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Macraucheniidae and Proterotheriidae (Mammalia, Litopterna) from Quebrada Fiera (Late Oligocene), Mendoza Province, Argentina

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ABSTRACT. In this contribution we present new specimens of Litopterna recovered during the last decade in Quebrada Fiera (Mendoza Province, Argentina), whose fossiliferous sediments, currently recognized as the base of Agua de la Piedra Formation, are assignable to Late Oligocene (Deseadan South American Land Mammal Age). Two remains mentioned in the first publication on this locality were neither detailed nor described, and they have not been located in the corresponding repository. The new material consists of postcranial fragmentary remains (astragali, calcaneum, and metapodials) of Macraucheniidae (Cramaucheniinae) and an incomplete upper molar (M3) of Proterotheriidae (Proterotheriinae). These few remains of litopterns contrast with the abundance of notoungulates at Quebrada Fiera. A comparative study was carried out with material from Patagonia (Argentina) and taxa recorded in Bolivia and Peru for the same temporal interval. The specimens of Cramaucheniinae are assigned to *Coniopternium andinum* and the molar of Proterotheriinae to cf. *Lambdaconus suinus*. This contribution allows us to extend the geographical range of *Coniopternium*, filling the gap between the Patagonian and lower latitude localities (Bolivia and Peru) in which this genus was found. The record of *L. suinus* in Quebrada Fiera expands the geographical range of this species outside from Patagonia.

Keywords: Litopterna, Coniopternium andinum, Lambdaconus suinus, Deseadan SALMA, Mendoza.

RESUMEN. Macraucheniidae y Proterotheriidae (Mammalia, Litopterna) de Quebrada Fiera (Oligoceno tardío), Mendoza, Argentina. En este trabajo se describen nuevos ejemplares de Litopterna recuperados durante la última década en la localidad de Quebrada Fiera (Mendoza, Argentina). Los sedimentos fosilíferos, actualmente reconocidos como la base de la Formación Agua de la Piedra, son asignables al Oligoceno tardío (Edad Mamífero Deseadense). Los dos restos mencionados en la primera publicación sobre esta localidad nunca se detallaron ni describieron, y no han sido localizados en el repositorio correspondiente. El nuevo material consiste en restos poscraneanos fragmentarios (astrágalos, calcáneo y metápodos) de Macraucheniidae (Cramaucheniinae) y un molar superior incompleto (M3) de un Proterotheriidae (Proterotheriinae). Esta escasez de litopternos contrasta con la abundancia de notoungulados en Quebrada Fiera. Se realizó un estudio comparativo con materiales de la Patagonia (Argentina) y de taxones registrados en Bolivia y Perú para el mismo lapso. Los restos de Cramaucheniinae se asignan a *Coniopternium andinum* y el molar de Proterotheriinae a cf. *Lambdaconus suinus*. Esta contribución permite ampliar el rango geográfico de *Coniopternium* a un área intermedia entre las localidades patagónicas y de latitudes más bajas (Bolivia y Perú) en donde se ha registrado este género. Asimismo, se extiende la presencia de *L. suinus* fuera de Patagonia.

Palabras clave: Litopterna, Coniopternium andinum, Lambdaconus suinus, Edad Mamífero Deseadense, Mendoza.

1. Introduction

The order Litopterna comprises several families of South American Native Ungulates (SANU). It has been recorded from the Early Paleocene (Bonaparte and Morales, 1997) to the Late Pleistocene/Early Holocene in South America (Tonni, 1990; Bond, 1999; Schmidt and Ferrero, 2014), and the Eocene in West Antarctica (Gelfo *et al*., 2015). There are various Paleogene groups (*i.e.,* Amilnedwardsiidae, Anisolambdidae, Indalecidae, Notonychopidae, Protolipternidae and Sparnotheriodontidae) that are commonly included in the order, but their relationships with Adianthidae, Macraucheniidae and Proterotheriidae are not well established (Cifelli, 1993; Rose, 2006; Forasiepi *et al*., 2016).

Phylogenetic relationships of SANU with other extant mammals still remain unresolved, with two different hypotheses following recent phylogenetic analyses at a large scale in which only a few taxa of SANU are included. One hypothesis relates the genera *Thomashuxleya* Ameghino, 1901 and *Carodnia* Simpson, 1935 to Proboscidea and Sirenia, forming the clade Paenungulata within Afrotheria, whereas the genus *Protolipterna* Cifelli, 1983 is related to didolodontids and other Condylarthra, being close to the clade Eungulata (O'Leary *et al*., 2013); therefore, the three genera of SANU included in the analysis are not recovered as a clade. The second hypothesis is based on proteomic analyses and recovers the two included genera of SANU (*Macrauchenia* Owen, 1838 and *Toxodon* Owen, 1837) as a clade that is the sister taxon of Perissodactyla (Buckley, 2015; Welker *et al*., 2015). More recently, a new study using mitochondrial genome (Westbury *et al*., 2017) places *Macrauchenia patachonica* (and thus Litopterna) as the sister taxon of living Perissodactyla, in agreement with prior works based on collagen sequences obtained from proteomic analyses.

