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News and Views

New early Miocene primate fossils from northern Patagonia, Argentina

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Introduction

There has been a long history of fossil primate discoveries in South America since the nineteenth century with the pioneering works of Peter Lund and Carlos and Florentino Ameghino. Most of the 26 described extinct genera come from two distant regions: Patagonia (Argentina and Chile) and La Venta (Colombia), ranging from the early to middle Miocene (e.g., Fleagle and Tejedor, 2002; Hartwig and Meldrum, 2002; Tejedor et al., 2006; Kay, 2010). The fossil record still remains limited, hampering the proper understanding of the history of the group, which is still a matter of debate.

The oldest records of primates in South America belong to *Branisella* and *Szalatavus*, derived from late Oligocene deposits at Salla, Bolivia (see Fleagle and Tejedor, 2002 and references therein), assigned to the Deseadan SALMA (South American Land Mammal Age). The second oldest series of platyrrhine primates is derived from early Miocene levels of central Patagonia and Chile, which are assigned to the Colhuehuapian SALMA, and includes *Dolichocebus*, *Tremacebus*, *Mazzonicebus*, and *Chilecebus* (Kay, 2010 and references therein).

In this work, we report the discovery and discuss the implications of two isolated primate teeth from early Miocene beds of northern Patagonia (Neuquén Province, Argentina, Fig. 1a). Due to the fact that platyrrhines are one of the rarest groups among South American Cenozoic mammals, even fragmentary new discoveries are relevant. Particularly, these new findings represent the first reports of early Miocene primates in northern Patagonia, and possibly the oldest in Patagonia, and thus extend the oldest primate records in southern latitudes. Primate specimens compared along the text are listed in Table 1.

Description and comparisons

MOZ-PV-927 (Fig. 2a–c) is an unworn left p4 with a single root that is grooved lingually (Table 1). The crown is 3.4 mm in length and 3.1 mm in width. The trigonid is higher and mesiodistally longer than the talonid, as in the holotype of *Carlocebus carmenensis* (MACN Pv SC266, Santacrucian SALMA, latest early Miocene) and in *Homunculus patagonicus* (the neotype MACN A 5757 and MACN Pv SC3026, Santacrucian SALMA). This contrasts with the situation in *Aotus* and extant pitheciines, in which the talonid is expanded, mesiodistally much longer than the trigonid. The buccal side of the crown is relatively flat, similar to *H. patagonicus* (MACN Pv SC3026), whereas *Soriacebus ameghinorum* (holotype MACN Pv SC2, Santacrucian SALMA), *Mazzonicebus almendrae* (MLP 69-III-12-1), *Aotus*, and living pitheciins have sloping buccal sides and apparently thicker enamel. The protoconid is higher, more robust than the metaconid, and as usual among platyrrhines, the metaconid is placed distolingual to the protoconid. The protoconid and metaconid are separated, resembling species of *Carlocebus* (early Santacrucian SALMA) and *H. patagonicus*, but not by as much as in *Aotus* and living pitheciins. Both the preprotocristid and (especially) premetacristid are weak. Unlike extant platyrrhines, the preprotocristid extends mesiolingually, leaving the trigonid opened as in *Dolichocebus gaimanensis* (MACN Pv CH898, Colhuehuapian SALMA; Kay et al., 2008), *M. almendrae*, and *H. patagonicus*. The talonid has at least three small distal cuspules, whose homologies with the entoconid and hypoconulid are uncertain.

MOZ-PV-1062 (Fig. 2d–f) is a right lower canine, 4.2 mm in length and 3.1 mm in width. The tooth is worn but the broken tip

Abbreviations: MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Buenos Aires); MLP, Museo de La Plata; MOZ-PV, Colección Paleontología de Vertebrados, Museo Prof. Juan Olsacher (Zapala, Neuquén).

