

# No evidence for an afrotherian-like delayed dental eruption in South American notoungulates

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**Abstract** The fossil South American ungulates are of great interest relative to the new phylogenetic framework elaborated for living placental mammals. In particular, studies on these endemic taxa can allow for testing congruence between southern placental phylogeny and plate tectonics, beyond what has already been suggested in the Atlantogenata hypothesis based on extant afrotherians and xenarthrans. The presence of delayed dental eruption relative to skull growth is one feature characterizing the extant afrotherians and possibly the xenarthrans. Late dental eruption has been mentioned previously in South American notoungulates, thus suggesting possible resemblance with afrotherians and perhaps xenarthrans. We provide here a detailed study of the dental eruption pattern relative to the skull growth in the notoungulates. In contrast to previous statements, our results demonstrate that there is currently no evidence for an afrotherian-like delayed dental eruption in this group. For now, the inferred absence of a delayed dental eruption in notoungulates does not support atlantogenatan/afrotherian affinities for the Notoungulata, but other atlantogenatan/afrotherian characteristics remain to be explored in more detail in this group and other South American ungulates.

**Keywords** Ontogeny · Phylogeny · Placental · Growth · Atlantogenata

## Introduction

Studies on the placental mammalian phylogeny recently reached a high level of agreement on the existence of four major extant clades with support from both morphological and molecular data (e.g., Asher et al. 2009; Murphy and Eizirik 2009; Wible et al. 2007). These clades are the Laurasiatheria, Euarchontoglires, Afrotheria, and Xenarthra, with the two former generally assembled as the northern Boreoeutheria and the two latter as the southern Atlantogenata (e.g., Hällstrom et al. 2007; Murphy et al. 2007; Wildman et al. 2007). The potential correspondence between this novel phylogenetic framework and plate tectonics is actually striking. Thus, for the Atlantogenata, Wildman et al. (2007) suggested that the divergence between the southern afrotherians and xenarthrans had been triggered by the Southern Atlantic Ocean aperture and the fragmentation of Gondwana during the Late Cretaceous. However, the paleontological record (Wible et al. 2007) and some molecular clock estimates (Kitazoe et al. 2007; Douzery et al. 2003) are too young to correspond with tectonic events older than 100 Ma as causal factor behind intra-placental divergences.

During the Cenozoic, endemic placentals in South America were not only represented by xenarthrans but also by diverse fossil groups usually referred to as “South American ungulates.” These taxa are of great interest for testing further the congruence between southern placental phylogeny and plate tectonics. They are traditionally recognized as five distinct orders: the Astrapotheria, Litopterna, Notoungulata, Pyrotheria, and Xenungulata (but see Billet 2010). Unfortunately, their phylogenetic position among placentals has been until now very poorly studied (Asher et al. 2008; Billet 2010; Horovitz 2004).

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One feature characterizing the extant afrotherians and possibly the xenarthrans is a delayed dental eruption relative to skull growth (Asher and Lehmann 2008). While dealing with this character, Asher et al. (2009) cited the possibility that Notoungulata have late tooth replacement based on a previous remark by Simpson (1967: 217). They noted that this might comprise a shared feature among notoungulates, afrotherians, and possibly xenarthrans, although they also acknowledged that some ungulate-grade boreoeutherians also show delayed tooth replacement. Asher et al. (2009) also pointed out that there already exists sufficient material to have a look at the dental eruption and growth skull across ontogenetic stages in South American ungulates and that this “may enable distinction of an ‘afrotherian’ vs. ‘northern ungulate’ pattern of late eruption” in notoungulates. More recently, Agnolin and Chimento (2011) claimed that notoungulates show a relatively late eruption of permanent cheek teeth like the afrotherians. We present here a detailed study on the dental eruption and skull growth in some Notoungulata, challenging the interpretation that this group exhibits delayed dental eruption.

**Abbreviations** The following abbreviations were used throughout the article:

MNHN-BOL V	Museo Nacional de Historia Natural in La Paz, Bolivia
MNHN-SAL	Salla collections of the Muséum National d’Histoire Naturelle in Paris, France
MNHN-SCZ	Santa Cruz collections of the Muséum National d’Histoire Naturelle in Paris, France
SGOPV	Museo Nacional de Historia Natural, Santiago, Chile
UF	Florida Museum of Natural History in Gainesville, USA
YPM-PU	Yale Peabody Museum, USA

