Tanque Loma, a new late-Pleistocene megafaunal tar seep locality from southwest Ecuador

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ABSTRACT

Fossil deposits in the petroleum-rich sediments of the Santa Elena Peninsula in southwestern Ecuador contain some of the largest and best-preserved assemblages of Pleistocene megafaunal remains known from the neotropics, and thus represent an opportunity to greatly expand our knowledge of Pleistocene paleoecology and the extinction of Quaternary megafauna in this region. This paper reports data from excavations at Tanque Loma, a late-Pleistocene locality on the Santa Elena Peninsula that preserves a dense assemblage of megafaunal remains in hydrocarbon-saturated sediments along with microfaunal and paleobotanical material. The megafauna bones are concentrated in and just above a ~0.5 m thick asphaltic layer, but occur sparsely and with poorer preservation up to 1 m above this deposit. Several meters of presumed-Holocene sediments overlying the megafauna-bearing strata are rich in bones of microvertebrates including birds, squamates, and rodents. These are interpreted as raptor assemblages. While over 1000 megafaunal bones have been identified from the Pleistocene strata at Tanque Loma, more than 85% of these remains pertain to a single species, the giant ground sloth *Eremotherium laurillardi*. Only five other megafauna taxa have been identified from this site, including *Glossotherium* cf. *tropicorum*, *Holmesina occidentalis*, cf. *Notiomastodon platensis*, *Equus (Amerhippus)* c.f. *santaeelenae*, and a cervid tentatively assigned to cf. *Odocoileus salinae* based on body size and geography. No carnivores have yet been identified from Tanque Loma, and microvertebrate remains are extremely rare in the Pleistocene deposits, although terrestrial snail shells and fragmented remains of marine invertebrates are occasionally encountered. Accelerator Mass Spectrometry radiocarbon dates on *Eremotherium* and cf. *Notiomaston* bones from within and just above the asphaltic layer yielded dates of ~17,000 − 23,500 radiocarbon years BP.

Taken together, the taxonomic composition, taphonomy, geologic context, and sedimentology of Tanque Loma suggest that this site represents a bone bed assemblage in a heavily vegetated, low-energy riparian environment with secondary infiltration of asphalt that helped to preserve the bones. The predominance of *Eremotherium* fossils at this site indicate that it may have been an area where these animals congregated, suggesting possible gregarious behavior in this taxon. The radiocarbon dates so far obtained on extinct taxa at Tanque Loma are consistent with a model positing earlier extinctions of megafauna in tropical South America than of related taxa further south on the continent, although this pattern may be an artifact of low sampling in the region.

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RESUMEN

Los depósitos de fósiles en los sedimentos de asfalto de la Península Santa Elena en el suroeste de Ecuador contienen uno de los más grandes y mejor preservados conjuntos de megafauna pleistocénica del neotrópico, por lo que representan una oportunidad para incrementar nuestro conocimiento de la paleoecología del Pleistoceno y la extinción de la megafauna cuaternaria en esa región. Este artículo reporta datos sobre las excavaciones en Tanque Loma, una localidad del Pleistoceno Tardío en la Península Santa Elena que preserva un conjunto denso de restos de megafauna en sedimentos saturados

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de hidrocarburos junto con restos de microfauna y plantas. Los huesos de megafauna se encuentran concentrados inmediatamente sobre y dentro de una capa de asfalto de ~0.5 m de grosor, pero también ocurren con menor frecuencia y peor estado de preservación hasta un metro sobre este depósito. Varios metros de sedimentos, presumiblemente Holocenicos, suprayacentes a las capas que contienen megafauna, son ricos en restos de microvertebrados como aves, escamosos, y roedores. Estos son interpretados como asociaciones producidas por aves rapaces.

Aunque más de 1.000 huesos de megafauna han sido identificados en los estratos del Pleistoceno en Tanque Loma, más del 85% de esos mismos pertenecen a una sola especie, el perezoso gigante *Eremotherium laurillardi*. Sin embargo, otros cinco taxones de megafauna han sido recuperados de este sitio, los cuales son: *Glossotherium cf. G. tropicorum*, *Holmesina occidentalis*, *cf. Notiomastodon platensis*, *Equus (Amerhippus)* c.f. *santaelenae* y un cérvido identificado tentativamente en base a tamaño y geografía como *cf. Odocoileus salinae.* Ningún carnívoro ha sido identificado aún en Tanque Loma, y los restos de microvertebrados son muy raros en los estratos del Pleistoceno, aunque las conchas de caracol terrestre y los restos fragmentados de invertebrados marinos son encontrados ocasionalmente dentro de esas capas. Los fechados de radiocarbono por espectrómetro de acelerador de masas (AMS) en huesos de *Eremotherium* y *cf. Notiomastodon* de la capa de asfalto y por encima de esta resultaron en ~17,000–23,500 años radiocarbónicos AP.

En conjunto, la tafonomía, la composición taxonómica, el contexto geológico, y la sedimentolgía del sitio Tanque Loma surgieren que esta localidad representa un yacimiento depositado en un ambiente ribereño con bajo flujo y vegetación densa, con infiltraciones secundarias de asfalto lo que ayudó a preservar los huesos. El predominio de fósiles de *Eremotherium* indican que esta podría haber sido una área donde estos animales se congregaban, sugiriendo un posible comportamiento gregario de este taxón.

Las fechas radiocarbónicas obtenidas hasta ahora en taxones extinguidos de Tanque Loma son consistente con el modelo postulado sobre la extinción de la megafauna, la cual habría sido más temprana en las regiones tropicales de Sudamérica que al sur del continente. Sin embargo, este patrón podría ser un artefacto del bajo muestreo en la región.

1. Introduction

Asphaltic paleontological localities (known colloquially as "tar pits") serve as unique repositories of Quaternary paleontological resources due to their extremely high preservation potential (Ho, 1965; McMenamin et al. 1982; Akersten et al. 1983). The rich accumulations of bone, along with insect remains and plant material, preserved in asphalt seeps allow a wide range of paleontological investigations, including paleoecological comparisons (e.g., Lemon and Churcher, 1961), studies of biology (e.g., Feranec, 2004) and behavior (e.g., Carbone et al. 2009) of prehistoric animals, and analyses of changes in the ecology of species and communities as ecosystems approached the terminal Pleistocene (e.g., Van Valkenburgh and Hertel, 1993; Coltrain et al. 2004). In addition many asphalt seeps, such as the famous Rancho La Brea locality in Los Angeles, California, USA, appear to have acted as "traps," preserving a cross-section of local ecosystems (Stock and Harris, 1992), and thus present researchers with a biodiversity baseline against which to measure the effects of later extinctions.

Asphalt seeps are also important because they can preserve biological material in geographic areas with otherwise poor preservation, such as the wet tropics, thus providing vital insight into the paleofauna and paleoecology of these little-known areas (e.g. Prevosti and Rincón, 2007). In the Neotropics, fossiliferous asphalt seeps are known from northwest Peru (Lemon and Churcher, 1961; Churcher, 1959, 1966; Czaplewski, 1990), southwest Ecuador (Hoffstetter, 1952; Campbell, 1976), Venezuela (Rincón, 2005, 2006, 2011; Czaplewski et al. 2005; Prevosti and Rincón, 2007; Rincón et al., 2006, 2008, 2009, 2011; Holanda and Rincón, 2012), Cuba (Iturralde-Vinent et al. 2000) and Trinidad (Blair, 1927; Wing, 1962). Unfortunately, only one of these localities — Las Breas de San Felipe in Cuba (Iturralde-Vinent et al. 2000) — has ever been excavated in a systematic, stratigraphically-controlled manner, which limits investigators' ability to draw meaningful conclusions about the formation, chronology, and faunal associations at these sites.

Here we present results of excavations at a new neotropical Pleistocene asphaltic locality, Tanque Loma, in southwest Ecuador. Tanque Loma comprises an extensive stratigraphic sequence of deposits stretching from at least the late Pleistocene through today. Thousands of bones of extinct megafauna are concentrated in and just above asphaltic sediments in the lower part of the deposit, which also contain abundant plant material and occasional invertebrate remains. Higher, presumably Holocene strata contain abundant microvertebrate bones interspersed with layers of charcoal. While the research presented here focuses predominantly on Tanque Loma's megafaunal deposits, the sedimentology and paleoclimatic implications of the younger strata will be discussed briefly as well.

This study constitutes the first stratigraphically-controlled paleontological excavation in the fossiliferous asphaltic deposits of the Santa Elena Peninsula in southwest Ecuador. The Santa Elena Peninsula is an important paleontological region because it contains numerous fossiliferous localities preserving a rich accumulation of late-Quaternary fauna in an area (tropical South America) where we currently have relatively little data regarding Pleistocene ecosystems and taxa. Quaternary vertebrate localities in the Neotropics are relatively rare, and only about a dozen published direct radiocarbon dates exist on any Quaternary mammals from this region (Barnosky and Lindsey, 2010). The Santa Elena Peninsula, with its vast fossil deposits preserved in petroleum-saturated sediments, thus represents one of the best opportunities to investigate Pleistocene fauna, ecosystems and extinction dynamics in the South American tropics.

2. Regional context

The Tanque Loma paleontological locality is located on the northern side of the Santa Elena Peninsula (SEP) in southwest Ecuador (Fig. 1). The site lies at 2° 13′ S, 80° 53′ W, between the municipalities of La Libertad and Santa Elena, approximately 800 m

from the modern coastline. The current elevation of the site is 69.5 m above sea level.

2.1. Geology

The Santa Elena Peninsula is relatively young, having emerged during the Pleistocene, and tectonic uplift has continued throughout the Holocene (Sheppard, 1930, 1937; Edmund, 1965; Stothert, 1985, 2011; Damp et al. 1990; Ficcarelli et al. 2003). The Peninsula comprises one or more Pleistocene marine terraces, known regionally as *Tablazos*. Some authors (Sheppard, 1928, 1937; Hoffstetter, 1948, 1952; Ficcarelli et al., 2003) recognize three wave-cut terraces, while others (Sarma, 1974; Pedoja et al. 2006) recognize four, at least in some parts of the Peninsula. Still others (Marchant, 1961; Ecuadorian Instituto Geografico Militar [IGM] 1974) propose a single, faulted terrace. Three *tablazos* have also been proposed for the nearby Talara region of northwestern Peru (Lemon and Churcher, 1961). Since the present study did not include a detailed regional geological analysis that would help to resolve this issue, we will refer to this feature simply as the *Tablazo formation* (*sensu* IGM, 1974; Pedoja et al. 2006). The Tablazo formation, which reaches a thickness of up to 40 m, is composed of calcareous sandstones, sands, sandy limestones and fine conglomerates, with abundant gastropod, bivalve, barnacle, and echinoid fossils that often occur in monotypic "beds" (Barker, 1933;

IGM, 1974). These deposits are cut by numerous dry riverbeds (*arroyos*), most of which only contain appreciable water during periods of high rainfall, generally associated with El Niño events (Spillmann, 1940).

The Tablazo formation unconformably overlies Tertiary (Eocene — Miocene) deposits of primarily limestones, shales, sandstones, and conglomerates (Sheppard, 1937; IGM, 1974). These include the Tosagua formation (upper Oligocene — lower Miocene), the Zapotal formation (Upper Eocene-lower Oligocene), the Ancon group (mid — upper Eocene), and the Azucar group (lower Paleocene — middle Eocene). The oil that seeps to the surface in the Tablazo deposits is thought to emanate from sandstones in these latter two groups (Sheppard, 1937; IGM, 1974; *but see* Jaillard et al. 1995). Two late Mesozoic deposits, the upper Cretaceous Cayo formation and the Jurassic-Cretaceous Piñon Complex, outcrop at a few points throughout the Peninsula (Fig. 1).

Industrial oil exploration began on the Santa Elena Peninsula in the late 19th Century (Peláez-Samaniego et al. 2007), but the surface tar seeps have been exploited since prehistoric times by indigenous cultures and, later, Spanish explorers to seal boats, a practice that continued into the 20th Century (Bengtson, 1924; Colman, 1970; Bogin, 1982). In the early 1900's, and continuing through at least the 1970's, shallow oil wells (*pozos*) were dug to extract oil by hand (Bengtson, 1924; Colman, 1970). Bones of Pleistocene megafauna can be seen protruding from the walls of
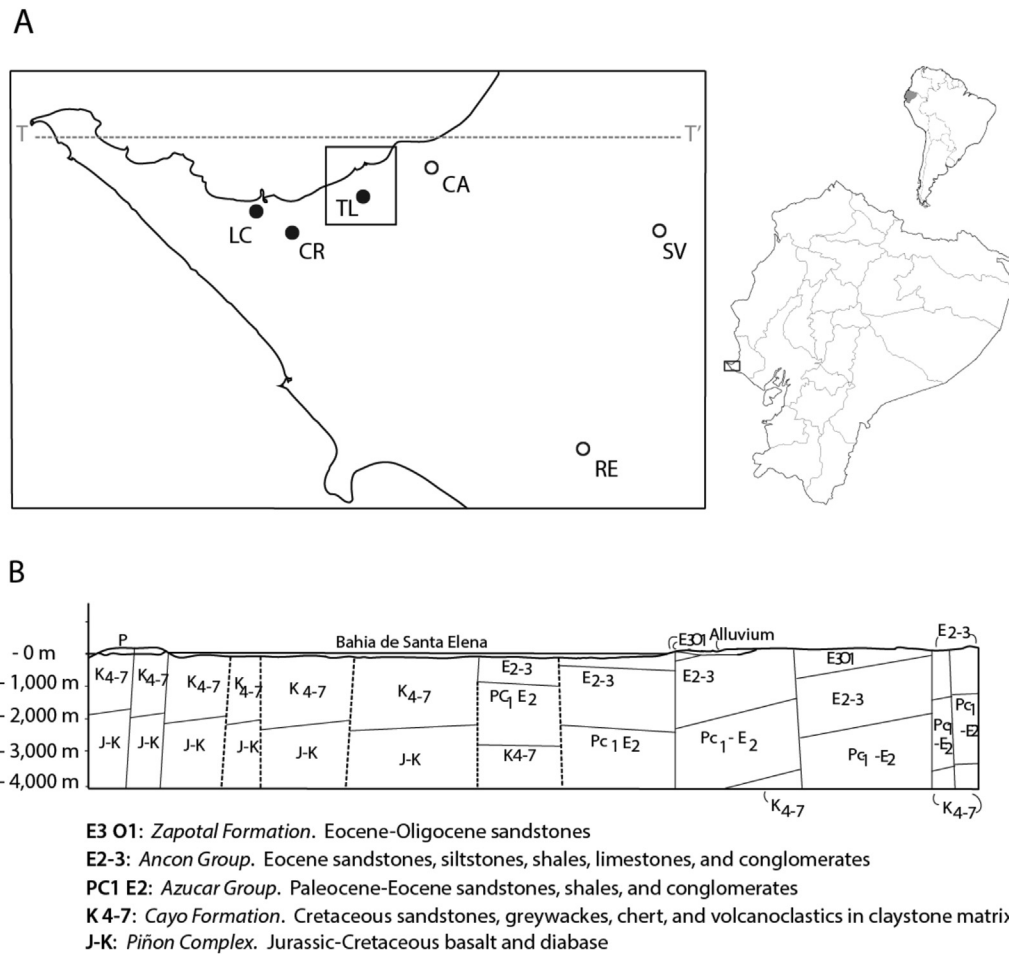

Fig. 1. (A) Map showing location of Tanque Loma locality and other published paleontological localities from the Santa Elena Peninsula, Ecuador. TL = Tanque Loma; LC = La Carolina (Hoffstetter, 1952); CR = Corralito (Spillmann, 1935); RE = Rio Engabao (Edmund, 1965); CA = Cautivo (Ficcarelli et al., 2003); SV = San Vicente (Lindsey, *unpublished data*). Black dots denote asphaltic localities; open dots denote non-asphaltic localities. (B) Generalized stratigraphic profile of the Santa Elena Peninsula along transect line T—T′. Modified from IGM (1974).

some of these pits today. Megafauna bones are also visible in the many dry riverbanks that riddle the Peninsula (Barker, 1933) and are commonly found in surface oil deposits (Colman, 1970).

