

FIRST EXTRA-PATAGONIAN RECORD OF *ASMODEUS* AMEGHINO (NOTOUNGULATA, HOMALODOTHERIIDAE) IN THE LATE OLIGOCENE OF MENDOZA PROVINCE, ARGENTINA



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Abstract. The Order Notoungulata is a large group of endemic mammals widespread throughout the Cenozoic of South America. Among them, the Family Homalodotheriidae is one of the less abundant and diverse, and geographically more restricted. Its record ranges from early Oligocene to late Miocene, but only a few genera were described, mainly known from Patagonia. This paper deals with the first homalodotheriid remains recovered from Deseadan levels outside Patagonia. The material comes from Quebrada Fiera, a late Oligocene locality in southern Mendoza Province (Argentina), and mainly consists of postcranial elements. A comparative study led to its placement in the Patagonian genus *Asmodeus* Ameghino, but with some significant differences from *Asmodeus osborni* Ameghino. Thus a new species –*Asmodeus petrasnerus* sp. nov.– is proposed for the taxon from Mendoza. It is characterized by: calcaneum with a subtriangular navicular facet, ectal facet with concave medial border, and not projected anterodistal end; astragalus with distal facet more medially placed than in *A. osborni*, without astragalar foramen, and with astragalar groove expanded; cuboid without contact with the astragalus; Mc III with posteriorly expanded proximal facet; and Mc IV with medial facets separated to the proximal edge. The material from Mendoza provides new data on the postcranial anatomy of *Asmodeus* and allows completing the diagnosis of this genus. The record of *A. petrasnerus* sp. nov. in Quebrada Fiera increases the diversity and the geographical distribution of the genus and the family during the late Oligocene.

Key words. Systematics. Homalodotheriids. *Asmodeus*. Quebrada Fiera. Deseadan. SALMA?

Resumen. PRIMER REGISTRO EXTRAPATAGÓNICO DE *ASMODEUS* AMEGHINO (NOTOUNGULATA, HOMALODOTHERIIDAE) EN EL OLIGOCENO TARDÍO DE MENDOZA, ARGENTINA. El Orden Notoungulata es un grupo amplio de mamíferos endémicos ampliamente repartidos a lo largo del Cenozoico de América del Sur. Entre ellos, la Familia Homalodotheriidae es una de las menos abundantes y diversas, y geográficamente más restringidas. Su registro comprende desde el Oligoceno temprano al Mioceno tardío, pero se han descrito pocos géneros, principalmente de Patagonia. En este trabajo, se describen los primeros restos deseadenses de homalodoteriidos extrapatagónicos. El material procede de Quebrada Fiera, una localidad del Oligoceno tardío de la Provincia de Mendoza (Argentina), y consiste principalmente en huesos postcraneales. El estudio comparativo permite reconocerlo como el género patagónico *Asmodeus* Ameghino, pero con diferencias significativas respecto a *Asmodeus osborni* Ameghino, lo cual lleva a proponer que el taxón de Mendoza corresponde a una nueva especie *Asmodeus petrasnerus* sp. nov. Se caracteriza por: calcáneo con faceta subtriangular para el navicular, faceta ectal con borde medial cóncavo, sin proyección del extremo anterodistal; astrágalo con la cabeza articular más desplazada medialmente que en *A. osborni*, sin perforación astragalar y con surco astragalar expandido; cuboides sin contacto con el astrágalo; Mc III con la faceta proximal expandida posteriormente; y Mc IV con el surco medial entre las facetas extendido hasta el borde proximal. El material proveniente de Mendoza proporciona nueva información sobre la anatomía postcraneal de *Asmodeus* y permite completar la diagnosis genérica. La presencia de *A. petrasnerus* sp. nov. en Quebrada Fiera, aumenta la diversidad y la distribución geográfica del género y de la familia Homalodotheriidae durante el Oligoceno tardío.

Palabras clave. Sistemática. Homalodoteriidos. *Asmodeus*. Quebrada Fiera. Edad mamífero Deseadense.

SOUTH AMERICA was an island continent during most the Cenozoic. Such paleogeographical context favored the development of a highly endemic biota, especially represented by exclusive groups of mammals (Simpson, 1980; Pascual, 1986; Benedetto, 2010). Among the native ungulates, the Order Notoungulata is the most abundant and diversified, including many different Paleocene–Pleistocene families (Billet, 2011). One of the rarest and less diversified families is Homa-

lodootheriidae. This group includes a small number of genera characterized by: complete and continuous dental series; palate short and concave, anteriorly rounded; open orbits; large, quadrate nasal opening; calcaneum with large fibular facet and articulating with navicular; astragalus with projected and convex articular head, and trochlea smoothly concave; carpus and tarsus bones in alternate rows; pentadactyl manus and pes; manus robust and digitigrade; pes plantigrade; metacarpus

with characteristic distal articulation, projected in an antero-proximal concavity, and cleaved third phalanges (Ameghino, 1891; Elissamburu, 2010; Cassini *et al.*, 2012). The best known homalodotheriid genus is *Homalodotherium* Flower, 1873, from the Santacrucian South American Land Mammal Age (SALMA) (Flower, 1873; Ameghino, 1891, 1894; Scott, 1930; Patterson, 1934; Riggs, 1937; Elissamburu, 2010; Cassini *et al.*, 2012). Older representatives are *Trigonolophodon* Roth, 1903, from the early Oligocene Tinguirirican SALMA (Croft *et al.*, 2008), and *Asmodeus* Ameghino, 1895, from the late Oligocene Deseadan SALMA of Patagonia (Ameghino, 1895, 1897, 1901, 1902). The only Neogene homalodotheriid so far described is *Chasicotherium* Cabrera and Kraglievich, 1931, from the late Miocene Chasicoan SALMA (Cabrera and Kraglievich, 1931; Ringuelet, 1957). Excepting the record of *Trigonolophodon cf. elegans* Roth, 1903, in Chile (Croft *et al.*, 2008) and *Chasicotherium rothi* Cabrera and Kraglievich, 1931, in Buenos Aires Province, Argentina, all other known homalodotheriids were collected in Patagonian localities. The faunal assemblage from Quebrada Fiera (Mendoza Province) dealt with in this paper reveals a new homalodotheriid taxon in central-western Argentina during Deseadan times.

