

## Quebrada Fiera (Mendoza), an important paleobiogeographic center in the South American late Oligocene

*Quebrada Fiera (Mendoza), un importante centro paleobiogeográfico en el Oligoceno tardío de América del Sur*

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### ABSTRACT

This contribution focuses on the main results and present researches on the Oligocene fauna from Quebrada Fiera (Mendoza, Argentina). This vertebrate assemblage is providing new data on the distribution and evolution of South American Deseadan (late Oligocene) mammals. Descriptions of notoungulate Notohippidae and Archaeohyracidae have been recently published. A new genus of notohippid was identified, while most archaeohyracid material was recognized as the same species present in Salla (Bolivia). Studies in progress on other native ungulates (Hegetotheriidae, Interatheriidae, Leontinidae, Homalodotheriidae, Toxodontidae, ?Protheroheriidae, and Pyrotheriidae), metatheria, xenarthra, and rodents from Quebrada Fiera will increase the knowledge of this fauna. Preliminarily, the faunal association appears as a mix of taxa. On the one hand, with Patagonian affinities, on the other hand, related to species known from lower latitudes (Bolivia), together with exclusive taxa such as *Mendozahippus* (Notohippidae). The ongoing research will allow a better understanding of the role of Mendoza area in the paleobiogeographic and biostratigraphic context of the South American Oligocene mammals.

**Key words:** Mammals, Notoungulata, Oligocene, Mendoza, Argentina

### RESUMEN

Esta contribución se centra en los principales resultados obtenidos en los últimos años sobre la fauna oligocena de Quebrada Fiera (Mendoza, Argentina) y las investigaciones en curso. La asociación faunística de Quebrada Fiera está aportando datos nuevos sobre la distribución y la evolución de los mamíferos sudamericanos de la Edad mamífero Deseadense. Recientemente, se han dado a conocer los restos de dos familias de notoungulados, Notohippidae y Archaeohyracidae. En el primer caso, se reconoció un género nuevo, mientras que los arqueohirácidos se identifican en su gran mayoría como la especie presente en Salla (Bolivia). Los estudios en curso sobre otras familias de ungulados nativos (Hegetotheriidae, Interatheriidae, Leontinidae, Homalodotheriidae, Toxodontidae, ?Protheroheriidae y Pyrotheriidae), así como de los restos de metaterios, xenartros y roedores recuperados en Quebrada Fiera, ampliarán el conocimiento detallado de esta fauna. De forma preliminar, el conjunto faunístico aparece como una mezcla de taxones; por un lado, con afinidades patagónicas y, por otro, relacionados con especies conocidas en latitudes bajas (Bolivia), al mismo tiempo que cuenta con representantes exclusivos como *Mendozahippus* (Notohippidae). El avance de las investigaciones permitirá comprender mejor el papel del área de Mendoza en las distribuciones paleobiogeográfica y bioestratigráfica de los mamíferos sudamericanos del Oligoceno tardío.

**Palabras clave:** Mamíferos, Notoungulata, Oligoceno, Mendoza, Argentina

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## Introduction

The Order Notoungulata gathers a group of herbivorous mammal families exclusive to South America. It was extremely abundant and diverse throughout the Cenozoic, being known from Paleocene to Pleistocene. Notoungulates, together with the orders Litopterna, Notopterna, Astrapotheria, and Pyrotheria, constitute the so-called South American native ungulates, all extinct and characteristic elements of the Cenozoic faunas of this subcontinent.

This chapter tries to summarize main results and researches in progress on the Quebrada Fiera site (Mendoza, Argentina), whose mammal association is providing new insights on the Oligocene South American faunas.

