

A report on late Quaternary vertebrate fossil assemblages from the eastern San Francisco Bay region, California

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Here we report on vertebrate fossil assemblages from two late Quaternary localities in the eastern San Francisco Bay region, Pacheco 1 and Pacheco 2. At least six species of extinct mammalian megaherbivores are known from Pacheco 1. The probable occurrence of *Megalonyx jeffersonii* suggests a late Pleistocene age for the assemblage. Pacheco 2 has yielded a minimum of 20 species of mammals, and provides the first unambiguous Quaternary fossil record of *Urocyon*, *Procyon*, *Antrozous*, *Eptesicus*, *Lasiurus*, *Sorex ornatus*, *Tamias*, and *Microtus longicaudus* from the San Francisco Bay region. While a radiocarbon date of 405 ± 45 RCYBP has been obtained for a single bone sample from Pacheco 2, the possibility that much of the assemblage is considerably older than this date is suggested by (1) the substantial loss of collagen in all other samples for which radiocarbon dating was unsuccessfully attempted and (2) the occurrence of *Microtus longicaudus* approximately 160 km to the west of, and 600 m lower in elevation than, its present range limit. The taphonomic data and limited stratigraphic information for the two localities suggest deposition of bones within a riparian system. Multiple lines of evidence including the taxonomic composition and the relative abundance of skeletal elements point to the original accumulation of most, if not all, of the small vertebrate remains at Pacheco 2 by owls. Based on taxonomic composition, Pacheco 1 appears to have been located in a mosaic of grassland and woodland habitats, and Pacheco 2 in moist woodland with dense underbrush and a body of freshwater.

INTRODUCTION

While the fossil record of large mammals from the Pleistocene of the San Francisco Bay region is robust and well-documented (Stirton 1939, Peabody 1945, Savage 1951), relatively little is known about the Quaternary history of small mammals in the same region (but see Wolff 1973, 1975). In this paper, we report taxonomic occurrences and taphonomic data for two vertebrate fossil localities (V77117 and V78027) in Contra Costa County, California. One of the assemblages from V78027 is particularly significant because it includes a diverse array of extant species of small mammals, some of which no longer inhabit the eastern San Francisco Bay region today.

The present-day mammalian fauna of the San Francisco Bay region is characterized by high species richness of California endemics (Davis et al. 2008). Documenting fossil occurrences of extant species is an essential step toward understanding the ecological underpinnings of this diversity in a historical context. Such knowledge, in turn, informs efforts to preserve the existing fauna (cf. Blois and Hadly 2009, Hadly and Barnosky 2009), and is urgently needed as this region faces substantial climatic changes in the next 100 years (Ackerly et al. 2010). The fossil record of small mammals is important in this regard because they constitute the majority of the regional mammalian diversity today, and because they are often sensitive indicators of environmental shifts at a wide range of spatiotemporal scales (Hadly 1996, Moritz et al.

2008, Myers et al. 2009, Blois et al. 2010, McGuire 2010).

Background on the localities

The vertebrate fossils reported here were collected in 1977 and 1978 by personnel of the University of California Museum of Paleontology (UCMP) during salvage excavation at a housing development site near the town of Pacheco (37.98°N , 122.07°W ; Fig. 1). Specimens were collected from two UCMP localities, Pacheco 1 (V77117) and Pacheco 2 (V78027), which were previously described by Hutchison (1987) as a series of cross-bedded alluvial deposits and a sedimentary pocket (of unspecified size) located within this depositional series, respectively. No additional stratigraphic

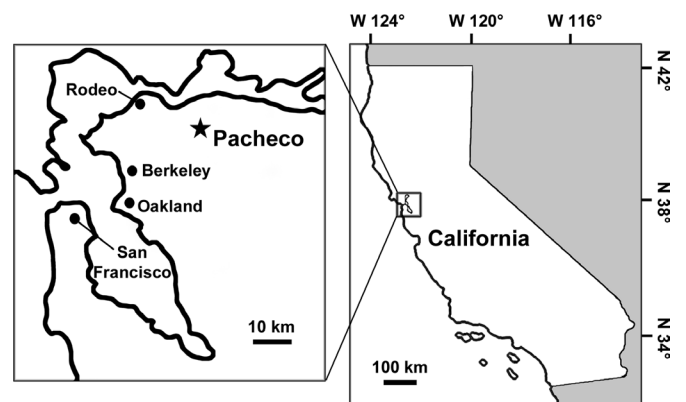


Figure 1. Map of UCMP Localities V77117 (Pacheco 1) and V78027 (Pacheco 2).

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information exists for either locality, and both localities were subsequently destroyed by construction activities. The matrix encasing some of the specimens from Pacheco 2 consists of a poorly-sorted clay-pellet conglomerate characteristic of deposition along river banks (Fig. 2).

Except for *Scapanus latimanus* from Pacheco 2 (Hutchison 1987), the fossils from the two localities have not been described in detail. Hutchison (1987) determined the late-Pleistocene age of Pacheco 1 from the composition of its megafauna, and tentatively considered Pacheco 2 to be equivalent in age, presumably based on the stratigraphic context. However, because no extinct species were definitively known from the latter, he also noted the possibility that the sedimentary pocket represented a Holocene cut and fill. We discuss below our current assessment of the age of Pacheco 2 based on the taxonomic composition of mammals and radiocarbon data.

MATERIALS AND METHODS

We examined 23 skeletal specimens from Pacheco 1 and 4,132 from Pacheco 2. All specimens are housed in the UCMP. Measurements were taken with Absolute Digimatic digital calipers (Mitutoyo, Japan) and a WILD M3C dissecting microscope with an ocular micrometer (Heerbrugg, Switzerland). Statistical analyses were performed in the R programming environment Version 2.10.1 for Windows (R Development Core Team 2009).

The small vertebrate fossils from Pacheco 2 had previously been collected by underwater sieving of bulk sediment. Although the precise quantity of this sediment is unknown, an undated document associated with the Pacheco specimens in the UCMP collection notes that the sediment sample was about the size of a display case meant to contain the bear skull (Fig. 2) and specimens of large mammals from Pacheco 1. Therefore, we suspect it was a few cubic meters in volume at most and possibly much smaller.

Taxonomic identification

The extinct mammals from Pacheco 1 were identified by direct examination of comparable museum specimens or, when these were not available, by consulting published descriptions and illustrations of North American Pleistocene taxa. Unless otherwise noted, the vertebrate taxa from Pacheco 2 were identified by direct examination of modern specimens of comparable extant species in California that were selected based on the morphological and geographic distributional information in Jameson and Peeters (2004) and Wilson and Reeder (2005). All comparative specimens are housed at the UCMP and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Following the taxonomic identification of dental elements, other skeletal elements were assigned to each taxon by comparison with modern specimens so far as possible.

Identification of species of *Microtus*—Specimens of *Microtus* from Pacheco 2 were identified at the species level by a discriminant function analysis of the occlusal surface shape

of the lower first molars (m1s) using the two-dimensional geometric morphometrics (for details of the method, see McGuire in press). The fossil specimens were compared to modern specimens of *M. californicus*, *M. longicaudus*, *M. montanus*, *M. oregoni*, and *M. townsendii*.

Identification of species of *Peromyscus*—Specimens of *Peromyscus* from Pacheco 2 were identified at the species level by a linear discriminant analysis of the anteroposterior and transverse lengths of the upper first molars (M1s). Four extant species in the Coast Ranges of central California, *P. boylii*, *P. californicus*, *P. maniculatus*, and *P. truei*, were selected as the reference groups, and 20 modern specimens of each species were measured. Although *P. crinitus* and *P. eremicus* also occur in California today, they were excluded from the analysis because of their primary association with rocky and arid environments, respectively (Veal and Caire 1979, Johnson and Armstrong 1987), which are unlikely to have existed at Pacheco considering the taxonomic composition of the rest of the assemblage. The predictive accuracy of the method was evaluated by jackknife re-classification of the reference specimens (Hammer and Harper 2006). The identification of each fossil M1 was accepted only when its posterior probability of group membership (i.e., specific affiliation) was equal to, or greater than, 0.950. This discriminant analysis was performed with the MASS package Version 7.3-5 for the R programming environment (Venables and Ripley 2010).

Identification of non-mammalian vertebrates—Although our focus here is on mammals, skeletal counts of other vertebrates from Pacheco 2 are reported to aid taphonomic interpretations. Non-mammalian vertebrates are not known from Pacheco 1.

Radiocarbon dating

Samples were analyzed by accelerated mass spectrometry (AMS) radiocarbon dating at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory (Livermore, California, U.S.A.). Eight bone samples from Pacheco 2, each from a different individual organism, were analyzed. We have not attempted radiocarbon dating of the fossil materials from Pacheco 1. Preparation procedures followed Brown et al. (1988) and Bronk Ramsey et al. (2004). To obtain collagen, samples were decalcified using 0.25N HCl. The collagen was then gelatinized at 58°C for 15 hours, and the gelatin samples were ultra-filtered to remove 30kD fractionation. Finally, the samples were lyophilized and then graphitized for AMS analysis.

Taphonomic analyses

For taphonomic and environmental interpretations of the fossil assemblages from Pacheco 1 and Pacheco 2, the number of identified specimens (NISP) and the minimum number of individuals (MNI) were counted for each taxon following the method of Lyman (1994). In this paper, the NISP is the number of individually-identifiable skeletal parts. In addition, we examined: (1) the weathering stages of mammalian bones

from the two localities following the criteria of Behrensmeyer (1978) and Andrews (1990: table 1.3); (2) selected skeletal elements from Pacheco 2 for digestive-acid etchings, breakages, and gnawing marks produced by predators and rodents; and (3) the proportions of adults and juveniles of small mammals based on epiphyseal fusion in humeri and femora. For the assessment of weathering stages of megaherbivore bones, we followed Behrensmeyer (1978) and recorded the most advanced stage of weathering present on at least 1 cm² of the bone surface.

