

SYSTEMATIC AFFINITIES OF THE EXTINCT METATHERIAN *EOBRASILIA COUTOI* SIMPSON, 1947, A SOUTH AMERICAN EARLY EOCENE STAGODONTIDAE: IMPLICATIONS FOR “EOBRASILIINAE”

LEONARDO M. CARNEIRO & ÉDISON V. OLIVEIRA

Laboratório de Paleontologia (PALEOLAB), Departamento de Geologia, Centro de Tecnologia e Geociências,
Universidade Federal de Pernambuco. Av. Acadêmico Hélio Ramos s/n, 50740-530, Recife, PE, Brazil.
leonardo.carneiro8@gmail.com, vicenteedi@gmail.com

ABSTRACT – *Eobrasilia coutoi* Simpson is currently considered one of the most enigmatic metatherian mammals of Itaboraí Basin, Brazil. A single badly broken and incomplete skull, with a single strongly worn M3, and an associated fragmentary dentary are the elements currently attributed to this taxon. This fragmentary condition contributes for its uncertain position within Metatheria. Herein, the preserved dental morphology of this species is re-analyzed. The morphology of these structures, such as a tiny, obliquely oriented, one-rooted P1; absence of retro-premolar spaces between the premolars and mesiodistally developed p3, supports the assignment of *Eobrasilia* as a South American stagodontid. This new result leads a systematic review of the affinities of “Eobrasiliinae”, currently represented by *Eobrasilia*, *Gaylordia* and *Didelphopsis*. The hypothesis that “Eobrasiliinae” represents a valid taxon is refuted in the phylogenetic analysis, which recovered *Eobrasilia* as more closely related to *Didelphodon* within Stagodontidae, *Gaylordia* as the sister taxon of *Tiulordia* and more closely related to *Minuscudelphis* and *Marmosopsis*, and *Didelphopsis* as the sister taxon of *Itaboraidelphys* and more closely related to *Herpetotherium*, *Carolopaulacoutoia* and *Derorhynchus*. The shared characters between *Eobrasilia*, *Gaylordia* and *Didelphopsis* were likely a result of convergent evolution, as these three lineages independently adapted to more durophagous diets. The phylogenetic analysis did not support the sister relation between *Fumodelphodon* and *Didelphodon* and *Eodelphis* and *Hoodooetherium*. The grouping of *Eobrasilia* and *Didelphodon* corroborates the previous hypothesis that Metatheria dispersed from North to South America during the Late Cretaceous.

Key words: Early Eocene, *Eobrasilia*, “Eobrasiliinae”, Itaboraí, Stagodontidae, systematics.

RESUMO – *Eobrasilia coutoi* Simpson é considerado atualmente como um dos metatérios mais enigmáticos da Bacia de Itaboraí, Brasil. Um crânio muito fragmentado e incompleto com um M3 muito desgastado, e um dentário fragmentado são os únicos elementos atribuídos a esse táxon. Essa “fragmentação” dos materiais associados ao gênero *Eobrasilia* contribui para a sua posição incerta dentro do clado dos Metatheria. Aqui, a morfologia dentária preservada dessa espécie é reanalizada. A presença de um P1 pequeno, com uma orientação oblíqua em relação aos P2-3 e com uma única raiz; ausência de espaços retro-premolares entre os pré-molares e o evidente desenvolvimento mesiodistal do p3 suportam a associação de *Eobrasilia* como um stagodontídeo sul-americano. Esse novo resultado levou a uma revisão sistemática das afinidades dos “Eobrasiliinae”, previamente representado por *Eobrasilia*, *Gaylordia* e *Didelphopsis*. A hipótese de que “Eobrasiliinae” representa um táxon válido é refutada pela análise filogenética, que recuperou *Eobrasilia* como grupo-irmão de *Didelphodon* e pertencente à família Stagodontidae; *Gaylordia* como táxon irmão de *Tiulordia*, sendo ambos mais próximos filogeneticamente de *Minuscudelphis* e *Marmosopsis*; e *Didelphopsis* como grupo-irmão de *Itaboraidelphys* e esses aparentados filogeneticamente a *Herpetotherium*, *Carolopaulacoutoia* e *Derorhynchus*. Os caracteres compartilhados entre *Eobrasilia*, *Gaylordia* e *Didelphopsis* são resultado de evolução convergente, visto que essas três linhagens se adaptaram independentemente para dietas mais durófagas. A análise filogenética não suporta a relação de grupo-irmão entre *Fumodelphodon* e *Didelphodon*, e de *Eodelphis* com *Hoodooetherium*. O agrupamento de *Eobrasilia* e *Didelphodon* corrobora a hipótese de que os metatérios se dispersaram da América do Norte para a América do Sul durante o Cretáceo Superior.

Palavras-chave: Eoceno Inferior, *Eobrasilia*, “Eobrasiliinae”, Itaboraí, Stagodontidae, sistemática.

INTRODUCTION

Eobrasilia coutoi Simpson, 1947, was discovered in fissure fillings of early Eocene Itaboraian South American Land Mammal Age (SALMA – ca 53-50 Ma; Woodburne *et al.*, 2014) in the Itaboraí Formation at São José de Itaboraí Municipality, State of Rio de Janeiro, 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 little 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 presence of large and inflated premolars, especially the p3, led *Eobrasilia* to be grouped by Marshall (1987) with *Didelphopsis* Paula Couto, 1952, *Tiulordia* Marshall & Muizon, 1988, and *Gaylordia* Paula Couto, 1952, into the subfamily Eobrasiliinae, within Didelphidae. Besides this feature, no other study has found diagnostic characters that support these taxa as constituting a monophyletic group.

A revision of petrosal and dental materials from Itaboráí placed *Eobrasilia* as more closely related to *Didelphodon* Marsh, 1889 than to *Didelphopsis* and *Gaylordia* (see Ladevèze & Muizon, 2010). Oliveira & Goin (2011) and Oliveira *et al.* (2016) considered *Gaylordia* as closely related to *Minuscudelphis* and *Marmosopsis*. Oliveira & Goin (2015) thought of *Gaylordia* as closely related to Pucadelphyidae and Peradectidae, but did not include a jaskhadelphyid or a closely related taxon in their analysis. Goin (2003) suggested the inclusion of *Didelphopsis*, *Itaboraidelphys* and *Carolopaulacoutoia* in the family "Sternbergiidae" (McKenna & Bell, 1997); but this result was not supported by Oliveira & Goin (2011), and Oliveira *et al.* (2016), that considered *Didelphopsis* as closely related to *Itaboraidelphys* as the sister lineage of *Carolopaulacoutoia*, *Peratherium*, *Derorhynchus* and *Djarthia*, refuting the validity of "Sternbergiidae". The validity of "Eobrasiliinae" 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 Oliveira & Goin (2012), the evolution of massive premolars was a result of convergent evolution. The same study also called attention to the morphology of the incisors present in *Eobrasilia*.

Marshall (1984) tentatively assigned the MCT 2830-M, the type of *Zeusdelphys complicatus* Marshall, 1987 (a single and isolated M1), as the upper molar of *Eobrasilia*. However, this occlusal relation has never been studied in detail due to the absence of preserved lower molars of *Eobrasilia*. In the same study, Marshall (1984) commented about the great number of similarities between *Eobrasilia* and Stagodontidae Marsh, 1889. The similarities between these two lineages were also previously mentioned by Simpson (1947) (for him Thlæodontinae, p. 7) and Ladevèze & Muizon (2010).

The Stagodontidae is currently considered as a North American Late Cretaceous endemic family (Clemens, 1966; Fox & Naylor, 1986, 2006; Lofgren, 1992; Eaton, 1993a, 2013; Cifelli, 2004; Williamson *et al.*, 2012, 2014; Scott & Fox, 2015). Currently represented by *Eodelphis* Matthew, 1916, *Didelphodon*, *Hoodootherium* Cohen, 2017, and *Fumodelphodon* Cohen, 2017, this lineage is characterized by the presence of inflated premolars, stout dentary, large size and lower molars with an enlarged paraconid (Clemens, 1966; Fox, 1981; Cohen, 2017). *Pariadens* is an enigmatic taxon with possible stagodontid affinities, following previous studies (Cifelli & Eaton, 1987; Cifelli, 2004; Eaton, 1993a; Williamson *et al.*, 2012, 2014; Wilson *et al.*, 2016). *Pariadens* is known from the Cenomanian, representing one of the oldest metatherians of North America (Cifelli & Eaton, 1987; Cifelli, 2004; Eaton, 1993a; Williamson *et al.*, 2012, 2014). The oldest confirmed record of a stagodontid is the Smoky Hollow Member of the Straight Cliffs Formation (Turonian), southern Utah, with *Hoodootherium* and *Fumodelphodon* (Cohen, 2017). The presence of a stagodontid in the Smoky Hollow Member of the Straight Cliffs Formation (Turonian) was firstly proposed by Cifelli (1990). The Stagodontidae represents a unique and rare lineage in North America (Scott & Fox,

2015), being evidently different from other Late Cretaceous taxa. As mentioned, previous studies commented about the similarities between *Eobrasilia* and this family (Simpson, 1947; Marshall, 1984; Ladevèze & Muizon, 2010), but none has ever tested this hypothesis so far.

Herein, it is presented a review of the diagnostic characters of "Eobrasiliinae" and a redescription of the preserved materials assigned to *Eobrasilia*.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; DGM, Divisão de Geologia e Mineralogia, Rio de Janeiro, Brazil; MCT (ex DGM), Museu de Ciências da Terra, Rio de Janeiro, Brazil; MNHN Vil, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, França; MN, Museu Nacional, Rio de Janeiro, Brazil; QMF, Queensland Museum, Australia; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UCM, University of Colorado Museum, Colorado, USA; UCMP, University of California Museum of Paleontology, Montana, USA; ZMH, Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China.

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

MATERIAL AND METHODS

The matrix is based mainly on dental characters from the upper and lower dentition of fossil and living metatherians presented in Carneiro (2017 and references therein), but it also includes cranial, dentary and postcranial characters from Ladevèze & Muizon (2010), Forasiepi *et al.* (2014), Wilson *et al.* (2016) and Beck (2017). The codification of the morphological matrix followed Carneiro (2017).

