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Mammalian Fauna From The Fullerton Gravel Pit (Ogallala Group, Late Miocene), Morton County, Kansas

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MAMMALIAN FAUNA FROM THE FULLERTON GRAVEL PIT
(OGALLALA GROUP, LATE MIOCENE),
MORTON COUNTY, KANSAS

being

A Thesis Presented to the Graduate Faculty
of the Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

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ABSTRACT

The Fullerton Gravel Pit, Morton County, Kansas is one of many sites in western Kansas at which the Ogallala Group crops out. The Ogallala Group was deposited primarily by streams flowing from the Rocky Mountains. Evidence of water transport is observable at the Fullerton Gravel Pit through the presence of allochthonous clasts, cross-bedding, pebble alignment, and fossil breakage and subsequent rounding.

Fluvial mechanisms also played an important role in the distribution of fossil material. When the fossils from the Fullerton Gravel Pit are placed in Voorhies Groups, it appears that a majority of them were removed from suspension gradually and transported through traction. This interaction created a distinct bias in the accumulation of specific specimens at the site.

The identity of the mammalian taxa recovered from the Fullerton Gravel Pit was determined by comparison with previously identified specimens, as well as previously utilized comparative techniques. Camels are the majority of identifiable elements at the site. In particular, the medium-sized camel, *Hemiauchenia* is best represented. The canid, *Osteoborus*, proboscideans, such as gomphotherids, and perissodactyls, predominantly horses, are also present. Conspicuous by its absence, *Teleoceras*, a common Miocene rhinoceros, has yet to be discovered. The absence of *Teleoceras* may in part be due to channel velocity and depth.

The presence of the canid *Osteoborus* restricts the Fullerton Gravel Pit to the Hemphillian age. The biochronologic range of the camels, *Aepycamelus*, *Protolabis*, and *Procamelus* end in the early Hemphillian, providing evidence restricting the Fullerton

Gravel Pit to an early Hemphillian age. Of the horse species found at the site, only *Neohipparion trampasense* partitions the Hemphillian, being confined to the late Barstovian to early Hemphillian. The biostratigraphic range of these genera results in an assignment of the Fullerton Gravel Pit to an early Hemphillian age.

Within the Equidae, hypsodont dentition and muzzle width indicate that horses were grazers. However, the varying degree of hypsodonty in the Camelidae indicates they were more diverse. Whereas, *Hemiauchenia*, exploited a grazing niche; others such as *Procamelus* occupied a browsing niche. Tooth condition and the percent δ^{13}C reinforce the interpretations obtained for camel feeding.

Grazing and browsing niches are supported in a savanna-grassland environment. Grasses would have sustained the grazers, and intermittent trees and brush the browsers. This interpretation of the Fullerton Gravel Pit is in agreement with analyses describing the spread of the savanna-grassland landscape across North America during the Miocene.

A number of factors influence fossil distribution at the Fullerton Gravel Pit. Niche specialization, fluvial filtering, and an evolving landscape each accounts for the abundance of camel material, as well as the distribution of other taxa.

ACKNOWLEDGMENTS

I dedicate this work to my parents, for their commitment to my education and my growth as a person. Thank you for allowing me to pursue this unconventional dream, which I have had for as long as we all can remember.

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INTRODUCTION

A late Tertiary deposit; the Ogallala Group crops out across parts of Colorado, Kansas, Nebraska, New Mexico, Oklahoma, South Dakota, Texas, and Wyoming (Fig. 1). The sediment is comprised of clay, silt, sand, and gravel and was deposited in a west to east fashion by streams draining from the Rocky Mountains, although there are accounts of eolian deposits preserved in the Ogallala Group (Winkler, 1987). Locally the sediment may be cemented by opal or calcium carbonate (Liggett et al., 1998).

Clastics in the central regions of Ogallala distribution are derived from the Front Range in Colorado and are silicic in composition. Clastics in the southern areas, however, are often derived from New Mexican basalts or Mesozoic sediments. Across its extant, additional clastics are derived from local bedrock (Liggett et al., 1998).

The fossil flora and fauna distinguish the Ogallala Group from other stratigraphic units of the late Miocene. Fossil leaves, anthoecia, achenes, nutlets, and endocarps have been identified in paleobotanical studies (Thomasson, 1979, 1990), whereas paleozoological studies have unearthed taxa ranging from mollusks to mastodons. When evidence from these two subdisciplines of paleontology is combined, the existence of subhumid and subtropical savannas or savanna parklands is indicated. Temperatures rarely dropped below 0° C or exceeded 38° C (Thomasson, 1990).

As a result of this geologic potential, studies (Liggett and Zakrzewski, 1997, Liggett et al., 1998) have set their goals on both the identification and description of the recovered specimens and lithology of the Ogallala Group. Within this particular study, both the depositional setting and mammalian fauna of the Fullerton Gravel Pit (FGP) are investigated.

Location

The FGP is located near the town of Elkhart in the extreme southwestern corner of Morton County, Kansas. (For the PLSS coordinates, contact the Sternberg Museum of Natural History at Fort Hays State University [FHSM].) The FGP is part of the Cimarron National Grassland (Fig. 2) and is the only site in Morton County from which Miocene vertebrate fossils have been reported.

As of November 2008, gravel production at the pit has been drastically reduced. Reclamation efforts have been instituted and terracing has progressed on a number of walls at the pit. Although this practice will undoubtedly lessen the effects of erosion, stratigraphic and paleontological studies may be disturbed by these efforts.

PREVIOUS WORK

Only two published papers deal with the FGP; Liggett and Zakrzewski (1997) and Liggett et al. (1998). Although the depositional setting and fossil fauna were briefly discussed, the papers represent preliminary surveys intended for resource management.

The relative abundance of fossil camels at the FGP was first noted by Liggett et al. (1998). However, the taphonomic filter of camel preservation was not determined at the time. The abundance of camel material is not common in other faunas from the Ogallala Group in Kansas, as the profusion of camel material observed at the FGP appears to be site specific. Mullin (2006) reported that rhinoceros, not camel, are more abundant at the Jack Swayze Quarry, Clark County, and Minium Quarry, Graham

County. Similarly, Liggett (1997) reported an apparent abundance of rhinoceros, a number of small, non-camel artiodactyls, and a single horse tooth (*Pseudhipparion*) from the Beckerdite site in Clark County (Fig. 2). This relative lack of horse material, comparatively speaking is shared with the FGP.

Although the research of Liggett et al. (1998) laid the foundation for future paleontological studies at the FGP, much of the fossil material needed to be described and assigned to a taxon. In addition, the exact reason for the abundance of camel material was unknown. This study is an attempt to rectify these issues.

METHODS

The fossils from the FGP were brought to my attention by Dr. Richard J. Zakrzewski in the spring of 2008. The fossil collection is housed at the FHSM, and consists of elements ranging from partial jaws to phalanges. All of the fossils and fragments were previously identified to family level; however, genus and species had yet to be determined for a number of specimens.

Prior to any field activity and fossil recovery for this study, members of the Cimarron National Grassland staff and Dr. Bruce A. Schumacher generously donated a number of fossils previously recovered from the FGP, ranging from fragmentary limb bones and individual teeth of a variety of mammals, to portions of turtle carapace and skeleton.

Field work was conducted November 21st through 23rd 2008. The reason for this expedition was twofold. First, a site review was established in the attempt to become familiar with the stratigraphy of the area. Sediment samples and a detailed log were collected from the surrounding area in the effort to document and fully understand the depositional environment of the site. Secondly, the trip was made for the acquisition of additional fossil material to enhance the observations of this study.

Depositional Environment

Compared to a previous study of the depositional environment of the Ogallala Group (Churchill, 1992), this study was less analytical. Sieve samples and acid dilutions were circumvented and substituted with written descriptions and surface samples taken at 0.3 m intervals. Although it was fully intended to record the orientation of the recovered fossils, which would have been a great aid in determining potential alignment, leading to further evidence for recreating the depositional environment, a number of difficulties (described later) prevented this goal from being achieved. The proceeding process was devised to ensure that the entire exposed section was documented, for future analysis, upon return from the field investigation.

In lieu of extensive sediment processing, a composite stratigraphic column of the study site was constructed (Fig. 3). As no stratigraphic column of the FGP existed prior to this point, this step will hopefully be of some value in future studies. A detailed description of each unit; including lithologic contacts, sediment type, fossils (if any), and sedimentary structures, was also recorded at 0.3 m intervals, with thicknesses being recorded to 0.01 m.

Fossil Recovery

The second goal of the field analysis was to collect additional fossil specimens that had become exposed since the last time the FGP was visited. Because the recovered fossils are considered to be float, the *in situ* location was not determined. As a result, no specific information, such as location above or below a certain contact or orientation of the fossil could be documented. There was one exception, however, where a single fossil was embedded within the planar sands and was recorded as *in situ*. All fossils when recovered were placed in a pre-labeled bag (recording the date of recovery and unit location in column), and packed securely.

Preparatory Processes

Mammalian specimens that could be classified, to an ordinal rank, were reassembled, when necessary, to further the probability of identification. Fragmentary bones that could not be recognized on their own accord were separated from the remaining material and disregarded for this study. Although classification of this fragmented material could not be established, it is in these fossils that fluvial rounding is best recorded. These fossil fragments will be referenced later. Upon restoration, these new specimens were accessioned into the vertebrate paleontology collection and assigned a catalog number (e.g., VP-XXXXX).

Mammalian Identification

Although this study has a particular focus on the fossil camels of the FGP, other mammalian families are represented. These taxa range from canids to horses and demonstrate the array of fauna present at the site. Measurements of appropriate variables, i.e., length, width, height, as well as any other pertinent characters, were taken with standard calipers and recorded to 0.1 cm. Tooth measurements were taken to 0.01 cm. These data were then used in conjunction with comparative osteology of previously identified specimens to identify the elements. When isolated teeth were studied, parameters such as degree of hypsodonty and the unique infolding of enamel were utilized for identification.

Teeth not only provide characters in generic assignment, but also to the establishment of an individual's age. Hulbert's (1984) method for determining classes of tooth wear was also implemented for fossil horses. Both the grade of wear and eruption of certain teeth, such as the m1, when available, were carefully noted (Fig. 4). In determining the wear stage of a particular specimen, one may assess the corresponding age of the individual at the time of death (Table 1), providing potential insight to herd age structure.

Although similarities exist in the process of equid and camel identification, there are also a number of alternatives in camel assignment. In addition to the degree of hypsodonty, is the development of llama buttressing. Llama buttressing, characteristic of the Camelidae and specific to a particular genus, is the labial extensions of the anterior most edge of the lower molars (Ruez, 2005). Combined with comparative morphology, these tooth characteristics were critical to taxon assignment.

Because most of the camel material was postcranial, primarily metapodials, Breyer's (1983) method, which utilizes the ratio of width to length of both metacarpals and metatarsals for generic assessment, was also implemented. For phalanges, muscle scarring on the proximal posterior surface is also diagnostic of genus. These additional techniques proved to be invaluable in camel identification when cranial material was not available.

DEPOSITIONAL ENVIRONMENT

Lithologic Description

The Ogallala Group exposed at the FGP can be divided into five discernable subdivisions (Fig. 3). Beginning in the stratigraphically lowest portion of the section, the bottom-most layer is mainly comprised of fine- to medium-sized sand with clasts ranging in size from pebbles to cobbles, resulting in a lithic arenite to arkosic conglomeratic gravel. Although the sand is relatively consistent in composition, being a light tan quartz; the composition of the clasts varies greatly. Vesicular basalts and quartzites are just two of the varieties of clasts found in this lower layer. The presence of these clasts indicates derivation most likely from sources in New Mexico or Oklahoma, as initially described by Liggett et al. (1998).

As a whole, this first layer can be described as being deposited in a planar manner, as the beds are mainly oriented in a horizontal fashion, with no additional bedding or structural features. It was within these planar sands that the one *in situ* specimen from the site was recovered. Besides the single specimen that was found in place, a number of other fossils, both mammalian and reptilian, were recovered from this layer. Here, the visible layer was measured to be approximately 1.83 m thick. The overall thickness of this layer can perhaps be extended downward, as the base is not exposed in cross-section.

The second unit is a 5.49 m layer of fine to medium sand with gravel; however, the clasts in this layer range from pebble to boulder size. These large clasts suggest an increase in both current velocity and carrying capacity. This higher velocity may be attributed to an increase in water shed from the Rocky Mountain region, possibly resulting from further uplift of the region, glacial outwash, or heavy rains. Again, the clasts range in composition, across the rock spectrum (from igneous, metamorphic, and sedimentary) and the source of these clasts is attributed to an allochthonous origin, as well as local bedrock.

Comparatively speaking, this layer had the most abundant fossil yield. Here, both mammalian and reptilian fossils were recovered; however, mammalian specimens were far more common. The mammalian specimens include post-cranial material, specifically metapodials of both the fore- and hind-limbs, as well as cranial material, including individual teeth.

The second layer can also be delineated from the first because of the presence of cross-bedding (Fig. 5). Within this layer, cross-bedding was noted in two locations, as well as pebble alignment, providing additional evidence for a fluvial environment.

The third unit is a 0.91 m layer composed of fine-grained, white calcareous material that reacted vigorously to dilute HCl. This layer was identified as a caliche and paleosol. Caliche forms when minerals from a developing soil are leached and accumulated in an underlying layer. Here, the paleosol would have been the source of these minerals; whereas the resultant caliche deposit marks the zone of accumulation. No fossils were recovered from this, or the remaining two layers.

Orange fine to medium sand characterizes the next unit. It, like the previous unit, measured 0.91 m in thickness. The difference in color is interpreted to reflect a change in the composition of the parent rock. The orange color is due to mineral impurities of a parent quartzite, likely iron oxide.

The uppermost layer in the section at the FGP is a 0.15 m layer of current soil. Here, the growth of short grasses is predominant and no fossils were recovered.

Interpretation

The previously described stratigraphy is critical to the interpretation of the depositional environment. To reiterate, the key evidence that was observed, such as cross-bedding, rounded clasts, and others, will be described in detail here, to support previous studies indicating that the sediment at the FGP is indeed fluvial in origin.

Although there is a large amount of sediment derived from local bedrock, the inclusion of basaltic clasts within the deposits of the FGP suggests fluvial transfer and subsequent deposition. Because the nearest volcanic source area to the FGP is approximately 64.7 km away (Black Mesa, Oklahoma), these igneous rocks were undoubtedly transported substantial distances to their present location.

As reported in the second layer of the stratigraphic column, there are two examples of cross-bedding (Fig. 5). Based on the orientation of the beds, it is evident that the direction of flow was to the southeast. The two instances of cross-bedding reflect the stream flow direction at this particular locality and may not reflect the overall stream direction for the site. As the number of exposed cross-beds is few, a rose diagram to fully interpret flow direction could not be implemented. Though cross-beds are also known to be formed through eolian processes, it is more likely in this event that they were formed by fluvial activity (Liggett and Zakrzewski, 1997). This interpretation is supported by a third piece of evidence.

Although subtle, there is evidence of pebble alignment at the FGP (Fig. 5). Along with the cross-bedding, pebble alignment of clasts approximately 1.6 cm in diameter, also serves as an indicator of a southeast flow direction. These pebbles are highly rounded, much like a number of fossils from the site. Jagged edges were smoothed by prolonged movement through water and the resulting erosion is now evident. Likewise, the size of the clasts and lack of evidence for eolian transport suggest it is unlikely that eolian processes were significant enough to produce both cross-bedding, as well as transport and align these clasts.

Breakage of fossils is a common result of water transport and a vast majority of the fossils recovered from the FGP are fragmentary. By being carried in water, fossil material often comes into contact with other large clasts. This contact results in the breakage of colliding fossils (Voorhies, 1969), whereas prolonged contact with other clasts rounds the fossil fragments. Much like the previously described pebbles, a number of fossil fragments (uncatalogued and unidentifiable) are relatively smooth and rounded at each end (Fig. 6). If these fragments were simply broken by collision, the edges would appear sharp and jagged. This is not the case, however, and the degree of rounding is directly correlated to the time in suspension and important evidence in the interpretation of the fluvial environment.

If the pebbles and fossils were transported via eolian means the probability of ventifact formation and pock-marking is increased. In this study, none of the gravel or fossils recovered from the FGP demonstrates any of these distinct eolian features; therefore, reducing the likelihood of an eolian environment. The combined observations of cross-bedding, pebble alignment, fossil breakage, and rounding of clasts and fossil fragments give credence to the interpretation of a fluvial depositional setting for the FGP.

The previously detailed evidence suggests that the fluvial environment at the FGP is most closely related to that of a pebbly-braided type stream environment. A modern analog to this interpretation would be the Platte River in Nebraska. A major variance; however, between the fluvial system at the FGP and that of the Platte River is that the carrying capacity and velocity of the channel at the FGP was far greater than the current Platte River system.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linneus, 1758

Order CARNIVORA Bowditch, 1821

Family CANIDAE Fischer, 1817

Osteoborus sp. Stirton and Vanderhoof, 1933

Specimen – VP-13344, posterior end of left dentary with m2.

Description – Portions of the ascending ramus and masseteric fossa are present, as well as nearly the entire mandibular condyle (Fig. 7). The m2 is highly worn and demonstrates a large metaconid (Fig. 8). The occlusal length of the m2 is 1.25 cm and the width is 0.79 cm. Crown height is 0.49 cm. There is no evidence of predation or scavenging.

Remarks – Recognition of VP-13344, first as a canid, comes from the retention of the m2 and the alveolus of the m3. The maintenance of the m3, due to an emphasis on molar crushing in canids, is lost in hyaenids (Werdelin, 1989). The large metaconid of the m2 is a trait indicative of the Borophaginae (Munthe, 1998).

Eucyon davisi ? Tedford and Qui, 1996

Specimen – VP-13316, vertebra (axis).

Description –The axis is small, measuring only 3.3 cm in length and 1.8 cm at the widest portion (anterior condyle). The height of the anterior condyle is 2.4 cm. Although the axis is small, the centrum itself is proportionately large. The anterior portion of the dorsal spinous process is preserved and very well defined, projecting anteriorly, but not extending beyond the prezygopophyses or the odontoid process. The posterior portion of the spinous process is broken.

Remarks – VP-13316 is the only representative postcranial material for the family. The small size of the axis suggests a small individual; a trait indicative of late Miocene canids (Miller and Carranza-Castañeda, 1998). The proportionately larger size of the centrum is indicative of *Canis*, whereas in *Osteoborus* the centrum is smaller in comparison. The anterior projection of the dorsal spinous process eliminates the likelihood of being from the genus *Osteoborus*, which demonstrates a posteriorly projecting spinous process (Harrison, 1983). Because the posterior portion of the spinous process is broken determining orientation and degree of posterior projection is impossible. In profile, VP-13316 most closely resembles an axis described by Harrison (1983) from the Edson Quarry, Sherman County, Kansas (F: AM-49456).

Similarities in measurements also support the assignment of VP-13316 to *E. davisi*. From Harrison (1983) parameter comparisons of the known *E. davisi* to specimen VP-13316 are as follows: width at the anterior condyle; 2.1 cm compared to 1.8 cm, height; 2.5 compared to 2.4 cm. When the width at the anterior condyle of VP-13316 is compared to *Osteoborus cyonoides* (F: AM-104718, Edson Quarry), the variability is ever greater being that of 1.8 cm to 3.5 cm (Harrison, 1983).

Order PROBOSCIDEA Illiger, 1811

Family GOMPHOTHERIIDAE Hay, 1922

Genus Indeterminate

Specimen – VP-13932, partial tusk.

Description – The partial tusk is dorso-ventrally flattened, with a lateral diameter of 4.5 cm (Fig. 9A). The band of enamel that is typical of the Gompheriidae is absent from the specimen. The distal most portion of the tusk is damaged and highly brittle. No further description of the specimen is possible.

Remarks – The dorso-ventrally flattened shape of the partial tusk is characteristic of the shovel-tusked gomphotheres, as in mammoths and mastodons the tusk is uniformly cylindrical. The reason for the lack of enamel band is unclear, as it may have been lost to wear through use or postmortem weathering. Generic assignment of VP-13932 is prevented due to the fragmentary nature of the specimen and lack of diagnostic characters.

Family Indeterminate

Specimens – VP-13313 and VP-13566 partial tusks; VP-13933, partial tooth.

Descriptions – Each partial tusk displays a high degree of physical weathering, and no signs of predation or scavenging are apparent. The diameter of VP-13313 is approximately 8.7 cm (Fig. 9B), whereas that of VP-13566 is 3.9 cm. Both specimens lack a band of enamel and are uniformly cylindrical in shape.

The partial tooth is poorly preserved; being broken along many surfaces and position in the jaw proves impossible to determine. What remains of the tooth would be classified as having a bunodont dentition.

Remarks – Beyond assigning these three specimens to the order Proboscidea, no further identification was possible as no diagnostic material is preserved. Each of the partial tusks is so badly damaged that attempts to recover the individuals' ages through core sampling would be problematic. The bunodont dentition of the partial tooth is distinct from mammoths; however, it is unclear if the tooth is from a mastodon or gomphothere (e.g. *Amebelodon*).

Order PERISSODACTYLA Owen, 1848

Family EQUIDAE Gray, 1821

Tribe EQUINI Gray, 1821

Subtribe PROTOHIPPINI Gidley, 1907

Calippus sp. Matthew and Stirton, 1930

Specimens – VP-13296, metacarpal III; VP-13297, partial metacarpal III.

Descriptions –VP-13296 is a well-preserved full metacarpal III, measuring 17.3 cm in length. The articular facets for the second and fourth metacarpals are well defined and a moderate posterior gully is also apparent in posterior view (Fig. 10A). The proximal head is preserved, maintaining the articular facets for the hamatum and magnum (Fig. 10B). Ligament scars are present on the medial sides of the distal portion of the specimen.

The distal surface of specimen VP-13297 (partial metacarpal III) is lost due to breakage; however, an estimate suggests that the specimen would have been approximately 17.1 cm in length. The proximal articular facets for hamatum and magnum are preserved. The facets for the second and fourth metacarpals are well defined and best viewed from the posterior side of the metacarpal. The posterior gully is moderate in depth.

Remarks – In contrast to other equid metacarpals from the FGP, the length of specimens VP-13296 and VP-13297 was comparably shorter. According to a previous study (Darnell, 2000), metacarpal length, in conjunction with physical description, can be used to determine genus. The measured and estimated sizes of VP-13296 and VP-13297 respectively and arrangement of the articulating facets for the hamatum and magnum are comparable to VP-8214 (*Calippus*), from the Minium Quarry, Graham County, Kansas. Although, one may suggest that specimens VP-13296 and VP-13297 are from the same individual, this is not the case because VP-13297 is slightly smaller than VP-13296 and that both specimens come from the right side.

Calippus ? sp. Matthew and Stirton, 1930

Specimens – VP-17362, partial Rp2; VP-13565, metacarpal III.

Descriptions – Figure 11 illustrates the generalized morphology of equid teeth. The ectoflexid of VP-17362 appears to be worn completely, whereas, the linguaflexid demonstrates a shallow V-shape. The metaconid and metastylid are near equal in size and closely spaced. Remnants of the protosylid are evident, but nearly lost to wear. The tooth demonstrates a high degree of physical and chemical wear and further description of characters is impossible.

The proximal surfaces for the hamatum and magnum are completely worn on specimen VP-13565 (metacarpal III). The posterior gully and ligament scarring on the medial sides of the distal portion of the specimen are preserved and moderately defined. VP-13565 is also small measuring 16.9 cm long and approximately 2.0 cm wide at the central part of the shaft.

Remarks – Specimen VP-17362 is similar in character to VP-7868 from the Minium Quarry, as described by Darnell (2000). The V-shaped linguaflexid, proportionately equal metaconid and metastylid, and evidence of the protostylid serve as justification for the assignment of VP-17362 to *Calippus*.

Identification of VP-13565 (metacarpal III) is difficult, due to the weathering of the hamatum and magnum facets. VP-13565 is the smallest identifiable metacarpal III from the FGP; being even smaller than VP-13296. As has been previously described, small metacarpal size can be indicative of *Calippus* sp, although generic assignment here is tentative due to the lack of comparable proximal articular facets. The size of VP-13565 may be a reflection of ontogentic state, rather than genus.

Protohippus supremus ? Leidy, 1869

Specimen – VP-17296, Rp3.

Description –Occlusal measurements of VP-17296 can be found in Table 2. The tooth has a moderate to high degree of hypsodonty (Fig. 12A) and a shallow V-shaped linguaflexid. The ectoflexid is deep and extends into the isthmus. The anterior fossetula is well defined, singularly lobed, and is directed posteriorly, whereas the posterior lobe of the posterior fossetula is considerably smaller than the anterior portion. The protoconid is well defined and the hypoconid is bulbous, demonstrating stylar folding toward the labial portion (Fig. 12C). The tooth displays a low to moderate degree of wear.

Remarks – Although not identical, VP-17296 shares a similar enamel pattern with VP-526, from an unknown locality in Kansas. The well-defined protoconid and bulbous hypoconid confirm the specimen to *Protohippus* and the similarities with VP-526 suggest that VP-17296 is *P. supremus*. Based on the expression of characters (i.e. protoconid and hypoconid) and wear, VP-17296 would best be described as between Hulbert's (1984) wear-stage 4 and 5 (Table 1, Fig. 4).

Protohippus sp. Leidy, 1869

Specimens – VP-13563, Lp2; VP-13292, partial right maxillary, with P3-M3; VP-13293, Rm3; VP-13345, partial distal end of left humerus; VP-17297, distal epiphysis of metapodial.

Descriptions – The ectoflexid of the Lp2 is very shallow, not even extending to the isthmus. The linguaflexid is also shallow, although shape could not be determined due to wear and breakage. A metasylid is present, though size comparison to the metaconid could not be determined because the metaconid is broken. The hypoconid is oval, and the entoconid is large and somewhat rounded. Labial borders of the protoconid and hypoconid are rounded. The posterior fossetula is bilobed and irregularly shaped; the anterior portion is larger, whereas the posterior is proportionately smaller.