## Fossil mammals from Mendoza Province

As most Cenozoic South American mammals, notoungulates were firstly recognized from Argentinean remains, particularly from Patagonia. The knowledge of extra-Patagonian mammal faunas in Argentina and other South American countries has a relatively short history in the context of the Paleontology of South America. A well-known area is the Pampean region, specially referring to Pliocene and Pleistocene faunas. Patagonian and Pampean mammals allowed establishing a rather complete biostratigraphic sequence of the South American Cenozoic, which only sporadically or in the last decades has incorporated faunal associations from other areas. In this context, the mammal fauna from Men-

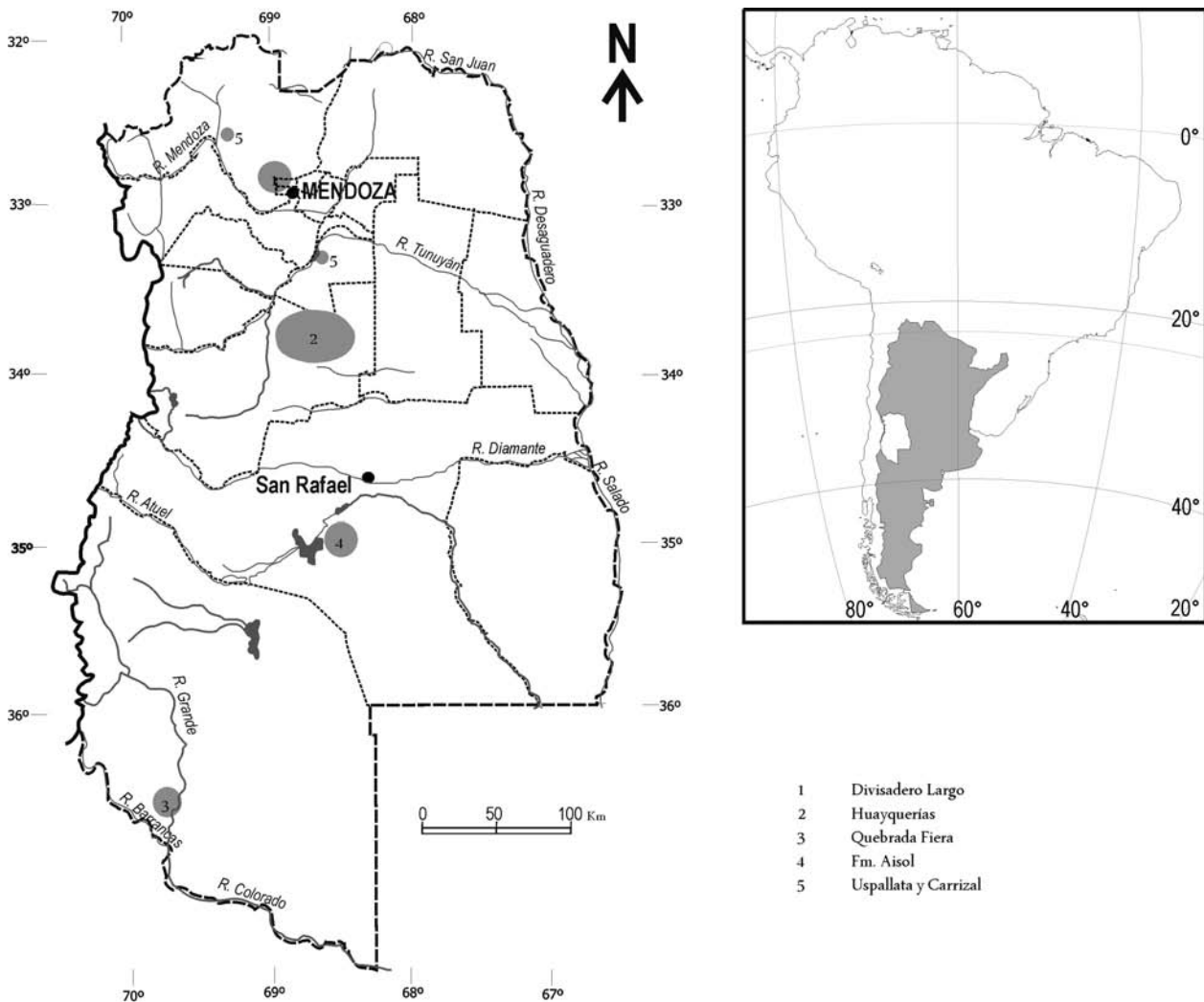


Fig. 1.— Main fossiliferous localities in Mendoza Province (Argentina).

