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Eocene archaeohyracids (Mammalia: Notoungulata: Hegetotheria) from the Puna, northwest Argentina

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ABSTRACT

A new genus and species of basal hegetothere mammal, *Punahyrax bondesioi*, is described from the middle-late? Eocene Geste Formation of northwestern (Catamarca and Salta provinces) Argentina. The new species is based on isolated teeth and mandibles and represents the first well-identified archaeohyracid from northwestern Argentina, and the earliest extra-Patagonian record of the family. It is characterized by its small-size and a short talonid on the molars. Though still poorly documented, this new taxon may provide key-data for the problem of the origin and basal of hegetotheres phylogeny. These fossils show the importance of northwestern Argentina (Puna area) in the early evolution of the extinct order Notoungulata and the poor state of our knowledge there.

1. Introduction

The Archaeohyracidae are a curious group of extinct notoungulates, known only from Paleogene deposits of South America (Simpson, 1967; Reguero et al., 2003; Croft et al., 2003). Florentino Ameghino (1906) believed that the Archaeohyracidae were ancestral to the extant Hyracoidea (hyraxes), and allied them with the Archaeopithecidae and Henricosborniidae. Roth (1903) was the first to include them in the extinct order Notoungulata.

Although archaeohyracids have been known for more than a century (Ameghino, 1897), it has only been in the last 15 years that they have been the subject of extensive study. Prior to this, the only significant studies of archaeohyracids were those of Patterson (1952) and Simpson (1967), which focused on the Patagonian representatives. Simpson (1967) defined archaeohyracids as ‘‘Early notoungulates with accelerated hypsodonty (not reaching continuous growth)”. These notoungulates experienced a great radiation in the late Eocene or earliest Oligocene, as indicated by their high diversity in earliest Oligocene Tinguiririrican age faunas of Chile and Argentina (Wyss et al., 1994; Croft et al., 2003; Flynn et al., 2003; Reguero et al., 2003). They are last recorded in late Oligocene Deseadan age faunas of Bolivia, Uruguay, and northeast of Argentina (Reguero et al., 1995; Reguero and Cifelli, 1997; Bond et al., 1998). Slightly older Oligocene representatives of this family are also known from several Deseadan local faunas of Argentina (Ameghino, 1897; Chaffee, 1952). Until now, no archaeohyracids of any age have been recorded from northwestern Argentina. Based on cladistic analysis, Croft et al. (2003) suggested that Archaeohyracidae (in its classical sense) is paraphyletic.

The present study describes a new archaeohyracid from the middle-late? Eocene fauna of Catamarca and Salta provinces, Argentina. Few specimens are referable to this new taxon, permitting just a detailed description of the dental morphology of some lower and upper teeth. It represents the earliest extra-Patagonian record of the family, and is one of the smallest archaeohyracids known. The moderately high-crowned cheek teeth of this new taxon are typical of the Archaeohyracidae and demonstrate the group's early tendency toward hypsodonty. Considering that this new taxon is based primarily on few specimens, intraspecific variation for pertinent characters cannot be determined. However, interspecific comparisons were made with specimens of Eocene and Oligocene archaeohyracids from Patagonia and Bolivia. In a broader phylogenetic context, these archaeohyracids are important because they display many of the character state transitions that occurred between advanced and primitive Typotheria.

We also provide geological information of the area, and the first detailed stratigraphic profile of the vertebrate-bearing horizons of the Geste Formation from Antofagasta de la Sierra, Catamarca province, NW of Argentina.

1.1. Materials and methods

All specimens of the new species described below are housed in the vertebrate paleontology collections of the Museo La Plata in La

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Plata, Argentina. Measurements of these and other specimens were made to the nearest 0.1 mm using digital calipers, unless otherwise noted. Comparative data were gathered from collections research at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN, Buenos Aires, Argentina); Museo Nacional de Historia Natural (SGOPV, Santiago, Chile); Museo Nacional de Historia Natural (MNHN, La Paz, Bolivia), American Museum of Natural History (AMNH, New York, USA), the Field Museum (FMNH, Chicago, USA), the Florida Museum of Natural History (UF, Gainesville, USA), and the Museo de La Plata (MLP, La Plata, Argentina); additional data were gathered from published sources.

The sequence of South American Land Mammal "Ages" (SALMAs) referred to in the present study essentially follows Flynn and Swisher (1995).

Dental terminology follows Reguero et al. (2003) and is illustrated in Fig. 1.

Tables 1 and 2 provide measurements.

1.2. Anatomical abbreviations

Upper tooth loci are indicated by upper case letters (e.g., I1, P2, M1) and lower tooth loci by lower case letters (e.g., i1, p2, m1).

2. Geographic and geologic setting

The present-day Puna yields few deposits with Paleogene faunas. Those that do currently lie at elevations between 3000 and 4000 m, and were likely deposited at significantly lower elevations (Kennan et al., 1997). The Puna is a high land region, close to the Andes Cordillera, that geographically comprises Catamarca, Salta and Jujuy provinces in Argentina.

Eocene mammals from the Geste Formation come from two localities: Antofagasta de la Sierra, Catamarca province, and Pozuelos, Salta province (Fig. 2). Antofagasta de la Sierra, at an elevation of about 3440 m, is located in the southernmost part of the Argentine Puna, 180 km northwest of the town of Belén, Catamarca province, at latitude 26° 04′ S, longitude 67° 26′ W (Fig. 3). The Pozuelos site, at an elevation of about 3900 m, is also located in the Puna, between Salar de Pozuelos and Salar de Pastos Grandes (24° 39′ 40″S; 60° 42′ 43″ W), near the Argentina–Chile border, Departamento de Los Andes, Salta province.