The infraorbital foramen of specimen VP-13292 is still fully intact, and although only partially present, the facial crest is also evident (Fig. 13). The P3-M3 series is still intact, demonstrating a moderate degree of hypsodonty. Each protocone is oval to circular and connected to the protocomule. The metastyle is sharply defined on each tooth. Both the prefossette and postfossette are worn to an L and J respectively in the P3, P4, and M2, whereas in the M3 the prefossette and postfossette have a U shape. Although evident on the entire series, the parastyle is most prominent on P3 and P4. The following is the measurement of tooth exposure above the jaw-line, all dimensions are in centimeters. P3, 1.92; P4, 1.5; M1, 1.6; M2, 1.2; M3, 1.32. Occlusal lengths and widths are found in Table 2. The teeth possess a high degree of wear; however, it is the M1 that demonstrates the highest degree, as none of the previously mentioned characters are observable (Fig. 14). No evidence of predation or scavenging is apparent.

The ectoflexid in the Rm3 (VP-13293) is moderate, extending to, but not through, the isthmus. The linguaflexid is shallow and V-shaped. A posteriorly elongated anterior fossetula is evident, although the posterior fossetula is broken from the tooth due to physical wear. The metaconid is lobate, whereas the metastylid is slightly pointed posteriorly. The degree of hypsodonty is moderate to high.

The proximal head and shaft of VP-13345 is broken, leaving only the distal end of the humerus intact. Distal grooves on the remaining articular surface are rounded and not sharply defined. VP-13345 displays a shallow coronoid fossa and intercondyloid groove.

The distal epiphysis of a metapodial is all that remains of specimen VP-17297. The attachments sites for the collateral ligaments on the lateral surfaces are small. The sagittal ridge is well defined and extends from the posterior portion to the anterior portion of the bone, an angle greater than 250°.

Remarks – Identification of specimen VP-13563 (Lp2) was based on the similarities shared with other *Protohippus* teeth (VP-9236 and VP-8679) previously described by Darnell (2000) from the Minium Quarry. Each of these specimens possesses similar shapes and orientations key characters, such as the hypo- and entoconids. Application of Hulbert's (1984) methods to determine wear-stage and corresponding age was not possible due to the fragmentary nature of the specimen.

VP-13292 represents the most complete cranial specimen recovered from the FGP. The well-defined metastyle and prominent parastyle on the P3 and P4 are distinguishing features of *Protohippus* (Hulbert, 1988). Although the protocones are connected to the protocomules in this specimen, in early stages of wear the protocones would have been isolated (MacFadden, 1998). Based on the high degree of wear of the M1, specimen VP-13292 would best be classified within Hulbert's (1984) wear-stage 9 (Table 1, Fig. 4). This tooth wear assessment also indicates that this specimen is the oldest equid recovered to date from the FGP. Specific assignment of the specimen was prevented due to the high wear of the teeth.

The degree of hypsodonty of specimen VP-13293 (Rm3) is comparable to that of specimens VP-9236 and VP-8679 (Minium Quarry). Generic assignment of VP-13293 to *Protohippus* is based on the comparable stylar folding to VP-7829 from the Minium Quarry.

The characters of the partial humerus (VP-13345) resemble *Equus*. The expression of the distal grooves of VP-13345 is in contrast to *Neohipparion* which are rounded, but more sharply defined (Gidley, 1903); marking the transition from a tapiroid to horse-like form (Cope, 1887). The shallow coronoid fossa and intercondyloid groove of *Protohippus* are sharper and better defined in *Neohipparion* (Gidley, 1903). VP-13345 compares favorably to VP-8380 as described by Darnell (2000) from the Minium Quarry.

Based on the fragmentary nature of VP-17297 (distal epiphysis of metapodial) assignment to *Protohippus* is tentative. What remains of the specimen (such as the expression of the sagittal ridge and ligament attachment facets); however, best compares to VP-7846 from the Minium Quarry, as described by Darnell (2000).

Tribe HIPPARIONINI Quinn, 1955

Neohipparion trampasense ? Edwards, 1982

Specimen – VP-13958, partial left dentary, with p4.

Description – Portions of the p2 and p3 are present in specimen VP-13958, but are broken below the jaw-line, the p4; however, is nearly complete. The p4 extends 1.11 cm above the jaw-line; occlusal measurements listed in Table 2. The ectoflexid is moderate, extending up to, but not through, the isthmus. Although damaged in weathering, the linguaflexid is shallow and U-shaped. The metaconid and metasylid are elongated anterio-posteriorly. The anterior-most portion of the anterior fossetula is lost to physical weathering, though the posterior portion is preserved and is lobate (Fig. 15). The posterior fossetula is well defined demonstrating two lobes. The p4 displays a moderate degree of wear through use.

Remarks – Only the p4 allows for specific assignment of specimen VP-13958. The broken nature of the p2 and p3 is attributed to fluvial transport, although it is unclear as to why the p4 would remain intact. The stylar foldings of the p4 of VP-13958 are analogous to those of *N. trampasense* (VP-5488) from the Bemis Ranch, Ellis County, Kansas. Wear patterns correspond to Hulbert's (1984) wear-class 5 (Table 1, Fig. 4).

Genus *Neohipparion* sp. Gidley, 1903

Specimens – VP-17365, Rm; VP-17368, lower molar (m); VP-17378, partial metatarsal III; VP-13924, metatarsal III.

Descriptions – The ectoflexid of the Rm (VP-17365) is shallow, and the linguaflexid is a shallow U-shape (Fig. 12B); occlusal measurements are presented in Table 2. Both the metaconid and metasylid are similar in size, but portions of both are broken (Fig. 12D). The anterior fossetula is slightly shortened anteriorly, but elongated posteriorly. The pli hypoconid is single lobed and extends posteriorly. The tooth displays a moderate degree of wear.

In VP-17368 (m), the ectoflexid is broken, but the linguaflexid is well preserved and is a shallow U. The metaconid is elongated, whereas the metastylid is shortened in comparison. The anterior fossetula is shortened anteriorly, but elongated posteriorly. The pli hypoconid is singularly lobed, extending to the anterior. The buccal portion of the tooth is lost to weathering. Although fragmentary, the tooth displays a moderate degree of wear through use.

VP-17378 is a partial metatarsal III. The distal end of the specimen is broken, leaving only the shaft and articular facet for the ectocuneiform. The articular facet for the second metatarsal is prominent in posterior view, whereas the articular facet for the fourth metatarsal becomes more apparent in proximal view. A gully on the posterior surface is shallow and flat. Before the distal break, the metatarsal appears to begin to bend posteriorly, suggesting an anterior bulge. An estimate of the complete length of the metatarsal is 20.9 cm.

Specimen VP-13924 is a well preserved, complete metatarsal III (Fig. 16A), measuring 19.9 cm in length. The ectocuneiform facet is preserved. The articular facet for the second metatarsal is apparent in posterior view and fourth metatarsal facet in proximal view (Fig. 16B). The posterior gully is flat. Scarring for the interosseous ligaments extend the posterior side, ending in shallow depressions. The sagittal ridge on the distal articular surface is oriented in a V. The distal end is bent posteriorly, resulting in an anterior bulge.

Remarks – The expression of the ectoflexid and linguaflexid in *Neohipparion* is variable among specimens (MacDonald, 1956). Identification of the Rm (VP-17365) was based on the comparison with VP-14856 from Ellis County, Kansas. Although there are similarities, the enamel foldings are distinct enough from other examples of

Neohipparion to prevent species identification. The wear due to usage corresponds to Hulbert's (1984) wear-class 5 (Table 1, Fig. 4).

Assignment of VP-17368 (m) was based on comparison to VP-14856 from Ellis County. The enamel pattern of between the two specimens was similar and allow for specimen VP-17368 to be identified as *Neohipparion* with a degree of confidence. As previously mentioned, the tooth is fragmentary; however, the remaining portion corresponds to wear-class 5 (Table 1, Fig. 4).

A comparison to specimen VP-8953, from the Minium Quarry, was utilized in the generic assessment of specimens VP-17378 and VP-13924 (metatarsal IIIs). The distal bending and anterior bulge of each metatarsal is a critical character shared between these three specimens. Although similar, the sagittal ridge and the adjacent valleys are less pronounced in VP-13924 than described by Darnell (2000); these features are lost in specimen VP-17378. Based on the estimated total length of the specimen, VP-17378 represents a larger individual than VP-13924. The similarities in facet orientation and anterior bulging of the distal end of the metatarsal III allow VP-17378 and VP-13924 to be confidently assigned to the genus *Neohipparion*.

Genus *Neohipparion* ? sp. Gidley, 1903

Specimens – VP-13417, distal end of metapodial III; VP-13564, 1st phalanx, 3rd digit.

Descriptions – The distal articular surface of VP-13417 is well preserved, whereas the shaft is completely broken. The sagittal ridge is V-shaped with moderately deepened adjacent valleys. The distal end appears slightly bent; as only a small portion of the shaft is preserved. The posterior gully and scarring for the interosseous ligaments cannot be determined.

VP-13564 is a well-preserved 1st phalanx from the 3rd digit. The specimen is long (6.9 cm) and slender (2.3 cm at the central portion of the phalanx), and on the proximal surface a groove for the sagittal ridge of a metapodial runs antero-posteriorly and is moderately deep. On the proximal head, the posterior medial sides appear to bulge out, resulting in a horseshoe-like orientation.

Remarks – Generic assignment of specimen VP-13417 is tentative due to the fragmentary nature of the specimen. Though the bent nature of the distal end is apparent, it is not as prominent as described in VP-13924 from the FGP. VP-13417 shares similar orientations of the sagittal ridge and adjacent valleys with VP-8854 from the Minium Quarry.

The depth of the groove for the sagittal ridge of VP-13564 is comparable to that of VP-7965 from the Minium Quarry. Assignment of VP-13564 to *Neohipparion* is tentative due to the fact that the medial sides of the proximal facet head of VP-7965 are sharply defined, whereas those of VP-13564 again bulge out. This sharply defined edge is consistent among a number of *Neohipparion* specimens from the Minium Quarry.

Pseudhipparion sp. Ameghino, 1904

Specimen – VP-17369, partial M2 ?

Description – The partial tooth demonstrates a high degree of physical wear; however, the metastyle remains intact and is prominent. A partial prefossette and full postfossette are preserved. The postfossette is a moderate and shallow U. Measurements of the occlusal length and width were not taken due to the fact that VP-17369 is poorly preserved. The degree of hypsodonty is high.

Remarks – Tentative identification of this specimen was established through comparative means. Although difficult to ascertain, VP-17369 shares similar stylar foldings of the (partial) pre- and postfossette with VP-4320 from the Borchers' Gravel Pit in Meade County, Kansas. Due to the fact that there is variation with the stylar folding, species identification could not be determined.

Tribe Indeterminate

Genus Indeterminate

Specimens – VP-13416, anterior portion of partial right dentary; VP-17387, partial cervical vertebra (axis); VP-13955, partial innominate; VP-17377 and VP-17383, partial distal end of tibiae; VP-13294, distal portion of partial tibia; VP-13295, right calcaneum.

Descriptions – VP-13416 is the anterior portion of a right dentary. A full alveolus for one tooth remains intact; whereas a second is partially preserved. Two foramina are present on the labial portion of the dentary, although they are not the result of predation or scavenging. No further description is possible.

VP-17387 is a partial cervical vertebra (axis) (Fig. 17), measuring 11.95 cm in length and 6.6 cm in width at the widest anterior portion. The odontoid process is preserved and well defined. The neural spine and transverse processes are completely broken. The anterior ventral crest that surrounds the odontoid process is separated by a deep depression. The posterior portion of the centrum is extremely concave, allowing for the articulation of the third cervical vertebra. Toward the anterior portion of the specimen, there are two grooves leading to foramina for ligament attachment.

VP-13955 is a partial innominate with a well-preserved acetabulum, which has an oval shape with the greatest diameter being 4.1 cm. A small portion of the neck of the ilium remains, although the lateral ischiatic notch is lost.

VP-17377, VP-17383, and VP-13294 (partial tibiae) display an intermedial ridge that is strongly angled between the lateral and medial malleolus. The proximal end and shaft in each of the specimens is broken and the medial ligament facets of VP-17383 are also lost.

Specimen VP-13295 (calcaneum) demonstrates a squared proximal head. The anteromedial sustentacular facet and cuboid facet are preserved, with the cuboid facet forming a slight L shape. A portion of the principal sustentacular facet is broken. The total length of the calcaneum is 8.9 cm and the depth is 3.8 cm.

Remarks – Assignment of VP-13416 (anterior end of the right dentary) to genus is prevented due to poor preservation and lack of diagnostic features. The size and depth of the alveoli suggest a high degree of hyposdonty indicative of equids and greater than that of any of the camels on record from the FGP. Family assignment is also tentative.

The proportions of VP-17387, partial cervical vertebra (axis), suggest a medium-sized animal. The incomplete ventral crest is indicative of the Equidae, as in camels (e.g. VP-8700, *Procamelus*, Minium Quarry) this crest is complete. The posterior concavity of the centrum is in contrast to camels which is flattened (VP-8700). Although roughly 70% of the size; VP-17387 shares the previously mentioned characteristics with

“Old Prince”, *Equus caballus* (NH-715). The poor preservation of VP-17387 prevents generic assignment.

Identification of the innominate (VP-13955) was based on comparative means. This particular specimen shared a similarly shaped and sized acetabulum and foramen as VP-446 from an unknown locality in Kansas. The small size of the innominate suggests a small, perhaps young, individual. As the majority of the innominate is lost, generic assignment of VP-13955 is impossible.

Assignment of the partial tibiae (VP-17377, VP-17383, and VP-13294) to the Equidae is based on comparative osteology. Perissodactyls are the only mammals in which the distal intermedial ridge is angled across the distal surface, rather than straight. In equids, the angle of the intermedial ridge is exaggerated more so than other fauna of the order (e.g. rhinoceros). In each of these specimens, this trait is clearly seen.

Although previous studies have utilized partial tibiae as a means of specimen assignment (e.g., Darnell, 2000), the comparative processes are not suitable in this case. There is not enough of the shaft in specimens VP-17377 and VP-13294 to observe ligament scarring and again in the instance of VP-17383; the medial ligament facets are broken.

The squared head of specimen VP-13295 is typical of the Equidae. Proportionately, the size of this calcaneum is similar to medium-sized horses such as *Protohippus*. Without comparison of the articular facets, assignment of this specimen remains undetermined, as the size of the specimen may reflect growth stage, as opposed to taxon similarity.

Order ARTIODACTYLA Owen, 1848

Family CERVIDAE Gray, 1821

Genus Indeterminate

Specimen – VP-13306, partial cannon bone.

Description – The condition of VP-13306 is poor. The outer surface is almost completely worn and the distal end is broken; however, an estimate of the total length can be established at 17.3 cm. The proximal head is so worn that attempts to describe the facet orientation are impossible. On the proximal end of the bone there is a large hole, typically uncharacteristic of the cannon bone.

Remarks – The metapodial appears superficially bovid-like, with the distal end illustrating the beginning of the distal split. Distinction from the Camelidae and Antilocapridae is found in the beginnings of the groove on the distal anterior surface of the metapodial, between what would be the distal epiphyses. This feature is absent in both camels and antilocaprids (Janis and Manning, 1998). Separation from the Bovidae, such as *Bison*, is in the lack of foramina for ligament attachment. In *Bison* there are four additional foramina; two on the anterior and two on the posterior side. These are all absent from specimen VP-13306. Additionally, VP-13306 is notably less robust than that of *Bison*, when metapodials of similar lengths are compared. The length to width (of the medial shaft) ratio of a similarly sized *Bison* metapodial (VP-5371) from Cowley County, Kansas, Feaster local fauna, is 4.8, whereas that of specimen VP-13306 is estimated to be nearly 9.2.

The size of VP-13306 is also similar to that of another cervid (VP-4199), from the Beckerdite Site in Clark County, Kansas. The length of VP-4199 (16.2 cm) is similar to that of VP-13306 (17.3 cm), especially when compared to that of an antilocaprid (*Antilocapra* [14125-11 from the comparative collection of the FHSM]), which measures 21.5 cm. It is for these reasons that specimen VP-13306 is assigned to the Cervidae.

This partial metapodial is an instance in which there may be evidence of predation or scavenging. On the proximal end of this specimen the large hole is not proportioned or positioned correctly for the site of ligament attachment. Therefore, it is interpreted to be a puncture mark due to carnivorous activity, although there is the distinct possibility that the hole is simply due to weathering.

Family ANTILOCAPRIDAE Owen, 1841

Genus Indeterminate

Specimens – VP-13931 and VP-17364 partial teeth; VP-13954, partial right dentary with p3-m1.

Descriptions –VP-13931 is fragmentary, as a portion of the crown and entire root are lost due to breakage. The degree of wear on the occlusal surface of the specimen is minimal and degree of hypsodonty is high. The tooth is simple and does not demonstrate complex infoldings of enamel or stylid development.

Specimen VP-17364 is a second partial tooth. Both the root and portions of the crown are lost. Degree of hypsodonty is high, though the occlusal surface displays a high degree of wear. There is a complete lack of accessory features.

The p3-m1 series of VP-13954 (Fig. 18) demonstrates a high degree of hypsodonty, high degree of occlusal wear, and a lack of accessory feautres. Measurements of the crown height above the jaw-line are as follows; p3, 0.87 cm; p4, 0.95; and m1, 1.1 cm. Occlusal lengths; p3, 0.8 cm; p4, 1.05cm; and m1, 1.32 cm. Occlusal widths (taken at the posterior end of each tooth); p3, 0.48 cm; p4, 1.15 cm; and m1, 1.21 cm.

Remarks – Justification in the assignment of specimens VP-13931, VP-17364, and VP-13954 to the Antilocapridae is as follows. Whereas cervids demonstrates a brachydont cheek tooth, the antilocaprids, by comparison, have a hypsodont dentition (Scott and Janis, 1987). Further evidence supporting the assignments of these specimens is in the lack of accessory features on the teeth, such as the ento- and ectostylids (Janis and Manning, 1998). Location in the jaw is difficult to determine due to the fragmentary nature of specimens VP-13931 and VP17364.

Although dentition plays an integral role in the identification of horses and camels, antilocaprid genera are distinguished primarily by their horn core morphology (Kelly, 1998; Kitts and Black, 1959); an osteological trait not available. Nevertheless, the recognition of the antilocaprid specimens is significant in that the paleoecological picture at the FGP becomes more complete.

Family CAMELIDAE Gray, 1821

Tribe PROTOLABIDINI Webb, 1965

Protolabis sp. Cope, 1876

Specimens – VP-13346, partial right dentary with p3 and p4; VP-13927 and VP-17366; dP4s.

Descriptions – Figure 19 illustrates the generalized morphology of camel teeth. The p3 and p4 of VP-13346 demonstrate brachydont dentition (Fig. 20). The p3 extends 0.87 cm above the jaw-line; whereas the p4 extends 1.95 cm. Occlusal measurements may be found in Table 3. The p3 is two rooted and demonstrates a well-defined posterior crescent that interrupts the posterior fossettid. The anterior crest is sub-rounded and the anterointernal groove is deep. The p4 possesses three roots and a prominent metastylid. The buccal anteroconid, protoconid, and hypoconid are sharply V-shaped, whereas the anterior, median, and posterior fossettids open lingually and also demonstrate a V-shape, although noticeably more shallow (Fig. 21). Llama buttressing is weak. Both teeth demonstrate a moderately low degree of wear and there is a degree of overlap between the posterior portion of the p3 and anterior portion of the p4.

VP-13927 is a partial molariform dP4, lacking portions of roots, and containing poorly-developed lama buttresses (Fig. 22A). Occlusal measurements can be found in Table 3. The anterior fossette is definitively more U-shaped than the posterior fossette, which exhibits more of a V-shape. Whereas the protocone is V-shaped, the hypocone is more of a U. The parastyle, mesostyle, and to some extent, metastyle are well defined

(Fig. 22B). The tooth demonstrates a brachydont dentition and ribbing of the external surfaces is also evident.

Specimen VP-17366 is a second dP4 indicating little wear. The tooth is nearly complete, possessing both crown and root and is fully molariform with an anterior basal cingulum, demonstrating a brachydont dentition. The protocone is markedly V-shaped, whereas, the hypocone is that of an U. Both the anterior and posterior fossae are a shallow V. A portion of the hypocone is removed, due to weathering. Llama buttresses are weakly developed. The parastyle is well defined, although the development of the meso- and metastyles could not be determined due to the fact that the enamel surface is lost.

Remarks – The brachydont dentition of specimen VP-13346 is typical of *Protolabis*. Whereas, the anterior crest is less rounded than described by Loring and Wood (1969), nearly all of the other defining characters including the anterointernal groove appear as initially described. Stylar folds are also similar to those present in other specimens of the genus. These characters are similar to those described in *Protolabis* (U. Cal. 32309) by Loring and Wood (1969).

Specimens VP-13927 and VP-17366 (dP4s) share a similar degree of brachydonty and development of llama buttressing. Although the defining characteristics of *Protolabis* are more prominent in VP-17366, both specimens compare favorably to that of U. Cal. 32309 (Loring and Wood, 1969). The less defined traits of VP-13927 are attributed to wear, both through use and postmortem weathering.

Protolabis ? sp. Cope, 1876

Specimen – VP-17359, dP4.

Description – VP-17359 is a partial dP4 (lacking roots), demonstrating a high degree of wear (Table 4). Llama buttresses are poorly developed. Ribbing is also apparent, but is weak. Style development although evident, is reduced.

Remarks – Assignment of VP-17359 is tentative due to the poor preservation of the specimen. The ribbing and expression of styles of VP-17359 is weaker than in specimens VP-13927 and VP-17366; however, this may be the result of postmortem wear through fluvial transport. Based on the evident characters; however, VP-17359 best compares with specimen U. Cal. 32309 (Loring and Wood, 1969).

Tribe LAMINI Webb, 1965

Genus *Hemiauchenia* sp. Gervais and Ameghino, 1880

Specimens –VP-17363, Rm1; VP-13414, distal end and partial shaft of humerus; VP-13930, partial proximal end of radius-ulna; VP-13398, partial distal end of radius; VP-13298, VP-13400, and VP-13401, partial proximal end of left metacarpals; VP-13317, right metatarsal; VP-13303 and VP-13403, partial proximal end of right metatarsals; VP-13402, partial right metatarsal; VP-13404, VP-13568, VP-17376, and VP-17379, partial proximal ends and shaft of metatarsals; VP-13405 and VP-17375, partial metapodials; VP-13567, partial distal end of metapodial; VP-17393, partial shaft of metapodial; VP-17382, distal epiphysis of metapodial; VP-13301, 1st phalanx; VP-13928, partial 1st phalanx.

Descriptions – VP-17363, Rm1, displays a high degree of wear, giving the false appearance of a less hypsodont tooth (Fig. 23A). On the labial and lingual sides the crown only extends above the root-line an average of 0.8 cm and on the anterior and posterior portions of the tooth the enamel is worn evenly with the root. The metastylid is prominent. The shape of the anterior fossettid cannot be determined due to wear; however, the posterior fossettid is a shallow U. Llama buttresses are also not apparent (Fig. 23B).

VP-13414 is the distal end and partial shaft of a humerus. The distal head is not robust, partial shaft appears slender, and the medial and lateral epicondyles are not flattened. The breadth of the distal ends measures 5.4 cm and the depth of the distal end is 5.6 cm. There is a broad, deep groove of the trochlea and on the lateral side there is a well-developed external condyle.

Specimen VP-13930 is a partial proximal end of a radius/ulna. The olecranon and a portion of the olecranon process are broken. Coronoid process, semilunar notch, and radial notch are well preserved. The remaining portion of the shaft appears uniform in width (an average of 3.7 cm) and thickness.

The lateral surface of VP-13398 (partial distal end of the radius) that articulates with the cuneiform is persevered and is confined posteriorly by a rounded crest. Only a small portion of the medial surface remains. Each of the surfaces is separated by a moderate crest. The lunar surface and shaft are broken.

Specimens VP-13298, VP-13400, and VP-13401 are the partial proximal ends of left metacarpals. In VP-13400, the magnum, trapezoid, and unciform facets are present.

The magnum and unciform facets are more triangular than trapezoidal or square. The trapezoid process is directed anteroposteriorly rather than medio-laterally. It should be noted that VP-13298 varies from VP-13400 and VP-13401 in that the proximal surface is wider, although the orientation of the proximal facets remains the same. A partial unciform facet is all that remains as the shaft and remaining facets are completely lost in VP-13401.

Length and distal width measurements of VP-13317, a right metatarsal, are listed in Table 4. The distal epiphyses are lost, as they were not fused to the metatarsal before preservation. The shaft of the metatarsal is long and slender and the posterior side demonstrates a deep concavity. The proximal articular surfaces (e.g. cuboid facet) are preserved and are triangular.

VP-13303 is the proximal end of a right metatarsal. Enough of the specimen is preserved to show a portion of the large, slender shaft and the concave posterior surface. The entocuneiform facet is preserved and begins to merge with the plantar process. The cuboid facet is triangular and extends medio-laterally, whereas the ectomesocuneiform facet is lobate. Preserved on the posterior surface are two fossae for additional ligament attachment.

In VP-13403, another partial right metatarsal, the plantar process is lost. The entocuneiform facet is present and begins to merge with the base of what would be the plantar process. Both the ectomesocuneiform and cuboid facets are broken medio-laterally. The entire shaft and distal end are broken.

Only the metatarsal shaft and small portion of the proximal articular surface are present in VP-13402. The entocuneiform facet is preserved and begins to merge with the ridge of the plantar process. The specimen exhibits a concave posterior surface, and long slender shaft.

VP-13404 is a poorly-preserved partial end and shaft of a metatarsal. The shaft is split, preserving only a fraction of the proximal surface facets and the plantar process is broken. Specimen shows a fair degree of fluvial deformation.

Although the shape of the facets in the left metatarsal (VP-13568) can be identified, the surfaces of each are nearly worn off. The ectomesocuneiform facet is triangular and directed medio-laterally, whereas the cuboid facet is more robust than the ectomesocuneiform and is directed more anteroposteriorly. The plantar process is broken. The partial shaft is slender and demonstrates a concave posterior surface. Ligament fossae are also preserved on the posterior surface.

Specimens VP-17376 and VP-17379 (partial metatarsals) share a similar triangular shape and medio-lateral orientation of the ectomesocuneiform facet. The plantar process and entocuneiform facet on both specimens are lost, although the weathered surface of the cuboid facet on VP-17376 is robust and directed more anteroposteriorly. Both bones have a slender shaft and a concave surface on the posterior surfaces.

