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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 Granorder 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.

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 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, Mastozoological 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 discussed 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 *Granastrapotherium 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 alveolous 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