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NANNIPPUS PHLEGON (MAMMALIA, EQUIDAE) FROM THE PLIOCENE (BLANCAN) OF FLORIDA

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NANNIPPUS PHLEGON (MAMMALIA, EQUIDAE) FROM THE PLIOCENE (BLANCAN) OF FLORIDA

BRUCE J. MACFADDEN AND JOHN S. WALDROP[1]

SYNOPSIS: Dental and postcranial remains of the three-toed horse, *Nannippus phlegon*, are described from four localities in Florida: Santa Fe River, Haile XVA, Sarasota, and Port Charlotte. As is the case elsewhere in North America, the presence of *N. phlegon* at these Florida localities appears to indicate a Blancan age, which spans a time interval from about 4.5 to 2 million years ago. Specimens of *N. phlegon* from Florida are similar to those found elsewhere in North America, e.g. the typotypic material from Mt. Blanco in the Texas Panhandle. Diagnostic characters of *N. phlegon* include: small and gracile stature, no preorbital facial fossa, elongate rostrum and symphysis, very hypsodont teeth, cement relatively thick above oval border, oval protocones, moderately complex enamel plications, deep ectoflexids, ectoparastylid absent, metapodials tridactyl and elongate, and trapezium absent. Postcranial remains demonstrate that *N. phlegon* was a functionally advanced and highly cursorial "antelope-like" hipparion. Several derived characters are presented here to support the hypothesis that a morphocline, which also is interpreted to represent an ancestral-decendent sequence, proceeds from *N. minor* (particularly from the Bone Valley district) to *N. beckensis* (from the early Blancan of Texas) to *N. phlegon*.

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INTRODUCTION

Nannippus phlegon is one of the most poorly known species of late Cenozoic horses. It is traditionally recognized as a hipparion, which is a horizontal or polyphyletic group of late Cenozoic (Neogene) horse genera with isolated protocones in their upper cheek teeth and tridactyl limbs. At present the phylogenetic interrelationships of *N. phlegon* to other hipparions remain obscure. Matthew and Stirton (1930) exanded the concept of the genus *Nannippus* to include the earlier species "*N.*" *lenticularis* and suggested a close interrelationship with *N. phlegon*, but this hypothesis has not been adequately justified.

N. phlegon is somewhat of an evolutionary curiosity as it was apparently adapted to a highly cursorial mode of life, even more so than most of the presumably more advanced one-toed horses. Its relatively small skelton is graceful and antelope-like. The limbs are long and slender, and the lateral digits are extremely reduced in function. The cheek teeth are the most hypsodont (index of crown area to height) of the Equidae. In short, *Nannippus phlegon* was an extremely progressive grazer and open-country runner.

It is extraordinary to find *N. phlegon* in the Blancan of Florida. The richest accumulations of this open-country antelope-like little horse are found at the Santa Fe River sites in some 10 m of water bordered by lush hydric hammock vegetation. The following evidence shows *N. phlegon* flourished in Florida only a few million years ago. Clearly, as indicated by studies of paleoclimate, there were significant fluctuations in Florida habitat types during the latest Cenozoic.

Cope (1893) originally described this hipparion as *Equus minutus* based on a fragmentary lower molar from Mt. Blanco in the Texas Panhandle. Hay (1899) provided the replacement name *Equus phlegon* because the name *minutus* had previously been used for a Eurasian species of *Equus*. Although referring *phlegon* to *Protohippus,* Gidley (1907) suggested that if upper cheek teeth had been available to him, he might have placed this species in either *Neohipparion* or *Hipparion.* Matthew (1926) proposed *Nannipus* as a subgenus of *Hipparion* for very hypsodont, small, and extremely graceful hipparions with three toes but without remains of the fifth digit or trapezium. His concept of this subgenus was based on the *N. phlegon* material collected from Crawfish Draw during the American Museum of Natural History expedition to Mt. Blanco in 1924 (for an anecdote about collecting at this locality, see Simpson 1951:93-95). This important 1924 collection has never been adequately described in the literature. Subsequently, *Nannippus* was elevated to generic rank (e.g. Stirton 1940), and numerous species of small North American hipparions have been included in it

without careful consideration of phylogenetic interrelationships. Morris F. Skinner (in Skinner and Hibbard 1972:117), one of the foremost students of the Equidae, stated that: "The practice of assigning all small forms of *Hipparion*-like equids to *Nannippus* without careful consideration of other characters clouds the relationship of many of the dwarf forms and prevents the recognition of true *Nannippus.*" Also, this practice lessens the temporal value of *Nannippus* and the other relatively unrelated small *Hipparion*-like forms.

Besides Mt. Blanco and other localities in Texas (see also Strain 1966, Akersten 1972, Dalquest and Donovan 1973, Dalquest 1975, Schultz 1977), *N. phlegon* has been reported from Arizona (Gazin 1942, Johnson, Opdyke, and Lindsay 1975), Kansas (e.g. Hibbard 1941, 1956, 1970), Nebraska (Skinner and Hibbard 1972), and two localities in Florida (Webb 1974, Robertson 1976). This horse apparently is restricted to sediments of Blancan (Pliocene) age, which spans a time interval from about 4.5 to 2 million years ago.

This report describes *Nannippus phlegon* from four localities in Florida and discusses its biostratigraphic significance and phylogenetic origin.

ACKNOWLEDGMENTS

We thank Beryl Taylor and Richard H. Tedford of the American Museum of Natural History, Clayton E. Ray of the National Museum of Natural History, and Ernest L. Lundelius of the Univerity of Texas at Austin for lending us specimens from their institutions. Roy H. Burgess of Venice, Florida, let us study an important specimen in his private collection. Walter W. Dalquest of Midwestern State University also helped us with our study of *Nannippus beckensis.* S. David Webb and Jon A. Baskin critically reviewed the manuscript. Waldrop would like to acknowledge assistance in the field from John Beaudua, C. David Frailey, and Henry Galiano. Work at the Santa Fe River sites was supported by National Geographic Society and National Science Foundation grants to Webb. The figures were prepared by Nancy Halliday; Rhoda J. Rybak typed and copystyled the manuscript.

ABBREVIATIONS

The following institutions are referred to in the text: AMNH; Department of Vertebrate Paleontology, The American Museum of Natural History, New York; BEG, Bureau of Economic Geology, now part of Texas Memorial Museum (TMM) collection, University of Texas, Austin; F:AM, Frick:American Mammals, Department of Vertebrate Paleontology, The American Museum of Natural History, New York; FGS, Florida Geological Survey (formerly at Tallahassee), now part of the Vertebrate Paleontology Collection, Florida State Museum, University of Florida, Gainesville; MU, Midwestern State University, Wichita Falls, Texas; RHB, Private Collection, Roy H. Burgess, Venice, Florida; TRO, Timberlane Research Organization, Lake Wales, Florida; UF, Vertebrate Paleontology Collection, Florida State Museum, University of Florida, Gainesville; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The dental nomenclature used in this paper and illustrated in Figure 1 follows Stirton (1941) and Skinner and Taylor (1967). The postcranial terminology follows Camp and Smith (1942), Sisson and Grossman (1953), Barone (1966), Sondaar (1968), and Hussain (1975).

Localities

Nannippus phlegon is now known from four localities in Florida (Fig. 2). Except for Haile XVA, which was collected in an isolated fissure, these localities represent at least several local sites in an area. This horse had previously been reported from only the first two localities listed below.

Santa Fe River I, IA, IB, and 4A: About 10 m underwater and consisting of collections found in deeper holes along the river bottom or *in situ* in the bank (IB), Columbia County, localities collected by B. Waller, R. R. Allen, C. E. Ray, J. H. Hutchinson, S. D. Webb, K. M. Ainslie, J. S. Robertson, and J. S. Waldrop (see Brodkorb 1963, Hibbard *et al.* 1965, Webb 1974).

Haile XVA: On land formerly owned by Parker Brothers Limestone Products, Inc., near Haile, Alachua County, locality collected by P. Kinsey, J. S. Robertson, S. D. Webb, and R. R. Allen (see Webb 1974, Robertson 1976).

Sarasota: A series of at least three localities in non-marine sediments that overlie the Pinecrest Formation west of Sarasota city, Sarasota County, locality collected by J. S. Waldrop, 1976-1977.

Port Charlotte: Canal spoil dumps on north edge of Port Charlotte, Charlotte County, localities collected by D. Wilson and field crews from the USNM during numerous field seasons, M. C. Thomas, and J. S. Waldrop in 1967; also a locality of Roy H. Burgess "collected from a canal bank (*in situ*) near Port Charlotte, Florida" (Skinner 1972:117).

For the Sarasota and Port Charlotte localities, detailed geographic and geologic data are available in Waldrop's field notes.

Systematic Paleontology

Class Mammalia Linnaeus 1758
Order Perissodactyla Owen 1848
Family Equidae Gray 1821
Genus *Nannippus* Matthew 1926
Nannippus phlegon (Hay) 1899
Figures 1-14, Tables 1-10

Holotype.—BEG 18586, fragmentary lower molar.

Type Locality.—Crawfish Draw, Mt. Blanco, Crosby County, Texas Panhandle (see discussion of type locality in Skinner and Hibbard 1972). The local fauna from Mt. Blanco typifies the Blancan North American Land Mammal Age (e.g. Schultz 1977).

Distribution.—Blancan (Pliocene, *sensu* Berggren and Van Couvering 1974, Lindsay, Opdyke, and Johnson 1975) of Florida, Texas, Kansas, Nebraska, and Arizona (see references in Introduction).

Diagnosis.—Small and gracile hipparion. No preorbital facial fossa. Elongate rostrum and symphysis. Teeth very hypsodont, even

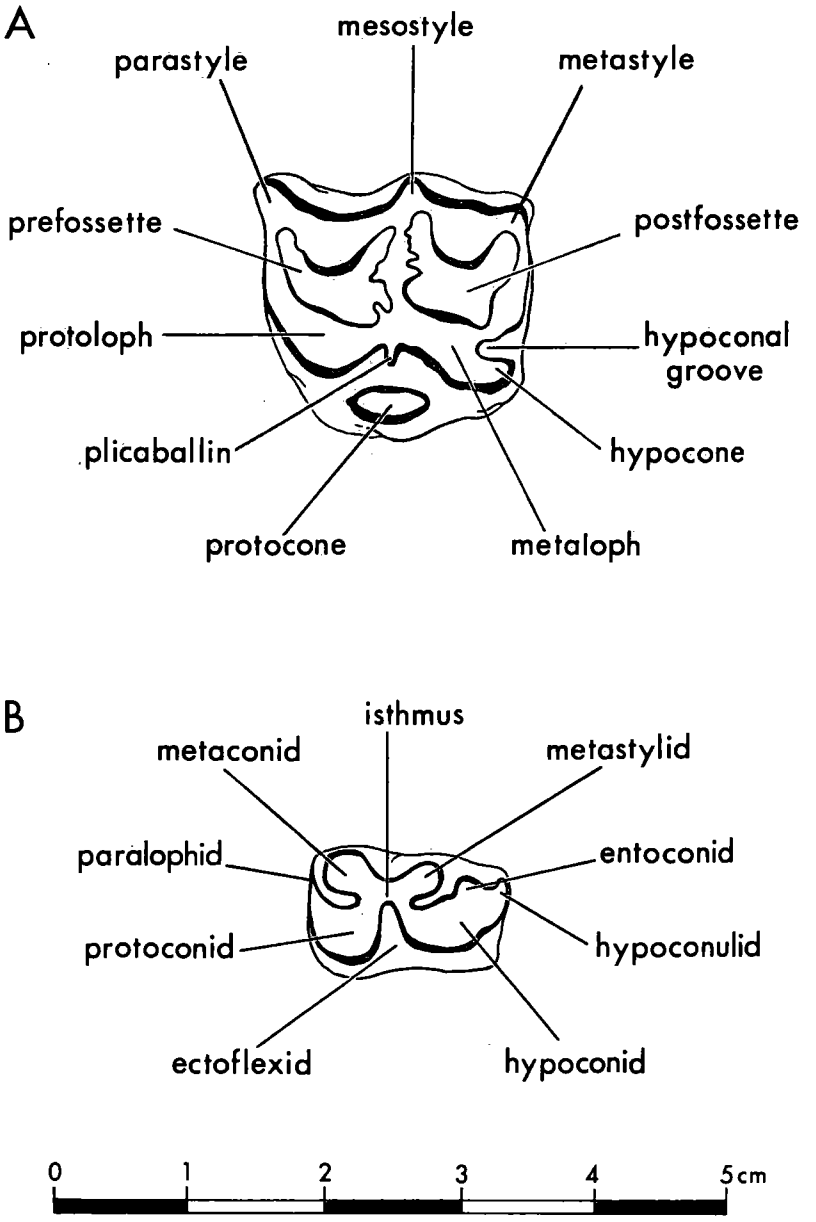

FIGURE 1.—Left upper (A) and lower (B) cheek teeth of *Nannippus phlegon* with dental nomenclature used in this study. Anterior is to the left.

more so than *N. minor,* and moderately curved in the anteroposterior plane; thick covering of cement above alveolar border; upper cheek teeth with oval protocones and moderately complex plications; lower cheek teeth with moderately deep ectoflexids and widely separated metaconids and metastylids; ectoparastylid absent in lower cheek teeth. Limbs functionally one-toed and metapodials relatively long and gracile. Facet for trapezium on the medial (III) metacarpal absent.