The preservation of VP-13405 and VP-17375 is similar. All that remains is the metapodial shaft, as the proximal articular surfaces are nearly completely lost in both specimens. The remaining shafts demonstrate a concave posterior surface and slender nature.

VP-13567 (partial metapodial) displays only one splayed epiphysis of the distal end and appears to be split in half, straight up the shaft. The sagittal ridge and adjacent valleys on the distal epiphysis are well defined. The attachment for the collateral ligament is moderately well defined. The shaft walls are not robust and average 0.7 cm thick.

The preservation state of VP-17393 (partial shaft of metapodial) is poor. On the posterior side of the bone there is a deep concavity that runs the full length of the slender partial metapodial. The proximal and distals ends of this metapodial are lost.

VP-17382 is a single distal epiphysis of a metapodial. The attachments for the collateral ligaments are well defined. Sagittal ridge is prominent as are the adjacent valleys. Not further description is possible.

VP-13301 is the only full *Hemiauchenia* phalanx recovered from the FGP. The phalanx is slender, measuring 9.7 cm in length, whereas the widths at the proximal and distal ends are 2.6 cm and 1.9 cm respectively. A carinal groove is apparent (Fig. 24A). On the proximal posterior side, there is a distinct W-shaped suspensory ligament scar (Fig. 24B).

VP-13928 is a partial phalanx in which the proximal end and portions of the shaft are lost. The remaining distal shaft is slender and the distal articular surface remains intact and is not robust. An estimate of the total length of the phalanx is 9.7 cm.

Remarks – Generic assignment of VP-17363 (Rm1) was based on comparison with specimen VP-8651 from the Minium Quarry. Both teeth share similar orientations of the posterior fossetid and wear patters. A comparison of the metastylids is impossible due to the fact that it is lost in VP-8651. The lack of llama buttresses in VP-17363 is attributed to the anterior portion of the m1 wearing against the posterior wall of the p4 (Breyer, 1977). The characters of VP-17363 are suggestive of *Hemiauchenia vera*; however, specific assessment is prevented due to the lack of direct metastylid comparison.

The broad, deep groove of the trochlea (VP-13414) is characteristic of camels, as in equids this feature is less defined. The lack of robust distal end and slender appearance of the partial shaft are characters indicative of *Hemiauchenia*, and in contrast to large camels (Harrison, 1979). The un-flattened epicondyles are characteristic of a number of species, preventing specific assessment. The ratio of the breadth of the distal end to the depth of the distal end is 0.96, well within range of species of *Hemiauchenia* (Meachen, 2005).

The remaining portions of VP-13930 (partial proximal end of a radius/ulna) allow for generic assessment of the specimen. The uniform thickness of the shaft is a trait indicative of *Hemiauchenia* and the average width of the shaft (3.7 cm) falls within those reported for *Hemiauchenia* (Meachen, 2005).

Although fragmentary, the partial radius, VP-13398, can still be generically assigned. The confinement of the lateral surface by the rounded crest and moderate size are traits specific to *Hemiauchenia* (Montellano, 1989).

The triangular shape of the magnum and unciform facets in specimens VP-13298 and VP-13400 is suggestive of *Hemiauchenia*. Assignment of VP-13401 is tentative due to the fragmentary nature of the specimen and lack of magnum and unciform facets for comparison.

The lack of fused distal epiphyses in specimen VP-13317 is indicative of a young individual. When plots of metatarsal length versus distal width and length versus ratio of length to distal width, were plotted against Breyer's (1983) data, the points were consistently among those of known *Hemiauchenia* specimens (Figs. 25 and 26). The plot of the metatarsal; however, is not within two standard deviations of the original length data (Breyer, 1983 [Fig. 27]) and may be a reflection of the individual's age.

The triangular shape of the cuboid facet, slender shaft, and orientation of the entocuneiform facet of specimen VP-13303 serve as justification in generic assignment. What is unique about the entocuneiform facet is that it begins to merge with the plantar process. In other camels such as *Alforjas* it is completely isolated. This particular orientation of the entocuneiform was also utilized in the assignments of VP-13403 and VP-13402 to the genus. The posterior fossae of VP-13303 are consistent across a number of specimens, including VP-13402 and VP-13569 and suggest a universal purpose (interpreted here as ligament attachment) as opposed to the being the result of physical weathering or predation or scavenging. In his description, Montellano (1989) noted that the bones of *Hemiauchenia* are also gracile in nature. Specimens VP-13303, VP-13403, and VP-13402 also demonstrate this defining character.

Assignment of specimen VP-13404 to *Hemiauchenia* was established through comparison of the partial facets. A notable difference between VP-13404 and other *Hemiauchenia* specimens is that the walls of the partial shaft are thicker (0.7 cm), although not as great as larger camels (e.g. *Alforjas*). Assignment to *Hemiauchenia* is tentative due to this variation.

The triangular shape and medio-lateral orientation of the ectomesocuneiform of specimens VP-13568, VP-17376, and VP-17379 (partial metatarsals) are characters previously associated with *Hemiauchenia*. The characteristic concavity of the posterior surface and slender nature of the remaining shafts are also observed in each specimen and are also indicative of *Hemiauchenia* (Montellano, 1989).

Identification of the partial metapodials (those that possess no articular facets [VP-13405, VP-17375, VP-13567, and VP-17393]) to the genus *Hemiauchenia* was based on the proportions of the shaft; as the gracile nature of the specimens is evident. Additionally, the posterior surface is deeply concave. These previously mentioned traits are again in contrast to larger camels, which typically possess more robust shafts and a lessened concavity on the posterior surface. Assignment of VP-17393 to *Hemiauchenia* is tentative, as it was exposed at the surface for an extended period of time, causing it to become brittle.

Generic assessment of VP-17382 (distal epiphysis) was based on comparative means. The development of the ligament attachment sites and sagittal ridge are parallel to those of VP-8860 from the Minium Quarry. Specific identification is prevented in this instance due to the fact that VP-8860 is first larger than VP-17382 and the lateral ligament attachment facets are deeper in VP-17382. It is unclear as to whether VP-17382 is from a young (thus marking a lack of ossification) or old individual (indicating postmortem breakage).

The W-shaped suspensory ligament scar on the proximal posterior surface of VP-13301 (first phalanx) is indicative of *Hemiauchenia* (Honey, et al., 1998) (Fig. 24B). In comparison to others on record from the FGP (e.g., VP-13300, *Megatylopus*) the phalanx is small and slender, with a ratio of length to medial shaft width of approximately 7.5. This ratio is also similar to that of VP-13928 (partial phalanx), in which the width of the distal articular facet and partial shaft is analogous between both specimens suggesting a similar length and width.

Aepycamelus sp. Macdonald, 1956

Specimen – VP-13415, distal end of metapodial.

Description – The shaft of specimen VP-13415 is lost and what remains is the distal end, which measures 8.3 cm in width (Table 4). The sagittal ridges are well defined and extend from the posterior, approximately 1/3 around each of the epiphyses. Adjacent valleys are moderate. The attachment sites for the medial collateral ligaments are also well defined and extend anteriorly.

Remarks – Attempts to utilize Breyer's (1983) methods were implemented, and due to the fragmentary nature of this specimen, the length of the shaft was estimated using a complete metatarsal of another large camel; *Megatylopus* (VP-7484 from the Hagerman local fauna, Twin Falls County, Idaho). VP-7484 has similar proportions to VP-13415; therefore, the former specimen was utilized for comparison in estimating the full length for assignment (Table 4). It must be noted, however, that the splaying of the distal end of VP-13415 is more exaggerated when compared with that of VP-7484. With the addition of the inferred length measurement, the ratios of metapodial measurements were plotted (Figs. 25, 26, and 27). The plot of specimen VP-13415 fell between plots of *Aepycamelus* and *Megatylopus* representing either a large *Megatylopus* or a small *Aepycamelus*. This discrepancy is likely the result of utilizing a *Megatylopus* metatarsal to estimate total length rather than that of an *Aepycamelus*.

Due to the potential of VP-13415 being recognized as one of two genera, additional comparative observations including the difference in splaying tendencies were utilized. In addition to the exaggerated splaying in VP-13415, another critical difference between the two specimens was the extension of the sagittal ridges on the distal epiphyses of the metapodial. In VP-13415 these ridges extend slightly further than in VP-7484. The orientation of the facets for collateral ligament attachment also varies, as in VP-7484 these sites extend posteriorly rather than anteriorly, as observed in VP-13415. When the ratios of the metapodial measurements were combined with physical characters, it was concluded that this specimen represents an individual from the genus *Aepycamelus*.

Alforjas sp. Harrison, 1979

Specimen – VP-17380, partial proximal end of metatarsal.

Description – The distal end of VP-17380 is lost, leaving only the shaft and proximal facet head. The walls of the shaft are thick, measuring an average of 1.0 cm. Within a moderate posterior concavity, two foramina exist. The entocuneiform facet of VP-17380 is completely separated from the medial plantar process (Fig. 28). There are also remnants of the accessory process of the anterior slope of the plantar process.

Remarks – The loss of the distal end prevented the application of Breyer's (1983) method of determining genus. The function of the two foramina is interpreted as additional ligament attachment as previously described (e.g. VP-13303). Proximal facets in VP-17380 are comparable to those of known *Alforjas* specimens from the Minium Quarry. Furthermore, the thickened shaft walls (Montellano, 1989), complete isolation of the entocuneiform facet, and remnants of the accessory process are all traits specific to *Alforjas* (LaGarry, 1988), allowing VP-17380 to be confidently assigned to the genus.

Tribe CAMELINI Webb, 1965

Procamelus ? sp. Leidy, 1858

Specimen – VP-13319, distal end of metapodial.

Description – The distal end and partial shaft characterize specimen VP-13319. What remains of the shaft is relatively thin, measuring 0.5 cm thick. The sagittal ridges extend approximately halfway around each of the distal epiphyses. The width of the splay is 5.7 cm (Table 4). The attachment sites for the collateral ligaments are moderately developed.

Remarks – A combination of Breyer's (1983) methods and comparative means were used to identify VP-13319. The shaft of this particular metatarsal was separated from the distal end, permitting Breyer's (1983) method to be applied when length was estimated. A comparison to specimen VP-717, from the Edson Quarry in Sherman County, Kansas, for an estimate on length was established. Splaying of the distal width was parallel in the two specimens, which suggested that both specimens were of a similar length. The extension of the sagittal ridge on the distal epiphyses is also similar between the two specimens. The tentative classification of VP-13319 as *Procamelus* is due to the ratio plots of the specimen using Breyer's (1983) methods (Figs. 25 and 26) and plot of the deviation as established in the original study (Fig. 27).

Megatylopus sp. Matthew and Cook, 1909

Specimens –VP-13570, centrum of cervical vertebra; VP-17381, partial proximal end of metatarsal; VP-13926, calcaneum; VP-13300 and VP-13925, 1st phalanges.

Descriptions – Although the transverse and spinous processes are missing, VP-13570 is a well-preserved centrum of a cervical vertebra (Fig. 29). The total length of the vertebra measures 14.6 cm and at the widest portion of the posterior end, measures 9.6 cm. The anterior head is highly rounded (convex); whereas the posterior surface is highly concave (opisthocoelous orientation). There are no signs of predation or scavenging on the specimen.

The state of VP-17381 is poor. The cuboid, ectomesocuneiform, and entocuneiform facets are missing, although the plantar process is still intact. It is impossible to determine whether or not the entocuneiform facet merges with the plantar process. There is a deep groove leading to the plantar process and two foramina are present on the posterior surface, which demonstrates a moderate concavity. Although fragmentary, the partial metatarsal is large, measuring 31.5 cm.

VP-13926 is the largest calcaneum from the FGP with a total length of 17.4 cm (Fig. 30A). The body of the shaft is relatively long and slender, and the cuboid facet is an irregular oval. The anteromedial sustentacular facet is broken although the principal sustentacular facet is preserved and is completely isolated. The distal most facets are lost to physical weathering, whereas a portion of the proximal head exhibits a series of three puncture marks with the corresponding grooves. The series runs for a total length of 0.9 cm and in cross-section the most prominent mark of the series appears triangular (Fig. 30B).

The total length of the first phalanx, VP-13300, is 14.6 cm. The widths at the proximal and distal ends are 5.6 cm and 3.9 cm, respectively. The carinal groove is strongly developed (Fig. 31A). There is a W-shaped posterior suspensory ligament scar on the posterior side and a slight expansion of the proximal head (Fig. 31B).

VP-13925 is another well-preserved first phalanx, with a length of 12.2 cm. The proximal and distal widths are 5.1 and 3.7 cm, respectively. A carinal groove and W-shaped ligament scar, on the posterior surface, are both apparent. The proximal head is slightly expanded, whereas the distal end is narrower.

Remarks – The proportions of VP-13570 (centrum of cervical vertebra) are similar to those of *Megatylopus*. The large size dwarfs those of smaller camels such as *Hemiauchenia*, but is less robust than that of *Camelops* and *Aepycamelus*. VP-13570 is the largest vertebra on record from the FGP.

The metatarsal is not supported by thickened walls and comparatively speaking VP-17381 is less robust than VP-17380 (*Alforjas*). As described by Montellano (1989), *Alforjas* limb bones are “short and thick with massive distal ends.” The lack of exaggerated posterior surface concavity and large size are in contrast to *Hemiauchenia*. The proportions of VP-17381 are most similar to those of VP-7484 (*Megatylopus*) from the Hagerman local fauna, Twin Falls County, Idaho. These characteristics are critical in supporting the assignment of VP-17381 to *Megatylopus*.

The elongated slender nature of the calcaneum body (VP-13926) is in contrast with *Camelops*, which is more robust. The irregular oval shape of the cuboid facet of the VP-13926 is indicative of *Megatylopus*, as in *Camelops* the cuboid facet is L-shaped (Voorhies and Corner, 1986).

The series of puncture marks and grooves are interpreted to be the result of predation or scavenging. The most prominent puncture mark of the series is distinguishable from the previously described ligament foramen, as again in cross-section this mark appears triangular. The distinct shape suggests a puncture from a tooth, most likely a premolar or molar. Based on the carnivores present at the site and size of the puncture, it is suggested that this mark is from an *Osteoborus*.

As exhibited in *Hemiauchenia*, there is a W-shaped posterior suspensory ligament scar on specimens VP-13300 and VP-13925 (although less pronounced in this particular specimen). The generic differentiation here, however, is in the stoutness of phalanges. The ratio of the length to medial shaft width is approximately 4.9 (VP-13300) and 4.7 (VP-13925) compared to 7.5 for the full specimen of *Hemiauchenia* (VP-13301). The slight lateral expansion of the proximal head and the narrow nature of the distal end in VP-13300 are in contrast to *Camelus*, *Gigantocamelus* (Voorhies and Corner, 1986), or *Aepycamelus* (Janis, et al., 2002).

Tribe Indeterminate

Genus Indeterminate

Specimens – VP-17370 and VP-17371, partial proximal ends of radii/ulnae; VP-13302, VP-13318, and VP-13348, partial proximal ends and shafts of metatarsals; VP-13569, partial proximal end of metatarsal; VP-13299, VP-13310, and VP-13349; partial distal ends of metapodials; VP-13305 and VP-13347, partial proximal ends and shafts of metapodials; VP-13320, VP-13406, and VP-13407 partial metapodials; VP-17372, VP-17373, and VP-17374, partial distal ends metapodials; VP-13304, right calcaneum; VP-13929, partial calcaneum; VP-13399, partial astragalus.

Descriptions – Specimens VP-17370 and VP-17371 are the partial proximal ends of radii/ulnae. In both instances the olecranon and a portion of the olecranon process are broken. The radial and semilunar notch in both specimens is partially preserved. In VP-17370 the coronoid process remains intact; however, in VP-17371 it is lost.

VP-13302, VP-13318, and VP-13348 are poorly preserved partial metatarsals. The cuboid and ectomesocuneiform facets in specimens VP-13302 and VP-13318 are broken laterally, whereas in VP-13348 the cuboid and ectomesocuneiform facets are worn. In all three instances the plantar process is lost. Only a portion of the anterior face of the metatarsal remains as the posterior portion is broken in each specimen.

VP-13569 is the partial proximal end of a metatarsal. The cuboid and ectomesocuneiform facets are preserved; however, the entocuneiform facet and plantar process are broken. The breadth of the metapodial across preserved facets is 6.0 cm. The specimen is preserved with a deep fossa on the partial shaft.

The preservation of VP-13299, VP-13310, and VP-13349 is similar. All three fossils are the partial distal ends of metapodials, preserving one distal portion of the typically splayed end. The extension of the sagittal ridge on specimens VP-13299 and VP-13349 extends from the posterior to approximately one third around each epiphysis. The ridge is well defined as are the adjacent valleys. The attachment sites for the collateral ligaments are evident, being more pronounced in VP-13299. There is a lack of ossification in specimen VP-13310 as the distal epiphysis is not fused with the bone and is, therefore, not preserved.

VP-13305 and VP-13347 are the partial proximal ends and shafts of metapodials in which the proximal facets of both specimens are broken laterally. In addition to the previous character, VP-13305 shows significant fluvial deformation and displays a relatively flat posterior surface.

VP-13320, VP-13406, and VP-13407 are also fragmentary metapodials. The proximal and distal ends are completely broken, whereas the shafts themselves are fragmentary. No ligament scarring is apparent on the remaining portions of each of these specimens; however, on specimen VP-13320 there is a moderate concavity to the posterior face of the partial shaft.

VP-17372, VP-17373, and VP-17374 are all partial shafts of metapodials; however, the preservation of each of these specimens varies from those previously described. The beginning of the separation of the distal splay is apparent in each of these samples. Ligament scarring is also absent in each of these specimens.

The body of VP-13304, a right calcaneum, is short (7.2 cm) but slender (1.9 cm deep). The cuboid and principal sustentacular facets are preserved. It appears that the principal sustentacular facet begins to merge with the anteromedial sustentacular facet, although this is impossible to determine because the latter is been broken.

The shape of the cuboid facet of the partial calcaneum (VP-13929) is an irregular oval. The body is broken and only the medial sustentacular facet is preserved. No further description of the specimen is possible.

The condyles of VP-13399 (partial astragalus) are sub-parallel to the axis and are unequal in size. The double articulating surface is broken, eliminating a potential keel. A portion of the posterior surface is also broken. The specimen also displays a lack of ossification.

Remarks – Although there are large enough portions of VP-17370 and VP-17371 (partial radii/ulnas) preserved to assign these specimens to the Camelidae, there is not enough to justify generic assignment. The small size is suggestive of *Hemiauchenia*; however, without any diagnostic features preserved these specimens cannot be assessed.

The partial facets of metatarsals VP-13302, VP-13318, and VP-13348 are distinct enough from equids to allow for familial assignment to the Camelidae; however, the partial nature of the facets prevents generic assessment. As the posterior portion of each of these specimens is broken, the potential to determine concavity is also eliminated.

Although better preserved than previous specimens (e.g. VP-13302 and VP-13318) generic assignment of VP-13569 still cannot be established. The lack of classification is due to the missing entocuneiform facet and plantar process; the orientation of which is critical in the assessment of medium-sized camels. The deep fossa on the partial shaft is not in the same location as those for ligament attachment and may be the result of fluvial weathering.

Because there is no way to measure width or shaft length, osteological comparison and Breyer's (1983) method for generic assignment could not be applied to the partial metapodials; VP-13299, VP-13305, VP-13310, VP-13320, VP-13347, VP-13349, VP-13406, VP-13407, VP-17372, VP-17373, and VP-17374. Also preventing generic assessment is the fact that each of the specimens is preserved with no diagnostic characteristics, such as the proximal facets. The lack of a fused distal epiphysis in specimen VP-13310 suggests a young individual, similar to that described in specimen VP-13317. The higher degree of fluvial deformation of VP-13305 implies a longer duration of transportation than other fossils.

Assignment of VP-13304 to the Camelidae is in the rounded orientation of the proximal head. The small, slender proportions of the specimen are suggestive of *Hemiauchenia*; however, generic assignment of the specimen in this instance is prevented due to a lack of comparable material. The small size may be indicative of age as opposed to generic identification.

The irregular oval-shaped cuboid facet observed on VP-13929 is similar to that of VP-13926 (*Megatylopus*). Without the body (to determine proportionality) and articular facets, such as the principal sustentacular facet, however, generic assignment cannot be established.

Generic assignment of the partial astragalus (VP-13399) is prevented due to the fragmentary nature of the specimen. The sub-parallel orientation and unequal size of the condyles are indicative of the Camelidae. Based on the lack of development and ossification, the specimen represents a young individual.

BIOSTRATIGRAPHY

The age of the site, based on the stage of evolution of the mammals from the FGP is considered to be early Hemphillian. One of the key taxa in this determination is the canid *Osteoborus*, which is restricted to the Hemphillian (Liggett, 1997).

Of the horses, only the identification of a single species further restricts the Hemphillian at the site. Although the biostratigraphic range of *Neohipparion* is from the late Barstovian to the end Hemphillian; that of *N. trampasense* is more constrained, being restricted to a range from the late Barstovian to the early Hemphillian (Hulbert, 1993).

Additional support for an early Hemphillian age comes from the camels. *Aepycamelus* has a biostratigraphic range that begins in the Barstovian and extends through the early Hemphillian (Breyer, 1983). The range of *Protolabis* also beings in the Barstovian, but extends through the late early Hemphillian. Although first appearing in the middle Barstovian, *Procamelus* has a range ending in the late early Hemphillian, similar to that of *Protolabis*. The extinction of *Neohipparion trampasense* and the three genera of camels, all support the assignment of the FGP to an early Hemphillian age (Fig. 32).

TAPHONOMY

Skeletal material from the Ogallala Group at the FGP possesses what one may call a typical fossilized appearance, demonstrating a high degree of mineral replacement with siliceous material and limited pore-space. The fossils also tend to possess a white to gray appearance depending on the portion of bone exposed to the surface. These fossils also demonstrate evidence of postmortem deformation from both abiotic and biotic factors.

The abiotic factors influencing preservation were discussed previously. Fluvial currents, as well as exposure to recent climatic conditions, have damaged a number of these fossils in distinct ways. Breakage and rounding are characteristic traits of fluvial activity, whereas exposure to the elements and fluctuating weather cause fossils that are exposed to become brittle.

The two instances in which the fossil material indicates the signs of predation or scavenging were described previously. The additional fossae are abnormal in size and location and are interpreted as puncture marks, possibly from the canid, *Osteoborus*. Further indication that these marks are due to scavenging is their triangular shape (Fig. 30B). With the preservation of predatory or scavenging activity, a fuller understanding of the paleoecology at the FGP is established.

Influences of Fossil Distribution

The fluvial processes responsible for the deposition of the Ogallala Group and physical weathering of its fossils also restrict the fossil yield at the site. Voorhies (1969) conducted a series of water table experiments to determine bone deposition from fluvial suspension. Even though all three groups (Groups I, II, and III [Table 5]) of bone are accounted for, it is Group II that is best represented at the FGP. Voorhies (1969) concluded Group II material is transported through traction, an understandably tumultuous process. If both fragile and stout bones, regardless of what animal they initially belonged to, are subjected to the same current activity, the likelihood of robust fossil survival appears far greater.

In this study a majority of fossils recovered from the FGP represent the most robust bones found within the mammalian skeleton. Cannon bones, vertebrae, and teeth, although often fragmentary, account for nearly 80% of the fossil assemblage. Although exceptions do exist, more fragile bones such as cranial elements are rare. The scarcity of delicate bones produces a bias in the fossil record and the presence of fossils, including taxa and their ontogentic stage may be skewed. For example, the number of camels, though abundant, may be overrepresented due to their potential of being more resistant to wear, and fossil horses underrepresented, due to the more fragile nature of the bones.

Bones from late Miocene camels are more robust than those of fossil horses of the same period. For example, camel metapodials are supported by a thickened shaft and are generally stouter, than those of horses. Similarly, horse teeth possess more surface area than those of camels; leading to an increased potential of wear. The abundance of fossil camel, therefore, may consequently be the result of fluvial filtering, rather than a reflection of the number of individuals and population size.

Not only is this bias evident in the ratio of horse to camel specimens, but a bias within the equid sample is also apparent. Hulbert's (1984) methods revealed that the representative age range at the time of death is from 2.2-3.5 years for the one specimen of *Protohippus supremus*, greater than 7 years for *Protohippus* (partial right maxillary [VP-13292]), and 2.5-3.5 for the *Neohipparion* specimens (Table 1). This spread hardly represents a full sample, and, therefore, population dynamics are impossible to establish. Further, without a full sample, it is impossible to determine whether or not the fossil assemblage represents attrition (Berger, 1983) or catastrophic event (Voorhies, 1981).

It is also unclear if the age spectrum obtained from the FGP is the result of fluvial activity or simply sampling. If the spread of samples is due to a fluvial bias, what makes teeth that are within the 2.2-3.5 year old range more susceptible to preservation than teeth that are younger or older? Fluvial activity may cause a bias in the fossil record; however, filtering alone cannot account for the distribution of material. It is only when other factors such as environmental shifts and ecological niches are considered that a more defined explanation as to fossil distribution at the FPG is established.

What the relative specimen numbers and functional morphology may represent is a shift from a previously equal distribution of feeding guilds in the early Miocene, to one of grazing; a succession of woodland to savanna (Prothero, 2006). The idea of an expanding savanna-grassland is also in agreement with the biostratigraphic range of the represented grazing camels. *Hemiauchenia* and *Camelops* are two of the genera of camel that extend through the Hemphillian and into the Blancan. It is no coincidence that the evolutionary adaptation of a grazing pattern may have been one of the key attributes allowing these particular genera to survive as the spread of savanna grassland continued through the Pliocene. The continuing expansion of the savanna, with a reduced number of trees, favored some genera and eliminated others. The combination of the grazing horse and camel specimens supports the idea of a savanna landscape.

To attribute the taxonomic distribution of fossils at the FGP to a single factor may be ill-advised. Most likely, the fossil allotment is the result of fluvial filtering and drop-out, as described by Voorhies (1969), the derivation of material from a specific habitat (MacFadden and Cerling, 1996), and a notable environmental shift. This combination of circumstances seems more likely. As has been previously stated, a savanna environment would sustain the different feeding guilds indicated by the fossil material. The grazing adaptation allowed the horses as well as a number of advanced camels to inhabit this particular region, while supporting the few taxa specifically requiring a browsing habit.

