

Phylogenetic revision of the South American notopithecines (Mammalia: Notoungulata)

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A phylogenetic analysis of all Eocene taxa assigned to Notopithecinae has been conducted, evaluating relationships amongst notopithecines, basal interatheriids and Interatheriinae. Other groups of native ungulates were also included. New dental and postcranial characters are considered with respect to previously published data; some characters are evaluated in notoungulates for the first time. Two different searches were performed under parsimony and equal weights. The inclusion of postcranial characters strongly influenced tree topology. The most significant result of the phylogenetic analysis was the identification of a novel monophyletic group, including species traditionally grouped as Patagonian Notopithecinae. The 'notopithecid' name is linked to the new clade defined as the clade stemming from the most recent common ancestor of the species Notopithecus adapinus, Antepithecus brachystephanus, Transpithecus obtentus and Guilielmoscottia plicifera. This phylogeny supports the main morphological differences of the new clade with respect to Interatheriinae Interatheriidae. In consequence, a diagnosis is proposed based on phylogenetic results, to which some other morphological characters are added. The Chilean basal interatheriids Johnbell and Ignigena as well as Punapithecus (Argentinean Puna) are excluded from the notopithecid clade, implying biostratigraphical and biogeographical changes. Notopithecid distribution now becomes restricted to the middle-late Eocene part of the Sarmiento Formation outcropping in central Chubut and north-east Santa Cruz provinces, Argentina. Other extra-Patagonian records of notopithecids are not confirmed. The resulting phylogeny resolves some relationships within basal interatheriids differently from previous analyses. Interatheriinae is not recovered as a monophyletic group, and Oldfieldthomasiidae and Henricosborniid are paraphyletic. The position of the Archaeopithecidae Acropithecus rigidus is controversial; it appears at the base of the Typotheria lineage or in the notopithecid clade, but systematic taxonomy and phylogenetic relationships amongst members of Archaeopithecidae remain to be established.

Keywords: phylogeny; notopithecines; Interatheriidae; Notoungulata; Eocene; Argentina

Introduction

The family Notopithecidae was established based on the description of the genus *Notopithecus* Ameghino, 1897. Ameghino considered it to fall within Prosimiae Haeckel, 1866 as the most ancient group of monkeys related to his (Ameghino 1891) protypotheriids, which currently includes the family Mesotheriidae. In the same paper, Ameghino (1897) established the family Archaeopithecidae, comprising seven species within the following four genera: *Archaeopithecus* Ameghino, 1897, *Ultrapithecus* Ameghino, 1901 and *Guilielmoscottia* Ameghino, 1901. These were considered to be prosimians because they share several traits with primates, such as brachydont dentition and a similar lower jaw.

Research on the families Notopithecidae and Archaeopithecidae has been scant but complex from a systematic point of view. In one of his last works, Ameghino (1906) recognized eight genera of Notopithecidae within the 'Notostylopense' fauna (Casamayoran South American Land Mammal Age – SALMA) of Patagonia (Argentina): *Notopithecus*, *Adpithecus* Ameghino, 1901, *Transpithecus* Ameghino, 1901, *Antepithecus* Ameghino, 1901, *Infrapithecus* Ameghino, 1901, *Epipithecus* Ameghino, 1903, *Acropithecus* Ameghino, 1901 and *Gonopithecus* Ameghino, 1903. For the 'Astraponotense' fauna (Mustersan SALMA), Ameghino mentioned *Adpithecus* within notopithecids and *Guilielmoscottia* in the family Archaeopithecidae.

Later, Scott (1913) included the families Notopithecidae and Archaeopithecidae in Typotheria, followed by Schlosser (1923) and Roth (1927), who discarded Ameghino's theory. The genus *Guilielmoscottia* was transferred to the family Notopithecidae by Schlosser (1923), which was accepted by Roth (1927), Scott (1937) and Simpson (1936, 1945, 1967). Riggs & Patterson (1935) considered Notopithecidae to be part of the family

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Interatheriidae Ameghino, 1897, which was the first report of this family for the Casamavoran SALMA. This transfer was based on Notopithecus, in which the authors observed diagnostic characters of Interatheriidae sensu Sinclair (1909), such as the jugal being excluded from the anterior edge of the orbit, and the morphology of the lower molars. However, in a footnote, Riggs & Patterson (1935, p. 202) stated that not all of the genera that Ameghino had placed in the family Notopithecidae could be considered Interatheriidae. Based on Riggs & Patterson's (1935) suggestion, Simpson (1945) proposed a new classification and divided the family Interatheriidae into two subfamilies, giving a new status to Ameghino's Notopithecidae: the subfamily Notopithecinae, including the Paleogene brachydont forms, and the subfamily Interatheriinae, grouping the hypsodont and euhypsodont forms that appear in the late Oligocene.

After Ameghino, the main systematic revision of Notopithecinae was that of Simpson (1967), who defined this subfamily based on Notopithecus and differentiated it from contemporaneous notoungulate groups such as Archaeopithecidae and Oldfielthomasiidae. Simpson's revision used the collections of Ameghino (MACN), Scarritt Pocket (AMNH), Tournouër (MNHN, Paris) and Roth (MLP), as well as others he had studied previously (Simpson 1932b, 1935a, b, 1936, 1964). Out of the eight genera and 20 species of Notopithecidae listed by Ameghino (1906), Simpson (1967) proposed a total of four genera and seven species of Notopithecinae, based on several synonymies and new combinations. Simpson recognized the following as valid names: Notopithecus adapinus adapinus, N. adapinus reduncus, ?N. amplidens, 'Notopithecus' summus, Antepithecus brachysthephanus, Transpithecus obtentus and Guilielmoscottia plicifera. Simpson (1967) transferred Acropithecus from the Notopithecidae, where Ameghino (1901) originally placed the genus, and proposed synonymies and combinations, regarding Archaeopithecidae as a family containing two genera and three species: Archaeopithecus rogeri Ameghino, 1897, A. fossulatus (Ameghino, 1897) and Acropithecus rigidus (Ameghino, 1901).

Subsequently, there was a remarkable find of the first extra-Patagonian notopithecine, *Punapithecus minor* López & Bond, 1995, from the middle levels of the Geste Formation in Antofagasta de la Sierra (Catamarca Province) and Salar de Pozuelos (Salta Province) in Argentina. The Geste Formation was considered to be Mustersan in age (Pascual 1983; Alonso *et al.* 1988; López 1997), although recent studies have proposed an older Casamayoran age (del Papa *et al.* 2010; Powell *et al.* 2011). López & Bond (1995) argued that *P. minor* was a conservative species because of its generalized notopithecine features, such as brachydont dentition and well-developed mesial and distal cingula in the upper molars, which would not be expected for a late Eocene taxon.

In a recent full revision of notopithecines, Vera (2013b) recognized only four genera of one species each for Notopithecinae sensu Simpson (1945, 1967): Notopithecus adapinus, Antepithecus brachystephanus, Transpithecus obtentus and Guilielmoscottia plicifera. The taxonomic status and nomenclatural issues concerning these taxa were rigorously examined by Vera (2012a, b, 2013a) and Vera & Cerdeño (2014). Phylogenetic analyses of the group (Vera 2013b, 2014) provide the basis for the present study. In these analyses, just the only complete archaeopithecid specimen AMNH 28782 (Acropithecus rigidus; Simpson 1967) was included, which grouped with notopithecines. Considering that the family Archaeopithecidae is now under taxonomic revision by the author, the inclusion of this unique specimen of the family is maintained in the present phylogeny.

