La Brea and Beyond: The Paleontology of Asphalt-Preserved Biotas

Edited by John M. Harris

Natural History Museum of Los Angeles County

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Cover Illustration: Pit 91 in 1915
An asphaltic bone mass in Pit 91 was discovered and exposed by the Los Angeles County Museum of History, Science and Art in the summer of 1915. The Los Angeles County Museum of Natural History resumed excavation at this site in 1969. Retrieval of the "microfossils" from the asphaltic matrix has yielded a wealth of insect, mollusk, and plant remains, more than doubling the number of species recovered by earlier excavations. Today, the current excavation site is 900 square feet in extent, yielding fossils that range in age from about 15,000 to about 42,000 radiocarbon years. Natural History Museum of Los Angeles County Archives, RLB 347.

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PREFACE

Rancho La Brea was a Mexican land grant located to the west of El Pueblo de Nuestra Señora la Reina de los Ángeles del Río de Porciúncula, now better known as downtown Los Angeles. The land grant derived its name from the asphaltic seeps that originated from the underlying Salt Lake oilfield and were a source of bitumen for Native Americans and European settlers. The seeps were known to trap unwary wildlife and domestic animals, but it was not until 1875 that they were documented as a source of prehistoric fossils. Systematic retrieval of the fossil remains did not take place until the early part of the 20th century. The history of investigation of these important fossil resources took place in three phases.

The first half of the 20th century saw collecting by the University of California, Berkeley, and several local southern California institutions between 1906 and 1913, after which the Hancock family granted sole right to excavate to the newly established Los Angeles County Museum and deeded the property to the County of Los Angeles in 1924. This early phase focused on well-preserved large specimens of the iconic Late Pleistocene megafauna; poorly preserved specimens were frequently discarded during excavation, and smaller elements of the biota were often flushed away while cleaning the asphalt from the bones. Some 300 species of animals and plants were documented during this interval and these led to the selection of the tar pits as the type locality of the Rancholabrean Land Mammal Age.

The second half of the 20th century saw the reopening of Pit 91 in 1969, using similar excavation techniques to the 1913–1915 excavations but enhancing the potential for taphonomic investigations by documenting the position and orientation of all fossils larger than 1 cm. More importantly, the matrix enclosing the bone accumulations was treated with solvent to remove the asphalt and, specifically, to recover the smaller elements of the biota. This process more than doubled the number of known species, and most of the plant, insect, and mollusk species from Rancho La Brea were first documented from Pit 91. The plant species represent the major habitats of the Los Angeles Basin during the Late Pleistocene—sagebrush scrub dotted with groves of oak and juniper with riparian woodland along the major stream courses and with chaparral vegetation on the surrounding hills. Other investigations focused on the function, diet, and behavior of species whose presence in the biota had been established earlier in the century.

The beginning of the 21st century has seen a shift in focus of La Brea studies to anatomical and behavioral changes through time, aided in part by an increase in the number and quality of radiometric dates from specimens collected during the previous century. New fossil assemblages recovered during construction at the neighboring Los Angeles County Museum of Art are being excavated with the same attention to detail as in the Pit 91 excavation. These are enabling us to better understand the process of formation of asphaltic fossil deposits, are providing a clearer picture of the local faunal composition, and afford the potential for documenting environmental changes through time. The Rancho La Brea sequence spans the last phase of global cooling and subsequent warming; changes in the Rancholabrean biota have much relevance to environmental changes taking place on earth today.

That Rancho La Brea is currently the world's most famous asphaltic fossil deposit–renowned for the immense number of its fossils and the diversity of its biota and serving as a standard for the recovery and interpretation of terrestrial asphaltic deposits elsewhere–owes much to its geographic location, the foresight of the Hancock family to preserve it for posterity, and the stewardship of the County of Los Angeles and its Natural History Museum to maintain its scientific integrity. This volume is dedicated to the museum's staff and their many volunteers who have recovered and curated this scientific resource over the course of the past century, to their many scientific associates who have helped with its interpretation, and to the generous donors who have supported different aspects of its research and curation programs.

John M. Harris
June 2015
Pasadena, California

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INTRODUCTION

H. Gregory McDonald,[1,2] John M. Harris,[2,3] and Emily Lindsey[4]

Humans have utilized naturally occurring surface deposits of oil in the form of natural asphalt (or bitumen) for thousands of years. The oldest evidence for its use is bitumen-coated flint implements that date to ca. 40,000 BC (Mousterian period) (Boëda et al. 1996; Connan, 1999), and ancient use of natural bitumen by different cultures is known from around the Middle East (Connan, 1999, and references therein), Asia (Kato et al., 2008), and the New World (Alliot, 1971; Wendt and Cyphers, 2008). Even though the science of paleontology is over 200 years old, the recognition that asphalt deposits may preserve unique records of past life is still relatively new, and the types of information that can be obtained from asphalt-preserved fossils is still evolving, especially as new technology enables the study of biomolecules preserved in these deposits (e.g., Coltrain et al., 2004; Ward et al., 2005; Fuller et al., this volume). Historically, the approach to studying tar-preserved biotas came primarily from techniques initially developed for Quaternary fossils preserved in more common contexts, such as burial in terrestrial sediments, peat bogs, and caves. While these approaches laid the groundwork for the study of tar-preserved biotas in terms of taxonomy, anatomy, and a general understanding of the paleoecology of the preserved biota, there has not yet been a comprehensive approach to understanding the taphonomic pathway(s) by which organisms may be preserved by asphalt or the positive and negative aspects of these deposits in terms of contributions to our understanding of the fossil record.

The formal study of the biota (vertebrates, invertebrates and plants), naturally preserved in tar and recovered from "tar pits," as a subdiscipline within paleontology, started in the early twentieth century with the formal excavations by the Los Angeles County Museum and the University California, Berkeley, at Rancho La Brea in southern California. Hence, Rancho La Brea can be thought of as the "holotype" of tar pit deposits as well as the type locality for the Rancholabrean North American Land Mammal Age (Savage, 1951). Certainly our current understanding of both deposition and preservation of past biotas in asphalt deposits is heavily dominated by the more than 100 years of ongoing research at Rancho La Brea, despite the recognition that tar-preserved biotas, just like the oil deposits that yield them, are present worldwide. Asphalt-preserved biotas are now known from several other localities in California (Carpinteria, McKittrick, Maricopa), as well as Peru, Ecuador, Trinidad, Venezuela, Cuba, Iran, Angola, and Azerbaijan. As might be expected, these other tar-preserved biotas are commonly compared to Rancho La Brea and it is often used as the model or reference by which these new sites are interpreted.

The simple Rancho La Brea standard model is that natural asphalt seeping to the surface forms a semiviscous sticky surface, which serves as a trap, much like a giant sheet of flypaper (Huseynov and Harris, 2010). Herbivores become mired in the tar, attracting predators or scavengers, which in turn become trapped as well. This process results in a disproportionate number of carnivores being preserved in the deposit and an ecologically unbalanced representation of the local ecosystem in terms of the number of individuals represented from different trophic levels. There is often an *a priori* assumption that any fauna preserved in asphalt should have a disproportionate number of carnivores (Behrensmeyer and Hook, 1992). Other aspects of the Rancho La Brea model include expectations of a high proportion of aquatic birds and arthropods, which are presumably attracted by a film of water overlying the seep, and an abundance of insects and plant material, which are often not preserved in nonasphaltic contexts.

However, recent studies on the paleobiology and taphonomy of different asphaltic localities from around world indicate that the picture may be much more complicated. Examination of the

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biota from other "tar pits" indicates that they do not always contain a disproportionately high number of carnivores, and carnivores may even be absent from the fauna. Also at these other sites, more easily perishable parts of the biota such as insects and plant remains, which are common at Rancho La Brea, may not be preserved. While in all of these sites, asphalt has contributed to the preservation of the fossils, at many of them, unlike at Rancho La Brea, the presence of the tar appears to be secondary and not the primary agent of fossil accumulation. In these cases a different taphonomic pathway led initially to the preservation of the biota present and hence our inferences about the local ecology and environment. The interpretation of site formation of any tar-preserved biota should be on a case-by-case basis, and the presence of asphalt should not lead to an *a priori* assumption that it was the primary cause of site formation.

This volume represents a compilation of papers presented at the symposium, *La Brea and Beyond: The Paleontology of Asphalt-Preserved Biotas*, held during the 73rd annual meeting of the Society of Vertebrate Paleontology hosted by the Natural History Museum of Los Angeles County. The goal of the symposium, and consequently of this volume, is twofold. First, as the many contributions clearly show, ongoing research continues to improve our understanding of the taphonomy and origin of the biota preserved at Rancho La Brea and, equally important, demonstrates that even after more than 100 years of research the unique aspects of Rancho La Brea in terms of the quality of preservation of the fossils and the large sample sizes for many taxa means it continues to contribute to our understanding of Pleistocene fauna, flora, climate, and environments in North America. Second, this collection of studies demonstrates that although Rancho La Brea is clearly a classic locality and world famous, there are many other less well known asphalt-preserved biotas around the world, and not all of them fall within the Rancho La Brea "paradigm" in terms of the origin of the deposit or the relative abundance of different taxa preserved therein. While sharing the common sobriquet of "tar pit," in reality each site is unique in terms of how it originated, how the preserved biota reflects the local climate and environment at the time of accumulation, and how well each site preserves the relative abundance and diversity of the fauna and flora at the time.

A number of the papers in this volume report novel studies that use the vast wealth of data from the world's best known asphaltic locality, Rancho La Brea, to glean new information about the evolution, ecology, and behavior of late-Quaternary taxa of southern California, as well as inform our understanding of tar pit formation and taphonomy. Campbell and Bochenski document the strigiform paleoavifauna from Rancho La Brea that comprises nine species represented by a minimum of 1,103 individuals. The commonest species was the extant Burrowing Owl, whereas the rarest is the extinct miniature owl *Asphaltoglaux cecileae*. Campbell and Bochenski note that owl specimens outnumber those of avian scavengers and were probably caught in the asphalt seeps because they were preying on trapped animals that were struggling to free themselves.

Brannick et al. used a two-dimensional landmark-based morphometric analysis to examine size and shape changes in dire wolf mandibles through time. They note that sexual dimorphism remained constant in the four samples from Pits 91, 2051, 13, and 61–67, but larger body sizes correlated with relatively warmer intervals, whereas smaller body sizes were inferred in samples from pits representative of cooler climates.

Scott et al. describe a fragmentary timber wolf femur from Rancho La Brea that shows evidence of a healed traumatic injury that occurred well before the death of the individual and which may have resulted in a tripedal lifestyle.

De Santis et al. interpreted the dental wear of the large La Brea carnivorans to be indicative of carcass utilization similar to that of comparable living analogs. They found no evidence that the larger carnivorans were more stressed, or dietary resources more limited, immediately before their extinction. *Puma concolor* survived the extinction event, and its generalist diet may have been the key to its survival.

Hartstone-Rose et al. survey the numerous carnivoran bacula from Rancho La Brea and compare them with modern analogues from the collections of the Smithsonian and American Museum of Natural History. The bacula of coyotes, and mustelids from the asphalt deposits are similar to those of their modern relatives. Those of dire wolves are much larger than those of *Canis lupus*, a difference that is much less subtle than the cranial features normally used to separate these species.

Additionally, El Adli et al. document the last years of life and season of death of a Columbian mammoth recovered in 2006 during the construction of the Los Angeles County Museum of Art's construction of an underground parking structure adjacent to the La Brea tar pits. It would appear that this 48–52 year-old male (named "Zed" by its preparators) died 37,000 years ago during the early summer as a result of soft tissue injuries resulting from a mating conflict.

Other papers in this volume highlight the history and potential of lesser studied Californian asphaltic localities. Brown et al. investigated the source of the type material of *Equus occidentalis* and concluded that this was probably from the McKittrick asphalt deposits rather than from Asphalto as attributed by Savage (1951) during his definition of the Rancholabrean North American Land Mammal Age. Meanwhile, Shaw and Quinn describe the first and only *Smilodon* specimen from Carpinteria, California. It represents a much younger individual than any juvenile from Rancho La Brea and is the first recorded preweaned specimen of *Smilodon fatalis*.

Another unique contribution of this volume is that it brings together several studies on lesser known and newly discovered asphaltic localities in South America that contribute to our understanding of the diversity in age, biota, and taphonomy of these deposits. Seymour provides an overview of the late Pleistocene fossils from the Talara tar seeps in northwestern Peru. The biota show similarities to Rancho La Brea in being carnivoran-dominated, but Anseriformes and Passeriformes predominate in the birds. The Talara assemblage represents a more humid environment than that present today, and although the biota shares some species with Rancho La Brea, it has a distinctive South American composition.

Lindsey and Seymour contrast the Talara tar seeps with three asphaltic Quaternary vertebrate localities from the Santa Elena Peninsula in southwestern Ecuador. They conclude that the sites of Talara and of La Carolina in Ecuador conform to the "typical tar pit trap," although Talara preserves a disproportionate number of juvenile individuals, and some bones at La Carolina may have accumulated before being impregnated with hydrocarbons. In contrast, the Ecuadorian sites of Coralito and Tanque Loma appear to represent fluvial or lacustrine bone bed deposits that were subsequently infiltrated by asphalt.

Northeast of these deposits, Solórzano et al. describe a new mammal assemblage designated ORS20 from the Late Pleistocene El Breal del Orocual in northeastern Venezuela. This assemblage is younger than the nearby Plio-Pleistocene assemblage of ORS16. Continual asphalt seepage over several million years may in part be due to the tectonically active location of the area vis-à-vis the junction of the American and Caribbean plates in northeastern Venezuela. The assemblage represents the last reported appearance of the peccary *Platygonus* sp. and of the armadillo *Pachyarmatherium leiseyi*.

Finally, papers in this volume report new methods for dealing with the particular challenges of tar pit research that will enable ever more detailed and informative studies of these valuable paleontological resources into the future. Fuller et al. describe a new sample preparation method that effectively recovers uncontaminated collagen from asphalt-impregnated bone, thereby facilitating accurate radiocarbon dates. They also assess previous bone radiocarbon dates from Rancho La Brea in terms of quality and discuss the dangers of using "pit average" dates for individual specimens. Additionally, Rice et al. discuss a new environmentally friendly method of recovering microfossils from asphaltic fossiliferous matrices.

We hope this volume will allow the reader both to better understand Rancho La Brea and to go Beyond and appreciate the many unique attributes of "tar pit" biotas in other parts of the world and how each contributes in its own way to our understanding the dynamics of past life on this planet.

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The Owls (Aves: Strigiformes) of Rancho La Brea

Kenneth E. Campbell, Jr.[1,2,4] and Zbigniew M. Bochenski[2,3]

ABSTRACT. The late Pleistocene strigiform, or owl, paleoavifauna of the Rancho La Brea asphalt deposits comprises nine species represented by a total of almost 8,000 specimens from a minimum of 1,103 individuals. Two of the eight represented genera are extinct, as are three of the represented species. The most common species present is the living, medium-sized Burrowing Owl (2,775 specimens from at least 378 individuals), whereas the rarest species is the extinct miniature owl *Asphaltoglaux cecileae*, which is represented by only four specimens from three individuals. A total of 31 pits, or excavation sites, produced owl specimens, although 11 pits had 10 or fewer specimens each. The top five pits produced approximately 73% of the total owl specimens, whereas the top ten pits produced 93% of the total owl specimens. The tarsometatarsus was the most commonly preserved bone, with 1,662 specimens, followed by the tibiotarsus (1,526 specimens) and humerus (1,110 specimens). Owls are almost strictly predatory birds; thus, it can be assumed that they were probably caught in the asphalt seeps because they were preying on entrapped animals that were struggling to free themselves. The number of owl specimens in the Rancho La Brea collections is larger than the number of true avian scavengers. This suggests that animals trapped, but still living, were more of an attraction to predators than dead animals were to scavengers, that acts of predation were more deadly for predators than feeding on carcasses was to scavengers, or that there were just more predators in the region than scavengers.

INTRODUCTION

Around 140 species of birds are known from the Rancho La Brea asphalt deposits, of which 17 are identified to family alone and nine just to genera. Twenty-three of the 114 taxa identified to species, or 20%, are extinct. Other extinct species are in the process of being described. The fossil bird collection housed at the La Brea Tar Pits and Museum, on which this report is based, is estimated to comprise ~250,000 specimens, of which approximately one-half are catalogued.

The first summary of the owl remains from Rancho La Brea was that of Miller (1916) based on collections in the University of California Museum of Vertebrate Zoology. He noted six species, of which the Barn Owl was "far the most common." In a later reassessment of the birds of Rancho La Brea based on most, if not all, collections available at that time, Miller (1925) recognized seven species. As before, the Barn Owl was "by far the most abundant" and the Burrowing Owl was rare. In both papers, he commented on the great range of variation in specimens of the Great Horned Owl, a major contributing factor of which was that bones of the extinct Brea Owl, *Oraristrix brea* (Howard, 1933), were later recognized to be mixed in with those of the former.

Among the currently identified strigiform specimens from Rancho La Brea are nine species of owls represented by ~8,000 specimens, or 8%, of the named species and ~3% of the estimated total number of specimens from Rancho La Brea. At least 1,103 individual owls are represented. Howard (1962) also listed nine species of owls from Rancho La Brea, although for some taxa the names she applied differ from those used here. In that study, she only considered specimens from 13 pits. She did not give the numbers of specimens identified for each species, and she identified the two species of *Asio* Brisson, 1760, with 1,730 only to genus. The total number of individuals in her tabulations was 757, whereas the total number of individuals from the same 13 pits presented here is 923. Other than the compilation by Howard (1962), no modern presentation discussing the entire strigiform avifauna from Rancho La Brea has appeared.

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The most common species of owl represented at Rancho La Brea is the living Burrowing Owl, *Athene cunicularia* (Molina, 1782), which is represented by 2,775 specimens from a minimum of 378 individuals (Table 1). It comprises 35% of the owl specimens and 34% of the individuals of owls. The large number of specimens of this species currently recognized stands in contrast to the statements by Miller (1916, 1925) that it was a rare species in the collections. The rarest species in the collection is the extinct miniature owl *Asphaltoglaux cecileae* Campbell and Bochenski, 2013, which is represented by only four specimens from three individuals. One of these specimens was probably that from Pit 16 referred to *Aegolius acadicus* (Gmelin, 1788) by Howard (1962). Together, the four most common owls in the collection comprise 93% of all owl specimens and 86% of the owl individuals represented.

Owls are highly predaceous birds, feeding almost exclusively on live-caught prey. Although their relative abundance in the fossil collections of Rancho La Brea was noted by Howard (1962), their abundance relative to that of true scavengers remains rather surprising. Also surprising is the fact that what are generally perceived as nocturnal hunters would be represented in the asphalt deposits in such numbers because the effectiveness of the asphalt seeps as traps is greatly reduced with the lower temperatures at night, as noted by Miller (1925).

The objectives of this paper are to present a picture of the entire strigiform avifauna from Rancho La Brea, to suggest reasons for the differential entrapment of the different species of owls in the asphalt seeps at Rancho La Brea, to outline the distribution of owl species among the 31 pits at Rancho La Brea producing owls, and to discuss the relative rates of preservation of different skeletal elements among the pits.

MATERIALS AND METHODS

The complete collection of fossil birds from Rancho La Brea housed at the La Brea Tar Pits and Museum, a branch facility of the Natural History Museum of Los Angeles County, comprises five different subsidiary collections, each catalogued separately. Each of these subcollections was thoroughly searched for specimens of owls, which resulted in ~1,000 newly catalogued specimens. The results reported here do not include an estimated 300 specimens of pedal and manual phalanges that can be identified as owl, but placed to genera and species only with difficulty, if at all.

To calculate the minimum number of individuals (MNI) for each species, the most abundant limb element was used. The number of complete specimens from one side (i.e., right or left) of the most abundant element was determined for each species from each pit. The element used could vary among the 31 pits, but it was usually the tarsometatarsus or tibiotarsus. To this was added the number of proximal or distal specimens of the same side of that element from that pit, depending on which was most abundant, to arrive at the MNI for each pit. This was repeated for each pit, and the numbers were added to reach the total for all pits. Limb elements were used in these calculations because they are far more numerous and better preserved than parts of the axial skeleton.

DISCUSSION

THE FORMATION OF FOSSIL-RICH ASPHALT DEPOSITS AT RANCHO LA BREA

To understand how owls could have been entrapped in the asphalt seeps at Rancho La Brea, it is necessary to understand the formation of the seeps and why they were effective traps. This is not difficult to determine because the asphalt seeps remain active today, and animals continue to be entrapped and die in the seeps just as they did thousands of years ago. The general image held by the public of the "tar pits" as "death traps," unfortunately reinforced by the industrial excavation site (aka, the "Lake Pit") in the southeast corner of Hancock Park alongside Wilshire Boulevard, is that of deep pools of "tar," into which animals would step and gradually sink out of sight in bubbling ooze. Although there were probably instances when pools of "tarry ooze" tens of centimeters deep might have formed, actual seep accumulations were predominately quite different.

The terrain in which the asphalt deposits occur lies near an oil field that was once an important industrial petroleum producer, the Salt Lake Oilfield (Quinn, 2001). The rock formations over the oil field are highly fractured because of the intermittent earthquakes resulting from tectonic movements in the Los Angeles Basin. Under pressure, natural petroleum finds its way to the surface along fracture zones until it reaches the surface through vents, or fissures, of varying sizes. The locations of modern vents are known to change after earthquakes, and occasionally changes occur for no apparent, visible reason. After exiting the vent at the surface, the liquid petroleum flows over the surface of the ground, flowing down any slope (Fig. 1). Occupying an alluvial plain less than 4 km south of the Santa Monica Mountains, the area of the asphalt seeps is not perfectly flat, and before human occupation, the ground surface and topography was probably in constant flux because of deposition and erosion resulting from outflow from the nearby mountains.

Table 1 Distribution of owls from the Rancho La Brea excavation sites (= pits). Species are listed in order by declining total abundance for ease in comparison. Specimens listed under *Asio* sp. are incomplete specimens referable to genus only; they do not indicate the presence of a third species of *Asio*.

	Pit 1		**Pit 2**		**Pit 3**		**Pit 4**		**Pit 9**		**Pit 10**		**Pit 13**		**Pit 16**	
Species	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
Athene cunicularia					122	14	23	4	2	1	958	111	1	1	140	24
Tyto alba	2	1	3	1	314	31	24	3	5	1	892	101			38	5
Asio flammeus			3	1	250	24	23	4	2	1	499	55	3	3	43	9
Bubo virginianus	1	1	2	1	52	6	154	20	5	2	65	6	31	5	644	40
Asio otus					19	9	7	3			41	8			43	8
Oraristrix brea					9	2	13	3			2	1			59	5
Asio sp.			1	1	19	5	5	1			78	14			9	2
Megascops kennicottii					2	1	1	1							20	5
Glaucidium kurochkini															1	1
Asphaltoglaux cecileae															1	1
Total NISP per pit	3		9		787		250		14		2,535		35		998	
Total MNI per pit		2		4		92		39		5		296		9		100

	Pit 27		**Pit 28**		**Pit 36**		**Pit 37**		**Pit 51**		**Pit 60**		**Pit 61**		**Pit 67**	
Species	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
Athene cunicularia			620	56	37	7	470	65					2	1	1	1
Tyto alba			166	23	91	12	174	17	1	1	1	1	42	11	12	3
Asio flammeus	1	1	179	19	66	8	135	14	3	1	1	1	11	4	4	2
Bubo virginianus			5	1	35	5					37	8	2	1	2	1
Asio otus					8	3	4	2					1	1		
Oraristrix brea			1	1	3	1			2	1			2	1		
Asio sp.			11	2	5	2	8	2					2	2	1	1
Megascops kennicottii					3	1	1	1								
Glaucidium kurochkini					1	1										
Asphaltoglaux cecileae					1	1										
Total NISP per pit	1		982		250		792		6		39		62		20	
Total MNI per pit		1		102		41		101		3		10		21		8

Table 1 Extended.

	Pit 77		Pit 81		Pit 83		Pit 90		Pit 91		Pit 96		Pit 98		Pit 99	
Species	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Athene cunicularia	1	1	39	6					5	3			7	2	1	1
Tyto alba	1	1	29	3	2	1			7	2			37	9	1	1
Asio flammeus	1	1	37	8			1	1	33	4			25	5	4	1
Bubo virginianus	5	1	1	1			1	1	41	6	1	1	33	3	15	3
Asio otus			3	1			1	1	2	1			7	4	1	1
Oraristrix brea			1	1					4	1			3	1	1	1
Asio sp.			1	1									1	1		
Megascops kennicottii									1	1			1	1		
Glaucidium kurochkini																
Asphaltoglaux cecileae																
Total NISP per pit	8		111		2		3		93		1		114		23	
Total MNI per pit		4		21		1		3		18		1		26		8

	Bliss 29		Pit A		Pit B		Academy		No data		LACM 7247		LACM 7297		Total	
Species	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	Specimens	Individuals
Athene cunicularia	101	37	197	33	1	1	11	2	36	7					2,775	378
Tyto alba	8	3	103	17			6	2	13	3					1,972	253
Asio flammeus	16	8	42	8			4	1	12	2					1,398	186
Bubo virginianus	7	2	132	12			3	1	6	3					1,280	131
Asio otus	4	2	30	4					1	1			1	1	173	50
Oraristrix brea	4	1	33	4	4	2			1	1	2	1			144	28
Asio sp.	2	2	13	7			2	2	1	1					159	46
Megascops kennicottii	13	5	36	5					1	1					79	22
Glaucidium kurochkini	4	3	6	1											12	6
Asphaltoglaux cecileae			2	1											4	3
Total NISP per pit	159		594		5		26		71		2		1		7,996	
Total MNI per pit		63		92		3		8		19		1		1		1,103

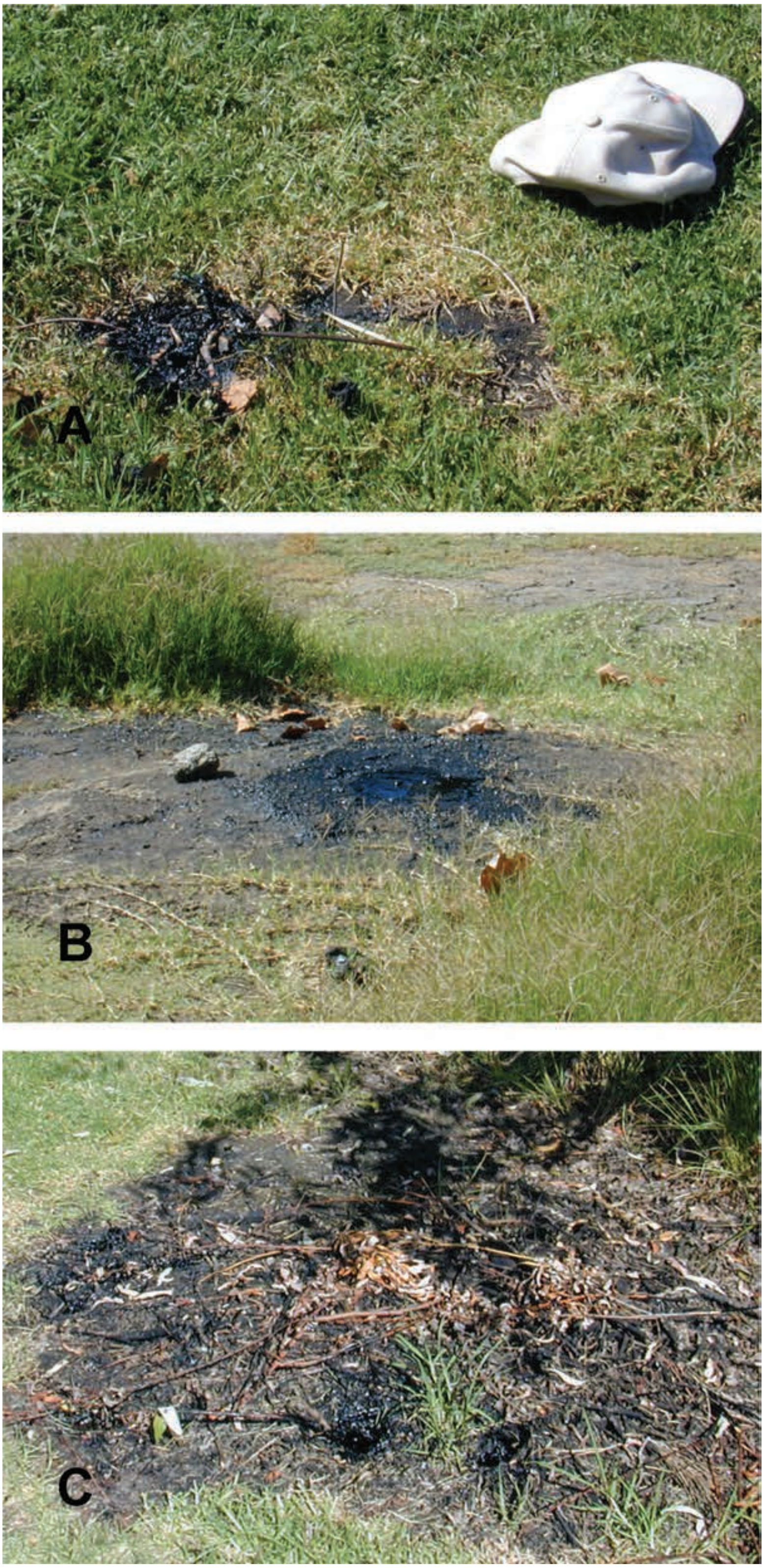

Figure 1 Images of modern seeps showing vent types. **A.** small seep showing flow away from vent; **B.** larger vent, showing downslope accumulation in several directions away from the elevated vent; **C.** seep with an inconspicuous vent and an accumulation of leaves and sticks, some of the latter a result of human curiosity.

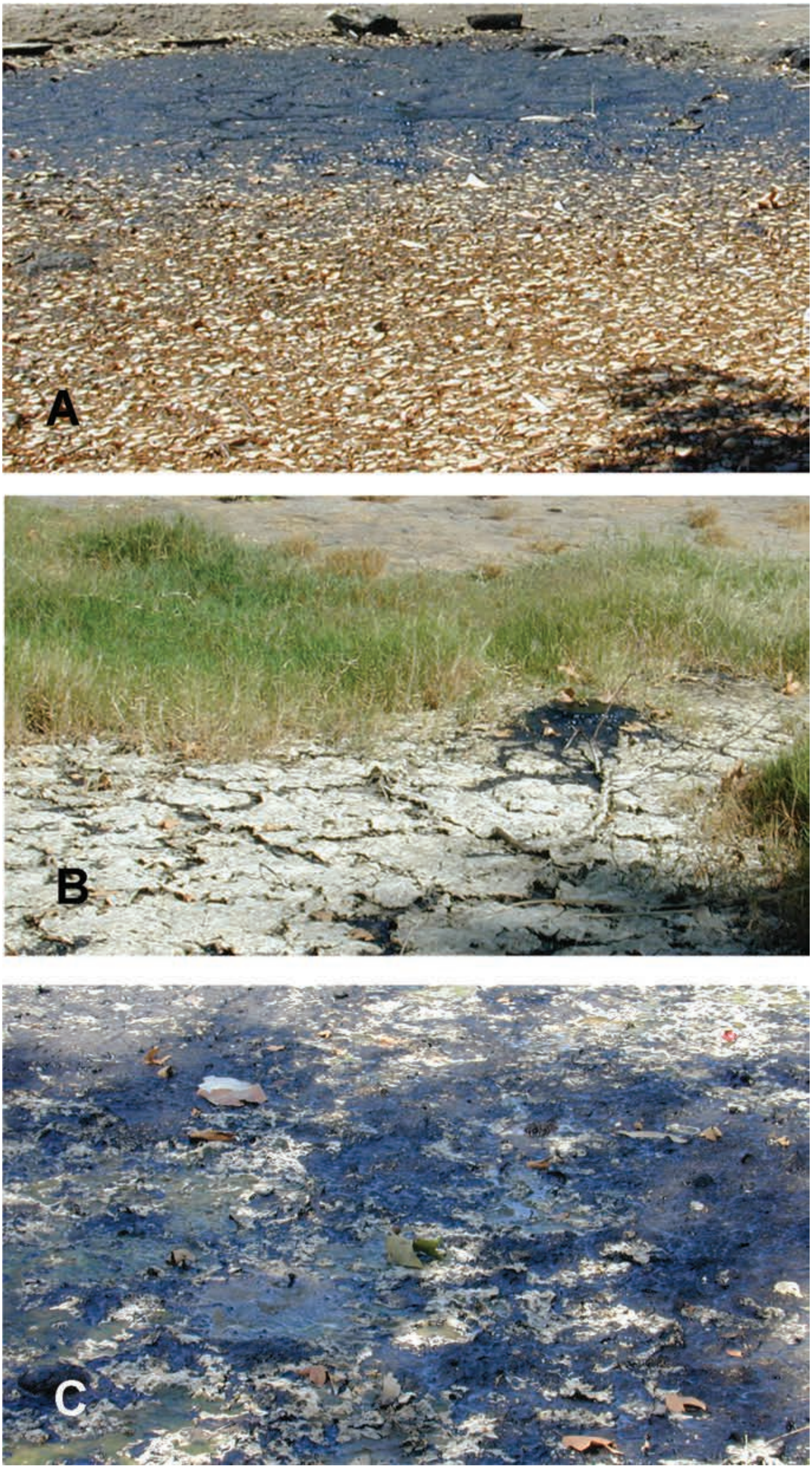

Figure 2 Images of modern seeps showing disguising coverings. **A.** blanket of leaves covers an artificial pool of asphalt; **B.** crust of dust and leaves covers the flow from a small vent; **C.** scattering of leaves and dust partially obscures an active seep.

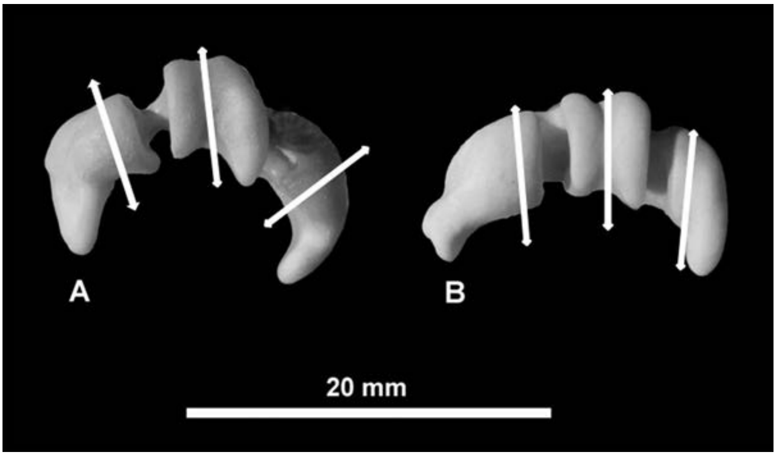

Figure 3 Images of distal ends of **A.** Great Horned Owl (*Bubo virginianus*) and **B.** Red-tailed Hawk (*Buteo jamaicensis*) tarsometatarsi showing general direction of movement, indicated by lines through trochleae, of first three pedal phalanges. The owl's phalanges tend to "box in" the prey more so than those of the hawk, which helps ensure their success as "pounce predators."

Once exiting the ground and on exposure to the atmosphere, the lighter volatile compounds of the petroleum dissipate, leaving the heavier compounds to accumulate on the surface of the ground over time. These deposits, more properly referred to as asphalt, as opposed to tar, are what ultimately form the traps that ensnare and preserve local wildlife. Unless there is a topographical depression near the vent, the petroleum residue does not accumulate to any depth in a "pool." Most of the soils in the region of Rancho La Brea have a high clay content; thus, the petroleum does not soak back into the ground once released from the pressure forcing it to the surface. Rather, the seeping material spreads laterally as long as there is a slope and the flow from the source continues. If the seep material encounters a permeable deposit, such as a sand accumulation in a stream channel, and if it remains of low viscosity, it might penetrate the coarse material and form a deeper potential trap.

The vents, or fissures, from which the petroleum flows onto the surface can vary in size, but they are not large or deep holes in the ground. Over time, however, continued venting of petroleum will cause the ground surface level around

Figure 4 Holotypical tarsometatarsus of *Oraristrix brea* is slightly smaller than small specimens of the largest North American owl, *Bubo virginianus*. Adapted from Campbell and Bochenski (2010). **A.** anterior, **B.** lateral, **C.** posterior, **D.** medial, **E.** proximal, **F.** distal views. Specimen coated with ammonium chloride for photography.

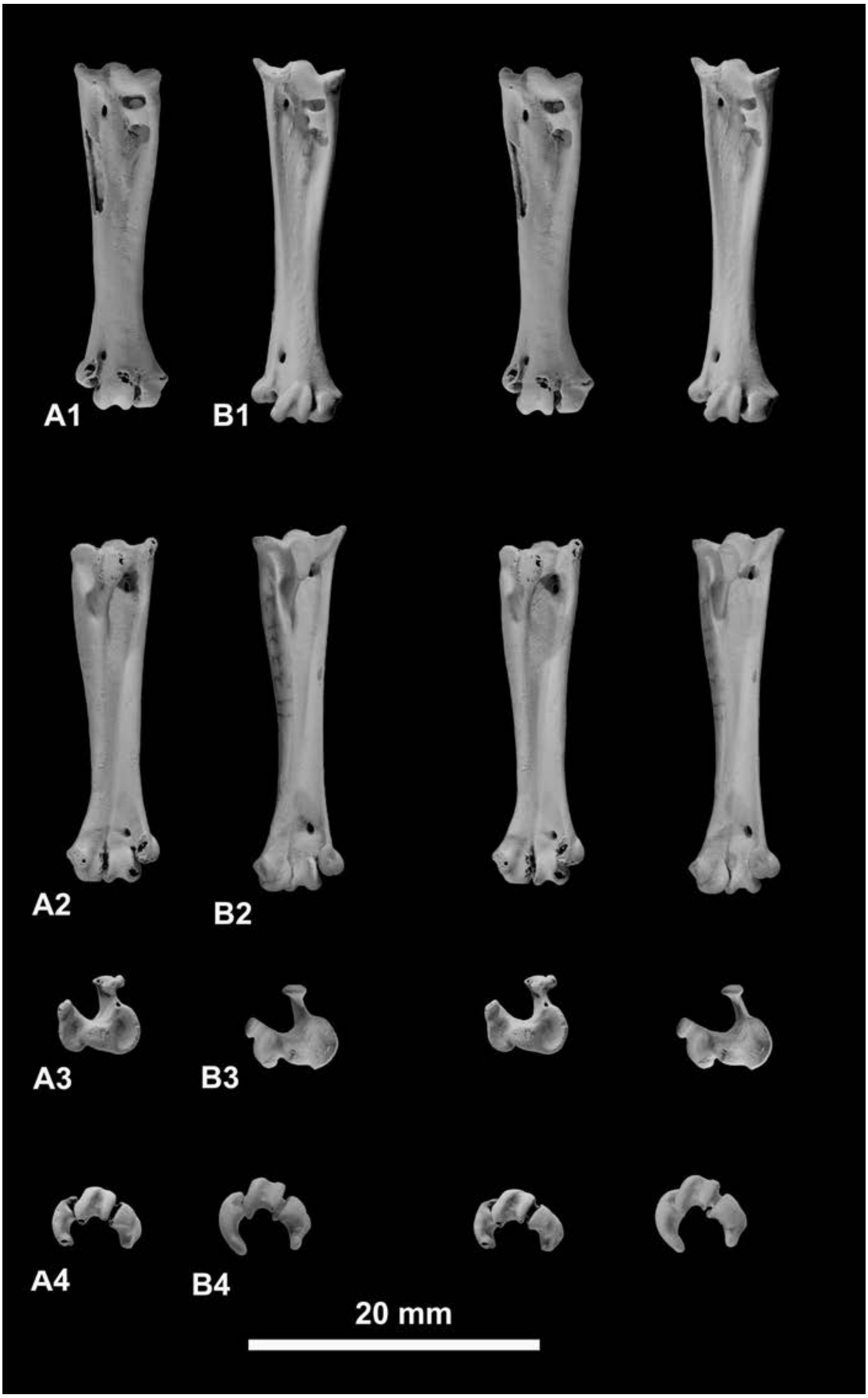

Figure 5 Stereopair views. Two miniature owls from Rancho La Brea (A1–A4, C1–C4) are shown next to the Recent species (B1–B4, D1–D4) that most closely resemble them. *Asphaltoglaux cecileae* **A1.** anterior, **A2.** posterior, **A3.** proximal, **A4.** distal; *Aegolius acadicus* **B1.** anterior, **B2.** posterior, **B3.** proximal, **B4.** distal.

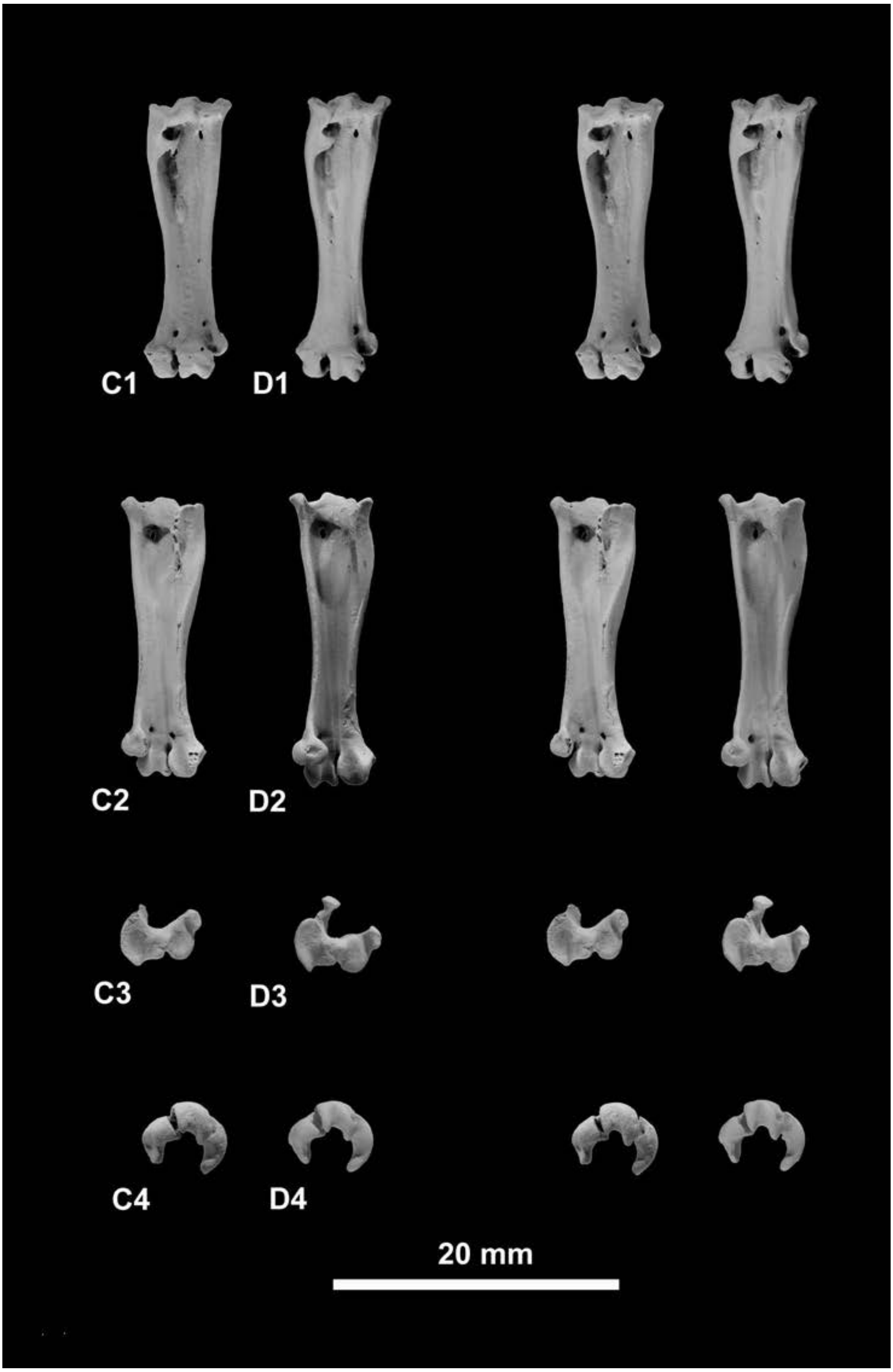

Figure 5 continued. *Glaucidium kurochkini* **C1.** anterior, **C2.** posterior, **C3.** proximal, **C4.** distal; *Glaucidium californicum* **D1.** anterior, **D2.** posterior, **D3.** proximal, **D4.** distal. Specimens coated with ammonium chloride for photography. Adapted from Campbell and Bochenski (2013).

Figure 6 Immature Burrowing Owl tarsometatarsi. **A.** very young with little fusion at proximal end; **B.** juvenile with proximal epiphysis not yet fused to shaft; **C.** immature adult with surface pitting at proximal end. Specimens coated with ammonium chloride for photography.

the vent to rise. The flow of petroleum away from a vent is dependent to a large part on temperature, so the season of the year and the hour of flow during the diurnal cycle are important factors in the formation and spread of a seep. Over time, after variations in seep flow for a variety of reasons, the spreading seep might also deepen away from the vent. Regardless of the depth of the accumulated asphalt, the fact that the seeps are predominately underlain by the compact surface of the ground prevents entrapped animals from sinking to any depth. Rather animals are generally stuck by their feet on or just below the surface of a seep as are flies on flypaper (Shaw and Quinn, 2001). Of course, the larger and heavier the passing animal is, the farther it will penetrate into the seep, if the seep has any depth at all.

As the seep spreads away from the vent it can become covered by a crust of dust and leaves, which can disguise it and hide it from view, as well as contribute to its depth (Fig. 2). Regardless of whether a seep is covered or not by a crust, the surface of a seep that can be traversed by an animal during times of seasonal or nocturnal low temperatures might prove quite effective as a fly-paper type of trap when air temperatures are high. Also, the presence of a crust might make the surface of a seep safe to traverse for some animals, but such a crust might give way to a heavier animal, immersing its feet into the sticky asphalt.

Animals trapped in the asphalt seeps do not die immediately, except perhaps some predatory birds. Rather, they are prone to struggle on the surface of a seep until dying of thirst or starvation. Howard (1962:9) referred to the seeps as acting "… as traps, baited with carcasses or struggling animals." Once deceased, the remains of entrapped animals, especially small-sized individuals, could be covered by continued outflow from the vent. If flow from the vent did not continue, the carcass could either be scavenged by other animals or lost to weathering. It is before the death of an entrapped animal that predatory birds, seeing a struggling animal, would deploy their particular hunting strategy and pursue the prey, which could lead to their being entrapped along with the prey or killed outright by impact with the ground via a "face plant," depending on their hunting style.

For additional information on entrapment at Rancho La Brea, see Stock (2001) and various papers in Harris (2001).

FEEDING IN OWLS

Owls are superb, highly adapted predators. They have a highly developed visual sense and acute hearing, which allow them to detect prey in very low light conditions and when the prey is moving under a cover of debris or snow. Also, owl feathers are uniquely structured to allow almost silent flight by suppressing the noise of air passing over the wings and body. Owls have powerful talons, with the outer pedal digit (IV) rotated partially to the rear (Fig. 3), which gives a more encompassing grasp on prey items. This differs from the structure seen in hawks and falcons, where the talons more strictly close from the front and rear.

Owls are very versatile, but primarily pounce predators, which means that they will rest on a perch, watching for movement or the sound of prey below. They frequently hunt in flight, commonly going into a "hover" mode before dropping onto their prey. Prey is often killed by the crushing of its skull by the owl's powerful beak while the talons are worked into the prey's body from multiple angles. Many owls will remain at the prey capture site after initial contact, ensuring that the prey is dead before carrying it to a perch to feed. Many owls are also capable of taking birds and bats in flight, and Burrowing Owls are noted for their long legs that enable them to run down prey on the ground.

THE STRIGIFORM AVIFAUNA

Six of the owl species occurring in the Rancho La Brea fossil collections are still extant. These are the Barn Owl, *Tyto alba* (Scopoli, 1769); the Burrowing Owl, *A. cunicularia*; the Short-eared Owl, *Asio flammeus* (Pontoppidan, 1763); the Long-eared Owl, *Asio otus* (Linnaeus, 1758); the Great Horned Owl, *Bubo virginianus* (Gmelin, 1788); and the Western Screech Owl, *Megascops kennicottii* (Elliot, 1867). Howard (1962) also recognized these species, although she did not separate the two species of *Asio*.

Three of the nine species of owls from Rancho La Brea are extinct. The first extinct owl to be described from Rancho La Brea was *O. brea* (Howard, 1933) (Fig. 4). Originally placed in the genus *Strix* Linnaeus, 1758, it was restudied and placed in its own genus by Campbell and Bochenski (2010) after the identification of numerous new specimens of the species. The last two extinct owl species described were the Brea Pygmy Owl, *Glaucidium kurochkini* Campbell and Bochenski, 2013, and the miniature owl *A. cecileae* Campbell and Bochenski, 2013 (Fig. 5). The latter two owls were miniature owls represented by only a few specimens (Table 1). Their small size was undoubtedly a contributing factor to their rarity because of the collection and preparation methodology used with the early collections from Rancho La Brea, although habitat and feeding preferences might have been of greater importance.

WHY SO MANY OWLS?

Although the “tar pits” are generally portrayed as a place where animals became mired in the asphalt seeps and perished, attracting large numbers of scavengers that fed on their decaying remains, and while it is undoubtedly true that scavengers were attracted by deceased animals, it has long been recognized that, overall, predators dominate in the collections from Rancho La Brea (e.g., Wyman, 1918; Howard, 1962). This is certainly true for the birds, where eagles, hawks, falcons, and owls vastly outnumber nonpredatory birds and true avian scavengers. Although the latter are often considered predatory birds, they do not take live prey. On the other hand, however, many predatory birds are opportunistic scavengers that will consume dead animals should they be encountered.

Of the predatory birds, owls alone, with ~1,100 individuals, outnumber the New World vultures and Old World vultures combined (~725 individuals). There are many reasons why the large number of owls relative to vultures is perhaps unexpected, especially given that the vultures are primarily large birds whose bones had a greater chance of surviving the collection and preparation procedures associated with the early collections. Owls are true predators and as far as is known do not regularly seek out and scavenge dead animals. There are exceptions, of course. At least five North American owl species have been documented as scavenging (Allen and Taylor, 2013), and long-term meat storage is reported for 18 species of North American owls (Poole, 2005). But owls are primarily nocturnal birds, which makes their feeding behavior difficult to observe, so scavenging might be more common than thought. As noted above, the nocturnal behavior of owls also becomes a factor in entrapment because the asphalt seeps are not as “sticky” at night when the air temperature is lower.

We cannot, at this time, explain why some owl species were more abundant in one pit over another. We can, however, look at the modern species and suggest reasons for their overall representation as fossils at the Rancho La Brea site. For details on each of the living species, see del Hoyo et al. (1999) and König and Weick (2008). We can recognize specific attributes through observations of living birds that might explain why the four most abundant owl species at Rancho La Brea occur in the numbers they do. These factors can be categorized under the following headings.

HABITAT

The environs of Rancho La Brea during the Pleistocene period of activity of the asphalt seeps are usually depicted as fairly open country. Although trees were present, there was no true forest. This description fits perfectly with the habitat preferred by the most abundant species, *A. cunicularia*, which is said to be “Open country with bushes or scattered trees, semi-desert and deserts, mountain slopes with ravine and scattered bushes, …” (König and Weick, 2008:432). Likewise, the preferred habitat of *T. alba* is characterized as open countryside or landscapes with scattered trees, whereas that of *A. flammeus* is more open grasslands. The fourth most common species, *B. virginianus*, tends to frequent a wide range of more wooded, semi-open landscapes, while preferring to forage in more open areas. Interestingly, the Burrowing Owl, Barn Owl, and Great Horned Owl are all present in highly urbanized, modern Los Angeles.

On the other hand, the Long-eared Owl, *A. otus*, and Western Screech-Owl, *M. kennicottii*, prefer more wooded habitat, but not necessarily closed canopy forest. Although we cannot know the preferred habitats of the extinct species, most species of the genus *Glaucidium* are inhabitants of woodlands of various types, which might be taken as the preferred habitat for *G. kurochkini* as well.

Table 2 Distribution of most common skeletal elements from the Rancho La Brea excavation sites (= pits). Elements are listed in order by decreasing total abundance. The total number of specimens per pit do not always equal the number per pit in Table 1 because not all skeletal elements are included in this table.

	Pit 1	Pit 2	Pit 3	Pit 4	Pit 9	Pit 10	Pit 13	Pit 16	Pit 27	Pit 28	Pit 36	Pit 37	Pit 51	Pit 60	Pit 61	Pit 67	Pit 77	Pit 81	Pit 83	Pit 90	Pit 91	Pit 96	Pit 98	Pit 99	Bliss 29	Pit A	Pit B	Academy	No data	LACM 7247	LACM 7297	
Element	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	NISP	Total specimens
Tarsometatarsus	1	2	151	55	4	561	12	209		200	33	90	1	15	15	11	3	29		1	18	1	39	5	35	146		6	17	1	1	1,662
Tibiotarsus		1	149	28		578	3	102		161	40	197	1	5	17	2	1	15			17		21		76	90	1	8	13			1,526
Humerus		3	127	33	2	424	4	111	1	112	56	120	1	3	16	8	2	14	1		5		15	2	1	36		1	12			1,110
Ulna		2	70	22	2	296	1	82		95	26	176			1			11			4		5		7	57			3			860
Femur	2		109	34	4	225	4	97		96	24	47		2	7	4	1	11		2	11		11	2	4	65	3	3	5			773
Carpometacarpus		1	66	24	1	213	5	93		81	16	32		4	1			10			5		8	4	6	50		3	8			631
Coracoid			70	15		91	4	102		90	13	15		4	3			13			6		10	6	12	51		3	5			513
Radius			13	12	1	104	1	59		68	11	79									8				8	41			6	1		412
Scapula			17	9		38	1	72		40	5	5		1	1			6			8		4	3	5	26		1	3			245
Total specimens/pit	3	9	772	232	14	2530	35	927	1	943	224	761	3	34	61	25	7	109	1	3	82	1	113	22	154	562	4	25	72	2	1	7,732

ACTIVITY PERIODS

The Burrowing Owl and the Short-eared Owl are largely diurnal, but most active at dusk, whereas the Barn Owl and Great Horned Owl are primarily nocturnal, but both are also active at dusk and dawn and occasionally at midday. The rarer Long-eared Owl and Western Screech-Owl, on the other hand, are more strictly nocturnal in habits. The period of activity is important because the asphalt seeps are much less effective as traps when the temperatures drop to nightly lows and the surface of a seep hardens and loses its "stickiness." Of course, the activity period of the prey must coincide with the times that seeps are most effective as traps for them to become entrapped and serve as bait.

SIZE

The size of the owl is important because of the feeding behavior of owls (i.e., dropping down on prey from above and killing it in place before flying off to consume it). The weight of an owl can be a factor in its being trapped in an asphalt seep because, as a pounce predator, the heavier the bird, the more likely it is to have its feet penetrate into a seep, and especially to break through any crust on the surface of a seep. The habit of staying at the site of the kill and balancing on the prey item while completing the kill also provides the opportunity to sink deeper into a seep, or break through a crust covering a seep. In terms of body weight, the six living owls present in the collections rank as follows: *B. virginianus*, *T. alba*, *A. flammeus*, *A. otus*, *A. cunicularia*, and *M. kennicottii*. Species of the genus *Glaucidium* are all very small, which leads to their being referred to as pygmy-owls. So, even though primarily nocturnal in behavior, the weight of the Great Horned Owl could have been a major factor in its being trapped in a seep in the course of predation.

PREY PREFERENCE

All of the living owls represented at Rancho La Brea feed on mammals, although they will also take a variety of other prey. The maximum size of the prey animal is generally proportional to the size of the owl, although most owls can and will take prey that is larger than themselves. Other vertebrates (i.e., amphibians, reptiles, and birds) will also be taken when available. Most owls will consume insects, and generally, but not always, the smaller the owl, the greater the proportion of its diet that is made up of insects. The low populations of some types of insects, which would be expected in the open environment of the asphalt seeps, might have been a factor in low populations of some species of owls.

EXPERIENCE

Owls can certainly remember past activities; otherwise, they could never return to continue consuming cached prey. However, we do not know if owls can "learn" from experience, such that getting partially stuck in an asphalt seep and escaping will lead an owl to avoid struggling animals stuck in asphalt. This would require their learning to recognize and avoid predation around asphalt seeps, the difficulty of which could vary significantly depending on the presence, absence, or degree of coverage of a debris crust.

This issue is notable because a survey of the Burrowing Owl specimens reveals that 71 of 196 complete right tarsometatarsi, or 36%, are judged to be from juveniles or immature adults based on the incomplete ossification of the proximal end of the bone as indicated by a pitted surface and incomplete ossification of the bone (Fig. 6). Although immature specimens of other species occur in the Rancho La Brea collections, especially of the extinct California Turkey, *Meleagris californica* (Miller, 1909) (Bochenski and Campbell, 2006), they are not common. For example, for *B. virginianus*, only two of 106 left and one of 89 right tarsometatarsi could be considered juvenile or immature based on the same criterion given above.

DISTRIBUTION OF SPECIES BY PIT

The 8,000+ specimens of owls in the Rancho La Brea collections discussed here are distributed through 31 pits (Table 1). Surprisingly, 32% of the specimens and 27% of the individuals came from a single pit, pit 10. The next two most productive pits were Pit 16 and Pit 28, each of which had 12% of the owl specimens. Pit 3 and Pit 37 round out the top five pits, with 10% of the total specimens each. These top five pits produced a total of 76% of the owl specimens and 62% of the individuals.

The next six most productive pits (4, 36, 81, 98, A, Bliss 29) produced over 100 specimens each for a combined total of 1,478 specimens, or 18% of the total specimens and 26% of the individuals. Eleven of the 31 pits produced 10 or fewer specimens each, with three having only a single specimen.

The composition of the strigiform avifauna varied widely among the pits (Table 1). In Pit 10, *A. cunicularia* was most abundant, with 958 specimens, followed by *T. alba* (892 specimens), *A. flammeus* (499 specimens), and *B. virginianus* (65 specimens). On the other hand, Pit 16 had 644 specimens of *B. virginianus*, 140 specimens of *A. cunicularia*, and only 38 specimens of *T. alba*. The extinct *O. brea*, which was only slightly smaller than *B. virginianus*, was more abundant in Pit 16 than in any other pit. In Pit 4, *B. virginianus* was over six times as common, in terms of specimens, as the next most common species, and *O. brea* was also relatively abundant. *Bubo virginianus* was also the most common owl in Pit 91 and Pit 99. The larger numbers of *O. brea* in pits with high numbers of *B. virginianus* suggests that they might have been attracted by the same prey items, or they had similar feeding habits. The 250 specimens of *A. flammeus* in Pit 3 were second only to those of *T. alba* (314 specimens) in that pit, whereas there were only 122 specimens of *A. cunicularia* in Pit 3.

The two extinct miniature owls, *A. cecileae* and *G. kurochkini*, are found together in three pits (16, 36, A), but *G. kurochkini* is also found in Bliss 29. In each case they are represented by only one to four specimens per pit. As noted above, this rarity is probably a result, in large part, to their very small size and the loss of small specimens in the older collections where the emphasis was on large animals. Still, the fact that these small owls, which might have fed primarily on insects, were found together in three different pits suggests that, at least at certain times, the habitats around these pits were more typical of the woodland habitats preferred by small owls.

An explanation for the varied composition of the strigiform avifauna among the 31 pits might lie with the local owl species' populations at the time each of the seeps was active, the presence of prey items stuck in a seep that were more attractive to one species or another, a preference for prey less likely to be entrapped in the asphalt (e.g., small birds customarily taken in flight), seasonal (i.e., migratory) movement of some owls through the region at times when one seep was more active than another, or differential preservation after death or during excavation and curation at each pit. There is no obvious answer to the question of why certain species are so overwhelmingly dominant in some pits and found in only low numbers in others.

As noted above, the large number of *A. cunicularia* specimens includes a high percentage of juvenile or immature birds, which might have been present at times when the seeps were active. For example, 63% of all owl specimens in Pit 28 were of *A. cunicularia*, and in Pit 37 this species comprised 59% of the total specimens. This might indicate the presence of nesting activity located in proximity to Rancho La Brea.

It would be interesting to compare the number of owls per pit to the number of prey animals found in each pit. Two factors prevent such a correlation, however. First, the prey animals would normally have been smaller than the owls. This means that their bones, if preserved in the asphalt, would have had a much greater chance of being destroyed or lost in the collection and preparation process. Small rodents, for example, are undoubtedly underrepresented in the collections. Second, there is no complete, computerized database of the mammalian collections from Rancho La Brea, so it would be a very difficult and time-consuming task to draw even an incomplete correlation between predators and prey.

DISTRIBUTION OF SKELETAL ELEMENTS BY PIT

The taphonomic factors at work in the formation of the collection of animal remains and how they are preserved in asphaltic deposits is different from those normally encountered in the formation of fossils. No taphonomic study of avian remains has ever been attempted at Rancho La Brea to elucidate these factors. A detailed taphonomic study is planned for the future, but this paper is intended as a general summary of our knowledge of the owls of Rancho La Brea. Consequently, here we have pooled the data for all owl species and focused only on the long bones of the skeleton, rather than looking at all bones of each species independently. We present the data in as basic a manner as possible, that is, by means of the number of identified skeletal specimens (NISP).

The numbers of specimens of the various skeletal elements preserved in the 31 excavation sites producing owls is as expected in asphaltic deposits, up to a point (Table 2). The tarsometatarsus is the most commonly preserved element, most probably because it is attached to the pedal phalanges that would be immersed in, or stuck to, the sticky asphalt seep. Not only is the tarsometatarsus strongly tied to the phalanges by major ligaments, at least its distal end would probably have been immersed in a seep as well. There is also very little muscle on the tarsometatarsus, which would make it of little interest to scavengers.

The tibiotarsus is a close second in terms of numbers. It is tied to the tarsometatarsus by strong ligaments, and it also has a high probability of being immersed in the seep as the bird struggled to free itself. It also would be less attractive to scavengers, having relatively little muscle mass, and that primarily on the proximal end.

The humerus is the third most commonly preserved element. This is a bit surprising because not only does it have a sizable muscle mass attached to it that should be attractive to scavengers, it attaches to the pectoral region of the body in close proximity to the breast muscles, the largest muscle mass of owls and a prime target for scavengers. It is attached to both the coracoid and scapula, which were preserved in relatively low numbers. The humerus is also one of the most thin-walled bones of the limb skeleton, which would make it more subject to destruction than many of the other bones.

The fairly high number of ulnae is probably related to the high number of humeri. The ulna is a long, thin bone with little attached muscle mass, and it has the secondary feathers attached to it, which would have made it difficult to scavenge.

Although the avian femur hosts a sizable muscle mass and is attached directly to the main body of the bird, it seems to have been preserved at a moderately high rate.

There are anomalies in preservation in the various pits. For example, in Bliss 29 and Pit 37 there are over twice as many tibiotarsi as there are tarsometatarsi. In Pit 36 the humeri are the most common element by a relatively large number. The pits with the most specimens follow most closely the overall trend in total numbers, whereas those with the fewest specimens tend to deviate more from the trend.

There are numerous factors that could influence what part of the skeleton would be preserved in an asphalt seep, beginning with what parts of the bird became covered by the seep material. For predatory owls, normally the feet and lower hindlimb bones would be the first to be affected, followed by the ends of the wings as the bird struggled to free itself. Unless the body was subsequently covered by additional seep material, exposure to the elements or scavenging by other animals would probably have resulted in their destruction. Scavenging of owl carcasses might have been deterred because the feathers of owls are particularly voluminous, which obscures the actual small size of an owl's body.

The relative preservation of particular skeletal elements at Rancho La Brea seems to show a unique pattern. It clearly differs from any other fossil, subfossil, or modern assemblages. In subfossil assemblages containing birds that died of natural causes, wing bones are usually more numerous than leg elements (Ericson, 1987). This is also true for uneaten food remains of diurnal birds of prey, as opposed to contents of pellets (Bochenski, 2005). Although Rancho La Brea can certainly be considered a natural accumulation and raptorial birds and/or scavengers are likely to have altered the prey, wing bones are underrepresented. Archaeological assemblages accumulated by birds of prey are characterized by the predominance of tarsometatarsi and either carpometacarpi or coracoids, depending on the size of prey (Mourer-Chauviré, 1983; Baales, 1992; but see also Bochenski, 2005). The two latter elements are rather poorly represented in our material, which is a significant difference.

