"Tar Pits" of the Western Neotropics: Paleoecology, Taphonomy, and Mammalian Biogeography

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ABSTRACT. Asphaltic deposits, or "tar pits," present a unique opportunity to investigate the paleobiology and paleoecology of Quaternary mammals due to their tendency to accumulate and preserve remains of numerous taxa. This role is especially important in areas with low preservation potential or incomplete sampling, such as the Neotropics. Currently, the most well known asphaltic paleontological locality in tropical South America is the Talara tar seeps in northwest Peru, which has yielded a great diversity of microfossils as well as extinct megafauna. Several other highly productive asphaltic localities have been excavated on the nearby Santa Elena Peninsula (SEP) in southwestern Ecuador. This project combines data from recent excavations on the SEP with analyses of fossils collected from southwest Peru and northwest Ecuador currently housed in the collections of the Museo de Historia Natural "Gustavo Orcés V." in Quito, Ecuador, the Royal Ontario Museum in Toronto, Canada, and the Muséum national d'histoire naturelle in Paris, France. In general, the communities of megaherbivores are comparable between these geographically close sites, but Talara and the La Carolina locality in Ecuador present a much more diverse assemblage of birds, micromammals, and carnivores compared to Coralito and Tanque Loma. Taxonomic, geomorphological, and taphonomic data indicate that these two sites were most likely tar pit–style traps analogous to the famous Rancho La Brea locality in California, USA, while the SEP sites Coralito and Tanque Loma likely represent fossil assemblages in marshy or estuarine settings with secondary infiltration of tar. Additionally, geological and taxonomic differences between the nearby localities Coralito and Tanque Loma suggest differences in local paleoenvironments and indicate gregarious behavior in certain species of extinct giant ground sloths.

RESUMEN. Las localidades asfálticas o "charcos de brea" presentan una oportunidad única para investigar la biología y paleoecología de mamíferos cuaternarios, por su característica de acumular numerosos fósiles de excelente preservación. Este papel esta especialmente importante en lugares con pobre preservación de fósiles, y/o muestreo incompleto, tal como las regiones neotropicales. La localidad asfáltica mas conocida de Sudamérica es el sitio La Brea en Talara, Perú, que ha proporcionado una gran diversidad de fósiles de micromamíferos así como megamamíferos pleistocénicos. Al mismo tiempo se encuentran localidades asfálticas muy productivas en la cercana Península Santa Elena, del suroeste del Ecuador. Este trabajo presente resultados de excavaciones recientes en la Península de Santa Elena, junto con análisis de fósiles provenientes de los sitios asfálticos del suroeste de Ecuador y noroeste de Perú alojados en las colecciones del Museo Gustavo Orcés en Ecuador, del Royal Ontario Museum en Canadá, y del Muséum national d'histoire naturelle en Francia. Por lo general, las comunidades de megaherbívoros son comparables entre estos localidades geográficamente cercanos. Sin embargo, Talara y La Carolina presentan una biodiversidad de carnívoros y micromamíferos considerablemente mas alta que la encontrada en los otros dos sitios. Datos taxonómicos, geomorfológicos, y tafonomicos indican que estos sitios probablemente funcionaron como "trampas de brea" parecidos al famoso sitio Rancho La Brea en California, EEUU, mientras las localidades Coralito y Tanque Loma mas probable representan acumulaciones de huesos en contextos fluviales o lacustres con

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infiltración secundaria de brea. Además, ciertas particularidades de algunas localidades sugieren diferencias en los paleoambientes locales y posiblemente comportamiento social en ciertas especies de perezosos gigantes extinguidas.

INTRODUCTION

Asphaltic paleontological localities, colloquially known as "tar pits," are important paleontological resources because of their tendency to collect and preserve organic remains regardless of exterior environmental conditions (Jull et al., 2004). These localities can serve as important repositories of information about extinct fauna and ecosystems, because they preserve both remains of organisms and materials such as isotopes and pollen that can be used in paleoenvironmental analyses (Akersten et al., 1983; Stock, 1992; Coltrain et al., 2004). Additionally, because most asphaltic paleontological localities are Quaternary in age, the faunistic information they preserve can be used in establishing "biodiversity baselines" for understanding ecosystems before and after the Late Quaternary extinction event.

Asphaltic localities are particularly important resources in the lowland Neotropics, because they preserve remains with otherwise scarce Quaternary paleontological data (Churcher, 1959; Rincón et al., 2006). This scarcity can be attributed to both physical and social factors. First, bone and collagen can be degraded by the elevated heat, ultraviolet radiation, and acidic soils that are typical of these regions (Lebon et al., 2011); second, because countries in these regions are often poorer and/or less politically stable than their temperate counterparts, even when fossils are preserved there may be logistical, economic, and political challenges to their recovery (Laurin, 2012). Currently the Neotropics has the least Pleistocene data for the South American continent, with fewer than a dozen direct radiocarbon dates on megafauna from this region (Barnosky and Lindsey, 2010).

Increasing Quaternary paleoecological data in the Neotropics is particularly important for several reasons. First, this region constitutes 80% of the South American continent, and thus understanding paleoecological dynamics such as biogeographical patterns of South American taxa, post–Great American Biological Interchange dynamics, or causes of Late Quaternary extinctions in South America is dependent upon good geographical and taxonomic coverage of the tropical zone. Second, this region is an area of exceptionally high extant biodiversity (Olson and Dinerstein, 1998) that will be disproportionately affected by modern environmental changes related to climate change and anthropogenic impacts (Brooks et al., 2002; Williams et al., 2007). Thus, having a better understanding of ecological dynamics and extinction drivers in past neotropical ecosystems could prove important in informing conservation efforts in this region today.