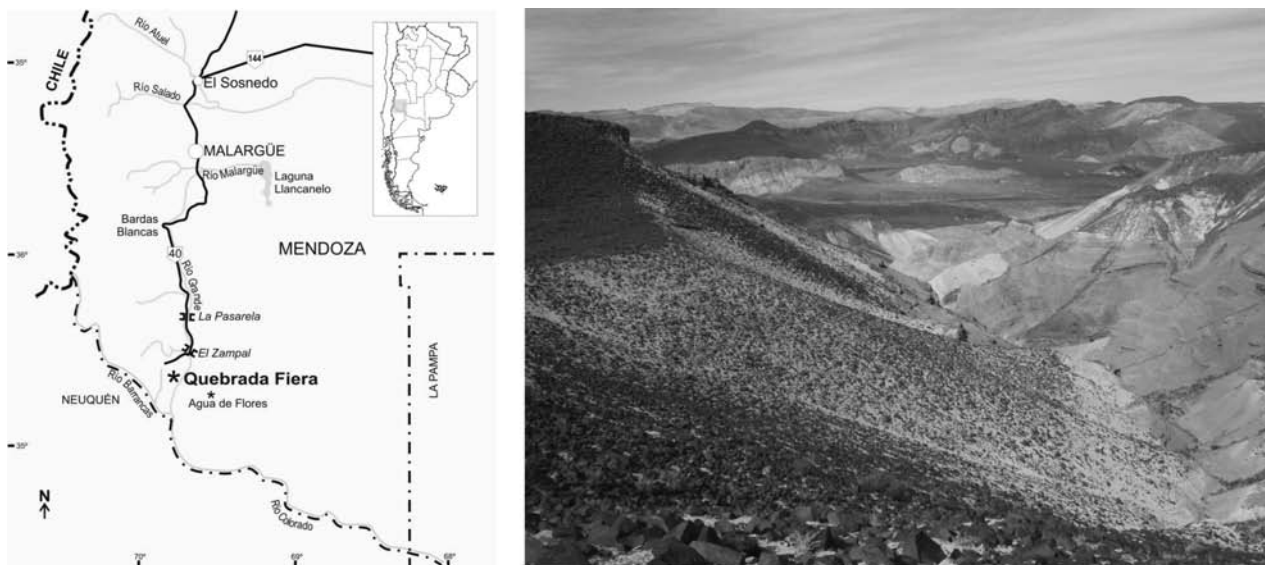


Fig. 2.— Geographical location of Quebrada Fiera site (Mendoza Province) and a general view of the fossiliferous levels.

doza Province had been scarcely studied, even though two faunal associations had given place to the definition of two mammal Ages in the mentioned biostratigraphic sequence: the Divisaderan and the Huayquerian (Pascual *et al.*, 1965).

The Divisaderan Age was defined upon the faunal association found in the Divisadero Largo area, near Mendoza city. Its faunal complex showed a mix of primitive taxa and two derived species (Simpson *et al.*, 1962), and was considered as Oligocene in age, older than the Deseadan faunas from Patagonia. Recent studies have demonstrated that the Divisaderan fauna is a mix of taxa of different origin. On the one hand, most of them come from the Divisadero Largo Formation, presently considered as Eocene (“Casamayoran” Age) (Cerdeño *et al.*, 2008; López, 2008). On the other hand, the previously supposed derived taxa would actually come from the overlying Mariño Formation (López & Manassero, 2008), assigned to early Miocene (Santacrucian Age) (Cerdeño *et al.*, 2006; Cerdeño, 2007; Cerdeño & Vucetich, 2007). Consequently, the Divisaderan Age became invalidated as it was formerly defined (Cerdeño *et al.*, 2008).

In turn, the Huayquerian Age was based on the mammal fossils recovered from the Huayquerías Formation, Huayquerías de San Carlos area, about 100 km south of Mendoza city. It is known since the beginning of the XXth century (De Carles, 1911; Frenguelli, 1930, among others), and the stratigraphy was later reviewed by Yrigoyen (1994).

