The Tule Springs local fauna: Rancholabrean vertebrates from the Las Vegas Formation, Nevada

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ABSTRACT

A middle to late Pleistocene sedimentary sequence in the upper Las Vegas Wash, north of Las Vegas, Nevada, has yielded the largest open-site Rancholabrean vertebrate fossil assemblage in the southern Great Basin and Mojave Deserts. Recent paleontologic field studies have led to the discovery of hundreds of fossil localities and specimens, greatly extending the geographic and temporal footprint of original investigations in the early 1960s. The significance of the deposits and their entombed fossils led to the preservation of 22,650 acres of the upper Las Vegas Wash as Tule Springs Fossil Beds National Monument. These discoveries also warrant designation of the assemblage as a local fauna, named for the site of the original paleontologic studies at Tule Springs.

The large mammal component of the Tule Springs local fauna is dominated by remains of *Mammuthus columbi* as well as *Camelops hesternus*, along with less common remains of *Equus* (including *E. scotti*) and *Bison*. Large carnivorans including *Canis dirus*, *Smilodon fatalis*, and *Panthera atrox* are also recorded. Micromammals, amphibians, lizards, snakes, birds, invertebrates, plant macrofossils, and pollen also occur in the deposits and provide important and complementary paleoenvironmental information. The fauna occurs within the Las Vegas Formation, an extensive and stratigraphically complex sequence of groundwater discharge deposits that represent a mosaic of desert wetland environments. Radiometric and luminescence dating indicates the sequence spans the last ~570 ka, and records hydrologic changes in a dynamic and temporally congruent response to northern hemispheric abrupt climatic oscillations. The vertebrate fauna occurs in multiple stratigraphic horizons in this sequence, with ages of the fossils spanning from ~100 to ~12.5 ka.

1. Introduction

Late Pleistocene vertebrate fossil assemblages are common from the Mojave Desert and southern Great Basin regions. In the upper Las Vegas Wash, Clark County, Nevada (Fig. 1), vertebrate fossils have been recognized for over a century. Spurr (1903) reported mastodon (?) bones and teeth from the wash between Corn Creek Springs and Tule Springs.[1] Later, as part of a paleontological investigation conducted under the auspices of the American Museum of Natural History (AMNH), Simpson (1933) reported vertebrate fossils in a contextual association with archeological artifacts. Subsequent intermittent work and excavations by the Southwest Museum from the 1930s through the 1960s (Harrington, 1934; Harrington and Simpson, 1961) concentrated on understanding this relation, and as a consequence of these inquiries the area became known as the Tule Springs site.

A multidisciplinary study conducted by the Nevada State Museum in 1962-63 sought to definitively establish the stratigraphic and geochronological positions of the Pleistocene megafauna and the artifacts (Wormington and Ellis, 1967). Vance Haynes directed the geological investigations, mapped the detailed stratigraphy of Tule Springs, and sought to integrate the site geology into that of the larger surrounding region (Haynes, 1967). He informally subdivided the Tule Springs sediments into discrete

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  [1] American mastodons, *Mammut americanum*, are largely unknown from Pleistocene deposits in the Mojave Desert (Jefferson, 1991; Scott and Cox, 2008), and the few available published reports (like that of Spurr, 1903) are not supported by fossil evidence. Given the preponderance of fossils of mammoth, *Mammuthus columbi*, in the upper Las Vegas Wash, we consider it more likely that the remains mentioned by Spurr (1903) were mammoth, rather than mastodon.
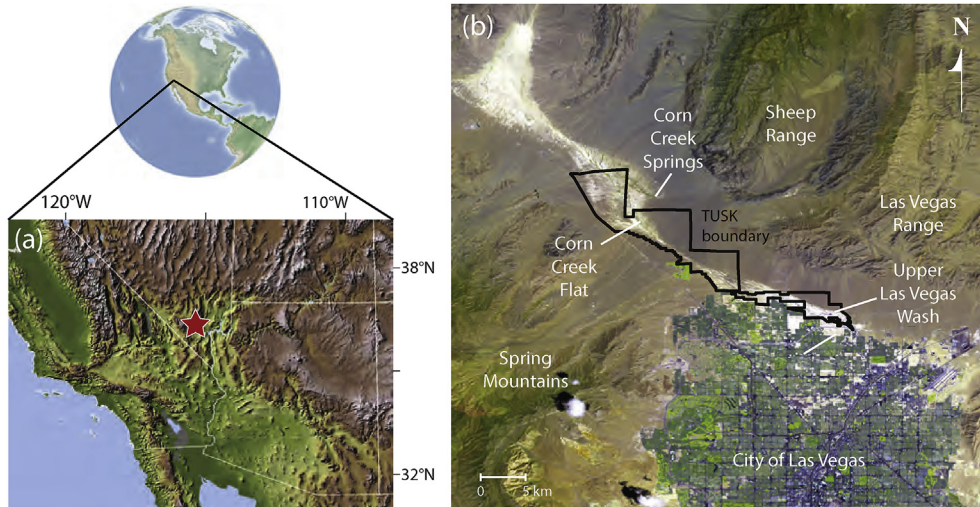
Fig. 1. (a) Site location map for the Las Vegas Valley of southern Nevada (red star); (b) aerial photograph of the Las Vegas Valley showing major physiographic features and the light-colored paleowetland deposits that are exposed in large parts of the upper Las Vegas Wash, including much of Tule Springs Fossil Beds National Monument (TUSK). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stratigraphic units, and referred to them where they occurred in the Las Vegas Valley proper as the "Las Vegas Formation" after Longwell et al. (1965). Mawby (1967) described the vertebrate remains from Tule Springs and discussed them within the informal units described by Haynes. The ultimate determination of the expedition was that human cultural artifacts were not in a temporally contextual position with respect to the vertebrate megafauna (Wormington and Ellis, 1967), and further investigations were suspended.

Few scientific inquires occurred in the Tule Springs area for the next four decades, save for some regional investigations focused on the mode and timing of paleoclimatic and hydrologic indicators of high groundwater discharge (paleospring deposits) in the southern Great Basin (Quade, 1983, 1986; Quade and Pratt, 1989; Quade et al., 1995, 1998, 2003). Vertebrate fossils recognized from these paleospring lithologies were little studied or reported upon.

From the 1990s to the present, scientists from the San Bernardino County Museum (SBCM) (Reynolds et al., 1991a; Springer et al., 2006, 2015; Scott and Springer, 2016), under permits from the Southern Nevada District Office of the Bureau of Land Management (BLM), discovered and documented hundreds of fossil localities, and added new taxa to the faunas described by Simpson (1933) and Mawby (1967). These ongoing paleontologic investigations, coupled with expanded and better-defined geologic interpretations and more refined dating of older sedimentary units (Page et al., 2005; Ramelli et al., 2011, 2012; Springer et al., 2015, 2017), have led to the determination that the assemblage of invertebrate and vertebrate fossil remains from the upper Las Vegas Wash comprises one of the most informative and significant late Pleistocene assemblages in the region.

The vertebrate fauna is derived from multiple discrete stratigraphic horizons within the middle to late Pleistocene Las Vegas Formation. The nature of this assemblage matches published definitions for local faunas; it is "local in both time and space" (after Taylor, 1960:10), consisting of "samples derived from localities, sites, quarries, pits, prospects, etc." that can be "organized into aggregates of species … which have a distribution in time and space, based on the record from a restricted geographic area"

(Tedford, 1970:686). Based upon these definitions, and because of the importance of these remains, this late Pleistocene assemblage warrants designation as a local fauna, herein named the Tule Springs local fauna (TSLF).

2. Background

2.1. Geologic setting and age of the fossil assemblage

The broad sedimentary basin of the Las Vegas Valley was created during the Neogene by extensional forces associated with the formation of the Basin and Range province of western North America (Fleck, 1970; Page et al., 2005). Normal and strike-slip faults cut across the region, including the Las Vegas Valley Shear Zone (LVVSZ), a northwest-striking, right lateral strike-slip fault system (Langenheim et al., 1997, 1998; Page et al., 2005). Thick basin-fill deposits mostly bury the LVVSZ, although surface expression occurs at Corn Creek Springs. The LVVSZ also marks the headward erosion of the upper Las Vegas Wash, and includes discontinuities and subsurface barriers that likely influence local and regional groundwater flow patterns.

The Quaternary-age Las Vegas Formation was first mapped and described by Longwell et al. (1965) from a series of light-colored clay and silt deposits exposed along the upper Las Vegas Wash. Due to their highly fossiliferous nature, including a number of extinct vertebrates, Longwell (1946) assigned the sedimentary sequence to the Pleistocene. Prior to extensive urbanization of the cities of Las Vegas and North Las Vegas, these sediments were exposed throughout the Las Vegas Valley (Longwell et al., 1965; Haynes, 1967; Matti et al., 1993; Donovan, 1996; Bell et al., 1998, 1999; Page et al., 2005). Today, exposures are primarily restricted to the upper Las Vegas Wash and Corn Creek Flat areas, coincident with the boundaries of Tule Springs Fossil Beds National Monument (Fig. 1).

