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First skeleton of the notoungulate mammal *Notostylops murinus* and palaeobiology of Eocene Notostylopidae

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Here, we describe the first skeletal remains of *Notostylops* recovered from middle Eocene levels of the Sarmiento Formation, Patagonia, Argentina. The remains include two teeth of *Notostylops murinus*, the axis, vertebral bodies, a rib, a left humerus, both radii, two metapodials, two phalanges, the pelvis, a right femur, a right calcaneus and several broken bones. Radial bones are not fused to ulnas, and are shorter than the humerus, very generalized, with an oval head, a marked neck and a radial tubercle. The humerus and the femur show pronounced insertion structures. Our analysis suggests that the appendicular skeleton of *Notostylops* is too generalized and shares several features with that of terrestrial rodents as Sciuridae. Unlike the appendicular skeletons of cursorial or saltatorial mammals, which restrict mobility, the skeleton of *Notostylops* indicates the ability to make a variety of different movements, as would be expected for terrestrial, fossorial or arboreal mammals. This skeleton gives new information about the locomotor behaviour of notoungulates, particularly in their basal forms. The results will also allow the identification of isolated notoungulate bones and raise questions about the previous taxonomic assignment of postcrania to *Pleurostylodon*. ☐ *Eocene, Meridiungulata, Notoungulata, Patagonia, postcranial anatomy.*

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The genus *Notostylops* Ameghino 1897 is one of the most characteristic basal genera of notoungulates from the middle Eocene strata from Patagonia. The abundance of this genus led Ameghino to recognize the so-called *Notostylops* beds Ameghino (1906) to distinguish them from the younger *Pyrotherium* beds. These faunas were subsequently the base for the recognition of Casamayoran (middle Eocene) and Deseadan (Oligocene) South American Land Mammal Ages (SALMAs) (Pascual *et al.* 1965; Madden & Scarano 2010). Later, *Notostylops murinus* was considered characteristic of the Barrancan subage, and *Notostylops pendens* and *Notostylops appressus* of the Vacan subage (Cifelli 1985a). Despite the abundance of this genus, *Notostylops* remains are mostly represented by skulls and isolated teeth, being two left astragali the only postcrania described in association with dental remains (Ameghino 1905; fig. 74; MACN-A 10940). Several isolated astragali morphologically similar to those assigned by Ameghino have been held in collections assigned either as *Notostylops* or as *Didolodus* (see Gelfo & Picasso 2003; Gelfo & Lorente 2012).

Here, we describe a partial skeleton comprising several vertebrae, a broken pelvis, and parts of the fore and hind limbs of an adult specimen of *Notostylops*. This partial skeleton was found in association with *Notostylops* teeth in 1982 in an expedition performed by researchers of the Museo de La Plata, La Plata, Argentina, led by Juan Carlos Quiroga to Valle Hermoso locality in Patagonia, Chubut Province, Argentina. This remain (MLP 82-V-1-8) is the most complete known fossil of *Notostylops* and represents one of the few basal notoungulates with dental and postcranial remains found in direct association. Other basal notoungulate with postcrania associated are the isotemnids *Thomashuxleya*, *Anisotemnus* and *Pleurostylodon* (Simpson 1967; Shockey & Flynn 2007; Carrillo & Asher 2017) and the oldfieldthomasiids *Colbertia* (Bond 1981; Bergqvist *et al.* 2007) and *Allalmeia* (Rusconi 1946a,b; Lorente *et al.* 2014).

The remains here presented were preliminarily and shortly compared with *Pleurostylodon* (Bergqvist & Metello 2011) before the specimen was prepared, but not fully described or illustrated. Here, we present a full description of the skeleton after its preparation and restoration, and a comparison with other related notoungulates, including the undescribed astragalus of the notostylopid *Boreastylops lumbrerensis* (MLP 79-XI-22-14) from the lower levels of the Lumbrera Formation, in Salta province, Argentina (middle? Eocene; Woodburne *et al.* 2014). The remains of *Boreastylops* are strongly deformed but preserve several broken appendicular bones,

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including a left astragalus (Vucetich 1980). In addition, we characterize the postcranial anatomy of the Notostylopidae and incorporate new information about the morphology and palaeobiology of notoungulates. These descriptions will be useful to append characters for phylogenetic hypotheses and to identify isolated remains of other possible notostylopids.

Material and methods

This study is based on the partial skeleton of an adult specimen of *N. murinus* Ameghino 1897 (MLP 82-V-1-8). To establish the most accurate homologies, several comments about the anatomical names are first needed. Each bone of *Notostylops* is described separately, and, when possible, with its topological name written at least once in Latin and cursive following the 'NAV' (Nomina Anatomica Veterinaria, 2012) attached to its colloquial name. The anatomy of the phalanges is based on Maiolino *et al.* (2011). Other names are based on several works as Davis (1964), Szalay (1994), Shockey & Flynn (2007) and Muizon *et al.* (2015). To avoid confusion, the crests or ridges that go down from the greater tubercle of the humerus and surround the deltoid tuberosity the medial one is called pectoral crest and the lateral one is referred as deltoid crest, following the works of Davis (1964) and Shockey & Flynn (2007). Although the NAV has the Latin name *Crista tuberculi majoris* (CTM) for what we called deltoid crest above, CTM is used for pectoral crest in primate anatomy (Netter 2011; Diogo *et al.* 2012). Calcaneus anatomy follows Tabuce *et al.* (2006). To compare the calcaneus, its orientation is considered as if sustentacular and fibular facets were always dorsal. The orientation of bones is present as follows: sagittal plane, medial/lateral (in appendicular bones); transverse plane, proximo/distal (in appendicular bones); craneo/caudal (in vertebrae); coronal plane, antero/posterior (in long bones); dorso/plantar (in calcaneus); and dorso/ventral (in vertebrae).

The remains were compared with extant and fossil remains, including the oldfieldthomasiids *Allalmeia atalaensis* Rusconi 1946a (MCNAM–PV 507; Lorente *et al.* 2014) and *Colbertia lumbrerense* Bond 1981 (PVL 4300, PVL 6227), the homalodotherid *Asmodeus* Ameghino 1894 (MACN-A 12326), the notostylopids *B. lumbrerensis* Vucetich 1980 (MLP 79-XI-22-14) and *Notostylops*? (MLP 56-XII-18-198; MLP 56-XII-18-199; MLP 56-XII-18-200; MLP 56-XII-18-201), the hegetotherid *Pachyrucos* Ameghino 1885 (MACN-A 7520), the interatherid *Protypotherium* Ameghino 1882 (MLP 90-XII-26-10), and the isotemnid *Thomashuxleya* Ameghino 1901 (PVL 331). The skeleton of *N. murinus* were also compared with a Notoungulata indet (PVL 323, LIEB-PV 4014 and LIEB-PV 4015), published data of basal skeletons of other notoungulates (Simpson 1967; Shockey & Anaya 2004; Bergqvist *et al.* 2007; Shockey & Flynn 2007; Bergqvist & Bastos 2009; Shockey *et al.* 2012; Vera 2012), as well as other mammalian postcranium (e.g. *Pyrotherium*, MLP 79-XII-18-29; *Callosciurus erythraeus*, MLP 2013; *Leontopithecus* MLP 20.iv.99.1; *Lycalopex*, MLP 1967; *Mazama*, MLP 4.VIII.98.1, MLP 4.X.94.2) and literature descriptions (Gaudry 1909; Cifelli 1983; Rose 1987; Bergqvist 1996; Shockey & Anaya 2004; Shockey *et al.* 2012).

Some of the bones of the skeleton of MLP 82-V-1-8 here described (i.e. axis, sacral and caudal vertebrae, humerus, radius, pelvis, femur and ungual phalange) were scanned in the 3D laboratory of the Museo de La Plata with a NextEngine HD 3D Laser Scanner and a Roland 3D laser Scanner LPX-600. The 3D image in.stl format can be downloaded from MorphoBank (http://www.morphobank.org/), project number 3326. Measurements were taken with an electronic digital calliper Schwyz, and the following six indices were taken from Samuels *et al.* (2012): FEI (femoral epicondylar index), FRI (femoral robustness index), GI (gluteal index), HEI (humeral epicondylar index), HRI (humeral robustness index) and SMI (shoulder moment index). These indices were compared with those obtained by Elissamburu & Vizcaino (2004), Samuels & Van Valkenburgh (2008) and Samuels *et al.* (2012). Locomotor habits (Supplementary material) are described following Samuels & Van Valkenburgh (2008) and Samuels *et al.* (2012).

