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PLEISTOCENE EQUIDAE FROM SHERIDAN COUNTY, NEBRASKA

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ABSTRACT—The horse metapodials collected by field parties of the University of Nebraska State Museum from the medial Pleistocene "Equus Beds" of northwestern Nebraska appeared to represent three species. Most of the specimens (219 metacarpals and 289 metatarsals) belonged to the asinid species *Equus* (*Asinus*) *niobrarensis* Hay (1913). Six metacarpals and three metatarsals represented a small hemionid, *E.* (*Hemionus*) *francisci* Hay (1915) and one metatarsal was that of the large hemionid *E.* (*H.*) *calobatus* Troxell (1915). The referral of each horse dentition in the Museum's collections was not possible because no known dental characteristics appeared to be reliable in distinguishing either the asinids from the hemionids or identifying any of three species indicated by the metapodials. However, based on the small number of hemionid metapodials most of the dentitions were assumed to be those of *E.* (*A.*) *niobrarensis* and provided a good example of the range of variation in a single fossil horse species, a range that was greater than had usually been accepted. One of the purposes of this study is to provide a quantitative picture of this range of variation.

INTRODUCTION

PALEONTOLOGISTS have frequently called the Pleistocene channel fills and depositional terraces bordering the Niobrara River in northwestern Nebraska the "Sheridan County *Equus* Beds." Although many different taxa were recovered from fossil quarries in these deposits, horse fossils were especially common. Among the specimens collected were the holotypes of *Equus niobrarensis* Hay (1913) and *Equus hatcheri* Hay (1915) which were incorporated in the collections of the United States National Museum. Several thousand additional specimens were collected by the University of Nebraska State Museum, and it is these specimens that are described in this paper.

Some controversy existed concerning the precise geologic age of the "Sheridan County *Equus* Beds." Schultz and Martin (1970) thought the strata were deposited during the Yarmouthian Interglacial, while Hibbard believed (Pers. commun., 1973) that the age was Yarmouthian or Illinoian. Though the discovery of several layers of datable volcanic ash of Pleistocene age (Izett et al., 1970) caused revision of the Pleistocene correlation charts, no ash layer was found in the Sheridan County quarries (Schultz and Martin, 1970, p. 347). Although the exact age of the "Sheridan County *Equus* Beds" remained unknown, a general age of medial Pleistocene was generally accepted.

MATERIAL AND MEASUREMENTS

All the specimens studied were located in the University of Nebraska State Museum collections and bore catalogue numbers of the Museum. A list of numbered specimens is available from the writer upon request.

Although a variety of skeletal elements were collected by the Museum, only the skulls, dentitions and metapodials were studied since these were the elements that furnished the holotypes for the described species and were therefore most valuable for comparative purposes.

Only six skulls (Table 1) were present in the Museum's collections and few conclusions could be reached concerning the total range of variation in skull characteristics for a species. The dentitions used as a basis for the statistical analyses did not include unassociated teeth. However, the unassociated teeth did not appear to be outside the range of variation indicated by the partial dentitions. The tooth nomenclature was derived from Quinn (1955, Fig. 1) and Skinner and Hibbard (1972, Text-fig. 57).

Measurements of the individual cheek teeth were as follows: The anteroposterior length of the crown was usually measured on the triturating (wear) surface along the midline parallel to the tooth row. However, when the P^2 or P_2 were included in the measurement the distance to the most anterior portion of the tooth was included and when the M^3 or M_3 was included

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TABLE *1*—Skull measurements and ratios for *Equus* (*Asinus*) *niobrarensis* from the Sheridan County quarries. All measurements are in millimeters.