REFERRED SPECIMENS.—*Santa Fe River I and IA:* UF 7258, partial right ramus with P_4-M_1; UF 7259, partial left ramus with P_3-M_2; UF 10696, articular condyle of left ramus; UF 22621, right dP^3 or dP^4; UF 22629, left dP^2; UF 22607, UF 22625, left dP^3 or dP^4; UF 11887, right ?P^3 or P^4; TRO 544, right P^3 or P^4; TRO 543, right M^3; UF 1143, left P^3 or P^4; UF 10694, left M^1 or M^2; UF 22627, left upper cheek tooth; UF

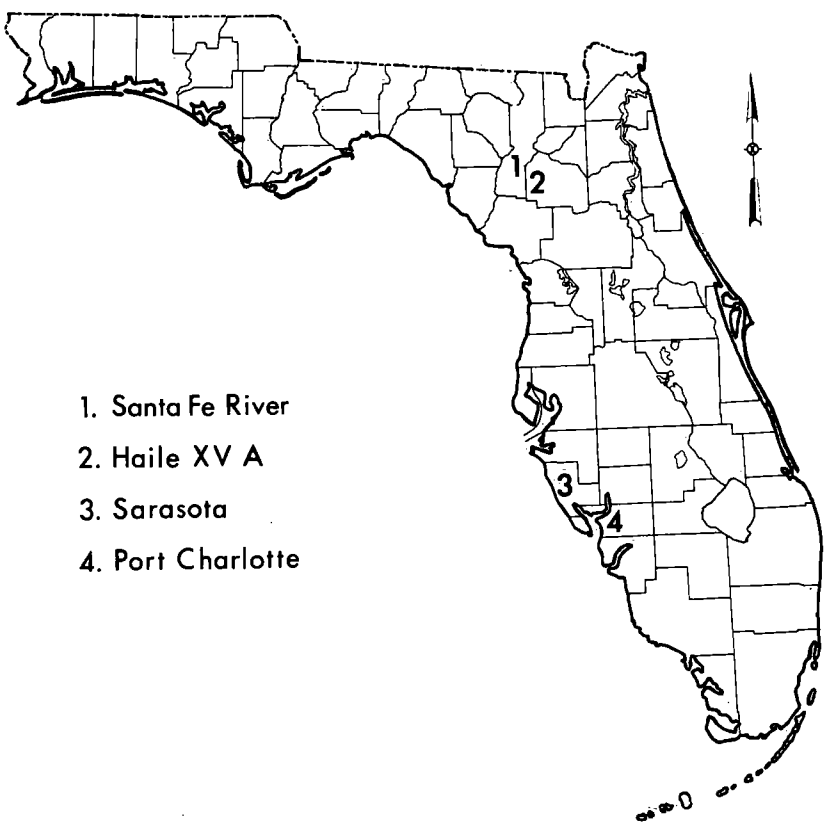

FIGURE 2.—*Nannippus phlegon* localities in Florida.

10593, UF 22626, upper cheek teeth fragments; UF 22624, left ?I_1; UF 22623, right dP_2; UF 22606, left P_3 or P_4; UF 22628, right M_1 or M_2; UF 7261, left M_1 or M_2; UF 7262, UF 7380, left lower cheek teeth fragments; UF 22622, ?left lower cheek tooth fragment; UF 7260, UF 7263, left radii with medial and distal portions of fused ulnae; UF 21325, right ?magnum; UF 7264, UF 22619, left metacarpal III; UF 7431, proximal right femur fragment; UF 7436, distal right femur fragment; UF 7256, left femur; UF 7432, left medial and distal femur fragment; UF 7435, left distal femur fragment; UF 21323, left astragalus fragment; UF 10697, right navicular; UF 21324, left navicular; UF 22630, right metatarsal III; UF 22620, left metatarsal III; UF 21326, proximal lateral metapodial (II or IV) fragment; UF 7388, medial metapodial (III); UF 7257, UF 7426, medial and distal medial metapodial (III) fragment; UF 7427, UF 22632, first medial phalanx (III); UF 10695, second medial phalanx (III).

SANTA FE RIVER IB: UF 11888a, left P^3 or P^4; UF 11888b, right M^3; UF 12226, left incisor; UF 11889, right ?P_2; UF 22644, ?left magnum; UF 21322, right navicular; UF 11890, UF 21321, distal lateral metapodial (II or IV) fragments.

SANTA FE RIVER 4A: UF 21319, partial right ramus with dP_2-dP_3; UF 21320, partial left ramus with dP_2-dP_3; UF 22609, left dP^2; UF 22617, right P^2; UF 22614, right P^3 or P^4; UF 22610, P^3; UF 22616, left P^3 or P^4; UF 22611, TRO 546, right M^1 or M^2; TRO 545, left M^1 or M^2 UF 21327, UF 22615, UF 22613, UF 22634, UF 22633, left upper cheek teeth; UF 22618, upper cheek tooth fragment; UF 22612, right M_3; UF 22608, left M_3; TRO 548, right lower cheek tooth; TRO 547, left lower cheek tooth; UF 22645, right humerus fragment.

HAILE XVA: UF 17484, left ?dP^3 or dP^4; UF 17485, upper cheek tooth fragment.

SARASOTA: TRO 553, right dP^3 or dP^4; TRO 554, upper cheek tooth fragment; TRO 552, right P_4-M_1; TRO 555, right M_3; TRO 556, left M_3 fragment.

PORT CHARLOTTE: UF 22631 (=RHB 1964 and =F:AM 104712), right ramus with symphysis, left C, left I_3-I_1, right I_1-I_3, right C, P_2, M_1-M_3; USNM 214432, right P_2, P_3, M_1-M_3; USNM 214820, left M^1 or M^2; TRO 550, left dP^3 or dP^4; UF 22646, upper cheek tooth fragment; TRO 549, left M_3; TRO 551, right lower cheek tooth; UF 17285a, UF 17285b, UF 22647, UF 22649, UF 22650-UF 22652, lower cheek teeth fragments.

DESCRIPTION

DENTITION.—Considering the small size of Florida *Nannippus phlegon*, the teeth are very hypsodont relative to other hipparions.

The Florida *N. phlegon* dentitions have a thinner covering of cement than do the AMNH specimens from Crawfish Draw, Mt. Blanco, although this difference may be related to diagenetic phenomena. Nevertheless, both these samples of *N. phlegon* have a relatively thick covering of cement above the alveolar border in contrast to those of many other late Cenozoic horses.

No complete upper dentition is known from the Florida sample, and the following description is based on isolated teeth. The upper molars are moderately curved in the anteroposterior plane and slightly curved in the transverse plane. In cross-section, P^2 is triangular and P^3-M^3 are rectangular, with the anteroposterior length being greater than the transverse width (Fig. 3, Table 1). P^2 has a moderately developed pseudoparastyle posterior to the true parastyle on the ectoloph. The protoloph connects directly to the true parastyle on P^2. The anterior part of P^2, including the parastyle, is often expanded in many Cenozoic

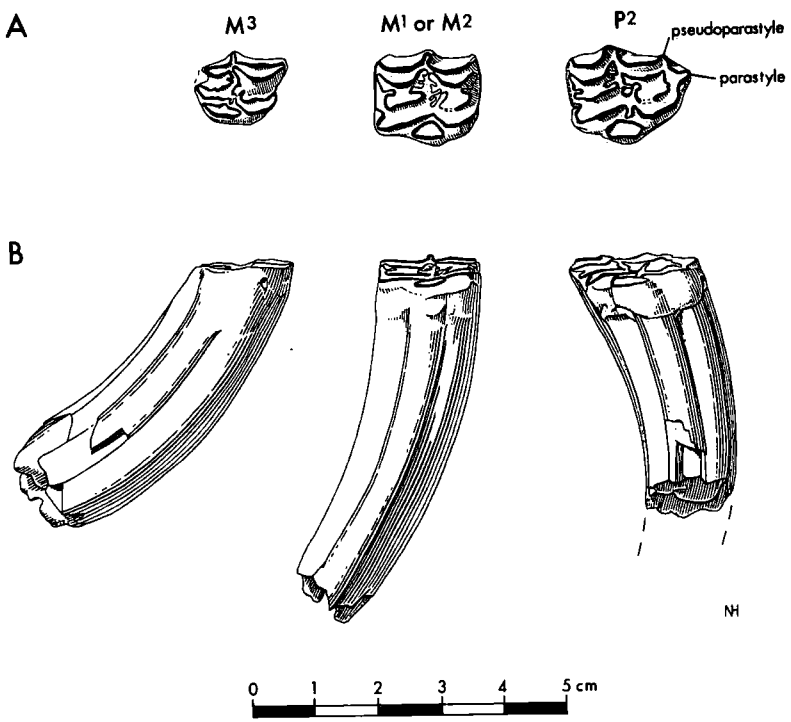

FIGURE 3.—Isolated upper cheek teeth of *Nannippus phlegon* from Florida. (A) occlusal view, M^3, UF 11888b, Santa Fe River 1B, M^1 or M^2, UF 22611, Santa Fe River 4A, P^2, UF 22617, Santa Fe River 4A; (B) medial (internal) view, UF 11888b, UF 22611, UF 22617.

horses resulting in a triangular outline for this tooth. However this area is not well developed in *N. phlegon*. In P^2-M^3 the parastyle and

TABLE 1.—MEASUREMENTS OF ISOLATED UPPER CHEEK TEETH OF *Nannippus phlegon* FROM FLORIDA.

Specimen		Tooth	AP* length	T width	HT †
UF	22617	R P^2	19.5	15.0	>40.6
UF	22621	RdP^3 or dP^4	26.6	11.3	—
TRO	553	RdP^3 or dP^4	21.4	12.6	—
UF	22614	R P^3 or P^4	18.0	16.4	51.0
TRO	554	R P^3 or P^4	17.2	17.3	35.9
UF	22611	R M^1 or M^2	16.3	14.9	59.1
UF	11888b	M^3	15.6	12.2	55.4
TRO	546	R M^1 or M^2	16.1	15.3	55.7
TRO	543	M^3	16.7	13.4	28.3
UF	11887	R upper	15.4	15.6	—
UF	22629	LdP^2	24.9	12.6	—
UF	22609	LdP^2	24.4	13.3	
UF	22607	LdP^3 or dP^4	20.5	11.1	—
UF	22634	?LdP^3 or dP^4	14.4	15.9	24.4
UF	22613	?LdP^3 or dP^4	12.8	14.7	21.4
UF	22610	LP^2 or P^3	19.7	14.7	42.1
UF	11888a	LP^3 or P^4	17.6	17.2	42.6
UF	1143	LP^3 or P^4	20.0	17.5	>46.3
UF	22616	LP^3 or P^4	18.5	15.5	55.0
UF	10810	LM^1 or M^2	17.1	16.4	55.8
UF	22615	LM^1 or M^2	17.9	14.1	62.8
TRO	545	LM^1 or M^2	17.0	13.7	66.0
USNM	214820	LM^1 or M^2	16.2	15.6	48.5
UF	7380	L upper	19.5	—	58.3‡
UF	21327	L upper	19.1	12.9	>54.9
UF	22627	L upper	17.0	14.3	22.2
UF	17484	L upper	17.3	19.9	24.9

*Anteroposterior length and transverse width measurements include cement.
†Greatest crown height measured from mesostyle to base of longest root. Maximum measurements indicate specimens in very early wear stages.
‡Measurement approximate.

TABLE 2.—MEASUREMENTS OF UPPER DECIDUOUS DENTITIONS OF *Nannippus phlegon* FROM MT. BLANCO, TEXAS.

		dP^2		dP^3		dP^4		M^1		M^2		M^3	
		AP	T	AP	T	AP	T	AP	T	AP	T	AP	T
AMNH	104708												
	Right	23.8	15.3	20.1	16.0	21.3	16.4	20.1	16.5	—	—	—	—
	Left	24.2	15.3	20.5	15.9	19.8	16.3	19.8	15.0*	—	—	—	—
AMNH	104709												
	Right	24.2	15.2	21.8	15.2	22.5	14.4	—	—	—	—	—	—
	Left	23.8	15.2	20.6	15.3	22.3	14.4	—	—	—	—	—	—

*Measurement approximate.

mesotyle are well developed; the metastyle is not so well developed. The anterior and posterior borders of the pre- and post-fossettes are moderately plicated, whereas the external and internal borders are relatively simple. The plicaballin is usually represented by a single loop, but in a few specimans this structure is absent. The protocone is oval or bean-shaped and does not exhibit the angular character seen in *"Nannippus" lenticularis.* The protocone is united with the protoloph in late wear stages. The hypoconal groove varies progressively from moderately developed during early and middle wear stages to absent during late wear stages.

The mandible has an elongate symphysis (Fig. 4.) in contrast to other small *"Hipparion"*-like horses such as *Calippus* and *Pseudhipparion.* The lower incisors have cement-filled infundibula not recessed below the occlusal surface. The incisor series is curved and relatively procumbent (or spatulate). The precanine diastema is very short in relation to the postcanine diastema. The mental foramen is approximately midway between C and P_2. P_1 is absent.

