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Cover: *Scaphohippus* sp. pes in lateral view, showing generalized skeletal anatomy. Illustration by Rob Soto.
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Taphonomic bias in collections of horse phalanges from the Barstow Formation (Miocene) and Rancho La Brea (Pleistocene) of California, USA

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Isolated equid phalanges are relatively common finds in the Barstow Formation (Miocene, 19 to 13 million years ago, southern California), but anecdotal observations suggested that not all positions (proximal, middle, and distal/ungual) of the primary digit (digit III) are recovered with equal frequency. Our sample includes primarily surface-collected phalanges from the Barstow Formation, which we compare with phalanges of Pleistocene horses from Pit 3 and Pit 77 from Rancho La Brea (Los Angeles, California). The null hypothesis is that the three positions of phalanges should be equally common. Our Barstow sample includes 228 proximal, 151 middle, and 36 distal phalanges. A chi-square test (p<0.001) is consistent with preservation bias in phalangeal frequency for the full Barstow Formation sample, and this pattern generally holds within sub-samples by locality or depositional environment. Pit 3 of La Brea produced 163 proximal, 144 middle, and 103 distal phalanges. A chi-square test with correction for multiple comparisons suggests that proximal and middle phalanges are preserved with statistically equal frequency (p=0.278) whereas distal phalanges are less common (p<0.001). For Pit 77, there are 54 proximal, 55 middle, and 51 distal phalanges; the chi-square test finds that all three types are equally common (p=0.922). Overall, differences in physical properties between phalangeal positions, such as surface area, density, shape, and size, could influence preservation within each environment. The observed differences between Barstow and La Brea might be caused by variations in depositional environment that influence the surface exposure time of fossils and disarticulation pre-burial, as well as by differences in the size of the horses at each locality. We suggest that when permitted by sample size, it is desirable to distinguish unguals from other phalanges when analyzing taphonomic patterns in the fossil record.

Keywords: Cenozoic, Equidae, fossil, taphonomy, ungual, tar pits

INTRODUCTION

Taphonomy is the filter through which life passes from the past to the present. Taphonomic processes not only subtract information through loss of anatomy and erasure of taxa, but also can add information about organisms, their behaviors, and their environments (e.g., Behrensmeyer et al. 1979, Behrensmeyer and Kidwell 1985, Sansom et al. 2010). Recent work in the Miocene-aged (~19–13 Ma) Barstow Formation of southern California (Loughney and Badgley 2017, 2020) used detailed taphonomic analysis of large, multi-locality samples to deepen and broaden understanding about a

classic North American locality. These large-scale studies of taphonomy are enabled by a long history of paleontological collection in the Barstow Formation by multiple institutions (summarized most recently in Pagnac et al. 2013 and Loughney and Badgley 2020).

Fieldwork in the Barstow Formation by the Raymond M. Alf Museum of Paleontology (RAM) stretches back to 1936, with the majority of fossils discovered and collected by high school students from The Webb Schools (Lofgren and Anand 2010). Horse phalanges from the central digit (digit III of both front and hind feet) are some of the most common finds, with hundreds cataloged in the RAM collection (Figs. 1, 2; Supplementary Material 1). Phalanges are relatively compact and durable elements, easing their transition into the fossil record and

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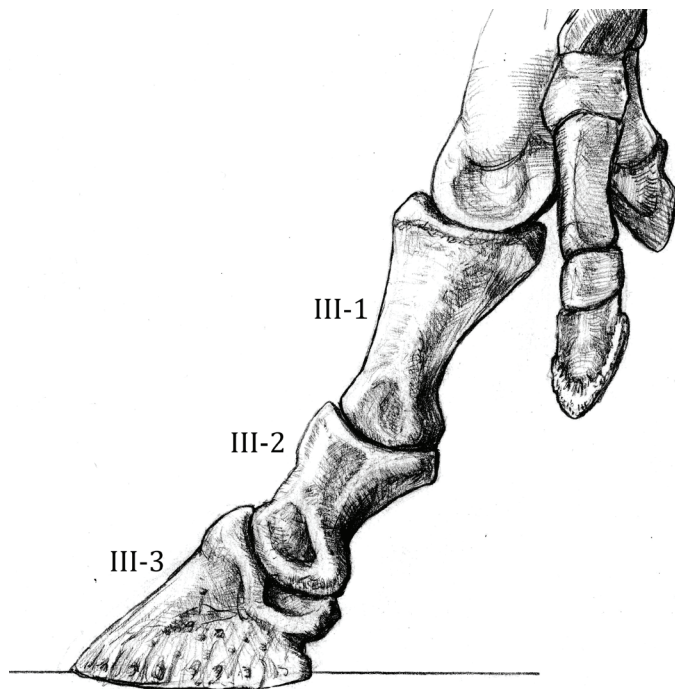YS and VWG contributed equally to this work.