Measurements and Ratios	Number (UNSM)					
	5982	1349	5979	5981	5978	5989
1. Lgth. med. basilar, for. mag. incisive border	—	465	—	540.5	553	569
2. Lgth. med. vertex, occipit-ant. incisive border	602	500	—	566.5	583	626
3. Lgth. med. facial, postorbit-ant. incisive border	429	365	—	410	434	442
4. Lgth. med. cranial, postorbit-occipital	209.5	150	—	199	211.5	196
5. Lgth. med. occip.-tip nas.	—	—	—	487	—	—
6. Lgth. med. occip.-nas. notch	411	209	—	387.5	401	408
7. Lgth. med. occip.-nas. overlap	—	292	—	295.5	—	—
8. Lgth. med. for. mag.-vomer	—	51	—	31.5	23	—
9. Lgth. med. for. mag.-postpalatine border	—	130.5	—	131	104	—
10. Lgth. med. for. mag.-post M^3	217.5	149.5	—	215	200	229
11. Lgth. med. for. mag.-post P^4	300	189	—	122	222	225.5
12. Lgth. med. for. mag.-ant. P^2	397	263.5	—	299	303	310
13. Lgth. med. for. mag.-postpalatine fissure	238	350	—	387	403	445
14. Lgth. med. muzzle, ant. P^2-Inion	523.5	224	—	141	266	238
15. Diastema I^3-C	424	440	—	(580.5)	477	—
16. Diastema C-P^2	80.5	—	—	31	38	41.5
17. Diastema I^3-P^2	116	—	—	84	73	85
18. Width, muzzle across 3d incisors	(78)	94	—	125.5	117	135.5
19. Width, muzzle narrowest point palatal side	—	61.5	—	—	76	86
20. Width, muzzle widest part ant, nares on premaxilla	68.5	42	—	51	55	—
21. Width antorbital, narrowest point	—	66	—	115	81	80
22. Width, postorbital rim, widest point	—	132	—	—	150	—
23. Width, outside temp. cond.	202	—	—	—	226	—
24. Width, zygomatic arch greatest	213.5	202	219.5	—	218	—
25. Width, cranial constriction, postorbital	86	200	221.5	210	221	235.5
26. Width, cranium, widest part on squamosal	105	85	—	75	—	—
27. Width, at alv. borders, ant. cont. parastyles P^2	75	(92.5)	—	97	—	130
28. Width, at alv. borders outside metastyles P^4	124	42	—	—	102.5	80
29. Width, at alv. borders outside parastyles M^3	131	115.5	—	125.5	122	127
30. Width, facial, ant. edge masseter ridge	131	115	80	—	121	128
31. Width, occipital, at tempero-occipital sutures	112	123	156.5	141.5	135	144.5
32. Width, across occipit on postemporal process	122	—	—	—	—	—
33. Width, across occ. cond.	89.5	—	—	—	130	—
34. Width, across base paraocc. proc.	116	75	—	93.5	91	—
35. Depth, top occipit-bottom condyles	110	—	—	115.5	116	118.5
36. Depth, plane of frontals-alv. border M^3	—	—	—	121	—	115
37. Depth, plane of nasals-alv. border P^2	—	109.5	—	143.5	—	144
38. Diam. orbit. horizontal	65	93	—	119	118	—
39. Diam. orbit. vertical	56	60	—	58.5	68	—
40. Temporal condyle (postcenter)-Inion (Direct)	92	55	—	55	48.5	—
41. P^2-M^3	182	—	—	264	—	—
42. P^2-P^4	121.5	163	—	166	183	182
43. M^1-M^3	86	89	—	94	104	94.5
44. P^2-A-P	26	79	86.5	74	82	85
45. Pr.	11.5	35	—	40	41	42.
46. Tr.	26	9.5	—	—	18	10
47. Ht.	—	25.5	—	25	20.5	26
48. P^3-A-P	29.5	—	—	—	—	—
49. Pr.	12	26.5	—	30	31	28
50. Tr.	29.5	14	—	—	16	—
51. Ht.	—	29	—	27.5	30	—
52. P^4-A-P	28	—	—	—	50	—
53. Pr.	13	6	31	25	30.5	28
54. Tr.	30.5	15	15	15	17	15
55. Ht.	—	29	31	30	29	52
56. M^1-A-P	25	—	—	—	—	15
57. Pr.	12	23.5	26.5	23	26	25
58. Tr.	29	14	12	—	13	14
59. Ht.	—	28	30	—	27	—
60. M^2-A-P	26.5	—	(40)	—	—	—
61. Pr.	14	25	28	23	27	27
62. Tr.	28.5	14	14	15	14	13.5
63. Ht.	—	27	29	25.5	26	29
64. M^3-A-P	31	—	—	—	—	—
65. Pr.	14.5	25	33	26	21	32.5
66. Tr.	26	15	14.5	15	12	16
67. Ht.	—	23	27	23	21	26.5
68. Ontogenetic age	Immature	Old	Mature	Old	Mature	Mature

the most posterior point of the tooth was measured. The crown width measured was the maximum width, including the cementum and was measured at right angles to the buccal surface of the tooth. The crown height was measured from a point between the base of the roots to the middle of the trituration surface. Other measurements made were the anterior-posterior protocone length, and the metaconid-metastylid columns length.

