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LEONARDO DE MELO CARNEIRO

A EVOLUÇÃO DOS METATHERIA: SISTEMÁTICA, PALEOBIOGEOGRAFIA, PALEOECOLOGIA E IMPLICAÇÕES PALEOAMBIENTAIS

RECIFE
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Dissertação de Mestrado apresentado à coordenação do Programa de Pós-graduação em Geociências, da Universidade Federal de Pernambuco, como parte dos requisitos à obtenção do grau de Mestre em Geociências

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"Somos todos visitantes deste tempo, deste lugar. Estamos só de passagem. O nosso objetivo é observar, crescer, amar... Depois vamos para casa" – Provérbio Aborígene. “Existem três coisas que não podem ser escondidas por muito tempo: o sol, a lua e a verdade” – Buda.

A todos vocês, meu mais sincero e verdadeiro obrigado!

"*Australia has long been known as the Land of Marsupials, but South America has also been a land of marsupials (...). In South America, (...) marsupials (...) had an adaptative radiation that led into many ways of life occupied by placentals on the northern continents and Africa.”*

(George G. Simpson)

RESUMO

Os marsupiais sul-americanos, dentre os quais se incluem os atuais “gambás” e “cuícas”, consistiram em dos grupos de mamíferos de maior diversidade no Paleogeno sul-americano. A literatura apresenta diversos estudos que enfocam na sistemática e paleobiogeografia dos taxa sul-americanos, entretanto, poucos apresentam resultados bem suportados. Essa incerteza sistemática resultou na análise de quase todas as famílias já descritas para a linhagem dos marsupiais (excluindo as quatro ordens endêmicas do continente Australiano) com o intuito de validar as características consideradas diagnósticas para as mesmas. Os resultados mostram que os Metatheria sul-americanos originaram-se durante o Cretáceo Inicial na América do Norte. A filogenia demonstrou que as grandes linhagens de Metatheria já haviam se diversificado na América do Norte antes da chegada à América do Sul, entretanto foi neste continente que a linhagem atingiu a sua maior diversidade. A provável rota de chegada a América do Sul envolveu a região do Caribe e América Central, constituindo os arcos-de-ilha e as regressões marinhas importantes fatores ambientais para a evolução do grupo. A paleoecologia do grupo demonstrou que os Metatheria sul-americanos evoluíram para ocupar diferentes nichos tróficos durante todo o Paleogeno-Neogeno, estando sua maior diversidade relacionada ao Máximo Termal do Paleoceno-Eoceno (MTPE). A redução das temperaturas globais durante o início do Oligoceno foi provavelmente o principal evento de extinção para a maioria das linhagens no Hemisfério Sul.

PALAVRAS-CHAVE: Metatheria. Paleobiogeografia. Paleoecologia. Sistemática.

ABSTRACT

The South American marsupials, which include the extant opossums, represented a diverse group in South America during the Paleogene. Most published studies focus on systematic and paleobiogeography of South American taxa, however, few present consistent results. This problematic resulted on the analysis of almost all described families of marsupials (excluding Australidelphia four endemic orders), in order to validate the characters considered as diagnostic for them. The results demonstrate that South American metatherians evolved in North America since Early Cretaceous, with almost all major lineages present in North America prior to the arrival in South America; nevertheless, the lineage reached its major diversity in the last continent. The probable dispersal rout was the Caribbean Plate, with 'aves ridge' and sea-level regressions during the Late Cretaceous representing important environmental events for the evolution of this group. The paleoecology demonstrated that South American taxa evolved to occupy different trophic niches during Paleogene and Neogene, with the greater diversity being recorded during the Paleocene-Eocene Thermal Maximum (PETM). The global cooling during the early Oligocene probably was the main environmental event for the extinction of the majority of Southern lineages.

KEY-WORDS: Metatheria. Paleobiogeography. Paleoecology. Systematics.

SUMÁRIO

1 INTRODUÇÃO

O clado Metatheria Huxley, 1880 inclui todos os marsupiais atuais, os extintos e todos os mamíferos mais próximos dos marsupiais do que dos placentários (ROUGIER, WIBLE e NOVACEK, 1998). Embora atualmente, os marsupiais viventes sejam mais diversos na Australásia, os Neotrópicos são o lar de impressionantes e diversificadas ordens (ALBUJA e PATTERSON, 1996). Eles são limitados em sua maioria à Austrália e América do Sul, enquanto que os poucos representantes da América Central e do Norte são imigrantes relativamente recentes da América do Sul através do Istmo do Panamá cerca de três milhões de anos atrás (HOROVITZ et al., 2009).

Durante o isolamento geográfico ocorrido na América do Sul em grande parte do Paleógeno, os metatérios se diversificaram ocupando zonas adaptativas extremamente diversas, e que em outras partes do mundo eram ocupadas por mamíferos eutérios (MARSHALL, 1977). Durante a maior parte do Cenozoico, os metatérios foram componentes notáveis dos ecossistemas terrestres da América do Sul (FORASIEPI, GOIN e MARTINELLI, 2009). Essa extinta fauna incluía insetívoros e onívoros da ordem Didelphimorphia, frugívoros das ordens Paucituberculata e Polydolopimorphia, e carnívoros da ordem Sparassodonta (FORASIEPI et al., 2006). Atualmente, os Metatheria estão restritos a um pequeno número de Didelphidae, Caenolestidae e Microbiotheridae (FLYNN e WYSS, 2004).

A maior parte dos materiais fósseis relacionados aos marsupiais sul-americanos é composta por dentes, materiais fragmentados e espécimes incompletos (ARGOT, 2004a, 2004b, 2004c; BABOT, POWELL e MUIZON, 2002; COZZUOL et al., 2006; FORASIEPI, GOIN e TAUBER, 2004; GOIN, 1996; GOIN, CANDELA, ABELLO et al., 2009). Dentre os conhecidos, os dentes apresentam excelente estado de preservação no registro fóssil (HUYSSEUNE, SIRE e WITTEN, 2009). Os dentes são muito importantes para definir os hábitos alimentares de animais viventes e extintos, e desde muito tempo é reconhecida a forte relação de forma x função entre a morfologia dentária e dieta de espécies fósseis (UNGAR, 2004). Estudos ecomorfológicos envolvendo a dentição dos extintos Metatheria são comuns na literatura (CHORNOGUBSKY, GOIN e REGUERO, 2009; FLYNN e WYSS, 2004; FORASIEPI, SANCHEZ-VILALGRA, GOIN et al., 2006; FORASIEPI, GOIN e

MARTINELLI, 2009; ZIMICZ 2011, 2012, 2014a); entretanto, a maioria foca nos hábitos alimentares de espécies de maneira isolada.

Em termos de adaptação, a grande diversidade de formas ocorreu em função de uma evidente irradiação adaptativa desses animais durante o isolamento da América do Sul; compreendendo táxons de pequeno porte (e.g. *Mayulestes*, com menos de 1 kg), animais do tamanho de ursos (e.g. *Borhyaena*), espécies com dentes de sabre (e.g. *Thylacosmilus*), arborícolas (e.g. *Mayulestes*) e cursoriais (e.g. *Pucadelphys* e *Borhyaena*) (ARGOT, 2004a). Após a extinção dos Thylacosmilidae, os metatérios sul-americanos passaram a ser representados por marsupiais de pequeno a médio porte com uma aparência bastante generalizada (FORASIEPI e CARLINI, 2010), embora estudos detalhados tenham demonstrado a existência de variações e diferenças na forma do crânio, mandíbula e elementos pós-cranianos em didelfídeos, caenolestídeos e microbioterídeos (ASTÚA, 2000; ASTÚA, HINGST-ZAHER, MARCUS et al, 2009).

Estudos envolvendo a origem e paleobiogeografia dos Metatheria são conhecidos (CASE, GOIN e WOODBURNE, 2005; GOIN et al., 2016). A maioria desses estudos defende uma origem norte-americana para o grupo e datam a sua chegada à América do Sul durante o Cretáceo Final (Maastrichtiano) através do Caribe. Entretanto, nenhum deles conseguiu encontrar resultados diagnósticos para a confirmação de suas teorias.

O presente estudo visou o estudo das relações sistemáticas, evolutivas, paleobiogeográficas e paleoecológicas dos Metatheria, em especial, os das Américas do Norte e do Sul.

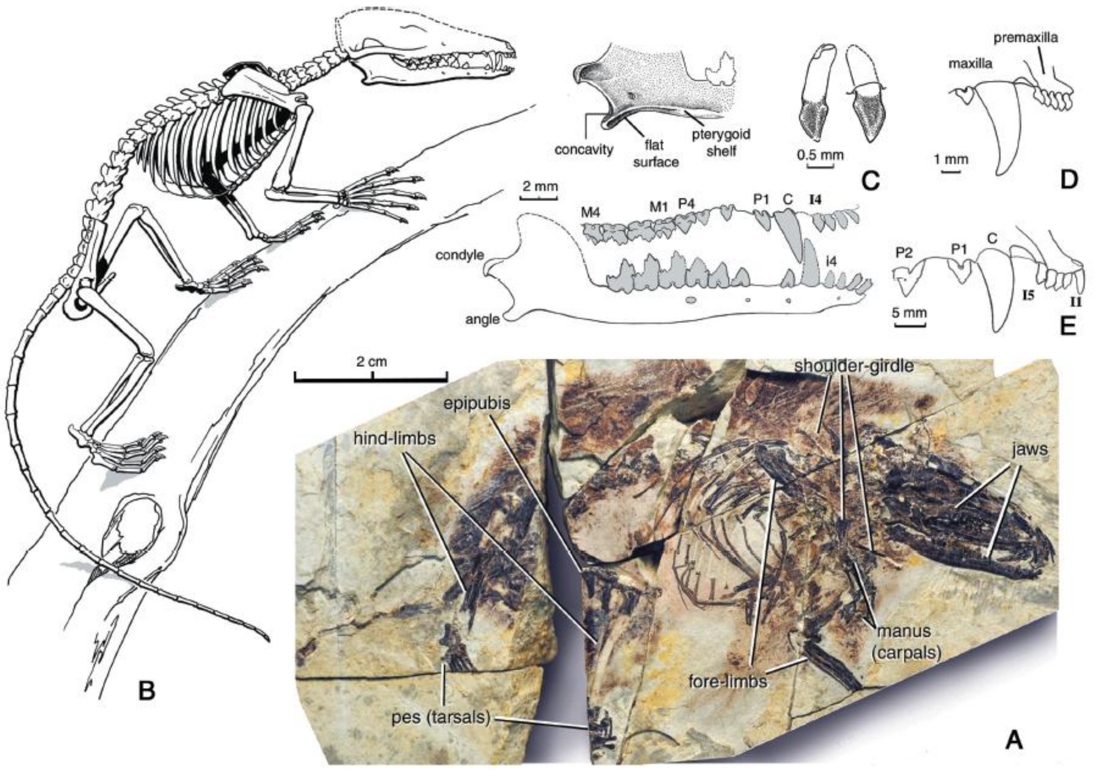
2 REVISÃO BIBLIOGRÁFICA

2.1 DEFINIÇÃO, ORIGEM E PALEOBIOGEOGRAFIA: ÁSIA

Segundo Kielan-Jaworowska, Cifelli e Luo (2004), Metatheria pode ser definido como a linhagem que compreende todos os animais mais próximos dos marsupiais do que dos placentários. Recentes estudos consideraram Metatheria como sendo representado por táxons basais, como *Sinodelphys szalayi*, Deltatheroida e Marsupialiformes (VULLO et al, 2009) (Fig. 1).

A origem dos Metatheria remonta há pelo menos 147,7 milhões de anos, quando se estima que essa linhagem tenha divergido da linhagem dos Eutheria Huxley, 1880, constituindo as duas a linhagem dos Theria Parker e Haswell, 1897 (BININDA-EMONDS et al., 2007); entretanto, *Juramaia sinensis* Luo et al. (2011) demonstraram que a divergência entre essas duas linhagens é ainda mais antiga, ocorrendo há pelo menos 160 milhões de anos. O mais antigo táxon associado com a linhagem dos Metatheria é *Sinodelphys szalayi* Luo et al, 2003, encontrado na Formação Yixian, China, datada em 125 Maa (Cretáceo Inicial). A presença desse táxon demonstra que os Metatheria já haviam se diversificado durante o Cretáceo Inicial (LUO et al, 2003).

Figura 1: Holótipo e reconstruções de *Sinodelphys szalayi*.



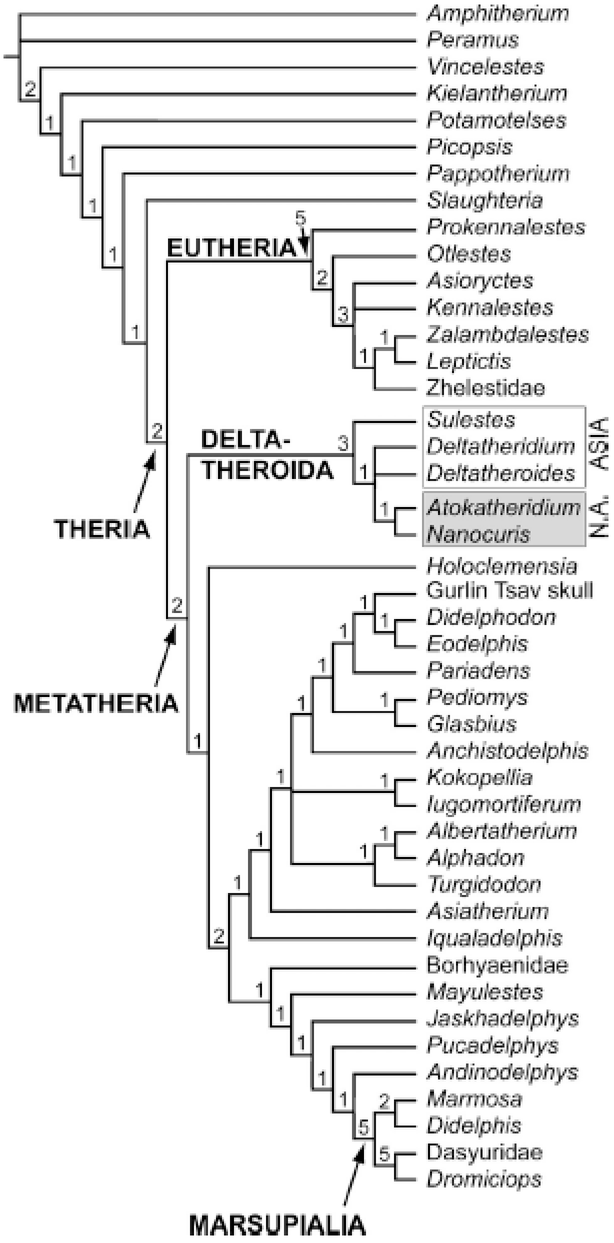
(LUO et al, 2003)

O Cretáceo da Ásia apresenta uma diversidade de Deltatheroida (AVERIANOV, ARCHIBALD e EKDALE, 2010; BI et al., 2015; ROUGIER, DAVIS e NOVACEK, 2015; ROUGIER, WIBLE e NOVACEK, 1998; 2004), *Asiatherium* (SZALAY e TROFIMOV, 1996; TROFIMOV e SZALAY, 1994) e *Marsasia* (AVERIANOV e KIELAN–

JAWOROWSKA, 1999), entretanto, nenhum Metatheria *strictu sensu* é encontrado nesse continente durante esse período.

Filogenias recentes apresentam quase que na totalidade uma relação de grupo-irmão entre Deltatheroida + Metatheria (AVERIANOV, ARCHIBALD e EKDALE, 2010; KIELAN-JAWOROWSKA e NESSOV, 1990; ROUGIER, WIBLE e NOVACEK, 2004; ROUGIER, DAVIS e NOVACEK, 2015; WILSON e RIEDEL, 2010) (Fig. 2), modificando a ideia inicial de que os Deltatheroida poderiam ser um grupo mais basal ao clado Eutheria + Metatheria (BUTLER e KIELAN-JAWOROWSKA, 1973). *Arcantiodelphys marchandi* Vullo, Gheerbrant, Muizon et al, 2009, foi descrito para o Cenomaniano da Europa (França); esse táxon foi considerado como filogeneticamente mais próximo dos Metatheria do que dos Deltatheroida (VULLO, GREERBRANT, MUIZON et al, 2009). A presença desse táxon na Europa poderia indicar que os primeiros verdadeiros Metatheria já haviam se irradiado na Ásia, indicando uma dispersão pela Ásia para a Europa, ou América do Norte, indicando uma rota de dispersão entre América do Norte e Europa durante o final do Cretáceo Inicial–início do Cretáceo Final; ainda assim, as duas hipóteses precisam de dados mais robustos a fim de serem corroboradas.

Figura 2: Filogenia entre Metatheria e Deltatheroida. É possível notar a relação de grupo irmão entre Deltatheroida + Metatheria.



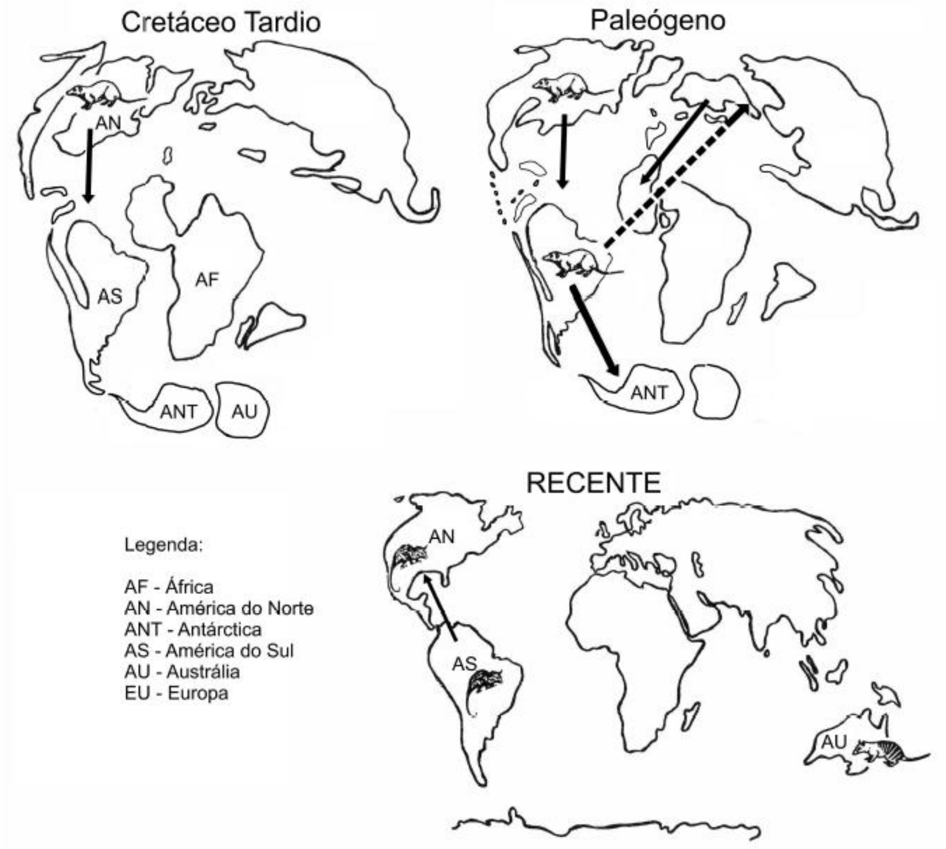
(WILSON e RIDLE, 2010)

Atualmente, é majoritariamente aceito que o grande grupo dos Metatheria (i.e. Deltatheroida + Metatheria) teve sua origem e irradiação basal durante o Cretáceo Inicial da Ásia (LUO et al, 2003), mas o local da irradiação dos Metatheria *strictu sensu* ainda não foi totalmente esclarecido. Dentre os Metatheria conhecidos, *Kokopellia juddi* Cifelli, 1993, é considerado atualmente como o mais antigo e basal Metatheria *strictu sensu* (CIFELLI, 1993; CIFELLI e MUIZON, 1997). A presença de outros grupos norte-americanos restritos as

Américas pode ser considerado como um indicativo de que a irradiação principal dessa linhagem ocorreu, de fato, na América do Norte durante o Cretáceo Inicial (CIFELLI, 2004).

Muitos estudos tentaram elucidar a origem dos Metatheria sul-americanos: Clemens (1968) defendia a ideia de que "didelfídeos" basais, como *Alphadon*, colonizaram a América do Sul e Austrália durante o Cretáceo Final e Cenozoico inicial, enquanto os Metatheria 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; o autor segue 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 propões 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 Metatheria norte-americanos, sul-americanos e africano-europeus nunca foi elucidada ou estudada propriamente (Fig. 3).

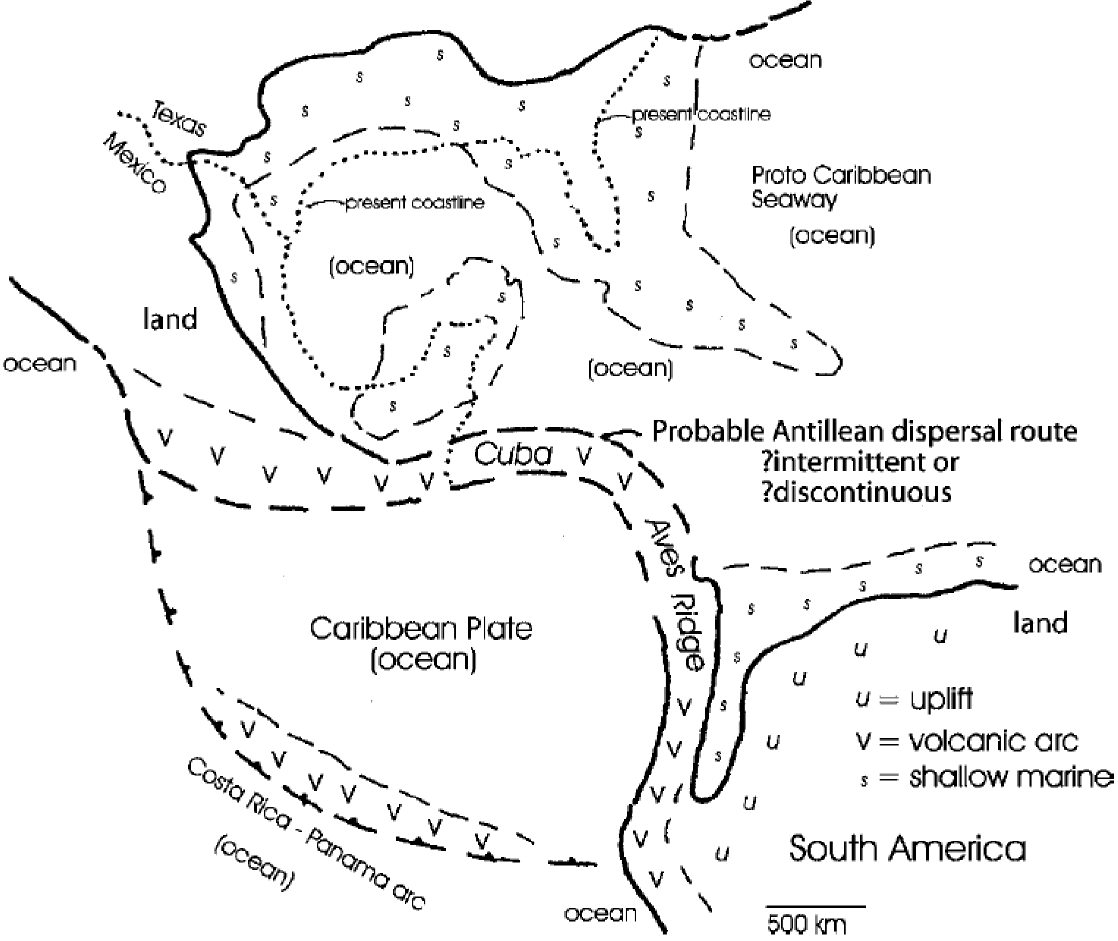
Figura 3: Principais propostas relacionadas à paleobiogeografia dos Metatheria durante o Cretáceo Final, Paleogeno e em períodos recentes**.**



(OLIVEIRA e GOIN, 2012)

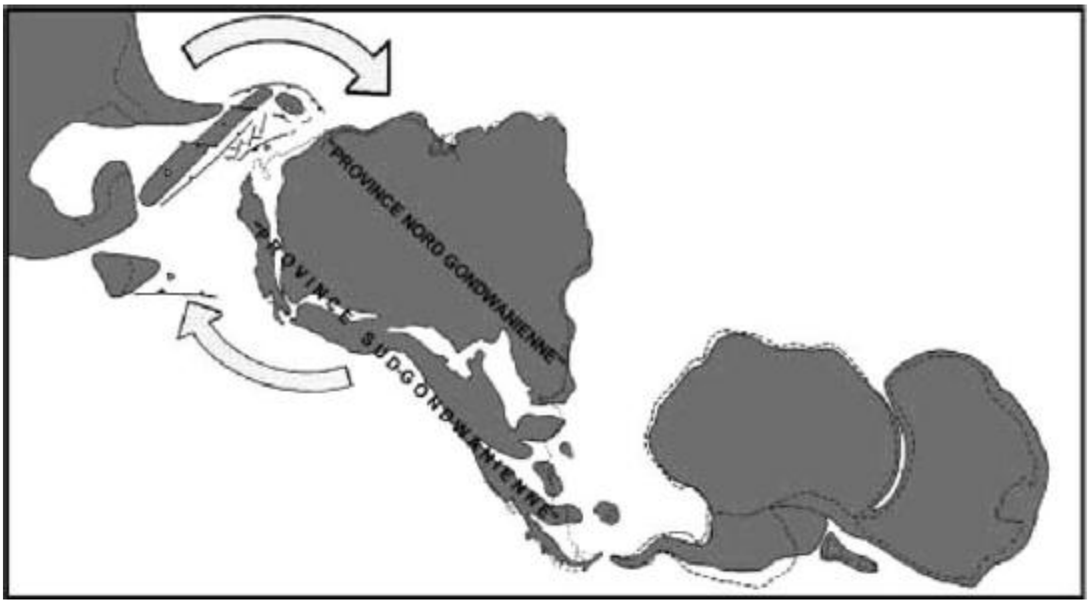
Szalay (1994) analisou os elementos pós-cranianos de muitos metatérios e propôs que todas as linhagens sul-americanas teriam derivado de um único ancestral norte-americano, pertencendo esse ancestral a um "*stock* peradectoideo". Entretanto, estudos recentes indicam que muitas linhagens de metatérios 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. 4). 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; WOODBORNE e CASE, 1996) (Fig. 5).

Figura 4: Reconstrução da Placa do Caribe apresentando as prováveis rotas paleobiogeográficas do grupo.



(PINDELL, 1994)

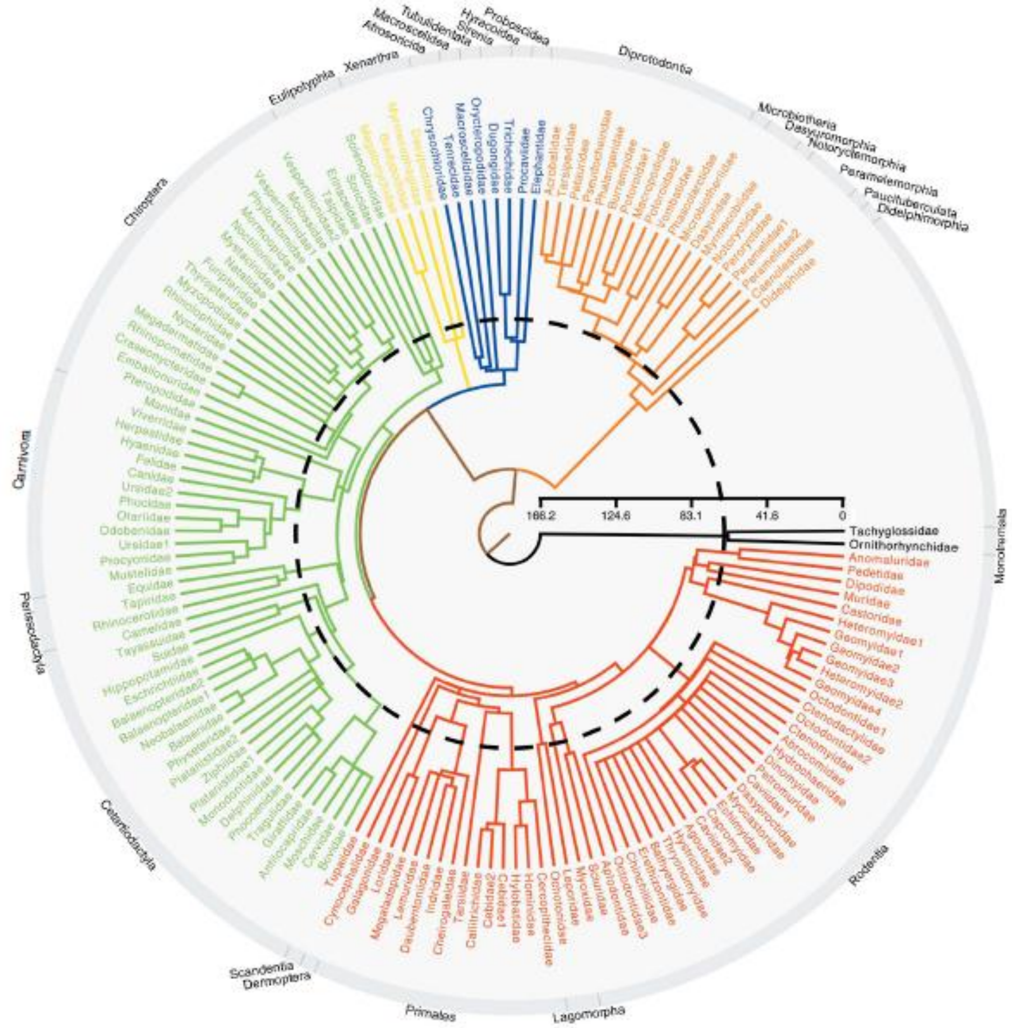
Figura 5: Reconstrução do posicionamento da América do Norte e de Gondwana durante o Cretáceo Final**.**



(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).

Figura 6: Filogenia dos Theria viventes calibrada no tempo geológico. É possível notar que Didelphimorphia, Paucituberculata e Peramelemorphia surgem ainda durante o Cretáceo Final.



(BININDA-EMONDS 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. 6). Beck (2008), por sua vez, classifica os Microbiotheria como a linhagem mais basal dos Australidelphia e Peramelemorphia como grupo irmão dos Dasyuromorpha + Notoryctemorphia.

2.2 PALEOBIOGEOGRAFIA: AMÉRICA DO NORTE

Os Metatheria são conhecidos na América do Norte desde o limite Albiano superior (Cretáceo Inicial)-Cenomaniano superior (Cretáceo Final), entre 100-98 Maa, na Formação Cedar Mountain, Utah, EUA. Dentre os taxa conhecidos destacam-se *Kokopellia juddi* (CIFELLI, 1993; CIFELLI e MUIZON, 1997; CIFELLI, 2004); *Pariadens mckennai* Cifelli, 2004, *Sinbadelphys schmidti* Cifelli, 2004, e *Adelodelphys muizoni* Cifelli, 2004 (CIFELLI, 2004). Atualmente, *Kokopellia*, *Sinbadelphys* e *Adelodelphys* não possuem posição taxonômica definida, entretanto estudos recentes são unânimes em considerar esses três taxa como membros basais da linhagem dos Metatheria (CIFELLI, 1993; CIFELLI e MUIZON, 1997; CIFELLI, 2004; WILLIAMSON, BRUSATTE, CARR et al, 2012; WILLIAMSON, BRUSATTE e WILSON, 2014). A posição de *Pariadens* Cifelli e Eaton, 1987, está atualmente em debate, sendo este táxon considerado um membro basal da família dos Stagodontidae Marsh, 1889 (EATON, 1993; CIFELLI, 2004; WILLIAMSON, BRUSATTE, CARR et al, 2012; WILLIAMSON, BRUSATTE e WILSON, 2014), posição contestada por Fox e Naylor (2006).

Durante o Cenomaniano superior, os Metatheria apresentam uma maior diversidade, sendo os principais taxa conhecidos para a Formação Dakota, Utah, EUA: *Dakotadens morrowi* Eaton, 1993, *Dakotadens* sp., *Eoalphadon clemensi* (Eaton, 1993), *Eoalphadon lillegraveni* (Eaton, 1993), *Eoalphadon woodburnei* Eaton, 2009, *Alphadon* sp., *Varalphadon* sp. e *Pariadens kirklandi* Cifelli e Eaton, 1987 (CIFELLI e EATON, 1987; EATON, 1993, 2009). A Formação Cedar Mountain, Utah, EUA, também apresenta prováveis Metatheria, como *Dakotadens pertritus* Cifelli, Cohen e Davis, 2016, e *Culicolestes kielanae* Cifelli, Cohen e Davis, 2016; sendo esta fauna datada em aproximadamente 97 Maa. Dentro os grupos apresentados, *Dakotadens* é considerado como um Theria *incertae sedis* (CIFELLI, COHEN e DAVIS, 2016; EATON, 1993), embora também seja considerado como um Metatheria basal também de posição incerta (WILLIAMSON, BRUSATTE, CARR et al, 2012; WILLIAMSON, BRUSATTE e WILSON, 2014); *Eoalphadon*, inicialmente considerado como uma espécie do gênero *Alphadon* por Eaton (1993), mantém a sua posição como um Alphadontidae (EATON et al, 1999; EATON, 1993, 2009); *Culicolestes*

Protalphadon sp. e o *Varalphadon* 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). Dentre os Metatheria conhecidos destacam-se ?*Anchistodelphys delicatus* Cifelli, 1990a (?*Varalphadon delicatus*, segundo Eaton e Cifelli, 2013), e alguns materiais não atribuídos a um gênero e espécie específicos (CIFELLI, 1990a). ?*Varalphadon* sp. foi identificado para o final do Coniaciano, sendo representado por um único molar inferior isolado (EATON, 2006a).

Os Metatheria do Santoniano-Campaniano inferior (Aquilan NALMA) são muito mais abundantes e mais diversos do que os conhecidos para o Cenomaniano, Turoniano e Coniaciano (CIFELLI, 1990b, 1990c; DAVIS, CIFELLI e COHEN, 2016; EATON, 2006a, 2006b, 2013). Dentre os taxa do Aquilan NALMA destacam-se *Varalphadon* (Johanson, 1996a), *Apistodon* (Davis, 2007), *Aquiladelphis* (Fox, 1971), *Alphadon* Simpson, 1927, *Albertatherium* Fox, 1971, *Protalphadon* Cifelli, 1990b, *Turgidodon* Cifelli, 1990b, *Eodelphis* Matthew, 1916, *Iugomortiferum* Cifelli, 1990c, *Anchistodelphys* Cifelli, 1990c, *Iqualadelphis* Fox, 1987, e outros taxa 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), *Pediomys* Marsh, 1889; *Eodelphis*, *Didelphodon* Marsh, 1889; e *Ectocentrocristus* 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*, *Ectocentrocristus* e *Bistius*), enquanto outras espécies sobrevivem após esse período (e.g. *Eodelphis*, *Didelphodon*, *Aquiladelphis*, *Leptalestes*, *Pediomys*, *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 (entretanto, veja os capítulos da dissertação), dentre as quais se destacam os “Alphadontidae” (Marshall, Case e Woodburne, 1990), os Pediomyoidea (Simpson, 1927) e os Stagodontidae

Marsh, 1889 (WILLIAMSON et al, 2014). Os Metatheria norte-americanos sofreram uma grande redução em sua diversidade durante o limite Cretáceo–Paleoceno, com a extinção de quase todas as linhagens conhecidas para o Cretáceo, à exceção dos Peradectidae e Herpetotheriidae (WILLIAMSON et al, 2014).

2.3 PALEOBIOGEOGRAFIA: HEMISFÉRIO SUL

O registro mais antigo confirmado de um Metatheria na América do Sul é o ?Polydolopimorphia basal *Cocatherium lefipanum* 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 material, 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 – Tiupampian 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 Maa (atualmente 64 Maa – 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 atribuídos aos Metatheria: "*Peradectes*" *austrinum*, *Chulpasia mattaueri* Crochet e Sigé, 1993; *Sillustania quechuense* Crochet e Sigé, 1996 (SIGÉ, 1971; CROCHET e SIGÉ, 1993, 1996). Sigé (1972) descreve vários materiais associados à linhagem dos Metatheria, mas, infelizmente, esses materiais não foram confidentemente atribuídos a nenhum táxon até o momento. Atualmente, a fauna de Laguna Umayo e Chulpas é tida como contemporânea a fauna de Itaboraí (i.e. Eoceno inferior – Itaboraian SALMA) (SIGÉ, SEMPERE, BUTLER et al, 2004).

A fauna de Santa Rosa, Peru, é tentativamente associada à Formação Yahuarango (?Eoceno – Barrancan-Mustersan? SALMA – WOODBURNE et al, 2014) 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 superior–Oligoceno inferior; Tinguirirican 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 Satacrucian SALMA (Mioceno inferior tardio, aproximadamente 17,5–16 Maa) 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 Km^2), mas, em contraste ao tamanho, ela é muito fossilifica. 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 (Itaboraian SALMA – WOODBURNE 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; WOODBURNE et al, 2014). É possível destacar ainda a presença de um provável Pucadelphyidae em Itaboraí (LADEVÈZE e MUIZON, 2010).