Phylogenetic background

The family Interatheriidae was subject to phylogenetic analysis by several researchers (Cifelli 1993; Hitz 1997; Reguero 1999; Hitz *et al.* 2000; Reguero *et al.* 2003; Hitz *et al.* 2006; Reguero & Prevosti 2010; García-López & Babot 2015). Most analyses have focused on the subfamily Interatheriinae without considering notopithecines and archaeopithecids. Based primarily on dental characters, Cifelli (1993) identified homoplasy in the group and recovered a single resolved node separating the subfamily Interatheriinae from the genus *Notopithecus*. He gave four synapomorphies for Interatheriidae: maxilla excludes jugal from orbit; i1–c bifd lingually; I2–P1 transversely compressed and blade-like; and lower molars bilobate with the trigonid separated from the talonid by deep labial and lingual sulci.

The next analysis performed by Hitz (1997), published by Hitz et al. (2000), proposed a more resolved phylogeny for interatheriids based on dental and cranial characters, which was the basis for a phylogenetic definition of the subfamily Interatheriinae and a list of synapomorphies shared by the taxa associated with this name. According to these authors, Interatheriinae is the clade stemming from the most recent ancestor of Santiagorothia chiliensis Hitz, Reguero, Wyss & Flynn, 2000 and Interatherium Ameghino, 1887, plus all its descendants. The clade is characterized by the following: deep parastyle/paracone groove on P2-4; very shallow parastyle/paracone groove on M1-3; smooth posterior ectoloph on M1-3; very high-crowned cheek teeth; distinctly bilobed p3-m3 with persistent labial and lingual sulci; a posterior portion of the auditory bulla overlapping the paraoccipital process; and maxilla excluded from the superior orbital border by an anteriorly projecting frontal sliver.

Reguero *et al.* (2003) presented a phylogenetic analysis of Interatheriidae focused on taxa of Interatheriinae.

They used Notopithecinae as the first out-group and the genus *Acropithecus* (Archaeopithecidae) as the second out-group. The results showed that Interatheriinae is a monophyletic group, in agreement with previous work (Cifelli 1993; Hitz *et al.* 2000), and defined it as the clade containing the most recent common ancestor of *Eopa-chyrucos* Ameghino, 1901, *Interatherium* and all of its descendants. According to Reguero *et al.* (2003), five synapomorphies unite *Eopachyrucos* and all other interatheriines: moderately high-crowned cheek teeth; cementum covering the teeth; lack of enamel on cheek teeth at mesiolabial angles; trigonid of p3 larger than the talonid; and prominent paracristid.

To the existing data set Hitz et al. (2006) added dental and postcranial characters and two species of 'basal interatheriids' from the Abanico Formation (central Chile), Ignigena minisculus from levels estimated to be Casamayoran in age and Johnbell hatcheri from levels considered to be Tinguirican SALMA (Flynn et al. 2003). They also incorporated *Punapithecus*. Antepithecus, the specimen SGO-PV 3604 (unclearly related to Antepithecus brachystephanus according to Hitz et al. 2006, but removed from this taxon by Vera & Cerdeño 2014), Eopachyrucos and Proargyrohyrax (Hitz et al. 2000; Reguero et al. 2003). Based on their results, Hitz et al. (2006) considered the configuration of the zygomatic arch (jugal between maxilla and squamosal, excluded from the orbit) in the interatheriids to be a diagnostic feature amongst notoungulates. This was the basis for naming the clade Interatheriidae, via an apomorphy-based phylogenetic definition (de Queiroz & Gauthier 1990, 1992). Hitz et al. (2006) did not identify synapomorphies shared by notopithecines that excluded them from other interatheriids, showing that Notopithecinae represent a paraphyletic assemblage. They suggested that the taxa formerly termed notopithecines are more appropriately referred to as 'basal interatheriids'. Within this group, the authors included the Patagonian genera Notopithecus, Antepithecus, Transpithecus and Guilielmoscottia, as well as Punapithecus from the Argentine Puna and the Chilean Ignigena and Johnbell.

Reguero & Prevosti (2010) performed a much broader analysis in order to interpret the phylogenetic relationships between the suborders of Notoungulata, Typotheria and Hegetotheria. The most relevant result was that Typotheria is the most inclusive monophyletic group, defined as the clade containing the most recent common ancestor of Notopithecus and Mesotherium plus all its descendants, including Campanorco inauguralis Bond, Vucetich & Pascual, 1984, Archaeohyracidae and Hegetotheriidae. In turn, the families Oldfielthomasiidae and Archaeopithecidae, previously considered to be Typotheria (Simpson 1967; Cifelli 1993), were excluded and formed the sister clade of Typotheria. Likewise, Reguero & Prevosti (2010) Interatheriidae defined the clade with five

synapomorphies: deep paracone/metastyle of the P3-4; very developed metacristid; postmetacristid present on p3-4; reduced jugal, between the maxilla and the squamosal; and moderately developed descending process of maxilla. It must be noted that the authors used the concept of Notopithecinae sensu Simpson (1945) as the subfamily comprising Notopithecus, Antepithecus, Transpithecus and Guilielmoscottia. However, Reguero & Prevosti (2010) only considered Notopithecus and Guilielmoscottia in their analysis. Subsequently, Billet (2011) analysed the relationships of all Notoungulata, where the suborders Typotheria and Toxodontia were recovered as monophyletic groups and, within Typotheria, this author recovered Interatheriidae, Mesotheriidae and Hegetotheridae as monophyletic assemblages. Shockey et al. (2012) obtained the same groups as Billet (2011) using a matrix that excluded postcranial characters; when including these characters, however, Typotheria was recovered as paraphyletic to the 'advanced Toxodontia', which form a clade with Interatheriidae. Therefore, Shockey et al. (2012) demonstrated that the inclusion of postcranial data has strong influence in the tree topology, differing from conventional analysis and changing long-standing ideas.

Very recently, García-López & Babot (2015) and García-López (2015) described the new interatheriid *Antofagastia turneri* from the middle section of the Geste Formation (Catamarca Province, Argentina), from where *Punapithecus* was also collected, and evaluated its phylogenetic position within Interatheriidae. Following Hitz *et al.* (2006), they recovered the clade Interatheriidae supported by the same synapomorphies. *Antofagastia* appeared to be related to other extra-Patagonian notopithecines, but did not fall within a clade.

Based on taxonomic revision of notopithecines (Vera 2012a, b, 2013a, b, 2014; Vera & Cerdeño 2014) and the previous research discussed above, a phylogenetic analysis is conducted here to examine the relationships of all the genera and species referred to as either Notopithecinae *sensu* Simpson (1945) or basal interatheriids *sensu* Hitz *et al.* (2006). The purpose is to elucidate the position of these controversial taxa within the interatheriids and their relationship with other contemporaneous groups such as Archaeopithecidae (*Acropithecus rigidus*) and Oldfieldthomasiidae.