However, the recognized taxa from the Huayquerías Fm. are few and scarcely represented. Nowadays, the Huayquerian fauna is better characterized in other Argentinean areas (La Pampa, Buenos Aires, Catamarca) than in the type locality.

Other areas can be added to these classical localities in Mendoza Province: 1) the Aisol Formation, near San Rafael city. New field works in this area are developed since 2007, discovering two Miocene levels with interesting mammals, including some probably new taxa (Forasiepi *et al.*, 2011); 2) Quebrada Fiera, south of Malargüe city, close to the southern border with Neuquén Province, which is the subject of the following contribution. All these areas and some isolated findings are compiled in figure 1.

### The vertebrates from Quebrada Fiera

The Quebrada Fiera site is located in an area of difficult access, in the Malargüe Department, at the southernmost end of Mendoza Province ( $36^{\circ} 33' 13.3''$  S,  $69^{\circ} 42' 3.5''$  W; 1406 m altitude; figure 2). The site was discovered during geological prospection carried out by Yacimientos Petrolíferos Fiscales (YPF) in the seventies. Gorroño *et al.* (1979) detailed some stratigraphic and tectosedimentary characteristics of this area and the preliminary studies on the recovered fauna assigned it to the Deseadan mammal Age, late Oligocene. The

faunal list presented at that time included a phorusrhacid bird and several mammals, including *Pyrotherium* Ameghino, 1888, a classic representative of the Patagonian Deseadan Age. Later, Pascual & de la Fuente (1993) added some taxa to the original faunal list, but only the carnivorous marsupial *Proborhyaena gigantea* Ameghino, 1897, another typical Deseadan element, was described in detail (Bond & Pascual, 1983).

From a geological point of view, the basal outcrops in Quebrada Fiera correspond to the Malargüe group, involving Loncoche and Roca formations (Campanian and Maastrichtian ages), followed by the Pircala-Coihueco Formation (Combina & Nullo, 2002). This is overlain by the so-called “Rodados Lustrosos” level, formed by clastic conglomerates in a silty matrix, considered as the stratigraphic evidence of the Pehuenche orogenic phase (Combina & Nullo, 2005). Above these conglomerates, 37 m of white-grayish tuffs and tobaceous paleosols, with laminated or massive parallel stratification constitute the fossiliferous level of Quebrada Fiera (figure 2). These are presently recognized as the base of the Agua de la Piedra Formation, which also outcrops in other areas of the Malargüe Department and seems to represent diachronic phases from southern to northern areas (Combina & Nullo, 2008). New sedimentological and stratigraphic studies are in progress (Pujos *et al.*, in preparation). No geochronological dating has been available in Quebrada Fiera, but its age is assumed to be older than 19 Ma, which is the dating obtained for the overlying Palaoco Basalt (Combina & Nullo, 2011).

New research projects (CONICET-PIP 5132 and PIP 1723) have focused on the Cretaceous-Tertiary outcrops in the south of Mendoza, and new field studies are developed in the Quebrada Fiera site since 2006 (Prámparo *et al.*, 2006; Cerdeño & Vera, 2007). The new recovered material has allowed increasing the known taxa. It includes small birds, new carnivorous marsupials (*Pharsophorus* Ameghino, 1897, and a small and rare metatherian), xenarthrans (Pujos *et al.*, 2008), and mainly native ungulates. All new specimens are stored in the Museo de Ciencias Naturales y Antropológicas “J. C. Moyano” of Mendoza (MCNAM-PV, vertebrate paleontology collection).

The notoungulates from Quebrada Fiera are notably enlarging the faunal association so far known and the Oligocene South American mammal landscape. At present, only two groups have been

studied in detail, the Notohippidae (Cerdeño & Vera, 2010) and the Archaeohyracidae (Cerdeño *et al.*, 2010).

The **Notohippidae** are middle to large-sized notoungulates of the Suborder Toxodontia, with brachydont, complete dentition, not enlarged canines, and ectolophodont molars. They have been usually differentiated into two subfamilies, Rhynchippinae and Notohippinae, but they do not constitute phylogenetically well-defined clades (Cifelli, 1993; Croft *et al.*, 2008a; Cerdeño & Vera, 2010), and the family results paraphyletic. The record of the group encompasses from Eocene to early Miocene.