Asphalt-trapped owls at Rancho La Brea can be compared with ice-trapped coots that were fed upon by bird scavengers (Oliver and Graham, 1994). Most of the coots were frozen in the life position with their belly and legs under ice, while wings, back and head were above the surface. Bird scavengers (Herring Gulls and crows) tended to strip flesh from the coots' bones and damage done by them was largely restricted to the sternum, and coracoids. Damage to the same body region (sternum, coracoid, scapula, and furculum) was also reported in the case of Manx Shearwaters preyed upon by the Great Black-backed Gulls (Serjeantson et al., 1993). The sternum and skeletal elements of the pectoral girdle are also relatively damaged and poorly represented in Rancho La Brea, but here the situation is more complex, and one cannot expect that the frequency of all skeletal elements would be similar to modern assemblages. Furthermore, thin-walled bones such as the sternum were undoubtedly damaged both by postpreservation movement within the asphalt deposits and early collection procedures. Whatever body parts get into asphalt, they are lost for the scavengers or predators but saved for the fossil record. As mentioned above, the distal portions of legs, including the feet and the tarsometatarsi, are most likely to get stuck in the asphalt. It can be expected that sooner or later the entrapped owl will end up with its belly or side on the sticky asphalt and the other parts exposed to predators, scavengers, and weathering. This would help explain relatively greater loss of some wing elements as well as the axial skeleton and the predominance of leg bones in the fossil record.

Although other bird species, such as the Golden Eagle and caracaras, are both scavengers and predators and common in the Rancho La Brea collections, it is not unreasonable to conclude that they, too, were, more often than not, going after prey that was entrapped but still alive and struggling. Avian predators, such as hawks and eagles, customarily move in at high speed for the kill and were probably killed instantly upon hitting the ground (i.e., a "face plant") when their targeted prey, pierced by sharp talons, could not be pulled free from the asphalt. Death or entrapment of owls could also have occurred in this way should they have tried to take prey while in flight. Scavengers, on the other hand, would more often have landed near carcasses and become entrapped while walking or hopping around them during feeding.

SUMMARY

A review of all owl specimens in the collections from Rancho La Brea housed at the La Brea Tar Pits and Museum confirms the presence of nine species in eight genera. Two of the genera and three of the species are extinct. Owls comprise only 8% of the named species from Rancho La Brea, but in terms of individual birds represented (1,103), they outnumber the four species of New World vultures, which are strict avian scavengers (~500). If the two species assigned to the Old World vultures are added to the avian scavengers, owls still dominate (1,103 to ~725). The reason that nocturnal, predaceous owls that

rarely scavenge are more numerous in the Rancho La Brea avifauna than strict avian scavengers is a result of their hunting behavior and the effectiveness of the asphalt seeps as baited traps.

The numbers of each species tend to correlate with the specific attributes of each species. Owls that prefer a more open landscape and are active during the day when the asphalt seeps are most effective as traps are represented in high numbers, whereas those that prefer more wooded areas and are nocturnal are present only in low numbers. The larger species are more likely to be entrapped because they feed more often on mammals serving as bait in a seep, whereas the smaller owls tend to feed more on insects that are more prevalent in wooded landscapes. The size of an owl is important because, as pounce predators, weight becomes a factor in the feet penetrating the surface layer of a seep, especially if a shallow crust has formed or the predation occurs at night when low temperatures will cause a "skin" to form over the seep.

Four of the nine species comprise 93% of all owl specimens in the collection. The relative numbers of specimens of each species vary among the pits, with each of the four most common species being the dominant species found in at least one pit. Pit 10, which is dominated by the Burrowing Owl, a primarily diurnal, terrestrial owl mostly active during the day when the asphalt seeps would be most effective as traps, produced an amazing 32% of all owl specimens.

The relative numbers of the different skeletal elements varied widely among the 31 pits preserving owls. The most common bone of the skeleton preserved is the tarsometatarsus, followed by the tibiotarsus. These bones would be those most likely to penetrate the surface of an asphalt seep in the course of predation by a pounce predator. Both the humerus and femur are preserved in higher than expected numbers, which suggests that owl carcasses were not heavily scavenged.

Although of much smaller body size than true avian scavengers, which was undoubtedly a factor in collection and preparation methodologies when the older La Brea collections were made, and although they represent only ~3% of the total number of avian specimens from Rancho La Brea, the higher number of individuals of owls compared with true avian scavengers demonstrates once again that predators dominated the Rancho La Brea paleofaunas.

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Microevolution of Jaw Shape in the Dire Wolf, *Canis dirus*, at Rancho La Brea

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ABSTRACT. The Rancho La Brea tar pits are classic fossil lagerstatten, famous for the deposition of episodic accumulations of large numbers of fossils over short intervals in the late Pleistocene. We analyzed *Canis dirus* hemimandibles from Rancho La Brea through a two-dimensional landmark-based morphometric analysis to examine size and shape changes through time. We scored 16 landmarks each on mandibles gathered from four pits: 61/67 (~13–14 ka), 13 (~17–18 ka), 2051 (~26 ka), and 91 (~28 ka). Analyses indicate size does change through time and shares a broad correlation with climate change. Largest body sizes are correlated with relatively warmer periods, whereas smaller body sizes are found in pits representative of colder climates. Shape variables—allometric size, coronoid process rotation, and molar position—also fluctuated from pit to pit. Additionally, some sexually dimorphic signals are also distinguishable among the mandibles. Global regressions of centroid size against specific molar distances indicated trends similar to those seen in the extant gray wolf (*Canis lupus*). While sexual dimorphism can be inferred, it appears to be constant over time, unlike other morphological aspects of the jaw.

INTRODUCTION

The Rancho La Brea tar pits are an excellent locality for examining late Pleistocene fossil communities. These asphaltic seeps range in age from ~50,000 to 10,000 years ago, spanning the late and terminal Pleistocene (O'Keefe et al., 2009). Each pit can be considered a distinct depositional episode in this larger time range; therefore, climate shifts can be broadly correlated with individual pits. This epoch saw numerous, extreme fluctuations in climate, as well as the demise of several genera of large mammals. The causality of this extinction event is contentious, but some combination of climate change and overkill by humans is the current consensus (Guthrie, 2006; Koch and Barnosky, 2006; Nogués-Bravo et al., 2008; Gill et al., 2009; MacDonald et al., 2012). By analyzing the structure of the fossil communities leading up to the end Pleistocene megafaunal extinction, a clearer interpretation of the causalities of this extinction may be ascertained.

The dire wolf *Canis dirus* (Leidy, 1854) was one of the last Pleistocene species to disappear during the megafaunal extinction, with radiocarbon dates of Rancho La Brea specimens dating as recent as 9850 ± 550 BP (Dundas, 1999). Furthermore, specimens from other sites date as young as 8200 ± 260 BP (Hester, 1960). Carnivores are found in higher proportions in the pits at Rancho La Brea: a ratio of 10 carnivores for every one herbivore, the opposite of what is seen in nature and at most fossil sites (Stock, 1992; Binder and Van Valkenburgh, 2010). This disparity is due to the capture mode at the tar pits, wherein one herbivore became mired in the tar and attracted a large number of carnivores, which then became mired themselves. Carbone et al. (2009) suggested a carcass domination scenario, where large, social carnivores were more likely to become entrapped due to a higher success rate of defending trapped prey against other predators. A recent study supported this hypothesis by reporting significantly higher social carnivoran abundance at Rancho La Brea compared with the fauna of Southern California and North America as a whole (McHorse et al., 2012). The most common species at Rancho La Brea is the dire wolf, comprising over 50% of the relative abundance of carnivorans there (McHorse et al., 2012). Because of the large numbers of dire wolves, they are an excellent species for the examination of shape over time.

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Here we use dire wolf mandibles to examine size and shape change and assess how these fluctuations may relate to climate change and other environmental factors.

The null hypotheses for this study are founded on the morphological variations seen in the extant gray wolf, *Canis lupus*. The wolf species are similar morphologically and behaviorally, making *C. lupus* an excellent model for the dire wolf. Previous studies on craniofacial measurements suggest that these two wolf species are not significantly different in most indices related to cranial proportions and jaw musculature, indicating similar feeding and killing behavior between the gray wolf and dire wolf (Biknevicius and Van Valkenburgh, 1996; Anyonge and Baker, 2006; Van Valkenburgh, 2007) However, *C. dirus* has larger dentition, including a more massive carnassial blade (Anyonge and Baker, 2006). *Canis dirus* also has broader zygomatic arches and relatively longer temporal fossae which suggest a slightly larger bite force from more massive temporalis muscles (Biknevicius and Van Valkenburgh, 1996; Anyonge and Baker, 2006). This dentition, in addition to larger, rounded canines, reveals that the dire wolf may have been able to resist the struggling of larger prey. Both species probably lived in packs, and they display cursorial hunting adaptations to a hypercarnivorous diet comprised primarily of ungulates, if available (Fox-Dobbs et al., 2007).

We have recently demonstrated significant shape and size difference in gray wolves with regard to geographic variation (O'Keefe et al., 2013). Gray wolves follow Bergmann's rule, an ecological trend stating that body size increases with increasing latitude and decreasing temperature (Jolicoeur, 1959; Skeel and Carbyn, 1977; Blackburn et al., 1999; O'Keefe et al., 2013). However, recent work has suggested that size differences in gray wolves are related to resource availability rather than surface to volume ratio as was originally suggested by Bergmann's rule (Geist 1987, McNab 2010). Although Bergmann's rule is predominantly seen as a latitudinal trend, this pattern may be applied temporally (Gardner et al., 2011). If dire wolves follow a temporal version of Bergmann's rule, we would expect to see the largest *C. dirus* specimens from pits with the coldest climates.

While climate may be influential in determining overall body size, other environmental effects may also affect the size and shape of dire wolf mandibles. Because canids almost solely rely on their crania in prey apprehension (Slater et al., 2009), mandibles should reflect functional changes as well. Functional changes may be induced by competition, nutritional stress, and prey preference change through time. Previous studies on dire wolf tooth breakage and wear show fluctuations between high and low breakage and wear frequencies (Binder et al., 2002; Binder and Van Valkenburgh, 2010; O'Keefe et al., 2014). High levels of breakage and wear indicate increased inter- and intraspecific competition and/or nutrient stress (decreased food availability) (O'Keefe et al., 2014; Binder et al., 2002; DeSantis et al., 2012). Because breakage and wear data reflect environmental effects, it is possible that the shape of the mandibles may change in response.

In addition to size patterns, sexual dimorphism is detectable in gray wolf skulls. Although levels of sexual dimorphism in canids are low, distinct characteristics are found in association with size variation among the sexes of *C. lupus* (Van Valkenburgh and Sacco, 2002). Females are smaller than males and have proportionally larger molars, whereas males have relatively larger coronoid processes (Jolicoeur, 1975; O'Keefe et al., 2013; O'Keefe et al., 2014). These features should be easily identifiable in the dire wolf mandibles if these ancient wolves displayed the same type and amount of sexual dimorphism. Assuming that sexual dimorphism does not vary over time, these particular signals should not segregate among pits.

Here we analyze dire wolf mandibular morphometrics to determine if shape and size remained static over time at Rancho La Brea. If change does occur, we explore these fluctuations in relation to Bergmann's rule on a temporal scale, as well as other environmental factors, and attempt to disentangle possible causalities of any observed change.

METHODS AND MATERIALS

We used two-dimensional geometric morphometrics to analyze jaws of *C. dirus*. We analyzed 157 complete, adult *C. dirus* hemimandibles. Digital photographs were taken of the labial side of specimens from Pits 91 (≈23–28 calibrated kyBP, majority of dates 27–28 kyBP; n = 22), 13 (≈17–18 calibrated kyBP; n = 36), and 61/67 (≈13–14 calibrated kyBP; n = 83) from the La Brea Tar Pits and Museum Hancock Collection (LACMHC), and Pit 2051 (≈21–30 calibrated kyBP, mean 26 kyBP; n = 16) from the University of California Museum of Paleontology at Berkeley (UCMP). We analyzed left hemimandibles only for all pits, except Pit 2051, where right hemimandibles were examined. Specimens from Pit 2051 were horizontally inversed, using Adobe Photoshop CS2 v.9.0, before analysis. All specimens were laid flat and photographed with a 5-cm scale bar. While camera angle and distance were held constant photographing LACMHC specimens, scale bars present in photographs were used to size UCMP specimen images properly to LACMHC specimen images in Adobe Photoshop CS2 v.9.0 before landmark digitization.

Table 1 Descriptions of the 16 homologous landmarks placed on *Canis dirus* hemimandibles.

1. Anterior edge of the canine at the tooth/mandible junction.
2. Posterior edge of the canine at the tooth/mandible junction. Together landmarks 1 and 2 will give the anteroposterior width of the canine.
3. Anterior edge of p1 at the tooth/mandible junction.
4. Posterior edge of the p4 at the tooth/mandible junction. Together landmarks 3 and 4 will give the length of the premolar arcade.
5. Point on the tooth/mandible junction directly below anterior edge of the talonid basin of the m1. Together landmarks 4 and 5 will give the length of the shearing area of m1.
6. Tooth/mandible junction of the posterior edge of m1. Together landmarks 5 and 6 will give the length of the grinding area of m1.
7. Posterior edge of m^2/m^3 at the tooth/mandible junction. Together landmarks 5 and 7 will give an estimate for the grinding area.
8. Anterior edge of the masseteric fossa. Disregard landmark movement in the coronal plane and focus only on movement in the anteroposterior plane.
9. Top edge of the coronoid process.
10. Point where the coronoid process meets the condyloid process. Together landmarks 8 and 10 give the total width of the masseteric fossa.
11. Posterior edge of the condyloid process. Together landmarks 1 and 11 give an estimate of the total jaw length.
12. Posterior edge of the angular process.
13. Point where the ramus of the jaw moves from a horizontal plane to a vertical plane to the angle of the jaw. Together landmarks 9 and 13 will give the height of the coronoid process.
14. Edge of mandible, directly below landmark 7. When taken with landmark 7, gives the height of the jaw in the coronal plane post-m1.
15. Edge of mandible, directly below landmark 5. When taken with landmark 5, gives the height of the jaw in the coronal plane post-p4.
16. Edge of mandible, directly below landmark 4.

We digitized 16 homologous landmarks on each specimen using the program tpsDig2 (Rohlf, 2013). Positions of landmarks were chosen to give a general outline of the mandible and capture information of functional relevance (Table 1, Fig. 1). Landmarks on the tooth row were placed on the tooth/mandible junction, so specimens with missing teeth could be included in our dataset. However, presence of the lower carnassial tooth was required in order to obtain landmark 5. Landmark 5 properly distinguishes the trigonid basin from the talonid basin of this tooth. The alveolus of the carnassial does not accurately differentiate between these basins, so the tooth itself must be present. All landmark data were collected by the same researcher (A.L.B.) to reduce bias and measurement error.

A Procrustes superimposition was performed on raw landmark *x*-*y* coordinates in Morphologika. A set of new *x*-*y* coordinates, with rotation and translation between specimens removed, was then used to calculate interlandmark relationships (Zelditch et al., 2004). To determine if the large sample size in Pit 61/67 affected the resulting Procrustes coordinates, 30 specimens from Pit 61/67 (total of 104 specimens) were randomly selected and subjected to a Procrustes superimposition. This process was replicated three times. No significant difference between the replicates and the original sample was detected; further analyses were conducted using the original sample of all 157 total specimens. Centroid size, a scaling variable, was also calculated and provided a relative representation of mandible size for each specimen. Since mandible size and overall body size in carnivorans have been shown to be highly correlated (Figueirido et al., 2011), we use centroid size as a proxy for overall body size. Differences in size between pit samples were determined through an analysis of variance (ANOVA) on centroid size.

A principal component analysis (PCA) was conducted on the Procrustes coordinates to investigate jaw shape variation within and between the pits sampled (Zelditch et al., 2004). The PCA was run in pcagen7_14a (Sheets, 2005), as well as the program JMP. A Procrustes mean specimen was generated through least squares fitting based on all data. Partial warp scores were then computed using that Procrustes mean specimen. Principal components were calculated from the covariance matrix of partial warp scores generated in pcagen7_14a and JMP. Principal component (PC) axes were used as shape variables to describe variance in shape among the specimens. Specimens were then identified by pit along each PC axis to evaluate mandibular shape. Both a Student's *t*-test and a set of analyses of variance (ANOVAs) on the first four PC scores were used to determine significant differences in shape among the pits.

Shape changes along PC axes were visualized as vectors of mean landmark position differences by 0.1 units in the positive direction (unless

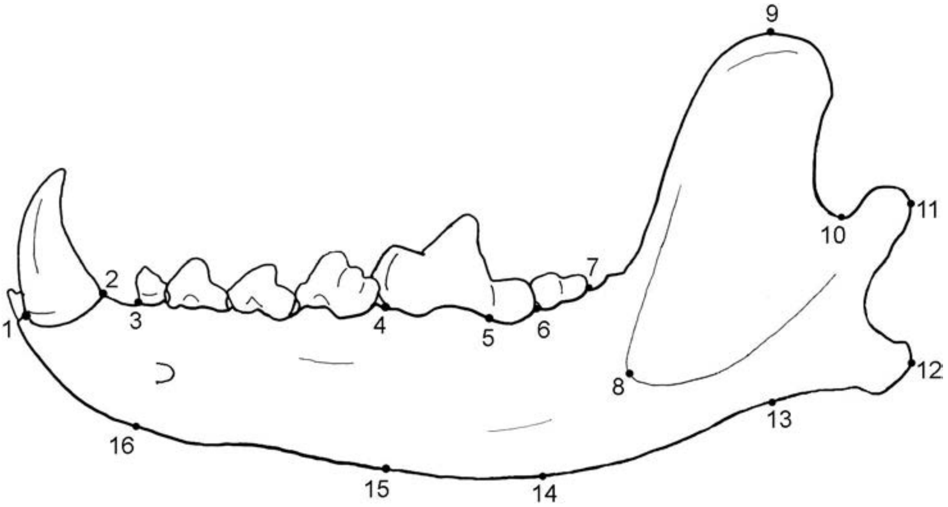

Figure 1 *Canis dirus* hemimandible in labial view. Locations of 16 landmarks are also shown. See Table 1 for corresponding list and descriptions for landmark placement.

described otherwise). The pcagen7_14a program was used to create the landmark vectors. The vectors showed the relative direction and magnitude of landmark displacement, allowing for a clearer interpretation of shape change along each PC axis. Additionally, distances between Procrustes coordinates for specific landmark combinations were calculated. These distances included the length of the grinding portion of the carnassial (between landmarks 5 and 6), the length of the second molar (between landmarks 6 and 7), and the coronoid height (between landmarks 9 and 13). Measurements of these features were analyzed to determine whether or not sexually dimorphic signals similar to those seen in *C. lupus* skulls were detectable (O'Keefe et al., 2013). The interlandmark distances chosen were regressed against centroid size to establish significant patterns of these elements in relation to overall body size. Regressions against centroid size first included all specimens and were not separated by pit. To ensure that patterns were consistent throughout all pits, regressions against centroid size were then separated by pit and examined.

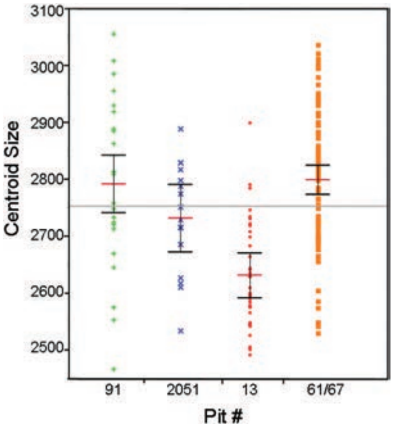

Figure 2 Plot of ANOVA of centroid size among pits; n = 157 hemimandibles. The red lines represent the estimates of the mean for each pit. Black lines indicate 95% confidence intervals. Pit 13 has a significantly smaller overall body size compared with the other three pits.

RESULTS

The ANOVA of centroid size showed that overall body size varied among the pits (Fig. 2). Pit 61/67 displayed the largest size but was significantly larger than only Pits 2051 and 13. The smallest body size was from Pit 13 and was significantly smaller than from all of the other pits. Although Pit 91 body size did not differ from either Pit 2051 or Pit 61/67, that from Pit 2051 was significantly smaller than Pit 61/67.

Thirty-two PCs resulted from the PCA, with PC1–PC6 explaining 67.2% of the variance (Table 2). While performing a PCA on the Procrustes coordinates should minimize the effect of size on shape variables, size significantly varied among the pits and should be taken into account when examining shape. For example, knowing the relationship between size and a PC axis may alter the interpretation of that axis. The first and fourth principal components are positively correlated with centroid size ($p < 0.001$, $R^2 = 0.099$ and $p < 0.0001$, $R^2 = 0.090$, respectively), whereas PC3 is negatively correlated with centroid size ($p < 0.0335$, $R^2 = 0.0288$; Table 2). Principal component 2 is not correlated with centroid size.

Table 2 One-way ANOVAs of principal components (PC) by pit. The first four PCs are shown and account for 52.8% of the variance. Regressions against centroid size are also shown. Significance at $P<0.05$ is denoted by an asterisk.

PC	% Explained	One-way ANOVA by pit	Means, T 61/67, 2051	61/67, 13	61/67, 91	13, 91	2051, 91	2051, 13	Regression, centroid size
1	17.91	F ratio 10.919, p<0.0001*	0.0157*	0.7741	<0.0001*	0.0001*	<0.0001*	0.0171*	F ratio 17.1757, p <0.0001*
2	13.02	F ratio 6.8112, p <0.0002*	<0.0001*	0.0194*	0.3131	0.3995	0.0055*	0.0216*	F ratio 1.6429, p <0.2018
3	11.92	F ratio 1.0209, p <0.3852	0.9019	0.1412	0.2246	0.9920	0.4323	0.3856	F ratio 4.6030, p <0.0335*
4	9.92	F ratio 5.8212, p <0.0009*	0.0533	0.0145*	0.0366*	0.0003*	0.0019*	0.8991	F ratio 15.3336, p <0.0001*

Principal component 1 explains 17.9% of variance and is interpreted to represent posterior jaw size increase. Principal component 1 is also correlated with size. Dire wolves scoring high on the PC1 axis have a larger jaw, largely represented by vectors from landmarks 8–13, in relation to the size of their teeth, as represented by vectors from landmarks 1–7. Negative values on the PC1 axis indicate animals with small jaws relative to tooth size. Significant differences among pits on PC1 were identified. Pit 91 significantly segregated from all other pits, as did pit 2051. Pits 13 and 61/67 were not different on PC1.

The second principal component represents significant reorientation of the jaw. Principal component 2 explains 13% of the variance and also displays segregation among groups. Negative loading on PC2 is associated with two shape changes: (1) the coronoid process and posterior portion of the jaw shifting both anteriorly and ventrally in a counterclockwise fashion and (2) the anterior portion of the jaw near the canine shifting posteriorly and dorsally in a clockwise rotation (Fig. 3). Positive loadings are associated with the anterior and posterior portions of the jaw rotating away from each other. Pit 2051 differed from all other pits, displaying the highest degree of the anterior and posterior portions of the jaw rotating in toward each other. Pit 61/67 differentiated from Pit 13 as well, with Pit 13 specimens displaying more reorientation of the anterior and posterior portions of the jaw toward each other than those from 61/67. However, Pit 13 did not differ significantly from Pit 91. A plot of the scores of the first two PCs can be seen in Figure 3.

Principal component 3 explains 11.9% of the variance and shows no significant differences among pits. Negative loadings on PC3 are associated with increases in canine size and length of the tooth row relative to the somatic jaw. Molars shift together posteriorly, with a slight decrease in size of the second molar. Positive loadings are associated with decreases in canine size and overall tooth row length.

Principal component 4 explains 9.9% of the variance and is correlated with size. Positive values on PC4 are associated with slight increases in jaw and tooth row length. Negative values are associated with a decrease in jaw size, especially the coronoid height, and a shift of the molar arcade forward. On this axis, wolves from Pit 91 are distinct from all other pits. Pit 61/67 differs from Pit 13, but not Pit 2051. Pits 13 and 2051 are not distinct. It is important to note that the landmark 13 vector dominates this PC axis; this is relevant because the variance of this landmark in the x dimension regarding the Procrustes coordinates is an order of magnitude greater than any other landmarks' variance in the x or y dimension. The placement of landmark 13 is more

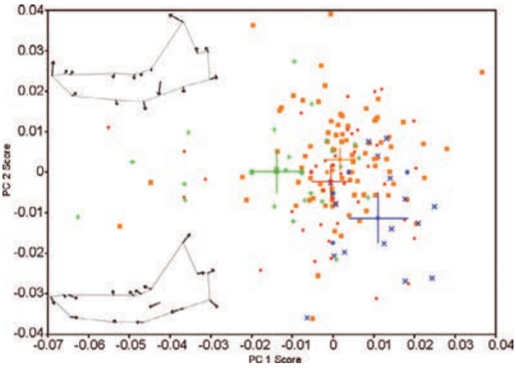

Figure 3 Plot of PC1 vs. PC2 scores. Crosses represent the mean pit score (center) and 95% confidence intervals. PC1 vectors are from the centroid in a positive direction, whereas PC2 vectors are from the centroid in a negative direction. Colors associated with pit numbers are as follows: orange, 61/67; red, 13; blue, 2051; green, 91.

subjective in the *x* dimension than any other landmark. However, landmark 13 still contributes to size decrease with negative values on the *x*-axis. The variance of landmark 13 in the y-dimension was similar to that of the other landmarks; this is important because the main purpose of the landmark 13 was to acquire coronoid height in conjunction with landmark 9.

The length of the grinding portion of the carnassial and the length of the second molar were negatively correlated with centroid size ($p = 0.0023$, $R^2 = 0.058$; $p = 0.0003$, $R^2 = 0.082$, respectively). These patterns were consistent throughout each pit. In terms of sexual dimorphism, these results are consistent with trends seen in the extant gray wolf. *Canis lupus* males have relatively larger body sizes and relatively smaller molars. The trend of decreasing molar size with increasing centroid size can be seen in both of these regressions (Fig. 4). While it is not possible to discern *C. dirus* male specimens from female specimens, these trends suggest that the dire wolf displayed the same degree of sexual dimorphism in their molars as extant gray wolves.

The same result does not hold for coronoid height. Male gray wolves have been shown to have relatively taller coronoid processes. As such, we expected to see a positive correlation of coronoid height with centroid size based on these trends. Regressions against centroid size, both

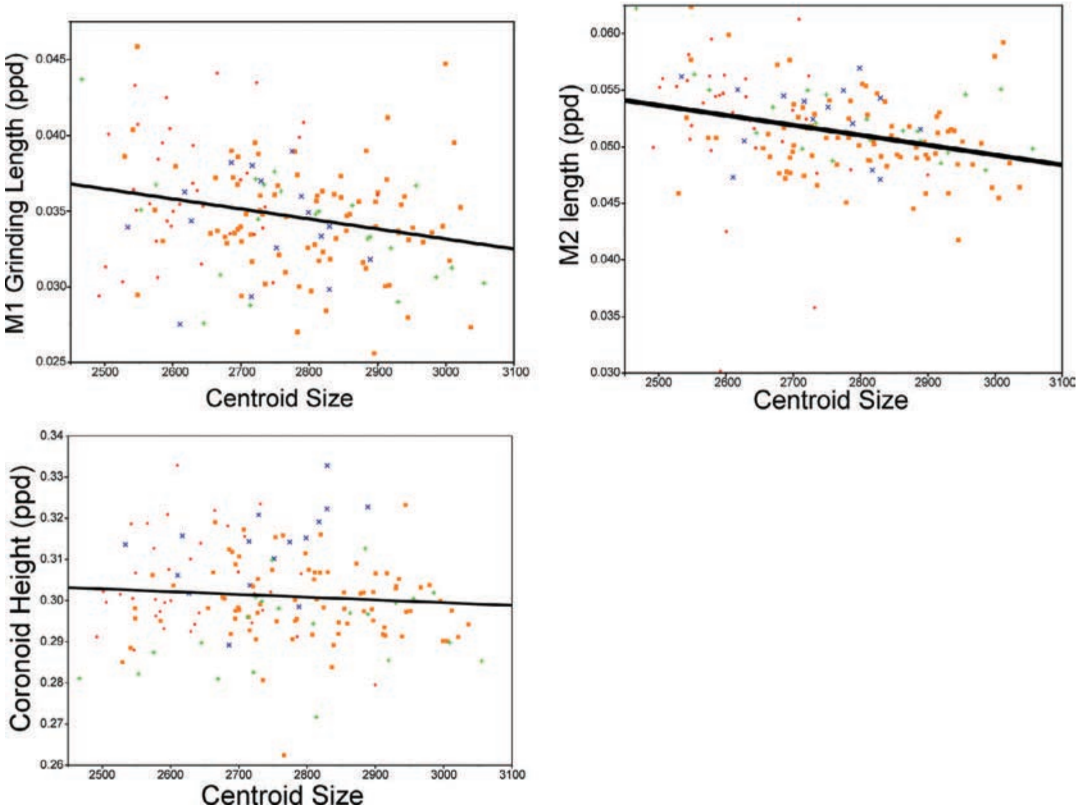

Figure 4 Global regressions of the length of the grinding portion of the carnassial against centroid size ($p = 0.0023$, $R^2 = 0.058$), the length of the second molar against centroid size ($p = 0.0003$, $R^2 = 0.082$), and the coronoid height against centroid size ($p = 0.302$, $R^2 = 0.007$). Colors associated with pit numbers are as follows: orange, 61/67; red, 13; blue, 2051; green, 91.

separated and not separated by pit, do not display a significant trend (global regression: $p = 0.302$, $R^2 = 0.007$).

DISCUSSION

Both shape and size in *C. dirus* change through time in Rancho La Brea, showing that evolution is occurring. Mean body size averages vary from pit to pit; the largest body size occurs in Pit 61/67, and wolves from Pit 91 are only marginally smaller than those from 61/67. Significantly smaller wolves are found in Pit 13. By examining Greenland Ice Core Project (GRIP) and North GRIP (NGRIP) climate records, we can begin to evaluate size and climate relationships, such as Bergmann's Rule (NGRIP, 2004). Pit 61/67 had the warmest climate, overlapping in deposition with the Bølling-Allerød warm interval, whereas Pit 13 was deposited during a relatively cool interval near the last glacial maximum. According to NGRIP data, Pit 2051 represents the coldest interval of this sequence, while Pit 91 is thought to be associated with rapid warming events, labeled Dansgaard-Oeschger events (Rahmstorf, 2003; Meachen et al., 2014; O'Keefe et al., 2014). However, more precise dating of all of these pits, especially Pits 61/67 and 13, will solidify these correlations. From these size changes it appears dire wolves did not follow a temporal Bergmann's rule. Instead, body size in relation to climate is opposite to what Bergmann's rule would have predicted; the colder pits (2051 and 13) display smaller body sizes and the warmer pits (91 and 61/67) show larger body sizes. This is particularly interesting because the gray wolf, our model species for the dire wolf, follows Bergmann's rule (O'Keefe et al., 2013). Many carnivores do not follow Bergmann's rule, including some canids, such as coyotes (Meiri and Dayan, 2003; Meachen and Samuels, 2012). This is thought to be related to levels of primary productivity and food availability rather than climate (Huston and Wolverton, 2011; Yom-Tov and Geffen, 2011). Huston and Wolverton (2011) suggest that carnivores may be indirectly affected by the amount of ecological and evolutionary net primary productivity (eNPP) during a given period of time. Higher outputs of eNPP, possibly due to warmer climatic conditions, may increase food availability for primary producers. With an increase of food for primary producers, larger populations of herbivores can be supported, which increases food availability for carnivores and allows for body size increases. Changing levels of primary productivity due to climate would have a cascading effect on carnivores, such as the dire wolf (Meachen et al., 2014).

Mandible shape also varies significantly from pit to pit. Fluctuating environmental pressures, such as changing nutrient stress, are a leading cause in changing the appearance and/or rate of development, or heterochrony, within a population (McNamara, 1990). Neoteny, decreased somatic growth relative to sexual maturation, in canids is recognizable through the identification of proportionally shorter snouts, smaller teeth, and a more steeply rising forehead region compared with the ancestral population (Gould, 1977; Paquet and Carbyn, 2003; O'Keefe et al., 2014). The largest amount of variance in shape is shown along PC1, representative of an allometric size vector, which displays evidence of neoteny in the dire wolf. A recent study on dire wolf cranial morphometrics found higher incidences of tooth breakage and wear (indicative of increased nutritional stress), along with neotenic characteristics in wolves of Pit 13. These specimens were also significantly smaller than those of other pits (O'Keefe et al., 2014). Our results are concurrent with this study; animals we examined are smallest in Pit 13. However, wolves of Pit 91 also had high tooth breakage and wear frequencies but were relatively large, using the centroid size of the entire skull as a metric (O'Keefe et al., 2014). These authors suggest nutrient stress for Pit 91 wolves was less severe than that for Pit 13 wolves or began after dental maturity was reached. Although wolves from Pit 91 were the second largest in this study, PC1 scores from our data suggest that Pit 91 wolves also show neotenic characteristics. These wolves have the smallest jaws relative to the size of their teeth. Since modern wolves reach dental maturity before they reach full somatic growth, it can be inferred that Pit 91 wolves experienced late-stage growth truncation (Kreeger, 2003; O'Keefe et al., 2014). This pattern was subtle but identifiable in the skull data.

The shape changes along PC1 primarily show allometric jaw growth but may contain some evolutionary effects as well. Pit positions along PC1 may also be in response to competition and prey availability. Taller coronoid processes allow increased area for the attachment of the temporalis muscle, which increases the speed and force of jaw closure (Anyonge and Baker, 2006; Wang and Tedford, 2008). Wolves of Pits 61/67 and 2051 have the largest jaws, including the coronoid process, relative to their teeth. Increased coronoid height suggests that these wolves are catching larger, faster prey, and tooth breakage and wear indicate that they are not under nutrient stress (O'Keefe et al., 2014). It follows that these wolves have a mechanical advantage in shearing when tooth breakage and wear indicates that they are not under nutrient stress. Wolves of Pits 91 and 13 have relatively the smallest jaws in comparison, including their coronoid processes. Having shorter coronoid processes decreases the mechanical advantage of the temporalis muscles in relation to the masseter muscle. Additionally, shorter, broader jaws produce larger bite forces. These wolves are more masseter dominated, which is active in crushing at the molars. It follows that these wolves are probably consuming more bone, making crushing abilities necessary, or prey preference was different in comparison to pits 61/67 and 2051.

In terms of shape, Pit 2051 wolves are interesting in that they discretely segregate from the other pits on the first two PC axes (Fig. 3). Pit 2051 wolves have anteroventrally oriented coronoid processes, while the anterior portion of the jaw orients posteriorly and dorsally. Additionally, these wolves do not display signs of neoteny, having the largest somatic jaws relative to their teeth. Wolves of Pit 13 score closest to Pit 2051 on the PC2 axis, which demonstrates reorientation of both ends of the jaw. Evidence of neoteny is present in Pit 13; further directional change of Pit 13 wolves toward the shape seen in Pit 2051 may have been hindered by nutritional stress or other factors. Because Pits 13 and 2051 were deposited during relatively colder climates than the other pits, it is possible that this anterior rotation of the terminal ends of the jaw may have been an adaptation for hunting in cold climates. The ecological drivers of the shape difference displayed in Pit 2051 are not clear, but our PCA analysis determined that shape evolution is evident.

Our results suggest that sexual dimorphism is present in the molars of *C. dirus* mandibles. PC3 seems to capture sexually dimorphic molar signals. This axis does not discriminate among the pits, and vectors are associated with movement and size fluctuations in the molars. PC3 is also significantly associated with size. Negative loadings (decrease in second molar size) on PC3 are associated with larger centroid size values; this would follow the trend we expected to see given the observed dimorphism seen in modern wolves. While PC3 represents sexual dimorphism, there is no clear evidence for dimorphism on PC4. PC4 is correlated with centroid size and captures shifts in the tooth row and slight fluctuations in jaw size. However, there is distinct segregation among the pits on this axis. We expect sexual dimorphism to remain constant through time, so variables indicating dimorphism should not differentiate between pits.

Regressions of molar interlandmark distances against centroid size also indicate sexual dimorphism. The length of the talonid basin, or grinding area, of the carnassial and the length of the second molar both decrease with increasing centroid size (Fig. 4). Small body sizes have relatively larger molars, which is consistent with patterns found in *C. lupus*. These trends are also evident in each individual pit, indicating this pattern did not change through time. Our molar interlandmark regressions agree with our interpretation of PC3. Both PC3 and molar regressions display the same relationship between centroid size and molar size and are not time dependent, indicating a sexually dimorphic molar signal in the dire wolf. However, our results do not support a sexually dimorphic signal in the coronoid process, as seen in the gray wolf. Our global regression shows no correlation between coronoid height and centroid size (Fig. 4). There are several possibilities for not detecting this trend in the dire wolf specimens. First, the coronoid height signal was not as strong as the molar signal in gray wolves, so we may not have the power to detect this pattern. Second, the coronoid process is subject to evolutionary change in orientation, as seen in PC2, which may be masking the signal. Third, the dire wolf may not display this trend at all and is not sexually dimorphic in coronoid height like *C. lupus*.

In summary, *C. dirus* mandible shape and size, and therefore overall body size, do not remain constant throughout time. Size comparisons reveal that dire wolves were largest in pits with warmer climates and smaller in cooler pits, the opposite of what a temporal Bergmann's rule would have predicted. Because the dire wolf does not seem to follow climate correlations similar to the gray wolf, its extant counterpart, it is appropriate to explore other environmental factors as possible causalities by examining shape change. Overall mandible shape shows certain microevolution, and nutrient stress and adaptations relating to food availability and competition are also influential factors. Because Pleistocene climate records reveal extreme variability, more precise dating of the La Brea tar pits would help more accurately define the existing environmental conditions of each deposit.

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A Pathological Timber Wolf (*Canis lupus*) Femur from Rancho La Brea Indicates Extended Survival After Traumatic Amputation Injury

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ABSTRACT. A fragmentary timber wolf (*Canis lupus*) femur from the late Pleistocene Rancho La Brea asphalt deposits of Los Angeles, California, shows evidence of healed traumatic injury incurred well before the death of the individual. The specimen, from San Bernardino County Museum (SBCM A3356-1), consists of proximal and metaphyseal portions of the right femur, including the complete femoral head, neck, and greater trochanter. The fragment terminates abruptly in a well-remodeled surface oriented caudally and oblique to the shaft axis. This surface consists primarily of smooth cortical bone that has almost completely covered the underlying trabecular bone. Two possibilities arise from the observation: (1) this fragment represents only the proximal portion of a pseudarthrosis (false joint) resulting from osseous nonunion of a femoral fracture, or (2) a complete amputation event occurred with subsequent healing of the remaining bony shaft. Either case indicates that the animal survived for a significant amount of time after the traumatic injury was inflicted. A premortem lesion on the caudomedial femoral head suggests that forced hyperextension of the hind limb occurred simultaneously with the femoral shaft breakage. A violent bite injury with subsequent shearing, torsion, and hip hyperextension provide the best fit for all the osseous evidence. The fact that the proximal femoral segment had adequate time to heal means the violent event could not have been itself the cause of death. Furthermore, that the individual lived for a significant amount of time postinjury means it must have retained adequate hunting and/or scavenging ability to survive. Alternatively, pack or other social provisioning and protection may have facilitated or, minimally, permitted the healing of the injured individual. Because no functional bony connection to the more distal limb elements appears to have been present, the individual must have had either an entirely missing or useless lower right leg, and may have adopted a completely tripodal lifestyle.

INTRODUCTION

The Rancho La Brea (RLB) asphalt deposits have the richest known concentration of Pleistocene terrestrial vertebrate fossils in the world. Nearly four million fossils representing over 660 species of animals and plants have been recorded from the "tar pits" in episodic excavations spanning more than a century (Stock, 1992). The sheer volume of vertebrate fossils preserved at RLB has enabled a wide variety of paleobiological, paleoecological, and paleopathological studies to be conducted over many decades. In this case the exceptional preservation afforded at RLB allows not only paleopathological assessment of an unusual specimen of timber wolf, but also permits reasonable speculation regarding part of that individual's life history.

The RLB assemblage is dominated by large carnivorans, particularly dire wolves (*Canis dirus*), saber-toothed cats (*Smilodon fatalis*), and coyotes (*Canis latrans*) (Stock, 1992). In contrast, timber wolves (*Canis lupus*) are comparatively rare at RLB, somewhat anomalously given the evident suitability of Pleistocene Los Angeles for carnivorans—especially canids—and the demonstrated proclivity

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of the RLB asphalt seeps to entrap and preserve these animals.

Here, we report and diagnose a pathological femur of *C. lupus* from RLB—the first published record of pathological remains of *C. lupus* from the site. Previous paleopathological investigations at RLB have generally been confined to specimens of much more abundant species (e.g., Moodie, 1930; Heald, 1986; Van Valkenburgh, 1998; Rooney and Scott, 1998; Binder et al, 2002; Shaw et al., 2008). This study therefore offers a rare opportunity to examine ancient injury in a substantially less abundant member of the assemblage.

MATERIALS AND METHODS

The proximal femur under study here, from the San Bernardino County Museum (SBCM A3356-1), was identified from a collection of fossils from RLB originally collected by the University of California between 1906 and 1913. These fossils were subsequently housed in the vertebrate paleontology collections of the Department of Biology, University of California, Los Angeles. In 1994, this collection was transferred to the Department of Biology, California State University, San Bernardino. SBCM A3356-1 was located in this collection among numerous partial and damaged limb elements ascribed to *C. dirus,* the dominant canid at RLB. Preliminary cleaning suggested that the partial element was not simply broken, but instead was a fractured and subsequently healed proximal femur. Subsequent visual comparison with specimens of *C. dirus* and specimens of extant *C. lupus* indicated that SBCM A3356-1 is closer in size range to the latter species, although it does exhibit a massive and rugose greater trochanter resembling the condition observed in *C. dirus*. Based upon size, it is here inferred to represent an individual of *C. lupus*.

Preparation included soaking the specimen for one week in GenTech, an *n*-propyl bromide (90%), 1,2-butylene oxide (2%), and a proprietary compounds (8%) solvent. Complete asphalt removal was accomplished using a toothbrush and dental pick.

Figure 1 SBCM A3356-1, *Canis lupus*, proximal right femur in anterior (left) and posterior (right) views.

PALEOPATHOLOGICAL ASSESSMENT

Various features bear on the pathology afflicting SBCM A3356-1 (Table 1). Most evident is the very advanced healing of the truncated femoral shaft in an oblique plane, distal to the neck of the femur medially and to the greater trochanter laterally (Fig. 1, right; Fig. 2, middle). Elevated rounded nodules form the flaring edge of a surface, whose center is largely smooth and planar. The edges have been distorted and broadened by advanced healing. There is some minimal exposure of underlying trabecular bone (<10% of the surface). The rounded and coarsened trabeculae are indicative of remodeling. No evidence of postmortem breakage is apparent along this plane or its edges. This contrasts with the caudal femoral head, where the complete lack of bone reaction on the exposed femoral head trabeculae indicates that this lesion is due to postmortem damage. No eburnation indicative of bone-on-bone rubbing or other indicators of *in vivo* bony articulation are evident. All evidence suggests that the marked alteration of this surface is the sequela of

Table 1 Pathological features of SBCM A3356-1, *Canis lupus*.

Feature	Description	Differential diagnosis
Plane of femoral truncation	Oblique well-remodeled surface with lateral edges distorted and broadened by advanced healing.	• Healed fracture • Amputation injury
Femoral head lesion	Oval, remodeled lesion with depressed center and slightly elevated margins on caudomedial femoral head.	• Dislocation injury • Localized traumatic necrosis • Primary avascular necrosis
Enthesopathy of greater trochanter	Projecting osteophytes at areas of gluteus medius/minimus insertion.	• Traumatic muscle injury • Various congenital and metabolic muscle-ossifying conditions
Marginal joint nodule	Proliferative excrescence at inferior femoral head margin.	• Traumatic joint capsule injury • Osteoarthritis
Erosive trabecular exposure	Caudal femoral head planar lesion.	• Postmortem damage pseudopathology

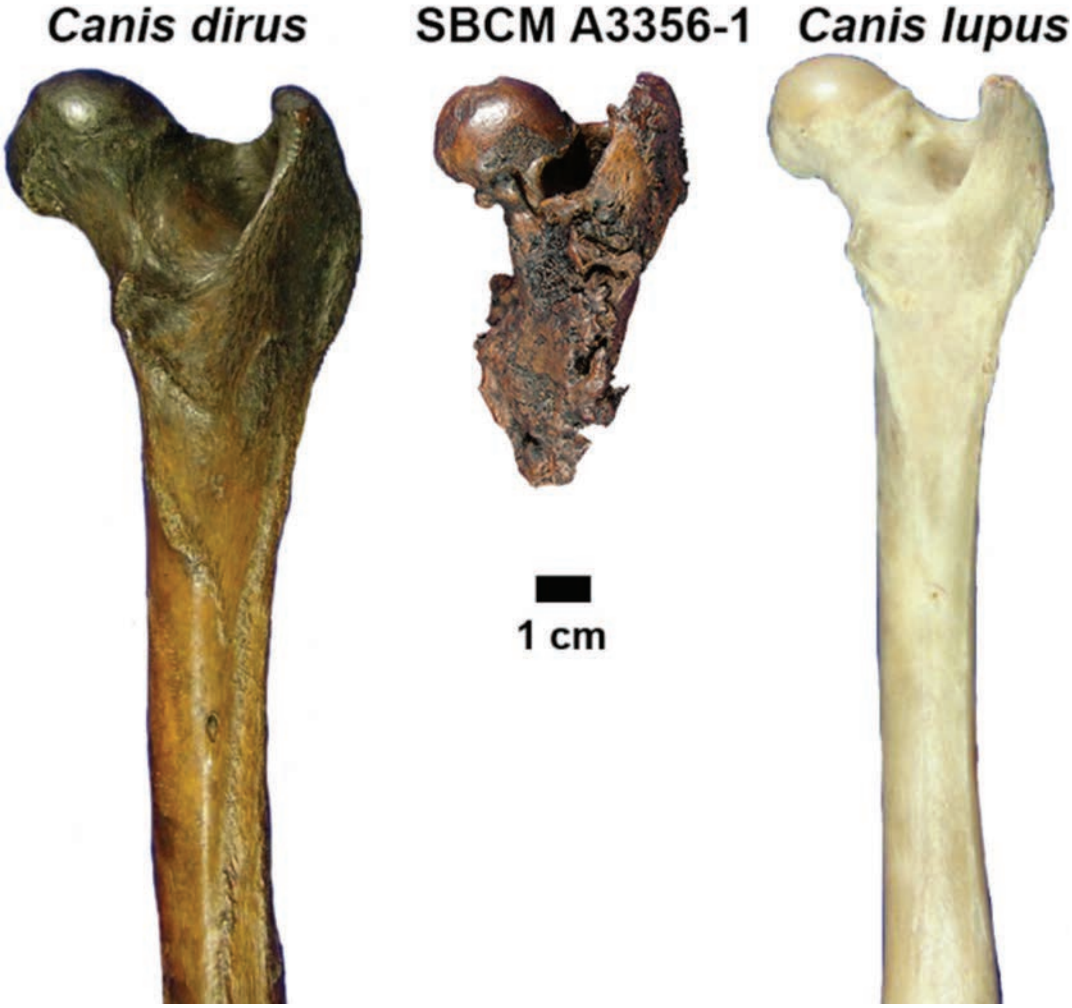

Figure 2 Anterior views of proximal portions of right femur of *Canis dirus* (left); SBCM A3356-1, pathological RLB *Canis lupus* (middle); and extant *C. lupus* (right).

complete oblique fracture and the separation of the femur distal to the break.

The femoral head itself provides additional clues to the injury scenario. The lesion on the posterior femoral head medioinferior to the fovea (see Table 1) is consistent with localized cartilage crush injury as a result of forceful hip hyperextension. Aside from this lesion and the postmortem pseudopathology, the femoral head itself is smooth and nondeformed, with no indications of osteoarthritis or avascular necrosis. The latter is significant in that the injury must have spared the medial circumflex femoral artery, which runs along the inside of the intertrochanteric crest and supplies the femoral head. Indeed, given the magnitude of the injury, the femoral head is remarkably intact. Some degree of hip movement must have been present in the individual in order to maintain cartilage nutrition and thus integrity postinjury. The area of the gluteus maximus femoral insertion is disrupted, but the gluteus medius and gluteus minimus insertions are intact and indeed marked by enthesophytes, consistent with the bite/hip hyperextension scenario.

Two separate possibilities are proposed to explain the observed pathological condition: (1) a pseudarthrosis (false joint) resulted from osseous nonunion, where bone ends remained separated by soft tissue in life, or (2) a complete amputation event occurred with subsequent healing of the remaining bony shaft. Either case indicates that the animal survived for a significant amount of time—likely years—after the traumatic injury was inflicted. The lack of femoral head degeneration suggests the hip joint was capable of some movement subsequent to the injury.

The oblique nature of the break and its location suggest that the bone failed as a result of extreme shear and torsional forces. The most obvious candidate is the violent snapping of the limb by another, larger carnivore. Fracture subsequent to fall injury at high velocity remains a possibility, although the fracture location and associated hyperextension damage to the femoral head render this scenario less likely. Massive trauma inflicted by large prey animals such as *Equus* or *Bison* is also a possibility, although, again, the hyperextension injury to the hip seems to slightly favor the bite injury hypothesis.

Several carnivoran candidates are larger than timber wolves in the fauna from RLB. The most abundant are *C. dirus*, whose calculated bite force is estimated at 129% of that of extant gray wolves (Therrein, 2005). Felids, include two species of saber-toothed cats (*S. fatalis* and *Homotherium serum*), and the North American lion, *Panthera atrox*, are also candidates—the bite force and bone shearing ability of the latter make it a prime candidate. Ursids, including short-faced bears (*Arctodus simus*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos horribilis*) are also present and could inflict such an injury. Intraspecific violence cannot specifically be ruled out, although the magnitude of forces necessary to inflict the observed injury seem to indicate a larger predator.

The fact that the proximal femoral segment had adequate time to heal means the violent event itself could not have been the cause of death. That the individual lived for a significant amount of time postinjury means it must have retained adequate hunting and/or scavenging ability to survive. Alternatively, if it was a member of a pack or other social group, that group may have facilitated, or minimally tolerated, the inclusion of the injured individual. Because there is no functional connection to the more distal limb elements, the individual must have had either a useless lower right leg, or may have adopted a completely tripodal lifestyle.

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Dental Microwear Textures of Carnivorans from the La Brea Tar Pits, California, and Potential Extinction Implications

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ABSTRACT. The tar pits at Rancho La Brea in southern California boast the richest fossil collection of Pleistocene carnivorans in North America. This important carnivoran collection accumulated as the result of a "carnivore trap" created by asphalt seeps, or tar pits. Tar pits such as those at La Brea provide rare opportunities to examine the ecology and evolution of carnivorous mammals—including many that went extinct during the terminal Pleistocene extinction event. We use this rich fossil record, resulting from 100 years of excavations, to study the dietary ecology of Pleistocene carnivorans and assess the hypothesis that these species were stressed just prior to their extinction. Specifically, through the examination of dental microwear textures on tooth enamel, we assess dietary behavior, including durophagy (e.g., bone processing) in an extinct canid, the dire wolf *Canis dirus*, and synthesize recent work on the dental microwear textures of extinct felids (the saber-toothed cat *Smilodon fatalis*, the extinct American lion *Panthera atrox*), an extant felid that survived the extinction (the cougar, *Puma concolor*), and an extinct ursid (the North American giant short-faced bear *Arctodus simus*). Baseline results from extant carnivorans reveal the need to analyze different teeth depending on phylogenetic relationships and functional morphology, with ursids and canids requiring analysis of second lower molars (teeth engaged in crushing or grinding) in contrast to lower first molars in feliforms. In sum, dental microwear texture attributes that are most indicative of bone consumption (i.e., complexity and textural fill volume) suggest that carcass utilization by La Brea carnivorans was similar to comparable living analogs. Thus, in contrast to earlier studies, we see no evidence that large carnivorans were more stressed, or dietary resources were more depleted, just prior to the extinction event. Further, *Puma concolor* survived the extinction, and results from both La Brea and extant specimens reflect the varying generalist diet for this species; this versatility may have been key to its survival.

INTRODUCTION

The La Brea Tar Pits in southern California (USA) have yielded one of the richest Late Pleistocene fossil collections in North America, represented by ~600 species and over 3.5 million specimens (Stock, 2001). After 100 years of excavation, this site reveals an extraordinary fossil record allowing researchers to better resolve the paleoecology and paleobiology of ice age flora and fauna in southern California over the past ~35,000 years (Stock, 2001; O'Keefe et al., 2009). The La Brea Tar Pits are most famous for their high abundance of fossil carnivorans, with up to ~90% of excavated mammals belonging to the order (Stock, 2001). Unlike most other fossil sites, where herbivores are typically more abundant, the asphalt seeps (more commonly referred to as "tar") found at La Brea functioned as carnivore traps. The general hypothesis is that prehistoric prey became stuck in the tar and this attracted carnivores; the carnivores also became mired, luring more and more carnivores to their entrapment and subsequent preservation.

Of the carnivorans present at La Brea, the dire wolf (*Canis dirus*) and saber-toothed cat

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(*Smilodon fatalis*) are most abundant (Stock, 2001; Carbone et al., 2009). Even carnivorans present in lower relative abundances at La Brea consist of some of the best preserved and best represented specimens from North America. For example, La Brea has produced more giant short-faced bear (*Arctodus simus*) individuals than any other site (Schubert et al., 2013), despite a relative abundance of only 1% (compared with other carnivorans at all pits; Carbone et al., 2009). Thus, the La Brea Tar Pits are a treasure trove for the study of Late Pleistocene carnivorans and can address hypotheses about their extinction.

The cause of the selective extinction of large-bodied carnivorans and other megafauna (animals with mass >45 kg) across the globe during the Late Pleistocene is hotly debated, with explanations including human hunting, climate change, or some combination of the two (e.g., Martin and Klein, 1984; Barnosky et al., 2004; Wroe et al., 2004, 2013; Koch and Barnosky, 2006). One hypothesis proposes that prehistoric predators may have competed directly and/or indirectly with humans for similar prey, as potentially occurred in 20th century rural Uganda (Treves and Naughton-Treves, 1999). To test this idea, Van Valkenburgh and colleagues quantified the relative frequency of broken teeth in extinct carnivorans (e.g., Van Valkenburgh and Hertel, 1993; Van Valkenburgh, 2009; Binder and Van Valkenburgh, 2010) to infer relative degrees of carcass utilization. High incidences of broken teeth, especially canines, were documented in La Brea carnivorans compared with their modern relatives (Van Valkenburgh and Hertel, 1993; Van Valkenburgh, 2009). Differences between extant and extinct taxa were quite extreme, with more than one-third of the extinct American lion (*Panthera atrox*) specimens having broken canines, compared with only 5%–10% of extant felids (Van Valkenburgh, 2009). These observations were used to suggest that La Brea carnivores were consuming carcasses more fully during "tough times" to compensate for food shortages (Van Valkenburgh and Hertel, 1993; Van Valkenburgh, 2009). This inference further suggests that large carnivorans and humans may have competed for prey and/or that prey resources were more limited during the Late Pleistocene.

Over the past decade, carnivoran research at La Brea has continued to expand on the classic works by Merriam (1911, 1918), Merriam and Stock (1932), and other early researchers and has employed studies of cranial and postcranial morphology to better understand carnivoran phylogenetic relationships and functional morphology (e.g., Christiansen and Harris, 2009, 2012; Meachen-Samuels, 2012). The paleobiology of extinct carnivores has also improved with the use of tools such as geochemistry and dental microwear. The stable isotope biogeochemistry work of Coltrain et al. (2004) suggests that carnivorans, including *C. dirus*, *S. fatalis*, and *P. atrox*, competed for similar prey items and were equally reliant on herbivorous ruminants and nonruminants. Most recently, dental microwear texture analysis (DMTA) was employed to better understand the dietary behavior of La Brea carnivorans and test the idea that tough times required La Brea carnivorans to consume carcasses more fully. As opposed to earlier dental microwear work that relied on human observers counting pits and scratches on scanning electron microscope images (i.e., Van Valkenburgh et al., 1990; Anyonge, 1996), DMTA quantifies wear in three dimensions and uses scale-sensitive fractal analysis (SSFA) to assess the topographic features produced when processing food materials (e.g., Ungar et al., 2003; Scott et al., 2005, 2006). Direct comparisons of two-dimensional and three-dimensional microwear methods in extant carnivores and herbivores reveal the advantages of using three-dimensional DMTA to assess the physical properties of food items consumed by carnivorans (DeSantis et al., 2013). For example, pitting (typically found in high abundances in hard-object consumers) is an unreliable dietary indicator in carnivorans, because increased pitting was not always observed in extant taxa engaging in durophagy (i.e., bone processing) and was occasionally found in lower numbers (often as larger pits) relative to bone avoiders (DeSantis et al., 2013). However, SSFA is able to successfully differentiate between hard object feeding and tough object feeding, which in extant carnivores reflect bone and flesh, respectively (Schubert et al., 2010; DeSantis et al., 2012, 2013).

Recent DMTA studies have focused on a variety of La Brea carnivorans (i.e., felids and a canid that went extinct, a felid that survived the Late Pleistocene extinction, and an extinct ursid), yet separate studies of these taxa have not been integrated into one synthetic review. Here, we build off of the work of Schmidt (2011) on the dental microwear textures of *C. dirus* compared with a modern canid baseline and further synthesize dental microwear evidence provided by dominant carnivorans at the La Brea Tar Pits in southern California. We aim to improve understandings of the paleobiology of Late Pleistocene carnivorans and clarify potential reasons for the extinction or survival of these taxa.

BACKGROUND OF THE DIRE WOLF

The dire wolf (*C. dirus*) is a common species in Pleistocene assemblages and represents one of the many large carnivores that existed during the epoch (Kurtén and Anderson, 1980; Dundas, 1999). The species occurred across the Americas and lived in a variety of environments, including forested areas and open grasslands at elevations ranging from sea level to 2,255 m (Dundas, 1999). *Canis dirus* is the most common canid and carnivoran at the La Brea Tar Pits (Stock, 2001; Carbone et al., 2009). It has been described as resembling a large gray wolf (*Canis lupus*) with a broader and more robust skull and dentition (Anyonge and Baker, 2006). Morphological research concerning sexual dimorphism of dire wolves suggests that they were pack oriented and likely shared similar behaviors of sociality as modern gray wolves (Van Valkenburgh and Sacco, 2002). Specifically, they were similar to most canids, with a low level of sexual dimorphism exhibited in the canine, suggesting a pair-bonded breeding system (Van Valkenburgh and Sacco, 2002).

Although similar in cranial and dental morphology (Anyonge and Baker, 2006), dire wolves have been proposed to differ from *C. lupus* in their degree of bone consumption (Biknevicius and Van Valkenburgh, 1996). Analysis of canine fracture frequencies of La Brea dire wolves indicates that ~19% are broken (Van Valkenburgh, 2009). The extant, durophagous African wild dog (*Lycaon pictus*) only exhibits 4.2% of broken canines, while the extant coyote (*Canis latrans*) and gray wolf, *C. lupus*, both exhibited a broken canine frequency of 9.8% (Van Valkenburgh, 2009). Previous studies employing DMTA questioned the inference that the frequency of broken canines directly reflects degree of carcass utilization (DeSantis et al., 2012), and we further assert this concern here. As an alternative hypothesis, a higher frequency of broken canines may have resulted from the acquisition and consumption of larger prey.

If dire wolves engaged in significant bone consumption, it is expected that they would also exhibit morphological features indicative of such behavior. Van Valkenburgh (2007) suggested that bone consumers evince dome-shaped skulls, a prominent sagittal crest, postcarnassial molars that can be reduced in size and number, and somewhat shortened snouts to increase the mechanical advantage of jaw-closing muscles. Dorsoventral deepening of the dentaries in species that consume bone was also noted, which may be a response to high loads placed on the jaws during bone cracking (Biknevicius and Ruff, 1992). There has also been an observed preference in utilizing posterior teeth during hard-object feeding, which has likely led to a thickening of the mandible in the posterior region of the dentary where these bone-crushing teeth are located. Both *C. dirus* and *C. lupus* are suggested to have used postcarnassial molars instead of the anterior premolars for bone consumption (Biknevicius and Van Valkenburgh, 1996). According to Anyonge and Baker (2006), the dire wolf shared some similarities in jaw strength and functionality with the occasional bone-consuming gray wolf; however, it also shared characteristics with the durophagous spotted hyena (*Crocuta crocuta*) and the extinct borophagine *Borophagus secundus*. The skull anatomy of *C. dirus* also suggests enhanced jaw musculature compared with *C. lupus* (Anyonge and Baker, 2006), and it has been estimated that the dire wolf had one of the largest canine bite forces among extinct and extant placental carnivorans (Wroe et al., 2005).

ECOLOGY OF COMPARATIVE CANIDS

The family Canidae is described as a diverse group of carnivorans distributed across the globe and exhibiting a wide range of body weights, habitat preferences, and phenotypic appearances (Van Valkenburgh and Koepfli, 1993; Geffen et al., 1996; Johnson et al., 1996; Wang and Tedford, 2008). It has been hypothesized that canids originated in North America and then dispersed to other continents during the Miocene (Wang, 1994; Munthe, 1998; Wang et al., 1999; Wang and Tedford, 2008). Currently, only gray wolves, coyotes, and red foxes (*Vulpes vulpes*) are sympatric in most of North America (Johnson et al., 1996). Just like their habitat preferences, the diet of this family has been described as highly variable, with most species considered to be opportunistic feeders; but some are specialized frugivores, insectivores, or hypercarnivores (Van Valkenburgh and Koepfli, 1993). Further, canids demonstrate a large amount of variation in their social structure and reproductive behaviors that are usually based on ecological conditions (Johnson et al., 1996). Some species, like the gray wolf, are social predators (Mech, 1970), whereas others like the maned wolf (*Chrysocyon brachyurus*) hunt alone (Biben, 1983).

The cranial morphology of *C. lupus* is not consistent with other habitual bone consumers. Since its forehead is not vaulted, the stress arc from biting passes between the infraorbital foramen and the orbit and crosses the frontal bones just above the orbits (Werdelin, 1989). This stress arc pattern does not occur in other known bone crushers such as the modern spotted hyena and the African wild dog (Werdelin, 1989; Anyonge and Baker, 2006; Tanner et al., 2008). However, both field observations and experimental studies indicate that the gray wolf engages in bone consumption (Mech, 1970; Haynes, 1980), with entire large carcasses being consumed in the wild (Mech, 1970). Prey limb elements can be completely consumed while only the skull, lower jaw, vertebrae, and hide are left (Mech, 1970; Haynes, 1982; D'Andrea and Gotthardt, 1984; Blumenschine, 1986, 1988). Like most canids, wolves tend to use their large cheek teeth to gnaw on bones and thereby leave characteristic marks on skeletal remains (Haynes, 1983). Further, wolves (like spotted hyenas) may favor the greasy, less dense, marrow-rich bones (Haynes, 1980, 1982; Blumenschine, 1988; Maraen and Spencer, 1991; Maraen et al., 1992).

The coyote is often sympatric with the modern gray wolf (Johnson et al., 1996). Due to this overlap in territories, partitioning prey by size for dietary resources is likely an essential survival strategy (Arjo et al., 2002). While gray wolves are described as highly predacious carnivores, coyotes are usually considered opportunistic feeders (Morey et al., 2007). The diet of *C. latrans* is highly varied, ranging from small rodents and rabbits to large ungulates and carrion (Arjo et al., 2002; Bartel and Knowlton, 2005; Morey et al., 2007). Coyotes tend to consume rabbits in proportion to their abundance and more fully consume carcasses (including bones and teeth) of these animals (Bartel and Knowlton, 2005). Along with natural prey items, recent encroachment of human civilizations into coyote habitat (and vice versa) has led to an increase in dietary variety of coyotes (Morey et al., 2007). Coyotes have been known to remain in human areas for access to unnatural food items such as domesticated pets, garbage, and vegetation (McClure et al., 1995), and this behavior would presumably leave characteristic patterns on the surfaces of their teeth.