As discussed below, the high concentration of bones and the taxonomic composition of vertebrates from Pacheco 2 suggested that the bulk of the skeletal remains were originally concentrated by owl pellets. Following the approach of Terry (2007), we further tested this hypothesis with a linear discriminant analysis that assigns a given bone assemblage to a predator type (owl, diurnal raptor, or mammalian carnivore) based on the frequencies of skeletal elements. The reference data on 38 modern assemblages of owl pellets (representing 11 species), diurnal raptor pellets (three species), and carniv-

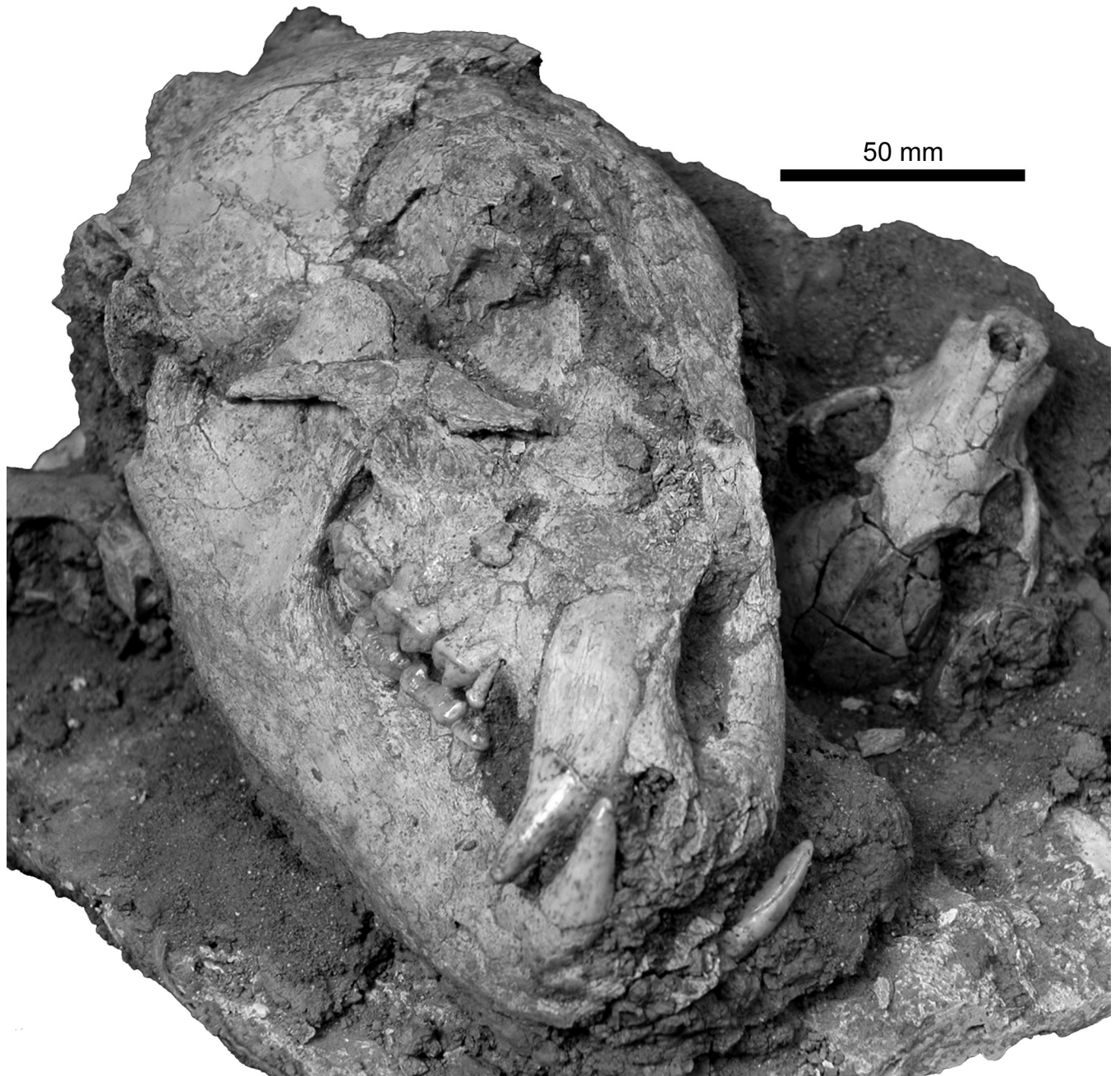


Figure 2. Skulls of *Ursus* cf. *U. americanus* (UCMP 190510), *Procyon lotor* (UCMP 190509), and *Neotoma fuscipes* (UCMP 190508) from Pacheco 2, embedded in a block of original sediment. Scale bar = 50 mm.

oran scats (seven species) were adopted from the compilation by Terry (2007: appendix 1). We recalculated some of the skeletal element frequencies by setting the number of incisors per individual organism to 4 instead of 2 (see Appendix), and applied square-root arcsine transformation to all frequencies. The jackknife re-classification success rates were then obtained for all possible combinations of 7 skeletal elements to select the set of elements with the highest classification accuracy, and the predator type for the Pacheco 2 mammalian assemblage (excluding the bones of *Procyon lotor* and *Ursus cf. U. americanus*) was retrodicted using this set of elements. This discriminant analysis was performed with the MASS package Version 7.3-5 for the R programming environment (Venables and Ripley 2010).

Institutional abbreviations: **MVZ**, Museum of Vertebrate Zoology, University of California, Berkeley, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, USA.

Other abbreviations: **APL**, anteroposterior length; **CV**, Haldane's (1955) sample-size adjusted coefficient of variation; **MNI**, minimum number of individuals; **NALMA**, North American Land Mammal Age; **NISP**, number of identified specimens; **RCYBP**, radiocarbon years before present; **TL**, transverse length.

SYSTEMATIC PALEONTOLOGY

The vertebrate taxa from Pacheco 1 and 2 are listed in Tables 1 and 2, respectively. Here we provide the criteria for the identification of mammalian taxa. Except for the genus *Otospermophilus* (for recent taxonomic revision of the genus *Spermophilus*, see Helgen et al. 2009), the classification of extant mammals follows Wilson and Reeder (2005). The supraspecific classification of extinct taxa follows McKenna and Bell (1997). Individual specimen data including skeletal elements represented are accessible through the online collection database of the UCMP (<http://ucmpdb.berkeley.edu/>).

ORDER: PILOSA Flower 1883

FAMILY: MEGALONYCHIDAE Gervais 1855

GENUS: *MEGALONYX* Harlan 1825

Megalonyx jeffersonii Desmarest 1822
(Figs. 3–5)

Referred specimens—UCMP locality V77117 (Pacheco 1): UCMP 149192, left tibia; UCMP 190483, anterior caudal vertebra.

Remarks—The left tibia (UCMP 149192; Figs. 3–5) differs from those of *Paramylodon* in being less robust and having two tendinal grooves on the medial malleolus (Stock 1925), and from those of *Nothrotheriops* in having a wider diaphysis (the narrowest portion measures 84 mm, which is 25–49% wider than those reported for *N. shastensis* (Stock 1925: table 37), a more triangular medial femoral facet, the greatest development of the tuberosity for the attachment of patellar ligament directly anterior to the gutter separating the medial and lateral femoral facets, and a medial malleolus

Table 1. Vertebrate taxa from Pacheco 1 (UCMP locality V77117) and their abundances.

Taxon	NISP	MNI
Mammalia		
Pilosa		
<i>Megalonyx jeffersonii</i>	1	1
<i>Paramylodon harlani</i>	1	1
Proboscidea		
Proboscidea indet.	3	1
<i>Mammuthus</i> sp.	5	1
<i>Mammut americanum</i>	1	1
Artiodactyla		
<i>Camelops</i> cf. <i>C. hesternus</i>	1	1
Perissodactyla		
<i>Equus</i> sp.	7	1
Mammalia indet.	4	1
Total:	23	6

with a shallower lateral tendinal groove (Stock 1925). UCMP 149192 is morphologically indistinguishable from the tibia of *Megalonyx jeffersonii* described and illustrated by Leidy (1855), and is referred to this species based on the linear dimensions (Table 3) that are very close to the measurements reported by Leidy (1855) but are considerably larger than those of *M. leptostomus* (Hirschfeld and Webb 1968) and those inferred for *M. wheatleyi* based on measurements of astragali reported by McDonald et al. (2000).

The anterior caudal vertebra (UCMP 190483; Table 3) differs from those of *Paramylodon* in having transverse processes that extend posterolateral (rather than directly lateral) to the axis of the centrum (Leidy 1855: plate 7, Stock 1925: plates 6, 18, 29, H.G. McDonald *personal communication*, May 3, 2011), and those of *Nothrotheriops* in having transverse processes with more bulbous ends (Leidy 1855, Stock 1925: plate 6). In addition, the bulbous protuberances lateral to the prezygapophyses appear to be characteristic of *Megalonyx* (Leidy 1855: plate 7). This specimen is tentatively referred to *M. jeffersonii* following the identification of the tibia described above.

FAMILY: MYLODONTIDAE Gill 1872

GENUS: *PARAMYLODON* Brown 1903

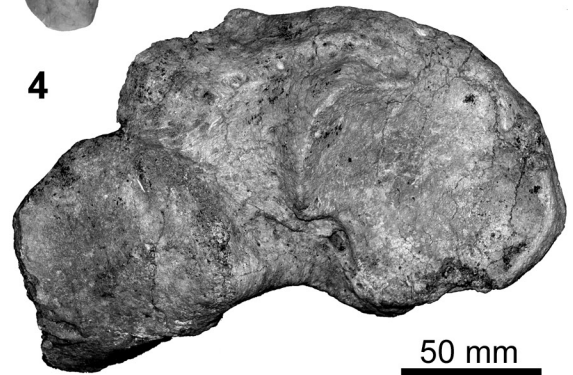
Paramylodon harlani Owen 1840

Referred specimen—UCMP locality V77117 (Pacheco 1): UCMP 190487, distolateral fragment of right femur.

Remarks—The referred specimen preserves most of the lateral epicondyle and the lateral condyle. The maximum diameter of the lateral condyle in lateral view is 83 mm, and is comparable to the mean for 26 specimens of *Paramylodon harlani* (88.7 mm) reported by Stock (1925). It differs from the corresponding portions of femora of *Megalonyx* and

Table 2. Vertebrate taxa from Pacheco 2 (UCMP locality V78027) and their abundance.

