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Original Investigation

Critical revision of the alleged delayed dental eruption in South American “ungulates”

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ABSTRACT

The endemic South American “ungulates” (SANU) were traditionally assumed to be a monophyletic offshoot of the Grandorder Ungulata, but the current reorganization of the extant ungulates in Laurasiatheria and Afrotheria (based on molecular data) leaved them in an undetermined systematic position. The delayed dental eruption versus cranial growth was proposed as a hard-tissue synapomorphy of Afrotheria. In a recent paper, at least some endemic SANU (Notoungulata, Astrapotheria, and possibly Pyrotheria) were interpreted as allied to Afrotheres by having a late replacement of deciduous cheek teeth. This statement was based on: (1) the usual occurrence within these groups of individuals with deciduous and permanent teeth; (2) the individual size (estimated comparing the length/width ratio of cheek teeth) of specimens with permanent premolars erupted is indistinguishable from that of specimens with deciduous premolars (putative juveniles), and (3) the retention of at least dP1–dP3 in adult specimens of *Parastrapotherium* (Astrapotheria). Herein we critically examine the presumed existence of delayed dental eruption in astrapotheres, pyrotheres and xenungulates and the assumptions on which it was based. The alleged evidences supporting the occurrence of delayed dental eruption in SANU arise from misinterpreted information from the literature and conceptual mistakes (i.e. delayed dental eruption versus cranial growth was confused with delayed replacement of premolars versus molar eruption). Based on examination of at-hand specimens, we found that there is no evidence for a delayed premolar replacement relative to the eruption of the molars in astrapotheres, pyrotheres, and xenungulates. A delayed dental eruption in relation to jaw growth does not occur at least in *Astrapotherium magnum*. Although a very recent study proposed close relationships among afrotheres and at least notoungulates and xenungulates, a more complete analysis is still needed to elucidate the evolutionary relationships of astrapotheres and pyrotheres.

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Introduction

Cenozoic South American ecosystems were inhabited by a wide diversity of enigmatic, endemic “ungulates” or ungulate-like mammals that diversified in geographic isolation from other continental masses (Simpson, 1980; see also Wilf et al., 2013). These endemic native “ungulates” are traditionally grouped in at least six orders: Condylarthra, Notoungulata, Litopterna, Astrapotheria, Xenungulata and Pyrotheria. The origins and phylogenetic relationships of SANU with the main eutherian clades were debated during more than a century (see Cifelli, 1993 and references therein). During the last decades, the most accepted posture was that of McKenna (1975), who proposed that all SANU would have diverged from a

common North American ancestor. The term Meridiungulata was proposed by this author to include all the SANU, as one of the divisions of the Grandorder Ungulata. Nevertheless, the introduction of molecular studies reorganized the extant ungulates in at least two separate clades, within Laurasiatheria and Afrotheria (Murphy et al., 2001; Waddell et al., 1999; Springer et al., 2007), but the higher level relationships of SANU and other extinct “ungulates” remain uncertain, leaving them in an undetermined systematic position.

In a recent paper, Agnolin and Chimento (2011), based on a bibliographic revision, concluded that all or most Notoungulata, Pyrotheria, and Astrapotheria share with the Afrotherian mammals a relatively late eruption of permanent cheek teeth versus cranial (or mandibular) growth, a feature previously proposed as an Afrotherian synapomorphy (Asher and Lehmann, 2008). Accordingly, Agnolin and Chimento (2011) interpreted this character as indicating a close phylogenetic relationship among

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SANU and Afrotherians. More recently, in a much more extensive analysis, O'Leary et al. (2013) concluded that at least *Carodnia* (Xenungulate) and *Thomashuxleya* (Notoungulata) are part of the Afrotherian clade, partially corroborating the proposal by Agnolin and Chimento (2011). Nevertheless, O'Leary et al. (2013) admitted that they were not able to corroborate the occurrence of a relatively late eruption of permanent cheek teeth in the two SANU taxa included in their analysis. A detailed critical discussion on the timing of tooth eruption in Notoungulata was provided by Billet and Martin (2011), concluding that there is no evidence for an afrotherian-like delayed dental eruption, except in few late diverging forms. Concerning the presence of delayed dental eruption in other SANU (Pyrotheria, Xenungulata and Astrapotheria), only a preliminary discussion was presented by Kramarz et al. (2011).

