

## Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters

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The Notoungulata is the richest order of South American endemic placentals, but phylogenetic relationships within this order are unclear. This work provides short descriptions of new cranial characters useful for phylogenetic research on notoungulates, argues for a redefinition of some characters on the dental cristae, and provides a long overdue treatment of notoungulate relationships – the most complete thus far – via a cladistic phylogenetic analysis comprising 50 notoungulate genera and 133 morphological characters of the skull and teeth. The monophyly of the Notoungulata (including *Pyrotherium*) is well supported by numerous cranial and dental apomorphies. The validity of most traditional notoungulates suprageneric taxa is tested, and the monophyly of the two traditional notoungulate suborders Toxodontia and Typotheria is supported. These two taxa are united in a clade supported by an original character on the morphology of the ectopterygoid crests. The Henricosborniidae, Isotemnidae and Oldfieldthomasiidae are paraphyletic, reflecting the fact that these families are mostly defined by plesiomorphic characters. The monophyly of Notohippidae is questioned, as well as the possibility of a close relationship between leontiniids and toxodontids on the basis of cranial arguments. It is observed that two major subclades diverge early within the Typotheria: the Interatheriidae and the clade Archaeohyracidae + Mesotheriidae + Hegetotheriidae. This new phylogeny of the notoungulates from cranial and dental anatomy is an essential step towards reconstructing the ancestral morphotype of the Notoungulata, and is crucial for research on the origin and phylogenetic affinities of these South American ungulates within the Placentalia.

**Keywords:** systematics; skull; Toxodontia; Typotheria; Pyrotheria; anatomy

### Introduction

Among the Placentalia, South American endemic notoungulates are one of the more enigmatic taxa. Billet (2010) investigated their possible relationships with some other South American ungulates, and suggested the inclusion of Pyrotheria within the group and close relationships with the Astrapotheria. However, the phylogenetic relationships of the Notoungulata with other placentals have been almost completely unexplored.

Notoungulates are known from most of the Cenozoic, i.e. from the late Palaeocene Itaboraian (Paula Couto 1952) to the beginning of the Holocene, where they have even been found in association with human remains (MacFadden 2005). As with other South American endemic ungulates (e.g. Litopterna, Astrapotheria), notoungulates show a surprising degree of morphological dualism, as emphasized by Simpson (1934, p. 1): “on one hand, they are remarkably exotic in comparison with the fossil or recent mammals of any other continent, and on the other they parallel these mammals in many features, now considered

largely adaptive or secondary, in a way often amazing”. This dualism has been a confounding factor in efforts to comprehend the origin and evolution of this clade, as evidenced by the long, complicated history of notoungulate classification and the diverse hypotheses that their unique morphology inspired.

Ameghino (1895, 1897, 1902), the pioneer of South American palaeomammalogy, classified notoungulates among many different orders of mammals: according to him, homalodotheriid notoungulates were related to chalicotheriid perissodactyls (within the Ancylopoda), notohippids were the meridional ancestors of equids, *Notopithecus* was a primate (Prosimiae), *Archaeohyrax* was a stem Hyracoidea, and the notostylopids were members of Tillodonta. The taxon ‘Notoungulata’ was eventually introduced by Roth (1903), who recognized the monophyly of this group based on a unique configuration of the temporal region of the skull. Roth already considered Notoungulata to have an evolutionary history based exclusively in South America, with no direct relationships with other ungulates. Simpson (1934, 1945) later considered

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Notoungulata in a similar light (Roth 1903), but added to it the holarctic family Arctostylopidae Schlosser, 1923 (Palaeocene–Oligocene?), based on their dental resemblance to notoungulates (Matthew 1915; Schlosser 1923; Matthew & Granger 1925; Matthew *et al.* 1929; Simpson 1934, 1945, 1948, 1980; McKenna 1980). More recently, Cifelli *et al.* (1989) argued that such a relationship was unlikely, and that arctostylopids did not belong in Notoungulata (McKenna & Bell 1997). The current extensional definition of Notoungulata corresponds to that provided by Cifelli (1993, followed by McKenna & Bell 1997), and includes 13 families formally described: Henricosborniidae, Notostylopidae, Isotemnidae, Homalodotheriidae, Leontiniidae, Notohippidae, Toxodontidae, Oldfieldthomasiidae, Archaeopithecidae, Interatheriidae, Archaeohyracidae, Mesotheriidae and Hegetotheriidae.

Simpson (1934, 1945, 1948, 1967) contributed much to the establishment of a clear classification within Notoungulata. However, certain groups he considered (e.g. Isotemnidae, Oldfieldthomasiidae) were assumed ‘primitive’ and thus probably paraphyletic. Cifelli (1993) provided the first cladistic analysis of Notoungulata. Cifelli’s results notably argued for the paraphyly of Notioprogonia (Henricosborniidae + Notostylopidae) and Entelonychia (Isotemnidae + Homalodotheriidae), which have since been abandoned. Cifelli’s study also supported the monophyly of the two traditional suborders of notoungulates: Typotheria in its usual extension, and Toxodontia *sensu lato* (including the Isotemnidae and Homalodotheriidae). However, Cifelli’s phylogeny was limited in its taxonomic sample, with only 13 taxa included in the analysis. These taxa were families, of which a number were suspected to be paraphyletic (e.g. Isotemnidae, Oldfieldthomasiidae, Archaeopithecidae). Few characters were used (23 for 13 taxa) and most of these derived from dental anatomy. Since Cifelli’s work, no other phylogenetic analysis has been undertaken on the entire Notoungulata. The present work provides a long overdue and more complete treatment of notoungulate systematics, by way of a cladistic phylogenetic analysis comprising 50 notoungulate genera and 133 morphological characters.

### Institutional abbreviations

**ACM:** Amherst College Museum, Amherst, Massachusetts, USA; **AMNH:** American Museum of Natural History, New York, USA; **FMNH:** Field Museum of Natural History, Chicago, Illinois, USA; **MACN:** Museo Argentino de Ciencias Naturales ‘Bernadino Rivadavia’, Buenos Aires, Argentina; **MLP:** Museo de La Plata, Argentina; **MNHN-BOL-V:** the Museo Nacional de Historia Natural, La Paz, Bolivia; **MNHN-CAS,** **MNHN-CLB,** **MNHN-DES,** **MNHN-SAL,** **MNHN-COL,** **MNHN-SCZ,** **MNHN-ACH,** **MNHN-AYO,** **MNHN-MHR** and **MNHN-PAM:** respectively Casamayor, Colombia, Deseado, Salla, Colhue-Huapi, Santa-Cruz, Achiri, Ayo-Ayo, Monte-

hermosan and Pampean collections of the Muséum national d’Histoire naturelle, Paris, France; **PVL:** Colección de Paleontología de Vertebrados Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina; **YPM-PU:** Princeton University collection housed in the Yale Peabody Museum, Yale University, New Haven, Connecticut, USA; **UF:** Florida Museum of Natural History, Gainesville, Florida, USA.

## Material and methods

### Selection of terminal taxa

Until now, no published cladistic analysis has focused on a detailed phylogeny of the whole Notoungulata. To address this, 58 taxa have been included in the present analysis. These are the non-placental eutherian mammals *Zalambdalestes* and *Leptictis* (Wible *et al.* 2007), the non-South American ‘condylarths’ *Phenacodus* and *Meniscotherium*, the South American ungulates *Astrapotheria* (*Trigonostylops*), *Litopterna* (*Protolipterna* and *Proterotherium*) and *Pyrotheria* (*Pyrotherium*), and numerous taxa among Notoungulata (50 genera). As there is no consensus on the phylogenetic position of Notoungulata within Eutheria, except perhaps with *Pyrotheria* (Patterson 1977; Billet 2010), any group of eutherian mammals might be viewed as a potential outgroup. For the present analysis however, the non-placental eutherian mammal *Leptictis* and *Zalambdalestes* were treated as *a priori* outgroups. The other non-notoungulate taxa were included to provide a larger basis for the character polarity determination within the Notoungulata.

All taxa in the analysis are at genus level. Several genera are coded using a single well-known species, specified in Appendix 3 (see online supplementary material). Character scoring relied mainly on direct observations of original specimens, but in some cases bibliographic data was also used (notably for outgroup taxa, see Appendix 3).

### Morphological characters and character scoring

The present analysis includes 133 characters, of which 65 are non-dental cranial characters. Many are original, while others were adapted from already published observations on dental and cranial anatomy of the Notoungulata (e.g. Patterson 1932, 1934a, b, 1936, 1977; Simpson 1948, 1967; Cifelli 1993; Shockey 1997).

Character scoring mostly follows the ‘C-method’ proposed by Pleijel (1995). However, some features that appeared to present logical intermediate states—for example, the characters concerning relative position, size or relative development of features (e.g. ch. (chapter) 19, 45, 78) – were scored here as multistate characters. Of these 11 multistate characters, 9 were ordered. A distinction was made between missing data, scored ‘?’, and non-applicable

characters, scored ‘–’. For example, for characters dealing with fossettes isolated by lophi, those taxa that do not present lophi or lophids are coded as non-applicable. Autapomorphies and invariant characters were excluded. Most species and/or specimens of the same genus were anatomically uniform regarding selected characters. There were, however, several instances of polymorphisms apparent within some genera. Such taxa were coded as polymorphic, (e.g. ‘0&1’) for the character considered.