The notohippid remains from Quebrada Fiera include a rather complete skull with two associated metatarsals, two palatal fragments of a same individual, and some isolated molars (figure 3A-B). These specimens have allowed the recognition of a new taxon, *Mendozahippus fierensis* Cerdeño & Vera, 2010. It shares several characters with the species of the genus *Rhynchippus* Ameghino, 1895 from Patagonia (Marani & Dozo, 2008) and Bolivia (Shockey, 1997), but presents other features that separates it from other known notohippids: closed dentition; incisors and canines subequal in size and morphology; rather parallel tooth rows, M3 with short metaloph and projecting protocone; and well-developed sagittal crest (see Cerdeño & Vera, 2010 for complete diagnosis and comparison). Within notohippids, *Mendozahippus* appears as a basal taxon to the other genera, as well as to toxodontids. The last field season carried out in Quebrada Fiera (November 2010) has provided new associated dental and postcranial notohippid remains, which would allow a better characterization of this notoungulate, particularly concerning its postcranial skeleton.

The **Archaeohyracidae** from Quebrada Fiera are known by maxillary and mandibular fragments (figure 3C-D) and isolated teeth. There are numerous isolated postcranial elements that match in size, but the absence of previous data on the skeleton of this group prevents a reliable assignation.

Archaeohyracids are small, rodent-like, hypsodont tyotherian notoungulates from the South American Paleogene (Croft *et al.*, 2003; Reguero *et al.*, 2003). They mainly diversified during late Eocene-early Oligocene, and are lastly recorded from the Deseadan Age (late Oligocene) of Bolivia, Argentina, and Uruguay. Phylogenetic analyses show this group as paraphyletic (Croft *et al.*, 2003;