The body mass of *Notostylops* was calculated using the regression formulas of Tsubamoto (2012), whereas other body mass estimations were taken from the literature (Croft 2000; Bergqvist & Metello 2011; Elissamburu 2012; Vizcaíno *et al.* 2012).

Institutional abbreviations are as follows: AMNH, American Museum of Natural History, New York, USA; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MACN-A, Colección Ameghino of MACN; MACN-Ma, Colección de Mastozoología of MACN. MLP, Museo de la Plata, La Plata, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio, Paleontología de Vertebrados, Trelew, Argentina; MCNAM-PV, Museo de Ciencias Naturales y Antropológicas J. C. Moyano, Paleontología de Vertebrados, Mendoza, Argentina; PVL, Instituto Miguel Lillo, Paleontología de Vertebrados, San Miguel de Tucumán, Argentina; SALMA, South

American Land Mammal Age; SANU, South American native ungulates.

Description

Notostylops murinus is a basal notoungulate characteristic from the lower levels of the Gran Barranca Member of the Sarmiento Formation (middle Eocene, Casamayoran SALMA, Barrancan subage), south-east of Chubut Province, Argentina. The specimen here presented (MLP 82-V-1-8) includes two isolated teeth, the axis, several broken vertebral bodies, a proximal portion of a rib, a left humerus, both radii, a complete metapodial and the distal half of another, an intermediate phalanx and an ungual phalanx, the broken pelvis with two sacral vertebrae, three caudal vertebrae and both coxal bones; a right femur, a right calcaneus and several broken bones. Besides these remains, 24 fragmentary bones of small size, which could not be identified with any particular skeleton bone, are also part of the same individual (Supplementary material). All the bones have suffered some deformation and are lightly flattened in the dorsoventral axis.

Dentition

Only two isolated teeth are preserved. One of them is complete, with only one curved root, matching an I1 morphology. In other specimens, the root of I2 is less curved and the crown more mesiodistally lanceolate (Figs 1F, 2B). We also discarded the possibility of it being other rooted teeth as I3 or C, since their roots are almost straight (Simpson 1948). The crown of I1 is shorter than its root, and the coating mesial enamel is thicker than the preserved remains in the distal portion. In occlusal view, the tooth is rounded, with the mesial edge sharp and chisel-like. It is interpreted as a left incisor since, in the inner side, the enamel is erased due to the contact with the right I1, in contrast to that observed in the labial side, where it is complete. The other preserved tooth is a left M3 without roots, and with the mesiolabial corner and the mesial half of the ectoloph (Fig. 2A). Only a small portion of the mesial cingulum, much lower than the distal one, is preserved at the base of the tooth, but it is enough to allow taxonomic determination. The protocone has a lingual column and a subcrescentic shape in occlusal view, with thicker enamel in the lingual side. There is an inverted V-shaped sulcus with a very acute angle, over the enamel of the distolingual side of the protocone. The preserved part of the protoloph is projected mesiolabially from the protocone and its internal enamel edge continues in the inner margin of the ectoloph. The distal part of the protoloph, equivalent to the postprotocrista, ends in an enamel promontory. There is no trace of the hypocone, and the distal cingulum is lower than the metaloph. The metaloph is short, with a thick portion that contacts the base of the protoconid and continues mesially, with a long crochet, and a fine distolabial portion connected to the ectoloph. The scarce wear of the tooth allows identifying that this part of the metaloph is formed by a tiny cusp plus a short and narrow crest, which ascends to the ectoloph. The crochet is almost straight and divided by a constriction in the enamel margins in a small mesial portion (lingual to the paracone portion of the ectoloph) and a larger distal structure in contact with the metaloph. An oval fossette is limited by the crochet, the ectoloph and the metaloph. This fossette continues mesially in a deep furrow that completely surrounds the crochet, which is wider at the base of the protocone. This occlusal morphology allows referring to these molars as belonging to *N. murinus*.

Axis

This remain is slightly deformed, with the right side more cranially placed than the left one (Figs 1G, 3A). It is longer dorsoventrally (27.81 mm from the preserved part of the neural spine to the vertebral body) than craniocaudally (26.37 mm from the odontoid process up to the caudal part of the vertebral body). It has a large and rounded neural canal (*Foramen vertebrale*; Fig. 3A, nc), slightly larger than the vertebral body (*Corpus vertebrale*, cranially 9.06 mm tall and 6.58 mm transverse), and small transverse processes and transverse foramina. The neural spine (*Processus spinosus*; Fig. 3A, ns) is broken in the dorsal, cranial and caudal ends, but the preserved part is higher than the vertebral body. The odontoid process (*Dens*; Fig. 3A, o) has an oblique, large articulation surface in the ventral side of the atlas. Both prezygapophyses (*Processus articularis cranialis*; Fig. 3A, ap) are strong and separated from the odontoid process by a wide and deep furrow. The prezygapophyses are as large as the odontoid process, cranially oriented, slightly convex, with mostly flat surfaces, while the postzygapophyses (*Processus articularis caudalis;* Fig. 3A, cp) are less of the half of the prezygapophyses and ventrolaterally oriented. The transverse processes (*Processus transverses*; Fig. 3A, tp) are small and equal in size to the postzygapophyses.

Lumbar vertebrae

Three isolated vertebral bodies are also preserved (Fig. 1H). Because they are wider than high, with a

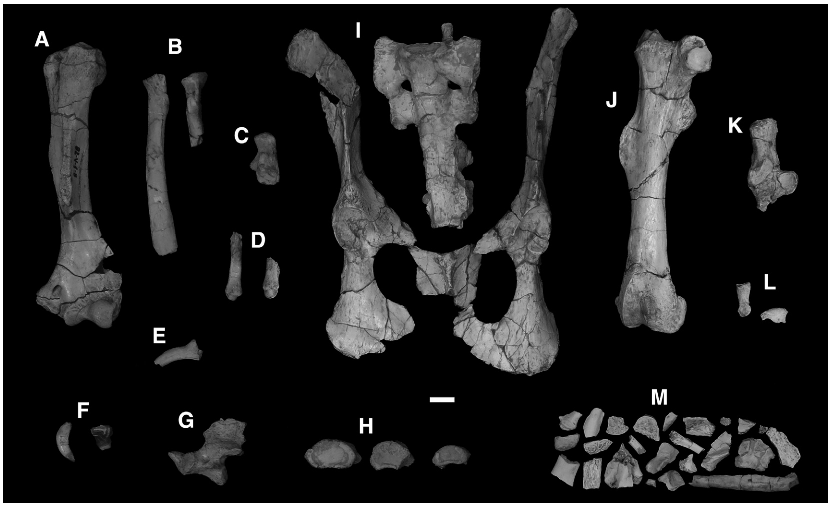

Fig. 1. Notostylops murinus MLP 82-V-1-8 skeleton from Valle Hermoso, Province del Chubut, Argentina. A, left humerus; B, radii; C, left ulna; D, metapodials; E, rib fragment; F, teeth; G, axis; H, vertebral bodies; I, sacral and caudal vertebrae, and pelvis; J, right femur; K, right calcaneus; L, phalanges; M, undetermined fragments. Scale bar = 10 mm.

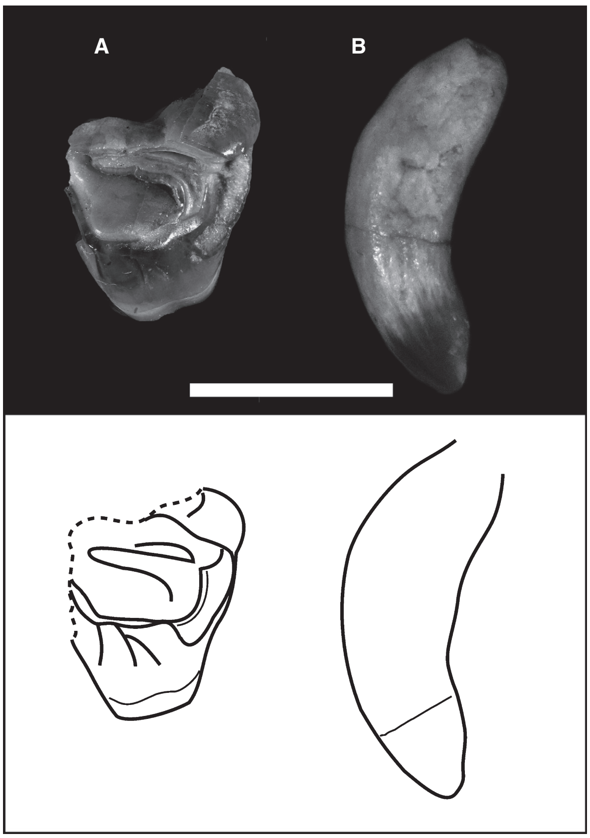

Fig. 2. Notostylops murinus MLP 82-V-1-8 dental elements. A, left M3; B, left I1. Scale bar = 10 mm.

convex ventral margin and neither of them shows any facet for the head of ribs or haemal processes, they are considered as lumbar vertebrae. Two of them preserve a pair of vascular foramina in the dorsal surface of the body. Part of the right pedicle that delimits the neural canal is preserved in one specimen.

