



A new nothrotheriid xenarthran from the early Pliocene of Pomata-Ayte (Bolivia): new insights into the caniniform–molariform transition in sloths

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Tardigrade xenarthrans are today represented only by the two tree sloth genera *Bradypus* and *Choloepus*, which inhabit the Neotropical rainforests and are characterized by their slowness and suspensory locomotion. Sloths have been recognized in South America since the early Oligocene. This monophyletic group is represented by five clades traditionally recognized as families: Bradypodidae, Megalonychidae, Mylodontidae (†), Megatheriidae (†) and Nothrotheriidae (†). A new nothrotheriid ground sloth represented by a dentary and several postcranial elements, *Aymaratherium jeani* gen. nov., sp. nov., from the early Pliocene locality of Pomata-Ayte (Bolivia) is reported. This small- to medium-sized species is characterized especially by its dentition and several postcranial features. It exhibits several convergences with the 'aquatic' nothrotheriid sloth *Thalassocnus* and the giant megatheriid ground sloth *Megatherium* (*M.*) *americanum*, and is interpreted as a selective feeder, with good pronation and supination movements. The tricuspid caniniform teeth of *Aymaratherium* may represent a transitional stage between the caniniform anterior teeth of basal megatherioids and basal nothrotheriids (1/1C-4/3M as in *Hapalops* or *Mionothropus*) and the molariform anterior teeth of megatheriids (5/4M, e.g. *Megatherium*). To highlight the phylogenetic position of this new taxon among nothrotheriid sloths, we performed a cladistic assessment of the available dental and postcranial evidence. Our results, derived from a TNT treatment of a data matrix largely based on a published phylogenetic data set, indicate that *Aymaratherium* is either sister taxon to *Mionothropus* or sister to the clade Nothrotheriini within Nothrotheriinae. They further support the monophyly of both the Nothrotheriinae and the Nothrotheriini, as suggested previously by several authors.

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INTRODUCTION

Xenarthra constitute one of the more peculiar groups of the South American endemic mammalian faunas, and are recognized as one of four main clades among placental mammals (O’Leary *et al.*, 2013). Xenarthrans include the sloths or Tardigrada, the anteaters or Vermilingua, and the armored xenarthrans, or Cingulata (armadillos and their fossil kin, Glyptodontidae and Pampatheriidae) (Pujos *et al.*, 2012c). Sloths and anteaters are sister clades and constitute Pilosa, the sister group of Cingulata (Gaudin & McDonald, 2008; Pujos *et al.*, 2012c). The three xenarthran clades are represented in modern ecosystems of South America. Tardigrada are today restricted to tree sloths that inhabit the Amazonian and Central American rainforests. According to the most recent and comprehensive phylogenetic analysis (Gaudin, 2004), sloths are distributed among five clades (generally considered as families, but also as superfamilies or subfamilies depending on the authors): Nothrotheriidae, Megalonychidae and Megatheriidae (grouped as Megatherioidea), Mylodontidae (or Mylodontoidea; St-André *et al.*, 2010) and the monogeneric Bradypodidae (Gaudin, 2004). Several small-sized forms such as *Hiskatherium*, *Hapalops* and *Analcimorphus* are commonly included in Megatherioidea (Pujos, De Iuliis & Mamani Quispe, 2011). Recently, De Iuliis, Gaudin & Vicars (2011) performed a phylogenetic analysis of nothrotheriids at the genus level, concluding that Nothrotheriinae and *Thalassocnus* are sister groups.

Over the last two centuries, palaeontologists have concentrated their investigations in South America mainly in the arid regions of Patagonia, whereas the northern areas of South America, and most particularly the Andean and Amazonian regions, have been less intensely studied. However, field efforts conducted in Bolivia over the past decades have allowed for the discovery of several new fossil-bearing localities (Marshall, Hoffstetter & Pascual, 1983; St-André, 1999). These localities, primarily from the Departments of Chuquisaca, La Paz, Oruro, Potosi and Tarija, have yielded well-diversified vertebrate faunas. The most notable Bolivian Cenozoic vertebrate localities include those from the Palaeocene [Tiupampa, early Palaeocene-Tiupampan South American Land Mammal Age (SALMA): de Muizon, 1991; Vilcapujio, late Palaeocene: Sigé *et al.*, 1984; Zack, Kay & Madden, 1999], late Oligocene (Salla, Deseadan SALMA: Hoffstetter, 1968a; Lacayani,

?Deseadan SALMA: Hoffstetter *et al.*, 1971a), middle and late Miocene (e.g. Cerdas and Choquecota, Collocuran SALMA: Croft *et al.*, 2009; St-André, 1994; Quebrada Honda, Laventan SALMA: Croft, 2007; Achiri, Chasicuan SALMA: Pujos *et al.*, 2012a), Pliocene (e.g. Ayo Ayo-Viscachani and Pomata-Ayte, Montehermosan SALMA: Hoffstetter *et al.*, 1971b; Hoffstetter, Martinez & Tomasi, 1972) and Pleistocene (e.g. Tarija, Ensenadan SALMA: Hoffstetter, 1963; Nuapua, Lujanian SALMA: Hoffstetter, 1968b).

The Pomata-Ayte locality, considered early Pliocene in age, is situated in the Oruro Department (Province of Carangas) near the city of the same name (Fig. 1), and was first reported by Hoffstetter *et al.* (1972). Hoffstetter *et al.* (1972), Marshall *et al.* (1983), Hoffstetter (1986), Marshall & Sempere (1991) and St-André (1994) provided preliminary faunal lists. The vertebrate assemblage includes the macraucheniid litoptern *Macrauchenia* sp. (St-André, 1994), the notoungulate toxodontid *Posnanskytherium* cf. *viscachanense* and another toxodontid of uncertain affinities (St-André, 1999), several pilosan xenarthrans including the mylodontid *Simomyodon uccasamamensis* (St-André, 1994 and St-André *et al.*, 2010; = *Simotherium uccasamamense*) and the megatheriid *Megatherium* (*Megatherium*) *altiplanicum* (see St-André & De Iuliis, 2001), three armored cingulates including a glyptodontid, a dasypodid and the pampatheriine *Plaina* sp. (see de Paula Couto, 1983), a rodent, and a giant carnivorous phorusrhacoid bird (St-André, 1994).

This fauna was collected from the Umala Formation, which lies above the Totorá and Pomata Formations (St-André, 1994). The fossiliferous levels occur approximately 100 m above a tuff that corresponds to the ‘Toba 76’ according to St-André (1994). This tuffaceous level was dated by Marshall *et al.* (1983), using $^{40}\text{K}/^{40}\text{Ar}$, as ranging between 5.42 ± 0.6 and 5.97 ± 0.4 Ma, which corresponds to the Montehermosan SALMA (latest Miocene/early Pliocene). This represents a floor age for the vertebrate locality. The upper parts of these levels are eroded and unconformably covered by Pleistocene alluvial deposits, from which remains of the Pleistocene macraucheniid litoptern *Macrauchenia patachonica* were recovered (St-André, 1994).

Our palaeontological campaigns in the Pomata-Ayte area (2012 and 2015) resulted in: (1) better appreciation of the great diversity of the Montehermosan fauna, which had previously only been

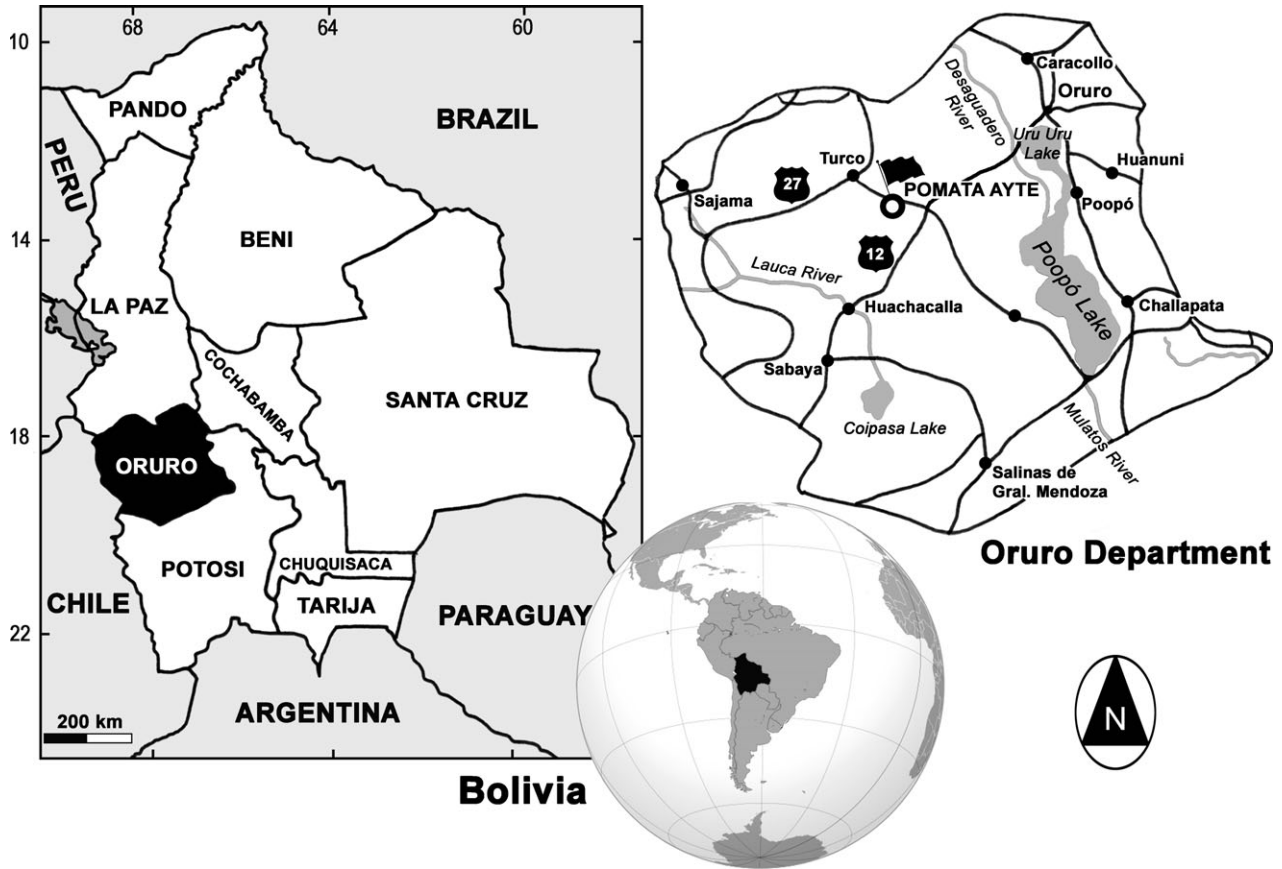


Figure 1. Location map of the fossil-bearing locality of Pomata-Ayte. Left and centre, general location map; right, geographical location of Pomata-Ayte from which *Aymaratherium jeani* gen. nov., sp. nov. was recovered.

partially described; (2) confirmation of the existence of a Pleistocene assemblage comprising *M. patachonica* (as noted above), but also a gomphotheriid proboscidean (cf. *Cuvieronius*), a machairodontine felid (cf. *Smilodon*), a giant megatheriine ground sloth (*Megatherium* sp.) and a glyptodontid (*Glyptodon* sp.); and (3) the first report of a late Miocene vertebrate fauna older than the commonly recognized Montehermosan fauna. In this older fauna (the dating and study of the relevant vertebrate specimens are in process), the mesotheriid notoungulates (cf. *Plesiotypotherium*) are extremely abundant and sloths are absent, whereas the reverse situation is observed in the Montehermosan assemblage.

In this work we describe a new small- to medium-sized nothrotheriid sloth from the Montehermosan SALMA of Pomata-Ayte (Bolivia). We assess its phylogenetic affinities with other Nothrotheriidae, drawing on the previous work of De Iuliis *et al.* (2011). Lastly, we describe the cuspid-and-lophid arrangements of its teeth, especially the caniniform tooth, and propose a caniniform/molariform transition pattern during sloth evolution.

MATERIAL AND METHODS

The descriptions and comparisons are based on the investigation of previously known specimens of Megatherioidea housed in the following institutions: AMNH, American Museum of Natural History, New York, USA; BMNH, British Museum of Natural History, London, UK; FMNH, Field Museum of Natural History, Chicago, USA; LACM, Los Angeles County Museum, Los Angeles, USA; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MCL, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; LV, Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Bogota, Colombia (material from ‘La Venta’ cf. Villarroel, 1998); MNHN, Muséum national d’Histoire naturelle, Paris, France; MNHN-Bol, Museo Nacional de Historia Natural de Bolivia, La Paz, Bolivia; MPM-PV, Museo Regional Provincial Padre M. J. Molina, Río Gallegos, Argentina; MUSM, Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima, Peru; NRM, Naturhistoriska

Riksmuseet, Stockholm, Sweden; SMNK, Staatliche Museum für Naturkunde, Karlsruhe, Germany; UATF, Universidad Autónoma Tomás Frías, Potosí, Bolivia; UCMP, Museum of Paleontology, University of California, Berkeley, USA; UNI, Universidad Nacional de la Ingeniería, Lima, Peru; UF, University of Florida, Florida State Museum, Gainesville, USA.

A revision of the collection of the MNHN-Bol in La Paz (Bolivia) and preparation in 2013 and 2015 of the newly discovered specimens during the 2012 and 2015 field campaigns in the Montehermosan SALMA of Pomata-Ayte resulted in the identification of a third sloth, a nothrotheriid, and the main subject of the current report. This new small- to medium-sized sloth is represented by a right dentary (MNHN-Bol-V 008954; Fig. 2, Supporting Information Appendix S1), three humeri (MNHN-Bol-V 003789, 012874 and 012875; Figs 4, 5 and Appendix S1), a right astragalus (MNHN-Bol-V 012983; Fig. 7A–H, Q, R and Appendix S1), and a right calcaneum (MNHN-Bol-V 003307; Fig. 7I–P, R and Appendix S1). This sloth is distinct in size and morphology from the megatheriine *Megatherium* (*Megatherium*) *altiplanicum* (St-André & De Iuliis, 2001) and the mylodontid *Simomyodon uccasamamensis* (St-André *et al.*, 2010), previously mentioned and extremely abundant in the Montehermosan level of the Pomata-Ayte locality.

Given that: (1) the three Montehermosan sloth taxa are radically different in size and morphology, and belong to distinct clades (i.e. Megatheriidae, Mylodontidae, and Nothrotheriidae), (2) the three sloth humeri are nearly identical in size and anatomy, and undoubtedly belong to the same species (Figs 4, 5), and (3) the astragalus and calcaneum belong to two individuals (discovered independently and at different times) but articulate almost perfectly, it is reasonable to consider that the smaller sloth elements from the Montehermosan levels belong to the new form. Four other osteological elements recovered from the same locality include a right ulna without distal epiphysis (MNHN-Bol-V 008951), a manual claw (MNHN-Bol-V 008951), a rib

(MNHN-Bol-V 008951) and the distal half of a fibula (MNHN-Bol-V 003800), which could possibly belong to this new nothrotheriid. However, given that these elements are fragmentary and less securely nothrotheriid in nature, they are not considered in the present study.

Based on the systematic arrangements of Gaudin (2004), De Iuliis *et al.* (2011), Pujos *et al.* (2011, 2014), the principal sloth dentaries, humeri, astragali and calcanei considered for comparisons are listed in the Tables 1, 2, 3 and 4, respectively.

For the mandible, the orientational terms anterior/posterior and lateral/medial are used; for teeth, mesial/distal and vestibular/lingual are employed. A majority of the mandibles considered for comparison are illustrated in Pujos *et al.* (2011, 2014). All specimens of the new taxon are housed in the MNHN-Bol (La Paz, Bolivia).

Abbreviations: C, upper caniniform tooth; c, lower caniniform tooth; HI, hypsodonty index; M, upper molariform tooth; m, lower molariform tooth; NALMA, North American Land Mammal Age; SALMA, South American Land Mammal Age.

SYSTEMATIC PALAEOLOGY

MAMMALIA LINNAEUS, 1758

XENARTHRA COPE, 1889

PILOSA FLOWER, 1883

TARDIGRADA LATHAM & DAVIES IN FORSTER, 1795

NOTHROTHERIIDAE AMEGHINO, 1920

Emended diagnosis [modified from McDonald & de Muizon (2002) and De Iuliis *et al.* (2011); characters added from Gaudin (2004) and De Iuliis *et al.* (2011)]. Sloths with small- to medium-sized caniniform (when present); molariforms quadrate, rectangular, or trapezoidal with transverse width less than or equal to twice mesiodistal length, with apicobasal grooves on lingual and vestibular surfaces (only on m3 of *Aymaratherium*); sagittal crest rudimentary or absent; postorbital process of jugal reduced or absent; hypoglossal foramen recessed dorsally, lies at same level as jugular foramen;

Figure 2. Right dentary of the holotype of *Aymaratherium jeani* gen. nov., sp. nov. (MNHN-Bol-V 008954). A–B, D–E and G–H, pictures and drawings of the specimen in medial, lateral and occlusal views, respectively; C and F, drawings in medial and lateral views, respectively, showing muscular origin and insertion areas; I, J, antero occlusal view of the tooth row and detail of c1; K, L, picture and drawing of the right tooth row in occlusal view (mesial towards left and lateral towards top). Abbreviations: A, cuspid A (distolingual); anp, angular process; B, cuspid B (distolabial); bf, buccinator fossa; C, cuspid C (mesial); C., lower caniniform tooth; condp, condyloid process; corp, coronoid process; emef, external mental foramina; hrm, horizontal ramus; mf, mandibular foramen; Msi; insertion of the muscle masseter pars superficialis; m1–m3, three lower molariform teeth; peomc, posterior external opening of the mandibular canal; Pmi, insertion of the muscle pterygoideus medius; spo, spout; symph, symphysis; Ti, insertion of the muscle temporalis; vg, vertical groove; Zo, origin of the muscle zygomaticomandibularis. Scale bars = 50 mm (A–H) and 20 mm (I–L).