At the original Tule Springs site, Haynes (1967) recognized and described five Pleistocene and two Holocene informal stratigraphic units (A-G, in ascending stratigraphic order with subunits designated with subscript numerals) and six intervening soils. He

attributed these informal units to the Las Vegas Formation, as coined by Longwell et al. (1965), and subsequently this usage was extrapolated throughout the upper Las Vegas Valley (Quade, 1986).

Through successive periods of dissection, deflation, and deposition, the formational units are laterally discontinuous, exhibit complex stratigraphic relations, and form a highly dissected, badland topography. Longwell et al. (1965) mapped the Las Vegas Formation as Quaternary lacustrine (Ql) based on the thin, regular and horizontal bedding, and together with the nature and abundance of fossil mollusk shells, interpreted the sediments as representing shallow lakes that once occupied the Las Vegas Valley. Others have also attributed these extensive deposits in the Las Vegas Valley to be strictly lacustrine in origin (Hubbs and Miller, 1948; Maxey and Jameson, 1948; Snyder et al., 1964; Longwell et al., 1965). Haynes (1967) determined that at least some of the sediments were deposited in ciénegas, or desert wetlands, although he too postulated the existence of "Pluvial Lake Las Vegas" based on the spatial distribution of full-glacial age deposits in the Las Vegas Valley. More recent studies have demonstrated that the sediments were deposited during past episodes of groundwater discharge, and thus the existence of "Pluvial Lake Las Vegas" is no longer accepted (Quade, 1986; Springer et al., 2015, 2017).

Springer et al. (2017) established the contemporary framework for the fossil-bearing groundwater discharge deposits (GWD) in the Las Vegas Valley with detailed geologic mapping, and stratigraphic and chronologic control aided by numerous ^{14}C and luminescence dates throughout the sedimentary sequence. Springer et al. (2017) also designated the Las Vegas Formation as a formal lithostratigraphic unit, with distinct and mappable members and beds. The nomenclature largely follows that of Haynes (1967) but with significant modifications to the lithostratigraphy and geochronology. The Las Vegas Formation now includes Members X, A, B, D, and E, which represent distinct groundwater discharge regimes and contain vertebrate and/or invertebrate fossils. Units F and G of Haynes (1967) are excluded as they represent dry conditions that prevailed during the Holocene and do not contain vertebrate materials. In addition, Unit C of Haynes (1967) has been dissolved based on revised stratigraphic and chronologic data and observations. In all, the GWD deposits of the Las Vegas Formation span the past ~570,000 ka.

The TSLF, within the Las Vegas Valley, occurs in 13 distinct beds within Members B, D and E. The primary physical characteristics, age ranges, and distribution of vertebrate fossils for each subunit within the Las Vegas Formation are presented herein as a composite stratigraphy (Fig. 2). Additional stratigraphic and chronologic details for all subunits are provided in Springer et al. (2017). Overall, the ages of fossil-bearing strata within the Las Vegas Formation span from ~100 to ~12.5 ka.

2.2. Paleoenvironment and paleoclimate

During the middle-late Pleistocene, a climate cooler and wetter than today supported a variety of groundwater discharge settings throughout the southwestern U.S., including seeps, springs, marshes, wet meadows, ponds, and spring pools. Alluvial, fluvial, and eolian sediment became trapped by wet ground conditions and dense plant cover around discharge points, and combined with organic material and chemical precipitates (carbonates, silicates) to form GWD deposits (Pigati et al., 2014). These deposits are distinguished from lake sediments using geomorphic, sedimentologic, and stratigraphic properties, and we are able to recognize specific hydrologic regimes within the

deposits that are analogous to modern spring ecosystems (Springer and Stevens, 2008). Evidence for limnocrene (ponding), helocrene (marshes or wet meadows), and rheocrene (spring-fed stream) flow is recognized within the Las Vegas Formation GWD sequence. The types of spring discharge and their spatial distribution throughout the upper Las Vegas Wash are directly related to subsurface structure (faults), aquifer complexity, and local and regional water table levels. The recognition of specific hydrologic environments within a given member or bed allows past environmental and hydrologic conditions to be further constrained.

The highly resolved chronologic and paleohydrologic record of the GWD deposits in the upper Las Vegas Wash shows that wetlands in the valley were extremely sensitive to climate change during the recent geologic past (Springer et al., 2015). Over the last 35 ka, for example, multiple cycles of deposition, erosion, and soil formation demonstrate that wetland ecosystems in the valley expanded and contracted many times, often collapsing entirely, before disappearing altogether as the last glacial period came to a close. These events exhibit temporal congruence with episodes of abrupt climate change, including Dansgaard-Oeschger (D-O) cycles and other millennial and submillennial-scale climatic perturbations (Fig. 3). Drought-like conditions, as recorded by widespread erosion and the formation of desert soils, typically lasted for a few centuries, which would have severely impacted the flora and fauna that depended on the springs and wetlands for water in an otherwise arid landscape. The TSLF occurs throughout the members and beds of the Las Vegas Formation, each of which represents a discrete "bin of time" that can be queried to evaluate changes in local faunal assemblages, reconstruct past ecosystems and environments on millennial and submillennial timescales, and determine the response of these systems to past episodes of abrupt climate change.

2.3. Recent history of investigation

The San Bernardino County Museum (SBCM) recovered fossils and associated contextual data from Tule Springs and the upper Las Vegas Wash from 2002 to 2014. Initial survey and excavation efforts were conducted in conjunction with the mitigation program for the Harry Allen—Northwest 500 kV transmission line (HANWTL) in North Las Vegas, under Paleontologic Resources Use Permits #N75218 (for survey) and #N76154 (for excavation) from the BLM, as well as under the auspices of Nevada Antiquities Permit #449.

The paleontologic sensitivity of the Las Vegas Formation in the upper Las Vegas Wash later assumed particular significance when the wash was included in the Las Vegas Valley Disposal Boundary (LVVDB). The LVVDB comprised public lands administered by the BLM that were slated to be disposed of by the Las Vegas Field Office, consistent with the Southern Nevada Public Land Management Act of 1998 (SNPLMA). However, the SNPLMA did not authorize the BLM to transfer title of land if such transfer would not conform to other laws, including the National Environmental Policy Act of 1970 (NEPA).

