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PYRAMIODONTHERIUM ROVERETO (XENARTHRA, TARDIGRADA, MEGATHERIINAE) FROM THE EARLY PLIOCENE OF SAN FERNANDO, CATAMARCA PROVINCE, ARGENTINA

RICARDO A. BONINI[1] AND DIEGO BRANDONI[2]

[1]División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Paseo del Bosque S/ N, B1900FWA La Plata, Buenos Aires, Argentina. *rbonini@fcnym.unlp.edu.ar*

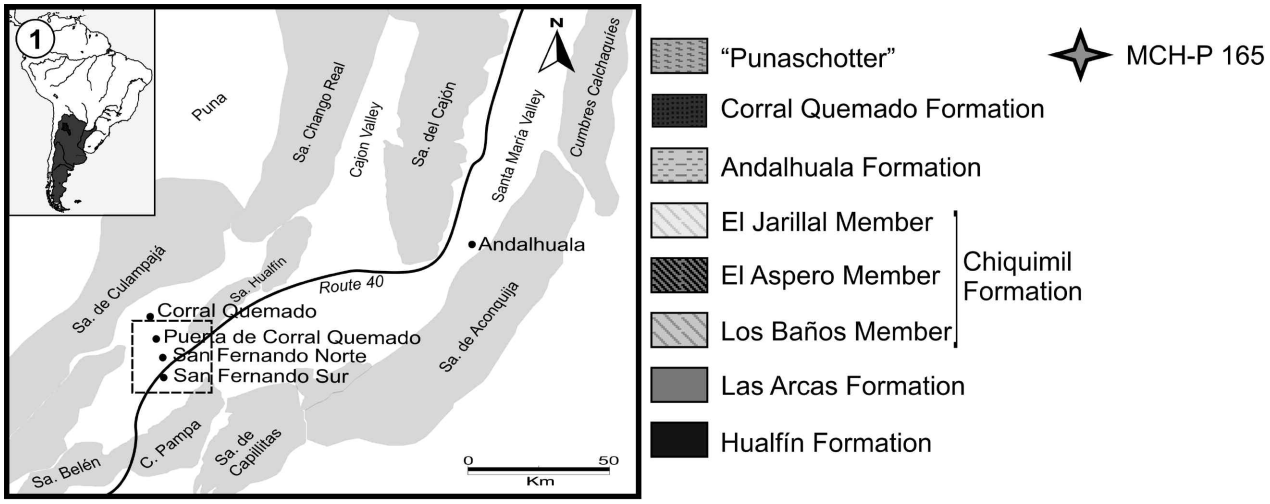
[2]Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICYTTP-CONICET), Materi y España, E3105BWA Diamante, Entre Ríos, Argentina. *dbrandoni@cicyttp.org.ar*