The Brazilian taxa were directly examined (*i.e.* fossil specimens and casts). In addition, literature descriptions, casts, digital and Scanning Electron Microscope (SEM) pictures were also analyzed. The Brazilian studied taxa come from the Itaboráí fossil locality in southeastern Brazil (Figure 1). The North American stagodontids were studied based on literature digital and SEM pictures, and original descriptions. The materials from Naturita (formerly Dakota) Formation (upper Cenomanian – Carpenter, 2014) were examined by casts and pictures. These casts were sent by Richard L. Cifelli and Joshua E. Cohen from the Oklahoma Museum of Natural History, OK, USA. The list of casts is given in the supplementary material.

The SEM pictures of DGM 919-M was made with the Scanning Electron Microscope JEOL JSM-6390LV at the Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional, Rio de Janeiro, Brazil.

The analysis was conducted using a traditional search with TNT 1.1 (Goloboff *et al.*, 2008) with 1000 replications and 1000 random seeds, saving 10 trees for replication. The morphological matrix is available as a supplementary material. Bremer supports and tree scores were calculated with TNT 1.1. The phylogeny presents 584 unordered characters,



Figure 1. Location map showing the region and coordinates of the Itaboraí Basin, São José de Itaboraí, Rio de Janeiro, Brazil ($22^{\circ}45'9.9144''S$, $42^{\circ}51'53.5536''W$).

including cranial, dentary, dental and postcranial characters, and 123 therian taxa, including more than 100 metatherians, from the Cretaceous and Cenozoic of North America, Asia and Gondwana.

The best way to test the validity of a character or to establish the affinities of a taxon is through a phylogenetic analysis (Simões *et al.*, 2017). This study is based on the results of the phylogenetic analysis, as *a priori* systematic and taxonomical conclusions are not accepted as valid evidence in a systematic study without a phylogenetic analysis supporting it.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Infraclass METATHERIA Huxley, 1880

Supercohort MARSUPIALIFORMES Vullo *et al.*, 2009

†Order ARCHIMETATHERIA Szalay, 1994

†Family STAGODONTIDAE Marsh, 1889

Emended diagnosis. Large, Late Cretaceous and Paleogene, North and South American metatherians in which trigonids are anteroposteriorly shortened, and paraconid and protoconid are of subequal height, and higher than the metaconid (modified from Clemens, 1966); first upper premolars are obliquely oriented and present well-developed anterior and posterior cusps; upper and lower premolars are closely spaced, with no

evident retro-premolar spaces separating these teeth; lower incisors are semi-procumbent and not “staggered”, third upper and lower premolars are inflated and the dentary is robust.

Included genera. *Hoodootherium*, *Fumodelphodon*, *Eodelphis*, *Didelphodon* and *Eobrasilia*.

†*Eobrasilia* Simpson, 1947

1947 *Eobrasilia* Simpson, p. 2, figs. 2–4.

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 (Bergqvist *et al.*, 2009). Early Eocene, Itaboraian SALMA (ca. 53–50 Ma; Woodburne *et al.*, 2014).

†*Eobrasilia coutoi* Simpson, 1947

(Figure 2)

1947 *Eobrasilia coutoi* Simpson, p. 2, figs. 2–4.

1984 *Eobrasilia coutoi* Marshall, p. 174, figs. 1–2.

1987 *Eobrasilia coutoi* Marshall, p. 100, figs. 10–11.

Emended diagnosis. Differs from other Metatheria in the following combination of characters: two large semi-procumbent lower incisors (i1 and i3); massive and incipiently three-rooted p3 that is much larger than p2, inflated and deep dentary below p3, and narrow and markedly curved anterior part of the dentary.

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

Hypodigm. The type and DGM 919-M, a fragment of a right dentary with alveoli of incisors, canine and p1; complete p2-3 and anterior part of m1.

Occurrence. As for the genus.

Remarks. *Eobrasilia* can be securely identified as a metatherian due to the presence of three premolars and four molars (Simpson, 1947; Paula Couto, 1962; Marshall, 1984, 1987). The dental formula of *Eobrasilia* differs from the one of eutherians, which presents four premolars and three molars. The idea that *Eobrasilia* may represent another mammalian lineage than Metatheria presents no reliable evidence based on current fossil record.

When compared to most of the 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 an evident mesio-distal elongation and one-rooted P1.

PHYLOGENETIC ANALYSIS

The analysis found four most parsimonious trees (trees scores = 2045; CI = 0.3400; HI = 0.6600; RI = 0.6580) (Figure 3). Following the results, *Eobrasilia* is more closely 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), who assigned this taxon to Didelphidae; however, supports Ladevèze & Muizon (2010).

The association between *Eobrasilia* and *Zeusdelphys* as a single taxon (Marshall, 1984) was not supported as the last taxon does not show any of upper dentition synapomorphies of the Stagodontidae, and was recovered as the sister taxon of *Hatcheritherium alpha* Case, Goin & Woodburne, 2005, within Hatcheriformes. Similar affinities for *Zeusdelphys* were found by Carneiro & Oliveira (2017) and Carneiro (2017). This hypothesis, proposed by Marshall (1984), will be commented in detail later.

Pariadens was recovered as closely related to stagodontid, following Cifelli & Eaton (1987), Cifelli (2004), Eaton (1993a), Williamson *et al.* (2012), and Wilson *et al.* (2016), who supported the affinities of this taxon with Stagodontidae. The results refute Fox & Naylor (2006) and Williamson *et al.* (2014), who considered this taxon as not closely related to Stagodontidae.

The Turonian stagodontids *Hoodooetherium* and

Fumodelphodon are the sister taxa of *Eodelphis* and (*Eobrasilia* + *Didelphodon*). This result does not support Cohen (2017), who considered *Hoodooetherium* as the sister taxon of *Eodelphis* and *Fumodelphodon* as the sister taxon of *Didelphodon*.

The validity of “*Eobrasiliinae*” was not supported in the analysis, as *Gaylordia* + *Tiulordia* constitutes a monophyletic lineage more closely related to Jaskhadelphyidae Muizon, 1992. *Didelphopsis cabrerai* is more closely related to *Itaboraidelphys camposi* Marshall & Muizon, 1984, both are the sister taxon of *Herpetotherium* Cope, 1873, *Derorhynchus* Paula Couto, 1952, and *Carolopaulacoutoia* (McKenna & Bell, 1997); and *Eobrasilia* is closely related to *Didelphodon*.

The close relation of Pediomyoidea + Stagodontidae supports the validity of Archimetatheria proposed by Szalay (1994) (Figure 3). The Marsupialiformes and Deltatheroida are recovered in the analysis as sister taxa. The Pappotheriidae is the sister taxon of the clade that comprehends Marsupialiformes and Deltatheroida. These three lineages represent the mammalian Infraclass Metatheria (see Figure 3).

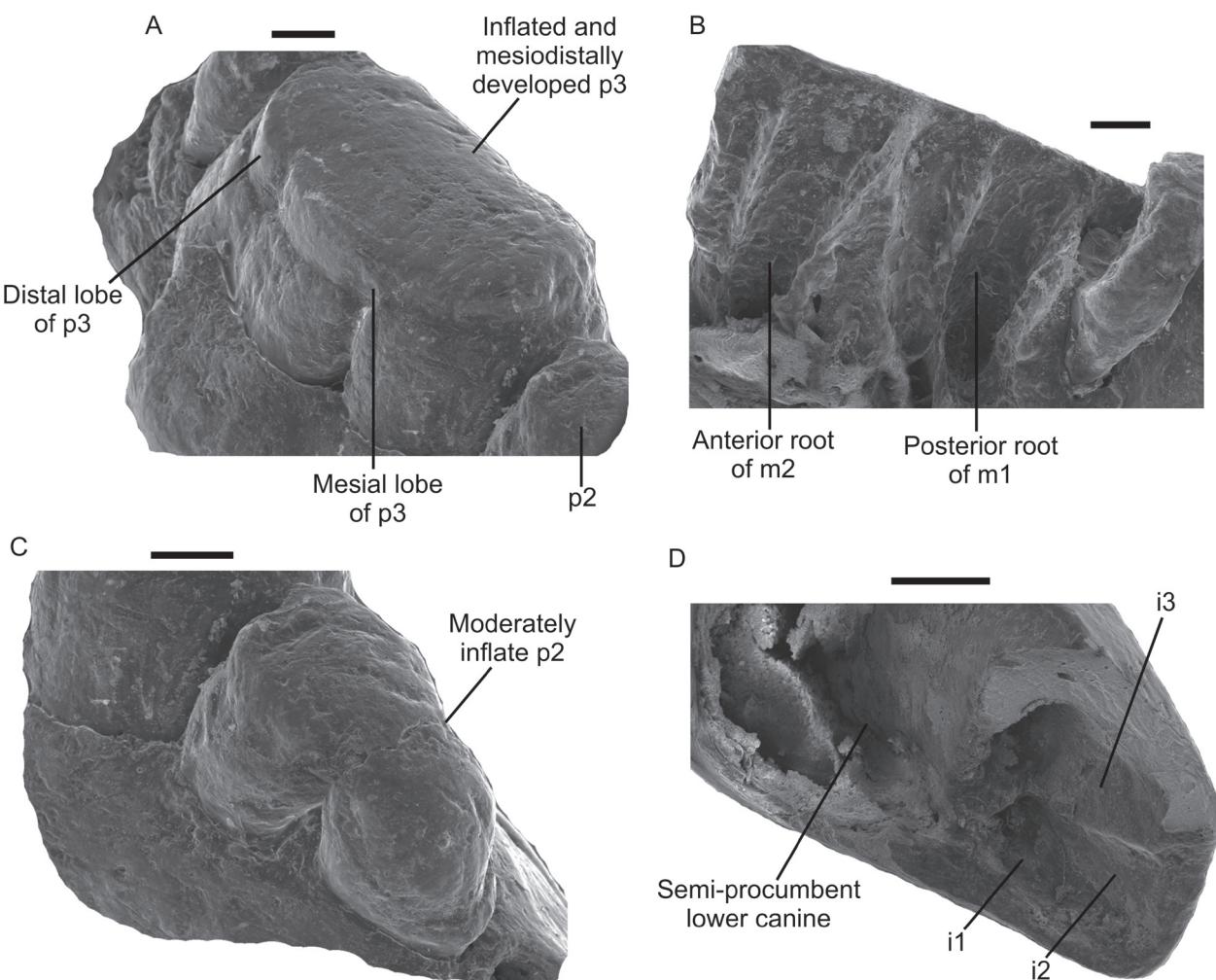


Figure 2. SEM photographies of the preserved dentary of *Eobrasilia* (DGM 919-M). **A**, p3 in antero-lingual view; **B**, alveoli of m1 roots, with partially preserved paraconid of the right m1, and alveoli of m2 anterior root; **C**, p2 in antero-lingual view showing the lingual flexid; **D**, incisors and canine alveoli. Scale bars = 1 mm.

