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Taxonomy, paleoecology and taphonomy of ground sloths (Xenarthra) from the Fairmead Landfill locality (Pleistocene: Irvingtonian) of Madera County, California

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ABSTRACT

The Fairmead Landfill locality contains a diverse middle Irvingtonian, (0.78–0.55 Ma), vertebrate fauna that includes three sloths, *Megalonyx wheatleyi*, *Nothrotheriops shastensis* and *Paramylodon harlani*. The co-occurrence of these three genera in a single fauna is relatively rare in both the Irvingtonian and Rancholabrean and this is only the fourth documented Irvingtonian fauna to contain all three sloth genera. The presence of the three different sloths, each of which had different ecological requirements, indicates the presence of a variety of different habitats at this time and a heterogeneous landscape. Preliminary analysis of pollen from the site supports the interpretation of the existence of a mosaic of plant communities, but a landscape dominated by a mesic grassland. This interpretation is also supported by the total faunal diversity that includes taxa associated with woodlands as well as open habitat and taphonomic differences in the preservation and relative abundance of the different sloths. Evolutionarily the Fairmead Landfill sloths show a suite of morphological, size and proportional characters that indicate they represent transitional populations between older and younger members of their respective lineages.

Introduction

The number of vertebrate faunas from the Irvingtonian North American Land Mammal Age (NALMA) (ca. 1.9 or 1.72 Ma to ca. 0.4 or 0.15 Ma) (Bell et al., 2004) is considerably smaller than that of the later Rancholabrean NALMA. Construction of Fairmead Landfill in Madera County has provided an opportunity to recover a diverse fauna from sediments deposited in the eastern San Joaquin Valley of California during the middle Irvingtonian. The recovered biota consists of 69 taxa (1 fish, 2 amphibians, 3 reptiles, 5 birds, 28 mammals, 1 bivalve, 1 gastropod, 12 plants, 16 diatoms) (Table 1) and enhances our knowledge of the middle Pleistocene fauna and flora of the West Coast. It complements the record provided by similar age faunas in Anza-Borrego Desert State Park (Cassiliano, 1994), San Timoteo Badlands (Albright, 1999) and El Golfo, Sonora, Mexico to the south (Shaw, 1981), and the type Irvington fauna to the north (Savage, 1951). This paper will focus only on the ground sloths from the fauna; other taxa will be addressed in subsequent publications.

Materials and methods

Initially, specimens found during construction of the landfill were placed in the University of California, Museum of Paleontology at Berkeley (UCMP). Subsequently, all specimens recovered have been curated and cataloged in the Madera County Paleontology Collection (MCPC), Madera, California. All measurements were taken in mm with digital calipers. AP = anteroposterior, ML = mediolateral.

Geography and geology

Paleontological monitoring of Fairmead Landfill began in 1993 and has covered an area of 40 acres to date. Continued excavation is planned over the next couple of decades and it is expected that the recovered fauna will increase in both taxonomic diversity and number of specimens. The landfill is located at 37° 04′ N latitude and 120° 12′ W longitude (Fig. 1). Ground surface is at 73.2 m elevation. Fossils at Fairmead Landfill have been collected from the Turlock Lake Formation and Riverbank Formation at depths of 4 m to 20 m below the surface. The upper unit of the Turlock Lake Formation has produced over 99% of the fossils from the locality, including all sloth specimens.

Excavation at the landfill has exposed all three middle to late Pleistocene formations of the eastern San Joaquin Valley. The formations are subdivided into informally named units. In ascending stratigraphic order they are the Turlock Lake Formation (lower and upper), Riverbank Formation (lower, middle and upper), and Modesto Formation

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Table 1
Fairmead Landfill Vertebrate Fauna. Compiled from Dundas et al. (1996), Tovar and Dundas (2008), Tovar et al. (2008), Dundas (2009), Kottachchi et al. (2009), Asami et al. (2011), Dundas et al. (2011), Kottachchi et al. (2011), Ngo et al. (2011).

Taxon
Class Actinopterygii (ray-finned fishes)
Order Perciformes (perch-like fishes)
Family Centrarchidae (sunfishes)
Archoplites interruptus (Sacramento perch)
Class Amphibia (amphibians)
Order Caudata (salamanders, newts, etc.)
Order Anura (frogs and toads)
Class Reptilia (reptiles)
Order Testudines (turtles and tortoises)
Family Emydidae (turtles)
Clemmys marmorata (western pond turtle)
Family Testudinidae (tortoises)
Xerobates agassizi (desert tortoise)
Order Squamata (scaled reptiles)
Family Colubridae (snakes)
Class Aves (birds)
Order Anseriformes (waterfowl)
Family Anatidae (ducks, geese, swans)
Branta canadensis (Canada goose)
Tadorna tadorna (common shelduck)
cf. *Aythya* sp. (diving duck)
Order Strigiformes (owls)
Family Strigidae (typical owls)
Athene cunicularia (burrowing owl)
Order Columbiformes (pigeons, doves, dodo)
Family Columbidae (pigeons, doves)
Zenaida macroura (mourning dove)
Class Mammalia (mammals)
Order Soricomorpha (shrews and moles)
Family Soricidae (shrews)
Sorex sp. (shrew)
Order Xenarthra (anteaters, armadillos, sloths)
Family Mylodontidae (ground sloths)
Paramylodon harlani (Harlan's ground sloth)
Family Nothrotheriidae (giant ground sloths)
Nothrotheriops shastensis (Shasta ground sloth)
Family Megalonychidae (two-toed sloths)
Megalonyx wheatleyi (Wheatley's ground sloth)
Order Carnivora (carnivores)
Family Canidae (canids (i.e. dogs))
Canis latrans (coyote)
Canis dirus (dire wolf)
Vulpes velox (swift fox)
Family Felidae (cats)
Homotherium sp. (Scimitar cat)
Smilodon sp. (Saber-tooth cat)
Miracinonyx sp. (American cheetah)
Panthera cf. P. onca (jaguar)
Family Mustelidae (weasels, badgers, skunks, etc.)
Taxidea taxus (badger)
Family Ursidae (bears)
Arctodus sp. (Giant short-faced bear)
Order Rodentia (rodents)
Family Sciuridae (squirrels, etc.)
Spermophilus sp. (ground squirrels)
Family Cricetidae (rats, mice)
Neotoma sp. (woodrat)
Peromyscus sp. (deer mouse)
Microtus sp. (vole)
Family Geomyidae (gophers)
Thomomys sp. (pocket gopher)
Family Heteromyidae (rats)
cf. *Dipodomys* sp. (kangaroo rat)
Order Lagomorpha (rabbits and hares)
Family Leporidae (rabbits and hares)
Lepus sp. (rabbit)
Order Proboscidea (proboscideans)
Family Elephantidae (elephants)
Mammuthus columbi (Columbian mammoth)
Order Perissodactyla (perrisodactyls)
Family Equidae (horses)
Equus sp. (horse)
Order Artiodactyla (artiodactyls)
Family Camelidae (camels)
Camelops sp. (camel)
Hemiauchenia sp. (llama)
Family Antilocapridae (pronghorns)
Tetrameryx irvingtonensis (Irvington pronghorn)
Capromeryx sp. (small-sized pronghorn)
Family Cervidae (deer)
Odocoileus sp. (deer)
Family Tayassuidae (peccary)
Platygonus cf. *P. vetus* (Leidy's peccary)

(lower and upper). Member contacts are marked by unconformities and paleosols (Marchand and Allwardt, 1981). Marchand (1976) mapped the surficial geology at Fairmead Landfill as predominantly the middle unit of the Riverbank Formation, with minor exposures of Modesto Formation represented by incised channel fills in the south-central area of the landfill. Dundas et al. (1996) recognized a previously unmapped upper unit of the Riverbank Formation at the surface. Locally, the lower unit of the Riverbank Formation is missing. In the subsurface, the middle unit of the Riverbank Formation unconformably overlies the upper unit of the Turlock Lake Formation (Dundas et al., 1996).

The eastern San Joaquin Valley's Pleistocene strata accumulated during glacial periods, with each unit recording one or more alluvial episodes. The unconformities and paleosols that separate units represent significant time intervals between periods of alluviation (Marchand and Allwardt, 1981). Fairmead Landfill is located on the Chowchilla River alluvial fan. Fossils are preserved in sediments representing distal alluvial fan channel, distal fan overbank flood or sheetflood, and marsh/lacustrine deposits (Dundas et al., 1996) (Fig. 2). Detailed descriptions of the stratigraphy are provided in Dundas et al. (1996) and are not repeated here.

Between the summer of 1993, when the first fossils were reported from the site, and the most recent excavations in the summer of 2008, 84 specimens attributable to the Xenarthra have been documented. Although small numbers of sloth specimens have been found throughout the history of paleontological efforts at Fairmead Landfill, the majority were recovered from bone beds discovered during the 1993 and 2006 field seasons.

Excavation records from the 1993 five-acre landfill expansion cell indicate that most sloth specimens that year were collected from 12.2 m (40 ft) to 12.8 m (42 ft) below the surface, or 61 m (200 ft) to 60.4 m (198 ft) in elevation (ground surface is at 73.2 m [240 ft]). Sloth material was collected from three distinct areas in 1993.

Area 1. *Megalonyx* (UCMP 140262, upper caniniform) (Figs. 3B, C, D) was found in close proximity to an *Odocoileus* antler base (UCMP 140399), one of only five deer specimens thus far identified from Fairmead Landfill. *Mammuthus columbi* was also recovered at the same location. These specimens were collected in the northeastern area of the 1993 excavation, about 25 m southeast of the bonebed mentioned below as area 3.

Area 2. *Megalonyx* (UCMP 140393), *Nothrotheriops* (UCMP 140260 (Figs. 3E, F) and UCMP 140261), and *Paramylodon* (UCMP 140263) were found at the south end of the 1993 excavations, all within approximately 25 m laterally. Other taxa occurring in this bone cluster include: *Clemmys marmorata*, Anatidae, *Smilodon*, *Homotherium*, *Miracinonyx*, *Canis dirus*, *Canis latrans*, *Camelops*, *Hemiauchenia*, *Capromeryx*, *Tetrameryx*, *Equus*, *M. columbi*, and *Thomomys*. The *Homotherium*, *Miracinonyx*, *C. latrans*, *Tetrameryx*, and *Capromeryx* were likely collected about 0.5 m deeper than the sloth material.