The lower molars are moderately curved in the anteroposterior plane and slightly curved in the transverse plane. The lower deciduous premolars, e. g. UF 21319 and UF 21320 (almost certainly from the same individual), are more elongate anteroposteriorly and narrower transversely than are the permanent premolars and molars (Fig. 5, Tables 3, 4). The protoconids and hypoconids have flattened external borders and are narrow transversely. The ectoflexid is relatively shallow. The metaconids and metastylids are anteroposteriorly elongated (transversely compressed) and are widely separated. The entoconid is much larger than the hypoconulid. These two parts are distinct and widely separated. The enamel foldings are simple except for some plications on the anterointernal border of the hypoconid. In summary, the individual teeth, as well as the constituent parts, such as conids, lophids, and stylids, are anteroposteriorly more elongate in the deciduous dentition than in the permanent dentition. The elongate character of the deciduous dental row (both lower and upper), which is characteristic of horses in general, is related to a maximum occlusal surface needed during early growth stages after weaning. The lower deciduous dentition from Florida is similar to that of *Nannippus phlegon* from Mt. Blanco (e.g. AMNH 104710), although the former has a thinner investment of cement.

In cross-section the lower permanent premolars and molars are longer than wide (Figs. 4,6,7). The paralophid is slightly expanded anteriorly in P_2, but much less so than in most hipparions. The external borders of the protoconids and hypoconids are rounded. The ectoflexid varies (either within an individual tooth row or with pro-

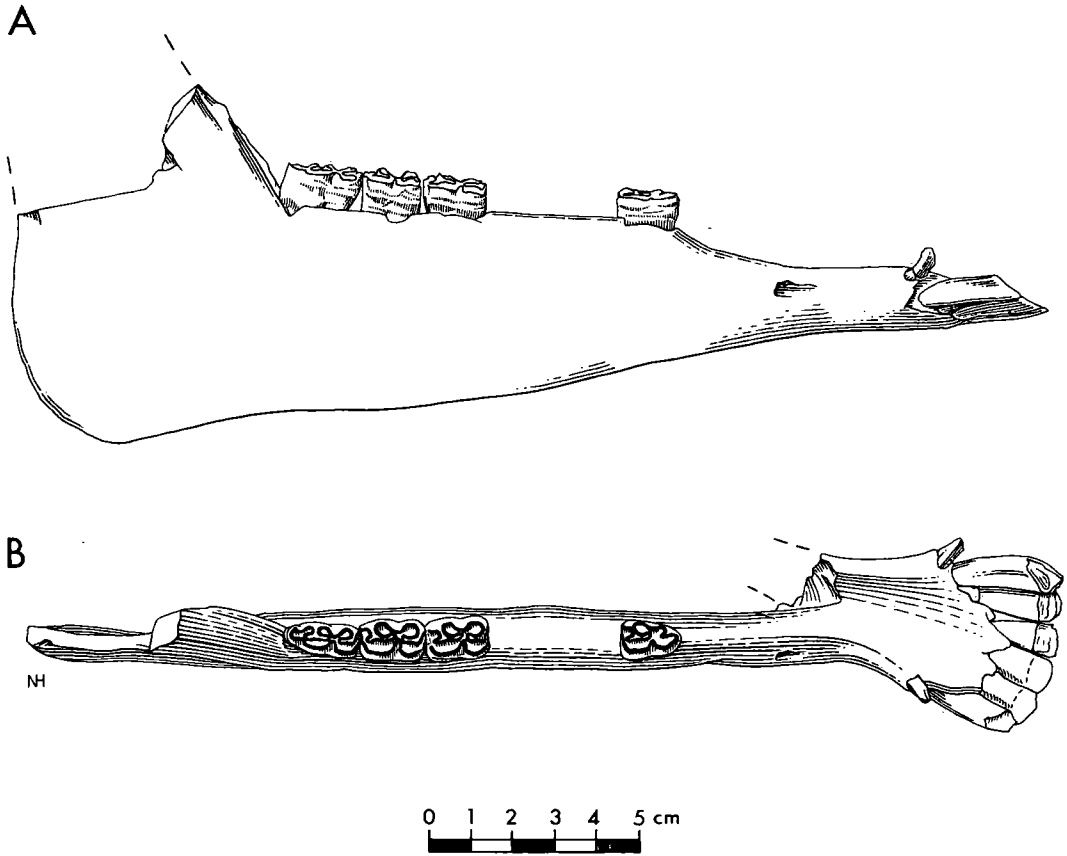

FIGURE 4.—Right mandibular ramus of *Nannippus phlegon*, UF 22631 (=RHB 1964 = F:AM 104712) from Port Charlotte, Florida. (A) right lateral view with symphysial dentition, P_2, M_1-M_3; (B) occlusal view.

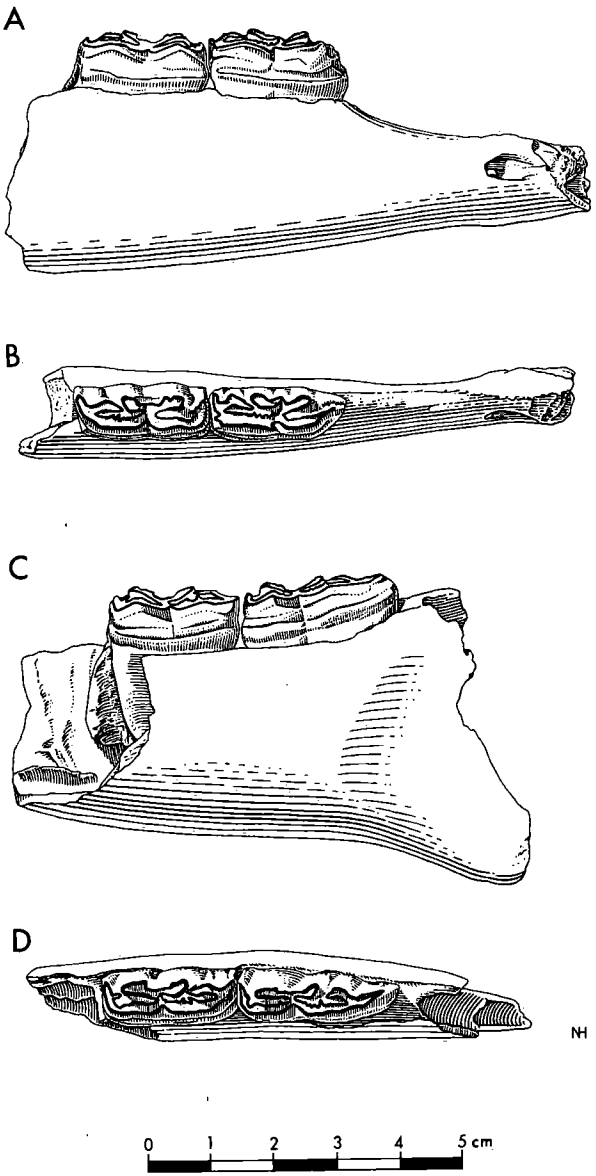

FIGURE 5.—Immature *Nannippus phlegon* from Santa Fe River 4A, Florida. (A) UF 21319, lateral view of right mandibular ramus with dP_2 - dP_3; (B) UF 21319, occlusal view; (C) UF 21320, lateral view of left mandibular ramus with dP_3 - dP_4; (D) UF 21320, occlusal view. Because of the same provenance and stage of wear, these two specimens are almost certainly from the same individual.

gressive wear) from shallow to moderately developed, in which case it can partially divide the isthmus (into the anteroisthmus, metaisthmus,

TABLE 3.—MEASUREMENTS OF LOWER DENTITIONS OF *Nannippus phlegon* FROM FLORIDA AND SELECTED SPECIMENS FROM MT. BLANCO, TEXAS.

		P_2		P_3		P_4		M_1		M_2		M_3	
		AP	T	AP	T	AP	T	AP	T	AP	T	AP	T
UF	7259 Left	-	-	14.3	10.6	14.8	11.2	12.9	9.9	15.0	9.4	-	-
TRO	552 Right	-	-	-	-	15.5	11.2	15.5	9.9	-	-	-	-
AMNH (Mt. Blanco)	104710* Left	23.0	11.0	21.7	16.8	26.7	10.3	-	-	-	-	-	-
AMNH (Mt. Blanco)	104711 Right	17.2	11.4	18.0	13.2	17.3	12.9	16.5	11.7	16.7	11.5	-	-
UF (sharp cast of RHB 1964)	22631 Right	14.4	9.6	-	-	-	-	15.3	10.5	15.7	10.4	18.0	7.9
UF	21319* Right	21.0	8.6	20.7	8.7	-	-	-	-	-	-	-	-
UF	21320* Left	-	-	21.1	8.5	24.2	8.1	-	-	-	-	-	-
UF	7258 Right	-	-	14.2	10.9	14.7	11.1	12.9	9.4	-	-	-	-
USNM	214432 Right	16.2	11.2	16.8	11.0†	-	-	17.4	10.5	15.3	9.6	16.6	9.4

*Includes deciduous premolars.
†Could also be P_4.

TABLE 4.—MEASUREMENTS OF LOWER ISOLATED CHECK TEETH OF *Nannippus phlegon* FROM FLORIDA.

Specimen	Tooth	AP length	T width	Ht*
UF 22623	RdP_2	22.7	7.0	—
UF 11889	RP_2	19.4	8.3	—
UF 22633	RdP_2 or dP_3	20.4	6.5	—
UF 22628	R M_1 or M_2	19.0	9.7	63.0
UF 22612	R M_3	20.7	8.0	60.2
UF 22625	L dP_3 or dP_4	21.4	9.4	—
UF 22606	L P_3 or P_4	15.3	12.1	—
UF 22608	L M_3	18.5	9.0	—
UF 7262	L lower	17.8†	9.3†	—
UF 7261	L lower	17.0†	10.5†	>56.2

*Greatest crown height (see Table 1).
†Measurement approximate.

and postisthmus). There is generally a progressive deepening of the ectoflexid posteriorly in the tooth row. The plicaballinid is rudimentary or absent. The metaconids and metastylids are rounded, widely separated, and approximately equal in size. The entoconids and hypoconulids have rounded margins and are not widely separated. The enamel is very simple with few plications. The lower permanent dentitions described here are similar to those of *N. phlegon* from Mt. Blanco (e.g. AMNH 104711).

Although no comprehensive list of dental measurements has been published for *N. phlegon* from Mt. Blanco, the specimens from this

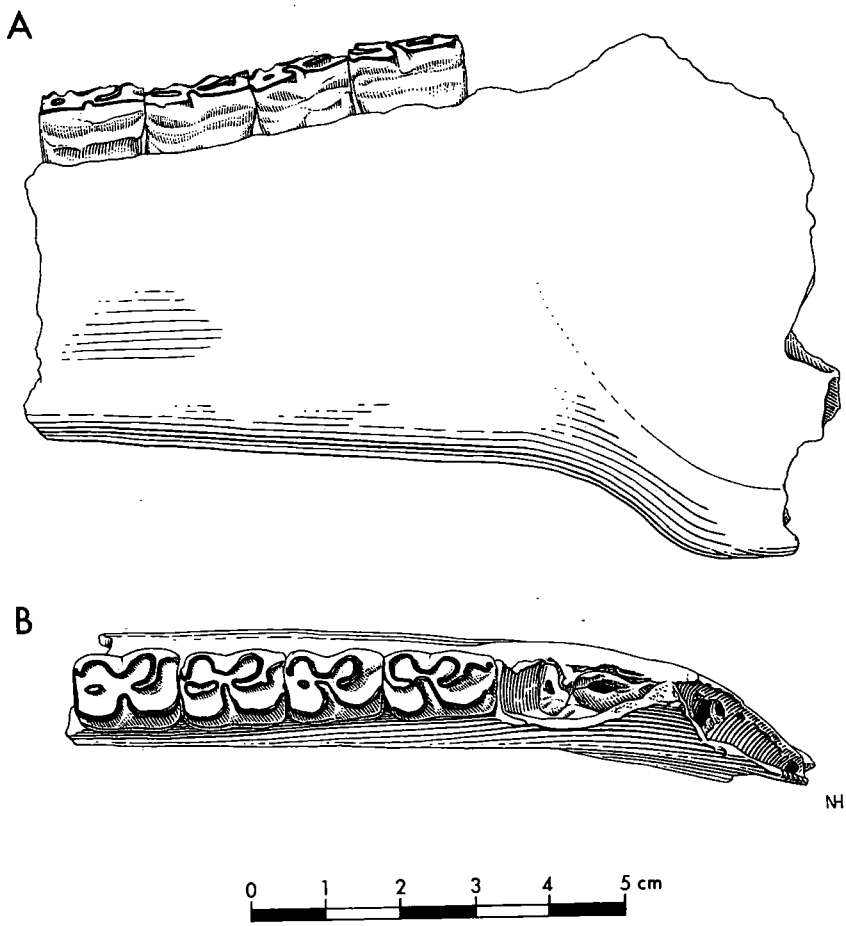

FIGURE 6.—*Nannippus phlegon*, UF 7259, from Santa Fe River 1, Florida. (A) lateral view of left mandibular ramus with P_4 - M_3; (B) occlusal view.