Macraucheniidae (Late Oligocene-Late Pleistocene/Early Holocene; Schmidt and Ferrero, 2014) currently comprises two subfamilies: Cramaucheniinae and Macraucheniinae (Soria, 1981; Dozo and Vera, 2010; Schmidt and Ferrero, 2014; Forasiepi *et al*., 2016), while Proterotheriidae (Late Paleocene-Late Pleistocene, Villafañe *et al*., 2006) is composed of Anisolambdinae, Megadolodinae and Proterotheriinae (Cifelli and Villarroel, 1997; Villafañe *et al*., 2006, 2012; Schmidt, 2015). Macraucheniids include medium to very large herbivores with body masses estimated about 35.3-54.6 kg for *Llullataruca shockeyi* McGrath *et al.,* 2018, 121 kg for *Theosodon gracilis* Ameghino, 1891, 250 kg for *Huayqueriana* cf. *H. cristata* (Rovereto, 1914), 400 kg for *Promacrauchenia* Ameghino, 1904, 830-1100 kg for *Macrauchenia patachonica*, and 1200 kg for *Macraucheniopsis ensenadensis* Paula Couto, 1945 (Fariña *et al*., 1998; Cassini *et al*., 2012; Vizcaíno *et al*., 2012; Forasiepi *et al*., 2016; McGrath *et al*., 2018). Other characteristics of macraucheniids are long neck and limbs, three digits, complete dentition and browser-grazer or typically browser diet (Bond, 1999; Cassini *et al*., 2012; Croft, 2016). Their nares were positioned posteriorly with very small nasal bones in macraucheniines such as *Huayqueriana*, *Macrauchenia* and *Xenorhinotherium* Cartelle and Lessa, 1988 (Schmidt and Ferrero, 2014; Forasiepi *et al*., 2016), although primitive forms (*e.g., Cramauchenia* Ameghino, 1902) present the nasal notch anteriorly placed (Dozo and Vera, 2010).

Proterotheriids comprise small to medium-sized herbivores, characterized by the reduction of lateral digits (II and IV). Their body mass ranges from ~10 kg for *Lambdaconus colombianus* (Hoffstetter and Soria, 1986) to ~395 kg for *Diplasiotherium robustum* Rovereto, 1914 (Ortiz Jaureguizar *et al*., 2003; Villafañe *et al*., 2006), though the latter seems to be overestimated. According to Soria (2001:97), the skull of *D. robustum* was around 30 cm similar to that of the macraucheniid *Theosodon*, but body mass estimations for the latter are rather smaller (*e.g.,* 125-170 kg for *T. lallemanti*, Croft, 2016). For the proterotheriids of Santacrucian SALMA, Cassini *et al*. (2012) calculated a mean body mass from ~24 kg (*Thoatherium minusculum* Ameghino, 1887) to ~82 kg (*Diadiaphorus majusculus* Ameghino, 1887). These values are lower than those calculated by Villafañe (2005), but close to those provided by Croft (2016; *e.g., T. minusculum*: 15-28 kg). Proterotheriids occupied diverse environments, from forested to semi-open areas (Bond *et al*., 2001, Ubilla *et al*., 2011). The Santacrucian *Thoatherium* exhibited a noticeable tendency towards monodactyly, due to a reduction of the lateral digits even greater than in Equinae horses. This is why proterotheriids have been usually compared with little horses (Soria, 2001; Bond *et al*., 2001).

Since 2006, new field works to Quebrada Fiera locality (Mendoza Province, central-west Argentina) have greatly increased the knowledge of its Deseadan

fauna that encompasses typical Patagonian taxa, exclusive elements and a species shared with Salla, Bolivia (Cerdeño, 2011, 2014a, b; Cerdeño and Reguero, 2015; Cerdeño and Vera, 2010, 2014, 2015, 2017; Cerdeño *et al*., 2010; Forasiepi *et al*., 2014; Hernández del Pino *et al*., 2017; Miquel and Cerdeño, 2016; Seoane and Cerdeño, 2014; Vera *et al*., 2017). In this opportunity, this contribution focuses on the Litopterna from Quebrada Fiera, a group whose presence at this locality was only referred to as Macraucheniidae indet. (Gorroño *et al*., 1979), mentioning two specimens stored at MLP (Museo de La Plata, Buenos Aires, Argentina), which have not been located at present. We include herein a full description of the new remains, their comparison with other Deseadan taxa and some biogeographical remarks.

2. Geological context

The Quebrada Fiera site is situated in the Malargüe Department, south of Mendoza Province, Argentina, at the foothill of the Andes Range (Fig. 1). The fossiliferous levels are located at around 36°33'13.3"S, 69°42'3.5"W, 1300-1406 m of altitude. The site was discovered during a geological prospection carried out by Yacimientos Petrolíferos Fiscales (YPF) in the late seventies (Gorroño *et al*., 1979). Later on, other fossil bearing levels were found at the southern side of the ravine, located at around 36°33'26"S, 69°41'35"W, 1316 m (see Cerdeño and Vera, 2014, 2017).

The geological characterization and the preliminary faunal list were published by Gorroño *et al*. (1979). The faunal assemblage was then assigned to the Late Oligocene (Deseadan SALMA) based on the presence of two typical representatives of the Deseadean fauna of Patagonia: *Pyrotherium* Ameghino, 1888 and *Proborhyaena gigantea* Ameghino, 1897 (Gorroño *et al*., 1979; Bond and Pascual, 1983; Cerdeño and Vera, 2017). New faunal data confirm the Deseadan age, but absolute dating is lacking for Quebrada Fiera.

The stratigraphic section consists of a heterogeneous conglomeradic level, followed by uniform sequences, variable in thickness, of whitish-ocher tuffaceous paleosols with concretions and whitish-gray tuffs with intercalations of pyroclastic deposits (Gorroño *et al*., 1979). These deposits are currently recognized as the base of the Agua de la Piedra Formation (Combina and Nullo, 2008, 2011; Cerdeño and Vera, 2014).

