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A Comparison of the Clarendonian Equid Assemblages from the Mission Pit, South Dakota and Ashfall Fossil Beds, Nebraska

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The Mission Pit locality (SDSM V5314), near Mission, South Dakota, has produced a large collection of equid teeth obtained from the Miocene Ash Hollow (=Thin Elk) Formation. Ashfall Fossil Beds (UNSM Ap-116), near Royal, Nebraska, has yielded an extensive collection of equid cranial elements and teeth derived from the Cap Rock Member, Ash Hollow Formation. The two sites are interpreted to be Clarendonian in age [12.5 to 9.0 Ma], but may contain faunal assemblages from differing Clarendonian subages.

The two sites exhibit a notably similar composition of equid genera, including the tribes Equini (*Plihippus*, *Calippus*, and *Protohippus*), and Hipparionini (*Cormohipparion*, *Neohipparion*, and *Pseudhipparion*). Both sites share the same proportion of the equid tribes Hipparionini and Equini. Approximately seventy-five percent of the equids at both sites are members of the Hipparionini tribe, whereas twenty-five percent are of the Equini tribe. The comparative composition within the Equini tribe between the two sites is nearly identical with differences in the absence of *Calippus* at Ashfall and a larger proportion of *Protohippus* at Mission. Only slight differences are observed in the composition of genera within the Hipparionini tribe between the two sites, with the Mission Pit containing a higher percentage of *Neohipparion*. The striking taxonomic similarity between the two sites is not only unique but also rare, suggesting a correlative relationship within the early to medial Clarendonian (Cl1 or Cl2). This similarity also suggests unique paleoecological relationships among equids and has a potential for insight into plant ecology and equid niche partitioning during this time interval.

Introduction

The Mission Pit of South Dakota contains a middle-to-late Miocene assemblage preserved in a series of fluvial channel deposits. Although generally recognized as a Clarendonian assemblage based on the presence of *Paratomarctus* (= *Tomarctus*) *euthos*, *Aelurodon taxoides*, *Epicyon saevus* (= *Aelurodon* cf. *inflatus*), *Carpocyon robustus*, *Ischyrocyon gidleyi* (= *Pliocyon walkerae*), *Merychippus* sp., *Hypohippus* sp., *Cormohipparion* (= *Neohipparion*) *occidentale*, *Neohipparion affine* (= *whitneyi*), *Pseudhipparion* (= *Nannippus*) *gratus*, *Plihippus pernix* (= *lullianus*), *Ustatochoerus* sp., and *Cosoryx* sp. (MacDonald, 1960; Tabrum, 1981; Wang et al., 1999) there is yet no definitive referral to a Clarendonian subage. The assemblage from the Mission Pit has not been extensively described other than a primary work by MacDonald (1960).

The fossil bearing units of the Ash Hollow Formation within Ashfall Fossil Beds State Historical Park in Nebraska have been dated to 11.83 Ma (Perkins et al., 1998) and represent a watering hole environment preserved during an ashfall event. Based on the occurrence of *Mioheteromys* cf. *M. amplissimus*, cf. *Ischyrocyon* sp., *Epicyon* cf. *E. saevus*, *Cynarctus* cf. *C. voorhiesi*, *Aelurodon* sp., cf. *Eubelodon* sp., *Hypohippus* sp., *Cormohipparion occidentale*, *Neohipparion affine*, *Pseudhipparion gratum*, *Plihippus pernix*, *Ustatochoerus major* (= *skinneri*), *Cranioceras* sp., cf. *Plioceras* sp., and *Longirostromeryx wellsi* (Voorhies, 1990, 2006) this assemblage is referred to the Clarendonian North American Land Mammal Age

(NALMA). Unfortunately, the fossil assemblage at Ashfall Fossil Beds has been extensively studied, but remains unpublished.

Both sites have a particularly large sample of equids from both the Equini and Hipparionini tribes, common constituents in many medial to late Miocene assemblages. A comparison of equid taxa from both sites would provide improved understanding of the relative age of the assemblage at the Mission Pit, and would provide unique insight into environmental variation within the northern Great Plains during the medial to late Miocene.

