Postcranial remains of basal typotherian notoungulates from the Eocene of northwestern Argentina

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Notoungulates represent the most taxonomically diverse and temporally and geographically widespread group among South American native ungulates. Here, we analyze anatomical and systematic aspects of proximal tarsal bones recovered from the Lower and Upper Lumbrera formations (middle and late middle Eocene) in northwestern Argentina. We provide detailed descriptions, comparisons, and infer foot stances and range of movements for the taxa implicated. Material studied includes astragali belonging to the oldfieldthomasiid *Colbertia lumbrerense* (Lower Lumbrera Formation), a set of proximal tarsals referred as Typotheria indet. (Lower Lumbrera Formation), and tarsals (also including navicular and cuboid) of the informal taxon "*Campanorco inauguralis*" (Upper Lumbrera Formation). The comparison of the tarsals of *Colbertia lumbrerense* (middle Eocene of Argentina) with *Colbertia magellanica* (early Eocene of Brazil) reveals several differences including variations on the development and arrangement of articular facets, and the size of the dorsal astragalar foramen in the Argentinean species. The specimen of Typotheria indet. shows morphological affinities with basal interatheriid taxa. However, its larger size contrasting with the overall small body sizes of Eocene interatheriids precludes an indisputable taxonomic assignment. Concerning "*Campanorco inauguralis*", our observations indicate that there is no morphological evidence for a close phylogenetic relationship with Mesotheriidae. It presents a "reversed alternating tarsus" condition, which is also observed in Leontiniidae, "Notohippidae", Toxodontidae, and some typotherians. However, the spectrum of singularities exhibited by this form precludes the assessment of its relationships in the context of the Paleogene radiation of Typotheria and it is necessary to extend the comparison to Eocene notoungulates. Finally, in a morphofunctional context a plantigrade foot posture is inferred for the specimens here reported. These observations have the potential to provide functional proxies for paleoecological reconstructions to be applied to the study of the early radiation of these notoungulate faunas.

Key words: Mammalia, Notoungulata, calcaneum, astragalus, plantigrade, foot stances, Paleogene, South America.

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Introduction

The South American Paleogene vertebrate record is plethoric of well-known mammalian groups, which enclose several peculiar forms. Of these, the order Notoungulata stands as one of the most prolific, diverse, and geographically widespread clades (Cifelli 1993; Bond et al. 1995; Billet 2011; Bond 2016). During the Paleogene, the notoungulates reached a high degree of taxonomic diversity (Cifelli 1983, 1993; Billet 2011; and references herein), although the basal radiations of the group show a relatively low morphological disparity (Giannini and García-López 2014), sometimes hindering a clear assessment of intra order affinities.

Two monophyletic major groups are usually recognized within Notoungulata: Toxodontia and Typotheria (Reguero and Prevosti 2010; Billet 2010, 2011). Nevertheless, the basal relationships of the order are controversial, as some Paleogene taxa fall in basal polytomies outside these groups in integrative phylogenetic hypotheses (Reguero and Prevosti 2010; Billet 2011; García-López and Powell 2011). The vast majority of these phylogenetic studies are based on cranial and dental characters. Conversely, despite postcranial remains also provide phylogenetic information, they were only included in a few analyses, which received relatively little attention (e.g., Cifelli 1983, 1993; Szalay 1985; Shockey and Flynn 2007; Shockey and Anaya 2008). More recently, they started to be more frequently used for complementing cranial and dental character matrices (e.g., Shockey et al. 2012; Vera 2015).

Among postcranial elements, the calcaneum and astragalus (i.e., proximal tarsals) provide valuable and highly useful information at systematic and morphofunctional levels (e.g., Matthew 1909; Cifelli 1983; Szalay 1994; Rose et al. 2008; Shockey et al. 2012; Vera 2012; Armella et al. 2016; Hernandez del Pino et al. 2017). They are compact bones of the hind limb that form the joint between the zeugopodium and autopodium (Carrano 1997), and thus their importance as a functional unit is related to the locomotor adaptations of the studied animals (Argot 2004; Elissamburu and Vizcaíno 2004; Candela and Picasso 2008; Argot and Babot 2011; Ginot et al. 2016). Also, since each element functions as an integrated part of the hind limb, it is generally stable, as any modification of one element changes its role in relation to the remaining pieces of the functional complex (Shockey and Anaya 2008). Consequently, their morphology can bear valuable information about the group they belong to (Matthew 1909; Cifelli 1983; Prasad and Godinot 1994; Szalay 1994), spurring an increasing interest in studies of these elements.

More interestingly, the calcaneum and astragalus are frequently found in the fossil record, only outcompeted by the teeth, which are usually the most common remains recovered (Fostowicz-Frelik et al. 2018). The Paleogene levels from northwestern Argentina are not an exception to that pattern. In late Eocene outcrops of the Geste Formation (Catamarca Province), Armella et al. (2016) reported sev-
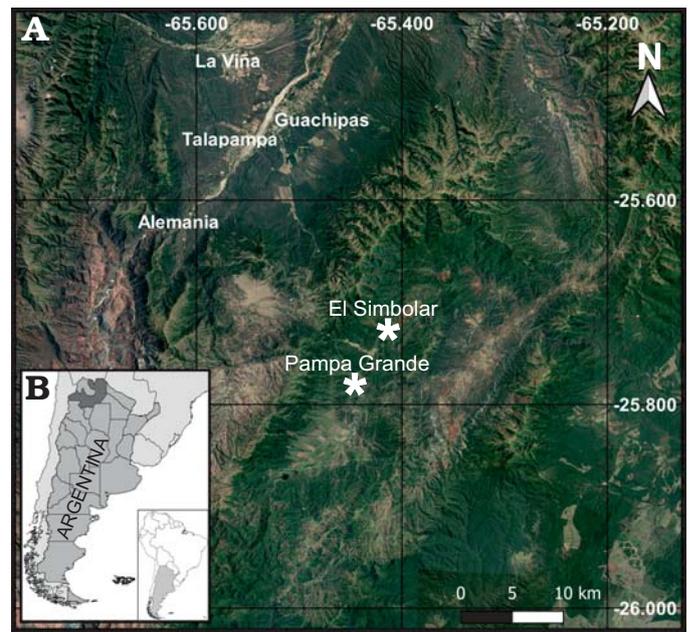

Fig. 1. Satellite images showing location of Guachipas Department, Salta Province, Argentina (**B**, dark grey) and of the fossil-bearing localities Pampa Grande and El Simbolar (**A**, asterisked).

eral proximal tarsals assigned to early-diverging notoungulate taxa and archaic members of several lineages of South American native ungulates (SAnu). Moreover, middle–late middle Eocene sequences, recognized by del Papa et al. (2010) as the Lower and Upper Lumbrera formations, respectively (Salta Province), yielded several vertebrate faunas (see Babot et al. 2017). Within these faunas, notoungulates are very frequent, represented by well-preserved, mostly cranial remains, often associated with postcranial elements. Particularly, Typotheria taxa were described in detail, but all of the studies focused on cranial and dental elements (e.g., Bond 1981; Bond et al. 1984; Bergqvist et al. 2007; García-López and Powell 2009, 2011; García-López 2011; Powell et al. 2011).

In this contribution we analyze anatomical and systematic aspects for tarsals of notoungulates recovered from the Lower and Upper Lumbrera formations (see Fig. 1 for geographic provenance). Most of these elements are associated with cranial remains and are described here for the first time; the fact that they are well preserved and articulated allows us to undertake a detailed analysis. Finally, we consider several morphological features of the tarsals to infer mammalian foot stances and range of movements. Given that the Paleogene is considered a period of major importance for the evolution and diversification of Notoungulata (Croft et al. 2008; Reguero and Prevosti 2010), this contribution enhances the tarsal morphology as a trait to assess phylogenetic affinities and morphofunctional patterns in early forms within Typotheria.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; IBIGEO-P, Instituto de Biología y Geología, Colección Paleontología, Salta, Argen-

tina; MACN-A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional Ameghino, Ciudad Autónoma de Buenos Aires, Argentina; MACN-PV, Museo Argentino de Ciencias Naturales "Bernardino Riva-davia", Colección Nacional Paleovertebrados, Ciudad Autó-noma de Buenos Aires, Argentina; MCNAM-PV, Colección Paleontología de Vertebrados, Museo de Ciencias Naturales y Antropológicas "J.C. Moyano", Mendoza, Argentina; MCT, Museu de Ciências da Terra, Río de Janeiro, Brasil; MHAS, Museo del Hombre de Antofagasta de la Sierra, Catamarca, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MPEF-PV, Museo Paleontológico "Egidio Feruglio", Paleontología de Vertebrados, Chubut, Argentina; MUSM, Museo de Historia Natural-Universidad Nacional Mayor de San Marcos, Lima, Perú; PVL, Colección Paleontología Vertebrados Lillo, Tucumán, Argentina; UF, University of Florida, Gainesville, Florida, USA.

Other abbreviations.—SALMA, South American Land Mammal Age; SAnu, South American native ungulates.

Material and methods

Most of the fossil bones studied here are part of skeletons preserving also cranial and dental remains; therefore, tax-onomic assignments are reliable. In the case of isolated re-mains, assignment to particular taxa was achieved by com-parison with previously described skeletons, both directly and from the literature.

The recovered material was directly compared with fossil specimens of different mammalian groups housed in IBIGEO-P, MACN-A, MACN-PV, MLP, and PVL. The comparative analyses were developed using up to date spe-cific literature. Measurements are reported in Table 1, fol-lowing Carrano (1997: fig. 2) and Armella et al. (2016: fig. 3).

The anatomical terms used herein are those commonly employed in classical papers (e.g., Cifelli 1983) and more recent contributions (Carrano 1997; Muizon et al. 1998; Cerdeño and Vera 2010; Vera 2012; Armella et al. 2016). General characters mentioned in the text are illustrated in Fig. 2; additionally, some specific structures are also detailed
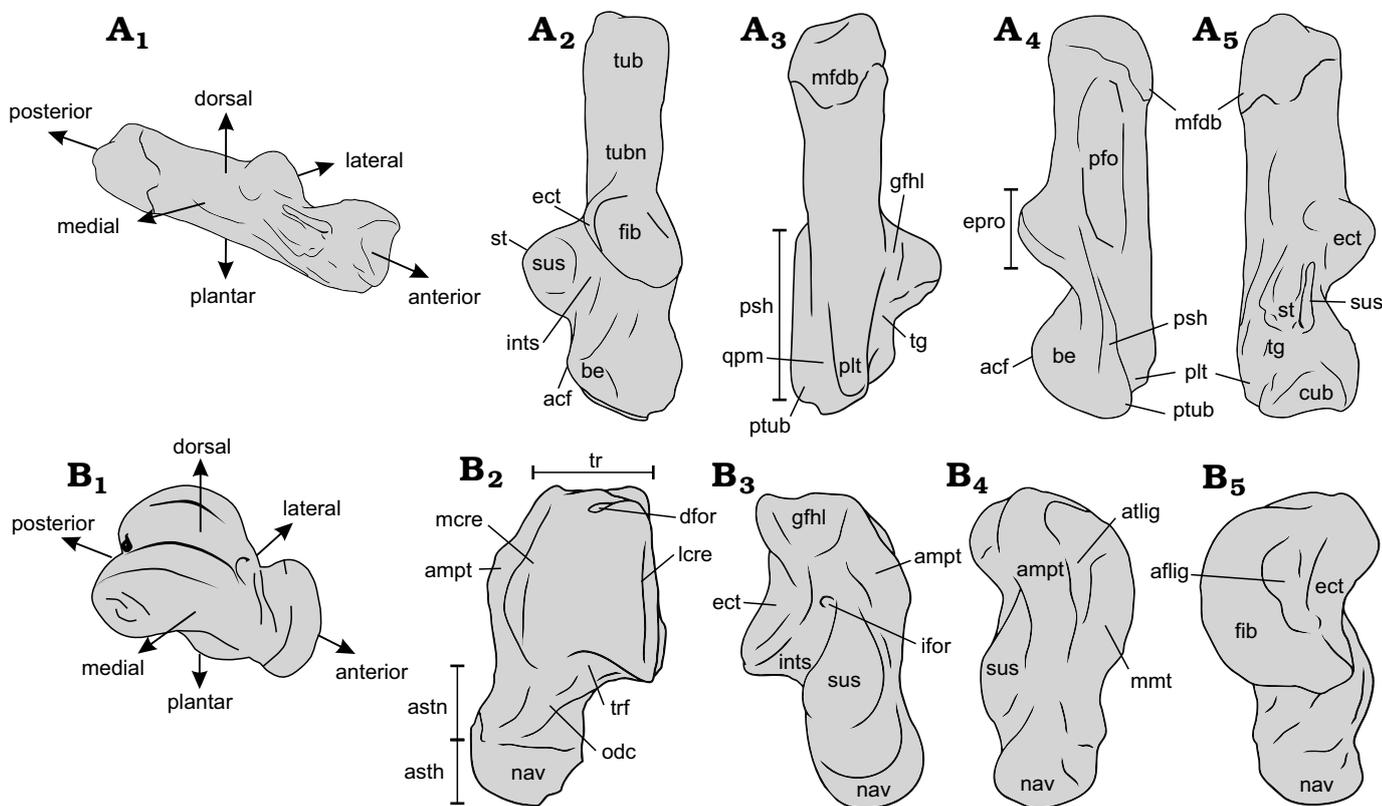