Sacral and caudal vertebrae

There are two sacral and two caudal vertebrae preserved together embedded in the rock, which were separated from the matrix after laboratory preparation (Figs 1I, 4). In ventral view, the suture (*Lineae transversae*) between these vertebrae is present. The remains are slightly deformed by compression, so the right side is turned over the left one. The most anterior sacral vertebra preserved the left prezygapophysis but not the right one. There is only the base of the neural spine, and both transverse processes are dorsoventrally flattened and craniocaudally expanded in the contact with the pelvis. The neural canal is squashed but lesser than the vertebral body. The second sacral vertebra is better preserved and has a laterally flat neural spine. It is similar but proportionally smaller in every detail than the former vertebra. The caudal vertebrae present no transverse process, their neural arcs are bent to the left, and the neural canal of the last caudal vertebra is completely collapsed over the vertebral body.

Ribs

A fragmentary right rib is preserved, with the tuberculum (*tuberculum costae*) and a small *facies articularis tuberculi costae* over it (Fig. 1E). The capitulum (*crista capitis costae*) is absent. A wide *sulcus costae* is present along the caudal side of the rib. There is a prominence over the cranial side of the rib, which could be compared to the *tuberositas m. longissimi* of equids. Another bone, long and tubular, seems to be a rib, since it is too thin to be a long bone (Fig. 1M).

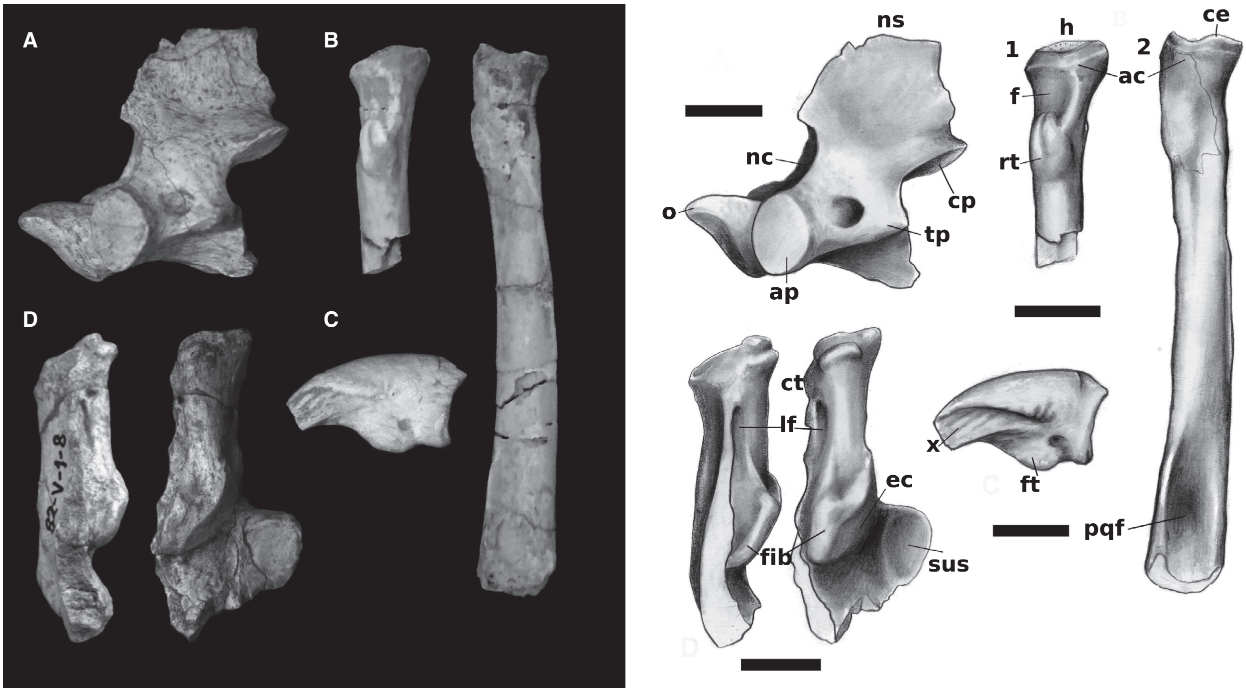

Fig. 3. *Notostylops murinus* MLP 82-V-1-8. A, axis; B, radii; C, ungual phalanx; D, right calcaneus; (ap, articular process; nc, neural canal; ns, neural spine; o, odontoid process; tp, transverse process); 1, right radius; 2, left radius; (ac articular circumference; ce, capitular eminence; f, fossa?; h, head; pqf, Pronatus quadratus fossa; rt, radial tuberosity; ft, flexor tubercle; x, observe the marked grooves as in hoof-like phalanges; ct, calcaneal tuber; ec, ectal facet; fib, fibular facet; lf, lateral fossa; sus, sustentacular facet. Scale bar = 10 mm.

Slender long bones in notoungulates (e.g. fibulae and ulnae) are much more robust.

Humerus

Only the left humerus is preserved. It is 116 mm long, compressed antero-posteriorly, probably due to postmortem deformation, particularly in the epiphyses affecting the head and the capitulum, respectively (Figs 1A, 5A,B). The head (*Caput humeri,* Fig. 5B, h) is oval, and the greater and lesser tubercles (*Tuberculum majus* and *Tuberculum minus;* Fig. 5A, hgt, hlt) are well developed. The greater tubercle is as high as the head and has marked fossae for *Supraspinatus* and *Infraspinatus* muscle insertions. The bicipital groove (*Sulcus intertubercularis*; Fig. 5A, bg) is open to the medial side of the bone. There is a slender and almost drop-shaped deltoid tuberosity (*Tuberositas deltoidea*), surrounded by the pectoral crest and a less marked deltoid crest. The pectoral crest is well marked and extends over almost 60% of the length of the humerus. It is smoother in the middle of its extension. The deltoid crest is less developed and goes to the lateral side but does not reach the greater tubercle. After a smooth space, another crest goes on proximally, and may be a continuation of the deltoid crest or a *Linea M. Tricipitis*. There is a tubercle for the *Teres major* muscle (*Tuberositas teres major*, Fig. 5: A, B, ttm) in the medial side, almost in the middle of the humerus but slightly more proximally. The humeral crest (*Crista humeri*) goes down from the deltoid tuberosity towards the medial epicondyle and is barely marked. The distal epiphysis is wider than the proximal epiphysis and has a large medial epicondyle (*Epicondylus medialis*; Fig. 5A, B, me). There is an epicondylar foramen (*Foramen supracondylare*; Fig. 5A, ef), which opens antero-posteriorly oblique to the main axis of the bone. The capitulum (*Capitulum humeri*) is ovoid and with a smooth transition to the trochlear lateral crest, which is well marked in the posterior side. There is no supratrochlear foramen (*Foramen supratrochleare*). The olecranon fossa (*Fossa olecrani*, Fig. 5B, of) is scarcely marked. The lateral epicondyle (*Epicondylus lateralis*) is narrow and continues proximally in a sharp and flattened lateral supinator crest (*Crista supracondylaris lateralis*; Fig. 5A, B, sc).