Area 3. *Megalonyx* (UCMP 194840) (Fig. 3A) and *Paramylodon* (UCMP 140392) (Fig. 8E) were collected from a bonebed in the northern part of the 1993 excavation. Associated taxa include: *M. columbi*, *Tetrameryx*, *Camelops*, *Equus*, *Lepus*, and *Dipodomys*. Voids (molds) in some of the bonebed sediment appeared to represent branches and

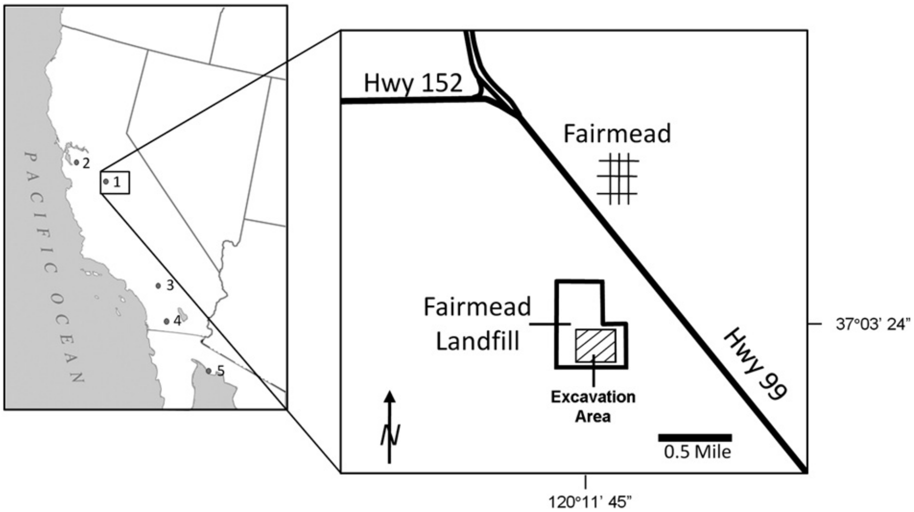

Figure 1. Location of the Fairmead Landfill locality near the junction of highways 152 and 99 in Madera County, California. Fairmead Landfill is one of five Irvingtonian sites in the southwestern United States and northern Mexico that contain sloth specimens: 1) Fairmead Landfill, California, 2) Irvington, California, 3) San Timoteo Badlands, California, 4) Anza-Borrego Desert State Park, California, and 5) El Golfo, Sonora, Mexico.

other vegetation that accumulated with the fauna. This bonebed was 90 m north of area 2.

More than half of the sloth specimens recovered from Fairmead Landfill came from a single alluvial fan channel-fill deposit discovered in August 2006. Located at the south end of landfill Unit 3 Cells 1B and 2A, the deposit consists of poorly sorted pebbly, silty sand with abundant inclusions of fossil bone. The deposit lies between 58.5 and 57.3 m (192–188 ft) in elevation, or approximately 14.6–15.8 m (48–52 ft) below the modern land surface. It extends approximately 40 m east–west by 15 m north–south, with the highest concentration of bone found in the westernmost 15 m. In addition to specimens recovered in situ, fossils continue to be recovered from a large stockpile of channel-fill sediment from the year 2006 excavation. Many of the fossils from this context have been rounded or polished by fluvial transport. Of sloth material collected from the processed bulk sediment sample, *Paramylodon* dermal ossicles occur most frequently.

To date, 46 sloth specimens have been identified from the year-2006 deposit, 36 of them from *Paramylodon*. The remaining ten elements, including fragments of vertebrae, manus/pes bones, a humerus, and fragments of teeth could not be assigned to genus, although they too are probably from *Paramylodon*. At least six individuals of *Paramylodon* representing individuals of all ages were recovered in the 2006 assemblage, which includes eight molariform teeth from at least two neonates (MCPC A37, A39, A40, A49, A52, A55, A56, and A60), a dentary with two molariforms from a juvenile (MCPC A77) (Fig. 8A), a dentary with three molariforms of a small adult (MCPC A54) (Fig. 8B), a right maxilla, neurocranium, right dentary, two cervical vertebrae, a fibula and a distal femur from one large adult (MCPC A70 [Figs. 8F,G], A74, A78 [Fig. 8C], A47a, A47b, A73, and A84, respectively), and 18 other specimens from adults. The additional adult specimens include part of a maxilla from a second large adult, six molariforms, two caniniforms, and two caudal vertebrae, as well as other cranial and manus elements. Dermal ossicles have not been included in specimen counts.

Other genera from the August 2006 bone bed include *Mammuthus*, *Equus*, *Camelops*, *Hemiauchenia*, Antilocapridae cf. *Tetrameryx*, *Platygonus*, *Vulpes*, *Thomomys*, and as-yet unidentified microtine, fish, and reptile. The proportionate representation of large mammal taxa in this assemblage differs markedly from that found in the Fairmead Landfill collection as a whole, as shown in Table 2. Among the 1376 cataloged elements of large mammals in the Fairmead Landfill collections at Madera County and UCMP, *Equus* and camelids (*Camelops* and *Hemiauchenia*) dominate, accounting for nearly 85% of the total. Antilocaprids, *Platygonus*, *Mammuthus*, and Xenarthrans are relatively rare. In contrast, Xenarthra, notably *Paramylodon*, dominate the August 2006 assemblage, and while cf. *Tetrameryx*, *Platygonus*, and *Mammuthus* are also disproportionately common, *Equus* and camelids are markedly under-represented. This taxonomic composition is probably indicative of similar habitat preferences by the represented animals.

Between 1993 and 2008, paleontological monitors recovered another 30 sloth specimens. Of those finds, all but one, a weathered cranium of *Nothrotheriops* (MCPC A91), are from *Paramylodon harlani*. Many of the finds were isolated bones and teeth, but 16 specimens discovered in 2003 were closely associated and appear to represent a single individual. Nicknamed “Bessie” by volunteer excavators, remains of that individual include a maxilla (MCPC A529), five teeth (MCPC A3, A6, A18, A25, A26), two vertebrae (MCPC A24, A71), a rib (MCPC A5), manus and pes elements (MCPC A2, A4, A10, A15, A22, A76), and a hemapophysis (MCPC A14).

Age

Age determination of the Fairmead Landfill biota is based on biostratigraphy, magnetostratigraphy, and radiometric age dating associated with the lithostratigraphy. Biostratigraphically, the mammal taxa support a middle to late Irvingtonian age assignment. The absence of *Bison*, a diagnostic taxon of the Rancholabrean NALMA, is significant, given that large herbivorous mammals dominate the thousands of fossils collected from the site (Dundas et al., 1996). *Mammuthus* is present, indicating a maximum biostratigraphic age of Irvingtonian (Bell et al., 2004).

Paleomagnetic analysis of the upper unit of the Turlock Lake Formation, to a depth of 14 m below the surface at Fairmead Landfill, yielded a normal remnant magnetic polarity (Dundas et al., 1996). Coupled with the radiometric age of the Friant Pumice Member of the upper unit of the Turlock Lake Formation, discussed below, the results of the paleomagnetic analysis are consistent with sediment deposited during the Brunhes normal magnetic polarity chron. This indicates a maximum age for the locality of ~774–780 ka, the Matuyama reversed-Brunhes normal paleomagnetic boundary (Baksi et al., 1992; Singer and Pringle, 1996; Tauxe et al., 1996; Sarna-Wojcicki et al., 2000).

Although an air-fall ash bed has not been documented at Fairmead Landfill, the upper unit of the Turlock Lake Formation elsewhere contains the Friant Pumice Member near its base (Marchand and Allwardt, 1981). Samples from the air-fall ash bed at the pumice member's type locality, 33 km (20.5 miles) southeast of Fairmead Landfill, produced $^{40}Ar/^{39}Ar$ dates with a weighed mean age of 750.1 ± 4.3 ka, only slightly younger than the updated weighted mean age of

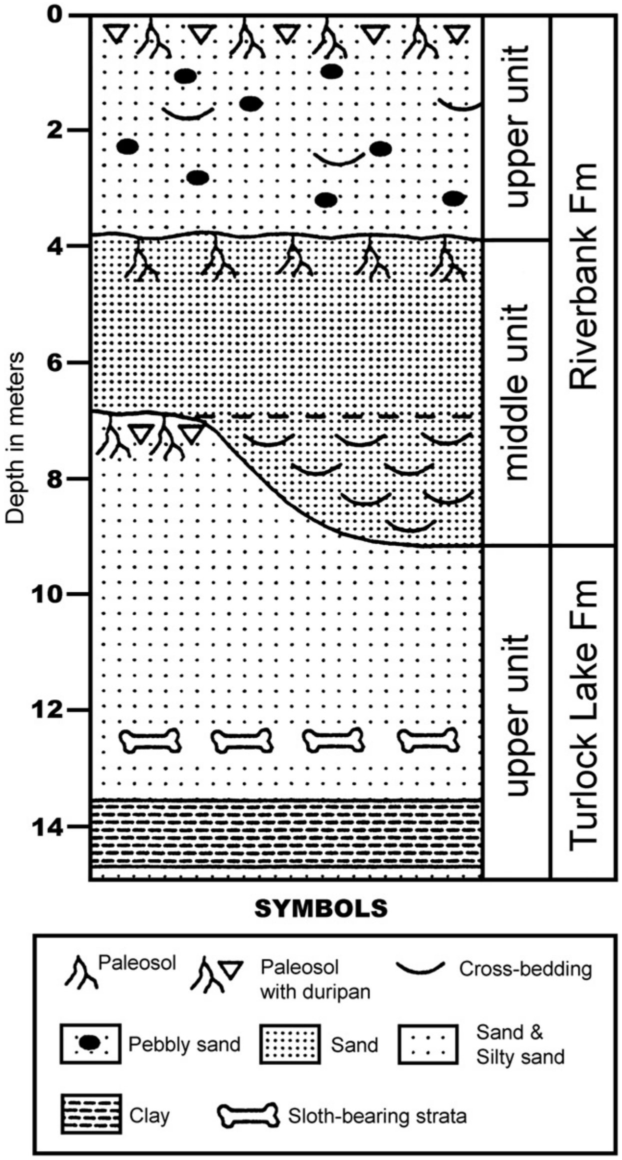

Figure 2. Stratigraphic section of the south wall at Fairmead Landfill in 1993, indicating the 12.2 m to 12.8 m zone from which remains of *Nothrotheriops*, *Megalonyx* and *Paramylodon* were collected that year. By comparison, the year 2006 bone bed which yielded more than half of all ground sloth specimens collected from Fairmead Landfill was at a slightly greater depth of approximately 14.6 to 15.8 m (48 to 52 ft) below ground surface. Modified from Dundas et al., 1996.

Bishop Tuff at 758.9 ± 1.8 ka (Sarna-Wojcicki et al., 2000). Sarna-Wojcicki et al. (2000) concluded that the basal air-fall ash of the Friant Pumice Member is Bishop Ash.

