PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2020, v. 35, 175–190
Research Article
DOI: http://dx.doi.org/10.2110/palo.2019.067

THE INFLUENCE OF DEPOSITIONAL ENVIRONMENT AND BASIN HISTORY ON THE TAPHONOMY OF MAMMALIAN ASSEMBLAGES FROM THE BARSTOW FORMATION (MIDDLE MIOCENE), CALIFORNIA

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ABSTRACT: **The Barstow Formation in the Mojave region of California was deposited in an extensional-basin setting of the Basin and Range province and preserves diverse middle Miocene mammalian assemblages. Six facies associations represent the dominant depositional environments in the basin, which changed through time from alluvial-fan and playa-dominated settings to floodplains and spring-fed wetlands. The majority of fossil localities and specimens occur in later-forming facies associations. We analyzed the taphonomic characteristics of fossil assemblages to test whether basin-scale facies associations or locality-scale facies exert more control on the preservational features of mammalian assemblages through the formation. We documented the facies settings of 47 vertebrate localities in the field in order to interpret depositional setting and the mode of accumulation for fossil assemblages. We evaluated skeletal material in museum collections for taphonomic indicators, including weathering stage, original bone-damage patterns, hydraulic equivalence, and skeletal-element composition. We evaluated four alternative modes of accumulation, including attritional accumulation on the land surface, accumulation by fluvial processes, carnivore or scavenger accumulations, and mass-death events. The majority of localities represent attritional accumulations at sites of long-term mortality in channel-margin, abandoned-channel, poorly drained floodplain, and ephemeral-wetland settings. Skeletal-element composition and taphonomic characteristics varied among facies, indicating an important role for depositional setting and landscape position on fossil-assemblage preservation. We find that locality-scale facies have a greater influence on the taphonomic characteristics of fossil assemblages; the taphonomy of each facies association is influenced by the facies that compose it. The facies composition and distribution within facies associations change through the formation, with a greater variety of depositional settings forming later in the history of the basin. Heterogeneous landscapes present more settings for fossil accumulation, contributing to the increase in fossil occurrence through the depositional history of the formation.**

INTRODUCTION

Bone accumulations in terrestrial settings form under a variety of circumstances that depend on processes occurring at the land surface. Processes of accumulation may be biological or geological in nature and may take place over time spans of minutes to thousands of years (Behrensmeyer 1975; Rogers and Kidwell 2007). By evaluating the taphonomic attributes of bones in fossil assemblages and the depositional setting of the sites of accumulation, we can interpret ancient processes and agents of bone accumulation and their facies context. As environments change through the history of a basin, the taphonomic processes acting on vertebrate material may result in changing preservation potential as facies change through a depositional sequence. The taphonomic patterns within a stratigraphic sequence can have implications for a range of paleontologic investigations, from systematics to paleoecology.

The Barstow Formation in southeastern California preserves an early to middle Miocene record of continental sediments and mammalian faunas. The type fauna of the Barstovian North American Land Mammal Age is documented from the type section of the Barstow Formation in the Mud Hills near Barstow, California (Fig. 1; Woodburne 2004), and large- and small-mammal biochronologies have been established for the formation (Lindsay 1972; Woodburne et al. 1990; Pagnac 2009). Most work on the mammal faunas of the formation has been systematic paleontology, and few studies have focused on the taphonomy or ecology of assemblages (Browne 2002; Pagnac 2005). Facies analysis (Loughney and Badgley 2017) and paleoenvironmental reconstruction (Loughney et al. 2020) provide new contexts for studying the taphonomy of the Barstow Formation in relation to the depositional history of the basin. Fossil localities are unevenly distributed through the major facies of the formation, as preservation potential of depositional environments changed in response to tectonics and climate (Loughney and Badgley 2017). Because taphonomic features of assemblages are typically linked to depositional environment (Behrensmeyer 1988), we evaluated whether taphonomic characteristics of fossil assemblages in the Barstow Formation covary more closely with changes in major facies associations (FAs) or with the facies representing specific depositional settings within FAs.

In this paper, we describe taphonomic features of the large-mammal ($>$ 1 kg) faunas of the Barstow Formation. We focused on large mammals because the majority of specimens from the formation represent large mammals, which have been more consistently collected than small mammals over the last 100 years. We examined fossil specimens to infer taphonomic processes of accumulation, evaluated the relationship of taphonomic processes to FAs and facies, and analyzed taphonomic patterns of fossil assemblages in relation to depositional setting and basin history. We address three questions: (1) Which depositional settings (facies) preserve large-mammal remains? (2) Do taphonomic characteristics of fossil assemblages vary by facies and FA? (3) How do taphonomic patterns

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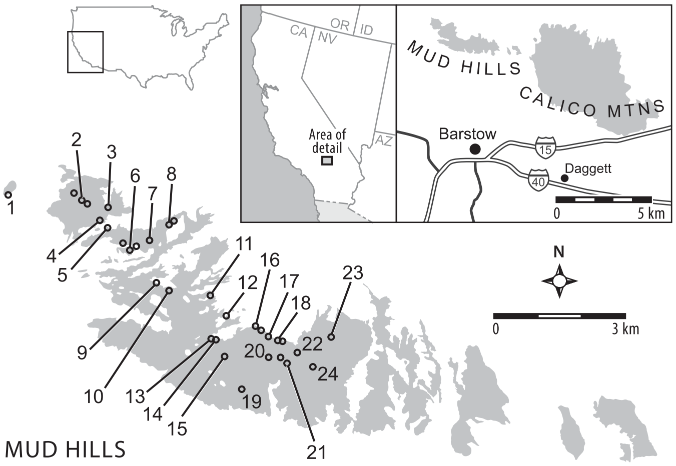

FIG. 1.—Map of the Barstow Formation in the Mud Hills, California, with the location of fossil localities shown in Figure 2. Key: 1 = SBCM 1.130.421; 2 = MMR-029, MMR-051, MMR-043; 3 = Margo Quarry; 4 = UCMP V6448; 5 = UCMP V6447; 6 = Rodent Hill Basin; 7 = Leader Quarry, Sunnyside Quarry; 8 = Robbins Quarry, Hidden Hollow Quarry; 9 = Lake Bed, RAM V200047; 10 = RAM V98004, Slugbed; 11 = *Hemicyon* Quarry; 12 = Easter Quarry; 13 = Steepside Quarry, Sunset Quarry; 14 = Oreodont Quarry, Turbin Quarry; 15 = Rak Quarry; 16 = Hailstone Quarry; 17 = May Day Quarry, New Year Quarry, MMR-049; 18 = Skyline Quarry, Starlight Quarry; 19 = Red Division Quarry; 20 = Deep Quarry; 21 = Camp Quarry; 22 = Valley View Quarry; 23 = Saucer Butte Quarry; 24 = Sunder Ridge. Modified from Loughney and Badgley (2017).

and processes change over the depositional history of the basin? If FAs control the taphonomy of fossil assemblages, then we expect each FA to have distinct taphonomic characteristics and to see changes in these assemblage characteristics through time. If locality-scale facies control the taphonomy of assemblages, then we expect each depositional setting of accumulation to have distinct taphonomic characteristics. The taphonomic influences of facies and FAs on fossil assemblages may underlie the patterns of fossil distribution through the formation.

We combined detailed facies descriptions of fossil localities to characterize depositional settings with taphonomic analyses of fossil assemblages to infer mode of accumulation for fossil assemblages. For each fossil locality, we interpreted the depositional setting in relation to its inferred landscape position and evaluated taphonomic features of the fossil assemblage. We distinguished among four possible modes of accumulation: long-term sites of mortality, fluvial accumulations, carnivore and scavenger accumulations, and mass-death events. The distribution of fossil assemblages and their inferred taphonomic processes through the formation indicate how fossil preservation changed over the history of the Barstow Basin.

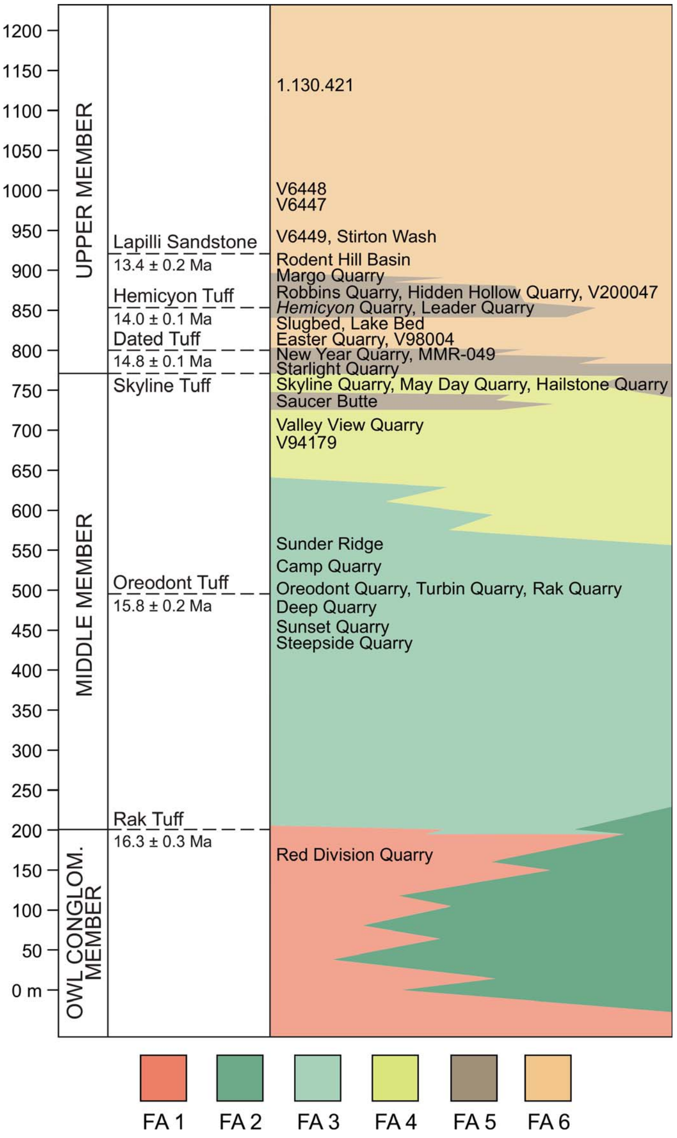

FIG. 2.—Stratigraphy of the Barstow Formation, showing dated tuff units (dates from MacFadden et al. 1990), relationships among major facies associations (FAs), and stratigraphic position of fossil localities shown in Figure 1.

Geological Background

The Barstow Formation crops out in the central Mojave Desert near Barstow, California (Fig. 1). Detachment faulting throughout the Mojave region created fault-block basins during the early Miocene (Glazner et al. 2002). The Barstow Formation was deposited after extension had ended in the central Mojave region and unconformably overlies the older Pickhandle and Mud Hills formations in the Mud Hills and Calico Mountains (Fig. 1; Ingersoll et al. 1996; Glazner et al. 2002).

The Barstow Formation is divided into three lithostratigraphic members in the Mud Hills: the Owl Conglomerate, Middle, and Upper members (Fig. 2; Woodburne et al. 1990). It has been dated through biostratigraphy (Woodburne et al. 1990; Pagnac 2009), magnetostratigraphy (MacFadden et al. 1990; Woodburne 1996), and radiometric dating of airfall tuffs (Woodburne et al. 1990; Miller et al. 2010; Miller et al. 2013). In the Mud Hills, the Barstow Formation ranges in age from ∼ 19 to ∼ 13 Ma (Woodburne et al. 1990).