3. Material and methods

The final repository of the new material studied is the Museo de Ciencias Naturales y Antropológicas "J.C. Moyano" (**MCNAM**) in Mendoza city, Argentina. Most remains correspond to postcranial elements (fragments of metapodials, astragali and one calcaneum) and there is only one incomplete upper molar (M3). The taxonomic identification was based on morphological and metrical comparisons with other Deseadan specimens from Argentina (Patagonia) through direct observation or published data. The compared material corresponds to specimens housed in the following institutions: **ACM** (Pratt Museum, Amherst College, Amherst, USA); **AMNH** (American Museum of Natural History, New York, USA); **FMNH** (Field Museum of Natural History, Chicago, USA); **MACN-A** (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Ameghino, Buenos Aires, Argentina); **MNHN-Bol** (Departamento de Paleontología, Museo Nacional de Historia Natural, La Paz, Bolivia); **MUSM** (Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Perú); **UF** (Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA).

FIG. 1. Geographical location of Quebrada Fiera site, Mendoza Province, Argentina (modified from Cerdeño and Vera, 2017).

4. Systematic paleontology

Litopterna Ameghino, 1889
Macraucheniidae Gervais, 1855
Cramaucheniinae Ameghino, 1902
***Coniopternium* Ameghino, 1894**
Coniopternium andinum Ameghino, 1894
Fig. 2A-F, Table 1

Material. astragali: MCNAM-PV 4490, left (complete); MCNAM-PV 4489, left head fragment; MCNAM-PV 4904, right trochlea fragment; MCNAM-PV 5250 and MCNAM-PV 5251, two trochlea portions. Calcaneum: MCNAM-PV 4092, proximal fragment. Metapodials: MCNAM-PV 3859, MCNAM-PV 4256, MCNAM-PV 4264, and MCNAM-PV 4275, distal fragments.

Occurrence. Quebrada Fiera locality, Malargüe Department, Mendoza Province, Argentina. Base of the Agua de la Piedra Formation, Late Oligocene, Deseadan SALMA.

Descriptions. the astragalus MCNAM-PV 4490 (Fig. 2A) has the trochlea rather symmetric. The external crest is slightly more developed and acute than the medial one and both are parallel to the astragalar body; this is also observed in the fragment MCNAM-PV 4904 (Fig. 2B). The neck is narrower than the trochlea, short, and in dorsal view, the fossa is slightly displaced to the lateral side. The articulation with the navicular is dorsoventrally convex with a dorsolateral expansion (also observed in MCNAM-PV 4489). In ventral view (Fig. 2A), the sustentacular facet is slightly depressed and with a proximodistal enlargement. There is a little astragalar foramen at the end of the astragalar groove that separates the ectal and sustentacular facets. The other fragments of astragali (MCNAM-PV 5250 and 5251) are coincident in morphology and measurements (Table 1) with MCNAM-PV 4490.

The calcaneum MCNAM-PV 4092 (Fig. 2C) preserves a long neck, laterally compressed and dorsoventrally broad. The medial and lateral sides are slightly depressed, and its dorsal border is narrower than the ventral one. The tuber is enlarged, subtriangular, rugose, and proximally projected.

All metapodials assigned to macraucheniids are distal fragments (Figs. 2D-F), one of them badly preserved and not figured. They present a strong keel, slightly displaced from the center, which occupies the whole length of the trochlea, being more prominent on the ventral side (better observed in the most complete specimen MCNAM-PV 3859, Fig. 2D). Ventrally and above the keel, there is a median ridge on the diaphysis (Fig. 2D-F). At both sides of the trochlea as well as above its ventral border, there are depressions for ligament insertions. In MCNAM-PV 3859, MCNAM-PV 4264 and MCNAM-PV 4275 (Figs. 2D-F), the asymmetry of the trochlea is interpreted as belonging to lateral digits.

Comments and comparison. the Macraucheniidae recognized for Deseadan SALMA are *Coniopternium andinum* Ameghino, 1894 (including *Notodiaphorus crassus* Loomis, 1914; Cifelli and Soria, 1983), ?*C. primitivum* Cifelli and Soria, 1983, *Pternoconius polymorphoides* Cifelli and Soria, 1983, and *Cramauchenia normalis* Ameghino, 1902 (including *C. insolita* Ameghino, 1902; Soria, 1981).

Morphologically, the astragalus MCNAM-PV 4490 (Fig. 2A) is undifferentiated from those assigned to *Coniopternium andinum* from La Flecha, Santa Cruz Province (MACN A-11701-02; Figs. 3A, B), from Cabeza Blanca, Chubut Province (MACN A-12206 and MACN A-12207; Figs. 3E, F), and that figured by Loomis (1914, Fig. 11 as *Notodiaphorus crassus*) also from Cabeza Blanca locality. Concerning the latter, Loomis indicated a tiny facet for the cuboid that is not observed either in MCNAM-PV 4490 or the Patagonian specimens. Similarities are also evident with the Bolivian specimens UF 172424 of ?*Coniopternium* sp. from the Principle Guide Level, Unit 4, at Calaboza Pata, and UF 172426 of *Coniopternium* cf. *C. primitivum* from Unit II at Pasto Grande (Shockey, 1999; Shockey and Anaya, 2008). The very little astragalar foramen described in MCNAM-PV 4490 is also observed in MACN A-12207 (Fig. 3F) and UF 172426. In turn, according to Shockey (1999), there would be a cuboid facet in UF 172426, but practically indistinct from the sustentacular facet; in fact, the author established the contact astragalus-cuboid after the presence of a facet in the cuboid, and suggested that this contact would occur only during the loaded portion of the locomotor cycle.

In contrast, MCNAM-PV 4490 is morphologically different from the astragalus of *Cramauchenia normalis* (MACN A-12238, Fig. 3G) described by Soria (1981). In dorsal view, the specimen from Mendoza has more concave trochlea, longer neck and wider head. Even though MACN A-12238 is ventrally eroded, it shows a similar astragalar foramen, but slightly displaced dorsally with respect to MCNAM-PV 4490.