In addition to North American canids, the African wild dog has the potential to reveal the dietary ecology of dire wolves. The African wild dog is a highly predaceous canid that hunts in large groups, allowing it to prey on massive African herbivores (Creel and Creel, 1995); however, they favor ungulates such as impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*) (Pole et al., 2004). These canids represent a monotypic group and have been shown to be phylogenetically distinct from all other wolf-like canids, including wolves and coyotes (Creel and Creel, 2002). Most importantly, *L. pictus* is a modern example of a durophagous canid. A population of African wild dogs in Selous, Tanzania, was often found to eat leg bones, ribs, vertebrae, and skulls (Creel and Creel, 2002). The fecal remains of this canid have also been found to turn white due to the high amount of digested bone, which is similar to spotted hyenas (Creel and Creel, 2002). The dietary behavior of African wild dogs is pertinent for comparative purposes of this study, and so their dental microwear should reflect bone-consuming behavior.

MATERIALS AND METHODS

Carnivorans included in this study consist of extant and extinct canids, felids, a hyaenid, and ursids. The extant canids include *C. latrans* (n = 12), *C. lupus* (n = 15), and *L. pictus* (n = 13). All of the *C. latrans* and a few of the *L. pictus* specimens are from Ungar et al. (2010) (see Table 1). The extinct *C. dirus* (n = 18) was examined from several of the pits at La Brea, including Pits 3, 13, 61–67, and 91 (ranging in time from approximately 29,000 to 11,500 calibrated radiocarbon years before present; O'Keefe et al., 2009). Extant feliforms reviewed in this paper include the cheetah *Acinonyx jubatus* (n = 9), the African lion *Panthera leo* (n = 15), the cougar *Puma concolor* (n = 38), represented by *Puma concolor cougar*, n = 17, and *Puma concolor coryi,* n = 21*)*, and *C. crocuta* (n = 12), all reported in Schubert et al. (2010), DeSantis et al. (2012), and DeSantis and Haupt (2014). Pleistocene felids from the La Brea Tar Pits, include *P. atrox* (n = 15), the cougar *Puma concolor* (n = 12), and *S. fatalis* (n = 15), all reported in DeSantis et al. (2012) and DeSantis and Haupt (2014). Extant ursids reviewed in this paper include the giant panda *Ailuropoda melanoleuca,* the spectacled bear *Tremarctos ornatus,* the black bear *Ursus americanus*, the sun bear *Ursus malayanus,* and the polar bear *Ursus maritimus*, all from Donohue et al. (2013). The extinct ursid, *A. simus*, was examined from La Brea pits spanning up to ~35,500 radiocarbon years before present (Donohue et al., 2013; based on dates from O'Keefe et al., 2009).

Extant specimens used in this study are housed at the American Museum of Natural History, New York, NY, USA (AMNH); Florida Museum of Natural History, Gainesville, FL, USA (FLMNH); Iziko South African Museum, Cape Town, South Africa (SAM); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Santa Barbara Museum of Natural History, Santa Barbara, CA, USA (SBMNH); and the University of Arkansas, Fayetteville, AK, USA (UA). Extinct specimens are housed at the La Brea Tar Pits and Museum in Los Angeles, California, USA (LACMHC, La Brea Tar Pits and Museum Hancock Collection; LACMRLP, Los Angeles County Museum, Pit 91). Between about 15% and 33% of specimens for each taxon from the La Brea Tar Pits have broken canines and/or premolars; thus, our sample is representative of both individuals lacking and containing antemortem tooth breakage.

The enamel region of the anterolingual surface of the hypoconid on the lower m2 was analyzed in canids, as postcarnassial teeth are used for hard-object processing, in contrast to the carnassial shearing facet on the lower m1 (Ungar et al., 2010). In feliforms, the lower carnassial shearing facet of the m1 trigonid was examined (as described in Schubert et al., 2010; DeSantis et al., 2012; DeSantis and Haupt, 2014). In ursids, the mesial facet of the lower m2 hypoconulid was sampled, as this facet captures grinding and food processing correlated with diet, in contrast to the buccal facet on the lower m1 protoconid (per

Table 1 All canid specimens examined and dental microwear characters. † denotes extinct taxon.

Taxon	Status/pit[a]	Collection	ID	*Asfc*	*epLsar*	*Tfv*	Data[b]
Canis dirus†	Pit 3	LACMHC	2301-130	4.694	0.0024	14,792	U
		LACMHC	2301-216	4.353	0.0022	9,716	U
		LACMHC	2301-124	3.776	0.0011	17,229	U
		LACMHC	2301-208	3.602	0.0027	12,884	U
		LACMHC	53834	4.437	0.0013	14,688	U
	Pit 13	LACMHC	2301-138	3.473	0.0015	14,701	U
		LACMHC	55145	2.827	0.0036	12,970	U
		LACMHC	55161	1.951	0.0028	11,414	U
		LACMHC	55172	5.273	0.0029	14,688	U
		LACMHC	55185	2.220	0.0042	18,568	U
		LACMHC	55191	2.034	0.0019	14,711	U
	Pit 61	LACMHC	55586	3.416	0.0015	13,706	U
	Pit 67	LACMHC	2301-511	4.730	0.0017	13,763	U
		LACMHC	55662	4.599	0.0028	13,826	U
		LACMHC	55672	2.965	0.0024	17,166	U
	Pit 91	LACMRLP	R39848	1.543	0.0028	11,493	U
		LACMRLP	R41748	1.988	0.0021	14,808	U
		LACMRLP	R52965	4.358	0.0023	17,220	U
Canis latrans	Modern	UA	261	4.829	0.0028	13,533	P
		UA	279	5.247	0.0010	14,247	P
		UA	280	4.857	0.0025	14,929	P
		UA	287	4.574	0.0040	15,030	P
		UA	298	6.586	0.0013	17,380	P
		UA	303	9.842	0.0018	11,778	P
		UA	304	10.108	0.0008	13,500	P
		UA	306	4.472	0.0022	10,516	P
		UA	308	4.963	0.0029	13,941	P
		UA	310	3.610	0.0026	10,200	P
		UA	315	3.911	0.0013	8,824	P
		UA	320	11.228	0.0008	14,710	P
Canis lupus	Modern	USNM	6218	5.684	0.0026	16,926	U
		USNM	99668	1.167	0.0036	11,164	U
		USNM	150421	2.566	0.0017	11,446	U
		USNM	175178	6.186	0.0023	12,759	U
		USNM	200693	0.910	0.0020	13,923	U
		USNM	231320	4.013	0.0016	15,063	U
		USNM	282819	2.358	0.0026	15,019	U
		USNM	283586	1.181	0.0030	15,248	U
		USNM	289933	2.535	0.0020	15,605	U
		USNM	290425	2.398	0.0014	9,603	U
		USNM	290428	1.651	0.0019	10,855	U
		USNM	291008	2.078	0.0038	10,936	U
		USNM	291012	5.398	0.0022	11,491	U
		USNM	507338	1.720	0.0036	7,063	U
		USNM	512023	2.555	0.0030	10,876	U
Lycaon pictus	Modern	SAM	12245	6.177	0.0028	15,987	P
		SAM	33303	2.026	0.0010	11,808	P
		SAM	33304	7.428	0.0011	14,448	P
		SAM	33359	4.947	0.0012	12,670	P
		SAM	33642	6.294	0.0013	16,585	P
		USNM	162878	1.784	0.0027	13,328	U
		USNM	181508	4.522	0.0021	10,982	U
		USNM	181509	5.577	0.0016	16,698	U
		USNM	251878	3.166	0.0020	15,731	U
		USNM	296105	2.602	0.0026	11,624	U
		USNM	368440	3.830	0.0022	15,934	U
		USNM	368441	5.350	0.0012	14,488	U
		USNM	368443	1.051	0.0020	14,083	U

Abbreviations: *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume.

[a] Status/Pit, if extinct only the pit is noted (all pits are from the La Brea Tar Pits, Los Angeles, California, USA).

[b] Note the source of respective data according to the following: P, published in Ungar et al. (2010); U, unpublished data new to this study. All teeth analyzed are lower second molars per "Materials and Methods."

Table 2 Descriptive statistics for each DMTA variable by canid species. † denotes extinct taxon.

Taxon	Statistic	n	*Asfc*	*epLsar*	*Tfv*
Canis dirus† (La Brea Tar Pits)	Mean	18	3.458	0.0023	14,352
	Median		3.538	0.0023	14,688
	Standard deviation		1.156	0.0008	2,255
	Minimum		1.543	0.0011	9,716
	Maximum		5.273	0.0042	18,568
	Total range		3.730	0.0031	8,852
	Skewness (Fisher)		−0.211	0.595	−0.057
	p for normality (Shapiro–Wilk)		0.228	0.578	0.514
Canis latrans (modern)	Mean	12	6.186	0.0020	13,216
	Median		4.910	0.0020	13,737
	Standard deviation		2.657	0.0010	2,437
	Minimum		3.610	0.0008	8,824
	Maximum		11.228	0.0040	17,380
	Total range		7.619	0.0032	8,556
	Skewness (Fisher)		1.116	0.484	−0.352
	p for normality (Shapiro–Wilk)		0.008*	0.402	0.621
Canis lupus (modern)	Mean	15	2.827	0.0025	12,532
	Median		2.398	0.0023	11,491
	Standard deviation		1.699	0.0008	2,692
	Minimum		0.910	0.0014	7,063
	Maximum		6.186	0.0038	16,926
	Total range		5.276	0.0024	9,863
	Skewness (Fisher)		1.012	0.471	−0.164
	p for normality (Shapiro–Wilk)		0.019*	0.296	0.474
Lycaon pictus (modern)	Mean	13	4.212	0.0018	14,182
	Median		4.522	0.0020	14,448
	Standard deviation		1.976	0.0006	1,967
	Minimum		1.051	0.0010	10,982
	Maximum		7.428	0.0028	16,698
	Total range		6.377	0.0018	5,716
	Skewness (Fisher)		−0.094	0.209	−0.286
	p for normality (Shapiro–Wilk)		0.843	0.192	0.318

Abbreviations: n, number of individuals sampled; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume. All teeth analyzed are lower second molars, per "Materials and Methods."

* Significant at the $p<0.05$ level.

Donohue et al., 2013). All tooth facets examined were first cleaned with cotton swabs soaked in acetone (to remove preservatives such as Butvar) and subsequently molded using a polyvinylsiloxane dental impression material (President's Jet regular body, Coltène/Whaledent Corp., Cuyahoga Falls, Ohio, USA). Tooth replicas were then prepared using Epo-Tek 301 epoxy resin and hardener (Epoxy Technologies Corp., Billerica, Massachusetts, USA).

Dental microwear texture analysis was performed on all replicas that preserved antemortem microwear using white-light confocal profilometry and SSFA (Ungar et al., 2003; Scott et al., 2005, 2006). All specimens were scanned in three dimensions in four adjacent fields of view for a total sampled area of 204 × 276 μm^2. All scans were analyzed using SSFA software (Toothfrax and Sfrax, Surfract Corp., www.surfract.com) to characterize tooth surfaces according to the variables of complexity (*Asfc*), anisotropy (*epLsar*), and textural fill volume (*Tfv*). Specifically, complexity is a scale-sensitive measure of roughness and is used to distinguish taxa that consume hard, brittle foods from those that eat softer ones, with greater complexity indicative of hard-object processing (such as bone) in carnivores (Ungar et al., 2003; Scott et al., 2005, 2006; Schubert et al., 2010; DeSantis et al., 2012). Anisotropy is the degree to which surface textures show a preferred orientation, such as the dominance of parallel striations that might be formed by carnassial action in meat slicing, given constraints to tooth–tooth movement during occlusion (Ungar et al., 2003; Scott et al., 2005, 2006; Schubert et al., 2010; DeSantis et al., 2012). Textural fill volume is a measure of the difference in volume filled by large-diameter (10-μm) and small-diameter (2 μm) square cuboids, with high values indicating many deep features between these sizes (Ungar et al., 2003; Scott et al., 2005, 2006; Schubert et al., 2010; DeSantis et al., 2012).

As the majority of DMTA variables are not normally distributed (as determined using Shapiro–Wilk tests), nonparametric statistical tests (e.g., Kruskal–Wallis) are used here to compare

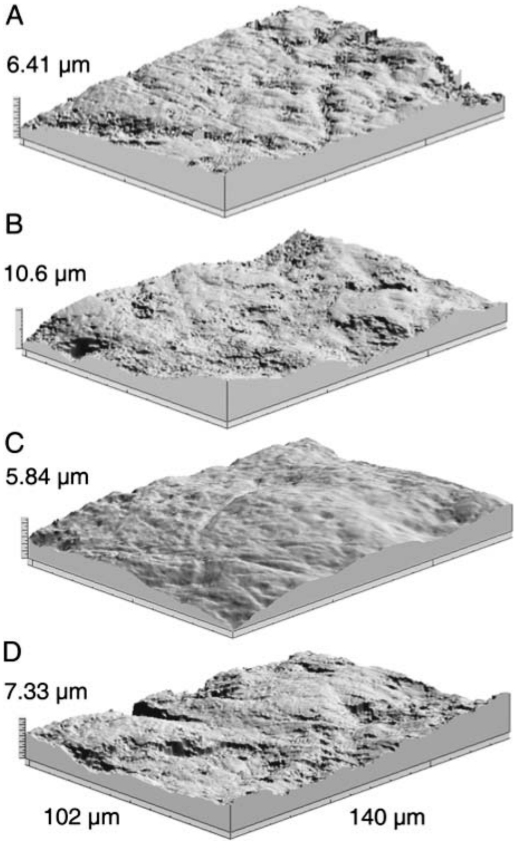

Figure 1 Three-dimensional photosimulations of canid lower second molars taken at $100\times$ magnification. **A.** *Canis dirus*, LACMHC 2301-124; **B.** *Canis latrans*, UA 304; **C.** *Canis lupus*, USNM 200693; **D.** *Lycaon pictus* SAM 33359. Length and width measurements of photosimulation D correspond to all.

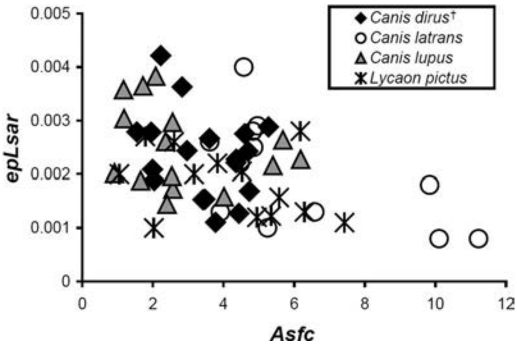

Figure 2 Bivariate plot of complexity (*Asfc*) and anisotropy (*epLsar*) for lower second molars of canids. † denotes extinct taxon.

differences among all canids. The feliform and ursid data have previously been published (Schubert et al., 2010; DeSantis et al., 2012; Donohue et al., 2013; DeSantis and Haupt, 2014); thus, the descriptive statistics are summarized below. The canids were analyzed using the same methods as the other carnivorans, with both nonparametric and parametric statistical tests applied when appropriate to assess differences between extant and extinct taxa. Because only the complexity values for *C. latrans* are not normally distributed, parametric analyses of variance, Fisher's LSD, and Tukey's HSD tests were used to compare anisotropy and textural fill volume. Significant results ($p < 0.05$) by Fisher's LSD test may be considered suggestive, or of marginal significance, in contrast to those for more conservative Tukey's HSD tests. We also used Dunn's procedure (Dunn, 1964) to conduct multiple comparisons of complexity between canids. (As specific p-values are not calculated for this test, we only note if significant with a $p < 0.05$ criterion.) Further, the Bonferroni correction is not used in either parametric or nonparametric comparisons. The Bonferroni correction is meant to reduce the likelihood of false positives (Type I errors) by taking into consideration the number of comparisons being made, but it also increases the probability of false negatives (Type II errors) and is therefore not appropriate for our analysis (Cabin and Mitchell, 2000; Nakagawa, 2004).

RESULTS

Dental microwear results of canids are presented in Tables 1 and 2 and illustrated in Figures 1 and 2. Of the extant canids analyzed, *C. latrans* has the greatest mean complexity value (6.186), followed by *L. pictus* (4.212) and *C. lupus* (2.827). *Canis dirus* has a mean complexity value of 3.458, intermediate between *C. lupus* and *L. pictus* and significantly lower than *C. latrans*. Further, *C. lupus* has significantly lower complexity than both *L. pictus* and *C. latrans*. In contrast, all anisotropy values are similar between most canids (mean values ranging from 0.0018 in *L. pictus* to 0.0025 in *C. lupus*). Despite these minor differences, *C. lupus* yields significantly greater values than *L. pictus* when less conservative critical values are used in Fisher's LSD comparisons ($p = 0.037$). However, *C. dirus* mean anisotropy, is not significantly different from that of any of the extant canids. Similarly, mean textural fill volume values are similar between canids, with no significant differences between extant taxa using Tukey's LSD tests. However, *C. dirus* is significantly greater than *C. lupus* when using the less conservative Fisher's LSD tests ($p = 0.031$).

Dental microwear results of extant feliforms from La Brea are summarized in Table 3 and illustrated in Figures 3–5. Dental microwear results of extant and extinct ursids are summarized in Table 4 and illustrated in Figures 6 and 7. As these data are already published in DeSantis et al.

Table 3 Descriptive statistics for each DMTA variable by feliform species, summarized from published data. † denotes extinct taxon.

Taxon	Statistic	n	*Asfc*	*epLsar*	*Tfv*
Acinonyx jubatus[a] (modern)	Mean	9	1.590	0.0049	5,071
	Median		1.767	0.0047	2,581
	Standard deviation		0.737	0.0011	5,372
	Minimum		0.759	0.0030	0
	Maximum		2.674	0.0064	14,638
	Total range		1.915	0.0034	14,638
Crocuta crocuta[a] (modern)	Mean	12	9.315	0.0031	12,320
	Median		7.070	0.0034	14,142
	Standard deviation		6.708	0.0011	5,666
	Minimum		2.280	0.0012	1,234
	Maximum		23.864	0.0052	17,531
	Total range		21.584	0.0040	16,297
Panthera leo[a] (modern)	Mean	15	4.616	0.0031	10,413
	Median		4.690	0.0033	11,358
	Standard deviation		1.729	0.0017	4,074
	Minimum		1.807	0.0009	3,710
	Maximum		7.354	0.0075	14,934
	Total range		5.547	0.0066	11,224
Puma concolor[b] (modern)	Mean	38	4.086	0.0035	9,035
	Median		4.039	0.0034	9,849
	Standard deviation		1.929	0.0017	4,597
	Minimum		1.075	0.0004	28
	Maximum		9.505	0.0071	16,887
	Total range		8.430	0.0067	16,859
Panthera atrox†[a] (La Brea Tar Pits)	Mean	15	1.812	0.0033	6,051
	Median		2.049	0.0029	7,063
	Standard deviation		0.562	0.0012	4,637
	Minimum		0.822	0.0017	341
	Maximum		2.438	0.0060	12,683
	Total range		1.616	0.0043	12,342
Puma concolor[b] (La Brea Tar Pits)	Mean	12	4.592	0.0035	12,860
	Median		3.222	0.0027	14,008
	Standard deviation		4.530	0.0021	3,609
	Minimum		0.804	0.0009	3,145
	Maximum		16.371	0.0080	16,597
	Total range		15.567	0.0071	13,452
Smilodon fatalis†[a] (La Brea Tar Pits)	Mean	15	2.900	0.0026	10,213
	Median		3.113	0.0023	12,819
	Standard deviation		0.845	0.0013	5,460
	Minimum		1.173	0.0010	190
	Maximum		4.590	0.0054	17,830
	Total range		3.417	0.0044	17,640

Abbreviations: n, number of individuals sampled; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume. All teeth analyzed are lower first molars, per "Materials and Methods."

[a] Taken from DeSantis et al. (2012).

[b] Taken from DeSantis and Haupt (2014).

(2012), Donohue et al. (2013), and DeSantis and Haupt (2014), we do not repeat results here but do discuss them in the context of carnivoran dental microwear results.

DISCUSSION

DENTAL MICROWEAR OF EXTANT CANIDS AND DIRE WOLVES FROM LA BREA

The dental microwear textures of extant canids can help clarify the dietary ecology of *C. dirus*. *Canis latrans* has a generalized diet and is classified as an opportunistic feeder (Arjo et al., 2002; Bartel and Knowlton, 2005; Morey et al., 2007). Its dental microwear is consistent with at least some hard-object feeding (high complexity values). Consumption of various animals, small bones, garbage, vegetation, and carrion may all contribute to the overall microwear texture complexity exhibited by the coyote sample. The more uniform and less complex microwear surfaces of the gray wolves is consistent with a diet of soft tissue and some bone. Dental microwear attributes exhibited by *C. lupus* are consistent with

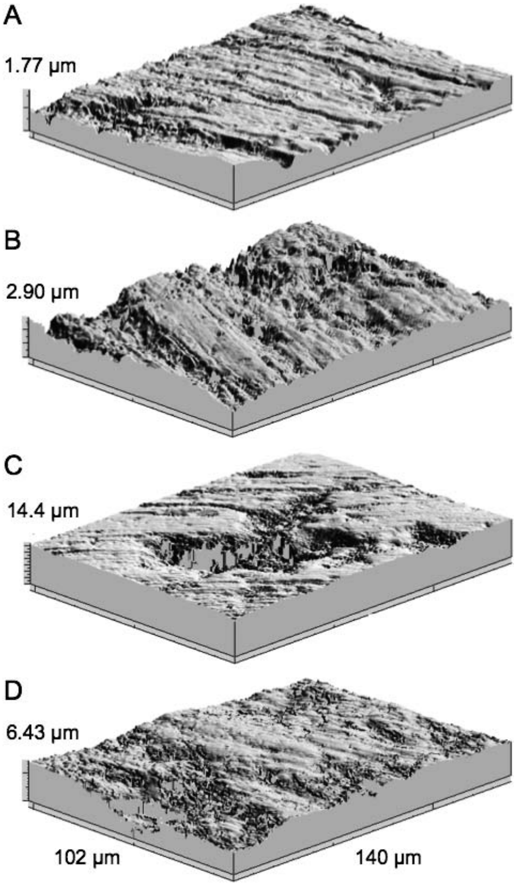

Figure 3 Three-dimensional photosimulations of extant feliform lower first molars taken at 100× magnification. **A.** *Acinonyx jubatus*, AMNH 161139; **B.** *Panthera leo*, USNM 236919; **C.** *Puma concolor*, SBMNH 886; **D.** *Crocuta crocuta*, AMNH 83592. Length and width measurements of photosimulation D correspond to all. All images are originally from DeSantis et al. (2012) and DeSantis and Haupt (in 2014).

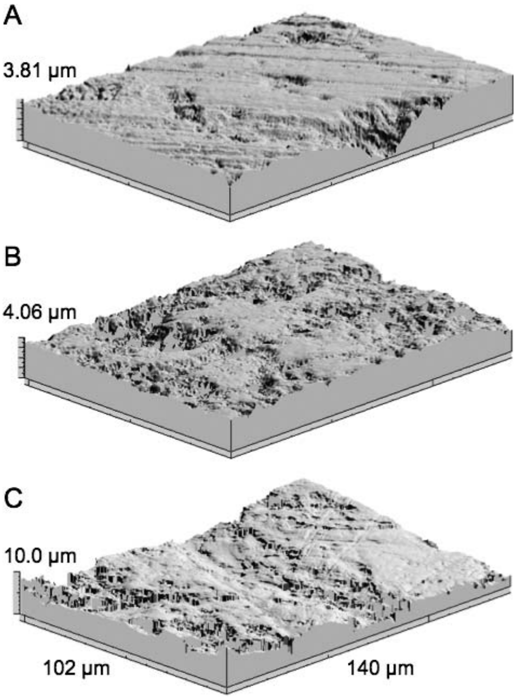

Figure 4 Three-dimensional photosimulations of feliform lower first molars from the La Brea Tar Pits taken at 100× magnification. **A.** *Panthera atrox*, LACMHC 6996; **B.** *Smilodon fatalis*, LACMHC 2002-298; **C.** *Puma concolor*, LACMHC x946. Length and width measurements of photosimulation C correspond to all. All images are originally from DeSantis et al. (2012) and DeSantis and Haupt (in 2014).

the lowest levels of durophagy for all analyzed canids (i.e., the lowest complexity and textural fill volume values and the highest anisotropy values). When gray wolves and coyotes overlap in territory, it is likely the coyotes eat the smaller animals, such as rodents and rabbits, while wolves prey on the larger ungulates that occur throughout their range (Arjo et al., 2002).

As noted, the canid with the greatest complexity is *C. latrans*, and this is likely due to its variable and opportunistic feeding behaviors. Since coyotes tend to focus more on smaller prey (Arjo et al., 2002; Bartel and Knowlton, 2005; Morey et al., 2007), the complexity differences between *C. latrans* compared with *C. dirus* and *L. pictus* may evince more common comminution of larger bones in the latter two taxa. Future work expanding on the canid baseline could address how prey size affects dental microwear attributes. The dental microwear texture results suggest that the dire wolves participated in some level of bone consumption, consistent with cranial morphology (Anyonge and Baker, 2006) and bite force

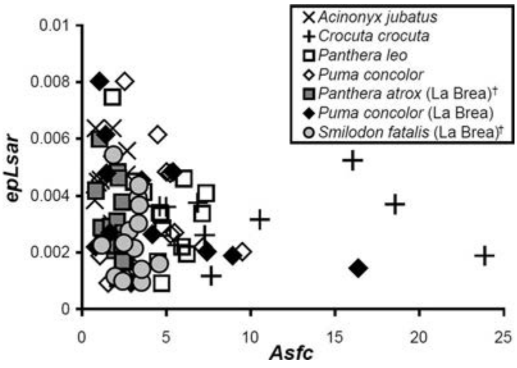

Figure 5 Bivariate plot of complexity (*Asfc*) and anisotropy (*epLsar*) for lower first molars of feliforms. Data summarized from DeSantis et al (2012) and DeSantis and Haupt (2014). † denotes extinct taxa.

Table 4 Descriptive statistics for each DMTA variable by ursid species, summarized from published data. † denotes extinct taxon.

Taxon	Statistic	n	*Asfc*	*epLsar*	*Tfv*
Ailuropoda melanoleuca[a] (modern)	Mean	11	1.996	0.0039	8,230
	Median		1.915	0.0035	11,433
	Standard deviation		1.010	0.0021	5,507
	Minimum		0.618	0.0004	211
	Maximum		3.895	0.0083	14,591
	Total range		3.277	0.0079	14,380
Tremarctos ornatus[a] (modern)	Mean	11	4.172	0.0028	12,987
	Median		3.538	0.0026	13,012
	Standard deviation		2.288	0.0009	4,410
	Minimum		1.256	0.0014	4,029
	Maximum		8.478	0.0043	19,630
	Total range		7.222	0.0029	15,601
Ursus americanus[a] (modern)	Mean	15	7.847	0.0022	12,192
	Median		6.792	0.0021	13,262
	Standard deviation		4.576	0.0011	4,528
	Minimum		1.530	0.0008	3,140
	Maximum		16.550	0.0045	1,6981
	Total range		15.020	0.0037	13,841
Ursus malayanus[a] (modern)	Mean	6	3.964	0.0023	10,639
	Median		3.972	0.0021	11,727
	Standard deviation		2.519	0.0009	3,715
	Minimum		1.052	0.0012	4,243
	Maximum		6.762	0.0038	13,791
	Total range		5.710	0.0026	9,548
Ursus maritimus[a] (modern)	Mean	16	8.486	0.0022	13,036
	Median		9.005	0.0019	13,358
	Standard deviation		3.640	0.0010	2,136
	Minimum		1.740	0.0008	10,574
	Maximum		14.690	0.0058	18,800
	Total range		12.950	0.0050	8,226
Arctodus simus[a]† (La Brea Tar Pits)	Mean	16	4.586	0.0022	15,028
	Median		4.115	0.0020	15,395
	Standard deviation		2.295	0.0010	1,753
	Minimum		1.160	0.0009	11,985
	Maximum		8.292	0.0041	17,652
	Total range		7.132	0.0032	5,667

Abbreviations: n, number of individuals sampled; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume. All teeth analyzed are lower second molars, per "Materials and Methods."

[a] Taken from Donohue et al. (2013).

estimates (Wroe et al., 2005). Further, *C. dirus* is not significantly different in any microwear attribute from *L. pictus*, suggesting that it likely engaged in some bone processing; however, it is unlikely they participated in this behavior more than *L. pictus* (or even spotted hyenas, as suggested based on tooth breakage data by Van Valkenburgh, 2009), despite prior work that implied that the dire wolf was a frequent bone crusher (Binder et al., 2002). It is also unclear whether *C. dirus* truly consumed bone more often than do modern-day wolves, as dental microwear textures are similar between these taxa (only significantly different in textural fill volume when using a less conservative statistical test). Microwear results are consistent with both *C. dirus* and *C. lupus* participating in some hard-object consumption. As modern observations of gray wolves show that this species does include bone as an occasional nutritional source (Mech, 1970; Stahler et al., 2006), it is possible that the extinct dire wolf behaved similarly.

DENTAL MICROWEAR OF CARNIVORANS FROM LA BREA AND EXTINCTION IMPLICATIONS

Dental microwear of carnivorans has largely focused on analyzing the lower m1 (carnassial) facet, as this is the largest wear facet and is homologous (although not necessarily analogous) among carnivorans (e.g., Van Valkenburgh et al., 1990; Peigné et al., 2009; Schubert et al., 2010; DeSantis et al., 2012). However, recent work shows that microwear variation along the tooth row reflects a functional division of labor between specific teeth (e.g., Goillot et al., 2009; Ungar et al., 2010; Donohue et al., 2013; Pinto-Llona, 2013).

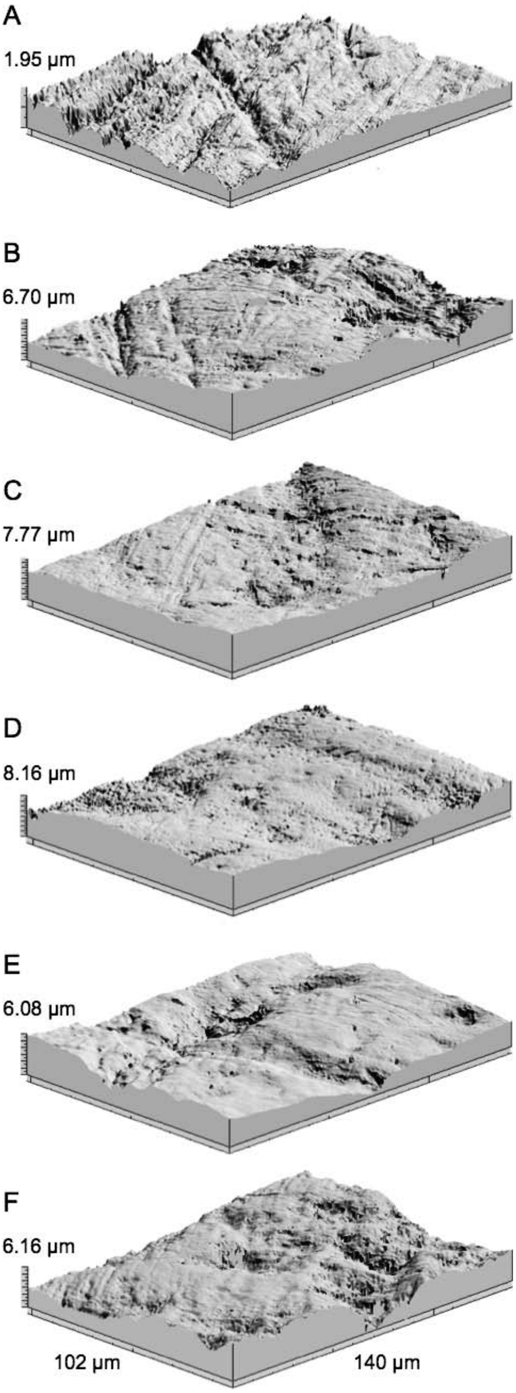

Figure 6 Three-dimensional photosimulations of ursid lower second molars taken at 100× magnification. **A.** *Ailuropoda melanoleuca*, USNM 259028; **B.** *Tremarctos ornatus*, USNM 271418; **C.** *Ursus malayanus*, USNM 151866; **D.** *Ursus americanus*, FLMNH 28436; **E.** *Ursus maritimus*, USNM 512117; **F.** *Arctodus simus*, LACMHC 1292. Length and width measurements of photosimulation F correspond to all. All images are originally from Donohue et al. (2013).

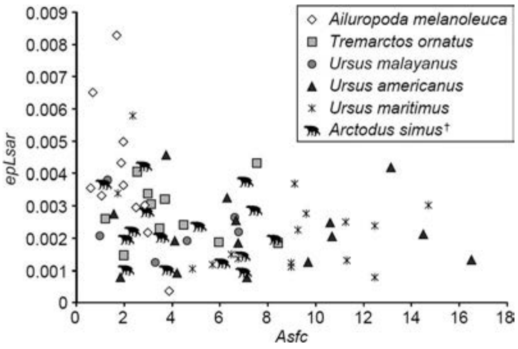

Figure 7 Bivariate plot of complexity (*Asfc*) and anisotropy (*epLsar*) for lower second molars of ursids. Data are from Donohue et al. (2013). † denotes extinct taxon.

While Goillot et al. (2009) suggest that the shearing facet on the lower m1 (buccal facet of the paraconid) is the most informative in carnivorans as a whole, work by others (Ungar et al., 2010; Donohue et al., 2013) suggests that lower second molars may be informative for capturing diet signals in canids and ursids, which both heavily depend on postcarnassial teeth for food processing. In canids, the presence of postcarnassial crushing teeth renders carnassials functionally distinct and nonanalogous with carnassials of felids and hyenas (Ungar et al., 2010). Specifically, lower m2s (the anterolingual surface of the hypoconid) have lower anisotropy and higher complexity and textural fill volume than lower m1s (the buccal facet on the protoconid), consistent with crushing functionality (Ungar et al., 2010). Similarly, lower m2s of bears are typified by lower anisotropy, higher complexity, and higher textural fill volume, consistent with grinding/crushing functionality for the mesial facet of the lower m2 hypoconulid (Donohue et al., 2013). Although these attributes and relationships do vary between bear species, microwear of m2 crushing facets is highly correlated with observed dietary behavior, in contrast to the slicing/shearing carnassial m1 facet (Donohue et al., 2013). This is not surprising, as postcarnassial molars are highly modified in bears in accordance with known dietary behavior, with increased dental ornamentation and mass-specific size in herbivorous bears compared with carnivorous bears (i.e., giant pandas, *A. melanoleuca*, and polar bears, *U. maritimus*, respectively; Evans et al., 2007). Thus, while lower first molar shearing facets are homologous across carnivorans, it is critical to document and control for differences in dental microwear between facets and teeth with disparate functions, as we have done in canids, feliforms, and ursids. Because we examine different facets in different carnivorans, the dietary behavior of extinct taxa is interpreted in the context of comparisons of closely related taxa using homologous and analogous facets.

Dental microwear texture analysis of *A. simus* from La Brea indicates it consumed food with similar textural properties to its closest living relative the spectacled bear *T. ornatus* (Donohue et al., 2013), an herbivore/omnivore from South America (Peyton, 1980). *Arctodus simus* from this region apparently consumed foods softer and tougher on average than does the hypercarnivorous polar bear *U. maritimus* (Bentzen et al., 2007; Thiemann et al., 2008) and the omnivorous American black bear *U. americanus* (Raine and Kansas, 1990; Stratman and Pelton, 1999), which both exhibited a large variance in complexity values. While further geochemical work is necessary to better understand the amount of plant material versus meat in this carnivoran's diet, dental microwear textures suggest that *A. simus* was not filling the role of a bone-consuming hyperscavenger (as suggested by Matheus, 2003).

The dental microwear of felids from the La Brea Tar Pits provides insight into the dietary behavior of extinct large cats that once roamed southern California (and more generally North America), include *S. fatalis* and *P. atrox*. Previous work by DeSantis et al. (2012) used dental microwear to assess the relative degree of carcass utilization and test the idea that extinct felids were experiencing tougher times than today (based on the hypothesis proposed by Van Valkenburgh and Hertel, 1993). In contrast to tooth fracture frequency data demonstrating that *P. atrox* had the greatest percentage of broken canines (36% compared with the co-occurring Pleistocene canids *C. dirus*, 18.8%; *C. latrans*, 19%; and *C. lupus*, 22.7% and the co-occurring felid *S. fatalis*, 11.2%), its dental microwear textures were most similar to extant cheetahs that are known to avoid bone and primarily consume flesh from fresh kills (DeSantis et al., 2012). Similarly, *S. fatalis* (with the lowest percentage of broken canines compared with other felids and canids at La Brea) has dental microwear suggestive of some bone processing—most similar to the African lion (DeSantis et al., 2012). Dental microwear texture results of both *P. atrox* and *S. fatalis* are consist with inferred hunting behavior based on percent abundance data (i.e., the lower percent abundance of *P. atrox* suggests it was less social than the second most abundant carnivoran, *S. fatalis*; Carbone et al., 2009). For example, if *P. atrox* was more solitary than its relatives, it is expected that *P. atrox* would utilize carcasses to a lesser extent than social animals like modern African lions and potentially *S. fatalis* (DeSantis et al., 2012) who have to share their kills, game densities being equal.

The stark disparity between tooth breakage data and dental microwear textural data in carnivorans, indicates that the proxies are not of equal value for indicating relative degree of carcass utilization (DeSantis et al., 2012). We suspect that tooth fracture frequency (especially of canines) is likely also a result of prey capture and/or defensive behaviors, especially as more posterior teeth are involved in the processing of bone (Van Valkenburgh, 2007). Van Valkenburgh (1988) corroborated this by documenting a higher frequency of broken canines in female lions and female hyenas, who do a greater share of the hunting and carcass defense, respectively, as further discussed by DeSantis et al. (2012). All else being equal, we expect that anterior teeth such as canines will incur more damage when used to take down larger prey, including the large herbivores dominating the landscape during the Late Pleistocene. Because larger teeth are more vulnerable to fracture (Van Valkenburgh and Ruff, 1987; Freeman and Lemen, 2006; Plavcan and Ruff, 2008), larger organisms that take down larger prey are expected to incur more damage and break teeth more frequently due to the mass of prey and exerted forces during their acquisition. We believe that microwear texture patterns, which have been shown to reflect degree of carcass utilization in extant feliforms (Schubert et al., 2010) are likely better indicators of proportions of meat and bone consumption than incidence of nonchewing tooth breakage (as suggested by DeSantis et al., 2012). Tooth breakage, on the other hand, is likely also related to prey size and hunting behavior.

Late Pleistocene cougars from La Brea exhibit significantly greater variance in complexity values than *S. fatalis*, which suggests that the former were more generalized in their dietary behavior, including the processing of bone. Relatively complete carcass utilization by cougars is also observed today and reflected in their dental microwear (both in southern California and southern Florida; DeSantis and Haupt, 2014). However, this strategy did not make them impervious to whatever caused the extinction, as genetic work shows a severe bottleneck and possible localized extinctions for the group around this time (Culver et al., 2000). As cougars are one of only two large cats to survive the Late Pleistocene extinction event in North America (the other being the jaguar, *Panthera onca*; Kurtén and Anderson, 1980), it may be that their generalized diet was a key to their survival (DeSantis and Haupt, 2014). Similar work examining the dental microwear of La Brea's smaller felids (e.g., bobcats *Lynx rufus*) and canids that survived the Late Pleistocene extinction (i.e., *C. latrans and C. lupus*) may further reveal effective dietary strategies to buffer against extinction. We also note that the smaller cougar (at least in the context of extinct felids; Stock, 2001) and smaller canids that likely more fully consumed smaller prey items, survived the Late

Pleistocene extinction. However, future work on Pleistocene La Brea *C. latrans* and local modern specimens can help reveal potential keys to success for the canids.

SUMMARY

Collectively, dental microwear textures of all extinct carnivorans at the La Brea Tar Pits (i.e., *A. simus, C. dirus, P. atrox,* and *S. fatalis*) suggest that carnivorans were engaging in less hard-object consumption than modern analogues known to more fully consume carcasses, including polar bears, African wild dogs, and spotted hyenas (DeSantis et al., 2012; Donohue et al., 2013). The only carnivoran with more variable complexity than *S. fatalis* and greater textural fill volume than modern cougars in southern California (indicating a more generalized diet including scavenging and/or bone processing), is the cougar from La Brea, which again, survived the Late Pleistocene extinction. The absence of any evidence of more complete carcass utilization in extinct La Brea carnivorans compared with modern analogous known to process bone suggests that carnivorans were not consuming less-preferred parts of their prey during tough times (as suggested by Van Valkenburgh and Hertel, 1993). Further, the absence of significant differences in other stress markers (i.e., Harris lines, osteological markers indicative of poor health and/or arrested growth) between healthy mammals and Pleistocene mammals from La Brea (*C. dirus*, *C. latrans*, *S. fatalis*, the bison *Bison antiquus*, the camelid *Camelops hesternus*, and horse *Equus laurentius*) suggests tough times were not apparent (Duckler and Van Valkenburgh, 1998). In fact, the Pleistocene mammal fossils from La Brea have significantly fewer Harris lines than the likely stressed and highly endangered Florida panther (*Puma concolor coryi;* Duckler and Van Valkenburgh, 1998).

Evidence from all La Brea carnivorans examined and reviewed here suggests that they were not stressed just prior to the extinction event. Thus, DMTA provides no evidence for scarcer prey resources during the Late Pleistocene of La Brea and, by extension, provides no indication of competition between humans and carnivorans for similar prey items and/or that these resources were in short supply. Instead, high incidences of tooth breakage likely suggest different challenges experienced by carnivorans in terms of hunting and prey acquisition. While more work is needed to better compare dental microwear textures through time at a finer temporal resolution and corresponding to a better understanding of potential climatic fluctuations occurring during the preservation of certain pits (and with increased samples sizes than was done in prior work; DeSantis et al., 2012), this is not always possible for all taxa (i.e., all specimens of *A. simus* and *P. concolor* that were excavated over 100 years with antemortem wear were included). To date, the rich fossil record at the La Brea Tar Pits can provide us with an improved understanding of carnivoran dietary behavior and can help eliminate potential extinction hypotheses.

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The Bacula of Rancho La Brea

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ABSTRACT. The Rancho La Brea (RLB) fossil collection at the La Brea Tar Pits and Museum represents one of the largest assemblages of carnivoran fossils in the world. This is certainly true of the bacula; the collection houses several hundred bacula of *Canis dirus*, more than a dozen of *Canis latrans*, two *Mustela* sp., one *Taxidea taxus*, and a one baculum previously described as belonging to *Urocyon cinereoargenteus*. Unfortunately, no bacula from any of the RLB felids or ursids have yet been recovered. In the current study, we compare the RLB fossil bacula to those of all of the modern analogues curated at the American Museum of Natural History and the Smithsonian. Nine measurements were taken on each complete specimen, and three of these were combined to create an overall volumetric size proxy. The *Mustela* and *Taxidea* specimens are both similar to their modern congeners, but the *Urocyon* specimen is smaller than the three modern specimens available for comparison. The sample of 18 *C. latrans* fossils is nearly statistically indistinguishable from the 21 modern conspecific samples from across their current geographic range, though the mean of the fossil sample is slightly larger than the modern sample for eight of the 10 metrics.

Of the large La Brea Tar Pits and Museum collection of *C. dirus* bacula, 159 are complete. They have been recovered from nearly all of the fossiliferous RLB deposits and span the entire Late Pleistocene accumulations represented at the site. The *C. dirus* bacula are almost five times as large as those of *C. lupus* (N = 10) in terms of a volumetric proxy, and the *C. dirus* mean total bacular length exceeds that in *C. lupus* by 44%. The *C. dirus* bacular width and height variables are even more dramatic in comparison, ranging up to 236% the size of those of *C. lupus*. No statistically discernable size or shape pattern emerges when considering the chronological sequence of the specimens, though the chronology of the deposits is complicated by the substantial mixing that is becoming evident, for instance, with Project 23 (John R. Southon and Benjamin T. Fuller, personal communication). However, the sample is large enough to see ontogenetic differences within it. In this respect, though, there are a few clearly juvenile bacula; the sample heavily skews to older, more robust, apparent age classes. Furthermore, several *C. dirus* bacula in the RLB sample are clearly broken and healed. Perhaps the extreme robusticity in this bone is an evolutionary response to aggressive mating competition—a hypothesis supported by the presence of several broken and healed bacula in the RLB sample.

INTRODUCTION

Modern mammal species in general and carnivorans in particular can be distinguished based on their bacular morphology (Didier, 1946, 1948, 1949, 1950; Burt, 1960). This is true in fossil carnivorans as well (Matthew, 1907; Olsen, 1959; Harrison, 1982; Wang, 1994; Abella et al., 2013), though these fossils are rarely found and described, and when they are, the description seldom includes any functional interpretation (Abella et al., 2013). As is the case for other rare bones (Hartstone-Rose et al., 2012), the rich fossil deposits at Rancho La Brea (RLB) preserve many delicate details that offer a unique opportunity to evaluate the bacular morphology of several extinct species.

The extraordinary occurrence of fossils at RLB is due to the presence of asphalt (Shaw, 2007), which both trapped the organisms and also preserved their remains in such remarkable condition. The site, dating from 11,000 to 45,000 years BP (Marcus and Berger, 1984; O'Keefe et al., 2009), is

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the richest source of late Pleistocene terrestrial fossils known (Akersten et al., 1983; Shaw and Quinn, 1986) and is the standard for the Rancholabrean North American Land Mammal Age (Savage, 1951; Savage et al., 1954). These accumulations are the result of a complex system of faulting within the Newport–Inglewood fault zone (Quinn et al., 2000). This geology is defined by folding and dipping of subsurface strata containing structural traps filled with petroleum, and migration of degraded petroleum (asphalt) to the ground surface as the result of up-dip leakage from oil sands (Wright, 1987) and/or along fractures and fissures within clayey siltstones (Quinn et al., 1997). At the ground surface, "stratiform" deposits develop around active vents and often produce sticky, sheet-like deposits in which animals become stuck, and their remains become preserved by asphalt saturation (Shaw and Quinn, 1986; Quinn, 1992). Some of these individual asphaltic discharges vented for thousands of years, typically resulting in cone-shaped deposits of petroleum-saturated sediment mixed with the remains of plants and animals (Woodard and Marcus, 1971), although rare, shallow, laterally extensive deposits have also been described as containing fossils accumulated over shorter depositional periods (Shaw and Quinn, 1986).

From 1913 to 1915, the Natural History Museum of Los Angeles County (LACM) was given exclusive excavation rights to the site, after which 23 acres of land containing the most extensive fossil deposits were donated to the County of Los Angeles. More than 1 million specimens were recovered during these two years of LACM excavation. These specimens comprise the Hancock Collection and are housed at the La Brea Tar Pits and Museum. Unfortunately, the early excavators focused their efforts on "perfectly preserved" items, so they rarely noticed or collected remains of smaller organisms or noted important information pertaining to geology and taphonomy. Newer excavations have resulted in a much more thorough understanding of the fauna from the site (Shaw, 1982). This has allowed the recovery of fossil items rarely preserved during in the early excavations, including some hyoid elements, bacula, auditory ossicles, and clavicles (Hartstone-Rose et al., 2012).

CARNIVORAN AND CANID BACULA

Though the baculum has often been ignored in carnivoran morphometric studies, the few studies that have focused on this bone have found it to be highly variable between closely related species and yet fairly morphologically uniform within them; thus, the baculum is a valuable bone for species differentiation (Didier, 1946, 1948, 1949, 1950; Burt, 1960; Long and Frank, 1968; Patterson and Thaeler, 1982; Mondolfi, 1983; Patterson, 1983; Tarasov, 1984; Decker, 1991; Johnson, 1991; Baryshnikov and Abramov, 1997, 1998; Lariviere and Ferguson, 2002; Baryshnikov et al., 2003; Sovova et al., 2007; Sharir et al., 2011; Abella et al., 2013). Many studies have discussed the anatomy of the baculum for specific carnivoran taxa—especially specific species of mustelids (Didier, 1948; Friley, 1949; Wright, 1949, 1950; Elder, 1951; Burt, 1960; Walton, 1968; Harrison, 1982; Hancox, 1987; Johnson, 1991; King, 1991; Kierdorf, 1996; Baryshnikov and Abramov, 1997, 1998; Frost et al., 1997; Harding et al., 1999; Aulerich et al., 2000; Baryshnikov et al., 2003; Tumanov, 2005; Abramov et al., 2008; Albayrak et al., 2008; Elsasser and Parker, 2008; Miller and Nagorsen, 2008; Harding and Smith, 2009; Krawczyk et al., 2011; Persson et al., 2011; Schulte-Hostedde et al., 2011; Vercillo and Ragni, 2011; Yu et al., 2011), pinnipeds (Scheffer, 1950; Burt, 1960; Ryg et al., 1991; Vanbree, 1994; Dixson, 1995; Miller et al., 1998, 1999, 2000; Capasso, 1999; Oosthuizen and Miller, 2000; Morejohn, 2001; Born, 2003; Yurkowski et al., 2011), and to a lesser extent viverrids (Jia et al., 2001), procyonids (Didier, 1950; Burt, 1960; Decker, 1991; Lutz, 1991; Martucci et al., 2011), ursids (Didier, 1950; Burt, 1960; Mondolfi, 1983; Dyck et al., 2004; Thiemann et al., 2006; Sonne et al., 2007; Abella et al., 2013), and felids (Didier, 1949; Burt, 1960; Schauenberg, 1979; Tumlison and McDaniel, 1984), but only a few have focused on canid bacula (Didier, 1946; Burt, 1960; Eleftheriou and Stanley, 1963; Sharir et al., 2011). While many of these studies have focused on age determination based on the baculum—an important variable given the RLB *Canis dirus* (dire wolf) sample (see below)—the two studies (Didier, 1946; Burt, 1960) that discuss wild canid bacula describe only the adult morphology. The only two studies to examine the ontogeny of this bone in canids (Eleftheriou and Stanley, 1963; Sharir et al., 2011) studied only a small sample of domestic dogs. No study has examined the functional morphology of variation in canid bacular shape. Though we attempted to gather an ontogenetic canid bacular sample from the American Museum of Natural History (AMNH) and Smithsonian (USNM), the relatively few canid bacula preserved in these collections are all from adult specimens of similar osteological maturity. Not only are there no juvenile large canid bacula in these collections, there are no bacula from subadult or senescent specimens either. Thus, although the scant literature on canid comparative bacular anatomy is thorough enough to contextualize the significance of the differences between the bacula of *C. dirus* and other canids, our efforts to sort the RLB *C. dirus* specimens into age classes and discuss the functional interpretation of this morphology is conjecture based on findings of more thoroughly studied carnivoran species.

THE COMPARATIVE ANATOMY OF *CANIS DIRUS*

The vast majority of bacula recovered from RLB (those held in the La Brea Tar Pits and Museum as well as those at the University of California Museum of Paleontology (UCMP) and distributed to other collections—e.g., several specimens at the AMNH and USNM) belong to *C. dirus*. Although the baculum of *C. dirus* has been discussed previously (Ware, 2006), a detailed morphological and ontogenetic analysis has not been done, nor has this bone been thoroughly compared with that of other canids. However, qualitatively, it is clear that the dire wolf baculum is substantially different from that of *Canis lupus* (gray wolf)—the most obvious comparative taxon and the largest modern canid—and thus a review of the literature on phylogenetic and comparative postcrania of *C. dirus* is warranted.

Phylogenetically, *C. dirus* is the most derived member of the genus *Canis* in the Americas, possessing a suite of cranial characters that distinguish it from congeners (Nowak, 1979; Berta, 1988; Tedford et al., 2009). In addition to discrete cranial differences, an analysis using 15 cranial measurements completely separates *C. dirus* and *C. lupus* morphologically (Nowak, 1979). While examination of the dire wolf has focused on the skull for purposes of species identification and paleoecological inference, several studies have examined postcranial dimensions of *C. dirus*, making comparisons with *C. lupus* (Merriam, 1912; Stock et al., 1946; Nigra and Lance, 1947; Stock and Lance, 1948; Kurtén, 1984). These include examination of the lengths of dire wolf metapodials from RLB (Nigra and Lance, 1947) and study of the remaining limb elements and overall limb length, making comparisons to eight individuals representing three subspecies of *C. lupus* (Stock and Lance, 1948). The results indicate that *C. dirus* from RLB had relatively shorter hind limbs than *Canis lupus occidentalis,* a large Albertan subspecies, but the difference is slight (about 8%), with the disparity resulting from a significantly shorter tibia and metatarsus in *C. dirus*. This shortness is also evident in the lower bones of the forelimb, although it is not as pronounced. While the dire wolf is smaller in limb proportion than *C. l. occidentalis*, the same study noted that *C. dirus* is larger than *Canis lupus irremotus*, a subspecies occurring in the Rocky Mountains south of *C. l. occidentalis* (Stock and Lance, 1948). The gray wolf is geographically variable in skeletal measurements among subspecies, so it is not surprising that RLB *C. dirus* falls between some *C. lupus* populations in size. Of further significance is that these early studies considered only the RLB population of dire wolves.

Geographic differences in dire wolves were not evaluated in detail until 30 years ago when a study compared skeletal variation in dire wolves throughout North America and found marked differences between dire wolves from the west (California and Mexico) and east of the Continental Divide (Kurtén, 1984). Additionally, some temporal variation is indicated, with a reduction in size noted when comparing Sangamonian and late Wisconsinan *Canis dirus dirus*. Based mainly on limb proportions and a few craniodental differences, dire wolf material in California and Mexico was referred to a separate subspecies, *Canis dirus guildayi,* with specimens east of the North American Continental Divide referred to *C. d. dirus*. Little overlap in individual element length between the two subspecies suggests that size can be used to distinguish between the two populations. *Canis dirus dirus* has significantly longer limbs than *C. d. guildayi*, reflected by greater than 15% longer radii and metapodials, and about 10% longer humeri, femora, and tibiae. In overall limb proportions, *C. d. dirus* has a 14.3% longer forelimb and a 9.7% longer hindlimb. Compared with the *C. lupus* data from Stock and Lance (Stock and Lance 1948), *C. d. dirus* and *C. lupus* deviate from the RLB *C. d. guildayi* in the same manner. The Stock and Lance (Stock and Lance, 1948) *C. lupus* approaches *C. d. dirus* in absolute size of limb length. Furthermore, *C. d. dirus* not only has long limbs but the front limb to hind limb ratio is 94.6% compared with 90.8% for *C. d. guildayi* and about 92% for *C. lupus* (Kurtén, 1984). While the postcranial studies of dire wolf indicate some intraspecific variation, and interspecific variation when compared with *C. lupus*, the relatively modest variation is in stark contrast to the results of this study when comparing *C. dirus* and *C. lupus* bacula, suggesting that the distinct *C. dirus* baculum is an important taxonomic tool for species identification.

MATERIALS AND METHODS

SAMPLE

All the fossil bacula curated at the La Brea Tar Pits and Museum were compared with modern analogues held at the AMNH and USNM. The sample includes 18 *Canis latrans* bacula, two bacula of *Mustela*, one of *Taxidea*, and one baculum previously described as belonging to *Urocyon* (Fig. 1). It also contains bacula from ca. 400 *C. dirus* individuals. We measured and photographed all of the complete specimens (N = 159). No bacula from other taxa have yet been

Figure 1 The bacula of RLB excluding those of *C. dirus*. Lateral views. **a.** A representative *C. latrans* specimen (LACMHC 14169); **b, c.** *Mustela* sp. (LACMP23-2081 and LACMRLP R50903 reversed); **d.** *Urocyon cinereoargenteus* (LACMRLP R38303); **e.** *Taxidea taxus* (LACMRLP R18598). Distal is to the left.

identified in the La Brea Tar Pits and Museum collection.

The RLB specimens were compared with all of the modern relatives in the collections of the AMNH and USNM. These specimens are uncommonly curated in these collections but the comparative sample includes all 10 *C. lupus* bacula available in the two collections and bacula from one *C. rufus*, three *Urocyon*, three *Taxidea*, and four *Mustela frenata* (the most likely taxon represented at RLB). The AMNH and USNM do house relatively large samples of modern *C. latrans*, and we collected data on 21 specimens from throughout the entire modern range of the species.

MEASUREMENTS

Nine measurements (Fig. 2) were taken on each specimen using digital Mitutoyo calipers to the nearest 0.01 mm connected by cable directly to a spreadsheet. These were all instrumentally determined maximum or minimum measurements (see Fig. 2 caption for description).

In addition to these raw measurements, we created a volumetric size proxy modeling each baculum as an elliptical cylinder using the midshaft height (a) and width (b) along with total length (l), as follows: $V = \pi * 0.5a * 0.5b * l$.

ONTOGENETIC STAGE SCORING

Because of apparent variation in the developmental ages of the *C. dirus* individuals, it was important to sort the samples into ontogenetic stages before comparing their sizes and shapes within and across the species. As discussed above, no previous studies have described maturation stages of canid bacula, and unfortunately, there is not enough ontogenetic variation in the museum samples to establish correlates of this anatomy to actual ages or other measures of development

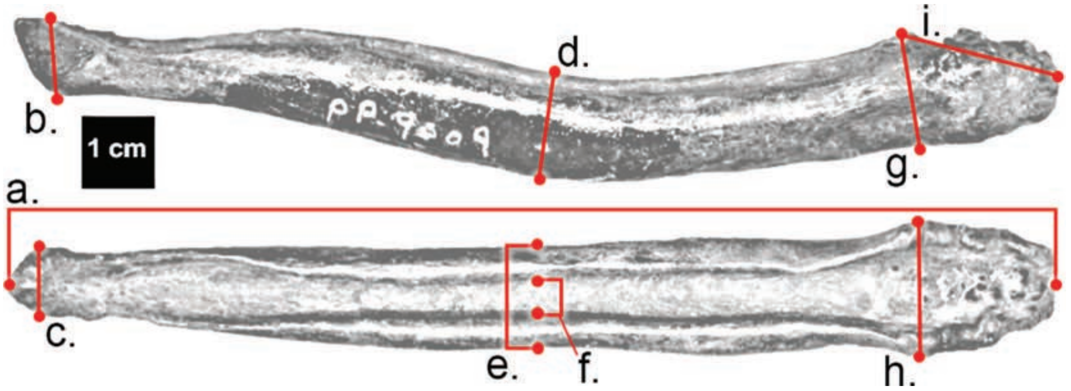

Figure 2 Measurements. *Canis dirus* (LACMHC PP9009) lateral view (top) and dorsal view (bottom). Distal is to the left. **a.** Total length, **b.** distal end height, **c.** distal end width, **d.** midshaft height, **e.** midshaft width, **f.** width of dorsal opening of the urethral canal at the midshaft (hereafter referred to as "urethral canal width"), **g.** proximal end height, **h.** proximal end width, **i.** proximal end length (measured from the line connecting the points represented by h and the proximal-most point of the baculum).

Figure 3 *Canis dirus* bacular ontogenetic stage scores compared with the baculum of *C. lupus*. Lateral (left) and dorsal (right) views. From top (stage 0.5) to bottom (*C. lupus*), these specimens are LACMRLP R30149, LACMHC PP8866, PP8649, PP9141, PP9009, PP8650, PP8854, PP8638, and AMNH 98230. *Canis lupus* is stage 3. Some images are reversed to align all distal ends to the left.

(e.g., dental or epiphyseal ages), and the morphology of the canid baculum is sufficiently different from the other carnivoran taxa for which ontogenetic studies have been published that we are reluctant to assign anything but relative maturation stages within this sample. To that end, we were able to divide the sample into four clear morphostages (and fairly apparent semistages between these) that almost certainly correspond to ontogenetic development from youngest (stages 0.5 and 1) to oldest (stages 3.5 and 4) individuals (Fig. 3; Table 1). Though securely associated specimens at RLB are rare, one relatively complete *C. dirus* skeleton preserves a baculum (LACMPMS 1012-5). This specimen, ontogenetic stage 3, corresponds to the relatively mature state that we would expect based on the dental wear of the associated cranium and mandible and the general robusticity of the postcranial elements. A juvenile baculum (stage score 1.5, LACMRLP R30149) was found in close proximity to postcranial elements with unfused epiphyses, as we would predict from this stage score, but the association of these specimens is unconfirmed in this highly jumbled deposit.

Data were collected in Excel (MS Office 2007 and 2013) and analyzed in JMP (SAS Institute Inc. version 10.0.2). Because of small sample sizes of comparative material, nonparametric tests (Kruskal–Wallis and Wilcoxon) were used to determine statistical differences (alpha = 0.05) between samples.

RESULTS

The non-*Canis* samples are too small to determine statistical differences between the RLB and modern congeners. Qualitatively, the mustelids fall within the variation of the formally studied AMNH and USNM samples, as well as other specimens of these taxa that we have observed. At 35.80 mm long, the "*Urocyon*" specimen is much smaller than the three modern congeners that we studied, which measure 59.40–70.80 mm. This specimen might be juvenile (though at this apparent level of ossification, it should probably be much longer at this stage), or it could have been misidentified. Clearly further research is warranted, especially if more small bacula are identified from RLB.

Statistically, the RLB coyotes cannot be differentiated from their modern conspecifics. Though they are larger in all but two of the 10 metrics, the samples overlap so substantially, both qualitatively and statistically, that differentiation of the fossil and modern samples would be unjustified based on this bone alone. However, there are additional RLB *C. latrans* bacula in the UCMP collection, and with expanded sampling of both fossil and modern specimens, more fine-grained functional hypotheses might be tested.

The most dramatic statistical finding of this study pertains to the substantial dire wolf sample: While these bones clearly separate *C. dirus* from *C. lupus* qualitatively, from a statistical perspective,

Table 1 Ontogenetic stage score definitions.

Stage	Definition
0.5	Length is up to 50% of maximum length, and bacula are not fully ossified.
1.0	Length is 50%–60% of maximum length, and they are the smallest ossified bacula with porous ends, a broad distal end, and a proximal end that is not yet fully defined. A substantial urethral groove runs the entire length of the baculum.
2.0	Length is 70%–80% of maximum length. A deep urethral groove extends up to 90% of the total length, and the baculum is fairly gracile.
3.0	Length is 80%–90% of maximum length. The more defined distal end is pointed or bulbous, and the proximal end is more substantial with increased ossification and rugosity. The urethral groove is deep, extends up to 80% of total length, and has encroaching dorsal edges (i.e., the dorsal edges of the groove are closer in approximation than the maximum mediolateral diameter of the canal).
4.0	Length is 90%–100% of maximum length. The well-defined distal ends are pointed or bulbous and the proximal ends are very substantially defined with substantial ossification and rugosity. The urethral groove extends approximately 70% of total length, appearing more constrained due to the lateral walls encroaching deeply at the dorsal edges. Dorsal edges of the urethral groove are highly rugose, forming a noticeable edge on the lateral sides of the baculum that extends approximately 50% of the way toward the ventral side, while the ventral surface appears as a smooth rounded crest. The rugosity starts approximately 20%–30% from the distal end and extends to approximately 60% from the distal end. This appears to be a tendinous origin, possibly of a tissue covering the urethral canal. Thus the presumably more mature animals would appear to have a stronger urethral cover.

the baculum separates these taxa more substantially than any other quantified morphology thus far described. That is, these two taxa have been distinguished based almost entirely on cranial features, particularly discrete morphological characters (Nowak, 1979; Berta, 1988; Tedford et al., 2009), and while these features reliably separate the species, they are markedly more subtle than the bacular differences. The two taxa are statistically distinct in nine of the ten metrics (Table 2).

When the dire wolf bacular variables are regressed (ordinary least squares) over geological time (dates taken from Stock, 1992; O'Keefe et al., 2009) three slopes are significant: *C. dirus* bacula get slightly, though statistically significantly, shorter over time, but their distal heights and widths become larger. These interpretations may change based on the ongoing reevaluation of the dates of the RLB deposits.

