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Postnatal ontogenetic scaling of Nesodontine (Notoungulata, Toxodontidae) cranial morphology

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Abstract

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Toxodontidae is a clade of endemic South American ungulates that comprises medium to very large animals, including strict megammamals, i.e., 1000 kg or more. *Adinotherium* at approximately 120 kg and *Nesodon* at 550 kg are, respectively, the smallest and the largest Nesodontinae of Santacrucian age (early Miocene). The large number of specimens recorded and the quality of preservation (including very young animals) permit a morphometric study of cranial ontogeny. We measured 17 cranial variables on an ontogenetic series of 23 specimens of *Adinotherium ovinum* and 11 of *Nesodon imbricatus*. Bivariate analysis (standardized major axis) was performed to obtain the coefficients of allometry using skull length as the independent variable. Results indicate that eight of 16 variables show an isometric trend, seven exhibit positive allometry, and only the height of the orbit in *N. imbricatus* exhibits negative allometry. Contrary to expectation, neurocranial variables are positively allometric or isometric. With respect to the splanchnocranium, most variables related to the rostrum, palate, and masticatory muscles show positive allometry, suggesting a strengthening of masticatory system in adults of both taxa. The splanchnocranial allometric trends fail to support previous inferences of specialized herbivory, suggesting generalized herbivory in nesodontines.

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Introduction

Toxodontids are endemic South American fossil ungulates, characteristic of the Cenozoic faunas of the continent. Although variable in size, their skulls present a conservative morphology that permits comparison of their ontogenetic trajectories within an established phylogenetic framework. The goal of this comparison is to detect possible patterns in the evolution of size within the group. Currently, toxodontids include two monophyletic groups: Toxodontinae and Nesodontinae (Nasif *et al.* 2000). Among them, the early Miocene (Santacrucian Age) nesodontines provide an unusually large sample for growth studies because of the availability of complete ontogenetic series. Recent fieldwork (Vizcaíno *et al.* 2010) yielded a large number of nesodontine skulls, which, together with collections made in the nineteenth century by Carlos Ameghino and John Bell Hatcher, make an excellent ontogenetic series of well-preserved putative juvenile, subadult, and adult individuals for the genera *Adinotherium* Ameghino 1887 (Fig. 1A–C) and *Nesodon* Owen 1846 (Fig. 1D–F).

Nesodontines have been compared with rhinos, because of their inferred general appearance, the grinding pattern of molar crowns, and some cranial features (Ameghino 1907; Scott 1912). Particularly for *Adinotherium ovinum* (Owen 1853), areas of roughness on the frontal bones suggest the presence of rhino-like horns, a character that could be considered evidence of sexual dimorphism, as they are more marked in putatively male specimens (Ameghino 1907; Scott 1912). *A. ovinum* is a rather small toxodontid, considered an

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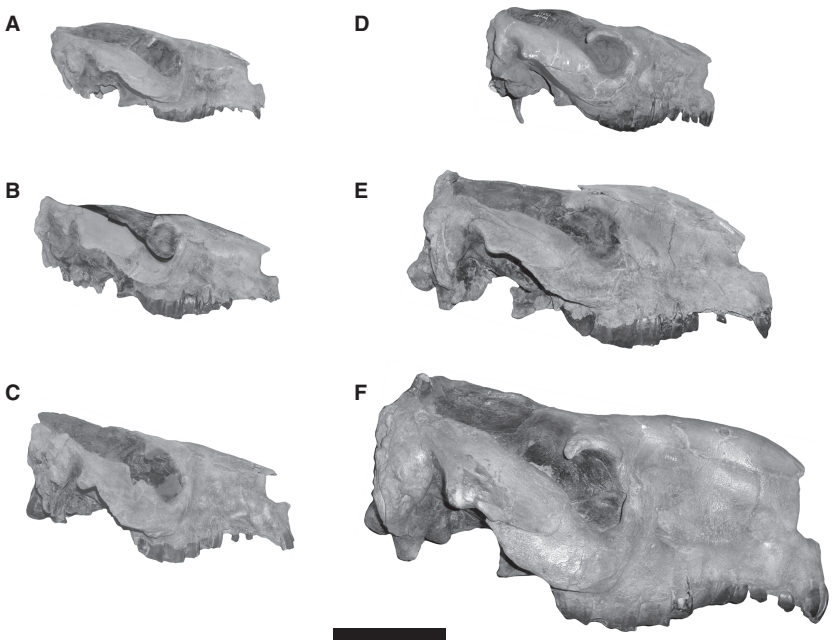

Fig. 1—Three ontogenetic stages in *Adinotherium ovinum* and *Nesodon imbricatus*. —A. Juvenile *Adinotherium* MPM-PV 3541 left side (mirror image); —B. Subadult *Adinotherium* MPM-PV 3666 right side; —C. Adult *Adinotherium* MPM-PV 3532 left side (mirror image); —D. Juvenile *Nesodon* YPM-PU 15354 right side; —E. Subadult *Nesodon* MPM-PV 3669 left side (mirror image); —F. Adult *Nesodon* YPM-PU 15252 right side. Scale bar 100 mm.

inhabitant of open environments, feeding mostly on grasses and/or other open-habitat vegetation (Patterson and Pascual 1968; Cifelli 1985; Cassini *et al.* in press), although some consider it a pure leaf browser (Townsend and Croft 2008). While the description of the genus was mostly drawn on the basis of specimens referred to *A. ovinum*, a few additional valid species are recognized, with the better preserved specimens belonging to *A. robustum* Ameghino 1891.