### Presentation and discussion of the characters used in the analysis

Characters and states are fully presented in Appendix 1 (see online supplementary material). The data matrix is displayed in Appendix 2 (see online supplementary material). Below is a presentation of some original characters derived from cranial anatomy that necessitate detailed description and/or illustration. Some dental characters are also discussed and reinterpreted. Numbers in parentheses correspond to the characters.

**Dental characters, cristae (26–27, 30–32).** The notoungulate upper molar presents a lophed pattern composed of an oblique protoloph, an ectoloph and a metaloph. A small crest runs mesially from the middle of the mesial edge of the metaloph; this crest is called the ‘crochet’ (Patterson 1934b; Simpson 1948, 1967). This basic pattern is easily observable in the oldest taxa (e.g. *Henricosbornia*, *Notostylops*, *Simpsonotus*). In many subsequent notoungulates, the dental pattern becomes more complicated with the development of a variety of accessory cristae. In all notoungulates except henricosborniids and notostyloids, a crest named ‘crista 2’ runs from the ectoloph to connect with the crochet and then isolates a posterolabial fossette (ch. 26, Fig. 1A, C–F). The presence of another crest, mesial to the crista 2, is less common within notoungulates. This additional crest is traditionally termed ‘crista 1’. The two major groups of notoungulates, the Typotheria and the Toxodontia, differ fundamentally in the configuration of ‘crista 1’. These differences seriously challenge the putative homology of ‘crista 1’ between these two groups:

1. Among the Typotheria, the crest mesial to crista 2 is a short crista running mesiolingually from the ectoloph to connect with the protoloph. The connexion of this crista with the protoloph isolates an anterolabial fossette. This crista is still termed ‘crista 1’ in the present work (ch. 27, Fig. 1E, F).
2. Among the Toxodontia, ‘crista 1’ is not present in every taxon. In the notohippid *Argyrohippus* and in the earliest toxodontids (Fig. 1D), this crista presents a well-individualized crest running distolingually from the ectoloph between the protoloph and crista 2. In *Argyrohippus*, this crest exhibits a thin connexion

(isthmus) with crista 2, whereas it is totally free lingually in early toxodontids. Some leontiniids and notohippids show a lingual ectoloph outgrowth or bulge (Fig. 1C) that clearly evokes a rough sketch of the well individualized crista of *Argyrohippus* and early toxodontids. As demonstrated by the morphologies described above, the crista mesial to crista 2, present in only some toxodontians, never presents a morphology comparable to that of tyotherian notoungulates. Therefore the ex-‘crista 1’ of some toxodontians might be better termed ‘crista intermedia’, as this crista may represent a less distal structure than crista 1 of Typotheria that connects to the protoloph. This term is proposed and used here (ch. 31–32).

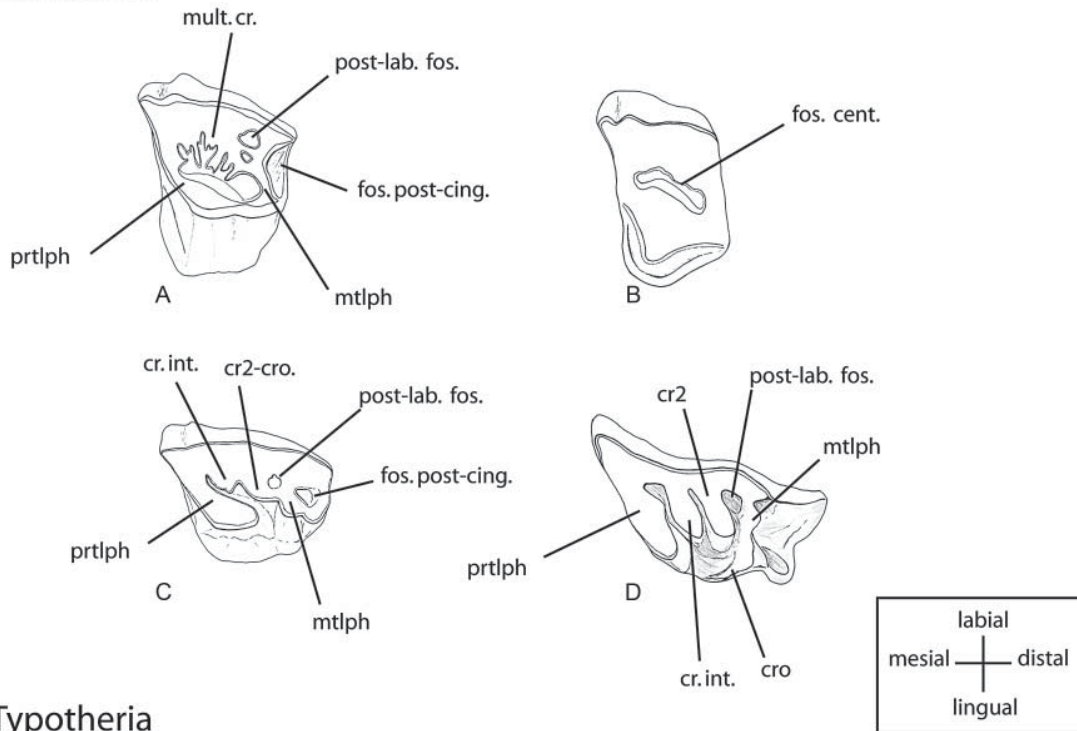
Even more complex occlusal morphology includes the presence of multiple cristae between the protoloph and metaloph on numerous early notoungulate cheek teeth (ch. 30, Fig. 1A). Character 30 in this feature corresponds to a modified version of character 25 of Shockey (1997) and is also inspired by suggestions in Patterson (1934b, p. 108). Compared with these preceding studies, the observation and scoring of notohippids has been modified. Notohippid cheek teeth most often do not exhibit multiple cristae; however, this feature is observable at least on unworn M3s of some notohippids (Fig. 2). These notohippids are scored ‘1’. Unexpected traces of these cristae have also been detected among tyotherians on worn molars of the archaeohyracids *Eohyrax* and *Pseudohyrax* (undulating ridges on the labial edge of the labial fossette) or on deciduous cheek teeth of the mesotheriid *Trachytherus* (Billet *et al.* 2008).

Phylogenetic information on the presence of multiple cristae (ch. 30) may partially overlap with information on the presence of the crista intermedia (ch. 31). The bulge scored in character 32 state 0 as a poorly individualized crista intermedia may be formed by the merging of multiple cristae in advanced wear stages. Some remnants of multiple cristae are distinct within the bulge on moderately worn teeth of some leontiniids (e.g. *Ancylocoelus*) or some notohippids (e.g. *Morphippus*, Fig. 2).

### Cranial characters, palate and pterygoid crests (74–75).

This region of the skull presents two crucial characters that have never been used before for phylogenetic purposes. Firstly, it has been recently noted that in tyotherians (Billet *et al.* 2008, 2009), a postpalatal platform made by the posteromedial extension of the palatines expands the palate posteriorly (ch. 74, Fig. 3A). This platform is fully continuous with the palate, and no medial relief is present to mark the boundary of these two structures. This is only known in tyotherians. Secondly, the lateral processes surrounding the choanae are also worthy of study. As demonstrated in *Trachytherus* (Billet *et al.* 2008), these processes or crests, exclusively formed by the palatine/alispheoid, are the