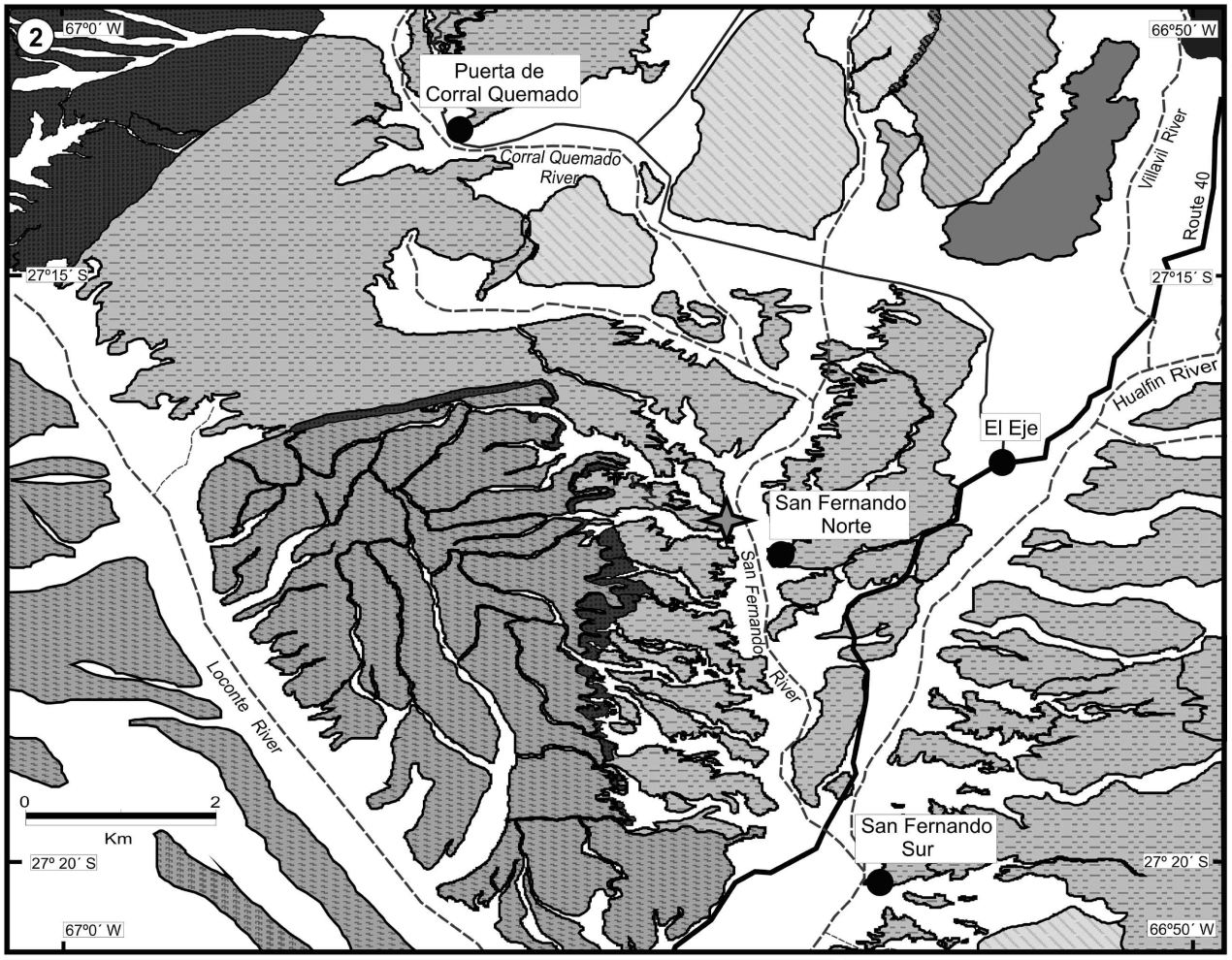
Key words. Zanclean Age. Biostratigraphy. Ground sloths. Tibia-fibula. Northwestern Argentina.

THE discovery of Neogene fossil vertebrates in Catamarca Province began in the 19th century (*e.g.*, Moreno and Mercerat, 1891; Lydekker, 1894). In 1889, Adolfo Methfessel collected several mammal remains from Bajo de Andalhuala (= Andalhuala de abajo), a locality located in the Santa María Valley (Moreno and Mercerat, 1891). Most of the vertebrates collected by Methfessel were later studied by Moreno and Mercerat (1891) and Lydekker (1894). However, several remains, including the holotypes of many species of ground sloths, glyptodontids, rodents, carnivores, and native ungulates were collected from these units without precise stratigraphic control.

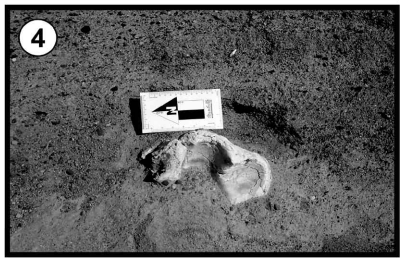
The terms "Araucanense", "Araucano", "formación araucana", and "estratos araucanos" have been used to refer to the fossil beds exposed in the Santa María Valley, (*e.g.*, Moreno and Mercerat, 1891; Rovereto, 1914). Stahlecker (in Riggs and Patterson, 1939) divided the "Araucanense" into three major lithostratigraphic units (from base to top: Chiquimil, "Araucanense", and Corral Quemado horizons) that were recognized in the Santa María Valley and also in the area of Puerta de Corral Quemado (Fig. 1.1). However, Cabrera (1944) did not accept this distinction between "Araucanense" and Corral Quemado, given that he identified the same species of glyptodontids (Mammalia, Xenarthra) in both horizons. The "Araucanense" horizon (*sensu* Riggs and Patterson, 1939) was used by Galván and Ruiz Huidobro (1965) to define the Andalhuala Formation (see also Bossi and Palma, 1982). Bossi *et al.* (1987) correlated the stratigraphic arrangement originally proposed for the Santa María Valley with the sedimentary sequence exposed in the area of Puerta de Corral Quemado. These authors also modified the boundary between the Andalhuala and Corral Quemado formations proposed by Stahlecker (in Riggs and Patterson, 1939) and Marshall and Patterson (1981), from level 19 to level 31.