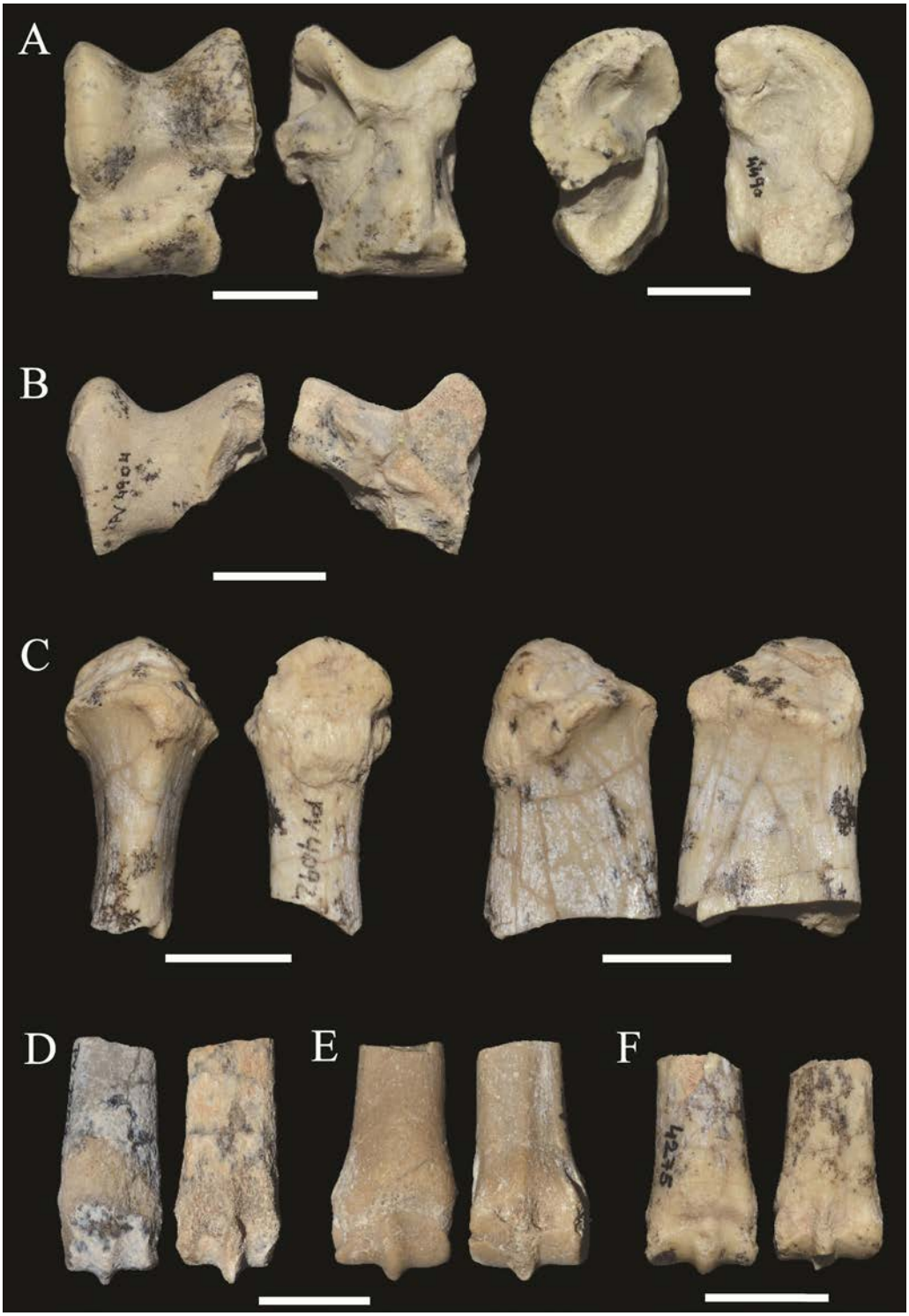

FIG. 2. *Coniopternium andinum*. **A**. MCNAM-PV 4490, left astragalus. From left to right: dorsal, ventral, lateral and medial views. **B**. MCNAM-PV 4904, right astragalus fragment. Dorsal and ventral views. **C**. MCNAM-PV 4092 proximal fragment of calcaneum. From left to right: dorsal, ventral, lateral and medial views. **D-F**. Distal fragments of metapodials in dorsal and ventral views. **D**. MCNAM-PV 3859, **E**. MCNAM-PV 4264, **F**. MCNAM-PV 4275. Scale bars: 20 mm.

TABLE 1. COMPARATIVE MEASUREMENTS (IN mm) OF POSTCRANIAL ELEMENTS OF MACRAUCHENIIDAE FROM QUEBRADA FIERA (MENDOZA PROVINCE).

Astragali	**TL**	**CD**	**HW**	**NW**
Coniopternium andinum				
MCNAM-PV 4490	47.6	33.6	29.5	25.2
MCNAM-PV 4489			26.1	
MCNAM-PV 4904		35.1		
MCNAM-PV 5250		*33.2		
MCNAM-PV 5251		*31.6		
MACN A- 11701	50.81	39.15	30.41	?
MACN A- 11702	43.39	35.2	25.86	
MACN A- 11703 (fragment)	44.17		28.21	
MACN A- 12206	50.67	39.64	30.73	
MACN A- 12207	51.32	37.6	28.05	
Notodiaphorus crassus [a]				
ACM 3287	48	38		
ACM 3275	44	35		
Coniopternium cf. *C. primitivum* [b]				
UF 172426	38.4	25.5		
cf. ?*Coniopternium* spp.[c]				
MNHN-BOL-V-005991	45.5	30.2		
MNHN-BOL-V-005986	43.1	29.8		
UF 172424	42.5	26.8		
Cramauchenia normalis				
MACN A-12238	46.4	*39.7	28.5	