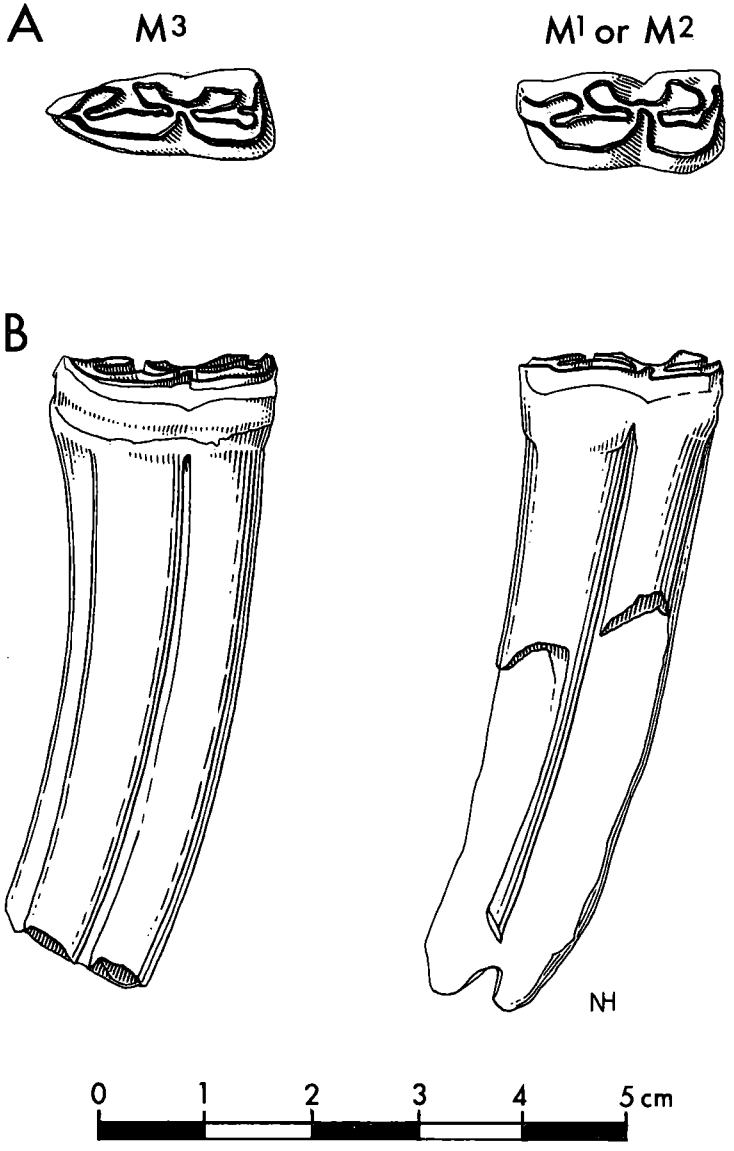

FIGURE 7.—Isolated lower molars of *Nannippus phlegon* from Florida. (A) occlusal view, M_3; UF 22612, Santa Fe River 4A, M_1 or M_2, UF 22628, Santa Fe River 1; (B) medial (internal) view, UF 22612, UF 22628.

type locality and from Florida are of generally similar size (compare Tables 1-4).

POSTCRANIAL SKELETON.—The following postcranial elements are represented in the Florida specimens of *Nannippus phlegon* (for individual numbers see Referred Material above): right humerus, left radius, left ulna, right magnum, ?left magnum, left medial (III) metacarpal, left lateral (II) metacarpal, right and left lateral (IV) metacarpals, femur, astragalus, navicular, right medial (III) metatarsal, left medial (III) metatarsal, medial (III) metapodials, lateral (II or IV) metapodials, first medial (III) phalanx, and second medial (III) phalanx. These postcranial elements are assigned to *N. phlegon* with some certainty because: (1) they are very much smaller than those associated with *Equus (Dolichohippus = Plesippus)*[1] in the same deposits; and (2) of their similarity to articulated *N. phlegon* material (in the AMNH) from Crawfish Draw, Mt. Blanco.

UF 22645 is a distal fragment of a right humerus. On the dorsal side the olecranon fossa is preserved. On the volar side the coronoid fossa is preserved. The medial epicondyle is smaller than the lateral epicondyle. On the distal trochlea the medial condyle is smaller than the lateral condyle, and these are separated by a well-developed parasagittal ridge.

The left radius and ulna are represented by two specimens, UF 7260 and UF 7263 (Fig. 8, Table 5). The proximal articular surface of the radius is divided into two facets for articulation with the medial and lateral condyles of the humerus. Approximately midway down the shaft the cross-section of the radius is roughly oval, although the volar surface is slightly concave. The distal articular surface of the radius consists of facets for the proximal row of carpal bones, i.e. scaphoid (this term is preferred to navicular, which is restricted here to the bone in the tarsus) and lunatum. The proximal shaft of the ulna is broken so that the olecranon process is not preserved. The proximal portion of the shaft that is preserved is separated (unfused) from the radius by the interosseous space. The remainder of the ulna, i.e. medially and distally, is fused to the radius. The distal articular surface of the ulna has facets for the triquetrum and pisiform.

The right and possibly left magna are represented by UF 21325 and UF 22644. Both specimens are somewhat waterworn, but several important features are preserved. The magnum of *N. phlegon* is relatively wider than in some more primitive horses. The medial facet for the scaphoid is concave and somewhat larger than the lateral facet for the lunatum. The posterior keel is not preserved in these specimens. The

[1]Following the synomy of Skinner and Hibbard (1972), the subgenus *Equus (Dolichohippus)* is used here in place of *E. (Plesippus)*.

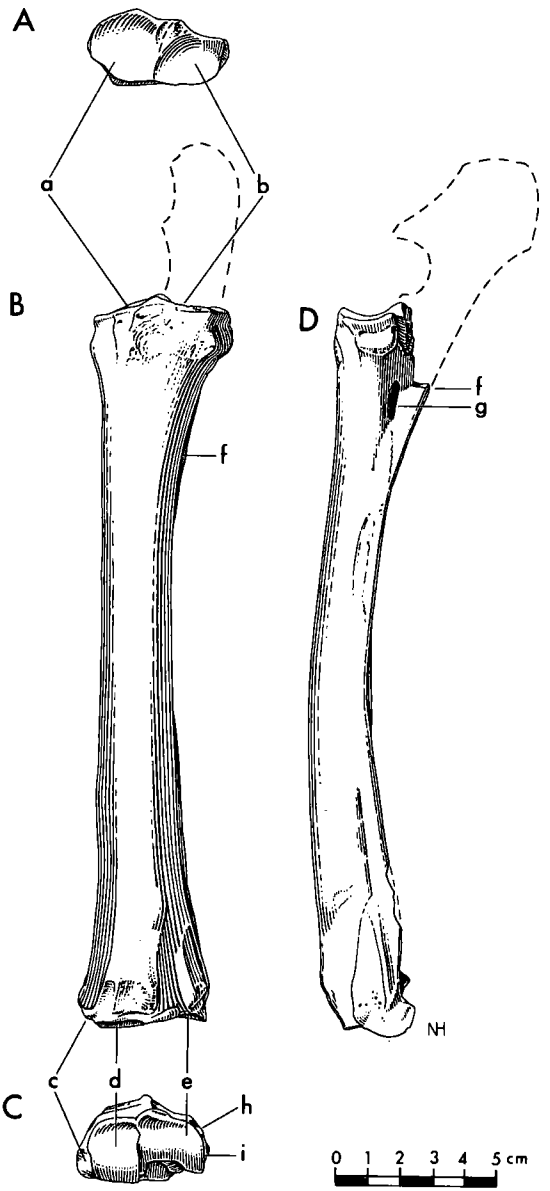

FIGURE 8.—Left radius and ulna, UF 7260. (A) proximal view; (B) dorsal view; (C) distal view; (D) lateral view; a, facet for medial condyle of humerus; b, facet for lateral condyle of humerus; c, ligament attachment; d, scaphoid facet; e, lunatum facet; f, ulna; g, interosseus space; h, pisiform facet on ulna; i, triquetrium facet on ulna.

TABLE 5.—MEASUREMENTS OF RADII FOR *Nannippus phlegon* FROM FLORIDA.

Specimen	Length	AP diam. prox. art. surface	Trans. width prox. art. surface	AP diam. dist. art. surface	Trans. width dist. art. surface*
UF 7260	224.6	22.8	41.3	23.6	38.3
UF 7263	197.7	19.5	34.8	20.7	32.4

*Includes tuberosity for medial ligament and distal articular surface of ulna.

distal articular surface is only slightly concave, which is the condition in advanced horses (Sondaar 1968).

The left medial metacarpal, represented by UF 7264 and UF 22619, is elongate with a relatively narrow shaft (Fig. 9, Table 6). On the proximal articular surface the transverse width is greater than the anteroposterior diameter, which is the condition in advanced horses (Sondaar 1968). This proximal surface consists of a large and roughly triangular facet for the magnum. Lateral to this facet is another facet for the hamatum. Sondaar (1968) noted that the angle between the facets for the magnum and hamatum is ±100° in *Mesohippus,* ±120° in *Parahippus,* and ±160° in *Equus.* This angle in the two Florida *N. phlegon* specimens is approximately 139° and 148° (Table 6). On either side of the volar part of the shaft, distal to the proximal articular surface, are concavities with small facets for the lateral metacarpals II and IV. The medial metapodial shaft is approximately oval in cross-section, although the volar surface is somewhat concave. About halfway down the volar side of the shaft is a nutrient foramen. On either side of the volar surface roughened elongate areas serve as attachments for the interosseous lateral metacarpal ligaments. These surfaces become poorly defined distally; they appear to extend at least

TABLE 6.—MEASUREMENTS OF MEDIAL (III) METACARPALS FOR *Nannippus phlegon* FROM FLORIDA.

	UF 7264 Left	UF 22619 Right
Length*	200.6	208.8
AP length prox. surf.	20.1	23.8
Trans. width prox. surf.	27.1	28.8
Angle on prox. surf. schaphoid/hamatum†	139°	148°
Width distal prominences	23.1	23.1
Width distal art. surf.	22.5	24.4
Ratio width dist. prom./width dist. art. surf.	1.02	.95
Angle inscribed dist. art. sag. ridge†	240°	265°

*Scaphoid facet on proximal articular surface to sagittal crest on distal articular surface.
†Probably accurate to approximately ±15°.

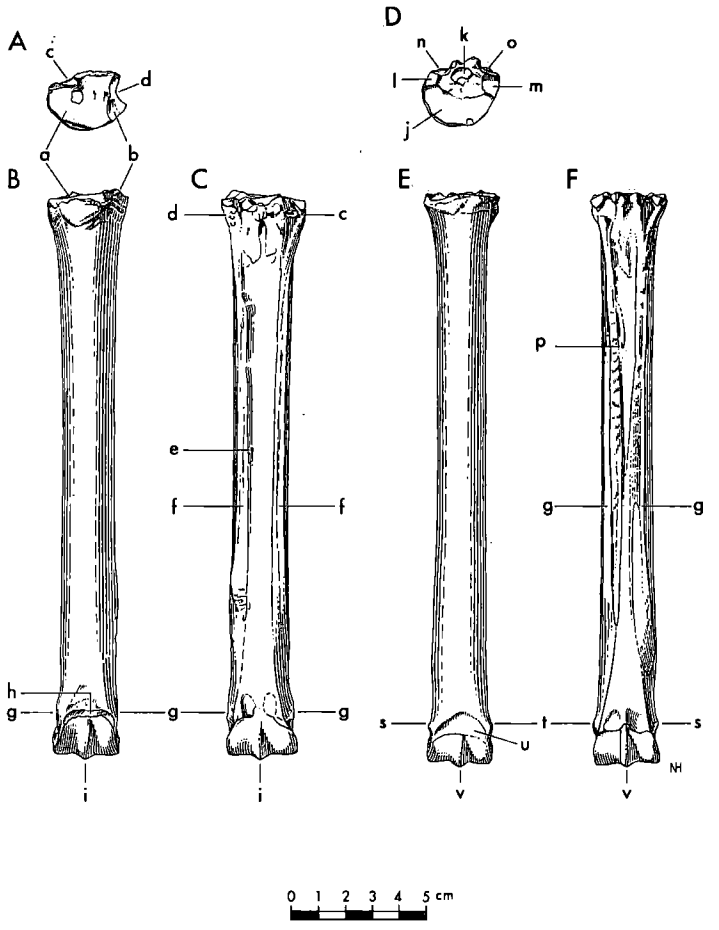

FIGURE 9.—Left medial (III) metacarpal, UF 22619, of Florida *Nannippus phlegon* from Santa Fe River 1A; (A) proximal view; (B) dorsal view; (C) volar view; a, facet for magnum; b, facet for hamatum; c, articular area for lateral metacarpal (II); d, articular area for lateral metacarpal (IV); e, nutrient foramen; f, roughened areas for attachment of interosseus lateral metacarpal ligaments; g, distal prominences for attachment of superficial collateral ligaments; h, depression that accommodates first medial (III) phalanx; i, sagittal ridge on distal trochlea.