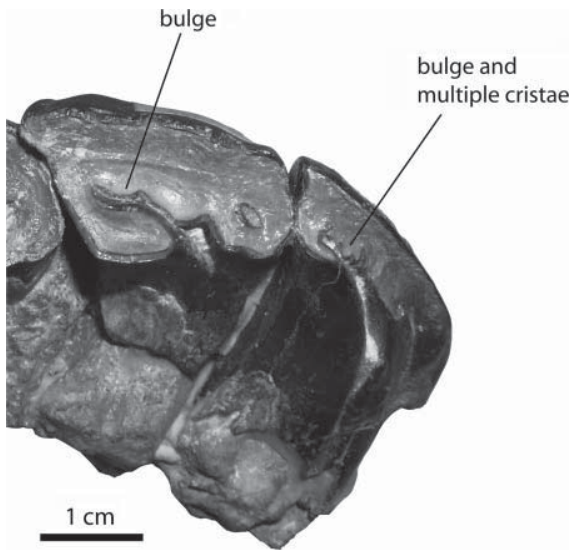
## Toxodontia



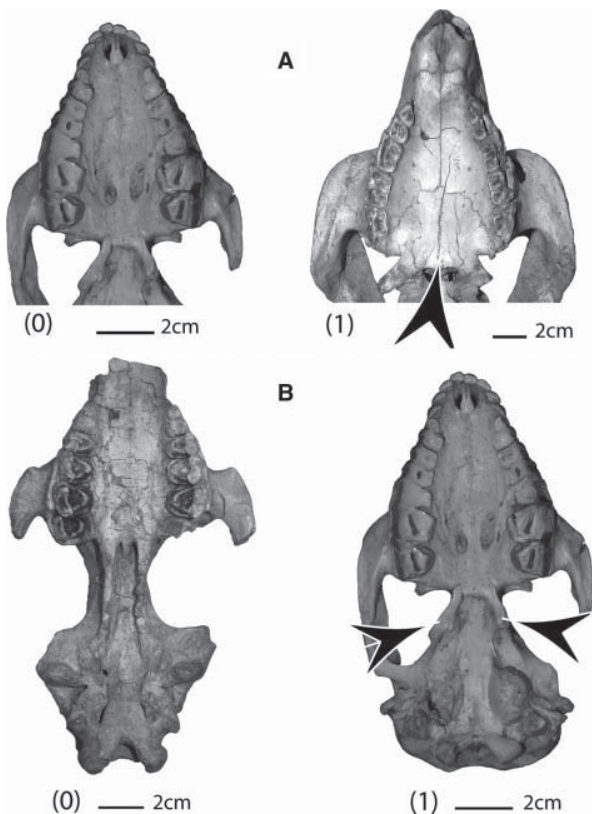
**Figure 1.** Occlusal views of notoungulate upper molars. **A**, *Isotemnus sp.*, MNHN-CAS 296 (M2); **B**, *Periphragis harmeri*, MLP 82-V-7-1 (M2); **C**, *Ancylocoelus frequens*, MNHN-DES 595 (M2); **D**, *Nesodon sullivani*, MNHN-SCZ 18 (M2); **E**, *Pseudhyrax eutrachytheroides*, MLP 61-IV-9-1 (M2); **F**, *Acropithecus rigidus*, AMNH 28782 (M3); **G**, *Plagiarthrus clivus*, FMNH P 13415 (M1); **H**, *Plesiotypotherium achirens*, MNHN-ACH 26 (M2). Abbreviations: ant-lab. fos.: antero-labial fossette; cr1: crista 1; cr2: crista 2; cr2-cro: crista 2 – crochet; cr int: crista intermedia; cro: crochet; fos. cent.: central fossette; fos post-cing.: post-cingulum fossette; med-lab. fos.: medio-labial fossette; mtlph: metaloph; mult. cr.: multiple cristae; post-lab. fos.: postero-labial fossette; prtiph: protoloph. Not to scale.

ectopterygoid crests. In both typotherians and toxodontians, these crests are robust and diverge posteriorly, whereas they are parallel (anteroposterior direction) in other notoungulates such as *Notostylops* and *Simpsonotus* and in other

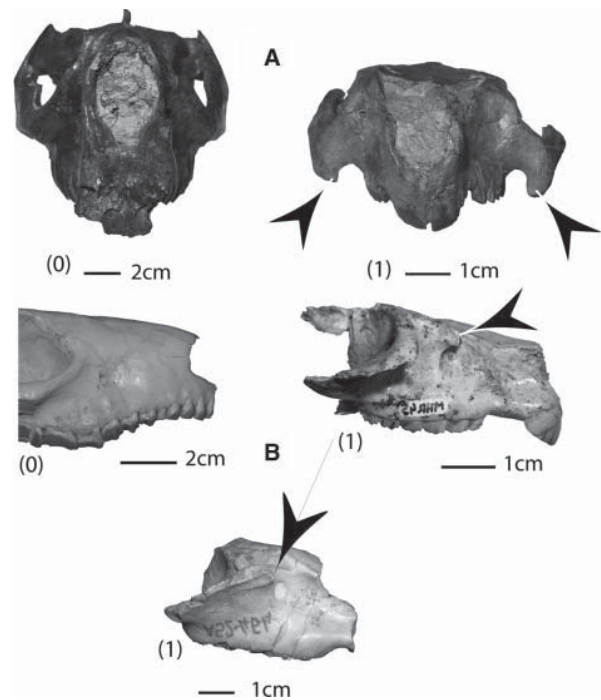
South American ungulates (ch. 75, Fig. 3B). The presence of the diverging ectopterygoid crests also corresponds to the presence of transverse dorsoposterior buttresses (see Billet *et al.* 2008).



**Figure 2.** Occlusal views of M2-3 of *Morhippus* sp., MNHN-DES 375 (reversed); mesial to the left, labial to the top.

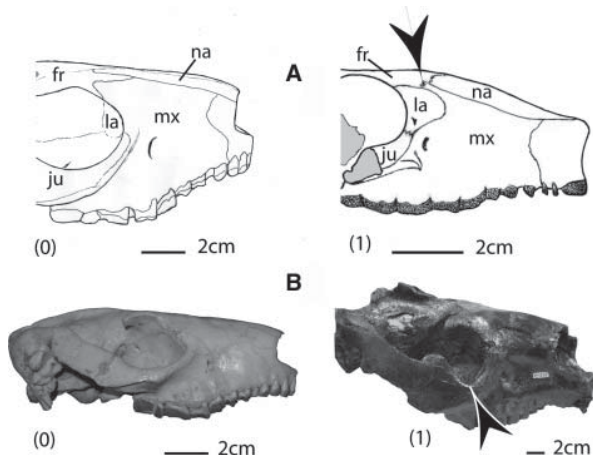


**Figure 3.** Palate and pterygoid crests. **A**, ventral views of palates; anterior to the top. Character 74: medial platform of the palatines expanding palate posteriorly and fully continuous with it; (0), absent, *Puelia* sp., MLP 67-II-27-27; (1), present; *Plesiotyotherium achirensense*, MNHN-ACH 26. **B**, ventral views of skulls; anterior to the top. Character 75: strong and diverging ectopterygoid crests formed exclusively by palatines/alispheonoids; (0), absent, *Trigonostylops wortmani*, AMNH 28700; (1), present, *Puelia* sp., MLP 67-II-27-27.



**Figure 4.** Descending process. **A**, anterior views of skulls. Character 80: strong vertical descending process of maxillary; (0), absent, *Adinotherium ovinum*, MNHN-SCZ 14; (1), present, *Interatherium robustum*, MNHN-SCZ 173. **B**, lateral views of snouts; anterior to the right. Character 81: descending process of maxillary developed as a horizontal spine lateral to the infra-orbital foramen; (0), absent, *Puelia* sp., MLP 67-II-27-27; (1) present, *Prosotherium triangulidens*, MACN A52-464 (bottom) and *Paedotherium imperforatum*, MNHN-MHR 45 (top right).

**Cranial characters, descending process (80–81).** The descending process, the configuration of which is explained in Billet *et al.* (2008), has a structure exactly corresponding to what is faintly indicated in many other mammals. In the latter, this faint structure is traditionally termed the ‘facial tubercle’. The facial tubercle or descending process of notoungulates represents the anterior end of the facial crest which usually runs along the lateral edge of the zygomatic arch (Barone 1997). The development of this process appears very variable in many notoungulate taxa: whereas the facial crest is almost always distinct, the descending process (or facial tubercle) is inconsistently marked and sometimes varies within species. Therefore, I have chosen not to code the presence of a faint descending process, the observation of which may be ambiguous, but to code only for the presence of a massive process (ch. 80, Fig. 4A). Character 80 on this feature corresponds to a modified version of Reguero *et al.* (2003) character 25 and Hitz *et al.* (2006) character 33. Another character concerns the descending process in notoungulates. In the pachyrhukhines, a horizontal spine is formed just lateral to the infraorbital foramen (ch. 81, Fig. 4B). This spine is here considered homologous with the descending process of other notoungulates.



**Figure 5.** Orbital region. **A**, lateral views of snouts; anterior to the right. Character 86: large facial extent of lacrimal toward nasal bone; (0) absent, *Puelia* sp., MLP 67-II-27-27; (1), present, *Archaeohyrax suniensis*, illustration modified from Billet *et al.* (2009). **B**, lateral views of skulls; anterior to the right. Character 93: orbit shape; (0), round, *Puelia* sp., MLP 67-II-27-27; (1), oval (higher than long, dorsal edge of zygomatic arch excavated below orbit), *Adinotherium ovinum*, MNHN-SCZ 14. Abbreviations: fr: frontal; ju: jugal; la: lacrimal; mx: maxillary; na: nasal.

This is evident from the configuration in the pachyrukhine *Prosotherium* (Fig. 4B state (1)) in which this spine is in continuity with the anterior root of the zygomatic arch. This is not the case in later diverging pachyrukhines like *Paedotherium*, in which the spine is situated far forward from the anterior root of the zygomatic arch (Fig. 4B state (1)).

