

# Ecomorphology of Mammalian Fossil Lineages: Identifying Morphotypes in a Case Study of Endemic South American Ungulates

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**Abstract** The notoungulates are one major clade of extinct native South American ungulate mammals. Several notoungulate morphotypes have been proposed by comparison with mammals from other large land masses, representing instances of convergent evolution in continental isolation. As with other entirely fossil lineages, the reconstruction of their functional biology is challenging, one major obstacle being the fragmentary and distorted nature of the fossil remains for which application of conventional quantitative data analysis techniques is compromised. Here we explored the patterns in morphospace of representatives of all notoungulate families on the basis of the qualitative scoring of 31 cranial characters that provided a basic description of shape and an approximation to sensory and mechanical functions of the skull. We calculated pairwise distances between all taxa with an index that proportionally corrected overall similarity by both character number and dissimilarities. The distances were used to generate a morphospace with a multivariate technique, Principal Coordinates Analysis. We recovered a tight group of basal Paleocene-Eocene notoungulates and a scattered group of Oligocene and Neogene forms. Lines drawn in that space connecting successive sister terminals clearly showed a departure from basal genera toward four diverging, previously proposed morphotypes, namely rabbit-, large-rodent-, small-horse-, and rhino-like forms. An extensive analysis identified the character basis of these morphotypes. Mapping additional information such as body size and degree of hypsodonty effectively aided in the interpretation of notoungulate

morphofunctional evolution. We briefly discuss the utility of the qualitative morphospace as a tool for exploring the ecomorphology of fossil lineages and the evolutionary implications of this reconstruction.

**Keywords** Notoungulata · Ecomorphology · Principal coordinates analysis · Paleogene · Morphospace

## Introduction

A major goal of Paleontology is the reconstruction of life in the past from available fossil evidence. One particularly challenging subject of study is the functional ecology of entirely fossil lineages (Van Valkenburgh 1994). The evolutionary history of many of the lineages without living representatives have been reconstructed using cladistic analysis, so today interpretations of diversification, function, or paleoecology, can be informed by phylogeny (e.g., Sidlauskas 2008). These include ecomorphology, or the study of the interrelationship of functional morphology and the ecology of organisms (e.g., Leisler and Winkler 1985; Wainwright and Reilly 1994), which assumes a predictable relationship between the two (e.g., Findley and Black 1983). In the case of entirely fossil lineages, the ecological function of their members is best inferred by comparison with convergent lineages with living representatives, so that the functional implications of preserved structures can be established with greater confidence (Van Valkenburgh 1994). One such fossil lineage is represented by a large clade of ungulate forms endemic to South America, the Meridiungulata (McKenna and Bell 1997). Comprising several orders, most taxa belong in the Notoungulata, likely also inclusive of Pyrotheria (see Billet 2010). The morphology of notoungulates has often been compared with that independently developed by mammals from other continents, and a few morphotypes have been proposed to have existed: rhino- and horse-like forms in

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the Toxodontia, and rabbit- or rodent-like forms in the Typotheria, groups that represent the major divisions of the order (Reguero et al. 2007; Croft and Weinstein 2008 and references therein). In turn, several recent studies have dealt with functional aspects of dentition, skull, and postcranium of notoungulates and other native South American ungulates (Croft 2001; Elissamburu 2004, 2010; Croft and Weinstein 2008; Townsend and Croft 2008; Billet et al. 2009a, b; Reguero et al. 2010; Cassini et al. 2011, 2012; Scarano et al. 2011; Cassini and Vizcaíno 2012).

Our goal is to objectively explore the morphofunctional space of notoungulates as a case study within the general framework of reconstructing the ecomorphology of entirely fossil lineages. To a great extent, measurements included in ecomorphological studies need to be proxies to functions like food acquisition and processing (e.g., Slater and Van Valkenburgh 2009; Cassini et al. 2011; Cassini and Vizcaíno 2012), body support (e.g., Elissamburu 2010, 2012; Giannini et al. 2012), locomotion (e.g., Scott 1985; Van Valkenburgh 1987; Elissamburu 2004, 2010), or a combination thereof (e.g., Findley and Black 1983; Leisler and Winkler 1985). Frequently, a multivariate approach has been chosen to face ecomorphological problems in which many variables and taxa were involved (e.g., Leisler and Winkler 1985; Morales and Giannini 2010, 2013). The morphospace generated in this way is a tool used to explore functional relationships among taxa as illuminated by the characters / variables included. The aforementioned studies described morphofunctional variation in extant assemblages; with fossils such as notoungulates, this approach is severely limited in at least two ways.

First, measurements should be taken from intact specimens, so measurement errors are minimized. This is a problem in fossils because specimens are often broken, crashed, or otherwise distorted by accidents that accumulated during thousands to millions of years of hazardous preservation (e.g., Abdala and Giannini 2000). Second, fragmentation frequently causes the specimen to be incomplete, with sometimes many missing values for the chosen characters. These two problems, so common in fossil data (see Billet [2010] for an example in notoungulates), preclude the direct use of metric multivariate methods such as Principal Components Analysis, which require complete design (i.e., no missing entries in the primary data matrix) for unbiased applications (e.g., Hair et al. 1995).

In addition to these statistical problems, other issues affect the study of ecomorphology of fossil lineages encompassing several periods of time. For instance, notoungulates are represented by diverse forms found in deposits from the Paleocene to the Holocene (Tonni et al. 1992; McKenna and Bell 1997). Therefore, in some way a stratigraphic component should be attached to the interpretation of results to account for the succession of forms that appeared and were replaced along the history of the lineage (e.g., Van Valkenburgh 1994: fig. 7–2). Without temporal considerations, similarities among

taxa that result in proximities in morphospace cannot be adequately interpreted in paleoecological terms because taxa that are close in morphospace may be distantly located in the geological time scale. That is, similar forms appearing close in morphospace may have never co-existed, thus representing cases of temporal morphotype replacement. In addition, variation along the time line is further complicated by specific sister-taxon relationships as dictated by the best phylogenetic hypothesis available, which brings about a fourth problem associated with the ecomorphology of fossils. Similar and contemporary forms may belong to the same or different sub-lineages within a clade; as a consequence, the interpretation of similarities (convergent versus phyletic, respectively) varies radically in each case and so does the corresponding paleoecological interpretation. In other words, the interpretation of relationships in the morphospace can be severely biased if phylogenetic relationships are not taken into account in some way (see examples in Van Valkenburgh 1994).

In this study we present a morphological analysis of the skull of notoungulates that includes a wide sample of representatives from all currently recognized families for which well-preserved cranial material is known, as well as other forms (Pyrotheria) not included in the traditional Notoungulata but recently recovered inside this clade (see Billet 2010). This fossil lineage gave us the opportunity to explore an analytical framework that copes with the problems of material quality and completeness by means of discrete-data encoding of morphofunctional information. In turn, this approach allowed us to map and interpret aspects of stratigraphy and phylogeny in the morphospace generated by this sample from an extinct clade. In this way, to the extent cranial morphology alone allowed it, we directly tested the existence of proposed morphotypes, established their specific morphofunctional relationships, and the way those morphotypes derived along the evolutionary time.

## Materials and Methods

**The Group** The “Southern Ungulates” (Order Notoungulata) represent the most diverse clade within a native, phylogenetically questioned South American group, the Meridiungulata, which also includes Litopterna, Xenungulata, Astrapotheria, Pyrotheria, and Notopterna (Soria 1989; Cifelli 1993; McKenna and Bell 1997; Reguero et al. 2007; Townsend and Croft 2008; Croft and Weinstein 2008). Notoungulata was erected by Roth (1903) on the basis of cranial characters and the monophyly of the group has been traditionally accepted by most authors (Cifelli 1993). Important studies were carried out on this fossil mammal order and many species were described already at the turn of the 20th century (Ameghino 1885, 1887a, b, 1897, 1901, 1902; Burmeister 1888). Notoungulate fossils were recovered from Paleocene to Quaternary deposits. *Perutherium altiplanense* was

postulated as a primitive notoungulate from Peruvian Cretaceous levels (Marshall et al. 1983). However, this age assignment was challenged by Bond (1986) and posteriorly the bearing sediments were re-assigned to the upper Paleocene—lower Eocene (Sigé et al. 2004). The last representatives of the order have been recorded in association with human remains (Tonni et al. 1992).