In order to make comparisons with earlier descriptions, several ratios between molar measurements were computed: length of crown to width of crown, length of crown to length of protocone, and length of crown to length of metastylid-metaconid columns.

Metapodial measurements and ratios included the maximum length of metapodial, the medial transverse width, the medial anterior-posterior depth, the transverse and antero-posterior measurements of the proximal and distal articulations. The ratios computed were maximum length to medial width, medial width to medial depth, transverse diameter to antero-posterior diameter of both the proximal and distal articulations, length to the proximal articulation transverse and distal articulation transverse.

The statistical descriptions included the arithmetic mean, mode, observed range, standard deviation, and coefficient of variability. All were used as defined by Cazier and Bacon (1949, p. 352, 361–363). The number of specimens from which the provided data were calculated was also included. The tables summarizing the statistical findings have been omitted to reduce publication costs but are available from the author upon request.

SYSTEMATIC PALEONTOLOGY

Most of the descriptions of Pleistocene horses were based on the characteristics of the metapodials or dentitions. Skinner and Hibbard (1972) indicated that the dentitions of the asinids, hemionids, and amerhippids all possessed an ectoflexid that did not project between the preflexid and postflexid; the amerhippids lacked cupped incisors, a characteristic that was present in the asinids and hemionids. In the dolichohippids and equids an ectoflexid that projected between the flexids was present. The Sheridan County horses in the Museum's collection all exhibited an ectoflexid that did not project between the preflexid and post flexid and also had cupped incisors. The presence of these characteristics indicated that the specimens represent either *Equus* (*Asinus*) or *Equus* (*Hemionus*). Skinner and Hibbard (1972) state that *E.* (*Hemionus*) could be identified on the basis of three characteristics: 1) the skull has a very light, small occipital region 2) the lower dentition has a direct isthmus uniting the metaconid metastylid columns with the protoconid and hypoconid and 3) the metapodials are long and slim. Although no measurements were given for the "light, small occipital region" of the hemionids, the occipits of the Niobrara horses do not appear to be light or small and therefore must be those of an asinid.

The lower dentitions of *E.* (*Asinus*) and *E.* (*Hemionus*) were alike in the construction of the isthmus and therefore this characteristic was of no value in distinguishing the two subgenera. However, the long slim metapodials of the hemionids were easily distinguished from the shorter, stouter leg bones of the asinids and were the best means of identifying the two subgenera.

EQUUS (ASINUS) NIOBRARENSIS

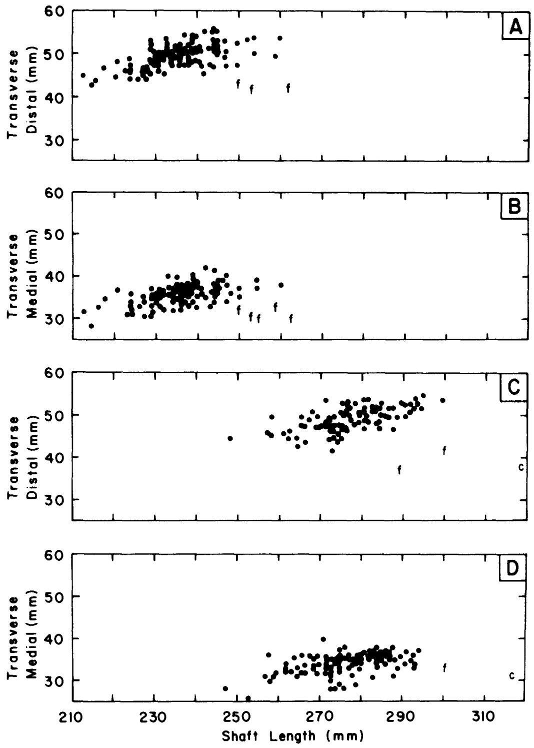
Equus niobrarensis HAY, 1913, p. 576–584, figs. 19–24.

Holotype.—Nearly complete skull U.S. National Museum (USNM) 4999.