Um dado importante, porém pouco explorado, reside no fato de que os materiais de Itaboraí são provenientes da mesma bacia, mas foram encontrados em fendas e anos diferentes, destacando-se as coletas de 1948, 1948–1949, 1950, 1953, 1958, 1961, 1964–1967, 1968 e 1976 (adaptado de BERGQVIST et al, 2009). O primeiro metatério publicado da Bacia de Itaboraí foi *Eobrasilia coutoi* por Simpson (1947); como é possível notar, o crânio muito fragmentado foi entregue ao pesquisador antes da coleta de 1948, indicando que poderiam existir outras fendas com metatérios que nunca foram referidas ou propriamente identificadas. As faunas de metatérios coletados durante os anos de 1948, 1949, 1958, 1961, 1964–1967, principalmente por Júlio da Silva Carvalho e Paula Couto, depositadas no Museu Nacional (MNRJ) e Museu de Ciências da Terra (MCT, ex DGM, afiliado ao DNPM – Departamento Nacional de Produção Mineral), parecem representar uma fauna característica e similar, entretanto, materiais coletados por Price e Campos em 1968, depositados no MCT, nunca foram devidamente estudados e não estão presentes na literatura. Os últimos estudos de Paula Couto com os metatérios de Itaboraí apresentam materiais coletados até 1967, mas não mencionam os materiais de 1968.

Marshall (1982a; 1984) mencionam uma visita em Dezembro de 1979 ao antigo DGM (hoje MCT), em que ele analisa materiais encontrados em uma coleção nunca antes estudada (e.g. *Eobrasilia* e *Procaroloameghinia*). É possível que esses dois materiais por ele estudado estejam associados à coleta de 1968.

Recentemente descoberta, a fauna da Formação Guabirotuba, 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 exemplar 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, Tinguiririican SALMA–Oligoceno inferior (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 inferior (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 materiais coletados na Patagonia por André Tournouër, incluindo metatérios das idades Casamayorense, Deseadense, Colhuehuapiense e Santacrucense 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 inferior (“Sapoan” 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: *Djarthia* e um gênero ainda não descrito. Beck (2008) descreve materiais cranianos e pós-cranianos e os associa com *Djarthia 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 (PETM, sigla em inglês) (WOODBURNE, GOIN, BOND et al, 2013; GOIN et al, 2016), que ocorreu por volta de 55,5 Maa (BOWEN, MAIBAUER, KRAUS et al, 2015). Esse período é compatível com o desenvolvimento de florestas tropicais e árvores frutíferas (WOODBURNE, 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 Maa, coincidindo com Óptimo Climático do Eoceno Inicial (EECO, sigla em inglês) (WOODBURNE, 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 (Tinguiririican) 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 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 nucal, 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 materiais 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 resitir 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 exemplares fósseis incompletos (BABOT, POWELL e MUIZON, 2002).

2.5 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 WOODBURNE, 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*. O grupo é mais diverso e abundante 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); paraconido desenvolvido, e entoconido comprimido ou levemente inflado (DAVIS, 2007).

As afinidades filogenéticas do Pediomyoidea de Itaboraí são discutidas no **Capítulo 1** (‘A new Pediomyoid (Mammalia, Metatheria) from the Paleogene of Brazil: insights about systematics and paleobiogeography of Microbiotheria and Pediomyoidea).

2.6 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 principiais 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).

As relações filogenéticas, paleobiogeográficas e paleoecológicas dos “Eobrasilinae” e Stagodontidae serão debatidas no **Capítulo 2** (‘Systematic review of dental homologies of

"Eobrasilinae" (Mammalia, Metatheria), with the description of the first preserved lower molar of *Eobrasilia coutoi* Simpson, 1947, a South American early Eocene Stagodontidae').

2.7 "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* – 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 materiais atribuídos a *Pariadens kirklandi* poderiam representar outra espécie de grande porte, o que representaria uma quimera; de forma interessante, alguns materiais 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 (Aquilan 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 a 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) (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*.

2.8 POLYDOLOPIMORPHIA (AMEGHINO, 1897); ARCHER, 1984

Os Polydolopimorphia representam um grupo conhecido para o Cretáceo Tardio da América do Norte (CASE, GOIN e WOODBUNE, 2005) 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 *Ectocentrocristus 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 homoplastico).

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 (?Eoceno) 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 um grande número de 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 materiais 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).

As afinidades de *Ectocentrocristus* serão debatidas nos **Capítulos 3** (‘*Zeusdelphys complicatus* Marshall, 1987, is not a Protodidelphidae Marshall, 1990, but a Hatcheriformes Case, Goin & Woodburne, 2005: paleobiogeographyc implications’).

2.9 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 WOODBURNE, 1990; PAULA COUTO, 1952a, 1970) ou como um Microbiotheria basal (CASE, GOIN e WOODBURNE, 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 mattaueri* 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 bunoides, o que indica hábitos alimentares frugívoros (SIGÉ, ARCHER, CROCHET et al, 2009). A subfamília foi inicialmente considerada como uma linhagem dos Bonapartheriiformes–Polydolopimorphia (CASE, GOIN e WOODBURNE, 2005), entretanto, estudos recentes indicam que essa linhagem seria basal aos Polydolopimorphia ou nem pertenceriam a esse grande grupo (CHORNOGUBSKY e GOIN, 2015).

As relações filogenéticas de *Zeusdelphys complicatus* e *Hatcheritherium alpha* serão discutidas nos **Capítulos 3** (‘*Zeusdelphys complicatus* Marshall, 1987, is not a Protodidelphidae Marshall, 1990, but a Hatcheriformes Case, Goin & Woodburne, 2005: paleobiogeographyc implications’).

2.10 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 materiais 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 (Itaboraian 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 and Chornogubsky, 2010, da Formação Sarmiento (Tinguiririca SALMA–Oligoceno inferior), Argentina.

2.11 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 Pucadelphyidae ainda não descrito para Itaboraí, sendo representado por petrosos isolados.

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, talonido levemente reduzido, a preparacrista e a pós-metacrista não é reduzida em comprimento e 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.

2.12 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 rostro, 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.

A validade do agrupamento de *Gaylordia* e *Tiulordia* na subfamília "Eobrasilinae" será debatida no **Capítulo 2** ('Systematic review of dental homologies of "Eobrasilinae" (Mammalia, Metatheria), with the description of the first preserved lower molar of *Eobrasilia coutoi* Simpson, 1947, a South American early Eocene Stagodontidae').

2.13 HERPETOTHERIIDAE TROUESSART, 1879; "STERNBERGIIDAE" SZALAY, 1994; 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, WOODBURNE et 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; TRAVOUILLON, GUROVICH, BECK et al, 2010; TRAVOUILLON, 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 didelfídeos atuais, em que os processos espinhosos são baixos e largos anteroposteriormente; 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).

A validade do agrupamento de *Didelphopsis* na subfamília "Eobrasilinae" será debatida no **Capítulo 2** ('Systematic review of dental homologies of "Eobrasilinae" (Mammalia, Metatheria), with the description of the first preserved lower molar of *Eobrasilia coutoi* Simpson, 1947, a South American early Eocene Stagodontidae').

2.14 MARSUPIALIA: DIDELPHIMORPHIA GILL, 1872; E "DIDELPHOIDEA" GRAY, 1821

A ordem Didelphimorphia é representada pelas famílias Didelphidae (GARDNER, 2008; VOSS e JANSA, 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 JANSA, 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 JANSA, 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 JANSA, 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 dolgopolae* (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 rostro 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 didelfóideos 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).

2.15 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, Abelo 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 (Deseadan SALMA). Atualmente, esse táxon é considerado como o grupo irmão de Bardalestes, Caenolestoidea + 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 (Tinguiririrican SALMA – GOIN, ABELLO e CHORNOGUBSKY, 2010) e para o Oligoneo inferior 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 que *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 – Casamayoran SALMA – GOIN e CANDELA, 1998) até o limite Mioceno médio-Mioceno superior (ABELLO, 2013; RINCÓN, SHOCKEY, ANAYA et al, 2015). A superfamília incluíu 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 inferior, entretanto, o grupo apresenta um lapso temporal durante o Eoceno médio-superior e Oligoceno. A família é considerada atualmente a linhagem mais basal dos Palaeothentoidea (ABELLO, 2013).

Sasawatsu e *Perulestes* são conhecidos para o Eoceno superior? do Peru (GOIN e CANDELA, 2004), enquanto *Pilchenia* é conhecida para o Oligoceno inferior e superior da Argentina (GOIN, ABELLO e CHORNOGUBSKY, 2010). A exceção dos Pichipilidae, as demais linhagens da ordem Paucituberculata não sobreviveram após o Oligoceno superior (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 plagiaulacóideos com trigonido laminar com cristas oblíquas bem desenvolvidas por quase toda a extenção do mesmo, e talonido 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).

Os Palaeothentidae representa a família mais diversa da superordem com pelo menos sete gêneros conhecidos e duas subfamílias descritas, sendo importantes componentes das faunas do Oligoceno-Mioceno médio (Deseadan-Santacrucian SALMAs) da América do Sul (RAE, BOWN e FLEAGLE, 1996). Dentre os gêneros conhecidos, *Palaeothentes* representa o gênero mais diverso 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-superior 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 inferior (Santacrucian SALMA). A presença desse animal durante o Mioceno indica que os Paucituberculata diversificaram-se após a extinção dos Polydolopidae e dos Bonapartheriiformes (PASCUAL e HERRERA, 1975; RINCÓN, SHOCKEY, ANAYA et al, 2015). Outro Caenolestidae fóssil é *Pliolestes* do Mioceno superior-Plioceno inferior (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).

2.16 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 36º a 43º 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 material com os Microbiotheria nunca foi confirmado.

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 OBJETIVOS GERAIS

O presente estudo corresponde a uma análise comparativa da morfologia dentária de táxons extintos e atuais da linhagem dos Metatheria com enfoque em suas relações filogenéticas, paleoecologicas e paleobiogeograficas.

3.2 OBJETIVOS ESPECÍFICOS

a) Realizar uma análise das homologias dentárias dos Metatheria, buscando elucidar as suas relações evolutivas e sistemáticas;

b) Associar dados sobre a idade dos fósseis, localização geográfica, climatologia, fitofisionomia e características geomorfológicas dos diferentes depósitos fossilíferos norte e sul-americanos associando-os com os resultados obtidos na análise filogenética.

c) Inferir a história paleobiogeografica do grupo, incluindo a sua provável data de chegada aos continentes austrais, em especial na América do Sul, e o seu provável local de origem; utilizando dados de eustasia, geocronologia, vulcanismo e deriva continental para traçar as suas prováveis rotas paleobiogeográficas;

d) Delimitar os diferentes caracteres dentários indicativos de dieta nos marsupiais fósseis e atuais para comparação entre eles com o intuito de inferir sua paleoecologia nos ambientes em que viveram.

4 METODOLOGIA

4.1 CONSTRUÇÃO DA MATRIZ MORFOLÓGICA: DIVERSIDADE DOS TAXA, POLARIZAÇÃO E HOMOLOGIAS DENTÁRIAS

A escolha dos caracteres dentários baseou-se em estudos prévios (ABELLO, 2013; CASE, GOIN e WOODBURNE, 2005; CHORNOGUBSKY e GOIN, 2015; CIFELLI e MUIZON, 1997; DAVIS, 2007; FOX, 1987; GOIN, CANDELA, ABELLO et al, 2009; HOROVITZ et al, 2009; JOHANSON, 1996a; MARSHALL, CASE e WOODBURNE, 1990; OLIVEIRA e GOIN, 2011, 2015; OLIVEIRA, ZIMICZ e GOIN, 2016); entretanto, muitos caracteres e estados passaram por revisões, visto que muitos estudos uniam diversos estados e caracteres como representando um caractere/estado homólogo (e.g. morfologia da centrocrista, grau de invasividade da centrocrista, grau de abertura da centrocrista, alinhamento da centrocrista com para- e metacone, todos considerados como um único caractere).

O estudo apresenta novos caracteres e estados, resultantes da reinterpretação de suas homologias. Interessantemente, muitas estruturas e estados apresentados nas descrições dos materiais nunca foram propriamente estudados ou adicionados a análises filogenéticas. Entretanto, tais estruturas representam, por muitas vezes, sinapomorfias de diversas linhagens (e.g. cíngulo anterobasal interrompido – GOIN e ABELLO, 2013; paracone com orientação oblíqua – GOIN e CANDELA, 2004; “vale” entre o metaconulo e protocone – CROCHET e SIGÉ, 1996). Além disso, muitas estruturas nunca antes descritas ou mesmo consideradas foram identificadas, descritas, comparadas e “testadas” na análise filogenética proposta (e.g. cônulos subdivididos dos Pediomyoidea). A reinterpretação das homologias dentárias dos materiais e a identificação/adição de novas estruturas na análise filogenética resultaram na redescrição de diversas linhagens (i.e. ordens, superfamílias, famílias, gêneros e espécies), todas justificadas e comentadas nos capítulos da dissertação.

A identificação dos caracteres e morfologias nos táxons estudados baseou-se em visitas diretas aos materiais das coleções do Museu de Ciências da Terra (MCT, ex DGM), Museu Nacional (MNRJ) e Universidade Federal do Rio de Janeiro (UFRJ), análises de moldes e fósseis dessas coleções presentes na Universidade Federal de Pernambuco (UFPE);

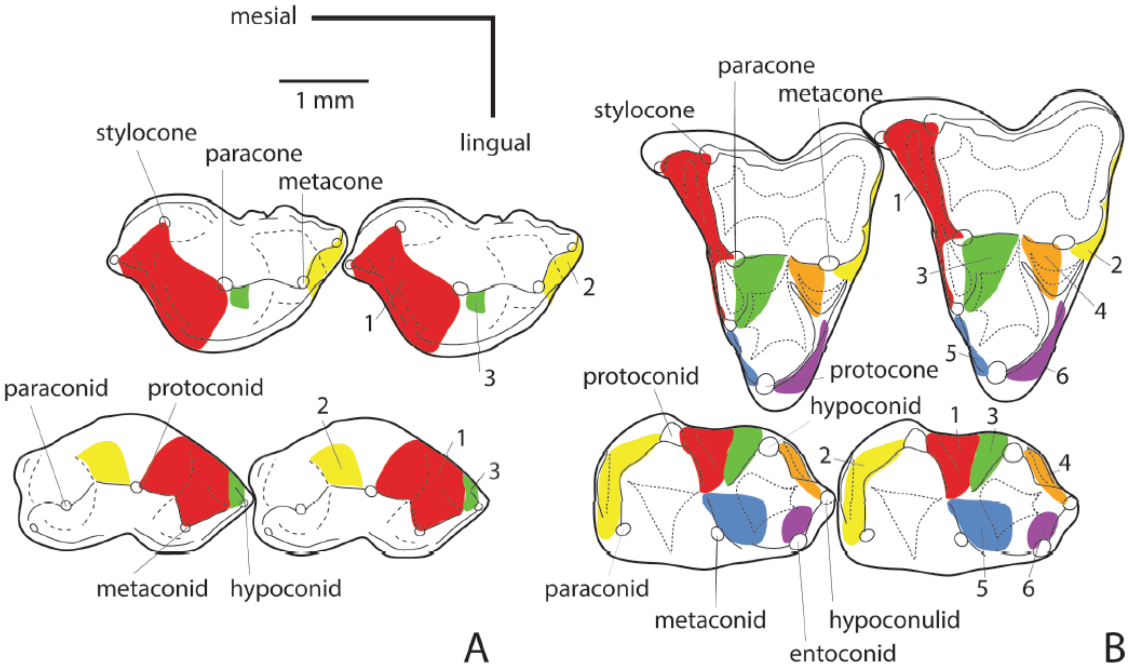
moldes de táxons norte-americanos enviados pelo Prof. Dr. Richard Cifelli; fotografias de Microscopia Eletrônica de Varredura (SEM) disponíveis na literatura; nas próprias descrições dos materiais e por desenhos esquemáticos disponíveis na literatura.

A polarização das estruturas seguiu os trabalhos citados no primeiro parágrafo desse tópico. Entretanto, muitas considerações com relação à polarização das estruturas e estados (i.e. plesiomorfias e apomorfias) não foram recuperadas na análise filogenética, visto que representavam apomorfias de linhagens basais e não plesiomorfias para a linhagem dos Metatheria (e.g. contato da cristida obliqua com a porção media do trigonido é uma apomorfia dos Metatheria e não uma plesiomorfia, visto que os Boreosphenida, Eutheria e Deltatheroida possuem a cristida obliqua em contato com o metaconid). Para corroborar a polarização dos estados e caracteres, o estudo comparou as morfologias presentes em materiais preservados para a linhagem dos Boreosphenida, Theria *incertae sedis*, Deltatheroida, Eutheria basais e Metatheria. Tais comparações serviram para recuperar a polarização dessas estruturas pela identificação do que são apomorfias e plesiomorfias para cada linhagem, como mencionado.

Os caracteres foram baseados nas diferentes estruturas presentes, principalmente, nos molares preservados dos diferentes táxons conhecidos. Algumas estruturas possuirão mais de um caractere relacionado, para que cada componente e propriedade do mesmo tenham suas devidas homologias identificadas (e.g. alinhamento da centrocrista com para- e metacone; morfologia da centrocrista dilambdodonte; grau de invasividade da centrocrista; morfologia da centrocrista com entalhe entre postparacrista e premetacrista). Muitas linhagens consideradas como “problemáticas” podem ser incluídas em análises desse tipo, o que por si só pode ser, por muitas vezes, suficiente para elucidar as relações evolutivas desses táxons *incertae sedis*.

As associações propostas para molares superiores e inferiores foram baseadas na morfologia, tamanho e relações oclusivas entre as estruturas (Fig. 7).

Figura 7: Oclusão dentária entre os molares superiores e inferiores, diferenciando um Metatheria de um Mammaliforme não Boreosphenida. As cores similares indicam relações oclusivas entre as estruturas dos molares superiores e inferiores.



(WILLIAMSON, BRUSATTE e WILSON, 2014)

A homologia dos caracteres e estados utilizados é de vital importância para uma análise filogenética (HENNING, DAVIS e ZANGERL, 1966). Em função disso, o estudo abrangeu a maior diversidade quanto possível para a linhagem dos Metatheria; infelizmente, nem todos os resultados desse projeto estão representados nessa dissertação. A parte disso, o grande número de gêneros representados na matriz filogenéticas suporta a validade das conclusões. Visto que conclusões relacionadas à homologia ou homoplasia/convergência só podem ser consideradas após uma análise filogenética, e não previamente, visto que o número de variáveis é muito grande para serem consideradas de maneira satisfatória (PORPINO, com. pes. X Simpósio Brasileiro de Paleontologia de Vertebrados), quanto maior a diversidade, mais robustos são os resultados, visto que a alegação da presença ou ausência de um táxon para refutar a análise não poderão ser propostas.

Outro fator é ainda mais importante: existem muitas teorias que propõem a presença de intercâmbios faunísticos entre as faunas norte e sul-americanas, incluindo uma origem norte-americana para as linhagens de metatérios sul-americanos (CASE e WOODBURNE, 1986; CASE, GOIN e WOODBURNE, 2005; GOIN et al, 2016; ORTIZ-JAUREGUIZAR, 2009; PASCUAL, 2006; SZALAY, 1994). Tendo em conta tais conclusões, não é prudente avaliar a diversidade sul-americana em filogenias restritas apenas com elementos endêmicos do Hemisfério Sul, o mesmo aplica-se a filogenias focadas a táxons norte-americanos, algo amplamente presente na literatura atual. Tal conclusão é válida especialmente para trabalhos que por conta de características muito marcantes para uma determinada linhagem acabam por restringir as filogenias apenas aos táxons aparentemente relacionados ao que se quer estudar, o que acaba por "induzir" uma relação próxima entre eles, visto que a abrangência de comparação é muito restrita. A sistemática, origem e paleobiogeografia dos metatérios sul-americanos foi proposta como um objetivo do projeto; portanto, os metatérios norte-americanos são uma peça chave para a elucidação da história evolutiva da América do Sul, e, por isso, foram incluídos na filogenia.

A paleoecologia dos metatérios sul-americanos foi cuidadosamente estudada por Zimicz (2011; 2012; 2014a; 2014b). As relações evolutivas dos metatérios estudados foram comparadas com os dados apresentados nesses estudos, auxiliando na reconstrução das paleocomunidades nos diferentes ecossistemas conhecidos com metatérios na América do Norte e do Sul. Para inferência das hipóteses e teorias paleobiogeográficas e paleoecológicas foram utilizados dados de geomorfologia, paleoclimatologia e eustasia (CASE e WOODBURNE, 1986; CASE, GOIN e WOODBURNE, 2005; GOIN et al, 2016; HAQ, 2014; ORTIZ-JAUREGUIZAR, 1996, 2009; PASCUAL, 2006; PINDELL, 1994; WOODBURNE et al, 2013; WOODBURNE et al, 2014).

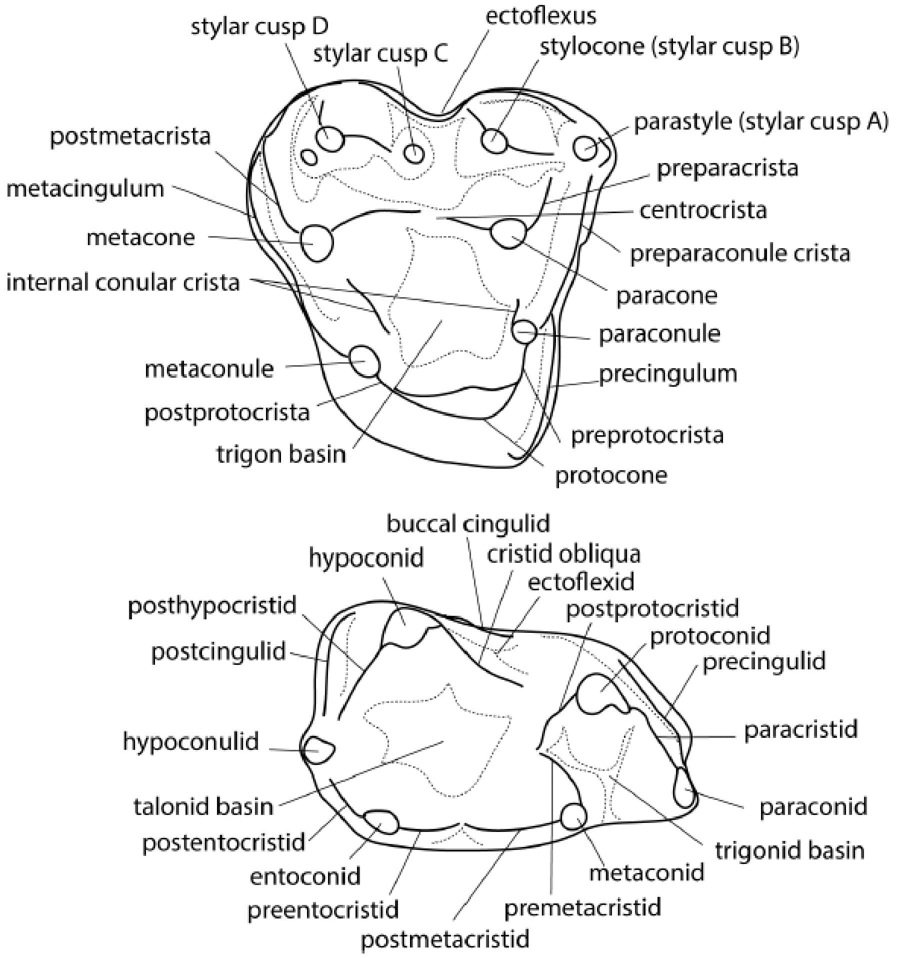
4.2 ANÁLISE FILOGENÉTICA

A maior parte dos materiais fósseis relacionados aos marsupiais sul-americanos é composta por dentes, materiais fragmentados e espécimes incompletos (ARGOT, 2004a, 2004b, 2004c; BABOT, POWELL e MUIZON, 2002; COZZUOL, GOIN, DE LOS REYES et al., 2006; FORASIEPI, GOIN e TAUBER, 2004; GOIN e PARDIÑAS, 1996; GOIN, ZIMICZ, DE LOS REYES et al., 2009). Dentre os conhecidos, os dentes apresentam excelente estado de preservação no registro fóssil (HUYSSEUNE, SIRE e WITTEN, 2009). A presença de materiais dentários como os únicos elementos fósseis preservados para a maior parte dos Metatheria conhecidos implica na construção de filogenias baseadas principalmente em caracteres dentários para que se possa incluir a maior diversidade quanto possível de metatérios fósseis.

Os Metatheria da Bacia de Itaboraí, RJ, foram diretamente analisados (análise dos materiais fósseis), entretanto, a morfologia das características e a identificação das estruturas foram baseadas em fotografias de MEV, visto que muitas estruturas só podem ser identificadas por essas fotografias. Moldes desses animais também foram estudados. Dentre os Metatheria da América do Norte, *Pariadens*, *Dakotadens*, *Varalphadon* e *Protalphadon* foram estudados tendo como base moldes enviados pelo professor Richard Cifelli e Joshua Cohen, ambos do Museu de Oklahoma, e por fotografias de MEV presentes na literatura. Os demais taxa da América do Norte, América do Sul, Austrália, Europa, África, Antartida e Ásia foram estudados baseados em fotografias de MEV presentes na literatura. É importante salientar que a análise dos materiais baseou-se principalmente nas fotografias de MEV, pois muitas estruturas só são visualizadas nessas fotografias. A análise de materiais originais ou moldes em estereomicroscópio não proporcionou resultados satisfatórios, visto que diversas estruturas encontram-se reduzidas em muitos taxa, ou seja, análises baseadas unicamente em visualizações diretas de fósseis e moldes em estéreomicroscópio não proporcionam resultados seguros para análises filogenéticas com materiais fósseis muito pequenos como os dentes dos Metatheria. Portanto, todos os capítulos aqui apresentados nessa dissertação basearam-se majoritariamente nas fotografias em MEV tiradas pelo discente e docente dos materiais de Itaboraí e nas imagens de MEV disponíveis na literatura.

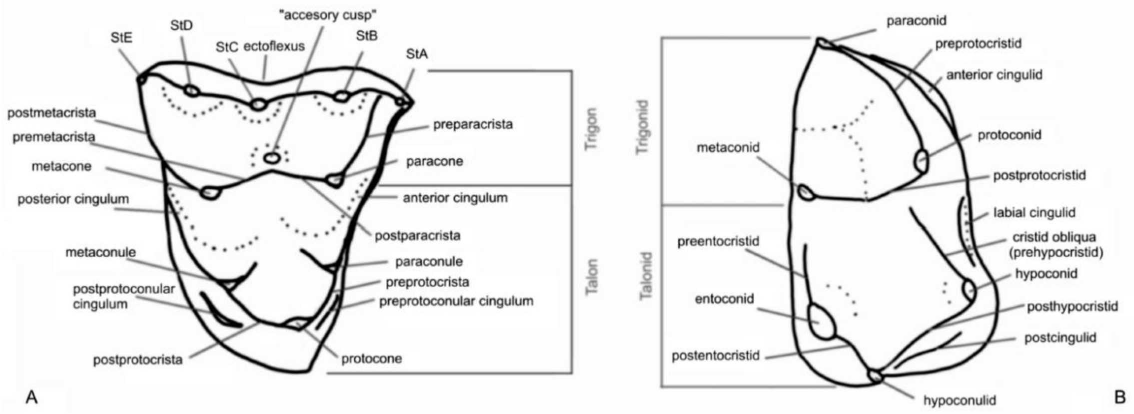
Baseando-se nisso, foi construída uma das maiores filogenias com metatérios fósseis já apresentadas na literatura até o presente momento. A filogenia compreende mais de 120 gêneros, sendo oito gêneros viventes da América do Sul e Austrália. Dentre os táxons fósseis, a filogenia compreende quase todos os gêneros já descritos para a América do Norte, América do Sul e Antártica. Foram incluídos também táxons fósseis da Austrália (fauna de Tingamarra e gêneros ‘problemáticos’ do Paleogeno e Neogeno) e alguns metatérios da Europa, África e Ásia. A filogenia conta com mais de 200 caracteres, sendo 188 relacionados a caracteres dentários (Figs. 8, 9). Os caracteres restantes estão relacionados à morfologia do dentário, crânio, petrosos e pós-crânio quando possível.

Figura 8: Desenho esquemático dos molares superiores e inferiores de *Glasbius intricatus* apresentando uma lista geral dos principais caracteres utilizados na construção da matriz morfológica.



(WILLIAMSON, BRUSATTE e WILSON, 2014)

Figura 9: Desenho esquemático dos molares superiores e inferiores de um metatério "polyprotodonte" generalizado apresentando uma lista geral dos principais caracteres utilizados na construção da matriz morfológica.



(OLIVEIRA e GOIN, 2011)

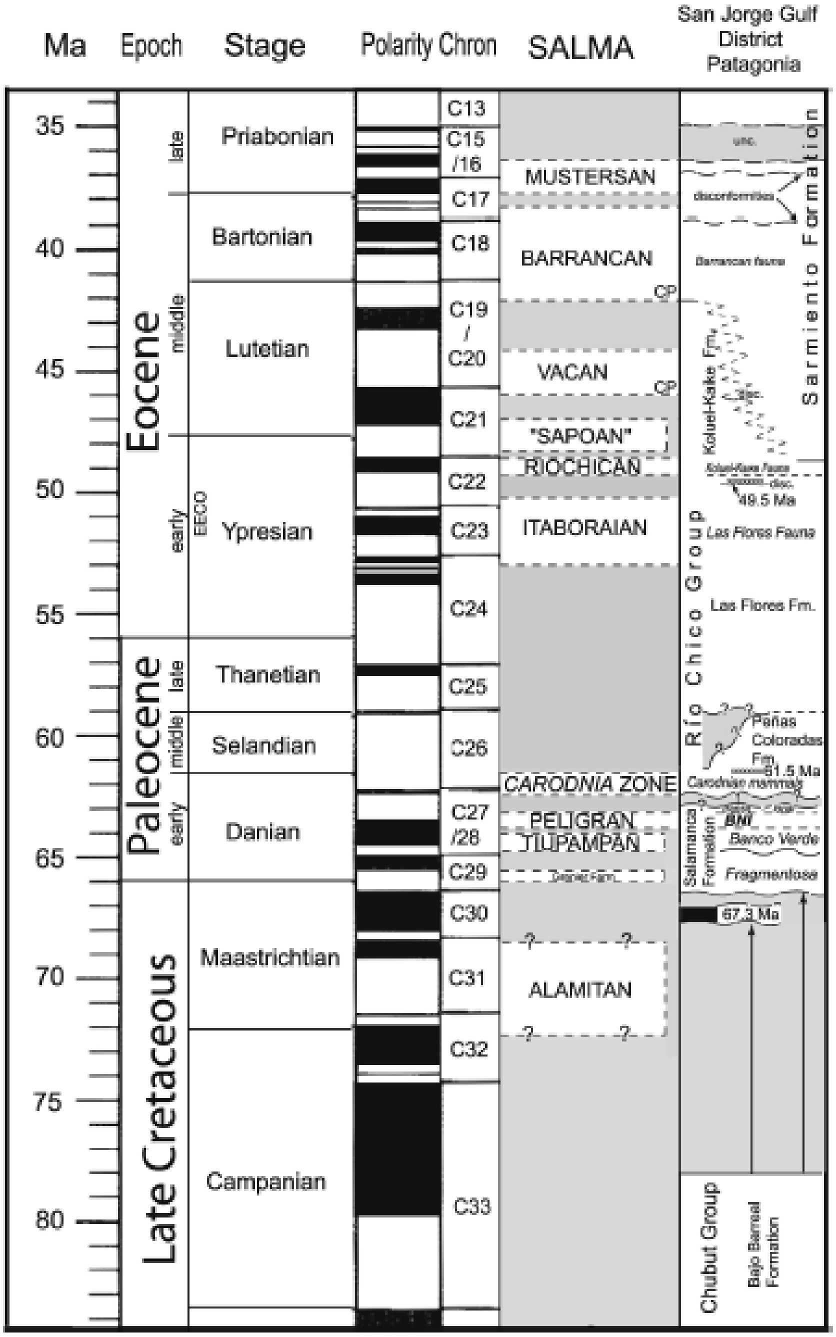
A matriz de caracteres e estados por táxon foi construída no *software* NEXUS, sendo as matrizes salvas em arquivos '.nex'. As análises filogenéticas utilizaram o *software* TNT 1.1 (GOLOBOFF et al, 2008). Foi escolhido o método de máxima parcimônia com 1000 *replications* por 1000 *random seeds*, salvando 10000 árvores na memória da análise. O algorítimo utilizado foi o TBR (tree bisection reconnection). Para inferência da estabilidade robustez e suporte dos ramos foi utilizado o 'Suporte de Bremer', também calculado com o TNT 1.1.

4.3. INFORMAÇÕES PALEOAMBIENTES: PALEOCLIMATOLOGIA, EUSTASIA, GEOCRONOLOGIA E GEOMORFOLOGIA

As idades das comunidades de metatérios fósseis seguidas na dissertação basearam-se nos trabalhos de Gelfo et al (2009) e Woodburne et al (2014) para as Idades de Mamíferos Terrestres Sul-americanos (South American Land Mammal Ages – SALMAs) (Fig. 10). Para as Idades de Mamíferos Terrestres Norte-americana (North American Land Mammal Ages – NALMAs) foram utilizados os trabalhos de Cifelli et al (2012) e Williamson, Brusatte e Wilson (2014) (Fig. 11).

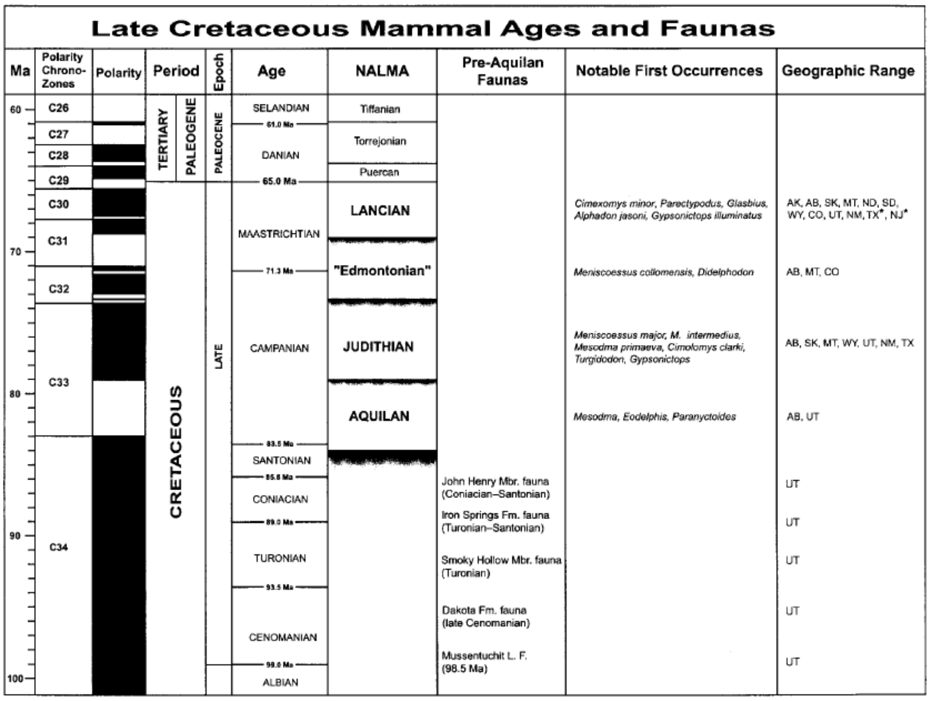
As idades das transgressões e regressões marinhas durante o Cretáceo Final e Paleoceno inferior foram obtidas de Haq (2014) (Fig. 12). As reconstruções geomorfológicas da América do Norte, América do Sul e Caribe foram, dentre elas, obtidas de Pindell (1994); Pascual e Ortiz-Jaureguizar (2007). A idade do Máximo Termal do Paleoceno-Eoceno (MTPE – PETM em inglês) foi obtida de Woodburne et al (2014) e Bowen et al (2015). As reconstruções paleoclimáticas foram obtidas de Woodburne et al (2013).

Figura 10: Geocronologia das SALMAs atualizadas. A figura apresenta os prováveis Estágios e Épocas das SALMAs, estimando a sua idade em Maa.



