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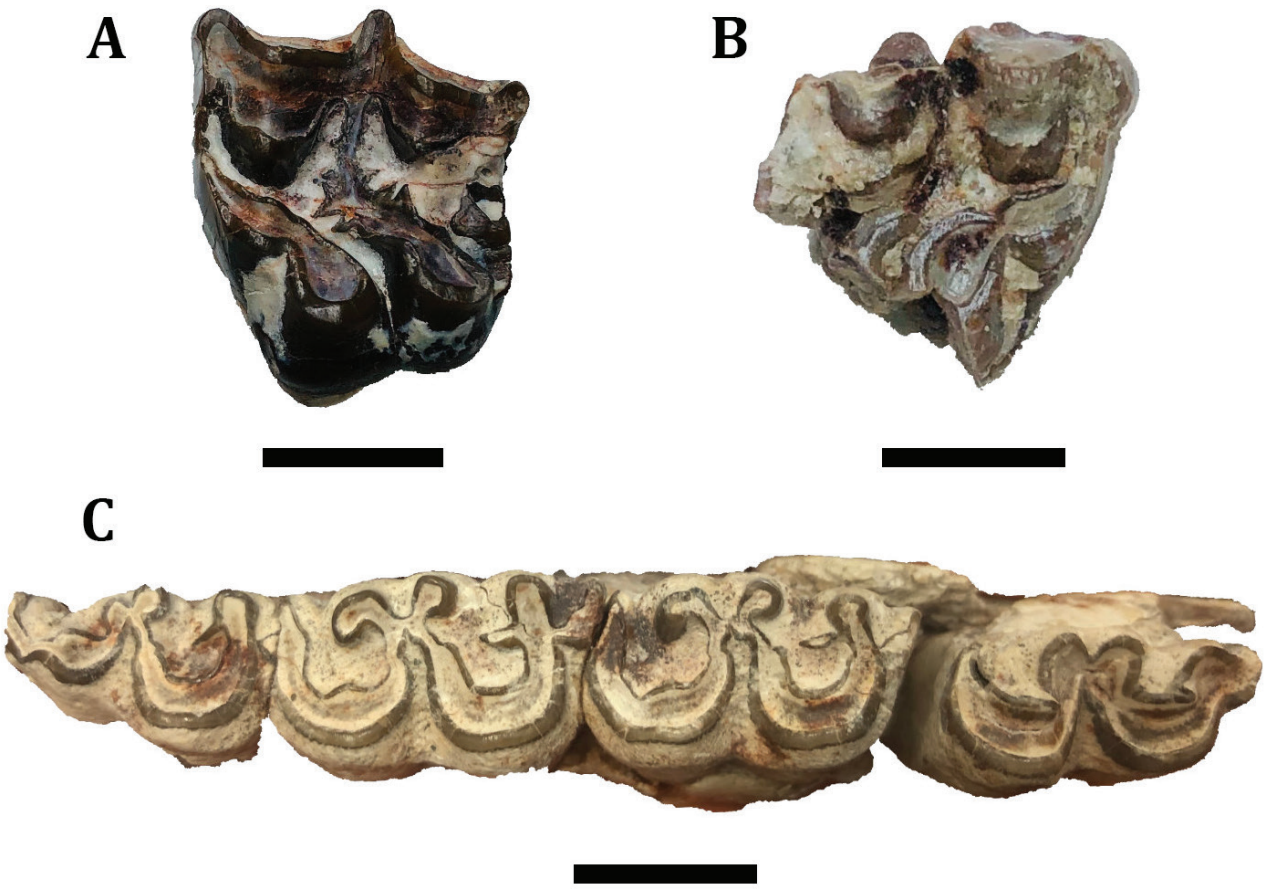


## BRITTNEY E. STONEBURG, ANDREW T. MCDONALD, ALTON C. DOOLEY JR., ERIC SCOTT, & CHARLOTTE J. H. HOHMAN (2021). New remains of middle Miocene equids from the Cajon Valley Formation, San Bernardino National Forest, San Bernardino County, California, USA.

**Cover:** A selection of Miocene horse teeth figured in this paper. **A.** *Parahippus brevidens*, WSC 8914 upper left M1. **B.** *Archaeohippus mourningi*, WS 8826 upper right M3. **C.** *Scaphohippus sumani*, WSC 8922 partial right dentary, p4–m3. Scale bars=1 cm.

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# New remains of middle Miocene equids from the Cajon Valley Formation, San Bernardino National Forest, San Bernardino County, California, USA

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New material of three equids is described from the middle Miocene Cajon Valley Formation in San Bernardino National Forest, San Bernardino County, California. The material includes teeth of *Archaeohippus mourningi*, *Scaphohippus sumani*, and *Parahippus brevidens*. *Scaphohippus intermontanus* is considered a junior subjective synonym of *S. sumani*. *Parahippus brevidens* is identified from an upper molar that closely resembles the morphology of the holotype as well as referred specimens of *Pa. brevidens* from the Mascall Formation in Oregon and the Temblor Formation in California. The presence of *Pa. brevidens* in the Cajon Valley Formation represents a geographic range extension for the taxon of over 400 km. Interesting ecological implications emerge for the Cajon Valley Formation when compared to the nearby Barstow Formation, including the presence of chalicotheres and apparent lack of *Hypohippus affinis* and *Megahippus mckennai*.