The Paleogene is the period of greater notoungulate diversity (Croft and Weinstein 2008; Croft et al. 2008; Reguero and Prevosti 2010). In Argentina, the country with the richest record, most Paleogene forms come from Patagonia (Simpson 1948, 1967) but the provenance of important findings also includes midwestern (Simpson et al. 1962) and northwestern Argentina (Pascual et al. 1978; Vucetich 1980; Pascual et al. 1981; Bond 1981; Vucetich and Bond 1982; Bond et al. 1984; Bond and López 1993, 1995; López and Bond 1995; López 1995, 1997; Reguero et al. 2008; Deraco et al. 2008; García-López and Powell 2009, 2011). Remarkable Paleogene notoungulates also have been discovered in Brazil, Chile, Uruguay, and Bolivia (de Paula Couto 1954, 1983, 1952; Cifelli 1983; Soria and Ferraz de Alvarenga 1989; Shockey 1997; Bond et al. 1998; Ubilla et al. 1999; Flynn et al. 2002a, b, 2003; Croft et al. 2003; Hitz et al. 2006; Billet et al. 2008).

Notoungulata is a fossil order with a great morphological diversity (Simpson 1948; Cifelli 1993; Reguero et al. 2007; Croft and Weinstein 2008) including, for example, remarkably small forms (López and Bond 1995; Hitz et al. 2006) and very large forms (e.g., *Trigodon*, *Chasicotherium*), tusk-bearing animals (Madden 1997), representatives with complete dentition (e.g., *Griphotherion*), clades with early development of diastemata (e.g., Notostylopidae), and forms with possible nocturnal and arboreal habits (López 2008). Two main lineages have been recognized, Toxodontia and Typotheria—both abundantly recorded from the Paleogene to the Quaternary. These lineages show a clear transition from early brachyodont forms, traditionally regarded as browsers, to late hypselodont forms considered grazers.

Although Pyrotheria has been traditionally considered as a separated clade, recent phylogenetic analyses recovered *Pyrotherium* nested within Notoungulata in association with two middle Eocene notoungulate genera (*Boreostylops* and *Notostylops*; see Billet 2010; García-López and Powell 2011). As a consequence, we included *Pyrotherium* in our ecomorphological analysis of the notoungulate lineage.

**Specimens and Characters** We scored 29 genera that cover all 14 currently recognized families (McKenna and Bell 1997). Taxa were selected to represent each group of notoungulates on the basis of best-preserved specimens, i.e., those specimens that allowed scoring of the maximum number of characters per taxon. The specimens examined are listed in Appendix 1. We also collected specific character information from the following sources: Billet (2010: *Pyrotherium*); Billet

et al. (2009a, b: *Archaeohyrax*; 2008: *Trachytherus*); Cassini and Vizcaíno (2012: *Adinotherium*, *Interatherium*, *Pachyrhukhos*); Cassini et al. (2012: *Adinotherium*, *Nesodon*); Cerdeño and Bond (1998: *Paedotherium*); Chaffee (1952: *Scarrittia*); Marani and Dozo (2008: *Eurygenium*); Pascual et al. (1966: *Trigodon*), Patterson (1934: *Homalodotherium*); Scott (1912: *Adinotherium*, *Hegetotherium*, *Interatherium*, *Nesodon*, *Pachyrhukhos*, *Protypotherium*); Simpson (1967: *Thomashuxleya*); and Simpson et al. (1962: *Brachystephanus*). In addition to these sources, we scored *Leontinia* and partially *Scarrittia* from photographs (see Appendix 1 for details).

We developed 31 craniodental characters chosen to represent some important function of the skull and / or describe a prominent feature of it (Fig. 1). Characters include absence / presence of structures (e.g., character 2: zygomatic plate); relative size or development (e.g., character 5: tympanic bulla); orientation (e.g., character 3: external acoustic meatus); shape (e.g., character 9: anterior palate); length, height, or width (e.g., character 6: height of rostrum); position (e.g., character 12: nasal aperture); relative size of two structures (e.g., character 17: length of upper premolar row relative to the upper molar row); and overall skull size (character 31). Some of these characters have been used in phylogenetic analyses (e.g., character 4: development of the epitympanic sinus, included in Billet [2010]).

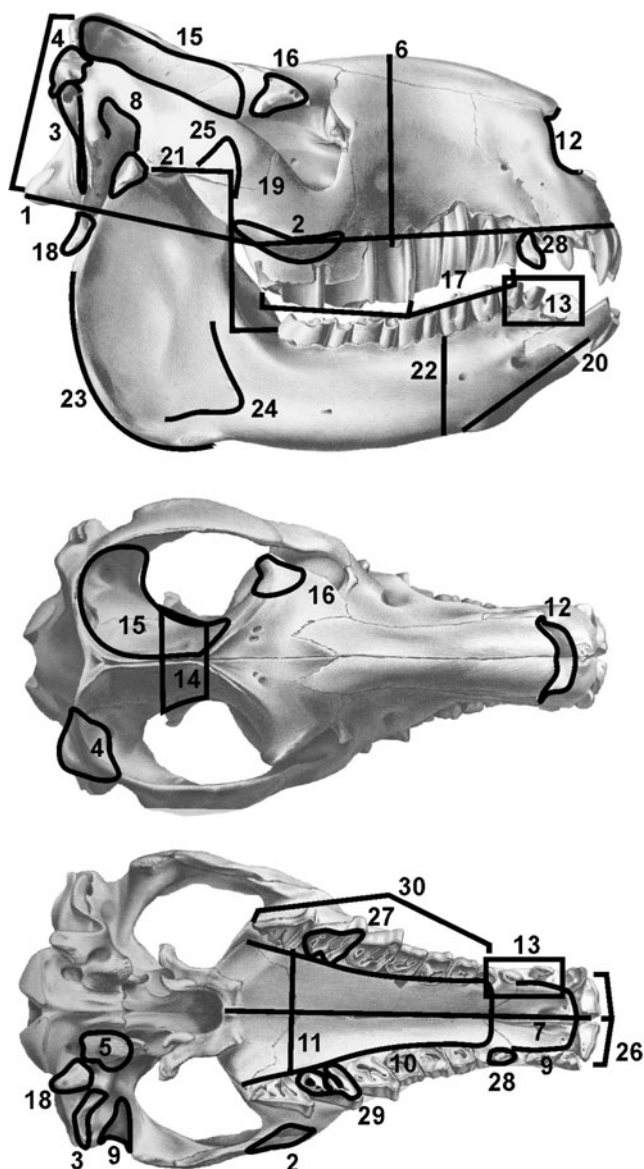
In this strategy, coding of functionally important traits on a discrete-data scale, as opposed to precise, continuous-data scale, allows scoring of imperfectly preserved material while maintaining the ability of making meaningful comparisons across taxa, and establishing degrees of dis- / similarity for the entire assemblage (see below). For instance, a broken tympanic bulla can hardly be measured with precision, but in most cases it can be readily classified as small (state 0 in our character 5) versus well developed, prominent (state 1). More ambiguous cases were scored as missing (Table 1).

**Analytical Techniques** In order to depict the basic craniodental structure of the notoungulate lineage, we choose Principal Coordinates Analysis (hereafter PCORD; Rohlf 1990). PCORD is an ordination technique that generates a multivariate space from a dis- or similarity matrix. The input similarity matrix was constructed with the widely used *RT* index originally proposed by Rogers and Tanimoto (1960; see also Rohlf 1990):

$$RT_{a,b} = m / (n + u)$$

where *m* is the number of identical character states and *u* is the number of dissimilar states, for any pair of taxa *a* and *b*, for *n* characters. This measure was chosen among many available given its intuitive simplicity and the proportional correction applied to absolute similarities (*m*) by both character number





**Fig. 1** Illustration of the qualitative characters used in this study. Character states and a discussion of each character are presented in Appendix 2. Character list: 1. Basicranial angle; 2. Presence of zygomatic plate; 3. External auditory meatus orientation; 4. Development of epitympanic sinus (squamosal); 5. Development of tympanic bulla; 6. Height of rostrum; 7. Length of rostrum; 8. Shape of mandibular (= glenoid) fossa; 9. Shape of anterior palate (on the premaxilla); 10. Shape of upper tooth row; 11. Posterior width of palate; 12. Position of nasal aperture; 13. Diastema; 14. Development of postorbital constriction; 15. Size of temporal fossa; 16. Development of postorbital process; 17. Length of upper molar row relative to upper premolar row; 18. Development of jugular (= paracondylar) process; 19. Development of zygomatic arch; 20. Orientation of mandibular symphysis; 21. Position of articular process (= mandibular condyle) relative to lower molar row; 22. Mandibular depth at level of lower premolars; 23. Expansion of angular process; 24. Anterior extent of insertion of masseteric muscle on mandible; 25. Height of coronoid process; 26. Relative size of upper incisors; 27. Aspect of occlusal surface of upper molars; 28. Development of upper canine; 29. Morphology of upper molars; 30. Differentiation of upper cheekteeth. Character 31 (Skull size) not depicted. Image is a lithograph original of the artist Bruce Horsfall, first published in Scott (1912), depicting different views of specimens YPM VPPU 015000 (skull) and YPM VPPU 015260 (mandible) of the toxodontid *Nesodon imbricatus*

(here notoungulate taxa) in the chosen combination of axes (e.g., the plane of axes 1 and 2).