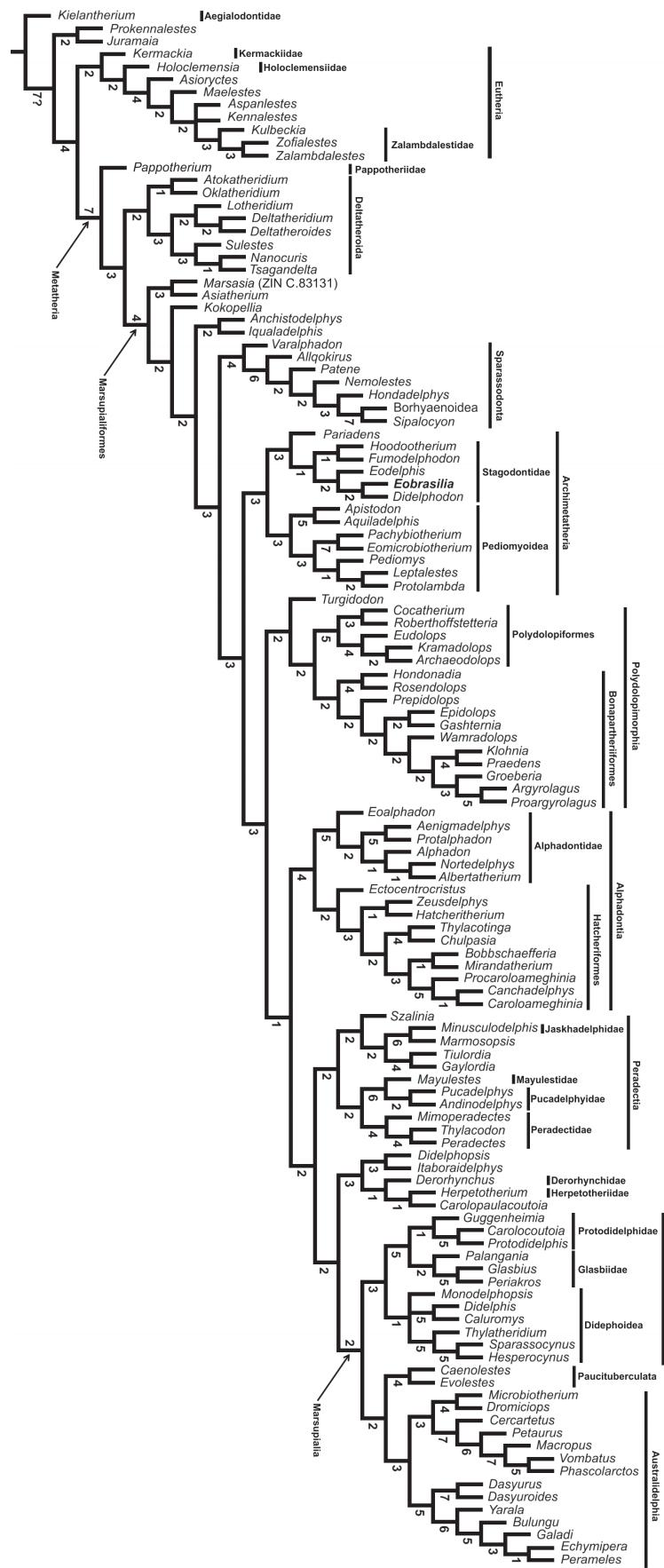


Figure 3. Result of phylogenetic analysis. Strict consensus tree of the four most parsimonious trees found in the analysis. The metatherian lineages are identified by vertical bars. Numbers below the branches indicate the Bremer Support.

DENTAL HOMOLOGIES

Morphology of first premolar

The presence of a single-rooted P1 was identified in *Didelphodon vorax* and *Eobrasilia coutoi* (Figure 4). A preserved maxilla assigned to *Eodelphis browni* presents a two-rooted P1 (Fox & Naylor, 2006), unlike *Didelphodon vorax* (Lofgren, 1992) and *Eobrasilia coutoi* (Marshall, 1984, 1987) (Figure 4). Other North and South American taxa such *Pucadelphys*, *Herpetotherium*, *Didelphopsis*, Sparassodonta, *Roberthoffstetteria*, *Mimoperadectes*, *Szalinia*, *Gaylordia macrocynodonta*, and almost all South American Marsupialia Illiger, 1811, also present a two-rooted P1.

Some Deltatheroida (e.g. *Lotheridium*) and Australidelphia also present a single-rooted P1. The similar condition between *Eobrasilia* + *Didelphodon*, Australidelphia and Deltatheroida is recovered in the phylogenetic analysis as result of independent origins (*i.e.* convergent evolution). Following the analysis, this condition shows a significant level of homoplasy among Metatheria; nevertheless, the one-rooted P1 was recovered by the analysis as valid evidence for the grouping of *Eobrasilia* + *Didelphodon*.

The P1 of Stagodontidae is minute when compared to P2 or P3 and is obliquely orientated with respect to the dental row axis. *Eodelphis*, *Didelphodon*, *Eobrasilia*, *Didelphopsis* and *Lotheridium* show that the anterior root of this tooth is 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) (Figure 4). The minute P1 of *Eobrasilia*, *Eodelphis* and *Didelphodon* are in contact with the canine and P2, a condition absent in *Gaylordia*, *Didelphopsis* and *Lotheridium*, as the P1 is evidently separated from P2 (*i.e.* these teeth are not in contact, Figures 5, 6).

The P1 of *Eobrasilia* presents two accessory cusps anteriorly and posteriorly placed to its main cusp (see Simpson, 1947); morphology also found in *Eodelphis* and *Didelphodon* (Figure 4). These cusps are developed and visible even in worn teeth. The P1 of *Didelphopsis* (Paula Couto, 1962), *Gaylordia* (Oliveira & Goin, 2015), *Szalinia* (Muizon & Cifelli, 2001), *Herpetotherium* (Fox, 1983), *Acyon* (Forasiepi *et al.*, 2006), *Roberthoffstetteria* (Muizon, 1992) and *Lotheridium* (Bi *et al.*, 2015) do not present developed anterior and posterior cusps. Similar accessory cusps are also present on the upper premolars of Didelphidae and Sparassocynidae (Reig *et al.*, 1987); however, the phylogenetic analysis did not recover these morphologies as homologous (228:1).

A partially preserved maxilla of *Didelphopsis cabrerai* (MN 2884-V) presents a minute, obliquely placed and two-rooted P1, with a better developed P2 and a much larger P3 (based on preserved alveoli) (Figure 5). The P1 of *D. cabrerai* is separated from P2 by a developed and visible space between P1 and P2 (these spaces between the premolars are identified in this study as retro-premolar spaces), which differs from the characteristic pattern present in Stagodontidae (Figures 4, 5). The partially preserved skull of *Gaylordia macrocynodonta* (DGM 329-M) also presents a minute and two-rooted P1, but

differs from *Didelphopsis* and Stagodontidae, in having the P1 aligned in the same axis as the P2 and P3. The P1 of *Gaylordia* shows a similar morphology to the P1 of *Didelphopsis*, as both present a developed retro-premolar space separating P1 and P2 (Figure 5).

The Tiupampian *Roberthoffstetteria nationalgeographic* presents a better developed P3 compared to P1–2, a premolar series with all premolars closely spaced and nearly in contact, and an slightly oblique oriented P1 (Muizon, 1992). However, this species differs from Stagodontidae in the relatively larger size of P1 and relatively lesser inflation and development of the P3 (Figure 6). This taxon was recovered as closely related to Polydolopidae (Goin *et al.*, 2003; Chornogubsky & Goin, 2015).

Malleodectes mirabilis Arena *et al.*, 2011, presents a reduced P1 comparing to P2–3 as in referred South and North American taxa (Arena *et al.*, 2011; Archer *et al.*, 2016). Nevertheless, the pattern of its upper premolars is divergent from the one present in American taxa. The P1 is two-rooted, poorly developed, but not as vestigial as in Stagodontidae, aligned with dental row axis and separated by a small retro-premolar space from P2 (Arena *et al.*, 2011; Archer *et al.*, 2016) (Figure 6). Its morphology is more similar to *Gaylordia*. *Malleodectes* represents an independent evolutionary event of its lineage in Australia, not directly linked to any South American taxa, including *Gaylordia*. This conclusion is supported by Archer *et al.* (2016), who described new materials assigned to this taxon, grouping it in the family Malleodectidae, within Dasyuromorpha Gill, 1872.

Despite the presence of an oblique oriented and single-rooted P1 in *Lotheridium mengi* (Bi *et al.*, 2015), this taxon does not show any inflation of the premolars, present a visible retro-premolar space separating P1 from P2, and undoubtedly differs from Marsupialiformes based on its dental morphology. The P1 is relatively larger than the one of Stagodontidae, *Gaylordia*, *Didelphopsis* and *Malleodectes* (Figure 6).

The phylogenetic analysis demonstrated that a single-rooted, obliquely oriented and tiny P1, independently evolved several times in the evolution of Metatheria, probably as an adaptation to durophagous diet. Nevertheless, the stagodontids are the only metatherians that present a tiny P1, obliquely oriented, closely spaced to remaining premolars (with no developed retro-premolars space), with two accessory cusps, and associated with large, but not plagiulacloid third premolars.

The phylogenetic analysis recovered the obliquely oriented, one-rooted, tiny and closely spaced P1 compressed between the canine and P2, as evidences for the grouping of *Eobrasilia* within Stagodontidae (229:1, 230:1, 231:1 and 232:1, respectively). The same result was recovered for the accessory cusps of P1 (228:1).