Calcanei	**Tuber**	
	TD	**APD**
Coniopternium andinum		
MCNAM-PV 4092	24.74	26.95
MACN A-11700 (lectotype)	22.37	30.85
MACN A-12205	24.9	27.99
Cramauchenia normalis		
MACN A-12238	17.4	25.5

Metapodials	**Distal epiphysis**	
	TD	**APD**
Coniopternium andinum		
MCNAM-PV 3859	18.9	
MCNAM-PV 4256	21.1	*16.5
MCNAM-PV 4264	20.3	
MCNAM-PV 4275	19.1	
cf. *Coniopternium* sp.[d]		
UF 173216	19.4	
MUSM 349	18.2	

[a]Loomis (1914), [b]Shockey and Anaya (2008), [c]Shockey (1999), [d]Shockey *et al.* (2009), *approximate measurements.

APD: anteroposterior diameter; **CD**: distance between crests; **HW**: head width; **NW**: neck width; **TD**: transverse diameter; **TL**: total length.

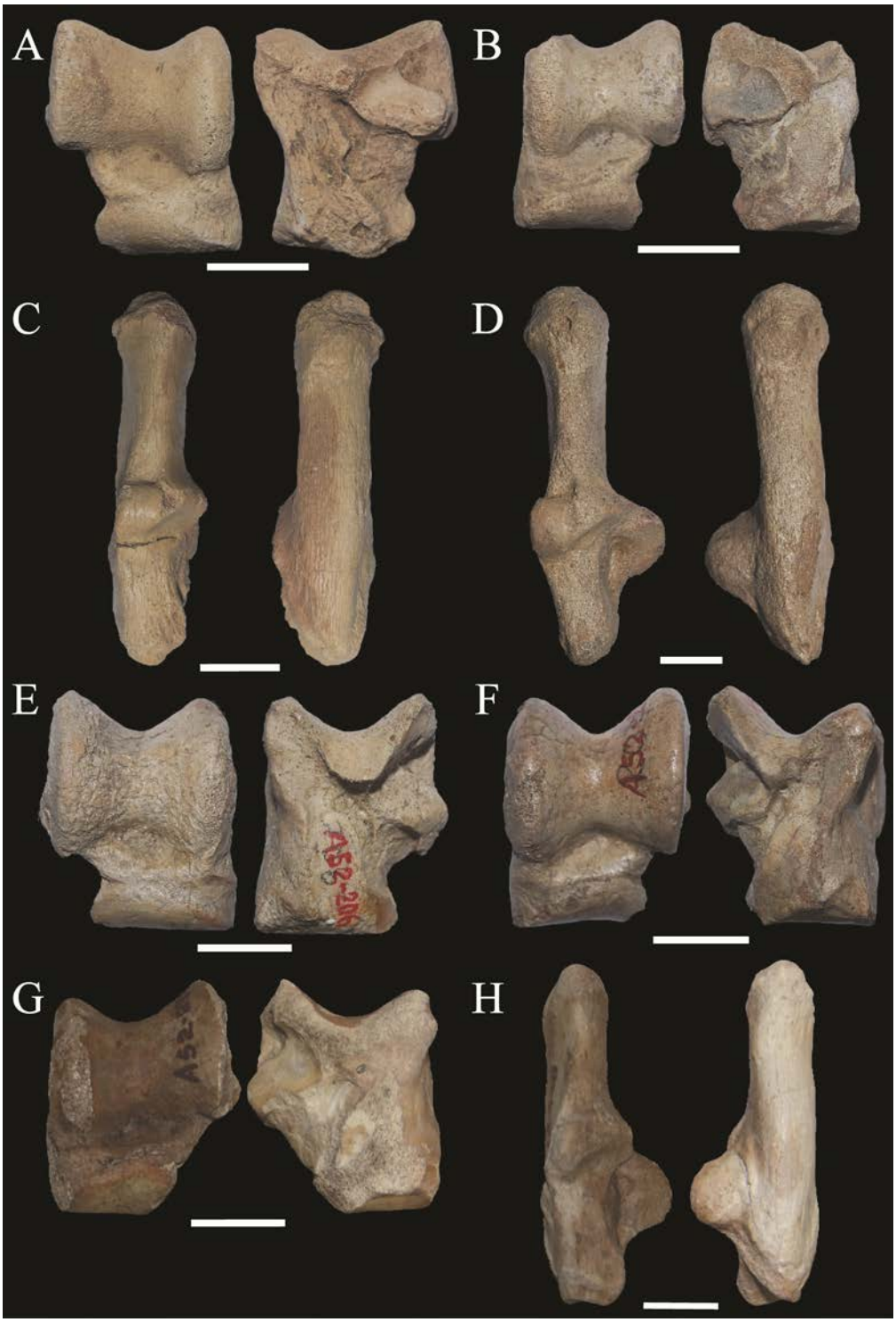

FIG. 3. *Coniopternium andinum*. **A**. MACN A-11701, right astragalus. **B**. MACN A-11702, left astragalus. **C**. MACN A-11700, right calcaneum. **D**. MACN A-12205, right calcaneum. **E**. MACN A-12206, right astragalus. **F**. MACN A-12207, left astragalus. *Cramauchenia normalis*. **G**. MACN A-12238, left astragalus, **H**. MACN A-12238, right calcaneum. All figures in dorsal and ventral views. Scale bars: 20 mm.