Material

Institutional abbreviations

The phylogenetic analysis is based on an extensive literature review and re-study of all taxa, using specimens from the palaeontological collections of the following institutions: **ACM**: Amherst College Museum of Natural History, Amherst, Massachusetts, USA; **AMNH**: American Museum of Natural History, New York, USA; **DGM**: ex-Direção Geologia y Mineralogia, Rio de Janeiro, Brazil; FMNH: Field Museum of Natural History, Chicago, Illinois, USA; MACN: Museo Argentino de Ciencias Naturales, 'Bernardino Rivadavia', Buenos Aires, Argentina; MCNAM-PV: Vertebrate Palaeontology collection, Museo de Ciencias Naturales y Antropológicas de Mendoza 'J. C. Moyano', Mendoza, Argentina; MCT: Museu de Ciências da Terra, Rio de Janeiro, Brazil; MGP: Museo di Geologia e Paleontologia, Università degli Studi di Padova, Italy; MLP: Museo de La Plata, La Plata, Argentina; MN: Museu Nacional, Rio de Janeiro, Brazil; MNHN-Bol: Museo Nacional de Historia Natural, La Paz, Bolivia (material revised at the University of Florida); MNHN-CAS: Casamayoran Collection, Muséum National d'Histoire Naturelle, Paris, France; SGO-PV: vertebrate palaeontology collections, Museo Nacional de Historia Natural, Santiago, Chile; UCMP: Museum of Paleontology. University of California. Berkeley, USA: UF: Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; YPMVPPU: Vertebrate Paleontology Princeton University Collection, Yale Peabody Museum, New Haven, Connecticut, USA.

Morphological abbreviations

C/c, upper/lower canine; DC/dc, upper/lower deciduous canine; DI/di, upper/lower deciduous incisor; DP/dp, upper/lower deciduous premolar; I/i, upper/lower permanent incisor; LLD, labiolingual diameter; M/m, upper/lower molar; MDD, mesiodistal diameter; P/p, upper/lower premolar.

Phylogenetic analysis

Cladistic methodology

The parsimony analyses were conducted with an original data matrix of 28 terminal taxa (17 interatheriids *sensu lato*) and 86 morphological characters (0–56, upper and lower dentition; 57–69, skull and mandible; 70–85, post-cranial). Some of these are used for the first time (based on personal observations of numerous specimens), whereas others have been evaluated and modified from previous research (Sinclair 1909; Hitz *et al.* 2006, 2008; Billet *et al.* 2009; Reguero & Prevosti 2010; Billet 2011), selecting the most informative characters. When no information was known for a taxon, characters were scored as missing data; when a character was not present in a taxon, it was scored as non-applicable. All characters with the character state in superscript.

Terminal taxa were chosen as the best-represented or better-known species of the families of Order Notoungulata, both temporally and phylogenetically more related to notopithecines: Notostylopidae, Oldfieldthomasiidae, Henricosborniidae, Archaeopithecidae, Interatheriidae as well as other Typotheria such as Hegetotheriidae, and Mesotheriidae. The recently described *Antofagastia turneri* is only known from a maxillary fragment with four teeth and two other partial fragments (García-López & Babot 2015; García-López 2015); its incompleteness causes significant instability in the topologies so it was excluded from the analysis. The polarization of the characters was based on out-group comparison using the most complete and geologically oldest notoungulate *Simpsonotus praecursor* Pascual, Vucetich & Fernández, 1978, a Henricosborniidae from Mealla Formation (Jujuy Province), middle–late Paleocene (Selandian–Thanetian: Marquillas *et al.* 2005).

The taxa and characters used in this analysis are explained in Supplemental Appendices 1 and 2, respectively. The data matrix (Supplemental Appendix 3) was assembled with Mesquite (Maddison & Maddison 2009). Maximum parsimony under equal weights was assumed. The computer program TNT 1.1 (Goloboff *et al.* 2008) was used to conduct heuristic searches with the Tree Bisection Reconnection swapping algorithm (TBR) using 1000 random addition sequences and saving 10 trees. Subsequent searches were repeated from previously obtained trees. Branch support was estimated by absolute Bremer support (Bremer 1990) and Symmetric Resampling (Goloboff *et al.* 2003). Two different searches were performed, using the original matrix and excluding postcranial characters.

Characters. Comments are necessary for some of the characters.

Character 3. The sequence of eruption of permanent premolars amongst notoungulates is not well known. This character has not been used in phylogenetic analyses with native ungulates. Variation is observed amongst notoungulates. For example, in toxodontids (Scott 1912) and archaeohyracids (Billet et al. 2009), eruption is in an anterior-posterior direction from P/p2 to P/p4 [3⁰], while Billet et al. (2008) and Billet & Martin (2011) described a simultaneous pattern of premolar eruption for mesotheriids [3²]. Vera (2013b) and Vera & Cerdeño (2014) noted that the Patagonian notopithecines Notopithecus, Antepithecus and Guilielmoscottia show a posterior-anterior direction of premolar replacement [3¹]. Amongst the specimens studied, the same pattern described for Notopithecus and Antepithecus was also observed, surprisingly, in other species of different groups, such as Henricosbornia lophodonta (Henricosborniidae), the Interatheriinae Federicoanava sallaensis and Brucemacfaddenia boliviensis (Bolivia), Plagiarthrus clivus (Vera et al. in progress), Protypotherium australe, Cochilius volvens, Interatherium robustum (Argentina) and Miocochilius anamopodus (Colombia).

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Character 4. Like the premolar eruption sequence (Character 3), the timing of eruption between permanent premolars and molars is not well known and is variable amongst notoungulates. For example, D/d4 are maintained during eruption of M/m3 [4¹] in the Miocene mesotheriid 'Plesiotypotherium' minus (Townsend & Croft 2010), the Miocene toxodontids Adinotherium ovinum and Nesodon imbricatus (Scott 1912), and in the Mustersan notopithecine Guilielmoscottia (Vera & Cerdeño 2014). However, P/p4 erupt before M/m3 $[4^0]$ in taxa such as Antepithecus and Notopithecus (Vera & Cerdeño 2014), the Oligocene mesotheriid Trachytherus alloxus (Billet & Martin 2011) and Eopachyrucos pliciferus, Notostylops murinus, Colbertia magellanica and Henricosbornia lophodonta. In all interatheriines showing replacement from P/p4 to P/p2 [3¹], D/d4 are maintained throughout M/m3 eruption $[4^1]$.

Character 11. P/p1 overlapped by C/c and P/p2 [11⁰] is diagnostic for *Notopithecus adapinus*, and is also observed in *Johnbell hatcheri*. In *Transpithecus obtentus*, C overlaps P1 [11¹]. This character could not be scored for *Antepithecus brachystephanus*, whose complete dentition is unknown. In *Guilielmoscottia plicifera*, P2 overlaps P1, but C is unknown.

Character 12. Hitz *et al.* (2006) scored 'absence' of P1 parastyle in *Antepithecus brachystephanus* without clarifying which specimen this was based on. P1 is in fact unknown for *A. brachystephanus* (Vera & Cerdeño 2014), so in the present data matrix the character is scored as missing.

Characters 13 and 14. These are character 10 in Hitz *et al.* (2006) and refer to the dimensions of P3–4. Here they are treated as independent characters based on observed differences. For example, in *Transpithecus obtentus* and *Punapithecus minor*, P3 is longer than it is wide $[13^1]$ whereas P4 is wider than it is long $[14^0]$.

Character 20. According to Billet (2011) and Billet *et al.* (2008), the presence of a distal cingulum in M1-2 [20⁰] is typical of basal notoungulates (e.g. oldfieldthomasiids, notopithecines, archaeopithecids). However, it is also present in some interatheriines such as *Brucemacfaddenia boliviensis*, *Santiagorothia chiliensis* and *Eopachyrucos pliciferus*.