A preliminary faunal list of the Antofagasta de la Sierra fauna (Alonso et al., 1988) indicated a scarce but diverse vertebrate assemblage including turtles, sebecid crocodiles, boid snakes, marsupials, dasypodid edentates, "condylarths", notoungulates, and pyrotheres (López, 1997). In contrast, the fauna of Pozuelos is poorly known and includes few taxa; two marsupials (Pascual, 1983) and one notoungulate (López and Bond, 1995), have been described. Goin et al. (1998) revised the taxonomic status of the Pozuelos marsupials.

Table 1
Measurements (in mm) of upper cheek teeth of *P. bondesioi*, new genus and species, and other species of Archaeohyracidae. Measurements in parentheses are estimated

	M1		M2	
	L	*W*	*L*	*W*
Punahyrax bondesioi gen. et sp. nov.				
MLP 83-XI-3-4	4.9	5.9		
MLP 81-XI-15-4			5.0	5.2
Eohyrax isotemnoides				
AMNH 28844	8.2	10.3	9.0	11.9
Pseudhyrax eutrachytheroides				
SGOPV 2877	7.6	8.6	9.8	7.9
MLP 12-2199	(9.5)	(11.0)	10.8	(13.5)
Protarchaeohyrax gracilis				
MLP 12-1522	6.7	5.0	7.5	5.0
MLP 52-XI-4-168	6.4	3.4		
SGOPV 2982	6.9	4.3		
Archaeotypotherium propheticus				
MLP 12-1524a	13.6	10.5	13.7	9.1
MLP 12-1549a	10.1	9.5	11.5	9.8
AMNH 28955	10.9	(11.0)	13.0	(10.0)
Archaeotypotherium pattersoni				
SGOPV 2918	10.1	–	10.3	(9.1)
Archaeohyrax patagonicus				
MACN A-52-617*	9.1	8.6	10.2	8.3
MLP 83-I-12-4	8.2	9.8	12.0	9.0
AMNH 15911	8.9	10.5	11.3	10.5

* Holotype.

The Geste Formation has been identified only in three areas in northwest Argentina (from south to north): Antofagasta de la Sierra, Salar de Tolillar (67°05′W; 25°05′S and 4000 m elevation), and Salar de Pastos Grandes.

The mammals from Antofagasta de la Sierra come from small outcrops hundreds of square meters in size of red beds around the village. These Paleogene rocks lie to the west above marine shales and turbidites of Ordovician age and are covered by Pleistocene ignimbrites of the Galan caldera (Fig. 4). The red bed sequence is composed of fluvial sediments dominated by conglomerates, sandstones, siltstones and claystones. The total thickness is less than 500 m. The sediments are immature and were deposited in alluvial plains with rivers flowing to the east. Fossil bones are preserved in different lithologies such as sandstones, pelites or fine channel conglomerates. Sedimentary structures such as intraclast, cross bedding, and cut and fill are present. Secondary gypsum and carbonate in thin veins occur as part of the epigenetic process. Also, green discoloration centers

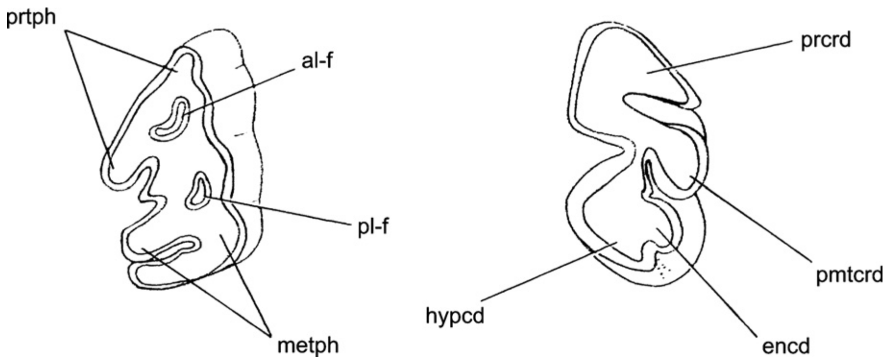

Fig. 1. Dental morphology and terminology in the upper and lower molars of primitive archaeohyracids. Abbreviations: al-l. anterolabial fossette; encd. entoconid; hypcd. hypoconid; metph. metaloph; pl-f. posterolabial fossette; pmtcrd. postmetacristid; prcrd. paracristid; prtph. protoloph.