On the Absence of Rhinoceros

In addition to inquiries on the abundance of camel material, another question regarding fossil distribution is raised; why are rhinoceros not present at the FGP? *Teleoceras*, a semi-aquatic rhinoceros and biostratigraphic indicator of the Hemphillian (Gustafson, 1978), is abundant throughout Ogallala deposits in the Great Plains (Voorhies and Thomasson, 1979), but has yet to be described from the FGP. The following ideas represent the initial steps in explaining this anomaly.

Teleoceras is an analogue of the modern hippopotamus (*Hippopotamus amphibius*). It is thought that *Teleoceras* lived in herds and spent the daylight hours wading in rivers and along its banks, leaving the water at night to graze on grasses (Voorhies and Thomasson, 1979). As the FGP is interpreted to have been a pebbly braided stream environment and supportive of grazing fauna, it would appear this would be an appropriate environment to support the genus.

The size of the deposited clasts at the site may explain the lack of *Teleoceras* material. Utilizing the Hjulström curve for transport and deposition, the minimum velocity needed to carry the smallest of boulder-sized clasts is 600 cm/sec at a flow depth of 1 m (Nichols, 1999), and an increase in clast size, leads to an increase in velocity and flow depth. This velocity is incredible and may have been one of the main variables that prevented *Teleoceras* from living at the site.

A second suggestion into the absence of *Teleoceras* is related to the intermittency of the channel at the FGP. Similar to the effects of a channel that is too deep, a channel that is too shallow would prevent the establishment of the genus. As a stable water supply is critical to hippopotamus survival, so would it be to *Teleoceras*. Although a channel was evident at the FGP, the influx of water may reflect a seasonal event, possibly from ice melt or heavy rains. These seasonal trends would not support *Teleoceras* year round.

Although determining the depth of the channel at the FGP is beyond the scope of this study, it is proposed that the hypothetical depth may have also played a part in the absence of *Teleoceras*. In a study conducted by Olivier and Laurie (1974), it was noted that as river depth increased, individuals dispersed and the mean group size of hippopotami decreased. Because *Teleoceras* is thought to be comparable to the hippopotamus, factors limiting the spatial distribution may be similar between the genera. Although conjecture, as there is no direct evidence, it is suggested that the depth of the channel at the FGP was too great to support *Teleoceras*.

PALEOECOLOGY

Feeding Ecology and Source Area Environment

The late Miocene represents a world in transition, a fauna once dominated by browsers, was being replaced by grazers. This would be in agreement with the climatic changes that North America underwent in the late Miocene to early Pliocene. A savanna landscape contains both grasslands with intermittent trees, allowing for the presence of both grazers and browsers. With time, however, the continued expansion of grasslands would dominate the landscape, forcing some species to migrate or go extinct.

Great strides have been taken in the attempt to determine the habitat in which fossil perissodactyls and artiodactyls once lived. Such studies (e.g., Prothero, 2006) have utilized the functional morphology of cranial elements to explore the potential feeding ecologies of these now extinct animals. When considered together the degree of hypsodonty, relative number of specimens collected of each family, and climatic changes of the Late Miocene, yield a more complete reconstruction of the paleoecology of the FGP.

Dental durability is a direct evolutionary response to an established feeding ecology. The trend toward hypsodonty in both horses and camels of the late Miocene increases enamel on the labial and lingual surfaces; whereas on the occlusal surface, enamel in increased through elaborate infoldings (MacFadden, 1992). The feeding opportunity of those individuals with an even slightly increased amount of enamel selects them for differential survival. The selection of the survivors continues through generations, favoring those with an ever increasing amount of enamel. When combined with other biological adaptations, such as an elongated cecum, the grazing guild is eventually fully exploited. The hypsodont character; however, is a key attribute that is observable in the specimens from the FGP, as no soft tissues have been recovered. The occlusal enamel patterns are not only diagnostic for identification, but are also useful in the interpretation of a grazing behavior.

Although the camel teeth from the FGP are comparatively hypsodont to others within the family, the degree of hypsodonty as a whole is dwarfed by that of the equids. The lesser degree of hypsodonty, however, has still allowed some camels to adapt to a grazing pattern, whereas permitting others, such as *Protolabis*, to occupy the browsing niche. For example, the degree of hysodonty, among other characters, indicates that *Hemiauchenia* represents a grazing camel, rather than a browser (Prothero, 2006).

As previously stated, horses represent a smaller percentage of the material recovered from the FGP, whereas that of the camels is proportionately more. The important factor here, however, is the type of camel that is best represented at the site, which is *Hemiauchenia*, a grazer. In environmental interpretation, it is more important to note that grazers are more abundant than browsers, rather than camels to horses. Although grazing was the most predominant method of feeding at the FGP, there are also some browsers or mixed feeders.

The evolution of the landscape in the late Miocene represents the transition of woodland to savanna and one of browsing to grazing (Prothero, 2006). The savanna landscape incorporates both vast grasslands and intermittent trees, thereby, allowing for both grazers and browsers. This landscape appears to best support the fauna, because both browsers and grazers have been described from the FGP. Development of the savanna landscape, however, does give credence to this interpretation.

Janis (1982) expanded the habitat categories established by Jarman (1974) to include both living and fossil ungulates, supporting the aforementioned feeding guilds. Of particular interest are the additions to Jarman's C_2 and D_1 categories. As woodland-savanna and open woodland-savanna-grassland, respectively, there was a notable shift in biota. These two categories appear to support a number of the genera at the FGP and give credence to the presence of a savanna within the study area.

Janis (1982) further expands the savanna and extrapolates the data to other periods in time, explicitly targeting that of the late Miocene of North America. Here, the established woodland-savanna, specifically Grades 1 and 2 can be shown to contain most of the fauna from the FGP. Grade 1 represents an area supportive of medium- to large-sized grazers and browsers, whereas the environment of Grade 2 supports the grazers and browsers of Grade 1, in addition to mixed feeders. Well represented at the FGP, *Hemiauchenia* is interpreted as a grazer and an outlier of Grade 1. In Grade 2, *Neohipparion* has been established as a tridactyl grazing equid, whereas *Aepycamelus* is a browsing camel. In summary, aepycameline camels would have been outlier of the woodland-savanna, whereas the grazing equids and protolabine and cameline camels would have been supported in the woodland-savanna-grassland. This interpretation of the early Hemphillian landscape is also in agreement with what has been established in Thomasson's (1979, 1990) paleobotanical investigation of the Ogallala Group.

Equid Muzzle and Symphysis Width—Although traditional interpretation indicates that hypsodonty is an adaptive response to grazing in horses, there are a number of other characters that suggest that the family Equidae was indeed predominantly a grazing taxon. Janis and Ehrhardt (1988) indicated muzzle width, along with hypsodonty and symphysis shape, are indicators of feeding habits. Those genera which possessed a broad muzzle, wide symphysis, and a linear arrangement of incisors, are grazers. Genera such as *Neohipparion*, *Protohippus*, and *Pseudhipparion* (those well represented at the FGP) have a broad muzzle and hypsodont dentition, although they differ in the fact that the symphyses vary in the degree of curvature, indicating a less specialized grazing habit. Those genera with a narrow muzzle (*Megahippus*) and a brachydont dentition are considered to be browsers, and have yet to be described from the FGP. The interpretation of feeding habit, based solely on the degree of hypsodonty, is reinforced with the hypothetical muzzle and symphysis width noted by Janis and Ehrhardt (1988).

Implications of Crown Height and Percent δ^{13}C Studies—MacFadden and Cerling (1996) studied the feeding ecologies of mammalian herbivore communities from the Neogene of Florida. Among the orders studied were the Perissodactyla (most notably horses) and Artiodactyla and within Artiodactyla, the Camelidae, and even more specifically, a number of *Hemiauchenia* and *Procamelus* samples (two genera represented at the FGP). Based on the parameters of relative crown height and percent δ^{13}C, four feeding types, or ecologies, were established. These niches include C3 browsers, C3 grazers, mixed feeders, and C4 grazers.

The fossil record of the Equidae marks a classic example of an ecological shift leading to morphological evolution. Between 20-15 mya (middle Miocene) horses underwent rapid diversification and the development of hypsodonty. The alteration of dental condition was interpreted to signify the shift in feeding pattern from browsing to grazing. This dietary transition, therefore, may have been the result of a shift from relatively soft browse to more abrasive grasses. Based on the $\delta^{13}C$ obtained from MacFadden and Cerling (1996) the late Miocene is characterized by a shift in C3 diets (either browse or grass, depending on the clade) to C4 grass.

The shorter crowns of fossil camels (e.g., *Procamelus*) generally indicate browsers or browser/mixed feeders, as is the modern *Camelus*. The isotopic data of the study suggests that extinct camels in the Florida region fed on C3 plants although the lone specimen of *Hemiauchenia* possibly represents a potential pure-C4 grazer. As stated in the same report, these findings may not come as a surprise as extinct llamas and their relatives are predominately grazers. There is another explanation, however, for these findings, as this single specimen may have been a specialized feeder on rare C4 shrubs, which are uncommon in modern communities (MacFadden and Cerling, 1996).

Although the data cannot be directly transferred to the FGP, the findings of MacFadden and Cerling (1996) are certainly intriguing. The results of the $\delta^{13}C$ study reinforce those based on the functional morphology of the specimens. The savanna must have supported such a large group of grazers, and the remaining browsers. The continued spread of grassland-savanna across North America allowed grazers to radiate and diversify, and reduced strict browsers to relatively low numbers.

FUTURE RESEARCH

This study would greatly benefit from a series of $\delta^{13}C$ tests. No such studies have been conducted on samples from the Ogallala Group in western Kansas and the results obtained from the horse and camel teeth of the FGP would likely support those claims established by MacFadden and Cerling (1996), as well as those established within this report.

There is one drawback to this form of research, however, when considered in the light of this particular study. Beyond the detailed carbon isotopic measurements of the camel and horse teeth mentioned in the original experiment, this process outlined by MacFadden and Cerling (1996) depends upon the presence of fossil plants to support the data. A $\delta^{13}C$ test at the FGP would be strictly based on faunal data due to the lack of fossil flora.

A thorough investigation into the absence of *Teleoceras* would further the paleoecology of the FGP. Although I have suggested potential reasons for this anomaly, a number of the ideas are not currently supported and represent the preliminary efforts of future research.

Continued paleontological research at the FGP is important, as it is one of only a relatively few localities in southwestern Kansas where fossils from the Ogallala have been recovered. This provides researchers with an opportunity to investigate a site with critical geological and paleontological implications.

CONCLUSIONS

The FGP is one of the many instances in which the Ogallala Group crops out in Kansas but the only one in Morton County from which Miocene vertebrate fossils are reported. The Ogallala was deposited primarily by fluvial activity (Liggett et al., 1998), depositing sediments across portions of Texas, Oklahoma, Wyoming, Colorado, New Mexico, Nebraska, South Dakota, and Kansas. Evidence from the FGP supporting this claim includes the prevalence of allochthonous clasts, including those of igneous origin, cross-bedding, pebble alignment and size, and fossil breakage and subsequent rounding of fossil and clastic material.

The fluvial environment also played an integral role in fossil distribution. A vast majority of the recovered material from the FGP falls within Voorhies' (1969) Group II. Fossils within this group are removed gradually from suspension and are transported by traction. As a result of these processes, robust bones are those that are most likely to be preserved and identifiable to the generic or specific level. Combined with the environment, this scenario creates a bias in the observable fossil record and may play a part in the apparent abundance of camel specimens.

Previous observations that fossil camels outnumber those of other families at the FGP are supported. Most of the identifiable skeletal elements recovered from the site were those of the Camelidae. The medium-sized camel, *Hemiauchenia*, was best represented at the site.

The age of the FGP was established based on the stratigraphic ranges of the fossil taxa. The presence of the canid *Osteoborus* restricts the FGP to the Hemphillian

(Liggett, 1997). The biostratigraphic range of *Neohipparion trampasense* supports an early Hemphillian assignment of the FGP. Likewise, the biostratigraphic ranges of *Aepycamelus*, *Protolabis*, and *Procamelus* have been shown to end in the early Hemphillian. When combined the data supports an assignment of the FGP to the early Hemphillian; an age that is in agreement with those reported in previous studies.

Functional morphology played an important role in the reconstruction of the paleoecology of the FGP. Hypsodont dentition within the Equidae indicates that the horses grazed, whereas the camels varied in their feeding preference. Some camels, such as *Hemiauchenia*, grazed; others such as *Procamelus* browsed. Both ecological guilds are supported in a savanna-grassland environment, where grazers would be supported through various grasses and browsers through intermittent trees or brush. This interpretation of the FGP is in also in agreement with previous studies (Thomasson, 1990).

There are a number of factors that have been shown to influence fossil distribution at the FGP. Ecological niche specialization, fluvial filtering, and the climatic evolution of landscape may account for the apparent abundance of camel material, as well as the distribution of the comparatively low number of horse specimens. The fauna, particularly grazers, however, corresponds to the continued spread of the grassland across the North American landscape.

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TABLE 1. Hulbert's (1984) wear classes and corresponding age range at the time of death.

Class	Estimated Age Range at Time of Death
1	0 to 2 Weeks
2	0.5 to 1.2 Years
3	1.3 to 2.2 Years
4	2.2 to 2.8 Years
5	2.5 to 3.5 Years
6	3.6 to 4.6 Years
7	4.6 to 5.6 Years
8	5.6 to 7 Years
9	Greater than 7 Years

TABLE 2. Measurements (in cm) for horse teeth from the FGP.

Speicmen Number	**Genus**	**Species**	**Tooth Position**	**Length**	**Width**	**Wear (Y/N)**
VP-13563	*Calippus*	-	Lp2	2.1	1.15	Y
VP-17296	*Protohippus*	*supremus* (?)	Rp3	2.49	1.83	Y
VP-17362	*Protohippus*	-	Rp2	2.55	1.04	Y
VP-13292	*Protohippus*	-	P3	2.35	2.45	Y
VP-13292	*Protohippus*	-	P4	2.35	2.65	Y
VP-13292	*Protohippus*	-	M1	1.78	2.79	Y
VP-13292	*Protohippus*	-	M2	2.15	2.51	Y
VP-13292	*Protohippus*	-	M3	2.71	2.28	Y
VP-13293	*Protohippus*	-	Rm3	2.48	1.05	
VP-13958	*Neohipparion*	*trampasense* (?)	P4	2.13	1.44	Y
VP-17365	*Neohipparion*	-	molar	2.21	1.43	Y
VP17368	*Neohipparion*	-	molar	2.09	1.32	Y

TABLE 3. Measurements (in cm) for camel teeth from the FGP.

Specimen Number	**Genus**	**Tooth Position**	**Length**	**Width**	**Crown Height**	**Wear (Y/N)**
VP-13927	*Protolabis*	RM1	2.8	2.2	1.5	Little
VP-17359	*Protolabis*	RM1	2.68	1.87	2.43	Y
VP-17366	*Protolabis*	RM1	2.87	2.29	2.01	N-Little
VP-13346	*Protolabis*	p3	1.4	0.5	0.87	Little
VP-13346	*Protolabis*	p4	3	0.8	1.7	Little
VP-17363	*Hemiauchenia*	Rm1	2.17	1.48	0.9	Y

TABLE 4. Camelidae metatarsal measurements (on the following two pages). Specimens with catalog numbers were collected from the FGP, Morton County, Kansas and are housed at the FHSM. Remaining measurements are those from Breyer (1983). All measurements are recorded to the nearest 0.1 cm in correspondence to the initial study. n, number of specimens; $\bar{x}$, mean; s, standard deviation.

		Length			Distal Width		
		n	$\bar{x}$	s	n	$\bar{x}$	s
Aepycamelus							
	1) Early Clarendonian	13	71	4.5	13	9	0.9
	2) Early Hemphillian	58	69	-	1	13	
	3) Early Hemphillian	5	58	2	11	10	0.3
VP-13415	4) Early Hemphillian	1	56	-	1	8.3	-
Hemiauchenia							
	5) Late Clarendonian	1	39	-	1	6	-
	6) Early Hemphillian	5	39	2.6	5	5	0.4
VP-13317	7) Early Hemphillian	1	28.6	-	1	3.7	-
	8) Late Hemphillian	38	30	1.6	38	4	0.3
	9) Late Hemphillian	7	26	1.1	7	4	0.4
	10) Late Hemphillian	7	38	2	7	6	0.3
	11) Blancan	2	40	-	2	6	-
	12) Late Blancan	1	42	-	1	6	-
Alforjas							
	13) Late Hemphillian	11	30	2.1	11	6	0.4
	14) Late Hemphillian	2	36	0.7	2	5	0.1
	15) Late Hemphillian	9	33	2.6	8	7	0.6

		Length			Distal Width		
		n	$\bar{x}$	s	n	$\bar{x}$	s
Procamelus							
	16) Late Barstovian	4	36	1	4	6	0.1
	17) Late Barstovian	13	35	1.8	13	6	0.4
	18) Late Barstovian	72	35	2.5	72	6	0.5
	19) Early Clarendonian	7	33	1.5	7	6	0.3
	20) Early Clarendonian	23	32	1.7	21	5	0.7
	21) Late Clarendonian	14	35	1.3	14	7	0.8
	22) Early Hemphillian	30	36	1.4	30	7	0.5
	23) Early Hemphillian	1	38	-	1	7	-
VP-13319	24) Early Hemphillian	1	30.7	-	1	5.7	-
Megatylopus							
	25) Late Clarendonian	10	40	2	10	7	0.5
	26) Early Hemphillian	6	43	2.4	6	9	0.6
	27) Late Hemphillian	8	48	2	8	9	0.5
	28) Late Hemphillian	5	51	0.9	5	10	0.3

TABLE 5. Elements of the mammalian skeleton grouped according to their characteristic susceptibility to transport. Elements in lower-case type are intermediate between the two groups in which they appear. Elements in italicized type are those recovered from the FGP (Modified from Voorhies, 1969).

Group I	**Group II**	**Group III**
Immediately removed, transported by saltation or floatation	Removed gradually transported by traction	Lag deposit
RIBS	FEMUR	*SKULL*
VERTEBRAE	*TIBIA*	*MANDIBLE*
SACRUM	*HUMERUS*	
STERNUM	*METAPODIA*	*ramus*
	PELVIS	
scapula	*RADIUS*	
phalanges		
ulna	scapula	
	ramus	
	phalanges	
	ulna	

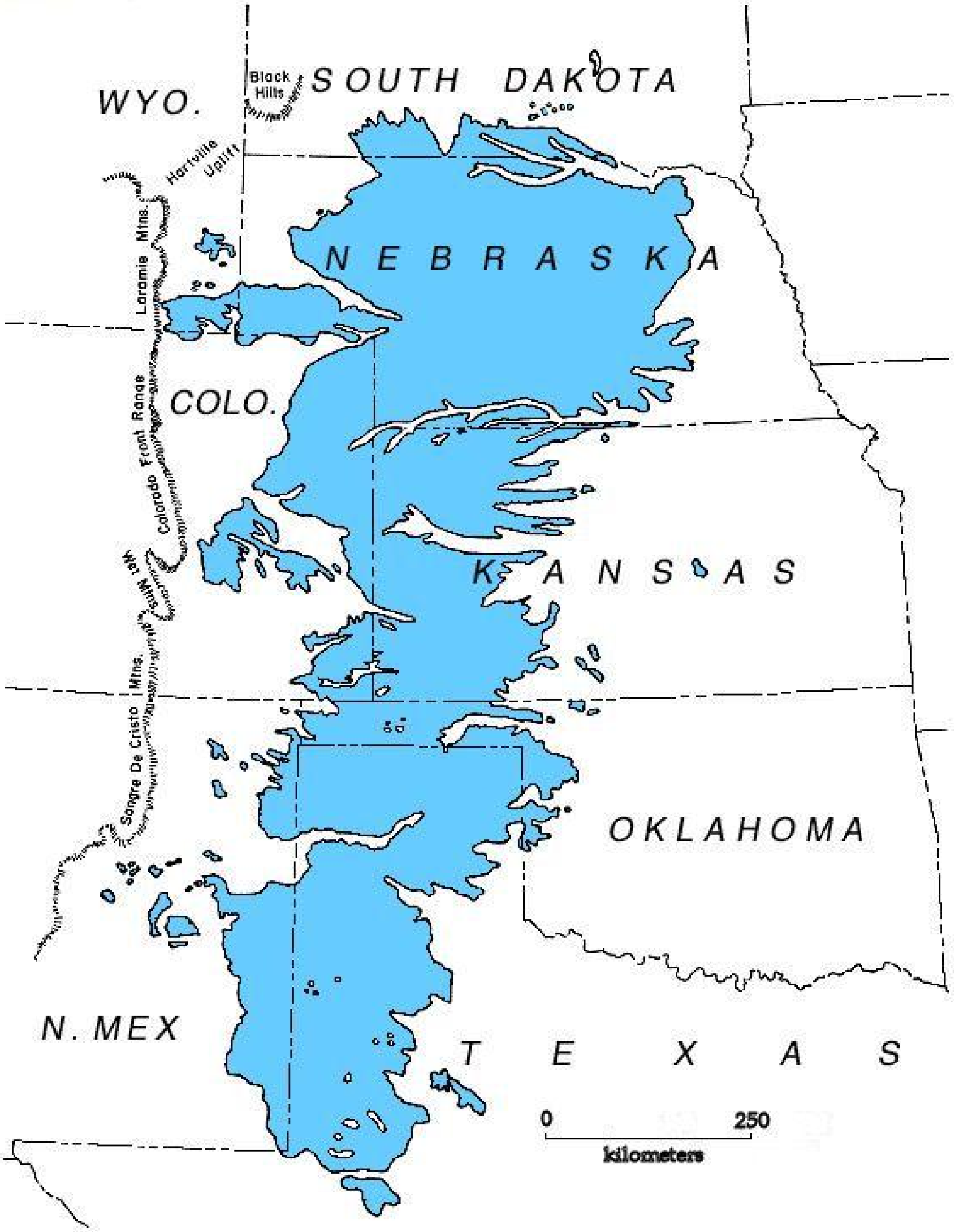


FIGURE 1. Distribution of the Ogallala Group

(Modified from Kansas Geological Survey, 2006).

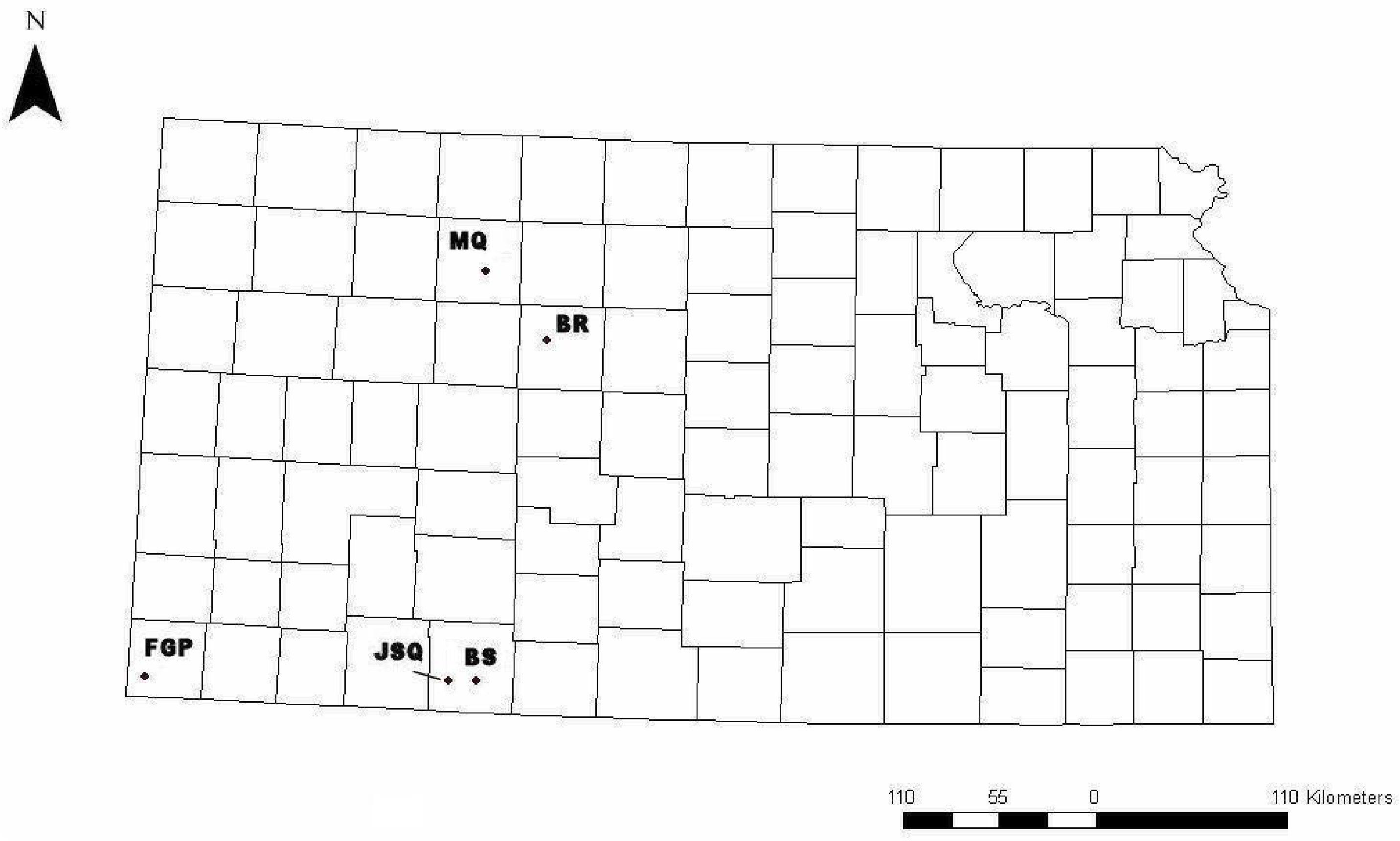


FIGURE 2. Location of the FGP (Morton County, Kansas) in relation to previous thesis studies. **JSQ**: Jack Swayze Quarry, Clark County; **BS**: Beckerdite Site, Clark County; **BR**: Bemis Ranch, Ellis County; **MQ**: Minium Quarry, Graham County.

