Paleoenvironmental analysis of the Neotropical fossil mammal site of Cerdas, Bolivia (middle Miocene) based on ichnofossils and paleopedology

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Abstract

The early middle Miocene (Langhian age) site of Cerdas in the southern Bolivian Altiplano has produced a diverse fauna of extinct mammals (15 species in seven orders and 11 families). In this study, we use paleosols and ichnofossils to reconstruct its paleoenvironment and the conditions in which its fossils were preserved. The described paleosols represent three pedotypes and three distinct landscape surfaces in an alluvial system. Type 1 paleosols are interpreted as Haplusteps (Inceptisols) that formed on a proximal floodplain in a subhumid to humid, patchy shrubland with seasonal variation in precipitation and associated changes in soil moisture conditions (Landscape 1). Type 2 paleosols are interpreted as Dystrudepts that formed on a well-vegetated, distal floodplain in a seasonal, humid climate with ground covering

shrubland vegetation (Landscape 2). Type 3 paleosols are interpreted as Calciustolls (Mollisols) that formed in a shifting alluvial environment in a seasonal, sub-humid to semi-arid open environment (Landscape 3). Ichnofossil assemblages of Cerdas include *Skolithos*, *Planolites*, *Macanopsis*, *Parowanichnus*, rhizohaloes, and rhizotubules. These were produced by detritivorous, herbivorous, and faunivorous soil arthropods as well as plant roots and represent soil communities not normally preserved as body fossils that were living within a heterogeneous alluvial environment. The physical and geochemical properties of the paleosols and associated ichnofossil assemblages indicate that the paleolandscapes were composed of shrublands and open environments that experienced changes in moisture regimes due to seasonal precipitation and flooding events and had varying degrees of temporal stability. Our analysis is the first detailed study of pre-Pleistocene Cenozoic paleosols and trace fossils from the southern tropics (mid-latitudes) of South America and one of the few focused on important fossil-mammal bearing sediments.

Key Words: Alluvial, Continental, Neogene, Paleoenvironment, Provinciality

1. Introduction

South America has a rich record of Cenozoic mammal evolution (Patterson and Pascual 1968; Simpson 1980; Flynn and Wyss 1998). Most of this record prior to the late Miocene comes from the southern third of the continent (Pascual and Ortiz Jaureguizar 1990; Croft 2007; Flynn et al. 2012). The faunas and paleoenvironments of many of these high latitude (primarily Patagonian) localities have been studied extensively (see Bown and Ratcliff 1988; Bown and Laza 1990; Genise and Bown 1994; Bellosi and González 2010; Bellosi et al. 2010; Melchor et al.

2010; Sánchez et al. 2010). In many cases, paleoenvironmental interpretations have been based on paleopedological and ichnologic data, including lithology, geochemistry, degree of development, ichnofacies, and trace fossil assemblages. Such studies are essential for understanding the paleoecology of extinct species and how climates and habitats have changed during the Cenozoic.

In contrast to the higher latitudes of South America, only a single pre-Pleistocene locality north of 22°S (La Venta, Colombia) has been the subject of similarly detailed paleoenvironmental studies (Guerrero 1997; Kay and Madden 1997a). Although this is due in large part to the scarcity of well-described pre-Pleistocene Cenozoic sites, such sites are not absent. For example, a variety of fossil localities have been identified in northern Chile and Bolivia that range in age from Paleocene to Pliocene (Marshall and Sempere 1991; Croft et al. 2007; Flynn et al. 2012). The mammals and other vertebrates of these sites have been studied to varying degrees (e.g., Villarroel 1974; Oiso 1991; Anaya and MacFadden 1995; Muizon and Cifelli 2000; Croft 2007; Shockey and Anaya 2008; Townsend and Croft 2010; Cerdeño et al. 2012; Muizon et al. 2015), and many Oligocene to Pleistocene assemblages in Bolivia are found in paleosol-bearing sequences including: Salla (28.5 – 24 Ma) (MacFadden et al. 1985; Leier et al. 2013), Cerdas (16.5 – 15.3 Ma) (MacFadden et al. 1995; Croft et al. 2009), Quebrada Honda (13.0 – 12.7 Ma) (MacFadden et al. 1990), Callapa (11.4 – 4.6 Ma) (Quade et al. 2007), Quehua (9.0 – 7.1 Ma) (Garzzone et al. 2014; Auerbach et al. unpublished data), Choquecota (6.0 – 5.5 Ma) (Bershaw et al. 2010), Ayo Ayo (5.7 – 3.6 Ma) (Marshall et al. 1984; MacFadden et al. 1993) and Tarija (1.0 – 0.7 Ma) (Coltorti et al. 2006; MacFadden et al. 2013). Nevertheless, these paleosols have only been described superficially in terms of general lithology and degree of

pedogenic carbonate development. As a consequence, paleoenvironmental interpretations for these sites have relied primarily on their vertebrate (principally mammal) faunas and, in a few cases, data from stable isotopes (Garzione et al. 2008; Auerbach et al. unpublished data).

Paleosols and ichnofossils are often associated with one another and provide direct and complimentary evidence of ancient landscape surfaces from both biotic and abiotic perspectives. Soil formation and maturation are influenced by a variety of environmental factors including parent material, climate, organisms, topography, and time (Buol et al. 2003). The ways in which these factors influence the physical and chemical properties of modern soils are well documented; as a result, paleosols can be used to answer diverse paleoenvironmental and paleoecological questions (Retallack and Mindszenty 1994; Kraus 1999; Hembree and Hasiotis 2008; Smith et al. 2008; Sheldon and Tabor 2009; Hembree and Nadon 2011). Ichnofossils are biologically produced, *in situ* structures that result from the movement of organisms through or on a medium in direct response to their environments (Bromley 1996). Ichnofossils are also not transported beyond their original depositional setting and are thus representative of the environments in which they are preserved. Soft-bodied organisms such as plants, worms, and arthropods are not typically preserved as body fossils, but the ichnofossils produced by them can help refine paleoecological reconstructions. Combined with paleopedology, ichnology is invaluable for reconstructing paleoenvironments and paleoclimates across various terrestrial landscapes (Rhoads 1975; Retallack 2001, 2004; Kraus and Hasiotis 2006; Hembree and Hasiotis 2007, 2008; Gingras et al. 2007; Smith et al. 2008; Hembree and Nadon 2011).

The goal of the present study is to use paleosols and ichnofossils to reconstruct the paleoenvironment of an important Neogene mammal-bearing locality from the southern tropics (middle latitudes) of South America known as Cerdas. This site is located in the southern Bolivian Altiplano and has produced the remains of some 15 species of mammals that were living in the area during the latter part of the middle Miocene Climatic Optimum or MMCO (Croft et al. 2015). Cerdas is noteworthy in being one of only two presently well-sampled fossil mammal localities outside of southern South America from a 12-million-year interval spanning the early and middle Miocene (Aquitanian through Langhian ages; Croft et al. 2016), a time period that saw the onset and development of significant provinciality in South American mammal faunas (Croft et al. 2004). An accurate understanding of the site's paleoenvironmental context is essential for clarifying the factors responsible for regional differentiation of faunas during this interval and changes in mammal distributions following the MMCO (Croft et al. 2016).

2. Geographic and geologic setting

The Cerdas locality (20° 52' S, 66° 19' W) encompasses the badlands located 65-70 km southeast of Uyuni, between the towns of Cerdas and Atocha (Fig. 1A; MacFadden et al. 1995; Croft et al. 2009). It is situated at an elevation of approximately 4,000 m (Croft et al. 2009) near the eastern edge of the Bolivian Altiplano, an internally drained, 200-km-wide, east-west trending plateau that is the dominant feature of the central Andean region (DeCelles and Horton 2003; Garziona et al. 2006). The Altiplano is bounded by the Eastern Cordillera, a Paleozoic fold-thrust belt formed in metasedimentary rocks, and the Western Cordillera, an

active magmatic arc consisting of stratovolcanoes and thick ignimbrite sheets (Kennan et al. 1997; DeCelles and Horton 2003; Garzzone et al. 2006; Strecker et al. 2007).

During the Eocene to Miocene interval, crustal contraction of the Western Cordillera, Altiplano, and Eastern Cordillera formed numerous coalesced sedimentary basins within the Bolivian Altiplano (DeCelles and Horton 2003; Strecker et al. 2007; Hoke and Garzzone 2008). The Neogene sediments that were deposited within these basins are typically horizontally to sub-horizontally oriented, undeformed, and composed of continental evaporites, volcanics, and fluvio-lacustrine sediments (DeCelles and Horton 2003, Strecker et al. 2007). Local deformation of the Eastern Cordillera waned by approximately 10 Ma, and basin subsidence and deposition within the Bolivian Altiplano largely ceased as a consequence (Grubbels et al. 1993; Allmendinger et al. 1997). Regional erosional surfaces then developed within the basins of the Altiplano (Grubbels et al. 1993).