Table 2
Measurements (in mm) of lower cheek teeth of *P. bondesioi*, new genus and species, and other species of Archaeohyracidae

	p3		p4		m1		m2		m3	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
Punahyrax bondesioi gen. et sp. nov.										
MLP 86-V-6-8							5.6	3.1		
MLP 86-V-6-11	3.8	2.8	4.5	3.5	6.2	4.4				
MLP 88-V-10-6*									8.0	4.1
Eohyrax isotemnoides										
MACN 10776			8.3	5.8	8.0	5.9	8.6	6.3	–	5.4
AMNH 28665	7.3	4.5	8.2	5.6	8.3	(6.0)	9.0	6.4	13.5	6.2
AMNH 28629	7.2	4.2	7.8	5.2	7.4	5.6	9.0	6.0	12.4	5.5
Pseudhyrax eutrachytheroides										
SGOPV 2985							–	6.8	12.7	5.8
SGOPV 2887							8.1	5.3	(8.2)	4.5
SGOPV 2901					(7.2)	(6.5)	(8.1)	(7.3)	(10.0)	(5.3)
AMNH 29458			7.7	4.8	7.9	5.3	8.6	5.5		
MLP 12-2198	6.9	5.6	7.2	5.8	7.6	6.5	9.2	6.5	15.0	6.7
MLP 12-1740	9.0	6.0	9.0	6.5	8.5	7.0	10.0	7.0	15.0	6.5
Protarchaeohyrax gracilis										
MLP 12-1518	4.7	3.0	5.1	2.6	4.7	3.3	5.2	3.5	7.1	3.1
MLP 12-1513b	5.5	2.6	5.6	2.6	6.2	3.4	7.4	3.5	7.1	3.5
SGOPV 2954	3.5	2.8	3.8	3.6	4.2	4.0	5.2	4.3	7.4	3.5
Archaeotypotherium propheticus										
MACN A52-618*	8.4	6.0	8.8.	6.5						
MLP 12-1516					9.0	7.0	10.3	6.3	16.1	5.4
MACN 10905b					10.6	6.5				
MACN 10905e					11.8	6.6				
Archaeotypotherium pattersoni										
SGOPV 2917	8.4	5.2	8.3	6.0	8.8	6.4	11.0	5.9	12.2	5.0
Archaeohyrax patagonicus										
MACN A-52-617*	7.2	5.5	7.1	5.4	8.8	5.4	9.4	5.3	14.4	4.4
MACN A-52-624	8.8	4.9	9.1	7.0	9.8	7.0	10.3	4.3	12.1	3.5
MLP 93-XI-21-14					8.9	5.6	9.4	5.1	17.8	4.3
AMNH 15911					7.8	5.2	8.5	4.8		
FMNH P14681							8.1	6.0	14.9	4.8

Measurements in parentheses are estimated.
* Holotype.

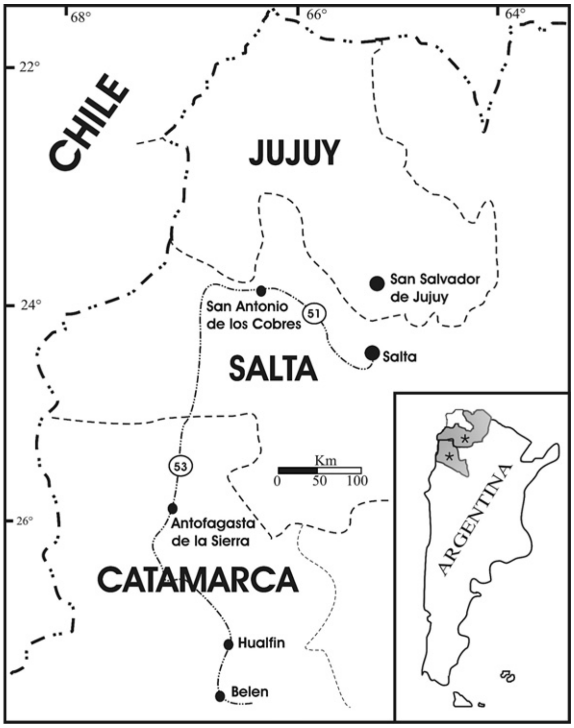

Fig. 2. Map of Northwestern Argentina, with geographical names and localities (indicated by an asterisk) mentioned in the text.

are distributed in the red beds. The sedimentary facies of Antofagasta de la Sierra are similar in lithology, color, stratigraphic position and mammal content to other facies situated 200 km to the north in the Pastos Grandes basin. They are part of alluvial plains and rivers developed during the Cenozoic Andean basin evolution (Jordan and Alonso, 1997).

3. Systematic paleontology

Order Notoungulata Roth, 1903
Suborder Hegetotheria Simpson, 1935
Family Archaeohyracidae Ameghino, 1897
Genus *Punahyrax* gen. nov.

Type species – *Punahyrax bondesioi* sp. nov.
Diagnosis – *Punahyrax* is most easily distinguished from other archaeohyracids in possessing small-size (30% smaller than *Archaeohyrax* and 40% smaller than *Archaeotypotherium*) and short talonid in the molars. It differs from species of *Eohyrax* in a more expanded entoconid and absence of the anterolingual cingulum on the upper molars. *Punahyrax* differs from *Pseudhyrax* in the presence of lower crowned cheek teeth, in having a more transverse protoloph, and in the absence of trigonid fossette. *Punahyrax* differs from *Archaeotypotherium*, *Protarchaeohyrax*, and *Archaeohyrax* in having low crowned cheek teeth, an antero-posteriorly-shortened talonid on the molars, and an entoconid very expanded. Posterior extension of the fossettid between the labial and lingual sides of the

Fig. 3. Photo of Antofagasta de la Sierra, showing the fossiliferous layer of the Geste Formation cropping out (indicated by arrows). To the right the homonymous village.

talonid appears to be greater in both *Eohyrax* and *Pseudhyrax* than in *Punahyrax*.

Etymology – Puna, from the Quechuan indigenous language meaning "a high land region"; hyrax, the common suffix for archaeohyracids.

3.1. *Punahyrax bondesioi sp. nov*

Holotype – MLP 88-V-10-6 (Fig. 5), left m3.