Previous paleontological work on the Peninsula by Spillmann (1931, 1935, 1940), Hoffstetter (1948a, 1952), Edmund (1965 and *unpublished field notes*) and Ficcarelli et al. (2003) has yielded numerous mammal fossils, in both asphaltic and non-asphaltic contexts (Table 1). The Peninsula has been inhabited since at least 10,800 BP (Stothert et al. 2003) and a significant amount of archaeological research has been conducted in this region (Bushnell, 1951; Sarma, 1970; Stothert, 1983, 1985, 2011; Stothert et al. 2003). However, with the possible exception of the Cautivo locality (Ficarrelli et al. 2003), there is no documented evidence of associations between ancient humans and extinct Pleistocene megamammals.

2.2. Paleoenvironment

Modern climate in western Ecuador is heavily influenced by upwelling of the Humboldt Current, the Intertropical Convergence Zone (ITCZ), and the El Niño Southern Oscillation (ENSO) (Tellkamp, 2005), and these factors were probably major drivers of the regional climate during the Pleistocene as well. Some researchers (Campbell, 1976; Koutavas et al. 2002) have suggested that during the Pleistocene, ENSO conditions — which today result in

significantly higher rainfalls on the western SEP (Sheppard, 1937; Bogin, 1982) — may have been a persistent phenomenon in this region. However, this does not appear to have resulted in the establishment of wet tropical forest ecosystems as are typical of the northern Ecuadorian coast today. Rather, sea core isotopic and pollen data (Heusser and Shackleton, 1994) indicate that western Ecuador experienced cool, dry conditions during the last glacial, between approximately 28,000–16,000 BP, and this aridity resulted in the expansion of grasslands at least in the Andes. The same pattern is noted in pollen records of neighboring Colombia (Van der Hammen, 1978) and Peru (Hansen et al. 1984). Precipitation in southwest Ecuador appears to have reached its lowest levels around 15,000 years before present (uncalibrated radiocarbon years — RCYBP) (Tellkamp, 2005).

The end of the Pleistocene (approximately 14,000 to 10,000 RCYBP) was marked by warmer temperatures and a dramatic increase in precipitation (Heusser and Shackleton, 1994; Tellkamp, 2005) which, combined with the resultant erosional runoff and rising sea levels, resulted in the widespread establishment of mangrove swamps along the Ecuadorian coast, including the SEP (Heusser and Shackleton, 1994). Sarma (1974) notes a trend of increasing aridity throughout the Holocene, with brief returns to fluvial conditions around 7500 and 4000 years ago. In the last century, vegetation cover has been substantially reduced through human activities, including deforestation (Marchant, 1958; Bogin, 1982; Stothert, 1985, 2011).

Today, the Santa Elena Peninsula is a coastal desert with very little vegetation except where underground springs provide permanent standing-water in otherwise usually dry arroyos (Stothert, 1985). Whether this modern landscape is due primarily to early Holocene climatic changes (Sarma, 1974), to mid-Holocene uplift (Damp et al. 1990), or to relatively recent intervention by humans (Stothert, 1985; Ficarrelli et al. 2003), is still a matter of debate.

3. Materials and methods

The megafaunal deposit at Tanque Loma was discovered in 2003 by Ecuador's state-run oil company, PetroPenínsula, when an excavator removed the edge of a hill during maintenance on an adjacent spring and naturally-occurring oil seep. Initial excavations were conducted in 2003–2006 by a team of archaeology and tourism students from the Universidad Estatal Península de Santa Elena (UPSE) under the direction of the second author of this study (EXLR). The Museo Paleontologico Megaterio (MPM) was constructed at UPSE to house the excavated remains. Additional excavations were conducted in 2009–2011 by teams from the University of California–Berkeley, UPSE, and the George C. Page Museum led by the first author of this study (ELL). The name of the locality derives from the hill (*loma*) whose eastern margin overlies the deposit, on which sit a number of large oil cisterns (*tanques*).

All bones excavated from Tanque Loma are reposited at the MPM in Santa Elena, Ecuador. Fossils excavated during the 2003–2006 excavations have been fully prepared and were included in the faunal analyses in this study. Fossils excavated between 2009 and 2011 are still in process of preparation, and were included in the taphonomic studies of the deposits, but not the quantitative faunal analyses. However, in general the material recovered during the later field seasons appears to conform to the patterns noted for the earlier excavations, comprising predominantly intact, large bones of megathere sloth and occasionally gomphothere. The one notable addition is the discovery, in 2010, of a few rib fragments that appear to belong to a large carnivore, possibly *Smilodon*, though these have yet to be prepared and definitively identified.

Table 1
Mammal taxa reported from Pleistocene localities on the Santa Elena Peninsula, Ecuador. Data are from Hoffstetter (1952, La Carolina), Edmund (1965, Rio Engabao), Ficcarelli et al. (2003, Cautivo), Lindsey & Lopez (this publication, Tanque Loma) and Lindsey (*in prep.*, Corralito and San Vincente).

	La Carolina	Corralito	Tanque Loma	Rio Engabao	Cautivo	San Vicente
MARSUPIALIA						
Didelphidae						
Didelphis		X				
XENARTHRA						
CINGULATA						
Pampatheridae						
Holmesina	X	X	X	X		
PILOSA						
Mylodontidae						
Glossotherium	X	X	X		X	
Scelidodon	X	X				
Megaheriidae						
Eremotherium	X	X	X	X		X
RODENTIA						
Caviidae						
Neochoerus	X					
CARNIVORA						
Canidae						
Dusicyon	X	X				
Protocyon	X					
Felidae						
Puma	X					
Smilodon	X	X		X		
Mustelidae						
Lutra				X		
PROBOSCIDEA						
Gomphotheriidae						
Notiomastodon	X	X	X		X	
PERISSODACTYLA						
Equidae						
Equus	X	X	X	X	X	
ARTIODACTYLA						
Camelidae						
Palaeolama	X	X				
Cervidae						
Odocoileus	X	X	X	X		
Tayassuidae						
Tayassu		X				

3.1. Excavation

A grid made of irregular rectangular units each measuring 2−4 m in width by 3−5 m in length was established in December of 2003, and added to throughout 2005 and 2006 (Fig. 2). The 2009−2011 excavations proceeded in the pre-established units, three of which (units 8, 9, and 10) had been partially excavated during 2005 and 2006, leaving material in the western portion of these grid units *in-situ* in the hopes of establishing a Paleontological Park at the site. This material was removed during the 2009 excavations, as negotiations with the local governments had unfortunately stalled, making the designation of a Paleopark unlikely. Each of the rectangular units in the grid was excavated in 10 cm−20 cm layers, and the positions of all fossil remains and large (>15 cm) clasts and wood pieces within each layer were mapped. Three-dimensional positional data was taken for all mapped objects, and in 2010 and 2011, 3-D orientation within the deposit was determined using a Brunton compass for all objects >10 cm that had a length equal to at least twice their width.

3.2. Stratigraphy and sedimentology

Detailed stratigraphic studies of the Pleistocene and Holocene deposits at Tanque Loma were made by ELL in 2009−2011. These descriptive studies were supplemented with laboratory analyses of sediment grain size, soil pH, and organic carbon content, conducted by ELL at the University of California−Berkeley in 2011−2012.

For the sediment grain size analyses, approximately 200 g of sediment from each stratum was passed through a series of nested screens ranging from −3ϕ to 3ϕ. Continuously running water was
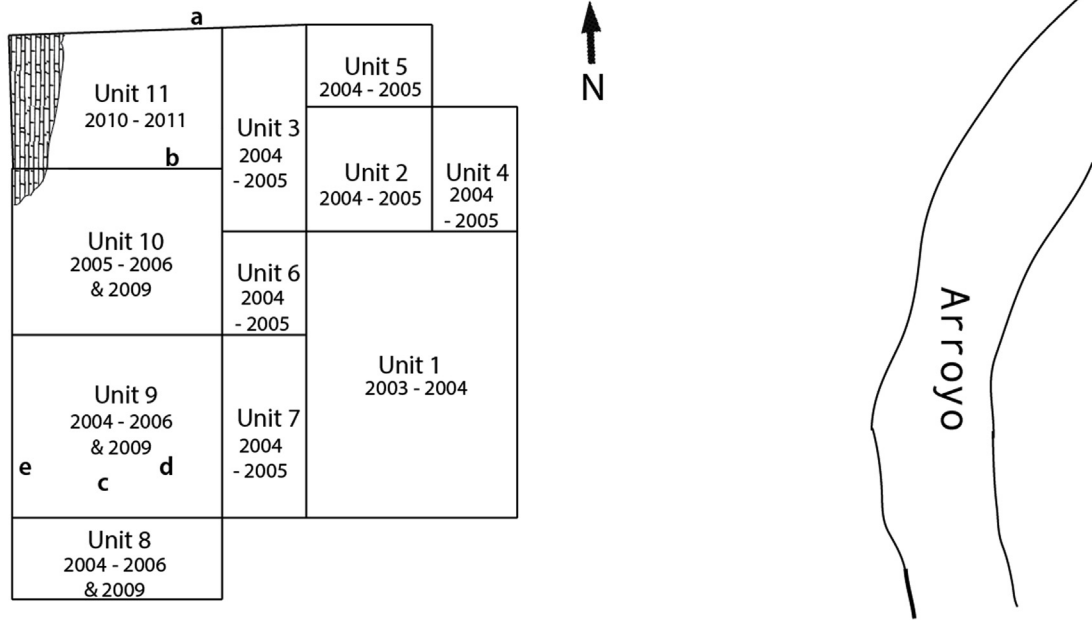

Fig. 2. Detail of the box in Fig. 1A showing area of the Tanque Loma locality, and map of Tanque Loma field site showing excavated grid units, years of excavation, and locations of radiocarbon-dated bones. **a, b, c, d,** & **e** indicate locations of the following samples collected for radiocarbon-dating: Aves phalanx, *Eremotherium* vertebral epiphysis, MPM291 (cf. *Notiomastodon platensis* caudal vertebra), MPM325 (cf. *Notiomastodon platensis* metapodial), and HE616 (*Eremotherium laurillardi* phalanx), respectively. Map data: Google, DigitalGlobe.

used to ensure that clumps of sediment were fully disintegrated. Dried sediment samples were weighed before and after screening to determine the percentage of sediment grains and clasts in each size class.

The pH of sediment samples was measured using a pH meter (Oakton Acorn series pH 5). Ten grams of dry sediment were weighed and combined with 20 mL of deionized water. Samples were allowed to sit in the water for 30 min, after which the calibrated pH and temperature probes were immersed and stirred in the sediment mixture. Measurements were repeated three times for each sample, and then averaged.

Organic carbon content of the different sediment layers was determined by Loss-on-Ignition analysis (sensu Dean, 1974). Oven-dry sediment samples were weighed in pre-weighed crucibles, then baked in a Thermoline 30400 oven at 560 °C for one hour. After one hour in the oven, some samples still had papery, black, charred material clinging to the crucibles; in this case baking continued for up to six hours, until all charred material had disappeared. Baked samples were cooled in a desiccator, then re-weighed to determine the amount of carbon combusted.

To comply with U.S. Department of Agriculture standards, all sediment samples were sterilized prior to analysis by baking in a Thermo Scientific Precision 6526 oven at 155 °C for 0.5 h. This protocol should have had no effect on the conclusions of any of the analyses reported here.

3.3. Faunal analyses

Prepared bones housed in the MPM collections were identified and analyzed by ELL in collaboration with H.G. McDonald of the U.S. National Parks Service. Because material collected during the 2009–2011 field seasons has not been fully prepared, only specimens collected during the 2004–2006 field seasons were considered in the faunal analyses, including species composition, population demographics, number of identified specimens (NISP), minimum number of individuals (MNI), and element counts. For each specimen, information regarding taxon, element, age of organism, percent present, and part preserved was recorded. In addition, notes were taken on taphonomic markings including scratches, weathering, breakage, erosion, and punctures. Taxonomic, demographic, and taphonomic data were compared with published information from other localities of known origin to investigate the environmental and depositional context of the site.

3.4. Radiocarbon analyses

Accelerator mass spectrometry (AMS) radiocarbon dating was attempted on five ultrafiltered collagen samples from the Tanque Loma locality. The bones analyzed included 1) a manual phalanx from an adult *Eremotherium* (Field # HE 616) found during the 2009 field season at the interface of Strata IV and V; 2) a *Notiomastodon* caudal vertebra (MPM291) and 3) a *Notiomastodon* metapodial (MPM325) excavated during the 2004 field season from the lower part of Stratum IV; 4) an *Eremotherium* vertebral epiphysis excavated during the 2009 field season from the upper part of Stratum IV; and 5) an Aves phalanx recovered during screening in 2011 from the lower part of Stratum III (Figs. 2 and 3).

All bone samples were prepared by ELL at the Center for Accelerator Mass Spectrometry (CAMS) at Lawrence Livermore National Laboratories in Livermore, California, USA. Bone samples were collected and the outermost layer of bone from each sample was removed using a Dremel Tool to avoid contamination from adhering sediments. Samples consisting of 120 mg–150 mg of uncrushed bone were decalcified in 0.5N HCl at 38 °C for 24–72 h, until the bone had a spongy texture. Decalcified samples were placed in 0.01N HCl at 58 °C for 16 h to unwind the collagen. Collagen samples were filtered through Whatman® quartz fiber filters with vacuum suction and then ultrafiltered in Centriprep® centrifugal filters that had been pre-rinsed via centrifuge four times in Milli-Q purified water. The ultrafiltered collagen was freeze-dried then combusted with copper oxide (CuO) and silver, and the resultant carbon dioxide was graphitized. Graphite targets were analyzed in an accelerator mass spectrometer by Tom Guilderson at CAMS.

Because all bones were found at or above the top of Stratum V, and did not on first inspection show any evidence of contamination by asphalt, no solvents were used for tar extraction on any of these five samples.