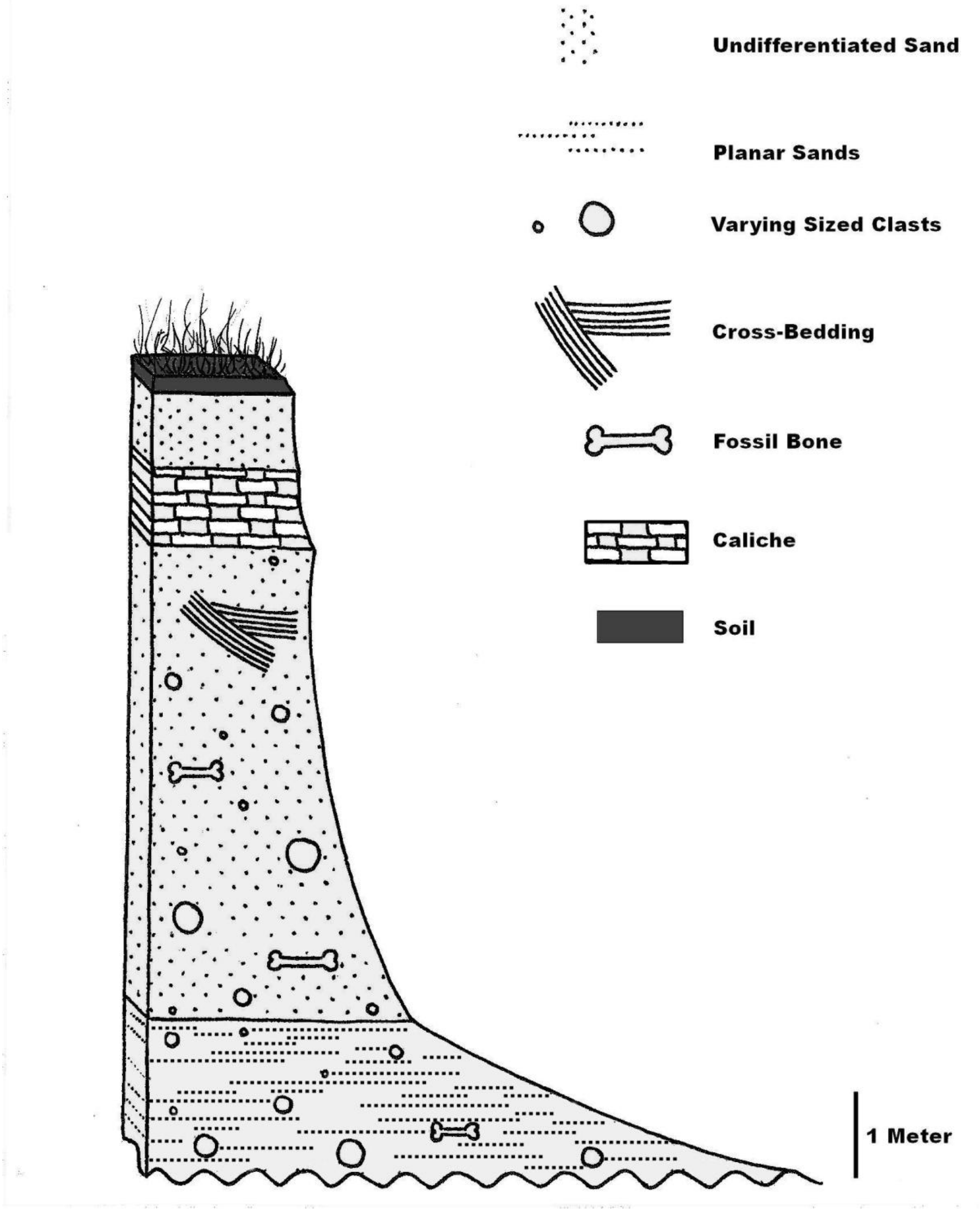


FIGURE 3. Composite stratigraphic cross-section of the FGP.

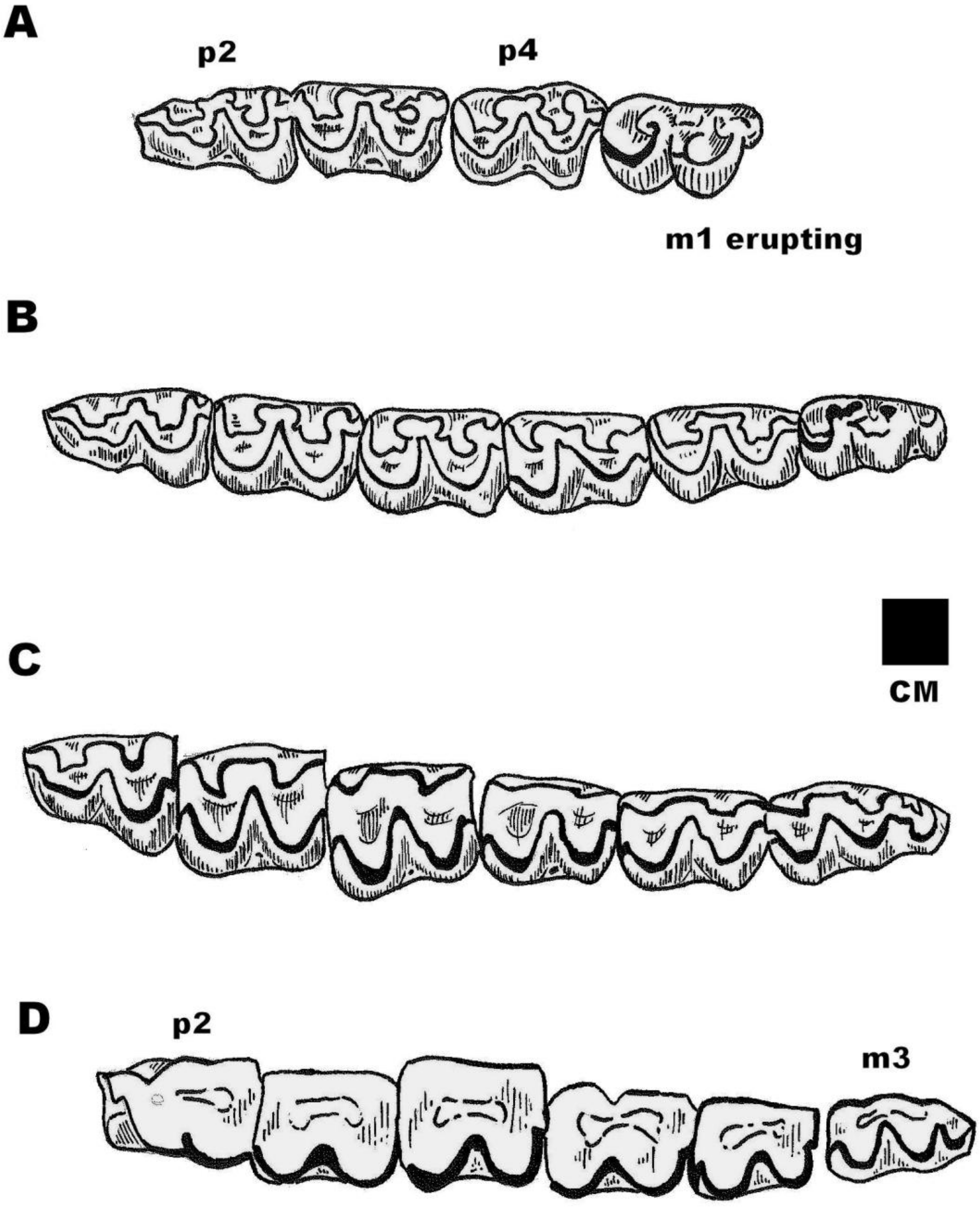


FIGURE 4. Hulbert's (1984) wear-class stages as observed in *Parahippus leonensis*. **A**, wear-class 2; **B**, wear-class 5; **C**, wear-class 7; **D**, wear-class 9 (After MacFadden, 1992).

FIGURE 5. Cross-bedding and pebble alignment found at the FGP.

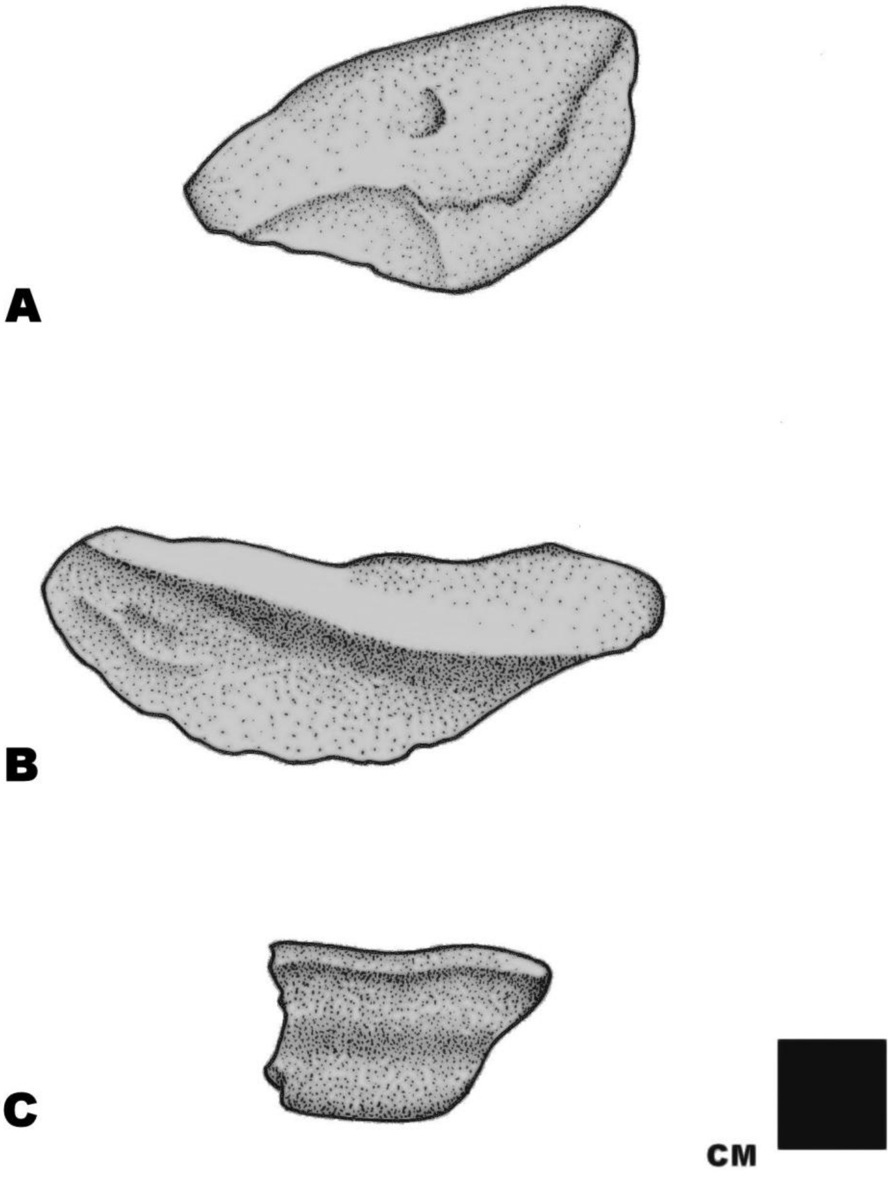


FIGURE 6. Specimens demonstrating rounding through current transport. Illustrations are of un-catalogued float material. Degree of rounding is a result of duration in suspension. **B** suggests prolonged suspension, whereas **C** possesses edges that are still sharp, and **A** represents an intermediate condition, comparatively speaking.

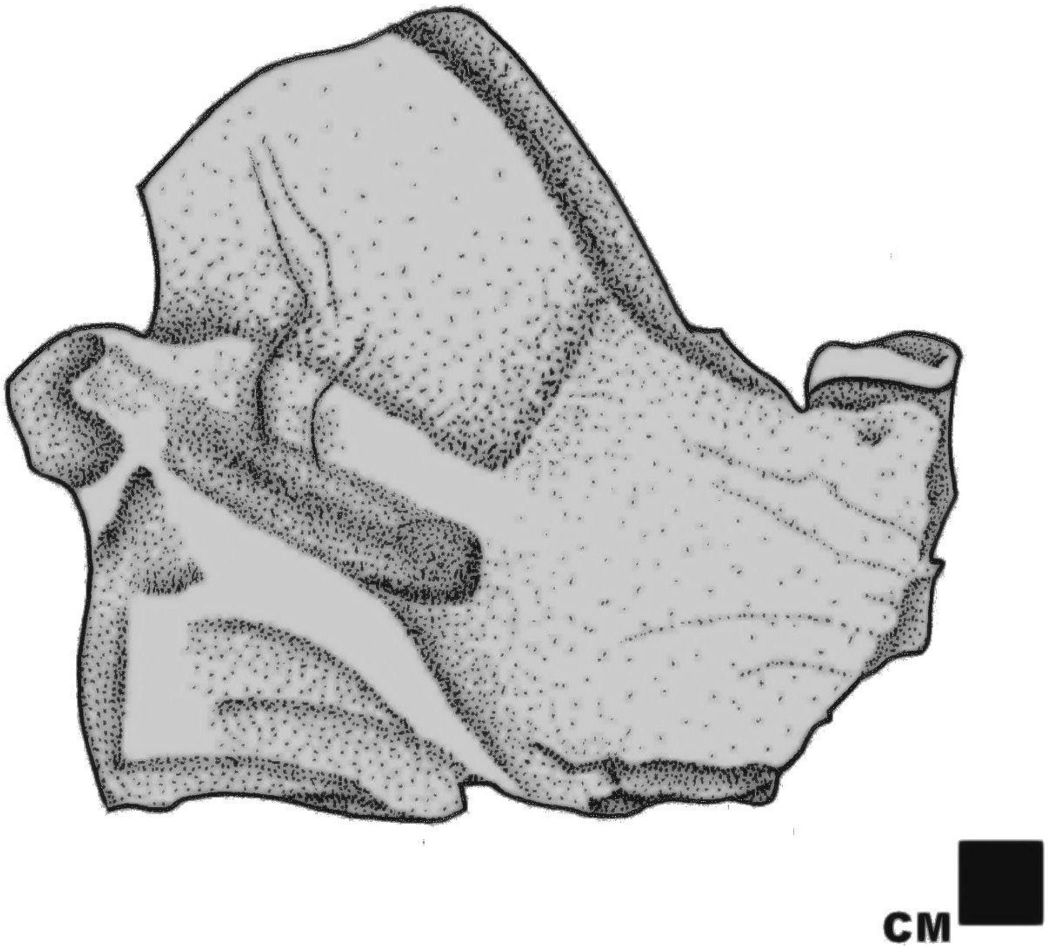


FIGURE 7. Partial left dentary with m2 of *Osteoborus* sp. (VP-13344) in lingual view.

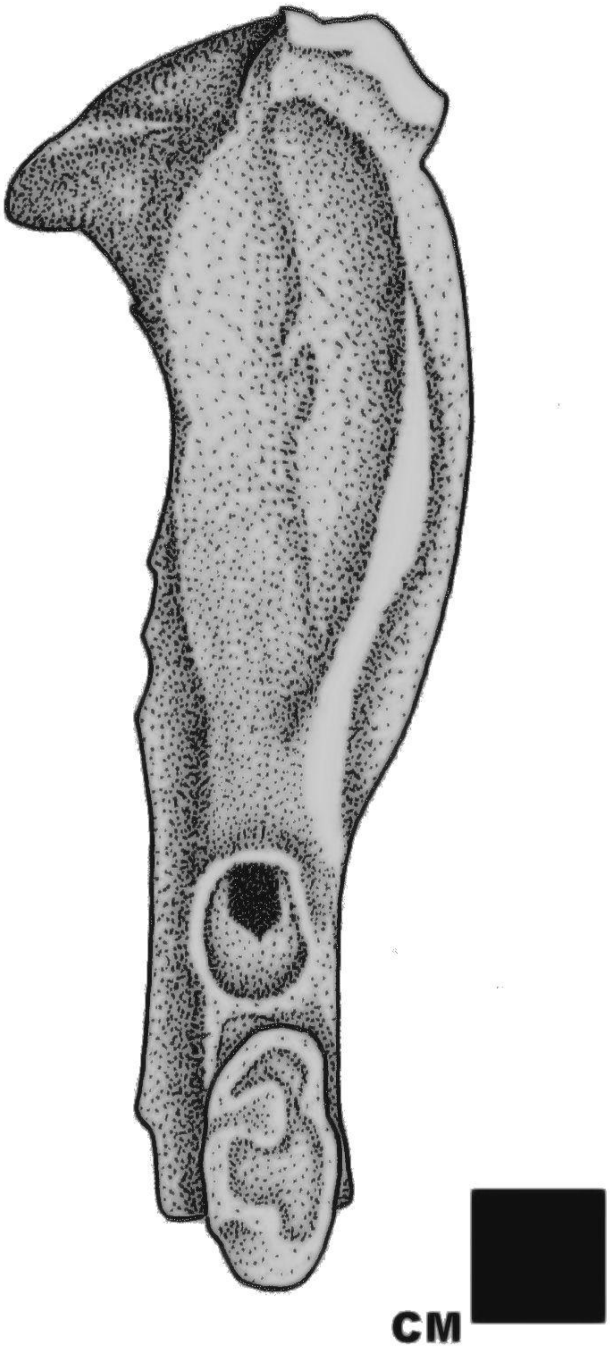


FIGURE 8. Partial left dentary with m2 and alveolus for m3 of *Osteoborus* sp. (VP-13344) in occlusal view.

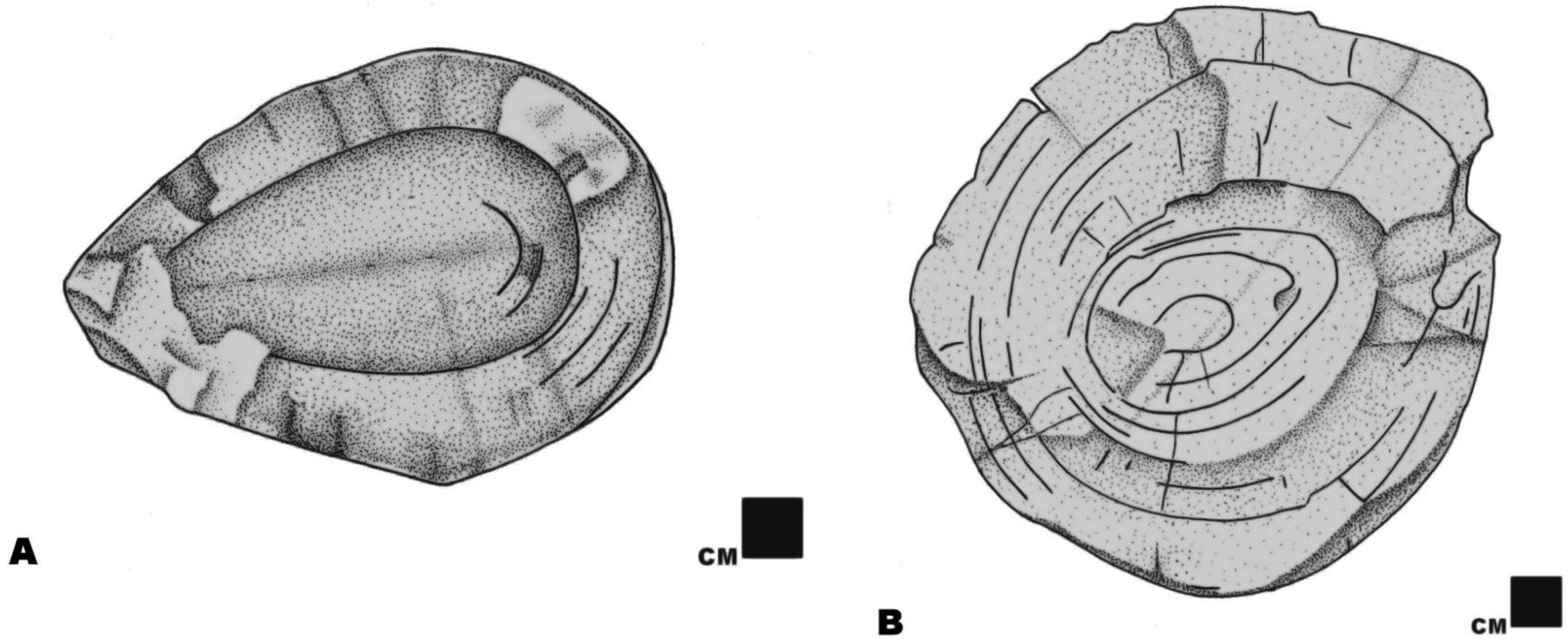


FIGURE 9. Comparison of tusk morphology. **A**, Gomphotheriidae (VP-13932) and **B**, indeterminate proboscidian (VP-13313).

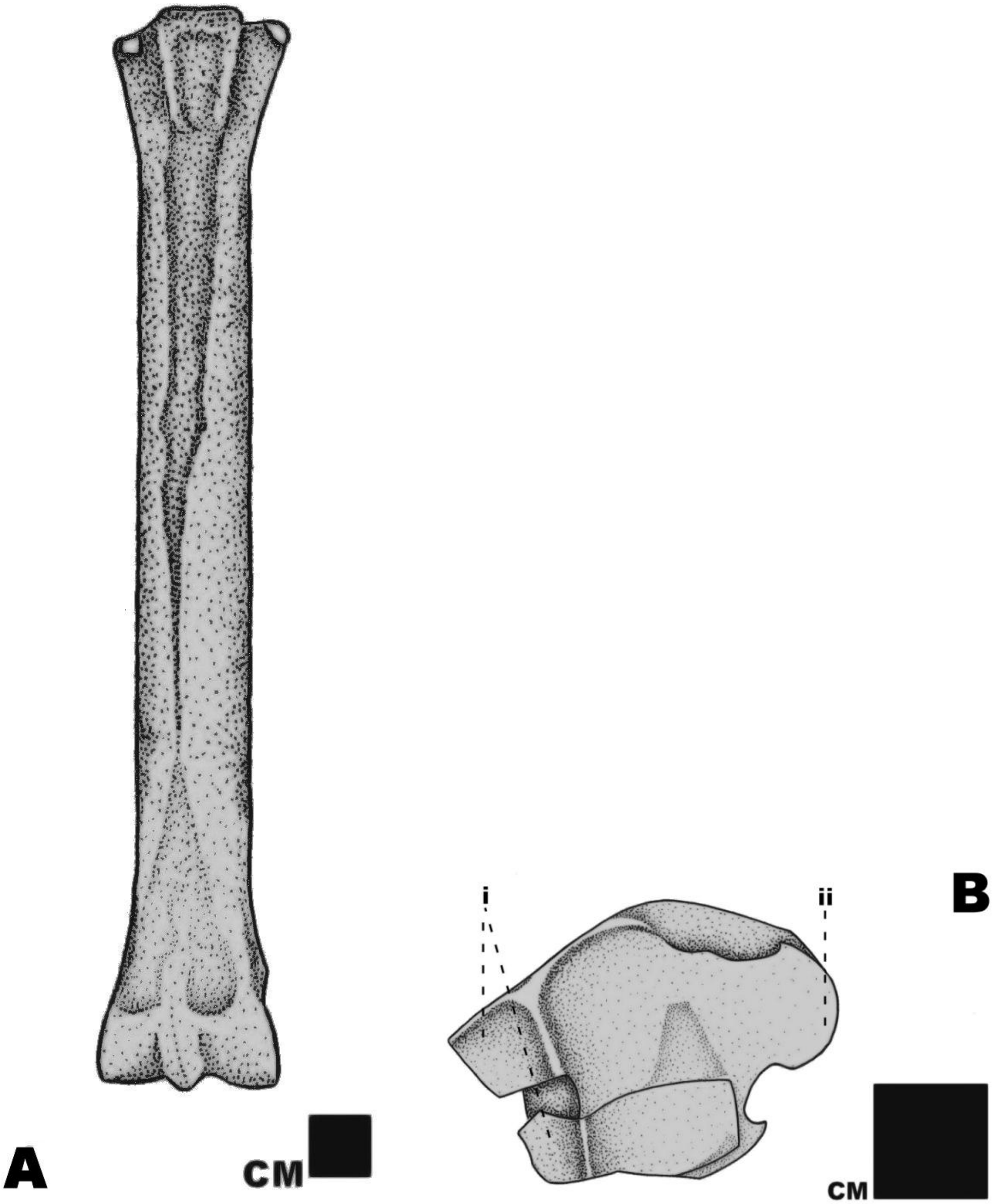


FIGURE 10. Metacarpal of *Calippus* sp. (VP-13296) from the FGP. **A**, posterior view; **B**, proximal view; **i**, articular facet for the hamatum; **ii**, articular facet for the magnum.

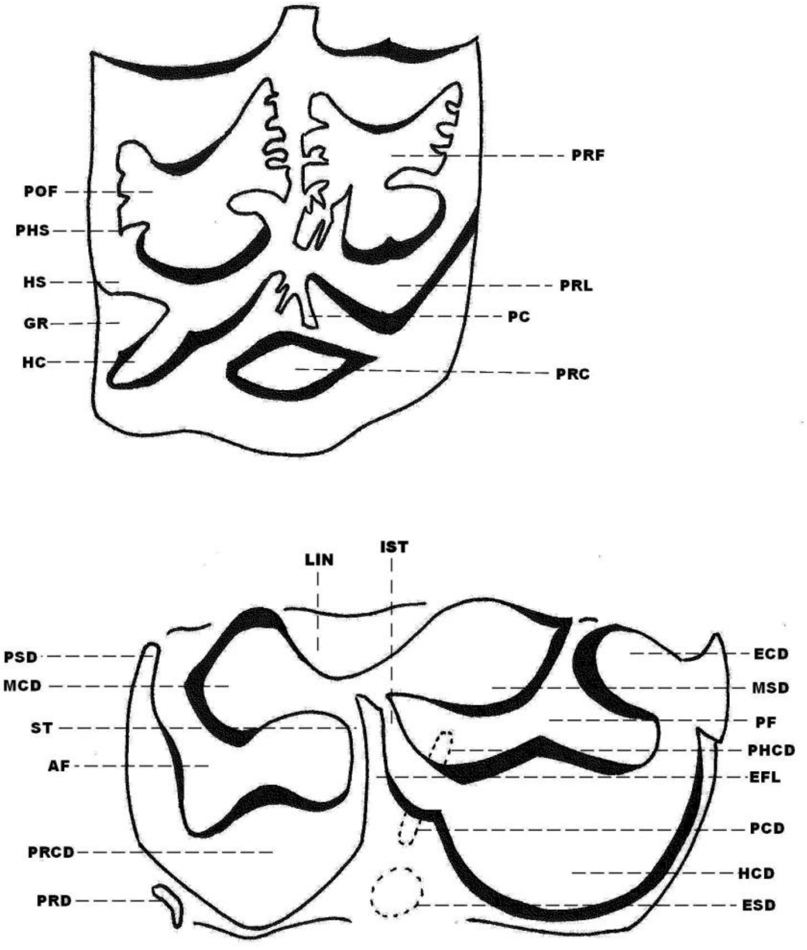


FIGURE 11. Morphology of cheek teeth in varying groups of equid. **AF**, anterior fossetula; **ECD**, entoconid; **EFL**, ectoflexid; **ESD**, ectostylid; **GR**, hypoconal groove; **HC**, hypocone; **HCD**, hypoconid; **HS**, hypostyle; **IST**, isthmus; **LIN**, linguaflexid; **MCD**, metaconid; **MS**, mesostyle; **MSD**, metastylid; **PC**, pli caballin; **PCD**, pli calballinid; **PF**, posterior fossetula; **PHCD**, pli hypoconid; **PHS**, pli hypostyle; **POF**, postfossette; **PRC**, protocone; **PRCD**, protoconid; **PRD**, protostylid; **PRF**, prefossette; **PRL**, protocomule; **PSD**, parastylid; **ST**, stalk (After Forstén, 1978). (Not to scale.)