The p1 of *Didelphodon*, *Eodelphis* and *Eobrasilia* is two-rooted, as remaining metatherians (Scott & Fox, 2015); however, these three taxa differ from other metatherians as they show the anterior root of p1 lingually positioned to the canine (Figure 7). *Lotheridium* shows an oblique p1, but the anterior root is labially positioned to the canine and the canine and p1 are not in contact, indicating a non-homologous

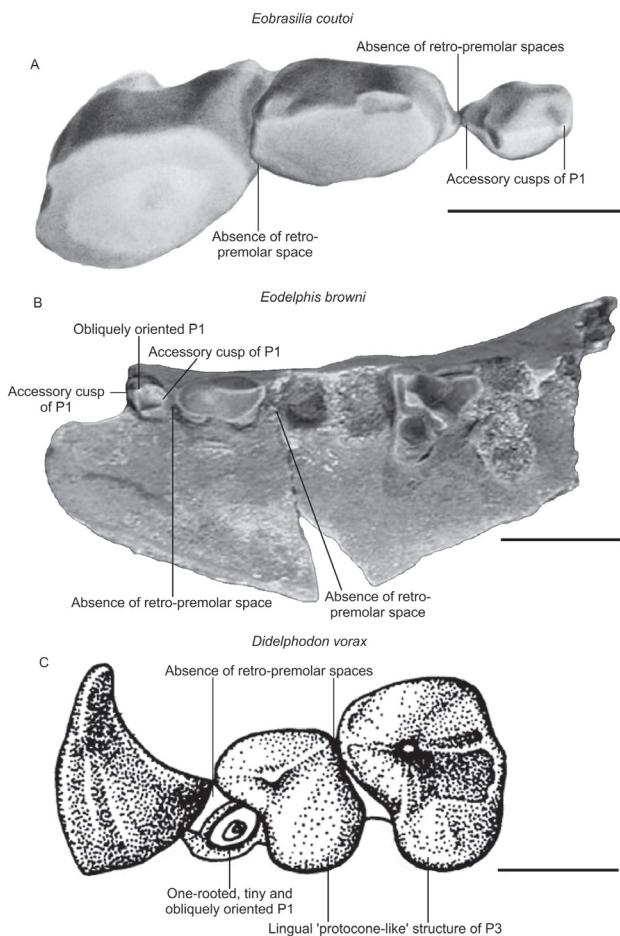


Figure 4. Upper premolars comparative morphology of Stagodontidae taxa. **A**, AMNH 39424 (type) of *Eobrasilia coutoi*, with right P1–3, adapted from Marshall (1984, p. 174, fig. 1); **B**, TMP 1985.053.0003, incomplete left maxilla of *Eodelphis browni*, with incomplete P1–2, M1 and alveoli for C, P3 and M2, adapted from Scott & Fox (2015, p. 686, fig. 3); **C**, UCMP 134795, reconstruction of edentulous left maxilla fragment of *Didelphodon vorax*, adapted from Lofgren (1992, p. 163, fig. 1). Scale bars = 5 mm.

condition to Stagodontidae. The lingual positioning of the anterior root of p1 to the canine can be considered as synapomorphy of Stagodontidae (233:1).

Morphology of the second and third premolars

The morphology of P2 and P3 in *Eobrasilia*, *Didelphopsis*, *Eodelphis*, *Gaylordia*, *Didelphodon* and *Malleodectes* are divergent for the condition present in remaining metatherians: the second and third premolars are very large and inflated, growing as large as or even larger than upper and lower molars (Figures 4–7). The presence of this pattern is an evidence for durophagous habits among these taxa (Fox & Naylor, 2006; Arena *et al.*, 2011; Scott & Fox, 2015; Archer *et al.*, 2016). Aside from this resemblance, these teeth present diagnostic morphologies that represent independent acquisitions for them.

Gaylordia presents a bulbous P3 that is much more massive than P2, but this pattern is not true for the lower dentition,

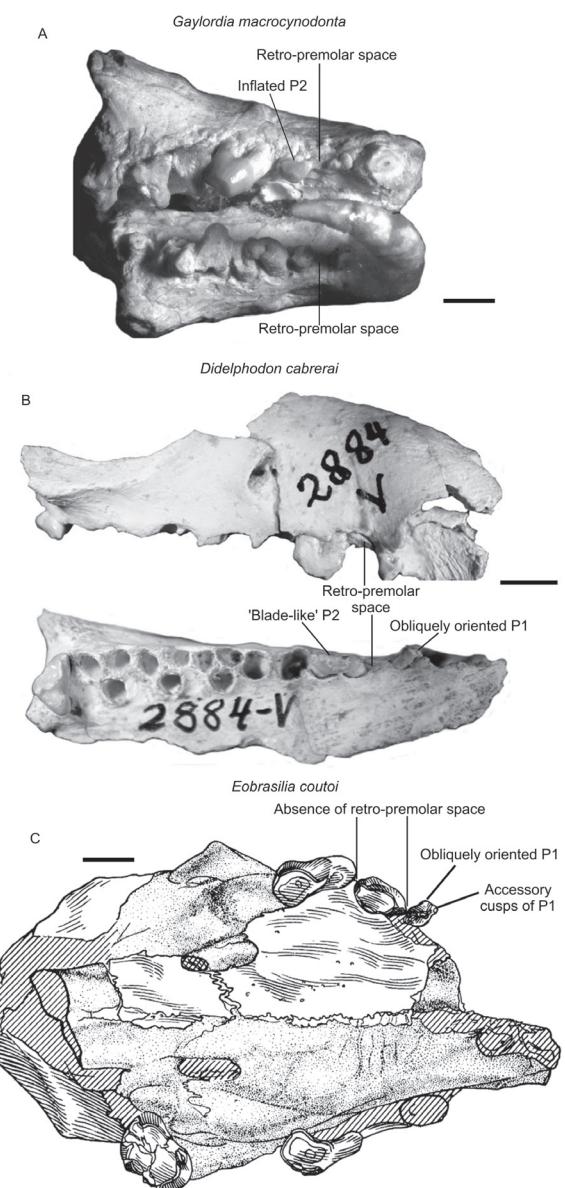


Figure 5. Comparative morphology of "Eobrasiliinae" upper premolars. **A**, DGM 329-M, partial skull of *Gaylordia macrocynodonta* in palatal view, adapted from Oliveira & Goin (2015, p. 100, fig. 2); **B**, MN 2884-V, right maxilla of *Didelphopsis cabrerai* with preserved p1, p2 and m4 in labial (superior) and occlusal (below) views; **C**, AMNH 39424, incomplete facial part of skull of *Eobrasilia coutoi* adapted from Simpson (1947, p. 5, fig. 2). Scale bars = 1 mm.

as the second lower molar is only slightly less inflated and smaller than the third (Figure 8). In upper premolars, the P3 is inflated and rounded, but the P2 still retains a mesiodistal elongation and is not as inflated as the P3. The first premolars are evidently less developed and less inflated than the second premolars (Figure 5). This reduction in the size of P1 is not as evident as the one present in *Eobrasilia*, *Didelphodon* and *Eodelphis*, in which the first premolars are strikingly smaller than the second or the third premolars.

In *Didelphopsis*, the third premolars are strikingly larger and more inflated than the second premolars, which present a

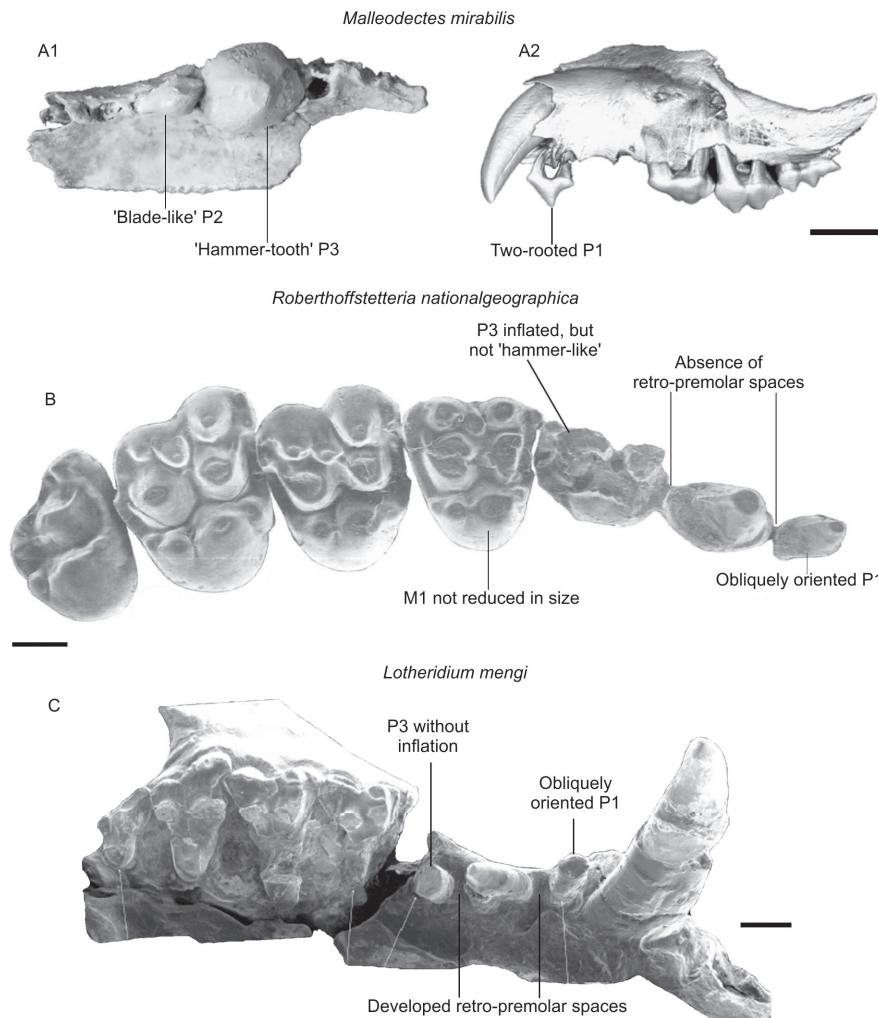


Figure 6. Upper premolars of *Malleodectes*, *Roberthoffstetteria* and *Lotheridium*. **A1**, QM F50847 (type), left maxillary fragment with P2–3 and alveoli of C–M2 of *Malleodectes mirabilis*, adapted from Archer et al. (2016, p. 4, fig. 4); **A2**, QM F57925, left maxilla with P1, DP3, M1–2 and alveoli of P2 of *Malleodectes mirabilis*, adapted from Archer et al. (2016, p. 4, fig. 4); **B**, MNHN Vil 99 (type), right maxilla with P1–M4 of *Roberthoffstetteria nationalgeographica*, adapted from Muizon (1992, p. 581, fig. 2); **C**, ZMHM M9032, upper canine, premolars and molars of *Lotheridium mengi*, adapted from Bi et al. (2015, p. 6, fig. 4). **Abbreviations:** **M1**, first upper molar; **P1**, first upper premolar; **P2**, second upper premolar; **P3**, third upper premolar. Scale bars: A1–2 = 5 mm; B = 1 mm; C = 2 mm.

more labiolingually compressed morphology and an incipient inflation. The second upper and lower premolars are more “blade-like” than the ones of *Gaylordia* (Oliveira & Goin, 2015).