Fig. 2. Ungulate left proximal tarsal terminology. **A**. Calcaneum; orientation used for description (A_1), dorsal (A_2), plantar (A_3), lateral (A_4), and medial (A_5) views. **B**. Astragalus; orientation used for description (B_1), dorsal (B_2), medial (B_3), medial (B_4), and lateral (B_5) views. Abbreviations: acf, astraga-localcaneal facet; aflig, attachment for the fibuloastragalar ligament; ampt; astragalar medial plantar tuberosity; asth, astragalar head; astn, astragalar neck; atlig, attachment for the tibioastragalar ligament; be, "beak" (Cifelli 1983, 1993); cub, cuboidal facet; dfor, dorsal astragalar foramen; ect, ectal facet; epro, ectal protuberance; fib, fibular facet; gfhl, groove for the tendon of the flexor hallucis longus muscle (groove for deep digital flexor tendon in Cifelli 1983; groove for the tendon of muscle flexor fibularis in Szalay 1985); ifor, inferior astragalar foramen; ints, interarticular sulcus; lcre, lateral crest; mcre, medial crest; mfdb; muscle flexor digitorum brevis (attachment of flexor digitorum superficialis muscle in Cifelli 1983); mmt, facet for the medial malleolus of the tibia; nav, navicular facet; odc, oblique dorsal crest (nuchal crest or tibial stop); pfo, peroneal fossa; plt, plantar tubercle; psh, peroneal shelf; ptub, peroneal tubercle; qpm, attachment of the quadratus plantae muscle (Cifelli 1983); st, sustentaculum; sus, sustentacular facet; tg, tendinous groove (for the attachment of calcaneocuboid ligaments; Muizon et al. 1998); tr, tibial trochlea; trf, fossa trochlear; tub, tuber calcis; tubn, tuber neck.

in the corresponding figures for each specimen. For descriptive purposes, we considered six main faces on each tarsal bone: anterior, posterior, medial, lateral, dorsal, and plantar (Cerdeño et al. 2012); with the terms anterior and posterior referring to the head and opposite position respectively, the terms medial and lateral referring to the aspects facing toward the sagittal plane or opposite to it on each side considering the actual anatomical position and, finally, the terms dorsal and plantar referring to the aspects facing opposite or towards the substrate considering the resting position of the foot. For practical reasons, some taxonomic names recognized as informal (e.g., "*Campanorco inauguralis*"; García-López and Babot 2017) are used throughout the text.

For morphofunctional inferences, we use restrictively the terms plantigrade, digitigrade, and unguligrade for the foot in resting position, following Carrano (1997). In plantigrades the flexure occurs at the calcaneum-astragalus joint; in unguligrades (highly specialized condition), it occurs at the phalangeo-ungual joint. In digitigrades, the foot may technically be flexed at any joint between these two, though it most commonly occurs at the metatarso-phalangeal joint.

Systematic palaeontology

Panperissodactyla Welker, Collins, Thomas, et al., 2015

Notoungulata Roth, 1903

Typotheria Zittel, 1893

Genus *Colbertia* Paula Couto, 1952

Type species: *Colbertia magellanica* (Price and Paula Couto, 1950); São José de Itaborai, Brazil; early Eocene.

Included species: *Colbertia magellanica* (Price and Paula Couto, 1950); *Colbertia lumbrerense* Bond, 1981.

Colbertia lumbrerense Bond, 1981

Material.—PVL 6227; right calcaneum and left and right astragali, part of a skeleton of an adult individual also preserving the skull and mandibles, from Pampa Grande, Guachipas Department, Salta Province, Argentina (Fig. 1); Lower Lumbrera Formation, middle Eocene (Vacan subage of the Casamayoran SALMA; del Papa et al. 2010).

Description.—The calcaneum is poorly preserved. This element has suffered a dorsoplantar compression that altered its main features and it will not be described here (Fig. 3A). The astragali are complete, but the right one is also compressed (dorsoplantarly); the following description is based on the better-preserved left element. In dorsal view, the tibial trochlea is shallow, asymmetric (see Table 1), and trapezoidal in shape, the lateral crest being more developed and conspicuous than the medial crest, which is more rounded (Fig. 3B$_1$). The trochlear fossa is shallow and almost smooth. The astragalar neck is short compared to other Paleogene taxa (e.g., *Thomashuxleya externa* Ameghino, 1901, *Notopithecus ada-*

Table 1. Measurements (in mm) of the proximal tarsals described in the text. After Armella et al. (2016: fig. 3.3, 4): LAn, length of the anterior region of the calcaneum; LTr, length of the trochlea; LTub, length of the tuber calcis; MDTub, maximum diameter of the tuber calcis; MiDTub, minimum diameter of the tuber calcis; TLA, total length of the astragalus; TLC, total length of the calcaneum; WC, width of the calcaneal body; WH, width of the astragalar head; WTr, width of the trochlea. Values in italics after Carrano (1997: fig. 2C): ASTCS, astragalar condyle symmetry (ASTW1/ WTr); ASTD, depth of the astragalar trochlea; ASTRD, astragalar trochlea concavity (ASTD/WTr); ASTW1, width of medial condyle. – measurement not available; * approximate.

Specimen		*Colbertia lumbrerense* (PVL 6227)	Typotheria indet. (PVL 4292)	"*Campanorco inauguralis*" (IBIGEO-P 105)
Calcaneum	TLC	–	45.49	–
	WC	–	17.78	15.42
	LTub	–	*28.71*	*19.03**
	LAn	–	*16.78*	*10.25*
	MiDTub	–	8.61	7.51
	MDtub	–	11.52	7.74
Astragalus	TLA	13.76	25.75	17.89
	WTr	5.29	7.63	8.89
	LTr	9.06	14.35	11.66
	WH	5.64	8.54	9.13
	ASTWl	*2.31*	*2.82*	*3.96*
	ASTD	*0.67*	*0.81*	*0.94*
	ASTCS	*0.42*	*0.36*	*0.44*
	ASTRD	*0.12*	*0.11*	*0.10*

pinus Ameghino, 1897) and other specimens here studied (see below), representing almost 28% of the total length of the astragalar body (Table 1). The oblique dorsal crest (nuchal crest or tibial stop) is robust, oriented posterolateral-anteromedially and it occupies the entire surface of the neck (it forms an angle of approximately 62° with the anteroposterior axis of the astragalus; Fig. 3B$_1$). The head is slightly eroded on its medial side; however, it can be observed that it is spherical, being roughly as wide as the neck but not expanded (a shallow groove surrounding the head separates both structures; Fig. 3B$_1$). The navicular facet occupies the entire anterior surface of the astragalar head and it is slightly extended on the medial surface (Fig. 3B$_1$).

In plantar view, the astragalus shows some eroded areas; nevertheless, the articular facets are well-preserved (Fig. 3B$_2$). The ectal facet is subtrapezoidal, with the major axis anteroposteriorly oriented. It is represented by a deep concavity that faces lateroplantarly (Fig. 3B$_2$). In contrast, the sustentacular facet is convex, oval, and it occupies the plantar surface of the astragalar neck. This facet exhibits well-defined edges. Although a small, smooth surface connects the sustentacular and navicular facets, the strong concavity of this surface indicates that both facets are functionally separated (Fig. 3B$_2$, B$_4$).

The interarticular sulcus is deep and anterolateral-posteromedially oriented. Moreover, in its posterior area, the inferior astragalar foramen is small and faces anteroplantarly (Fig. B$_2$). The groove for the tendon of the flexor hallucis lon-
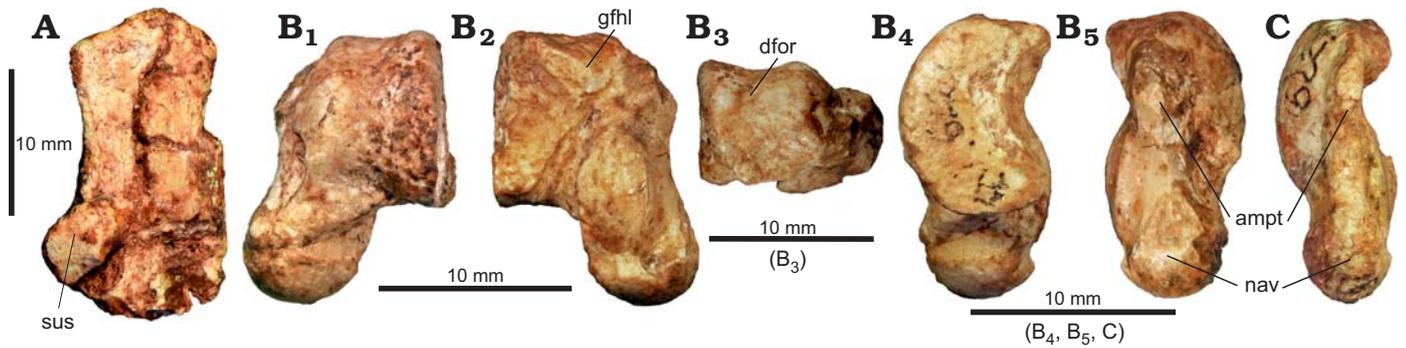
Fig. 3. Tarsal bones of typotherian notoungulate *Colbertia lumbrerense* Bond, 1981 (PVL 6227) from Pampa Grande, Salta Province, Argentina, Lower Lumbrera Formation, middle Eocene (Vacan subage of the Casamayoran SALMA). **A**. Left dorsoplantarly compressed calcaneum in dorsal view. **B**. Left astragalus in dorsal (B_1), plantar (B_2), posterior (B_3), lateral (B_4), and medial (B_5) views. **C**. Right dorsoplantarly compressed astragalus in medial view. Abbreviations: ampt, astragalar medial plantar tuberosity; dfor, dorsal astragalar foramen; gfhl, groove for the tendon of the flexor hallucis longus muscle; nav, navicular facet; sus, sustentacular facet.

gus muscle is poorly developed compared to other specimens such as PVL 4292 (see below) and it is roughly continuous with the trochlea (Fig. B_3). The lateral crest that limits the groove is broken; nevertheless, the rest of the structure is clearly visible. The dorsal astragalar foramen is present but very small and located near the lateral crest of the trochlea (Fig. $3B_1$, B_3). On the medial area, the astragalar medial plantar tuberosity (medial protuberance in Cifelli 1993; medial process in Shockey and Flynn 2007; tibial protuberance in Vera 2012) is small but well pronounced, defined by the anteromedial portion of the medial crest (Fig. $3B_2$). The orientation of the facet for the medial malleolus of the tibia is similar to the astragalar medial plantar tuberosity, but the former is smooth and less projected (Fig. $3B_5$). The attachment for the tibioastragalar ligament is located between these two structures, forming a shallow groove.