## Material and methods

We investigated and compared the timing of dental eruption and skull growth of the mesotheriid tyotherian *Trachytherus alloxus* Billet et al. 2008 from the Deseadan (late Oligocene) Salla Beds of Bolivia (Billet et al. 2008) and the toxodontid toxodontians *Adinotherium ovinum* and *Nesodon imbricatus* from the Santacrucian (early Miocene) of Patagonia (Scott 1912), three species known by abundant and well-preserved remains. As mandibles for these species are all incompletely preserved, no measurements of this bone can be provided. However, for some skulls representing

different ontogenetic dental stages, the skull length and the hard palate length could be measured or estimated. The length values for the specimens lacking the premaxillary part have been estimated by adding to the measured value the documented premaxillary length of a specimen of the same or immediately later dental stage (see Tables 1 and 2). Cranial specimens investigated are housed in MNHN-BOL V, MNHN-SAL, YPM-PU, and UF collections. Body masses estimated for these species are: 19 kg for *Trachytherus*, 34 kg for *Adinotherium*, and 294 kg for *Nesodon*, according to Croft (2000), or 120 kg for *Adinotherium* and 550 kg for *Nesodon*, according to Cassini et al. (2011a).

The skull and hard palate length of specimens have been measured either directly or from scaled photos (i.e., some *T. alloxus* specimens). The skull length has been measured from the anterior extremity of the skull at I1 to the posterior extremity at the occipital vertical wall (condyles often not preserved; Fig. 1). For *T. alloxus*, the hard palate length has been measured from the anterior edge of I1 (or dI1) to the most posterior point on the posterolateral edge of the palate, which explains why some measured values may be slightly greater than the I1-M3 measured values provided by Billet et al. (2008: Appendix 4, Table A3). For *A. ovinum* and *N. imbricatus*, the common preservation of the anterior border of the choanae on the observed rostrums allows us to provide an additional measurement of the hard palate up to this posterior structure (Fig. 1). The degree of eruption was quantified, following the procedure of Asher and Lehmann (2008), by expressing the number of permanent, occluding cheek teeth as a percentage of the norm for the species. The degree of eruption was further specified by assigning one of the 14 dental stages defined by Billet et al. (2008: Appendix 2) for the upper dentition of *T. alloxus*.

Details on the dental eruption sequence and wear stages in *T. alloxus* have been provided by Billet et al. (2008: Appendix 2) from tens of specimens. It is noteworthy that all specimens referred to this taxon—almost 300 when also counting jaw fragments exhibiting at least two teeth (Billet et al. 2008: Appendix 1)—do not deviate from the sequence described therein. In this sequence, adults can easily be recognized by their fully erupted permanent dentition, although this is also associated with typical wear stages/features such as the presence/absence of some fossettes on the cheek teeth (see upper cheek teeth stages 10–16 in Billet et al. 2008: Appendix 2). Particularly, there is no *T. alloxus* specimen with incompletely erupted cheek teeth showing an adult-like wear. This means that there should be no adult specimens incorrectly identified as juveniles, which is of great importance for the present study. The same holds true for *Adinotherium* and *Nesodon* specimens investigated herein [see also the adult stages determined for these species by Scott 1912 (pp. 130–131) and Cassini et al. 2011b].

**Table 1** Data on skull dimensions (in centimeters) and dental developmental stages in *T. alloxus*

Specimens	Stage	No. of permanent cheek teeth erupted	% permanent cheek teeth erupted	Hard palate length	Specimen/adult mean	Skull length
UF 91651 <sup>a</sup>	3	0	0	5.8+2.1=7.9	0.65	9.4+2.1=11.5
MNHN-BOL V004271	4	2	16.67	7.8	0.64	
MNHN-BOL V004302	5	2	16.67	8.3	0.69	
UF 136062 <sup>a</sup>	5.5	2	16.67	6.4+2.3=8.7	0.72	11.7+2.3=14
UF 137845	5.5	2	16.67	8.8	0.73	14.2
MNHN-BOL V003459 <sup>a</sup>	6	2	16.67	6.5+2.5=9	0.74	
MNHN-SAL 297 <sup>a</sup>	6	2	16.67	6.9+2.5=9.4	0.78	
MNHN-BOL V003825 <sup>a</sup>	7	4	33.33	7.0+2.5=9.5	0.78	
MNHN-BOL V009027 <sup>b</sup>	9	10	83.33	10.2	0.84	
YPM-PU 20687	9.5	10	83.33	10.3	0.85	15.9
MNHN-BOL V003328	10	12	100	12.8	1.06	
UF 90955	11	12	100	13	1.07	22.8
MNHN-BOL V006355	11	12	100	11.4	0.94	17.4
MNHN-BOL V005710	11	12	100	11.3	0.93	
MNHN-BOL V004360 <sup>c</sup>	11	12	100	11.7	0.97	
MNHN-SAL 7	11	12	100	11.8	0.97	
UF 91933	11.5	12	100	13.3	1.10	22.3
MNHN-BOL V004374 <sup>c</sup>	12	12	100	11.8	0.97	
MNHN-BOL V006918	12	12	100	12	0.99	
MNHN-BOL V005011	13	12	100	12.5	1.03	
MNHN-SAL 289	14	12	100	11.6	0.96	
Mean adult				12.11		20.83
CV adult				5.62		14.32

