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## Paleosol and ichnofossil evidence for significant Neotropical habitat variation during the late middle Miocene (Serravallian)

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#### ABSTRACT

We use paleopedology and ichnology to elucidate the habitat of the late middle Miocene fossil site of Quebrada Honda, southern Bolivia. The paleosols represent three pedotypes, Type 1 and Type 2 paleosols are interpreted as Inceptisols (Eutrudepts) and Entisols (Udifluvents), respectively, which formed on proximal and distal floodplains in a seasonal, sub-humid to humid wooded grassland-like vegetative community. Type 3 paleosols are interpreted as Inceptisols (Calciustepts) that formed in more densely vegetated wooded grassland-like vegetative communities on distal floodplains in a strongly seasonal sub-humid to semi-arid environment. The ichnofossil assemblage of Quebrada Honda includes Celliforma, Coprinisphaera, Taenidium, Fictovichnus, Planolites, Skolithos, Katarrhedrites, and root traces and represents heterogeneous communities dominated by soil arthropods and plants. The physical and geochemical properties of the paleosols, including low maturity, poor development of horizons, and the overall moderate estimates of mean annual precipitation, indicate changes in soil moisture due to seasonal precipitation and flooding and low but varying degrees of temporal stability. The diverse ichnofossil assemblage of Quebrada Honda reflects environments with greater primary productivity and temporal stability than those of nearby Cerdas, Bolivia, which are several million years older. Quebrada Honda's inferred paleoenvironments differ markedly from those of La Venta, Colombia, indicating that dissimilar habitats may partly or principally account for the vastly different faunas of these two well-sampled and contemporaneous fossil localities.

#### 1. Introduction

The modern tropics of Central and South America (Neotropics) have been the focus of myriad ecological studies that have provided insights into the biodiversity and functioning of modern tropical floras, faunas, and ecosystems (Sarmiento, 1984; Hoorn et al., 2010a; Hughes et al., 2013; Rull, 2014; Smith et al., 2014). By contrast, comparatively little is known about the structure and functioning of ancient Neotropical ecosystems. This is largely the result of a sparse terrestrial fossil record (Flynn and Wyss, 1998; MacFadden, 2006). Only a handful of relatively well-sampled paleontological sites older than a few million years are known from tropical latitudes of South America (Croft, 2007; Carrillo et al., 2015; Antoine et al., 2016a). Of these, only a small proportion derive from a thick sedimentary sequence that not only preserves a diverse fossil fauna, but also is suitable for associated geochronologic, paleoenvironmental, and paleoecological studies (e.g., Kay and Madden, 1997a; Cozzuol, 2006; Croft, 2007; Tejada-Lara et al., 2015; Antoine et al., 2016b; Croft et al., 2016; Kerber et al., 2016). Therefore, applying new analyses to known Neotropical sites is just as important as the search for new fossil sites.

The fossil site of Quebrada Honda is among the richer Neotropical mammal sites presently known (MacFadden and Wolff, 1981; Marshall and Sempéré, 1991; Croft, 2007, 2016; Engelman et al., 2016). > 30 species of well-preserved mammals have been described there in addition to several types of non-mammalian vertebrates (Croft et al., 2013; Cadena et al., 2015). Among Neotropical sites of Miocene age, Quebrada Honda is second only to La Venta, Colombia (Fig. 1A), in the total number of well-documented mammal species that have been recorded, but the ancient depositional environments and habitats preserved there have never been studied in detail. As a result, little is known about this ecosystem as a whole and the factors potentially responsible for similarities and differences between the mammals of Quebrada Honda and those of other Neotropical localities.

The principal aim of the present study is to use paleosols and

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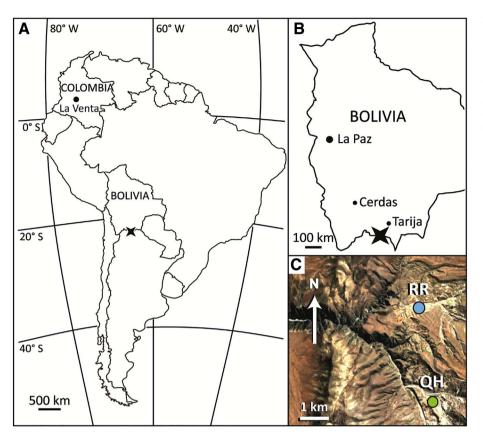
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**Fig. 1.** A) Locations of Quebrada Honda (star) and La Venta (black dot) in South America; B) Inset box showing Quebrada Honda (star, 21° 57′ S, 65′ 25′ W) and Cerdas (C, 20° 52′ S, 66° 19′ W) in Bolivia (modified from Croft, 2007); C) Google Earth image showing outcrops of the Quebrada Honda local area (QH, green dot) and the Río Rosario local area (RR, blue dot) (Image © 2017 CNES/Astrium, © 2017 Google). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ichnofossils as independent lines of evidence to reconstruct the middle Miocene paleoenvironment of Quebrada Honda. Quebrada Honda is highly suitable for such a study because the thick sedimentary sequence includes abundant paleosols that, in turn, preserve abundant ichnofossils and vertebrate fossil remains (Croft et al., 2013; Catena et al., 2015). We also compare paleopedological and paleoichnological data from Quebrada Honda to similar data from both La Venta and the slightly older locality of Cerdas, Bolivia to test previous hypotheses about the paleoecologies of Quebrada Honda mammals and possible reasons for their taxonomic distinctiveness relative to La Venta and Cerdas.