In lateral view, the fibular facet is flat, crescent-like (with a blunter, although somewhat eroded, posterior end), and lacking projections (Fig. $3B_4$). The attachment for the fibuloastragalar ligament is represented by a deep and conspicuous kidney-shaped depression, with the major axis being anteroposteriorly oriented. In medial view, the medial aspect of the astragalar medial plantar tuberosity is elliptical, with the major axis being anteroposteriorly oriented (Fig. $3B_5$). Although there is an eroded area on the medial surface, this structure is not connected with the navicular facet (this is more evident on the right astragalus; Fig. 3C).

Remarks.—The genus *Colbertia* includes two species of small-sized notoungulates: *Colbertia magellanica*, from the early Eocene of Brazil (Itaboraí) and *Colbertia lumbrerense*, recorded from middle Eocene rocks of the Lower Lumbrera Formation in Salta Province, Argentina. Although Bergqvist et al. (2007) and Bergqvist and Fortes Bastos (2009) studied postcranial remains of both species, these authors did not provide detailed descriptions of the tarsal bone morphology, since these elements were not fully prepared and poorly preserved in the specimens available to them. In the particular case of *C. lumbrerense*, the specimen analyzed by Bergqvist et al. (2007) was the postcranium PVL 6218, currently not

available to us, and proximal tarsals were not figured in detail. The recently prepared PVL 6227 allows us to compare in detail the two species of *Colbertia*. Concerning the astragalus, the shared features between *C. magellanica* (MCT 2456M; Bergqvist et al. 2007: fig. 5; Bergqvist and Fortes Bastos 2009: fig. 2) and *C. lumbrerense* (Fig. 3) are the spherical astragalar head, where the sustentacular and navicular facets are separated by a deep sulcus, and the navicular facet slightly extended on the medial surface, which is not connected with the astragalar medial plantar tuberosity.

Bergqvist et al. (2007) considered that, at least regarding the features exposed in the specimen PVL 6218, the trochlea and ectal facet morphology are traits shared by *C. magellanica* and *C. lumbrerense*. Nevertheless, PVL 6227 shows an asymmetric and trapezoidal tibial trochlea (Fig. $3B_1$), in contrast to *C. magellanica* (MCT 2456M), where the trochlear crests are parallel and inclined to the lateral side (Bergqvist et al. 2007: fig. 5; Bergqvist and Fortes Bastos 2009: fig. 2). Other traits of *C. lumbrerense* differing from *C. magellanica* are the ectal and fibular facets not projected laterally, smaller astragalar medial plantar tuberosity on the medial face, longer neck (made of the oblong sustentacular facet), and very small dorsal astragalar foramen (in *C. magellanica* this foramen is well developed and located in a depression on the trochlea).

In summary, the mentioned differences are opposed to a previous point of view that considers the morphologies of *Colbertia magellanica* and *Colbertia lumbrerense* being similar (Bergqvist et al. 2007). Hence, these comparisons indicate a source of diagnostic traits potentially useful to the further characterization of both species.

Stratigraphic and geographic range.—Lower Lumbrera Formation, middle Eocene (Lutetian); Pampa Grande, Salta Province, Argentina.

Typotheria indet.

Material.—PVL 4292; left calcaneum, astragalus, and associated distal fragment of the fibula; from Pampa Grande, Guachipas Department, Salta Province, Argentina (Fig. 1);

Lower Lumbrera Formation, middle Eocene (Vacan subage of the Casamayoran SALMA; del Papa et al. 2010).

Description.—The elements are well preserved and the articular facets can be clearly observed (Fig. 4). Nevertheless, there are broken areas and surfaces that have been eroded, as evidenced by angular edges (e.g., the middle region of the calcaneum and the astragalus neck).

Calcaneum: It is an elongated and relatively robust bone, compared with the other specimens here studied. In dorsal view, the tuber calcis represents almost 45% of the calcaneum total length (Table 1). The dorsal surface is narrower than the plantar face; hence, the cross section of the tuber is subtriangular. The apical region is also wider than the dorsal aspect of the tuber and its posterior surface is rugose and dorsoplantarly sloping (Fig. 4A$_1$). On the tuber neck, a small concavity can be observed posteriorly and laterally to the fibular and ectal facets, respectively. The ectal facet is convex and medially oriented (Fig. 4A$_1$); it is crescent-shaped with a wider posterior area. Adjacent to this, the fibular facet is also markedly convex but it is larger (in comparison to other Eocene ungulates; see below) and anterodorsally oriented. It is subrectangular with markedly rounded edges, with the major axis obliquely arranged compared to the major axis of the calcaneum (Fig. 4A$_1$). Both ectal and fibular facets form a conspicuous ectal protuberance. The sustentaculum is larger than the ectal protuberance and anteromedially located. The sustentacular facet is smaller than the ectal and fibular facets. It is dorsally oriented, slightly concave, and subcircular; however, its anterior edge is slightly projected (Fig. 4A$_1$). Between the sustentacular and ectal facets, there is a broken area which prevents the assessment of the dimensions and morphology of the interarticular sulcus. In the anteromedial end of the calcaneum and separated from the sustentacular facet, the anterior astragalocalcaneal facet is slightly elongated on a large dorsal projection (named as "beak" by Cifelli 1983, 1993; Fig. 4A$_1$).

In plantar view, the surface for the attachment of the muscle flexor hallucis brevis has rounded edges and occupies the entire width of the tuber apex (Fig. 4A$_2$). The groove for the tendon of the flexor hallucis longus muscle is broad and limited by a shallow longitudinal crest on the plantar aspect (tendinous groove, see bellow; Fig. 4A$_2$). Toward the anterior region, the most prominent feature is the plantar tubercle. It is a robust structure that is developed parallel to the major axis of the calcaneum for the plantar ligaments (to the cuboid and cuneiforms) and tarsal fibrocartilage (sensu Cifelli 1983) (Fig. 4A$_2$).

On the lateral side, the peroneal fossa is bounded by the ectal protuberance and two longitudinal crests (Fig. 4A$_3$). This fossa occupies almost 42% of the calcaneum total length ant it is much longer than the anteroposterior extension of the fibular facet. The peroneal tubercle is a robust process located on the anterior end of the lateral face. Despite being posteriorly broken, it seems to be extended from the anterior edge of the ectal protuberance to the anterolateral end of the calcaneum, forming a peroneal shelf (Fig. 4A$_3$).

Anterolaterally, on the peroneal shelf, a well-marked groove for the attachment of the quadratus plantae muscle (Cifelli 1983) is more exposed in plantar view (Fig. 4A$_2$).

In medial view a tendinous groove is located medial to the plantar tubercle and separated from the anterior edge of the sustentaculum (Fig. 4A$_4$). It is slightly concave, oblique, and does not extend to the anterior face. According to Muizon et al. (1998), this is a site for attachment of calcaneocuboid ligaments. The calcaneum cuboidal facet is clearly observed in this view; it is strongly concave and has an elliptical shape with an anteroplantar to posterodorsally oriented major axis, reaching almost a complete medial exposure (Fig. 4A$_4$).

Astragalus: The astragalus is more robust than the calcaneum and represents 53% of the calcaneum total length (Table 1). In dorsal view, the tibial trochlea is asymmetric, trapezoidal, and has a slightly excavated trochlear concavity (see Table 1; Fig. 4B$_1$). The lateral trochlear crest is wider than the medial crest, which shows more rounded edges. The trochlear concavity leads anteriorly to a moderately deep trochlear fossa, which is in turn bounded by the anterior end of the lateral trochlear crest (Fig. 4B$_1$). The oblique dorsal crest is well defined and developed in a posterolateral-anteromedial direction; it forms an angle of approximately 58° with the anteroposterior axis of the astragalus. The astragalar neck is longer and narrower than the astragalar body; it is slightly oblique, causing a minimum medial displacement of the astragalar head. The head is spherical and almost as wide as the neck; both areas are separated by a shallow groove (Fig. 4B$_1$). The navicular facet extends on the medial surface of the neck.

In plantar view, the ectal facet is well defined; it is sub-triangular with a vertex pointing anterolaterally (Fig. 4B$_2$). This facet is strongly concave and faces laterally. In contrast, the sustentacular facet is slightly convex, teardrop-shaped, and occupies a large portion of the astragalar neck. This facet exhibits well-defined edges, and it is separated from the navicular facet by a deep sulcus (Fig. 4B$_2$). The articular facet arrangement of the proximal tarsals PVL 4292, results in a transverse articulation plane (side by side), rather than an overlapping disposition of both elements (Fig. 4C$_1$). Between the ectal and sustentacular facets, the interarticular sulcus is deep, anterolateral-posteromedially oriented, and it leads to a small inferior astragalar foramen (Fig. 4B$_2$). In the posterior area, the groove for the tendon of the flexor hallucis longus muscle is wide and defined by two sharp crests. This groove is not continuous with the tibial trochlea (Fig. 4B$_3$). With the astragalus and calcaneum in articulation, the groove is continuous with a similar structure on the calcaneum, completing the passage for the flexor hallucis longus muscle (Fig. 4C$_2$). There is a small notch or fossa developed on the surface separating the trochlea and flexor groove, clearly visible in posterior view (Fig. 4B$_3$). This structure probably houses the dorsal astragalar foramen; however, the bottom is filled with sediment matrix and the presence of an aperture is not certain. If present, the foramen would be very small.