Adinotherium is closely allied to *Nesodon* (Madden 1997; Nasif *et al.* 2000). Probably due to their highly conservative cranial shape, Owen (1853) thought both belonged to a single genus, *Nesodon*. Both *Nesodon* and *Adinotherium* are known from complete dentitions with hypertrophied lateral incisors and high-crowned non-evergrowing cheek teeth (protohypsodonty *sensu* Mones 1982). Neither has a diastema, but each has large masseter and temporalis attachment areas. Although Scott (1912) followed Ameghino's view and maintained them as different genera, he still stated that '…the skull of *Adinotherium* is so very closely like that of *Nesodon*, that it is difficult to find any tangible points of distinction'. However, in his comprehensive revision, Scott (1912) remarked a series of anatomic characters that clearly differentiate both genera. For instance, the species of *Adinotherium* are all smaller than those of *Nesodon* (approximately 120 and 550 kg, respectively; Vizcaíno *et al.* 2010), the upper premolars exhibit a simpler pattern, the anterior lobe of the lower molars is relatively broader, the rostrum is broadened, and apparently males of *Adinotherium* exhibit dermal bone in the frontal region, which seems to be absent in *Nesodon*. Several additional differences in cranial and postcranial morphology between these genera are reported and discussed in the monograph (Scott 1912).

Although some ontogenetic inferences were made in other toxodontids such as the late Miocene *Pericotoxodon platygnathus* Madden 1997 and the Pleistocene *Toxodon platensis* Owen 1837 (Madden 1997; Pérez García 2004), they were principally based on tooth eruption and wear, without the use of cranial regressions. As mentioned earlier, the conservative morphology and the variable size of toxodontids allow us to compare the ontogenetic trajectories of *Adinotherium* and *Nesodon* to look for patterns in size-correlated evolution in the group. The existence of common trajectories of skull growth in *Adinotherium* and *Nesodon* might represent the plesiomorphic condition for the toxodontid clade. Detection of common patterns of cranial growth in closely related groups is essential to assess a possible common plan in growth patterns within a more inclusive phylogenetic context. Thus, comparisons of the trajectories found in the well-represented *Adinotherium* with those of closely related toxodontids (e.g., *Nesodon*) are of special importance for understanding the evolutionary size change in the family. In this contribution, we also investigated the way in which the cranial configuration of *A. ovinum* and *Nesodon imbricatus* Owen 1846 changes from juveniles to aged adults, offering a quantitative approach based on an ontogenetic series of skulls of different inferred life stages. The ontogenetic series studied also permit us to evaluate the morphological changes on functional grounds and for a period of

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development in which critical changes occur. Interactions between growth of neurocranial and splanchnocranial components through developmental stages cause modifications to functions of the skull that are linked to the transition from juvenile to adult diets. Finally, the allometric analyses allow us to study the relative growth of different cranial components in these species.

Material and methods

Study specimens

We analyzed 23 specimens of *A. ovinum* and 11 specimens of *N. imbricatus* housed at the vertebrate paleontology collections in Argentina at the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN, Buenos Aires), Museo de La Plata (MLP, La Plata), Museo Regional Provincial Padre 'M. J. Molina' (MPM-PV, Rio Gallegos, Santa Cruz) and in the USA at the American Museum of Natural History (AMNH, New York) and Yale Peabody Museum (YPM-PU, New Haven) (Table 1). We choose the most complete, well-preserved specimens with the least qualitative litostatic deformation for both species. Age stages (juveniles, subadults, and adults) were estimated from dental formulae and observations of sutural fusion at basicranium (see Scott 1912; Morris 1972). Specimens with deciduous dentition without M3 erupted were considered juveniles; specimens with erupted M3 without or with little wear were considered as subadults; specimens with complete permanent dentitions with M3 fully erupted and fused basicranium

Table 1 List of Toxodontidae skulls examined with teeth replacement and assigned age

Catalog	Species	dP4	P4	M1	M2	M3	Age	TSL
AMNH 9276	*Adinotherium ovinum*	Erupted/worn	–	Very early erupting			J	147.864
MPM-PV 3541	*A. ovinum*	Erupted/worn	–	Almost fully erupting			J	172.739
YPM-PU15986	*A. ovinum*	Erupted/worn	–	Erupted/worn			J	194.365
MPM-PV 3675	*A. ovinum*	Erupted/worn	–	Erupted/worn			J	195.02
YPM-PU 15114	*A. ovinum*	Erupted/worn	–	Erupted/worn	Very early erupting		J	187.413
MPM-PV 3666	*A. ovinum*	Erupted/worn	–	Erupted/worn	3/4 erupting		J	205.319
YPM-PU 56890	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Almost fully erupting	S	216.239
MLP 84-III-9-10	*A. ovinum.*	–	Almost fully erupting	Erupted/worn	Erupted/worn	Almost fully erupting	S	222.043
MPM-PV 3543	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	222.789
YPM-PU 15983	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	226.983
MPM-PV 3532	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	227.192
AMNH 9171	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	227.413
AMNH 9571	*A. ovinum*	–	Fully worn	Fully worn	Fully worn	Erupted/worn	A	232.697
YPM-PU 15382	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	233.96
MACN-A 926	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	234.989
MPM-PV 3667	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	235.197
AMNH 9140	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	235.294
MLP 12-5	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	236.116
MPM-PV 3668	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	238.113
YPM-PU 15118	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	239.38
MACN-A 5352	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	246.179
MPM-PV 3535	*A. ovinum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	249.363
MPM-PV 3476	*A. ovinum*	–	Erupted/worn	Broken	Broken	Broken	A	255.169
AMNH 9532	*A. robustum*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	249.537
AMNH 9497	*A. robustum*	–	Fully worn	Fully worn	Fully worn	Fully worn	A	252.557
YPM-PU 15354	*Nesodon imbricatus*	Erupted/worn	–	1/2 erupting			J	214.931
YPM-PU 15001	*N. imbricatus*	Erupted/worn	–	1/2 erupting			J	252.146
MPM-PV 3669	*N. imbricatus*	Erupted/worn	–	Erupted/worn	3/4 erupting		J	310.28
YPM-PU 15135	*N. imbricatus*	–	Almost fully erupting	Erupted/worn	Erupted/worn	Almost fully erupting	S	369.78
YPM-PU 15256	*N. imbricatus*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	421.872
YPM-PU 15000	*N. imbricatus*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	421.898
MACN-A 5305	*N. imbricatus*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	421.914
YPM-PU 15252	*N. imbricatus*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	425.392
YPM-PU 15141	*N. imbricatus*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	445.828
YPM-PU 15336	*N. imbricatus*	–	Erupted/worn	Erupted/worn	Erupted/worn	Erupted/worn	A	450.18
AMNH 9128	*N. imbricatus*	–	Erupted/worn	Fully worn	Erupted/worn	Erupted/worn	A	462.245
YPM-PU 16012	*N. cornutus*	–	Broken	Broken	Broken	Broken	A	383.524

J, juvenile; S, subadult; A, adult; TSL, total skull length in millimeters.

