Postcranial anatomy of the early notoungulate Allalmeia atalaensis from the Eocene of Argentina

Malena Lorente, Javier N. Gelfo & Guillermo M. López
Published online: 26 Mar 2014.

PLEASE SCROLL DOWN FOR ARTICLE

Postcranial anatomy of the early notoungulate *Allalmeia atalaensis* from the Eocene of Argentina

MALENA LORENTE, JAVIER N. GELFO and GUILLERMO M. LÓPEZ

We redescribe and interpret the postcranial elements of *Allalmeia atalaensis* Rusconi, found in the Divisadero Largo Formation, Mendoza, Argentina. *Allalmeia* is one of the few basal notoungulates with preserved postcranial remains. Rusconi initially documented a skull, several vertebrae and part of the appendicular skeleton but these specimens were subsequently lost. Recently though, distal components of the holotype humeri, the proximal portion of the right femur, several broken diaphyses and most of the left and right pes (MCNAM-PV 507), were relocated. Preparation of this material has revealed new details, especially from the plantar side of the feet. The calcaneum has a distal peroneal process with marked rugosity in the lateral end, a well-developed calcaneal plantar tubercle and a large sustentaculum tali. The naviculars exhibit a well-developed medial tuberosity and slightly contact the calcaneum on the dorsal side, a condition called a 'reverse alternating tarsus'. The disposition and morphology of the cuneiforms are similar to those of more recent typotheres and the archaic ungulate *Tetraclaenodon puercensis*. The phalangeal rows are oblique to each other, as in some extant digitigrade mammals. The ungual phalanges are claw-like suggesting that they might have borne claws. Long bones are gracile in comparison with other notoungulates, but with well-developed muscle origins and insertions. The use of body-mass allometric equations and a comparison with extant analogues suggests that *Allalmeia* was a small, generalized, digitigrade animal. An estimated body mass of approximately 3 kg is consistent with oldfieldthomasiids and archaic ungulates.

Malena Lorente [mlorente@fcnym.unlp.edu.ar] (author for correspondence), Javier N. Gelfo [jgelfo@fcnym.unlp.edu.ar], Guillermo M. López [glopez@fcnym.unlp.edu.ar], División Paleontología de Vertebrados, Museo de La Plata. Paseo del Bosque s/n B1900FWA, La Plata, Buenos Aires, Argentina; First and second authors also associated with CONICET. Received 1.10.2013, revised 6.1.2014, accepted 16.1.2014.

NOTOUNGULATA was the most diverse group of South American native ungulates, incorporating at least 13 families, six of which were already differentiated by the early–middle Eocene. The notoungulate clade includes herbivores of various adaptive types, many of which are convergent to Holarctic mammals (Simpson 1978, López *et al*. in press). Hypotheses on the relationships within Notoungulata, and their placement relative to other mammals, have been derived largely on the basis of dental and cranial features (Billet 2010), or in conjunction with only a few incompletely documented postcranial traits (Cifelli 1993, Shockey *et al*. 2012). Basal notoungulates have rarely been found with dental and postcranial remains in close association. Examples include the notostylopid *Notostylops* (Bergqvist & Metello 2011, Lorente *et al*. 2013), the isotemnids *Thomashuxleya*, *Anisotemnus* and *Pleurostylodon* (Simpson 1967, Shockey & Flynn 2007) and the oldfieldthomasiid *Colbertia* (Bergqvist & Bastos 2009). Consequently, the appendicular morphology, locomotor adaptations and phylogenetic relationships of this group are poorly understood.

Allalmeia atalaensis is a basal notoungulate recovered from the Divisadero Largo Formation in Mendoza province (central western Argentina; López 2008). The faunal assemblage recovered from this unit was used to define the Divisaderan South American Land Mammal Age (SALMA; Pascual *et al*. 1965) and was originally characterized by taxa with a mix of generalized and derived morphologies. The particular nature of this association was considered to fill the gap between the Mustersan and Deseadan SALMAs during the late Eocene (Pascual *et al*. 1965). However, the Divisaderan is now no longer recognized and could be considered a local fauna probably equivalent in age to the Vacan or intercalated between the Vacan and Barrancan (López 2010).

The lower and middle levels of Divisadero Largo Formation have yielded a vertebrate fauna composed essentially of mammals and a few reptiles (i.e., turtles, crocodiles and boas). Mammals comprise more than 95% of the fossils collected from these levels and, remarkably, almost all of them can be referred to South American native ungulates (López 2010). Postcranial remains are uncommon in this assemblage and *A. atalaensis* is the only species recognized from both dental and postcranial remains.

Allalmeia atalaensis was named by Carlos Rusconi (1946a), who documented the skull, isolated vertebrae and part of the appendicular skeleton (MCNAM-PV 507). However, these fossils, and others housed in Museo de Historia Natural de Mendoza (now Museo de

Ciencias Naturales y Antropológicas J. C. Moyano), have been lost. López (2008) assigned new cranial and dental remains to *A. atalaensis*, and also presented a more comprehensive description. Recently, a small portion of the holotype of *A. atalaensis*, composed of the distal parts of both humeri, a proximal portion of the right femur, several broken diaphyses and most of the pedal elements were relocated and prepared. These materials were still labeled with the original repository number from Rusconi (1946a, b, c) and match his published description.

Originally, Rusconi (1946a, c) referred *A. atalaensis* to Notostylopidae, and (Simpson *et al.* 1962, p. 254) considered it to be a possible olfieldthomasiid and emphasized that this reference was '... based more on the absence of special characters of other defined families than on the presence of special resemblances to *Oldfieldthomasia* and other known, more surely allied early forms'. López & Bond (2003) proposed that *Allalmeia atalaensis* had close phylogenetic affinities with *Brachystephanus postremus* Simpson, Minoprio & Patterson, 1962, *Xenostephanus chiottii* Simpson, Minoprio & Patterson, 1962, *Colbertia lumbrerense* Bond, 1981 (Eocene, Northwestern Argentina) and *Colbertia magellanica* Price & Paula Couto, 1950, (late Paleocene—early Eocene, São José de Itaboraí, Brazil), and designated them as a new but yet unnamed family.

Here we review and redescribe the appendicular skeleton of *Allalmeia* in order to better understand the early evolution of notoungulates via identification of novel phylogenetic characters and functional interpretations.

Materials and methods

MCNAM-PV 507. Part of the holotype of *Allalmeia atalaensis*. The originally documented skull, vertebrae, a partial scapula, ulna, a patella, right tibia, left femur, left astragalus and left calcaneum are still missing. The relocated elements described here include: the distal epiphysis of both humeri, the proximal half of the right femur, the distal epiphysis of the left fibula, several broken diaphysis and most of the foot bones. The pedal components were cleaned and separated from the rock matrix. The tarsals, metatarsals and phalanges were retained in their articulated position. Most of the glue present in the upper ankle joint of the right foot was removed and cleaned by technical staff of Museo de La Plata. This procedure exposed the trochlea of the right astragalus and a broken bone, which might be a fragment from the calcaneum. Measurements were taken with a point digital caliper (Schwyz) and expressed in millimetres. Locomotor patterns were described following Samuels & Van Valkenburgh (2008). Bone topological names are written in Latin following the Nomina Anatomica Veterinaria (Schaller 1996) attached to their colloquial names. We compare *A. atalaensis* with extant and fossil remains housed in different museums mentioned below, and also with published

data of other notoungulate skeletons. Orientation of the bones was based on the proposal of Sisson & Grossman (1982).

Body-mass estimations. The mass inferences for *Allalmeia* and extant mammals of similar size were inferred, depending of the available material, following allometric equations from Janis (1990) and Scarano *et al.* (2011) for dental measures, and Scott (1990) and Tsubamoto (in press) for postcranial parameters. Dental dimensions of the type material are from Rusconi (1946c), as are the length of the humerus, femur and the femoral diameter. Additional dental measures are from López (2008). For each equation we obtained a range of mass values, their mean and standard deviation. Following the analyses by Elissamburu (2012), the frequency distribution of the corporal mass was evaluated in order to avoid under and overestimation of mass.

Institutional abbreviations. AMNH, American Museum of Natural History, USA; MLP, Museo de la Plata, Argentina; MACN-A, Museo Argentino de Ciencias Naturales, 'Bernardino Rivadavia', colección Ameghino, Argentina; MACN-Ma, Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, colección Mastozoología, Argentina; MCT PV, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MCZ, Museum of Comparative Zoology, Harvard, USA; MMCNMP, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia', Mar del Plata, Argentina; MCNAM-PV, Colección Paleontología de Vertebrados, Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano', Mendoza, Argentina.

Systematic palaeontology

Infraclass EUTHERIA Gill, 1872
Order NOTOUNGULATA Roth, 1903
Family ?OLDFIELDTHOMASIIDAE Simpson, 1945

Allalmeia Rusconi, 1946a

Allalmeia atalaensis Rusconi, 1946a (Figs 1–4, Table 1; see also Simpson *et al.* 1962, p. 266).

Holotype. MCNAM-PV 507, incomplete individual consisting of a maxillar fragment with the alveoli of I and C, right P1–M3 and left P2–M3, partial right jaw with i3–m3 and left jaw with i3–p4 (at present lost). A partial postcranial skeleton represented by elements of the vertebral column, scapular and pelvic girdles, left and right humeri, cubits, radii, femurs and several elements of the hind and forelimb autopodium.