Radii

Both radii are preserved (Figs 1B, 3B). The left radius has the proximal epiphysis and most of the diaphysis, until the *Pronatus quadratus fossa* (Fig. 3B, pqf), while the right radius has the proximal epiphysis and a small portion of the diaphysis. If they were complete, they would have been shorter than the humerus. In the left radius, the radial tubercle (*Tuberositas radii*; Fig. 3B, rt) has been reconstructed with plaster, while in the right radius, it is complete and well marked and developed, oval in outline, divided by a soft furrow and with the larger axis proximodistally oriented (Fig. 3B, rt). Between the head and the radial tubercle, there is a deep fossa (Fig. 3B, f), which is common in basal Notoungulata (Lorente 2015), but which significance is unknown. There is a strong crest which connects the radial tubercle with the head of the radius. The head (*Caput radii*; Fig. 3B, h) is oval, almost round, with a marked neck (*Collum radii*). The fovea (*Fovea capitis radii*) is an oval depression with a higher edge in the medial side. There is a small capitular eminence (Shockey & Flynn 2007; Fig. 3B, ce) in the dorsal side of the proximal radius like in other notoungulates. The articular circumference (*Circunferentia articularis*) (Fig. 3B, ac) is thin and surrounds the head, which could indicate an unrestricted radius rotation.

Ulna

Only the left olecranon is preserved. Its medial ridge projects medially, forming a triangular process (Fig. 1C). This structure may expand the insertion surface of the *flexor carpi ulnaris* muscle, which moves the carpal articulation. To our knowledge, this process is not very common or even described in mammals, being found in some Carnivora, for example the small Indian civet (*Viverricula indica*) (AMNH 113770, see Morphobank media number M139571 from O'leary *et al.* 2013).

Metapodials

There are two metapodials, one complete and another broken, preserving only the diaphysis and the distal epiphysis (Fig. 1D). The complete metapodial is flat (larger transversally), while the broken one seems larger and has a dorsoplantarly larger distal epiphysis and an ovoid diaphysis, with the larger axis oblique. The distal epiphysis has a well marked longitudinal crest and developed, round condyles. The complete metapodial has the plantar side of the proximal end slightly broken, lateral and medial condyles in this end, being a left second, third or more probably the fourth metacarpal, based on the morphology of the proximal epiphysis and the small size.

Phalanges

An intermediate phalanx and an ungual phalanx are preserved (Figs 1L, 3C). Both are larger dorsoventrally. The intermediate phalanx has large and very marked articulations. The ungual phalanx is very narrow, with a claw-like shape but, in the distal end, it has very pronounced, proximodistally oriented grooves as in hoof-like phalanges (Fig. 3C, x). The distal point is broken. The body is triangular in cross-section and has a round and ventrodistally oriented *Tuberculum flexorium* (Fig. 3C, ft), a pair of foramina, lateral and medial dorsally to the tuberculum, and a sulcus above the grooves. Due to the large size, they are probably pedal phalanges.

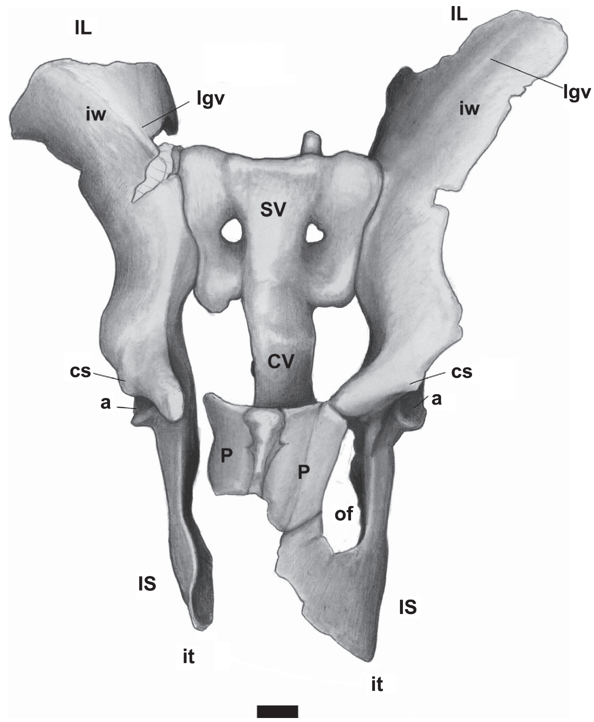

Fig. 4. *Notostylops murinus* MLP 82-V-1-8 pelvis. A, acetabulum; cs, caudal spina iliaca; CV, caudal vertebrae; IL, ilium; IS, ischium; it, ischium tuberosity; iw, ilium wing; lgv, linea glutea ventralis; of, obturator foramen; P, pubis; SV, sacral vertebrae. Scale bar = 10 mm.

Pelvis

The pelvis is the most complete structure of the skeleton (Figs 1I, 4). The ilium, ischium and pubis (Fig. 4 IL, IS, P) are completely fused, without any remain of the sutures. The ilium wing (*Ala ossis ilium*, Fig. 4 iw) is narrow and concave dorsally, and its ventral side is divided in half by the presence of the *Linea glutea ventralis* (Fig. 4 lgv). The facet for the insertion of the sacrum is convex. The *Spina ischiatica* is broad. The ischium is large, with a round ischial tuberosity (*Tuber ischiadicum*, Fig. 4 it), a sharp external border and smooth surfaces. The *Foramen obturador* is large and oblong (Fig. 4 of). Pubis bones are fused together, and the suture is erased in the dorsal side and forms a robust

Fig. 5. *Notostylops murinus* MLP 82-V-1-8. Humerus: A, dorsal; B, plantar. Femur: C, dorsal; D, plantar, bg, bicipital groove; c, capitulum; d, diaphysis; dc, deltoid crest; dt, deltoid tuberosity; ef, epicondylar foramen; fgt, greater trochanter; flt, lesser trochanter; h, head; hgt, greater tuberosity; hlt, lesser tuberosity; if, intercondylar fossa; lc, lateral trochlear crest; lco, lateral condyle; mc, medial trochlear crest; mco, medial condyle; me, medial epicondyle; of, olecranon fossa; pc, pectoral crest; sc, supinator crest; t, trochlea; tf, trochanteric fossa; tt, third trochanter; ttm, tuberosity for teres major muscle. Scale bar = 10 mm.

protuberance ventrally. The caudal half of the right pubis bone is lacking. The fusion areas of the pubis with the ischium, and particularly the one between the pubis and the ilium, are small. The acetabulum (Fig. 4 a) is large and deep, with a broad acetabular notch (*Incisura acetabuli*). Near the superior margin of the acetabulum is the caudal spina iliaca (*Spina iliaca dorsalis caudalis*, Fig. 4 cs), which descends like a crest but ends like a callosity almost in the acetabulum border.

In contrast with the other remains of the skeleton, the pelvis is of light contexture, with a very thin ilium and ischium, but with the fused pubis bones more robust.

Femur

The right femur is preserved. It is slightly larger than the humerus (Figs 1J, 5C, D). The head (*Caput ossis femoris*; Fig. 5C, D, h) is broken, but it can be observed than it was lower than the *Trochanter major* (Fig. 5C, D, fgt). The *fossa trochanterica* (Fig. 5 D, tf), insertion for the *obturatorius externus*, *obturatorius internus* and the *gemelli* muscles, has a long and narrow shape, not as marked as in other notoungulates as *Allalmeia atalaensis* (Lorente *et al.* 2014). The lesser and the third trochanters (*Trochanter minor* and *Trochanter tertius;* Fig. 5C, D, flt, tt) are well developed. The lesser trochanter starts at the level where the trochanteric fossa ends, being triangular in outline and very robust in the anterior side. The third trochanter starts at the same height where the lesser trochanter ends and continues almost to the middle of the diaphysis with prominent shelf rugosity over the posterior side. The diaphysis is longer transversally and flattened. From the distal base to its proximal end, the trochlea (Fig. 5C, t) bends to the lateral side of the femur and is long and narrow, as in most notoungulates. The lateral crest of the trochlea is higher and larger than the medial trochlea crest, which is broken in its distal end. The lateral condyle (Fig. 5D, lco) is broken in its lateral half, but with the *Fossa extensoria* and the *Fossa m. poplitei* well preserved. The medial condyle (Fig. 5D, mco) is larger and somewhat flattened antero-posteriorly and has a deep fossa for the *Collaterale mediale* ligament. The distal ends of the femur can have some plastic deformation, particularly affecting the medial side.