Left medial (III) metatarsal, UF 22620, of Florida *Nannippus phlegon* from Santa Fe River 1A; (D) proximal articular surface; (E) dorsal view; (F) plantar view; j, dorsal ectocuneiform facet; k, plantar ectocuneiform facet; l, mesentocuneiform facet; m, cuboid facet; n, depression for articulation of lateral (II) metatarsal; o, depression for articulation of lateral (IV) metatarsal; p, nutrient foramen; q, roughened areas for attachment of interosseus lateral metatarsal ligaments; r, distal trochlea; s, medial prominence for superficial collateral ligaments; t, lateral prominence for superficial collateral ligaments; u, depression that accommodates the first medial (III) phalanx; v, sagittal ridge on distal trochlea.

two-thirds to three-quarters of the way down the volar side of the metacarpal.

On the shaft, just proximal to the distal trochlea, are prominences (medially and laterally) for the attachment of the superficial collateral ligaments. Sondaar (1968) noted that these prominences are more dorsal in *Hipparion* than in, for example, *Anchitherium* or *Pliohippus*, where they are more centrally located on the medial and lateral surfaces of the metacarpal. In relatively primitive horses such as *Parahippus*, a depression just proximal to the dorsal surface of the distal trochlea accommodates the first medial (III) phalanx. Sondaar (1968:30-31) stated that this depression: "gives the proximal [first medial] phalanx more freedom when the fetlock joint is flexed." This depression is reduced or absent in advanced horses such as *Equus*. In Florida *N. phlegon* this depression is very poorly developed relative to, for example, *Parahippus*. The distal trochlea is bilaterally symmetrical with a strong sagittal ridge. This distal ridge is very well developed in Florida *N. phlegon*, as in other more advanced horses. Also, the distal ridge increases in circumference in more advanced horses; it extends about 180° in *Parahippus* whereas it spans about 220° in *Equus* (Sondaar 1968). In the two UF specimens this distal ridge extends from roughly 240° to 265° around the trochlea (Table 6). Apparently this distal ridge was most progressively developed in *N. phlegon*, but this should be confirmed by more than the two specimens available in the present study.

Sondaar (1968) noted that the ratio of width of the deep collateral ligament prominences to the width of the distal trochlea is greater than 1 in relatively primitive horses and less than 1 in relatively advanced horses. This ratio is close to 1 (.95 and 1.02) for the two UF specimens of Florida *N. phlegon*.

The right and left lateral (IV) metacarpals are represented by UF 22637 and UF 22636 (Fig. 10). Proximally there is an articular facet for the unciform and two articular facets for the medial (III) metacarpal. It is difficult to determine from these specimens whether or not metacarpal V was present. The shaft is three-sided, relatively slender, and tapered. On its medial surface are rugose areas for attachment with the interosseus metacarpal ligaments. The distal trochlea for articulation with the lateral phalanges is not preserved (see discussion of distal lateral metapodials below).

The left lateral (II) metacarpals are represented by UF 22635 and UF 21326 (Fig. 10). Proximally there is a triangular-shaped facet for articulation with the trapezoideum. Proximodorsally are two small facets for articulation with the medial (III) metacarpal and the magnum. The proximovolar area, which is well preserved, has no ar-

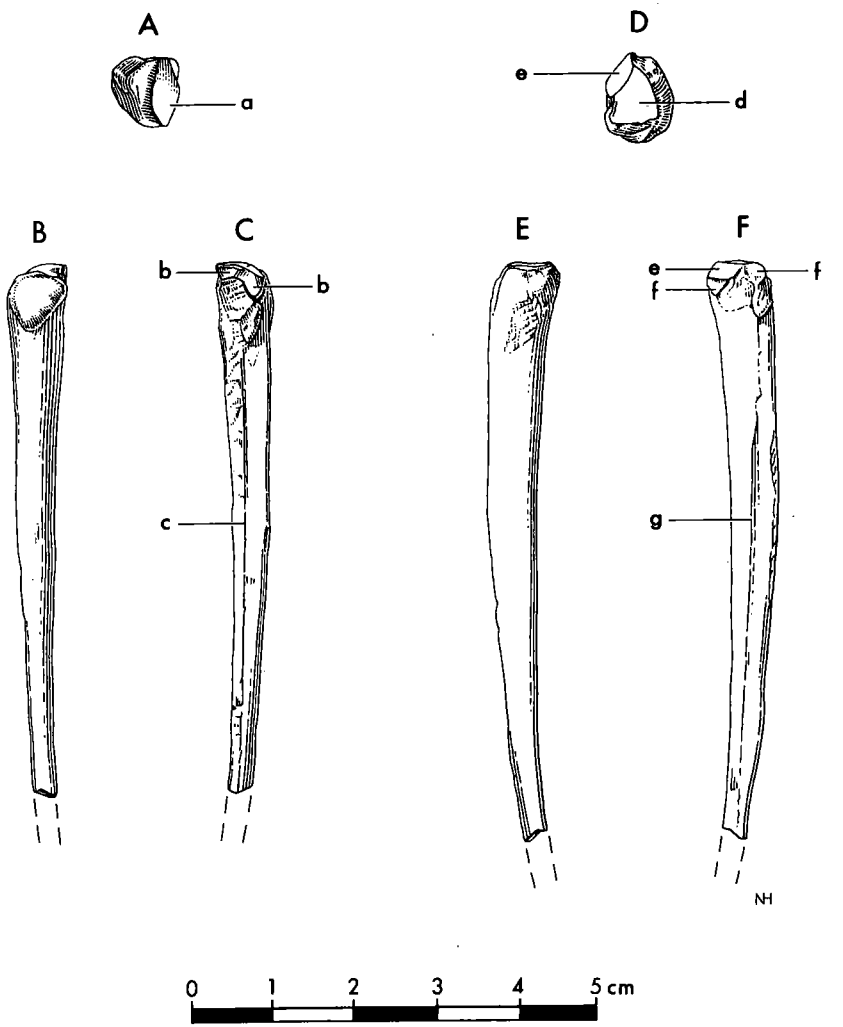

FIGURE 10.—Left lateral (IV) metacarpal, UF 22636, from Santa Fe River 1A. (A) proximal view, (B) external view, (C) internal view; a, facet for articulation with unciform; b, facets for articulation with medial (III) metacarpal; c, rugose area for attachment of collateral ligaments.

Left lateral (II) metacarpal, UF 22635, from Santa Fe River 1A. (D) proximal view, (E) external view, (F) internal view; d, facet for articulation with trapezoideum; e, facet for articulation with magnum; f, facets for articulation with medial (III) metacarpal; g, rugose area for attachment of interosseous lateral metacarpal ligaments.

ticular facet for the trapezium. Evidently the trapezium was absent. Primitive horses normally have a trapezium (Sondaar 1968), and Chubb (1912) found this bone in 57% of the *Equus* specimens that he examined. Matthew (1926) stated that the absence of the trapezium is one of the characters of *Nannippus,* which the *N. phlegon* specimens from Florida support. The shaft of metacarpal II is three-sided, relatively slender, and tapers below the proximal articular region. Again, the distal articular areas are not preserved in these specimens (see discussion of metapodials below).

UF 7256 is a virtually complete left femur (Fig. 11, Table 7). Fragmentary femora are represented by UF 7436 (right), UF 7432 (left), and UF 7435 (left). Proximally the head does not have a complete and distinct rim, in contrast to the condition seen in *Equus* (Hussain 1975 for example). The fovea capitus, which serves for attachment of ligaments, is triangular in outline. As in all horses, the greater, lesser, and third trochanters are well developed. The nutrient foramen is approximately halfway down the shaft, which is oval in cross-section. The medial epicondyle is well developed. The distal trochlea is assymetrical and relatively deep. The medial condyle is larger than the lateral condyle. UF 7256 shows an additional thickening of spongy bone on the medial condyle (this is also developed in some UF specimens of *Equus*), whereas the three other specimens, UF 7432, 7436, and 7435 have no bony thickening.

The astragalus (UF 21323) is too water-worn to be described here.

The navicular (Fig. 12, Table 8) is represented by UF 21324 (right), UF 10697 (left), and UF 21322 (left). Hussain (1975) noted a trend in the evolution of the equid navicular for the transverse width to become greater than the anteroposterior length. This feature is clearly related to its increased importance in transmitting weight to the medial (III) metatarsal. Hussain's "navicular diameter/width index" (ratio × 10)

TABLE 7.—MEASUREMENTS OF FEMORA FOR *Nannippus phlegon* FROM FLORIDA.

Specimen	Length[1]	AP length[2] proximal articular surface	Transverse[3] width prox. articular surface	AP length[4] distal trochlea	Transverse[5] width distal trochlea
UF 7436, Right	-	-	-	59.0	46.6
UF 7256, Left	272.5	53.2	79.4	73.3	64.1
UF 7432, Left	-	-	-	66.9	56.2*
UF 7435, Left	-	-	-	68.1	-

[1]Proximal tip of greater trochanter to distal-most part of medial ridge.
[2]Distance between dorsal-most and plantar-most points of greater trochanter.
[3]Medial-most point on head and lateral-most point of greater trochanter.
[4]Dorsal-most and plantar-most points on medial condyle.
[5]Medial-most point on medial epicondyle to lateral-most point on lateral epicondyle.
*Measurement approximate.

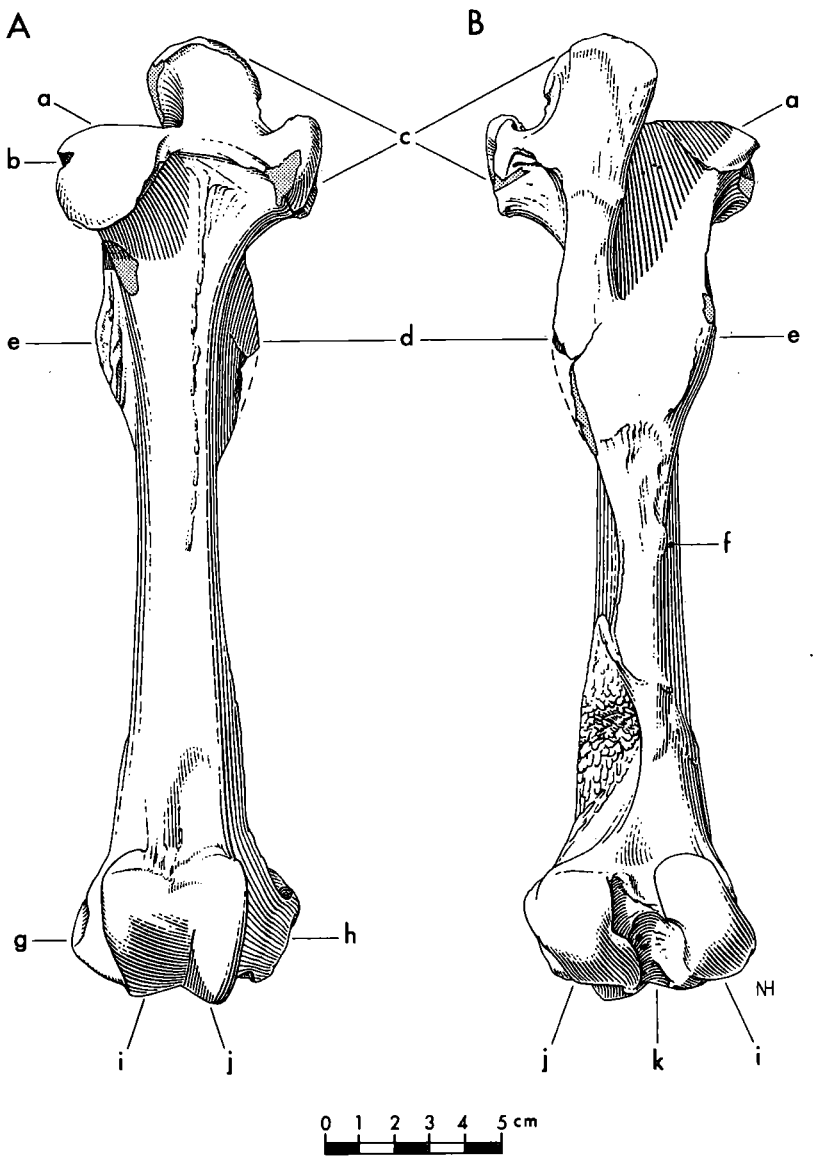

FIGURE 11.—Left femur, UF 7256, of Florida *Nannippus phlegon* from Santa Fe River 1. (A) dorsal view; (B) plantar view; a, head; b, fovea capitus; c, greater trochanter; d, lesser trochanter; e, third trochanter; f, nutrient foramen; g, medial epicondyle; h, lateral epicondyle; i, medial condyle of distal trochlea; j, lateral condyle of distal trochlea; k, intercondyloid fossa.

ranges from 10.0-11.3 for *Mesohippus* to 7.2-8.9 for *Equus*. This same index for Florida *N. phlegon* ranges between 9.3-10.2, which is greater than Hussain's study predicted for advanced three-toed horses. The proximal surface, which articulates with the navicular, is concave and has a well-developed medial non-articular groove, which is poorly developed or absent in such primitive horses as *Mesohippus* or *Parahippus*. The distal articular surface has two (dorsal and lateral) confluent ectocuneiform facets, one cuboid facet, a non-articular area, and one mesentocuneiform facet. In the Florida *N. phlegon* specimens the mesentocuneiform facet and lateral-most portion of the ectocuneiform facet are confluent, as in *Hipparion* illustrated by Hussain (1975:199, Fig. 7C).