CV with standard deviation expressed as a percentage of mean palate (or skull) length among specimens with all cheek teeth erupted

<sup>a</sup> With premaxillary length estimated (measured value up to pmx–mx suture+pmx estimate=hard palate length)

<sup>b</sup> Maximal length estimate considering M3 length while not erupted through the alveolus

<sup>c</sup> Palate length measured from I1 to M3 (real hard palate length is likely some millimeters greater)

## Results

Concerning the sequence of dental eruption, it is worth noting that *T. alloxus* exhibits an almost simultaneous eruption of P2-4 and M2 (M2 slightly earlier; Billet et al. 2008), which explains the absence of any specimen presenting a percentage of erupted permanent cheek teeth between 34% and 82%. More precisely, the sequence in *T. alloxus* is P1, M1, M2, P2-4, M3 (Billet et al. 2008). In *A. ovinum* and *N. imbricatus*, the sequence is M1, (P1), M2, P2-3, M3, P4 (Scott 1912).

Asher and Lehmann (2008) found that all the afrotherian genera they sampled represented specimens with 95% median adult jaw length that had <60% of their permanent, occluding premolars and molars erupted; in other words, they found adult size to be frequently reached prior to the eruption of many permanent teeth in afrotherians and not in non-afrotherians, except for one specimen of the primate *Eulemur*. They also found similar

results from another index of skull size, the condylobasal length.

The few measurements taken for the skull length in *T. alloxus*, *A. ovinum*, and *N. imbricatus* suggest a non-delayed dental eruption when compared with dental stages (Tables 1 and 2 and Fig. 2). Measurements of the hard palate also allow quantification of skull growth. The more numerous data for this part of the skull provide more significant results than the skull length. In *T. alloxus*, *A. ovinum*, and *N. imbricatus*, all examined specimens with incompletely erupted permanent cheek teeth have non-fully grown palates (Fig. 3). This parallels the rare occurrence of adult-sized lower jaws among specimens with incompletely erupted cheek teeth in non-afrotherians (Asher and Olbricht 2009: Fig. 3). Actually, not a single specimen of the three investigated notoungulates presents more than 95% adult size (skull or palate length) with <100% of its permanent cheek teeth (Tables 1 and 2 and Fig. 3; see below for a discussion of di/polymorphism).

**Table 2** Data on skull dimensions (in centimeters) and dental developmental stages in *A. ovinum* and *N. imbricatus*

	No. of permanent cheek teeth	% permanent erupted	Skull length	Hard palate length (to posterolateral extremity)	Hard palate length (to choanae)	Specimen/adult mean
<i>Adinotherium ovinum</i>						
MNHN-SCZ uncataloged rostrum with dP2-4, M1 <sup>a</sup>	2	16.67		7.6+2.8=10.4	8.0+2.8=10.8	0.71
MNHN-SCZ uncataloged skull with dP2-4, M1, M2 <sup>a</sup>	4	33.33	18.0+2.8=20.8	9.3+2.8=12.1	8.9+2.8=11.7	0.76
MNHN-SCZ uncataloged rostrum with P4 and M3 in crypt <sup>a</sup>	8	66.67		11.7+2.8=14.5	11.4+2.8=14.2	0.93
MNHN-SCZ 14	12	100	25.2	14.7	15.1	0.99
MNHN-SCZ 12	12	100	25.1	15.4	14.9	0.97
MNHN-SCZ 20	12	100		15	15.6	1.02
MNHN-SCZ 4	12	100		15.3	15.6	1.02
Mean adult					15.3	
CV adult					2.33	
<i>Nesodon imbricatus</i>						
MNHN-SCZ uncataloged rostrum with dP2-4, unworn M1	0	0		16.3(?)		
MNHN-SCZ uncataloged rostrum with DP2-4, M1	2	16.67			17.6	0.59
MNHN-SCZ 17	2	16.67			17.9	0.60
MNHN-SCZ 18	2	16.67			18.1	0.60
MNHN-SCZ 41	4	33.33	34	21.6	20.8	0.69
MNHN-SCZ uncataloged crushed skull, unworn P4 and M3	8	66.67		25.6	24.6	0.82
MNHN-SCZ 47	10	83.33	43.1	26.6	26.5	0.88
MNHN-SCZ 46	12	100		29.5	29.2	0.97
MNHN-SCZ 40	12	100		30	30.5	1.02
MNHN-SCZ 42	12	100		30.6	30.9	1.03
MNHN-SCZ 51	12	100	46.1	27.5	29.1	0.97
MNHN-SCZ 36	12	100	47	29.1	30.2	1.01
MNHN-SCZ 52	12	100	46.5	28.9	29.6	0.99
MNHN-SCZ 50	12	100	47.3	30.1	30.4	1.01
MNHN-SCZ 35	12	100		28.1		
Mean adult					29.99	
CV adult					2.31	