Calcaneus

Only the right calcaneus is preserved (Figs 1K, 3D). It is quite flattened due to deformation. It has an oblique tuber (the longest circumference axis is oblique, not sagittal). The ectal facet (Fig. 3D, ec) is long and convex. The fibular facet (Fig. 3D, fib) is thin and almost half of the ectal facet length. The sustentacular facet (Fig. 3D, sus) is round, concave and fused with a thin distal sustentacular facet, forming an invert teardrop-like articular facet. In dorsal view, the articular surface is slightly larger than the tuber. In the lateral side of the calcaneal tuber, there is an elongated and very distinct fossa (Fig. 3D, lf), which is bordered by a broken crest-like peroneal process that extends below the ectal and fibular facets, to the cuboid facet. There is no distinct flexor groove in the plantar side of the sustentaculum. The distal edge is broken where the characteristic 'beak' is in most notoungulates. This 'beak' has been described in the archaic ungulate *Arctocyon* and in calcanei ascribed to SANU (Cifelli 1983; Bergqvist 1996), but is very conspicuous in notoungulates (Bergqvist 1996).

Other non-identified bones

There are 24 unidentified broken bone fragments (Fig. 1M).

Discussion

Comparison with Pyrotheria

Notostylops was proposed by Billet (2010, 2011) as the sister taxon of Pyrotheria, a group traditionally considered as a separate order of SANU (Gaudry 1909; Simpson 1967, 1978, 1980; McKenna & Bell 1997). This statement was based on the observations of Patterson (1977) and a large data matrix (Billet 2010, 2011). In the analysis, when the basal pyrothere *Proticia* was removed from the data set, *Notostylops* grouped with pyrotheres (Billet 2010). In the unconstrained analysis of Muizon *et al.* (2015), *Notostylops* clustered together with *Adinotherium*, *Colbertia*, *Protypotherium* and *Plesiotypotherium*, as part of an unresolved polytomy of notoungulates, which are basal to the clade which joins *Pyrotherium* and Paenungulata.

Pyrotheria share the bilophodont morphology of their teeth with Xenungulata, and are considered as more related between them than to Notoungulata (Simpson 1945; Lucas 1986, 1993). Xenungulates were not included in the phylogenetic analysis of Billet (2010, 2011), so the position of pyrotheres is contentious. However, since the inclusion of *Carodnia* and the results of the analysis of Muizon *et al.* (2015), a comparison with the present remains of *Notostylops* is deserved.

Simpson (1978) accepted the observations of Patterson (1977) about the notoungulate-like ear of Pyrotheria, but rejected its inclusion in Notoungulata. He proposed that Pyrotheria and Notoungulata shared a bunodont archaic ungulate ancestor with the modifications in the ear but not in the dentition, and so that the two orders were different enough to remain as two different taxa. To propose Pyrotheria as the sister taxa of Notostylopidae, the dentition of basal pyrotheres must be derived from the specialized dentition of basal Notoungulata, which does not seem the case, as the basal pyrothere *Proticia* has more bunodontoid teeth than basal notoungulates (Patterson 1977), being more 'primitive' or 'less specialized'.

According to the descriptions of *Pyrotherium* (Gaudry 1909; Loomis 1914), its postcranium is very different from the one of *Notostylops*. The humerus of *Pyrotherium* is short, stout and very flattened from front to back, and the deltoid crest is very extended, making a crest along the outer side of the bone, which, at the lower end, rises in a prominent process. This is similar to the humerus of elephants or *Carodnia*, particularly in the distal epiphysis, with a short compressed trochlea, and both epicondyles well developed. The radius and ulna of *Pyrotherium* are intimately united and apparently fused in one specimen referred by Gaudry (1909). The fusion of these elements is present in adult individuals of the litoptern *Macrauchenia* but is unknown among notoungulates. The *Pyrotherium* femur is a bit longer than the humerus and has a short trochlea, with globular and subequal condyles with a narrow intercondylar fossa. This trochlea is similar to that of graviportal mammals such as *Loxodonta* (O'leary *et al.* 2013), but different from that of *Notostylops* and the rest of the known notoungulates, in which the trochlea is elongate with a larger intercondylar fossa. The calcaneus of *Pyrotherium* is flatter dorsoplantarly. It has a thin cuboid facet, fused ectal and sustentacular facets, and a tuber that is much wider transversally than dorsoplantarly (Gaudry 1909; Shockey & Anaya 2004; Shockey *et al.* 2012), like in most graviportal mammals (e.g. *Elephas*, *Rhinoceros*, *Hippopotamus*). The astragalus of *Pyrotherium* (MLP 79-XII-18-29) shows a well-developed, distal cuboid facet, which indicates the presence of an alternating tarsus such as in Perissodactyla and Artiodactyla, but not in Notoungulata, which have a serial or reverse alternating tarsus (Cifelli 1993; Shockey *et al.* 2012; Lorente 2015). The navicular bone described by Gaudry (1909) is a small bone that lacks a navicular process or a medial tubercle, both characteristic of Notoungulata. The *Notostylops* postcranium, and even the known postcrania of Notoungulata, is markedly different from that of *Pyrotherium*, which clearly exhibits graviportal adaptive features. Only the great development of the fibula could be interpreted as a common character state between the postcranium of Pyrotheria and Notoungulata or even Litopterna. An important point to highlight is that the postcrania of basal pyrotheres still remain unknown. *Pyrotherium* is probably too derived in its postcranium characters to be directly compared with basal SANU or the more generalized Paleogene notoungulate skeleton, to infer accurate phylogenetic relationships.

Comparison with Notoungulata Typotheria

Among other known notoungulates, the skeleton of *Notostylops* resembles that of some Eocene notoungulates such as *Allalmeia atalaensis* (Lorente *et al.* 2014), *Colbertia lumbrerense* and *C. magellanica* (Bergqvist 1996; Bergqvist *et al.* 2007), as well as that of other typotherians in most features, but, the general aspect is more massive, with better developed crests, fossae and tuberosites. For example, in the humerus, the evident tubercle for the *Teres major* of *Notostylops* is not marked in the Eocene *Notopithecus* (Vera 2012). Opposite to that observed in both typotherians and toxodontids, whose humerus has a thin region or even a supratrochlear foramen in the olecranon fossa, the olecranon fossa region of *Notostylops* is thick. In the pelvic girdle, the obturator foramen is smaller in *Notostylops* than in *Protypotherium* (MLP 90-XII-26-10), with shorter pubis and ischium.

Comparison with Notoungulata Toxodontia

The postcranium of *Notostylops* has been considered morphologically closer to that of toxodontians by Bergqvist & Metello (2011). *Notostylops* shares some features, such as a wider humeral distal epiphysis and a smaller fibular facet in the calcaneus, with the isotemnid *Pleurostylodon* (AMNH 28904: Simpson 1967; Shockey & Flynn 2007) and with Homalodotheriidae (e.g. *Asmodeus*, MAC-A 12326), but not with other isotemnids or later toxodontians (Toxodontidae, Leontiniidae and Notohippidae). These features are also present in some Typotheria and could be primitive for Notoungulata. Toxondontia share several modifications that are absent in *Notostylops* as (1) a more lateral projected deltoid tuberosity connects the radial tubercle with the head in the humerus; (2) a lateral projection of the greater tubercle; (3) a narrower humeral entepicondyle; (4) a more developed humeral ectepicondyle; (5) a thin olecranon fossa wall; (6) a femoral trochanter minor less projected than the third trochanter; (7) an expanded ilium wing; (8) the fibular facet of the calcaneus as wide as the ectal facet (except in isotemnids and homalodotherids); (9) a marked plantar groove in the sustentaculum; and (10) a calcaneal tuber almost round, while in most mammals, including *Notostylops*, it is markedly narrower transversally, being more oval than round. This last feature could be exemplified with the calcaneus of *Nesodon* (MLP 12–90), in which the ratio between the calcaneal tuber dorsoplantar diameter and the transversal diameter (DPT/ATT) is 0.88, while in *Notostylops,* DPT/ATT = 0.57. A round calcaneal tuber is associated with graviportal mammals. Graviportality can be hard to ascribe to the smaller toxodontids, as isotemnids, notohippids or the toxodontid *Adinotherium*, but, in general, all Toxodontia show weight-bearing adaptations.