Concerning size (Table 1), MCNAM-PV 4490 falls within the range of both *Coniopternium andinum* and *Cramauchenia normalis*. Furthermore, all of them are larger than UF 172426 of *Coniopternium* cf. *C. primitivum*. Up to now, there is no record of postcranial remains assigned to *Pternoconius polymorphoides*, but its postcranial bones might be similar to the former species if we consider their coincidence in dental measurements (Cifelli and Soria, 1983).

On the other hand, we discard the assignment of the astragali from Quebrada Fiera to Proterotheriidae. They are clearly larger and more robust than those of proterotheriids of Salla (Bolivia), which also differ in morphology by its long and columnar neck and gracile appearance (Shockey, 1999).

The fragment of calcaneum MCNAM-PV 4092 (Fig. 2C) is morphologically and metrically very similar to those of *Coniopternium andinum* (MACN A-11700, lectotype, and MACN A-12205, Figs. 3C, D, Table 1), although the neck of MCNAM-PV 4092 is barely shorter dorsoventrally than in MACN A-11700. Besides, it is comparable to that figured by Loomis (1914) as *Notodiaphorus crassus* and UF 172426 of *Coniopternium* cf. *C. primitivum*. Instead, it is different from MACN A-12238 of *Cramauchenia normalis* (Fig. 3H) due to the greater width of the tuber in MCNAM-PV 4092.

The asymmetric trochlea of the metapodials MCNAM-PV 3859, MCNAM-PV 4264 and MCNAM-PV 4275 (Fig. 2) coincides with lateral metapodials (digits II or IV) of the specimens ACM 3275 from Cabeza Blanca (Chubut Province) assigned to *Notodiaphorus crassus* (Loomis, 1914), UF 172425 from Salla (Bolivia) assigned to ?*Coniopternium* sp. (Shockey, 1999), and MUSM 349 from Moquegua (Peru) determined as cf. *Coniopternium* sp. (Shockey *et al*., 2009). Moreover, our specimens have the keel somewhat developed dorsally, which differs from what is observed in central metapodials (digit III) (Loomis, 1914; Shockey *et al*., 2009). The presence of well-developed keels in lateral digits likely contributed to the transversal stability of the central metapodial (Shockey, 1999).

According with the previous paragraphs and agreeing with the synonymy between *C. andinum* and *N. crassus* established by Cifelli and Soria (1983), the described postcranial bones from Quebrada Fiera are identified as *Coniopternium andinum*.

Proterotheriidae Ameghino, 1887
Proterotheriinae Ameghino, 1887
***Lambdaconus* Ameghino, 1897**
cf. *Lambdaconus suinus* Ameghino, 1897
Fig. 4A

Material. MCNAM-PV 4673, incomplete left M3.

Occurrence. Quebrada Fiera locality, Malargüe Department, Mendoza Province, Argentina. Base of the Agua de la Piedra Formation, Late Oligocene, Deseadan SALMA.

Description. the only specimen from Quebrada Fiera so far assigned to Proterotheriidae is an incomplete M3 (MCNAM-PV 4673; Fig. 4A), barely worn and lacking the labial side and roots. The anteroposterior valley is shallow and sinuous; the anterolingual cingulum is strong and forms a small fossette without reaching lingually the base of the protocone. The prominent protocone is joined to a small paraconule by a ridge. The metaconule is absent and the hypocone is bunoid and very close to the postcingulum. Between the hypocone and the protocone there is a low and short crista. The anteroposterior length is 11.5 mm, and the width of the fragment is 9 mm.

Comments and comparison. During the Deseadan SALMA, the Argentinean Proterotheriidae from Patagonia (Chubut and Santa Cruz provinces; Soria, 2001; Kramarz and Bond, 2005; Villafañe *et al*., 2006) are *Lambdaconus suinus* Ameghino, 1897, *L. inaequifacies* (Ameghino, 1904), and *Protheosodon coniferus* Ameghino, 1897.

Another species of *Lambdaconus* from Patagonia is *L. lacerum* (Ameghino, 1902), but it is registered in Early Miocene Colhuehuapian and Santacrucian SALMAs (Soria, 2001; Kramarz and Bond, 2005; Villafañe *et al*., 2006). Outside Argentina, the species *L. colombianus* has been recognized in the Middle Miocene of Colombia (Laventan SALMA; Cifelli and Guerrero, 1989; Villafañe *et al*., 2006), but see comments below about its generic ascription.

The specimen studied here (MCNAM-PV 4673, Fig. 4A) presents a well-defined hypocone and lacks metaconule, two features that coincide with the M2-3 of *Lambdaconus suinus*, whereas in *L. inaequifacies* and *L. lacerum* the upper molars have metaconule (Soria, 2001). In turn, MCNAM-PV 4673 differs from *Protheosodon coniferus* in the presence of the hypocone, as it is absent in the M3 of this species (Soria, 2001).