4. Results

4.1. Stratigraphy and sedimentology

Seven distinct sedimentary strata have been identified overlying the limestone bedrock at Tanque Loma (Fig. 3). The lower strata (IV − VII) are presumed to be latter-Pleistocene (Lujanian: 0.781 Ma − 0.012 Ma) in age, based on the presence of bones of extinct megafauna including ground sloths, horse, and gomphothere in these layers. Radiocarbon dates obtained on some of these megafauna bones (reported herein) support this conclusion. The overlying layers (Strata I − III) are inferred to be Holocene, based on a marked change in deposition and the absence of extinct taxa. (It should be noted that extant megafauna have not been recovered from Strata I − III either, and attempts at radiocarbon dating of material from these layers have so far proved unsuccessful. However, a stark change in depositional characteristics along with other indicators of paleoenvironmental change detailed below, cause us to tentatively assign a Holocene age to these strata).

The uppermost stratum (Stratum I) is modern colluvium measuring 30 cm–45 cm thick, washed down from the hill overlying the deposit. This stratum consists of uncompacted, poorly-sorted, friable, brown (Munsel assignation 10YR 4/3) sediment with abundant plant material (mostly modern plant roots) and angular limestone clasts up to 3 cm in diameter. The sediments are composed of roughly 26% gravels, 20% sands, and 50% muds (silts or clays). The sediments have a pH of 6.6 and contain only about 3% organic carbon (Table 2). Sixty liters of sediment from Stratum I were sifted through nested 2- 4- 8- and 16-mesh screens, but no vertebrate remains were encountered.

Stratum II is a 45 cm–80 cm thick grey-brown (10YR 5/2) silty paleosol, with poorly-sorted very small (2 mm) clasts and $CaCO_3$ nodules throughout. Approximately 2% of Stratum II sediments are gravels, 15% are sands and >82% are muds. This stratum was likely deposited in slow-moving water, probably a meandering river. Organic carbon content of this stratum is very low (about 4%) and pH of the sediments is 7.6. Twenty liters of Stratum II sediments were sifted through 2- 4- 8- and 16-mesh screens, but no vertebrate remains were encountered.

Stratum III is 95 cm–160 cm thick and comprises 15 distinct unconsolidated sedimentary layers (Table 2). Some of these layers occur as graded beds probably deposited during flooding events, while others appear as laminated beds that would have been deposited in still water. Repeated episodes of desiccation and paleosol development are evident in this stratum. Some of the layers are very thin (<1 cm thick) and appear to contain substantial amounts of charcoal. Such layers have a very high organic carbon content (>40%) and contain macroscopic pieces of charcoal. The various layers of Stratum III vary widely in sediment composition, from 1% to >50% gravels, 6%–52% sands, and 22% to >92% muds. The pH of the sediments generally increases from the upper to
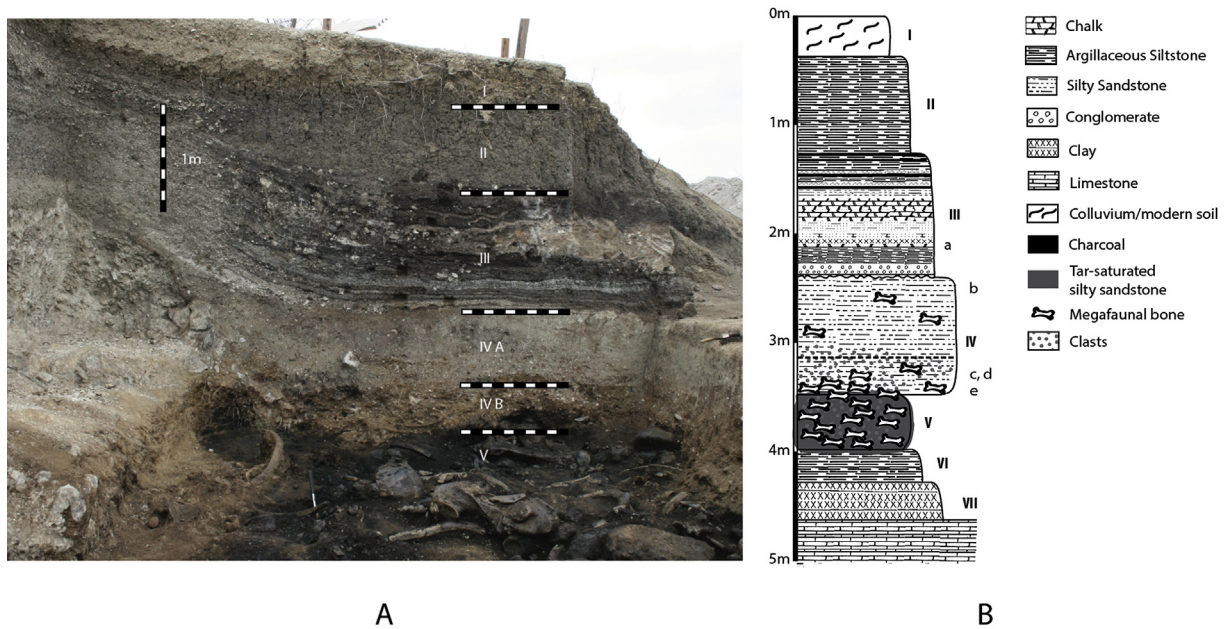
Fig. 3. (A) Photo of north wall of Tanque Loma grid unit 11. (B) Generalized stratigraphic profile for Tanque Loma locality. **a, b, c, d,** & **e** indicate stratigraphic positions of the radiocarbon dated Aves phalanx, *Eremotherium* vertebral epiphysis, MPM291 (cf. *Notiomastodon platensis* caudal vertebra), MPM325 (cf. *Notiomastodon platensis* metapodial), and HE616 (*Eremotherium laurillardi* phalanx), respectively.

lower layers, ranging from 5.7 at the top to 7.8 in the lowermost layer. Stratum III is extremely rich in microvertebrate remains, and thousands of bones of birds, squamates, and small mammals have been recovered through dry- and wet-screening of these layers. No remains of extinct megafauna have been encountered in Stratum III.

Strata IV − VII comprise the Pleistocene (Lujanian) deposits at Tanque Loma. Stratum IV unconformably underlies Stratum III. At the contact with Stratum III there is occasionally present a 1 mm−2 mm thick layer of black powdery sediment with some plant material, apparently charcoal. Below this thin line, and extending irregularly down into the top of Stratum IV, occasionally forming rootlet casts, is a calcareous deposit interpreted as caliche. Stratum IV is a compact, silt-sand paleosol that has a maximum thickness of 110 cm, reduced to 55 cm towards the west side of the excavated grid where the underlying bedrock protrudes upward. Stratum IV can be divided into upper and lower segments of about equal thickness in most of the site, distinguishable by color (7.5 YR 4/4 vs. 10 YR 4/3, respectively) as well as clast size and abundance. These two sub-strata may represent separate episodes of sediment deposition and paleosol development. The upper sub-stratum is a weakly-graded, sandy matrix supporting abundant small (mostly 1−2 cm) clasts. Small (1 mm−3 mm) carbonate nodules are also present in this sub-stratum, especially the upper section. The lower sub-stratum contains numerous clasts, with 90%−95% of the clasts being moderately-to- largely-spherical, angular clasts 1 cm−25 cm in diameter and the remaining 5%−10% of the clasts being moderately spherical, rounded (fluvial) rocks, 0.5−5 cm diameter. This layer is moderately graded, containing ~40% 0.5 cm-diameter angular clasts in the lower 40 cm of the deposit, 20% 2−3 cm diameter subangular-angular clasts in the lower 25 cm, and 10% 4−5 cm subangular-angular clasts in the lower 10 cm. Fragments of sea urchin spines and bits of shell are found throughout this layer, and small (1 cm−2 cm long, 2 mm−3 mm diameter) twig fragments are abundant in the lower part near the contact with Stratum V.

The matrix sediments of Stratum IV are made up of approximately 6% gravels, 25% sands and 68% muds, and contain about 11% organic carbon. The pH of Stratum IV sediments is 7.4. Cobbles

up to 20 cm in length are occasionally encountered. Megafauna bones are present throughout Stratum IV, but are sparse and fragmentary towards the top of the deposit, growing more abundant and better preserved towards the bottom (Fig. 4). Megafauna bones are highly abundant in the lower 20 cm of this stratum. Despite methodical excavation techniques and extensive screening, fewer than five microvertebrate bones have been discovered in Stratum IV. However, a substantial amount of paleobotanical material, including twigs, needle vesicles, and thorns, was recovered during screening.

Stratum V consists of sediments similar to the lowermost portion of Stratum IV, but these sediments are saturated with asphalt. In this layer megafaunal bones are so abundant as to constitute a clast-supported breccia of bones, cobbles and plant material. Wood pieces (up to 15 cm long) and cobbles (5 cm−20 cm diameter) are relatively common. In many places, there is a "mat" of plant material (mostly consisting of 1 cm−2 cm long twigs) lying immediately on top of bones. Stratum V extends in a continuous layer of approximately 50 cm thickness throughout the entirety of the locality. In some places, this layer is seen to undercut the bedrock forming the nucleus of the hill. Sediments in certain areas of the deposit contain a substantial amount of liquid tar (sometimes in amounts sufficient to impede excavations), while the sediments in other areas are drier, though still completely saturated. The wettest sediments contact fissures where oil is actively seeping. Many additional active seeps are visible on the land surface in riverbeds and hillsides in the immediate vicinity of the site.

Stratum VI is a silty, grey-green, anoxic sediment that oxidizes quickly to dark brown-black when exposed to air. This stratum is interpreted as a gley.

Stratum VII is a compact, sterile green clay. The depth of this layer varies substantially depending on the location of the underlying bedrock.

The bedrock layer at Tanque Loma consists of highly friable white limestone. This rock appears to form the nucleus of the hill overlying the locality. It protrudes into the upper part of Stratum IV

Table 2
Results of sediment analyses (pH, Loss on Ignition, and grain size analysis) for Strata 1–4 at Tanque Loma locality.

Sample#	Provenance	Avg pH	% organic carbon	%-4 phi	%-3 phi	%-2 phi	%-1phi	%0 phi	%1 phi	%2 phi	%3 phi	% >3 phi
SS-11-304	Stratum I	6.58	3%	0%	6%	11%	9%	6%	5%	4%	6%	52%
SS-11-305	Stratum II	7.56	4%	0%	2%	0%	0%	1%	1%	3%	11%	82%
SS-11-290	Stratum III, level 4	5.65	11%	0%	0%	0%	1%	1%	1%	1%	3%	92%
SS-11-291	Stratum III, level 5	6.03	11%	0%	0%	4%	9%	10%	7%	7%	15%	49%
SS-11-292	Stratum III, level 6	6.32	39%	0%	4%	2%	4%	7%	9%	13%	20%	41%
SS-11-293	Stratum III, level 7	6.88	41%	0%	1%	3%	5%	6%	6%	7%	6%	66%
SS-11-294	Stratum III, level 8	6.87	n/a	0%	0%	0%	4%	8%	6%	13%	17%	52%
SS-11-295	Stratum III, level 9	7.55	8%	0%	1%	6%	8%	13%	13%	15%	9%	35%
SS-11-296	Stratum III, level 10	7.31	51%	0%	0%	6%	8%	10%	13%	10%	8%	45%
SS-11-297	Stratum III, level 11	7.74	21%	0%	0%	2%	1%	3%	4%	11%	5%	74%
SS-11-298	Stratum III, level 12	7.39	19%	0%	0%	1%	1%	2%	4%	4%	4%	84%
SS-11-299	Stratum III, level 13	7.41	18%	0%	1%	1%	1%	3%	4%	5%	6%	79%
SS-11-300	Stratum III, level 14	7.84	8%	0%	29%	11%	11%	11%	7%	5%	4%	23%
SS-11-301	Stratum IV	7.43	11%	0%	3%	2%	2%	2%	2%	6%	16%	68%

at the western edge of the excavation (Fig. 2) and slopes steeply downward to the east.

4.2. Faunal composition and taphonomy

To date, approximately 200 m^3 of megafauna-bearing deposit have been excavated at the Tanque Loma locality. The full extent of the deposit is still unknown, but the fossiliferous layer is observed to continue to the north, south and southwest of the excavated sections. In the 2003–2006 excavations, a minimum 663 megafaunal bone elements (MNE) were excavated and prepared from approximately 140 m^3 of deposit. Bones deposited in and just above the tar-saturated sediments at Tanque Loma are generally in good condition and not very fragmented. 68% of bones, excluding vertebrae, ribs, and cranial elements, are ≥75% complete. 45% of these are 100% complete.

4.2.1. Systematic paleontology

The megafaunal specimens so far prepared from the Tanque Loma locality comprise two species of ground sloth, one species of gomphothere, one species of pampathere, one species of horse, and a cervid.
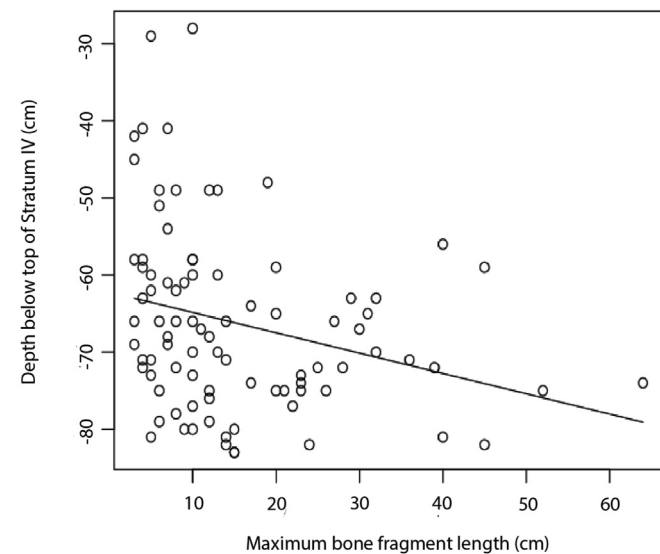

Fig. 4. Distribution and size of megafaunal bones within Stratum IV of grid unit 11 at the Tanque Loma locality. Bones toward the bottom of the stratum are more abundant and larger, whereas those toward the top are more fragmentary and scarce. Pearson's product–moment correlation, cor = −0.28, p = 0.009.

ORDER: XENARTHRA Cope, 1889
SUBORDER: PILOSA Flower, 1883
FAMILY: MEGATHERIIIDAE Owen, 1842
GENUS: _EREMOTHERIUM_ Spillmann, 1948
Eremotherium laurillardi (Lund), 1842
For synonymies see Cartelle and De Iuliis (1995)

4.2.1.1. Referred material. MPM702, cranium; MPM703, left and right mandibles, fused; MPM681, right mandible; MPM791 and MPM841, right femora; MPM787, MPM541 and MPM542, left femora; MPM34, metacarpal III.

4.2.1.2. Remarks. The premaxillary contact exhibits a triangular suture. This is typical of the suture in _Eremotherium laurillardi_, and is in contrast with the suture in _Megatherium americanum_ which is rectangular, and in which the premaxilla is well-fused to the maxilla (Cartelle and De Iuliis, 1995). The mandibular symphysis terminates at the m1 (Fig. 5D); this is different from _M. americanum_, in which the posterior margin of the mandibular symphysis ends at the m2 (Cartelle and De Iuliis, 1995).