**Cranial characters, orbital region (86, 93).** The lacrimal bone presents a typical large facial extent in the archaeohyracids, mesotheriids and hegetotheriids (Billet *et al.* 2009), whereas it is much reduced and largely intra-orbital in all other notoungulates (ch. 86, Fig. 5A). This large facial extent of the lacrimal generally adopts a semi-oval outline. It reduces the posterodorsal extension of the maxillary to a thin strip of bone between nasal and lacrimal. The non-formal taxon ‘*Campanorco*’ is here considered to present a well-developed facial extension of the lacrimal toward the nasal bone. Its lacrimal is still less developed than in *Archaeohyrax* or *Trachytherus*, but more extended than in interatheriids or *Oldfieldthomasia*. Concomitantly, the posterodorsal extent of the maxillary is narrower in *Campanorco* than in interatheriids or *Oldfieldthomasia*. It is noteworthy that the facial extent of the lacrimal is slightly less in the late pachyrukhine *Paedotherium bonaerense* relative to other hegetotheriids, mesotheriids and archaeohyracids. This smaller extent is concomitant with the enormous development of the zygomatic plate in front of the orbit of this taxon (Cerdeño & Bond 1998).

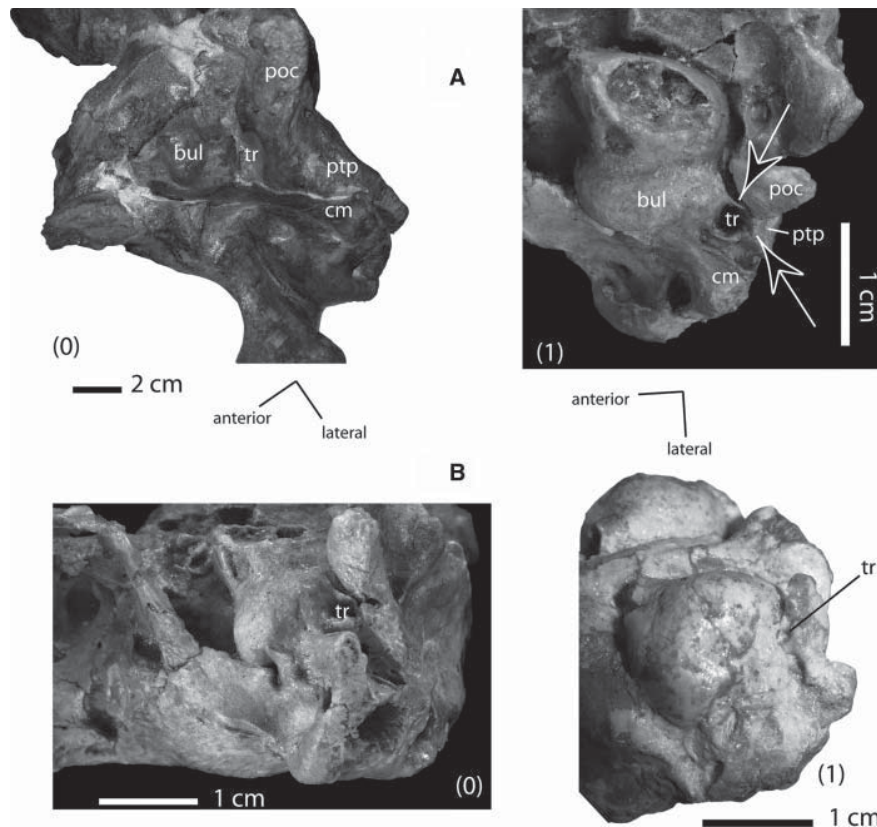
The orbit shape also provides interesting new characters. The orbit of the leontiniids, some nothippids and

the toxodontids presents an oval outline due to being higher than it is long, and the ventral outline of their orbit is marked by an excavation within the dorsal edge of zygomatic arch (ch. 93, Fig. 5B). Other notoungulate orbits instead exhibit a round shape and no mark on the dorsal edge of the zygomatic arch.

**Cranial characters, tympanohyal recess (120–121).** The tympanohyal recess is defined as the fossa housing the insertion of the hyoid apparatus on the cranium of notoungulates (Billet *et al.* 2008, 2009; Billet 2010). Patterson (1932, 1934a) noted that the posterior border of the tympanohyal recess was formed by different structures among notoungulates. In most tyotherians, a tympanic extension from the bulla and/or the post-tympanic process forms the posterior border of the tympanohyal recess. In other notoungulates, the paroccipital process that forms this posterior border (ch. 120, Fig. 6A). Moreover, the tympanohyal recess presents as a deep fossa strictly posterolateral to the bulla in most notoungulates. In all interatheriids, however, the tympanohyal recess appears as a minute fossa located not strictly posterolateral to the bulla but rather on the posterolateral slope of the bulla (ch. 121, Fig. 6B).

**Cranial characters, petrosal and tympanic cavity (125, 128).** Few studies have been interested in the petrosal of notoungulates. Gabbert (2004) suggested that the tympanic face of the petrosal of toxodontian notoungulates was expanded, fanlike, toward the occipital bone and was heavily crenulated. Observations on non-toxodontian notoungulates indicate that all currently known notoungulate petrosals present an expanded and fanlike medial margin of their tympanic face. This morphology is always associated with a promontory well demarcated from the remaining tympanic face of the petrosal, the outline of the promontory being highlighted by a very distinct breakslope. The promontory of these petrosals always presents a bean-shaped morphology (ch. 125, Fig. 7A). The medial crenulation of the petrosal observed in toxodontians by Gabbert (2004) is apparently not a feature present in all notoungulates, as it is notably absent in *Notostylops*. However, these observations are based on a very poor taxonomic sample and the crenulation, or its absence, would require more observations to be scored.

Within the tympanic cavity, the crista tympanica and tympanic sulcus, which are structures surrounding the internal aperture of the ossified external auditory meatus, also appear to present interesting phylogenetic information. The tympanic sulcus is defined as a groove channelling the inner circumference of ectotympanic, to which the tympanic membrane is attached by means of the fibrocartilaginous ring (MacPhee 1981). The crista tympanica is defined as a low semicircular ridge, representing the dorsal margin of the tympanic sulcus (MacPhee 1981). In notoungulates, the crista tympanica that surrounds the tympanic sulcus



**Figure 6.** Tympanohyal recess. **A**, ventral views of right auditory regions. Character 120: posterior border of tympanohyal recess; (0), formed by paroccipital process, *Nesodon sullivanii*, MNHN-SCZ uncatalogued; (1), formed by a tympanic extension and/or post-tympanic process, *Archaeohyrax suniensis*, MNHN-SAL 4. **B**, latero-ventral view of right auditory regions; anterior to the left, ventral to the top. Character 121: tympanohyal recess; (0), large, posterolateral to the bulla, *Archaeohyrax suniensis*, MNHN-SAL 4; (1), very small, located on the posterolateral slope of the bulla, *Federicoanaya sallaensis*, MNHN-SAL 418. Abbreviations: bul: tympanic bulla; cm: crista meatus; poc: paroccipital process; ptp: post-tympanic process; tr: tympanohyal recess.

may be either (i) in relief, i.e. the external auditory meatus protrudes within the tympanic cavity; or (ii) faint, i.e. the external auditory meatus aperture is in retreat within the tympanic cavity (ch. 128, Fig. 7B). This character has been partly inspired by illustrations in the work of Patterson (1936, figs 44 & 51).

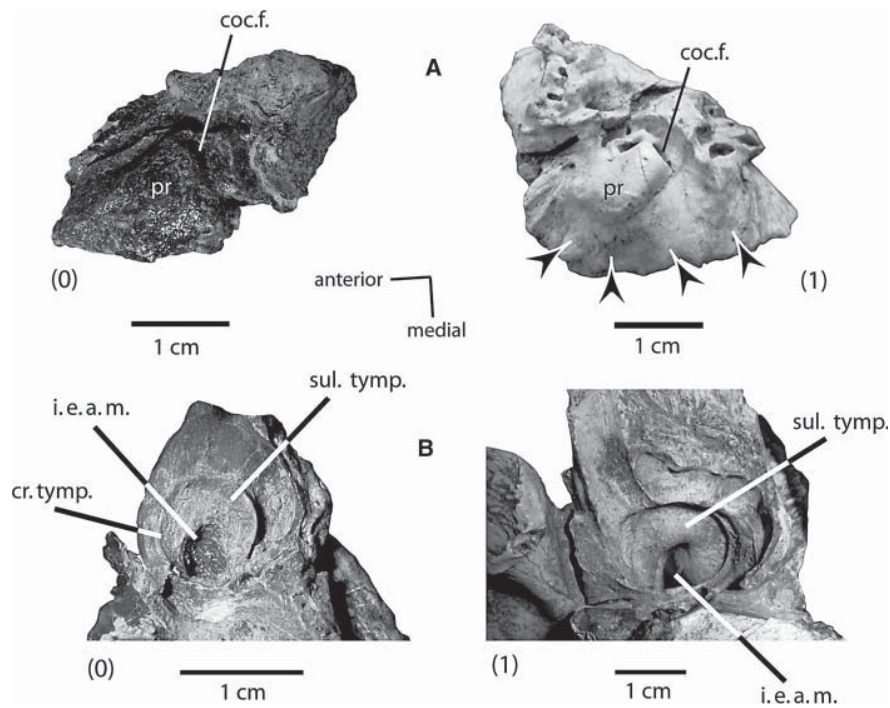
**Cranial characters, mastoid region (129).** The occipital face of the notoungulate cranium exhibits an intriguing small lamina (or strip) of bone that squeezes in between squamosal and occipital. The mastoid foramen opens just lateral to this lamina. The bony composition of the lamina has always been a matter of debate among notoungulate workers. The squamosal, occipital, petrosal (mastoid) and even adventitious bone have been in turn hypothesized to form this bony lamina (e.g. Patterson 1932, 1936, 1977; Simpson 1936; Gabbert 2004). To settle this question, computed tomography has been used to study the intracranial anatomy of the mesotheriid *Plesiopottherium achirensis* MNHN-ACH 26. This determined that the mastoid portion of the petrosal actually forms the small

bony lamina exposed on the occiput (Fig. 8). Character 129 deals with this lamina, which is unique to notoungulates.