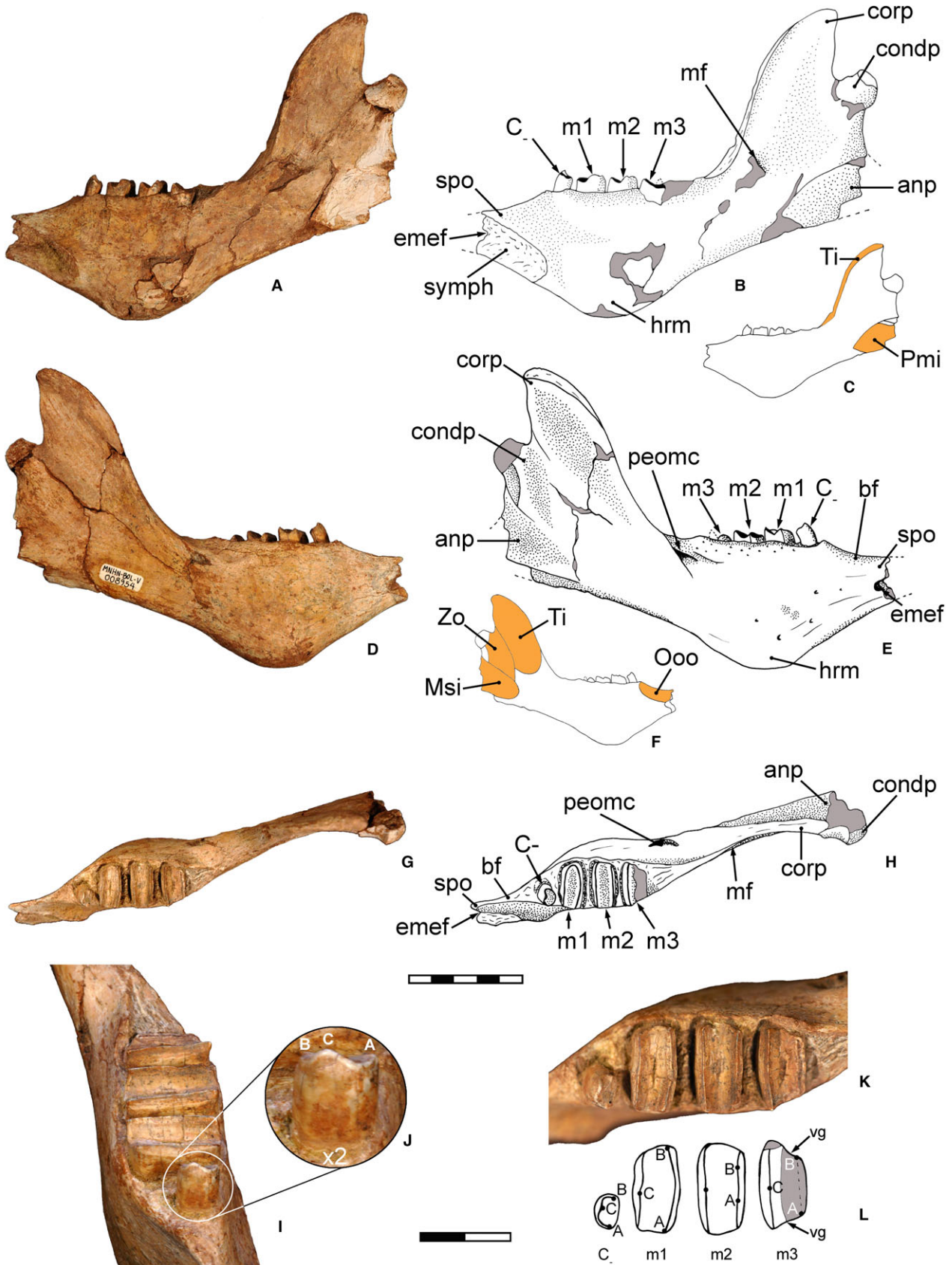




Figure 3. Photographs of mandibles of several Megatherioidea, Nothrotheriidae (A–H), and Megatheriidae (I–J) in occlusal (A, C, E, G, I) and lateral (B, D, F, H, J) views. A, B, *Xyophorus villarroeli* (holotype, MNHN ACH 43) from the Huayquerian SALMA of Achiri (Bolivia); C, D, *Hiskatherium saintandrei* (holotype, MNHN-Bol-V 003633) from the Laventan SALMA of Quebrada Honda (Bolivia); E, F, *Lakukullus anatisrostratus* (holotype, MNHN-Bol-V 006601) from the Laventan SALMA of Quebrada Honda (Bolivia); G, H, *Mionothropus cartellei* (holotype, LACM 11753) from the Huayquerian SALMA of Río Acre (Peruvian/Brazilian Amazon); I, J, *Megatherium (Pseudomegatherium) tarijense* from the Ensenadan/Lujanian of Tarija (Bolivia). Scale bar = 50 mm.

occipital condyles sessile, with posterior edges at the same level as or anterior to posterior edge of foramen magnum; mastoid process (= paroccipital process of Wible & Gaudin, 2004) bulbous, expanded mediolaterally; dorsally directed branch of the occipital artery that perforates mastoid process, emerging in a foramen on the dorsal side of the mastoid process [foramen apparently absent (lost?) in *Nothrotherium*]; Glaserian fissure opens into weak groove on ventral or posteroventral surfaces of entoglenoid process; coronoid process of mandible without medial ridge along anterior edge; radial bicipital tuberosity projecting mainly posteriorly; pronator teres insertion at proximal one-third of radial diaphyseal length (= relatively elongated distal radial diaphysis); cuneiform deep proximodistally, nearly rectangular in dorsal view; ungual process of ungual phalanx of manual digit 2 semicircular in cross-section and not triangular as in other manual unguals; astragalus with medial trochlea enlarged and modified into an odontoid process; calcaneum with tuberos tuberc calcis enlarged mediolaterally and anteroposteriorly.

AYMARATHERIUM JEANI GEN. NOV., SP. NOV.
(FIGS 2, 4, 5, 7, APPENDIX S1)

Holotype. MNHN-Bol-V 008954 (Fig. 2, Appendix S1), nearly complete right dentary, missing only posterior extremities of angular and condyloid processes, anterior extremity of the ‘spout’, and distal lophid of m3.

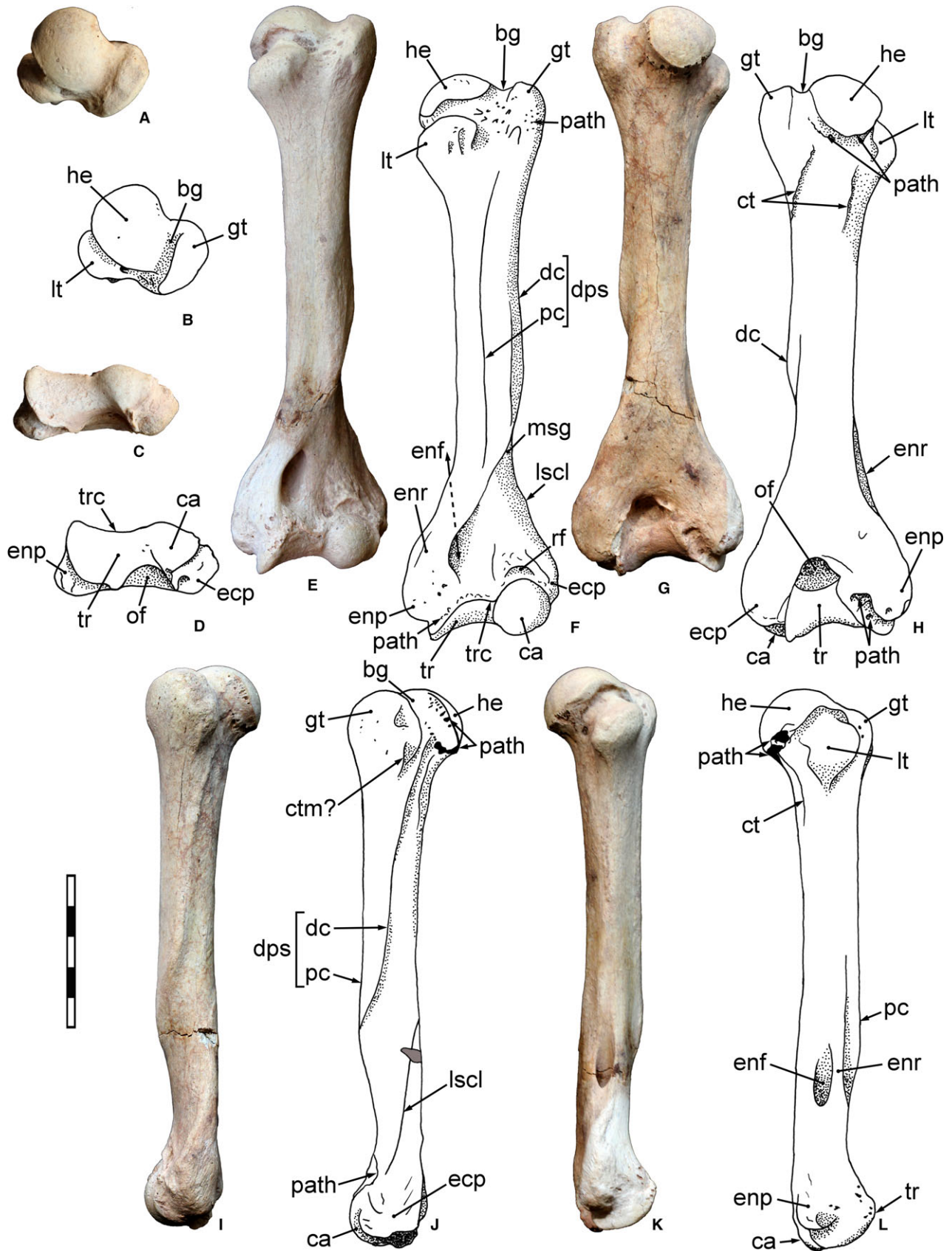
Etymology. In reference to the Aymara (*Aymar aru*), a native ethnic group and language from the Andes, from where the specimens were recovered; and, the specific epithet for Jean Joinville Vacher (successively Director of the French Institute of Andean Studies – IFEA, Advisor of the Institute for Development Research – IRD in Bolivia, Advisor of Regional Cooperation for Andean Countries of the French Embassy during 2000/2012, and currently Assistant to General Executive Officer for Science of the IRD) for his friendship and constant support for palaeontological investigations over the years.

Hypodigm (Figs 4, 5, 7, Appendix S1). Three humeri (MNHN-Bol-V 003787, 012874 and 012875), a

complete astragalus (MNHN-Bol-V 012983) and a complete calcaneum (MNHN-Bol-V 003307).

Type locality and age. All specimens were discovered in the Montehermosan SALMA (late Miocene/early Pliocene) levels of the Pomata Ayte locality, 100 m above ‘Toba 76’ dated by St-André (1994: 83), using $^{40}\text{K}/^{40}\text{Ar}$, as between 5.42 ± 0.6 and 5.97 ± 0.4 Ma.

Diagnosis. Small- to medium-sized sloth, similar in size to *Thalassocnus* and *Nothrotherium*; lower dentition comprising a single small caniniform and three large molariform teeth; absence of diastema between c1 and m1; very high hypsodonty index (1.14), as in the most hypsodont specimens of *Megatherium* and *Megalonyx*; deep buccinator fossa and extremely thin dorsal margin of the spout; c1 is distally curved and bears three isolated cuspids (mesiovestibular, distoventibular and distolingual); m1–m3 mesiodistally compressed, m1–m2 rectangular and m3 subtriangular (as for m4 in Megatheriinae); molariforms constituted by mesial and distal lophids perpendicular to the mesiodistal axis of the tooth row and separated by a deep transverse valley, open vestibularly and lingually as in Megatheriinae (open vestibularly only in other Nothrotheriidae and Megatherioidea of uncertain affinities such as *Hiskatherium*); apicobasal grooves not present on m1–m2, in contrast to other typical Nothrotheriidae; shallow apicobasal grooves are present on distolingual and distoventibular surfaces of m3; the mesial lophid is shorter than the distal lophid in m1; in m2 and m3 the relationship is reversed; the angle between the dorsal edges of ascending and horizontal rami is close to 110° ; the humerus is slender, with the greater and lesser tubercles well developed and strongly asymmetric with the greater tubercle larger than the lesser and the head medially inclined, in contrast to other Megatherioidea (except *Diabolotherium*), which never have this combination; the deltopectoral shelf begins laterally, expands anterolaterally and is not well developed; the entepicondyle is rounded as in *Thalassocnus*, particularly *T. natans*, and poorly developed medially, in contrast to *Pronothrotherium* and *Mionothropus*; the epicondyles are similar in size; in anterior view of the astragalus the discoid and odontoid facets meet at a right angle as in *T. natans*, the caput tali is positioned centrally and its dorsal



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Figure 4. Photographs and drawings of the left humerus MNHN-Bol-V 008954 referred to *Aymaratherium jeani* **gen. nov., sp. nov.** in proximal (A, B, posterior towards top and medial towards left), distal (C, D, anterior towards top, medial towards left), anterior (E, F, proximal towards top, medial towards left), posterior (G, H, proximal towards top, lateral towards left), lateral (I, J, proximal towards top, anterior towards left) and medial (K, L, proximal towards top, posterior towards left) views. Abbreviations: bg, bicipital groove; ca, capitulum; ct, crests for triceps muscle; ctm?, crest for teres minor muscle?; dc, deltoid crest; dps, deltopectoral shelf; ecp, ectepicondyle (lateral epicondyle); enf, entepicondylar foramen; enp, entepicondyle (medial epicondyle); enr, entepicondylar ridge; gt, greater tubercle; he, head; lscl, lateral supracondylar line (= supinator crest); lt, lesser tubercle; msg, musculospiral groove; of, olecranon fossa; path, osteological pathology; pc, pectoral crest; tr, trochlea; trc, anterior edge of the trochlear cavity. Scale bar = 50 mm.

border is located just below the discoid surface as in *Thalassocnus*; the odontoid process is well defined, perpendicular to the main anteroposterior axis of the discoid facet and does not bear a strong plantar extension; the transverse width of the odontoid process is less than that of the discoid process, in contrast to *Thalassocninae* and *Megatheriinae*; the calcaneum is massive and bulky and its general morphology is comparable to that of *Thalassocninae* (particularly *T. natans*); the tuber calcanei is approximately symmetrical in dorsal view and slightly elongated posteriorly, rather than tapered, in contrast to other nothrotheriids; the ectal facet for the astragalus is oriented in an almost dorsoplantar plane (as in *T. carolomartini*) and bordered by a dorsal groove; the sustentacular facet for the astragalus and cuboid facet are contiguous, as in *Thalassocninae* and *Megatheriinae*, and separated from the ectal facet by the deep sulcus calcanei; the dorsal portion of the tuber calcanei bears a tuberosity, as in *Megatheriinae* and *Thalassocninae*.

DESCRIPTION OF AYMARATHERIUM

MANDIBLE (HOLOTYPE; FIG. 2, AND APPENDIX S1)

MNHN-Bol-V 008954 is a nearly complete right dentary (Fig. 2). In occlusal view, the molariform teeth are mesially convex and the most mesial tooth closely approaches the dorsolateral margin of the mandible. Following Cartelle & De Iuliis (2006) for megatheriines and Pujos *et al.* (2011, 2014) for megatherioids, this latter characteristic suggests that this specimen probably belonged to an adult individual. The nearly complete dentary preserves four teeth, missing only the distal lophid of the last tooth. It preserves the horizontal ramus, missing only the tip of the spout. The dentary also lacks parts of the extremities of the coronoid and condyloid processes, and most of the angular process (Fig. 2K, L). This specimen pertains to a small- to medium-sized megatherioid, similar in size to the nothrotheriids *Thalassocnus*, *Lakukullus*, *Nothrotherium* and *Mionothropus*, and the planopsines, larger than *Hiskatherium*, *Xyophorus* and *Hapalops*, and consider-

ably smaller than large megatheriines such as *Megatherium* (Fig. 3I, J) and *Megathericulus* (Pujos *et al.*, 2013). The dentition of *Aymaratherium jeani* includes a caniniform followed by three molariform teeth, which is characteristic of basal tardigrade taxa such as *Pseudoglyptodon* and *Octodontotherium* (Tinguirirican and Deseadan SALMAs: Engelmann, 1987; McKenna, Wyss & Flynn, 2006; Pujos & De Iuliis, 2007; Pujos *et al.*, 2012a), as well as the nothrotheriids *Nothropus*, *Mionothropus* and *Pronothrotherium*, and several other Miocene basal megatherioid sloths (Santacrucian SALMA: e.g. Scott, 1903, 1904; De Iuliis *et al.*, 2014).