***Keywords***: *Parahippus brevidens*, *Scaphohippus sumani*, *Scaphohippus intermontanus*, *Archaeohippus mourningi*, Equidae, Cajon Pass

## INTRODUCTION

The Cajon Valley Formation in the San Bernardino National Forest has been excavated by multiple institutions for over 40 years. Originally considered part of the Punchbowl Formation and located in the southwestern Mojave Desert province of southern California, the Cajon Valley Formation is subdivided into six units dating between approximately 18.0–12.7 Ma (Loughney and Smiley 2019). It is temporally overlapping but distinct from the adjacent Crowder Formation (Woodburne and Golz 1972, Morton and Miller 2003, Reynolds et al. 2008, Coombs and Reynolds 2015, Loughney and Smiley 2019) (Fig. 1). This paper follows Morton and Miller (2003) and uses the name Cajon Valley Formation for these six units that were previously referred to as the Punchbowl Formation.

Specimens found in the Cajon Valley Formation generally span the late Hemingfordian to middle Barstovian North American Land Mammal Ages (NALMA) (Coombs and Reynolds 2015, Loughney and Smiley 2019). Previous investigations of fossils from the Cajon Valley Formation reported multiple perissodactyls (Pagnac and Reynolds 2010, Loughney and Smiley 2019), including the equids *Archaeohippus mourningi* (Merriam, 1913) Osborn (1918) and *Scaphohippus sumani* (Merriam, 1915) Pagnac (2006), as well as chalicotheres (Coombs and Reynolds 2015). Specimens collected by Western Science Center (WSC) personnel on six separate expeditions in 2018, 2019, and 2020, represent three morphologically distinct middle Miocene equid species. The WSC material consists primarily of teeth with scattered postcranial fragments. These teeth not only indicate the presence of equids previously known from the Cajon Valley Formation, such as *Ar. mourningi* and *S. sumani*, but also the first description of *Parahippus brevidens* (Marsh, 1874) Gidley (1907) from the formation. These fossils provide further insight into the understudied Cajon Valley Formation, as well as opportunities for comparison to the fauna of

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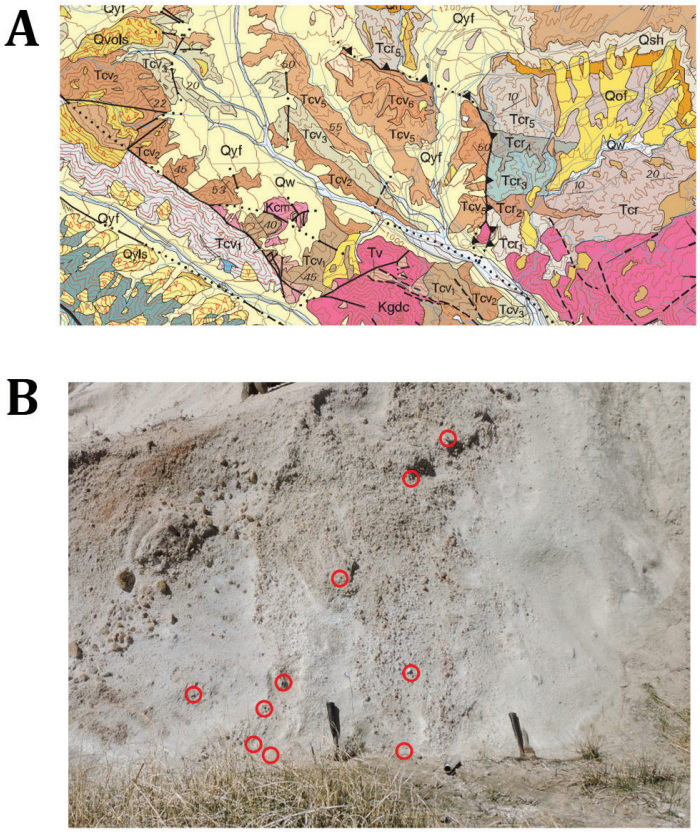


**Figure 1. A**. Geology of the Cajon Pass area; image taken from the United States Geological Survey geological map of the San Bernardino Quadrangle (Morton and Miller 2003). Divisions of the Cajon Valley Formation listed as $Tcv_1$ through $Tcv_6$. WSC Locality No. 381 located in $Tcv_5$. **B.** Photograph of the locality at which the Western Science Center collected the equid specimens described herein. The outcrop is composed of conglomeratic sandstone. Places at which equid teeth or mammalian bone fragments were collected are highlighted by red circles. For scale, two rock hammers (~ 33.0 cm long) are leaning upright against the outcrop near the bottom of the photograph.

surrounding areas, such as the nearby and partially coeval Barstow Formation, which is approximately 19–13 Ma (Loughney and Smiley 2019).

## MATERIALS AND METHODS

We collected over a dozen equid teeth over the course of six collection trips from January 2018 to January 2020. These are housed at the Western Science Center (WSC) in Hemet, California and were collected under United States Forest Service (USFS) permits R5-SBNF-MGM-FY18-001 and R5-SBNF-MGM-FY19-001. The teeth were collected from the ground surface as loose float and *in situ* from WSC Locality No. 381, a conglomerate sandstone bed within unit 5 of the Cajon Valley Formation (Morton and Miller 2003) (Fig. 1). This formation consists of beds of conglomeratic sandstone, siltstone, and minor occurrences of lignite, limestone, and carbonaceous shale (Woodburne and Goltz 1972).

Digital 3D models of select specimens were created at the WSC through laser scanning with a NextEngine 3D scanner. Resultant scans were processed in Meshmixer. The 3D models are available for viewing and download on Sketchfab (https://sketchfab.com/WesternScienceCenter/collections/miocene-horses).

All equid dental nomenclature used in this paper follows MacFadden (1984): lowercase **p**/uppercase **P**=lower and upper premolar; lowercase **dp**/uppercase **DP**=lower and upper deciduous premolar; lowercase **m**/uppercase **M**=lower and upper molar.

Specimens and images of Miocene equid teeth from the following institutions were used for comparative purposes: **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California; **RAM**, Raymond M. Alf Museum of Paleontology, Claremont, California; **SBCM**, San Bernardino County Museum, Redlands, California; **UCMP**, University of California Museum of Paleontology, Berkeley, California; and **YPM**, Yale Peabody Museum, New Haven, Connecticut.