### 2. Geographic and geologic setting

The fossil site known as Quebrada Honda (ca. 21°57′S, 65°25′W) is located in the Eastern Cordillera of southern Bolivia, 65 km southwest of the city of Tarija (Fig. 1A, B). The Neogene sedimentary rocks at Quebrada Honda are mapped as part of the Honda Group by the Servicio Geológico de Bolivia and are composed of tan to reddish brown claystones, siltstones, and fine-grained sandstones; interbedded tuffaceous horizons, and local conglomerates and coarser-grained sandstones (MacFadden and Wolff, 1981; MacFadden et al., 1990; Auerbach et al., 2015). Modern elevation is approximately 3500 m, but it was probably much lower during the middle Miocene (see below).

Four broad areas of badland exposures (local areas or LAs) have been recognized near the town of Quebrada Honda: Quebrada Honda LA, Río Rosario LA, Papachacra LA, and Huayllajara LA. Collectively, these comprise the "Quebrada Honda" site, and their local faunas comprise the Quebrada Honda Fauna (Croft, 2007; Croft et al., 2011; Engelman et al., 2015, 2016; Brandoni et al., 2017). Most geological and paleontological studies have focused on the Quebrada Honda and Río Rosario LAs (e.g., MacFadden et al., 1990; Sánchez-Villagra et al., 2000; Goin et al., 2003; Engelman and Croft, 2014; Garzione et al., 2014) (Fig. 1C); therefore, we examined the same areas for in this study. The Quebrada Honda LA (abbreviated throughout as QH) includes badlands with approximately 300 m of stratigraphic section located 1–2 km southeast of the town of the same name. The Río Rosario LA (abbreviated throughout as RR) includes approximately 300 m of section located 5–6 km north of the town of Quebrada Honda. Although stratigraphic units cannot be laterally traced between QH and RR, the two local areas have been correlated with one another based on lithology and local paleomagnetic sections (MacFadden et al., 1990).

The entire QH section has been constrained to approximately 13.0–11.9 Ma (Serravallian Age; Polarity Chrons C5AA and C5A of the Geomagnetic Polarity Time Scale or GPTS (Ogg, 2012)) by the local paleomagnetic sections combined with two  ${}^{40}$ K/ ${}^{40}$ Ar dates, one on sanidine (12.83  $\pm$  0.07 Ma at approximately 85 m) and another from biotite (11.96  $\pm$  0.11 Ma at approximately 260 m) derived from volcanic tuffs (MacFadden et al., 1990). The most fossiliferous zones of QH are near the base of the section, below the 12.83  $\pm$  0.07 Ma dated "Unit 9" tuff of MacFadden et al. (1990). These zones are within the local magnetic polarity zone N1 which correlates to Polarity Chron C5AAn (MacFadden et al., 1990) and spans 13.18–13.03 Ma based on Ogg (2012).

The RR section has an estimated age of 13.0–11.9 Ma and has been tentatively correlated to the lower and middle portions of Polarity Chron C5A via the QH section (MacFadden et al., 1990). Its most fossiliferous portion is the lowest 100 m (MacFadden et al., 1990; personal observation), which is primarily of reversed polarity (MacFadden et al., 1990) and correlates to zone C5Ar.3r of the GPTS (13.03–12.89 Ma; Ogg, 2012). The mammals of QH and RR are considered to represent a single, relatively contemporaneous fauna (Croft and Anaya, 2006; Croft, 2007; Croft et al., 2011).

The lower 100 m of both the QH and RR sections are composed of siltstones, sandy siltstones, sandstone, conglomerates, and laterally continuous volcanic tuffs, some of which have been reworked into biotite sandstones (Fig. 2). The biotite sands and tuffs can be traced laterally for hundreds of meters and are useful for stratigraphic

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