## Results

The parsimony analysis performed in TNT (Goloboff *et al.* 2008) (traditional search, 100 replications, TBR swapping algorithm) resulted in 480 trees of 334 steps (CI = 0.44, RI = 0.80). The strict consensus (Fig. 9; 367 steps, CI = 0.40, RI = 0.76) presents an interesting resolution among monophyletic Notoungulata (including *Pyrotherium*; Billet 2010). The Homalodotheriidae, Leontiniidae, Toxodontidae, Interatheriidae, Mesotheriidae and Hegetotheriidae are monophyletic, whereas other notoungulate families are either para- or polyphyletic (Fig. 9).

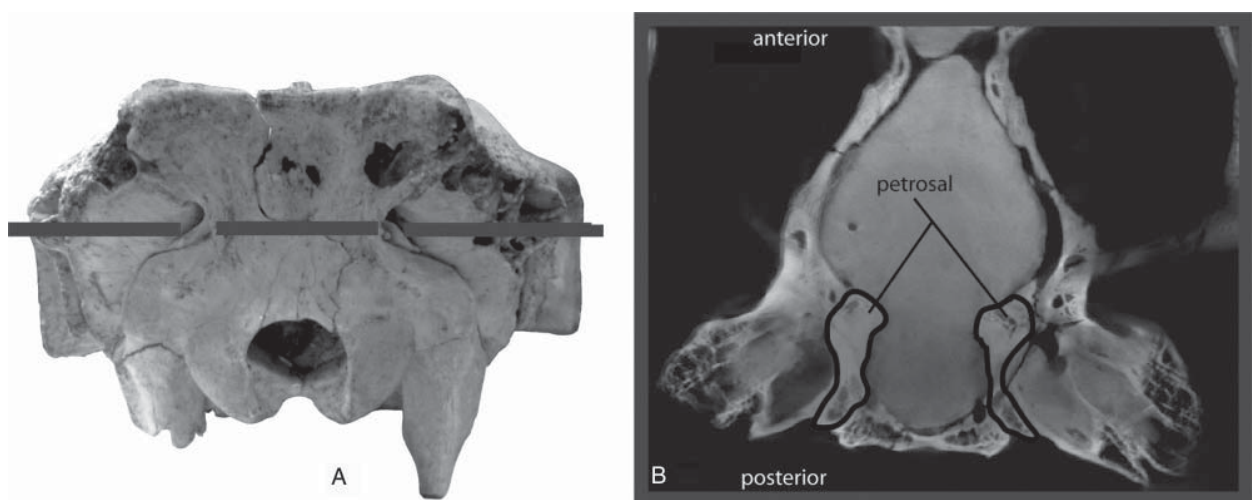
As demonstrated in a recent study (Billet 2010), the Astrapotheria (represented by *Trigonostylops*) and the Pyrotheria (represented by *Pyrotherium*) are supported as, respectively, the sister-group of the Notoungulata and part of the Notoungulata. Characters supporting these relationships have been discussed in Billet (2010).



**Figure 7.** Petrosal and tympanic cavity. **A**, ventral views (tympanic face) of left petrosals. Character 125: expanded and fanlike medial margin of tympanic face of petrosal, well demarcated from the bean-shaped promontory; (0), absent, *Diadiaphorus* sp. (Litopterna, petrosal like *Proterotherium*), MNHN-SCZ uncatalogued; (1), present, *Scarrittia canquelensis*, AMNH 26914. **B**, medial views of the tympanic cavity; anterior to the left, ventral to the top. Character 128: crista tympanica surrounding the tympanic sulcus at the internal aperture of the external auditory meatus; (0), in relief and external auditory meatus protrudes within the tympanic cavity, *Hegetotherium mirabile*, FMNH P 13194; (1), faint crista tympanica and external auditory meatus aperture in retreat within the tympanic cavity, *Posnanskytherium* sp., MNHN-AYO 191. Abbreviations: coc.f.: cochlear fenestra; cr. tymp.: crista tympanica; i.e.a.m.: internal aperture of the external auditory meatus; pr: promontory; sul. tymp.: sulcus tympanicus.

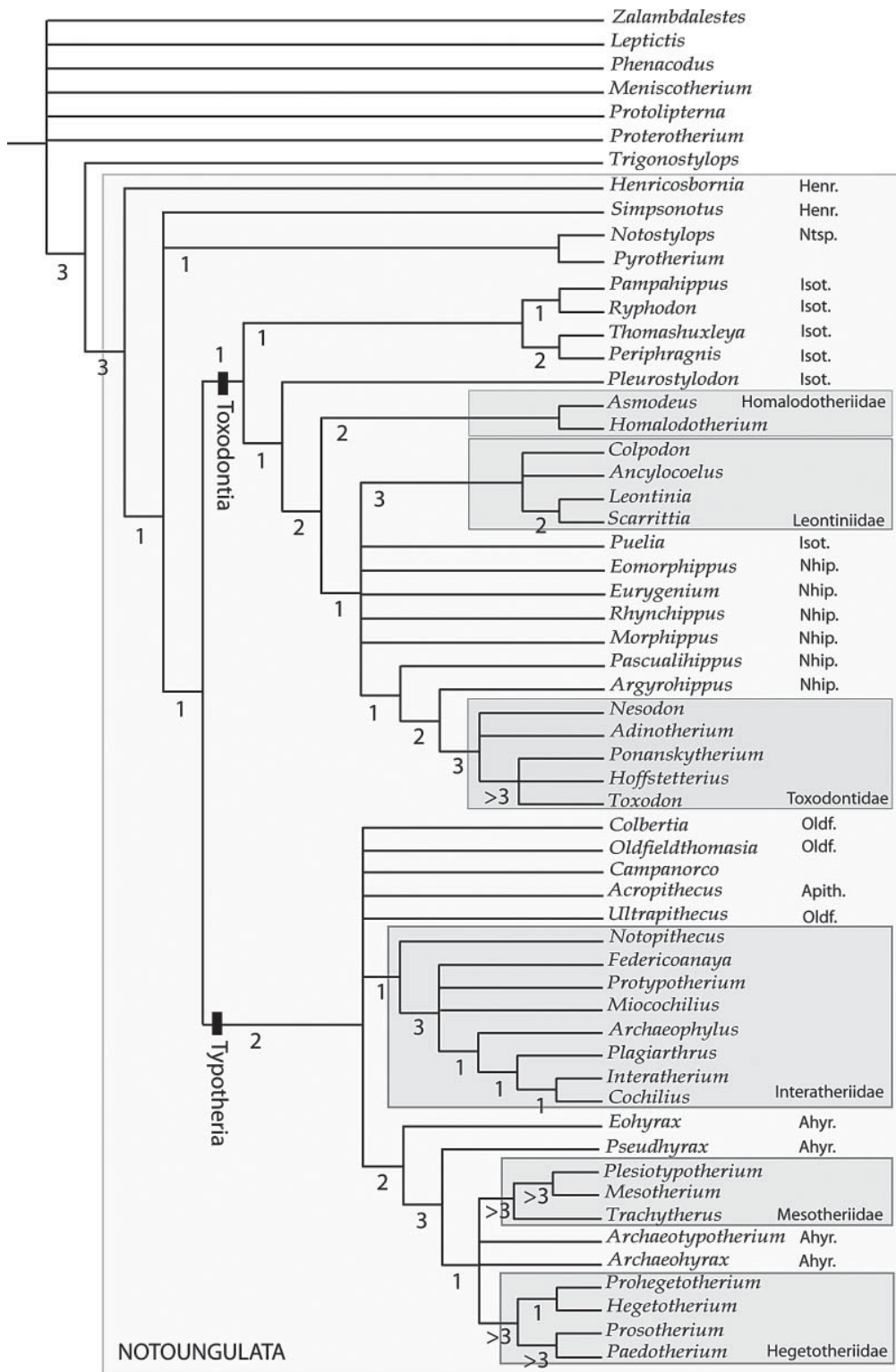
Within Notoungulata, *Henricosbornia* is the earliest diverging genus and is therefore the sister taxa of all other notoungulates. The immediately less inclusive clade shows a basal tritomy from which branches *Simpsonotus*, the

clade (*Notostylops*, *Pyrotherium*) and a clade clustering all the remaining notoungulates. These remaining notoungulates are composed of the Typotheria and Toxodontia, both monophyletic, and therefore sister taxa. Basal resolution is



**Figure 8.** **A**, posterior view of the occipital face of the cranium of *Plesiotypotherium achirens*, MNHN-ACH 26, showing a paired thin strip of bone (where the horizontal grey line disrupts), appearing between in squamosal and exoccipital; **B**, virtual coronal slide made at the level of the grey line in **A**, and showing that the thin strip of bone corresponds to the petrosal (pars mastoidea). Not to scale.