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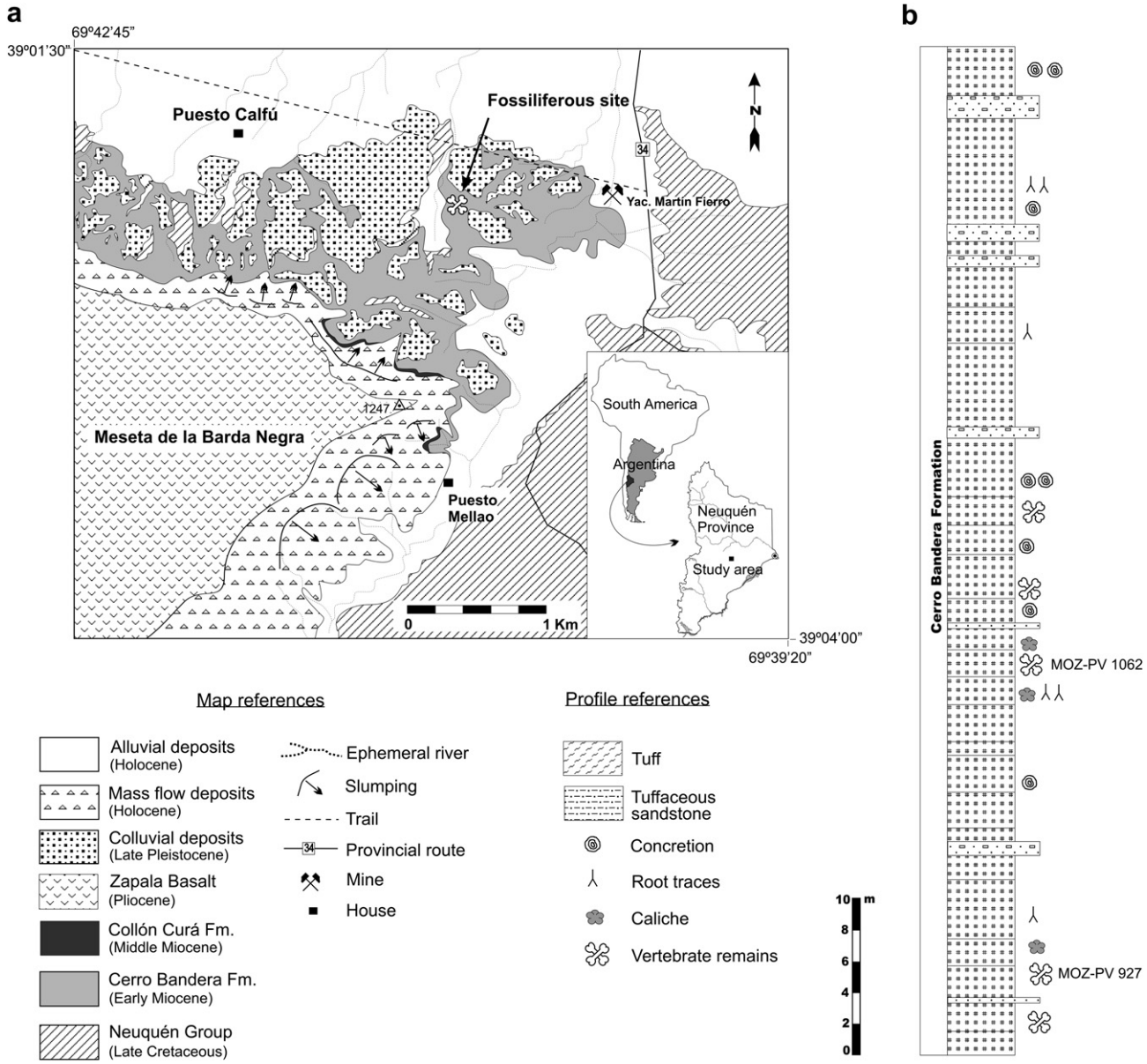

Figure 1. (a) Geologic map of the northeastern slope of the Barda Negra hill (Neuquén Province, Argentina), showing the location of the site bearing primate remains of the Cerro Bandera Formation. (b) Stratigraphic section of the Cerro Bandera Formation at Puesto Calfú locality showing the provenance of the primate remains MOZ-PV-927 (S 39°02′06.3″/W 69°40′54.3″) and MOZ-PV-1062 (S 39°02′26.21″/W 69°40′53.36).

appears to turn outward, suggesting that the canine had an everted crown. This condition is typical of pitheciids (including *Aotus*), being extremely pronounced in some living forms of pitheciines (e.g., *Pithecia*, *Chiropotes*, *Cacajao*). There is a continuous lingual cingulum ascending to the tip of the crown. The shape of the entocristid is obscured by wear, but an approximately triangular cross section of the canine, certainly more compressed buccolingually, suggests that this structure was moderately developed, as in *Aotus*, but not as sharp as in advanced pitheciins. Although no Miocene homunculine specimens preserve intact lower canine crowns, the overall appearance of this tooth matches well some isolated canines reported for the early Santacrucian Pinturas Formation (Tejedor, 2002), especially MACN Pv SC22 and SC243 (both classified as Lower Morph 1, cf. *C. carmenensis*; Tejedor, 2002), thus approximating the alleged homunculine condition. In available homunculine isolated canines, the crown eversion is less evident than in the Cerro Bandera specimen.