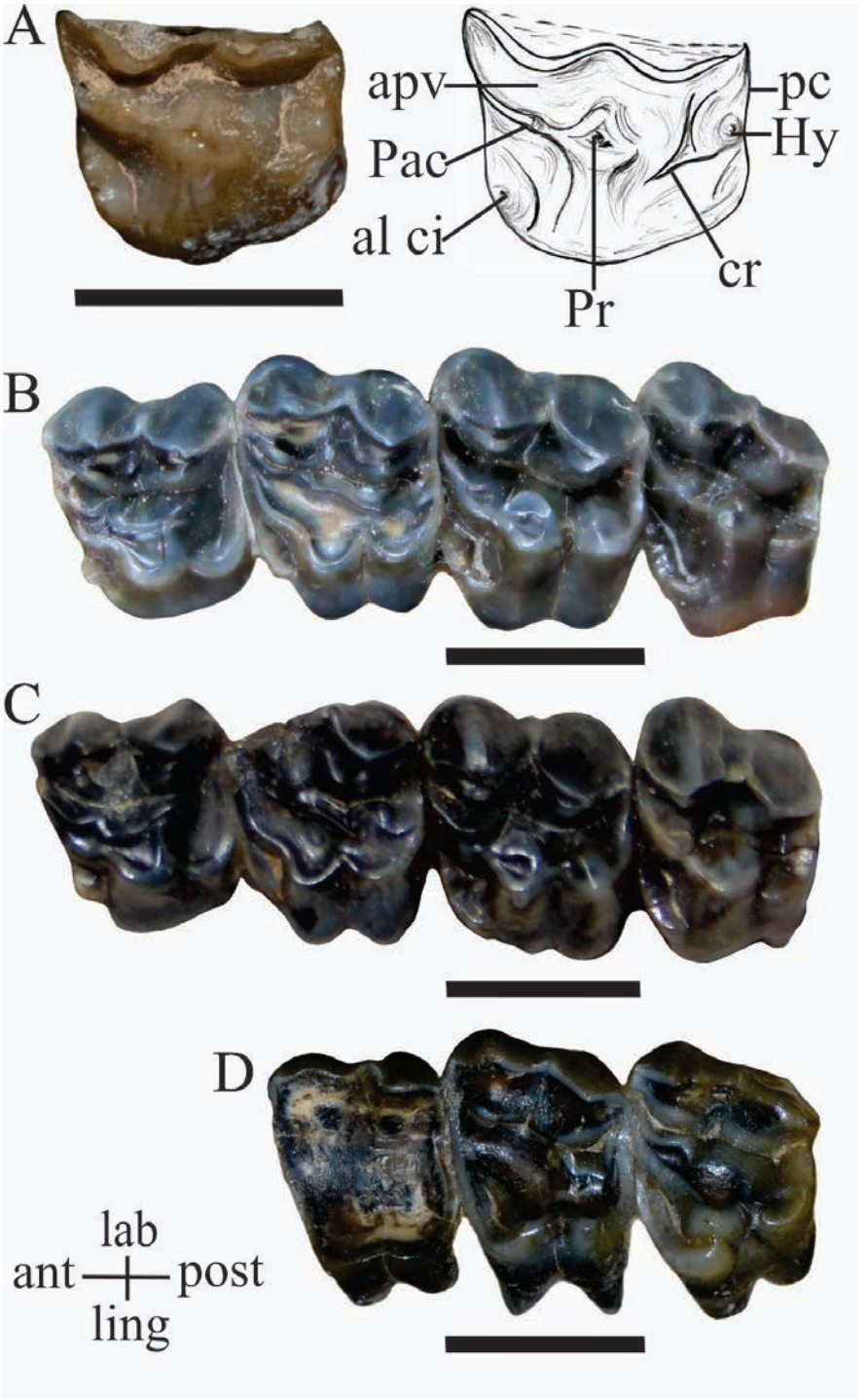

FIG. 4. cf. *Lambdaconus suinus*. **A**. MCNAM-PV 4673, incomplete left M3. Original and schematic drawing with anatomical references: **al ci**, anterolingual cingulum; **ant**, anterior; **apv**, anteroposterior valley; **cr**, crista; **Hy**, hypocone; **lab**, labial; **ling**, lingual; **Pac**, paraconule; **pc**, postcingulum; **post**, posterior; **Pr**, protocone. *Lambdaconus suinus.* **B**. MACN A-12198, partial right maxilla with P4-M3 (reversed). **C**. MACN A-12655, partial left maxilla with P4-M3. **D**. AMNH 29554, left M1-M3 (detail). Scale bars: 10 mm.

Some specimens originally included in *Deuterotherium distichum* Ameghino, 1897 were reassigned to *Lambdaconus suinus* by Soria (2001), such as MACN A-12198 (Roth, 1927, and Fig. 4B), a right maxilla with P4-M3, and MACN A-12655, a partial left maxilla with P4-M3 (figured by Ameghino, 1904, Loomis, 1914, and in Fig. 4C), both probably from La Flecha, Santa Cruz Province (Soria, 2001), and AMNH 29554, a skull badly preserved from Cabeza Blanca (Chubut Province; Simpson, 1932, and Fig. 4D). The specimen MCNAM-PV 4673 from Quebrada Fiera differs from MACN A-12198 (Fig. 4B) because the former has the anterolingual cingulum less developed and the hypocone more noticeable. Moreover, MCNAM-PV 4673 presents the hypocone more conspicuous than MACN A-12655 (Fig. 4C), and lacks the posterolingual groove. In turn, MCNAM-PV 4673 also differs from AMNH 29554 (Fig. 4D) because the latter has the hypocone more developed and joined to the postcingulum as a thick border, presents a posterolingual groove and a well-developed anterior cingulum that reaches the anterolingual base of the protocone. Despite these differences, all of them share the absence of metaconule and a shallow anteroposterior groove.

In summary, the absence of metaconule in MCNAM-PV 4673 indicates that it could belong to *Lambdaconus suinus*. Nevertheless, the scarce development of the anterior cingulum, the lack of posterolingual groove, and the position and development of the hypocone generate some doubts for an accurate taxonomic determination; therefore, we prefer to identify the molar MCNAM-PV 4673 as cf. *Lambdaconus suinus*.