**Figure 9.** Strict consensus cladogram of the analysis (367 steps, CI = 0.40, RI = 0.76). Bremer support values and notoungulate families are indicated. Abbreviations: Henr.: Henricosborniidae; Ntsp.: Notostylopidae; Nhip.: Notohippidae; Isot.: Isotemnidae; Oldf.: Oldfieldthomasiidae; Apith.: Archaeopithecidae; Ahyr.: Archaeohyracidae.

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rather good within the Toxodontia, contrary to Typotheria (Fig. 9).

The Toxodontia presents two basal clades, the smaller clade composed of three isotemnid and an uncertain 'notohippid' or isotemnid' (*Periphragmis*, *Thomashuxleya*), (*Pampahippus*, *Ryphodon*). The second, much larger clade notably includes the isotemnid *Pleurostylodon* as its earliest diverging member. The Isotemnidae may therefore be polyphyletic. The large clade of toxodontians includes a clade of homalodotheriids as sister taxa of a clade clustering the leontiniids, most 'notohippids' and the toxodontids. This latter clade exhibits a basal polytomy from which branches *Puelia*, the notohippids *Eomorphippus*, *Morphippus*, *Eurygenium* and *Rhynchippus*, a leontiniid clade and a clade clustering the remaining 'notohippids' and the toxodontids. The Notohippidae may be at least diphyletic (*Pampahippus*, others) on this cladogram, whereas the monophyly of the Leontiniidae is unambiguously supported. The notohippids *Pascualhippus* and *Argyrohippus* appear as successive outgroups to the monophyletic Toxodontidae (Fig. 9).

Clade Typotheria presents a large basal bush from which branch the oldfieldthomasiids *Oldfieldthomasia*, *Colbertia* and *Ultrapithecus*, the archaeopitheciid *Acropithecus*, the taxon *Campanorco*, the Interatheriidae and a clade uniting the Archaeohyracidae, Mesotheriidae and Hegetotheriidae. The monophyly of the Oldfieldthomasiidae is therefore uncertain. The less rich of the two clades within the Typotheria is the Interatheriidae. The genus *Notopithecus* is the earliest diverging interatheriid; others constitute an interatheriine clade with the taxa *Protypotherium*, *Miocochilius*, *Federicoanaya* and a clade of *Interatherium* relatives. The earliest diverging taxon of this latter clade is *Archaeopithecus*, then *Plagiarthrus* is the sister taxa of the clade (*Interatherium*, *Cochilius*). The clade clustering archaeohyracids, mesotheriids and hegetotheriids presents two archaeohyracids as the earliest diverging taxa, successively *Eohyrax* and *Pseudhyrax*. Then a clade gathering the Mesotheriidae, the Hegetotheriidae and the archaeohyracids *Archaeotypotherium* and *Archaeohyrax* presents a basal polytomy. The Archaeohyracidae are then paraphyletic. Within the Mesotheriidae, *Trachytherus* is the sister taxon to the mesotheriine clade composed of *Plesiotypotherium* and *Mesotherium*. The Hegetotheriidae are represented by two clades: one corresponding to the hegetotheriines *Prohegetotherium* and *Hegetotherium*, the other corresponding to the pachyrhines *Prosotherium* and *Paedotherium* (Fig. 9).

Bremer supports are provided in Fig. 9. Character distribution on the strict consensus cladogram is provided in Fig. 10 (unambiguous synapomorphies) and Appendix 4 (optimized synapomorphies) (see online supplementary material). The original characters detailed above present an interesting distribution and are weakly homoplastic.

## Discussion

### Cristae

The presence of the crista intermedia (ch. 31) and of crista 1 (= anterolabial fossette, ch. 27) (Fig. 1C–F) appear in this analysis as two synapomorphies of two unrelated clades. On one hand, the presence of the crista intermedia is a synapomorphy of the clade that unites the leontiniids, most notohippids and the toxodontids (Fig. 10B). On the other hand, the anterolabial fossette-crista 1 is a synapomorphy of the Typotheria (Fig. 10A). This finding therefore supports the hypothesis that these cristae are not homologous (as argued above), as they occur in two distant unrelated clades. Furthermore, the putative (see above) formation of the crista intermedia by the merging of multiple cristae is possible according to the results of the analysis, given that the presence of multiple cristae is a symplesiomorphy within the clade (leontiniids + notohippids + toxodontids) where the crista intermedia appears. The clear individualization of the crista intermedia (ch. 32) of the clade (*Argyrohippus*, Toxodontidae) even corresponds with the complete disappearance of multiple cristae with Deltran optimization (reversion of ch. 30) (see Fig. 10B and Appendix 4).

### Notoungulata

As the focus of the present study is phylogeny within the Notoungulata, relationships outside the group will not be commented on (see Billet 2010 for details on this subject). The earliest diverging notoungulate is *Henricosbornia*. This result is the same as in Billet (2010) and the same as that supposed by Cifelli (1993). In the present analysis, *Henricosbornia* presents a metacone fold on the upper premolars, a plesiomorphic feature relative to other notoungulates (ch. 38) (Fig. 10A). Cranial data for *Henricosbornia* are unknown. Therefore, the presence in this taxon of the derived cranial features present in all other notoungulates is uncertain and depends on optimization. The apomorphic cranial features of notoungulates (including or excluding *Henricosbornia*; Appendix 4) are numerous, as already shown by Billet (2010). This supports the widespread idea that notoungulates are strongly original in the anatomy of their skull (e.g. Patterson 1932, 1936). Among these characters are the above-described characters 125 and 129, respectively on the medial margin of the petrosal and on the small petrosal lamina visible on the occipital face (Appendix 4). The monophyly of the Notoungulata is well supported in terms of number of synapomorphies as well as via Bremer support (Fig. 9).

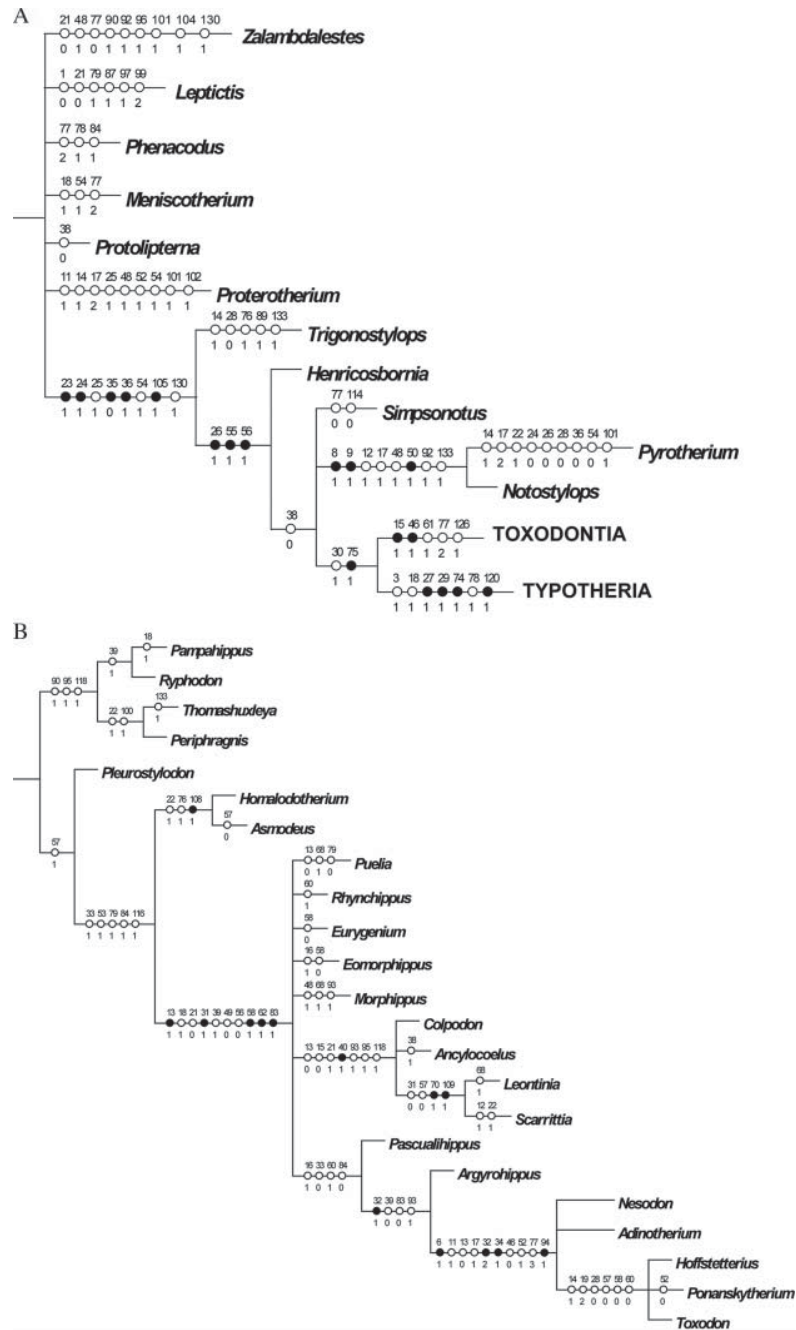
The position of *Simpsonotus* as member of a clade uniting all notoungulates except *Henricosbornia* unsurprisingly confers a paraphyletic status to the Henricosborniidae. The relationships of *Notostylops* and *Pyrotherium* have been extensively discussed elsewhere (Billet 2010).