Six major FAs record the dominant environments and associated landscapes of the Barstow Formation (Fig. 2; Loughney and Badgley 2017). Environments changed from closed-drainage, alluvial-fan and playa-lake settings to open-drainage fluvial systems in response to changes in subsidence and accommodation. FA 1 represents channels and interfluves of alluvial fans that drained into playa-lake deposits of FA 2. FA 1 and FA 2 formed early in the basin history when rates of subsidence and sediment accumulation were high. As rates of subsidence decreased, meandering streams were established; FA 3 represents the channel and proximal-floodplain deposits of these fluvial environments. Deposits of FA 3 grade into those of FA 4, which are stacked sandstone bodies that represent channel deposits of braided streams. FA 5 and FA 6 are mudstone-dominated and represent interfingering poorly drained and well-drained floodplain deposits and spring-fed wetlands, which formed when rates of sediment accumulation and subsidence were low (Loughney and Badgley 2017).

Barstow Fauna and Fossil Localities

Fossils from the Barstow Formation have been collected and described since the early twentieth century (e.g., Merriam 1919; Woodburne et al. 1990). Important early collections were made by the University of California Museum of Paleontology (UCMP) and the American Museum of Natural History (AMNH). The American Museum parties under Childs Frick established many fossil localities throughout the Mud Hills, and some of the largest and most productive localities are Frick-era quarries. Collectors from the University of California, Riverside; the San Bernardino County Museum in San Bernardino, California; and the Webb Schools and affiliated Raymond Alf Museum (RAM) in Claremont, California, began making collections in the 1960s (Pagnac et al. 2013). The San Bernardino County Museum (SBCM) and the Webb Schools continue to add to their collections from the Barstow Formation. Fossil material was collected through excavation and surface collection sporadically throughout the twentieth century (Woodburne et al. 1990; D.L. Lofgren personal communication 2018; R.E. Reynolds personal communication 2018) and to the present day.

The mammal faunas of the Barstow Formation are characteristic for North America during the middle Miocene (Pagnac et al. 2013). The most abundant herbivorous groups are equids (eight species), camelids (seven species), and antilocaprids (six species). Other ungulates that occur in low abundance include oreodonts (three species), tayassuids (three species), palaeomerycids (two species), proboscideans (two genera), and rhinoceros (one species). The carnivore fauna is dominated by canids, with 13 species recognized in the formation. Other important carnivores are amphicyonids (four species), mustelids (three species), felids (two species), ursids (one species), and procyonids (one species). Many small-mammal species are also recognized from the formation, including numerous rodents and insectivores (Lindsay 1972).

Fossils occur unevenly throughout the formation in the Mud Hills. Few large-mammal fossils occur in FA 1, and imprecise stratigraphic information exists for localities in this interval (Woodburne et al. 1990). Red Division Quarry (AMNH) is the most important quarry from FA 1 and is the oldest locality included in this study. Only mammal trackways are known from FA 2, and no fossils from this FA were included in our analysis. Many fossil localities occur in FA 3 and FA 4, including several localities that have produced hundreds of specimens, primarily through excavation. Steepside, Camp, and Deep Quarries (AMNH) in FA 3, and Valley View and Skyline Quarries (AMNH) and RAM V94179 in FA 4 are among the prominent localities of these two FAs. The majority of fossil localities occur in FA 5 and FA 6. New Year and *Hemicyon* Quarries (AMNH) and Robbins Quarry (SBCM) are productive localities in FA 5. RAM V98004, Rodent Hill (UCMP), and UCMP V3849 are rich localities in FA 6 (Figs. 1, 2).

Taphonomic Indicators and Modes of Accumulation

The mode of accumulation represents the combination of biological and physical processes that result in distinct patterns of taphonomic modification. Attrition in specific sites over years to decades, fluvial processes, carnivore accumulations, and mass-death or catastrophic events are possible modes of accumulation that may be distinguished based on sedimentological criteria and taphonomic indicators in fossil assemblages. Facies characteristics and lateral extent of the fossiliferous horizon are the sedimentological basis for inferring depositional setting. Taphonomic indicators include patterns of original bone damage (abrasion, tooth marks), weathering stage, degree of articulation, and skeletal-element composition. The frequency of these indicators varies among assemblages that accumulated under different processes (Table 1; Badgley 1986a; Behrensmeyer 1991; Eberth et al. 2007).

TABLE 1.—*Taphonomic characteristics of generalized assemblages formed through four modes of accumulation common in terrestrial environments. For each accumulation mode, generalized degree of articulation and completeness, types of original damage patterns, range of weathering stages, spatial dimensions of the locality, and amount of material in hydraulic equivalence with sediment matrix are given.*

Mode of accumulation	Features of the assemblage
Long-term site of mortality	Specimens articulated and disarticulated; multitaxic; elements complete, partial, or fragmentary; tooth marks and breakage common (present on > 25% of material); wide range of weathering stages; assemblage is laterally and vertically extensive; little to no hydraulic equivalence (< 10% of elements)
Fluvial accumulation	Specimens disarticulated, not associated; multitaxic; elements complete, partial, or fragmentary; tooth marks variable (present on < 25% of material); abrasion, rounding, and polish common; wide range of weathering stages; assemblage is laterally and vertically concentrated; high hydraulic equivalence (> 50% of elements)
Carnivore or scavenger accumulation	Specimens articulated or disarticulated; multitaxic; elements partial or fragmentary; tooth marks and punctures abundant (present on > 50% of material), breakage common; variable range of weathering stages; assemblage is laterally concentrated; no hydraulic equivalence (0% of elements)
Mass-death or catastrophic event	Specimens articulated or disarticulated, many associated; mono- or paucitaxic; elements complete or partial; tooth marks, breakage variable; uniform weathering stage; assemblage may be laterally extensive, vertically concentrated; high to no hydraulic equivalence (0% to > 50% of elements)

We assessed four modes of accumulation for fossil assemblages in the Barstow Formation. (1) Long-term sites of mortality are places where animals live, interact, and die over years to decades. Biological activities, including predation, seasonal migration, or breeding behavior, typically cause individuals and species to concentrate spatially or temporally at certain sites (Rogers and Kidwell 2007); (2) Fluvial accumulations are created by transport and sorting by stream currents, and the ability of water to move skeletal elements depends on flow velocity and element size, shape, and density (Voorhies 1969; Hanson 1980); (3) Carnivores and scavengers can modify bone assemblages by collecting individual elements or by disarticulating and dispersing remains from a mortality site (Lansing et al. 2009); and (4) Mass-death or catastrophic events may include floods, volcanic activity, or drought and typically result in concentrations of individuals with little post-mortem modification (Table 1; Rogers and Kidwell 2007).

METHODS

We used field observations of facies to interpret depositional processes along with taphonomic indicators to infer mode of accumulation (Table 1). Combining lithological description from the field and evaluation of taphonomic features from fossil assemblages is a robust means of interpreting taphonomic modes of accumulation (Behrensmeyer 1991), even when these data are collected separately.

Field Description

We documented facies characteristics for 61 fossil localities in the Mud Hills. Sites were selected based on the amount of material in museum collections, FA occurrence, and paleontological significance. Localities that are representative for their FAs were visited in FA 1 (Owl Conglomerate Member), FA 3 and FA 4 (Middle Member), and FA 5 and FA 6 (Upper Member) in the Mud Hills (Fig. 2).

We located fossil sites using aerial photographs, topographic maps, Google Earth, and field maps and notes from museum archives. Coordinates of localities were recorded with a Garmin eTrex GPS unit. The stratigraphic position of each locality was tied into the nearest stratigraphic reference section from Loughney and Badgley (2017) using a Jacobs staff and Brunton compass. Most localities in the Barstow Formation have been collected by several institutions and many have multiple names or institution numbers; we assigned a University of Michigan locality number (MMR) to each locality.

In order to interpret the depositional setting, we described the sedimentology and stratigraphy of the 61 fossil localities, including lithology, bed thickness and geometry, sedimentary structures and ichnofossils, vertical and lateral extent of the locality, and number of fossil layers (Loughney 2018). The number of productive layers was documented from positions of *in situ* bones and teeth or estimated if *in situ* elements were not observed. Ideally, the position of *in situ* bones would be noted in the field at the time of collection; however, this information was not available for most of the localities examined here. At most localities, excavation scars were evident, and it was possible to trace elements in float toward source horizons. At localities without *in situ* elements, we traced float material to probable source horizons and estimated at least one source layer and more than one if the locality had multiple excavation scars. This approach may underestimate the actual number of productive layers, as bones were likely deposited in multiple layers in some depositional settings. We made surface collections of bone and tooth fragments where appropriate.

Taphonomic Data from Museum Collections

During 2015–2017, KML visited four museums with significant collections of fossil material from the Barstow Formation: the American Museum of Natural History (AMNH), University of California Museum of Paleontology (UCMP), Raymond Alf Museum of Paleontology (RAM), and the San Bernardino County Museum (SBCM). We examined 3,285 specimens of bones, teeth, and fragments of mammals from 93 localities to document features useful for interpreting taphonomic history. Specimens examined from these localities were originally collected via excavation (approximately 44%) or surface collection (approximately 56%).

We evaluated each specimen for original surface features and damage, including breakage patterns, abrasion, rounding, tooth marks, number of punctures, and weathering stage (Fig. 3). We assessed weathering stage based on the categories of Behrensmeyer (1978). In many instances, we encountered material with weathering features that were intermediate between two stages; we recorded these features as "advanced" (e.g., advanced 1). Broken edges of bones were characterized as smooth or irregular, and fracture outlines were characterized as transverse, stepped, or saw-toothed (Villa and Mahieu 1991; Pesquero et al. 2013). Saw-toothed and irregular edges of broken bones are typically produced during chewing by carnivores, whereas smooth, transverse breaks are diagenetic (Alcalá and Escorza 1998; Fernández-Jalvo and Andrews 2016). Stepped or curved fractures may further indicate whether bones were broken when dry or fresh, respectively. Bone may become abraded or rounded from prolonged interaction with sediment grains in stream channels or from trampling (Olsen and Shipman 1988; Eberth et al. 2007; Fernández-Jalvo and Andrews 2016). Specimens for which these features could not be determined (due to preservation quality, preparation, or repairs) were omitted from further analyses; we did, however, include all elements in skeletal-element analyses. We recorded the completeness of all specimens based on presence of original breakage patterns and categorized each fossil as complete, partial, or fragmentary. Complete specimens were 90% to 100% complete, partial elements were 40% to 90% complete, and fragmentary specimens were less than 40% complete. We chose these percentages in order to increase element identification and to accommodate a range of skeletal elements with varying shapes. We also measured length, width, and height of all specimens in order to calculate hydraulic equivalence.

Skeletal-Element Composition and Depositional Contexts

For each fossil assemblage, we determined the skeletal-element composition. The relative frequency of skeletal elements in a fossil assemblage can be compared to the skeletal-element composition of the average whole mammal (e.g., Badgley 1986a) as a way to estimate the degree of modification of the death assemblage. The average Neogene ungulate contains approximately 210 bones, which can be grouped into morphologically functional and taphonomically similar categories (e.g., vertebrae, podials, long bones). We omitted ribs and sesamoids, as these elements were rare in Barstow assemblages, and grouped elements into nine categories containing approximately 170 bones for an average ungulate. We chose a Neogene ungulate for comparison, as ungulates dominate Barstow faunal assemblages. The frequency of over- and under-represented elements indicates how assemblage composition differs from the composition of the original skeletons and potentially reveals agents of modification associated with particular depositional settings.