In general morphology, MOZ-PV-927 and MOZ-PV-1062 closely approximate the pitheciid pattern. The overall morphology of both teeth is more similar to those of basal forms of homunculines (e.g., *Homunculus*, *Carlocebus*) than to strict pitheciines, including the non-typical Patagonian forms, such as *Soriacebus* and *Mazzonicebus* (Fleagle et al., 1987; Fleagle, 1990; Tejedor, 2005; Kay, 2010). The scarcity and isolated nature of the new specimens do now allow more precise attribution, but they provide additional evidence for a broader homunculine radiation among the southernmost primates of South America.

Geology and age of the Cerro Bandera Formation

The primate specimens come from the Cerro Bandera Formation at the northeastern slope of the Barda Negra hill (Neuquén Province), in the vicinity of the Puesto Calfú locality (Fig. 1a). The Cerro Bandera Formation is a 45 m thick succession of reworked

Table 1
List of fossil primate specimens compared in the text.

Specimen	Description	Locality and age
MACN A 5757 (*H. patagonicus*; neotype)	Mandible with almost complete dentition	Corrigüen Aike, SCF
MACN Pv CH898 (*D. gaimanensis*)	Left p4	Gaiman, SF
MACN Pv SC2 (*S. ameghinorum*; holotype)	Mandible with right p2-m3, and roots for left and right i1-2, c1	Portezuelo Sumich Norte, PF
MACN Pv SC266 (*C. carmenensis*; holotype)	Right mandible with p4-m2.	Estancia El Carmen, PF
MACN PV SC3026 (*H. patagonicus*)	Right p4	Monte Observación, SCF
MLP 69-III-12-1 (*M. almendrae*)	Symphysis and part of the left ramus with p4.	Gran Barranca, SF
MACN Pv SC22 (cf. *C. carmenensis*)	Lower right canine	Rio Pinturas, PF
MACN Pv SC243 (cf. *C. carmenensis*)	Lower left canine	Portezuelo Sumich Norte, PF

Abbreviations: PF, Pinturas Formation, 'Pinturan' (early Santacrucian SALMA); SCF, Santa Cruz Formation, Santacrucian SALMA (late-early Miocene); SF, Sarmiento Formation, Colhuehuapian SALMA (early Miocene).

pyroclastic deposits, alternating with primary pyroclastic and scant sandstone levels (Fig. 1b), exposed in isolated areas at east central Neuquén Province, Northwestern Patagonia. These outcrops represent the relicts of an old alluvial filling developed on small local valleys eroded on late Cretaceous and Paleocene deposits (Leanza and Hugo, 1997; Kramarz et al., 2005).

The mammal-bearing deposits of the Cerro Bandera Formation were assigned to the Colhuehuapian SALMA on the basis of a diverse mammalian fauna collected from outcrops in the vicinity of the new locality of Puesto Calfú (Kramarz et al., 2005). Those findings included *Cramauchenia normalis* (Litopterna), *Proadinotherium* cf. *P. muensteri* (Notoungulata), *Eosteiromys* sp., and *Caviocricetus lucasi* (Rodentia), and an undescribed species of *Protypotherium* (Notoungulata) with primitive features. Most of these taxa are also recorded in Puesto Calfú, in the same levels preserving the primate remains (Fig. 1b). Other mammals recently