The right and left medial (III) metatarsals are represented by UF 22630 and UF 22620, respectively (see Fig. 9, Table 9). The proximal articular surface is transversely wider than it is anteroposteriorly long and bears two large ectocuneiform facets (dorsal and plantar), one

TABLE 8.—MEASUREMENTS OF NAVICULARS OF *Nannippus phlegon* FROM FLORIDA.

Specimen	AP length	Width	Index*
UF 21324, Right	26.0	28.1	9.3
UF 10697, Left	28.2	29.2	9.7
UF 21322, Left	27.6	27.2	10.2

*Ratio length/width x 10 (Hussain 1975).

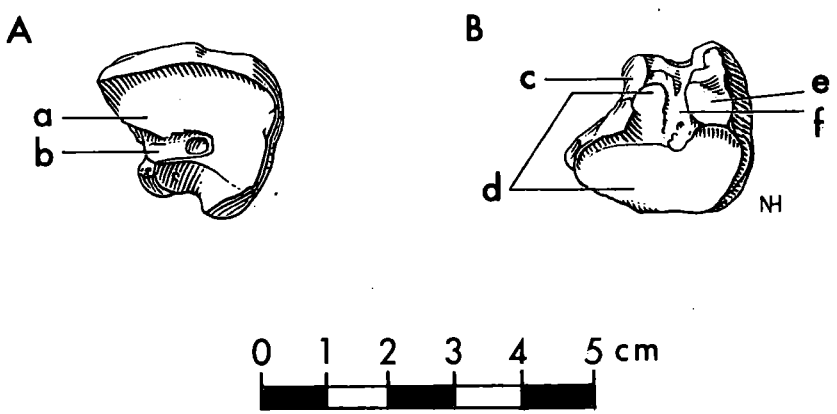

FIGURE 12.—Right navicular, UF 21324, of Florida *Nannippus phlegon* from Santa Fe River 1A. (A) proximal articular surface (dorsal view); a, astragalar facet; b, non-articular area; (B) distal articular surface (plantar view); c, cuboid facet; d, ectocuneiform facets; e, mesentocuneiform facet; f, non-articular area.

mesentocuneiform facet (medial), and one cuboid facet (lateral). These mesentocuneiform and cuboid facets, which are as well developed as in other advanced horses, indicate a functional de-emphasis of the lateral (II and IV) metatarsals (Hussain 1975). Just below the proximal articular surface, on the plantar portion of the shaft, are medial and lateral depressions with facets for the lateral (II and IV) metartarsals. The nutrient foramen is approximately one-quarter of the distance down the plantar side of the shaft, which is oval in cross-section. It has roughened areas that extend about two-thirds to three-quarters of the distance down the plantar surface for attachments of the interosseous lateral metatarsal ligaments. The distal portion of the medial (III) metatarsal is very similar to the medial (III) metacarpal of *N. phlegon* described above. Proximal to the distal trochlea are medial and lateral prominences for the superficial collateral ligaments. In between these prominences on the dorsal side is a shallow depression for the first medial (III) phalanx. A well-developed sagittal ridge on the distal trochlea extends approximately 260° around the trochlea (see Table 9). Hussain (1975) noted that the distal tuberosities (superficial collateral ligament prominences) are wider than the distal trochlea in three-toed horses, except in *Nannippus*, where he noticed the reverse. This condition in *Nannippus* is similar to that of one-toed horses. The measurements for the two Florida *N. phlegon* specimens (.98 and 1.00, Table 9) appear to be intermediate, i.e. the widths of both the distal prominences and distal trochlea are approximately the same.

Several incomplete specimens represent metapodials whose exact position in the manus or pes cannot be determined. UF 7257, UF 7426, and UF 7388 are fragmentary or water-worn medial (III) metapodials. UF 22639 and UF 22640 are fragments of the medial region of the lateral (II or IV) metapodials. Three specimens, UF 11890, 21321, and 22638 show the distal articular surface of lateral (II or IV)

TABLE 9.—MEASUREMENTS OF MEDIAL (III) METATARSALS FOR *Nannippus phlegon* FROM FLORIDA.

	UF 22630 Right	UF 22620 Left
Length*	227.2	210.7
AP length prox. surf.	24.8†	26.5
Trans. width prox. surf.	27.7	28.2
Width distal prominences	21.5	23.1
Width distal art. surf.	22.0	23.0
Ratio width dist. prom./width dist. art. surf.	.98	1.00
Angle inscribed dist. art. sag. ridge‡	260°	260°

*Cuboid facet on proximal articular surface to distal sagittal ridge.
†Measurement approximate.
‡Probably accurate to approximately ± 15°.

metapodials. As in more advanced horses, these specimens of *N. phlegon* do not have sagittal ridges on the distal articular surfaces. (Stirton [1940] noted that faint sagittal ridges are developed on primitive species of "*Nannippus.*")

The great similarity in the distal trochlea of the medial (III) metacarpal and metatarsal makes it difficult or nearly impossible to distinguish between the first medial phalanx of the manus and pes. The classic work on equid digital ligaments by Camp and Smith (1942) and later studies (Sondaar 1968; Hussain 1975) showed these phalanges have many characters of functional significance. UF 2427 and UF 22632 are first phalanges of the medial (III) metapodial (an additional specimen, UF 17548, is discussed in Robertson 1976). These phalanges are relatively long and slender (Fig. 13, Table 10). Sondaar (1968) noted that in the manus the length of the first phalanx increases from about 1/6 that of the medial (III) metacarpal in *Mesohippus* to about 1/3 that of the medial (III) metacarpal in *Equus.* In the two UF specimens of *N. phlegon* the length of the first phalanx is about 1/4 the length of the medial (III) metapodials.

The proximal articular surface is concave with a deep groove to accommodate the well-developed sagittal ridge on the distal trochlea of the medial (III) metacarpal. This deep groove and well-defined ridge system is characteristic of advanced horses and is related to restriction of lateral movement in the fetlock. In more primitive horses lateral movement was somewhat restricted by the presence of more elongate lateral metapodials (Sondaar 1968). In this regard *N. phlegon* is more like one-toed horses, for example *Equus,* than it is to other three-toed horses, such as *Hipparion.*

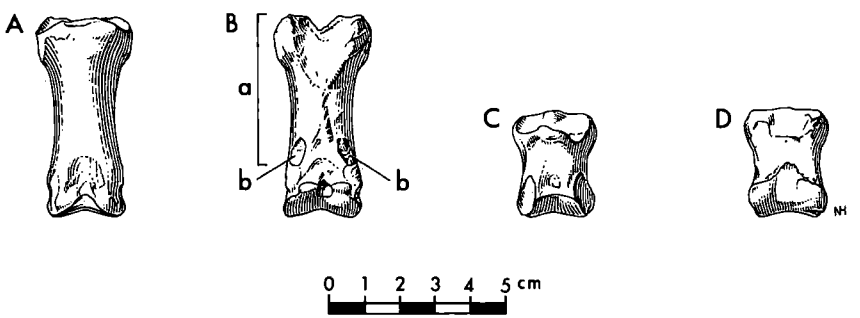

FIGURE 13.—Medial (III) phalanges of Florida *Nannippus phlegon* from Santa Fe 1A. First phalanx, (A) dorsal view; (B) volar or plantar view; a, V-scar; b, oval perforatus scars. Second phalanx, (C) dorsal view; (D) volar view.

TABLE 10.—MEASUREMENTS OF PHALANGES OF MEDIAL (III) METAPODIALS FOR *Nannippus phlegon* FROM FLORIDA.

Specimen	Length	Width prox. art. surface	Width dist. art. surface	Length V-cscar first phalanx	Length V-scar/length first phalanx
UF 7427					
First phalanx	52.5	25.6	20.5	41.7	.79
UF 22632					
First phalanx	54.2	27.0	21.4	42.7	.79
UF 10695					
Second phalanx	29.7	23.7	22.1	-	-

The volar, or plantar, surface of the first phalanx bears a complex of scars that serve as attachments for the digital ligaments. During the course of equid evolution the length of the V-scar (Fig. 13) increased greatly relative to the length of the phalanx. Sondaar (1968) stated that in advanced horses this scar extends about 1/2 the length of the phalanx in *N. phlegon* and "primitive" *Equus (Dolichohippus)* and about 2/3 the length of the phalanx in "advanced" *Equus*. (Figures of *Equus* in Camp and Smith [1942:100] and Sondaar [1968:36] suggest that the V-scar extends far more than 2/3 the length of the phalanx, but as Camp and Smith noted, it is indeed difficult to delimit the distal extent of this scar.) Based on the two UF specimens of Florida *N. phlegon* (Table 10), the V-scar extends for more than 3/4 the length (.79) of the phalanx. Lateral to the distal apex of the V-scar are two well-developed oval perforatus scars (Fig 13B, b).

The second medial phalanx is represented by one specimen, UF 10695. As in other three-toed horses, the length of this phalanx exceeds the width, whereas the reverse is true in one-toed horses (Table 10, Hussain 1975).

DISCUSSION

Nannippus phlegon FROM FLORIDA.—In size, degree of hypsodonty, and dental pattern the Florida *N. phlegon* specimens resemble the topotypic material from Mt. Blanco. The Florida sample is also comparable to published descriptions of this species from other localities (Hibbard 1941, 1956, Gazin 1942, Dalquest 1975). Prior to this study *N. phlegon* was reported from only two localities in Florida, Haile XVA (Robertson 1976) and Santa Fe River (Webb 1974). Two additional localities are now known, Sarasota and Port Charlotte.

Evidently this horse was not rare in Florida, and its apparent scarcity reflected the meager sample of appropriate age. With its northernmost occurrence in Nebraska (Skinner and Hibbard 1972), *N. phlegon*

was apparently Neotropical in distribution (although Blancan faunas are not known in Central America). In the well-sampled more northern Hagerman L. F. and Grand View L. F. of equivalent age in Idaho, *N. phlegon* is not represented (Gazin 1936, Shotwell 1970). Its presence in Florida seems to be another example of the Neotropical influence of late Cenozoic faunas of the Gulf Coastal region.

Fossil horses, because of their rapid evolution and wide distribution both geologically and geographically, are among the best indicators of time in terrestrial Cenozoic sequences. The occurrence of *Nannippus phlegon* is also consistent with this generally held view. In organizing the biochronology of the North American continental Tertiary, the Wood Committee (1941) presented a synthesis of the stages of mammalian evolution. The Blancan North American Land Mammal Age was proposed in that report. This time term is a faunal characterization that includes a combination of first appearances, last appearances, index fossils, and characteristic fossils. As a result of the recent advent of precise geochronological tools such as radiometric and paleomagnetic dating, it is now known that the Blancan spans a period of time from about 4.5 to 2 million years ago (although not in total agreement, see Berggren and Van Couvering 1974, Johnson, Opdyke, and Lindsay 1975, Lindsay, Opdyke, and Johnson 1975, Tedford *et al.*, in press).

With regard to horses, "primitive" *Equus (Dolichohippus)* is considered an index fossil of Blancan time. *Nannippus* is stated to last appear during this time (Wood *et al.* 1941). Besides the last occurrence of this genus, the species *N. phlegon* is taken as an index of Blancan time, with its presence in characteristic faunal assemblages (based on other constituent taxa) such as the type Blancan of the Texas Panhandle, Arizona, Kansas, and Nebraska. Similarly, Webb (1974) stated that the presence of *Nannippus phlegon* in Florida, again based on associated characteristic faunal elements, is consistent with an interpretation of Blancan time for the Santa Fe River and Haile localities.

The two additional localities reported here also appear to be of Blancan age. Besides *Nannippus phlegon,* the Sarasota TRO localities include the following taxa collected *in situ: Equus (Dolichohippus)* cf *simplicidens, Kraglievichia* cf *floridanus, Megalonyx, leptostomus, Hemiauchenia macrocephala, Tapirus* cf *veroensis, Cuvieronius* sp., primitive capybara, and *Chrysemys platymarginata.* This assemblage is taxonomically similar to the Santa Fe River and Haile Blancan localities (Webb 1974, Robertson 1976). The field associations and small faunal assemblages of the Port Charlotte localities are of doubtful significance; besides *Nannippus phlegon,* only primitive *Equus* and *Chrysemys platymarginata* have been collected from spoil piles.

However, the concurrent range zone of *N. phlegon* and *Equus* is an indicator of Blancan time at all other published localities of this time interval. Also, the turtle *Chrysemys platymarginata* appears to be restricted to the Blancan (Webb 1974). More work is needed to increase the faunas from southwestern Florida. The complex interfingering of marine and non-marine facies in that region (see e.g. DuBar 1958) would provide an excellent opportunity to analyze late Cenozoic faunal correlation and geological history of the Gulf Coast.