A table of identifications, anatomical descriptions, and measurements for all equid teeth in the WSC collections from the Cajon Valley Formation can be found in Supplementary Materials 1.

## SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
EQUIDAE Gray, 1821
ARCHAEOHIPPUS Gidley, 1906
*Archaeohippus mourningi* (Merriam, 1913) Osborn, 1918
*Parahippus* (?) *mourningi* Merriam, 1913
*Archaeohippus mourningi* Osborn, 1918
Fig. 2

**Referred specimens**—WSC 8801 lower left p2; WSC 8816 upper left DP4; WSC 8826 upper right M3; WSC 8911 worn upper tooth; WSC 8912 partial dentary; WSC 8913 worn upper tooth; WSC 9969 upper DP?.

**Occurrence**—Cajon Pass, San Bernardino National Forest, San Bernardino County, California. Exact locality data are on file at the USFS and WSC. Subdivision $Tcv_5$, Cajon Valley Formation (Woodburne and Golz 1972, Morton and Miller 2003); middle Miocene, late Hemingfordian–middle Barstovian NALMA; $Tcv_5$ (unit 5) spans approximately 16.5–14 Ma (Liu 1990).

**Description**—Several teeth from a small brachydont horse were collected by WSC personnel from the Cajon

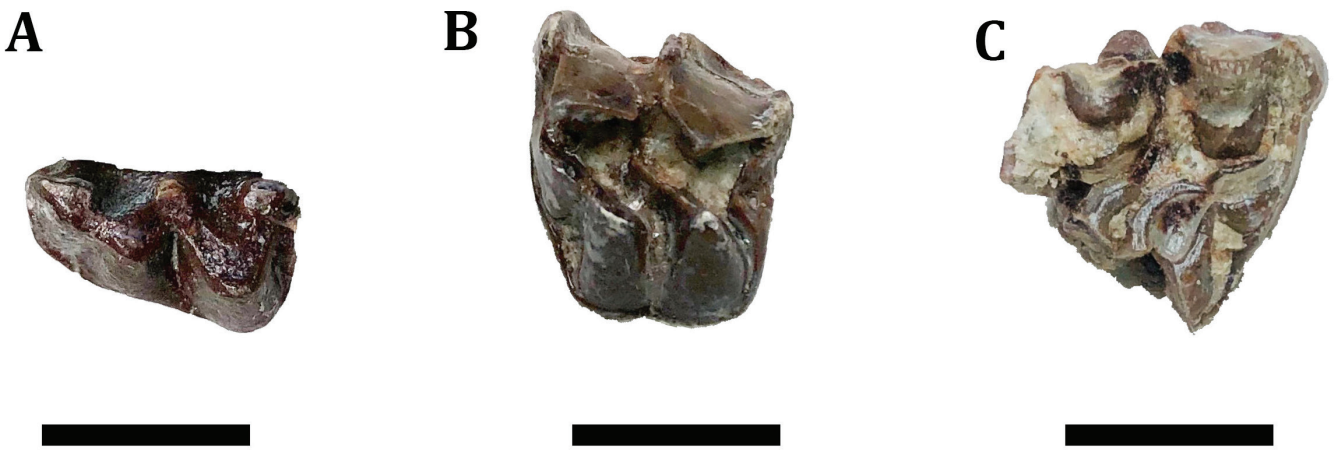


**Figure 2**. Teeth of *Archaeohippus mourningi* from the Cajon Valley Formation, San Bernardino County, CA. **A.** Lower left p2 of WSC 8801. **B.** Upper left DP4 of WSC 8816. **C.** Upper right M3 of WSC 8826. Scale bar=1 cm.

Valley Formation, in subdivision $Tcv_5$. These teeth, based upon their small size, lack of cement, and absence of a well-developed crochet, are best referred to the genus *Archaeohippus* (Pagnac 2005) (Fig. 2). WSC 8826, the only adult molar in the WSC sample, lacks a crochet completely and so is referred to *Ar. mourningi* (Pagnac 2005). Because of size and brachydont condition, all other referred specimens in the WSC sample are also referred to *Ar. mourningi*. Pagnac and Reynolds (2010) also described *Ar. mourningi* material from the Cajon Valley Formation, including a juvenile skull from $Tcv_5$. Merriam (1913) originally named this species as *Parahippus* (?) *mourningi*, which was then transferred to the genus *Archaeohippus* by Osborn (1918).

SCAPHOHIPPUS Pagnac, 2006
*Scaphohippus sumani* (Merriam 1915) Pagnac 2006
*Merychippus sumani* Merriam, 1915
*Merychippus intermontanus* Merriam, 1915
*Scaphohippus sumani* Pagnac, 2006
*Scaphohippus intermontanus* Pagnac, 2006
Figs. 3, 4

**Referred specimens**—WSC 8922 partial right dentary, p4–m3; WSC 8933 upper right DP3; WSC 8934 upper left M2; WSC 9618 highly worn upper left DP2; WSC 9967 lower left p4.

**Occurrence**—Cajon Pass, San Bernardino National Forest, San Bernardino County, California. Exact locality data are on file at the U.S. Forest Service and WSC. Subdivision $Tcv_5$, Cajon Valley Formation (Woodburne and Golz 1972, Morton and Miller 2003); middle Miocene, late Hemingfordian–middle Barstovian NALMA; $Tcv_5$ (unit 5) spans approximately 16.5–14 Ma (Liu 1990).