PCORD as applied here does not provide a simultaneous way of evaluating the contribution of each character in the ordination (see Rohlf 1990). However, this is possible within the frame of indirect gradient analysis (see ter Braak 1995): axis coordinates are associated with either the original or external variables by way of any variant (depending on the nature of the variables) of general linear modeling (GLM). Here we used ANOVA-like GLM to detect whether contrasting (e.g., 0 versus 1) states in any original character were associated with variation along the PCORD axes. We limited our exploration to axes 1 and 2, so the analysis consisted of a separate GLM for each original discrete character as explanatory variable (factor) of each set of axis coordinates. In order to avoid increased type I error rate due to multiple testing on the same data (axis coordinates), we fixed alpha at a conservative 0.01 value as a compromise between a strict Bonferroni correction (at  $\alpha = 0.05 / 31 = 0.001$ ) and the conventional 0.05 value. A few characters had too few (<5) scorings per state and so were either not tested due to this scoring unbalance, or the states with few scorings were removed (i.e., the state coded non-applicable). These analyses were done using simple R scripts (see GLM commands in R Development Team 2010).

( $n$ ) and dissimilarities ( $u$ ).  $RT$  varies between 0 (no common states between  $a$  and  $b$  across the matrix) and 1 (all states identical). We introduced a minor modification to the  $RT$  index by allowing missing data to be excluded from comparisons between pairs of taxa. Specifically, for any pairwise comparison, we defined  $p$  as the number of characters with missing entries and set  $n$  to  $n-p$  calculating  $m$  and  $u$  solely on the basis of characters without missing entries for both taxa. The final  $RT$  matrix was double-centered and submitted to PCORD with default settings as implemented in the program NTSYS-pc v. 2.1 (Rohlf 1990). Goodness of fit was estimated with the approximate scale provided by Rohlf (1990) and a broken-stick model generated by NTSYS was used to choose the axes retained for interpretation. Results of PCORD include an ordination diagram that reconstructs, to the extent allowed by the underlying data structure, the (dis)similarity among objects

**Mapping** In the cranial morphospace, we mapped phylogenetic and climatic / age information associated with the taxa, as well as two key functional attributes, overall size and degree of molar development (brachyodonty / hypsodonty). Phylogenetic information was mapped by superimposing lines connecting successive sister taxa onto the tree based in Fig. 2 derived from Billet (2010) and

**Table 1** Data matrix resulting from scoring 31 craniodental characters (columns) for 29 notoungulate taxa (rows) at the genus level, representing all currently recognized families (inclusive of Pyrotheria,

see text). Taxa ordered in phylogenetic sequence following tree in Fig. 2. Missing values indicated “?”

Genus \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
<i>Simpsonotus</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	
<i>Brachystephanus</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	?	1	?	1	0	1	0	0	0	1	0	0	1	0	0	0	
<i>Notostylops</i>	1	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	
<i>Boreastylops</i>	1	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	
<i>Pyrotherium</i>	2	0	0	0	0	1	1	0	2	0	0	2	2	?	1	0	1	?	2	1	1	1	0	0	?	0	1	0	3	1	2	
<i>Tomashuxleya</i>	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	?	1	1	2	1	1	0	0	0	0	0	0	2	1	0	1	
<i>Pampahippus</i>	1	0	0	0	1	1	0	0	0	0	1	0	0	0	1	?	0	?	1	0	?	0	?	?	?	?	?	0	1	0	0	1
<i>Homalodotherium</i>	2	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	1	2	?	1	0	0	0	1	0	0	1	1	0	1	
<i>Coquenia</i>	2	0	1	0	0	1	1	1	0	0	1	0	0	0	1	1	1	1	1	0	1	0	1	0	1	0	0	1	0	0	1	
<i>Scarrittia</i>	2	0	0	0	0	1	1	1	0	0	1	1	0	0	1	0	1	0	2	0	0	0	1	0	1	0	0	1	1	0	1	
<i>Leontinia</i>	2	0	0	0	0	1	1	1	0	0	1	1	0	1	0	1	1	1	2	0	1	1	?	0	1	0	0	1	1	0	2	
<i>Eurygenium</i>	2	0	0	0	0	1	1	1	1	1	2	0	0	0	1	1	1	?	2	?	?	?	?	?	?	0	0	1	1	0	1	
<i>Adinotherium</i>	2	0	1	0	0	0	1	1	1	0	1	0	1	0	1	1	1	1	2	1	1	1	1	0	0	1	1	1	1	0	2	
<i>Nesodon</i>	2	0	1	0	0	1	1	1	1	0	2	0	1	0	1	1	0	1	2	1	1	1	1	0	0	1	1	1	1	0	2	
<i>Toxodon</i>	2	0	1	0	0	0	1	1	1	0	2	1	2	0	1	1	1	1	2	1	1	1	1	1	0	1	1	0	1	0	2	
<i>Trigodon</i>	2	0	1	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	2	1	1	1	1	1	0	0	1	1	2	0	2	
<i>Colbertia</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0
<i>Oldfieldthomasia</i>	1	0	0	0	1	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	?	0	?	0	0	1	0	0	0	0
<i>Campanorco</i>	1	0	0	1	1	0	1	0	0	0	1	0	1	0	1	1	1	0	1	?	?	?	?	?	?	1	0	1	0	0	0	0
<i>Notopithecus</i>	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1	0	0	0	0
<i>Protypotherium</i>	1	0	0	1	0	0	1	1	0	1	2	0	0	0	1	1	0	1	1	1	1	1	1	0	1	0	0	1	2	0	0	0
<i>Interatherium</i>	1	0	0	1	0	0	1	1	0	1	2	0	2	0	1	1	0	1	2	0	1	1	1	1	1	1	1	0	2	0	0	0
<i>Griphotherion</i>	1	1	0	0	1	0	1	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0
<i>Trachytherus</i>	1	2	1	1	0	1	1	1	0	0	2	0	2	0	1	1	1	?	2	1	1	1	?	?	?	1	1	1	1	0	1	1
<i>Mesotherium</i>	1	2	1	1	0	1	1	1	0	1	2	0	2	0	1	1	1	1	2	1	1	1	1	1	0	1	1	0	2	0	1	1
<i>Archaeohyrax</i>	1	1	1	1	1	0	1	0	0	0	2	0	1	0	1	0	0	1	1	1	1	1	?	0	?	1	1	1	1	0	0	0
<i>Hegetotherium</i>	0	2	1	1	0	0	1	0	0	0	2	0	1	1	1	1	1	1	0	1	1	1	1	0	0	1	0	1	2	0	0	0
<i>Pachyrukhos</i>	0	2	1	2	0	0	1	0	0	1	2	0	2	1	0	0	1	1	0	1	1	0	1	1	0	1	0	0	2	0	0	0
<i>Paedotherium</i>	0	2	1	2	0	0	1	0	0	1	2	0	2	1	0	0	1	1	0	1	1	0	1	1	0	1	0	0	2	0	0	0

García-López and Powell (2011). We selected the most significant age-specific variable affecting these taxa, mapping the climatic transition during the Tertiary of South America (and, in fact, all over the world) that occurred across the Eocene-Oligocene boundary (Prothero and Berggren 1992). This was shown by tracing a line separating taxa younger and older than the transition. We mapped size as encoded in our three-states character 31 (small, medium, and large; see description in Appendix 2), as well as condition of molars: brachyodontology (low-crowned) versus hypsodontology (high-crowned). The latter defined as a height-to-width ratio of the largest molar greater than 1 (see Mendoza and Palmqvist 2007) and including hypselodontology (a extreme case of hypsodontology; see Janis 1986). Finally, we provide a map of each original character on the ordination diagram (see Supplemental Figs. S1–S31).

## Results and Discussion

**Data and Similarity Scoring** of our notoungulate sample resulted in the data matrix shown in Table 1, with 36 missing values (or 7.7 % of 465 cells) representing principally the mandible missing in several taxa. From this data matrix the modified *RT* index was calculated and the resulting similarity matrix is shown in Table 2. Although *Paedotherium* and *Pachyrukhos* (Hegetotheriidae) are distinct taxa, they scored the same for our morphofunctional characters (Table 1) and so all pair-wise comparisons with other taxa were identical between the two genera (Table 2).