This analysis clusters the Toxodontia and the Typotheria together in a clade, as in Cifelli (1993) and Billet (2010). This clade (Toxodontia, Typotheria) is notably supported by an original character presented above: the presence of strong and diverging ectopterygoid crests formed by the palatines/alisphenoid (ch. 75, state 1) (Fig. 10A). Even if not well supported in terms of Bremer support (Fig. 9), the

clade (Toxodontia, Typotheria) is strongly supported in its particular morphology of the ectopterygoid crests.

### Toxodontia

The monophyly of the Toxodontia is supported by five unambiguous synapomorphies: the presence of a fossa formed by lingual cingulum on upper incisors (ch. 15,



**Figure 10.** Strict consensus cladogram of the analysis (367 steps, CI = 0.40, RI = 0.76) with positioned unambiguous synapomorphies. **A**, basal part of cladogram; **B**, detail among Toxodontia; **C**, detail among Typotheria. Black-filled circles indicate autapomorphic features whereas white-filled ones indicate homoplastic synapomorphies. (Continued)

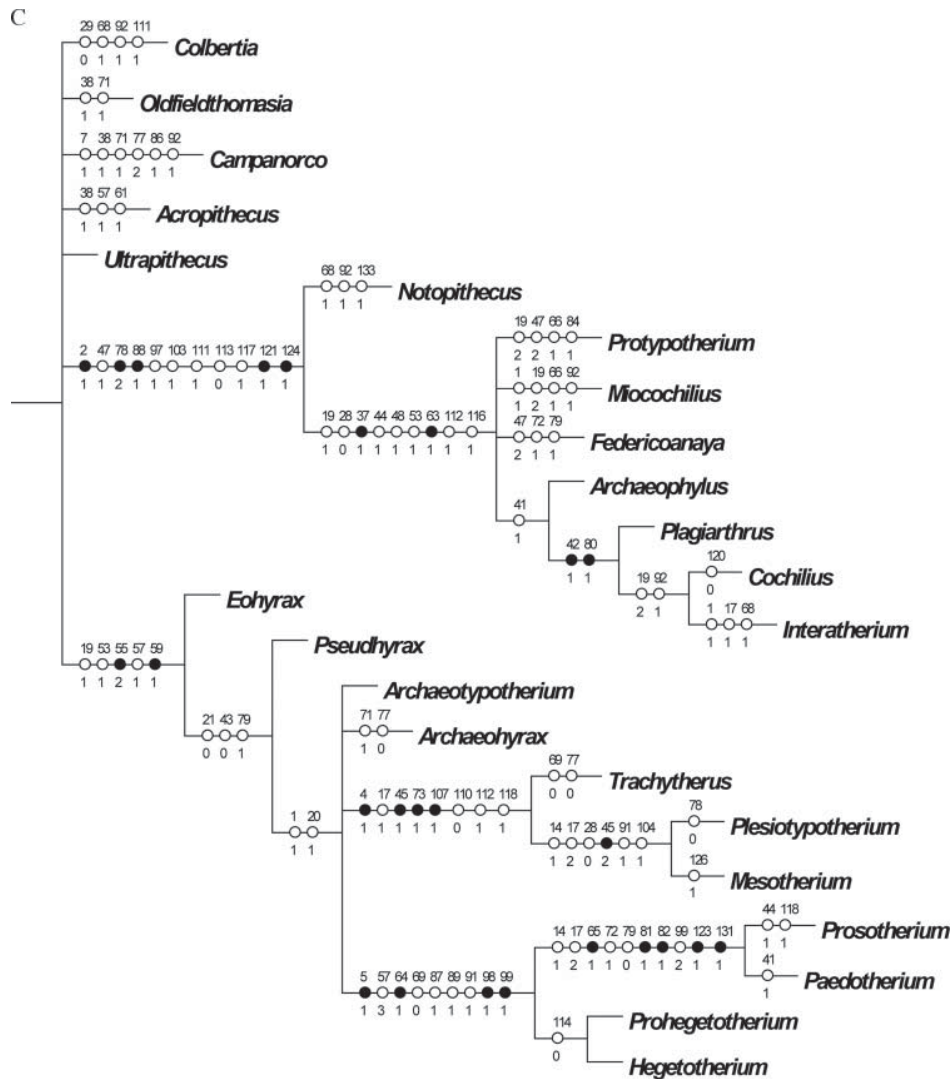


Figure 10. (Continued).

state 1), the presence of a lingual vertical ridge on lower incisors and canine (ch. 46, state 1), the presence of a distolabial crest on trigonid of lower premolars made by a distolabial extension of protolophid (ch. 61, state 1), the premaxillary–maxillary suture course directed posteriorly in its medial part on the palate (ch. 77, state 2), a shallow subarcuate fossa that is reduced in surface (ch. 126, state 1) (Fig. 10A). The Bremer support value is, however, weak (Fig. 9). Shockey *et al.* (2009) argued that postcranial anatomy does not support the monophyly of the Toxodontia (particularly the inclusion of isotemnids within the toxodontians). However, cranial and dental data do provide arguments for monophyly (see also Cifelli 1993). The suborder Toxodontia is a long-standing taxon and its composition in the present phylogenetic analysis agrees, for example, with the extensional definition of ‘Toxodonta’ by Simpson (1967).

Relationships within Toxodontia are different here from those of Shockey (1997) that were obtained exclusively from dental data. The main differences concern the location of notohippids and of taxa inconsistently referred to as notohippids, such as *Puelia* and *Pampahippus* (Bond & López 1993; McKenna & Bell 1997; Shockey 1997). First, traditional notohippids (*sensu* Simpson 1967) are not found to be closer to toxodontids than are leontiniids, except for the genera *Pascualihippus* and *Argyrohippus*. The resemblance between the notohippid *Argyrohippus* and early diverging toxodontids like *Nesodon* and *Adinotherium* has been noted by Loomis (1914), who thought that the former was closer to some toxodontids (nesodontiines) than to the rest of notohippids. Patterson (1934b) strongly contradicted Loomis and considered *Argyrohippus* and its allies as true notohippids. Shockey (1997) found that *Pascualihippus* is the notohippid closest to toxodontids. The present analysis

indicates that *Pascualhippus* constitutes the sister taxon to the clade (*Argyrohippus*, Toxodontidae). The position of *Argyrohippus* as sister taxon to toxodontids is supported by the morphology of the crista intermedia of upper molars (ch. 32) (Fig. 10B), discussed above.

Whereas some other notohippids present some dental resemblances to the clade (*Pascualhippus* (*Argyrohippus*, Toxodontidae)) (notably ch. 13, 16, 60), the leontiniids share cranial characters with toxodontids and *Argyrohippus* (unknown in *Pascualhippus*). Although not mentioned in any taxonomic framework, a close resemblance of the cranial anatomy of toxodontids and leontiniids has been noted in the descriptive work of Patterson (1936, p. 225), but all subsequent studies have acknowledged from dental anatomy the closer position of notohippids than leontiniids to toxodontids (e.g. Simpson 1967; Shockey 1997). However, cranial characters concerning the oval orbit shape (ch. 93; described above), the crista meatus and post-tympanic process of squamosal very close to or appressed against each other (ch. 118), and the auditory region (basicranium) being large and short (ch. 100), are strong arguments for a sister-taxon relationship between the Toxodontidae and Leontiniidae (the two former characters also include *Argyrohippus* in this relationship; Fig. 10B and Appendix 4). Postcranial anatomy may help resolve the apparent contradiction between dental and cranial data relative to the relationships between notohippids, leontiniids and toxodontids. It appears to support an exclusive relationship between leontiniids and toxodontids (Bergqvist 1996), or at least supports that the leontiniids are closer to toxodontids than are some notohippids (e.g. *Eurygenium*; B. Shockey pers. comm.). In all cases, the monophyly of the Notohippidae (*sensu* Simpson 1967) is seriously challenged, and this group may even be polyphyletic.