The sedimentary units of the Cerdas locality have previously been mapped as belonging to the Quehua Formation (Marshall and Sempere 1991), which has a type locality approximately 125 km to the north (MacFadden et al. 1995). However, the exact relationship between the Quehua Formation and Cerdas strata is poorly constrained; as a result, these units are informally referred to as the “Cerdas beds” (MacFadden et al. 1995; Croft et al. 2009). The Cerdas beds consist of over 250 m of flat-lying red to brown, silty claystones, siltstones, silty sandstones, and conglomerates (MacFadden 1985). The lower 50 m of the Cerdas beds (Fig. 2A) contain a mix of fine-grained sedimentary rocks including mudstones and fine sandstones, as well as coarse-grained sedimentary rocks including coarse sandstones. These units have been interpreted as braided alluvial deposits that include both fine-grained overbank deposits and

coarse channel deposits (Croft et al. 2009). The upper 150 m of the Cerdas beds are composed of poorly sorted volcanoclastic rocks (Croft et al. 2009); this stratigraphic interval is capped by a 100-m-thick regionally extensive ignimbrite.

Fossils are found within several stratigraphic levels of the lower Cerdas beds but primarily occur at the base of the lower interval (Croft et al. 2009). Based on radioisotopic dates and magnetostratigraphy by MacFadden et al. (1995), the fossiliferous zone is extrapolated to span 16.5–15.3 Ma and falls within the middle Miocene Climatic Optimum (MMCO; Zachos et al. 2001, 2008; Croft et al. 2009). Several paleosols within the middle portion of the Cerdas beds were noted by Garzzone et al. (2014) and classified as argillic calcisols. These paleosols contain root traces and green-grey mottling, and the upper surfaces of the paleosols are defined by scour surfaces at the bases of sandstone or conglomerate beds (Garzzone et al. 2014). Clumped ^{13}C and ^{18}O (expressed as Δ_{47}) isotope thermometry of pedogenic carbonate nodules from Cerdas suggests soil temperatures ranged from 30°–40°C and mean annual air temperature from 10°–28°C. Based on these temperatures, the paleoelevation of Cerdas (and the southern Bolivian Altiplano) is estimated to have been 1.1 ± 0.7 km during the early middle Miocene (Garzzone et al. 2014).

3. Methodology

The lowermost 30 m of the exposed section in the Cerdas locality was studied approximately 12.5 km northwest of the town of Atocha (Fig. 1A). The major lithologic units exposed in the Cerdas locality were measured and described from four closely spaced sub-sections within 150 m of each other and one sub-section 350 m (Fig. 1B) to the northeast to

produce a composite stratigraphic section (Fig. 2B). Paleosols were identified within the fine-grained units in the section based on field observations. Five 0.8–1.3 m sections from the lower, middle and upper zones of the composite section were chosen for paleopedogenic and ichnologic analysis. Individual detailed stratigraphic columns were constructed for each paleosol-bearing section. The lithology, sedimentary structure, grain size, texture and color of the paleosols were described, as were the size, abundance and distribution of ichnofossils and mottles. The types and thicknesses of paleosol horizons (genetically related units of a paleosol profile) were measured and documented based on these observations, and samples were collected from each paleosol horizon for thin section preparation and bulk geochemical analysis.

Thirty-four thin sections, mounted on 2.5 x 5.0 cm ($n = 22$) and 4.0 x 7.4 cm ($n = 12$) slides, were prepared in a commercial laboratory (Texas Petrographic Services, Inc., Houston TX, USA). The thin sections were studied under a polarizing microscope (Motic BA300) to identify micromorphological features including lithic fragments, grain fabrics, plasmic microfabrics, peds, illuviated clays, and small trace fossils. Micromorphological descriptions of the thin sections follow the nomenclature of Brewer (1976) and Fitzpatrick (1993).

Twenty-two samples, one from each paleosol horizon, were prepared in the Department of Geology at Ohio University (Athens, Ohio) for X-ray fluorescence (XRF) analysis. The samples were dried, pulverized, and analyzed using lithium borate fusion XRF. The bulk geochemical data are reported in oxide weight percent (Appendix 1). These weight percents were then normalized to their molecular weight to calculate various molecular weathering ratios (MWR) including base loss, calcification, leaching, lessivage, oxidation and salinization

(Retallack 2001; Sheldon and Tabor 2009) as well as the chemical index of alteration minus potash (a weathering index) (CIA-K) and mean annual precipitation (MAP) (Sheldon and Tabor 2009) (Tables 1–2; Supplementary Figures 1–3). Values for base loss, calcification, leaching, lessivage and oxidation that ranged from 0.0–0.50 were considered low, values from 0.51–1.00 were considered moderate, and values greater than 1.00 were considered high. For CIA-K, values from 0–50%, 51–75%, and 76–100% were considered low, medium and high, respectively. MAP estimates are low (arid to semi-arid; 0–800 mm), moderate (temperate sub-humid to humid; 801–1600 mm) and high (wet tropical; 1600+ mm) (modified from Kottek et al. 2006).

4. Results

4.1 Sedimentology

The measured Cerdas beds consist of red, tan and brown alluvial sandstones, siltstones and claystones, generally with sharp contacts (Figs. 2B, 2C, 3–5). Sandstones are the most common lithological units in the Cerdas beds. The sandstones in the lower 6 m of the section are medium to thick bedded (< 0.5 m), medium-grained, and fine upward to silty sandstones and siltstones. The lower sandstones commonly contain mottles, clay clasts, and volcanic-derived lithic clasts. Fine-grained sandstones containing clay clasts and grey mottles are common throughout the middle 14 m of section and range in thickness from 0.3–2.8 m. The siltstones of the Cerdas beds range in thickness from 0.2–3.0 m and commonly contain mottles and volcanic-derived lithics. The claystones of the Cerdas beds range in thickness from 0.1–1.0 m; the claystones in the lower and upper portions of the section contain planar laminations and rare volcanic-derived lithic fragments.

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199 4.2 Continental Ichnology

200 4.2.1 Rhizoliths

201 Rhizoliths, or root traces, are common features of paleosols and are among the more
202 definitive criteria for recognizing them (Retallack 2001). Rhizoliths are the result of interactions
203 among soils, roots, and microorganisms (Kraus and Hasiotis 2006). The abundance, distribution
204 and modes of preservation of roots on paleolandscapes are dependent on environmental
205 conditions such as soil moisture, drainage conditions, nutrient availability, and temporal
206 stability, and are thus critical for paleoecological reconstructions (Klappa 1980; Retallack 1988;
207 Retallack 2001; Kraus and Hasiotis 2006). Two major types of rhizoliths occur in Cerdas
208 paleosols, rhizohaloes and rhizotubules.

209 4.2.1.1 Rhizohaloes

210 Organic compounds produced by roots and microbes preferentially reduce pedogenic
211 iron and manganese in the rhizosphere, the area of the soil adjacent to a root (Kraus and
212 Hasiotis 2006). These processes result in elongate, drab-colored mottles that extend into the
213 paleosol matrix (Kraus and Hasiotis 2006). The lower and middle Cerdas paleosols contain
214 elongate, gray and red rhizohaloes that are vertically oriented, downward tapering, and
215 horizontally branching (Figs. 3, 6A). The rhizohaloes are circular in transversal section and 0.1–
216 1.2 cm in diameter. The centers of the rhizohaloes are 0.5–2.5 mm in diameter and are similar
217 in color and composition to the surrounding matrix.

218 4.2.1.2 Rhizotubules

Root molds are the tubular voids left in a soil after a root decays (Klappa 1980).

Rhizotubules form when calcium carbonate, precipitated from evaporating soil water, fills the cylinders that form in these root molds (Buol et al. 2003). As a result, the cemented portion preserves the root morphology. The inner mold may then be filled with sediment (Klappa 1980, Kraus and Hasiotis 2006). The upper Cerdas paleosols contain abundant, 0.5–1.0 cm long, vertically oriented, downward tapering, horizontally branching calcareous rhizotubules with 0.5–1.0 mm diameter, circular to ellipsoidal cross sections (Figs. 5, 6B, 6C).

4.2.2 Burrows

4.2.2.1 Skolithos

Vertically and subvertically oriented, non-branching, unlined shafts with sharp walls are common in all Cerdas paleosols (Figs. 3–5, 6D, 6E). The shafts are linear to J-shaped, circular in cross section, and have an observed length of 3.5–7.0 cm and observed diameter of 1.1–1.6 cm. The burrows are filled with a massive sandstone that is coarser grained than the surrounding matrix and, in some burrows, reduced in iron relative to the surrounding paleosol. These burrows are interpreted as temporary shelters and dwelling structures of small soil arthropods (Hasiotis 2002).

4.2.2.2 Planolites

Horizontally oriented, branching and non-branching tunnels are common in all Cerdas paleosols (Figs. 3–5, 4F–I). The shafts are 2.0–5.3 cm long and have a 0.5–1.0 cm diameter, circular cross sections. The burrows are generally non-branching, but small, vertical branches are present in a number of specimens. The burrows are filled with a massive sandstone that is coarser grained than the surrounding matrix. In the lower Cerdas paleosols, the fill of some

burrows is reduced in iron relative to the surrounding paleosol. These burrows are interpreted as temporary shelters and dwelling structures of small soil arthropods (Hasiotis 2002).

4.2.2.3 Macanopsis

Unlined, 3.5–7.0 cm long, subvertical to vertical shafts with sharp walls ending in 1.0–1.5 cm diameter, terminal chambers are rare in Cerdas paleosols (Figs. 4–5, 7A). The shafts and chambers are filled with massive sandy siltstone that is coarser than the surrounding matrix. The burrows are interpreted as dwelling and reproduction structures of small arthropods such as spiders, millipedes, or beetles (Hasiotis 2002; Hembree 2009; Mikus and Uchman 2013), and they occur in the middle and upper Cerdas paleosols.