Of the ca. 400 *C. dirus* bacula in the La Brea Tar Pits and Museum collection, only about eight show evidence of pathology. Most of these demonstrate some degree of twisting along the long axis that may have been either congenital or the result of trauma. Only a few of the specimens show clear signs of antemortem breakage and healing (Fig. 4). This is a far lower percentage of antemortem trauma than one would expect from a population of animals that demonstrates such high levels of injuries in other regions of their skeletons (Van Valkenburgh and Hertel, 1993; Ware, 2006). This is especially true given that this bone has a notable propensity for breakage in other lineages of carnivores (Kierdorf, 1996; Capasso, 1999; Bartosiewicz, 2000, 2008; Lariviere and Ferguson, 2002).

DISCUSSION AND CONCLUSIONS

Given that bacula are so rare in the fossil record, the collections at Rancho La Brea give us the perfect opportunity to examine this bone. No doubt, as more microfossils are recovered, and

Table 2 Size comparison between *C. dirus* and *C. lupus* bacular variables.

	C. dirus (N = 137[a]) mean (SD)	*C. lupus* (N = 10) mean (SD)	Wilcoxon p-value
Volumetric proxy (mm^3)	25,748.1 (9,670.9)	5,637.0 (1,413.8)	<0.0001
Total length (mm)	159.4 (19.7)	109.8 (8.1)	<0.0001
Proximal end length (mm)	29.9 (5.5)	16.73 (5.7)	<0.0001
Proximal end width (mm)	15.4 (2.0)	7.72 (1.6)	<0.0001
Proximal end height (mm)	20.7 (3.4)	8.9 (1.6)	<0.0001
Midshaft width (mm)	14.3 (2.6)	8.2 (1.3)	<0.0001
Midshaft height (mm)	13.9 (2.0)	7.9 (0.7)	<0.0001
Urethral canal width (mm)	4.35 (0.8)	4.2 (0.8)	0.7192
Distal end height (mm)	6.36 (1.6)	4.41 (0.3)	<0.0001
Distal end width (mm)	7.44 (1.5)	4.42 (1.3)	<0.0001

[a] Specimens that were categorized into stage scores below 2.0 were excluded from statistical analysis.

Figure 4 A broken, displaced, and healed *C. dirus* baculum (LACMHC 8291). Dorsal view, distal is left, proximal end not shown.

with a more specific search image, it is likely only a matter of time before bacula of the felids (especially the ubiquitous *Smilodon fatalis*) and ursids will be identified. While the small sample sizes of bacula of the several species for which they have been recovered precludes differentiation of these specimens from their modern relatives, the large sample of *C. dirus* bacula has yielded important results. Namely, *C. dirus* bacula are radically different than *C. lupus* bacula—a difference that far exceeds, both qualitatively and quantitatively, that found in any other element commonly used to differentiate the taxa.

But what explains this difference? Previously, larger (mainly, *longer*) bacula have been correlated to colder environments (Ferguson and Lariviere, 2004), but most commonly they are associated with higher levels of male–male competition and multimale mating structures (Dixson, 1987, 1995; Hosken et al., 2001; Dixson et al., 2004; Ferguson and Lariviere, 2004; Schulte-Hostedde et al., 2011; Abella et al., 2013). Though dire wolf bacula are significantly longer than gray wolf bacula, the difference in length is not as dramatic as that seen in other lineages (e.g., ursids; Abella et al., 2013). However, they are much more massive. We believe that this accounts for the notable relative scarcity of healed bacula at RLB: Though La Brea was clearly a place of great interspecific competition among the carnivores, and presumably great intraspecific competition given the propensity of specimens accumulated there, it is possible that dire wolves damaged their bacula relatively rarely because they had evolved increased robusticity to withstand aggression. Bartosiewicz (2000) predicted that fractures would occur in carnivorans during copulation when fights between males cause the mating male to jump suddenly and snap the bone. Perhaps the robusticity that we have observed is an evolutionary response to that type of aggression.

In all but one metric, dire wolf bacula are more substantial than those of their modern congener, but that one metric may be quite telling: The urethral canals of the two taxa are statistically indistinguishable. This structure is likely simply a bony correlate of the soft tissue anatomy. If this is the case, then, as in other elements of their postcranial anatomy, dire wolf urethrae were not substantially larger those of gray wolves; however, their penises were—especially in terms of their cross-sectional geometries. Perhaps this was an evolutionary response to a more competitive sociosexual environment—evolution that likely preceded the late Pleistocene if the large baculum of *C. dirus* was autapomorphic. The distinctive characteristics of the dire wolf baculum have been present throughout the geologic range of the species, as indicated by the proximal end of a *C. dirus* baculum (UCMP 67930) from the mid-Pleistocene Irvington site (Dundas, 1999; Tedford et al., 2009). Irvington documents one of the oldest occurrences of *C. dirus* in the fossil record, at least 0.78 Ma and possibly older than 1.21 Ma in age (Bell and Bever, 2006). Unfortunately, knowledge of bacula for other Pleistocene canid taxa, such as *Canis armbrusteri*, is lacking.

Eleftheriou and Stanley (1963) found that testosterone propionate and growth hormone influenced the size of the baculum in two breeds of domestic dogs, but only in puppies less than 18 weeks old. If this is the mechanism that controls the growth of the baculum in *C. dirus*, then the extreme robusticity in this bone was likely developed long before sexual maturity. Hopefully more bacula of canids spanning the evolutionary gap between *Hesperocyon* and *C. dirus* will be described and help explain this extraordinary morphology.

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Last Years of Life and Season of Death of a Columbian Mammoth from Rancho La Brea

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ABSTRACT. Excavations near the Los Angeles County Museum of Art in 2006 uncovered Pleistocene-age fluvial deposits containing the disarticulated skeleton of an adult Columbian mammoth (*Mammuthus columbi*). The skeleton is about 80% complete, with osteological and dental features suggesting a male with a Laws' Age Class of XXVI, representing an adult of prime reproductive age. A sample was excised from near the proximal end of the left tusk to evaluate the last years of life and assess season of death. This sample was scanned by microCT then thin-sectioned. Viewing microCT data in transverse section, the dentin is organized in concentric zones paralleling the pulp cavity surface. Between the dentin–cementum interface and the pulp surface, there are somewhat regularly spaced, abrupt transitions (inward, in the direction of dentin apposition) from higher to lower x-ray attenuation, suggesting shifts from higher to lower density. Similar transitions have been interpreted previously as reflecting winter–spring boundaries. These same loci are associated consistently with periradicular topographic features on the external surface of the alveolar portion of the tusk. Analysis of approximately weekly incremental features in a transverse thin section shows little systematic seasonal variation in rates of dentin apposition—not surprising for southern California—but shorter term patterns of rate variation do help confirm some of our identifications of year boundaries. Daily dentin increments are visible in parts of the sequence, but not consistently. Judging from rates of tusk growth in the last years of life, death appears to have come in early summer, the season identified in prior work as normal for musth, the period of heightened aggression and sexual activity in which mating and male–male conflict would be expected to occur. We suspect that this male died as a result of soft-tissue injuries sustained in a musth conflict.

INTRODUCTION

In 2006, construction of an underground parking structure by the Los Angeles County Museum of Art in southern California exposed abundant fossil vertebrate specimens from the Rancholabrean North American Land Mammal Age. This assemblage was preserved in fluvial deposits that had been postdepositionally permeated by asphalt (Harris et al., 2013), and it contained a nearly complete but mostly disarticulated skeleton of a large Columbian mammoth, *Mammuthus columbi* (Falconer, 1857). Approximately 80% of the skeleton was recovered.

This mammoth, nicknamed "Zed," is the largest and most complete proboscidean collected from Rancho La Brea. An uncalibrated radiocarbon date on Zed (second thoracic vertebra P23-1316) returned an age of 36,770 ± 750 radiocarbon years before present (Fuller et al., 2014). The left tusk of this individual (P23-10910) is 318 cm long, measured along its outer curve, and has a maximum diameter of 24 cm at a position 90 cm from the proximal margin (Fig. 1). Tusk dimensions, especially length and circumference, confirm that this individual is a male (Smith and Fisher, 2011, 2013). Furthermore, the stage of molar replacement and wear suggests a Laws' Age Class (1966) of XXVI, representing an adult of prime reproductive age (Fig. 2).

As in other proboscideans, the tusks of Columbian mammoths record a remarkable diversity of information on life history. This information can be extracted from structural and compositional

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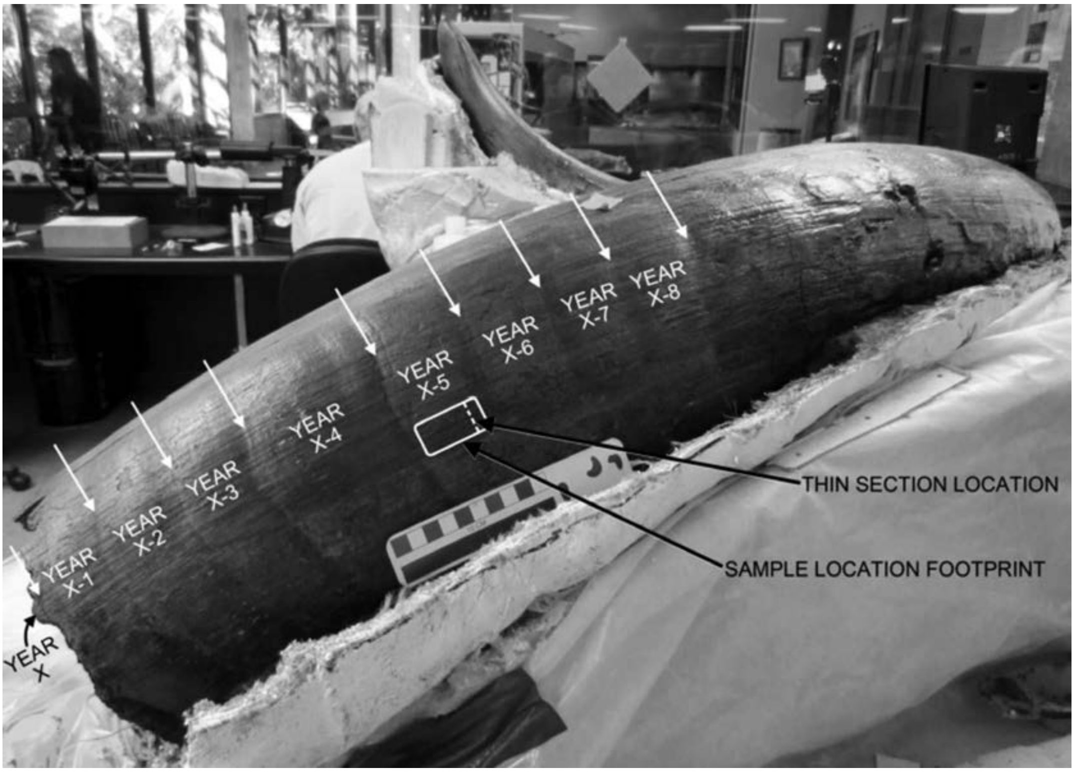

Figure 1 Zed's left tusk, with proximal end in foreground (distal end in background), showing location of sample block used for microCT analysis, thin section production (for increment thickness analysis), and stable isotope sampling. White arrows mark boundaries of the last eight periradicular bands on the external surface. Breakage of the proximal margin has removed all but a small fragment of the extensional increment for the partial year (Year X, black font) that terminates the tusk record. The previous eight years of tusk extension are labeled (white font) within their respective periradicular bands. Scale bar = 10 cm.

variation within annual (first-order), weekly (second-order), and daily (third-order) growth increments observable in tusks (Fisher, 2001). First-order dentin increments can also be observed in data from computed tomography on a micro scale (microCT) (Fisher et al., 2014). Because incremental features form periodically, increment thickness can be used to assess growth rates, which are in turn related to nutrition and health of the individual (Fisher, 1996). By comparing rates of dentin apposition (thickness increase) and extension (length increase) with compositional changes and with external growth features of the tusk, it is often possible to recover information on specific life history events, including season of death.

MATERIALS AND METHODS

The left tusk of Zed was prepared at the La Brea Tar Pits and Museum. This tusk is largely intact, with only minor fracturing along its proximal margin. A sample block approximately 5 cm long and 2.5 cm wide, extending from the outermost cementum, inward to the pulp cavity surface, was removed from the tusk using a Dremel hand-held grinder and a carbide bit. Given the conical geometry of the pulp cavity, the sample block was 46 mm thick (along a tusk radius) at its distal end and 36 mm thick at its proximal end. The sample site was located along the outer curve of the tusk (to maximize increment thickness), about 23 cm from the broken proximal margin, within a sequence of relatively well-defined periradicular topographic features (Fig. 1).

During removal of the sample block, the dentin sequence separated along a parting that followed a former position of the appositional surface. The outer block of dentin, with attached cementum, was set aside, and cutting was continued on the remainder of the sample block. This was removed intact, and the two parts were assembled with quick-setting epoxy. Inspection of the block revealed that the dentin was somewhat chalky (suggesting degradation of much of its original collagen matrix), but still structurally sound.

Following repair of the sample block, a region near its distal end was imaged in the MicroCT Core Facility at the University of Michigan School of Dentistry, using a Scanco Medical μCT 100 operating at 90 kV, 78 μA, and 500 ms,

Figure 2 Occlusal view of Zed's mandible, showing left and right lower m3s.

yielding uniform cubic voxels 60 μm on a side. To observe patterns of variation in x-ray attenuation within the tusk cross section, the CT scan was processed using Amira 5.4.1. Zones of high and low x-ray attenuation were noted by eye (Fig. 3A) and quantified by luminance measurements. Time-dependent luminance variation was documented using the Measure tool in ImageJ (Rasband, 1997) on a swath of pixels extending along a transect in the direction of dentin apposition (normal to appositional features). Grayscale values of 10 neighboring pixels (the swath width) paralleling appositional features were averaged (in Adobe Photoshop CS5) for each position along the transect to reduce the influence of more highly localized factors (e.g., CT artifacts, vacuities, dentinal tubules).

For additional analyses, two adjacent 5-mm-thick slabs were cut from the sample block along transverse planes normal to the appositional surface using a Buehler Isomet saw with a diamond wafering blade. Ethanol was used as a lubricant during cutting; unlike cutting oils, ethanol evaporates quickly from the sample leaving no residue. We avoid using water or aqueous solutions because the collagen in dentin is hygroscopic and expands in the presence of water, fracturing adjacent dentin that has not yet absorbed comparable amounts of water. A transverse thin section was made from one of the slabs using ethanol for cutting and polishing (Fisher and Fox, 2003). This thin section was examined initially at 25× with a stereomicroscope (Wild) and then at 40× with a petrographic microscope (Leitz). Sixteen photomicrographs (e.g., Fig. 3B) were taken along a transect from the cementum to the pulp cavity surface using plane-polarized light, with kerosene added to the slide to reduce scattering of light and enhance contrast. Thicknesses of second-order (approximately weekly) increments were measured from these micrographs using the ImageJ plug-in Inc Meas 1.3c (Rountrey, 2009).

The second slab cut from the sample block was used as a source for a time series of samples for analyzing stable isotope changes in the tusk during the last years of life. Mill paths for individual samples were laid out on a high-resolution scan of the polished slab surface, which was also aligned with a virtual section from the microCT scan. Comparing both records allowed us to limit

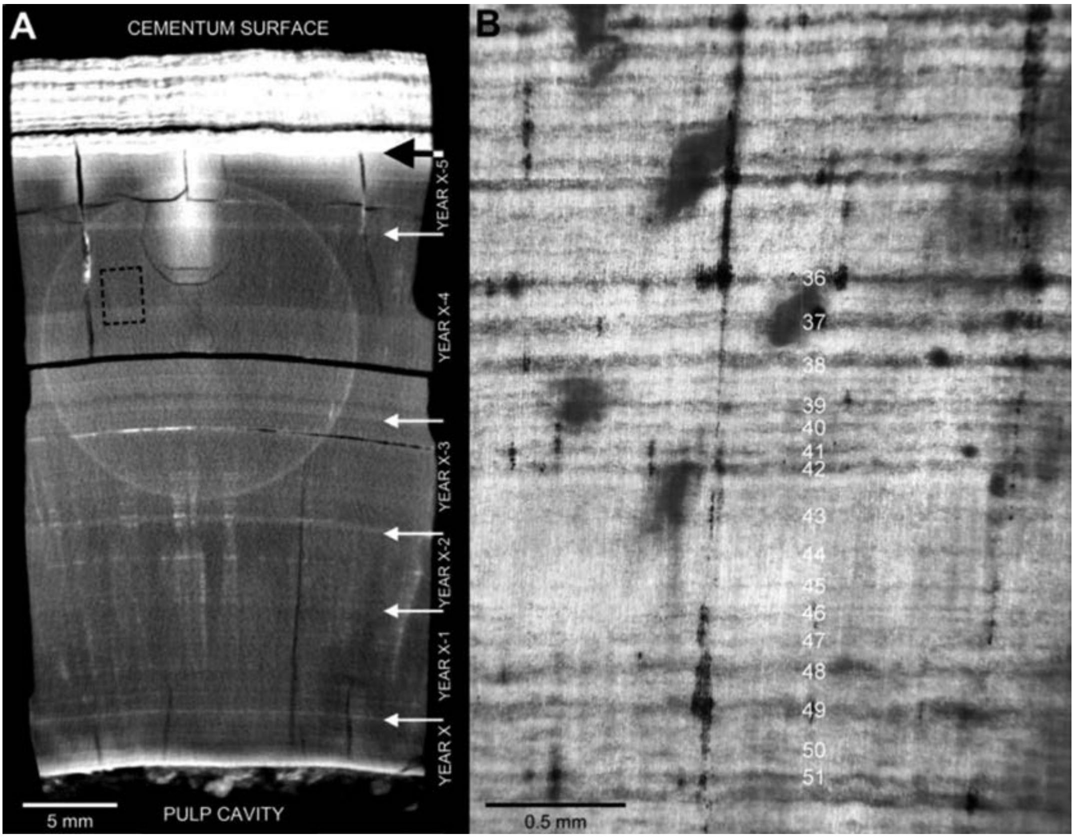

Figure 3 **A.** MicroCT image of a virtual transverse section of tusk cementum (brighter zone near upper, outer surface) and dentin (generally darker) extending from the dentin–cementum interface (large black arrow along right margin) to the surface of the pulp cavity (lower border of section). Smaller white arrows mark locations where there is an abrupt change (moving in the direction of apposition) from dentin with higher x-ray attenuation (brighter) to dentin with lower attenuation (darker). We hypothesize that these transitions mark approximate winter–spring boundaries. Annual increments of dentin apposition are labeled along the right margin, between white arrows, and correspond to years labeled in Figure 1. The bright circle in the upper part of the image is a ring artifact from the CT scan. **B.** Photograph of a region (indicated in A by a black dashed rectangle) of the transverse thin section of tusk dentin showing weekly, and some daily, increments; numbers mark second-order increments included in the profile of variation in second-order increment thickness.

samples to areas bounded by growth lines (time-dependent appositional discontinuities). Mill paths were later transferred to the slab surface, and dentin powders from 30 samples of equal thickness (0.7 mm) were collected using a carbide bit and a manual drilling stage under a stereomicroscope (Fig. 4).

Samples were pretreated for isotope analysis of structural carbonate following methods described in Rountrey (2009). About 6.25 mg of each powder sample was vortexed in 0.5 ml of 30% H_2O_2 and then left for 24 hours in a fume hood. Samples were subsequently rinsed in five separate washes of 1.0 ml ultrapure water with vortexing, followed by centrifugation (five minutes at 6,000 rpm), and then by removal of supernatant between each wash. The rinsed samples were then vortexed in 0.5 ml of a 1 M acetic acid–calcium acetate buffer solution and left in a fume hood for an additional 24 hours. Following this, the samples were again rinsed five times in ultrapure water, as described above. Samples were then freeze-dried overnight to remove all water. Using a microbalance, we measured 0.75 mg of each sample, loaded samples into boats, and then analyzed carbon and oxygen isotope ratios using a Thermo Finnigan GasBench II, coupled to the inlet of a Thermo Finnigan Delta V+ mass spectrometer.

RESULTS

EXTERNAL FEATURES OF THE TUSK

About 55 cm from the proximal end of the tusk, we noted a discontinuity in surface texture characterized by a greater degree of abrasion and polish evident distally and more surface

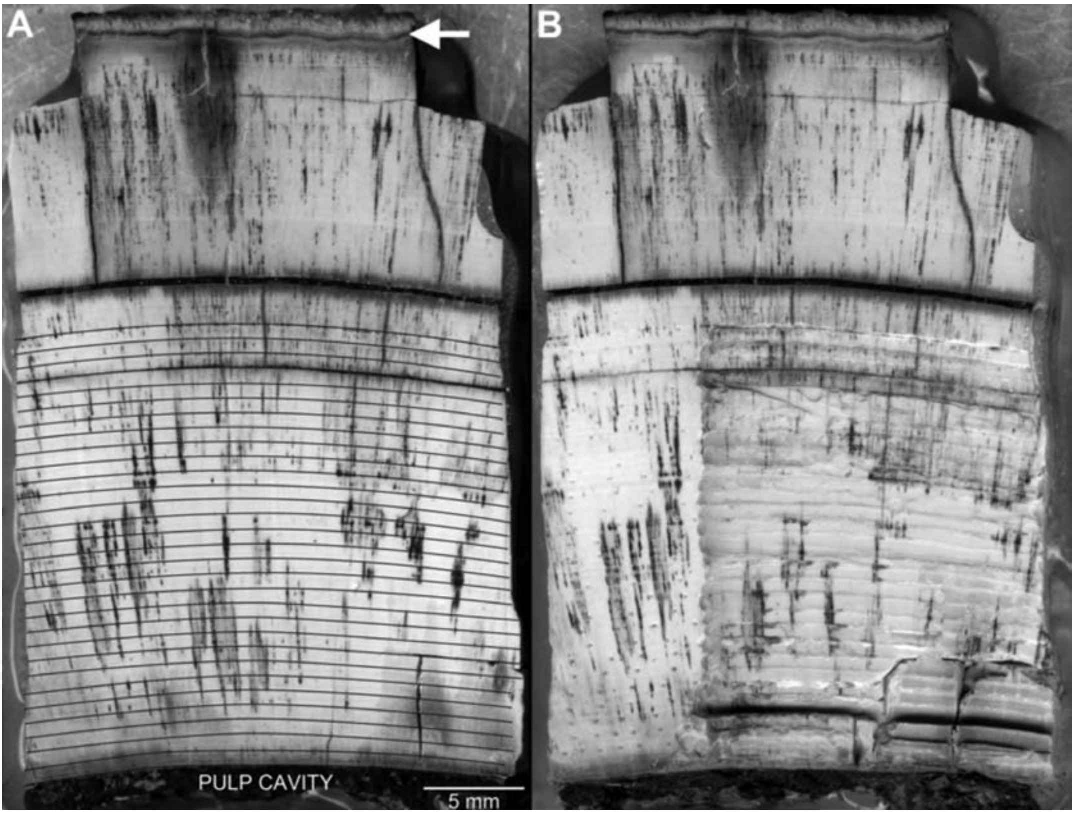

Figure 4 Sample slab used for stable isotope analysis. Internal fractures allowed several fragments to separate from the upper part of the slab (including most of the cementum layer; cementum–dentin interface indicated by white arrow) during polishing of this surface. **A**. Black curved lines parallel to pulp cavity surface (lower border of sample slab) represent boundaries between planned serial samples to be collected along paths following second-order dentin increments. **B**. Slab after milling, showing consistency of planned and implemented serial sampling.

roughness (consistent with original attachment of periodontal ligament) preserved proximally. This shift marks the gingival (or alveolar) margin, separating the erupted part of the tusk that was subjected to use-wear during life (creating the smoother surface) from the proximal portion that was surrounded by and attached to periodontal ligament within the tusk alveolus. The external surface of the alveolar portion of the tusk displays a series of circumferential, undulatory topographic features referred to as "periradicular bands" (Dean, 1995; Fisher, 2008), where a single "band" is one cycle of proximodistal variability in surface relief. Complicating this picture, many tusks (and other teeth), including this one, show two (or even three) different scales of periradicular features in the form of finer scale features with short wavelengths and only subtle relief co-occurring with coarser scale features that have much longer wavelengths and more pronounced relief. Descriptions of this system of features confront several terminological issues (discussed below), but our usage follows Fisher (2008), where "periradicular features" include any of the circumferential topographic elements on tooth roots that represent structural increments of root extension. Such elements include sinuous, but locally linear, topographic features both positive ("ridges") and negative ("grooves") that roughly parallel the proximal, growing margin of the root. They also include areas that are bounded by such linear elements, though for clarity, we always distinguish between *increments* (the entirety of mass or surface added to an appositional system during an interval of time) and *boundaries* (features that demarcate increments and generally approximate a delimiting edge or interface of the appositional system at a point in its history).

Periradicular features originate as primary (original) relief on the dentin–cementum interface and therefore are usually most easily observed near the proximal margin of roots, where the cementum layer is thinnest. Farther from the proximal margin, where a greater accumulation of cementum mantles the topography of the dentin–cementum interface, periradicular features are often more difficult to distinguish (Laws, 1952). Additionally, when viewing periradicular

Table 1 Measurements of periradicular bands on Zed's left tusk. Bands are labeled backward in time, from the incomplete Year X, located at the proximal margin.

Distal margin of year	Distance to proximal end (cm)	Extensional length (cm), of year
X − 10	54.7	
X − 9	48.5	6.2, X − 10
X − 8	43.4	5.1, X − 9
X − 7	37.5	5.9, X − 8
X − 6	32.6	4.9, X − 7
X − 5	26.8	5.8, X − 6
X − 4	21.6	5.2, X − 5
X − 3	13.7	7.9, X − 4
X − 2	9.2	4.5, X − 3
X − 1	4.6	4.6, X − 2
X	0.6	4.0, X − 1
	0	0.6, X (incomplete)

features through the cover of cementum, some of the subtler features in a sequence may be obscured.

Periradicular features have a structural aspect in addition to their topographic expression, and this corresponds directly to elements of the hierarchy of incremental features documented in dentin cross sections (transverse or longitudinal; Fisher, 1984, 1987) or volumes (as in CT analyses; Fisher et al., 2014). We refer to the largest scale periradicular features as "first-order" and these reflect the same units of internal dentin structure that we describe as first-order and that have been demonstrated to recur with periods of about one year (Fisher, 1987, 1996, 2001; Koch et al., 1989). The next largest scale features are "second-order," corresponding to the second-order increments normally studied in dentin thin sections, and in mammoth tusks, these typically recur with periods of about one week (Fisher, 2001). On the external surface of Zed's tusk, there is generally a most-accentuated (within the local sequence) second-order negative periradicular feature, or groove, located within a broader, deeper trough separating successive positive first-order elements (ridges). We treat these grooves within troughs as bounding successive first-order periradicular bands and use their spacing along the outside curve of the tusk for quantifying the extensional magnitude of first-order periradicular bands. These features are shown in Figure 1, where low-angle lighting emphasizes the topography of first-order periradicular bands, and white arrows mark the boundaries of the last eight first-order features for which both distal and proximal boundaries are observed. Two additional first-order periradicular bands, distal to the last eight, were discerned during direct inspection but are not clear under the illumination used for Figure 1.

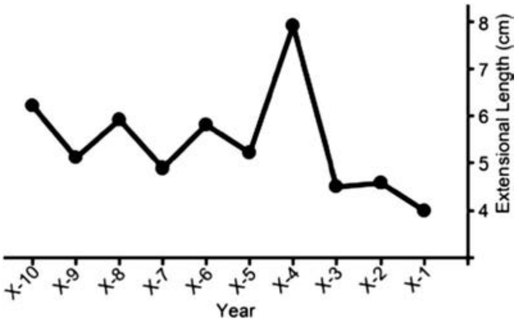

Figure 5 Graph showing extensional length of first-order periradicular bands between the gingival margin and the proximal margin of the tusk (data in Table 1). Years are numbered as in Figure 1, with Year X excluded because it is incomplete.

Extensional lengths of first-order periradicular bands on Zed's tusk are presented in Table 1. This series of measurements starts near the gingival margin simply because distal to this position, boundaries of periradicular features cannot be clearly distinguished on the external surface. There is no direct concordance between periradicular bands and the gingival (alveolar) margin because they represent separate aspects of anatomy—the first controlled by the geometry of the proximal margin of the tusk and the second by the geometry of the tusk "lip line." The measurements in Table 1 end with a year that is incomplete in two respects: (1) If we correctly interpret a short groove (marked by the proximal-most white arrow in Figure 1, offset from the others, near the proximal margin of the tusk) as a last boundary between first-order periradicular bands, death appears to have befallen this individual before the expected end of this last year of life, Year X, leaving it narrower than preceding years, and (2) the proximal margin of the tusk is broken all around its circumference, so that Year X is nowhere seen with the extensional magnitude that was in fact realized in life.

The pattern of variation in extensional length of first-order periradicular bands is shown in Figure 5. In this graph, we do not show Year X because it is incomplete and thus not directly comparable to the preceding 10 years. We provisionally accept the location of the periradicular feature marking the boundary between Years X and X − 1, despite its preservation on only a small portion of the tusk margin. The average extensional length over Years X − 1 through X − 10 is then 5.4 cm, with a general pattern of declining values, except for the unusually long Year X − 4.

Table 2 Molar measurements for Zed.

Tooth	RM3	LM3	Rm3	Lm3
Occlusal length (cm)	25.8	27.0	23.7	23.4
Number of lophs	>14	16	>15	>15
Lophs/occlusal surface	9	10	10	10.5
Maximum width (cm)	12.0 @ 5	12.3 @ 5	12.0 @ 5	12.3 @ 5
Crown height (cm)	>25	>25	[in mand.]	[in mand.]
Lamellar frequency	3.5	3.7	4.0	4.0
Enamel thickness (mm)	3.0	3.0	3.5	3.7

Abbreviations: [in mand.], tooth in mandible, measurement not accessible; >, specimen incomplete or obscured by associated bone; @, loph number at which width is greatest.

STAGE OF DENTAL DEVELOPMENT AND SEX

Close spatial association, lack of duplication of elements, and consistent sizes and stages of development provide compelling evidence that the dental and skeletal elements discussed here are associated remains of a single individual. Only one molar is present within each quadrant of the dentition, and in each case, dimensions and loph counts (Table 2) confirm identification as a third molar. Dental traits are consistent with other reports for *M. columbi*, although the lamellar frequency is low compared with other material attributed to this species in current taxonomic practice (e.g., Saunders, 1970; Agenbroad, 1994).

An occlusal view of Zed's mandible with lower molars is shown in Figure 2. Upper molars are in a similar, but slightly less advanced stage of wear, especially in regard to attrition of the anterior margin. Similar differences in wear between uppers and lowers are reported for *Loxodonta africana* (Laws, 1966). Stages of molar eruption and wear in Columbian mammoths and African elephants are not identical, but the best approximation to the configuration seen in Zed is to Laws' Age Class XXVI (Laws, 1966). Although there has been no formal calibration of the dental eruption and wear schedule of *M. columbi*, most investigators accept the working hypothesis that ages assigned to *Loxodonta* at comparable stages of eruption and wear are a reasonable estimate of Columbian mammoth ages (e.g., Graham, 1986; Agenbroad, 1994). This would place Zed at about 49 ± 2 years old.

Zed's tusk length and diameter are consistent with an age estimate of this magnitude. Accepting that first-order periradicular bands recur with approximately annual periodicity, the fact that 10 such periradicular bands occur within barely more than the proximal one-sixth of tusk length could be taken to imply an even greater age. However, years prior to the last 10 were likely characterized by greater extension rates than were realized during the last decade (judging from the life-long pattern of variation in extension rate documented for mastodons; Fisher, 2008). Zed's tusk diameter declines from 24 cm at a position 90 cm from the proximal margin to a value of 19.5 cm at the proximal margin, a pattern typical of fully mature individuals. Asphalt and sediment were not completely removed from the pulp cavity at the time of sampling, but the pulp cavity is clearly not as shallow as would be expected for a very old individual. Without further sampling and analysis, knowledge of Zed's age will remain imprecise, but we have no reason to reject the Laws' age estimate.

Zed was originally identified as male on the basis of molar width (male molars being appreciably wider than those of females). Zed's tusk length and circumference also support identifying him as a male. One of the best-studied assemblages of *M. columbi* is from the Hot Springs Mammoth Site of South Dakota, and most of the individuals preserved there are interpreted as sexually mature, but still young males (Agenbroad, 1994; Lister and Agenbroad, 1994). Zed's tusk is longer than published values for Hot Springs *M. columbi*, but his tusk circumference is near the mean for their distribution (Agenbroad, 1994:fig. 77). Given normal patterns of sexual dimorphism in proboscidean tusks (Fisher, 2008; Smith and Fisher, 2013), these measures are too great to consider this specimen female. Zed's pelvic aperture is not sufficiently intact to use its dimensions to evaluate sex (following Lister and Agenbroad, 1994), but the posterior aspect of his ischial tuberosities shows the relatively narrow V-shaped profile characteristic of males (Fisher, 2008:text-fig. 12C). The size and advanced state of epiphysis fusion on Zed's postcranial skeletal elements likewise corroborate his age and sex.

COMPUTED TOMOGRAPHIC FEATURES

X-ray microCT was used to assess density features within the sample block removed from the tusk. Within this three-dimensional dataset, the pulp cavity surface is a clear interface inclined relative to the outer surface of the block. The dentin–cementum interface is marked as a sharp transition in attenuation values (from higher values within cementum to generally lower values in dentin) that parallels the outer surface. Within the dentin sequence, smaller-scale transitions in attenuation value, some gradual and some abrupt, broadly parallel the pulp cavity surface and represent time-dependent variation in the attenuation value of coevally deposited dentin. We digitally extracted a slice oriented as a transverse section, perpendicular to the pulp cavity surface and to the transitions in attenuation value that parallel it. This slice was located near (and parallel to) the sample slabs that would later yield the thin section (dashed white line crossing the sample location footprint in Fig. 1). Viewing this virtual slice perpendicular to its principal plane and averaging attenuation through a thickness of 1 mm, we generated the image shown in Figure 3A. Luminance values in this image are a summation of attenuation values throughout the slice thickness, analogous to the optical summation of density that occurs in light microscopy.

Some luminance features in Figure 3A have nothing to do with time-dependent variation in properties of dentin. Air- or epoxy-filled cracks are much darker than average dentin values. The bright, ring-shaped feature in the upper part of the image is an artifact of the density reconstruction algorithm, and some of the vertically oriented (radially in the tusk) bright swaths represent so-called “dead tracts” (Avery, 1988), where the lumina of dentinal tubules have been partially filled with mineral, often as a response to some inflammatory process. The zone of high luminance adjacent to the pulp cavity could indicate early-diagenetic (postmortem) precipitation of carbonate within dentin pores most directly exposed to groundwater following burial. Globular loci of high luminance within the pulp cavity represent clastic sediments, surrounded by asphalt, that were left in place to protect the integrity of the pulp cavity surface.

Shifting to the more clearly zonal patterns of variation that parallel the pulp cavity surface, brighter zones (higher attenuation) suggest higher density of mineralization of the dentin, and darker zones suggest lower density, but the causes of these contrasting values are not self-evident. Without some external frame of reference, the concentric patterns of density variation in Figure 3A, clear as they are, might still be difficult to interpret in terms of first-order features. However, prior work on premaxillary and mandibular tusks of mastodons and molar roots of mammoths (Fisher, 1987; Fisher et al., 2014) suggests that dentin is often more highly mineralized in late winter and less mineralized in spring, with relatively abrupt transitions between these conditions. Low-density dentin often continues to form into the summer, and the rest of the year may be characterized either by a gradual or stepwise increase in dentin density. We thus interpret abrupt transitions from higher to lower dentin luminance as suggestive of some approximation of a winter–spring boundary. Based on this search image, we placed white arrows along the right margin of Figure 3A, demarcating putative first-order dentin increments.

In this fashion, we provisionally identify four complete years in the intermediate portion of this dentin sequence and two partial years, one at the beginning of the sequence and one at the end. Starting near the pulp cavity, we interpret the dentin that formed subsequent to the last winter–spring boundary as the initial portion of a final year of life that is thinner than other years and even at this scale of analysis appears to be incomplete. We propose that this year corresponds to the incomplete final year inferred from the record of tusk extension and identify it in Figure 3A as Year X. Extending attributions backward in time, the incomplete year recorded just inside the dentin–cementum interface would be Year X − 5, and its incompleteness in this plane is simply a function of the proximodistal location of this slice of the data. Year X − 4, just inside of Year X − 5, has the greatest appositional thickness of any of these last years of life, matching its unusually great extensional length (Fig. 5). The luminance transitions noted above are also documented quantitatively in Figure 6B for the part of the sequence sampled isotopically. Provisionally accepting the winter–spring boundaries proposed in Figure 3A, annual appositional thickness averaged 6.4 mm in the last four complete years of life.

SECOND-ORDER INCREMENT PROFILE

When high-speed polishing of the thin section was complete, we examined it in reflected light under a stereomicroscope. Most of the zones of high x-ray attenuation in the microCT record, immediately preceding transitions to lower attenuation that we interpreted as associated with a winter–spring boundary, displayed slightly elevated topography of the section surface and a higher degree of polish than adjoining areas—implying greater hardness and confirming our inference of greater density. These observations confirmed placement of all of the first-order increment boundaries except for the one between Years X − 1 and X − 2, which offered little corroboration of its placement.

Examination of the thin section in plane-polarized transmitted light reveals moderately distinct second-order dentin increments presenting typically as dark–light couplets whose thickness can be measured from one dark zone to the next. These couplets generally represent approximately weekly growth intervals and sometimes contain about seven third-order (daily) increments

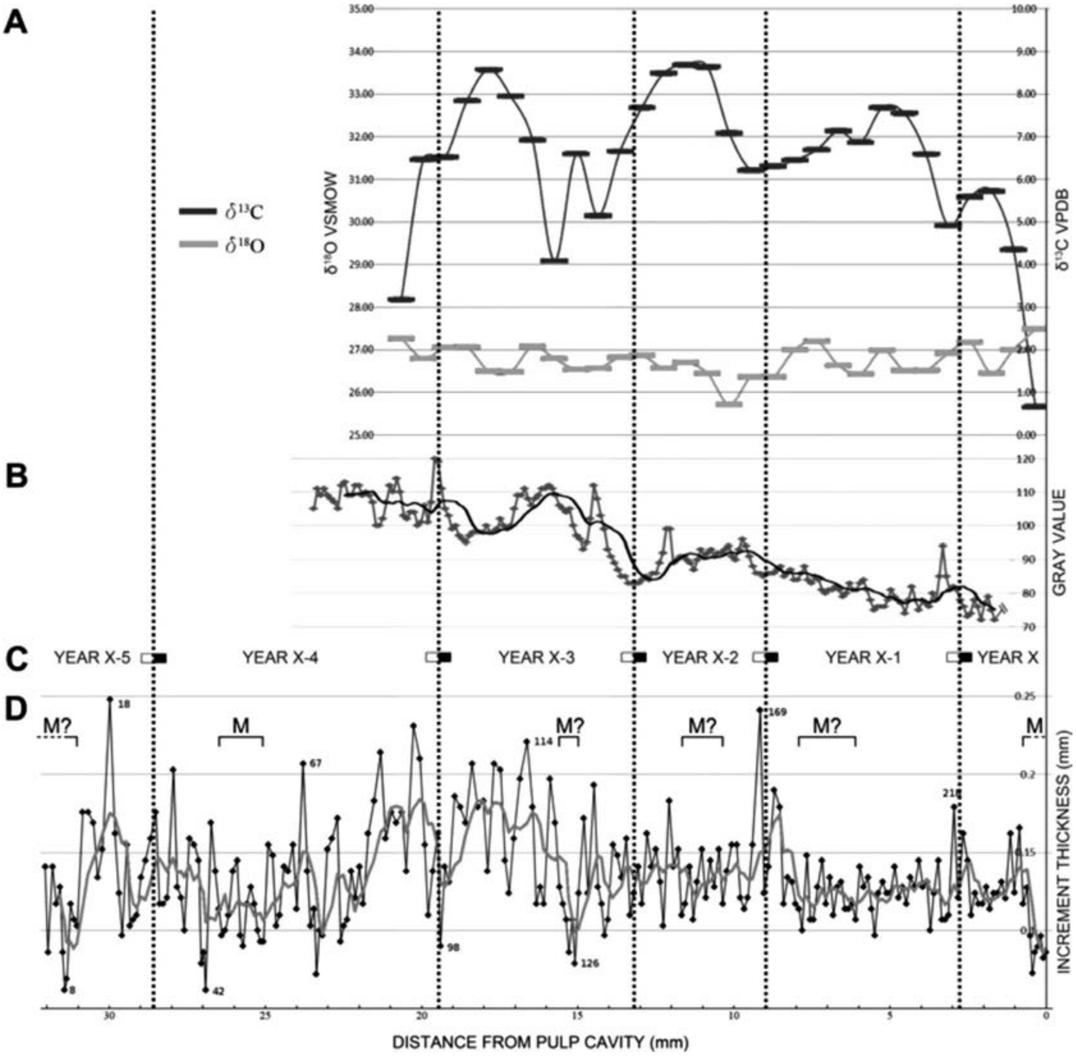

Figure 6 **A.** Results of serial isotope analysis showing changes in $\delta^{13}C$ and $\delta^{18}O$ values through the last years of life; **B.** luminance values measured along a transect normal to appositional surface, acquired from a virtual section (microCT data) of the same years shown in A (this curve is truncated just before the high-luminance zone adjacent to the pulp surface); **C.** positions of density features observed in microCT images (symbolized by rectangles with left-to-right, white-to-black transitions); **D.** profile showing variation in thickness of weekly (second-order) appositional increments (increment numbers labeled for notably thick or thin increments); continuous gray curve shows five-point moving average; bracketed intervals labeled "M" or "M?" denote probable or possible musth episodes marked by low rates of dentin apposition during summer months; vertical dotted lines represent hypothesized winter–spring boundaries demarcating years (labeled in C, matching labels in Figs. 1 and 3).

between them, although third-order increments are not always visible within each second-order increment in this specimen. In ideal conditions, second-order increments are distinguished from third-order increments by broader and often darker dark zones within their dark–light couplets. However, in intervals where third-order increments are not consistently developed, an anomalously dark third-order increment could be mistaken for a second-order increment. In this way, or worse, if there were aperiodic structural features mixed in with and indistinguishable from periodic increments, increment counts and thickness profiles could be subject to large errors. When increment numbers and thicknesses match expected patterns, they combine to yield a well-corroborated history of apposition, with growth rates documented by thickness variation of periodically formed increments. However, when expected patterns fail to emerge, it can be difficult to assess what aspect of the system has been misinterpreted.

Table 3 Measured isotope values for $\delta^{13}C$ (relative to VPDB, Vienna Pee Dee Formation Belemnite) and $\delta^{18}O$ (relative to VSMOW, Vienna Standard Mean Ocean Water) for hydroxylapatite in dentin. Distance is measured from the pulp cavity (PC) to the center of the sampling site.

Sample	$\delta^{13}C$	$\delta^{18}O$	Distance (mm)
PC	0.65	27.49	−0.35
PC-1	4.35	27.00	−1.05
PC-2	5.72	26.45	−1.75
PC-3	5.58	27.18	−2.45
PC-4	4.92	26.91	−3.15
PC-5	6.59	26.52	−3.85
PC-6	7.56	26.52	−4.55
PC-7	7.69	26.99	−5.25
PC-8	6.87	26.44	−5.95
PC-9	7.14	26.63	−6.65
PC-10	6.69	27.20	−7.35
PC-11	6.45	27.00	−8.05
PC-12	6.31	26.37	−8.75
PC-13	6.21	26.37	−9.45
PC-14	7.08	25.72	−10.15
PC-15	8.64	26.45	−10.85
PC-16	8.69	26.70	−11.55
PC-17	8.49	26.57	−12.25
PC-18	7.68	26.87	−12.95
PC-19	6.66	26.82	−13.65
PC-20	5.14	26.56	−14.35
PC-21	6.60	26.54	−15.05
PC-22	4.09	26.79	−15.75
PC-23	6.92	27.08	−16.45
PC-24	7.96	26.49	−17.15
PC-25	8.58	26.50	−17.85
PC-26	7.85	27.06	−18.55
PC-27	6.52	27.05	−19.25
PC-28	6.47	26.79	−19.95
PC-29	3.18	27.27	−20.65

Thicknesses of second-order increments in thin section were measured perpendicular to the appositional surface from the pulp cavity nearly to the dentin–cementum interface. These increments were fairly regular throughout the last few years of the animal's life and averaged 0.14 mm in thickness with a standard deviation of 0.04 mm. Both the raw data and a summary provided by a five-point moving average reveal weak annual fluctuations in apposition rate, with slight increases in what we interpret (based on x-ray attenuation features discussed above) as late winter–early spring and slower apposition in the summer. We do not see a strong pattern of sinusoidal seasonal variation comparable to patterns documented for specimens from temperate latitudes (Fisher, 1987; Koch et al., 1989). One exception to the generally smooth trend is a series of seven second-order increments that record low rates of apposition (averaging 0.087 mm per increment) at the very end of life (Fig. 6D). This series begins about 16 increments after the last inferred winter–spring boundary and extends to the last increment, marking the time of death, about 23 increments into the last year of life. Several other intervals of low growth rate are observed in the tusk and are displaced comparably from a marked transition in x-ray attenuation. However, none of these is sustained for as long as at the end of life.

ISOTOPE DATA

Thirty serial samples from Zed's last approximately four years of life were analyzed for the carbon and oxygen isotope compositions of structural carbonate in tusk dentin. Measured $\delta^{18}O$ values from Zed's tusk show little seasonal variation, with fluctuations of ca. 1‰ around an average of ca. 26.75‰ SMOW (Standard Mean Ocean Water, Table 3; Fig. 6A). Thus, no clear evidence of season is available from this time series.

The time series of carbon values from the tusk shows relatively pronounced variation on an approximately annual scale, with fluctuations of up to ca. 5‰ VPDB within a given year (Table 3; Fig. 6A). Within interpreted years, winters usually have lower, but still positive, $\delta^{13}C$ values, while summers have higher (more enriched in ^{13}C) values. However, the $\delta^{13}C$ values recovered from the tusk are all abnormally high (averaging 6.4‰ VPDB), even for herbivores with a strictly C_4 diet living in dry conditions (Koch et al., 1994). One final observation is that the series of $\delta^{13}C$ values appears to be inversely correlated with attenuation value of the dentin, measured as luminance in the microCT slice near the isotope sampling site (Figs. 3A, 6B).

DISCUSSION

Taken individually, each data series from Zed's left tusk, with the possible exception of periradicular bands, might be considered as offering only weak evidence of season of formation. The microCT features are somewhat faint, and the pattern of variation in attenuation within years is variable. Second-order growth increments show only hints of seasonal variation in thickness. Oxygen isotope values vary about a mean that is not unexpected, but the range of variation is so limited that this time series is uninformative with respect to season. Carbon isotope values show the only conspicuous pattern of variation on the timescale of years, but the actual values are unlike any observed previously in a proboscidean tusk. However, further probing of each data source and associations between them reveals greater cohesion.

The periradicular bands on the alveolar portion of Zed's tusk at least represent a clearly repeating pattern with a prior history of study. They were first described in proboscideans by Osborn

(1936), who referred to them as "annulations," a generic noun referring to their ring-like configuration relative to the tusk axis, although he also proposed that their period of recurrence might approximate one year, opening the door to some risk of confusion of "annular" features and "annual" features. Lest this seem unlikely, in another application of dental histology, "cementum annuli"—incremental features of cementum apposition that can indeed be seen as "annuli" when viewed in transverse sections of roots (although their three-dimensional geometry would be better described as quasi-cylindrical)—are routinely treated as annual and used in determinations of age and season of death. As evidence of the potential for confusion, Keiss (1969:175), discussing cementum annuli in elk, cites Scheffer (1950) as the earliest report of "annular rings in the dental cementum," but "annular rings" would seem to be redundant, suggesting he may have meant "[annual] rings." Furthermore, Scheffer (1950) does not in fact address cementum annuli at all, describing instead features that are, in our terminology, first-order periradicular bands. Keiss (1969) also cites Laws (1952), but this paper deals with what we would call first-order dentin increments seen in transverse cross sections of tooth roots and is mainly concerned with demonstrating their annual nature, making no reference whatsoever to cementum annuli. Because of this potential for misunderstanding, Fisher (1987) cited Osborn's "annulations," illustrated and described first- and second-order "undulations" of the dentin–cementum interface traced in longitudinal section, and related them to first- and second-order features of dentin structure but did not adopt Osborn's term.

Use of the phrase "periradicular bands" is generally traced to Komai and Miyauti (1938), but Smith and Reid (2009) suggest that the features Komai and Miyauti illustrated are not identical to what Dean (1995) describes as the basis for most recent applications of the concept. Dean's periradicular bands are manifestations at the dentin–cementum interface of what are called in the primate literature "long-period lines" equivalent to our second-order increments (except for the focus on the "line" rather than the whole increment). Still, Smith and Reid (2009) cite and appear to accept the usage of Rinaldi and Cole (2004), who describe periradicular bands that are manifestations of daily (third-order) dentin increments (although in their usage, the "band" is the "line" or "groove"). Smith and Reid (2009:90) likewise cite Scheffer's (1950) annual (first-order) features, although they describe his topographic features as "regular concentric lines on mammalian root surfaces." On balance, we accept that periradicular features occur on a range of different scales, requiring only an appropriate modifier and description of details of expression to clarify usage. We prefer to treat "bands" as having measurable width on the dentin–cementum interface, rather than being infinitesimally narrow boundaries, but bands cannot be adequately described without stipulating how their boundaries are defined. The "short-period"/"long-period" dichotomy used for increments of different scale in the primate literature works well there, where annual-scale features are not usually evident, but for a dental system with at least three clear hierarchical levels, our reference to first-order, second-order, and third-order features seems preferable.

One aspect of the periradicular pattern that we have not seen before is variation in surface color, which seems to be correlated with first-order periradicular topography (with darker shades just proximal to first-order periradicular band boundaries; Fig. 1). Cementum can vary in color seasonally, with darker shades usually associated with winter (Fisher, 1996), but the entire outer surface of cementum on the alveolar portion of a tusk is usually represented as forming at approximately the same time and is therefore expected to have about the same color. It is possible that cementum apposition is conditioned by some factor related to periradicular topography, but characterizing this further will require additional investigation.

The causal basis for first- and second-order periradicular features is not well resolved, but as explained elsewhere (Fisher, 1987, 2001), first-order periradicular bands appear to reflect a shifting balance (one cycle per year) between appositional and extensional growth of the tusk. When extension is suppressed relative to apposition, tusk circumference is reduced. Since Zed's second-order increment profile shows little seasonal variation in rate of apposition, we suspect that the changing "balance" was mainly due to a reduction and later increase in extension rate. When extension rate regains its relative magnitude, its trajectory (more or less aligned with the pulp cavity surface) generally increases tusk circumference again. Rate of dentin apposition is probably a function of access to nutrients for both formation of organic matrix and mineralization, but rate of tusk extension is fundamentally constrained by tusk eruption, which requires extensive remodeling of the periodontal ligament, a process that is probably protein-limited. Where the seasonal pattern of these interactions has been worked out in most detail, for a Great Lakes region adult male mastodon (Fisher, 2008; Fisher, 2009), we suspect that protein limitation is most pronounced during the winter and is relieved with access to new plant growth in the spring. We suspect that Zed's well-defined periradicular bands originated in a similar fashion and imply at least moderate seasonality in diet quality (emphasizing protein content) even if the quantity of apposition-limiting nutrients was not markedly variable.

The rates of extensional growth implied by the pattern of first-order periradicular bands on Zed's tusk correspond to values that would be expected for an adult male (Fisher, 2001:fig. 13.6A). Additionally, the trend toward lower values approaching the proximal end of the tusk is closely comparable to the pattern of tusk growth in a mature male American mastodon in his prime reproductive years, experiencing musth regularly (Fisher, 2008:text-fig. 24). If there is anything surprising about Zed's values, it is that his tusk is growing as rapidly at an inferred age on the order of 50 as was the tusk of the mastodon Fisher studied, in its mid-30s. Of course, differences in local climate, among other factors, could be responsible for Zed's relative vigor.

Zones of abrupt transition from high to low x-ray attenuation in microCT of tusk dentin, proposed here as part of the annually recurring syndrome of traits marking first-order features, are not as clearly defined as the year-long gradients in attenuation value observed in tusks from the high-elevation Ziegler Reservoir site in Colorado (Fisher et al., 2014). This can be explained in terms of the much greater seasonality to which proboscideans high in the Colorado Rockies would have been exposed. Still, the general nature of these features is similar, and the *number* of microCT features recognized in Zed's sample block between the cementum and the pulp surface corresponds to the *number* of periradicular bands between the location of the sample block and the proximal margin of the tusk. This match is highlighted by the consistent numbering of years in Figures 1 and 3A.

Rates of appositional growth implied by the microCT features we recognize in the sample block also match expectations for a mature male (Fisher, 2001:fig. 13.6B). For this variable, no great diminution is expected with advancing age (Fisher, 2008:text-fig. 24), nor is any seen in this short sequence.

Focusing even more closely on comparing the appositional record contained in the sample block with the extensional record visible as periradicular bands on the tusk surface, we have compared appositional thicknesses of successive years with their extensional lengths. Year X − 4 is both the thickest and the longest, with subsequent years being more or less similar in thickness and length. The correlation between thickness and length for the four Years X − 1 through X − 4 (the only complete years for which we have both values) is moderate ($R^2 = 0.70$), but not significant ($p = 0.16$), primarily because we only have data for four years. As explained above, apposition and extension are probably controlled by different factors. The topographic relief associated with first-order periradicular bands itself implies a decoupling of these two processes on an intra-annual time scale, and even modest decoupling extending beyond the bounds of a single year would lead to some lack of strict proportionality between these two variables. Without further work, we cannot even be certain that the microCT features that we use to mark boundaries of first-order dentin increments meet the dentin–cementum interface at precisely the position of the features we recognize as boundaries of first-order periradicular bands. Our best opportunity to check this on Zed's tusks was to compare the distance between the last microCT feature and the pulp cavity surface in the sample block (2.66 mm, measured on our photomicrographs using Inc Meas 1.3c) to the tusk thickness along the broken proximal margin, near the boundary separating periradicular Year X and Year X − 1. This latter value was 2.95 mm, and it must include some cementum as well as the dentin thickness associated with Year X. This close correspondence means that at least this last microCT feature must match the last periradicular year boundary very closely.

Another approach to evaluating the degree to which microCT features can be confirmed as annual involves shifting to the record of appositional growth provided by second-order dentin increments. In mammoth tusks these are understood as generally having a periodicity of about one week (Fisher, 2001; confirmed following documentation of a similar periodicity in *Gomphotherium* by Fox, 2000; Fisher et al., 2003). We were able to count third-order (daily) increments in some parts of our thin section, confirming a periodicity close to weekly for parts of the record. Nevertheless, the tally of weeks recognized in Years X − 4 through X − 1, the only complete years for which we have data, is 69, 42, 31, and 49, respectively, compared with an expected value near 52. At first, this variation seemed large enough to cast doubt on the supposition that these increments were strictly periodic. However, as argued by Fisher et al. (2008), the factors that influence the timing of the changes in dentin structure and composition that we use to recognize boundaries of first-order increments likely involve elements of local weather, behavior, and food resources that vary from season to season and year to year. Although these are influenced by astronomical patterns, they need not show strict regularity, especially in environments of low overall seasonality. In any case, the tally of weeks above implies a mean of 47.8—close enough to 52 to reawaken interest. In fact, we are not concerned at all about small departures from documented periodicities because the physiological rhythms that appear to control second- and third-order increments (or long-period and short-period features of Dean and Scandrett, 1996) display individual and species-level variation like any other aspect of the phenotype. We therefore consider the annual nature of Zed's microCT features as reasonably secure.

Despite the lack of any strong pattern of seasonal (intra-annual) variation in rate of dentin apposition, we observe scattered occurrences of thicker than normal second-order increments in the weeks shortly before and after most of the winter–spring boundaries. This suggests that climate and dietary amelioration from whatever set of conditions is here recognized as "winter" (no doubt different from this season at temperate latitudes) typically began before the winter–spring boundary and continued into early spring. Lower rates of dentin apposition in summer could reflect drier conditions and/or lower forage quality, but we offer another interpretation below. Overall, this pattern of apposition is consistent with a relatively mild climate and adequate nutritional resources during most of the year. This degree of evenness is not surprising, given the relatively moderate climate reconstructions for southern California during the late Pleistocene (Spaulding, 1990; Minnich, 2007).

An alternative interpretation of the low rates of dentin apposition during a portion of the inferred summer is that this was Zed's season of musth, the period of hormonally induced aggression and mate-seeking known also in extant elephants (e.g., Poole and Moss, 1981). Musth in elephants can last up to three months. In dominant adult males, it normally recurs annually and is associated with fasting behavior that would be expected to reduce rates of dentin apposition. Even in environments of relatively low seasonality, a season with elevated chance of rainfall, such as late winter and spring, judging from Zed's record of tusk growth, could be an optimal season for birth (e.g., based on food availability for a nursing mother), and given an elephant-like gestation period of about 22 months, summer would be an optimal mating season. In elephants, dominant males are especially likely to mate according to this optimal schedule (Poole, 1996).

Less is known for mammoths, but observations on the development of the deciduous dentition in woolly mammoths suggest birth in the spring and a gestation period similar to that of extant elephants (based on the duration of intrauterine development in dp2; Rountrey et al., 2012). Late spring to early summer has also been proposed as the normal musth season for Columbian mammoths from the North American Great Plains (Fisher, 2004), for woolly mammoths in northern Yakutia (Fisher, 2007), and for American mastodons in temperate North America (Fisher and Fox, 2007; Fisher, 2008).

Numerically, the $\delta^{18}O$ values we observe in Zed's tusk are similar to those recorded for *Bison* and *Equus* from Rancho La Brea (Feranec et al., 2009, reporting values relative to PDB rather than VSMOW), but Zed's intra-annual range of variation is only about 1‰, and his profile shows little repeated pattern from year to year. In contrast, Feranec et al. (2009) report annual ranges of ca. 1.5‰–5‰ per year in *Equus* and ca. 1‰–5‰ in *Bison*, with some patterns looking more like seasonal cycles than what we see in Zed. Either Zed experienced a lower level of variation in oxygen isotope ratio and less seasonally structured variation than did bison or horses, or his values could have been to some degree homogenized by diagenetic alteration, as dentin is generally understood to be less stable diagenetically than enamel (Ayliffe et al., 1994).

Zed's $\delta^{13}C$ profile stands in marked contrast to his $\delta^{18}O$ profile, in that it shows conspicuous variation of about 3‰–5‰ within years and an intra-annual pattern that is at least somewhat consistent among years. However, the numerical values are much more positive than expected. Even herbivores with diets dominated by C_4 vegetation would not normally show values above about 2‰ (Koch et al., 1994). In this light, only the last $\delta^{13}C$ value measured for Zed, adjacent to the pulp cavity, seem plausible as a primary value, although even this may be questionable given that both Coltrain et al. (2004) and Feranec et al. (2009) found no evidence of C_4 vegetation in the diets of Rancho La Brea herbivores they analyzed (although neither included mammoths). Analysis of Zed's molar enamel could clarify this discrepancy.

We have considered factors beyond diet that might elevate $\delta^{13}C$ values, such as severe water stress, but it seems difficult, not to mention inconsistent with the absence of seasonal enrichment in the $\delta^{18}O$ profile and with characterizations of contemporary climate as cool and mesic (Heusser, 1998), to explain the values observed here as unaltered, primary indicators of diet and climate. We do, however, note an apparent inverse association between dentin density, measured as luminance in the microCT record (Fig. 6B), and the $\delta^{13}C$ record. One possible explanation of this is that the structural carbonate of Zed's dentin may have been diagenetically altered, shifting values in a positive direction, and to a greater degree in zones of lower density, where greater permeability may have increased the effective volume of porewater interacting with the dentin. Higher density zones might thus retain less altered values. Most of these higher density zones are primary features of dentin structure, but the *highest* density dentin, adjacent to the pulp cavity, was interpreted above as having been altered postmortem by deposition of exogenous carbonate within dentin pores. This would have reduced the potential for further interaction with groundwater and could explain why it is only in this zone that we find a plausibly primary $\delta^{13}C$ value. The sample pretreatment methods for analysis of structural carbonate in bioapatites are designed precisely to remove this type of secondary carbonate (Koch et al., 1997), so ironically, we may be seeing original isotope values only where dentin was "sequestered" within early-postmortem secondary carbonate. If the carbon isotope ratio of this last sample before death is intact, perhaps the oxygen isotope ratio is as well, but unfortunately, there is little we can do with a single value. We recognize that this explanation of our isotope results is incomplete, but it suggests that some scrap of meaning may yet remain in a record that otherwise failed to yield the quality of data we had hoped would be recovered.

For most of his last years of life, Zed's tusk growth record, most notably his rate of tusk extension, suggests excellent health, especially given his probable age. The first significant interruption of this pattern occurs near the end of life where the terminal series of seven second-order increments records a marked drop in weekly rate of apposition (Fig. 6D). As this pattern is sustained for nearly two months, we interpret it as a significant deterioration of condition.

Placing this terminal interval of low growth rate into context, it is immediately preceded by two thin, but not so dramatically thin, increments that occur 15 increments after the final inferred winter–spring boundary, or about a month into what might be considered summer (in the absence of more detailed information, we treat seasons as lasting about three months). Looking to previous years, we see similar intervals of low growth rates at about this same time of year, indicated in Figure 6D by bars labeled "M" or "M?" (depending on how clearly they stand out), alluding to our suggestion above that these intervals reflect musth periods. The duration of these periods ranges from about six increments in Year X − 3 to about 16 increments in Year X − 1, and although this last value seems high (relative to a maximum musth duration of about three months in African elephants; Poole, 1996), low rates of apposition could in some cases continue beyond the musth interval itself into a "recovery period." When introduced above, considering only year-to-year comparisons, our interpretation of these intervals as musth episodes was admittedly speculative. However, with recognition of the last instance of this phenomenon as a preface to even lower rates of apposition, followed by death, this interpretation gains explanatory power.

Musth conflict between males is known to cause death in extant elephants (e.g., Buss, 1990) and has been interpreted as a cause of death in adult male Columbian mammoths (Fisher, 2004) and American mastodons (Fisher and Fox, 2007; Fisher, 2008). Zed's tusk does not show cementum defects like those that record musth battles in mastodons (Fisher, 2008), but with the more helical tusk geometry of mammoths, tusks might have been used less for "stabbing," and the peak stresses of tusk use may have been associated with rotation about the tusk axis rather than impingement of the proximal margin against the back of the tusk alveolus. We thus do not consider absence of cementum defects as evidence against musth battles.

We observe no damage on Zed's skeleton that is clearly perimortem, but there are multiple examples (healed rib fractures and vertebral damage) of injuries that occurred earlier in life and could have been sustained in musth battles. Without a clear record of perimortem skeletal damage, we suspect his death may have been caused by soft-tissue injuries. We suspect his final, nearly two-month interval of low tusk growth rate represents a period of decline during which he may have been capable of limited feeding and drinking, but from which he never managed to recover.

CONCLUSIONS

Zed's left tusk shows a pattern of variation in external topography and internal structure that corresponds closely to other proboscidean tusks that have been studied in even greater detail. Only our analysis of stable isotope values (δ^{18}O and δ^{13}C) of structural carbonate of tusk dentin failed to reveal a periodic pattern that was independent of other variables. Accepting the largest-scale features of topographic and structural modulation as recurring on an annual basis, we have evidence of relatively steady and high tusk growth rates that suggest Zed was in good condition during most of the last decade of his life. Based on the association of first-order (annual) periradicular bands, microCT features, and patterns of variation in rate of dentin apposition in the last four to five years of life, death appears to have come in midsummer, shortly after the start of a musth episode that was not sustained for the normal duration. Instead, it devolved quickly into an interval characterized by rates of dentin apposition as low as any observed in the last five years of life. This interval lasted for almost two months and ended with Zed's death. We suspect that this terminal interval was initiated by musth conflict, during which Zed sustained a serious soft-tissue injury. Following this injury, locomotion and feeding were probably difficult, but Zed would not have lasted as long as he did without some access to food and water.

