SYSTEMATICS AND PHYLOGENY OF *HIPPARION, NEOHIPPARION, NANNIPPUS,* AND *CORMOHIPPARION* (MAMMALIA, EQUIDAE) FROM THE MIOCENE AND PLIOCENE OF THE NEW WORLD

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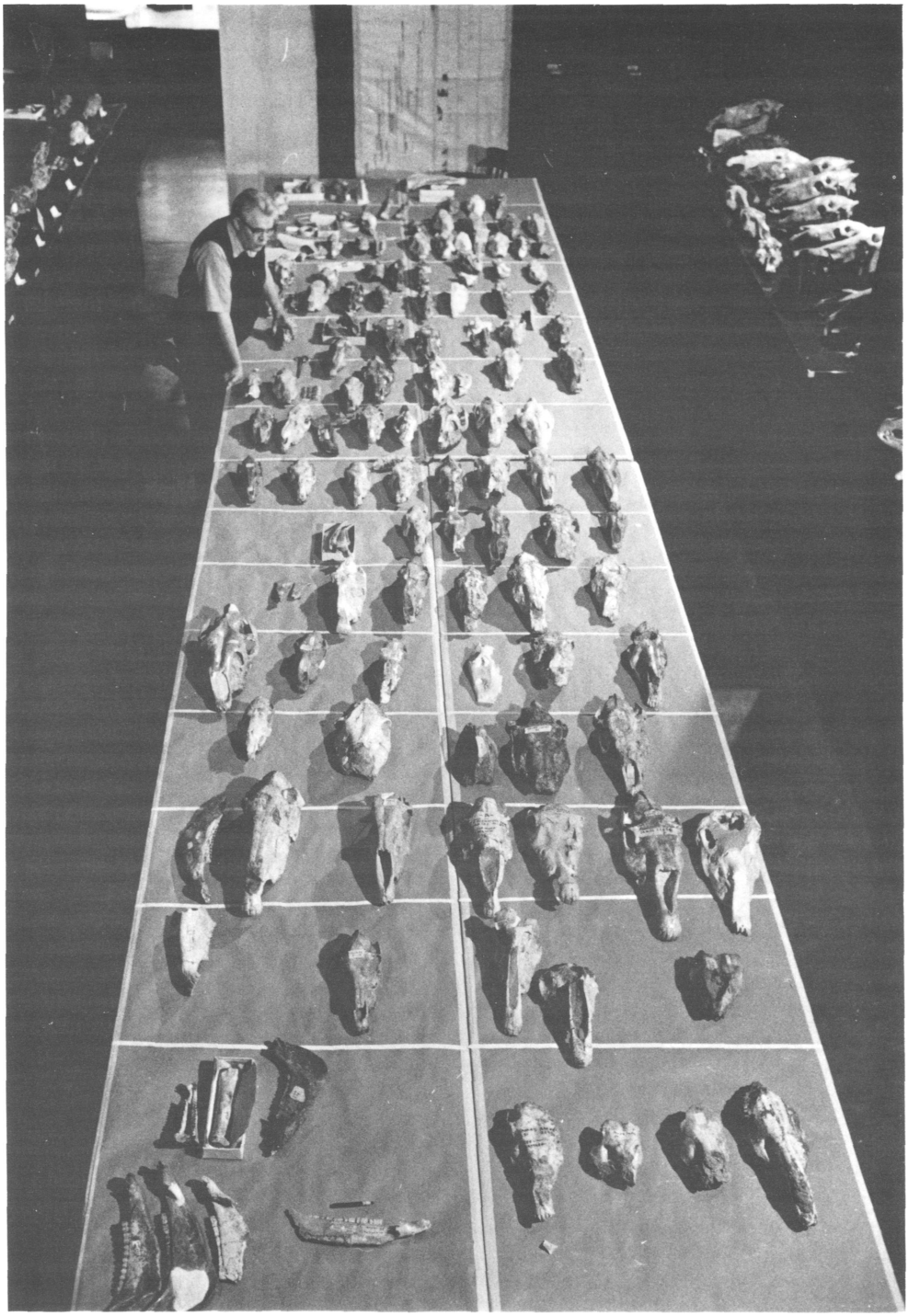

FIG. 1 (FRONTISPIECE). Dr. Morris F. Skinner, Frick Curator Emeritus, and the unexcelled array of Tertiary horse skulls in the Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History. The Frick horses serve as the principal source of reference for an understanding of the systematics of extinct Equidae. Of particular importance to the present report, this collection contains the single best sample of the North American representatives of the genera *Hipparion, Neohipparion, Nannippus,* and *Cormohipparion.*

ABSTRACT

Hipparions are a polyphyletic assemblage of three-toed horses that lived during the Miocene and Pliocene in the Old and New worlds. Four hipparion genera are recognized from Central and North America, they are: *Hipparion sensu stricto, Neohipparion, Nannippus,* and *Cormohipparion.* Of the 41 previously named species of New World hipparions, 15 are referred to the existing genera and the remaining 26 species names are considered to be either junior synonyms, *incertae sedis, nomina nuda,* or *nomina dubia.* One new species, *Hipparion shirleyi,* is described from the late Barstovian of the Texas Gulf Coastal Plain. This paper presents the systematics of New World hipparions in a scheme that principally includes an integration of quantitative and qualitative dental and cranial characters such as the configuration of the dorsal preorbital fossa. Statistical analyses of crania and dentitions provide determinations of the amount of character variation for North American hipparions.

The hipparion from Mt. Léberon in southern France, *Hipparion prostylum* de Christol, 1832, is the genotypic species of *Hipparion sensu stricto.* In the New World, *Hipparion sensu stricto* is represented by three species; *H. shirleyi,* new species, *H. tehonense* (Merriam), 1916a, and *H. forcei* Richey, 1948, collectively known from the late Barstovian to the early Hemphillian of North America. Six species comprise the genus *Neohipparion*: *N. coloradense* (Osborn), 1918, *N. affine* (Leidy), 1869, *N. trampasense* (Edwards), 1982, *N. leptode* Merriam, 1915a, *N. eurystyle* (Cope), 1893, and *N. gidleyi* Merriam, 1915a, collectively known from the Clarendonian through late Hemphillian of Central and North America. Four species comprise the genus *Nannippus*: *N. minor* (Sellards), 1916, *N. ingenuus* (Leidy), 1885, *N. beckensis* Dalquest and Donovan, 1973, and *N. peninsulatus* (Cope), 1885, collectively known from the Clarendonian through late Blancan of Central and North America. In the New World, the genus *Cormohipparion* consists of three species, *C. goorisi* MacFadden and Skinner, 1981, *C. sphenodus* (Cope), 1889, and *C. occidentale* (Leidy), 1856, collectively known from the early Barstovian through early Hemphillian of North America.

Hipparions are closely related to, or arose from, at least two separate taxa within the merychippine horse complex. The earliest North American hipparion, *C. goorisi,* is known from the 15-million-year old early Barstovian Gulf Coastal Plain of Texas. The peak of hipparion diversity in North America occurred about 12 to 8½ million years ago during the height of the Clarendonian chronofauna. Hipparion diversity dropped during the Hemphillian. Only the genus *Nannippus* is known from the Blancan. Some previous workers state that all Old World hipparions were monophyletically descended from the oldest Old World species *H. primigenium.* However, based on similar hipparion facial morphotypes represented in both the Old and New worlds, it is possible that there were at least two hipparion dispersal events across Beringia, resulting in a polyphyletic assemblage in the Old World.

INTRODUCTION

During the Miocene and Pliocene the three-toed hipparion horses were a geographically and temporally widespread element of terrestrial mammalian faunas throughout North America and the Old World. Their dispersal across Beringia resulted in their first occurrence in the Old World, or the so-called "Hipparion Datum," one of the most striking biochronological reference points in the terrestrial Neogene. In the New World, particularly North America, hipparions were the dominant horses and among the most common ungulates during the height of the Clarendonian chronofauna (Webb, 1969). The ubiquitous nature of these horses has given rise to the term "Hipparion faunas" for Neogene mammalian assemblages, particularly in the Old World.

De Christol (1832) described the genus *Hipparion* based on material from the late Turolian Mt. Léberon locality in southern France. Since this original description, several other genera and numerous species (certainly more than a hundred) of hipparions have been named from the Neogene record of the New and Old worlds. The taxonomy of hipparions has traditionally been based on dental, and to a lesser extent postcranial, characters. Because of the large number of named species, the taxonomy of this group has become very unwieldy. In the past, some workers have unsuccessfully attempted to

refer a local sample to a preexisting species. As a result of this, they sometimes have named new species based on minor dental or postcranial characters of dubious significance. There have been attempts in recent years to reconcile this unwieldy taxonomy of Old World hipparions (see Gromova, 1955; Forstén, 1968; Hussain, 1971; Sondaar, 1974). However, a comprehensive taxonomic synthesis of New World hipparions has not been presented since the publication of some of the classic works on this subject earlier in this century (see Osborn, 1918; Stirton, 1940). In addition two new genera, one of which is here considered valid, and several new species of North American hipparions have been named since these classic works. In recent years North American students of equid paleontology have investigated the significance of character complexes such as the configuration of facial fossae as well as the more traditional dental and postcranial characters (see Skinner and MacFadden, 1977; Woodburne and Bernor, 1980). As is also the case with Old World forms, prior to Forstén (1968), the high number of North American hipparion species is an artifact of the preexisting unwieldy taxonomy.

The purpose of this study is to present the systematics and phylogeny of North American hipparions and to discuss the biochronological and paleobiogeographical significance of this important group. This research has been stimulated by the extraordinary array of relevant specimens, particularly the hundreds of well-preserved skulls and meticulous stratigraphic control that are part of the Frick horse collection (see fig. 1). As a result of more than a half-century of study on this collection by Morris F. Skinner, and more recent research by his students, a new taxonomic approach to the study of fossil horses centers on the significance of cranial characters, particularly in the development of preorbital facial fossae, as well as an integration of the more traditional dental and postcranial characters. This approach is particularly applicable to hipparions and provides, along with the Frick Collection, the impetus for the present revision. Rather than attempting to demonstrate the monophyly of hipparions, which has been done by many previous workers, the present study is based on the premise that this "group" is polyphyletic. Different hipparion taxa are probably most closely related to two or more taxa within the genus *Merychippus* (*sensu lato, fide* Stirton, 1940) or perhaps even *Parahippus*. Therefore, in order to present a monophyletic study of the separate hipparion taxa and their closest relatives, it would also be necessary to revise at least the "merychippine" complex, which is beyond the scope of this report. In addition, other hipparion-like equid genera, such as *Pseudhipparion,* are not considered in this paper because they seem more distantly related to the genera traditionally considered to be "true hipparions."

In summary, the polyphyletic term "hipparion" is of little use in a strict taxonomic sense. However, throughout the text, the term hipparion is used, *faute de mieux,* to describe a complex of four genera, i.e., *Hipparion, Neohipparion, Nannippus,* and *Cormohipparion,* of Mio-Pliocene horses with similar (although independently acquired) characters such as the presence of isolated protocones in the upper molars and tridactyl feet. A comparative synopsis of North American hipparion character states is presented in table 1. These character states are also discussed in detail below. However, they are not used to interrelate these taxa because this group is clearly polyphyletic.

I hope that this study will result in a clearer and phylogenetically significant taxonomy for North American hipparions. As mentioned above, in many instances it was previously very difficult, if not impossible, to refer a given hipparion sample to a preexisting North American species or species group. Although there is little hope in every instance for fitting isolated finds (e.g., single teeth) into an existing taxonomic framework, this study attempts to present a taxonomy that will allow medium to large quarry samples to be referred to recognized species and appropriate genera. This study also significantly reduces the "diversity" of North American hipparion species to a situation that seems more consistent with the apparent evolutionary history of this group.

ACKNOWLEDGMENTS

Special thanks are extended to Drs. Morris F. Skinner and Richard H. Tedford of the

TABLE 1

Comparison of Selected Character States and Other Descriptive Information for the Hipparion Genera Discussed in this Report[a]

Character or Data	*Hipparion*	*Neohipparion*	*Nannippus*	*Cormohipparion*
Number of species recognized in this report	3	6	4	3
Size relative to all hipparions	Small to medium	Medium to very large	Very small to small	Small to large
Mean length of upper cheek tooth row, P^2–M^3 (TRL)	105.35 to 133.50 mm	127.31 to *ca.* 150 mm	*Ca.* 90 to 115.90 mm	116.83 to 138.00 mm
Hypsodonty relative to all hipparions	Mesodont to hypsodont	Hypsodont to very hypsodont	Hypsodont to extremely hypsodont	Mesodont to hypsodont
Estimated-approximate M^1 mesostyle crown height (M1MSTHT) for little-worn specimens	25 to 50 mm	35 to 71 mm	37 to 66 mm	22 to 43 mm
SKULL				
Nasal notch	Moderate to deep, in some cases retracted dorsal to P^2	Moderate, dorsal to postcanine diastema	Moderate, dorsal to postcanine diastema	Small to moderate, dorsal to postcanine diastema
Position of dorsal preorbital fossa (DPOF)	On nasal and maxillary bones anterior to lacrimal	On nasal, maxillary, and lacrimal bones	Absent (except possibly in *N. ingenuus*)	On nasal, maxillary, and sometimes lacrimal bones
Configuration of dorsal preorbital fossa (DPOF)	Anterior rim poorly defined or absent, posterior rim continuous and well defined, posterior pocket shallow or absent	Depending upon species, varies from shallow and poorly defined to virtually absent, posterior pocket absent	Absent (in *N. ingenuus* there is a small depression principally on nasal and maxillary bones)	Anterior and posterior rims well defined and usually continuous, posterior pocket moderate to deep
UPPER DENTAL PATTERN[b]				
Protocone	Mostly rounded to oval; primitive species (*H. shirleyi*) with anterior spur (relict of connection to protoloph); advanced forms elongate (advanced *H. forcei*)	Oval to very elongate, frequently with angular anterior and posterior borders in advanced species	Usually sub-oval to oval with rounded borders	Usually oval to elongate; primitive species (*C. goorisi*) with anterior spur; advanced species without well-developed angular borders and not as elongated as *N. eurystyle*

TABLE 1—(*Continued*)

Character or Data	*Hipparion*	*Neohipparion*	*Nannippus*	*Cormohipparion*
Enamel plications on fossettes	Very simple to moderate	Simple to complex	Simple to moderate	Moderate to complex
Pli caballin	Usually well-developed single or double loop	Usually well-developed single or double loop, advanced species can exhibit more loops	Moderately to poorly developed, usually single loop	Usually well-developed single or double loop; *C. occidentale* sometimes more complicated
LOWER DENTAL PATTERN[b]				
Protostylid	Usually moderately developed	Usually moderate to well developed	Moderately developed to rudimentary or absent	Moderately to well developed; sometimes an isolated conid; frequently developed in some Old World relatives
Ectoflexid	Deep to moderate	Moderate to very shallow	Deep to moderate	Deep to moderate
Plications on lower cheek tooth enamel	Simple	Simple to moderate	Simple	Simple
Plications on isthmus	Absent	Absent in primitive species; can be well developed in advanced species	Absent	Absent
Pli caballinid	Moderate to poorly developed, rudimentary or absent	Moderate to well developed; extremely well developed and complicated in advanced species	Moderate, poorly developed, frequently rudimentary, or absent	Moderate to poorly developed
Metaconid-metastylid complex	Approx. equal or subequal in size; distinctly separated; rounded borders	Approx. equal or subequal in size; distinctly separated; usually with rounded borders, in advanced species oftentimes very expanded	Approx. equal or subequal in size; distinctly separated with rounded borders	Approx. equal or subequal in size; distinctly separated usually with rounded borders
Entoconid-hypoconulid complex	Entoconid larger than hypoconulid; distinctly separated; usually with rounded borders	Entoconid larger than hypoconulid; distinctly separate; rounded or angular borders; in advanced species very angular borders	Entoconid slightly larger than hypoconulid; distinctly separated, rounded borders	Entoconid larger than hypoconulid, distinctly separated; rounded borders, infrequently angular

TABLE 1—(*Continued*)

Character or Data	*Hipparion*	*Neohipparion*	*Nannippus*	*Cormohipparion*
POSTCRANIAL ELEMENTS				
Digits	Tridactyl	Tridactyl	Tridactyl	Tridactyl
Trapezium	Present (so far as is known)	Present (so far as is known)	Absent in *N. minor* and *N. peninsulatus*; condition unknown in other species	Present (so far as is known)
Metapodials (exemplified by MC III and MT III)	Moderate to robust and elongate	Moderately robust, moderately to very elongate	Relatively gracile, moderately to very elongate	Moderately to relatively robust, moderately elongate
MISCELLANEOUS				
Known stratigraphic range in North America	Barstovian to early Hemphillian	Early Barstovian to latest Hemphillian	Late Clarendonian to late Blancan	Early Barstovian to probably early Hemphillian
Known paleobiogeographic distribution	United States[c] and the Old World	North America and Central America, possibly Old World	United States[c] and Central America	United States[c] and Central America, Old World

[a] A detailed analysis of these character states is presented separately for each genus in the individual sections of Systematic Paleontology.
[b] Unless otherwise noted, the descriptions of dental characters are representative of early and medial wear stages.
[c] Although United States is a political and not a natural entity, it is used here to be more restrictive than North America.