4.2.2.4 Parowanichnus

Lined, grey, sandy siltstone-filled, complex burrow systems occur in the lower Cerdas paleosols (Fig. 3A, 7B). The lining is 0.5–1.0 mm thick and is a darker grey than the central portion of the burrows. The burrow systems are composed of boxworks with central, vertical, 1.0–1.5 cm diameter shafts that are intersected by smaller, 0.3–0.5 cm diameter, horizontally oriented, straight tunnels with a maximum exposed length of 6.5 cm. The branching patterns are T- to Y- shaped. Laterally expanded chambers (1.0 cm W x 0.5 cm H) also radiate from the shafts; the chambers are typically ovoid to elliptical in cross section, but chambers that are roughly circular in cross section are also present. The burrow systems are interpreted as ant nests (Genise 2004).

4.2.3 Mottles

The lower and middle Cerdas paleosols commonly contain lined and unlined, branched and unbranched, amorphous, red and grey mottles (Figs. 3–5, 7C–F). The contact between the

matrix and the lined mottles is always sharp, whereas the contact between the unlined mottles and matrix are generally sharp, but also include gradational boundaries. The mottles have irregular exposed widths, but are typically 0.7–1.3 cm wide; in cross section the mottles are typically circular with diameters of 0.5–1.0 cm. The mottles commonly occur in distinct horizons and may cut across one another. These indicate that they are the result of organism-substrate interactions; however, given their irregular morphology, it is not possible to identify the potential trace makers with certainty. Mottles can form in a variety of ways. Amorphous drab, grey mottles can be produced by reduction and mobilization of iron in areas adjacent to roots during periods of wet, reducing conditions (Retallack 2001; Kraus and Hasiotis 2006). Burrowed zones with increased porosity and permeability also allow for the preferential movement of water through the soil profile and may produce zones of localized gleization (Gingras 1999). In drier soils, roots and open burrows may form channels that increase the movement of oxygen into the sediment, producing reddened mottles (Kraus and Hasiotis 2006).

4.3 Cerdas Paleosols

Paleosols were identified and described in four intervals within the 30 m measured section, at 5, 9, 19, and 28 m (Fig. 2B). Three pedotypes were identified within these intervals: Type 1 paleosols at 5 and 9 m, Type 2 paleosols at 19 m, and Type 3 paleosols at 28 m. The three pedotypes were distinguished by macro- and micromorphological pedogenic properties, ichnofossil assemblages, and bulk geochemistry.

4.3.1 Type 1 Paleosol (T1P)

T1Ps (n=6) are present in two localities, CS1 and CS2 (Fig. 3A, B). T1Ps occur as multiple (CS1: profiles 1–3, CS2: profiles 1–3), 32–54 cm thick, stacked paleosol profiles below massive,

285 fine-grained, plagioclase-rich grey to brown sandstones. Individual T1P profiles are composed
286 of alternating layers of solid to variegated, weak red (10R 5/3) and red (10R 4/6) silty
287 sandstones and reddish brown (2.5YR4/3) and grey (5YR 5/1) sandstones. The upper portion of
288 CS1 is moderately calcareous, whereas the lower portion of CS2 is mildly calcareous. Both silty
289 sandstones and sandstones have angular blocky texture and gradational contacts between each
290 unit. The color of the sandstones remains relatively constant throughout each of the sections.
291 The sandstones of CS2 contain common angular to subangular, fine- to coarse pebble-sized
292 pumice intraclasts and iron nodules. The upper CS2 sandstone also contains claystone clasts.
293 The red color of the silty sandstones is strongest in the upper and middle portions of CS1 and
294 CS2 then becomes more variegated toward the bases of both sections. One silty sandstone unit
295 in CS1 contains relict lamination and two contain angular to subangular, fine- to coarse pebble-
296 sized pumice intraclasts. Claystone intraclasts are common all in silty sandstones in CS1
297 averaging 0.5 cm thick and 2–3 cm wide with some larger, 4–12 cm wide, laminated clasts
298 occurring in the upper portions of the paleosols (Fig. 8A).

299 The ichnofossil assemblage associated with the silty sandstones of T1Ps is dominated by
300 clumped and patchily distributed, vertically oriented rhizohaloes and amorphous mottles that
301 occur throughout both CS1 and CS2. The rhizohaloes and mottles are predominantly grey, but
302 both red rhizohaloes and lined and unlined, red mottles are also present throughout the
303 profiles. The cores of the grey rhizohaloes are commonly coarser grained than the surrounding
304 matrix, whereas the red rhizohaloes are commonly finer grained than the surrounding matrix.
305 *Parowanichnus* occurs in P1 of the CS1 locality; *Skolithos* and *Planolites* are abundant in P1 and
306 P3 of CS1 as well as throughout the silty sandstone portions of P1–3 in CS2.

The micromorphology of T1P is characterized by intertextic fabric (dominated by larger framework grains with voids between grains (Brewer 1976)) to agglomeroplastic fabric (silt- and clay-sized fines form an incomplete matrix around framework grains (Brewer 1976)) with some rarer areas of porphyroclastic fabric (silt to clay dominated fabric with fines forming a dense matrix around dispersed framework grains (Brewer 1976)). The matrix microfabric is mostly ineptic (small, isolated patches of high birefringence, oriented clay) to skelseptic (high birefringence, oriented clay around skeleton grains) with some silaseptic (abundant silt and sand-sized particles within a microfabric that lacks high birefringent streaks) (Fig. 9A–C). The framework grains are mostly plagioclase with common mica and pumice that often possess thin weathering rinds. Small pedogenic iron oxide nodules are also present within the samples. Biological features visible in thin section include isolated, elongate areas of coarse-fill that are circular in cross section (Fig. 6E).

Eleven samples from CS1 (n=5) and CS2 (n=6) were analyzed for bulk geochemistry to calculate molecular weathering ratios (Appendix 1, Table 1, Supplementary Figure 1). Lessivage is low and shows little variability throughout the profiles and between CS1 and CS2. Oxidation is also low overall and increases from P1 to P3 in both sections. Base loss is the lowest in P3 of CS1 but is otherwise moderate and shows little variability throughout the profiles and between both sections. Leaching is moderate to high and peaks in P1 of CS1 and P3 of CS2. Salinization is moderate to high throughout both sections and peaks in P1 of CS1 and P2 of CS2. Calcification peaks in P3 of CS2, but is otherwise moderate and shows little variability throughout the profiles and between both sections. With the exception of P3 of CS2, the CIA-K values are moderate. The CIA-K value decreases from P3 to P1 of CS1 and increases from P3 to P1 of CS2.

4.3.2 Type 2 Paleosol (T2P)

T2Ps (n=6) were observed at two laterally continuous localities, CS3 and CS4, approximately 15 m apart (Fig. 4). T2Ps consist of 20–40 cm thick, multiple (CS3 profiles 1–3, CS4 profiles 1–3), vertically successive, overlapping, stacked profiles that occur below massive, poorly sorted and consolidated, angular and medium-grained, plagioclase-rich brown sandstones (Fig. 2). Individual T2P profiles are characterized by poorly defined horizons composed of a brown (7.5YR 5/3) to reddish brown (2.5YR 4/4) silty sandstone and a light olive grey (5Y 5/3) silty claystone with sharp contacts (Fig. 4). The color of the horizons is relatively constant throughout the sections. The profiles are separated by narrow layers of less modified sediments with higher concentrations of tuffaceous lithics and clasts. The pedogenic and ichnologic features of the overlying paleosol profiles, however, partially extend into and overprint the upper surfaces of the underlying profiles. The silty sandstone units in CS3 and CS4 have a coarse, angular blocky structure. Angular to subangular, fine to coarse pebble-sized tuffaceous lithic fragments occur in the silty sandstone units of P1 and P2 in both CS3 and CS4, but are more common in CS4. Elongate, 0.5–2.5 cm, clay clasts are common throughout CS4 and in P2 and P3 of CS3; the clay clasts within CS3 commonly contain mm-scale laminations. One silty sandstone unit at the top of CS3 also contains some relict lamination. The silty claystone unit in P1 of CS3 and CS4 has a finer subangular blocky texture, and the silty claystone in CS4 contains claystone clasts.

The ichnofossil assemblage associated with T2Ps includes vertically oriented, grey rhizohaloes and mottles in P1 and P2 of CS3 and P1, P2 and P3 of CS4 (Figs. 7D–F). Red

rhizohaloes and both lined and unlined red mottles also occur in P1 and P2 of both CS3 and CS4, but are more common in CS3. Grey rhizohaloes and mottles are commonly of the same grain size as the surrounding matrix, whereas the red rhizohaloes and mottles are finer. T2Ps also contain abundant *Skolithos* and *Planolites* in P1 and P2 of both CS3 and CS4 (Figs. 6D,E,G; 7A); *Macanopsis* are less common and occur in P2 of CS3.

The micromorphology of T2Ps is characterized by granular (framework grain dominated with little to no plasma between the grains (Brewer 1976)) to porphyroskelic grain fabric (Fig. 9D–F). The matrix microfabric is insepic to mosepic (highly birefringent streaks of oriented clay that are partially adjoining) (Fig. 9F). The framework grains primarily consist of plagioclase, quartz, pumice and micas; these have thin weathering rinds in better developed paleosol horizons. Small iron oxide nodules are also visible in thin sections. Angular blocky peds (1.2–6.0 mm) are visible in thin sections from P2 of CS3 (Fig. 8B). The peds are distinct at a single horizon that occurs 35 cm below the uppermost surface of CS3. Biological features include linear, horizontally oriented silt- to sand-filled zones that cut across the surrounding fine-grained plasma (Fig. 6H).