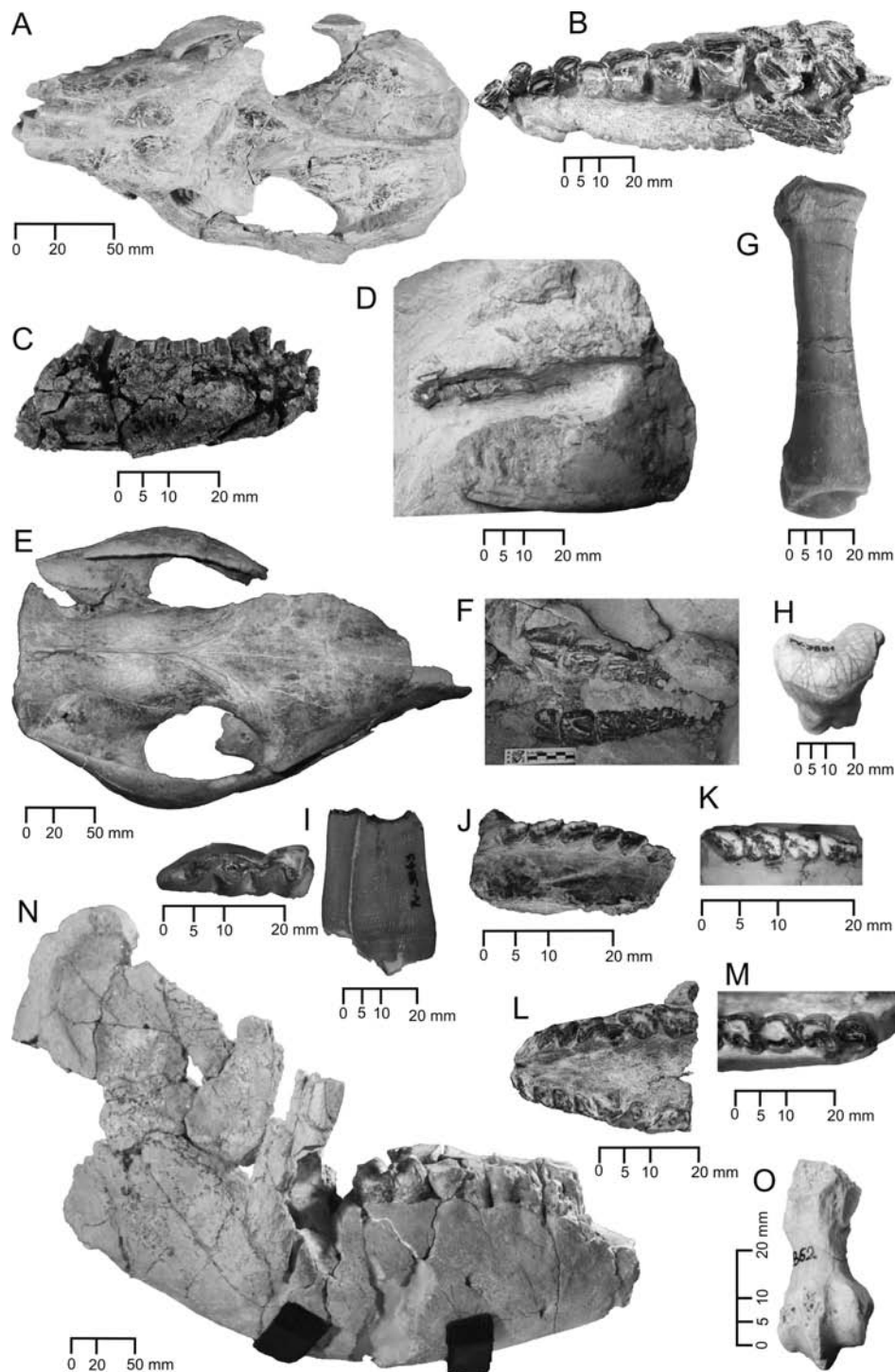


Fig. 3.— Mammal remains from Quebrada Fiera, Mendoza, Argentina. *Mendozahippus fierensis* (Notohippidae): A, MCNAM-PV 4004, skull, dorsal view; B, MCNAM-PV 3846, palatal fragment with left I1-M2, occlusal view. *Archaeohyrax suniensis* (Archaeohyracidae): C, MCNAM-PV 3844, right mandible with i1-m3, labial view; D, MCNAM-PV 3849, right cranial and mandibular fragments as they were found within a nodule. *Scarrittia* sp. (Leontinidae): E, MCNAM-PV 4003, skull, dorsal view; F, tooth series of the skull as they were found in the field, occlusal view. *Asmodeus*? (Homalodotheriidae): G, MCNAM-PV 3869, left Mc IV, anterior view; H, MCNAM-PV 3881, first phalanx, antero-proximal view. *Proadinothereum* sp. (Toxodontidae): I, MCNAM-PV 3843, right m3, occlusal and labial views. Hegetotheriidae: Hegetotheriinae, J, MCNAM-PV 3848, right P2-M3; Pachyrukhinae, K, MCNAM-PV 4189, left P4-M3, occlusal view. Interatheriidae: L, MCNAM-PV 3968, palatal fragment with deciduous dentition; M, MCNAM-PV 4055, right m2-m3. Pyrotherium (Pyrotheriidae): N, MCNAM-PV 4073, mandible, labial view. Megalonychidae?: O, MCNAM-PV 3862, left ?Mc II.

Reguero & Prevosti, 2010) or polyphyletic (Billet *et al.*, 2009).

The archaeohyracid material from Quebrada Fiera is relatively abundant and it has been mostly recognized as *Archaeohyrax suniensis* Billet *et al.*, 2009 (Cerdeño *et al.*, 2010). This species was extremely well represented and the only recognized archaeohyracid at Salla, Bolivia (Billet *et al.*, 2009), a well-dated Deseadan site between 27 and 25.8 Ma (Kay *et al.*, 1998). Both Salla and Quebrada Fiera remains have permitted the characterization of different ontogenetic stages that show the tooth morphological variation with wear. Together with *A. suniensis*, Cerdeño *et al.* (2010) recognized a second archaeohyracid at Quebrada Fiera, only represented by a lower premolar (p2). This tooth clearly differs from the other remains by its larger size, less hypsodonty, presence of roots, and open W-shaped occlusal outline. This morphology resembles that described for *Archaeotypotherium propheticus* Roth, 1903 from Chile (Croft *et al.*, 2003). Considering this only specimen, Cerdeño *et al.* (2010) identified it as cf. *Archaeotypotherium*. Up to now, this genus has been recognized in the Tinguirirican Age (early Oligocene) both in Chile and Argentina and maybe in the Deseadan Age in Uruguay (Croft *et al.*, 2003). If the latter and its presence in Quebrada Fiera are confirmed, the biochron of this taxon would extend to the late Oligocene.

