

A NEW SPECIES OF *GAYLORDIA* PAULA COUTO (MAMMALIA, METATHERIA) FROM ITABORAÍ, BRAZIL

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ABSTRACT – We describe a new metatherian of the genus *Gaylordia* Paula Couto, from the early Eocene Itaboraí Basin, Brazil. This new species (estimated body mass ~60-90.9 g) is based on lower and upper dentition elements and is characterized by a more plesiomorphic dental morphology with respect to *G. macrocynodonta* Paula Couto (with a larger body mass, estimated in ~74-103 g for large individuals or males). The species *G. doelloi* Marshall, represented by small individuals or females, is regarded a junior synonym of *G. macrocynodonta*. A phylogenetic analysis as well as details of the occlusal surface of its upper and lower molars suggests that *Gaylordia* is closely related to the Pucadelphyidae, a non-marsupial “ameridelphian” group previously recorded at the early Paleocene locality of Tiupampa, Bolivia.

Key words: systematics, Paleogene, Mammalia, Metatheria, body mass, Brazil.

RESUMO – Descreve-se um novo marsupial basal do gênero *Gaylordia* Paula Couto, do Eoceno inicial da bacia de Itaboraí, Brasil. Esta nova espécie (massa corporal estimada ~60-90.9 g) está baseada na dentição superior e inferior, e é caracterizada por uma morfologia dentária mais plesiomórfica em relação a *G. macrocynodonta* Paula Couto (cuja maior massa corporal é estimada em ~74-103 g para grandes indivíduos ou machos). A espécie *G. doelloi* Marshall, representada por indivíduos pequenos ou fêmeas, é considerada um sinônimo junior de *G. macrocynodonta*. Uma análise filogenética, bem como detalhes da superfície oclusal de seus molares superiores e inferiores sugerem uma relação próxima de *Gaylordia* aos Pucadelphyidae, um grupo de ameridélfos não marsupiais previamente registrados no Paleoceno inicial da localidade de Tiupampa, Bolívia.

Palavras-chave: sistemática, Paleógeno, Mammalia, Metatheria, massa corporal, Brasil.

INTRODUCTION

The early Paleogene Itaboraí fauna in eastern Brazil represents one of the richest localities of metatherian diversity from the whole Cenozoic of South America. A taxonomic revision of the Itaboraí taxa is crucial to the understanding of early metatherian phylogeny, in particular those traditionally referred to the “Didelphimorphia” (Marshall *et al.*, 1990). This aspect is of particular importance taking in account that recent phylogenetic studies involving some Paleogene taxa (*e.g.* *Herpetotherium* Cope, 1873 and *Peradectes* Matthew & Granger, 1921, previously referred to the Didelphidae and Peradectidae, respectively), supported their exclusion from the crown-group Marsupialia (Sánchez-Villagra *et al.*, 2007; Beck, 2012; Beck *et al.*, 2014; Engelman & Croft, 2014, but see Horovitz *et al.*, 2009). In this context, the closer relationship of several Itaboraí metatherians with respect to crown-group Marsupialia, especially to “Didelphimorphia”, has been a topic of discussion (Goin, 2003; Forasiepi & Rougier, 2009; Ladevèze & Muizon, 2010; Oliveira & Goin, 2011).

Here we review the type material and undescribed specimens of *Gaylordia*, a Paleogene genus previously assigned to the Didelphidae (Marshall *et al.*, 1990), which allowed the recognition of several new cranial and dental characters. This genus is one of the few Itaboraí taxa defined on the basis of a skull and includes a large hypodigm (Paula Couto, 1952; Marshall, 1987; Oliveira, 1998). In addition, in their comprehensive study of metatherian postcranials Szalay (1994) and Szalay & Sargis (2001) referred to representatives of this genus several isolated postcranial materials only with *Gaylordia*. The new species of *Gaylordia* here described is based on a previously unreported upper dentition and on dentaries (including lower molars) previously referred to *Derorhynchus singularis* Paula Couto, 1952 and *Marmosopsis juradoi* Paula Couto, 1962 (Marshall, 1987). Morphological details of the upper and lower molars are described for the first time for *Gaylordia*.

The type species (*Gaylordia macrocynodonta*) was erected by Paula Couto (1952) on the basis of an anterior part of a skull with incomplete, worn teeth. Later, Paula Couto (1962)

recognized a new genus and species, *Xenodelphis doelloi*, and finally he described an additional species of *Gaylordia*, *G. mendesi* Paula Couto, 1970. The type materials of *X. doelloi* and *G. mendesi* were reviewed by Marshall (1987), who concluded that both are inseparable in size and structure and suggested that they should be regarded as synonyms, establishing the combination *G. doelloi*. Later, Marshall *et al.* (1990) included *Gaylordia* within Didelphidae: Eobrasiliinae, along with other early Paleogene taxa such as the Itaboraian *Didelphopsis* Paula Couto, 1952, and *Eobrasilia* Simpson, 1947 and the Tiupampian *Tiulordia* Marshall & de Muizon, 1988. Goin (2003) and later Oliveira & Goin (2011) transferred *Didelphopsis* to Sternbergiidae, ruling out closer affinities between *Eobrasilia* and *Gaylordia*. The genus *Gaylordia* is of special interest regarding its affinities with the early Paleocene Tiupampian genus *Tiulordia*, from the locality of Tiupampa, Bolivia (Muizon, 1991; Muizon & Brito, 1993; Oliveira & Goin, 2011). Previous works recognize the Pucadelphyidae as encompassing *Pucadelphys* Marshall & de Muizon, 1988 and *Andinodelphys* Marshall & de Muizon, 1988 (Muizon, 1998; Ladevèze & Muizon, 2010). Goin (2003) suggested the inclusion in this family of *Mizquedelphys* Marshall & de Muizon, 1988 and *Incadelphys*. In addition, a recent phylogenetic study has considered the Tiupampian genus *Mayulestes* Muizon, 1994 as a member of Pucadelphyidae (Engelman & Croft, 2014).

MATERIAL AND METHODS

All studied materials come from the Itaboraí fossil locality in southeastern Brazil (Figure 1). Details on the geology and age were summarized in previous works (*e.g.* Medeiros & Bergqvist (1999), Oliveira & Goin (2011)). More recently, an absolute Ar/Ar dating of a tuff in the (also Itaboraian-aged) levels of Las Flores, in central Patagonia, supported an early Eocene age for the Itaboraian SALMA (see Woodburne *et al.*, 2014).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCT (*ex* DGM), Museu de Ciências da Terra, Rio de Janeiro, Brazil; MN, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; UFPE, Universidade Federal de Pernambuco, Recife, Brazil.

Anatomical abbreviations. C1, upper canine; c1, lower canine; p1, p2, p3, lower premolars; M1/m1, M2/m2, M3/m3, M4/m4, upper and lower molars; StA, StB, StC, StD, StE, styler cusps. Molar cusp and crest nomenclature follows Oliveira & Goin (2011).

Abbreviations for descriptive statistics. In table 1 (dental measurements); L, maximum anteroposterior length and W, maximum labiolingual width. An asterisk (*) after some measurements indicates that they are approximate.

Other abbreviations. g, grams; CI, consistency index; RC, rescaled consistency index; RI, retention index; SALMA, South American Land Mammal Age.