An Environmental Impact Statement (EIS) was completed to update the BLM's analysis of SNPLMA land sales and other BLM-authorized land uses in light of the requirements of NEPA and the BLM's NEPA Handbook, and to analyze impacts of disposing and authorizing uses of federal public lands within the new disposal boundary adopted by the U.S. Congress. As part of this effort, the SBCM field surveyed the entire LVVDB, including much of the upper Las Vegas Wash, in 2003—2004. This survey resulted in the
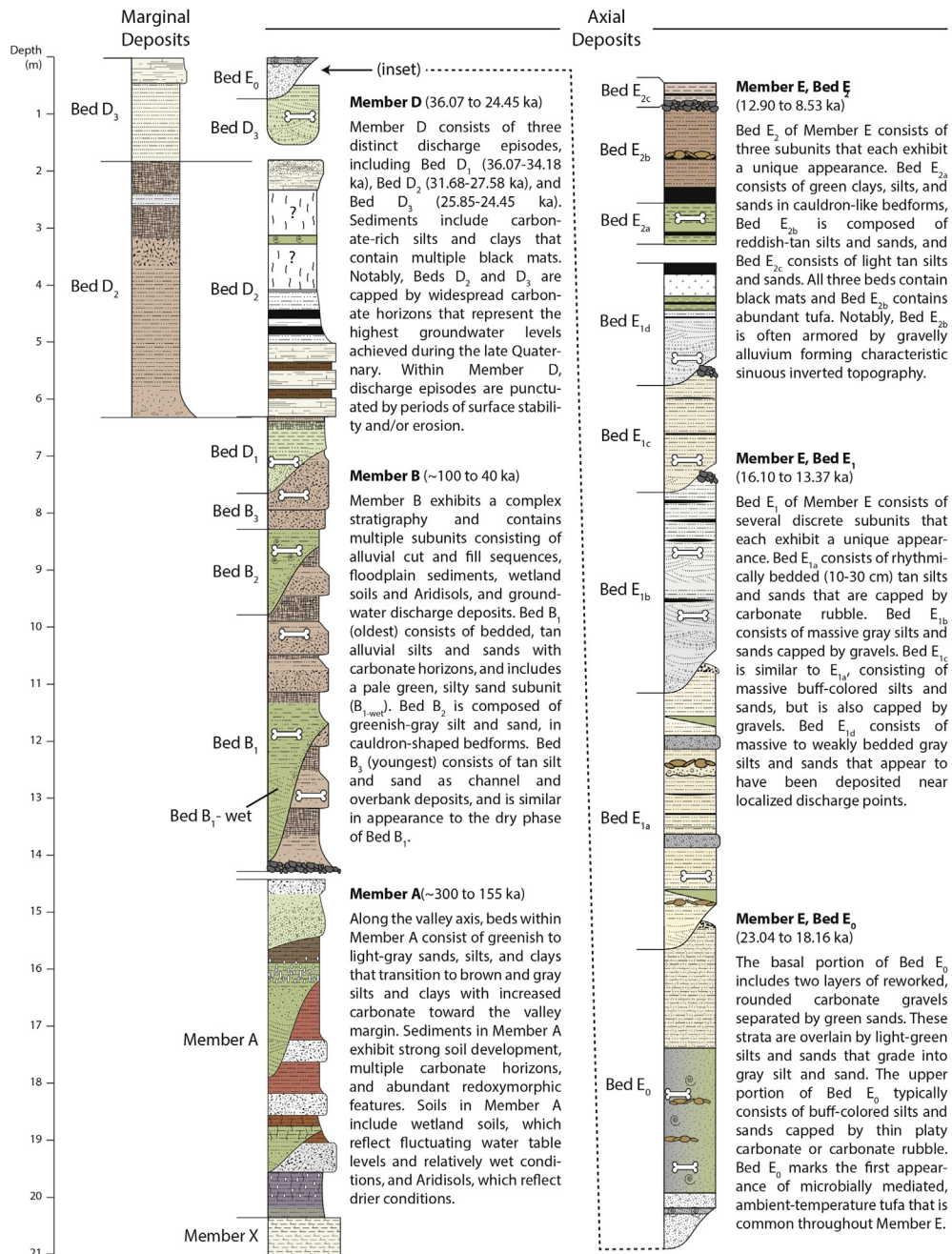
Fig. 2. Composite stratigraphy and brief unit descriptions of the members and beds of the Las Vegas Formation. The occurrence of vertebrate fossils within discrete discharge units are depicted by bone symbol. Age control is based on a combination of radiocarbon (^{14}C) and luminescence (IRSL) dating.
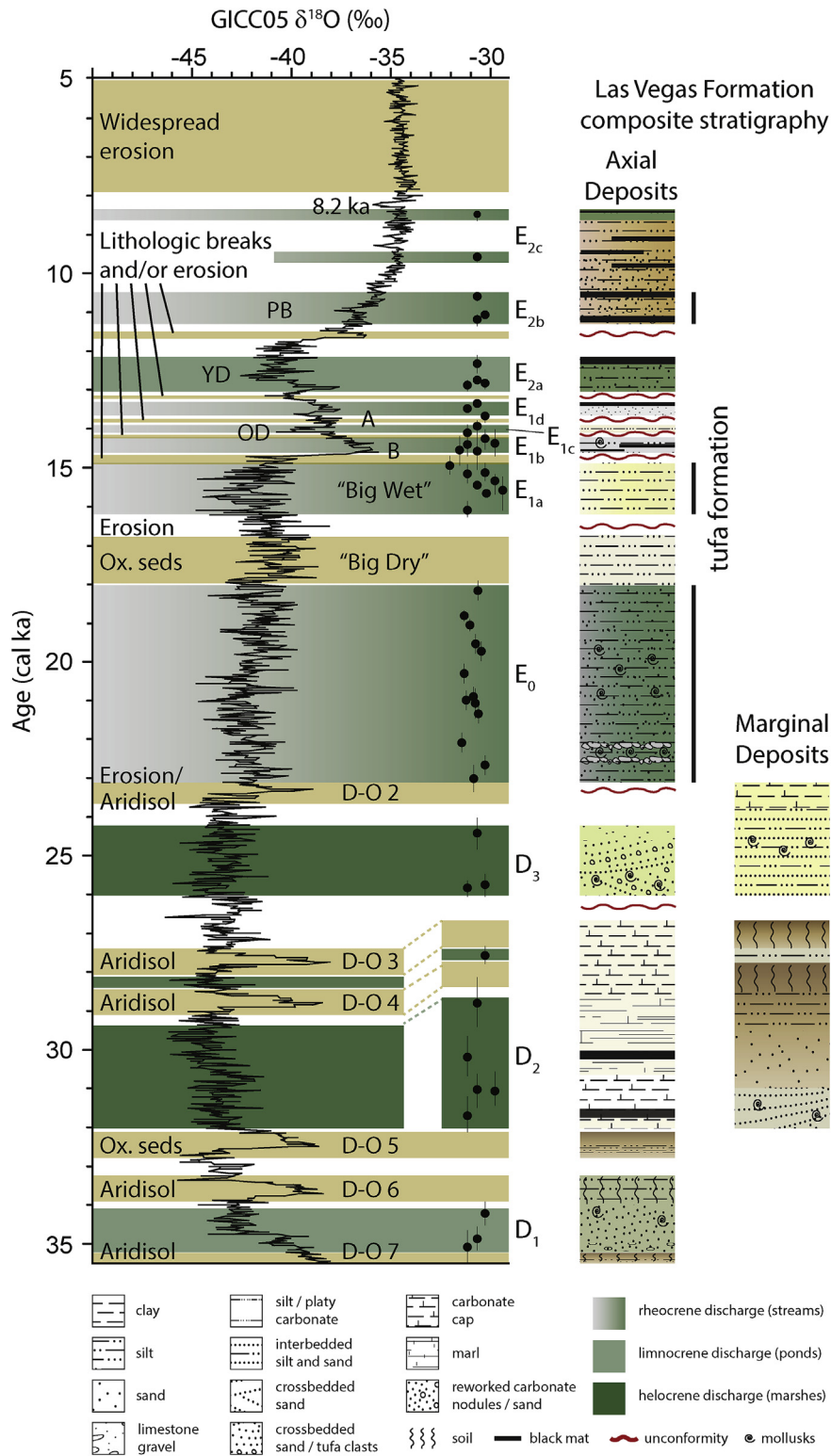
Fig. 3. Stratigraphic and chronologic records of groundwater discharge deposits in the Las Vegas Valley of southern Nevada (after Springer et al., 2015) compared to δ^18O data from Greenland ice core records using the GICC05 chronology (Svensson et al., 2008). Filled circles are calibrated radiocarbon ages of the GWD deposits with uncertainties presented at the 95% (2σ) confidence level. Wetland discharge (by type) is shown in graduated shades of green. Tan horizontal bars indicate periods of aridity as evidenced by surface stability and/or erosion. D-O = Dansgaard-Oeschger cycles; "Big Wet/Big Dry" after Broecker et al. (2009); B = Bølling; OD = Older Dryas; A = Allerød, YD = Younger Dryas; PB = Pre-Boreal; 8.2 ka = 8.2 ka cold event. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

discovery of 438 previously undocumented fossil localities within the Las Vegas Formation.

In light of this dramatic increase in the number of known localities in the upper Las Vegas Wash, a Conservation Transfer Alternative (CTA) was developed to analyze the impacts of selling certain lands if disposal could occur with protection of sensitive environmental resources and mitigation of significant impacts to those resources. The nearly 11,000 acre CTA was developed to provide protection and mitigation for sensitive fossils and other biological and cultural resources while continuing to dispose of lands as authorized under SNPLMA.

In 2008, the Las Vegas District Office of the Nevada BLM requested proposals for treating and curating the paleontologic resources discovered by the SBCM in 2003–2004. This culminating effort was awarded to the SBCM (K. Springer, P.I.) as Federal Assistance Agreement #L08AC13098 entitled, "The Upper Las Vegas Wash Conservation Transfer Area, Clark County, NV: Treatment, Protection, and Interpretation of Heritage Paleontological Resources through Public Involvement."

3. Methods

All work described herein was conducted from 2008 to 2014 under BLM Scientific Paleontological Collecting Permit #N85806 (K. Springer, P.I.) and Field Work Authorizations that were renewed annually. Standard geological and stratigraphic practices were employed during the course of the study. Geologic mapping, combined with description and measurement of multiple stratigraphic sections throughout the upper Las Vegas Wash were used to construct the composite stratigraphy. Sediment samples were collected and curated at the SBCM. All sites, including radiocarbon dating localities and stratigraphic sections, were photodocumented and their positions recorded with handheld GPS units. All physical and digital data reside at the SBCM in Redlands, CA.

Large fossils were jacketed with plaster bandages or strips of burlap saturated with plaster, then removed and returned to the SBCM's paleontology laboratory for preparation, identification, and permanent storage. Smaller fossils were documented and collected without jackets. For taphonomic studies, true north was determined and then written on the fossil specimens. Where accumulations of fossils were identified as part of a single, localized assemblage, the positions and relationships of the fossils in the assemblage were mapped in detail. Samples of fossiliferous sediments were recovered from fossil localities where appropriate; this sedimentary matrix was returned to the SBCM and processed by screen washing through 20-mesh (841 μm) and 30-mesh (595 μm) screens. Specimens recovered in this manner were identified and curated.

Radiocarbon (^{14}C) dating of charred vascular plants (charcoal) and, to a lesser extent, small terrestrial gastropod shells was used to establish the chronologic framework of the Las Vegas Valley groundwater discharge deposits for the past ~35 ka. Charcoal samples were treated using either the standard acid-base-acid treatment or acid-base-wet oxidation methods prior to combustion online in the presence of excess high-purity oxygen. All ^{14}C ages were calibrated using the IntCal13 dataset and CALIB 7.1html (Stuiver and Reimer, 1993; Reimer et al., 2013). Ages are presented in calibrated radiocarbon years or ka BP (ka = thousands of years; BP = before present; present = 1950 AD). Luminescence techniques were also used to date sediments beyond the practical limit of ^{14}C dating (~35−40 ka) or where materials suitable for ^{14}C dating were not present. These ages are also presented in ka BP. Uncertainties of ages derived from both techniques are presented at the 95% (2σ) confidence level. Additional details of both techniques are presented in Springer et al. (2017).