The Australian *Malleodectes* presents a poorly inflated P2 closely spaced to P3 (Arena et al., 2011; Archer et al., 2016). The P3 is rounded, massive and much more developed than the remaining teeth. This condition is quite similar to *Gaylordia* and *Didelphopsis*. These taxa present a “dome-like” P3 and a “blade-like” P2. *Malleodectes* differs from them in the presence of incipiently three-rooted P3 (Figure 6).

Eobrasilia resembles *Eodelphis* and *Didelphodon* in the larger size of the third premolars in comparison with the second ones (Figures 4, 7). The inflation of second premolars in stagodontids varies from species to species: *Eodelphis cutleri* shows “blade-like” or slightly inflated second upper and lower premolars, which differs from *E. browni* that presents a slightly more inflated condition. *Didelphodon*

coyi and *D. vorax* present an evident inflation of the second premolars. Among the species of *Didelphodon*, *D. vorax* shows the greatest degree of inflation of p2 in comparison with any other metatherian, an autapomorphy of this species. The p2 of *Eobrasilia* is twice the size of p1 (see Marshall, 1984), and is heavily worn. Judging by the size and outline, this tooth is more inflated than the one of *Eodelphis browni*, but less inflated than the one of *Didelphodon*.

The p3 of *Eobrasilia* and *Didelphodon* presents an evident mesio-distal elongation, a unique morphology among Metatheria (Figures 2, 7). Scott & Fox (2015) describe this morphology as an autapomorphy of *Didelphodon*; however, the presence of a similar morphology in *Eobrasilia* was recovered by the analysis as a synapomorphy of *Eobrasilia* + *Didelphodon* (241:1). This character supports the assignment of *Eobrasilia* as a Stagodontidae. *Eobrasilia* differs from *Didelphodon* in the presence of an incipiently three-rooted condition. Marshall (1987) first identified this condition and

it is confirmed in this study. This condition can be identified as an autapomorphy of *Eobrasilia* (see paleoecological implications of incipient three-rooted premolars).

Cohen (2017) recovered *Fumodelphodon* as the sister taxon of *Didelphodon*. However, the absence of a mesiodistally developed p3 in *Fumodelphodon* indicates that this taxon may represent an older divergent lineage than the one of *Eobrasilia* + *Didelphodon* (see the phylogenetic analysis in Figure 3). *Eodelphis*, *Didelphodon* and *Eobrasilia* show a developed distal lobe in third lower premolars, which is absent or incipiently developed in the p3 of *Hoodooetherium* and *Fumodelphodon*. This distal lobe in third lower premolars is recovered as a shared synapomorphy (242:1) of *Eodelphis* and *Didelphodon* + *Eobrasilia*.

The presence of an incipiently three-rooted P3 in *Malleodectes* and *Fumodelphodon*, and in the p3 of *Eobrasilia* can be identified as an adaptation to the ingestion and crushing of harder food resources. Cohen (2017, p. 9) suggested the working hypothesis that the three-rooted condition in *Fumodelphodon* is morphologically and functionally antecedent to that of *Didelphodon*. Nevertheless, the phylogenetic analysis indicates that both morphologies represent independent adaptations to increase durophagy. The presence of an incipiently three-rooted p3 in *Eobrasilia*, three-rooted P3 in *Fumodelphodon* and “the single, expanded distal root in *Didelphodon*” (Cohen, 2017, p. 9) indicates that the stagodontids developed independent morphologies to increase durophagous adaptations.

Didelphodon vorax and *D. coyi* show a lingual projection in P2 and P3. This morphology produces a “protocone-like” structure on the lingual border of the upper premolars in this genus (Figure 4), which probably is an adaptation to increase the crushing of hard food resources. The absence of upper premolars with preserved crowns of *Eobrasilia* does not allow the identification of a “protocone-like” cusp in third upper premolars of this taxon. Based on this, it is not possible to conclude if the presence of a “protocone-like” cusp in upper premolars is an ancestor adaptation of *Eobrasilia* + *Didelphodon* or an adaptation that evolved in *Didelphodon*. The Turonian *Fumodelphodon* shows a “protocone-like” cusp on the lingual border of P3, similar to *Didelphodon*; nevertheless, the phylogenetic analysis recovered this similar adaptation as result of homoplasy.

The inflated third and second lower premolars represent independent acquisitions for *Tiulordia* + *Gaylordia*, *Didelphopsis* and Stagodontidae (240:1), as indicated by the phylogeny (Figure 3). This conclusion is evident by the analysis of the condition present in most basal taxa of each grouping.

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 compared to the former, which represents an autapomorphy of this species. *Gaylordia mater* represents a mosaic condition between the basal *Tiulordia* and the specialized *Gaylordia macrocynodonta* (see Oliveira & Goin, 2015).

The Stagodontidae presents a similar pattern, as *Eodelphis*, *Hoodooetherium* and *Fumodelphodon* present less inflated premolars than *Eobrasilia* and *Didelphodon* (Figure 7). The result is the same for *Didelphopsis cabrerai*, which presents inflated and large third premolars and less inflated second premolars, again indicating an evolutionary tendency for the inflation of the last premolars.

Closely spaced premolars and robust dentary

The absence of retro-premolar spaces separating the lower premolars in the lower dentition and the robust dentary were considered by Marshall (1987) as strong evidences for the grouping of *Eobrasilia*, *Gaylordia*, *Tiulordia*, and *Didelphopsis* within “Eobrasiliinae”. However, other taxa also lack these spaces between the premolars (*e.g.* *Roberhoffstetteria nationalgeographic*, Stagodontidae and some Borhyaenoidea). A robust dentary is also present in other metatherians, such as *Pachybiotherium*, *Protolambda*, *Didelphodon* and *Roberhoffstetteria*.

Interestingly, the presence of these characters is considered as adaptations to durophagy (*e.g.* Stagodontidae), granivory (*e.g.* *Pachybiotherium*), and carnivory (*e.g.* Sparassodonta) (see Zimicz, 2012), as the reduction in the length of dentary represents an adaptation to increase the bite force (Thomason, 1991).

Among Cretaceous North American taxa, the presence of a robust dentary, strong premolars, and an absence of retro-premolar spaces in the upper and lower dentition represent diagnostic features of the Stagodontidae. Regarding South America, the conclusion is not similar as many lineages acquired some degree of durophagy. As previously mentioned the upper dentition of Stagodontidae shows a minute, obliquely placed, and strongly compressed P1, which is placed between the much larger canine and P2. These two premolars are also compressed to an even larger P3 (Figure 4). This absence of retro-premolar spaces between the upper premolars was recovered as an important character for Stagodontidae (232:1), excluding *Tiulordia* + *Gaylordia* and *Didelphopsis* from this lineage, and treating their similarities as result of independent acquisitions (see phylogeny and the previous topic).

The robust dentary and the strong wear pattern can be treated as important evidences for supporting durophagous feeding habits for *Eobrasilia* (see the paleoecology discussion), but these characters on their own could not be considered as strong phylogenetic evidence. Interestingly, the presence of these features in addition to the exclusive morphology and patterns present in the premolar series could be treated as compelling evidence for supporting stagodontid affinities for *Eobrasilia*.

The dentary of *Eobrasilia* shows evident labiolingual inflation around the p3 and its deepest point is below the p3; this morphology is probably a result of the enlarged condition of this tooth. These characters represent the main autapomorphies of *Eobrasilia coutoi* (Figure 7).

The dentary of *Eobrasilia* and *Gaylordia macrocynodonta* show an evident curvature of the anterior portion (Figures 7, 8).