The humerus of *Notostylops* here described is similar to that assigned by Simpson (1967) to *Pleurostylodon similis* (AMNH 28904) from the Eocene of Patagonia. Both share an elevated deltoid tuberosity (although more lateral in *Pleurostylodon*), an expanded lateral ridge, a distal region dorsoventrally compressed and a shallow olecranon fossa (Shockey & Flynn 2007). In contrast, the humerus of *Pleurostylodon* lacks the proximal half, which has diagnostic features for Toxodontia. So, the similarity with *Notostylops* rests in the distal half of the humerus which retains basal characters for notoungulates. Unlike other Eocene forms such as *Anisotemnus*, *Thomashuxleya* and *Pleurostylodon* (Shockey & Flynn 2007), *Notostylops* shows the following features: (1) the greater tubercle is not high but even with the head; (2) radial-ulnar fossae are not marked; (3) the olecranon fossa is not deep; (4) the lateral trochlear crest is not marked; and (5) the medial crest does not form a ridge continuous with deltoid tuberosity. These differences could be interpreted as phylogenetic or functional, as toxodontids were heavily built beyond their size while *Notostylops*, although robust, has no significant weight-bearing adaptations.

Other postcranial remains cf. Notostylopidae

Several specimens assigned to different basal notoungulates are here discussed in the context of the skeleton of *Notostylops*. Shockey & Flynn (2007) described an indeterminate isotemnid (AMNH 28690; Figs 6B, 7E) represented by an almost complete left hind limb, with a partial femur, tibia, fibula, tarsals and three metapodials. In spite of its size, these authors considered it probably related to *Pleurostylodon*, because 'it is probably too large and morphologically distinct to represent any of the notostylopids or oldfieldthomasiids' already found in 'Oficina del Diablo', Cañadón Vaca, Argentina, as mentioned by Simpson (1967). Although the dentition of *N. murinus* is around 60% smaller than that of *Pleurostylodon similis*, its skeleton is large and robust, being the femur around 80% of that of *P. similis*. The measures of AMNH 28690 are similar to the skeleton of *Notostylops* (MLP 82-V-1-8), even being slightly smaller. The similarity between AMNH 28690 and MLP 82-V-1-8 is remarkable at tarsi level. There is an elongated fossa in the lateral side of the calcaneal tuber, which is dorsal to an expanded sharp crest of the peroneal process. The femur of both specimens shares a greater trochanter just slightly higher than the head, a lesser trochanter that begins about 1 cm below the head and continues distally for about 2 cm, and a third trochanter that starts near the end of the lesser trochanter. Additionally, the femur of AMNH 28690 resembles more that of *Notostylops* (MLP 82-V-1-8) than that of *Pleurostylodon similis* (AMNH 28904), which has a larger and more constrict trochlea, less developed trochanters, and a more plantar lesser trochanter.

Another evidence of the possibility that AMNH 28690 belongs to *Notostylops* is based on the astragali described by Ameghino (1905; fig. 74; both under the repository number MACN-A 10940; Fig. 7). These are the only two of the isolated astragali described by Ameghino as found with dental remains, while this condition was not clarified in the assignation of any other astragali. The astragalus of specimen AMNH 28690 shares with them a similar size and morphology (Supplementary material). Morphological features include: (1) length greater than width; (2) a large, oval sustentacular facet with the medial sulcus thin, almost erased; (3) distal medial extension of the trochlea in the dorsal side over the neck; (4) large trochlea that surrounds the astragalar foramen at sides; (5) medial plantar tuberosity distinct but small in comparison with other notoungulates; (6) a marked flexor groove, more proximal than the trochlea (as in *Homalodotherium*, but less developed); and (7) a gap between the lateral trochlear crest and the flexor groove. Several of these features are also shared with the astragalus of *B. lumbrerensis* (MLP 79-XI-22-14) and also with that of a large notoungulata, also recovered from Cañadón Vaca (PVL 323), which, considering its size and especially the enlarged medial crest and the high flexor groove, could probably belong to *Edvardotrouessartia sola* (Fig. 7).

In contrast to that observed in *Notostylops*, a very different astragalar morphology is present in isotemnids. We have six astragali from ?*Thomashuxleya* (MLP 75-II-1-7 to -11 in Supplementary material and Fig 7A) and three from ?*Isotemnus* (LIEB-PV 4014, LIEV PV-4015, LIEB-PV 4056, Supplementary material). These isotemnid? astragali are (1) wide; (2) with broad, smooth trochleas of parallel but asymmetrical crests; (3) medial crest slightly smaller and rounder than lateral; (4) astragalar foramen more lateral; (5) no extension of the trochlea over the neck; and (6) large medial tubercle with a ridge that starts in the middle of the medial facet (Lorente 2015).

Notostylops pendens, slightly smaller than *N. murinus*, is present in Cañadón Vaca (Simpson 1948, 1967). Considering the similarities between AMNH 28690 and MLP 82-V-1-8, here we propose that AMNH 28690 could be assigned to *Notostylops pendens.*

Another specimen from Cañadón Vaca, comprising a femur and a tibia (AMNH 28635), was also considered as a *Pleurostylodon similis* by Shockey & Flynn (2007). This sample also fits well with the present description of *N. murinus* and also with AMNH 28690 and probably represents another notostylopid. It is larger than *Notostylops* and AMNH 28690, and around 8% smaller than *Pleurostylodon* (AMNH 28904) based on the femur (Fig. 6C). However, in Cañadón Vaca, there is another notoungulate of the size of *Pleurostylodon similis*, the large notostylopid *Edvardotrouessartia sola* (around 91% of the size of

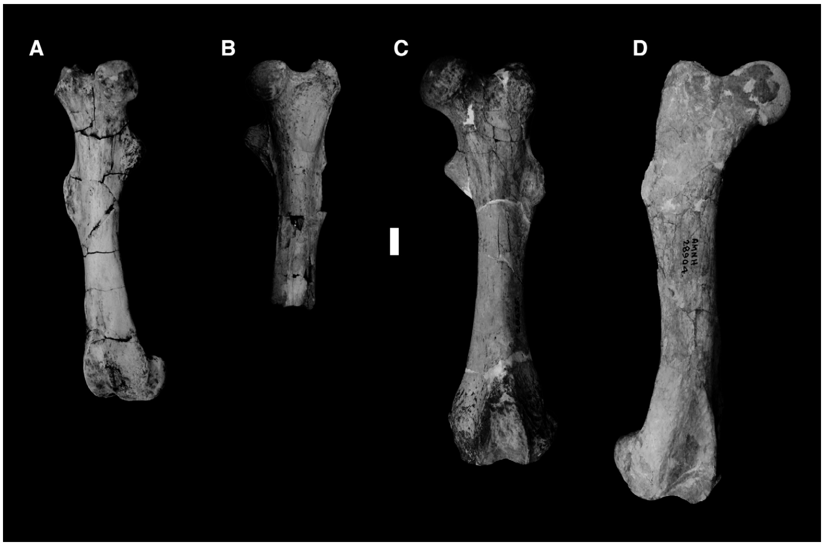

Fig. 6. A, *Notostylops murinus* MLP 82-V-1–8 right femur; B, AMNH 28690 left femur (Isotemnidae indet. Shockey & Flynn 2007; *Notostylops pendens*?, this work); C, AMNH 28635 left femur (*Pleurostylodon similis*, Shockey & Flynn 2007; *Edvardotrouessartia sola*?, this work); D, *Pleurostylodon similis* AMNH 28904 right femur (part of a partial skeleton that includes teeth). Scale bar = 10 mm.

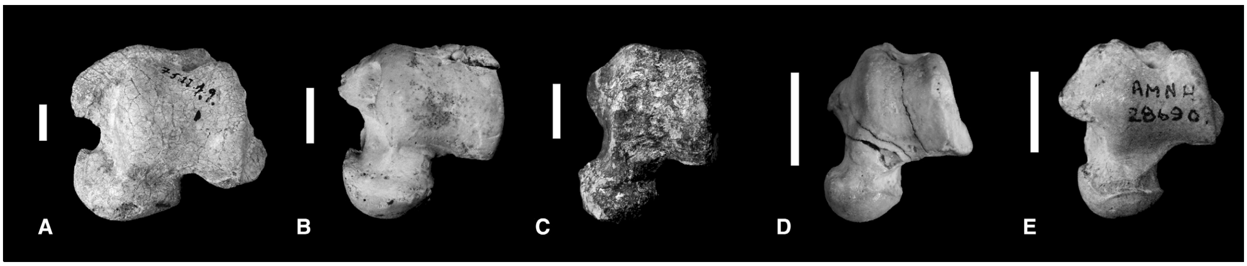

Fig. 7. Scalated left astragali of A, Loma Verde MLP 75-II-1-9, *Thomashuxleya*?; B, La Barda LIEB-PV 4014 *Isotemnus*?; C, Cañadón Vaca PVL 323, *Edvardotrouessartia*?; D, *Notostylops* MACN-A 10940; E, AMNH 28690, *Notostylops pendens*?. Scale bar = 10 mm.