Although our view of Zed's life covers only his last decade and offers interesting temporal resolution only for the last five years, it suggests that local weather conditions 37,000 years ago presented few extremes, with only low to moderate seasonality. In this environment, Columbian mammoths thrived to the degree that their sometimes tumultuous lives permitted. Zed's tusk record is important not only for the view it offers of his life and times, but as a basis for comparison with mammoth life histories of other regions and times, especially closer to the last phases of mammoth history, just prior to extinction.

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Equus occidentalis Leidy from "Asphalto," Kern County, California

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ABSTRACT. The species *Equus occidentalis* Leidy, 1865, was initially described from three teeth, one recovered from an unknown locality in Tuolumne County, California, and the others from asphalt deposits inset into sediments of the Tulare Formation, Kern County, California. The single tooth from Tuolumne County is the lectotype. None of these teeth is sufficiently diagnostic to warrant specific distinction, and so *E. occidentalis* is generally interpreted to be a *nomen dubium*.

Another less common interpretation suggests that *E. occidentalis* may be a valid plesippine equid dating to the Blancan North American Land Mammal Age. This view is based upon plesippine characters exhibited by teeth of large *Equus* from the Asphalto fossil locality. At this site, lower cheek teeth of large *Equus* from outcrops of the Tulare Formation exhibit deep ectoflexids, a diagnostic character of plesippine equids.

Our investigation relocated the Asphalto site and its fossiliferous asphalt beds, examined equid fossils from the Tulare Formation to confirm their plesippine character, and directly examined the original types of *E. occidentalis* in order to assess their similarity to nonasphaltic fossils from the Tulare Formation. Efforts to relocate Asphalto were successful, but encountered only oil-saturated sands of the Tulare Formation—not asphalt beds. Nonasphaltic localities in the Tulare Formation contain abundant remains of plesippine equids, but these fossils—and other vertebrate remains from the formation—lack the deep asphalt staining characteristic of Leidy's types from this region. In contrast, fossils in Leidy's original type series are heavily impregnated with asphalt, resembling abundant fossil remains from the nearby McKittrick asphalt deposits. Leidy's type series also includes previously unpublished topotypes representing a derived, nonplesippine equid similar to the Late Pleistocene large horse species represented at McKittrick.

We propose that Leidy's original fossils of *E. occidentalis* from northwest of Buena Vista Lake are most likely from the McKittrick asphalt deposits, rather than from the Asphalto paleontological locality. Based upon actual topotypes comprising Leidy's original type series, *E. occidentalis* is a derived horse closely resembling the large Pleistocene horses from localities such as McKittrick, Maricopa, and Rancho La Brea. The species cannot be considered a plesippine horse and is unlikely to date to the Blancan NALMA.

INTRODUCTION

Pleistocene horses (genus *Equus*) in North America are emblematic of taxonomic confusion, due in part to the prevalence of skeletal remains of these animals in the fossil record. Bones and especially teeth of horses are common components of numerous Pleistocene terrestrial vertebrate faunas and have been since the early days of paleontology. Because many fossils of *Equus* were discovered in years when the naming of species was not strictly codified and the full morphological variability of those remains had not been quantified, nominal species names proliferated. While many of these early names have retreated into obscurity, some have continued in use despite inadequate type material.

The species *Equus occidentalis* Leidy, 1865, is a case in point. Originally named from two upper premolars and one lower molar from two widely separated geographic localities, the species has subsequently been the subject of much confusion. Interpretations include (1) *E. occidentalis* as a valid Late Pleistocene species (e.g., Merriam, 1913; Bennett, 1980; Kurtén and Anderson, 1980), (2) *E. occidentalis* as a valid early Pleistocene plesippine species (e.g., Savage, 1951; see also MacFadden, 1998), and (3)

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E. occidentalis as a *nomen dubium* and/or a *nomen vanum* (e.g., Miller, 1971; Winans, 1985; Scott, 2004).

Of these, the interpretation advanced by Savage (1951:246) that *E. occidentalis* was "a valid species of plesippine affinity" is considered here.

ABBREVIATIONS

BVM	Buena Vista Natural History Museum, Bakersfield, California
SBCM	San Bernardino County Museum, Redlands, California
UCMP	University of California Museum of Paleontology
VPM	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

BACKGROUND

The species *E. occidentalis* Leidy, 1865, was named on the basis of three teeth: a left P3 from the auriferous clays of Tuolumne County, California (VPM 9129), and a right P3 (VPM 9130) and right m3 (VPM 9131) from "a bed of asphaltum … near Beuna [sic] Vista Lake" (Leidy, 1865:94) in Kern County, California. None of these was selected as a holotype, likely because the need for designation of a type was not yet fully recognized at the time the species was named (see Dayrat, 2010). The defining character of *E. occidentalis* was interpreted to be "the remarkable degree of simplicity of the enamel folding, as seen on the triturating surfaces" (Leidy, 1865:94). This definition was augmented (Leidy, 1869:267) to note "the absence of the little fold of enamel … near the bottom of the deep valley between the median- and posterior internal folds of the triturating surface" (i.e., the pli caballin).

Although the discussion of enamel simplicity in the initial publication could be readily ascribed to all of the available teeth, the subsequent mention of the lack of plis caballin could only apply to the upper teeth, since this feature does not occur in lower teeth. This is actually a point of some significance, because subsequent to Leidy's (1865) naming of the species, the available literature makes no mention of the right m3 referenced in the initial description.

Leidy's 1869 paper considered the fossils previously assigned to *E. occidentalis* to resemble upper teeth of the species *Equus excelsus* Leidy, 1858, in both the simplicity of the enamel patterns on the wear surface and in the lack of plis caballin. Although the fossils of *E. excelsus* derived from Nebraska, Leidy (1869) nevertheless considered the California teeth to belong to that same species. This interpretation was promulgated by Leidy (1873), although in this later paper taxonomic priority was erroneously assigned to *E. occidentalis*.

Whitney (1880:256) published some of Leidy's notes on the fossils, with the view that it was "proper to publish in full the notes furnished by [Leidy] in regard to the equine remains examined, although some years have elapsed since [these notes] were written." These notes describe in somewhat more detail fossils previously mentioned in passing by Leidy (1869, 1873) as belonging to *E. occidentalis* (or *E. excelsus*) in addition to the type material—although, as noted, the "last lower molar" referred to by Leidy (1865:94) is not included. Whitney (1880:256) is more specific as to the locality producing the specimens "imbued with bitumen," again referencing the Buena Vista Lake region but stating in a footnote that "[t]he exact locality is believed to be the 'Sta. Maria Oil Springs', about twelve miles northwest of the north end of Buena Vista Lake."

Cope (1884) and Gidley (1901) considered *E. occidentalis* to be distinct from *E. excelsus*; the latter review selected the Tuolumne County premolar (VPM 9129) as the lectotype of *E. occidentalis*. This was largely the state of affairs when Merriam (1913) assigned the entire sample of horses from Rancho La Brea, Los Angeles County, California, to *E. occidentalis*. At this point, there is a substantial shift in the literature, as most subsequent papers making reference to *E. occidentalis* reference the fossil horses from Rancho La Brea rather than Leidy's original suite of fossils.

Savage (1951) disagreed with Merriam's (1913) interpretation, considering *E. occidentalis* to be a valid species separate from the Rancho La Brea equid. Because Savage's analysis is a primary focus of the present study, his reasoning is presented here verbatim:

"*Equus occidentalis* Leidy [1865] was based on an upper cheek tooth from the 'Pleistocene auriferous gravels' in Tuolumne County, California, and two upper cheek teeth from an asphalt bed near Buena Vista Lake in Kern County, California. The latter locality is now usually called Asphalto. These teeth are all characterized by a simple and somewhat rectilinear enamel pattern and a broad lingual groove on the protocone. It is impossible to get topotypes of the Tuolumne County specimen, because the exact locality was never specified; it may or may not be Pleistocene in age. [University of California Museum of Paleontology director R.A.] Stirton (oral communication, 1948) has called to my attention that topotypal lower cheek teeth from Asphalto bear the plesippine V-shaped groove between the metaconid and metastylid [= the linguaflexid]. Merriam [1913] referred the abundant horse material from Rancho La Brea to *E. occidentalis*. Although there is remarkable identity in characters between the Rancho La Brea horse and the types of *E. occidentalis*, the La Brea horse is a true caballine … and must be referred to some other species. *E. occidentalis* is believed to be a valid species of plesippine affinity…. The Blancan [North American Land Mammal Age] age assignment for [*E. occidentalis*] is supported by the recovery of *Ischyrosmilus* and *Borophagus* from Asphalto." (Savage, 1951:246)

A key point in this discussion is Savage's (1951) mention of the locality name Asphalto; this is the first occurrence of this locality in this context, as the name did not occur in Leidy's original (1865) description of *E. occidentalis* nor in any of his subsequent discussions of the species. The Asphalto region, located around present-day McKittrick, was named for early exploration and asphalt mining camps northwest of Buena Vista Lake; the original camp was established in the later 1860s, but the first camp was not actually named Asphalto until 1891 (Brewer, 2001). The third and final Asphalto camp was renamed McKittrick in 1900 (Brewer, 2001).

The issue is further confused in that there is also a fossil locality named Asphalto from the same general region. The Asphalto paleontological locality, UCMP 1365, is recorded approximately 2.6 km (1.6 miles) southeast of present-day McKittrick in Kern County, California. The locality is documented from outcrops of the Tulare Formation, a thick succession of nonmarine, poorly consolidated sandstone, conglomerate, and claystone beds exposed intermittently along the western border of the San Joaquin Valley (Woodring et al., 1932; Maher et al., 1975). The formation is composed of two distinct lithologic units, separated on the basis of the color of the mudstones. The lower unit is made up of alternating layers of olive-grey gypsiferous mudstone and cross-bedded grey feldspathic sandstone containing lenses and irregular stringers of conglomerate; the upper lithologic unit resembles the lower unit, save that the mudstone layers are buff in color while the sandstone layers near the top of the unit include pebbles representing a diversity of rock types (Maher et al., 1975). The formation has been dated from 2.5 to 0.6 Ma (Scheirer and Magoon, 2007).

The Asphalto locality yielded the holotype left and right dentaries (UCMP 8139) of "*Hyaenognathus pachyodon* Merriam, 1903" (= *Borophagus diversidens* Cope, 1892) and the genotype mandible (UCMP 8140) of "*Ischyrosmilus* Merriam, 1918" (= *Homotherium* Fabrini, 1890). Both these carnivorans date to the Blancan North American Land Mammal Age (NALMA), which is consistent with the proposed geologic age of the Tulare Formation (Scheirer and Magoon, 2007). These fossils are light in color, showing no evidence of asphalt staining or impregnation.

Other vertebrate fossils have also been reported from the Tulare Formation, but most have not previously been described in any detail. Repenning (1980, unpublished report reprinted in part in Miller, 1999) listed multiple taxa from the formation, including two species of horse, *Equus* (*Hemionus*) "*callobatus*" (= *Equus calobatus* Troxell, 1915) and "*E.* (*H.*) *occidentalis*." However, the morphological characters upon which these species assignments were made have not been published, and so these assignments remain unverified. Repenning (1980) also reported the presence of *Hypolagus furlongi* Gazin, 1934, and *Sigmodon medius* Gidley, 1922, in the assemblage from the Tulare Formation; these taxa are also indicators of a Blancan NALMA date for the fossils.

It appears that Savage (1951) and subsequent researchers conflated Asphalto as a general geographic region with Asphalto the specific paleontological locality. Following from this, the assertion that lower cheek teeth of plesippine *Equus* from the region could be used to supplement the definition of *E. occidentalis* Leidy (which was based upon upper teeth) seems reasonable. Further, the Blancan age for the fossils from the Tulare Formation could be applied to *E. occidentalis* if Asphalto was actually the site producing Leidy's fossils.

Some subsequent reviews have called Savage's (1951) interpretation into question. For example, Dalquest (1978) argued that Gidley's (1901) selection of the specimen from Tuolumne as the lectotype of *E. occidentalis* should be retained under Article 73 of the International Rules of Zoological Nomenclature. The plesippine character of the "topotypal" lower cheek teeth from Asphalto described by Savage (1951) was therefore not considered relevant in the diagnosis of the taxon. In contrast, MacFadden (1998) considered *E. occidentalis* to be roughly synonymous with the Blancan plesippine equid *Equus simplicidens* Cope, 1892, which suggests that this study agreed at least in part with *E. occidentalis* being a plesippine as proposed by Savage (1951).

However, in this context it is important to emphasize that Leidy (1865, 1869, 1873) and Whitney (1880) never mentioned Asphalto in any of their discussions of *E. occidentalis*. In fact, they could not have done, since the first Asphalto settlement was not established until 1891 (Brewer, 2001). Rather, Leidy and Whitney made repeated mention of Buena Vista Lake as their point of reference, probably because that was the major geographic feature of the region in the mid-nineteenth century. Here, Whitney's (1880) reference to the Santa Maria Oil Springs northwest of the north end of Buena Vista Lake may be telling, since there are extensive asphalt beds in this general region: the McKittrick asphalt seeps (Schultz, 1937; Church, 1968), located approximately 27 km (17 miles) northwest of the northern extent of former Buena Vista Lake. These extensive beds of asphalt, situated adjacent to the southern end of the Little Santa Maria Valley, are inset into older sediments of the Tulare Formation but postdate that unit (Schultz, 1937). The McKittrick seeps have yielded abundant remains of Late Pleistocene megafauna, of which *E. occidentalis* is reported to be the most abundant large herbivore, based upon minimum numbers of individuals (Torres, 1989). The fossils excavated from these deposits are all dark stained due to impregnation by asphalt.

Based upon this review, there are two well-established paleontological localities, Asphalto and McKittrick, that might have produced the type series of *E. occidentalis* Leidy from "northwest of the north end of Buena Vista Lake" (Whitney, 1880:256). Since these localities are of differing geologic ages—Asphalto dating to the Blancan NALMA, McKittrick to the Rancholabrean NALMA—the assumption by Savage (1951) that the Asphalto locality yielded some of Leidy's original type series of *E. occidentalis* is called into question. The present study examines this concern.

METHODS

In order to assess the viability of Savage's (1951) interpretation of the validity of *E. occidentalis* Leidy, a three-pronged approach included (1) field visits to the Asphalto region, including to established paleontological localities, to assess whether or not exposed beds of asphaltum were present regionally; (2) direct examination of fossils from the Tulare Formation in museum collections, to confirm or refute whether or not they possess plesippine characters; and (3) examination of Joseph Leidy's original series of fossils assigned to *E. occidentalis*, including the types as well as additional, previously undescribed fossils.

A field survey of the Asphalto region was conducted by two of us (K.E.B. and E.S.) in August 2013; the area had been previously visited by W.A.A. in 1972. The survey was based upon historic maps and early United States Geological Survey topographic quadrangle maps showing Asphalto as a geographic locale. The survey also examined paleontological locality UCMP 1365 and the surrounding area, based upon locality data from the UCMP online locality database. Survey was conducted on foot.

Fossils of large *Equus* from the Tulare Formation were examined by K.E.B. and E.S. in the collections of the Buena Vista Natural History Museum and the San Bernardino County Museum.

Leidy's original type series of *E. occidentalis* was directly examined and photodocumented by E.S. in the collections of the Museum of Comparative Zoology in June and December 2013.

RESULTS AND DISCUSSION

RELOCATING ASPHALTO

The field survey relocated geographic (as opposed to paleontological) Asphalto as documented on early US Geological Survey maps near a railroad line extending from the community of McKittrick in an east-southeast direction, then veering toward the northeast. Asphalto was marked on these maps near the center of section 22, Township 30 south, Range 22 east, Mount Diablo Base and Meridian, roughly 2 km (1.2 miles) due east of present-day McKittrick. Finding this original locality was instrumental in determining where the fossils were collected. Satellite photographs of the area from Google Maps revealed the old railroad grade, establishing that this was indeed the site of an old rail line. Historical artifacts were also discovered at the site, including broken bottles, railroad ties, and rail spikes, verifying the presence of an old railroad. However, we found no evidence of asphaltum deposits, confirming that the fossils were not found at this locality.

Paleontological locality UCMP 1365 is situated in the western half of section 27. Foot surveys of this area revealed multiple outcrops of petroleum-impregnated sands and gravels, consistent with published descriptions of the Tulare Formation (Fig. 1), but located no substantive beds of asphaltum. No fossils were observed at either of these two sites.

LARGE *EQUUS* FROM THE TULARE FORMATION

Teeth of large *Equus* from the Tulare Formation in the collections of the BVM include both upper and lower cheek teeth collectively catalogued under number BVM 6001. Lower molars in this collection clearly exhibit plesippine characters including a V-shaped or narrow U-shaped linguaflexid discussed by Savage (1951), as well as a deep ectoflexid (Fig. 2A). The equid represented by these specimens appears to be of moderate to large size.

Similarly, fossils of large *Equus* in the collections of the SBCM also include specimens of upper and lower cheek teeth. Here, too, lower molars exhibit plesippine characters, including the narrow linguaflexid and molar ectoflexids that penetrate the isthmus (Fig. 2B). These fossils represent a very large plesippine horse, likely *Equus idahoensis* Merriam, 1918, or a closely related form.

All of these fossils exhibit a very light, white or off-white color and show no trace of asphalt staining or impregnation. This coloration is consistent with other fossils reported from the Tulare Formation, including the holotype of "*Hyaenognathus pachyodon*" and the genotype of "*Ischyrosmilus*."

LEIDY'S TYPE SERIES AND SUPPLEMENTAL FOSSILS OF *EQUUS OCCIDENTALIS*

Specimens VPM 9129, VPM 9130, and VPM 9131 collectively constitute Leidy's type series for

Figure 1 Outcrop of the Tulare Formation in the near vicinity of the Asphalto paleontological locality, UCMP 1365. The outcrop consists of well-sorted sands saturated with oil. View is to the southeast. Author K. Brown for scale.

E. occidentalis. VPM 9129 is the left P3 from Tuolumne County, selected by Gidley (1901) as the lectotype; this specimen is not considered further here. VPM 9130 is the right P3 "obtained from a bed of asphaltum, *in company with a last lower molar*, near [Buena] Vista Lake" (Leidy, 1865:94; emphasis added).

VPM 9131 is an adult right m3 in full wear (Fig. 3). Because it is numbered sequentially with VPM 9129 and VPM 9130, and because it is the only m3 available in Leidy's type series as presently constituted, and because it is asphalt stained, as is VPM 9130, it is almost certainly the "last lower molar" from the Buena Vista Lake region referenced by Leidy (1865:94) in his initial description of *E. occidentalis*. (This is contrary to the mistaken assertion by Savage [1951:246] that the type series included "two upper cheek teeth from an asphalt bed near Buena Vista Lake.") The tooth exhibits a shallow, broad, U-shaped linguaflexid and a shortened ectoflexid that does not penetrate the molar isthmus (Fig. 3). These characters differ markedly from the plesippine condition observed in lower molars of *Equus* from the Tulare Formation, which possess narrow linguaflexids and ectoflexids that penetrate the molar isthmus.

In addition to Leidy's type series, the collections of the Museum of Comparative Zoology also hold additional fossils mentioned by Leidy (1869, 1873) and Whitney (1880) that have otherwise remained undocumented. Like the type series, these other fossils also derive from "the Asphaltum bed or spring, near Buena Vista Lake, California" (Leidy, 1869:267). Among these fossils, a partial mandible (including VPM 9143, left horizontal ramus; VPM 9144, right horizontal ramus; and VPM 9146, symphyseal region) also clearly exhibits a number of nonplesippine characters, including broad, U-shaped molar linguaflexids and molar ectoflexids that do not penetrate the molar isthmus (Fig. 4). These characters are also exhibited by a partial left dentary, VPM 9141 (Fig. 5).

It is apparent that these asphalt-impregnated specimens, mentioned although never fully described by Leidy (1869, 1873) and Whitney (1880), are actual topotypal fossils of *E. occidentalis*. None of the fossils exhibits any plesippine characters but, instead, resemble more derived Late Pleistocene *Equus*—including specimens of large *Equus* from the McKittrick asphalt seeps, as well as from other asphalt localities in southern California including Rancho La Brea (Stock, 1992) and Maricopa (Torres, 1989). Their morphology contrasts sharply with the description provided by Stirton to Savage in 1948 (as reported by Savage, 1951) referencing plesippine characters in "topotypal" cheek teeth from Asphalto; this description very likely refers to horse teeth from the Early to

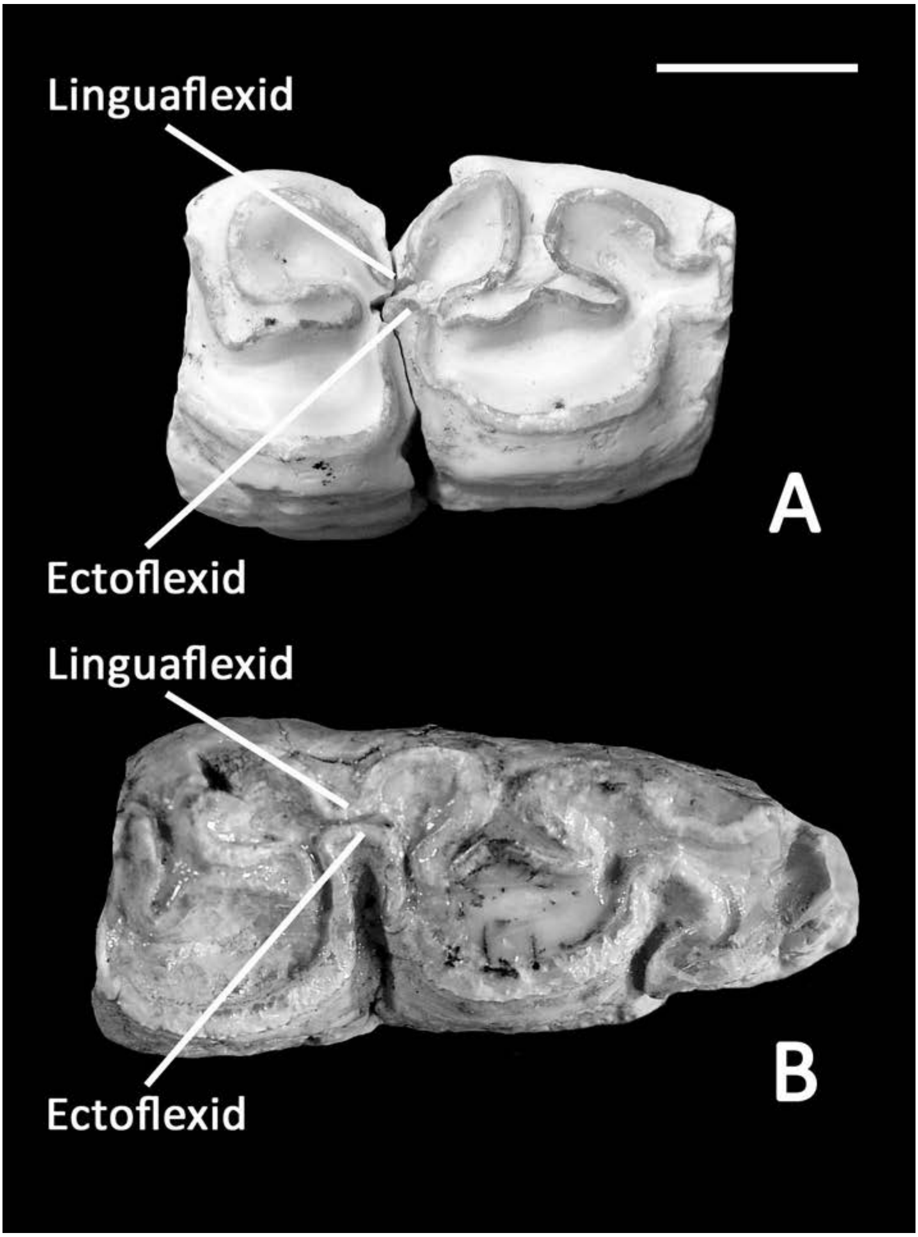

Figure 2 Lower molars of *Equus* from the Tulare Formation. Anterior is to the left. **A.** BVM 6001, left lower molar, occlusal view; **B.** SBCM A3029-1977, left m3, occlusal view. Both specimens exhibit plesippine characters, including a narrow linguaflexid and a long ectoflexid that penetrates the molar isthmus. Scale = 1 cm.

Middle Pleistocene age Tulare Formation, which despite their potential geographic proximity are likely not true topotypes *sensu stricto*.

CONCLUSIONS

The species *E. occidentalis* Leidy, 1865, was named in part from specimens obtained from asphalt beds northwest of Buena Vista Lake in Kern County, California. Although the lectotype of the species is from a different locality, some researchers (notably Savage, 1951) proposed that the Kern County fossils can be used, together with other horse fossils from that region, to establish *E. occidentalis* as a valid plesippine equid species dating to the Blancan NALMA. This interpretation assumes that Leidy's Kern County fossils derived from the Asphalto paleontological locality, or from a site of similar age and depositional constraints.

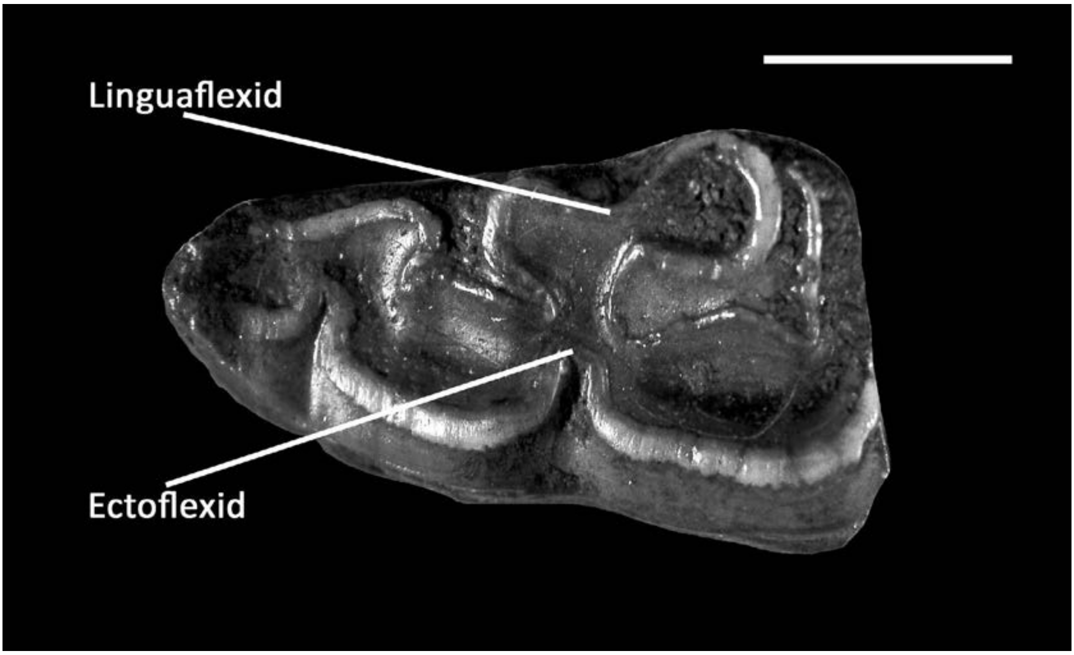

Figure 3 VPM 9131, right m3, occlusal view. Anterior is to the right. This specimen is the "last lower molar" referenced by Leidy (1865) in his initial description of *Equus occidentalis*; this specimen, part of the original type series for the species, has not previously been described or figured. VPM 9131 possesses a broad, shallow linguaflexid and an ectoflexid that approaches but does not penetrate the molar isthmus; compare with the plesippine condition observed in SBCM A3029-1977 (Fig. 2). Scale = 1 cm.

We propose that the teeth of Leidy's type series of *E. occidentalis*, stated to derive from near Buena Vista Lake, are in fact from the McKittrick asphalt beds, and not from Asphalto at all. This interpretation is consistent with the geography and geology of the region, with the original published mentions of the locality in question, and with the nature of the fossils themselves. Nor is this interpretation new. Schultz (1937) stated:

"The first mention of vertebrate remains from the McKittrick region seems to have been made by Joseph Leidy (1865, p. 94), who described two horse teeth from the vicinity of Buena Vista Lake and referred them to *Equus occidentalis* [underlined in original]. Additional horse material from this locality was described and figured by Leidy in 1873 (pp. 242–244, pl. 33, fig. 1). Whitney (1880, p. 256) stated that Leidy's specimens were obtained from Santa Maria Oil Springs, a locality

Figure 4 VPM 9144, right lower cheek tooth row with p2 through m2, occlusal view. Anterior is to the right. These teeth are part of a partial mandible mentioned by Leidy (1869, 1873) and Whitney (1880) as belonging to *Equus occidentalis* and deriving from the same locality yielding the original type series. This specimen has not previously been figured. The molars (left two teeth) lack any plesippine characters but, instead, exhibit broad, rounded linguaflexids and shortened ectoflexids. Scale = 1 cm.

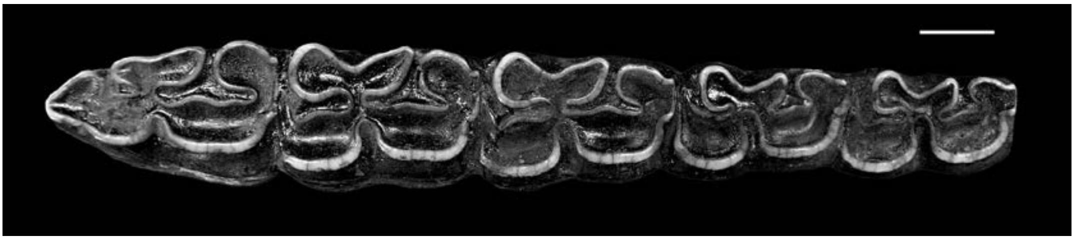

Figure 5 VPM 9141, left lower cheek tooth row with p2 through m2, occlusal view. Anterior is to the left. These teeth are from material mentioned by Leidy (1869, 1873) and Whitney (1880) as *Equus occidentalis* from the same locality yielding the original type series. This specimen has not previously been figured. The molars (right two teeth) exhibit broad, rounded linguaflexids and shortened ectoflexids. Scale = 1 cm.

approximately two miles to the southwest of McKittrick." (Schultz, 1937:5)

We agree with Schultz's (1937) interpretation. We emphasize that this does not indicate that the McKittrick and Asphalto paleontological localities are one and the same; different and geographically separate locality data are available for each, demonstrating that they are separate localities (Holroyd, personal communication, 2013).

It is of course possible, given the extensive asphalt mining and petroleum extraction conducted in and around the McKittrick region since Leidy first published on the remains of *E. occidentalis*, that any fossiliferous asphalt beds once located in the Asphalto area may have been completely excised. However, given that similar asphalt mining also took place at the McKittrick asphalt seeps, which remain extant, we conclude that the beds of asphaltum referenced by Leidy (1865, 1869, 1873) are more likely to be the McKittrick beds themselves. The nature of the fossils included in Leidy's type series supports this contention.

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The Addition of *Smilodon fatalis* (Mammalia: Carnivora: Felidae) to the Biota of the Late Pleistocene Carpinteria Asphalt Deposits in California, with Ontogenetic and Ecologic Implications for the Species

Christopher A. Shaw[1,2] and James P. Quinn[1]

ABSTRACT. A well-preserved Late Pleistocene flora and fauna was collected in 1927 and 1930 from an asphalt quarry located southeast of the city of Carpinteria in Santa Barbara County, California. In 1985, an edentulous left maxilla from a very young saber-toothed cat, *Smilodon fatalis,* was identified during organization of the California Institute of Technology collection from the Carpinteria locality at the Natural History Museum of Los Angeles County. This is the first and only *Smilodon* material identified from Carpinteria. Except for 13 mm of the permanent canine (located deep within the bifurcated canine alveolus), all developing deciduous and permanent cheek teeth have been lost. The Carpinteria specimen is from a much younger animal than any juvenile found in the Rancho La Brea collection at the La Brea Tar Pits and Museum and represents the first preweaned individual of this species to be identified anywhere.

Studies of the biota indicate that the Carpinteria fossil deposits accumulated in a coastal closed-cone pine forest with an understory consisting of ferns and shrubs, whereas the Rancho La Brea environment was inland coastal, with more open areas close to the asphalt traps. We suggest the Carpinteria habitat, with its dense patches of undergrowth, may have been a desirable area for birthing and/or denning and that the more open habitat at Rancho La Brea favored herds of open-country grazers and was more suitable for hunting prey.

INTRODUCTION

In Santa Barbara County, California, the city of Carpinteria is located on the coast approximately 133 km northwest of Rancho La Brea. Just southeast of the city, extensive asphaltic deposits were located on the now emergent Punta Gorda marine terrace (40–60 ka) in alluvial sands and gravels along approximately 2 km of the coastline (Arnold, 1907; Jackson, 1980; Lajoie and Sarna-Wojcicki, 1982). These asphaltic deposits are locally known as the "Carpinteria Formation" and extend inland for about 1.2 km (Chaney and Mason, 1933). They were exploited for paving beginning in 1875 (Caldwell, 2000), apparently exhausting the commercial resources by the 1930s (Miller, 1931).

A well-preserved Late Pleistocene biota was collected in 1927 (Hoffmann et al., 1927), and another separate site was recovered in 1930 (Miller, 1931; Chaney and Mason, 1933) from an asphalt quarry on the Lucien Higgins ranch (Fig. 1). These collections were procured by the Santa Barbara Museum of Natural History (SBMNH), the California Institute of Technology (CIT), and the University of California, Museum of Paleontology (Miller and Peck, 1979). Since its purchase in 1957, the CIT collections have been housed at the Natural History Museum of Los Angeles County (LACM). All fossil materials were removed from both sites and subsequent mining removed all of the asphalt deposits; in the 1940s, the County used the open mine "pits" as a refuse burn dump, which has since obscured the locations of the original fossil deposits (Miller and Peck, 1979; Guthrie, 2009).

Previous studies identified a robust biota of 204 species which includes 25 plants (Chaney and Mason, 1933; Miller, 1979), 57 marine mollusks (Grant and Strong, 1934), at least 12 insects (Lance, 1946; Miller, 1978; Moore and Miller, 1978; Ashworth, 1979; Miller and Peck, 1979; Doyen and Miller, 1980), five reptiles (Brattstrom, 1955; Jefferson, 1991), 79 birds (Miller, 1931, 1932; DeMay, 1941; Guthrie, 2009), and 26 mammals (Wilson, 1933). These plant and animal remains accumulated during Late Pleistocene time. Two samples of wood were dated using radiocarbon at greater than 38,000

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Figure 1 Aerial photograph taken in 1938 showing the locations of the asphalt mines southeast of Carpinteria, California. Fossiliferous deposits were recovered from the Higgins Ranch open pit asphalt mine.

(UCLA-180 and 181) years BP (Fergusson and Libby, 1964), and two pine cones yielded dates greater than 44,500 (QC-468) and 53,000 (QC-467B) years BP (Miller and Peck, 1979).

During curation of the CIT collection [locality LACM(CIT) 139] in 1985, a left maxilla of *Smilodon fatalis* (Leidy, 1868) was identified, which was apparently overlooked by Wilson (1933). The specimen (LACM 124681) represents a very young individual. An examination of the CIT and SBMNH Carpinteria collections yielded no other skeletal elements of this individual or of this taxon. LACM 124681 is the first record of *S. fatalis* identified in the Carpinteria biota.

DESCRIPTION

The Carpinteria left maxilla is small when compared with the youngest *S. fatalis* maxillae from the Rancho La Brea collections at the La Brea Tar Pits and Museum. Except for the ventrolateral portion of the canine alveolus, LACM 124681 is complete (Fig. 2). All deciduous teeth are missing. The alveoli for the cheek teeth (DP3–4) and deciduous canine are deep,

Figure 2 *Smilodon fatalis* (Leidy, 1868), LACM 124681, left maxilla: **A.** lateral view; **B.** anterior view; **C.** medial view.

Figure 3 *Smilodon fatalis* (Leidy, 1868), comparison between two left maxillae, one a weaned cub from Rancho La Brea (LACMHC 28832, to the left in each photograph) and the Carpinteria cub (LACM 124681): **A.** lateral view; **B.** occlusal (ventral) view; **C.** anterior view. Note how the maxillary bone anchors the roots of the deciduous premolars of the weaned cub (view 3B, left), as opposed to that of the Carpinteria specimen.

enlarged, and spacious, which without doubt facilitated the loss of the milk teeth and permanent tooth buds or crowns once the connective and other soft tissue decayed. With increasing maturity, alveolar bone normally forms around tooth roots of deciduous cheek teeth, thus anchoring teeth to the maxillae. This condition is found in all of the youngest juveniles recovered from Rancho La Brea (Fig. 3), but it is not the condition seen in LACM 124681.

At the time we recognized the taxonomic identity of LACM 124681, the alveolus for the upper deciduous and permanent canines was filled with asphaltic sediment. As some of this sediment was carefully removed, the tip of a tooth crown was revealed. About 13–15 mm of the permanent canine crown was uncovered and is still located deep within the anterior chamber of the bifurcated canine alveolus. The anterior edge of the developing cusp is not clearly serrated, and without extracting the tooth from the alveolus, it is impossible to see what posterior serrations may exist. Serrations cannot be detected on the x-ray (Fig. 4).

DISCUSSION

The small size of LACM 124681 compared with the Rancho La Brea sample of juvenile specimens and the open, spacious appearance of the cheek teeth alveoli indicate that this specimen belonged to an extremely young individual of *Smilodon fatalis*, younger than any juvenile *S. fatalis* represented at Rancho La Brea (Tejada-Flores and Shaw, 1984). It is clear that the deciduous canine and premolars had not fully erupted when this cub died and thus represents the first preweaned (i.e., pre-Stage 1 juvenile of Tejada-Flores and Shaw, 1984) individual found anywhere. The presence of 13–15 mm of developing permanent canine implies a growth period of about two months (Feranec, 2004, 2005), part of which may have been accomplished *in utero*. It appears from Feranec's (2004, 2005) stable isotope work that the timing of *Smilodon* dental eruption and maturity is roughly comparable to African lions, where the deciduous dentition is completely erupted by 2–3 months and the permanent dentition by 18–24 months (Smuts, et al., 1978), even though the sequence of tooth eruption is quite different (Tejada-Flores and Shaw, 1984). This would, therefore, imply that the preweaned cub from Carpinteria was less than 8–12 weeks old when it died.

Previous studies of the Carpinteria flora (Chaney and Mason, 1933), birds (Miller, 1931, 1932; DeMay, 1941), and mammals (Wilson, 1933) suggested that the Carpinteria fossil deposits accumulated in, or at the edge of, a coastal closed-cone pine forest that had essentially the same composition as the forest which now exists on the Monterey Peninsula. Beneath the pine forest there were dense ground-layer shrubs of lilac, manzanita, and bay, occasionally broken by sparser vegetation and patches of open grassland. The site was situated on a seaward slope, and the climate was cooler than today, with moister summers and more summer fog. In contrast, the biota at Rancho La Brea indicates an inland coastal environment, with more open areas close to the asphalt traps supporting coastal sage scrub, with wooded areas restricted to the occasional stream crossing the plain or distant upslope areas.

Chaney and Mason (1933) also concluded that the plant materials were deposited with the alluvial sediments of the "Carpinteria Formation" and were secondarily preserved by asphalt saturation. It seems likely, however, that some of the vertebrate remains found in the Carpinteria asphalt deposits accumulated in or adjacent to asphalt seeps, similar to the chief mode of bone accumulation observed at Rancho La Brea (Shaw and Quinn, 1986, 2001; Stock, 2001; Shaw,

Figure 4 *Smilodon fatalis* (Leidy, 1868), anterioventral view of LACM 124681 showing the tip of the permanent canine in the medial portion of the bifurcated canine alveolus (left). The x-ray (center and right) clearly shows the developing permanent canine deep within the alveolus.

2007). The absence of adult *Smilodon fatalis* skeletal elements in the same asphalt deposit implies that this juvenile did not die *in utero*, but was a victim of passive entrapment (Shaw and Quinn, 1986, 2001). We suggest that this individual wandered from the relative safety of a den and became mired in an asphalt seep.

The concept of sociality in *Smilodon* has been proposed using several lines of evidence (Gonyea, 1976; Tejada-Flores and Shaw, 1984; Heald and Shaw, 1991; Shaw, 2001; Carbone et al., 2008). *Smilodon fatalis* is represented by over 166,000 specimens at Rancho La Brea, dominated by subadult and juvenile specimens, whereas only one bone of a preweaned individual is recorded from Carpinteria. Sociality may be the reason so many postweaned individuals have been recovered from Rancho La Brea. Preweaned cubs were probably not physically strong, or neurologically developed, enough to participate in the hunt and, like African lions, were kept apart from the rest of the social group until after weaning. We suggest the Carpinteria habitat, with its dense patches of undergrowth, may have been a desirable area for birthing and/or denning. The habitat at Rancho La Brea favored herds of open-country grazers and apparently was a more suitable area, with its low vegetation, for hunting prey.

CONCLUSIONS

1. A left maxilla of a young saber-toothed cat, *S. fatalis* (Leidy, 1868), is the first record of this species from the Carpinteria asphalt deposits, Santa Barbara County, California.
2. Late Pleistocene Carpinteria may have been an ideal place for birthing and/or denning by *Smilodon*, whereas Rancho La Brea may have been a favored hunting area.
3. This specimen is from the youngest *Smilodon* identified from any site and represents a preweaned individual who likely wandered from its den to become mired in an asphalt seep.

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Perusing Talara: Overview of the Late Pleistocene Fossils from the Tar Seeps of Peru

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ABSTRACT. A. G. Edmund collected more than 28,000 fossil bones from the Late Pleistocene tar seep deposit near Talara, Piura, Peru, more than 50 years ago, in January 1958. Of the identified 27,072 specimens reported here, 63.4% represent Mammalia, 34.5% Aves, and 2.1% Reptilia, with trace amounts of Amphibia remains. Two families of Amphibia and eight families of Reptilia have been identified but remain unpublished. Fourteen nonpasserine avian orders represented by 6,322 identified specimens have been published, while the almost 3,000 passerine bones remain under study. Considering the fossil bird remains, Anseriformes (37.2%) and Passeriformes (32%) predominate, in contrast to the similarly aged Rancho La Brea, California, assemblage where diurnal birds of prey (60%) form the majority. Of the 17,167 mammalian specimens, Carnivora represent over 79%, indicating a classic carnivore trap situation, as at Rancho La Brea. Eight species of Carnivora have been identified (minimum number of individuals, MNI, in parentheses): the canids *Lycalopex sechurae* (101) and *Canis dirus* (51), the felids *Smilodon fatalis* (20), *Panthera onca* (3), *Puma concolor* (3) and *Leopardus* sp. (2), the mustelid *Conepatus talarae* (7) and a single bone of another as yet unidentified mustelid. The MNI is usually based on podial elements. Although *Panthera atrox* was reported from Talara, this report was in error, as the specimen is *P. onca*. Within the mammalian herbivores only the cervids and camelid have been studied and published. There are two cervids, *Odocoileus virginianus* (18) and *Mazama* sp. (1); a camelid, *Palaeolama aequatorialis* (3); a tayassuid, *Pecari tajacu* (1); an equid, *Equus* cf. *E. santaeelenae* (8); a gomphotheriid, *Notiomastodon platensis* (2); and at least five xenarthrans, *Holmesina occidentalis* (3), *Eremotherium laurillardi* (3), an unidentified nothrothere (1), *Glossotherium tropicorum* (2), and *Catonyx chiliense* (12). Rodentia are represented by *Neochoerus* sp. (1) and an undetermined number of smaller species still under study. Finally there is a single bat specimen assigned to *Lophostoma* cf. *L. occidentalis* and two didelphids to *Didelphis* sp. (1) and *Marmosa* sp. (1). The mammalian remains compare well with the famous Rancho La Brea deposits; carnivorans dominate, a high proportion of juveniles and subadults are present (35% to 69% depending on the species), and a significant number of *C. dirus* specimens show skeletal pathologies. A habitat with more water than is present today is indicated by this fauna, which has a distinctive South American component as well as a number of species in common with the Rancho La Brea assemblage.

INTRODUCTION

Next to the famous Rancho La Brea (RLB), California, tar pit fossil collection, the Talara site in Piura, northwest Peru, probably preserves the next largest tar seep collection of fossil vertebrates in the world; yet, no faunal summary of this site has been published since the preliminary listing presented in Lemon and Churcher (1961). Significant work has been accomplished since that time; in particular, a number of student theses have been completed which have identified and described large portions of this fauna, but most of this work remains unpublished. The whole catalogued collection has been inventoried, and in so doing many re-identifications were made. Additionally, all specimens have been registered in a database, allowing for accurate counts of numbers of specimens and a better basis upon which to judge the minimum number of individuals represented by each species. Although much work remains to be done, the symposium on tar pit faunas at the 2013 Society of Vertebrate Paleontology meeting in Los Angeles seemed an appropriate time to provide a summary of the work to date (Seymour, 2013), expanded here along with some comments on the paleoecology and taphonomy of the site.

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The Talara locality is located at 4°33′S, 81°7′W. A map of the location is provided in Campbell (1979) and Lindsey and Seymour (2015).

The history of the collection was outlined in Lemon and Churcher (1961), so only a few additional comments will be added here. In 1958, A. G. Edmund excavated at least one sublocality at Talara in a grid (Site II). The grid numbers are written in white ink on all the bones, but so far no one has investigated any associations via these field numbers. Recent work on the sedimentology by Alván et al. (2009) has clarified the work of Lemon and Churcher (1961).

Carbon dates published by Churcher (1966) are as follows: 13,616 ± 600 BP and 13,790 ± 535 BP on small chewed sticks, as well as 14,150 ± 564 BP and 14,418 ± 500 BP on large pieces of wood associated with fossil bones. Due to the refinements made in carbon dating since that time, several attempts have been made to date bone directly, but none have met with success yet because of the confounding effects of the presence of tar.

To date 27,072 fossil bones have been identified and catalogued into the Royal Ontario Museum collections. Additional unidentified and uncatalogued material remains in the Royal Ontario Museum, Toronto, Canada, collections. The purpose of this overview is to present an updated and annotated list of the species preserved at this site, as is known at the present time.

MATERIALS AND METHODS

All fossil material was examined to confirm taxonomic and element identification, and the ROM database was updated accordingly. Specimens were counted in order to establish number of specimens (NISP) and minimum number of individuals (MNI) counts for each taxon. All specimens are preserved in the Vertebrate Palaeontology collections of the Department of Natural History at the Royal Ontario Museum in Toronto, Canada.

The observation that many of the mammal specimens preserved in this deposit represent juvenile individuals led to an attempt to estimate the proportion of juveniles in the Talara sample at ROM. Since the proximal and distal epiphyses may not fuse to the shaft of a limb bone at the same time, the estimation of age of a proximal or distal portion of a limb bone is problematic, as the portion present may look adult but the missing portion may have looked juvenile. Disregarding this fact, the following method was used. For complete limb bones, if one or more of the epiphyses were not fused to the shaft, it was considered juvenile. For proximal or distal portions, their adult or juvenile status was scored considering that portion only. All limb bones, as well as proximal and distal portions, were examined and scored as adult or juvenile. For each species an MNI was tallied for both adults and juveniles for each limb bone. Then the ratio of the largest MNI for juvenile versus adult was calculated, even if not from the same limb bone. For instance, if the largest MNI for juvenile limb bones was represented by eight femora (e.g., which might be four complete and four proximal portions) and the MNI for adult limb bones was four adult radii, then the proportion juvenile for that particular species would be 8/12 or 67%. For those species with an overall MNI of 3 or less, no calculation was attempted due to the small sample size.

Calculations of frequency of bones for different regions of the body were tallied using the database records for the three most common carnivores: *Lycalopex sechurae, Canis dirus*, and *Smilodon fatalis*. Since each specimen was given a separate record, the number of records was tallied, and the percentage of specimens in each of seven body regions was calculated. Body regions were defined as: skull + mandible, teeth, vertebrae, ribs + sternebrae, girdles, limbs, and manus + pes. For comparison, the number of bones in a domestic dog and domestic cat were counted and the proportion calculated for them as well, with the exception that only 13 caudal vertebrae were counted for the cat, as it is thought (but probably not well established) that *S. fatalis* had an abbreviated tail. In this way, if a complete skeleton was fossilized, recovered and counted, the bones should be found to be in the proportion of a complete recent skeleton.

ABBREVIATIONS

MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Brazil
RLB	Rancho La Brea site, Los Angeles, California, USA
ROM	Royal Ontario Museum, Toronto, Ontario, Canada
UCMP	University of California Museum of Paleontology, Berkeley, California. USA
Undet.	Undetermined

RESULTS AND DISCUSSION

SYSTEMATIC PALEONTOLOGY

PLANTAE

The plant material from Talara remains unstudied. A. G. Edmund claimed that some of the plant remains represented stomach contents of ground sloths, but this was not well-documented at the time of collection. Much of the plant material does appear to be chewed or cropped into similar-sized fragments, supporting this claim.

INSECTA

Churcher (1966) published a summary of some of the insects preserved at Talara. These results are summarized in Table 1. Most of the identifications

Table 1 Fossil Insecta from Talara.[a]

Order	Family	Genus and species	Common name	NISP
Coleoptera	Hydrophilidae	*Hydrophilus* sp.	Water beetles	45
	Hydrophilidae	*Tropisternus* sp.	Water beetles	1
	Dytiscidae	Undetermined	Diving beetles	9
	Gyrinidae	Undetermined	Whirligig beetles	0[b]
	Scarabaeidae	Undetermined	Scarab beetles	19
	Scarabaeidae	*Copris incertus*	Scarab beetles	3
	Tenebrionidae	Undetermined	Darkling beetles	14
	Curculionidae	*Sphenophorus* sp., *Ryssomatus* sp.	Weevils	12
	Carabidae	Undetermined	Ground beetles	3
	Haliplidae?	Undetermined	Crawling water beetles	Undet.
	Silphidae?	Undetermined	Carrion beetles	Undet.
	Dermestidae?	Undetermined	Carpet beetles	Undet.
	Histeridae?	Undetermined	Clown beetles	Undet.
	Cicindelidae?	Undetermined	Tiger beetles	Undet.
	Cerambycidae?	Undetermined	Long-horned beetles	Undet.
Lepidoptera	Sphingidae	Undetermined	Sphinx moths	1
Orthoptera	Acrididae	Undetermined	Grasshoppers	1
Total				108

[a] Based on Churcher (1966).

[b] Gyrinidae specimen listed by Churcher (1966) re-identified as *Tropisternus* sp.

are not more refined than the family level, and there are still many hundreds of fossils, particularly beetle elytra, that remain unstudied. The Gyrinidae specimen listed by Churcher (1966) has been re-identified as *Tropisternus* sp., a hydrophilid, hence removing Gyrinidae from the fauna at this time.

AMPHIBIA AND REPTILIA (2.1% of the fossil bones)

Philip Currie, now of dinosaur fame, completed a preliminary study of the amphibians and reptiles from the Talara site as a student project in the 1970s. This paper was not published, and none of these specimens have been re-evaluated since that time; consequently, the identifications presented here are his, with only minor modifications, such as updating the taxonomy. Only the number of specimens in the database are listed in Table 2, as these specimens are in need of further study.

AVES (34.5% of the fossil bones)

Kenneth E. Campbell, Jr., completed his Ph.D. dissertation on the nonpasserine bird fossils from Talara, and these specimens were published by him (Campbell, 1979). Campbell (1979:table 1) lists the 89 species described, including six new genera and 21 new species, plus the NISP and MNI for each species, giving a total of 742 individual birds, represented by 6,258 specimens. This table is reproduced here as Table 3, with updated taxonomy (following such sources as Clements, 2007; Baker et al., 2012), updated common names, and a few adjustments in NISP and MNI taken from the ROM database. Note that there are more specimens and a slightly adjusted total MNI than the summary published by Campbell (1979); any numbers changed from Campbell's table 1 are in bold.

Few workers have re-examined any parts of the nonpasserine collection, except Suárez and Olson (2009), who reassigned the hawk *Miraquila terrestris* to *Buteogallus terrestris*. Additionally, they described the small caracara specimens (published by Campbell [1979] as *Polyborus plancus*) as a new species in the genus *Caracara* (Suárez and Olson, 2014).

Jessica Oswald (University of Florida) presently is studying the passerine specimens (2,986 specimens). To date she has identified specimens from the following families: Furnariidae, Thamnophilidae, Tyrannidae, Hirundinidae, Mimidae, Thraupidae, Cardinalidae, and Icteridae, with the great majority representing Icteridae (Jessica Oswald, personal communication, 2013). A preliminary list of a few of these species was published (Oswald and Steadman, 2010), and this list has been appended to Table 3.

MAMMALIA (63.4% of the fossil bones)

Eight orders of mammals are preserved, as discussed below. NISP and MNI are in Table 4.

Didelphimorphia (5 specimens)

Four of these specimens have tentatively been assigned to *Didelphis* sp. and the fifth to *Marmosa* sp. and remain undescribed.

Xenarthra (1,873 specimens, 10.9% of the mammal specimens)

Table 2 Fossil Amphibia and Reptilia from Talara.[a]

Order	Family	Genus and species	Common name	NISP
Anura	Bufonidae	Undetermined	Toad	13
	Ranidae	Undetermined	Frog	1
Crocodilia	Alligatoridae	*Caiman crocodilius*	Spectacled caiman	160
Squamata	Boidae	*Boa* sp.	Boa	15
	Colubridae	Undetermined	Snake	64
	Phyllodactylidae	*Phyllodactylus* sp.	Leaf-toed gecko	3
	Iguanidae	*Iguana* sp.	Iguana	24
	Iguanidae	Undetermined	Iguanid	1
	Gymnophthalmidae	*Cercosaura* sp.	Spectacled lizard	3
	Teiidae	*Callopistes* sp.	False monitor	70
	Teiidae	*Dicrodon* sp.	Desert tegu	23
	Emydidae	*Trachemys* sp.	Slider	2
	Geoemydidae	*Rhinoclemmys melanosterna*	Colombian wood turtle	158
	Testudinidae	*Chelonoidis* sp.	Tortoise	48
Total				585

[a] Updated data from a student project (P. Currie, unpublished data).

Megatheriidae

Eremotherium laurillardi (Lund)

The giant ground sloth material from Talara is unusually small and has been given the name *Eremotherium elenense* (Hoffstetter, 1949) in the past. However, Cartelle and De Iuliis (1995) studied the variation in this genus throughout North and South America and came to the conclusion that there was only one variable species in the Quaternary and it was *E. laurillardi*. Consequently the small eremothere from Talara is here identified as *E. laurillardi*.

Undetermined nothrothere. A single tooth (ROM 12686) is thought to represent an undetermined nothrothere. Further study is required to confirm or deny this tentative identification.

Mylodontidae

Catonyx chiliense (Lydekker)

McDonald (1987) completed his Ph.D. dissertation on a systematic review of the South American scelidothere sloths, and he concluded that the Talara specimens should be referred to the species *C. chiliense* (McDonald, 1987), which was originally described as *Scelidotherium chiliense* by Lydekker (1886).

Glossotherium tropicorum Hoffstetter

The fossils of this sloth remain unstudied, but were tentatively identified by Greg McDonald when he was a graduate student in Toronto. Perhaps it remains unstudied because no significant skull material was preserved, with only one mandible present (ROM 02122); however, there is a reasonably complete skull and jaw from the nearby Coralito site in Ecuador in the ROM collections (ROM 3146).

Pampatheriidae

Holmesina occidentalis (Hoffstetter)

In presenting a systematic review of the Quaternary Pampatheriidae of North and South America, Edmund (1996) identified the pampathere from Talara and nearby La Carolina, Ecuador, as belonging to this species based on the size and ornamentation of the preserved osteoderms, which form a large portion of the remains. Many more specimens of this species from Coralito, Ecuador, also are preserved in the ROM collections.

Chiroptera (1 specimen)

Phyllostomidae

Czaplewski (1990) published on the sole identified bat fossil in the ROM collections (ROM 35105), identifying the specimen as *Tonatia* cf. *T. silvicola*. Since that time, the genus *Tonatia* has been split into two, *Tonatia* and *Lophostoma* (Lee et al, 2002), resulting in the combination *Lophostoma silvicolum* being accepted for this species. More recently, Velazco and Cadenillas (2011) recommended that the living subspecies from northern Peru, *Lophostoma sylvicolum occidentalis*, be raised to species status as *Lophostoma occidentalis*. This would render Czaplewski's original referral to *Lophostoma* cf. *L. occidentalis*.

A hand-written note by C. S. Churcher suggested that there were other bat specimens that compared well with *Eptesicus*, but these specimens cannot be located at ROM at the present time. Continued work by Cadenillas and Martínez (2006) and Cadenillas et al. (2013) document *Eptesicus* cf. *E. innoxius*, *Myotis* sp., and other bat fossils from Talara. Several bat postcranial elements recently located amongst unidentified material at ROM are under study by Moretto and Lim (in prep).

Table 3 Fossil Aves from Talara.[a]

Order	Family	Genus and species	Common name or X = extinct	NISP	MNI	MNI based on
Tinamiformes	Tinamidae	*Crypturellus* cf. *C. transfasciatus*	Pale-browed Tinamou	1	1	
Anseriformes	Anatidae	*Dendrocygna autumnalis*	Black-bellied Whistling-Duck	301	33	Right humerus
		Chloephaga melanoptera	Andean Goose	91	7	Left humerus
		Cairina moschata	Muscovy Duck	33	4	Left scapula
		Nannonetta invisitata	X	112	10	Right coracoid
		Anas talarae	X	13	2	Right coracoid
		Anas amotape	X	29	5	Right tibiotarsus
		Anas sanctaehelenae	X	5	1	
		Anas bahamensis	White-cheeked Pintail	**2,877**	243	Right coracoid
		Nomonyx dominicus	Masked Duck	1	1	
		Undetermined gen. et sp.		**5**	1	
Galliformes	Cracidae	*Penelope* cf. *P. purpurascens*	Crested Guan	4	1	
Podicipediformes	Podicipedidae	*Tachybaptus dominicus*	Least Grebe	4	2	Left femur
		Podilymbus podiceps	Pied-billed Grebe	4	2	Right femur
Ciconiiformes	Ciconiidae	*Jabiru mycteria*	Jabiru	47	5	Right carpal
		Mycteria americana	Wood Stork	1	1	
Pelecaniformes	Phalacrocoracidae	*Phalacrocorax brasilianus*	Neotropic Cormorant	**135**	15	Left coracoid
		Phalacrocorax bougainvillii	Guanay Cormorant	1	1	
Pelecaniformes	Ardeidae	*Ardea cocoi*	Cocoi Heron	6	2	Left carpometacarpus
		Ardea alba	Great Egret	11	4	Right coracoid
		Egretta thula	Snowy Egret	7	2	Right scapula
		Egretta caerulea	Little Blue Heron	1	1	
		Egretta sp.		15	5	Left tarsometatarsus
		Syrigma sanctimartini	X	1	1	
		Nycticorax nycticorax	Black-crowned Night-Heron	54	10	Right coracoid
Pelecaniformes	Threskiornithidae	*Eudocimus peruvianus*	X	10	2	Left tarsometatarsus
		Eudocimus albus	White Ibis	10	3	Left coracoid
		Theristicus wetmorei	X	2	1	
		Platalea ajaja	Roseate Spoonbill	1	1	
Accipitriformes	Cathartidae	*Geronogyps reliquus*	X	**39**	4	Right femur
		Coragyps cf. *C. atratus*	Black Vulture	26	3	Right tibiotarsus
		Cathartes aura	Turkey Vulture	**83**	6	Left tibiotarsus
		Gymnogyps howardae	X	30	4	Left tarsometatarsus
		Vultur gryphus	Andean Condor	17	3	Left femur
		Sarcoramphus? *fisheri*	X	3	1	
		Undetermined gen. et sp.		**2**	1	

Table 3. Continued.

Order	Family	Genus and species	Common name or X = extinct	NISP	MNI	MNI based on
Accipitriformes	Accipitridae	*Buteogallus terrestris*	X	8	2	Right tarsometatarsus
		Amplibuteo hibbardi	X	53	7	Right tarsometatarsus
		Parabuteo unicinctus	Harris's Hawk	31	4	Right tibiotarsus
		Geranoaetus polyosoma	Variable hawk	31	4	Left coracoid
		Geranoaetus melanoleucus	Black-chested Buzzard-Eagle	33	4	Left tarsometatarsus
		Buteo sp. 1		4	2	Left ulna
		Buteo sp. 2		10	4	Right tibiotarsus
		Undetermined gen. et sp.		3	1	
Gruiformes	Rallidae	*Porzana carolina*	Sora	3	1	
Charadriiformes	Burhinidae	*Burhinus superciliaris*	Peruvian Thick-knee	29	4	Left humerus
Charadriiformes	Charadriidae	*Viator picis*	X	1	1	
		Pluvialis squatarola	Black-bellied Plover	3	1	
		Pluvialis dominica	American Golden-Plover	32	6	Left humerus
		Vanellus edmundi	X	3	2	Left humerus
		Charadrius collaris	Collared Plover	3	1	
		Charadrius semipalmatus	Semipalmated Plover	1	1	
		Charadrius vociferus	Killdeer	7	2	Left coracoid
		Undetermined gen. et sp.		1	1	
Charadriiformes	Thinocoridae	Undetermined gen. et sp.		1	1	
		Thinocorus rumicivorus	Least Seedsnipe	1	1	
		Thinocorus koepckeae	X	1	1	
Charadriiformes	Jacanidae	*Jacana spinosa*	Northern Jacana	1	1	
Charadriiformes	Scolopacidae	*Actictis macularius*	Spotted Sandpiper	1	1	
		Tringa solitaria	Solitary Sandpiper	21	5	Left coracoid
		Tringa melanoleuca	Greater Yellowlegs	11	2	Right tarsometatarsus
		Tringa semipalmata	Willet	16	4	Left humerus
		Tringa flavipes	Lesser Yellowlegs	72	14	Left humerus
		Tringa ameghini	X	2	1	
		Numenius cf. *N. borealis*	Eskimo Curlew	1	1	
		Nuntius solitarius	X	2	1	
		Arenaria interpres	Ruddy Turnstone	2	1	
		Calidris himantopus	Stilt Sandpiper	1	1	
		Calidris minutilla	Least Sandpiper	28	12	Right humerus
		Calidris melanotos	Pectoral Sandpiper	221	57	Left humerus
		Calidris mauri	Western Sandpiper	17	3	Left humerus
		Caldris chapmani	X	1	1	
		Phalaropus tricolor	Wilson's Phalarope	68	11	Right humerus
		Phalaropus lobatus	Red-necked Phalarope	2	2	Left humerus
		Phalaropus graui	X	1	1	

Table 3. Continued.

Order	Family	Genus and species	Common name or X = extinct	NISP	MNI	MNI based on
Charadriiformes	Laridae	*Leucophaeus atricilla*	Laughing Gull	**32**	6	Right humerus
		Leucophaeus pipixcan	Franklin's Gull	95	17	Left coracoid
Columbiformes	Columbidae	*Zenaida asiatica*	White-winged Dove	7	2	Right humerus
		Zenaida auriculata	Eared Dove	102	**12**	Right ulna
		Columbina talpacoti	Ruddy Ground-Dove	3	2	Left coracoid
		Columbina cruziana	Croaking Ground-Dove	**599**	68	Left humerus
Strigiformes	Tytonidae	*Tyto alba*	Barn Owl	83	8	Right coracoid
Strigiformes	Strigidae	*Bubo virginianus*	Great Horned Owl	103	11	Left tarsometatarsus
		Athene cunicularia	Burrowing Owl	6	1	
		Asio flammeus	Short-eared Owl	12	2	Right coracoid
Caprimulgiformes	Caprimulgidae	*Chordeiles acutipennis*	Lesser Nighthawk	6	1	
		Caprimulgus piurensis	X	2	1	
Falconiformes	Falconidae	*Caracara seymouri*	X	**306**	27	Right tarsometatarsus
		Milvago brodkorbi	X	**164**	17	Right carpometacarpus
		Falco sparverius	American Kestrel	55	6	Left carpometacarpus
		Falco femoralis	Aplomado Falcon	7	2	Right coracoid
		Falco peregrinus	Peregrine Falcon	34	3	Right humerus
		Falco sp.		7	1	
		Undetermined gen. et sp.		**1**	1	
Psittaciformes	Psittacidae	*Forpus coelestis*	Pacific Parrotlet	1	1	

[a] Reproduced from Campbell (1979:table 1) with data appended from Oswald and Steadman (2010). Numbers changed from Campbell's table are in bold.