Hypodigm – the holotype, MLP 86-V-6-8, right dentary fragment with m2; MLP 86-V-6-11 (Fig. 6), left dentary fragment with p3-m1; MLP 86-V-6-9 (Fig. 7A), left dp4.

Referred specimens – MLP 81-XI-15-4, right M2 (Fig. 7B); MLP 83-XI-3-1, left M1, broken labially; MLP 83-XI-3-4, right M1 (broken); MLP 83-XI-3-5, left M1 (broken); MLP 83-XI-3-6, left M1.

Locality and horizon – the hypodigm comes from Antofagasta de la Sierra, Catamarca province, Argentina, and the referred specimens come from Salar Pozuelos, Salta province, Argentina. Middle Member of the Geste Formation, Pastos Grande Group (Alonso, 1992).

Age – middle-late? Eocene. Mustersan? SALMA.

Etymology – the species name honors Professor Pedro Bondesio for his contributions to the knowledge of Cenozoic fossil vertebrates from Argentina.

Diagnosis – as for genus, this being the only currently recognized species.

3.1.1. *Description*

3.1.1.1. Lower dentition. The cheek–teeth are relatively low crowned and rooted. The major characters of the lower dentition of this species are listed in the generic diagnosis. The talonid of the holotype MLP 88-V-10-6 (left m3; Fig. 5) is proportionately shorter than that of any other archaeohyracid taxon (30% smaller than *Archaeohyrax* and 40% smaller than *Archaeotypotherium*) (Tables 1 and 2). In the trigonid, the paracristid is small and the metaconid is prominent, extending lingually and posteriorly. The trigonid is square, with a small postmetastylid projecting posteriorly. The talonid of m3 differs from those of m1-2 in its more posteriorly projecting hypoconulid, which forms a continuous, blade-like lophid. A broad posterolingual groove separates the entoconid and hypoconulid.

As is typical in archaeohyracids, the entoconid of the molars is expanded transversely into an entolophid. In *Punahyrax* the entolophid is extended somewhat obliquely, attaching to the talonid crest (posterolophid). No medial fossettid is present in MLP 88-V-10-6. There is a small papilla or pillar between the entoconid and hypoconulid, likely homologous to that present in some specimens of *Pseudhyrax eutrachytheroides*; it has not yet fused with the small hypoconulid, which is cuspidate and is lower than the hypolophid. The posterior premolars (p3-4) of MLP 86-V-6-11 (Fig. 6) are similar to those of *Eohyrax isotemnoides* except for their smaller size and more robust appearance. Additionally, p4 is proportionately larger than p3, and is non-molariform. On the lingual face of p4 the attachment of the postmetastylid to the anterior face of the entoconid forms a closed talonid fossettid. Unfortunately, the m1 of this specimen is broken on the lingual side but the general morphology of the talonid suggests that it is proportionally smaller than the corresponding tooth of *Eohyrax*. The lower molars lack secondary fossetids. The m2 is short and robust. In the lower molariforms of *Punahyrax* the protoconid does not have a posteriorly projecting protometastylid as is seen in the rest of the species of Archaeohyracidae (no central fossetid is formed).

3.1.1.2. Lower deciduous teeth. Only one tooth is identified as deciduous; MLP 86-V-6-9 (Fig. 7A), is tentatively identified as a left dp4 (*L*: 6.1 mm., *W*: 3.4 mm.). It displays essentially the same