Geological setting

The locality of Quebrada Fiera is placed in southwestern Mendoza Province (Malargüe Department; Fig. 1). It was discovered during the decade of 1970, but little was published (Gorroño *et al.*, 1979; Bond and Pascual, 1983; Pascual and de la Fuente, 1993) before new fieldworks restarted in 2006. The mammal-bearing horizons are exposed along a ravine, and most fossils come from the north side ($36^{\circ} 33' 13.3''$ S; $69^{\circ} 42' 3.5''$ W; about 1406 m a.s.l.), though others have been found at the south side ($36^{\circ} 33' 26''$ S; $69^{\circ} 41' 35''$ W; 1316 m a.s.l.), in the same sedimentary level and revealing the same faunal composition (Cerdeño and Vera, 2014). The fossil beds of Quebrada Fiera are composed of white-grayish tuffs and tuffaceous paleosols and appear to represent the base of the Agua de la Piedra Formation exposed in other areas of the Malargüe Department, but a diachronic deposition has been proposed for the different outcrops (Combina and Nullo, 2008, 2011).

The faunal assemblage from Quebrada Fiera has provided a high number of notoungulates, together with other native ungulates, rodents, xenarthra, and carnivorous metatheria, as



Figure 1. Geographic location of Quebrada Fiera site, South Mendoza Province. Modified from Cerdeño (2011).

well as some remains of phorusrhacids and small birds (see Cerdeño, 2011 for a summary), and a mandibular fragment of a small lizard. Some groups have been studied in detail, such as Notohippidae (Cerdeño and Vera, 2010, 2014), Archaeohyracidae (Cerdeño *et al.*, 2010), Hegetotheriidae (Cerdeño and Reguero, in press), Leontiniidae and metatherian taxa (Forasiepi *et al.*, 2014). Preliminary data on toxodontids and homalodotheriids were recently presented (Hernández Del Pino *et al.*, 2013), but other groups are pending full description such as interatheres, xenarthra, pyrotheres and rodents (Pujos *et al.*, 2008; Cerdeño, 2011). This fauna reveals an interesting composition, because it shares some taxa with higher latitude faunas (Patagonia), other taxa with lower latitude faunas (Bolivia), and at the same time it contains several endemic taxa (presently one notohippid, one hegetotherid and one carnivorous metatheria).

MATERIAL AND METHODS

The studied material consists of 29 isolated postcranial elements and one tooth fragment coming from Deseadan beds of Quebrada Fiera. Specimens are temporarily stored at Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Centro Científico Tecnológico CONICET-Mendoza, although their final repository is the Museo de Ciencias Naturales y Antropológicas “J. C. Moyano”

(MCNAM) in Mendoza city. We also tentatively include a badly preserved juvenile cranial fragment belonging to the Vertebrate Paleontology collection of the Museo de La Plata (MLP).

A comparative study was carried out by direct observation of Oligocene and Miocene remains of different homalodotheriid taxa: *Asmodeus*, *Homalodotherium* and *Chasicotherium*. The comparative material belongs to the Ameghino Collection within the Vertebrate Paleontology Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-A), Buenos Aires, and the Vertebrate Paleontology Collection of the Museo de La Plata (MLP). In addition, we used photographs of specimens curated at the American Museum of Natural History (AMNH), New York, and the Field Museum of Natural History (FMNH), Chicago.

Anatomical description mainly follows Scott (1930), Riggs (1937) and Elissamburu (2010). Linear measurements were taken with a digital caliper and are expressed in millimeters. For metrical and descriptive purposes, the orientation of bones follows Cerdeño *et al.* (2012), considering six faces for each element: proximal, distal, anterior, posterior, medial and lateral, being the anterior to the head of the animal, medial to the sagittal plane and lateral to the external side of the body. Limb bones are considered in a unique vertical axis independently from the actual anatomical position.

Anatomical abbreviations. **Ant**, anterior; **APD**, anteroposterior diameter; **cub**, cuboid; **dia**, diaphysis; **DP**, upper deciduous tooth; **epi**, epiphysis; **ext**, external; **fac**, facet; **h**, head; **int**, internal; **M**, upper molar; **Mc/Mt**, metacarpal/metatarsal; **P**, upper premolar; **PDD**, proximodistal diameter; **post**, posterior; **prox**, proximal; **TD**, transversal diameter.

SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903

Suborder TOXODONTIA Owen, 1853

Family HOMALODOTHERIIDAE Huxley, 1870

Genus *Asmodeus* Ameghino, 1895

Type species. *Asmodeus osborni* Ameghino, 1895.

***Asmodeus petrasnerus* sp. nov.**

Figures 2–6

Derivation of name. From Greek words *petra* (stone, piedra

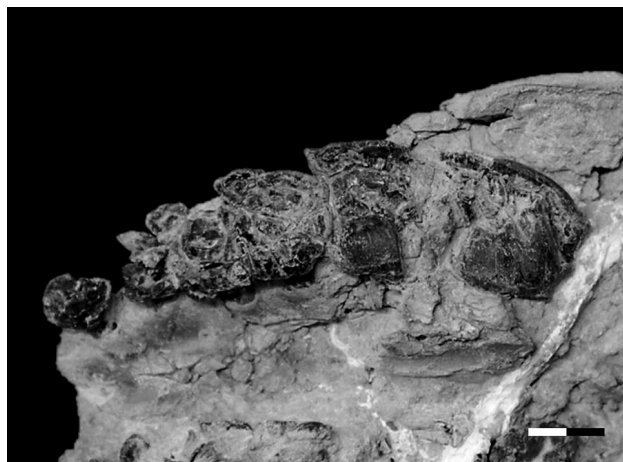


Figure 2. *Asmodeus petrasnerus* sp. nov., MLP 96-XI-20-1, occlusal view of fragment of juvenile skull tentatively assigned. Scale bar= 1 cm.

in Spanish) and *nero* (referred to water, agua in Spanish) in reference to the fossiliferous sediments of the Agua de la Piedra Formation.