CV with standard deviation expressed as a percentage of mean palate (or skull) length among specimens with all cheek teeth erupted

<sup>a</sup>With premaxillary length estimated (from adults): measured value up to pmx–mx suture+pmx estimate=hard palate length

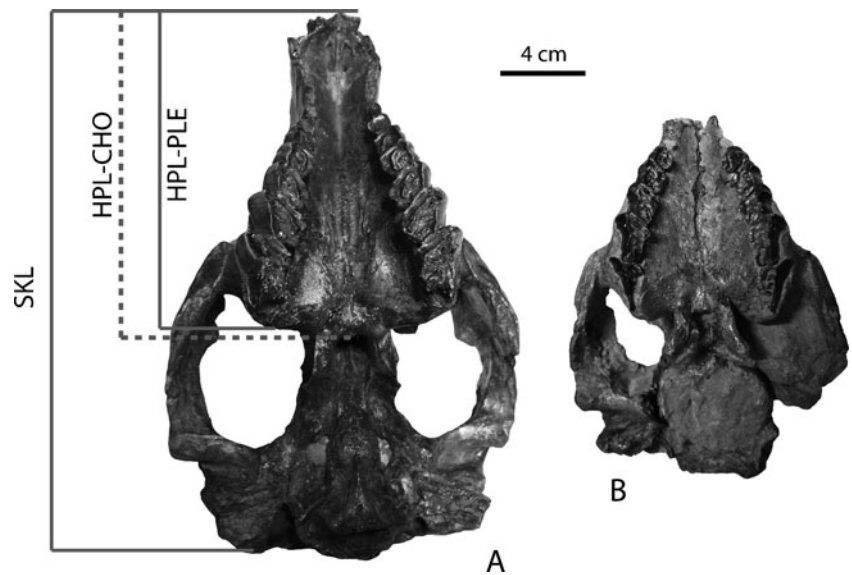
## Discussion

### Different definitions for “delayed dental eruption”

In the literature dealing with late eruption in placentals, two different patterns have been studied. The first one concerns the late replacement of the deciduous premolars dP2-4 by permanent premolars P2-4 relative to the eruption of the molars, especially the M3. This latter pattern has notably been observed in the hyracoid, tenrecid, and macroscelidean afrotherians; phenacodontid and pleuraspidotheriid condylarths; some tillodonts; and some artiodactyls and

primates; as well as in some lipotyphlans, carnivorans, and scandentians (Asher and Olbricht 2009; Holroyd 2008, 2009; Slaughter et al. 1974; Smith 2000). The second pattern rather concerns the delayed eruption of the permanent dentition relative to the skull growth and not only constitutes a synapomorphy for afrotherian mammals according to Asher and Lehmann (2008) but also sporadically occurs in some artiodactyls and primates (Asher and Olbricht 2009; Asher et al. 2009). When speaking about late tooth replacement in notoungulates, Simpson (1933, 1967) certainly referred to the late replacement of deciduous premolars relative to the third molar. Actually, it is