The goal of this work is to provide a detailed critical analysis of the presumed occurrence of afrotherian-like delayed dental eruption in SANU, based primarily on examinations of at-hand specimens, as well as a critical revision of the empiric and bibliographic sources indicated by Agnolin and Chimento (2011) as supporting their statement. Since this feature in notoungulates was extensively discussed by Billet and Martin (2011), we will focus herein on the discussion of Astrapotheria and Pyrotheria, with some additional remarks on notoungulates other than those analyzed by previous works.

Institutional abbreviations

AMNH, American Museum of Natural History, USA; FMNH, Field Museum of Natural History, USA; MACN-Ma, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina, Mastozoológico Collection; MACN-A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina, Ameghino Collection; MLP, Museo de La Plata, Argentina; MPM, Museo Padre Molina, Santa Cruz, Argentina; YPM PU, Yale Peabody Museum, Princeton University Collection, USA.

Reassessment of the evidences supporting delayed dental eruption in Astrapotheria and Pyrotheria

Agnolin and Chimento (2011) stated that Astrapotheria, and possibly Pyrotheria, share with afrotheres a late replacement of the deciduous cheek teeth. The authors based this statement essentially on the three following arguments upon which legitimacies are herein discussed.

The usual occurrence within Astrapotheria and Pyrotheria of individuals with deciduous cheek-teeth together with totally erupted permanent molars

This statement was substantiated by a list of pyrothere and astrapothere specimens with coexisting deciduous premolars and molars taken from the literature (Agnolin and Chimento, 2011: supp. material). As noted by Billet and Martin (2011), two different patterns concerning the late dental eruption in placental mammals can be recognized: the late replacement of the deciduous premolars by permanent premolars relative to the eruption of the molars, and the delayed eruption of the permanent dentition relative to the skull growth. They are different patterns that should not be equated, although they may coexist in some afrotherians (e.g. hyracoids, tenrecids, and macroscelideans) (Billet and Martin, 2011). Asher and Lehmann (2008) proposed that a delayed eruption of the permanent dentition relative to skull growth is an afrotherian synapomorphy, but they did not discuss the phylogenetic meaning of the late replacement of the deciduous premolars relative to the eruption of the molars. The list of specimens with coexisting deciduous premolars and molars presented by Agnolin

and Chimento (2011) only would provide support for a putative late replacement of the deciduous premolars relative to the eruption of the molars. Conversely, it is not an evidence of a delayed eruption of the permanent dentition relative to skull growth because no comparison with the skull (or other skeletal elements) size is provided. Regardless, the coexistence of deciduous premolars and M1/1–M2/2 in most of the specimens listed by Agnolin and Chimento (2011) does not necessarily indicate a late replacement, given that in most eutherians with normal dental replacement the complete substitution of premolars occurs before the eruption of M3/3 (Simpson, 1933; Billet and Martin, 2011 and references therein). Only the co-occurrence of dP4/4 and M3/3 in two of the listed specimens could be considered a significant deviation. However, in one of those specimens, listed as *Granstrapotherium snorki* and having DP4 and M3 (UCMP 38007), the teeth are not physically associated, and their assignation to a single individual is merely speculative. The other specimen, listed as *Astrapotherium ruderarium?* with complete dp3–m3 series, belongs to the MACN A 52–524 (Kramarz and Bond, 2010: fig. 12.2). In this specimen, the m3 is still unerupted, as well as the p4 below the dp4, but the crown of the m3 is well exposed in lingual and occlusal view because the lingual wall of the dentary and the ascending ramus were not preserved. There is no evidence suggesting that in this specimen the complete premolar replacement would have occurred after the eruption of m3. In other astrapotheres the eruption of P4/4 before the M3/3 is well documented in juveniles or sub-adults (with fully erupted P4/4 and erupting or still unerupted M3/3) of *Eoastrapostylops* (PVL 4216; Soria, 1987) *Trigonostylops* (e.g. AMNH 28700; Simpson, 1933), *Astraponotus* (MLP 69 – III – 24 – 295; Kramarz et al., 2010), *Parastrapotherium* (FMNH 13492, 13504, 13413, 13505, 13579), and *Astrapotherium* (FMNH 14259, MACN A 8603).

In the pyrothere *Griphodon peruvianus*, the only known specimen has erupted dp4–m1 and encrypted p3–4 (Patterson, 1942), and was also presented by Agnolin and Chimento (2011) as illustrating delayed dental replacement in Pyrotheria. In this specimen the m2 is not preserved, but the mesial part of its alveolus is as deep in the dentary as the p4 (Fig. 1), suggesting that both teeth would have erupted almost simultaneously, before the m3.