The Mission Pit is a gravel pit on the Thomas Fox Ranch near Mission, Mellette County, South Dakota (Fig. 1). The sediments preserve a paleo-channel deposit, consisting of unconsolidated yellow to brown sands and gravels with limited occurrence of caliche and minor amounts of volcanic ash (MacDonald, 1960; Harsken and Green, 1971). The deposits at the Mission Pit are of a typical cut and fill stream channel with interbedded lenses of fine, garnet-rich sands within layers of gravel and cobbles (MacDonald, 1960). The Mission Pit is also the type section of the now invalidated Thin Elk Formation of South Dakota, lithologic correlative of the Ash Hollow Formation (Harsken and Green, 1971; Wang et al., 1999).

Ashfall Fossil Beds contains a 2-m-thick bed of volcanic ash in the Cap Rock Member, a ledge-forming sandstone (Skinner et al., 1972), of the Ash Hollow Formation in the drainage basin of Verdigre Creek, Antelope County, northeastern Nebraska

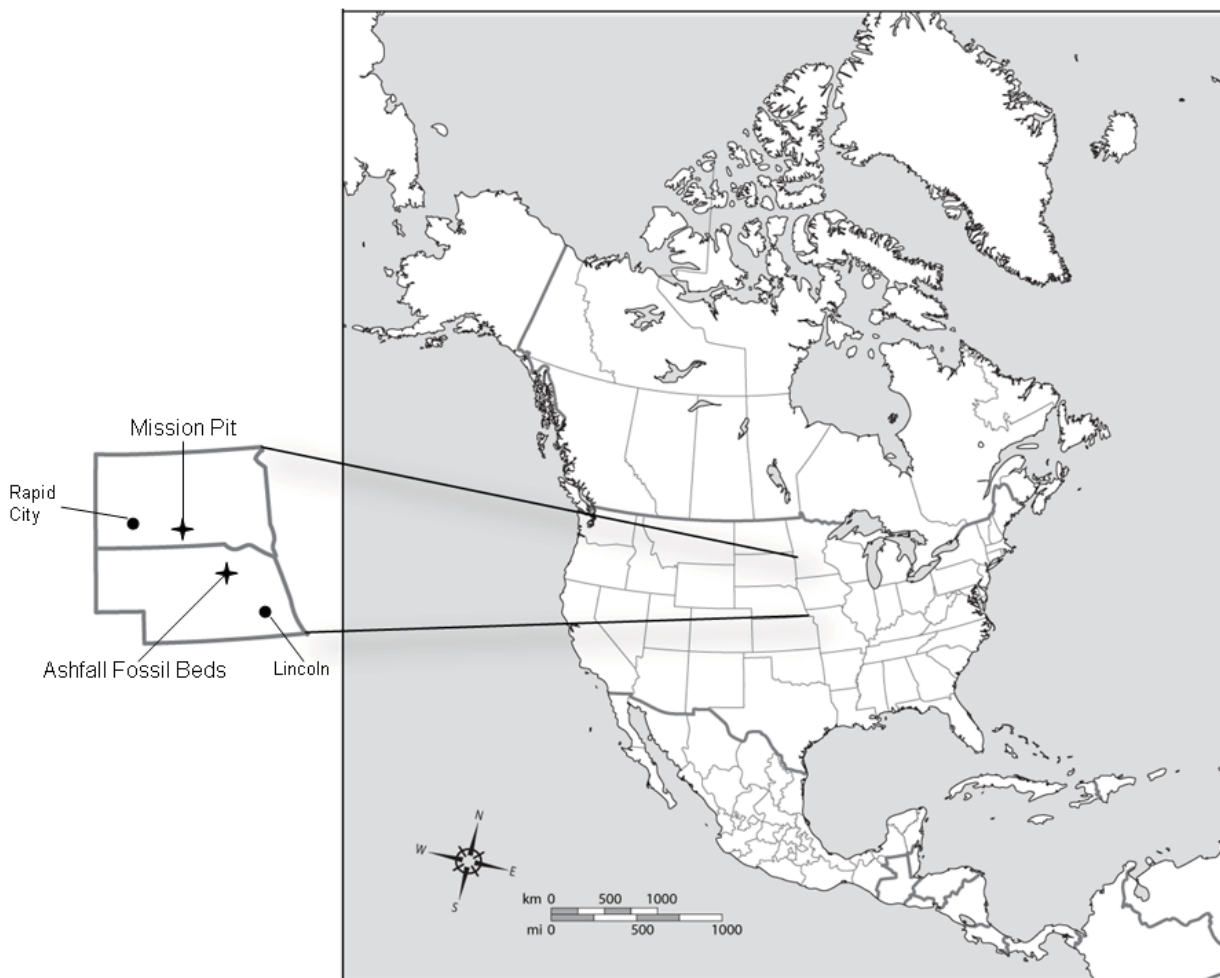


Figure 1. Map Showing General Location of Mission Pit and Ashfall Fossil Beds.

(Voorhies and Thomasson, 1979; Voorhies, 1992). The site is underlain by the older Valentine Formation and overlain by the younger Long Pine Formation (Voorhies, 2006). The site has been exposed by Colson Creek near Royal, Antelope County, Nebraska (Fig. 1).

The Mission Pit faunal assemblage has been studied briefly. MacDonald (1960) identified six equid taxa from Mission that include *Hypohippus* sp., *Cormohipparion* (= *Neohipparion*) cf. *C. occidentale* and/or *Neohipparion affine* (= *whitneyi*), *Neohipparion* sp., *Pliohippus* sp., *Pliohippus* cf. *P. martini*, and *Pseudhipparion* (= *Nannippus*) *gratus*. Tabrum (1981) re-described the equids at the Mission Pit and assigned them to six taxa including *Merychippus* sp., *Calippus* sp., *Protohippus* sp., *Pliohippus pernix* (= *lullianus*), *Pseudhipparion* n. sp., and *Cormohipparion* (= *Neohipparion*) *occidentale*. He also suggested the possibility of two additional equid taxa at Mission Pit, but these remain undescribed. Based on the equids, Tabrum (1981) dated the assemblage as intermediate between the early Clarendonian Burge

fauna and late Clarendonian Big Springs Canyon fauna, i.e., early medial Clarendonian. Tabrum (1981) and MacDonald (1960) concluded that the sediments at the Mission Pit site were deposited under fluvial conditions.

Ashfall Fossil Beds has been extensively researched in comparison, although primarily through unpublished work. Ashfall Fossil Beds contains a 0.5 m to 2.0 m thick ash bed (Skinner et al, 1972; Rose, et al., 2003) that also occurs in Morrill County, western Nebraska (Diffendal, 1982, 1995; Diffendal et al., 1996), and has been tentatively associated with an eruption from the Bruneau-Jarbridge Volcano of western Idaho (Perkins, 1998), about 1400 km west (Rose, et al., 2003). The Ashfall ash is correlated to the Ibex Hollow Ash dated at 11.83 Ma (Perkins et al., 1998). Five taxa of equids were described from the ash bed by Voorhies (2006), including *Neohipparion affine*, *Pseudhipparion gratum*, *Cormohipparion occidentale*, *Pliohippus pernix*, and *Protohippus simus*. *Hypohippus* sp. has been identified from the sands below the ash (Herbel, 1994; Voorhies,