Figure 1. *Scaphohippus* sp. pes in lateral view, showing generalized skeletal anatomy. Illustration by Rob Soto.

subsequent discovery by collectors. One of the authors (A. Farke) anecdotally observed that ungual phalanges seem to be surprisingly rare in the field and in the museum collection, whereas the middle and proximal phalanges are much more common. If a genuine pattern, what factors might be causing it, and what does it mean for preservation of horse toes in particular and taphonomy of the Barstow Formation in general?

Numerous taphonomic studies have observed differences in preservation potential between skeletal elements, influenced by intrinsic skeletal characteristics such as shape, size, mass, and density, among others (e.g., Voorhies 1969; Behrensmeyer 1975; Moore and Norman 2009). Within the skeleton of a given animal, phalanges may be selectively winnowed out in fluvial conditions relative to larger and denser elements such as femora or metapodials (e.g., Voorhies 1969). However, differences in preservation potential, preservation frequency, and overall taphonomic trajectories between phalangeal positions are rarely documented. Hill and Behrensmeyer (1984) documented differences in patterns of phalangeal disarticulation between mammalian taxa, and other studies have addressed element-level material properties (density, volume, etc.) or differences in preservation frequency both in modern settings and the fossil record (e.g., Behrensmeyer 1975, Lam et al. 1999, Lyman 1994, Stiner 2004, Moore and Norman 2009, Moore and

Varricchio 2018). However, most studies in taphonomy treat phalanges as a single category, an understandable simplification to streamline data collection or increase sample sizes within element categories. Additional data on intra-phalangeal preservation potential are thus fairly sparse.

In this paper, we document and interpret the abundance of horse phalanges from the Barstow Formation, at the level of locality, depositional environment, and formation. The null hypothesis is that each phalangeal position should be preserved with equal frequency in the fossil record, matching the frequency in live animals. These observations are compared with those for Rancho La Brea (La Brea Tar Pits), a famous Pleistocene-aged locality also in southern California that preserves abundant horse material (Stock 1992). As outlined below, each general locality represents very different depositional environments, and thus they provide interesting points of comparison. From these results, we then discuss implications for future taphonomic studies.

GEOLOGICAL BACKGROUND

Barstow Formation

The sample of fossil horse toe bones from the Barstow Formation studied here is housed at the Raymond M. Alf Museum of Paleontology, located on the campus of The Webb Schools, an independent high school in southern California. The museum's history of fossil collection in the Barstow Formation started in 1936, when the science teacher Raymond Alf and his students discovered the holotype for the peccary *Dyseohyus fricki* Stock (1937). Webb students have collected in the Barstow Formation nearly continuously since then (Lofgren and Anand 2010), amassing a large collection of fossils.