Because the number of localities and specimens varies within and among each depositional setting and FA, we calculated confidence intervals on mean skeletal-element compositions. We calculated the bootstrapped mean proportion of skeletal elements from assemblages within each depositional setting and FA. Confidence intervals were calculated as twice the standard deviation of the bootstrapped mean proportions. We used pairwise Kolmogorov-Smirnov tests to compare the skeletal-element composition of fossil assemblages in each depositional setting and FA against that of the average ungulate. This non-parametric test enabled us to assess whether the mean proportion of skeletal elements was significantly altered from its initial composition in assemblages from the different depositional settings and FAs. We adjusted *p*-values using the Bonferroni correction on multiple comparisons of depositional settings (28 comparisons) and FAs (15 comparisons).

Hydraulic Equivalence

Hydraulic equivalence involves comparison of the settling velocities of fossils to clasts in their encasing sediment matrix to estimate whether they could have been transported and deposited by the same flow velocities (Behrensemeyer 1975). The settling velocity of a grain in a fluid describes the balance between gravitational acceleration and the drag exerted on the grain by the fluid (Bridge 2003). Hydraulically equivalent fossil specimens and sediment could have been transported and deposited together, whereas non-hydraulically equivalent specimens and sediment cannot have a shared transport history. Assemblages accumulating through fluvial processes should have a high proportion of material in hydraulic equivalence with the sediment matrix, whereas a lack of hydraulic equivalence indicates that fluvial processes were not the dominant mode of accumulation (although it does not rule out fluvial influence). Hydraulic equivalence alone, however, is not sufficient evidence that elements in an assemblage were transported, an inference which must be based on additional features of the fossil assemblage (Badgley 1986b).

Hydraulic equivalence is determined by calculating the diameter of a quartz sphere (d_q) with equivalent density to a bone or tooth

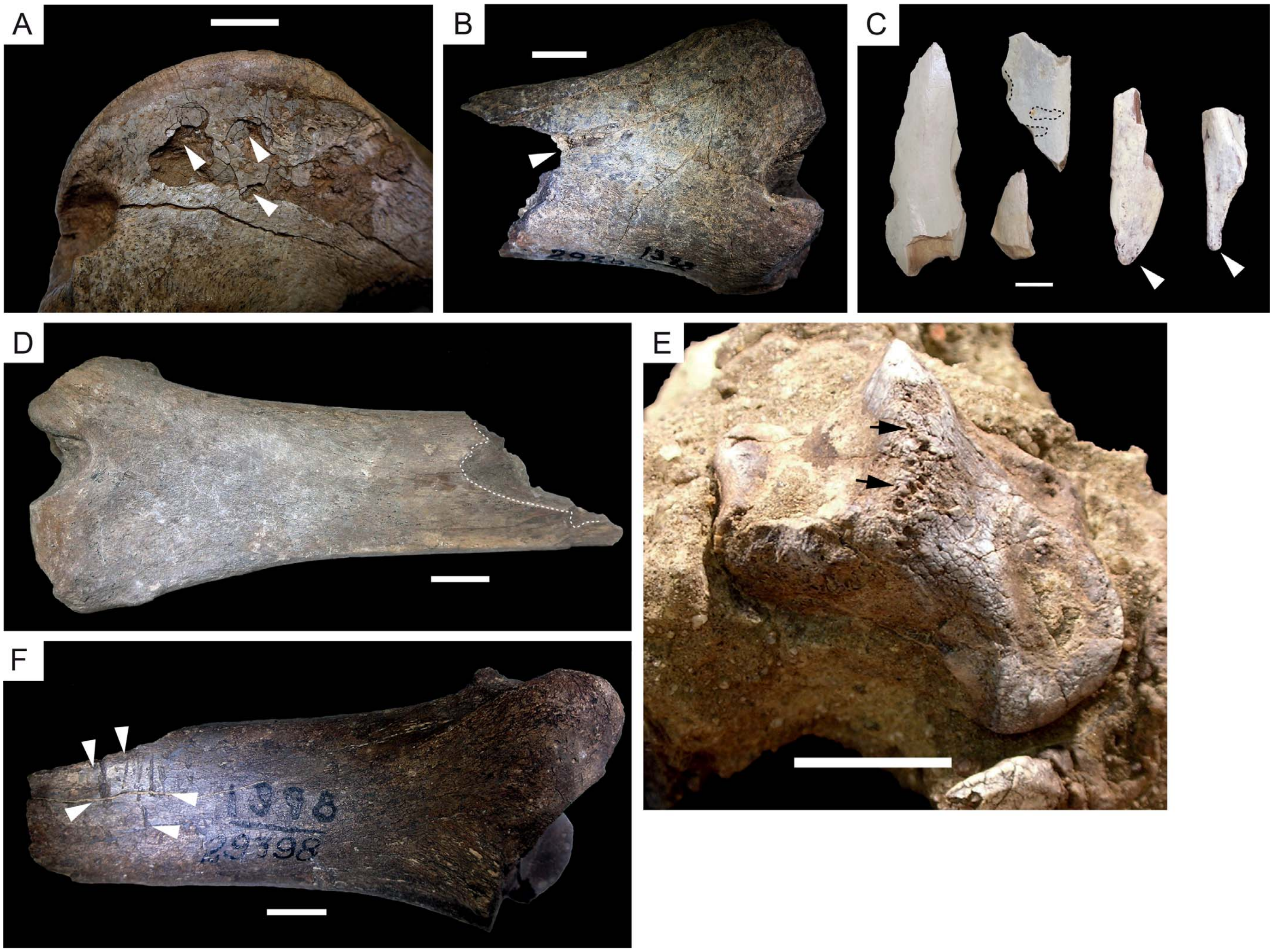

FIG. 3.—Examples of taphonomic features of fossils from the Barstow Formation. **A**) Tooth marks on a distal femur (white arrows) indicative of carnivore modification. **B**) Saw-toothed, irregular fractures on a distal tibia indicative of gnawing. **C**) Bone chips with conchoidally fractured edges, tooth marks (dashed lines), and rounded edges (white arrows) indicative of carnivore processing. **D**) Shallow-angled, flaked edge (dashed line) on an irregular fracture on a distal tibia indicative of breakage from impact or trampling. **E**) Abraded edges (black arrows) of an equid phalanx in coarse-grained sandstone indicative of sedimentary abrasion. **F**) Tooth marks (white arrows) around a shallow-angled, irregularly fractured edge of a distal tibia indicative of breakage and gnawing by a carnivore. Scale bars = 1 cm.

(Behrensmeyer 1975; Badgley 1986a):

$$d_q = (\rho_b - 1) \times \frac{d_b}{1.65} \tag{1}$$

where ρ_b is bone density, which varies depending on the amount of cancellous and compact bone in an element, and d_b is the nominal diameter of bone, calculated from the volume (v_b) of a specimen:

$$d_b = \sqrt[3]{1.91 \times v_b}. \tag{2}$$

We used the dimensions of specimens measured in museum collections and the measured densities of modern bone and teeth in Badgley (1986a) to calculate nominal bone diameters for the equivalent densities of quartz spheres.

Mode of Accumulation

We distinguished among four possible modes of accumulation that are common in terrestrial environments: attrition in long-term sites of mortality, fluvial accumulation, carnivore and scavenger accumulations, and mass-death or catastrophic events (Table 1). We used the spatial dimensions of the locality to infer whether the agent of accumulation concentrated or dispersed remains. For each locality, we assessed taphonomic features of individual specimens and evaluated the properties of the entire assemblage to infer mode of accumulation. We used weathering stage and degree of articulation as indications of the duration of exposure before burial (Behrensmeyer 1978; Eberth et al. 2007), and we evaluated element completeness, articulation, and damage patterns for evidence of carnivore or scavenger modification and trampling (Pesquero et al. 2013; Fernández-Jalvo and Andrews 2016). In addition to hydraulic equivalence of elements, we considered abrasion and the degree of articulation and association of material in interpreting fluvial transport (Voorhies 1969; Behrensmeyer 1975).

Each mode of accumulation imparts characteristic taphonomic features on the resulting assemblage that are useful for discriminating among them (Table 1). Long-term sites of mortality contain time-averaged assemblages that show little or no evidence of fluvial transport and have a variety of articulation and association patterns, weathering stages, and bone damage (Table 1). Typically, many individuals and species are present in the

TABLE 2.—*Taphonomic characteristics of fossil assemblages from the Barstow Formation by depositional setting. For breakage, abrasion, rounding, polish, and tooth marks, the number of specimens exhibiting that taphonomic feature is given relative to the total number of specimens assessed for that feature. Number of genera is the number identified for all localities combined. TNS = total number of specimens evaluated. Mean NS = mean number of specimens per locality; total number of specimens divided by number of localities ± one standard deviation. WS = weathering stage.*

Depositional setting	Channel lag[1]	Crevasse splay	Channel margin	Abandoned channel	Poorly drained floodplain	Ephemeral wetland	Well-drained floodplain
No. localities	2	2	16	10	9	7	1
TNS	14	60	1095	434	450	982	125
Mean NS	7 ± 3	30 ± 10	68 ± 88	43 ± 69	50 ± 50	140 ± 331	125
Median NS	7	30	22	19	38	7	125
No. genera	6	2	32	27	29	12	1
Articulation	0/14	0/60	95/1095	55/434	11/450	6/982	102/125
Association	0/14	3/60	301/1095	31/434	54/450	27/982	19/125
Breakage	8/14	30/60	292/888	116/260	127/327	124/718	2/125
Abrasion	10/12	28/52	345/981	87/255	72/308	294/865	0/125
Rounding	1/14	20/44	94/969	13/319	22/309	48/860	0/125
Polish	0/14	2/35	46/970	5/319	26/307	76/806	0/125
Tooth marks	3/14	2/37	191/1081	35/280	70/354	362/982	?
WS range	1 to 2	1 to 3	0 to 4	1 to adv. 3	1 to 3	0 to 3	1 to adv. 1
Mean WS	Adv. 1	Adv. 1	Adv. 1	1 to adv. 1	1 to adv. 1	Adv. 1	1
Median WS	Adv. 1	Adv. 1	Adv. 1	1	1	Adv. 1	1
Hydraulic Equivalence	92.9% (13)	56.8% (25)	0% (553)	2.8% (185)	0% (188)	0% (646)	0% (0)

[1] Does not include RAM 7648

assemblage (Rogers and Kidwell 2007). Fluvial accumulations comprise non-associated material that is typically abraded, rounded, or polished. Although fluvial deposition can occur in discrete events, fluvial accumulations may be time-averaged because the remains of many individuals are assimilated from different sources (Aslan and Behrensmeyer 1996). Carnivore and scavenger collections typically include partial skeletons and fragmentary material that shows carnivore damage (tooth marks, punctures); predators and scavengers may concentrate remains at dens, burrows, or roosting sites (Rogers and Kidwell 2007; Lansing et al. 2009; Fosse et al. 2012). Characteristics of mass-death assemblages vary depending on the nature of the mortality agent; floods, volcanic eruptions, or droughts typically occur over short time spans (minutes to weeks) and can result in the deaths of up to hundreds of individuals (Capaldo and Peters 1995; Rogers and Kidwell 2007). Such assemblages may be monotaxic or paucitaxic with a high degree of articulation or association of elements (Table 1; Voorhies 1969; Martin 1999).