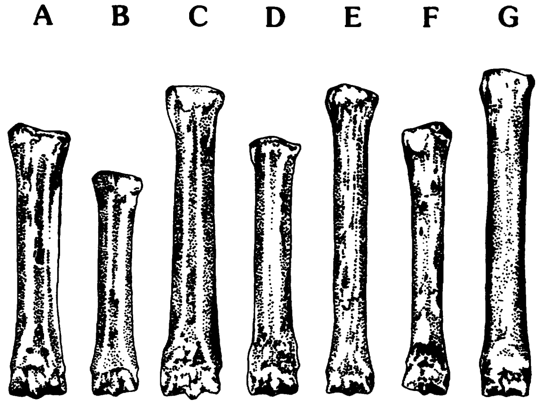
Description.—In describing his new species Hay indicated it was "characterized by teeth of rather large size, the length of the grinding surface of the first molar being about 27 mm., the width about the same. Enamel of the lakes of rather simple pattern." Hay also made several statements concerning the characteristics of the skull, noting that it was wide and had a short nose, and compared its measurements with that of a modern horse skull. He also indicated that the braincase in *E.* (*A.*) *niobrarensis* was wider than the domestic horse and the nose shorter.

Discussion.—The most numerous metapodials in the Sheridan County collections were the shorter, stouter forms (Text-figs. 1 and 2) that are indicative of the asinids. All but seven of the metapodials from these quarries were those of asinids (98%).

It also appeared that only one asinid species was present. This conclusion was based on two criteria. First, a plot of the lengths and



TEXT-FIG. *1*—Ratio of transverse distal and transverse medial measurements to the length of the shaft in metapodials from Sheridan County. dots = *Equus* (*Asinus*) *niobrarensis*, f = *E.* (*Hemionus*) *francisci*, c = *E.* (*H.*) *calobatus*. All measurements are in millimeters. *A* and *B*, metacarpals; *C* and *D*, metatarsals.



TEXT-FIG. *2*—Metapodials of Sheridan County horses. Longest and shortest metacarpals (*A,B*) and metatarsals (*C,D*) of *Equus* (*Asinus*) *niobrarensis*. Metatarsal (*E*) and metacarpal (*F*) of *E.* (*Hemionus*) *francisci*. Metatarsal (*G*) of *E.* (*H.*) *calobatus*. See Text-fig. 1 for measurements.

widths of the heavy metapodials did not appear to produce a bimodal distribution in either measurement and secondly, the range of metapodial length found in these specimens was very similar to that found in several species of living horses.

The identification of a bimodal distribution was difficult. From the statistical point of view a population was truly bimodal if the differences between the two modes approaches twice the standard deviation of what appears to be the bimodal curve. It is of course possible that two species were present whose size ranges were very similar. In such an instance, size could not be used as a diagnostic characteristic. Seldom was any fossil collection so ideal as to produce a perfect bell-shaped distribution for a single measurement and some class intervals would usually be poorly represented. This situation was not necessarily an indication of bimodality or the presence of several species.

Second, the range of 51 mm in the length of the heavy metatarsals from the Sheridan County quarries was similar to that found in some modern horse species. Lundelius and Stevens (1970, Text-fig. 3) found a range in metatarsal length of 40 mm for *Equus asinus* and 60 mm for *E. prezewalskii*.

As indicated previously, all the skulls apparently represent members of this species. Unfortunately, the dentition did not possess characteristics that made it possible to isolate the teeth of the hemionids from the asinids.

Referred Specimens.—Partial Skulls—6. Metacarpals—139 complete; 80 partial. Metatarsals—137 complete; 152 partial.

