

A new Hypsodont Notungulate (Hegetotheriidae, Pachyrukhinae) from the late Miocene of the Eastern Cordillera, Salta province, Northwest of Argentina

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ABSTRACT. Late Miocene fluvial strata of the Palo Pintado Formation are broadly exposed to the northwest of the town of Angastaco, Salta province, Northwest of Argentina. These strata accumulated in the extensional Angastaco Basin. Recent field work at the Palo Pintado Formation (late Miocene), Valle Calchaquí, Salta province, Argentina has provided fossil remains that greatly increased the knowledge of the faunal assemblage of this site. A number of notungulates and rodents were collected. A partial left jaw was collected at Quebrada Peñas Blancas along the west bank of the Río Calchaquí. Morphological and morphometric comparisons permit referral of this specimen to a new species of hegetotheriid notungulate *Paedotherium kakai* sp. nov. It represents the first report of *Paedotherium* for the Eastern Cordillera and one of the few well-documented occurrences of this genus outside of middle-high latitudes Argentina. The widespread geographic range of *Paedotherium*, combined with its restricted temporal range, suggest it may be one of the most useful biostratigraphic indicator taxa for Neogene faunas. *Paedotherium kakai* would have been a mixed feeder that lived in gallery forests, feeding close to water bodies of a system river and lagoons, in food plains developed under humid and subtropical climate.

Keywords: Eastern Cordillera, Palo Pintado Formation, Valle Calchaquí, Late Miocene, Hegetotheriidae, *Paedotherium*.

RESUMEN. Un nuevo Notungulado Hipsodonte (Hegetotheriidae, Pachyrukhinae) del Mioceno tardío de la Cordillera Oriental, provincia de Salta, Noroeste de Argentina. Los estratos fluviales asignados al Mioceno tardío de la Formación Palo Pintado están ampliamente expuestos al noroeste de la localidad Angastaco, provincia de Salta, noroeste de Argentina. Estos estratos fueron acumulados en la Cuenca de Angastaco. Recientes trabajos de campo en la Formación Palo Pintado (Mioceno tardío), Valle Calchaquí, provincia de Salta, Argentina ha provisto restos fósiles que han incrementado el conocimiento de la asociación faunística de ese sitio. Un número discreto de especímenes (notungulados y roedores) fueron colectados. Una porción de cuerpo mandibular izquierdo fue colectado en la localidad Quebrada Peñas Blancas a lo largo del margen oeste del río Calchaquí. Comparaciones morfológicas permiten referir a este espécimen a una nueva especie de notungulado hegetotérido, *Paedotherium kakai* sp. nov. Esta nueva especie representa el primer registro de *Paedotherium* para la Cordillera Oriental y una de las pocas bien documentadas ocurrencias de este género fuera de las latitudes medias y altas de Argentina. El amplio rango de registro geográfico de *Paedotherium*, combinado con su restringido rango temporal sugiere que este género puede considerarse como un buen indicador bioestratigráfico para las faunas del Neógeno. *Paedotherium kakai* puede ser considerado un 'mixed feeder' que vivió en bosques, en galerías, alimentándose en las proximidades de los cuerpos de agua de un río, lagunas o en planicies de inundación bajo un clima húmedo y subtropical.

Palabras clave: Cordillera Oriental, Formación Palo Pintado, Valle Calchaquí, Mioceno tardío, Hegetotheriidae, *Paedotherium*.

1. Introduction

Study of Neogene South American fossil mammals has traditionally focused on faunas from the middle-high latitudes in Argentina (Patterson and Pascual, 1972; Simpson, 1980; Cione and Tonni, 1995). The discovery of low latitude faunas elsewhere in Argentina (NW and NE of Argentina) and other countries of South America (*e.g.*, Bolivia, Brazil, Chile, Colombia, Perú) have contributed to more complete understanding of the evolution of South American mammals. These low latitudes faunas demonstrate, for one, that latitudinal provinciality characterized South American mammal faunas for much of the Neogene, necessitating sampling of a wide geographic range for any given time slice to gain a fuller understanding of mammal evolution on the continent (Riggs and Patterson, 1939; Pascual *et al.*, 1985; Flynn *et al.*, 2002; Wyss *et al.*, 2003; Reguero *et al.*, 2007b; Reguero and Candela, 2011).

Fossil mammals previously collected from the lower levels within the Palo Pintado Formation near Calchaquí River indicate a late Miocene to early Pliocene age and palaeoenvironments characterized by relative humidity (Marshall *et al.*, 1983; Anzótégui, 1998; Starck and Anzótégui, 2001).

Our research team has been working to uncover and study Miocene/Pliocene fossil mammal faunas throughout the northwestern area of Argentina (Jujuy and Salta provinces). In March 2010, one of the authors (D. Voglino) collected a small fossil mandible of a pachyrukhine (Notoungulata: Hegetotheriidae) from the upper levels of the Palo Pintado Formation at Quebrada Peñas Blancas in the area of Angastaco, Salta province (Fig. 1). From the same horizon more vertebrates were recovered, preliminary identifications of the unprepared specimens suggest the presence of at least three rodents, in addition to the small notoungulate specimen collected at Quebrada Peñas Blancas described below. The finding of a jaw with teeth in this unit has renewed the interest of this paleontological area, since represents the first hypsodont notoungulate remains from this formation.

Assignment of the Palo Pintado hegetotheriid to the subfamily Hegetotheriinae is precluded by the morphology of m3 and the small size; the Palo Pintado taxon has a trilobed m3, whereas in all known hegetotheriines this tooth is sharply bilobed.