Pyramiodontherium Rovereto, 1914, one of the best known genera of Neogene Megatheriinae (Xenarthra, Tardigrada, Megatheriidae), is represented by *P. bergi* (Moreno and Mercerat, 1891); *P. brevirostrum* Carlini, Brandoni, Scillato-Yané and Pujos, 2002; and *P. scillatoyanei* De Iuliis, Ré, and Vizcaíno, 2004. A fourth, though probably invalid species, *Pyramiodontherium*? *carlesi* Kraglievich, 1930, has also been proposed. *Pyramiodontherium bergi* and *P. brevirostrum* were collected from the "Araucanense" (Late Neogene) in Catamarca Province; whereas *P. scillatoyanei* is from Pliocene deposits in La Rioja Province. The holotype of *P. bergi* –a nearly complete skeleton– was recovered by Methfessel from Bajo de Andalhuala, Santa María Valley (Moreno and Mercerat, 1891; Cabrera, 1928), but its stratigraphic provenance is uncertain. The type material of *P. bergi* is part of the older collections of Museo de La Plata, from a time when the distinction between Andalhuala and Corral


1
Puna
Sa. Chango Real
Cajon Valley
Sa. del Cajón
Santa María Valley
Cumbres Calchaquíes
N
Andalhuala
Sa. de Culampajá
Sa. Hualfín
Route 40
Corral Quemado
Puerta de Corral Quemado
San Fernando Norte
San Fernando Sur
Sa. de Aconquija
Sa. Belén
C. Pampa
Sa. de Capillitas
0
50
Km
"Punaschotter"
MCH-P 165
Corral Quemado Formation
Andalhuala Formation
El Jarillal Member
El Aspero Member
Los Baños Member
Chiquimil Formation
Las Arcas Formation
Hualfín Formation


2
67°0´ W
66°50´ W
Puerta de Corral Quemado
Corral Quemado River
Villavil River
Route 40
27°15´ S
Hualfín River
El Eje
San Fernando Norte
San Fernando River
Loconte River
0
2
Km
27° 20´ S
San Fernando Sur


3
"Punaschotter"
Andalhuala Formation
Corral Quemado Formation


4

Quemado Formations had not yet been proposed. According to the original description (see Carlini *et al.*, 2002; Brandoni and Carlini, 2009; but see Bonini, 2014), *P. brevirostrum* was also recovered from Bajo de Andalhuala; as is the case with *P. bergi* its stratigraphic provenance is doubtful.

Bonini (2014) considered the diversity and biostratigraphy of the Neogene mammals from the localities of Puerta de Corral Quemado and San Fernando, both in Belén Department, Catamarca Province (Fig. 1.1–2). In addition to the study of specimens already housed in the collections, several new specimens with strict stratigraphic control were collected by Bonini and collaborators in San Fernando. Among the newly collected material, a megatheriine tibia-fibula was recovered from the Andalhuala Formation at San Fernando Norte.

In this contribution we describe this tibia-fibula and assign it to *Pyramiodontherium* sp. We also discuss its taxonomic, stratigraphical, and geochronological relevance.

Institutional abbreviations. **AMU-CURS,** Colección de Paleontología de la Alcaldía de Urumaco, Urumaco, Venezuela; **FMNH-P,** Field Museum of Natural History, Chicago, USA; **MACN Pv,** División Paleontología Vertebrados, Colección Nacional, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MCH-P,** Sección Paleontología, Museo Arqueológico Provincial "Condor Huasi", Belén, Argentina; **MLP,** División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

GEOGRAPHICAL AND GEOLOGICAL SETTING

San Fernando is located in Belén Department of, northwestern Catamarca Province, an area lying in the northwestern Sierras Pampeanas. San Fernando is divided into two villages: San Fernando Sur or Capillanía and San Fernando Norte or La Villa (27° 16′ S; 66° 54′ W; Fig. 1.1). The Neogene sediments are represented by the following lithostratigraphic units, from base to top: Hualfin, Las Arcas, Chiquimil, Andalhuala, and Corral Quemado formations, and the informal unit "Punaschotter" (Fig. 1.2–3) (Bonini and Georgieff, 2014).