The lateral margin of the femur is relatively rectilinear, rather than more convex as is typical of femora in _Megatherium_ (De Iuliis and St-André 1997), and the greater trochanter is not expanded nor posteriorly deflected as is seen in _M. americanum_ (Fig. 5E). The femoral head is wide and close to the body of the femur, not constricted and elongated as in _Eremotherium sefvei_ (De Iuliis and St Andre 1997). The referred (all adult) femurs at Tanque Loma are also much larger than the femur of _E. sefvei_, with proximodistal lengths ranging from 73.0 cm to nearly 86.6 cm, whereas the lateral proximodistal femur length reported for _E. sefvei_ (De Iuliis and St Andre 1997) is only 39.1 cm.

The metacarpal is relatively stout, as compared with those of _Megatherium americanum_ and _Eremotherium eomigrans_, which are more gracile (De Iuliis and Cartelle 1999), and does not exhibit an articular facet for mcII. There is also no evidence of second metacarpals (as possessed by _M. americanum_ and _E. eomigrans_) or first phalanges (as are present in _E. eomigrans_) among the 24 megathere metacarpals and 26 phalanges prepared from Tanque Loma. The diagnostic metacarpal–carpal complex bone (De Iuliis and Cartelle, 1994) has not yet been recovered at Tanque Loma.

4.2.1.3. Biogeographic context. _Eremotherium laurillardi_ is known from late-Pleistocene deposits in lowland tropical and subtropical areas from Rio Grande do Sul, Brazil, to South Carolina, U.S.A. (Cartelle and De Iuliis, 1995). The assignment of the megathere remains at Tanque Loma to _E. laurillardi_ is consistent with the
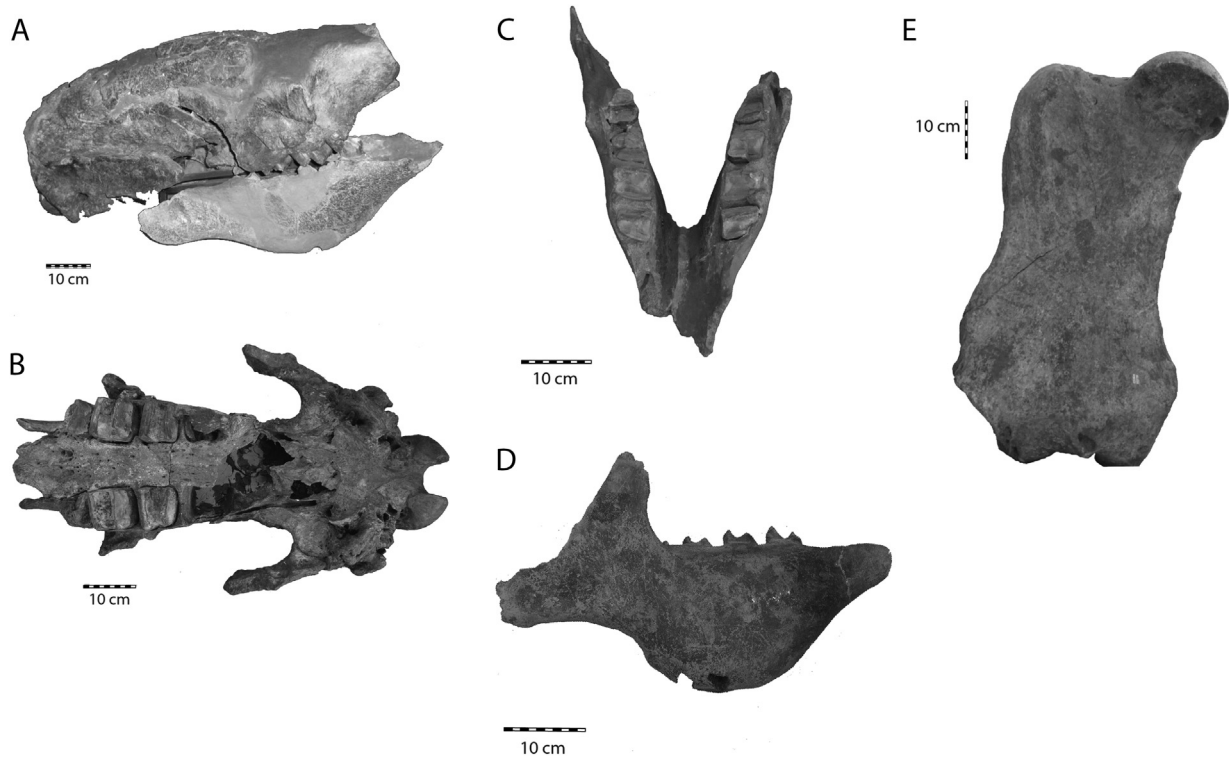
Fig. 5. *Eremotherium laurillardi* bones from Tanque Loma. (A) MPM702, cranium, right lateral view. (B) MPM702, ventral view. (C) MPM703, mandibular symphysis, occlusal view. (D) MPM681, right mandible, lateral view (E) MPM841, right femur, anterior view.

assertion (Cartelle and De Iuliis, 1995; 2006) that there were only two megatheriid sloth species − *Megatherium americanum* and *Eremotherium laurillardi* – in the late-Pleistocene of South America, and with the fact that *M. americanum* is not known to be associated with tropical lowlands (Cartelle and De Iuliis, 1995; Bargo et al. 2006). Some authors (e.g., Pujos and Salas, 2004; Tito, 2008) recognize the presence of a second, smaller megathere species, *Megatherium* (= *Pseudomegatherium* = *Eremotherium*) *elenense*, in coastal Ecuador, however other analyses (Cartelle and De Iuliis, 2006) indicate that this may simply represent ontogenetic growth and sexual dimorphism in *E. laurillardi*. The present study yields no evidence for the occurrence of multiple megathere species at Tanque Loma.

ORDER: XENARTHRA Cope, 1889
SUBORDER: PILOSA Flower, 1883
FAMILY: MYLODONTIDAE Gill, 1872
GENUS: *GLOSSOTHERIUM* Owen, 1840
Glossotherium cf. *G. tropicorum* Hoffstetter, 1952

4.2.1.4. Referred material. MPM823, left mandible; MPM800, left humerus; MPM454, proximal right ulna.

4.2.1.5. Remarks. The referred mandible (Fig. 6A) is more modeled and complex than the mandible of *Mylodon* or *Scelidotherium*. The depth of the horizontal ramus increases posteriorly to a maximum of 8.5 cm. The referred specimen lacks dentition and is missing the alveoli for m1 − m3, but the m4 alveolus indicates a bilobate tooth, which is diagnostic for mylodont sloths. However, this specimen likely pertains to a juvenile as the m4 is not very elongated and the lobes are not well defined, making it of little diagnostic utility below the family level.

The deltoid tuberosity of the humerus (Fig. 6B) is very well-developed, but does not protrude as in scelidotheriines. And, the humerus lacks an entepicondylar foramen, which is present in scelidotheres. The ulna (Fig. 6C) is stout, with a well-developed olecranon process, typical of mylodont sloths, however this feature does not project as much as would be expected in *Scelidotherium* (Bargo et al. 2000).

While the referred specimens are indicative of *Glossotherium* (Hoffstetter, 1952; Román-Carrión, 2007; Pitana et al. 2013), the available material is insufficient to diagnose a species. We tentatively assign the referred material to *Glossotherium* cf. *G. tropicorum*, which was first described from the close-by La Carolina locality (Hoffstetter, 1952), as this is the only *Glossotherium* species that has been definitively identified from coastal Ecuador.

4.2.1.6. Biogeographic context. *Glossotherium* species known from Ecuador include *G. tropicorum* from the Santa Elena Peninsula, *G.* (*Oreomylodon*) *wegneri* (=*Glossotherium robustum*) in the Andes, and a possibly new undescribed species from Puná Island (Román-Carrión, 2007). *Glossotherium* has also been identified from the contemporaneous Talara tar seeps in northwest Peru (Lemon and Churcher, 1961), and the species represented there is probably *G. tropicorum* given the very similar mammal faunas shared by this locality and the sites on the Santa Elena Peninsula. *Glossotherium* cf. *G. tropicorum* has also been reported from Venezuela (Bocquentin-Villanueva, 1979) and Panama (Gazin, 1956) but these isolated reports probably warrant further analysis.

ORDER: XENARTHRA Cope, 1889
SUBORDER: CINGULATA Illiger, 1811
FAMILY: PAMPATHERIIDAE Paula Couto, 1954
GENUS: *HOLMESINA* Simpson, 1930
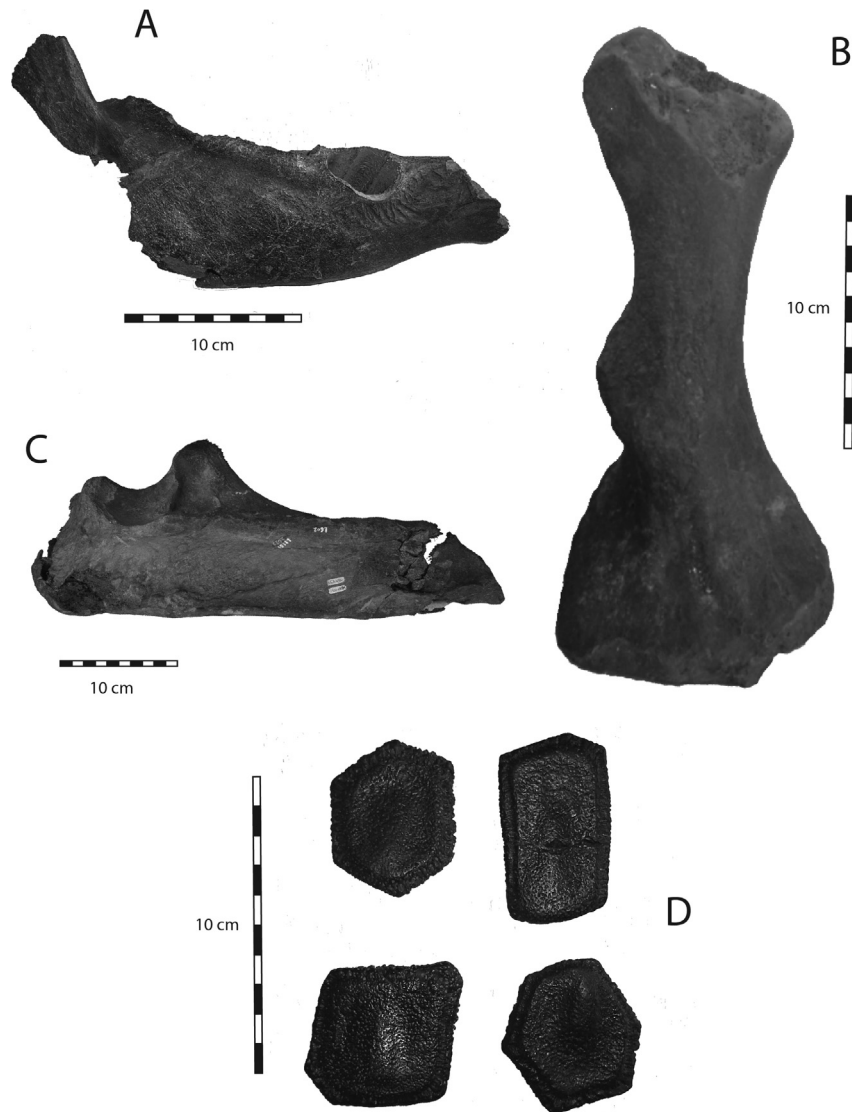*Holmesina occidentalis* (Hoffstetter), 1952

Fig. 6. (A) MPM823, *Glossotherium* cf. *tropicorum* left mandible, lingual view. (B) MPM800, juvenile *Glossotherium* cf. *tropicorum* left humerus, anterior view. (C) MPM454, cf. *Glossotherium* proximal right ulna. (D) MPM830, MPM831, MPM832, MPM833, *Holmesina occidentalis* buckler osteoderms.

4.2.1.7. Referred material. MPM830, MPM831, MPM832, and MPM833, buckler osteoderms.

4.2.1.8. Remarks. The osteoderms (Fig. 6D) are subrectangular or hexagonal. Each posesses a narrow, well-defined, raised central figure that extends vertically across most of the scute. They differ in this respect from buckler osteoderms of *Pampatherium*, which exhibit a central figure that is wider, flatter, and less distinct, and also from those of *Holmesina paulacoutoi* which has a wide, gentle ridge across the lower margin of the scute only. On the surface of the scutes, smooth bone extends almost all the way to the lateral margin, which is distinct from *Pampatherium* and also from *H. majus* as scutes in these these taxa have relatively wider rugose margins. The osteoderms are also relatively thin (3 mm − 5 mm), unlike those of *H. paulacoutoi* which tend to be more robust (Edmund, 1996; Scillato-Yané et al. 2005).

4.2.1.9. Biogeographic context. Holmesina occidentalis has been reported from sites along the northwest coast of South America from southern Peru to northern Venezuela (Scillato-Yané et al. 2005). However, some authors argue that the southern occurrences actually pertain to *H. paulacoutoi* (Pujos and Salas, 2004) or *H. majus* (Martinez and Rincón, 2010). It has been suggested that these two species may be conspecific (Edmund, 1996).

ORDER: PROBOSCIDEA Illiger, 1811
FAMILY: GOMPHOTHERIIDAE Cabrera, 1929
GENUS: CF. *NOTIOMASTODON* Cabrera, 1929
Notiomastodon cf. *N. platensis* (Ameghino), 1888

4.2.1.10. Referred material. MPM847, left femur; MPM849, left tibia; MPM851, left astragalus; MPM852, left calcaneum.

4.2.1.11. Remarks. The referred femur (Fig. 7A) presents general proboscidean characters, with a head that is rounded, well-defined and located proximal to the greater trochanter. Like in *Cuvieronius*, the margins of the diaphysis are slightly convex, but unlike in *Cuvieronius*, the tibial crest is not well-defined, and the malleolus is

very well-developed. The medial condyle of the tibia is proximal to the lateral condyle, which is typical in proboscideans. The astragalus is robust with the ectal and sustancular facets well-differentiated. The *tuber calcanei* on the calcaneum is elongated and lacks protuberences, and the articular facet for the cuboid is concave.

Unfortunately, Lujanian gomphothere postcrania are not currently well-enough studied to be taxonomically diagnostic (e.g.: Ficcarelli et al. 1995; Prado et al. 2005; Ferretti, 2008; Lucas and Alvarado, 1991). Historically, three species of gomphothere have been recognized in the Lujanian, *Cuvieronius hyodon* from the Andes, *Haplomastodon chimborazi* (= *H. waringi*), from the tropical lowlands, and *Stegomastodon* (= *Haplomastodon*) *platensis* from the temperate lowlands (Sánchez et al., 2004; Mothé et al. 2012). However, the most recent taxonomic revision (Mothé et al. 2012) taking into account craniodental morphological variation across the continent, synonymizes the latter two species, recognizing only one species of lowland gomphothere, *Notiomastodon platensis*, in the South American Pleistocene. Because we have only recovered postcrania so far, we follow the most recent and comprehensive analysis and tentatively assign the gomphothere species present at Tanque Loma to cf. *Notiomastodon platensis* pending the recovery of more taxonomically diagnostic material.