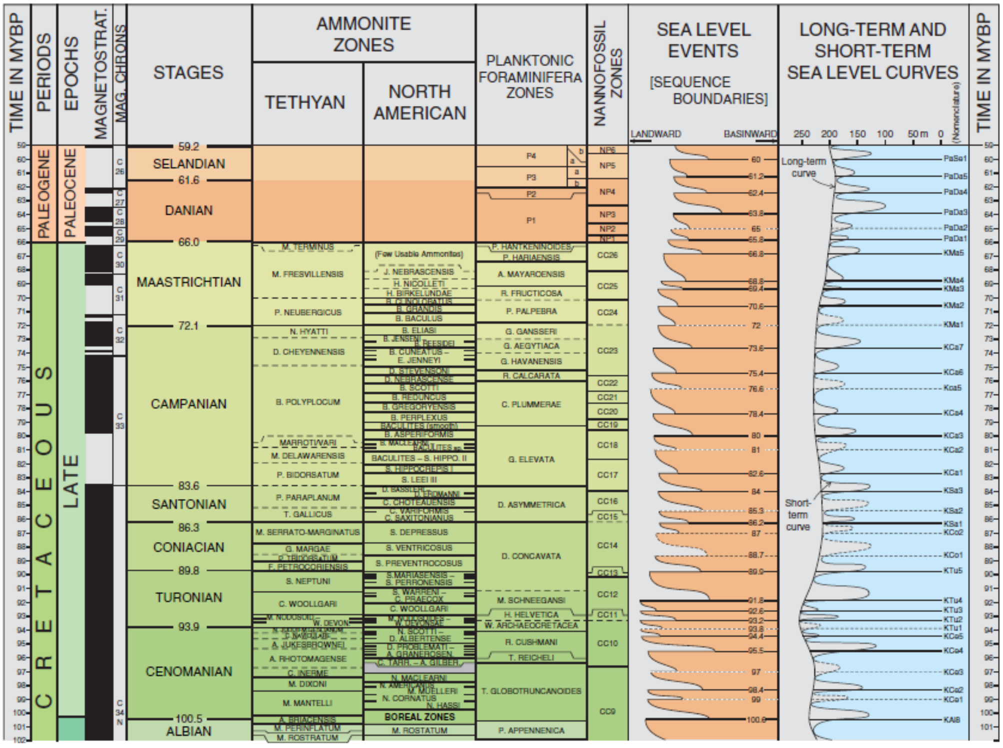
(WOODBURNE et al, 2014)

Figura 11: Geocronologia das NALMAs atualizadas. A figura apresenta os prováveis Períodos, Estágios e Épocas das NALMAs, estimando a sua idade em Maa.



(CIFELLI et al, 2014)

Figura 12: Regressões e Transgressões marinhas durante o Cretáceo Final e Paleoceno inferior.



(HAQ, 2014)

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A NEW PEDIOMYOID (MAMMALIA, METATHERIA) FROM THE PALEOGENE OF BRAZIL: INSIGHTS ABOUT SYSTEMATICS AND PALEOBIOGEOGRAPHY OF MICROBIOTHERIA AND PEDIOMYOIDEA

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RH: CARNEIRO & OLIVEIRA—A NEW PEDIOMYOIDEA FROM BRAZIL

Abstract

The Pediomyidae is considered an endemic lineage from the Cretaceous of North America, although some latest Cretaceous and Palaeogene forms from South America seem to present affinities with them. The description of *Austropediomys marshalli* gen. et sp. nov. provides a reliable evidence for the presence of Pediomyoidea in South America during the Paleogene. The phylogenetic analysis recovered several Paleogene "Microbiotheriidae" taxa within Pediomyoidea and not Microbiotheria. The grouping of these taxa with Pediomyidae indicates a possible paraphyletic state for Microbiotheria. The description of *Austropediomys* allowed the identification of subdivided conules lingual to para- and metaconule on Pediomyidae and most of Paleogene-Neogene "Microbiotheriidae", a feature never discussed or identified in previous studies. We also reinterpreted the validity of the "linear" centrocrista, which represents two different morphologies. The straight or linear centrocrista was considered as a plesiomorphy and is identified by its alignment with para- and metacone apices; while the derived state, the pseudolinear centrocrista, shows a "straight" shape, but is not aligned with paracone and metacone apices. The morphology of lower molars of Pediomyidae and Microbiotheria was also discussed in order to support the positioning of *Austropediomys* within Pediomyoidea, and not Microbiotheria. The presence of several Pediomyoidea during the Paleogene of South America increases the temporal and biogeographical range of this lineage and supports a North American origin and dispersal to South America during the Late Cretaceous.

Key words: Microbiotheria, Paleobiogeography, Pediomyoidea, Systematics

INTRODUCTION

The Pediomyidae Simpson, 1927, is an endemic lineage from the Late Cretaceous of North America. The fossil record of this family are known from the late Santonian to the KPg boundary (late Maastrichtian-Paleogene boundary), with no described taxa crossing this time span (Clemens, 1966; Eaton, 2006; 2013; Davis, 2007; Williamson *et al.*, 2012; Williamson *et al.*, 2014). In South America, possible “pediomyids” have been reported in the Maastrichtian of Peru (Sigé, 1972), in the early Paleocene of Bolivia (Case & Woodburne, 1986; Oliveira & Goin, 2006; Woodburne *et al.*, 2013) and in the early Eocene of Brazil (Marshall, 1987; Marshall *et al.*, 1990). Nevertheless, no study has ever corroborated the presence of Pediomyoidea in South America.

Marshall (1987) identified as a Pediomyinae the Itaboraí genus *Monodelphopsis* in a concept that considers this subfamily as belonging to Microbiotheriidae, along with Microbiotheriinae. For him, the specimen DGM 808-M represents the upper dentition of *Monodelphopsis*. The grouping of *Monodelphopsis* within Pediomyidae was previously discussed by Muizon (1992). However, none study has ever corroborated the affinities of this taxon; consequently, none pediomyid is formally described in South America. However, DGM 808-M represents new taxa, distinct of *Monodelphopsis*.

Herein, we describe the specimens DGM 808-M and MN 2354-V, previously misinterpreted as *Monodelphopsis*, and discuss its affinities in relation to North and South American forms.

Institutional abbreviations. CMCVF, Carnegie Museum Catalog of Vertebrate Fossils, Pittsburgh, Pennsylvania, USA; **DGM**, Divisão de Geologia e Mineralogia, Rio de Janeiro, Brazil; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MCT** (ex

DGM), Museu de Ciências da Terra, Rio de Janeiro, Brazil; **MN**, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; **MNA V**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MOR**, Museum of the Rockies, Montana State university, Bozeman, Montana, USA; **MPEF-PV**, Museu Paleontológico “Egidio Feruglio”, Sección Paleontología Vertebrados, Trelew, Argentina; **MPM-PV**, Museu Regional Provincial “Padre Manuel Jesús Molina”, Rio Gallegos, colleción Paleontología Vertebrados, Argentina; **OMNH**, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; **UALVP**, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; **UNM-B**, U.S. Bureau of Land Management collections housed at the University of New Mexico, Albuquerque, New Mexico, USA; **YPFB Pal**, Colecciones de Paleontología del Centro de Tecnología Petrolera de Yacimientos Petrolíferos Fiscales de Bolivia, Santa Cruz, Bolívia.

Other abbreviations. m, lower molars with the numbers corresponding to its positioning; **M**, upper molars; **p**, lower premolars; **P**, upper premolars; **StA**, stylar cusp A; **StB**, stylar cusp B; **StC**, stylar cusp C; **StD**, stylar cusp D; **StE**, stylar cusp E. **NALMA**, North American Land Mammal Age. **SALMA**, South American Land Mammal Age.

MATERIALS AND METHODS

We present a new matrix with new proposed characters and codification based on the interpretation of singular patterns and evolutionary tendencies that have never been proposed or studied in any phylogeny published so far. The matrix is mainly based on dental characters from upper and lower dentition of fossil and living Metatheria, with the polarization of characters following the conclusions of previous studies (Fox, 1987; Marshall *et al.*, 1990; Johanson, 1996; Cifelli & Muizon, 1997; Oliveira & Goin, 2011; Oliveira *et al.*, 2016).

We consider the specimens herein studied as a new genus and species on the basis of materials previously described as *Monodelphopsis travassosi* by Paula Couto (1962, 1970) and Marshall (1987), which include DGM 808-M and MN 2354-V (Fig. 1). Because MN 2354-V significantly differs from the holotype of *M. travassosi* in having a slightly smaller size, paraconid lingually placed and better developed, cristid obliqua ending anteriorly in a position labial to the postprotocristid notch (near the labial face of the protoconid), talonid much wider and longer than trigonid, preentocristid less developed, entoconid significantly more robust, smaller hypoconulid and less labially extended postcingulid; we exclude this material from the hypodigm of *Monodelphopsis*.

We conducted a traditional search using TNT 1.1 (Goloboff *et al*., 2008) with 1000 replications and 1000 random seeds, saving 10 trees for replication. Bremer supports were calculated using TNT 1.1. The phylogeny presents 37 metatherian taxa, including five extant genera, from Cretaceous and Cenozoic from North America and Southern hemisphere (*i.e.* South America and Australia).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Infraclass METATHERIA Huxley, 1880

†Superfamily PEDIOMYIODEA (Simpson, 1927)

Family *INCERTAE SEDIS*

†Genus *Austropediomys* gen. nov.

(Fig. 1)

1987 *Monodelphopsis travassosi* (part.) Marshall, p. 115, figs. 31-32.

Etymology. *From Latin 'austro' = south; 'Pediomys*', in reference to its North American Pediomyidae family affinities. *marshalli*, in honor to North American paleontologist, by his contributions to fossil marsupials knowledge.

Type species. *Austropediomys marshalli* sp. nov.

Included species. The type only.

Diagnosis. Differs from all other Pediomyoidea in the following combination of features: not winged conules, anterior cingulum reduced to the anterolabial face of the paracone, absence of posterior-, pre- and postprotoconal cingula, paracone much lower and less voluminous than the metacone, pyramidal paracone and rounded metacone, StB much better developed, protocone with anteroposterior compression and more elongated, and lower molars without accessory cuspids on the preentocristid and accessory cuspids e and f.

Holotype. DGM 808-M, incomplete left maxilla with M2-4.

Occurrence. Itaboraí Basin and Formation, Itaboraí, state of Rio de Janeiro, Brazil. Early Eocene, Itaboraian SALMA (ca 53-50 Ma) (Woodburne *et al*., 2014).

Remarks. When compared to most of Late Cretaceous and Paleogene metatherians, the new taxa herein described is recovered as closely-related to the North American "*Protolambda*" *clemensi* (Sahni, 1972), and the South American *Eomicrobiotherium*, *Clenia*, *Oligobiotherium* and *Pachybiotherium* than any other Pediomyoidea. This new lineage was recovered as the sister group of remaining Pediomyidae (Fig. 2).

†*Austropediomys marshalli* sp. nov.

(Fig. 1)

1987 *Monodelphopsis travassosi* (part.) Marshall, p. 115, figs. 31-32.

Etymology. *'marshalli*', in honor to North American paleontologist, by his contributions to fossil marsupials knowledge.

Diagnosis. As for the genus.

Holotype. DGM 808-M, incomplete left maxilla with M2-4.

Hypodigm. MCT 2798-M, incomplete left M1; MCT 2799-M, complete left M3; MCT 2800-M, incomplete right M4; MCT 808-M(a), left M1; MN 2354-V (Fig. 1), incomplete left dentary with intra-alveolar portion of the p3 and with m1-4.

Occurrence. As for the genus.

Description

Upper molars. M1 (MCT 808-M(a)) differs from the M2 by the stylar shelf very reduced, vestigial stylar cusps with supernumerary cusps; no vestige of ectoflexus; the paracone is very close to StB; vestigial preparacrista pointing to StA; vestigial conules; central protocone; straight centrocrista and reduced cingula.

The M2 (DGM 808-M) present a poorly developed stylar shelf and a lingually expanded talon; the StA is poor projected mesially and places in the same level in relation to StB, so that there is no vestige of fissure; the StB is the higher and robust style, being located more lingually than the remaining styles; vestigial styles, place very close to StD on the C position; the StD is very compressed labiolingually; the preparacrista is clearly oriented anterolingually, and ends very close to StA; the ectoflexus is very deep; the postmetacrista shows a trajectory only slightly more long than that of the preparacrista; although low the centrocrista is clearly straight; the metacone is higher and more labially convex than the paracone, which is labiolingually compressed; the protocone is expanded lingually and anteriorly turned; para- and metaconule are moderately developed, subdivided (see definition below), being the metaconule slightly stronger; the anterior cingulum is very short, with trajectory limited to the labial half of the paracone.

The M3 is structurally equal to M2, differing in the slightly larger size, StB more convex labially, StA somewhat compressed anteriorly, StC more developed, StD slightly less developed, preparacrista slightly more long and ectoflexus more deep.

The M4 differs from M1-3 in having its posterolabial half transversely reduced, the antero-lingual angle is more salient labially and the StA more compressed anteriorly, the StC is places anteriorly to the ectoflexus, the paracone is less developed than the metacone, the protocone is compressed anteroposteriorly, the paraconule is absent and the metaconule is very developed. MCT 2800-M differs from the DGM 808-M by the parastylar region anterolabially more developed and by the metaconule less developed.

Lower Dentition. Regarding the premolars of MN 2354-V, the intra-alveolar portion of p3 has, in section, an oval outline, suggesting that the tooth was well developed transversely. The portion of p1 and p2 was not preserved.

The lower molars present slightly inflate cuspids; the talonid is wide transversely; the trigonid is compressed anteroposteriorly; the paraconid is not so reduced in relation to the metaconid, being slightly less robust than the metaconido; the metaconid is placed slightly posterior to the protoconid; the pre- and postprotocristid have the same length with both fissures situated in the same horizontal plan; the anterocingulid shows an almost horizontal trajectory; the talonid is wide transversely, well basined; the entoconid is placed slightly posterior to the distal wall of the trigonid and is very compressed labiolingually; the entoconid is higher than the hypoconid; the hypoconulid is smaller and placed very lingually to the posterior face of the entoconid; the hypoconid is very salient labially; the cristida obliqua is poor developed and open, ends anteriorly at labially to the postprotocristid notch; the posthypocristid is long and poor transversal to the dental axis; the postentocristid is connected to the anterolingual face of the hypoconulid; the postcingulid is only vestigial.

The m2 differs from m1 as the tooth is slightly smaller in size, the trigonid is more compressed anteroporsteriorly, the posthypocristid is more transversely oriented, and the hypoconulid is slightly more developed. The tooth has a postentocristid running posterolabially.

The m3 differs from m2 in being narrower and by the more anterior position of the metaconid in relation to protoconid; the apex of the protoconid is acute; the metaconid is slightly higher than the paraconid.

The m4 differs from m1-3 by the smaller size, talonid poor developed transversely, so that it is subequal to trigonid, the cristida oblíqua is shorter and the hypoconulid is more developed and more labially placed, the entoconid is notably lingually oriented; the protoconid is moderately high and with the apex very acute.

Wear facets. On all teeth are observed apical wear facets in all cuspids of the trigonid, cristid obliqua and posthypocristid. The wear pattern is similar to the one present in Pediomyidae.

PHYLOGENTIC ANALYSIS

The results found a single most parsimonious tree (tree score = 98) (Fig. 2). *Austropediomys marshalli* was recovered as closely-related to “*Protolambda*” *clemensi* (Sahnii, 1972), *Eomicrobiotherium* Marshall, 1982, *Clenia* Ameghino, 1904, “*Clenia*” *brevis*

Goin, Abello & Chornogubsky, 2010, *Oligobiotherium divisum* (Ameghino, 1902), *Kirutherium paititiensis* Goin & Candela, 2004, and *Pachybiotherium* Ameghino, 1902. This lineage was recovered as the sister-group of Pediomyidae, within Pediomyoidea.

The results do not support the grouping of "Microbiotheriidae" along with Polydolopimorphia and *Glasbius*, as proposed by Goin *et al.* (2009); indeed, "Microbiotheriidae", *Glasbius* (*i.e.* Glasbiidae) and Polydolopimorphia do not form a monophyletic group. Polydolopimorphia was found as a basal metatherian lineage. *Glasbius*, on his turn, was found to be a Didelphimorphian marsupial, closely related to *Protodidelphis* Paula Couto, 1952, and *Carolocoutoia* Goin, Oliveira & Candela, 1998.

The phylogeny also shows an unexpected result: *Eomicrobiotherium, Oligobiotherium, Clenia*, "*Clenia*" *brevis, Kirutherium* Goin & Abello, 2004, and *Pachybiotherium* are closely-related to *Austropediomys marshalli* and "*Protolambda*" *clemensi* than any other metatherian lineage. This lineage was recovered as the sister group of Pediomyidae, which included *Khasia cordillerensis, Pediomys elegans, Leptalestes* Davis, 2007, and *Protolambda* Osborn, 1898. This clade is considered as one of the most basal groups recovered in the phylogeny. The basal positioning of *Khasia* recovered by Oliveira *et al*. (2016) agrees with this review as *Khasia* belong to one of the most basal lineages recovered in the phylogeny.

"Microbiotheria" was recovered as a paraphyletic group represented by *Woodburnodon casei* Goin *et al.*, 2007, *Microbiotherium* spp. and *Dromiciops gliroides*, not showing direct affinities with Pediomyoidea, in contrast to Oliveira & Goin (2011), but resembling Oliveira *et al.* (2016). *Eomicrobiotherium, Oligobiotherium, Clenia, Kirutherium,* and *Pachybiotherium* do not belong to Microbiotheria *sensu strictu*, in contrast to Goin & Abello (2013).

DISCUSSION

Subdivided conules

The identification of the subdivided conules was a crucial feature of the analysis. These new features are identified by the presence of an additional pair of “conular-like” structures associated with the pre- and the postprotocrista lingual to para- and metaconule on upper molars of *Austropediomys marshalli* (we will call these structures as subdivided conules) (Fig. 3). This condition is also observed in other South American Paleogene taxa, such *Clenia* and *Eomicrobiotherium*, actually regarded as “Microbiotheriidae”. *Oligobiotherium divisum*, shows on M2 only traces of subdivided conules, and almost no evidence on M3. In North America, the Cretaceous taxa “*Protolambda*” *clemensi* and *Pediomys elegans* also show these structures. *Protolambda*, “*Leptalestes*” *cooki* and *Leptalestes* show only traces of these structures on M1-3, but these structures are easily identifiable on M4. *Khasia* shows a single para- and metaconule (*e.g.* YPFB Pal 6133 and YPFB Pal 6486), a condition recovered as an autapomorphy, following the phylogenetic analysis. Unfortunately, the condition present on *Pachybiotherium* could not be distinguishable due to bad preservation of the referred M3 (*i.e.* MPM-PV 1806) (Goin *et al.*, 2010).

The late Eocene-?early Oligocene Peruvian taxon *Kirutherium paititiensis* shows similar condition. On its description, the accessory conules were identified as: “both para- and metaconule are vestigial, elongated, and partially fused with the labial ends of the pre- and postprotocrista, respectively” (Goin & Candela, 2004). Regarding the presence of subdivided conules, it is important to observe that pediomyoid metatherians seem to possess a particular upper molar wear pattern that strongly worn the conules, talon basin, anterobasal cingulum and protocone. This condition can also be identified on some pediomyid upper molars – *e.g.* UALVP 2410 M2 assigned to *Leptalestes krejcii* (Clemens, 1966), UNM-B1737 M2 assigned to *Leptalestes prokrejcii* (Rigby & Wolberg, 1987), and CMCVF 3706, M3 assigned to *Pediomys elegans* (Lillegraven, 1969). The Pediomyidae teeth show similar pattern as seen on M3 of *Pachybiotherium illuminatum* (Goin *et al.*, 2010). The exemplar OMNH 64262 shows a lesser degree of wear on the upper molars of *Pediomys elegans*, in which the subdivided conules are worn, giving the impression that para- and metaconule are indeed elongated; same condition is also present on *Kirutherium paititiensis*, which support the conclusions about the presence of subdivided conules on this taxon.

As seen above, the Oligocene *Oligobiotherium divisum* shows poorly developed subdivided conules on M2, but this condition represents a secondarily reduction of these structures, as the tooth does not present a high level of wear. However, these structures are identifiable by the presence of a notch separating the conules on unworn to slightly worn teeth. On upper molars with some degree of wear, the subdivided conules are normally identified as a heavy, wide and elongated pre- or postprotocrista.

Chornogubsky & Kramarz (2012) figurate a left M2 (*i.e.* MACN SC3648) that also presents subdivided conules. An accessory conule lingual to metaconule is easily visible, but the one lingual to paraconule is more reduced. The presence of these conules allowed the conclusion that this upper molar does not belong to *Microbiotherium* (see systematic review topic for more details). The morphology and location of the conules present in MACN SC3648 resemble the one present in "*Clenia*" *brevis,* in which the paraconule is more lingually shifted.

The presence of subdivided conules in most basal Pediomyoidea indicates a symplesiomorphic condition for the superfamily. Following the results, the presence of subdivided conules is an ancestral condition for the lineage and their subsequent loss is regarded as apomorphic, being independently acquired in both North and South American lineages. The Cretaceous *Aquiladelphis,* regarded as the sister group to all Pediomyoidea (Davis, 2007) or as a true Pediomyidae (Williamson *et al*., 2014), also present subdivided conules, observation that support its inclusion among this lineage.

Identification of these structures very probably is associated with a deep notch separating the subdivided structures. The Pediomyidae shows these features still merged with the pre- and postprotocrista, when these structures are easily identifiable and independent from pre- and postprotocrista on "*Protolambda" clemensi*, *Austropediomys* and South American "Microbiotheriidae". Some North American taxa, such *Turgidodon* (Cifelli, 1990) and *Dakotadens* Eaton, 1993, present similar structures associated to postprotocrista (Eaton, 1993; Hunter *et al*., 2010). These structures were identified as non-homologous structures to the subdivided conules of Pediomyoidea by the phylogenetic analysis. *Turgidodon* and *Dakotadens* present multiple "conules" only on postprotocrista. These species present a variable presence of these structures, with some taxa presenting two or more structures (*e.g.* MOR 2509 *Turgidodon russelli* (Hunter *et al*., 2010) and MNA V5825, V6037, V5828 *Dakotadens morrowi* and V5345 *Dakotadens* sp. (Eaton, 1993).

Dromiciops, *Microbiotherium* and *Woodburnodon* do not show any sign of subdivided conules (Fig. 3), as the remaining metatherians. Indeed, the presence of these accessory structures represents a strong and unique acquisition of Pediomyoidea among Metatheria, which supports its monophyletic origin.

Straight centrocrista

A usual character regarded as a plesiomorphy of Metatheria is the straight centrocrista. In fact, most of traditionally regarded as basal metatherian present a straight centrocrista: Caroloameghiniidae, Peradectidae, Pediomyidae, Stagodontidae, Aquiladelphidae, Sparassodonta, *Kokopellia* and “Microbiotheriidae”. Although, quite accepted in literature, the homology of this structure has never been studied in detail. In the revision, we attempted to different morphologies regarding this structure, which implies a homoplastic acquisition. We noted that the straight centrocrista shows, at least, two different morphologies.

Several taxa (Sparassodonta, Pediomyidae, Stagodontidae, *Kokopellia*, Aquiladelphidae and some Peradectidae) present a centrocrista that is aligned with para- and metacone apices (condition for me considered as the true straight centrocrista), while others have a straight centrocrista that is more labial shifted in position regarding the cone apices (Caroloameghiniidae, “Microbiotheriidae”, some Didelphidae and Peradectidae), condition identified as ‘pseudolinear centrocrista’.

The labial displacement indicates a derived state, comprehending an apomorphy for this character and, consequently, a non-homologous origin. Based on this, the straight centrocrista morphology must be considered as a plesiomorphy, present just in basal lineages and taxa; while the derived condition (*i.e.* pseudolinear centrocrista) can be considered as an apomorphy, that was independently acquired many times in Metatherian evolution (*e.g.* *Andinodelphys*, *Procaroloameghinia*, *Szalinia*, *Dromiciops* and *Microbiotherium*). The straight centrocrista can be considered as a truly plesiomorphic state for Metatheria lineage.

The South and North American Pediomyoidea taxa present a straight centrocrista (Fig. 3). The labial displacements (*e.g.* ‘V-shape’, ‘U-shape’, ‘arc-shape’, pseudolinear and open states) can be considered variations in the dilambdodont morphology, being independently acquired at least five times in Metatherian evolution, as suggested by (Williamson *et al.*, 2012). The posterior displacement of metacone apex on *Oligobiotherium divisum*, *Clenia minuscula* and "*Clenia*" *brevis* slightly affects the morphology of premetaconular crista, which gives to centrocrista a slightly sinuous trajectory; nevertheless, the centrocrista still remains aligned with para- and metacone apex (*i.e.* straight centrocrista condition). *Austropediomys marshalli* presents a straight centrocrista on all upper molars.

Woodburnodon casei, *Dromiciops gliroides* and *Microbiotherium tehuelchum* present the derived centrocrista state (Fig. 3). The pseudolinear centrocrista present on these taxa assume a more dilambdodont appearance on the extant taxon, *D. gliroides*; and a more "U-shape" morphology on *Woodburnodon* and *Microbiotherium*. Despite this little difference, the centrocrista of these taxa is shifted at stylar shelf comparing to para- and metacone apices, an undoubtedly independent condition from the one present on Pediomyoidea.

In short, the results do not consider as a plesiomorphy the centrocrista state of *Woodburnodon*, *Microbiotherium* and *Dromiciops*. However, the state present on Pediomyidae, Aquiladelphidae and most of Paleogene "Microbiotheriidae" was recovered as a plesiomorphy, supporting the basal positioning of these taxa.

Morphology of lower molars

Austropediomys marshalli presents a metaconid just slightly posteriorly placed to protoconid. Similar condition is also present on "*Protolambda*" *clemensi* and remaining Pediomyidae. The posterior displacement of metaconid is more evident on Paleogene "Microbiotheriidae". In addition, these taxa present a strongly reduced metaconid than the protoconid, an exclusive feature of this lineage among Pediomyoidea. The plesiomorphic condition of *Austropediomys marshalli* and "*Protolambda*" *clemensi* does not refute the affinities with this group, as the condition present on both taxa constitutes a retained plesiomorphy, following the phylogenetic analysis (Fig. 4).

The Microbiotheria presents a slightly posteriorly placed metaconid than the protoconid on *Microbiotherium tehuelchum* and an aligned one on *Dromiciops gliroides*. On both taxa, the metaconid is lower and less developed than the protoconid, but does not reach the strong reduction present on m1 of remaining "Microbiotheriidae" (Fig. 4).

The talonid of Paleogene "Microbiotheriidae" resemble Pediomyidae pattern, with a labiolingually compressed and better developed entoconid than the hypoconid, and a lingually placed hypoconulid. The posterobasal cingulid is better developed in "*Protolambda*" *clemensi*, less developed on *Austropediomys marshalli* and *Eomicrobiotherium*; and is nearly vestigial on remaining taxa of this lineage. The Microbiotheriidae *sensu strictu* present the talonid of m3 with a straight preentocristid, which forms the lingual border of the talonid. However, different from Paleogene taxa, the hypoconid is labially projected, giving to the cristid obliqua a more sinuous trajectory and forming a concave and labially projected inflexion, instead. The projection of hypoconid results on a wider talonid than trigonid.

The morphology of the cristid obliqua on m2 and m3 separates Paleogene "Microbiotheriidae" and Microbiotheriidae *sensu strictu*. The Paleogene taxa, such *Oligobiotherium divisum*, *Clenia minuscula* and "*Clenia*" *brevis* present a cristid obliqua that contacts the posterior wall of trigonid at the lingual border of protoconid. MACN SC520 and MPEF-PV 4750 evidence an interesting and exclusive pattern, their cristid obliqua recurves at the anteriormost portion, not reaching the trigonid wall, but curving towards talonid basin in a more perpendicular patter. This morphology was identified as a synapomorphy.

For Microbiotheriidae *sensu strictu*, the cristid obliqua presents a more sinuous trajectory, and differing from Paleogene taxa by the labial contact on m1-3. In short, the

Paleogene “Microbiotheriinae” presents a subequal talonid and trigonid with a straight cristid obliqua contacting the labial border of talonid, due to the absence of the displacement of hypoconid. For Microbiotheriidae, the hypoconid presents a labial displacement and the cristid obliqua presents a sinuous trajectory, reaching the labial border of trigonid.

The Pediomyidae presents a moderately developed anterobasal cingulid with equal degree of development on all lower molars. This family also presents a nearly subequal m4 and m3. “*Protolambda*” *clemensi* presents similar pattern. *Austropediomys marshalli* shows a moderately reduced m4 than m3, condition also present on Paleogene “Microbiotheriidae”, but with a greater reduction. The reduction of these taxa is evidently less developed than the one present on Microbiotheriidae *sensu strictu*. In fact, the m4 of this lineage is extremely reduced. The Antarctic *Marambiotherium glacialis* presents a moderately developed m4 than m3 (Goin *et al*., 1999), a condition that is present on Pediomyoidea, as mentioned. Unfortunately, *Marambiotherium* is only known by a single m4, restricting more comparisons with remaining taxa. The morphology of basal Australidelphia is quite similar to the one present on *Marambiotherium glacialis,* as both differs from Pediomyidae and Paleogene “Microbiotheriidae” by the presence of aligned proto- and metaconid in m4. Based on this, we followed Goin *et al*. (1999), which considered *M. glacialis* as a basal Microbiotheria.

The comparative morphology demonstrates that the lower molars of Paleogene “Microbiotheriidae” are more similar on general shape to Pediomyidae than any Microbiotheriidae *sensu strictu*. This discussion results on preliminary conclusions about the phylogenetic affinities of Paleogene “Microbiotheria”. Future focused studies could help to better understand the proper systematic affinities of these taxa with Microbiotheriidae *sensu strictu* and Pediomyidae.

Systematic implications of *Austropediomys marshalli* and Paleogene "Microbiotheriidae"

Austropediomys marshalli share with other pediomyoids the following set of characters: accessory conular structures lingual to para- and metaconule, poorly developed stylar cusps, enlarged StA, accessory cusp twinned to StC, StC closely-spaced to StD, reduced and labiolingualy compressed StD; para- and metacone appressed at bases, straight and sharp centrocrista, protocone wide and slightly anteriorly displaced, talon longer than stylar shelf, developed metacone and metaconule on M4; reduced anterobasal cingulid, well-developed and labiolingually compressed entoconid, labial and lingual border with slightly difference in height, talonid something wider than trigonid, para- and metaconid with little difference in high; paraconid closer to metaconid, with both aligned at lingual border; cristid obliqua connecting the trigonid at labial border, hypoconulid appressed to entoconid and less developed than this one; and m4 with sharp and tall protoconid, that is higher than para- and metaconid.

The presence of developed subdivided conules lingual to para- and metaconule is easily identifiable on M2-3 of *Austropediomys marshalli*. These subdivided conules are also present in Paleogene "Microbiotheriidae", such *Eomicrobiotherium mykerum*, *Clenia brevis*, "*Clenia*" *minuscula* and *Kirutherium*. The presence of similar conular structures on several Pediomyidae (*e.g. Pediomys elegans*, "*Protolambda*" *clemensi*, *Leptalestes*? *cooki*) indicates a closely-relation between these taxa and Paleogene "Microbiotheriidae". The conular structures of *Austropediomys* are evidently more developed than any other Pediomyoidea, recovering this degree of development as an autapomorphy of Brazilian taxon. These conular accessory structures were considered as a valid feature for the grouping of these taxa, following the phylogenetic analysis.

Austropediomys marshalli presents a unique morphology regarding all Pediomyoidea, being autapomorphic by the reduction of the anterobasal cingulum and absence of posterobasal cingulum, absence of protoconal cingula, absence of interrupted anterobasal cingulum, better development of StB, accessory cuspule twinned to StA on M2, mesio-distally compressed upper molars, nearly subequal stylar shelf on M2 and subequal on M3, better development of the stylar shelf, and twinned StC on M2-3.

This taxon is closely-related to "*Protolambda*" *clemensi* and several Paleogene "Microbiotheriidae" based on the presence of the asymmetric development of the subdivided conules, and strong labial projection of the hypoconid on m4.

The grouping of *Clenia minuscula*, "*Clenia*" *brevis*, *Eomicrobiotherium*, *Pachybiotherium*, *Kirutherium*, "*Microbiotherium*" *gallegosense* and *Oligobiotherium divisum* within Pediomyoidea was an unexpected and surprising result of the phylogenetic analysis. Regarded as "Microbiotheriidae" (Goin & Abello, 2013), these taxa share with Pediomyidae the following set of characters: presence of paraconule, posterobasal cingulum (well-developed only in *Eomicrobiotherium* and reduced in the remaining taxa), crested conules, accessory cusp twinned with StC (*Oligobiotherium* and *Pachybiotherium*), StC closer to StD, developed preprotoconal cingulum (*Eomicrobiotherium*), presence of subdivided conules, and a rounded paracone and pyramidal metacone (the last three are synapomorphies of Pediomyoidea).

The large size of subdivided conules, frequently as large as para- and metaconule, groups "*Protolambda*" *clemensi*, *Austropediomys* and Paleogene "Microbiotheriidae". These taxa differ from Pediomyidae by the presence of smaller lingual conular structures than para- and metaconule (Fig. 3).

The results agree with Goin & Abello (2013) that found these taxa as a monophyletic lineage independent from Microbiotheriidae *sensu strictu,* although the cited study only focuses on traditionally considered “Microbiotheriidae”. When compared with a larger metatherian assemblage, most of Paleogene and Neogene “Microbiotheriidae” are closely-related to Pediomyidae than any Microbiotheria *sensu strictu*.

Dromiciops gliroides and *Microbiotherium* differ from Pediomyoidea on the absence of paraconule, absence of crested conules, equally reduced stylar shelf (when the parastylar shelf is more reduced than metastylar shelf in Pediomyoidea), vestigial to absent M4 metacone, absence of conules on M4, absence of preprotoconal cingulum, centrocrista not aligned with the apices of para- and metacone (*i.e.* absence of a straight centrocrista), absence of a twinned cusp to StC and absence of posterobasal cingulum and eccentric protocone; the Neogene taxa also lacks the two unambiguous synapomorphies of Pediomyoidea (*i.e.* subdivided conules and interrupted anterobasal cingulum).

The preliminary results of this study indicate that the similar morphology between Pediomyoidea and “Microbiotheria” could be a result of convergent evolution, implying a “paraphyletic” state for “Microbiotheria”. Future more focused studies will help to elucidate the true affinities of Paleogene “Microbiotheria” taxa.

The North American Cretaceous origin of Pediomyoidea and the Late Cretaceous arrival in South America

The result of the phylogenetic analysis extends the temporal and biogeographical distribution of Pediomyoidea from the Late Cretaceous of North America (Santonian – Aquilan NALMA – Eaton 2006; 2013) to the Neogene of South America (middle-late Miocene boundary) (Fig. 5). In opposition to previous studies (Williamson *et al*., 2012;

Williamson *et al*., 2014), the Pediomyidae survived after the KPg boundary in South America, surviving until, at least, early Paleocene in Tiupampa (Muizon, 1992). The presence of a lower molar in Laguna Umayo Basin (?late Maastrichtian - Late Cretaceous) of Peru appears to constitute an evidence for a Late Cretaceous transcontinental arrival for the lineage in South America during the ?late Maastrichtian, as suggested by Case *et al.* (2005).

The grouping of "*Protolambda*" *clemensi* with *Austropediomys* and several Paleogene "Microbiotheriidae" supports a North American origin of this lineage, and indicates a maximum early Campanian dichotomy time between *P. clemensi* and South American taxa. The results corroborate previous theories about the presence of pediomyoid metatherians in South America (Muizon, 1992; Oliveira & Goin, 2012).

These new data indicate a complex evolutionary history for the lineage. The presence of sea level lowstands during the Campanian and late Maastrichtian (Haq, 2014) could indicate asynchronous arrivals in South America. It seems that the basal dichotomy between "*Protolambda*" *clemensi* and South American taxa probably happened during early Campanian stage, with the lineage of *P. clemensi* restricted to North America and remaining taxa to "insular Central America" or South America.

During the Late Cretaceous, current Central America was a place of intense volcanic activity, and recent geological models reconstructed this area as a set of islands (*i.e.* 'Aves Ridge' concept) (Pindell, 1994). Previous studies considered the 'Aves Ridge' and adjacent Cuba in the Campanian and especially in the Maastrichtian as one of the best pathway candidates for the dispersal rout between Americas (Woodburne & Case, 1996). The separated South American continent, always situated south of the North American plate, drifted north-northwest during the Campanian, when its mutual connection by the Panamanian "Bridge" began. Around 80 Ma, the Caribbean Sea was not yet defined, although intermediate volcanic islands enabled the first interamerican faunal exchange: hadrosaurid dinosaurs from the rising North American continent and titanosaurid saltasaurine dinosaurs from the South America continent (Pascual, 2006). The Late Cretaceous-Paleogene faunal correlation between the North and South Americas was previously proposed (Case & Woodburne, 1986; Pascual, 2006; Pascual & Ortiz-Jaureguizar, 2007; Case *et al*., 2005). The arrival in South America probably happened during late Maastrichtian (around 66 Ma), time span compatible with a strong sea-level lowstand; although, Muizon & Cifelli (2001) supposed an arrival of the South American Metatheria from North America older than late Maastrichtian based on the great diversity of this group than South American Native Ungulates. The group survived in South America until middle-late Miocene boundary (Goin *et al.*, 2010; Goin & Abello, 2013; Goin *et al*., 2013).