**Ordination** The first PCORD axis accounted for 25.4 % of total variance (sum of all eigenvalues; Table 3). Together with axis 2, they accumulated 38.9 % of total variance, which nearly doubles the value expected under a broken-

stick null model (Table 3). By contrast, the third and subsequent axes had eigenvalues similar or below the null expectation and thus are not considered further.

An ordination diagram of the plane of axes 1 and 2 is presented in Fig. 3a. Two groups of notoungulate genera were apparent: small and primitive taxa tightly grouped in the negative side of axis 1 (*Simpsonotus*, *Colbertia*, *Brachystephanus*, *Pampahippus*, *Oldfieldthomasia*, *Nothopithecus*, *Notostylops*, *Boreastylops*, *Griphotherion*, and *Campanorco*), and a more dispersed group from the center to the right hand side of the diagram including the remaining taxa. All members of the former group are Paleocene or Eocene taxa; by contrast, only two taxa (*Thomashuxleya* and *Coquenia*) are of Eocene age in the latter group (see line depicting the Eocene-Oligocene boundary line in Fig. 3b).

**Character Analysis** The analysis recovered 18 original characters significantly associated with PCORD axis 1 only, ten characters with axis 2 only, four characters with none, and four characters associated with both axes (Table 4). The last were glenoid fossa shape, diastema development, upper canine development, and skull size. Three characters were not tested due to unbalanced scoring (see Methods). For character interpretation, we divided the morphospace in quadrants. The first division was negative versus positive side of axis 1. The primitive notoungulates lying on the negative side were associated with a short rostrum, a lateral auditory meatus, a comparatively large bulla, and slender protoloph and metaloph in upper molars. The progressively more derived notoungulates lying on the positive side of axis 1 tended to possess comparatively longer rostrum, smaller bulla, auditory meatus dorsolaterally oriented, wide palate, larger paracondylar process, mandibular condyle higher than toothrow, molars with flat occlusal surface and derived lophs, and a deep mandible with procumbent symphysis, expanded angular process, anterior insertion of masseter, and high coronoid process. Altogether, the states associated with the positive side of axis 1 represent mainly specializations of the masticatory apparatus common to derived notoungulates. Variation along axis 2 was also divided in negative and positive sides. Basicranial angle, rostrum height, robustness of zygoma, and relative size of I1 versus I2 were all greater on the negative side of axis 2. The positive side was associated with a greater development of the zygomatic plate and the epitympanic sinus. In turn, four characters were associated with both axis 1 and 2 (see above and Table 2); a large diastema was associated with positive sides of both axes, whereas a transversal glenoid fossa, a developed upper canine, and a large skull appeared associated with positive side of axis 1 and negative side of axis 2.

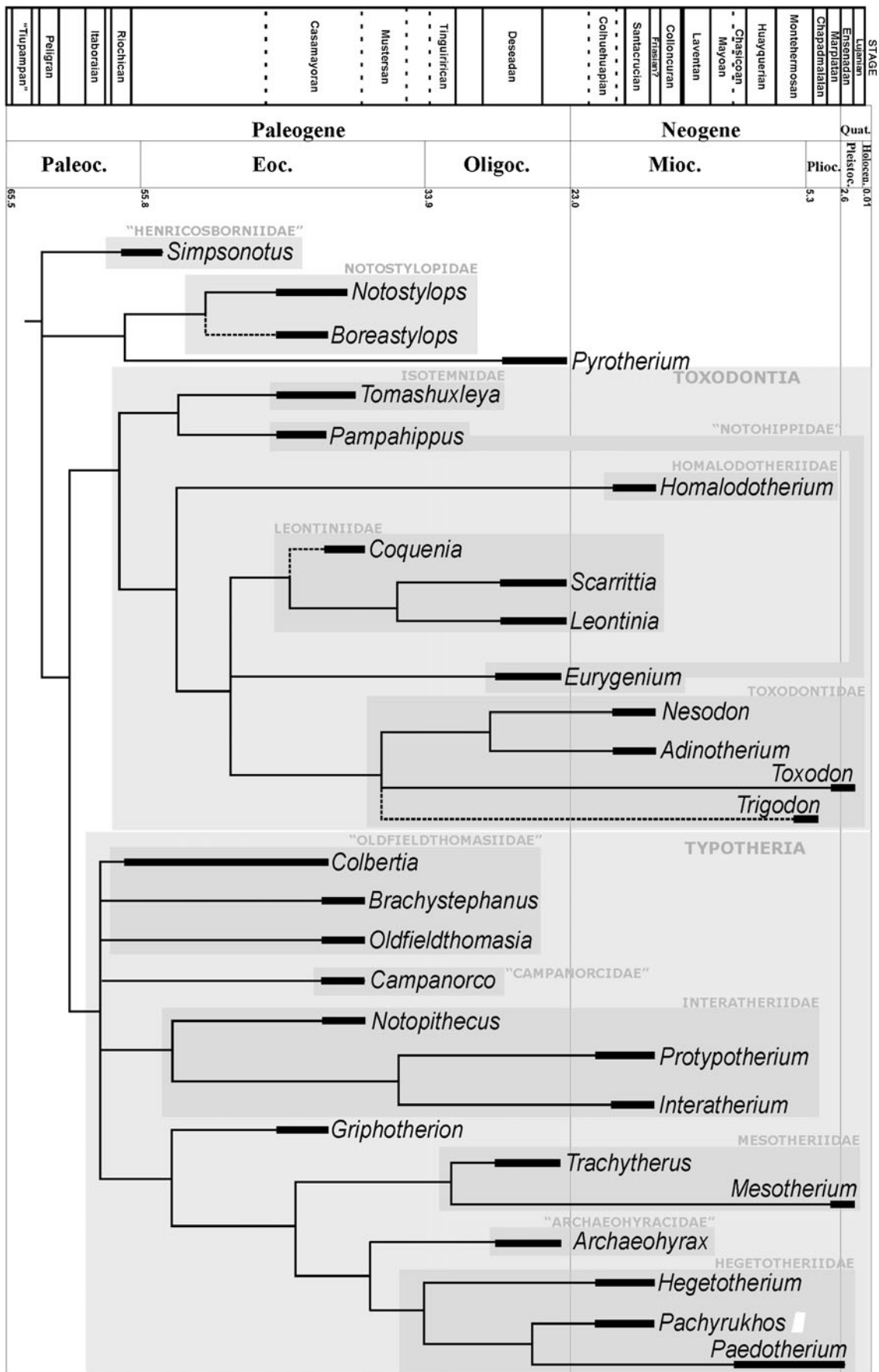
**Patterns in Morphospace** In terms of character variation, the notoungulate skull morphospace (see character analysis

**Fig. 2** Cladogram modified from Billet (2010) and García-López and Powell (2011) depicting the relationships of genera included in this study. Families are included in boxes. A stratigraphic reference and time scale are provided on top

above) can be interpreted as composed of two regions on each side of axis 1 of structurally “primitive” versus “derived” notoungulates. The latter depicted two diverging trends, one toward the quadrant of positive axis 1 and 2 characterized by small skulls with large diastema, zygomatic plate, and epitympanic sinus, which together compose the rabbit-like morphotype; and one toward the quadrant of positive side of axis 1 and negative side of axis 2 characterized by large skulls with transverse glenoid and developed upper canines that compose, together with the set of derived states on axis 1, a heavy herbivore, or the rhino-like morphotype. In between the two appeared the mesotheriids as intermediate forms, here likened to a large rodent (see below and Shockey et al. 2007).

When phylogenetic connections were mapped onto the ordination diagram, the cranial morphospace becomes considerably more informative (Fig. 3b). Lines in morphospace joining successive sister taxa showed clear, initially parallel trends across morphospace of several lineages from typical Paleogene forms (negative side of axis 1) toward increasingly more derived, divergent forms (positive side of axis 1 in Fig. 3). Of the lineages sampled in this study, those reaching the Quaternary appeared in the edges of the diagram: late Hegetotheriidae (top), Mesotheriidae, and Toxodontidae (right). These represent the three derived rabbit-like, large-rodent-like, and rhino-like morphotypes, respectively, with Interatheriidae recovered as intermediate forms between rabbit-like and large-rodent-like forms (see above). Alternatively, Shockey et al. (2007) likened mesotheres to wombats (terrestrial diprotodont marsupials that resemble large fossorial rodents). An additional, previously identified as a small-horse morphotype, represented by the Oligocene *Eurygenium*, also appeared in the (bottom) edge of the diagram.