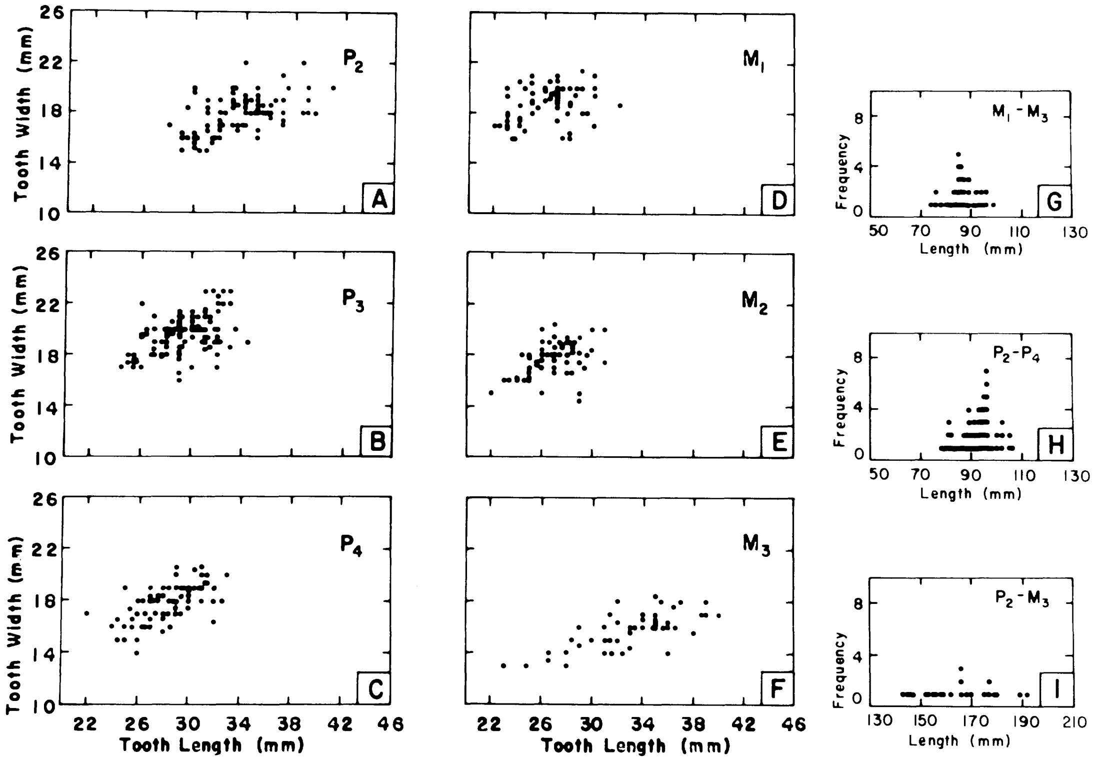
EQUUS (HEMIONUS) FRANCISCI

Equus francisci HAY, 1915, pp. 535–549.

Holotype.—Skull, mandible and partial skeleton, Texas Agricultural and Mechanical University Specimen number 2518.

Description.—Hay described the species as a small Pleistocene horse which was about the size of *Equus tau* Owen, but unlike *E. tau*, with the last premolar and anterior two molars wider than long. He also noted that the enamel pattern of the cheek teeth was simple.

Discussion.—The statement by the original author (Hay, 1915) that the last premolar and anterior two molars were wider than long and



TEXT-FIG. *3*—Frequency of the longer dental measurements and the relationship of the length to width measurements in the lower permanent cheek teeth of the horses from the Sheridan County quarries, species indeterminant (interpreted to be 98% *Equus* (*Asinus*) *niobrarensis*). All measurements are in millimeters.

that the enamel pattern was simple did not appear to be diagnostic in the light of our current knowledge of the amount of variation in Pleistocene horse species (Howe, 1966; 1970).

Lundelius and Stevens (1970) restudied the holotype and several referred specimens and concluded that the species was also characterized by small teeth with simple enamel patterns, V-shaped metaconid-metastylid grooves (linguaflexids), a rounded metaconid, a posteriorly pinched metastylid and thin metapodials. The shape of the metaconid, metastylid and linguaflexid appear to be of little use in hemionid species identification. However, when the dental length measurements given by Lundelius and Stevens, (1970) for *E.* (*H.*) *francisci* were compared to those of the Sheridan County horses the measurements given for the *E.* (*H.*) *francisci* were about three standard deviations from the mean and not represented in the Sheridan County population. If Lundelius and Steven's small-sized specimens actually represented the largest specimens of that species the species may have been identifiable on the basis of the small tooth size. If so, teeth of *E.* (*H.*) *francisci* were absent from the Sheridan County horse collection. If the measurements given by Lundelius and Stevens did not include the largest individuals, there must have been considerable overlap in dental size of *E.* (*A.*) *niobrarensis* and *E.* (*H.*) *francisci,* and tooth size was diagnostic for only the smallest members of the species *E.* (*H.*) *francisci.*

The most diagnostic characteristic in the identification of *E.* (*H.*) *francisci* was the narrowness of the metapodial articulations when compared to the overall length of the shaft (Text-fig. 1). A comparison of the measurement of the Sheridan County hemionid specimens with those of *E.* (*H.*) *francisci* (Lundelius and Stevens, 1970) indicates the presence of a hemionid of similar size.

Referred Specimens.—Metacarpals—2

complete, 4 partial. Metatarsals—2 complete, 1 partial.