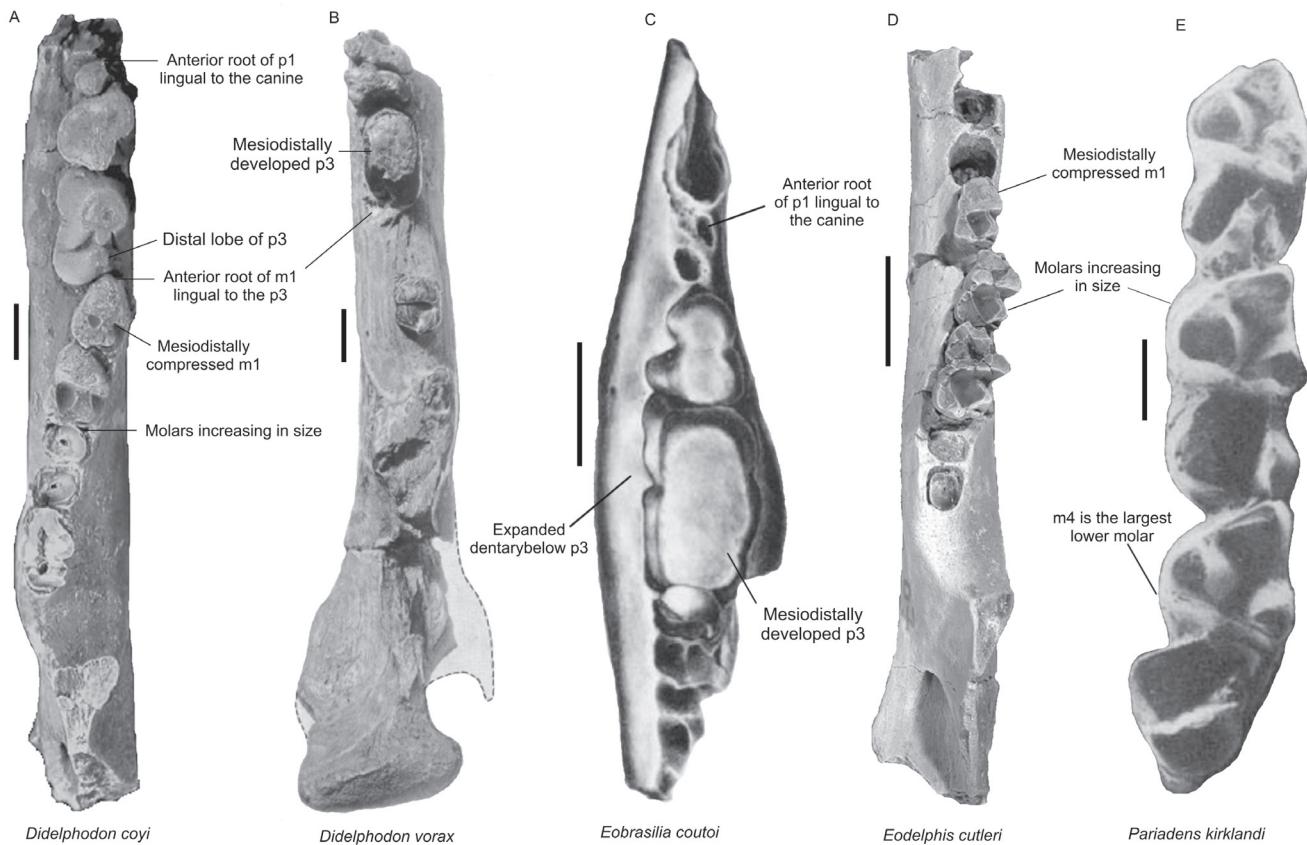


Figure 7. Comparative lower dental morphology of stagodontids. **A**, TMP 91.161.1, incomplete right dentary of *Didelphodon coyi* in occlusal view with p1–m2 and roots of m3 and m4, adapted from Fox & Naylor (2006, p. 17, fig. 1); **B**, AMNH 3013, incomplete dentary of *Didelphodon vorax* with preserved p2, p3, m3 and posterior root of m4 in occlusal view, adapted from Matthew (1916, pl. 5, fig. 1); **C**, DGM 919-M, incomplete dentary of *Eobrasilia coutoi* with p2, p3, anterior root of m1 and alveoli for m2, p1, C and lower incisors, modified from Marshall (1964, p. 174, fig. 2); **D**, TMP 2002.012.0007, incomplete right dentary of *Eodelphis* sp., cf. *E. cutleri* with m1–3 and alveoli for p3 and m4 in occlusal view, adapted from Scott & Fox (2015, p. 692, fig. 8); **E**, UCM 54155 (type), part of left mandibular ramus preserving the last three molars m2–4 of *Pariadens kirklandi*, adapted from Cifelli & Eaton (1987, p. 521, fig. 1). Abbreviations: m1, first lower molar; p3, third lower premolar. Scale bars: A–D = 5 mm; E = 1 mm.

Marshall (1987) as evidence of their close relation considered this morphology. However, the phylogenetic analysis recovered this morphology as independent acquisitions for *Gaylordia* and *Eobrasilia*, constituting a convergent adaptation probably for more durophagous diets (258:1).

Eobrasilia differs from *Eodelphis* and *Didelphodon* by the strong curved condition of the anterior half of its dentary (Figure 8). Marshall (1987) compared the dentary of *Eobrasilia* with the one of *Didelphopsis* and *Gaylordia*: “The mandibular rami in *Didelphopsis* and *Gaylordia* are robust anteriorly, while in *Eobrasilia* the anterior part is narrow...” (Marshall, 1987, p. 133). A narrow anterior part of the dentary is also present in *Eodelphis* (Figure 8), but not as narrow and curved as in *Eobrasilia*.

Didelphodon coyi shows a curvature of the anterior part of the dentary similar to *Eobrasilia*; but they differ in the more robust constitution of this structure in *Didelphodon*. The dentary of *Didelphodon* is more similar to the one of *Gaylordia* and *Didelphopsis* in the more robust constitution and lesser degree of curvature comparing to *Eobrasilia*. *Didelphodon* is autapomorphic by the stronger compression

of the anteriormost portion of the dentary, which strongly compressed the premolars, canine and incisors. The robust anterior part of the dentary is a convergent adaptation between *Didelphopsis*, *Didelphodon* and *Gaylordia* (Figure 8).

Based on the results of the phylogenetic analysis, the curvature of the dentary (258:1) and its robust constitution (259:1) represent independent acquisitions between Stagodontidae, *Gaylordia*, and *Didelphopsis* (Figure 3).

Large size, mesiodistal compression of m1 and increasing in lower molar series

Eobrasilia is considered as one of the largest metatherians from Itaboraí, being only slightly smaller than *Zeusdelphys complicatus* (based on upper or lower molars linear size). The large size of *Eobrasilia* and *Zeusdelphys* could indicate a compatible occlusal relation between the upper and lower teeth, as proposed by Marshall (1987). The type 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).

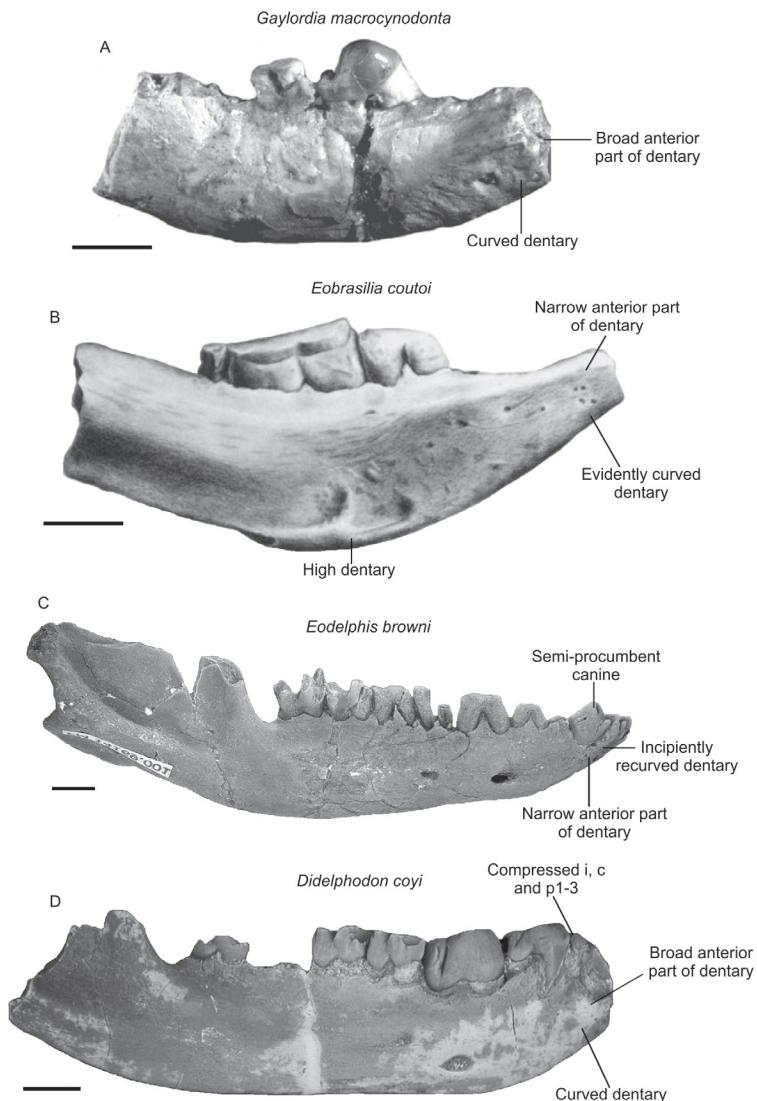


Figure 8. Comparative dentary morphology of “Eobrasiliinae” and Stagodontidae. **A**, DGM 329-M (type), incomplete dentary with p3 and worn m1 of *Gaylordia macrocynodonta*, adapted from Oliveira & Goin (2015, p. 101, fig. 3); **B**, DGM 919-M, incomplete dentary of *Eobrasilia coutoi* with p2, p3, anterior root of m1 and alveoli for m2, p1, C and lower incisors, modified from Marshall (1964, p. 174, fig. 2); **C**, AMNH 14169, incomplete left dentary with i1–3, C, p1–3, m2–4 and roots of m1 of *Eodelphis browni*, adapted from Scott & Fox (2015, p. 685, fig. 2); **D**, TMP 91.161.1, incomplete dentary with i2–3, C, p1–3, m1–4 of *Didelphodon coyi*, modified from Fox & Naylor (2006, p. 21, fig. 2). Abbreviations: **i**, incisor; **c**, canine; **p1**, first lower premolar; **p2**, second lower premolar. Scales bars: A = 2 mm; B–D = 5 mm.

The M1 of *Zeusdelphys* cannot be considered as the M1 of *Eobrasilia* based on its relative size: this tooth reaches 8.30 mm in length and 8.47 mm in width (Oliveira & Goin, 2011); this size is considerably larger than the one preserved in the alveoli of m1 of DGM 919-M (5.5 mm in length). The evident difference in size between the first molar of *Zeusdelphys* and *Eobrasilia* indicates that this occlusal relationship is not possible. In addition, *Zeusdelphys* does not present stagodontid upper molar synapomorphies, being recovered in the phylogenetic analysis as a hatcheriform, supporting Carneiro & Oliveira (2017).

The m1 of *Eobrasilia* is smaller than the m2 (based on preserved alveoli) (Figure 2). Similar condition is also recognizable in the skull and dentary of *Didelphodon vorax*,

which presents an M1 much smaller than M2 (Wilson *et al.*, 2016), and a strongly mesiodistally compressed m1 (Matthew, 1916; Clemens, 1966). *Didelphodon coyi* shows a relatively lesser mesiodistal compression of m1 (Fox & Naylor, 1986, 2006). The relative size between m1 and m2 in *Eobrasilia* is more similar to the one of *Didelphodon coyi*. The m1 of *Eodelphis browni* is slightly smaller than m2, but the one of *E. cutleri* is more mesiodistally compressed (Figure 7). *Didelphodon* is autapomorphic by the lingual positioning of the anterior root of m1 to p3 (Fox & Naylor, 1986; Scott & Fox, 2015).