Character 21. Amongst notopithecines, a difference was observed between the hypocone and the protocone on M1-2. *Notopithecus* has both cusps rather equally developed [21⁰], whereas in *Antepithecus* the protocone protrudes more lingually than the hypocone [21²]. The opposite is true for *Transpithecus* and *Guilielmoscottia*, whose hypocone projects more lingually than the protocone [21¹]. *Punapithecus* is like *Antepithecus* in this respect.

Characters 26 and 27. Character 13 of Hitz *et al.* (2006) is the presence of fossettes and sulcus on M1-2. Here this is treated as two independent characters: the absence or presence and characterization of the lingual sulcus in M1-2 [26], and the presence or absence of fossettes in adult M1-2 [27].

Character 32. Three different states can be observed in notoungulates i1: absence $[32^0]$ or presence $[32^1]$ of a lingual sulcus or a biphid condition $[32^2]$. The latter is scored when the tooth is completely divided into two sections by a vertical slit (called 'bicolumnar' by Reguero & Prevosti 2010), as seen in *Federicoanaya*, *Progaleopithecus* and *Protypotherium*.

Character 47. This is modified from character 37 of Billet *et al.* (2009). In the Patagonian *Notopithecus, Antepithecus, Transpithecus* and *Guilielmoscottia*, the mesial extension of entolophid on the lower molars does not reach the external face of the metalophid [47¹]. In contrast, *Acropithecus rigidus* has a very developed extension in contact with the metalophid and forms a fossettid [47²], which is also seen in *Pleurostylodon modicus*.

Character 60. The jugal being excluded from the orbit was treated as a diagnostic feature for the family Interatheriidae by Sinclair (1909). Based on the presence of this character in the cranium of *Notopithecus adapinus*, Riggs & Patterson (1935) and later Simpson (1945) suggested that Ameghino's (1897) Notopithecidae also belonged to Interatheriidae (see above). However, the crania of other genera of Notopithecinae *sensu* Simpson (1945), such as *Antepithecus*, *Transpithecus* and *Guilielmoscottia*, are completely unknown. The same applies to *Johnbell* and *Ignigena*. The feature was only recently identified in *Punapithecus* (García-López & Babot 2015) and is similar to *Notopithecus*. It cannot be evaluated for other interatheriids such as *Eopachyrucos*, *Progaleopithecus* and *Brucemacfaddenia*.

Characters 62 and 63. The presence and position of a dorsal-posterior maxillary process, Hitz *et al.*'s (2006) character 34, is evaluated as two separate characters. The exclusion of the maxillary from the dorsal border of the orbit [62^1] is a feature shared by Interatheriinae, hegetotheriids, archaeohyracids and mesotheriids, but the origin is different. In interatheriines, the frontal projects anteriorly like a sliver separating the maxillary from the orbit [63^1], which is diagnostic for this group, whereas in hegetotheriids, archaeohyracids and mesotheriids this occurs because of the significant expansion of the lacrimal in the facial region (Billet *et al.* 2008). In *Notopithecus adapinus* the maxillary comprises both the anterior and dorsal borders of the orbit [62^0], as well as in *Colbertia*, *Oldfieldthomasia* and *Acropithecus*. **Character 68.** The antorbital foramen positioned above molars in adults $[68^1]$ is diagnostic for hegetotherids and mesotherids, but it is also present in *Federicoanaya*, which is the only interatherid with this feature.

Characters 70–85. The appendicular skeleton of notopithecines is only known for *Notopithecus adapinus*, which shows significant differences compared to the most complete interatheriines, such as *Federicoanaya* and *Eopachyrucos* from Deseadan SALMA, and *Interatherium* and *Protypotherium* from Santacrucian SALMA (Vera 2012b, 2013b). Amongst studied notoungulates with humeri, the entepicondylar foramen is absent [70¹] only in *Interatherium* and hence is an apomorphic character for this taxon.

Regarding the astragalus, Sinclair (1909) considered the bilaterally symmetrical astragalar trochlea to be diagnostic of Interatheriidae, but this was only based on Santacrucian Interatheriinae. The character [79¹] was also observed in Deseadan interatheriines from Bolivia (Shockey & Anaya 2008; UF 173204 and UF 259809). According to Shockey & Flynn (2007), the astragalar foramen is common in Paleocene and Eocene notoungulates such as Colbertia magellanica (Cifelli 1983) and Eocene isotemnids (Thomashuxleya and Anisotemnus), but is rare in Oligocene mammals. The presence of this foramen [82⁰] was corroborated in *Notopithecus adapinus* by Vera (2012b). Likewise, it was scored for Transpithecus obtentus based on Ameghino (1904, fig. 63); however, the figured astragalus was not found in the MACN collection (see Cifelli 1983). In contrast, the foramen is absent [82¹] in Neogene interatheriines such as *Cochilius*, *Mio*cochilius, Interatherium and Protypotherium, which means that there is a morphofunctional differentiation between Notopithecus and interatheriines. In turn, Notopithecus and Colbertia magellanica have a well-developed peroneal tubercle in the calcaneum $[75^{\circ}]$, an obliquely orientated fibular facet on the astragalus [83⁰] (also present in Trachytherus alloxus) and an oblique medial protuberance (medial malleolar facet) on the astragalus [85⁰], whereas interatheriines lack the peroneal tubercle $[75^1]$, the fibular facet on the astragalus is proximodistally orientated [83¹] and the medial protuberance on the astragalus is vertical $[85^1]$ or absent $[85^2]$.

Sinclair (1909) mentioned that *Protypotherium* does not have a calcaneum–navicular contact. In contrast, Shockey *et al.* (2012) noted that this contact occurs in the interatheriids *Federicoanaya* and *Protypotherium*. Amongst interatheriines, a difference is noted in the calcaneum–navicular contact: both *Cochilius* (Simpson 1932a) and *Interatherium* lack the contact [78⁰], whereas it is present [78¹] in *Miocochilius*, *Protypotherium* and *Federicoanaya*, following Shockey *et al.* (2012). The absence of the calcaneum–navicular contact [78⁰] is a trait shared by *Notopithecus*, *Colbertia* and *Trachytherus*.

According to Shockey & Anaya (2008), the interatheriid tarsus shares several traits with the 'advanced Toxodontia' (sensu Cifelli 1993), including the following: well-developed, dorsoventrally orientated calcaneumfibular articulation [76¹]; absence of the astragalar peroneal process [84¹]; nearly vertical lateral and medial sides of the astragalar body [79¹]; and steeply inclined orientation of the articulation of the calcaneum and astragalus and their ectal contact. Shockey & Anava (2008) suggested that these characters provide support for excluding Interatheriidae from Typotheria, which contradicts the traditional interpretation (Simpson 1945; Cifelli 1993; Reguero & Prevosti 2010). Indeed, the interatheriine interatheriids Federicoanaya and Protypotherium included in the analysis performed by Shockey et al. (2012) form a sister group to the 'advanced Toxodontia', which is supported exclusively by postcranial synapomorphies.