Other notoungulates in Quebrada Fiera, whose study is still pending, are the following:

1. **Leontinidae**: an almost complete skull (figure 3E-F), maxillary and mandibular fragments, and postcranial elements are preliminarily assigned to the genus *Scarrittia*. A detailed comparison with Patagonian and Brazilian species is presently in progress.

2. **Homalodotheriidae**: this family is recognized upon metapodials and phalanges, but no dental remain has been ascribed to it. Metacarpals and anterior phalanges of homalodotheriids are characteristic (figure 3G-H), and have been classically compared with those of the holarctic chalicotheres (*Perissodactyla*). Other postcranial bones are also assigned to homalodotheriids based on their similarities with fossil rhinoceroses (pers. observ.). The homalodotheriid genus described for Deseadan times in Patagonia is *Asmodeus* Ameghino, 1894, poorly known in contrast to its younger relative *Homalodotherium* Huxley, 1870 from the Santacrucian Age (early Miocene) (Scott, 1930).

3. **Toxodontidae**: they are poorly represented, but a lower tooth can be preliminarily assigned to

*Proadinothierium* Ameghino, 1894, a genus known from Deseadan beds in Patagonia (figure 3I).

4. **Hegetotheriidae and Interatheriidae**: these two other families of tyotherian notoungulates are represented by rather good material (maxillaries, mandibles, and isolated teeth) and their study is in progress. Among interatheres (figure 3J-K), the common Patagonian *Plagiarthrus* Ameghino, 1896 is identified, as well as a probable new taxon. Hegetotheriid remains reveal the presence of both subfamilies of the group, Hegetotheriinae and Pachyrukhinae. Hegetotheriines (figure 3J) seem to be represented at least by a species comparable to *Prohegetotherium schiaffinoi* (Kraglievich, 1932) from Salla. Pachyrukhines include some specimens (figure 3K) close to the genus *Prosotherium* Ameghino, 1897, which was previously mentioned by Reguero (1999) in Quebrada Fiera. Within tyotherians, the outstanding absence of **Mesotheriidae** in Quebrada Fiera is in contrast with other Deseadan localities.

Other native ungulates from Quebrada Fiera include **Pyrotheriidae** and **Litopterna**. Recently, Billet (2009) has proposed that pyrotheres should be included in Notoungulata. Previous pyrothere remains from Quebrada Fiera were scarce, but a partial skull and associated mandible (figure 3N) together with dental remains and large postcranial elements have been now recovered. The detailed study of this material would allow a specific determination after comparing it with the best known species from Patagonia, *P. romeroi* Ameghino, 1889 (Billet, 2009), and that from Salla, *P. macfaddeni* (Shockey & Anaya, 2004). Litopterns are very scarcely represented, not allowing an accurate determination, though some remains point to the Family Proterotheriidae.

With respect to other mammal groups, Quebrada Fiera yielded several representatives of **Xenarthra**, including sloths, gliptodonts, and armadillos, mainly identified after postcranial elements (figure 3O) and scutes. They show some Patagonian affinities and are different from the Salla material, although are comparable to the specimens from the Bolivian Lacayani site (Pujos *et al.*, 2008).

**Rodents** are very scarce. A nice mandibular fragment under study seems to belong to *Acaremyidae*, very similar to that present in Salla (M. E. Pérez & A. Candela, pers. comm.).