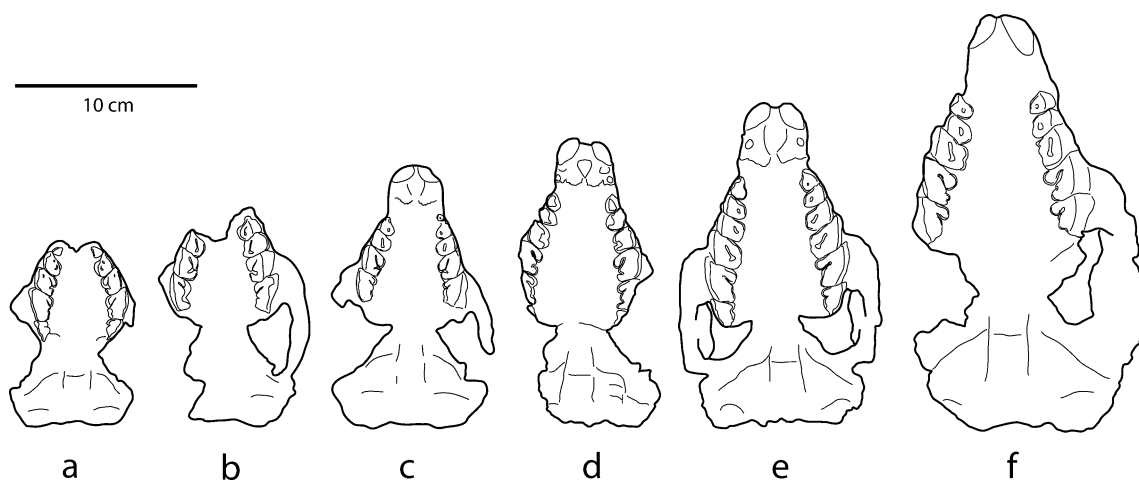
**Fig. 1** *A. ovinum* adult and juvenile skulls and illustration of the measurements taken. **a** Adult, *A. ovinum*, MNHN-SCZ 14, all permanent cheek teeth erupted. **b** Juvenile, *A. ovinum*, MNHN-SCZ uncataloged skull with right and left dP2-4, M1, M2. *HPL-CHO* hard palate length up to choanae, *HPL-PLE* hard palate length up to posterolateral extremity of palate, *SKL* skull length



noteworthy that Simpson (1932, 1933, 1948, 1967) only used the expression “late replacement” and never “late eruption” in his descriptive works on South American ungulates. In notoungulates, the term “replacement” concerns loci with two generations of teeth, i.e., the incisors, canines, and premolars, but not the molars. Even if he did not state it explicitly, Simpson very likely meant a premolar vs. molar timing of eruption as each time he dealt with “late replacement,” he detailed this along with a timing comparison of the premolar replacement and molar eruption (Simpson, 1932: 4, 1933: 4, 1948: 179, 1967: 217). At the same time, he never discussed skull growth along with these statements on late tooth replacement. Furthermore, when available, he figured ontogenetic series, e.g., for *Notostylops* (Simpson, 1948: 182–183), but he never used them to make

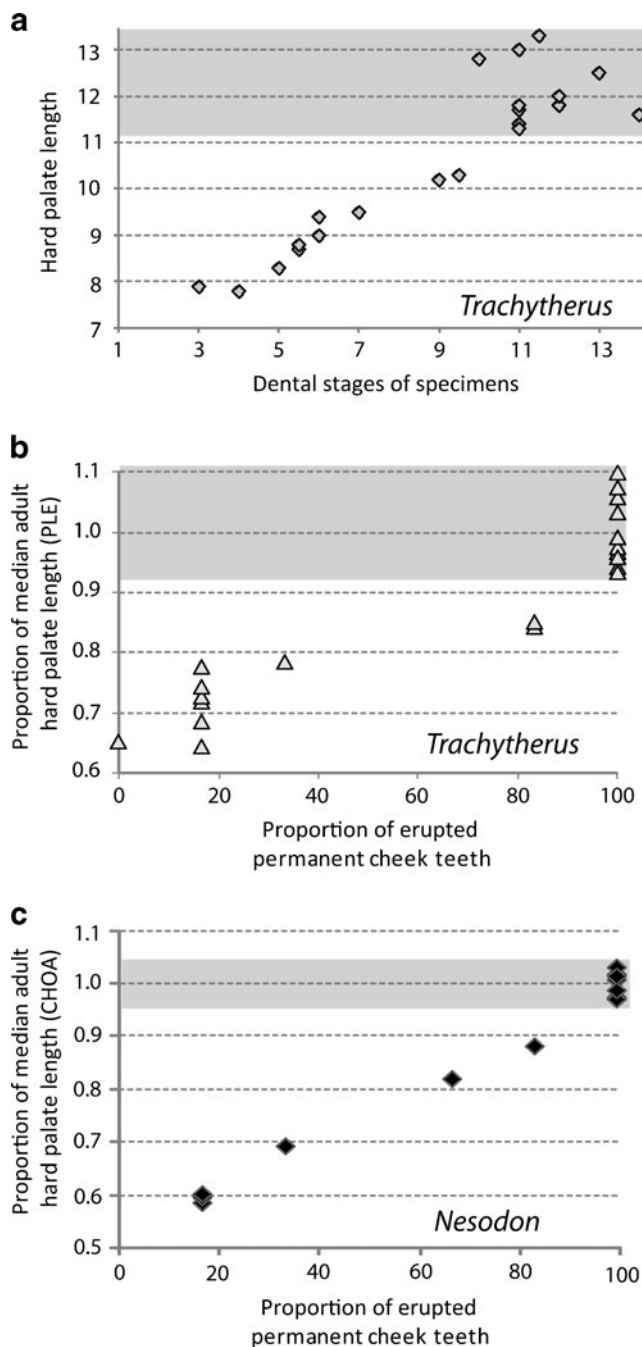
general comments on the timing of dental eruption relative to skull growth. It is also likely that Simpson did not have many notoungulate cranial ontogenetic series available for a detailed study of the dental eruption relative to skull growth. At least, such a putative study would have encompassed the Santacrucian material like *Adinotherium*, *Nesodon*, or *Protypotherium*, which are discussed here. All these arguments make a strong case that Simpson only meant a late eruption of premolars vs. molars when stating a “late replacement.”