Aymaratherium bears one of the highest HI values reported for a sloth (1.14), equivalent to that reported for some specimens of the Pampean megatheriine *M. (M.) americanum* (1.14) and the North American giant megalonychid *Megalonyx* (1.17) (Pujos *et al.*, 2011). The HI is generally higher among *Megatheriinae* (0.77–1.14) and lower in *Nothrotheriidae* (0.40–1.06). In nothrotheriids that retain a plesiomorphic dental formula (i.e. the presence of a caniniform tooth), HI is considerably lower: between 0.43 in *Pronothrotherium typicum* and 0.86 in *Mionothropus cartellei*. In advanced nothrotheriids, which lack the caniniform, given the reduction of the length of the tooth row, the HI reaches higher values, and ranges between 0.52 in *Nothrotherium maquinense* to 1.05 in *Thalassocnus antiquus* (see Pujos *et al.*, 2011: table 2 for further details and an overview of HI in sloths).

In lateral view, the ventral margin of the horizontal ramus is more convex than in other nothrotheriids, planopsines and *Hapalops*, and is thus similar to that of *Megatherium* and *Huilabradys magdalenensis* from La Venta (Laventan SALMA: Villarroel, 1998). In MNHN-Bol-V 008954, the maximum convexity (and by extension the depth of the mandible) is located between m1 and m2 (Fig. 2A, B, D, E) as in *Thalassocnus antiquus* and *Planops martini*. In *Xyophorus bondesioi* (MLP 32-IV-20-1) and *Mionothropus cartellei*, the maximum convexity of the mandible is located at the level of m2, between m2 and m3 in the Megalonychidae *Eucholoeops* and in *Megatherium (P.) tarijense*, and at the level of m3

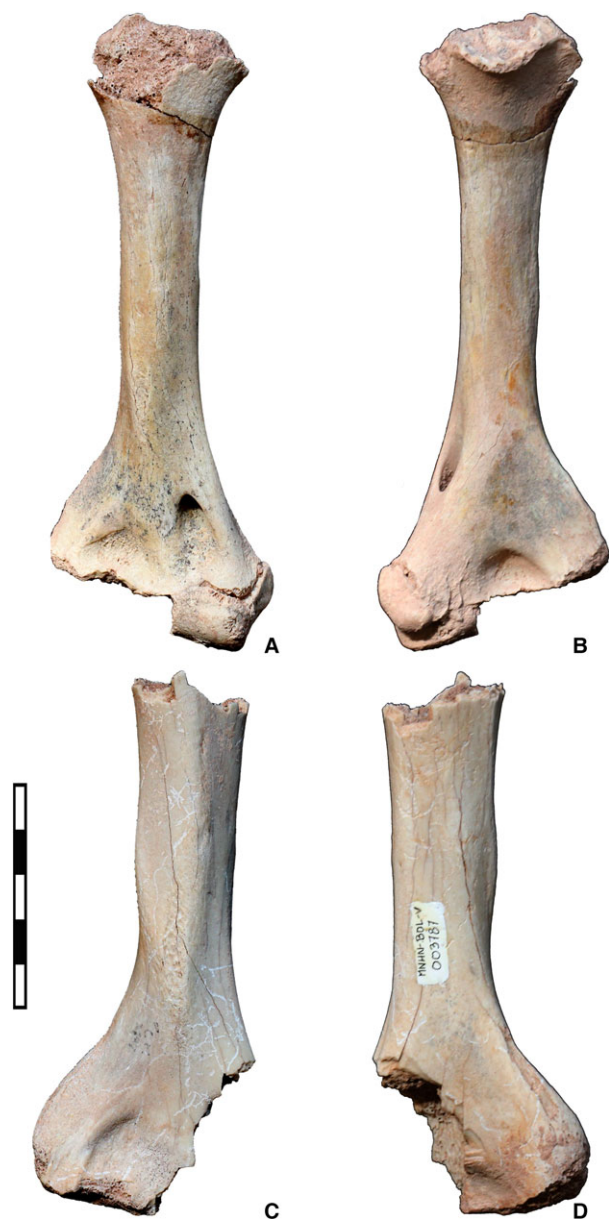


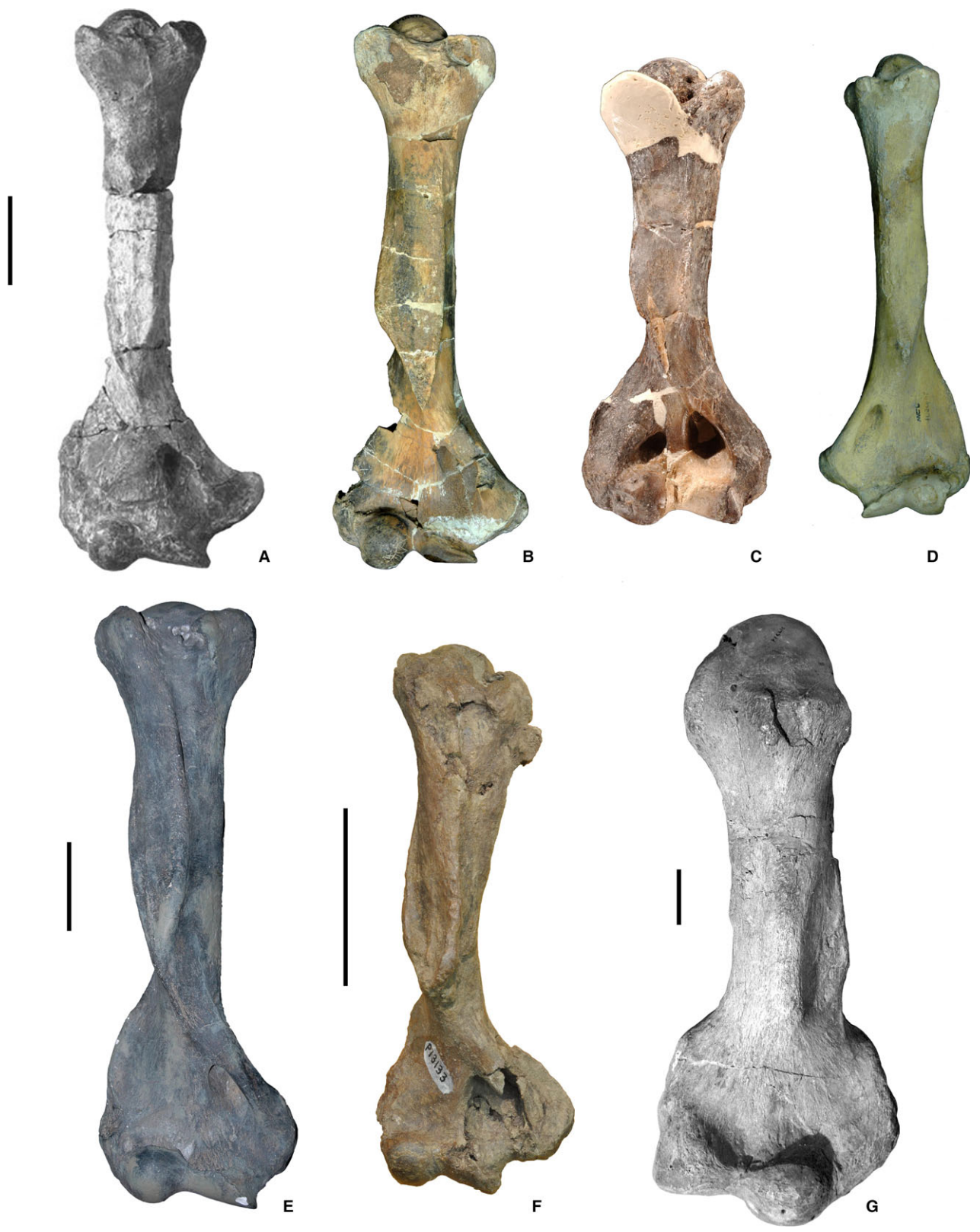
Figure 5. Photographs of the left humeri MNHN-Bol-V 012875 (A, B) and MNHN-Bol-V 003787 (C, D) referred to juvenile specimens of *Aymaratherium jeani* gen. nov., sp. nov. in anterior (A, C, proximal towards top and medial towards left) and posterior (B, D, anterior towards top, medial towards left) views. Scale bar = 50 mm.

in *Prepoplanops* (Carlini, Brandoni & Dal Molin, 2013). The deep buccinator fossa is located anterolaterally to c1 (Fig. 2D–H). The posterior half of the external mental foramen is preserved (Fig. 2A–H). This large foramen is located on the lateral margin of the spout, 25 mm in front of c1 and 10 mm below the dorsal margin of the dentary. Anteriorly to c1, the dorsal border of the spout is thinner than in most other sloths (2.2 mm), especially *Lakukullus* (Pujos *et al.*, 2014; Fig. 3E) and Megatheriinae, and comparable to the condition in *Thalassocnus antiquus*.

The anterior extremity of the spout is broken but it is possible to estimate its anterior extension. Based on the position of the external mental foramina and the depth of the anterior portion of the mandible, the spout of *Aymaratherium* extends far anteriorly, a condition somewhat similar to that observed in *X. villarroeli* UF 2668, *Mionothropus cartellei* and *Nothrotheriops shastensis*, and in megatheriine sloths such as *M. (P.) tarijense* (see De Iuliis, Pujos & Tito, 2009) and *M. (M.) altiplanicum* (St-André & De Iuliis, 2001). In occlusal view, the lateral surface of the horizontal ramus is strongly convex, as in *Mionothropus* (Fig. 3G) and in contrast to *Diabolotherium* (Pujos *et al.*, 2007: fig. 6B, G, H); the medial surface is rectilinear as in most nothrotheriids. In anterior view, the lateral surface of the ramus is dorsoventrally rectilinear and the medial surface slightly concave.

The posterior external opening of the mandibular canal opens laterally. It is located below the tooth row, posterior to m3, at the base of the ascending ramus of the coronoid process (Fig. 2D–H). In *Thalassocnus natans* (see de Muizon *et al.*, 2004a), it is located at the same level as the tooth row and opens more anteriorly, whereas in *Mionothropus cartellei* (De Iuliis *et al.*, 2011; Fig. 3G, H), it opens laterally but at the level of m3. The angle between the ascending and horizontal rami is close to 110°, as in *Nothrotherium maquinense*, *Nothrotheriops texanum*, *Xyophorus bondesioi*, *Pronothrotherium typicum*, *Hapalops* and *Planops martini*. In most nothrotheriids, this value ranges between 100 and 115°, except in *Mionothropus cartellei* in which the posterior portion of the mandible is inclined posteriorly and this

Figure 6. Photographs of humeri of several Megatherioidea in anterior view (proximal towards top). A, right humerus of *Mionothropus cartellei* (LACM 4609 modified from De Iuliis *et al.*, 2011) from the Huayquerian SALMA of Brazil–Peruvian Amazonia; B, right humerus of *Pronothrotherium typicum* (FMNH P14515) from the Huayquerian SALMA of Argentina; C, right humerus of *Thalassocnus natans* (MNHN SAS 734) from the Montehermosan SALMA of Peruvian coast; D, left humerus of *Nothrotherium maquinense* (MCL 1020-42-1) from the Lujanian SALMA of Brazil; E, right humerus of *Planops martini* (BMNH M 9207) from the Santacrucian SALMA of Patagonia Argentina; F, right humerus of *Hapalops* sp. (FMNH P13133) from the Santacrucian SALMA of Patagonia Argentina; G, left humerus of *Megatherium (Pseudomegatherium) tarijense* from the Ensenadan SALMA of southern Bolivia. Scale bars = 50 mm.



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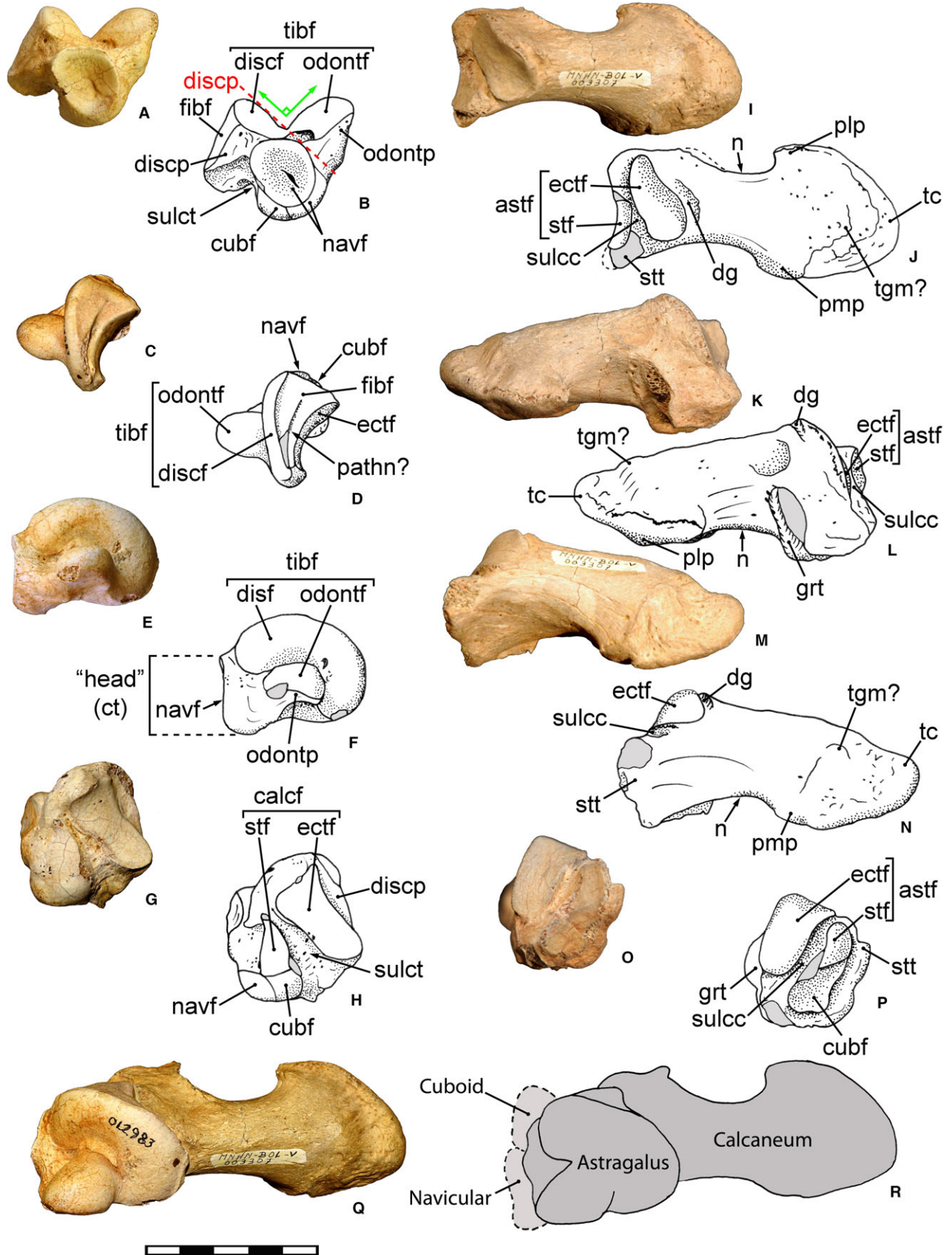


Figure 7. Photographs and drawings of the right astragalus MNHN-Bol-V 012983 and right calcaneum MNHN-Bol-V 003307 referred to *Aymaratherium jeani* gen. nov., sp. nov. A–H, right astragalus in distal (A, B, dorsal towards top, lateral towards left), lateral (C, D, anterior towards top, dorsal towards left), medial (E, F, dorsal towards top, anterior towards left) and plantar (G, H, posterior towards top, medial towards left) views; I–P, right calcaneum in dorsal (I, J, lateral towards top anterior towards left), lateral (K, L, dorsal towards top, posterior towards left), medial (M, N, dorsal towards top and anterior towards left) and anterior (O, P, dorsal towards top and lateral towards left) views; Q, the astragalus and calcaneum in dorsal view (lateral towards top, anterior towards right); R, hypothetical reconstruction of the pes of *Aymaratherium jeani* gen. nov., sp. nov. Abbreviations: astf, astragalus facets; ct, caput tali ('head' of the astragalus); cubf, cuboid facet; dg, dorsal groove; discf, discoid facet; discp, discoid process; ectf, ectal facet; fibf, fibular facet; grt, groove for the tendon; n, neck; navf, navicular facet; odontf, odontoid facet; odontp, odontoid process; pathn?, pathological notch?; plp, posterolateral process; pmp, posteromedial process; sulcc, sulcus calcanei; sulct, sulcus tali; stf, sustentacular facet; stt, sustentaculum tali; tc, tuber calcanei; tgm?, tuberosity for the gastrocnemius muscle?; tibf, tibial facet. Scale bar = 50 mm.

angle is close to 125° (Fig. 3H). In Megatheriinae and *Prepoplanops*, the ascending ramus is generally more upright and the angle with the horizontal ramus lower, approximating 100° (see variation in megatheriines in De Iuliis, 1996). In relation to the strong hypsodonty of *Aymaratherium*, the posterior portion of the mandible (i.e. coronoid, condyloid and angular processes) is located dorsally relative to the horizontal ramus in comparison to its position in other nothrotheriids and planopsines. The anterodorsal margin of the ascending ramus is rough and corresponds to the insertion of the temporalis muscle (Fig. 2C, F). Laterally, this muscle is located above the origin of the zygomaticomandibularis muscle and the insertion of the masseter pars superficialis muscle (Fig. 2F; Naples, 1987; Naples & McAfee, 2012; Pujos *et al.*, 2014). In *Aymaratherium*, these muscle attachments occupy the entire medial surface of the posterior portion of the dentary. Such expanded mandibular musculature is unusual in Nothrotheriidae, except *Lakukullus* (Fig. 3E, F; Pujos *et al.*, 2014), but much more common in Megatheriinae, such as *M. (P.) tarijense* (Naples & McAfee, 2012).