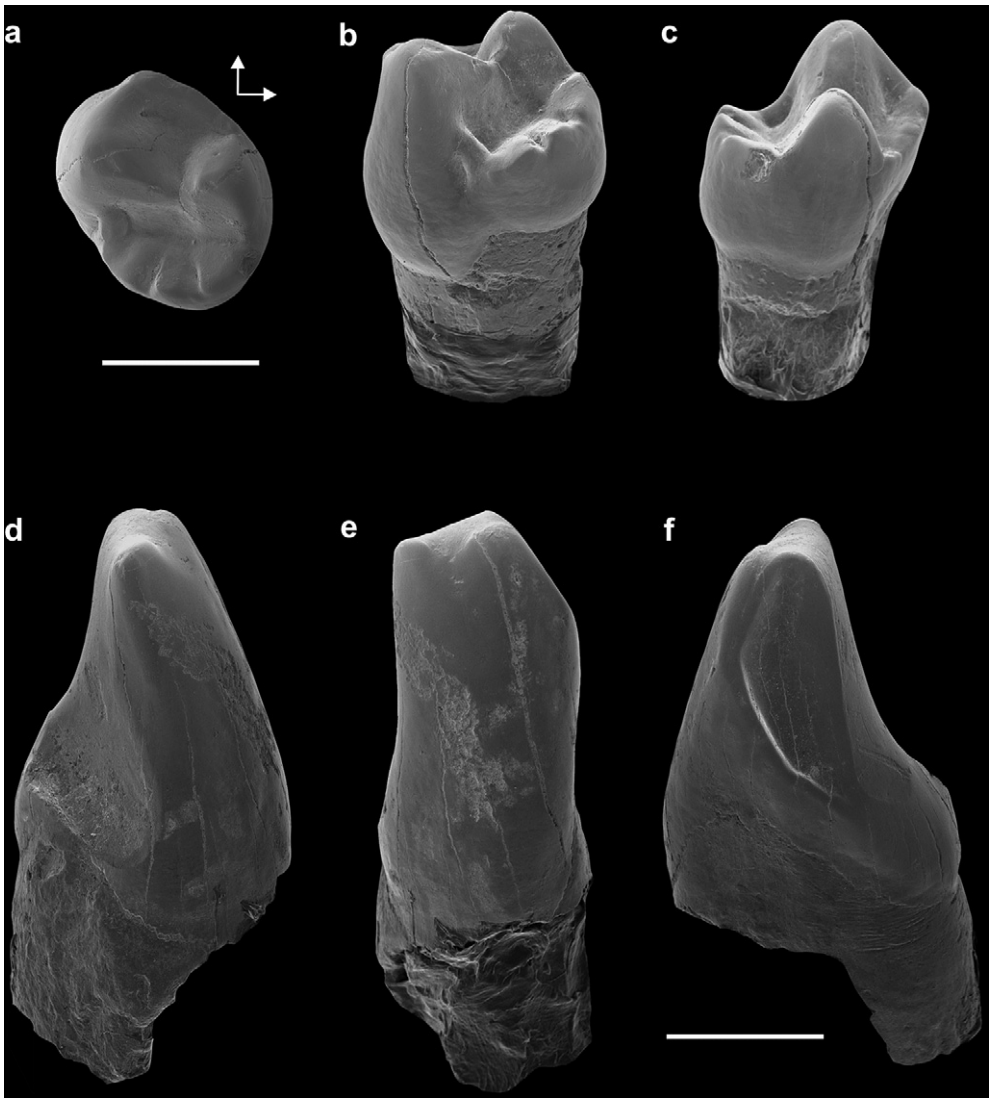

Figure 2. Primate remains from the Cerro Bandera Formation. MOZ-PV-927, isolated left p4 in occlusal (a), posterolabial (b), and lingual (c) views. MOZ-PV-1062, right lower canine in labial (d), anterior (e), and lingual (f) views. Arrows show anterior and lingual sides. Scale bar = 2 mm.

found in these levels also support a Colhuehuapian age (e.g., *Cochilius*, *Australoprocta*, *Hypsosteiromys*, *Branisamyopsis*, *Galileomys*). However, these deposits also provided several specimens referable to *Cephalomys* (Rodentia), exclusively known in the immediately older Deseadan SALMA (Loomis, 1914; Wood and Patterson, 1959; Marshall et al., 1983; but see; Frailey, 1981; Croft, 2007), an archaeohyracid (Notoungulata), not known in post-Deseadan faunas (see Billet et al., 2009 and references therein), and few isolated molars of a litoptern strongly resembling those described as *Deutherotherium distichum* by Ameghino (1897) from the typical Deseadan locality of La Flecha (Soria, 2001). Moreover, Dozo and Vera (2010) reported the occurrence of *C. normalis* (previously considered as an exclusively Colhuehuapian species) in the Deseadan Cabeza Blanca Locality (central Patagonia), revealing that its presence in the Cerro Bandera Formation does not necessarily indicate a Colhuehuapian age for these deposits.

The precise biochronological significance of this particular combination of typical Colhuehuapian mammals with some putative Deseadan elements is still uncertain. A preliminary interpretation suggests that the mammal-bearing deposits of the Cerro Bandera Formation correlate with the Lower Faunal Zone of the Colhue Huapi Member of the Sarmiento Formation at Gran Barranca, south of Colhue Huapi Lake and dated at 20.4–20.0 Ma (millions of years ago) (Ré et al., 2010), which is virtually the type section for the Colhuehuapian SALMA. The occurrence of some Deseadan taxa in Cerro Bandera would document the survival in northern Patagonia of some mammals that had already become extinct in central and southern Patagonia before the early Miocene. Because mammal associations assigned to the Colhuehuapian SALMA in lower latitudes are very scant and poorly documented (e.g., Castillo Formation, Venezuela), further comparisons are not available at the moment. As an alternative interpretation, the Cerro Bandera assemblage would represent a transitional association between the typical Deseadan and Colhuehuapian faunas, corresponding to a pre-Colhuehuapian age, not recorded elsewhere in South America. This latter interpretation implies that the platyrrhine remains here described may represent the oldest record of primates in Patagonia and the second-oldest in South America, however, further studies and absolute dates are necessary for a better interpretation of the Cerro Bandera primates and their associated mammals.

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