CONCLUSIONS

The description of *Austropediomys marshalli* increases the diversity of non-marsupial metatherian in South America. The positioning of several Paleogene “Microbiotheriidae” within Pediomyoidea and the description of *A. marshalli* increase the geographic and temporal range of this lineage. The presence of these taxa provides new information for this group that survived in South America until middle Miocene.

The systematic positioning of “*Protolambda*” *clemensi* indicates a North American origin for the South American pediomyoid clade (*i.e. Austropediomys*, *Eomicrobiotherium*, *Oligobiotherium*, *Clenia*, “*Clenia*” *brevis*, *Pachybiotherium* and *Kirutherium*). The presence of strong sea-level lowstands during Cretaceous seems to be a major factor in the paleobiogeography of the group, allowing these taxa to reach South America thorough

Caribbean still in Late Cretaceous. Same pattern should be true for Pediomyidae, as the latest taxon, *Khasia cordillerensis,* was found in South America during early Paleocene.

The assignment of many Paleogene "Microbiotheriidae" as pediomyoid metatherians restricted Microbiotheriidae in South America to only four genera: *Woodburnodon, Marambiotherium*, *Microbiotherium* and *Dromiciops*.

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FIGURES CAPTIONS

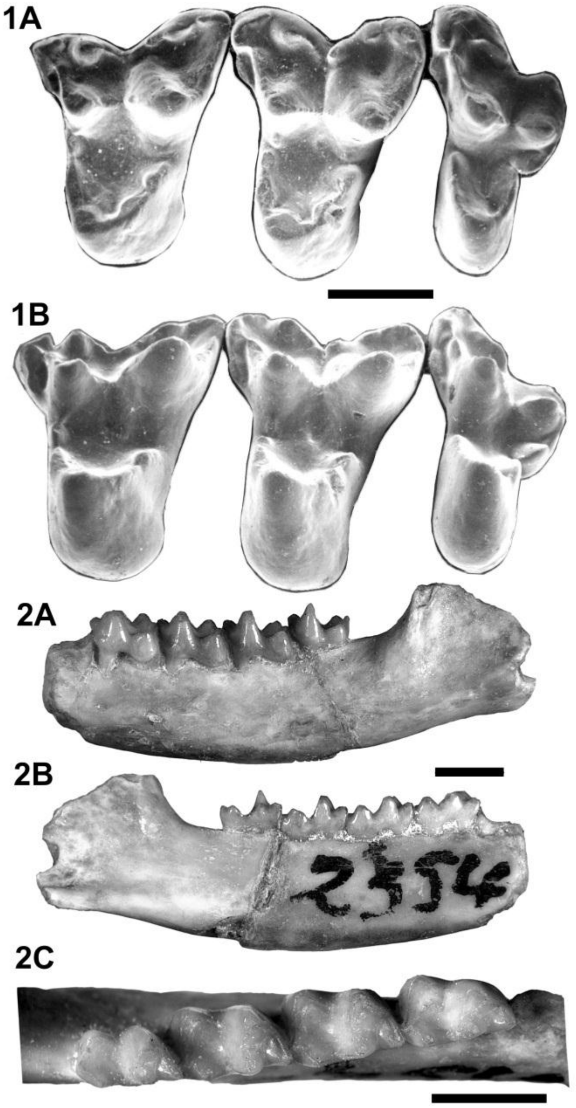
Fig. 1. Upper and lower dentition of *Austropediomys marshalli*. **1.** DGM 808-M (type specimen): **A.** occlusal view; **B.** oblique view. Scale bar: 1mm. **2.** MN 2354-V: **A.** labial view; **B.** lingual view; **C.** occlusal view of left incomplete dentary with preserved m1-4 and alveolus of posterior root of p_3. Scale bar: 2 mm.

Fig. 2. Result of phylogenetic analysis. Single most parsimonious tree found in analysis. The metatherian lineages are identified by vertical bars. Numbers below the ramus indicate the Bremer Support.

Fig. 3. Comparative morphology of studied taxa. Schematic drawings of *Austropediomys marshalli*, *Pediomys elegans*, *Eomicrobiotherium mykerum* and *Microbiotherium tehuelchum* evidencing main autapomorphies of each taxa and lineage. **Ps**, parastylar shelf; **Ms**, metastylar shelf. Scale bar: 1 mm.

Fig. 4. Comparative morphology of m1. Schematic drawings of the first lower molar of *Microbiotherium tehuelchum* and *Pachybiotherium acclinum* evidencing the two main synapomorphies of Microbiotehria and Pediomyoidea on m1. Scale bar: 1 mm.

Fig. 5. Temporal and geographical distribution of Pediomyoidea. Phylogeny of Pediomyoidea calibrated in time, based on the phylogeny present in the figure 2. The wide bars indicate the recorded temporal range of Pediomyoidea genera. The NALMAs and SALMAs that present Pediomyoidea taxa are identified.



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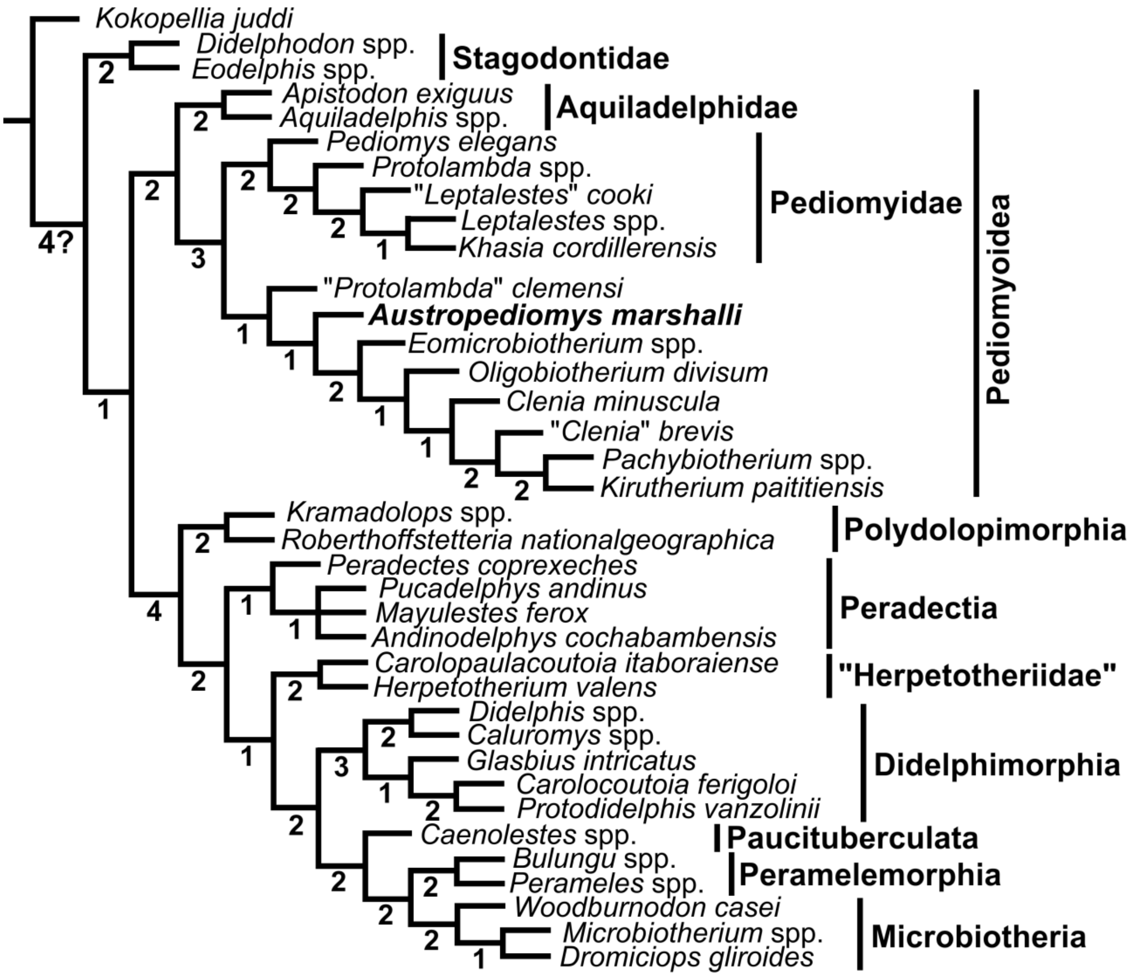

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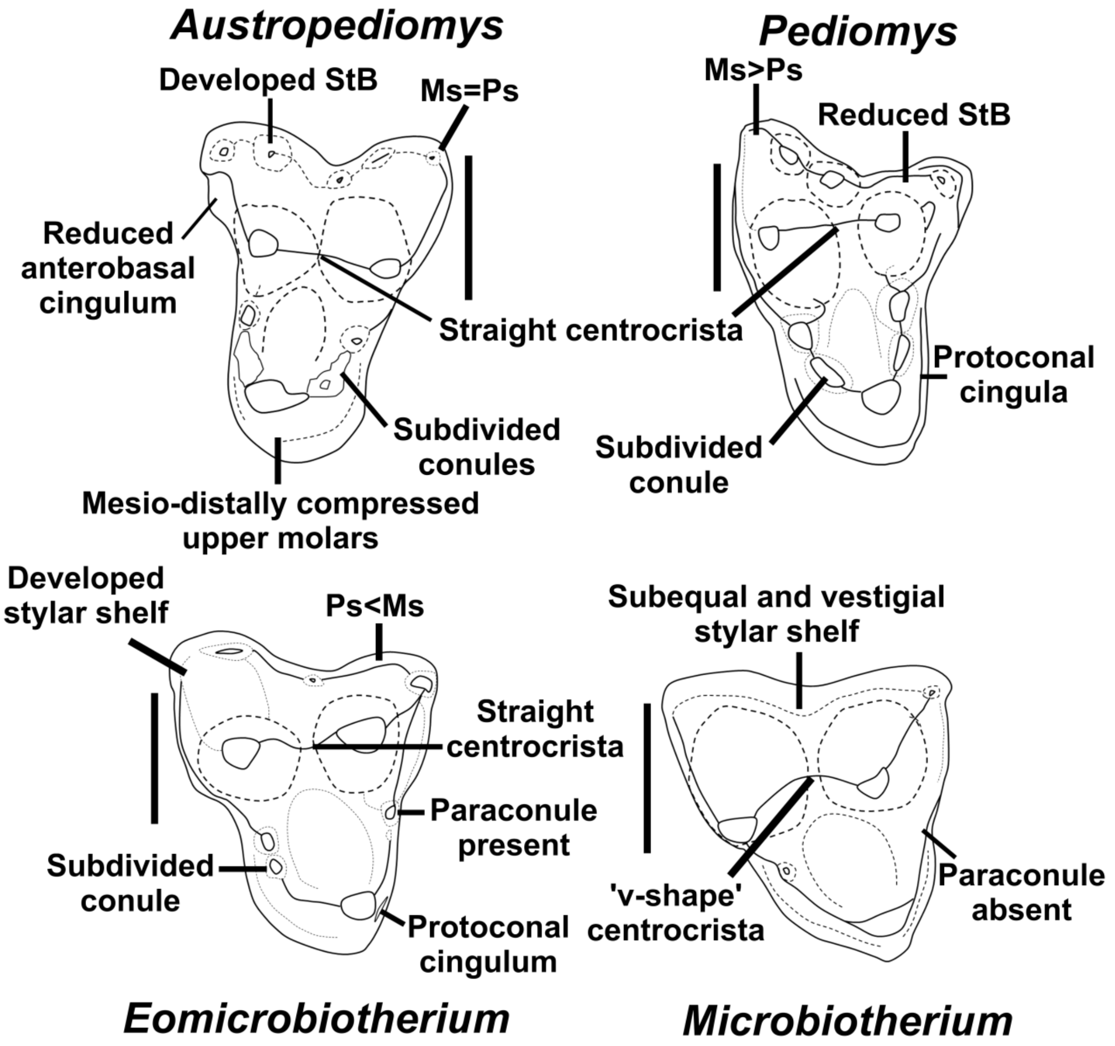

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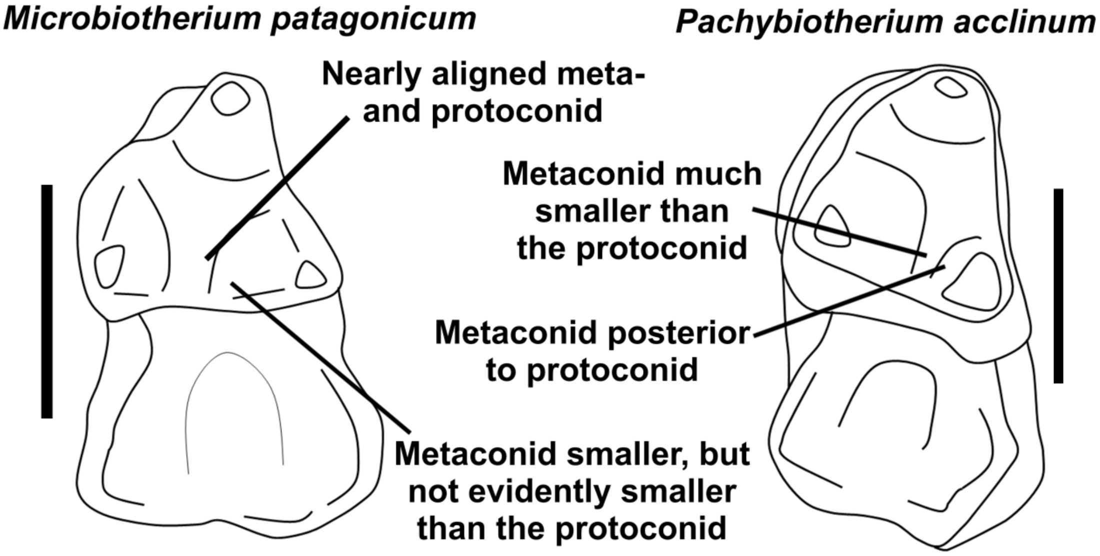

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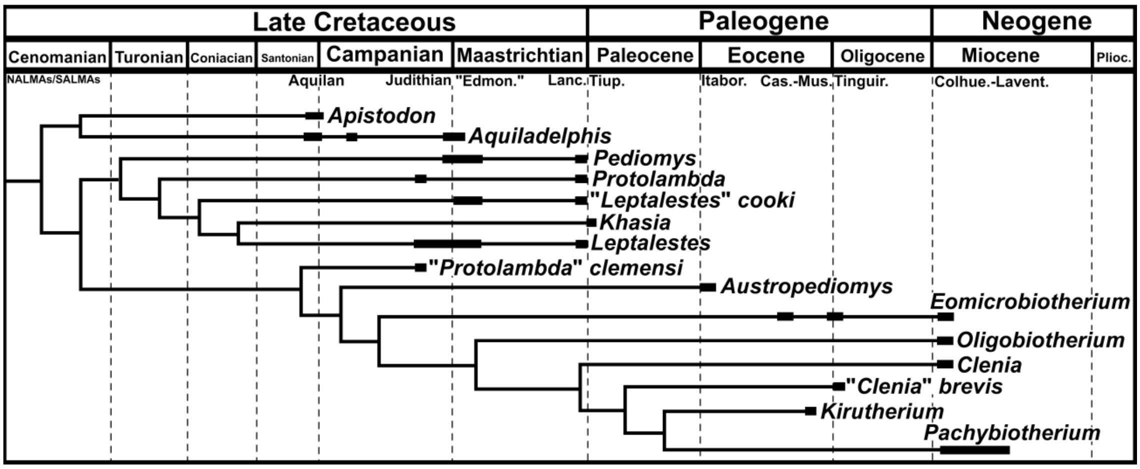

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Appendix 1

Characters and states of phylogenetic analysis. Characters and states used in the phylogenetic analyses. Characters are polarized with respect to *Lotheridium mengi* as outgroup. All characters are treated as unordered.

1. Wing-like parastyle: (0) absent, (1) present.
2. Development of parastyle: (0) developed, (1) reduced or vestigial.
3. Lingually shifted parastyle on M2-3: absent (0), present (1).
4. Development of StA in comparison to StB (Muizon and Cifelli, 2001): enlarged (0), small (1), vestigial (2).
5. Development of StB: developed (0), vestigial or absent (1).
6. Sinuous crest connecting StB and StD: (0) absent, (1) present.
7. StB with distolabial accessory cuspule (StB1): (0) absent, (1) present.
8. StB1 position in comparison to StC: (0) more labial than StC, (1) at same level of StC.
9. Well-developed StB1: (0) absent, (1) present.
10. Centro-labial StB1: (0) absent, (1) present.
11. Pyramidal StB: (0) absent, (1) present.
12. Broad and well-developed labial accessory crest of pyramidal StB: (0) absent, (1) present.
13. Reduced lingual accessory crest of pyramidal StB, which does not contact StC: (0) absent, (1) present.
14. Invasive lingual accessory crests of pyramidal StB and StD in stylar shelf: (0) absent, (1) present.
15. Invasive lingual accessory crests of pyramidal StB and StD merging at the center of stylar

shelf: (0) absent, (1) present.

16. StB massively larger than paracone: absent (0), present (1).
17. 'Twinned' cusp to StB: absent (0), present (1).
18. StB salient labially on M3: absent (0), salient (1).
19. StC development: (0) not truly identifiable, (1) identifiable.
20. Presence of StC: present (0), vestigial or absent on all molars (1).
21. Pyramidal StC: absent (0), present (1).
22. StC mesiolingually twisted on M1: absent (0), present (1).
23. Lingual shifting of StC: (0) not evidently lingual, (1) evidently lingual.
24. Lingual accessory crest of StC: absent (0), present (1).
25. Well-developed StC: absent (0), present (1).
26. Alignment of StB, StC and StD: (0) absent, (1) present.
27. Labiolingually compressed StC: absent (0), present (1).
28. StC merging with StD on M3: absent (0), present (1).
29. Twinned StC: present (0), absent (1).
30. StD development: (0) not truly identifiable, (1) identifiable.
31. Medium accessory crest of StD: (0) absent, (1) present.
32. Pyramidal StD: (0) absent, (1) present.
33. Pyramidal StD on all upper molars: absent (0), present (1).
34. StD with lingual and labial accessory crests: (0) absent, (1) present.
35. Morphology of the pyramidal StD: (0) pyramidal without inflation or compression, (1) compressed and flattened, (2) inflated, reducing the concave medial border and the accessory crests.
36. Vertical posterior border of StD: (0) absent, (1) present.

37. Developed vertical posterior border of StD: (0) developed, (1) poorly developed or vestigial.

38. StD subdivided into three apices: (0) absent, (1) present.

39. StD with sinuous accessory crest on M2, but not M1 or M3: absent (0), present (1).

40. Sinuous crest connecting the incipiently developed StD and the labiodistal border of metacone: present (0), absent (1).

41. StD with multiple crenulations on its longitudinal axis: absent (0), present (1).

42. StD1 presence: absent (0), present (1).

43. Notch between StB and StD: absent (0), present (1).

44. Conical and developed StE: absent (0), present (1).

45. Twinned cusps on the posterior border of metastylar shelf of M3: absent (0), present (1).

46. Roll of reduced cuspules only at the anterior border of StD: (0) absent, (1) present.

47. Accessory cuspules. (0) present, (1) absent.

48. Presence of multiples cuspules on metastylar shelf, with one usually slightly more developed than the remaining, but it could not be considered as a "true" StD: present (0), absent (1).

49. M3 with 'metastylar-wall': absent (0), present (1).

50. Flattened and reduced StB, StC and StD. (0) absent, (1) present.

51. Subequal, labially aligned, conical and closely-spaced StB, StC and StD: absent (0), present (1).

52. Well-developed stylar shelf with subequal parastylar and metastylar shelf: absent (0), present (1).

53. Epiconular plataform: absent (0), present (1).

54. Low parallel crest connecting the apex of the paracone with StB: (0) absent, (1) present.

55. Low parallel crest connecting the apex of the metacone with StD: (0) absent, (1) present.

56. Preparacrista orientation: StB (0), StA (1).

57. Preparacrista labially notched due to the absence of the mesiolingual crest of StB: absent (0), present (1).

58. Reduced preparacrista that points toward StA and does not contact the mesiolingual crest of StB: (0) absent, (1) present.

59. Parastylar shelf development on M2 and or M3: developed (0), reduced to a narrow cingulum or rim (1).

60. Postmetacrista with three accessory cuspules: (0) absent, (1) present.

61. Well-developed postmetacrista accessory cusps: (0) absent, (1) present.

62. Postmetacrista accessory crest: (0) absent, (1) present.

63. Well-developed metastylar wing, distally projecting on M3: absent (0), present (1).

64. Comparative development of asymmetric reduced parastylar shelf and developed metastylar shelf: absent (0), metastylar much larger than parastylar (1), metastylar slightly larger than parastylar (2), metastylar slightly larger or nearly subequal to parastyle.

65. Labial border of metastylar shelf oblique oriented on M1, being twice the size of the parastylar shelf labial border: (0) absent, (1) present.

66. Labial border of metastylar shelf evidently rounded: absent (0), present (1).

67. Labial cingulum: absent (0), present (1).

68. Vestigial stylar shelf: absent (0), present (1).

69. Ectoflexus very deep, reaching the level of lingual border of StB: present (0), absent (1).

70. Ectoflexus deep and broad ('ridge-like' ectoflexus): absent (0), present (1).

71. Para- and metacone with apices lingually projected: (0) absent, (1) present.

72. Metacone apex evidently posteriorly projected: absent (0), present (1).

73. Morphology of the labial borders of para- and metacone: (0) both rounded, (1) metacone rounded and paracone pyramidal, (2) both compressed, (3) paracone rounded and metacone

pyramidal.

74. Labial alignment of para- and metacone: aligned (0), paracone more labial than metacone (1).

75. Paracone evidently more labial than the metacone on M2-3: absent (0), present (1).

76. Twisted paracone: (0) absent, (1) present.

77. Degree of paracone twisting: (0) poorly twisted, (1) evidently twisted.

78. Medium sharp crest on lingual border of metacone: absent (0), present (1).

79. Accessory crest labially and oblique oriented on the midline of metacone: (0) absent, (1) present.

80. Development of the accessory crest labially oriented on the midline of metacone: (0) developed, (1) poorly developed.

81. Accessory crest labially oriented on the midline of paracone: (0) absent, (1) developed.

82. Development of the accessory crest labially oriented on the midline of paracone: (0) developed, (1) poorly developed.

83. Alignment of centrocrista with para- and metacone: (0) straight, (1) lingually displaced.

84. Notched straight centrocrista: (0) absent, (1) present.

85. Morphology of labially displaced centrocrista: pseudolinear (0), dilambdodont (1), 'arc-shape' (2), 'U-shape' (3), open (4), vestigial (5), notched (6).

86. Invasive centrocrista: (0) absent, (1) present.

87. Morphology of labially displaced notched centrocrista: (0) discontinuous, (1) some degree of 'arc-shape', (2) sinuous, (3) pseudolinear.

88. Accessory cusp to the ectoloph of the centrocrista: (0) absent, (1) present.

89. Protocone displacement (Oliveira and Goin, 2011): (0) absent, (1) eccentric.

90. Morphology of protocone: fusiform or indiferenciated (0), mesio-distally expanded (1), labio-lingually developed (2), conical (3), hypocone (4), compressed (5).

91. Inflation of protocone: absent (0), present (1).

92. Spire-like protocone: (0) absent, (1) present, (2) compressed.

93. Fusiforme protocone on M3, but not on M1-2: (0) absent, (1) present.

94. M1 with fusiform and eccentric protocone ('Peradectoid M1'): absent (0), present (1).

95. Protocone with a pair of oblique grooves: absent (0), present (1).

96. Preprotocrista with half the length of postprotocrista, but the protocone is not eccentric: absent (0), present (1).

97. Accessory cuspules associated with postprotocrista with a variable number: absent (0), present (1).

98. Presence of dental basal expansions: absent (0), present (1).

99. Development of dental basal expansions: poorly developed (0), well-developed (1).

100. Conules separated from the pre- and postprotocrista by a deep notch: (0) absent, (1) present.

101. Accessory conules presence: (0) absent, (1) present.

102. Accessory conules with similar development to para- and metaconule and independently developed from protocristae: absent (0), present (1).

103. Development of conules: with some degree of development, but not reduced or enlarged (0), reduced or absent (1), enlarged (2).

104. Paraconule much more reduced than the metaconule: (0) absent, (1) present.

105. Morphology of metaconule: pyramidal (0), pseudoinflated (1), inflated (2), 'hypocone-like' (3), 'spire-like' (4), mesio-distally compressed (5), pseudohypocone (6).

106. Paraconule enlarged, being larger than the vestigial metaconule on M3: (0) absent, (1) present.

107. Paraconule lingually shifted, but not the metaconule: absent (0), present (1).

108. Aligned paraconule, protocone and metaconule: (0) absent, (1) present.

109. M3 with conules lingually shifted, subequal and aligned, but not on the lingual border: (0) absent, (1) present.
110. Straight preparaconular crista separating the talonid basin from the mesiolingual cingulum: absent (0), present (1).
111. Invasive preparaconular crista: absent (0), present (1).
112. Morphology of invasive preparaconular crista: oblique oriented, but not so invasive (0), oblique oriented and well-invasive (1), straight (2).
113. Straight invasive preparaconular crista with sinuous lingual third trajectory: absent (0), present (1).
114. Discontinuous postmetaconular crista on M1: absent (0), present (1).
115. Internal metaconular crista development, when the metaconule is developed: developed (0), reduced or absent (1).
116. Furrow between protocone and metaconule: absent (0), present (1).
117. Proto-paraconule wear pattern: absent (0), present (1).
118. Anterobasal cingulum contacting the talon in a lower position (discontinuous anterobasal cingulum with talon basin): (0) absent, (1) present.
119. Merging of discontinuous anterobasal cingulum and talon basin: absent (0), present (1).
120. Reduced anterobasal cingulum only on M3: (0) absent, (1) present.
121. Mesial expansion of anterobasal cingulum: absent (0), with the labial half gently recurved and mesially expanded (1), broad and evidently mesially expanded (2), broad, but with sinuous trajectory (3).
122. Anterobasal cingulum with a lower trajectory: (0) absent, (1) present.
123. Posterobasal cingulum development: developed (0), reduced or poorly developed (1), vestigial or absent (2).

124. Posterobasal cingulum with a lower contact than stylar shelf: absent (0), present (1).

125. External shape of upper molars: 'yoke-like' (0), trapezoid (1), ovoid (2), subquadrangular (3), piriform (4), rectangular (5).

126. Hexacuspate upper molars: absent (0), present.

127. Hypsodonty: (0) absent, (1) present.

128. Mesiodistally compressed upper molars: (0) absent, (1) present.

129. Elongated talon that is longer than stylar shelf on all molars: (0) absent, (1) present.

130. Talon longer than stylar shelf only on M3: (0) absent, (1) present.

131. Compressed talon: (0) absent, (1) present.

132. M4 with centrally placed paracone: (0) absent, (1) present.

133. Dilambdodont centrocrista connecting para- and metacone on M4: (0) absent, (1) present.

134. M4 with large, inflated and labiocentral stylar cusps: (0) absent, (1) present.

135. Inflated M4: (0) absent, (1) present.

136. M4 with paracone apex anteriorly shifted: absent (0), present (1).

137. M4 with paracone more labial than the metacone: absent (0), present (1).

138. M4 more reduced than M3, but is not mesiodistally or labiolingually compressed: absent (0), present (1).

139. M1 with elongated shape that does not present a strong labiolingual compression of trigonid, which is much shorter than the talonid: (0) absent, (1) present.

140. M1 strongly labiolingually compressed: present (0), absent (1).

141. Anteroposteriorly compressed m1: (0) absent, (1) present.

142. M1 with well labially salient hypoconid: absent (0), present (1).

143. Protoconid and metaconid nearly merged on m1: absent (0), incipiently merged (1), merged (2).

144. Mesiodistally elongated a labiolingually compressed trigonid on m1: absent (0), present (1).

145. Labiolingual expansion of trigonid: absent (0), present (1).

146. Compression of trigonid: compressed (0), not compressed (1).

147. Relative size between paraconid and metaconid: (0) both well-developed and subequal, (1) paraconid with some degree of reduction, (2) metaconid with some degree of reduction, (3) paraconid with evident increasing in size.

148. Paraconid as taller as the protoconid: (0) absent, (1) present.

149. Paraconid medially placed: absent (0), present (1).

150. Paraconid broad and with its apex anteriorly shifted ('blade-like' paraconid) on m2-4: absent (0), present (1).

151. Paraconid with compressed mesial border: absent (0), present (1).

152. Metaconid positioning in comparison to the protoconid: metaconid complete posterior to protoconid (0), metaconid posterior to protoconid (1), both aligned (2), metaconid anterior to protoconid (3).

153. Keeled distolingual angle of metaconid (Eaton, 2006): absent (0), present (1).

154. Protoconid strongly labiolingually shifted on m2-3: absent (0), present (1).

155. Metastylid (Goin, 2006): (0) absent, (1) present.

156. Ectostylid: absent (0), present (1) (Zimicz, 2011).

157. Entostylid: absent (0), present (1).

158. Morphology of hypoconid: (0) compressed, (1) spire-like, (2) 'tower-like'.

159. Hypoconid labially projected, resulting in a wider talonid comparing to the trigonid: (0) absent, (1) present.

160. Development of the entoconid: (0) not truly identifiable, (1) identifiable and with some degree of development.

161. Morphology of entoconid: flattened and poorly developed (0), conical (1), compressed (2), 'spire-like' (3), flattened (4), inflated (5).

162. Entoconid and hypoconid with similar size: (0) absent, (1) present.

163. Conical and vestigial entoconid: (0) absent, (1) present.

164. Massive hypo- and entoconid: absent (0), present (1).

165. Cristid obliqua position of contact with the posterior wall of the trigonid (m1-3): slightly lingual (0), carnassial notch (1), slightly labial (2), more labial (3), at labial border (4).

166. Metacristid short and recurved due to the merging with the cristid obliqua: absent (0), present (1).

167. Cristid obliqua progressively more lingual through the lower molar series: absent (0), present (1).

168. Sinuous and reduced cristid obliqua: absent (0), present (1).

169. Recurved cristid obliqua on m2, does not contacting trigonid posterior wall: absent (0), present (1).

170. Hypo-hypoconulid wear pattern: absent (0), present (1).

171. Hypoconulid position: central (0), more lingual (1), distolingual (2), slightly lingual (3).

172. Hypoconulid central, well-developed and distally projected (occupies more than the half of the posterior wall of talonid): absent (0), present (1).

173. Aligned entoconid, hypoconulid and hypoconid on distal border of talonid: absent (0), present (1).

174. Accessory cuspids e and f: (0) with at least one present, (1) both vestigial or absent.

175. Short talonid: (0) absent, (1) present.

176. Low and broad lower molars: (0) absent, (1) present.

177. Protoconid labially projected on m4: absent (0), present (1).

178. M3 and or m4 cristid obliqua with posterior sinuous compression and straight trajectory: (0) absent, (1) present.

179. M4 hypoconid aligned or anterior to the entoconid: (0) absent, (1) present.

180. M4 size in comparison to m3, but not reduced to a single root: (0) nearly subequal, (1) moderately smaller, (2) much smaller, (3) larger.

181. M4 with elongated talonid: not elongated (0), shorter and narrower than the trigonid (1), evidently elongated (2), elongated, but evidently shorter than the trigonid (3).

182. M4 with conical and small entoconid ('tower-like'): absent (0), present (1).

183. M4 with conical and central hypoconulid: absent (0), present (1).

184. Cristid obliqua contacting the metaconid only on m4: absent (0), present (1).

185. M4 with labial cingulid: absent (0), poorly developed (1), evidently developed (2).

186. M4 with well-developed anterobasal cingulid: absent (0), present (1).

187. 'Didelphid-like' m4: absent (0), present (1).

188. Number of premolars: four (0), three or less (1).

189. P1 with two developed anterior and posterior cusps: (0) absent, (1) present.

190. P1 oblique oriented in comparison to P2-3: aligned (0), oblique oriented (1).

191. P1 with single-root: absent (0), present (1).

192. P2 larger than p3: absent (0), present (1).

193. Morphology of the mesial border of p2: rounded or convex (0), with anterior projection (1), laminar or without cusps or projections (2).

194. Flexids in the p2: (0) absent, (1) present.

195. Bulbous and inflated P3/p3: absent (0), present (1).

196. P3 with anteroposterior elongation: (0) absent, (1) present.

197. Plagiaulacoid P3-p3: absent (0), present (1).

198. Bilobed third lower incisor: absent (0), present (1).

199. Angular process of the dentary development: (0) not so developed, (1) evidently developed.

200. Recurved dentary: (0) absent, (1) present.

201. Recurvation of dentary below p1: absent (0), present (1).

202. Retropremolars spaces development: with diastem between p1-p2, but not p2-4 (0), spaces absent, with premolars in contact (1), with short retropremolar space between p1-2, but not p2-3 (2), with spaces between p1-2 and p2-3 (3), p1 and-or p2 absents (4).

203. Fossa incudis and epitympanic recess: continuous (0) or separated by a distinct ridge (1) (Ladevèze and Muizon, 2010 - character 28).

204. Mastoid tympanic process: small, slanted, and nodelike, on the posterolateral border of the stylomastoid notch and continuous with squamosal (0), indistinct to absent (1) (Beck, 2012).

205. Deep groove for internal carotid artery excavatedon anterior pole of promontorium: absent (0), present (1) (Ladevèze and Muizon, 2010 - character 10).

206. Tympanic sinus formed in the lateral trough (orlateral expansion of the pars canalicularis): absent (0), present (1) (Ladevèze and Muizon, 2010 - character 15).

207. Third trochanter presence: absent (0), present (1).

208. Positioning of the third trochanter: distal to the lesser trochanter, but with proximal portion nearly at same level (0), proximal to the lesser trochanter (1), more distal than the lesser trochanter, being complete more distal (2).

209. Lesser trochanter distomedially displaced: absent (0), present (1).

210. Calcaneocuboid facets: without subfacets (0), subdivided into pCaCu and dCaCu (1), subdivided into pCaCu, mCaCu and dCaCu (2) (Szalay, 1994).

211. CLAJP presence: absent (0), present (1) (Szalay, 1994).

212. Postorbital processes: absent or formed only by the frontals (0), formed by the parietals and

frontals (1) (Voss e Jansa, 2009).

213. Development of postorbital process: absent or indistinct (0), with some degree of development (1).

214. Posterior palate morphology: without distinct lateral corners, the choanae unconstricted behind (0), or posterior palate with distinct lateral corners, choanae constricted (1) (Voss e Jansa, 2009 - character 69).

SYSTEMATIC REVIEW OF DENTAL HOMOLOGIES OF “EOBRASILINAE” (MAMMALIA, METATHERIA), WITH THE DESCRIPTION OF THE FIRST PRESERVED LOWER MOLAR OF *EOBRASILIA COUTOI* SIMPSON, 1947, A SOUTH AMERICAN EARLY EOCENE STAGODONTIDAE

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RH: CARNEIRO AND OLIVEIRA—SYSTEMATIC REVIEW OF “EOBRASILINAE”

Abstract

Eobrasilia coutoi Simpson, 1947, is currently considered to be one of the most enigmatic metatherian mammals from Itaboraí Basin, Brazil. A single badly broken and incomplete skull and an associated fragmentary dentary are the elements currently attributed to this taxon, with a single strongly worn M3, which contributes for the uncertain position within Metatheria. Herein, it is described the first lower molar assigned to *Eobrasilia coutoi*, represented by an isolated m1 lacking the lingual half of the trigonid. In addition, we also re-analyze the preserved premolars morphology of this species. The morphology of this new molar supports the assignment of *Eobrasilia* as a South American Stagodontidae. This new result leads a systematic review of the accepted dental homologies of “Eobrasilinae”, currently represented by *Eobrasilia*, *Gaylordia* and *Didelphopsis*. The hypothesis that “Eobrasilinae” represents a valid taxon is refuted mainly due to the morphology of the lower molars, which recovered *Eobrasilia* as closely-related to *Didelphodon* within Stagodontidae, *Gaylordia* to Jaskhadelphyidae, and *Didelphopsis* to Herpetotheriidae. *Gaylordia* and *Tiulordia* were grouped in the new family Gaylordiidae. *Didelphopsis* and *Itaboraidelphys* were grouped as the sister-group of *Herpetotherium*. The presence of many shared characters between *Eobrasilia*, *Gaylordia* and *Didelphopsis* was a result of convergent evolution, as these three lineages independently adapted to more durophagous diets. The abundant presence of snails in Itaboraí could explain why three lineages independently adapted to more durophagous diets. The grouping of *Eobrasilia* and *Didelphodon* corroborates previous hypothesis that Metatheria dispersed from North to South America during Late Cretaceous.