Multivariate Analysis of Skeletal-Element Composition

We performed principal coordinate analysis (PCO) on counts of skeletal elements from fossil localities in different depositional settings. Principal coordinate analysis is a distance-based ordination method that enables visualization of group differences (Zuur et al. 2007). We thereby evaluated the covariation among skeletal elements and their variation among depositional environments. Because processes that accumulate and disperse skeletal elements operate within each depositional setting, the absence of a particular skeletal element at a locality is potentially as informative as the presence of that element. We therefore used the Euclidean distance matrix to preserve the distance among sites. We included counts of 2,702 skeletal elements in 13 element categories from 27 localities with observations from both the field and museum collections. Specimen counts per locality ranged from 10 to 862; we excluded localities with fewer than 10 specimens, including those from channel-lag deposits. We also excluded the well-drained floodplain assemblage as an outlier in our ordination. To minimize absolute differences in the number of elements among localities, counts were transformed by taking the natural log of (count + 1). We calculated the Euclidean distance matrix on counts using the "vegan" package (Oksanen et al. 2017) in R version 3.6.2 (R Core Team 2019).

RESULTS

For 47 localities, we had both field descriptions and data from museum collections. These localities are distributed throughout the fossiliferous facies associations (FAs) of the Barstow Formation and include many of the most productive localities (Figs. 1, 2). These localities represent a range of facies settings, taphonomic features, and taxonomic composition. Taphonomic features of fossil assemblages are summarized in Table 2 and detailed in the Online Supplemental File (Table S1).

Depositional Settings of Fossil Localities

Within the FAs of the Barstow Formation, we identified nine facies that occur in varying proportions (Fig. 4). The 47 fossil localities documented in detail occur in seven of these facies (Table 3), distributed throughout the formation, with the majority of localities occurring in FA 5 and FA 6 of the Upper Member (Fig. 2). No vertebrate localities occur in lacustrine facies (FA 2). Based on the lithology, sedimentary features, facies relationships, and bed geometry at the localities, we interpret the depositional setting of fossil-bearing facies in terms of original landscape positions and processes in a fluvial system: active channel, crevasse splay, channel margin, abandoned channel, poorly drained floodplain, ephemeral wetland, and well-drained floodplain (Fig. 5). Lithological descriptions of facies and interpretations of depositional settings are summarized in Table 3 (also see Loughney 2018).

Skeletal-Element Composition of Fossil Assemblages

The skeletal-element composition of assemblages varied at the scale of facies and depositional settings (Fig. 6). The skeletal-element composition of the seven depositional settings did not differ significantly from that of the average ungulate (adjusted $p > 0.05$; Online Supplemental File Table S2). Serial elements that are numerous in the average whole ungulate differed among assemblages from different depositional settings. Teeth were abundant in most assemblages, whereas the occurrence of vertebrae ranged from abundant (e.g., in well-drained floodplain) to absent (e.g., in

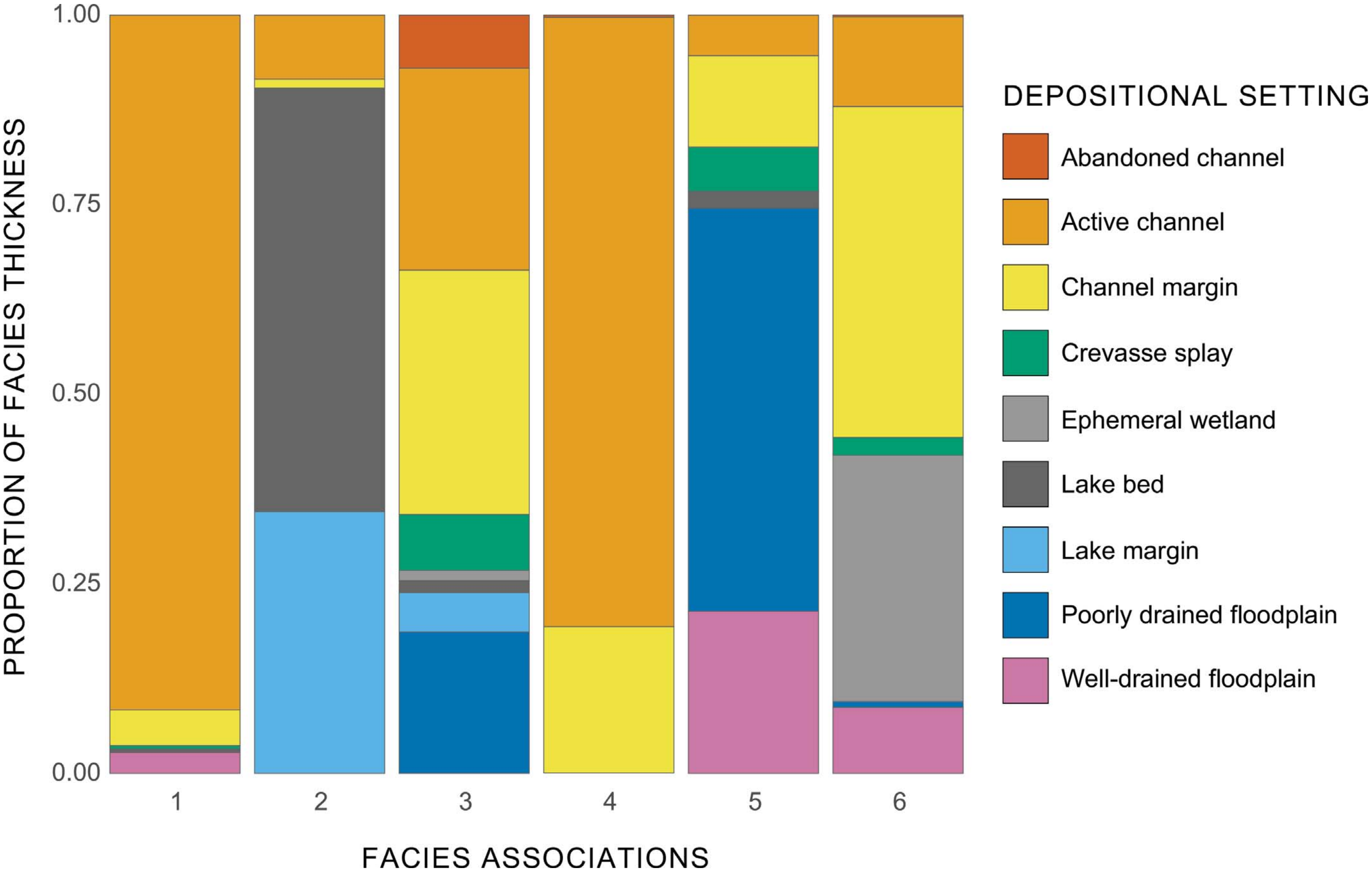

FIG. 4.—Stacked barplot of the proportional thickness of nine facies that occur within six facies associations, measured from 25 stratigraphic sections in the Barstow Formation in the Mud Hills.

channel lag). Assemblages that were modified by fluvial processes (channel lag and crevasse splay) showed distinct differences from assemblages without fluvial modification and had high proportions of limb elements, including shafts of long bones and podials (Fig. 6). In pairwise comparisons, assemblages from channel-lag and crevasse-splay settings differed significantly from those from channel-margin, poorly drained floodplain, and ephemeral-wetland settings, and channel-margin assemblages differed from the well-drained floodplain assemblage (Online Supplemental File Table S2).

Among FAs, the skeletal-element composition of FA 1, FA 5, and FA 6 differed significantly from the composition of the average ungulate (adjusted $p < 0.05$; Online Supplemental File Table S3). Teeth were abundant in the assemblages of most FAs, as were podials and metapodials. Cranial elements, vertebrae, and girdles were present in fewer assemblages, and their occurrence was variable among FAs (Fig. 7). The skeletal-element composition of FA 1, which included only one fluvially modified assemblage, differed significantly from those of all other FAs (adjusted $p < 0.05$; Online Supplemental File Table S3).

The principal coordinate analysis (PCO) of skeletal-element composition of localities separated localities by depositional settings of fossil preservation and by FA (Figs. 8, Online Supplemental File Fig. S1, Table 4). In Figure 8, the first principal coordinate axis, with 52% of the variance, separates localities with a high frequency of vertebrae, metapodials, distal long bones, and girdle elements from localities with a high frequency of long-bone shafts. Notably, many of the elements that dominate the positive side of PCO 1 include those that are most susceptible to fluvial transport (Voorhies 1969; Moore and Varricchio 2018), thereby indicating that these assemblages experienced little winnowing from fluvial action. PCO 2, with 13% of the variance, separates localities with a high frequency of cranial elements (skull, dentary) and proximal long bones from localities with a high frequency of isolated teeth, vertebrae, and distal limb elements (podials, phalanges).

On the ordination biplot (Fig. 8), the convex hulls that span localities from depositional settings largely overlap but also show moderate separation for certain settings. Fossil assemblages from channel-margin settings are roughly centered around the origin and have a high degree of overlap with those from three other well-represented depositional settings, especially with those from poorly drained floodplains along PCO 2. Assemblages from ephemeral wetlands have the most variable composition. Fossil assemblages from abandoned channels lie mainly in the lower-left quadrant of the biplot and contain a high frequency of skulls (Figs. 6, 8). These assemblages are the most dissimilar from those in other depositional settings and show minimal overlap in composition. There is no overlap of these assemblages with those from ephemeral wetlands, which extend to the upper-right quadrant and show a high frequency of distal limb elements (Figs. 6, 8).

The convex hulls of FAs show moderate separation and overlap (Online Supplemental File Fig. S1). The skeletal-element compositions of FA 3, FA 4, and FA 6 overlap the least in composition, whereas FA 5 overlaps with the compositions of the other FAs. FA 3 separates the most along PCO 2, whereas FA 4 and FA 6 separate the most along PCO 1. The skeletal-element composition of FA 6 is heavily influenced by the presence of distal limb elements, and the composition of FA 3 is similar to that of abandoned-

TABLE 3.—*Lithological descriptions of facies settings for 47 fossil localities in the Barstow Formation. Interpretation of depositional setting is based on lithological characteristics and sedimentary features documented in the field. Depositional settings correspond to those shown in Figure 5 and discussed in the text.*

Facies and locality description	Interpretation	Depositional setting category	No. of localities
Cross-stratified to massive, coarse- to fine-grained sandstone with pebble- or cobble-sized clasts, fining upwards to cross-stratified sandy siltstone with slickensides, mottles, sand-filled burrows, clay-filled root traces, manganese concentrations; *Celliforma* nests and root traces; scoured or sharp upper and lower contacts. Lateral extent 2 to 4 m.	Channel and channel-bar deposits	Channel lag	2
Coarse- to fine-grained sandstone with pebble or coarse-sand lags and ripple-cross stratification with locally preserved palm-frond impressions; thin, tabular or wedge-shaped beds 25–30 cm thick, sharply overlie siltstone with fine to medium root casts. Lateral extent 4 to 30 m.	Crevasse-splay deposits on the proximal floodplain	Crevasse splay	2
Medium- to fine-grained cross-stratified sandstone fining upwards to laminated to massive siltstone and fine sandstone; bioturbated and brecciated marl layers (10–20 cm thick) may be present; root traces, root casts, mottling; upper boundaries truncated by coarse- to medium-grained sandstone beds. Lateral extent 3 to 40 m.	Levee and chute deposits	Channel margin	16
Siltstone and claystone with abundant root casts and traces, thin-bedded marls (2–3 cm thick) with bioturbated or brecciated upper surfaces, oncolites; low-chroma coloration; in sharp vertical and lateral contact with coarse- to medium-grained cross-stratified sandstone or pebble conglomerate. Lateral extent 4 to 10 m.	Abandoned-channel fill	Abandoned channel	10
Siltstone and claystone interbedded with numerous bioturbated marl layers (4–40 cm thick), abundant root casts, *Lymnaea* and *Planorbula* snails; low-chroma coloration, mottling, pedogenic features absent or poorly developed; gradational or sharp vertical contacts. Lateral extent 5 to 40 m.	Low-lying floodplain, floodplain pond, or perennial wetland	Poorly drained floodplain	9
Siltstone interbedded with nodular or brecciated marl layers (10–90 cm thick) with abundant root casts; *Lymnaea* and *Planorbula* snails, *Celliforma* nests; carbonate nodules, clay pore linings, slickensides, weak to moderate pedogenic structure; gradational or sharp vertical contacts. Lateral extent 6 to ~100 m.	Ephemeral or seasonal spring-fed wetland	Ephemeral wetland	7
Sandy siltstone grading to claystone with high-chroma coloration and moderate pedogenic development; medium blocky peds, slickensides, few mottles, bioturbated; sharp contact with overlying fine sandstone. Lateral extent ~10 m.	Well-drained distal floodplain	Well-drained floodplain	1

channel assemblages in having many cranial and proximal long bone elements (Fig. 7, Online Supplemental File Fig. S1).