Carnivore **marsupials** are represented by two Deseadan Patagonian taxa: *Proborhyaena gigantea* (Bond & Pascual, 1983) and *Pharsophorus* Amegh-

ino, 1897 (Forasiepi, pers. comm.). At the same time, a tiny specimen recovered in 2009, associated maxilla and mandible, has revealed the presence of a rare metatherian with unique characteristics, which represents a new taxon (Forasiepi *et al.*, 2010).

Aside mammals, **birds** are represented by a large phorusrhacid, cf. *Andrewsornis* (Gorroño *et al.*, 1979), as well as by some remains of small indeterminate birds. In addition, two inner moulds of a terrestrial **Gastropoda** were recovered.

### Paleobiogeographic remarks

The late Oligocene Deseadan faunal associations are firstly known from classical Patagonian localities such as Cabeza Blanca and Scarrit Pocket, Chubut Province, and La Flecha, Santa Cruz Province. Later, the rich Deseadan fauna from the Bolivian locality of Salla (Kay *et al.*, 1998) showed significant differences with the Deseadan complex from Patagonia. Other known Deseadan faunas come from the Fray Bentos Formation, outcropping in Argentina and Uruguay (Mones & Ubilla, 1978; Ubilla *et al.*, 1994; Bond *et al.*, 1998), other Bolivian localities such as Lacayani (Hoffstetter *et al.*, 1971; Vucetich, 1989), the Moquegua Formation in Peru (Shockey *et al.*, 2006), the Tremembé Formation in Brazil (Berqvist & Ribeiro, 1998; Soria & Alvarenga, 1989; Vucetich & Ribeiro, 2003), Río Maipo-Abanico Formation in Chile (Croft *et al.*, 2008b), and maybe the locality of Santa Rosa (Peru), whose notoungulates present affinities with Deseadan taxa (Shockey *et al.*, 2004). Despite this number of localities, published data are still scarce, which limit available comparisons. Now, Quebrada Fiera is providing new information that increases the knowledge on late Oligocene South American faunas. Concerning archaeohyracids, the sample from Quebrada Fiera allows a clear correlation with Salla, with the presence of *A. suniensis* (Billet *et al.*, 2009; Cerdeño *et al.*, 2010). In Patagonian localities, the genus is scarcely represented by *A. patagonicus* Ameghino, 1897. If the presence of *Archaeotypotherium* in Mendoza is confirmed, it would represent a greater similarity between older Tinguirirican and Deseadan faunas.

The notohippid from Quebrada Fiera, *Mendozahippus*, is a basal taxon that is not as close to other Deseadan species as might be expected (Cerdeño & Vera, 2010). This family is also recorded in the

Moquegua Formation by a distinct genus (Shockey *et al.*, 2006), while Salla yielded three notohippid species (Shockey, 1997), two of them corresponding to known Patagonian genera. Soria & Alvarenga (1989) described a notohippid species from the Tremembé Formation included in the Patagonian genus *Rhynchippus*.

As mentioned before, hegetotheriids from Quebrada Fiera correspond to both Hegetotheriinae and Pachyrukhinae subfamilies; the presence of the latter approaches the Mendoza fauna to those from Patagonia, where there is a remarkable diversity of pachyrukhines (Reguero *et al.*, 2007) in contrast to Bolivian and Uruguayan faunas.

The absence of Mesotheriidae (at least not recognized by dental remains) in Quebrada Fiera is striking as they are well represented in other Deseadan localities both in Patagonia and lower latitudes (Billet *et al.*, 2008). In addition, marsupial, xenarthran, and rodent remains from Quebrada Fiera also show similarities and differences with respect to Bolivian and Patagonian Deseadan taxa.

In summary, mammals from Quebrada Fiera are supporting the idea of a mixed faunal association that includes known southern and northern taxa together with exclusive species. This assemblage could be explained by the intermediate latitudinal position of Mendoza in the paleogeographical context of South American Oligocene. New researches in Mendoza as well as in the other mentioned Deseadan localities in Bolivia, Brazil, Chile, and Peru will provide important data to increase the knowledge of the diversity, evolution and geographical distribution of the Oligocene mammal faunas.

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