In other astrapotheres, pyrotheres and xenungulates where no juveniles are known, the eruption of p4 before the m3 can be easily deduced in adults by comparisons among the stages of wear of the permanent teeth (i.e. P4/4 is consistently more worn than M3/3) (Bergqvist, 2010).

The retention of at least dP1–dP3 in adult or senile specimens of Parastrapotherium

This statement has neither empirical nor bibliographic support, and it is entirely contradicted by previous interpretations (Ameghino, 1904; Gaudry, 1904; Loomis, 1914; Scott, 1937; Soria, 1984; Frailey, 1987; Cifelli, 1993; Johnson and Madden, 1997; Kramarz and Bond, 2008, 2009, 2010). Adult specimens of *Parastrapotherium* have five upper and lower cheek teeth, as stated by Kramarz and Bond (2008) and accepted by Agnolin and Chimento (2011: 103). If dP1–dP3 would be retained in adult stages, the adult dental formula would be dP1–M1, representing an extraordinary case of dental reduction among eutherians. Juvenile specimens of *Parastrapotherium* have at least three, much worn molariform teeth in front of M1, which clearly represent dP2–dP4 (e.g. AMNH 29596, see also Scott, 1937). In adult specimens, there are two non-molariform teeth (noticeably different from the deciduous ones, Scott, 1937) in front of M1, consistently less worn than M1 (e.g. AMNH 29575, FMNH P. 13329, 13413, 13505, MACN A 52–604), which correspond to P3–P4. The replacement of at least the dp4 is observable in the juvenile mandible FMNH 13473, which preserves the crown of the p4 encrypted within the mandible below

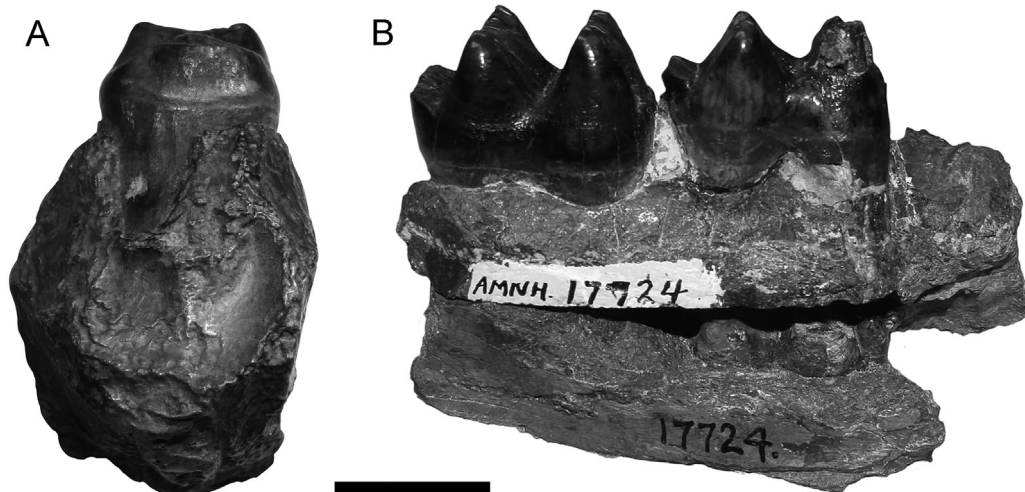


Fig. 1. *Griphodon peruvianus* Anthony, 1924. AMNH 17724, A, left mandible in posterior view showing the crown of m1 and the mesial wall of the alveolus for m2 (the contour nearly reproduces the profile of the trigonid); B, the same in lingual view showing the p4 encrypted below the dp4 (dp3 was removed). Scale bar = 2 cm.

the dp4. Consequently, in all known adult specimens of *Parastrapotherium* the cheek teeth formula is unmistakably P3/3, P4/4, M1–3/1–3 (Kramarz and Bond, 2008), and there is no retention of deciduous teeth in adult stages (Scott, 1937; Kramarz and Bond, 2008). In contradiction to the statement by Agnolin and Chimento (2011: 102–103), the juvenile dentition is much better known in *Astrapotherium* than in *Parastrapotherium*; an almost complete ontogenetic series for *A. magnum* and for *Astrapotherium? ruderarium* reveals a normal premolar replacement for these species as well (Ameghino, 1904; Scott, 1928, 1937; Kramarz and Bond, 2010). Such replacement is undoubtedly shown in the specimen MACN Pv 19888 (Fig. 2), in which DP3–DP4 are still in position and P3–P4 are encrypted within the maxillary. There is no evidence suggesting that the deciduous premolars were retained in adult stages of all the remaining astrapotheres.