Results

Analysis including postcranial characters. The first analysis yielded 66 most parsimonious trees, 273 steps long, with a consistency index (CI) of 0.40 and a retention index (RI) of 0.69. The 50% majority-rule consensus is shown in Figure 1. The main novelty of this analysis is that the Patagonian members of the traditionally known notopithecines Notopithecus, Antepithecus, Guilielmoscottia and Transpithecus are recovered as a monophyletic group, herein named as the notopithecid clade. In 72% of the trees, this group includes only the notopithecine taxa mentioned before (Fig. 2A), while in the rest of the trees Acropithecus rigidus appears nested within the clade (Fig. 2B). Differences amongst the trees are interesting. In one of the 66 possible solutions (Fig. 2A), Acropithecus rigidus splits from node A as sister taxon to the remaining taxa, node B, which is supported by four synapomorphies: I1 labiolingually compressed [6⁰]; I2-C labiolingually compressed [9¹]; P1 overlapped by C and P2 [11⁰]; and p1 overlapped by c and p2 $[36^{2}]$; $[6^{0}]$, $[9^{1}]$ and $[11^{0}]$ are autapomorphic. Under low optimization, three additional synapomorphies appear at this node: eruption of premolars in a posterior-anterior direction [3¹] (autapomorphic); a lingual shallow groove on i1 [32¹]; and absence of the astragalar peroneal process [84¹], which is present in hegetotheriids [84⁰]. Node C is at the base of the notopithecid clade, which is supported by two autapomorphic synapomorphies: poorly developed mesial extension of the entolophid on molars [47¹]; and asymmetrical astragalar trochlea with higher lateral side more oblique than the medial side [79⁰]. Under low optimization, one additional non-homoplasic synapomorphy appears supporting node C: absence of mesial cingulid on m1-2 [53¹]. Two lineages can be recognized within the notopithecid clade.



Figure 1. A 50% majority-rule consensus tree (273 steps, CI = 0.40, RI = 0.69) of the 66 most parsimonious trees obtained in the first phylogenetic analysis using the original data matrix and under equally weighted characters. Numbers above branches indicate the percentage of times that a particular group was recovered. Numbers below branches indicate absolute Bremer support (left) and Symmetric Resampling values (right).

B. Vera



Figure 2. Two of the 66 most parsimonious trees obtained in the first phylogenetic analysis, showing different configurations of the ingroup: **A**, *Acropithecus rigidus* outside the notopithecid clade; **B**, *Acropithecus rigidus* within the notopithecid clade; the name 'INTERATHERIINAE' is used to save space and refers to species from *Santiagorothia chiliensis* to *Interatherium robustum* of **A**. Upper-case letters indicate nodes. Black and white circles indicate autapomorphic and homoplastic synapomorphies, respectively. Numbers above and below circles indicate characters and states, respectively.

First, *Transpithecus obtentus* + *Guilielmoscottia plicifera* (Fig. 2A, node D), which is characterized by five unambiguous synapomorphies: mesial cingulum absent on P3–4 [17¹]; mesial cingulum absent on M1–3 [18¹]; lingual sulcus present on P3 [24¹]; lingual sulcus present on P3 [24¹]; lingual sulcus present on P4 [25¹]; and p2–3 with a labiodistally well-developed protoconid [37⁰]. Secondly, the clade *Notopithecus adapinus* + *Antepithecus brachystephanus* (node E) is supported by one unambiguous synapomorphy: eruption of P/p4 before M/m3 [4⁰], also present in the interatherine *Eopachyrucos* and the mesotheriid *Trachytherus*. The first clade (*T. obtentus*, *G. plicifera*) was identified by García-López & Babot (2015) by two synapomorphies

[17¹] and [18¹], whereas *Notopithecus* and *Antepithecus* were not recovered as a clade.

It is interesting to note the position of the 'henricosbornid-olfieldthomasid' clade (Kibenikhoria, (Oldfieldthomasia, Henricosbornia)) as the sister group (Fig. 2A, node G) of the clade including interatheriids + hegetotheriids mesotheriids (node +I). This 'henricosboriid-oldfieldtomasiid clade' (node G) also separates the Patagonian notopithecines (node C) from the basal interatheriids and interatheriines. Within this clade (node G), the henricosborniid Henricosbornia lophodonta is the sister group of a more inclusive group formed by the oldfielthomasiids Kibenikhoria and Oldfielthomasia

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(node H) due to a single synapomorphy: presence of mesial extension(entostylid) on the metalophid of lower molars [51⁰]. In the present analysis the families Oldfield-thomasiidae and Henricosborniidae are paraphyletic assemblages, as noted by Billet (2011). A large clade includes the remaining taxa (node I), linked to the 'henricosboriid-oldfieldtomasiid clade' by node F which is supported by four synapomorphies: P3 longer than it is wide [13¹]; labial fossettes of P3–4 absent in adults [27¹]; i3 < i2 (autapomorphic) [29¹]; and cingulid uniting hypoconulid and entonconid on m3 absent [56⁰].

The present analysis does not identify Interatheriinae as a monophyletic group, as in other analyses (Hitz et al. 2006; Reguero & Prevosti 2010). Instead, 'basal interatheriids' sensu Hitz et al. (2006) (Punapithecus, Ignigena and Johnbell) + interatheriinae (nodes L-T) form a paraphyletic group related to node U, which comprises mesotheriids (Trachytherus) + hegetotheriids (Hegetotherium mirabile + Pachyrukhos moyani, node V). Five synapomorphies separate *Punapithecus* from other interatheriids. node J: P4 with DLL < DMD (autapomorphic) [14¹]; mesial cingulum absent on P3-4 $[17^{1}]$; mesial cingulum absent on M1-3 [18¹]; M1-2 DLL<DMD (autapomorphic) $[22^{1}]$; and hypocone on M3 present $[23^{1}]$. The clade including the Interatheriinae defined by Hitz et al. (2000) plus Eopachyrucos and remaining taxa (node L) is supported by seven synapomorphies: hypsodont cheek teeth (autapomorphic) $[2^1]$; parastyle sulcus deep on P3-4 [16¹]; lingual sulcus present on P3 [24¹]; lingual sulcus present on P4 [25^{1}]; bifid lingual sulcus on M1-2 [26^{1}]; p1 overlapping by c $[36^{1}]$; and ectoflexid on m1-2 reach until the base of the crown (autapomorphic) $[48^{1}]$. Between nodes I and P, the interatherids show a successive phylogenetic sequence of the species Punapithecus minor, Ignigena minisculus, Johnbell hatcheri, Santiagorothia chiliensis, Federicoanaya sallaensis, Brucemacfaddenia boliviensis, Eopachyrucos pliciferus and Plagiarthrus clivus, which is the sister taxon of a more inclusive clade (node Q). Within the latter, two lineages can be recognized amongst interatheriines. In the topology of Fig. 2A, node R (Progaleopithecus tournoueri (Miocochilius anamopodus, Protypotherium australe)) is supported by two unambiguous synapomorphies: a single lingual sulcus on M1–2 $[26^{\circ}]$, and a deep hypoflexid on m3 [55²]. *Protypotherium* forms a monophyletic group with Miocochilius supported by three synamoporphies: hypocone absent on P3–4 $[15^{0}]$; talonid < trigonid on p4 $[43^{0}]$; and auditory bullae moderately developed $[67^{1}]$. The close relationship between Deseadan Progaleopithecus and Santacrucian Protypotherium was previously suggested by Cifelli (1993). As he noted, the data in his analyses were insufficient to indicate such branching within the subfamily (Cifelli 1993, p. 208). The same two groups were identified by Reguero et al. (2003, fig. 8). Node T links Interatherium robustum and Cochilius

volvens based on two unambiguous synamoporphies: height of the mandibular horizontal ramus at the m2 level is at least twice as high as at the incisor level [57^{1}]; and auditory bullae moderately developed [67^{1}]. The clade *Interatherium* + *Cochilius* is the sister group of the clade mesotheriids + hegetotheriids (node U). Both clusters are grouped based on three synamopomorphies (node S): c is absent or smaller than incisors [34^{0}]; the talonid is larger than or equal to the trigonid on p2 [41^{2}]; and short rostrum [58^{0}].