In lateral view, the fibular facet and the attachment for the fibuloastragalar ligament are similar to those observed
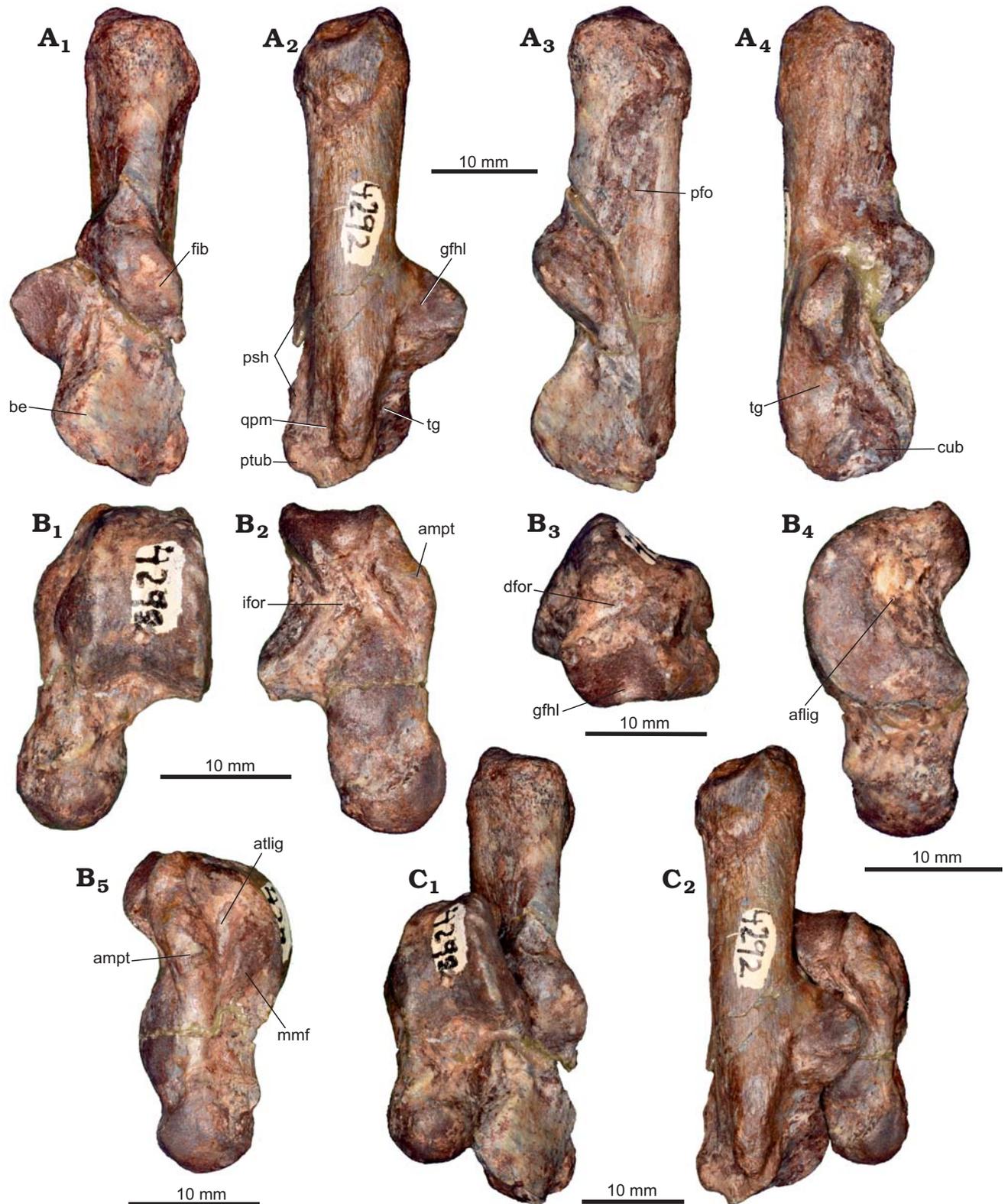
Fig. 4. Tarsal bones of Typotheria indet. (PVL 4292) from Pampa Grande, Salta Province, Argentina, Lower Lumbrera Formation, middle Eocene (Vacan subage of the Casamayoran SALMA). **A**. Left calcaneum in dorsal (A_1), plantar (A_2), lateral (A_3), and medial (A_4) views. **B**. Left astragalus in dorsal (B_1), plantar (B_2), posterior (B_3), lateral (B_4), and medial (B_5) views. **C**. Articulated proximal tarsals in dorsal (C_1) and plantar (C_2) views. Abbreviations: aflig, attachment for the fibuloastragalar ligament; ampt, astragalar medial plantar tuberosity; atlig, attachment for the tibioastragalar ligament; be, "beak" (Cifelli 1983, 1993); cub, cuboidal facet; dfor, dorsal astragalar foramen; fib, fibular facet; gfhl, groove for the tendon of the flexor hallucis longus muscle; ifor, inferior astragalar foramen; mmt, facet for the medial malleolus of the tibia; pfo, peroneal fossa; psh, peroneal shelf; ptub, peroneal tubercle; qpm, attachment of the quadratus plantae muscle (Cifelli 1983); tg, tendinous groove.

in *Colbertia lumbrerense* (PVL 6227; see above) (Fig. 4B$_4$). On the medial side, the astragalar medial plantar tuberosity is larger and wider than the facet for the medial malleolus of the tibia. It is fusiform in medial view, with the major axis antero-posteriorly oriented (Fig. 4B$_5$). The facet for the medial malleolus of the tibia is adjacent to the aforementioned tuberosity and presents almost the same development and orientation (Fig. 4B$_5$). Both structures are separated by the attachment for the tibioastragalar ligament. It is a deep groove, wider on the posterior region and narrower toward the anterior area.

Remarks.—Cifelli (1983, 1993) recognized several synapomorphies in the astragalus of Notoungulata: astragalar neck constricted and well-differentiated from the head and the body, presence of the oblique dorsal crest, marked astragalar medial plantar tuberosity, and sulcus extended laterally from the dorsal astragalar foramen (generally absent in derived notoungulates). Moreover, Bergqvist (1996) added the medially extended navicular facet as a diagnostic feature for the clade. The presence of this set of distinctive traits results in the identification of PVL 4292 as a notoungulate.

Several notoungulate tarsals are known for the Paleogene (e.g., Cifelli 1983; Muizon et al. 1998; Shockey and Flynn 2007; Shockey and Anaya 2008; Gelfo and Lorente 2010; Shockey et al. 2012; Vera 2012; Lorente et al. 2013, 2019; Armella et al. 2016; Hernandez del Pino et al. 2017; among others); however, only a few records came from Eocene levels. In this context, PVL 4292 was initially compared with specimens sharing temporal affinities.

The basal notoungulate *Notostylops murinus* Ameghino, 1897 (Notostylopidae) was reported for the middle Eocene of Chubut, Argentina (Lorente et al. 2013, 2019). Its astragali (MACN-A 10940) differ from PVL 4292 in parallel trochlear crests, laterally inclined; short astragalar neck, narrower than the head; small astragalar medial plantar tuberosity; lateral process well developed; ectal facet more plantarly exposed; and a large dorsal astragalar foramen. Regarding *Allalmeia atalaensis* Rusconi, 1946, another basal form found in middle Eocene levels of Mendoza, Argentina (Lorente et al. 2014), several features distinguish it from PVL 4292. Although the calcaneum of *A. atalaensis* (MCNAM-PV 507) is poorly preserved, it shows a more circular sustentaculum, well-developed peroneal tubercle, and a more horizontal orientation of the cuboidal facet. Besides this, the astragalus MCNAM-PV 507 differs from PVL 4292 in the presence of well-developed lateral process and astragalar medial plantar tuberosity, and small facet for the medial malleolus of the tibia.

The Eocene toxodontians that preserve the proximal tarsals are the genera *Thomashuxleya* Ameghino, 1901 and *Periphragnis* Roth, 1899 ("Isotemnidae"). Regarding the calcaneum, only the PVL 316 (*Thomashuxleya* sp.) was available for comparison; it is almost two times larger than PVL 4292 and shows a robust tuber calcis with a globose posterior region. Also, the fibular facet is very small, the ectal facet is large (pointing to the lateral and anterior faces), and the cuboidal facet is more transversely oriented than in

PVL 4292. As for the astragalus, both *Thomashuxleya* (PVL 332; Carrillo and Asher 2017) and *Periphragnis* (Shockey and Flynn 2007) differ from PVL 4292 in the presence of a wide trochlea, large dorsal astragalar foramen, well-projected astragalar medial plantar tuberosity, short neck, and a shallow oblique dorsal crest. Additionally, Shockey and Flynn (2007) described another middle Eocene indeterminate isotemnid from Patagonia, Argentina, which preserves an almost complete foot. In overall terms, this specimen (AMNH 28690, but see Lorente et al. 2019) also displays the differences mentioned above, except for the ectal facet, which is more plantarly oriented in the astragalus, and the tuber calcis, which is dorsoplantarly wider than in PVL 4292.

Within Typotheria, the astragalus of PVL 4292 differs from the oldfieldthomasiid *Colbertia lumbrerense* (PVL 6227) in several traits: larger size, which is 46% longer than PVL 6227 (Table 1); presence of a longer neck; narrow trochlea compared to the ratio between total length of the astragalus and width of the trochlea; ectal facet exposed mostly on the lateral side; and presence of a notch or fossa housing the dorsal astragalar foramen (although this last character is not fully visible; see above). Regarding *C. magellanica*, the same differences are observed, with the remarkable exception of the notch for the dorsal astragalar foramen, present also in this species (Bergqvist et al. 2007). As for the calcaneum (which cannot be compared with C. *lumbrerense*) PVL 4292 differs from *C. magellanica* (MCT 1263M) in a more vertically oriented ectal facet; well-developed fibular facet; and a subcircular sustentacular facet.

The tarsal morphology is also known for Eocene interatheriids. Vera (2012) described the postcranial morphology of *Notopithecus adapinus*, from the middle Eocene of the Argentinean Patagonia. Although the tarsals show a few similarities (e.g., well-developed peroneal fossa, one concavity near the ectal prominence in the calcaneum, asymmetric, shallow, and narrow astragalar trochlea, and a long neck with spherical head in the astragalus), PVL 4292 differs from this specimen (MPEF-PV 1113) in a longer tuber calcis compared to the calcaneal body; low development of the peroneal shelf in the calcaneum; and a larger astragalar medial plantar tuberosity and greater development of the medial trochlear crest in the astragalus. In addition, the PVL 4292 remains are almost four times larger than the tarsals of *Notopithecus*.

In NWA, the Eocene Geste Formation yielded several proximal tarsals (García-López and Babot 2015) that were assigned to Interatheriidae (two calcanei and one astragalus; Armella et al. 2016). Morphologically, the calcanei MHAS 046 and MHAS 047 (Armella et al. 2016: fig. 5) share with PVL 4292 a long tuber calcis; wide peroneal fossa; fibular facet markedly convex and obliquely arranged regarding the major axis of the calcaneum; projected ectal protuberance; small and slightly concave sustentacular facet with its anterior edge slightly projected; presence of a small concavity posteriorly and next to the fibular and ectal facets, respectively; and robust plantar tubercle. Furthermore, although the astragalus MHAS 048 lacks the lateral crest of

the trochlea (Armella et al. 2016: fig. 6), it shows a long neck and spherical astragalar head similar to the astragalus PVL 4292. However, the discrepancy in size between these tarsals and the specimen PVL 4292 is remarkable and reaches the same values as that mentioned for *Notopithecus adapinus* (see Table 1; and Armella et al. 2016: tables 1 and 2).

At this point, a recent taxonomic proposal made by Vera (2015) should be considered. This author performed a cladistic analysis including both cranial and postcranial characters and proposed a drastic change in the systematic of the forms usually considered as basal interatheriids. In this contribution, *Notopithecus*, *Transpithecus*, *Antepithecus*, and *Guilielmoscotia* are recovered as a monophyletic clade named Notopithecidae and defined by two unequivocal synapomorphies: small mesial extension of the entolophid and asymmetrical astragalar trochlea with higher lateral side more oblique than the medial side. Considering these traits, the specimen PVL 4292 should be included as a member of Notopithecidae. Moreover, other general characters are mentioned for the group and are present in the material studied here: inclined fibular facet, oblique astragalar medial plantar tuberosity, and absence of astragalar-cuboid contact. Nevertheless, in addition to the already mentioned differences with *Notopithecus* (which include a much larger size; see below), it should be noted that postcranial traits are only known for this latter genus within the focus group studied by Vera (2015), and that this particular morphology for the astragalar trochlea is widely distributed among other Paleogene notoungulates (e.g., *Allalmeia*, *Colbertia*, "*Campanorco*", *Trachytherus*). It is clear that this taxonomic proposal should be evaluated in light of new materials and may be challenged in future analyses, and thus we follow here a more traditional taxonomic approach.

It is also important to mention that several of the aforementioned features are shared with interatheriids recorded from the late Oligocene (e.g., *Federicoanaya* Hitz, Billet, and Derryberry, 2008 from Salla, Bolivia) and the middle Miocene (e.g., *Protypotherium* Ameghino, 1882 from Santa Cruz, Argentina). Additionally, these post-Eocene taxa show a well-defined facet in the calcaneum for the articulation with the navicular. The last trait is also observed in some toxodontians (e.g., leontiniids, notohippids, and early toxodontids; Cifelli 1993; Shockey et al. 2012), but it is absent in PVL 4292.

In summary, there is a set of similarities that would indicate that the specimen PVL 4292 is close to basal interatheriids (in a traditional taxonomic scheme). Nevertheless, it is clear that the remarkable larger size of the former represents an important difference compared to any basal interatheriid taxon, which show mostly small body sizes (Hitz et al. 2006; Vera 2015). In addition, although the Lower and Upper Lumbrera formations levels are highly fossiliferous, there is so far no record of that family therein. A direct assignment is thus difficult, as it would imply the presence of a very large, and thus rather unusual, basal interatheriid morphotype in these levels. We therefore refrain from referring PVL 4292 to this clade, provisionally favoring its identification as a basal Typotheria.