The Friant Pumice provides an important radiometric age for the base of the upper unit of the Turlock Lake Formation. Whether the fossil-bearing strata in the upper unit of the Turlock Lake Formation at Fairmead Landfill are stratigraphically above or below the Friant Pumice is undetermined at this time. It may be that the Friant Pumice was stratigraphically higher and eroded away prior to deposition of the unconformably overlying Riverbank Formation, in which case the Friant Pumice is not preserved at the site. Alternatively, given that the fossil-bearing strata are magnetically normal and that the Friant Pumice lies stratigraphically close to, but above, the Matuyama–Brunhes boundary, it is more likely that the Friant Pumice Member lies below the fossil bearing strata and has yet to be encountered. It is unlikely that the Friant Pumice was not deposited at Fairmead Landfill, given the known limits on the geographic distribution of the Bishop Ash and Friant Pumice and its 9 cm air-fall thickness at the nearby type locality (Janda, 1966; Sarna-Wojcicki et al., 2000). United States Geological Survey driller's log data near Madera and Chowchilla, California indicate that the Friant Pumice's area of distribution should include Fairmead Landfill and extends beyond it (Janda, 1966). The possibility that the Friant Pumice has been encountered by excavators at Fairmead Landfill, but not recognized, cannot be discounted.

Although the age of the Friant Pumice provides good age control at the base of the upper unit of the Turlock Lake Formation, the age of the top of the unit is less well-constrained. Uranium-trend dating of two soils at the top of the upper unit yielded dates of 560 ± 80 ka and 540 ± 50 ka (Marchand and Allwardt, 1981). Unit ages of the unconformably overlying Riverbank Formation range from 130 ka to 450 ka (Marchand and Allwardt, 1981).

We conclude that the age of the Fairmead Landfill biota recovered from the Turlock Lake Formation is constrained between ~550 ka and ~780 ka. This corresponds to the middle Irvingtonian land mammal age (Bell et al., 2004). Future excavation at the locality may provide further age refinement if the Friant Pumice Member is discovered.

Palynology

The initial analysis of pollen from finer sediments at the Fairmead Landfill site is consistent with the ecosystem indicated by the composition of the mammalian community. Thirty-nine samples have been extracted by Global Geolab Ltd. and the pollen residues identified by Peter Van der Water of California State University Fresno. Pollen yields in most cases amount to only a few grains, but counts of up to 240 palynomorphs have been obtained.

Poaceae (grass) is almost uniformly the dominant pollen type, with *Pinus* second most common. In many samples, only these two types occur. Chenopodeaceae/Amaranthaceae (Cheno/Am) and Cupressaceae (probably representing *Juniperus*) also occur in a number of samples. The largest count included over 45% Poaceae, 16% each of *Pinus* and Cheno/Am, 6% Cupressaceae, and 6% *Ambrosia* (ragweed). *Picea* (spruce), *Abies* (fir), *Quercus* (oak), *Alnus* (alder), *Betula* (birch) and longspine Asteraceae (daisy family) are surprisingly rare at less than 2% and *Artemisia* (sagebrush) is represented by a single grain.

The record differs distinctly from the Asteraceae and xeric shrub assemblage obtained by Davis (1999) from mid to late Wisconsinan through early Holocene sediments at Tulare Lake, California, which he inferred to represent a semiarid steppe flora similar to that found today in the Great Basin. The pollen samples from Fairmead, in contrast, appear to indicate a mesic grassland with ephemeral ponds surrounded by halophytic shrubs and either distant stands of forest or small, highly dispersed groves of trees. Much of the arboreal pollen might also be accounted for as allochthonous and was probably deposited with the fine-grained sediment brought in by streams flowing from the nearby Sierra Nevada foothills.

Additional analysis may clarify the record, particularly if intact pollen assemblages can be found in association with the larger bone beds. However, these preliminary findings indicate a mosaic of plant communities, but dominated by a mesic grassland. This could account for both the diversity of ground sloth species represented at the site, and the dominance of *P. harlani*, which has been previously interpreted as an open-country grazer (Stock, 1925).

Systematic paleontology

Order Xenarthra Cope (1889)
Family Megalonychidae Gervais (1855)
Megalonyx Harlan (1825)
Megalonyx wheatleyi Cope (1871)

Material: UCMP 140262 left upper caniniform (Figs. 3B, C, D); UCMP 140393 molariform; UCMP 194840 left humerus (Fig. 3A).

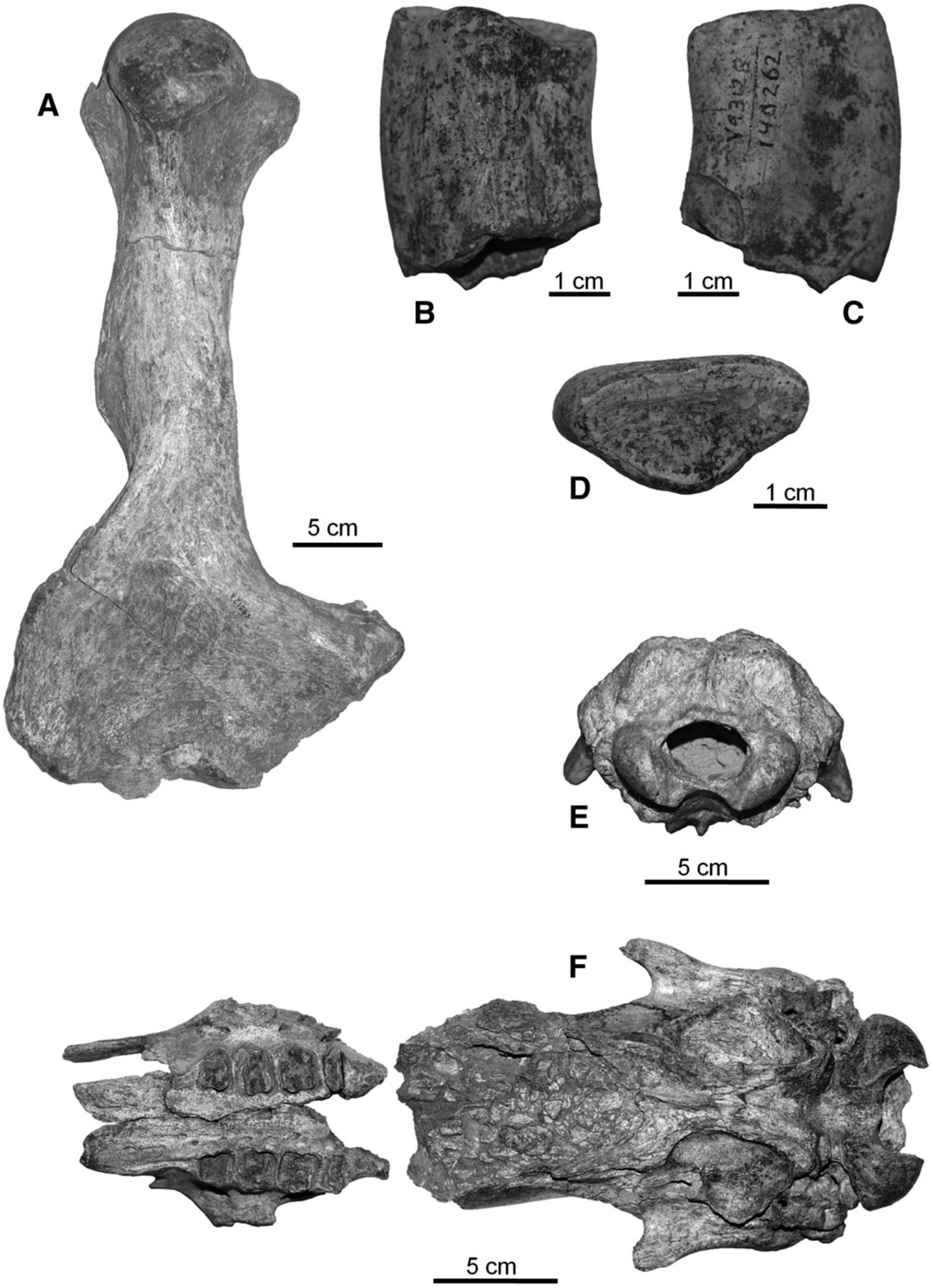

Figure 3. A. *Megalonyx wheatleyi* left humerus (UCMP 194840); B–D. *Megalonyx wheatleyi* left upper caniniform (UCMP 140262), medial, lateral and occlusal views respectively; E–F. *Nothrotheriops shastensis* cranium (UCMP 140260), occipital and ventral views respectively.

While there is clearly an evolutionary increase in size in the *Megalonyx* lineage from the Hemphillian to Rancholabrean NALMAs, size alone, although useful to a certain degree, provides an insufficient basis for assignment to a specific species of *Megalonyx*. For example, the left-upper caniniform of *Megalonyx* (UCMP 140262) (AP length 34.2 mm, ML width 18.4 mm) from Fairmead Landfill falls within the overlap in the size distribution between earlier members of *Megalonyx jeffersonii* and the youngest members of *M. wheatleyi* (Fig. 4). Given the potential variability in size, whether due to stage of ontogenetic development, sexual dimorphism, or geographic variation such as a Bergmann's response, size cannot be used as a primary criterion for species assignment. Discrete morphologically-based criteria are essential. Based on morphological criteria, the relative development of the longitudinal grooves anterior and posterior to the lingual column on the tooth, which are less pronounced in their development than in *M. jeffersonii* and are comparable to that of other Irvingtonian specimens assigned to *M. wheatleyi*, the Fairmead specimen is assigned to *M. wheatleyi*. The Fairmead Landfill fauna is close in age to the Cudahy fauna of Kansas (Paulson, 1961) and the Camelot fauna of South Carolina (Fields, 2009), which also include upper caniniforms of *M. wheatleyi*. All of these samples fall at the upper end of the size range for the Irvingtonian sample. Likewise, the size of the humerus – length 414 mm; mediolateral width of proximal end 122 mm; mediolateral width of head 77.9 mm; anteroposterior diameter of head 85 mm; mediolateral width of distal end 220.8 mm – shows it is smaller than the available sample of *M. jeffersonii*, although still larger than the only other *M. wheatleyi* humerus, from the Irvingtonian at McLeod Limerock Mine, Florida (Fig. 5). Although the exact age of the McLeod fauna is

Table 2
Comparison of percentages of large mammal specimens from the year 2006 bonebed with the total cataloged assemblage from Fairmead Landfill.