Hypodigm. López (2008) referred the following specimens: MLP 49-XI-21-21, right maxilla with M2–M3; MLP 66-XII-12-22 A–B, (A) right maxillar fragment with P3–M2 and erupting M3; (B) right jaw fragment with p4 talonid, m1–2, and erupting m3; MLP 87-II-20-5, right maxilla with P4–M3; MLP 87-II-20-11,
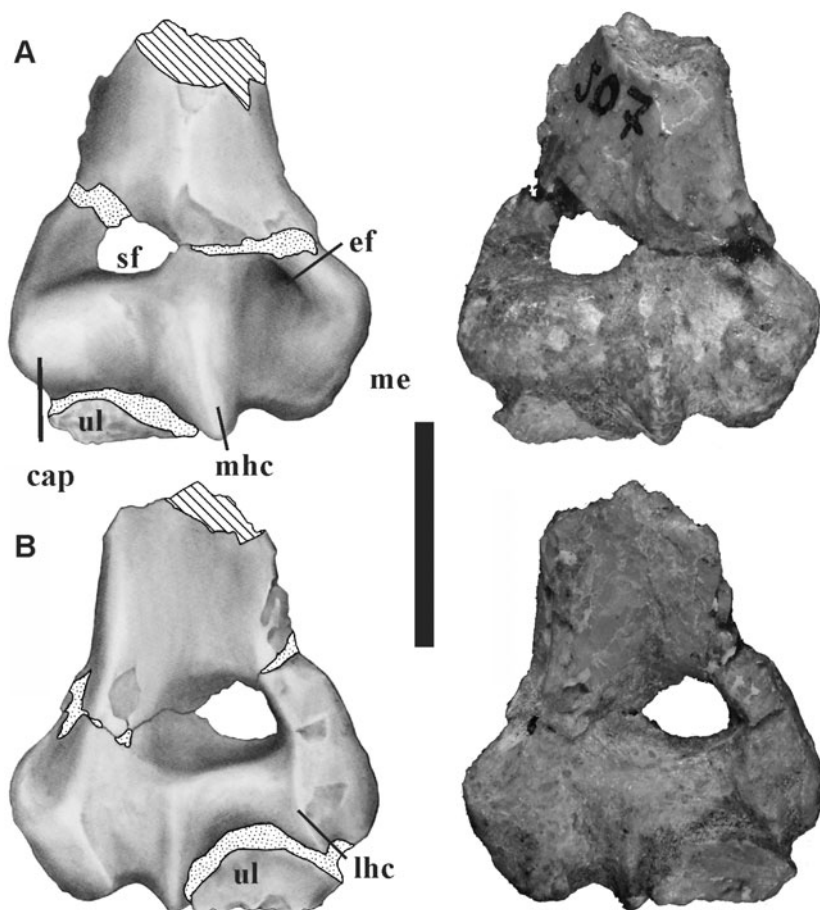
Fig. 1. Allalmeia atalaensis distal epiphysis of the right humerus. **A,** dorsal; **B,** palmar; **cap**, capitulum; **ef**, epicondylar foramen; **lhc**, lateral humeral trochlear crest; **me**, medial epicondyle; **mhc**, medial humeral trochlear crest; **sf**, supratrochlear foramen; **ul**, ulna. Scale bar = 10 mm.

almost complete skull with left and broken P1–M2 and right I2, roots of I3, C, P1, and P2–M3, and left jaw with i2, roots of i3, p1, p2, and p3–m3; MLP 87-II-20-13, left maxillar fragment with P2–M3; MLP 87-II-20-54, anterior part of the skull with complete left and right I1-M3; MLP 87-II-20-59, right maxillar fragment with P3–M1; MLP 88-V-15-9, right maxilla with broken M2 and M3; MMCNMP 734 S, right maxilla with broken P2–P3, P4–M2 and part of the right jaw with i3–p1, p3–m3 and roots of left p1–p3; MCZ 7412, left maxillar fragment with M1–M2.

Type locality. Divisadero hill, 8 km west of Mendoza city, Mendoza province, Argentina.

Age and stratigraphy. All specimens derive from the middle Eocene, Divisadero Largo Formation. This unit is exposed as a NNE–SSW-oriented ledge extending from the Divisadero Largo hill up to the Papagallos locality, approximately 2200 m long and 60–250 m wide. The Divisaderan SALMA was originally proposed as an Eocene biochronological unit (Pascual *et al.* 1965), older than the Tinguirirican and younger than the Mustersan. This unit was originally characterized by the coexistence of taxa with non-specialized morphology (e.g., *Allalmeia atalaensis, Brachystephanus postremus, Xenostephanus chiottii, Acamana ambiguus* Simpson, Minoprio &

Patterson, 1962) together with taxa with more specialized characters (e.g., *Ethegotherium carettei* Simpson, Minoprio & Patterson, 1962, *Trachytherus? mendocensis* Simpson & Minoprio, 1949) comparable with closely related taxa in Deseadan and post-Deseadan faunas (Oligocene). Cerdeño (2007) noted the similarity between the Divisadero Largo and the Mariño mesotheriids. Subsequently, López (2008) showed that the two last species do not come from beds in the Divisadero Largo Formation but rather come from the overlying Mariño Formation. A detailed study of the Divisaderan fauna revealed that it has more affinities with faunas of Casamayoran Age (Vacan and Barrancan) than with those of Mustersan Age (Cerdeño *et al.* 2008, López 2008, López & Manassero 2008). Consequently, the Divisaderan SALMA is no longer considered to be a valid unit (López 2008, 2010).

Description

Humerus. Only the distal epiphyses of both right and left humeri are preserved. The epiphysis of the right humerus is the most complete (Fig. 1). It has a supratrochlear foramen (Foramen supratrochleare) and an epicondylar foramen (Foramen supracondylare). These characters are variable in more recent typotheres, as *Protypotherium* lacks the supratrochlear foramen but instead has a deep

Table 1   Postcranial measurements of *Allalmeia atalaensis* MCNAM-PV 507.

Humerus			
hew	htw	htwme	hmtl
right	17.63	11.6	17.59	6.89

	Humerus			
	hew	htw	htwme	hmtl
right	17.63	11.6	17.59	6.89

	Femur	
	ftl	ftd
right	8.47	3.71

	Astragalus				
	lltca	lmtc	tdat	dpdt	tdn
right	8.8	8.31	6.35	5.49	5.02

	Cuboid				
	ctw	cdpw	capw	cfw	cfdp
right	7.18	5.85	8.39	6.13	3.89
left	7.14	6	8.35	6.69	4.55

	Navicular		
	ntw	ndpw	ndw
right	9.51	6.56	8.3

	Metatarsals				
	digit	mml	mmdd	mmtd	mdedd	mdetd
right	II	24.46	2.35	3.33	-	-
	III	29.42	-	3.21	-	-
	IV	29.47	-	3.08	-	-
left	V	22.98	1.93	2.26	2.97	4.3
	I	10.66	2.45	2.63	2.99	2.93
	II	23.91	-	3.21	3.31	4.6
	III	29.65	-	3.54	3.49	5.43
	IV	29.83	2.18	3.21	3.67	5.23

	Phalanges length		
	digit	proximal	intermediate	ungueal
right	I	9.57	-	-
	IV	12.42	8.33	6.97
left	I	-	7.57	-
	II	11.29	-	-

All values expressed in mm. Abbreviations: **capw**, cuboid distal width; **cdpw**, cuboid dorsoplantar width; **cfdp**, calcaneal facet dorsoplantar width; **cfw**, calcaneal facet width; **ctw**, cuboid trasversal width; **dpdt**, mid disto proximal diameter of the astragalar throclea; **ftd**, fossa throcanterica depth; **ftl**, fossa throcanterica largest axis length; **hew**, humeral epiphysis width; **hmtl**, humeral medial trochlear crest length; **htw**, humeral trochlea width; **htwme**, humeral trochlea width plus medial epicondyle; **lltc**, length of the lateral trochlear crest of the astragali; **lmtc**, length of the medial astragalar trochlear crest; **mdedd**, metatarsal distal epiphyseal dorsoplantar diameter; **mdetd**, metatarsal distal epiphyseal transverse diameter; **mmdd**, metatarsal middle dorsoplantar diameter; **mml**, metatarsal maximum length; **mmtd**, metatarsal middle transverse diameter; **ndpw**, navicular dorsoplantar width; **ndw**, navicular distal width; **ntw**, navicular transversal width; **tdn**, transversal diameter of the neck of the astragali; **tdt**, transversal diameter of the astragalar trochlea.

oleocraneal fossa, and both foramina are present in *Hegethotherium* but absent in *Interatherium* (Sinclair 1908). The olecraneal fossa (Fossa olecrani) or supratrochlear foramen (if it is perforated) is part of the elbow articulation capsule. Animals with a supratrochlear foramen are able to hyperextend the elbow joint (Lamb 1890, De Wilde *et al.* 2004, Voisin 2011). The epicondylar foramen, passage for the medial nerve and the branchial artery, was obliterated during the original preparation, but has now been re-exposed during our work on the material. The presence of an epicondylar foramen is considered a primitive condition within Mammalia and is retained in most notoungulates (Landry 1958, Shockey *et al.* 2012). *Allalmeia* has a wide medial epicondyle that is almost the same size as the trochlea (including the capitulum); this resembles the condition in