Hegetotheriid pachyrukhines are similar in size to other small- to medium- sized notoungulates, *i.e.*,

interatheriids, and some of the later representatives were very similar to modern rabbits (leporids) or certain 'caviomorph rodents' (*e.g.*, *Lagostomus*, *Dolichotis*) in overall morphology (Sinclair, 1909; Kraglievich, 1926; Elissamburu, 2004). The hegetotheriids become abundant during the late Oligocene Deseadan SALMA (Loomis, 1914; Simpson, 1945). They are last recorded in the Pleistocene of Argentina (Cerdeño and Bond, 1998). Two sub-groups are generally recognized within Hegetotheriidae: Hegetotheriinae and Pachyrukhinae (Simpson, 1945). Pachyrukhinae is universally considered monophyletic (Cerdeño and Bond, 1998) and the clade is certainly recognizable as early as the Deseadan SALMA (Loomis, 1914; Simpson, 1945; Reguero *et al.*, 2007b). In contrast, Hegetotheriinae is likely paraphyletic, though it may include a monophyletic subset of Miocene taxa (Cifelli, 1993; Flynn *et al.*, 2002; Croft *et al.*, 2004; Croft and Anaya, 2006; Reguero and Prevosti, 2010).

Herein is described a new species of *Paedotherium* from the late Miocene Palo Pintado Formation, Salta province, Argentina. The new species provides insight into Pachyrukhinae diversity during the Neogene and allow valuable comparisons between low latitude late Miocene faunas and similarly aged middle-high latitude faunas. In addition, the presence of a hypsodont fossil ungulate species in a forested environment is discussed.

2. Materials and methods

The specimen of the new species described below is housed in the vertebrate paleontology collections of the Museum of San Carlos, Salta province, Argentina. Measurements of this 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 de La Plata (Argentina); additional data were gathered from published sources.

Hypsodont dentition is characterized by high-crowned teeth, as opposed to brachyodont dentition, which is low-crowned. Hypselodonty refers to ever-growing, rootless or open-rooted dentition. Hypsodonty index follow Reguero *et al.* (2007a), and were calculated by dividing the m1 height by the m1 anterobuccal-posteriorlingual length.

S.Sal.Scar.Paleo.2012-045 was found *in situ* in the sandy facies of the bearing horizon and the adhering

