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Original Investigation

Afrotherian affinities for endemic South American “ungulates”

Federico L. Agnolin^{a,b}, Nicolás R. Chimento^{c,*}^a Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470 (C1405BDB), Buenos Aires, Argentina^b Fundación de Historia Natural “Félix de Azara”, Departamento de Ciencias Naturales y Antropología, CEBBAD – Universidad Maimónides, Valentín Virasoro 732 (C1405BDB), Buenos Aires, Argentina^c División Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n (B1900FWA), La Plata, Buenos Aires, Argentina

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ABSTRACT

The phylogenetic relationships of endemic South American ungulates are a highly debated topic. Among them, the most well-known clades are the Notoungulata and the Astrapotheria. Three unambiguous hard-tissue features characteristic of afrotherian mammals potentially indicate a relationship with the two South American clades: delayed cheek-tooth replacement, more than 19 thoracolumbar vertebrae, and the presence of a well defined astragalar cotylar fossa. New data based on many fossil specimens preserving deciduous dentition and a morphometric assessment of those specimens, together with a revision of available postcranial anatomy in relevant fossils are used to examine the distribution of the three characters in placental phylogeny.

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Introduction

The clade Afrotheria includes six living mammalian clades: Proboscidea (elephants), Hyracoidea (hyraxes), Sirenia (dugongs and manatees), Tubulidentata (aardvarks), and Macroscelidea, and Tenrecoidea (african “insectivorans”) (Tabuce et al., 2008). This clade, first recognized by Stanhope et al. (1998) (see also De Jong et al., 1981) has been recovered by most recent molecular analyses, and there is a strong consensus about its monophyly (De Jong et al., 1981, 1993; Stanhope et al., 1998; Madsen et al., 2001; Murphy et al., 2001; Eizirik et al., 2001; Redi et al., 2007; Springer and Murphy, 2007; Nikolaev et al., 2007; Nishihara et al., 2007; Wildman et al., 2007; Asher et al., 2009). In contrast to its stable monophyly, afrotherian relationships are still in state of flux. Most authors recognize a monophyletic Paenungulata, including Hyracoidea, Proboscidea, and Sirenia (Lavergne et al., 1996; Springer et al., 1999; Shoshani and McKenna, 1998; Asher et al., 2009).

Mammalian ‘orders’ encompassed within Afrotheria have first occurrences in Africa (except Sirenia) and in some cases (i.e. Tenrecoidea, Macroscelidea) have remained endemic to the Afro-Malagasy region (Tabuce et al., 2008). However, possible stem afrotheres are not restricted to Africa, including some extinct fossil forms, such as the Euramerican “hyopsodontids” and Asian

tethyteres (Asher et al., 2003; Zack et al., 2005; Seiffert, 2007; Tabuce et al., 2007).

Throughout the Tertiary, the South American continent has been populated by a large array of native ungulate-like mammals. Up to now, at least five mammalian ungulate ‘Orders’ have been recognized: Litopterna, Notoungulata, Astrapotheria, Xenungulata, and Pyrotheria (Simpson, 1945; Pascual and Ortiz Jaureguizar, 2007). The notoungulates existed during the Paleocene–Pleistocene time span; it was the most successful and diverse group of native South American “ungulates”. The Astrapotheria is known from the Middle Paleocene to the Late Miocene, constituting a small group of rhino-sized taxa including less than ten genera (Cifelli, 1993).

The pyrotheres and xenungulates are two small groups of Paleogene ungulates of poorly known morphology and fossil record. Due to its incomplete knowledge, their relationships are matter of debate, being pyrotheres often considered as *Mammalia incertae sedis* (Cifelli, 1993).

Although relatively well-known, the affinities of these South American ungulate clades are still in state of flux, and most proposals of their relationship with other mammalian groups await further investigations. One example appears to be the clade Litopterna (including the Didolodontidae) with affinities are with some North American “archaic ungulates” (De Muizon and Cifelli, 2000; but see Williamson and Carr, 2007).

In the present paper we hypothesize close affinities of the Notoungulata and Astrapotheria, with the Afrotheria. Moreover, afrotherian affinities are also suggested for Xenungulata and Pyrotheria.

* Corresponding author.

E-mail addresses: fedeagnolin@yahoo.com.ar (F.L. Agnolin), nicochimento@hotmail.com (N.R. Chimento).

Material and methods

We follow the nomenclature for deciduous teeth employed by Villarroel (1997). Although adult size is difficult to quantify on fossil specimens, we follow the criteria of Madden (1997), who analyzed relatively complete ontogenetic series of the notoungulate *Pericotodon platignathus*.

Following the criteria of Sánchez-Villagra and collaborators (2007) the number of thoracolumbar vertebrae of individual species of most extant mammalian orders is reviewed and recorded (see S1). In addition, several bibliographical sources were consulted to include some relevant fossil specimens (S2–3).