**Description**—WSC 8933 and WSC 8934 exhibit fewer than ten plications and moderately oval-shaped isolated protocones, supporting referral to the genus *Scaphohippus* (Pagnac 2006). Furthermore, metric data (Supplemental Material 1) indicate that the occlusal surfaces of all referred teeth are consistent in size with *Scaphohippus* rather than the larger penecontemporaneous *Acritohippus* (Kelly 1995), with its larger occlusal surface (Pagnac 2006: figure 3). Additional cranial and dental diagnostic features described by Pagnac (2006) cannot be assessed at this time.

Having demonstrated that our sample is best referred to *Scaphohippus*, the question of which species it is becomes paramount. *Scaphohippus intermontanus* and *S. sumani* were originally referred to the genus *Merychippus* by Merriam (1915) before being referred to the new genus *Scaphohippus* by Pagnac (2006), who defined the two species by differences in tooth morphology and temporal and geographic range. In terms of range, *S. intermontanus* is restricted to the Barstow Formation of Southern California, stratigraphically located in the informal faunal subdivisions Barstow Fauna and Second Division Fauna (Pagnac 2006). *Scaphohippus sumani* is assigned a much larger range; found throughout California, Nebraska, New Mexico, and Colorado, it is also found in the Barstow Formation, in the Barstow Fauna and Second Division (Pagnac 2006). This results in the two species overlapping stratigraphically and geographically.

According to previous descriptions, *S. intermontanus* dentition exhibits "higher crown height and simpler enamel complexity" (Pagnac 2006: p. 49) than *S. sumani*. Merriam (1915) in part used complexity of plications ("enamel bordering fossettes," the phrase then used by

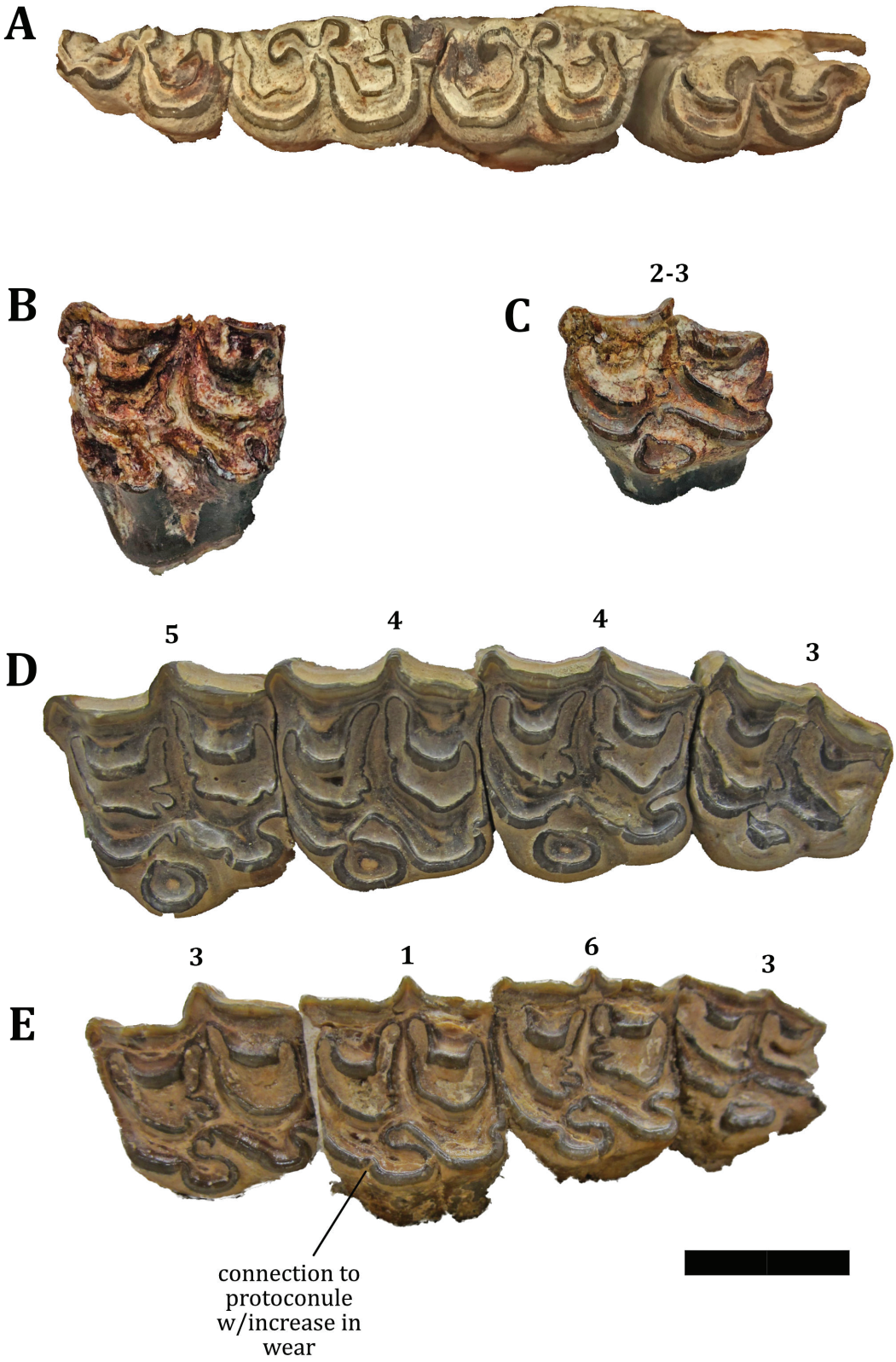


**Figure 3**. Teeth of *Scaphohippus sumani*, comparing rows from the Cajon Valley (**A–C**) and Barstow (**D–E**) formations of San Bernardino County, CA. **A.** WSC 8922 partial right dentary, p4–m3. **B.** WSC 8934 upper left M3?. **C.** WSC 8933 upper right DP3. **D.** LACM 4941 upper left P4–M3. **E.** LACM 33847 upper left P4–M3. Scale bar=2 cm. Numbers above each tooth indicate number of inner plications.