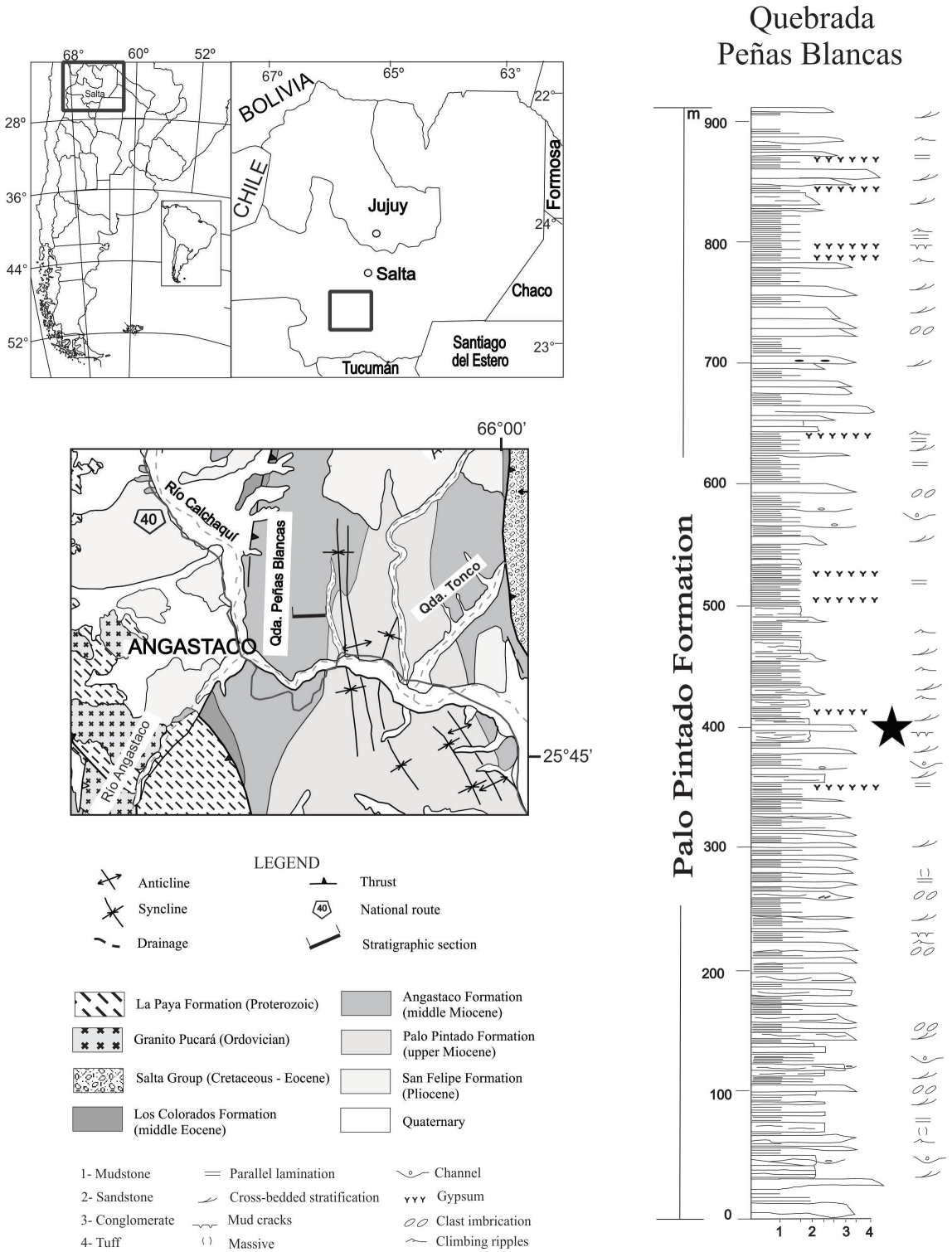


FIG. 1. Geography and geology of the Palo Pintado Formation. **Left:** map showing location of Quebrada Peñas Blancas in Salta. **Right:** measured stratigraphical column of the Palo Pintado Formation at Quebrada Peñas Blancas and the mammal-bearing horizon (star).

matrix is a fine sandstone which was deposited by large subaqueous dunes in fast-flowing confined channels (Fig. 2). Further, the preservation of this specimen indicates that it was not transported far, and there are no other potential source horizons in the immediate vicinity. Some taphonomic characteristic of the teeth show no abrasion by sedimentary transport, *i.e.*,

1. the amount and distribution of cementum (dentine-cementum boundary indicated in figure 3) is normal and suggests that little abrasion has occurred; **2.** no rounding and no enamel loss at the edges of occlusal surfaces; **3.** no removal of enamel along the salient angles. Histologic features of the crowns teeth also indicate that little, if any, dentine has been removed, other than by normal processes of occlusal attrition.

Institutional Abbreviations: MLP: Museo de La Plata, Buenos Aires, Argentina. S.Sal.Scar.Paleo: Museo de San Carlos, Salta, Argentina.

Other Abbreviations: Lower tooth loci are indicated by lower case letters (*e.g.*, p2, m1). **HI:** hypsodonty index. **SALMA:** South American Land Mammal Age, Stage/age; cronostatigraphic unit.

3. Geographic and geologic setting

The Eastern Cordillera area in Argentina is situated to the northwest between 22°05' and 27°00'S and 64°40' and 66°10' W; it represents the southern extremity of the same mountain range known from Bolivia. The narrow, NS trending Angastaco basin is located in the distal part of a once contiguous Paleogene Retroarc Foreland basin (Jordan and Alonso, 1987). The Angastaco basin is located in the southern part of the Eastern Cordillera. This basin includes >6 km of Eocene-Pliocene continental clastic strata of the Payogastilla Group (*e.g.*, Díaz and Malizzia, 1983; Starck and Vergani, 1996). This basin is bounded to the west by the Precambrian-early Cambrian metasedimentary Puncoviscana Formation over the Cenozoic basin strata. To the east, the Cretaceous rocks of the Sierra de Los Colorados over the basin strata (*e.g.*, Carrera and Muñoz, 2008).

The Palo Pintado Formation comprises fluvial systems deposits which are well exposed at Peñas Blancas outcrops. The lithofacies boundaries and the



FIG. 2. *Paedotherium kakai*, holotype, S.Sal.Scar.Paleo.2012-045 *in situ* in the sandy facies of the bearing horizon and the adhering matrix is fine sandstone which was deposited by large subaqueous dunes in fast-flowing confined channels.

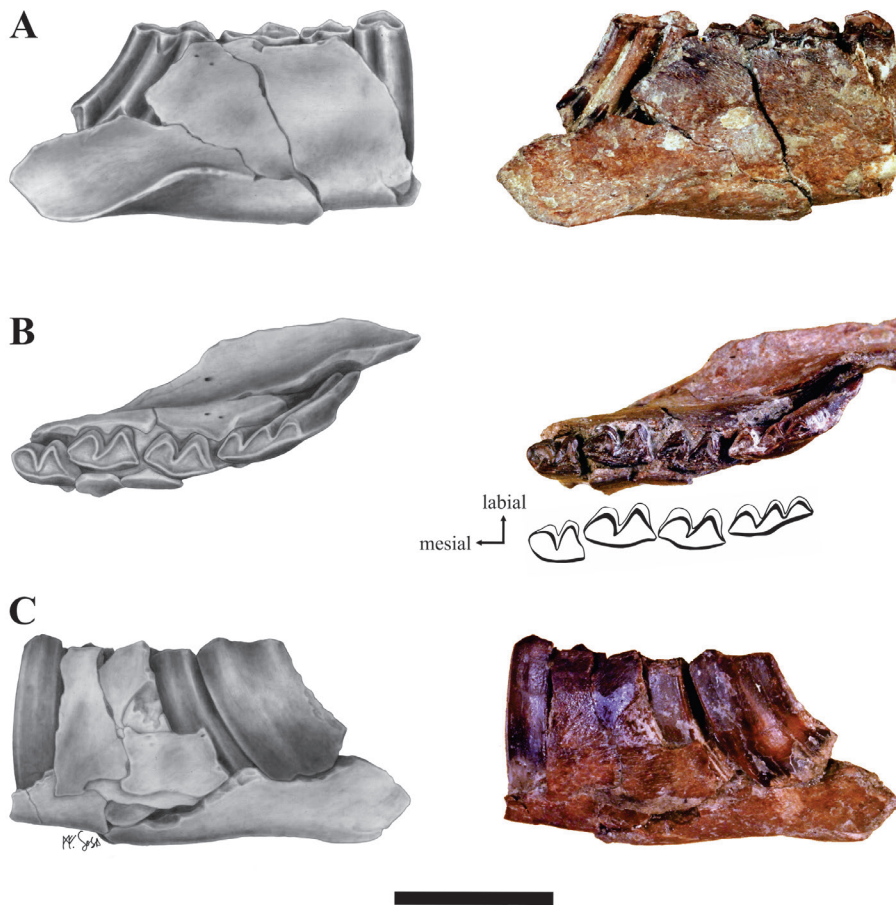


FIG. 3. *Paedotherium kakai*, holotype, S.Sal.Scar.Paleo.2012-045; right mandibular fragment with p4-m3; **A**. Labial view; **B**. Occlusal view; **C**. Lingual view. Scale bars=1 cm.