Fortunately, several known asphaltic localities preserve rich accumulations of Late Pleistocene fauna in the neotropical region. Of these localities, the most well known is Pampa La Brea (also called "Talara") in Talara, Peru (e.g., Lemon and Churcher, 1961; Churcher, 1966; Campbell, 1979; Czaplewski, 1990; Martínez and Cadenillas, 2004). Several fossiliferous asphaltic sites are also known from the nearby Santa Elena Peninsula in southwest Ecuador. These include the La Carolina (Hoffstetter, 1952; Campbell, 1976) and Coralito (Spillmann, 1935; Edmund, unpublished field notes) localities, excavated in the early to middle part of the 20th century, as well as a new locality, Tanque Loma (Lindsey and Lopez, 2015) (Fig. 1). Two additional highly fossiliferous asphaltic localities have been reported in the past decade from Venezuela: Mene de Inciarte in Zulia State (Czaplewski et al., 2005; Rincón, 2005, 2006, 2011; Rincón et al., 2006, 2008, 2011; Prevosti and Rincón, 2007); and El Breal de Orocual in Monagas State (Rincón et al., 2009, 2011; Holanda and Rincón, 2012). Finally, asphaltic vertebrate localities are known from some Caribbean islands, including Trinidad (Blair, 1927) and Cuba (Iturralde-Vinent et al., 2000).

The purpose of this study is to compare the taphonomy, paleoecology, and biogeographic faunal patterns of the Late Quaternary (Lujanian South American Land Mammal Age) asphaltic vertebrate localities from the western Neotropics—the three reported localities from the Santa Elena Peninsula in Ecuador (La Carolina, Coralito, and Tanque Loma) and the better studied Talara locality on the north coast of Peru (Fig. 1). These sites all fall in a shared biogeographic zone (Udvardy, 1975) and probably have a similar recent geological history. Multiple authors (Sheppard, 1928, 1937; Hoffstetter, 1948a, 1952; Lemon and Churcher, 1961; Ficcarelli et al., 2003) have noted the presence of three marine terraces uplifted during the Early/Middle and later Pleistocene in both regions. Although it is not known whether the individual terraces (known in both regions as *Tablazos*) are homologous, they are similar in age and composition, comprising series of calcareous sandstones, sands, sandy limestones, and fine conglomerates with abundant mollusk fossils (Barker, 1933; Lemon and Churcher, 1961; Instituto Geográfico Militar, 1974). Also in both regions, the *Tablazo* deposits overlie Paleogene rocks, some of which seep oil that emerges onto the surface in numerous locations.

Both on the Santa Elena Peninsula and in northern Peru, the modern ecosystem is a coastal desert and the surface is cut by numerous dry

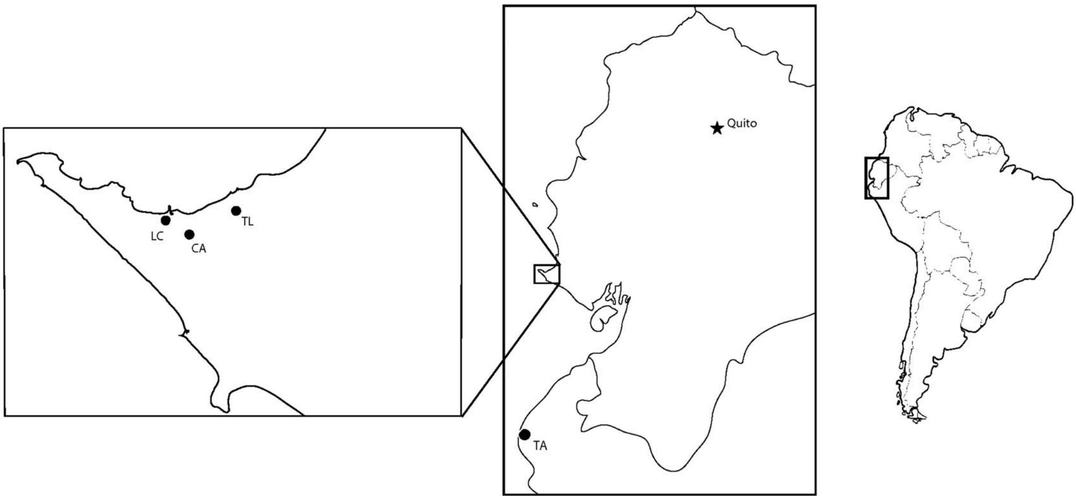

Figure 1 Asphaltic Quaternary vertebrate localities in southwestern Ecuador and northwestern Peru. Abbreviations: TA = Talara, LC = La Carolina, CA = Cautivo, TL = Tanque Loma.

riverbeds (*arroyos*), most of which carry water only seasonally or interannually during El Niño events (Spillmann, 1940). Paleoclimatic data (Churcher, 1966; Tellkamp, 2005) suggest that these areas were also arid during the Pleistocene; however, they must have been more heavily vegetated to support the abundance of large animals found in the local fossil deposits. Most data suggest that Late Pleistocene ecosystems in both regions comprised open grassland savannah crossed by permanent or semipermanent river courses supporting dense wetland vegetation (Lemon and Churcher, 1961; Sarma, 1974; Campbell, 1976; Tellkamp, 2005; Stothert, 2011).