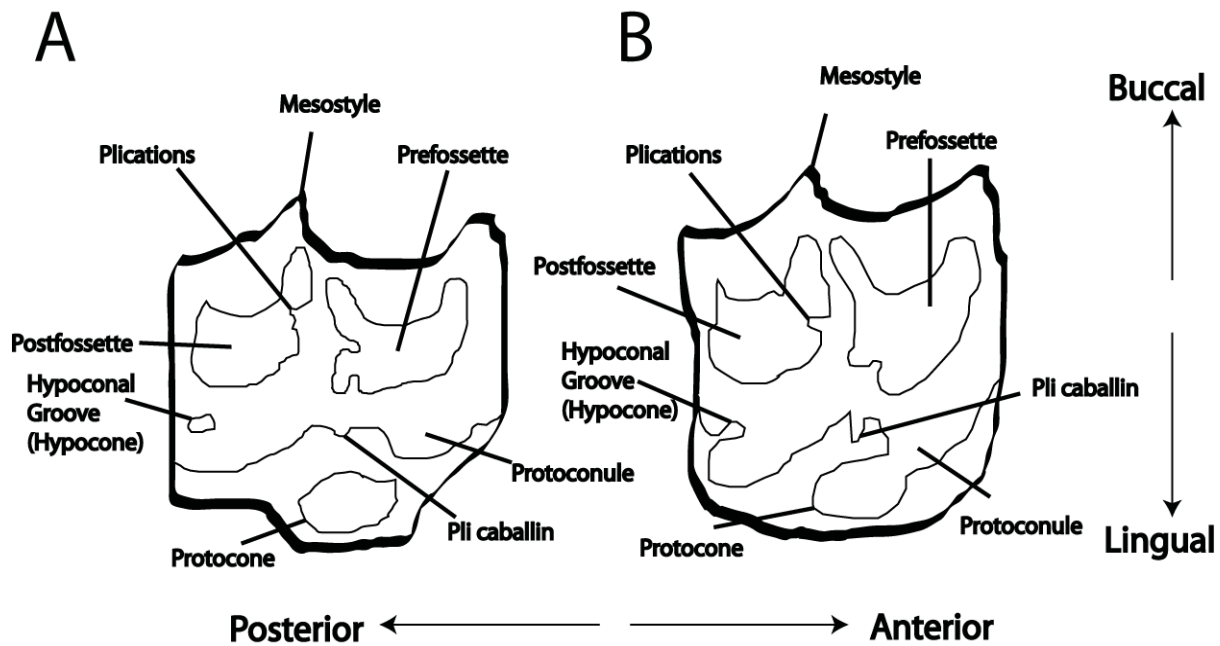


Figure 2. General Tooth Morphology of Hipparionini (A) and Equini (B) Tooth. Occlusal view, terminology after McFadden (1984).

2006). These equid occurrences closely resemble the composition of the medial Clarendonian Chokeycherry Quarry and Minnechaduzha faunas of Nebraska (Voorhies, 1990). Ashfall Fossil Beds represents a perennial watering hole where several of the present taxa congregated (Voorhies, 1992). Work on the paleotopography of the sands below the ash indicates that Ashfall represents a seasonally water-filled deflation basin (Herbel, 1994). The objective of this research is to compare the equid assemblages from Ashfall Fossil Beds and the Mission Pit localities.

Methods

To compare the equid assemblages from the two localities we analyzed a sample of 384 isolated teeth from the Mission Pit locality and 81 skulls with teeth from Ashfall Fossil Beds. Most of the specimens from Mission Pit are in the collections of the South Dakota School of Mines and Technology (SDSM), whereas most of those from Ashfall Fossil Beds are in the collections at the University of Nebraska State Museum (UNSM), Lincoln, Nebraska.

Figure 2 shows the tooth morphology utilized in the study (after MacFadden, 1984). Several diagnostic structures are present on the occlusal surface of equid teeth. Structures analyzed include the mesostyle, prefossette, postfossette, pli-caballin, protocone, protoconule and hypoconal groove.

The specimens at Ashfall Fossil Beds allowed examination of the cranial structures as there are two

fossae that are generically distinctive and can be used to support the identifications based only on dentition. These distinctive features include the dorsal preorbital fossa (DPOF) and the malar fossa. Terminology of these fossae follows Woodburne (2007).

Measurements taken on the upper premolars and molars include mesostyle crown height (MSTHT), length of tooth (APL), width of tooth (TRNW), protocone length (PRTL), protocone width (PRTW), and number of plications. Terminology of some measurements follows MacFadden (1992) and Woodburne (2007). Measurements were taken by using a Cen-Tech 6" digital caliper with an error of ±0.001" (0.03 mm). A hand lens was used to aid in counting plications. An examination of the presence of occlusal surface structures was also preformed. A Spearman-Kendall rank coefficient test was performed to ascertain the similarity of the two assemblages.