Keywords: *Eobrasilia*, *Gaylordia*, *Didelphopsis*, “Eobrasilinae”, Gaylordiidae, Stagodontidae

INTRODUCTION

Eobrasilia coutoi Simpson, 1947, was discovered in fissure fillings of early Eocene in the Itaboraí formation at São José de Itaboraí, Brazil (Marshall, 1984). Represented by a badly broken and incomplete skull with heavily worn teeth (Simpson, 1947), and by a fragmentary dentary (Marshall, 1984), *Eobrasilia* received poorly attention since its formal description, being traditionally identified as a potential "missing-link" between Borhyaenoidea and "Didelphoidea" metatherians (*sensu* Simpson, 1947) and as a Didelphidae (*sensu* Paula Couto, 1962), though its position among "Didelphoidea" was supported by Marshall (1984).

The dental adaptations toward durophagy led *Eobrasilia* to be grouped with *Didelphopsis* Paula Couto, 1952, *Tiulordia* Marshall & Muizon, 1988, and *Gaylordia* Paula Couto, 1952, into the subfamily Eobrasilinae, within Didelphidae by Marshall (1987). Aside the durophagous adaptations, no other study founded diagnostic characters that support these taxa as constituting a monophyletic group.

A revision of petrosal and dental materials from Itaboraí placed *Eobrasilia* as closer-related to *Didelphodon* Marsh, 1889, and not to *Didelphopsis* and *Gaylordia*, though, the validity of Eobrasilinae was not properly discussed (Ladèveze & Muizon 2010). Oliveira & Goin (2011), and Oliveira *et al*. (2016) recovered *Gaylordia* as closely-related to *Minusculodelphis* and *Marmosopsis*, while Oliveira & Goin (2015) recovered *Gaylordia* as closely-related to *Pucadelphyidae* and *Peradectidae*. Goin (2003) suggested the inclusion of *Didelphopsis*, *Itaboraidelphys* and *Carolopaulacoutoia* in the family Sternibergiidae (McKenna & Bell 1997); but this result was not supported by Oliveira & Goin (2011), and Oliveira *et al*. (2016) that recovered *Didelphopsis* as closely-related to *Itaboraidelphys* as a monophyletic lineage basal to *Carolopaulacoutoia, Peratherium, Derorhynchus* and *Djarthia*, refuting the validity of Sternibergiidae. The validity of "Eobrasilinae" was previously contested by Oliveira & Goin (2012) based on the fact that *Didelphopsis*, *Gaylordia* and

Eobrasilia do not constitute a monophyletic lineage, as commented. For the authors, the evolution of bulbous and large premolars was a result of convergent evolution. The same study also called the attention to the morphology of the incisors present in *Eobrasilia*.

Marshall (1984) tentatively assigned MCT 2830-M, the holotype of *Zeusdelphys complicatus* Marshall, 1987 (a single and isolated M1), as the upper molar of *Eobrasilia*. However, this occlusal relation was never properly studied in details based on the absence of preserved lower molars of *Eobrasilia*. In the same study, the author commented about the greater number of morphological similarities between *Eobrasilia* and Stagodontidae taxa, but due to the absence of comparable materials, Marshall preferred not to assign the Brazilian taxon to this family.

The discovery of an undescribed “stagodontid-like” lower molar in DNPM Mammal Collection demonstrates that Stagodontidae Marsh, 1889, was present during the early Eocene of Brazil, in South America. Among all metatherians from Itaboraí, the lower dentition is not known for *Eobrasilia coutoi*, *Carolocoutoia ferigoloi* and *Zeusdelphys complicatus* both regarded as the largest species of this fauna. Interestingly, this lower molar is compatible in size with the alveoli roots of the m1 of *Eobrasilia coutoi* (DGM 919-M); this tooth even shows an anteroposterior compression expected for the m1 of this species based on the morphology of its preserved dentary. In addition, the dental adaptations of *Eobrasilia* and its larger size are also compatible with Stagodontidae.

The absence of diagnostic characters of “Eobrasilinae” and the discovery of the new lower molar resulted in the morphological review of the validity of dental homologies of “Eobrasilinae” herein present.

Institutional abbreviations. AMNH, American Natural History Museum; **DGM**, Divisão de Geologia e Mineralogia, Rio de Janeiro, Brazil; **MCN-PV**, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brasil; **MCT (ex DGM)**, Museu de Ciências da Terra, Rio de Janeiro, Brasil; **MNRJ**, Museu Nacional, Rio de Janeiro, Brasil; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.

Other abbreviations. **i**, lower incisors with the numbers corresponding to its positioning; **m**, lower molars; **M**, upper molars; **p**, lower premolars; **P**, upper premolars.

MATERIALS AND METHODS

In order to provide a proper association of the new lower molar, it was compared with the lower molars of Itaboraí taxa present in the collections of Brazil cited in the Institutional Abbreviations. The morphology of the dentition of Stagodontidae, Deltatheroida and some Australian groups were also studied and compared with this new material, with the objective to evaluate the proper homology of the presented dental durophagous adaptations. The polarization of the characters followed the conclusions of previous studies (Fox, 1987; Marshall *et al*., 1990; Johanson, 1996; Cifelli & Muizon, 1997; Oliveira & Goin, 2011; Oliveira *et al*., 2016).

The SEM pictures of DGM 919-M and MCT 1342-LE were made with the Scanning Electron Microscope JEOL JSM-6390LV at the Centro de Microscopia Eletrônica de Varredura do Departamento de invertebrados do Museu Nacional.

The phylogenetic analysis was conducted as a traditional search using TNT 1.1 (Goloboff *et al*., 2008) with 1000 replications and 1000 random seeds, saving 10 trees for replication. Bremer supports were calculated using TNT 1.1. The phylogeny includes 41 metatherian taxa, including 5 extant genera, from Cretaceous and Cenozoic from Asia, North America and Southern hemisphere (*i.e.* South America and Australia).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Infraclass METATHERIA Huxley, 1880

†Family STAGODONTIDAE Marsh, 1889

Emended diagnosis. Family supported by the presence of a single-rooted and oblique P1, presence of developed anterior and posterior cusps in P1, closely-spaced upper and lower premolars, with no evident retro-premolars spaces separating these teeth; development of semi-procumbent incisors, enlarged paraconid that is the tallest cuspid in the trigonid or present similar development to the protoconid in most basal taxa; small to reduced metaconid that is always the smallest cuspid in the trigonid; tall and flattened ento- and hypoconid, wide talonid, anteroposteriorly compressed m1, anteroposteriorly compressed trigonid, inflated third upper and lower premolars, large size and robust dentary.

Included genera. *Eodelphis* Matthew, 1916, *Didelphodon* and *Eobrasilia*.

†Genus *Eobrasilia* Simpson, 1947

1947 *Eobrasilia* Simpson, p. 2, fig. 2-4.

1984 *Eobrasilia* Marshall, p. 174, fig. 1-2.

1987 *Eobrasilia* Marshall, p. 100, fig. 10-11.

Type species. *Eobrasilia coutoi* Simpson, 1947.

Included species. The type only.

Occurrence. Itaboraí Basin and Formation, municipality of Itaboraí, state of Rio de Janeiro, Brazil. Early Eocene, Itaboraian SALMA (ca 53-50 Ma; Woodburne *et al*., 2014).

†*Eobrasilia coutoi* Simpson, 1947

(Fig. 1)

1947 *Eobrasilia* Simpson, p. 2, fig. 2-4.

1984 *Eobrasilia* Marshall, p. 174, fig. 1-2.

1987 *Eobrasilia* Marshall, p. 100, fig. 10-11.

Emended diagnosis. Differs from other Metatheria by the presence of two large semi-procumbent lower incisors, massive p3 that is much larger than p2 and even larger than the one present in *Didelphodon*; incipient three-rooted p3, talonid reduced to a rim in the m1; ento- and hypoconid contacting the posterior border of metaconid and protoconid, respectively, with the entoconid nearly fused with the metaconid; and enlarged and well-anteriorly projected paraconid that is the largest cuspid in the m1. The main autapomorphies of this species are the rim condition of the talonid, the merging condition between the entoconid and metaconid, and the stronger development of the paraconid.

Holotype. AMNH 39424, incomplete facial part of skull, with right P1-3, left P3 and M3.

Hypodigm. Holotype and DGM 919-M, a fragment of a right dentary with alveoli of incisors, canine and p1, p2-3 complete and anterior part of m1; MCT 1342-LE, left m1 lacking most of lingual portion of the trigonid.

Occurrence. Itaboraí Basin and Formation, municipality of Itaboraí, state of Rio de Janeiro, Brazil. Early Eocene, Itaboraian SALMA (ca 53-50 Ma; Woodburne *et al*., 2014).

Remarks. When compared to most of Late Cretaceous and Paleogene metatherians, *Eobrasilia coutoi* is closely-related to *Didelphodon* from the Late Cretaceous of North America by the massive size of p3 with a strong anteroposterior elongation, and strong compression of the m1.

†Family GAYLORDIIDAE fam. nov.

Diagnosis. Family supported by the presence of inflated third premolars with no anteroposterior development, mesio-distally compressed upper molars, elongated talon, mesio-distally wide protocone, moderately developed StB and StD, dilambdodont centrocrista, compressed para- and metacone, reduced conules, anteroposteriorly compressed trigonid, paraconid evidently less developed than the metaconid, wide and short talonid, conical and poorly developed entoconid, slightly lingual contact of the cristid obliqua, entoconid fused to the hypoconulid in m4, and sinuous cristid obliqua in the m4. The main synapomorphy of the family is the presence of an elongated talon that is longer than stylar shelf width.

Included genera. *Gaylordia* and *Tiulordia*.

PHYLOGENETIC ANALYSIS

Our results found a single most parsimonious tree (tree score = 122) (Fig. 2). Following the results, *Eobrasilia* is closer-related to *Didelphodon* within Stagodontidae. This result does not support proposals of Simpson (1947), Paula Couto (1962), Marshall (1984; 1987) or Marshall *et al*. (1990), which assigned this taxon to Didelphidae. The association between *Eobrasilia* and *Zeusdelphys* as a single taxon (Marshall, 1984) was not supported as the last taxon does not show any of Stagodontidae upper dentition synapomorphies, being recovered as the sister-taxon of *Hatcheritherium alpha* Case, Goin & Woodburne, 2005, within Hatcheriformes Case, Goin & Woodburne, 2005. The hypothesis proposed by Marshall (1984) will be commented in details later.

The validity of "Eobrasiliinae" was not supported by the analysis, as *Gaylordia* + *Tiulordia* constitutes a monophyletic lineage (*i.e.* Gaylordiidae fam. nov.) more closely-related to Jaskhadelphyidae Muizon, 1992, and Peradectidae Crochet, 1979 + Pucadelphyidae Marshall & Muizon, 1988; while *Didelphopsis* is closely-related to *Itaboraidelphys camposi* Marshall & Muizon, 1984, both as the sister-taxon of *Herpetotherium* Cope, 1873.

The closely-relation of Pediomyoidea + Stagodontidae supports the Archimetatheria taxon proposed by Szalay (1994). This cohort was recovered as one of the most basal lineages of Metatheria. Sparassodonta was recovered as a basal lineage to remaining Metatheria, a condition compatible with the tall and nearly subequal size of para- and metaconid that is present only in most basal taxa, such *Sinodelphys szalayi* (Luo *et al*., 2003) and *Kokopellia juddi* (Cifelli, 1993; Cifelli & Muizon, 1997). Deltatheroida was recovered in a polytomy with *Kokopellia juddi* Cifelli, 1993, following previous studies regarding the basal positioning of these two taxa among Metatheria (Cifelli, 1993; Luo *et al*., 2003).

DENTAL HOMOLOGIES

Morphology of lower molars

The lower molar of *Eobrasilia coutoi* (*i.e.* MCT 1342-LE) shows distinctive characters regarding remaining metatherians from Itaboraí. Its large size (nearly 6 mm considering the length of the paraconid in occlusal view) excludes any association with smaller taxa, such *Gaylordia macrocynodonta*, *Gaylordia mater*, *Minusculodelphis* spp., *Derorhynchus singularis*, *Gugghenheimia crocheti*, *Bobbschaefferia fluminensis*, for example. The dimension of this tooth is comparable to larger taxa such *Patene simpsoni*, *Protodidelphis mastodontoides*, *P*. *vanzolinii*, *Didelphopsis cabrerai*, *Nemolestes* sp., *Eobrasilia coutoi*, *Zeusdelphys complicatus*, and *Carolocoutoia ferigoloi*.

Interestingly, the lower molars of the last two taxa are not known. However, *Carolocoutoia ferigoloi* was recovered as a Protodidelphidae (Oliveira & Goin, 2011) and *Zeusdelphys complicatus* was recovered as a Hatcheriformes by the analysis. Initially considered the upper dentition of *Eobrasilia coutoi* (Marshall, 1984), the systematic positioning of *Zeusdelphys* have changed since its formal description: later it was considered a Polydolopimorphia Protodidelphinae (Marshall, 1987), a Kollpaniidae (Marshal *et al*., 1990), and more recently as a basal Protodidelphidae (Oliveira & Goin, 2011). In the last study, the authors compare *Zeusdelphys* to *Hatcheritherium alpha*, mentioning that these two genera share many similarities, conclusion supported by the presented phylogeny analysis (Fig. 2).

The idea that MCT 1342-LE represents the lower dentition of one of these two taxa is not supported, as Protodidelphidae present inflated cuspids, and a reduced paraconid, which differs from the one present in the new tooth. Comparisons with *Zeusdelphys* are more restrict as this taxon and *Hatcheritherium alpha* do not show any preserved lower molar. Despite that, a crucial feature of MCT 1342-LE refutes any attempt to associate this tooth with *Zeusdelphys*: it is slightly larger than the half length of the M1 of *Zeusdelphys complicatus* and it is evidently narrower than this tooth; which indicates that MCT 1342-LE belongs to a smaller species (but see complementary explanation below). In addition, the upper molars of *Zeusdelphys* evidence brachyo-bunodont adaptations, which is morphology not compatible with the morphology of the new lower molar.

Associations of this molar with *Patene simpsoni* Paula Couto, 1961, or *Nemolestes* Ameghino, 1902, are also refutable. The preserved lower dentition of *Patene simpsoni* does not resemble the condition present in MCT 1342-LE, as at least one of the lower molars of this species is preserved in the studied collections. Association with *Nemolestes* sp. is not supported as well, mainly based on the different morphology from the new material. The new lower molar is slightly “inflated”, but it could not be considered as brachyodont or bunodont (the inflation here mentioned indicates that this tooth is more rounded that the expected condition present in *Nemolestes*). Aside this, the original description of Ameghino (1902) and schematic drawings of the dentition of this taxon (Forasiepi *et al.*, 2014) show that the lower dentition of *Nemolestes* is evidently different from the new tooth (*i.e.* relative longer talonid, more inflated entoconid, entoconid not contacting the metaconid, paraconid not larger than the protoconid, developed and tall hypoconulid).

This new lower molar is autapomorphic based on the strong anteroposterior reduction of the talonid that is reduced to a rim. This reduction is so evident that the entoconid and the hypoconid are appressed against the posterior wall of metaconid and protoconid, with entoconid almost complete merged with metaconid (it is possible to identify in labial view two worn apexes, one representing the entoconid and other the metaconid – Fig. 1B). This morphology excludes any association with any known species of Itaboraí with preserved lower dentition. Unfortunately, most of metaconid and the lingual half of the paraconid are missing, but, despite this, it is possible to reach some conclusions: the hypoconid is as developed as the entoconid, the entoconid is flattened and developed, the metaconid is lower and much less developed than the paraconid and protoconid (it can be identifiable by the presence of a developed premetacristid and postprotocristid connecting the protoconid and metaconid); the paraconid is evidently developed, and judging by the missing portion this cusp is the largest cuspid in the lower molars (the preserved portion in the dentary of *Eobrasilia* DGM 919-M represents the antero-ventral portion of the paraconid, which demonstrates how broad and developed is this cuspid). The paraconid is voluminous, representing half of the length of the trigonid. No other metatherian lineage shows such great development of the paraconid. Similar morphology is found in the m3 assigned to "*Boreodon matutinus*" (Sahnii, 1972), *Didelphodon coyi* Fox, 1986, (Fox, 1986; Fox & Naylor, 2006), and *Eodelphis* (Scott & Fox, 2015), in which the relative size of stylar cusps undoubtedly resemble the condition present in the m1 of *Eobrasilia*.

The expected size of the metaconid is deduced by the fragmentary portion that represents this structure and by the presence of a developed premetacristid. The expected size of the paraconid is based on the absence of its antero-ventral portion and the breakage of its apical and lingual portions; even with the breakage, the paraconid is evidently more voluminous than the protoconid.

Comparisons of MCT 1342-LE with Stagodontidae resulted in evident and interesting similarities: MCT 1342-LE, *Eodelphis* and *Didelphodon* share the enlarged paraconid as tall as or taller than the protoconid (the paraconid is much larger than the protoconid in the new tooth); relative wide talonid, anteroposterior compression of the trigonid, tall and flattened entoconid (the entoconid is as tall as the metaconid), large and nearly subequal entoconid and hypoconid, and hypoconulid not larger than the entoconid (the hypoconulid is extremely reduced, but identifiable as a small elevation labially appressed to the entoconid + metaconid). The trigonid of the new tooth is compressed, judging by the closely-spaced cuspids. The great enlargement of the paraconid could create the false impression that the trigonid is not compressed, which is not the case.

Among these characters, the enlargement of the paraconid is the most evident feature in the dentition of Stagodontidae. A similar condition occurs in Sparassodonta, but this comparison is not supported as none Sparassodonta present such degree of enlargement of the paraconid and this cusp never reaches a size equal to or larger than the protoconid, which is always the larger cuspid of the lower molars in this group (Ameghino, 1902; Paula Couto, 1961; Marshall, 1976; Muizon, 1992; Forasiepi *et al*., 2014). Based on this, any attempt of association with Sparassodonta is easily discarded (Table 1).

Aside the striking large size of the paraconid, MCT 1342-LE presents another interesting morphology shared with Stagodontidae: the anteroposterior compression of the m1. *Eodelphis cutleri*, *E. browni*, *Didelphodon coyi*, and *D. vorax* show a reduction in size of the m1 in comparison with remaining molars; in fact, this reduction in length is a result of the anteroposterior compression of this tooth, an evolutionary tendency among the group as the most plesiomorphic taxon, *E. browni*, presents the lesser degree of reduction; and *D. vorax* presents a stronger degree of compression, resulting in its singular morphology. The only taxon that presents great reduction of the talonid in the m1 in comparison to *D. vorax* is *Eobrasilia coutoi*.

The anteroposterior compression of MCT 1342-LE is also attested by the length of the preserved alveoli roots of m1 and m2 in DGM 919-M. The talonid of this tooth is extremely compressed, as comment. This particular morphology diverges from the condition present in

Sparassodonta, which present a labiolingual compression of the m1 and not an anteroposterior compression, again discarding any association of MCT 1342-LE with this lineage.

The possibility that this singular condition present in *Didelphodon vorax* and *Eobrasilia coutoi* represents two independent events was not supported by the phylogeny. The anteroposterior compression of m1 present in Stagodontidae is uncommon in other groups of Metatheria. In short, the common ancestor of Stagodontidae probably presented an anteroposterior compression of the m1 (conclusion based on the phylogeny results), being more evident in most apical taxa, but identifiable in all remaining members of the family. This conclusion demonstrates that the compression of the m1 had begun early in the evolutionary history of the family, with each taxon presenting different degrees of compression.

The preserved morphology demonstrates that the posterior root is evidently larger than the anterior one, in a degree very distinct from remaining taxa of Itaboraí. The dentary of *Eobrasilia coutoi* (*i.e.* DGM 919-M) presents a breakage in the area of the m1, showing the expected morphology of the roots of this tooth (Fig. 2C). The m1 of *Eobrasilia* shows a reduced anterior root in comparison with the posterior ones, which is evidently more developed. This morphology is compatible with the alveoli present in DGM 919-M. To test this association, MCT 1342-LE was positioned in same place of this breakage, fitting quite well with the morphology and size expected for the m1 of *Eobrasilia coutoi*. In addition, the preserved anterior root of the m2 in DGM 919-M demonstrates that this structure is evidently larger than the m1, reaching more than half of the size of the first lower molar. MCT 1342-LE is also compatible with this proportional development, as the preserved alveolus of the anterior root of m2 is longer than the half of the length of the new tooth.

Interestingly, the lower molar and dentary were collected in same year and in same fissure by the collector (Price & Campos in 1967). In addition, the colour of these two materials is similar, which could be considered as an evidence that same materials belong to same individual, though this argument is debatable. The skull of *Eobrasilia* was collected in 1947, year of its description, but the proper local of its founding, as for the remaining materials can't be properly assigned. Based on this, we are cautious in considering the skull, the jaw and the m1 as belonging to a single individual.

Deltatheroida taxa share with Stagodontidae an enlarged paraconid that is evidently developed and a moderately reduced metaconid, but differ by the relative larger protoconid that is the larger cuspid of the trigonid (Fox *et al*., 2007; Bi *et al*., 2015). Despite similar morphology, the lower molars of Stagodontidae and Deltatheroida can be easily distinguishable, as the second group present labiolingually compressed lower molars, reduced hypoconid and entoconid, and "elongated" and narrow talonid; while Stagodontidae present oppose tendencies. Based on this, the grouping of *Eobrasilia* with Deltatheroida is not supported. The lower molar described in this study refutes any attempt to associate *Eobrasilia* with this group (Table 1).

It is evident that the enlargement of the paraconid evolved several times during the evolution of Metatheria, but the strong enlargement of this structure is only present in *Eobrasilia*, *Didelphodon* and *Eodelphis*, which is an evidence for the closely-relation between these taxa, result recovered in the phylogenetic analysis (Fig. 2).

The validity of "Eobrasiliinae" has never been tested in any study, mainly based on the absence of preserved molars of *Eobrasilia*. The discovery of this first lower molar allows better conclusions.

Comparisons between *Eobrasilia* and *Gaylordia* show the fragility of this supposed monophyletic lineage: *Gaylordia* presents mesio-distally compressed upper molars, small paraconid, developed metaconid; short, but not reduced talonid; reduced entoconid, and tiny size. It is remarkable that all of these characters are also shared by *Minusculodelphis* and *Marmosopsis*. This combination of characters grouped these three taxa, along with *Szalinia gracilis* Muizon & Cifelli, 2001, in a monophyletic lineage as performed by Oliveira & Goin (2011), and Oliveira *et al.* (2016). The grouping of *Gaylordia* with these two taxa was also supported in our analysis (Fig. 2). Interestingly, *Didelphodon* also shows mesio-distally compressed upper molars, similar to Jaskhadelphyidae and Gaylordiidae fam. nov. Despite that superficial similarity, the phylogeny recovered this morphology as independent acquisitions between these two lineages (Fig. 2).

The presence of oppose evolutionary tendencies between *Gaylordia* and *Eobrasilia* regarding the molars morphology and size is verifiable (Table 2). *Eobrasilia* is one of the largest metatherians from Itaboraí, while *Gaylordia* and closely-related taxa represent the smallest taxa; the M3 of *Eobrasilia* is described with a “rounded” external shape, while the teeth of *Gaylordia* and closely-related taxa are mesio-distally compressed. The degree of development of the entoconid in *Eobrasilia* represents the strongest argument for the invalidation of “Eobrasiliinae”, as the strong reduction of the entoconid is one of the main synapomorphies of the lower molars of *Gaylordia*, *Minusculodelphis*, *Marmosopsis* and *Szalinia*. In addition, the strong development of the paraconid and the apparently reduction of the metaconid in *Eobrasilia* represent a divergent pattern from the one present in the lineage of *Gaylordia*, as this last group shows an evolutionary tendency among the development of the metaconid and great reduction of the paraconid. This analysis refutes any attempt to group *Eobrasilia* and *Gaylordia* in a monophyletic lineage.

Comparisons with *Didelphopsis* provide similar results, as this taxon share all main synapomorphies present in the lineage of Herpetotheriidae and Derorhynchidae, with an invasive dilambdodonty centrocrista, accessory cusp labial to the ectoloph of the centrocrista, more anteriorly displaced protocone, and cristid obliqua contacting the trigonid in the middle of the tooth only in the m4. Interestingly, none of these characters are preserved in *Eobrasilia*; but the relative morphology of remaining lower molars is distinct: *Didelphopsis* shows a small paraconid in comparison with metaconid, the entoconid present some degree of inflation, and the m1 are not compressed. Regarding all mentioned characters the possibility of closely-relations between these two taxa is not supported (Table 1).

Based on roots morphology and size expected for the m1 of *Eobrasilia coutoi*, MCT 1342-LE is assigned to the hypodigm of this species. Remarkably, the enlarged paraconid as the larger cuspid of the tooth, the relative reduction of the metaconid, the anteroposterior compression of the m1, the large size, the absence of labiolingual strong compression of the lower molars, and the greater development of the flattened entoconid are features present in Stagodontidae. The phylogeny results endorse the great number of shared characters between *Eobrasilia* and Stagodontidae as evidences for the closely-relation between these taxa.

Morphology of P1

The presence of a single-rooted P1 was identified in *Didelphodon vorax* and *Eobrasilia coutoi*. Other North and South American taxa such *Pucadelphys*, *Herpetotherium, Didelphopsis cabrerai*, Sparassodonta, *Roberthoffstetteria nationalgeographica* Marshall, Muizon & Sigé, 1983, Peradectidae, *Szalinia gracilis, Gaylordia macrocynodonta* Paula Couto, 1952, and almost all South American Marsupialia Illiger, 1811, present a two-rooted P1. Some Deltatheroida (*e.g. Lotheridium*) also develop a single-rooted P1 (Bi *et al*., 2015).

The preserved maxilla assigned to *Eodelphis browni* present a two-rooted P1 (Fox & Naylor, 2006), while *Didelphodon vorax* (Lofgren, 1992) and *Eobrasilia coutoi* (Marshall, 1984; 1987) show a single-rooted P1, as mentioned. The presence of similar condition in

Australidelphia and Deltatheroida do not refute the phylogeny results, as Australidelphia is more closely-related to Paucituberculata within Marsupialia cohort, and Stagodontidae is a basal lineage of the phylogeny. The presence of this condition apparently shows significant level of homoplasy among Metatheria.

The best way to test the validity of a character is testing it in a phylogenetic analysis (Simões *et al.*, 2016). Based on the phylogeny results, the presence of a single-rooted P1 was recovered as a good evidence for the grouping between *Eobrasilia* and *Didelphodon*. The idea that a highly homoplastic character could not be used to evidence closely-relations between taxa can only be set after a phylogenetic analysis. The presence of highly homoplastic characters, if pointed like this by the analysis, will be "weighted" (do not confuse with 'imply weighting' mechanism of phylogenies) with other characters in order to proper elucidates the evolutionary tendency of a lineage. For example, it is possible that the absence of preserved molars could be pointed as a limitation for the inclusion of a fragmentary taxon, such *Eobrasilia* in phylogenies, as the great absence of identifiable characters could "negatively" influence the analysis, as the comparative morphology is quite limited, as was the case before this study. Interestingly, the discovery of the first lower molar of *Eobrasilia* nullifies this critic, as the lower molars provide a more reliable result, comparing to the premolars that could present a highly level of homoplasy. Based on this, the inclusion of lower molar characters in our phylogenetic analysis represents additional evidence for the indication of a single-rooted P1 as an evidence of Stagodontidae affinities for *Eobrasilia*. In fact, considering a closer-relation of *Eobrasilia* and *Gaylordia* is undoubtedly less parsimonious than considering the presence of single-rooted P1 as common ancestor feature of *Didelphodon* and *Eobrasilia*.

The P1 of Stagodontidae is minute when compared to P2-3 and presents an anterolingually-posterolabially elongation, which results in an oblique orientation in comparison with dental row axis. All studied taxa that present this feature (*i.e. Eodelphis*, *Didelphodon*, *Eobrasilia*, *Didelphopsis* and *Lotheridium*) show the anterior root of this tooth labially oriented, while the posterior root is lingually oriented (*i.e.* the anterior root is oriented to the external border of the maxilla – labial; while the posterior one is oriented to the internal buccal space - lingual).

The minute P1 of *Eobrasilia*, *Eodelphis* and *Didelphodon* are strongly appressed against the larger canine and P2, condition absent in *Lotheridium*, *Gaylordia* and *Didelphopsis* as the P1 is evidently separated from P2 (*i.e.* these teeth are not in contact – Fig. 3). This condition was recovered as a valid character for the grouping of *Eobrasilia* within Stagodontidae following the phylogenetic analysis. The P1 of *Eobrasilia* presents two accessories and developed cusps anteriorly and posteriorly placed to its main cusp (Simpson, 1947), morphology also found in *Eodelphis* and *Didelphodon*. These cusps are developed and visible even in worn teeth. Interestingly, the P1 of *Didelphopsis* (Paula Couto, 1962), *Gaylordia* (Oliveira & Goin, 2015), *Szalinia* (Muizon & Cifelli, 2001), *Herpetotherium* (Sánchez-Villagra *et al*., 2007), *Acyon* (Forasiepi *et al*., 2006), *Roberthoffstetteria nationalgeographica* (Muizon, 1992) and *Lotheridium* (Bi *et al*., 2015) does not present developed anterior and posterior cusps. The presence of developed cusps in the P1 was recovered as a positive evidence for the grouping of *Eobrasilia* within Stagodontidae following the phylogenetic analysis.

In order to test the possibility that a reduced P1 could represent a homoplastic state between Stagodontidae and “Eobrasiliinae”, we analyzed the morphology present in these three taxa (Table 2).

A partially preserved maxilla of *Didelphopsis cabrerai* (*i.e.* MNRJ 2884-V) Paula Couto, 1952, presents a minute, oblique and two-rooted P1, with a better developed P2 and a much larger P3 (based on preserved alveoli). The P1 of *D. cabrerai* is separated from P2 by a developed and visible space between P1 and P2 (I will call these space between the premolars as retro-premolar spaces), which differs from the characteristic pattern present in Stagodontidae (Fig. 3). The partially preserved skull of *Gaylordia macrocynodonta* (*i.e.* DGM 329-M) also presents a minute and two-rooted P1, but differs from *Didelphopsis* and Stagodontidae, in having the P1 aligned in same axis of P2-P3. The morphology of P1 is similar to the one present in *Didelphopsis* as both present a developed retro-premolar space separating P1 and P2 (Fig. 3).

The Tiupampian *Roberthoffstetteria nationalgeographica* presents a better developed P3 comparing to P1-2 and a premolar series with all premolars closely-spaced and nearly appressed, but presents a developed P1 that is aligned in same axis of P2-P3 (Muizon, 1992), condition that separates this taxon from *Gaylordia*, *Didelphopsis*, *Eobrasilia*, *Didelphodon* and *Eodelphis*. This taxon was identified as closely-related to Polydolopidae (Goin *et al.*, 2003; Chornogubsky & Goin, 2015).

Comparisons with the Australian *Malleodectes mirabilis* Arena *et al*. 2011, which presents a reduced P1 comparing to P2-3 as in referred South and North American taxa (Arena *et al*., 2011). Nevertheless, the pattern of its upper molars is divergent from the one present in the American taxa. The P1 is poorly developed, but it is not as vestigial as in Stagodontidae. The P1 is two-rooted, aligned with dental row axis and separated by a small retro-premolar space from P2 (Arena *et al*., 2011). Its morphology is similar to *Gaylordia*, but the Australian taxon presents an independent evolutionary event of its lineage in Australia, not directly linked to any South American taxa. This conclusion is corroborated by Archer *et* *al*. (2016) that described new materials assigned to this taxon, grouping it in a new family, Malleodectidae, within Dasyuromorpha Gill, 1872. Australidelphia (represented by Peramelemorphia and Microbiotheria) and *Gaylordia* do not constitute a monophyletic lineage based on the phylogeny results (Fig. 2).

The comparative morphology demonstrates that a single-rooted, oblique oriented and tiny P1 independently evolved several times in the evolution of Metatheria, probably as adaptation for a more durophagous diets. The idea that the tiny, oblique oriented and single-rooted P1 is a poorly informative character is not supported, as stagodontid taxa are the only metatherians that present a tiny P1, oblique oriented, closely-spaced to remaining premolars (with no developed retro-premolars spaces), and associated with bulbous, but not plagiaulacoid premolars. Based on this, any attempt to justify the grouping of *Gaylordia* + *Tiulordia* and *Didelphopsis* with *Eobrasilia* in a monophyletic group (*i.e.* “Eobrasiliinae”) presents no substantial or informative evidence, while the grouping of *Eobrasilia* as a Stagodontidae is quite supported as both taxa present same pattern, which is unique among Metatheria. In addition, the absence of anterior and posterior cusps in the P1 of *Gaylordia* excludes this taxon from Stagodontidae and does not support its grouping with *Eobrasilia*.

Despite the presence of an oblique oriented, tiny and single-rooted P1 in the Deltatheroida *Lotheriudium mengi* (Bi *et al*., 2015), this taxon does not show any tendency of the inflation of the premolars, present a visible retro-premolar space separating the P1 from P2, and undoubtedly differs from others metatherians based on its dental morphology.

In short, the arguing that highly homoplastic characters could not be used as a validity characters to defining a group can be considered as an important argument, but it falls in a matter of philosophy: a character can only be treated as highly homoplastic after a phylogenetic analysis, and could not be discarded *a priori*, as commented (Simões *et al*., 2016). Based on this, we add these characters in the character matrix as the validity of such characters could only be attested after a phylogenetic analysis. The phylogeny recovers the oblique orientation and single-rooted condition of P1 as a valid evidence for the grouping of *Eobrasilia* within Stagodontidae. Even with the presence of similar condition in *Lotheridium*, *Gaylordia* and *Didelphopsis* (*i.e.* this characters are indeed result of homoplasy), the analysis found a single most parsimonious tree with *Eobrasilia* well-nested within Stagodontidae. The homoplastic state of this character among Metatheria does not affect the stability of the phylogeny (Fig. 2).

The presence of developed accessory cusps in the P1 of these three taxa was also supported by the phylogeny as a synapomorphy of Stagodontidae.

Morphology of the second and third upper and lower premolars

The morphology of P2 and P3 in *Eobrasilia*, *Didelphopsis*, *Gaylordia*, *Didelphodon* and *Eodelphis* are divergent for the condition present in remaining Metatheria: the second and third premolars are very large and bulbous, growing as larger as or even larger than upper and lower molars. The presence of this pattern is an evidence for durophagous habits among these taxa (Fox & Naylor, 2006; Scott & Fox, 2015). Aside this resemblance, these teeth present diagnostic morphologies that represent independent acquisitions for them, as explained.

The third premolars of *Gaylordia macrocynodonta* are much larger than the second premolars, although the relative size between the second and the first premolars are not so extreme. It is evident that P1/p1 are less developed and inflated than P2/p2, but this comparative development is not so visible when compared to *Eobrasilia*, *Didelphodon* and *Eodelphis*, in which the first premolars are striking smaller than the second and third premolars. *Didelphopsis* presents a relative development of premolars that superficially resemble the pattern present in Stagodontidae.

In relation to the morphology of the second and the third upper and lower molars, these taxa are undoubtedly divergent. *Gaylordia* presents a bulbous P3 that is much more voluminous than P2, but this pattern is not truth for the lower dentition, as the second lower molar is only slightly less inflated and smaller than the third. In upper premolars, the P3 is inflated and rounded, but the P2 still retains an anteroposterior elongation and is not as inflated as the P3.

The Australian *Malleodectes* presents a poorly inflated P2 that is appressed to P3 (Arena *et al*., 2011). The P3 is rounded, massive and much more developed than remaining teeth, which resemble the condition present in *Gaylordia*.

Didelphopsis presents a P3 that is striking larger and inflated in comparison to P2, which presents a more laminar morphology and incipient inflation. The elongation of this tooth is even more visible than the one present in *Gaylordia* (Oliveira & Goin 2015).

For Stagodontidae, the pattern present in *Eodelphis* resemble the one present in *Didelphopsis* as both present a less inflated P2 in comparison to a larger and more inflated P3. Despite that, the condition present in the second upper premolar of *Eodelphis* is better developed in comparison with *Didelphopsis* (*i.e.* the P2 of *Eodelphis* is more inflated than the one present in *Didelphopsis*). The pattern present in the P2 and P3 of *Eobrasilia* resembles *Eodelphis* more than any other metatherian. *Didelphodon* presents a P3 that is much more developed than P2. The P2 is inflated, well developed and does not present the elongated and more “laminar” condition of remaining taxa. It differs from *Gaylordia* as both upper and lower second premolars are evidently inflated.

Regarding the lower dentition of Stagodontidae, the relative size difference between the p3 and p2 in *Eobrasilia* and *Didelphodon* is striking remarkable as p3 is antero-posteriorly elongated. In fact, the p3 is nearly twice the length of the p2. This morphology represents a unique morphology of these two genera; with the anteroposterior elongation of *Eobrasilia* being greater in comparison to *Didelphodon*.

The p3 of *Didelphodon vorax* and *D. coyi* present a massive inflation of the crown. Unfortunately, no description of the crown of *Eobrasilia* could be made due to the strong worn condition of the only known p3 assigned to this species, but, judging by the labio-lingual inflation of this tooth, some degree of inflation is expected for the crown. The incipient three-rooted condition of *Eobrasilia* is an autapomorphy of this taxon. The p3 assigned to *D. padanicus* is also evidently worn, not allowing better conclusion regarding its morphology, but an anteroposterior development is evident.