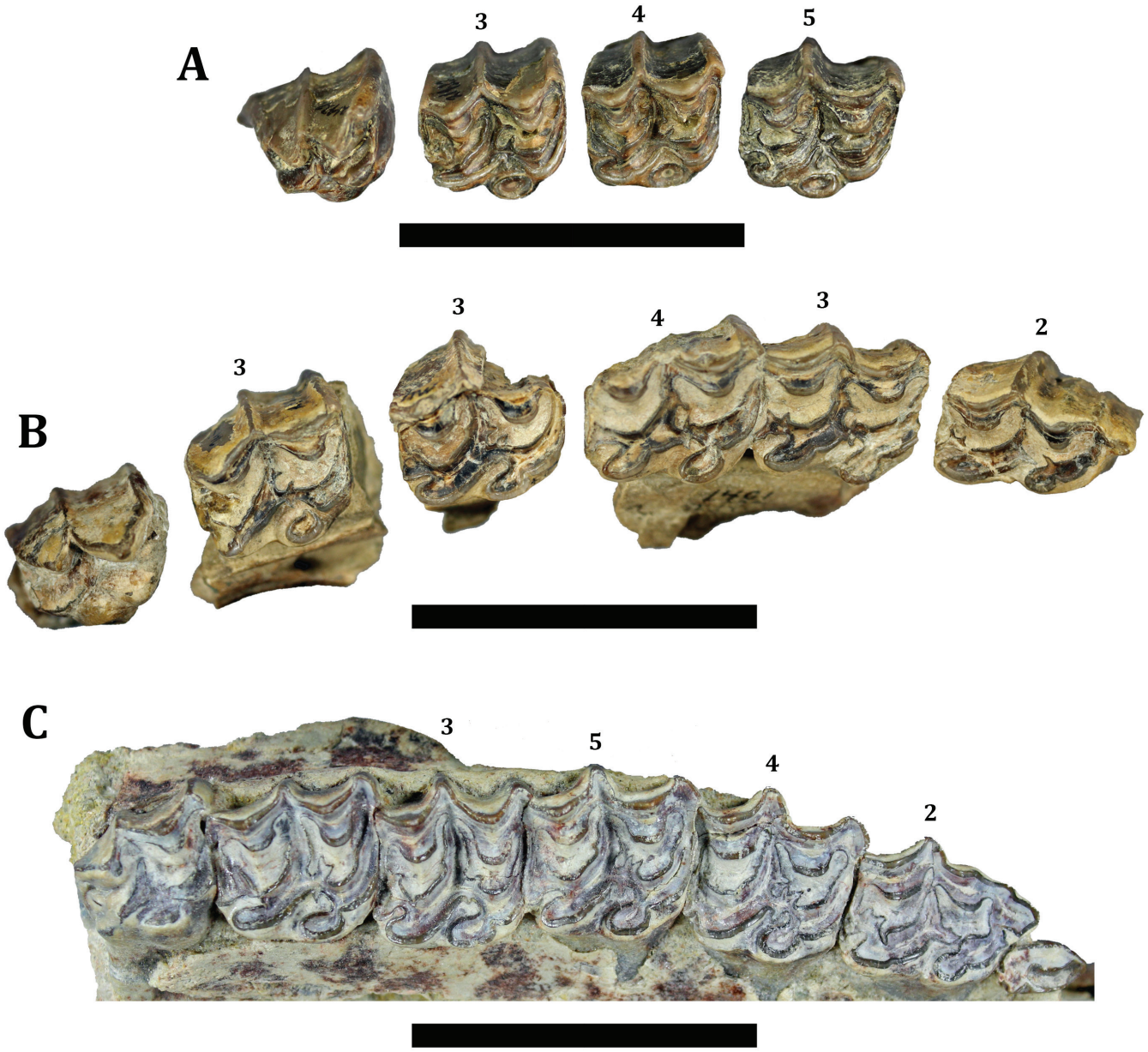


**Figure 4**. Teeth of *Scaphohippus sumani*. **A.** Holotype of *S. sumani*, showing P4–M3 from right to left, UCMP 21422. **B.** Holotype of *S. intermontanus* showing P2–M3 from right to left, UCMP 21400. **C.** Referred specimen of *S. intermontanus* palate (Pagnac 2006) showing P1–M3 from right to left, UCMP 316891. Scale bar=5 cm. Numbers above each tooth indicate number of inner plications.

Merriam to describe plications) in order to distinguish *S. sumani* from *S. intermontanus*. Pagnac (2006) quantified this, stating that the average number of plications in *S. intermontanus* is two, with a maximum of four; for *S. sumani*, the average number is three with a maximum of seven. However, complex inner plications can be found in both *S. sumani* and *S. intermontanus*, depending on tooth position and wear state (Figs. 3, 4). For example, in the right tooth row of UCMP 316891, assigned to *S. intermontanus*, P4 displays five plications, as in the holotype of *S. sumani* (UCMP 21422; Fig. 4A, C). In the holotype of *S. intermontanus* (UCMP 21400), P4 has four plications. Given the considerable overlap in the number of plications observed between the two species, we regard the difference between four and five plications as having no taxonomic significance. Although this feature might be a species-level difference, it might also result from other sources of variation, such as stratigraphic placement of specimens, population variation, and taphonomic artifacts.

Specimens of both species display an isolated protocone on the upper molars that connects to the protoconule with increased wear; however, only a 5–10% difference in wear (with an upper limit of 30% of wear) is used to characterize this particular morphological difference between the dentitions of the two species (Pagnac 2006). It is possible that other factors, such as stratigraphic, ecological, or population differences could account for this minor dissimilarity in the appearance of certain occlusal surface features, rather than it being a defining feature of two separate taxa.