Diagnostic Equid Morphology

Hipparionine and equine taxa are defined by several characteristics within the cranial and dental morphology. A high degree of distinctive variation is present within the DPOF) within both tribes. Hipparionines have a greater number of plications, in the tooth enamel thereby increasing the most durable part of the tooth to resist wear (Fig. 2A). In hipparionines, the protocone is closed and isolated and the hypoconal groove is open to the base of the crowns (Quinn, 1955). Equines adapted relatively

tall teeth with simple enamel borders (Fig. 2B). The upper teeth exhibit heavy styles and deep valleys (Quinn, 1955). The protocones are elongate, and are usually grooved and heeled (Quinn, 1955). Protolophs are also connected to the protoselene in the later forms and unconnected in early forms (Quinn, 1955). Additionally, the hypoconal groove opens with wear (Quinn, 1955). MacFadden, 1998, provides detailed diagnoses of each of the genera utilized in this study.

In *Pseudhipparion* the DPOF is poorly developed and has indistinct boundaries. The malar fossa is absent. The protocone is large and elliptical. It is isolated during early wear but is connected in later wear stages.

In *Neohipparion* the DPOF is relatively poorly defined. The malar fossa is absent. The protocone is isolated and is an elongate- to very elongate oval shape. Teeth were compared to MacFadden (1984, Fig. 63).

In *Nannippus* the DPOF is moderately well developed to absent. Teeth are very hypsodont with moderately complex enamel plications. The protocone is oval and isolated. Teeth were compared to MacFadden and Waldrop (1980, Fig. 15).

In *Cormohipparion* the DPOF is teardrop shaped and is well developed on the anterior and posterior rims. The DPOF contains a distinct posterior "pocket". The malar fossa is absent. Fossette borders are moderately to highly plicated. The pli caballin is well developed. The protocone is isolated. Teeth were compared to Hulbert (1988a, Fig. 6).

In *Protohippus*, the DPOF is large and oval-shaped. The lacrimal is large and is included within the posterior portion of the DPOF. The malar fossa is absent. The protocone is isolated during early wear stages. Fossette enamel borders are simple. Teeth were compared to Osborn (1918, Plate 22).

In *Calippus*, the DPOF, when present, is long, shallow, and not pocketed. The malar fossa is absent. The protocone is open, large, and oval to elongate. The pli caballin is rudimentary or absent. The hypoconal groove is shallow and frequently forms hypoconal lakes. Teeth were compared to Hulbert (1988, Fig. 15).

In *Pliohippus*, the DPOF and malar fossa are well developed and are often strongly pocketed and complex. The cheek teeth are strongly curved. The protocone is connected. The hypoconal groove is shallow. Teeth were compared to Osborn (1918, Fig. 120).

In *Dinohippus*, the malar fossa is small or absent. The DPOF is rudimentary or absent. The cheek teeth are moderately curved. The protocone is strongly connected. The hypoconal groove is well developed.

Table 1. Total Number of Skulls Identified for Each Genus at Ashfall Fossil Beds.

Genus	Total
<i>Pseudhipparion</i>	46
<i>Neohipparion</i>	3
<i>Cormohipparion</i>	14
<i>Pliohippus</i>	13
<i>Protohippus</i>	5
<i>Calippus</i>	0

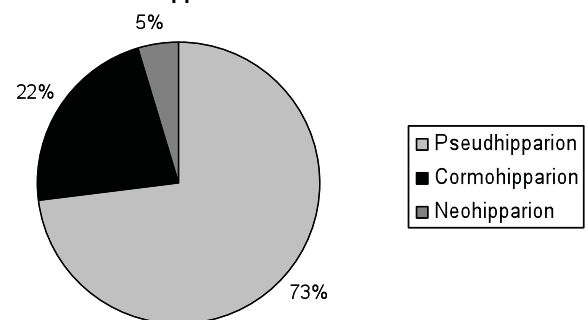
The enamel plications are simple. Skulls and teeth were compared to Osborn (1918, Fig. 130). *Dinohippus* is generally regarded as a Hemphillian or Blancan genus, but many specimens from this study were referred to *Dinohippus* based on older diagnoses.