Diagnosis. Calcaneum with mediodistal facet for the navicular as *A. osborni*, but subtriangular in outline; ectal facet with concave medial border as *A. osborni* and different from *Homalodotherium*; anterodistal end and distal facet little projected in contrast with *A. osborni* and *Homalodotherium*; astragalus with articular head very convex and more medially placed than in *A. osborni*, separated by a wider neck from the corpus; astragal groove expanded as in *A. osborni*; absence of astragal foramen as in *Homalodotherium*; cuboid relatively wider than in *Homalodotherium* and without contact with the astragalus; Mc III with proximal facet more extended posteriorly than in *Homalodotherium*, crescent-shaped and at an acute angle with lateral facets; Mc IV with the groove between medial facets extended to the proximal edge in contrast with *Homalodotherium*.

Holotype. MCNAM-PV 4101, incomplete right calcaneum.

Referred material. MCNAM-PV 3927, right pisiform; MCNAM-PV 3888, MCNAM-PV 4111, MCNAM-PV 4236 and MCNAM-PV 4483, right unciforms; MCNAM-PV 4348, distal fragment of right astragalus; MCNAM-PV 4481, proximal fragment of right astragalus; MCNAM-PV 3906, MCNAM-PV 4101 and MCNAM-PV 4289, fragments of right calcanei; MCNAM-PV 4119 and MCNAM-PV 4382, right cuboids; MCNAM-PV 3923 and MCNAM-PV 4091, proximal fragments of Mc III; MCNAM-PV 3869, left Mc IV; MCNAM-PV 4118, proximal fragment of right

Mc IV; MCNAM-PV 3870, left Mc V; MCNAM-PV 3878, proximal fragment of left Mc V; MCNAM-PV 4102, proximal fragment of right Mc V; MCNAM-PV 4212, distal epiphysis of Mc V; MCNAM-PV 4316, distal fragment of metapodial; MCNAM-PV 3880, MCNAM-PV 3881, MCNAM-PV 3882, MCNAM-PV 4270 and MCNAM-PV 4313, first phalanges; MCNAM-PV 3883, second phalanx; MCNAM-PV 4105 and MCNAM-PV 4340, incomplete third phalanges. We add tentatively the juvenile cranial fragment MLP 96-XI-20-1.

Geographic and stratigraphic occurrence. Quebrada Fiera, Malargüe Department, Mendoza Province, central-western Argentina, late Oligocene, Deseadan SALMA.

Description

Dentition. As expressed before, the poor preservation and the juvenile condition of specimen MLP 96-XI-20-1 (Fig. 2) prevent an appropriate comparison and we assign it tentatively to the homalodotheriid taxon. MLP 96-XI-20-1 is a very crushed juvenile cranial fragment preserving some parts of the zygomatic arches, basicranium, and jugal series; a remnant of the narrow sagittal crest is also observable. Only a few dental features can be described. Preserved left cheek teeth are the incomplete P1, DP2, DP3, DP4, M1 and M2 erupting; from the right series, only the M2 is observable. The P1 has a strong lingual cingulum, a wide anterior fossa, and part of the occlusal face worn. Its ectoloph is incomplete. Both right and left DP2 are very badly preserved. The broken left DP3 presents a central fossa. The better preserved DP4 (length 26.3 mm; width 23.9 mm) also bears a central fossa, and a smooth paracone fold on the ectoloph; no lingual or labial cingula are present. The M1 has smooth parastyle and paracone fold and separated from each other by a wide sulcus. The lingual cingulum of M1 is barely a basal rugosity, similar to that on M2. The latter shows a posteriorly convex ectoloph and the presence of a crochet. Approximate length of the ectoloph is 35.4 mm in M1 and 38.1 mm in M2.

This specimen was preliminarily labeled as Leontiniidae together with other remains from Quebrada Fiera in the MLP collection. However, some features such as the convexity of the ectoloph, the lingual junction of protoloph and metaloph in molars (better observed on left M2), which is higher in homalodotheriids than in leontiniids, and the less distally expanded protocone bring MLP 96-XI-20-1 closer to the former

group. These features are observed for instance in the isolated molar FMNH P 14711 from La Flecha, Santa Cruz, labeled as *A. osborni* (B. Vera's original photograph), although some variation exists (e.g., skull MLP 82-V-6-1 of *A. osborni* from El Pajarito, Chubut). In addition, the juvenile mandible MLP 96-XI-20-3 from Quebrada Fiera recognized as a leontiniid shows a similar ontogenetic stage, bearing the deciduous dentition together with erupting m1 and m2, but it is larger and relatively longer (the p1–dp2–4–m2 series, 163 mm long versus P1–DP2–4–M2, 125 mm long), which would also support the separation of the juvenile skull from the leontiniid of Quebrada Fiera. Anyway, we acknowledge that observed characters on MLP 96-XI-20-1 are not fully conclusive, and its assignment to *Asmodeus petrasnerus* sp. nov. is tentative.

Pisiform. This is a subrectangular, robust bone (Fig. 3.1; Tab. 1). The anterior face bears an articulation composed of two subfacets; the antero-proximal one is smaller and concave in the ulna; the anterodistal subfacet is convex and articulates with the pyramidal. As a whole, the articulation is triangular. The posterior face has a large tuberosity occupying a third of the bone.