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were considered adults. Our sample of *A. ovinum* included six juvenile specimens that retain deciduous dentition and only M1 and/or M2 erupted, two subadult with M3 emerging and little wear, and twelve specimens with a complete adult dentition at different stages of wear, one of them (AMNH 9571) with most heavily worn dentition (Table 1). For the allometric analyses, we also included a moderately well-represented ontogenetic series of 11 specimens of the sister group *N. imbricatus* (Table 1). Our sample of *N. imbricatus* included three juvenile specimens that retain deciduous dentition with M1 and/or M2 emerging, one subadult specimen with some deciduous premolars and M3 emerging with little wear, and seven specimens with adult dentition at different stages of wear (Table 1). Two adult specimens of *A. robustum* and one adult of *N. cornutus* Scott 1912 were not used to calculate allometric trends but were included in the graphics to explore their position along the ontogenetic trajectory observed for their congeners.

Study of growth and measurements

Allometry of growth explicitly considers timing of changes throughout the life of an individual (Kunz and Robson 1995; Prestrud and Nilssen 1995; Maunz and German 1996; Stern and Kunz 1998). By contrast, allometry of size compares changes against overall size along a growth series; the time frame is implicitly incorporated but not specified. Allometry of size may in turn be interspecific with the purpose of studying functional changes from an evolutionary perspective within a lineage (Davis 1962; Radinsky 1984; Hayssen and Kunz 1996; Silva 1998) or intraspecific with an aim similar to studying the allometry of growth (Nelson and Shump 1978), that is, to describe relative modifications in structures as the animal grows.

For the allometric analysis, we used 17 cranial variables (Fig. 2) including length, width, and height of several neurocranial and splanchnocranial components. Overall size was estimated by the total length of the skull because this measurement is considered a good estimator of body mass for all living ungulates and in most mammals in general; also, it is not affected by allometric trends (Janis 1990; Emerson and Bramble 1993). We interpreted coefficients of allometry as growth rates, although they actually represent rates of size increase (Simpson *et al.* 1960; Gould 1966; Nelson and Shump 1978). Thus, we ultimately assumed that intraspecific allometry of size closely reflects true allometry of growth. The relation of each variable to overall size (total length of the skull) was examined with the equation of allometry:

$$\log(y) = \log(b_0) + b_l \log(x) + log(e);$$

where y is any of the measured skull variables, $a = \log(b_0)$ is the y-intercept (and b_0 is the constant term of growth function), b_l is the slope of the line or coefficient of allometry, x is the total length of the skull, and e is the error term.

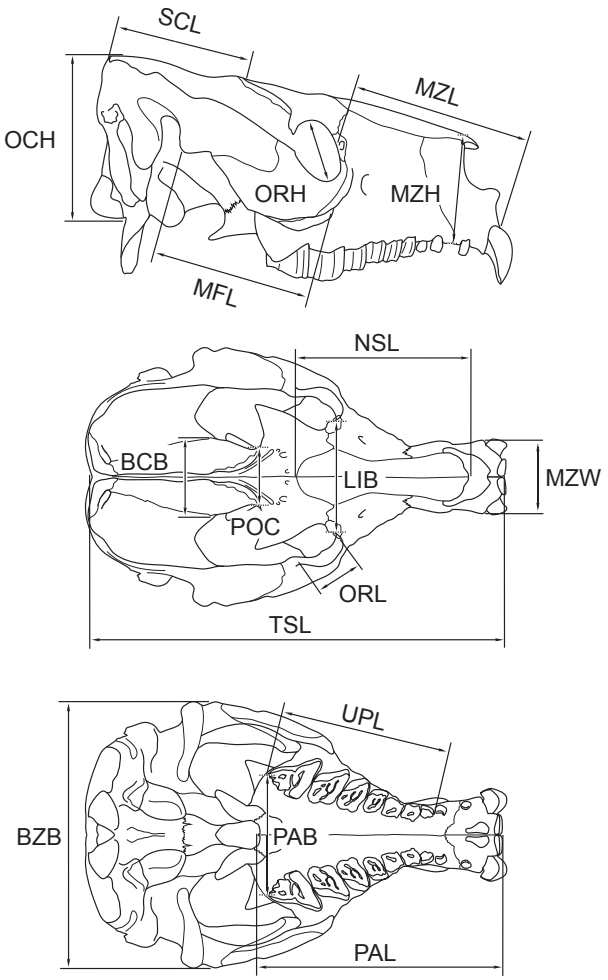

Fig. 2—Cranial measurements of *Adinotherium ovinum* used in this study. BCB, braincase breadth; BZB, bizygomatic breadth; LIB, least interorbital breadth; MFL, masseteric fossa length; MZH, muzzle height; MZL, muzzle length; MZW, muzzle width; NSL, nasal suture length; OCH, occipital height; ORH, orbital height; ORL, orbital length; PAB, palate breadth; PAL, palate length; POC, postorbital constriction; SCL, sagittal crest length; TSL, total skull length; UPL, upper postcanine tooth row length.