The pattern of skull size mapped onto the morphospace is also remarkable: small-sized forms appeared on top of the occupied space, mid-sized forms in the middle and lower portions, whereas large-sized forms were confined to the bottom-right region of the morphospace. Likewise, a clear pattern of brachydonty versus hypsodonty emerges when a line separating notoungulates with each type of dentition is superimposed in the diagram: hypsodont forms included all the four morphotypes and their closely related taxa. Hypsodonty was clearly independent of the size pattern (derived hypsodont forms span the whole size spectrum from rabbit-like to rhino-like notoungulates), and more responsive to the age pattern given that most hypsodont taxa are Neogene; exceptions of *Eurygenium*, *Trachytherus*, and *Archaeohyrax* which are late Oligocene hypsodont forms.



**Table 2** Similarity matrix based on the Rogers and Tanimoto (1960) index (source matrix in Table 1)

Genus	SIM	BRA	NOS	BOR	PYR	TOM	PAM	HOM	COQ	SCA	LEO	EUR	ADI	NES
<i>Simpsonotus</i>	1.00													
<i>Brachystephanus</i>	0.87	1.00												
<i>Notostylops</i>	0.72	0.81	1.00											
<i>Boreastylops</i>	0.63	0.71	0.88	1.00										
<i>Pyrotherium</i>	0.22	0.26	0.30	0.33	1.00									
<i>Tomashuxleya</i>	0.46	0.54	0.46	0.46	0.38	1.00								
<i>Pampahippus</i>	0.85	0.92	0.66	0.66	0.24	0.55	1.00							
<i>Homalodotherium</i>	0.46	0.57	0.43	0.43	0.38	0.66	0.59	1.00						
<i>Coquenina</i>	0.44	0.57	0.41	0.41	0.27	0.60	0.60	0.74	1.00					
<i>Scarritia</i>	0.48	0.45	0.38	0.38	0.33	0.50	0.50	0.67	0.63	1.00				
<i>Leontinia</i>	0.30	0.36	0.28	0.30	0.38	0.45	0.37	0.66	0.58	0.62	1.00			
<i>Eurygenium</i>	0.30	0.32	0.23	0.26	0.31	0.53	0.63	0.60	0.57	0.66	0.60	1.00		
<i>Adinotherium</i>	0.22	0.29	0.27	0.22	0.37	0.45	0.23	0.40	0.48	0.38	0.46	0.50	1.00	
<i>Nesodon</i>	0.19	0.21	0.19	0.22	0.37	0.36	0.26	0.36	0.44	0.35	0.43	0.55	0.82	1.00
<i>Toxodon</i>	0.13	0.18	0.24	0.27	0.40	0.36	0.14	0.33	0.35	0.32	0.40	0.45	0.72	0.68
<i>Trigodon</i>	0.19	0.26	0.19	0.22	0.40	0.40	0.26	0.40	0.51	0.38	0.46	0.52	0.77	0.72
<i>Colbertia</i>	0.94	0.93	0.77	0.68	0.24	0.50	0.78	0.49	0.48	0.51	0.33	0.33	0.24	0.17
<i>Oldfieldthomasia</i>	0.81	0.74	0.57	0.49	0.20	0.47	0.85	0.47	0.49	0.45	0.41	0.33	0.26	0.23
<i>Campanorco</i>	0.61	0.73	0.67	0.61	0.18	0.47	0.83	0.43	0.43	0.35	0.32	0.30	0.39	0.28
<i>Notipithecus</i>	0.72	0.81	0.68	0.68	0.24	0.43	0.66	0.43	0.48	0.44	0.40	0.30	0.29	0.22
<i>Protypotherium</i>	0.41	0.46	0.32	0.32	0.22	0.43	0.37	0.36	0.48	0.35	0.30	0.50	0.38	0.41
<i>Iteratherium</i>	0.27	0.27	0.35	0.35	0.24	0.30	0.26	0.25	0.32	0.27	0.25	0.37	0.38	0.41
<i>Griphotherion</i>	0.68	0.71	0.68	0.59	0.19	0.43	0.60	0.45	0.44	0.41	0.30	0.30	0.32	0.24
<i>Trachytherus</i>	0.17	0.24	0.26	0.32	0.30	0.41	0.41	0.35	0.42	0.35	0.38	0.45	0.54	0.59
<i>Mesotherium</i>	0.11	0.16	0.22	0.27	0.27	0.33	0.20	0.25	0.35	0.24	0.38	0.41	0.44	0.48
<i>Archaeohyrax</i>	0.38	0.38	0.38	0.38	0.23	0.37	0.41	0.30	0.29	0.21	0.23	0.20	0.45	0.49
<i>Hegetotherium</i>	0.22	0.29	0.27	0.27	0.22	0.36	0.20	0.28	0.35	0.22	0.30	0.26	0.48	0.44
<i>Pachyrhynchus</i>	0.17	0.21	0.29	0.24	0.19	0.30	0.14	0.18	0.24	0.17	0.20	0.20	0.27	0.24
<i>Paedotherium</i>	0.17	0.21	0.29	0.24	0.19	0.30	0.14	0.18	0.24	0.17	0.20	0.20	0.27	0.24

Genus	TOX	TRI	COL	OLD	CAM	NOT	PRO	INT	GRI	TRA	MES	ARC	HEG	PAK	PAE
<i>Simpsonotus</i>															
<i>Brachystephanus</i>															
<i>Notostylops</i>															
<i>Boreastylops</i>															
<i>Pyrotherium</i>															
<i>Tomashuxleya</i>															
<i>Pampahippus</i>															
<i>Homalodotherium</i>															
<i>Coquenina</i>															
<i>Scarritia</i>															



**Table 2** (continued)

Genus	TOX	TRI	COL	OLD	CAM	NOT	PRO	INT	GRI	TRA	MES	ARC	HEG	PAK	PAE
<i>Leontinia</i>															
<i>Eurygenium</i>															
<i>Adinootherium</i>															
<i>Nesodon</i>															
<i>Toxodon</i>	1.00														
<i>Trigodon</i>	0.63	1.00													
<i>Colbertia</i>	0.15	0.22	1.00												
<i>Oldfieldthomasia</i>	0.16	0.23	0.76	1.00											
<i>Campanorco</i>	0.25	0.32	0.67	0.67	1.00										
<i>Notopithecus</i>	0.19	0.27	0.77	0.61	0.72	1.00									
<i>Protypotherium</i>	0.32	0.38	0.38	0.45	0.47	0.53	1.00								
<i>Interatherium</i>	0.48	0.38	0.24	0.29	0.39	0.33	0.65	1.00							
<i>Griphotherium</i>	0.19	0.24	0.72	0.71	0.85	0.55	0.35	0.29	1.00						
<i>Trachytherus</i>	0.54	0.50	0.20	0.20	0.37	0.29	0.42	0.50	0.29	1.00					
<i>Mesotherium</i>	0.55	0.51	0.13	0.14	0.28	0.22	0.44	0.63	0.19	0.80	1.00				
<i>Archaeohyrax</i>	0.35	0.32	0.35	0.35	0.52	0.45	0.49	0.41	0.45	0.47	0.38	1.00			
<i>Hegetotherium</i>	0.38	0.41	0.24	0.32	0.47	0.35	0.48	0.38	0.35	0.50	0.48	0.53	1.00		
<i>Pachyrhinos</i>	0.35	0.27	0.19	0.21	0.25	0.22	0.32	0.38	0.22	0.32	0.48	0.32	0.59	1.00	
<i>Paedotherium</i>	0.35	0.27	0.19	0.21	0.25	0.22	0.32	0.38	0.22	0.32	0.48	0.32	0.59	1.00	1.00

**Table 3** Summary of ordination results from Principal Coordinates Analysis based on a double-centered Rogers and Tanimoto (1960) similarity matrix. Here we report values for the first four of the axes extracted, including eigenvalues ( $\lambda_i$ ), proportions of variance expected using a broken-stick null model (% Expected), actual proportion of variance accounted for by each individual axis (% Observed), and cumulative percentage of observed variance (last column)

Axis	$\lambda_i$	% Expected	% Observed	% Cumulative
1	4.27	13.66	25.36	25.36
2	2.29	10.21	13.58	38.94
3	1.41	8.49	8.38	47.31
4	1.12	7.34	6.68	53.99
Total	16.83*	NA	NA	100.00

NA non-applicable

\*  $16.83 = \sum \lambda_i$

The pattern of hypsodonty in Fig. 3b, with several lineages separately emerging as hypsodont from a the primitive, brachyodont nucleus in morphospace, is consistent with the many (at least four) independent originations of hypsodonty proposed by several authors (see Croft and Weinstein 2008; Billet et al. 2009a, b; Billet 2011).