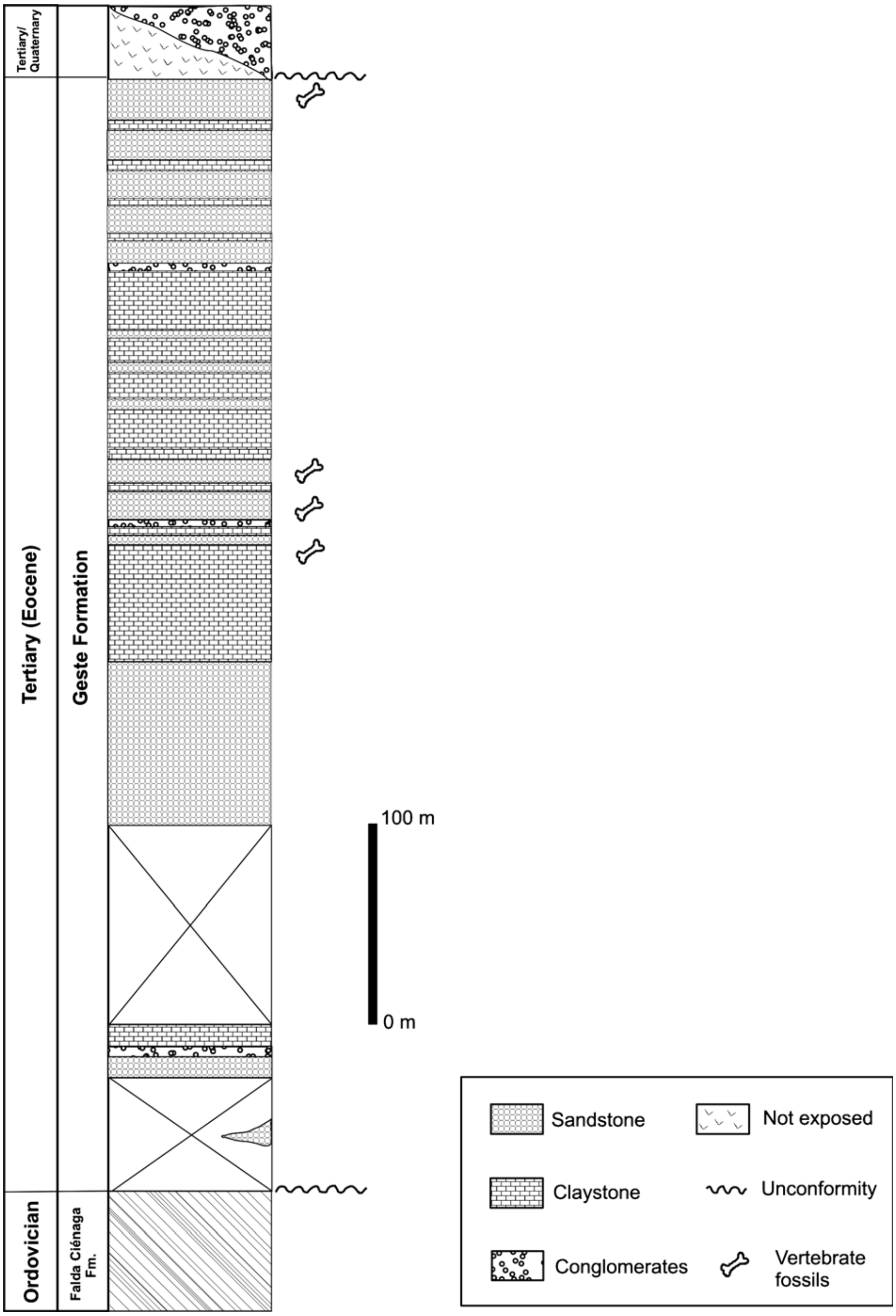

Fig. 4. Generalized lithostratigraphic profile of the Geste Formation at Antofagasta de la Sierra, Catamarca, Argentina.

morphology as its permanent counterpart but is smaller and has thinner enamel. It is unworn and lacks roots. The trigonid is squared and the paralophid is not reduced. The protoconid is the largest cusp and its posterior wall is smooth, lacking the protometastylid. The talonid is rounded and is slightly larger than the trigonid. The entoconid is large, very expanded, and connected to the hypolophid by a short entocristid. There is a small and low cuspid between the metaconid and the entoconid.

3.1.1.3. Upper dentition. Five upper molars from Pozuelos are provisionally assigned to P. bondesioi. This association is based on evidence from the overall morphology and size of the specimens and their stratigraphic provenance (the mammal-bearing horizons are equivalent in age). Only M1 and M2 of this species are preserved. The morphology of a very lightly worn M1 is exhibited by MLP 81-XI-15-4 (Fig. 7B). This molar is subquadrate and the height of the crown is as high as in Eohyrax. It has a large, obliquely oriented (antero-external to postero-internal) central fossa. It evidently had a fairly large hypocone, which is completely fused by wear to the protocone. The post-cingulum is low, enclosing a deep fossette. The paracone is more prominent than the metacone and a lingual bifid sulcus persists through early wear, delimiting a tiny median lobe. The metastyle is moderately large and the posterior cingulum is low and a labial fossette is present close to the metacone groove. The hypocone is somewhat differentiated, separated from the protocone by deep sulcus. Posteriorly, a weak and blade-shaped metastyle is present. The protoloph is orientated obliquely and its end is free (not forming a closed central fossa); the metaloph is strongly transverse.

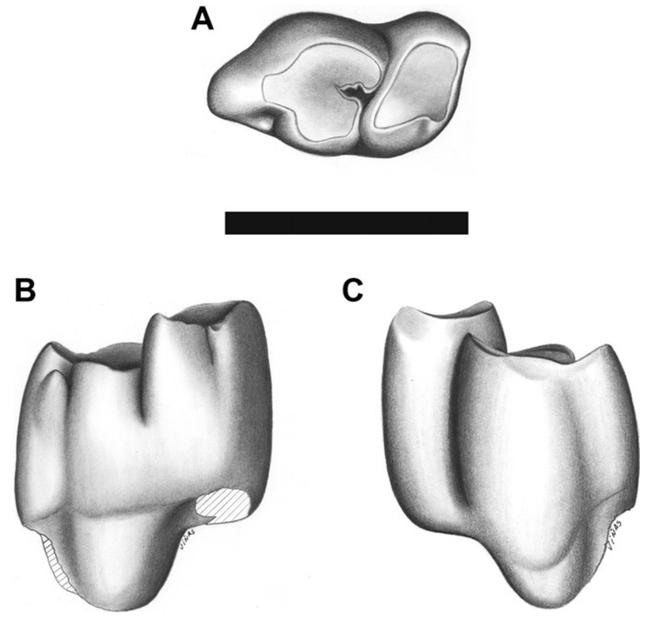

Fig. 5. Holotype of *Punahyrax bondesioi*, gen. et sp. nov., MLP 88-V-10-6, left m3 in (A) occlusal (above), (B) lingual (lower left), and (C) labial (lower right) views. Scale bar equals 0.75 mm.