Body mass. Body mass estimates (in g) were calculated for the species of *Gaylordia* following regression equations for upper and lower molars crown area by multiplying

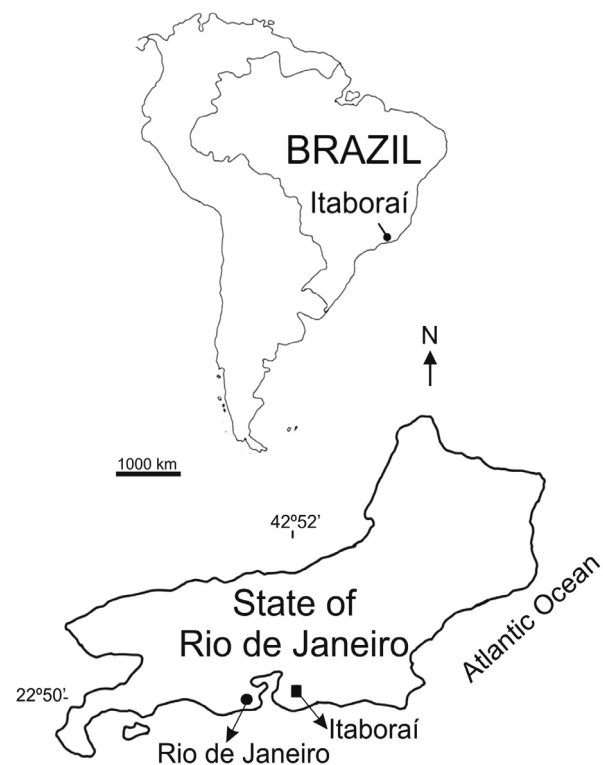


Figure 1. Location map showing the region of the Itaboraí Basin.

maximum length and maximum width (lengthxwidth) from two different datasets provided by Gordon (2003): the Didelphidae (*Caluromys* excluded) and pooled Didelphidae and Dasyuridae.

Phylogenetic analysis

In order to determine the position of *Gaylordia* within the Metatheria, we performed a maximum parsimony analysis based on the morphological matrix of Beck (2012) and Beck *et al.* (2014). This morphological matrix has been modified from previous studies (Horovitz & Sánchez-Villagra 2003; Sánchez-Villagra *et al.* 2007; Beck *et al.* 2008b; Horovitz *et al.* 2008, 2009; Abello & Candela 2010; Beck, 2012). Parsimony analysis of the matrix was carried out using the heuristic search algorithm of PAUP* 4.0b 10 (Swofford, 2002) with an initial search of 2000 replications. The morphological matrix comprised 262 characters and 38 taxa. We analyzed two hypotheses: the first analysis including craniodental characters of the present paper and petrosal type I from Ladevèze & Muizon (2010); the second analysis including craniodental and petrosal type VI characters from Ladevèze & Muizon (2010). Coding of the morphological characters from the first analysis on the craniodental and petrosal type I for *Gaylordia* is ?????????(10) ?????????(20) ?????????(30) ?????????(40) ?????????(50) ?????????(60) ?????????(70) ?? ?????????(80) ?????????(90) ?????????(100) ?????????-?(110) ?????????(120) ??? ?????????(130) ?????????(140) ?????????00

(150) 0 2 1 0 0 1 1 ? 1 2 (160) 2 ? ? ? 1 2 0 1 ? 0 (170) 0 ? ? ? 1 0 0 0 ? 1 (180) 0 ? ? ? ? ? ? ? ? ? (190) ? ? ? ? ? ? ? ? ? (200) ? ? ? ? ? ? ? ? ? ? (210) ? ? ? ? ? ? ? ? ? 2 (220) ? ? ? 0 2 ? – 1 1 0 1 (230) 0 1 0 1 0 0 0 1 0 1 (240) 1 0 0 0 1 1 1 0 0 1 (250) - 1 1 1 1 1 0 ? ? 1 (260) ? ? (262). Coding of the morphological characters from the craniodental and petrosal type VI differs from the first analysis in the following characters: 228 (state 0), 234 (state 0), 235 (-inapplicable), 236 (state 1), 239-242 (unknown), 245 (state 0), 247 (unknown), 249-253 (unknown).

SYSTEMATIC PALAEOLOGY

Class MAMMALIA Linnaeus, 1758
 Infraclass METATHERIA Huxley, 1880
 Order *INCERTAE SEDIS*

Genus *Gaylordia* Paula Couto, 1952

Type species. *Gaylordia macrocynodonta* Paula Couto, 1952.

1952 *Gaylordia* Paula Couto, p. 16, fig. 16.
 1962 *Gaylordia* Paula Couto, p. 151, fig. 9.
 1962 *Xenodelphis* Paula Couto, p. 160.
 1970 *Xenodelphis* Paula Couto, p. 21, fig. 1.
 1970 *Gaylordia* Paula Couto, p. 22, figs. 2, 3.
 1987 *Gaylordia* Marshall, p. 103, figs. 12-18.

Revised diagnosis. Small metatherian with body mass estimated between 20.8 and 103 g and characterized by the following combination of features: skull with relatively short rostrum, relatively short dentary, lower premolars subequal in size, p2 bulbous and with a well-developed posterior accessory cusp, lower molars with elevated trigonids relative to talonids, m2-3 with metaconid anteriorly displaced in relation to protoconid, very low paraconid in relation to metaconid, long preprotocristid, talonids subequal to or narrower than trigonids and progressively shortened from m1-4, small entoconids, anterior cingulid well-developed in m1-4, M1-3 wider than long, with large StC and anteroposteriorly compressed protocones, and conular crests absent. Differs from *Pucadelphys* in the smaller StA (parastyle), less developed conules and lower molars with shorter talonids. Differs from *Tiulordia* in having the StC undivided, m2 with a less compressed trigonid and a more robust and acute hypoconid, so that the cristid obliqua ends slightly labial to a point below the postprotocristid notch. Differs from *Mizquedelphys* and *Incadelphys* in its much greater StC on M2 and M3, smaller StA, and less developed conules; the protocone in *Gaylordia* is more expanded lingually than in *Incadelphys*. Differs from *Andinodelphys* (a questionable Pucadelphyidae) in having the StC undivided, V-shaped centrocrista instead straight, absence of conular crests on the metaconule, expanded protocone, less developed anterior cingulum, and absence of cutting edge crests. Differs from *Mayulestes* in having the styler shelf less developed in width, paracone and metacone twinning (i.e. the paracone and the metacone are coalescent at their bases), talonid

shorter, paraconid more reduced, and the hypoconulid lower in relation to hypoconid.

Gaylordia macrocynodonta Paula Couto, 1952
 (Figures 2, 3A,B; Table 1)

1962 *Xenodelphis doelloi* Paula Couto, p. 160.
 1970 *Xenodelphis doelloi* Paula Couto, p. 22, fig. 1.
 1970 *Gaylordia mendesi* Paula Couto, p. 23, fig. 3.
 1987 *Gaylordia doelloi* Marshall, p. 104, figs. 12-13.

Holotype. DGM 329-M, incomplete rostrum with right P2-M2, root of C1, roots of P1, and incomplete M3; left C1, roots of P1-P3, worn M1, anterolabial root of M2, and root of M3; and an incomplete left dentary with p3 and m1, roots of p1-2, and crowns of m2-3.