Relative abundance was assessed based upon numbers of specimens assigned to a given taxonomic rank within the catalogued assemblage (i.e., number of identifiable specimens [NISP]), following Marshall and Pilgram (1993). Minimum numbers of individuals for these same taxa are presently being determined. Measurements for metric analyses were taken following the procedures outlined by Von den Driesch (1976) and Eisenmann et al. (1988) as appropriate. Data were acquired using Mitutoyo Digimatic calipers connected by a Mitutoyo USB digital interface to a PC laptop. Graphic plots were generated using SigmaPlot 13.0.

All collected fossils were curated at the SBCM. In June 2015, the fossils obtained during the HANWTL mitigation program were transferred to the Nevada State Museum, Las Vegas, where they presently reside.

4. Results and discussion

A total of 550 localities identified from the upper Las Vegas Wash by the SBCM yielded the fossils discussed herein. Previous studies reported fossils from units B$_2$, D and E$_1$ (Haynes, 1967; Mawby, 1967); we document here that vertebrate fossils composing the TSLF occur throughout the entire Las Vegas Formation sequence in the upper Las Vegas Wash, except for Member A. Members B, D and E and their subordinate beds B$_1$, B$_2$, B$_3$, B$_{1-wet}$, D$_1$, D$_2$, D$_3$, E$_0$, E$_{1a}$, E$_{1b}$, E$_{1c}$, E$_{1d}$, and E$_{2a}$ all host vertebrate fossils (see Fig. 2). Beds E$_{2b}$ and E$_{2c}$ are not fossiliferous. Overall, as stated above, the age range of the vertebrate fauna in the Las Vegas Formation spans ~100 to ~12.5 ka.

Previously unrecorded taxa are identified in this study (see Table 1, new records in boldface), although most species identified conform to published faunal lists for the Tule Springs area (Simpson, 1933; Mawby, 1967). Newly recognized faunal components include the microvertebrates Perciformes, *Rana* sp., Xantusiidae, *Masticophis* sp., cf. *Arizona elegans*, *Marmota flaviventris*, *Neotoma* sp. cf. *N. lepida*, *Reithrodontomys* sp., and cf. *Onychomys* sp. The list of medium- and large-sized mammals is expanded to include *Lynx rufus* and a medium- to large-sized bovid approaching *Euceratherium* in size.

4.1. Character of the Tule Springs local fauna

Mammoths (*Mammuthus columbi)* dominate the large mammal assemblage from the TSLF. This strong representation is not unusual for this locale; both Simpson (1933) and Mawby (1967) also remarked upon the relative abundance of mammoth fossils in the samples under their respective study. However, these earlier investigations were based upon comparatively small sample sizes. The present study, based upon remains from several hundred localities, confirms that the observed profusion of remains of *Mammuthus* is indicative of the true prevalence of these animals in the region during the late Pleistocene.

The high proportion of mammoths in the TSLF indicates the presence of abundant forage in the valley during the later Pleistocene, sufficient to support herds of such large animals over tens of thousands of years. This contrasts somewhat with large mammal faunas from other open sites elsewhere in the Mojave Desert (e.g., Lake Manix; see Jefferson, 2003), where mammoths are present but make up a much smaller percentage of the assemblage.

We note that fossils of *Mammuthus* may be somewhat overrepresented in the overall assemblage, based upon NISP. Adult mammoth teeth are larger than those of other Pleistocene mammals; the cheek tooth enamel of mammoths is easily recognized and identified, even when fragmented; and the massive tusks can, when damaged or broken, produce thousands of small but diagnostic pieces. Contrast this with the tooth enamel of smaller

Table 1
Composite Vertebrate Fauna, Las Vegas Formation. [Includes taxa reported previously (Simpson, 1933; Mawby, 1967; McDonald, 1996; Scott and Cox, 2008; Scott and Springer, 2016); new records in boldface. "cf." = compares favorably based upon direct comparison, but not fully diagnostic; "?" = uncertain, but resembles assignment and cannot be referred to other known taxa].

Animalia	
Chordata	
Osteichthyes	
Perciformes	**fish**
Amphibia	
Anura	
Bufonidae	
Bufo sp.	toad
Hylidae	
Hyla sp. (large)	large frog
Hyla sp. (small)	small frog
Ranidae	
***Rana* sp.**	**pond frog**
Reptilia	
Chelonia	
Testudinidae	
Gopherus sp.	tortoise
Lacertilia	
Iguanidae	
Sceloporus sp. cf. *S. occidentalis*	sagebrush lizard
Callisaurus sp. cf. *C. draconides*	zebra-tailed lizard
Phrynosoma sp.	horned lizard
Xantusiidae	**night lizard**
Serpentes	
Colubridae	nonvenomous snakes
***Masticophis* sp.**	**coachwhip snake**
cf. *Arizona elegans*	**glossy snake**
Aves	
Anseriformes	
Anatidae	
Mareca americana	widgeon
Aythya collaris	ring-necked duck
Aythya affinis	lesser scaup
Mergus merganser	common merganser
Ciconiiformes	
Teratornithidae	
Teratornis merriami	extinct teratorn
Accipitriformes	
Accipitridae	
Buteoninae	indeterminate soaring hawk
Gruiformes	
Rallidae	
Fulica americana	coot
Fulica americana minor	extinct small coot
Strigiformes	
Strigidae	
Bubo sp.	owl
Mammalia	

Xenarthra
    Megalonychidae
        Megalonyx jeffersonii   Jefferson's ground sloth
    Megatheriidae
        Nothrotheriops shastensis   Shasta ground sloth
Lagomorpha
    Leporidae
        Sylvilagus sp.   cottontail rabbit
        Lepus sp.   jack rabbit
        ?*Brachylagus idahoensis*   possible pygmy rabbit
Rodentia
    Sciuridae
        Ammospermophilus leucurus   antelope ground squirrel
        Marmota flaviventris   **yellow-bellied marmot**
    Geomyidae
        Thomomys bottae   Botta's pocket gopher
    Heteromyidae
        Dipodomys sp. (large)   large kangaroo rat
        Dipodomys sp. (small)   small kangaroo rat
        Perognathus sp.   pocket mouse
    Cricetidae
        Peromyscus sp. cf. *P. maniculatis*   deer mouse
        ***Reithrodontomys* sp.**   **harvest mouse**
        ***Onychomys* sp.**   **grasshopper mouse**
        Neotoma* sp. cf. *N. lepida   **desert wood rat**
        Microtus sp. cf. *M. californicus*   meadow vole
        Ondatra zibethicus   muskrat
Carnivora
    Mustelidae
        Taxidea taxus   badger
    Canidae
        Canis dirus   **dire wolf**
        Canis latrans   coyote
    Felidae
        Puma sp. cf. *P. concolor*   probable puma
        Lynx rufus   **bobcat**
        Panthera atrox   extinct North American lion
        Smilodon fatalis   **sabre-toothed cat**
Proboscidea
    Elephantidae
        Mammuthus columbi   extinct Columbian mammoth
Perissodactyla
    Equidae
        Equus scotti   **extinct Scott's horse**
        Equus spp. (small)   extinct small horses
Artiodactyla
    Camelidae
        ***Hemiauchenia* sp.**   **extinct llama**
        Camelops hesternus   extinct giant camel
    Cervidae
        Odocoileus sp.   deer
    Antilocapridae   pronghorn
    Bovidae
        Bison sp. cf. *B. latifrons*   probable long-horned bison
        Bison antiquus   extinct bison
        ? *Euceratherium*   **possible shrub-ox**

Fig. 4. SBCM L3160-4, *Mammuthus columbi*, left and right M3 in early wear, lateral view, in field jacket with scale. The closer tooth possesses 22 enamel plates, with enamel thickness ranging from 1.8 mm to 2.9 mm; the lamellar frequency is 7.

mammalian herbivores such as camels or bison, which when broken or fragmentary, can be more difficult to identify to genus and so would often be more conservatively assigned to "Mammalia (large)." For these reasons, mammoth fossils would likely be somewhat overrepresented in any assessments of relative abundance based upon NISP. We anticipate that ongoing efforts to determine minimum numbers of individuals (MNI) for the TSLF will provide a more accurate interpretation of the abundance of *Mammuthus* in the Las Vegas region during the Pleistocene.

Previous studies that reported *Mammuthus* from the upper Las Vegas Wash (Simpson, 1933; Harrington, 1955; Mawby, 1967; Rowland, 2010; Rowland and Bonde, 2015) did not describe the morphology of the recovered fossils in any detail. Simpson (1933) assigned mammoth remains from the region to "*Parelephas columbi*" (= *Mammuthus columbi*), but did not delve deeply into the rationale behind this referral, stating only that the available "isolated teeth and other fragments appear to represent a single species, considered as the Columbian mammoth" (Simpson, 1933:5). In like manner, Mawby (1967:115) discussed contemporary views about mammoth taxonomy and concluded that the mammoth specimens recovered by the 1962 team "seem best referable to <u>Mammuthus columbi</u>" (underlined in original) with no discussion of the anatomical features upon which this referral was based.