Pleurostylodon). *Edvardotrouessartia* is less known, and its specimens are scarcer than those of *Pleurostylodon*.

Summarizing, considering the previous statements, we assign the remains of AMNH 28690 and AMNH 28635 to the notostylopids *N. pendens* and *E. sola*, respectively.

Anatomical and palaeobiological implications

Notostylops has been compared by its dental morphology to rodents and lagomorphs, and has been represented for example as a rabbit-like mammal (Dixon *et al.* 1988). However, the postcranium of *Notostylops* is more robust and shows more generalized features than that of lagomorphs. As in the rest of notoungulates, the radius of *Notostylops* is not fused to the ulna. It is shorter than the humerus and very generalized, which means that it has an oval head, a marked neck and a radial tubercle, more similar to those of some arctocyonids (e.g. *Chriacus*; Rose 1987). The humerus and the femur show pronounced insertion structures as trochanters, tuberosities, fossae and crests. In rabbits, the medial humeral epicondyle is not developed, and the capitulum is small and lower than trochlea, which has a marked lateral crest, whereas, in *Notostylops*, the capitulum is more elevated than the trochlea and there is not a marked lateral trochlear crest. The humerus of lagomorphs also has a supratrochlear foramen; the deltoid tuberosity is more proximal and less developed, there is no tuberosity for *Teres major*, and there is no supinator crest (Fig. 9).

Superficially, the postcranial skeleton of *Notostylops* resembles more that of Sciuridae rodents (e.g. *Callosciurus erythraeus*, MLP 2013; Fig. 8C). As *Notostylops*, squirrels have a humerus with well-developed greater and lesser tuberosities, high deltoid tuberosity that extends over almost two-thirds length of the humerus, pronounced deltoid tuberosity, marked tuberosity for *Teres major*, large medial epicondyle with an epicondylar foramen, ovoid capitulum, well-marked medial but not lateral trochlear crest, no supratrochlear foramen, well-marked olecranon fossa and a sharp lateral ridge. In squirrels

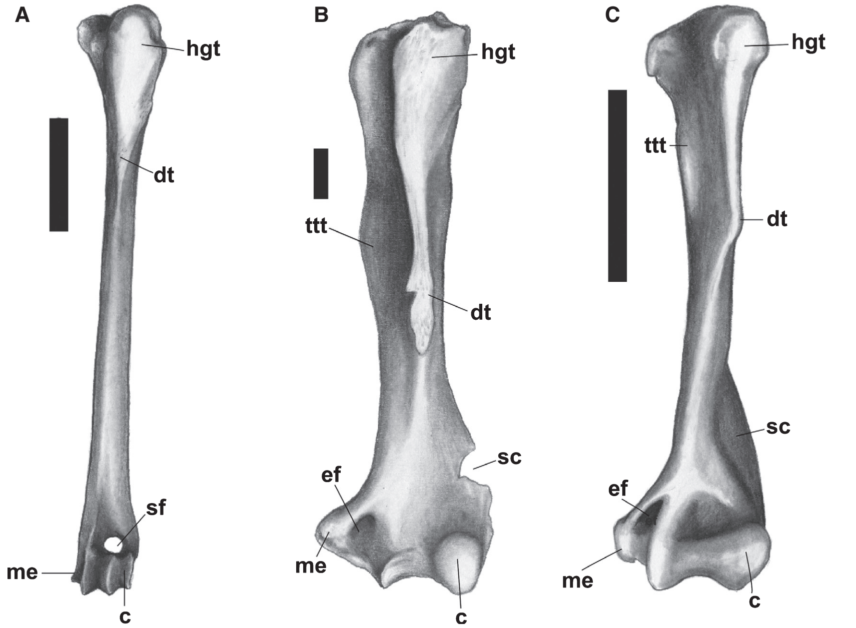

Fig. 8. Comparison of humeri of A, the lagomorph *Lepus callotis* MLP 1082; B, *Notostylops murinus* MLP 82-V-1-8; C, the sciuridae rodent *Callosciurus erythraeus* MLP 2013. c, capitulum; dt, deltoid tuberosity; ef, epicondylar foramen; hgt, greater tuberosity; me, medial epicondyle; sc, supinator crest; sf, supratrochlear foramen; ttt, tuberosity for teres major muscle. Scale bar = 10 mm.

and *Notostylops*, the radius head is oval and almost round, and there are no fusions with the ulna. The femur has similarly developed trochanters. Despite these similarities, some differences between *Notostylops* and sciurids could be mentioned. For example, in squirrels, the humeral supinator lateral crest is more developed, which may be due to their arboreality, and the third trochanter is larger and in a lower position than the lesser trochanter in *Notostylops.* This last character is the most common state in basal notoungulates and litopterns and probably represents the plesimorphic condition for the lesser trochanter in these groups. Additionally, the femoral trochlea of *Notostylops* bends to the lateral side, while in most squirrels, it is straight, being prairie dogs, *Cynomys*, a possible exception (France 2009).

The inferences for body mass calculated for *Notostylops* (see below) indicate that *Notostylops* is too large to be compared with extant arboreal squirrels, since the largest known tree squirrel, *Ratufa indica*, has a body mass range of 1.5 to 2 kg (Nowak 1999). Ground sciuromorphs, as *Marmota* or *Cynomys*, could be a better analogy since they are morphologically alike but larger in size (Bezuidenhout & Evans 2005). The locomotor habit of *Notostylops* appears to have been more similar to that of ground squirrels (see below).

The body mass of *Notostylops* has been calculated in 3.119 kg through inferences based on the M1 (Croft 2000), in around 11.91 kg based on several dental measures (Elissamburu 2012), between 18 and 55 kg using the humerus and between 7 and 27 kg using the femur (Bergqvist & Metello 2011), and in 50 kg by a comparison with *Ovis aries* (Vizcaíno *et al.* 2012). In the present work, with measures of the MLP astragali assigned to *Notostylops* (MLP 56-XII-18-198 to -201 in Supplementary material), using the regression formulas of Tsubamoto (2012), the body mass was calculated between 5.02 and 13.56 kg (Supplementary material). Based on head-body length of another notostylopid, *Otronia muhlbergi*, Croft (2016) estimated a mass between 5 and 9 kg.

Based on the previous statements about skeletal traits of *Notostylops* and the locomotor habit inferred from other sources, some comparisons could be made. Macrini *et al.* (2010) studied the morphology of the ear of *N. murinus* and, based on its agility scores and particularly the range of locomotor patterns inferred in previous works for other notoungulates, concluded that *Notostylops* was a generalized mammal, with cursorial tendencies. The agility scores calculated for *Notostylops* range from 3.4 to 3.9, suggesting that this taxon had an 'average' agility, which, in extant mammals, corresponds to terrestrial, cursorial, fossorial, arboreal and semi-aquatic species, but not to gliding, flying, ricochetal or fully aquatic species (Spoor *et al.* 2007; Macrini *et al.* 2010). This wide range of locomotor possibilities inferred for *Notostylops* shows the weakness of these scores, at least for fossil mammals without direct extant relatives. Macrini *et al.* (2010) thus advised that their results should be tested with

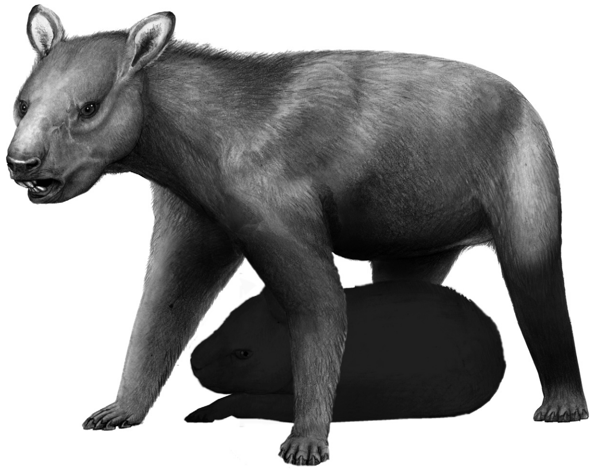

Fig. 9. Reconstruction of an adult *Notostylops murinus* with its calf. *Notostylops* was a remarkably robust animal, which probably looked more like 'archaic ungulates' than like extant ones.

postcrania. Here, we reduced the possible spectrum of locomotor behaviours in *Notostylops* by eliminating the cursorial behaviour, based on the absence of cursorial traits in its postcranium, as could be the reduction of the humeral distal epiphysis, low humeral capitulum, complex radial head, reduction of third trochanter, high greater trochanter and high astragalar trochlear crests (Van Valkenburgh 1987). The characteristics of the foot of the specimen here assigned to *Notostylops pendens* (AMNH 28690), being pentadactyl, with short metatarsals, and shallow astragalar trochlear crests, indicate that it could be a plantigrade mammal (Carrano 1997; Shockey & Flynn 2007). The development of tuberosities, insertion fossae and trochanters, and the radial head of the specimen of *Notostylops* here analysed (MLP 82-V-1-8) suggest that it was a robust animal, able to fully supinate the arm, with no indication to be adapted to parasagittal movements, predominant in cursorial species.