On the basis of the large amount of fossil specimens of Notoungulata and Astrapotheria still retaining deciduous lower and upper premolars, a bivariate analysis with the aim to evaluate the ontogenetic stage of adult and juvenile specimens was performed. This analysis was made using m1/M1, m2/M2, and m3/M3 maximum length vs. maximum width when preserved, and measurements were taken in millimetres (S3). This ratio was used in order to demonstrate that in specimens that carried deciduous teeth the molars exhibit proportions comparable to those seen in fully adult specimens. We also analyzed the same parameter in artiodactyls, with the aim to compare it with South American taxa (S3). The length vs. width ratio is a useful parameter in order to evaluate total size of the individual as indicated by previous authors (Billet et al., 2008, 2009; Townsend and Croft, 2010). We opt to include selected Astrapotheria and Notoungulate taxa in which large amount of specimens are known, and measurements were given in the bibliography (S3).

Abbreviations

MACN-Ma, Sección Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina. MACN-PV, Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina. MLP, División Paleontología de Vertebrados, Museo de La Plata, La Plata, Buenos Aires, Argentina; DUNUC, D’Arcy Thompson Zoology Museum, University of Dundee, Nethergate, Dundee, Scotland (available in <http://www.dundee.ac.uk/museum/zoology/skeletons.htm>). TVL, Thoracolumbar vertebrae.

Results

Afrotherians are highly morphologically divergent from each other, making shared derived characters hard to identify (Cote et al., 2007); possibly, its long endemic evolution may have overwritten morphological afrotherian synapomorphies (Robinson and Seiffert, 2004). Although some putative shared derived characters were recognized previously as synapomorphies of Afrotheria (see overview in Tabuce et al., 2008), only two hard-tissue features are actually unambiguous synapomorphies of Afrotheria: more than 19 thoracolumbar vertebrae (Sánchez-Villagra et al., 2007), and late eruption of permanent dentition (Asher and Lehmann, 2008). Moreover, another probable synapomorphy of Afrotheria is the presence of an astragalar cotylar fossa, as proposed by Tabuce et al. (2007; see also Tabuce et al., 2008; Asher et al., 2009). Here, we analyze these morphological features among the clades Notoungulata and Astrapotheria.

Relatively late eruption of the permanent dentition (Asher and Lehmann, 2008)

Eruption of permanent cheek teeth well past sexual maturity is uncommon among mammals, except in hyracoids, proboscideans, manatee, and African “insectivorans” (Asher and Lehmann, 2008),

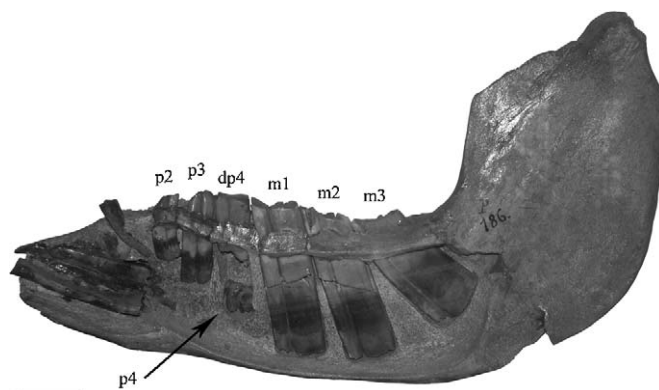


Fig. 1. Left mandible of *Toxodon platensis* Owen, 1837 (MLP-P.186) showing permanent p2–m3, and deciduous p4. At base of the mandible the unerupted permanent p4 is present. Scale: 5 cm.

as well as selected artiodactyl genera (Asher and Olbricht, 2009). The Tubulidentata does not erupt a functional, deciduous dentition, and the ontogeny of this clade is still poorly known (Asher and Lehmann, 2008; Lehmann, 2009). In this way, and in contrast with most mammals, adult size among afrotherians is frequently reached prior to the eruption of many permanent teeth. However, the same condition was acquired convergently by selected primates, perissodactyls, and artiodactyls (Asher and Olbricht, 2009). Non-afrotherian mammals show that less than 60% of erupted permanent cheek teeth in individuals with median adult length well under the 90% of adult-sized individuals. On the other hand, in afrotherians most specimens show less than 60% of permanent cheek teeth when the jaw length surpasses 95% of adult-sized individuals (Asher and Lehmann, 2008). In sum, afrotherian permanent cheek-teeth finish erupting generally after these taxa have reached adult body size.

In Notoungulata the deciduous dentition is extremely similar to the permanent dentition (Villarroel, 1997). Deciduous and permanent teeth may be distinguished because the formers are smaller, proportionally longer, and more brachyodont (Villarroel, 1997). Usually in notoungulates both the permanent and deciduous dentition are found in the same individual (Ameghino, 1906). In Notoungulata, as exemplified by the toxodontids *Nesodon* and *Toxodon*, most deciduous teeth are retained in adult-sized individuals (a condition resembling Afrotheria), a fact well-known by most authors since the XIX century (Fig. 1; Ameghino, 1889, 1904a; Roth, 1927; Simpson, 1933, 1967; see Asher et al., 2009). Because of the availability of only poorly known ontogenetic series in most notoungulates, the retention of deciduous teeth is not well known in most taxa, with the exception of the two above mentioned genera. However, retention of most deciduous teeth in adult-sized specimens has been also corroborated in the toxodontid *Adinotherium*, the isotemnid *Asmodeus*, and the leontiniid *Huilatherium*, the homalodotheriid *Homalodotherium* and the notohippid *Rhynchippus* (Ameghino, 1904a; Scott, 1912; Loomis, 1914; Villarroel, 1997). Moreover, among the notoungulate clade Typotheria, a similar condition was recognized in the interatheriid *Protypotherium* and the hegetotheriid *Propachyrucos* (Sinclair, 1909; Chaffee, 1952). In addition, in the two latter genera, as well as in other derived notoungulates, the deciduous teeth reach the full depth of the mandibular ramus, with no sign of permanent teeth below them, as also occur in proboscidean premolars (Chaffee, 1952; Asher and Lehmann, 2008).