Rodentia (134 specimens, 0.79% of the mammal specimens)

Besides the small rodent remains on loan to Michael Carleton (United States National Museum), the remaining rodent, the extinct giant capybara *Neochoerus* sp., is represented by 20 postcranial elements, with an MNI of 1. The phalanges of this animal were probably the source of the previous uncertain report of tapir from this site by Lemon and Churcher (1961).

Carnivora (13,636 specimens, 79.5% of the mammal specimens)

Canidae

Lycalopex sechurae (Thomas)

Beebe (1976) completed her Ph.D. dissertation on this species, which was then named *Dusicyon sechurae*. Since that time the species has been transferred to the genus *Lycalopex* (Cossíos, 2010). Beebe (1976) found only one species amongst the cranial and dental specimens preserved at Talara and assumed the postcranial also represented only one species. By NISP, this is by far the most common animal found at the Talara site, with almost all skeletal elements represented in the collection. Martínez and Cadenillas (2006) concluded that the subspecies proposed by Hoffstetter (1952) for the fossil form (*D. sechurae elenensis*) was not warranted.

This species, called the Sechuran desert fox, still lives in the area today. It is a nocturnal omnivore that can survive for some period of time on a completely herbivorous diet, but most commonly eats insects, rodents, birds eggs, and carrion (Asa and Wallace, 1990). This would make it particularly vulnerable to being entrapped by the tar seeps, given the number of avian and insect remains that have been preserved there.

Canis dirus Leidy

Churcher (1959) first identified this canid from Talara (although with some doubt as to the species allocation), at which time it was the first

Table 4 Fossil Mammalia from Talara.

Order	Family	Genus and species	Common name or X = extinct	NISP	MNI	MNI based on
Didelphimorphia	Didelphidae	*Didelphis* sp.	Opossum	4	1	No duplication
		Marmosa sp.	Mouse opossum	1	1	No duplication
Chiroptera	Phyllostomidae	*Lophostoma* cf. *L. occidentalis*	Round-eared bat	1	1	No duplication
Rodentia	Hydrochoeridae	*Neochoerus* sp.	X	20	1	No duplication
	Undetermined	Undetermined		114	?	
Carnivora	Canidae	*Lycalopex sechurae*	Sechuran fox	7,326	101	Left calcaneum
		Canis dirus	X	4,216	51	Right calcaneum
	Felidae	*Smilodon fatalis*	X	1,874	20	Right astragalus
		Panthera onca	Jaguar	93	3	Right calcaneum
		Puma concolor	Puma	48	3	Left third metatarsal
		Leopardus sp.		6	2	Right humerus
	Mustelidae	*Conepatus talarae*	X	89	7	Left humerus
		Undetermined		1	1	No duplication
Xenarthra	Megatheriidae	*Eremotherium laurillardi*	X	99	3	Age of radii
		Undetermined	X	1	1	No duplication
	Mylodontidae	*Catonyx chiliense*	X	602	12	Left femur
		Glossotherium tropicorum	X	14	2	Left petrosal
	Pampatheriidae	*Holmesina occidentalis*	X	1,157	3	Right third metatarsal
Artiodactyla	Cervidae	*Odocoileus virginianus*	White-tailed deer	675	18	Left astragalus
		Mazama sp.	Brocket deer	2	1	No duplication
	Tayassuidae	*Pecari tajacu*	Collared peccary	1	1	No duplication
	Camelidae	*Palaeolama aequatorialis*	X	136	3	Right astragalus
Perissodactyla	Equidae	*Equus* cf. *E. santaeelenae*	X	505	8	Left calcaneum
Proboscidea	Gomphotheriidae	*Notiomastodon platensis*	X	182	2	Age, no duplication
Total				17,167	246	

report of this species from South America. Berta (1988) confirmed the presence of this species from Talara with more detailed comparative analyses, and in this publication, she listed many of the ROM specimens (Berta, 1988:38–40). In contrast to all other animals preserved at Talara, there are a large number of pathological bones (at least 60), mostly representing healed wounds or bone overgrowths. A. G. Edmund had assembled radiographs and completed some analysis but never published on these specimens.

Kisko (1967) completed a study of the metapodials of the Talaran dire wolf. He found them to be slightly larger than the California population from RLB described by Nigra and Lance (1947) but to lie within the limits of variation of a single species.

Almost all skeletal elements are represented in the collection. Although there is an MNI of 51 for this species, strangely only one baculum has been identified, which contrasts with RLB, where several hundred bacula have been identified (Hartstone-Rose et al., 2013).

Felidae

Smilodon fatalis (Leidy)

C. S. Churcher studied the *Smilodon* material, but to date he has not published on this animal. Instead, he supplied data to Kurtén and Werdelin (1990) who concluded that the Talara *Smilodon* represented *S. fatalis*. Their conclusions were based primarily on the elongated proportions of the foot bones, as well as most skull proportions. Kurtén and Werdelin (1990) noted that this North American species may have immigrated along the western coastline of northern South America along with the dire wolf and the American lion, although we now know that this last species is not present. Almost all skeletal elements of *Smilodon* are represented in the collection, probably even including several hyoid bones.

Panthera onca (Linnaeus)

Seymour (1983) described the jaguar fossils in some detail, demonstrating that the large cat skull (ROM 2115) was one of the largest known jaguar fossils and that it did not belong to *P. atrox* as suggested by Lemon and Churcher (1961). Many publications since Lemon and Churcher (1961) have repeated the claim of *P. atrox* from South America based on this sole specimen, in particular Kurtén and Anderson (1980). Therefore there are no valid records of *P. atrox* from South America to date. The most southerly known records are from Tequixquiac, Mexico, published by Freudenberg (1910). Unfortunately, Freudenberg's specimens were lost during World War II, although casts exist of a few of the specimens (e.g., UCMP 27604, a right mandible). Additionally, Seymour (1983) demonstrated sexual dimorphism in the Talara jaguar fossils, the first such demonstration for this species in the fossil record.

Puma concolor (Linnaeus)

Seymour (1983) described the puma fossils, showing that there was little difference between the Talara form and the living species. This species was not identified by Lemon and Churcher (1961) as present at Talara.

Leopardus sp.

Seymour (1983) described two incomplete right humeri of a small leopardine, one adult (ROM 29752) and one subadult (ROM 29751). Since that time four additional postcranial fossils of a leopardine have been located, but none allow a specific identification due to the similarity of leopardine postcranial elements. This genus was not identified by Lemon and Churcher (1961) as present at Talara.

Mustelidae

Conepatus talarae Churcher and van Zyll de Jong

Churcher and van Zyll de Jong (1965) described this extinct species of skunk based on the Talara fossils. The main differences from living species of *Conepatus* are in the shapes of the upper P4 and particularly the upper M1. I examined a selection of *Conepatus* specimens at MACN and found most did not look like *C. talarae*, although one specimen of *Conepatus chinga* (MACN 28.184) closely approached the *C. talarae* condition. With the larger samples of recent comparative material available today, it might be worth re-examining the validity of the species.

Undetermined mustelid. A single proximal part of a juvenile femur (ROM 60500) does not fit into any of the other carnivoran taxa already described and appears to represent a medium-sized mustelid, possibly representing *Eira* sp. Subadult comparative material would be required to confirm this identification.

Artiodactyla (815 specimens, 4.8% of the mammal specimens)

Cervidae

Odocoileus virginianus (Zimmerman)

When Churcher (1962) published on the deer fossils from Talara, there was still some doubt as to the taxonomic status of the local living species of Peruvian *Odocoileus*, complicating the identification of the fossils. Hoffstetter (1952) considered that the fossil species *Odocoileus salinae* might not be specifically different from the living *Odocoileus gymnotis*, which Hershkovitz (1958) in turn included in *O. virginianus*. Additionally, Hershkovitz had a chance to examine some of the Talara material and commented that it looked to be conspecific with the living whitetails (see quote in Churcher, 1962:6). Since this time, the living species has indeed been included in *O. virginianus* (Emmons, 1990), and so here I refer the Talara deer fossils to *O. virginianus* and not *O. salinae*, as did Churcher (1962).

Mazama sp.

Churcher (1962) identified two specimens, a juvenile atlas and a small antler tine, as not consistent with *Odocoileus*, and hence mostly likely representing *Mazama* sp.

Tayassuidae

Pecari tayassu (Linnaeus)

Only a single specimen of this species has been identified so far. This family, the Tayassuidae, was noted as absent from Talara by Lemon and Churcher (1961).

Camelidae

Palaeolama aequatorialis Hoffstetter

Churcher (1965) published on the camel from Talara, identified it as *P. aequatorialis* and named a new subgenus for this species, *Astylolama*. He mentioned that with degree of development and relatives sizes, he thought there might be five adults and three juveniles represented in this material, whereas using strict duplication of elements I can find no more than three individuals represented. I have reported an MNI of three here since the method is the same as that which I have used for MNI counts of all the other species. Additional, and better, material of this species from Coralito, Ecuador, is in the ROM collections.

Perissodactyla (505 specimens, 3.0% of the mammal specimens)

Equidae

Equus santaeelenae (Spillmann)

Although Churcher studied and identified the Talara equid specimens, he didn't publish directly upon them. He referred to his identification as *E. santaeelenae* in an abstract only (Churcher, 1985). Recently this species, originally described by Spillmann (1938), was identified from the Inciarte site in Venezuela by Rincón et al. (2006). Prado and Alberdi (1994), in their review of the South American horses, considered this species valid.

Table 5 Percent juveniles for select Talara fossil mammals.

Genus and species	% Juvenile	% Juvenile based on
Lycalopex sechurae	35	76 adult left ulnae, 40 juvenile right tibiae
Canis dirus	43	28 adult right tibiae, 21 juvenile left humeri
Smilodon fatalis	41	10 adult right humeri, 7 juvenile left ulnae
Conepatus talarae	57	3 adult left humeri, 4 juvenile left humeri
Catonyx chiliense	69	4 adult left femora, 9 juvenile right humeri
Odocoileus virginianus	64	8 adult right humeri, 14 juvenile right radii
Equus cf. *E. santaeelenae*	57	3 adult right ulnae, 4 juvenile left femora

Proboscidea (182 specimens, 1.1% of the mammal specimens)

Gomphotheriidae

Notiomastodon platensis (Ameghino)

Mothé et al. (2012) studied the Quaternary gomphotheres from South America and concluded that there was only one lowland species. Although they did not examine the Talara material, they identified remains of *N. platensis* from coastal areas of central Peru and northern Ecuador, implying that this is the most likely identification for the material from coastal areas of northern Peru and southern Ecuador as well. The Talara material is represented by parts of two individuals, one juvenile and one older adult.

JUVENILE SPECIMENS

Percentages of juvenile specimens are presented in Table 5. The percentages of juveniles for three herbivores (*Catonyx*, *Odocoileus*, and *Equus*) ranged between 57% and 69%, while those for three carnivores (*Lycalopex*, *Canis*, and *Smilodon*) were the same or lower, ranging from 35% to 57%. It is not certain if there is any significance to a higher proportion of juvenile herbivores preserved. Although these percentages of juveniles seem to be high, it is difficult to know what constitutes a high proportion of juveniles because of a lack of comparative data. Comparative data for RLB is not available from Stock (1992), as this summary gives proportions of the fauna only. Miller (1968) gave a summary of 2,100 *Smilodon* specimens and showed that, based on skulls, the proportion of juvenile specimens differed between pits from 11% to 25%. This would seem to indicate that 41% for the Talara *Smilodon* is relatively high, but the Talara calculation was based on limb material and not skull material, and the sample size is much smaller than at RLB (MNI of 20 versus 2,100 for RLB), so these data may not be directly comparable. There does not seem to be similar comparative data available from RLB for any of the other five species presented in Table 4.

The ROM holds significant numbers of Plio–Pleistocene mammal specimens from a series of localities of in southwest Florida, USA, primarily from fluvial deposits of Charlotte and Sarasota counties. In order to compare with Talara, the ROM database was queried as to the number of juvenile and nonjuvenile mammal specimens from this collection. The count was 252 juvenile versus 14,477 adult, or about 1.7% juvenile. If the Florida collection is at all representative of fossil sites in general, then the Talara site does indeed have a high proportion of juvenile specimens.

Several reasons might be suggested for the high proportion of juveniles seen in the Talara fauna. Juveniles at certain times of the year (e.g., post-breeding) might make up the majority of the number of individuals in a population and hence by chance alone might be more likely to become trapped in the tar pits. Also the juveniles might be relatively naïve about the tar pits or relatively weaker and less able to extract themselves once ensnared.

BODY SECTION PRESERVATION

The MNI for many of the Talara mammals was based on podial elements (see Table 4) leading to the hypothesis that since terrestrial animals tend to get stuck in tar feet-first, that the manus + pes category might be overrepresented in the fossil material. This idea is not particularly supported by the data presented in Table 6. While there are more bones preserved in the manus + pes category than for any other category for all three taxa considered, if the proportions are compared to the proportion of bones found in a complete dog or cat skeleton, then the manus + pes category is not overrepresented. In fact, the manus + pes category is underrepresented for *L. sechurae* and *C. dirus* compared with the complete dog skeleton. Perhaps due to their small size, some of the manus + pes bones may not have been recovered or remain unidentified. For the larger saber-toothed cat, the manus + pes category is preserved in the approximate proportion of a complete cat skeleton.

Because there is an observed and expected proportion to this table, a chi-square test might be run for significance, but this was not done for two reasons: Zar (1974) states that chi-square tests should never be run on proportions or percentages, and the breakage of bones means that one skull, or one limb bone for instance, may produce many fragments, all of which could be identifiable and counted. It seems that all the larger bones (skull + mandible, limb, and girdle categories) are overrepresented in the proportions of fossil material in Table 6, suggesting that breakage of these larger bones into many pieces

Table 6 Inventory of body regions preserved for the three most common carnivores from Talara, in percent, compared with living *Canis familiaris* and *Felis catus*.

Category	*Lycalopex sechurae*	*Canis dirus*	*Canis familiaris*	*Smilodon fatalis*	*Felis catus*
Skull + mandible	14.2	9.3	**1.1**	6.1	**1.2**
Teeth	12.1	16.5	**15.7**	7.5	**10**
Vertebrae	16.2	12.8	**17.5**	16.3	**15.8**
Ribs + sternebrae	5.5	2.5	**12.7**	5.5	**13.1**
Girdles	4.8	3	**1.5**	2.1	**1.5**
Limbs	17.2	15.6	**4.5**	9.8	**4.6**
Manus and pes	29.9	40.2	**47**	52.8	**53.9**
Total[a]	99.9	99.9	**100**	100.1	**100.1**

[a] Total percentages may not add to 100 due to rounding.

may account for this. The rib + sternebrae are probably underrepresented due to the difficulty in determining their identity or because they are actually preferentially scavenged and removed before fossilization. Given the vagaries of fossilization and recovery, it is actually somewhat surprising how closely the *S. fatalis* body section proportions match the proportions of *Felis catus*.

COMPARISON WITH RANCHO LA BREA (RLB), CALIFORNIA

Of the 17,167 mammal specimens identified from Talara, 13,636 (or 79.5% of the mammals) represent eight species in the order Carnivora. This is very high proportion of the fauna, considering that carnivores normally make up between 2% and 3% of modern faunas (Eisenberg and Thorington, 1973; Odum et al., 2004). This indicates a classic carnivore trap situation, such as the tar pits at RLB, California (Stock, 1992), or in select other environments such as lava blisters (White et al., 1984), where carnivores are selectively preserved, far out of proportion to their presence in the ecosystem.

RLB preserves a much larger sample than does Talara, by an order of magnitude. The MNI for RLB *S. fatalis* mentioned in Marcus (1960) was 1,029, while in Miller (1968) it was listed as 2,100. Since that time another 400 or so individuals have been tallied (Chris Shaw, personal communication, 2013), making the MNI about 2,500 compared with 20 at Talara. The MNI for *C. dirus* from Marcus (1960) was reported as 1,646 but is now thought to be about twice that, in the order of 3,200 to 3,500 individuals (Chris Shaw, personal communication, 2013), compared with 51 at Talara.

Several species are common to both RLB and Talara. Amongst the mammals, the carnivores *C. dirus*, *S. fatalis*, *Panthera onca*, and *Puma concolor* all occur at the two locations, but no mammalian herbivorous species were in common. Within the nonpasserine birds, 16 species are in common, all widespread species on the two continents: the grebe *Podilymbus podiceps*; the herons *Ardea alba*, *Egretta thula*, *Egretta caerulea*, and *Nycticorax nycticorax*; the spoonbill *Platalea ajaja*; the vulture *Cathartes aura*; the falcons *Falco sparverius* and *Falco peregrinus*; the plovers *Pluvialis squatarola* and *Charadrius vociferus*; the shorebirds *Tringa melanoleuca* and *Tringa semipalmata*; and finally three owls *Bubo virginianus*, *Athene cunicularia*, and *Asio flammeus*.

At this point, there are only three passerine families in common to the two sites: Tyrannidae, Mimidae and Emberizidae. Once the passerines are fully identified, it would be expected that few species would be in common between the sites, given the amount of passerine endemism in the tropics, although some migrants might be expected in common.

Nine families of mammals found at RLB are not found at Talara: Megalonychidae, Leporidae, Procyonidae, Ursidae, Mammutidae, Elephantidae, Tapiridae, Antilocapridae, and Bovidae. In turn, four families of mammals found at Talara are not found at RLB: Didelphidae, Phyllostomidae, Pampatheriidae, and Gomphotheriidae. A similar pattern is found in the birds. Six families of nonpasserines are found at RLB and not Talara: Teratornithidae, Phasianidae, Gruidae, Recurvirostridae, Cuculidae, and Picidae, and six families are found at Talara but not at RLB: Tinamidae, Cracidae, Burhinidae, Thinocoridae, Jacanidae, and Psittacidae. Much, but not all, of these differences reflect the geographic location of the Talara site in tropical South America. The lack of a record for some families at Talara (e.g., Procyonidae and Tapiridae) may represent the paleoecology of the area or the chance nonpreservation of these taxa.

Both RLB and Talara preserve substantial bird remains, making them particularly valuable resources, because bird remains are often lacking or poorly represented from many non–tar pit locations. Stock (1992) lists 138 bird species from RLB, whereas Table 3 lists at least 107 species from Talara. Of the 9,328 bird specimens preserved at Talara, over two-thirds are either Anseriformes (37.2% of the birds) or Passeriformes (32.0% of the birds), with only 10.2% representing diurnal birds of prey (Accipitriformes or Falconiformes). This contrasts sharply with RLB, where 60% of the bird fauna are diurnal birds of prey (Stock, 1992). Perhaps at Talara, water pooled on top of the seeped oil, attracting ducks to land on this fatal arrangement. As well, it is possible that Talara was on a flyway for migrating ducks and passerines, accounting for their overabundance there. If the water-covered oil was relatively fluid, whole animals may have been entombed, leaving little exposed for scavengers.

PALEOECOLOGY

Today the Peruvian coast is dominated by arid desert scrub habitat, but several kinds of animals represented by fossils from Talara indicate a moister environment (Campbell, 1982; Martínez and Cadenillas, 2004). These include such animals as water and diving beetles, frogs, caimans, pond turtles, ducks, grebes, herons, ibises, rails, plovers, sandpipers, and capybaras, most of which do not occur in the area today in any numbers due to the aridity of the environment. Martínez and Cadenillas (2004) however suggested caution in the interpretation of the paleoenvironment because of the great variety of animals which can occur in similarly arid areas.

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“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

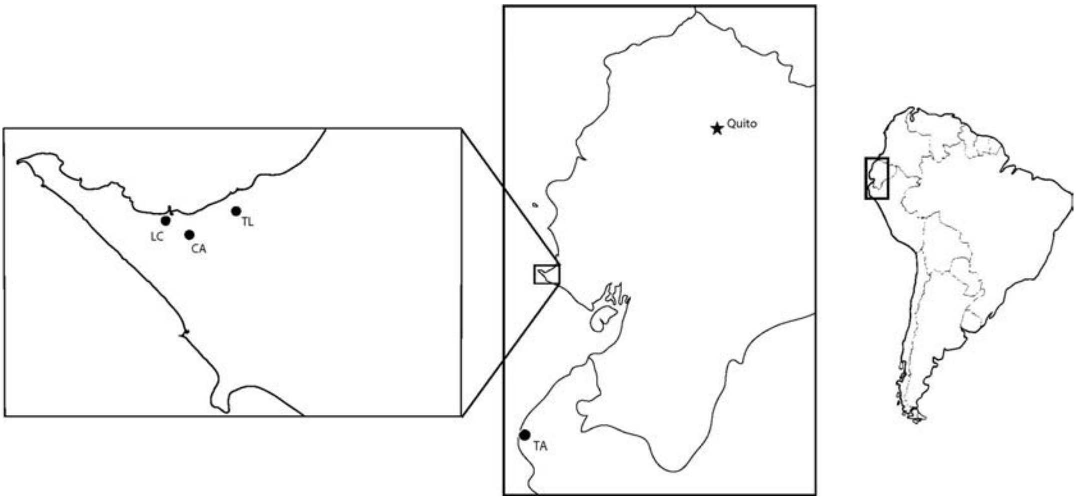

Figure 1 Asphaltic Quaternary vertebrate localities in southwestern Ecuador and northwestern Peru. Abbreviations: TA = Talara, LC = La Carolina, CA = Cautivo, TL = Tanque Loma.

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

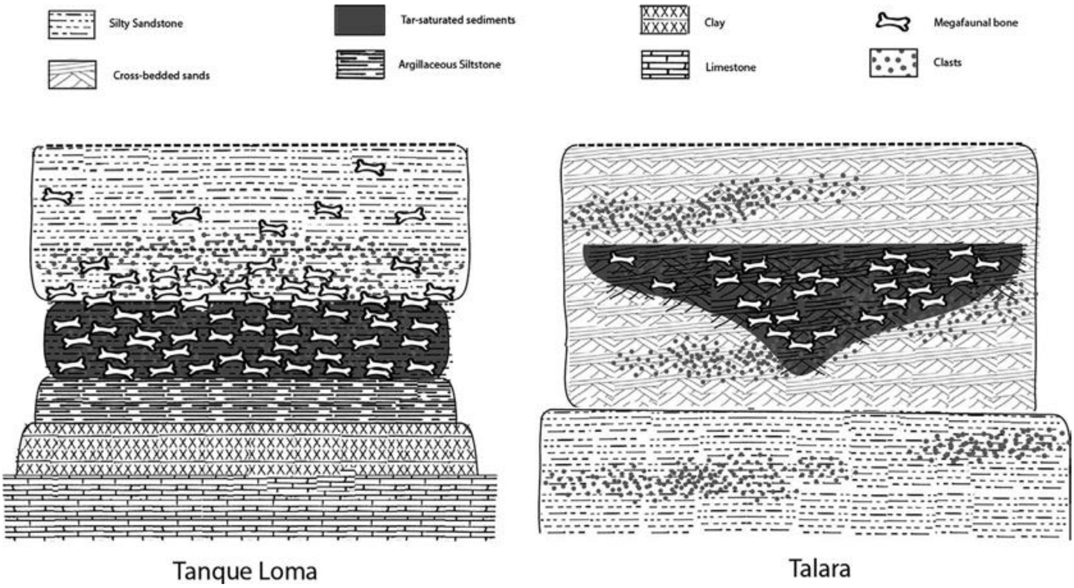

Figure 2 Generalized stratigraphic profiles showing geomorphology and bone and clast distribution in asphaltic deposits at Tanque Loma, Ecuador, and Talara, Peru.

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

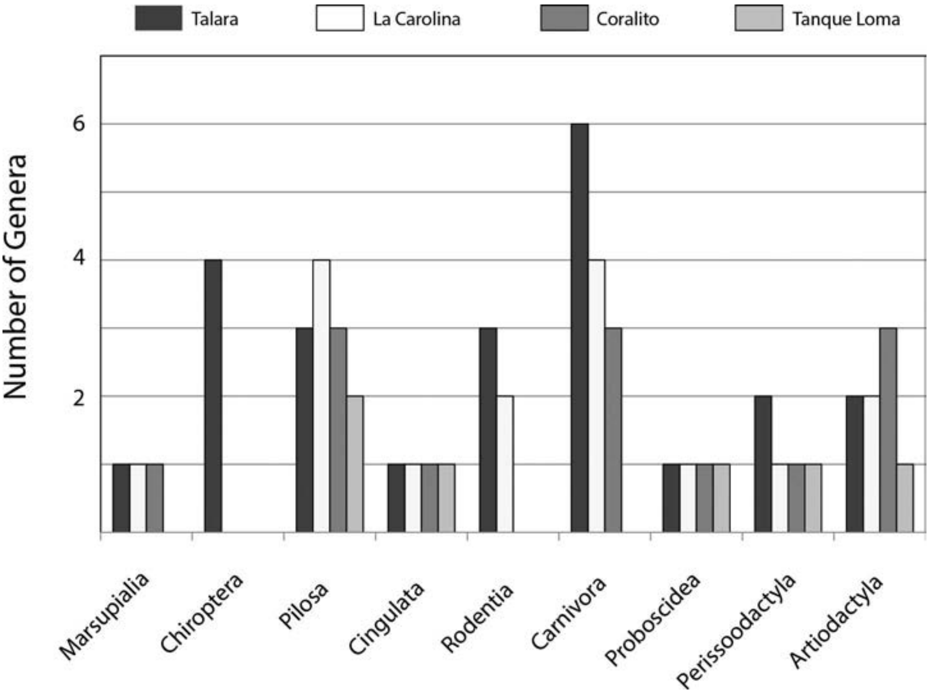

Figure 3 Bar graph showing taxonomic richness of different mammalian clades at asphaltic Quaternary vertebrate localities in the western Neotropics. Abbreviations: TA = Talara, LC = La Carolina, CA = Cautivo, TL = Tanque Loma.

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,

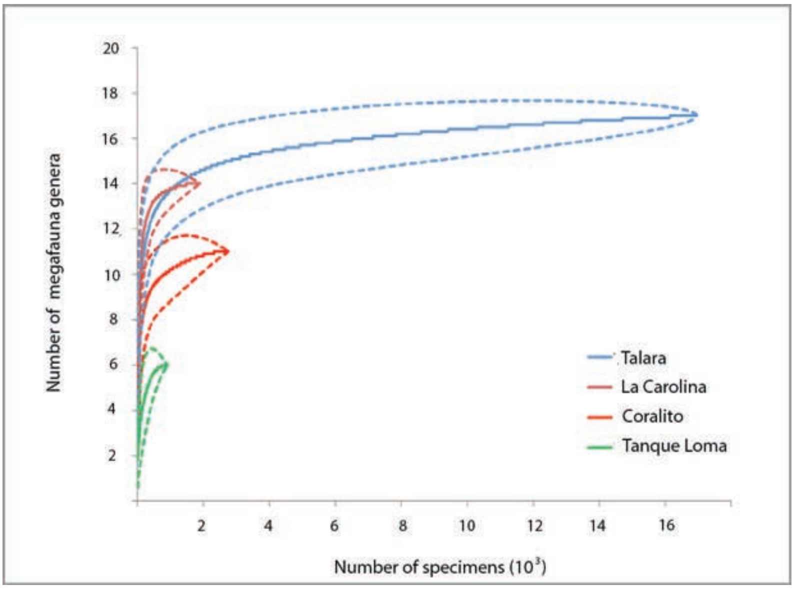

Figure 4 Rarefaction curves of generic richness versus number of specimens sampled for the neotropical asphaltic vertebrate localities Talara, La Carolina, Coralito, and Tanque Loma. Dashed lines indicate 95% confidence intervals.

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

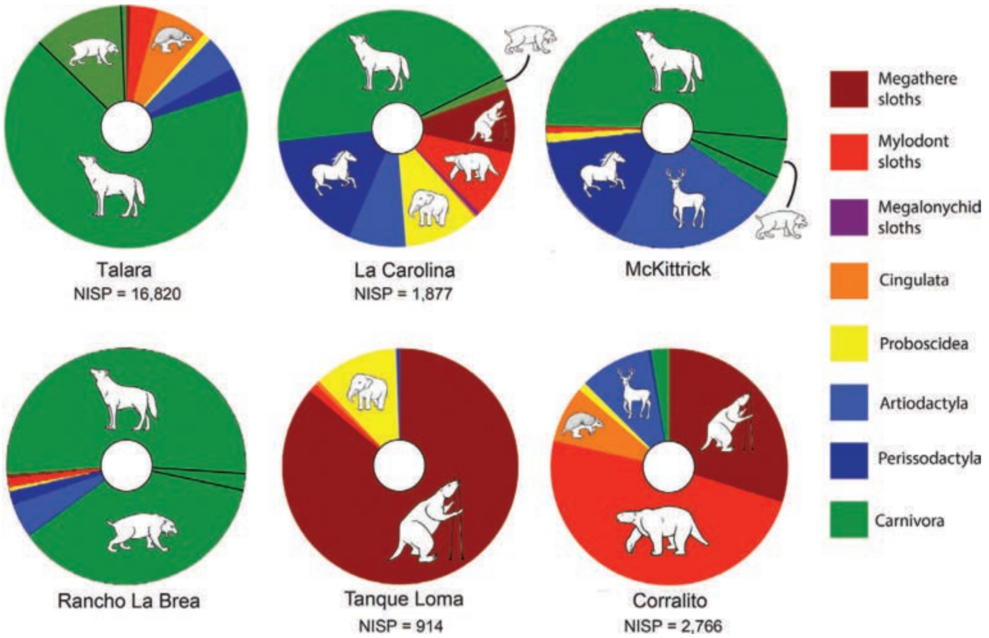

Figure 5 Pie charts showing relative representation of mammalian taxa at neotropical asphaltic localities Talara, La Carolina, Coralito, and Tanque Loma, as well as the California, USA, localities Rancho La Brea and McKittrick. Dominant groups represented by icons. While the South American locality graphs 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

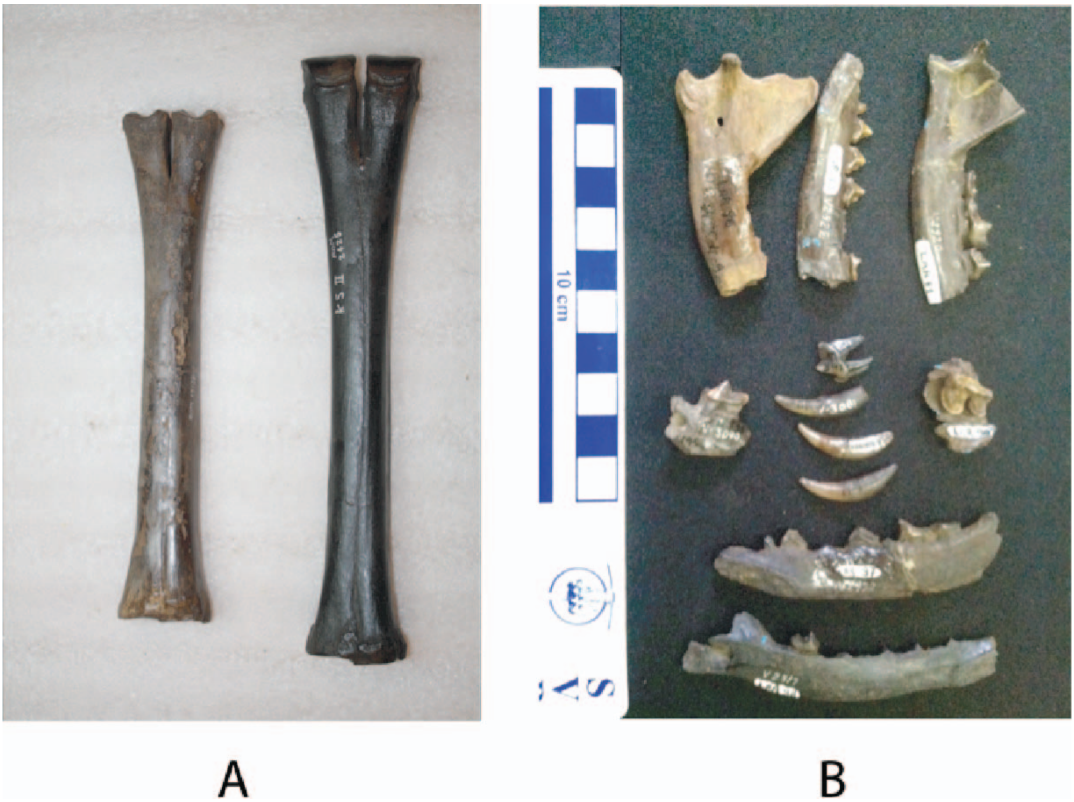

Figure 6 **A.** *Palaeolama* metapodials collected from Coralito (left) and Talara (right), showing typical coloration of bone from the two localities. **B.** Carnivore bones from La Carolina, showing range of asphalt saturation observed on bones from this deposit.

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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A New Mammal Assemblage from the Late Pleistocene El Breal de Orocual, Northeast of Venezuela

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ABSTRACT. In the last decade, intensive paleontological fieldwork has been carried out in Venezuela, resulting in many new fossil vertebrate localities being found. Two sites of special significance are the fossil-rich tar pits of El Breal de Orocual and Mene de Inciarte. El Breal de Orocual is located in Monagas State in the northeast of Venezuela. Multiple individual pits have been identified and a fauna with 24 mammalian taxa was reported from an inactive tar pit (ORS16) with an estimated Plio–Pleistocene age. However, the fossils so far collected and described from this locality represent only a miniscule fraction of the total fossil material preserved there. Three hundred meters west of the original site is a still active tar pit from which we describe a new mammal assemblage named ORS20. This new mammal assemblage (ORS20) is chronologically and taxonomically different from the previously reported fauna (ORS16). Our taxonomic identifications of the mammals from ORS20 and their known or inferred ages suggest a Late Pleistocene age for this fauna. The multiple pits in the area of El Breal de Orocual contain a diverse fauna which accumulated during distinctive episodes of deposition from the Late Pliocene/Early Pleistocene (ORS16) until the Late Pleistocene (ORS20), indicting that surface exposures of asphalt and the subsequent accumulation of vertebrate remains occurred over a long period of time (about 2 My?), a situation that to date has not been observed for other tar pits localities in North, Central, or South America. The presence of the peccary *Platygonus* sp. and the armadillo *Pachyarmatherium leiseyi*, in the Late Pleistocene of ORS20 represent the youngest appearances of these taxa in the fossil record of South America.

INTRODUCTION

The paleontological potential of tar pits or asphaltic seep deposits has been recognized since the beginning of the 19th century with the discovery of Rancho La Brea in the United States (Stock, 1930). Similar deposits have since been reported at McKittrick and Carpinteria, California, USA (Nowak, 1979; Stock, 1992); Talara, Peru (Hoffstetter, 1952; Campbell, 1979); La Carolina, Ecuador (Hoffstetter, 1952); Pitch Lake, Trinidad and Tobago (Wing, 1962); Las Breas de San Felipe, Cuba (Iturralde-Vinent et al., 2000); and most recently in Venezuela at Mene de Inciarte and El Breal de Orocual (McDonald et al., 1999; Czaplewski et al., 2005; Rincón, 2006; Rincón et al., 2006, 2008, 2009; Prevosti and Rincón, 2007). El Breal de Orocual is located in eastern Venezuela, and consists of a series of open asphalt pits that acted as animal traps. From this locality, Rincón et al. (2009, 2011) described a diverse continental mammal assemblage of 24 taxa; four were new records from Venezuela (*Hoplophorus* sp., Erethizontidae indet., *Hippidion* sp., *Platygonus* sp.), and three (*Pachyarmatherium leiseyi, Smilodon gracilis*, and *Homotherium venezuelensis*) were the first records of these taxa in South America. Biochronologically, El Breal de Orocual is Late Pliocene or Early Pleistocene in age, and is the oldest known fossiliferous tar pit locality in South America. The fossils collected and described from this locality represent only a miniscule fraction of the total fossil material preserved there, considering that the site may have at least 18,000 m^2 of potential fossil-bearing sediments (Rincón et al., 2009). The discovery of the well-preserved biota at El Breal de Orocual provides an important first step in filling a major gap in our understanding of

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Figure 1 Landscape of ORS20 tar pits. Left. pits and mounds with fossils, Right. several big bone fragments.

the Pliocene–Pleistocene vertebrate history of the Neotropics (Rincón et al., 2009; Fortier and Rincón, 2013).

In this paper we describe a new continental mammal assemblage from El Breal de Orocual that is geographically close to the fauna previously reported by Rincón et al. (2009) but is distinctly different in terms of the species present in the fossil assemblage and its age. Furthermore, we discuss some of the paleoenviromental, biochronological, and taphonomical implications of these new discoveries from El Breal de Orocual.

GEOLOGIC SETTING

The original vertebrate fauna described from El Breal de Orocual (Rincón et al., 2009, 2011; Holanda and Rincón, 2012; Fortier and Rincón, 2013) was collected during 2006 and 2007 from a locality near the oil tower ORS16. These fossils were preserved in sediments that contained weathered hydrocarbons but were inactive in terms of fresh oil coming to the surface.

In late 2011, from an active seep located about 300 m west of the original site (ORS16), a new fossiliferous deposit was discovered. The discovery was initially made by the workers of Petróleos de Venezuela S.A. (Venezuelan Petroleum Company, PDVSA), who conducted excavations of at least 40 pits as part of an environmental impact study of the area (Fig. 1a). Sediments extracted from these excavations revealed the existence of an extensive bone bed well preserved in a highly asphalt impregnated sedimentary material. In some cases asphalt flowed from large bone fragments (Fig. 1b).

This new fossiliferous deposit was named ORS20 for its proximity to an oil tower with this name (Pozo Orocual Shell número 20). Both ORS16 and ORS20 are located 20 km northeast of the city of Maturín in Monagas State, northeastern Venezuela (Fig. 2). The recovered material from this new fossil locality includes a diverse fauna composed of mammals, birds, amphibians, turtles, crocodiles, and coleopterans. Wood and seeds are also present but have not yet been further identified. Montellano-Ballesteros et al. (2012, 2014) report several mandibles and isolated lower and upper teeth of two tayassuids species, *Platygonus* sp. and *Tayassu pecari* from ORS20.

The local geologic framework for the Orocual area includes a significant number of tar pits, especially in the area affected by a collapse structure denominated “La Hoya de Orocual” (Orocual hole). The collapse structure of Orocual is an almost circular depression of 3 km diameter formed by concentric normal faults, with nearly vertical sides and displacements between 30 and 300 m that divide the hole into different blocks (Gil, 2007). The origin of the collapse structure of Orocual is not yet clear but may have been caused by late dewatering of rocks by mechanical compaction, thereby reducing the volume of rock mass in the subsurface. Generally, this process also induces the formation of diapirs and mud volcanoes, which are characteristic for tectonic deformation fronts in the presence of overpressure mudstones (Cegarra, 2007). The presence of grey mudstones from the Carapita Formation (Oligocene–Miocene age) in the subsurface combined with the geodynamic location (interaction zone between the South American and Caribbean plates) of the Orocual area encourages the generation of tar pits.

Both the ORS20 and ORS16 deposits partially overlie the Mesa Formation (Hedberg and Pyre, 1944) that extends through the lowland savanna in eastern Venezuela (Guárico, Anzoátegui, and Monagas states). The Mesa Formation was deposited in a fluvial–deltaic paleoenvironment related to the ancestral Orinoco River during

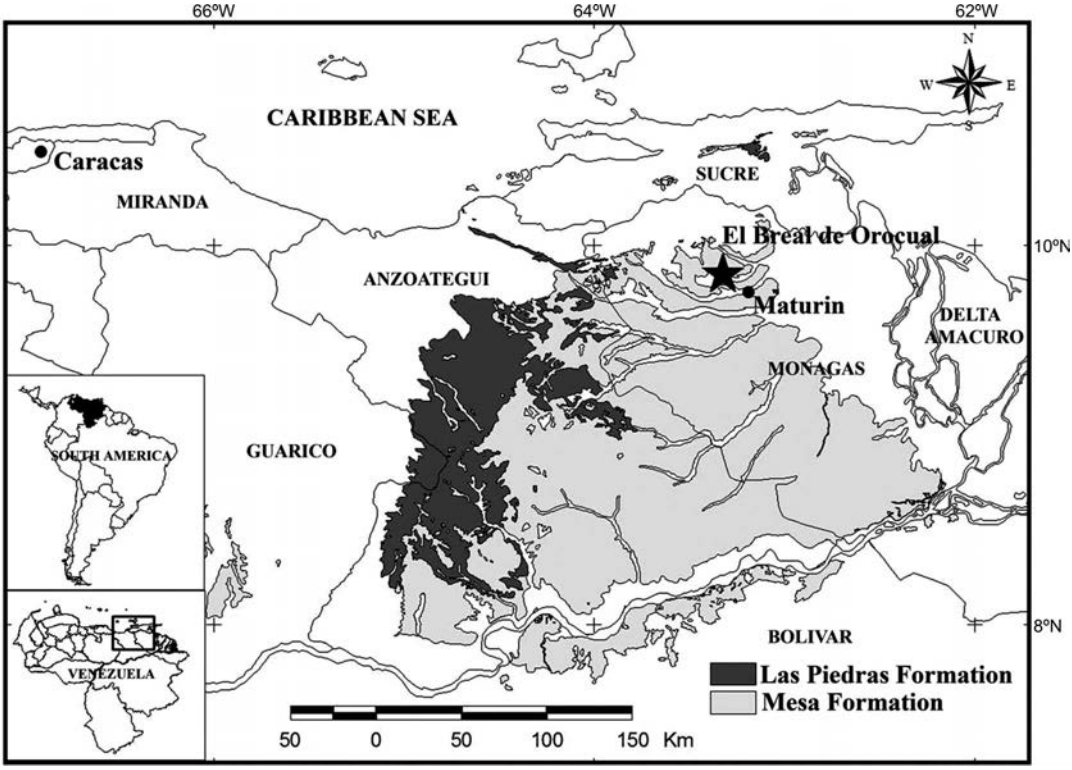

Figure 2 Geographical map showing the location of El Breal de Orocual tar pits, Monagas State, Venezuela, and the schematic geological map of eastern Venezuela, showing the main geological units, Mesa and Las Piedras Formations (after Hackley et al., 2006).

the Early to Middle Pleistocene (González de Juana et al., 1980). Thermoluminescence-based dates suggest a Middle Pleistocene age (between 0.5 and 1 Ma) for the Mesa Formation (Carbón et al., 1992). However, the presence of *S. gracilis* and cf. *Chapalmatherium* in the faunal assemblage of ORS16 suggest a Late Pliocene–Early Pleistocene age (Rincón et al., 2009, 2011; Costa and Rincón, 2011).

MATERIALS AND METHODS

All specimens reported here are housed at the Instituto Venezolano de Investigaciones Científicas (IVIC) in Caracas, Venezuela, and were cataloged and curated under the locality designation ORS20. Individual specimen numbers are listed below, but the ORS20 designation is provided only at the beginning of each Referred Material section. All measurements are in millimeters and were taken with a digital caliper. Dental terminology follows Wang et al. (1999) for Canidae, Berta (1987) for Felidae, Eisenmann et al. (1988) for Equidae, Butler (1952) and Holanda et al. (2011) for Tapiridae, Reig (1977) for Rodentia, Hershkovitz (1982) for Camelidae, and Reig et al. (1987) for Didelphidae.

INSTITUTIONAL ABBREVIATIONS

ORS20	ORS20 tar pit collection, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela
OR	Orocual (ORS16) tar pit collection, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela
ROM	Royal Ontario Museum, Toronto, Canada
MERO	Museu do Estado de Rondônia, Porto Velho, Rondônia, Brazil
UZM	Universitets Zoologisk Museum, Copenhagen, Denmark
MCL-PUC/MG	Museu de Ciências Biológicas, da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil
HMNS	Houston Museum of Natural Science, Houston, Texas, USA
IHNFG	Instituto de Historia Natural, Fósil Geográfico, Tuxtla Gutierrez, Chiapas, Mexico.

OTHER ABBREVIATIONS

D	deciduous
GABI	Great American Biotic Interchange
Ka	thousand years ago
Ma	million years ago

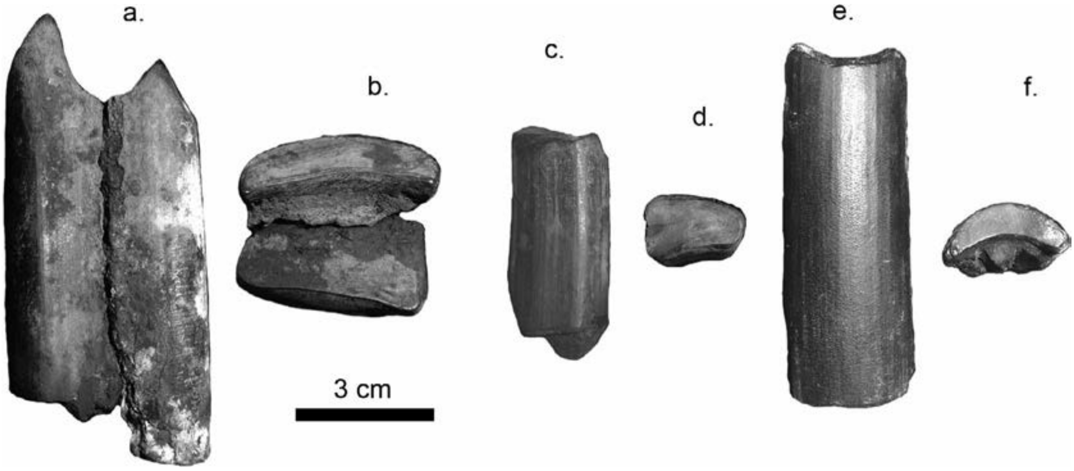

Figure 3 Phyllophaga isolated molariforms from ORS20. **a, b.** *Eremotherium* cf. *laurillardi* (**a** = dorsal view, **b** = occlusal view); **c, d.** Megalonychidae gen. et sp. indet. (**c** = lateral view, **d** = occlusal view); **e, f.** Mylodontidae gen. et sp. indet. (**e** = lateral view, **f** = occlusal view).

m/M	molars
NALMA	North American Land Mammal Age
p/P	premolars
SALMA	South American Land Mammal Age

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Xenarthra (Cope 1889)

Suborder Phyllophaga Owen 1842

Family Megatheriidae (Gray 1821)

Genus *Eremotherium* Spillman 1948

Eremotherium cf. *E. laurillardi* (Lund, 1842)

Figure 3a, 3b

REFERRED MATERIAL. ORS20-080, ORS20-081, ORS20-297: three fragments of molariform teeth.

DESCRIPTION. Hypsodont molariform teeth, quadrangular in shape, with two strong, almost parallel crests (one mesial and one distal), separated by a deep V-shaped valley.

REMARKS. The suborder Phyllophaga is composed of four families, each of which has characteristic molariform morphology. In the Megalonychidae, the molariforms (molar-like teeth) are subtrapezoid or subtriangular in shape with two transversely oriented low lophs (Borrello, 1966). In the Mylodontidae, the molariform are cylindrical or subcylindrical in shape with lateral grooves and tendency to bilobation (Borrello, 1966). Dentition of the Megatheriidae and Nothrotheriidae are generally similar, in that the molariforms are quadrangular in shape, with two strong, almost parallel crests (one mesial and one distal) separated by a deep V-shaped valley (De Iuliis and St-Andre, 1997). Teeth of the smaller nothrotheres are also distinguished by the presence of a longitudinal sulcus on the labial and lingual sides of the tooth, which is absent in the megatheres. Based on the size and absence of furrows on the tooth fragments recovered, the teeth ORS20-080 and ORS20-081 are of megatheres.

The anatomy of Megatheriinae is well known from the best represented genera, *Megatherium* and *Eremotherium* (Martinelli et al., 2012). *Megatherium* has molariforms that are extremely hypsodont, subequal in size, nearly square in cross section, and bilophodont (Bargo, 2001). In *Eremotherium* the transverse crests and valleys of the molariforms, particularly of the more mesial ones, tend to be more obliquely oriented, whereas in *Megatherium* the crests and valleys are more parallel (Cartelle and De Iuliis, 1995). ORS20-080 and ORS20-081 molariforms show the latter feature of *Eremotherium*.

Four species of *Eremotherium* are recognized: the largest is *Eremotherium laurillardi*, with a Pan-American distribution during the Pleistocene (Cartelle and De Iuliis, 1995, 2006), a smaller species *Eremotherium elenense* (Hoffstetter, 1952) is known from the Late Pleistocene of Ecuador, *Eremotherium sefvei* from Late Pliocene/Early Pleistocene of Bolivia (De Iuliis and Saint-André, 1997), and *Eremotherium eomigrans* (De Iuliis and Cartelle, 1999) from the Late Pliocene and Early Pleistocene of Florida, USA. The wide distribution of *E. laurillardi* in the Pleistocene of northern South America includes Venezuela (Bocquentin, 1979; Cartelle and De Iuliis, 1995, 2006; Rincón, 2003; Rincón et al., 2009), and the oclusal teeth morphology of ORS20-080 and ORS20-081 suggest that this material is *E. laurillardi*.

Family Megalonychidae Gervais, 1855

Megalonychidae gen. et sp. indet.

Figure 3c, 3d

REFERRED MATERIAL. ORS20-082, ORS20-083, ORS20-298, ORS20-299: four fragments of molariform teeth.

DESCRIPTION. The molariforms are wider than long, subtrapezoid in shape, with rounded corners; each has two transversely oriented low lophs, one mesial and one distal converging to form the apex of a triangle.

REMARKS. As described above, the Orocual material (ORS20-082, ORS20-083) displays all the features of the dentition of members of the Megalonychidae (Borrello, 1966), but generic allocation is not possible with the material recovered so far. Megalonychid sloths are known since the Oligocene (Deseadan SALMA; Carlini and Scillato-Yané, 2004), although their Late Pleistocene record in South America is poor compared with other groups of sloths and with that of megalonychids from the Antillean Islands or North America (White and MacPhee, 2001; McDonald et al., 2013). In Venezuela, the only Pleistocene record of Megalonychidae is the recently described *Megistonyx oreobios* (McDonald et al., 2013) and the currently indeterminate molariform remains from ORS16 (Rincón et al., 2009).

Family Mylodontidae (Gill, 1872)

Mylodontidae gen. et sp. indet.

Figure 3e, 3f

REFERRED MATERIAL. ORS20-084: molariform fragment.

DESCRIPTION. Molariform cylindrical or subcylindrical in shape with lateral grooves.

REMARKS. ORS20-084 preserves molariform features indicative of the Mylodontidae (Borrello, 1966), but generic allocation is not possible on the basis of material recovered thus far. Mylodontidae sloths of the genus *Paroctodontotherium* are known since the Late Oligocene (Shockey and Anaya, 2011). During the Late Pleistocene–Early Holocene of South America (Lujanense SALMA), the genera *Mylodon*, *Glossotherium*, *Lestodon*, and *Paraglossotherium* are the most common (Oliva and Brandoni, 2012). Venezuelan Late Pleistocene Mylodontidae remains are usually assigned to *Glossotherium* (Nectario María, 1938; Bocquentin, 1979), but the material is poorly preserved. ORS20-084 does however provide the first unequivocal evidence for the presence of members of the Mylodontidae at Breal de Orocual.

Suborder Cingulata

Family Glyptodontidae Gray 1869

Genus *Glyptodon* Owen, 1839

Glyptodon clavipes Owen, 1839

Figure 4a

REFERRED MATERIAL. ORS20-086 to ORS20-214: 129 buckler osteoderms.

DESCRIPTION. Osteoderms generally thick (between 119 and 265 mm) and hexagonal or pentagonal in shape; dorsal surfaces covered with typical rosette sculpturing pattern, with central figure larger to subequal in size compared with the peripheral figures; single row of six to 10 peripheral figures; central figure sometimes depressed above plane of peripheral figures and separated by relatively wide and shallow groove.

REMARKS. Osteoderms of *Glyptodon* are thicker than those of other late Pleistocene members of the family, with a subcircular or polygonal central figure separated by a well-marked sulcus from a single row of peripheral figures, which are usually of smaller diameter than the central figure (Rincón and White, 2007; Rincón et al., 2008). This combination of characters suggests the presence of *Glyptodon* Owen, 1839, at ORS20.

Numerous species of *Glyptodon* have been described, but from the Late Pleistocene (Lujanian SALMA) only *Glyptodon clavipes*, *Glyptodon reticulatus*, and *Glyptodon elongatus* are considered to be valid species (Rincón et al., 2008). *Glyptodon reticulatus* osteoderms are thicker (>4 cm) and smaller in size than those of *G. clavipes*. The dorsal surfaces of the central and peripheral figures of each osteoderm are convex and in the same plane in *G. reticulatus*, whereas in *G. clavipes* the dorsal surfaces of the central and peripheral figures are flat, with the central figure slightly depressed below the plane of the peripheral figures (Duarte, 1997; Rincón et al., 2008). *Glyptodon elongatus* has a larger central figure than the peripheral figures, which distinguishes it from both *G. clavipes* and *G. reticulatus* (Rincón and White, 2007). The osteoderms from ORS20 are assigned to *G. clavipes* based on the combination of characters: osteoderm larger but less thick than in *G. reticulates*; radial and central grooves wide and shallow; central figure larger to subequal than peripheral figures; and single row of six to 10 peripheral figures.

The surface of the dorsal carapace osteoderms is very rugose in the North American genus *Glyptotherium*, whereas in *Glyptodon* they are smoother (Carlini et al., 2008). The annular and radial sulci in *Glyptodon* are somewhat wider than those observed in *Glyptotherium*, with almost vertical sides and a wide, almost flat

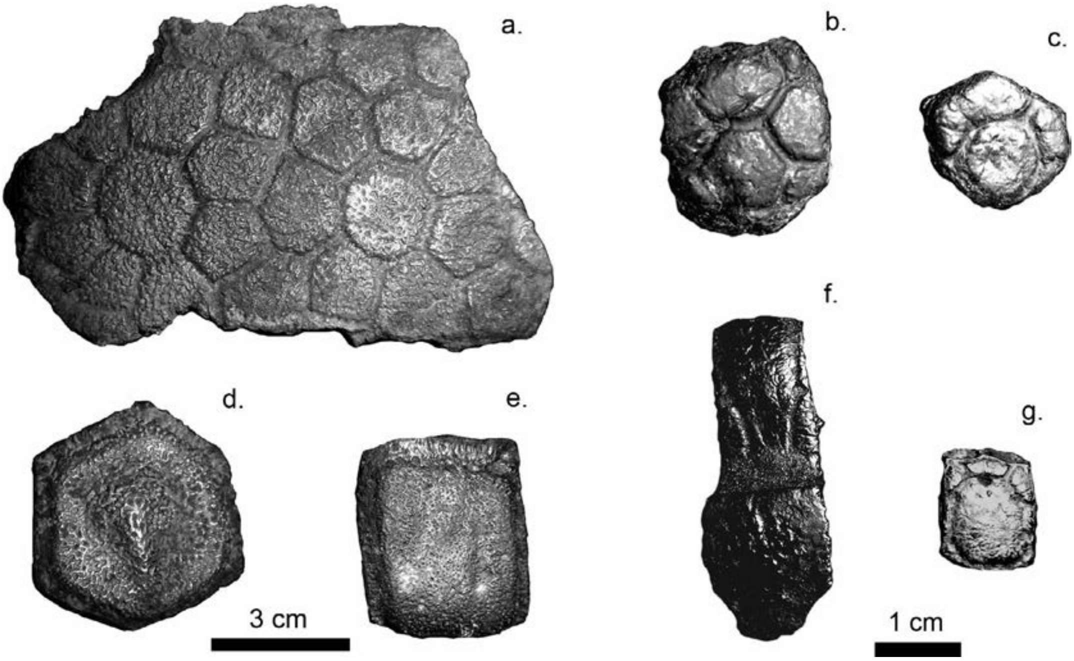

Figure 4 Cingulate osteoderms from ORS20 in external view. **a.** fused osteoderms of *Glyptodon clavipes*; **b, c.** isolated buckler osteoderms of *Pachyarmatherium leiseyi*; **d.** *Holmesina occidentalis* isolated buckler osteoderm; **e.** *Pampatherium humboldtii* isolated osteoderm; **f, g.** *Propraopus sulcatus* (**f** = moveable osteoderm [ORS20-269], **g** = buckler osteoderms [ORS20-014]).

bottom, forming an angle of 90°, whereas in *Glyptotherium* the sulci show a more concave morphology (Zurita et al., 2012). According Oliveira et al. (2010) *Glyptotherium* has eight to nine peripheral figures on average; in contrast, *Glyptodon* has a smaller number of peripheral figures (six to seven). However, the number of peripheral figures is common to both genera according to Dantas et al. (2013) and is probably useless for taxonomic identification. *Glyptodon* and *Glyptotherium* not only share skull and postcranial features (Gillette and Ray, 1981), both genera are very similar at the exoskeleton level; isolated osteoderms are difficult to distinguish (Zurita et al., 2011). A recent review of the taxonomic relationship of these two genera interpret them as distinct and distinguished by features of the skull and mandible, carapacial osteoderms, and the caudal shield (Carlini et al., 2008). There is no consensus on this conclusion, so additional research to test this requires a rigorous phylogenetic and taxonomic analysis that documents and incorporates patterns of individual, ontogenetic, sexual, and other forms of variation within both nominal taxa. We suspect that the taxa are most likely synonymous.

In Venezuela, *Glyptodon* has been reported from the Early Pleistocene ORS16 tar pit, and the Late Pleistocene of Mene de Inciarte, Cueva del Zumbador, and San Miguel (Simpson, 1939; Rincón et al., 2008, 2009). Carlini et al. (2008) reported *Glyptotherium* osteoderms from several localities in Falcon State, Venezuela.

Genus *Pachyarmatherium* Downing and White, 1995

Pachyarmatherium leiseyi Downing and White, 1995

Figure 4b, 4c

REFERRED MATERIAL. ORS20-001 to ORS20-013, and ORS20-272 to ORS20-296: 38 buckler osteoderms.

DESCRIPTION. Osteoderms hexagonal in shape, small and thick. The hexagonal central figure displaced toward posterior edge and separated from five to six smaller peripheral figures by well-defined groove (sulcus) around central figure; peripheral figures well developed, separated from each other by radial sulci, but not along the posterior margin; peripheral figures flat; hair follicle pits or foramina large and few (none to two in number) and located at the intersections of the sulcus around central figure and in radial grooves. Sulcus and radial sulci deep and narrow. For measurements, see Table 1.

REMARKS. *Pachyarmatherium* has a biochronological range from the Late Pliocene to Late

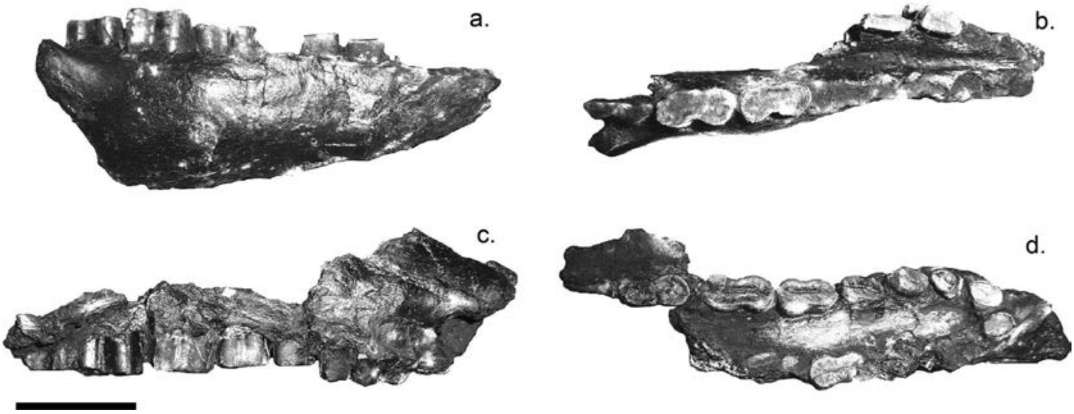

Figure 5 *Holmesina occidentalis* remains from ORS20. **a, b.** fragment of mandible (**a** = labial view, **b** = occlusal view); **c, d.** fragment of maxilla (**c** = labial view, **d** = occlusal view). Scale bar = 5 cm.

Pleistocene of North America, Costa Rica, Venezuela, Brazil, Uruguay, and Peru (Rincón and White, 2007, Bostelmann et al., 2008; Oliveira et al., 2009; Porpino et al., 2009; Rincón et al., 2009; Martínez and Rincón, 2010; Valerio and Laurito, 2011; Oliveira et al., 2013). Three species have been described: *P. leiseyi* Downing and White, 1995, *Pachyarmatherium tenebris* Rincón and White, 2007, and *Pachyarmatherium brasiliense* Porpino et al., 2009. Martínez and Rincón (2010) and Valerio and Laurito (2011) suggest *P. tenebris* and *P. brasiliense* species cannot be distinguished on morphology and biometry of the osteoderms. As *P. tenebris* has priority over *P. brasiliense*, we regard the latter a junior synonym of *P. tenebris*.

Pachyarmatherium leiseyi is smaller and thinner than *P. tenebris* (see Table 1). *Pachyarmatherium leiseyi* has convex peripheral figures, whereas in *P. tenebris* they are almost flat. Also *P. tenebris* has a sulcus and radial sulci that are wider and less deep than in *P. leiseyi* (Rincón and White, 2007). ORS20 osteoderms have the typical morphology of *P. leiseyi*. Morphometrically the isolated buckler osteoderm means (n = 38) are 13.70 mm in length, 15.81 mm in width, and 7.49 mm in thickness. These sizes are in the range observed for *P. leiseyi* from Florida (Downing and White, 1995) and smaller than has been reported for *P. tenebris* (Table 1; Rincón and White, 2007; Porpino et al., 2009; Oliveira et al., 2013), confirming the presence of *P. leiseyi* at ORS20.

Family Pampatheriidae Edmund 1987

Genus *Holmesina* Simpson 1930

Holmesina occidentalis (Hoffstetter, 1952)

Figures 4d, 5a–d

REFERRED MATERIAL. ORS20-029 (Fig. 5a, 5b) fragment of mandible with right molariform series of m6–m8 (m8 broken) and left series with m3 and m4 (m4 broken); ORS20-028 (Fig. 5c, 5d) skull fragment with the right molariform series M1–M8 (M8 broken) and left series of M1–M5; ORS20-031; ORS20-032; ORS20-236 to -242; ORS20-244 to -254; ORS20-256 to -259: 24 isolated buckler osteoderms.

DESCRIPTION. Fragment of mandible with right molariform series (m6–m8, m8 broken) and left series with m3 and m4 (m4 broken). The m3 is oval in shape, m4 is reniform, and m5 alveolus suggests the m5 was bilobed. The members of

Table 1 Measurements of different species of *Pachyarmatherium*.

Taxon	Length	Width	Thickness
P. leiseyi[a]	8.1–22.9	—	5.5–13.3
P. leiseyi (ORS20)	11.2–19	13.0–21.7	5.4–11.8
P. tenebris[b]	12.4–23.2	13–22.5	5.2–14.1
P. brasiliense (= *P. tenebris*)[c]	10.1–26.7	14.5–28	7–18.4
P. brasiliense (= *P. tenebris*)[d]	14–30	15–26	6–15

[a] Downing and White (1995).
[b] Rincón and White (2007).
[c] Porpino et al. (2009).
[d] Oliverira et al. (2013).

Table 2 Anteroposterior length of upper molars in *Holmesina* species (in mm) (*sensu* Góis et al., 2012).

Holmesina species	M1	M2	M3	M4	M5	M6	M7	M8	M9
H. rondoniensis sp., MERO-002	8.1	12	17.5	19	24	27	26.5	21	17.1
H. occidentalis, ROM 3881	10	13	16	17.1	25	27.9	26	23.5	14.5
H. majus, UZM 2314	8.1	11	13	19.1	24.1	26	24.1	22	18
H. paulacoutoi, MCL-501/01	—	12	19	20.4	26.4	26	26.2	22.8	15
H. septentrionalis, HMNS 173	10	12	14.2	17.2	21.2	23.2	23.5	21.2	13.2
H. occidentalis, ORS20-028	9.9	11.5	12.5	15.2	18.5	23.7	21.1	—	—

m6–m8 series are also bilobed in shape. The m8 is smaller than the m7. The mandibular ramus is narrow. The base of the coronoid process is at the level of the m8. The mandibular symphysis is not fused and the two dentaries are separate at the m5. The molariforms are arranged in a linear form. The lower molariforms are arranged in a stepwise progression, and this is clearly observed in the m6–m8 series (Fig. 5a). The skull fragment with the right molariform series M1–M7 is well preserved, but the M8 is broken, and the left series includes the M1–M5. M1, M2, and M3 are oval in shape. M3 is longer and less wide than M2. M1, M2, and M3 are clearly imbricated. M4 is reniform in shape and M5, M6, M7, M8 (fragment) are bilobed. M5 is the most bilobed in appearance of the molariforms. The M1–M4 series is imbricated. The maxillary suture is not visible. The infraorbital foramen is located anterior to the M1. In general, the lobation of both the upper and lower molariforms is more pronounced on the labial side. For molariform measurements see Table 2.