"*Campanorco*" informal taxon

Remarks.—The name "*Campanorco inauguralis*" was introduced by Bond et al. (1984) in one of the abstracts of a scientific meeting (*I Jornadas Argentinas de Paleontología de Vertebrados*). Although in this abstract even a family name was also included (Campanorcidae) no formal definition or illustration was provided; hence, the erection of this taxonomical entity does not fit in the standards of the International Commission of Zoological Nomenclature. Nevertheless, this term has been widely used in literature, sometimes regarded as an "informal taxon" (e.g., Reguero and Castro 2004; Billet 2010, 2011; Reguero and Prevosti 2010; García-López and Powell 2011). Additionally, a formal description of the first material mentioned as "*Campanorco*" and other new specimens is currently under way, dealing also with the proper use of this term. Thus, here we maintain the use of both the generic and specific epithets between quotation marks in order to link our observations with previous contributions and to avoid further confusion until this nomenclatural issue is resolved.

"*Campanorco inauguralis*" informal taxon

Material.—IBIGEO-P 105; articular portion of left calcaneum, almost complete right calcaneum, complete left astragalus, trochlear portion of right astragalus, and left cuboid and navicular. These elements are part of an incomplete skeleton including limbs, pelvis, vertebral column, and cranial remains; from El Simbolar, Guachipas Department, Salta Province, Argentina (Fig. 1); Upper Lumbrera Formation, late middle Eocene (Barrancan subage of the Casamayoran SALMA; del Papa et al. 2010).

Description.—The bones belong to a juvenile individual (this is inferred by the presence of deciduous dentition; García-López and Babot 2017).

Calcaneum: Both tuber calcanei are incomplete, preventing from estimating the total length of this element (Fig. 5A, B_1, Table 1). In dorsal view, it seems to be more robust than the calcaneum PVL 4292; however, both present a plantar surface that is wider than the dorsal surface (Fig. 5A). The tuber neck has a small concavity on the posterior region of the ectal protuberance. The ectal facet is convex (although less than in the calcaneum PVL 4292), elliptical in shape, and medially oriented (Fig. $5B_1$). The fibular facet is also convex; it is more slender than in PVL 4292 but shows the same arrangement (Fig. $5B_1$). Both facets are better observed in the right calcaneum, where they are differentiated by a change of orientation of the surface (Fig. $5B_1$). The sustentaculum is well developed medially and the sustentacular facet is larger than the fibular facet but subequal in size to the ectal facet. The sustentacular facet is also dorsally oriented, slightly concave, and circular with crested and well-defined edges (Fig. 5A, B_1). In the anteromedial end

of the calcaneum, the astragalocalcaneal facet is small and well separated from the sustentacular facet.

In plantar view, the groove for the tendon of the flexor hallucis longus muscle is narrower and shallower than in the calcaneum PVL 4292 (Fig. 5B$_2$). The plantar tubercle is slightly projected although developed on the anterior surface of the element; it is smaller than in the PVL 4292; however, this could have been affected by erosion.

On the lateral aspect, the peroneal fossa is poorly developed and located above the level of the ectal protuberance (Fig. 5C). This condition is opposite to that seen in the calcaneum PVL 4292 (see above). The peroneal tubercle is weak and rugose; it does not form a peroneal shelf (Fig. 5D$_1$). In medial view, the tendinous groove is slightly concave and restricted to a small area, medial to the plantar tubercle and anteroplantar to the navicular and sustentacular facets (Fig. 5D$_2$). The cuboidal facet is strongly concave and elliptical with the major axis anteroplantar to posterodorsally oriented. It is smaller and less inclined than in the calcaneum PVL 4292.

A remarkable feature of these calcanei, clearly visible on the right one, is the presence of a facet for the navicular bone. It is evident on medial view, between the anterior region of the sustentaculum and the cuboidal facet, and it is much smaller than the sustentacular facet, slightly concave, and elliptical (Fig. 5D$_2$).

Astragalus: This bone is somewhat flattened dorsoplantarly; despite this, it can be observed that this is mid-sized regarding the other astragali reported here (Table 1). It is 23% smaller than the astragalus PVL 4292 and 28% larger than the astragalus of *Colbertia lumbrerense* (PVL 6227). In dorsal view, the tibial trochlea is slightly asymmetric, trapezoidal, and more excavated than in the astragali described above (see Table 1, Fig. 5E$_1$). The medial crest is well developed, reaching the medial side of the astragalar neck (a somewhat similar condition is present in *C. lumbrerense*, although in this case the anterior end of the crest is weaker). The trochlear fossa is deeper than in the astragalus of *C. lumbrerense*, but shallower than in PVL 4292. Anterior to this fossa, the oblique dorsal crest is conspicuous but short; it forms an angle of approximately 45° with the anteroposterior axis of the astragalus. Unlike other notoungulate astragali this crest is confined to the lateral area of the astragalar neck. This neck is slightly narrower than the head, in which the navicular facet occupies the entire anterior extension (Fig. 5E$_1$). The main exposure of this facet is dorsal; in plantar view it is almost completely hidden (Fig. 5E$_2$). Moreover, it extends on the medial surface of the astragalar neck. Such a condition was observed in the other astragali described here. The astragalar head seems to be more developed transversely. However, this condition is related to dorsoplantar deformation, since the astragalar facet of the navicular bone (in which the head articulates) is markedly concave and hemispherical (see below).

In plantar view, the arrangement of the articular facets of IBIGEO-P 105 is similar to that in *Colbertia lumbrerense* (Fig. 5E$_2$). Nevertheless, the ectal facet is pro-portionally larger and more laterally extended than in the latter. Furthermore, the sustentacular facet is subcircular, with well-defined medial and lateral crested edges, and it is well separated from the navicular facet by a deep sulcus (Fig. 5E$_2$). The sustentacular facet is larger than in *C. lumbrerense*. Between the ectal and sustentacular facets, the interarticular sulcus houses the inferior astragalar foramen, which is posteriorly located. As in *C. lumbrerense* (PVL 6227), the groove for the tendon of the flexor hallucis longus muscle is not well developed (Fig. 5E$_3$). The dorsal astragalus foramen is large and located on the surface between the astragalar trochlea and flexor groove (interrupting the contact between both structures; Fig. 5E$_3$). Although the edges of this foramen are broken, it seems to have been rounded. This condition is different from the astragalus PVL 4292, in which it is located into a notch, and from *C. lumbrerense*, in which this foramen is very small and more dorsolaterally placed. On the medial area, the astragalar medial plantar tuberosity is projected medially (Fig. 5E$_2$).

In lateral view, the fibular facet is concave and crescent-like, with the major axis anteroposteriorly and obliquely oriented (Fig. 5E$_4$). Moreover, the lateral process is prominent, a feature not observed in the astragali described above. The attachment for the fibuloastragalar ligament is shallower and proportionally smaller than in *Colbertia lumbrerense* and the astragalus PVL 4292. On the medial aspect, the astragalar medial plantar tuberosity is elliptical, with the major axis anteroposteriorly oriented, and it does not reach the astragalar neck (Fig. 5E$_5$). The facet for the medial malleolus of the tibia is smaller than the astragalar medial plantar tuberosity, and both structures are separated by a slight depression corresponding to the attachment for the tibioastragalar ligament (Fig. 5E$_5$).

Navicular: This bone is not affected by deformation (Fig. 5F$_1$). It only preserves the corpus, which is robust and anteroposteriorly short. In posterior view, there is a facet for the astragalar head occupying the entire surface. It is very concave and circular (Fig. 5F$_1$). On the anterior surface, there are three main facets and a prominent tuberosity (Fig. 5F$_2$). The facet located on the lateral end is for the cuboidal bone; it forms a right angle with a small lateral facet for the calcaneum. The cuboidal facet is elliptical, slightly convex, and faces medially. Between this and the other facets, there is a deep sulcus dorsolaterally to medioplantarly oriented (Fig. 5F$_2$). The remaining facets are separated from each other by a shallow crest. The medial facet (which is larger) articulates with the mesocuneiform, while that for the ectocuneiform is lateral. The mesocuneiform facet is subtriangular and concave-convex, whereas the ectocuneiform facet is teardrop-shaped and slightly convex. There is no articulation for the entocuneiform. On the plantar region, there is a robust tuberosity that would be connected with the plantar apophysis (Fig. 5F$_2$). Finally, there is a triangular broken surface on the medial aspect of the navicular. This area may have corresponded to the navicular medial tuberosity present in basal notoungulates
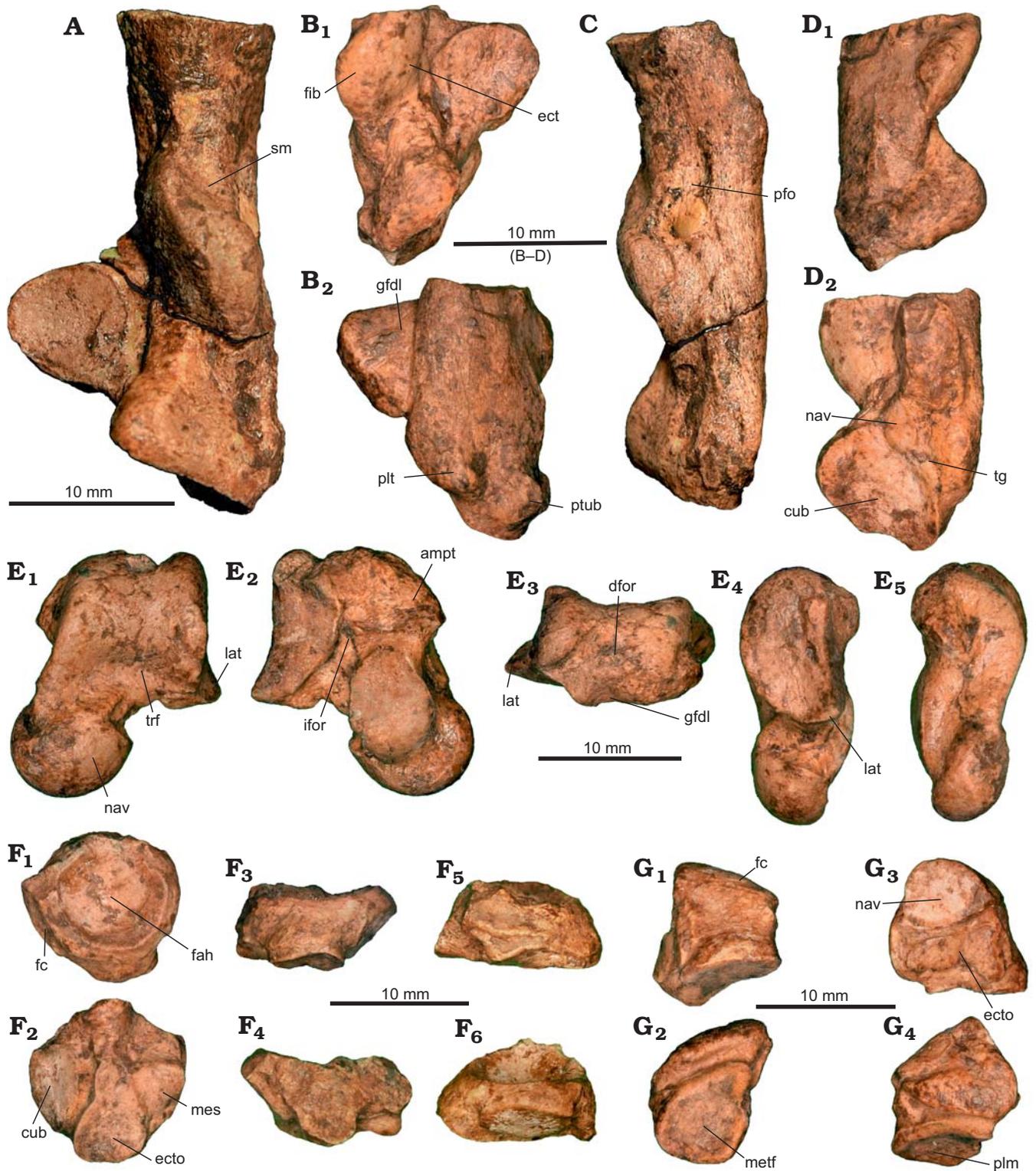
Fig. 5. Tarsal bones of typotherian notoungulate "*Campanorco inauguralis*" Bond, Vucetich, and Pascual, 1984 (IBIGEO-P 105) from El Simbolar, Salta Province, Argentina, Upper Lumbrera Formation, late middle Eocene (Barrancan subage of the Casamayoran SALMA). **A**. Left calcaneum in dorsal view. **B**. Right calcaneum in dorsal (B_1) and plantar (B_2) views. **C**. Left calcaneum in lateral view. **D**. Right calcaneum in lateral (D_1) and medial (D_2) views. **E**. Left astragalus in dorsal (E_1), plantar (E_2), posterior (E_3), lateral (E_4), and medial (E_5) views. **F**. Left navicular in posterior (F_1), anterior (F_2), dorsal (F_3), plantar (F_4), medial (F_5), and lateral (F_6) views. **G**. Left cuboid in dorsal (G_1), plantar (G_2), medial (G_3), and posterior (G_4) views. Abbreviations: ampt, astragalar medial plantar tuberosity; cub, cuboidal facet; dfor, dorsal astragalar foramen; ect, ectal facet; ecto, ectocuneiform facet; fah, facet for the astragalar head; fc, facet for the calcaneum; fib, fibular facet; gfhl, groove for the tendon of the flexor hallucis longus muscle; ifor, inferior astragalar foramen; lat, lateral process; mec, mesocuneiform facet; metf, metatarsal facet; nav, navicular facet; pfo, peroneal fossa; plm, tendon of the peroneous longus muscle; sm, small concavity; tg, tendinous groove; trf, fossa trochlear.