Eight samples from CS3 (n=4) and CS4 (n=4) were analyzed for bulk geochemistry (Appendix 1, Table 1, Supplementary Figure 2). Oxidation values are low and generally increases from P1 to P3 in both sections. In both CS3 and CS4, lessivage is low and calcification is moderate; both values show little variability among the profiles and between the sections. Base loss is moderate to high in both sections and also shows little variability. Salinization is moderate to high in both sections, with the highest values in P1 and the lowest values in P3 for each section. Leaching is also moderate to high in both CS3 and CS4 with the lowest values in

P1 and the highest values in P3 for each section. The CIA-K values peak in P3 of CS3, but are otherwise moderate throughout and show general increases from P1 to P3.

4.3.3 Type 3 Paleosol (T3P)

T3Ps (n=2) were described from a single locality, CS5 (Fig. 5E). T3Ps consist of multiple (CS5 profiles 1–2), 25–30 cm thick, stacked profiles that occur below a massive, plagioclase-rich, poorly sorted, brown sandstone with angular- to subrounded grains and a granular- to intertextic microfabric. Individual T3P profiles are characterized by moderately well-defined soil horizons that are composed of brown (7.5YR 5/4) silty sandstone and brown (7.5YR 4/4) silty claystone with coarse (5.0–8.0 cm), angular blocky structure and sharp contacts. The lower silty sandstone contains abundant, fine pebble- to cobble-sized tuffaceous lithics (Fig. 8C), whereas the upper silty sandstone contains both clay clasts and tuffaceous lithics. Clay clasts (0.5–1.0 cm) are also common throughout the silty claystone. P1 contains abundant, small, calcareous rhizotubules and common *Skolithos*, *Planolites* and *Macanopsis* (Figs. 6B,C, I; 9I).

The micromorphology of T3P is characterized by agglomeroplastic to porphyroclastic grain fabrics (Fig. 9G–I). The matrix microfabric is insepic and skelsepic. The framework grains include plagioclase and quartz as well as pumice lithics all with thin weathering rinds. Small iron oxide nodules are also present in the samples. Well-defined, 3.0–4.5 mm wide, granular peds were observed in samples from profile 1, 28 cm below the uppermost surface of the section (Fig. 9H). Biological features include stringy, branching micritic rhizotubules that are circular to ovoid in cross section (Figs. 6C, 9I).

Three samples were analyzed for bulk geochemistry (Appendix 1, Table 1, Supplementary Figure 3). The base loss and lessivage are low and show little variability between the profiles. Oxidation peaks in P1, but is low throughout the section. Calcification and leaching are moderate to high, with both ratios peaking in P1. Salinization values are lowest in P1, but are high throughout the section. The CIA-K is low to moderate and increases from P1 to P2.

5. Discussion

5.1 Terrestrial Landscapes of the Cerdas Beds

The paleosols and ichnofossils of the lower Cerdas beds record paleoenvironmental, paleoecological and paleoclimatic data that allow for the reconstruction of terrestrial landscapes within the Bolivian Altiplano during the early middle Miocene. The five studied paleosol-bearing sections of the lower Cerdas beds represent soils forming on three distinct types of landscape surfaces within an alluvial system, and are useful for interpreting temporal paleoenvironmental changes across a dynamic landscapes as a result of local changes in sedimentology, topography and hydrology. The results of this study can also be used to help assess the effects of local environments on mammalian paleofaunas.

5.1.1 Landscape 1

Landscape 1 is represented by the three T1P profiles in CS1 and CS2. The physical structures, geochemistry, and ichnofossil assemblages of the T1Ps in CS1 allow the recognition of three genetically distinct, compound paleosols with Bw and B/C or Bw and C horizons (Fig. 3A). Bw horizons are composed of modified silty sandstones with no remaining primary sedimentary structures whereas B/C horizons are composed of partially modified silty

416 sandstone that contains primary sedimentary structures in the form relict laminations and of
417 clay clasts with moderate to weak millimeter-scale planar laminations. C horizons are
418 composed of weakly modified, massive sandstone. Clay-clast rich zones separate the Bw and
419 B/C horizons. The three profiles in CS2 also represent three compound paleosols (Fig. 3B). Bw
420 horizons are composed of modified silty sandstone that contains no primary sedimentary
421 structures whereas C horizons are composed of weakly modified silty sandstone containing iron
422 nodules and tuffaceous lithics fragments.

423 Compound paleosols occur as stacked profiles separated by minimally modified
424 sediment with no overlapping soil horizons (Kraus 1999). In compound paleosols rapid
425 sedimentation events truncate the active soil surface and bury it beyond the reach of
426 pedogenesis (Kraus 1999). Compound paleosols usually form in areas such as natural levees
427 where erosion is minimal and sedimentation events are rapid and episodic (Kraus 1999). The
428 lack of overprinting of the buried soil surfaces in the T1Ps could either be caused by large-scale
429 depositional events that precluded modification of buried paleosols or slow rates of
430 pedogenesis (Kraus 1999). The presence of moderately well-developed pedogenic features such
431 as weathering rinds around framework grains, areas of agglomeroplastic microfabric, patches
432 of high birefringence clay and areas of dense bioturbation features within the B and B/C
433 horizons indicates that the former explanation is more likely.

434 Due to the presence of poorly to moderately defined soil horizons, high base status,
435 abundant feldspar and volcanic rock fragments, and ferric nodules in thin section, the T1Ps are
436 classified as Eutric Ferric Protosols (Mack et al. 1993) and interpreted as Inceptisols, or more
437 specifically Haplustepts (Buol et al. 2003; Soil Survey Staff 2010). Both Protosols and Inceptisols

438 are characterized by weak development and poorly to moderately developed soil horizons
439 (Mack et al. 1993; Buol et al. 2003; Soil Survey Staff 2010) whereas Haplustepts are Inceptisols
440 with a high base status that may also have calcareous horizons (Buol et al. 2003; Soil Survey
441 Staff 2010).

442 The ichnofossils preserved in the T1Ps suggest that the landscape consisted of a patchy,
443 shrubland-like vegetative community in a subhumid- to humid climate with periodically or
444 seasonally wet conditions. The clumped, irregular distribution of rhizohaloes is typical of a
445 shrubland where vegetative cover and, therefore, root distribution is patchy (Retallack 2001;
446 Trendell et al. 2013). The occurrence and the pattern of overprinting of both grey and red
447 rhizohaloes and mottles indicate the T1Ps experienced fluctuating moisture conditions (Kraus
448 and Hasiotis 2006). Under anoxic conditions, iron reduction occurs adjacent to roots and
449 organics within the soil (Kraus and Hasiotis 2006). The iron is reduced and translocated outward
450 from flowpaths such as root channels and infilled burrows. Thus, the grey rhizohaloes and
451 mottles indicate periods of soil saturation when the water table was high (Retallack 2001; Kraus
452 and Hasiotis 2006). The red mottles and rhizohaloes indicate the presence of hematite and
453 imply oxidized and at least moderately well-drained conditions (Kraus and Hasiotis 2006). Ant
454 nests (*Parowanichnus*) typically occur in the A and upper B horizons of soils constrained by the
455 upper vadose zone to the upper phreatic zone; based on modern occurrences, ant nests
456 suggest soil formation in well-drained and at least temporarily stable conditions (Wagner et al.
457 1997; Genise et al. 2000; Hasiotis 2002; Wilson and Hölldobler 2005; Halfen and Hasiotis 2010).
458 Rhizohaloes and passively filled burrows that are left open to the surface (*Skolithos*, *Planolites*)
459 are also constrained to the upper vadose to the upper phreatic zones; the presence of these

ichnofossils in conjunction with red and grey mottles also supports the interpretation of moderately- to well-drained, cohesive and at least temporarily stable soils (Hasiotis 2002; 2007).

Geochemical and micromorphological features of the T1Ps also indicate fluctuating soil moisture conditions during the development of each paleosol profile. Low oxidation and lessivage values are indicative of periods when soil moisture levels were high, drainage was low, and base cations were not transported through the soil profile (Retallack 2001). In contrast, the moderate to high salinization and calcification values suggest water-table fluctuation and periods of dry soil conditions. Salts and carbonates precipitate from the top of and within the zone of water-table fluctuation during these alternating cycles of oxidizing and reducing conditions (Retallack 2001). High leaching values, which suggest good drainage, along with the patchy distribution of illuviated clay deposited by the downward movement of water through the soil profile, and the presence of pedogenic iron oxide nodules precipitated during redox cycles, also suggest that soil moisture regimes and drainage conditions fluctuated (Retallack 2001; Stiles et al. 2001; Kraus and Hasiotis 2006). These types of variations in chemical weathering indices and micromorphology in a single soil profile typically form as a result of soil moisture variations due to seasonality (Retallack 2001; Schaetzl and Anderson 2009). As soil-forming processes change through wet and dry seasons, the soil is continuously altered and new physical and chemical pedogenic features may form during each phase. In young or immature soils in particular, pedogenic features of different seasons can be preserved together (Schaetzl and Anderson 2009). Flooding events are indicated by the gravel-sized lithics and the laminated clay clasts. Therefore, it is likely that intermittent or seasonal floods also had

at least a minor influence on pedogenesis and varying soil moisture regimes. The CIA-K values indicate low to mostly moderate MAP that ranged from approximately 520–1050 mm/year. The largest shift in MAP, from 991 mm/yr to 518 mm/yr occurred between P2 and P3 in CS1 (Fig. 7B). This shift suggests a substantial drop in precipitation corresponding to a change in climate from sub-humid to semi-arid. MAP returns to moderate levels (921 mm/yr) in P1 of CS2, however, and increases to its highest (1049 mm/yr) by P3. These changes in estimated MAP suggest variations in soil moisture conditions at longer timescales.