The tibia-fibula (MCH-P 165) was collected from the Andalhuala Formation at San Fernando Norte, about 50 m above the base of the section there exposed. This specimen comes from facies of medium grained light brown cross-stratified sandstone and interbedded facies of coarse-grained sandstone to conglomerate with lenticular stratification (Fig. 1.4). $_{39}Ar/_{40}Ar$ dates indicate an age of c. 4.8 Ma for the tuff bed overlying (37.9 m above) the sediments from which MCH-P 165 was recovered (Fig. 2; Bonini and Georgieff, 2014). Based on the sedimentation rate estimated for the upper levels of the Andalhuala Formation at Puerta de Corral Quemado (*i.e.*, 0.33 m/1000 years, see Esteban *et al.*, 2014), an approximate age of 4.91 Ma (Zanclean Age, *i.e.*, early Pliocene) is herein proposed for the deposition of the fossil-bearing bed.

MATERIALS AND METHODS

MCH-P 165 was compared with the tibia-fibula of the following species and specimens: *Pyramiodontherium bergi* (MLP 2-66, holotype), *P. scillatoyanei* (MLP 68-III-14-1, holotype), *P. brevirostrum* (MLP 31-XI-12-25, holotype), *Megathericulus patagonicus* Ameghino, 1904 (MLP 91-IX-7-18), and *Megatherium americanum* Cuvier, 1796, (MLP 75, MLP 2-207, MLP 2-29, MLP 27-IV-4-1, MLP 44-XII-28-1, MLP 74-26-1-1). In addition, other specimens of *Megatherium* Cuvier, 1796, referred to species of doubtful validity were also considered (*i.e.*, MLP 2-30, MLP 2-31).

SYSTEMATIC PALEONTOLOGY

XENARTHRA Cope, 1889

TARDIGRADA Latham and Davies in Forster, 1795

MEGATHERIOIDEA Gray, 1821

MEGATHERIIDAE Gray, 1821

MEGATHERIINAE Gray, 1821

Genus ***Pyramiodontherium*** Rovereto, 1914

Figure 1. Study area. **1,** Location map of study area; **2,** Map of lithostratigraphic units recognized in the study area including the site yielding **MCH-P** 165; **3,** Panoramic image of outcrops around San Fernando Norte; **4,** Detail of facies of the medium grained sandstone unit yielding **MCH-P** 165.

Type species. *Pyramiodontherium bergi* (Moreno and Mercerat, 1891).

Geographic and stratigraphic occurrence. Bajo de Andalhuala, Santa María Valley, Catamarca Province; Andalhuala Formation?, precise stratigraphic level unclear (Brandoni and Carlini, 2009).

Pyramiodontherium sp.