This equation was derived from the power growth function, $y = b_0.x^{b1}.e$, by converting each side to its (base 10) logarithm (Alexander 1985; Silva 1998). We assumed that the error term e is multiplicative, that is, it interacts with x, as expressed in the second equation, so log transformation allows the function to take the form of the first equation. Significance of allometry coefficients was evaluated by means of two-tailed t-tests at a significance level set to $P = 0.05$. Deviations from isometry were assessed by comparing the allometric coefficient with that expected under geometric similarity (Alexander 1985). Expected coefficients under isometry are equal to 1.0 for variables involved, because they all are linear measurements. Consequently, we perform

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F-tests with the null coefficient set at 1.0 to assess significant deviations from isometry (Warton and Weber 2002). Negative allometry refers to the case of a coefficient significantly less than expected by isometry, and positive allometry is when it is significantly higher (Emerson and Bramble 1993). Ordinary least squares regression (OLS) is a method of fitting lines for the prediction of the *Y*-variable that assumes a clearly identifiable independent variable with neither measurement error nor natural variation (Hair *et al.* 1995; Zar 1999). The major axis (MA) and standardized major axis (SMA) are other ways of determining an axis or line-of-best-fit. Here, the purpose of line-fitting is not to predict *Y* from *X*, but to summarize the relationship between two variables. The major axis is the line that minimizes the sum of squares of the shortest distances from the data points to the line, so in this method residuals are measured perpendicular to the line. The SMA is the major axis calculated on standardized data, then rescaled to the original axes that allowed variation in both dimensions, so residuals were oblique with *X* and *Y* directions without equal weight when measuring departures from the line. Both MA and SMA are more appropriate for dealing with allometric approaches (for extensive overviews on the subject, see Warton *et al.* 2006). Therefore, we calculated SMA and MA coefficients of allometry for all variables. All regression coefficients, statistical parameters, and tests were performed using smart package of R software (Warton and Weber 2002).

Results

All regressions were significant except those including the postorbital constriction (POC) for *A. ovinum* and *N. imbricatus* (shaded variable in Tables 2 and 3). Regressions for *Adinotherium* showed high values of correlation in all dependent variables, except in POC. In both analyses (MA and SMA), the observed allometric trend was isometry in eight of 16 variables: muzzle height and width (MZH, MZW), occipital height (OCH), orbital height and length (ORH, ORL), least interorbital breadth (LIB), masseteric fossa length (MFL), and braincase breath (BCB). In contrast, slopes for bizygomatic breadth (BZB), palate breadth and length (PAB, PAL), sagittal crest length (SCL), muzzle length (MZL), nasal suture length (NSL), and upper postcanine tooth row length (UPL) showed a positive allometric trend, with no variable showing negative allometry (Table 2). Despite the small sample size for *Nesodon*, the ontogenetic series examined allowed us to detect allometric trends in all variables considered. As for *Adinotherium*, trends observed were similar in both analyses (MA and SMA), with high values of correlation, except in POC. However, the allometric trends for *Nesodon* were

Table 2 Regression results for *Adinotherium ovinum*

				Major axis (MA)				Standardized major axis (SMA)				
Variable	***n***	**R^2**	$F_{(1, n-2)}$	$\log(bo)_{MA}$	$t_{(n-2)}$[b]	$b_{1\text{-}MA}$	Trend	$\log(bo)_{SMA}$	$t_{(n-2)}$[b]	$b_{1\text{-}SMA}$	Trend	$F\text{iso}_{(1, n-2)}$[c]
MZH	**16**	**0.882**	104.373	**−0.583**	−2.509*	**1.014**	**iso**	**−0.581**	−2.664*	**1.013**	**iso**	0.020
OCH	**8**	**0.734**	16.520	**−0.447**	−0.772	**1.005**	**iso**	**0.445**	−0.898	**1.004**	**iso**	<0.001
ORH	**17**	**0.732**	40.958	**−0.269**	−0.924	**0.800**	**iso**	**−0.330**	−1.280	**0.826**	**iso**	2.081
BZB	**16**	**0.865**	89.615	**−0.927**	−2.835*	**1.327**	**+**	**−0.868**	−2.909*	**1.302**	**+**	7.376
BCB	**19**	**0.589**	24.410	**0.090**	0.255	**0.746**	**iso**	**−0.030**	−0.105	**0.798**	**iso**	2.156
MZW	**22**	**0.780**	71.001	**−0.636**	−2.360*	**0.970**	**iso**	**−0.644**	−2.696*	**0.974**	**iso**	0.065
LIB	**16**	**0.778**	48.956	**−0.372**	−1.209	**0.924**	**iso**	**−0.392**	−1.432	**0.932**	**iso**	0.309
PAB	**19**	**0.869**	112.739	**−0.992**	−3.672**	**1.226**	**+**	**−0.953**	−3.837**	**1.209**	**+**	4.737
POC	**20**	**0.094**	1.869[a]	**−2.662**	−0.860	**1.812**		**−1.259**	−1.982	**1.212**		
SCL	**16**	**0.742**	40.293	**−1.520**	−2.874*	**1.433**	**+**	**−1.362**	−3.137*	**1.366**	**+**	5.442
MZL	**23**	**0.935**	300.078	**−0.730**	−4.550**	**1.187**	**+**	**−0.715**	−4.632**	**1.180**	**+**	8.920
MFL	**19**	**0.871**	114.519	**−0.904**	−3.457**	**1.197**	**iso**	**−0.871**	−3.611**	**1.183**	**iso**	3.747
NSL	**17**	**0.927**	189.336	**−1.236**	−5.325**	**1.366**	**+**	**−1.200**	−5.432	**1.351**	**+**	19.038
ORL	**19**	**0.755**	52.483	**−0.501**	−1.775	**0.875**	**iso**	**−0.537**	−2.151*	**0.80**	**iso**	0.944
PAL	**21**	**0.934**	267.757	**−0.690**	−3.994**	**1.207**	**+**	**−0.672**	−4.053**	**1.200**	**+**	9.631
UPL	**23**	**0.909**	210.933	**−1.118**	−5.348**	**1.297**	**+**	**−1.083**	−5.493**	**1.282**	**+**	14.604

The more common parameters, number of observations, R-square value, estimators of regression coefficients and allometric trends are in bold; BCB, braincase breath; BZB, bizygomatic breadth; LIB, least interorbital breadth; MFL, masseteric fossa length; MZH, muzzle height; MZL, muzzle length; MZW, muzzle width; NSL, nasal suture length; OCH, occipital height; ORH, orbital height; ORL, orbital length; PAB, palate breadth; PAL, palate length; POC, postorbital constriction; SCL, sagittal crest length; UPL, upper postcanine tooth row length.

iso, isometric trend, *F* iso-test, no significant differences from expected value of one; (−) negative allometric trend and (+) positive allometric trend, both F_{iso}-tests for slope were significantly different from the expected value of one. Gray-shaded rows show non-significant regressions.