The articular head of the condyloid process is partially missing but located above the tooth row and in a slightly more dorsal position than in *Mionothropus cartellei* (Fig. 3H), *Xyophorus* sp. (UAFT V-000871, Croft *et al.*, 2009), Planopsinae and Megatheriinae. The posterior extremity of the condyloid process lacks a ventral concavity, as it also occurs in most ground sloths. In posterior view, the base of the angular process inclines laterally. The ventral margin of the angular process is flat. The mandibular foramen is very large (10 mm), opening posterodorsally, and is located at the base of the medial side of the ascending ramus, just dorsal to the tooth row (Fig. 2A, B, G, H). In *Xyophorus*, *Eucholoeops* and *Hapalops*, this foramen is located at the same level as or ventral to the tooth row. The medial side of the ascending ramus bears a long dorsal and a ventral

insertion site for the temporalis and pterygoideus medius muscles, respectively (Fig. 2C).

The lower dentition of *Aymaratherium* includes a caniniform and three molariforms (Fig. 2). The c1 is posteriorly recurved, with its mesial surface convex and its distal slightly concave. It lies medial to the sagittal axis of the tooth row. In occlusal view, c1 is oval and slightly compressed mesiodistally (Fig. 2K, L), rather than transversely, as occurs in *Xyophorus villarroeli* (Fig. 3A, B) and *Lakukullus anatisrostratus* (Fig. 3E), or circular as in *Pronothrotherium typicum*, *Mionothropus cartellei* and *Prepoplanops boleadorensis*. During the evolution of the nothrotheriids, several taxa such as *Thalassocnus*, *Nothrotheriops* and *Nothrotherium* have lost the most anterior tooth, whereas others (e.g. *Pronothrotherium* and *Mionothropus*) have retained four lower teeth, including a caniniform first tooth. In some sloths such as *Hiskatherium* (Fig. 3C), *Diabolotherium* and Megatheriinae (Fig. 3I), four teeth are also present, with the anterior most molarized instead of being canine-shaped (Pujos *et al.*, 2007, 2011).

In *Aymaratherium*, c1 is slightly larger than in some other nothrotheriids such as *Mionothropus cartellei* (Fig. 3G, H), *Xyophorus villarroeli* (Fig. 3A, B) and *Pronothrotherium typicum* (Ameghino, 1907; FMNH P14467), Planopsinae (*Planops martini*, FMNH P13148, Hoffstetter, 1961), and most of the species of *Hapalops* (e.g. MACN A-6368). It is similar in robustness to that in *Pseudortotherium australis* (MLP 68-I-17-5, Scillato-Yané, 1981) and *Lakukullus anatisrostratus* (Pujos *et al.*, 2014; Fig. 3E, F), but smaller than that in *Huilabradys magdaleniensis* and in Megalonychidae (e.g. *Eucholoeops ingens*, De Iuliis *et al.*, 2014), and than that in some Mylodontiidae that possess a robust caniniform.

It is worth noting that the c1 of *A. jeani* differs from that of other Tardigrada in bearing three cusps, a pattern usually recognized only in molariform teeth (e.g. *Eucholoeops* Bargo, Vizcaíno & Kay, 2009;

Table 1. List of principal megatherioid sloths dentaries considered for comparison with *Aymaratherium jeani* gen. nov., sp. nov.

Taxon	Specimen	Age and locality	Reference(s)
Megalonychidae			
<i>Eucholoeops ingens</i>	MPM-PV 3401	Santacrucian SALMA of Patagonia Argentina	De Iuliis <i>et al.</i> (2014)
Megatheriidae Planopsinae			
<i>Planops martini</i>	FMNH P13148	Santacrucian SALMA of Patagonia Argentina	Hoffstetter (1961)
<i>Prepoplanops boleadorensis</i>	MLP 97-XI-3-1 [holotype]	Miocene [dubious age] of Patagonia Argentina	Carlini <i>et al.</i> (2013)
Megatheriinae			
<i>Megatherium</i> (<i>Megatherium</i>) <i>altiplanicum</i>	MNHN AYO 101 [holotype]	Montehermosan SALMA of Bolivian altiplano	St-André & De Iuliis (2001)
<i>Megatherium</i> (<i>Pseudomegatherium</i>) <i>tarijense</i>	MNHN-Bol-V 011564 (Fig. 3I, J), FMNH P14216, and UNI 1	Lujanian SALMA of Bolivian altiplano and Peru	Pujos & Salas (2004); De Iuliis <i>et al.</i> (2009)
Nothrotheriidae Thalassocninae			
<i>Thalassocnus antiquus</i>	MUSM 228	Huayquerian SALMA of southern Peruvian coast	de Muizon <i>et al.</i> (2003)
<i>Thalassocnus natans</i>	MNHN.F.SAS 734	Montehermosan SALMA of southern Peruvian coast	de Muizon <i>et al.</i> (2003)
<i>Thalassocnus littoralis</i>	MNHN.F.SAS 1615	Montehermosan SALMA of southern Peruvian coast	McDonald & de Muizon (2002); de Muizon <i>et al.</i> (2004b)
<i>Thalassocnus yaucensis</i>	MUSM 434	Early Uquian SALMA of southern Peruvian coast	de Muizon <i>et al.</i> (2004a)
<i>Thalassocnus carolomartini</i>	SMNK PAL 3814 [holotype] and MNHN SAO 203	Chapadmalalan SALMA of southern Peruvian coast	McDonald & de Muizon (2002); de Muizon <i>et al.</i> (2004b)
Nothrotheriinae			
<i>Mionothropus cartellei</i>	LACM 11753 [holotype] (Fig. 3G, H)	Huayquerian SALMA of Brazil-Peruvian Amazon	De Iuliis <i>et al.</i> (2011)
<i>Pronothrotherium typicum</i>	FMNH P14467 and MACN Pv 8140 [holotype]	Huayquerian SALMA of Patagonia Argentina	Ameghino (1907)
<i>Nothrotherium maquinense</i>	MCL 1020	Ensenadan SALMA of Brazil	Cartelle & Fonseca (1983)
<i>Nothrotheriops shastensis</i>	LACM 1801-7	Rancholabrean NALMA of USA	Stock (1925)
<i>Lakukullus anatisrostratus</i>	MNHN-Bol-V 006601 [holotype] (Fig. 3E, F)	Laventan SALMA of Bolivia	Pujos <i>et al.</i> (2014)
<i>Nothrotheriops texanum</i>	UF 86889	Irvingtonian NALMA of USA	McDonald (1995)
<i>Xyophorus villarroeli</i>	MNHN ACH 43 [holotype] (Fig. 3A, B) and UF 2668	Huayquerian SALMA of Achiri and Laventan SALMA of Quebrada Honda, Bolivia	St-André (1996)
<i>Xyophorus bondesioi</i> or <i>X. cf. bondesioi</i>	MLP 32-IV-20-1 [holotype] and UATF-V-000871	Chasicoan SALMA of Argentina and Laventan SALMA of Bolivia	Scillato-Yané (1979), Croft <i>et al.</i> (2009)
<i>Nothropus priscus</i>	MACN Pv 975 [holotype]	Lujanian SALMA of Argentina	Burmeister (1882)

Table 1. *Continued*

Taxon	Specimen	Age and locality	Reference(s)
Megatherioidea of uncertain phylogenetic affinities			
<i>Hiskatherium saintandrei</i>	MNHN-Bol-V 003633 [holotype] (Fig. 3C, D)	Laventan SALMA of Bolivian altiplano	Pujos <i>et al.</i> (2011)
<i>Diabolotherium nordenskioldi</i>	NMR-PZ M 4287 [paratype] and MNHN CPN 9-1	Lujanian SALMA of Peru, Chile, and Argentina	Pujos <i>et al.</i> (2007)
<i>Huilabradys magdaleniensis</i>	LV-4-11 [holotype]	Laventan SALMA of Colombia	Villarroel (1998)
<i>Hapalops</i> sp.*	Various specimens from MACN and MLP collections	Santacrucian SALMA of Patagonia Argentina	Scott (1903)

**Hapalops* will be considered at the generic level until intraspecific variation and revision of this genus is undertaken (De Iuliis & Pujos, 2006).

Hiskatherium Pujos *et al.*, 2011). These cusps, which are not homologous to ‘true’ cusps present in most other placentals, are in this case exclusively formed by wear during functional occlusion with the opposite upper tooth. Indeed, erupting teeth in sloths do not bear cusps but instead represent a rounded cap (see examples in Gervais, 1873; Naples, 1982, 1990; Cartelle & De Iuliis, 2006). The c1 of *Aymaratherium* bears a mesial central cuspid (Fig. 2J, L), termed cuspid ‘C’, following the terminology suggested by Bargo *et al.* (2009). It is well defined and its extremity is rounded but not as prominent as in *Mionothropus* (which bears a single distal cuspid, Fig. 3H) and *Megalonychinae*, but more pronounced than in species of *Xyophorus*. Additionally, two distal cuspids are present in the c1 of *A. jeani*, one distolingually (cuspid ‘A’) and the other distovestibularly (cuspid ‘B’) on the margin of the occlusal surface (Fig. 2A–C, J, L). A large concave wear facet occupies the central part of the occlusal surface. A diastema is not present between c1 and m1, in contrast to other Nothrotheriidae, Planopsinae and *Hapalops*.

The three molariform teeth (m1–m3) are approximately rectangular and compressed mesiodistally. Similarly to c1, three cuspids also shaped by wear processes are present on each tooth, but located on two transverse lophids that are perpendicular to the mesiodistal axis of the tooth row, and separated by a deep transverse valley (Fig. 2K, L). The general form of the molariform teeth of *Aymaratherium* combines several features in a distinct pattern for Tardigrada, although the condition is closely approached in the most basal megatheriine *Megathericulus* (De Iuliis, Brandoni & Scillato Yané, 2008; Pujos *et al.*, 2013). In occlusal view, m1–m2 are very similar in shape, and mesiodistally compressed as in *Megathericulus*; m3 is more triangular in section with a reduced distal lophid. A similar condition for the last lower

molariform tooth occurs in Megatheriidae such as *M. (P.) tarijense* (Ensenadan SALMA; Fig. 3I). The central transverse valley of m1–m3 is open vestibularly and lingually as in Megatheriinae. In other Nothrotheriidae, the valley is open only vestibularly. The apicobasal grooves are missing in m1–m2, in contrast to other Nothrotheriidae, Megatheriidae and *Hapalops*, and morphologically similar taxa.

The mesial lophid of m1 is slightly convex mesially and the distal lophid convex distally in occlusal view. The transverse width of the mesial lophid is less than that of the distal lophid. In occlusal view, the mesial lophid is concave mesially, and the distal lophid convex distally (Fig. 2I). In lateral view, the distal lophid is higher than the mesial lophid. Cuspid ‘C’ lies at the centre of the mesial lophid, and cuspids ‘B’ and ‘A’ at the vestibular and lingual extremities of the distal lophid (Fig. 2K, L). In medial view, the apicobasal height of the distal wear facet is reduced medially. In posterior view, the apicobasal height of the distal wear facet is constant. The maximal apicobasal height of the mesial and distal wear facets is 2.6 mm.

As in m1, m2 also bears two transverse lophids which are nearly straight and partially joined lingually, as the margin of the tooth is raised in this region. This condition is in sharp contrast to the typical condition observed in megatheriine molariform teeth (see De Iuliis, 1996). The transverse width of the distal lophid is slightly shorter than that of the mesial lophid; as in m1, the distal lophid is higher than the mesial lophid. In posterior view, the distal lophid is slightly concave at its lingual third. In m2, cuspid ‘C’ is at the centre of the mesial lophid, but cuspids ‘B’ and ‘A’ are located closer to the centre of the distal lophid (Fig. 2L). In mesial and distal views, the apicobasal heights of the wear facets are constant. The maximal apicobasal height of the mesial and distal wear facets is 2.4 and 2.0 mm,

Table 2. List of principal sloths humeri considered for comparison with *Aymaratherium jeani* gen. nov., sp. nov.

Taxon	Specimen	Age and locality	Reference(s)
Megalonychidae			
<i>Euchloeops ingens</i>	MPM-PV 3401 [neotype]	Santacrucian SALMA of Patagonia Argentina	De Iuliis <i>et al.</i> (2014)
<i>Mesocnus browni</i>	AMNH 49918, 49927	Pleistocene of Cuba	Not figured
Megatheriidae Planopsinae			
<i>Planops martini</i>	BMNH M 9207 (Fig. 6E)	Santacrucian SALMA of Patagonia Argentina	Hoffstetter (1961)
<i>Prepoplanops boleadorensis</i>	MLP 97-XI-3-1 [holotype]	Miocene [dubious age] of Patagonia Argentina	Carlini <i>et al.</i> (2013)
Megatheriinae			
<i>Megatherium (Pseudomegatherium) tarijense</i>	FMNH P14216 (Fig. 6G)	Lujanian SALMA of Bolivian altiplano and Peru	Pujos & Salas (2004); De Iuliis <i>et al.</i> (2009)
<i>Megatheriops rectidens</i>	MACN 2818	Huayquerian SALMA of Mendoza Province, Argentina	De Iuliis (2003)
<i>Megathericulus patagonicus</i>	MLP 91-IX-7-18	Friasian SALMA of Chubut and Santa Cruz Provinces, Argentina	De Iuliis <i>et al.</i> , 2008
Nothrotheriidae Thalassocninae			
<i>Thalassocnus natans</i>	MNHN.F.SAS 734 (Fig. 6C)	Montehermosan SALMA of southern Peruvian coast	Amson <i>et al.</i> (2015a)
<i>Thalassocnus littoralis</i>	MNHN.F.SAS 53	Late Huayquerian or early Montehermosan SALMA of southern Peruvian coast	Amson <i>et al.</i> (2015a)
Nothrotheriinae			
<i>Mionothropus cartellei</i>	LACM 4609 [holotype] (Fig. 6A)	Huayquerian SALMA of Brazil-Peruvian Amazon	De Iuliis <i>et al.</i> (2011)
<i>Pronothrotherium typicum</i>	FMNH P14515 (Fig. 6B)	Huayquerian SALMA of Patagonia Argentina	Not figured
<i>Nothrotheriops texanum</i>	UF 86897	Irvingtonian NALMA of North America	Not figured
<i>Nothrotherium maquinense</i>	MCL 1020 (Fig. 6D)	Ensenadan SALMA of Brazil	Cartelle & Fonseca (1983)
Unnamed	UCMP 39949	Laventan SALMA of La Venta, Colombia	Hirschfeld (1985)
Nothrotheriidae			
Megatherioidea of uncertain phylogenetic affinities			
<i>Diaboloatherium nordenskioldi</i>	NMR-PZ M 4286 [holotype] and MNHN CPN 9-1	Lujanian SALMA of Peru, Chile, and Argentina	Pujos <i>et al.</i> (2007)
<i>Hapalops</i> sp.	FMNH P13133	Santacrucian SALMA of Patagonia Argentina	Scott (1903)
Mylodontidae			
<i>Catonyx cuvieri</i>	MCL 22751	Lujanian SALMA of Brazil	Cartelle, De Iuliis & Ferreira (2009)
<i>Simomylodon uccasamamensis</i>	MNHN AYO 10	Montermosan-Chapadmalalan of Ayo-Ayo, Viscachani, and Pomata-Ayte, Bolivia	St-André <i>et al.</i> (2010)

respectively. In vestibular view, the central valley is deeper than in m1.

As in *Hapalops* and most Nothrotheriidae, such as *Xyophorus* (Fig. 3A) and *Lakukullus* (Fig. 3E), the m3 of *Aymaratherium* shows a distinct pattern. In Megatheriinae and *Aymaratherium*, the transverse

diameter of the last lower molariform tooth is strongly reduced distally. The distal lophid of *Aymaratherium* is broken at the crown, but shallow and distovestibular apicobasal sulci are present (Fig. 2K, L). In occlusal view, the mesial lophid is mesially convex and cuspid 'C' is reduced. The transverse valley is

Table 3. List of principal sloths astragali considered for comparison with *Aymaratherium jeani* gen. nov., sp. nov.