ORIGIN OF *Nannippus phlegon.*—Dental characters have traditionally been used to distinguish fossil horse taxa. In many cases the phylogenetic significance of minor dental variations so used is poorly understood. This practice has been especially true for hipparions, which consist of an unnatural or horizontal group of several genera of predominantly Mio-Pliocene horses with isolated protocones in the upper molars and tridactyl feet. Attempts have been made to resolve this undesirable taxonomic assemblage by recognizing discrete groups of hipparions based on other characters, as well as those of the dentition. The configuration of facial fossae has recently been shown to be of great significance in determining phylogenetic interrelationships of fossil horses (MacFadden and Skinner 1977, Skinner and MacFadden 1977, MacFadden 1980).

As stated above, *Nannippus phlegon* is one of the rarest and least-studied members of the late Cenozoic Equidae. It is instructive to examine the cranial morphology of this horse in order to discuss its phylogenetic affinities later in this section. Until now, skulls of this horse have not been described in the literature. Unfortunately no skulls of this horse are known from Florida. There is one skull in the AMNH collected during the 1924 expedition to Crawfish Draw, Mt. Blanco, Texas[1].

AMNH 104708 is a fairly well-preserved skull of a subadult *N. phlegon* (Fig. 14). The cheek teeth include right and left dP^2-M^1. Despite some crushing, the preorbital region of this specimen preserves some important characters. The nasal notch is not retracted and it lies above the buccinator fossa anterodorsal to dP^2. The premaxillary bone extends posteriorly to a position that lies over dP^2. There is a moderately inflated malar crest. The lacrimal bone extends anteriorly to a position that lies over M^1. The preorbital region is smooth with no trace of a facial fossa. The infraorbital foramen lies over dP^3-dP^4.

Numerous workers have speculated on the origin of *N. phlegon.* Matthew and Stirton (1930), Webb (1969), and Dalquest and Donovan (1973) stated that "*Nannippus*" *lenticularis* appears to be closely

[1]Two other partial skulls of *Nannippus phlegon*, JWT (Johnston — West Texas) 771 and JWT 1028, from Cita Canyon, Texas, are housed in the Panhandle Plains Museum, Canyon, Texas.

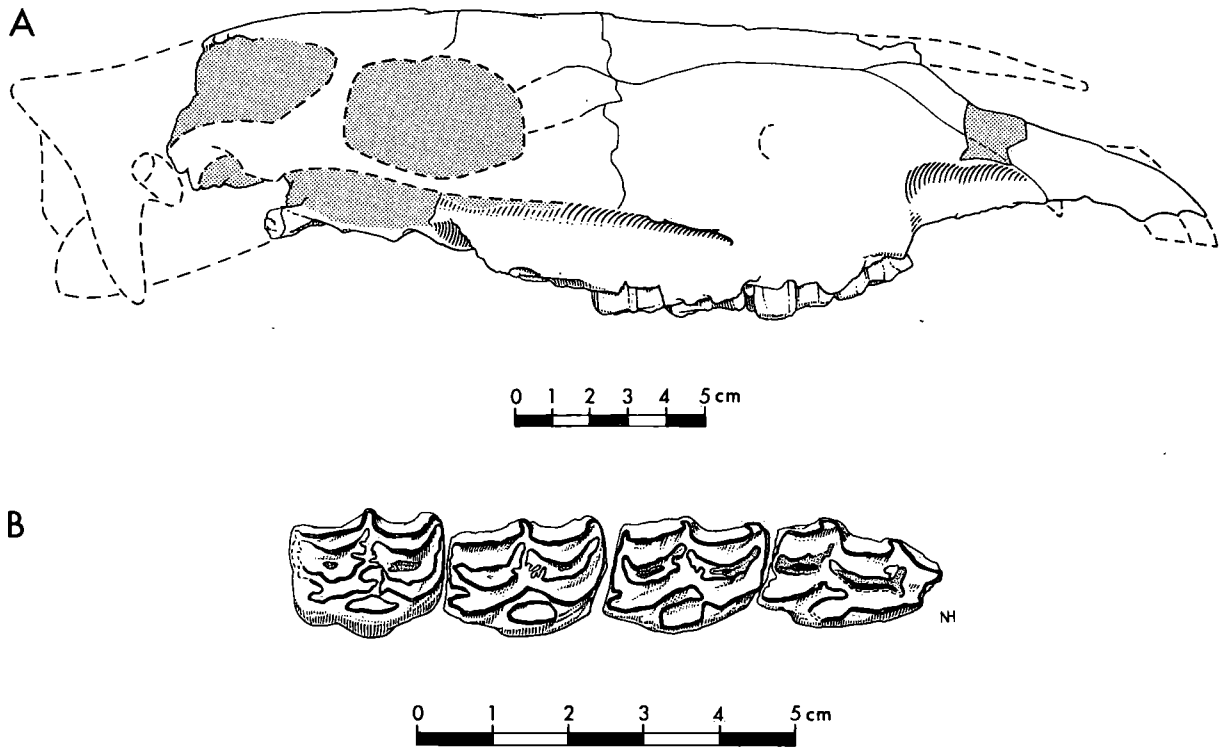

FIGURE 14.—*Nannippus phlegon*, AMNH 104708, collected by the AMNH expedition of 1924 from Crawfish Draw, Mt. Blanco, Crosby Co., Texas Panhandle (Blancan Land Mammal Age). (A) right lateral view of skull (reconstructed areas indicated by dashed lines, matrix stippled); (B) occlusal view of right upper cheek teeth.

related, or ancestral, to *N. phlegon.* Cope (1893) originally described the species *Protohippus lenticularis* based on two upper molars of late Hemphillian age from Mulberry Canyon, near Goodnight, in the Texas Panhandle. Gidley (1907) described more complete material (particulary a well-preserved skull, AMNH 10584) of what he called *Neohipparion lenticularis* from older deposits of Clarendonian age in Donley County of the Texas Panhandle. In Osborn's (1918) monograph on the fossil Equidae, he listed AMNH 10584 as the neotype of *Hipparion lenticulare* [sic], but as Cope's original type specimens were never lost, designation of a neotype was not necessary. Matthew and Stirton (1930) refer hipparion material from the late Hemphillian Coffee Ranch locality in the Texas Panhandle to *Hipparion lenticularis.*

The recognition of the species "*Hipparion*" or "*Nannippus*" *lenticularis* is difficult because of the lack of well-preserved specimens from the type locality. As envisioned by some workers, the broad definition of this species that includes Clarendonian through latest Hemphillian material is certainly open to question. Thus it is difficult to defend an ancestral-descendent relationship for "*N*" *lenticularis* and *N. phlegon* until the former species becomes better defined.

It should also be noted that in Sondaar's (1968) discussion of the equid manus, he stated that (p. 69): "There are smaller *Hipparion*-like animals that do not belong to the genus *Nannippus,* for example the species *lenticulare* [sic], which do not have the generic characters." This statement suggests that the species "*N.*" *lenticularis* and *N. phlegon,* the latter of which is the genotypic species of *Nannippus,* are not very closely related based on an analysis of postcranial remains.

We suggest the hypothesis that *Nannippus minor, N. beckensis,* and *N. phlegon* are relatively closely related. *N. minor* is best known from Mio-Pliocene deposits of central and northern Florida (Sellards 1916, Simpson 1930), and it has also been described from Georgia (Voorhies 1974)[1], Texas (Akersten 1972), and Chihuahua, Mexico (Lance 1950, Mooser 1968[2]). It should be noted that the holotype of *N. minor,* FGS 5867, from the Bone Valley district, has been lost since about the 1920's (see original description in Sellards 1916). We designate here the neotype of *N. minor,* UF 17570, consisting of left P^3-M^3 and right M^2-M^3 from Palmetto Mine in the Bone Valley district, Polk County, Florida (Fig. 15, Table 11).

Dalquest and Donovan (1973, also see Dalquest 1978) described a new species, *Nannippus beckensis,* from the early Blancan Beck Ranch

[1]Leidy (1860) described a small and poorly known *N. minor*-like horse, "*Hipparion*" *venustum,* from the Ashley River of South Carolina.

[2]*Nannippus aztecus,* described by Mooser (1968) from the Ocote L. F. of Mexico, is probably a junior synonym of *N. minor* (Waldrop 1971).

L.F. of Scurry County, Texas. They stated that (1973:34): "The new form is intermediate in most respects between the middle Pliocene (Hemphillian) *Nannippus lenticularis* and *N. phlegon* of the latest Pliocene and earliest Pleistocene, with some distinctive characters of its own." Despite the conclusion that "*Nannippus*" *lenticularis* is closely related to both *N. phlegon* and *N. beckensis,* Dalquest and Donovan presented important information with regard to the present study that supports a close relationship among *N. minor, N. beckensis,* and *N. phlegon.*

In most hipparions the anterior regions of both P^2 and P_2 are expanded. In the P^2 this expansion includes the presence of a pseudoparastyle and true parastyle (Fig. 3). In the P_2 the paralophid usually exhibits a triangular anterior projection. In *N. minor, N. beckensis,* and *N. phlegon* the anterior regions of both P^2 and P_2 are unexpanded relative to other hipparions (compare Fig. 17 with Fig. 4, also see Dalquest and Donovan 1973:38, text-fig. 4B).

TABLE 11.—MEASUREMENTS OF *Nannippus minor,* NEOTYPE, UF 17570, FROM PALMETTO MINE IN THE BONE VALLEY DISTRICT, POLK COUNTY, FLORIDA.

Tooth	AP Length	T Width	Ht*
LP^3	16.1	15.3	28.9
LP^4	15.6	15.0	32.8
LM^1	14.0	13.7	27.8
LM^2	14.3	13.7	31.7
LM^3	12.8	9.7	31.5
RM^2	14.7	13.5	32.3
RM^3	13.0	9.3	31.9
Length LP^3-LM^3:72.1			

*Greatest crown height (see Table 1).

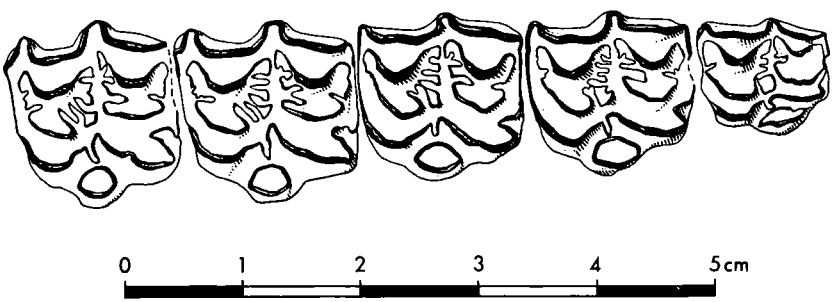

FIGURE 15.—Left upper cheek tooth row, P^3-M^3, of *Nannippus minor,* UF 17570, neotype, from Palmetto Mine, Bone Valley district, Polk County, Florida. (Remainder of neotype, M^2-M^3, not illustrated here.)

Many hipparions have an ectoparastylid (projection or isolation of paralophid, also called parastylid by some workers) developed on the anteroexternal region of P_2-M_3. Primitive *N. minor* shows a reduction in the presence of the ectoparastylid, which is further reduced in both advanced *N. minor* and *N. beckensis*. In *N. phlegon* the ectoparastylid is normally absent (see Waldrop 1971 and Dalquest and Donovan 1973 for quantitative data). In other words, a character morphocline proceeds from primitive hipparions (ectoparastylid present) to primitive *N. minor* (reduction in frequency of ectoparastylid) to advanced *N. minor-N. beckensis* (further reduction in frequency of ectoparastylid) to *N. phlegon* (ectoparastylid normally absent).

N. minor, N. beckensis, and *N. phlegon* have numerous other dental characters that support a hypothesis of close relationship, for example, complexity of enamel plications and shape of dental parts. Both *N. minor* and *N. beckensis* are smaller in maximum crown height (in both the uppers and lowers) than *N. phlegon.* The maximum crown height of *N. minor* is normally less than 50 mm (Waldrop 1971) whereas the maximum crown height of *N. phlegon* is somewhat greater than 50 mm (see Tables 1,4). For *N. beckensis* Dalquest and Donovan (1973) noted crown heights of 56.2 mm to 60.0 mm (lowers) and 51.2 mm to 55.7 mm

TABLE 12.—MEASUREMENTS OF LEFT LOWER CHEEK TEETH OF *Nannippus minor,* TRO 567, FROM PALMETTO MINE, BONE VALLEY DISTRICT, POLK COUNTY, FLORIDA.

Tooth	AP length	T width	HT*
P_2	13.3	7.5	25.2
P_3	13.6	7.9	—
P_4	14.0	7.6	33.5
M_1	13.0	6.4	35.0
M_2	13.4	6.6	—
M_3	16.6	5.3	39.3

*Crown height at mesostyle.