[a]Not significant at 0.05 level, the remaining *F*-tests for slope coefficients (b_1) were significant ($P < 0.0001$) except for OCH ($P < 0.007$).

[b]*t*-test for intercept coefficients **log** (b_0). * Differences that were significant (*$P < 0.05$; **$P < 0.005$).

[c]Same *F*-test value for both slopes (MA and SMA) for each isometric test.

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Table 3 Regression results for *Nesodon imbricatus*

				Major axis (MA)				Standardized major axis (SMA)				
Variable	***n***	R^2	$F_{(1, n-2)}$	$\log(bo)_{MA}$	$t_{(n-2)}$[b]	b_{1-MA}	Trend	$\log(bo)_{SMA}$	$t_{(n-2)}$[b]	b_{1-SMA}	Trend	$F\text{iso}_{(1, n-2)}$[c]
MZH	**8**	**0.963**	157.246	**−1.408**	−5.201**	**1.332**	**+**	**−1.390**	−5.260**	**1.325**	**+**	13.288
OCH	**6**	**0.977**	171.697	**−0.243**	−1.392	**0.909**	**iso**	**−0.246**	−1.421	**0.910**	**iso**	1.568
ORH	**9**	**0.944**	118.778	**−0.669**	−2.963 *	**0.965**	**iso**	**−0.672**	−3.057 *	**0.966**	**iso**	0.154
BZB	**7**	**0.981**	259.347	**0.396**	3.348 *	**0.752**	–	**0.391**	3.329 *	**0.754**	–	21.570
BCB	**7**	**0.954**	103.662	**0.536**	3.900 *	**0.553**	–	**0.519**	3.815 *	**0.560**	–	40.790
MZW	**9**	**0.938**	106.670	**−0.437**	−2.039	**0.865**	**iso**	**−0.447**	−2.143	**0.869**	**iso**	2.250
LIB	**8**	**0.885**	46.069	**−0.305**	−0.910	**0.893**	**iso**	**−0.320**	−1.009	**0.899**	**iso**	0.596
PAB	**8**	**0.947**	107.626	**−0.159**	−0.745	**0.861**	**iso**	**−0.168**	−0.804	**0.865**	**iso**	2.410
POC	**8**	**0.433**	4.589[a]	**0.921**	2.329	**0.333**		**0.617**	1.744	**0.452**		
SCL	**7**	**0.949**	92.292	**−0.066**	−0.322	**0.778**	**iso**	**−0.079**	−0.391	**0.783**	**iso**	5.948
MZL	**10**	**0.992**	951.658	**−0.604**	−6.458**	**1.125**	**+**	**−0.602**	−6.473**	**1.124**	**+**	13.236
MFL	**10**	**0.904**	75.760	**−0.895**	−2.632 *	**1.155**	**iso**	**−0.874**	−2.722*	**1.147**	**iso**	1.587
NSL	**10**	**0.963**	210.289	**−0.957**	−4.454**	**1.215**	**+**	**−0.946**	−4.501**	**1.211**	**+**	8.105
ORL	**10**	**0.883**	60.384	**0.010**	0.044	**0.675**	–	**−0.030**	−0.139	**0.690**	–	9.828
PAL	**10**	**0.992**	941.127	**−0.400**	−4.415**	**1.084**	**+**	**−0.399**	−4.424**	**1.083**	**+**	6.081
UPL	**11**	**0.961**	224.592	**−0.638**	−3.380 *	**1.099**	**iso**	**−0.632**	−3.426*	**1.097**	**iso**	2.015

The more common parameters, number of observations, R-square value, estimators of regression coefficients and allometric trends are in bold; BCB, braincase breath; BZB, bizygomatic breadth; LIB, least interorbital breadth; MFL, masseteric fossa length; MZH, muzzle height; MZL, muzzle length; MZW, muzzle width; NSL, nasal suture length; OCH, occipital height; ORH, orbital height; ORL, orbital length; PAB, palate breadth; PAL, palate length; POC, postorbital constriction; SCL, sagittal crest length; UPL, upper postcanine tooth row length.

iso, isometric trend, *F* iso-test, no significant differences from expected value of one; (−) negative allometric trend and (+) positive allometric trend, both F_{iso}-tests for slope were significantly different from the expected value of one.

Gray-shaded rows show non-significant regressions.

[a]Not significant at 0.05 level, the remaining *F*-tests for slope coefficients (b_1) were significant ($P < 0.0001$).

[b]*t*-test for intercept coefficients **log** (b_0). * Differences that were significant (*$P < 0.05$; **$P < 0.005$).

[c]Same *F*-test value for both slopes (MA and SMA) for each isometric test.

notably different than those for *Adinotherium*. Although also 8 of 16 variables were isometric (OCH, ORH, MZW, LIB, PAB, SCL, MFL, UPL), four variables were positively allometric (MZH, MZL, NSL, PAL) and three were negatively allometric (BZB, BCB, ORL).