Figure 3

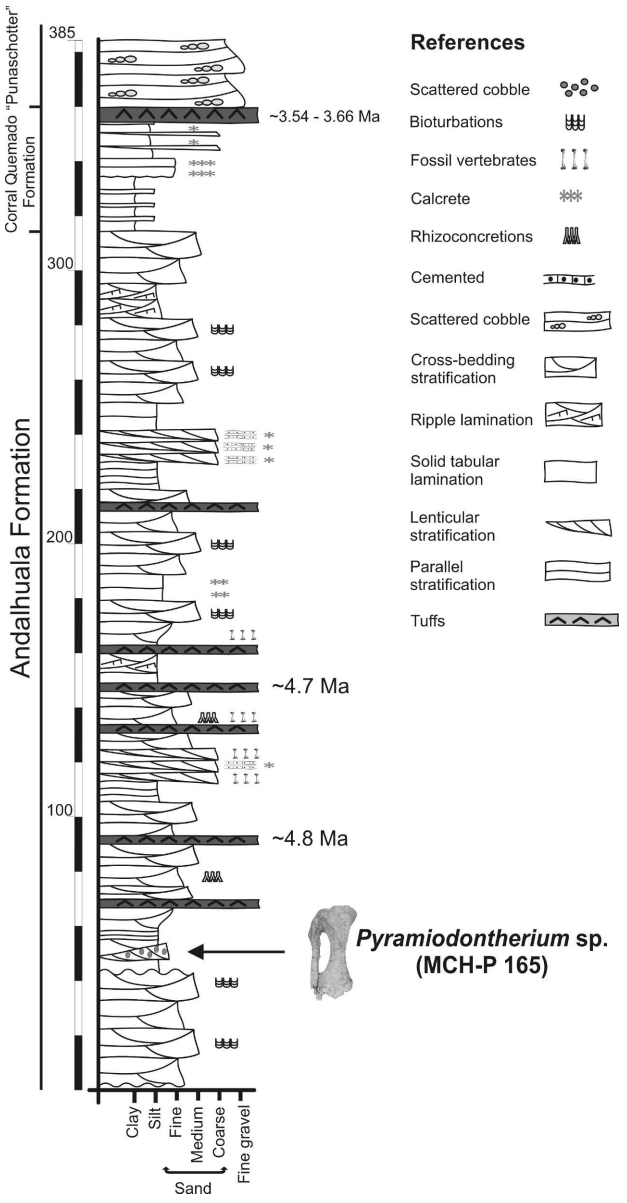


Figure 2. Stratigraphic section at San Fernando Norte (modified from Bonini and Georgieff, 2014).

Referred material. MCH-P 165, right tibia-fibula (Fig. 3.1–4).

Geographic provenance of the referred specimen. 27° 17′ 5.92″ S; 66° 54′ 30.88″ W, San Fernando Norte, Belén Department, Catamarca Province, Argentina (Fig. 1.2).

Stratigraphic provenance of the referred specimen. Upper levels of the Andalhuala Formation (Fig. 2).

Description and Comparisons

The tibia of MCH-P 165 (Fig. 3.1–4) is relatively elongated and gracile, resembling that of *Pyramiodontherium bergi* (MLP 2-66) among other megatheriines. Proximally, the tibia is fused with the fibula, but distally they are separated as in most megatheriines, except in adult specimens of *Megatherium americanum* and *M. tarijense* Gervais and Ameghino, 1880 (see De Iuliis *et al.*, 2009). The proximal surface bears two main articular facets for the femoral condyles, *i.e.*, the lateral articular facet and the medial articular facet (Fig. 3.1). The lateral articular facet is oval to subcircular; its surface is gently convex anteroposteriorly and transversely. Anteriorly and posteriorly to this facet, there are two small facets for sesamoid bones (see De Iuliis, 1996; De Iuliis *et al.*, 2015); the anterior one for the lunula or meniscal sesamoid (De Iuliis, 1996) is small and semicircular in outline; the posterior, for the cyamella, is larger, nearly rectangular in outline and faces posteromedially. In *P. bergi* the lateral facet is similar to that described for MCH-P 165, whereas in *P. scillatoyanei* (MLP 68-III-14-1) the facet is subrectangular in outline. As in most megatheriines, the medial articular facet is oval in outline, concave transversely and anteroposteriorly. In MCH-P 165 the longitudinal axis is oblique, forming an angle of approximately 60° with the transverse axis, and it is posteriorly projected. The intercondylar surface is wide but not to the same degree as in *P. bergi*. In *P. bergi* the intercondylar surface is nearly as wide as the lateral facet; in MCH-P 165 the intercondylar surface is not as wide as the lateral facet, whereas in *P. scillatoyanei* the intercondylar area is narrower than MCH-P.

As in *P. bergi*, the tibial diaphysis is gracile; the lateral and medial walls of the diaphysis are concave (Fig. 3.2–3). The cnemial crest is well-developed, as in MLP 2-66 (Figs. 3.2, 4.1). The crest is obliquely oriented, from the proximolateral to the distomedial end of the epiphysis. The proximal half of the crest is particularly prominent (Fig. 3.2). Thus, as in *P. bergi* (Fig. 4.1), the middle section of the diaphysis is

Figure 3. ***Pyramiodontherium*** **sp., MCH-P** 165, right tibia-fibula. **1,** proximal view; **2,** anterior view; **3,** posterior view; **4,** distal view. Scale bar= 100 mm.