MATERIALS AND METHODS

Of the four localities examined in this study, only Tanque Loma was originally excavated using modern paleontological techniques, including stratigraphic control. Controlled excavations were conducted at Tanque Loma in 2003–2006 and 2009–2011 (Lindsey and Lopez, 2015). Detailed geostratigraphic, taphonomic, and sedimentological studies were made of the site during the 2009–2011 excavations. Geomorphological investigations at the still-active Talara locality were made by E.L.L. and Jean-Noel Martinez, and these were compared with published accounts. Finally, the La Carolina and Coralito localities were relocated by E.L.L. in collaboration with Erick X. Lopez and Aisling Farrell in order to attempt to investigate the geological context of these deposits.

Investigations were made of the fossil material collected at La Carolina, Coralito, Tanque Loma, and Talara localities now held in museum collections. These include material from: **La Carolina** at the Escuela Politécnica Nacional (EPN) in Quito, Ecuador, and the Muséum national d'histoire naturelle (MNHN) in Paris, France; **Coralito** and **Talara** at the Royal Ontario Museum (ROM) in Toronto, Canada; and **Tanque Loma** at the Museo Paleontológico Megaterio (MPM) in La Libertad, Ecuador.

Fossil material was examined to confirm taxonomic identification in the museum records; establish number of individual specimens (NISP), minimum number of elements, and minimum number of individuals (MNI) counts for different taxa; and compare taphonomic characteristics of the bones between different localities. Geomorphological, taxonomic, and taphonomic data from these four localities were compared with published data from the Rancho La Brea and McKittrick localities in California, USA. In the case of the EPN collections, only a cursory examination of the fossil material was possible, and so we rely on the unpublished museum database provided by José Luis Román Carrion for most of the analyses involving these fossils.

To test whether differences in taxonomic richness between localities could be attributed to unequal sampling, rarefaction analyses of generic richness at each locality were conducted using the program Analytic Rarefaction, version 1.3 (Holland, 2003). To control for differences in microfauna collection and publication effort by different researchers, only megafauna taxa were included in these analyses.

RESULTS AND DISCUSSION

CHRONOLOGY

The faunal composition at all four sites studied place them in the late Pleistocene (Lujanian land mammal age). Additionally, radiocarbon dates

Table 1 Radiocarbon dates obtained for asphaltic vertebrate localities in Ecuador and Peru.

Locality	Lab number	Material	Date (RCYBP)	Reference
Talara	SM 852	Sticks	13,616 ± 600	Churcher 1966
Talara	SM 853 (1)	Wood[a]	14,418 ± 500	Churcher 1966
Talara	SM 853 (2)	Wood[a]	14,150 ± 564	Churcher 1966
Talara	SM 854	Sticks[b]	13,790 ± 535	Churcher 1966
La Carolina	GX0339	Sticks[b]	18,400 ± 600	Churcher 1966
Tanque Loma	CAMS 147211	*Eremotherium* phalanx	23,560 ± 180	Lindsey and Lopez, 2015
Tanque Loma	CAMS 160800	*Notiomastodon* caudal vertebra	17,170 ± 920	Lindsey and Lopez, 2015
Tanque Loma	CAMS 160801	*Notiomastodon* metapodial	19,110 ± 1,260	Lindsey and Lopez, 2015

RCYP = radiocarbon years before present;
[a] wood associated with bones.
[b] *Eremotherium* fodder?

have been obtained on material from three of the localities. Four dates have been reported for Talara: two on plant material purportedly representing stomach contents of the giant ground sloth *Eremotherium*, and two on "large piece(s) of wood associated with the bones" (Churcher, 1966: p.992). Each of these samples was purified in a Soxhlet extractor with carbon tetrachloride until the solvent was clear. All four dates cluster closely between 13,500 and 14,500 radiocarbon years before present (BP) (Table 1). One date of 18,400 ± 600 BP has been reported for La Carolina, also on twigs supposedly "chewed" by *Eremotherium* (Churcher, 1966); the sample preparation method used for this specimen was not reported. Finally, three dates were obtained on bone of extinct megafauna from Tanque Loma—one date on an *Eremotherium* phalanx yielded an age of 23,560 ± 180 BP, and dates on a caudal vertebra and metapodial of the gomphothere cf. *Notiomastodon* from slightly higher in the deposit yielded ages of 17,170 ± 920 and 19,110 ± 1,260 BP, respectively (Lindsey and Lopez, 2015). These three samples were prepared using ultrafiltration, but no solvent was used, as no asphalt was visible on the exterior of the bones analyzed. No dates have yet been obtained for Coralito.

While all of the available dates for these localities place them after the last glacial maximum, none of these sites appears to reach the Pleistocene–Holocene boundary. This is consistent with a previously noted pattern of earlier disappearances of Quaternary megafauna in the tropics compared with the temperate regions of South America (Barnosky and Lindsey, 2010) and is also consistent with the fact that there is no evidence of interaction between Late Pleistocene humans and extinct megafauna on the Santa Elena Peninsula, despite substantial archaeological research in the area (Stothert, 2011). Nonetheless, all the dates reported here should be considered equivocal, both due to their limited number and because of the problems inherent in dating hydrocarbon-contaminated materials (Aufderheide et al., 2004).

GEOMORPHOLOGY

The two sites where geomorphological investigations were conducted, Tanque Loma on the Santa Elena Peninsula and Talara in Peru, present dramatically different geomorphologies. At Talara, the asphaltic sediments occur as numerous isolated, irregular, lenticular deposits often in the form of inverted cones (Lemon and Churcher, 1961; Churcher, 1966). These deposits range up to 2 m in thickness and can extend for up to 10 m in length. Vertebrate remains are encountered only in some of these deposits. These characteristics are similar to the geomorphological context reported for Rancho La Brea in California, USA (Stock, 1992), which is suggestive of accumulation of remains via entrapment in exposed pools of asphalt.