The comparison of slopes and intercepts for *Adinotherium* and *Nesodon* (Table 4) shows that both groups exhibit divergent patterns of cranial growth, demonstrating strong differences, but some similarities, in slopes and intercepts of several variables. For instance, although 11 of 16 variables (OCH, ORH, BCB, MZW, LIB, MZL, MFL, NSL, ORL, PAL, UPL) shared a common slope, only seven of them (OCH, ORH, BCB, LIB, ORL, PAL, UPL) showed agreement among intercepts of the common slopes obtained for the two sister taxa. In general, the differences in allometric trends indicate that the slopes observed for *Adinotherium* were higher than those observed for *Nesodon,* except in MZH, where the slope for *Nesodon* was higher (Table 4, Fig. 3). Similarly, in those variables that showed differences in the intercepts, their values were always statistically higher in *Adinotherium*. The data for specimens of *A. robustum* always lie on the SMA regression line or within the range of the data of *A. ovinum*, except for BCB in which are far above (Fig. 3). In the case of *N. cornutus* only, data for NSL and ORL lie far from the SMA regression line, above and below it, respectively, whereas the rest of variables lie within the range of the data of *N. imbricatus* (Fig. 3).

Discussion

In the ontogenetic series of both species, we detected several measurements exhibiting deviation from isometry. Many of them are clearly related to functional demands in the neurocranial and splachnocranial components. The different largest sizes attained by *Adinotherium* and *Nesodon* are also accompanied by different patterns of cranial growth, with some variables exhibiting distinct signs in the trends of each group (Tables 2 and 3). However, in spite of some timing differences in the growth pattern, the ontogeny of the muzzle results in some clear trends in both sister groups. For instance, MZL and related variables such as nasal length and palate length grow with positive allometry, resulting in a muzzle relatively lengthened with respect to younger individuals. *Toxodon*, the genus from which the name Toxodontidae is derived, was named by Richard Owen. *Toxodon* means 'bow-tooth,' from the strongly curved grinding teeth – tooth roots on opposite sides almost meet in the midline above the hard palate (Scott 1913, p. 463). Although neither Miocene taxon studied here is euhypsodont *sensu* Mones (1982), the general configuration of the grinding teeth described earlier

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Table 4 Test for common slope and common intercept for both taxa

	Common slope			Common intercept		
Variable	Lr_{b1}	P_{b1}	b_{1com}	$W_{(logbo)}$	$P_{(logbo)}$	$\log(b_0)_{com}$
MZH	4.196	**0.041**	Ne > Ad			
OCH	0.174	0.677	**0.919**	1.471	0.225	**−0.122**
ORH	0.897	0.344	**0.924**	0.103	0.748	**−0.513**
BZB	12.519	**<0.001**	Ad > Ne			
BCB*	3.392	0.065	**0.609**	0.320	0.572	**0.538**
MZW	0.619	0.431	**0.911**	8.581	**0.003**	Ad > Ne
LIB	0.037	0.848	**0.916**	0.108	0.743	**−0.279**
PAB	5.308	**0.021**	Ad > Ne			
SCL	8.164	**0.004**	Ad > Ne			
MZL	0.550	0.458	**1.137**	6.182	**0.013**	Ad > Ne
MFL*	0.046	0.830	**1.168**	15.020	**<0.001**	Ad > Ne
NSL	1.169	0.280	**1.274**	22.780	**<0.001**	Ad > Ne
ORL*	2.041	0.153	**0.782**	1.707	0.191	**−0.395**
PAL	2.146	0.143	**1.106**	0.349	0.555	**−0.419**
UPL*	2.579	0.108	**1.184**	0.050	0.823	**−0.846**

b_{1com}, common slope from standardized major axis; $\log(b_0)_{com}$, common intercept from standardized major axis (common slope and intercept values are in bold); ***Lr***, likelihood ratio (Warton *et al.* 2006); ***w***, Wald statistic (Warton *et al.* 2006); P_{b1}, p-value of ***Lr*** parameter; $P_{(logbo)}$, p-value of ***W*** parameter, (p-values significant at 0.05 level are in bold); BCB, braincase breath; BZB, bizygomatic breadth; LIB, least interorbital breadth; MFL, masseteric fossa length; MZH, muzzle height; MZL, muzzle length; MZW, muzzle width; NSL, nasal suture length; OCH, occipital height; ORH, orbital height; ORL, orbital length; PAB, palate breadth; PAL, palate length; SCL, sagittal crest length; UPL, upper postcanine tooth row length.
*Differences are between the common slope trend and the slope observed for each genus.

does pertain to *Adinotherium* and *Nesodon* (Fig. 4). Thus, the allometric trends for palate and nose morphology suggest that along ontogenetic growth, additional space is needed to accommodate growing protohypsdont teeth. However, vertical and transverse dimensions of the muzzle do not seem to be shared in both groups, because of the positive allometry of PAB in *Adinotherium* but isometry in PAB in *Nesodon*. This is also inferred from the isometry of MZH in *Adinotherium*, but positive allometry of MZH in *Nesodon*. In this sense, although the general morphology of the rostrum is conservative in nesodontines, the generalized structure in both taxa differs principally in its ontogenetic trends, resulting in a proportionally broader muzzle in *Adinotherium* and a higher muzzle in *Nesodon*.

Indeed, variables with significant differences in intercept values (Table 4), always higher in *Adinotherium*, are closely related to the muzzle and the masseteric fossa (MZW, MZL, MFL, NSL), indicating a proportionally strong rostrum in this genus, independently of the maximum size attained.