Body size (inferred through cheek teeth proportions) of specimens with permanent premolars (adults) is indistinguishable from specimens with deciduous premolars (putative juveniles)

This argument was substantiated by a bivariate plot of cheek-teeth maximum length vs. width for *Astrapotherium magnum*

(Agnolin and Chimento, 2011: Fig. 2A), based on dental measurements provided by Scott (1928). This figure shows that M1/1 length/width ratio of a specimen retaining deciduous premolars (putative juvenile) do not differ significantly from M1/1 of specimens with fully erupted permanent dentition. Agnolin and Chimento (2011: 103) stated that “On the contrary, in remaining mammals, including artiodactyls (see S3), adult individuals exhibit a length/width ratio very different from that of juvenile specimens (carrying deciduous premolars)”. The authors interpreted that in *Astrapotherium magnum* the body size of a specimen retaining dp4 is similar to specimens with fully erupted permanent dentition, and thus concluded that the replacement of the premolars was completed after the adult body size is reached, as seen in afrotheres.

On one hand, Agnolin and Chimento (2011) assumed that the body size of the individual can be estimated using the cheek teeth length vs. width ratio, citing Billet et al. (2008, 2009) and Townsend and Croft (2010) as the source of this methodology. As noted by Billet and Martin (2011), these citations are erroneous because those analyses used the cheek teeth length vs. width ratio to compare ontogenetic trajectories, but not to evaluate the total individual size at a determined ontogenetic stage.

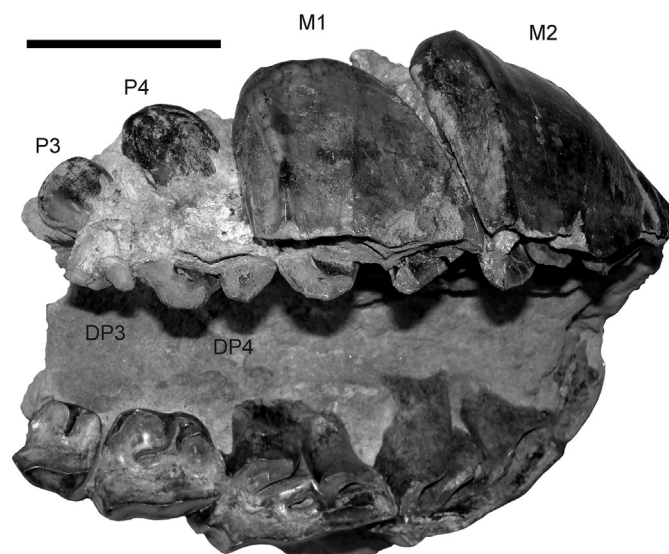


Fig. 2. Juvenile palate of *Astrapotherium magnum* (Owen, 1853) MACN Pv 19888, with erupted left and right DP3–M2 (left DP3–DP4 preserved only their lingual portion) in lateroventral view, showing the crowns of left P3–P4 encrypted below DP3–DP4. M3s of both sides are also encrypted (not shown). Scale bar = 5 cm.

Table 1

Comparisons between dental developmental stages and mandibular length for *A. magnum*. Mean adult jaw length calculated as the mean of specimens with fully erupted permanent cheek teeth.

Specimen	Erupted teeth (×2)	Number of permanent cheek teeth	% Permanent erupted	Complete jaw length (cm)	% Specimen/adult mean
YPM PU 15117	i1, i2, i3, c, p4, m1, m2, m3	8	100	57.00	105.0369841
MACN A 3207	i1, i2, i3, c, p4, m1, m2, m3	8	100	55.00	101.3514759
AMNH 9278	i1, i2, i3, c, p4, m1, m2, m3	8	100	50.80	93.61190861
MPM PV 3715	i1, i2,?, c, p4, m1, m2	6	75	48.32	89.04187843
YPM PU 15332	i1, di2, i3, c, dp4, m1, m2	4	50	44.00	81.08118069
MACN A 8600	i3, c, dp3, dp4, m1	2	25	26.00	47.91160677
MACN A s/nro.	di2?, dc, dp2, dp3, dp4	0	0	19.90	36.67080672
Mean adult	–	–	100	54.267	100