Taxon	NISP	MNI
Actinopterygii	12	1
Amphibia	135	17
Testudines	22	1
Squamata	324	9
Aves	374	23
Mammalia		
Soricomorpha		
Soricidae		
<i>Sorex ornatus</i>	76	21
Talpidae		
<i>Scapanus latimanus</i>	25	2
<i>Scapanus</i> sp.	1	1
<i>Scapanus</i> total	26	2
Chiroptera		
Vespertilionidae		
<i>Antrozous</i> sp.	19	3
<i>Eptesicus</i> sp.	3	1
<i>Lasiurus</i> sp.	2	1
Unidentified chiropterans	2	1
Chiroptera total	26	5
Carnivora		
Canidae		
<i>Urocyon cinereoargenteus</i>	1	1
Procyonidae		
<i>Procyon lotor</i>	45	1
Ursidae		
<i>Ursus</i> cf. <i>U. americanus</i>	114	1
Lagomorpha		
Leporidae		
<i>Sylvilagus bachmani</i>	86	6
Rodentia		
Sciuridae		
<i>Otospermophilus beecheyi</i>	131	6
<i>Tamias</i> sp.	1	1
Geomyidae		
<i>Thomomys</i> sp.	1007	57
Heteromyidae		
Perognathinae indet.	25	3
Cricetidae		
<i>Microtus californicus</i>	15	15
<i>Microtus longicaudus</i>	3	3
<i>Microtus</i> sp.	438	51
<i>Microtus</i> total	456	51
<i>Neotoma fuscipes</i>	744	39
<i>Peromyscus californicus</i>	20	7
<i>Peromyscus maniculatus</i>	6	3
<i>Peromyscus truei</i>	2	1
<i>Peromyscus</i> sp.	497	60
<i>Peromyscus</i> total	525	60
<i>Reithrodontomys</i> sp.	2	1
Mammalia total:	3265	255

**Figures 3-5.** Left tibia of *Megalonyx jeffersonii* (UCMP 149192) from Pacheco 1. **3.** Anterior view. **4.** Proximal view, anterior to the top. **5.** Distal view, anterior to the top. Scale bars = 50 mm.

Nothrotheriops in having a more prominent lateral epicondyle and a deeper, more cylindrical lateral condyle that is anteriorly confluent with the patellar groove (Leidy 1855: plate 11, Stock 1925: plates 12, 13, 38, 39).

ORDER: PROBOSCIDEA Illiger 1811

FAMILY: ELEPHANTIDAE Gray 1821

GENUS: *MAMMUTHUS* Brookes 1828

Mammuthus sp.

Referred specimens—UCMP locality V77117 (Pacheco 1): UCMP 153920, tooth fragments; UCMP 190482, right tibia.

Remarks—The tooth specimens (UCMP 153920) are too fragmentary to be identified as specific teeth or to allow for accurate calculation of lamellar frequencies necessary for species identification (cf. Maglio 1973).

The right tibia (UCMP 190482) lacks both proximal and distal epiphyses, and is missing most of the anterior surface due to breakage. This specimen is tentatively referred to *Mammuthus* based on the broad shelf lateral to the two longitudinal ridges on the posterior surface of the diaphysis, which distinguishes it from the tibiae of the gomphotheres *Stegomastodon* and *Rhynchotherium*. Furthermore the proximolateral surface of the diaphysis is more concave than in *Mammuth americanum* (Olsen 1979: fig. 27).

FAMILY: MAMMUTIDAE Hay 1922

GENUS: *MAMMUT* Blumenbach 1799

Mammuth americanum Kerr 1792

Referred specimen—UCMP locality V77117 (Pacheco 1): UCMP 119071, mandible with Rm3 and Lm3.

Remarks—The specific identification is based on the presence of well-developed pentalophid on m3 (Saunders 1996). The mean dimensions of m3 are approximately 177 mm in anteroposterior length and 77 mm in transverse length. The former is comparable to the mean m3 length of 164.0–194.0 mm reported for *Mammuth americanum* (Lambert and Shoshani 1998).

Proboscidea indet.

Referred specimens—UCMP locality V77117 (Pacheco 1): UCMP 190480, cranial fragment with right occipital condyle; UCMP 190481, cranial fragment; UCMP 190485, proximal fragment of radius.

ORDER: ARTIODACTYLA Owen 1848

FAMILY: CAMELIDAE Gray 1821

GENUS: *CAMELOPS* Leidy 1854

Camelops cf. *C. hesternus* Leidy 1873

Referred specimens—UCMP locality V77117 (Pacheco 1): UCMP 190486, lumbar vertebra.

Remarks—The referred specimen is distinguishable from similarly sized vertebrae of *Bison* based on the shallower ventrolateral excavation of the centrum. The effectively platycoelous articular surfaces of the centrum, dorsoventrally thick

Table 3. Measurements (mm) of specimens of *Megalonyx jeffer-sonii* from Pacheco 1.

Measurement	UCMP 139261
Tibia	
Greatest length ¹	347
Length of anterolateral surface	295
Maximum breadth of proximal end	200
APL of proximal end	101
Maximum breadth of distal end	160
Minimum mediolateral width of diaphysis	84
	UCMP 190483
Caudal vertebra	
Centrum APL	39
Centrum mediolateral width	63
Centrum dorsoventral depth	55
Width across transverse processes	134

¹Measured between the proximal extremity of the gutter separating the medial and lateral femoral facets and the distal extremity of the medial malleolus

transverse processes, and notably well-developed episphenial processes above the postzygapophyses are all consistent with the description of lumbar vertebrae for the genus *Camelops* (Webb 1965). The size of the specimen (57.0 mm in width across the postzygapophyses, 89.5 mm in centrum APL) is also comparable to those reported for *Camelops hesternus* from Rancho La Brea, California (Webb 1965: table 8).

ORDER: PERISSODACTYLA Owen 1848

FAMILY: EQUIDAE Gray 1821

GENUS: *EQUUS* Linnaeus 1758

Equus sp.

Referred specimen—UCMP locality V77117 (Pacheco 1): UCMP 147540, isolated LDP2, LDP3, LDP4, RDP3, Rdp3, probable fragment of Rdp2, and RM1.

Remarks—Because of the roughly equivalent wear stages of all deciduous premolars, the tight fit of the left upper deciduous premolars, and the presence of an unworn upper molar, these elements appear to have belonged to the same young individual. Specific identification has not been attempted because the permanent teeth are not well-preserved and the taxonomy of North American *Equus* in the fossil record is unresolved (Scott 2004).

ORDER: SORICOMORPHA Gregory 1910

FAMILY: SORICIDAE Fischer 1814

GENUS: *SOREX* Linnaeus 1758

Sorex ornatus Merriam 1895

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190557, left dentaries; UCMP 190973, right dentaries; UCMP 190974, right maxillae; UCMP 190975, left maxillae; UCMP 190976, right incisors; UCMP 190977, isolated left incisors and left lower molars.

Remarks—All sorcid fossils from Pacheco 2 are assigned to the same species based on very limited size variation ($CV = 2.2\%$ for m1 APL) and the lack of qualitative morphological variation that would clearly indicate the presence of multiple species.

In comparison to the 12 extant species of sorcids in California, the craniodental elements from Pacheco 2 differ from those of: *Notiosorex* in having strongly-pigmented tooth enamel and molars with more angular outline in occlusal view; subgenus *Sorex* of genus *Sorex* in lacking postmandibular foramen (Junge and Hoffmann 1981); *S. bendirii*, *S. palustris*, and *S. sonomae*, in having significantly smaller m1 APL ($n = 19$, mean = 1.44 mm, $P < 0.001$ for the Welch's test); *S. tenellus* in having significantly larger m1 APL ($P < 0.001$); *S. preblei* and *S. lyelli* in having the upper third unicuspid tooth that is shorter than the upper fourth unicuspid tooth (Junge and Hoffmann 1981, Cornely et al. 1992); *S. monticolus* and *S. vagrans* in having significantly smaller m3 trigonid relative to m3 talonid (Table 4); and *S. vagrans* in having less angular ectoloph of upper molars and less flat labial wall of m3. In contrast, the presence of pigmented ridges on the lingual cingula of unicuspid teeth in the Pacheco 2 dental remains is diagnostic of the subgenus *Otiosorex* of genus *Sorex* (Junge and Hoffmann 1981), and the anteroposterior length of m1 as well as the size of m3 trigonid relative to m3 talonid is indistinguishable from those of the extant *S. ornatus* (Table 4).

These specimens represent the first unambiguous record of the species from Quaternary fossil localities in the San Francisco Bay region (cf. Graham and Lundelius 2010).

FAMILY: TALPIDAE Fischer 1814

GENUS: *SCAPANUS* Pomel 1848

Scapanus latimanus Bachman 1842

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 119287, clavicle; UCMP 125567, right and left maxillae, dentary, isolated Rp4, isolated upper and lower right and left molars, fragments of humerus, fragments of ulna, distal fragment of femur, intermediate phalanx.

Remarks—The referred specimens were described by Hutchison (1987).

Scapanus sp.

Referred specimen—UCMP locality V78027 (Pacheco 2): UCMP 190719, fragment of edentulous left dentary.

Remarks—The referred specimen lacks the pronounced labial excursion of molar alveoli that typifies *Scapanus latimanus* (cf. Hutchison 1987), and has a significantly longer m3 (anteroposterior length across m3 alveoli = 5.3 mm) than in the dentary fragment of UCMP 122567 and the modern

Table 4. Mean m3 trigonid/talonid size ratios of *Sorex*. The size was calculated as the product of the anteroposterior length and the labiolingual width. The Bonferroni-adjusted P -values are for the Welch's test for an equal mean with the Pacheco sample.

Species	n	Mean trigonid/ talonid		P
		s		
<i>S. monticolus</i>	10	0.62	0.06	< 0.001
<i>S. vagrans</i>	10	0.59	0.07	0.019
<i>S. ornatus</i>	10	0.53	0.06	0.248
Pacheco 2	17	0.50	0.07	—

specimens of *S. latimanus* that we examined. In these respects, the specimen resembles *Scapanus townsendii*, but is still distinct in having a relatively short tooth row.

ORDER: CHIROPTERA Blumenbach 1779

FAMILY: VESPERTILIONIDAE Gray 1821

GENUS: *ANTROZOUS* Allen 1862

Antrozous sp.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190559, right dentaries; UCMP 190560, isolated Rc1s and Rp3; UCMP 190561, left dentaries; UCMP 190563, isolated RC1, RP4, and right and left upper molars; UCMP 190564, right maxilla with P4-M3; UCMP 190804, right maxilla with P4.

Remarks—In comparison to the corresponding elements of extant vespertilionids in California, the dental remains from Pacheco differ from those of: *Euderma*, *Lasionycteris*, *Myotis*, *Pipistrellus*, and *Plecotus* in being considerably larger; *Lasiurus* in having longer P4, M1, M2, and p4 (P4 APL = 1.43–1.49 mm, M1 APL = 2.00–2.20 mm, M2 APL = 2.20–2.34 mm, p4 APL = 1.34 mm), and an m3 with a smaller talonid relative to the trigonid; *Eptesicus* in having longer P4, M2, and p4, more robust lower cheek teeth, and M3 with reduced protocone and no metacone (Allen 1893, Czaplewski et al. 2008). Additionally, UCMP 190564 has M1 and M2 with the preprotocrista extending to the anterior base of paracone and the postprotocrista extending to the base of metacone, which are characteristic of the genus *Antrozous* (Czaplewski et al. 2008). The lingual portions of M1 and M2 of UCMP 190564, however, have more quadrate outline than in the sole extant species of the genus, *A. pallidus*, owing to greater posterolingual expansion of the teeth. The specific identity of the specimens is thus uncertain.