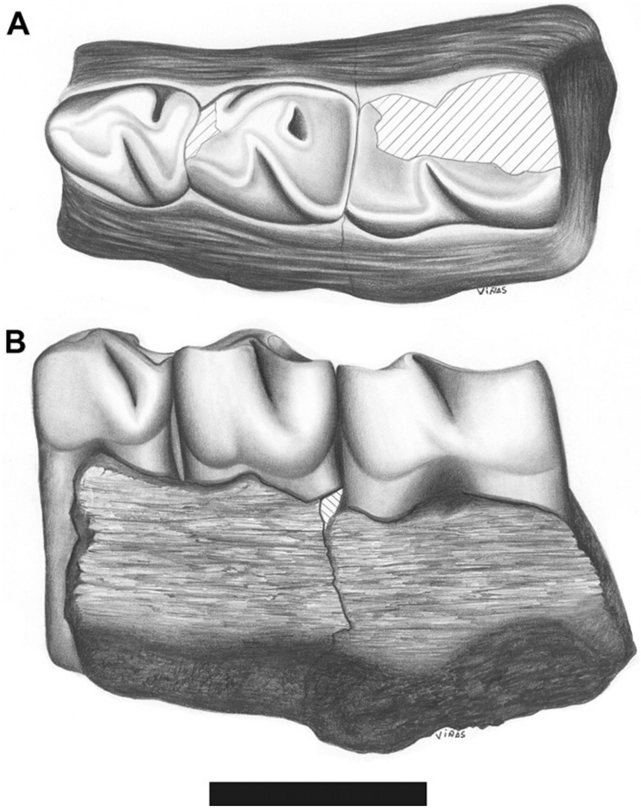

Fig. 6. *Punahyrax bondesioi* gen. et sp. nov., MLP 86-V-6-11, partial left mandible bearing p3-m1 in occlusal (above) and labial (below) views. Scale bar equals 0.75 mm.

In size, Punahyrax is smaller than any other known species of this family except Protoarchaeohyrax. Dental measurements are given in Tables 1 and 2.

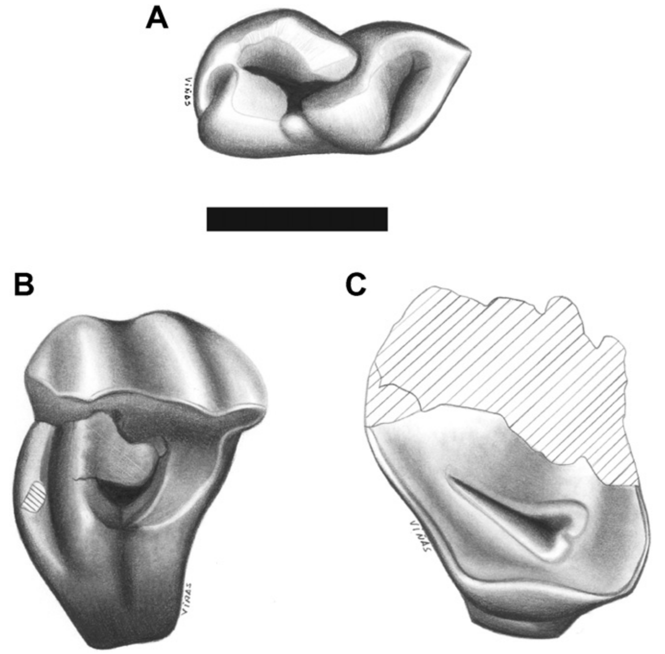

Fig. 7. *Punahyrax bondesioi* gen. et sp. nov., (A) MLP 86-V-6-9, left dp4, in occlusal view. (B) MLP 81-XI-15-4, left M1 in occlusal view. (C) *cf. Punahyrax*, MLP 86-V-6-10, right M1 or M2 in occlusal view. Scale bar equals 0.75 mm.

3.2. Punahyrax sp.

Referred specimens – MLP 86-V-6-10, left M1 or M2 broken on the labial side (Fig. 7C) and MLP 93-VI-1-11, right M1 or M2 broken on the labial side, both from Antofagasta de la Sierra, Catamarca province.

These teeth are assigned to *Punahyrax* based on overall molar morphology of the crests, the shape of the central fossette and the hypsodonty (HI = 0.95). Although they are broken and fragmentary, these specimens are considerably larger than *P. bondesioi* (MLP 86-V-6-10, *L*: 6.4 mm, *W*: 5.9 mm; MLP 93-VI-1-11, *L*: 6.4 mm, *W*: 5.7 mm.). The paucity of these teeth precludes specific designation at this time. MLP 86-V-6-10 and MLP 93-VI-1-11, may represent a new species or might be conspecific with *P. bondesioi*.

4. Discussion

We describe a new genus and species, *P. bondesioi*, from the early-middle Eocene of Geste Formation from the Puna area of Salta and Jujuy provinces, Argentina. The taxon is based on a partial jaw, and isolated upper and lower teeth.

Punahyrax bondesioi is a small-sized archaeohyracid. Only *Protarchaeohyrax minor* from the Tinguiririćan (early Oligocene) of Chile is smaller (10%) than this species.

The anterior upper and lower dentitions of *P. bondesioi* are not known, but the lower and upper molars indicate it to be unmistakably distinct from any described archaeohyracid genus possessing an antero-posteriorly-shortened talonid on the molars, and an enlarged entoconid.