Modes of Accumulation

Based on taphonomic and facies data from each locality, we interpret the majority of fossil assemblages to represent either time-averaged accumulations at long-term sites of mortality or accumulations formed through fluvial processes. Thirty-nine localities represent long-term sites of mortality, four localities represent fluvial accumulations, three localities represent carnivore or scavenger accumulations, and one locality may represent a mass-death event (Table 5). Full descriptions of fossil assemblages from each depositional setting are given in the Online Supplemental File.

Long-Term Sites of Mortality.—The majority of localities we investigated represent long-term sites of mortality. These sites encompass 2,869 specimens from 39 localities occurring in channel-margin, abandoned-channel, poorly drained floodplain, and ephemeral-wetland settings (Table 2, Fig. 5). These localities occur in FA 3, FA 4, FA 5, and

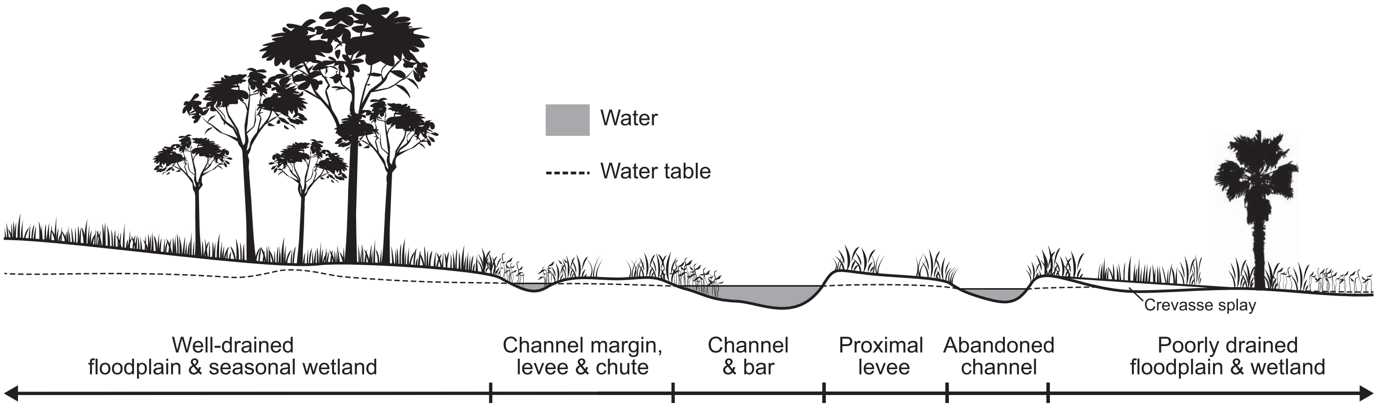

FIG. 5.—Schematic transect across a generalized fluvial landscape showing the lateral distribution of depositional settings represented by 47 fossil localities in the Barstow Formation. See text and Table 3 for facies descriptions. Gray shading indicates water; dashed line indicates water table. Not to scale.

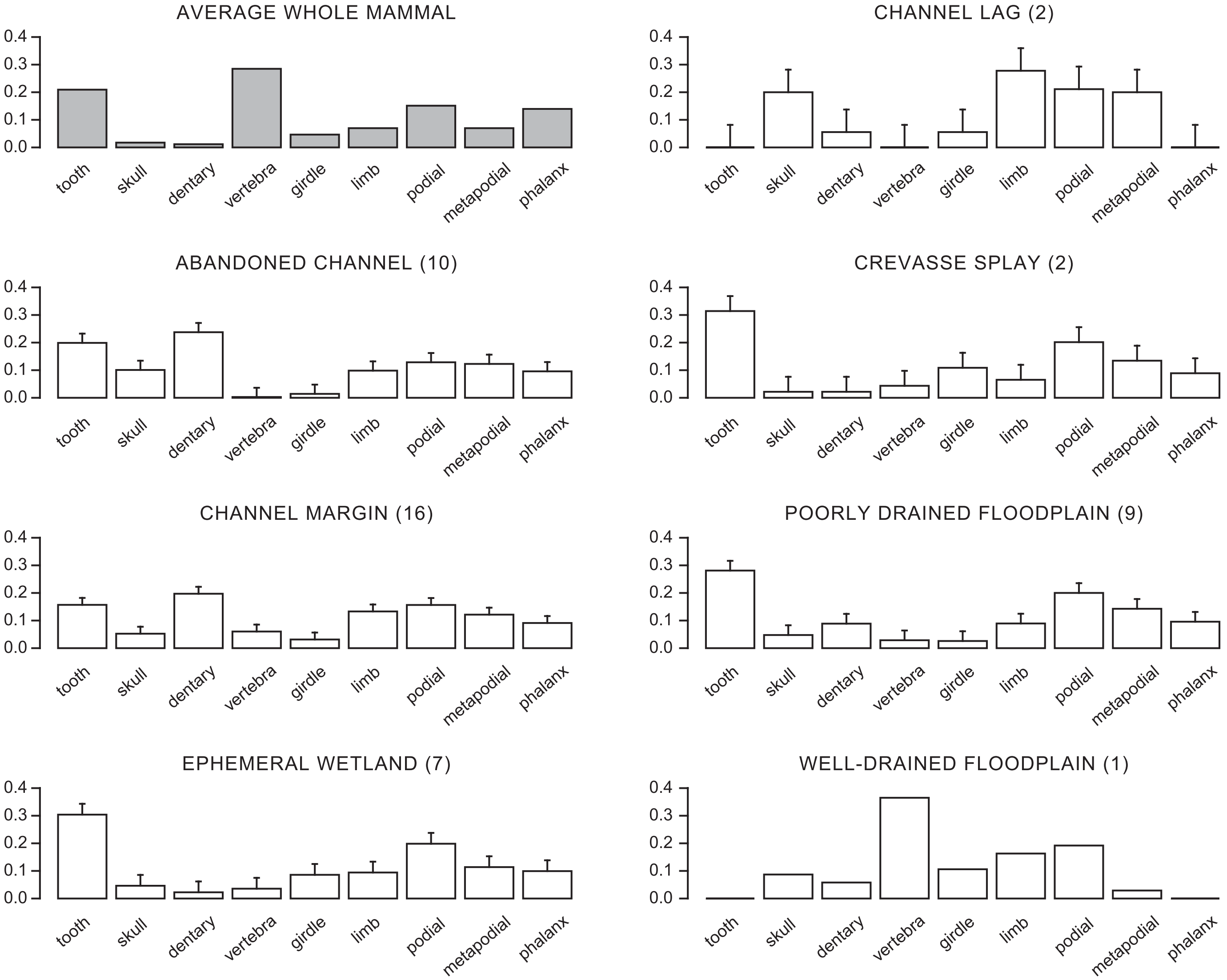

FIG. 6.—Mean skeletal-element composition of fossil assemblages of seven depositional settings in Table 3 compared with the skeletal-element composition of an average whole ungulate mammal with 172 elements in nine categories. Error bars are 2× the standard deviation of bootstrapped skeletal-element proportions of localities in each depositional setting. Number of localities indicated in parentheses; RAM 7648 is not included in the skeletal-element composition of the channel-lag assemblages.

FA 6 (Table 5). Most specimens were isolated elements (80%), yet the degree of articulation and association varied widely among assemblages, ranging from 0% to 74% (Online Supplemental File Tables S1, S4). Articulated and associated material comprised 20% of these assemblages (Online Supplemental File Table S4). A variety of skeletal elements occurred in these assemblages, differing slightly by depositional setting (Fig. 6, Online Supplemental File Table S2). Elements that were rare in other assemblages, such as ribs and vertebrae, were associated with partial skeletons. Weathering stages ranged from 0 to 4, and few elements were hydraulically equivalent with the sediment matrix (Table 2, Online Supplemental File Table S4). Taxonomic richness of assemblages from long-term sites of mortality were higher than in other assemblages (Table 2, Online Supplemental File Table S4), and body sizes ranged from small ($<$ 1 kg) to very large ($>$ 900 kg; Loughney 2018).

Most elements from these localities were complete (44%), and approximately one third of bones from these assemblages displayed original breakage and abrasion. Original breaks had irregular, conchoidal, stepped, or saw-toothed outlines (Fig. 3). Tooth marks, punctures, or irregularly broken edges consistent with carnivore gnawing were identified on 24% of elements (Fig. 3, Online Supplemental File Table S4). Over half of elements (55%) had smooth, transverse breaks that typically occur in mineralized bone during diagenesis (Villa and Mahieu 1991; Alcalá and Escorza 1998; Pesquero et al. 2013; Fernández-Jalvo and Andrews 2016).

We interpreted these assemblages as attritional accumulations at long-term sites of mortality (Table 5). The relatively high frequency of associated and articulated material indicates that these assemblages were mostly autochthonous, and the moderate amount of carnivore damage indicates some modification of the assemblages by carnivores and scavengers during accumulation.