According to the Faunmap II database (Graham and Lundelius 2010), chiropteran fossils from the Quaternary of northern California are known from only three other localities, all of which are located more than 250 km from Pacheco 2.

GENUS: *EPTESICUS* Rafinesque 1820

Eptesicus sp.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190535, RM2; UCMP 190562, right dentary; UCMP 190783, LM2.

Remarks—The same characters that distinguish *Antrozous* from *Euderma*, *Lasionycteris*, *Lasiurus*, *Myotis*, *Pipistrellus*, and *Plecotus* are observed for these specimens. In addition, the specimens from Pacheco differ from those of *Antrozous* in having anteroposteriorly shorter M2 (APL = 1.91–1.94 mm) with greater posterolingual expansion and m3 with anteroposteriorly more compressed trigonid. Consistent with the characteristics of the genus *Eptesicus*, the upper molars from Pacheco lack both paraloph and metaloph, and the myotodont m3 (i.e., the postcrisid reaches the entoconid rather than hypoconulid) has a thick labial cingulum (Czaplewski et al. 2008). The talonid of m3 is labiolingually wider (talonid TL = 0.43 mm) than in modern specimens of the only species in California, *Eptesicus fuscus*, so the specific identity of fossil specimens is uncertain. The specimens reported here represent only the second record of the genus from Quaternary fossil localities in the west coast of North America (cf. Graham and Lundelius 2010).

GENUS: *LASIURUS* Gray 1831

Lasiurus sp.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190776, RP4; UCMP 190949, left dentary.

Remarks—The fossil elements resemble those of *Lasiurus cinereus* and differ from those of *Antrozous pallidus* and *Eptesicus fuscus* in: (1) the rounded curvature of the anterior end of the dentary, reflecting the anteriorly-wide snout; (2) the ventral projection of the anteroventral border of the dentary along the mandibular symphysis; (3) the ventrally expansive masseteric fossa; and (4) the anteroposteriorly highly-compressed P4, p3, and p4 (P4 APL = 0.91 mm, APL across p3 and p4 alveoli = 1.09 mm). The specimens reported here represent the first record of the genus from Quaternary fossil localities in northern California (cf. Graham and Lundelius 2010).

ORDER: CARNIVORA Bowdich 1821

FAMILY: CANIDAE Fischer 1817

GENUS: *UROCYON* Baird 1857

Urocyon cinereoargenteus Schreber 1775

Referred specimen—UCMP locality V78027 (Pacheco 2): UCMP 190558, RM1.

Remarks—The heavily-worn M1 is distinguishable from the available comparative specimens of *Vulpes macrotis* and *V. vulpes* in (1) lacking a clear indication of paraconule, (2) having the metaconule that is nearly as robust as the protocone, (3) having anteroposteriorly more symmetrical lingual border, (4) having a metacone that is more or less aligned with the metaconule and the hypocone, (5) being intermediate in size between *V. macrotis* and *V. vulpes*. The specimen is indistinguishable from the M1s of *Urocyon cinereoargenteus*, the sole extant species of the genus in continental North

America (Wilson and Reeder 2005).

This specimen represents the first unambiguous record of the genus from Quaternary fossil localities in the San Francisco Bay region (cf. Graham and Lundelius 2010).

FAMILY: PROCYONIDAE Gray 1825

GENUS: *PROCYON* Storr 1780

Procyon lotor Linnaeus 1758

(Fig. 2)

Referred specimen—UCMP locality V78027 (Pacheco 2): UCMP 190509, cranium; UCMP 190913, isolated vertebrae, sternebra, fragments of left pelvis, left ulna, left fibula, left calcaneum, right and left metapodials, phalanges, and incisors.

Remarks—The variety of skeletal elements and the MNI of 1 suggest that they belonged to a single individual. The skeletal elements from Pacheco do not differ appreciably from those of modern specimens of *P. lotor*, the only extant species of the genus in continental North America (Wilson and Reeder 2005).

These specimens represent the first record of the genus from Quaternary fossil localities in the San Francisco Bay region (cf. Graham and Lundelius 2010).

FAMILY: URSIDAE Fischer 1817

GENUS: *URSUS* Linnaeus 1758

Ursus cf. *U. americanus* Pallas 1780

(Fig. 2)

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190510, skull; 190565, fragmentary postcrania including vertebrae, sternebrae, ribs, left ischium, right and left scapulae, right and left humeri, left radius, left ulna, right and left femora, right and left fibulae, podials, metapodials, phalanges, sesamoids, and incisors.

Remarks—The variety of skeletal elements, the MNI of 1, and the consistent lack of fused epiphyses in long bones suggest that they belonged to a single young individual.

According to Gordon (1977), an M2 APL of less than 31 mm and an m1 APL of less than 20.4 mm reliably distinguish modern specimens of *Ursus americanus* from those of *U. arctos*. By these criteria, the M2 APL of UCMP 190510 (28.8 mm) is indicative of *U. americanus*, while the m1 APL of 21.9 mm suggests that it represents *U. arctos*. With respect to the m1 length, however, one of the modern specimens of *U. americanus* that we examined (MVZ 81581, collected in California in 1938) measured 21.6 mm. Further, m1 APLs exceeding 20.4 mm are not uncommon in fossil specimens of *U. americanus* from late-Pleistocene localities of North America (Graham 1991: tables 5, 6). On the other hand, M2 APLs of less than 34 mm are rare in *U. arctos* (Kurtén and Anderson 1980) and an M2 APL less than 31 mm is apparently unknown in fossil specimens (Graham 1991: fig. 4). The widest portion of the M2 located in the middle one-third of the M2 length and the M2 APL/M1 APL ratio of 1.47 are consistent with *U. americanus* (cf. Gordon 1977).

ORDER: LAGOMORPHA Brandt 1855

FAMILY: LEPORIDAE Fischer 1817

GENUS: *SYLVILAGUS* Gray 1867

Sylvilagus bachmani Waterhouse 1839

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190484, left maxillae; UCMP 190512, right calcanea; UCMP 190518, left calcanea; UCMP 190521, fragments of left humeri; UCMP 190523, distal fragment of femur; UCMP 190526, left tibiae; UCMP 190529, right dentaries; UCMP 190530, metapodials; UCMP 190533, right maxillae; UCMP 190534, left dentaries; UCMP 190566, isolated upper and lower premolars and molars; UCMP 190567, cranial fragments; UCMP 190656, LP2; UCMP 190699, right upper premolar or molar; UCMP 190769, Rm3; UCMP 190809, left ulna; UCMP 190810, right tibiae; UCMP 190857, right scapulae; UCMP 190878, right ulnae; UCMP 190891, left astragali; UCMP 190892, right astragali; UCMP 190902, vertebrae.

Remarks—The craniodental elements are considerably smaller than those of *Lepus* but larger than those of *Brachylagus*. The lack of strongly-crenulated ridges separating the anterior and posterior lobes of P4, M1, and M2 is characteristic of *Sylvilagus bachmani*, and distinguishes the Pacheco specimens from *S. audubonii* as well as *S. nuttallii* (Chapman 1974, 1975, Chapman and Willner 1978). The sub-equal transverse widths of the anterior and posterior lobes of p4-m2 further distinguish the fossil specimens from *S. nuttallii* (Chapman 1975).

ORDER: RODENTIA Bowditch 1821

FAMILY: SCIURIDAE Fischer 1817

GENUS: *OTOSPERMOPHILUS* Brandt 1844

Otospermophilus beecheyi Richardson 1829

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190537, left dentaries; UCMP 190538, left maxillae; UCMP 190539, right maxillae; UCMP 190540, RP3s; UCMP 190541, RM1s; UCMP 190542, RP4s; UCMP 190543, LM1s; UCMP 190544, Rm2; UCMP 190545, Lm2s; UCMP 190546, Rm3s; UCMP 190547, Lm3s; UCMP 190548, Lp4s; UCMP 190549, LP4s; UCMP 190550, RM3; UCMP 190551, RM2s; UCMP 190552, LM3s; UCMP 190553, LM2s; UCMP 190554, Rp4s; UCMP 190555, Rm1s; UCMP 190556, right dentaries; UCMP 190784, right scapulae; UCMP 190785, left scapulae; UCMP 190786, right humeri; UCMP 190787, left humerus; UCMP 190802, right astragali; UCMP 190803, left astragali; UCMP 190805, right calcanea; UCMP 190806, left calcanea; UCMP 190808, right ulnae; UCMP 190811, right tibia; UCMP 190812, left tibiae; UCMP 190816, left ulnae; UCMP 190861, left radii; UCMP 190864, right radii; UCMP 190888, vertebra.

Remarks—The ratio of m3 transverse length to antero-posterior length distinguishes the fossil specimens ($n=7$, mean = 1.039) from modern specimens of *Otospermophilus variegatus* ($n=38$, mean = 0.953, Bonferroni-adjusted P

< 0.001 for the Welch's test) but not from the modern specimens of *O. beecheyi* ($n=32$, mean = 1.060, Bonferroni-adjusted $P=0.53$).

GENUS: *TAMIAS* Illiger 1811

Tamias sp.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190887, Lm3.

Remarks—The referred specimen differs from the m3s of *Ammospermophilus* in having more triangular (rather than rectangular) outline in occlusal view due to more pronounced narrowing of the tooth toward its posterior end, and is distinguishable from all other sciurid genera in California except for *Tamias* sp. based on the small size (m3 APL = 2.16 mm, m3 TL = 1.70 mm). Compared to similar-sized extant species of *Tamias* sp. in California, the m3 from Pacheco resembles those of *T. merriami* and generally differs from those of *T. sonomae* in having (1) a relatively long posterolabial segment of the outline in occlusal view and (2) a relatively wide angle between this segment and the posterolingual segment of the outline (in occlusal view). With only a single tooth available, and without a major quantitative analysis of various species, we are unable to determine the specific identity of the specimen.

The occurrence of *Tamias* sp. at Pacheco 2 is significant because there is no other fossil or modern record of the genus in the eastern San Francisco Bay region (Jameson and Peeters 2004, Graham and Lundelius 2010). The absence of the chipmunks in the eastern Bay region appears to have gained little attention, and is perplexing considering the variety of habitats occupied in the northern Bay region by *T. sonomae* (Best 1993) and in the San Francisco Peninsula and southern Bay region by *T. merriami* (Best and Granai 1994). Drought is considered a major cause of population decline in *T. merriami* (Larson 1987), so the disappearance of the genus from the eastern Bay region may be related to local aridification since the time of deposition at Pacheco 2.