(see Lorente et al. 2014, 2019). Nevertheless, this cannot be ascertained.

Cuboid: The cuboid is well preserved. The corpus is robust and trapezoidal. The posterior surface is occupied by the facet for the calcaneum, better observed in dorsal view (Fig. 5F$_3$); it is strongly convex and mediolaterally inclined. Medially, there are two facets separated by a deep sulcus. The posterior facet is that for the navicular and the anterior facet represents the articulation for the ectocuneiform (Fig. 5F$_4$). The navicular facet is almost elliptical and larger than the ectocuneiform facet, which is dorsoplantarly elongated and seems to be formed by two lobes with a smooth concavity between them. In anterior view, the metatarsal facet is concave and teardrop-shaped (Fig. 5F$_5$). On the plantar side there is a deep sulcus running mediolaterally, which houses the tendon of the peroneous longus muscle (Szalay 1985). The posterior edge of this sulcus is formed by a robust tuberosity that occupies almost the entire plantar surface of the cuboid (Fig. 5F$_6$).

Remarks.—"*Campanorco inauguralis*" is one of the most frequent notoungulates from the Upper Lumbrera Formation (García-López and Babot 2017). Even though it was only informally reported in nomenclatural terms, it was included in several phylogenetic analyses within Notoungulata (Reguero and Castro 2004; Reguero and Prevosti 2010; Billet 2011; García-López and Powell 2011). Initially, Bond et al. (1984) considered "*C. inauguralis*" close to Mesotheriidae, based on several dental and cranial features. Later, it was grouped into Typotherioidea, along with Mesotheriidae, Hegethotheriidae, and polyphyletic Archaeohyracidae (Reguero and Castro 2004; Reguero and Prevosti 2010). In turn, postcranial remains of "*C. inauguralis*" were unknown so far, and therefore their description could contribute to assessing these proposed phylogenetic affinities.

Among basal notoungulates, the astragali of *Notostylops murinus* (MACN-A 10940) show a similar size regarding "*Campanorco inauguralis*"; nevertheless, these bones differ in the marked asymmetrical trochlea with parallel and laterally inclined crests, and a lateral process strongly projected. The basal typotherian *Colbertia lumbrerense* (PVL 6227) differs from IBIGEO-P 105 in a small-sized astragalus, an astragalar medial plantar tuberosity longitudinally extended, and a small lateral process. Additionally, *C. magellanica* (MCT 2456M; Bergqvist and Fortes Bastos 2009: fig. 2) shows a short and robust astragalar neck and more developed astragalar medial plantar tuberosity and lateral process than in "*C. inauguralis*". The calcaneum of *C. magellanica* (MCT 1263M) is also markedly different in shape and the arrangement of the articular facets (e.g., ovoid sustentacular facet, ectal facet more obliquely oriented) compared to "*C. inauguralis*".

Concerning Interatheriidae, recovered as the sister clade of Typotherioidea by Reguero and Prevosti (2010), *Notopithecus adapinus* (MPEF-PV 1113; Vera 2012: fig. 5) displays a slender and small astragalus, with a markedly asymmetrical trochlea. The calcaneum of *N. adapinus* differs from "*Campanorco inauguralis*" in the presence of a robust tuber calcis, a low inclination and development of the cuboid facet, and a small and oblique fibular facet. In addition, interatheriid calcanei from the Geste Formation (see above) present two concavities adjacent to the ectal protuberance, while there is one concavity in "*C. inauguralis*", and they have an ectal facet that is less vertical.

Finally, comparisons among the known postcranial remains for basal mesotheriids are crucial due to the aforementioned hypothesis relating this family with "*Campanorco inauguralis*". In this sense, Paleogene tarsals are known for *Trachytherus alloxus* Billet et al. 2008 and *Trachytherus ramirezi* Shockey, Billet, and Salas-Gismondi 2016, from the late Oligocene of Salla, Bolivia (Shockey et al. 2016). The astragali of these taxa (UF 172437; Shockey and Anaya 2008: fig. 7.8; and MUSM 961; Shockey et al. 2016: fig. 5) differ from "*C. inauguralis*" in the presence of a markedly asymmetrical trochlea, short neck, and small head in relation to the astragalar body. In addition, the calcaneum UF 172514 (*T. alloxus*) shows a small sustentaculum, an oblique orientation of the ectal facet, lesser development of the fibular facet, and an almost transverse cuboid facet. Furthermore, in derived mesotheriids such as *Mesotherium* Serres, 1867, the mentioned features do not show any significant modification in the observed tarsals (i.e., MACN-PV 1950, 1975, 7760) compared basal representatives of the family and, therefore, the morphology is also different from "*C. inauguralis*".

One of the most remarkable features in the calcaneum of "*Campanorco inauguralis*" is the presence of a facet for the navicular bone. This is considered by Cifelli (1993) as a "reversed alternating tarsus" condition, where the astragalus lacks its contact with the cuboid while the calcaneum articulates with the navicular bone. The calcaneal-navicular articulation was observed also in Leontiniidae, "Notohippidae", Toxodontidae, and some typotherians (e.g., *Protypotherium* and *Federicoanaya*), as well as in lagomorphs and arctostylopids (Shockey and Anaya 2008; Shockey et al. 2012; Lorente 2019). This fact, added to the differences observed with the compared mesotheriids (i.e., *Trachytherus* and *Mesotherium*), such as a reduced fibular-calcaneal contact, oblique ectal facet of the calcaneum, and the astragalus overlying the calcaneum, among others, highlight the singular condition of the proximal tarsals of "*C. inauguralis*".

Based on the comparative analysis and the combination of features exhibited by "*Campanorco inauguralis*", the proximal tarsals contain useful information for diagnostic purposes. In turn, there are no characters to support the hypothesis of phylogenetic affinities between this form and the Mesotheriidae clade, and the specimen analyzed here shows a generalized morphology within Notoungulata, considering both basal and derived taxa. This is in agreement with previous hypotheses (i.e., García-López and Powell 2011) that locate campanorcids in an unclear and basal position within Typotheria.

Stratigraphic and geographic range.—Upper Lumbrera Formation, late middle Eocene (Bartonian); El Simbolar, Salta Province, Argentina.

Morphofunctional aspects

The significance of tarsals for paleobiology stems from the fact that they are usually in direct contact with the substrate; thereby, these elements are immediately related to locomotor habits and foot postures (Carrano 1997; Davidovits 2012; Fostowicz-Frelik et al. 2018). Even though the articulation between calcaneum and astragalus is usually a relatively static joint, this assemblage works as a hinge between the tibia-fibula and the foot bones. In most mammals, the proximal tarsals articulate through a complex arrangement of contact facets. Given that, the morphology of the calcaneum and astragalus makes possible the inference of mammalian foot posture and range of posterior limb movements (Szalay and Decker 1974; Carrano 1997; Polly 2008).

The mammalian foot can assume a range of postures: plantigrady, digitigrady, and unguligrady (Carrano 1997). Both plantigrady and digitigrady are widespread conditions among basal terrestrial mammals, including several taxa among the SAnu (Shockey and Flynn 2007), whereas unguligrady is a highly specialized condition associated with several morphological changes and restricted to more derived taxa (Carrano 1997).

Biomechanically, the calcaneum is the bone where the astragalus rests, functioning together, along with other elements, as a crurotarsal lever system with reference to the foot (Carrano 1997; Davidovits 2012). In this model the calcaneum acts as a moment arm or in-lever, whereas the metatarsals represent the out-lever (see Carrano 1997: fig. 3). The functional principle of these components is that a relatively longer in-lever increases the amount of out-force produced by a given in-force. In this context, the calcaneum in Typotheria indet. and "*Campanorco inauguralis*" presents a long tuber calcis compared to total length (Tables 1, 2, Figs. 4, 5), which would be effective in an animal that requires greater power in the foot stroke, but not velocity (Carrano 1997; Bergqvist and Fortes Bastos 2009). This arrangement is common in plantigrade mammals.

Concerning the astragalus, the trochlea articulates with the tibia and moves anteroposteriorly during locomotion. Likewise, the position of the astragalus on the calcaneum sets the plane of the major axis of the tibia. The three specimens analyzed here (i.e., *Colbertia lumbrerense*, Typotheria indet., and "*Campanorco inauguralis*") show an asymmetric trochlea with crests of different sizes (the lateral one is the largest) (Fig. 6, Table 2). In this configuration, Carrano (1997) recognized that in plantigrade mammals the tibia goes through trajectories of different radii over the two crests, and that it does not move in a strictly parasagittal plane. It tends to move along the smaller radius (i.e., the narrower crest), since if it moves along the larger radius (i.e., the trochlear concavity and greater crest) it would produce dislocation on the other radius. Added to this, a shallow trochlear concavity allows mediolateral movements of the foot (also seen in the tarsals here reported; Tables 1, 2, Fig. 6A, C–E), and thus, the resulting instability is offset by the open position of the phalanges, observed in plantigrade forms (Bergqvist and Fortes Bastos 2009). In the case of a symmetric astragalar trochlea (Fig. 6B), the tibia describes an arc along the midpoint and rotates without significant mediolateral movements (Carrano 1997; Bergqvist and Fortes Bastos 2009). This latter arrangement is important given the metatarsals-phalanges setting in digitigrade mammals.