The osteoderms are more highly ornamented dorsally and may be rectangular pentagonal or hexagonal in shape. The submarginal band of each osteoderm has a sharply raised ridge that extends above the lower marginal band. The central figure is usually raised and keel-like and is clearly separated from the submarginal band by a sulcus that is usually horseshoe shaped. Numerous follicular pits are present; they are shallow and elongate and positioned along the marginal band. The marginal band is continuous around most of the osteoderm but may become indistinct posteriorly and may merge somewhat with the central ridge. Osteoderms measurements (n = 24): average thickness 10.35 mm (observed range 13.8–7.5 mm); mean area 2,280 mm^2 (observed range 719–3,305 mm^2).

REMARKS. As previously mentioned, there are only two Late Pleistocene genera in the Pampatheriidae, *Pampatherium* and *Holmesina*. The two genera can be differentiated using the general characters of the osteoderms (Scillato-Yané et al., 2005), and molariforms (Góis et al., 2012).

Pampatheres have heterodont dentition, consisting of nine upper and nine lower molariforms. The molariforms may comprise a short anterior series that are oval or kidney-shaped, peg-like teeth, and a posterior molariform series that are either bilobed or trilobed. Both the upper and lower series are arranged in a complementary step-like arrangement, so the occlusal surfaces are not in the same plane (Vizcaíno, 2009; Góis et al., 2012). The first and second upper molariforms of *Holmesina* are imbricated, whereas these teeth in *Pampatherium* are not imbricated (Góis et al., 2012). The posterior dental series (M5–M9) is trilobed in *Pampatherium* and generally bilobed in *Holmesina* (Góis et al., 2012). ORS20-028 material has a bilobate MF5–MF7 series as in *Holmesina*.

Five species of *Holmesina* are recognized: *Holmesina majus*, *Holmesina paulacoutoi*, and *Holmesina rondoniensis* from Brazil; *Holmesina septentrionalis* from the United States and Mexico; and *Holmesina occidentalis* from Peru, Ecuador, Colombia, and Venezuela (Rincón et al., 2009; Góis et al., 2012). The total interdentary space in the upper molariform series in *Holmesina* species is 6.4 mm in *H. rondoniensis*, 7.4 mm in *H. paulacoutoi*, 14 mm in *H. occidentalis*, 17 mm in *H. septentrionalis*, and 22.5 in *H. majus* (Góis et al., 2012). As can be seen, *H. rondoniensis* and *H. paulacoutoi* are distinguished by having the least interdentary space in the upper molariform series (M1–M9; Cartelle and Bohórquez, 1985; Góis et al., 2012). Although ORS20-028 is poorly preserved and slightly deformed, the interdentary space for the M1–M7 series is 12 mm so is longer than those of *H. rondoniensis* and *H. paulacoutoi*, shorter than *H. majus*, and close to the values observed in *H. occidentalis* and *H. septentrionalis* (Góis et al., 2012).

Besides the interdentary space, ORS20 specimens differ from *H. rondoniensis,* which has a reniform M5 (Góis et al., 2012), whereas in ORS20-028 this tooth is bilobate. The M5 of *H. paulacoutoi* has a slight development of a third labial lobe, but this tooth is perfectly bilobed in *H. occidentalis, H. majus, H. septentrionalis*, and ORS20-028 (Góis et al., 2012). The M7 of *H. majus* has a well-marked third labial lobe, but this tooth is perfectly bilobed in *H. occidentalis, H. septentrionalis*, and ORS20-28. *Holmesina occidentalis* and *H. septentrionalis* can be differentiated by the size of the M6 and M7. In the first species the M6 is larger than the M7, while in the second species the M6 and M7 are almost the same size (Simpson, 1930). In ORS20-028 the M6 (length = 23.7 mm) is larger than the M7 (length = 21.1 mm), allowing us to infer that this specimen can be assigned to the species *H. occidentalis*. It should be noted that the overall size of the molariform series of the Orocual material is slightly smaller (about 20%) than that of *H. occidentalis* ROM 3881 from Talara, Peru (see Table 2). Currently ORS20-028 and ORS20-029 are the only known cranial material of pampatheres in Venezuela.

In general, the ornamentation of the osteoderms in *Holmesina* is more pronounced than in *Pampatherium*. Also, the osteoderms of *Holmesina* are thicker than in *Pampatherium* (Edmund, 1996; Rincón et al., 2008). One of the most diagnostic features for distinguishing these genera is the presence of a raised keel-like central figure in *Holmesina*, which is absent (or nearly so) in *Pampatherium* (broad, flat, low, and elongated when present; Rincón et al., 2008). The osteoderms of *H. occidentalis* have a continuous marginal band, with numerous shallow and elongated hair follicles, generally radiating outward. They differ from those of *H. septentrionalis* as being less thick, being less ornamented, and having thinner follicles in the marginal band. *Holmesina occidentalis* differs from *H. majus* and *H. paulacoutoi* in being less ornamented and having a narrower marginal band and more developed sulcus. These features allow us to determine that the osteoderms found at the site ORS20 (ORS20-031; ORS20-032; ORS20-236 to -242; ORS20-244 to -254; ORS20-256 to -259) are from *occidentalis*. But we do note that the osteoderms from ORS20 have a greater mean area (2,280 mm^2) than the averages reported by Rincón et al. (2009) from ORS20 (1,041 mm^2) and Edmund (1996) for *H. occidentalis* from Talara, Peru (1,806 mm^2), and Santa Elena, Ecuador (1,933 mm^2).

Genus *Pampatherium* Ameghino, 1875

Pampatherium humboldtii (Lund, 1839)

Figure 4e

REFERRED MATERIAL. ORS20-227 to 234, ORS20-243, and ORS20-260: 10 buckler osteoderms.

DESCRIPTION. The osteoderms are poorly ornamented dorsally and are rectangular pentagonal or hexagonal in shape. The central figure is broad, elongate, low, and flat and is isolated from the submarginal band. The central figure is often not perceptible and sometimes is posteriorly tapered. The sulcus around the central figure is shallow and continuous posteriorly. The submarginal band is narrow and slightly elevated, and although it often completely surrounds the sulcus, it occasionally is absent anteriorly. The marginal band is wide and continuous around the osteoderm but is narrow posteriorly. Measurements (n = 10): average thickness 7.57 mm (observed range 6.4–8.6 mm); mean area 1,356 mm^2 (observed range 951.9–1,774.52 mm^2).

REMARKS. As previously noted, the two different genera of South America Quaternary Pampatheriidae—*Holmesina* and *Pampatherium*—can be distinguished by the general characters of the osteoderms, (Edmund, 1996; Scillato-Yané et al., 2005). Osteoderms of *Pampatherium* are typically poorly ornamented, the marginal band may be absent or may be represented by a narrow band of follicular pits on the posterior and lateral margins and is not significantly depressed below the submarginal band (Edmund, 1996; Rincón et al., 2008). In South America only two *Pampatherium* species are currently recognized: *Pampatherium humboldtii* from the Late Pleistocene of Brazil, Uruguay, and Venezuela (Edmund, 1996; Rincón et al., 2008, 2009) and *Pampatherium typum* from Bolivia, Brazil, Paraguay, and Argentina (Scillato-Yané et al., 2005). A single North American species, *Pampatherium mexicanum,* is known only from Mexico (Edmund, 1996).

Pampatherium humboldtii has a narrow and slightly elevated submarginal band, whereas in *P. typum* it is smooth and in *P. mexicanum* it is almost imperceptible. In *P. humboldtii* the central figure is more elongated than in *P. typum*, usually does not rise posteriorly, and is isolated from the submarginal band. The central figure in *P. typum* is broad and flat, rises slightly posteriorly and may join with the submarginal band, whereas in *P. mexicanum* it is broad and tapers posteriorly, extremely low in relief, and often has a feeble union with the submarginal band (Rincón et al., 2008). In the ORS20 pampathere material the central figure is broad, elongated, low, and flat; it is sometimes imperceptible and has a narrow and slightly elevated submarginal band. These characters justify assignment of these osteoderms to *P. humboldtii*.

Family Dasypodidae Gray, 1821

Genus *Propraopus* Ameghino, 1881

Propraopus sulcatus (Lund, 1842)

Figure 4f, 4g

REFERRED MATERIAL. ORS20-014, ORS20-268, buckler osteoderms; ORS20-269, moveable osteoderm.

DESCRIPTION. The buckler osteoderms are hexagonal, isometric, and ornamented with a central figure almost circular in shape, with peripheral figures smaller than the central figure. All of the peripheral figures are separated from the central figure by a sulcus that completely encircles the central figure separating it from the three smaller peripheral figures. There are four hair pits within the sulcus between central and peripheral figures. The moveable or imbricating osteoderm is elongated, with two divergent sulci forming a subtriangular inverted figure 'V' in shape, the base of which covers almost the entire posterior border where a few hair pits are located. Buckler osteoderms measurements ($n = 2$): average thickness 4.55 mm (observed range 4.4–4.7 mm); mean area 179.97 mm^2 (observed range 174.3–85 mm^2).

REMARKS. In *Propraopus,* the sulci that delimit the principal figure on the moveable osteoderms are subparallel anteriorly compared with the V-shaped pattern in *Dasypus*. The principal figure on the fixed osteoderms has a hexagonal to circular outline, with foramina that are not situated on the confluence between the radial sulci and the principal sulcus as in *Dasypus* (Rincón et al., 2008; Oliveira and Pereira, 2009). This genus is common in faunas from the Pleistocene to Early Holocene of Argentina (Ensenadan–Lujanian SALMA) and Pleistocene of Brazil, Venezuela, Uruguay, and Bolivia (Rincón et al., 2008, 2009; Castro et al., 2013b). Recently it has been suggested that there is only one valid species of *Propraopus*: *Propraopus sulcatus* (Castro et al., 2013a, 2013b). Among the other previously recognized species, *Propraopus punctatus* was recently assigned to *Dasypus* (Castro et al., 2013) and *Propraopus grandis* does not have the morphologic characteristics that clearly distinguish it from *P. sulcatus* and is regarded as a junior synonym of *P. sulcatus* (Castro et al., 2013a). The presence of foramina not situated on the confluence between the radial sulci and the principal sulcus support the identification of ORS20-014 specimens as *P. sulcatus*.

Order Didelphimorphia Hill, 1872

Family Didelphidae Gray, 1821

Genus *Didelphis* Linnaeus, 1758

Didelphis sp.

Figure 6a–c

REFERRED MATERIAL. ORS20-038, almost complete right dental ramus with c1 to m4; the tip of the dentary and the canine are missing.

DESCRIPTION. The ramus is robust. The masseteric fossa is deep, and the posterior mental foramen is positioned below the m1 with a second mental foramen below the p1. The posterior margin of the symphysis is located below the anterior root of the p2. There is a short diastema between the p1 and p2, which is longer than the diastema between the c1 and p1. The molars are tribosphenic with the trigonid slightly longer than wide. The talonid is shorter than the trigonid. The molars decrease in length anteriorly ($m4 > m3 > m2 > m1$). The molars have an anterior cingulum that is highly developed and increases in prominence from m1 to m4. A smaller posterolabial cingulum and posterobasal cuspule that is talonid-like are present on the m1 and m2 but absent in the m3 and m4. The paraconid is well separated from the protoconid by a sharp cleft. The talonid of the m4 is triangular in shape and narrower than the trigonid. The hypoconulid is well developed, especially in the m1, m2, and m3 and projects posteriorly so it overlaps with the anterior cingulate of the following tooth. In the m4 the hypoconulid is almost the same size as the entoconid, while the m1 to m3 have a hypoconulid smaller than the entoconid. The hypoconulid and entoconid are separated by a narrow valley. On the m4 the entoconid is slightly bicuspid, while the m3 to m1 have a single cuspid entoconid. The premolars are double rooted. The p2 is larger than the p3, which is larger than the p1. The p3 is conical with a well-developed posterolingual and posterolabial cingulum. All of the premolars are double rooted. Measurements (in mm) of the dental elements: tooth row length p1–m4 = 37, p1L = 3.1, p1W = 1.1, p2L = 5, p2W = 2.4, p3L = 5.5, p3W = 2.8, m1L = 5.1, m1W = 3.1, m2L = 5.5, m2W = 3.1, m3L = 6, m3W = 3.2, m4L = 6.3, m4W = 3.3, cL = 4.6, cW = 2.5.

REMARKS. The tribe Didelphini includes *Didelphis*, *Philander*, *Lutreolina, Chironectes, Hyperdidelphis,* and *Thylophorops* (McKenna and Bell, 1997), with the last two genera only known from fossils. Morphological features of the mandible distinguish *Didelphis* from the other Didelphinae (Reig et al., 1987). *Didelphis* is the only Didelphinae with a well-developed anterior cingulum on the lowers molars (Reig et al., 1987), and this is observed in ORS20-038. *Didelphis* has four extant species—*Didelphis albiventris, Didelphis aurita, Didelphis marsupialis,* and *Didelphis virginiana*—and three species known only from the fossil record—*Didelphis solimoensis, Didelphis reigi,* and *Didelphis crucialis* (Cozzuol et al., 2006). The oldest record of *Didelphis* is *D. solimoensis* from the Late Miocene of Brazil (Cozzuol et al., 2006). *Didelphis* is also present in the fauna from ORS16. The ORS16 specimen (see Rincón et al., 2009:fig. 2) has a posterolabial cingulum and a talonid-like posterobasal cuspule in all molars and a gracile mandibular ramus, whereas ORS20-038 has an almost imperceptible posterolabial cingulum, a posterobasal cuspule that is talonid-like on the m1 and m2, and a more robust mandibular ramus. Given the small available sample it is possible that the last difference is merely due to intraspecific variation or sexual dimorphism, or it is possible they represent two different species, given the difference in age of the

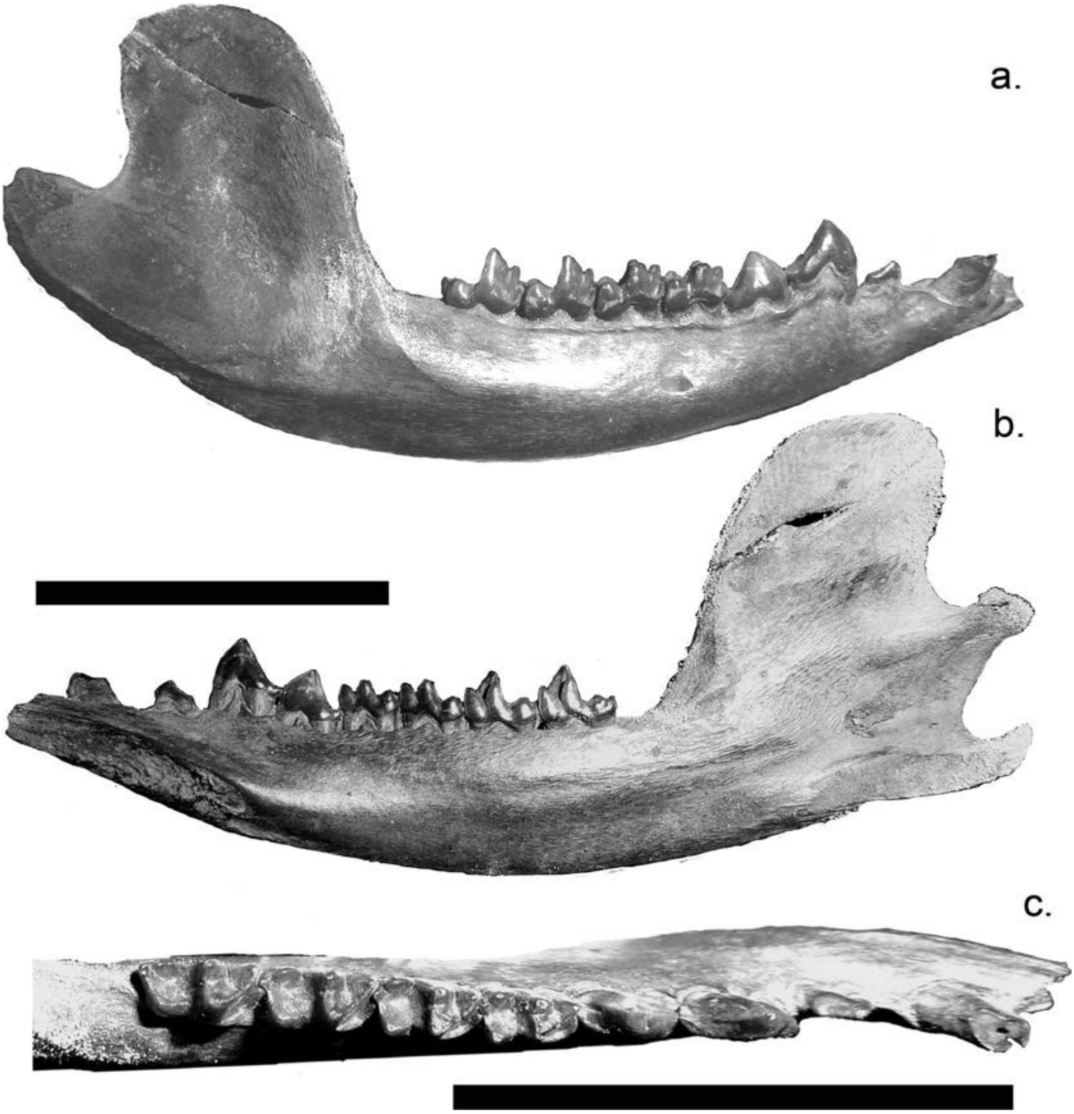

Figure 6a–c. Right dentary ramus (ORS20-038) of *Didelphis* sp. from ORS20 (**a** = labial view, **b** = lingual view, **c** = zoom of occlusal view). Scale bar = 3 cm.

two faunas. This can only be resolved with the collection of a larger sample with more diagnostic materials to compare living and fossil *Didelphis* species.

Order Artiodactyla Owen, 1848

Family Camelidae Gray, 1821

Genus *Palaeolama* Gervais, 1869

Palaeolama sp.

Figure 7a–c

REFERRED MATERIAL. ORS20-017: right m3.

DESCRIPTION. The m3 is brachyodont and selenodont. In occlusal view the protoconid and hypoconid are V-shaped. The parastylid, protostylid, and metastylid are small. The endostylid is almost imperceptible, and the trigonid fossa is narrow and V-shaped. The protoconid is longer than the hypoconid, with a small third lobe (hypoconulid) and without fossae.

REMARKS. Three genera of South American Camelidae are recognized: *Lama*, *Palaeolama*, and *Hemiauchenia*. *Lama* possesses a well-marked parastyle, mesostyle, and metastyle on the m2 and m3 (Viret, 1961), while in some *Palaeolama* species these are absent or reduced on the m2 and m3

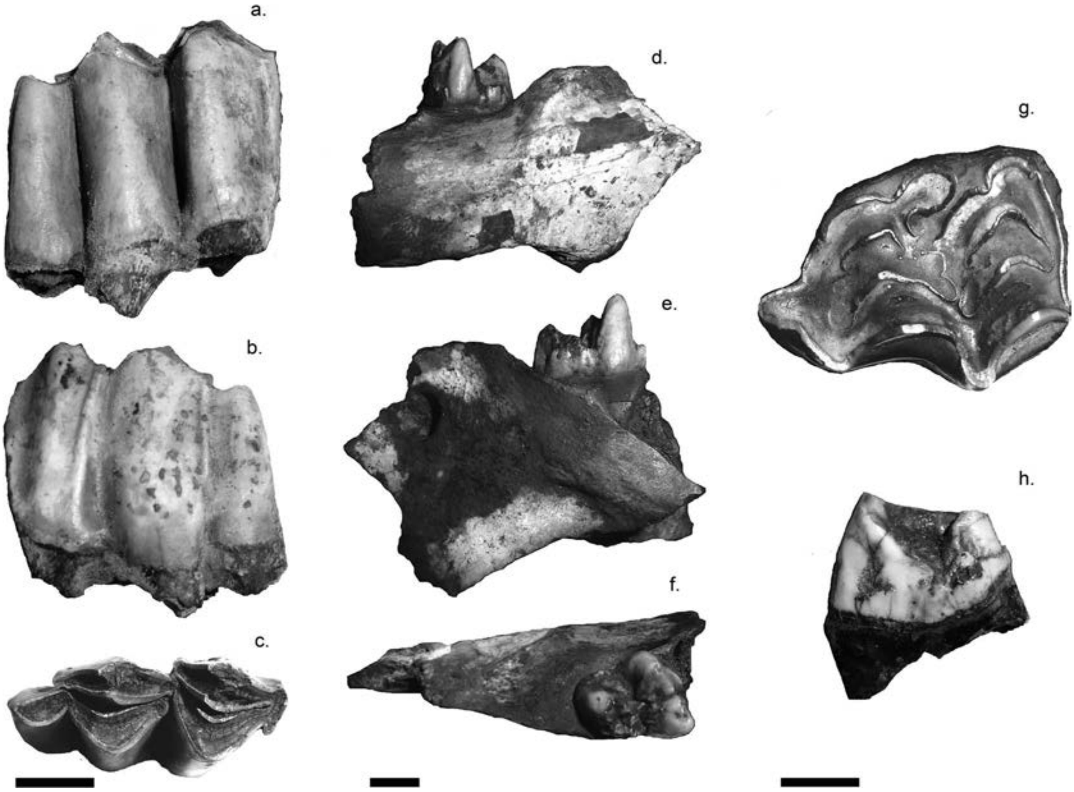

Figure 7 Artiodactyla and Perissodactyla remains from ORS20. **a–c.** right m3 of *Palaeolama* sp. (ORS20-017) (**a** = labial view, **b** = lingual view, **c** = occlusal view); **d–f.** posterior fragment of left dentary of *Platygonus* sp. (ORS20-304) with broken m3 (**d** = labial view, **e** = lingual view, **f** = occlusal view); **g.** isolated upper right premolar (P2) of *Equus* sp. (ORS20-265), occlusal view; **h.** fragment of posterior part of left M2? of cf. *Tapirus* (ORS20-061), distal view. Scale bar = 1 cm.

(Hoffstetter, 1952). In *Hemiauchenia*, the protoconid and hypoconid (labial lophids) form a U shape, and the protostylid and parastylid are pronounced. In *Palaeolama* the labial lophids are V-shaped, and the protostylid and parastylid are almost imperceptible (Scherer et al., 2007. Scherer, 2013), as is seen in ORS20-017. *Palaeolama* remains are known from Ensenadan of Bolivia (Marshall et al., 1984; MacFadden and Shockey, 1997) and the Lujanian of Brazil, Chile, Peru, Venezuela, Bolivia, Ecuador, and Paraguay (Marshall et al., 1984; Scherer et al., 2007. Scherer, 2013).

Family Tayassuidae Palmer, 1897

Genus *Platygonus* Le Conte 1848

Platygonus sp.

Figure 7d–f

REFERRED MATERIAL. ORS20-304, posterior fragment of left dentary with a broken m3; ORS20-304, partial m3; ORS20-060, right P2.

DESCRIPTION. The premolar is simple with two cusps, bunolophodont, mesodont and with a cingulum surrounding the entire tooth. While the m3 is broken, it was probably pentacuspidate with an accessory cuspule between the hypoconulid and posterior crest.

REMARKS. Tayassuidae represent one of the first North American mammalian immigrants, entering South America after the procyonids (Carnivora) and cricetid rodents (Prevosti and Vizcaíno, 2006; Woodburne et al., 2006). Late Pleistocene genera of the family currently recognized are the extinct *Platygonus* and *Mylohyus*—known only from North America—and the extant *Tayassu* and *Catagonus* (Menegaz and Jaureguizar, 1995).

Platygonus and *Catagonus* have high-crowned teeth, while *Mylohyus* and *Tayassu* have lower crowned teeth (Rincón et al., 2009). In *Platygonus*, the premolars have a single pair of high cusps, and the molars have a cingulum surrounding the entire tooth (Season, 2007; Gasparini and Ubilla, 2011). The enamel cingulum never surrounds the entire tooth in *Catagonus* and *Tayassu* but may be present on two or three sides (e.g., anterior, labial, and posterior) of the teeth

(Gasparini and Ubilla, 2011). The peccary from ORS20 has the following diagnostic morphological characters: simple premolars with two major cusps, bunolophodont crown morphology, mesodont crown height, and the enamel cingulum surrounds the entire tooth; that allows us to refer the material to *Platygonus*. However the currently available material lacks diagnostic characters permitting assignment to the species level.

In North America, *Platygonus* is represented by four species: *Platygonus pearcei* and *Platygonus bicalcaratus* (Blancan–early Irvingtonian), *Platygonus vetus* (late Irvingtonian–early Rancholabrean), and *Platygonus compressus* (middle–late Rancholabrean; Season, 2007). In South America this genus is represented by five species: *Platygonus kraglievichi, Platygonus scagliai*, *Platygonus chapadmalensis*, *Platygonus marplatensis*, and *Platygonus cinctus* (Gasparini, 2007). *Platygonus* was reported from Colombia, Bolivia, Uruguay, Argentina, and Venezuela (Rincón et al., 2009; Gasparini and Ubilla, 2011), and its time range in South America extends from the Middle Pliocene to Middle Pleistocene (Gasparini and Ubilla, 2011). *Platygonus* sp. was previously described from ORS16 (Rincón et al., 2009), but the molars from ORS20 possess an accessory cuspule between the hypoconulid and posterior crest, which is not present for example in the specimens from ORS16 (Rincón et al., 2009). This suggests the presence of two different species in Orocual, but the absence of more diagnostic characters does not permit assignment to species at this time.

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Genus *Equus* Linnaeus, 1758

Equus (Amerhippus) sp.

Figure 7g

REFERRED MATERIAL. ORS20-265, isolated upper right premolar (P2).

DESCRIPTION. The highly worn upper right premolar is indicative of an adult (old) individual. It has a well-marked mesostyle, parastyle, and anterostyle. The prefossette and postfossette folds are reduced. The protocone is subtriangular in shape and smaller than the hypocone. The pli caballine is connected with the anterofossette.

REMARKS. In *Equus* (*Amerhippus*) the upper teeth have a triangular protocone with the prefossette and postfossette folds reduced as seen in ORS20-265. Five species of *Equus* (*Amerhippus*) are recognized from the Ensenadan and Lujanian SALMA of South America: *Equus* (*Amerhippus*) *andium*, *Equus* (*Amerhippus*) *insulatus*, *Equus* (*Amerhippus*) *neogeus*, *Equus* (*Amerhippus*) *santaeelenae*, and *Equus* (*Amerhippus*) *lasallei* (Prado and Alberdi, 1994). In Venezuela, *E.* (*Amerhippus*) *santaeelenae* is known from the Mene de Inciarte tar pits and Taima-taima in western Venezuela. The morphology of the upper premolar is characteristic of *Equus*, but its morphology, while similar to that of *E. santaeelena*e, is not definitely diagnostic for this species. With larger samples, species can be differentiated by size, but current sample sizes are too small to permit species identification. This is the first record of *Equus* at El Breal de Orocual.

Family Tapiridae Burnett, 1830

Genus cf. *Tapirus* Brünnich, 1771

cf. *Tapirus* sp.

Figure 7h

REFERRED MATERIAL. ORS20-061, fragment of posterior part of left M2?.

DESCRIPTION. The tooth fragment is brachyodont and bunolophodont. There is a well-developed parastyle. The hypocone is more elevated than the metacone. The hypocone is connected with the metaloph, ectoloph, and posterior arm of the metacone. There is a labial cingulum below the metacone and a small cingulum below the posterior part of the hypocone.

REMARKS. The upper molars of Tapiridae are characterized by the presence of two transverse crests formed by the protoloph and metaloph and a high ectoloph formed by the joining of the paracone and metacone (Paula Couto, 1979). These last features are present in ORS20-061, but the material is very fragmentary. The genus *Tapirus* is the only member of family Tapiridae since the Ensenadan SALMA, and the fossil record includes Brazil, Bolivia, Peru, Argentina, Venezuela, and Uruguay (Rincón et al., 2009; Holanda et al., 2011; Holanda and Rincón, 2012).

Order Rodentia Bowdich, 1821

Suborder Myomorpha, Brant, 1855

Family Muridae Illiger, 1815

Subfamily Sigmodontinae Wagner, 1843

Tribe Sigmodontini Wagner, 1843

Genus *Sigmodon* Say and Ord, 1825

Sigmodon sp.

Figure 8a

REFERRED MATERIAL. ORS20-073, old adult right dentary; ORS20-074, young adult dentary.

DESCRIPTION. The teeth are brachyodont. The m1 is tetralophodont, while the m2 and m3 are trilophodont. The procingulum of the m1 is wider than long. The m1 has only three roots. On the lower first molar the lingual root is absent. The anterolophid and mesolophid are absent on all lower teeth. The m2 and m3 have a smaller

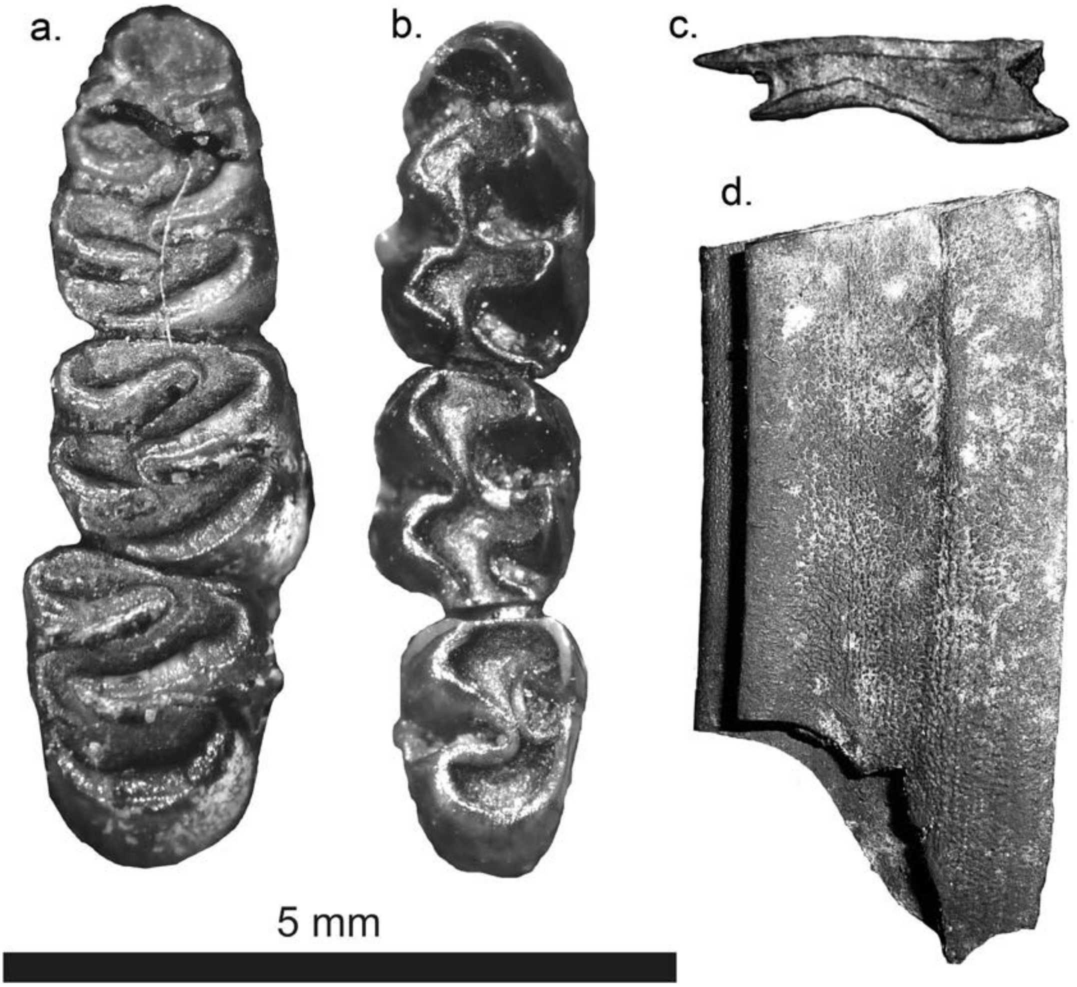

Figure 8 Rodents from ORS20. **a.** right dentary of *Sigmodon* sp. (ORS20-074), occlusal view; **b.** left dentary of *Zygodontomys brevicauda* (ORS20-075), occlusal view; **c–d.** fragment of molar of Hydrochoeridae gen. et sp. indet. (ORS20-063).

anterolabial cingulum. The metaflexid is present on the m1 but absent on the m2 and m3. The posterolophid is poorly developed on the m1 and m2 and fused with the entoconid on the m3. The mesoflexid and hypoflexid on the m2 and m3 are deep. The anterolabial conulid is positioned more distally than the anterolingual conulid. The anterior conulid of the m1 is undivided. The labial and lingual cuspids are positioned in a stepwise pattern. Measurements (in mm) of the dental elements, ORS20-073 (old adult): Length m1–m3 series: 6.1 mm, m1L = 2.4, m1W = 1.5; m2L = 1.6, m2W = 1.9; m3L = 2.5, m3W = 1.7; ORS20-074 (young adult): Length m1–m3 series: 6.4 mm, m1L = 2.5, m1W = 1.7; m2L = 2.1, m2W = 1.9; m3L = 2.3; m3W = 1.9.

REMARKS. Diagnostic characters of Sigmodontinae include reduced and simplified molars characterized by the obsolescence of a functional mesolophid in, at least, the m1 and m3 and the presence of an S-shaped enamel pattern on the m3 (Hershkovitz, 1955). The Sigmodontinae include at least eight tribes, including the Sigmodontini. The Sigmodontini is monotypic with *Sigmodon,* a genus known since the Blancan NALMA of the United States as the only extant genus (Czaplewski, 1990). The modern distribution of *Sigmodon* includes North, Central, and South America (Pardiñas et al., 2002). *Sigmodon* has an anterolabial–anterolingual conulid of the ml that is undivided; anterolophid and mesolophid absent on all lower teeth; the posterolophid well developed on ml and m2, absent (or fused with entoconid) on the m3; the ml with three or four roots, and the m2 and m3 each with three roots (Hershkovitz, 1955; Martin, 1969, 1979; Voss, 1992). All of these characters are clearly observed in ORS20-073 and ORS20-074.

Around 15 extant species of *Sigmodon* are currently recognized with at least six extinct species (Pelaez-Campomanes and Martin, 2005). The *Sigmodon* from ORS20 has dental morphology similar to the extant species, *Sigmodon hispidus* and *Sigmodon alstoni*. According Voss (1992) these two species can be differentiated by the lower first molar lingual root; this is well developed but always smaller than the anterior and posterior roots in *S. hispidus* but either absent, or very small and weak in *S. alstoni*, as in the specimens from ORS20. However, we consider this character as insufficient for a definitive assignment to species.

Tribe Oryzomyini Vorontsov, 1959

Genus *Zygodontomys* J.A. Allen, 1897

Zygodontomys brevicauda J.A. Allen and Chapman, 1893

Figure 8b

REFERRED MATERIAL. ORS 10-075, left dentary with m1–m3 dental series.

DESCRIPTION. Brachyodont and terraced molars, with the m1 tetralophodont, m2 trilophodont, and m3 bilophodont. On the m1 the lingual conids are slightly distally displaced relative to the labial conids, showing a stepwise pattern. On the m2 and m3 the conid labial and lingual are face to face. The procingulum is well developed on the m1 but never completely isolated from either the protoconid and/or metaconid due to the confluence of the protoflexid and metaflexid—which is absent on the m2 and m3. The anterolophid, ectostylid, metastylid, and mesostylid are absent from all lower teeth. The hypoflexid is deep and wide on all lower molars and increases in width posteriorly. There is a well-marked accessory cuspid at the base of the hypoflexid on all molars. There is a posteroflexid present on the m1 and m2, which is absent on the m3. The posteroflexid of the m1 is larger than in the m2. The posterolophid of the m1 and m2 is posteriorly elongated but is absent from the m2. Measurements (in mm) of the dental elements: Length m1–m3 series: 5.7; m1L = 1.9; m1W = 1.2; m2L = 1.5; m2W = 1.2; m3L = 1.4; m3W = 1.0.

REMARKS. The Tribe Oryzomyini is composed of around 36 extant and fossil genera and more than 130 species (Weksler and Percequillo, 2011). It is characterized by low-crowned (brachyodont) and terraced molars (except *Holochilus*, which have high-crowned molars) and generally pentaloph molars (tetraloph in *Holochilus*, *Pseudoryzomys,* and *Zygodontomys*), with a well-developed mesoloph and mesolophid (Pardiñas et al., 2002).

Zygodontomys has an anteroconid of the ml that is undivided by an anteromedian flexid; the anterolophid is absent on all lower teeth; an anterolabial cingulum present on the unworn m2 and m3; a mesolophid absent on all lower teeth; and a well-developed posterolophid present on the ml and m2, but absent from the m3 (Voss, 1991), all features present in ORS20-075. The latest comprehensive review of the genus *Zygodontomys* recognizes only two valid species: *Zygodontomys brunneus* and *Zygodontomys brevicauda* (Voss, 1991). The morphology of the lower molars is distinctive in each species; *Z. brunneus* has lophids and conids with an orthogonal shape, while they are in a slanted position in *Z. brevicauda* (Voss, 1991). This allows us to assign ORS20-075 to the extant species *Z. brevicauda*, which usually inhabits open vegetation in Central America and northern South America (Voss, 1991). The only other evidence of *Zygodontomys* in the fossil record comes from Trinidad Island (Wing, 1962). This specimen is the first fossil record of the short-tailed cane mouse *Zygodontomys* in Venezuela, and probably in northern South America.

Suborder Hystricognathi Tullberg, 1899

Family Hydrochoeridae Gray, 1825

Hydrochoeridae gen. et sp. indet.

Figure 8c, 8d

REFERRED MATERIAL. ORS20-063, m3 broken in several places along the individual enamel plates

DESCRIPTION. A very fragmented lower molar that is very hypsodont.

REMARKS. The Hydrochoeridae (capybaras) are notable for their large size and euhypsodont and multilaminated cheek teeth (Vucetich et al., 2005). Three subfamilies are recognized: Hydrochoerinae, Cardiatheriinae, and Protohydrochoerinae. The preserved dental morphology of ORS20-063 is more similar to members of the Hydrochoerinae, which have molars that are more complicated than the Cardiatheriinae and have a larger number of transverse plates (Paula Couto, 1979). Due the fragmented nature of the material, a definitive identification is not possible, but the specimen can at least be identified to the family level.

Order Carnivora Bowdich, 1821

Family Felidae Gray, 1821

Subfamily Machairodontinae Gill, 1872

Genus *Smilodon* Lund 1842

Smilodon populator Lund, 1842

Figure 9a–c

REFERRED MATERIAL. ORS20-037, partial left ramus containing a broken dp3 and dp4; the

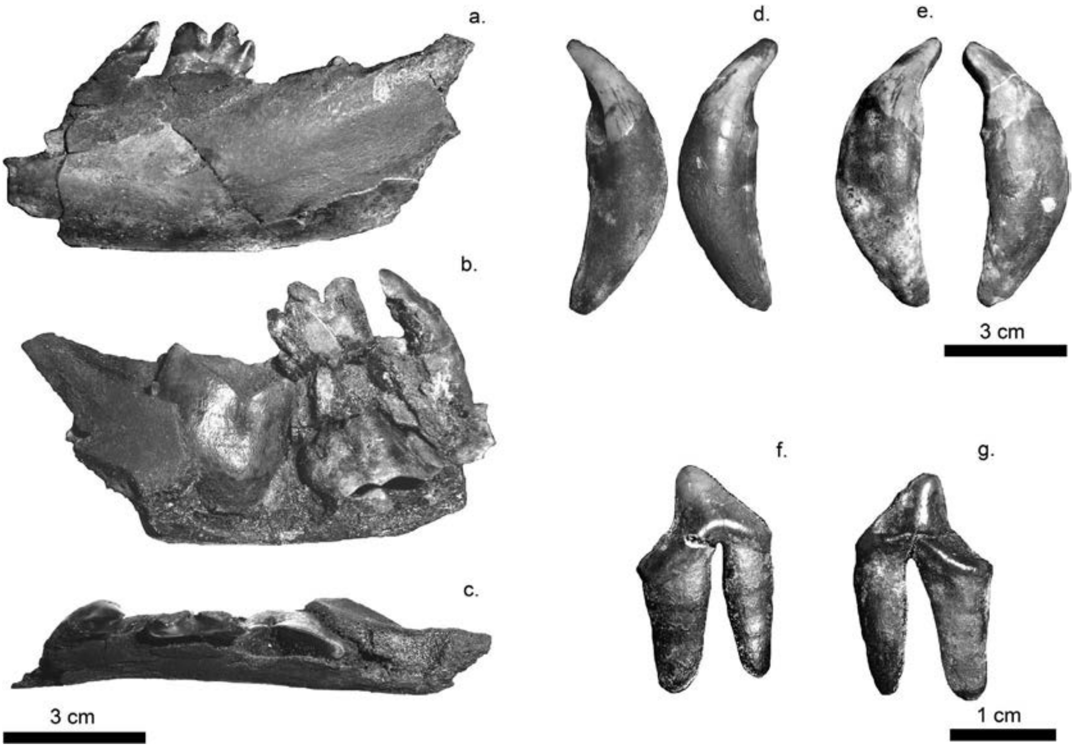

Figure 9 Carnivores from ORS20. **a–c.** *Smilodon populator* (**a** = labial view, **b** = lingual view, **c** = occlusal view); **d, e.** *Panthera* cf. *onca*, (**d** = right lower canine, **e** = left lower canine); **f, g.** cf. *Protocyon* sp. (ORS20-076), right lower premolar (p2) (**f** = labial view, **g** = lingual view).

p4 is present but not erupted, and the m1 is starting to erupt, indicating a young individual.

DESCRIPTION. The dp3 is reduced, double-rooted, and probably bicuspidate; the root is long (>17 mm). The dp3 is tricuspidate. Below the dp3, the p4 is not yet erupted. The p4 is composed of a principal cusp flanked by a relatively small anterior cusplet and two progressively smaller posterior cusps, a posterior cusplet, and a posterior cingulum. On the m1 the paraconid blade is clearly shorter anteroposteriorly than the protoconid, and both have the serrations typical of many members of the Machairodontinae. The protoconid is more elevated than the paraconid. A small basal posterior cingulum behind the protoconid is clearly marked. See Table 3 for measurement.

REMARKS. Berta (1987) recognized two species of *Smilodon*, the small, slender *S. gracilis* from Late Pliocene–Middle Pleistocene localities in North America and the larger, and more robust, *Smilodon populator* from Middle–Late Pleistocene localities in North and South America. Morphometric data provided for several authors (Berta, 1985, 1987; Kurtén and Werdelin, 1990) suggest that species of *Smilodon* species are distinguished based primarily on size (Rincón, 2003). The measurements of the m1 and p4 of ORS20-037 are within the range of variation observed for *S. populator* and are greater than those of *S. gracilis* (see Table 3). Additionally, the presence of coarser serrations on the teeth also suggests affinities with *S. populator* (very fine serrations on teeth in *S. gracilis*; Rincón et al., 2011). The combination of the dental morphology and measurements suggest that ORS20 can be assigned to *S. populator*. *Smilodon populator* is commonly reported from Late Pleistocene (Lujanian SALMA) faunas of Brazil, Bolivia, Venezuela, and Argentina and for the Middle Pleistocene (Ensenadan SALMA) of Argentina (Berta, 1985; Kurtén and

Table 3 Comparison between p4 and m1 measurements (mm) in *Smilodon populator* and *Smilodon gracilis*.

Species	Length p4	Length m1
S. populator[a]	31.8–23.5	31.9–26.6
S. gracilis[b]	22.0–18.2	25.2–20.8
S. populator[c]	27.6[d]	28.4

[a] Kurtén and Werdelin (1990).

[b] Berta (1987).

[c] Present work (ORS20-037).

[d] Estimated measurements.

Table 4 Lower incisive measurements (in mm) of *Puma concolor*, *Panthera onca*, and *Panthera leo*.

Species	Height	Width	Depth	Observations
Puma concolor[a]	23.8	77	12.08	Average of 16 individuals, Mexico.
Panthera onca[a]	32.7	12.24	15.95	Average of 29 individuals, Mexico
P. onca augusta[bc]	—	14.6	19.35	Average of 5 individuals, USA
P. leo atrox[cd]	—	15.1–22.0	21.8–30.4	Data from Rancho La Brea, USA
Panthera onca[cf]	25.5[g]	12.7	17.3	ORS20-078, Venezuela
Panthera onca[cf]	25.4[g]	12.6	17.3	ORS20-079, Venezuela

[a] Morales-Mejía et al. (2010).
[b] Kurtén (1965).
[c] Fossil record.
[d] Merriam and Stock (1932).
[e] Montellano-Ballesteros and Carbot-Chanona (2009).
[f] ORS20 material.
[g] Estimated measurements.

Werdelin, 1990; Rincón, 2003, 2006). In Venezuela, *S. populator* has been reported from the western localities (Mene de Inciarte tar pits and Zumbador Cave; Rincón, 2006). This is the first evidence of *S. populator* at El Breal de Orocual.

The presence of light wear on the dp3 and heavy wear on dp4 with a no more than one-third of the m1 erupted in ORS20-037 indicates a stage 3 of the mandible ontogenetic development (*sensu* Tejada-Flores and Shaw, 1984), indicating the occurrence of a juvenile *S. populator* at El Breal de Orocual.

Subfamily Pantherinae Pocock, 1917

Genus *Panthera* Oken, 1816

Panthera cf. *P. onca* Linneo, 1758

Figure 9d, 9e

REFERRED MATERIAL. ORS20-078, ORS20-079, left and right lower canine probably from the same individual.

DESCRIPTION. The canine is mostly conical in shape and oval in cross section, with the mesiolabial border highly eroded, suggesting an older individual. The distal crest is completely eroded. The base of the mesial crest is present. Although the mesial and distal crests are eroded, they are clearly not connected toward the canine's crown. For measurements see Table 4.

REMARKS. Comparison of lower canine measurements of the extant felid species *Puma concolor* and *Panthera onca* and the fossils *Panthera onca augusta* and *Panthera leo atrox* (see Table 4) suggest that the genus *Panthera* has a wider and longer lower canine than *Puma*. Furthermore the mesial and distal crests in *Puma* are connected toward the canine crown but remain unconnected in *Panthera* (Morales-Mejía et al., 2010). These last features allow to us to refer the specimens from ORS20 to *Panthera*. The ORS20 specimens are smaller than *P. onca augusta* (Kurtén, 1965) and *P. leo atrox* (Merriam and Stock, 1932; Montellano-Ballesteros and Carbot-Chanona, 2009), and their size is closer to those of extant *P. onca*. The fossil record of *P. onca* probably extends from the Middle Pleistocene to the Recent, with a distribution in mostly southern North America (with the northernmost record in Oregon) and Central and South America (Eizirik et al., 2001). This is the second fossil record of *P. onca* in Venezuela, after the Muaco locality in western Venezuela (Bocquentin, 1979).

Family Canidae Fischer, 1817

Genus *Protocyon* Siebel, 1855

cf. *Protocyon* sp.

Figure 9f, 9g

REFERRED MATERIAL. ORS20-076, right lower premolar (p2).

DESCRIPTION. The premolar has two roots. The posterior root is larger than the anterior root. The principal cusp is acute and weak but lacks accessory or cingular cusps. Measurements (in mm): length = 12.4, width = 5.1.

REMARKS. The presence of an acute and weak principal cusp in the premolars, which is observed in ORS20-076, separates *Protocyon* from *Canis*, *Theriodictis*, and *Chrysocyon* (Prevosti and Rincón, 2007). *Protocyon* is restricted to South America (Prevosti et al., 2005). Only two species of *Protocyon* are currently recognized; *Protocyon troglodytes* and *Protocyon scagliarum* (Prevosti and Rincón, 2007). The unequivocally oldest record of *Protocyon* is younger than 0.78 Ma (Prevosti et al., 2005). The age of *P. scagliarum* is between 0.78 and 0.5 Ma, while the oldest record of *P. troglodytes* is probably older than 0.5 Ma but extends into the Late Pleistocene (Prevosti et al., 2005). The premolars from ORS20 have lower and less acute principal cusps than in *P. scagliarum*, suggesting closer affinities with *P. troglodytes*, but the available material is insufficient for a species level assignment.

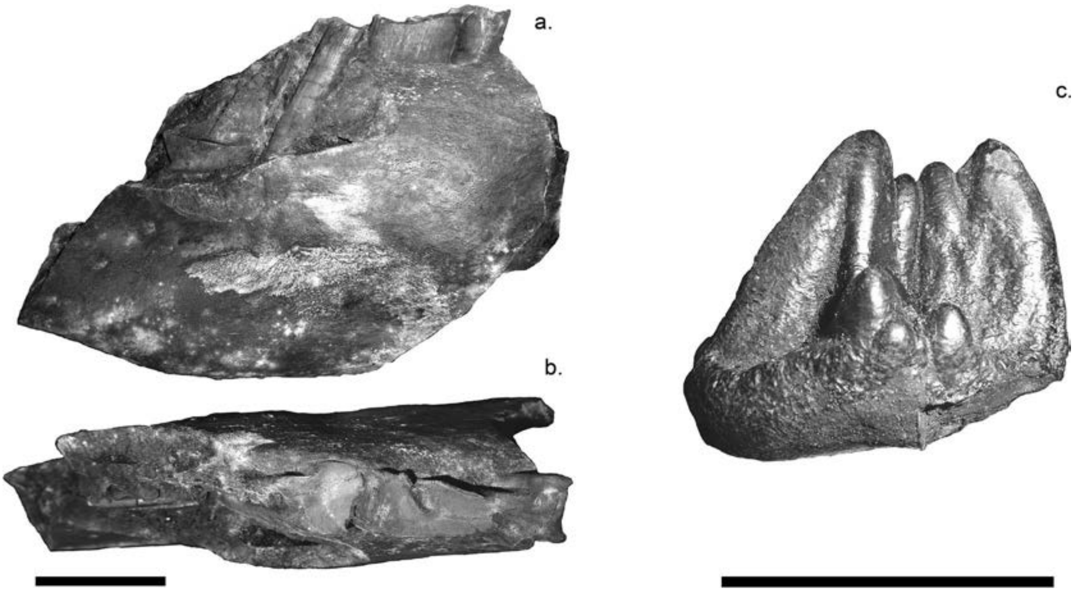

Figure 10a, b. *Mixotoxodon larensis,* fragment of right dentary (ORS20-069) (**a** = labial view, **b** = occlusal view); **c.** molar fragment of Gomphotheriidae gen et sp. indet. (ORS20-263). Scale bar = 5 cm.

Order Notoungulata Roth, 1903

Family Toxodontidae Gervais, 1847

Genus *Mixotoxodon* van Frank, 1957

Mixotoxodon larensis van Frank, 1957

Figure 10a, 10b

REFERRED MATERIAL. ORS20-069, fragment of right dentary with m1–m3.

DESCRIPTION. The molars are hypsodont, with discontinuous enamel arranged in vertical bands. The molars have paraconids and the lingual border of the hypoconid without enamel. The m1 has a pronounced meta-entoconid fold, with a bigger metaconid than the m2, while the rest of dental structure is eroded. The m2 shows a meta-entoconid fold less developed and not well marked, a metaconid with an enamel band on the labial part, a pronounced enamel ento-hypoconid fold, and hypoconid triangular in shape and lacking enamel on its labial side. While the m3 is eroded, it still shows a deep and pronounced ento-hypoconid and meta-entoconid fold, with an entoconid smaller than that of the m2.

REMARKS. The toxodont genera *Toxodon* and *Mixotoxodon* were large to very large herbivorous mammals endemic in South America and the Neotropics during the late Cenozoic (MacFadden, 2005a), although *Mixotoxodon* has recently been reported as far north as Texas (Lundelius et al., 2013). *Toxodon* can be differentiated from *Mixotoxodon* based on the presence of well-developed meta-entoconid and ento-hypoconid folds I on the m1 and m2 (Pascual, 1957); while in *Mixotoxodon* the meta-entoconid fold is lacking on the m2 and m3, but is present on the m1. The ento-hypoconid fold is present on the m1 and m2, but is lacking on the m3 (van Frank, 1957; Saint-Andre, 1999; Rincón, 2011). *Mixotoxodon* is a monotypic genus, with the single species *Mixotoxodon larensis*. Rincón (2011) suggested that this species could be recognized by the absence of the meta-entoconid fold on the m2 and m3, but present in m1, and a ento-hypoconid fold present in the m1 and m2, but lacking in the m3. These features are present in ORS20-069 and permit assignment to *M. larensis*. The genus is known only from the Late Pleistocene. Its paleogeographic distribution ranges from United States to Bolivia, which indicates an intertropical distribution for this species (Rincón, 2011; Lundelius et al., 2013).

Order Proboscidea Illiger, 1811

Family Gomphotheriidae Cabrera, 1929

Gomphotheriidae gen. et sp. indet.

Figure 10c

REFERRED MATERIAL. ORS20-263, fragment of molar.

DESCRIPTION. Fragmented tooth with heavy, crenulated enamel, preserving only a strongly developed anterior cingulum that is oblique toward mesial side.

REMARKS. The fossil record of gomphotheres in South America apparently begins during the glacial phases of the Early or Middle Pleistocene (Ensenadan SALMA) or maybe earlier, the Pliocene or Plio–Pleistocene boundary (Casamiquela et al., 1996). A first appearance in South America during the Late Miocene has been proposed (Campbell et al., 2000), but no conclusive data exists that confirms this early arrival (Alberdi et al., 2004). During the Pleistocene only two species of proboscideans were presented in South America, *Cuvieronius hyodon* and *Notiomastodon platensis* (Mothé et al., 2012, 2013). These two species spread throughout the continent following two different "corridors." In the highland corridor via the Andes, *C. hyodon* was dominant and is present in Colombia, Ecuador, Bolivia, Peru, and Chile. *Notiomastodon platensis* inhabited the lowland corridor and is found in Brazil, Ecuador, Venezuela, Colombia, Argentina, Uruguay, Paraguay, and the western coastal areas of Peru and Chile (Mothé et al., 2013). Based strictly on known distribution of the two taxa, we refer the limited material from ORS20 to *Notiomastodon* but recognize that the recovery of better preserved specimens may require a revision of this assignment. The time range of *N. platensis* is currently from at least 530 ka (Middle Pleistocene) until 6 ka (Early Holocene; Dantas et al., 2013). Although the dental morphology of South American proboscideans is complex, Prado et al. (2003) and Alberdi et al. (2002, 2004) noted that some tooth fragments can be identifiable. Unfortunately, our material is too fragmentary for any reliable identification.

DISCUSSION

AGE

The tar pit deposits that preserve fauna at El Breal de Orocual overlie the Mesa Formation (Rincón et al., 2009). The Mesa Formation is considered Pleistocene in age based on its stratigraphic position above the Pliocene Las Piedras Formation (González de Juana, 1946). The age of the Las Piedras Formation is based on its stratigraphic position above the Freites and La Pica Formations, considered being Middle to Late Miocene (Sulek, 1961). However, in the Orocual area the Las Piedras Formation is overlying the Carapita Formation mudstones (Late Oligocene–Middle Miocene; Sulek, 1961). This demonstrates that the chronologies of late Cenozoic Venezuelan geologic formations which lack marine fossils are poorly known in terms of age assignment and consequently at this time should be considered unreliable. Thermoluminescence ages obtained for the Mesa Formation at Maripe, State of Anzoátegui, suggest that the formation dates to between 0.5 and 1 Ma, whereas two other thermoluminescence dates suggest an age in excess of 2 Ma (Carbón et al., 1992). The preliminary taxonomic identifications of the mammalian component of the fauna from ORS16 suggest that, based on the known or inferred ages of these taxa (or their morphologically close kin) elsewhere in North or South America, the oldest faunas from the El Breal de Orocual deposit dates to somewhere between the Late Pliocene to Early Pleistocene (Rincón et al., 2009, 2011).

Given the absence of absolute geochronological dates, the common biochronological ranges of the mammals described here for ORS20 suggest a Late Pleistocene age for the fauna. This indicates that, although ORS16 and ORS20 tar pits are geographically close, their assemblages are of different ages, as indicated by the differences in their mammalian taxa.

One of major differences between the asphaltic mammalian assemblages of ORS16 and ORS20 is the presence of *S. gracilis* in the earlier ORS16 fauna and the presence of the larger and chronologically later species *S. populator* in the fauna from ORS20. These two *Smilodon* species have distinctive biochronological ranges (Bell et al., 2004). Prior to its discovery at ORS16, *S. gracilis* had been only known from the late Blancan to late Irvingtonian faunas in the United States (Bell et al., 2004; Rincón et al., 2011). Ferrusquía Villafranca et al. (2010) also mention *S. gracilis* from the Pleistocene (Trans-Mexican Volcanic Belt) of Mexico, but insufficient detail on the referred specimens is provided, and it is not possible to corroborate the assignment of their specimens to that species (Rincón et al., 2011). Nonetheless, *S. gracilis* is generally more typical of the Irvingtonian (Bell et al., 2004), while the other saber-tooth, *S. populator,* is commonly reported for the Late Pleistocene (Lujanian SALMA) of Brazil, Bolivia, Venezuela, and Argentina and the Middle Pleistocene (Ensenadan SALMA) of Argentina (Berta, 1985; Kurtén and Werdelin, 1990; Berman, 1994; Rincón, 2004, 2006).

Of the horses, *Equus* is present in ORS20, but only *Hippidion* is present in ORS16. *Hippidion* first appeared in the South American fossil record around 2.5 Ma, shortly after the Great American Interchange, whereas *Equus* first appeared in South America only around 1 Ma (Orlando et al., 2008). The presence of these two different genera is consistent with the marked difference in age between ORS16 and ORS20. The presence of *Platygonus* remains is significant, as this taxon is less common than *Tayassu* in ORS20 but more common in ORS16. In South America, *Platygonus* has been reported from Colombia, Bolivia, Uruguay, Venezuela, and Argentina (Rincón et al., 2009; Gasparini and Ubilla, 2011). The oldest unquestionable record of *Platygonus* comes from the Chapadmalal "Formation" and is referred to the species, *P. marplatensis*, known from the beginning of the Middle Pliocene of Argentina (Gasparini and Ubilla, 2011). The greatest diversity of *Platygonus* species in South America occurs during the Late Pliocene but during the Early to Middle Pleistocene the numbers of records of this genus markedly decrease (Gasparini and Ubilla, 2011). The presence of several remains of *Platygonus* in ORS20 represent the latest record of this genus in South America, expanding its biochron from Middle Pliocene to the Late Pleistocene.

The jaguar *Panthera* cf. *P. onca* is only reported from ORS20. *Hoplophorus* (Cingulata; Glyptodontidae) is absent in ORS20 but present in ORS16. The rodents *Echimys* and Erethizontidae are only present in ORS16, whereas *Sigmodon* and *Zygodontomys* are only found in ORS20. These last taxa suggest a replacement in the faunal assemblage in the vicinity of Orocual from the Pliocene? to Pleistocene and that the multiple tar pits at the site are sampling the several stages of GABI in South America (Woodburne, 2010).

Pachyarmatherium leiseyi is currently known from the Late Pliocene and Early Pleistocene of Florida, USA (Leisey Shell Pit, Hillsborough County and Haile 16A, Alachua County), Late Pliocene of Dorchester County, South Carolina, USA (Downing and White, 1995; Hulbert et al., 2001), Blancan to Irvingtonian (SALMA) of Costa Rica (Laurito et al., 2005; Valerio and Laurito, 2011), and the Plio–Pleistocene of the Breal de Orocual at ORS16, Venezuela (Rincón, et al., 2009). The new material of *P. leiseyi* found in ORS20 with an estimated Late Pleistocene age is the youngest appearance of this species and expands our knowledge of the biochronological record of *P. leiseyi* in South America. The two different species of *Pachyarmatherium*, *P. leiseyi*, and *P. tenebris*, are present in South America during the Late Pleistocene, but they appear to be allopatric as there is no evidence of their sympatric coexistence in the same locality. *Pachyarmatherium tenebris* was originally described from Late Pleistocene deposits of Cueva del Zumbador in northwestern Venezuela (Rincón and White, 2007). Until now *P. tenebris* is restricted to the Late Pleistocene of South America in Venezuela, Peru, Uruguay, and Brazil (Rincón and White, 2007; Bostelmann et al., 2008; Oliveira et al., 2009; Porpino et al., 2009; Rincón et al., 2009; Martínez and Rincón, 2010; Oliveira et al., 2013), while the geologically earlier species *P. leiseyi* is dominant in North and Central America during the Blancan and Irvingtonian (NALMA) and in northern South America as documented at El Breal de Orocual from the Pliocene–Pleistocene of ORS16 until the Late Pleistocene of ORS20.

TAPHONOMICAL ASPECTS

The fauna from Rancho La Brea is a composite of remains recovered from several pits (e.g., Pits 3, 4, 9, 13, 16, 60, 61–67, 77, 91, and 2051). As at Orocual, the overall depositional history of the Rancho La Brea complex spans from beyond the limit of accurate radiocarbon dating greater than 50 ka to less than 10 Ka, with some of the deposits recording one or more pulses of accumulation (Friscia et al., 2008; O'Keefe et al., 2009). A recent taphonomic analysis of Pit 91 documents at least two different episodes of deposition: one from 45 to 35 ka and another, shorter interval from 26.5 to 23 ka (Friscia et al., 2008).

Other South America and Caribbean tar pit localities with radiocarbon dates include Las Breas de Talara (Peru) with an age between 13 and 14 ka (Churcher, 1966; Bryan, 1973), Las Breas de San Felipe (Cuba) dating between 5 and 12 ka (Jull et al., 2004), and Mene de Inciarte (Venezuela), dating between 25.5 and 27 ka (Jull et al., 2004). These other asphaltic fossiliferous localities have vertebrate assemblages representing a relatively short time interval (compared with a maximum of 60–50 ky at Rancho La Brea). However, at El Breal de Orocual the different tar pits contain a diverse fauna which accumulated during distinctive episodes of deposition, from the Late Pliocene–Early Pleistocene of ORS16 until Late Pleistocene of ORS20 during an interval of time, about 2 My, that is longer than any other locality in North or South America.

Continued work at additional tar pits at El Breal of Orocual, formed by successive episodes of natural oil seeping to the surface along fractures formed at different times caused by the displacement of tectonically controlled fault blocks, has the potential to document successive stages of the biotic change that occurred from the Pliocene through Pleistocene. This hypothesis is supported by the presence of the two different mammalian faunal associations of dramatically different ages: ORS16 (Plio–Pleistocene) and ORS20 (Late Pleistocene). The older site (ORS16) is currently inactive in terms of oil emanations and comprises a mixture of weathered hydrocarbons and sediments, whereas the younger site (ORS20) is a currently still an active tar pit.

PALEOENVIRONMENTS

The dominant fauna in ORS20 consists of forms adapted to open savanna environments or ecotone savanna forest, with some specialist grazers such as *G. clavipes*, *P. humboldtii*, *H. occidentalis*, *Sigmodon* sp., *Z. brevicauda*, *Platygonus* sp., and Hydrochoeridae; some browsers like Megalonychidae and *Eremotherium* sp.; and some mixed feeders (grazer and browsers) like *T. pecari*, *Palaeolama* sp., *M. larensis*, and Mylodontidae. Also represented are the myrmecophagous *P. leiseyi*, the omnivorous *P. sulcatus* and *Didelphis* sp., and the hypercarnivores *S. populator*, *P. onca*, and *Protocyon* sp. The mammal assemblage from the El Breal de Orocual indicates high paleoenvironmental heterogeneity, with a savanna and/or seasonally dry forest and probably almost continuous water flow in the area during the Late Pleistocene. This is consistent with the pronounced conditions of aridity and cold temperatures during the long glacial phases, which particularly stimulated the development of open and homogeneous environments in South America during the Pleistocene (MacFadden, 2005b; Woodburne, 2010).