In contrast, the asphaltic sediments at Tanque Loma occur as one continuous deposit approximately 75 cm in thickness with a broad lateral extent (Fig. 2). Bones in this deposit are distributed densely and uniformly throughout the asphaltic layer and 10–20 cm above it. Overall, the character is much more typical of a bone bed, suggesting that the asphalt infiltrated the sediments secondarily after the bones were deposited and buried.

Unfortunately, the La Carolina and Coralito localities are no longer accessible for geological investigation, and no formal studies were made at the time of their excavation. Therefore, the origin of these deposits must be inferred through taxonomic and taphonomic characteristics of the fossil collections alone.

TAXONOMIC COMPOSITION

Mammalian taxonomic richness for Talara, La Carolina, Coralito, and Tanque Loma was calculated by examination of museum collections and museum databases and from published records in the literature. Of these four localities, Talara presents the highest diversity of mammals (Fig. 3; Table 2). One explanation for this may be increased sampling effort (more than 17,000 prepared mammal specimens from Talara are reposited in the ROM, and approximately 5,000

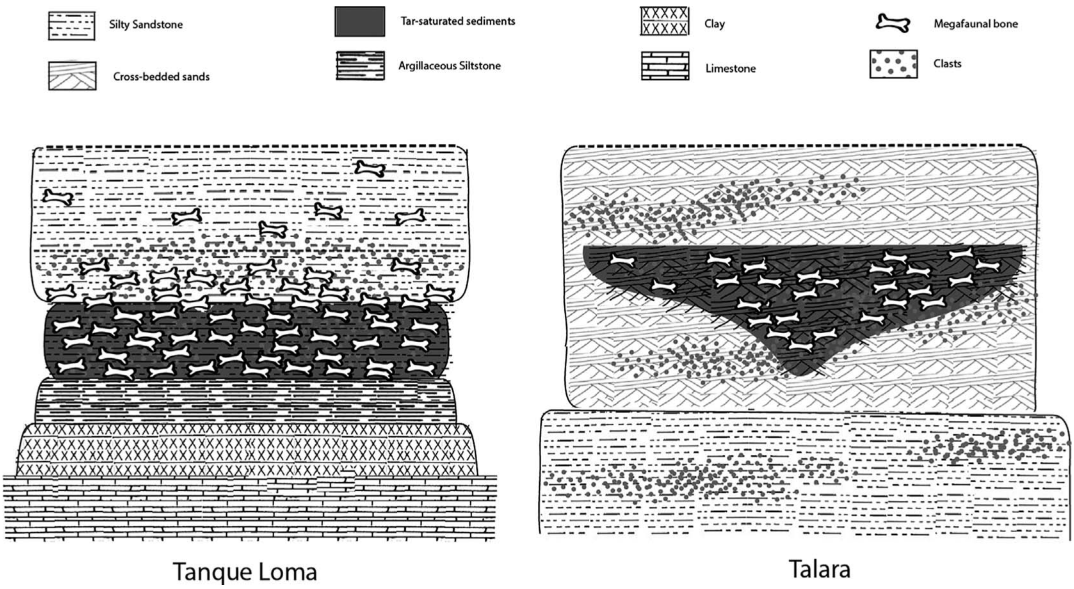

Figure 2 Generalized stratigraphic profiles showing geomorphology and bone and clast distribution in asphaltic deposits at Tanque Loma, Ecuador, and Talara, Peru.

more specimens have been collected over the past 10 years that are now reposited at the Universidad Nacional de Piura in Peru [J. N. Martínez, personal communication, 2013]). This is in comparison with a little over 4,000 mammal specimens from Coralito in the ROM collections; 2,000 specimens from La Carolina that are reposited in the EPN, and the MNHN; and 1,000 specimens from Tanque Loma in the MPM.

A second factor that may have contributed to the observed pattern is increased study and publication of these collections: More than a dozen published studies exist reporting taxa from Talara (e.g., Churcher, 1959, 1962, 1965, 1966; Lemon and Churcher, 1961; Churcher and van Zyll de Jong, 1965; Campbell, 1979; Czaplewski, 1990; Martínez and Cadenillas, 2004; Alván et al., 2009; Cadenillas and Martínez, 2006; Oswald and Steadman, 2010), and several of these were made on the more recently collected fossils that focused on smaller and/or extant taxa that were often overlooked during earlier excavations. In comparison, only about half that number report fauna from La Carolina (Hoffstetter, 1948a–c, 1949, 1952; Campbell, 1976; Martínez and Cadenillas, 2006), and most of these are older publications dealing exclusively with the megafauna, much of which has since been synonymized. Finally, only a couple of studies have been made so far on the fauna of Coralito and Tanque Loma (Spillmann, 1931, 1948; Lindsey and Lopez, 2015). Thus, publication bias also could have played a role in the observed differences in taxonomic richness between localities (Davis and Pyenson, 2007).

Nonetheless, at least some of the differences in observed mammalian diversity between the four localities cannot be explained by differences in either sampling or publication effort and are more likely related to factors inherent in the formation of the deposits. For instance, the locality in this study with the lowest observed diversity is Tanque Loma, with only six mammalian taxa discovered in the asphaltic deposit. While this locality has the fewest identified specimens of all the localities in this study, it was excavated the most recently, and substantial efforts were made during the excavations to recover all faunal remains in the deposit, including screening for small elements and use of solvent to look for microfossils. Thus, the low diversity at this site (principally dominated by one species of ground sloth, *see below*) must be explained by some other factor.