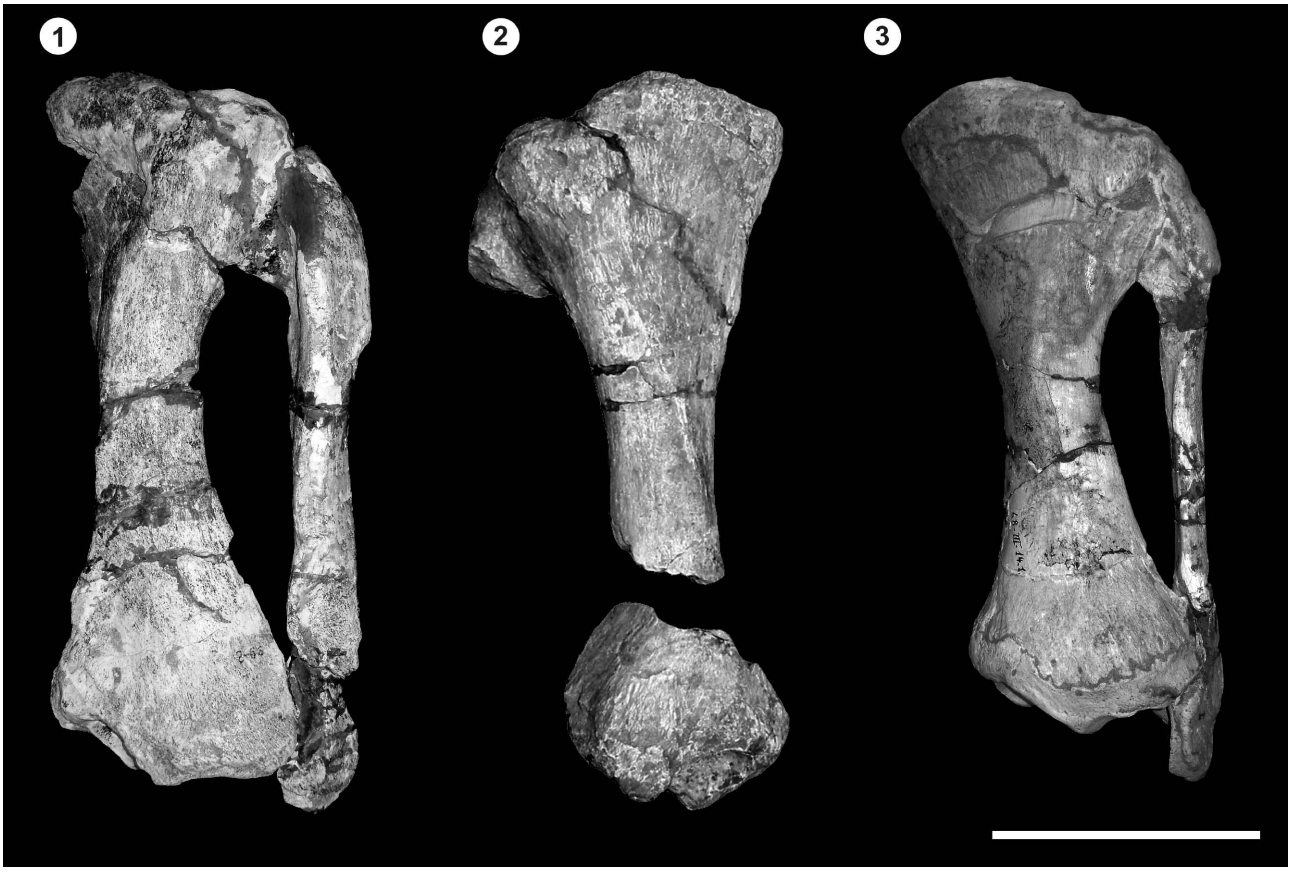


Figure 4. Tibia-fibula of ***Pyramiodontherium*** species in anterior view. **1, *Pyramiodontherium bergi*, MLP** 2-66; **2, *Pyramiodontherium brevirostrum*, MLP** 31-XI-12-25; **3, *Pyramiodontherium scillatoyanei*, MLP** 68-III-14-1. Scale bar= 100 mm.

subtriangular, whereas in *P. brevirostrum* (Fig. 4.2), *P. scillatoyanei* (Fig. 4.3) and *Megathericulus patagonicus* the tibia is oval to suboval in section.

As in all described species of *Pyramiodontherium* and *Megathericulus patagonicus*, the posterodistal surface of the tibia bears three grooves defined by two crests; these are for the long digital flexor tendons (De Iuliis, 1996; De Iuliis *et al.*, 2008) (Fig. 3.3). In *Megatherium americanum* a single, wide groove (*e.g.*, MLP 75, MLP 74-IV-26-1) or two grooves separated by a crest (*e.g.*, MLP 27-IV-4-1) are present (see also De Iuliis, 1996).