Results

Approximately 78% of the equids at Ashfall represent the Hipparionini tribe, whereas 22% represent the Equini tribe (n = 81) (Fig. 3B). There are three genera present from the Hipparionini tribe, *Pseudhipparion*, *Neohipparion*, and *Cormohipparion*. Of the Hipparionini, *Pseudhipparion* comprises 72%, *Neohipparion* 5%, and *Cormohipparion* 23% (n = 63) (Fig. 3A). Table 1 shows the number of individuals (skulls) for each genus at Ashfall and the distribution of all equid genera is shown in Fig. 3B.

An analysis was conducted on the equid teeth at Ashfall Fossil Beds. Measurements are presented in

A. Distribution of Hipparionini Genera at Ashfall Fossil Beds



B. Distribution of Equid Genera at Ashfall Fossil Beds

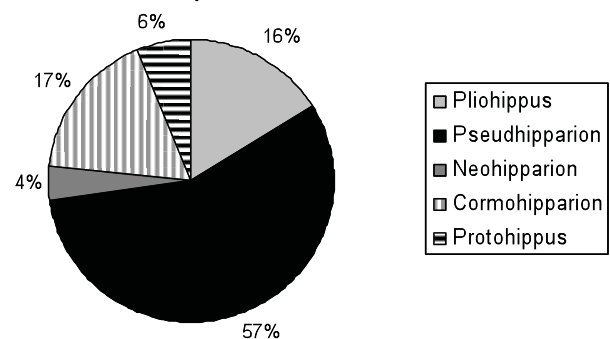


Figure 3. Distribution of Hipparionini and Equid Genera at Ashfall Fossil Beds.

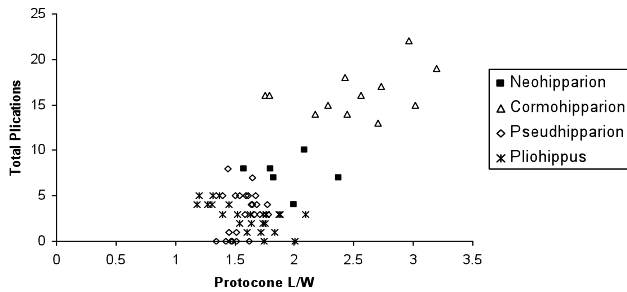


Figure 4: The Relationship Between the Ratio of Protocone Length to Width and Total Plication Count for Ashfall Fossil Beds Equid Genera.

Appendix A. A relationship between the ratio of protocone length to width and the total number of plications was discovered on all genera sampled at Ashfall Fossil Beds (Fig. 4). The Equines fall near *Pseudhipparion*, which is the most basal Clarendonian Hipparionine. The more advanced hipparionines appear to increase the surface area of enamel through an increased number of plications.

Figure 4 shows the relationship between protocone length multiplied by width versus total plication count for Ashfall Fossil Beds genera. When calculating a linear regression line for the data we find an *R* value of 0.752 indicating a strong positive relationship. We see that the positive relationship correlates with the phylogenetic relationship of the Hipparionini genera. MacFadden (1992) indicates that *Pseudhipparion* is the most basal Hipparionini, while *Cormohipparion* is the most derived. This is reflected in the dentition of each genus, as represented in the plot in Figure 4. We expect *Pseudhipparion* to have the lowest number of plications among the hipparionines, and the data in Figure 4 supports this hypothesis. The Equini in this graph plot in the same area of the graph as *Pseudhipparion*, which is also expected considering the adaptations of low plication counts for the Equini tribe. An interesting correlation is also observed between a more elongate protocone and an increased number of plications.

The sample population for the Mission Pit was compiled from individual upper teeth. The summary of the Mission Pit data can be found in Table 2.

Approximately 75% of the equids at the Mission Pit represent the Hipparionini tribe, while 25% represent the Equini tribe (n = 384) (Fig. 5B). The three genera present within the Hipparionini tribe include *Pseudhipparion*, *Neohipparion*, and *Cormohipparion*. Of the Hipparionini, *Pseudhipparion* represents 60%, *Neohipparion* represents 19%, and *Cormohipparion* represents 21% (n = 288) (Fig. 5A). The distribution of all equid genera at the Mission Pit

Table 2. Total Number of Upper Teeth Identified for Each Genus at the Mission Pit.