The extinct Thylacoleonidae Gill, 1872, presents an anteroposterior elongation of the p3; development that could also be used as argument to invalid the hypothesis of a monophyletic origin of *Eobrasilia* and *Didelphodon*, as this character could be a homoplastic character. However, the lower molar of Thylacoleonidae is evidently different from the one present in Stagodontidae. The p3 of Thylacoleonidae resembles a ‘carnassial tooth’, and not a ‘hammer-tooth’ (*sensu* Arena *et al*., 2011), observation that identifies different ecological roles for these teeth. Another question relays in the discovery of a basal Thylacoleonidae in Australia, *Microleo attenboroughi* (Gillespie *et al*., 2016), which presents a plesiomorphic condition for the P3 of this family. A quick look allows the conclusion that the morphology present in Stagodontidae and Thylacoleonidae are evidently different. In addition, the upper and lower dentition excludes any possibility that Stagodontidae and Thylacoleonidae constitute a monophyletic lineage.

The presence of two developed flexids is visible in the p2 of *Didelphodon padanicus* and *Eobrasilia coutoi*. In fact, this morphology of the p2 is so characteristic of these two taxa that we were unable to recover similar morphology in any other North American, South American and Australian taxa. In order to test the identification of these structures as a natural morphology of the p2, we analyze these flexids searching for signs of wear. Interestingly, no sign of wear is identified in these flexids, which recovers them as natural structures. These two taxa differ in the degree of development of these flexids, which are strongly developed in the Late Cretaceous taxa and poorly developed, but still identifiable, in *Eobrasilia coutoi*.

Didelphodon coyi presents a small and poorly developed swelling on the lingual border of the p2, which is for us identified as a reduced flexid (*e.g.* TMP 91.161.1). *Didelphodon vorax* present no sign of these flexids. This observation supports the identification of these structures as natural structures of the p2 of *Eobrasilia* and *Didelphodon*, as these features are present in different degrees of worn. To test the importance of this morphology, we added this character in the phylogeny. The analysis recovers these flexids as a synapomorphy of *Didelphodon* and *Eobrasilia*. For *D. coyi* and *D. vorax* the presence of a stronger inflation of the p2 is regarded as the main explanation for the reduction of these flexids. The p2 incipient inflation in *D. coyi* reduced, but not “erases” the presence of these flexids. In *Didelphodon vorax* this inflation reaches its greater development among the family and in comparison with any other North and South American metatherians, adaptation that complete reduced the presence of such flexids. The condition present in *Didelphodon padanicus* is more developed than remaining taxa, as its tooth is the one that present the lesser degree of inflation among the genus. The condition present in *Eobrasilia coutoi* is a mosaic of the condition present in *D. padanicus* and *D. coyi*, indicating that the secondary loss of these flexids represents an evolutionary tendency of the group.

On the upper molars, *Didelphodon vorax* and *D. coyi* shows a lingual projection of the P3. This tooth is bulbous and massive, and presents a lingual inflation and development. The P3 of *Didelphodon padanicus* shows a strong development, being also inflated, but it differs from the condition present in other species of *Didelphodon* by the presence of a developed and larger talon in this tooth, and a less developed lingual projection. The condition present in *D. padanicus* could be regarded as the most plesiomorphic among the three species of the genus, as the talon is better developed and the lingual projection is less developed in comparison with *D. coyi* and *D. vorax*. The lingual projection of the P3 was recovered as an autapomorphy of *Didelphodon*.

Based on the discussion above, the flexids of the p2 and the evident anteroposterior expansion of the p3 shared by *Eobrasilia* and *Didelphodon* are strong evidences of its monophyletism, supporting *Eobrasilia* within Stagodontidae. Both characters were recovered as synapomorphies of these taxa based on the results of the phylogenetic analysis.

The inflated second and third lower premolars represent independent acquisitions for *Tiulordia* + *Gaylordia*, *Didelphopsis* and Stagodontidae, as indicated by the phylogeny. This conclusion is evident by the analysis of the condition present in most basal taxa of each referred lineage.

Tiulordia floresi and *Gaylordia mater* Oliveira & Goin, 2015, present an incipient inflation of p3, resulting in a tooth that is quite similar to the plesiomorphic condition of Metatheria (*i.e.* poorly inflated). In *Gaylordia macrocynodonta* the p3 and p2 are much more inflated and larger comparing to the formers, which represents an evolutionary tendency of this lineage. In Stagodontidae the pattern is similar, as *Eodelphis* presents an inflated p2 and a bulbous p3; and *Eobrasilia* and *Didelphodon* present more inflated p2 and p3 comparing to the former. The morphology in *Didelphopsis cabrerai* presents inflated third premolars, but less inflated second premolars, again indicating an evolutionary tendency towards the inflation of the last premolars. The presence of a bulbous and developed p3 was tested in the phylogeny and was recovered as independent acquisitions of these three groups (*i.e. Didelphopsis*; *Tiulordia* + *Gaylordia*; and Stagodontidae).

Closely-spaced premolars, stout dentary and wear pattern

The absence of retro-premolars spaces separating the lower premolars in lower dentition, the wear pattern and the stout dentary were considered by Marshall (1987) as strong evidences for the grouping of *Eobrasilia*, *Gaylordia*, *Tiulordia*, and *Didelphopsis* in "Eobrasiliinae". However, other taxa also lack these spaces between the premolars (*e.g. Roberthoffstetteria nationalgeographica*, Stagodontidae and some Borhyaenoidea). The stout dentary is present in *Pachybiotherium*, *Didelphodon* and *Roberthoffstetteria*, for example.

Interestingly, the presence of these characters is considered adaptations to durophagy (*e.g.* Stagodontidae), granivory (*e.g.* Pachybiotherium) and carnivory (*e.g.* Sparassodonta) feeding habits among Mammalia, as the reduction in the length of dentary represents an adaptation to increases bit force (Thomason, 1991). The combination of characters presented by these taxa should be considered as an evidence of similar paleoecological feeding habits, convergent acquired by their own lineages.

Among Cretaceous North American taxa, the presence of a stout dentary, strong premolars wear pattern and absence of retro-premolars spaces in upper and lower dentition represent diagnostic features of Stagodontidae. Regarding South America, the conclusion is not similar as many lineages evolved towards some degree of durophagy, as commented.

As exhaustively mentioned in this paper, the upper dentition of Stagodontidae shows a minute, oblique placed and strongly compressed P1, which is placed between the much larger canine and P2. These two premolars are also appressed against an even larger P3. This absence of retro-premolars spaces between the upper premolars was recovered as an important character for Stagodontidae, excluding *Tiulordia* + *Gaylordia* and *Didelphopsis* from this lineage and treating their similarities as result of homoplastic acquisitions (see phylogeny and the previous topic).

It is important to comment that the heavy wear pattern and the high dentary could not be regarded as strong phylogenetic characters, as commented. In order to avoid misinterpretations among the description of these adaptations, the use of these adaptations as characters in the matrix is discarded. Again, the large dentary and the strong wear pattern can be treated as important evidences for supporting durophagous feeding habits for *Eobrasilia* (see the discussion regarding the paleoecology of *Eobrasilia*), but these characters by its own could not be considered as strong phylogenetic evidences. Interestingly, the presence of these features in addition to the exclusive morphology and patterns present in the new lower molar and in the premolars series could be treated as compelling evidence for supporting Stagodontidae affinities for *Eobrasilia*.

The dentary of *Eobrasilia* and *Gaylordia macrocynodonta* show an evident curvature of the anterior portion. This morphology could be an evidence for supporting the closely-relation of these two taxa, as proposed by Marshall (1987), or it could be a convergent adaptation towards durophagous feeding habits. As explained, the best way to test the validity of a character (*i.e.* a homologous origin) is testing it in a phylogenetic analysis. The results recovered this morphology as independent acquisitions for *Gaylordia* and *Eobrasilia*, constituting a convergent adaptation for more durophagous diets. *Eobrasilia* differs from *Eodelphis* and *Didelphodon* by the strong recurved condition of the anterior half of its dentary.

Large size

Eobrasilia is considered as one of the largest metatherians from Itaboraí, being only slightly smaller than *Nemolestes* sp. and *Zeusdelphys complicatus* (based on upper or lower molars linear size), as previously commented. The large size of *Eobrasilia* and *Zeusdelphys* could indicate an occlusal relation between the upper and lower teeth described independently for them, as proposed by Marshall (1987). The holotype of *Eobrasilia* shows a strongly worn M3, not allowing details of its morphology. Direct comparisons could not be conducted as *Eobrasilia* presents a preserved M3, while *Zeusdelphys* presents a preserved M1 (Oliveira & Goin, 2011). The lower molar of *Eobrasilia* does not help on the study of occlusal relations, but refutes this possibility.

The lower molar of *Eobrasilia* presents all main synapomorphies and characteristic features of the lower dentition of Stagodontidae, while the M1 of *Zeusdelphys complicatus* does not show any common character with homologous tooth of Stagodontidae. Despite that, some could argue that this conclusion could not be made as these taxa could not be directly compared, which is, again, easily refutable. The preserved upper molar of *Zeusdelphys* is a M1 (the external shape and the position of the protocone confidently identifies this tooth as a M1), when the one present in *Eobrasilia* is an m1. Interestingly, the M1 of *Zeusdelphys* reaches 8.30 mm in length and 8.47 mm in width (Oliveira & Goin, 2011); this size is considerably larger to the one presented by the m1 of *Eobrasilia* (*i.e.* 5.5 mm in length, and apparently 4 mm of width). In fact, this occlusal relationship could not be acceptable.

The Stagodontidae *Eodelphis* and *Didelphodon* were the largest metatherians during the Late Cretaceous of North America (Fox & Naylor, 2006; Williamson *et al.*, 2012; Williamson *et al.*, 2014; Scott & Fox, 2015). Following the results, the larger size of

Eobrasilia can also be considered as another evidence for its grouping within Stagodontidae. As commented, the large size of *Eobrasilia* is incompatible with *Gaylordia* and closely-related taxa that evolved towards a tiny size, as they are among the smallest species of Itaboraí (Paula Couto, 1962; Marshall, 1987) (Table 2). It is important to comment that the shared large size by its own could not be recovered as a strong systematic character (reason why we do not include this feature in the character matrix, as its use could result in long and unnecessarily discussion regarding this study), but the association of this feature with the results of the phylogenetic analysis endorsed by the discussed morphology of the preserved dentition can be treated as another evidence for the grouping of *Eobrasilia* within Stagodontidae.

Interestingly, *Gaylordia* is considered one of the smallest species of Itaboraí, along with *Minusculodelphis* and *Marmosopsis* (Oliveira & Goin, 2015; Oliveira *et al*., 2016). In fact, the smaller size seems to be an evolutionary tendency of this group. This character undoubtedly differs from the condition present in *Eobrasilia*, as it is one of the largest species of metatherians from Itaboraí. The difference in size could not be considered as a definitive evidence for the unrecognizing of "Eobrasiliinae" as a valid group, as commented, but this strong divergence in size associated with the commented characters can be considered as compelling evidence of the polyphyletic state of "Eobrasiliinae" (Table 2).

Semi-procumbent lower incisors

The presence of semi-procumbent lower incisors in *Didelphodon* was discussed by Fox & Naylor (2006). *Eodelphis* present three unequally-sized lower incisors, with the second (i3) much larger than i2 and i4. The presence of a staggered condition for i3 in *Eodelphis* is not clear as it seems that the enlargement and "semi-procumbence" of i3 creates this impression (Fox & Naylor, 2006). In fact, the enlargement of lower incisors is also visible in *Eobrasilia coutoi* (Marshall, 1984) and *Didelphodon coyi* (Fox & Naylor, 2006).

The preserved dentary of *Eobrasilia* evidences the presence of three lower incisors alveoli (Fig. 1). Marshall (1984) described *Eobrasilia* as presenting two large and anteriorly inclined incisors, with one lying above the other. Marshall (1987) mentioned the presence of a small third incisor and a possible even smaller fourth incisor. DGM 919-M was reanalyzed and did not present any evidence of the fourth lower incisor alveoli. In fact, the two lingualmost alveoli of the i2 and i4 are easily identifiable, but the i3 is barely seen (following Oliveira & Goin, 2011, which considered the incisors as i2, i3, i4 and i5). As described by Marshall (1984) these teeth show, along with the canine, some degree of procumbence. In *Eobrasilia* the i3 is a compressed lower incisor, with its apparently 'staggered' condition being a result of the extreme degree of procumbence of i2 and i4 that compressed the referred tooth in the middle, creating the false impression that it is 'staggered'.

Interestingly, this morphology is quite similar to the one present in *Eodelphis* spp. and *Didelphodon coyi* in which the incisors are better developed, lying above the others and with some degree of semi-procumbence. *Eobrasilia* present two large semi-procumbent lower incisors, *Eodelphis cutleri* and *E. browni* present a single and not so enlarged one i3 (Scott & Fox, 2015), *Didelphodon vorax* does not evidence any degree of procumbence, and *D. coyi* presents a single and well developed semi-procumbent i2 (Fox & Naylor, 2006). It is quite possible that the idea of the presence of a 'staggered' incisor is a result of the morphology of the semi-procumbent lower incisors, which creates an apparent 'staggered' condition, as the semi-procumbent and large incisors lay one above the other in the dentary of these animals due to the strong procumbence morphology. This hypothesis is confirmed by the study of the alveoli morphology of *D. vorax* that does not evidence any sign of a "staggered" lower incisor, as its incisors are equally sized and located at same level; this result agrees with Fox & Naylor (2006).

The semi-procumbence pattern is different in the three genera of Stagodontidae: *Eodelphis* shows the i3 as the most procumbent incisor, *Didelphodon coyi* shows the i2, and *Eobrasilia* the i2 and i4. This variable condition for the semi-procumbence of the lower incisors represents an evolutionary tendency among the family, being independently acquired. However, the presence of a large semi-procumbent i2 in *D. coyi* and *E. coyi* could be considered as an ancestor condition for them, but the absence of preserved lower incisors in *D. padanicus* and the absence of this condition in *D. vorax* represent negative evidences against this conclusion. Based on this, the semi-procumbence is considered as an evolutionary tendency of Stagodontidae, as the morphology of *D. padanicus* is not known and the ancestor condition could not currently proved.

Semi-procumbent lower incisors are absent in Pucadelphyidae, Peradectidae, Didelphidae, *Marmosopsis*, *Minusculodelphis*, Sparassodonta, and Microbiotheriidae. Oliveira & Goin (2012) propose focused studies regarding the morphology of the incisors of *Eobrasilia*, Herpetotheriidae and Protodidelphidae. The presence of two semi-procumbent incisors is reported for *Herpetotherium fugax* (Fox, 1983), but their condition is striking divergent from the one present in Stagodontidae as this taxon shows small and slightly procumbent i2 and i3 that are slightly larger and more procumbent than i4 and i5. In addition, *Herpetotherium* shows four alveoli, while *Eobrasilia* shows only three. Protodidelphidae show poorly procumbent incisors, which striking diverge from the condition present in *Eobrasilia*.

In short, the morphology of lower incisors in *Eobrasilia* resemble the one present in Stagodontidae. The procumbence of lower incisors can be considered as an evolutionary tendency among this family as all taxa show some degree of procumbence of these teeth. This condition could not be recovered as an evidence of Herpetotheriidae affinities for *Eobrasilia* based on the different pattern regarding the size, number and degree of semi-procumbence of the lower molars.

SYSTEMATIC REVIEW

Systematic position of "Eobrasiliinae" taxa

Eobrasilia, *Gaylordia* and *Didelphopsis* do not constitute a natural group. The association of the upper molar assigned to *Zeusdelphys* with *Eobrasilia* was not supported as well.

Eobrasilia, *Didelphodon* and *Eodelphis* share the following combination of characters: P1 minute, oblique placed and appressed against the canine and P2; P1 with two developed accessory cusps, upper and lower premolars series closely-appressed against each other (*i.e.* absence of retro-premolars spaces), third premolars very large and heavy; semi-procumbence condition of lower incisors (exception for *Didelphodon vorax*, but is more probable that this morphology represents a reversion state), large size, and stout dentary. *Eobrasilia* share with *Didelphodon* the presence of a single-rooted P1, anteroposterior elongation of p3, flexids in the p2, and the strong anteroposterior compression of m1.

Gaylordia and *Tiulordia* share with Jaskhadelphyidae the presence of a poorly developed entoconid, a fused entoconid with hypoconulid in m4, mesio-distally compressed upper molars, poorly developed paraconid, reduced conules and tiny size. These taxa share with Pucadelphyidae + Peradectidae the presence of a sinuous cristid obliqua in m4, slightly labial contact of the cristid obliqua, pyramidal para- and metacone, dilambdodont centrocrista and straight dentary (exception for *Gaylordia macrocynodonta*, as commented). *Gaylordia* and *Tiulordia* constitute the monophyletic Gaylordiidae fam. nov. based on the presence of broader talonids, inflated third premolars, and elongated talon that is longer than the developed stylar shelf.

Didelphopsis and *Itaboraidelphys* share with Herpetotheriidae and Derorhynchidae the presence of an accessory cusp labial to the ectoloph of centrocrista, invasive dilambdodont centrocrista, subdivided StC, StD with three apexes, cristid obliqua contacting the carnassial notch only in m4, and morphology of m4. These two taxa were recovered as a monophyletic lineage based on the presence of a compressed entoconid, inflated metaconule, and broad protocone.

The strong divergent morphology of the lower molars of *Eobrasilia* in comparison with *Gaylordia* refutes any attempt to group these taxa in a monophyletic lineage. A hypothesis that could be used to justify the grouping of *Gaylordia* and *Eobrasilia* in a monophyletic lineage is the loss of all diagnostic characters of *Gaylordia* lineage in *Eobrasilia*, and the independent acquisition of all Stagodontidae features in *Eobrasilia*, which in other words means that the only possibility that these two taxa constitute a monophyletic lineage is if *Eobrasilia* had lost all synapomorphies of *Gaylordia* and convergently developed all synapomorphies of Stagodontidae. This is easily refuted due to the complex parsimonious explanation required in order to prove it, which is undoubtedly less parsimonious than considering *Eobrasilia* as an early Eocene Stagodontidae, result indeed evidenced by the phylogeny.

PALAEOBIOGEOGRAPHIC AND PALEOECOLOGICAL IMPLICATIONS

The recovery of *Eobrasilia coutoi* as a Stagodontidae increases the palaeobiogeographic and temporal range of this family. Previously considered endemic from Late Cretaceous of North America, the presence of *Eobrasilia* evidences an early Eocene taxon, extending the temporal range of this family in about 10 Ma. These conclusions evidence a North American origin for *Eobrasilia* lineage, with the dichotomy between *Eobrasilia* + *Didelphodon* probably happening during the late Campanian (*i.e.* Judithian NALMA) to Maastrichtian (*i.e.* Lancian NALMA).

Regarding the probable dispersal rout between North and South Americas, the 'Aves Ridge' and adjacent Cuba were indicated as the best pathway candidates for the dispersal rout between both landmasses (Woodburne & Case, 1996; Case *et al*., 2005). The volcanic activity during Late Cretaceous (Pindell 1994) associated with strong sea-level lowstands during late Campanian (around 73 Ma) and Late Cretaceous (around 66 Ma) (Haq, 2014) probably allowed a sweepstakes dispersal pattern for them; with a hopping-island model as the best concept for their dispersal. The marine regressions associated with intense volcanic activity should have created temporary land pathways between isolated islands until the arrival in South America.

In North America, Stagodontidae is considered as a not abundant group in any given local fauna (Scott & Fox, 2015). *Eobrasilia* follows the group pattern, as only a partially preserved skull, a partially preserved dentary, and the isolated and fragmentary lower molar are the only elements assigned to this taxon, which identifies this taxon as one of the rarest taxa of Itaboraí fauna. The diagnostic and extreme adaptations of Stagodontidae undoubtedly associate their feeding habits to durophagous diets.

In Australia, the extinct *Malleodectes* had its ‘hammer-tooth’ P3 associated with a snail-eating diet (Arena *et al*., 2011; Archer *et al*., 2016). This conclusion can also be inferred for Itaboraian taxa, as these species show similar adaptations.

The tiny size of *Gaylordia macrocynodonta* could be an indication for consume of small snail taxa, hard exoskeleton insects or even seeds, which demands durophagous adaptations. The mesio-distal compression of the upper molars of *Gaylordia* supports this conclusion, as other taxa with similar morphology present more insectivorous feeding habits, such *Minusculodelphis* (Oliveira *et al*., 2016). The mesio-distally compression of the upper molars, the short rostrum and the robust dentary are adaptations towards durophagy (Thomason, 1991). The slender morphology of *Minusculodelphis* is more compatible with consume of soft insects or worms (Oliveira *et al*., 2016), while the more developed protocone of *Gaylordia* evidently recovers the ingestion of harder food items. *Gaylordia mater*, a larger species, shows incipient development of durophagous feeding habits in comparison to *Gaylordia macrocynodonta*, but similar to this species, *G. mater* can also be considered a durophagous species. The tiny size and the durophagous adaptations of *Gaylordia* can be interpreted as indication of a specialized diet. The presence of tiny snail taxa is recorded for Itaboraí (Ferreira & Coelho, 1989), which could explain the presence of the tiny specialist *Gaylordia macrocynodonta* in Itaboraí.

Eobrasilia and *Didelphopsis* show large size and durophagous adaptations, as commented. The more “rounded and inflated” external shape of their upper molars is compatible with the ingestion of large and harder items in comparison with *Gaylordia*. Interestingly, the limestones of Itaboraí Basin (Early Eocene in age), Rio de Janeiro, Brazil, harbour a rich fossil fauna of pulmonate snails (Salvador & Simone, 2012; 2013). The abundant presence of these animals can be directly linked with the dental durophagous adaptations present in *Eobrasilia* and *Didelphopsis*.

This great abundancy of snails could explains why at least three different lineages evolved towards durophagous adaptations, corroborating the results of the phylogeny that “Eobrasiliinae” represents a polyphyletic lineage. The tiny size of *Gaylordia* indicates that this taxon did not directly compete with *Didelphodon* and *Eobrasilia*, as the last two species are evidently larger, and probably consumed larger food items (*e.g.* larger snail species). The similar size between *Eobrasilia* and *Didelphopsis* could indicate a niche overlapping between these two taxa. Currently, it is not possible to test the semi-aquatic adaptations of Stagodontidae (Szalay, 1994), which includes *Eobrasilia*, as no postcranial element can be securely assigned to these taxa. Interestingly, a complete skeleton of *Didelphodon* is known, but its formal description has never been presented so far. If this conclusion were indeed correct, it could be inferred that the niche overlapping between *Eobrasilia* and *Didelphopsis* was minimized by different use of habitat.

The abundant presence of these pulmonate mollusks in Itaboraí Basin allowed the presence of a Stagodontidae. Based on this conclusion, it is quite possible that the paleobiogeographic distribution of this family was directly linked with the presence of these animals. In South America, the extinction of Stagodontidae could be related to the reduction in diversity and abundancy of snail taxa as *Eobrasilia* seems to be a specialist species. Interestingly, *Didelphopsis* is also considered extinct after Itaboraian SALMA. The sister-group of *Didelphopsis*, *Itaboraidelphys* survived during the early Eocene, being identified in the local fauna of Paso del Sapo (Tejedor *et al*., 2009). *Itaboraidelphys* presents more carnivorous adaptations in comparison to *Didelphopsis*, but this taxon could not be regarded as specialized faunivorous species, such *Patene* and *Nemolestes*. It is possible that this more generalist feeding habits allowed the surviving of this species, while the great specialization of *Eobrasilia* and *Didelphopsis* could be regarded as the main reason for their extinction.

CONCLUSIONS

The discovery of the first partially preserved lower molar of *Eobrasilia coutoi* allowed the recovering of this species as an early Eocene South American Stagodontidae. This result indicates a North American origin for Stagodontidae and a Late Cretaceous-early Paleocene dispersal event to South America.

Based on the phylogeny, *Eobrasilia*, *Gaylordia* and *Didelphopsis* do not constitute a monophyletic lineage. This phylogeny result increases the Metatheria diversity in South America during the Paleogene.

The strong divergences regarding the lower molars and premolars morphologies, in addition to other evolutionary tendencies conclude that any attempt to group *Gaylordia* and *Eobrasilia* in a monophyletic lineage is not acceptable, as the referred lineages of both taxa show divergent evolutionary tendencies; aside that, the presence of all main characters and evolutionary tendencies of Stagodontidae in *Eobrasilia* represent an undeniable result of this study.

The diagnosis of “Eobrasiliinae” was based on homoplastic and morpho-ecological adaptations, which resulted in the polyphyletic state of this subfamily. As commented, “Eobrasiliinae” cannot be considered as a valid taxon.

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FIGURES CAPTIONS

Fig. 1. SEM photographies of MCT 1342-LE and DGM 919-M of *Eobrasilia coutoi*. **1.** MCT 1342-LE: **A**. Occlusal view; **B**. Labial view. **2**. DGM 919-M: **A**. p3 in antero-lingual view; **B**. p2 in antero-lingual view showing the lingual flexid; **C**, alveoli of m1 roots, with partially preserved paraconid of the right m1, and alveoli of m2 anterior root; **D**, incisors and canine alveoli. **art**, anterior root; **C**, canine; **i**, incisor; **ent**, entoconid; **flx**, flexid; **hyp**, hypoconid; **hypl**, hypoconulid; **lab**, labial; **met**, metaconid; **par**, paraconid; **port**, posterior root; **prt**, protoconid; **rps**, retro-premolar space. Scale bar: 1 mm [planned for page width]

Fig. 2. Result of phylogenetic analysis. Single most parsimonious tree found in analysis. The metatherian lineages are identified by vertical bars. Numbers below the ramus indicate the Bremer Support. [planned for page width]

Fig. 3. Comparative Morphology of “Eobrasilinae” taxa. **A.** DGM 329-M, partial skull of *Gaylordia macrocynodonta* in palatal view; **B**. MCT 2776-M, right m3 of *Gaylordia mater* in occlusal, lingual and labial views (both pictures are from Oliveira and Goin 2015); **C**. MNRJ 2884-V, right maxilla of *Didelphopsis cabrearai* with preserved p1, p2 and m4 in labial (superior) and occlusal (below) views; **D**. MCN-PV 1786, m1 of *Didelphopsis cabrerai* in occlusal (left) and lingual (right) views; **E**. AMNH 39424, incomplete facial part of skull of *Eobrasilia coutoi* presented in Simpson (1947); **F**. MCT 1342-LE, left m1 of *Eobrasilia coutoi* in labial view. **ant**, anterior; **ent**, entoconid; **hyp**, hypoconid; **lab**, labial; **met**, metaconid; **par**, paraconid; **prt**, protoconid; **rps**, retro-premolar space. Scale bars: 1 mm. [planned for page width]

Table 1. Morphological characters shared by *Eobrasilia* and other metatherians. The ‘X’ indicates that the character is present. It is possible to see that *Gaylordia* share the lesser number of similarities with *Eobrasilia*, while Stagodontidae share all cited characters with the

referred species. It is possible to recover a highly level of homoplasy among many characters, but most of these features are shared only by *Eobrasilia* and Stagodontidae. [planned for page width]

Table 2. Morphological patterns of Stagodontidae, and Jaskhadelphyidae + Gaylordiidae. The table highlight the main differences between the lineage of *Gaylordia* (*i.e.* Gaylordiidae) and the lineage of *Eobrasilia* (*i.e.* Stagodontidae). It is possible to identify divergent evolutionary tendencies between these two lineages. [planned for page width]

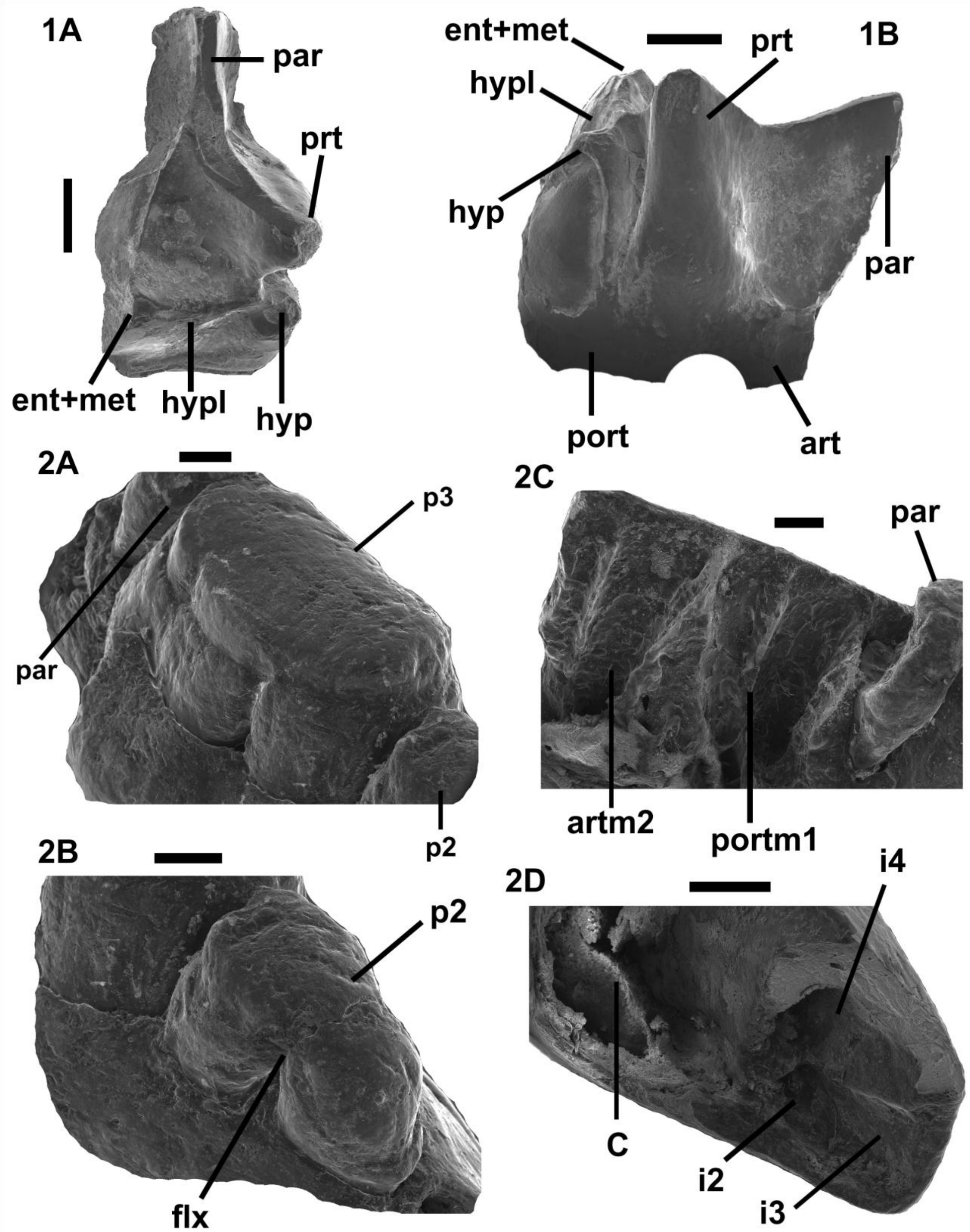
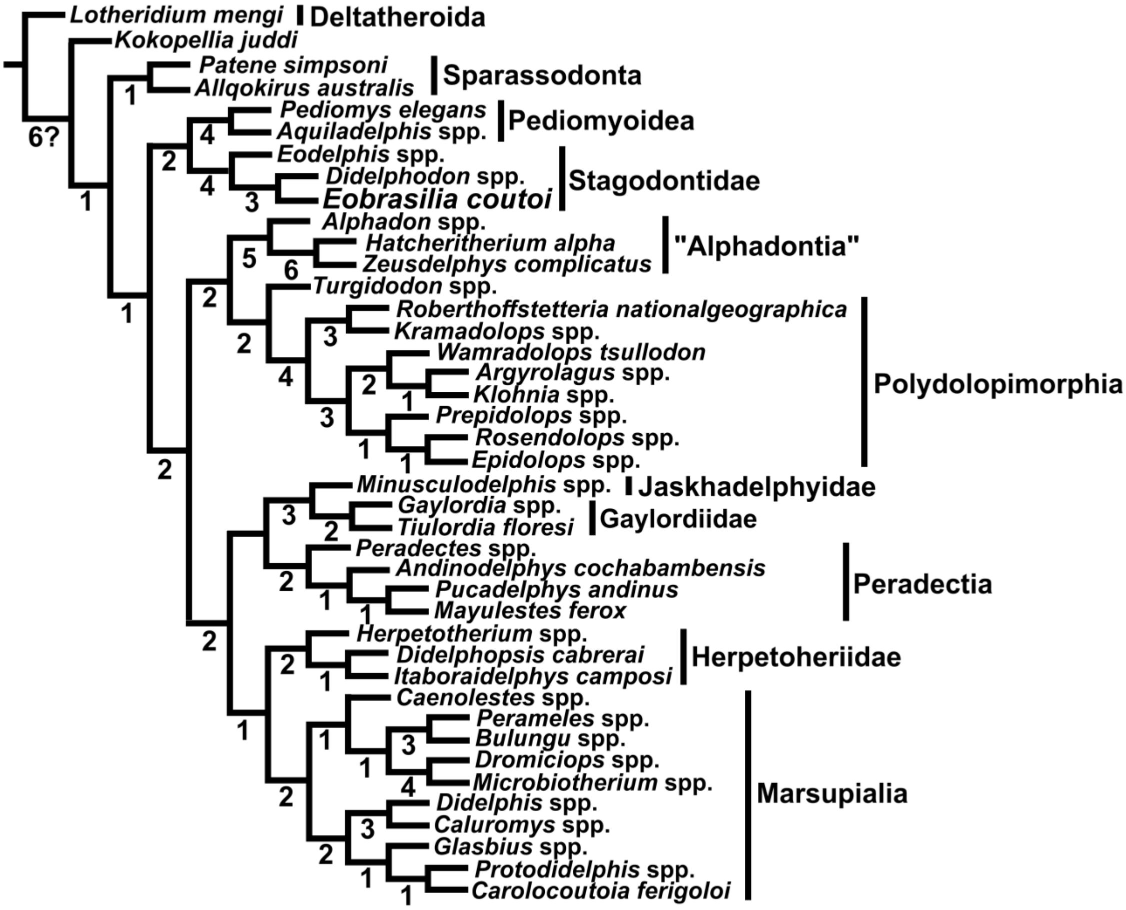


Fig. 1. SEM photographies of MCT 1342-LE and DGM 919-M of *Eobrasilia coutoi*. **1.** MCT 1342-LE: **A**. Occlusal view; **B**. Labial view. **2**. DGM 919-M: **A**. p3 in antero-lingual view; **B**. p2 in antero-lingual view showing the lingual flexid; **C**, alveoli of m1 roots, with partially preserved paraconid of the right m1, and alveoli of m2 anterior root; **D**, incisors and canine alveoli. **art**, anterior root; **C**, canine; **i**, incisor; **ent**, entoconid; **flx**, flexid; **hyp**, hypoconid;

hypl, hypoconulid; **lab**, labial; **met**, metaconid; **par**, paraconid; **port**, posterior root; **prt**, protoconid; **rps**, retro-premolar space. Scale bar: 1 mm [planned for page width]



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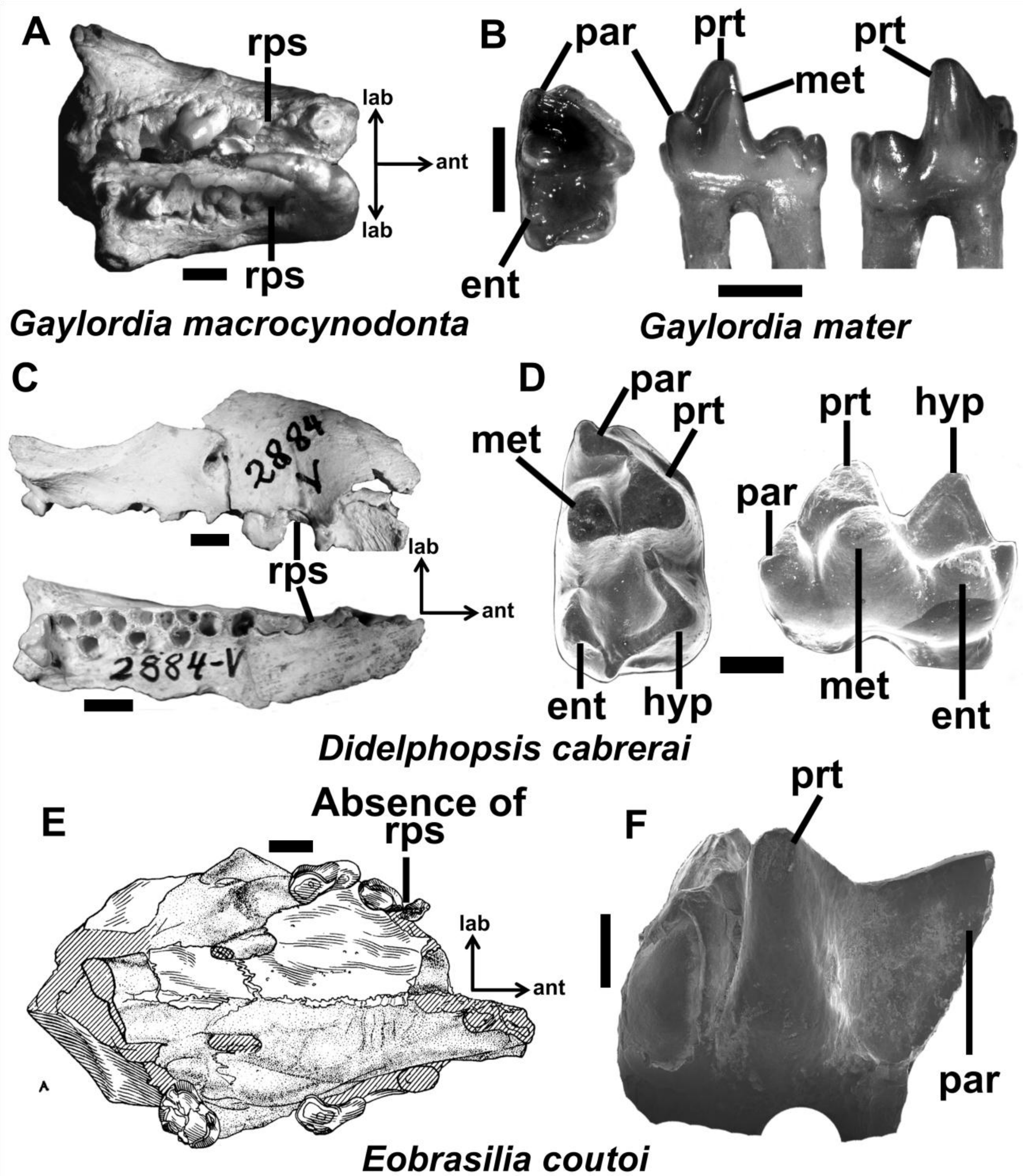

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Eobrasilia coutoi presented in Simpson (1947); **F**. MCT 1342-LE, left m1 of *Eobrasilia coutoi* in labial view. **ant**, anterior; **ent**, entoconid; **hyp**, hypoconid; **lab**, labial; **met**, metaconid; **par**, paraconid; **prt**, protoconid; **rps**, retro-premolar space. Scale bars: 1 mm. [planned for page width]

Char./Tax.	*Eobrasilia*	Stagodontidae	*Lotheridium*	*Didelphopsis*	*Gaylordia*	Sparassodonta
Accessory cusps in the P1	X	X				
Single-rooted P1	X	X	X			
Oblique oriented P1	X	X	X	X		
Absence of retro-premolar space between P1 and P2	X	X				
Anteroposterior development of p3	X	X				
Developed and flattened entoconid	X	X				
Anteroposte	X	X				

rior compression of m1						
Enlarged paraconid	X	X	X			X
Large size	X	X		X		X
Inflated and large second and third premolars	X	X		X	X	
Labiolingual compression of lower molars			X			X
Labial contact of the cristid obliqua	X	X				
Relative reduction of metaconid	X	X	X			X
Paraconid as the	X	X				

largest cuspid in the trigonid						
Robust dentary	X	X	X	X	X	X
Recurved dentary	X				X	

Character/Lineages	*Gaylordia*, *Tiulordia* (Gaylordiidae) and Jaskhadelphyidae	*Eobrasilia*, *Eodelphis* and *Didelphodon* (Stagodontidae)
Size	Tiny	Large
Relative size of paraconid	Small to vestigial, being the lowest cuspid in the trigonid	Enlarged, being the largest cuspid of lower molars
Development of metaconid	Well-developed, being nearly as tall as the protoconid in some taxa	Developed, but can always be considered as the lowest cuspid in the trigonid; sometimes present some degree of reduction
Size of entoconid	Small to vestigial	Well-developed
Morphology of entoconid	Conical	Flattened
Contact of cristid obliqua	Slightly labial to the carnassial notch	Labial contact in comparison to the carnassial notch
Anteroposterior compression of m1	m1 with no evidence of anteroposterior compression	m1 with evident anteroposterior compression
Upper and lower premolars closely-	Absent	Present (*i.e.* all premolars are closely-spaced and in

spaced (absence of retro-premolars spaces)		contact)
Mesio-distal compression of upper molars	Present in all taxa	Absent (exception for *Didelphodon vorax*); *Eobrasilia* present a “rounded” upper molar (Simpson 1927)

Appendix 1

Characters and states of phylogenetic analysis. Characters and states used in the phylogenetic analyses. Characters are polarized with respect to *Lotheridium mengi* as outgroup. All characters are treated as unordered.