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METHODS, TERMINOLOGY, AND ABBREVIATIONS

This study is based on research at various institutions that has been in progress for several years. The Frick horse collection served as a nucleus for this study. The other North American collections that were principally consulted during this research include those at Yale University, the National Museum of Natural History, Smithsonian Institution, the University of Florida, the Panhandle Plains Historical Museum and West Texas State University, the University of Nebraska State Museum, the Texas Memorial Museum, the Natural History Museum of Los Angeles County, and the University of California Mu-

seum of Paleontology. Specimens borrowed from other institutions are listed below. For a better understanding of Old World hipparions, I examined collections at the British Museum (Natural History), London; the Institut de Paléontologie, Paris; the Institut für Paläontologie und historiche Geologie, Munich; Geologische Instituut, Utrecht; Department of Zoology, University of the Punjab, Lahore; and the Geological Survey of India, Calcutta.

As outlined in the Introduction, emphasis is placed on localities and specimens that have well-preserved cranial material as well as associated dentitions and other skeletal elements. All the presently recognized species of North American hipparions except *Neohipparion gidleyi* and *Nannippus minor* are now known from crania as well as dentitions. With regard to the figures, emphasis is placed on specimens not previously published in the literature or on poorly illustrated critical specimens. Excellent figures of many of the early type and important specimens are found in Osborn (1918); therefore, many of these are not included in this report. Material studied in the institutions listed herein from almost all relevant localities was examined, but it is not possible to identify with certainty which hipparion taxa come from numerous small localities and isolated prospects. The map in figure 2 indicates representative, important, and well-known sites, fossil fields, and local faunas for which abundant and well-preserved hipparion specimens have been studied or are known in the literature.

TYPE SPECIMENS AND REFERRED SAMPLES: Many of the late nineteenth and early twentieth century paleontologists introduced equid species' names into the literature without critically assessing ranges of variation in diagnostic characters (e.g., Merriam named nine new hipparion species from the western United States between 1913 and 1916, see table 2 and references cited below). The early names were frequently based on single, fragmentary specimens with only general provenance data. In addition, Osborn (1918) influenced subsequent research with the use of "neotypes" to expand or better understand the concept of certain species. When a type specimen was fragmentary or consisted of perhaps an isolated tooth, Osborn would choose a better-preserved specimen (e.g., skulls for "*Hipparion lenticulare*" or "*Merychippus sphenodus*") as the neotype even though the holotype still existed. He defined his concept of the neotype as (Osborn, 1918, p. 35): "The specimen chosen in a subsequent paper by the original or another author as referable to the same species and amplifying the characters of the type by affording fuller material for description." With the advent of the International Code of Zoological Nomenclature (Stoll et al., 1964), the neotype can only be designated when no holotype, lectotype, or syntype is available. In some cases Osborn chose neotypes that now appear to represent taxa different from the original type, thereby engendering much confusion in subsequent literature (e.g., see discussion of the nomen *Hipparion lenticulare* below).

During the present study, all available types and associated topotypic samples of North American hipparions were examined. Despite the problems that afflict some of the earlier-named types, those nomen that possess diagnostic characters were conserved. Following current procedures, all junior taxa were subsumed regardless of whether or not these are better-known in the literature or represented by better samples (e.g., *Nannippus phlegon* from Mt. Blanco, herein a junior synonym of *N. peninsulatus*). Samples from other representative localities are then described below in order to present a comprehensive description of the morphology (and variation) and limits of geographic and temporal distribution of each species. Some previously named species do not possess any diagnostic characters that would facilitate allocation to a valid name or recognition of synonymy. These *nomina dubia* are relegated to "Hipparionine Indeterminate" below. One other problematical name, "*Hippotherium plicatile,*" has a diagnostic suite of characters that justify recognition of a distinct species. However, this species cannot be unambiguously allocated to one genus; it is herein considered *incertae sedis.*

SYSTEMATIC METHODOLOGY AND PHYLOGENY RECONSTRUCTION: In recent years ample space in the professional literature has been devoted to controversies in systematic methodology. I do not intend to reiterate this subject, but briefly outline the methodology

TABLE 2
Descriptions of North American Hipparion Species Discussed in this Report in Chronological Order

Original Name, Author, and Year	Locality	Age	Present Reference
Hipparion occidentale Leidy, 1856	Little White River, South Dakota	Late Clarendonian	=*Cormohipparion occidentale*
Hipparion venustum Leidy, 1860	Ashley River, South Carolina	"Post-Pliocene"	*Nomina vanum* et *oblitum*, =*Nannippus minor*
Hipparion affine Leidy, 1869	Niobrara River, Nebraska	Late Clarendonian	=*Neohipparion affine*
Hippotherium sinclairi Wortman, 1882	Cottonwood Creek, Oregon	Early Hemphillian	*Nomen dubium*
Hippotherium montezuma Leidy, 1883	near Lacualtipan, Hidalgo, Mexico	Exact provenance uncertain	*Nomen dubium*
Hippotherium ingenuum Leidy, 1885	Mixson's Bone Bed, Florida	Early Hemphillian	=*Nannippus ingenuus*
Hippotherium peninsulatum Cope, 1885	Tehuichila, Mexico	Exact provenance uncertain	=*Nannippus peninsulatus*
Hippotherium rectidens Cope, 1886	Tehuichila, Mexico	Exact provenance uncertain	*Nomen dubium*
Hippotherium plicatile Leidy, 1887	Mixson's Bone Bed, Florida	Early Hemphillian	="*Hippotherium*" *plicatile*, *Incertae sedis*
Hippotherium sphenodus Cope, 1889	Sand Canyon, Colorado	Late Barstovian	*Cormohipparion sphenodus*
Protohippus lenticularis Cope, 1893	Mulberry Canyon, Goodnight, Texas	Late Hemphillian	=*Nannippus ingenuus*
Equus eurystylus Cope, 1893	Falls of the Palo Duro Canyon, Texas	Late Hemphillian	=*Neohipparion eurystyle*
Equus phlegon Hay, 1899	Mt. Blanco, Texas	Blancan	Replacement name for *Equus minutus* Cope, 1893, =*Nannippus peninsulatus*
Neohipparion whitneyi Gidley, 1903	Rosebud Agency, South Dakota	Late Clarendonian	=*Neohipparion affine*
Neohipparion dolichops Gidley, 1906	Little White River, Big Spring Canyon, South Dakota	Late Miocene	=*Neohipparion affine*
Hipparion (?) *mohavense* Merriam, 1913	Mohave Desert, Ricardo, California	Early Clarendonian	=*Cormohipparion occidentale*
Neohipparion gidleyi Merriam, 1915a	San Francisco Bay (Petaluma), California	Late Hemphillian	*Neohipparion gidleyi*
Neohipparion molle Merriam, 1915a	North Coalinga Region, California	?Late Hemphillian	=*Neohipparion eurystyle*
Neohipparion leptode Merriam, 1915a	Thousand Creek, Nevada	Early Hemphillian	*Neohipparion leptode*
Hipparion platystyle Merriam, 1915a	San Francisco Bay, California	Early Clarendonian	=*Cormohipparion occidentale*
Hipparion condoni Merriam, 1915a	Ellensberg, Washington	Late Miocene	*Nomen dubium*

TABLE 2—(*Continued*)

Original Name, Author, and Year	Locality	Age	Present Reference
Hipparion mohavense callodonte Merriam, 1915b	Mohave Desert, Ricardo, California	Early Clarendonian	=*Cormohipparion occidentale*
Hipparion minor Sellards, 1916	Bone Valley phosphate district, Florida	Probably Hemphillian	=*Nannippus minor*
Hipparion anthonyi Merriam, 1916a	Ironside, Oregon	Unknown	*Nomen dubium*
Neohipparion gratum tehonense Merriam, 1916b	South Tejon Hills, California	Early Clarendonian	=*Hipparion tehonense*
Hipparion coloradense Osborn, 1918	Sand Canyon, Colorado	Late Barstovian	=*Neohipparion coloradense*
Nannippus cragini Hay, 1917	Meade and Clark counties, Kansas	Blancan	=*Nannippus peninsulatus*
Neohipparion occidentale sodalis Osborn, 1918	?Upper Snake Creek, Nebraska	Unknown	*Nomen nudum, fide* Stirton (1940)
Hipparion phosphorum Simpson, 1930	Bone Valley phosphate district, Florida	Hemphillian	=*Neohipparion eurystyle*
Neohipparion sanfondensis Frick, 1933	Upper Santa Fe, New Mexico	Miocene	*Nomen nudum, fide* Stirton (1940)
Neohipparion sanjuanensis Frick, 1933	Upper Santa Fe, New Mexico	Miocene	*Nomen nudum, fide* Stirton (1940)
Neohipparion floresi Stirton, 1955	Yepómera, Chihuahua, Mexico	Late Hemphillian	=*Neohipparion eurystyle*
Neohipparion arellanoi Stirton, 1955	Yepómera, Chihuahua, Mexico	Late Hemphillian	=*Neohipparion eurystyle*
Neohipparion otomii Mooser, 1960	Ocote, Guanajuato, Mexico	Late Hemphillian	=, in part, *Neohipparion eurystyle* and, in part, *N. gidleyi*
Neohipparion monias Mooser, 1964	Ocote, Guanajuato, Mexico	Late Hemphillian	=*Neohipparion eurystyle*
Nannippus aztecus Mooser, 1968	Ocote, Guanajuato, Mexico	Late Hemphillian	=*Nannippus minor*
Nannippus hesperides Mooser, 1968	Ocote, Guanajuato, Mexico	Probably early Blancan	?=*Nannippus peninsulatus*
Nannippus beckensis Dalquest and Donovan, 1973	Beck Ranch, Texas	Blancan	*Nannippus beckensis*
Cormohipparion goorisi MacFadden and Skinner, 1981	Trinity River, Gulf Coast, Texas	Early Barstovian	*Cormohipparion goorisi*
Hesperohipparion stirtoni Dalquest, 1981	Coffee Ranch, Texas	Late Hemphillian	=*Neohipparion eurystyle*
Hipparion trampasense Edwards, 1982	San Francisco Bay region, California	Late Clarendonian	=*Neohipparion trampasense*
Hipparion shirleyi, new species this report	Gulf Coast, Texas	Late Barstovian	—

followed here. Since Hennig's (1966) work became available, many interpretations and modifications of phylogenetic systematics, or "cladism" have been proposed. It is clear that the method as stated by Hennig (1966) provides an elegant foundation of rigorous

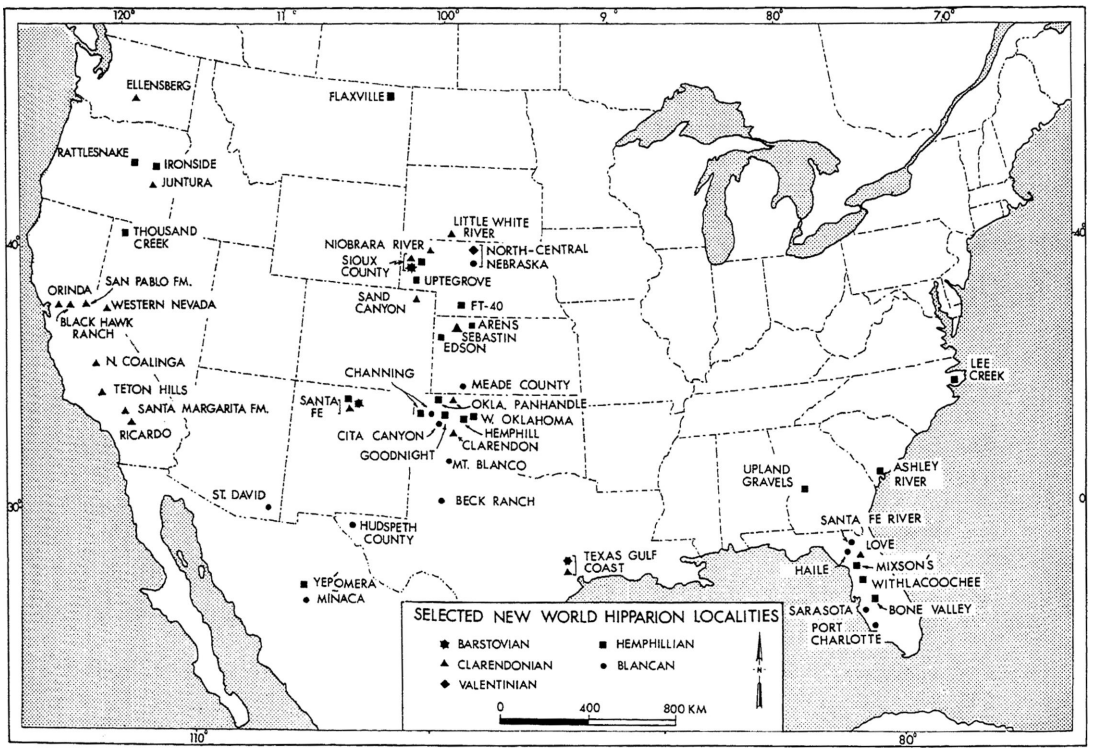


FIG. 2. Selected localities of *Hipparion, Neohipparion, Nannippus,* and *Cormohipparion* in the New World. These represent most of the large hipparion samples discussed in text. In addition, extensive fossiliferous areas represented by numerous localities are indicated by a symbol near center of the region, e.g., Meade (and adjacent Clark) counties, Kansas; north-central Nebraska, which encompasses Brown and Cherry counties and adjacent South Dakota; the Bone Valley region of Polk and adjacent Hillsborough counties, Florida. See text and figure 7 for an interpretation of the North American Land Mammal "Ages."

criteria for constructing hypotheses of relative relatedness of taxa with the use of intrinsic (e.g., morphological) data. However, as workers such as Gaffney (1979) have pointed out, there are philosophical problems with cladism as well as the other "schools" of systematic methodology. In addition, few systematists adhere to exactly the same methodology. An article entitled "Cladism and common sense" by Eldredge (1979) and an earlier article by Schaeffer, Hecht, and Eldredge (1972) best exemplify the methodology followed in the present report.