The space for the temporal musculature is a function of differential growth and interaction between the zygomatic bone and the braincase; this space is generated by different patterns in each species. In *Adinotherium*, zygomatic breadth shows positive allometry as development progresses, whereas the braincase is isometric. Although the isometry of the braincase is unusual in mammals (Emerson and Bramble 1993), the interaction of both trends generates considerable space for the temporal musculature in adults. Although the allometric trends are different, the interaction of these two variables produced the same situation for the temporal muscles in the development of *Didelphis albiventris* (Abdala *et al.* 2001). This led the authors to relate these changes to the transition from suckling to active mastication. Indeed, the positive allometry of the length of the braincase also permits the development of an important cranio-caudal space for the temporal musculature of *Adinotherium*. By contrast, the allometric trends in *Nesodon* also leave a considerable space for the temporal musculature, although to a lesser degree than in *Adinotherium*, because of the negative allometry in both variables. However, the negative allometry of the braincase of *Nesodon* is more strongly pronounced than the negative allometry of zygomatic breadth, and thus, an extensive space is still generated. Although the masseteric fossa grows in an isometric way in both taxa, a lateral transposition of the trajectories is observed, indicating a proportionally larger fossa in *Adinotherium*, in spite of the larger size of *Nesodon*. This suggests that *Adinotherium* has proportionately greater muscle volume than *Nesodon*, particularly for the temporalis. This is not in agreement with previous work that postulates a more hard-object diet (e.g., bark) for *Nesodon* (Townsend and Croft 2008), nor does it support a more dedicated grazing habit for *Adinotherium* as proposed by Cassini *et al.* (in press). Following Cox (2008), their morphology corresponds in broad terms to the generalized feeding group of Turnbull (1970) with an apparent (but not complete) dominance of temporal musculature, with a relatively long and wide rostrum, and with a small lacrimal bone. Values of enamel carbon isotopes for Santacrucian *Nesodon* fall in the range of herbivorous mammals feeding on a pure C3 diet with δ13C values of about −17 to −10‰ (MacFadden *et al.* 1996). Based on isotopic data, MacFadden (2005) concluded that the Quaternary Toxodontinae (*sensu* Nasif *et al.* 2000), *Toxodon* and *Mixotoxodon*, that spread all over South America had the evolutionary capacity to be dietary generalists, i.e., eating the dominant local vegetation with a niche differentiation based on body size. Although evaluating hypotheses about diet and niche partitioning is not our principal aim, the morphological traits related to the trophic apparatus lead us to postulate generalized herbivory for both nesodontines. This seems to be a conservative condition among toxodontids.

The neurocranial components exhibit strong differences in the pattern of growth between taxa. The trends observed in *Adinotherium* are unusual because of the absence of negative allometry in the variables associated with sensory capsules such as the orbit and braincase (Table 2). The orbit is isometric in both dimensions, a pattern that is uncommon in mammals (Emerson and Bramble 1993), even though this pattern was found in some australidelphian marsupials like *Dasyurus albopunctatus* and *Dromiciops gliroides* (Giannini *et al.* 2004; Flores *et al.* 2006). By contrast, neurocranial variables in

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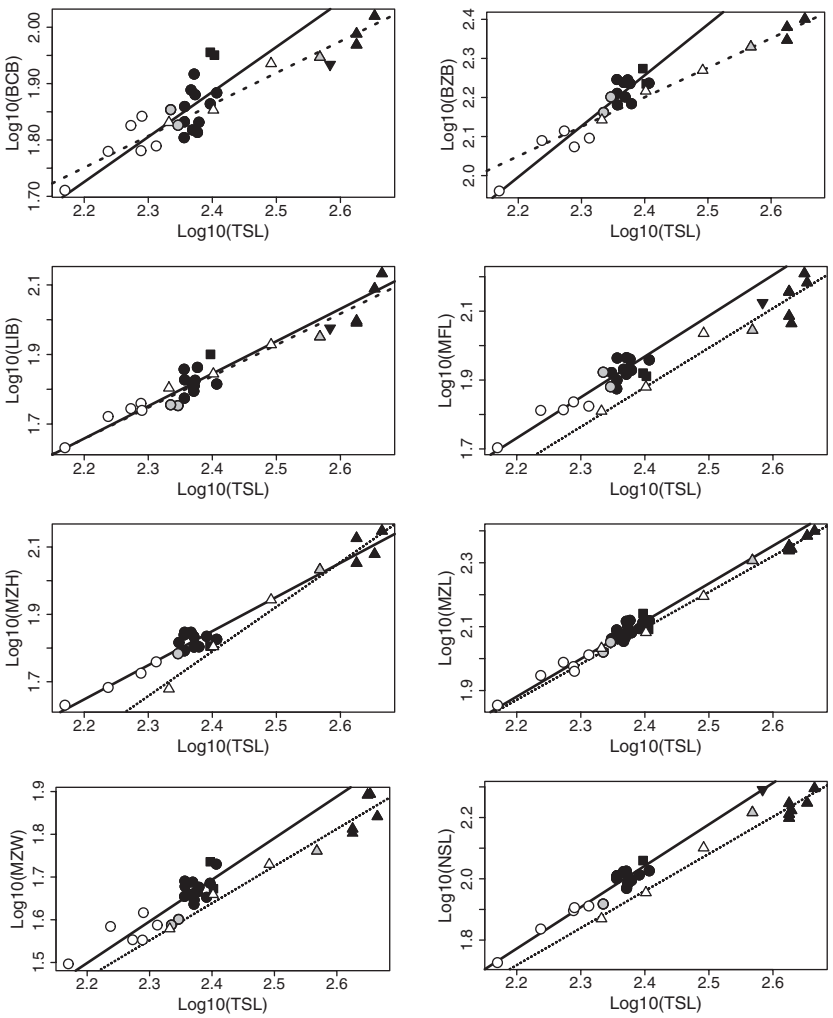

Fig. 3—Biplots of 16 log-transformed linear measurements versus log-transformed total skull length. circles *Adinotherium ovinum* specimens; squares *A. robustum*; triangles *Nesodon imbricatus*; inverted triangle *N. cornutus*. White symbols juveniles; gray symbols subadults; black symbols adults. See Fig. 2 for variables names.