The polytomies observed in the majority consensus tree (Fig. 1) are due to the shifting position of *Acropithecus rigidus, Eopachyrucos pliciferus* and the 'henricosbornidolfieldthomasid' clade (node G, Fig. 2A), causing low values of branch support; in turn, there are no synapomorphies uniting *Ignigena minisculus* and *Johnbell hatcheri*. With respect to the position of *Eopachyrucos pliciferus*, Hitz *et al.* (2000), Reguero *et al.* (2003) and Reguero & Prevosti (2010) recognized this species as the most basal member of the interatheriines, whereas Hitz *et al.* (2006) stated that *E. pliciferus* could not be considered a member of Interatheriinae. The present analysis shows a different situation, where *E. pliciferus* is not only included in Interatheriinae but in some topologies it is in a more derived position within the group (Fig. 2A).

The clade formed by mesotheriids + hegetotheriids (Fig. 2A, node U) is supported by 11 synapomorphies: distribution of enamel on cheek teeth is discontinuous or absent (autapomorphic) $[0^1]$; parastyle is absent on P1 $[12^0]$; there is a shallow parastyle sulcus on P3-4 $[16^0]$; lingual sulcus is absent on P3 $[24^0]$; lingual sulcus is absent on P3 $[24^0]$; lingual sulcus is absent on P4 $[25^0]$; jugal is not reduced $[60^0]$; descending process of the maxillae is absent $[61^0]$; sliver of frontal is not anteriorly projected $[63^0]$; lacrimal is external $[64^1]$; antorbital foramen is above molars in adults $[68^1]$; and the astragalar trochlea has parallel sides with the lateral side higher than the medial side (autapomorphic) $[79^2]$. Reguero & Prevosti (2010) also recovered the 'unnamed clade' Hegetotheriidae + Mesotheriidae diagnosed by five unequivocal synapomorphies.

As mentioned above, the group of Patagonian notopithecines including *Notopithecus*, *Antepithecus*, *Transpithecus* and *Guilielmoscottia*, was recovered as a clade in the majority of the 66 trees (Fig. 2A). However, in the remaining trees (28%), the Archaeopithecidae *Acropithecus rigidus* (represented by AMNH 28782) appears grouped with the notopithecines (node B, Fig. 2B), which is supported by three synapomorphies: i1–2 implantation no procumbent [33⁰]; poorly developed mesial extension of the entolophid on molars (autapomorphic) [47¹]; and asymetrical astragalar trochlea with higher lateral side that is more oblique than the medial side (autapomorphic) [79⁰]. Only the non-procumbent implantation on i1–2 is a common character between *Acropithecus* and notopithecines, while [47²] is an autapomorphy for *Acropithecus* and [79] is not known for this taxon. Under low optimization, three additional unambiguous synapomorphies support node B: $[44^1]$, $[45^1]$ and $[61^1]$. Within node B (Fig. 2B), *Acropithecus* appears as a sister taxon of a more inclusive clade grouped by *Transpithecus* and *Guilielmoscottia*, which is supported by three unambiguous synapomorphies: P3–4 mesial cingulum absent $[17^1]$; hypocone more developed than protocone and lingually protruding on M1–2 $[21^1]$; and p2–3 with a labiodistally well-developed protoconid $[37^0]$. In this topology (Fig. 2B), no assemblages were recovered within node G.

Support values (Bremer and Symmetric Resampling) are relatively low in the topology (Fig. 1), excepting some nodes. These parameters are a measure of the robustness of the cladogram; in this respect, the values obtained indicate a moderate fit between them and the data, due in part to the presence of homoplasy and missing entries (ambiguities) for many species.

Analysis excluding postcranial characters. Eliminating characters 70-85 (Supplemental Appendix 2) from the analysis, 96 most parsimonious trees were obtained, 239 steps long, with a CI of 0.38 and RI of 0.70. The strict consensus tree is shown in the Figure 3. The grouping of Patagonian notopithecines, such as recovered in previous analyses, does not appear in any topology amongst the 96 solutions. Except for the most basal taxa which form a polytomy (Fig. 3, nodes A and B), the relationships amongst interatheriids, hegetotheriids and mesotheriids (Fig. 3, node C) remain similar to that shown in Figure 2A, in particular for the clades including the most derived taxa (nodes D-F). It is interesting to note that when performing the 50% majority-rule consensus (not shown), Guilielmoscottia + Transpithecus, and Notopithecus + Antepithecus each group together. In addition, the clade formed by Kibenikhoria, Henricosbornia and Oldfieldthomasia is also recovered.

Discussion

Phylogeny

The most important result obtained in the phylogenetic analysis is that a notopithecid clade is identified. The Patagonian members of the classically named notopithecines *Notopithecus adapinus*, *Antepithecus brachystephanus*, *Transpithecus obtentus* and *Guilielmoscottia plicifera* form a monophyletic group. Within this group, two more inclusive clades are identified: *Transpithecus* and *Guilielmoscottia*, sharing six ambiguous synapomorphies, and *Notopithecus* and *Antepithecus*, with a single synapomorphy. In the 50% majority-rule consensus, the notopithecid clade is recovered in 72% of the topologies (Fig. 1). This particular configuration grouping Patagonian notopithecine taxa (Fig. 2A) is supported by two autapomorphies, one of them being a postcranial character; under low optimization, one additional synapomorphy supports the clade. In the minority of the topologies (Fig. 2B), *Acropithecus rigidus* is nested into the notopithecine clade as the sister taxon of *Guilielmoscottia plicifera* and *Transpithecus rigidus*. As mentioned above, the family Archaeopithecidae is presently under revision by the author, which is why only *Acropithecus rigidus* (represented by the most complete known specimen, AMNH 28782) is included. Clearly, *Acropithecus* behaves like an erratic taxon due to its variable phylogenetic position, introducing instability into the analysis.

When postcranial characters are excluded, the Patagonian notopithecine taxa are not recovered as a clade in any topology. In this sense, and as was concluded by Shockey *et al.* (2012), the inclusion of postcranial data strongly influences tree topology, mainly concerning the relationships of basal taxa, even though notoungulate skeletons are scarcely known. The asymmetrical astragalar trochlea with the lateral side higher and more oblique than the medial side is a synapomorphy that unequivocally supports the notopithecid clade. However, this feature is only reliably known in *Notopithecus*, doubtfully in *Transpithecus* and unknown in *Antepithecus* and *Guilielmoscottia*.

On one hand, the notopithecid clade comprises solely of Patagonian species from the Casamayoran and Mustersan SALMAs (middle-late Eocene) and excludes the extra-Patagonian members of notopithecines such as *Punapithecus minor*, *Ignigena minisculus* and *Johnbell hatcheri*. On the other hand, the notopithecid clade is separated from, but phylogenetically related to, basal interatheriids and interatheriines. The present analysis places *Guilielmoscottia plicifera* within the notopithecid clade, contrary to Ameghino's (1897) suggestion but agreeing with Schlosser (1923).