As is discussed in the next section, a standard series of measurements was taken for relevant specimens for each species. These data were then analyzed to obtain statistical parameters that can be used to quantitatively discriminate among various species. It needs to be mentioned here that these statistical parameters were not used for phenetic linking in phylogeny reconstructions; they do however provide many important characters used in the alpha-level taxonomy of the North American hipparion species. Once these and numerous qualitative characters were analyzed for the different species, then the relative interrelatedness was assessed by cladistic methodology (as I ascribe to it; see discussion elsewhere in this section).

In the systematics section of this paper, particular emphasis is placed on the recognition of morphocline polarities (Gaffney, 1979, notwithstanding) and shared-derived (synapomorphic) character states. There will

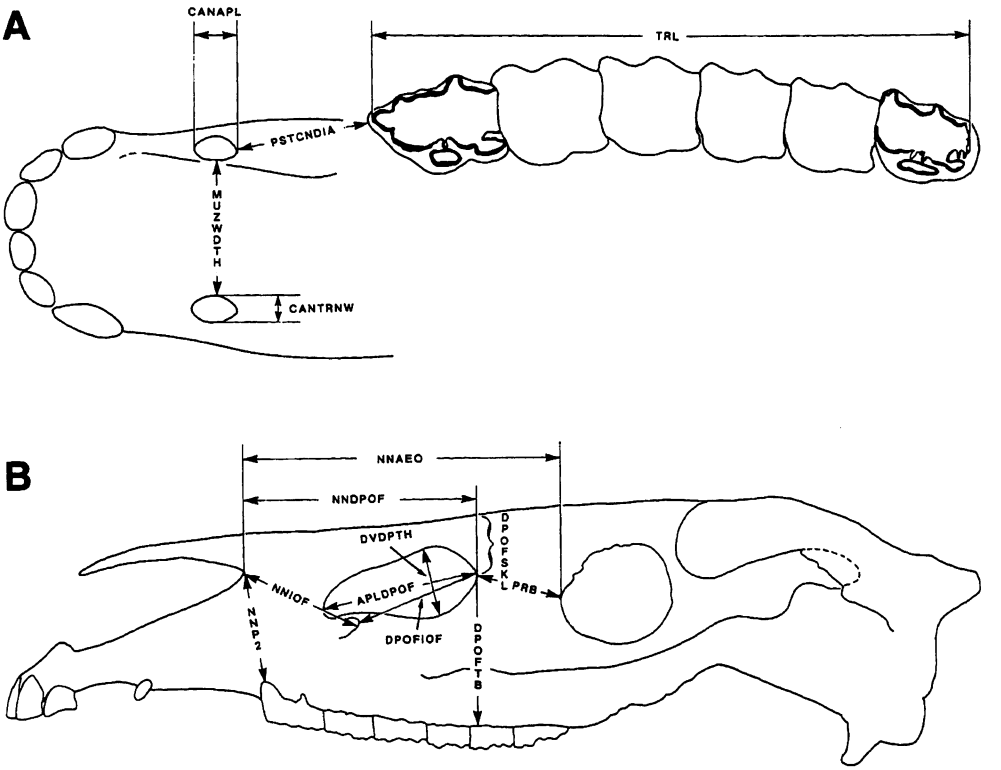


FIG. 3. Conventions for measured cranial characters. A. Ventral view of muzzle and palate. B. Left lateral view of skull. See explanation and abbreviations in text.

be two parts in the section entitled Phylogenetic Interrelationships. The first involves construction of cladistic hypotheses of interrelationships for the North American hipparion species. The second uses the cladograms and relevant temporal data to suggest possible phylogenetic trees, i.e., ancestral-descendant relationships through geological time. The succeeding sections contain hypotheses concerning biostratigraphy and paleobiogeography of New World hipparions as well as their relevance to Old World forms.

PREORBITAL FACIAL FOSSAE AND CRANIOMETRY: In hipparions and other horses the cheek region usually has one or more preorbital facial fossae. All horses have the anteroventralmost buccinator fossa that lies on the premaxillary and maxillary bones. Posterior to the buccinator fossa there can be developed a complex of fossae. Hipparions do not have the malar fossa that is found in many other genera of horses (which is developed on the maxillary, jugal, and lacrimal bones just dorsal to the facial, or malar crest). Above the site of the malar fossa is oftentimes developed what has been commonly referred to as the lacrimal fossa. This fossa is situated differently in the four genera of hipparions discussed here. When present, this fossa can occur on only the nasal and maxillary bones, or these two plus the lacrimal bone. Because the lacrimal bone is not involved in the fossa of some hipparions, the term lacrimal fossa is somewhat misleading. In order to circumvent this problem in nomenclature, this structure will be referred to in this report as the "dorsal preorbital fossa" (abbreviated DPOF).

Throughout the history of investigation of late Tertiary Equidae, various workers have commented on the taxonomic significance and utility of preorbital facial fossae. In recent years this controversial fire has been rekindled and a discussion of this topic is

presented below. During the present study, a detailed suite of measurements was taken on a sample of 42 individual crania of *Hipparion tehonense* from the early Clarendonian MacAdams Quarry from the Texas Panhandle in order to present a quantitative and comparative description of cranial (including the DPOF) character variation and possible sexual dimorphism. Many of the characters measured for these skulls are similar to those recommended by the Hipparion Conference.[1] The characters measured for the MacAdams Quarry sample are as follows (fig. 3):

1. Anteriorposterior canine length (CANAPL); taken at alveolar border.
2. Transverse canine width (CANTRNW); taken perpendicular to CANAPL at alveolar border.
3. Muzzle width (MUZWDTH); transverse distance between labialmost parts of right and left canines taken at alveolar border.
4. Postcanine diastema (PSTCNDIA); distance from posteriormost border of canine to anteriormost part of P^2 (both measurements are taken at the alveolar border).
5. Cheek tooth row length (TRL); taken from anteriormost enamel of anterostyle on P^2 to posteriormost enamel on M^3.
6. Distance from posteriormost part of nasal notch to anteriormost edge of the orbit (NNAEO).
7. Distance from posteriormost part of nasal notch to posteriormost edge of rim of the DPOF (NNDPOF), probably precise[2] to ±5 mm.
8. "Preorbital bar" length (PRB); distance from posteriormost edge or rim of the DPOF to the anteriormost edge of the orbit; in cases where the posterior rim of the DPOF is indistinct (see below), this measurement is probably precise to ±5 mm.
9. Maximum anteriorposterior length DPOF (APLDPOF); as with PRB, this measurement is probably precise to ±5 mm.
10. Dorsoventral depth of DPOF perpendicular to APLDPOF (DVDPTH), as with PRB, this measurement is probably precise to ±5 mm.
11. Distance from posteriormost edge or rim of DPOF to posteriormost opening of the infraorbital foramen (DPOFIOF): as with PRB, this measurement is probably precise to ±5 mm.
12. Distance from posteriormost edge of infraorbital foramen to posteriormost part of nasal notch (NNIOF).
13. Height of nasal notch (NNP2); minimum distance (frequently in the dorsoventral plane) from the posteriormost part of the nasal notch to the alveolar border of P^2.
14. Height of DPOF (DPOFTB); minimum distance from posteriormost edge or rim of DPOF to alveolar border.
15. Cranial height above DPOF (DPOFSKL); minimum (in vertical, i.e., dorsoventral plane) distance from posteriormost edge or rim of DPOF to midline of skull (at frontal suture); this measurement is probably precise to within ±1 mm but it is also greatly affected by crushing (see below).

In addition, several coded variables were recorded to indicate the states of certain characters:

1. Tooth directly below DPOFHT (TOOTH); 1, P^2; 2, P^3; 3, P^4; 4, M^1; 5, M^2; 6, M^3.
2. Position of lacrimal bone (LACBN); 0, posterior to, and does not touch, DPOF; 1, touches or enters DPOF; 2, indeterminate.
3. Posterior half of DPOF (SHPDPOF); 0, continuous rim; 1, rim absent.
4. Posterior pocket of DPOF (POSTPOCK); 0, absent; 1, rudimentary or shallow (*ca.* 0–3 mm); 2, deep (*ca.* 5–10 mm or greater); 3, indeterminate.
5. Anterior margin of DPOF (ANTMARG); 0, poorly defined; 1, moderately well defined, rim not continuous; 2, well defined, rim continuous; 3, well-defined dorsally but not ventrally; 4, indeterminate.

Certain other variables were used in the study of the MacAdams Hipparion sample for subsequent grouping into subsets by variables such as ontogeny (ONT) and sex (SEX). The use of these is described in more detail below. Several of the characters of the cheek region, particularly those that pertain to the configuration of the DPOF, were also measured and recorded for relevant cranial material of the other hipparions; the results of this analysis are presented in the section entitled Systematic Paleontology for each species.

[1] This workshop was held at the American Museum of Natural History in New York on November 2–10, 1981. Subsequent references in this text to the "1981 Hipparion Conference" is based on the author's personal observations while attending that workshop.

[2] The term precise is used in the sense presented by Sokal and Rohlf (1981, p. 13) to mean "the closeness of repeated measurements to the same quantity."

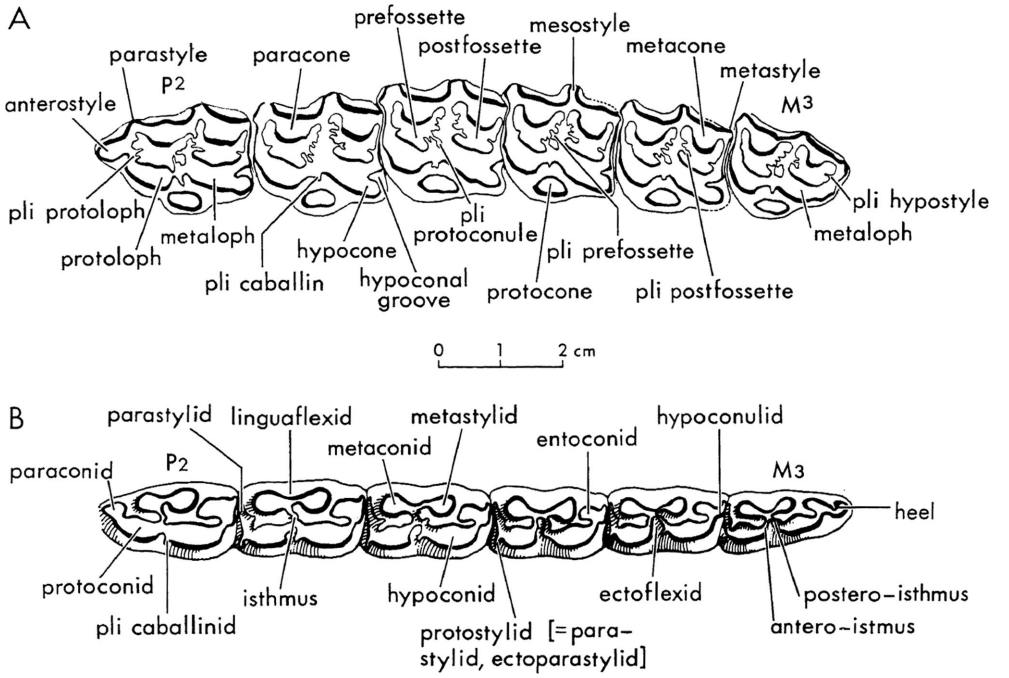


FIG. 4. Dental nomenclature used in this report: A. Upper cheek teeth, P^2–M^3. B. Lower cheek teeth, P_2–M_3.

DENTAL NOMENCLATURE, MENSURATION, AND STATISTICS: The dental nomenclature presented in figure 4 follows a combination of Stirton (1941), Skinner and Taylor (1967), Skinner and MacFadden (1977), and the consensus of the 1981 Hipparion Conference. With regard to the use of the term protostylid, which is commonly well developed in hipparions, figure 4 indicates synonymy with two other equivalent names that are frequently encountered in the literature, parastylid and ectoparastylid.

In order to provide a series of quantitative size parameters which were used along with qualitative characters in alpha-level discrimination, 24 measurements or counts were taken on samples of upper cheek tooth dentitions of each North American hipparion species. Whenever possible, upper cheek tooth dentitions associated with cranial material were chosen. Although lower cheek teeth can provide valuable taxonomic information, it is difficult in many instances to unambiguously associate lower dentitions with corresponding cranial and upper dental material. Therefore, although the lower cheek teeth are used for qualitative character analysis, they are not used in the morphometric study. Whenever possible, the upper cheek tooth measurements used here are the same as those recommended by the 1981 Hipparion Conference. The major exception is that crown height is measured at the mesostyle (consistent with most previous studies) rather than the parastyle. (It was impossible to shift to the parastyle because numerous measurements on the mesostyle had already been made during the earlier phases of this study.)

In an attempt to correct for the problems encountered with ontogenetic variation of hypsodont horse teeth, many previous workers have not taken these same measurements at the occlusal surface. For example, Sondaar (1961) and Hussain (1971) take their measurements on only isolated teeth 10 mm above the base. However, Hussain (1971, p. 12) also states that "teeth embedded in the jaws and skulls were measured on their occlusal surfaces and these measurements are treated separately." Forstén (1968, p. 6) states that:

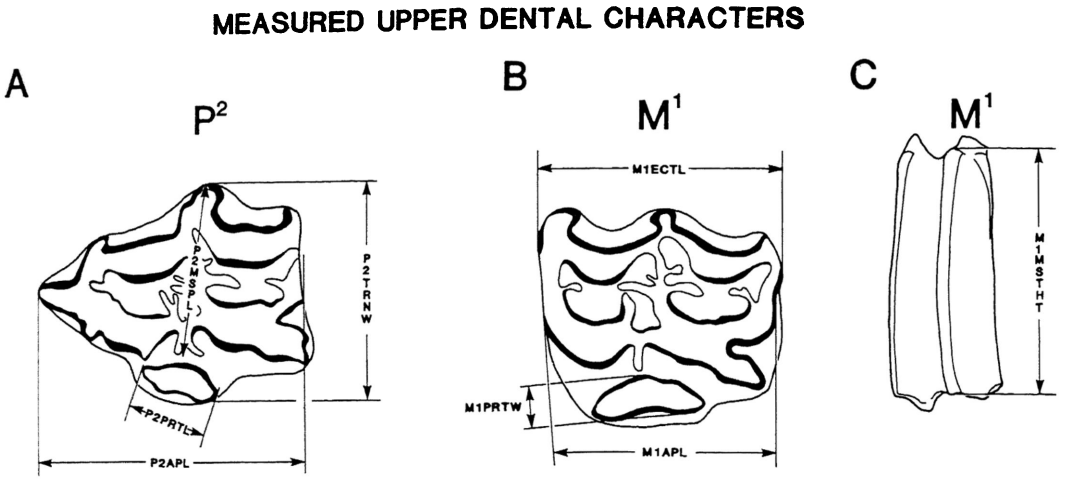


FIG. 5. Conventions for measured characters of upper dentitions. For simplicity, analagous measurements are only shown once on either P^2 or M^1 (these are as follows: P2TRNW = M1TRNW, P2PRTL = M1PRTL, P2PRTW = M1PRTW, P2MSPL = M1MSPL, P2MSTHT = M1MSTHT). Also see discussion in text. A. Occlusal view of P^2. B. Occlusal view of M^1. C. Lateral (labial) view of M^1.