Genus	Total
<i>Pseudhipparion</i>	173
<i>Neohipparion</i>	54
<i>Cormohipparion</i>	61
<i>Pliohippus</i>	75
<i>Protohippus</i>	10
<i>Calippus</i>	11

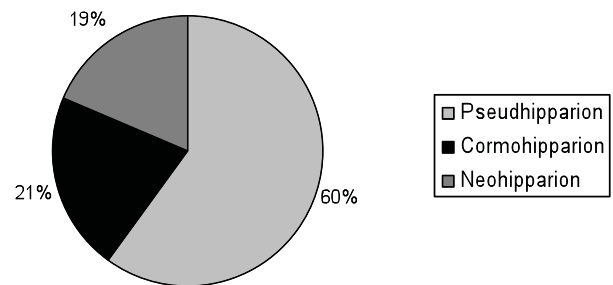
can be seen in Figure 5B.

Measurements of the Mission Pit samples are presented in Appendix B.

Statistical tests

A nonparametric test for abundance correlation, the Spearman-Kendall test, was performed using PAST analytical software (Hammer et al., 2001). This test was utilized to test the correlation of abundance rank between the two sites based on the percentage of each genus as a portion of the whole sample for each locality (Fig. 3). The analysis on the overall population yielded a Spearman *r_s* of 0.77, and Kendall *tau* of 0.6 (Table 4). When we remove *Calippus*, the Spearman *r_s* becomes 0.8 and the Kendall *tau* remains the same (Table 5).

A. Distribution of Hipparionini Genera at the Mission Pit



B. Distribution of Equid Genera at the Mission Pit

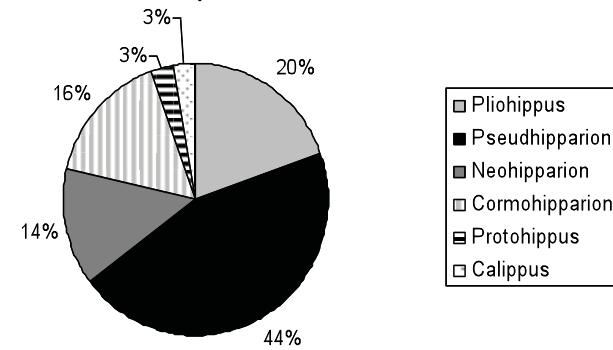


Figure 5. Distribution of Hipparionini and Equid Genera at the Mission Pit.

Table 3. Population Values.

Genus	Ashfall	Mission Pit
<i>Pseudhipparion</i>	56.790	45.052
<i>Neohipparion</i>	3.704	14.063
<i>Cormohipparion</i>	17.284	15.885
<i>Pliohippus</i>	16.049	19.531
<i>Protohippus</i>	6.173	2.604
<i>Calippus</i>	0.000	2.865

Table 4. Results of Spearman-Kendal Test for total Population Including *Calippus*.

	Values	<i>p</i> (uncorrected)	Permutation <i>p</i>
<i>D</i>	8.00	0.08	0.10
<i>r_s</i>	0.77	0.10	0.10
<i>tau</i>	0.60	0.09	0.13

Table 5. Results of Spearman-Kendal Test for total Population Excluding *Calippus*.

	Values	<i>p</i> (uncorrected)	Permutation <i>p</i>
<i>D</i>	4.00	0.11	0.13
<i>r_s</i>	0.80	0.08	0.13
<i>tau</i>	0.60	0.14	0.23

Interpretation of the Spearman-Kendall statistics shows a strong abundance rank correlation between Ashfall and Mission, with *r_s* values between 0.75 and 0.8, and a *tau* value of 0.6. The associated *p* values are greater than 0.05 allowing acceptance of the null hypothesis (*H*₀) that the two localities contain statistically similar abundance rankings. The main differences lie in the abundances between *Neohipparion*, *Pliohippus*, *Protohippus* and, of course, *Calippus* (only present at a one locality).