In the anterior region, the astragalar head is involved in foot rotation, which is associated with the relation among the mediolateral axis of the astragalar head, trochlear crests and metatarsal planes, and the major axis of the tibia (Fig. 6A, B). In *Colbertia lumbrerense*, Typotheria indet., and "*Campanorco inauguralis*" the mediolateral axis of the astragalar head is parallel to the plane of the trochlear crests, so that the trochlear plane draws an angle with the metatarsal plane (Fig. 6, Table 2). As a result, when the metatarsals flex and extend, they do so at an oblique (rather than perpendicular) angle with respect to the major axis of the tibia (Fig. 6A, C–E). This arrangement is common in plantigrade forms, whereas in digitigrade mammals the mediolateral

Table 2. List of tarsal features analyzed to infer the foot postures among the specimens herein reported. – not available; * approximate.

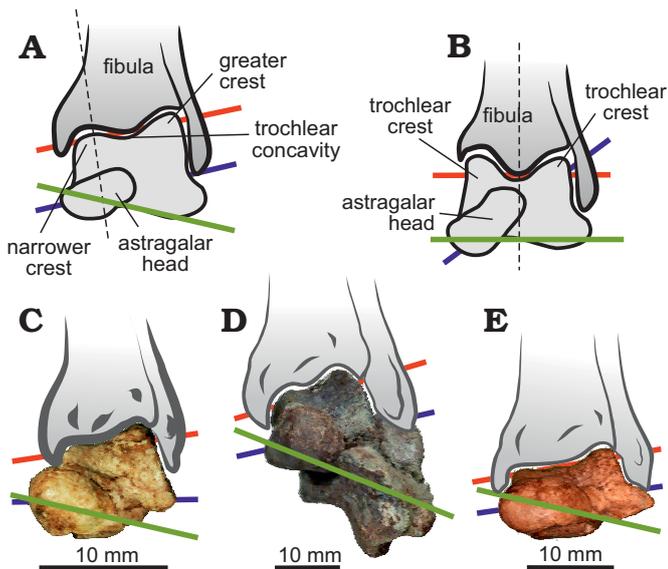| Feature	References	*Colbertia lumbrerense* (PVL 6227)	Typotheria indet. (PVL 4292)	"*Campanorco inauguralis*" (IBIGEO-P 105)
Development of tuber calcis	Carrano 1997; Bergqvist and Fortes Bastos 2009	–	long	long*
Development of the dorsal astragalar foramen	Wang 1993; Shockey and Flynn 2007	very small	present in a notch	well-developed
Development of the oblique dorsal crest	Shockey and Flynn 2007	well-developed	well-developed	well-developed
Shape of the astragalar trochlea	Carrano 1997; Table 1	0.42 (asymmetric)	0.32 (asymmetric)	0.44 (slightly asymmetric)
Astragalar trochlea concavity	Carrano 1997; Table 1	0.12 (shallow)	0.11 (shallow)	0.10 (shallow)
Orientation of the astragalar body on the calcaneum	Carrano 1997	obliquely (according to the location of the articular facets)	obliquely	obliquely*
Mediolateral axis of the astragalar head	Carrano 1997	parallel to the plane of the trochlear crests	parallel to the plane of the trochlear crests	parallel to the plane of the trochlear crests*
Mammalian foot posture inferred	this paper	plantigrade	plantigrade	plantigrade

Fig. 6. Illustration of the foot rotation in typotherian notoungulates. Schematic anterior view of the ankle of a plantigrade (**A**) and digitigrade (**B**) mammal. *Colbertia lumbrerense* PVL 6227 (**C**), Typotheria indet. PVL 4292 (**D**), and "*Campanorco inauguralis*" IBIGEO-P 105 (**E**) in anterior view. The colored lines represent the hypothetical tibia long axis (black line), mediolateral axis of the astragalar head (blue line), the plane of the trochlear crests (red line), and the hypothetical metatarsal plane (green line).

axis of the astragalar head is oblique to the trochlear crests (Fig. 6B); thereby, the trochlear and metatarsal planes are parallel. Thus, the metatarsals rotate in a plane perpendicular to that of the long axis of the tibia in digitigrades (see Carrano 1997: fig. 4).

Lastly, the presence of a dorsal astragalar foramen (frequent in plantigrade mammals) is considered as a feature that limits dorsoplantar movements (Wang 1993; Shockey and Flynn 2007; Bergqvist and Fortes Bastos 2009; for a different approach see Schaeffer 1947). The fact that this foramen is usually associated with a structure that interrupts the connection between the astragalar trochlea and the groove for the deep digital tendons supports this inference. Additionally, the development of a robust oblique dorsal crest on the astragalar neck also restricts the foot flexion and extension (mentioned as "tibial stop" sensu Shockey and Flynn 2007). All these features are present in the studied taxa.

In summary and following the aforementioned authors (i.e., Wang 1993; Carrano 1997; Shockey and Flynn 2007; Bergqvist and Fortes Bastos 2009), we infer a plantigrade foot posture for the specimens here reported (Table 2). Concerning *Colbertia lumbrerense*, our results are different from those proposed by Bond (1981), who suggests a semidigitigrade-digitigrade posture based on the presence of long and slender tibia and fibula, and a long tuber calcis observed on PVL 6218 (poorly preserved; sensu Bond 1981: 528). At this point, the new tarsal remains (PVL 6227) allow us to consider structures and features more directly related to the foot posture, many of which support a plantigrade

condition. This is in agreement with the posture inferred for *C. magellanica* (Bergqvist and Fortes Bastos 2009).

Shockey and Flynn (2007) inferred that notoungulates evolved from fully plantigrade and pentadactyl (common in the Paleocene and Eocene) to digitigrade forms (frequent in Oligocene and younger faunas). Furthermore, the foot posture was found to be related with the degree of hypsodonty along the Cenozoic, with high percentages of plantigrade and brachydont taxa in the Eocene, whereas digitigrade morphologies and hypsodont taxa are more common from the middle–late Cenozoic across much of South America. The specimens from Lower and Upper Lumbrera Formation show morphologies consistent with this scenario, supporting the previously proposed trend.

Conclusions

The proximal tarsals of notoungulates from the Lower and Upper Lumbrera formations are suitable materials for detailed taxonomic analyses. Several morphological features can be clearly distinguished in most cases and provide new anatomical data for several Eocene typotherian notoungulates.

The comparison of the tarsals of *Colbertia lumbrerense* with *Colbertia magellanica* reveals several differences, mainly on the astragalus. Most of them include variations on the development and arrangement of articular facets, and the small size of the dorsal astragalar foramen in the specimen of the Lower Lumbrera Formation. These differences between the two species of the genus *Colbertia* highlight the importance of proximal tarsals as a source of useful diagnostic traits to further characterize species.

The PVL 4292, referred to as Typotheria indet., shows morphological affinities with basal interatheriid taxa. Notwithstanding these similarities, the notable larger size of PVL 4292 compared to the overall small body sizes of Eocene interatheriids and the absence of that family so far in the highly fossiliferous levels of the Lower and Upper Lumbrera formations preclude an indisputable taxonomic assignment.

Concerning "*Campanorco inauguralis*", the tarsals exhibit a combination of unique features useful for diagnostic purposes. Our observations indicate that there is no particular morphological evidence for a close phylogenetic relationship with the Mesotheriidae clade, although it should be noted that the considered features were not included in a cladistic analysis so far. Moreover, "*C. inauguralis*" shows a "reversed alternating tarsus" condition, also observed in Leontiniidae, "Notohippidae", Toxodontidae, and some typotherians. However, the spectrum of singularities exhibited by these forms precludes, at this point, the assessment of its relationships in the context of the Paleogene radiation of Typotheria. In this sense, it is necessary to expand the comparative basis among Eocene notoungulates, so that their evolutionary significance can be fully appreciated.

On the other hand, the detailed anatomical description in

a morphofunctional context performed here allows us to infer a plantigrade foot posture for the studied specimens. These inferences could potentially be used as functional proxies for paleoecological purposes, especially informative for the study of the early radiation of these notoungulate faunas.

Acknowledgements

References

Ameghino, F. 1882. Catálogo de las colecciones de Antropología prehistórica y paleontología de Florentino Ameghino, Partido de Mercedes. *Catálogo de la Sección de la Provincia de Buenos Aires (República Argentina), Anexo* A: 35–42.

Ameghino, F. 1897. Mammifères Crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. *Boletín del Instituto Geográfico Argentino* 18: 406–429, 431–521.

Ameghino, F. 1901. Notices préliminaires sur des ongulés noveaux des terrains Crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* 16: 349–426.

Armella, M.A., García-López, D.A., Lorente, M., and Babot, M.J. 2016. Anatomical and systematic study of proximal tarsals of ungulates from the Geste Formation (Northwestern Argentina). *Ameghiniana* 53: 142–159.

Argot, C. 2004. Evolution of South American mammalian predators (Borhyaenoidea): anatomical and paleobiological implications. *Zoological Journal of the Linnean Society* 140: 487–521.

Argot, C., and Babot, M.J. 2011. Postcranial morphology, functional adaptations and palaeobiology of *Callistoe vincei*, a predaceous metatherian from the Eocene of Salta, North-western Argentina. *Palaeontology* 54: 447–480.

Babot, M.J., García-López, D.A. Deraco, V., Herrera, C.M., and del Papa, C. 2017. Mamíferos paleógenos del subtrópico de Argentina: síntesis de estudios estratigráficos, cronológicos y taxonómicos. *In*: C.M. Muruaga and P. Grosse (eds.), *Ciencias de la Tierra y Recursos Naturales del NOA. XX Congreso Geológico Argentino, Relatorio* 730–753. CGA Publisher, Tucumán.

Bergqvist, L. 1996. *Reasociaçao de pós-crânio às espécies de ungulados da Baciade S.J. Itaboraí (Paleoceno), Estado do Rio de Janeiro, e Filogenia dos "Condylarthra" e ungulados Sul-Americanos com base no pós-crânio*. 401 pp. Ph.D. Thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre.

Bergqvist, L.P. and Fortes-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., Furtado, M.R., Souza, C.P., and Powell, J.E. 2007. *Colbertia magellanica* (Bacia de Itaboraí, Brasil) × *Colbertia lumbrerense* (Grupo Salta, Argentina): a morfologia pós-craniana confrontada. *In*: I.S. Carvalho, R.C.T. Cassab, C. Schwanke, M.A. Carvalho, A.C.S. Fernandes, M.A.C. Rodrigues, M.S.S. Carvalho, M. Arai, and M.E.Q. Oliveira (eds.), *Paleontologia: Cenários de Vida*, 765–775. Editora Interciência, Rio de Janeiro.

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.

Billet, G. 2011. Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters. *Journal of Systematic Palaeontology* 9: 481–497.

Billet, G., Muizon, C. de, and Mamani Quispe, B. 2008. Late Oligocene mesotheriids (Mammalia, Notoungulata) from Salla and Lacayani (Bolivia): implications for basal mesotheriid phylogeny and distribution. *Zoological Journal of the Linnean Society* 152: 153–200.

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

Bond, M. 2016. Ungulados nativos de Sudamérica. Una corta síntesis. *Contribuciones del MACN* 6: 231–247.

Bond, M., Cerdeño, E., and López, G.M. 1995. Los ungulados nativos de América del Sur. Evolución biológica y climática de la región pampeana durante los últimos cinco millones de años. *Monografías del Museo Nacional de Ciencias Naturales* 12: 257–277.

Bond, M., Vucetich, M.G., and Pascual, R. 1984. Un nuevo Notoungulata de la Formación Lumbrera (Eoceno) de la Provincia de Salta, Argentina. *I Jornadas Argentinas de Paleontología de Vertebrados, Actas* 20: 1–20.

Candela, A.M. and Picasso, M.B. 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): Indicators of locomotor behavior in Miocene porcupines. *Journal of Morphology* 269: 552–593.

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.

Carrillo, J.D. and Asher, R.J. 2017. An exceptionally well-preserved skeleton of *Thomashuxleya externa* (Mammalia, Notoungulata), from the Eocene of Patagonia, Argentina. *Palaeontologia Electronica* 20: 1–33.