EQUUS (HEMIONUS) CALOBATUS

Equus calobatus TROXELL, 1915, p. 615.

Holotype.—Metacarpal in Yale Peabody Museum.

Description.—Troxell (1915) identified the species as having limb bones that were "unusually long and slender." He also stated that the metapodials were 19.4% longer than those of the modern Arabian horse and more than one and one-half times as long as the metapodials of *E. asinus.*

Discussion.—Troxell (1915) indicated that the ratio of shaft length to median width to be a diagnostic characteristic. His statements concerning the comparison of the metapodials to those of the Arabian horse and *E. asinus* would have been more meaningful had he also included the measurements of the metapodials of the ass and the Arabian he was using, since we do not know if they were large or small representatives of their species. The measurements of my specimen are presented in Text-fig. 1.

The dentition of this species was evidently not diagnostic. Although Hibbard (1953, p. 120) indicated that the lower dentition resembled the dolichohippids with "V"-shaped linguaflexids, Skinner and Hibbard (1972) later stated that these characteristics were only of use in identifying the dolichohippids. Skinner and Hibbard (1972, p. 120) also called attention to the fact that the *Equus* (*Hemionus*) specimens in their collection possessed the following characteristics in the M_1 and M_2.

1) The protoconid is united with the metastylid by a plain isthmus.

2) The hypoconid is united to the posterior portion of the protoconid-isthmusial complex.

3) The metastylid is united with the metaconid remaining free of the hypoconid.

Of the 78 lower dentitions from the Sheridan County quarries that possessed both the M_1 and M_2, only seven (14%) specimens definitely exhibited the condition indicated. Two specimens possessed the characteristic in either the M_1 or M_2 but not both and there were ten specimens that appeared to be intermediate between the asinid and hemionid condition. Due to the comparative high percentage of specimens possessing the characteristic (1 versus less than 1% hemionid metapodials) plus the intermediate nature of many specimens, it appeared doubtful that the characteristic was diagnostic for either *E. (H.) calobatus* or the hemionids in general.

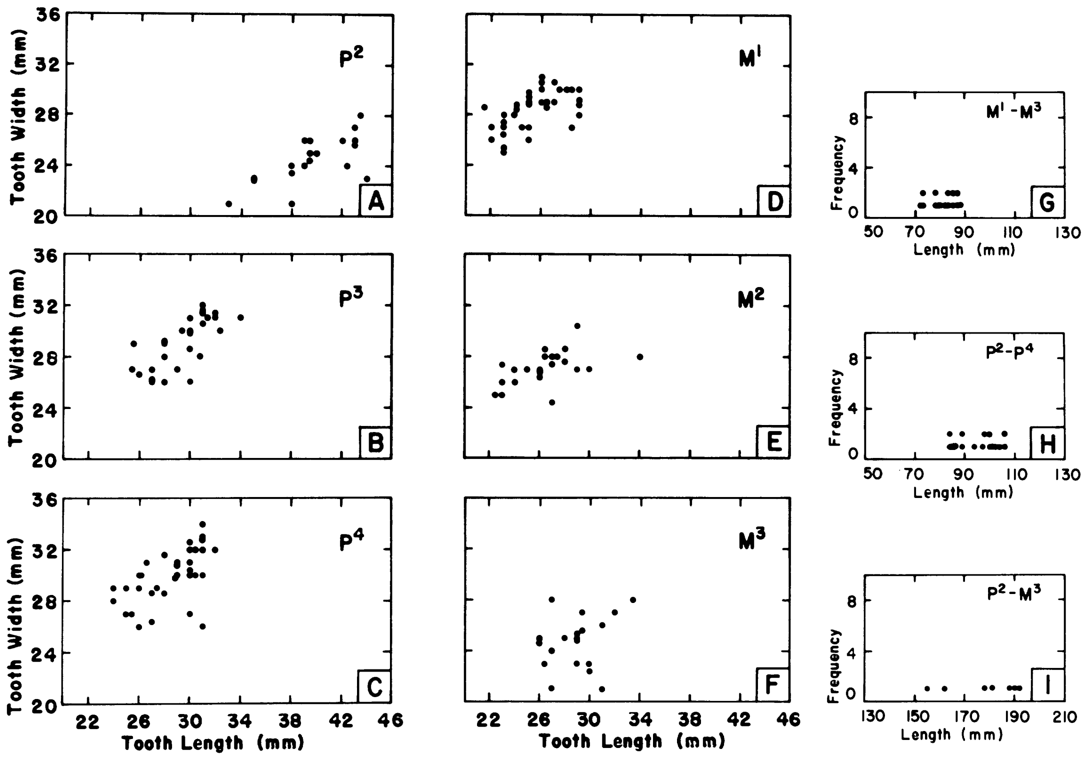
Referred Specimens.—1 complete metatarsal.