1. Wing-like parastyle: (0) absent, (1) present.
2. Development of parastyle: (0) developed, (1) reduced or vestigial.
3. Lingually shifted parastyle on M2-3: absent (0), present (1).
4. Development of StA in comparison to StB (Muizon and Cifelli, 2001): enlarged (0), small (1), vestigial (2).
5. Development of StB: developed (0), vestigial or absent (1).
6. Sinuous crest connecting StB and StD: (0) absent, (1) present.
7. StB with distolabial accessory cuspule (StB1): (0) absent, (1) present.
8. StB1 position in comparison to StC: (0) more labial than StC, (1) at same level of StC.
9. Well-developed StB1: (0) absent, (1) present.
10. Centro-labial StB1: (0) absent, (1) present.
11. Pyramidal StB: (0) absent, (1) present.
12. Broad and well-developed labial accessory crest of pyramidal StB: (0) absent, (1) present.
13. Reduced lingual accessory crest of pyramidal StB, which does not contact StC: (0) absent, (1) present.
14. Invasive lingual accessory crests of pyramidal StB and StD in stylar shelf: (0) absent, (1) present.
15. Invasive lingual accessory crests of pyramidal StB and StD merging at the center of stylar

shelf: (0) absent, (1) present.

16. StB massively larger than paracone: absent (0), present (1).
17. 'Twinned' cusp to StB: absent (0), present (1).
18. StB salient labially on M3: absent (0), salient (1).
19. StC development: (0) not truly identifiable, (1) identifiable.
20. Presence of StC: present (0), vestigial or absent on all molars (1).
21. Pyramidal StC: absent (0), present (1).
22. StC mesiolingually twisted on M1: absent (0), present (1).
23. Lingual shifting of StC: (0) not evidently lingual, (1) evidently lingual.
24. Lingual accessory crest of StC: absent (0), present (1).
25. Well-developed StC: absent (0), present (1).
26. Alignment of StB, StC and StD: (0) absent, (1) present.
27. Labiolingually compressed StC: absent (0), present (1).
28. StC merging with StD on M3: absent (0), present (1).
29. Twinned StC: present (0), absent (1).
30. StD development: (0) not truly identifiable, (1) identifiable.
31. Medium accessory crest of StD: (0) absent, (1) present.
32. Pyramidal StD: (0) absent, (1) present.
33. Pyramidal StD on all upper molars: absent (0), present (1).
34. StD with lingual and labial accessory crests: (0) absent, (1) present.
35. Morphology of the pyramidal StD: (0) pyramidal without inflation or compression, (1) compressed and flattened, (2) inflated, reducing the concave medial border and the accessory crests.
36. Vertical posterior border of StD: (0) absent, (1) present.

37. Developed vertical posterior border of StD: (0) developed, (1) poorly developed or vestigial.

38. StD subdivided into three apices: (0) absent, (1) present.

39. StD with sinuous accessory crest on M2, but not M1 or M3: absent (0), present (1).

40. Sinuous crest connecting the incipiently developed StD and the labiodistal border of metacone: present (0), absent (1).

41. StD with multiple crenulations on its longitudinal axis: absent (0), present (1).

42. StD1 presence: absent (0), present (1).

43. Notch between StB and StD: absent (0), present (1).

44. Conical and developed StE: absent (0), present (1).

45. Twinned cusps on the posterior border of metastylar shelf of M3: absent (0), present (1).

46. Roll of reduced cuspules only at the anterior border of StD: (0) absent, (1) present.

47. Accessory cuspules. (0) present, (1) absent.

48. Presence of multiples cuspules on metastylar shelf, with one usually slightly more developed than the remaining, but it could not be considered as a "true" StD: present (0), absent (1).

49. M3 with 'metastylar-wall': absent (0), present (1).

50. Flattened and reduced StB, StC and StD. (0) absent, (1) present.

51. Subequal, labially aligned, conical and closely-spaced StB, StC and StD: absent (0), present (1).

52. Well-developed stylar shelf with subequal parastylar and metastylar shelf: absent (0), present (1).

53. Epiconular plataform: absent (0), present (1).

54. Low parallel crest connecting the apex of the paracone with StB: (0) absent, (1) present.

55. Low parallel crest connecting the apex of the metacone with StD: (0) absent, (1) present.

56. Preparacrista orientation: StB (0), StA (1).

57. Preparacrista labially notched due to the absence of the mesiolingual crest of StB: absent (0), present (1).

58. Reduced preparacrista that points toward StA and does not contact the mesiolingual crest of StB: (0) absent, (1) present.

59. Parastylar shelf development on M2 and or M3: developed (0), reduced to a narrow cingulum or rim (1).

60. Postmetacrista with three accessory cuspules: (0) absent, (1) present.

61. Well-developed postmetacrista accessory cusps: (0) absent, (1) present.

62. Postmetacrista accessory crest: (0) absent, (1) present.

63. Well-developed metastylar wing, distally projecting on M3: absent (0), present (1).

64. Comparative development of asymmetric reduced parastylar shelf and developed metastylar shelf: absent (0), metastylar much larger than parastylar (1), metastylar slightly larger than parastylar (2), metastylar slightly larger or nearly subequal to parastyle.

65. Labial border of metastylar shelf oblique oriented on M1, being twice the size of the parastylar shelf labial border: (0) absent, (1) present.

66. Labial border of metastylar shelf evidently rounded: absent (0), present (1).

67. Labial cingulum: absent (0), present (1).

68. Vestigial stylar shelf: absent (0), present (1).

69. Ectoflexus very deep, reaching the level of lingual border of StB: present (0), absent (1).

70. Ectoflexus deep and broad ('ridge-like' ectoflexus): absent (0), present (1).

71. Para- and metacone with apices lingually projected: (0) absent, (1) present.

72. Metacone apex evidently posteriorly projected: absent (0), present (1).

73. Morphology of the labial borders of para- and metacone: (0) both rounded, (1) metacone rounded and paracone pyramidal, (2) both compressed, (3) paracone rounded and metacone

pyramidal.

74. Labial alignment of para- and metacone: aligned (0), paracone more labial than metacone (1).

75. Paracone evidently more labial than the metacone on M2-3: absent (0), present (1).

76. Twisted paracone: (0) absent, (1) present.

77. Degree of paracone twisting: (0) poorly twisted, (1) evidently twisted.

78. Medium sharp crest on lingual border of metacone: absent (0), present (1).

79. Accessory crest labially and oblique oriented on the midline of metacone: (0) absent, (1) present.

80. Development of the accessory crest labially oriented on the midline of metacone: (0) developed, (1) poorly developed.

81. Accessory crest labially oriented on the midline of paracone: (0) absent, (1) developed.

82. Development of the accessory crest labially oriented on the midline of paracone: (0) developed, (1) poorly developed.

83. Alignment of centrocrista with para- and metacone: (0) straight, (1) lingually displaced.

84. Notched straight centrocrista: (0) absent, (1) present.

85. Morphology of labially displaced centrocrista: pseudolinear (0), dilambdodont (1), 'arc-shape' (2), 'U-shape' (3), open (4), vestigial (5), notched (6).

86. Invasive centrocrista: (0) absent, (1) present.

87. Morphology of labially displaced notched centrocrista: (0) discontinuous, (1) some degree of 'arc-shape', (2) sinuous, (3) pseudolinear.

88. Accessory cusp to the ectoloph of the centrocrista: (0) absent, (1) present.

89. Protocone displacement (Oliveira and Goin, 2011): (0) absent, (1) eccentric.

90. Morphology of protocone: fusiform or indiferenciated (0), mesio-distally expanded (1), labio-lingually developed (2), conical (3), hypocone (4), compressed (5).

91. Inflation of protocone: absent (0), present (1).

92. Spire-like protocone: (0) absent, (1) present, (2) compressed.

93. Fusiforme protocone on M3, but not on M1-2: (0) absent, (1) present.

94. M1 with fusiform and eccentric protocone ('Peradectoid M1'): absent (0), present (1).

95. Protocone with a pair of oblique grooves: absent (0), present (1).

96. Preprotocrista with half the length of postprotocrista, but the protocone is not eccentric: absent (0), present (1).

97. Accessory cuspules associated with postprotocrista with a variable number: absent (0), present (1).

98. Presence of dental basal expansions: absent (0), present (1).

99. Development of dental basal expansions: poorly developed (0), well-developed (1).

100. Conules separated from the pre- and postprotocrista by a deep notch: (0) absent, (1) present.

101. Accessory conules presence: (0) absent, (1) present.

102. Accessory conules with similar development to para- and metaconule and independently developed from protocristae: absent (0), present (1).

103. Development of conules: with some degree of development, but not reduced or enlarged (0), reduced or absent (1), enlarged (2).

104. Paraconule much more reduced than the metaconule: (0) absent, (1) present.

105. Morphology of metaconule: pyramidal (0), pseudoinflated (1), inflated (2), 'hypocone-like' (3), 'spire-like' (4), mesio-distally compressed (5), pseudohypocone (6).

106. Paraconule enlarged, being larger than the vestigial metaconule on M3: (0) absent, (1) present.

107. Paraconule lingually shifted, but not the metaconule: absent (0), present (1).

108. Aligned paraconule, protocone and metaconule: (0) absent, (1) present.

109. M3 with conules lingually shifted, subequal and aligned, but not on the lingual border: (0) absent, (1) present.

110. Straight preparaconular crista separating the talonid basin from the mesiolingual cingulum: absent (0), present (1).

111. Invasive preparaconular crista: absent (0), present (1).

112. Morphology of invasive preparaconular crista: oblique oriented, but not so invasive (0), oblique oriented and well-invasive (1), straight (2).

113. Straight invasive preparaconular crista with sinuous lingual third trajectory: absent (0), present (1).

114. Discontinuous postmetaconular crista on M1: absent (0), present (1).

115. Internal metaconular crista development, when the metaconule is developed: developed (0), reduced or absent (1).

116. Furrow between protocone and metaconule: absent (0), present (1).

117. Proto-paraconule wear pattern: absent (0), present (1).

118. Anterobasal cingulum contacting the talon in a lower position (discontinuous anterobasal cingulum with talon basin): (0) absent, (1) present.

119. Merging of discontinuous anterobasal cingulum and talon basin: absent (0), present (1).

120. Reduced anterobasal cingulum only on M3: (0) absent, (1) present.

121. Mesial expansion of anterobasal cingulum: absent (0), with the labial half gently recurved and mesially expanded (1), broad and evidently mesially expanded (2), broad, but with sinuous trajectory (3).

122. Anterobasal cingulum with a lower trajectory: (0) absent, (1) present.

123. Posterobasal cingulum development: developed (0), reduced or poorly developed (1), vestigial or absent (2).

124. Posterobasal cingulum with a lower contact than stylar shelf: absent (0), present (1).

125. External shape of upper molars: 'yoke-like' (0), trapezoid (1), ovoid (2), subquadrangular (3), piriform (4), rectangular (5).

126. Hexacuspate upper molars: absent (0), present.

127. Hypsodonty: (0) absent, (1) present.

128. Mesiodistally compressed upper molars: (0) absent, (1) present.

129. Elongated talon that is longer than stylar shelf on all molars: (0) absent, (1) present.

130. Talon longer than stylar shelf only on M3: (0) absent, (1) present.

131. Compressed talon: (0) absent, (1) present.

132. M4 with centrally placed paracone: (0) absent, (1) present.

133. Dilambdodont centrocrista connecting para- and metacone on M4: (0) absent, (1) present.

134. M4 with large, inflated and labiocentral stylar cusps: (0) absent, (1) present.

135. Inflated M4: (0) absent, (1) present.

136. M4 with paracone apex anteriorly shifted: absent (0), present (1).

137. M4 with paracone more labial than the metacone: absent (0), present (1).

138. M4 more reduced than M3, but is not mesiodistally or labiolingually compressed: absent (0), present (1).

139. M1 with elongated shape that does not present a strong labiolingual compression of trigonid, which is much shorter than the talonid: (0) absent, (1) present.

140. M1 strongly labiolingually compressed: present (0), absent (1).

141. Anteroposteriorly compressed m1: (0) absent, (1) present.

142. M1 with well labially salient hypoconid: absent (0), present (1).

143. Protoconid and metaconid nearly merged on m1: absent (0), incipiently merged (1), merged (2).

144. Mesiodistally elongated a labiolingually compressed trigonid on m1: absent (0), present (1).

145. Labiolingual expansion of trigonid: absent (0), present (1).

146. Compression of trigonid: compressed (0), not compressed (1).

147. Relative size between paraconid and metaconid: (0) both well-developed and subequal, (1) paraconid with some degree of reduction, (2) metaconid with some degree of reduction, (3) paraconid with evident increasing in size.

148. Paraconid as taller as the protoconid: (0) absent, (1) present.

149. Paraconid medially placed: absent (0), present (1).

150. Paraconid broad and with its apex anteriorly shifted ('blade-like' paraconid) on m2-4: absent (0), present (1).

151. Paraconid with compressed mesial border: absent (0), present (1).

152. Metaconid positioning in comparison to the protoconid: metaconid complete posterior to protoconid (0), metaconid posterior to protoconid (1), both aligned (2), metaconid anterior to protoconid (3).

153. Keeled distolingual angle of metaconid (Eaton, 2006): absent (0), present (1).

154. Protoconid strongly labiolingually shifted on m2-3: absent (0), present (1).

155. Metastylid (Goin, 2006): (0) absent, (1) present.

156. Ectostylid: absent (0), present (1) (Zimicz, 2011).

157. Entostylid: absent (0), present (1).

158. Morphology of hypoconid: (0) compressed, (1) spire-like, (2) 'tower-like'.

159. Hypoconid labially projected, resulting in a wider talonid comparing to the trigonid: (0) absent, (1) present.

160. Development of the entoconid: (0) not truly identifiable, (1) identifiable and with some degree of development.

161. Morphology of entoconid: flattened and poorly developed (0), conical (1), compressed (2), 'spire-like' (3), flattened (4), inflated (5).

162. Entoconid and hypoconid with similar size: (0) absent, (1) present.

163. Conical and vestigial entoconid: (0) absent, (1) present.

164. Massive hypo- and entoconid: absent (0), present (1).

165. Cristid obliqua position of contact with the posterior wall of the trigonid (m1-3): slightly lingual (0), carnassial notch (1), slightly labial (2), more labial (3), at labial border (4).

166. Metacristid short and recurved due to the merging with the cristid obliqua: absent (0), present (1).

167. Cristid obliqua progressively more lingual through the lower molar series: absent (0), present (1).

168. Sinuous and reduced cristid obliqua: absent (0), present (1).

169. Recurved cristid obliqua on m2, does not contacting trigonid posterior wall: absent (0), present (1).

170. Hypo-hypoconulid wear pattern: absent (0), present (1).

171. Hypoconulid position: central (0), more lingual (1), distolingual (2), slightly lingual (3).

172. Hypoconulid central, well-developed and distally projected (occupies more than the half of the posterior wall of talonid): absent (0), present (1).

173. Aligned entoconid, hypoconulid and hypoconid on distal border of talonid: absent (0), present (1).

174. Accessory cuspids e and f: (0) with at least one present, (1) both vestigial or absent.

175. Short talonid: (0) absent, (1) present.

176. Low and broad lower molars: (0) absent, (1) present.

177. Protoconid labially projected on m4: absent (0), present (1).

178. M3 and or m4 cristid obliqua with posterior sinuous compression and straight trajectory: (0) absent, (1) present.
179. M4 hypoconid aligned or anterior to the entoconid: (0) absent, (1) present.
180. M4 size in comparison to m3, but not reduced to a single root: (0) nearly subequal, (1) moderately smaller, (2) much smaller, (3) larger.
181. M4 with elongated talonid: not elongated (0), shorter and narrower than the trigonid (1), evidently elongated (2), elongated, but evidently shorter than the trigonid (3).
182. M4 with conical and small entoconid ('tower-like'): absent (0), present (1).
183. M4 with conical and central hypoconulid: absent (0), present (1).
184. Cristid obliqua contacting the metaconid only on m4: absent (0), present (1).
185. M4 with labial cingulid: absent (0), poorly developed (1), evidently developed (2).
186. M4 with well-developed anterobasal cingulid: absent (0), present (1).
187. 'Didelphid-like' m4: absent (0), present (1).
188. Number of premolars: four (0), three or less (1).
189. P1 with two developed anterior and posterior cusps: (0) absent, (1) present.
190. P1 oblique oriented in comparison to P2-3: aligned (0), oblique oriented (1).
191. P1 with single-root: absent (0), present (1).
192. P2 larger than p3: absent (0), present (1).
193. Morphology of the mesial border of p2: rounded or convex (0), with anterior projection (1), laminar or without cusps or projections (2).
194. Flexids in the p2: (0) absent, (1) present.
195. Bulbous and inflated P3/p3: absent (0), present (1).
196. P3 with anteroposterior elongation: (0) absent, (1) present.
197. Plagiaulacoid P3-p3: absent (0), present (1).

198. Bilobed third lower incisor: absent (0), present (1).

199. Angular process of the dentary development: (0) not so developed, (1) evidently developed.

200. Recurved dentary: (0) absent, (1) present.

201. Recurvation of dentary below p1: absent (0), present (1).

202. Retropremolars spaces development: with diastem between p1-p2, but not p2-4 (0), spaces absent, with premolars in contact (1), with short retropremolar space between p1-2, but not p2-3 (2), with spaces between p1-2 and p2-3 (3), p1 and-or p2 absents (4).

203. Fossa incudis and epitympanic recess: continuous (0) or separated by a distinct ridge (1) (Ladevèze and Muizon, 2010 - character 28).

204. Mastoid tympanic process: small, slanted, and nodelike, on the posterolateral border of the stylomastoid notch and continuous with squamosal (0), indistinct to absent (1) (Beck, 2012).

205. Deep groove for internal carotid artery excavatedon anterior pole of promontorium: absent (0), present (1) (Ladevèze and Muizon, 2010 - character 10).

206. Tympanic sinus formed in the lateral trough (orlateral expansion of the pars canalicularis): absent (0), present (1) (Ladevèze and Muizon, 2010 - character 15).

207. Third trochanter presence: absent (0), present (1).

208. Positioning of the third trochanter: distal to the lesser trochanter, but with proximal portion nearly at same level (0), proximal to the lesser trochanter (1), more distal than the lesser trochanter, being complete more distal (2).

209. Lesser trochanter distomedially displaced: absent (0), present (1).

210. Calcaneocuboid facets: without subfacets (0), subdivided into pCaCu and dCaCu (1), subdivided into pCaCu, mCaCu and dCaCu (2) (Szalay, 1994).

211. CLAJP presence: absent (0), present (1) (Szalay, 1994).

212. Postorbital processes: absent or formed only by the frontals (0), formed by the parietals and

frontals (1) (Voss e Jansa, 2009).

213. Development of postorbital process: absent or indistinct (0), with some degree of development (1).

214. Posterior palate morphology: without distinct lateral corners, the choanae unconstricted behind (0), or posterior palate with distinct lateral corners, choanae constricted (1) (Voss e Jansa, 2009 - character 69).

Zeusdelphys complicatus Marshall, 1987, is not a Protodidelphidae Marshall, 1990, but a Hatcheriformes Case, Goin & Woodburne, 2005: paleobiogeographic implications

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RH: CARNEIRO AND OLIVEIRA—SYSTEMATIC REVIEW OF *ZEUSDELPHYS COMPLICATUS*

Abstract

Zeusdelphys complicatus Marshall, 1987, is currently as one of the most enigmatic metatherians from Itaboraí Basin. The type and only known specimen was previously considered the upper dentition of *Eobrasilia*; an M4 of a new taxon; an M3 of a Kollpaniidae; a probable M1 of an *incertae sedis* taxon; and as an M1 of a Protodidelphidae. However, the affinities with Protodidelphidae could be a result of convergent evolution, as this taxon is quite similar to *Hatcheritherium alpha* from the Late Cretaceous of North America. Herein, we present a morphological revision of the dental structures of *Zeusdelphys complicatus*, presenting new interpretations and comparing it with other North and South American taxa. We also perform a phylogenetic analysis in order to test the affinities of *Zeusdelphys* and the validity of most studied characters. The results recovered *Zeusdelphys complicatus* as more closely related to *Hatcheritherium alpha* than to any other metatherian. Glasbiidae was recovered as the sister lineage of Protodidelphidae within Didelphimorphia, as true marsupials. *Ectocentrocristus* was recovered as the sister taxon of *Zeusdelphys* + *Hatcheritherium*, as a Hatcheriformes. The analysis recovered this suborder as an independent lineage from Polydolopimorphia, being more closely related to "Alphadontidae". The results support a North American origin for Hatcheriformes. The presence of strong sea-level lowstands and islands in the Caribbean Plate during the Late Cretaceous provide valid data to support a faunal interchange between Americas during the end of the Late Cretaceous. Based on the results, *Zeusdelphys* represents a South American early Eocene surviving Hatcheriformes, increasing the diversity of metatherian fauna during the Paleogene of South America.

Key words: Hatcheriformes, Metatheria, Paleobiogeography, Systematics, *Zeusdelphys*

Introduction

Zeusdelphys complicatus Marshall, 1987, currently considered the largest “opossum-like” species from Itaboraí, is recognized only by a single M1. The tooth of this species was firstly considered to be the upper dentition of *Eobrasilia coutoi* Simpson, 1947, as it was compatible in size (Marshall 1984). Three years later, Marshall (1987) considered this tooth as an M4 of a new genus et species, *Zeusdelphys complicatus*, with the name identifying the largest and most important Itaboraí taxon due to its size, and ‘*complicatus*’ in reference to the wrinkle enamel. Marshall et al. (1990) considered *Zeusdelphys* as a basal Paucituberculata, in the subfamily Kollpaniidae (currently, this family is considered as a subfamily of ‘condylarths’), reconsidering this tooth as an M3. Goin *et al*. (1998) identified this tooth as an M1, however, due to the autapomorphic state of this taxon, the authors considered it as an *incertae sedis* Didelphimorphian. Oliveira and Goin (2011) recovered *Zeusdelphys* as a Protodidelphidae, closely related to *Protodidelphis* and *Carolocoutoia* than to *Guggenheimia*. The same conclusion was recovered in Oliveira *et al*. (2016). *Zeusdelphys* was grouped with Protodidelphidae based on the presence of wrinkle enamel, absence of StC, bunoid molars, large and inflated StB and StD, eccentric protocone, and absence of conules.

Oliveira and Goin (2011) superficially discussed the shared similarities between *Zeusdelphys complicatus* and *Hatcheritherium alpha* Clemens, 1966, from the Lancian NALMA (Late Cretaceous) of North America (Clemens 1966). Following the authors, both taxa share an open centrocrista, which connects to a centrally place cuspule; but this taxon could not be assigned to Polydolopimorphia as it lacks a more developed protocone, a metaconule, and the transversally twinning of StB and StD with para- and metacone, respectively. However, *Zeusdelphys* and *Hatcheritherium* share all mentioned characters, including a labial compression of StB and StD, the presence of three developed accessory cusps on the postmetacrista, broad anterobasal cingulum, and the presence of lingual and labial accessory crests on the distal and mesial borders of StB and StD, respectively.

Herein, we present a comparative study of the shared features between *Zeusdelphys*, *Hatcheritherium*, Glasbiidae, Protodidelphidae and Polydolopimorphia in order to try to elucidate the affinities of *Zeusdelphys*.

Institutional abbreviations.—MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; YPM, Yale University Peabody Museum, New Haven, Connecticut.

Biochronology.—EECO, Early Eocene Climatic Optimum; NALMA, North American Land Mammal Age; SALMA, South American Land Mammal Age; PETM, Paleocene-Eocene Thermal Maximum.

Dental nomenclature.—**M**, upper molars.

Materials and methods

The study presents a detailed review of the homology of preserved materials associated to Hatcheriformes taxa. The new matrix was constructed based on the interpretation of singular patterns and evolutionary tendencies that have never been proposed or studied in any phylogeny published so far; which implies in new proposed characters and codifications. The polarization of the characters followed the conclusions of previous studies (Fox, 1987; Marshall *et al*. 1990; Johanson 1996; Cifelli and Muizon 1997; Oliveira and Goin 2011;

Oliveira *et al*. 2016). The matrix is mainly based on dental characters from upper and lower dentition of fossil and living Metatheria.

We conducted a traditional search using TNT 1.1 (Goloboff *et* al. 2008) with 1000 replications and 1000 random seeds, saving 10 trees for replication. The data matrix was plotted in Nexus and is available at supplementary materials. For Bremer supports and tree scores were used TNT 1.1. The phylogeny presents 38 metatherian taxa, including 5 extant genera, from Cretaceous and Cenozoic from North America and Southern hemisphere (*i.e.* South America, Antarctica and Australia).

Systematic Palaeontology

†Mammalia Linnaeus, 1758

†Metatheria Huxley, 1880

†Polydolopimorphia (Ameghino, 1987)

†Hatcheriformes Case, Goin and Woodburne, 2005

Family *incertae sedis*

†Genus *Zeusdelphys* Marshall, 1987 (Fig. 2)

1984 *Eobrasilia* Marshall, p. 174, fig. 4.

1987 *Zeusdelphys* Marshall, p. 124, fig. 45.

Type species: *Zeusdelphys complicatus* Marshall, 1987.

Included species: The type only.

Type Locality: Fresh water travertine deposits at São José de Itaboraí, Rio de Janeiro, Brazil (Bergqvist *et al*. 2009).

Type Horizon: Itaboraí Basin and Formation, municipality of Itaboraí, state of Rio de Janeiro, Brazil. Early Eocene, Itaboraian SALMA (ca 53-50 Ma; Woodburne *et al*. 2014).

†*Zeusdelphys complicatus* Marshall, 1987 (Fig. 2)

Revised Diagnosis.—Differs from other Metatheria in the following combination of characters such as the presence of a large, lingually shifted and centrally placed StC; pyramidal shape of StB and StD; presence of labial and lingual accessory crests of StB and StD; developed labial cingulum, oblique crest that separates the parastyle from the anterobasal cingulum; broad and well developed anterobasal cingulum; lingual border of the metacone evidently more lingual in position than the lingual border of the paracone; presence of three large supernumerary cusps on the postmetacrista; reduced stylar shelf and postmetacrista; very compressed talon, and protocone not eccentric. Differs from Protodidelphidae and Glasbiidae in the absence of eccentric protocone, basal expansions of upper molars, the presence of pyramidal StB and StD, lingually shifted StC, and larger size of StC.

Holotype: MCT 2830-M, M1.

Referred specimens.—The type only.

Occurrence.—Itaboraí Basin and Formation, municipality of Itaboraí, state of Rio de Janeiro, Brazil. Early Eocene, Itaboraian SALMA (ca 53-50 Ma; Woodburne *et al*. 2014).

Remarks.—When compared to most of Late Cretaceous and Paleogene metatherians, *Zeusdelphys complicatus* is more similar to *Hatcheritherium alpha* from the Late Cretaceous of EUA than to any other metatherian.

Phylogenetic analysis

The analysis found a single most parsimonious tree (tree score = 97) (Fig. 1). Following the results, *Zeusdelphys complicatus* was recovered as the sister taxon of *Hatcheritherium alpha*. This result supported the previous hypothesis of Oliveira and Goin (2011), which mentioned similarities of both taxa. However, the results didn't support the assignment of *Zeusdelphys* as a Protodidelphidae, as proposed by Oliveira and Goin (2011), and Oliveira *et al*. (2016).

The North American *Ectocentrocristus* was recovered as the sister lineage of *Zeusdelphys* + *Hatcheritherium*, within Hatcheriformes. This result didn't support Polydolopiformes affinities, as proposed by Case *et al*. (2005). The phylogenetic analysis recovered *Zeusdelphys*, *Hatcheritherium* and *Ectocentrocristus* as Hatcheriformes. This suborder was recovered as the sister lineage of "Alphadontidae", a paraphyletic family, as *Turgidodon* is apparently more closely related to Polydolopimorphia than to any "Alphadontidae".

Glasbiidae and Protodidelphidae were considered as sister lineages within Didelphimorphia. The phylogenetic relation between Protodidelphidae and Polydolopimorphia were proposed by Marshall *et al*. (1990), but was refuted by Goin *et al*. (1998), and Goin and Candela (2010); this result was supported by the analysis. The exclusion of Glasbiidae from Hatcheriformes didn't agree with Case *et al*. (2005), which considered this taxon along with *Hatcheritherium* as the members of Hatcheriformes.

Discussion and conclusions

Presence of three accessory cusps on the postmetacrista

The presence of three accessory cusps in the postmetacrista is easily identifiable on the postmetacrista of *Zeusdelphys* and *Hatcheritherium*. The development of these structures is greater in *Zeusdelphys complicatus* than any other metatherian, which is the main autapomorphy of this species. In *Hatcheritherium*, these cusps are present through the postmetacrista, while they are appressed against each other in *Zeusdelphys*. The explanation for these two different morphologies is the strong reduction of the postmetacrista in the Itaboraian taxon, resulting in the compression of these structures.

Interestingly, several “Alphadontidae like-taxa” also present similar structures (e.g. *Nortedelphys*, *Alphadon* and *Albertatherium*), though much less developed than the ones of *Zeusdelphys* and *Hatcheritherium*. The greater degree of development of these two genera is unique among Metatheria.

Discontinuous centrocrista

The presence of an open centrocrista is identified in Polydolopimorphia, Hatcheriformes and *Zeusdelphys*. The condition present in *Zeusdelphys* is more similar to *Hatcheritherium* than to any other metatherian. Both taxa present a straight postparacrista and an oblique premetacrista, a unique pattern for Metatheria. *Hatcheritherium* presents the premetacrista merged with two small cuspules at the labiocentral portion of stylar shelf (Case et al. 2005), while *Zeusdelphys* presents the premetacrista merged with a large and lingually shifted StC, previously identified as a non-homologous cusp to the StC by Oliveira and Goin (2011). Based on this, *Zeusdelphys* presents a developed StC, condition not common for Protodidelphidae.

The open centrocrista of Polydolopimorphia is different from the one of *Hatcheritherium* + *Zeusdelphys*: the former lineage presents an evidently opened centrocrista, with postparacrista and premetacrista invasive on stylar shelf; for *Hatcheritherium* + *Zeusdelphys*, only the premetacrista is invasive on stylar shelf. The phylogenetic analysis didn't recover these two morphologies as homologous, which indicates that the condition of *Hatcheritherium* + *Zeusdelphys* is not plesiomorphic to the open state of Polydolopimorphia, then, representing two independent evolutionary events. This idea is supported by the sister relation between *Alphadon* + *Nortedelphys* with *Ectocentrocristus* and *Hatcheritherium* + *Zeusdelphys*.

Ectocentrocristus foxi Rigby and Wolberg, 1987, shows an 'arc-shape' centrocrista, with the postparacrista and the premetacrista not in contact, creating a notch between both. The condition is different from the one present in Polydolopimorphia, in which the centrocrista is evidently more invasive and opened. Case et al. (2005) considered the centrocrista of *Ectocentrocristus* as representing a probable plesiomorphic state of Polydolopiformes, but they didn't bring support to this hypothesis in a phylogenetic analysis. In order to test the affinities of this taxon with Hatcheriformes and Polydolopimorphia, it was included in the phylogenetic analysis. The results recovered its centrocrista state as more similar to the one present in *Hatcheritherium* and *Zeusdelphys* than to any Polydolopiformes.

The centrocrista of Glasbiidae and Protodidelphidae is more 'U-shape' than the one present by Polydolopimorphia and Hatcheriformes. The phylogenetic analysis does not recover this morphology as an evidence for the grouping of these two taxa with Polydolopimorphia or Hatcheriformes, but group both families as a monophyletic lineage within Didelphimorphia. Apparently, this morphology represents an apomorphy of a 'V-shape' centrocrista.

Based on the phylogenetic results, the Hatcheriformes represents an independent lineage from Polydolopimorphia, more closely related to Alphadontidae than to any other metatherian lineage.

Pyramidal shape of StB and StD

An important feature identified by this study is the presence of pyramidal shapes in *Zeusdelphys* and *Hatcheritherium*. Both taxa present a vertical distal border of the StD, which differs from remaining metatherians that present a more convex border. Other characteristic features of the StD is the presence of a bifurcated medium crest and two accessory and well-developed mesially oriented crests; similar crests are also present at the distal border of StB, resulting on a concave distal border of StB and a concave mesial border of StD. These structures change the external shape of StB and StD in lingual view, giving the appearance of two “pyramids”.