Values of morphofunctional indices were taken for *Notostylops* and compared with the values obtained by Samuels & Van Valkenburgh (2008) and Elissamburu & Vizcaino (2004). This allowed suggesting that *Notostylops* is comparable to fossorial, semifossorial and terrestrial (unspecialized) extant mammals, but differs from ricochetal mammals (higher HRI) and semiaquatic extant mammals (higher SMI), and differs in more than one index with arboreal (higher SMI and HRI), aquatic (higher SMI, lower GI and FRI) and cursorial (higher SMI, HRI and HEI, lower FRI and FEI) species. *Notostylops* shows higher values in all indices when compared with gliding forms like the flying squirrel *Petaurista petaurista*. These comparisons allow discarding ricochetal, semiaquatic, arboreal, aquatic, cursorial and gliding traits for *Notostylops*, leaving terrestrial, semifossorial and fossorial traits as the most probable functional behaviours for this taxon. Similar conclusions can be achieved considering other probable representatives of the Notostylopidae. The crural index (tibial length/femur length) of specimen AMNH 28635, here considered with doubts as *Edvardotrouessartia sola*?, is more similar to fossorial and semifossorial extant mammals than to any other.

Regarding its feeding habits, *Notostylops* has chisel-like upper incisors and a large diastema, a humerus with a large HEB index (31%), high and distally placed deltoid tuberosity, and a small radius. These features could be associated with chisel tooth-digging and particularly with scratch-digging mammals (Hildebrand 1985; Shockey *et al.* 2007). An approximation to the zygomatic index used for rodents (Verzi 2008) indicates that the small orbits of *Notostylops* based on an adult individual (CNHM 13319, Simpson 1948; fig. 68, B) have values of 0.54, which are equivalent to those expected for subterranean caviomorphs (Verzi 2008). The medial surface of the olecraneon extends to an unusual medial process, whereas in scratch diggers the olecraneon itself usually extends to the medial side, increasing the area of attachment of digital and carpal flexors to produce a greater strength to dig (Hildebrand 1985).

Previous interpretations of some notoungulates (e.g. Typotheria), as rabbit-like ungulates, had been based on dental analogies but not on a straight comparison with postcranial elements, which, by that time, were not available (Sinclair 1908; Kraglievich 1926; Simpson 1980; Cifelli 1985b). Even notoungulates with slender skeletons than *Notostylops* were robust in comparison to extant rabbits or rabbit-like rodents as *Dolichotis* or *Pediolagus*. No notoungulate seems to have the proportions of lagomorphs, where both the tibia and the radius are larger than the femur and the humerus respectively. As an example, the typotheria Hegetotheriidae were characterized by 'saltatorial postcranial adaptations' (Cifelli 1985b, p. 257), although they have larger tibias than femurs, but shorter radii than humeri. The proportions of notoungulates are comparable to those present in many rodents (e.g. *Microcavia*, Olivares 2009), artiodactyls (e.g. *Mazama*, MLP 4.VIII.98.1, MLP 4.X.94.2), primates (e.g. *Leontopithecus*, MLP 20.IV.99.1) and carnivores (e.g. *Lycalopex*, MLP 1967), but not to those present in specialized ricochetal mammals. So, it is improbable that notoungulates exhibited ricochetal habits, perhaps with the exception of some later forms of Hegetotheriidae (e.g. *Paedotherium*). However, it should be noted that even these hegetotheriids were more generalized in their morphology than other ricochetal mammals.

Unlike the appendicular skeletons of cursorial or saltatorial animals, which restrict their mobility antero-posteriorly, the skeleton of *Notostylops* indicates the possibility for a wide variety of different movements, including supination and pronation, as would be expected for terrestrial, fossorial or arboreal mammals. Fossoriality has been proposed for other notoungulates as Mesotheriidae (Shockey & Flynn 2007), and *Hegetotherium* and *Interatherium* may have occasionally digged (Cassini *et al.* 2012). Croft & Anderson (2008) suggested than fossoriality may be an ancestral attribute of Notoungulata, as they found that *Protypotherium* is similar in some aspects to fossorial and arboreal rodents.

The ungual phalanx of *Notostylops* (Fig. 3C) is unusual, although similar phalanges appear in other Eocene localities from Patagonia (e.g. Paso del Sapo, del Chubut province). The very pronounced proximodistally oriented grooves in the distal end resemble hoofed or nail-bearing phalanges (apical tuft; see Maiolino *et al.* 2011), but the presence of a symmetrical *Tuberculum flexorium* (insertion of deep digital flexor tendon) and the narrow shape rather suggest the presence of a claw. In extant unguligrade mammals, the *Tuberculum flexorium* is asymmetrical, with a reduced size or even not developed, in which case, there is a plate, the *Facies flexoria*, for the deep digital flexor tendon. These mixed features may indicate the presence of an intermediate condition between a true claw and a true hoof. Among notoungulates, *Allalmeia atalaensis* and *Homalodotherium* had claw-like phalanges, whereas *Nesodon* and *Toxodon* had hoof-like ones. The well-developed flexor tubercle indicates that *Notostylops* was able to flex its ungual phalanges more than most primates or ungulates.

Notostylops does not fit with the image of a prairie-dweller cursorial ungulate. It was a terrestrial, semifossorial or maybe fossorial mammal, which lived in a more transitional and woody environment and resembled generalized archaic ungulates such as *Protungulatum*, *Chriacus*, *Arctocyon* or *Hyopsodus* more than extant specialized ungulates (Fig. 9). The skeleton here studied (MLP 82-V-1-8) came from the lower levels of the Gran Barranca Member of the Sarmiento Formation. The phytoliths content of these middle Eocene outcrops indicate the presence of mixed vegetation with abundant palms associated with grasses, sedges and dicotyledons, including woody elements (Zucol *et al.* 2010). The analysis of these components suggests that *Notostylops* belonged to savanna and/or forest communities (Zucol *et al.* 2010). However, by using the leaf area index, Dunn *et al.* (2015) considered that the Patagonian landscape was composed of a closed forest that was just starting to open up by the middle-late Eocene.

Conclusion

The tentative assignation of the remains analysed by Shockey & Flynn (2007) to *Notostylops pendens*? (AMNH 28690) and *Edvardotrouessartia sola*? (AMNH 28635) and the description of the postcranial elements of *N. murinus* (MLP 82-V-1-8) here performed contribute to elucidating the morphology of the family. Notostylopids are characterized by their appendicular robustness and the great development of their muscular insertion and origin structures. Their morphology is very distinct, but with notoungulate affinities such as reduced lateral epicondyle and enlarged medial epicondyle of the humerus, high olecranon, low third trochanter and calcaneal beak. These features are different from the anatomy of other SANU orders, including Pyrotheria, which has been proposed as their sister taxa, based on their cranial anatomy (Billet 2010).

We conclude that *N. murinus* was a medium-sized, terrestrial, semifossorial or fossorial mammal, which lived in the forest communities of the middle Eocene of Patagonia. It was characterized by its grooved curved ungual phalanges, which probably supported an epidermal structure with an intermediate development between a claw and a hoof. Combined with the anatomy of *Nostostylops pendens*? (AMNH 28690), a plantigrade, and *Edvardotrouessartia sola*? (AMNH 28635), a probable semifossorial or fossorial mammal, our knowledge of the appendicular morphology, locomotion and ecology of the Notostylopidae has considerably increased.

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