4.2.1.12. Biogeographic context. *Notiomastodon platensis* has a broad lowland continental distribution, with records from every South American country except Bolivia and the Guyanas (Mothé et al. 2012). The absence of records from the Guyanas is probably simply due to the lack of any Quaternary vertebrate fossils known from this region.

ORDER: PERISSODACTYLA Owen, 1848
FAMILY: EQUIDAE Gray, 1821
GENUS: *EQUUS* Linnaeus, 1758
SUBGENUS: *EQUUS* (*AMERHIPPUS*) Hoffstetter, 1950
Equus (Amerhippus) cf. *E (A.) santaeelenae* Spillmann, 1938

4.2.1.13. Referred material. MPM827 and MPM828, upper molars; MPM829, lower molar.

4.2.1.14. Remarks. The referred material coincides with descriptions of *Equus (Amerhippus) santaeelenae* (Hoffstetter, 1952; Prado and Alberdi, 1994; Rincón et al., 2006). The enamel on the occlusal surface is complexly wrinkled, and the lower molar is quite wide relative to its length. The M3 (Fig. 7B) measures approximately 25 mm wide × 28 mm long, which is similar to the measurements of 23.6 mm–28.4 mm wide and 26.2 mm – 26.3 mm
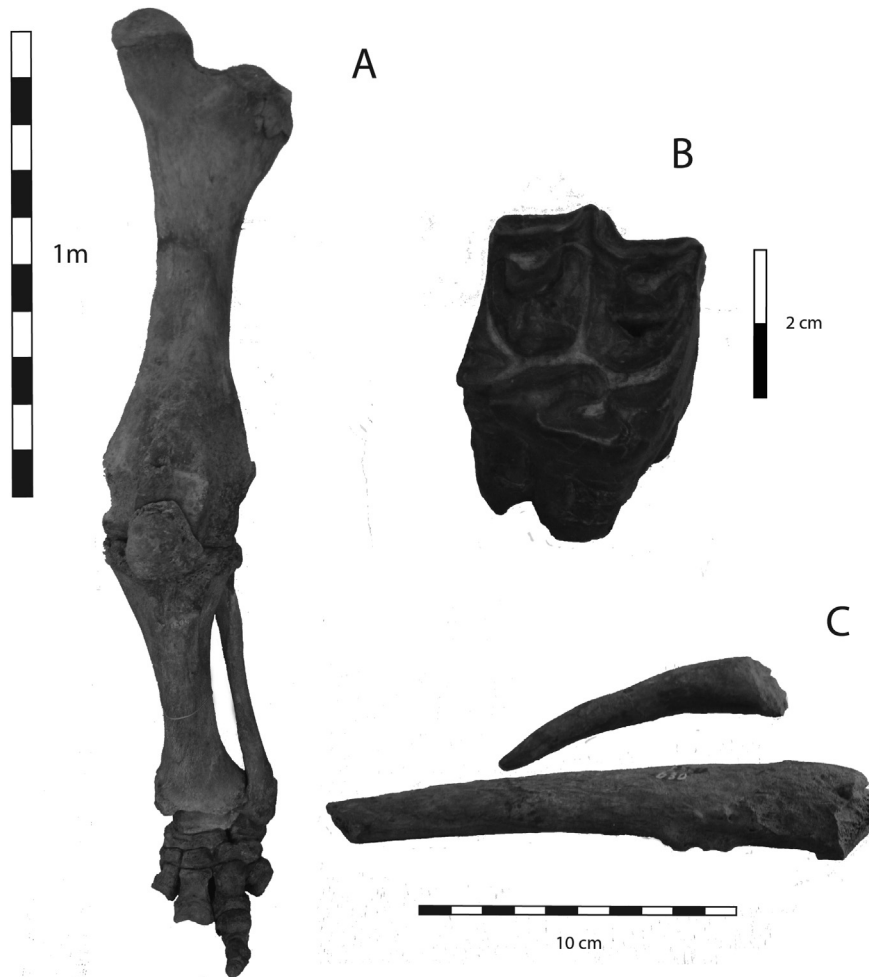

Fig. 7. (A) Articulated cf. *Notiomastodon platensis* left hind leg, anterior view. MPM847, femur; MPM848, patella; MPM849, tibia; MPM850, fibula; MPM851, astragalus; MPM852, calcaneum; MPM853, cuboid; MPM854, navicular; MPM855, ectocuneiform; MPM856, mesocuneiform; MPM857, entocuneiform; MPM858, metatarsal III; MPM859, metatarsal IV; MPM860, proximal phalanx IV; MPM861, medial phalanx IV; MPM862, distal phalanx IV; MPM863, metatarsal V; MPM864, metatarsal II. (B) MPM827, *Equus santaeelenae* upper right molar, occlusal view. (C) MPM834 and MPM835, cf. *Odocoileus salinae* antler fragments.

long given for this element by Hoffstetter (1952). This tooth also presents an island in the isthmus of the protocone, which is characteristic of *E. (A.) santaeelenae* (Hoffstetter, 1952).

4.2.1.15. Biogeographic context. Equus (Amerhippus) santaeelenae has been recovered from the Santa Elena Peninsula, Ecuador (Hoffstetter, 1952; Prado and Alberdi, 1994) and at Inciarte, Venezuela (Rincón et al., 2006).

ORDER: ARTIODACTYLA Owen 1848
FAMILY: CERVIDAE Gray 1821
GENUS: cf. *ODOCOILEUS* Rafinesque 1832
cf. *Odocoileus* cf. *O. salinae* (Frick) 1937

4.2.1.16. Referred material. MPM834 and MPM835, antler fragments.

4.2.1.17. Remarks. The larger of the referred antler fragments (Fig. 7C), measures approximately 22 mm in diameter at its base. This is smaller than the maximum antler diameter reported for *Odocoileus salinae* (28.5 mm), which is much smaller than *Odocoileus virgineanus* (maximum diameter 31.7 mm–52 mm) (Tomiati and Abbazzi, 2002). However, since neither specimen includes the pedicle, it is impossible to determine from which part of the antler the fragments came, and thus size cannot be a diagnostic criterion. We have tentatively assigned these remains to cf. *O. salinae* based on its small size, and because this is the only species of

cervid that has been reported for the late Quaternary of coastal Ecuador (Hoffstetter, 1952; Edmund, 1965; Tomiati and Abbazzi, 2002).

4.2.1.18. Biogeographic context. O. salinae has been reported from the Santa Elena Peninsula (Hoffstetter, 1952; Edmund, 1965) and also from the nearby Talara tar seeps in northern Peru, where it co-occurs with *Mazama* sp. (Churcher, 1962). *Mazama* has not yet been reported from the Santa Elena Peninsula.

4.2.2. Bone orientation

Aside from a few *Eremotherium* vertebrae, no clearly articulated megafaunal remains have been encountered at Tanque Loma, with one exception: the complete left hindquarters (including left ilium, femur, tibia, astragalus, calcaneum, metatarsals and some phalanges) of a juvenile *Notiomastodon* were found articulated in Stratum IV, 15 cm – 30 cm above the contact with Stratum V in grid unit 9 (Figs. 2 and 3).

An analysis of 91 bones and bone fragments excavated during the 2009–2011 field seasons from grid units 8, 9, 10, and 11 measuring greater than 30 cm in length and with at least a 2:1 length:width ratio did not show any significant directional orientation (Kolmogorov–Smirnov test, $p = 0.32$; Fig. 8A).

Dip data was collected using a Brunton compass for 98 megafaunal bones in Strata IV and V of grid unit 11. Dip angles were generally shallow, with 16 bones having no dip at all, and only three bones dipping steeper than 40° (Fig. 8B). The 80 bones with dip angles between 0° and 90° showed no pattern in directional
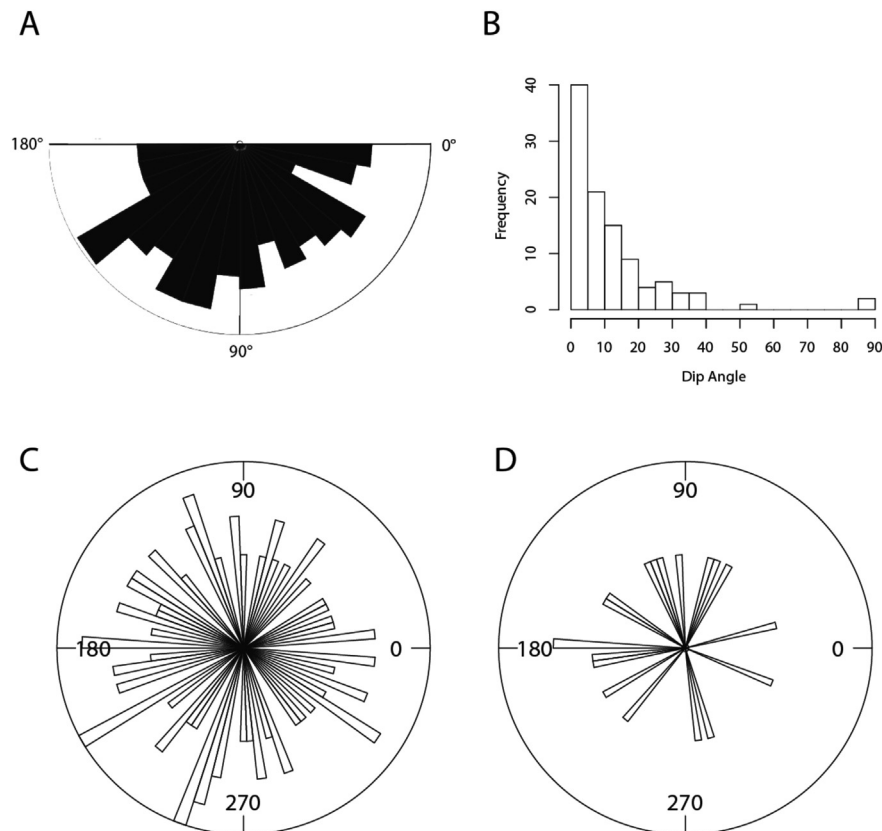

Fig. 8. (A) Rose diagram depicting orientation of all bones and bone fragments >30 cm in length, with a length:width ratio of at least 2:1, excavated in grid units 8, 9, 10, and 11 during the 2009–2011 field seasons. $N = 91$. Kolmogorov–Smirnov test, $p = 0.32$. Because bone orientation was taken without regard to bone polarity, orientation is plotted on a 180° axis. (B) Histogram depicting dip angles of bones and bone fragments >10 cm in length, with a length:width ratio of at least 2:1, collected in grid unit 11. $N = 98$. (C) Rose diagram depicting directional orientation of dipping end of bones included in (B), excluding horizontally- and vertically-oriented bones. $N = 80$. Kolmogorov–Smirnov test, $p = 0.65$. (D) Rose diagram depicting directional orientation of dipping end of only steeply-dipping (dip angle >/ = 20°) bones included in (B). $N = 19$. Kolmogorov–Smirnov test, $p = 0.33$.

orientation of the dipping end (Kolmogorov–Smirnov test, $p = 0.65$; Fig. 8C). An analysis of dip orientation of only steeply-dipping (dip angle $>/ = 20°$) bones ($n = 19$) still revealed no pattern in orientation (Kolmogorov–Smirnov test, $p = 0.33$; Fig. 8D). Only three of the bones in this analysis had a clear polarity (heavy end) so it was not possible to determine whether there was a consistent orientation to the heavy ends of the bones.

4.2.3. Bone condition and taphonomic markings

Most megafaunal bones in the lower (tar-saturated) part of Stratum IV are in good condition and do not exhibit substantial evidence of weathering (nearly all conform to weathering stages 0–1, *sensu* Behrensmeyer, 1978). However, some bones present unusual taphonomic features including deep, smooth, conical holes and extensive irregular erosions or breakages on the ends (Fig. 9). In addition, many bones are marked by abundant shallow, irregular, non-parallel scratches that are consistent with trampling abrasion (*sensu* Olsen and Shipman, 1988, Fig. 9B and F). On the other hand, bones in the upper substratum of Stratum IV, especially the top 40 cm or so, are extremely fragmentary and do exhibit substantial weathering (Behrensmeyer weathering stages 3–5). There is no evidence of unequivocally human-caused modifications on any bones, and no tools or other evidence of human presence have been found in the megafauna-bearing strata of Tanque Loma.

4.2.4. Associated fauna

Almost no small vertebrate remains have been encountered in the megafauna-bearing strata of Tanque Loma. During 2010, and 2011, a few microvertebrate bone fragments 2–10 cm in length were collected. These correspond to several long bones of birds and possibly one rodent, but have not yet been prepared and identified to more precise taxonomic levels. In addition, a dense micro-vertebrate assemblage, consisting primarily of small ($</ = 3$ cm) bird, squamate and rodent bones typical of the Stratum III assemblages, was found precisely at the top of Stratum IV and above the gomphothere skeleton in grid unit 9. These are being analyzed to learn more about the paleoecology of the Tanque Loma ecosystem.

The most prevalent invertebrate fossils encountered in the Pleistocene deposits are sea urchin spine fragments and terrestrial gastropods of the genus *Porphyrobaphe*. Complete, isolated *Porphyrobaphe* shells are found throughout Strata IV and V, often adjacent to megafaunal remains.

4.2.5. Megafauna NISP, MNE, MNI, and MAU

The megafaunal bones and bone fragments excavated and prepared during the 2004–2006 field seasons comprise a minimum of 663 individual elements (NISP = 887). 571 of these elements, or roughly 86%, pertain to the extinct giant ground sloth *Eremotherium laurillardi*, representing a minimum of 16 individuals (Fig. 10). These constitute a minimum of: nine adults, two juveniles, three neonates, and two individuals believed on the basis of their extremely small size to be fetuses. An additional 76 elements, comprising roughly 11% of the identified material, pertain to the gomphothere *Notiomastodon platensis*, representing a minimum of three individuals (two juveniles and one adult). Eight elements of the Mylodont sloth *Glossotherium* cf. *tropicorum* representing at least three individuals (one adult, one juvenile and one neonate or fetus); three *Equus santaeelenae* teeth (MNI = 2 adults), and two fragments of antler, most likely pertaining to the cervid *Odocoileus* (cf. *O. salinae*) (MNI = 1 adult) were also recovered during the first three years of excavation. In addition, four osteoderms from the Pampathere *Holmesina occidentalis* (MNI = 1 adult) were recovered from a test pit dug about 1 m east of Grid unit 1 (Fig. 2).