Taxon	Specimen	Age and locality	Reference
Megalonychidae			
<i>Pliometanastes prostitus</i>	UF 13782	Hemphillian NALMA	Hirschfeld (1981)
Megatheriidae			
Megatheriinae			
<i>Megathericulus patagonicus</i>	MACN-A-11151 [holotype] (Fig. 8A–C)	Friasian SALMA of Chubut and Santa Cruz Provinces, Argentina	De Iuliis <i>et al.</i> (2008)
Nothrotheriidae Thalassocninae			
<i>Thalassocnus antiquus</i>	MUSM 228 [holotype]	Huayquerian SALMA of southern Peruvian coast	Amson <i>et al.</i> (2015b)
<i>Thalassocnus natans</i>	MNHN.F.SAS 163	Montehermosan SALMA of southern Peruvian coast	Amson <i>et al.</i> (2015b)
Nothrotheriinae			
<i>Pronothrotherium typicum</i>	FMNH P15233 (Fig. 8D–F)	Huayquerian SALMA of Patagonia Argentina	Not figured
<i>Xyophorus villarroeli</i>	MNHN ACH 15 (Fig. 8J–L)	Huayquerian SALMA of Achiri, Bolivia	St-André (1996)
Megatherioidea of uncertain phylogenetic affinities			
<i>Hapalops</i> sp.	MLP 88-X-2-1.4	Santacrucian SALMA of Patagonia Argentina	Scott (1903)
<i>Diabolotherium nordenskioldi</i>	MNHN CPN 9-1	Lujanian SALMA of Peru, Chile, and Argentina	Pujos <i>et al.</i> (2007)

shallower than in m1–m2. In mesial view the mesial lophid is convex apically and the apicobasal height of the mesial wear facet is reduced lingually (4.8 mm vestibularly, 2.8 mm at the centre and 2 mm lingually).

HUMERUS (FIGS 4, 5 AND APPENDIX S1)

Aymaratherium is represented by three humeri from three individuals of distinct ontogenetic stages: an adult (MNHN-Bol-V 012874; Fig. 4) on which the description is mainly based, a sub-adult (MNHN-Bol-V 012875; Fig. 5A, B) and a juvenile (MNHN-Bol-V 003787; Fig. 5C, D). The sutures are easily distinguishable between unfused epiphysis and diaphysis on non-adult specimens, and the juvenile humerus is somewhat more robust than the sub-adult humerus (Fig. 5). Although these humeri represent different ontogenetic stages, they present a common general pattern we consider as characterizing this new nothrotheriid taxon. The three humeri bear slight pathological abnormalities, mainly in the epiphysis and especially in the most complete specimen (MNHN-Bol-V 012874; Fig. 4). Such pathologies are relatively common in ground sloths (McDonald, 1989) and consist of exostoses, which could possibly reflect injury repair.

In contrast to Mylodontidae, Megatheriinae and most Megalonychidae, the humeri of nothrotheriids

are generally slender with a moderately developed deltopectoral shelf and a prominent entepicondyle. Humeri of modern tree-sloths *Bradypus* and *Choloepus* are disproportionately elongated and secondarily modified in relation to their suspensory posture and locomotion, features and habits that probably evolved convergently in Bradypodidae and Megalonychidae (Nyakatura, 2012). The humerus of *Aymaratherium* is gracile as in *Mionothropus* (Fig. 6A), *Pronothrotherium* (Fig. 6B) and *Diabolotherium* (NMR-PZ M4286 and MNHN CPN 9-1; Pujos *et al.*, 2007). However, the general morphology of the humerus of the Bolivian nothrotheriid is more robust than that of *Nothrotherium maquinense* (Fig. 6D), and less robust than that of *Thalassocnus* species (and especially *T. natans*; Fig. 6C), megatheriid planopsines (e.g. *Planops martini*; Fig. 6E), *Hapalops* sp. (Fig. 6F) and megatheriines [e.g. *Megatherium (P.) tarijense*; Fig. 6G].

In *Aymaratherium*, the entire proximal epiphysis is modified in comparison with other Megatherioidea (except *Diabolotherium*) by a combination of an asymmetry of the greater and lesser tubercles with a medial inclination of the head (Fig. 4E, F). The greater tubercle is much more prominent and proximally extended than the lesser tubercle, and the latter is not well separated from the proximal epiphysis (Fig. 4A, E–H). A similar asymmetry of the tubercles is generally present in Megalonychidae but never so

Table 4. List of principal sloths calcanei considered for comparison with *Aymaratherium jeani* gen. nov., sp. nov.

Taxon	Specimen	Age and locality	Reference
Megalonychidae			
<i>Pliometanastes prostitus</i>	UF 13781	Hemphillian NALMA of North America	Hirschfeld (1981)
<i>Megalonyx jeffersonii</i>	LACM 20095	Rancholabrean NALMA of North America	Stock (1925)
Megatheriidae Planopsinae			
<i>Prepoplanops boleadorensis</i>	MLP 97-XI-3-1 [holotype]	Miocene [dubious age] of Patagonia, Argentina	Carlini <i>et al.</i> (2013)
Megatheriinae			
<i>Megatherium (Pseudomegatherium) tarijense</i>	FMNH P14216	Lujanian SALMA of Tarija, Bolivia	De Iuliis (1996)
<i>Eremotherium laurillardii</i>	ROM 14795	Irvingtonian and Rancholabrean SALMAs of North America	De Iuliis (1996)
Nothrotheriidae Thalassocninae			
<i>Thalassocnus antiquus</i>	MUSM 228 [holotype]	Huayquerian SALMA of southern Peruvian coast	Amson <i>et al.</i> (2015b)
<i>Thalassocnus carolomartini</i>	MNHN.F.SAO 16	Chapadmalalan SALMA of southern Peruvian coast	Amson <i>et al.</i> (2015b)
<i>Thalassocnus natans</i>	MNHN.F.SAS 234	Montehermosan SALMA of southern Peruvian coast	Amson <i>et al.</i> (2015b)
Nothrotheriinae			
<i>Nothrotheriops texanum</i>	UF 82938	Irvingtonian NALMA of North America	Not figured
<i>Nothrotherium maquinense</i>	MCL 1020	Ensenadan SALMA of Brazil	Cartelle & Fonseca (1983)
<i>Pronothrotherium typicum</i>	FMNH P14467	Huayquerian SALMA of Patagonia Argentina	Not figured
Megatherioidea of uncertain phylogenetic affinities			
<i>Hapalops</i> sp.	MLP 68-VI-25316	Santacrucian SALMA of Santa Cruz Province, Argentina	Scott (1903)

pronounced, except in *Eucholoeops* (see Pujos *et al.*, 2007: fig. 10). A similar condition is also present in *Diabolotherium* (see Pujos *et al.*, 2007: fig. 10A–D), but in the latter taxon, the tubercles are extremely reduced. Among other Nothrotheriidae (e.g. *Mionothropus* and *Thalassocnus*; Fig. 6A, C) and Planopsinae (e.g. *Prepoplanops*, see Carlini *et al.*, 2013: fig. 5A, B, and *Planops*; Fig. 6E), the greater and lesser tubercles display nearly the same proximal development and they are located at the same level. In *Nothrotherium maquinense* (Fig. 6D), the two tubercles are strongly reduced. In Megatheriinae, including in early middle Miocene forms such as *Megatheriops rectidens* (MACN 2818), the tubercles are extremely reduced (Fig. 6D). In proximal view, the greater tubercle is located laterally and expands anteroposteriorly, whereas the lesser tubercle is located anteromedially and expands posteromedially to anterolaterally (Fig. 4A, B). The articular

surface of the head of the humerus is oval with its major axis oriented posteromedially to anterolaterally (Fig. 4A, B).

In posterior view (Fig. 4G, H), the head of the humerus is much more medially inclined than in other nothrotheriids (especially *Thalassocnus*; Amson *et al.*, 2015a: fig. 6C) and Megatheriidae. A similar but less marked condition is present in *Diabolotherium* (Pujos *et al.*, 2007: fig. 10B, D). The bicipital groove is deep, anteroposteriorly elongated and pierced towards the greater tubercle by five large foramina. The presence of a well-developed bicipital groove is considered to be plesiomorphic for the clade Nothrotheriidae (Amson *et al.*, 2015a), and is observed in basal nothrotheriids such as *Mionothropus*, *Thalassocnus* and *Pronothrotherium*. The groove is poorly developed in *Nothrotheriops* and almost absent in *Nothrotherium*. In posterior view, the neck of the humeral head of MNHN-Bol-V 012874

presents several osteological pathologies that are also present on the anterior surface of the greater tubercle (Fig. 4E–H). In lateral view, the greater tubercle gives rise distally to a small crest (Fig. 4I, J) that possibly represents the insertion of the teres minor muscle (Amson *et al.*, 2015a).

In *Aymaratherium*, the lateral and medial crests on the proximal third of the posterior diaphyseal surface mark the origin of the triceps muscle (Fig. 4G, H). This insertion lies distal to the head of the humerus and extends proximomedially to posterolaterally. It widens slightly distally and is bordered laterally by the beginning of the deltoid crest. Two principal areas for muscle attachment are observable on the diaphysis of the humerus in *Aymaratherium*: proximoposteriorly for the triceps muscle and anteriorly – and anterolaterally – for the deltoid and pectoral muscles. According to De Iuliis (2003), the deltopectoral plate (or deltopectoral shelf following De Iuliis *et al.*, 2011) begins proximally on the lateral face of the diaphysis, just behind the greater tubercle (Fig. 4I, J). It continues distally, expanding anteriorly toward the central part of the diaphysis and then decreasing in width rapidly towards the distal epiphysis (Fig. 4E, F). In *Aymaratherium*, as in most ‘ground sloths’, the deltopectoral shelf is formed by the deltoid (laterally) and better developed (anteriorly) pectoral crests, and it corresponds to the insertion area for the strong deltopectoral musculature. The brachiocephalic crest identified in *Thalassocnus* species (except in *T. antiquus*; Amson *et al.*, 2015a), and generally located between the deltoid and pectoral crests, is not observable in *Aymaratherium* and most nothrotheriid sloths. The deltopectoral shelf extends through the entepicondylar ridge (= entepicondylar bar) in the direction of the entepicondyle (or medial epicondyle; Figs 4E, F, K, L and 5B, 6A–F). The deltopectoral shelf is generally poorly developed in Nothrotheriinae (Figs 4–6) in comparison with Thalassocninae (Fig. 6C and Amson *et al.*, 2015a), Mylodontidae, Megalonychidae (see Pujos *et al.*, 2007: fig. 10), Planopsinae (e.g. *Planops*; Fig. 6E) and *Hapalops* (Fig. 6F). In Pleistocene Megatheriinae, the deltoid and pectoral crests occur together on the centre of the anterior diaphyseal surface (De Iuliis, 2003), and form a relatively reduced V-shaped deltopectoral shelf (e.g. *Megatherium*; Fig. 6G), but in less derived megatheriines such as *Megathericulus* and *Megatheriops*, the general morphology of the humerus is more gracile, and the deltopectoral shelf resembles that of other sloths more closely. In *Aymaratherium*, the deltopectoral shelf is weakly developed especially anteriorly. The shelf is more developed than in *Nothrotherium* and *Diabolotheerium*, somewhat less than in *Mionthropus*, and considerably less than in

Nothrotheriops, *Pronothrotherium* and *Thalassocnus* (Fig. 6A–D).

The distal epiphysis of MNHN-Bol-V 012874 expands transversely and bears pathological growths (exostoses) above the trochlea and capitulum on the anterior and posterior surfaces (Fig. 4E–J). A large entepicondylar ridge connects the deltopectoral shelf to the entepicondyle, and delimits the entepicondylar foramen, which is oval, opens anteroposteriorly, and serves for the passage of the brachial artery and median nerve (Fig. 4E, F, K, L). The foramen is not present in *Diabolotheerium*, Megatheriinae, some Megalonychidae (e.g. *Parocnus* and *Mesocnus*) or Mylodontidae scelidotheriines (e.g. *Catonyx cuvieri*), but is present in all Nothrotheriidae, Planopsinae and *Hapalops*. The entepicondyle (or medial epicondyle) is rounded in outline, as in *Thalassocnus natans* (Fig. 6C), and does not bear a marked medial extension as in *Pronothrotherium*, *Mionthropus*, *Thalassocnus* and the unnamed nothrotheriid from the middle Miocene of La Venta (UCMP 39949; Hirschfeld, 1985). In *Aymaratherium*, the ectepicondyle (or lateral epicondyle) is slightly larger than in *Diabolotheerium*. The ectepicondyle is bordered anteriorly by the slightly sinuous lateral supracondylar line (= supinator crest, Fig. 4E–G). In *Aymaratherium*, the epicondyles are approximately equal in size, in contrast to other Nothrotheriidae, where the entepicondyle is larger than the ectepicondyle.

The trochlea is concave transversely, convex anteroposteriorly and slightly wider than the capitulum, as in *Mionthropus* and *Thalassocnus* (Figs 4B, C and 6A–C). The distal edge of the trochlea is oriented proximolateral/distomedial, not transversely as in *Diabolotheerium*. The capitulum is round and convex like most ‘ground sloths’, suggesting good pronation and supination, as in *Diabolotheerium* (Pujos *et al.*, 2007). The radial fossa is short, particularly well marked, and located proximal to the capitulum (Fig. 4E, F). We interpret this peculiar morphology as pathological. Indeed, in MNHN-Bol-V 003787 (Fig. 5A, C), the radial fossa appears as a uniformly curved arc as in the holotype of *Diabolotheerium* (NMR-PZ-M4286; Pujos *et al.*, 2007). It is smaller and shallower in the sub-adult *Aymaratherium* than in *Thalassocnus* (especially *T. natans* and *T. littoralis*; see Amson *et al.*, 2015a: fig. 5). The distal epiphysis exhibits pathologies on the anterior surface, at the level of the proximal border of the trochlea and on the posterior surface surrounding the olecranon fossa, and between the entepicondyle and the trochlea (Fig. 4E–H). Posteriorly, the olecranon fossa is deep.

The juvenile specimen, MNHN-Bol-V-003787 (Fig. 5C, D), is similar but slightly more robust than MNHN-Bol-V 012874; the deltopectoral shelf exhibits a similar development (Fig. 5C, D). The sub-adult

specimen, MNHN-Bol-V 012875 (Fig. 5A, B), is more slender than the adult specimen; the entepicondylar crest and entepicondyle are poorly developed and the deltopectoral shelf is barely visible. Except for the presence of an entepicondylar foramen, the humerus of *Aymaratherium* shares several similarities with *Diabolotherium* that are not present in other nothrotheriids (see Pujos *et al.*, 2007).

ASTRAGALUS (FIG. 7A–H, Q, AND APPENDIX S1)

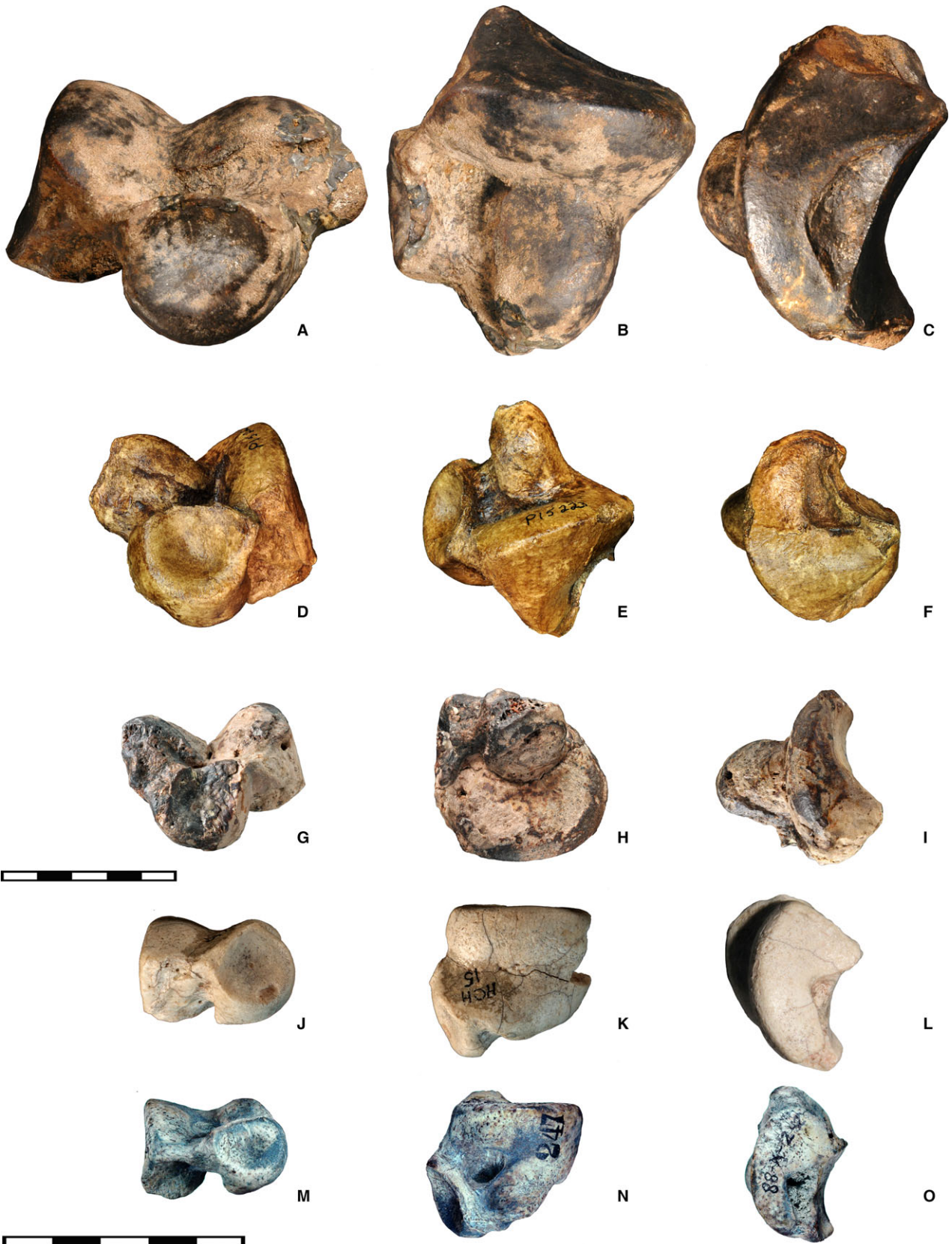
In addition to the humerus and femur, the astragalus of *Aymaratherium* is well preserved. It is a tarsal element that offers considerable phylogenetic and morphofunctional information. MNHN-Bol-V 012983 is a complete right astragalus (Fig. 7A–H); its plantar articular facets match almost perfectly with the corresponding facets of the calcaneum of a second individual, described below and also referred to *Aymaratherium* (Fig. 7I–Q). This astragalus shows the typical megatherioid morphology with a well-marked odontoid process (Fig. 7A–D).