characteristics and geometries of the architectural elements are documented in the stratigraphic column (Fig. 1). We interpret these facies as the deposits of laterally unstable shallow gravelly channels, perhaps in a braided fluvial system (e.g., Miall, 1996).

The Palo Pintado Formation (ca. 10 to 5 Ma) consists of ~1,200 m of colored fine to medium-grained sandstone beds with trough cross-stratified sandstones interpreted as fluvial channel sand bodies (e.g., Davis, 1983).

The geological context and the stratigraphic profile of the Palo Pintado Formation at the Quebrada Peñas Blancas area are fully detailed in figure 1. The new fossil material comes from about 410 m above the base of this unit, close to a left tributary of the Calchaquí River (Fig. 1). The age of this formation range between 10.29±0.11 Ma (Galli *et al.*, 2008, 2011) below

the bearing horizon, and 5.27±0.28 Ma (Coutand *et al.*, 2006) and 5.98±0.32 Ma (Bywater-Reyes *et al.*, 2010) on the top of the unit. Magnetostratigraphic study in progress of the Palo Pintado Formation has dated the mammal-bearing horizon at ca. 8.8 Ma (personal communication, C. Galli, 2013). This formation is correlated with the Guanaco Formation in the La Viña area (Sierra de Los Colorados) that has been dated at 8.73±0.25 Ma by K-Ar on biotite from an ash (Del Papa *et al.*, 1993) and by zircon U-Pb at 9.31±0.31 Ma (Hain *et al.*, 2011).

The Palo Pintado Formation at Quebrada Peñas Blancas is gradational with the Angastaco Formation (Fig. 1) and consists of ca. 1,000 m of green mud rocks and sandstones interbedded with green ripple- and planar-laminated mudstones interpreted as associated to a relatively fine grained, nonmarine

setting with meandering stream (Galli et al., 2011). The fluvial system interpreted for this unit is intermediate between fluvial braided (with low sinuosity and simple channels) and meandering rivers (with high sinuosity and multiple channels) (Miall, 1996). The trough cross-stratified conglomerates and sandstones were deposited by large subaqueous dunes (or large 3D ripples) in fast-flowing confined channels.

4. Systematic paleontology

Class MAMMALIA Linnaeus, 1758

Order NOTOUNGULATA Roth, 1903

Suborder TYPOTHERIA Zittel, 1893

(sensu Reguero and Castro, 2004)

Family HEGETOTHERIIDAE Ameghino, 1894

Subfamily PACHYRUKHINAE Kraglievich, 1934

(see diagnosis in Cerdeño and Bond, 1998)

Genus PAEDOTHERIUM Burmeister, 1888

PAEDOTHERIUM KAKAI sp. nov.

Figure 3

Holotype: S.Sal.Scar.Paleo.2012-045, right mandibular fragment with p4-m3.

Diagnosis: Similar in size to *P. typicum* and *P. bonaerense*. The fourth premolar (p4) proportionally longer than the molars, exhibits the trigonid more rounded than *P. typicum* and *P. bonaerense*. Differs from all other species of *Paedotherium* in having no cementum on the molariforms and the cheek teeth are less hypsodont (HI: 2.6) than *P. typicum* and *P. bonaerense*. The third molar (m3) is narrower, with shallow labial sulci and the last lobe is smaller and more rounded than *P. typicum* and *P. bonaerense*.

Etymology: *kakai*, from Cacán language spoken by Diaguitas and Calchaquíes tribes who inhabited the Valle Calchaquí, Salta province, this language became extinct since the mid-17th century or beginning of 18th century. When the Inca started extending their empire southwards in the 15th century, the Diaguita fiercely resisted the invasion.

Type Locality: Quebrada Peñas Blancas (S 66° 09.42'4.81"; W 25°67.18'5.43" and 1,857 m a.s.l.).

Age and Distribution: Palo Pintado Formation, Quebrada Peñas Blancas, Salta Province, northwest Argentina, Huayquerian (late Miocene) age.

Three species of *Paedotherium* are currently recognized (Cerdeño and Bond, 1998): *P. minor* from the late Miocene Chasicoan and Huayquerian stage/ages, *P. typicum* and *P. bonaerense* from Huayquerian.

Description: S.Sal.Scar.Paleo.2012-045 consists of a partial right mandible that has been partially prepared. Most of the horizontal ramus is preserved. The alveolar and inferior margins are roughly parallel, with the depth of the mandible averaging approximately 11.5 mm. All teeth are fully erupted and have undergone moderate wear, indicative of a fully mature animal.

Paedotherium kakai is similar to *P. typicum* in morphology and is comparable in size. It was compared with the lectotype of *P. typicum*, MLP 12-1782, from the Montehermosan Stage/age of Buenos Aires Province, Argentina (Fig. 4).