The two genera most similar to *Punahyrax* are *Eohyrax* and *Pseudhyrax*. *P. bondesioi* has its closest affinities with *Eohyrax*. *P. bondesioi* is different in size (smaller) and slightly less hypsodont (Table 3) to the known species of *Eohyrax*, *E. isotemnoides* and *E. rusticus*, of the Barrancan age (late Eocene) of Patagonia. The absence of posterior cingulum on M1-2 of *P. bondesioi* certainly involves a derived condition from *Eohyrax*, as this trait is present not only in *Eohyrax*, but in other basal typotheres. However, *Punahyrax* is more similar in several aspects to *Eohyrax* than *Pseudhyrax*,

Table 3
Calculation of hypsodonty index for Archaeohyracidae

	HI
Punahyrax bondesioi	0.88
Eohyrax isotemnoides	1.28
Pseudhyrax strangulatus	1.60
Archaeotypotherium propheticus	1.50
Protarchaeohyrax gracilis	1.73
Archaeohyrax patagonicus	2.74

e.g., low crowned cheek teeth; talonid of the lower molars does not form a second fossette, and small body size.

Punahyrax bondesioi has only one similarity with *Pseudhyrax* from the Mustersan (late Eocene) of Patagonia. This is especially illustrated by the presence of a small pillar between the entoconid and the hypoconulid in m3 (Fig. 5B). This feature is rare within Archaeohyracidae, and Simpson (1967) figured one specimen of *P. eutrachytheroides* (AMNH 29410) from the Mustersan of Cerro Blanco, Chubut province, Argentina, bearing this character. Simpson (1967) suspected that this feature might be constant when the tooth is not worn. Simpson's photograph of AMNH 29410 also shows that the lingual sulcus between the trigonid and talonid in the m3 extends far below the base of the pillar. In the holotype of *Punahyrax*, this sulcus only extends to the base of the pillar. This seems to suggest much lower hypsodonty in *Punahyrax*. The lingual talonid sulcus is much deeper in *Pseudhyrax* than in *Punahyrax* – this forms a talonid fossettid in *Pseudhyrax* but does not appear to form one in *Punahyrax*.

The phylogenetic position of *Punahyrax* is clearly basal to the rest of the genera of the family, except *Eohyrax*. *Eohyrax* is currently considered to be the earliest diverging archaeohyracid, sharing with the rest of the archaeohyracids a single derived character: lack of enamel on the posterior face of I1 (Croft et al., 2003). This character is unknown in *Punahyrax* since no I1 is known of this genus. It suggests that more material of this genus and more detailed analyses should be done prior to performing a new phylogenetic analysis. Based on the topology obtained in the phylogenetic analysis of Archaeohyracidae performed by Croft et al. (2003), we hypothesized that *Punahyrax* is located at the base of the tree, close to *Eohyrax*, in a polytomy with the two outgroup taxa (*Oldfieldthomasia* and *Ultrapithecus*) and the clade of remaining archaeohyracids + *Hegetotherium* (Fig. 8). Three synapomorphies diagnose *Pseudhyrax* and later-diverging archaeohyracids (including the hegetotheriid *Hegetotherium*), the most robustly supported clade in the analysis (Fig. 8, Node 1), to the exclusion of *Eohyrax* and *Punahyrax*(the earliest diverging archaeohyracids): (1) presence of lower molar central trigonid fossettid (lost in *Hegetotherium*); (2) presence of small fossettid between m3 entoconid and hypoconulid (either lost in *Protarchaeohyrax* and *Hegetotherium,*independently derived in *Pseudhyrax, Archaeotypotherium,* and *Archaeohyrax*; (3) labial surface of m3 talonid with sulcus between hypoconid and hypoconulid (lost in *Protarchaeohyrax*).

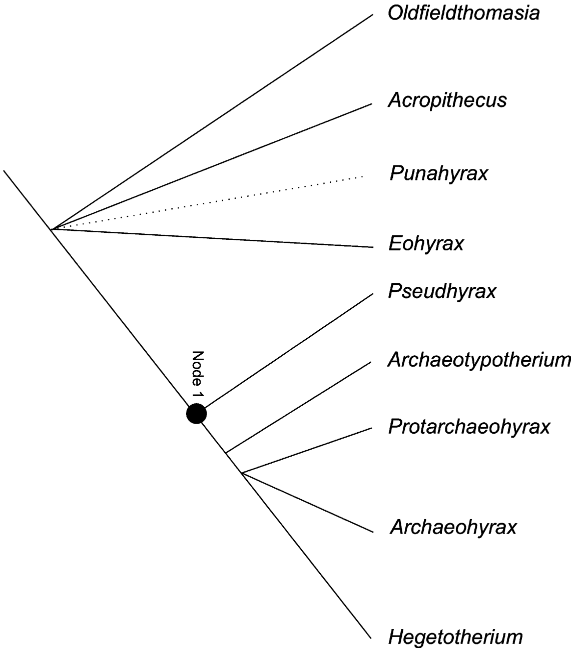

Fig. 8. Proposed phylogenetic position of *P. bondesioi* gen. et sp. nov. within "Archaeohyracidae", based largely on characters from Croft et al. (2003). This strict consensus tree shows *Punahyrax* located at the base of the tree in a polytomy with the two outgroup taxa, and *Eohyrax*.

Punahyrax bondesioi is most comparable in size to *P. minor* (Reguero et al., 2003) from Cañadón Blanco, Chubut province, Argentina, of probable Tinguirirican age (earliest Oligocene), which is approximately 10% smaller than the Puna taxon. Nevertheless, several features cited in the diagnosis, e.g., low crowned molars, somewhat expanded entoconid, and short talonid, distinguish *P. bondesioi* from *P. minor*.

When more material becomes available, a comparison of *Punahyrax* with *Eohyrax* sp. will be especially significant in determining primitive archaeohyracid dental morphology.