Regarding Astrapotheria, the lack of specimens of early ontogenetic age prevents analysis of the retention of deciduous teeth. However, the typical hyracoid-like condition appears to be present in at least *Parastrapotherium* (Ameghino, 1902, 1904a), the only

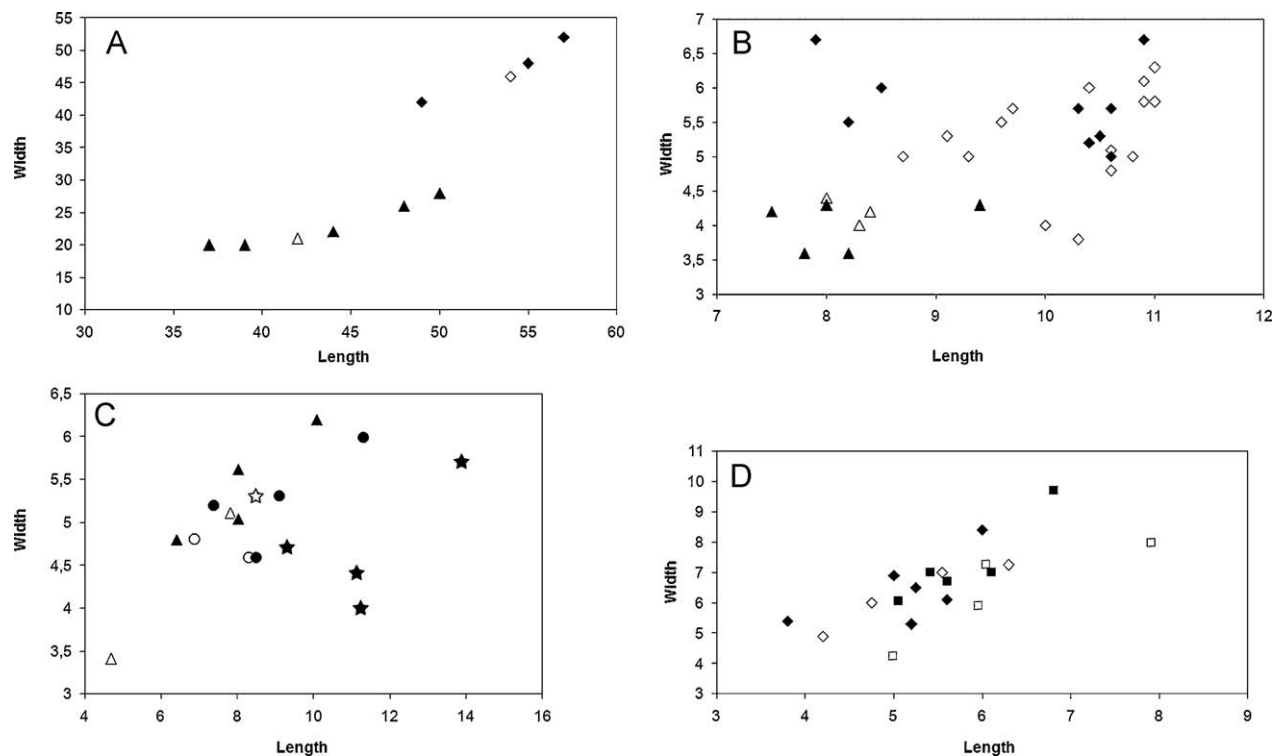


Fig. 2. Bivariate plots of cheek-teeth maximum length (abscissa) vs. maximum width (ordinate) of selected South American ungulates. A, *Astrapotherium magnum* (Astrapotheria: Astrapotheriidae) (Scott, 1928); B, *Archaeohyrax suniensis* (Notoungulata: Archaeohyracidae) (Billet et al., 2009); C, *Plesiotypotherium minus* (Notoungulata: Mesotheriidae) (Townsend and Croft, 2010); D, *Brachystephanus postremus* (Notoungulata: Oldfieldthomasiidae) (López, 2008). References: Black figures indicate adult specimens with fully erupted permanent dentition; White figures indicate specimens still retaining deciduous premolar teeth; Triangles: m1; Rhombus: M1; Circles: m2; Square: M2; Star: m3.

astrapothere in which the juvenile dentition is properly known. In adult *Parastrapotherium* the dental formula is composed of five cheek-teeth, of which at least dP1–dP3 are still retained in adult or senile specimens.