Minimum Animal Units (MAU) were calculated for *Eremotherium* by dividing the MNE for each element by the number of times that bone is represented in an individual skeleton (*sensu* Spencer et al. 2003). MAU is a metric used for determining completeness of skeletons and whether certain elements are over- or underrepresented relative to others, which can be useful in determining taphonomic process such as winnowing, predation, or human action (Voorhies, 1969; Lyman, 1994; Spencer et al. 2003). Percent MAU was calculated by dividing each MAU value by the MAU value for the most-represented element. For *Eremotherium*, the most common element (and thus, the one with 100% MAU) found in the
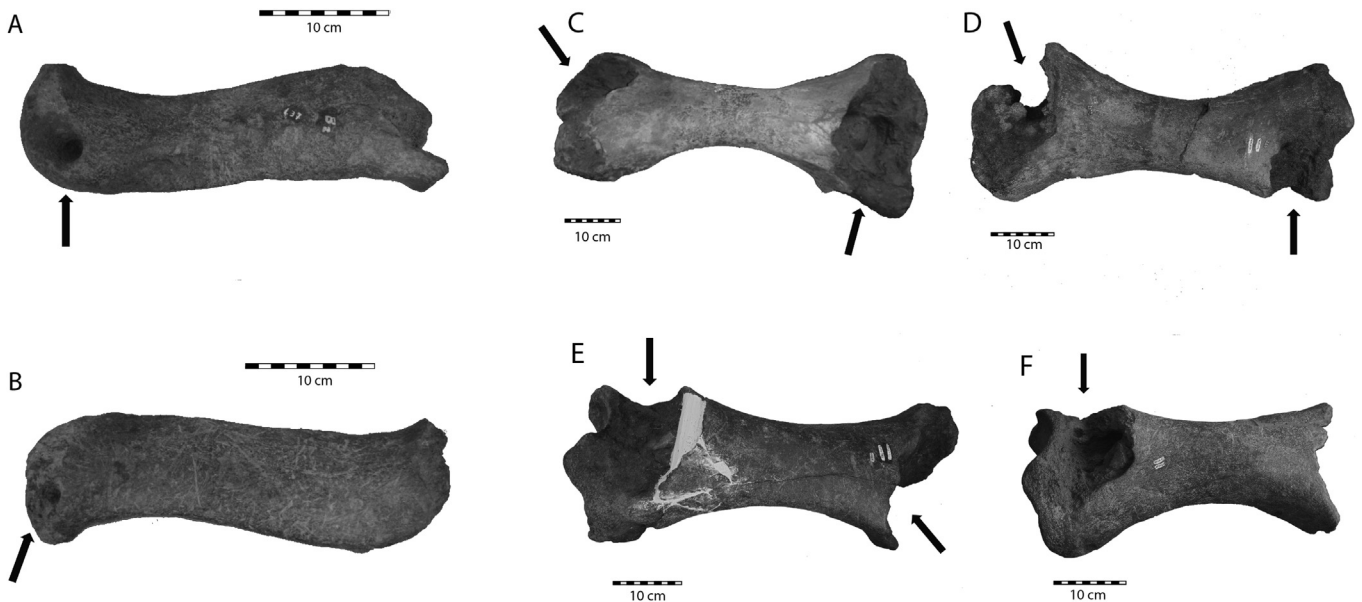

Fig. 9. Some unique taphonomic marks on bones from Tanque Loma locality. (A) Specimen MPM212, *Eremotherium laurillardi* clavicle, with smooth, conical hole on lateral end. (B) Reverse side of MPM212 with smaller hole. (C) Specimen MPM674, *E. laurillardi* tibia, showing deep erosions on both ends. (D) Specimen MPM340, *E. laurillardi* tibia, showing deep erosions on both ends. (E) Specimen MPM342 *E. laurillardi* tibia, showing significant erosion/breakage on both ends. (F) Specimen MPM675, *E. laurillardi* tibia, showing irregular excavations on proximal end (distal end broken off). Arrows indicate location of noted taphonomic features. (B) and (F) are covered in shallow scratch marks interpreted as trampling abrasion.
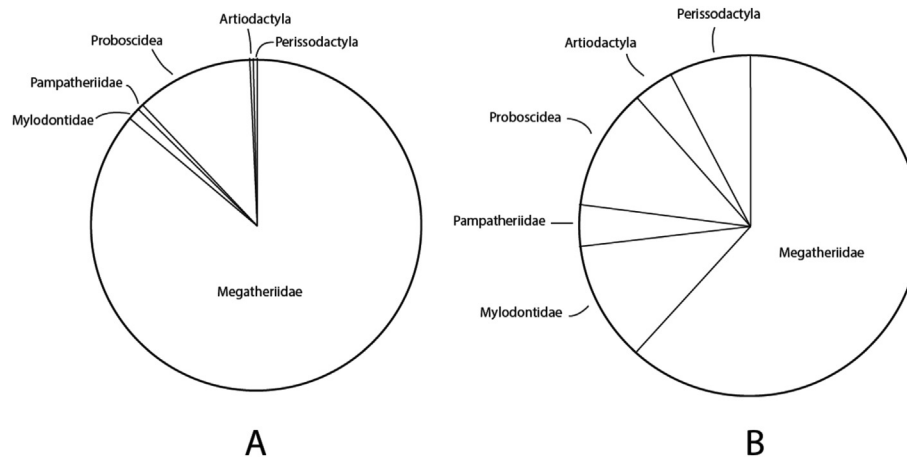
Fig. 10. Graphs showing proportions of (A) Minimum Number of Elements (MNE), and (B) Minimum Number of Individuals (MNI) for the different megafaunal taxa recovered at the Tanque Loma locality.

deposit was the tibia, followed by the humerus (74% MAU). Astragali, femora, radii, innominates, clavicles and dentaries all had about 50% representation in the deposit. Small bones (carpals, smaller tarsals, phalanges, sternebrae and sesamoids) and more fragile elements (ribs and certain vertebrae) tended to be underrepresented (1%–22% MAU; Table 3). Vertebrae and costal ribs were probably somewhat underestimated because some very fragmentary specimens collected during the 2004–2006 field seasons were never fully prepared and thus were not able to be included in the analyses. Additionally, several vertebrae (MNE = 17) were so incomplete that they could not be classified according to anatomical position.

MAU values were not calculated for the other five megafauna taxa found at the site, as numbers of elements represented for each taxon were too small to be informative.

In order to investigate the origin of the megafaunal deposit at Tanque Loma, percent MAU values for *Eremotherium* from this site were compared with %MAU values for large vertebrates from localities with differing depositional contexts, including a "tar pit" trap (Rancho La Brea Pit 91; Spencer et al. 2003) and a fluvial assemblage (the Pliocene Verdigre Quarry; Voorhies, 1969) (Table 4). *Eremotherium* from Tanque Loma and *Merycodus* from Verdigre have a similar under-representation of small bones (carpals, tarsals) and vertebrae, although vertebrae are better represented in the Tanque Loma deposits (9%–39% MAU for non-sacra) than at Verdigre (2%–9% MAU). Long bones and ribs are much better represented at Tanque Loma than at Verdigre, whereas metapodials and rami are more prevalent at Verdigre. A different pattern exists for comparisons with %MAU values for the three most common herbivores in Pit 91 at Rancho La Brea: *Bison antiquus, Equus occidentalis,* and *Paramylodon harlani*. In general, crania, mandibles, vertebrae, and small bones such as podials and metapodials were much better represented in the La Brea deposit than at Tanque Loma, while long bones had similar %MAU values at the two sites.

Relative element representations of *Eremotherium* at Tanque Loma were also compared qualitatively with large-mammal data for archaeological and paleoanthropological butchering accumulations (Behrensmeyer, 1987; Bunn, 1987), for a lacustrine assemblage with hardship-induced attritional mortality (Ballybetagh bog; Barnosky, 1985), and for a second Pleistocene "tar pit" (Maricopa; Muleady-Mecham, 2003). Butchering localities tend to have an underrepresentation of meaty, transportable elements such as limb bones and mandibles, which are presumably carried off by

human hunters. This pattern is not observed at Tanque Loma. The *Megaloceros* accumulation at Ballybetagh bog exhibits an over-representation of crania, mandibles, vertebrae, ribs, and podials; in contrast, the *Eremotherium* assemblage at Tanque Loma has less than 50% MAU for all of these elements, and less than 25% MAU for ribs, all vertebrae except the axis, and all podials except astragali and calcanea. Finally, skeletal element representation at the Maricopa tar seep locality is skewed in favor of appendicular elements, a fact which the authors attribute to the animals' limbs becoming trapped and buried in the tar, while axial elements were left exposed to scavengers and environmental processes. While large limb bones (femora, humeri, radii, ulnae, and tibias) are among the

Table 3
Number of Individual Specimens (NISP), Minimum Number of Elements (MNE), and Minimum Animal Units (MAU and %MAU) calculations for *Eremotherium laurillardi* elements excavated at Tanque Loma locality, 2004–2006.

Element	NISP	MNE	MNI	# in skeleton	MAU	%MAU
Cranium	21	4	4	1	4.00	26%
Mandible	21	15	8	2	7.50	48%
Molariform	38	38	5	18	2.11	14%
Atlas	4	3	3	1	3.00	19%
Axis	6	6	6	1	6.00	39%
Other Cervical Vertebra	18	17	4	5	3.40	22%
Thoracic Vertebra	93	65	5	16	1.33	9%
Lumbar Vertebra	4	4	1	3	1.33	9%
Sacral Vertebra	2	1	1	5	0.20	1%
Caudal Vertebra	64	57	7	18	3.17	20%
Scapula	15	11	6	2	5.50	35%
Clavicle	13	13	7	2	6.50	42%
Costal Rib	154	90	3	32	2.81	18%
Seternal Rib	21	15	1	16	0.94	6%
Sternebra	5	5	1	8	0.63	4%
Pelvis	10	7	7	1	7.00	45%
Humerus	34	23	11	2	11.50	74%
Radius	25	18	10	2	9.00	58%
Ulna	20	12	6	2	6.00	39%
Metacarpal	20	20	7	6	3.33	22%
Carpal	8	8	4	16	0.50	3%
Femur	30	14	7	2	7.00	45%
Tibia	38	31	16	2	15.50	100%
Fibula	7	6	4	2	3.00	19%
Patella	2	2	2	2	1.00	6%
Metatarsal	16	16	6	6	2.67	17%
Astragalus	17	14	8	2	7.00	45%
Calcaneum	11	10	6	2	5.00	32%
Other tarsal	11	11	3	12	0.92	6%
Phalanx	30	30	3	24	1.25	8%

Table 4
Comparison of %MAU values for *Eremotherium* at Tanque Loma, *Merycodus* at Verdigre Quarry (Voorhies, 1969) and the three most common herbivores in Pit 91 at Rancho La Brea (Spencer et al. 2003).

Element	Tanque Loma *Eremotherium*	Verdigre Quarry *Merycodus*	La Brea *Bison*	La Brea *Equus*	La Brea *Paramylodon*
Cranium	26	4	100	88	71
Mandible	48	100	91	81	100
Molariform	14	n/a	n/a	n/a	n/a
Atlas	19	4	11	25	29
Axis	39	9	11	100	0
Other Cervical Vertebra	22	4	15	40	17
Thoracic Vertebra	9	2	27	76	41
Lumbar Vertebra	9	7	24	46	0
Sacral Vertebra	1	1	13	21	6
Caudal Vertebra	20	n/a	3	12	29
Scapula	35	16	51	50	100
Clavicle	42	n/a	n/a	n/a	n/a
Costal Rib	18	1	25	38	26
Seternal Rib	6	n/a	n/a	n/a	n/a
Sternebra	4	n/a	0	9	41
Pelvis	45	23	51	88	100
Humerus	74	49	43	94	71
Radius	58	29	31	75	57
Ulna	39	10	43	31	29
Metacarpal	22	50	43	75	29
Carpal	3	1	17	19	29
Femur	45	13	37	63	71
Tibia	100	55	34	50	86
Fibula	19	n/a	20	6	71
Patella	6	n/a	14	31	0
Metatarsal	17	67	26	88	14
Astragalus	45	41	23	38	71
Calcaneum	32	42	34	25	43
Other tarsal	6	4	18	19	18
Phalanx	8	11	15	27	n/a

best-represented *Eremotherium* elements at Tanque Loma, smaller limb bones, especially podials and metapodials, tend to be under-represented at this site, which is inconsistent with an entrapment model.

4.3. Radiocarbon analysis

Dates were obtained on the two *Notiomastodon* bones (MPM291 and MPM325) and the *Eremotherium* phalanx (HE616) (Table 5). The *Eremotherium* vertebra and the Aves phalanx did not yield sufficient collagen for dating.

The *Notiomastodon* bones yielded overlapping dates. The caudal vertebra (MPM291) yielded a 14C date of 17,170 ± 920 RCYBP, and the metapodial (MPM325) yielded a date of 19,110 ± 1260 RCYBP.

The *Eremotherium* phalanx yielded a date of 23,560 ± 180 RCYBP. This date is consistent with the lower stratigraphic position of this bone relative to the dated *Notiomastodon* elements. However, a small amount of dark-colored liquid extracted during the decalcification process indicates that contamination by hydrocarbons cannot be ruled out. Such contamination would most likely result in an erroneously old date, because petroleum derivatives are depleted in carbon 14 (Venkatesan et al. 1982).

Experiments are now underway to establish a protocol for completely removing hydrocarbons from the Tanque Loma bones, which will hopefully allow us to corroborate the validity of these dates.

5. Interpretation and discussion

5.1. Geology and sedimentology

5.1.1. Depositional context

The overall geomorphology and sedimentological history of Tanque Loma is suggestive of a slow-moving riparian system alternately inundated and exposed throughout the later Pleistocene and Holocene. Strata IV and V, as well as many of the layers within Stratum III, consist principally of well-sorted, fine-grained sediments, containing a high proportion (70%–90%) of muds (Table 2), which is suggestive of deposition in a low-flow fluvial environment (Allen, 1982). In addition, in the lower 10 cm of Stratum III, several layers occur as thin, lamina-type deposits (Fig. 3), which is consistent with deposition in still water. A standing-water environment is also suggested in the Pleistocene deposits by the presence of a green anoxic gley (Stratum VI) which tends to form in freshwater marshes (Ponnamperuma, 1972), underlying the bone-bearing strata.

The interpretation of these sediments as low-flow fluvial deposits is consistent with the extreme scarcity of clasts larger than 0φ in most of these layers (Allen, 1982). Of those clasts that are present in the Tanque Loma deposits, nearly all are quite angular and match the friable limestone material of the bedrock, suggesting that they were transported only a short distance, most likely eroding out of the adjacent hillside. This hypothesis is supported by the fact that these clasts are extremely abundant close to the bedrock nucleus of the hill, and nearly absent from sediments just a few meters to the west, and that their deposition appears to follow the slope of the hillside (Fig. 3A). In addition, there is no evidence of rounding or smoothing of these clasts from fluvial transport. The few smooth, rounded stones encountered in the Stratum IV and V sediments most likely come from re-worked marine sediments of the *Tablazo* formation that were uplifted from the ocean floor during the Pleistocene. This is also the most probable explanation for the presence of sea urchin spine fragments and occasional marine shell fragments encountered in these layers.

Finally, a low-flow regime is also suggested by the extreme abundance of microvertebrate bones throughout Stratum III and small plant fragments in Strata IV − VI, as such lightweight materials would be expected to be removed from the deposit through hydraulic sorting in a high-flow environment (Dodson, 1973; Allen, 1982). Additionally, there is no evidence of rounding or abrasion on either the microvertebrate or the megafaunal bones, suggesting that any transport must have been minimal (Korth, 1979; Behrensmeyer, 1988).

5.1.2. Paleoenvironmental evidence

The fluvially-deposited sediments at Tanque Loma appear to have undergone repeated periods of desiccation and paleosol development, as evidenced by their characteristic blocky ped

Table 5
Results of radiocarbon dating analyses of extinct Pleistocene megafauna bones recovered from Tanque Loma locality, Santa Elena, Ecuador. All analyses were conducted by ELL in collaboration with Dr. T. Guilderson at the Center for Accelerator Mass Spectrometry, Livermore, CA, USA.