Mammoth fossils recovered by the SBCM from the upper Las Vegas Wash include teeth that can be definitively assigned to the species *Mammuthus columbi*. For example, a left and a right M3 in early wear, in parallel orientation but lacking any adhering maxillary bone (specimen SBCM L3160-4; Fig. 4), possess 22 enamel plates, with the enamel ranging from 1.8 mm to 2.9 mm in thickness, and have a lamellar frequency of 7. Similarly, a right m3 (SBCM L3160-647; Fig. 5) with 21 enamel plates exhibits an enamel thickness ranging from 1.7 mm to 2.4 mm, and a lamellar frequency of 6–7. These data match published diagnoses for *M. columbi* (Maglio, 1973; Agenbroad, 1984; Graham, 1986), confirming

previous species assignments.

In contrast to the possible overrepresentation of *Mammuthus*, the observed profusion of remains of *Camelops hesternus* in the TSLF is interpreted to reflect the true abundance of these animals. Based upon NISP, *C. hesternus* makes up over one-third of the large mammal sample (Table 2). This is a smaller proportion of the overall assemblage than that inferred from previously collected samples, particularly those recovered during the 1962-63 excavations (Mawby, 1967), where *Camelops* accounted for over half of the large mammal fossils based upon NISP (Table 2; NISP based upon a search of the UCMP online database). However, given that the sampled obtained by the SBCM is substantially larger and comes from a much larger geographic area, the smaller percentage is interpreted to more accurately reflect the relative abundance of *Camelops* in the living community.

The preponderance of *Camelops* in the TSLF is not unusual for late Pleistocene megafaunal assemblages from the Mojave Desert. Multiple other sites including Valley Wells, Lake Manix, and Lake Tecopa have all yielded assemblages dominated by camels, frequently *Camelops* (Jefferson, 1991; Scott and Cox, 2008). The relative abundance in the TSLF does differ substantially from that observed at more coastal localities such as Rancho La Brea, where camels are less represented respective to other large mammals such as *Equus* and *Bison* (Stock and Harris, 1992; Scott, 2010). In this context, it is interesting that the Diamond Valley Lake local fauna, reported from southwestern Riverside County, California, inland from the coast, exhibits a greater relative abundance of *Camelops* than at Rancho La Brea, but less than that reported from late Pleistocene localities in the Mojave Desert (Springer et al., 2010). Thus, it appears that there is a gradient of increasing relative abundance of this taxon from the coast to the high desert, at least among those localities where the assemblages are sufficiently large and diverse.

The next most abundant large mammals in the TSLF based upon

Fig. 5. SBCM 3160-647, *Mammuthus columbi*, right m/3, lateral view. Specimen has 21 enamel plates exhibits an enamel thickness ranging from 1.7 mm to 2.4 mm, and a lamellar frequency of 6–7.

NISP are horses (*Equus*). Despite their abundance, the majority of the fossil horse remains in the TSLF are fragmentary, and so for many decades reliable specific assignments have not been forthcoming. Both Simpson (1933) and Mawby (1967) noted the presence of at least two species of horse, one large and one small, from the area; Simpson (1933) also suggested the possible presence of a third species. The large horse fossils were assigned by Simpson (1933) to the species *Equus pacificus* Leidy, but the holotype of this species is a nondiagnostic tooth and therefore the species is invalid (Savage, 1951; Scott, 2016). Mawby (1967) avoided a firm specific assignment for the large horse remains, preferred to refer them to "*Equus*, large species, near *E. caballus*" (i.e., close to the living domestic horse).

The majority of horse fossils recovered by the SBCM follows this pattern, and are not sufficiently diagnostic to enable firm specific assignments. This fact emphasizes the significance of the recovery of a partial skull, mandible, and metapodial (SBCM L3160-1015A,B, L3160-1016A,B, and L3160-1017, respectively) of the large Pleistocene horse species *Equus scotti* from Member E, Bed E_{1d} of the Las Vegas Formation. These fossils—the first horse fossils from the Las Vegas Formation to be reliably referable to species—lacked sufficient collagen for direct dating, but are associated stratigraphically with a date of 13.69 ± 0.14 ka (Springer et al., 2015), making these the youngest and most southerly remains of this species in Nevada and among the youngest recorded anywhere in North America. The newly recovered fossils represent a large equid with stout metapodials and lower incisor infundibula, all features that characterize *E. scotti*.

Small horse fossils are also present in the TSLF, and Mawby (1967:119) noted that these fossils represented a "small *Asinus*-like species" that fell "within the size range of Equus tau (= E. francisi) (sic)" (underlined in original). At the time of Mawby's writing, the relation between *Equus tau* and *Equus francisci* (note correct spelling) had not been fully worked out. *Equus francisci* is a small "stilt-legged" North American horse species (Lundelius and Stevens, 1970; Scott, 2004). *Equus tau* was also a small horse, but the holotype was nondiagnostic and has been lost, so it remains unknown whether or not it was a stilt-legged form. *Equus francisci* has been considered a junior synonym of *E. tau* (Dalquest, 1979; Kurtén and Anderson, 1980), but Winans (1985) retained *E. francisci* while considering *E. tau* to be invalid. Both species have also been separately synonymized with the stout-legged species *E. conversidens* (Hibbard, 1955; Hibbard and Taylor, 1960), but the finding that *E. francisci* was a stilt-legged species (Lundelius and Stevens, 1970) demonstrated that the two were different species (see Scott, 2004, for a discussion of stilt-legged horses in Pleistocene North America). Dalquest and Schultz (1992) considered both *E. francisci* and *E. tau* to be potentially valid species. However, given that the holotype of *E. tau* offered no diagnostic characters other than small size, has been lost, and was not associated with any diagnostic topotypal material, we follow Winans (1985) in considering the species a *nomen dubium*.

A proximal phalanx (UCMP V-6246/272139) from Tule Springs plots in the low end of the size range of *Equus conversidens*, but somewhat outside the range of small stilt-legged horses (Fig. 6). This suggests that a small horse with relatively stout limbs, similar to *E. conversidens*, is present in the TSLF. In contrast, a partial metatarsal (UCMP V-6246/63476; Fig. 7) has the long, slender appearance of more stilt-legged horses, although the specimen is incomplete as well as juvenile and so this interpretation is subjective. Nevertheless, UCMP V-6246/63476 does resemble juvenile metapodials of small *Equus* from Pleistocene Lake Tecopa to the west. These bones have been interpreted to represent stilt-legged horses (Scott, 1997). In combination, these data suggest the likelihood that three species of horse are represented in the TSLF.

Although the evidence for a small stilt-legged horse from the

Table 2
Number of identified specimens (NISP) and percentage of the assemblage (%) for collections of large mammal fossils from the upper Las Vegas Wash at the Museum of Paleontology, University of California, Berkeley (UCMP) and the San Bernardino County Museum (SBCM). NISP includes specimens with "cf." and "?" designations. Data for UCMP obtained from the UCMP online database: http://ucmpdb.berkeley.edu/advanced.html.