This analysis indicates that most putative juvenile specimens of Astrapotheria and Notoungulata are indistinguishable from those of adult or senile individuals, showing a rather similar body size and tooth proportions (Fig. 2; S1; see also Appendix 3 of Billet et al., 2008; Appendix 2 of Billet et al., 2009; Fig. 14 of Townsend and Croft, 2010), a fact also noted by Billet et al. (2008) in some mesotheriids. This is in agreement with the condition seen in most afrotherians, in which specimens still retaining deciduous cheek-teeth are similar in size and proportions to adult specimens (Asher and Lehmann, 2008). On the contrary, in remaining mammals, including artiodactyls (see S3), adult individuals exhibit a length/width ratio very different from that of juvenile specimens (carrying deciduous premolars).

Among pyrotheres, in the holotype and only known specimen of *Griphodon peruvianus*, the mandible shows a dp4 and a well erupted m1, with p4 still at base of the mandible (Anthony, 1924). This suggests that Pyrotheria also exhibited a delayed tooth replacement. Regrettably, in Xenungulata no single deciduous tooth is known, and the presence or absence of delayed tooth replacement in this clade is ambiguous.

In conclusion, Astrapotheria, Notoungulata, and possibly Pyrotheria show a relatively late eruption of permanent cheek teeth, a condition considered a synapomorphy of the Afrotheria.

More than 19 thoracolumbar vertebrae (Sánchez-Villagra et al., 2007)

Plesiomorphically for eutherians, synapsids retain the vertebral number of 20 thoracolumbar vertebrae, showing a remarkable con-

servatism relative to the basal amniote condition (Müller et al., 2002; Sánchez-Villagra, 2010). In most mammals the number of thoracic and lumbar vertebrae together tends to be 19, and this number is the plesiomorphic condition for Mammalia, as observed in Monotremata and Marsupialia (S2). Afrotheria was diagnosed by Sánchez-Villagra et al. (2007) by having an increase in such number: Macroscelidia shows 20 thoracolumbars, Chrysochloridae shows between 22 and 24, Tenrecidae from 21 to 24, and tubulidentates 21 (S2). The clade Paenungulata (i.e. Sirenia, Proboscidea, Hyracoidea) includes taxa with more than 23 vertebrae, and hyracoids exhibit between 27 and 32 thoracolumbars (Fig. 3; S2; see detailed discussion in Sánchez-Villagra et al. (2007) and Asher et al. (2009)). Among mammals, more than 19 thoracolumbars have been also reported only in some selected members of Xenarthra, Primates (see Schultz, 1969), carnivores, erinaceids, soricids, lagomorphs and perissodactyls, among others (S2; Sánchez-Villagra et al., 2007; Asher et al., 2009).

Regrettably, the vertebral formula is poorly known among South American ungulates, since articulated specimens of most genera still remain unknown or undescribed. However, in all Notoungulata and Astrapotheria in which the vertebral formula is known, the number of thoracolumbars is more than 19 (S2–3).

Among this mammalian clade, a large number of thoracolumbar vertebrae are present in the genera belonging to the families Toxodontidae (e.g., *Nesodon*, *Adinotherium*, *Toxodon*; Fig. 3; Scott, 1912; Burmeister, 1879), Leontiniidae (e.g. *Scarritia*; Chaffee, 1952), Notohippidae (e.g., *Rhynchippus* Loomis, 1914), and Isotemnidae (e.g., *Thomashuxleya*; Simpson, 1936). These taxa show 20–21 thoracolumbar vertebrae (S2). Among most genera of Typotheria, for example in two Interatheriidae (e.g. *Protypotherium*, *Interatherium*; Sinclair, 1909), Hegetotheriidae (e.g. *Pachyrucos*; Scott, 1912), and Mesotheriidae (e.g., *Mesotherium*; Serrés, 1867), there are 22–23 thoracolumbar vertebrae (S2).