Unciform. This is a large and robust bone (Fig. 3.2–3; Tab. 1). Two facets along the distal face form a continuous surface, both are concave and differentiated by a slight depression; the lateral one articulates with Mc V and the medial one with Mc IV. The latter facet joins that of Mc III, which is mediolaterally placed. This facet, in turn, is composed of two subcircular subfacets; this feature differs from that of specimen MACN A-8618 of *Homalodotherium segoviae* Ameghino, 1891, in which the facet is triangular. Proximally placed on the medial face of the unciform is the articular facet for the magnum, which can be either separated by a small depression (MCNAM-PV 3888) from the MC III facet or forming a continuous surface with it (MCNAM-PV 4483), in a way similar to specimen MACN A-5989 of *Homalodotherium crassum* Ameghino, 1894. The proximal articulation for the semilunate is flattened or slightly concave, and continues proximo-laterally into the pyramidal facet. The latter is concave, strongly inclined and extended postero-distally. Its border does not reach the distal facet for the Mc V as it happens in specimen MACN A-3142 of *Homalodotherium cunninghami* Flower, 1873.

Astragalus. The throclea is slightly concave (Fig. 4.1–2; Tab. 1), with smooth medial and lateral borders, the latter

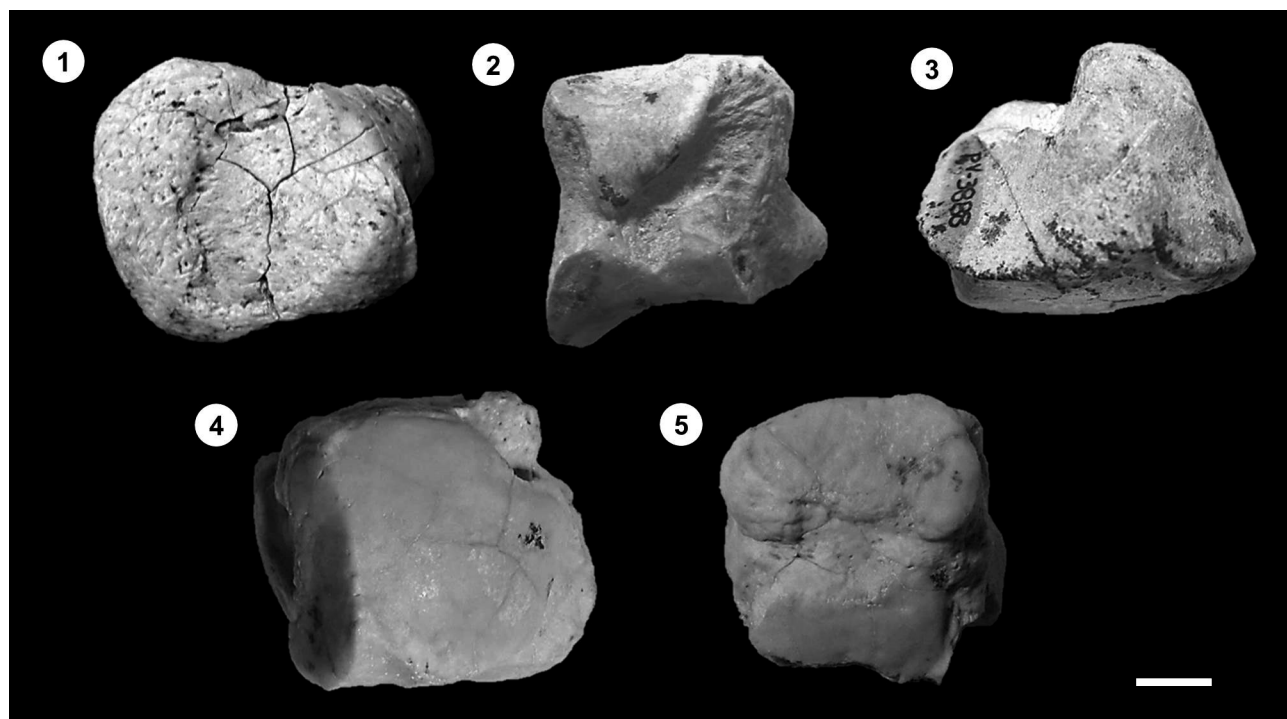


Figure 3. *Asmodeus petrasnerus* sp. nov. **1**, MCNAM-PV 3927, right pisiform, medial view; **2–3**, MCNAM-PV 3888, right unciform, medial and proximal views; **4–5**, MCNAM-PV 4382, left cuboid, proximomedial and medial views. Scale bar= 1 cm.

TABLE 1 – Dimensions (mm) of the carpal and tarsal bones of *Asmodeus petrasnerus* sp. nov. from Quebrada Fiera.

<i>Pisiform</i>						
MCNAM-PV	APD	TD post.	TD ant.	TD fac.	PDD	
3927	44	19	26	24	39	
<i>Unciform</i>						
MCNAM-PV	APD		TD		PDD	
3888	37		46		41	
4236	>32		>45		42	
4483	34.7		46.1		44.2	
<i>Astragalus</i>						
MCNAM-PV	TD distal	TD prox.	TD throcleaint.	TD throcleaext.	TD h.	APD h.
4348	49	58	38	46	>26	>24
4381			48			
<i>Calcaneum</i>						
MCNAM-PV	APD	TD lateral fac.*	PDD lateral fac.*	TD cub. fac.	APD fac. cub	
4101	68	45	36	30	34	
3906	71	(43)		>29	36	
<i>Cuboid</i>						
MCNAM-PV	APD		TD		PDD	
4382	38		45		37	
4119	41		>40		39	

*Measurement of lateral fibular and ectal facets together.