FAMILY: GEOMYIDAE Bonaparte 1845

GENUS: *THOMOMYS* Wied-Neuwied 1839

Thomomys (Megascapheus) sp. Elliot 1903

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 168144-168191, UCMP 168193-168195, UCMP 168197-168200, UCMP 168206-168223, UCMP 190569-190578, 190580-190629, 190631-190643, 190645-190655, 190657-190698, 190700-190711, 190713-190715, 190717, 190718, 190720-190752, 190754-190768, 190770-190775, 190777-190780, 190782, 190793, 190794, 190822, 190838, 190839, 190843, 190846, 190849, 190852, 190870, 190871, 190879, 190890. These specimens represent isolated maxillae, dentaries, teeth, vertebrae, scapulae, humeri, ulnae, fused tibiae and fibulae, calcanea, and astragali.

Remarks—The craniodental elements from Pacheco 2 differ from those of the subgenus *Thomomys* sp. in having: the base of P4 located anterior to the base of I1; P4 with

strong anterior tilt; the infraorbital foramina located anterior to the incisive foramina; narrow and flat anterior enamel plate on the anterior lobe of p4; and the angular process narrowly connected to the posteroventral flange of the dentary (Thaler 1980). When compared to extant species of the subgenus *Megascapheus* sp. in California, the lengths of p4-m2 of the Pacheco specimens ($n = 49$, mean = 6.05 mm) are significantly smaller than those of *Thomomys townsendii* from northeastern California ($n = 17$, mean = 9.96 mm, Bonferroni-adjusted $P < 0.001$ for the Welch's test), but indistinguishable from modern specimens of *T. bottae* from Contra Costa County ($n = 40$, mean = 5.90 mm, Bonferroni-adjusted $P = 0.28$) and from a sample of *T. townsendii* from northwestern Nevada ($n = 9$, mean = 5.93 mm, $P = 0.38$ for the Welch's test). While the occurrence of *T. bottae* would seem geographically more plausible, the occurrences of *Microtus longicaudus* (discussed below) and *Tamias* sp. in the Pacheco 2 assemblage caution against identification of the fossils based solely on the present geographic distributions of candidate species.

FAMILY: HETEROMYIDAE Gray 1868

SUBFAMILY: PEROGNATHINAE Coues 1875

Perognathinae indet.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190536, left dentaries; UCMP 190929, isolated p4s; UCMP 190930, left maxilla; UCMP 190931, isolated lower molars; UCMP 190932, isolated upper molars; UCMP 190936, isolated P4s.

Remarks—The dental remains from Pacheco 2 differ from the corresponding elements of *Dipodomys* in being considerably smaller, and from those of *Microdipodops* in being substantially larger, having M1 and M2 with anteroposteriorly less constricted lingual margin in the occlusal view, and showing less pronounced size decrease from M1 to M2 to M3. The Pacheco specimens can be assigned to the subfamily Perognathinae, but the extant genera *Chaetodipus* and *Perognathus* cannot be distinguished from each other on the basis of dental morphology alone (Wahlert 1993).

FAMILY: CRICETIDAE Fischer 1817

GENUS: *MICROTUS* Schrank 1798

Microtus sp.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190100-190183, 190185-190198, 190200-190206, 190208, 190210, 190212-190235, 190238, 190247-190250, 190252-190459, 190461, 190462-190464, 190466-190479, 190795, 190796, 190799, 190882. These specimens represent isolated maxillae, dentaries, and teeth.

Microtus californicus Peale 1848

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190184, 190199, 190207, 190211, 190236, 190237, 190239, 190240, 190242-190244, 190246, 190251, 190460, 190465. All specimens represent Lm1s.

Microtus longicaudus Merriam 1888

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190209, 190241, 190245. All specimens represent Lm1s.

Summary remarks for *Microtus*

All skeletal elements other than m1 are currently referred to *Microtus* sp. The referred m1s from Pacheco 2 were assigned to species using discriminant function analysis, the details of which were reported elsewhere (McGuire *in press*). Of the 30 fossil m1s analyzed, 15 specimens plotted with modern *M. californicus* and 3 with *M. longicaudus*, whereas the remaining 12 could not be assigned to a particular species with confidence. While *M. californicus* is extant in the San Francisco Bay region, the occurrence of fossil *M. longicaudus* at Pacheco 2 represents a range shift of 160 km eastward and 600 m higher in elevation (McGuire *in press*).

GENUS: *NEOTOMA* Say and Ord 1825

Neotoma fuscipes Baird 1857

(Fig. 2)

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 168189, 168192, 190491-190508, 190511, 190513-190517, 190519, 190520, 190522, 190524, 190525, 190527, 190528, 190712, 190716, 190753, 190781, 190788, 190789, 190813, 190814, 190817, 190821, 190836, 190837, 190844, 190847, 190850, 190853, 190881, 190884, 190889, 190901. These specimens represent isolated cranium, maxillae, dentaries, teeth, vertebrae, scapulae, humeri, radii, ulnae, fused tibiae and fibulae, astragali, and calcanea.

Remarks—In comparison to the five extant species of *Neotoma* in California, the craniodental elements from Pacheco differ from those of: *N. cinerea* in having M1 with shallow angle of anterolingual reentrant (Smith 1997); *N. albigula* in having M3 with medial inflection of the posterolabial fold; *N. lepida* in having M3 with deep lingual reentrant; *N. bryanti* in having a significantly greater mean m1-m3 length (9.64 mm, $n = 7$, Bonferroni-adjusted $P < 0.001$ for the Welch's test). The mean m1-m3 length of Pacheco 2 specimens does not differ significantly from that of a modern sample of *N. fuscipes* (Bonferroni-adjusted $P = 0.09$).

GENUS: *PEROMYSCUS* Gloger, 1841

Peromyscus sp.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190568, right dentaries; UCMP 190819, right humeri; UCMP 190820, left humeri; UCMP 190906, Lm1s; UCMP 190908, Rm3s; UCMP 190909, Lm3s; UCMP 190910, RM2s; UCMP 190911, left dentaries; UCMP 190914, RM1s; UCMP 190915, LM1s; UCMP 190928, Rm2s; UCMP 190933, Lm2s; UCMP 190935, left maxillae; UCMP 190937, Rm1s; UCMP 190941, LM2s; UCMP 190945, right maxillae.

Peromyscus cf. *P. californicus* Gambel 1848

Referred specimens—UCMP locality V78027 (Pacheco

2): UCMP 190912, Rm2s; UCMP 190916, RM1s; UCMP 190917, LM1s; UCMP 190919, LM2s.

Remarks—All specimens were assigned to *P. californicus* based on their large size compared to *P. boylii*, *P. maniculatus*, and *P. truei* (also see the summary remarks below).

Peromyscus cf. *P. maniculatus* Wagner 1845

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190925, RM1s; UCMP 190926, LM1s; UCMP 190939, Lm1.

Peromyscus cf. *P. truei* Shufeldt 1885

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190907, LM1; UCMP 190947, RM1.

Summary remarks for *Peromyscus*

The Shapiro-Wilk test did not reject the normality of measurements for any of the reference samples of extant species ($P=0.12-0.89$). The first and the second discriminant functions ($LD1 = 2.232 M1APL + 15.728 MITL - 23.272$, $LD2 = 14.081 M1APL - 19.050 MITL - 2.645$) account for 94.8% and 5.2%, respectively, of the interspecific variations. Using the jackknife method, 95% of modern specimens of *P. maniculatus* and *P. californicus* (the smallest and the largest of the four species, respectively) were correctly identified, but the classification success rate was only 60% for the modern specimens of *P. boylii* and *P. truei*. The classification function assigned 5 M1s to *P. californicus*, 6 to *P. maniculatus*, and 2 to *P. truei* with the posterior probability of 0.950 or greater (Fig. 6). The remaining 48 M1s could not be assigned to any particular species with the same level of confidence, and are therefore reported as unidentified species.

In addition to the dimensions of M1, we examined the occurrence of a mesostyle and mesoloph on M1, a feature that generally separates two subgenera of the genus considered here: the subgenus *Haplomylomys*, to which *P. californicus* belongs, typically lacks both the mesostyle and mesoloph, whereas the subgenus *Peromyscus*, which includes the other three species analyzed here, typically possesses the mesostyle, mesoloph, or both (Osgood 1909, Hooper 1957, Merritt 1978, Hoffmeister 1981). The absence of a mesoloph and mesostyle in all of the 8 M1s from Pacheco that were assigned to *P. (Haplomylomys) californicus* by the discriminant analysis corresponds to this general observation. With respect to the fossil M1s assigned to *P. maniculatus* and *P. truei*, the frequency of specimens lacking both a mesoloph and mesostyle is high (3 out of 7 and 2 out of 2, respectively) compared to those reported by Hooper (1957) for modern specimens of the two species (4% and 0% of 225 and 30 specimens, respectively). This apparent discrepancy may reflect geographic or temporal variation in molar morphology within each species (Hooper's (1957) sample of *P. maniculatus* and *P. truei* did not include specimens from California), or the presence of extinct morphotypes in the Pacheco sample.

GENUS: *REITHRODONTOMYS* Giglioli 1874

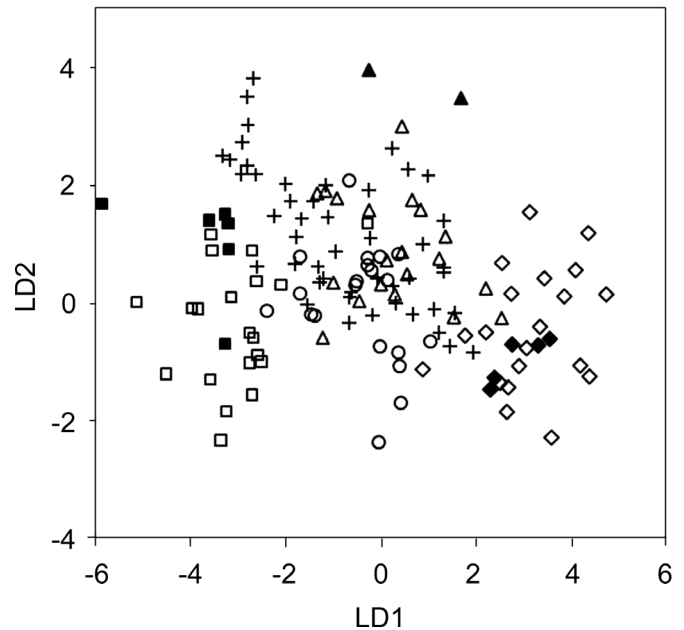


Figure 6. Discriminant function plot of *Peromyscus* species based on M1 dimensions. Open symbols, modern reference specimens; filled symbols, Pacheco 2 specimens. Symbols represent: *Peromyscus maniculatus* (squares); *P. truei* (triangles); *P. boylii* (circles); *P. californicus* (diamonds); and Pacheco 2 specimens that could not be assigned to a particular species with the posterior probability ≥ 0.950 (crosses).