The fourth premolar (p4) of *Paedotherium kakai* is similar to *P. typicum* in morphology but is less molariform, it has a very simple occlusal surface and exhibits a single deep labial sulcus separating the trigonid from the talonid. The sulcus is open and the lingual extremity has closely appressed sides. The talonid is wider than the trigonid in both p3 and p4 but is similar to it in length (mesiodistal). The lingual face of p4 is slightly convex. Enamel is absent from the distolingual and mesial surfaces, no cement covers the labial surface.

The molars are subequal in size, but gradually decrease from m1-m3. The first (m1) and second lower (m2) molars closely resemble p4 in size and morphology except that the lingual faces are slightly less convex and the labial sulci are deeper, extending more than halfway across the tooth. These attributes give the impression of a more slender tooth, but this is not reflected in dental measurements (Table 1).

The morphology of m3 is the most notable aspect of the dentition of *P. kakai*. A labial sulcus separating the trigonid and the talonid, and a second shallow labial sulcus is present in approximately the middle of the talonid. The resulting 'trilobed' condition is common to all pachyrukhines but the shape and locations of the sulci is variable between the species.

Comments: In overall morphology, *Paedotherium kakai* is similar to *P. typicum*. The most obvious difference between these two species is in morphology is the shape of the lobes and the locations of the labial sulci that conforms the tooth. *Paedotherium kakai* is a large pachyrukhine, but is significantly smaller than the Deseadan SALMA (late Oligocene) species *Prosotherium garzoni* and *Medistylus dorsatus* from Patagonia, the largest member of the subfamily; it is similar in size to *P. typicum* and *P. bonaerense*, overlapping in size some specimens described by Cerdeño and Bond (1998). Beyond of size features,

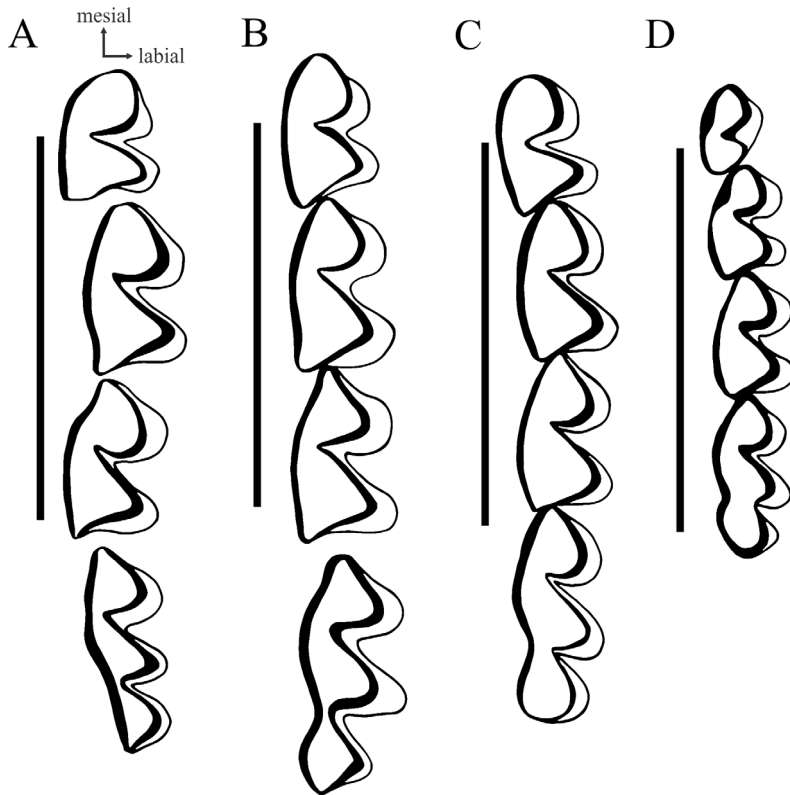


FIG. 4. Occlusal views of right p4-m3 series of **A.** *Paedotherium kakai* (holotype, S.Sal.Scar.Paleo.2012-045); **B.** *Paedotherium typicum* (lectotype, MLP 12-1782); **C.** *Paedotherium minor* (MLP 30-XII-10-29); **D.** *Tremacyllus impressus* (MLP 57-X-10-55). Scale bar=1cm.

the combined morphological difference cited in the diagnosis, clearly distinguish *Paedotherium kakai* from all previously described Neogene pachyrukhines.

5. Discussion

5.1. Biostratigraphic and biogeographic significance of the genus *Paedotherium*

Pachyrukhines are extremely common in the Miocene and Pliocene of Argentina. From the late Miocene (Chasicuan/Huayquerian) to late Pliocene (Marplatan), only two genera are represented, *Paedotherium* and *Tremacyllus*.

Paedotherium is best known from the rich Chasicuan and Huayquerian (late Miocene) deposits along the Atlantic coast of Buenos Aires. The temporal record of *Paedotherium* ranges from late Miocene to late Pliocene of Argentina, Chile and Bolivia; it is one of the most abundant mammals in

Montehermosan and Chapadmalalan faunas of the Buenos Aires (Monte Hermoso, Chapadmalal, Barranca de los Lobos, etc.) and La Pampa provinces (Zetti, 1972; Cerdeño and Bond, 1998).

The smaller species, *Paedotherium minor*, is recognized in the Arroyo Chasicó Formation (Vivero and Las Barrancas members) and the Epecuén Formation, which represent the late Miocene Chasicuan and Huayquerian ages, respectively (Cerdeño and Bond, 1998). Contreras and Baraldo (2011) mentioned *Paedotherium minor* from horizons assigned to the Chasicuan and Huayquerian ages in San Juan province. Brandoni *et al.* (2012) mentioned the presence of *Paedotherium minor* in the El Degolladito, La Rioja province, from sediments of Salicas Formation. This species also is recognized from sediments of Cerro Azul Formation assigned to the late Huayquerian for Verzi and Montalvo (2008) (but see Prevosti and Pardiñas, 2009 for a discussion about age of these bearing sediments).