continuing into the lateral facet for the fibula. The astragalar head is separated from the trochlea by a wide and deep groove, and is mediolaterally placed; the articulation for the navicular is very convex and posteriorly projected. The posterior face shows two subrectangular facets for the calcaneum, the lateral

one slightly concave and the medial one slightly convex; they are separated from each other by a wide astragalar groove, as in *Asmodeus osborni* (Fig. 4.3–4), and in contrast with *Homalotherium*, where this groove is narrower and both facets can even merge as in specimen MLP 67-VIII-15-1. On the other

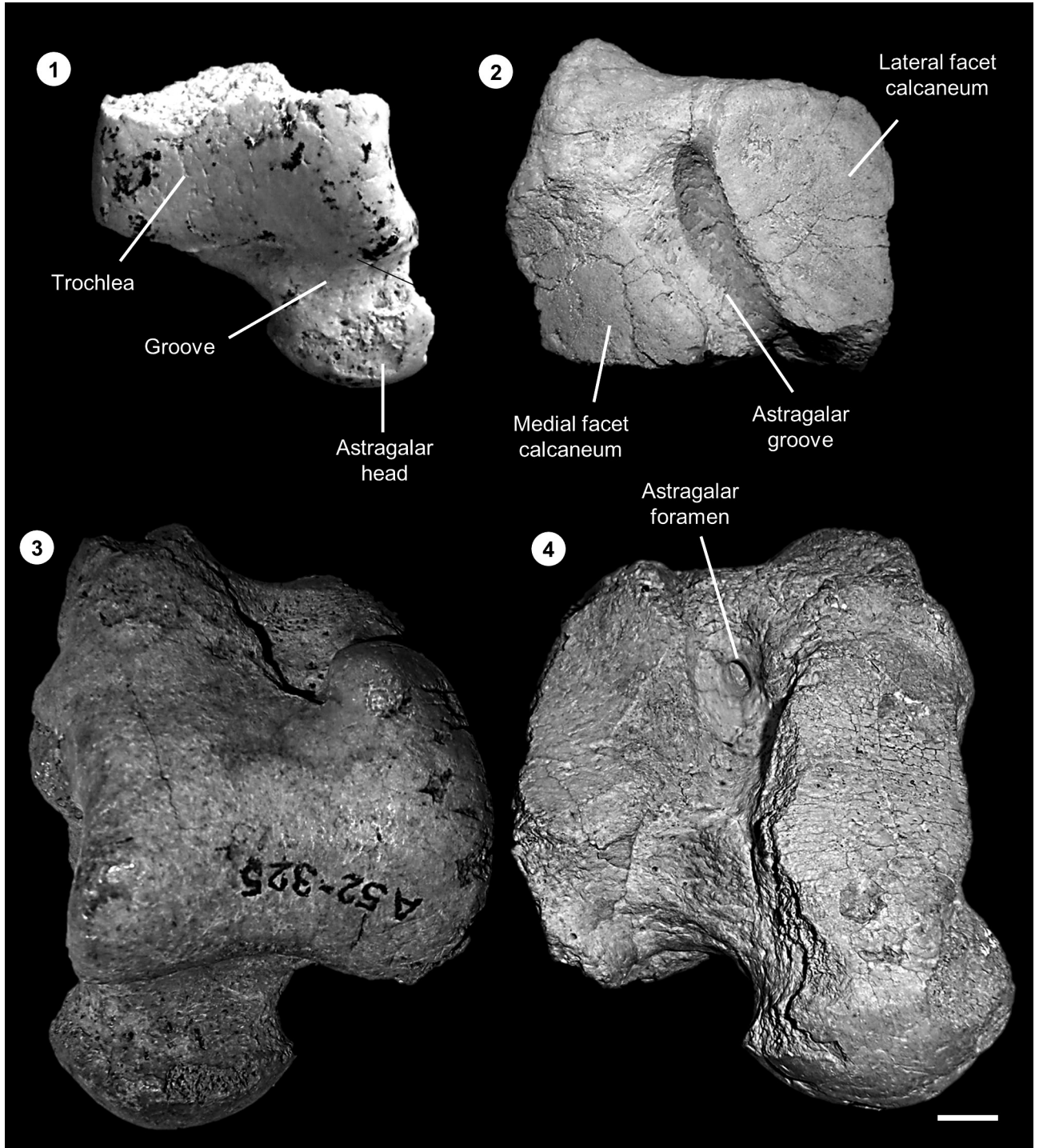


Figure 4. 1–2, *Asmodeus petrasnerus* sp. nov. 1, MCNAM-PV 4381, distal fragment of right astragalus, anterior view; 2, MCNAM-PV 4348, proximal fragment of right astragalus, posterior view. 3–4, *Asmodeus osborni*, MACN A 52-325, left astragalus, anterior and posterior views. Scale bar= 1 cm.