It is interesting to note the basal position of the notopithecid clade (Fig. 2A, node C) as the sister group of a major unnamed clade that includes henricosborniid + some oldfieldthomasiids + basal interatheriids + interatheriinae + mesotheriids + hegetotheriids (Fig. 2A, node F). This situation reflects, in this analysis, the lack of synapomorphies to support the traditional definition of the family Interatheriidae sensu lato and the need to examine relationships within this group. One character - jugal not being part of the orbit – has traditionally been considered a synapomorphy for the family Interatheriidae; however, it is homoplastic in the present analysis, as it is shared by interatheriines and Notopithecus adapinus. In turn, the frontal projecting anteriorly like a sliver that separates the maxillary from the orbit $[63^1]$ is absent in N. adapinus and constitutes a diagnostic character for interatheriines.

As mentioned above, *Punapithecus minor*, *Ignigena minisculus* and *Johnbell hatcheri* are not included in the



Figure 3. Strict consensus tree of the 96 most parsimonious trees (239 steps, CI = 0.38, RI = 0.70) obtained under equally weighted characters, excluding the postcranial characters. Upper-case letters indicate nodes mentioned in the text.

same group as the Patagonian species. Instead, they are nested with interatheriids, making them basal interatheriids, in agreement with Hitz *et al.* (2006).

With regard to the family Archaeopithecidae, *Acropithecus rigidus* appears as the sister group of Typotheria *sensu* Reguero & Prevosti (2010) that includes the notopithecid clade, but disagrees with the hypothesis of the authors grouping *A. rigidus* with *Oldfieldthomasia*; in turn, in a minority of the topologies *A. rigidus* also grouped into the notopithecid clade. However, the systematics of archaeopithecids is still under revision and further study should help to clarify their taxonomy and affinities.

The phylogenetic hypothesis presented here supports the grouping of species called Notopithecinae by Simpson (1967), but excluded from the interatheriids, and provides a basis for further studies and interpretations. Applying the phylogenetic system of taxonomy (de Queiroz & Guathier 1992), the name 'notopithecid' is proposed to define the node-base clade as the clade stemming from the immediate common ancestor of the species represented by *Notopithecus adapinus*, *Antepithecus brachystephanus*, *Transpithecus obtentus* and *Guilielmoscottia plicifera*. The exclusion of notopithecids from Interatheriidae sensu *lato* has relevance for the palaeobiogeography and evolution, as *Ignigena minisculus* is the oldest interatheriid (Fig. 4).

The notopithecid clade herein identified is phylogenetically characterized by two unequivocal synapomorphies: the little-developed mesial extension of the entolophid on lower molars [47¹]; and the asymmetrical and shallow astragalar trochlea [79⁰]. It includes the smallest known species of Notoungulata, with an estimated body mass of 1-5 kg (Vera 2013b). Other plesiomorphic features (Figs 5, 6) that characterize these taxa are: complete dentition without diastemata or small spaces between the anterior teeth: lophodont and brachydont dentition; continuous cheek tooth enamel around the crown and lack of a cement cover; eruption sequence of upper and lower premolars in posterior-anterior direction; I1 lingually compressed and subequal in size to, or slightly different from, I2; upper canine similar to incisors, labially compressed and without labial sulcus; parastyle absent in P1; P3-4 without hypocone and with shallow parastyle sulcus; P4-M3 with two labial fossettes and one central fossette, showing a 'face pattern' on occlusal surface; ectolophe undulated due to well-differentiated parastyle, paracone, metacone and metastyle columns; mesial cingulum on upper molars present in N. adapinus and A. brachystephanus and absent in T. obtentus and G. plicifera; distal cingulum and entolophe (uniting protocone and hypocone) present on molars; P4-M2 width greater than length; hypocone of M3 absent or indistinguishable; lower incisors labially compressed, not procumbent and with a lingual shallow groove; lower canine similar to and slightly larger than incisors; p3-4 with postmetacristid;

p2-4 with talonid smaller than trigonid; p4 not molarized; lower molars with trilobed lingual face, paralophid well developed and parallel to the metalophid, both posteriorly inclined, hypolophid well developed, labially convex and semicircular, conferring a mushroom-like talonid, and little-developed mesial extension of the entolophid; short and low rostrum; small descending process of the maxilla; moderately expanded root of the zygomatic arch; reduced jugal; maxilla forms the dorsal border of the orbit and the sliver of frontal not anteriorly projected; lacrimal external; prominent auditory bullae; horizontal ramus of the mandible low with nearly constant height; humerus with entepicondylar foramen; proximal facet of the radius is subrectangular; tibia much larger than fibula and without proximal fusion; calcaneum with a short neck, less-inclined cuboid facet, well-developed peroneal tubercle and inclined fibular facet; and astragalus with an asymmetrical and shallow trochlea, without astragalar-cuboid contact, oblique medial protuberance and dorsal foramen.

It is worth remarking that most of the cranial and postcranial characters are based on Notopithecus, which is the most complete and best-known notopithecid. The finding of an almost complete skeleton of N. adapinus made it possible to describe, for the first time, the characteristics of the tarsus within this group, which revealed significant differences from interatheriines (Vera 2012b, 2013b). The tarsus of N. adapinus differs from Santacrucian Interatherium and Protypotherium and Deaseadan Federicoanaya in having a shorter neck, less-inclined cuboid facet, and inclined fibular facet on the calcaneum. The astragalus has an asymmetrical and shallow trochlea and a dorsal foramen. In turn, the well-developed peroneal tubercle on the calcaneum, oblique astragalar medial protuberance, the lack of astragalar-cuboid contact and the presence of an astragalar foramen are shared with the basal notoungulate Colbertia magellanica from the Itaboraian SALMA.

Palaeobiogeographical and biostratigraphical contexts

Keeping in mind the previous concept of notopithecines as a subfamily of Interatheriidae that comprised species from Chile and the Puna, it was thought that the geographical distribution of this group included regions as distant as central Patagonia, the Argentine Puna and central Chile. In particular, the co-occurrence of both subfamilies, notopithecines (*Johnbell*) and interatheriine interatheriids (*Santiagorothia*), in Tinguiririca levels, Tinguirirican SALMA (Chile), was biogeographically relevant (Wyss *et al.* 1990; Flynn *et al.* 2003; Hitz *et al.* 2006). Taking into account this distribution, with small-sized interatheriid species inhabiting lower latitudes (*Punapithecus, Ignigena* and *Johnbell*) and larger species inhabiting higher latitudes (Patagonian notopithecines), Hitz *et al.* (2006)

Phylogenetic revision of the South American notopithecines



Figure 4. Stratigraphical position of the taxa relative to the phylogeny obtained in the first analysis. South American Land Mammal Ages after Reguero & Prevosti (2010) and Woodbourne *et al.* (2014).

suggested a geographical provincialism or a clinal variation to explain the pattern. Based on the recent systematic and phylogenetic revisions (Vera 2012a, b, 2013b, 2014; Vera & Cerdeño 2014) and the present study, the monophyletic group including the Patagonian species *Notopithecus adapinus, Antepithecus brachystephanus, Transpithecus obtentus* and *Guilielmoscottia plicifera* implies restricted stratigraphical and geographical distributions for the new notopithecid clade here defined, which is limited to the middle-late Eocene levels of the Sarmiento Formation in Patagonia. Hence, the presence of *Johnbell* and *Santiagorothia* at the same locality does not imply the co-occurrence of the two subfamilies.