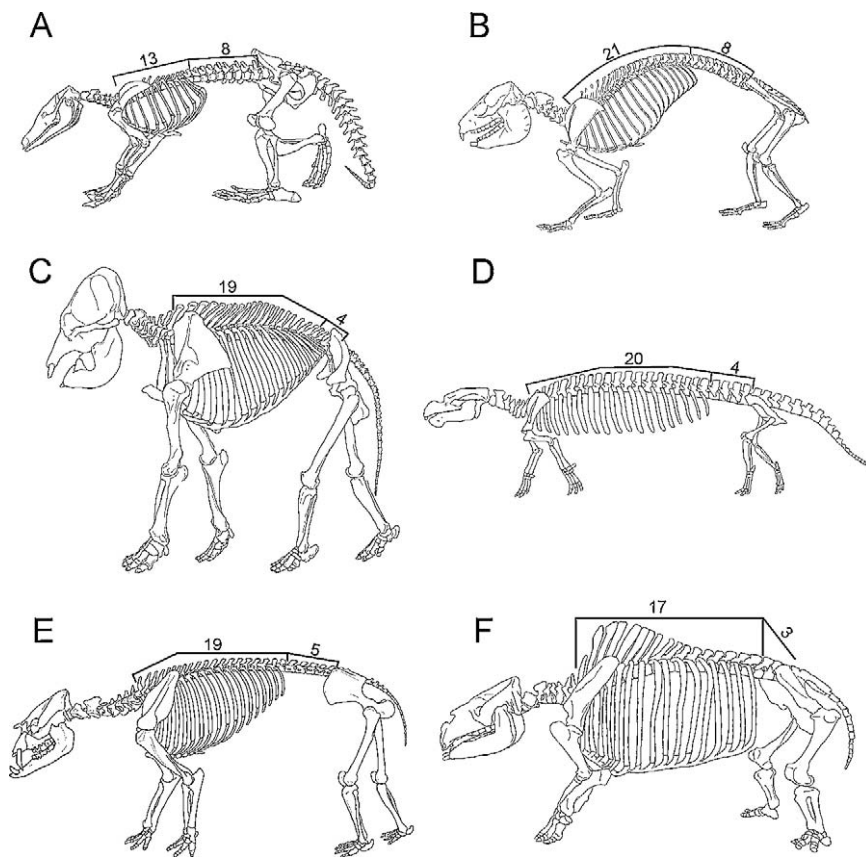


Fig. 3. Skeletal reconstructions of selected Afrotherian mammals showing TLV. A, *Orycteropus afer* (Tubulidentata) (MACN-Ma 13.99); B, *Procavia capensis* (Hyracoidea) (MACN-Ma 22.36); C, *Elephas maximus* (Proboscidea) (MACN-Ma 43.49); D, *Pezosiren portelli* (Sirenia) (modified from Domning, 2001); E, *Astrapotherium magnum* (Astrapotheria) (modified from Riggs, 1932); F, *Toxodon platensis* (Notoungulata) (MLP 12.II.26). Not to scale.

The number of thoracolumbar vertebrae seen among Notoungulata differs from that of Paenungulata, which invariably show more than 23 thoracolumbars (Sánchez-Villagra et al., 2007).

In Astrapotheria the vertebral formula is only known in *Astrapotherium*, which shows a number of at least 24 thoracolumbars (Fig. 3; Riggs, 1935; Scott, 1937), indicating that these animals exhibited an extremely elongate trunk.

In conclusion, the presence of more than 19 thoracolumbar vertebrae is another potential synapomorphy for the Notoungulata and Astrapotheria with the Afrotheria.

Cotylar fossa on the astragalus (Tabuce et al., 2007)

In mammals, the cotylar fossa of the astragalus is represented by a deep concavity located at the medial margin of the medial rim of the astragalar trochlea for receive the medial malleolus of the distal tibia (Szalay, 1977). As indicated by several previous studies, the absence of a medial cotylar fossa is the plesiomorphic condition for mammals, being absent in monotremes, metatherians, and xenarthrans (Fig. 4; Szalay, 1977, 1984; Asher et al., 2003; Salton and Szalay, 2004). Accordingly, in litopterns, as well as cetartiodactyls the astragalar body is spool-like, with strong, parallel medial and lateral rims, and a deep astragalar trochlea, lacking any sign of a cotylar fossa (Fig. 4; Cifelli, 1983; Gingerich et al., 2001). In most perissodactyls, phenacodontids, mesonychids, as well as the ungulate-like Olseniidae, the astragalus shows the rims of the astragalar trochlea nearly subparallel each other, and lack a cotylar fossa (Fig. 4; Radinsky, 1966; Guthrie, 1968; Erfurt and Averianov, 2005). Moreover, in pholidotan and palaeodont mammals the medial margin of the medial rim of the astragalar trochlea is slightly convex (Gheerbrant et al., 2005; Horovitz et al., 2005). In the same

way, in *Protungulatum*, the medial margin of the astragalar trochlea is nearly straight, without any sign of a medial fossa (Szalay, 1977). In Glires, including Lagomorpha, Rodentia, and Arctostylopida, the astragalus shows the medial margin of the medial rim of the astragalar trochlea straight or slightly convex, and a cotylar fossa appears to be invariably absent (Fig. 4; Asher et al., 2005; Missiaen et al., 2006).

On the other hand, the astragalus of Afrotheria was characterized as having a very deep cotylar fossa (Fig. 4; Zack et al., 2005; Tabuce et al., 2007). In fact, all known stem-Afrotheria show a wide cotylar fossa, that is secondarily lost only in some crown Tenrecidae and Chrysochloridae (Fig. 4; Salton and Szalay, 2004). The presence of a cotylar fossa for the malleolus of the tibia in the inner surface of the astragalar body was considered as a probable derived feature shared by Orycteropodidae, Hyracoidea, and Paenungulata by Le Gros Clark and Sonntag (1926). In this way, Tabuce et al. (2007) considered the presence of a cotylar fossa on the astragalus as a reliable afrotherian synapomorphy. Moreover, Tabuce et al. (2007) indicated the presence of this cotylar fossa not only in afrotherians, but also in South American “ungulates”, a fact previously noted by Ameghino (1905). The presence of a cotylar fossa has also been reported in some unrelated eutherian groups that acquired it convergently, as cercopithecoid primates, and some “creodonts” (Tabuce et al., 2007).