The Barstow Formation, deposited between 19 and 13 million years ago, preserves a diverse fossil assemblage, with most fossiliferous localities dating to the Middle Miocene (Woodburne et al. 1990). The formation is divided (from lowest to highest) into the Owl Conglomerate, Middle, and Upper members. The overall Barstow ecosystem is interpreted as wooded grasslands alongside more closed-canopy riparian environments, including shallow, sometimes seasonal, lakes (Loughney and Badgley 2017, Loughney et al. 2020). Channel margin, abandoned channel, floodplain, and ephemeral wetland depositional settings host the majority of vertebrate body fossil localities in the Barstow Formation, with primarily attritional modes of accumulation (Loughney and Badgley 2017, 2020). The best exposed and most
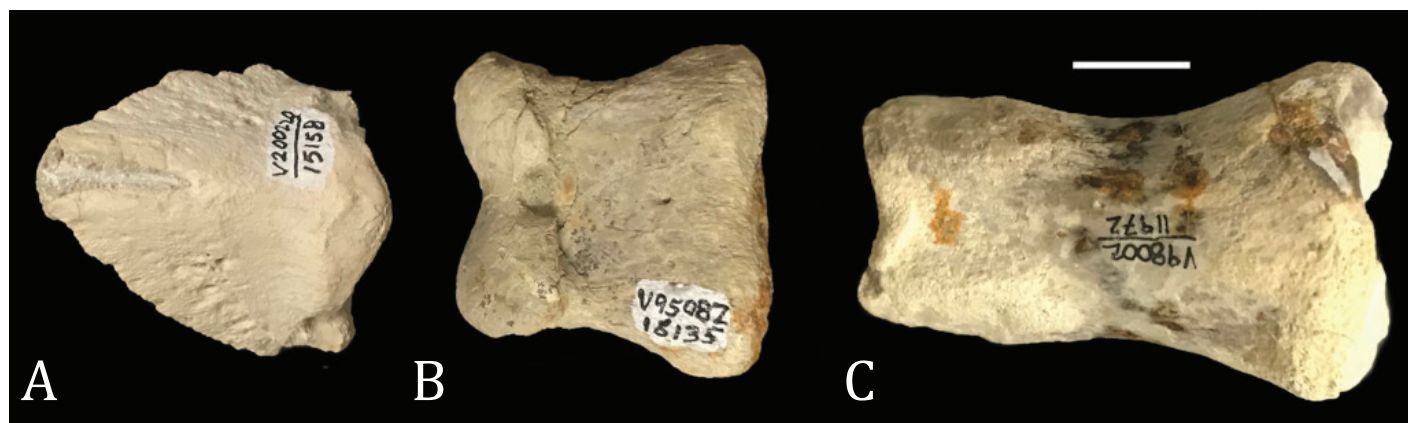
Figure 2. Horse phalanges from the Barstow Formation showing generalized phalangeal anatomy in equids. **A.** Distal phalanx (III-3), RAM 15158. **B.** Middle phalanx (III-2), RAM 18135. **C.** Proximal phalanx (III-1), RAM 11972. Scale bar=1 cm.

intensively studied outcrops of the Barstow Formation are located in the Mud Hills, north of Barstow, San Bernardino County, California (Fig. 3), with additional exposures continuing to the east through the Calico Mountains and Yermo Mountains. The sample for this study was collected entirely in the Mud Hills area, from the Middle and Upper members; a comprehensive list of specimens and localities is in Supplementary Material 2. The diverse large herbivorous mammal assemblage includes horses, rhinos, peccaries, camels, proboscideans, oreodonts, palaeomerycids, and antilocaprids; horse fossils are the most abundant (Pagnac 2009, Pagnac et al. 2013).

In the Barstow Formation, five genera of horse are currently recognized from the Middle and Upper members (Pagnac et al. 2013): *Scaphohippus* Pagnac (2006), *Megahippus* McGrew (1938), *Archaeohippus* Gidley (1906), *Hypohippus* Leidy (1858), and *Acritohippus* Kelly (1995). Based on identifiable dental remains, the most abundant horse in the Alf Museum collection was *Scaphohippus*. It was around a meter tall at the shoulder, with three toes on each foot (Fig. 1). *Acritohippus* is a slightly larger genus, and is the second most common horse in the Alf collection. None of the phalanges in our sample can be identified to genus level, but *Scaphohippus* and *Acritohippus* collectively comprise ~96 percent of the identifiable dental material in the Alf Museum collection. Thus, we speculate that *Scaphohippus* and *Acritohippus* are the most likely sources for the vast majority of the phalanges studied here.

Rancho La Brea

Rancho La Brea, or the La Brea Tar Pits, is located on the Santa Monica Plain in the Los Angeles Basin of southern California, in what is now downtown in the city of Los Angeles (Fig. 3). Sediments of this iconic

deposit were laid down during the mid and late Pleistocene (beginning ~50,000 years before present) and into the Recent, primarily as coarse-grained alluvial fan deposits, which were in turn permeated by petroleum to form asphalt (Stock 1992, Spencer et al. 2003, Friscia et al. 2008). Animals became trapped in the asphalt at the surface, with varying degrees of subsequent scavenging and disarticulation, in addition to weathering and erosion from abiotic forces both before and after burial (Stock 1992, Spencer et al. 2003, Friscia et al. 2008). The abundant fossils at Rancho La Brea include hundreds of plant and animal species, with vertebrates along a size spectrum from tiny rodents to mammoths. Western horses, *Equus occidentalis* Cope (1892), are one of the most common species from the assemblage (Spencer et al. 2003, DeSantis et al. 2011). A second, smaller species from Rancho La Brea is *Equus conversidens* Owen (1869), but it is significantly more rare (Stock 1992).