Colbertia magellanica, *Notostylops murinus* Ameghino, 1897 and in interatheriids (Bergqvist *et al*. 2007, Lorente *et al*. 2013). The capitulum (Capitulum humeri) is round and continuous with the trochlea. The lateral trochlear crest is visible only on the palmar side and is indistinguishable from the capitulum on the dorsal side. As in *Anisotemnus distentus* (Ameghino, 1901), the medial crest is high, pronounced and marks the distal end of the trochlea (Shockey & Flynn 2007: AMNH 28906). Conversely, the medial crest is not continuous with the deltoid crest (Crista humeris). The lateral epicondyle is so poorly developed that the capitulum marks the lateral border in dorsal view. The relation between the trochlea and the medial epicondyle is similar to those present in *N. murinus* (e.g., MLP 82-V-1-8). In contrast, Hegetotheriids (e.g., *Pachyrukhos*, MLP 99-X-2-1; *Paedoetherium*, MLP 50-X-5-29), leontiniids (e.g., *Scarritia*, AMNH 29585) and toxodontids (e.g., *Toxodon*, MLP 96-III-10-103; *Nesodon*, MLP 55-XII-13-46), have a more reduced medial epicondyle. The presence of a lateral supracondylar ridge (Crista supracondylaris lateralis) could be tenta-

tively inferred from the sharp and angular edge on the proximal side of the right humerus, but this side of the bone is broken. A small part of the proximal ulna is attached to the trochlea ventrally.

Femur. Only the proximal part of the right femur has been relocated (Fig. 2). The femoral head (Caput ossis femoris) is broken, but the greater trochanter (Trochanter major) and most of the proximal diaphysis are preserved. Rusconi (1946c) described a lower position of the femoral head than the greater trochanter, but in these remains it is not possible to determine if it was lower or higher, because the head is broken from the area of the lesser trochanter (Trochanter minor). The lesser trochanter seems poorly developed and there was a third trochanter (Trochanter tertius), but only its broken base is evident. The fossa trochanterica, insertion for the Obturatorius externus, Obturatorius internus and the Gemelli muscles, is well marked, deep and oval in outline. The diaphyseal lateral border forms a sharp ridge; judging from its position, it is a probable equivalent to a primate Linea aspera (White *et al*. 2011) or to a marked Labium laterale of Facies aspera of extant ungulates (Sisson & Grossman 1982). In both cases, this sharp ridge is the insertion area for several muscles, especially for the Glutæus superficialis, that abducts the leg (Sisson & Grossman 1982).

The femur of *Allalmeia* closely resembles those of *Colbertia lumbrerense* (Berqgvist *et al*. 2007) and interatheriids in its distinguishable trochanters, which are more prominent than in hegethotherids or toxodonts but comparatively less than in *Notostylops*. The femur of *Allalmeia* is longer than the tibia (Rusconi 1946c) like the isotemnid *Pleurostylodon* (e.g., AMNH 29604) but in contrast to interatheriids and hegetotheriids.

Fibula. Only the distal epiphysis of the left fibula is preserved. It is well developed and covers part of the lateral crest of the astragalus. The facet for the calcaneum is as large as that for the talus. Situated between these structures is a fossa for the talofibular ligament as occurs elsewhere in *Protypotherium* (MLP 90-XII-26-10). The lateral malleolus (Malleolus lateralis) forms a distinct tuberosity with a sulcus for the peroneal tendons. The fibula is not fused with the tibia (Rusconi 1946c) as it is in interatheriids, isotemnids, mesotheriids (Shockey *et al*. 2007) and toxodontids; the tibiofibula of hegetotheriids is fully fused (Croft *et al*. 2004, fig. 14).

Calcaneum. The distal half of the right calcaneum is preserved in articulation with the rest of the pes. It has a distal peroneal process with a marked rugosity at its lateral end, and a cuboid facet that is oblique to the long axis of the bone (most clearly observable in plantar view). The calcaneum also has a well-developed plantar tubercle and a large sustentaculum (Sustentaculum tali) of the same width as the calcaneal tuber (Tuber calcanei). The peroneal process, sustentacular groove and plantar tubercle of *Allalmeia* are similar to those of *Protypotherium* (e.g., MLP 90-XII-26-10) in morphology and disposition,

Fig. 2. Allalmeia atalaensis part of the right femur. **A**, dorsal; **B**, plantar; **ft**, trochanteric fossa; **gt**, greater trochanter. Scale bar = 20 mm.
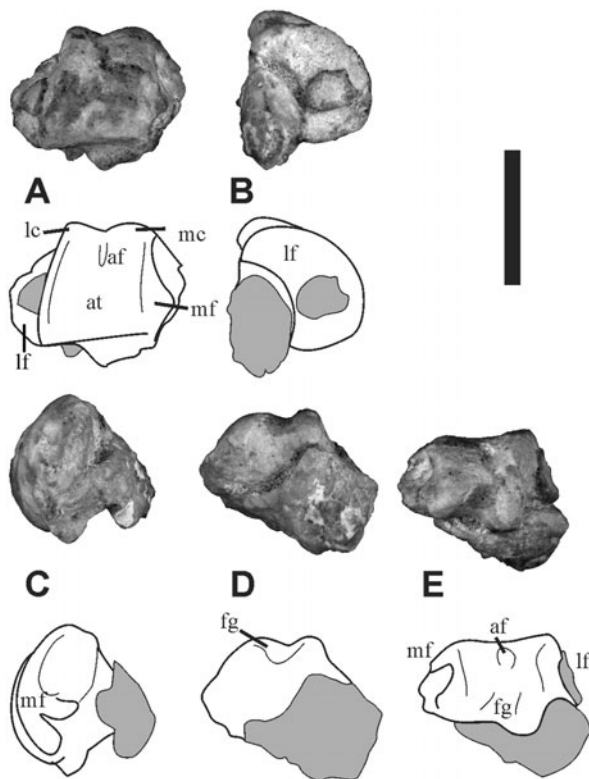
Fig. 3. *Allalmeia atalaensis* right astragalus. Grey surfaces indicate attached bone remains. **A**, dorsal; **B**, lateral; **C**, medial; **D**, plantar; **E**, proximal; **af**, astragalar foramen; **at**, astragalar trochlea; **lc**, lateral astragalar trochlear crest; **lf**, lateral or fibular facet; **fg**, flexor groove; **mc**, medial astragalar trochlear crest; **mf**, medial malleolar facet. Scale bar = 10 mm.

although the peroneal process is more expanded laterally, and the plantar tubercle is slightly more distally positioned. This is similar to the associated calcanei of *Paulacoutoia protocenica* (Paula Couto, 1952; e.g., AMNH 55390), *Lamegoia conodonta* Paula Couto, 1952 (e.g., MCN–PV 1271), *C. magellanica* (e.g., DNPM LE446B), and in particular, those those referred to the kollpaniines *Tiuclaenus minutus* Muizon & Marshall, 1987 (e.g., MHNC 8322) and *Molinodus* (e.g., MHNC 8318) from the early Paleocene of Tiupampa, Bolivia (Cifelli 1983, Bergqvist 1996, Muizon *et al.* 1998).

Astragalus. The trochlea (Trochlea tali) of the right astragalus is preserved. It has asymmetrical crests that diverge proximodistally (Fig. 3). The lateral trochlear crest is higher and larger than the medial. The astragalar foramen is small. The flexor groove is well developed; the medial facet is small and crescentic, and has a central projection; there is a broken medial plantar tuberosity, and the lateral crest was sharp with laterally projecting plantar border. The base of the astragalar neck projects medially (Collum tali), and overall the astragalus appears to have been broad. The astragalus of *Allalmeia* with its shallow crests and crescent medial facet with a central projection is reminiscent of that in *C. magellanica* (e.g., AMNH 55373), *Notostylops?* (e.g., MLP 56-XII-18-92 to 201), *Hegetotherium* (e.g.,

MACN-A 9866:80), *Thomashuxleya?* (e.g., MLP 75-II-1-10), as well as the kollpaniine *Tiuclaenus* (e.g., MHCN 8308), the archaic North American ungulate *Tetraclaenodon puercensis* (e.g., AMNH 3878), and also more basal eutherians such as *Protungulatum* and *Procerberus* (see Szalay & Decker 1974). Leontiniidae, Notohippidae and Toxodontidae are characterized by elongate astragali with a reduced neck and flexor groove; the medial malleolar facet also extends onto the neck. Later interatheriids and hegetotheriids, excluding *Hegethotherium*, have an astragalus with a deep trochlea. Mesotheriids, such as *Trachytherus* (e.g., MLP 61-IV-11-6), have a similar medial facet to *Allalmeia*, but with a markedly asymmetrical trochlea.

Cuboid. Both cuboids are preserved (Figs 4, 5) and are proximodistally elongate with an L-shaped tuberosity bearing a prominent groove for the Peroneus longus ligament. This is unique to *Allalmeia*; Isotemnidae indet. (AMNH 28690), *Nesodon* (e.g., MLP 55-XII-13-46), *Protypotherium* (e.g., MLP 90-XII-26-10) alternatively display a transversely oriented tuberosity.