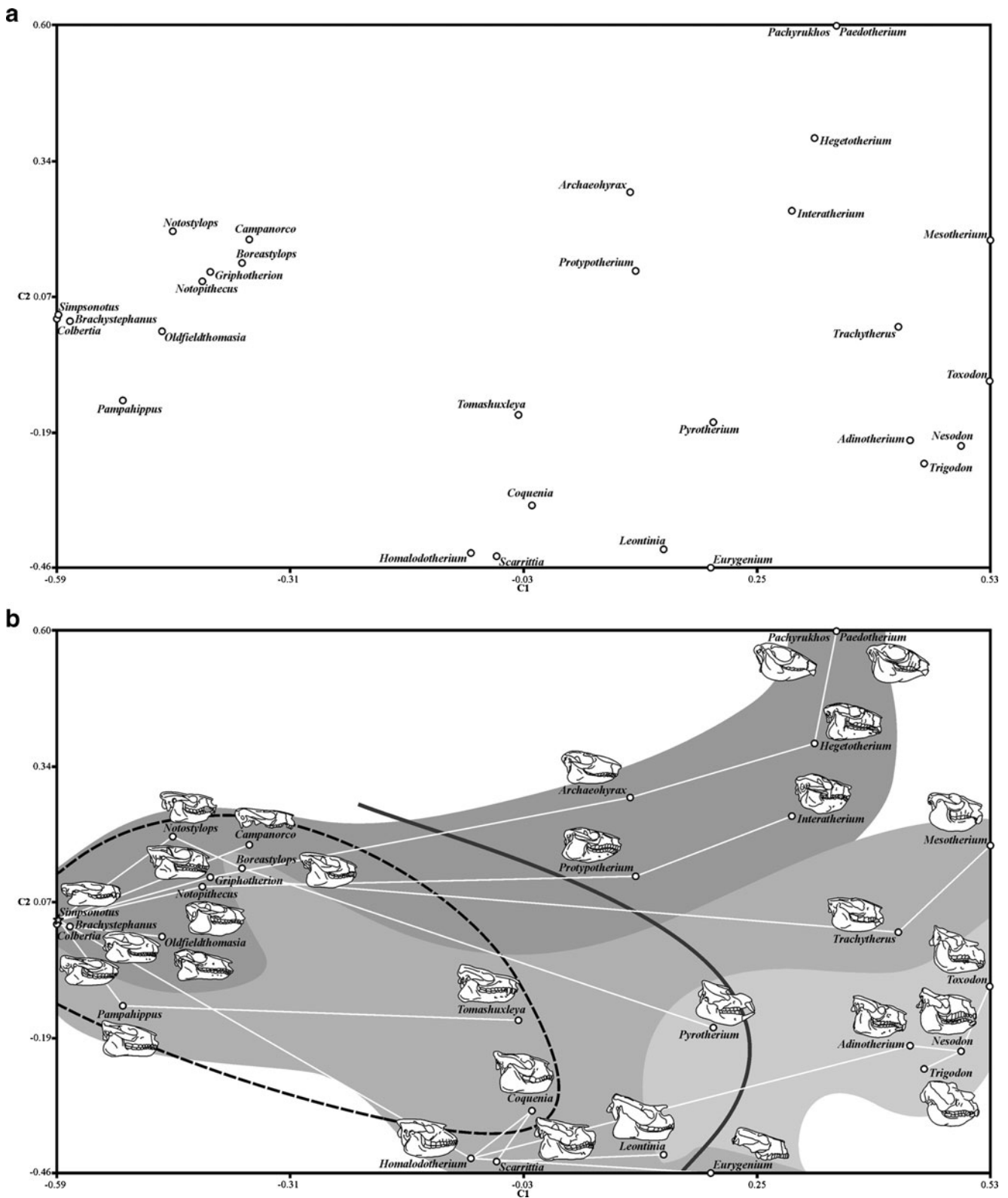
**Evolutionary Interpretations** In functional terms, notoungulate evolution consisted of a great expansion of the morphospace from a tight cluster of primitive forms that diverged in time toward several distinct morphotypes. This is evidenced in the lines connecting sister taxa when superimposed onto the ordination diagram, but there appear to be interesting exceptions. The Eocene *Coquenia* resembled closely the more advanced Oligocene relatives *Leontinia* and *Scarritia*, and another Eocene form, *Thomashuxleya*, joined this group. Another interesting example is represented by *Pyrotherium*, formerly included in an order of its own and recently recovered within Notoungulata (see Billet 2010). Although not an hypsodont form, this taxon is an Oligocene herald of more advanced, but unrelated Neogene forms in the Toxodontidae whose position in the morphospace clearly suggests a temporal replacement within the same morphotype.

The pattern in morphospace is reminiscent of the South American pattern of “faunal strata” advanced by Simpson (1980) and elaborated further by Flynn and Wyss (1998) and Croft et al. (2008). These authors defined a first stratum spanning from the Paleocene to the Eocene and dominated by “archaic” mammal communities represented mainly by primitive South American endemic ungulate groups (as well as Xenarthra and Metatheria). This fauna was replaced by the second stratum of the Oligocene and most part of the Miocene (see Croft et al. 2008) and is characterized by the “modernization” of several endemic lineages including notoungulates, as well as by immigration events including early representatives of “native” South American rodents and primates (but

note that recent evidence suggests that rodents entered the continent by the middle Eocene; Antoine et al. 2012). The third faunal stratum is characterized by the latest and most derived representatives of native clades (and the advent of GABI colonizers). The pattern in morphospace reflects with unexpected fidelity those faunal strata for notoungulates, with most forms of the first stratum of primitive notoungulates to the negative side of axis 1 and separated by a gap from forms of the second stratum in the middle. This important shift is associated with intense turnover in mammalian fossil communities and has received considerable attention. Known as the “Terminal Eocene Event” in North America and “Le Grand Coupure” in Europe (Pascual et al. 1996; MacFadden 2000; Flynn et al. 2003; Croft et al. 2008; Billet et al. 2009a, b), this climatic event was mainly characterized by the change from humid and warm environments during the Eocene to arid, colder, and open environment during the Oligocene (MacFadden 2000). Particularly in South America, this event also coincides with the complete isolation of the continent, marked by the separation from Antarctica. The effects on the endemic fauna of this region were substantial, including the spread of hypsodont forms since the Oligocene, a feature precociously acquired by South American forms as compared with other ungulates (Pascual et al. 1996; Kay et al. 1999; MacFadden 2000; Croft and Weinstein 2008; Billet et al. 2009a, b). Derived forms of the third stratum diverged toward the right-hand side of the diagram. Again, exceptions (as mentioned above) represent interesting cases of older forms resembling younger and more derived taxa (e.g., *Coquenia*).

As interesting as the pattern of occupied space were the areas devoid of notoungulate representatives. These areas included most of the top region of the space, the gap between the cluster of primitive and more derived forms, and the upper and lower right corners of the diagram. It is possible that these vacant areas were actually occupied by notoungulates not sampled in this study, or by taxa belonging to other orders that constrained the evolution of notoungulates, such as other members of the South American native fauna, or even the late North American colonizers. This hypothesis can be readily tested by scoring representatives of other taxa such as condylarths, litopterns, astrapotheres, xenungulates, and other pyrotheres (only *Pyrotherium* was included in the present analysis). Such analyses may also include non-ungulate taxa such as caviomorph rodents, as well as paenungulates and euungulates that colonized South America and presumably replaced some of the native forms (e.g., large notoungulates; cf. Webb 1991).

**Comments on Technique** The multivariate analysis applied here recovered meaningful patterns of variation in an extinct clade of mammals on the basis of a discrete-state coding of salient morphological features of the skull. The similarity index used was just one of many available, but clearly, a thorough exploration of indices and their properties is beyond



**Fig. 3** Ordination diagram (plane of axes 1 and 2, 38.9 % of total variation) showing the position of taxa in morphospace (a) and the same morphospace with additional information mapped onto the same diagram (b). Size include overall skull shape (drawings scaled to same length), body size mapped as colors (dark gray: small, intermediate shade: mid-

sized, light gray: large), and phylogenetic connections (lines connecting successive sister species in each major lineage). In addition, the dotted line separates Eocene-Paleocene forms (left) from Oligocene-Neogene forms (right), and the solid line separates brachyodont (left) from hypsodont (right) forms

**Table 4** Summary of general linear modeling applied to principal coordinates of axes 1 and 2 as dependent variables, with each discrete-state original character as independent variable (factor). Significant *P*-values for each axis are in bold (alpha  $\approx$  0.01; see text). Abbreviations: *d.f.* degrees of freedom. Full character and states description in Appendix 2