The m1 is not known for the type specimen of *Pariadens* (UCM 54155); however, the specimen MNA V5842 found in Naturita Formation (upper Cenomanian, southwestern

Utah, Carpenter, 2014) is smaller than remaining molars. Eaton (1993a), which indicates the presence of a smaller m1 than m2, m3 or m4 in *Pariadens* identified this specimen as an m1. The Stagodontidae, presents the m1 as the smallest molar due to a mesio-distal compression, which was recovered as a synapomorphy of Stagodontidae (156:1). The m1 of *Pariadens* is smaller than remaining molars, but is not mesio-distally compressed, which supports its exclusion of Stagodontidae. Eaton (1993a) discussed the affinities of *Pariadens* and suggested that this taxon may be more appropriately placed in a new family.

The Stagodontidae shows an increase in size through the lower molar series, with the m4 being the largest tooth. *Pariadens* presents the same pattern. An m4 larger than m3 is also present in some Borhyaenoidea (Forasiepi *et al.*, 2014), but the phylogenetic analysis recovered this adaptation as separate independent acquisitions. This character was recovered as a synapomorphy of *Pariadens* + Stagodontidae (224:1).

The stagodontids *Eodelphis* and *Didelphodon* were the largest metatherians during the Late Cretaceous in North America (Fox & Naylor, 2006; 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. It is important to comment that the shared large size by its own could not be recovered as a strong systematic character (reason why this character is not included in the morphological matrix, as its use could result in a long and unnecessary discussion regarding this study). Nevertheless, the association of this feature with the results of the phylogenetic analysis endorses the grouping of *Eobrasilia* within Stagodontidae.

Gaylordia is considered one of the smallest species of Itaboraí, along with *Minuscudelphis* and *Marmosopsis* (Oliveira & Goin, 2015; Oliveira *et al.*, 2016). In fact, the smaller size seems to be an evolutionary tendency of this group. This evidence undoubtedly differs from the condition present in *Eobrasilia*, as it is one of the largest species of metatherians of 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 1).

Semi-procumbent lower incisors and canines

Fox & Naylor (2006) discussed the presence of semi-procumbent lower incisors in *Didelphodon*. *Eodelphis* present three unequally sized lower incisors, with the second (i2) much larger than i1 and i3. The presence of a staggered condition of i2 in *Eodelphis* is not clear, as it seems that the enlargement and “semi-procumbence” of i2 create 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).

In the dentary of *Eobrasilia* (DGM 919-M) there are alveoli for three lower incisors (Figure 2). Marshall (1984)

described *Eobrasilia* as presenting two large and 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. The examination of DGM 919-M finds no evidence of a fourth lower incisor alveolus. In fact, the two lingual most alveoli of i1 and i3 are easily identifiable, but the i2 is barely seen. As described by Marshall (1984) these teeth show, along with the canine, some degree of procumbence. In *Eobrasilia* the i2 is a compressed lower incisor, with its apparently “staggered” condition being a result of the extreme degree of procumbence of i1 and i3 that compressed the referred tooth in the middle, creating the false impression that it is “staggered”. This hypothesis is confirmed by the study of the alveoli morphology of *Didelphodon 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).

Semi-procumbent lower incisors are absent in Pucadelphyidae, Peradectidae, Didelphidae, *Marmosopsis*, Sparassodonta, and Microbiotheriidae. Oliveira & Goin (2012) proposed 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 its condition is strikingly divergent from the one present in Stagodontidae, as *Herpetotherium* shows small and slightly procumbent i1, and i2 that are slightly larger and more procumbent than i3 and i4. In addition, *Herpetotherium* shows four alveoli, while *Eobrasilia* shows only three. Protodidelphidae does not show an evident procumbence of lower incisors, which diverge from the condition present in *Eobrasilia*.

The skull of *Didelphodon vorax* (see Wilson *et al.*, 2016) presents semi-procumbent first incisors (I1), which are evidently better developed than the remaining ones (Figure 5). This morphology could not be recovered for *Eobrasilia*, as the type and only known skull does not preserve the upper incisors. Nevertheless, the presence of upper semi-procumbent incisors in *D. vorax* supports this morphology as a valid feature for Stagodontidae. The skull of *Didelphodon* and *Eobrasilia* share the presence of developed palatine foramina, differing in relative size. *Eobrasilia* presents less developed foramina than *Didelphodon*. The reduction of these foramina could be interpreted as an apomorphy of *Eobrasilia* based on the current fossil record.

The lower canines of *Eodelphis browni* and *Eobrasilia coutoi* are evidently semi-procumbent (Figures 2, 8) and markedly larger in comparison with any of the living Didelphidae. Marshall (1984) described the canine of *Eobrasilia* as inclined anteriorly; a similar morphology is present in *Eodelphis* (Scott & Fox, 2015). The canines of *Didelphodon* are less anteriorly procumbent, being more “erect”.

In short, the morphology of the lower incisors and canines of *Eobrasilia* resemble the one present in North American stagodontids. The procumbence of lower incisors can be considered as an evolutionary tendency among this family, as all taxa show some degree of procumbence. The semi-

Table 1. Premolars and dentary characters shared between *Eobrasilia* and other metatherians. The ‘X’ indicates presence of the character; ‘?’ indicates unknown condition for the character; and blank spaces indicate absence of the character. *Eobrasilia* shares few similarities with *Gaylordia* and *Didelphopsis*, while it shares almost all characters with Stagodontidae. These characters show a highly level of homoplasy, however, most of these features are shared only by *Eobrasilia* and Stagodontidae.

Character/Taxon	<i>Eobrasilia</i>	Stagodontidae	<i>Lotheridium</i>	<i>Didelphopsis</i>	<i>Gaylordia</i>	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, P2 and P3	X	X				
Anterior root of p1 lingual to the canine	X	X				
Mesio-distal development of p3	X	X				
Mesio-distal compression of m1	X	X				
Large size	X	X		X		X
Inflated and large third and/or second premolars	X	X		X	X	
Semi-procumbent canines	X	X				
Semi-procumbent incisors	X	X			?	
Robust dentary	X	X	X	X	X	X
Recurved dentary	X					X

procumbent lower incisors and canines, and the narrow dentary represent retained plesiomorphies for Stagodontidae. The semi-procumbence of lower incisors is not an evidence of herpetotheriid affinities for *Eobrasilia* based on the different pattern regarding the size, number and degree of semi-procumbence of the lower incisors.

Systematic implications for *Eobrasilia* and “Eobrasiliinae”

Eobrasilia shares several characters that are recovered as synapomorphies of Stagodontidae: anterior root of p1 lingual to the lower canine, mesiodistal development of the p3, semi-procumbent and enlarged lower incisors, mesiodistal compression of m1, absence of retro-premolar spaces in upper and lower dentition and accessory cusps in P1. Despite the absence of preserved molars of this species, the combination of characters supports the assignment of *Eobrasilia* as a Stagodontidae.

The hypothesis that *Eobrasilia* represents an “aberrant” lineage of South America is not supported in the analysis based on the following evidences: (i) the affinities of *Eobrasilia* were tested along with Eutheria, Pappotheriidae, Deltatheroida, Sparassodonta, Stagodontidae, Pediomyoidea, “Alphadontidae”, Hatcheriformes, Polydolopimorpha, Peradectidae, Pucadelphyidae, Mayulestidae, Jaskhadelphyidae, Herpetotheriidae, Derorhynchidae, Didelphoidea, Protodidelphidae, Glasbiidae, Paucituberculata, Australidelphia, and several *incertae sedis* taxa. The phylogenetic analysis provides the largest morphological dataset ever published in literature; (ii) the great number of similar and unique adaptations between *Eobrasilia* and North American stagodontids is an important evidence, as no other metatherian lineage presents the anterior root of p1 lingual

to the canine or the p3 mesiodistally developed, for example; (iii) several previous studies proposed a North American origin for South American metatherians (discussed below), including Carneiro & Oliveira (2017) and Carneiro (2017), who discussed the North American origin and dispersal of Hatcheriformes and Sparassodonta, respectively, to South America. Based on these studies, the presence of stagodontids in South America should not be discarded *a priori*.

The discovery of new specimens of *Eobrasilia* should help the discussion about the affinities of this taxon; nevertheless, the great number of shared synapomorphies and the absence of diagnostic traits of other metatherian lineages support, with some reliability, the assignment of *Eobrasilia* to Stagodontidae. Until the discovery of new specimens, the taxonomical hypothesis of stagodontid affinities for *Eobrasilia* represents the most parsimonious explanation.

The “Eobrasiliinae” is not supported, as it was erected based on convergent durophagous adaptations between three independent metatherian lineages: *Gaylordia* + *Tiulordia*, *Didelphopsis* + *Itaboraidelphys* and Stagodontidae (Figure 3). Based on this, “Eobrasiliinae” has no systematic validity.

PALEOBIOGEOGRAPHIC AND PALEOECOLOGICAL IMPLICATIONS

Paleobiogeography of Stagodontidae

The consideration of *Eobrasilia coutoi* as a stagodontid increases the paleobiogeographic and temporal range of this family. Previously considered extinct in North America after the Late Cretaceous–Paleogene mass extinction (around 66 Ma, Williamson *et al.*, 2012, 2014; Wilson, 2014), the assignment of *Eobrasilia* to this family evidences an early

Eocene taxon (around 52 Ma, Woodburne *et al.*, 2014), extending the temporal range of this lineage by about 10 million years. These conclusions suggest a North American origin for *Eobrasilia*, with the dichotomy between *Eobrasilia* + *Didelphodon* probably proving to have occurred during the Campanian (Figure 9).

The oldest fossil records of *Didelphodon* are represented by *Didelphodon coyi* from the Judithian North American Land Mammal Age (NALMA, late Campanian) (Fox, 1981; Scott & Fox, 2015). The discovery of an isolated tooth assigned to *Eodelphis* dated from the Santonian (Aquilan NALMA) from the upper part of John Henry Member of Straight Cliffs Formation, Utah, USA, indicates that the lineage of *Didelphodon* + *Eobrasilia* already existed during the Aquilan NALMA. If the dichotomy between *Didelphodon* and *Eobrasilia* happened during the early Campanian, then the lineage of the Brazilian taxon independently evolved for more than 20 million years prior to the appearance of *Eobrasilia* in the Itaboraí Basin during the early Eocene (Woodburne *et al.*, 2014).