"Length and breadth of the cheek teeth have been measured at the base, i.e. at the neck of the tooth. Grouping into wear classes is thus got rid of." During the present study all measurements (except those of mesostyle crown height) were made on the occlusal surface. Realizing the problems with wear variation, in addition, the relative ontogenetic stage of each tooth was estimated (see discussion of techniques below). In the subsequent numerical analysis, parameters were calculated and reported below for each species in two groups: (1) all wear stages and (2) "middle wear," i.e., juvenile and late wear removed. A fuller discussion of the results and implications of this procedure is presented below. Mesostyle crown heights are reported for each species based on measurements taken for (1) all wear classes and (2) juveniles (middle and late wear classes removed). This latter group provides an approximation of the maximum mesostyle crown height.

The 14 measured characters are described as follows (fig. 5):

1. Anteriorposterior length of P^2 (P2APL); this measurement is taken from the anteriormost enamel of the anterostyle to the posteriormost enamel on the posterior edge (hypocone and cement are excluded).
2. Transverse width of P^2 (P2TRNW); this measurement is taken from the labialmost part of the mesostyle to the lingualmost part of the protocone (cement is excluded).
3. Anteriorposterior protocone length of P^2 (P2PRTL); maximum length of protocone excluding (1) rudimentary spur (in some primitive species) or (2) connection to protoloph (in some late wear stages).
4. Transverse protocone width of P^2 (P2PRTW); this measurement is taken perpendicular to P2PRTL.
5. Mesostyle-pli caballin distance on P^2 (P2MSPL); distance from labialmost part of mesostyle (excluding cement) to lingualmost part of pli caballin. If pli caballin is rudimentary or absent, then measurement is taken to labialmost junction of protoloph and metaloph.
6. Mesostyle crown height of P^2 (P2MSTHT); this measurement is taken from occlusal surface to base of mesostyle where the enamel ends (i.e., it excludes the root).
7. Anteriorposterior length of M^1 (M1APL); this measurement is taken from anteriormost enamel of protoloph to posteriormost enamel of tooth excluding the ectoloph and cement.
8. Anteriorposterior ectoloph length of M^1 (M1ECTL); this measurement is taken from the anteriormost enamel of the parastyle to the posteriormost enamel of the metastyle (excluding cement).
9. Transverse width of M^1 (M1TRNW); analogous to P2TRNW.

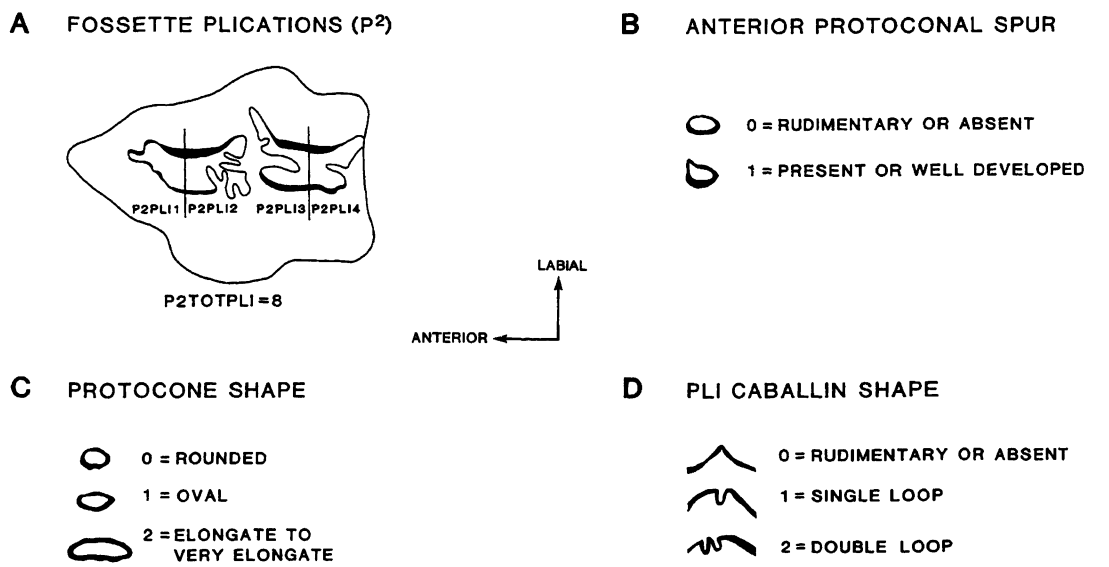


FIG. 6. Conventions for counted and coded characters of upper dentitions. A. Fossette plications on P^2 (and analogous characters for M^1, see text). In this example, the total plication count (P2TOTPLI) is 8 (1, 4, 2, 1). See discussion of counting criteria in text. B. Codes for anterior protoconal spur. C. Codes for protocone shape. D. Codes for pli caballin shape.

10. Anteriorposterior protocone length of M^1 (M1PRTL); analogous to P2PRTL.
11. Transverse protocone width of M^1 (M1PRTW); analogous to P2PRTW.
12. Mesostyle-pli caballin distance of M^1 (M1MSPL); analogous to P2MSPL.
13. Mesostyle crown height of M^1 (M1MSTHT); analogous to P2MSTHT.
14. Tooth row length P^2–M^3 (TRL); taken from anteriormost enamel of anterostyle on P^2 to posteriormost enamel on M^3 (fig. 3).

The complexity and number of enamel plications in the fossettes of upper cheek teeth has frequently been used in hipparion systematics. During the present study, for both P^2 and M^1 the number of plications were counted (fig. 6) for the anterior half of the prefossette (P2PLI1, M1PLI1), posterior half of the prefossette (P2PLI2, M1PLI2), anterior half of the postfossette (P2PLI3, M1PLI3) and posterior half of the postfossette (P2PLI4, M1PLI4). In certain cases plication counts become somewhat arbitrary. One has to make a decision about when a rudimentary fold should be ignored or counted. In this study (and following the recommendations of the 1981 Hipparion Conference), plications were only counted if their width is equal to, or exceeds, the maximum enamel width developed anywhere on the fossette. Also, in the case of "secondary plications" that develop on the ends of other plications, only the latter are counted. Three other variables for both P^2 and M^1 were computed during this study that were thought to have been potentially useful in species discrimination. These are (1) combined plication count for anterior half of the prefossette and posterior half of the postfossette (P2APPLI = P2PLI1 + P2PL14; M1APPLI = M1PLI1 + M1PL14); (2) combined plication count of posterior half of prefossette and anterior half of the postfossette (P2MDPLI = P2PLI2 + P2PLI3; M1MDPLI = M1PLI2 + M1PLI3), and (3) total plication count for tooth (P2TOTPLI = P2APPLI + P2MDPLI; M1TOTPLI = M1APPLI + M1MDPLI). The system employed here, i.e., separating the fossette plications into four counts (e.g., P2PLI1, P2PLI2, P2PLI3, P2PLI4) is consistent with that of many of the studies of Old World hipparions (e.g., Sondaar, 1961; Forstén, 1968). Although the use of P2APPLI, P2MDPLI, M1APPLI, and M1MDPLI might

seem to be an unnecessary addition of variables, as is presented below, the relative complexity of the anterior border of the prefossette and posterior border of the postfossette are more similar on the one hand and the posterior border of the prefossette and anterior border of the postfossette are equally similar to one another.

A series of coded variables were used to describe several important characters of the upper cheek tooth dentition. These were used either as a qualitative assessment of character states or a limiting variable for grouping of subsets during data analysis. These are as follows:

1. Tooth or tooth row side (P2SIDE, M1SIDE, TRWSD); 0, right; 1, left.
2. Preservation category (P2PRES, M1PRES); 0, complete and well preserved; 1, waterworn; 2, broken or cracked (partially or otherwise); 3, combination of 1 and 2; 4, cast; 5, pathological.
3. Anterior protocone spur development on P^2 (P2PRTSPR); 0, rudimentary or absent; 1, present or well developed. In practice this was difficult to assess in ontogenetic stages where P^2 connected to the protoloph.
4. Protocone shape on P^2 (P2PRTSHP); 0, rounded; 1, oval; 2, elongate to very elongate.
5. Pli caballin shape on P^2 (P2PLSHP); 0, rudimentary or absent; 1, single loop; 2, two or more loops that originate from the junction of protoloph and metaloph. The pli caballin was considered to be rudimentary or absent (code = 0) if the amplitude of the fold was smaller than the maximum enamel thickness developed on the occlusal surface of the tooth.
6. Anterior protocone spur on M^1 (M1PRTSPR); analogous to P2PRTSPR.
7. Protocone shape on M^1 (M1PRTSHP); analogous to P2PRTSHP.
8. Pli caballin shape on M^1 (M1PLSHP); analogous to P2PLSHP.
9. Ontogeny (ONT); an arbitrary variable that proved to be very important during data analysis. A qualitative assessment was made for each measured tooth whether it was isolated or within a cheek tooth row. These arbitrary groupings of wear stages are coded as follows; 0, juvenile–young adult, wear slight in cheek tooth row, M^3 virtually unworn; 1, "early maturity," wear moderate, in cheek tooth rows all teeth in wear and M^3 slightly worn; 2, "advanced maturity," all teeth in moderate wear including M^3; 3, "indeterminate," either codes 1 or 2, this was particularly useful for isolated teeth in middle wear in which the relative wear of M^3 was unavailable; 4, old age, teeth in relatively late wear, in cheek tooth rows usually the protocones are strongly connected to the protoloph.
10. Sex (SEX); 0, indeterminate; 1, male; 2, female; this character state was determined by the relative size of the canine. With the exception of the large sample of skulls from MacAdams Quarry, this character could only be evaluated in such a small number of cases that it was essentially rendered useless for its original purpose of studying sexual dimorphism.

All statistical parameters were computed through use of the BMDP (Dixon and Brown, 1979) programs. During this study the following BMDP programs were employed; (1) 1D, for simple univariate analysis and data screening; (2) 5D, for histograms and normal probability plots; (3) 7D, for univariate statistics and histograms of subset groups (particularly for ontogenetic studies), and (4) 6D, for bivariate (scatter) plots and regression statistics. With the exception of certain measurements for the one new species described below, the raw data are not presented in the species descriptions. Instead, for each species the selected data for measured variables are given with standard computed univariate statistics.

All measurements are in millimeters. Unless stated otherwise (i.e., certain cranial variables), measurements are taken and reported below to the nearest 0.1 mm. All counted or coded (meristic) variables are reported as whole integers. All computed statistics are reported to the nearest hundreth.

PRIMITIVE HIPPARION CHARACTER STATES: In the diagnoses and descriptions listed below, emphasis is placed on character states that are derived for each of the four recognized monophyletic groups (genera). For the sake of brevity and to avoid repetition, many primitive characters common to either hypsodont horses or the "hipparion grade" are not included in the diagnoses and descriptions. These shared-primitive character states include:

1. Isolated protocones in the upper cheek teeth;
2. Incisors with cement-filled infundibula (cups);
3. Tridactyl manus and pes (in many cases this is assumed because of the lack of definitely associated material);

4. Buccinator fossa is moderately developed;
5. Malar crest is moderately inflated;
6. In P^2, the anterior part is expanded to form an anterostyle which gives this tooth a triangular shape;
7. Mental foramen lies approximately midway between C and P^2;
8. Parastyles, mesostyles, and metastyles are moderately developed in the upper cheek teeth;
9. Hypoconal groove is moderate to deep;
10. Metaconids and metastylids have rounded borders and are widely separated;
11. Entoconids and hypoconulids have rounded borders and they are subequal in size; and
12. M^3 has a moderately well-developed heel.

Certain hipparion species exhibit the autapomorphic or synapomorphic state of some of the characters listed above; these are then described in the text. The shared-derived character states are so indicated in the text; these are used to relate species. The autapomorphic character state is unique to only one species within a monophyletic group; these are therefore not used in phylogeny reconstruction.