Reithrodontomys sp.

Referred specimens—UCMP locality V78027 (Pacheco 2): UCMP 190934, left dentary; UCMP 190938, right dentary.

Remarks—The anteroconid of m1 (UCMP 190938) is relatively narrow and lacks clear bifurcation of the lingual and labial conulids. Although these characters were used by Wolff (1971) to distinguish *R. raviventris* from *R. megalotis*, our observation of modern specimens suggests that they are not always diagnostic, and preclude definitive identification of the Pacheco specimens.

RESULTS

Radiocarbon dating

Collagen yields of seven of the eight bone samples were too small to produce reliable ages. One bone (CAMS N80421) from Pacheco 2 yielded an age of 405 ± 45 RCYBP.

Taphonomic analyses

Relative abundance of taxa—In total, 23 mammalian skeletal specimens from Pacheco 1 and 3,265 from Pacheco 2 were identified at various taxonomic ranks, representing the minimum of six individuals of six species from Pacheco 1 and 255 individuals of 20 species from Pacheco 2 (Tables 1, 2). In addition, 867 non-mammalian vertebrate fossils from Pacheco 2 were assigned to a ray-finned fish, salamanders, frogs, a turtle, lizards, snakes, and birds, representing at least

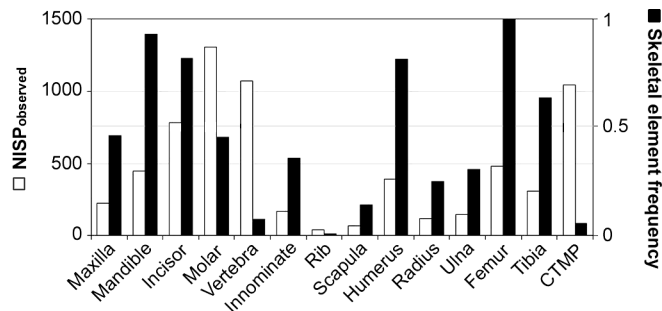


Figure 8. Abundance of skeletal elements of small mammals from Pacheco 2. Open bars, observed NISP; filled bars, untransformed skeletal element frequencies (see Appendix). Incisors and molars here represent isolated teeth. CTMP, the set of podials, metapodials, and phalanges.

numerous fine cracks of the enamel layer, and a narrow but deep trench that penetrates the enamel layer along the labial $\sim 1/2$ of the junction between the anterior cingulum and the rest of the crown. These features may reflect abrasion or digestive corrosion.

Age structure of the Pacheco mammalian assemblages—Among the mammalian remains from Pacheco 1, the tibial diaphysis of *Mammuthus* is the only postcranial element that shows incomplete skeletal growth. The unworn M1 indicates a young age for the individual of *Equus*.

As noted above, all skeletal elements of *Ursus* from Pacheco 2 likely belong to a single individual, and the consistent lack of epiphyseal fusion in the postcranial elements as well as the little-worn upper molars indicate a relatively young age for this individual. On the other hand, the limb bones of *Procyon lotor* have fused epiphyses, and probably represent a fully-grown adult. The limb elements of small mammals are marked by the preponderance of unfused epiphyses and diaphyses. For example, 88% of proximal humeral epiphyses and 87% of distal femoral epiphyses examined are not fused to the diaphyses. Thus, most of the small mammals had not completed skeletal growth at the time of death.

Discriminant analysis of predator type using skeletal element frequencies—Two sets of 3 elements and a set of 4 elements yielded the identical highest overall jackknife reclassification success rate of 86.8%. Of these, the sets of 3 elements were preferred over the set of 4 elements to minimize the number of parameters in the classification function. The

two sets of 3 elements yielded different predictive accuracies for individual predator groups: (1) the classification function based on the frequencies of scapula, vertebra, and innominate identified bone assemblages made by owls, diurnal raptors, and mammalian carnivores with jackknife re-classification success rates of 96% (24/25), 50% (3/6), and 86% (6/7), respectively; (2) the classification function based on the frequencies of scapula, vertebra, and maxilla identified the same assemblages with success rates of 100% (25/25), 33% (2/6), and 86% (6/7), respectively. In comparing these results, we considered the benefit of substantially higher predictive accuracy for diurnal raptor-pellet assemblages (50% vs. 33%) attained by the first set to outweigh the cost of its slightly lower predictive accuracy for owl-pellet assemblages (96% vs. 100%), and therefore selected the first set (consisting of scapulae, vertebrae, and innominates) for use in retrodicting the predator identity for the Pacheco 2 small mammal assemblage. For the selected set of elements, the first and the second discriminant functions ($LD1 = 5.647 f_{scapula} - 7.231 f_{vertebra} + 0.846 f_{innominate} - 1.424$, $LD2 = 4.438 f_{scapula} - 5.851 f_{vertebra} - 4.453 f_{innominate} + 2.834$, where f is the skeletal element frequency) account for 72.2% and 27.8%, respectively, of the variance among predator types.

The classification function using the frequencies of scapula, vertebra, and innominate retrodicted the owls to be the predator type of the Pacheco 2 small mammal assemblage, with a posterior probability of 69.5% (Fig. 10). The posterior probabilities of association with a mammalian carnivore or diurnal raptor were 25.6% and 4.8%, respectively.

DISCUSSION

Taphonomic histories of Pacheco fossils

Taken together, the taphonomic features of the Pacheco 1 assemblage and the limited information concerning the associated sediment are consistent with the death of large mammals in a riparian setting, followed by disarticulation and subaerial weathering for several years before burial in over-bank or stream deposits. As for the Pacheco 2 assemblage, the bulk of the vertebrate fossils appear to have accumulated as owl pellets. These inferences are based on the following considerations.

Accumulation of vertebrate bones at Pacheco 2—The high concentration of bones in the sedimentary pocket of Pacheco 2 (probably not exceeding a few cubic meters in

◀ **Figure 7.** Comparison of relative abundances of small mammals in Pacheco 2 and modern owl pellets. For the central California dataset (second from top), the relative abundance is the proportional number of occurrences in pellets (which should approximate the relative abundance of individuals; see Fitch 1947); for all other datasets, it is the number of individuals expressed as the proportion of total mammals recovered. Non-mammalian vertebrates are excluded from the total counts. Filled bars, great horned owl; open bars, barn owl. The total individual mammals (or occurrences for central California) in the pellets of the great horned and the barn owls are denoted as N_{gh} and N_{barn} , respectively. Data from: Fitch (1947) for central California; Rudolph (1978) for northern California; Boggiatto et al. (2003) for northeastern California; Aigner et al. (1994) for central eastern California; Foster (1926), Hall (1927), Smith and Hopkins (1936) for the San Francisco Bay region. *Counts of *Otospermophilus* include *Spermophilus*, and the counts of perognathines here consist of *Chaetodipus* and *Perognathus*.

Table 5. Frequencies of bone modifications in selected mammalian postcrania from Pacheco 2.

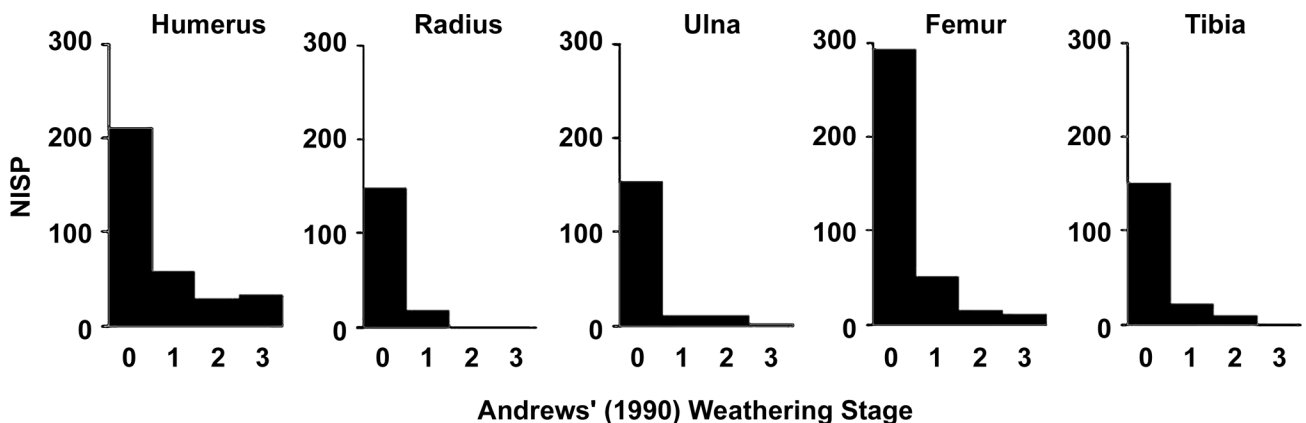
Element	<i>n</i>	Breakage	Acid etching	Punctures	Gnawing
humerus	245	196	6	5	5
radius	167	152	6	0	1
ulna	180	117	5	0	1
femur	368	318	14	3	4
tibia	148	99	3	3	2
Total	1,108	882 (80%)	34 (3%)	11 (1%)	13 (1%)

volume; see Materials and Methods), representing at least 306 individual organisms (Table 2), and the ecological diversity encompassed by the assemblage—from fish to snakes, moles and birds—are suggestive of original bone accumulation by a predator. With respect to the mammalian component of the assemblage, the low abundance of the primarily-diurnal ground squirrel, *Otospermophilus beecheyi* (Fig. 7; Linsdale 1946) seems indicative of pellets produced by nocturnal owls (Smith and Hopkins 1937, Fitch 1947, Maser et al. 1970, Marti and Kochert 1995), especially in the eastern San Francisco Bay region where the species is common today (S.T. *personal observation*, 2010) and abundant in late-Pleistocene fossil assemblages (Wolff 1971, 1975). Of the owls that are present in the region, the barn owl (*Tyto alba*) and the great horned owl (*Bubo virginianus*) are well-known for the breadth of their diet (Fitch 1947, Bosakowski and Smith 1992, Bogiatto et al. 2003). Although there is considerable interregional variation in the taxonomic composition of the prey of these species, the most abundant mammalian genera at Pacheco 2 (*Peromyscus*, *Thomomys*, *Microtus*, and *Neotoma*) appear to be important prey items for the owls where they occur (Fig. 7). The specific identity of the owl, however, cannot be inferred from the available data. We speculate that the more even distribution of the relative abundances of mammalian taxa at Pacheco 2 compared to those for several modern owl pellet assemblages (Fig. 7) may reflect

contributions from multiple owl species (see Andersen 1996 on interspecific nest reuse).