Navicular. The naviculars have a 'W-shaped' outline in plantar view, with a lateral projecting rim (Figs 4, 5). The medial tuberosity (which provides insertion for the Tibialis posterior) is well developed and extends proximally. Both naviculars have a narrow contact with the calcaneum on the dorsal side, as in *Protypotherium* (e.g., MLP 90-XII-26-10) termed a 'reverse alternating tarsus'. Cifelli (1993) considered this feature a synapomorphy of Leontiniidae, Notohippidae and Toxodontidae, but Shockey *et al.* (2012, p. 40) alternatively regarded it as a non-exclusive trait of 'advanced toxodontia' (being elsewhere in some Typotheria interatheriids such as *Protypotherium* and *Federicoanaya*). A reverse alternating tarsus is also present in some litopterns, where the calcaneocuboid articulation is placed more distally than that of the astragalonavicular. We identified that the medial tuberosity is well developed as in typotherians, basal toxodontians and the notoungulates of São José de Itaboraí.

Cuneiforms. The three cuneiforms are preserved. The ectocuneiform is cubic and the largest of the three, with a sesamoid in the plantar side of the left foot. The mesocuneiform is the smallest. The endocuneiform is longest proximodistally. *Protypotherium, Hegetotherium* and *Interatherium* and *Tetraclaenodon* have a similar cuneiform disposition and morphology (Matthew 1897, fig. 12; Sinclair 1908, pls II, V and VIII). This is unlike toxodontians and *Phenacodus*, which have a shorter endocuneiform.

Metatarsus. *Allalmeia* was pentadactyl, and although the first and fifth metatarsals were reduced, they were sufficiently developed to articulate with complete distal digits. The metatarsal of the hallux is less than half the
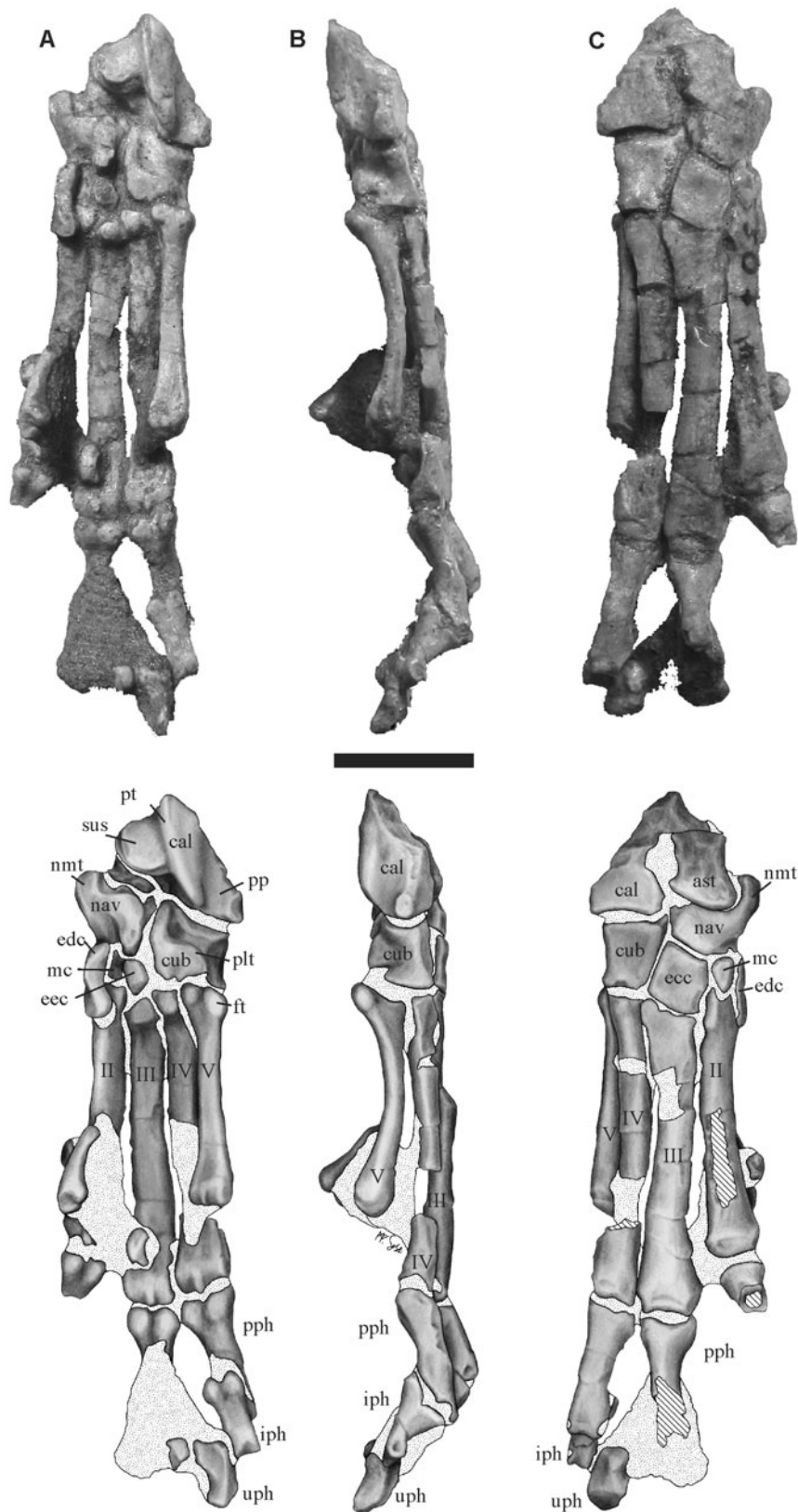
Fig. 4. *Allalmeia atalaensis* right foot. Metatarsals identified by roman numbers. **A**, plantar; **B**, lateral; **C**, dorsal; **ast**, astragalus; **cal**, calcaneum; **cub**, cuboid; **ecc**, ectocuneiform; **edc**, endocuneiform; **ft**, tuberosity for Flexor brevis minimi digiti; **iph**, intermediate phalanges; **mc**, mesocuneiform; **nav**, navicular; **nmt**, navicular medial tuberosity; **plt**, tuberosity for Peroneuss longus; **pp**, peroneal process; **pph**, proximal phalanges; **pt**, plantar tuberosity; **sus**, sustentaculum; **uph**, ungual phalanx. Scale bar = 10 mm.
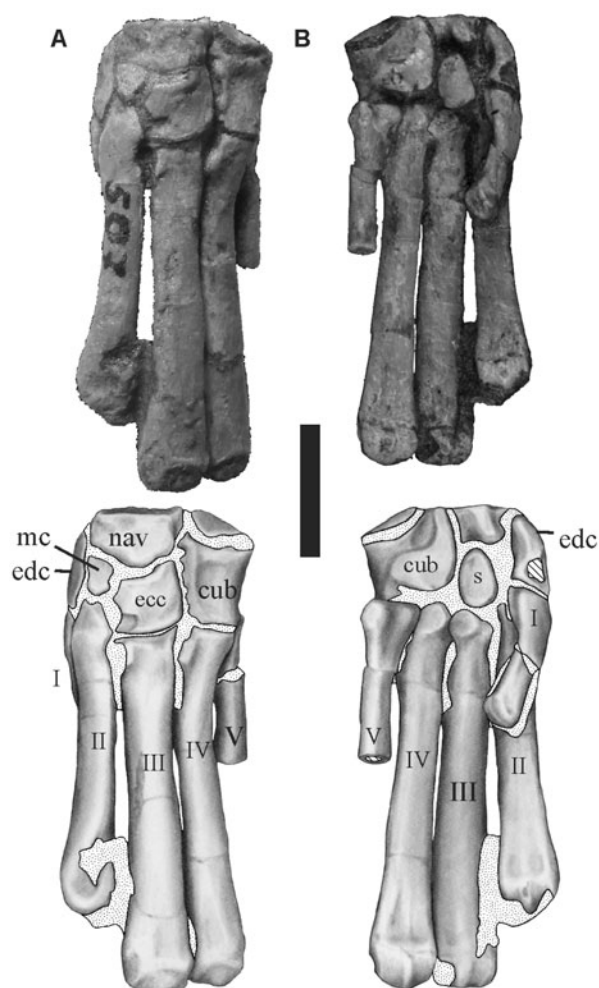
Fig. 5. Allalmeia atalaensis left foot. Metatarsals identified by roman numbers. **A**, dorsal; **B**, plantar; **cub**, cuboid; **ecc**, ectocuneiform; **edc**, endocuneiform; **mc**, mesocuneiform; **nav**, navicular; **s**, sesamoid. Scale bar = 10 mm.

length of the second metatarsal. The second metatarsal is positioned more proximally than the others; it articulates not only with the mesocuneiform but with the ectocuneiform and endocuneiform. The third and fourth metatarsals are parallel to each other; the fourth metatarsal is only slightly larger than the third. The fifth metatarsal is less reduced than the first, and it has a well-developed tuberosity for origin of the Flexor brevis minimi digiti (a flexor of the fifth digit). The metatarsals are wider in the distal epiphysis, with diameter constriction between the proximal epiphysis and the half of the diaphysis; they are also compressed dorsoplantarly. We observed that the metatarsals are thin and long, as in typotherians in contrast to toxodonts. In *Protypotherium* and *Interatherium*, as in *Allalmeia*, the third and fourth metatarsals are the longest, although in *Allalmeia*, the fifth is more reduced than the second, whereas the opposite is the case in *Protypotherium* (Sinclair 1908).