SUMMARY LIST OF ABBREVIATIONS

General

L.F., local fauna, a stratigraphically and geographically restricted vertebrate assemblage (*sensu* Tedford, 1970)
R, right
L, left
ONT, ontogeny
PRES, preservation (see discussion above)
I, incisor
C, canine
P, premolar
M, molar
myBP, million years before present

Statistical

ANOVA, analysis of variance
N, sample size
$\bar{x}$, sample mean
s, sample standard deviation
V, sample coefficient of variation
OR, sample observed range
t, t-value
F, variance ratio
p, probablity level

Cranial

ANTDPOF, development of anterior margain of dorsal preorbital fossa
APLDPOF, anteriorposterior length of dorsal preorbital fossa
DPOF, dorsal preorbital fossa
DPOFIOF, distance from posterior margin of dorsal preorbital fossa to infraorbital foramen
DPOFHT, height of dorsal preorbital fossa on face
DPOFSKL, distance from posterior margin dorsal preorbital fossa to frontal suture
DVDPTH, dorsoventral depth of dorsal preorbital fossa
IOF, infraorbital foramen
LACBN, development of lacrimal bone
MUZWDTH, muzzle width
NNAEO, distance from nasal notch to orbit
NNDPOF, distance from nasal notch to posterior margin of preorbital fossa
NNIOF, distance from nasal notch to infraorbital foramen
NNP2, distance from nasal notch to alveolar border P^2
POSTPOCK, development of posterior pocket of dorsal preorbital fossa
PRB, preorbital bar length
PSTCNDIA, length postcanine diastema
TOOTH, tooth ventral to posterior margin of dorsal preorbital fossa
SHPDPOF, shape of posterior margin of dorsal preorbital fossa

Dental

CANAPL, anteriorposterior canine length
CANTRNW, transverse canine width
P2APL, anteriorposterior P^2 length
P2APPLI, combined plication count anterior half of prefossette plus posterior half postfossette on P^2
P2MDPLI, combined plication count posterior half of prefossette plus anterior half of postfossette of P^2
P2MSPL, distance from mesostyle to pli caballin on P^2
P2MSTHT, P^2 mesostyle height
P2PLI1, plication count anterior half of prefossette on P^2
P2PLI2, plication count posterior half of prefossette on P^2
P2PLI3, plication count anterior half of postfossette on P^2
P2PLI4, plication count posterior half of postfossette on P^2
P2PLSHP, shape pli caballin on P^2
P2PRTL, protocone length on P^2
P2PRTSHP, protocone shape on P^2
P2PRTSPR, anterior protoconal spur on P^2

P2PRTW, protocone width on P^2
P2TOTPLI, total fossette plication count on P^2
P2TRNW, transverse width P^2
M1APL, anteriorposterior M^1 length
M1APPLI, total plication count anterior half of prefossette plus posterior half of postfossette on M^1
M1ECTL, ectoloph length M^1
M1MDPLI, combined plication count posterior half of prefossette plus anterior half of postfossette on M^1
M1MSPL, distance from mesostyle to pli caballin on M^1
M1PLI1, plication count anterior half of prefossette on M^1
M1PLI2, plication count posterior half of prefossette on M^1
M1PLI3, plication count anterior half of postfossette on M^1
M1PLI4, plication count posterior half of postfossette on M^1
M1PLSHP, shape pli caballin on M^1
M1PRTL, protocone length on M^1
M1PRTSHP, protocone shape on M^1
M1PRTSPR, anterior protoconal spur on M^1
M1PRTW, protocone width on M^1
M1TOTPLI, total fossette plication count on M^1
M1TRNW, transverse width M^1
TRL, tooth row length

INSTITUTIONS AND COLLECTIONS

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York
ANSP, Academy of Natural Sciences, Philadelphia
BMNH, British Museum (Nat. Hist.), London
CIT, California Institute of Technology Collection, now part of the Natural History Museum of Los Angeles County, Los Angeles, California
F:AM, Frick American Mammals, Department of Vertebrate Paleontology, American Museum of Natural History, New York
FMNH, Field Museum of Natural History, Chicago
FGS, Florida Geological Survey, Tallahassee, now part of the UF Collection
JWT, Johnston West Texas Collection, Panhandle Plains Historical Museum, Canyon, Texas
LACM, Natural History Museum of Los Angeles County, Los Angeles
MSU, Midwestern State University, Wichita Falls, Texas
NMNHP, Institut de Paléontologie, Paris
PU, Princeton University, Princeton, New Jersey
TMM, Texas Memorial Museum, University of Texas, Austin, Texas
UALP, University of Arizona Laboratory of Paleontology, Tucson
UCMP, University of California Museum of Paleontology, Berkeley, California
UCR, Department of Earth Sciences, University of California, Riverside
UF, Vertebrate Paleontology Collection, Florida State Museum, University of Florida, Gainesville, Florida
UNSM, University of Nebraska State Museum, Lincoln, Nebraska
UO, University of Oregon Museum, Eugene, Oregon
USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UTBEG, Bureau of Economic Geology, University of Texas, Austin, now part of TMM Collection
WTSU, Kilgore Research Center, West Texas State University, Canyon, Texas

CHRONOLOGICAL FRAMEWORK

The chronological terminology and conventions followed in this report are presented in figure 7. This chart spans the time interval for the known ranges of North American hipparions, that is, from 16 to 2 myBP. The following references were used for correlation among the different temporal schemes: Tedford et al. (in press) for absolute age equivalents (fig. 7A) and North American Land Mammal "Ages" (fig. 7C), La Brecque, Kent, and Cande (1977) and Mankinen and Dalrymple (1979) for Geomagnetic Polarity Chrons (fig. 7B), Berggren and Van Couvering (1974) and Fahlbusch (1976) for European mammal stages (fig. 7D), and Berggren and Van Couvering (1974) for planktonic foraminiferal zones (fig. 7E) and the Miocene-Pliocene boundary (fig. 7F). The conventions employed here for the North American Land Mammal "Ages" and temporal equivalents consist of the following:

BARSTOVIAN: Medial Miocene, 16 to 12 myBP, Magnetic Chrons 16 to early 12, Astaracian Mammal Stage, and planktonic foraminiferal zones N7 to N13. Astaracian is the preferred European Mammal Stage rather than the Vindobonian or Oeningian (see Fahlbusch, 1976).

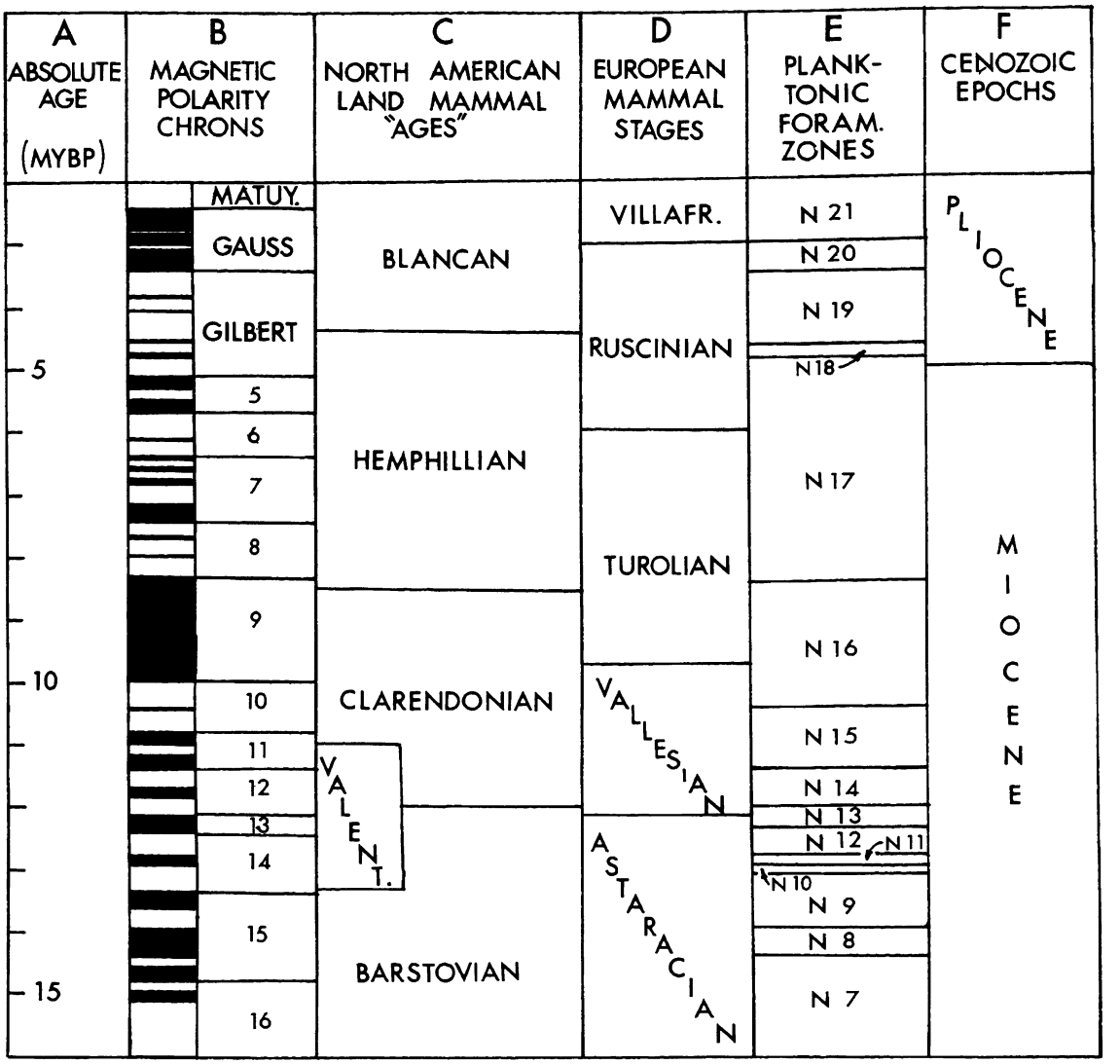


FIG. 7. Chronological framework used in this report. A. Absolute time scale in millions of years before present (myBP). B. Geomagnetic Polarity Time Scale (from LaBrecque, Kent, and Cande, 1977; Mankinen and Dalrymple, 1979). C. North American Land Mammal "Ages" (from Tedford et al., in press). D. European Mammal Stages (from Berggren and Van Couvering, 1974; Fahlbusch, 1976). E. Planktonic foraminiferal zones (from Berggren and Van Couvering, 1974). F. Cenozoic epochs (from Berggren and Van Couvering, 1974). See text for discussion.

VALENTINIAN: Partially overlaps with late Barstovian and early Clarendonian, late medial Miocene, 13½ to 11 myBP, Magnetic Chrons 14 to 11, late Astaracian to early Vallesian European Mammal Stage, and planktonic foraminiferal zones N9 to N15. There is some disagreement among North American mammalian paleontologists as to the need for the Valentinian because it partially overlaps with, and is less widely recognizable than, the Barstovian and Clarendonian mammal ages. However, in the type area, i.e., north-central Nebraska and adjacent South Dakota, the Valentinian faunas

are extensive, taxonomically distinctive, and represent a time interval apparently intermediate between the youngest faunas from the Barstovian of California and oldest faunas from the Clarendonian (*sensu stricto*) of Texas (Tedford et al., in press). In the present report, the Valentinian is recognized as a valid biochronological term representing distinct faunas contained within the Valentine Formation. However, this term is not used outside the areal distribution of this rock unit, i.e., it is restricted to faunas from northern Nebraska and adjacent South Dakota (also see Breyer, 1975).

CLARENDONIAN: Medial to early late Miocene, 12 to 8½ myBP, Magnetic Chrons 12 to 9, Vallesian and, in part, Turolian European Mammal stages, and planktonic foraminiferal zones N14 to N16. The Clarendonian *sensu lato* overlaps with the late Valentinian, and it is used here for faunas outside the areal extent to the Valentine Formation.

HEMPHILLIAN: Late Miocene to earliest Pliocene, 8½ to 4½ myBP, Magnetic Chrons 8 to early Gilbert, medial Turolian to medial Ruscinian European Mammal Stage, and planktonic foraminiferal zones N16 to N18. Tedford et al. (in press) discuss the term "Kimballian" for the time interval equivalent to early Hemphillian (although it was originally proposed for a post-Hemphillian time interval, see Schultz and Stout, 1961; Schultz, Schultz, and Martin, 1970). The Kimballian has been used for the time represented by the sediments and faunas of the "Kimball Formation" of western Nebraska. However, the expanded concept of the Kimball Formation, which was first described by Lugn (1938), is actually a series of laterally discontinuous calcareous intervals overlying the Sidney Gravels within the Ash Hollow Formation (Ogallala Group) in this region. Because the Kimball Formation is not a lithologically diagnostic or mappable unit, Breyer (1975, 1981) correctly concluded that it is not of formational rank. In addition, the "fauna" from the "Kimball" used to characterize this Land Mammal age is not temporally homogeneous among the various sites. The Kimballian is only represented by a few small sites in addition to the best-known Cambridge L.F. (UNSM Ft-40 = *Amebelodon fricki* Quarry). The faunas from these sites are not coeval with each other and they do not represent a distinct biochronological unit (Breyer, 1975, 1981). Therefore, from both faunal and lighological criteria, the Kimballian is not used in the present report.

BLANCAN: Spans most of the Pliocene; 4½ to 2 myBP, Gilbert to early Matuyama Magnetic Chrons, Ruscinian and early Villafranchian European Mammal stages, and planktonic foraminiferal zones N19 to N21. Until recently, the Blancan was considered early Pleistocene. However, with the revised late Cenozoic time scale and the Pliocene-Pleistocene boundary at about 2 myBP, the Blancan is almost equivalent to the entire Pliocene.

HISTORY OF INVESTIGATIONS

As might be expected from a geographically and temporally widespread group, the hipparions have had a very complex history of discussion in the paleontological literature. The present review concentrates on the literature that pertains to the North American hipparion genera. Although every relevant paper cannot be cited here, this discussion attempts to highlight studies that have been important to an understanding of New World hipparions. Also, certain studies of the Old World representatives of this group is discussed. For the interested reader, comprehensive reviews of Old World hipparion literature are presented in numerous studies, such as Gromova (1955), Forstén (1968), and Hussain (1971).

De Christol (1832) is correctly credited with the original description of the genus *Hipparion* based on specimens from Mt. Léberon (also called Mt. Luberon or Cucuron) in the province of Vaucluse in southern France. Some later workers (e.g., Cope, 1889) considered *Hipparion* to be a *nomen nudum*. De Christol's original description of *Hipparion* did relate this name to a brief characteriza-

tion of the appropriate specimens. De Christol did not designate a type species for the genus. Gervais (1849) described three species of *Hipparion, H. prostylum, H. mesostylum,* and *H. diplostylum,* from Mt. Léberon based on minor variations in lower cheek tooth morphology. In that study, *H. prostylum* was designated the type species of the genus, although no type specimen was indicated. Sondaar (1974), in a revision of *Hipparion* from the type locality, designated a type specimen consisting of a right maxillary fragment with P^4–M^3 illustrated by Gervais (1859, pl. 19, fig. 2) and probably housed in the Musée Requien, Avigon. Therefore, as recommended in the International Code of Zoological Nomenclature (Stoll et al., 1964) and because of its common usage, *Hipparion* constitutes a valid genus.

Kaup (1833) proposed the new genus of hipparion *Hippotherium* for material from Eppelsheim in West Germany. For about two decades European paleontologists considered *Hippotherium* to be generically distinct from *Hipparion.* For example, Gervais (1849) believed that *Hipparion* was geographically restricted to southern France. However, during the late 1850s, 1860s, and consistently thereafter as indicated in the European literature, *Hipparion* was considered to be the senior synonym of *Hippotherium* (e.g., Gaudry, 1867; Gaudry, 1873, see historical listing of early usage in Pirlot, 1956, pp. 7–8).

Leidy (1856) was the first to apply either of the Old World generic names to North American species when he described *Hipparion occidentale* that was collected by the Hayden Survey from the Little White River of South Dakota (table 2). In this short description there is no justification for the use of the Old World genus nor is there any discussion of the implications for Holarctic faunal interchange (see below). In later descriptions of New World hipparions by Leidy (e.g., 1859, 1883, 1885; also see Osborn, 1918, p. 174) *Hipparion* was replaced by *Hippotherium* for numerous species. In a very important paper, Cope (1889) reviewed the North American hipparions and referred all these species to *Hippotherium.* Cope's justification was that the genus *Hipparion* had been inadequately characterized in De Christol's (1832) original description and it was therefore considered invalid and replaced by *Hippotherium* Kaup, 1833. Based on a survey of the literature, it appears that *Hippotherium* remained the preferred generic name for hipparions by North American paleontologists until nearly the end of the nineteenth century.

Leidy and Lucas (1896), in their description of fossil vertebrates from the Alachua Clays of northern Florida, present one of the last studies in which *Hippotherium* was the preferred generic name for North American hipparions. It is interesting to note here that the Florida hipparions described in that paper, particularly "*Hippotherium*" *plicatile* were later stated to be very similar to Old World hipparions in characters such as the small protocone. As a result of these similarities, workers such as Gidley (1907), Osborn (1918), and Stirton (1940) indicated a close phylogenetic affinity between the Florida and Old World hipparions.