Discussion

Ashfall Fossil Beds and the Mission Pit demonstrate minor differences in equid taxonomic composition. All genera, except *Calippus*, are present at both localities based on the identification of upper dentition. The two sites have the same abundance between the Hipparionini tribe and the Equini tribe. There are, however, differences in the generic level composition. Mission and Ashfall vary most significantly in the abundance of *Neohipparion* and *Protohippus* as well as the absence of *Calippus* at Ashfall. We see the same relative distribution of higher taxonomic groupings (tribes) at the two sites. This stands in slight contrast to the different generic level abundance. The differences observed among genera could be due to preservation and collection biases. The two sites were deposited under different conditions. Additionally, the manner in which the specimens were collected was different. Ashfall specimens were collected with traditional excavation techniques and consist of more complete elements. The Mission specimens were collected in a more

unorthodox manner. The Mission Pit was a functioning gravel pit during investigations; the easiest way to collect specimens was by examining the sediment being conveyed by belts on the machinery (MacDonald, 1960). MacDonald used a rake to pull specimens off of the conveyer belts. This method produced more incomplete elements at the Mission pit, and a much higher percentage of isolated teeth.

It is important to note that the Ashfall ash bed represents a short period of time, roughly four weeks. The Ashfall ash bed does not include all taxa present in this area, as the fragmental zone beneath the ash bed contains over 35 mammalian taxa while the ash bed contains only 12 mammalian taxa (Voorhies, 2006). The Mission Pit represents an accumulative attritional assemblage, with specimens deposited over a much longer span of time.

In the process of conducting this study a rudimentary taxonomic review was performed on the equids at each site. The identification of specimens from the Mission Pit were conducted in the early 1960s. The specimens labeled *Nannippus* were re-identified as either *Pseudhipparion* or *Calippus*. Specimens labeled *Neohipparion* were determined to be *Neohipparion* or *Cormohipparion*. Specimens labeled *Merychippus* were generally at an early wear stage obscuring diagnostic features. These teeth were then referred at the familial level to Equidae. There were also some minor issues with the specimens in the Ashfall Fossil Beds collection. These specimens were identified in the late 1970s. Several specimens were identified as *Dinohippus*; these were determined to be referable to *Pliohippus*, while a few were referred to *Protohippus*. Two specimens labeled *Calippus* were determined to be individuals of *Pseudhipparion* in later stages of tooth wear.

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Appendix A. Measurements of Teeth From Ashfall Fossil Beds State Historical Park A key to measurements is provided at the end of Appendix B

Table with columns: Spec. Num, Field Num, Taxon, Tooth, Locality, Side, Mesostyle Cwn hght, Length, Width, L x W, LW, Proto-loph-Metaloph conn, Pre-fossette, Post-fossette, Hypocone open, Hypoconal groove, Nature of Protocone, Protocone Length, Protocone Width, Protocone LW, Pli cab, Pli prtiph, Pli prf, Pli psf, Pli hyst, Total plications, Comments (Measurements in mm)

Appendix B. Measurements of Teeth From Mission Pit, continued

Table with columns: Spec. Num, Field Num, Taxon, Tooth, Locality, Side, Mesostyle Crwn hght, Length, Width, L x W, L/W, Protoloph-Metaloph conn, Pre-fossette, Post-fossette, Hypocone open, Hypoconal groove, Nature of Protocone, Protocone Length, Protocone Width, Protocone L/W, Pli cab, Pli prtlph, Pli prf, Pli psf, Pli hyst, Total plications, Comments (Measurements in mm)

Key: Appendices depict measurements of upper check teeth (in mm) of specimens from the Ashfall Fossil Beds (Appendix A) and Mission Pit (Appendix B) samples. + and - indicate presence or absence of characteristics (e.g. open hypocone). Numbers expressed without decimal value indicate presence and number of plications. N/A indicates a feature which was broken and not available for measurement. Mesostyle Crwn hght, Mesostyle Crown Height; L x W, Length times Width; L/W, Length divided by Width; Protoloph-Metaloph conn, Protoloph-Metaloph connected; Pli cab, Pli-caballin; Pli prtlph, Pli-protoloph; Pli prf, Pli-prefossette; Pli psf, Pli-postfossette; Pli hyst, Pli-hypostyle.