TABLE 1. MEASUREMENTS OF LOWER DENTITION OF *PAEDOTHERIUM KAKAI* SP. NOV. AND OTHER PACHYRUKHINES.

	<i>Paedotherium kakai</i> S.Sal.Scar.Paleo.2012-045	<i>Paedotherium minor</i> MLP 29-X-10-90	<i>Paedotherium minor</i> MLP 29-X-10-88	<i>Paedotherium minor</i> MLP 31-XI-12-16	<i>Paedotherium minor</i> SF 13	X <i>P. minor</i> Cerdeño and Bond, 1998	X <i>P. typicum</i> Cerdeño and Bond, 1998	X <i>P. bonaerense</i> Cerdeño and Bond, 1998	<i>Tremacyllus</i> sp. MLP 76-VI-12-130	X <i>T. impressus</i> Cerdeño and Bond, 1998
L p2	-	1.6	1.97	-	-	2.36	2.52	2.59	1.96	2.07
W p2	-	1.08	1.57	-	-	1.44	1.49	1.53	1.19	1.17
L p3	-	3.06	2.64	-	2.49	3.25	3.37	4.14	2.53	2.52
W p3	-	1.68	1.78	-	1.77	2.04	2.18	2.48	1.58	1.65
L p4	3.80	2.99	2.87	-	3.09	3.76	2.8	4.38	2.86	2.65
W p4	2.60	1.88	1.99	-	2.02	2.23	2.34	2.57	1.86	1.72
L m1	4.43	3.85	4.24	3.25	3.93	4.11	4.26	4.52	3.8	3.45
W m1	2.24	2.2	2.18	1.96	2.42	2.32	2.45	2.65	2.27	2.04
L m2	4.71	-	4.21	3.4	3.68	4.13	4.37	4.53	3.99	3.57
W m2	2.36	-	2.3	2.42	2.42	2.3	2.48	2.59	2.29	2.13
L m3	5.66	-	-	4.87	5.6	5.66	6	6.05	-	4.74
W m3	2.18	-	-	2.09	2.35	2.19	2.32	2.36	-	1.97

One of the largest species, *Paedotherium typicum*, is abundantly recorded in the Monte Hermoso (Monterhermosan age; Tomassini *et al.*, 2013) and the Chapadmalal (Chapadmalalan age) formations in Buenos Aires province. It is coeval with *P. bonaerense*, but *P. typicum* occurs more frequently in the Montehermosan (Tomassini *et al.*, 2013), while *P. bonaerense* is more abundant in the Chapadmalalan age. Some scarce remains indicate the persistence of *P. typicum* in the younger Marplatan levels of the Barranca de Los Lobos and Vorohué formations. Also this species has been mentioned from late Miocene Río Quinto Formation of San Luis province (Prado *et al.*, 1998). *Paedotherium* cf. *typicum* also is recorded in the Pliocene Alvear Formation (Candela *et al.*, 2007). The size of *P. typicum* and *P. bonaerense* is very similar (Table 1).

In a biostratigraphic context the last appearance of *Paedotherium* is in the *Paractenomys chapadmalensis* Zone (Marplatan Age, Sanandresian subage, late Pliocene, Cione and Tonni, 1995). The probable persistence of *Paedotherium* in the Ensenadan age of Buenos Aires Province involves scarce remains assigned to *P. bonaerense*. Nevertheless, the stratigraphic provenance of these remains is doubtful (Bond *et al.*, 1995).

Except for the records of *Paedotherium minor* in the late Miocene (Chasicoan-Huayquerian) from the Guandacay Formation in Bolivia (Marshall and Sempere, 1991), middle Miocene from Cura Mallín Formation in Chile (Wyss *et al.*, 2003), and from the late Miocene of the Catamarca, Argentina (Valle del Cajón) and *Paedotherium kakai* in the late Miocene from Palo Pintado Formation, Salta in Argentina, the genus *Paedotherium* had a strictly middle latitude Pampean distribution. This contrasts with most high- and middle-latitude faunas (*i.e.*, those south of 23°S) in which *Paedotherium* account for the majority or entirety of hegetotheriid remains (*e.g.*, Sinclair, 1909; Zetti, 1972; Cerdeño and Bond, 1998). *Paedotherium kakai* is the first unambiguous record of the genus in the Eastern Cordillera NW of Argentina. At Quebrada Peñas Blancas, the Palo Pintado Formation (*i.e.*, fluvial association; Fig. 5) ranges in age between 10.29±0.11 Ma and 5.27±0.28 Ma (Galli *et al.*, 2011; Carrapa *et al.*, 2006). Additionally, interfingering of this Palo Pintado Fm. with the Guanaco Formation at La Viña area (Sierra de Los Colorados, a laterally equivalent facies) has been dated at 8.73±0.25 Ma by K/Ar on biotite from an

ash (Del Papa *et al.*, 1993) and by zircon U-Pb at 9.31±0.31 Ma (Hain *et al.*, 2011).

The Quebrada Peñas Blancas specimen was collected from near the top of the middle part of the Palo Pintado Formation (*i.e.*, fluvial association), suggesting an age slightly older than 6 Ma and younger than 10 Ma. Magnetostratigraphic study in progress of the Palo Pintado Formation has dated the mammal-bearing horizon at *ca.* 8.8 Ma (late Miocene, personal communication, C. Galli, 2013).