Characters	<i>d.f.</i>	Axis 1		Axis 2	
		<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value
1. Basicranial angle	27	0.93	0.343	121.90	<b>&lt;0.001</b>
2. Zygomatic plate development	27	6.04	0.021	18.61	<b>&lt;0.001</b>
3. Auditory meatus orientation	27	32.11	<b>&lt;0.001</b>	1.74	0.198
4. Epitympanic sinus development	27	3.76	0.063	42.87	<b>&lt;0.001</b>
5. Tympanic bulla development	27	77.86	<b>&lt;0.001</b>	0.58	0.454
6. Rostrum height	27	3.22	0.084	21.82	<b>&lt;0.001</b>
7. Rostrum length	27	31.77	<b>&lt;0.001</b>	0.38	0.541
8. Glenoid fossa shape	27	19.28	<b>&lt;0.001</b>	7.23	<b>0.012</b>
9. Anterior palate shape*	27	9.48	<b>0.004</b>	5.31	0.030
10. Upper tooththrow shape	27	5.33	0.029	4.98	0.034
11. Posterior palate width	27	13.70	<b>&lt;0.001</b>	5.69	0.024
12. Nasal aperture position	27	—	—	—	—
13. Diastema development	27	8.93	<b>0.006</b>	10.90	<b>0.003</b>
14. Postorbital constriction width	26	0.82	0.370	4.32	0.048
15. Temporal fossa size	27	—	—	—	—
16. Postorbital process development	24	4.68	0.041	3.33	0.080
17. Molar row relative lengths	27	0.39	0.540	0.27	0.609
18. Paracondylar process development	22	67.20	<b>&lt;0.001</b>	0.03	0.859
19. Zygomatic arch shape	27	3.58	0.069	33.38	<b>&lt;0.001</b>
20. Mandibular symphysis orientation	24	43.74	<b>&lt;0.001</b>	1.19	0.287
21. Mandibular condyle position	24	11.58	<b>0.002</b>	0.29	0.598
22. Mandible depth	25	14.33	<b>&lt;0.001</b>	0.01	0.974
23. Angular process development	20	22.62	<b>&lt;0.001</b>	0.36	0.554
24. Masseteric insertion extent	23	12.97	<b>0.002</b>	4.26	0.050
25. Coronoid process height	20	29.24	<b>&lt;0.001</b>	1.14	0.297
26. Upper incisors size	26	4.33	0.047	14.52	<b>&lt;0.001</b>
27. Upper molars occlusal surface	27	22.56	<b>&lt;0.001</b>	0.09	0.770
28. Upper canine development*	27	3.38	<b>0.135</b>	7.14	<b>0.013</b>
29. Upper molar morphology*	27	57.75	<b>&lt;0.001</b>	1.63	0.213
30. Upper cheek teeth heterodonty	27	—	—	—	—
31. Skull size	27	10.38	<b>0.003</b>	22.73	<b>&lt;0.001</b>

\*Tested with one character state coded as non-applicable (see text)

the scope of this contribution. Suffice to say here that other indices merit exploration, and that the intuitively simple *RT* index as applied in the present study, which also corrects for dissimilarities and missing entries, appeared to effectively capture meaningful morphological similarities among taxa. How faithfully these similarities translate into patterns in the actual morphospace is difficult to assess but it was clear that the subsequent PCORD analysis was able to recover structured patterns of morphofunctional variation in this case study (notoungulates). Thus, ordination diagrams likely represent the morphospace to the extent sampled by our character set. In addition, linear modeling of axis scores allowed to identify

the characters that were important in each region of the ordination diagram. This discrete-state procedure, devised to cope with problems of material fragmentation and distortion that preclude the application of more conventional metric techniques such as Principal Components Analysis, appears as an effective alternative for the study of fossil lineages.

## Conclusions

The discrete-state multivariate analysis recovered a remarkable pattern of cranial variation across taxa representing all



currently recognized notoungulate families from all ages. Three cranial morphotypes were clearly identified by this analysis, and they largely correspond with those previously proposed (e.g., Reguero et al. 2007; Croft and Weinstein 2008). It is important to note that in this contribution we do not test the actual resemblance of these morphotypes to their models (i.e., true rabbits, rhinos, etc.), but that can be done by including them in a new analysis. A fourth morphotype also appeared as a derived form (*Eurygenium*). These morphotypes did not cluster in morphospace; instead, they were end points of lineages that evolved from a remarkably uniform ancestral Paleogene stock and diverged during the Tertiary, some eventually reaching the Quaternary as highly derived forms. In many of these lineages, the analysis showed consistent patterns of successive taxa replacement. Also, the morphospace depicted interesting patterns of size, molar morphology, age, and possibly, responses to climate change, as well as phylogenetic relatedness. The discrete-state coding strategy effectively circumvented problems that arise with metric techniques when applied to fragmentary or deformed fossil material. It is suggested that this technique may be used to test constraints in morphofunctional evolution of other groups as done here with notoungulates.

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## Appendix 1 Specimens Examined in the Present Study

Institutional abbreviations: AMNH: American Museum of Natural History, New York; MACN: Museo Argentino de Ciencias naturales Bernardino Rivadavia, Buenos Aires, Argentina; MLP: Museo de La Plata, Buenos Aires, Argentina; MMMP: Museo Municipal de Historia Natural “Lorenzo Scaglia”, Mar del Plata, Argentina; PVL: Colección Paleontología de Vertebrados Lillo, Tucumán, Argentina.

Specimen list (alphabetical):

*Archaeohyrax* MACN-A 52-617; *Boreostylops* MLP 78-V-6-5, PVL 4261; *Brachystephanus* MLP 68-X-17-2; *Campanorco* MLP 79-VI-16-1, PVL 6225; *Colbertia* PVL 4183, PVL 4184 (1-2), PVL 4293, PVL 4300, PVL 4608, PVL 6218, PVL 6227; *Coquenia* PVL 5853, PVL 6397; *Griphotherium* PVL 5903; *Hegetotherium* PVL 91; *Interatherium* MACN-A 3444; *Leontinia* MACN-A 52-573 (photographs provided by Virginia Deraco); *Mesotherium* MACN 2036, MACN 8690; *Notopithecus* MACN-A 10790, MACN-A 10787; *Notostylops* MACN-A 10499, MACN-A 10466; *Oldfieldthomasia* MACN-A 10376, MACN-A 10772; *Pachyrhukhos* PVL 84, MACN-A 3313;

*Paedotherium* MACN-A 1184, MACN-PV 1081, MACN-PV 7214, MACN-PV 10178, MMMP 226-S, MMMP 698-S, MMMP 710-S, PVL 503, PVL 2272, PVL 2274, PVL 2377, PVL 3386; *Pampahippus* PVL S-4192; *Protypotherium* MACN-A 3882, MACN-A 3920, MLP 84-III-9-12; *Scarrittia* AMNH 29581, AMNH 29583, AMNH 29584 (photographs provided by Virginia Deraco); *Simpsonotus* MLP 73-VII-3-11; *Toxodon* MLP 12-II-26, PVL uncatalogued specimen; *Trachytherus* MACN-A 52-490.

## Appendix 2 Commented List of Characters Used in this Study

See Fig. 1 for illustration of characters.

1. Basicranial angle: less than 180° (0); or approximately 180° (1); or greater than 180° (2). The basicranial angle is defined as the angle between the horizontal plane of the basicranium with respect to the rostrum of the skull. The former is defined by the ventral aspect of the presphenoid, basisphenoid, and basioccipital, and the latter by the upper alveolar line, specifically the plane including the points at the base of left and right canines and last molars. The angle is assessed on a lateral view of the skull.
2. Zygomatic plate: absent (0); or incipient (1); or well developed (2). The term “zygomatic plate” refers here to a lateral widening of the anterior root of the zygomatic arch, associated with a flat or concave smooth ventral area for the origin of enlarged anterior tracts of the masseter muscle. The skulls with incipient plates present a moderately widened ventral edge of the anterior root of the arch and a comparatively small flattened area. In taxa with a well-developed plate (state 2), the anterior root of the arch is greatly widened and a large, concave, and smooth area is present.
3. External auditory meatus orientation: nearly horizontal (0); or dorsolateral (1). In the groups considered here, the external auditory meatus is a lateral tubular projection of the ectotympanic. Orientation of the tube is independent of the length of the meatus. In state 1, the tube extends laterally, dorsally, and usually posteriorly, reaching the level of the skull roof.
4. Development of the epitympanic sinus (squamosal): absent or inconspicuous (0); or well developed (1); or prominent (2). The epitympanic sinus of the squamosal is a singular feature of notoungulates and pyrotheres (see Billet 2010). This structure is a hollow space developed inside the squamosal bone. The sinus is located at the posterolateral corner of the skull, and connected to the tympanic cavity ventrally. This feature is present in all notoungulates (Cifelli 1993) and in