In notoungulates, a late replacement of deciduous premolars vs. molars has been documented for some late diverging interatheriids and mesotheriids (Townsend and Croft 2010; Simpson 1932; Sinclair 1909) and some toxodontids (Bond et al. 2006: Fig. 1; Roth 1895; Scott



**Fig. 2** Skull growth series of *T. alloxus*. **a** UF 91651, dP2-4, unworn erupting M1, cf. dental stage 3 in Billet et al. (2008). **b** UF 136062 dP2-4, slightly worn M1, stages 5–6. **c** UF 137845, dP2-4, slightly worn M1, stages 5–6. **d** YPM-PU 20687, very slightly worn P2-4,

M1, slightly worn M2, M3 in crypt, stages 9–10. **e** MNHN-BOL V 006355, P2-M3, stage 11. **f** UF 90955, P2-M3, stage 11. **e**, **f** Two extreme sizes among the adult specimens



**Fig. 3** Hard palate length and dental eruption in *T. alloxus* and *N. imbricatus*. **a** Palate length in centimeters compared with the dental stages of specimens in *T. alloxus* (Billet et al. 2008). **b** Proportion of median adult hard palate length (y-axis, median value=1.0) in relation to the proportion of erupted permanent cheek teeth (x-axis, all permanent cheek teeth erupted=100) in *T. alloxus*; hard palate length measured from anterior border of I1/dI1 alveolus to the most posterior point on the posterolateral edge of palate (PLE). **c** Same as **b** for *N. imbricatus*; hard palate length measured from anterior border of I1/dI1 alveolus to anterior border of choanae (CHOA). Gray shaded areas represent the range of hard palate length in specimens with all permanent cheek teeth erupted. Note the absence of adult-sized hard palates among specimens with incompletely erupted cheek teeth. Data are based on Table 1

1912). Conversely, in the early diverging mesotheriid *T. alloxus* and many other notoungulates, M3 erupts after P2-4 and there is no late replacement of upper premolars vs. molars.

Only the pattern of a delayed eruption of the permanent dentition relative to skull growth has been explicitly proposed as an afrotherian synapomorphy (Asher and Lehmann 2008). Indeed, a late replacement of deciduous premolars relative to molar eruption may at times overlap with this former pattern, as is the case in some afrotherians (e.g., hyracoid, tenrecid, and macroscelidean). However, as shown for *Erinaceus europaeus* (European hedgehog; Asher and Olbricht 2009) and as found here for *Nesodon* and *Adinotherium*, these two patterns are not fully coincidental and thus should not be equated. Therefore, Simpson's comments on late tooth replacement are not directly comparable with eruption patterns recently characterized for afrotherians.

#### Poly/dimorphism and dental eruption in notoungulates

For *T. alloxus*, the general coefficient of variation (CV) of adult palate length is 5.62 (Table 1), which is significant but much less than the values exceeding 10 for the mandible lengths of the di/polymorphic genera *Tenrec* and *Didelphis* (Asher and Lehmann 2008). However, the three measurements of skull length for adults *T. alloxus* show a considerable CV of 14.32 and might suggest a possible di/polymorphism, which would therefore be much more conspicuous on total skull length than on hard palate length. Previous measurements taken on individual cheek teeth of *T. alloxus* have shown not only a considerable metric variation but also a great continuity (Billet et al. 2008). Shockey and Anaya (2008: 144) also acknowledge a wide variation in the size of *T. alloxus* individuals from observations of elements of the entire skeleton, but they argue that the absence of any discontinuity in size does not suggest the presence of sexual dimorphism in this taxon.