Consistent with predation by an owl (or owls) is the rarity of bones with corrosion or puncture marks, which would likely have been more prevalent had the remains been ingested by diurnal raptors or mammalian carnivores (Andrews and Nesbit Evans 1983, Andrews 1990). The prevalence of young individuals (i.e., those with unfused epiphyses) is also in agreement with predation by an owl (Lyman et al. 2001 and references therein).

Although the patterns of bone breakage in a pellet or scat assemblage can be useful for identifying the predator(s) that produced it (Andrews 1990, Terry 2007), such patterns may be distorted in fossil assemblages by postburial breakage of skeletal elements. In the present study, we expect such breakage to have reduced the frequency of scapula more than those of vertebra and innominate, assuming that fragmented scapulae are particularly prone to destruction or are difficult to identify. This expectation is based on our observation (*unpublished data*) that almost all identified scapular remains are broken and are missing much of the flat body bearing the supra- and infraspinous fossae. In comparison, although remains of innominates are likewise almost all broken, several parts of this element are individually identifiable as belonging to an innominate and have, in fact, been recovered. Vertebrae appear to be the most robust of the 3 elements selected for

**Figure 9.** Weathering stages of selected small mammal bones from Pacheco 2.

discriminant analysis, and, like innominates, broken parts are relatively well-preserved and are usually readily identifiable. Considering the direction of this potential bias in our analysis, we suspect that the original small mammal assemblage from Pacheco 2 was more firmly associated with the modern owl pellet assemblages (Fig. 10), and that the 69.5% posterior probability of owl-mediated accumulation for Pacheco 2 is likely an underestimate.

Occurrences of raccoon bones in association with nests of great horned owls have been documented but are apparently rare (Bosakowski and Smith 1992), and there are no published records of predation on gray foxes (*Urocyon cinereoargenteus*) by any owl. With regard to the carnivoran remains from Pacheco 2, it is notable that the relatively intact skeletons of the raccoon and the black bear show no clear signs of predation or scavenging, suggesting that the individuals died at or near the site of deposition, and that their carcasses were largely, if not entirely, inaccessible to scavengers. Perhaps these carnivorans used a crevice or a small cave (excavated into the alluvial deposit of Pacheco 1) as a shared den, and were drowned when sediment-laden water flooded this space. Alternatively, their carcasses may have been carried by a current and buried after being caught against an obstruction in the river, such as a cut bank, where the current also concentrated bone-laden pellets from a roosting or nesting owl. The cause of death for the gray fox, which is known from a single molar, remains a mystery.

Durations of subaerial exposure—Although the sample size is small, the bones from Pacheco 1 show degrees of weathering corresponding to Stages 1 to 3 of Behrensmeier (1978). In Behrensmeier's (1978) study, these weathering stages were observed for bones of large mammals that had been subaerially exposed for 0 to 15 years under the seasonally-arid climate of Amboseli Basin, Kenya. The majority of Pacheco 1 bones show only minor weathering (Stages 1 or 2) that would correspond to 0 to 6 years of exposure at Amboseli (Behrensmeier 1978). Because of the complexity of environmental factors influencing the rate of weathering (Behrensmeier 1978, Lyman 1994), however, direct comparison of weathering stages between the two sites would be inappropriate without sufficient paleoclimate data for the Pacheco locality. Finally, the wider distribution of weathering stages for Pacheco 1 fossils compared to that for the mammalian bones from Pacheco 2 (Fig. 9) is suggestive of more varied individual taphonomic histories of the former.

Among the selected mammalian postcranial elements from Pacheco 2, more than 90% show either no modification or minor weathering (Fig. 9). These conditions are equivalent to Stages 0 and 1 of Andrews (1990), which he observed for small mammal bones (originally encrusted in owl pellets) after subaerial exposure of 0–2 and 1–5 years, respectively, under the wet temperate climate of Wales (Andrews 1990). Whether similar absolute weathering rates apply to Pacheco 2 fossils is unknown, but the predominance of bones in Stage 0 across all the elements indicates minimum subaerial exposure

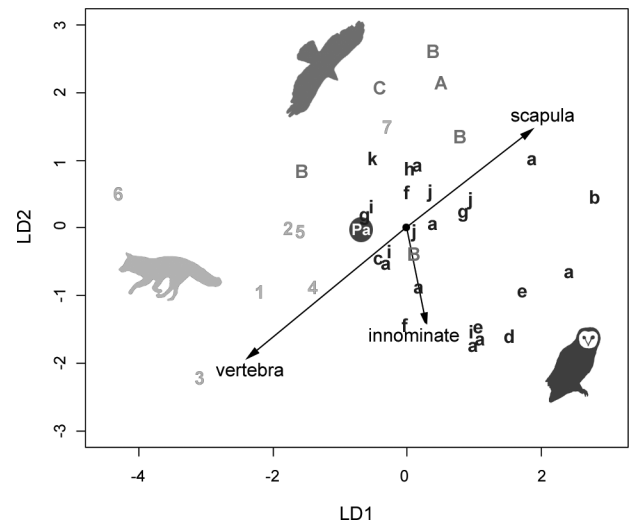


Figure 10. Discriminant function plot of modern predator pellet and scat assemblages and the Pacheco 2 assemblage. Owls (lower-case letters), diurnal raptors (capital letters), and mammalian carnivores (numbers) are plotted based on the frequencies of scapulae, vertebrae, and innominates of their prey. Vectors indicate relative contributions of the elements to the axis scores. Data modified from Terry (2007: appendix 1). See Appendix. Pa, mammalian assemblage from Pacheco 2 (excluding carnivorans); a, Barn owl; b, Great grey owl; c, Great horned owl; d, Snowy owl; e, Long-eared owl; f, Short-eared owl; g, Verreaux eagle owl; h, Spotted eagle owl; i, European eagle owl; j, Tawny owl; k, Little owl; A, Peregrine; B, Common kestrel; C, Hen harrier; 1, White-tailed mongoose; 2, Small-spotted genet; 3, Bat-eared fox; 4, Coyote; 5, Red fox; 6, Arctic fox; 7, Pine marten.

and more homogeneous taphonomic histories of individual elements compared to those of Pacheco 1 fossils.

Skeletal dissociation, transport, and burial—The Pacheco 1 and Pacheco 2 assemblages differ markedly in the completeness of skeletal remains. Each of the taxa from Pacheco 1 is represented by only one or a few elements (Table 1; the isolated teeth of *Equus* are probably derived from paired upper and lower jaws of a single individual). Assuming reasonable sampling effort at Pacheco 1, this indicates high degrees of skeletal dissociation and loss of elements. Because the preserved elements vary widely in size, shape, and density, hydrodynamic sorting does not appear to have been a dominant factor in the formation of this assemblage. At the same time, there is no clear evidence of predation or scavenging for the bones from Pacheco 1. Thus, the incompleteness and the apparently random sampling of skeletal elements at Pacheco 1 may reflect long-distance transportation from the locations of death to the depositional site.

In contrast, much lower levels of skeletal dissociation and loss of elements are evident for *Ursus* and *Procyon lotor* from Pacheco 2, and for the small mammals from the same locality based on the comparatively high ratio of MNI to NISP. These observations suggest relatively rapid burial, which is

also consistent with the short periods of subaerial exposure inferred from the weathering stages of mammalian bones.

Ages of Pacheco localities

A Pleistocene age for the Pacheco 1 assemblage is secure based on the presence of *Mammuthus* (Bell et al. 2004). More precisely, the probable occurrence of *Megalonyx jeffersonii* suggests a later Pleistocene age for the locality. We have not attempted radiocarbon dating of specimens from Pacheco 1.

With respect to Pacheco 2, the applicability of the single radiocarbon age (405 ± 45 RCYBP for CAMS N80421) to the assemblage in general is questionable because all other samples from the locality did not have enough collagen to provide reliable ages. Although it is possible that the successfully-dated bone had escaped weathering by chance, the state of preservation may reflect its mixture with chronologically-older fossils in the same sedimentary pocket, possibly as a result of bioturbation by a burrowing rodent, or the construction activities that accompanied fossil recovery. The anomaly of the radiocarbon age for the Pacheco 2 fossils is further suggested by the extralimital occurrence of *Microtus longicaudus*, which indicates a substantial range shift that is in line with the major distributional changes of small mammals from the late Pleistocene to early Holocene in northern California and North America in general (Graham et al. 1996; but see Moritz et al. 2008 for an example of drastic species range shifts in recent years). The nearly identical taxonomic compositions of the mammalian assemblage from Pacheco 2 and those of the late-Pleistocene Montezuma Formation near Rodeo, California (~18 km northwest of Pacheco; Wolff 1971, 1973, 1975) also make Pacheco 2 compatible with a late-Pleistocene age. Overall, however, the available data are insufficient to refute the possibility that much of the Pacheco 2 assemblage is only a few hundred years old. Additional radiocarbon data are necessary to determine the precise age or a range of ages for the assemblage and establish its temporal relationship to the Pacheco 1 assemblage.

Paleoenvironmental interpretations

The taxonomic composition of the Pacheco 1 assemblage is suggestive of a mosaic of grassland and woodland, and the depositional setting indicates the presence of a stream system. Mixed vegetation is inferred based on the combination of: (1) wide ranges of diet for late Pleistocene *Mammuthus* and *Equus*, with preference for C4 grasses where available (Feranec 2004) but elsewhere subsisting primarily on C3 eudicots (Coltrain et al. 2004); (2) mainly browsing diet reported for *Camelops hesternus* (Akersten et al. 1988) and *Mammuth americanum* (Koch et al. 1998); and (3) co-occurrence of *Paramylodon harlani* and *Megalonyx jeffersonii*, which likely had different habitat preferences (McDonald 1996). It is, however, possible that such taxonomic composition reflects temporal, rather than spatial, heterogeneity of habitat structure (McDonald 1996).

Although most of the mammalian taxa from Pacheco 2 are extant in the eastern San Francisco Bay region, the occurrences of *Microtus longicaudus* and *Tamias* sp. hint at a cooler and wetter local climate than today (cf. Larson 1987, McGuire 2010, in press). Compatible with this interpretation is the presence of several vertebrate taxa with affinities for moist soil, wetlands, or freshwater bodies such as *Microtus californicus*, *Scapanus latimanus*, *Sorex ornatus*, a duck, a heron, a pond turtle, amphibians, and a fish (Table 2 and unpublished data). Also notably, most of the small mammals from Pacheco 2 as well as various reptiles and amphibians are known to associate with stick houses of *Neotoma fuscipes* (Carraway and Verts 1991), so the fossil assemblage likely represents a spatially coherent sample of vertebrates from a typical habitat of *N. fuscipes* in woodland with dense underbrush (Carraway and Verts 1991).