In the *Aymaratherium* astragalus, the discoid and odontoid facets of the trochlea tali meet approximately at a right angle (approximately 85°) in anterior view (Fig. 7A, B). This angle is slightly wider in *Thalassocnus antiquus*, *T. natans* (Fig. 8G), *Pronothrotherium* (Fig. 8D) and Megatheriinae such as *Megathericulus* (Fig. 8A), and considerably wider in Planopsinae, Nothrotheriini, *Xyophorus* (Fig. 8K) and *Hapalops* (Fig. 8N). The odontoid and discoid processes are convex transversely and anteroposteriorly. In dorsal view, the odontoid process is well defined, bulky and almost perpendicular to the anteroposterior main axis of the discoid facet, whereas in *Xyophorus* (Fig. 8J), *Hapalops* (Fig. 8M) and *Diabolotherium* (Pujos *et al.*, 2007: fig. 14), it is poorly differentiated. In anterior view, the odontoid process of the *Aymaratherium* astragalus does not bear a strong plantar extension (Fig. 7A, B) in contrast to the condition observed in astragali of other Megatheriidae (Fig. 8A), *Pronothrotherium* (Fig. 8D) and Thalassocninae (Fig. 8G and Amson *et al.*, 2015b). It is shallow, as in Megatheriinae. In anterior view, the transverse diameter of the odontoid process is shorter than that of the discoid process (Fig. 7A, B); the opposite condition occurs in Thal-

socninae (Amson *et al.*, 2015b: fig. 24; Fig. 8G) and Megatheriinae (e.g. *Megathericulus*; Fig. 8A). A fossa lies between the anterior extremity of the discoid process and the head (Fig. 7E).

On the head of the astragalus the navicular facet is medially positioned, and the cuboid facet is lateral and ventral (Fig. 7A, B) as in Megatheriinae (Fig. 8A), Thalassocninae (Fig. 8G), Nothrotheriini and *Pronothrotherium* (Fig. 8D). In *Diabolotherium*, *Xyophorus* and *Hapalops* (Fig. 8J, M), the navicular and cuboid facets extend medially to the extremity of the odontoid process. Two typical distinct astragalar patterns exist in Megatheriinae and *Hapalops*, whereas the condition in Planopsinae is approximately intermediate (e.g. *Planops*; see Hoffstetter, 1961: fig. 12). In anterior view, the dorsal aspect of the head in *Aymaratherium* is located just below the discoid surface (Fig. 7A, B) as in *Thalassocnus*, a condition intermediate between that observed in Megatheriinae, in which the head is more plantar (e.g. *Megathericulus*; Fig. 8A), and *Hapalops* (Fig. 8M), in which the head is more dorsolateral relative to the discoid surface. The cuboid facet, mainly plantar in position, is convex anteroposteriorly and transversely. It is bordered medially by the navicular facet and posteriorly by the sustentacular facet (Fig. 7A, B, G, H). In contrast to *Thalassocnus* species (see Amson *et al.*, 2015b: fig. 23C, D), in anterior view the cuboid facet does not extend onto the base of the discoid facet. The navicular facet comprises a deep and concave anterior cupula, and a reduced medioplantar portion that is convex dorsoplantarly and transversely as in all Megatherioidea and in the majority of sloths. The navicular facet constitutes the medial border of the head. In plantar view it is bordered laterally by the cuboid facet and contacts the sustentacular facet posterolaterally (Fig. 7G, H). As in almost all sloths, the lateral surface of the astragalus of *Aymaratherium* is entirely occupied by the fibular facet. It is slightly convex anteroposteriorly and dorsoplantarly, triangular in shape, and its apex orientated posteriorly (Fig. 7C, D). In MNHN-Bol-V 012983, a deep anteroposterior notch, possibly pathological, almost completely separates the fibular facet into dorsal and plantar portions (Fig. 7C, D). In anterior view, the angle between the discoid and fibular facets is less than 90° (Fig. 7A, B).

Figure 8. Photographs of astragali of several Megatherioidea in anterior (A, D, G, J, M), dorsal (B, E, H, K, N) and lateral or lateroplantar (C, F, I, L, O) views. A–C, right astragalus of *Megathericulus patagonicus* (MACN-A-11151, holotype) from the Friasian SALMA of Laguna Blanca, Chubut, Argentina; D–F, left astragalus of *Pronothrotherium* sp. (cast of FMNH P15223) from the early Pliocene of Catamarca Province, Argentina; G–I, *Thalassocnus natans* (MNHN.F.SAS 163) from the Montehermosan SALMA of Peruvian coast; J–L, *Xyophorus villarroeli* (MNHN ACH 15) from the Huayquerian SALMA of Achiri, Bolivia; M–O, *Hapalops* sp. from the Santacrucian SALMA of Patagonia Argentina. Scale bar = 50 mm.



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The astragalar plantar surface bears the cuboid and navicular facets, and the two calcaneal facets (ectal and sustentacular). The ectal facet is elongated and rectangular, extended anterolaterally to posteromedially, and concave along its main axis (Fig. 7G, H) as in Megatheriidae, Nothrotheriini, Thalassocninae and *Pronothrotherium*; in *Xyophorus*, *Hapalops*, *Diabolootherium* and some Megalonychidae, such as *Pliometanastes prostitus* (Pujos et al., 2007: fig. 15), the ectal facet is L-shaped. The sustentacular facet is smaller and concave anteroposteriorly. It extends anteriorly to the cuboid facet, and narrows posteriorly. The sulcus tali extends anterolaterally to posteromedially, and is narrower posteromedially.

CALCANEUM (FIG. 7I–P, R, AND APPENDIX S1)

The complete right calcaneum MNHN-Bol-V 008954, referred to *Aymaratherium* (Fig. 7I–P), resembles that of the thalassocnine lineage recently described by Amson et al. (2015b) and especially that of *Thalassocnus antiquus*. It is approximately intermediate between the slender and elongated calcaneum typical of nothrotheriids (e.g. *Nothrotheriops*, *Nothrotherium*, and *Pronothrotherium*) and megalonychids (e.g. *Pliometanastes* and *Megalonyx*), and that of megatheriines [e.g. *Megatherium (P.) tarijense* and *Eremotherium laurillardii*], in which the diaphysis is markedly robust and relatively short. The diaphyseal shaft or neck is oval in section (Fig. 7I, O), as in *Thalassocnus* and Megatheriinae, in contrast to other Nothrotheriinae, Planopsinae, *Hapalops* and allied genera, in which the neck is generally dorsoplantarly compressed and flattened. The form of the tuber calcanei reflects the form of the neck, being rounded in the former group of taxa and flattened in the latter group.

The posterior end of the calcaneum, including the tuber calcanei, resembles that of megatheriines and *Thalassocnus*, in which the tuber is tapered posteriorly and elongated in the middle. In genera such as *Hapalops*, *Prepoplanops* and nothrotheriines, the tuber is, by contrast, broad and relatively short, and of approximately constant length (i.e. the distance between the epiphyseal line and end of the tuber is uniform across its width), as well as flattened (as noted above), thus imparting an axe-like appearance to this part of the calcaneum. In *Aymaratherium*, the tuber resembles that of megatheriines and *Thalassocnus*, but is not drawn posteriorly to the same degree.

The posterolateral and posteromedial processes of the tuber calcanei are nearly symmetric in dorsal view, although the posterolateral process is slightly more prominent and projects to a greater degree than the posteromedial process (Fig. 7I, J). In

Nothrotherium and *Pronothrotherium*, only the proximal margin of the tuber calcanei contacts the ground (Amson et al., 2015b), whereas in *Thalassocnus*, *Aymaratherium* (Fig. 7K–N) and Megatheriinae (e.g. *Megatherium* and *Eremotherium*), only the lateral and medial processes of the tuber calcanei contact the ground. As in species of *Thalassocnus*, the dorsal portion of the tuber calcanei bears a small tuberosity visible especially in lateral view (Fig. 7K–N). Amson et al. (2015b) noted that this tuberosity is also present in megatheriines, such as *Megatherium (P.) americanum*, and perhaps served for the insertion of the gastrocnemius muscle.

The arrangement of the astragalar and cuboidal articular facets in *A. jeani* (Fig. 7O, P), at the anterior end of the calcaneum is similar to that in *Thalassocnus carolomartini*, with the major axis of the ectal facet for the astragalus orientated almost dorso-plantarly. In several species of *Thalassocnus* (i.e. *T. natans* and *T. antiquus*), a medial torsion of the anterior epiphysis of the calcaneum results in the main axis of the ectal facet, extending mediodorsally to lateroplantarly (see Amson et al., 2015b). In *Megatherium* [e.g. *M. (P.) tarijense*], the main axis of the ectal facet is transverse and the sustentacular facet for the astragalus and the cuboidal facet are located on the plantar portion of the anterior epiphysis (De Iuliis, 1996). In *Aymaratherium*, the ectal facet is the largest articular facet and the sustentacular the smallest one. In anterior view, the ectal facet for the astragalus is oval and occupies the dorsolateral portion of the anterior epiphysis; it is convex dorsoplantarly and transversely (Fig. 7O, P). The ectal facet is bordered dorsally by a transverse groove that is absent in other Nothrotheriidae. As usual in sloths (but not in all Mylodontidae), the ectal facet is separated from the sustentacular and cuboidal facets by a deep sulcus calcanei. The sustentacular and cuboidal facets are not separated as in Planopsinae (e.g. *Prepoplanops*), Nothrotheriini, *Diabolootherium*, *Hapalops* and allied genera, but contiguous as in *Thalassocnus* (and especially *T. carolomartini*) and Megatheriinae. In *Aymaratherium*, the sustentacular facet is oval, transversely concave, and its main axis is dorsoplantar. The cuboid facet is plantar to the sustentacular facet. It is transversely and dorsoplantarly concave, and extends lateroplantarly on the anterior surface of the calcaneum.

PHYLOGENETIC ANALYSIS

PHYLOGENETIC DATASET

A cladistic assessment of the cranial and postcranial evidence so far available was performed to investi-

gate and formalize the phylogenetic position of *Aymaratherium* among nothrotheriids. The phylogenetic data matrix was slightly modified from the data set recently published by De Iuliis *et al.* (2011). The present analysis included a new character (character 67 – shape of the calcaneum). We also modified the states of character 34 (presence of labial and lingual grooves in the molariform teeth), and supplemented the coding of *Thalassocnus* based on the recent work of Amson *et al.* (2015a,b).

The phylogenetic data set for nothrotheriid ground sloths comprised seven taxa and 67 characters. The ingroup included the nothrotheriid taxa that are represented by sufficiently abundant cranial and postcranial osteological information (see De Iuliis *et al.*, 2011; for further details): *Thalassocnus*, *Mionthropus*, *Pronothrotherium*, *Nothrotherium* and *Nothrotheriops*, to which the current analysis added *Aymaratherium*. *Thalassocnus* is a peculiar Mio-Pliocene sloth, secondarily adapted to a sub-aquatic life style, that lived in the Pacific desert coast region of Peru and Chile. The *Thalassocnus* lineage from the Peruvian Pisco Formation is represented by five species (e.g. McDonald & de Muizon, 2002; de Muizon *et al.*, 2004a; Amson *et al.*, 2014; table 1) that range in age from the Huayquerian to the Chapadmalalan SALMAs. *Mionthropus cartellei*, the only Amazonian nothrothere, is represented by a single reasonably complete specimen from the Huayquerian SALMA of Acre (Peruvian–Brazilian frontier; De Iuliis *et al.*, 2011). *Pronothrotherium typicum*, the first nothrotheriid genus and species erected (at the beginning of the 19th century by Ameghino, 1907), is represented by a partial skeleton from the Araucano Formation of Entre Rios Province (Argentina) and isolated elements from the Huayquerian SALMA of Argentina and Uruguay. In addition to these three Neogene taxa, the Pleistocene forms *Nothrotheriops* and *Nothrotherium*, from North America and Brazil, respectively (e.g. Stock, 1925; Cartelle & Fonseca, 1983), were added in the ingroup. The early Miocene (Santacrucian SALMA) basal Megatherioidea *Hapalops*, from the Santa Cruz Province of Argentina, was employed as an outgroup. This taxon is the most basal megatherioid represented by several complete specimens (Toledo *et al.*, 2014), and as such, it is frequently treated as an outgroup in megatheriid and nothrotheriid phylogenetic analyses (e.g. McDonald & de Muizon, 2002; Pujos, 2006; De Iuliis *et al.*, 2011).

Following De Iuliis *et al.* (2011), nine characters were considered as additive (ordered): characters 3 (posterior palatal shelf), 5 (morphology of pterygoid pneumatic sinus), 37 (proximal projection of lesser tubercle of humerus), 38 (height of deltopectoral shelf and size of pectoral ridge on anterior humeral

diaphysis), 51 (morphology of dorsolateral surface of scaphoid), 53 (aspect of the magnum), 59 (position of greater trochanter of femur relative to crest between head and greater trochanter), 60 (position of third trochanter of femur) and 62 (position of patellar and medial tibial articular facets of femur). The multi-state osteological characters concern variation of the skull (characters 1–28), lower jaw (29–31), upper and lower teeth (32–34), forelimb (35–56, humerus, radius, ulna, carpals, metacarpals and phalanges) and hind limb (57–67, femur, patella, astragalus, calcaneum, and metatarsals) (see Supporting Information Appendix S2 for morphological characters and character state lists). In the text characters are identified by number and their states appear in superscript (i.e. 1², character state 2 of character 1).

PHYLOGENETIC ANALYSIS

The character matrix was compiled using Mesquite (Maddison & Maddison, 2011; Appendix S3); unknown character states were coded as ‘?’. Phylogenetic analyses were performed using cladistic methodology (Kitching *et al.*, 1998). The phylogenetic dataset presented in Appendix S3 was analysed with equally weighted parsimony (equally weighted character analysis – EWA; Goloboff, 1993) using the parsimony software TNT v. 1.0 (Goloboff, Farris & Nixon, 2008a, b). Considering the low number of taxa (i.e. seven), the data matrix was analysed using the implicit enumeration algorithm. Support values for each node were calculated using Total Bremer Support (TBS; Bremer, 1994; Goloboff & Farris, 2001), Standard Bootstrap (Hillis & Bull, 1993; Gaudin, 2004) and Standard Jackknife resamplings, the values of which are reported in absolute frequencies (Fig. 9).