Interestingly, the similar condition is also present in *Ectocentrocristus foxi*, currently considered as a basal Polydolopiformes. However, the phylogenetic analysis recovered *E. foxi* as a Hatcheriformes, more closely related to *Hatcheritherium* + *Zeusdelphys* than to any other taxa. *Ectocentrocristus* share the “pyramidal” shape of StB and StD, the distal vertical border of StD, the lingual and labial accessory crests of StB and StD, but lacks the bifurcated medium crest of StD. *Alphadon* and *Nortedelphys* also present the “pyramidal” shape of StB and its accessory crests, but lacks the accessory crests of StD (have only a single crest), and the medium crest of StD is not so developed. Based on the phylogenetic analysis, the presence of a “pyramidal” StD is a synapomorphy of Hatcheriformes, while the “pyramidal” StB is a synapomorphy of Alphadontidae and Hatcheriformes.

The Glasbiidae and Protodidelphidae do not present the “pyramidal” shape of StB and StD, distal vertical border of StD, the medium accessory crest of StD, and the labial and lingual accessory crests of StB and StD. The absence of these structures, considered as synapomorphies of Hatcheriformes by the phylogenetic analysis, excludes Glasbiidae and Protodidelphidae from Polydolopimorphia and Hatcheriformes.

Broad anterobasal cingulum and development of the labial cingulum

The anterobasal cingulum of *Zeusdelphys* and *Hatcheritherium* is more anteriorly expanded than any other metatherian lineage, which was recovered as a synapomorphy on the phylogenetic analysis. The presence of a developed labial cingulum is evident in *Zeusdelphys* and several Glasbiidae (e.g. *Glasbius*) and Protodidelphidae (e.g. *Carolocoutoia* and *Protodidelphis*), which can be considered as an evidence of their close relation. Interestingly, the phylogenetic analysis considered the greater development of the labial cingulum as an independent evolutionary event between *Zeusdelphys* and Glasbiidae + Protodidelphidae. The species of *Didelphis* also presents the similar development of labial cingulum.

Hatcheritherium alpha shows a poorly developed labial cingulum (Case *et al*. 2005), *Guggenheimia* presents a moderately developed labial cingulum (Paula Couto 1952, 1962, 1970); *Alphadon* (Johanson 1996), *Nortedelphys* (Case *et al*. 2005), *Sillustania* (Chornogubsky and Goin 2015), *Ectocentrocristus* (Sahni 1972; Rigby and Wolberg 1987; Case *et al*. 2005) and *Roberthoffstetteria* (Marshall *et al*. 1983; Muizon *et al*. 1984; Muizon 1992; Goin *et al*. 2003) do not developed a labial cingulum. The greater degree of development of this cingulum appears to be an adaptation to more frugivorous diets, a conclusion that agrees well with that proposed for *Zeusdelphys* and *Protodidelphis* (Zimicz 2012). Unfortunately, without a more focused study, this idea can only be treated as a plausible hypothesis. The idea that this feature could indicate a close relation between *Zeusdelphys* and Protodidelphidae was not supported by the phylogenetic analysis, but the same analysis recovered this morphology as an evidence for the sister relation between Glasbiidae and Protodidelphidae.

Systematic review

The results of this study indicate that Hatcheriformes is more diverse than previously accepted. The current definition of this lineage is paraphyletic, with Glasbiidae representing a Didelphimorphian lineage, being more closely related to Protodidelphidae than to any other metatherian lineage. *Ectocentrocristus* should be included among Hatcheriformes, as it presents all main synapomorphies of this lineage: pyramidal shape of StB and StD, vertical posterior border of StD, presence of labial and lingual accessory crests on pyramidal StB and StD, which forms concave medial borders on these cusps; discontinuous centrocrista, with postparacrista and premetacrista do not contact at the center of the tooth; presence of three developed cusps on the postmetacrista; and absence of an eccentric protocone.

The currently status of Protodidelphidae is paraphyletic, as *Zeusdelphys complicatus* represents a Hatcheriformes. Following the analysis, *Zeusdelphys* is the sister taxon of *Hatcheritherium alpha*. Both, along with *Ectocentrocristus*, represents the Hatcheriformes, the sister lineage of "Alphadontidae" and not Polydolopimorphia. The results demonstrate that Polydolopimorphia represents an independent lineage from Hatcheriformes, excluding this lineage from this order. The systematical state of Polydolopimorphia appears to polyphyletic, as Hatcheriformes belongs to ?Alphadontia, along with "Alphadontidae"; Glasbiidae represents a family of Didelphimorphia; and *Ectocentrocristus* is a Hatcheriformes. In order to recover the monophyletic state of Polydolopimorphia, *Ectocentrocristus*, Hatcheriformes and Glasbiidae must be excluded from this order.

The results indicate that *Zeusdelphys complicatus* is closely related to *Hatcheritherium alpha*. These taxa share the presence of a discontinuous centrocrista, pyramidal StB and StD with a strong labial compression, well-developed three accessory cusps of the postmetacrista, the bifurcated medium accessory crest of StD, and broad anterobasal cingulum.

These two taxa also share with *Ectocentrocristus* the presence of the pyramidal StB and StD, compressed talon, notched centrocrista, labial and lingual accessory crests, the vertical distal border of StD, and greater development of the medium accessory crest of StD. These characters are the main synapomorphies of Hatcheriformes lineage.

Alphadon and *Nortedelphys* share with Hatcheriformes the presence of a well-developed StC, three accessory cusps on the postmetacrista, pyramidal StB, and lingually oriented crest connecting the apex of StC with the centrocrista. “Alphadontidae” + Hatcheriformes represent the sister-lineage of Polydolopimorphia + *Turgidodon*; with both sharing the presence of a frequently present distolabial cusp to StB, a synapomorphy for them.

The inclusion of *Zeusdelphys* within Protodidelphidae probably results of a convergent evolution related to more frugivorous diets. Oliveira and Goin (2011) considered *Zeusdelphys* as lacking a StC, but this taxon presents a well-developed cusp lingually shifted on stylar shelf. The presence of developed labial cingulum, wrinkle enamel, bunoid molars, relatively large size, developed protocone, and reduction of the conules are adaptations for frugivorous diets (Zimicz 2012). Despite the presence of these shared adaptations between Protodidelphidae and *Zeusdelphys*, these characters represent independent adaptations to increase the ingestion of fruits.

It is possible the negative argument that is more “plausible” or parsimonious that *Zeusdelphys* represents a Protodidelphidae that converged to acquire all main synapomorphies of *Hatcheritherium* and *Ectocentrocristus*. However, this hypothesis is not supported by the phylogenetic analysis, which tested all main characters shared between Hatcheriformes, Polydolopimorphia, Glasbiidae and Protodidelphidae. It is important to comment that a phylogenetic analysis is currently considered as the most reliable analysis to test the affinities between different taxa, as the number of variables is too high to be considered without a statistic analysis (Simões *et al*. 2016). Based on this, the arguments that defend convergent evolution between *Zeusdelphys* and *Hatcheritherium* or the idea that taxa from two different continents could not represent a single lineage was not supported by the analysis. The idea that *Zeusdelphys* is restricted to a single specimen is not supported as well, as the present characters were strongly supported by the analysis. Following this idea implies in the exclusion of several metatherians from phylogenetic analysis, which is not acceptable. Besides, other studies also included *Zeusdelphys* on their phylogenetic analysis, without methodological problems (Marshall 1987; Oliveira and Goin 2011; Oliveira *et al*. 2016). The greatest "problem" of these studies was the absence of Hatcheriformes in the analysis, which restricted the possibilities for the grouping of *Zeusdelphys*. The presence in our analysis of several metatherians lineages supported the grouping of *Zeusdelphys* within Hatcheriformes and not Protodidelphidae.

Paleobiogeography

The grouping of *Zeusdelphys* + *Hatcheritherium* indicates a North American origin for this lineage. Based on recent studies, several South American metatherians represent Paleogene surviving taxa of Late Cretaceous North American lineages (Woodburne and Case, 1996; Case, Goin and Woodburne, 2005; Oliveira and Goin, 2012; Goin *et al*. 2016). These studies defend the Caribbean Plate as the main pathway for the arrival of North American lineages in South America, through the 'Aves Ridge' (Pindell, 1994). The late Maastrichtian (Lancian NALMA) is considered the most probable time-span for the arrival of metatherians in South America (see FABI in Goin *et al*. 2016).

Interestingly, strong sea-level regressions are registered for the Late Cretaceous, including one around 66 Maa (Haq 2014). This sea-level regression probably was enough to create land connections between these islands and South America, allowing the dispersal of North American lineages to South America. The idea of a faunal interchange between Americas during the Late Cretaceous is also known for other groups, such dinosaurs (Bonaparte 1984; Pascual 2006; Pascual and Ortiz-Jaureguizar 2007) and “ungulates” (Muizon and Cifelli 2001).

The results of the phylogenetic analysis support a North American origin for Hatcheriformes, with *Zeusdelphys* representing one of the last members of this lineage. The ancestors of *Zeusdelphys* probably reached South America during the Late Cretaceous and survived until the early Eocene (Itaboraian SALMA) in Itaboraí (Fig. 3). Recent studies proposed that Itaboraí represents a faunal assemblage during the early Eocene Climatic Optimum (EECO) (Woodburne *et al*. 2014; Goin *et al*. 2016), after the Paleocene-Eocene Thermal Maximum (PETM), around 55.2 Maa (Bowen *et al*. 2014). This climatic event increased the presence of tropical rainforests, warm temperatures and is considered the main event for the evolution of Metatheria during the Paleogene (Woodburne *et al*. 2013; Goin *et al*. 2016). The large size and the bunoid adaptations of *Zeusdelphys* identify this taxon as a specialized metatherian, probably with a strict frugivorous diet (Zimicz 2012). The reduction in global temperatures during the middle and late Eocene can be considered as the main responsible for the extinction of *Zeusdelphys* and many other frugivorous lineages (Goin *et al* 2016).

In short, *Zeusdelphys complicatus* represents an early Eocene South American surviving lineage of Hatcheriformes, which indicates that a North and South American land connection existed during the Late Cretaceous. This result also increases the diversity of metatherians during the early Paleogene of South America.

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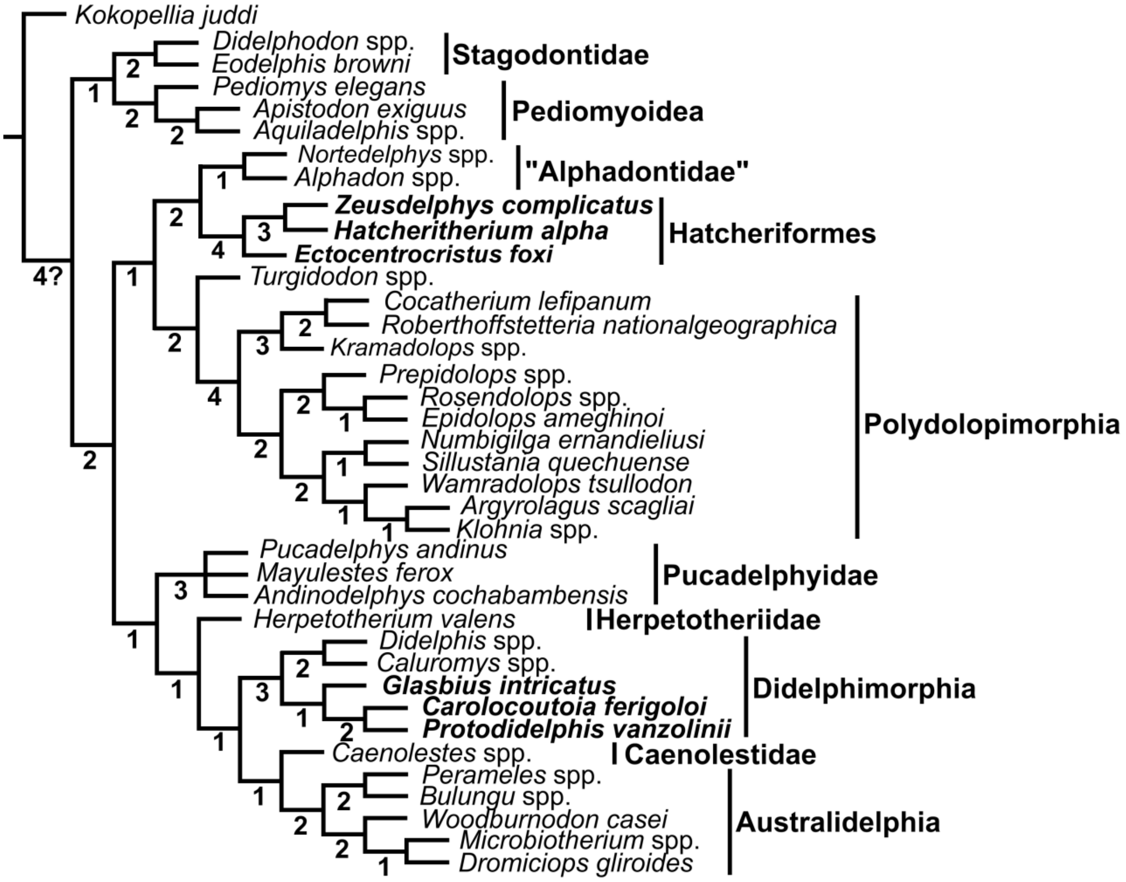
Figure captions

Fig. 1 Result of phylogenetic analysis. Single most parsimonious tree found in the analysis. The metatherian lineages are identified by vertical bars. Numbers below the ramus indicate the Bremer Support. The Hatcheriformes, Glasbiidae and Protodidelphidae are in bold. [planned for page width]

Fig. 2 *Zeusdelphys* autapomorphies and characters. MCT 2830-M (*Zeusdelphys complicatus*) showing its main autapomorphies and general characters. Scale bar: 1 mm. [planned for page width]

Fig. 3 Temporal and geographical distribution of Hatcheriformes. Phylogeny of Hatcheriformes calibrated in time, based on the phylogeny present in the figure 1. The wide bars indicate the recorded temporal range of Hatcheriformes taxa. The NALMAs and SALMAs that present Hatcheriformes taxa are also identified. [planned for page width]



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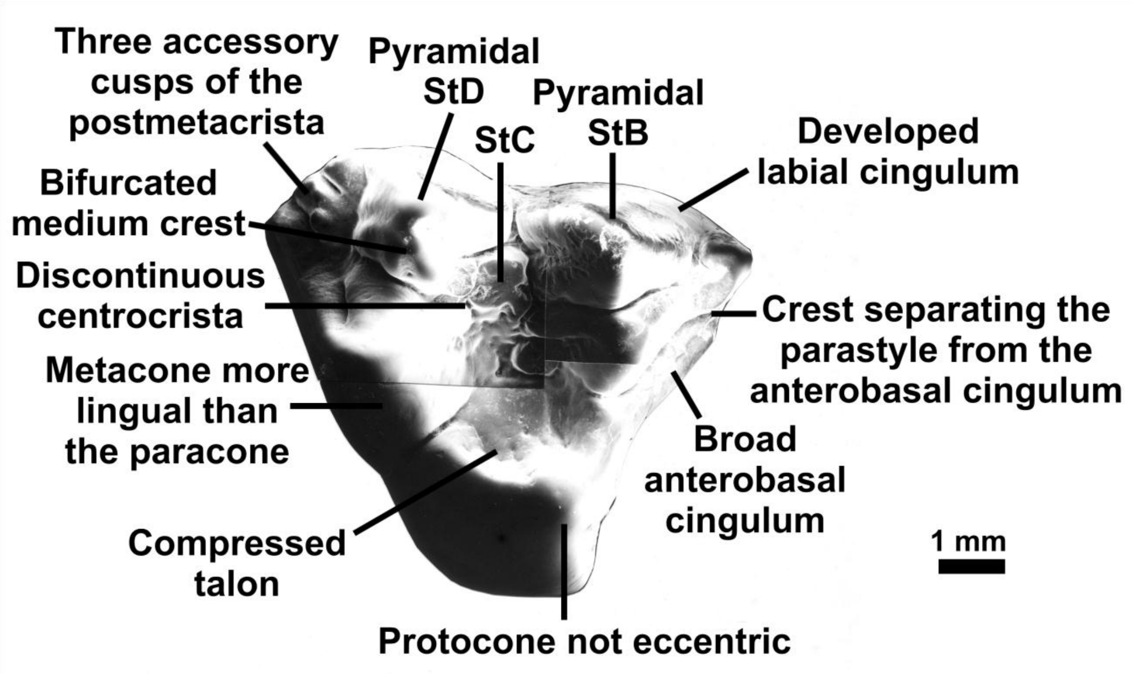

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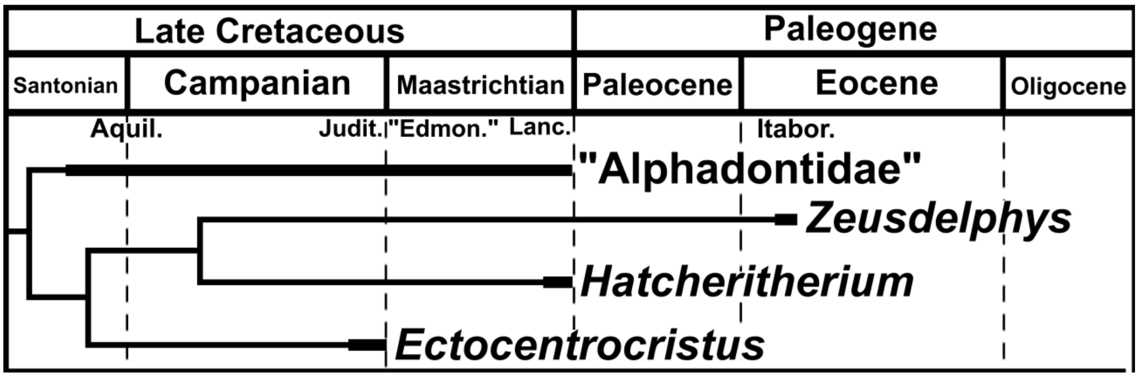

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Appendix 1

Characters and states of phylogenetic analysis. Characters and states used in the phylogenetic analyses. Characters are polarized with respect to *Lotheridium mengi* as outgroup. All characters are treated as unordered.

1. Wing-like parastyle: (0) absent, (1) present.
2. Development of parastyle: (0) developed, (1) reduced or vestigial.
3. Lingually shifted parastyle on M2-3: absent (0), present (1).
4. Development of StA in comparison to StB (Muizon and Cifelli, 2001): enlarged (0), small (1), vestigial (2).
5. Development of StB: developed (0), vestigial or absent (1).
6. Sinuous crest connecting StB and StD: (0) absent, (1) present.
7. StB with distolabial accessory cuspule (StB1): (0) absent, (1) present.
8. StB1 position in comparison to StC: (0) more labial than StC, (1) at same level of StC.
9. Well-developed StB1: (0) absent, (1) present.
10. Centro-labial StB1: (0) absent, (1) present.
11. Pyramidal StB: (0) absent, (1) present.
12. Broad and well-developed labial accessory crest of pyramidal StB: (0) absent, (1) present.
13. Reduced lingual accessory crest of pyramidal StB, which does not contact StC: (0) absent, (1) present.
14. Invasive lingual accessory crests of pyramidal StB and StD in stylar shelf: (0) absent, (1) present.
15. Invasive lingual accessory crests of pyramidal StB and StD merging at the center of stylar

shelf: (0) absent, (1) present.

16. StB massively larger than paracone: absent (0), present (1).
17. 'Twinned' cusp to StB: absent (0), present (1).
18. StB salient labially on M3: absent (0), salient (1).
19. StC development: (0) not truly identifiable, (1) identifiable.
20. Presence of StC: present (0), vestigial or absent on all molars (1).
21. Pyramidal StC: absent (0), present (1).
22. StC mesiolingually twisted on M1: absent (0), present (1).
23. Lingual shifting of StC: (0) not evidently lingual, (1) evidently lingual.
24. Lingual accessory crest of StC: absent (0), present (1).
25. Well-developed StC: absent (0), present (1).
26. Alignment of StB, StC and StD: (0) absent, (1) present.
27. Labiolingually compressed StC: absent (0), present (1).
28. StC merging with StD on M3: absent (0), present (1).
29. Twinned StC: present (0), absent (1).
30. StD development: (0) not truly identifiable, (1) identifiable.
31. Medium accessory crest of StD: (0) absent, (1) present.
32. Pyramidal StD: (0) absent, (1) present.
33. Pyramidal StD on all upper molars: absent (0), present (1).
34. StD with lingual and labial accessory crests: (0) absent, (1) present.
35. Morphology of the pyramidal StD: (0) pyramidal without inflation or compression, (1) compressed and flattened, (2) inflated, reducing the concave medial border and the accessory crests.
36. Vertical posterior border of StD: (0) absent, (1) present.

37. Developed vertical posterior border of StD: (0) developed, (1) poorly developed or vestigial.
38. StD subdivided into three apices: (0) absent, (1) present.
39. StD with sinuous accessory crest on M2, but not M1 or M3: absent (0), present (1).
40. Sinuous crest connecting the incipiently developed StD and the labiodistal border of metacone: present (0), absent (1).
41. StD with multiple crenulations on its longitudinal axis: absent (0), present (1).
42. StD1 presence: absent (0), present (1).
43. Notch between StB and StD: absent (0), present (1).
44. Conical and developed StE: absent (0), present (1).
45. Twinned cusps on the posterior border of metastylar shelf of M3: absent (0), present (1).
46. Roll of reduced cuspules only at the anterior border of StD: (0) absent, (1) present.
47. Accessory cuspules. (0) present, (1) absent.
48. Presence of multiples cuspules on metastylar shelf, with one usually slightly more developed than the remaining, but it could not be considered as a "true" StD: present (0), absent (1).
49. M3 with 'metastylar-wall': absent (0), present (1).
50. Flattened and reduced StB, StC and StD. (0) absent, (1) present.
51. Subequal, labially aligned, conical and closely-spaced StB, StC and StD: absent (0), present (1).
52. Well-developed stylar shelf with subequal parastylar and metastylar shelf: absent (0), present (1).
53. Epiconular plataform: absent (0), present (1).
54. Low parallel crest connecting the apex of the paracone with StB: (0) absent, (1) present.
55. Low parallel crest connecting the apex of the metacone with StD: (0) absent, (1) present.
56. Preparacrista orientation: StB (0), StA (1).

57. Preparacrista labially notched due to the absence of the mesiolingual crest of StB: absent (0), present (1).

58. Reduced preparacrista that points toward StA and does not contact the mesiolingual crest of StB: (0) absent, (1) present.

59. Parastylar shelf development on M2 and or M3: developed (0), reduced to a narrow cingulum or rim (1).

60. Postmetacrista with three accessory cuspules: (0) absent, (1) present.

61. Well-developed postmetacrista accessory cusps: (0) absent, (1) present.

62. Postmetacrista accessory crest: (0) absent, (1) present.

63. Well-developed metastylar wing, distally projecting on M3: absent (0), present (1).

64. Comparative development of asymmetric reduced parastylar shelf and developed metastylar shelf: absent (0), metastylar much larger than parastylar (1), metastylar slightly larger than parastylar (2), metastylar slightly larger or nearly subequal to parastyle.

65. Labial border of metastylar shelf oblique oriented on M1, being twice the size of the parastylar shelf labial border: (0) absent, (1) present.

66. Labial border of metastylar shelf evidently rounded: absent (0), present (1).

67. Labial cingulum: absent (0), present (1).

68. Vestigial stylar shelf: absent (0), present (1).

69. Ectoflexus very deep, reaching the level of lingual border of StB: present (0), absent (1).

70. Ectoflexus deep and broad ('ridge-like' ectoflexus): absent (0), present (1).

71. Para- and metacone with apices lingually projected: (0) absent, (1) present.

72. Metacone apex evidently posteriorly projected: absent (0), present (1).

73. Morphology of the labial borders of para- and metacone: (0) both rounded, (1) metacone rounded and paracone pyramidal, (2) both compressed, (3) paracone rounded and metacone

pyramidal.

74. Labial alignment of para- and metacone: aligned (0), paracone more labial than metacone (1).
75. Paracone evidently more labial than the metacone on M2-3: absent (0), present (1).
76. Twisted paracone: (0) absent, (1) present.
77. Degree of paracone twisting: (0) poorly twisted, (1) evidently twisted.
78. Medium sharp crest on lingual border of metacone: absent (0), present (1).
79. Accessory crest labially and oblique oriented on the midline of metacone: (0) absent, (1) present.
80. Development of the accessory crest labially oriented on the midline of metacone: (0) developed, (1) poorly developed.
81. Accessory crest labially oriented on the midline of paracone: (0) absent, (1) developed.
82. Development of the accessory crest labially oriented on the midline of paracone: (0) developed, (1) poorly developed.
83. Alignment of centrocrista with para- and metacone: (0) straight, (1) lingually displaced.
84. Notched straight centrocrista: (0) absent, (1) present.
85. Morphology of labially displaced centrocrista: pseudolinear (0), dilambdodont (1), 'arc-shape' (2), 'U-shape' (3), open (4), vestigial (5), notched (6).
86. Invasive centrocrista: (0) absent, (1) present.
87. Morphology of labially displaced notched centrocrista: (0) discontinuous, (1) some degree of 'arc-shape', (2) sinuous, (3) pseudolinear.
88. Accessory cusp to the ectoloph of the centrocrista: (0) absent, (1) present.
89. Protocone displacement (Oliveira and Goin, 2011): (0) absent, (1) eccentric.
90. Morphology of protocone: fusiform or indiferenciated (0), mesio-distally expanded (1), labio-lingually developed (2), conical (3), hypocone (4), compressed (5).

91. Inflation of protocone: absent (0), present (1).

92. Spire-like protocone: (0) absent, (1) present, (2) compressed.

93. Fusiforme protocone on M3, but not on M1-2: (0) absent, (1) present.

94. M1 with fusiform and eccentric protocone ('Peradectoid M1'): absent (0), present (1).

95. Protocone with a pair of oblique grooves: absent (0), present (1).

96. Preprotocrista with half the length of postprotocrista, but the protocone is not eccentric: absent (0), present (1).

97. Accessory cuspules associated with postprotocrista with a variable number: absent (0), present (1).

98. Presence of dental basal expansions: absent (0), present (1).

99. Development of dental basal expansions: poorly developed (0), well-developed (1).

100. Conules separated from the pre- and postprotocrista by a deep notch: (0) absent, (1) present.

101. Accessory conules presence: (0) absent, (1) present.

102. Accessory conules with similar development to para- and metaconule and independently developed from protocristae: absent (0), present (1).

103. Development of conules: with some degree of development, but not reduced or enlarged (0), reduced or absent (1), enlarged (2).

104. Paraconule much more reduced than the metaconule: (0) absent, (1) present.

105. Morphology of metaconule: pyramidal (0), pseudoinflated (1), inflated (2), 'hypocone-like' (3), 'spire-like' (4), mesio-distally compressed (5), pseudohypocone (6).

106. Paraconule enlarged, being larger than the vestigial metaconule on M3: (0) absent, (1) present.

107. Paraconule lingually shifted, but not the metaconule: absent (0), present (1).

108. Aligned paraconule, protocone and metaconule: (0) absent, (1) present.

109. M3 with conules lingually shifted, subequal and aligned, but not on the lingual border: (0) absent, (1) present.

110. Straight preparaconular crista separating the talonid basin from the mesiolingual cingulum: absent (0), present (1).

111. Invasive preparaconular crista: absent (0), present (1).

112. Morphology of invasive preparaconular crista: oblique oriented, but not so invasive (0), oblique oriented and well-invasive (1), straight (2).

113. Straight invasive preparaconular crista with sinuous lingual third trajectory: absent (0), present (1).

114. Discontinuous postmetaconular crista on M1: absent (0), present (1).

115. Internal metaconular crista development, when the metaconule is developed: developed (0), reduced or absent (1).

116. Furrow between protocone and metaconule: absent (0), present (1).

117. Proto-paraconule wear pattern: absent (0), present (1).

118. Anterobasal cingulum contacting the talon in a lower position (discontinuous anterobasal cingulum with talon basin): (0) absent, (1) present.

119. Merging of discontinuous anterobasal cingulum and talon basin: absent (0), present (1).

120. Reduced anterobasal cingulum only on M3: (0) absent, (1) present.

121. Mesial expansion of anterobasal cingulum: absent (0), with the labial half gently recurved and mesially expanded (1), broad and evidently mesially expanded (2), broad, but with sinuous trajectory (3).

122. Anterobasal cingulum with a lower trajectory: (0) absent, (1) present.

123. Posterobasal cingulum development: developed (0), reduced or poorly developed (1), vestigial or absent (2).

124. Posterobasal cingulum with a lower contact than stylar shelf: absent (0), present (1).
125. External shape of upper molars: 'yoke-like' (0), trapezoid (1), ovoid (2), subquadrangular (3), piriform (4), rectangular (5).
126. Hexacuspate upper molars: absent (0), present.
127. Hypsodonty: (0) absent, (1) present.
128. Mesiodistally compressed upper molars: (0) absent, (1) present.
129. Elongated talon that is longer than stylar shelf on all molars: (0) absent, (1) present.
130. Talon longer than stylar shelf only on M3: (0) absent, (1) present.
131. Compressed talon: (0) absent, (1) present.
132. M4 with centrally placed paracone: (0) absent, (1) present.
133. Dilambdodont centrocrista connecting para- and metacone on M4: (0) absent, (1) present.
134. M4 with large, inflated and labiocentral stylar cusps: (0) absent, (1) present.
135. Inflated M4: (0) absent, (1) present.
136. M4 with paracone apex anteriorly shifted: absent (0), present (1).
137. M4 with paracone more labial than the metacone: absent (0), present (1).
138. M4 more reduced than M3, but is not mesiodistally or labiolingually compressed: absent (0), present (1).
139. M1 with elongated shape that does not present a strong labiolingual compression of trigonid, which is much shorter than the talonid: (0) absent, (1) present.
140. M1 strongly labiolingually compressed: present (0), absent (1).
141. Anteroposteriorly compressed m1: (0) absent, (1) present.
142. M1 with well labially salient hypoconid: absent (0), present (1).
143. Protoconid and metaconid nearly merged on m1: absent (0), incipiently merged (1), merged (2).

144. Mesiodistally elongated a labiolingually compressed trigonid on m1: absent (0), present (1).

145. Labiolingual expansion of trigonid: absent (0), present (1).

146. Compression of trigonid: compressed (0), not compressed (1).

147. Relative size between paraconid and metaconid: (0) both well-developed and subequal, (1) paraconid with some degree of reduction, (2) metaconid with some degree of reduction, (3) paraconid with evident increasing in size.

148. Paraconid as taller as the protoconid: (0) absent, (1) present.

149. Paraconid medially placed: absent (0), present (1).

150. Paraconid broad and with its apex anteriorly shifted ('blade-like' paraconid) on m2-4: absent (0), present (1).

151. Paraconid with compressed mesial border: absent (0), present (1).

152. Metaconid positioning in comparison to the protoconid: metaconid complete posterior to protoconid (0), metaconid posterior to protoconid (1), both aligned (2), metaconid anterior to protoconid (3).

153. Keeled distolingual angle of metaconid (Eaton, 2006): absent (0), present (1).

154. Protoconid strongly labiolingually shifted on m2-3: absent (0), present (1).

155. Metastylid (Goin, 2006): (0) absent, (1) present.

156. Ectostylid: absent (0), present (1) (Zimicz, 2011).

157. Entostylid: absent (0), present (1).

158. Morphology of hypoconid: (0) compressed, (1) spire-like, (2) 'tower-like'.

159. Hypoconid labially projected, resulting in a wider talonid comparing to the trigonid: (0) absent, (1) present.

160. Development of the entoconid: (0) not truly identifiable, (1) identifiable and with some degree of development.

161. Morphology of entoconid: flattened and poorly developed (0), conical (1), compressed (2), 'spire-like' (3), flattened (4), inflated (5).

162. Entoconid and hypoconid with similar size: (0) absent, (1) present.

163. Conical and vestigial entoconid: (0) absent, (1) present.

164. Massive hypo- and entoconid: absent (0), present (1).

165. Cristid obliqua position of contact with the posterior wall of the trigonid (m1-3): slightly lingual (0), carnassial notch (1), slightly labial (2), more labial (3), at labial border (4).

166. Metacristid short and recurved due to the merging with the cristid obliqua: absent (0), present (1).

167. Cristid obliqua progressively more lingual through the lower molar series: absent (0), present (1).

168. Sinuous and reduced cristid obliqua: absent (0), present (1).

169. Recurved cristid obliqua on m2, does not contacting trigonid posterior wall: absent (0), present (1).

170. Hypo-hypoconulid wear pattern: absent (0), present (1).

171. Hypoconulid position: central (0), more lingual (1), distolingual (2), slightly lingual (3).

172. Hypoconulid central, well-developed and distally projected (occupies more than the half of the posterior wall of talonid): absent (0), present (1).

173. Aligned entoconid, hypoconulid and hypoconid on distal border of talonid: absent (0), present (1).

174. Accessory cuspids e and f: (0) with at least one present, (1) both vestigial or absent.

175. Short talonid: (0) absent, (1) present.

176. Low and broad lower molars: (0) absent, (1) present.

177. Protoconid labially projected on m4: absent (0), present (1).

178. M3 and or m4 cristid obliqua with posterior sinuous compression and straight trajectory: (0) absent, (1) present.

179. M4 hypoconid aligned or anterior to the entoconid: (0) absent, (1) present.

180. M4 size in comparison to m3, but not reduced to a single root: (0) nearly subequal, (1) moderately smaller, (2) much smaller, (3) larger.

181. M4 with elongated talonid: not elongated (0), shorter and narrower than the trigonid (1), evidently elongated (2), elongated, but evidently shorter than the trigonid (3).

182. M4 with conical and small entoconid ('tower-like'): absent (0), present (1).

183. M4 with conical and central hypoconulid: absent (0), present (1).

184. Cristid obliqua contacting the metaconid only on m4: absent (0), present (1).

185. M4 with labial cingulid: absent (0), poorly developed (1), evidently developed (2).

186. M4 with well-developed anterobasal cingulid: absent (0), present (1).

187. 'Didelphid-like' m4: absent (0), present (1).

188. Number of premolars: four (0), three or less (1).

189. P1 with two developed anterior and posterior cusps: (0) absent, (1) present.

190. P1 oblique oriented in comparison to P2-3: aligned (0), oblique oriented (1).

191. P1 with single-root: absent (0), present (1).

192. P2 larger than p3: absent (0), present (1).

193. Morphology of the mesial border of p2: rounded or convex (0), with anterior projection (1), laminar or without cusps or projections (2).

194. Flexids in the p2: (0) absent, (1) present.

195. Bulbous and inflated P3/p3: absent (0), present (1).

196. P3 with anteroposterior elongation: (0) absent, (1) present.

197. Plagiaulacoid P3-p3: absent (0), present (1).

198. Bilobed third lower incisor: absent (0), present (1).

199. Angular process of the dentary development: (0) not so developed, (1) evidently developed.

200. Recurved dentary: (0) absent, (1) present.

201. Recurvation of dentary below p1: absent (0), present (1).

202. Retropremolars spaces development: with diastem between p1-p2, but not p2-4 (0), spaces absent, with premolars in contact (1), with short retropremolar space between p1-2, but not p2-3 (2), with spaces between p1-2 and p2-3 (3), p1 and-or p2 absents (4).

203. Fossa incudis and epitympanic recess: continuous (0) or separated by a distinct ridge (1) (Ladevèze and Muizon, 2010 - character 28).

204. Mastoid tympanic process: small, slanted, and nodelike, on the posterolateral border of the stylomastoid notch and continuous with squamosal (0), indistinct to absent (1) (Beck, 2012).

205. Deep groove for internal carotid artery excavatedon anterior pole of promontorium: absent (0), present (1) (Ladevèze and Muizon, 2010 - character 10).

206. Tympanic sinus formed in the lateral trough (orlateral expansion of the pars canalicularis): absent (0), present (1) (Ladevèze and Muizon, 2010 - character 15).

207. Third trochanter presence: absent (0), present (1).

208. Positioning of the third trochanter: distal to the lesser trochanter, but with proximal portion nearly at same level (0), proximal to the lesser trochanter (1), more distal than the lesser trochanter, being complete more distal (2).

209. Lesser trochanter distomedially displaced: absent (0), present (1).

210. Calcaneocuboid facets: without subfacets (0), subdivided into pCaCu and dCaCu (1), subdivided into pCaCu, mCaCu and dCaCu (2) (Szalay, 1994).

211. CLAJP presence: absent (0), present (1) (Szalay, 1994).

212. Postorbital processes: absent or formed only by the frontals (0), formed by the parietals and

frontals (1) (Voss e Jansa, 2009).

213. Development of postorbital process: absent or indistinct (0), with some degree of development (1).

214. Posterior palate morphology: without distinct lateral corners, the choanae unconstricted behind (0), or posterior palate with distinct lateral corners, choanae constricted (1) (Voss e Jansa, 2009 - character 69).