This conclusion is supported by the rarefaction analyses. Rarefied to 900 samples (the approximate NISP count for Tanque Loma, the locality with the fewest identified specimens), Talara yields a taxonomic richness of 13.5 megafaunal genera, La Carolina 13.7 genera, Coralito 10.1 genera, and Tanque Loma a mere six genera (Fig. 4). Aside from highlighting the depauperate nature of the Tanque Loma fauna, these results suggest that La Carolina and Talara may be more similar than the raw species counts indicate.

The fact that La Carolina and Talara both exhibit a higher proportion of carnivores and small mammals than Coralito and Tanque Loma may indicate that the former two localities functioned as Rancho La Brea–style traps, as these groups tend to be the best represented mammal taxa in such

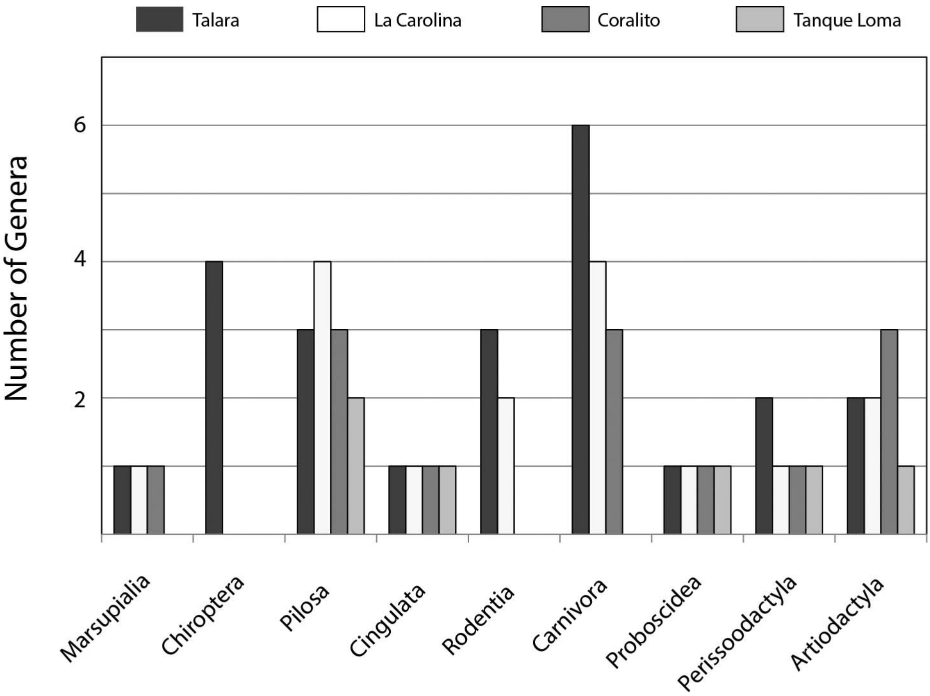

Figure 3 Bar graph showing taxonomic richness of different mammalian clades at asphaltic Quaternary vertebrate localities in the western Neotropics. Abbreviations: TA = Talara, LC = La Carolina, CA = Cautivo, TL = Tanque Loma.

deposits (Lemon and Churcher, 1961; Stock, 1992). This model is also supported by the great abundance of bird fossils found at La Carolina and Talara. Birds, particularly water fowl, are among the most abundant organisms in tar pit traps, presumably because they are attracted by the perception of a watering hole given by a film of water covering the surface of the asphalt (Churcher, 1966; Campbell, 1979; Stock, 1992). Moreover, studies made of the avifauna from Talara and La Carolina (Campbell, 1976, 1979) reveal that the bird taxa at these localities bear a close resemblance both to one another and to that found at the well-studied asphalt trap locality Rancho La Brea. The beetle fauna at Talara also corresponds to the model of entrapment of hydrophilic taxa, as it comprises a large proportion of species typical of standing-water habitats, and is also similar to that found at Rancho La Brea (Churcher, 1966). Despite directed searching for microvertebrates, Tanque Loma has yielded fewer than half a dozen remains of Aves in the megafaunal deposit, and only a half dozen bird bones are in the ROM collections from Coralito, although 50 sacks of matrix were collected and processed in hot kerosene to search for microfauna during the excavations (Edmund, unpublished field notes); in fact, Edmund (unpublished field notes, 1959) notes that at Coralito, "small bones were not nearly as abundant as … at Talara."

Other associated fauna at these sites suggest differences in local paleoenvironments between the four localities. In addition to the mammalian, avian, and insect fauna, Talara has yielded remains of reptiles, including crocodilians and turtles, indicative of nearby aquatic environments (Lemon and Churcher, 1961). La Carolina has produced a few remains of frogs, caiman, and indeterminate testudinates, as well as terrestrial tortoises and lizards, so overall the signature is less aquatic than that of Talara. Tanque Loma, on the other hand, has no remains of aquatic taxa, only a few bird bones, and no reptiles; the most abundant invertebrates at this locality are terrestrial snails of the genus *Porphyrobaphe*. This genus still occurs on the Ecuadorian coast today but is associated with somewhat wetter climates farther north (Barker, 1933). Finally, the associated fauna at the Coralito locality has a strongly marine signature, comprising beds containing abundant marine shell and shark teeth (Edmund, unpublished field notes). Turtle, tortoise, and otter remains are also present at this locality.

Abundance Data

Perhaps even more interesting than the differences in species richness between the four localities is the great difference in the relative abundances of

Table 2 Taxon lists for all mammalian taxa reported from Talara, La Carolina, Coralito, and Tanque Loma localities, excluding Chiroptera and nonmegafauna rodents.