Fluvial Accumulations.—We interpreted the assemblages from four localities as fluvial accumulations in channel and crevasse-splay deposits in FA 1, FA 5, and FA 6 (Table 5). The majority of specimens consist of isolated elements, including long bones, podials, girdle and axial elements, and teeth (Fig. 6). Most specimens were partial or fragmentary, showing a combination of original and recent breakage. A high proportion of

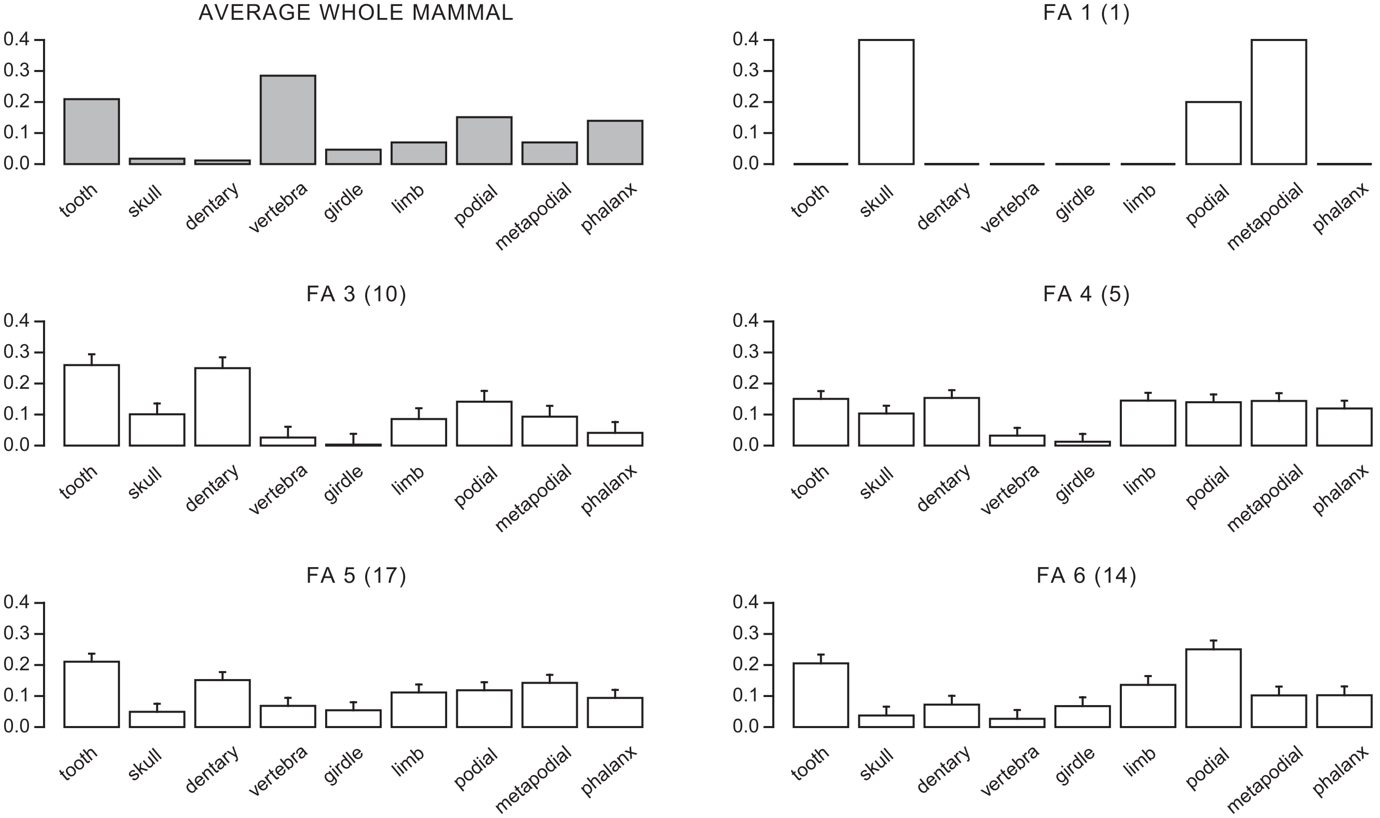

FIG. 7.—Mean skeletal-element composition of fossil assemblages of five fossiliferous facies associations (FAs) in the Barstow Formation compared with the skeletal-element composition of an average whole ungulate mammal with 172 elements in nine categories. Error bars are 2× the standard deviation of bootstrapped skeletal-element proportions of localities in each FA. Number of localities indicated in parentheses; RAM 7648 is not included in the skeletal-element composition of the FA 6 assemblages.

elements was broken (51%), abraded (58%), rounded (36%), or hydraulically equivalent with the sediment matrix (Table 2, Online Supplemental File Table S4). Weathering stages ranged from 1 to 3. In addition to isolated elements, one articulated, partial camel skeleton (RAM 7648) was collected from a channel deposit (RAM V200047; Figs. 1, 2). The skeleton was articulated at the time of collection and was nearly complete, missing the skull, mandible, and several distal forelimb elements (Lofgren and Anand 2010). Few elements showed original breakage or abrasion, and weathering stage for all elements was incipient (1 to advanced 1). Taxonomic diversity was low in these assemblages (Table 2), and specimens were predominantly of small- to medium-sized mammals (10–200 kg; Loughney 2018).

The assemblages from these four localities represent several taphonomic processes that occur within channels or during deposition on the proximal floodplain. We interpreted the isolated elements as settling in channel-lag, channel-bar, or crevasse-splay deposits during waning flow, and RAM 7648 as a floating carcass deposited with the isolated specimens of RAM V200047 as flow velocities in the channel subsided. These assemblages are time-averaged, given the range of weathering stages and high degree of abrasion and rounding (Table 2), indicating the incorporation of heavily reworked material into the assemblage.

Carnivore and Scavenger Accumulations.—Assemblages from three localities occurring in poorly drained floodplain deposits in FA 5 and FA 6 (Table 5) were distinct in having a greater proportion of carnivore-damaged material than other assemblages ($p < 0.01$, χ^2 test of proportion). Fossils at these three localities were spatially concentrated over < 20 m^2, and the 92 specimens from these assemblages were predominantly fragmentary and partial. No specimens were hydraulically equivalent with sediment matrix at the site of deposition, and weathering stages ranged from 1 to 3. Tooth marks and punctures occurred on 40% of specimens, and many bone fragments had conchoidal breakage or were diamond-shaped shaft fragments, sometimes with smoothed or rounded edges (Fig. 3C). Such shapes are characteristic of breakage by carnivores, and rounding or polishing of bone fragments can result from partial digestion by carnivores (Fosse et al. 2012; Fernández-Jalvo and Andrews 2016). Taxonomic richness of these assemblages was moderate (< 7 genera), and body sizes were generally smaller than in other assemblages, ranging from small to medium (1–200 kg; Loughney 2018). We interpreted these assemblages as carnivore and scavenger accumulations, due to the spatial concentration of elements, the high degree of fragmentation, and the predominance of conchoidal breakage. These features are typical of carnivore damage and are similar to features of assemblages in modern carnivore dens (Andrews and Evans 1983; Lansing et al. 2009).

Mass-Death Assemblage.—One locality in FA 5 (Saucer Butte Quarry) occurred in well-drained floodplain deposits (Table 5). At least six partial, articulated camel skeletons referred to *Miolabis* were collected by AMNH parties (Honey 2004); we evaluated four of these skeletons. Skeletons were still in jackets, allowing observation of the degree of articulation, disassociation, and orientation of elements, but precluding close examination of the elements themselves. Weathering stages of these specimens ranged from 1 to advanced 1, and long bones typically had smooth, transverse fractures indicative of recent breakage (Table 2). Thoracic and lumbar vertebrae were articulated, often with ribs, complete pelves, and scapulae articulated or associated; three skeletons had

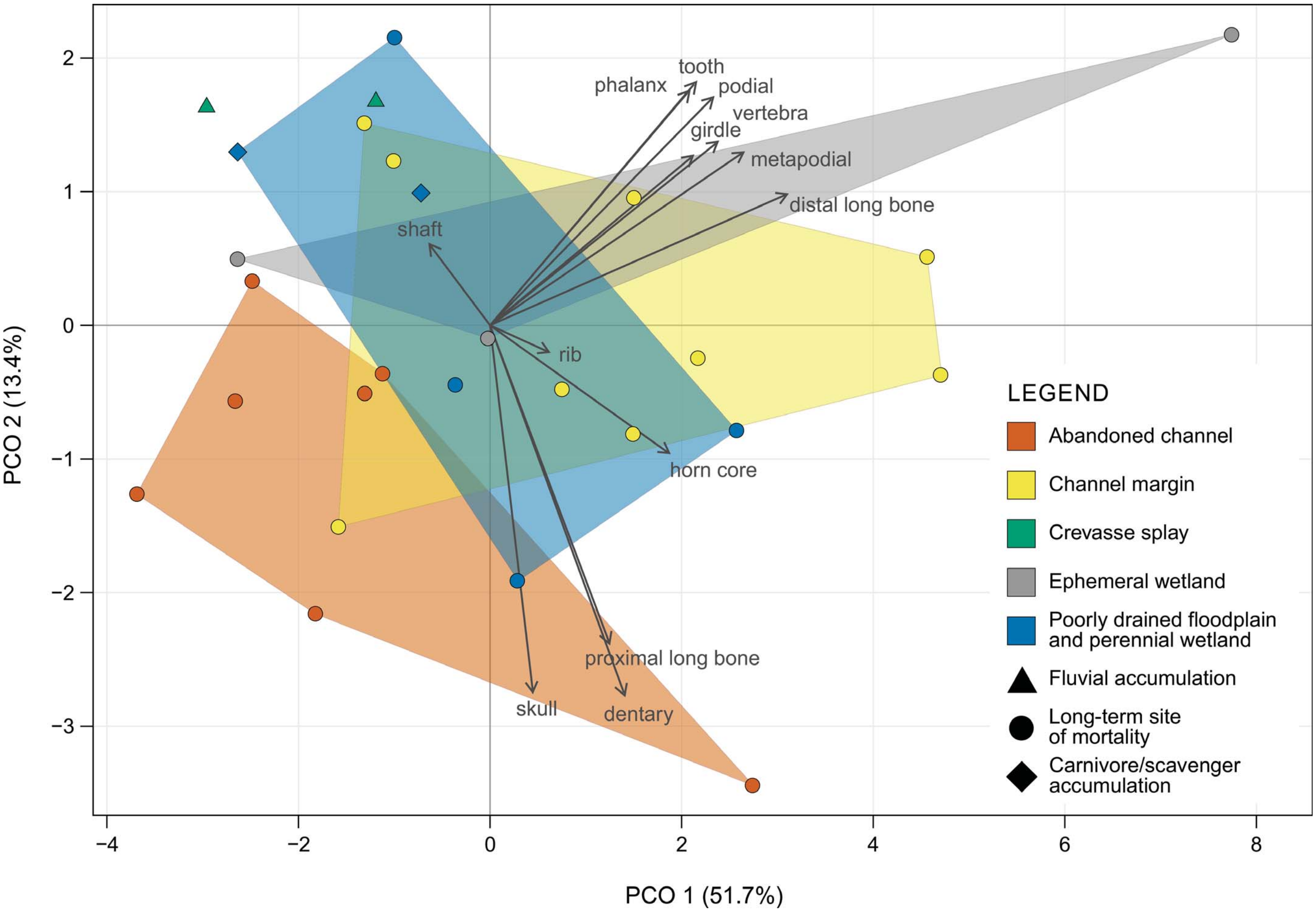

FIG. 8.—Principal coordinate analysis (PCO) of fossil-assemblage composition based on counts of 2,702 skeletal elements from 27 fossil localities with more than 10 specimens. Localities from channel-lag and well-drained floodplain deposits are not included. Polygons group localities by depositional setting. Key: circles = sites interpreted as accumulations from long-term mortality; triangles = fluvial accumulations; diamonds = carnivore and scavenger accumulations.

associated cranial material. If limb bones were present, femora were articulated and humeri were disarticulated but associated; distal forelimb elements were either associated or missing. This assemblage represents a different taphonomic history from the largely disassociated material and taxonomically diverse assemblages from other localities in the Barstow Formation. Saucer Butte Quarry may represent a mass-death event or a predator kill site from which elements were removed by scavengers. Environmental stressors (i.e., drought) could have contributed to the deaths of multiple individuals at the same locality.

DISCUSSION

The fossil localities included in this taphonomic assessment (47 of > 400 documented localities in the Mud Hills) are among the most productive and represent the major modes of fossil accumulation in the Barstow Formation. The majority of fossil assemblages that we examined accumulated at long-term sites of mortality forming in channel-margin, abandoned-channel, poorly drained floodplain, and ephemeral-wetland deposits (Tables 3, 5), and few specimens accumulated through purely fluvial processes in channel lags and crevasse splays. There is overlap among FAs in the occurrence of modes of accumulation, and taphonomic characteristics of assemblages are more closely associated with specific facies than with FAs. The distinct characteristics of assemblages indicate that taphonomic processes varied among depositional settings and across landscapes.