Phalanges. Six proximal phalanges are preserved. Only one proximal phalanx in the left foot is complete and, judging from its *in situ* position and comparison with

phalanges from the right foot, was probably a proximal phalanx of the second digit. In the right foot, the first and fourth digits have complete proximal phalanges; those of the second, third and fifth digits are represented only by their proximal ends. The proximal phalanges are less than half the size of the metatarsals, except for the first metatarsal, which is greatly reduced but the first digit phalanges are not reduced, so the proximal first phalanx is almost the size of the first metatarsal. The distal articulation in the proximal phalanges is plantarly oriented.

There are two intermediate phalanges, the fourth of the right foot and probably the first of the left foot; there is also an impression of the third right intermediate phalanx in the matrix. The fourth intermediate phalanx of the right foot is like a triangular prism, with the distal end more constricted and smaller than the proximal one. This articulates with the plantar side of the proximal phalanx such that the intermediate phalangeal row is positioned oblique in relation to the proximal one (Fig. 4). The distal articulation of intermediate phalanges is also plantar, making the entire ungual row oblique.

There are two ungual phalanges on the right foot: an isolated proximal portion of an ungual phalanx and a fourth digit ungual phalanx. They are claw-like; the fourth is flat dorsoplantary and convex but it is broken on the lateral border. The isolated ungual is eroded so the outline is difficult to determine. The bone is larger dorsoplantarly as expected for a claw-like phalanx, the Tuberculum flexorium is flat and barely marked on the ventral side of the phalanx.

As in *Protypotherium*, and in contrast to most known notoungulates, the second phalangeal row is oblique to the proximal one. This morphology is similar to that observed among some extant digitigrades, as for example, felines: *Leopardus geoffroyi* (e.g., MLP 27-XII-01-15) and *Panthera leo* (e.g., MLP 1046), foxes: *Lycalopex* (e.g., MLP 22-V-02-5), and *Marmota* and *Sciurus vulgaris* among Sciuridae (Pander & D'Alton 1823, tables 4, 6). A similar posture of the phalanges was observed in *Callosciurus erythracus* (e.g., MLP 2013) but without modification of the articulations.

The preserved unguals are claw-like but different to those of *Homalodotherium* (e.g., MACN-A 11721), which are bifurcated and claw-like but as those present in the cimolestan *Stylinodon* (Coombs 1983) or the creodont *Oxyaena* (Rose & Emry, 1993).

Lost postcranial elements. Rusconi (1946c) described five cervical, some sacral and caudal vertebrae that he considered similar to those of *Paedotherium* and *Pachyrukhos* in their general aspect. The ulna was apparently robust, with an arched diaphysis and triangular crosssection. The left femur was complete, and the lesser and third trochanter were enlarged into 'wings' with the third trochanter extending below the mid-diaphysis; the femoral trochlea was thin, long and well excavated,

articulating with a thin patella. The tibiae were reportedly with robust proximal tibial epiphysis, shallowly excavated articulations for the astragalus and a robust medial malleolus. The almost complete right fibula was completely separated from the tibia. Rusconi (1946a) described the left astragalus as having a longer neck than those of *Pachyrukhos* or *Paedotherium*; the plantar aspect was not observed because it was articulated with the calcaneum. The left calcaneum was not discussed in detail by Rusconi (1946a), and the scapula, radii and manual bones were all fragmentary. Rusconi (1946a) depicted the pelvis with a large obturator foramen; there were one or two sacral vertebrae as in *N. murinus* (Lorente *et al.*, 2013). The cleaning of several portions of the hindlimb, which were not originally prepared, allowed us to reinterpret characters of several bones and provide new anatomical information about this taxon. Rusconi's (1946a) figures of the pes are inverted with left representing right (Rusconi 1946c, figs 20, 21). In contrast to the original observations of Rusconi (1946c), there is an aperture that we identified as the supratrochlear foramen in the right humerus; based on its smooth border it does not seem to be a taphonomic artefact.

Discussion

Morphological comparisons and lifestyle

Among notoungulates, phylogenetic analyses and palaeobiological inferences have been based mostly on dental and cranial features. Knowledge of the postcranial characters in this group is important for testing these inferences and to add new information about the evolutionary trends in the locomotor system and lifestyle.

Allalmeia was first considered by Rusconi (1946a, b, c) as a member of Notostylopidae. In *Notostylops*, from the middle Eocene of Patagonia, the humerus (i.e., MLP 82-V-1-8) is similar to *Allalmeia* in its wide proximal portion and the poorly developed lateral epicondyle. However, *Notostylops* is more robust with a proportionately smaller and less spherical capitulum, a less prominent medial crest, the supratrochlear foramen is absent and a smooth oleocraneal fossa is present instead, and the medial epicondyle is slightly narrower and more proximally oriented. The femur of *Notostylops* has a large but thinner and shallower trochanteric fossa, and more robust trochanters.

As observed by Simpson *et al.* (1962), the postcranial character states of *Allalmeia* are mostly non-diagnostic, but there are some traits that differentiate *Allalmeia* from other notoungulates: the low crural index and the shape of the Peroneus longus groove on the cuboid (although the cuboid morphology is unknown in most other taxa). In general, *Allalmeia* is morphologically comparable with the oldfieldthomasiid *Colbertia magellanica* (Bergqvist *et al.* 2007), but differs in the medial epicondyle of the humerus being larger, the epicondylar foramen being smaller and more

proximally positioned, and the femur possessing a deeper trochanteric fossa. The astragalus of *C. magellanica* has more parallel trochlear crests, a more distally situated medial facet, a more medial and larger medial plantar tuberosity, and a shallower flexor groove. Both, *C. magellanica* and *Allalmeia* share a well-developed navicular medial tuberosity that articulates with the medial extension of the navicular facet on the astragalus. In contrast, the spring or collateral ligaments contact the astragalus in North American archaic ungulates (e.g., *Arctocyon*). This well-developed navicular medial tuberosity is present in all typotheres and basal toxodontians (Shockey & Flynn 2007), but is absent in the more recent toxodontids such as *Nesodon* (e.g., MLP 55-XII-13-46) and *Toxodon* (e.g., MLP 12-1125), as well as Deseadan leontiniids, such as *Scarritia* (e.g., AMNH 29585). These forms also lack a medial extension on the astragalus. Litopterns and astrapotheres lack a medial navicular tuberosity, and its condition is unknown in xenungulates and pyrotheres. Litopterns lack a medial tuberosity and have a plantar, instead of a medial, extension of the navicular facet in the astragalus. Astrapotherians have a medial extension of the navicular facet in the astragalus, but an almost flat navicular. If the proximally expanded navicular medial tuberosity can be confirmed in more basal notoungulates, it could be a derived character for Notoungulata. Astragali of both *Allalmeia* and *Colbertia* are similar to those attributed to the early Paleocene kollpaniines *Tiuclaenus* and *Pucanodus* (morph 1 and 2), and the calcanei of *Tiuclaenus* and *Molinodus* (morph 1 and 3, Muizon *et al.* 1998): the lateral process, astragalar medial facet and medial plantar tuberosity of *Tiuclaenus* are more similar to those of *Allalmeia* than to *C. magellanica*, but the trochlea and flexor groove bear greater resemblance to those of *Colbertia*. *Tiuclaenus* also possesses a crest in the astragalar neck, called 'tibial stop', which is similar although not identical to that of *Colbertia*. We observed that in *Colbertia* and other ungulates, this crest appears to be related to the trochlea, whereas in *Tiuclaenus* it develops from the head, as in the protoliptern *Miguelsoria parayirunhor* (MCT PV 1353), which otherwise possesses a 'litoptern-like' astragalus. At least for notoungulates, this crest has been considered a possible derived character (Shockey & Flynn 2007). The calcaneum of *Tiuclaenus* has a well-marked plantar tuberosity and a distal peroneal process like those of *Allalmeia*. The ectal facet is also oval in outline, and the fibular facet is half the size of the ectal; there is also an inverted lacriform sustentacular facet as expressed in the notoungulate calcanei from the Eocene of Paso del Sapo, Patagonia (Lorente *et al.* 2012). In the *Pucanodus* astragalus, the proximal half of the trochlea is broken, but the distal part shows a morphology compatible with that of *Allalmeia*. The plantar side is more similar, and head and neck more different to notoungulates than *Tiuclaenus*. The *Molinodus* calcaneum resembles that of *Tiuclaenus* (Muizon

Table 2 Measurements and inferred body mass of *Allalmeia atalaensis*.