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APPENDIX

Discriminant analysis of predator types using skeletal element frequencies: Methodological details

Selection and preparation of data—We adopted the skeletal element frequency data compiled by Terry (2007: appendix 1), and applied square-root arcsine transformation to all frequencies. The transformed data on mandibles were excluded from the analysis because of their non-normal distribution (Shapiro-Wilk test, $W = 0.867$, $P < 0.01$). The frequencies of isolated incisors, isolated molars, ribs, and the combined set of podials, metapodials, and phalanges are reported below but were excluded from the analysis because we suspected these to be particularly sensitive to postburial breakage and loss, including those resulting from the underwater sieving of sediment used to recover the fossils. Likewise, the frequencies of femora and humeri were excluded because of the prevalence of isolated epiphyses in the Pacheco 2 fossil assemblage.

Following Terry (2007), the frequency of each element in each bone assemblage was calculated as the ratio of the observed NISP to the expected NISP, where the latter is the product of the number of the selected element in an individual organism and the minimum number of individuals required to produce the most abundant element in the assemblage. For this calculation, Terry (2007: appendix 1) apparently set the number of incisors per individual to 2, so we recalculated all the skeletal element frequencies reported in her paper by setting this number to 4 (N.B. Even though the frequencies of incisors are excluded from our analysis, they affect the frequencies of other elements when incisors are incorrectly identified as the most abundant element in a bone assemblage) and using the original data (in the form of raw counts of elements) in Andrews and Nesbit Evans (1983: table 1) and Andrews (1990: table 2.2, appendix table 12). The per-individual numbers of all other elements used in our calculation are as in Terry (2007): mandible, 2; maxilla, 2; molar, 12; vertebra, 58; rib, 26; scapula, 2; humerus, 2; radius, 2; ulna, 2; pelvis, 2; femur, 2; tibia, 2; podials, metapodials, and phalanges combined, 78. Because of the variations in per-individual numbers of elements among taxa, selecting a single set of these numbers contributes to the error in calculated skeletal element frequencies. Nevertheless, we consider the numbers used here to be reasonable for the analysis of assemblages dominated by rodents such as the Pacheco 2 mammal assemblage.

The square-root arcsine transformed data are reported at right. It should be noted that two of the three assemblages in the compilation by Terry (2007: appendix 1) that are labeled as pellet assemblages of the Peregrine are in fact those of the Common kestrel (Andrews 1990: appendix table 12).

Square-root arcsine-transformed skeletal element frequencies for reference assemblages and Pacheco 2 small mammals. Original data from: Terry (2007: appendix 1) for the Great horned owl; Andrews (1990: table 2.2, appendix table 12) for all other raptors; Andrews and Nesbit Evans (1983: table 1) for mammals. **Abbreviations:** **Mand.**, mandible; **Max.**, maxilla; **I/i**, isolated incisors; **M/m**, isolated molars; **Scap.**, scapula; **Hum.**, humerus; **Rad.**, radius; **Vert.**, vertebra; **Inn.**, innominate; **Fem.**, femur; **Tib.**, tibia; **CTMP**, podials, metapodials, and phalanges combined.

Predator	Location	Mand.	Max.	I/i	M/m	Scap.	Hum.	Rad.	Ulna	Rib	Vert.	Inn.	Fem.	Tib.	CTMP
Barn owl	Stratton	1.508	0.664	0.127	0.402	0.694	0.91	0.967	1.077	0.454	0.386	0.807	0.855	1.055	0.554
Barn owl	Barton Turf	1.571	0.774	0.145	0.209	1.19	1.466	1.315	1.425	1.147	0.729	1.239	1.571	1.362	0.669
Barn owl	Makapanang	1.481	1.1	0.306	0.465	1.161	1.129	0.989	0.998	0.925	0.714	1.244	1.09	1.161	0.507
Barn owl	Boomplaas	0.854	1.571	0.264	0.272	0.683	0.83	0.796	0.785	0.335	0.477	0.808	0.866	0.819	0.294
Barn owl	Salthouse	1.01	0.827	0.328	0.183	0.869	0.973	0.785	0.853	0.386	0.294	1.263	1.571	1.571	0.177
Barn owl	Gedi	1.571	1.107	0.226	0.168	0.421	0.651	0.504	0.58	0.09	0.183	0.615	0.651	0.818	0.114
Barn owl	Hula	1.44	1.345	0.514	0.409	0.802	0.956	0.835	0.92	0.486	0.517	0.956	0.973	0.991	0.386
Barn owl	Wookey Hole	1.571	0.892	0.32	0.498	0.813	1.019	1.12	0.863	1.143	0.279	0.849	1.011	1.571	0.432
Great grey owl	Oulu	1.444	1.186	0.542	0.467	0.864	1.209	0.895	1.012	0.488	0.219	1.103	1.143	1.259	0.214
Great horned owl	San Juan Island, WA, USA	1.571	0.58	0	0	0.785	1.107	0.991	0.991	1.061	0.564	0.785	0.685	0.886	0.764
Snowy owl	Bathurst Island	1.007	0.857	0.388	0.333	0.968	1.134	1.007	0.93	1.138	0.499	1.301	1.238	1.38	0.81
Long-eared owl	Hindshill	1.476	1.202	0.325	0.33	0.645	1.115	0.766	0.926	0.318	0.209	1.217	1.295	1.231	0.171
Long-eared owl	Prestwick-Carr	1.206	1.139	0.23	0.268	0.947	1.286	1.257	1.231	0.836	0.537	1.206	1.35	1.481	0.455
Short-eared owl	Ross	1.15	1.107	0.262	0.53	0.752	1.388	1.15	1.197	0.583	0.515	1.028	1.15	1.249	0.524
Short-eared owl	Cefn Wilfre	1.571	0.637	0.723	0.317	0.392	1.179	0.764	0.785	0.226	0.188	0.659	0.956	0.89	0.355
Verreaux eagle owl	Serengeti	1.234	1.571	0.279	0.459	0.851	0.963	0.873	0.895	0.597	0.627	0.631	0.72	0.785	0.478
Verreaux eagle owl	Olduvai	1.571	1.345	0.376	0.571	0.917	1.187	1.266	1.095	0.573	0.499	0.846	1.217	1.173	0.389
Spotted eagle owl	Lake Baringo	1.571	0.747	0.478	0.25	0.343	0.757	0.386	0.612	0.162	0.135	0.602	0.852	0.691	0.221
European eagle owl	Oster Malma (pellets)	1.115	0.926	0.54	0.375	0.491	0.842	0.702	1.047	0.214	0.315	0.785	1.403	0.926	0.221
European eagle owl	Oster Malma (nest)	1.433	0.513	1.037	0.717	0.596	1.126	0.555	0.879	0.256	0.414	0.615	0.86	0.897	0.422
European eagle owl	Qatar	1.117	1.142	0.609	0.501	1.117	1.433	1.225	1.256	0.425	0.682	1.195	1.328	0.962	0.729
Tawny owl	Ross	1.266	1.134	0.682	0.27	0.454	0.889	0.889	0.823	0.296	0.127	0.836	1.343	1.457	0.219
Tawny owl	Kirkby	1.571	0.968	0.503	0.11	0.388	0.93	0.524	0.714	0.055	0.142	0.714	0.785	0.749	0.127
Tawny owl	Rhulen	1.38	0.821	0.544	0.221	0.481	0.714	0.678	0.821	0.27	0.256	0.785	0.968	0.821	0.241
Little owl	Wornack	1.09	0.481	0.524	0.577	0.388	1.09	0.388	0.785	0.27	0.235	0.481	1.183	1.571	0.335
Peregrine	Rhulen	0.702	0.869	0.615	0.688	0.615	0.956	0.421	1.047	0.486	0.26	0.421	1.279	1.047	0.346
Common kestrel	Rhulen	1.571	1.571	1.209	0.594	0	0.785	0.361	0.659	0	0.063	0.361	0.785	0.785	0.1
Common kestrel	Bleadney	1.415	1.461	1.033	0.775	0.524	0.857	0.577	0.761	0.159	0.194	0.313	0.881	0.773	0.336

Square-root arcsine-transformed skeletal element frequencies for reference assemblages and Pacheco 2 small mammals. (cont.)

Predator	Location	Mand.	Max.	I/i	M/m	Scap.	Hum.	Rad.	Ulna	Rib	Vert.	Inn.	Fem.	Tib.	CTMP
Common kestrel	Somerdale	1.466	0.785	1.022	0.698	0.584	1.022	0.664	0.818	0.232	0.223	0.619	0.84	0.895	0.283
Common kestrel	Ross	1.319	0.785	0.627	0.292	0.594	1.124	0.849	0.849	0.346	0.352	0.849	0.978	0.785	0.432
Hen harrier	Orkney	1.422	1.362	0.987	0.552	0.258	0.785	0.485	0.459	0.235	0.095	0.299	0.485	0.459	0.232
White-tailed mongoose	Meswa Bridge, Kenya	0.972	0.923	1.357	0.793	0.497	1.571	0.441	0.877	0.48	0.563	0.599	1.13	0.648	0.545
Small-spotted genet	Naboomsprit, South Africa	1.493	0.745	0.774	0.344	0.185	0.796	0.355	0.413	0.063	0.25	0.493	0.884	0.652	0.114
Bat-eared fox	Lainyamok, Kenya	1.571	1.571	0.922	0.243	0.403	1.29	0.501	0.588	0.281	0.629	0.708	1.29	0.501	0.168
Coyote	Powell, WY, USA	1.301	0.857	0.857	0.577	0.388	1.571	1.007	0.93	0.27	0.383	0.714	1.571	1.183	0.454
Red fox	Dorset, UK	0.785	0.524	0.912	0.594	0.361	1.047	0.524	0.659	0.281	0.367	0.524	1.571	0.912	0.508
Arctic fox	Bathurst Island, Canada	1.571	1.15	0	0.615	0	0.785	0.421	0.421	0.256	0.396	0	0.421	0.615	0.593
Pine marten	Kinlochewe, Scotland	0.956	0.785	1.047	0.702	0.615	1.571	0.421	0.956	0.281	0.372	0.421	0.615	0.421	0.437
Pacheco 2	Contra Costa Co., CA, USA	1.305	0.748	1.130	0.738	0.389	1.129	0.524	0.584	0.084	0.281	0.639	1.526	0.925	0.239