Taxonomic group	Total cataloged	August 2006 bonebed
Xenarthra[a]	6.7	44.0
Equus	63.9	25
Camelidae[b]	20.5	5.0
Antilocapridae[c]	1.2	7.0
Odocoileus virginianus	0.2	0
Platygonus	0.2	2.0
Mammuthus	5.8	16.0
Carnivora[d]	1.5	1.0

[a] *Paramylodon*, *Nothrotheriops*, *Megalonyx*.
[b] *Camelops* and *Hemiauchenia*.
[c] *Tetrameryx* (primarily) and *Capromeryx*.
[d] *Canis*, *Vulpes*, *Homotherium*, *Smilodon*, *Miracinonyx*, *Arctodus*, *Taxidea*.

unknown, it is currently placed chronologically around the Matuyama–Brunhes Boundary, so may be roughly coeval with the Fairmead Landfill fauna (Bell et al., 2004). However, given the limited sample of humeri of Irvingtonian *Megalonyx*, it is likely that, once a larger sample becomes available, there will be overlap between the two species similar to that seen in the caniniform. It should be also noted that, while there is an increase in caniniform size, it is strictly isometric and there is no positive allometry. Even the largest and smallest individuals of the genus have essentially the same proportions. This was noted by Fields (2009) in the proportions of the mandible in different species of *Megalonyx*. In this regard, the Fairmead *Megalonyx*, while a limited sample, seems to be like the *Megalonyx* from the chronologically similar Camelot fauna from South Carolina and thus to represent a transitional population between *M. wheatleyi* and *M. jeffersonii* (Fields, 2009).

Family Nothrotheriidae
Nothrotheriops Hoffstetter (1954)
Nothrotheriops shastensis Sinclair (1905)

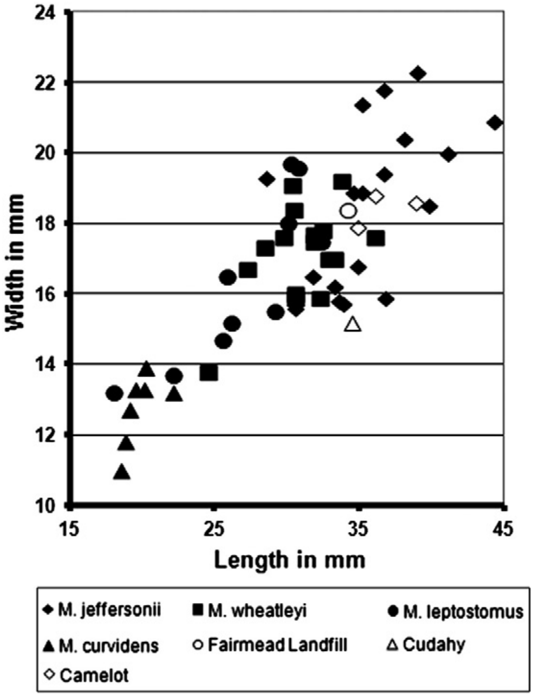

Figure 4. Comparison of the length and width of the upper caniniform of *Megalonyx* from Fairmead Landfill to other species of *Megalonyx*.

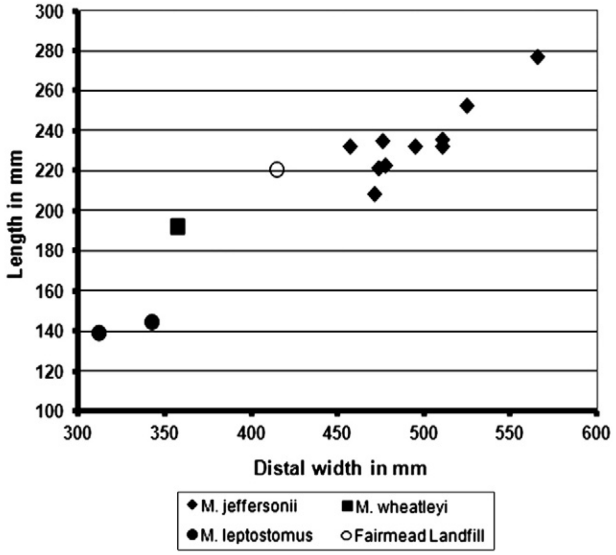

Figure 5. Comparison of length and distal width of humerus of *Megalonyx* from Fairmead Landfill to other species of *Megalonyx*.

Material: UCMP 140260 cranium (Figs. 3E, F); MCPC A91 severely weathered cranium; UCMP 140261 tooth; UCMP 175276 diaphysis of right femur.

Other than the severely weathered cranium (MCPC A91), no additional specimens of *Nothrotheriops* have been recovered to complement those originally reported from the site by Dundas et al. (1996). Based on the sample from the early Irvingtonian Leisey Shell Pit in Florida, McDonald (1995) considered the differences in the skull proportions between specimens from the Irvingtonian and Rancholabrean to allow them to be distinguished. He referred the Irvingtonian material to the species *Nothrotheriops texanum*. In this earlier species, the alveolar length of the upper tooth row is less than the predental length of the skull (Range 0.73–0.91, N = 5) while in the later species, *N. shastensis*, the tooth-row length is the greater (Range 1.02–1.29, N = 7). The ratio of the tooth row to the predental length in the Fairmead Landfill specimen is 1.16, placing it in *N. shastensis*. The length of the skull (UCMP 140260) is about 271 mm, alveolar length is 57.2 mm; predental length of skull 49.5 mm; width of palate at first molariform 54.2 mm; width of occiput 103.1 mm; height of occiput 65.4 mm; width across occipital condyles 75.7 mm, indicating that the Fairmead specimen is a small individual (Figs. 6, 7).

As McDonald (1995) noted in his discussion of the *Nothrotheriops* from the Leisey fauna, it is often difficult in a continuum of an evolving lineage to demarcate the boundaries distinguishing two species, especially two that appear to have an ancestor–descendant relationship. Although smaller samples often make the distinction initially easy, it becomes more blurred with additional materials. The Fairmead Landfill *Nothrotheriops* is such an example. The Fairmead Landfill fauna is estimated as being between 780,000 and 550,00 years old, making it younger than the Leisey fauna, which is considered to be approximately 1.2 Ma by Morgan and Hulbert (1995). While we might expect the Fairmead Landfill *Nothrotheriops* to be intermediate in size between the Leisey sample and late Rancholabrean NALMA members of the genus, it is a small individual compared to both the younger and older samples. Its small size may simply reflect simple size variation, as the stage of cranial suture closure indicates it is an adult. Despite the individual's smaller size, including the size of the skull, the proportionately longer tooth row places it within *N. shastensis*. Consequently *N. texanum* and *N. shastensis* cannot be considered strictly as Irvingtonian and Rancholabrean NALMA taxa, respectively. It appears, that based

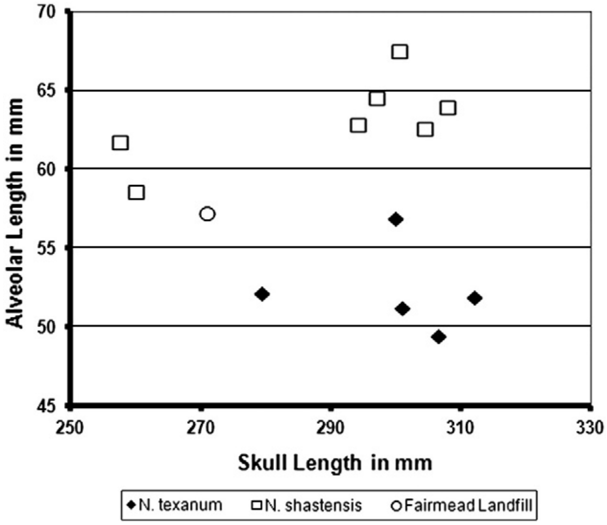

Figure 6. Comparison of the alveolar length of skull and skull length in the *Nothrotheriops* from Fairmead Landfill to *N. texanum* and *N. shastensis*.

on the ratio of tooth-row length to predental length in the single specimen available from Fairmead Landfill, the transition from *N. texanum* to *N. shastensis* had already occurred by the middle Irvingtonian NALMA.

Unlike the *Megalonyx* lineage, which first appears in North America in the Hemphillian NALMA, and the *Paramylodon* lineage, which first appears in the Blancan NALMA (as *Glossotherium chapadmalense*), *Nothrotheriops* first appears in North America in the Irvingtonian. Therefore, it represents a later stage of the Great American Biotic Interchange (McDonald, 2005). The earliest records in North America indicate that it was initially widespread (California to Florida), but by the Rancholabrean NALMA, its range was reduced to the West Coast, southwestern United States, and northern Mexico, prior to its extinction (McDonald and Jefferson, 2008). While the larger number of early Irvingtonian records clearly documents the genus' initial widespread distribution in North America, the small number of late Irvingtonian and early Rancholabrean NALMA faunas containing *Nothrotheriops* does not currently permit the timing of the contraction of its range to be determined. Neither does it permit the change to be correlated with climatic or environmental events in the middle Pleistocene.

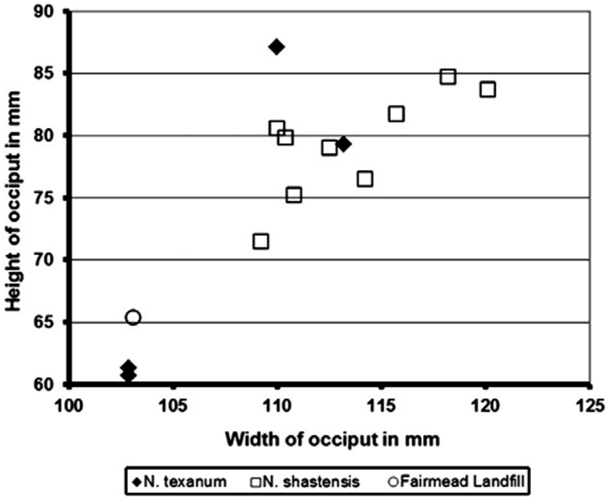

Figure 7. Comparison of the height and width of the occiput in the *Nothrotheriops* from Fairmead Landfill to *N. texanum* and *N. shastensis*.

The diaphysis of a right femur (UCMP 175276) with intact growth ends indicates the presence of juveniles in the Fairmead population.

Family Mylodontidae Gill (1872)
Paramylodon Brown (1903)
Paramylodon harlani Owen (1840)

Material: caniniforms — MCPC A92, AP 15.3, ML 14.7; MCPC A58, AP 16.8, ML 15.5; and MCPC A6, AP 16.7, ML 13.8; MCPC A944; molariforms — UCMP 140263, MCPC A3, A18, A25, A26, A36, A37, A39, A40, A49, A52, A53, A55, A56, A57, A59, A60, A66, A93 and A945; neurocranium — MCPC A74; right maxilla lacking teeth — MCPC A70 (length of total tooth row 148.6 mm; length of molariform series 121.4 mm); left maxilla lacking teeth — MCPC A1064 (length of total tooth row 155.5 mm; length of molariform series 127 mm); partial occiput — MCPC A1063 (width across occipital condyles 124 mm); crushed partial cranium with two molariforms — MCPC A529; palatine portion left and right maxillae MCPC A41; right dentary missing teeth — UCMP 140392 (Fig. 8E); posterior right dentary missing teeth — MCPC A78 (Fig. 8C); right dentary with m3–m4 — MCPC A77 (Fig. 8A); partial right dentary with m2–m4 — MCPC A54 (Fig. 8B); partial right dentary lacking teeth — MCPC A85 (Fig. 8D); right scapula — MCPC A83, length along spine 323 mm, greatest width of blade 425 mm, length along posterior border 354 mm; synsacrum — MCPC A82, A86; left femur minus proximal end — UCMP 197855; right distal femur — MCPC A84; left fibula — MCPC A73; left partial tibia and fibula — MCPC A825; left partial tibia — MCPC A828; unciform MCPC A33; third manus phalanges — MCPC A4, A61; other phalanges MCPC A2, A10, A15, A76; cervical vertebrae — MCPC A47a, A47b, A71; caudal vertebrae — MCPC A24, A67, A69, A 87, A88, A89, A90, A946, A947; hemapophysis — MCPC A14 (Table 3).