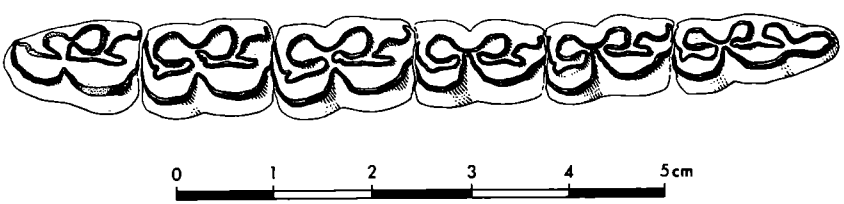

FIGURE 16.—Left lower cheek teeth, P_2-M_3, of *Nannippus minor,* TRO 567, from Palmetto Mine, Bone Valley district, Polk County, Florida.

(uppers), and, for the topotypic material of *N. phlegon* from Crawfish Draw, Mt. Blanco, 60.0 mm to 63.4 mm (lowers) and 66.7 mm to 72.7 mm (uppers). It should be noted that only the maximum crown height is significant; broken or well-worn teeth should not be considered.

Other characters besides dental similarities support a close relationship between *N. beckensis* and *N. phlegon* (unfortunately relevant material is not available for *N. minor*). Both *N. beckensis* and *N. phlegon* have an elongate rostrum and correspondingly elongate symphysis. Also the lower incisors are relatively procumbent and spatulate (Dalquest and Donovan 1973, this report). As discussed above, the one skull of *N. phlegon* examined during this study, AMNH 104708, has no facial fossa (Fig. 14). The only skull of *N. beckensis*, MU 8362 (now TMM 41542), is crushed but it also appears not to have either a malar fossa or dorsal (also called lacrimal or nasomaxillary) fossa.

Based on the dental similarities discussed here, we conclude that *N. minor, N. beckensis,* and *N. phlegon* share derived characters that imply a close relationship among these species. Within this species group is a morphocline, chronocline, and ancestral-descendent sequence from *N. minor* to *N. beckensis* to *N. phlegon.* Even though *N. beckensis* appears intermediate based on reduction in the presence of the ectoparastylid and crown height, it is clearly unique in one very distinctive character complex: the occlusal surface area of the cheek teeth is larger than either *N. minor* or *N. phlegon.* This hypothesis of close relationship is also consistent with the paleobiogeography of these species; it appears that *N. minor, N. beckensis,* and *N. phlegon* were essentially Neotropical in their distributions.

Dalquest and Donovan (1973) noted what they interpreted to be an ecological exclusion between species of *Nannippus* and other contemporaneous horses. For example, at Beck Ranch, *N. beckensis* is relatively abundant, whereas *Equus (Dolichohippus)* of *simplicidens* is relatively rare. At Mt. Blanco *N. phlegon* is relatively rare in contrast to abundant *Equus,* except at one site associated with a diatomite. Dalquest and Donovan conclude that *N. beckensis* and *N. phlegon* were probably adapted to pond-margin or swamp habitats. At the Florida Bone Valley sites *N. minor* occurs in association with several taxa of horses and other open-country forms like antilocaprids and deer (Webb and Tessman 1968). Similarly Florida *N. phlegon* is found at four sites in association with *Equus (Dolichohippus)* cf *simplicidens,* and, notably, with abundant *Capromeryx arizonensis* in the Santa Fe River Sites (Webb 1974, this report). In short, if Dalquest and Donovan's observations about High Plains *Nannippus* and *Equus* are a true reflection of ecological preferences, then there does not appear to

have been a similar ecological exclusion among equids and other large herbivores in the Gulf Coastal region during Hemphillian and Blancan times.

Literature Cited

Akersten, W. A. 1972. Red Light local fauna (Blancan) of the Love Formation, southeastern Hudspeth County, Texas. Texas Mem. Mus. Bull. 20: 1-53.

Barone, R. 1966. Anatomie comparée des mammifères domestiques. Tome Premier. Lab. d'Anat. Ecole Natl. Veterinaire, Lyon. 811 p.

Berggren, W. A., and J. A. Van Couvering. 1977. The late Neogene: Biostratigraphy, geochronology and paleoclimatology of the last 14 million years in marine and continental sequences. Palaeogeogr., palaeoclimat., palaeoecol. 16(1/2): 1-216.

Brodkorb, P. 1963. A giant flightless bird from the Pleistocene of Florida. Auk 80(2): 111-115.

Camp, C.L., and N. Smith. 1942. Phylogeny and functions of the digital ligaments of the horse. Mem. Univ. California 13(2): 69-124.

Chubb, S. H. 1912. Notes on the trapezium in the Equidae. Bull. Amer. Mus. Nat. Hist. 31(7): 113-115.

Cope, E. D. 1893. A preliminary report on the vertebrate paleontology of the Llano Estacado. Texas Geol. Surey, 4th Ann. Report: 1-137.

Dalquest, W. W. 1975. Vertebrate fossils from the Blanco local fauna of Texas. Occ. Pap. Mus. Texas Tech. Univ. 30:1-52.

_____. 1978. Early Blancan Mammals of the Beck Ranch Local Fauna of Texas J. Mamm. 59(2):269-298.

_____, and T. J. Donovan. 1973. A new three-toed horse (*Nannippus*) from the late Pliocene of Scurry County, Texas. J. Paleont. 47(1):34-45.

DuBar, J. R. 1958. Stratigraphy and paleontology of the late Neogene strata of the Caloosahatchee River area of southern Florida. Bull. Florida Geol. Surv. 40:1-267.

Gazin, C. L. 1936. A study of the fossil horse remains from the upper Pliocene of Idaho. Proc. U. S. Natl. Mus. 83(2985):281-320.

_____. 1942. The late Cenozoic vertebrate faunas from the San Pedro Valley, Ariz. Proc. U. S. Natl. Mus. 92(3155):475-518.

Gidley, J. W. 1907. Revision of the Miocene and Pliocene Equidae of North America. Bull. Amer. Mus. Nat. Hist. 23(35):865-934.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. London Med. Repository Rev. 15:296-310.

Hay, O. P. 1899. On the nomenclature of certain American fossil vertebrates. Amer. Geol. 24:345-349.

Hibbard, C. W. 1941. Mammals of the Rexroad fauna from the Upper Pliocene of southwestern Kansas. Trans. Kansas Acad. Sci. 44:265-313.

_____. 1956. Vertebrate fossils from the Meade Formation of southwestern Kansas. Pap. Michigan Acad. Sci. 41:145-200.

_____. 1970. Pleistocene mammalian local faunas from the Great Plains and central lowland provinces of the United States; pp. 395-433 *In* W. Dort and J. K. Jones (eds.). Pleistocene and Recent environments of the central Great Plains. Dept. Geol. Univ. Kansas Spec. Pub. 3, Univ. Kansas Press, Lawrence.

_____, C. E. Ray, D. E. Savage, D. W. Taylor, and J. E. Guilday. 1965. Quaternary mammals of North America; pp. 509-525 *In* H. E. Wright and D. G. Frey (eds.) The Quaternary of the United States. Princeton Univ. Press, Princeton.

Hussain, S. T. 1975. Evolutionary and functional anatomy of the pelvic limb in fossil and Recent Equidae (Perissodactyla, Mammalia). Anat., Histol., Embryol. 4:179-222.

Johnson, N. M., N. D. Opdyke, and E. H. Lindsay. 1975. Magnetic polarity stratigraphy of Pliocene-Pleistocene terrestrial deposits and vertebrate faunas. San Pedro Valley, Arizona. Bull. Geol. Soc. Amer. 86(1):5-12.

Lance, J. F. 1950. Paleontologia y estratigrafia del Plioceno de Yepómera, estado de Chihuahua. 1ª Parte: Equidos, excepto *Neohipparion*. Univ. Nac. Autonoma Mexico. Inst. Geol. Bol. 54:1-81.

Leidy, J. 1860. Description of vertebrate fossils; pp. 99-122 *In* F. S. Holmes (ed.). Post-Pliocene Fossils of South Carolina.

Lindsay, E. H., N. M. Johnson, and N. D. Opdyke. 1975. Preliminary correlation of North American land mammal ages and geomagnetic chronology; pp. 111-119 *In* G. E. Smith and N. E. Friedland (eds.). Studies on Cenozoic paleontology and stratigraphy in honor of Claude W. Hibbard. Mus. Paleont. Univ. Michigan Papers Paleont. 12.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae. Secundum Classes, Ordines, Genera, Species, cum Characteribus Differentiis Synonymiis Locis. Editia decima, reformata. Laurentii, Stockholm, Salvi, 1:824p.

MacFadden, B. S. 1980. The Miocene horse *Hipparion sensu stricto* from North America and the type locality in southern France. Palaeontology. In press.

_____, and M. F. Skinner. 1977. Earliest known *Hipparion* from Holarctica. Nature. 265:532-533.

Matthew, W. D. 1926. The evolution of the horse; a record and its interpretation. Quart. Rev. Biol. 1:139-185.

_____, and R. A. Stirton. 1930. Equidae from the Pliocene of Texas. Univ. of California Pub. Bull. Dept. Geol. Sci. 19(17):349-396.

Mooser, O. 1968. Fossil Equidae from the middle Plocene of the Central Plateau of Mexico. Southwest. Nat. 13:1-12.

Osborn, H. F. 1918. Equidae of the Oligocene, Miocene, and Pliocene of North America. Iconographic type revision. Mem. Amer. Mus. Nat. Hist., New Ser. 2:1-326.

Owen, R. 1848. Description of teeth and portion of jaws of two extinct anthracotheroid quadrupeds *(Hypotamus vectianus* and *H. bovinus)* discovered by the Marchioness of Hastings in the Eocene deposits on the N. W. coast of the Isle of Wight, with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of toes. Quart. J. Geol. Soc. 5:380-383.

Robertson, J. S. 1976. Latest Pliocene mammals from Haile XV A, Alachua County, Florida. Bull. Florida State Mus., Biol. Sci. 20(3):111-186.

Schultz, G. E. (ed.). 1977. Guidebook: Field conference on late Cenozoic biostratigraphy of the Texas Panhandle and adjacent Oklahoma, August 4-6, 1977. Kilgore Res. Center, Dept. Geol. and Anthropol., West Texas State Univ., Spec. Pub. 1:1-160.

Sellards, E. H. 1916. Fossil vertebrates from Florida. A new Miocene fauna, new Pliocene species, the Pleistocene fauna. Florida Geol. Survey, 8th Ann. Report:77-119.

Shotwell, J. A. 1970. Pliocene mammals of southeast Oregon and adjacent Idaho. Bull. Mus. Nat. Hist. Univ. Oregon. 17:1-103.

Simpson, G.G. 1930. Tertiary land mammals of Florida. Bull. Amer.Mus. Nat. Hist. 59(3):149-211.

Simpson, G. G. 1951. Horses. Oxford Univ. Press, New. York, 247 p.

Sisson, S., and J. D. Grossman. 1953. The anatomy of domesticated animals. W. B. Saunders Co., Philadelphia, 972 p.

Skinner, M. F., and B. E. Taylor. 1967. A revision of the geology and paleontology of the Bijou Hills, South Dakota. Amer. Mus. Nat. Hist. Nov. 2300:1-53.

Skinner, M. F., and C. W. Hibbard. 1972. Early Pleistocene pre-glacial and glacial rocks and faunas of north-central Nebraska. Bull. Amer. Mus. Nat. Hist. 148(1):1-48.

Skinner, M. F., and B. J. MacFadden. 1977. *Cormohipparion* N. Gen. (Mammalia, Equidae) from the North American Miocene (Barstovian-Clarendonian). J. Paleont. 51(5):912-926.

Sondaar, P. Y. 1968. The osteology of the manus of fossil and Recent Equidae with special reference to phylogeny and function. Koninkl. Nederl. Akad. Wetenschappen. 25(1):1-76.

Stirton, R. A. 1940. Phylogeny of North American Equidae. Univ. California Pub. Bull. Dept. Geol. Sci. 25(4):165-198.

_____. 1941. Development of characters in horse teeth and the dental nomenclature. J. Mamm. 22(4):434-446.

Strain, W.S. 1966. Blancan mammalian fauna and Pleistocene formations, Hudspeth County, Texas. Texas Mem. Mus. Bull. 10:1-55.

Tedford, R. H., T. Galusha, M. F. Skinner, B. E. Taylor, R. W. Fields, J. R. Macdonald, T. H. Patton, J. M. Rensberger, and D. P. Whistler. In press. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through late Miocene epochs), North America. Univ. California Press, Berkeley.

Voorhies, M. R. 1974. The Pliocene horse *Nannippus minor* in Georgia: Geologic implications. Tulane Stud. Geol. Paleont. 11(2):109-113.

Waldrop, J. S. 1971 The Pliocene Equidae of Florida. M. S. thesis, Univ. Florida, Gainesville, 170p.

Webb, S. D. 1969. The Burge and Minnechaduza Clarendonian mammalian faunas of north-central Nebraska. Univ. California Dept. Geol. Sci. Pub. 78:1-191.

_____. 1974. Chronology of Florida Pleistocene mammals; pp. 5-31 *In* S. D. Webb (ed.). Pleistocene mammals of Florida. Univ. Presses of Florida, Gainesville.

_____, and N. Tessman. 1968. A Pliocene vertebrate fauna from low elevation in Manatee County, Florida. Amer. J. Sci. 266:777-881.

Wood, H. E., R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Bull. Geol. Soc. Amer. 52:1-48.

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