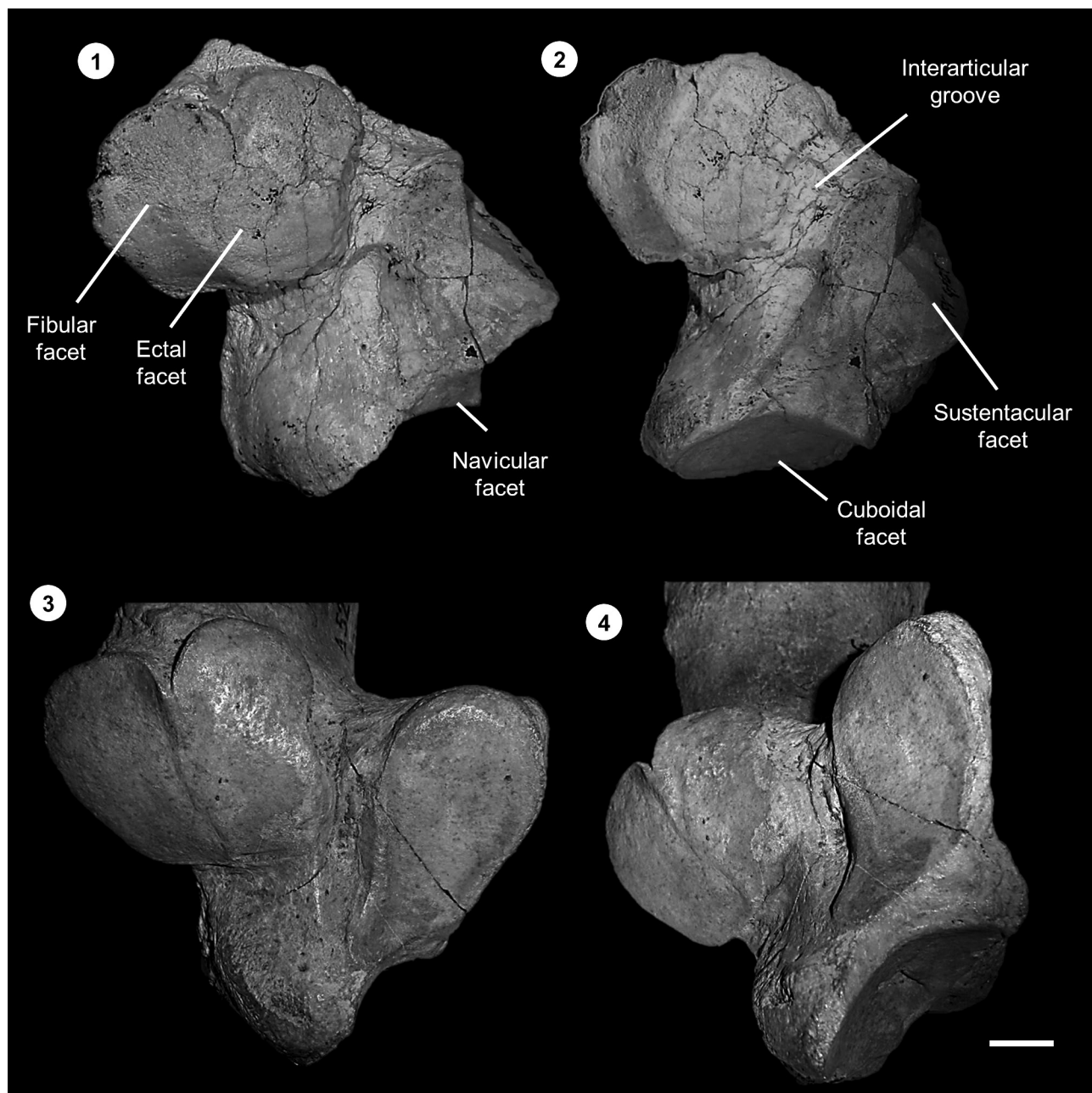


Figure 5. 1–2, *Asmodeus petrasnerus* sp. nov., MCNAM PV 4101 (holotype), right calcaneum, anteromedial and mediolateral views. 3–4, *Asmodeus osborni*, detail of MACN-A 52-326 (holotype), right calcaneum, anteromedial and mediolateral views. Scale bar= 1 cm.

hand, the astragalar foramen described by Ameghino (1897, 1902) for Patagonian *Asmodeus* is not observed in MCNAM-PV 4481.

Calcaneum. It is a large, robust bone with a great anterior development of the articular area (Fig. 5.1–2; Tab. 1). Fibular and ectal facets are in a continuous surface, limited by a smooth crest between them and a V-shaped notch at the same level. The fibular facet has its lateral border strongly convex and the surface is slightly convex. The ectal facet is also con-

vex but its medial border is concave. This morphology agrees with *Asmodeus osborni* (Fig. 5.3–4) and differs from *Homalodotherium*, whose medial border is straight or slightly convex. Both facets are subequal in size as in *Asmodeus* and differing from *Homalodotherium*. The sustentacular facet is large, slightly concave, and separated from the ectal facet by a wide and deep interarticular groove. The distal face bears the subcircular, concave facet for the cuboid, with a small posterior projection, less developed than in the compared speci-