	Talara	La Carolina	Coralito	Tanque Loma
Marsupialia				
Didelphidae				
Didelphis	X		X	
Marmosa	X			
Xenarthra				
Cingulata				
Pampatheriidae				
Holmesina	X	X	X	X
Pilosa				
Mylodontidae				
Glossotherium	X	X	X	X
Catonyx	X	X	X	
Megatheriidae				
Eremotherium	X	X	X	X
Rodentia				
Caviidae				
Neochoerus	X	X		
Carnivora				
Canidae				
Canis	X			
Lycalopex	X	X	X	
Protocyon		X		
Felidae				
Leopardus	X			
Panthera	X			
Puma	X	X		
Smilodon	X	X	X	
Mustelidae				
Conepatus	X			
Lutra			X	
Proboscidea				
Gomphotheriidae				
Notiomastodon	X	X	X	X
Perissodactyla				
Equidae				
Equus	X	X	X	X
Artiodactyla				
Camelidae				
Palaeolama	X	X	X	
Cervidae				
Odocoileus	X	X	X	X
Mazama	X			
Tayassuidae				
Tayassu	X		X	

taxa at these sites (Fig. 5). Broadly, these localities fall into two categories. Talara and La Carolina are both dominated by carnivores, principally canids. Coralito and Tanque Loma, on the other hand, both predominantly comprise remains of giant ground sloths.

Overabundance of carnivores is one of the classic characteristics of tar pit–style traps (Stock, 1992) and is the pattern observed at the well-known North American site Rancho La Brea, as well as the less studied McKittrick locality, both in California, USA. When compared against these sites, La Carolina is seen to most closely resemble the McKittrick locality, as both contain similar proportions of canids, felids, and equids and similar relative proportions of carnivores and herbivores. Talara, on the other hand, is more similar to Rancho La Brea, in having more than 75% of the specimens represented by carnivores, and similar low proportions of perissodactyls,

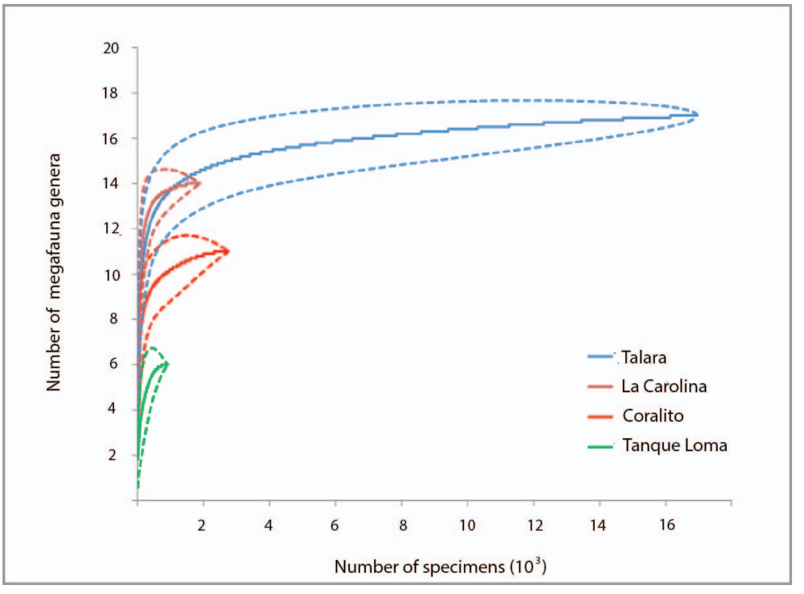

Figure 4 Rarefaction curves of generic richness versus number of specimens sampled for the neotropical asphaltic vertebrate localities Talara, La Carolina, Coralito, and Tanque Loma. Dashed lines indicate 95% confidence intervals.

artiodactyls, proboscideans, and sloths. Furthermore, while Talara does not have the very high proportion of felids that is seen at Rancho La Brea, the proportion is significantly higher than at La Carolina. These differences are interesting, as they reinforce the idea that fossil accumulations generated through entrapment in asphalt may be more complex than originally thought, as even geographically close localities with presumably similar paleocommunities may preserve different segments of the population in different proportions.

Intriguing taxonomic differences are also evident in the case of Coralito and Tanque Loma. Although both of these localities are heavily dominated by giant ground sloths and are separated by only a few kilometers, the most common taxon at Coralito—*Catonyx*—is not found at Tanque Loma. Remains of another sloth, *Eremotherium*, are abundant at both localities. At both of these sites, the dominant taxa are represented by multiple age classes. At Coralito, a minimum of five *Eremotherium* sloths are represented, at least one of which is a neonate, and at least eight *Catonyx* individuals are preserved at this site, most of which appear to be juveniles or neonates. At Tanque Loma, *Eremotherium* is represented by at least 16 individuals, including three neonates, two subadults, six or seven prime adults, and two to three very old individuals, as well as two probable fetuses. Other taxa are also represented by multiple individuals at these sites. At Coralito, these include *Glossotherium* (MNI = 3), *Didelphis* (MNI = 4), *Holmesina* (MNI = 5), *Palaeolama* (MNI = 5), and *Odocoileus* (MNI = 3) and at Tanque Loma, *Notiomastodon* (MNI = 3) and *Glossotherium* (MNI = 3). However, these taxa are represented by many fewer elements than are *Catonyx* and *Eremotherium*. Thus, both localities appear to comprise multigenerational assemblages of ground sloths, with limited input from other taxa. Such monodominant assemblages can form either through attritional (e.g., Agenbroad, 1984; Barnosky, 1985) or catastrophic (e.g., Voorhies, 1985; Hunt, 1990) mortality. Either situation strongly implies gregarious behavior in these sloths, a phenomenon that has been previously suggested at least in the case of *Eremotherium* (Cartelle and Bohòroquez, 1982; Rossetti et al., 2004) but never conclusively demonstrated (Hubbe et al., 2013).