- Pyrotherium*; however, in some Paleogene genera the internal space of the squamosal is not associated with an external inflation and the sinus is not evident in intact skulls (state 0). Thus, the first state also contemplates the possibility that the sinus is absent. Nevertheless, the presence of the sinus was confirmed in some genera assigned 0, such as *Colbertia*, even in the absence of the external inflation (see García-López 2011).
5. Development of the tympanic bulla: small (0); or well developed, prominent (1). All notoungulates exhibit a tympanic bulla that is part of the ectotympanic bone (see Gabbert 2004). In the first state, the bulla is small with respect to the area of the basicranium in ventral view, and not particularly prominent ventrally. In the second state, the bulla is a large, balloon-like structure, usually occupying a large surface of the basicranial area in ventral view.
  6. Height of the rostrum: low (0); or high (1). This character is considered as the relation between the length of the rostrum in lateral view (from the rostral edge of the orbit to the tip of the premaxilla) and the height of the rostrum immediately rostral to the orbit. In skulls with a high rostrum, both measures are similar. In a low rostrum, the first measure is clearly greater than the second.
  7. Length of the rostrum: short (0); or long (1). This character is measured as the proportion of the length of the palate (from the edge of the choanae to the rostral edge of the premaxilla), relative to the total skull length. A long rostrum is one comprising more than 50 % of the total length of the skull in ventral view.
  8. Shape of the mandibular (= glenoid) fossa: shallow, rostral border not well defined (0); or transversal, rostral border well defined (1). The first state of this character is referred to a shallow fossa where width is subequal to the length and where rostral limit is not marked by a well-developed process on the ventral edge of the zygomatic arch. This is related to the shape of the articular process of the mandible, and, therefore, this last feature was not included in the analysis to avoid redundancies.
  9. Shape of the anterior palate (on the premaxilla): semi-circular (0); or subrectangular (1); or *Pyrotherium*-like (2). Most genera show state 0, with a roughly semicircular dental arcade. Some genera (e.g., *Toxodon*) exhibit a truncated rostrum with a transversally straight arcade (state 1). The condition observed in *Pyrotherium* is of irregular shape due to the great development of the incisor alveoli (state 2). This character has been used to assess dietary adaptations of extinct ruminants (Solounias and Moelleken 1993).
  10. Shape of the upper toothrow: straight (0); or bowed, toothrow medially concave (1). State 0 applies to either parallel or divergent toothrows as the character refers to one side of the upper dental arcade.
  11. Posterior width of the palate: very narrow (0); or narrow (1); or wide (2). State 0 refers to the singular condition observed in *Pyrotherium*, which presents an unusual narrow palate. State 1 is scored when the posterior width of the palate represents less than two times the buccolingual length of the molars. In state 2 the posterior width exceeds that measure.
  12. Position of the nasal aperture: terminal (0); or slightly retracted (1); or retracted (2). The lateral edges of the nares and the rostral end of the nasals can be located at the level of the first incisors (state 0), slightly behind this position (state 1), or located at the level of the postcanine teeth (state 2, only present in *Pyrotherium*).
  13. Diastema: absent (0); or present, small (1); or present, well developed (2). A diastema is any space in the dental arcade between the canines and cheekteeth, existing as a consequence of evolutionary loss of dental pieces or separation between them (usually associated with some reduction of the teeth).
  14. Postorbital constriction: narrow (0); or wide (1). The confluence of the temporal lines just posterior to the postorbital processes may determinate a strong postorbital constriction (state 0).
  15. Temporal fossa: small (0); or large (1). The extent of the temporal fossa is determined dorsally by the temporal lines and the sagittal crest, which mark the perimeter of the area for the origin of the temporal muscle in the skull. Small fossae (state 0) are shallow and retracted to the surface of the parietal, with sagittal crests weak or absent. In large fossae (state 1), the temporal lines begin immediately posterior to the postorbital processes and converge in a strong sagittal crest that joins the lambdoid or nuchal crest.
  16. Development of the postorbital process: small (0); or large (1). A small postorbital process (state 0) is either a tubercle-like structure with a limited base, or a sharp, needle-like process. In either case the tip of the process does not reach far into the orbit. A large process (state 1) exhibits either a wide base, or it is long, thus approaching the zygomatic arch.
  17. Length of the upper molar row relative to upper premolar row: similar length (0); or molar row longer (1). This difference could be due to a lesser mesiodistal development of the premolars (being all present) or to the evolutionary loss of one or more of the anterior premolars.
  18. Development of the jugular (= paracondylar) process in occipital view: short, not exceeding the extent of the

- tympenic bulla ventrally (0); or long, greatly exceeding the tympanic bulla ventrally (1).
19. Development of the zygomatic arch in lateral view: slender (0); or intermediate (1); or robust (2). Slender arches (state 0) are thin bars of bone. Arches are scored as robust (state 0) when its depth is comparable to the height of the orbit.
  20. Orientation of the mandibular symphysis: sub-vertical (0); or procumbent (1). In the procumbent state, the mental surface of the symphysis forms an angle of 45° or less with the horizontal (ventral edge of the mandible).
  21. Position of the articular process (= mandibular condyle) relative to the lower molar row: slightly dorsal to the molar row level (0); or much higher than the molar row level (1). In all the studied genera the articular process is located above the level of the lower molar row. The character is scored as 0 when this difference in height is less than twice the height of lower molars. In *Campanorco* the mandible is unknown. We scored this taxon on the basis of the relative position of the glenoid fossa with respect to the occlusal surface of the upper molars.
  22. Mandibular depth at the level of the lower premolars: shallow (0); or deep (1). This character is scored as 1 when the depth of the mandibular body is greater than three times the height of the lower premolar crowns.
  23. Development of the angular process: not expanded (0); or expanded (1). In most Paleogene genera the angular process is a rounded prominence on the mandibular ramus, which is more developed caudally than ventrally. Expanded processes (state 1) describe a wide, continuous curve from the articular process (= mandibular condyle) to the rostral end of the masseteric line, on the ventral edge of the mandibular body.
  24. Anterior extent of the insertion of the masseteric muscle on the mandible: at the level of the distal end of the lower molar row (0); or anterior to the level of the caudal end of the lower molar row (1).
  25. Height of the coronoid process: low, not well developed (0); or high, well developed (1). The top of the coronoid process is the area of insertion of the temporal muscle, and its size is associated with the development of this element. Low processes do not exceed dorsally the height of the articular process (state 0). High processes (state 1) greatly exceed the height of the articular process.
  26. Size of upper incisors: I1 similar to I2 (0); or I1 larger than I2 (1). In this character only the size of the first upper incisor is considered and not its morphology. The character is scored as state 1 when the mesiodistal length or the crown of the I1 greatly exceed that of I2.
  27. Aspect of the occlusal surface of the upper molars at average condition of wear: dominated by the ectoloph (0); or roughly flat (1). The cusps of the ectoloph (paracone and metacone) are usually well developed in most notoungulates. This character considered the height of these cusps. In the state 0, the paracone and the metacone are greatly exceed in height the protocone and the hypocone, which are the other two main cusps of the notoungulate upper molar; so the ectoloph is the most prominent structure of the occlusal surface. In state 1, height is comparable across all the cusps, and the occlusal surface appears roughly flat.
  28. Upper canine: absent (0); or moderately developed (1); or hypertrophied (2). The upper canine can be absent (state 0) or present with two degrees of development as compared with the size of upper incisors. The canine can be of comparable size relative to the incisors (state 1) or be significantly larger than the incisors (state 2; present in only one of the included genera, *Thomashuxleya*).
  29. Morphology of the upper molars: protoloph and metaloph moderately developed (0); or wide lophs (1); or occlusal surface without fossettes (2); or bilophodont (3). Although this character is easily influenced by wear, the development of the lophs can be discriminated by other features, like the orientation of the walls of the lophs. State 0 refers to slender lophs and state 1 to strong lophs, which occupy a large occlusal area. State 2 refers to a continuous occlusal surface, without fossettes. State 3 is proper of *Pyrotherium*, which exhibits two lophs likely homologous to a protoloph and metaloph (see Billet 2010).
  30. Differentiation of the upper cheekteeth: heterodont, premolars and molar well differentiated (0); or virtually homodont (1). Despite the different degrees of molarization in notoungulate premolars, most representatives of this group bear well-differentiated premolars and molars. *Pyrotherium* was scored 1 given that all but the first cheektooth are bilophodont with just minor differences in size across the row.
  31. Skull size: small (0); or medium (1); or large (2). Assessment of skull sizes in this study is only approximate and relied on visual comparisons of skulls rather than on metric estimates given the degree of fragmentation and deformation of several key representatives of notoungulate families.

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