| Taxon:	UCMP		SBCM		Total:	
	NISP	%	NISP	%	NISP	%
Megalonyx sp.	4	2%	–	–	4	<1%
Nothrotheriops	1	<1%	–	–	1	<1%
Canis dirus	–	–	1	<1%	1	<1%
Smilodon fatalis	–	–	3	<1%	3	<1%
Puma concolor	1	<1%	–	–	1	<1%
Panthera atrox	1	<1%	–	–	1	<1%
Mammuthus columbi	19	8%	187	28%	206	22%
Equus spp.	45	19%	125	19%	170	18%
Camelops hesternus	133	55%	222	33%	355	38%
Hemiauchenia sp.	–	–	1	<1%	1	<1%
Antilocapridae	10	4%	8	1%	18	2%
Odocoileus sp.	1	<1%	7	1%	8	1%
Bison spp.	28	12%	110	17%	138	15%
Total:	243	100%	664	99%	907	96%
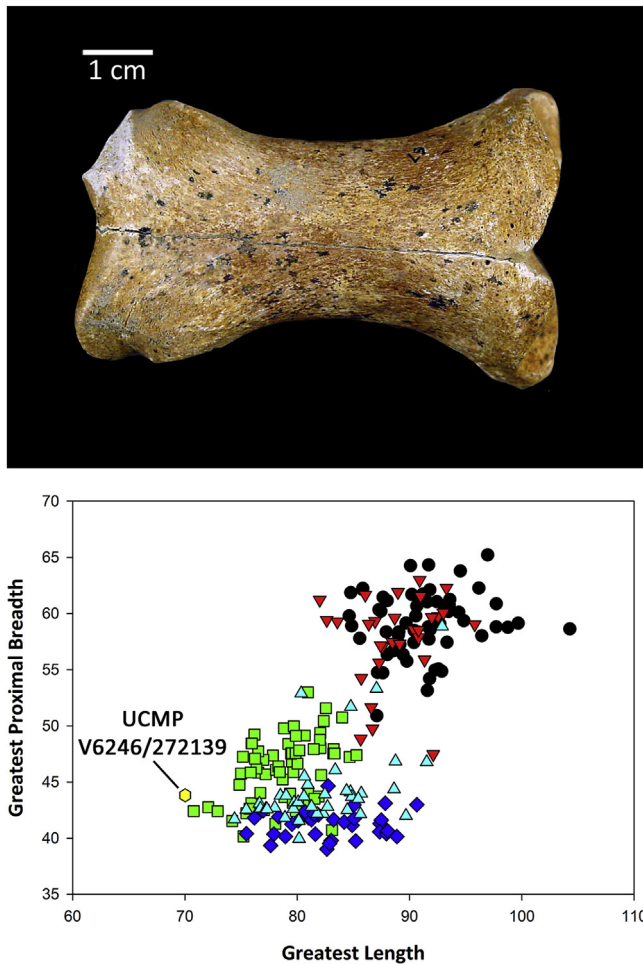
Fig. 6. UCMP V-6246/272139, uncatalogued proximal phalanx of small *Equus* from TSLF. A: dorsal view of specimen; proximal is to the right. B: bivariate plot of length and proximal breadth measurements in millimeters of UCMP V-6246/272139 against data from other Pleistocene species of large and small *Equus*. Black circles = *Equus occidentalis*, Rancho La Brea, California; red triangles = *E. scotti*, Rock Creek, Texas; green squares = *E. conversidens*, San Josecito Cave, Mexico; dark blue diamonds = *Equus* NWSL (= New World stilt-legged) from Dalhart Horse Quarry, Channing, Texas; light blue triangles = *Equus* NWSL from Natural Trap Cave, Wyoming; yellow hexagon (labeled) = UCMP V-6246/272139 from TUSK. Measurements of UCMP V-6246-272139 are observed to fall within the range of *E. conversidens* rather than any of the NWSL species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wash is not yet conclusive, these animals are known to have lived elsewhere in the Mojave Desert during the late Pleistocene (Scott, 1997), for example at Gypsum Cave, Nevada, just east of the Las Vegas Wash (Weinstock et al., 2005; Scott and Lutz, 2014). If additional, more complete remains confirm the presence of three horse species from the Las Vegas Formation, it would be incongruent with molecular studies that suggest only two species of *Equus* were present in late Pleistocene North America (Weinstock et al., 2005; Orlando et al., 2008).

Bison are also common in the assemblage from the upper Las Vegas Wash, although less so than elsewhere in the southwestern U.S. (Simpson, 1933; Mawby, 1967; de Narvaez, 1995; Scott and Cox, 2008; Scott, 2010). Remains of this genus are frequently incomplete, and consequently have previously been assigned to a wide variety of species, including *Bison* sp. aff. *B. occidentalis* (Simpson, 1933), *B. alleni* (Skinner and Kaisen, 1947), *Bison* sp. (Mawby, 1967), *B. antiquus antiquus* (McDonald, 1981), and *Bison* sp. cf. *B. antiquus* (Scott and Cox, 2008).

Because of the large number of names, more detailed discussion of bison is warranted here, particularly with respect to the specimens discussed by Simpson (1933). These consist of two largely complete bison skulls, NMC 8775 (formerly AMNH 30051; transferred from the AMNH to the Canadian Museum of Nature in 1936) and AMNH 30052. These skulls were interpreted by Simpson (1933) to belong to a "general group" including *B. occidentalis*, *B. crassicornis*, *B. chaneyi*, *B. taylori*, and *B. texanus*. Based upon sedimentary and stratigraphic descriptions provided by Simpson (1933), these skulls were likely recovered from unit B_2 (=Member B, Bed B_2) of the Las Vegas Formation. Simpson's taxonomy included many putative species that were later synonymized; see Skinner and Kaisen (1947), Guthrie (1970, 1990), McDonald (1981), and Scott and Cox (2008) for discussions. Regardless, the skulls from the upper Las Vegas Wash were interpreted to be sufficiently unique that they did not resemble any other species "closely enough for specific reference" (Simpson, 1933:6). The skulls were characterized by their robustness, broader frontals, and longer, straighter horn cores relative to *B. occidentalis*, although no metric data were presented (Simpson, 1933).

Skinner and Kaisen (1947) later interpreted these two skulls to represent small-sized variants of the species *B. alleni*, and proposed that the size and morphology of the skulls "represent[ed] either individual variation or a geological variety." *Bison alleni* has been subsequently synonymized with *B. priscus* by Wilson (1974) as well as with *B. latifrons* by Kurtén and Anderson (1980) and McDonald (1981). If these interpretations are correct, then the Las Vegas bison skulls could be assigned to either of these species. Skull

Fig. 7. UCMP V-6246/63476, partial left metatarsal of *Equus* from TSLF. Distal is to the right. Scale = 1 cm.

Fig. 8. AMNH 30052, partial skull of *Bison* sp. cf. *B. latifrons*, oblique lateral view.
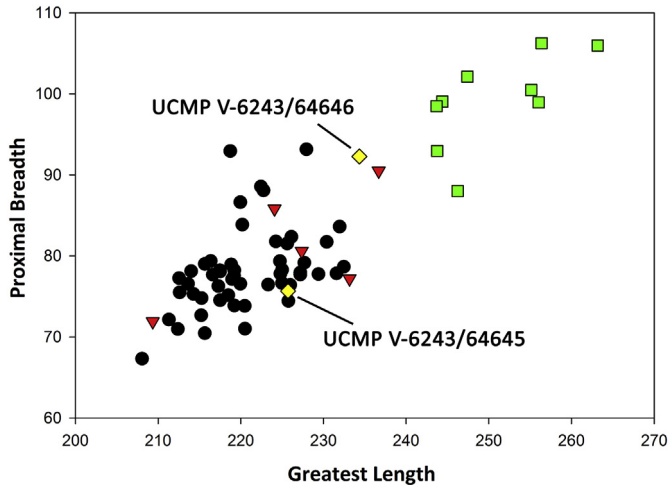

Fig. 9. Bivariate plot of metacarpals of Pleistocene *Bison*. Measurements in millimeters. Black circles = *Bison antiquus*, Rancho La Brea, California; red triangles = *B. antiquus*, Folsom, New Mexico; green squares = *B. latifrons*, American Falls Reservoir, Idaho; yellow diamonds = UCMP V-6243/64645 (presumed female) and V-6243/64646 (presumed male) from TUSK. Measurements of the metacarpals from TUSK are observed to fall within the range of *B. antiquus* rather than *B. latifrons*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

AMNH 30052 (Fig. 8) has also been considered a "probable hybrid" between populations of *B. priscus* or *B. alaskensis* and *B. latifrons* or *B. a. antiquus* by McDonald (1981:225).

For fossils of *Bison* recovered during the Tule Springs Expedition of 1962-63, Mawby (1967) preferred an assignment of *Bison* sp. with no specific epithet. Bison fossils recovered during these excavations consisted of two largely complete skeletons, an adult male and a somewhat younger female (Mawby, 1967:124), from one locality, as well as isolated teeth from other sites. All localities were identified from unit B_2 (=Member B, Bed B_2) of the Las Vegas Formation; Mawby (1967) emphasized that no bison fossils were recovered from the younger units of the formation. The two skeletons unfortunately lacked complete or even partial skulls; only one fragment of a horn core, interpreted to be from the female individual, was recovered (Mawby, 1967:124), which was insufficient for specific assignment of the fossils. No additional specimen descriptions or diagnoses were advanced by Mawby (1967), although he did present photos of a left dentary and a left metacarpal. McDonald (1981) examined the horn core fragment mentioned by Mawby (1967) (UCMP V-6243/64688), which led him to assign the fossils to *Bison antiquus antiquus*.

Scott and Cox (2008) reviewed the taxonomic status of bison fossils from throughout the Mojave Desert, including the upper Las Vegas Wash, and concluded that the Nevada fossils were best assigned to *Bison* sp. cf. *B. antiquus*. Measurements of two metacarpals from the Tule Springs Expedition sample, UCMP V-6243/64645 and V-6243/64646, indicated that the fossils fell within the size range of *B. antiquus* from Rancho La Brea and Folsom (Scott and Cox, 2008) (Fig. 9). The male metacarpal, UCMP V-6243/64646, also plotted very near the low end of the size distribution of *B. latifrons*.

More recent discoveries of fossils of *Bison* by the SBCM include a partial skull with an intact horn core (SBCM L3160-781) from the full-glacial deposit of Member D, Bed D_1 (Fig. 10). Although incompletely preserved, precluding most standard measurements, the horn core is visibly short and small at the base, extending directly laterally from the skull rather than angling posterolaterally. The specimen compares favorably with crania of *B. antiquus*, and can be differentiated on the basis of its horn core size and orientation from other late Pleistocene species including *B. latifrons* (including *B. alleni*), *B. alaskensis*, *B. priscus*, and *B. occidentalis*. SBCM 3160-781 is herein assigned to *B. antiquus*.