Paramylodon is the most common of the three sloth species recovered from the fauna and is the only one represented by partial associated skeletons. The other genera are represented by isolated bones and teeth.

A right edentulous maxilla (MCPC A70) and left edentulous maxilla (MCPC A1064) preserve the alveolus for the caniniform. Although the loss of the caniniform was one of the characters used by Brown (1903) to diagnose the genus *Paramylodon*, the loss only occurs in Rancholabrean NALMA individuals; all Irvingtonian NALMA and older members of the lineage retain the caniniform (McDonald, 2006). Even in the Rancholabrean NALMA, the pattern of loss is variable and may only occur on one side or not at all (Stock, 1925). All three of the recovered caniniforms have the occlusal surface worn perpendicular to the axis of the tooth. This is one of the two different patterns of occlusal wear that occurs on the caniniforms of *Paramylodon*, a difference that is attributed to sexual dimorphism (McDonald, 2006). Both morphs have been observed in Blancan through Rancholabrean specimens (McDonald, 1995, 2006). McDonald (2006) noted that the dimensions of the caniniforms with both types of occlusal wear in the Blancan and Irvingtonian forms were larger than those from the Rancholabrean, indicating a reduction in the size of this tooth over time. In the Blancan and Irvingtonian specimens, there is a more pronounced difference in the size of the two tooth morphs, while both morphs are essentially the same size in the Rancholabrean. Comparison of the Fairmead specimens with other *Paramylodon* caniniforms with perpendicular occlusal wear shows they are at the small end of the size range compared to other Irvingtonian specimens, but are still larger than most individuals from the Rancholabrean (Fig. 9). As no caniniforms with acute wear have been recovered yet, it is not possible to see if they follow the pattern already observed from other Irvingtonian specimens.

McDonald (1995) noted that the depth of the mandible relative to the length of the tooth row in *Paramylodon* increased from the Irvingtonian to Rancholabrean. One mandible (UCMP 140392) (Fig. 8E) is sufficiently preserved to provide these measurements. As can be seen in Figure 10, the proportions of the Fairmead specimen are comparable to those of Rancholabrean individuals and not other

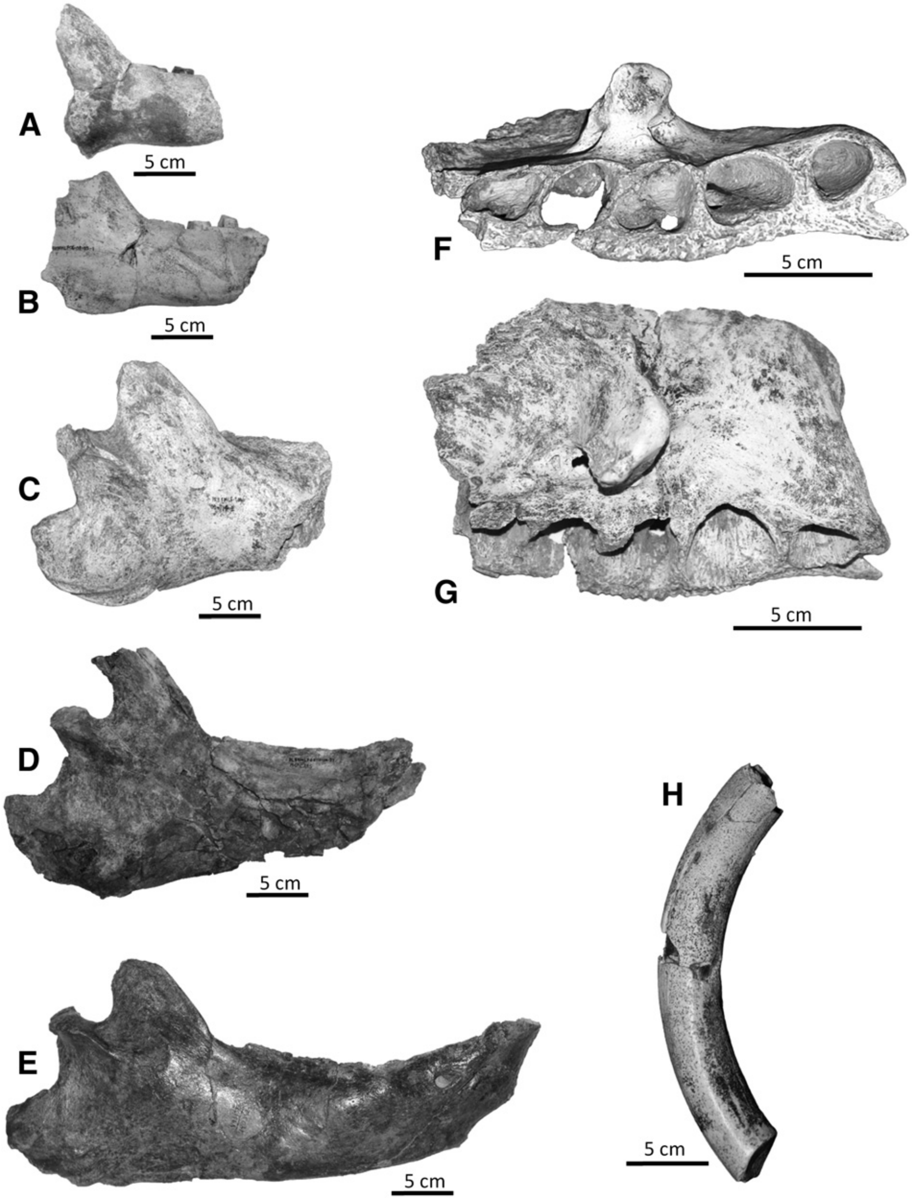

Figure 8. A–E. *Paramylodon harlani* right dentary series in lateral view, A. juvenile (MCPC A77), B. subadult (MCPC A54), C. adult (MCPC A78), D. adult (MCPC A85), E. adult (UCMP 140392). F–G. *Paramylodon harlani* right maxilla (MCPC A70), occlusal and lateral views respectively; H. *Paramylodon harlani* caniniform (MCPC A58) lateral view.

Table 3
Measurements of lower dentition of *Paramylodon harlani* from Fairmead Landfill. a = alveolar measurement.

	UCMP 140392	MCPC A78	MCPC A54	MCPC A77
m1 AP	26.1a			
m1 ML	16.8a			
m2 AP medial	28.3a		16.9	
m2 ML ant	20.8a		15.1	
m2 ML post	26.5a		17.0	
m3 AP med	21.6a	27.5a	11.5	8.6
m3 AP lat	18.6a	27.3a	15.1	9.6
m3ML ant	20.5a	20.2a	19.9	15.0
m3 ML post	27.0a	15.2a	21.1	15.4
m4 length	58.7a	50.6a	37.9	23.9
m4 ML ant lobe	32.7a	29.0a	21.3	14.3
m4ML post lobe	17.8a	20.3a	15.3	10.8
m4 width isthmus between lobes	9.0a	9.5a	7.7	5.9

Irvingtonian individuals. The Irvingtonian sample includes Leisey (McDonald, 1995) and Tri-Britton, Florida and Gilliland, Texas, (Hibbard and Dalquest, 1966) all of which are older than the Fairmead Landfill fauna.

The fourth molariform in one dentary (MCPC A54) (Fig. 8B) has an extra column; this variation was also seen in the molariforms of *P. harlani* from Leisey (McDonald, 1995).

The large sample of *Paramylodon* from the Fairmead Landfill also includes remains of juveniles, including a partial lower jaw (MCPC A77) (Fig. 8A) and neonatal or late-term fetal individuals, represented by eight molariforms.

Discussion

Two aspects of the Fairmead Landfill sloth collection are of particular interest. It constitutes an evolutionarily intermediate assemblage between earlier Irvingtonian and later Rancholabrean representatives of the taxonomically better-represented respective species, thus providing a window into the evolution of North American ground sloths. The

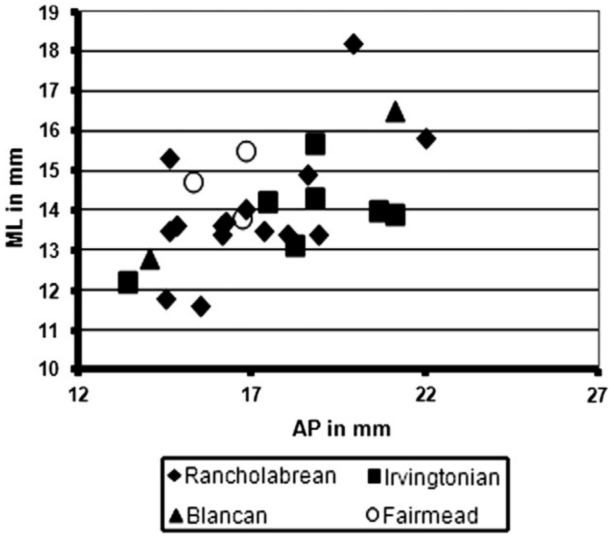

Figure 9. Comparison of the dimensions of the caniniforms with perpendicular occlusal wear of *Paramylodon harlani* from Fairmead Landfill with those of *Paramylodon harlani* from different North American Land Mammal Ages.

structure and species composition of the faunal assemblages with which the sloths are associated at Fairmead also provide information about the structure of local faunal communities during the middle Irvingtonian and provides insights into changes in these communities.

In contrast to the 64 Rancholabrean records of *Paramylodon* in California listed by McDonald (1996), the genus is rare in the Irvingtonian with only two localities listed in McDonald's (1995) summary of Irvingtonian records of the genus. These are the type locality for the Irvingtonian North American Land Mammal Age, Irvington, Alameda County and Vallecito Creek, San Diego County. In California, there are 18 records of *Nothrotheriops* from the Rancholabrean and 5 from the Irvingtonian (McDonald and Jefferson, 2008). *Megalonyx* is known from 7 Irvingtonian and 32 Rancholabrean localities in California (McDonald, 1996).