Cerdeño, E. and Vera, B. 2010. *Mendozahippus fierensis*, gen. et sp. nov., new Notohippidae (Notoungulata) from the late Oligocene of Mendoza (Argentina). *Journal of Vertebrate Paleontology* 30: 1805–1817.

Cerdeño, E., Vera, B., Schmidt, G.I., Pujos, F., and Quispe, B.M. 2012. An almost complete skeleton of a new Mesotheriidae (Notoungulata) from the Late Miocene of Casira, Bolivia. *Journal of Systematic Palaeontology* 10: 341–360.

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. *Mammal Phylogeny* 2: 195–216.

Croft, D.A., Flynn, J.J., and Wyss, A.R. 2008. The Tinguiririca fauna of Chile and the early stages of "modernization" of South American mammal faunas. *Arquivos do Museu Nacional* 66: 191–211.

Davidovits, P. 2012. *Physics in Biology and Medicine*. 343 pp. Cambridge Academic Press, Cambridge.

del Papa, C.E., Kirschbaum, A., Powell, J., Brod, A., Hongn, F., and Pimentel, M. 2010. Sedimentological, geochemical and paleontological insights applied to continental omission surfaces: a new approach for reconstructing an Eocene foreland basin in NW Argentina. *Journal of South American Earth Sciences* 29: 327–345.

Elissamburu, A. and Vizcaíno, S.F. 2004. Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). *Journal of Zoology* 262: 145–159.

Fostowicz-Frelik, Ł., Li, Q., and Ni, X. 2018. Oldest ctenodactyloid tarsals from the Eocene of China and evolution of locomotor adaptations in early rodents. *BMC Evolutionary Biology* 18: 150.

García-López, D.A. 2011. Basicranial osteology of *Colbertia lumbrerense* Bond, 1981 (Mammalia: Notoungulata). *Ameghiniana* 48: 3–12.

García-López, D.A. and Babot, M.J. 2015. Notoungulate faunas of north-western Argentina: new findings of early-diverging forms from the Eocene Geste Formation. *Journal of Systematic Palaeontology* 13: 557–579.

García-López, D.A. and Babot, M.J. 2017. Adiciones al conocimiento de los "Campanorcidae" (Notoungulata, Typotheria) en el Noroeste ar-

gentino. *XX Congreso Argentino de Geología, Simposio del Paleógeno de América del Sur, Actas* 9: 15–17.

García-López, D.A. and Powell, J.E. 2009. Un nuevo Oldfieldthomasiidae (Mammalia: Notoungulata) del Paleógeno de la provincia de Salta, Argentina. *Ameghiniana* 46: 153–164.

García-López, D.A. and Powell, J.E. 2011. *Griphotherion peiranoi*, gen. et sp. nov., a new Eocene Notoungulata (Mammalia, Meridiungulata) from northwestern Argentina. *Journal of Vertebrate Paleontology* 31: 1117–1130.

Gelfo, J.N. and Lorente, M. 2010. Asociaciones de elementos postcraneales en ungulados nativos del Paleógeno. *Revista Ciencias Morfológicas* 12: 1–6.

Giannini, N.P. and García-López, D.A. 2014. Eco-morphology of mammalian fossil lineages: identifying morphotypes in a case study of endemic South American ungulates. *Journal of Mammalian Evolution* 21: 195–212.

Ginot, S., Hautier, L., Marivaux, L., and Vianey-Liaud, M. 2016. Ecomorphological analysis of the astragalo-calcaneal complex in rodents and inferences of locomotor behaviours in extinct rodent species. *PeerJ* 4: e2393.

Hernández Del Pino, S., Seoane, F.D., and Cerdeño, E. 2017. New postcranial remains of large toxodontian notoungulates from the late Oligocene of Mendoza, Argentina and their systematic implications. *Acta Palaeontologica Polonica* 62: 195–210.

Hitz, R.B., Billet, G., and Derryberry, D. 2008. New interatheres (Mammalia, Notoungulata) from the late Oligocene Salla beds of Bolivia. *Journal of Paleontology* 82: 447–469.

Hitz, R.B., Flynn, J.J., and Wyss, A.R. 2006. New basal Interatheriidae (Typotheria, Notoungulata, Mammalia) from the Paleogene of central Chile. *American Museum Novitates* 3520: 1–33.

Lorente, M. 2019. What are the most accurate categories for mammal tarsus arrangement? A review with attention to South American Notoungulata and Litopterna. *Journal of Anatomy* [published online http://doi.org/10.1111/joa.13065].

Lorente, M., Gelfo, J.N., and López, G.M. 2014. Postcranial anatomy of the early notoungulate *Allalmeia atalaensis* from the Eocene of Argentina. *Alcheringa* 38: 398–411.

Lorente, M., Gelfo, J.N., López, G.M., and Bond, M. 2013. Restos postcraneanos de *Notostylops murinus* (Mammalia: Notoungulata, Notostylopidae) del Eoceno medio de Chubut. Argentina. *Ameghiniana* 50 (4 Supplement): R21–R22.

Lorente, M., Gelfo, J.N., and López, G.M. 2019. First skeleton of the notoungulate mammal *Notostylops murinus* and palaeobiology of Eocene Notostylopidae. *Lethaia* 52: 244–259.

Matthew, W. 1909. The Carnivora and the Insectivora of the Bridger basin, middle Eocene. *Memoirs of the American Museum of Natural History* 9: 1199–1203.

Muizon, C., Cifelli, R.L., and Bergqvist, L.P. 1998. Eutherian tarsals from the early Paleocene of Bolivia. *Journal of Vertebrate Paleontology* 18: 655–663.

Paula Couto, C.1952. Fossil mammals of the beginning of the Cenozoic in Brazil: Notoungulata. *American Museum Novitates* 1568: 1–16.

Polly, P.D. 2008. Adaptive zones and the pinniped ankle: a three-dimensional quantitative analysis of carnivoran tarsal evolution. *In*: E. Sargis and M. Dagosto (eds.), *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay*, 165–194. Springer, Dordrecht.

Powell, J.E., Babot, M.J., García-López, D.A., Deraco, M.V., and Herrera, C. 2011. Eocene vertebrates of northwestern Argentina: annotated list. *In*: J.A. Salfity and R.A. Marquillas (eds.), *Cenozoic Geology of the Central Andes of Argentina*, 349–370. SCS Publisher, Salta.

Prasad, G.V.R. and Godinot, M. 1994. Eutherian tarsal bones from the Late Cretaceous of India. *Journal of Paleontology* 68: 892–902.

Price, L.I. and Paula Couto, C. 1950. Vertebrados terrestres do Eoceno na Bacia calcárea de Itaboraí, Brasil. *Segundo Congreso Panamericano de Engenharia de Minas e Geologia, Anais* 3: 149–173.

Reguero, M.A. and Castro, P.V. 2004. Un nuevo Trachytheriinae (Mammalia, Notoungulata) del Deseadense (Oligoceno tardío) de Patagonia, Argentina: implicancias en la filogenia, biogeografía y bioestratigrafía de los Mesotheriidae. *Revista Geológica de Chile* 31: 45–64.

Reguero, M.A. and Prevosti, F.J. 2010. Rodent-like notoungulates: Typotheria. Phylogeny and Systematic. *In*: R. Madden, A.A. Carlini, M.G. Vucetich, and R. Kay (eds.), *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*, 148–165. Cambridge University Press, Cambridge.

Rose, K.D., Burke De Leon, V., Missiaen, P., Rana, R.S., Sahni, A., Singh, L., and Smith, T. 2008. Early Eocene lagomorphs (Mammalia) from Western India and the early diversification of Lagomorpha. *Proceedings of the Royal Society B* 275: 1203–1208.

Roth, S. 1899. Aviso preliminar sobre mamíferos Mesozoicos encontrados en Patagonia. *Revista del Museo de La Plata* 9: 381–388.

Roth, S. 1903. Noticias preliminares sobre nuevos mamíferos fósiles del cretáceo superior y terciario inferior de la Patagonia. *Revista del Museo de La Plata* 11: 133–138.

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

Schaeffer, B. 1947. Notes on the origin and function of the artiodactyl tarsus. *American Museum Novitates* 1356: 1–24.

Serres, M. 1867. De l'ostéographie du *Mesotherium* et de ses affinitiés zoologiques. *Comptes Rendus de l'Académie des Sciences* 65: 6–7.

Shockey, B.J. and Anaya, F. 2008. Postcranial osteology of mammals from Salla, Bolivia (Late Oligocene): Form, function, and phylogenetic implications. *In*: E. Sargis and M. Dagosto (eds.), *Mammal Evolutionary Morphology: A Tribute to Frederick S. Szalay*, 135–157. Springer, Dordrecht.

Shockey, B.J. and 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., Billet, G., and Salas-Gismondi, R. 2016. A new species of *Trachytherus* (Notoungulata: Mesotheriidae) from the late Oligocene (Deseadan) of Southern Peru and the middle latitude diversification of early diverging mesotheriids. *Zootaxa* 4111: 565–583.

Shockey, B.J., Flynn, J.J., Croft, D.A., Gans, P. B., and 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.

Szalay, F.S. 1985. Rodent and lagomorph morphotype adaptations, origins, and relationships: some postcranial attributes analyzed. *In*: W.P Luckett and J.L. Hartenberger (eds.), Evolutionary Relationships among Rodents. *NATO Advanced Science Institutes Series, Series A: Life Sciences* 92: 83–132.

Szalay, F.S. 1994. *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*. 480 pp. Cambridge University Press, Cambridge.

Szalay, F.S., and Decker, R.L. 1974. Origins, evolution, and function of the tarsus in Late Cretaceous Eutheria and Paleocene primates. *Primate Locomotion* 1: 223–259.

Vera, B. 2012. Revisión del genero *Transpithecus* Ameghino, 1901 (Notoungulata, Interatheriidae) del Eoceno medio de Patagonia, Argentina. *Ameghiniana* 49: 6074.

Vera, B. 2015. Phylogenetic revision of the South American notopithecines (Mammalia, Notoungulata). *Journal of Systematic Palaeontology* 14: 461–408.

Wang, X. 1993. Transformation from plantigrady to digitigrady: Functional morphology of locomotion in *Hesperocyon* (Canidae: Carnivora). *American Museum Novitates* 3069: 1–26.

Welker, F., Collins, M.J., Thomas, J.A., Wadsley, M., Brace, S., Cappellini, E., Turvey, S.T., Reguero, M., Gelfo, J.N., Kramarz, A., Burger, J., Thomas-Oates, J., Ashford, D.A., Ashton, P.D., Rowsell, K., Porter, D.M., Kessler, B., Fischer, R., Baessmann, C., Kaspar, S., Olsen, J.V., Kiley, P., Elliott, J.A., Kelstrup, C.D., Mullin, V., Hofreiter, M., Willerslev, E., Hublain, J.J., Orlando, L., Barnes, I., and MacPhee, R.D. 2015. Ancient proteins resolve the evolutionary history of Darwin's South American ungulates. *Nature* 522: 81–84.

Zittel, K.A. von 1893. *Handbuch der Palaeontologie, Abteilung I, Palaeozoologie, Band IV, Vertebrata (Mammalia)*. 799 pp. R. Oldenbourg, Munich.

Fig. 6. Illustration of the foot rotation in typotherian notoungulates. Schematic anterior view of the ankle of a plantigrade (**A**) and digitigrade (**B**) mammals. *Colbertia lumbrerense* PVL 6227 (**C**), Typotheria indet. PVL 4292 (**D**), and "*Campanorco inauguralis*" IBIGEO-P 105 (**E**) in anterior view. The lines represent the hypothetical tibia long axis (thin black line), mediolateral axis of the astragalar head (gray line), the plane of the trochlear crests (thick black line), and the hypothetical metatarsal plane (dotted line). {Olu ten caption dla printed version}