On the other hand, the support for the statement that in non-afrotherian mammals (including artiodactyls) the adult M1/1 length/width ratio is very different from that of juveniles are bivariate plots for two fossil artiodactyls, *Palaeotragus tungurensis* and *Pipestoneia douglasi*, provided in the supplementary material (Agnolin and Chimento, 2011: S3). These plots are based on some of the dental measurements of M1 and m1 published by Colbert (1936) and Tabrum and Métais (2007). However, we found no relevant difference between length/width ratio of juveniles and adults in both species, especially when all dental measurements provided by Colbert (1936) and Tabrum and Métais (2007) are analyzed, as some juvenile specimens are closer to adults than to other juveniles. Additionally, we plotted the m1 length/width for samples of adults and juveniles of the extant artiodactyl *Tayassu tajacu*, the extant perissodactyl *Tapirus terrestris*, and the litoptern *Diadiaphorus majusculus* (see Appendix 1). We found that neither in these non-afrotherian mammals are there significant differences between juveniles and adults, concluding that the criterion used by Agnolin and Chimento (2011) for body size evaluation is methodologically incorrect.

In the case of *Astrapotherium magnum*, and as in many notoungulates (Billet and Martin, 2011), the cheek teeth have particular ontogenetic trajectories for each locus, and there is no compelling evidence to indicate that individual body size can be inferred through cheek teeth proportions. The specimen plotted by Agnolin and Chimento (2011: fig. 2A) as having dp4 belongs to the YPM PU 15332 (m1 length = 42 cm, m1 width = 21 cm, Scott, 1928: 339). The nearest plotted specimen has complete permanent dentition and belongs to the YPM PU 15117 (m1 length = 44 cm, m1 width = 22 cm, Scott, 1928: 338), with identical length/width ratio. On the contrary, the mandibular and cranial measurements of the YPM PU 15117 are in average 30% larger (see Scott, 1928: 340). Additionally, in the skull of the YPM PU 15332 the frontal and parietal bones are still not fused, unlike the YPM PU 15117 and all other available skulls of *Astrapotherium* with complete permanent dentition, indicating unambiguously that the YPM PU 15332 have not reached adult size. Consequently, the evidence put forward by Agnolin and Chimento (2011) does not support that premolar replacement was completed after the adult body size was reached in *Astrapotherium*.

Dental eruption relative to jaw growth in *Astrapotherium*

The evaluation of the timing of dental eruption/replacement relative to body growth requires comparisons of the dental stages with the size of non-dental anatomical elements. Asher and Lehmann (2008) used the complete mandibular length as an indirect measurement of the body size because jaws are better represented in museum collections. Billet and Martin (2011) used the skull length and the hard palate length to evaluate the timing of dental eruption in some selected notoungulates. The few known complete

jaws of pyrotheres and xenungulates and the only complete skull of *Pyrotherium* belong to adult specimens with the complete permanent dentition in use. Among astrapotheres, *Astrapotherium magnum* is the most abundant and best known species so far. However, all available complete skulls belong to specimens with complete permanent dentition, except one (YPM PU 15332). Here we evaluate the dental eruption in *Astrapotherium magnum* relative to the complete jaw length because more complete juvenile mandibles are available.

In Table 1 we compare the dental stage of seven specimens of *A. magnum* (the only ones with complete or almost complete mandibles available to us) with their corresponding complete jaw length and with the percentage of the jaw length of adult mean. The available evidences for this species indicate that specimens with less than 95% adult jaw length mean have all (100%) their permanent lower cheek teeth erupted, and specimens with less than 60% of erupted cheek teeth are all below 85% of adult jaw length, as seen in YPM PU 15332 (Fig. 3). Asher and Lehmann (2008) concluded that in all the afrotherian genera they sampled, there were specimens with 95% adult jaw length that have less than 60% of permanent cheek teeth, indicating that the eruption of the permanent teeth is frequently completed after reaching the adult size. These results suggest that the eruption of the permanent teeth in *A. magnum* is completed well before reaching the adult size, unlike in afrotherian mammals. More specimens would obviously be needed to confirm these results, but, pending more fossils are available, it is clear that there is currently no evidence for an afrotherian-like delayed dental eruption in astrapotheres.