These observations from both species lead us to conclude that previously proposed differences in enamel complexity and wear states are not sufficient to distinguish between the two taxa. We refer all specimens of *S. intermontanus* to *S. sumani*, which has taxonomic priority (Merriam 1915).

PARAHIPPUS Leidy, 1858
*Parahippus brevidens* (Marsh 1874) Gidley, 1907

*Anchippus brevidens* Marsh, 1874
*Parahippus brevidens* Gidley, 1907
Fig. 5

**Referred specimens**—WSC 8914 upper left M1; WSC 8918 lower right p3; WSC 9968 highly worn lower molar.

**Occurrence**—Cajon Pass, San Bernardino National Forest, San Bernardino County, California. Exact locality data are on file at the U.S. Forest Service and WSC. Subdivision $Tcv_5$, Cajon Valley Formation (Woodburne and Golz 1972, Morton and Miller 2003); middle Miocene, late Hemingfordian–middle Barstovian NALMA; $Tcv_5$ (unit 5) spans approximately 16.5–14 Ma (Liu 1990).

**Description**—A brachydont horse larger than *Ar. mourningi* but smaller than *S. sumani* is represented by several specimens that include a well-preserved upper left M1 (WSC 8914), a lower right p3 (WSC 8918), and a worn lower molar or premolar (WSC 9968) (Fig. 5). WSC 8914 exhibits two characters of the genus *Parahippus* (following Osborn 1918: p. 74): 1) "protocone and hypocone relatively large as compared with the simple

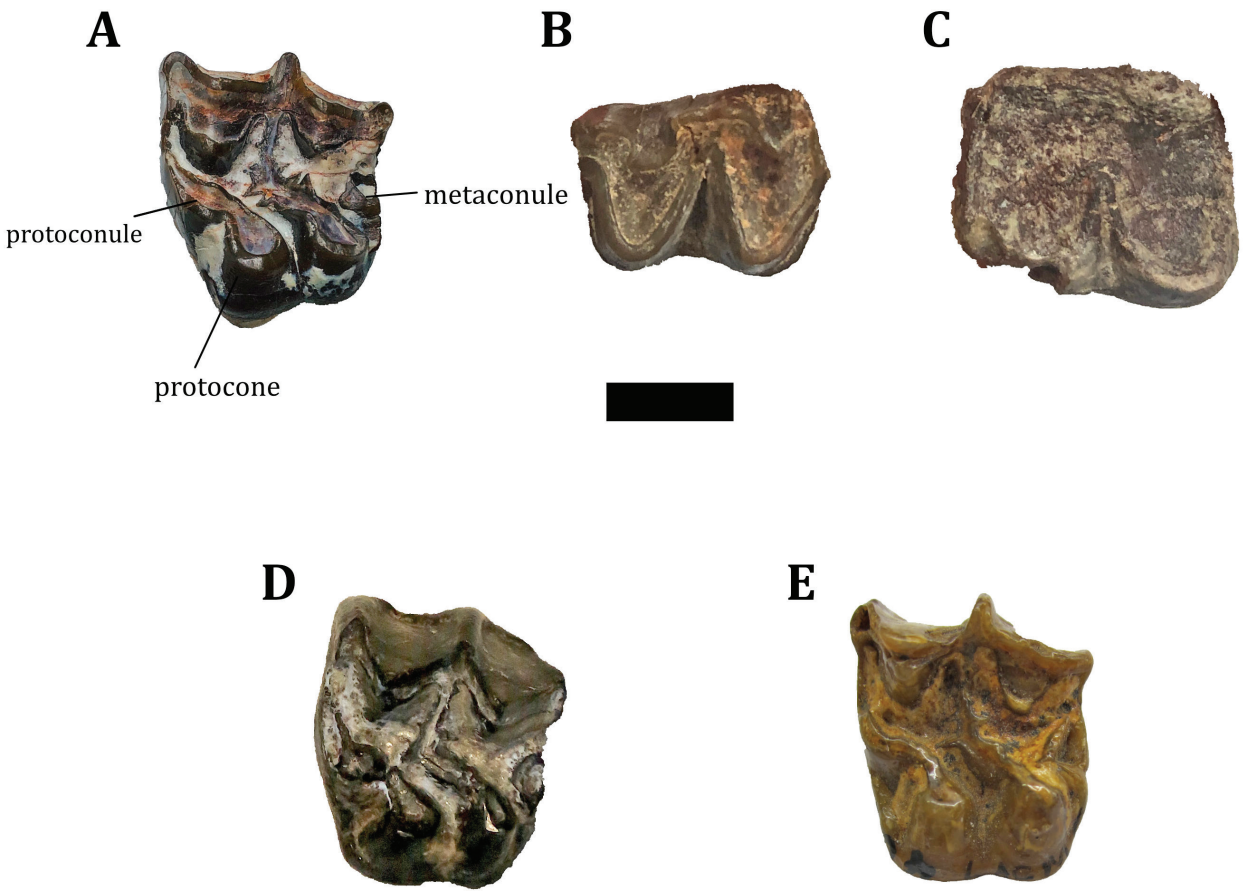


**Figure 5**. Teeth of *Parahippus brevidens* from the Cajon Valley Formation, San Bernardino County, California (**A–C**); the Mascall Formation, Grant County, Oregon (**D**); and Temblor Formation, Fresno County, California (**E**). **A.** WSC 8914 upper left M1. **B.** WSC 8918 lower right p3. **C.** WSC 9968 highly worn *Parahippus* lower tooth. **D.** YPM 11274 (holotype), upper left M1 or P4. **E.** LACM 1146 upper M?. Scale bar=1 cm.

lophoid protoconule and metaconule"; and 2) "hypostyle prominent, subtriangular" (Figs. 5, 6). According to the UCMP online database (https://ucmp.berkeley.edu/collections/databases/), material in the UCMP collection from the Cajon Valley Formation has been previously identified as *Parahippus* by Michael Woodburne. However, none of these teeth have been formally described as *Parahippus*. All Cajon Valley Formation specimens listed in the UCMP online database are, as of this publication, currently under the listing "Punchbowl Formation."