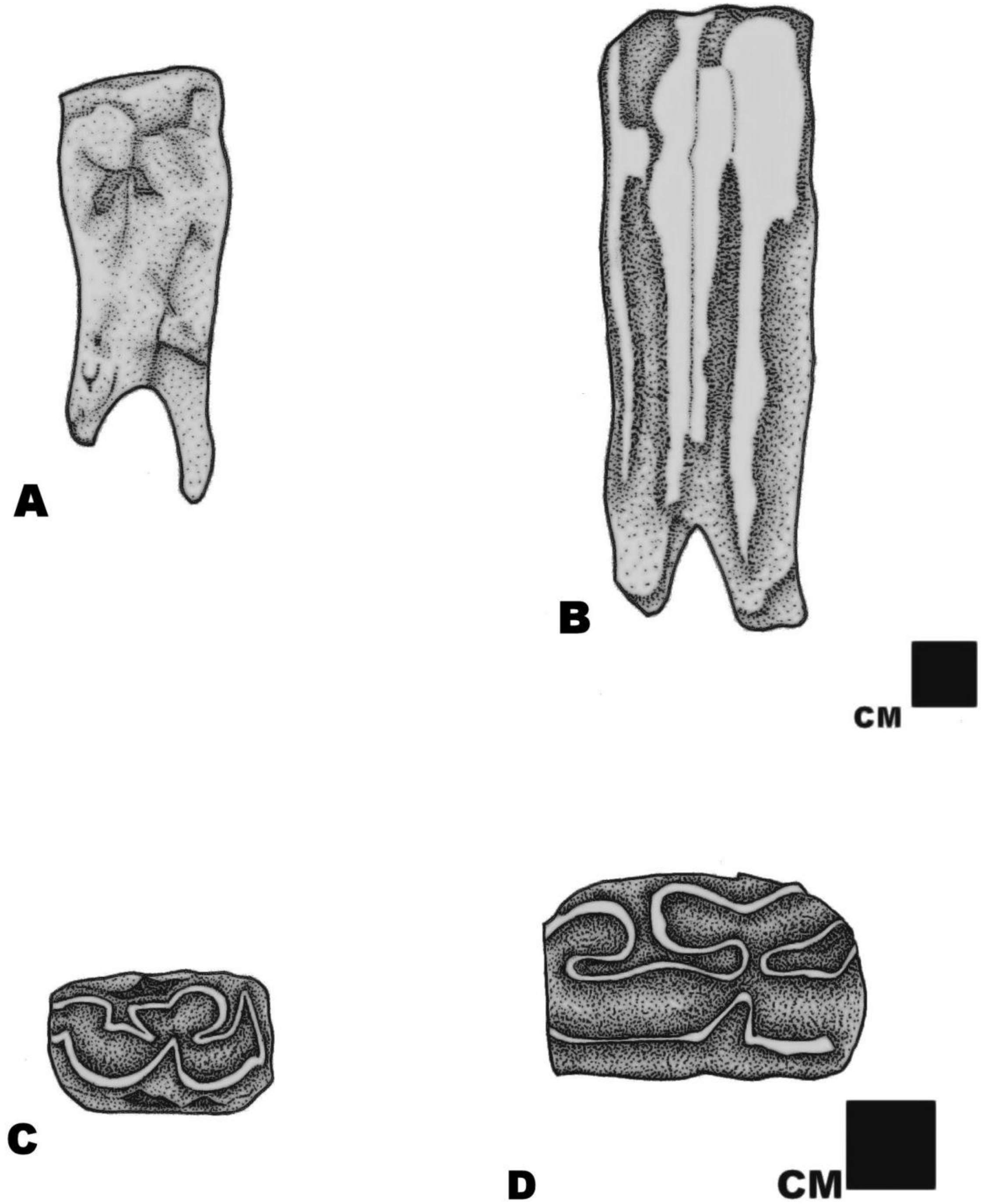


FIGURE 12. Representative equid teeth from the FGP. *Protohippus supremus* ? (VP-17296) **A**, labial view; **C**, occlusal view; *Neohipparion* sp. (VP-17365) **B**, labial view; **D**, occlusal view.

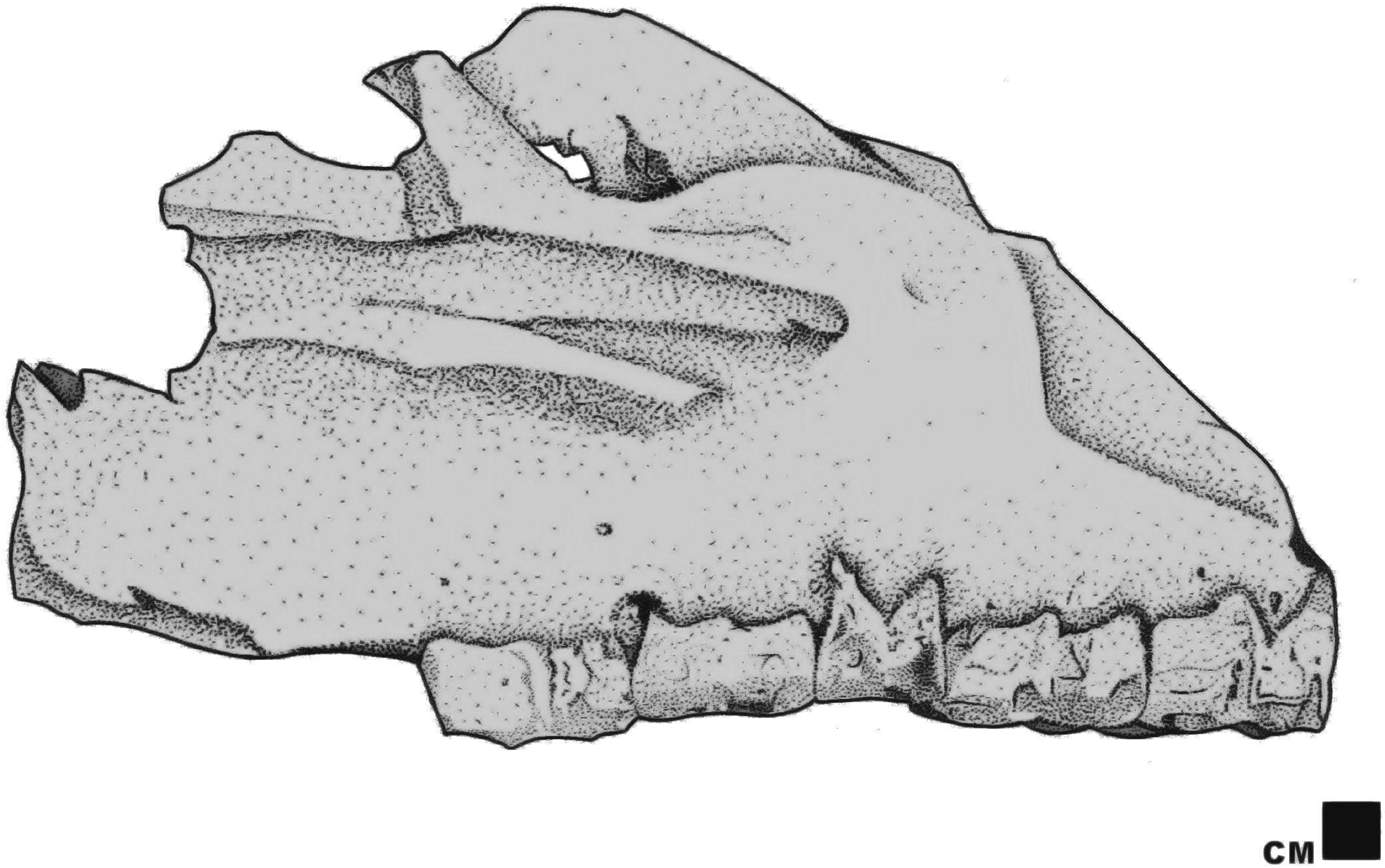
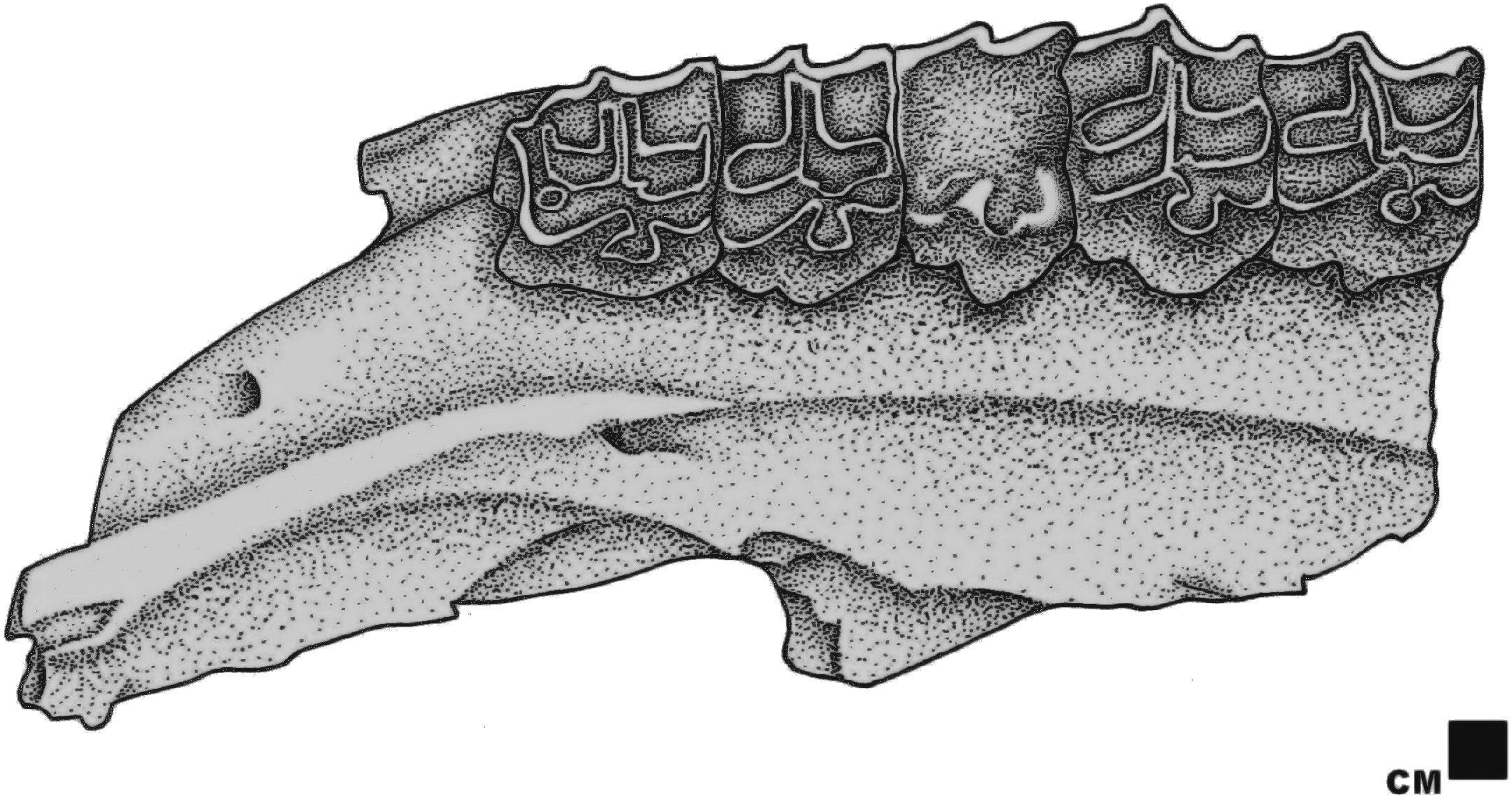


FIGURE 13. Partial right maxillary of *Protohippus* sp. (VP-13292) with P3-M3, infraorbital foramen and partial facial crest. in labial view.



FGIURE 14. Partial right maxillary of *Protohippus* sp. (VP-13292) with P3-M3 in occlusal view.

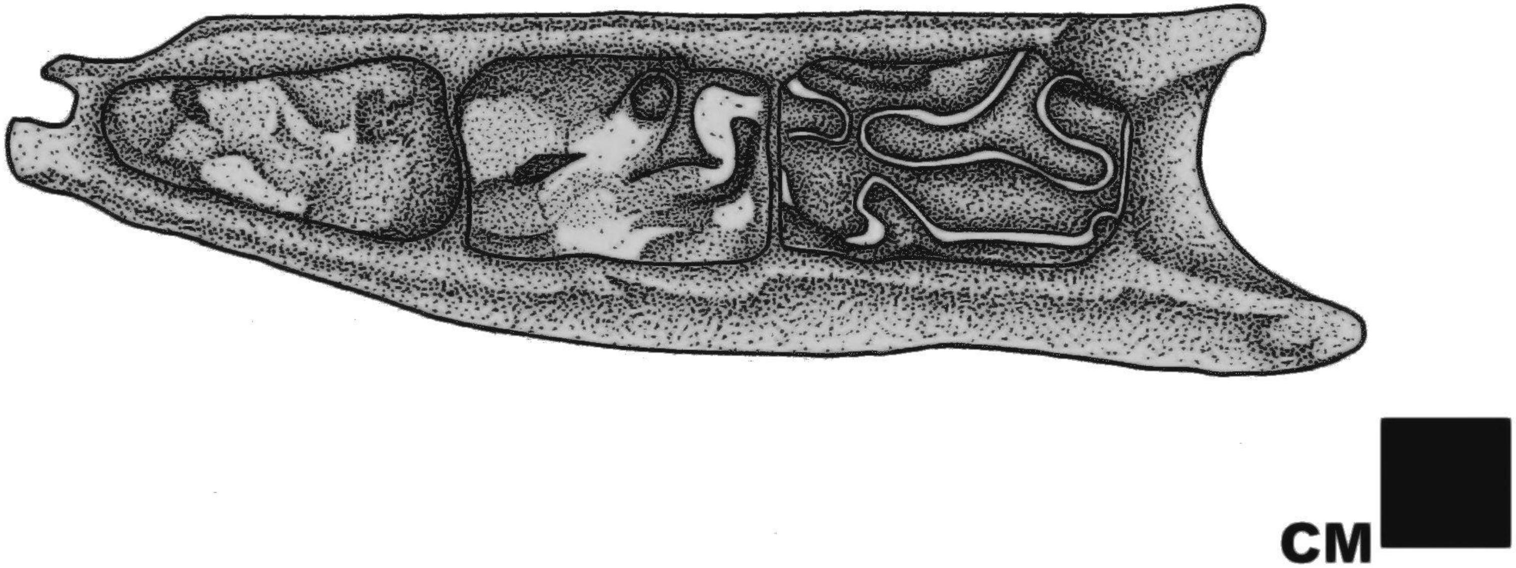


FIGURE 15. Partial left dentary of *Neohipparion trampasense* ? (VP-13958) with fragments of p2 and p3 in alveoli and full p4 in occlusal view.

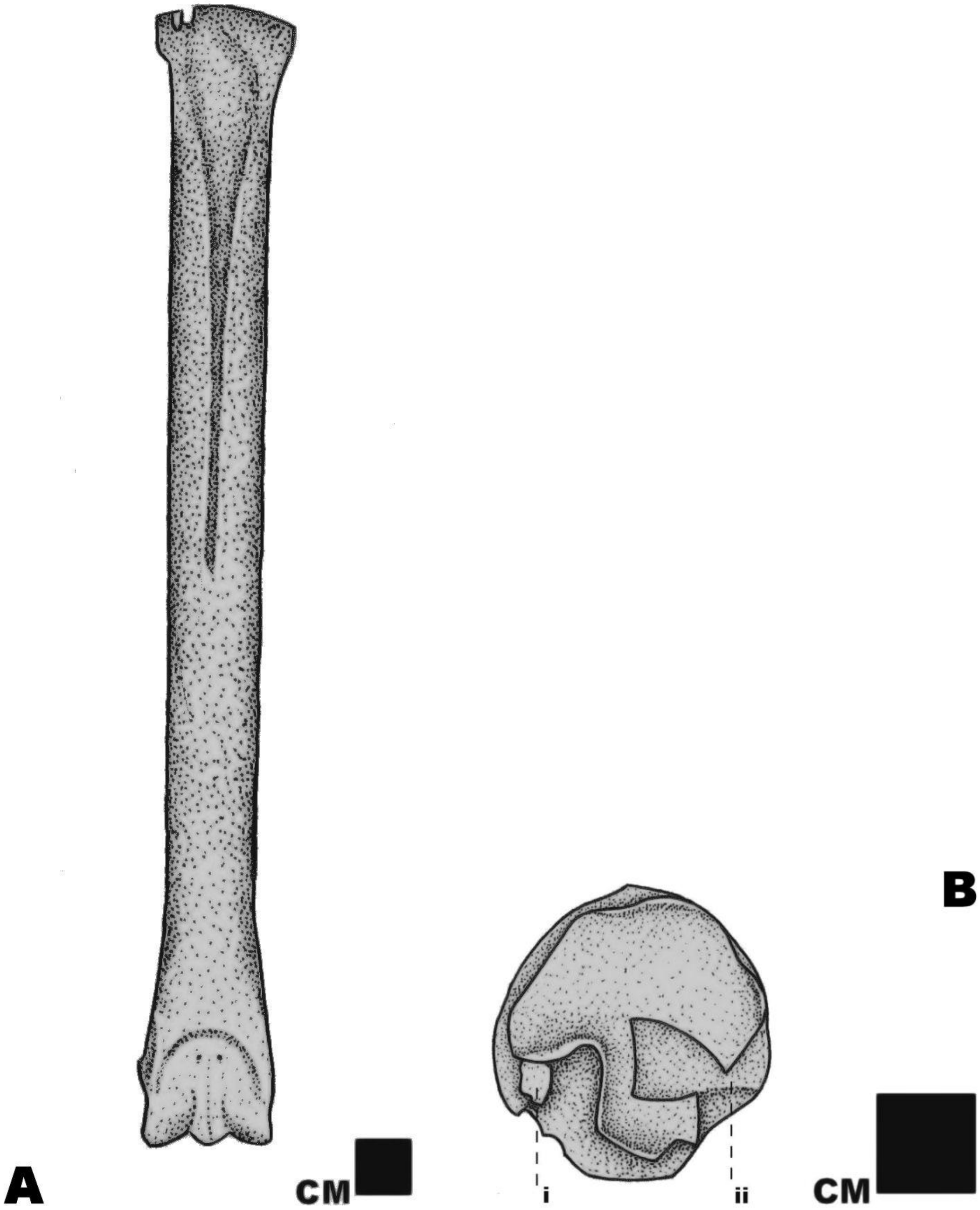


FIGURE 16. Metatarsal of *Neohipparion* sp. (VP-13924) from the FGP.

A, posterior view; **B**, proximal view; **i**, articular facet for the second metatarsal;

ii, articular facet for the fourth metatarsal.

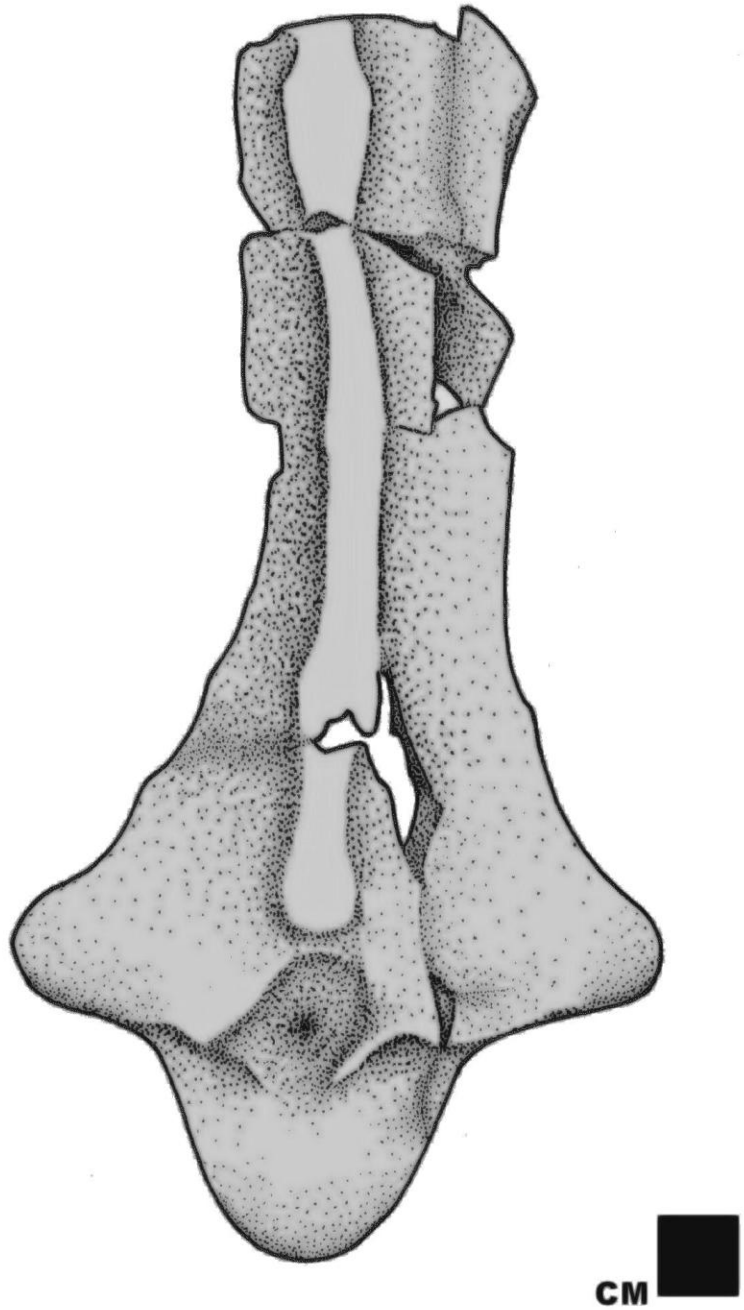


FIGURE 17. Partial cervical vertebra (axis) of indeterminate equid (VP-17387) in ventral view.