As noted, Mawby (1967) reported fossils of extinct *Bison* from unit B_2 (=Member B, Bed B_2) at two localities within the Las Vegas Formation, but not from any of the younger fossil-bearing units; this dearth of bison fossils in younger strata led to cautious inferences with respect to increasing desertification of the region through time. However, more recent efforts by the SBCM confirmed the presence of *Bison* in both the oldest and the youngest Pleistocene members of the Las Vegas Formation. Specifically, numerous fossils of *Bison* were recovered from exposures of Beds B_1, B_2, D_1, and E_0 of the Las Vegas Formation (*Bison* in Bed E_1 is unconfirmed at this time). The Bed E_0 *Bison* locality are associated with a date of 18.16 ± 0.19 ka (Springer et al., 2015); these fossils are the youngest reliably dated remains of extinct bison from anywhere in the Mojave Desert.

Other megafaunal taxa are not as well represented in the TSLF as the animals discussed above (Table 2). Ground sloths have been previously reported from the region, but their remains are quite rare. Simpson (1933) mentioned a partial cranium that he assigned to "*Nothrotherium*" (= *Nothrotheriops*), and Mawby (1967) reported an upper left cheek tooth of "*Nothrotherium shastense*" (= *Nothrotheriops shastensis*). The evident paucity of remains of *Nothrotheriops* is buttressed by the lack of any additional sloth fossils recovered during the extensive SBCM investigations documented here, and stands in surprising contrast to the well-documented presence of *N. shastensis* at nearby Gypsum Cave (Harrington, 1933). Mawby (1967) also documented fossils of *Megalonyx* sp. from Tule Springs, but declined to refer them to species although noting that they did not represent the common late Pleistocene species *M. jeffersonii*.

Antilocaprids are present in the TSLF, but make up only a small percentage of the large mammal fauna. Mawby (1967) assigned antilocaprid fossils to *?Tetrameryx*, because no skulls or horn cores were available in the sample under study. Rather than continue to use this genus, however tentatively, when discussing antilocaprid remains from the Las Vegas Formation, it is more conservative to

Fig. 10. SBCM L3160-781, partial skull of *Bison antiquus* from TUSK, in field jacket, dorsal view. The short horn core, extending directly laterally from the cranium, is consistent with *B. antiquus* rather than *B. latifrons*.
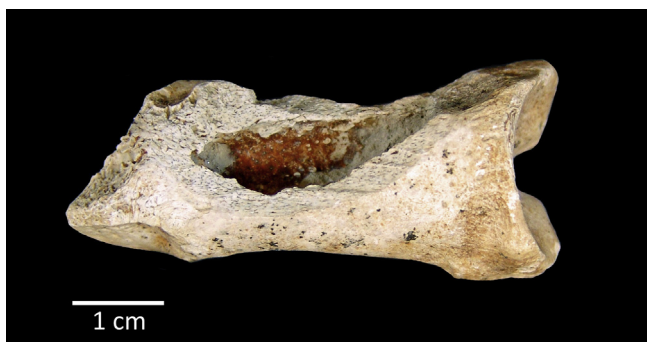

Fig. 11. UCMP 3552/23918, proximal phalanx of *Panthera atrox* from TUSK, dorsal view; proximal is to the right. This specimen, collected by paleontologist Chester Stock in 1919, represents the first record of *P. atrox* in the TSLF, although the fossil was not published at the time.

simply assign the recovered elements to the family Antilocapridae (R.S. White, oral communication).

Megafaunal carnivorans are also present in the TSLF, but are rare as would be expected in a normally distributed large mammal assemblage. Mawby (1967) reported the presence of *Panthera atrox*, based upon an incomplete mandible retaining part of the m/1 (UCMP 64321). Additionally, the UCMP houses a proximal phalanx from digit IV of the right hind foot (UCMP 23918; Fig. 11), originally discovered by paleontologist Chester Stock and his student Richard J. Russell in 1919, but not reported at that time (Springer et al., 2011). Mawby (1967) also included *Puma concolor* among the carnivoran megafauna from the Las Vegas Formation, based upon a few tooth fragments (UCMP 64523) from one locality.

More recent research by the SBCM has added to the list of large mammalian carnivores present in the TSLF. A right patella of *Canis dirus* from Member E, Bed E_{1b} represents the first confirmed record of dire wolves from the Las Vegas Formation (Scott and Springer, 2016); a large canid metapodial fragment has also been reported from "unit D" of the formation (Rowland and Bonde, 2015). Additionally, a partial left humerus, left radius, and sacrum of a single individual of *Smilodon fatalis* recovered from Member E, Bed E_{1a} are the first remains of sabre-toothed cat from the TSLF. These two specimens are discussed more fully by Scott and Springer (2016).

4.2. New vertebrate records for the Tule Springs local fauna

Perciformes: Remains of fish are previously unknown from the Las Vegas Formation; Mawby (1967:108) emphasized that he did not recognize remains of fish in the collections nor did he find evidence of fish in the field. Consequently, the discovery of three fish otoliths (specimens L3160-497, −502, and −503) from locality SBCM 2.6.308 provides the first record of fish in the TSLF. The presence of fish is consistent with paleoenvironmental reconstructions of the region as including numerous spring-fed ponds.

Rana sp.: Multiple postcranial fossils representing the true frog, *Rana* sp., were recovered from throughout the sequence of the Las Vegas Formation (Members B through E). Present day members of this genus in the southern Nevada region frequent springs, slow-moving streams, marshes, bogs, and ponds, usually where there is permanent water and aquatic vegetation such as cattails (Stebbins, 2003). In the Pleistocene fossil record of the Mojave Desert, *Rana* has been reported previously in the Daggett region

(Reynolds and Reynolds, 1985). Mawby (1967:108) reported the presence of "a few scraps of bone of a small anuran, a frog or toad" from the Las Vegas Formation, but provided no more detailed identifications.

Xantusiidae: A single right dentary with five teeth (SBCM L3160-396, from locality SBCM 2.6.330 = Member B, Bed B_{1-wet}) represents the first record of night lizard (Xantusiidae) from the Las Vegas Formation. Present-day xantusiid lizards prefer to live beneath fallen branches of yucca trees, in crevices or under rocks, and beneath bark or other plant debris (Stebbins, 2003). Fossils assigned to the genus *Xantusia* have been described from the earlier Pliocene White Narrows local fauna elsewhere in Clark County (Mead and Bell, 2001).

Masticophis sp.: A partial vertebra (L3088-334) of whipsnake, *Masticophis* sp. is added to the TSLF. *Masticophis* has not been previously reported from the fossil record of the Las Vegas Valley. Present-day individuals of *Masticophis* are diurnal, and are found in a variety of habitats. *Masticophis flagellum*, the coachwhip, frequents deserts, prairies, scrublands, juniper-grasslands, woodlands, thornforests, and farmlands; *M. taeniatus*, the striped whipsnake, is found in shrublands, grasslands, sagebrush flats and canyons, piñon-juniper woodlands, and open pine-oak forests (Stebbins, 2003). *Masticophis flagellum* has previously been recorded from Gypsum Cave (Brattstrom, 1953), which is the only other record of this animal from Clark County, NV (Harris, 1985; Weinstock et al., 2005; Scott and Lutz, 2014). Both *M. flagellum* and *M. taeniatus* occur in Nevada today (Stebbins, 2003).

cf. *Arizona elegans*: Four vertebrae (L3088-662) that compare favorably with vertebrae of the glossy snake, *Arizona elegans*, were identified from the base of one of the many spring outflow streams of Member E, Bed E_0 and are associated with a date of 19.52 ± 0.22 ka (Springer et al., 2017). This species has not been previously reported from the Las Vegas Formation. *Arizona elegans* is primarily nocturnal, preferring open areas with loose soils that are suitable for burrowing. However, the species can inhabit a wide variety of habitats, including light shrubby to barren desert, sagebrush flats, grasslands, chaparral covered slopes, and/or woodlands (Stebbins, 2003). *Arizona elegans* is common in Nevada today (Stebbins, 2003), but fossils resembling this species have not previously been described from the fossil record of southern Nevada.

Marmota flaviventris: A fossilized left P3 of marmot (*Marmota flaviventris*), L3088-934, was also recovered from Bed E_0 ($23.04–18.16$ ka; Springer et al., 2017). This is the first record of marmots from the Las Vegas Formation. Although relatively common in the western United States, *M. flaviventris* has not been frequently reported from the eastern Mojave Desert. The only other Pleistocene record of *M. flaviventris* from Clark County was that identified from Mercury Ridge in the Spotted Range (Harris, 1985). Additionally, a late Pleistocene record of *M. flaviventris* has been reported from Mormon Mountain Cave in southern Lincoln County, approximately 125 km northeast of the Las Vegas Valley in the southern Great Basin (Brattstrom, 1953). Present-day marmots do not occur in southern Nevada; however, their presence in the region during the late Pleistocene is consistent with paleoenvironmental reconstructions for the region. In California, fossil remains of *Marmota flaviventris* are recorded from the eastern Mojave Desert at Antelope Cave (Reynolds et al., 1991b), Kokoweef Cave (Reynolds et al., 1991c), and possibly Mescal Cave (UCMP V-38064; Harris, 1985) and Mitchell Cavern (LACM 3497; Jefferson, 1991).