Hypodygm. The holotype and AMNH 49801, an incomplete right dentary with p2-m2 and alveoli of m3; DGM 186-M, left dentary with p3-m1 and alveoli for the rest of the molar teeth; DGM 925-M, left dentary with complete p1-m1; MCT 2385-M (DGM 646-M), incomplete left dentary with m1-2 and roots of m3-4; MN 1355-V, incomplete right dentary with alveoli of p1 and complete p2-m4; MN 1357-V, left dentary with p3 and m3, and alveoli of p1-2, m1-2 and m4; MN 1358-V, right dentary with p3, alveoli of p1-2 and of m1-4; MN 1366-V, left dentary with m1, alveoli of p2-3 and of m2-4. Also included here are the specimens referred by Marshall (1987) to “*Gaylordia doelloi*”.

Description of the skull and upper dentition. The specimen DGM 329-M is deformed because of lateral compression; the skull is broken anteriorly to the canines and behind the lacrimals. The rostrum includes maxillae, palatines, nasals, anterior part of frontals, and lacrimals (Figure 2). The infraorbital foramen is large and located in the maxilla above the anterior root of P3 (Figure 2A); the infraorbital canal is wide and the maxillary foramen opens into the anterior region of the orbit, where it is surrounded by the maxilla and the lacrimal (Figure 2B). Palatines are flat and, judging from the left one, palatal vacuities are absent. The maxillary-frontal contact is broad, much wider than in didelphids. The nasals are posteriorly expanded, reaching their maximum width at the level of the M1. On the left side of the skull the lateralmost suture with the frontal bone can be observed, which is aligned with the lacrimal foramen (Figure 2A).

The left lacrimal is better preserved. Sutures with the maxilla, frontal, and part of the palatine are visible, but the ventral suture with the maxilla is difficult to distinguish. There is a single, large lacrimal foramen, opening inside the orbit (Figure 2B). In contrast, in most didelphids there are usually two separate openings exposed on the face (but see Voss & Jansa, 2009). There is no evidence of a lacrimal tubercle. The anterior edge of the orbit, which is almost coincident with the lacrimal-maxillary suture, is placed dorsal to the middle part of M2 (Figures 2A,D). This condition resembles that of *Herpetotherium* according to Sánchez-Villagra *et al.* (2007) rather than that of *Pucadelphys*, where it is aligned dorsally with M1.

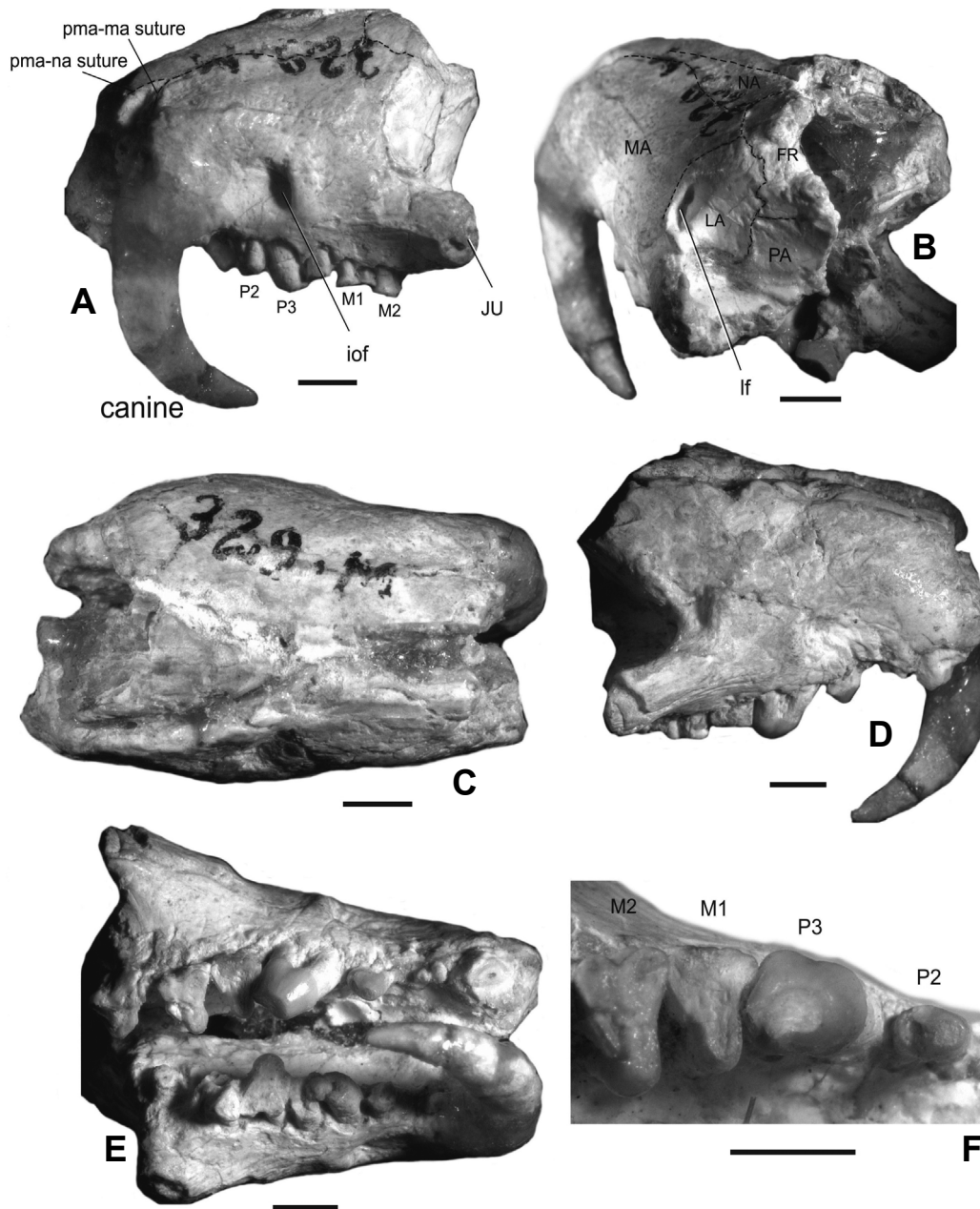


Figure 2. *Gaylordia macrocynodonta*, a partial skull, DGM 329-M (holotype). **A**, left lateral view; **B**, lateral oblique view; **C**, dorsal view; **D**, right lateral view; **E**, palatal view; **F**, left P2-M2 teeth in occlusal view. **Abbreviations:** iof, infraorbital foramen; If, lacrimal foramen; FR, frontal; JU, jugal; LA, lacrimal; PA, palatine, Pma, premaxilla; ma, maxila; na, nasal. For other abbreviations see Material and Methods. Scale bars = 2 mm.

Based on what is preserved on the left side of the skull and in the lower dentition (see below), the post-incisor dental formula of *Gaylordia macrocynodonta* is C1/c1; 3P/3p; 4M/4m. The single-rooted canine is very large, long, curved and laterally compressed. Measurements of left C: height, 5.80; width at base, 1.78; length at base 2.42. There is no diastema between the canine and P1. Short diastemata, nearly equal in length, occur between P1 and P2, and P2 and P3 (Figures 2E,F). There is no diastema between P3 and M1 (Figure 2F). The best preserved molars are the left M1-

2, although they are much worn; they are wider than long (Figures 2E,F).

Dentary and lower dentition. The dentary of the type specimen is badly preserved (Figures 3A,B). The mandibular symphysis is unfused, and extends backwards to a point below the anterior root of p3 (Figure 3A). A large mental foramen, probably representing the anterior, is located below p2 (Figure 3B). The posterior foramen is not preserved. The P3 is inflated, ovate in outline and has a large posterior accessory cusp. The M1 is worn and very small in relation to p3.