Janis (1990)

	SUML	SUMW	SUMA	FLML	FLMW
PV 507	1.35681 (0.5)	21.456 (0.9)	5.4105 (0.45)	1.605 (0.45)	6.42082 (0.38)
MLP 87-II-20–5*	2.69138 (0.62)	24.445 (0.94)	8.1159 (0.583)	–	–
MLP 66-XII-12–22	1.35681 (0.5)	6.1894 (0.595)	2.8277 (0.298)	2.414 (0.51)	–
MCZ 7412	3.96088 (0.7)	34.092 (1.05)	11.677 (0.735)	–	–
MLP 87–11-20–54	1.35681 (0.5)	22.92 (0.92)	5.6002 (0.46)	–	–
MLP 88-V-15–8	2.55558 (0.61)	21.456 (0.9)	7.3901 (0.549)	–	–
MLP 87-II-20–11	0.7788 (0.42)	15.635 (0.81)	3.4895 (0.34)	2.263 (0.5)	3.89477 (0.32)
MMCNMP 734S*	2.55558 (0.61)	22.92 (0.92)	7.6492 (0.561)	–	–
MLP 87-II-20–13	2.97767 (0.64)	7.004 (0.62)	4.4418 (0.397)	–	–
AVERAGE	2.00816	20.885	6.2891	2.094	5.15779
SD	1.0215	8.7799	2.7365	0.43	1.78619

Janis (1990)

	FLMA	SLML	SLMW	SLMA
PV 507	77144 (0.17)	1.4669 (0.5)	5.64043 (0.4)	2.8087 (0.2)
MLP 87-II-20–5*	–	–	–	–
MLP 66-XII-12–22	–	2.7723 (0.61)	–	–
MCZ 7412	–	–	–	–
MLP 87–11-20–54	–	–	–	–
MLP 88-V-15–8	–	–	–	–
MLP 87-II-20–11	1.58201 (0.16)	1.4205 (0.495)	2.17238 (0.29)	1.6084 (0.1)
MMCNMP 734 S*	–	2.4917 (0.59)	10.6144 (0.495)	1.6084 (0.1)
MLP 87-II-20–13	–	–	–	–
AVERAGE	1.67672	2.0378	6.14239	2.2086
SD	0.13395	0.6958	4.24332	0.693

Scarano et al. (2011)
Scott (1990)

	FLML	SLML	TUL	FLF	APDF
PV 507	1.887 (0.45)	1.638 (0.5)	1.98 (7.5)	2 (8.4)	3.23 (0.7)
MLP 87-II-20–5*	–	–	–	–	–
MLP 66-XII-12–22	2.596 (0.51)	2.752 (0.61)	–	–	–
MCZ 7412	–	–	–	–	–
MLP 87–11-20–54	–	–	–	–	–
MLP 88-V-15–8	–	–	–	–	–
MLP 87-II-20–11	2.468 (0.5)	1.596 (0.5)	–	–	–
MMCNMP 734 S*	–	2.523 (0.59)	–	–	–
MLP 87-II-20–13	–	–	–	–	–
AVERAGE	2.317	2.127	1.98	2	3.23
SD	0.597	0.597	–	–	–

	Li1	Li2	Li3	Li1 x Li2	Li1 x Li3	Statistics for all equations AVERAGE	SD
Tsubamoto (in press)	(6.35)	(8.8)		(8.3)		(73[a])	(52.8[a])
PV 507	1.384	2.467	2.48	2.7	1.84		
AVERAGE	1.384	2.467	2.48	2.7	1.84	2.786	4.4

Allometric equation from Janis (1990), Scarano et al. (2011), Scott (1990) and Tsubamoto (in press). Measures between brackets in mm, estimated values expressed in kg. Abbreviations indicate the measure used in each of the equations; APDF, anteroposterior diameter of the femur; FLMA, first lower molar area; SUMA, second upper molar area; SUML, second upper molar length; SUMW, second upper molar width; Li2, second upper molar area; FLF, functional length of the femur; FLML, first lower molar length; FLMW, first lower molar width; Li1, transverse width of the tibial trochlea; Li2, proximodistal length of the lateral trochlear ridge of the tibial trochlea; Li3, proximodistal length of the medial trochlear ridge of the tibial trochlea; SLMA, second lower molar area; SLML, second lower molar length; SLMW, second lower molar width; TUL, total length of the ulna;
*Approximated value.
[a]Values expressed in mm².

et al. 1998), but has a marked rugosity in the lateral end of the peroneal process as in *Allalmeia*. The lateral side of the calcaneum of *Molinodus* has equivalent structures to the notoungulate *Notostylops murinus* (Lorente *et al*. 2013), but the fibular facet is smaller. The sustentacular facet is also more rounded than that of notoungulates.

Several palaeobiological features, such as *Allalmeia* body mass and their locomotor posture can be inferred from the postcranium. Rusconi (1946c) considered *Allalmeia* to be a digitigrade runner that could have employed jumping at high speeds, and suggested close comparisons in lifestyle with *Pachyrukhos moyani* and *Paedotherium imperforatum*. Structurally, however, *Allalmeia* differs from these taxa (e.g., *Pachyrukhos*, MLP 99-X-2-1; *Paedoetherium*, MLP 50-X-5-29) in its wider humeri, unfused zeugopods, more prominent trochanters, the higher position of the greater trochanter (positioned below the head in *Paedotherium* and *Pachyrukhos*), and the wider and shallower astragalar trochlea. *Allalmeia* also had a shorter tibia relative to its femur (Rusconi 1946c), a feature thought to be characteristic of fossorial, terrestrial, arboreal and some cursorial extant mammals, as opposed to ricochetal (Samuels & Van Valkenburgh 2008). Furthermore, the epicondyle is broadened, suggesting substantial Pronator teres and Flexor digitorum musculature as in fossorial, terrestrial or arboreal taxa (Salton & Sargis 2008). Rusconi (1946c) calculated the pes length index (III metatarsal length/femur length) and crural index (tibia length/femur length) for *Allalmeia* as 0.33 and 0.809 respectively, which are additionally compatible with arboreal, fossorial and especially semifossorial habits (Samuels & Van Valkenburgh, 2008), such as the American badger *Taxidea taxus*; some cursorial/terrestrial mammals such as the South American tapir (*Tapirus terrestris*, MLP 1) and the guinea baboon, *Papio papio* (e.g., MACN 23,383); and some arboreal marsupials (Jungers 1980) such as the koala *Phascolarctos cinereus*. Nevertheless, the long, thin metatarsal and the low astragalar trochlea would argue against a fossorial or cursorial lifestyle (Van Valkenburgh 1987, Carrano 1997), and instead we propose that *Allalmeia* was probably a terrestrial (non-cursorial) or arboreal animal.

The foot posture of *Allalmeia* can be inferred from its metatarsal length–width ratio (*sensu* Carrano 1997), which falls between those of plantigrades and digitigrades, but lower than subunguligrades. Oblique positioning of the intermediate versus proximal phalangeal rows implies a digitigrade posture, as extant animals with this disposition are digitigrades.

Body mass estimations

Several measures were considered in order to infer body mass. Considering a normal distribution of the data (Table 2), the confidence interval for the mean at 99% was calculated between 1.140 kg and 6.336 kg. The

Table 3 Astragalar measures and body masses.

Species	Specimen	lltc	lmtc	tdt	dpdt	tdn	Body mass	
Allalmeia atalaensis	PV 507	8.8	8.31	6.35	5.49	5.02	–	2.786[a-b]
Lepus callotis	MLP 1082	8.38	7.87	7.4	6.58	5.31	2.7[1]	2.164[b]
Moschiola meminna	MACN 21970	7.56	8.13	6.92	–	6.23	2.47[2]	1.959[b]
Potos flavus	MLP 1740	10.38	8.64	7.44	7.17	4.86	2.5[3]	2.970[b]
Lemur catta	MLP 993	8.25	8.32	7.54	8.26	5.89	2.269[4]	2.312[b]
Dasyprocta azarae	CFA Ma 13,094	9.59	9.28	7.9	7.77	5.68	3[5]	3.035[b]
Conepatus chinga	MLP 19-XII-02–2	6.35	6.61	5.75	5.18	3.43	1.96[6]	1.144[b]

Linear dimensions in mm and body mass in kg. Extant animals are ranked from the most similar to the most different based on linear values. Abbreviations: **dpdt**, mid disto proximal diameter of the astragalar throclea; **lltc**, length of the lateral trochlear crest of the astragali; **lmtc**, length of the medial astragalar trochlear crest; **tdn**, transversal diameter of the neck of the astragali; **tdt**, transversal diameter of the astragalar trochlea. Mean of weighted body mass from [1]Feldhamer *et al.* (2003), [2]Janis (1984), [3]Walter & Cant (1977), [4]Simmen *et al.* (2010), [5]McWilliams (2009) and [6]Kasper *et al.* (2012). Inferred body mass using allometric equations of: [a]Janis (1990), Scarano *et al.* (2011) and Scott (1990); [b]Tsubamoto (in press).

allometric equation using SUMW (Table 2) was rejected because the mean of their inferences (20.885 kg) falls outside of the estimated range. No underestimation was detected, the lowest mass estimation being 1.384 kg with the L1 equation of Tsubamoto (in press). The mean of the inferred corporal mass values taking into account all the equations with estimations inside the confidence interval is 2.786 kg with a standard deviation of 4.4 kg. Although inclusion of *Allalmeia atalaensis* within Oldfieldthomasiidae is doubtful (Simpson *et al.* 1962), their estimated body masses are compatible. Vizcaíno *et al.* (2012) calculated mass estimates of around 50 kg for *Oldfieldthomasia* and *Paginula* using *Ovis aries* as an analogue. However, we considered this to be an overestimation because the teeth of *O. aries* are four times larger than those of *Oldfieldthomasia*. In contrast, Elissamburu (2012), based on allometric equations for dental and postcranial remains, estimated the body mass for several oldfieldthomasiids, and derived a mean of 5.567 kg for *Oldfieldthomasia*, 5.73 kg for *Maxschlosseria*, 3.98 kg for *Colbertia* and 5.98 kg for *Ultrapitecus*. These corporal masses agree approximately with the expected values if a comparison with a living analogues of the same size is undertaken.