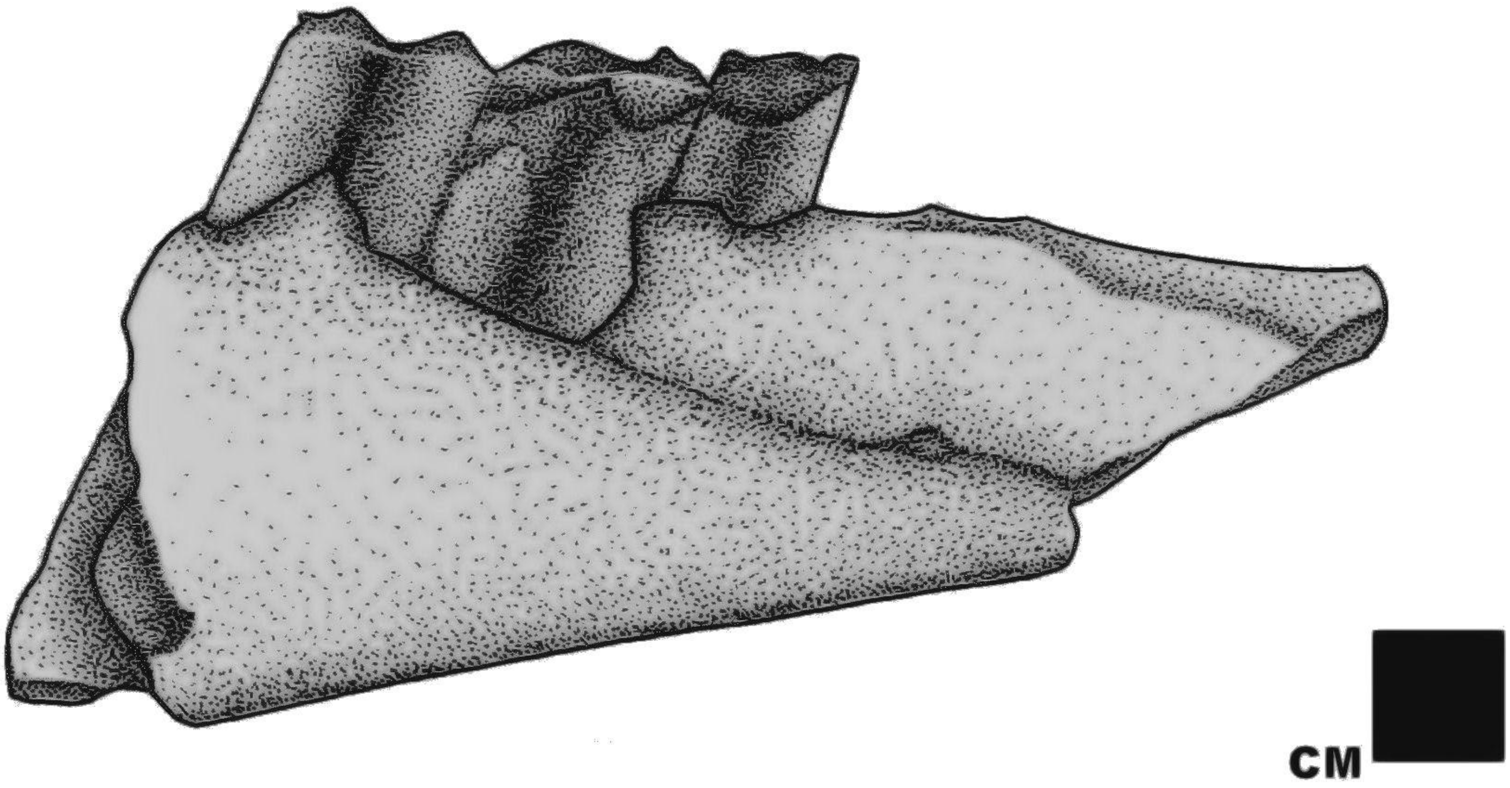
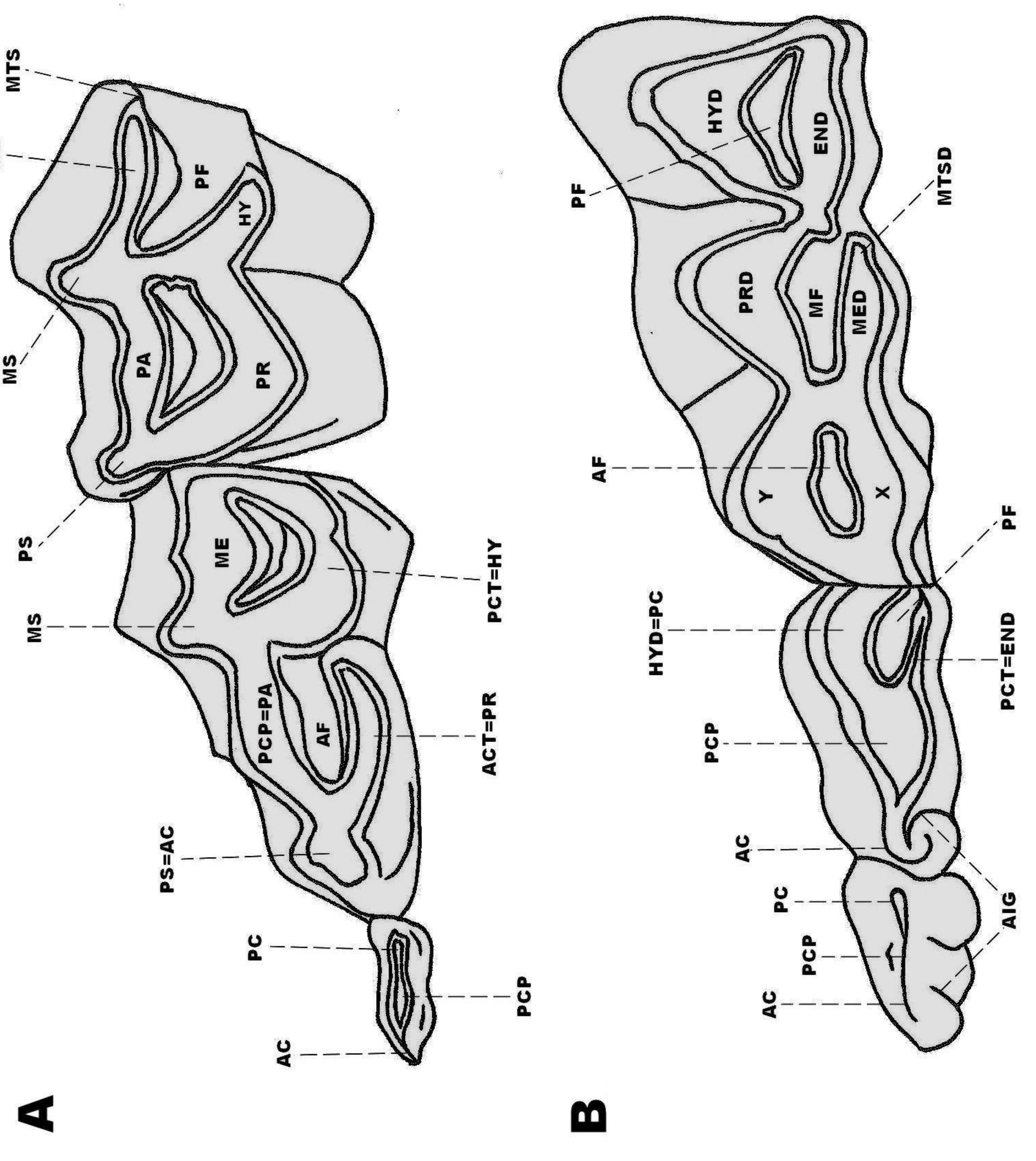


FIGURE 18. Partial right dentary of antilocaprid (VP-13954) with p3-m1 in labial view.

FIGURE 19. Morphology of camel milk teeth (on facing page).

A, left dP2-4; **B**, right dp2-4; **AC**, anterior crest; **ACT**, anterior crescent; **AF**, anterior fossette or fossettid; **AIG**, anterointernal groove; **END**, entoconid; **HY**, hypocone; **HYD**, hypoconid; **ME**, metacone; **MED**, metaconid; **MF**, median fossettid; **MS**, mesostyle; **MTS**, metastyle; **MTSD**, metastylid; **PA**, paracone; **PC**, posterior crest; **PCP**, primary cusp; **PCT**, posterior crescent; **PF**, posterior fossette or fossettid; **PR**, protocone; **PRD**, protoconid; **PS**, parastyle; **X**, lingual anteroconid; **Y**, buccal anteroconid (After Loring and Wood, 1969). (Not to scale.)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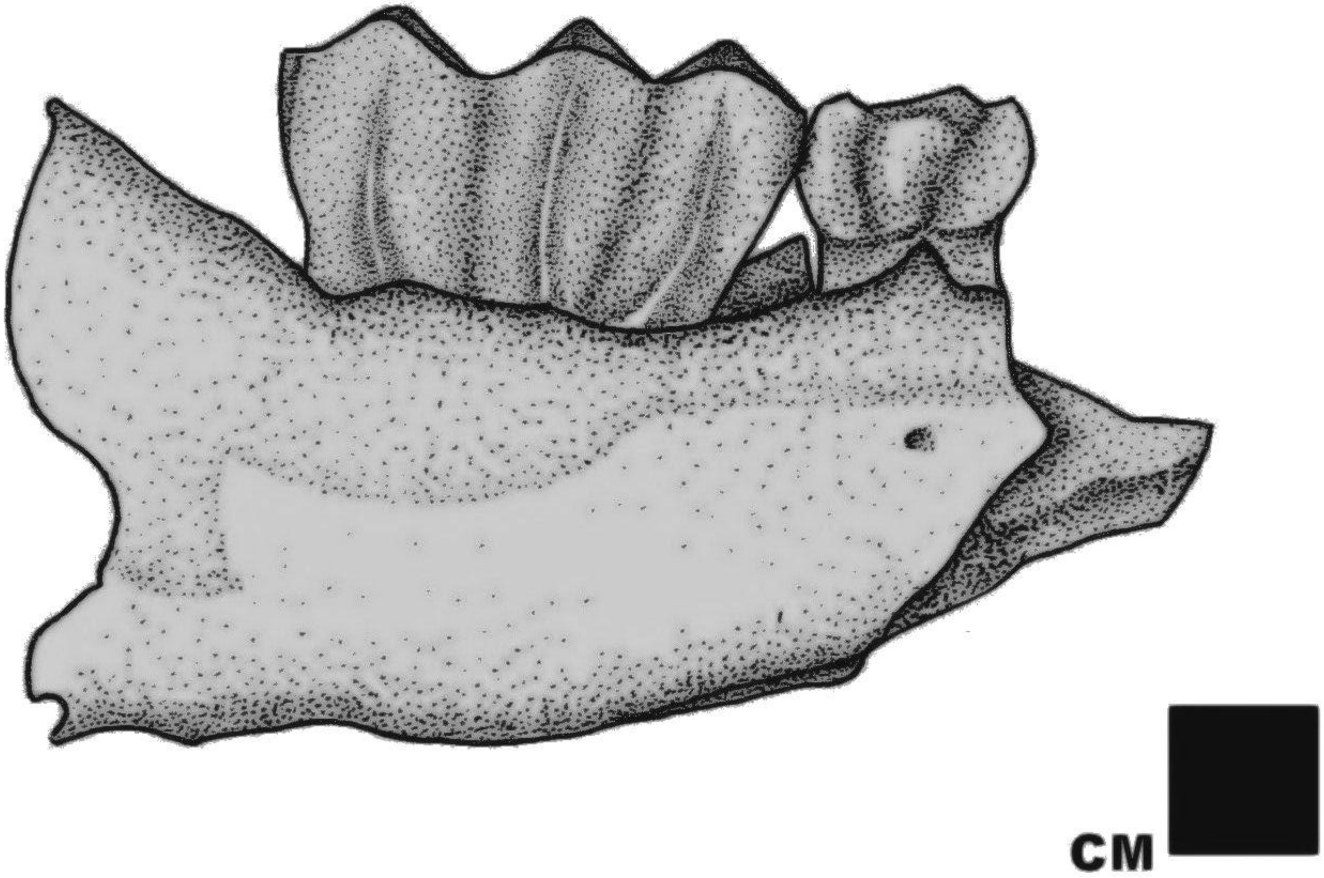

FIGURE 20. Partial right dentary of *Protolabis* sp. (VP-13346) with p3-p4 in labial view.

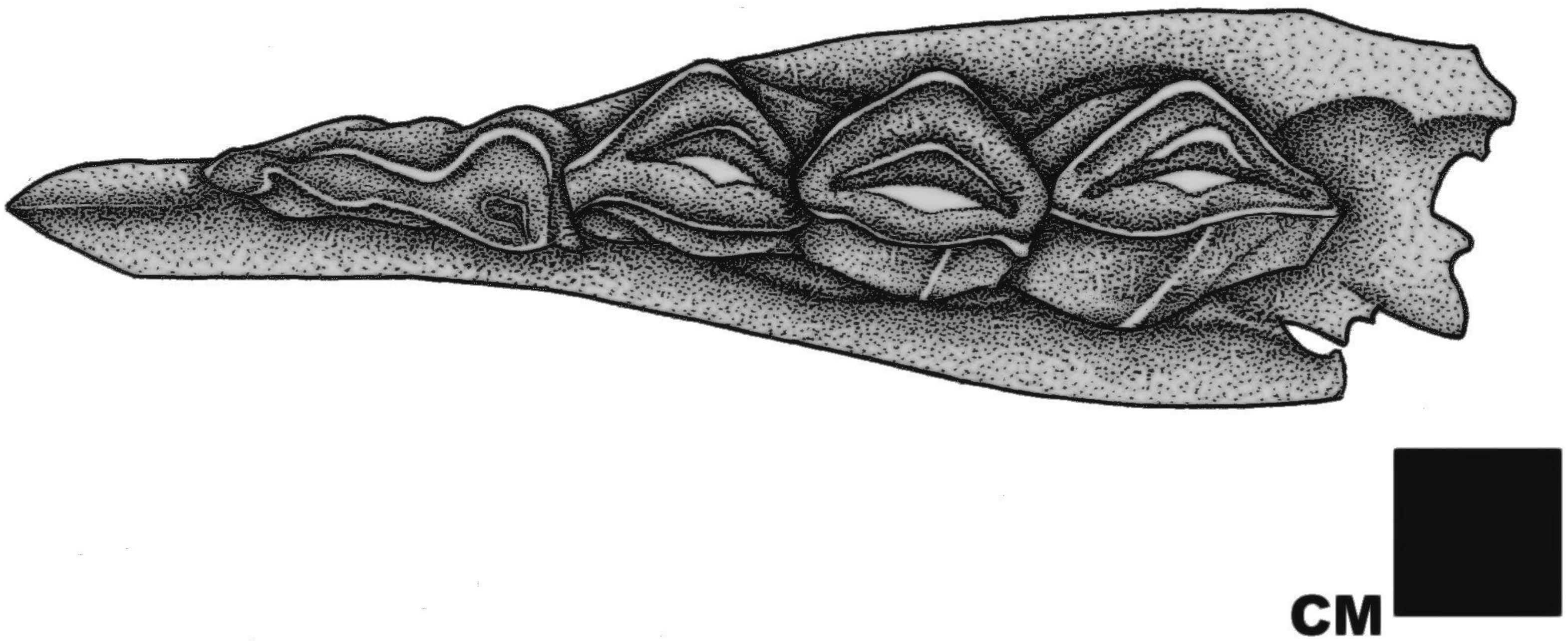

FIGURE 21. Partial right dentary of *Protolabis* sp. (VP-13346) with p3-p4 in occlusal view.

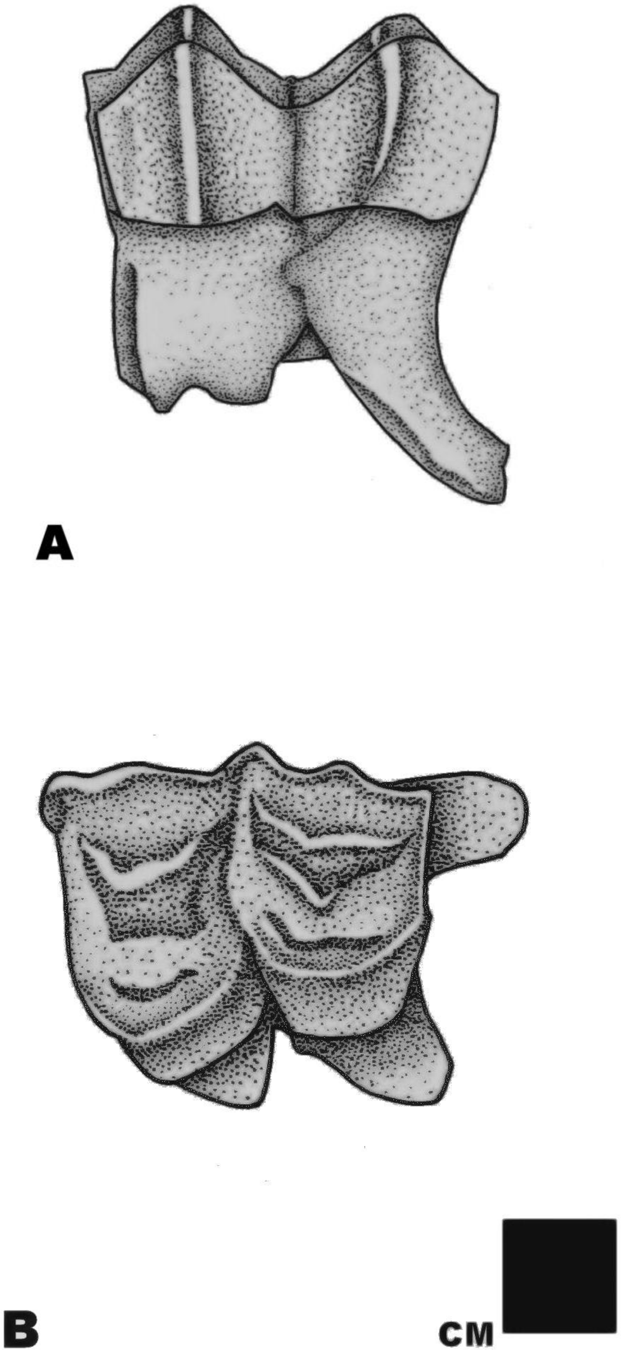

FIGURE 22. *Protolabis* sp. tooth (LdP4) from the FGP (VP-13927) in **A**, labial view and **B**, occlusal view.

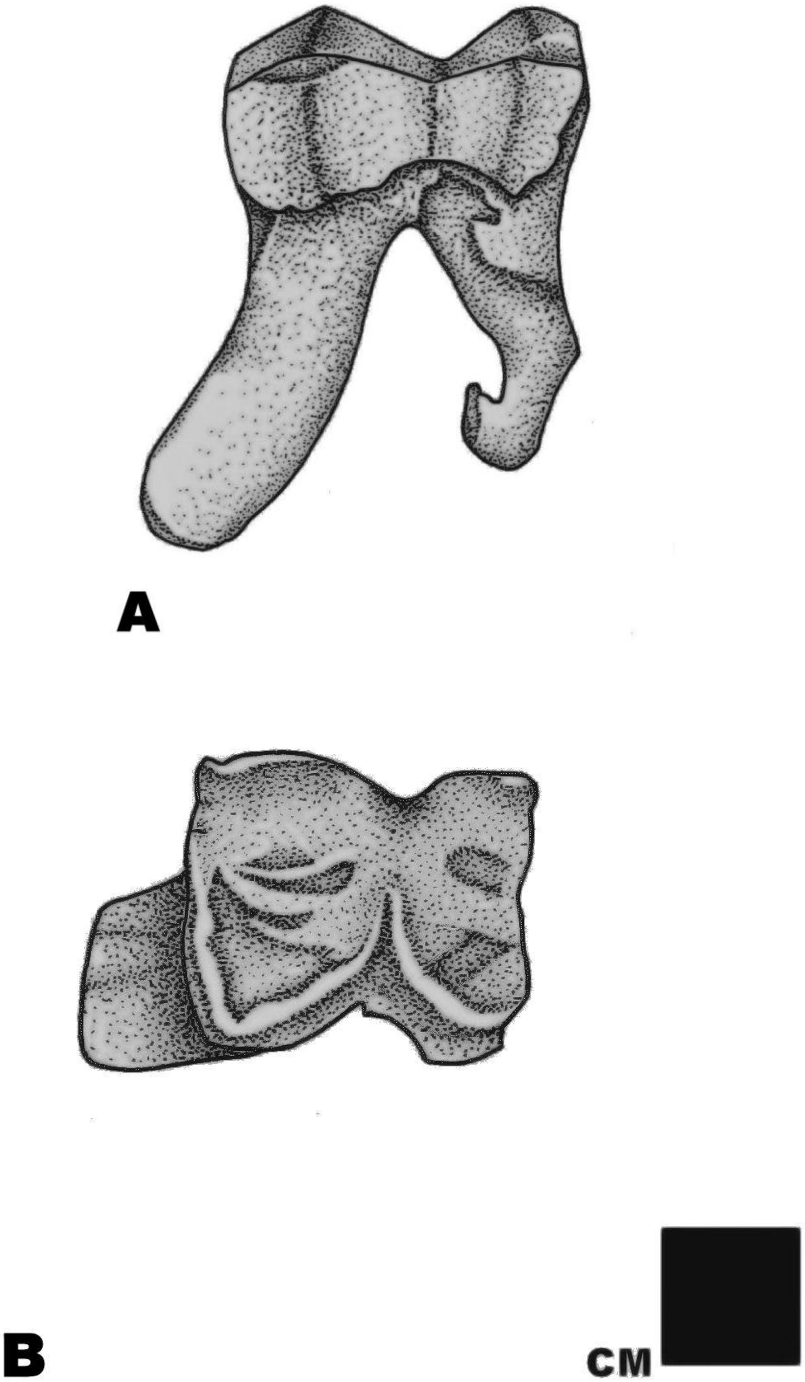

FIGURE 23. *Hemiauchenia* sp. tooth (Rm1) from the FGP (VP-17363) in **A**, labial view and **B**, occlusal view.

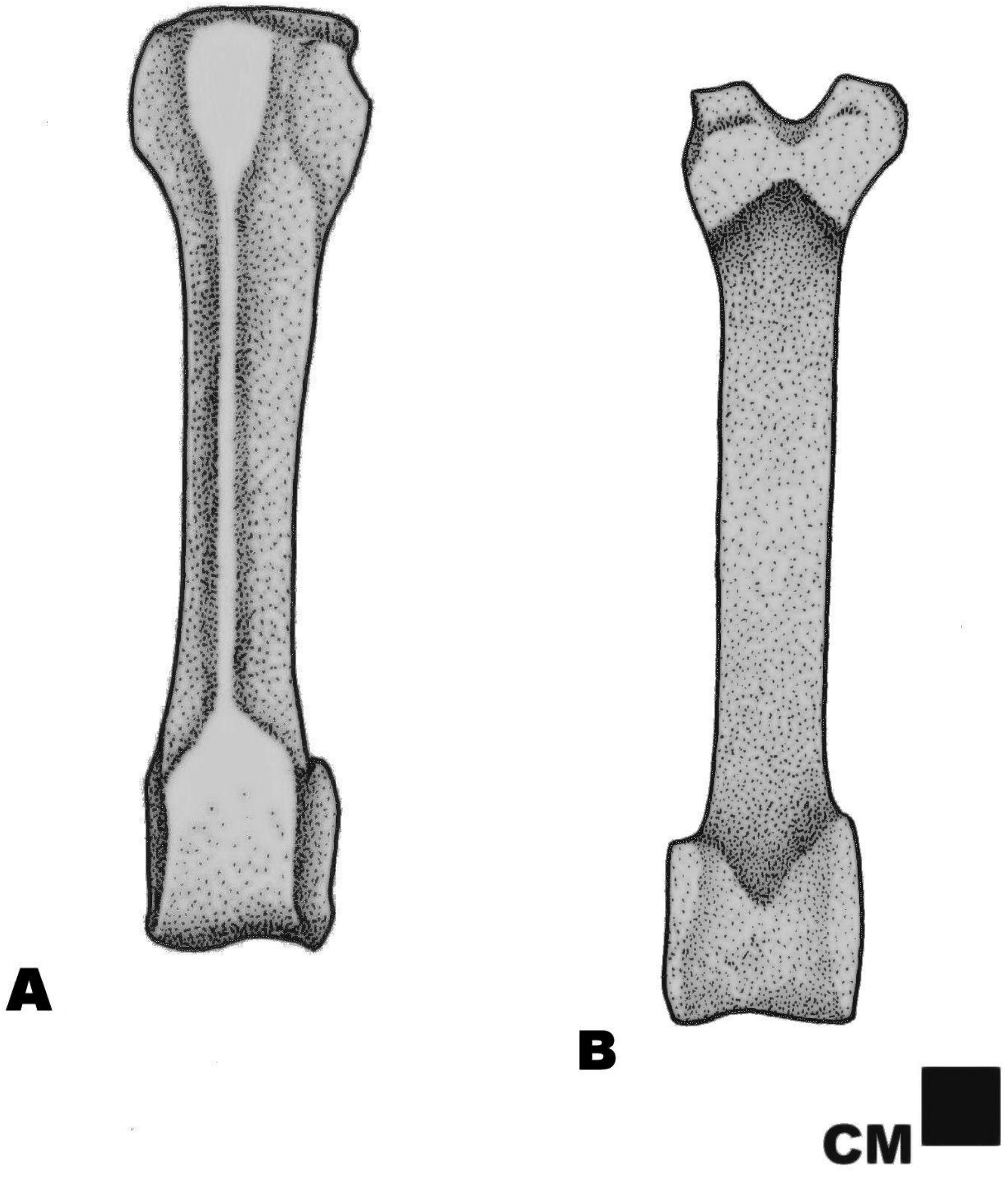

FIGURE 24. First phalanx of *Hemiauchenia* sp. (VP-13301) in **A**, anterior view and **B**, posterior view.

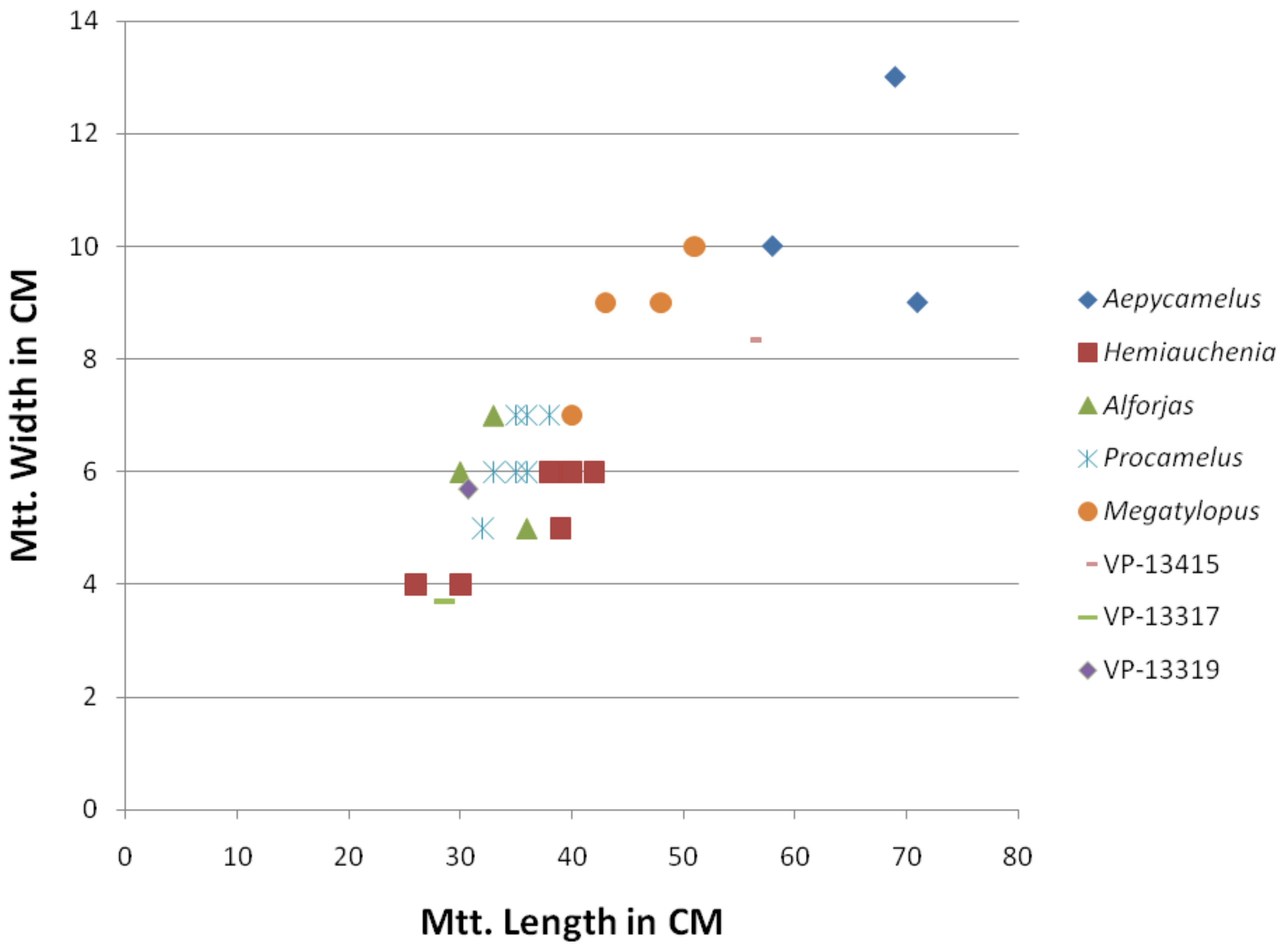

FIGURE 25. Plot of metatarsal length vs. distal width. Plots are based on values presented in Table 5 (Modified from Brever, 1983).