The location of *Puelia* within the clade clustering leontiniids, notohippids and toxodontids differs greatly from the study of Shockey (1997). However, this difference may be due to scoring on different specimens possibly representing different taxa. *Puelia* has been scored here based on the observation of only one specimen, MLP 67-II-27-27, a fine skull with complete but worn dentition, from the Mustersan locality 'La Gran Hondonada' in Patagonia. This skull has been referred to *Puelia sp.* by Bond & López (1993) but these authors, unfortunately, did not provide their argument. In contrast, Shockey (1997) scored *Puelia* from the work of Simpson (1967) which included only cheek teeth remains for *Puelia coarctatus*. Detailed studies are needed to decide on the correspondence of these remains to the same taxon. For now, the present analysis argues for the inclusion of the taxon represented by MLP 67-II-27-27 in the clade allying leontiniids, notohippids and toxodontids. The location of *Pampahippus* within an early diverging clade of Toxodontia with some isotemnids argues for the polyphyly of the Notohippidae *sensu* Bond & López (1993). The only character it shares with other notohippids is an incisiform

canine subequal to other incisors (ch. 18) (Fig. 10B). Therefore, if the present results are confirmed in future studies, Notohippidae should be reduced to the Notohippidae *sensu* Simpson (1967) or even to a more reduced monophyletic version, if any exists. There is no monophyletic subset of Notohippidae on the cladogram presented here.

The Homalodotheriidae are the sister taxon of the clade uniting the leontiniids, notohippids and toxodontids. This relationship is only supported by homoplastic characters; however, there are no fewer than five unambiguous synapomorphies from both dental and cranial anatomy (Fig. 10B). The inclusion of *Periphragnis* within Homalodotheriidae, defended by Flynn *et al.* (2003), is not supported. The character of the continuous cingulum on the lingual margin of upper cheek teeth (ch. 22, state 1), traditionally regarded as supporting this relationship, is here convergent in the two taxa (Fig. 10B).

The polyphyly of Isotemnidae is unsurprising, as this family is only defined by plesiomorphic features (Simpson 1967) among the Toxodontia. Notably, the branches concerning the isotemnids on the cladogram are supported only by homoplastic characters. This emphasizes the necessity of new studies and data on these early diverging Toxodontia to better understand their phylogenetic relationships. An intriguing resemblance is present in the skull of *Periphragnis* and *Thomashuxleya* (and possibly *Ryphodon* to a lesser degree) to that of leontiniids and toxodontids in the strong relief of the dorsal edge of the posterior root of the zygomatic arch (ch. 95), the auditory region (basicranium) large and short (ch. 100), and the crista meatus and post-tympanic process of squamosal very close to or appressed against each other (ch. 118) (Fig. 10B and Appendix 4). Even if a direct relationship with leontiniids and toxodontids seems unlikely regarding dental morphology, further investigation into these characters and taxa should be undertaken.

### Typotheria

The monophyly of the other traditional suborder of notoungulates, the Typotheria, is supported by seven unambiguous synapomorphies: the I1 enlarged relative to other incisors (ch. 3), the canine (upper and lower) incisiform and subequal to other incisors (ch. 18), the presence of an anterolabial fossette on upper cheek teeth (ch. 27), the presence of a deep labial extension of central fossette between the protoloph (-crista 1) and the crochet (-crista 2) on upper molars (ch. 29), the presence of a medial platform of palatines expanding the palate posteriorly and fully continuous with it (ch. 74), the posterodorsal extremity of maxillary contacting nasal does approximately reach the posterior extremity of nasals (ch. 78), the posterior border of tympanohyal recess formed by a tympanic extension and/or post-tympanic process (ch. 120). This also differs from the results of the study of Shockey *et al.* (2009) from postcranial data which do not support the monophyly of the Typotheria.

Here, both cranial and dental morphology provide support for the existence of such a group, and notably for some original characters detailed above, such as the medial platform of the palatines (ch. 74) and the posterior border of the tympanohyal recess formed by a tympanic extension and/or post-tympanic process (ch. 120) (Fig. 10A).

As expected by Cifelli (1993), the Oldfieldthomasiidae are paraphyletic. Bond (1981) clearly suggested that oldfieldthomasiids may be diphyletic by identifying two possible unrelated groups: on the one hand *Oldfieldthomasia*, *Ultrapithecus*, *Paginula*, *Tsamnichoria* and *Kibenikhoria*; on the other hand *Maxschlosseria*, *Colbertia*, *Brachystephanus*, *Xenostephanus* and *Allalmeia*. López & Bond (2003) even proposed the creation of a new family for this latter subset. These two groups have not been obtained by the present analysis, though two taxa of each supposed group have been included. The present oldfieldthomasiid sample is still too small to find the topology hypothesized by Bond (1981) and López & Bond (2003), as most characters mentioned by them are uninformative in the present context. This clearly needs further investigation. From this analysis, oldfieldthomasiids all represent early diverging typotherians; however, no more can be said about their relationships given the poor resolution at the base of the Typotheria clade.

The Interatheriidae are monophyletic, as supported by recent studies on this group (Reguero *et al.* 2003; Hitz *et al.* 2006). The interatheriids present a novelty, with *Archaeophylus* emerging as the sister taxa of (*Plagiarrhynchus* (*Interatherium*, *Cochilius*)). The phylogeny of Reguero *et al.* (2003) places *Archaeophylus* as an early diverging member of the following clade (*Archaeophylus*, *Progalearpithicus* ((*Protypotherium*, *Miocochilius*), (*Cochilius*, *Interatherium*))). In the more recent study of Hitz *et al.* (2006), *Archaeophylus* appears as an early diverging taxon in a polytomy of a clade gathering all Oligocene and younger interatheriids. The new position of *Archaeophylus* is supported here by the partial molarization of the upper premolars of this taxon, which is intermediate between the plesiomorphic triangular premolar conditions and the fully molarized premolars of the clade (*Plagiarrhynchus* (*Interatherium*, *Cochilius*)) (ch. 41–42) (Fig. 10C). Other relationships within interatheriids are similar to those already supported in previous studies (Reguero *et al.* 2003; Hitz *et al.* 2006).

The informal taxon ‘*Campanorco*’ (Bond *et al.* 1984) and the archaeopithecid *Archaeopithecus* branch in the basal polytomy of the Typotheria clade, as do the oldfieldthomasiids. ‘*Campanorco*’ has been reported from the cladistic studies of Reguero *et al.* (1996), Reguero (1999) and Reguero and Prevosti (2010) to be the sister taxa of the clade Typotherioidea (Reguero and Castro 2004) that clusters the Archaeohyracidae, Mesotheriidae and Hegetotheriidae. From the basal polytomy obtained in the present analysis, such a relationship for ‘*Campanorco*’ is not supported, but also not excluded. Two characters offering potential

support to such a clade are scored in the data matrix: ch. 7, I1 obliquely implanted, meeting at tips; ch. 86, large facial extent of lacrimal toward nasal (see above). These characters are homoplastic in the strict consensus cladogram of the analysis (Fig. 10C and Appendix 4). The analysis of Reguero and Prevosti (2010), focused on the Typotheria, encompasses more characters supporting a relationship between ‘*Campanorco*’ and the Typotherioidea clade.

The clade clustering archaeohyracids, mesotheriids and hegetotheriids of the present analysis shows some differences from that of Billet *et al.* (2009). These concern the relative positions of the archaeohyracids *Archaeotypotherium* and *Archaeohyrax*, the mesotheriids and the hegetotheriids. As the taxonomic sample among these groups is less complete and adapted to resolve their phylogeny in the present work, this is not discussed further (for more extensive results and discussion on phylogenetic relationships among archaeohyracids, mesotheriids and hegetotheriids, see Croft *et al.* 2003 and Billet *et al.* 2009).

## Conclusion

The cladistic analysis presented here is the first applied to the entirety of Notoungulata. However, it is not exhaustive. The taxonomic sample essentially includes taxa with well-known craniodental anatomy. Future work should analyse a similar character sample with a larger taxonomic sample, including other probable early diverging taxa such as *Acoelohyrax*, *Kibenikhoria* (Simpson 1967) or *Pampatenuus* (Vucetich & Bond 1982), even if less completely known, to see if a different topology is obtained. Obviously, the addition of postcranial characters to the craniodental data should also be undertaken.

This study provides numerous new hypotheses that future analyses should test. The Notoungulata (including *Pyrotherium*) is a well supported clade with numerous cranial and dental apomorphies. The monophyly of the two traditional notoungulate suborders Toxodontia and Typotheria is also supported. These two taxa are united in a clade supported by an original character on the morphology of the ectopterygoid crests. The Henricosborniidae, Isotemnidae and Oldfieldthomasiidae are paraphyletic, a reflection of the fact that these families are mostly defined by plesiomorphic characters. If confirmed by future analyses (especially those including post-cranial data), these taxonomic clusters should be abandoned. The monophyly of Notohippidae is questioned, as well as the possibility of a close relationship between leontiniids and toxodontids on the basis of cranial arguments. Analysis also suggests that two major subclades diverge early within the Typotheria: the Interatheriidae and the clade Archaeohyracidae + Mesotheriidae + Hegetotheriidae.

The study and use of cranial anatomy for phylogenetic reconstruction within notoungulates has here proven

effective, as many newly observed cranial characters provide support for many clades within notoungulates. In conclusion, this new phylogeny of notoungulates is an essential step towards reconstructing the ancestral morphology of the Notoungulata. This, in turn, is crucial for further research on the origin and phylogenetic affinities of notoungulates within the Placentalia.

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## Supplementary material

Appendix 1, 2, 3 and 4 are available via the Supplementary Content on the article's online page.

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