The second-half of the nineteenth century must have been a very exciting time for the formulation of biogeographical theory based both on fossil and extant evidence and, in particular, from horses. It is surprising that paleontologists at that time who studied horses such as hipparions did not clearly state the striking paleobiogeographical consequences of fossil horse distributions, although they implied intercontinental continuity by the use of the same generic designations such as *Hipparion* for both Old and New world species. The great British naturalist Sir Thomas Henry Huxley was one of the first to clearly realize the biogeographic implications of the distribution of fossil mammals throughout Holarctica when he stated (1870, p. 372): "That there was a continuity of dry land between Europe and North America during the Miocene epoch, appears to me to be a necessary consequence of the fact many genera of terrestrial mammals, such as . . . *Hipparion* . . . are common to the Miocene formations of the two areas, and have as yet been found (except perhaps *Anchitherium*) in no deposit of earlier age." Since the end of the nineteenth century the dispersal of hipparions across the Bering Land Bridge has become increasingly more important in discussions of intercontinental paleobiogeography and correlations within the Holarctic Realm (see below).

Gidley (1903, and reiterated in 1907) named the genus *Neohipparion* based on a fine skeleton collected by the AMNH 1902 Whitney expedition to the Little White River of South Dakota. The type species was named *N. whitneyi.* Gidley stated that, in contrast to Old World hipparions, New World hipparions have differences such as more elongate protocones, less complex enamel plications, and more slender metapodials. As a result of these differences in character states, Gidley proposed that all Old World hipparions be assigned to *Hipparion* and all New World hipparions be assigned to *Neohipparion* except those from Florida which he questionably referred to *Hipparion* (Gidley, 1907).

In a series of papers, Merriam (1913, 1915a, 1915b, 1916a, 1916b) described nine new hipparion species from the Pacific Coast and Great Basin provinces. The validity and distinction of these species is somewhat doubtful because in most cases Merriam based these descriptions on isolated teeth with poor stratigraphic data. Certain of these species, such as "*Hipparion*" *mohavense,* "*H.*" *anthonyi,* and "*H.*" *condoni* were later claimed, along with the Florida hipparions, to be very closely related to Old World *Hipparion* (Stirton, 1940).

Osborn (1918) published the classic monograph on the Oligocene, Miocene, and Pliocene Equidae of North America. Although some of the work contained in this monograph has since become out of date, the exhaustive compilations, descriptions, and illustrations make this a required reference for studies of equid paleontology. The contributions to this subject are far too numerous to list here; however, one of the most important points in that monograph was that Osborn did not follow Gidley's ideas about the generic differences between *Hipparion* and *Neohipparion,* and considered both of these to be synonymous.

Matthew, first working at the AMNH and later at the UCMP, was a very important force in equid paleontology during the 1920s and 1930s. During the early 1920s Matthew led expeditions to the Texas Panhandle and worked at Mt. Blanco (for delightful anecdotes about fieldwork in this region with Matthew during 1924, see Simpson, 1951, pp. 91–97, and Simpson, 1978, p. 35). Remains of a graceful antelope-like hipparion were collected from this locality. Matthew (1926) gave the name *Nannippus* to this tiny hipparion and considered it a subgenus of *Hipparion.* It is surprising that the important topotypic material of *Nannippus* "*phlegon*" (=*peninsulatus*) from Crawfish Draw, Mt. Blanco, collected during the AMNH expedition of 1924 has not been adequately described in the literature.

In Matthew's (1924) description of the Snake Creek fauna from Sioux County, Nebraska, a detailed section was devoted to hipparions. Matthew did not agree with Gidley's (1903, 1907) idea that Florida hipparions were very closely related to Old World hipparions. Matthew (1924, pp. 173–174) presented an obvious refutation of the French paleontologist Joleaud's hypothesis that there was a Miocene ("Pliocene") transatlantic bridge ("Atlantis") from North America to the Antilles, to Spain (and North Africa), and to elsewhere in Europe. Joleaud had relied heavily upon the supposed close relationships between Florida and Old World hipparions. Matthew did not agree with the paleontological evidence based on Florida hipparions and stated that Joleaud had ignored the Old World affinities of the California hipparions such as *H. mohavense.*

During the mid-1920s Matthew studied hipparion collections from the Siwalik Hills of India (and what is also now Pakistan). In Matthew's (1929) article on this fauna, he discussed the idea that the first occurrence of *Hipparion* in both the New and Old worlds represented a geologically synchronous event that could be used to approximately define the Miocene-Pliocene boundary. This event, which has been referred to as the "Hipparion Datum" has received much attention in subsequent discussions of hipparion phylogeny, paleobiogeography, and biochronology (see below).

In 1927 Matthew moved to the University of California at Berkeley (Gregory, 1939). During that time and up to 1929, large collections of fossil vertebrates were made from the Texas Panhandle by Berkeley paleontologists and associates. Matthew and Stirton (1930) described the late Miocene horses from the Texas Panhandle. They reviewed the genera of Pliocene horses and described the hip-

parions from the Coffee Ranch locality, the fauna which typifies the Hemphillian Land Mammal Age. In that paper (pp. 355–356) they suggest that hipparions are polyphyletic. Matthew died in 1930 and his studies of equid paleontology were continued by R. A. Stirton, who was then a graduate student at Berkeley.

Colbert (1935a, 1935b) published on the Siwalik fauna represented in the AMNH collection. In these studies he reiterated the earlier concept of the first arrival or dispersal of *Hipparion* into the Old World as the herald of the Pliocene. This biochronological event has subsequently been termed the "Hipparion Datum" or "Hipparion FAD" (first appearance datum, see below). Colbert also realized the remarkable dental similarities between Siwalik hipparions and those of the "Republican River beds" (Clarendonian) of midcontinental North America. Stirton (1939), in a discussion of Pliocene Holarctic intercontinental correlations and the dispersal ability of land mammals, also underscored the idea that the first occurrence of *Hipparion* in the Old World indicated the base of the Pliocene. However, based on revised radiometric calibrations, this occurrence is now accepted by most workers to be late Miocene (see discussion below).

Stirton (1940) published a review of North American Tertiary horses, which along with Osborn (1918), has become a principal reference in equid paleontology. Stirton recognized three genera of North American hipparions, *Neohipparion, Nannippus,* and *Hipparion.* Stirton believed that *Neohipparion,* which was represented by a diversity of species, was the most common hipparion in Tertiary deposits of North America. *Nannippus* was less common and represented by several small species. Following earlier workers, *Hipparion* was considered to be common in the Old World but rare in North America and restricted to several species (cited above) from Florida and California. The systematics presented in Stirton's (1940) and later papers on fossil horses were essentially based on dental, and, to a lesser degree postcranial, characters because of the abundance of these remains in Cenozoic deposits of North America.

Drescher (1941) described additional remains of Merriam's species *H. tehonense* and *H. mohavense* from the Tejon Hills of the southern San Joaquin Valley, California. Gregory (1942) contributed to our knowledge of late Clarendonian Great Plains hipparions in his work on the Big Springs Canyon L.F. of South Dakota. Stock (1945, 1951) described an extraordinary well-preserved skeleton and other associated individuals of *Neohipparion leptode* from the early Hemphillian Thousand Creek locality of Nevada.

Richey (1948) described a new species, *Hipparion forcei,* from the late Clarendonian Black Hawk Ranch L.F. of the San Francisco Bay region. Of particular importance to an understanding of the facial morphology of *Hipparion sensu stricto* as represented by the Pacific Coast localities, the topotypic material includes a relatively complete skull. This represents one of only a few skulls of any hipparion from that region.

Lance (1950) described *Nannippus* cf. *minor* from the late Hemphillian Yepómera L.F. of Chihuahua, Mexico, based on the collections made by the California Institute of Technology. Also from Yepómera, Stirton (1955) named two new hipparion species, *Neohipparion floresi* and *N. arellanoi.* The Yepómera L.F. is important because, based on abundant material, it provides knowledge of hipparions from near the southern extent of their known geographic range. Olson and McGrew (1941) described specimens of *Neohipparion montezuma* from the late Clarendonian of Honduras. Mooser (1960, 1964, 1968) described several new species and occurrences of *Neohipparion* and *Nannippus* from Mexico.

Quinn (1955) presented a revision of Miocene horses from the Gulf Coastal Plain of Texas. Diverse faunas have been collected from this region, but many groups including the horses were relatively poorly known until works such as Quinn's. His work is difficult to interpret because of the numerous new taxa he named, the extreme vertical splitting, and otherwise unorthodox taxonomic methodology (see critique in Webb, 1969). Quinn (1955) recognized hipparions from the Texas Gulf Coastal Plain, but did not describe relevant specimens in the text (see also Quinn, 1952). Forstén (1975) studied the same material and did much to unravel the compli-

cated taxonomy of these horses. Of relevance to the present discussion, she recognized the presence of *Nannippus, Neohipparion,* and "*Merychippus* near *Hipparion.*" Despite the confusion engendered from Quinn's taxonomic methodology, one important consequence was that facial characters, i.e., the development of facial fossae in *Dinohippus,* were considered important in equid systematics (see below).

In two comprehensive studies, Sondaar (1968) and Hussain (1975) discuss the osteology and function of, respectively, the manus and pes in fossil and Recent horses. Both of these works provide important discussions on hipparions. One interesting note is that advanced *Nannippus* appears to have been extremely cursorial, even more so than in certain *Equus.*

For about half a century from the late 1920s to the present, large collections of later Tertiary horses were amassed by the Frick Laboratory (now part of the AMNH). During this time, Morris F. Skinner has been largely responsible for building and studying the Frick horse collection. With the integration of the Frick and AMNH equids during the 1970s, this combined collection is unquestionably the most complete and comprehensive record of horse morphology, evolution, and biostratigraphy in the world. Since the collection became accessible for unrestricted study during the 1960s, it is now recognized as the center for any serious comparative studies of fossil horses. One very obvious feature of the hundreds of skulls in this collection is that the development of facial fossae in medial and late Tertiary horses is of primary importance and that systematic studies using only dentitions (as has commonly been the practice) are oversimplified because of numerous instances of parallel evolution.

During the late 1960s and 1970s, North American paleontologists began to unravel the hipparion complex using the differences in facial fossae as well as dental and postcranial characters. Webb (1969) was one of the first to publish serious consideration of the value of facial fossae in North American equid taxonomy (also see below). Skinner and MacFadden (1977) described a new genus *Cormohipparion,* which was based largely on the configuration of the DPOF, that was widespread during the Miocene in North America. MacFadden and Bakr (1979) referred the large Siwalik hipparion "*H.*" *theobaldi* to *Cormohipparion* thereby implying some degree of Holarctic continuity for this genus. MacFadden and Waldrop (1980) described a large sample of *Nannippus* "*phlegon*" (*peninsulatus*) from Florida. In that paper a skull of *N. peninsulatus* collected during the AMNH 1924 expedition to Mt. Blanco was described along with the phylogenetic interrelationships of this species to other hipparions. Woodburne and Bernor (1980) presented a comprehensive survey of facial morphotypes for Old World hipparions and related some of these to New World forms. MacFadden (1980) described the facial morphology of *Hipparion sensu stricto* from the type locality at Mt. Léberon and recognized this genus at several localities in the Great Plains and Pacific coastal regions. In contrast to previous workers who stated that *Hipparion* was rare in North America (known only from Florida and California), MacFadden (1980) demonstrated that *Hipparion sensu stricto* was common in North America and there was a generic-level continuity of this hipparion throughout Holarctica.

A further consequence of recent systematics of hipparions relates directly to the concept of the "Hipparion Datum." Many workers (e.g., Forstén, 1968) state that *Hipparion* arose in the New World and subsequently dispersed in one event that defines the base of the Vallesian in the Old World. It is also implied that all Old World hipparions were monophyletically descended from the ancestral species involved in the Hipparion Datum, "*H.*" *primigenium.* Van Couvering and Miller (1967), Berggren and Van Couvering (1974) and Van Couvering and Berggren (1977) radiometrically calibrated this single "Hipparion Datum" at about 12.5 myBP. Recent analyses of the dating from Höwenegg, which is one of the critical sites (Becker-Platen, Benda, and Steffans, 1977; also see discussion in Bernor, Woodburne, and Van Couvering, 1980), indicate that this event is slightly younger, probably between 12.5 and 10.8 myBP. MacFadden and Skinner (1981; also see MacFadden and Skinner, 1977; Skinner and MacFadden, 1977) describe the earliest Holarctic hipparion, *Cormohipparion*

goorisi, from the early Barstovian of the Texas Gulf Coastal Plain. Based on biochronological correlations to faunas with associated radiometric control, this represents an occurrence of about 15 myBP. It is therefore clear that the so-called "Hipparion Datum" is not a synchronous dispersal event throughout Holarctica.

Bernor, Woodburne, and Van Couvering (1980), based on the radiometrically controlled succession of Miocene mammals from Maragheh (Iran), suggest the possibility that the facial morphotype represented by *Hipparion sensu stricto* was perhaps descended from an immigrant form similar to, or a species of, *Cormohipparion.* Based on a detailed comparison of hipparion facial morphotypes from Holarctica, Woodburne, MacFadden, and Skinner (1981) state that *Cormohipparion,* probably *C. sphenodus* from the Valentinian of North America, is the closest relative of Old World Vallesian hipparions. The Old World hipparions during this time represent one consistent facial morphotype that is derivable from *Cormohipparion.* Other facial morphotypes, e.g., *Hipparion sensu stricto,* are not represented at Old World localities until the Turolian when the diversity of hipparions in that region increased dramatically. In contrast to the Old World origin for the diverse suite of Turolian hipparions (*sensu* Bernor, Woodburne, and Van Couvering, 1980), studies such as MacFadden (1980) and Woodburne, MacFadden, and Skinner (1981) hypothesize two or more dispersal waves across Beringia. The earliest of these would represent the "Hipparion Datum." Subsequent events during the later Neogene could explain the allochthonous origin of forms such as *Hipparion sensu stricto* in the Old World. It is generally stated that *Neohipparion* is not represented in the Old World. However, in a novel interpretation Zhegallo (1978) suggests the origin of "*Hipparion* (*Neohipparion*) *houfenense*" from the dispersal of a New World species of *Neohipparion* about 6 myBP (see discussion below).

Returning to the New World, Dalquest (1981) described a new genus, *Hesperohipparion,* from the late Hemphillian of the southern United States and Mexico. His concept of the genus includes five species formerly assigned to *Neohipparion* as well as a new species, *H. stirtoni,* from the Coffee Ranch L.F. of the Texas Panhandle. Edwards (1982) described a new species, *Hipparion trampasense,* from the late Clarendonian of the San Francisco Bay region, California.

In summary, prior to the present report, 41 species of North American hipparions have been named in the literature. These taxa have been based principally on dental characters and, to a lesser extent, postcranial characters. Within the last decade, some workers have placed a significant emphasis on the value of cranial characters in hipparion systematics. Revised phylogenetic interpretations and new chronological data indicate a considerably more complex biochronological and paleobiogeographic history for these horses. The consequences of the recent work on hipparion systematics is also discussed in subsequent sections presented below.