Resembling the afrotherian condition, the oldest known unambiguous notoungulates (i.e. *Colbertia*, *Itaboraitherium*, *Camargomendesia*) show a well developed cotylar fossa that extends from the dorsal astragalar foramen to the base of the navicular facet, along the medial margin of the astragalar body (Cifelli, 1993). This morphology is also present in most remaining notoungulates, a fact well described and defined by Ameghino (1904b,

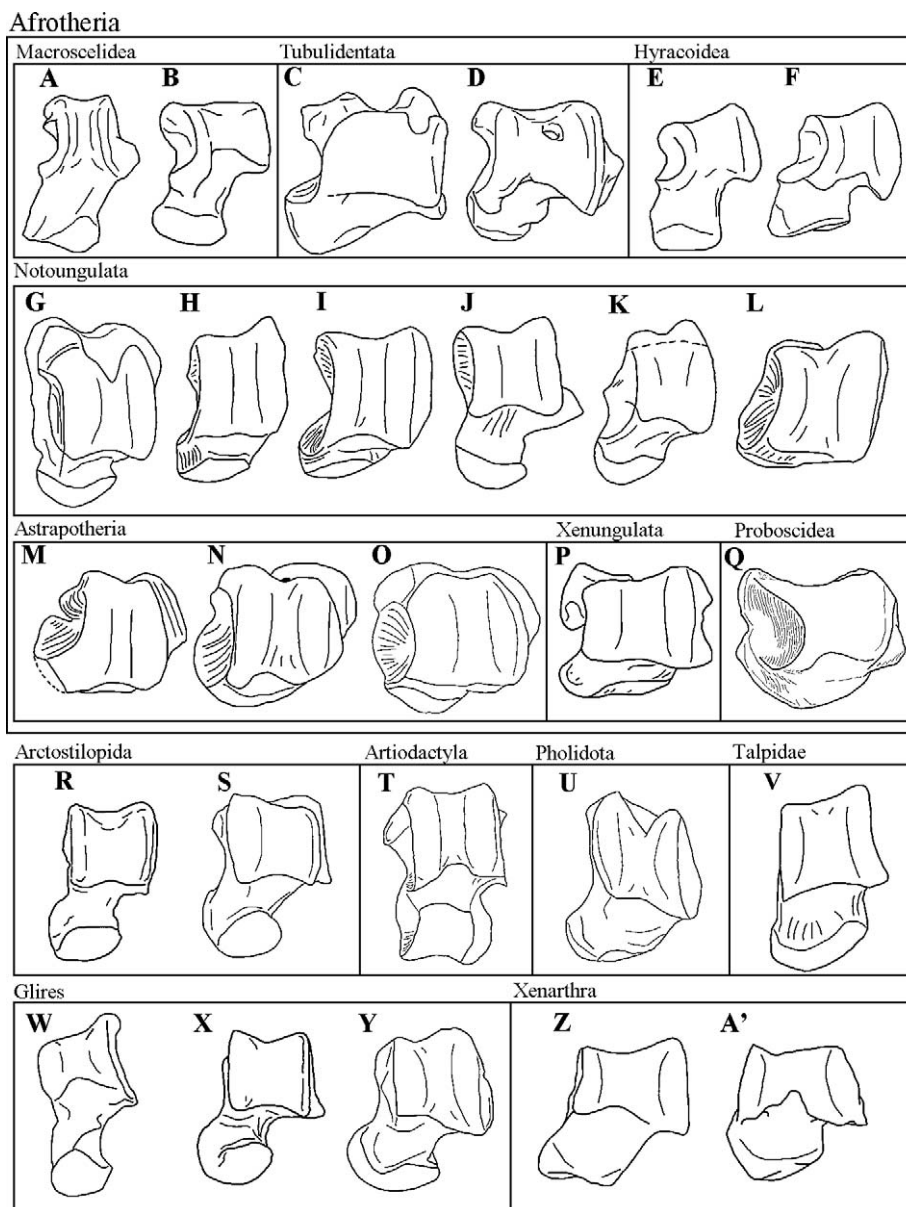


Fig. 4. Dorsal view of right astragalus of selected afrotherian, South American ungulates, and other eutherian taxa. A, *Rhynchocyon* sp. (Macroscelidea); B, *Chambius kasserinensis* (Macroscelidea); C, *Plesiorycteropus madagascariensis* (Tubulidentata, Bibimalagasia); D, *Orycteropus afer* (Tubulidentata, Orycteropiidae); E, *Microhyrax lavocati* (Hyracoidea); F, *Dendrohyrax dorsalis* (Hyracoidea); G, *Homalodotherium segoviae* (Notoungulata, Homalodotheria); H, *Morphippus fraternus* (Notoungulata, Notohippidae); I, *Nesodon imbricatus* (Notoungulata, Toxodontidae); J, *Pachyrucos typicus* (Notoungulata, Interatheriidae); K, *Tomashuxleya wortmani* (Notoungulata, Isotemnidae); L, *Toxodon platensis* (Notoungulata, Toxodontidae); M, *Liarthrus copei* (Astrapotheria, Astrapotheriidae); N, *Astrapotherium magnum* (Astrapotheria, Astrapotheriidae); O, *Parastrapotherium* sp. (Astrapotheria, Astrapotheriidae); P, *Carodnia vieirai* (Xenungulata, Carodniidae); Q, *Palaeomastodon beadnelli* (Proboscidea); R, *Arctostylops* sp. (Arctostylipida); S, *Paleostylops iturus* (Arctostylipida); T, *Diacodexis* sp. (Artiodactyla); U, *Patriomanis americana* (Pholidota); V, *Talpa europaea* (Talpidae); W, *Palaeolagus haydeni* (Glires, Lagomorpha); X, *Rhombomylus turpanensis* (Glires, Eurymylidae); Y, *Paramys copei* (Glires, Rodentia); Z, *Tamandua tetradactyla* (Xenarthra, Vermilingua); A', *Dasyurus novemcinctus* (Xenarthra, Cingulata). A, modified from Zack et al., 2005; B, E, Tabuce et al., 2007; C, D, F, Y, Z, A', modified from McPhee, 1994. G–N, modified from Ameghino, 1904b; O, modified from Weston et al., 2004; P, modified from Cifelli, 1993; Q, modified from Andrews, 1906; R and S, W and X modified from Missiaen et al. 2006; T, modified from Schaeffer, 1947; U, modified from Gaudin et al., 2009; V, modified from Ameghino, 1905. Not to scale.