We compared several astragalar measures of *Allalmeia* with those of a sample of extant mammals with known body mass (Table 3). We also applied to this sample the procedure of Tsubamoto (in press) in order to estimate their body mass from astragalar dimensions. The greatest difference between weighted and estimated body mass was 0.816 kg for *Conepatus chinga*, with the least (0.035 kg) being for *Dasyprocta azarae*. *Allalmeia* is closer to *Lepus callotis* in astragalar measures with a weighted body mass of 2.7 kg, but if the inferred body mass of these extant mammals is considered, it is closer to the Kinkajou *Potos flavus* at 2.970 kg.

Palaeoenvironmental implications

Sedimentological analysis by Kokogian *et al.* (1988) concluded that the Divisadero Largo Formation was deposited on an extensive alluvial plain with semi-permanent water bodies associated with ephemeral rivers in interdune areas. However, this reconstruction seems to be inconsistent with the faunal assemblage recovered from the unit. Certainly, microscopic, palaeosol and facies assessments by López (2008), indicated at least five distinct lithofacies reflecting different and contrasting depositional systems. A predominance of ephemeral and episodically high-energy river systems confined to channels was distinguished within the lower and middle stratigraphic levels. In contrast, shallow lacustrine facies incorporating epilimnic open environments predominated up-sequence. The presence of palaeosols indicates subaerial exposure. Climatic conditions are reconstructed as warm and humid, with abundant availability of water, which probably promoted the development of trees and abundant vegetation cover (López 2008). This complies with the abundant small mammals, such as *Allalmeia*, with low-crowned teeth and a non-specialized or even an arboreal morphology; and is different to the specialized high-crowned notoungulates of Mariño Formation that correspond to a time of drier conditions correlated with the initial uplift of the Andes range (López 2008).

Summary

Allalmeia was a small, digitigrade generalist notoungulate that could have been either terrestrial or arboreal, but with a capacity to hyperextend the elbow as in modern canids and suids. Like its relative *Colbertia*, the generally gracile postcranial skeleton of *Allalmeia* is more closely compatible with archaic ungulates and Typotheria (e.g., *Protypotherium*) rather than notostylopids such as *Notostylops*, or the basal toxondontian isotemnids *Thomashuxleya*, *Anisotemnus* and *Pleurostylodon*. This resemblance might have been both morphofunctional and phylogenetic. The latitudinal provenance (32°53′S) of *Allalmeia*, suggests that it could have been a possible link between Patagonian notoungulates and those recorded from the northwest of Argentina.

Acknowledgments

References

AMEGHINO, F., 1897. Mammifères Crétacés de l'Argentine. Deuxìme contribution à la connaissance de la faune mammalogique des conches à *Pyrotherium. Boletín del Instituto Geográfico Argentino 18*, 406–521.

AMEGHINO, F., 1901. Notices préliminaires sur des ongue's nouveaux des terrains Crétacés de Patagonie. *Boletin de la Academia Nacional de Ciencias de Córdoba 16*, 1–349.

BERGQVIST, L.P., 1996. *Reassociação do Pós-Cránio ás Espécies de Ungulados da Bacia de S. J. de Itaboraí (Paleoceno), Estado do Rio De Janeiro, e Filogenia dos 'Condylarthra' e Ungulados Sul-Americanos com Base no Póscrânio*. PhD thesis, Universidade Federal do Rio Grande Do Sul, Rio De Janeiro, Brasil, 407 pp. (unpublished)

BERGQVIST, L.P. & BASTOS, A.C., 2009. A postura locomotora de *Colbertia magellanica* (mammalia, Notoungulata) da Bacia de São José de Itaboraí (Paleoceno Superior), Rio de Janeiro. *Revista Brasileira de Paleontologia 12*, 83–89.

BERGQVIST, L.P. & METELLO, M.T., 2011. The first postcranial bones of *Notostylops* Simpson, 1948, from Chubut, Argentina (Barrancan). *Ameghiniana 48* (4R), 143.

BERGQVIST, L.P., FURTADO, M.R., SOUZA, C.P. & POWELL, J.E., 2007. *Colbertia magellanica* (bacia de Itaboraí, Brasil) x *Colbertia lumbrerense* (Grupo Salta, Argentina): a morfologia pós-craniana confrontada. In *Paleontologia: Cenários de Vida 1*. CARVALHO, I.S., CASSAB, R.C.T., SCHWANKE, C., CARVALHO, M.A., FERNANDES, A.C.S., RODRIGUES, M.A.C., CARVALHO, M.S.S., ARAI, M. & OLIVEIRA, M.E.Q., eds, Editora Interciência, Rio de Janeiro, 765–775.

BILLET, G., 2010. New observations on the skull of *Pyrotherium* (Pyrotheria, Mammalia) and new phylogenetic hypotheses on South American ungulates. *Journal of Mammalian Evolution 17*, 21–59.

BOND, M., 1981. Un nuevo Oldfieldthomasiidae (Mammalia, Notoungulata) del Eoceno inferior (Fm. Lumbrera, Grupo Salta) del NW Argentina. *Anais II Congreso Latino-Americano de Paleontología (Porto Alegre) 2*, 521–536.

CARRANO, M.T., 1997. Morphological indicators of foot posture in mammals: a statistical and biomechanical analysis. *Zoological Journal of the Linnean Society 121*, 77–104.

CERDEÑO, E., 2007. Systematic position of the Mesotheriidae (Notoungulata) from the Mariño Formation (Miocene) in Divisadero Largo, Mendoza, Argentina. *Geobios 40*, 767–773.

CERDEÑO, E., LÓPEZ, G.M. & REGUERO, M.A., 2008. Biostratigraphical considerations on the Divisaderan faunal assemblage. *Journal Vertebrate Paleontology 28*, 574–577.

CIFELLI, R.L., 1983. Eutherian tarsals from the late Paleocene of Brazil. *American Museum Novitates 2761*, 1–31.

CIFELLI, R.L., 1993. The phylogeny of the native South American ungulates. In *Mammal Phylogeny: Placentals*. SZALAY, F.S., NOVACEK, M.J. & McKENNA, M.C., eds, Springer-Verlag, New York, 195–216.

COOMBS, M.C., 1983. Large mammalian clawed herbivores, a comparative study. *American Philosophical Society 73*(7), 1–96.

CROFT, D.A., FLYNN, J.J. & WYSS, A.R., 2004. Notoungulata and Litopterna of the early Miocene Chucal Fauna, Northern Chile. *Fieldiana: Geology, N.S. 50*, 1–49.

DE WILDE, V., DE MAESENEER, M., LENCHIK, L., VAN ROY, P., BEECKMAN, P. & OSTEAUX, M., 2004. Normal osseous variants presenting as cystic or lucent areas on radiography and CT imaging: a pictorial overview. *European Journal of Radiology 51*, 77–84.

ELISSAMBURU, A., 2012. Estimación de la masa corporal en géneros del Orden Notoungulata. *Estudios Geológicos 68*, 91–111.

FELDHAMER, G.A., THOMPSON, B.G. & CHAPMAN, J.A., 2003. *Wild Mammals of North America: Biology*. JHU Press, Baltimore, Management and Conservation, 1216 pp.

GILL, T., 1872. Arrangement of the families of mammals and synoptical table of the characters of the subdivisions of mammals. *Smithsonian Miscellaneous Collections 11*, 1–98.

JANIS, C.M., 1984. Tragulids as living fossils. In *Living Fossils. Casebooks in Earth Sciences*. ELDREDGE, N. & STANLEY, S.M., eds, Springer Verlag, New York, 87–94.

JANIS, C.M., 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids. In *Body Size in Mammalian Paleobiology*. DAMUTH, J. & MACFADDEN, B.J., eds, Cambridge University Press, New York, 255–300.

JUNGERS, B.W.L., 1980. Adaptive diversity in subfossil Malagasy prosimians. *Zeitschrift für Morphologie und Anthropologie 71*, 177–186.

KASPER, C.B., SOARES, J.G.B. & FREITAS, T.R.O., 2012. Differential patterns of home-range, net displacement and resting sites use of *Conepatus chinga* in southern Brazil. *Mammalian Biology 77*, 358–362.

KOKOGIAN, D.A., BOGGETTI, D. & REBAY, G., 1988. Interpretación paleoambiental de la Formación Divisadero Largo (Eoceno superior), Cuenca Cuyana. Mendoza. *Actas de la Segunda Reunión Argentina de Sedimentología*, Mendoza, 135–139.

LAMB, D.S., 1890. The olecranon perforation. *American Anthropologist 3*, 159–174.

LANDRY, S.O.J., 1958. The function of the entepicondylar foramen in mammals. *American Midland Naturalist 60*, 100–112.

LÓPEZ, G.M., 2008. *Los Ungulados de la Formación Divisadero Largo (Eoceno Inferior?) de la Provincia de Mendoza, Argentina: Sistemática y Consideraciones Bioestratigráficas*. PhD Thesis, Universidad Nacional de La Plata, Argentina, 415 pp. (unpublished)

LÓPEZ, G.M., 2010. Divisaderan: land mammal age or local fauna? In *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*. MADDEN, R., CARLINI, A., VUCETICH, M.G. & KAY, R., eds, Cambridge University Press, New York, 410–420.