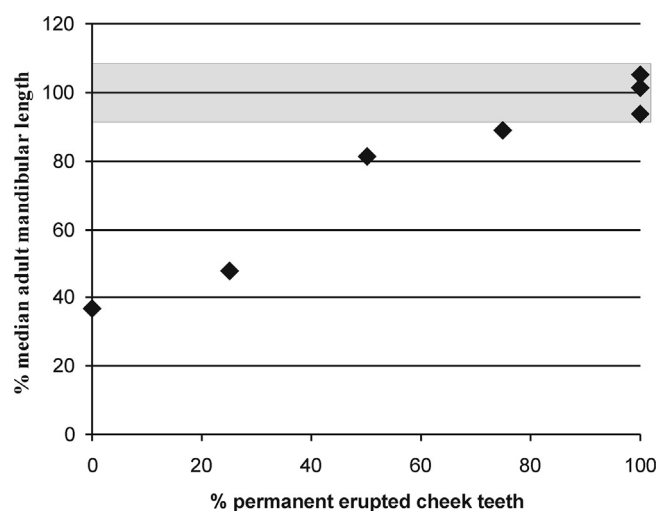


Fig. 3. Proportion of median adult mandibular length plotted against percentage of erupted cheek teeth for seven specimens of *Astrapotherium magnum* (Owen, 1853). Data are based on Table 1. Gray shaded area represents the range of mandibular length in specimens with all permanent cheek teeth erupted.

On the putative delayed dental eruption in *Toxodon* (Notoungulata)

Billet and Martin (2011) provided an exhaustive critical discussion of this character in notoungulates, concluding that there is no evidence for an afrotherian-like delayed dental eruption, except in few late diverging forms. Here we wish to add a brief comment concerning the archetypical notoungulate *Toxodon* (not discussed by Billet and Martin, 2011). Agnolin and Chimento (2011: fig. 1) presented a specimen referred to *Toxodon platensis* (MLP-P.186) with permanent p2–m3, deciduous p4, and unerupted p4. The authors interpreted this specimen as an adult-sized individual retaining deciduous teeth, thus exemplifying the afrothere-like delayed dental eruption in notoungulates. However, the authors did not take into account that the mandibular length of the MLP-P.186 is nearly 28% smaller than in specimens of *Toxodon platensis* with fully erupted permanent dentition (see Appendix 2), the incisors are still erupting, and the dentary is scarcely ossified. The more reasonable interpretation for this specimen is that it is a juvenile which has not reached adult size and shows a precocious eruption of the molars instead of an adult with late replacement of premolars.

Concluding remarks

The proposal by Agnolin and Chimento (2011) of a delayed dental eruption in SANU was herein reassessed. We found that the evidences presented by the authors as supporting their statements are founded on conceptual mistakes and inexactitudes; the information from literature is frequently misinterpreted or distorted, and some data are arbitrarily selected. Our examination of at-hand specimens led us to conclude that there is currently no evidence for a delayed premolar replacement relative to the eruption of the molars in astrapotheres and pyrotheres, but the phylogenetic significance of this feature, at least in SANU, has not yet been discussed. The occurrence of delayed dental eruption in relation to jaw growth, as recognized by Asher and Lehmann (2008) as an afrotherian synapomorphy, could be assessed only in *Astrapotherium magnum*. At least in this species the eruption of the permanent teeth is completed well before reaching adult size, unlike in afrotherian mammals. These results, in addition to those obtained by Billet and Martin (2011) for notoungulates, led us to interpret that there is no feature regarding the timing of tooth eruption that supports a phylogenetic affinity among SANU and afrotheres.

The recent published analysis by O'Leary et al. (2013) gives support to the alleged afrotherian affinities of xenungulates (represented by *Carodnia*) and notoungulates (represented by *Thomashuxleya*). However, no astrapotheres and pyrotheres were sampled in that study, and thus their relationships with other eutherian clades are still uncertain. Additionally, the analysis by O'Leary et al. (2013) neither includes representatives of extinct groups (e.g. pantodonts, dinocerates) proposed by previous workers as potentially related to some SANU. Therefore, a more complete taxonomic sample is still needed to elucidate the evolutionary relationships of astrapotheres and pyrotheres, as well as to confirm the systematic position of notoungulates and xenungulates.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2013.11.001>.

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