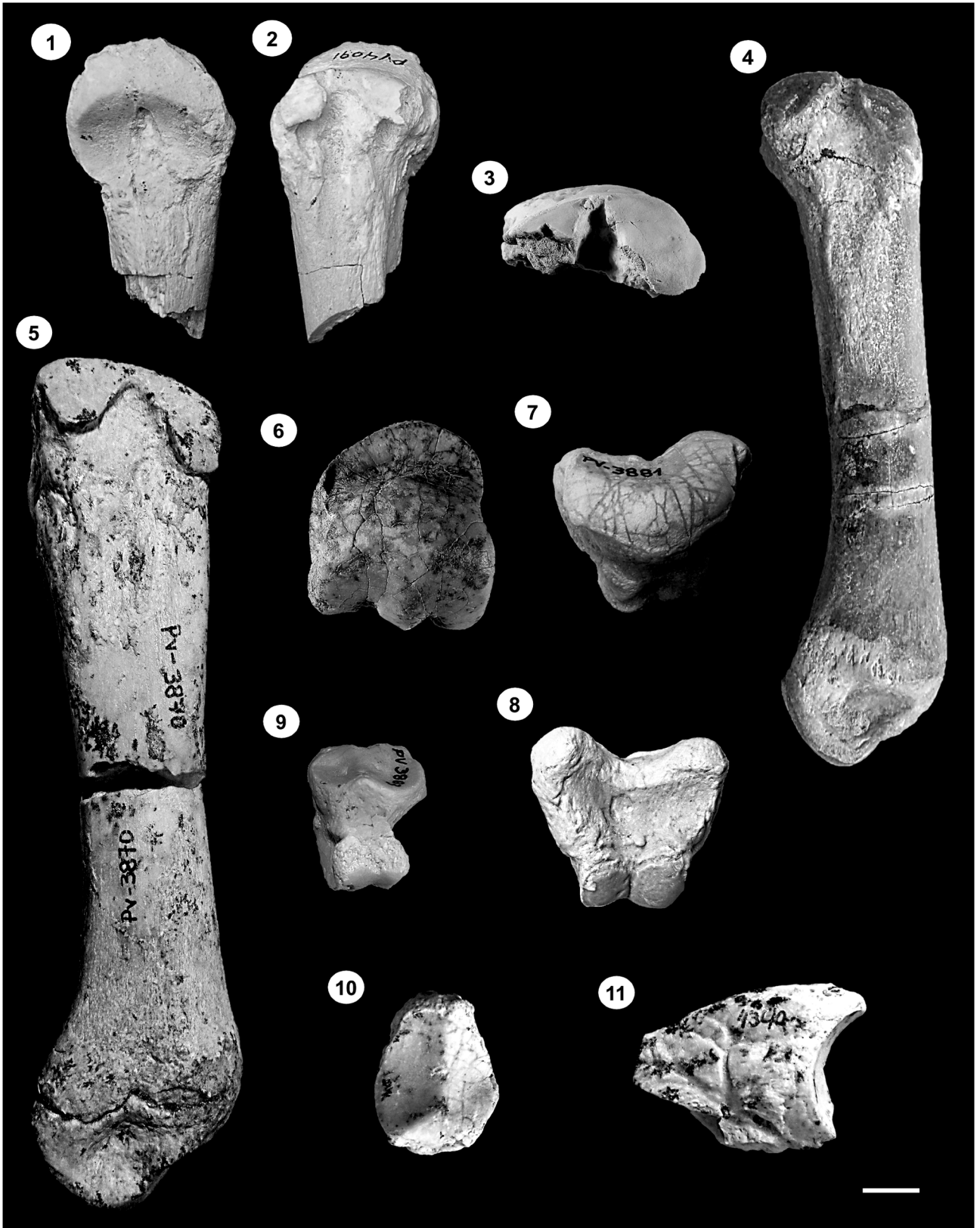


Figure 6. *Asmodeus pretrasnerus* sp. nov., 1–2, MCNAM-PV 4091, proximal fragment of right Mc III, lateral and medial views; 3, MCNAM-PV 4118, proximal epiphysis of right Mc IV, medial view; 4, MCNAM-PV 3869, left Mc IV, medial view; 5, MCNAM-PV 3870, left Mc V, medial view; 6, MCNAM-PV 4212, distal epiphysis of Mc V, distal view; 7–8, MCNAM-PV 3881, first phalanx, anterior and posterior views; 9, MCNAM-PV 3883, second phalanx, anteroproximal view; 10–11, MCNAM-PV 4340, third phalanx, proximal and lateral views. Scale bar = 1 cm.

mens of *A. osborni*. Anteromedially, between the cuboidal and sustentacular facets, there is a small, subtriangular, concave facet that would articulate with the navicular. This facet is observed in *A. osborni*, but with different size and inclination, and is lacking in *Homalodotherium*.

Cuboid. The proximal face is mostly occupied by the calcaneum facet; this is subcircular, with a posterolateral notch, convex and inclined laterally (Fig. 3.4–5; Tab. 1). The medial face bears two facets, a slightly concave one for the navicular, forming a smooth crest with the proximal facet and showing two small notches on its distal border; the second medial facet articulates with the ectocuneiform; it is convex, smaller and distally placed. Both facets are separated by a wide and shallow groove. On the distal face, two concave facets constitute a continuous surface with a smooth depression between them; the lateral one is subcircular and articulates with Mt V whereas the smaller, subtriangular medial one is for Mt IV. There is no articulation for the astragalus, in contrast with that observed in specimens of *Homalodotherium* (Scott, 1930; Elissamburu, 2010).

Mc III. The proximal face is occupied by the articular facet for the magnum, which is anteroposteriorly convex and slightly concave transversely, highly elevated laterally (Fig. 6.1–2; Tab. 2). This facet forms an acute crest with the proximo-lateral

facet for the unciform, the latter being fusiform, different from the subtriangular homologous facet in *Homalodotherium*. Below this facet, laterally placed and at a very acute angle, there are two facets for Mc IV, which are united at their proximal end and well-separated distally. The medial face of Mc III shows two convex facets for the Mc II; they are also in contact at their proximal end and well-separated distally. The diaphysis at the breakage level is rounded.

Mc IV. This bone (Fig. 6.3–4; Tab. 2) proximally articulates with the unciform by an anteroposteriorly convex and transversely concave facet. The medial face show two convex facets, well-separated from each other, and joined to the proximal facet forming acute crests. In *Homalodotherium* the two facets are joined at their proximal end. On the lateral face of Mc IV, two facets for Mc V are widely separated from each other by a shallow groove. The distal epiphysis shows the articulation for the first phalanx with two different areas: the anterior one concave and anteriorly projected and the other constituted by the distal trochlea, strongly convex, with a posterior keel. This distal morphology is typical of Homalodotheriidae. The section of the diaphysis is medially rounded.

Mc V. This is the most robust metacarpal in homalodotheriids (Fig. 6.5–6; Tab. 2). The proximal epiphysis presents a

TABLE 2 – Dimensions (mm) of metacarpal bones of *Asmodeus petrasnerus* sp. nov. from Quebrada Fiera.