5.2. Hypsodonty of *P. kakai* and the paleoenvironment of the Valle Calchaquí in the late Miocene

The Pachyrukhinae are small terrestrial herbivorous hegetotheriids easily recognized by their specialized anterior dentition, ‘rabbit-like’ and ever-growing (rootless) incisors and cheek teeth. They were extremely abundant in the mid-Cenozoic of Argentina. Based on dental dimensions, their body mass would have ranged from about 1.8 to 2.2 kg (Castro, 2001; Elisamburu, 2011; Cassini *et al.*, 2011); it is interesting to note that the only extant ungulate with similar size is the ruminant Asian tragulid mouse deer, the smallest artiodactyl known. Pachyrukhines are generally reconstructed as grassers and open habitat specialists that might have lived in burrows and resembled rabbits (leporids) or various South American rodents (caviids, chinchillids) in lifestyle (Sinclair, 1909; Kraglievich, 1926; Cifelli, 1985; Genise, 1989; Dozo, 1997; Cerdeño and Bond, 1998; Elisamburu, 2004).

The hypsodonty of *Paedotherium kakai* offers other possible paleoecological interpretation which is in agreement with the palaeoclimate and palaeoenvironment inferred for the Palo Pintado Formation, characterized by habitats forested, with system of sinuous rivers, marsh and lagoons developed under a humid and subtropical climate, with short dry seasonality (Galli *et al.*, 2011; Anzótégui and Horn, 2011) (Fig. 5). Study of megaflore of Palo Pintado indicate four paleocommunities: fresh water, marsh (*e.g.*, *Blechnum serrulatiformis*, *Acrostichum paleoaureum*), riparian (*e.g.*, *Cedrella fissiliformis*, *Sapium haemospermoides*, *Nectandra saltensis*, *Ficus tressensii* in the arboreal stratum, and the climbing *Ranunculodendron anzoteguiiae*) and xerophytic forests areas (Anzótégui and Horn, 2011), without evidence of development of grasslands or open savannas. So, open habits with predominant

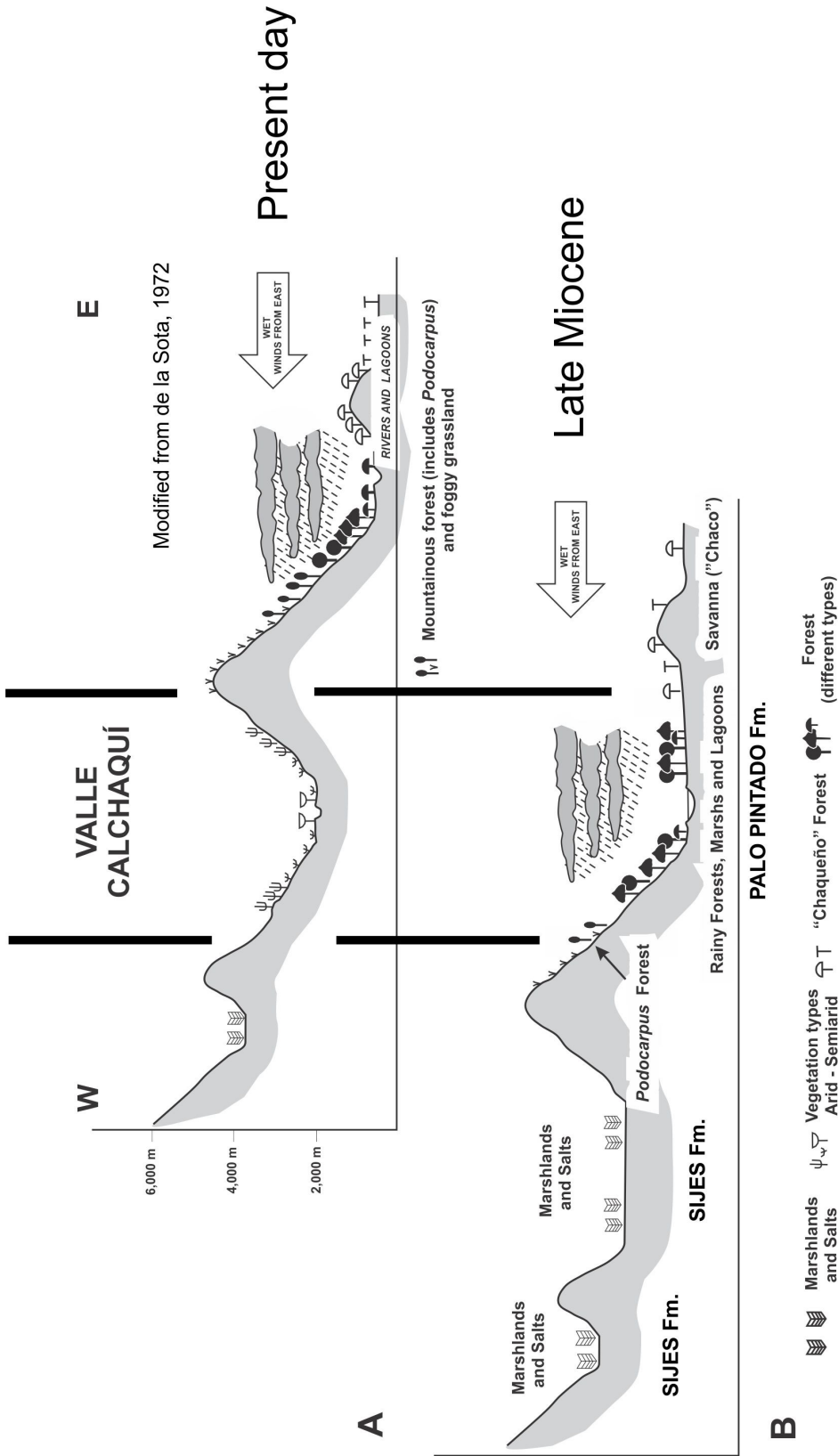


FIG. 5. Schematic topographic profiles showing the paleoenvironment distribution (modified from Starck and Anzótegui, 2001). **A.** Present day; **B.** Late Miocene (deposition time for the upper section of the Palo Pintado Fm.).