1905). Thus, the presence of a deep and concave cotylar fossa is shown by all known notoungulates, including isotemnids, leontiniids, notostyloids, notohippids, mesotheriids, archaeohyracids, interatheriids, homalodotheriids, nesodontine and toxodontine toxodontids (e.g., *Asmodeus*, *Tomashuxleya*, *Scarritia*, *Notostylops*, *Rhynchippus*, *Protypotherium*, *Interatherium*, *Mesotherium*, *Homalodotherium*, *Nesodon*, *Toxodon*; Fig. 4; Ameghino, 1904b; Scott, 1912; Sinclair, 1909; Chaffee, 1952). Moreover, in the latter taxa (e.g. *Toxodon*, *Nesodon*) the cotylar fossa is very wide and deep, and occupies most of the medial margin of the astragalus body (Ameghino, 1904b). Furthermore, this condi-

tion has also been noticed in other South American clades, as for example in the xenungulate *Carodnia* (Fig. 4; Paula Couto, 1952) and in the astrapotheres *Tetragonostylops*, *Trigonostylops*, *Astraponotus*, *Liarthrus*, *Parastrapotherium*, *Granastrapotherium* and *Astrapotherium* (Fig. 4; Ameghino, 1904b; Cifelli, 1993; Weston et al., 2004). These similarities were considered by some authors as indicative of phylogenetic affinities between astrapotheres and notoungulates (Van Valen, 1988). In addition, in astrapotheres the medial fossa is strongly expanded and is greatly excavated, occupying most of the medial margin of the astragalus body. Regrettably, in pyrotheres, the only genus in which the astragalus is known