EQUUS, Subgenus and Species Indeterminant

As stated earlier in this paper, no known characteristic appeared to be valid for distinguishing the hemionid dentitions from those of the asinids. It was therefore necessary to refer the partial dentitions to the genus *Equus,* but not to any particular subgenus or species. However, at least 95% (and probably 98%) of the horse dentitions from the Sheridan County quarries, here listed as "*Equus* subgenus indeterminate" probably belonged to a single species *E.* (*A.*) *niobrarensis* (Text-figs. 3–6). This assumption was based on the belief that the hemionid dentitions would occur in about the same percentage of the total number as do the metapodials, 2% for *E.* (*H.*) *francisci* and 0.2% for *E.* (*H.*) *calobatus.*

Although the range of variation in the measurements of these teeth may have seemed extreme to some, they apparently represented one species. The basis for this conclusion rested partially on evidence provided by the metapodials here referred to *Equus* (*Asinus*) *niobrarensis.* These metapodials also exhibited a wide range of variation (Text-fig. 1). There was no reason why a similar range of variation could not occur in the dentition. In addition, there was no evidence of bimodality in the length to width scatter diagrams (Text-figs. 3, 4) of the Sheridan County dentitions.

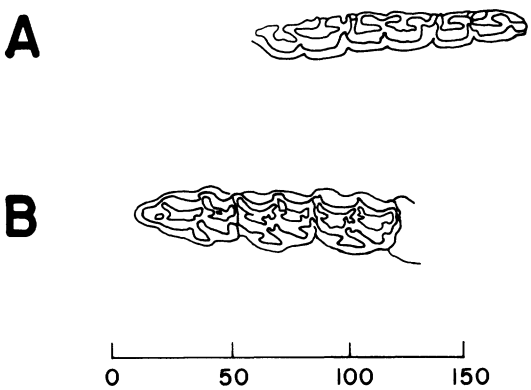
However, the coefficients of variability were somewhat large for the protocone length in the P^2, P^3, P^4, and M^3; the crown length for the P^4, M^1, M^2, M^3 and M_3; and the metaconid–metastylid length of the P_2. Simpson, Roe and Lewontin (1960, p. 91) indicated that this particular coefficient usually fell between four and ten and that five and six were good average values. They also stated that a coefficient of less than four was usually due to an inadequate sample and figures greater than ten indicated a mixed sample containing either animals of different ages or taxonomic divisions. The source of the few high coefficients of variability of the Sheridan County horses ap-



TEXT-FIG. *4*—Frequency of the longer dental measurements and the relationship of the length to width measurements in the upper permanent cheek teeth of the horses from the Sheridan County quarries, species indeterminant (interpreted to be 98% *E.* (*A.*) *niobrarensis*). All measurements are in millimeters.

peared to be the presence of different age groups and the associated change in the tooth's measurements and crown pattern as the hypsodont dentition was worn down. The crown lengths, protocone lengths and metastylid–metaconid lengths were especially susceptible to change with wear while the crown widths appeared to change the least (Howe, 1966, pp. 15–17). It was also true that the ratios computed were usually more variable than the measurements on which they were based.

The enamel pattern of the cheek teeth was evidently of minimal value in speciation. Some of the teeth of the younger animals (not juveniles) had very weakly crenulate enamel on the wear surface while other teeth of the same ontogenetic age were highly crenulate with most teeth falling somewhere between the two extremes. None of the slightly worn teeth totally lacked crenulations, a condition quite common in early Pleistocene zebras (Howe, 1970). The moderately worn teeth exhibited a great variety of crown patterns being highly, moderately and weakly crenulate and contained some teeth which lacked folding of the enamel. The well worn teeth of the old individuals lacked highly crenulate enamel and non-crenulate cheek teeth were much more common than in younger animals. The changes in the percentage of each age group possessing complex folds in the enamel of the wear surface was due to changes in the growth pattern in the long prismatic cheek teeth. Sectioning of the dentition indicated that most of the teeth that have complex enamel folds in a youthful state lost those folds as the tooth was worn down to the root. It was also noted that teeth in the same dental series seldom if ever possessed the same complexity of enamel pattern and never was the pattern actually duplicated. The two teeth that exhibited the greatest complexity of enamel pattern were the P^3 and P^4. If two upper or lower dental series from the same animal were compared, teeth