The Cerdas T1Ps likely formed on active floodplains proximal to channels of an alluvial system. The T1Ps are thin and have weakly to moderately developed profiles; these features, combined with the compound, stacked pattern observed at both CS1 and CS2, indicate soil formation in areas proximal to active channels, such as crevasse splays (Kraus 1999). The presence of *Parowanichnus* as well as both horizontal (*Planolites*) and vertical (*Skolithos*) burrows is also typical of proximal floodplain soils (Hasiotis 2007). Based on the compound profiles and the level of pedogenic development in both the macro- and micromorphological features, the time of formation of the T1Ps was likely from 10^1 – 10^2 years, consistent with Inceptisol development in alluvial environments (Birkeland 1999; Buol et al. 2003).

5.1.2 Landscape 2

Landscape 2 is represented by the T2Ps of CS3 and CS4, which consist of three separate but overlapping soil profiles composed of Bw, Bt, B/C and C horizons (Fig. 4). The Bw horizons are composed of modified silty sandstones with no primary sedimentary structures; whereas the B/C horizons are composed of partially modified silty sandstones with planar laminations,

clay clasts, and tuffaceous lithics. The Bt horizons are composed of moderately modified and clay-rich silty claystones or siltstones and the C horizons are composed of clay clasts and weakly modified silty sandstone with abundant tuffaceous lithics (Fig. 8C). In the T2Ps, the overlapping profiles are separated by narrow layers of less modified sediments, and the ichnofossils of the overlying profiles partially extend into the upper surface of the underlying profiles. The layers of less modified sediment represent the tops of the truncated and buried paleosol profiles, and indicate intervals of high rates of deposition and pauses in pedogenesis.

The multiple, overlapping profiles of C3 and C4 are indicative of composite paleosols. Composite paleosols form when the rate of pedogenesis is not steady because it is interrupted by episodically high rates of deposition (Kraus 1999). Unlike compound paleosols which are buried beyond the reach of pedogenesis and not modified further; in composite paleosols depositional events bury old soils, and over time, development of the overlying active soil extends into the buried paleosol (Kraus 1999). This results in partially overlapping, vertically successive profiles that at depth have a combination of features from both the overlying and underlying soils (Kraus 1999).

Due to the presence of high base status, abundant feldspars and rock fragments in hand sample and thin section, clay-rich horizons, and argillans and illuviated clay in thin section, the T2Ps are classified as eutric argillic Protosols (Mack et al. 1993) and interpreted as Inceptisols, or, more specifically, Dystrudepts, which are Inceptisols that lack free carbonate (Buol et al. 2003; Soil Survey Staff 2010).

The ichnofossils of the T2Ps represent a dense, shrubland vegetative community composed of ground-covering vegetation and a dense community of soil-dwelling animals in a

526 humid environment that experienced periodic changes in moisture conditions. The abundant
527 cm-scale, vertically oriented mottles and rhizohaloes represent the roots of small- to medium-
528 sized, ground-covering plants. The occurrence of both grey and red mottles and rhizohaloes
529 indicates fluctuations in moisture conditions and, therefore, redox conditions (Retallack 2001;
530 Kraus and Hasiotis 2006). In addition, the density of passively filled burrows such as *Skolithos*
531 and *Planolites* suggests that T2Ps were moderately to well drained, cohesive soils that formed
532 on stable landscape surfaces (Hasiotis 2002; 2007). *Macanopsis* are rarely found in areas with
533 very high or standing water tables (Hasiotis 2002); therefore, the presence of these traces in
534 the T2Ps also suggests moderately to well-drained soils.

535 The geochemical and micromorphological features of the T2Ps provide additional
536 evidence of fluctuating soil moisture conditions during the development of each paleosol
537 profile as well as moderate levels of precipitation. The low values for oxidation and lessivage
538 throughout the sections indicate periods of high soil moisture conditions and limited drainage
539 (Retallack 2001; Schaetzl and Anderson 2009). In contrast, the moderate levels of calcification
540 and the high levels of base loss and leaching suggest periods of improved drainage and
541 correspondingly drier soil moisture conditions (Retallack 2001). The brown argillans and zones
542 of mosaic high birefringence clay are characteristic of well-drained soils above the water table,
543 whereas the pedogenic iron nodules that form during wetting and drying (redox) cycles are
544 indicative of variations in soil moisture and drainage conditions (Retallack 2001; Stiles et al.
545 2001; Kraus and Hasiotis 2006). The geochemistry combined with the presence of illuviated
546 clays and redox features is similar to that observed in the T1Ps and suggests that variations in
547 soil moisture in the T2Ps were also largely the result of seasonality (Retallack 2001; Schaetzl

and Anderson 2009). Laminated clay clasts and the fine to coarse gravel-sized lithics indicate that periodic, potentially seasonal, flooding events likely influenced the soil moisture regime as well, but the lack of surface gley features indicates that this influence was relatively minor. The CIA-K values indicate moderate MAPs ranging from approximately 815–1050 mm/year that steadily increased from P1 to P3 of CS3, and generally increased from P1 to P3 of CS4. While the level of variation falls mostly within the range of error for the MAP estimate (± 181 mm/yr), the upward increasing trend from both CS3 and CS4 suggest an increase in precipitation over the time of the formation of the three T2P profiles.

The T2Ps likely formed in an area distal to an alluvial system, such as a floodplain away from the active channel. The T2Ps have profiles that overlap and are better developed than the T1Ps, which indicates lower sedimentation rates and higher rates of pedogenesis that exceeded rates of deposition (Kraus 1999; Hasiotis 2007). The T2Ps likely formed in areas with greater temporal stability that experienced fewer disturbances (Hasiotis 2007). The stacking pattern of the T2Ps and the presence of the Bt horizons are also characteristic of soil formation in areas of overbank deposition (Kraus 1999). Given their level of development, macro-, and micromorphological features the time of formation for the T2Ps was likely from 10^2 – 10^3 years (Birkeland 1999; Buol et al. 2003). While these paleosols are better developed than the T1Ps, they are still relatively thin and pedogenically immature overall. The greater pedogenesis of the T2Ps compared to the T1Ps is attributed to increased temporal stability due to a more distal position, and greater moisture and vegetative cover of the T2P landscape, rather than significantly longer formation times.

5.1.3 Landscape 3

Landscape 3 is represented by the T3Ps, which occur as two compound paleosols with Bw and C horizons (Fig. 5). The Bw horizons consist of a clay clast rich siltstone, whereas the C horizons are composed of weakly modified sandstones with clay clasts and abundant pebble- to cobble-sized lithic clasts. Due to the presence of poorly to moderately developed soil horizons, moderate to high rates of calcification, and ferric nodules in thin section, the T3Ps are classified as calcic ferric Protosols (Mack et al. 1993) and interpreted as Mollisols or, more specifically, Calciustolls due to the moderate to high levels of carbonate within the profiles (Buol et al. 2003; Soil Survey Staff 2010). The Mollisol interpretation is based on the Bw horizon of the T3Ps, which exhibits greater pedogenic development beyond than an Inceptisol, the abundant fine root traces, and the discrete horizon of well-defined granular peds (Buol et al. 2003; Soil Survey Staff 2010). A clay-rich horizon is also present in the T3Ps; however, the low lessivage values of T3P suggest that the clay-rich siltstone was deposited by flooding events and later pedogenically modified and is not a Bt horizon (Retallack 2001; Buol et al. 2003).

The ichnofossils of the T3Ps represent a soil ecosystem in an open environment that experienced regular drying. The abundant mm-scale calcareous rhizotubules represent the roots of small plants such as herbaceous dicots (Retallack 1988; Rodríguez-Aranda and Calvo 1996; Retallack 2001). Calcareous rhizotubules are typically found in soils that undergo periodic drying (Buol et al. 2003); the calcite forming the rhizotubules precipitates from evaporating soil water that filled open soil channels created by the decay of roots (Buol et al. 2003). The abundance of *Skolithos* and *Planolites* and the abundance of *Macanopsis* also indicate well-drained, cohesive soils and at least temporarily stable landscape conditions (Hasiotis 2002).

592 The geochemical and micromorphological features of T3P are indicative of fluctuating
593 moisture conditions and low levels of precipitation. The low levels of base loss and oxidation
594 throughout both profiles and the high level of leaching in P1 indicate high periods of soil
595 moisture with poor to moderate drainage, whereas the high values of salinization throughout
596 the profile and the high calcification in P1 indicate drier soil conditions (Retallack 2001).
597 Pedogenic iron nodules also indicate fluctuating soil moisture regimes (Stiles et al. 2001). As
598 with T1Ps and T2Ps, these combined pedogenic features are likely the results of seasonality
599 (Retallack 2001; Schaetzl and Anderson 2009). The CIA-K values indicate MAP values that
600 increase from approximately 550 mm in P1 to approximately 760 mm in P2, but are overall low.
601 This low level of precipitation, combined with the calcareous rhizotubules, indicates a sub-
602 humid to semi-arid seasonal climate (Retallack 2001).