The taxonomy of *Megalonyx* does not neatly divide at the Irvingtonian–Rancholabrean boundary. While early Irvingtonian *Megalonyx* have been assigned to *M. wheatleyi*, by the late Irvingtonian NALMA (sometime after the Fairmead Landfill fauna) the species had evolved into what can be morphologically identified as *M. jeffersonii*. Based on the skull of *Nothrotheriops*, this also appears to be true for this genus, since its proportions are those of *N. shastensis* and not *N. texanum*. Likewise, based on the available specimens of *Paramylodon*, this genus at Fairmead Landfill seems to show a mixture of characters that are characteristic of other Irvingtonian specimens but also has features similar to those from the Rancholabrean. The sample is limited, and many of the skeletal elements that would be useful to evaluate the evolutionary stage of each of the sloth lineages have not yet been recovered. However, based on what is currently available for each of the sloths, the Fairmead Landfill fauna shows a stronger similarity to the Rancholabrean than to the Irvingtonian. We consider the sloths to represent morphologically intermediate populations between those from the earlier Irvingtonian and the later Rancholabrean.

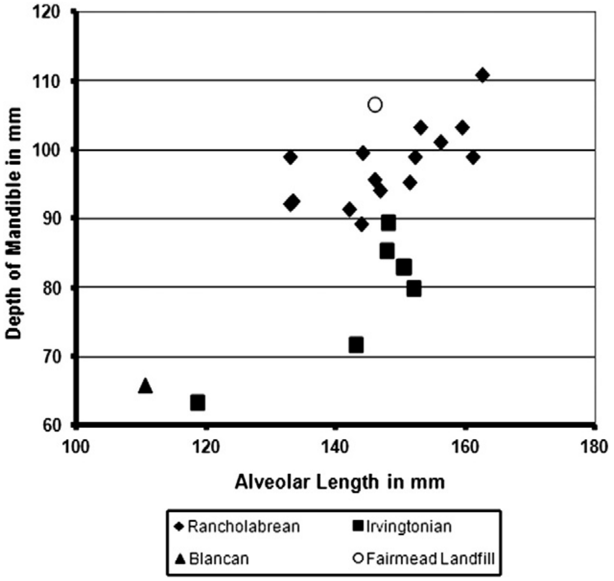

Figure 10. Comparison of the depth of the mandible relative to the alveolar length in *Paramylodon*.

The Fairmead Landfill fauna is derived from normally magnetized sediments of the upper unit of the Turlock Lake Formation and is inferred to have been deposited during the Brunhes normal magnetic polarity chron, placing an upper age limit on the age of the fauna at ca. 0.78 Ma (Dundas et al., 1996). Coupled with the radiometric age of the Friant Pumice Member of the Turlock Lake Formation at ca. 0.75 Ma and the uranium series ages of soils at the top of the upper unit at ca. 0.55 Ma, the Fairmead Landfill fauna is 0.78 to 0.55 Ma in age. The sediments from which the type Irvingtonian fauna was recovered are reversely magnetized and considered to be in the upper part (C1r) of the Matuyama chron ca. 1.07 Ma (Lindsay et al., 1975). Many of the traditional "Irvingtonian" faunas that include sloths, such as the Sandahl and Kanopolis faunas in Kansas and the Hay Springs, Angus, and Gordon faunas in Nebraska, lack external age control and may in fact be earliest Rancholabrean. Likewise, many sloth-containing faunas in Florida, originating from sinkholes such as Haile 16A and the McLeod Limerock Mine, also lack external age controls. Age assignment for these sites is limited to biostratigraphic comparisons or the stage of evolution of various species. One of the few exceptions is the Leisey fauna, although there is not a consensus as to its age. Strontium values in the mollusk deposits place it at ca. 2.08 ± 0.56 Ma (Jones et al., 1995), although MacFadden (1995) considers the fauna younger and places it between 1.66 and 1.4 Ma based on the reversed magnetic polarity of the sediments, while Morgan and Hulbert (1995) place it at 1.2 Ma. Despite the range of inferred ages, the Leisey fauna is clearly older than the type Irvingtonian and Fairmead Landfill faunas. *Paramylodon* has also been recovered from the Badger Room in Porcupine Cave, Colorado (Shabel et al., 2004). The paleomagnetic polarities of sediments in the cave place that site between 0.8 and 0.9 Ma, so it is somewhat older than the Fairmead Landfill fauna.

The Fairmead Landfill fauna is unusual, in that it contains three different taxa of sloth. McDonald (1996) noted that during the Rancholabrean, despite their broad overlap in distribution, these same three genera (although represented by different species) were rarely found together in a single fauna, reflecting their different ecological requirements. A summary of the sloths present in Irvingtonian faunas is provided in Table 4. As a grazer, or at least a mixed feeder, *Paramylodon* would have utilized more open grassland habitat than the other sloths (McDonald and Pelikan, 2006). This is supported by the dominance of horses, camelids, and Columbian mammoth in the Fairmead assemblage, as well as its association in relatively high frequency with *Tetrameryx* in the August 2006 bone bed. In contrast, both *N. shastensis* and *Megalonyx jeffersonii* are considered to have been browsers, although they utilized quite different habitats; *Nothrotheriops* utilizing more xeric adapted vegetation (Hansen, 1978) while *Megalonyx* probably utilized riparian habitat (Hoganson and McDonald, 2007). The co-occurrence of one of only three *Megalonyx* elements with one of only five specimens of *Odocoileus virginianus* at Fairmead Landfill is again consistent with this inference. Modern *O. virginianus* of more arid western North America are typically found in or near riparian habitats. In those cases where the three sloth genera do co-occur, their relative abundance is disproportionate, with one

Table 4
Irvingtonian records of *Megalonyx wheatleyi/jeffersonii*, *Nothrotheriops texanus/shastensis* and *Paramylodon harlani*. IMNH — Idaho Museum of Natural History, SBCM — San Bernardino County Museum, UF — Florida Museum of Natural History, USNM — United States National Museum of Natural History.
Modified from McDonald (1995) and McDonald and Jefferson (2008).

Locality	Age	*Megalonyx wheatleyi/ jeffersonii*	*Nothrotheriops texanus/shastensis*	*Paramylodon harlani*	Reference
California					
Bautista Creek, Riverside Co.	IRV	*wheatleyi*			Frick (1921)
Borrego Badlands, San Diego Co.	IRV		X		McDonald and Jefferson (2008)
El Casco, San Bernardino Co.	IRV I 1.3–1.4 Ma	*wheatleyi*			Albright (1999) F:AM 17835 skull
Gypsum Ridge, San Bernardino Co.	Latest Blancan to Earliest Irvingtonian		X		McDonald and Jefferson (2008)
Fairmead Landfill, Madera Co.	IRV II ca. .55–.78 Ma	*wheatleyi*	*shastensis*	X	Dundas et al. (1996) This paper
Irvington, Alameda Co.	IRV II ca. 1.07 Ma	*jeffersonii*	X	X	Savage (1951)
SBCM locality 5.6.155, Riverside Co.		*wheatleyi*			SBCM
Temecula, Antelope Road, Riverside Co.		*wheatleyi*			SBCM
Fish Creek-Vallecito Creek, San Diego Co.	Irv I 0.78–1.77 Ma	*wheatleyi*	X		
Canada					
Medicine Hat Fauna 9, Province of Alberta	IRV			X	Harington (1978)
Colorado					
Badger Room, Porcupine Cave, Park Co.	ca. 800–900 ka			X	Shabel et al. (2004)
Florida					
Tri-Britton Site, Hendry Co.	IRV No age control	*wheatleyi*		X	UF
Haile 16A, Alachua Co.	IRV No age control	*wheatleyi*			
Leisey 1A, Hillsborough Co.	1.2–1.21 Ma		*texanus*	X	McDonald (1995)
McLeod Limerock Mine, Levy Co.	IRV No age control	*wheatleyi*			
Pool Branch, Polk Co.	IRV No age control		*texanus*		McDonald (1985)
Kansas					
Butler Spring Locality 4 (Adams Local Fauna), Meade Co.	IRV Normal polarity	*wheatleyi*			Hibbard and Taylor (1960)
Courtland Canal, Jewell Co.	IRV			X	Eshelman and Hager (1984)
Cudahy, Meade Co.	IRV II 0.67 Ma	*wheatleyi*			Paulson (1961)
Kanopolis, Ellsworth Co.	RLBI No age control			X	Hibbard et al. (1978)
Sandahl Fauna, Harper Township, McPherson Co.	RLBI No age control	*jeffersonii*			Lindahl (1891); Semken (1966)
Maryland					
Cumberland Cave, Allegheny Co.	IRV II	*wheatleyi*			Gidley and Gazin (1938)
Mexico					
El Golfo, State of Sonora	IRV ca. 1.6–1.8 Ma	*wheatleyi*	*texanus*	X	Shaw (1981)
New Mexico					
Adobe Ranch Doña Ana Co.	IRV ca. 1.32–1.59 Ma	*wheatleyi*		X	Morgan (2008)
Nebraska					
Angus, Nuckolls Co.	RLBI No age control			X	Schultz and Martin (1970)
Gordon, Sheridan Co.	RLB No age control			X	Schultz and Stout (1948)
Hay Springs, Sheridan Co.	RLBI No age control			X	Allen (1913); Brown (1903)
Oklahoma					
Curtis, Woodward Co.	IRV No age control		*texanus*	X	Akersten and McDonald (1991)
Holloman, Tillman Co.	IRV ca.0.9–1.1 Ma	*wheatleyi*		X	Meade (1953); Dalquest (1977)
Oregon					
Rome. Malheur Co.	IRV No age control			X	IMNH
Pennsylvania					
Port Kennedy Cave, Montgomery Co.	IRV No age control	*wheatleyi* (Type Locality)		X	Cope (1871, 1899)
South Carolina					
Camelot, Dorchester Co.	IRV No age control	*wheatleyi*			Fields (2009)
South Dakota					
Kuchta Sand Pit Locality, Yankton Co.	IRV No age control	*wheatleyi*			Heaton and McDonald (1993)

Table 4 (*continued*)

Locality	Age	*Megalonyx wheatleyi/ jeffersonii*	*Nothrotheriops texanus/shastensis*	*Paramylodon harlani*	Reference
Texas					
Gilliland, Baylor and Knox Cos.	IRV I ca. 1.2–1.6 Ma		*texanus*	X	Hibbard and Dalquest (1966)
Rock Creek, Briscoe Co.	IRVII ca. 0.8 Ma			X	Lull (1915)
Wheeler Co. (Type *N. texanus*)	No age control		*texanus*		Hay (1916)
Washington					
Delight, Adams Co.	No age control			X	Matthew (1902)
West Virginia					
Scott Hollow Cave Monroe Co.	No age control	*wheatleyi*			USNM

genus dominating and the others being relatively rare, as is the case at Fairmead Landfill. At Fairmead, the most common sloth is *Paramylodon*, represented by multiple individuals of both adults and juveniles, while both *Nothrotheriops* and *Megalonyx* are represented by fewer specimens and consequently fewer individuals. The limited sample for *Nothrotheriops* does, however, include both adults and a juvenile. The presence of all three genera of sloth probably reflects the heterogeneous environment that existed in the Fairmead area during the Irvingtonian. Alluvial fan, fan channel, and marsh/lacustrine environments are all indicated by the sediments. Despite the thickness of sediments and time span represented in the Fairmead fauna, remains of the different genera have all been recovered from a relatively narrow stratigraphic zone and from close horizontal proximity to each other, so it is likely that the three genera were contemporaneous but also it should be considered that they may have moved in and out of the area, depending on climatic and environmental conditions. Although it is uncommon for the three genera to co-occur (Table 4) all three also co-occur in the Irvington, El Golfo and Anza-Borrego faunas.