CAMS#	Sample name	Element	d^{13}C	Fraction Modern	D^{14}C	^{14}C age
147211	HE616	*Eremotherium* phalanx	−20	0.0532 ± 0.0011	−946.8 ± 1.1	23560 ± 180
160800	MPM291	*Notiomastodon* caudal vertebra	−20	0.1180 ± 0.0134	−882.0 ± 13.4	17170 ± 920
160801	MPM325	*Notiomastodon* metapodial	−20	0.0927 ± 0.0144	−907.3 ± 14.4	19110 ± 1260

structures and lack of bedding features (Retallack, 2008). In addition, the orange coloration observed in Stratum IV is typical of some paleosols (Retallack, 1997). There appear to have been two separate episodes of paleosol development in Stratum IV, represented by the lighter and darker orange colors of the upper and lower substrata, respectively (Fig. 3). Further evidence for paleosol development in Stratum IV is provided by the rhizoliths visible in the top few cm of

Fig. 11. Present-day marshy riparian areas in river arroyos sustained by underground springs, in the vicinity of the Tanque Loma locality. (A) Shows orange paleosol believed to correspond to the lower part of Stratum IV at Tanque Loma. (B) A similar marshy context is proposed for the formation of some of the Pleistocene deposits at Tanque Loma. (C) Shows regionally-extensive terrace (dotted line) believed to correspond to the top of Stratum II at Tanque Loma. (A) and (C) photos courtesy of AD Barnosky.

the upper sub-stratum (Retallack, 1988). These periods of exposure at the site may have resulted from the river meandering away from the site, or from it drying up entirely as can be observed today in the many dry *arroyos* throughout the area. However, the characteristic dark orange coloration of the lower substratum of Stratum IV is visible at other points within 0.5−1.0 km of the Tanque Loma locality (Fig. 11), suggesting that at least this period of land exposure and establishment of a terrestrial plant community may have resulted from regional climatic change, rather than a mere redirection of the river course.

Other aspects of the sediments give evidence for climatic events at Tanque Loma. One substantially dry period appears to have occurred at the top of Stratum IV resulting in the chalky caliche layer separating this from overlying layers, as well as the calcareous rhizoliths and abundant small carbonate nodules found in the upper sub-stratum (Reeves, 1976). As noted previously (*see* Section 4.1), this feature is thought to divide the Pleistocene and Holocene strata at Tanque Loma. However, because Stratum III unconformably overlies Stratum IV, and because radiocarbon analyses from the upper part of Stratum IV and lower part of Stratum III have so-far been unsuccessful, it is not known whether this contact represents the Pleistocene−Holocene transition, or another time. One plausible scenario is that this period of extreme aridity occurred during the region's precipitation low, around 15,000 years ago.

In addition, throughout Stratum III, thin deposits of dark sediment with very high (approximately 20%−50%) organic carbon content, including macroscopic pieces of charcoal (Fig. 3, Table 2), suggest a marked change in fire regime starting at the base of the Stratum (inferred to be early Holocene). Such an increase in fire frequency and intensity is often observed in the South American Holocene (Markgraf and Anderson, 1994; Power et al. 2008), and could be attributed to a variety of factors including climatic changes (Marlon et al. 2009), anthropogenic causes (Pausas and Keeley, 2009), loss of megafauna from the ecosystem (Gill et al. 2009), or a combination of factors (Markgraf and Anderson, 1994).

At least one brief flooding event appears to have occurred in the lower part of Stratum III, (Table 2: Stratum III, levels 14−13); these layers comprise a depositional couplet of a small $(-3\phi - -1\phi)$ clast matrix overlain by fine-grained sediments, typical of a flood progression (Nichols, 2009). This event would be consistent with the increased rainfall inferred for the latest Pleistocene/earliest Holocene approximately (14,000 − 10,000 years ago; Heusser and Shackleton, 1994; Tellkamp, 2005), or with a return to wet conditions on the Santa Elena Peninsula, which Sarma (1974) notes for 7500 BP, 4500 BP and 4000 BP. However, the position of this layer within the Stratum III series of loose sedimentary deposits and regular, intense fires − as indicated by charcoal layers − suggests that it more likely was deposited during the Holocene rather than in the Pleistocene.

5.1.3. Asphaltic deposit

The tar-saturated layer at Tanque Loma − Stratum V − extends laterally with a more-or-less consistent depth throughout the deposit. Bones are distributed densely and relatively uniformly throughout this layer. Such geomorphology is typical of a bone-bed assemblage, and differs markedly from the geomorphology described for tar pit traps, which tend to form as numerous, isolated, often conical, asphaltic deposits (Lemon and Churcher, 1961; Woodard and Marcus, 1973). The implication of this morphology is that the Tanque Loma locality was not asphaltic at the time of the formation of the megafaunal assemblage, but rather that the sediments became secondarily infiltrated with tar at some point after the burial of the bones. Such a scenario has been proposed for a small number of other asphaltic paleontological localities, including the Corralito locality on the Santa Elena Peninsula (A.G.
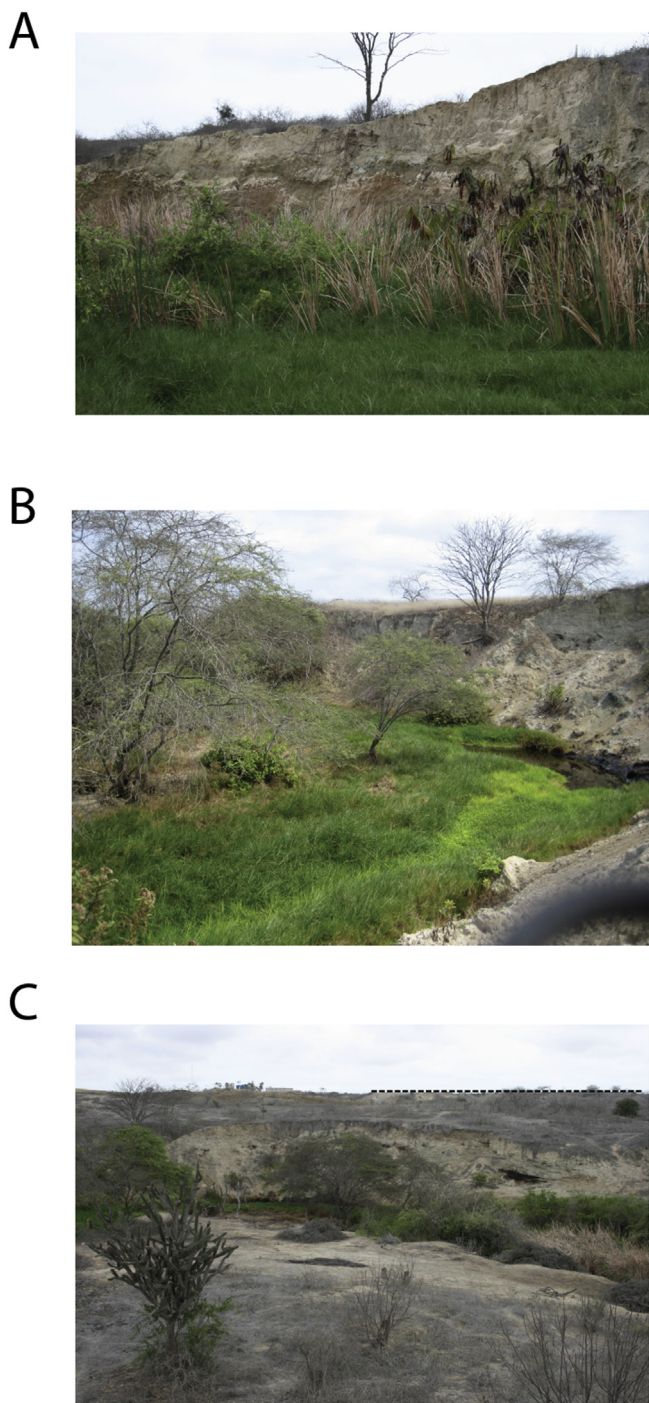
Edmund *unpublished field notes*), and Las Breas de San Felipe in Cuba (Iturralde-Vinent et al. 2000).

5.1.4. Context of the megafaunal deposits

Taken together, the relatively well-sorted sedimentary layers, the high proportion of muds, the scarcity of clasts anywhere except very close to their apparent source, the lack of evidence for long-distance transport of clasts and bones, the geomorphology of the primary bone bed, the evidence for the secondary infiltration of the asphalt, and the presence of at least two separate paleosols — the lower of which appears to be a regionally-extensive feature — suggest that the megafauna-bearing strata at Tanque Loma likely represent low-energy fluvial deposits separated by a period of regional aridity. This fluvial system apparently comprised a slow-moving river abutting against a limestone cliff — now the nucleus of the hill overlying the Pleistocene bone bed. During the first period of deposition (Strata VI and V and the lower sub-stratum of Stratum IV) at least, this slow-moving riparian system appears to have resulted in the establishment of a freshwater marshy habitat, as suggested by the abundant plant material in these strata and the underlying green anoxic gley. Other paleontological localities in the vicinity, including Cautivo (Ficcarelli et al. 2003) and Corralito (A.G. Edmund, *unpublished field notes*) have been interpreted as mangrove swamps; this does not appear to be the case at Tanque Loma, as the sediments are finer (i.e., less sandy) and contain very little of the marine material — such as saltwater mollusks and shark teeth — that are noted at these nearby localities. Instead, Tanque Loma more resembles a marshy freshwater riparian ecosystem such as those that persist in the immediate area today. For example, about 0.5 km north of the Tanque Loma deposit, the Arroyo Seco contains permanent, spring-fed ponds surrounded by marshy sediments and vegetation abutting steep, loose-sediment cliffs (Fig. 11A and B). A change in depositional context in the upper substratum of Stratum IV is suggested by the lesser amount of plant material as well as the relative scarcity and significantly greater fragmentation and weathering of the megafaunal bones recovered from this layer. Further paleontological and sedimentological studies in the vicinity of the Tanque Loma locality are required to determine if this reflects a regional environmental change.

5.1.5. Site context

The top of Stratum II appears to be coincident with a terrace level that is present throughout at least the immediate vicinity of the site (Fig. 11C). At the time of deposition of Strata VII − II, the Tanque Loma locality would have been closer to sea-level; Holocene uplift (Stothert, 1985; Damp et al. 1990; Ficcarelli et al. 2003) would have resulted in down-cutting of the river course (the bottom of the modern arroyo is approximately two meters below the Tanque Loma megafaunal deposit), and brought the site to its present elevation. At least one major period of uplift is known to have occurred in the area between 5500 and 3600 BP (Damp et al. 1990).

5.2. Taxonomic composition

The Pleistocene strata at Tanque Loma present an extremely low taxonomic diversity of vertebrates. The 2003−2006 excavations recovered 993 individual specimens (NISP), excluding very fragmented ribs and vertebrae, pertaining to only six distinguishable species, and the material recovered during the 2009−2011 excavations appears to conform to this pattern. With the possible exception of a few ribs excavated in 2010, no predators have yet been identified from the megafauna-bearing layers, and microvertebrates, including birds, are extremely rare in these strata (except for the one isolated deposit found in grid unit nine at the interface between Stratum IV and Stratum III). This pattern stands in stark contrast to that observed for tar pit traps, which generally contain an overabundance of carnivores and microvertebrates, particularly waterfowl. This pattern has been noted in the asphaltic deposits at Rancho La Brea (Stock and Harris, 1992), McKittrick (Miller, 1935), Talara (Campbell, 1979; Seymour, 2010), and Inciarte (Rincón, 2011). The standard explanation for this phenomenon is that large mammals as well as small vertebrates would have been attracted by the apparent presence of a water source. In attempting to drink from (or, in the case of birds, land upon) the source, these animals would have become mired in the asphalt-saturated sediments. Additional large carnivores would have been attracted to the trapped prey, and would themselves have become entrapped (McHorse et al. 2012).

Large carnivores, including *Smilodon*, *Puma*, and a couple of mid-sized canids have been identified from several late-Pleistocene localities on the Santa Elena Peninsula (Table 1). An abundance of birds, including waterfowl, have been identified from the asphaltic Santa Elena Peninsula locality La Carolina (Campbell, 1976). The absence of these animals from the asphaltic Pleistocene deposit at Tanque Loma supports the hypothesis proposed above that the formation of this site was fundamentally different from that proposed for traditional tar pit traps, and most likely that the asphalt was not present at the time the bones were deposited.

The number of individual specimens (NISP) and minimum number of individuals (MNI) counts for megafaunal taxa at Tanque Loma are both heavily skewed in favor of one species, the giant ground sloth *Eremotherium laurillardi*. This species is represented by 571 of the 663 elements excavated between 2003 and 2006, and constitutes 16 of the 25 minimum individual animals identified based on these bones. Such monodominant localities (paleontological assemblages where > 50% of the remains are represented by a single taxon) are fairly common in the fossil record (Eberth et al. 2010), and several explanations have been invoked to explain their formation, including selective geologic forces (Sander, 1992), gregarious behavior with attritional (e.g. Barnosky, 1985) or mass (e.g. Ryan et al. 2001; Bai et al. 2011) mortality, and selection by predators, including humans (e.g. Haury et al. 1959; Reeves, 1978). For reasons noted herein, human action seems unlikely to explain the concentration of one megafaunal species at this locality. Gregarious behavior has been posited previously for *E. laurillardi* (Cartelle and Bohòrquez, 1982) and this may explain the preponderance of this species at Tanque Loma.

5.3. Bone taphonomy

5.3.1. Bone condition

Megafaunal bones at Tanque Loma tend to be relatively intact. The main exceptions are more fragile elements such as ribs, vertebral processes, cranial elements, scapulae, and pelvises. Breakage of fragile elements can result from several processes including exposure to the elements, transport in high flow, carnivore action, and crushing (Behrensmeyer and Hill 1988).

Most bones in Stratum V and the lower substratum of Stratum IV exhibit little to no evidence of weathering, suggesting that they generally were not exposed on the surface for a great length of time. However, there was a wide range in the degree of abrasion on these bones – many elements did not show any marks whatsoever, while others had a large number of shallow, non-parallel scratches that were consistent with trampling abrasion, but not fluvial transport (Olsen and Shipman, 1988). These data suggest that bones were deposited in or near water and submerged fairly quickly, but were not transported a great distance after submersion. Some elements would have become buried by sediment on the bottom relatively rapidly, but others could have remained exposed

underwater where they may have been trampled by large animals wading in the water source, as commonly occurs around African watering holes today (Haynes, 1988).