A partial dentary (MCT 2385-M) with m1-2 is more robust than that of the type specimen (Figures 3C-E), probably reflecting intraspecific variation. It is very deep below the molars (4.66 mm), being comparatively deeper than that of the type specimen (4.10 mm) and also that of the new species of *Gaylordia* (4.40 mm). The retromolar space between the last molar and the anterior edge of the ascending process is short, corresponding to less than half of m4 length.

Gaylordia mater sp. nov.
(Figures 4-8; Table 1)

Holotype. DGM 810-M, a partial right dentary with complete m2-4.

Hypodigm. The type and MCT 2383-M (DGM 644-M), incomplete left dentary with m1-2 and m4; MCT 2384-M (DGM 645-M), incomplete left dentary with p3, m1-2, incomplete m3 and complete m4; MCT 2386-M, incomplete right dentary with m3 and alveoli of p3 (only the posterior alveolus is complete), m1, m2 and m4; MCT 2387-M, incomplete right dentary with complete p3 and m1, alveoli of p2, and m2; MCT 2774-M, complete left m4; MCT 2775-M, incomplete right m3; MCT 2776-M, complete right m3;

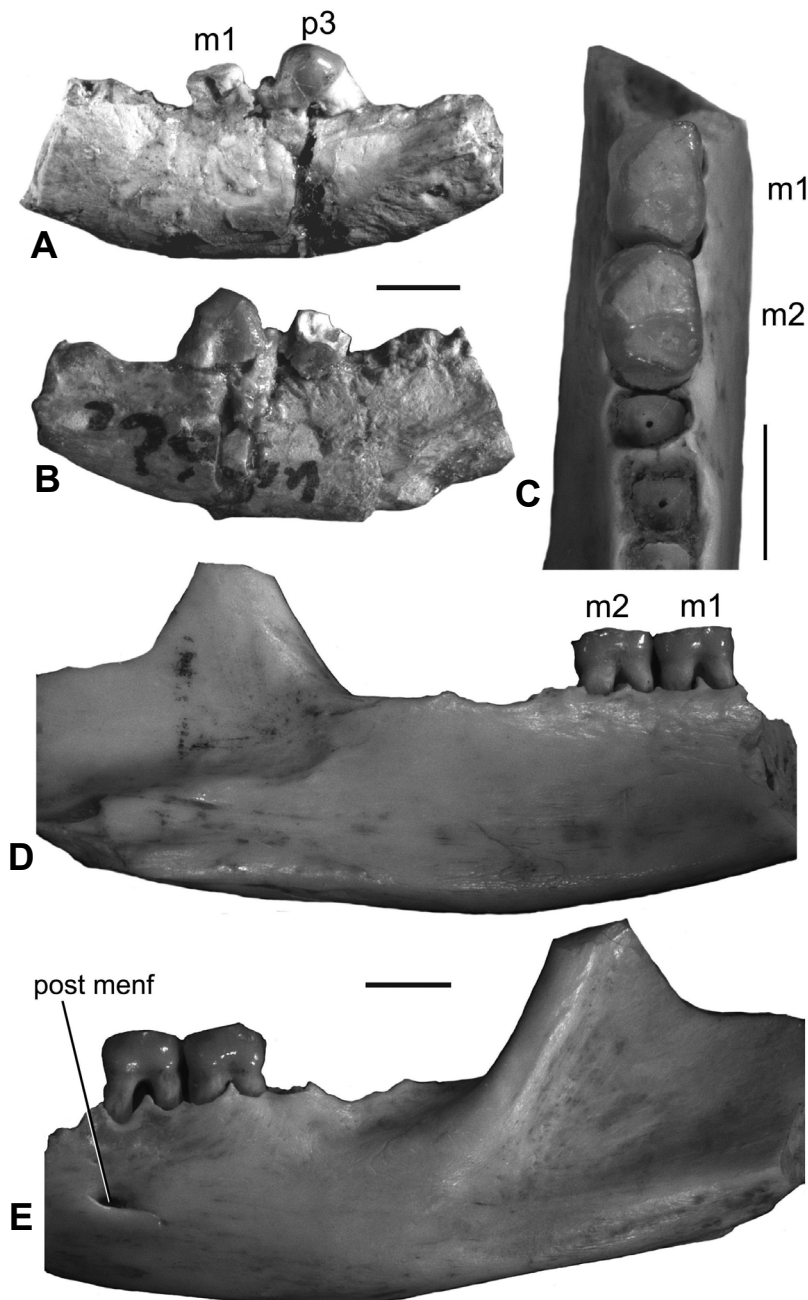


Figure 3. *Gaylordia macrocynodonta*, partial dentaries. **A-B**, DGM 329-M (holotype). **A**, in lingual view; **B**, in labial view. **C-E**, MCT 2385-M. **C**, m1-2 in occlusal view; **D**, dentary in lingual view; **E**, dentary in labial view. **Abbreviation:** post menf, posterior mental foramen. For other abbreviations see Material and Methods. Scale bars = 2 mm.

Table 1. Measurements (mm) of upper and lower molars of *Gaylordia macrocynodonta* and *Gaylordia mater* sp. nov. **Abbreviations:** see Material and Methods.

	LP2	WP2	LP3	WP3	LM1	WM1	LM2	WM2	LM3	WM3	LM4	WM4	
<i>Gaylordia macrocynodonta</i>													
DGM 329-M	1.38	0.80	2.06	1.60	1.78	1.98	1.68	2.14					
<i>Gaylordia mater</i> sp. nov.													
MCT 2777-M							2.12	2.52					
MCT 2778-M							2.10	2.52					
MCT 2779-M							2.19	2.56					
MCT 2780-M									1.96	2.76			
MCT 2781-M									1.97	-			
	Lp2	Wp2	Lp3	Wp3	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm4	Wm4	Lm1-4
<i>Gaylordia macrocynodonta</i>													
DGM 329-M			2.48	1.32									
MCT 2385-M					2.04	1.42	2.06	1.52					
MN 2882-V	1.24	0.75	1.60	1.00	1.45	1.00	1.48	1.02	1.48	1.02	1.46	0.98	5.60
<i>Gaylordia mater</i> sp. nov.													
DGM 810-M							2.10	1.42	2.04	1.48	1.90*	1.34	
MCT 2386-M									1.88	1.38			
MCT 2383-M					1.94	1.37	2.12	1.44			1.94	1.28	7.44
MCT 2384-M			1.70	1.13	1.95	1.36	2.10*	1.44			2.00	1.26	7.80
MCT 2387-M			1.72	0.93	1.95	1.37							
MCT 2474-M											1.92	1.50	
MCT 2775-M									2.25	1.66			
MCT 2776-M									2.01	1.45			

MCT 2777-M, complete right M2; MCT 2778-M, incomplete left M2; MCT 2779-M, incomplete right M2; MCT 2780-M, complete left M3; MCT 2781-M, incomplete right M3.

Etymology. *-mater*; Latin for “mother”; in reference to the more generalized morphology of its molars as compared with the type species of the genus and closely related forms.

Locality and age. São José de Itaboraí, State of Rio de Janeiro, Brazil; Itaboraí Basin, early Eocene, Itaboraian SALMA.

Diagnosis. Small metatherian with an estimated body mass of ~60.6-90.9 g. Differs from *Gaylordia macrocynodonta* in its lack of a bulbous p3, which is smaller than the m1; dentary with slightly longer retromolar space (~half of m4 length), lower molars with the metaconid more transversally aligned with the protoconid, and talonid anteroposteriorly less compressed.