Concerning *Nesodon* and *Adinotherium*, there is much less variation in size among the studied adult specimens (skull and hard palate length; Table 2). The metric variation among the numerous skulls of *N. imbricatus* and *A. ovinum* measured by Scott (1912) and Cassini et al. (2011b) shows a similar low range.

A particular potential problem with fossil taxa with intraspecific size variation is the fact that the "adult" size range might be biased by (di/polymorphic) large specimens and that smaller specimens have not been preserved. However, the size variation range of the studied adult *T. alloxus* specimens is already significant (moderate for hard palate length, high for the skull), which suggests that this is a representative sample of the size variation in this species. For *Nesodon* and *Adinotherium*, the measured size variation is much smaller.

In any case, there is no specimen of *Trachytherus*, *Nesodon*, or *Adinotherium* that falls within 90% of the median adult palate length (or skull length) without all the cheek teeth erupted. This may parallel the case of the marsupial *Didelphis marsupialis* which shows considerable intraspecific size polymorphism, but no specimen falling within 90% of the median adult jaw length has less than two thirds of its cheek teeth erupted (Asher and Lehmann 2008). In contrast, some specimens of the afrotherian *Tenrec ecaudatus*, another taxon with large intraspecific size di/polymorphism, approximate adult jaw length with less than half of their permanent cheek teeth erupted, which suggests a delayed dental eruption (Asher and Lehmann 2008). Therefore, the present observations at the notoungulates *Trachytherus*, *Nesodon*, and *Adinotherium*, even if limited, do not provide evidence for a delayed dental eruption.

#### Dental eruption pattern in notoungulates

Agnolin and Chimento (2011) recently claimed that notoungulates, similar to Afrotheria, present a relative late eruption of permanent cheek teeth. Their argumentation is based on the assumption that a molar of a specimen with deciduous cheek teeth can, in some cases, be distinguished by its length/width ratio from a molar of the same locus in a specimen with a fully erupted permanent dentition. According to Agnolin and Chimento (2011: 3 and Fig. 2), in taxa with non-delayed dental eruption, this distinction should be possible, whereas it should not be possible in taxa with delayed dental eruption. Actually, to link their bivariate analysis to the theme of dental eruption and skull growth, Agnolin and Chimento (2011) argue that length vs. width ratio of cheek teeth in notoungulates is a useful parameter for the evaluation of the total size of an individual, and they erroneously cite Billet et al. (2008, 2009) and Townsend and Croft (2010) as supporting this statement. However, there is a typical trend for many notoungulate cheek teeth to show dramatic changes in their occlusal dimensions with increasing wear also after replacement of the deciduous premolars, as explicitly stated by Croft et al. (2003), Billet et al. (2008, 2009), and Townsend and Croft (2010). These trends may be quite different on M1, M2, or M3, and measurements from different tooth loci therefore might indicate different body size variation trends for the same individual. Even if such metric data were pertinent for this purpose, the measurements used by Agnolin and Chimento (2011) for their bivariate analysis are strongly biased by the incompleteness of the sample. Measurements of a large number of adult specimens of “*Plesiotypotherium*” *minus* and *Archaeohyrax suniensis* that were provided respectively by Townsend and Croft (2010: Fig. 14.2) and Billet et al. (2009: Appendices 2 and 3) were not included in the

analysis by Agnolin and Chimento (2011). These adult specimens with moderate to heavily worn M1/m1 would have contradicted their results. Therefore, the bivariate analysis by Agnolin and Chimento (2011) actually does not permit the detection of a delayed dental eruption.

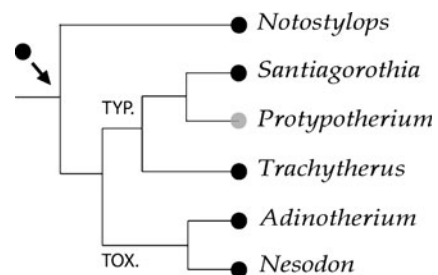
In most of the references (e.g., Roth 1903, 1927; Scott 1912) cited by Agnolin and Chimento (2011) in support of their interpretation, we were not able to find any clear statement that adult size is associated with the retention of milk teeth in notoungulates (except for one possible exception in late diverging *Prototypotherium*; see below). Some of these references, such as Ameghino (1904) who argued for three generations of cheek teeth in *Nesodon*, are clearly outdated.