The fact that the most abundant mammal in the Coralito deposits, *Catonyx*, is not present at all at the nearby Tanque Loma locality, may be attributable to one of several factors. One possibility is that the localities are asynchronous and that *Catonyx* either arrived later on the Peninsula than the other megafauna taxa present at both localities (if Coralito is younger than Tanque Loma) or became extinct earlier than other taxa (if Tanque Loma is younger). No radiocarbon dates yet exist for Coralito, and additional dating efforts may allow us to rule out one or both of these possibilities. A second possibility is that the two sites reflect a true habitat preference of *Catonyx*—as mentioned previously, Coralito appears to comprise an estuarine deposit, whereas Tanque Loma appears to have been formed in a freshwater marsh. Finally, it may be that the Tanque Loma locality

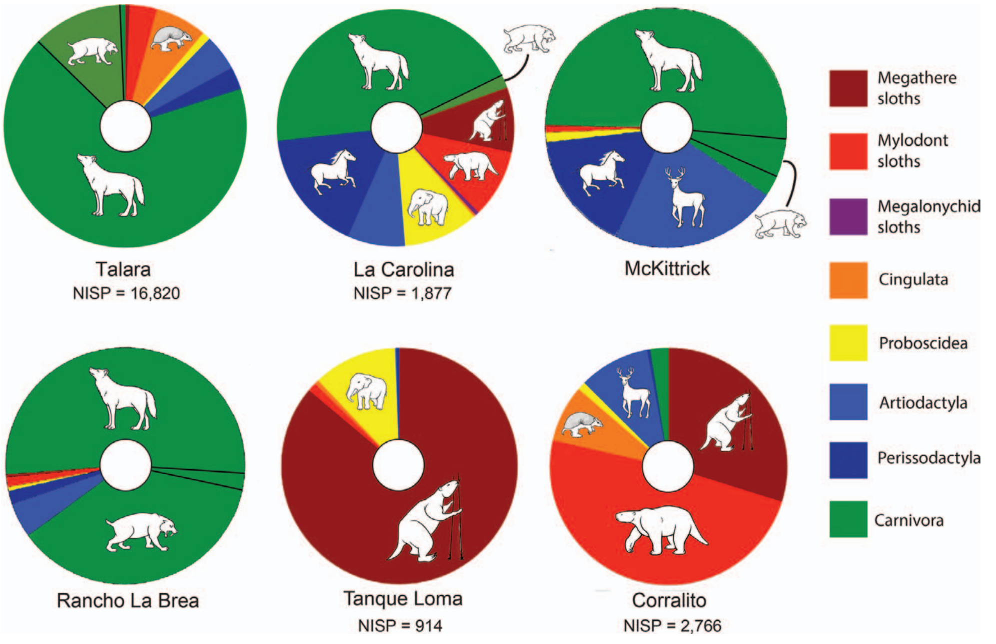

Figure 5 Pie charts showing relative representation of mammalian taxa at neotropical asphaltic localities Talara, La Carolina, Coralito, and Tanque Loma, as well as the California, USA, localities Rancho La Brea and McKittrick. Dominant groups represented by icons. While the South American locality graphs are based on number of individual specimen (NISP) counts, the California locality graphs are based on minimum number of individuals (MNI) calculations. However, because the numbers in the latter two are so large, the proportions of MNI should not be substantially different from NISP counts.

simply captured a narrower swath of the Santa Elena Peninsula ecosystem than did Coralito, either because the former locality was formed in a shorter period of time, because it comprises faunal input from a smaller or less heterogeneous geographic zone, or through chance. The fact that Tanque Loma has the lowest overall diversity of all sites in this study and that most taxa at this locality are represented by fewer than 10 specimens is consistent with the latter hypothesis.

TAPHONOMY

In comparing bones from the four localities in this study, two features are particularly striking. First, the bones collected from Talara tend to be substantially darker in color than those from Coralito, while bones from Tanque Loma and La Carolina present a range of shades, from light brown to black (sometimes on different parts of the same bone) (Fig. 6). This is consistent with the hypothesis that the Talara fossils were accumulated in pools of asphalt, while Coralito, and at least some parts of Tanque Loma and La Carolina, represent bone bed deposits in which the sediments were later saturated—sometimes incompletely—with asphalt. While the taxonomic composition at La Carolina (presented above) is similar to that from tar pit traps such as Rancho La Brea, these taphonomic data coincide with Hoffstetter's (1948a) interpretation of this locality as an estuarine deposit, rather than an entrapment scenario. The variations in color of the Tanque Loma bones are clearly associated with the degree of asphalt saturation of the sediments in which they are found. Unfortunately, not enough information is available from the La Carolina and Coralito localities to ascertain whether this is the case for these deposits as well.

The second notable pattern is that the Coralito, Tanque Loma, and Talara localities contain very high proportions of juvenile taxa. Between 45% and 55% of megafauna individuals at these localities are neonates or juveniles. In contrast, more than 90% of megafauna specimens at La Carolina pertain to adult individuals. This pattern also may be related to the formation of the localities: If Tanque Loma and Coralito represent assemblages formed through either attritional or drought- or disease-related catastrophic mortality, these deposits would be expected to comprise an overabundance of juveniles, as these are the members of a population most likely to succumb to "natural" mortality agents (Conybeare and Haynes, 1984; Olsen and Shipman, 1988). Meanwhile, if most of the fossil deposits at La Carolina were formed by entrapment in asphalt, juvenile animals may have been light enough not to become mired in the seeps. The high abundance of juvenile individuals encountered at