Here, we focused on Pit 3 and Pit 77, the two deposits within Ranch La Brea that preserve the largest numbers of cataloged equid phalanges. Pit 3 has been dated to a mean calibrated age of ~18.6 ka, and Pit 77 to ~35.4 ka (O'Keefe et al. 2009). Detailed taphonomic studies, beyond general discussions of Rancho La Brea taphonomy, are not yet available for these pits (Noriega et al. 2019 and Cohen et al. 2020 have preliminary work that includes Pit 3, but it has not yet been formally published).

MATERIALS AND METHODS

For this study, we concentrated on digit III, the central digit of both the manus and pes in most equids. Although Miocene-aged horses had additional vestigial digits with phalanges (II and IV), they are much less commonly found (AAF, personal observation of RAM collections) and have a very different morphology from digit III phalanges

Figure 3. Location map of Barstow Formation and Rancho La Brea within California, relative to the United States of America.

(Fig. 1). Thus, we did not consider them here for the sake of simplicity. Equids have three phalanges in digit III, including the proximal phalanx (III-1), the middle phalanx (III-2), and the distal phalanx (III-3, ungual or terminal phalanx) (Figs. 1, 2). These phalanges are easily distinguished in dorsal view (e.g., Dalquest and Hughes 1965), in that the proximal phalanx (III-1) is rectangular, the middle phalanx (III-2) is square and proportionately shorter than the proximal, and the distal (III-3, or ungual) is triangular with a roughened surface texture, forming the core of the hoof (see Fig. 2).

After identification, each phalanx was entered into a spreadsheet with specimen number, locality number, and completeness. Completeness was characterized as complete, distal end incomplete, proximal end incomplete, distal end entirely missing, or proximal end entirely missing; this was used primarily to track which specimens were not measured completely. Because taphonomic damage to individual bones was not studied here, we did not differentiate between specimens that were broken pre- and post-fossilization. In order to explore potential connections between size and preservation, we used

digital calipers to measure the maximum, preserved proximodistal length and maximum, preserved mediolateral width of each element from the Barstow Formation (Fig. 4). A grand mean (GM) of length and width were used as a proxy for element size. Measurements and specimen information were recorded in a spreadsheet for calculation of basic statistics in R 4.0.3 (R Core Team 2020). Specimens with missing measurements, such as phalanges with one end missing, were excluded from size analysis, but were retained in the overall taphonomic comparisons.

For the Rancho La Brea sample, we concentrated on the two deposits—Pit 3 and Pit 77—that had the largest sample of cataloged equid phalanges. This was done in order to focus efforts, given the massive number of specimens collected at Rancho La Brea, and control for potential effects of variation in taphonomy or collecting practices between pits, while also maximizing statistical power. The Barstow Formation was analyzed at the formational level, with additional analyses focused on selected individual localities and depositional environments. A sample size of n>20 for total collected phalanges

Figure 4. Proximal horse phalanx RAM 8490 from the Barstow Formation showing measurement standards. **A.** Dorsal view, with maximum length (proximal end at right of image). **B.** Proximal view, with mediolateral width of the proximal articular surface (dorsal surface at top of image). Scale bar=1 cm.

within a locality or depositional environment was arbitrarily chosen as the cutoff for each category. Depositional environments were assigned for localities following Loughney and Badgley (2020), shown in Appendix 1. Only two specific environments, channel margin and abandoned channel, had sufficient sample size to be considered here. All of the individual localities that were both included in our study and classified by Loughney and Badgley (2020) are characterized as long-term mortality accumulation mode, which represents attritional accumulation at a constrained location.

We used chi-square goodness of fit to test if each phalanx type was equally common. Based on the condition in the live animal, the three positions of phalanges should be equally abundant within the sample (1:1:1). Deviations from the null would be consistent with taphonomic or collection bias (or both). Statistical calculations were conducted in R version 4.0.2, using the "stats" package (R Core Team 2020). Critical p value was considered as 0.05 for initial tests. Tests within groups (multiple comparisons) used a Bonferroni correction (p=0.0167 as critical value where three comparisons were possible).

RESULTS

The frequency of each phalangeal position varies sharply between formations (Table 1; Fig. 5, raw data provided in Supplementary Material 1 and 2). Unguals are almost always underrepresented relative to other positions, with few exceptions.

Considering the entire sample of horse phalanges from the Alf Museum Barstow collection, positions are preserved with significantly unequal frequencies (p<0.001; Table 1). Frequencies also depart from the 1:1:1 expected ratio for both subsamples by depositional setting. For the six Barstow Formation locality subsamples, all but one depart significantly from the expected ratio at p<0.05 (Table 2). Unguals are generally underrepresented both at the bulk as well as subsample levels, with the notable exception of locality RAM V2002020 (Table 1 and 2). Here, middle phalanges are underrepresented relative to unguals and proximal phalanges.