In addition, among the genera cited by Agnolin and Chimento (2011) as presenting delayed dental eruption are *Adinotherium* and *Nesodon*, which, in our metric analysis (and others, see below), clearly do not show any evidence of a delayed dental eruption relative to skull growth. Therefore, we cannot follow the conclusions of Agnolin and Chimento (2011) claiming a delayed dental eruption for notoungulates.

According to our results, the tyotherian mesotheriid notoungulate *T. alloxus* and the toxodontid toxodontians *A. ovinum* and *N. imbricatus* do not present evidence for a delayed dental eruption relative to skull growth. Additional data, even if currently more limited, can be provided for some other notoungulates.

Among early diverging notoungulates, an ontogenetic series of three skulls has already been described for *Notostylops murinus* (Simpson 1948: Fig. 69); it also suggests a craniodental growing pattern with no delay in dental eruption relative to skull growth.

For Toxodontia, except for the investigated early diverging toxodontids *Adinotherium* and *Nesodon*, few data are available. Madden (1997) showed that the mandible of the later diverging toxodontid *Pericotoxodon perignathus* keeps on growing in depth after complete eruption of the



**Fig. 4** Phylogenetic relationships and inferred pattern of dental eruption relative to skull growth among the Notoungulata: delayed dental eruption (gray circle); non-delayed dental eruption (black circle). Pattern of relationships from Billet (2011) and Hitz et al. (2000). Parsimony suggests that non-delayed eruption is a plesiomorphic condition within Notoungulata. TYP Typotheria, TOX Toxodontia

permanent cheek teeth. Unfortunately, no data are available on the longitudinal growth of the mandible in this taxon. Concerning *Nesodon* and *Adinotherium*, further data can be found in Scott (1912) and Cassini et al. (2011b). Particularly, their measurements are fully congruent with our results that among their sample, all specimens retaining deciduous teeth are smaller than those with a fully erupted permanent dentition.

Among the Typotheria, in addition to *Trachytherus*, the Early Oligocene typotherian interatheriid *Santiagorothia chiliensis*, with P3-4 erupting after M3, does not present evidence for a delayed dental eruption relative to skull growth: the hard palate of SGOPV 2827 with dP3-4 and erupting M3 is definitely smaller than those of the adult specimens SGOPV 2914 and 2812 in the scaled photos presented by Hitz et al. (2000). Actually, evidence for adult-sized specimens still retaining deciduous teeth in Notoungulata is, to our knowledge, only (possibly) present in the late diverging interatheriid *Protypotherium* where M3 also erupts before P3-4 (see Sinclair 1909: plate V), but some other late diverging interatheriids like *Cochilius* may also exhibit this pattern (Simpson 1932).

When mapping on a cladogram the pattern of dental eruption relative to skull growth assumed for each investigated notoungulate taxon, parsimony suggests that non-delayed eruption represents the ancestral state for the Notoungulata (Fig. 4). The case of some late diverging interatheriids like *Protypotherium* thus appears isolated within the investigated notoungulates. Although these results are based on a small number of observations due to limitations of the fossil record, they demonstrate that there is currently no evidence available for an afrotherian-like delayed dental eruption in notoungulates, in contrast to the statement by Agnolin and Chimento (2011).

The possibility of relationships between Atlantogenata and South American ungulates obviously comes to mind when thinking about a scenario of southern placental biogeographic diversification congruent with plate tectonics. As mentioned above, delayed dental eruption has been proposed as a synapomorphy for afrotherians and also possibly for xenarthrans (Asher and Lehmann 2008; Asher et al. 2009). For now, the inferred absence of a delayed dental eruption in notoungulates does not support atlantogenatan/afrotherian affinities for the Notoungulata.

Other afrotherian (or atlantogenatan) apomorphic features like deviation of vertebral formulae and abundance of vertebral anomalies have been suggested as possibly linked to delayed dental eruption through a common developmental mechanism (Asher et al. 2009; Sánchez-Villagra et al. 2007). Though delayed dental eruption is here inferred to be absent in notoungulates, other putatively associated afrotherian apomorphies still deserve scrutiny in this group. Incidentally, Agnolin and Chimento

(2011) recently suggested the number of vertebrae and the cotylar fossa on the astragalus (see also Tabuce et al. 2007) to be common synapomorphies of afrotherians, notoungulates, and astrapotherians.

Concerning other South American ungulates, few data are known on the timing of their dental eruption (for litopterns, see Bergqvist 2010) as well as for their vertebral morphologies (Sánchez-Villagra et al. 2007). The cotylar fossa on the astragalus present in afrotherians (Tabuce et al. 2007) also needs to be further studied in South American ungulates to evaluate the extent to which this structure is comparable across “southern” placental mammals (i.e., atlantogenatans).

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