Although consistently found in small numbers throughout the Fairmead Landfill deposits, ground sloth remains were abundant in two bone beds, those exposed during summer 1993 and August 2006. The 1993 bonebed contained all three species in low frequencies, while the other contains a large number of specimens and individuals of a single species. Discovery of all three sloths common to the Pleistocene of western North America in a single bone bed is unusual, since the three are understood to have had distinct habitat preferences (McDonald, 1996). The 1993 bone bed is unique within the Fairmead locality in its total species diversity. Among the approximately 150 identified specimens it is known to contain at least 25 animal taxa. In addition to all three sloths, it contains all other large herbivores that have been recovered from elsewhere in the locality. As is typical of the locality as a whole, *Equus*, *Mammuthus*, and the large camelids dominate. The assemblage (Table 5) includes taxa associated with a variety of habitat preferences including presumed grazers (*Mammuthus*, *Equus*, *Paramylodon*), open county xerophyte browsers (*Tetrameryx* and *Nothrotheriops*), mesic habitat browsers (*Odocoileus*, *Megalonyx*, and perhaps *Capromeryx*) and mixed feeders (camelids). The array of carnivores is also broad. Along with *C. dirus*, *Canis latrans*, and *Smilodon*, which occur elsewhere at the locality, this bonebed preserved the only specimens of *Homotherium*, *Miracinonyx*, *Panthera*, and *Arctodus* yet recovered at the site.

In contrast, the August 2006 bone bed has only ten taxa based on approximately 100 identified specimens, but in this case, one species of sloth, *P. harlani*, is the dominant taxon, while *Equus* and the camelids are rare relative to the site as a whole (Table 2). *Tetrameryx* and *Platygonus* are also unusually well-represented, occurring at more than five times their frequency in the total assemblage. In fact, this bone bed produced nearly half of the *Tetrameryx* and *Paramylodon* specimens recovered to date. The habitat diversity represented by this bonebed is not as great, because all species represented in this bone bed are indicative of open country habitats of grassland or shrub steppe.

The differences between the lithology of the two bonebeds and the associated small animals help explain as the co-occurrence of species of Xenarthrans with inferred habitat differences in one bonebed compared to the monospecific assemblage in the other. The 2006 faunal remains were often subrounded to rounded fragments comingled in a very poorly sorted deposit of silt to gravel, which we interpret as channel and overbank flood deposits typical of a distal alluvial fan setting. The bones appear to have been entrained in the sediment as sand- to cobble-size clasts picked up from beside or within a small ephemeral stream channel. In marked contrast, the sediments in the 1993 bonebed range from gravelly sand to moderately well-sorted silty-clay, indicating a range of depositional environments from alluvial fan channel, overbank flood, and marsh/abandoned fan-channel/lake-margin sediments. Bones found in these facies were typically broken by trampling but lacked the rounding seen in the 2006 deposit. The fauna associated with the clay-rich deposits include three species of waterfowl and fragments of pond turtle are common. The presence of these animals indicates the existence of a permanent source of still water.

Table 5
Taxonomic composition of summer 1993 and August 2006 bone beds.

Class	Order	Species	1993	2006
Aves	Anseriformes	*Branta canadensis* (Canada goose)	+	
		Tadorna tadorna (shelduck)	+	
Mammalia	Artiodactyla	*Capromeryx sp.* (dwarf pronghorn)	+	
		Camelops sp. (giant camel)	+	+
		Hemiauchenia sp. (extinct llama)	+	+
		Odocoileus virginianus (whitetail deer)	+	
		Platygonus vetus (Leidy's peccary)		+
		Tetrameryx irvingtonensis (Irvington pronghorn)	+	+
	Carnivora	*Arctodus sp.* (giant short-faced bear)	+	
		Canis latrans (coyote)	+	
		Canis dirus (dire wolf)	+	
		Smilodon sp. (sabertooth cat)	+	
		Homotherium sp. (scimitar cat)	+	
		Miracinonyx sp. (American cheetah)	+	
		Panthera cf *P. onca* (jaguar)	+	
	Lagomorpha	*Lepus sp.* (hare)	+	
	Perissodactyla	*Equus sp.* (horse)	+	
	Proboscidea	*Mammuthus columbi* (Columbian mammoth)	+	+
	Rodentia	cf *Dipodomys sp.* (kangaroo rat)	+	
		Microtus sp. (vole)	+	+
		Thomomys sp. (pocket gopher)	+	+
	Xenarthra	*Nothrotheriops shastensis* (Shasta ground sloth)	+	
		Megalonyx wheatleyi (Wheatley's ground sloth)	+	
		Paramylodon harlani (Harlan's ground sloth)	+	+
Reptilia	Testudines	*Clemmys marmorata* (western pond turtle)	+	
	Squatamata	Colubridae (snake)		+
Pelecypoda	Unionidae	*Anodonta* (floater mussel)	+	

The sediments of the1993 bonebed, along with the diverse faunal assemblage that included waterfowl and turtle, is indicative of ponded, perennial water. As such, it attracted animals from an array of habitats, including animals probably resident in surrounding deciduous woodland as well as those that occupied open grassland and desert scrub beyond the woodland margins. The 2006 bone bed was formed by an ephemeral stream that only drew fauna from the nearby xeric, open habitat that supported a much more limited faunal community.

Summary

The middle Irvingtonian Fairmead Landfill fauna includes three species of sloth, *M. wheatleyi*, *N. shastensis* and *P. harlani*. This makes it one of a small number of faunas in which all three genera co-occur, although there is a significant difference in their relative abundance, with *P. harlani* being the most common taxon. This suggests that the local environment during the Irvingtonian was sufficiently heterogeneous to meet the ecological requirements of all three genera, an inference that is supported by the variety of depositional environments represented in the sediment, and by the differences in the faunal composition of two bonebeds at the site. While only mid-Irvingtonian in age, the Fairmead Landfill fauna is the youngest Irvingtonian fauna in California to contain sloths. It is considerably younger than the other well-documented faunas from the type Irvington (ca. 1.1 Ma), Vallecito Creek (ca. 1–2 Ma) (Cassiliano, 1994) and El Casco (ca. 1.3–1.4 Ma) (Albright, 1999). Despite the mid-Irvingtonian age of the fauna, the evolutionary stage of each of the individual sloth taxa suggests they represent a transitional population for each sloth lineage, as the preserved specimens include characters that are not only similar to older Irvingtonian members of their respective lineages but also to younger Rancholabrean members. Continuing study of the rest of the fauna may indicate this is the case for other taxa as well.

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References

Akersten, W.A., McDonald, H.G., 1991. *Nothrotheriops* (Xenarthra) from the Pleistocene of Oklahoma and paleogeography of the genus. The Southwestern Naturalist 36, 178–185.

Albright 3rd, L.B., 1999. Biostratigraphy and vertebrate paleontology of the San Timoteo Badlands, southern California. University of California Publications in Geological Sciences 144, 1–121.

Allen, G.A., 1913. A new *Mylodon*. Memoirs of the Museum of Comparative Zoology 40, 319–346.

Asami, R., Ibarra, Y., Scott, E., Dundas, R.G., 2011. *Equus* from the Middle Irvingtonian Fairmead Landfill Locality, Madera County, California. Supplement to the online Journal of Vertebrate Paleontology, November 2011, Program and Abstracts: Society of Vertebrate Paleontology Annual Meeting 2011, Las Vegas, Nevada, p. 64.

Baksi, A.K., Hsu, V., McWilliams, M.O., Farrar, E., 1992. ^{40}Ar/^{39}Ar dating of the Brunhes–Matuyama geomagnetic field reversal. Science 256, 356–357.

Bell, C.J., Lundelius Jr., E.L., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez Jr., D.R., Semken Jr., H.A., Webb, S.D., Zakrzewski, R.J., 2004. The Blancan, Irvingtonian, and Rancholabrean mammal ages. In: Woodburne, M.O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York, pp. 232–314.

Brown, B., 1903. A new genus of ground sloth from the Pleistocene of Nebraska. Bulletin of the American Museum of Natural History 19, 569–583.

Cassiliano, M.L., 1994. Paleoecology and taphonomy of vertebrate faunas from the Anza-Borrego Desert of California. Doctoral Dissertation, Department of Geosciences, University of Arizona, Tucson, 421 pp.

Cope, E.D., 1871. Preliminary report on vertebrata discovered in the Port Kennedy Bone Cave. Proceedings of the American Philosophical Society 12, 73–102.

Cope, E.D., 1899. Vertebrate remains from the Port Kennedy Bone Deposit. Journal of the Academy of Natural Sciences of Philadelphia 2 (2), 193–267.

Dalquest, W.W., 1977. Mammals of the Holloman local fauna, Pleistocene of Oklahoma. The Southwestern Naturalist 22, 255–268.

Davis, O.K., 1999. Pollen analysis of Tulare Lake, California: Great Basin-like vegetation in Central California during the full-glacial and early Holocene. Review of Palaeobotany and Palynology 107, 249–257.

Dundas, R.G., 2009. The Late Irvingtonian Fairmead Landfill Locality, Madera County, California: partnership in management and research at the local level. Proceedings of the Eighth Conference on Fossil Resources, St. George, Utah, pp. 113–114.

Dundas, R.G., Smith, R.B., Verosub, K.L., 1996. The Fairmead Landfill locality (Pleistocene, Irvingtonian), Madera County, California: preliminary report and significance. PaleoBios 17, 50–58.

Dundas, R.G., Ibarra, Y., Asami, R., Ngo, M., Canchola, J.A., 2011. Fairmead Landfill, a diverse Middle Irvingtonian biota in California's Central San Joaquin Valley. Supplement to the online Journal of Vertebrate Paleontology, November 2011, Program and Abstracts: Society of Vertebrate Paleontology Annual Meeting 2011, Las Vegas, Nevada, p. 102.