Description. Lower dentition: The p3 (DGM 2384 and 2387-M) is smaller than the m1, slightly inflated, and presents a low and broad posterobasal heel (Figures 5A-B). The m1 is heavily worn in 2387-M and DGM 2384 (Figures 5B,D). The trigonid is slightly longer than the talonid, but it is equal in width, and the paraconid is placed less lingually than the metaconid (Figures 5 B,D,H). The m2 (DGM 810-M) (Figure 4C) exhibits the trigonid anteroposteriorly compressed, higher crowned and wider in relation to the

talonid. Although it is slightly inclined posteriorly, the protoconid is not posteriorly located in relation to the metaconid. The paraconid and the metaconid are lingually placed, and are close to each other. The anterior cingulid is short, but anteriorly salient. The talonid is not reduced in width but anteroposteriorly compressed, being shorter than the trigonid. The entoconid is small, conical and located close to the metaconid. The preentocristid is absent. The hypoconulid is moderately sized and is located at the posterolingual corner of the tooth. The cristida obliqua is short and ends slightly labial to the postprotocristid notch. The posthypocristid is longer than the prehypocristid. The postcingulid is present but vestigial. The m3 (DGM 810-M) differs from m2 in having the protoconid even more transversely aligned with the metaconid, less developed anterior cingulid and more developed posterior cingulid (Figure 4C). The specimen MCT 2776-M is better preserved in relation to the holotype (Figures 6A-C); a remarkable feature of this tooth is that the hypoconulid is stronger and higher than the entoconid. In occlusal view, the metaconid is circular in outline. The m4 (DGM 810-M; Figure 4C) lacks the lingual and distal parts of the talonid. It differs from m3 in having a slightly smaller trigonid and a less labially salient hypoconid (Figure 4C). A small labial cingulid is

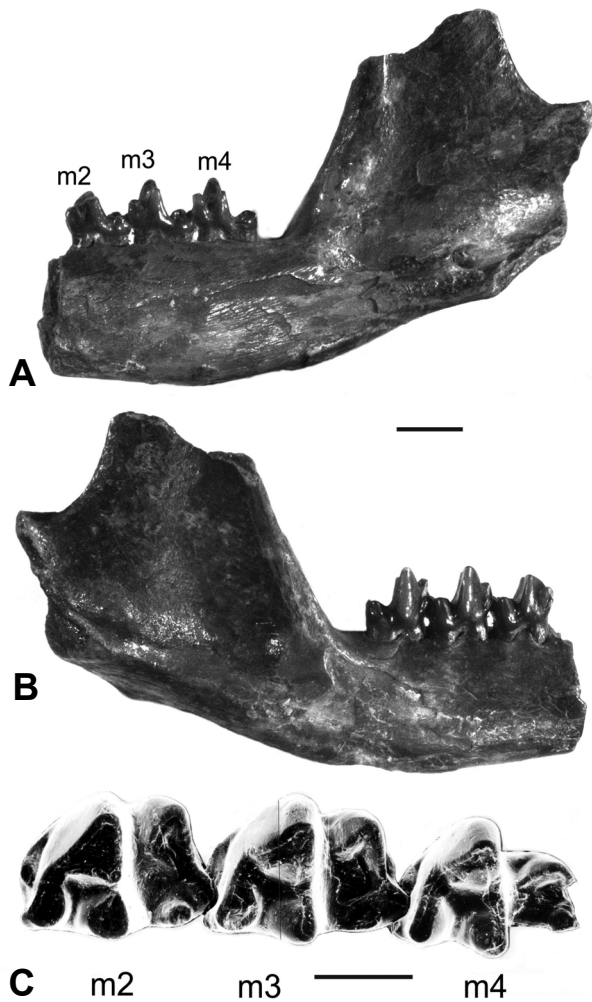


Figure 4. *Gaylordia mater* sp. nov., DGM 810-M (holotype). **A**, partial dentary in lingual view; **B**, partial dentary in labial view; **C**, m1-m3 in occlusal view. **Abbreviations:** see Material and Methods. Scale bars: A, B = 2 mm, C = 1 mm.

present. The m4 in the specimen MCT 2383-M (Figures 5E,F,H) is complete and bears a talonid that is not greatly reduced as in the other species of the genus; the talonid bears a well-developed hypoconulid, which is located at the posterolingual corner of tooth. The posterior cingulid is not reduced. The posthypocristid is less transversely oriented with respect to the long axis of the tooth, extending to a point near the postero-lingual corner, and connects with the hypoconulid at its base.

Dentary: The deepest part of the dentary is developed below the m4 (Figures 4A,B). Unlike "*Gaylordia doelloi*" and *G. macrocynodonta*, a well-developed retromolar space, corresponding in size to half the length of m4, is present (Figures 4A,B; 5A,E,F). The anterior edge of the coronoid process forms an angle of approximately 120° with respect to the horizontal axis of the dentary. MCT 2383-M has a quite large mandibular foramen located nearer to the angular process than to the anterior base of the condyle (Figures 5A,E). The mandibular condyle is placed well above the alveolar margin (Figures 5E,F). The angular process is medially inflected

(Figure 5G). There are two mental foramina: one below the anterior root of the p2 and the posterior one below the posterior half of m1 (Figures 5A,F). In MCT 2387-M the posterior foramina is located below the anterior root of m2 (Figure 5C).

Upper dentition: MCT 2777-M has a shallow ectoflexus and the styler shelf is moderate in width (Figures 7A,B). The tooth is worn, but exhibits a large and ovate StC, which is located inside the styler shelf. Both the StB and StC are placed closer to each other than StD. The presence of a metaconule is suggested by the convex postprotocrista at its distal end. The MCT 2779-M (Figure 7C) has strongly worn styler shelf and talon, especially on StC region and postmetacrista. MCT 2778-M (Figures 8A,B) is the only tooth without advanced wear, lacking due to breakage only the StC. A small and pointed cusplule is present on the labial margin of the tooth, immediately labial to the broken region of StC. The ectoflexus is shallow. The well-preserved centrocrista is slightly v-shaped and weakly invasive labially. The trigon cusps are high and with sharp crests. The metacone is much larger than the paracone. Both these cusps are laterally compressed. The base of the metacone extends further lingually than that of the paracone. The preparacrista ends labially at the anterolingual face of StB. The para- and metaconule are very compressed laterally. The anterior cingulum is shallow. The M3 (MCT 2780-M and MCT 2781-M) is transversally wider than M1-2. The StB is similar in size to StC. The StC is large, ovate, and slightly more compressed than in M2 (Figures 7D-F). The StD is less robust than in M2, and is connected to StC by a low crest. The ectoflexus is better developed than in M1 and M2, with the deepest point between StC and StD. The StA is proportionally smaller than in M1 and M2. The conules are vestigial.

PHYLOGENETIC ANALYSIS

Two phylogenetic analyses presented here resulted in distinct topologies. The first topology (987 steps, CI 0.3435, RI 0.6482, RC 0.2226) resulted from a matrix version with craniodental + petrosal type I characters (Ladevèze & Muizon, 2010), showing *Gaylordia* occupying a sister taxon position to the pucadelphyids (Figure 9A). When the maximum parsimony analysis included data on the craniodental and petrosal type VI (Ladevèze & Muizon, 2010), four most parsimonious trees were obtained (988 steps, CI 0.3431, RI 0.6475, RC 0.2222), and the strict consensus tree recovered *Gaylordia* in a polytomy with pucadelphyids, and *Herpetotherium* + Marsupialia (Figure 9B). The strict consensus of two trees from the first matrix data is better resolved than the second matrix analyzed (Figure 9A). All main clades obtained in these analyses are similar to those obtained by Beck (2012) and Beck *et al.* (2014, 164: fig. 17A).