WSC 8914 bears closest resemblance to *Pa. brevidens*. It exhibits complex plications on both sides of the metaloph ("metaloph ptychoid on both sides" [Osborn 1918: p. 90]) (Figs. 5, 6) in contrast with "*Protohippus*" *avus* (Marsh 1874) (later assigned to the genus *Parahippus* [Gidley 1907] or *Desmatippus* [MacFadden 1998]) which lacks these plications entirely, and *D. crenidens* (Scott 1893), which exhibits them only on the mesial side (Osborn 1918). The protoconule does not align with the protocone, resulting in the curvature of the mesial edge (Osborn 1918). The metaconule is isolated, and resembles an "ear-shaped lobe" with interior cement with wear (Osborn 1918). The tooth lacks a median ridge between the metacone and the paracone, and the metaloph connects with the hypocone, but not the hypostyle (Osborn 1918).

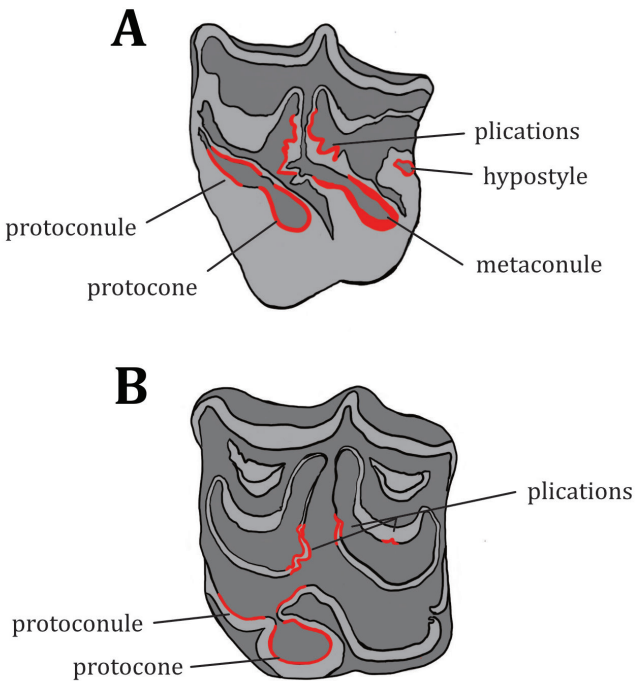


**Figure 6. A.** Upper molar of *Parahippus brevidens* labeled with anatomical features based upon WSC 8914. **B.** Upper molar of *Scaphohippus sumani* labeled with anatomical features based upon WSC 8934.

Marsh (1874) named *Protohippus avus* and *Anchippus brevidens*, both from the Miocene of Oregon. However, Gidley (1907) transferred the type species of *Anchippus*, *An. texanus* (Leidy 1868), into *Parahippus*, thus subsuming the genus *Anchippus* and creating the new combination *Parahippus brevidens*. He also placed the species "*Protohippus*" *avus* into *Parahippus*, which later authors (Osborn 1918, Bode 1933) continued. Downs (1956) argued that *Pa. brevidens* was synonymous with *Pa. avus*. However, he based this on nomenclatural arguments, and did not justify the synonymy with morphological characters.

Although we refer our specimens to *Pa. brevidens*, we acknowledge that the taxonomy of both *Parahippus* and *Anchippus* is in need of revision (see discussion by Albright 1999) but is beyond the scope of the present work.

## DISCUSSION

The differences among the horse teeth discussed in this paper highlight the diverse ecology represented in sediments of the Cajon Valley Formation (Fig. 7). Pagnac and Reynolds (2010) previously discussed the high prevalence of *Ar. mourningi* from the Cajon Valley Formation versus the coeval Barstow Formation, where it is comparatively rare. *Scaphohippus sumani* is present in both formations, but *Acritohippus* does not occur in the Cajon Valley Formation. The confirmation of *Pa. brevidens* in the Cajon Valley Formation extends the geographic range of this species southward by 400 km; the nearest previously described occurrence is in the Temblor Formation north of Coalinga, California (Bode 1933, 1935), at approximately 19–15 Ma (Bridges and Castle 2003) with the holotype described from the Mascall Formation of Oregon (Marsh 1874), at approximately 16–14.8 Ma (Maquire et al. 2018) (Fig. 8). The ages of these three formations are consistent with the known occurrences of *Pa. brevidens* being roughly contemporaneous. *Parahippus brevidens* is not found in the Barstow Formation (Pagnac 2005), again highlighting the differences in fauna between the two formations. There are numerous potential causes for these differences in faunal dispersal between these formations, which are less than 100 km from each other, and this is worth further research. In addition, collection biases could potentially affect our knowledge of California Miocene equids among these various formations; it is entirely possible that *Pa. brevidens* might be discovered in Miocene deposits throughout the California coast.