CONCLUSIONS

The mammal assemblage described in the present work plus *T. pecari* reported by Montellano-Ballesteros et al. (2012, 2014) document a minimum of 22 species recovered during preliminary salvage excavations in El Breal de Orocual at a tar pit named ORS20. As with previous work undertaken at the older ORS16, the relatively small assemblage of specimens collected in ORS20 so far represents a minuscule fraction of the total amount of material preserved there that, with additional excavation, has the potential to produce millions of fossil specimens just like Rancho La Brea.

The presence of a Late Pleistocene fauna in the tar pits El Breal de Orocual, in addition to the previously described and older fauna for the area, suggests the existence of particular conditions that are not present at other fossiliferous tar pits in the Americas. This condition (generating numerous sites which preserve distinctive faunas) can be attributed to the collapse structure "La Hoya de Orocual" in first place, and to the continued activity of the deformation front associated to the interaction between South American and Caribbean plates in the northeast of Venezuela in the second place. This unique combination permits the prediction of the existence of several sites within the area Orocual, each with a distinctive fauna reflecting significant differences in the timing of its accumulation over a 2-million-year period. The potential to document changes in the local biota, the impact on the endemic fauna, and possibly extinction by the appearance of exotic species from North America at different stages of the GABI and their subsequent evolutionary adaptations to the new landscape is remarkable and will provide the raw materials to create, test, and modify many hypotheses over the next few years.

For the moment, the faunas discovered in the tar pits at ORS20 and ORS16 (El Breal de Orocual), as well as Mene de Inciarte in western Venezuela, represent the most diverse and best preserved assemblages of mammals and other vertebrates in northern South American during the Quaternary. The interactions between North America and South America biotas during the Great American Biotic Interchange is well documented by fossil sites in the United States, Mexico, and Argentina, but there are few known faunas in northern South America, especially during the Early Pleistocene. The strategic location of the Venezuelan tar pits (El Breal de Orocual and Mene de Inciarte) will no doubt provide the critical data to improve our understanding of the phases of this event and the timing of the first appearance of many North American taxa in South America. The importance of these sites is demonstrated by the recent discoveries in ORS20 of *Platygonus* sp. and *P. leiseyi* during the Late Pleistocene, representing the last appearances of these taxa in the fossil record of South America. The jaguar *Panthera* is documented for the second time from the Pleistocene of Venezuela, and the cane mouse *Zygodontomys* is reported in fossil state for first time from Venezuela, and probably from South America.

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Sample Preparation for Radiocarbon Dating and Isotopic Analysis of Bone from Rancho La Brea

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ABSTRACT. Accurate radiocarbon dating and stable isotope ratio analysis of bone from Rancho La Brea and other tar seep sites is complicated by the necessity for the efficient and complete removal of asphalt from collagen. In this paper we review a new sample preparation method specifically designed for this purpose, that utilizes sonication in solvents, gelatinization, and selection of a specific molecular weight fraction by successive ultrafiltrations at 30 and 3 kDa. The middle fraction (3–30 kDa) produces white spongy collagen with excellent atomic C:N ratios between 3.2 and 3.5 and %C (42.0 ± 2%) and %N (15.0 ± 1%) values indicative of uncontaminated collagen. We also list past bone radiocarbon dates from Rancho La Brea and assess them in terms of quality and discuss the dangers of using "pit average" dates for individual specimens. Given the overall lack of stratigraphy at Rancho La Brea, more direct radiocarbon dates on bone specimens will be required to take full advantage of the amazing wealth of paleontological material available.

INTRODUCTION

Millions of specimens of plant, insect, reptile, bird, and mammal remains ranging in age from modern to more than 50 ky have been recovered and continue to be excavated from asphalt seeps ("tar pits") at the Rancho La Brea (RLB) site (for reviews, see Marcus and Berger, 1984; Quinn, 1992; Stock, 1992; Harris, 2001; Ward et al., 2005; Friscia et al., 2008; Gerhart et al., 2012). A key feature of these specimens is the exceptional preservation; the vast majority of the vertebrate skeletal material contains near modern amounts of bone collagen because skeletal elements were quickly immersed and impregnated with asphalt after death (Stock, 1992; Holden et al., 2013). This inhibited the processes of collagen breakdown and degradation, but the same asphalt that afforded such unique preservation must now be removed from the collagen for accurate radiocarbon dating and isotopic analysis, and this presents a significant challenge.

Ho et al. (1969) were the first to develop an effective method for radiocarbon dating of asphalt-impregnated material, and subsequent efforts have been summarized by Marcus and Berger (1984) and O'Keefe et al. (2009). Several food web studies based on isotopic studies of collagen from RLB have been published (Coltrain et al., 2004; Chamberlain et al., 2005; Fox-Dobbs et al., 2006, 2007; Bump et al., 2007), of which only one (Fox-Dobbs et al., 2006) combined stable isotope studies with direct radiocarbon dates on the same bones. These investigations have shown that asphalt can be successfully removed from collagen, but the contrast between this handful of studies and the sheer volume and diverse nature of the specimens available at RLB is striking and can be attributed to the fact that asphalt removal is still considered difficult, time consuming, and costly. If large-scale research projects requiring good chronologies are to be conducted at RLB, a rapid, less expensive, and more efficient technique is needed for the removal of petroleum products from bone collagen.

Here we summarize a novel protocol for asphalt removal and collagen purification (Fuller et al., 2014). We also examine past bone radiocarbon dates from RLB compiled by O'Keefe et al. (2009) and discuss why some of these ^{14}C ages (bioapatite and carbonate dates) are highly unreliable and why others are possibly in error due to residual collagen contamination with hydrocarbons. We highlight the importance of quality control indicators of collagen purity for radiocarbon dates from RLB, and we discuss the dangers of "pit averaging," where an average age of entrapment is used for undated specimens from a given asphalt deposit.

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METHODS

SAMPLE PREPARATION

The new method for the extraction of collagen from asphalt-impregnated bone at RLB utilizes sonication in solvents, followed by gelatinization and successive ultrafiltrations at two different molecular weight cutoffs, and is described in detail in Fuller et al. (2014).

In common with all published pretreatment protocols for RLB specimens, our technique begins with solvent treatment to remove bulk asphalt. Bone is sectioned using a handheld Dremel rotary tool and samples of ~150 mg are crushed to small pieces (1–2 mm) and placed in test tubes. Samples are sonicated repeatedly in a 2:1 toluene:methanol mixture until the solution remains clear (four to six 1-hour cycles with the solvent replaced every hour), followed by sonication in methanol (1 hour) and Milli-Q water (1 hour). Cold tap water is circulated through a plastic hose in the sonicator bath to keep the temperature around 45°C, well below the 58°C melting point of collagen (Piez and Reddi, 1984). Our tests (Fuller et al., 2014:table A.2) showed that samples treated with this protocol produced similar ages to aliquots of the same bones subjected to prolonged solvent soaking and Soxhlet solvent extractions following Coltrain et al. (2004) and Ward et al. (2005), but the sonication method is much quicker and requires no specialized Soxhlet apparatus.

Solvent-treated bone is demineralized in 0.5 N HCl for 24–36 hours at room temperature. The resultant collagen pseudomorphs are rinsed with Milli-Q to pH > 3 and gelatinized (Longin, 1971) in a 0.01 N HCl solution at 75°C in a hot block for ~14 hours. An intermediate molecular weight fraction (3–30 kDa) is isolated from the gelatin solutions by centrifuging, using precleaned (Beaumont et al., 2010) Centriprep ultrafiltration devices (Fisher Scientific). Following an initial ultrafiltration carried out using a 30-kDa molecular weight cutoff device, the high molecular weight fractions (>30 kDa) are discarded and the less than 30-kDa fractions are retained and ultrafiltered again at 3 kDa. The concentrated (≈1 ml) high molecular weight fractions from the second ultrafiltration (3–30 kDa) are frozen with liquid nitrogen and lyophilized overnight in a vacuum centrifuge (Fig. 1).

Collagen quality is checked (C:N ratio, %C, %N), and stable isotope ratios are determined by flash combustion of ~0.7 mg samples of collagen in tin capsules and analysis of the gas products using a Fisons NA1500NC elemental analyzer/Finnigan DELTAplus isotope ratio mass spectrometer combination. Replicate measurement errors on known standards are approximately ±0.1‰ for δ^{13}C and 0.2‰ for δ^{15}N. Accelerator mass spectrometry dating is performed as described by Southon and Santos (2004) on graphitized CO_2 derived from ~2 mg of collagen. All samples are run with oxalic acid standards (OX1), known age bone standards, plus modern (19th century cow) and "radiocarbon dead" blanks (Beaufort Sea whale, 60–70 ky), all prepared in the same manner as the unknowns.

RESULTS AND DISCUSSION

To date, approximately 85 bones from a variety of mammal, reptile, and bird species from various pits at RLB have been processed for radiocarbon dating and carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes, with over 90% of these yielding useable collagen. The seven specimens that failed had a darker color and brittle texture, suggesting that they had possibly accumulated in an aquatic environment before being impregnated with asphalt. Collagen yields in the 3–30-kDa fraction are typically 1%–9% and are usually sufficient to permit multiple isotopic and radiocarbon measurements. The technique produces white spongy lyophilized collagen with atomic C:N ratios between 3.2 and 3.5 and %C (42.0 ± 2%) and %N (15.0 ± 1%) values close to modern bone (Ambrose, 1990; van Klinken, 1999), all consistent with minimal residual contamination by hydrocarbons (Fig. 1).

The rationale for the method is as follows. Our own tests and previous studies (Ho et al., 1969; Friscia et al., 2008; T. Stafford, personal communication) all show that solvent extraction techniques for removing the hydrocarbons from bone are only partially effective. An insoluble residue, probably consisting of large aggregates of tar constituent molecules, remains trapped within the bone matrix and must be removed by other means. Likely suspects are colloidal asphaltenes (Mullins et al., 2007; Goual, 2012), which have been called "the cholesterol of the oil industry" for their strong tendency to aggregate into pipeline-clogging macroscopic deposits. An elevated gelatinization temperature of 75°C permits well-preserved collagen molecules to be broken down to sizes less than 30 kDa but leaves hydrocarbon aggregates essentially intact and unable to pass through the 30-kDa ultrafilter. The second ultrafiltration step using a 3-kDa filter discriminates against low molecular weight contaminants, including exogenous proteinaceous material, soil humics, and any free asphaltenes or other small hydrocarbon fragments lost from the large aggregates during gelatinization.

ULTRAFILTRATION VERSUS XAD

As a test of accuracy, we compared ultrafiltration dates against published ^{14}C ages from the same RLB bones obtained using the well-established total amino acid extraction (TAA)/XAD resin

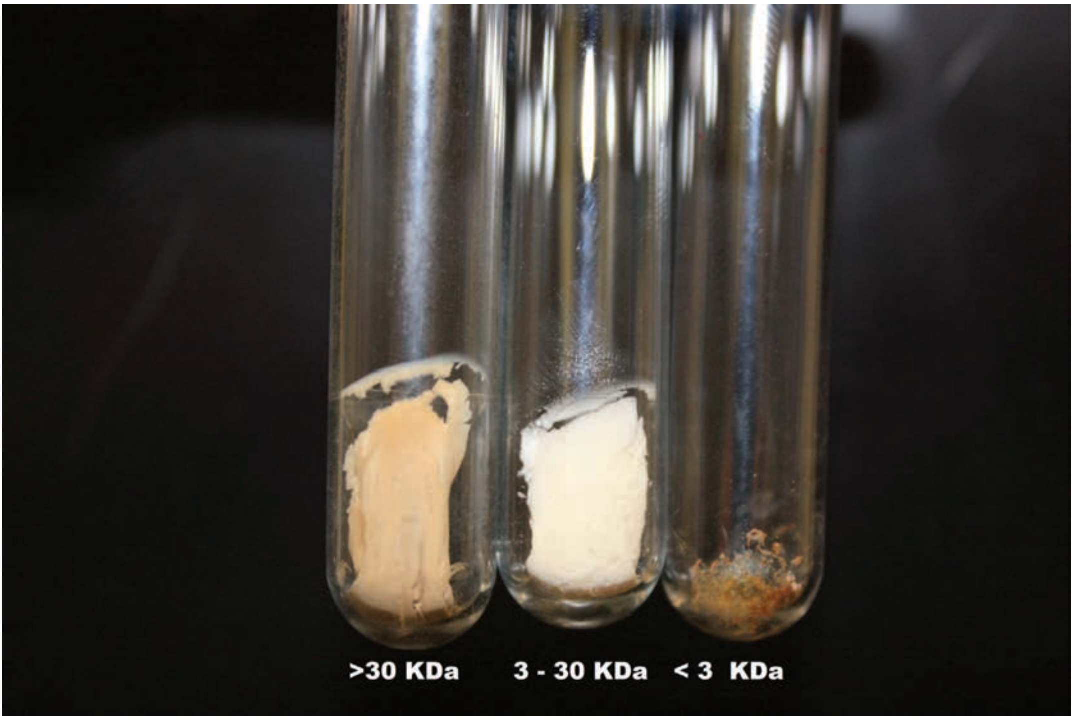

Figure 1 Collagen fractions obtained from ultrafiltration at >30 kDa (left), 3–30 kDa (center), and <3 kDa (right). The 3–30 kDa fractions were frozen with liquid nitrogen and lyophilized overnight in a vacuum centrifuge prior to mass spectrometer analysis.

purification technique (Friscia et al., 2008). TAA/XAD is time consuming but is viewed as an effective sample preparation technique for poorly preserved, conserved, or contaminated bone (Stafford et al., 1988, 1991; Minami and Nakamura, 2000, 2005; Minami et al., 2004; O'Keefe et al., 2009). Of the six RLB bones studied, five yielded sufficient 3–30-kDa collagen for ultrafiltration dates (Table 1; Fig. 2). The ultrafiltration and XAD dates for samples 1 and 2 were very similar, but samples 3 and 4 had ultrafiltration ages that were younger than those obtained with XAD by four and two standard deviations, respectively; the ultrafiltration age for sample 5 was four standard deviations older than the XAD result. It is unclear which of the discrepant radiocarbon dates is more accurate: Incomplete removal of radiocarbon-free tar would result in older radiocarbon dates, while soil contaminants (humics) are more likely to be young. Ultrafiltration cannot remove contaminants that are covalently crosslinked to the collagen, but this process is commonly associated with brown coloration of the collagen that was not observed in the 3–30-kDa fractions. Since Friscia et al. (2008) did not report stable isotope or elemental data, we cannot directly compare the extract quality between the two protocols.

This comparison showed no systematic age bias between the two methods, but the TAA/XAD technique did produce an age from sample 6, which yielded insufficient 3–30-kDa collagen for an ultrafiltration date. Thus, for RLB samples with poor collagen preservation, the TAA/XAD protocol should be used for isotopic analysis and radiocarbon dating. However, given the ease of sample preparation with the ultrafiltration method, we recommend it as an effective, faster, and simpler alternative to TAA/XAD for the well-preserved bones that constitute the great majority of samples from RLB.

PREVIOUS BONE RADIOCARBON DATES FROM RLB

O'Keefe et al. (2009) compiled a detailed and comprehensive list of all radiocarbon dates from Rancho La Brea. Here we list the bone ages from O'Keefe et al. (2009) (n = 148) and discuss the quality of these dates (Table 2). While the great majority are accurate or close to accurate, some are clearly seriously incorrect (bold entries in Table 2) and should not be used.

The most common sample preparation technique used to radiocarbon date bone at RLB involves the production of amino acids from

Table 1 A comparison of radiocarbon ages obtained using XAD-purified amino acids (Friscia et al., 2008) and collagen purified by ultrafiltration (Fuller et al., 2014) for the same six bones from Pit 91 at Rancho La Brea. No systematic offset was found, but the XAD procedure obtained datable amino acids from specimen 6 (LACMRLP R15406) and should be used in cases where there is little or poorly preserved collagen.

Sample no., museum catalogue no.	Study	Species	Collagen fraction analyzed	Collagen yield (%)	δ^{13}C (‰)	δ^{15}N (‰)	%C	%N	Atomic C:N	Uncalibrated ^{14}C age (yBP)	+/−
1 LACMRLP R16695	Friscia et al. (2008)	*S. fatalis*	XAD resin amino acids	—	—	—	—	—	—	27,350	120
	Fuller et al. (2014)	*S. fatalis*	3–30 kDa	3.8 ± 1.8	−18.0 ± 0.2	11.4 ± 0.1	42.5 ± 1.6	15.0 ± 0.3	3.31 ± 0.1	27,280	230
2 LACMRLP R34802	Friscia et al. (2008)	*S. fatalis*	XAD resin amino acids	—	—	—	—	—	—	28,170	160
	Fuller et al. (2014)	*S. fatalis*	3–30 kDa	5.8 ± 1.4	−18.2 ± 0.1	12.2 ± 0.2	42.6 ± 0.6	15.2 ± 0.1	3.26 ± 0.04	28,200	280
3 LACMRLP R42645	Friscia et al. (2008)	*S. fatalis*	XAD resin amino acids	—	—	—	—	—	—	44,300	850
	Fuller et al. (2014)	*S. fatalis*	3–30 kDa	3.8	−18.8	10.7	40.1	14.2	3.30	40,660	960
4 LACMRLP R49462	Friscia et al. (2008)	*C. dirus*	XAD resin amino acids	—	—	—	—	—	—	43,000	720
	Fuller et al. (2014)	*C. dirus*	3–30 kDa	4.4	−18.5	11.4	30.6	10.6	3.36	41,300	1,200
5 LACMRLP R14493	Friscia et al. (2008)	*C. dirus*	XAD resin amino acids	—	—	—	—	—	—	14,040	50
	Fuller et al. (2014)	*C. dirus*	3–30 kDa	6.4	−18.9	11.6	42.2	15.2	3.24	14,280	60
6 LACMRLP R15406	Friscia et al. (2008)	*C. dirus*	XAD resin amino acids	—	—	—	—	—	—	41,800	800
	Fuller et al. (2014)	*C. dirus*	Collagen could not be extracted	0	None	None	None	None	None	None	None

Abbreviation: LACMRLP, Specimen from Pit 91

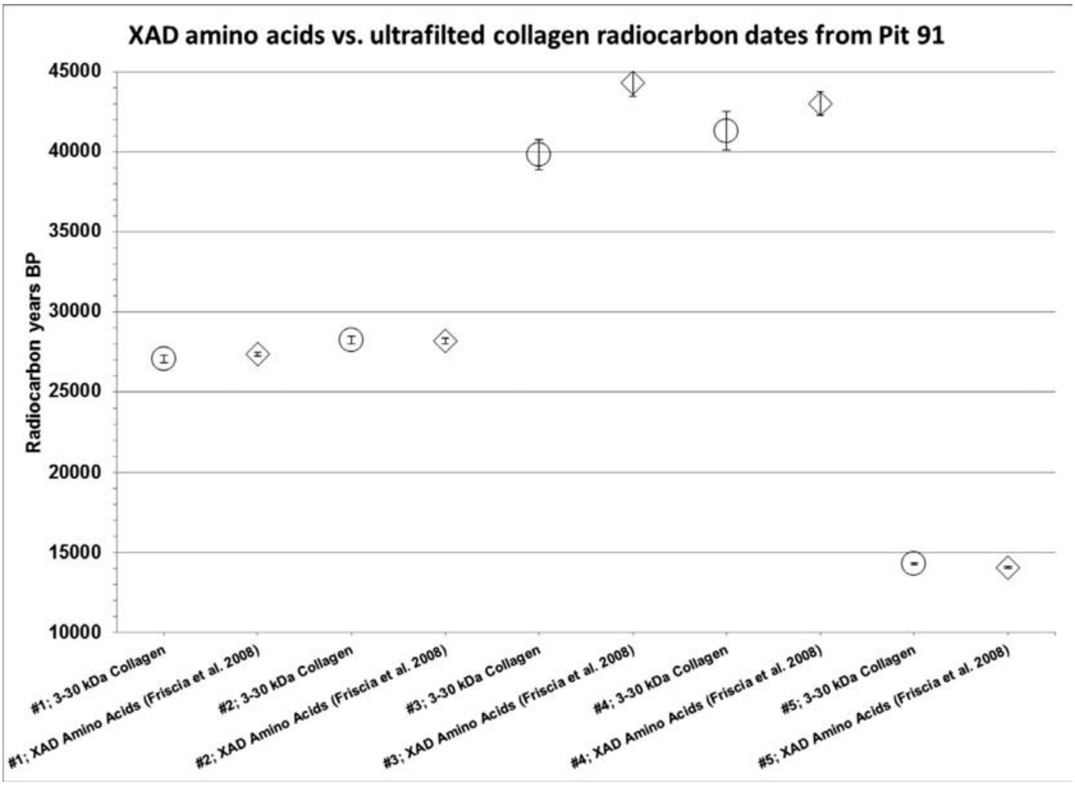

Figure 2 Graph contrasting ultrafiltrated collagen dates from Pit 91 with dates obtained for the same samples by the TAA/XAD resin purification technique that were reported by Friscia et al. (2008).

collagen by strong acid, followed by purification over ion exchange or XAD resins (Ho et al., 1969; Marcus and Berger, 1984; Friscia et al., 2008). Given the specificity of the resin purification procedures (Ho et al., 1969; Stafford et al., 1988, 1991), we believe that radiocarbon ages from RLB produced using these methods are generally accurate. Methods based on conversion of collagen to gelatin (Longin, 1971) were used by Fox-Dobbs et al. (2006) and O'Keefe et al. (2009) for RLB specimens. Our tests (Fuller et al., 2014:table A.1) found that extracts from these procedures typically retain some asphalt contamination that would add to the radiocarbon age, although the errors were relatively small (<~400 years). This suggests that dates on Longin-extracted gelatin (without the additional molecular weight selection steps used here) should be treated cautiously, but that the age biases may not be too serious, particularly for samples that are tens of thousands of years old. Some dates on inorganic fractions of bone (listed as bioapatite or carbonate) from Marcus and Berger (1984) are included in O'Keefe et al. (2009). Marcus and Berger concluded that these bone fractions are seriously contaminated by CO_2 exchange with the environment, and our own tests (Fuller et al., 2014:table A.2) yielded bone carbonate dates many thousands of years younger than collagen ages for the same specimens. Hence bioapatite or carbonate ^{14}C dates should never be used for RLB specimens (see Table 2). Finally, some limiting ("greater than") RLB radiocarbon ages from Marcus and Berger (1984) that are listed in O'Keefe et al. (2009) are from the early years of radiocarbon dating, and the limits are rather young (>~25–35 kyBP), reflecting high analytical blanks. These determinations are not inaccurate, but since limiting ages for bone collagen are now ~45–50 kyBP, redating these specimens would probably yield finite radiocarbon ages in some cases.

Currently, many radiocarbon facilities will not report a bone date unless the sample preparation yield and the extract composition (%C, %N, and C:N ratios) are within acceptable ranges. Given the high potential for asphalt contamination, adherence to strict quality control limits and reporting of collagen quality indicators is particularly important for bone dates from tar seep sites. Boundaries set by DeNiro (1985) of 2.9–3.6 for acceptable atomic C:N ratios for stable isotope studies are often cited in the radiocarbon literature (e.g., van Klinken, 1999; Higham et al.,

Table 2 List of all previously published bone radiocarbon ages by pit site for Rancho La Brea (after Marcus and Berger, 1984; Fox-Dobbs et al., 2006; Friscia et al., 2008; O'Keefe et al., 2009). Corrections are marked with an asterisk (*). All dates are assessed in terms of quality (amino acid dates = accurate; unfiltered collagen = possibly slightly older than true age; carbonates and bioapatites = not accurate and should not be used [bold]). Note the large range in radiocarbon dates for many pits. Reader is directed toward O'Keefe et al. (2009) for more details and information.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
Pit 3										
LACMHC 16124	***Canis dirus***	**E-3**	**22–25**	**Rt. humerus**	**Geo**	**9,860**	**550**	**Carbonates**	**Incorrect**	**Marcus and Berger (1984)**
LACMHC A642	*Smilodon fatalis*	C-4	7	Lt. femur	UCLA 1292B	12,650	160	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Z4360	*Equus* sp.	E-2	9	Terminal phalanx	ACRF833	12,820	90	Unfiltered collagen	Possibly slightly older than true age	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC A667	*S. fatalis*	E-3	6	Lt. femur	QC279	13,035	275	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC 6161	*S. fatalis*	E-3	6	Rt. humerus	QC414	13,745	275	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC 6166	*S. fatalis*	E-4	1–4.5	Lt. femur	QC401	13,820	840	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Z4450	*Equus* sp.	E-2	11.5	Terminal phalanx	ACRF830	14,250	40	Unfiltered collagen	Possibly slightly older than true age	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC Z6009	*Mammut americanum*	C-4*	14	Rt. ulna	UCLA1292T	14,350	175	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A883	*S. fatalis*	D-5	18.5	Rt. femur	ACRF827	14,360	35	Unfiltered collagen	Possibly slightly older than true age	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC A835	*S. fatalis*	C-4	11.5	Rt. femur	UCLA1292E	14,400	2,100	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC 1268	*M. americanum*	C-3	15	Lt. tibia	UCLA1292AA	14,430	200	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A398	*S. fatalis*	E-2	12	Lt. femur	UCLA1292C	14,500	190	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC 28501	*Equus* sp.	C-3	17.5	Terminal phalanx	ACRF832	14,745	40	Unfiltered collagen	Possibly slightly older than true age	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC K3407	*S. fatalis*	E-4	26	Rt. femur	UCLA1292K	19,300	395	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC K3407?	*S. fatalis*	E-4	26	Rt. femur	QC283	19,555	820	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A511	*S. fatalis*	E-5	22	Lt. femur	UCLA1292J	20,500	900	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A511	*S. fatalis*	E-5	22	Lt. femur	UCLA1292A	21,400	560	Amino acids	Accurate	Marcus and Berger (1984)

Total valid bone ^{14}C dates = 16 (+ 1 incorrect carbonate date)

Average age of Pit 3 based on bone radiocarbon dates = 15,491 ± 2,899 uncalibrated radiocarbon years BP

Range 12,650–21,400 uncalibrated radiocarbon years BP

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
Pit 4										
LACMHC 133499	*Ovis* sp.	Caved		Atlas	ACRF816	185	30	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC A1077	*S. fatalis*	B-5	18.5	Rt. femur	UCLA1292N	12,760	150	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Y6738	*Bison latifrons*	D-3+4	10.5	Lt. scapula	UCLA1292Q	13,500	170	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC T6101	*S. fatalis*	C-2	11.5	Tibia	UCLA1292L	15,200	800	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A657	*S. fatalis*		4.5–8.5	Lt. femur	UCLA1292R	19,800	300	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC 6152	*Equus* sp.	A-5	9	Lt. femur	QC412	22,000	1,200	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A846	*S. fatalis*	D-2+4	8	Lt. femur	UCLA1292G	26,700	900	Amino acids	Accurate	Berger and Libby (1968)
LACMHC 6167	*S. fatalis*	F-4+5	15	Lt. femur	QC386	26,995	4,000	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Y5664	*Bison antiquus*			Axis	UCLA1292Z	27,000	1,600	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A411	*S. fatalis*	D-2	15.5	Lt. femur	UCLA1292D	28,000	1,400	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Z4482	*Equus* sp.	D-2	8	Terminal phalanx	ACRF831	28,600	190	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC A768	*S. fatalis*	E-5*	23.5	Lt. femur	UCLA1292O	29,600	1,100	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A1176	*S. fatalis*	F-4+5	18	Lt. femur	UCLA1292S	35,500	2,200	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A641	*S. fatalis*	F-4+5	20–22	Lt. femur	UCLA1292M	>36,000		Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 14										
Average age of Pit 4 based on bone radiocarbon dates = 23,804 ± 7,142 uncalibrated radiocarbon years BP										
Range 12,760–>36,000 uncalibrated radiocarbon years BP										
Pit 10										
LACMHC 133	*Ursus arctos*		5.5	Lt. femur	QC916R	5,270	155	Unfiltered collagen	Accurate	Marcus and Berger (1984)
LACMHC 1323	*Homo sapiens*	F-10	6–9	Lt. femur	UCLA1292BB	9,000	80	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC 6945	*Equus* sp.	F-11	4–5.5	Lt. femur	UCLA1292CC	15,700	530	Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 3										
Average age of Pit 10 based on bone radiocarbon dates = 9,990 ± 5,285 uncalibrated radiocarbon years BP										
Range 5,270–15,700 uncalibrated radiocarbon years BP										
Pit 13										
LACMHC 6156	*B. antiquus*	F-11	20–23	Rt. femur	QC420	14,310	920	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A797	*S. fatalis*	E-11	11	Lt. femur	UCLA1292F	14,950	430	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A4436	*S. fatalis*	F-10	14.5	Rt. femur	UCLA1292I	15,300	200	Amino acids	Accurate	Marcus and Berger (1984)

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
LACMHC A1089	*S. fatalis*	G-10	13	Rt. femur	QC339	15,360	480	Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 4										
Average age of Pit 13 based on bone radiocarbon dates = 14,980 ± 482 uncalibrated radiocarbon years BP										
Range 14,310–15,360 uncalibrated radiocarbon years BP										
Pit 16										
	C. dirus		**8–12**	**Humerus**	**GEO**	**10,710**	**320**	**Carbonates**	**Incorrect**	**Marcus and Berger (1984)**
LACMHC Y2451	*B. antiquus*		3–6*	Metacarpal	QC371	12,275	775	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Y5611	*B. antiquus*		12–14	Rt. metatarsal	QC278	24,400	535	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC X9982	*Canis latrans*	Caved		Rt. ulna	ACRF814	29,860	190	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC Y5495	*B. antiquus*		3–6	Lt. metacarpal*	QC277II	>32,850		Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 4 (+ 1 incorrect carbonate date)										
Average age of Pit 16 based on bone radiocarbon dates = 22,178 ± 9,000 uncalibrated radiocarbon years BP										
Range 12,275–>32,850 uncalibrated radiocarbon years BP										
Pit 60										
LACMHC 6139	***Paramylodon harlani***	**F-11**	**12**	**Rib**	**QC361**	**7,600**	**195**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
LACMHC 6124	***Equus* sp.**	**C-12**	**14**	**Rt. tibia**	**QC410**	**22,330**	**1,060**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
LACMHC 6139	*P. harlani*	F-11	12	Rib	QC361	23,420	350	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A4435	*S. fatalis*	C-10	9–12	Rt. femur	UCLA1292H	23,700	600	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC 6124	*Equus* sp.	C-12	14	Rt. tibia	QC410	24,900	3,360	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Z4579	*Equus* sp.	E-12	18	Lt. metatarsal	ACRF826	26,320	240	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC A686	*S. fatalis*		8–9	Lt. femur	QC280	27,900	2,700	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC Z4767	***Equus* sp.**		**9–9.5**	**Lt. metacarpal***	**QC365**	**>24,460**		**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
LACMHC Z4767	*Equus* sp.		9–9.5	Lt. metacarpal*	QC365	>28,850		Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 6 (+ 3 incorrect bioapatite dates)										
Average age of Pit 60 based on bone radiocarbon dates = 25,248 ± 1,874 uncalibrated radiocarbon years BP										
Range 23,420–>28,850 uncalibrated radiocarbon years BP										

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
Pit 61-67										
LACMHC V5203	*Canis petrolei* (= *familiaris*)	Caved		Mandible	ACRF829	6,360	30	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMHC 6129	*S. fatalis*	B-9	18–20	Rt. humerus*	QC413	11,130	275	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A979	*S. fatalis*	F-10	16–18.5	Lt. femur	QC302A	11,640	135	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A979	*S. fatalis*	F-10	16–18.5	Lt. femur	QC302B	11,980	260	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A498	*S. fatalis*	D-16	10	Lt. femur	UCLA1292X	12,000	125	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A503	*S. fatalis*	H-10	15–20	Lt. femur	UCLA1292Y	12,200	200	Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 6										
Average age of Pit 61-67 based on bone radiocarbon dates = 10,885 ± 2,248 uncalibrated radiocarbon years BP										
Range 6,360–12,200 uncalibrated radiocarbon years BP										
Pit 77										
LACMHC A977	*S. fatalis*		9–11	Lt. femur	UCLA1292W	28,200	980	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A439	*S. fatalis*	F-10	18.5–21	Lt. femur	UCLA1292V	31,300	1,350	Amino acids	Accurate	Marcus and Berger (1984)
LACMHC A465	*S. fatalis*	G-11	13–15	Lt. femur	UCLA1292U	33,100	600	Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 3										
Average age of Pit 77 based on bone radiocarbon dates = 30,867 ± 2,479 uncalibrated radiocarbon years BP										
Range 28,200–33,100 uncalibrated radiocarbon years BP										
Pit 81										
LACMHC 6131	***Equus* sp.**	**Caved**		**Tibia**	**QC405**	**10,940**	**510**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
LACMHC 6131	*Equus* sp.	Caved		Tibia	QC405	14,415	3,250	Amino acids	Accurate	Marcus and Berger (1984)
Total valid bone ^{14}C dates = 1 (+ 1 incorrect bioapatite date)										
Pit 91										
LACMHC Z3245	***Equus* sp.**		**6–8**	**Lt. radius**	**QC384**	**8,850**	**455**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
LACMRLP R14493	*C. dirus*	L-11	8.5–9	Rt. radius	SR-5272	14,040	50	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R32497	*C. dirus*	H-7	10.5–11	Lt. tibia	SR-5444	23,060	90	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R21648	*S. fatalis*	M-11	7.5–8	Rt. astragalus	SR-5822	24,930	240	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R51288	*S. fatalis*	I-6	8.5–8.8	Rt. humerus	UCLA1738A	25,100	850	Amino acids	Accurate	Marcus and Berger (1984)
LACMRLP R51286	*S. fatalis*	L-10	8–8.3	Tibia	UCLA1738F	25,100	1,100	Amino acids	Accurate	Marcus and Berger (1984)

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
LACMRLP R25591	*S. fatalis*	L-10	8.5–9	Lt. tibia	SR-5276	25,710	140	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R27932	*S. fatalis*	L-10	9.5–10	Caudal vertebrae	SR-5588	25,740	100	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R36301	*S. fatalis*	L-11	9.5–10	Lt. calcaneum	SR-5826	26,120	280	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R35212	*S. fatalis*	L-10	10.5–11	Lt. humerus	SR-5825	26,150	280	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R29708	*C. dirus*	I-6	10.5–11	Lt. radius	SR-6146	26,840	120	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R22719	*S. fatalis*	H-7*	8.5–9	Lt. humerus	SR-5449	27,220	140	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R19258	*Arctodus simus*	N-11	9	Lt. humerus	ACRF820	27,330	140	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMRLP R16695	*S. fatalis*	I-6	9.5–10	Rt. radius	SR-5586	27,350	120	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R22420	*C. dirus*	I-6	8.5–9	Lt. radius	SR-6136	27,460	130	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R16837	*C. dirus*	M-4	7.5–8	Lt. radius	SR-5445	27,560	130	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R48706	*S. fatalis*	L-11	11.5–12	Rt. astragalus	SR-6004	27,620	150	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R28227	*C. dirus*	H-7	9.5–10	Rt. humerus	SR-5274	27,660	120	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R54035	*C. dirus*	I-6	12.5–13	Rt. radius	SR-6143	27,680	140	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R45830	*S. fatalis*	L-10	11.5–12	VIII thoracic vertebrae	SR-6003	27,820	150	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R50699	*C. dirus*	I-6	12–12.5	Lt. radius	SR-6142	27,860	140	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R50952	*C. dirus*	I-6	11.5–12	Rt. radius	SR-6140	27,890	130	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R36962	*C. dirus*	M-11	10.5–11	Rt. humerus	SR-5589	28,070	130	XAD purified amino acids	Accurate	Friscia et al. (2008)

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
LACMRLP R54077	*A. simus*	H-9	13.6	Rt. metatarsal	ACRF834	28,130	330	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMRLP R23755	*S. fatalis*	H-6	8.5–9	Lt. tibia	SR-5823	28,150	360	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R34802	*S. fatalis*	H-8	10.5–11	Rt. humerus	SR-5275	28,170	160	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R22376	*S. fatalis*	I-6	8.5–9	Rt. radius	SR-6000	28,240	160	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R39006	*C. dirus*	I-6	11.5–12	Lt. radius	SR-6141	28,270	130	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R50546	*C. dirus*	M-11	11.5–12	Lt. tibia	SR-5271	28,310	170	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R26134	*S. fatalis*	I-7	9.5–10	Rt. tibia	SR-5587	28,320	140	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R30312	*C. dirus*	I-6	11–11.5	Lt. radius	SR-6144	28,330	200	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R22385	*Nothrotheriops shastensis*	I-11	10.5–11	Lt. calcaneum	SR-6713	28,350	240	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R42063	*A. simus*	F-11	11.5	VI cervical vertebra	ACRF819	28,350	470	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
LACMRLP R23621	*C. dirus*	I-7	8.5–9	Lt. femur	SR-5447	28,360	160	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R27065	*C. dirus*	I-6	9–9.5	Lt. radius	SR-6139	28,400	130	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R41785	*C. dirus*	I-6	9.5–10	Lt. radius	SR-6137	28,430	140	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R39292	*C. dirus*	I-7	10.5–11	Rt. radius	SR-5827	28,510	380	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R38722	*N. shastensis*	K-8	11.5–12	Rt. astragalus	SR-6712	28,530	240	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R29823	*C. dirus*	I-6	10.5–11	Rt. humerus	SR-5824	28,580	380	XAD purified amino acids	Accurate	Friscia et al. (2008)

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
LACMRLP R36388	*N. shastensis*	I-8	11–11.5	Lt. cuboid	SR-6711	28,590	240	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R39320	*C. dirus*	I-7	11–11.5	Rt. humerus	SR-6002	28,620	200	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R22811*	*Puma concolor*	H-7	8.5–9	Lt. humerus	SR-6714	28,650	250	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R54033	*P. concolor*	I-11	10–10.5	Lt. radius	SR-6715	28,650	240	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R51289	*S. fatalis*	F-11	8.1–8.5	Rt. femur	UCLA1738C	29,100	1,200	Amino acids	Accurate	Marcus and Berger (1984)
	S. fatalis	L-5	6–7	Sacrum	UCLA1718	30,800	600	Amino acids	Accurate	Marcus and Berger (1984)
LACMRLP R51285	*S. fatalis*	M-3+4	7.2–7.5	Rt. femur	UCLA1738D	32,600	2,800	Amino acids	Accurate	Marcus and Berger (1984)
LACMRLP R51287	*S. fatalis*	N-11	8.8–9	Lt. humerus	UCLA1738B	33,000	1,750	Amino acids	Accurate	Marcus and Berger (1984)
LACMRLP R34667	*C. dirus*	M-11	9.5–10	VII thoracic vertebra	SR-6001	35,800	400	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R37351	*C. dirus*	L-11	10.5–11	Rt. humerus	SR-5273	39,090	580	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R18896	*C. dirus*	M-4	7.5–8	Lt. radius	SR-6138	41,010	580	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R15406*	*C. dirus*	M-4	7–7.5	Rt. tibia	SR-5999	41,800	800	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R39004	*C. dirus*	I-6	11.5–12	Rt. humerus	SR-5446	41,940	790	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R49462	*C. dirus*	H-7	11.5–12	Lt. innominate	SR-5591	43,000	720	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R42645	*S. fatalis*	H-8	11.5–12	Lt. II metacarpal	SR-5590	44,300	850	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R49462*	*C. dirus*	H-7	11.5–12	Lt. innominate	SR-6005	44,600	1,100	XAD purified amino acids	Accurate	Friscia et al. (2008)
LACMRLP R15199	*C. dirus*	M-4	6.5–7	Lt. ulna	SR-5821	44,650	2,830	XAD purified amino acids	Accurate	Friscia et al. (2008)

Total valid bone ^{14}C dates = 55 (+ 1 incorrect bioapatite date)
Average age of Pit 91 based on bone radiocarbon dates = 29,890 ± 5,948 uncalibrated radiocarbon years BP
Range 14,040–44,650 uncalibrated radiocarbon years BP

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
Pit 2051										
UCMP	***Equus* sp.**	**I-3**	**6**	**Femur**	**QC430**	**6,160**	**530**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
UCMP	*S. fatalis*	G-5	6.8	Humerus		13,950	1,570	Amino acids	Accurate	Marcus and Berger (1984)
UCMP	***Camelops hesternus***	**D-7**	**17**	**Metacarpal**	**QC442**	**17,630**	**1,400**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
UCMP	*S. fatalis*	D-7	16	Humerus	QC435	18,475	320	Amino acids	Accurate	Marcus and Berger (1984)
UCMP 148877	*Gymnogyps californianus*			Rt. ulna		19,030	280	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
UCMP 24334	*C. dirus*			Skull		19,380	100	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP	*P. harlani*	D-13	15	Rib	QC381	19,480	550	Amino acids	Accurate	Marcus and Berger (1984)
UCMP 24346	*C. dirus*			Skull		19,580	190	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP 24314	*C. dirus*			Skull		19,640	100	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP	*C. hesternus*	D-7	17	Metacarpal	QC442	20,300	1,750	Amino acids	Accurate	Marcus and Berger (1984)
UCMP	***S. fatalis***	**G-5**	**6.8**	**Humerus**	**QC436**	**20,410**	**2,450**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
UCMP	*P. harlani*	T-22	8	Rib	QC390	20,450	460	Amino acids	Accurate	Marcus and Berger (1984)
UCMP	***S. fatalis***	**D-7**	**16**	**Humerus**	**QC435**	**20,900**	**2,700**	**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
UCMP 148880	*G. californianus*			Rt. ulna	UCMP	21,260	370	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
UCMP	*S. fatalis*	J-13	11	Rib	QC431	22,355	3,400	Amino acids	Accurate	Marcus and Berger (1984)
UCMP 148878	*G. californianus*			Lt. ulna	UCMP	22,710	450	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
UCMP	*P. harlani*	N-21	5	Rib	QC443	22,890	500	Amino acids	Accurate	Marcus and Berger (1984)
UCMP 24332	*C. dirus*			Skull	UCMP	23,080	150	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP 24346	*C. dirus*			Skull	UCMP	23,110	160	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP 24319	*C. dirus*			Skull	UCMP	23,600	330	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP	*S. fatalis*	H-19	15	Femur	QC440	23,850	1,200	Amino acids	Accurate	Marcus and Berger (1984)

Table 2 Continued.

Catalog no.	Taxon	Grid	Depth (feet)	Element	Institution sample no.	Uncalibrated ^{14}C age (yBP)	+/−	Bone fraction	Assessment of ^{14}C date	Reference
UCMP 24345	*C. dirus*			Skull	UCMP	24,000	340	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP 148875	*G. californianus*			Rt. ulna	UCMP	24,230	550	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
UCMP 148885	*G. californianus*			Rt. ulna	UCMP	24,900	600	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
UCMP 24343	*C. dirus*			Skull		25,240	400	Unfiltered collagen	Possibly slightly older than true date	O'Keefe et al. (2009)
UCMP	*Equus* sp.	I-3	6	Femur	QC430	26,140	2,200	Amino acids	Accurate	Marcus and Berger (1984)
UCMP	*S. fatalis*	Q-19	16	Ulna*	QC438	28,250	1,030	Amino acids	Accurate	Marcus and Berger (1984)
UCMP	***S. fatalis***	**Q-19**	**16**	**Ulna**	**QC438**	**>29,760**		**Bioapatite**	**Incorrect**	**Marcus and Berger (1984)**
UCMP 148881	*G. californianus*			Lt. ulna		30,700	1,300	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
UCMP 148876	*G. californianus*			Rt. ulna		30,900	1,300	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
UCMP 148884	*G. californianus*			Rt. ulna		31,000	1,300	Unfiltered collagen	Possibly slightly older than true date	Fox-Dobbs et al. (2006)
Total valid bone ^{14}C dates = 26 (+ 5 incorrect bioapatite dates)										
Average age of Pit 2051 based on bone radiocarbon dates = 23,019 ± 4,095 uncalibrated radiocarbon years BP										
Range 13,950–31,000 uncalibrated radiocarbon years BP										
Pit A										
*LACMHC 116051	*C. latrans*			Lt. ulna*	ACRF815	46,800	2,500	Unfiltered collagen	Possibly slightly older than true date	Coltrain et al. (2004) protocol in O'Keefe et al. (2009)
Total valid bone ^{14}C dates = 1										

Abbreviations: ACRF, Archaeological Center Research Facility, University of Utah; LACMHC, Los Angeles County Museum Hancock Collection; LACMRLP, Specimen from Pit 91; Lt., left; QC, Queen's College; Rt., right; SR, Stafford Research; UCLA, University of California, Los Angeles; UCMP, University of California Museum of Paleontology.

2006; Brock et al., 2007; Talamo and Richards, 2011), but C:N ratios for ultrafiltered collagen from uncontaminated bones are almost always within the range 3.2–3.5. Hence we suggest that collagen C:N ratios greater than 3.5 in specimens from tar seeps should be viewed as suspicious: Excess carbon from residual petroleum contamination is likely present and will potentially skew the radiocarbon ages older than the true age.

PIT AVERAGING AT RLB

Due to the difficulties and cost of directly radiocarbon dating skeletal elements, only 138 reliable bone radiocarbon dates have been produced from RLB (Table 2). Thus, in some cases researchers have been forced to assign a general age to unknown specimens based on the average of the few radiocarbon dates available for a given pit (Coltrain et al., 2004; Chamberlain et al., 2005; Bump et al., 2007; Fox-Dobbs et al., 2007; Meachen and Samuels, 2012; Prothero et al., 2012), a practice known as "pit averaging."

Unfortunately, this procedure can lead to serious errors of chronology and interpretation, because unlike most paleontological or archaeological sites, tar seeps do not have a well-defined stratigraphic context: The liquid and gaseous nature of the seeping hydrocarbons plus churning by trapped animals results over time in separation and admixture of skeletal elements (Woodward and Marcus, 1973; Stock, 1992; Friscia et al., 2008; O'Keefe et al., 2009). While average ^{14}C pit ages may allow the detection of gross temporal trends, bones from a single pit can have very large age variations, and without direct radiocarbon measurements it is dangerous to assume that specimens found near each other date to a similar interval. For example, the best dated deposit at RLB is Pit 91, for which a total of 55 bone radiocarbon ages have been measured (Table 2). While ~60% of these fall between 27 and 29 kyBP, there is an enormous overall range of 14–44 kyBP, and some of the oldest dates represent bones recovered from the shallowest depths within the pit (Friscia et al., 2008). Similarly, a recent excavation (Project 23 Box 1) has yielded bone dates ranging from 33 kyBP to greater than 43 kyBP (unpublished data) from a small deposit roughly 1 × 1 × 2 m. Since age spreads of this magnitude can mix samples from very different climate regimes and potentially blur or even obliterate important temporal changes in morphological or isotopic data, radiocarbon dates should be directly obtained from RLB bone specimens wherever possible. The diminished cost and increased speed of the method described here will facilitate the development of better chronologies for RLB and will thereby help shed light on how species have adapted to climate change and on the causes of extinction and survival across the Pleistocene–Holocene transition.

CONCLUSIONS

We have reviewed a novel ultrafiltration method for asphalt removal from bone collagen that is simpler and less expensive than techniques used previously. Collagen quality indicators suggest that the new technique removes hydrocarbon contamination efficiently, and comparison of ultrafiltration and XAD radiocarbon dates from the same bones found no systematic offsets, indicating that the two methods are likely comparable in terms of accuracy. The protocol is summarized as follows:

1. Crush bones to 1–2-mm fragments.
2. Sonicate bone fragments repeatedly in 2:1 toluene:methanol solution until clear, sonicate in methanol (1 hour), sonicate in Milli-Q water (1 hour). Keep the temperature of sonication bath ≤45°C.
3. Demineralize bone fragments in 0.5 N HCl for 24–36 hours at room temperature.
4. Rinse collagen pseudomorph with Milli-Q water to pH >3.
5. Gelatinize in 0.01 N HCl at 75°C ~14 hours.
6. Ultrafilter at 30 kDa.
7. Discard the >30 kDa fraction; ultrafilter the <30 kDa fraction at 3 kDa.
8. Discard the <3 kDa fraction; lyophilize the 3–30 kDa fraction.
9. Record percent collagen yield and check collagen quality (δ^{13}C, δ^{15}N, %C, %N, and C:N).
10. If collagen is of good quality, process for radiocarbon dating.

We have assessed previous bone radiocarbon measurements from RLB, and we conclude that while the majority are likely accurate or close to accurate, ^{14}C ages based on bone carbonate or bioapatite are seriously in error and should not be used. Given that there is little defined stratigraphy in the pits at RLB, the dating of bones by pit averaging should be avoided, and direct radiocarbon dating of bone should be carried out wherever possible. Finally, while this protocol was specifically designed to extract collagen from samples at Rancho La Brea, we hope that it can also be used at other localities where bones have been recovered from tar seeps: These include sites in Cuba (Suarez and Olson, 2003), Venezuela (Prevosti and Rincón, 2007), Ecuador (Lindsey, 2011), Peru (Campbell, 1973), and Ukraine (Kuc et al., 2012).

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New Technique to Remove Asphalt from Microfossil-rich Matrix from Rancho La Brea

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ABSTRACT. Asphalt-preserved fossils present specific cleaning and preparation challenges not encountered with permineralized fossils. Asphalt is a complex mixture of mainly large hydrocarbon molecules that are totally insoluble in water and only sparingly soluble in many organic solvents. This study attempts to develop a faster and better procedure for dissolving asphalt, ideally making use of cheaper and greener solvents. One of the more promising of these is biodiesel. Pure biodiesel, or B100, is a liquid consisting of methyl esters of fatty acids produced by refining vegetable oil triglycerides and having similar properties to (petroleum-derived) diesel fuel. While biodiesel is not an effective asphalt solvent at room temperature, it becomes very effective when heated to temperatures greater than 70°C. We here provide a detailed guide and recommendations on the use of hot biodiesel as a solvent to process asphalt-impregnated fossiliferous matrix.

INTRODUCTION

The asphalt seeps at Rancho La Brea, located in Hancock Park, Los Angeles, California, are one of the world's richest terrestrial late Pleistocene fossil localities (e.g., Akersten et al., 1983; Shaw and Quinn, 1986; Stock, 1992) and present a unique window on the world at the end of the last ice age. Intensive collection at intervals during the past century has resulted in the recovery of hundreds of thousands of exceptionally well preserved mammalian bones ranging from saber-toothed cats to squirrels, plus large quantities of other vertebrates, invertebrates, and plant remains (Stock, 1992). Typical Rancho La Brea fossils are composed of unaltered organic material—bone, plant remains, shells, and insect exoskeletons. Extraordinary preservation of Rancho La Brea fossils is due principally to asphalt impregnation that helps protect the material from diagenetic changes. Vertebrate fossils from Rancho La Brea rarely display permineralization.

Early excavations between 1905 and 1915 concentrated on the recovery of larger and more spectacular fossil plants and animals; smaller organisms and important information pertaining to geology and taphonomy were rarely collected or documented. Pit 91 was reopened in 1969 by the Los Angeles County Museum of Natural History to rectify these collecting biases. New excavation techniques were developed in accordance with established paleontological and archaeological methods to sample intensely and carefully record biological and geological data (Shaw, 1982). A main goal of the excavation was the recovery of microvertebrate fossils, which have been shown to provide a wealth of information about past environments and ecosystems. The process of isolating large numbers of tiny and potentially fragile asphalt-preserved fossils presents specific cleaning and preparation challenges that are not encountered with permineralized fossils.

Asphalt comprises a complex mixture of hydrocarbon molecules of varying size and chemical makeup. Although asphalt composition can vary substantially between sources and even over time, in general it is composed of relatively large (>400 Da), nonpolar, highly condensed aromatic molecules that are totally insoluble in cold water (polarity index of 10) and only slightly soluble in nonpolar solvents like pentane (0.0). Historically, the asphalt-impregnated matrix was treated in a vapor degreaser unit at 73.3°C using 1,1,1-trichloroethane (methyl chloroform) as solvent (Shaw, 1982). Trichloroethane is highly effective in liberating the smaller fossils from the asphalt but has several significant drawbacks: It is hazardous to human health and the environment, difficult to dispose of, and potentially harmful to the earth's ozone layer. Trichloroethane

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production has been phased out in most of the world under the terms of the Montreal Protocol, an international treaty designed to protect the ozone layer by phasing out the production of numerous substances believed to be responsible for ozone depletion. To maintain the present processing methods, it was necessary to find a less hazardous alternative solvent that would be suitable to replace trichloroethane. Ideal solvents for asphalt should be slightly polar, such as dichloromethane (polarity index of 3.1), diethyl ether (2.8), or toluene (2.4), but all of these also have significant environmental and/or health and safety issues. Biodiesel is a liquid fuel generated by the hydrolysis and methylation of common vegetable oils, resulting in a series of fatty acid methyl esters of chain length C_{12}–C_{20}. With its long *n*-alkyl chains and single ester group, B100 has an overall polarity index of ca. 4. Thus asphalt should be moderately soluble in biodiesel.

The term "biodiesel" arises because of the similarity in physical properties and combustibility to diesel fuel, making it a direct replacement in diesel engines. However, unlike petroleum-derived diesel fuel, biodiesel is entirely renewable, nontoxic, nonvolatile, and rapidly degraded in the environment. It is flammable but, with a flash point greater than 130°C, it is quite difficult to ignite. Its low volatility also minimizes emissions that are problematic for air quality and for those using it. These characteristics make it a very environmentally friendly liquid, though it is not typically used as a solvent. As a commodity fuel, biodiesel is also cheaper than most industrial solvents. Unfortunately, the dissolution kinetics of asphalt are also problematical, as the relatively high molecular weight and aromatic character of asphaltene molecules cause them to dissolve very slowly. Dissolution rate favors solvents of smaller molecular size; accordingly, asphalt dissolves more rapidly in dichloromethane and trichloroethane than in toluene or most other hydrocarbon solvents. With its relatively large molecular size, biodiesel will dissolve asphalt exceedingly slowly at room temperature. However, dissolution rate is an exponential function of temperature, and—in our tests of asphalt dissolution—roughly doubled about every 10°C. Thus by heating the biodiesel to greater than 70°C, we were able to achieve sufficiently rapid dissolution to make this a practical choice.

MATERIALS AND METHODS

The fossiliferous asphaltic-impregnated sediment used in this study comes from Project 23. Project 23 is an ongoing excavation of 16 asphaltic fossiliferous deposits recovered from the western edge of Hancock Park in 2006 (Harris et al., 2011). The deposits were exposed, crated into 23 wooden boxes, and transported to a nearby, enclosed compound for future excavation of the fossils. Typical fossil deposits consist of dense bone accumulations surrounded by asphalt-saturated fine to coarse sand and coarse sand lenses with subangular to rounded pebbles and cobbles. Because matrix composition affects processing time and ease, we separate matrix by sediment type—focusing on asphaltic fossiliferous matrix rather than sterile sediment.

The technique for the biodiesel de-asphalting operation is based on our own observations and experiments. The methods and results presented here should be viewed as a case study rather than a definitive process.

While biodiesel itself is relatively nontoxic, the fumes emitted after the introduction of asphaltic matrix and heat may be hazardous. There are no guidelines for exposure to a mixture of heated biodiesel and asphalt, but existing literature on exposure to bitumen fumes and, separately, cooking oil fumes suggests respiratory protection is warranted (Binet et al., 2002; DHHS/NIOSH, 2003; Pan et al., 2008). Our process also involves a second solvent, *n*-propyl bromide (1-bromopropane), a known neurotoxin and possible carcinogen (DHHS/NIOSH, 2013). Accordingly we advocate the use of a half-face respirator with organic vapor cartridges, gloves (we use 11-mm nitrile gloves), a chemical-resistant apron, safety glasses or goggles, and a well-ventilated space in which to perform the operation. Biodiesel heated to around 80°C (175°F) is hot but is well below temperatures used in deep frying (175°C–200°C/350°F–375°F). At our advocated working temperatures, a gloved hand can be immersed briefly without burns; nevertheless, hot biodiesel and drum heaters should be treated with caution.

To set up the biodiesel de-asphalting station, place 8-gallon (30-L) metal drums in a plastic chemical spill tray large enough to contain the amount of biodiesel in the drums. The chemical spill tray should be set to a comfortable working height, for example, on top of a wood pallet or cinder blocks. Additionally, placing the heated biodiesel wash drum on paving bricks will insulate the hot drum from the plastic spill tray. Position the drum heater on the lower half of the metal drum and adjust so it sits snuggly against the outside of the drum (Fig. 1). Magnetic clips can be used on the outside of the drums to hold matrix information tags and are easily moved through steps of the processing. We found that partially filling the metal drums with 5 gallons (19 L) of biodiesel B100 works best.

Because biodiesel is quite involatile, it does not air-dry, and so cleaned matrix will remain solvent-wet for a very long time. To remove this oily residue, we currently use a rinse with room temperature *n*-propyl bromide that also removes any remaining asphalt. Ethanol also works well for removing biodiesel but is both more volatile

Figure 1 Eight-gallon metal drum with drum heater attached in chemical spill tray.

and more flammable. A solvent rinse station is set up adjacent to the biodiesel processing station rinse station and consists of a plastic chemical spill tray with up to five 8-gallon metal drums each containing 2 gallons of *n*-propyl bromide (see "Processing Methodology" below).

We provide a list of recommended materials in Table 1 and a materials resource list in the Appendix. Some of these items may be purchased, but others will have to be fabricated (e.g. 5-gallon (19-L) metal buckets with screened bottoms).

PROCESSING METHODOLOGY

Here we present a detailed guide to processing asphalt-impregnated sediment with biodiesel, but see Table 2 for an abridged version. Our multistep process involves soaking and agitating asphaltic matrix in hot biodiesel followed by rinsing in room temperature *n*-propyl bromide.

Fill an 8-gallon steel wash drum with 5 gallons of biodiesel B100 and heat to between 80°C and 90°C. Biodiesel will begin to emit visible fumes around 100°C. Drum heaters with adjustable heat and thermostat settings are used to heat biodiesel and maintain a relatively constant temperature. Use of a thermostat is essential to prevent accidental overheating of the biodiesel, which would then present a significant fire risk. A thermometer or thermocouple is also used to monitor the biodiesel temperature as it heats. Drum heater settings for desired temperature will

Table 1 List of materials for setting up a biodiesel processing station.

Item	Purpose
Biodiesel B100	Solvent
n-propyl bromide	Solvent
5-Gallon metal buckets with stainless steel 20-mesh screened bottoms	Screened washing containers
8-Gallon metal drums with lids	Washing tanks
Containment tray	Chemical spill containment
Drum heater with adjustable temperature and thermostat to fit around washing drum	Heat biodiesel
Drying rack to hold 5-gallon buckets	Drying processed condensate
Immersible thermometer	Measure biodiesel temperature, calibrate drum heaters
Hanging scale	Weigh matrix and condensate (optional but handy for quantifying reduction)
Magnetic clips	Attach matrix identification labels/tags to wash drums
55-Gallon drums with open tops and lids	Store liquid and solid biodiesel and *n*-propyl bromide solvent waste

vary depending on wattage of the band heater, amount of biodiesel to be heated and ambient temperature.

Matrix is processed in batches of 8–10 pounds (3.6–4.5 kg). We have found that this is a manageable amount of matrix to handle physically and ensures a greater solvent to matrix ratio with faster dissolution of the asphalt. The weighed matrix is placed in a screened bucket. These can be constructed by removing the bottom of a 5-gallon metal bucket and attaching stainless steel No. 20 mesh screen (850-µm openings) with machine screws and a large-diameter hose clamp (Fig. 2). Gently lower the screened bucket with matrix into the heated biodiesel wash drum. We recommend agitating slowly by rotating the bucket back and forth to saturate the matrix thoroughly and start dissolution. Agitate once or twice more depending on rate of breakdown until most of the matrix is disaggregated and sand and larger clasts and fossils are visible on the bottom of the bucket when lifted out of the biodiesel. When the majority of asphalt has dissolved and fine sediment (<No. 20 mesh) has been screened out, pull the bucket out of the solvent and angle it within the opening of the wash drum so that the bucket is stable, and allow it to drain completely.

Matrix composition affects the speed and ease of processing. We have observed that highly asphaltic sand matrix will dissolve and disaggregate rapidly in as little as 10–15 minutes. When the mineral matrix contains appreciable silt and/or clay, processing time slows considerably, requiring more agitation and, when necessary, manual break down of sediment clumps. Stubborn fine-grained matrix benefits from overnight soaking in solvent. Other factors that influence processing time are the degree of asphalt oxidation (weathering), ratio of matrix to solvent, and loading of solvent with dissolved asphalt.

Following soaking in biodiesel, the concentrate goes through five sequential rinses of *n*-propyl bromide, each in a separate drum. The number of *n*-propyl bromide wash drums isn't fixed. Fewer would work, too, but would require more frequent replacement of the biodiesel and asphalt-saturated *n*-propyl bromide. After the concentrate has been rinsed, the 5-gallon screened bucket is hung on a rack to dry. When concentrate has dried it is bagged and weighed, gravel-size clasts are removed, and it is stored in 1-gallon (4-L) cans. Depending on the nature of the matrix, a bucket of 4–5 gallons (15–19 L) of asphaltic matrix will reduce to a gallon or less

Table 2 Guide to processing asphalt-impregnated fossiliferous matrix in biodiesel.

Processing guide
1. Fill wash drums with 5 gallons of biodiesel.
2. Heat biodiesel to 80°C.
3. Weigh out 8–10 pounds of asphaltic matrix in 5-gallon screened bucket.
4. Slowly immerse bucket and matrix in heated biodiesel and agitate by gently rotating back and forth.
5. Soak matrix. Check after 15–30 minutes for dissolution. Agitate again if necessary.
6. Pull bucket out to drain when asphalt has dissolved and matrix has disaggregated. Drain completely.
7. Move bucket with concentrate through series of *n*-propyl bromide rinse drums. Agitate, and allow to soak in each drum.
8. Remove bucket with concentrate from final *n*-propyl rinse and hang to dry.

Figure 2 Five-gallon metal-screened bucket is constructed by removing the bottom of the bucket and attaching stainless steel 20-mesh screen with machine screws and a large-diameter hose clamp.

of concentrate (10%–35% of starting weight). A batch of 5 gallons of biodiesel can be used to de-asphalt about 10 gallons (38 L) or 80–100 pounds (36–45 kg) of asphaltic matrix before becoming too saturated and viscous.

Maintenance of the processing operation entails removing the fine sediment waste that builds up on the bottom of wash drums and replacing the asphalt-saturated solvents when they are no longer effective. Fine sediment buildup (fine sand, silt, and clay) will need to be removed after processing 5–10 gallons of asphaltic matrix. This sediment can be scooped from the bottom of wash drums when the biodiesel is cool using metal coffee cans with holes poked in the sides to allow liquid to drain. When biodiesel and *n*-propyl bromide become saturated with asphalt, wash drums need to be cleaned out and refilled with fresh solvent. Waste solvent and any solids should be placed in labeled 55-gallon (208-L) drums and disposed of as hazardous waste.

CONCLUSIONS

Hot biodiesel is an effective and efficient solvent for separation of microvertebrates in asphalt-impregnated sediments from Rancho La Brea. While biodiesel is not an effective solvent at room temperature, it becomes very effective when heated to temperatures between 70°C and 80°C, which is still well below its flash point of 130°C. Residual biodiesel can subsequently be removed from the treated fossil materials by rinsing in *n*-propyl bromide or ethanol. Our current excavation, Project 23, has yielded large quantities of microfossil-rich asphaltic sand. We have found heated biodiesel to be a safe, effective, and efficient solvent for processing these asphaltic sediments.

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Appendix

MATERIALS RESOURCE LIST

Drum heater: Wrap-It Heat drum heater model TRX-16L15 low heat range 1500W, http://www.thermalinc.com

Respirator and cartridges: North Model 7700 Silicone half-mask respirator with organic cartridges 75SCP 100L or 7581P100L, http://www.northernsafety.com

Gloves: Ansell Sol-Vex 11-mm chemical-resistant nitrile gloves, model 37-145, http://www.ansellpro.com

Spill trays and 8-gallon drums: Eagle spill containment basin model 1631; Skolnik 8-gallon carbon steel drum model HM0802, http://www.grainger.com

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La Brea and Beyond: The Paleontology
of Asphalt-Preserved Biotas

Edited by John M. Harris