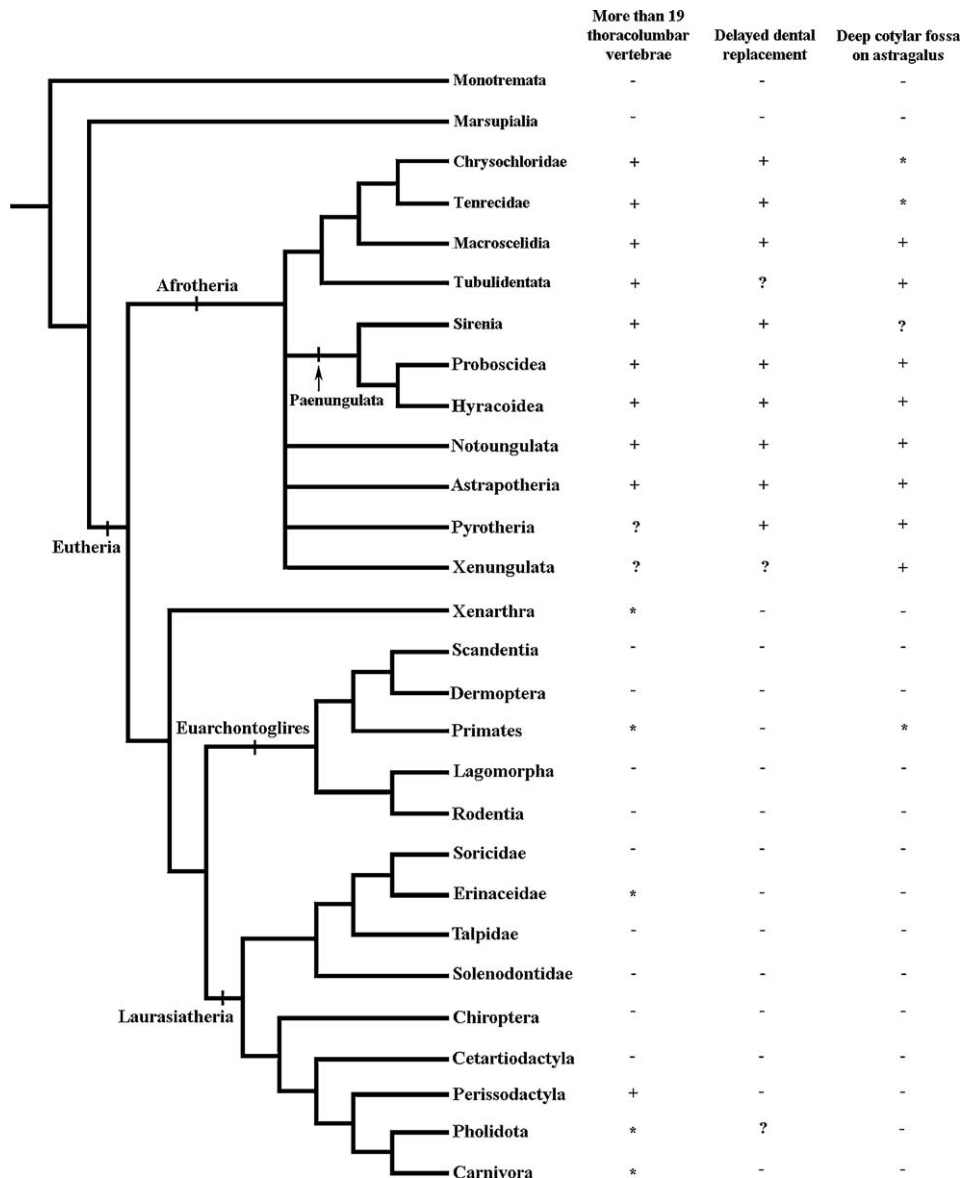


Fig. 5. Cladogram showing the phylogenetic position of South American Ungulate clades Notoungulata, Astrapotheria, Pyrotheria, and Xenungulata among Afrotherian mammals based on Amrine-Madsen et al. (2003; see also Asher et al., 2009). The presence of more than 19 TLV, late eruption of cheek teeth, and deep cotylar fossa on astragalus among mammalian clades is indicated at right side (modified from Sánchez-Villagra et al., 2007). References: +, present; -, absent; ?, unknown; *, variable.

is *Pyrotherium* (Shockey and Anaya Daza, 2004). In this genus the astragalus is strongly modified by a graviportal lifestyle, and thus, the morphology of the medial side of the astragalus could not be properly observed due to its strong dorsoventral compression and transverse expansion; consequently we consider the presence or absence of the cotylar fossa in Pyrotheria as uncertain.

In conclusion, we propose that the presence of a cotylar fossa on the astragalus is a synapomorphy shared by most Afrotheria, and includes Notoungulata, Astrapotheria, and Xenungulata.

Conclusions

The Notoungulata and Astrapotheria are here regarded as closely related to the Afrotheria. This hypothesis is sustained on the basis of three morphological characters recovered in previous analyses as diagnostic of Afrotheria: more than 19 thoracolumbar vertebrae, late replacement of deciduous cheek teeth, and cotylar fossa on astragalus (Fig. 5).

Hence, South American ungulates appear to belong to at least two different lineages. On one hand, the Litopterna (including Didolodontidae), are probably related to some Mioclaenidae that arrived to South America through the Panama isthmus at the end of the Cretaceous (De Muizon and Cifelli, 2000).

On the other hand, the Notoungulata and Astrapotheria, are close to the Afrotherian clade. Some morphological attributes are also shared between notoungulates and astrapotheres with some afrotherian mammals, as noticed by previous authors (Soria and Powell, 1982; Soria, 1984; Van Valen, 1988). Both notoungulates and astrapotheres share with afrotherian clade Paenungulata the serial (in line) arrangement of the carpal elements (Novacek and Wyss, 1986). Moreover, Notoungulata resembles afrotherians in having a tympanic bullae composed of both ectotympanic and entotympanic components (Prothero, 1993). However, these similarities are currently not considered as unambiguous synapomorphies.

Regarding remaining South American mammalian clades, the Pyrotheria appears to be related to the Notoungulata (Patterson

and Pascual, 1972; Patterson, 1977; Reig, 1981; Soria, 1984; Billet, 2010). The same appears to be true for the Xenungulata, which were usually regarded as related to Notoungulata and Astrapotheria (Soria and Powell, 1982; Soria, 1984, 1988; Cifelli, 1993; Berqvist, 1996). Moreover, most alternative hypotheses about the major relationships of pyrotheres and xenungulates ally both clades to mammalian groups currently included within Afrotheria (e.g. Ameghino, 1902, 1906; Loomis, 1914; Simpson, 1934, 1945; McKenna, 1975, 1980; Cifelli, 1983, 1993; Shockey and Anaya Daza, 2004). Additionally, pyrotherians shows similarities in cranial morphology to some afrotherians, including their tympanic bullae composed of both ectotympanic and entotympanic components (Prothero, 1993). In fact, some authors noted striking resemblances among Pyrotheria and Proboscidea (Ameghino, 1906; Loomis, 1914), which suggest that the similarities between these two clades are synapomorphies (Simpson, 1935; Schoch and Lucas, 1985; Van Valen, 1988). Among other traits, pyrotherians are reminiscent of proboscidean including an enlarged I1 and enlarged I2 tusks, tendency to lophodonty of cheek teeth, and orbit opening in the maxilla (Ameghino, 1906; Loomis, 1914; Tabuce et al., 2007; Gheerbrant, 2009; see also Billet, 2010). However, although afrotherian affinities for this clade are plausible, the supposedly shared derived features between both Orders may be convergences, rather than synapomorphies, as proposed by Patterson (1977), and we must await the discovery of further material to analyze in detail the phylogenetic relationships of both pyrothere and xenungulate mammals (Fig. 5).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.mambio.2010.12.001.

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