RESULTS (FIG. 9 AND APPENDIX S4)

This TNT analysis provided two most parsimonious trees (MPTs; Fig. 9) of 114 steps (consistency index = 0.719, retention index = 0.584); a strict consensus (SC) was calculated on which the synapomorphies common to the two MPTs were plotted. From these results, and given that only a single outgroup taxon was included (i.e. *Hapalops*), the monophyly of Nothrotheriidae was not tested. In both MPTs (MPT1 and MPT2) within Nothrotheriidae, *Thalassocnus* (= Thalassocninae) is sister taxon to Nothrotheriinae (clade B = all other Nothrotheriidae), a topology that mirrors the results of the analyses performed by de Muizon *et al.* (2003) and De Iuliis *et al.* (2011). Nothrotheriinae, which includes *Aymaratherium*, *Pronothrotherium*, *Mionthropus*, *Nothrotherium* and *Nothrotheriops*, is monophyletic

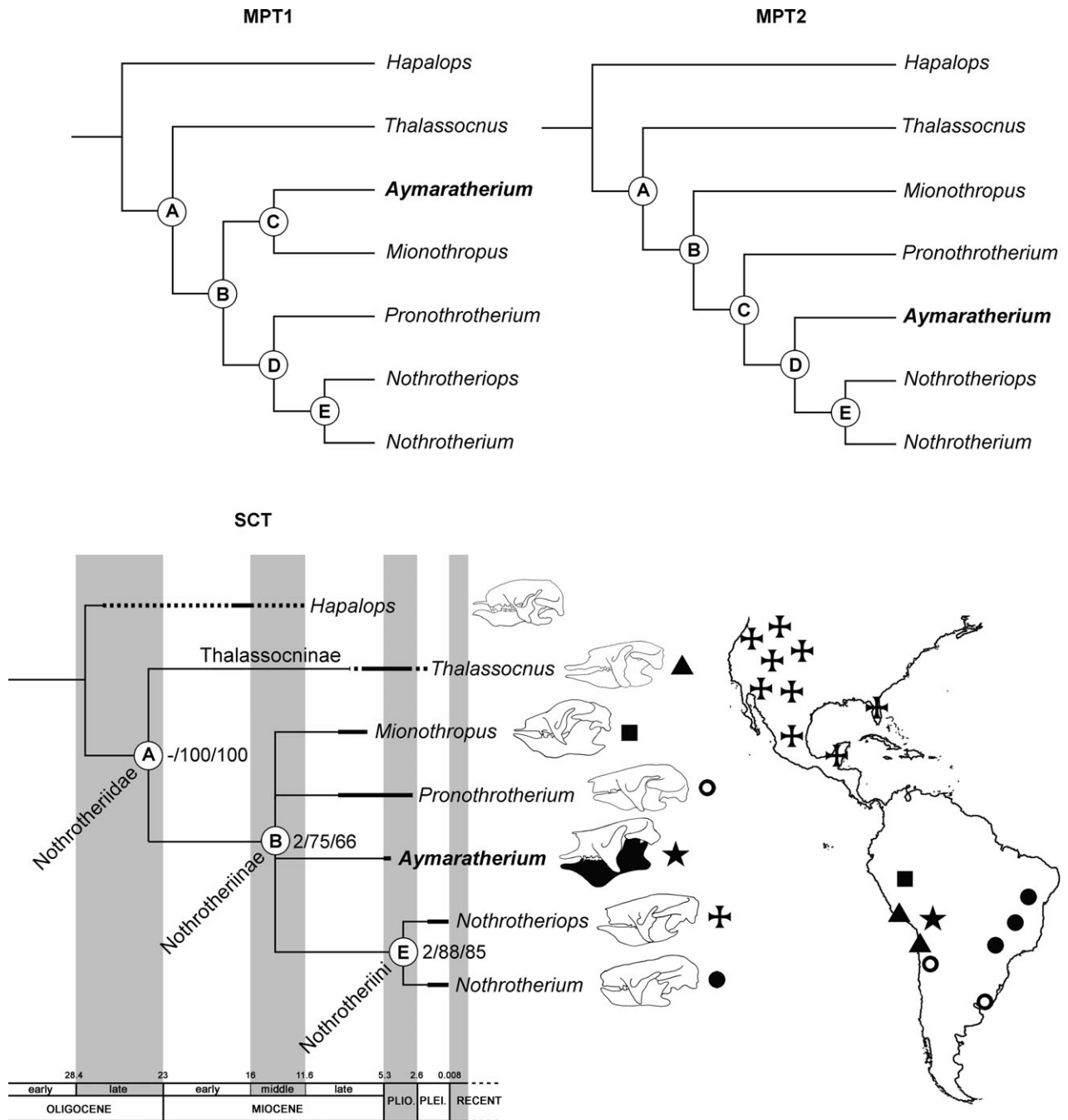


Figure 9. Most parsimonious trees (MPT1 and MPT2) and strict consensus tree (SCT) obtained based on phylogenetic analysis of nothrotheres using TNT (Goloboff *et al.*, 2008a,b). Tree length = 114 steps, CI = 0.719, RI = 0.584; numbers at each node represent, from left to right, Bremer support, Bootstrap and Jackknife values. The SCT is illustrated in chronostratigraphic context, following the known stratigraphical ranges for the relevant taxa.

and diagnosed by 11 unambiguous (= exclusive) synapomorphies (6^1 , 7^1 , 14^1 , 27^1 , 28^1 , 29^1 , 51^2 , 57^1 , $59^{2,3}$, 61^1 and 62^1), identical in both MPTs.

Based on fragmentary material, *Aymaratherium* could only be scored for 13 mandibular, dental and

postcranial characters, which may explain its unresolved phylogenetic position among Nothrotheriinae. In MPT1, *Aymaratherium* and *Mionothropus* constitute the clade C, which is the sister group to other Nothrotheriinae. Clade C is supported by a single



Figure 10. Hypothetical life reconstruction of *Aymaratherium jeni* gen. nov., sp. nov. by Jorge Gonzalez.

unambiguous synapomorphy, a straight anterior edge of symphyseal spout in lateral view (30⁰). Node D [*Pronothrotherium* [*Nothrotheriops*, *Nothrotherium*]] is strongly supported by eight unambiguous synapomorphies (3¹, 8¹, 15¹, 21¹, 58¹, 60¹, 62² and 64¹; Appendix S4-1). The Pleistocene *Nothrotheriops* and *Nothrotherium* comprise, as suggested by De Iuliis *et al.* (2011), the monophyletic Nothrotheriini, which is diagnosed by seven unambiguous synapomorphies (4¹, 5², 39¹, 43¹, 46¹, 47¹ and 63¹).

In MPT2, *Mionothropus* appears as the earliest diverging nothrotheriine and sister group to clade C, which is formed by [*Pronothrotherium* [*Aymaratherium* [*Nothrotheriops*, *Nothrotherium*]]]. Clade C is supported by the same six unambiguous synapomorphies as clade D of MPT1 (i.e. [*Pronothrotherium* [*Nothrotheriops*, *Nothrotherium*]], Appendix S4-1). MPT2 clade D comprises *Aymaratherium* and Nothrotheriini, and is supported by a single unambiguous synapomorphy, a humerus with little raised deltopectoral shelf and weakly developed pectoral ridge (38²). Finally, Nothrotheriini [*Nothrotheriops*, *Nothrotherium*] is supported by a single unambiguous synapomorphy (39¹).

In the strict consensus tree (SCT), the clades Nothrotheriinae (node B) and Nothrotheriini (node E) are not strongly supported (Bremer supports = 2) but display moderately high Bootstrap supports (75 and 88%, respectively) and Jackknife supports (66 and 85%, respectively) (Fig. 9). Nothrotheriinae and Nothrotheriini are monophyletic and supported by 11 and two unambiguous synapomorphies, respectively (Appendix S4-2). Using the pruning option of TNT,

among Nothrotheriinae, *Aymaratherium* appears as the unstable taxa (due to the lack of scored characters) and occupies an uncertain position with respect to *Mionothropus* and *Pronothrotherium*, forming a polytomy.

In the SCT, *Aymaratherium* is characterized by one unambiguous autapomorphy, a large and bulky calcaneum (67¹, convergent with *Thalassocnus* and *Thalassocninae* in general) and one ambiguous synapomorphy, a humerus with little raised deltopectoral shelf and weakly developed pectoral ridge (38²), also present in Nothrotheriini.

DISCUSSION ON THE ANATOMY AND PHYLOGENETIC AFFINITIES OF *AYMARATHERIUM*

Aymaratherium displays a combination of characters that is somewhat unusual for a megatherioid sloth, a situation reminiscent of that of *Thalassocnus* (nothrotheriid megatherioid), *Pseudoglyptodon* ('proto-sloth' of disputed affinities; McKenna *et al.*, 2006) and *Diabolootherium* (megatherioid sloth; Pujos *et al.*, 2007). This may be interpreted as indicating that our knowledge of South American mammals, especially Xenarthra, is far from being complete, an assertion that is bolstered by several recent discoveries (e.g. Billet *et al.*, 2011) in areas of South America other than Patagonia. The latter region was for a long time the principal source of fossil mammals, and the pattern and timing of South American mammalian evolution was mainly based on these fossils and the deposits from which they were recovered. Moreover, the Patagonian region was regarded as central in the evolution of endemic South American groups such as notoungulates and xenarthrans. However, recent discoveries in other fossiliferous areas of South America, such as the Andes and the Amazon basin, have substantially improved our understanding of fossil vertebrates, particularly mammals. Among these discoveries, we note new remains of 'ground sloths' belonging to the four commonly recognized Tardi-grada clades (traditionally ranked as families) from Bolivian deposits dating from the Oligocene to the Pliocene: the megalonychid *Deseadognathus riggsi* (Carlini & Scillato-Yané, 2004); the mylodontids *Parotodontotherium calleorum* (Shockey & Anaya, 2011), *Pleurolestodon dalenzae* and *Simomy-lodon uccasamamensis* (St-André *et al.*, 2010); the giant megatheriids *Megatherium (M.) altiplanicum* (St-André & De Iuliis, 2001), *Megatherium (Megatherium) tarijense* (De Iuliis *et al.*, 2009) and *Eremotherium sefvei* (De Iuliis & St-André, 1997); the nothrotheriids *Lakukullus anatisrostratus* (Pujos *et al.*, 2014) and *Xyophorus villarroeli* (St-André, 1996); the megatherioid *Hiskatherium saintandrei*

(Pujos *et al.*, 2011); and the ‘proto-sloth’ *Pseudoglyptodon sallaensis* (formally the oldest sloth genus, Engelmann, 1987; Pujos & De Iuliis, 2007). More locally, the discovery of new nothrotheriids enhances the palaeobiodiversity of this clade in Bolivia, where three taxa are now recognized: *Xyophorus villarroeli*, *Lakukullus anatisrostratus* and *Aymaratherium jeni* (Fig. 10).

ANATOMY

Mandible and teeth of Aymaratherium and the caniniform–molariform transition in sloths

The dentary of *Aymaratherium jeni* possesses one caniniform tooth and three molariform teeth, a pattern corresponding to the typical plesiomorphic lower dental formula in sloths (Engelmann, 1987; Pujos & De Iuliis, 2007; McDonald & De Iuliis, 2008; Pujos *et al.*, 2012c). This arrangement is observed in Oligocene Tardigrada, as represented in *Deseadognathus*, *Octodontotherium*, *Orophodon*, *Paroctodontotherium* and *Pseudoglyptodon* from Argentina, Bolivia and Chile (Hoffstetter, 1956; Carlini & Scillato-Yané, 2004; McKenna *et al.*, 2006; Pujos & De Iuliis, 2007; Shockey & Anaya, 2011).

The dentary of *Aymaratherium* is particularly interesting inasmuch as it exhibits an unexpected combination of characters for a sloth: a very high HI, a tricuspid caniniform and three rectangular molariforms, with apicobasal sulci present only on m3, and three cuspids organized on two transverse lophids separated by a deep valley that opens vestibularly and lingually. This combination of characters is new for Tardigrada.

HI is often used for comparisons among sloths. It is calculated as the ratio (in %) between the maximal mandibular height and the tooth row length (Bargo, De Iuliis & Vizcaíno, 2006). As suggested by Pujos *et al.* (2011), a consideration of the dental formula is essential for homologous comparison of HI in each lineage. For instance, the caniniform of Mylodontinae and Megalonychidae is homologous to the m1 of Megatheriinae, Scelidotheriinae and Megatherioidea such as *Diabolotherium* and *Hiskatherium*. The high degree of hypsodonty in *Aymaratherium* is comparable to that of *Huilabradys* (Villarroel, 1998) and *Megatherium (M.) americanum* (Pujos *et al.*, 2011). In addition to the presence of very high coronoid and condyloid processes, *Aymaratherium* bears prominent musculature attachment sites on the medial and, especially, lateral surfaces of the posterior portion of the dentary, which served for the insertions of the temporalis and masseter pars superficialis and zygomaticomandibularis muscles (Fig. 2A–F). The spout was probably anteriorly extended as in *Thalassocnus* and *Megatherium*, thereby suggesting the

presence of a relatively long tongue. *Aymaratherium* possessed a small caniniform tooth and three large molariform teeth with two transverse lophids, which are reminiscent of those of giant megatheriine and nothrotheriid ground sloths, particularly of Plio-Pleistocene taxa such as *Megatherium* and *Eremotherium*. The presence in *Aymaratherium* of strongly hypsodont molariform teeth, a relatively dorsal position of the mandibular condyle, well-developed mandibular musculature, a probably long spout and large molariforms with two transverse shearing lophids is clearly convergent with some giant megatheriines, particularly those with a high HI, such as *Megatherium*. These features may indicate that *Aymaratherium* was a selective feeder preferring shrubs, leaves, twigs and fruit, as hypothesized for *Megatherium (M.) americanum* (for more details see Bargo & Vizcaíno, 2008). Among the Pomata-Ayte Montehermosan fauna, at least three ground sloths cohabited with cingulates, rodents, native ungulates and birds. The giant mylodontoid *Simomyiodon* (St-André *et al.*, 2010) was probably a ‘bulk-feeder’ grazing on herbaceous plants and/or grass, as was suggested for other wide-muzzled sloths such as *Lestodon* and *Glossotherium* (Bargo & Vizcaíno, 2008). Although *Megatherium (M.) altiplanicum* and *Aymaratherium jeni* were selective feeders, it is unlikely that they competed for resources because they did not occupy the same ecological niche, as indicated by the large size difference between them (1000–2000 kg for the megatheriine vs. several dozen kilograms for the nothrotheriine). *Megatherium* was probably in search of fruits and leaves in trees, while *Aymaratherium* may have preferred small shrubs.

In *Aymaratherium*, the three lower molariforms are mesiodistally compressed, bearing two transverse crests separated by a deep transverse valley open labially and lingually; m1–m2 are rectangular and m3 more triangular (Fig. 2K, L). This molariform pattern is new in sloths and distinct from other Nothrotheriinae, Thalassocninae and Megatheriinae. In other nothrotheriid sloths, Thalassocninae and Nothrotheriinae, the molariforms are clearly less compressed mesiodistally, the lophids are not perpendicular to the principal anteroposterior axis of the mandible, and mesial and distal lophids are convex mesially and distally, respectively. The apicobasal grooves are also present on the labial and lingual sides of the lower molariforms. In Megatheriinae, including late Miocene forms (Pujos *et al.*, 2013: fig. 6A–C), molariforms are not as compressed mesiodistally, except in *Anisodontherium halmyronomum* (Brandoni & De Iuliis, 2007). In this latter, the most mesial tooth is not caniniform, however, and m2–m3, equivalent of m1–m2 of *Aymaratherium*, are less compressed mesiodistally. Also, the last

molariform tooth of *Anisodontherium* is rounded and not compressed as in the new Bolivian form. The molariform pattern of *Aymaratherium* exhibits more analogies with Megatheriinae and especially *Anisodontherium* than with other Nothrotheriidae. This probably reflects similarity in dietary preferences and masticatory apparatus rather than phylogenetic affinities.

In *Aymaratherium*, c1 is sloped lingually (Fig. 2G–L) as in other Nothrotheriidae, and not vestibularly as in Mylodontidae and Megalonychidae. The presence of three cuspids on the caniniform tooth of *Aymaratherium* is unique for Xenarthra. The c1 of the other sloths may have one or two cuspids (e.g. *Xyophorus villarroeli*; Fig. 3A, B). Cusps or cuspids shaped by wear are not always observable in the molariforms of sloths (e.g. in Megatheriinae; Pujos *et al.*, 2013), but when discernible, there are often three, one at the centre of the mesial lophid and two at the vestibular and lingual extremities of the distal lophid, as in *Eucholoeps* (Bargo *et al.*, 2009), *Hiskatherium* (Pujos *et al.*, 2011), *Lakukullus* (Pujos *et al.*, 2014) and *Proscelidodon* (Pujos *et al.*, 2012b). Five cuspids may be present in some taxa, such as in the lower last tooth of some Mylodontidae (e.g. *Octodontotherium*; F. Pujos, pers. observ.). A similar arrangement of these three cuspids on the c1 of *Aymaratherium* suggests that this combination might have represented a transitional stage from either a caniniform to a molariform morphology, or the reverse in the most mesial lower tooth. According to the most recent phylogenetic analyses of Megatherioidea by Gaudin (2004) and Pujos *et al.* (2007), the Nothrotheriidae and Megatheriidae are sister groups. In *Megathericulus*, the oldest and most basal megatheriine, known from the middle Miocene of Patagonia and Peruvian Amazonia (De Iuliis *et al.*, 2008; Pujos *et al.*, 2013), the most mesial lower tooth is already molariform. A reduced caniniform is present in planopsine megatheriids (e.g. *Planops martini*; Hoffstetter, 1961) and some nothrotheriids (e.g. *Xyophorus*; Fig. 3A, B). However, several nothrotheriids, such as *Thalassocnus*, *Nothrotherium* and *Nothrotheriops*, have lost the caniniform, although the two earliest nothrotheriines (i.e. *Mionthropus* and *Pronothrotherium*) retain it. Interestingly, *Hiskatherium* (a megatherioid of uncertain affinities) possesses four lower molariforms (Pujos *et al.*, 2011), as does *Diabolootherium* (Pujos *et al.*, 2007; see also Shockey *et al.*, 2009: fig. 4.1). Assuming that the tricuspid caniniform of *Aymaratherium* represents a transitional morphology, two hypotheses may be advanced to explain its presence. Given that *Hiskatherium* occurred during the late middle Miocene (i.e. Laventan SALMA) in Bolivia, the tricuspid caniniform of *Aymaratherium* may represent a tran-

sition from a molariform (megatherioid *Hiskatherium*-like state) to a caniniform (nothrotheriid *Pronothrotherium* state) condition, which would correspond to a reversion to the plesiomorphic condition in sloths. A second scenario suggests a transformation from the plesiomorphic condition, a large caniniform with a single cuspid, to a molariform condition (with the appearance of the two posterior cuspids), as is observed in the Pleistocene *Diabolootherium* and in megatheriines. Dental formulae would have evolved independently in the four main sloths clades (i.e. Megatheriidae, Nothrotheriidae, Megalonychidae and Mylodontidae).