The presence of three small- to mid-sized equids and a distinct, consistent lack of larger equids such as

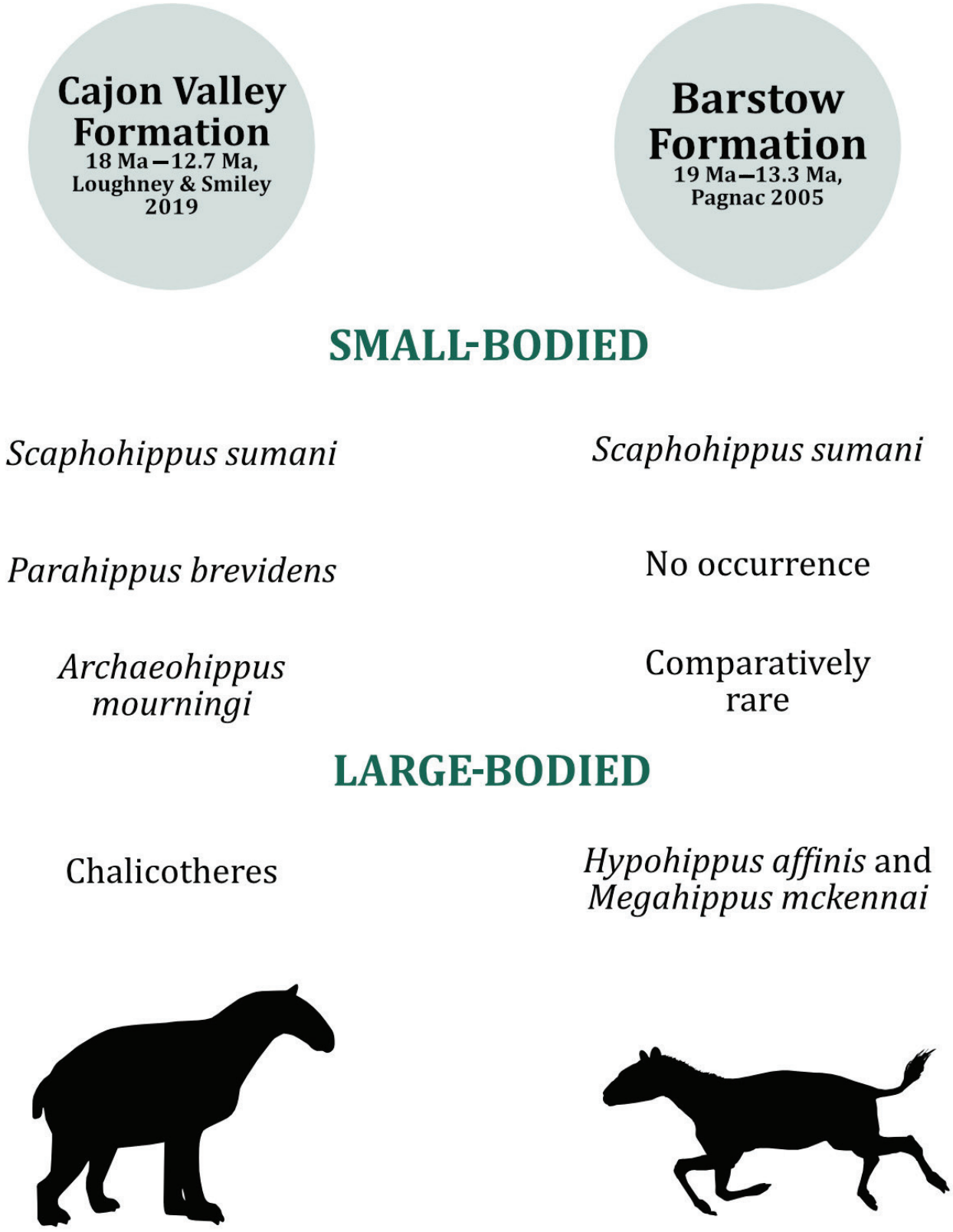


**Figure 7**. A faunal comparison of horses and chalicotheres of the Cajon Valley Formation and the Barstow Formation. Chalicothere silhouette from PhyloPic, created by Zimices; license: https://creativecommons.org/licenses/by-nc/3.0/. Horse silhouette from PhyloPic, created by Heinrich Harder and vectorized by T. Michael Keesey; license: https://creativecommons.org/publicdomain/mark/1.0/.


**Figure 8.** Published occurrences of *Parahippus brevidens* in Oregon and California, now including the material from the Cajon Valley Formation. Horse silhouette from PhyloPic, created by Jay Matternes and vectorized by Zimices, with no changes except the color; license: https://creativecommons.org/licenses/by/3.0/.

*Hypohippus affinis* (Leidy 1858) and *Megahippus mckennai* (Tedford and Alf 1962) in the Cajon Valley Formation may be due to sampling bias, but could also point to interesting ecological comparisons with the otherwise similar faunal list of the nearby Barstow Formation (Fig. 7). Three specimens of chalicotheres have been described in the Cajon Valley Formation, all referred to *Moropus* sp. Marsh, 1877 (Coombs and Reynolds 2015). Like *Pa. brevidens*, chalicotheres are absent in the Barstow Formation (Pagnac 2005). *Parahippus brevidens* has been previously found in units that lack chalicotheres including the Mascall and Temblor formations (Bode 1935, Downs 1956). However, in the Cajon Valley Formation they co-occur. The Cajon Valley Formation, in contrast to other described localities containing *Pa. brevidens* on the Pacific Coast, lacks the larger equids *Hypohippus* and *Megahippus*. The abundance of *Ar. mourningi* and the presence of *Pa. brevidens* suggest that the Cajon Valley Formation may have more in common with the Temblor and Mascall formations, apart from the presence of chalicotheres, than the geographically much closer Barstow Formation, which as previously noted is just under 100 km away. If this is not due to a temporal difference between our locality in the Cajon Valley Formation and the Barstow Formation, this could point to an environmental disparity, perhaps with a similar factor contributing to the abundance of *Pa. brevidens* and *Ar. mourningi* in the Cajon Valley, Temblor, and Mascall formations. Further studies on the paleoflora and comparative isotope analysis might reveal more about the ecological nature of these formations.

## ACKNOWLEDGEMENTS

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