DISCUSSION

Since the description of the type materials of *Gaylordia macrocynodonta* by Paula Couto (1952), details of the occlusal surface of its upper molars were unknown. The

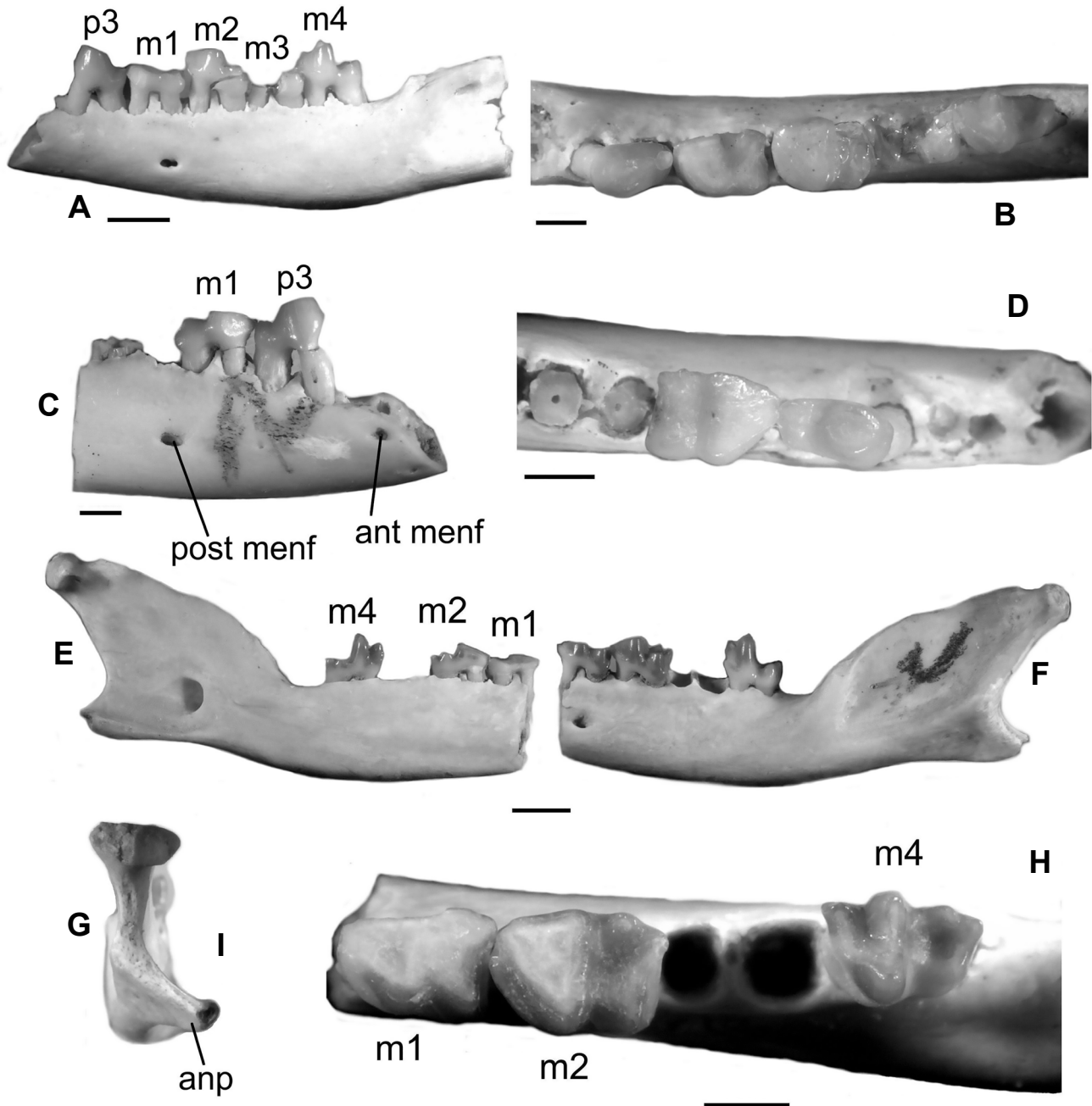


Figure 5. *Gaylordia mater* sp. nov., dentaries and lower dentition. **A**, MCT 2384-M, labial view; **B**, MCT 2384-M, occlusal view; **C**, MCT 2387-M, labial view; **D**, MCT 2387-M, occlusal view; **E**, MCT 2383-M, lingual view; **F**, MCT 2383-M, labial view; **G**, MCT 2383-M, posterior view; **H**, MCT 2383-M, occlusal view. **Abbreviations:** **ant menf**, anterior mental foramen; **post menf**, posterior mental foramen; **anp**, angular process. For other abbreviations see Material and Methods. Scale bars: A, E-F = 2 mm; B-D, G-H = 1 mm.

new specimens here described reveal that *G. mater* sp. nov. has a well-developed StC, at least on M2-3. In M2, the StC is robust, ovate in outline, and is located closer to StB than to StD. In M3 the StC is slightly more labiolingually compressed and is located more lingually. In both molars, the maximum depth of the ectoflexus locates labial to StC, being probably related to very labially expanded metastylar areas. The M3 is anteroposteriorly less developed than M2, in such a way that the postmetacrista is nearly parallel to the transverse axis of the tooth. In both M2 and M3, the

protocones are anteroposteriorly compressed (a feature that correlates with the moderate talonid reduction in the lower molars), the styler shelf is moderately reduced and the centrocrista is V-shaped but poorly invasive. In the lower molars the trigonid is shorter than the talonid (from m2-m4), the entoconid is very small relative to the hypoconid, and the hypoconulid is larger than the entoconid.

In comparison with *Gaylordia macrocynodonta*, the new species *G. mater* sp. nov. exhibits some plesiomorphic characters. The anteroposterior compression of the talonid in

Table 2. Body mass estimates for *Gaylordia* spp. discussed in the text. **Abbreviations:** see Material and Methods.

		Equation (from Gordon, 2003)	Body mass <i>Gaylordia</i> <i>macrocnodonta</i> , MCT 2385	Body mass <i>Gaylordia</i> <i>macrocnodonta</i> MN 2882	Body mass <i>Gaylordia</i> <i>mater</i> sp. nov.)
Didelphidae	m1 L x W	2.924+1.56*ln	97.8	33.2	86.2 (MCT 2387)
	m2 L x W	2.557+1.629*ln	82.8	25.2	76.5 (holotype)
	m3 L x W	2.581+1.564*ln	-	25.2	74.4 (holotype)
	m4 L x W	2.77+1.503*ln	-	27.3	62.6 (MCT 2383)
	M2 L x W	1.349+1.707*ln	-	-	66.2 (MCT 2778)
	M3 L x W	1.35+1.638*ln	-	-	61.3 (MCT 2780)
Pooled sample (Didelphidae and Dasyuridae)	m1 L x W	2.933+1.605* ln	103.6	34.1	90.9 (MCT 2387)
	m2 L x W	2.403+1.67*ln	74.4	22.0	68.6 (holotype)
	m3 L x W	2.363+1.635* ln	-	20.8	64.7 (holotype)
	m4 L x W	2.681+1.564* ln	-	25.6	60.6 (MCT 2383)
	M2 L x W	1.267+1.708*ln	-	-	61.1 (MCT 2778)
	M3 L x W	1.356+1.66*ln	-	-	64.0 (MCT 2780)