PREORBITAL FACIAL FOSSAE IN EQUID SYSTEMATICS, WITH SPECIAL REFERENCE TO NEW WORLD HIPPARIONS

Based principally on the fabulous array of fossil horse skulls in the F:AM-AMNH collection, many North American paleontologists (led by Morris F. Skinner) have reaffirmed the significance of preorbital facial fossae in equid systematics. These structures have been described in the literature for over a century. However, they were not usually employed as diagnostic taxonomic characters (although for a notable exception, see discussion of early work on Siwalik hipparions in MacFadden and Woodburne, 1982). Facial fossae have not generally been used in equid taxonomy for several reasons: (1) Well-preserved skulls showing the details of the preorbital region are much less common in contrast to the ubiquitous occurrence of teeth and postcranial elements. (2) The functional

morphology of preorbital facial fossa is not completely understood. (3) Earlier workers (e.g., Osborn, 1918) stated that the development of preorbital facial fossae was ontogenetically variable and sexually dimorphic.

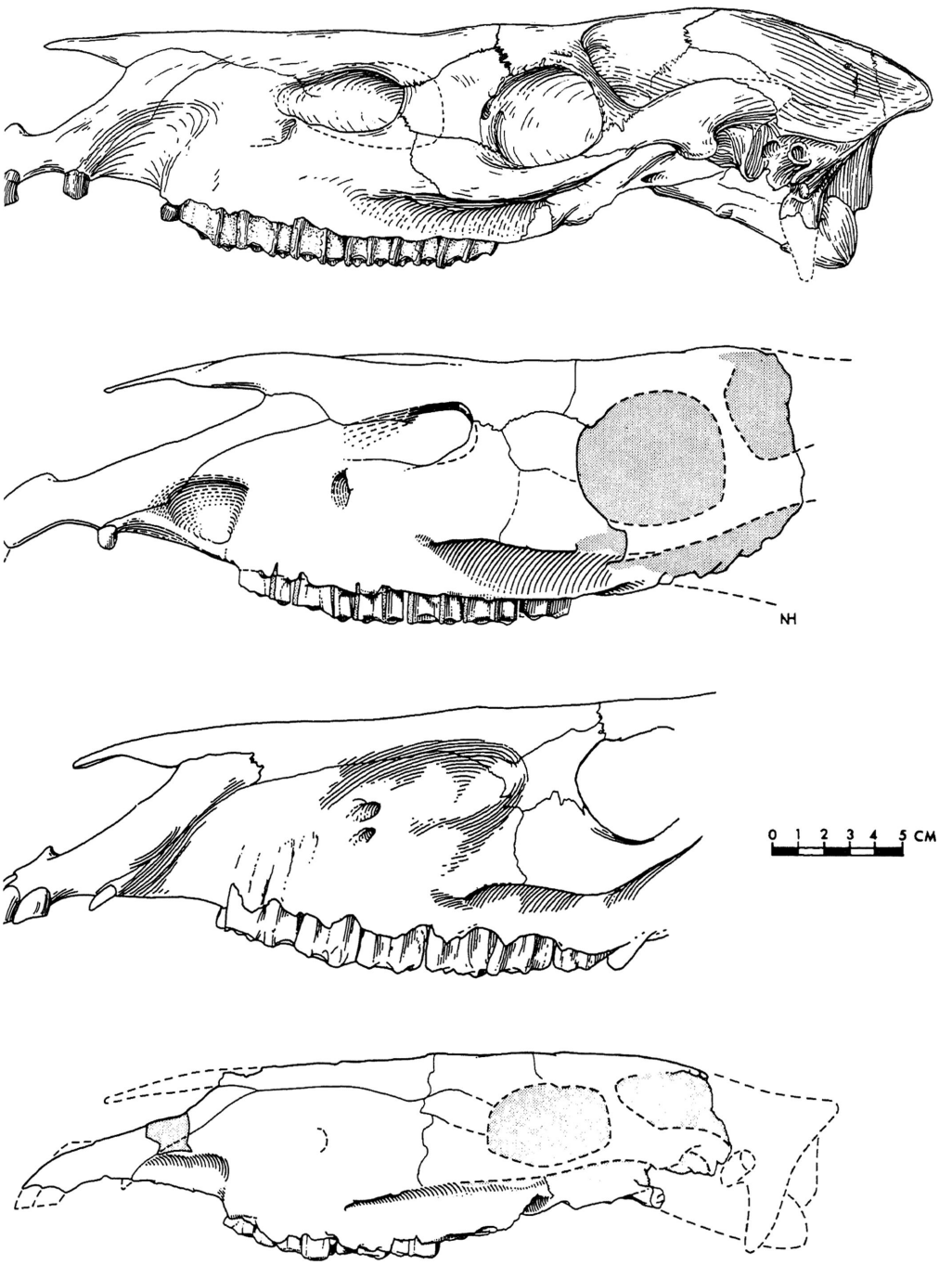
Gregory (1920) presented the most insightful discussion of preorbital facial fossae in Equidae. In many fossil horses this complex consists of the buccinator, dorsal (also called lacrimal or nasomaxillary, here referred to as "dorsal preorbital fossa," abbreviated DPOF), and ventral (malar) fossae. The function of the buccinator fossa, which is found in both fossil and Recent horses, is for origin of the buccinator musculature (Gregory, 1920; Sisson and Grossman, 1953). Gregory (1920) concluded that, based on analysis of Recent skulls of horses, zebras, and asses, the well-developed malar fossa in fossil horses served as the site of origin of the maxillo-labialis superior.

The origin and function of the DPOF is somewhat controversial. To further complicate matters, in hipparions and some other fossil horses, this fossa is of variable development in different taxa. In some hipparions, for example *Neohipparion affine* (fig. 8C), the posterior margin of the DPOF is developed relatively far back on the lacrimal bone (hence "lacrimal" fossa) close to the orbit (i.e., there is a narrow preorbital bar between the posterior margin of the fossa and anterior margin of orbit). In other hipparions, for example *Cormohipparion* (fig. 8A), the posterior margin of the DPOF is developed on the nasal and maxillary bones (hence "nasomaxillary" fossa) relatively far anterior of the orbit (i.e., there is a wide preorbital bar). These and other differences in development of the DPOF in hipparions might imply different functions and separate phylogenetic origins. Gregory (1920) reviewed the various hypotheses concerning the preorbital fossae in horses and concluded that the dorsal structure did not serve as a site for muscular attachment nor did it house a "larmier" (or facial) gland as in some artiodactyls. He concluded that the DPOF, which is rudimentary in extant horses such as *Equus grevyi* (Grevy's zebra), accommodated an expanded nasal diverticulum. Gregory did not discuss the probable function of this structural complex. The greatest diversity of development of facial fossae in horses occurred during the late Miocene (Clarendonian chronofauna, *sensu* Webb, 1969) when there was the greatest diversity of taxa. In addition to smell, present-day horses also use their olfactory organs, including the nasal diverticulum, for producing nasal sounds. Tedford (personal commun.) suggests that this would have been useful for intra- and interspecific recognition. Possibly related to this hypothesis is the observation that when equid diversity subsequently dropped after the demise of the Clarendonian chronofauna, so too did the diversity of preorbital morphologies decrease in equids. Although Gregory's (1920) study was insightful, he did not discuss whether facial fossae could be used in equid systematics.

Cope (1889) was one of the earliest North American paleontologists to discuss the taxonomic significance of equid facial fossae. He stated that species of North American hipparions could be distinguished by differences in the development of facial fossae. Osborn (1918) thought that the development of facial fossae was sexually dimorphic. However, as Webb (1969) noted, Osborn used the presence of a shallow DPOF to diagnose the species "*Pliohippus*" (=*Dinohippus*) *leidyanus*. Matthew (1924, p. 162) stated that:

> The fossae in *Merychippus* vary widely with age and apparently the individual or sex differences are great; nevertheless, some differences appear to be specific . . . . Ontogenetic changes appear to result in filling of the malar and contraction of the lacrymal . . . . The adult skulls of *M. isonesus,* however, still show an extensive although rather shallow fossa, chiefly in the lacrymal fossa area. The deep, restricted, sharply outlined lacrymal fossa of *M. paniensis* and *sphenodus,* the obscure shallow fossae of *M. sejunctus* and *republicanus,* etc. are probably valid specific characters; at all events, they are not age variations . . . . It should be observed, however, that the distinction of *Pliohippus* from *Protohippus* or *Hipparion* by the facial fossa cannot be maintained, as the malar fossa disappears in adult *Pliohippus,* in some species at least.

Pirlot (1953) presented a short note on the structure, function, and taxonomic significance of facial fossae in *Hipparion.* He concurred with Gregory's (1920) hypothesis that the DPOF in *Hipparion* probably accom-



8. Representative skulls of the four genera of hipparions, with particular emphasis on the tal region. A. *Cormohipparion sphenodus,* UNSM 1352, from Devil's Gulch Horse Quarry, Devil's Member of the Valentine Formation, Valentinian (early Clarendonian) of Brown County, north- Nebraska. B. *Hipparion tehonense,* F:AM 74478, from MacAdams Quarry, Clarendon Beds, a Group, early Clarendonian of Donley County, Texas Panhandle. C. *Neohipparion affine,* AMNH dapted from Osborn, 1918, pl. 32, fig. 1), from Little White River, near Rosebud Indian Agency, Miocene," late Clarendonian of South Dakota. D. *Nannippus peninsulatus,* AMNH 104708 d), from Blanco Beds, Crayfish Draw, Mt. Blanco, late Blancan of Crosby County, Texas Pan-

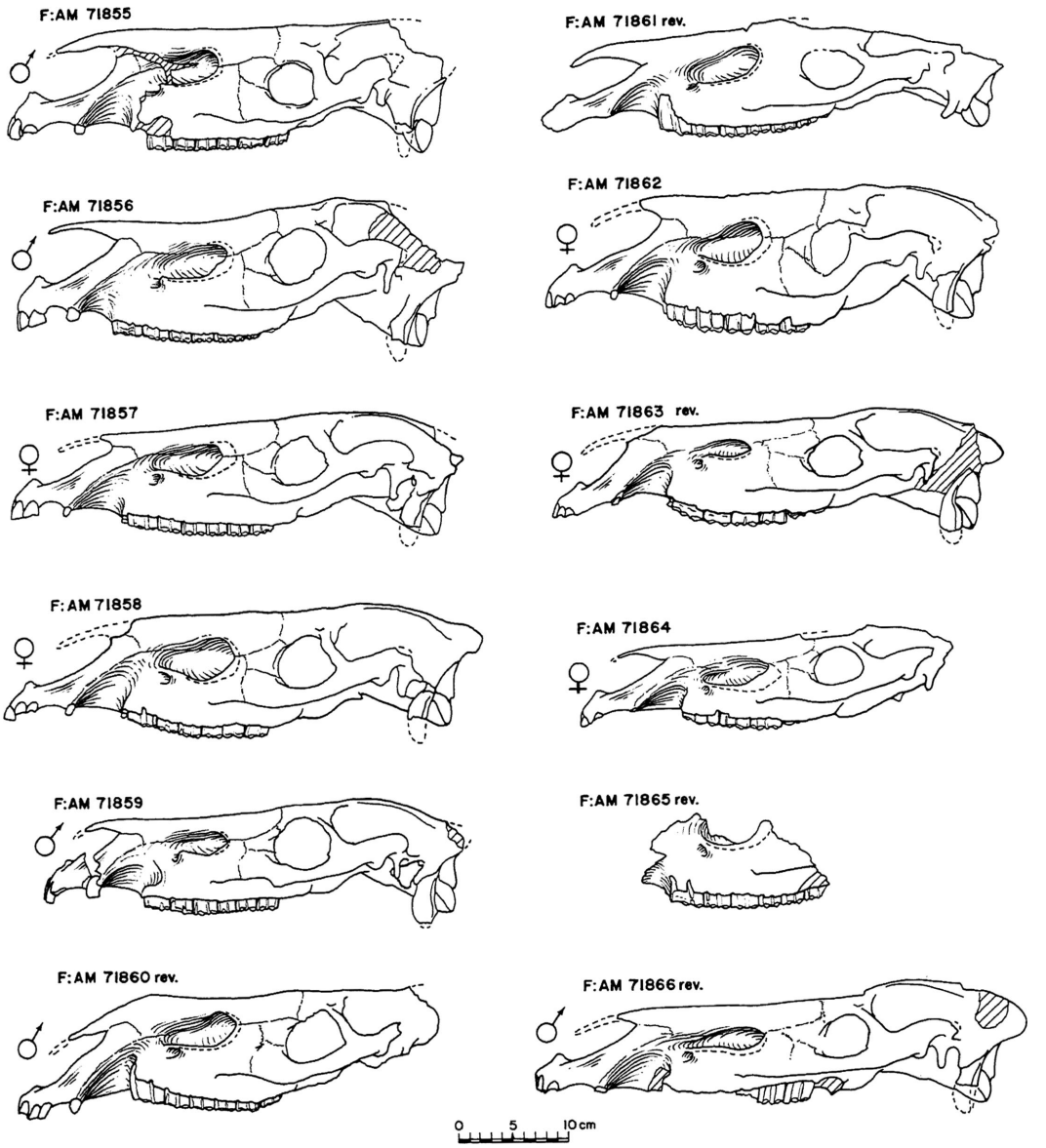


FIG. 9. Outline drawings of 12 individuals of both sexes of *Cormohipparion occidentale,* with emphasis on the detail of the preorbital region. This largest known sample of *Cormohipparion* (in which the DPOF is preserved) is from Hans Johnson Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska.

modated a nasal diverticulum. However, the paper concluded with the statement that (p. 311): "The preorbital fossa was probably of very little physiological importance to the individual and was likely to be an instable [*sic*] character."

Webb (1969) in his study of the Burge and Minnechadaza faunas, presented a review of facial fossae in horses. He concluded that (pp. 136, 138): "it seems possible that if individual variation is taken into account, the conformation of the preorbital fossae might

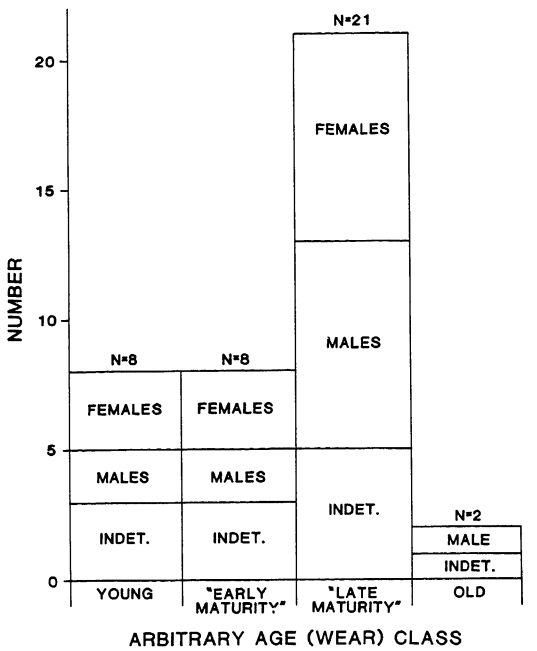


FIG. 10. Population age structure and distribution of sexes for the cranial sample (N = 39) of *Hipparion tehonense* from MacAdams Quarry, Clarendon Beds, Ogallala Group, early Clarendonian of the Donley County, Texas Panhandle. See discussion of arbitrary age (wear) classes in text.