Several interpretations were considered to explain the unusual, pit-like taphonomic features noted on some of the bones (Fig. 9). These include: 1) human modification; 2) predation or scavenging by carnivores; and 3) bore-holes of aquatic mollusks. None of these explanations is completely satisfactory. First, there is no other evidence of human modification of these bones, including cut marks; no artifacts, debitage, or human remains have been found at the site; and the youngest radiocarbon date so-far obtained for the megafaunal deposit pre-dates evidence for human arrival on the Santa Elena Peninsula by >5000 years (Stothert, 1985) and on the South American continent by >1000 years (Barnosky and Lindsey, 2010). Second, while the location of the excavations at the ends of the tibiae is highly suggestive of predation by canids (Haynes, 1983), there are no gnaw marks or pit impressions surrounding the broken and eroded areas, as would be expected if this were the source of the excavations, and there are no cracks or scratches around the smooth, conical holes on the clavicle (Fig. 9 A–B) as should be observed were they produced from a bite (Njau and Blumenschine, 2006). Finally, the conical holes are the wrong shape to have been produced by a bivalve or *Teredo* worm, which produce holes with a narrow opening and wider interior; the excavations are too regularly-sized for barnacles; and boring freshwater mollusks are very rare (DR Lindberg *personal communication*, 23 January 2013). Therefore, the mechanism that produced these features is as yet unresolved.

5.3.2. Bone orientation

The fact that overall bones at the site were randomly oriented suggests that there was no significant, consistent water flow transporting bones at this locality. However, the possibility of rapid, short-distance transport, as would occur during a flash flooding event, cannot be ruled out, as such events do not result in directional orientation of bones, especially if elements are still articulated during transport and/or retain adhering chunks of flesh that could dramatically alter the shape and hydrodynamic properties of the bones.

5.3.3. Element representation

There is a wide range in the relative representation (%MAU) of *Eremotherium* skeletal elements at Tanque Loma. The primary phenomena invoked to explain differential representation of skeletal elements in the fossil record are differential preservation (Conard et al. 2008), water transport (e.g. Voorhies, 1969), predation and scavenging (Spencer et al. 2003; Muleady-Mecham, 2003), and selection by humans (e.g. Metcalfe and Jones, 1988). Comparison of relative element representation values for Tanque Loma *Eremotherium* remains with those from other assemblages of known origin (the Verdigre flood deposit, Rancho La Brea Pit 91 tar pit trap, Maricopa clay-mud traps, Ballybetagh bog lacustrine assemblage, and anthropogenic accumulations) were made in order to elucidate the origin of the Tanque Loma megafauna deposit.

A river or flood deposit, as Verdigre is presumed to be (Voorhies, 1969), would be expected to retain a relatively low percentage of elements, because 1) fossils collected in the deposit are likely to be washed in from surface exposures, where bones might have accumulated and been dispersed over a long period of time; 2) water flow would also carry some accumulated elements out of the site, and 3) without a preserving agent, such as hydrocarbons, preservation after deposition would not necessarily be particularly high. Moreover, which elements become preserved in a fluvial assemblage depends upon the flow regime and the physical characteristics of the bones. Voorhies (1969) identifies

three groups of elements based on their hydrodynamic properties. These were compared with the elements encountered at Tanque Loma to evaluate the hypothesis that this locality constitutes a fluvial assemblage. It should be noted, however, that Voorhies' experiments were performed using bones of mid-sized ungulates and carnivores (sheep and coyotes), and thus the hydrodynamic properties of the different elements observed in his experiments might not be completely applicable to the larger and differently-shaped *Eremotherium* bones. We expect these differences would most likely be observed in *Eremotherium* femora, humeri, tibiae, and metapodials, all of which have substantially different relative dimensions than those observed in more cursorial carnivores and ungulates. It is also worth considering that in the case of a short-term high water flow event, such as a flash flood, bone winnowing might occur differently or not at all, especially if corpses were not fully decomposed.

Voorhies Group I, or those most likely to be transported in a current (and thus least likely to be found in a bone bed assemblage deposited in rapidly-flowing water), includes ribs, vertebrae, sacra, and sterna. All of these elements are underrepresented in the Tanque Loma deposit (1%–20% MAU). Voorhies group II, those bones with intermediate water-transport properties, include long bones (femora, humeri, radii, tibias), metapodials and pelvises. Most of these bones tend to be relatively well-represented in the Tanque Loma deposit (>/ = 45% MAU), especially tibiae, which are the most common element encountered (100% MAU). However, metapodia are quite under-represented (17%–22% MAU). Voorhies Group III, those bones most likely to be left behind in a lag deposit, include crania and mandibles. These elements are moderately represented in the Tanque Loma deposit (26% MAU for crania; 48% MAU for mandibles). In general, fragile elements and long bones are much better represented at Tanque Loma than in the Verdigre Quarry, while Verdigre has greater proportions of metapodials and rami, and podials show equally low representation at both localities.

Of the depositional contexts considered here, tar pit traps should tend to have the most complete overall representation of elements because for any individual corpse there would be only a short interval of exposure during which bones could be transported away from the site (primarily through carnivory/scavenging), after which preservation by immersion in tar would be extremely high. Many smaller Eremothere elements − podials, metapodials, and mandibles − and more fragile bones − crania, vertebrae, ribs, scapulae and pelvises − are far less prevalent at Tanque Loma as compared with the Rancho La Brea deposits, while larger and sturdier elements show comparable representation. Tanque Loma also exhibits no clear bias towards preservation of appendicular elements such as that observed at Maricopa (Muleady-Mecham, 2003) − the long bones are better-preserved than the axial elements, but podials are very poorly represented.

The Ballybetagh bog *Megaloceros* assemblage represents an attritional assemblage presumably accumulated over multiple years with relatively rapid burial and minimal transport of bones after deposition. The best-represented elements in this assemblage were found to be crania (including antlers), mandibles, ribs, vertebrae, and podials, which were interpreted as the elements that would have been most robust to dispersion and breakage by trampling (Barnosky, 1985). While these particular elements are generally poorly-represented at Tanque Loma, the assemblages are similar in that the *Eremotherium* elements with the highest %MAU values at Tanque Loma − principally longbones − tend to be larger, heavier, less-breakable elements that would be less likely to be dispersed far or heavily fragmented through trampling.

Finally, anthropogenically-accumulated assemblages tend to have an overrepresentation of nutritious (meaty), easily-

transportable parts, including mandibles and longbones (Behrensmeyer, 1987; Bunn, 1987). While these elements all have relatively high representation at Tanque Loma, the similarly high representation of other elements such as clavicles, axis vertebrae and pelvic elements, is not consistent with transportation of isolated elements to (or away from) the site by anthropic agents. These data are not surprising, as there are no artifacts or evidence of human activity at the site, and the radiocarbon dates so-far obtained for the megafauna deposit pre-date any established human arrival in the region by more than 5000 years (Stothert, 1985).

Overall, the pattern of relative representation of *Eremotherium* elements at Tanque Loma does not closely match any of the considered contexts − the Rancho La Brea and Maricopa tar pit "traps," the Verdigre fluvial deposit, the Ballybetagh bog lakeside assemblage or a butchering locality. However, it is most similar to the lacustrine example in that many of the more underrepresented elements − in this case ribs, vertebrae, and cranial elements − are bones that would probably be more likely to be fragmented through trampling. As noted, several vertebrae ($n = 17$) were excluded from the analysis because they were too fragmentary to identify to anatomical position. An additional group of vertebrae ($N \sim 100$) and ribs ($N \sim 98$) that were collected during the 2004−2006 excavations are so fragmented that they have not yet been prepared, and thus we were not able to include them in this analysis. This differential fragility of different elements could also explain the under-representation of *Eremotherium* crania in the deposit; this explanation was also invoked by Voorhies (1969) to explain the dearth of crania at Verdigre.

Trampling would not, however, likely explain the extreme paucity of *Eremotherium* podial (3%−6% MAU) or metapodial (17%−22% MAU) bones at Tanque Loma, which should be largely protected from crushing by their compact shapes and dense structure. Neither would fluvial transport, as these elements are roughly the same size and shape as, and thus probably no more likely to be transported away from the site than, the largest rock clasts encountered in Stratum V. One plausible explanation for their scarcity is that these relatively small, distal elements may have been selectively exposed due to biotic forces: dense plant growth, as may be encountered in marshy settings such as that hypothesized for the Pleistocene deposit at Tanque Loma, tends to push up smaller, lighter elements above the substrate, while burying larger heavier ones (A.K. Behrensmeyer, *personal communication*, 20 February 2013). These exposed elements may then have been broken up by weathering processes or carried off by scavengers.

5.4. Paleoecological implications

5.4.1. Paleoenvironmental change

The Tanque Loma locality offers important opportunities to investigate paleoenvironmental and faunistic change in the western coastal Neotropics during the late Pleistocene, across the Pleistocene−Holocene transition and throughout the Holocene. Today the western Santa Elena Peninsula is dry and sparsely vegetated, with dense vegetation present only in riverbeds supplied with year-round water from subterranean springs (Stothert, 1985). However, the region must have been more verdant during the Pleistocene in order to support the great quantity of megafauna that were evidently present on the Peninsula during this period. Various authors (Lemon and Churcher, 1961; Sarma, 1974; Stothert, 2011) have proposed that the Pleistocene ecosystem in this region would have comprised permanent or semi-permanent rivers supporting dense vegetation corridors between areas of open grassland savannah. This model is supported by pollen and climatic data (Heusser and Shackleton, 1994) indicating dry conditions and significant extent of grassland in the western Andes, as well as by bird

fossils recovered from the late-Pleistocene La Carolina locality on the Santa Elena Peninsula that indicate the presence of substantial wetlands in this area (Campbell, 1976; Tellkamp, 2005). Sea core data suggests that cool, arid, glacial conditions persisted until about 15,000 years ago, after which temperatures and precipitation increased until the earliest Holocene, around 10,000 years ago. This may have resulted in an expansion of dense forested habitat across the landscape, negatively impacting savannah-adapted megafauna populations (Ficcarelli et al. 2003). Such a phenomenon has been proposed as a factor in the extinction of the large mammal fauna of South America at the end of the Pleistocene (Cione et al. 2009).

Sedimentological features at the Tanque Loma locality may correspond to some of these paleoecological data. At the time of deposition of most of the Pleistocene sediments at Tanque Loma, the site was moist and heavily vegetated. We interpret this as representing a lush habitat in a river bottom. However, the Stratum IV sediments indicate the desiccation of this marshy habitat and establishment of a regionally-extensive terrestrial plant community − represented by the dark orange paleosol in the lower substratum of this layer − followed by a change in depositional regime constituting similar fluvially-deposited silty sands, but with fewer, smaller clasts and the near-cessation of the accumulation of fossil remains. A second, more pronounced change occurs at the top of Stratum IV, with the development of a layer of caliche − a sign of extreme aridity − followed by a marked change in depositional pattern, with occasional flooding and much more frequent desiccation episodes. Also very notable in the Stratum III (presumed-Holocene) deposits are the repeated appearance of charcoal-intensive layers, indicative of increased fires that may be related to a drier climate, the loss of large ecosystem engineers such as proboscideans, anthropogenic burning, or a combination of these forces.

Unfortunately microvertebrates, which can serve as excellent paleoecological indicators (e.g. Blois et al. 2010; McGuire, 2010), are nearly absent in all but the highest Pleistocene sediments at Tanque Loma. However, other taxa may provide some paleoenvironmental insight. For instance, the presence of the terrestrial snail *Porphyrobaphe*, common in Strata IV and V of Tanque Loma, has been noted in Pleistocene and Pliocene deposits throughout the Peninsula (Barker, 1933; Pilsbry and Olsson, 1941), but today it appears to be restricted to wetter coastal regions further to the north (Barker, 1933, *but see* Breure and Borrero, 2008). Detailed analyses of the paleobotanical material recovered from Strata IV and V, and of the rich microvertebrate assemblages present at the Stratum IV-III interface and throughout Stratum III − which, based on size-selectivity, we preliminarily interpret as raptor assemblages − will provide a much better picture of the late-Quaternary paleoenvironmental history of the western Santa Elena Peninsula.

5.4.2. Implications for late-Quaternary extinctions

Although the available chronological evidence places the primary megafaunal deposit at Tanque Loma several thousand years before the end of the Pleistocene, this locality may have implications for continental-scale investigations of the late-Quaternary extinction event. The radiocarbon dates of 17,000−19,000 RCYBP on cf. *Notiomastodon platensis* and of 23,500 RCYBP on *Eremotherium laurillardi* from Tanque Loma represent a significant augmentation of the fewer than one dozen direct 14C dates on neotropical megafauna. The date on *E. laurillardi* is one of fewer than five direct dates on South American *Eremotherium* (Rossetti et al. 2004; Hubbe et al. 2013) and the only one outside of Brazil. The cf. *N. platensis* dates double the number of direct dates on this taxon, and overlap completely with the other two, which include one from northern Ecuador and one from Brazil (Coltorti et al. 1998; Rosetti et al. 2004). The antiquity of these dates is consistent with

the pattern, noted by Barnosky and Lindsey (2010), of Last Appearance Dates on Pleistocene taxa occurring earlier in northern South America than in the southern, temperate part of the continent, and also with models predicting a greater reduction in preferred habitat for *Eremotherium* than for its temperate sister taxon *Megatherium* during late-Quaternary climatic shifts (Lima-Ribeiro et al. 2012). However, additional radiocarbon dating studies are currently underway to ensure that the presence of tar at Tanque Loma did not result in erroneously old dates.

6. Conclusions

The sedimentological, taphonomic, and taxonomic information for the Pleistocene megafauna assemblage at Tanque Loma suggest that, unlike most well-known asphaltic deposits such as Rancho La Brea in Los Angeles, USA, the Inciarte locality in Zulia province, Venezuela, and the Talara asphalt seeps in Talara, Peru, this locality was not a "tar pit" style trap, capturing and preserving organisms through entrapment in asphalt. Rather, this site most likely represents a bone bed assemblage, formed in a shallow, anoxic marshy setting, with secondary infiltration of tar. Several lines of evidence support this conclusion, including 1) the consistent lateral extent of the primary bone bed and asphaltic sediments; 2) the near-absence of carnivores, small mammals and birds from the Pleistocene layers; and 3) the abundance of plant material in the Pleistocene sediments and the presence of an anoxic gley underlying these strata. There is no evidence that Tanque Loma was a mangrove swamp estuary as has been proposed for other sites on the Santa Elena Peninsula. The relative representation of megafaunal elements and lack of evidence of high-energy fluvial activity suggests that probably most of the remains present in these layers pertain to animals that died in or around this marsh ecosystem, although small, isolated elements such as teeth and osteoderms may have washed in from further away. And, the overabundance of *Eremotherium laurillardi* remains in this deposit relative to other taxa may lend support to the hypothesis that this species was gregarious.

The megafauna remains associated with this inferred riparian environment appear in dense accumulations apparently spanning several thousands of years (at least roughly 23,400–18,000 BP); they then become much more scarce after a period of apparently regional desiccation, and disappear entirely after an extremely arid event. Efforts to bracket this event with radiocarbon dates have so-far proved unsuccessful, however it may pertain to an inferred precipitation low around 15,000 years ago. There is no evidence of humans in the megafauna-bearing strata.

Finally, the three radiocarbon dates so far obtained on megafaunal bones from Tanque Loma are consistent with the pattern of older Last Appearance Dates on Neotropical megafauna relative to their temperate South American counterparts. This pattern is intriguing and may have important implications for our understanding of climatic and biogeographic drivers of these extinctions, but additional radioisotopic dating is required to verify that this observed pattern is not simply an artifact of low sampling in the region.

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