603 The T3Ps likely formed on stable landscape surfaces with low rates of sedimentation
604 that were subject to occasional, rapid influxes of sediments. The features of the parent
605 material, which include sharp-based sandstone beds, clay intraclasts, and lithics, indicate rapid,
606 high energy sedimentation, potentially from avulsion or crevasse-splay deposition in the
607 proximal floodplain prior to the development of the T3Ps (Reading 1996; Krauss 1997; Kraus
608 1999; Egenhoff et al. 2015; Miall 2006). The features of the Bw horizon of P1, which include thin
609 (cm-scale), clay-rich siltstone units, small, shallow rhizotubules, and temporary dwelling
610 burrows of soil invertebrates, reflect deposition in a more stable, distal area of the floodplain
611 (Reading 1996; Kraus 1999; Egenhoff et al. 2015). The rapid influxes of sedimentation in an
612 otherwise temporally stable environment could have been caused by shifting channels within
613 the alluvial system (Reading 1996). Based on the higher level of pedogenesis and the lower soil

moisture content, the time of formation of the T3Ps was likely on the order of 10^2 – 10^3 years (Birkeland 1999).

6. Comparisons to paleosols and ichnofossils of Patagonian localities

As noted in the introduction, few paleosol and ichnofossil studies have focused on pre-Pleistocene sites in South America, and none of these has examined a site in tropical latitudes. We, therefore, compare the results of our study to those of well-studied, older, more southerly sites in order to highlight similarities and differences between Cerdas and the southerly localities. The paleosols of the Cerdas beds represent lithologies and ichnofossil assemblages that are distinct from those of several well-studied Patagonian localities. Paleosols described from the middle Eocene – early Miocene Sarmiento Formation of Gran Barranca (Chubut, Argentina) are derived from pyroclastic and fluvial parent materials including tephric loessites, tufoarenites, and conglomerates (Bellosi 2010; Bellosi and Gonzalez 2010; Bellosi et al. 2010). These paleosols have been classified as Aridisols, Alfisols, calcic Entisols, and calcic to non-calcic Andisols (Bellosi and Gonzalez 2010; Bellosi et al. 2010). Their associated ichnofossils mainly include fine, branching root traces and arthropod brood structures such as *Coprinisphaera*, *Celliforma*, *Teisseirei*, and *Feoichnus* (Bellosi et al. 2010; Sanchez et al. 2010). Based on the paleosols and trace fossils, the corresponding paleoenvironments have been interpreted as grasslands, shrubby grasslands, and seasonal subhumid to humid woodlands and wooded grasslands (Bellosi and Gonzalez 2010; Sanchez et al. 2010; Bellosi and Krause 2014). A recent phytolith study that calculated leaf area indices from several Patagonian localities including Gran Barranca suggested that scrub, shrubland and dry sclerophyllous forests habitats

predominated at Gran Barranca from approximately 43.0–30.8 Ma and 21.8–18.8 Ma (Dunn et al. 2015).

Like the paleosols of the Sarmiento Formation, those of the early Miocene (18–17 Ma) Pinturas Formation (Santa Cruz Province, Argentina) are also found within strata composed primarily of pyroclastic deposits including tuffaceous shales, carbonaceous shales, and volcanic mudrocks and sandstones (Bown and Laza 1990; Genise and Bown 1994). The ichnofossils of Pinturas paleosols record paleoenvironmental changes; termite nests (*Syntermesichnus fontanae*) are present in mature paleosols in the lower third of the formation and suggest a humid, forested environment (Bown and Laza 1990; Buatois et al. 1998). Ichnofossil assemblages within upper portions of the Pinturas Formation, however, are similar to those of less mature paleosols of the Sarmiento Formation, including *Celliforma* and calcified roots and stumps. This ichnofossil assemblage is interpreted to represent drier conditions produced after the onset of ashfalls and deforestation (Bown and Larriestra 1990; Bown and Laza 1990; Genise and Bown 1994; Buatois et al. 1998).

The paleosols of the late early Miocene Santa Cruz Formation (costal Santa Cruz Province, Argentina) are found within strata mainly composed of pyroclastic deposits, claystones, and mudstones that are interpreted to represent low-energy, laterally stable floodplain and distal overbank deposits (Tauber 1994, 1997; Krapovikas 2012). Santa Cruz ichnofossils bear some similarities to those of Cerdas, but represent a distinct assemblage overall. The ichnofossils include *Celliforma*, passively filled dwelling structures (*Palaeophycus*), deposit feeding structures (*Planolites*, *Taenidium*), dwelling structures of freshwater crabs (*Capayanichnus*) and mammals (large horizontal tubes), as well as a variety of root traces that

658 include rhizohaloes and calcareous rhizoconcretions (Krapovickas 2012). The Santa Cruz
659 Formation paleosols and ichnofossils are interpreted as recording a transition from humid to
660 drier climates (Krapovickas 2012).

661 Differences in parent material between the paleosols of Cerdas and the Patagonian
662 localities could account for some differences in ichnofossils and paleoenvironmental
663 interpretations. Although some fluvial deposits are present in the Sarmiento Formation, most
664 sediments at Gran Barranca and other Patagonian localities are volcanic in origin. Soils with
665 volcanic parent materials tend to have higher water retention and organic matter content than
666 soils in similar environments derived from other parent materials, such as alluvium (Retallack
667 2001; Buol et al. 2003). For this reason, Cerdas soils may have had relatively lower moisture
668 levels and total organic content making them less well suited for supporting a density of
669 vegetation equal to that interpreted for Patagonian paleoenvironments.

670 The differences in ichnofossil assemblages between Cerdas and the Patagonian localities
671 could also result from lower organic content and lower levels of primary productivity at Cerdas.
672 The ichnofossil assemblages of the Sarmiento Formation and the lower sequence of the
673 Pinturas Formation are primarily composed of root traces and brood structures produced by
674 termites, dung beetles, moths, and bee-like insects that are indicative of productive
675 environments and stable landscapes (Hasiotis 2002; 2003; 2007). Insect brood chambers are
676 packed with plant material or mammalian herbivore dung. Consequently, concentrations of
677 brood traces of a diverse number of insects are generally associated abundant vegetation, high
678 soil organic content resulting from the addition of organic material by the insects, and
679 potentially a large number of herbivores (Hasiotis 2002). Deposit-feeders cycle nutrients and

organic matter through soils through feeding and excretion (Hasiotis 2002; 2007). Like brood structures, high concentrations of deposit-feeding structures such as *Planolites* and *Taenidium* (such as in the Santa Cruz Formation) indicate soils with high organic content (Hasiotis 2002; Hasiotis 2007).

7. Comparison to the Cerdas mammalian fauna

A diverse mammal fauna has been collected at Cerdas, including of 15 species pertaining to 11 families and seven orders (Table 3). However, many other types of mammals were almost certainly living there during the middle Miocene even though their fossil remains have yet to be discovered (e.g., octodontoid and cavioid rodents, paucituberculatan marsupials, glyptodonts). This is likely the result of both the comparatively small number of specimens that have been collected at Cerdas (approx. 250 as of this writing; pers. observ.) as well as a preservational bias against very small bones and teeth (no species smaller than about 2 kg have yet been identified). As a result, the characteristics of its mammal fauna as a whole cannot be used as an accurate indicator of its paleoenvironment. Nevertheless, it is likely that some information can be gleaned from the most abundant group at the site, mesotheriid notoungulates, commonly known as mesotheres.

Approximately two-thirds of identifiable specimens collected at Cerdas are from mesotheres of the subfamily Mesotheriinae (Croft et al. 2009), which were small to medium-sized (generally 10–40 kg) herbivores with robust skeletons, rodent-like incisors, and ever-growing (hypsodont) cheek teeth (Croft 1999; Croft et al. 2004; Shockey et al. 2007; Townsend and Croft 2010; Macrini et al. 2013). Mesotheres were likely fossorial mammals

(scratch diggers) that had locomotor habits similar to the modern armadillo (*Orycteropus afer*), North American badger (e.g., *Taxidea taxus*), and/or wombats (family Vombatidae) (Shockey et al. 2007), all of which tend to live in relatively open environments such as shrublands, open woodlands, and grasslands (MacDonald 2009). Mesotheres have generally been interpreted as grazers (grass-eaters) and/or open habitat folivores based on their hypselodont cheek teeth (e.g., Pascual and Ortiz 1990). An analysis of macroscopic tooth wear (mesowear) in the basal mesothere *Trachytherus alloxus* from the late Oligocene of Salla, Bolivia, supports at least some open-habitat feeding in this species (Croft and Weinstein 2008). Wombats may be particularly appropriate modern analogs for mesotheres, as the two groups share a variety of craniodental characteristics that presumably represent independently evolved adaptations for herbivory (Shockey et al. 2007). Given that modern wombats prefer relatively open environments such as forests with open understories and low shrub cover (Catling et al. 2000; Roger et al. 2007), the presence of abundant mesothere remains throughout the Cerdas beds suggests similar vegetational structure during the early middle Miocene.