TEXT-FIG. 5—Deciduous dentition of *Equus* (*Asinus*) *niobrarensis*. The scale is in millimeters. *A*, Lower cheek teeth. *B*, Upper cheek teeth.

on opposite sides of the maxilla or mandible did not possess identical crown pattern.

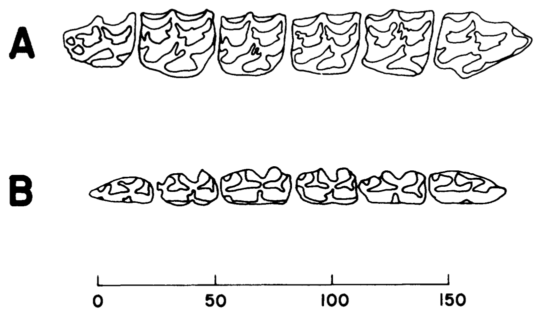
It therefore appeared that 90% of the dentitions were those of *Equus* (*Asinus*) *niobrarensis* and provided a very good indication of the range of variation in that paleospecies.

Referred Specimens.—Upper Dentitions—mature 50, immature 21. Lower Dentitions—mature 140, immature 58.

CONCLUSIONS

The fossil horse remains from the medial Pleistocene "Sheridan County *Equus* Beds" of Nebraska were interpreted to represent three species. Two of these species belonged to the subgenus *E.* (*Hemionus*) and possessed the long and/or thin metapodials characteristic of that group. The hemionid species present were *E.* (*H.*) *francisci* Hay a small hemionid and *E.* (*H.*) *calobatus* Troxell a much larger form. A third group possessed the shorter, broader metapodials of the subgenus *E.* (*Asinus*) and was referred to the species *E.* (*A.*) *niobrarensis* Hay.

Upper dentitions were of little value in identifying Pleistocene horse species or subgenera except for the incisors of the amerhippids which lacked cups. The lower molars could be used to distinguish the zebras and true horses from the asinids and hemionids but were of questionable value in telling the asinids from the hemionids or in identifying either of the two hemionid species in the Sheridan County collection. Unfortunately, most of the holotypes of Pleistocene horses consisted of denti-



TEXT-FIG. 6—Permanent dentition of *Equus* (*Asinus*) *niobrarensis*. The scale is in millimeters. *A*, Upper cheek teeth. *B*, Lower cheek teeth.

tions or single teeth without associated skulls or skeletal elements, thus referrals of a group distinguished by metapodials to a named species which was based on dentition was controversial.

Although the collection probably contained a few hemionid dentitions, the number of dentitions representing the subgenus was approximately the same as the percentage of hemionid metapodials in the collection (over 95% asinid). The dentitions were therefore mostly those of *E.* (*A.*) *niobrarensis* and provided an excellent indicator of the range of variation in that species.

The knowledge gained from the evidence supporting a wide range of variation in the species *Equus* (*Asinus*) *niobrarensis* was important in horse classification. In the past the identification of a particular species had frequently been based on the comparison of a newly found specimen with the holotype of a previously described species. It was sometimes assumed that all the organisms comprising a species would closely resemble the holotype in some characteristic, usually the size or enamel pattern of the dentition. As a result of misinterpretation of species variability, the members of what was at one time a single interbreeding population had been referred to several species. It now appears that Pleistocene horses can most accurately be classified on the basis of population studies and size differences will be best indicated by the arithmetic mean, standard deviation and coefficient of variability. Although specimens that are the largest or smallest in a species population (for example the small specimens referred to *E.* (*Hemionus*) *francisci* as opposed to the smallest member of the *E.* (*A.*) *niobrarensis* population or those with very complex enamel pattern (for example the most complex patterns in the P^3 and P^4 of *E.* (*A.*) *niobrarensis* being more wrinkled than the most complex patterns found in those teeth in *E.* (*Dolichohippus*) *simplicidens* of the early Pleistocene) may be useful in dating, it is very doubtful if these unusual specimens are worthy of separate species rank.

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