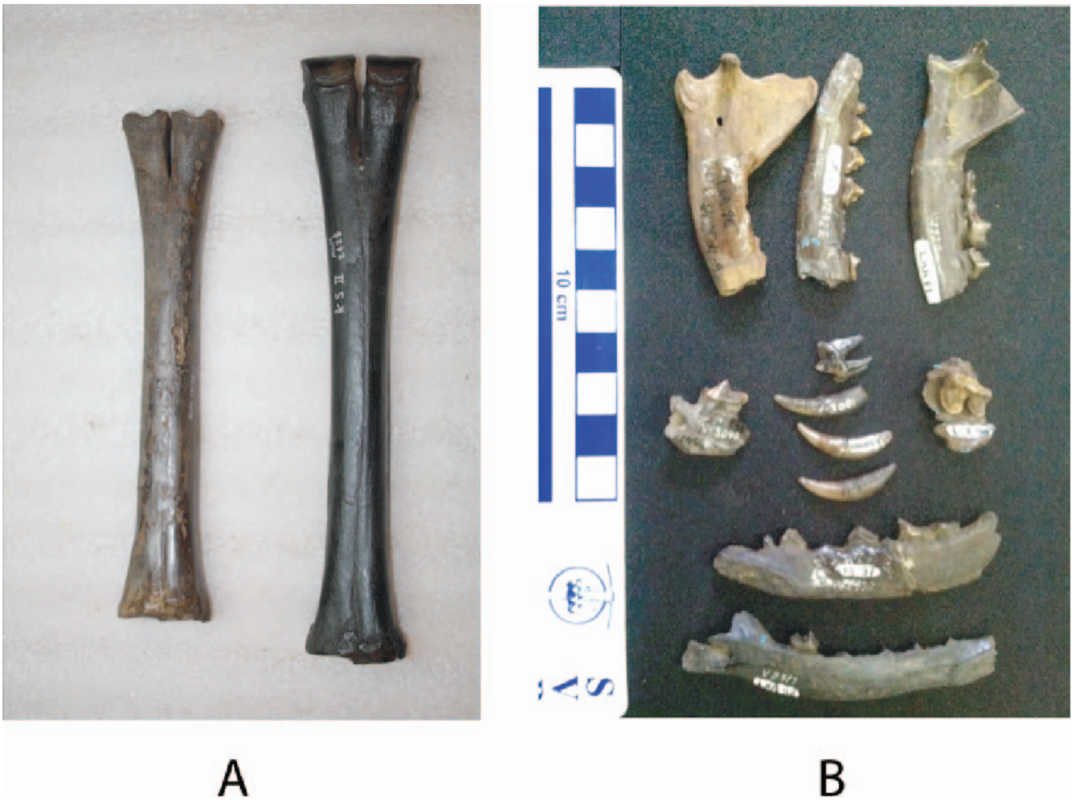

Figure 6 **A.** *Palaeolama* metapodials collected from Coralito (left) and Talara (right), showing typical coloration of bone from the two localities. **B.** Carnivore bones from La Carolina, showing range of asphalt saturation observed on bones from this deposit.

Talara is perplexing. One possible explanation is that the asphalt at this site was more liquid than at La Carolina, and therefore more likely to capture small individuals. A second possibility is that the Talara deposit was formed during a period of greater environmental stress than the other two tar pit trap localities and thus more closely resembles the catastrophic assemblages. Additional paleoenvironmental reconstructions and improved chronological resolution of these localities may help to resolve this mystery.

CONCLUSIONS

There is great variation in geomorphology, taxonomic composition, and taphonomy of the asphaltic vertebrate deposits in the western Neotropics. Of the localities examined in this study, the Ecuadorian localities Coralito and Tanque Loma have taxonomic, taphonomic, and, where discernable, geomorphological signatures suggestive of fluvial fossiliferous deposits with secondary infiltration of asphalt.

On the other hand, La Carolina in Ecuador and Talara in Peru conform to the typical tar pit trap in terms of taxonomic composition and (at least in the case of Talara) geomorphology. However, Talara differs from La Carolina in preserving a disproportionate number of juvenile individuals (similar to Tanque Loma and Coralito), while variations in color among the La Carolina specimens suggest that some bones at this locality may have been deposited before the sediments became saturated with hydrocarbons. When compared with better studied North American asphaltic localities, Talara is most comparable in taxonomic composition and relative abundance to Rancho La Brea, while La Carolina is more similar to the McKittrick locality.

Tanque Loma and Coralito probably comprise mass mortality assemblages of large intergenerational populations of extinct giant ground sloths, which may imply gregarious behavior in these taxa. The fact that the dominant ground sloth species at these two sites are different may be due to a true ecosystem chronological difference, such as the later arrival or earlier extinction of *Catonyx* on the Santa Elena Peninsula, but more likely reflects behavioral and/or habitat differences between these taxa or simple chance.

Radiocarbon dates currently exist for three of the localities in this study: Talara in northwest

Peru and La Carolina and Tanque Loma in southwest Ecuador. The chronology of these localities places all of them after the last interglacial, but well before the beginning of the Holocene. These data are consistent with an apparent paleoecological pattern of earlier extinctions of Pleistocene megafauna in the tropics compared with more temperate regions of South America. However, given the paucity of dates that currently exist in this region, as well as the difficulty of obtaining reliable dates on asphalt-impregnated materials, further chronological analyses will be required at these and other localities to verify this pattern.

Finally, it is notable that despite the rich fossil assemblages described here, very few publications exist for any of these localities. The data presented in this study highlights the fact that asphalt seeps warrant further investigation by paleoecologists, especially in the Neotropics, which represent one of the best possibilities for preservation of Quaternary fossils, and thus for understanding recent paleocommunities in these important ecological regions.

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