With respect to other records of notopithecids, Ortega (unpublished report in GEOBOL, La Paz, 1967; Marshall *et al.* 1983) mentioned *Notopithecus* in Bolivia.



Figure 5. Upper dentition of notopithecids in occlusal view. **A**, *Notopithecus adapinus*, MACN-A 10829, left maxillary fragment with C–M3; **B**, *Antepithecus brachystephanus*, MACN-A 10859a, right maxillary fragment with P2–M2 (reversed); **C**, *Transpithecus obtentus*, MNHN CAS 2700, right maxillary fragment with I1–C and P2–M3 (reversed); **D**, *Guilielmoscottia plicifera*, MLP 61-VIII-3-17, left maxillary fragment with P1–M3; **E**, line drawing showing main dental structures described in the text, modified from Vera (2013b). Scale bar: 5 mm.



Figure 6. Lower dentition of notopithecids in occlusal view. **A**, *Notopithecus adapinus*, FMNH P14718a, right mandibular fragment with i2–m2; **B**, *Antepithecus brachystephanus*, AMNH 28849, left mandibular fragment with p3–m3 (reversed); **C**, *Transpithecus obtentus*, AMNH 28861, right mandibular fragment with p2–m3; **D**, *Guilielmoscottia plicifera*, MLP 61-IV-9-10, right mandibular fragment with p2–m3. **E**, line drawing showing main dental structures described in the text, modified from Vera (2013b). Scale bar: 5 mm.



Figure 7. Palaeontological sites (black squares) in the Sarmiento Formation from which specimens of notopithecids have been recorded.

Unfortunately, this specimen has not been described or figured, nor was it found in the GEOBOL collections (Madden pers. comm. 2010). Tejedor et al. (2009) mentioned, but did not figure, dental remains ascribed to Notopithecus from Laguna Fría (Chubut Province), whose horizons were dated between 49.5 and 45 Ma (older than middle-late Eocene). Antoine et al. (2012) listed the presence of the Notopithecinae cf. Notopithecus sp. in the middle Eocene of Contamana, Peru, but the authors provided neither description nor figures of this specimen. There are some specimens in the MACN collection catalogued by Bordas as being from a Casamayoran locality near San Rafael, Mendoza Province, Argentina; however, in the vicinity of the city of San Rafael, the known fossiliferous Cenozoic levels belong to the late Miocene-Pliocene Río Seco del Zapallo Formation; the specimens are indeed notopithecids (Vera, 2013b), but they probably came from Patagonia (Forasiepi pers. comm. 2012). More recently, Silva et al. (2014) also referred to Notopithecinae some lower teeth from the Guabirotuba Formation, Curitiba Basin (southern Brazil), without providing further data. As a whole, these extra-Patagonian records are still uncertain and, therefore, can be discarded as definite notopithecids. If proven, they would extend the chronological range of notopithecids back to the early Eocene (Fig. 4), and the geographical extent of the group to such low latitudes as Peru and Brazil.

Members of the notopithecid clade as identified here are restricted to the Sarmiento Formation, which outcrops in central Chubut Province and north-east Santa Cruz Province (Fig. 7). Stratigraphically, the biochron of the group spans from the Barrancan Subage (Casamayoran SALMA) to Mustersan SALMA (middle–late Eocene; Fig. 4; Woodbourne *et al.* 2014).

Conclusions

The analyses reported here are based on an exhaustive phylogenetic analysis of all Eocene taxa called Notopithecinae and evaluate their relationships with basal interatheriids, Interatheriinae and other groups of notoungulates. Taxa usually included in the subfamily Notopithecinae (Simpson 1945, 1967; Cifelli 1993) had never been phylogenetically revised by means of a cladistic analysis. New dental and postcranial characters were added to previously published data, augmenting and improving observations with respect to previous studies on interatheriids: some of these characters are evaluated in notoungulates for the first time. The most relevant result of the analysis is that species traditionally known as Notopithecinae (Notopithecus adapinus, Antepithecus brachystephanus, Transpithecus obtentus and Guilielmoscottia plicifera) were recovered as a monophyletic group for the first time, changing the traditional concept of this assemblage. Two different searches were performed. When the original matrix was analysed, the notopithecid clade was recovered in most of the topologies supported by two synapomorphies: poorly developed mesial extension of the entolophid on molars and asymmetrical astragalar trochlea with the lateral side higher and more oblique than the medial. In a minor number of topologies recovered Acropithecus rigidus appears nested with the notopithecines, forming a more inclusive clade with Guilielmoscottia and Transpithecus; this hypothesis should be tested in future analyses, after completing taxonomic revision of Archaeopithecidae or when better evidence becomes available. Excluding postcranial characters, the Patagonian notopithecines are not recovered as a monophyletic group, meaning that they are potentially informative in phylogenetic analysis despite the scarcity of postcranial data in many taxa.

The basal interatheriids *Ignigena* and *Jonhbell* (central Chile) and *Punapithecus* (Argentinean Puna) are excluded from the Patagonian assemblage herein identified for the first time. In addition, the recognized synapomorphies exclude the notopithecid clade from other interatheriid interatheriines. In this sense, the traditional definition of the family Interatheriidae should be re-examined.

Oldfieldtomasiidae and Henricosborniidae are defined as paraphyletic groups; the henricosborniid Henricosbornia appears nested with Olfieldthomasia and Kibenikhoria. In some topologies, this 'henricosborniidoldfieldthomasiid clade' appears as the sister group of a large clade that includes the notopithecid clade, basal interatheriids, interatheriines, mesotheriids and hegetotheriids; in other topologies, in turn, the 'henricosborniid-oldfieldthomasiid clade' appears in a more derived position separating interatheriids from the notopithecid clade.

Interatheriinae is not identified as a monophyletic group. Interatheriines and basal interatheriids are shown to be a paraphyletic assemblage relative to mesotheriids and hegetotheriids. The earliest divergent taxa of interatheriines are *Santiagorothia chiliensis* and *Eopachyrucos pliciferus*, but in some topologies *E. pliciferus* appears in a more derived position than in previous analyses. Two well-differentiated lineages of interatheres are identified: a clade with *Progaleopithecus tournoueri* + (*Miocochilius anamopodus, Protypotherium australe*), and another with *Interatherium robustum* + *Cochilius volvens*.

The notopithecid clade identified here and previous taxonomic revisions of their species constitute strong support to consider this group at a familial level, a hypothesis to be tested with ulterior analyses including archaeopithecids, for example. A modified diagnosis is provided for this group of Eocene notoungulates including the Patagonian species Notopithecus adapinus, Antepithecus brachystephanus, Transpithecus obtentus and Guilielmoscottia plicifera. The exclusion of the Chilean basal interatheriids (Jonhbell hatcheri and Ignigena minisculus) and Punapithecus from the notopithecid clade has biostratigraphical and geographical implications. Both were thought to represent the latest record of the group (early Oligocene, Tinguirirican SALMA), which implied the coexistence of the two subfamilies of Interatheriidae as well as a distribution outside Patagonia. Based on results presented here, and until other extra-Patagonian records of notopithecids are confirmed, the stratigraphical and geographical distribution of the group is restricted to the middle-late Eocene levels of the Sarmiento Formation in central Chubut Province and north-east Santa Cruz Province, Patagonia, Argentina.

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Supplemental material

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