Considering all positions together (proximal, middle, and distal), horse phalanges from Rancho La Brea Pit 3 are preserved with differing frequencies (p<0.001). However, the proximal and middle phalanges do not show a statistically significant difference in frequency from each other (p=0.278; Table 1). In contrast, proximal, middle, and distal positions are preserved with equal frequency for Pit 77 (p=0.922; Table 1).

When calculating mean sizes for phalanges from the Barstow Formation, the middle phalanx is on average the smallest (mean GM=26.1 mm; standard deviation=3.83; 95% confidence interval=25.4–26.8), followed by the distal phalanx/ungual (mean GM=31.4 mm; standard deviation=2.11; 95% confidence interval=30.1–32.6), and the proximal phalanx (average GM=33.7 mm; standard

deviation=2.89; 95% confidence interval=33.2–34.2).

DISCUSSION

Equid phalanges show highly variable preservational frequencies. In one case (the Pit 77 sample from Rancho La Brea), the frequency of proximal, middle, and distal (ungual) phalanges matched the 1:1:1 ratio seen in living animals. In the Barstow Formation collection studied here, unguals were drastically underrepresented, and a similar but less pronounced bias was seen in Rancho La Brea's Pit 3. We suggest several explanations for these patterns. As outlined below, differences in depositional environment and disarticulation patterns may be primary factors, as well as collection bias. Furthermore, differences in physical properties of the individual bones also could influence preservation patterns within each environment.

Environmental influences

As seen in our data and consistent with some previously reported results (e.g., Moore 2012), preservation frequency of phalanges varies both by position and depositional setting. The Barstow Formation and Rancho La Brea have very different taphonomic histories primarily due to the process of asphalt entrapment at the latter (e.g., Spencer et al. 2003, Holden et al. 2013, Loughney and Badgley 2017, 2020), which undoubtedly impact the patterns of phalangeal preservation at each locality.

The sample examined here from the Barstow Formation generally represents attritional accumulations. Many bones were likely exposed to the elements and effects of scavengers, erosion, water, transport, etc., for at least some time (Loughney and Badgley 2017, Loughney et al. 2020, Loughney and Smiley 2019). Fossils from Rancho La Brea, on the other hand, had a very different depositional history, and the bones may have been buried relatively rapidly and with minimal transport (Stock 1992, Spencer et al. 2003, Friscia et al. 2008), at least as compared to the Barstow assemblage. This could be one reason why phalanges of *E. occidentalis* from Rancho La Brea—especially Pit 77—show less marked preservational bias than in the Barstow Formation equids.

Influence of disarticulation patterns

Patterns of disarticulation vary by element, taxon, and environmental conditions, and this may in turn affect preservation potential. In actualistic taphonomic studies of modern zebra in a tropical savanna, the ungual disarticulates from the rest of the animal prior to more proximal phalangeal elements (Hill and Behrensmeyer 1984). In environments where the bones are exposed at the surface for an extended time prior to burial, this early separation from the rest of the carcass might hasten overall disintegration of the ungual relative to other elements. We would predict that in environments with rapid burial (including those in which elements are buried with close association and minimal transport), unguals should be more evenly represented. That may partially explain differences between the La Brea and Barstow samples. It is unknown if the equids in the Barstow Formation, most of which are much smaller than modern equids and with a slightly different manual/pedal configurations, had the same disarticulation patterns as seen in contemporary animals. Studies of artiodactyls at different sizes with broadly similar toe morphology show variation in phalangeal disarticulation patterns (Hill and Behrensmeyer 1984), so we are hesitant to extrapolate from modern organisms to ancient ones.

Finally, temperature and moisture levels influence rates of decay and resulting patterns of disarticulation

Table 1. Element counts for each combined sample, with chi-square test results. Statistical significance (bold-faced values) was designated at p<0.05 for whole-group tests, and p<0.0167 for pairwise comparisons.