LÓPEZ, G.M. & BOND, M., 2003. Una nueva familia de ungulados (Mammalia, Notoungulata) del Paleógeno sudamericano. *Ameghiniana 40*(4 Supplement), R60.

LÓPEZ, G.M. & MANASSERO, M., 2008. Revision of the stratigraphic provenance of *Ethegotherium carettei* (Notoungulata, Hegetotheriidae) by sedimentary petrography. *Neues Jahrbuch für Geologie und Paläontologie 248*, 1–9.

LÓPEZ, G.M., GELFO, J.N., BOND, M., LORENTE, M. & REGUERO, M., In press. Towards the origin of South American native ungulates and their diversity in Paleocene and Eocene setting. In *Origins and Evolution of Cenozoic South American Mammals*. ROSEMBERGER, A.L. & TEJEDOR, M.F., eds, Springer, Dordrecht, 1–49.

LORENTE, M., GELFO, J.N. & TEJEDOR, M.F., 2012. Morfotipos de calcáneos de los mamíferos del Eoceno temprano de Paso del Sapo (Patagonia, Argentina). *Ameghiniana 49*(4 Supplement), R50.

LORENTE, M., GELFO, J.N., LÓPEZ, G.M. & BOND, M., 2013. Restos postcraneanos de *Notostylops murinus* (Mammalia: Notoungulata, Notostylopidae) del Eoceno medio del Chubut. *Argentina. Ameghiniana 50*(4 Supplement), R21–R22.

MATTHEW, W.D., 1897. A revision of the Puerco fauna. *Bulletin of the American Museum of Natural History 9*, 259–323.

McWILLIAMS, D.A., 2009. Determinants for the diet of captive Agoutis (*Dasyprocta* spp.). *Veterinary Clinics of North America—Exotic Animal. Practice 12*, 279–286.

DE MUIZON, C. & MARSHALL, L.G., 1987. Deux nouveaux condylarthres (Mammalia) du Maastrichtien de Tiupampa (Bolivie). *Comptes Rendus de l'Academie des Sciences 304*, 947–950.

DE MUIZON, C., CIFELLI, R.L. & BERGQVIST, L.P., 1998. Eutherian tarsals from the early Paleocene of Bolivia. *Journal of Vertebrate Paleontology 18*, 655–663.

PANDER, C.H.R. & D'ALTON, E., 1823. Die skelete der Nagetiehre, adgebilder und vergliche. In *Vergleichende Osteologie.* PANDER, C.H.R. & D'ALTON, E., eds, Commission bei Eduard Weber, Bonn, Vol. 5.

PASCUAL, R., ORTEGA HINOJOSA, E.J., GONDAR, D. & TONNI, E.P., 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquéllas del territorio bonaerense. *Anales de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires 6*, 165–193.

PAULA COUTO, C., 1952. Fossil mammals from the beginning of the Cenozoic in Brazil. Condylarthra, Litopterna, Xenungulata and Astrapotheria. *Bulletin of American Museum of Natural History 99*, 355–394.

PRICE, L.I. & PAULA COUTO, C., 1950. Vertebrados fósseis do Eoceno na Bacia calcárea de Itaboraí. *2º Congresso Panamericano de Engenharia de Minas e Geologia* (Petrópolis). *Anais 3*, 149–173.

ROSE, K.D. & EMRY, J.E, 1993. Xenarthra, Pholidota and fossil edentates. In *Mammal Phylogeny.* SZALAY, F.S., NOVACEK, M.J. & MCKENNA, M.C., eds, Spinger-Verlag, New York, 81–102.

ROTH, S., 1903. Los ungulados sudamericanos. *Anales del Museo de La Plata, Sección Paleontológica 5*, 1–36.

RUSCONI, C., 1946a. Nuevo mamífero fósil de Mendoza. *Boletín Paleontológico de Buenos Aires 20*, 1–2.

RUSCONI, C., 1946b. Aves y réptiles oligocenos de Mendoza. *Boletín Paleontológico de Buenos Aires 21*, 1–3.

RUSCONI, C., 1946c. Algunos mamíferos, reptiles y aves del Oligoceno de Mendoza. *Revista de la Sociedad de Historia y Geografía de Cuyo 2*, 1–37.

SALTON, J.A. & SARGIS, E.J., 2008. Evolutionary morphology of the Tenrecoidea (Mammalia) forelimb skeleton. In *Mammalian Evolutionary Morphology, A Tribute to Frederick S. Szalay.* SARGIS, E.J. & DAGOSTO, M., eds, Springer, Dordrecht, 51–71.

SAMUELS, J.X. & VAN VALKENBURGH, B., 2008. Skeletal indicators of locomotor adaptations in living and extinct rodents. *Journal of Morphology 269*, 1387–1411.

SCARANO, A.C., CARLINI, A.A. & IULLIS, A.W., 2011. Interatheriidae (Typotheria; Notoungulata), body size and paleoecology characterization. *Mammalian Biology–Zeitschrift für Säugetierkunde 76*, 109–114.

SCHALLER, O., ed., 1996. *Nomeclatura Anatómica Veterinaria Ilustrada.* Editorial Acribia, Zaragoza, Spain, 614 pp.

SCOTT, K.M., 1990. Postcranial dimensions of ungulates as predictors of body mass. In *Body Size in Mammalian Paleobiology: Estimation and Biological Implications.* DAMUTH, J. & MACFADDEN, B.J., eds, Cambridge University Press, New York, 301–336.

SHOCKEY, B.J. & FLYNN, J.J., 2007. Morphological diversity in the postcranial skeleton of Casamayoran (? Middle to Late Eocene) Notoungulata and foot posture in notoungulates. *American Museum Novitates 3601*, 1–26.

SHOCKEY, B.J., CROFT, D.A. & ANAYA, F., 2007. Analysis of function in the absence of extant functional homologues: a case study using mesotheriid notoungulates (Mammalia). *Paleobiology 33*, 227–247.

SHOCKEY, B.J., FLYNN, J., CROFT, D., GANS, P. & WYSS, A.R., 2012. New leontiniid Notoungulata (Mammalia) from Chile and Argentina: comparative anatomy, character analysis and phylogenetic hypotheses. *American Museum Novitates 3737*, 1–64.

SIMMEN, B., BAYART, F., RASAMIMANANA, H., ZAHARIEV, A. & BLANC, S., 2010. Total energy expenditure and body composition in two free-living sympatric lemurs. *Plos One 5*, e9860.

SIMPSON, G.G., 1945. The principles of classification and a classification of mammals. *Bulletin American Museum of Natural History 85*, 1–350.

SIMPSON, G.G., 1967. The beginning of the age of mammals in South America. Part II. *Bulletin of the American Museum of Natural History 137*, 1–259.

SIMPSON, G.G., 1978. Early mammals in South America: fact, controversy and mystery. *Proceedings of the American Philosophical Society 122*, 318–328.

SIMPSON, G.G. & MINOPRIO, J.L., 1949. A new adianthine litoptern and associated mammals from a deseadan faunule in Mendoza, Argentina. *American Museum Novitates 1434*, 1–27.

SIMPSON, G.G., MINOPRIO, J.L. & PATTERSON, B., 1962. The mammalian fauna of the Divisadero Largo Formation. Mendoza, Argentina. *Bulletin of Museum of Comparative Zoology 127*, 239–293.

SINCLAIR, W.J., 1908. Mammalia of the Santa Cruz Beds. Part I. Typotheria. In *Reports of the Princeton University Expeditions to Patagonia, 1896–1899, Volume VI, Paleontology III.* SCOTT, W.B., ed., Princeton University, New Jersey, 1–110.

SISSON, S. & GROSSMAN, J.D., 1982. *Anatomía de los Animales Domésticos*, 5th Edition. Salvat, Barcelona, 2302 pp.

SZALAY, F.S. & DECKER, R.L., 1974. Origins, evolution and function of the tarsus in Late Cretaceous Eutheria and Paleocene primates. In *Primate Locomotion.* JENKINS, F.A., ed., Academic Press, New York, NY, 223–259.

TSUBAMOTO, T., In press. Estimating body mass from the astragalus in mammals. *Acta Palaeontologica Polonica.*

VAN VALKENBURGH, B., 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. *Journal of Vertebrate Paleontology 7*, 162–182.

VIZCAÍNO, S.F., CASSINI, G.H., TOLEDO, N. & BARGO, M.S., 2012. On the evolution of large size in mammalian herbivores of cenozoic faunas of southern South America. Chapter 5 in *Bones, Clones and Biomes: The History and Geography of Recent Neotropical Mammals.* PATTERSON, B.D. & COSTA, L.P., eds, University of Chicago Press, 576–101.

VOISIN, J.L., 2011. Les caractères discrets des membres supérieurs: un essai de synthèse des données. *Bulletins et Mémoires de la Société d'Anthropologie de Paris 24*, 107–130.

WALTER, P.L. & CANT, J.G.H., 1977. A population survey of kinkajous (*Potos flavus*) in a seasonally dry tropical forest. *Journal of Mammalogy 58*, 100–102.

WHITE, T.D., BLACK, M.T. & FOLKENS, P.A., 2011. *Human Osteology.* Academic Press, San Diego, 688 pp.