Taphonomic Characteristics of Facies Associations

The taphonomic characteristics of FAs are strongly influenced by the depositional properties and mode of accumulation of individual localities. The similarity in skeletal-element composition among assemblages in FA 3, FA 4, FA 5, and FA 6 (Fig. 7; Online Supplemental File Table S3) derives from the dominance of long-term mortality as the mode of accumulation for the prominent localities across the formation. The composition of FA 1 differs from that of the average ungulate and the other FAs (Online Supplemental File Table S3) because it is composed of few elements that accumulated mainly through fluvial processes (Fig. 7). Carnivore and scavenger accumulations and the possible mass-death assemblage add comparatively little material to the entire assemblage composition of FA 5 and FA 6 and have only minor influence on the cumulative skeletal-element composition.

Modes of accumulation appear to have stronger associations with particular facies than with FAs. Long-term sites of mortality occur in four depositional settings within FA 3, FA 4, FA 5, and FA 6, and fluvial accumulations occur in channel-lag and crevasse-splay deposits in FA 1, FA 5, and FA 6 (Table 5). Carnivore and scavenger accumulations and the possible mass-death accumulation seem to be associated only with poorly

TABLE 4.—*Results of principal coordinate analysis on skeletal-element counts of 2,702 specimens from 27 fossil localities in the Barstow Formation.* ***A****) Eigenvalue and proportion of variance for the first three principal coordinate dimensions (PCO).* ***B****) Loadings and correlation coefficient (r) values of the 13 skeletal-element categories for the first two PCO axes.*

A) Principal Coordinate Axis	Eigenvalue		Proportion of variance
1	190.89		0.5172
2	49.52		0.1342
3	39.84		0.1079
B) Loadings	PCO 1	PCO 2	r
Skull	0.1609	–0.9869	0.7847
Horn core	0.8899	–0.4561	0.5875
Dentary	0.4530	–0.8915	0.8720
Tooth	0.7629	0.6465	0.7889
Vertebra	0.8581	0.5135	0.6909
Rib	0.9505	–0.3107	0.1756
Girdle	0.8661	0.4999	0.7692
Proximal long bone	0.4643	–0.8857	0.7564
Distal long bone	0.9534	0.3018	0.9162
Metapodial	0.8981	0.4398	0.8304
Podial	0.8067	0.5910	0.8091
Phalanx	0.7640	0.6452	0.7621
Shaft	–0.7223	0.6916	0.2413

drained and well-drained floodplain deposits, respectively; these strong associations, however, are likely due to the small sample size of localities with these modes of accumulation. Among the long-term sites of mortality, the taphonomic characteristics of assemblages can be distinguished based on depositional setting (Fig. 8).

Mode of Accumulation and Facies Context

Long-term sites of mortality and fluvial accumulation were the most common modes of accumulation for fossil localities in the Barstow Formation. Long-term sites of mortality occur in many depositional settings, whereas fluvial accumulations occur only in channel-lag and crevasse-splay deposits. Modes of accumulation are related to the specific depositional settings that occur in each FA. Differences in taphonomic characteristics of assemblages likely reflect the combination of taphonomic modes of accumulation, characteristics of the facies setting, and collecting bias.

Long-Term Sites of Mortality.—The wealth of material from localities forming at long-term sites of mortality reflects the attritional accumulation of bones at particular places on the land surface. Individual fossiliferous sites are fairly spatially concentrated, ranging in size from < 10 to ~ 300 m^2. The occurrence of fossil concentrations at restricted sites, rather than widely dispersed accumulations of material, suggests that these localities represent places where animals congregated. Animals tend to congregate around water sources, which increases predation frequency and mortality (Behrensmeyer 1975). The fossiliferous facies of the Barstow Formation represent depositional settings that formed in association with permanent or ephemeral water sources and may have been environments that were frequented by the mammals of the Barstow Basin. Time-averaged, autochthonous assemblages forming at such long-term sites of mortality feature material from many individuals and many taxa over time, and taxonomic richness is higher at these localities than in fluvial accumulations or at potential mass-death sites such as Saucer Butte Quarry (Online Supplemental File Table S4).

TABLE 5.—*Distribution of taphonomic modes of accumulation for 47 fossil assemblages among* ***A****) five facies associations (FAs) and* ***B****) seven depositional settings.*

	Long-term site of mortality	Fluvial accumulation	Carnivore and scavenger accumulation	Mass-death event
A) Facies association				
FA 1		1		
FA 3	10			
FA 4	5			
FA 5	12	2	2	1
FA 6	12	1	1	
B) Depositional setting				
Channel lag		2		
Crevasse splay		2		
Channel margin	16			
Abandoned channel	10			
Poorly drained floodplain	6		3	
Ephemeral wetland	7			
Well-drained floodplain				1

In the Barstow Formation, long-term sites of mortality occur in channel-margin, abandoned-channel, poorly drained floodplain, and ephemeral-wetland deposits, and in all fossiliferous FAs except FA 1 (Table 5). Overall, assemblages from these depositional settings have similar skeletal-element compositions (Figs. 6, 8, Online Supplemental File Table S2) and taphonomic features (Online Supplemental File Fig. S2), as they represent the remains of many individuals accumulating over long periods of time (months to hundreds of years). Although taphonomic characteristics of assemblages from long-term sites of mortality are broadly similar, there are differences in skeletal-element composition and taphonomic features among assemblages from different depositional settings. Assemblages from abandoned-channel settings differ more in terms of skeletal-element composition from other facies settings, in particular ephemeral-wetland settings (Fig. 8, Online Supplemental File Fig. S2, Table S2).

Abandoned-channel, channel-margin, and poorly drained floodplain deposits were typical settings for fossil accumulation in the Barstow Formation. These settings share some lithological properties, although channel-margin localities showed evidence of better drainage (mottling, brecciated marls) than localities in abandoned channels and poorly drained floodplains (Table 3). Abandoned channels and moist, low-lying floodplains are common sites of fossil accumulation and preservation (Behrensmeyer 1988; Therrien and Fastovsky 2000), partly because animals congregate and interact near water sources, and partly because ponded water or impeded drainage are conducive to preservation (Loughney et al. 2011). Waterlogged sediments reduce microbial and fungal activity and may impede decomposition processes (Nicholson 1996).

Rapid burial of elements would also have contributed to preservation in these depositional settings. Low-lying areas and areas close to active channels receive frequent sediment input (Bridge 2003) that would increase the chance of burying remains. Regular sediment accumulation in channel-margin and abandoned-channel settings may have contributed to the preservation of articulated and associated material, which was higher than in other settings (40% and 20%, respectively) (Table 2, Online Supplemental File Fig. S2). Notably, cranial elements were only 14% of articulated and associated material in channel-margin assemblages, compared with 37% in abandoned-channel assemblages. Several partial skeletons comprising mostly postcrania occurred in channel-margin assemblages, including elements, such as ribs and vertebrae that were generally rare in assemblages from other depositional settings.

Ephemeral-wetland assemblages shared taphonomic characteristics with channel-margin and poorly drained floodplain assemblages and differed most from abandoned-channel assemblages (Fig. 8, Online Supplemental File Fig. S2). The different lithological and drainage characteristics of ephemeral-wetland and abandoned-channel deposits likely influenced the difference in fossil preservation in these facies. Brecciated and bioturbated marls, carbonate nodules, and slickensides in ephemeral-wetland deposits indicate that these settings experienced episodic variations in moisture and drainage compared to more consistently wet abandoned channels (Table 3; Loughney et al. 2020). The dominance of isolated teeth and distal podial elements in ephemeral-wetland assemblages reflects a greater duration of accumulation than in other depositional settings that may have been more active sites of deposition. We infer that sedimentation rates were low in ephemeral wetlands, based on the moderate pedogenic development and the low proportion of articulated and associated material at these localities (Table 3, Online Supplemental File Fig. S2). On persistent land surfaces, vertebrate remains stay at the surface and are subject to repeated scavenging, scattering, and trampling for long periods of time before burial. Although breakage was common in ephemeral-wetland assemblages (Table 2, Online Supplemental File Fig. S2), many elements were isolated complete teeth and podials. Long limb bones and ribs are easily broken and fragmented during trampling or predation, whereas teeth, podials, and phalanges resist degradation and destruction from carnivores and scavengers (Behrensmeyer and Dechant Boaz 1980). The high incidence of tooth marks (Table 2) indicates that carnivores and scavengers modified the assemblages over the history of accumulation; this activity may have resulted in the paucity of long bones and vertebrae compared with the skeletal-element composition of other depositional settings. In addition, wet-dry cycles may have contributed to the modification of death assemblages from ephemeral wetlands. Alternating wet-dry cycles contribute to bone weathering and destruction at the surface (Behrensmeyer 1978; Nicholson 1996), and weathered bones are more easily broken (Behrensmeyer 1991). Very few bones from ephemeral-wetland assemblages were weathered past stage 2 (Online Supplemental File Table S1), and more weathered bones may have been destroyed before they were buried. In contrast, small elements such as podials and teeth are easily buried from trampling (Behrensmeyer and Dechant Boaz 1980), making these elements more likely to be buried during wet phases and perhaps contributing to the abundance of this material in ephemeral-wetland assemblages (Fig. 6).

Fluvial Accumulations.—Fossil assemblages resulting from fluvial processes have a variety of taphonomic characteristics and range from articulated skeletons to isolated fragments (Behrensmeyer 1988). Relatively little fossil material from fluvial accumulations is represented in museum collections from the Barstow Formation, potentially because less material was concentrated by fluvial processes, material may not have been as well preserved in these depositional settings, or this material was not collected.

The skeletal-element composition of crevasse-splay and channel-lag assemblages differs significantly from most other attritional assemblages accumulating in channel-margin or floodplain settings (Online Supplemental File Table S2). Although they do not differ significantly from one another, the crevasse-splay and channel-lag assemblages have different skeletal-element compositions (Fig. 6) that likely represent different processes of accumulation. Skeletal elements in active channels are sorted and winnowed by stream flow, and fluvial assemblages may be modified over time as flow volume and velocity fluctuate. Many specimens from the crevasse-splay assemblages (limb bones, vertebrae, girdle elements) have different potential for sorting in fluvial settings (Hanson 1980; Aslan and Behrensmeyer 1996; Moore and Varricchio 2018). The processes that produce crevasse splays are influenced by characteristics of the stream such as sinuosity, channel geometry, and discharge. These characteristics can contribute to the mixing of elements with different susceptibility to transport, producing assemblages of elements with different shapes and densities. However, skeletal elements are typically dispersed by fluvial action if they originate from a common source, and the concentration of elements in channel or near-channel deposits may depend on the presence of preexisting accumulations (Rogers and Brady 2010). Crevasse splays remobilize bones in channels, channel margins, and on the floodplain surface and incorporate them into the splay deposit. Crevasse-splay assemblages are then likely to represent the reworking of material on the floodplain as much as the concentration of transported material. Starlight Quarry occurs in siltstone and sandstone beds, and few elements are hydraulically equivalent with the sediment matrix; this crevasse-splay assemblage likely represents a mix of reworked floodplain material and material emplaced through fluvial action.