Nesodon are characterized by lower slopes than in *Adinotherium*. For instance, coefficients of variables related to the orbit indicate that it becomes proportionally taller because of the interaction of the isometry of its height and the negative allometry of its length. The orbit size of nesodontines, together with the great size of the rostrum (wider in *Adinotherium* and higher in *Nesodon*), suggests a reliance on olfaction and tactile senses using the nose and vibrissae together with a more developed visual system. Alternatively, the braincase of *Nesodon* shows a complex pattern of growth, becoming longer and taller, according to the negative allometry of its breadth and the isometry of its height and length (Table 3). The isometry of the height of the occipital plate in both species is indicative of a strong cervical musculature from early stages of growth.

In addition, the rarity of negative allometry, especially in neurocranial variables, indicates a particular mode of growth in nesodontines, uncommon in other mammals (Emerson and Bramble 1993).

In summary, the general trends detected in most variables are in agreement with the conservative morphology of nesodontines, and perhaps of toxodonts in general, given the similarity of the trajectories followed by both sister groups. Size differences are accompanied by shape conservation, indicating that the trajectory of *Nesodon* represents an extension of the trajectory of *Adinotherium*. However, differences in allometric trends and intercepts indicate that additional processes are acting as well in the evolution of the cranial ontogeny in nesodontines. Although the similarity of toxodontids to other ungulates has been highlighted since the earliest studies (Patterson 1932), the neurocranial allometric trend seems to be more similar to australidelphian marsupials. The splanchnocranial allometric trends fail to support the inference of specialized herbivory (see Townsend and Croft 2008; Cassini *et al.*

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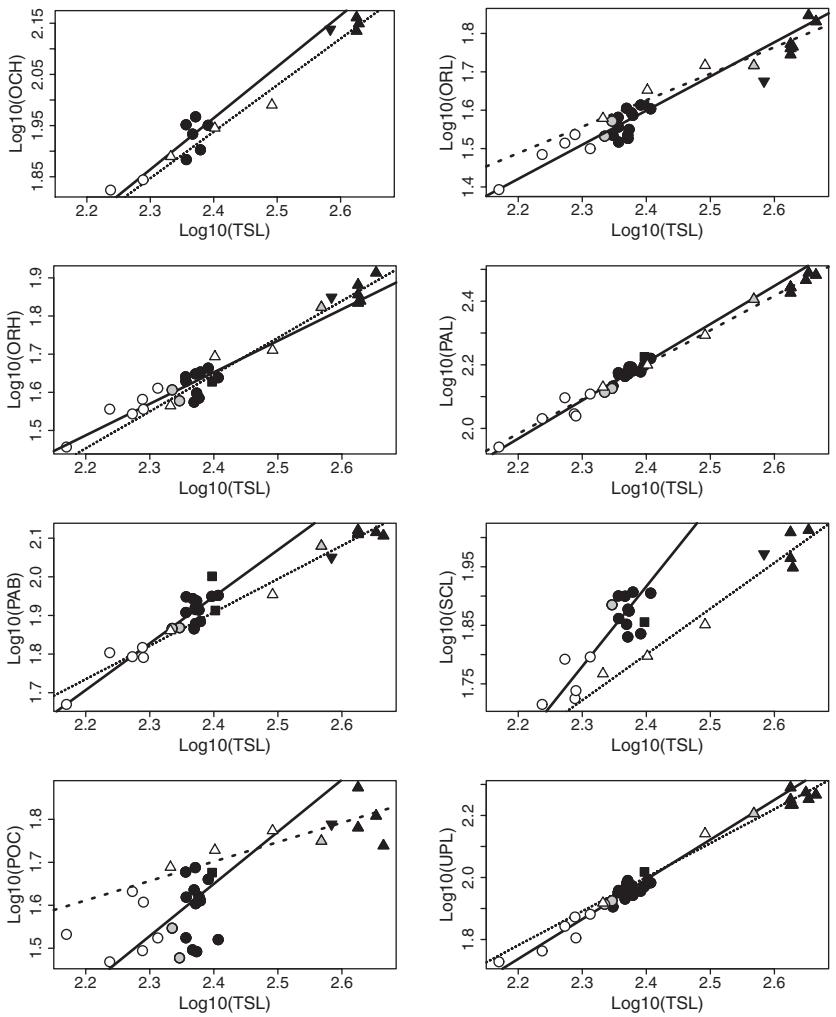

Fig. 3—(Continued).

in press and references therein), instead suggesting generalized herbivory in nesodontines. This constitutes a basal state in toxodontids, and because of the highly conservative morphology of toxodontids, it might also pertain to later forms (MacFadden 2005). This hypothesis remains to be tested within the family in an ecomorphological and ontogenetical morphometric framework and in a phylogenetic context.

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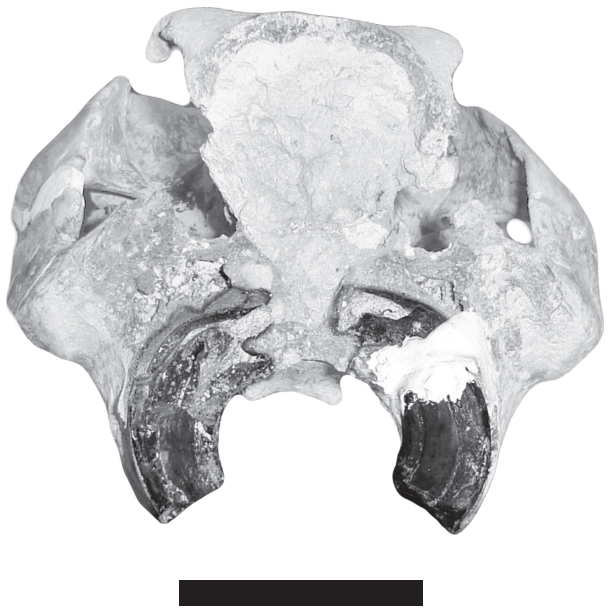

Fig. 4—Anterior view of the rostrum of *Adinotherium* YPM-PU 15003, broken just in front of orbits, showing how the molar roots nearly meet in the middle. Scale bar 50 mm.

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