The recent discovery of an astrapothere at Cerdas (Croft et al. 2015, 2016) may provide additional insights into the site's paleoenvironmental conditions. These very large (> 1,000 kg; Johnson and Madden 1997; Kramarz and Bond 2011), proboscis-bearing, rhinoceros-like ungulates ranged throughout South America during the Oligocene and early Miocene but became restricted to tropical latitudes following the middle Miocene Climatic Optimum (Croft et al. 2008; Goillot et al. 2011; Croft et al. 2015, 2016). Their remains are often found in fluvial and lacustrine deposits, sometimes alongside fully aquatic animals such as fishes, turtles, and crocodilians (Marshall et al. 1990). As a result, astrapotheres, particularly members of the

subfamily Uruguaytheriinae, have been interpreted as semi-aquatic and indicative of permanent bodies of water (Kay and Madden 1997b). The presence of an uruguaytheriine astrapothere at Cerdas suggests that relatively mild conditions and permanent bodies of water were present when the corresponding fossil-bearing levels were deposited (Croft et al. 2016).

Paleosol and ichnofossil data from the Cerdas beds are compatible with the paleoenvironmental implications of Cerdas mammals. The parent material of the Cerdas paleosols is interpreted as alluvially sourced (Croft et al. 2009). The compound and composite stacking patterns of the Cerdas paleosol profiles represent deposition in proximal and distal floodplains, respectively (Kraus 1999); likewise, the ichnofossil assemblage of Cerdas, including *Parowanichnus* and *Macanopsis*, represents soil fauna commonly found in proximal to distal alluvial environments (Hasiotis 2002; 2007). Together, the paleosols and ichnofossils of Cerdas represent landscapes in close proximity to alluvial systems that could have satisfied the environmental needs of astrapotheres. The size and distribution of rhizoliths in Cerdas paleosols indicate semi-open to open landscapes with patchy- to dense groundcover that could be favorable to mesotheriids.

8. Conclusions

The studied interval of the Cerdas beds contains three distinct pedotypes that represent three temporally separate landscapes and ecosystems within an alluvial system. Landscapes 1 and 2 represent patchy- to densely-vegetated, seasonal, humid environments and preserve a greater diversity of ichnofossils, whereas landscape 3 represents an open, seasonal, semi-humid to sub-arid environment with a low diversity of ichnofossils. These landscapes also vary

in their temporal stability and proximity to active channels, with landscape 3 paleosols being the most distal and most stable and landscape 1 paleosols being the most proximal and least stable.

The paleosols and ichnofossil assemblages of Cerdas are dissimilar from those of well-studied Patagonian localities and represent different environmental conditions. Cerdas paleosols are derived from alluvial sediments and preserve ichnofossils that represent passively-filled, temporary to permanent dwellings (e.g. *Skolithos*, *Planolites*, *Macanopsis*, *Parowanichnus*) as well as roots of small plants such as grasses and small- to medium sized shrubs. The paleosols of middle Eocene to early Miocene high-latitude Patagonian localities are primarily derived from volcanics and preserve ichnofossils that represent dwelling, brooding (*Coprinisphaera*, *Celliforma*, *Teisseirei*, *Feoichnus*), and deposit-feeding structures (*Taenidium*, *Planolites*) in organic-rich soils that likely supported dense vegetation and large numbers of herbivores.

Investigations such as this have great utility in elucidating patterns of ancient mammal evolution and can be used as sample sets with which to compare to both tropical and temperate fossil localities. Differences in environmental conditions likely account for the dissimilarity of the soil, and vertebrate faunas, of the Cerdas and the Patagonian localities. Environmental differences likely also account for faunal differences observed among Neotropical fossil localities; however, additional paleoenvironmental reconstructions that incorporate data from sedimentary environments, paleosols, and ichnofossils are needed to test potential explanations for such patterns.

This research presents the first independent, non-mammal based paleoenvironmental reconstruction of the middle Miocene Cerdas beds of Bolivia. Paleosol and trace fossil investigations of mammal-producing localities such as Cerdas provide robust, multidisciplinary paleoenvironmental interpretations that are essential for accurate habitat reconstructions, especially in localities where insufficient sampling may preclude body fossil based reconstructions. The similarities between the mammal faunas of Cerdas and the slightly older (late early Miocene) site of Chucal, Chile (Croft et al. 2009), suggest that paleoenvironmental interpretations for Cerdas may also extend to that site. By contrast, the differences between the mammal faunas of Cerdas and the slightly younger (late middle Miocene) site of Quebrada Honda, Bolivia, suggest these two site differed significantly in some aspect of their climate and/or vegetational structure. Ongoing studies of paleosols and ichnofossils at Quebrada Honda (Croft et al. 2013, Catena et al. 2015), as well as investigations of its faunal structure (Sameh and Croft 2010), will permit this hypothesis to be tested in coming years. Combined with similar analyses of the late middle Miocene fossil site of La Venta, Colombia (Guerrero 1997; Kay and Madden 1997a, b), such studies will also test whether paleoenvironmental heterogeneity was a significant contributing factor to provinciality in South American tropical mammal faunas during the middle Miocene (Croft 2007).

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Figure 1. A) Location of Cerdas in Bolivia (star); **B)** Google Earth image with the locations used to make the composite stratigraphic section (green bars), and the locations of the paleosol sections (blue stars) (Image © 2016 CNES/Astrium, © 2016 Google).

Figure 2. Stratigraphy of the lower Cerdas beds. **A)** Generalized stratigraphic section of the lower 50 m (modified from Croft et al. 2009); the bar indicates the 30 m of section studied in detail; **B)** Composite stratigraphic section of the lower 30 m and locations of paleosol sections; paleosols approximately colored to match outcrops; **C)** Typical paleosol sequence in the lower Cerdas beds; photo from CS1.

1273 **Figure 3.** Stratigraphic columns of CS1 and CS2. **A)** Three compound Type 1 paleosol profiles
1274 (P1–P3) from CS1. Each profile is marked by brackets and interpreted horizons are labeled. **B)**
1275 Three compound Type 1 paleosol profiles (P1–P3) from CS2.

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Figure 4. Stratigraphic columns of CS3 and CS4 **A)** Three composite Type 2 paleosol profiles (P1–P3) from CS3. Each profile is marked by brackets and interpreted horizons are labeled. **B)** Three composite Type 2 paleosol profiles (P1–P3) from CS4.

1308 **Figure 5.** Stratigraphic section of the two compound Type 3 paleosol profiles (P1–P2) from CS5.

1309 Each profile is marked by brackets and interpreted horizons are labeled.

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Figure 6. Rhizoliths and passively filled burrows. **A)** Grey rhizohaloes with diffuse contacts (from PS3 of CS2). **B)** Small, branching, calcareous rhizotubules (at arrows) with an enlarged view (insertion) (from P1 of CS5). **C)** Thin section of a branched, calcareous rhizotubule (from P1 of CS5). **D)** Top views of cross-sections of passively filled burrows assigned to *Skolithos* (from P2 of CS2). **E)** Thin section of a passively filled, vertical burrow assigned to *Skolithos* (from P2 of CS2). **F)** Horizontal, passively filled burrow classified as *Planolites* (from P3 of CS1). **G)** Horizontal, passively filled burrow with small vertical branches classified as *Planolites* (from P3 of CS3). **H)** Thin section of the passively filled burrow from (G). **I)** Elongate passively filled burrow (outlined, at arrow) classified as *Planolites* (from P1 of CS5).

Figure 7. Burrows with chambers, complex burrows and mottles. **A)** Passively filled burrow with a terminal chamber (outlined and at arrow) classified as *Macanopsis* (from P2 of CS3). **B)** Complex burrow system classified as *Parowanichnus* (from P1 of CS1). **C)** Red mottles overprinting grey mottles (from P1 of CS1). **D)** Grey mottles (from P3 of CS4). **E)** Hand sample of grey and red mottles; the red mottles overprint the gleyed area (from P1 of CS4). **F)** Hand sample of the sharp contact between gleyed and oxidized areas; small grey mottles overprint the oxidized area (top) (from P2 of CS4); and small red mottles overprint the gleyed area (bottom) (from P1 of CS4).

Figure 8. Pedogenic features of the Cerdas paleosols. **A)** Large clay clasts with mm-scale planar laminations (from P2 of CS1). **B)** Thin section of angular blocky peds that indicate the soil surface (from P2 of CS3). **C)** Typical sample of brown, silty sandstone with tuffaceous lithics (from P1 of CS4).

Figure 9. A–C) Matrix microfabrics from the Type 1 paleosols: **A)** Intertextic grain fabric within a matrix of insepic plasmic microfabric; **B)** Localized area of insepic clay surrounded by an intertextic grain fabric; **C)** Localized area of high birefringence clay. **D–F)** Matrix microfabrics from the Type 2 paleosols: **D)** Porphyroscopic grain fabric within a matrix of insepic plasmic microfabric; small iron nodules are present within the matrix (at arrows); **E)** Argillasepic microfabric of a laminated clay clast; **F)** Localized area with a mosaic microfabric. **G–I)** Matrix microfabrics from the Type 3 paleosols. **G)** Agglomeroplastic grain fabric within a matrix of insepic plasmic microfabric; small iron nodules are present in the matrix; **H)** Horizon of granular peds that indicate the soil surface; **I)** Cross section of a calcareous rhizotubule in a porphyroscopic grain fabric.