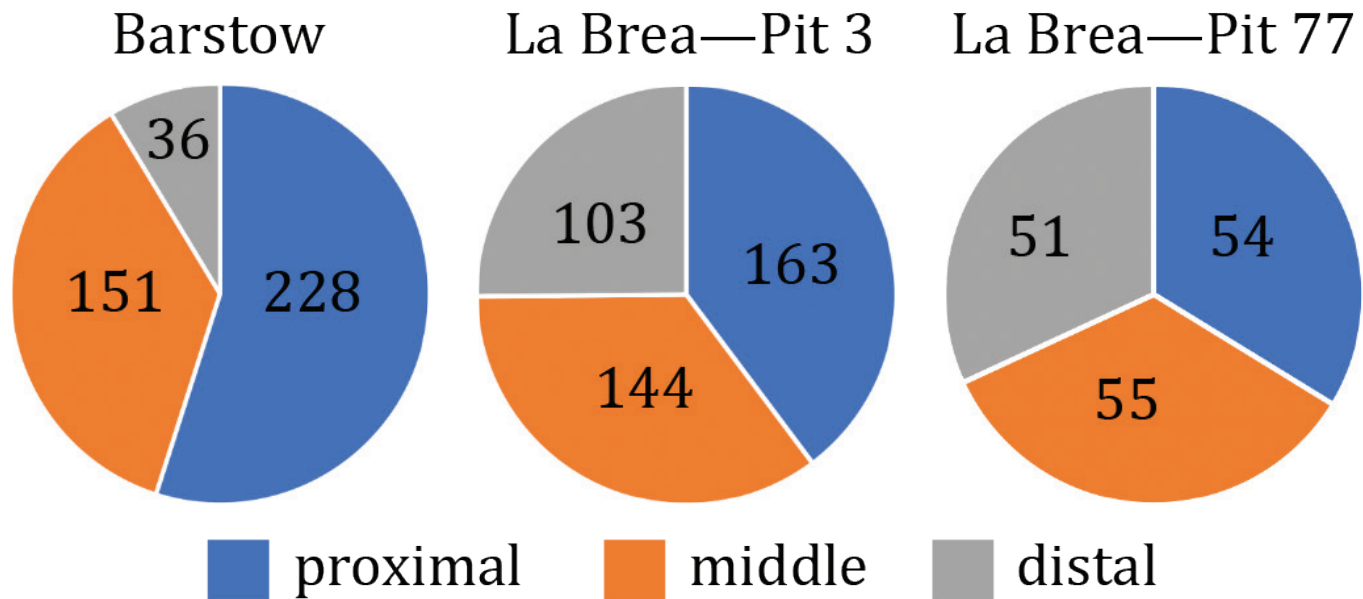| Sample	Phalanx Position			Chi-square test results	Comparison Pair Results		
	Proximal	Middle	Distal	All Positions	Proximal vs. Middle	Proximal vs. Distal	Middle vs. Distal
Barstow Formation	228	151	36	**p<0.001**	**p<0.001**	**p<0.001**	**p<0.001**
Rancho La Brea, Pit 3	163	144	103	**p<0.001**	p=0.278	**p<0.01**	**p<0.01**
Rancho La Brea, Pit 77	54	55	51	p=0.922	p>0.70	p>0.70	p>0.70

Figure 5. Pie charts comparing frequency of phalanges from different localities. The Barstow Formation sample aggregates across all localities. The numbers on the pie chart indicate the number of phalanges in each category for that sample.

and preservation (see Hill 1979 as well as references summarized in Lyman 1994), although that could not specifically be tested here. Hill (1979) noted that mummification under dry conditions can restrict disarticulation and separation of phalanges from each other and the rest of the foot. We speculate that this should lead to more closely matched frequencies for phalangeal positions.

With very few exceptions, the Barstow Formation fossils were disarticulated and disassociated elements; this is true of our sample as well as the formation as a whole (Loughney and Badgley 2020). Because the La Brea bones are nearly all disarticulated and densely packed with evidence of movement even after burial (e.g., Friscia et al. 2008), associations are similarly difficult to determine.

Influence of carnivores

Feeding by carnivores also influences pre-burial disarticulation (Hill and Behrensmeyer 1984) as well as overall bone preservation. According to Spencer et al. (2003), almost all fossils from Pit 91 of Rancho La Brea were disarticulated due to the feeding activities of carnivores. That could possibly apply to Pit 3 and Pit 77 as well, although similarly detailed studies have not been conducted for them, and different levels of carnivore activity might explain differences between the two, as well as the sharp difference of the sample from the Barstow Formation.

Approximately 2% of specimens in Pit 91 at Rancho La Brea (431 out of 18,270 specimens; Spencer et al.