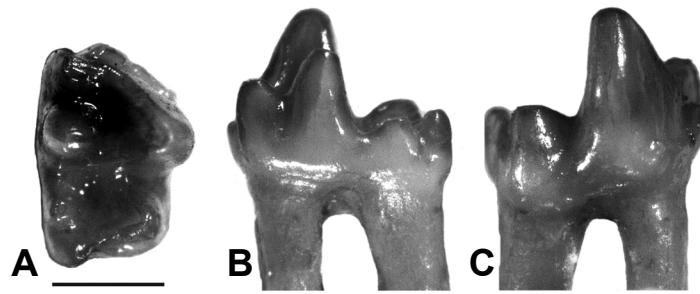


Figure 6. *Gaylordia mater* sp. nov., an isolated right m3, MCT 2776-M. **A**, occlusal view; **B**, lingual view; **C**, labial view. Scale bars = 1 mm.

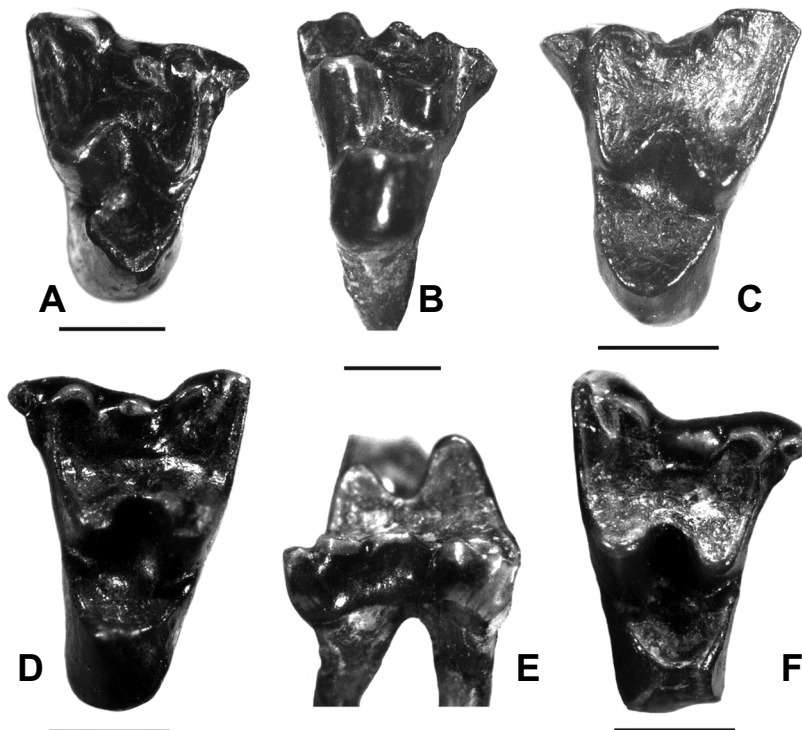


Figure 7. *Gaylordia mater* sp. nov., isolated upper molars. **A**, MCT 2777-M, M2 in occlusal view; **B**, MCT 2777-M, M2 in lingual view; **C**, MCT 2779-M, M2 in occlusal view; **D**, MCT 2780, M3 in occlusal view; **E**, MCT 2781, M3 in labial view; **F**, MCT 2781-M, M3 in occlusal view. Scale bars = 1 mm.

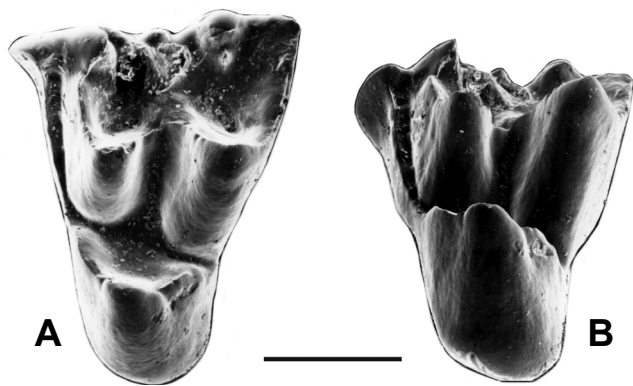


Figure 8. *Gaylordia mater* sp. nov., an isolated left M2 (MCT 2778-M). **A**, occlusal view; **B**, lingual view. Scale bar = 1 mm.

G. mater is much less developed than in *G. macrocynodonta*. In *G. mater* sp. nov. the m1-3 trigonids exhibit a narrower anterior cingulid than in *G. macrocynodonta*. Another plesiomorphic feature in *G. mater* sp. nov. is related to the absence of the hypertrophied p3, which is present in *G. macrocynodonta*. In this regard, an interesting possibility would be that “*G. doelloi*” represents small individuals (or female specimens) of *G. macrocynodonta*. Regarding the molar morphology both species are inseparable. As seen above, skull is available only for *G. macrocynodonta*. However, dentaries are relatively well-represented in the other species of the genus. *G. mater* sp. nov. shows its dentaries as high as in *G. macrocynodonta*, and “*G. doelloi*” has dentaries which are lower than *G. macrocynodonta*. Marshall (1987) diagnosed “*G. doelloi*” as the smaller species of the genus (30% smaller than the type species), with a p3 typically smaller relative to m1. However, a review of the MN 2882-V, described as “*G. doelloi*” by Marshall (1987), reveals that the p3 is larger than the m1. Thus, size is the only character that differentiates “*G. doelloi*” from the type species. In Recent marsupials, as small didelphids and dasyurids, differences in body size as well as in canine size represent sexual dimorphism (see Ladevèze *et al.*, 2011; Fisher & Cockburn, 2006). For example, hypertrophied canines in *Monodelphis dimidiata* are more characteristic of males than in females (Pine *et al.*, 1985). Ladevèze *et al.* (2011) described a strong sexual dimorphism for *Pucadelphys andinus* as revealed by size differences in the skull, dentaries and canines, with males representing larger individuals. In conclusion, we regard size differences used up to now for the recognition of “*G. doelloi*” as very likely related to sex. Thus, we consider now *G. doelloi* as a junior synonym of *G. macrocynodonta*.

Putting aside previous studies including *Gaylordia* within the Didelphidae (Paula Couto, 1970; Marshall, 1987; Marshall *et al.*, 1990), an alternative placement of this taxon was proposed by the phylogenetic study of Ladevèze & Muizon (2010), that recovered *Gaylordia* inside the crown-group Marsupialia as a taxon closely related to Paucituberculata + Australidelphia clade. As shown above, a phylogenetic test utilizing craniodental and petrosal type I data (see Ladevèze

& Muizon, 2010) recovered *Gaylordia* as a sister taxon to pucadelphyids (Fig. 9A). The idea that most or some Tiupampian and Itaboraian are closely related taxa have been advocated by Marshall *et al.* (1990), Muizon (1991), Muizon & Brito (1993), Oliveira & Goin (2006, 2011). These results reopen the question regarding the phylogenetic position of Itaboraian forms in relation to Paleogene forms and crown-group marsupials, which except *Patene*, are absent in denser sample taxa analyses (*e.g.* Sánchez-Villagra *et al.*, 2007; Forasiepi, 2009; Horovitz *et al.*, 2009; Beck, 2012; Beck *et al.*, 2014; Engelman & Croft, 2014). In several phylogenetic analysis pucadelphyids have been recovered as occupying a position near the crown-group, sometimes with *Herpetotherium* placed between them and Marsupialia, or as a sister group to Marsupialia (see *e.g.* Beck, 2012; Engelman & Croft, 2014).