In summary, among the Megatheriidae, the Planopsinae exhibit a small caniniform tooth (1/1C–4/3M), whereas in the Megatheriinae, the first tooth is molariform (5/4M; Fig. 3J), a condition present since at least the early late Miocene. Among the Mylodontidae, the Scelidotheriinae possess a molariform first tooth as early as the earliest offshoots of the clade, which can be found in the late early Miocene (5/4M in the Santacrucian *Nematherium*, Simpson, 1941). Members of the Mylodontinae (Mylodontini + Lestodontini according to St-André *et al.*, 2010) retained the plesiomorphic sloth condition (1/1C–4/3M), which can be observed at least from the Deseadan SALMA with *Octodontotherium*, or a second upper tooth that we interpret as secondarily modified into a caniniform tooth (i.e. 2C–3M), as in *Lestobradys sprechmanni* (see Rinderknecht *et al.*, 2010 for the original description) and *Ocnotherium giganteum* (F. Pujos *et al.*, unpubl. data). All members of the Megalonychidae, including the modern two-toed sloth *Choloepus*, possess a caniniform that is often well developed (1/1C–4/3M; see McDonald, Rincón & Gaudin, 2013). In the Bradypodidae represented only by the three-toed sloth *Bradypus*, the caniniform is less developed (Gaudin, 2004). Early nothrotheriines (e.g. *Mionthropus*; Fig. 3G, H) possess a small caniniform, which is lost in the thalassocnines and in most advanced nothrotheriines. However, the presence in *Aymaratherium* of a tricuspid caniniform tooth may suggest reconsideration of the ancestral state of the dentition for the Nothrotheriidae. Indeed, the strong cranial and post-cranial affinities of *Hiskatherium* (Pujos *et al.*, 2011; Fig. 3C, D) and *Diabolootherium* (Pujos *et al.*, 2007) with the Nothrotheriidae may, once the basal condition of the dentition is established, require a re-evaluation of the relationships of these taxa with this family. However, these aspects are beyond the scope of the current study.

Post-cranial anatomy of Aymaratherium

The humerus of *Aymaratherium jeani* (Figs 4, 5), as in nothrotheriids generally, is gracile and its

musculature less powerfully developed in comparison with the Megatheriidae (De Iuliis, 2003), the Megalonychidae (Pujos *et al.*, 2007: fig. 10) and the Mylodontidae (e.g. *Simomyodon*; St-André *et al.*, 2010). However, it appears less elongated than that of modern sloths (e.g. *Choloepus didactylus*; Nyakatura & Fischer, 2010), a feature that is related to their suspensory posture and locomotion. The humerus of *Aymaratherium* strikingly resembles that of *Diabolotherium* in bearing a prominent greater tubercle that is extended proximomedially, a reduced lesser tubercle, a medially inclined articular head and a weakly developed deltopectoral shelf, which is smaller in the Peruvian taxon. *Diabolotherium* differs in the absence of an entepicondylar foramen (Pujos *et al.*, 2007: fig. 10A–D), which is in contrast well marked in *Aymaratherium* (Fig. 3E, F). As in *Thalassocnus*, the medial epicondyle is short and rounded, and does not expand medially. The lateral epicondyle of *Aymaratherium* extends to approximately the same degree as in *Thalassocnus natans*. The presence in *Aymaratherium* of a prominent and medially sloped humeral head suggests extensive mobility of the shoulder joint. In addition, the round and convex capitulum for the radius suggests significant pronation and supination movements (Amson *et al.*, 2015a). These characteristics are accompanied by poor development of the deltopectoral musculature, a condition which is in sharp contrast to the giant terrestrial and fossorial mylodontid ground sloths. In the climbing sloth *Diabolotherium* (Pujos *et al.*, 2007), this musculature was less developed, as in *Aymaratherium*.

The right astragalus MNHN-Bol-V 012983 (Fig. 7A–H) and calcaneum MNHN-Bol-V 003307 (Fig. 7I–P) belong to different individuals referred to *Aymaratherium jeani* (Fig. 7Q), but these two elements articulate together almost perfectly and they allow for a better understanding of the foot motions. The general morphology of the astragalus is highly similar to that of the earliest Thalassocninae and Megatheriinae, particularly *Thalassocnus antiquus* (see Amson *et al.*, 2015b) and *Megathericulus patagonicus* (Fig. 7A): for example, the presence of a right angle in anterior view between the discoid and odontoid facets (Fig. 7B). However, the astragalus of *Aymaratherium* differs from that of the last two in the transverse diameter of the odontoid process, which is shorter than that of the discoid process (Fig. 7A, B). Consideration of megatherioid astragali reveals two distinct patterns in dorsal view: (1) the typical megatherioid morphology with a well-defined odontoid process perpendicular to the anteroposterior main axis of the discoid facet (e.g. Megatheriinae, Thalassocninae and *Aymaratherium*), and (2) an odontoid process (i.e. medial trochlea) that is poorly

differentiated from the discoid process (i.e. lateral trochlea), and bearing the head of the astragalus at its end. This second pattern includes taxa generally considered as phylogenetically distant, such as *Hapalops*, *Diabolotherium*, *Xyophorus* and *Pliometanastes*.

The calcaneum of *Aymaratherium* is large and bulky (Fig. 8I–P). It is not axe-shaped, in contrast to the condition found in other known nothrotheriines. Its morphology is reminiscent of that of the calcaneum of thalassocnines (i.e. *Thalassocnus antiquus*) and megatheriines, such as *Megatherium*. As in these last two genera, the calcaneum of *Aymaratherium* also bears a dorsal tuberosity that may have served for the insertion of the gastrocnemius muscle (Fig. 8I, J). In *Aymaratherium* the lateral and medial processes of the tuber calcanei, as well as the anterior epiphysis of the calcaneum, were in contact with the substrate. As in most ground sloths, the largest articular facet of the calcaneum was the ectal facet for the astragalus. In *Aymaratherium*, the main axis of this convex facet is almost dorsoplantar (Fig. 8O, P), and not obliquely orientated as in other nothrotheriids.

PHYLOGENETIC RELATIONSHIPS OF AYMARATHERIUM

Based on the work of De Iuliis *et al.* (2011), a phylogenetic analysis of the Nothrotheriidae was conducted to assess the position of *Aymaratherium* with respect to other well-known nothrotheriids, and the evolution and distribution of characters at major nodes. Three families (in addition to the monogeneric Bradypodidae) have long been considered as monophyletic, as noted by Gaudin (1995, 2004): the Megatheriidae, Mylodontidae and Megalonychidae. A fourth major grouping of small- to medium-sized forms was long recognized that included those that have recently been considered nothrotheriids plus several others, mainly late early Miocene genera (e.g. *Hapalops*) that were traditionally allied to them. The term ‘nothrotheres’ was commonly applied to this group. More recently, Gaudin (2004) removed the early late Miocene taxa, considering them as basal megatherioids, and this scheme has since been followed (e.g. De Iuliis *et al.*, 2011). The question of nothrotheriid relationships is clouded by the inclusion of several other genera, such as *Chasicobradys* and *Amphibradys*, many of which are based on such woefully inadequate remains as to preclude their inclusion in phylogenetic analyses (see De Iuliis *et al.*, 2011).

Although De Iuliis (1994) critically assessed the use of some characters in analyses that suggested affinities of the Nothrotheriidae with the Megatheriidae, De Iuliis *et al.* (2011) analysed the monophyly

of the Nothrotheriidae based on well-known nothrotheriids (i.e. *Nothrotherium*, *Nothrotheriops*, *Pronothrotherium*, *Mionothropus*, and *Thalassocnus*), and information on the nearly complete remains of the recently described late Miocene *Mionothropus cartellei* and the Mio-Pliocene genus *Thalassocnus*. Their analysis used PAUP (version 4.0b10) with the DELTRAN optimization option (see Gaudin, 1995, for justification) and involved a data matrix of 66 characters, 13 of which were multistate and nine were ordered. *Hapalops* was considered as outgroup.

Despite the recent advances in our understanding of nothrotheriids, we nonetheless sought here to re-examine nothrotheriid relationships using more recently developed phylogenetic tools. Our analyses include the same taxa and are based mainly on the data matrix presented by De Iuliis *et al.* (2011), except that one character is modified (see above and Supporting Information, Appendices S2, S3) and we include the new taxon *Aymaratherium*, and additional information on *Thalassocnus* derived from the recent descriptions and interpretations of Amson *et al.* (2015a,b). Our parsimony analysis was performed using TNT v. 1.0. We obtained two MPTs (Fig. 9) in which *Thalassocnus* (= Thalassocninae) is always sister group to Nothrotheriinae, as suggested by earlier studies (de Muizon *et al.*, 2003; De Iuliis *et al.*, 2011). The *Thalassocnus* lineage comprises five taxa that evolved on the Pacific coast (i.e. desert coasts) of Peru and Chile from the end of the Miocene to the end of the Pliocene, probably endemically in relation to their particular lifestyle and diet (see McDonald & de Muizon, 2002; de Muizon *et al.*, 2003, 2004a,b) and independently of the nothrotheriid nothrotheriines, as confirmed by the present phylogenetic analysis. The nothrotheriine clade is supported by 11 unequivocal synapomorphies (Appendix S4-1) and has been present in South America since at least the Huayquerian SALMA. It persisted in North and South America until the end of the Pleistocene, as represented by the genera *Nothrotheriops* and *Nothrotherium*, respectively. In one hypothesis (MPT1), *Aymaratherium* is sister taxon to *Mionothropus*, with which it forms a weakly supported clade, united by a single unequivocal synapomorphy. This clade is the sister group of [*Pronothrotherium* [*Nothrotheriops*, *Nothrotherium*]]. In a second hypothesis (MPT2), *Aymaratherium* is the sister group to [*Nothrotheriops*, *Nothrotherium*] and lies crownward with respect to *Mionothropus* and *Pronothrotherium*. The *Aymaratherium*/Nothrotheriini clade is also supported by six unequivocal synapomorphies. Using the pruning option of TNT, *Aymaratherium* is the unstable nothrotheriid taxon that generates the two distinct phylogenetic scenarios figured as MPT1 and MPT2. The instability of

the new taxon is due to the conflict generated by characters 30⁰ and 38², already discussed, and is also related to the fact that its skull and much of its postcranial skeleton have not been yet discovered, so that 80% of its coding is scored as unknown (Appendix S3). In the consensus tree, *Mionothropus*, *Pronothrotherium*, *Aymaratherium* and the [*Nothrotheriops*, *Nothrotherium*] clade form a polytomy (Fig. 9). In the two MPTs, *Nothrotheriops* and *Nothrotherium* constitute the Nothrotheriini clade, but the root of each tree, which groups together all of the ingroup taxa, is not supported by unequivocal synapomorphies.

CONCLUSION

1. The revision of the material deposited in the MNHN-Bol (La Paz, Bolivia) and the preliminary results of two recent palaeontological field campaigns (2012 and 2015) organized by members of MNHN-Bol, ISE-M (Montpellier, France) and CONICET (Argentina) in the fossiliferous locality of Pomata-Ayte (Oruro Department) reveal the great diversity of the Montehermosan vertebrate fauna (consisting almost entirely of mammals), the presence of a Pleistocene (Lujanian SALMA?) assemblage, and the existence of a late Miocene vertebrate mammalian fauna older than the commonly recognized Montehermosan fauna.
2. The Montehermosan fauna is dominated by xenarthrans, including three cingulates (a glyptodontid, a dasypodid and the pampatheriine *Plaina* sp.) and three tardigrades [the mylodontid *Simomylodon uccasamamensis*, the megatheriid *Megatherium (Megatherium) altiplanicum* and the new nothrotheriid *Aymaratherium jeani*]. Native South American ungulates are represented by a macrauchenid litoptern (*Macrauchenia* sp.), and two toxodontid notoungulates (*Posnanskytherium* cf. *viscachanense* and a taxon of uncertain affinities). A rodent and a phorusrhacoid bird are also present.
3. This fauna was recovered from the Umala Formation, 100 m above a tuff in the same section. This ash was dated, using ⁴⁰K/⁴⁰Ar, as between 5.42 ± 0.6 and 5.97 ± 0.4 Ma, which points to a post-Miocene age for the fossil assemblage, likely to coincide with an early Pliocene age (Montehermosan SALMA).
4. The nearly complete dentary, three humeri, astragalus and calcaneum of the small- to medium-sized sloth from Pomata-Ayte are described as belonging to a new nothrotheriid species, *Aymaratherium jeani* sp. nov. It is characterized by: a highly hypsodont dentition (HI = 1.14) consisting of a small caniniform and three large and

mesiodistally compressed molariform teeth and the absence of a diastema; a posteriorly inclined c1 bearing three cuspids; molariforms with a mesial and a distal lophid, orientated perpendicular to the anteroposterior axis of the tooth row and separated by a deep transverse valley that is open vestibularly and lingually; shallow distolingual and distolabial apicobasal grooves present on m3, but not m1 and m2; a gracile humerus, with a medially inclined head, prominent and asymmetric greater and lesser tubercles, and a poorly developed deltopectoral shelf; an astragalus with discoid and odontoid facets meeting at a right angle in anterior view, a centrally positioned caput tali with its dorsal border located just below the discoid surface, a well-developed odontoid process lying perpendicular to the main anteroposterior axis of the discoid facet and lacking a prominent plantar extension, and a transverse diameter of the odontoid process shorter than the discoid process; and a large calcaneum generally comparable to that of the Thalassocniinae and Megatheriinae, with the tuber calcanei tapered posteriorly and approximately symmetrical in dorsal view.

5. *Aymaratherium jeani* has strongly hypsodont teeth, high condyloid and coronoid processes, prominent adductor musculature attachment sites, and large molariform teeth with two transverse shearing lophids. Similar traits were independently acquired in some giant megatheriine ground sloths, further suggesting that the new Bolivian species was a selective feeder, similar to megatheriines such as *Megatherium (M.) americanum*.
6. The presence in *Aymaratherium jeani* of a tricuspid caniniform tooth and strongly mesiodistally compressed molariform teeth bearing mesial and distal lophids perpendicular to the anteroposterior axis of the tooth row and separated by a deep transverse, vestibularly and lingually open valley represents a new dental pattern in Xenarthra.
7. The phylogenetic analysis of nothrotheriid sloths based on 67 characters (nine ordered) using the parsimony software TNT confirms the monophyly of the Nothrotheriinae (*Aymaratherium*, *Mionothropus*, *Pronothrotherium*, *Nothrotherium* and *Nothrotheriops*) and Nothrotheriini (*Nothrotherium* and *Nothrotheriops*). *Aymaratherium* is sister taxon of *Mionothropus* (MPT1) or the sister clade of Nothrotheriini [*Nothrotheriops*, *Nothrotherium*] within Nothrotheriinae (MPT2).
8. The discovery of this new peculiar nothrotheriid sloth extends our knowledge of the palaeobiodiversity of ground sloths in Bolivia. The sloths are represented by the megalonychid *Deseadognathus*

riggsi, the mylodontids *Paroctodontotherium calleorum*, *Pleurolestodon dalenzae* and *Simomyiodon uccasamamensis*, the giant megatheriids *Megatherium (M.) altiplanicum*, *Megatherium (Megatherium) tarijense* and *Eremotherium sefvei*, the megatherioid *Hiskatherium saintandrei*, the basal *Pseudoglyptodon sallaensis*, and the nothrotheriids *Lakukullus anatisrostratus*, *Xyophorus villarroeli* and *Aymaratherium jeani*.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article:

- Appendix S1.** Measurements for *Aymaratherium jeani* gen. nov., sp. nov.
- Appendix S2.** Data matrix for the phylogenetic analysis.
- Appendix S3.** List of characters used in the phylogenetic analysis.
- Appendix S4.** Character distribution at nodes and terminal taxa.