Reithrodontomys sp.: two small, grooved upper incisors (L3160-424 and −425) were recovered from Bed D_3 and are associated with a date of 24.45 ± 0.39 ka at locality SBCM 2.6.409 (Ramelli et al., 2011; Springer et al., 2015). Both specimens exhibit a generally rounded cross-section and possess a groove that evenly divides the tooth, characteristic indicators for this genus. These specimens represent the first confirmed occurrence of *Reithrodontomys* from the Las Vegas Formation. Living harvest mice are usually associated with stands of short grass; their preferred altitudinal range is from below sea level in places to above the tree line on some Central American mountains (Nowak, 1991). Fossil remains of *Reithrodontomys* are not common from the Pleistocene of the American Southwest. In Nevada, the genus has been reported from Bonneville Estates Rockshelter in the northern Bonneville Basin (Schmitt and Lupo, 2012), and in California *Reithrodontomys* is present at Dove Spring Wash (Whistler, 1990), Anza-Borrego (Remeika et al., 1995), Costeau Pit, Emery Borrow Pit and Newport Bay Mesa (Miller, 1971), Kokoweef Cave (Reynolds et al., 1991c), Daggett (Reynolds and Reynolds, 1985), and Rancho La Brea (Stock and Harris, 1992). A possible record (?*Reithrodontomys*) is also recorded from McKittrick (Harris, 1985).

cf. *Onychomys* sp.: A left lower molar (L3088-625, left m/1) resembling the grasshopper mouse genus *Onychomys* was identified in the TSLF. The tooth exhibits high molar cusps and deep troughs closely similar to *Onychomys* but distinct from the lower cusps seen in other, like-sized mice such as *Peromyscus*; however, because the specimen is an isolated tooth, a more conservative "cf." designation is preferred here. Fossils suggestive of affinity with *Onychomys* are not previously known from the Las Vegas Formation. The nearest recorded Pleistocene localities that have yielded fossil remains of *Onychomys* are Glendale and Pintwater Cave (Harris, 1985; Hockett, 2000); Harris (1985) and Jefferson (1991) did not list any additional records of the taxon from the Pleistocene of the Mojave Desert. Present-day grasshopper mice generally occur in shortgrass prairies and desert scrub (Nowak, 1991). The common grasshopper mouse of the southwestern United States, *Onychomys torridus*, prefers relatively xeric areas at low elevations (Nowak, 1991). This species is present today in Clark County and southern Nevada, while a related species, *O. leucogaster*, inhabits the northern half of the state (Mantooth and Riddle, 2005).

Neotoma sp. cf. *N. lepida*: Fossils resembling the wood rat species *Neotoma lepida* (L3088-1037, left M1; L3088-1023, right M1; L3088-1020, left M3; L3088-1021 and −1024, right M3s) are also represented in the TSLF from multiple localities. The reduced anterior lingual reentrant angle of the M1s and the morphology of the posterolabial fold on the M3s all suggest affinity with *N. lepida* rather than other species of *Neotoma*. *Neotoma lepida* is common in fossil vertebrate faunas from the southwestern U.S. Other late Pleistocene localities from Clark County include Glendale, Mercury Ridge, Pintwater Cave, and the Sheep Range (Harris, 1985; Hockett, 2000). Desert wood rats are desert dwellers that prefer regions with relatively abundant vegetation; they do not thrive in open, arid regions with little or no brush cover (Hoffmeister, 1986).

Lynx rufus: A partial right humerus lacking the proximal end (L3160-146) from locality SBCM 2.6.369 represents the first Pleistocene record of bobcat from the upper Las Vegas Wash. This specimen was recovered from Bed E_0 and is associated with a date of 21.04 ± 0.52 ka (Springer et al., 2015). Bobcat fossils are actually relatively common in North America, first appearing in latest Pliocene deposits and continuing throughout the Pleistocene and into recent times (Kurtén and Anderson, 1980). Present-day bobcats are remarkably eurytopic carnivorans, inhabiting most kinds of environments from dense forest to desert, although they generally prefer broken country with cliffs and rock outcrops interspersed with open grasslands, woods, or deserts (Hoffmeister, 1986). Other Pleistocene records of *Lynx rufus* from the Mojave Desert include Kokoweef Cave (Reynolds and others, 1991c) and Mitchell Caverns (Jefferson, 1991); a Pleistocene record of *Lynx* sp. is also known from Schuiling Cave (Harris, 1985).

Hemiauchenia sp.: The TSLF differs markedly from other fossil

assemblages in the Mojave in that despite its size it offers little evidence of the extinct North American llama, *Hemiauchenia macrocephala*. This taxon is common from other, smaller late Pleistocene localities in the central and eastern Mojave Desert including Lake Manix (Jefferson, 1987, 1991), Bitter Springs Playa at Fort Irwin (Reynolds and Reynolds, 1994; Scott, 2000), and Lake Tecopa (Woodburne and Whistler, 1991; Reynolds, 1991). We therefore consider the infrequency of *Hemiauchenia macrocephala* from the Las Vegas Formation to be unusual. Clearly the Pleistocene environment of the upper Las Vegas Wash offered a different suite of options for niche partitioning than those provided at other localities in the Mojave Desert region at that time. *Hemiauchenia* has been interpreted to have been an intermediate feeder with a preference for browse, based upon isotopic data (Feranec, 2003), and so the Las Vegas region would appear to have been eminently suitable. Whether plants, topographic features, or other environmental conditions preferred by *Hemiauchenia* were more common outside the Las Vegas region remains to be explored.

A few specimens in the collections of the LACM and the SBCM are suggestive of the presence of a camel genus smaller than *Camelops*; these remains include a right P3 and an incisor in the collections of the LACM (unnumbered), as well as a distal femur (L3088-875) and a left M2 (SBCM L3088-1003). Unfortunately, none of these remains are sufficiently complete or diagnostic to warrant specific or even generic assignment.

Locality SBCM 2.6.617 yielded a proximal right radio-ulna (SBCM L3160-1159) of a small adult camelid. Although incomplete and lacking reliable points of measurement, the specimen is sufficiently small that estimated dimensions fall well within the published size range of *Hemiauchenia* (e.g., Meachen, 2005). Visual comparison with like elements of *Camelops hesternus* from Rancho La Brea confirms that this specimen is too small to be assigned to that species. Given the small size and apparent adult age of the fossil, it is here assigned to the genus *Hemiauchenia*. The incomplete nature of the fossil precludes assignment to species. This is the first record of *Hemiauchenia* from the Las Vegas Formation.

Bovidae (indeterminate): An unfused distal epiphysis of a bovid metapodial (L3088-876) was recovered from spring outflow stream deposits of Member E, Bed E_0. The fossil is substantially larger than either deer (*Odocoileus*) or sheep (*Ovis*), and exhibits morphology more closely resembling the latter genus. L3088-876 also compares favorably in size and shape to metapodials in the SBCM collections that have been informally interpreted to resemble the extinct shrub ox genus *Euceratherium*. Unfortunately, L3088-876 is not sufficiently complete or diagnostic to confirm a generic assignment, and so this fossil is herein identified as a bovid, although its resemblance to *Euceratherium* is noted.

The identification of L3088-876 raises the question of whether or not *Euceratherium* might have been present in the Las Vegas Valley during the latest Pleistocene. The Las Vegas Valley is within the geographic range of *Euceratherium*, and the habitat preferred by members of the genus—lower hills rather than high mountains (Kurtén and Anderson, 1980)—would have been readily available in the Las Vegas region. Continued recovery of vertebrate fossils from the Las Vegas Formation may help confirm whether or not *Euceratherium*, or a like-sized bovid, was present in the region during the latest Pleistocene.

5. Conclusions

The Tule Springs local fauna (TSLF) as it is presently understood is recognized as the largest and most diverse open-site assemblage from the Mojave Desert and southern Great Basin region. Multiple new discoveries presented here significantly augment the Pleistocene vertebrate faunal assemblage from the upper Las Vegas Wash.

The large mammal component of the TSLF is dominated by remains of *Mammuthus columbi*, which appear more common here than at some other late Pleistocene localities in the Mojave Desert. Remains of *Camelops hesternus* are also abundant; less common are remains of *Equus* and *Bison*. The llama *Hemiauchenia* is poorly represented. Large carnivorans including *Canis dirus*, *Smilodon fatalis*, and *Panthera atrox* were also part of the assemblage. Microvertebrate remains have also been recovered from the deposits.

The fossils of the TSLF are entombed in groundwater discharge deposits of the Las Vegas Formation, which preserve lithologic, sedimentological, and fossil evidence of hydrologic changes that occurred in response to significant climatic shifts during the late Pleistocene. Future studies of the TSLF will address how animal populations responded in kind to the changing hydrologic conditions, which will have implications for living fauna that depend on springs and desert wetlands for water in the harsh desert landscapes of the southwestern U.S.

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