The distal epiphysis of the tibia shows three articular facets, two distal for the astragalus and a single lateral one for the fibula (Fig. 3.4). The cochlea tibiae, for articulation with the astragalus, consist of a medial part for the astragalar odontoid facet and a larger lateral part for the astragalar discoid facet. In MCH-P 165 the angle between the facets is approximately 87°, while it is also 87° in *P. bergi*, nearly 90° in *P. scillatoyanei*, 114° in *P. brevirostrum*, and 135° in *Megathericulus patagonicus*. In MCH-P 165, as in *P. bergi*, *P. scillatoyanei*, *P. brevirostrum*, and most megatheriines, the odontoid facet is approximately adjacent to the central part of the discoid facet. As is usual in megatheriines, the facet for the fibula is contiguous medially with the discoid facet and is crescentic in outline.

As already noted, the tibia and fibula are fused proximally but not distally in MCH-P 165 (Fig. 3.2–4). The proximal third of the fibula of MCH-P 165 is subcircular in section. Its central portion is mediolaterally compressed and oval in section, whereas the distal third is subtriangular in section. In *P. bergi* the diaphysis is nearly subtriangular in section along its shaft, and in *P. scillatoyanei* it is more slender than in *P. bergi* and MCH-P 165, while it is subtriangular in section. Distally, the tibial facet of MCH-P 165 resembles that of other megatheriines, but it is wider, particularly posteriorly. The astragalar facet is not well preserved but it seems to be similar to that of *P. bergi* given that the anterior portion is relatively oval and the posterior portion is narrow,

whereas in *P. scillatoyanei* the facet is larger than in MCH-P 165 and *P. bergi*, and it is subtriangular in outline.

DISCUSSION

The general morphology MCH-P 165 more closely resembles the tibia-fibula of *Pyramiodontherium bergi*; but also has similarities with that of *P. brevirostrum*. Although slightly larger, the tibia-fibula of MCH-P 165 is similar in size to that of *Pyramiodontherium bergi* (Table 1) and shares several features with the tibia-fibula of this species such as: 1) shape of the proximal articular surfaces (*e.g.*, angle of the main axis of the medial articular facet with respect to its transverse width); 2) a well developed cnemial crest and a subtriangular section of the tibia; 3) arrangement of the distal facets for articulation with the astragalus (*e.g.*, angle between the discoid facet and the odontoid facet); 4) general shape, size, and distal section of the diaphysis of the fibula; and 5) shape of the astragalar facet of the fibula. However, MCH-P 165 differs from the tibia-fibula of *P. bergi* in the width of the intercondylar area. Based on these similarities and differences, and considering the individual variability proposed for other Neogene megatheriines (Brandoni and Carlini, 2009; Brandoni *et al.*, 2012), specimen MCH-P 165 is assigned to *Pyramiodontherium* sp.

Pyramiodontherium bergi –based on MLP 2-66 (Fig. 4.1)– was recovered from Bajo de Andalhuala in the Santa María Valley, south of Entre Ríos, Catamarca Province (Fig. 1.1). Its stratigraphic provenance is unclear, given that at least three lithostratigraphic units (Chiquimil, Andalhuala, and Corral Quemado formations) crop out in the area of Entre Ríos and at the time of the collection of the remains the distinction between these formations had not yet been proposed. Brandoni and Carlini (2009) suggested that the holotype probably comes from the Andalhuala Formation, although its exact stratigraphic provenance (*i.e.*, level within the Formation) is uncertain and thus so is its age. In addi-

TABLE 1. Tibia measurements in mm.

Taxon	*Specimen*	*Length*	*Proximal width*	*Distal width*	*Diaphysis medial width*
Pyramiodontherium *sp.*	*MCH-P 165*	*530*	*250*	*245 approx.*	*100*
Pyramiodontherium bergi	*MLP 2-66 Left*	*514*	*230*	*222*	*87*
Pyramiodontherium bergi	*MLP 2-66 Right*	*–*	*220*	*210*	*90*
Pyramiodontherium brevirostrum	*MLP 31-XI-12-25*	*500*	*210*	*170*	*–*
Pyramiodontherium scillatoyanei	*MLP 68-III-14-1*	*472*	*215*	*205*	*81*
Pyramiodontherium *sp.*	*MLP 31-XI-12-26 Left*	*425*	*195*	*150*	*–*
Pyramiodontherium *sp.*	*MLP 31-XI-12-26 Right*	*435*	*180*	*160*	*–*
Megathericulus patagonicus	*MLP 91-IX-7-18*	*270*	*120 approx.*	*150*	*55*
Megatherium *sp.*	*MLP 2-30*	*446*	*246*	*222*	*81*
Megatherium *sp.*	*MLP 2-31*	*445*	*235*	*245*	*97*
Megatherium americanum *	*MLP 2-207*	*560*	*360*	*–*	*115*
Megatherium americanum *	*MLP 2-29*	*620*	*355*	*305*	*141*
Megatherium americanum *	*MLP 2-79*	*539*	*342*	*–*	*123*
Megatherium americanum *	*MLP sala 9*	*568*	*330*	*290*	*100*
Megatherium americanum *	*MLP 44-XII-28-1*	*550*	*302*	*290*	*120*
Megatherium americanum *	*MACN Pv 10147*	*475*	*275*	*–*	*112*
Megatherium tarijense **	*FMNH-P 14216*	*408*	*214*	*202*	*85*
Urumaquia robusta	*AMU-CURS 169*	*440*	*–*	*130*	*69*