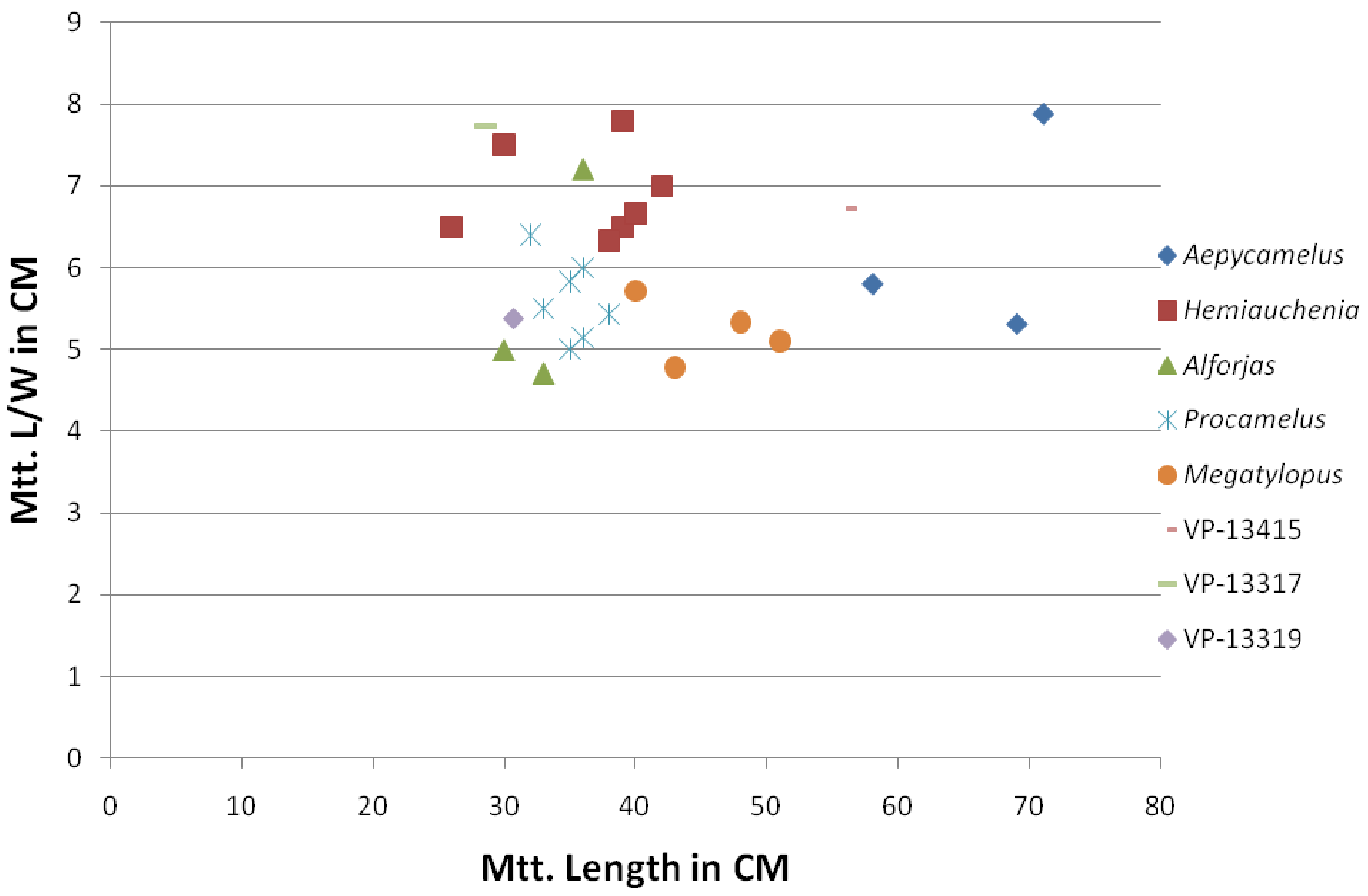

FIGURE 26. Metatarsal length vs. ratio of length to distal width. Plots are based on measurements presented in Table 5 (Modified from Breyer, 1983).

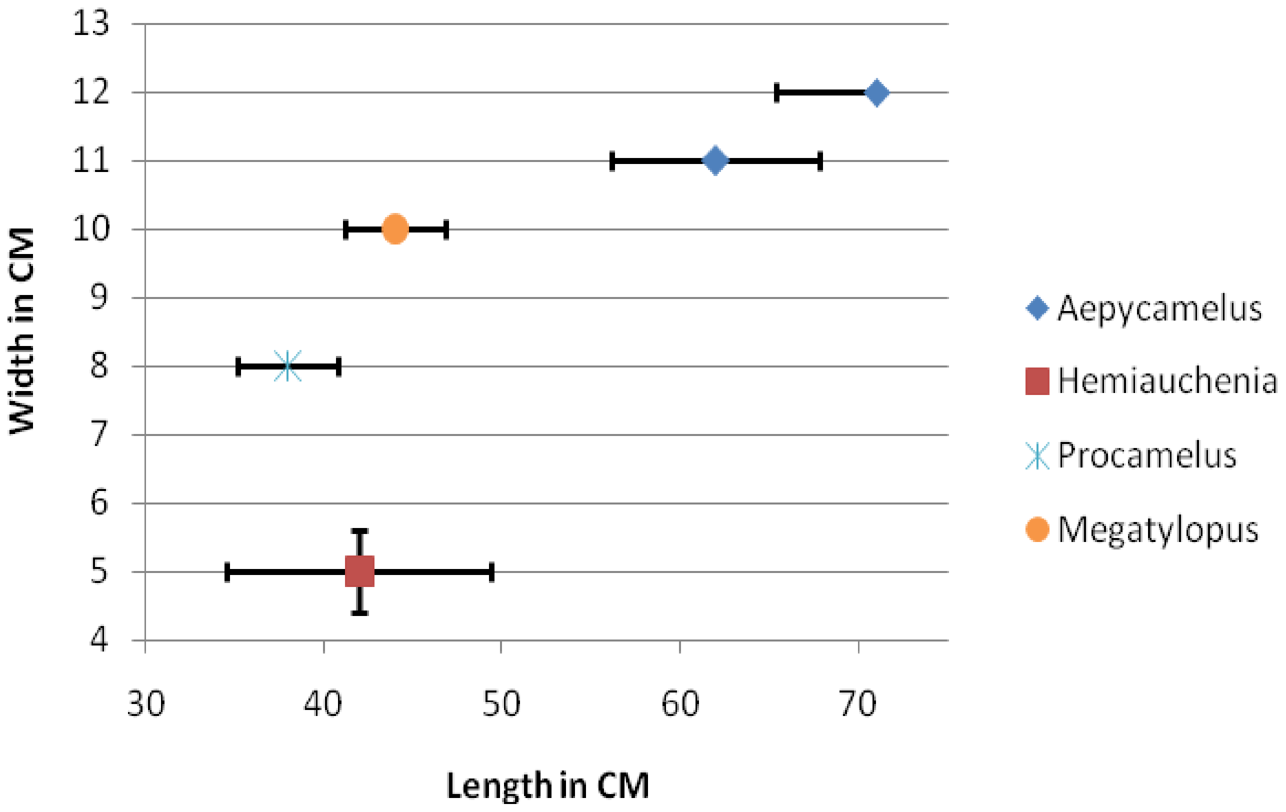

FIGURE 27. Metatarsal length vs. distal width for early Hemphillian camels. Plots are based on measurements from Table 5.

Bars drawn to include two standard deviations about the mean length for sample sizes of four or more (Breyer, 1983).

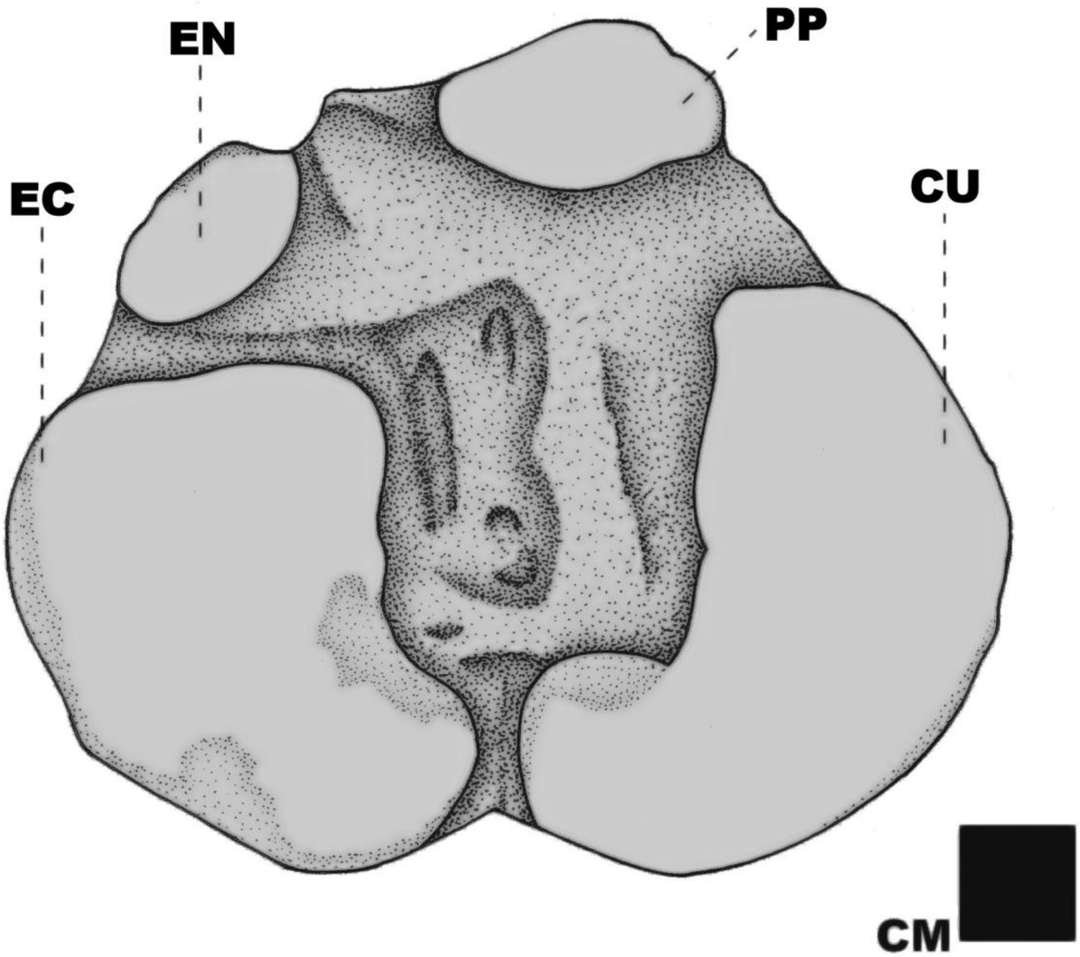

FIGURE 28. Proximal metatarsal osteology of *Alforjas* sp. (VP-17380)

CU, Cuboid Facet; **EC**, Ectomesocuneiform Facet; **EN**, Entocuneiform Facet;

PP, Plantar Process.

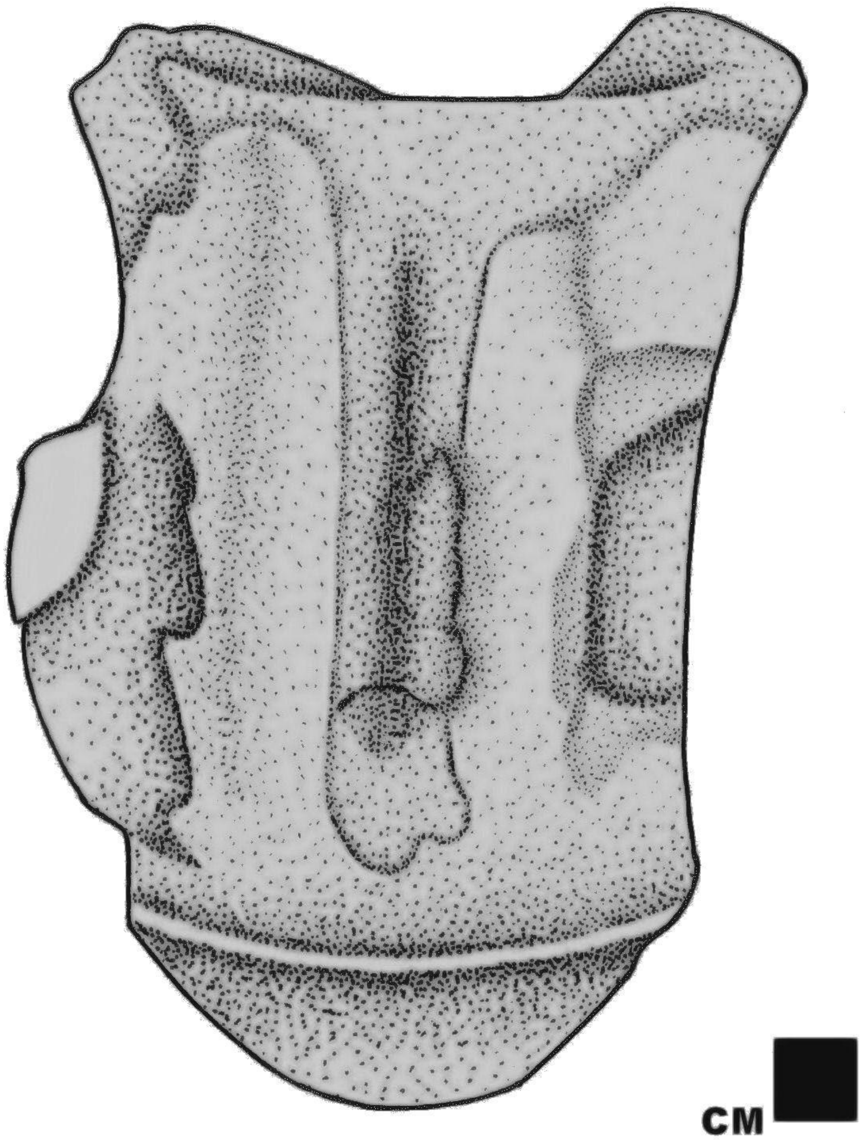

FIGURE 29. Partial vertebra of *Megatylopus* (VP-13570) in dorsal view, demonstrating an opisthocoelous orientation. Neural spine and transverse processes are broken.

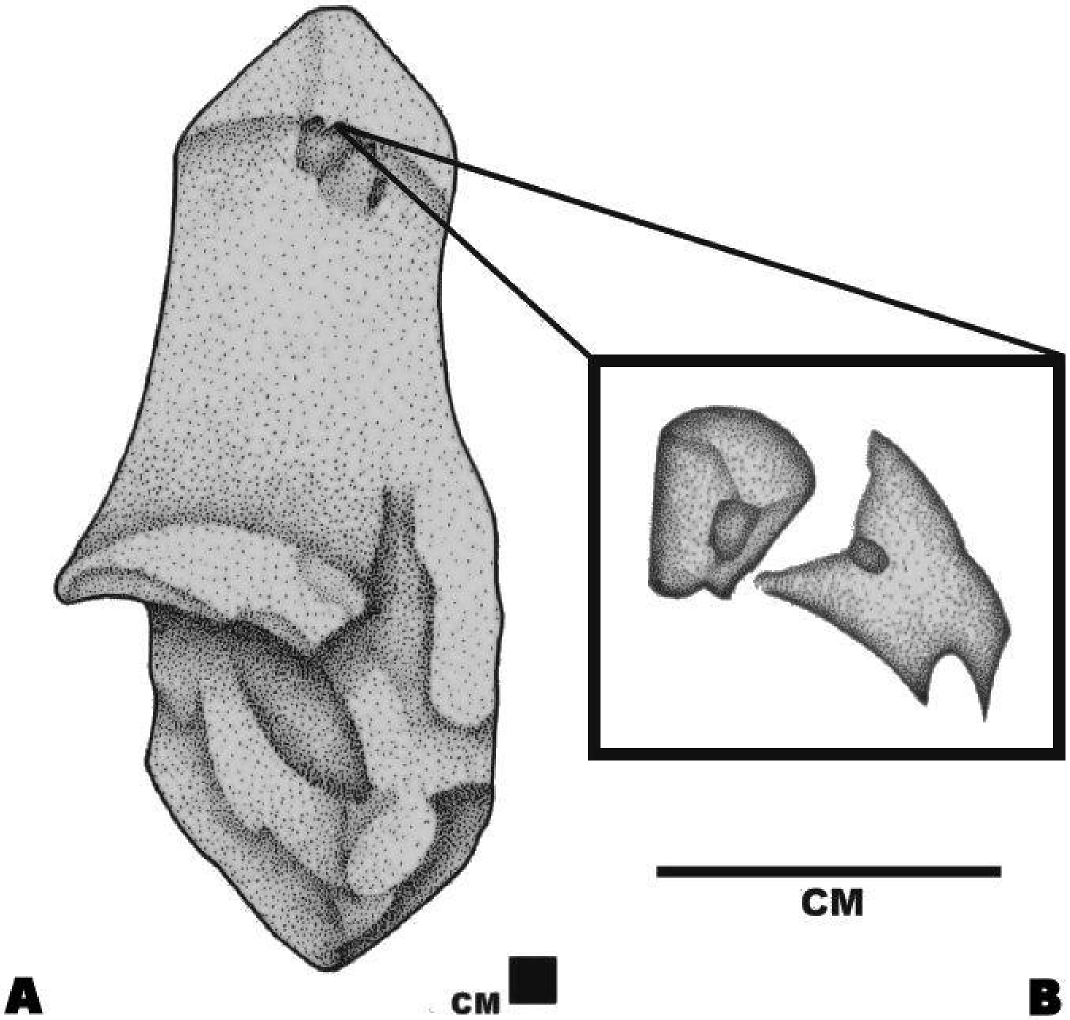

FIGURE 30. Calcaneum of *Megatylopus* sp. (VP-13926) in **A**, anterior view and **B**, emphasized view to highlight potential predation or scavenging.

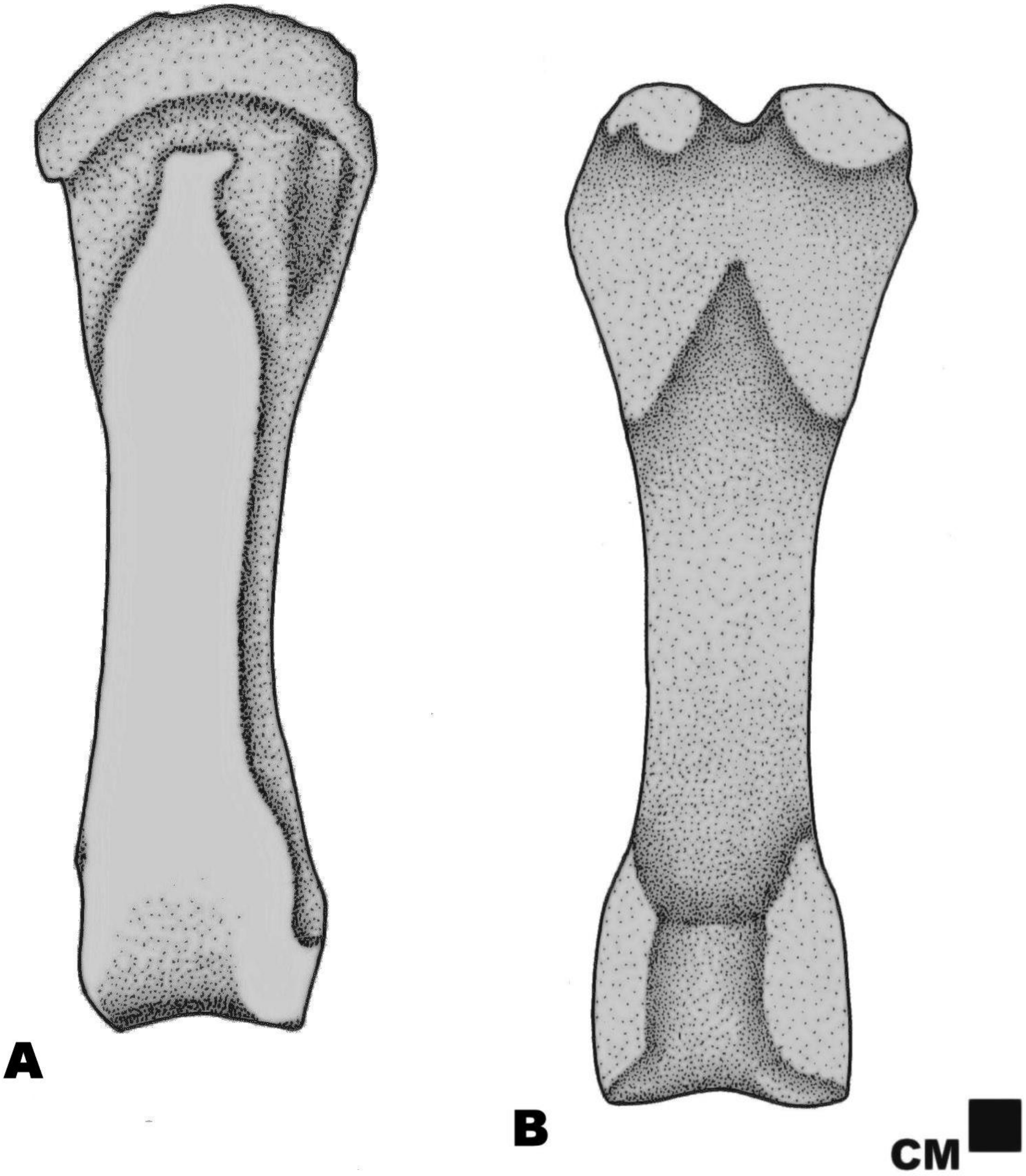

FIGURE 31. First phalanx of *Megatylopus* sp. (VP-13300) in **A**, anterior view and **B**, posterior view.

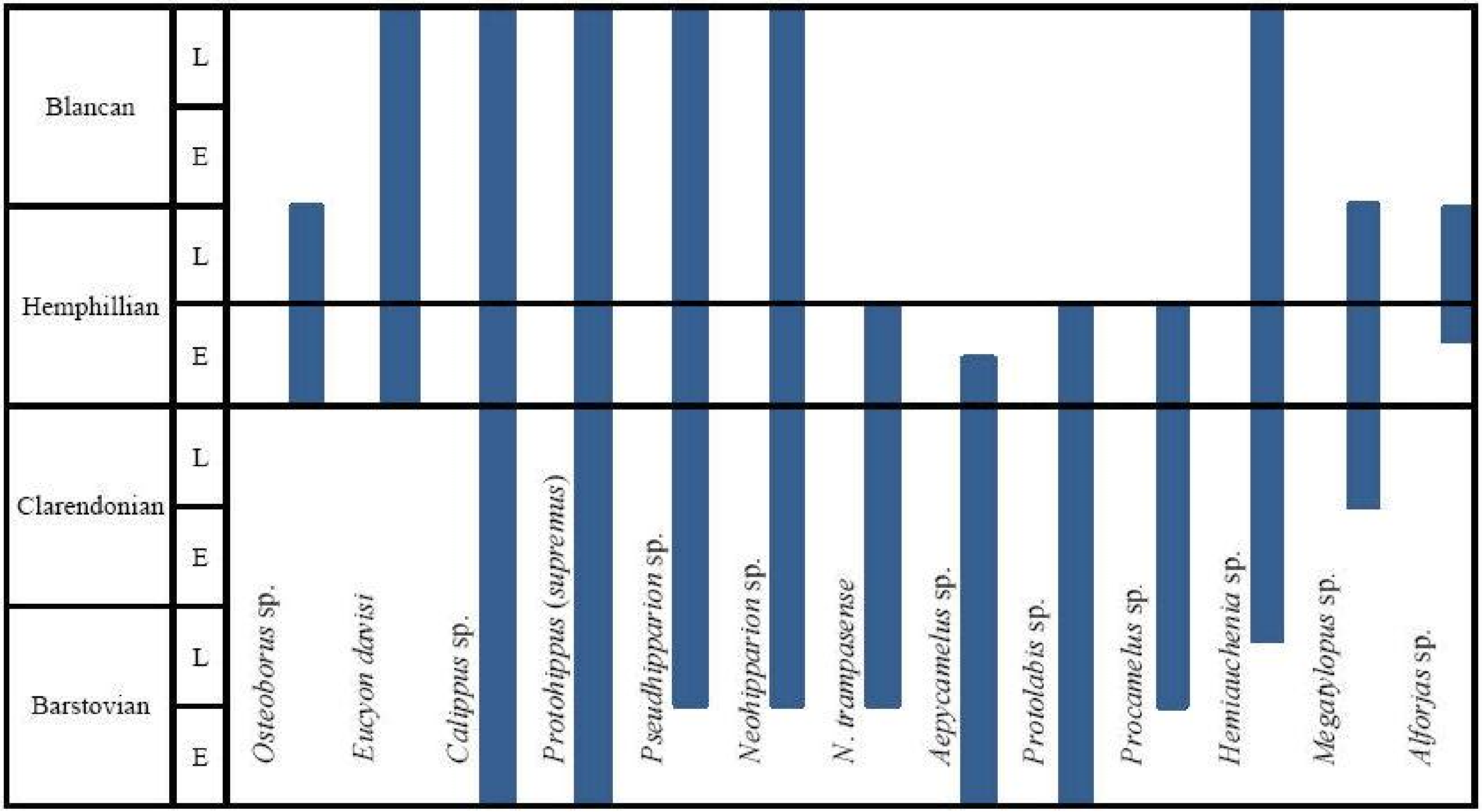

FIGURE 32. Biostratigraphic ranges of the mammalian fauna from the FGP.