The recovered timespan for the independent evolution between *Eobrasilia* and *Didelphodon* can be considered as plausible evidence for explaining the great number of autapomorphies separating these two taxa: *Eobrasilia* retained the semi-procumbent lower canines and the narrow anterior part of the dentary, considered by the analysis as stagodontid plesiomorphies, while *Didelphodon* is apomorphic for these characters. *Didelphodon* is plesiomorphic in the presence of two-rooted p3 and not inflated dentary, which are three-rooted and inflated in *Eobrasilia* (autapomorphies of this species). However, despite the presence of these autapomorphies, both taxa share a great number of synapomorphies, supporting their monophyletic origin. Unfortunately, there are no confirmed metatherian fossil records during the Late Cretaceous of South

America, and *Eobrasilia* is restricted to the early Eocene of Itaboraí Basin. This long ‘ghost-lineage’ between the first fossil record of *Didelphodon* and *Eobrasilia* may explain the number of morphological differences between them.

Regarding the probable dispersal route between North and South America, the ‘Aves Ridge’ and adjacent Cuba were indicated as the best pathway candidates for the dispersal route between both landmasses (Bonaparte, 1984; Woodburne & Case, 1996; Case *et al.*, 2005; Pascual, 2006; Pascual & Ortiz-Jaureguizar, 2007; Goin *et al.*, 2016; Carneiro & Oliveira, 2017). The volcanic activity during the Late Cretaceous (Pindell, 1994) associated with strong sea-level lowstands during the late Campanian (around 73 Ma) and the late Maastrichtian (around 66 Ma) (Eaton, 1993b; Haq, 2014; Carneiro & Oliveira, 2017; Carneiro, 2017) probably allowed a sweepstakes dispersal pattern for them; with a hopping-island model as the best model for their dispersal. The marine regressions associated with intense volcanic activity probably created temporary land pathways between isolated islands until their arrival in South America.

In North America, Stagodontidae is considered as a rare group in any given local fauna (Scott & Fox, 2015). *Eobrasilia* follows the group pattern, as only a partially preserved skull and a partially preserved dentary are the only elements confidently assigned to this taxon, which identifies this species as one of the rarest taxa of Itaboraí. The diagnostic and extreme adaptations of Stagodontidae undoubtedly associate their feeding habits to durophagous diets.

Paleoecological implications

In Australia, the extinct *Malleodectes* had its ‘hammer-tooth’ P3 associated with a durophagous diet (Arena *et al.*, 2011; Archer *et al.*, 2016). This conclusion can also be inferred for *Eobrasilia*, *Gaylordia* and *Didelphopsis*, as these species

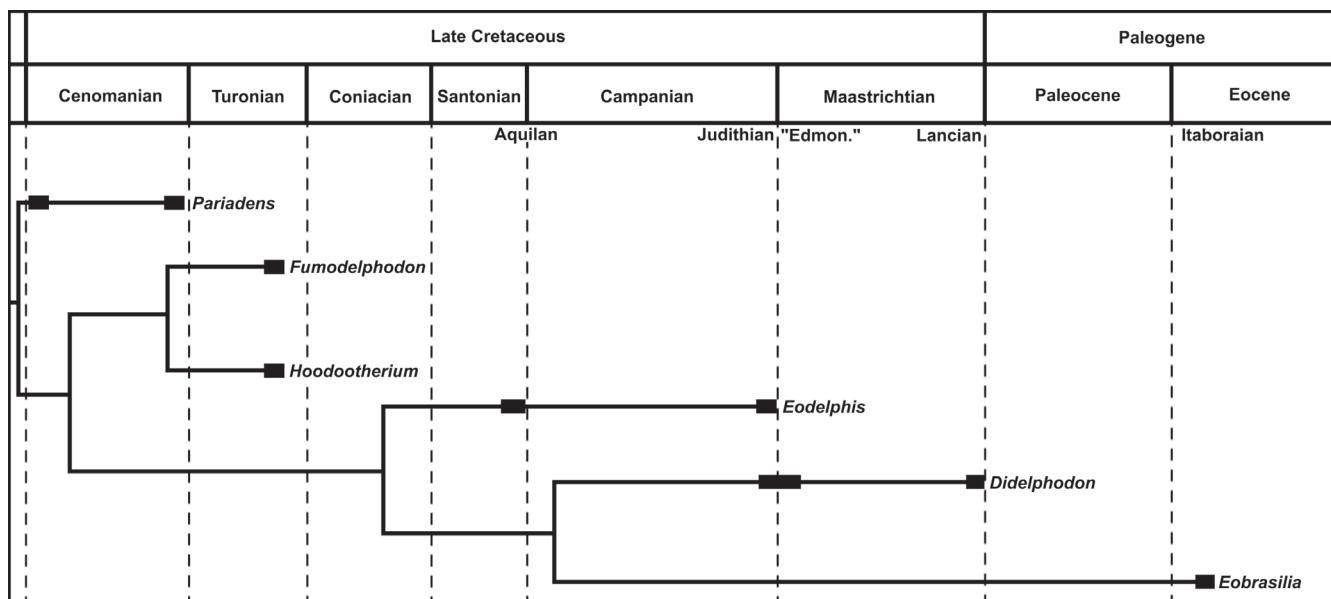


Figure 9. Temporal and geographical distribution of Stagodontidae. Phylogeny of Stagodontidae calibrated in time, based on the phylogeny present in the Figure 3. The wide bars indicate the recorded temporal range of stagodontids genera. The NALMAs and SALMAs that present stagodontids are identified.

show similar adaptations to *Malleodectes* (Figure 6). Herein, the same method and explanation used by Arena *et al.* (2011) and Archer *et al.* (2016) is followed.

The tiny size of *Gaylordia macrocynodonta* could be an indication of the ingestion of small snail taxa, hard exoskeleton insects or even seeds, which demands durophagous adaptations. The mesiodistal compression of the upper molars, the short rostrum and the robust dentary are adaptations to increase durophagy (Thomason, 1991). The vestigial entoconid and the short talonid are adaptations for increasing carnivory or insectivory (Zimicz, 2012; Oliveira *et al.*, 2016). The mesio-distal compression of the upper molars is also compatible with consume of soft insects or worms, as proposed for *Minusculedelphis* (Oliveira *et al.*, 2016). The presence of a robust protocone, high dentary and inflated premolars in *Gaylordia* indicates the ingestion of harder food items (Oliveira & Goin, 2015) (Figure 8). The tiny size and the durophagous adaptations of *Gaylordia* can be interpreted as indication of a specialized diet.

The results of Zimicz (2012) suggest a more frugivorous diet for *Didelphopsis cabrerai*, a result compatible with the global conditions during the early Eocene (Woodburne *et al.*, 2013, 2014). The presence of inflated molars, large Stylar cusps B and D, inflated and enlarged metaconule, reduction of the paraconule and low ‘U-shaped’ centrocrista are more compatible with frugivory, granivory, or frugivory-durophagy (see Zimicz, 2012) (Figure 8). The presence of similar adaptations in the upper dentition of *Malleodectes*, including the reduction of the centrocrista, inflated Stylar cusps B and D, compressed talon and inflated premolars (see Archer *et al.*, 2016) supports a durophagous diet for *Didelphopsis*. Based on these characters, *Didelphopsis* probably were a frugivorous-durophagous taxon.

The results of Wilson *et al.* (2016) suggest an omnivore diet for *Didelphodon vorax*; following the authors, this taxon probably consumed a range of vertebrate, plant and hard-shelled invertebrate resources but few insects, spiders and annelids (Wilson *et al.*, 2016). The idea that this animal consumed plants is weakly supported, as the enlarged paraconid more typically occurs in carnivorous species (Zimicz, 2012). *Didelphodon* was more likely to be a carnivorous-durophagous taxon than an omnivore one. *Eobrasilia* shows evident durophagous adaptations: thickened and raised palate near the P3, incipient three-rooted p3, mesiodistally developed p3, labiolingually expanded dentary around the p3, curvature of the dentary; tiny and oblique P1 and closely spaced premolars (Simpson, 1947; Marshall, 1984). Most of these characters are also present in *Malleodectes* (Arena *et al.*, 2011; Archer *et al.*, 2016) and *Didelphodon* (Wilson *et al.*, 2016). Based on available evidence, stagodontids should be considered as carnivorous-durophagous taxa, as proposed by Wilson *et al.* (2016) and Cohen (2017). The Turonian *Fumodelphodon* and the late Campanian-Maastrichtian *Didelphodon* independently acquired durophagous adaptations (e.g. “protocone-like” cusp in P3).

The presence of three independent metatherian lineages adapted to specialized durophagous diets in the metatherian assemblage of Itaboraí should be discussed: (i) *Eobrasilia* is one of the largest metatherians of the fauna and probably presented a carnivorous-durophagous diet; (ii) *Didelphopsis* is a relatively large species for Itaboraí standards and probably presented a frugivorous-durophagous diet; (iii) *Gaylordia* is among the smallest taxa of Itaboraí fauna and probably presented a insectivorous-durophagous diet. These differences in preferential food resources and size probably resulted on a low niche overlapping among these taxa, allowing their co-existence.

Similarly, to the conclusions of Arena *et al.* (2011) and Archer *et al.* (2016) for *Malleodectes*, the ingestion of snails should not be discarded for *Eobrasilia*, *Didelphopsis*, and *Gaylordia*.

Based on current fossil record, the reduction in global temperatures and floral replacement after the Early Eocene Climatic Optimum (Woodburne *et al.*, 2013, 2014; Goin *et al.*, 2016), and the specialized durophagous diet of *Eobrasilia*, *Gaylordia* and *Didelphopsis* may explain their apparently extinction after the early Eocene (Itaboraian SALMA, around 52 Ma, Woodburne *et al.*, 2014).

CONCLUSIONS

The presence of several characters and evolutionary tendencies supports the inclusion of *Eobrasilia* within Stagodontidae. This result indicates a North American origin for its lineage, and a Late Cretaceous-early Paleocene dispersal event to South America. This family survived in South America until the early Eocene (Itaboraian SALMA, around 52 Ma).

Based on the phylogenetic analysis, *Eobrasilia*, *Gaylordia* and *Didelphopsis* do not constitute a monophyletic lineage. The strong divergences regarding the premolars and evolutionary tendencies imply that any attempt to group *Gaylordia*, *Didelphopsis* and *Eobrasilia* in a monophyletic lineage is not recommended. The diagnosis of “Eobrasiliinae” was based on homoplastic characters and ecomorphologically similar adaptations (e.g. inflated premolars), which resulted in the polyphyletic state of this taxon. As discussed here, “Eobrasiliinae” cannot be considered as a valid taxon.

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