<i>Mc III</i>							
MCNAM-PV		APD prox. epi.	TD prox. epi.	APD diaphysis	TD diaphysis		
4091		34	28	20	19		
3923		35	27	21	20		
<i>Mc IV</i>							
MCNAM-PV	PDD	APD prox. epi.	TD prox. epi.	APD distal epi.	TD distal epi.	APD dia.	TD dia.
3869	122	33	29	33	30	21	19
4118		36	30				
<i>Mc V</i>							
MCNAM-PV	PDD	APD prox. epi.	TD prox. epi.	APD distal epi.	TD distal epi.	APD dia.	TD dia.
4102		28	>23			19	21
3878		40	34			22	25
3870	>157	37	34	42	36	25	22
4212				43.5	39.4	24.8*	25.9*

*Measured at bone fracture level, more distally than MCNAM-PV 3870.

subtriangular outline due to the continuity of lateral and anterior faces. The articulation for the unciform occupies the whole proximal face; it is antero-posteriorly convex and transversely concave. The medial face shows two Mc IV facets proximally joined; the anterior one projects anteriorly forming a crest that continues with the proximal facet; this morphology differs from that observed in the specimens of *Homalodotherium*, where the proximal facet does not project anteromedially. The distal epiphysis and the diaphysis section are comparable to those of Mc IV.

First phalanx. It is short and robust (Fig. 6.7–8; Tab. 3). Proximally, it has a concave articular surface that expands anteriorly, becoming strongly convex, accordingly to the distal morphology of metacarpals, which allows the identification of anterior phalanges. The proximal face presents two differently developed tuberosities, with a median notch. The convex, subrectangular distal facets form a continuous surface with a median groove. One of these facets is more developed, corresponding to the less developed proximal tuberosity, indicating the direction of the body weight.

Second phalanx. It is smaller than the first one (Fig. 6.9; Tab. 3). The proximal face is occupied by two subcircular, concave facets with a smooth median crest between them. The distal face also bears two facets in a continuous, convex surface, with a slight median groove.

Third phalanx. It is longer and more robust than the other phalanges (Fig. 6.10–11; Tab. 3). Proximally, there are two narrow, elongate and strongly concave facets, limited by a smooth crest between them. Posterior to them, there is a small, subtriangular facet that would articulate with a sesamoid bone. The anterior face is distally curved and shows a longitudinal groove in its medial zone.

DISCUSSION AND CONCLUSIONS

Unciform, cuboid, Mc III, Mc IV, Mc V and second phalanx are not known for *Asmodeus osborni* and the comparison of these bones was focused on *Homalodotherium*, establishing some differences with this genus (e.g., distal facet in the unciform, absence of astragalar facet in the cuboid, and morphology and position of articular facets in metacarpals). On the other hand, the morphology of the calcaneum and astragalus renders evident the greater similarity of the studied material with *A. osborni* than with *Homalodotherium*. This leads us to identify the homalodotheriid from Quebrada Fiera as belonging to the genus *Asmodeus*. This is mainly due to: (1) calcaneum: ectal facet with concave medial border, fibular and ectal facets subequal, and presence of navicular facet; (2) astragalus: astragalar groove greatly expanded proximally.

Asmodeus osborni is different from our material by the navicular facet in the calcaneum (Fig. 5) and the astragalar

TABLE 3 – Dimensions (mm) of phalanxes of *Asmodeus petrasnerus* sp. nov. from Quebrada Fiera.

First phalanx					
MCNAM-PV	PDD	APD prox.	APD distal	TD prox.	TD distal
4313	41	30.5	28.5	39	23
3881	38	30.5	18	41	22
3880	38	>28	18.5	39	24
3882	35	28	16.5	32	20
4270	34	22.5	14	34	20
Second phalanx					
MCNAM-PV	PDD	APD prox.	APD distal	TD prox.	TD distal
3883	28	19.2	17.5	23	15
Third phalanx					
MCNAM-PV	PDD	APD prox.	APD distal	TD prox.	TD distal
4340	>41	32	>13	27	20
4105	>33	28.5	18	23	17

foramen (Fig. 4). The navicular facet not only differs in size but also in its orientation on the bone, which supports its interpretation as a diagnostic character. As to the astragalar foramen, Ameghino (1897, 1902) interpreted its presence or absence as a genus-level diagnostic feature differentiating *Asmodeus* from *Homalodotherium*. Although Shockey and Flynn (2007) stated that the Santacrucian homalodotheriid retains this foramen, our observations indicate that it is absent (e.g., MACN-A-3138, MLP 55-XII-13-230, MLP 59-XII-14-10, MLP 12-104) or vestigial when present (e.g., MACN-A-3205, MACN-A-8614, MLP 58-IX-3-3), and very different from the large foramen in *Asmodeus osborni* (MACN-A 52-205). Despite the similarity concerning this feature, the taxon from Quebrada Fiera clearly differs from *Homalodotherium* by its metacarpals, unciform, cuboid and calcaneum (see description). Accepting that the specimens from Quebrada Fiera to belong to *Asmodeus*, the absence of an astragalar foramen appears as a variation within this genus.

The lack of astragalar foramen has been interpreted as a derived condition in many Deseadan native ungulates compared with Paleocene and Eocene taxa, in which the presence of this foramen is related to a full plantigrade foot stance (Shockey and Flynn, 2007, and references therein); a plantigrade condition has been established for *Homalodotherium* (Elissamburu, 2010, and references therein). Shockey and Flynn (2007) highlighted the absence of the astragalar foramen among the native ungulates from Salla (Bolivia), whereas it is well developed in the Patagonian *Asmodeus* and vestigial in the astrapothere *Parastrapotherium* Ameghino, 1895. The absence of an astragalar foramen in *A. pretasnerus* sp. nov. could thus be interpreted as a more derived condition of this species with respect to *A. osborni*.

Even though the comparable material is still very scarce, the combination of both mentioned characters supports the recognition of a species of *Asmodeus* different from the Patagonian *A. osborni*. The record of *Asmodeus petrasnerus* sp. nov. in Quebrada Fiera increases the diversity and geographic distribution of both the genus *Asmodeus* and the Family Homalodotheriidae, as this is the first extra-Patagonian locality with Deseadan homalodotheriid remains. The description of postcranial elements so far unknown for *A. osborni* also increases the anatomical knowledge of *Asmodeus* and allows establishing new differences with respect to the better known *Homalodotherium*.

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