Eshelman, R., Hager, M., 1984. Two Irvingtonian (Medial Pleistocene) vertebrate faunas from north-central Kansas. In: Genoways, H.H., Dawson, M.R. (Eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: Carnegie Museum Natural History Special Publication, 8, pp. 384–404.

Fields, S.E., 2009. Hypsodonty in the Pleistocene ground sloth *Megalonyx*: closing the "diastema" of data. Acta Palaeontologica Polonica 54, 155–158.

Frick, C., 1921. Extinct vertebrate faunas of the badlands of Bautista Creek and San Timoteo Canon southern California. University of California Publications Bulletin of the Department of Geology 12, 277–424.

Gidley, J.W., Gazin, C.L., 1938. The Pleistocene vertebrate fauna from Cumberland Cave, Maryland. Bulletin of the United States National Museum 171, 1–99.

Hansen, R.M., 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. Paleobiology 4, 302–319.

Harington, C.R., 1978. Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence. Syllogeus 15, 1–105.

Hay, O.P., 1916. Descriptions of two extinct mammals of the Order Xenarthra from the Pleistocene of Texas. Proceedings of the United States National Museum 51, 107–123.

Heaton, T.H., McDonald, H.G., 1993. Additions to the vertebrate fauna of the Kuchta Sand Pit Locality (Late Blancan–Early Irvingtonian), Yankton County, South Dakota. Current Research in the Pleistocene 10, 101–103.

Hibbard, C.W., Dalquest, W.W., 1966. Fossils from the Seymour Formation of Knox and Baylor counties, Texas, and their bearing on the late Kansan climate of that region. Contributions of the Museum of Paleontology, 21. University of Michigan, pp. 1–66.

Hibbard, C.W., Taylor, D.W., 1960. Two late Pleistocene faunas from southwestern Kansas. Contributions of the Museum of Paleontology, 16. University of Michigan, pp. 1–223.

Hibbard, C.W., Zakrzewski, R.J., Eshelman, R.E., Griggs, C.D., Griggs, C., 1978. Mammals from the Kanopolis local fauna, Pleistocene (Yarmouth) of Ellsworth County, Kansas. Contributions of the Museum of Paleontology, 25. University of Michigan, pp. 11–44.

Hoganson, J.W., McDonald, H.G., 2007. The first report of the occurrence of Jefferson's ground sloth (*Megalonyx jeffersonii*) in North Dakota and its paleobiogeographical and paleoecological significance. Journal of Mammalogy 88, 73–80.

Janda, R. J., 1966. Pleistocene History and Hydrology of the Upper San Joaquin River, California. Unpublished Ph.D. Dissertation, University of California at Berkeley, 425 pp.

Jones, D.S., Mueller, P.A., Acosta, T., Shuster, R.D., 1995. Strontium isotopic stratigraphy and age estimates for the Leisey Shell Pit faunas, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37, 93–105 (Pt. 1).

Kottachchi, N., Canchola, J.A., Dundas, R.G., 2009. *Platygonus* cf. *P. vetus* from the Middle Pleistocene (Late Irvingtonian) Fairmead Landfill Locality, Madera County, California. Geological Society of America 41 (7), 453 (Abstracts with Programs).

Kottachchi, N., Ibarra, Y., Dundas, R.G., 2011. *Camelops* from the Middle Pleistocene (Middle Irvingtonian) Fairmead Landfill Locality, Madera County, California. Supplement to the online Journal of Vertebrate Paleontology, November 2011, Program and Abstracts: Society of Vertebrate Paleontology Annual Meeting 2011, Las Vegas, Nevada, p. 139.

Lindahl, J., 1891. Description of a skull of *Megalonyx leidyi* n. sp. Transactions of the American Philosophical Society 17, 1–10.

Lindsay, E.H., Johnson, N.M., Opdyke, N.D., 1975. Preliminary correlation of North American land mammal ages and geomagnetic chronology. In: Smith, G.R., Friedland, N.E. (Eds.), Studies on Cenozoic Paleontology and Stratigraphy in honor of Claude W. Hibbard, Claude W. Hibbard Memorial Volume 3: The Museum of Paleontology Papers on Paleontology, 12, pp. 111–119.

Lull, R.S., 1915. A Pleistocene ground sloth, *Mylodon harlani*, from Rock Creek, Texas. American Journal of Science 39, 327–385.

MacFadden, B.J., 1995. Magnetic polarity stratigraphy and correlation of the Leisey Shell Pits, Tampa Bay, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37, 107–116 (Pt. 1).

Marchand, D.E., 1976. Preliminary Geologic Maps (1:24:000) Showing Quaternary Deposits of the Eastern San Joaquin Valley, California. United States Geological Survey, Open-File Report 76-839.

Marchand, D.E., Allwardt, A., 1981. Late Cenozoic Stratigraphic Units, Northeastern San Joaquin Valley, California. United States Geological Survey Bulletin 1470 (70 pp.).

Matthew, W.D., 1902. List of the Pleistocene fauna from Hay Springs, Nebraska. Bulletin of the American Museum of Natural History 16, 317–322.

McDonald, H.G., 1985. The Shasta ground sloth, *Nothrotheriops shastensis* (Xenarthra, Megatheriidae) in the middle Pleistocene of Florida. In: Montgomery, G.G. (Ed.), The Evolution and Ecology of Armadillos, Sloths and Vermilinguas. Smithsonian Institution Press, pp. 95–104.

McDonald, H.G., 1995. Gravigrade Xenarthrans from the middle Pleistocene Leisey Shell Pit 1A, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History, Biological Sciences 37, 345–373 (Pt. II).

McDonald, H.G., 1996. Biogeography and paleoecology of ground sloths in California, Arizona and Nevada. San Bernardino County Museum Association Quarterly 43, 61–65.

McDonald, H.G., 2005. Paleoecology of extinct Xenarthrans and the Great American Biotic Interchange. Bulletin of the Florida Museum of Natural History 45, 313–333.

McDonald, H.G., 2006. Sexual dimorphism in the skull of Harlan's ground sloth. Natural History Museum of Los Angeles County Contributions to Science 510, 1–9.

McDonald, H.G., Jefferson, G.T., 2008. Distribution and habitat of *Nothrotheriops* (Xenarthra, Nothrotheridae) in the Pleistocene of North America. In: Wang, X., Barnes, L.G. (Eds.), Geology and Vertebrate Paleontology of Western and Southern North America, Contributions in Honor of David P. Whistler: Natural History Museum of Los Angeles County Science Series, 41, pp. 313–331.

McDonald, H.G., Pelikan, S., 2006. Mammoths and mylodonts: exotic species from two different continents in North American Pleistocene faunas. Quaternary International 142–143, 229–241.

Meade, G.S., 1953. An early Pleistocene vertebrate fauna from Frederick, Oklahoma. Journal of Geology 61, 452–460.

Morgan, G.S., 2008. Vertebrate fauna and geochronology of the Great American Biotic interchange in North America. New Mexico Museum of Natural History and Science Bulletin 44, 93–140.

Morgan, G.S., Hulbert Jr., R.C., 1995. Overview of the geology and vertebrate biochronology of the Leisey Shell Pit Local Fauna, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37, 1–92 (Pt 1).

Ngo, M., Canchola, J.A., Dundas, R.G., 2011. Avifaunas of the Middle Pleistocene Irvington and Fairmead Landfill Localities in California. Supplement to the online Journal of Vertebrate Paleontology, November 2011, Program and Abstracts: Society of Vertebrate Paleontology Annual Meeting 2011, Las Vegas, Nevada, p. 166.

Paulson, G.R., 1961. The mammals of the Cudahy fauna. Papers of the Michigan Academy of Science, Arts, and Letters 46, 127–152.

Sarna-Wojcicki, A.M., Pringle, M.S., Wijbrans, J., 2000. New ^{40}Ar/^{39}Ar age of the Bishop Tuff from multiple sites and sediment rate calibration for the Matuyama–Brunhes boundary. Journal of Geophysical Research 105 (B9), 21,431–21,443.

Savage, D.E., 1951. Late Cenozoic vertebrates of the San Francisco Bay region. University of California Publications, Bulletin of the Department of Geological Sciences 28, 215–314.

Schultz, C.B., Martin, L.D., 1970. Quaternary mammalian sequence in the central Great Plains. In: Dort Jr., W., Jones Jr., J.K. (Eds.), Pleistocene and Recent Environments of the Central Great Plains; Special Publication of the Department of Geology, 3. University of Kansas, pp. 341–353.

Schultz, C.B., Stout, T.M., 1948. Pleistocene mammals and terraces in the Great Plains. Bulletin of the Geological Society of America 59, 553–588.

Semken Jr., H.A., 1966. Stratigraphy and paleontology of the McPherson *Equus* beds (Sandahl local fauna), McPherson County, Kansas. Contributions of the Museum of Paleontology, 20. University of Michigan, pp. 121–178.

Shabel, A.B., Barnosky, A.D., Van Leuvan, T., Bibi, F., Kaplan, M.H., 2004. Irvingtonian mammals from the Badger Room in Porcupine Cave, age taphonomy, climate and ecology. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene, the Porcupine Cave Fauna from Colorado. University of California Press, Berkeley, pp. 295–317.

Shaw, C.A., 1981. The middle Pleistocene El Golfo Local Fauna from northwestern Sonora, Mexico. Master's Thesis, Department of Biology, California State University, Long Beach, 141 pp.

Singer, B.S., Pringle, M.S., 1996. Age and duration of the Matuyama–Brunhes geomagnetic polarity reversal from ^{40}Ar/^{39}Ar incremental heating analyses of lavas. Earth and Planetary Science Letters 139, 47–61.

Stock, C., 1925. Cenozoic gravigrade edentates of western North America with special reference to the Pleistocene Megalonychinae and Mylodontidae of Rancho La Brea. Carnegie Institute of Washington 331, 1–206.

Tauxe, L., Herbert, T., Shackleton, N.J., Kok, Y.S., 1996. Astronomical calibration of the Matuyama–Brunhes boundary: consequences for magnetic remanence acquisition in marine carbonates and the Asian loess sequences. Earth and Planetary Science Letters 140, 133–146.

Tovar, D.H., Dundas, R.G., 2008. Irvingtonian occurrences of *Homotherium* from Irvington and Fairmead Landfill in California. Journal of Vertebrate Paleontology 28 (3 supplement), 152A–153A.

Tovar, D.H., Canchola, J.A., Dundas, R.G., 2008. Columbian Mammoth (*Mammuthus columbi*) from the Late Irvingtonian Fairmead Landfill Locality, Madera County, California. Geological Society of America 40 (1), 44 (Abstracts with Programs).