It should be noted that most potentially derived features observed in *Gaylordia* are present in some early Paleocene Tiupampian taxa such as the pucadelphyids *Mizquedelphys*, *Incadelphys* and *Pucadelphys* (Muizon, 1991; Goin, 2003), thus suggesting its belonging to, or close relation with, the Pucadelphyidae. Goin (2003) identified the following combination of features for Pucadelphyidae: retention of well-developed para- and metaconules, complete set of styler cusps, StA and StB separated by a notch, expanded protocone, long preparacristae which, in the M3, is almost as long as the postmetacrista, weakly V-shaped centrocrista, and the labially (not posterolabially) oriented postmetacrista (especially in M3, where it is almost parallel to the preparacrista). Additionally, we note that at its deepest point, the ectoflexus is located between StC and StD on M2 and M3. On the lower molars, the hypoconulid is slightly larger than the entoconid, and the metaconid is aligned transversely to the protoconid (mainly on m2 and m3). Taking in account the incipient V-shaped centrocrista, expanded protocone, smaller entoconid relative to the hypoconulid, and the alignment of the protoconid and metaconid, we also consider *Tiulordia*, another Tiupampian genus, as a member of, or closely related to, the Pucadelphyidae. Muizon (1998) and later Ladevèze & Muizon (2010) assigned *Andinodelphys* to the Pucadelphyidae. However, regarding the upper molar (holotype) *Andinodelphys* differs from the Pucadelphyidae in its straight instead of V-shaped centrocrista, smaller protocone, in that the deepest point of the ectoflexus is located labial to StC, and in having a crested metaconule. The lower molar associated to *Andinodelphys* by Muizon (1991) agrees well with the Pucadelphyidae in its transversely aligned protoconid and metaconid, and hypoconulid larger than the entoconid. Oliveira & Goin (2006) suggested that *Andinodelphys* is better compared to peradectids than to the didelphids. Pending a review of the type materials of *Andinodelphys*, we are cautious regarding its inclusion in the Pucadelphyidae. Another problematical taxon included within Pucadelphyidae is *Mayulestes* (see Engelman & Croft, 2014). This genus originally was included by Muizon (1994) in its own family (Mayulestidae), within the Sparassodonta. In some phylogenetic studies

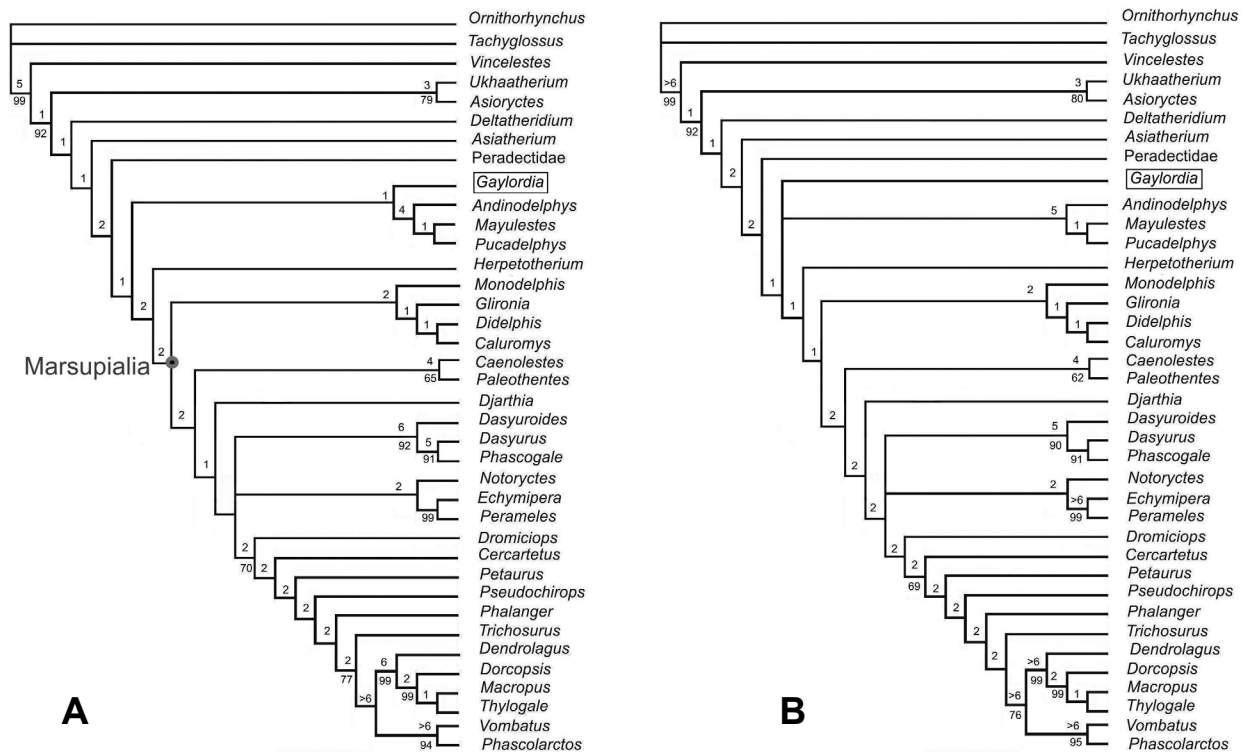


Figure 9. **A**, strict consensus cladogram of two trees obtained of the matrix with craniodental characters/petrosal type I. **B**, strict consensus cladogram of four trees obtained of the matrix with craniodental characters/petrosal type VI. Values to the upper left of each node represent Bremer supports, and numbers to the lower left represent bootstrap values (bootstrap values below 50 not shown).

Mayulestes has been frequently recovered as a sister taxon to *Pucadelphys*+*Andinodelphys* (e.g. Sánchez-Villagra *et al.*, 2007; Horovitz *et al.*, 2009; Forasiepi, 2009; Beck, 2012; Beck *et al.*, 2014). Goin (2003) suggested that the molar morphology of *Mayulestes* fits well in the peradectid pattern, mainly in characters related to wide styler shelf, styler cusps moderately developed, preparacrista not reduced in length, paraconid not reduced or shifted antero-medially, and hypoconulids high. As stated before for *Andinodelphys*, we are cautious regarding inclusion of *Mayulestes* in the Pucadelphyidae.

Regarding dental adaptations, Marshall (1987) suggested that the presence of a bulbous P3/p3 in *Gaylordia macrocynodonta* constitutes an adaptation to crushing. Most upper and lower teeth identified as *G. macrocynodonta* have strongly worn and flattened occlusal surfaces. We also note that teeth belonging to *G. mater* sp. nov. exhibit a wear pattern which is similar to that of the type species (see e.g. Figure 5). The holotype of *G. mater* has stronger wear on m2 than on m3-4 (Figure 4), a feature also observable in MCT 2383-M (Figures 5F,H), where the m1 is the most strongly worn tooth, while m3 almost lacks any wear signal at all. These data suggest that the most crushing teeth are the anteriormost molars and the posteriormost premolars. Dental adaptations where m1 and m2 become heavily worn have been identified in carnivorous marsupials, especially in bone-eating and invertebrate-crushing consumers (see Jones, 2003).

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