Concerning *Lambdaconus colombianus* some comments are deserved. The taxon *Neodolodus colombianus* Hoffstetter and Soria, 1986 was originally described as a didolodontid condylarth, recovered from the Monkey Unit of the Villavieja Formation, near Villavieja, Huila Department, Colombia. Posteriorly, based on new dental and postcranial remains collected from Miocene levels (Laventan SALMA) of the same area, Cifelli and Guerrero (1989) reassigned the species to the genus *Prothoatherium* Ameghino, 1902, an advanced proterotheriid. More recently, Villafañe (2005; Villafañe *et al*., 2006) has referred this species to the genus *Lambdaconus*, but without further comments. The generic correspondence of this species deserves a deep revision that is beyond the scope of this work. In any case, after Cifelli and Guerrero's (1989, Fig. 2, Tab 1) data, *L. colombianus* differs from MCNAM-PV 4673 in having a conspicuous metaconule, a poorly developed hypocone on M3, and smaller size.

5. Final remarks

The presence and diversity of the Litopterna in Quebrada Fiera are scarce (Cerdeño, 2011) as it occurs in the Deseadan localities of Patagonia (Santa Cruz and Chubut provinces), Salla (Bolivia), and Moquegua (Peru). Indeed, the amount of specimens of Litopterna is really scanty compared with other native ungulates, especially notoungulates that represent around 80% of native ungulate remains from Quebrada Fiera identified at family level (Cerdeño, 2014a; see also Supplemental data).

The initial radiation of Macraucheniidae happened during Deseadan times, but it is not until Colhuehuapian or Santacrucian SALMAs that they become well known (Cifelli, 1985, and references therein). Classically, two genera of macraucheniids were known from the Deseadan of Argentina, Peru and Bolivia: *Coniopternium* (*C. andinum*, *Coniopternium* cf. *C. primitivum*, ?*Coniopternium* sp.) and *Pternoconius* (*P. polymorphoides*) (Cifelli and Soria, 1983; Shockey, 1999; Shockey and Anaya, 2008; Shockey *et al*., 2009). More recently, Dozo and Vera (2010) extended back to the Deseadan the biochron of *Cramauchenia*, originally registered in the Colhuehuapian SALMA. In the Late Oligocene context, the presence of *Coniopternium andinum* at Quebrada Fiera (Mendoza Province) extends the geographical distribution of the genus, and adds to other mammals from this locality that fill the record at an intermediate latitudinal position between higher (Patagonia, Argentina) and lower latitudes (Bolivia and Peru) (Cerdeño, 2011, 2014a,b; Cerdeño and Reguero, 2015; Cerdeño and Vera, 2010, 2014, 2015, 2017; Cerdeño *et al*., 2010; Seoane and Cerdeño, 2014; Hernández del Pino *et al*., 2017; Vera *et al*., 2017).

Regarding proterotheriids, they are represented in the Late Oligocene of Argentina by the last Anisolambdinae (*Protheosodon coniferus*) and the first record of Proterotheriinae (*Lambdaconus suinus*, *L. inaequifacies*) (Bond, 1986; Soria, 2001). The recognition of cf. *Lambdaconus suinus* in the Deseadan levels of Quebrada Fiera constitutes the first

Argentinean evidence of this genus outside Patagonia. The ascription of the Colombian *L. colombianus* to the genus *Lambdaconus* needs to be discussed in detail; if confirmed, this species would represent the temporal and geographical extension of the genus in Middle Miocene of northern South America.

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Supplemental data

List of published taxa of South American Native Ungulates from Quebrada Fiera.

Taxon	Family	Order	Source	Published specimens
Archaeohyrax suniensis	Archaeohyracidae	Notoungulata	Cerdeño *et al*., 2010	11*
cf. *Archaeotypotherium*	Archaeohyracidae	Notoungulata	Cerdeño *et al*., 2010	1
Hegetotheriopsis sulcatus	Hegetotheriidae	Notoungulata	Cerdeño and Reguero, 2015 (as *Prohegetotherium* sp.); Kramarz and Bond, 2017	2
Prohegetotherium sp.	Hegetotheriidae	Notoungulata	Cerdeño and Reguero, 2015	4
P. schiaffinoi	Hegetotheriidae	Notoungulata	Cerdeño and Reguero, 2015	23
P. malalhuense	Hegetotheriidae	Notoungulata	Cerdeño and Reguero, 2015	3
Propachyrucos cf. *P. smithwoodwardi*	Hegetotheriidae	Notoungulata	Cerdeño and Reguero, 2015	11
Argyrohyrax proavus	Interatheriidae	Notoungulata	Vera *et al.*, 2017	38
Progaleophitecus sp.	Interatheriidae	Notoungulata	Vera *et al.*, 2017	1
Trachytherus cf. *T. spegazzinianus*	Mesotheriidae	Notoungulata	Cerdeño, 2014	1
Mendozahippus fierensis	Notohippidae	Notoungulata	Cerdeño and Vera, 2010, 2014	21
Notohippidae indet.	Notohippidae	Notoungulata	Cerdeño and Vera, 2014	1
Asmodeus petrasnerus	Homalodotheriidae	Notoungulata	Seoane and Cerdeño, 2014; Hernández Del Pino *et al.*, 2017	28
Gualta cuyana	Leontiniidae	Notoungulata	Cerdeño and Vera, 2015; Hernández Del Pino *et al.*, 2017	16
Proadinotherium sp.	Toxodontidae	Notoungulata	Hernández Del Pino *et al.*, 2017	5
Toxodontidae indet.	Toxodontidae	Notoungulata	Hernández Del Pino *et al.*, 2017	1
Pyrotherium romeroi	Pyrotheriidae	Pyrotheria	Cerdeño and Vera, 2017	12
Coniopternium andinum	Macraucheniidae	Litopterna	present work	10
cf. *Lambdaconus suinus*	Proterotheriidae	Litopterna	present work	1

Note: In addition to published material, many postcranial remains from Quebrada Fiera, mostly assignable to notoungulates, are still pending a confident taxonomic determination.

* After 2010, more dental remains assignable to *A. suniensis* were collected, but they remain unpublished.