2003:table 1) showed carnivore tooth marks. By contrast, 24% (663 out of 2,748) of specimens from the Barstow Formation (Loughney and Badgley 2020:table 2) showed tooth marks. This varied somewhat between depositional settings (e.g., 18% of bones from channel margin settings showed tooth marks, contrasting with 37% of bones from ephemeral wetland settings), but was nonetheless much more frequent than in the Pit 91 sample. Although the Barstow and La Brea samples are not strictly comparable due to different observers, different collection types, and different taphonomic histories, the higher degree of carnivore activity at Barstow is intriguing. We did not specifically look for tooth marks in our study, although analysis of tooth mark frequency between elements in the Barstow Formation assemblage holds research potential.

The ungual, which is of lower density than other phalanges, potentially could be more easily destroyed by carnivore action. Borophagine canids, some of which were durophagous (Wang et al., 1999), were some of the most common carnivores in the Barstow Formation. Pokines and Kerbis Peterhans (2007) noted that distal phalanges were unexpectedly common for smaller ungulates in hyena-generated bone accumulations, but rare for larger ungulates. It was speculated that small unguals were swallowed whole and survived digestion, with the implication being that larger unguals were destroyed. A similar pattern occurs in many Barstow Formation localities (Table 2), although we are hesitant to ascribe the rarity of unguals to specifically carnivore action.

Furthermore, in modern hyena accumulations the middle phalanges were drastically less common than proximal phalanges, contrasting with the more equal distribution seen in the Barstow Formation (Table 2)

Density, shape, and size

We hypothesize that variations in physical characteristics between phalanges of a single individual may also have affected subsequent preservation. For instance, density is correlated with resistance to physical damage and decreases the ease of transport. The expectation is that denser elements would show a higher percentage of completeness, and the completeness of fossils also impacts the probability of preservation because individual fragments are more susceptible to physical damage than are complete bones (Moore and Norman 2009). According to Lam et al. (1999), the proximal and middle phalanges are slightly denser than the distal phalanx (ungual) in modern horses, although density values greatly overlap between each position. To what extent do minor density differences between phalanges influence preservation? In our sample of Barstow proximal phalanges, proximal end fragments (n=38) are more common than distal end fragments (n=15), which corresponds to the relatively greater density of the proximal end as reported by Lam et al. (1999) and also summarized by Lyman (1994 and citations therein). Although we have not distinguished pre-fossilization versus post-fossilization damage here, density differences would presumably affect preservation potential at both stages.

Human bias during fossil collection may be another factor. Although the controlled excavations at Rancho La Brea would potentially reduce many aspects of bias, different priorities for preparation or retention of specimens could still have an effect. By contrast, the Barstow Formation sample was primarily collected via surface prospecting. The triangular ungual, with its roughened surface texture, is different from what might typically be perceived as bone shape or texture by the typical students who have collected many of the specimens in the Alf Museum collection (Gu and Shi, personal observation). We note, however, that there is little difference between localities that are predominantly from surface collection of "spoil piles" at historic Frick quarries (e.g., Skyline Quarry, RAM V1994178), and those that were not associated with quarries (e.g., Rodent Hill Flat, RAM V1994185; Table 2). This suggests that collection bias may not be as large of a factor as feared.

Overall, different phalangeal positions are more equally preserved in the Rancho La Brea samples than in the Barstow Formation. Size is one potential explanation. Phalanges from Rancho La Brea are significantly larger than the ones from Barstow (Fig. 6). Smaller taxa (and smaller bones) are more likely to be destroyed prior to fossilization or after exposure, and thus the larger unguals of La Brea horses might be more equally preserved relative to other phalanges than those of Barstow horses. However, it is also important to note that size is not necessarily the most important factor that causes preservation bias during fossilization (Moore and

Table 2. Element counts for subsamples of the Barstow Formation equid phalanges, with chi-square test results. Depositional setting follows interpretations by Loughney and Badgley (2020) and are summarized in Appendix 1; others are individual locality numbers within the Alf Museum catalog.