Table 1. Calculated chemical index of alteration (CIA-K), mean annual precipitation (MAP), and molecular weathering ratios for Cerdas paleosols.

Table 2. Molecular weathering ratio formulas and explanations (from Retallack 2001; Sheldon and Tabor 2009).

1437 **Table 3.** Faunal list of the mammals from the Cerdas Beds (Croft et al.2016).

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1454 **Appendix 1.** Bulk geochemical data, including major oxides and loss on ignition, derived from X-
1455 ray fluorescence. Values are reported in weight percent.

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Figure 1

Figure 2

Figure 3

Figure 4

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Figure 7

Figure 8

Figure 9

Table 1

Pedotype	Site	Sample	Depth (cm)	Weight (g)	CIA-K	MAP	Base Loss	Calcification	Leaching	Lessivage	Oxidation	Salinization
1	CS1	S1S11A	110	0.85	60	822	1.00	0.55	0.98	0.15	0.06	1.48
		S1S12B	90	0.85	70	959	0.98	0.52	3.03	0.14	0.14	0.70
		S1S13D	70	0.85	72	991	0.93	0.52	1.78	0.14	0.14	0.49
		S1S14D	40	0.85	59	798	0.84	0.71	1.63	0.14	0.11	1.00
		S1S15A	20	0.85	39	518	0.48	1.60	0.93	0.15	0.12	1.09
1	CS2	S4U1-A	110	0.85	67	921	0.76	0.86	1.58	0.15	0.18	1.27
		S4U1-2B	95	0.85	66	904	0.73	0.90	1.37	0.15	0.18	1.26
		S4U3A	70	0.85	66	898	0.71	0.92	1.36	0.14	0.19	1.29
		S4U4A-2	50	0.85	73	1007	0.83	0.70	1.30	0.14	0.21	0.87
		S4U5A	30	0.85	75	1028	0.82	0.71	1.09	0.14	0.23	0.77
		S4U6A-1	10	0.85	76	1049	0.87	0.62	2.12	0.14	0.21	0.86
2	CS3	S1S11C	80	0.85	62	851	0.16	0.57	0.83	0.14	0.16	1.83
		S2S12D	65	0.85	66	907	0.18	0.57	0.95	0.14	0.18	1.07
		S2S13C	50	0.85	69	953	0.22	0.55	1.47	0.14	0.22	0.82
		S2S13L	30	0.85	72	995	0.25	0.53	2.54	0.14	0.25	0.60
		S2S13U	10	0.85	76	1047	0.26	0.53	6.78	0.13	0.26	0.54
2	CS4	S2S21C	100	0.85	60	813	0.93	0.68	0.66	0.14	0.16	1.88
		S2S22C	70	0.85	60	815	0.96	0.64	0.80	0.14	0.11	1.74
		S2S23E	40	0.85	70	974	0.98	0.58	2.37	0.14	0.25	0.57
3	CS5	S341B	40	0.85	43	571	0.02	1.30	0.95	0.14	0.15	1.64
		S342F	25	0.85	41	549	0.01	1.50	1.58	0.13	0.23	1.03
		S343B	10	0.85	56	765	0.03	0.80	0.83	0.14	0.19	1.32

Table 2

Molecular Weathering Ratio	Formula	Explanation
Base Loss	$\text{Al}_2\text{O}_3/\text{CaO}+\text{MgO}+\text{Na}_2\text{O}+\text{K}_2\text{O}$	Accumulation of alumina relative to base cations
Calcification	$\text{CaO}+\text{MgO}/\text{Al}_2\text{O}_3$	Accumulation of Ca, Mg in the subsurface
Leaching	Ba/Sr	Ba solubility relative to Sr solubility
Lessivage	$\text{Al}_2\text{O}_3/\text{SiO}_2$	Downward transport of clay particles
Oxidation	$\text{Fe}_2\text{O}_3+\text{FeO}+\text{MnO}/\text{Al}_2\text{O}_3$	Accumulation of manganese, mobile and immobile iron relative to alumina
Salinization	$\text{Na}_2\text{O}/\text{K}_2\text{O}$	Accumulation of salts in the subsurface
CIA-K	$[(\text{Al}_2\text{O}_3)/(\text{Al}_2\text{O}_3 + \text{CaO} + \text{Na}_2\text{O})] \times 100$	Weathering of feldspars and the formation of clay minerals
MAP	$14.265(\text{CIA-K})-37.632$	Estimate of precipitation

Table 3

Order	Family	Genus/Species
†Sparassodonta	(uncertain)	gen. et sp. nov.
Xenarthra - Cingulata	Dasypodidae	Euphractini gen. et sp. nov.
	†Peltephilidae	Gen. et sp. nov.
Xenarthra - Phyllophaga	†Megatheriidae	Megatheriinae sp. indet.
	†Nothrotheriidae	"Xyophorus" cf. bondesioi
Rodentia - Caviomorpha	Chinchillidae	Lagostominae sp. indet.
†Litopterna	†Macrauchiidae	gen. et sp. nov.
†Notoungulata	†Toxodontidae	<i>Palyeidodon obtusum</i>
	†Interatheriidae	<i>Protypotherium cf. attenuatum</i>
		<i>Protypotherium</i> sp. nov.
	†Mesotheriidae	" <i>Plesiotypotherium</i> " minus
		<i>Microtypotherium cf. choquecotense</i>
	†Hegetotheriidae	<i>Hegetotherium cerdasensis</i>
†Astrapotheria	†Astrapotheriidae	Uruguaytheriinae gen.? et sp. nov.

Appendix 1

Pedotype	Site	Sample	Depth(m)	Weight(g)	SiO ₂	TiO ₂	AlO ₃	Fe ₂ O ₃	MgO	MnO	CaO	Na ₂ O	K ₂ O	P ₂ O ₅	BaO	SrO	lg	Total
1	CS1	S1S11A	110	085	63.16	0.55	16.48	2.41	1.02	0.03	3.53	2.71	2.77	0.28	0.04	0.04	690	9991
		S1S12B	90	085	60.64	0.74	14.88	5.11	1.73	0.04	1.82	1.89	4.07	0.19	0.07	0.02	886	9988
		S1S13D	70	085	55.44	0.68	13.30	5.08	1.66	0.04	1.50	1.47	4.60	0.15	0.03	0.01	1596	9991
		S1S14D	40	085	57.84	0.62	14.03	4.06	1.35	0.07	3.62	2.02	3.08	0.20	0.04	0.02	1295	9990
		S1S15A	20	085	49.87	0.54	12.55	3.79	1.35	0.24	9.14	1.85	2.58	0.16	0.03	0.03	1780	9993
1	CS2	S4U1-A	110	085	59.73	0.49	14.89	3.91	1.48	0.10	4.95	2.33	2.79	0.17	0.06	0.03	898	9990
		S4U1-2B	95	085	58.27	0.48	14.47	3.87	1.43	0.11	5.19	2.26	2.73	0.19	0.05	0.03	1084	9991
		S4U3A	70	085	58.25	0.47	14.10	3.88	1.48	0.10	5.07	2.34	2.76	0.18	0.04	0.03	1123	9992
		S4U4A-2	50	085	56.35	0.53	13.77	4.56	1.63	0.03	3.07	1.96	3.42	0.17	0.05	0.04	1433	9992
		S4U5A	30	085	56.13	0.51	13.74	4.88	1.82	0.04	2.81	1.84	3.65	0.17	0.04	0.04	1423	9990
		S4U6A-1	10	085	57.72	0.52	14.13	4.66	1.80	0.04	2.33	2.08	3.69	0.18	0.05	0.02	1269	9990
2	CS3	S2S11C	80	085	61.45	0.52	14.49	3.65	1.30	0.03	2.73	2.31	1.91	0.16	0.02	0.03	1133	9993
		S2S12D	65	085	61.81	0.53	14.57	4.08	1.57	0.03	2.37	1.89	2.68	0.18	0.02	0.02	1015	9991
		S2S13C	50	085	61.50	0.50	14.34	4.93	1.70	0.04	1.98	1.64	3.05	0.17	0.03	0.02	1003	9992
		S2S13L	30	085	61.82	0.55	14.22	5.43	1.76	0.04	1.70	1.41	3.58	0.18	0.04	0.01	917	9989
		S2S13U	10	085	60.32	0.52	13.57	5.52	2.07	0.05	1.09	1.39	3.90	0.23	0.06	0.01	1118	9990
2	CS4	S2S21C	100	085	61.77	0.51	14.97	3.63	1.55	0.03	3.42	2.38	1.93	0.18	0.02	0.03	950	9992
		S2S22C	70	085	63.36	0.49	14.88	2.58	1.31	0.02	3.37	2.37	2.06	0.18	0.03	0.04	924	9993
		S2S23E	40	085	59.17	0.46	14.12	5.34	1.85	0.04	1.94	1.39	3.69	0.21	0.04	0.01	1166	9990
3	CS5	S341B	40	085	56.77	0.41	13.71	2.90	1.17	0.11	8.21	2.11	1.95	0.17	0.03	0.03	1236	9993
		S342F	25	085	54.48	0.53	12.16	3.96	1.44	0.19	8.00	1.72	2.53	0.19	0.03	0.02	1465	9991
		S343B	10	085	58.96	0.58	14.44	4.20	1.57	0.07	4.18	2.19	2.52	0.19	0.02	0.03	1098	9991