Assemblages from the channel-lag deposits visibly differ the most from the composition of the average whole mammal, and the most abundant elements in an average mammal skeleton (teeth, vertebrae) are missing from the channel-lag assemblages (Fig. 6). It is surprising that isolated teeth are absent from these assemblages, as teeth are common in lag deposits (Behrensmeyer 1991); teeth do occur, however, in fragmentary maxillae. The geometry of the stream bed affects where elements of different densities come to rest during waning flow, as has been documented in modern examples (Hanson 1980; Aslan and Behrensmeyer 1996; Moore and Varricchio 2018). Similar to the sorting expected in crevasse-splay deposits, stream beds or bar forms should accumulate elements of different sizes and densities during different stages of flow (Hanson 1980). Dense elements such as teeth may concentrate in the thalweg of channels (true lag deposits), whereas lighter elements or carcasses may become stranded on emergent bars as flow subsides (Moore and Varricchio 2018). The overall paucity of specimens occurring in channel lags is a possible factor contributing to the absence of isolated teeth and other small elements, such as phalanges, that might be expected in lag deposits.

Collection bias could also have affected the patterns of skeletal-element composition at long-term sites of mortality and fluvial accumulations. Most of the excavated sites were AMNH localities, and most of the cranial material or partial skeletons we examined were from these localities. The Frick parties targeted cranial or other well-preserved material, potentially resulting in its over-representation in abandoned-channel and channel-margin deposits (Fig. 6). Surface collections made subsequently by other institutions have helped to offset the biases of the AMNH collections. Nevertheless, differences are evident in skeletal-element composition among AMNH collections from abandoned-channel, channel-margin, and poorly drained floodplain deposits (Fig. 8, Online Supplemental File Fig. S2) and may reflect real taphonomic trends. Collecting bias may also affect the amount and distribution of skeletal elements in channel lags, as fragmentary or unidentifiable material is often not collected.

Distribution of Fossil Localities Among Facies Associations

Local depositional settings are part of the larger-scale environment and landscape. As environments and landscapes change over the history of a basin, the frequency of depositional settings changes as well, imparting different taphonomic characteristics to assemblages through time. Animal behavior and habitat, local depositional setting, and the wider landscape of the basin all contribute to a hierarchy of taphonomic influences that builds from the local scale to the basin scale. The taphonomy of FAs depends on the taphonomy of the facies within them. In the Barstow Formation, locality-scale facies and mode of accumulation exert the main influence on the taphonomy of fossil assemblages. Although the facies that host fossil accumulations occur in most FAs, the frequency and proportion of these

TABLE 6.—*Distribution of the depositional settings of 47 fossil localities in the Barstow Formation among facies associations (FAs). Total number of specimens given in parentheses. See text and Loughney and Badgley (2017) for lithological descriptions of FAs.*

Depositional setting	FA 1	FA 3	FA 4	FA 5	FA 6[1]
Channel lag	1 (5)				1 (129)
Crevasse splay				2 (60)	
Channel margin		2 (43)	5 (561)	6 (108)	3 (383)
Abandoned channel		8 (420)		1 (9)	1 (5)
Poorly drained floodplain				7 (413)	2 (37)
Ephemeral wetland					7 (982)
Well-drained floodplain				1 (125)	

[1] Includes RAM 7648

facies differ among FAs (Fig. 4, Table 6) and thereby shape the taphonomic characteristics of fossil assemblages through the formation. FA 1 is dominated by channel deposits and has few exposures of channel-margin facies that could host long-term sites of mortality (Fig. 4). Fluvial accumulations also occur in FA 5 and FA 6, but these assemblages form a small proportion of the total fossil material from these FAs, and channel deposits represent low proportions of these FAs (Fig. 4). Abandoned-channel deposits constitute a greater proportion of FA 3 than other FAs and host the majority of fossil assemblages from FA 3. Ephemeral-wetland deposits are a significant proportion of the fossil-bearing facies in FA 6. For FA 3, FA 5, and FA 6, the overall distribution of skeletal elements is strongly correlated with the composition of assemblages from the facies that dominate these FAs.

Facies Distribution and Basin History.—The distribution of fossil localities follows changes in depositional environments through time. In FA 1, FA 3, and FA 4, localities occur in channel-lag, channel-margin, and abandoned-channel deposits but not in other depositional settings; in FA 5 and FA 6, localities occur in all depositional settings described here (Table 6). Changes in skeletal-element composition and taphonomic features among FAs follow a temporal trend (Online Supplemental File Figs. S1, S2), and the taphonomic characteristics of fossil assemblages in aggregate therefore change through the history of the basin. The sequence of FAs follows the changes in accommodation as subsidence and sediment-accumulation rates decreased (Loughney and Badgley 2017). During the evolution of the basin, moisture patterns and vegetation structure changed from wet, closed-canopy habitats during the Middle Miocene Climatic Optimum to drier, open-canopy habitats as climate cooled (Loughney et al. 2020). Early-forming depositional environments were homogeneous in terms of landscape position and settings that accumulate fossils, and more heterogeneous landscapes formed later in the Barstow Basin.

FA 1 has yielded little material, and much of it comes from the sparse assemblage from the channel deposits of Red Division Quarry (Galusha et al. 1966; Woodburne et al. 1990). Preservation potential was limited on alluvial fans of FA 1, and fluvial processes were the dominant agents of fossil accumulation. The resulting assemblage has highly fragmentary and disassociated specimens, and consequently, little identifiable material is known from the oldest deposits of the Barstow Formation (Woodburne et al. 1990). The lacustrine facies of FA 2 were not life habitats for mammals and do not preserve vertebrate body fossils (Loughney and Badgley 2017).

As rates of accommodation and sediment accumulation in the basin decreased, basin-center fluvial landscapes became prevalent and were more conducive to fossil preservation. Sequences of sandstone and mudstone in FA 3 represent channel and proximal-channel floodplain deposits of meandering streams, and the amalgamated sandstone beds of FA 4 represent channel and bar deposits of braided streams (Loughney and Badgley 2017). Aggradation was relatively high during the formation of FA 3, resulting in avulsion and channel abandonment. Many localities in FA 3 occur in abandoned-channel fill or in channel-margin deposits because these represent widespread depositional environments forming at that time. Sedimentation rates in FA 3 and FA 4 were low enough to allow for the accumulation of mammal remains in abandoned channels but high enough to bury remains, resulting in assemblages that preserved articulated and associated material (Online Supplemental File Table S1). From FA 3 to FA 4, the occurrence of articulated material decreased and abrasion increased, reflecting the shift from a meandering system to a braided-channel system that may have more heavily reworked its deposits. Distal floodplain deposits are not preserved or not exposed in FA 3 and FA 4, limiting the occurrence of fossil localities to proximal-channel deposits (Fig. 5).

As rates of subsidence and sediment accumulation continued to decline (Loughney and Badgley 2017) and the climate became drier and cooler (Loughney et al. 2020), fluvial landscapes in the Barstow Formation became more heterogeneous. The poorly drained and well-drained floodplain deposits of FA 5 interfinger with the proximal-channel and ephemeral-wetland deposits of FA 6 (Figs. 2, 5). Slower rates of aggradation resulted in the formation of stable land surfaces and allowed for preservation of the crevasse-splay assemblages from FA 5 and the mass-death assemblage at Saucer Butte Quarry. A broader range of fluvial depositional settings is preserved in FA 5 and FA 6 than in earlier FAs, providing additional settings for fossil accumulation and preservation (Table 6). Diverse habitats reflect variable water availability (Loughney et al. 2020), and animals congregated near sources of water. Carnivore and scavenger activity was concentrated in these areas, resulting in the high proportion of carnivore-damaged material. Lower rates of sediment accumulation in these FAs allowed bones to accumulate over longer periods of time, and fossil assemblages in FA 5 and FA 6 may represent longer time spans than those in FA 3 or FA 4. These deposits are also well exposed, adding to the number of localities documented in the upper part of the formation.

The spatial behaviors of animals and processes of fossil accumulation did not differ substantially between the middle and upper part of the Barstow Formation, but depositional environments and landscapes changed with the evolution of the basin. More heterogeneous landscapes in the upper part of the formation created more opportunities for fossil preservation under varying local depositional conditions. The taphonomic characteristics of fossil assemblages in FA 5 and FA 6 reflect the accumulation of material through a variety of processes, rather than the taphonomically more similar assemblages accumulating in depositional settings in FA 1, FA 3, and FA 4. Landscape history, therefore, played an important role in determining the spatial distribution of plants and animals, depositional settings, taphonomic processes, and the resulting fossil assemblages.

CONCLUSIONS

The taphonomic history of a fossil locality encompasses aspects of depositional setting, physical processes, and biological agents that influence the accumulation of fossils on the landscape. Fossil localities in the Barstow Formation represent a variety of landscape settings, including deposits of active channels, crevasse splays, channel margins, abandoned channels, poorly drained floodplains, ephemeral wetlands, and well-drained floodplains. Within these settings, assemblages formed at sites of long-term mortality, as fluvial accumulations, as carnivore and scavenger accumulations, and in mass-death events. Taphonomic features such as articulation, completeness, original breakage and abrasion, and skeletal-element composition of assemblages varied among depositional settings, reflecting variation in sorting from fluvial processes, duration of accumulation, and degree of carnivore and scavenger modification. These factors exert strong control on the taphonomic characteristics of assemblages in each facies, which in turn influences the taphonomic characteristics of assemblages within each FA. This hierarchy of taphonomic influences contributes to the patterns observed in the Barstow Formation. As depositional environments changed through the history of the Barstow Basin, landscapes became more heterogeneous, increasing the number of microhabitats available for accumulation and burial of mammal remains.

The change in environments in the Barstow Formation from alluvial fans and playa lakes to streams and floodplains over time reflects the tectonic evolution of the basin and climatic trends. With the changes in depositional environments, local landscapes became more heterogeneous, preservation potential increased, and modes of fossil accumulation became more diverse. A wide range of depositional settings and taphonomic processes resulted in more detailed records of paleoecosystems. Different depositional settings preserved different aspects of faunal assemblages, including skeletal-element and taxonomic composition, potentially reflecting predictable patterns of preservation across fossil-bearing sequences. Systematic variation in taphonomic assemblages among fluvial facies has been documented in other contexts, including the Triassic Chinle Formation in Arizona (Therrien and Fastovsky 2000; Loughney et al. 2011), the Cretaceous Two Medicine and Judith River formations in Montana (Rogers and Kidwell 2000), the Eocene Willwood Formation of Wyoming (Bown and Kraus 1981), and the Miocene Siwalik sequence of Pakistan (Badgley 1986a). In the Barstow Formation, taphonomic trends track environments through the tectonic evolution of the basin. Elucidating taphonomic trends through a formation is crucial for studying the composition and ecology of the fauna and flora and the patterns of turnover that are the basis for reconstructions of biostratigraphy, evolution, and biogeography.

ACKNOWLEDGMENTS

We thank Bob Reynolds, Mike Woodburne, Don Lofgren, and Everett Lindsay for providing help and resources for accessing and locating fossil localities in the field. We also appreciate the assistance of Rachel Thorpe, Tara Smiley, and Anna Harkness in the field. Thanks to Pat Holroyd and Diane Erwin at UCMP, Andy Farke and Gabe Santos at RAM, Ian Gilbert and Melissa Russo at SBCM, and Judy Galkin at AMNH for granting access to museum collections and providing resources during collections visits. We also thank Carol Abraczinskas for advice on figures and John Finarelli and Miriam Zelditch for their statistical guidance. This work was supported by the University of Michigan Department of Earth and Environmental Sciences Scott Turner Award. We thank reviewers and the associate editor for their valuable comments and help in improving this manuscript.

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: https://www.sepm.org/supplemental-materials.

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Received 21 July 2019; accepted 31 March 2020.