| Sample	Phalanx Position			
	Proximal	**Middle**	**Distal**	**Chi-square test results**
Abandoned channel depositional setting (4 localities)	39	33	3	p<0.00001
Channel margin depositional setting (8 localities)	41	38	9	p<0.00001
RAM V1994026 (Quarry 5)	11	15	1	p=0.003
RAM V1994178 (Frick Skyline Quarry)	12	15	3	p=0.020
RAM V1994185 (Rodent Hill Flat)	11	9	2	p=0.048
RAM V1995082 (Frick Oreodont Quarry)	10	11	1	p=0.016
RAM V1998004 (Fuller's Canyon East)	10	9	2	p=0.067
RAM V2002020 (Frick Unknown)	10	1	10	p=0.021
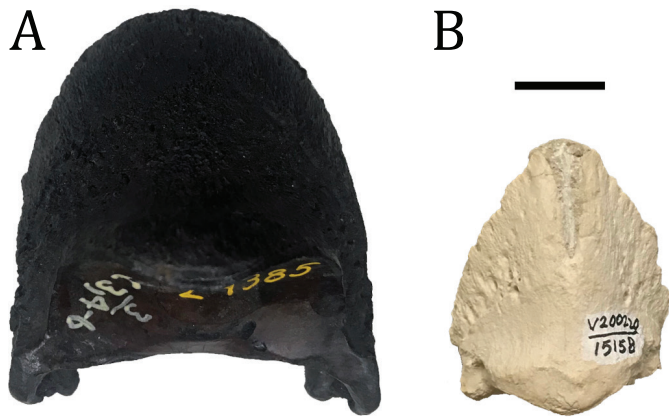
Figure 6. Distal phalanges for fossil equids. A. Rancho La Brea, Pleistocene, LACMHC Z4385 (La Brea Tar Pits and Museum Hancock Collection). B. Barstow Formation, Miocene, RAM 1518. Scale bar=1 cm.

Norman 2009). Within the Barstow Formation itself, we examined overall size of phalanges to see how that may relate to preservational frequency. The sizes of proximal and middle phalanges bracket the average size of unguals (see Results). Thus, the data suggest that size has little impact on phalangeal preservation within the Barstow sample itself. Additionally, although the largest (proximal) phalanges are most common in the overall Barstow sample, individual localities have fairly equal abundances of phalanges III-1 and III-2 (Tables 1, 2). Thus, size alone cannot be the major factor to explain rarity of unguals within a sample.

One notable exception to the patterns observed here is shown by locality RAM V2002020, in which unguals are heavily overrepresented (Table 2). We are at a loss for an explanation of this occurrence, speculating that it may be simply a fluke of preservation or collecting luck.

Future studies

Why is there a preservation bias in phalanges between Pit 3 and Pit 77 at Rancho La Brea, even though both pits presumably have similar environments? Expanding the data set may explain some of the mysteries, and more detailed studies of intra-pit taphonomy and collection bias will undoubtedly be illuminating (e.g., Noriega et al. 2019, Cohen et al. 2020). Given the patterns observed here, we suggest that additional detailed statistical analysis of phalangeal elements for horses (and other abundant taxa) across pits at La Brea, coupled with additional actualistic taphonomy experiments could be an important facet of future taphonomic studies at this locality. Future research could also divide data from the Barstow Formation by specific environments or

delve more deeply into quarried samples to augment the primarily surface collected sample considered here. Interestingly, we note that the bulk sample of Barstow Formation phalanges shows proximal phalanges much more common than middle phalanges, whereas they are more evenly distributed when looking at individual localities or depositional environments (Tables 1, 2). We do not have a good explanation for this feature of the data, although suspect it may be capturing some type of collecting bias. This, too, is worth future examination.

This study also suggests that different phalangeal positions within a single taxon may have very different taphonomic profiles. When sample size permits for quantitative studies, we recommend separate consideration of terminal phalanges from more proximal positions. This is in line with previous actualistic taphonomy observations, which noted that for some taxa, the ungual may disarticulate prior to the rest of the phalanges in many environments (Hill and Behrensmeyer 1984, Moore and Varrichio 2018). Thus, it would be expected that the ungual could be preserved less frequently or separated more easily in many taphonomic scenarios.

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APPENDIX

Appendix 1. Localities from the Barstow Formation that produced fossils studied here, with depositional setting interpretations from Loughney and Badgley (2020).

Locality name	RAM Locality	Depositional setting
Barstow Below Skyline	V1994179	channel margin
Doc's Level	VI-2000047	channel lag
Easter Quarry	V1994067	abandoned channel
Fuller's Canyon East	VI-1998004	channel margin
Hailstone Quarry	V1994055	channel margin
Hemicyon Quarry	V2008001	poorly drained floodplain
May Day Quarry	V2012014	channel margin
New Year Quarry	V1994029	channel margin
Oreodont Quarry	V1995082, V1998002	abandoned channel
Rak Quarry	V1994047, V1994057, V1994063	channel margin
Rodent Hill	V1994028	ephemeral wetland
Skyline Quarry	V1994178	channel margin
Steepside Quarry	V1994058	abandoned channel
Sunder Ridge	V1994177	channel margin
Sunset Quarry	V1998006	abandoned channel