** from De Iuliis (1996).*
*** from De Iuliis et al. (2009).*

tion, Reguero and Candela (2011) included *P. bergi* in the *Cyonasua brevirostris* Biozone (Moreno and Mercerat, 1891). Carlini *et al.* (2002) indicated that the holotype of *P. brevirostrum* was also recovered from Bajo de Andalhuala in the Santa María Valley, but its stratigraphic provenance is also doubtful. However, based on a Cabrera's report (dated from 27th march of 1930) of the activities carried out in the third expedition in Catamarca Province, Bonini (2014), suggested that the type specimen of *P. brevirostrum* was collected by Cabrera and his staff during fieldwork in the area of Puerta de Corral Quemado and not at Bajo de Andalhuala.

Reguero and Candela (2011) defined the *Cyonasua brevirostris* Biozone for the lower levels of Andalhuala Formation at Puerta de Corral Quemado. Taxa included in this biozone range from level 14 (c. 7.14 Ma) at the base of the Andalhuala Formation to level 21 (c. 6 Ma) (Reguero and Candela, 2011). The biozone it was based on the First Appearance Datum (FAD) of the procyonid *Cyonasua brevirostris* (Fig. 5) and is assigned a Messinian Age (7.24–5.33 Ma). Reguero and Candela (2011) considered that *P. bergi* was exclusive of this biozone; however, as already stated, the precise level from where the remains of *P. bergi* (*i.e.*, MLP 2-66) were collected is unknown.

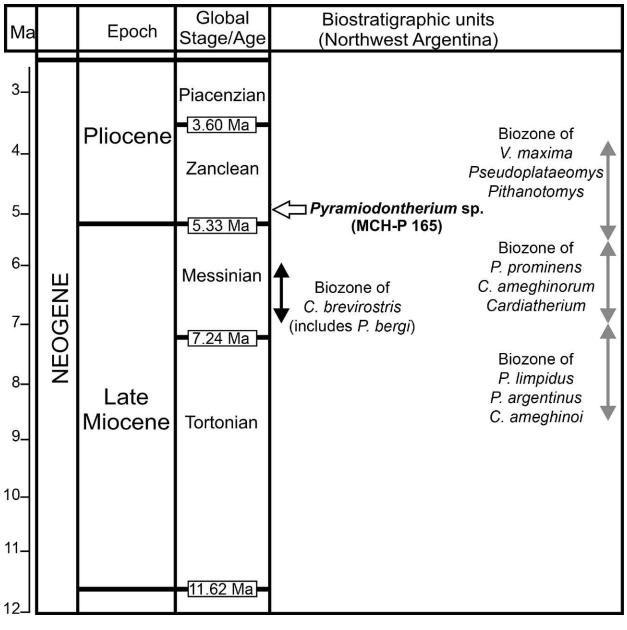


Figure 5. Chronological chart with the temporal occurrence of **MCH-P** 165. Biostratigraphic units from Reguero and Candela (2011, black arrow) and Esteban *et al.* (2014, grey arrows).

As noted, MCH-P 165 was collected in the upper levels of the Andalhuala Formation at San Fernando Norte, Catamarca Province. An age of approximately 4.91 Ma is herein proposed for the levels bearing this specimen, which suggests a Zanclean Age (5.33–3.60 Ma) for these beds of the Andalhuala Formation (Fig. 5). Although *Pyramiodontherium bergi* was traditionally considered as late Miocene in age (Brandoni and Carlini, 2009; Reguero and Candela, 2011), the results of the current study suggest that a form close to *P. bergi* (*i.e.*, *Pyramiodontherium* sp.) is present in the early Pliocene (Zanclean Age) of Catamarca Province.

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