grass were not the environments dominant inferred for Palo Pintado Formation. Note that the case of *Paedotherium kakai* is in contrast with the majority of the late Miocene extinct South American ungulates, for which no information on the paleoenvironment conditions of its bearing-units is little or not available. In this context, we assume that hypsodonty in *P. kakai* is not a feature associated with grasser feeding habits and strictly open habits. Then, if unquestionably hypsodont indicates high rates of tooth wear (Fortelius, 1985), we must explore which are the abrasive factors that explain the relatively high rate of tooth wear in *P. kakai* (Table 2).

At least partially, hypsodonty is here interpreted as feature reflecting the evolutionary history of the group previously acquired in the Pachyrukhinae during late Oligocene in Patagonia, when extensive grasslands were certainly absent (Palasezzi and Barreda, 2012; Billet *et al.*, 2009; Kay *et al.*, 1999; Reguero *et al.*, 2010; Strömberg *et al.*, 2011). On the other hand, hypsodonty in *P. kakai* is understood as feature associated to abrasive particles consumption during feeding.

Janis (1988) concluded that hypsodonty alone could not be taken as evidence for grazing behavior in extinct ungulates and suggest that, although do not the only factor; the grit had an important role for hypsodonty. Likewise, other authors (*e.g.*, Williams and Kay, 2001; Mendoza and Palmqvist, 2008; Damuth and Janis, 2011 and citations herein) indicated

that soil ingestion in ungulates has a considerable explanatory power of hypsodonty, irrespective of the proportion of the grass in the diet.

In line with these ideas, soil consumption, including abrasive particles such as sand, dust, volcanic glass, etc., adhered to surface of food or accidentally ingested, could explain, at least partially, the high degree of hypsodonty in *P. kakai*. Examples of living ungulates indicate that hypsodonty and wear rates vary with levels of soil ingestion, but not entirely with proportion of grass in the diet (Damuth and Janis, 2011). Currently the pronghorn antelope (*Antilocapra americana*) is an examples of an hypsodont not grasser but mixed-feeding species, in which soil intake explains, at least as an important factor, the tooth wear (Damuth and Janis, 2011). On the other hand, among extant ungulates, these authors given examples of some populations of grazing or mixed-feeding species that live in rainforest regions (*e.g.*, *Bubalus mindorensis*, buffalo, *Syncerus caffer*), where the grass is essentially absent.

Ungar *et al.* (1995) support the presence of hypsodont species in forested habits obtaining source of wear on dust particles found in the canopies of tropical dry forests and rainforests.

Therefore, soil consumption, including probably sand near of border of rivers or lagoons, or consumption of dust or abrasive particles of soil adhered to food surfaces in floodplains or riparian forest could have acted as wear tooth in *Paedotherium kakai*. Compared with *Paedotherium typicum* and *P. minor*, the lesser degree of hypsodonty and the absence of cement of *P. kakai* would be indicative of a lesser amount of abrasive particle in the diet. *P. kakai* must have had a relatively lesser rate of abrasive particle consumption, indicative of a diet (food?) not highly abrasive, perhaps because it was being foraged close to water and so more free of grit. A high hypsodonty and the presence of cementum in *Paedotherim typicum* and *P. minor* evidence an increasing dietary abrasion as consequence of the grasslands became more widely available in the more open habits of Pampean region. These features common to these species suggest that their feeding habits were influenced by Cenozoic climate and its impact on paleoenvironment and habitat structure.

As discussed above, *Paedotherium kakai* probably was a mixed feeder compared with *P. minor* and *P. typicum*, consuming a variable diet obtained close to the ground. In the context of hypsodont species,

TABLE 2. HYPSONDONTY INDEX (HI) FOR SMALL-/MEDIUM SIZED HEGETOTHERES.

Species	Age	HI
<i>Medistylus dorsatus</i>	Late Oligocene	2.41
<i>Prosotherium garzoni</i>	Late Oligocene	2.72
<i>Pachyrukhos moyanoi</i>	Middle Miocene	3.52
<i>Tremacyllus impressus</i>	Late Miocene/Pliocene	3.23
<i>Paedotherium bonaerense</i>	Pliocene/Pleistocene	4.10
<i>Paedotherium typicum</i>	Pliocene	4.06
<i>Paedotherium kakai</i> sp. nov.	Late Miocene	2.61
<i>Prohegetotherium sculptum</i>	Late Oligocene	2.23
<i>Hegetotherium mirabile</i>	Middle Miocene	2.42

this ungulate was probably a wide ranging species that lived in gallery forests, being able to eat close to water bodies of a system river and lagoons that occurred in the foodplains developed under humid and subtropical climate.

Other hypsodont species, the giant rodent *Eumegamys paranensis* from the late Miocene of Argentina, adds to the examples of hypsodont but not grasser species (Candela et al., 2013) dwellers of forested habits, developed under warm and humid climate, where the grasses were not predominant.

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