4.1. Age of the Punahyrax-bearing horizons

The age of the Geste Formation (Pozuelos Formation in Pascual, 1983; nec Turner, 1960) is somewhat problematic. Although a few taxa are known from the Pozuelos fauna (e.g., the marsupial, *Punadolops alonsoi*; the "notopithecine," *Punapithecus minor*; and the new species described here, *P. bondesioi*) all of these are shared with the Antofagasta de la Sierra fauna suggesting that these two faunas are similar in age. However, endemism complicates efforts to determine the temporal relationships between the Puna faunas and those from Patagonia. Based on scarce biochronologic evidence, some authors (López, 1997; Goin et al., 1998) suggested that the Antofagasta de la Sierra fauna is Mustersan in age. The Antofagasta de la Sierra fauna contains one taxon known elsewhere only from Mustersan, the pyrothere *Propyrotherium*. However, the Antofagasta de la Sierra pyrothere, a broken tusk, is very fragmentary and vaguely diagnostic, and does not permit a more precise identification. The Mustersan SALMA was recently calibrated by Kay et al. (1999, 2002) as late Eocene.

The absence of high-crowned notoungulates (later-diverging archaeohyracids, "rhynchippine" notohippids, interatheriine interatheriids) strongly suggests that Antofagasta de la Sierra and Pozuelos are older than the Tinguiririca SALMA which is characterized by communities dominated by high-crowned herbivores (Wyss et al., 1994; Flynn and Wyss, 1999; Flynn et al., 2003).

Other evidence suggests an age older than late Eocene for the Middle Member of the Geste Formation. Marshall et al. (1997) correlated the basal part of the fluvial sandstone assigned to the Geste Formation (see Jordan and Alonso, 1997) with the lower part ("Faja Verde" Member, Salfity and Marquillas, 1994) of the Lumbrera Formation of Pampa Grande, Salta province, northwestern Argentina, and with the lower part (La Cabaña Member) of the Potoco Formation in the Cordillera Oriental, Bolivia. Palynological evidence indicates a late Paleocene or early Eocene age for the Lumbrera Formation (Quatrocchio, 1978). Magnetostratigraphic studies indicate that the Faja Verde Member of the Lumbrera Formation is correlated with chrons 26n and 24n. Assuming that depositional rates were constant for the lower Lumbrera, the predicted age would be ~54.5 Ma (earliest Eocene; Marshall et al., 1997).

In contrast, the marsupial species associated with *Punahyrax* (*P. alonsoi*, *Bonapartherium serrensis*) possess a greater number of derived character states compared to those from Lumbrera Formation (*Prepidolops didelphoides*, *Bonapartherium hinakusijum*). This suggests that the *Punahyrax*-bearing fossiliferous localities may be younger than the Lumbrera fauna. Additionally, in Pampa Grande, the Casa Grande Formation overlies the Lumbrera Formation and seems to be partially equivalent to the Middle Member of the Geste Formation. Stratigraphic correlation between these units was suggested by Alonso and Fielding (1986). Based on the presence of an undescribed isotemnid notoungulate in both horizons, Bond and López (1995) supported the correlation between the vertebrate-bearing horizons of Geste and Casa Grande Formations.

Based on stratigraphic studies, Voss (2002) recently suggested a correlation between the Geste Formation and the lower member of the Quiñoas Formation (Campo Negro Member). The Campo Negro Member has been dated in 37.6 ± 0.3 Ma. (Kraemer et al., 1999). Based on this correlation the Geste Formation could be late Eocene in age as Alonso et al. (1988) suggested.

Given the lack of magnetostratigraphic and adequate micropaleontological data, as well as the endemism of the mammal faunas of the Puna, our assessment of the absolute age of these faunas is preliminary. We regard the Antofagasta de la Sierra and Pozuelos faunas to be middle and possibly late Eocene in age. The new information provided here regarding the record of primitive new archaeohyracids in the Eocene at low latitudes of Argentina strongly supports that northwestern Argentina could have played an important role as center of origin of the Archaeohyracidae. The affinity of Archaeohyracidae with the primitive notoungulate, *Campanorco inauguralis*, from the Paleocene Lumbrera Formation of Salta province, regarded by Reguero et al. (1996) as the sister group of the clade formed by Mesotheriidae plus Hegetotheria (= Archaeohyracidae + Hegetotheriidae), presents a biogeographic as well as phylogenetic puzzle. *C. inauguralis* is endemic to this area (Puna) and exhibits characters ancestral for archaeohyracids (e.g., low crowned cheek teeth, little enlarged I1, obliquely implanted I1). Geographically and phylogenetically, the presence of this family in the northwest of Argentina supports the point of view that the ancestral notoungulates close to the stem of Archaeohyracidae were differentiated in South America in the Paleocene/Eocene interval.

In Patagonia, the Archaeohyracidae are unquestionably known since the late Eocene Barrancan age. The presence of this family in strata older than Barrancan is dubiously accepted. Simpson (1967) and Bond et al. (1995) mentioned, but did not confirm, the presence of archaeohyracids in Paleocene strata of Patagonia. The absence of archaeohyracids in the well-sampled Vacan (early Eocene) of Cañadón Vaca (Cifelli, 1985) and Laguna Fría, Paso del Sapo, Chubut province (Goin et al., 2000; Bond et al., 2002) suggests the family was not present prior to the Barrancan (late Eocene) in Patagonia.

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