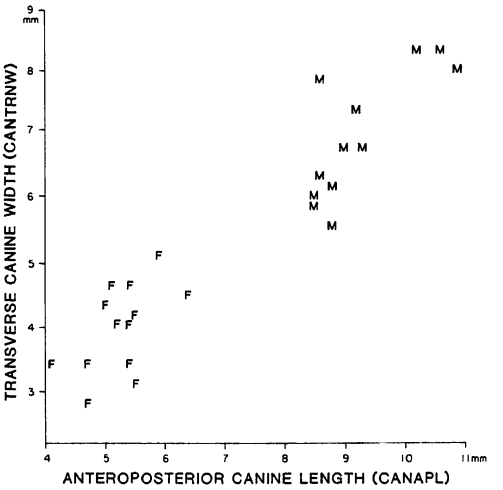


FIG. 11. Bivariate plot of CANAPL and CANTRNW for individuals of MacAdams *Hipparion tehonense* that preserve these characters to show sexual dimorphism of males (M) and females (F).

reveal phylogenetic relationships at the superspecific level . . . . When sizable single-quarry samples become available, it should be possible to show whether such variation [in the preorbital fossae] occurs, and, if so, whether it represents interspecific or intraspecific variation."

Skinner and MacFadden (1977) diagnosed a new genus of hipparion, *Cormohipparion,* based principally on the development of the DPOF. In this study, relatively large quarry samples of *Cormohipparion* were investigated in order to better understand the intraspecific and sexual variation in the DPOF (fig. 9). MacFadden (1980) analyzed a large sample of skulls of *Hipparion tehonense* from the Frick MacAdams Quarry of early Clarendonian age in Donley County, Texas. In both of these samples, as is the case in other hipparions, the variation in development of the DPOF seems to fall within a range that demonstrates that this character complex is of potential taxonomic value. In addition, other workers have also employed preorbital facial fossae in their taxonomic studies. It is interesting that Forstén, who at various times has been critical of the use of preorbital facial fossae in equid systematics (e.g., Forstén, 1982b), nevertheless uses this character complex in her studies of Samos hipparions (Forstén, 1980) and the brachydont Miocene *Sinohippus* (Forstén, 1982a). Also, other workers recently have continued to question the taxonomic use of the DPOF (Eisenmann, 1981).

In order to further investigate the utility of the DPOF as applied to hipparion systematics, a quantitative study was made of skulls and upper dentitions of *Hipparion tehonense* from the early Clarendonian MacAdams Quarry of Donley County in the Texas Panhandle (the systematics of this sample was presented in MacFadden, 1980). This quarry sample was chosen because it provides a large number of individuals to analyze ontogenetic and sexual variation of characters. (There are other cranial samples that could have been used, but, to my knowledge, the MacAdams sample far surpasses that of any other hipparion in North America in terms of number of available individuals from a single quarry.)

TABLE 3

Cranial Characters and Tests for Sexual Dimorphism for *Hipparion tehonense* from the Early Clarendonian MacAdams Quarry of Donley County, Texas Panhandle[a]

	Males					Females					*t*-test	
Character	N	$\bar{x}$	*s*	*V* (%)	OR	N	$\bar{x}$	*s*	*V* (%)	OR	*t*	?Null[b]
CANAPL	13	9.19	0.84	9.14	8.5–10.9	14	5.26	0.55	10.46	4.1–6.4	14.52***	Rejected
CANTRNW	12	6.91	0.94	13.60	5.6–8.2	13	4.02	0.67	16.67	2.9–5.1	8.92***	Rejected
MUZWDTH	10	31.76	4.50	14.17	21.1–36.9	6	33.73	2.47	7.32	29.4–36.8	0.98	Accepted
PSTCNDIA	11	48.16	4.69	9.74	42.0–54.3	14	50.44	3.77	7.47	44.2–56.8	1.34	Accepted
TRL	12	123.70	5.59	4.52	115.6–132.6	13	123.70	5.21	4.21	116.0–134.6	0.31	Accepted
NNAEO	6	113.72	7.71	6.78	102.2–125.7	3	114.83	9.17	7.99	108.2–125.3	0.88	Accepted
NNDPOF	9	75.20	7.36	9.79	63.9–83.7	6	77.97	11.26	14.44	67.2–98.2	0.70	Accepted
PRB	8	40.26	4.81	11.95	33.9–45.8	7	37.60	4.34	11.54	33.2–46.2	1.35	Accepted
APLDPOF	10	49.72	3.70	7.44	43.3–54.3	11	48.98	4.85	9.90	39.7–54.8	0.35	Accepted
DVDPTH	10	23.58	4.35	18.44[c]	16.2–31.5	11	24.42	3.80	15.56	19.3–30.5[c]	0.37	Accepted
DPOFIOF	8	45.41	6.73	14.82	38.6–56.7	9	40.79	4.61	11.30	33.5–46.7	1.29	Accepted
NNIOF	7	48.81	5.02	10.28	44.3–59.2	6	49.82	8.29	16.64	42.7–64.8	0.85	Accepted
NNP2	8	61.55	4.98	8.09	52.6–67.7	6	58.43	5.99	10.25	51.3–67.9	0.87	Accepted
DPOFTB	10	61.45	6.08	9.89	52.4–72.2	11	58.78	3.32	5.65	53.0–63.9	1.13	Accepted
DPOFSKL	7	21.86	2.91	13.31	18.0–26.0	7	20.71	3.55	17.14	17.0–26.0	3.55	Accepted

[a] See abbreviations above.

[b] Test of null hypothesis; accepted indicates no signficant difference and rejected indicates significant differences between males and females.

[c] DVDPTH is particularly sensitive to postmortem crushing. A combined sample (N = 14) of males and females with crushed specimens removed yielded $\bar{x}$ = 24.21, S = 3.05; V = 12.59; OR = 19.72–29.0.

*** Probability level ≤ 0.001.

TABLE 4

ANOVA for Cranial Characters of Sample of *Hipparion tehonense* from MacAdams Quarry as a Test for Significant Differences Based on Ontogeny

Character	Source of Variation	Sum of Squares	Degrees of Freedom	Mean of Squares	F-value	?Null Hypothesis[a]
CANAPL	Between groups	8.9714	2	4.4857	1.00	Accepted
	Within groups	107.7760	24	4.4907		
	Total	116.7474	26			
CANTRNW	Between groups	11.2375	2	5.6187	2.20	Accepted
	Within groups	56.0921	22	2.5496		
	Total	67.3296	24			
MUZWDTH	Between groups	0.9484	2	0.4742	0.03	Accepted
	Within groups	225.9918	13	17.3840		
	Total	226.9402	15			
PSTCNDIA	Between groups	45.6989	2	22.8494	1.29	Accepted
	Within groups	390.7811	22	17.7628		
	Total	436.4797	24			
TRL	Between groups	161.5231	2	80.7615	3.18	Accepted
	Within groups	710.4850	28	25.3745		
	Total	872.0081	30			
NNAEO	Between groups	125.1021	1	125.1021	2.28	Accepted
	Within groups	823.5952	15	54.9063		
	Total	948.6973	16			
NNDPOF	Between groups	58.0670	3	19.3557	0.26	Accepted
	Within groups	1431.3176	19	75.3325		
	Total	1489.3845	22			
PRB	Between groups	47.5689	3	15.8563	0.84	Accepted
	Within groups	413.6006	22	18.8000		
	Total	461.1694	25			
APLDPOF	Between groups	39.8411	3	13.2804	0.72	Accepted
	Within groups	534.9006	29	18.4448		
	Total	574.7415	32			
DVDPTH	Between groups	52.1680	3	17.3893	1.44	Accepted
	Within groups	349.1220	29	12.0387		
	Total	401.2898	32			
DPOFIOF	Between groups	30.4016	3	10.1339	0.28	Accepted
	Within groups	799.6537	22	36.3479		
	Total	830.0552	25			
NNIOF	Between groups	66.9033	3	22.3011	0.57	Accepted
	Within groups	587.8407	15	39.1894		
	Total	654.7439	18			
NNP2	Between groups	45.6734	2	22.8367	0.86	Accepted
	Within groups	370.4761	14	26.4626		
	Total	416.1494	16			
DPOFTB	Between groups	66.4603	3	22.1534	1.09	Accepted
	Within groups	586.8385	29	20.2358		
	Total	653.2988	32			
DPOFSKL	Between groups	50.3181	3	16.7727	1.08	Accepted
	Within groups	296.1167	19	15.5851		
	Total	346.4346	22			

[a] $P \leq 0.01$; accepted indicates no significant difference among four arbitrary age classes (also see discussion in text).

For the MacAdams cranial study, a maximum of 25 characters were measured, counted, or coded for each of 39 individuals (see "Craniometry" section above). The ontogeny and sex of each individual (fig. 10) was determined by, respectively, arbitrary wear classes (see Methods above) and canine size. From this analysis it appears that the MacAdams *H. tehonense* is well-suited to a statistical study with the above-mentioned goals because: (1) The population age structure does not seem to be overrepresented in young and old age classes. (It seems to be a catastrophic rather than attritional assemblage. This fact becomes even more critical in an analysis of the dentitions below where attritional assemblages could reflect statistics biased by an overabundance of old and possibly young individuals.) (2) With 13 males and 14 females determined from this sample, possible sexual dimorphism of certain characters can be compared.

For each the 15 measured skull characters (these are described in detail in the Craniometry part of the Methods section above), a *t*-test was performed to test the null hypothesis that no significant statistical difference exists between males and females. As presented in table 3, 15 of these same characters indicate no significant difference between the males and females. The only two characters that differ significantly (at the $p \leq 0.001$ level) in size between males and females are CANAPL and CANTRNW (fig. 11). It is not at all surprizing that these two characters are sexually dimorphic in the MacAdams sample; they also are in other horses (and many other mammals).

In order to study possible ontogenetic changes in the same 15 measured cranial characters, Model I ANOVA (see Sokal and Rohlf, 1981) was used to simultaneously test the null hypothesis of no significant difference among four arbitrary wear (age) classes (see Methods section above). The total number of individuals in each class (males, females, and those of indeterminate sex) is shown in figure 10. As presented in table 4, the null hypothesis is accepted (at the $p \leq 0.01$ level) for all 15 of these measured characters. There are no significant differences in each of these characters that are attributable to ontogeny.

In order to study the amount of variation for each of the same 15 characters,[3] a variability profile was constructed for the cranial sample of *Hipparion tehonense* from MacAdams Quarry (fig. 12). In variability profiles, characters are arranged on the abscissa from left to right in sequence of descending mean values (e.g., TRL has the largest mean and CANTRNW has the smallest mean value). After the characters are ordered in this fashion, then the *V*s are plotted along the ordinate. Coefficients of variation provide a rough comparative guide to variability of characters with different means; however, other studies (e.g., Yablokov, 1974) have noted that characters with smaller means oftentimes exhibit larger *V*s than characters with larger mean values. This phenomena gives rise to a slight trend (or "drift" *sensu* Yablokov, 1974) toward an increase in *V*s as exemplified in figure 12. With regard to characters related to the DPOF (particularly APLDPOF and DVDPTH), the *V*s are consistent with "expected" values for their respective means value (i.e., position on variability profiles) relative to other skull characters based on the MacAdams sample of *Hipparion tehonense.*

The development of DPOF appears to be a taxonomically valid character complex. Despite claims to the contrary by some workers, the variation in development of facial fossae within equid taxa is not strongly controlled by either ontogeny or sexual dimorphism. Other studies of European hipparion quarry samples provide additional evidence for the constancy in development of hipparion facial fossa within taxa (Woodburne and

[3] Sokal and Braumann (1980; also see Yablokov, 1974) discuss the use of variability profiles and comparative studies of coefficients of variation. They state that (1980, p. 61): "persons wishing to employ coefficients of variation should first test whether the sample [character] distributions they are working with are normally or at least symmetrically and unimodally distributed." In the present study inspection of histograms indicate that all of the cranial characters satisfy these requirements except for CANAPL and CANTRW, which are distinctly bimodal in distribution. In addition, one of the reasons why the coded characters (see Methods above) are not used in this comparative study is because many of these do not satisfy the requirements stated by Sokal and Braumann (1980).

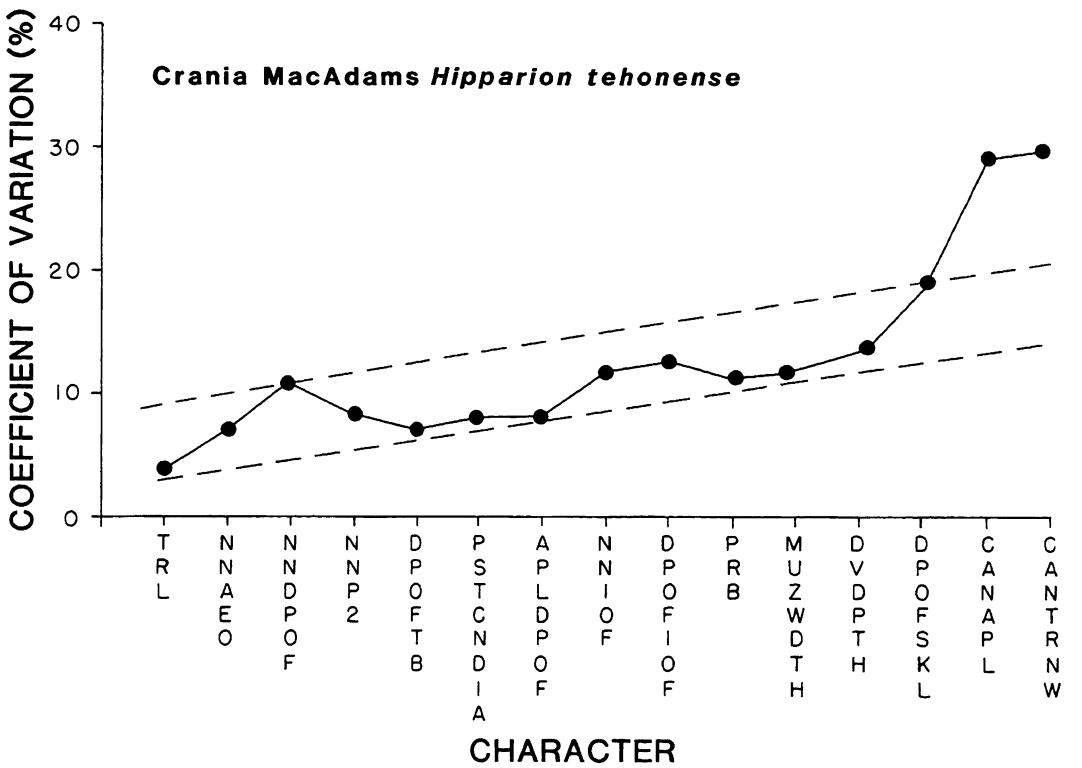


FIG. 12. Variability profiles for measured cranial characters of MacAdams *Hipparion tehonense*. The dashed lines show a trend (or "drift," *sensu* Yablokov, 1974) toward increased *Vs* for smaller mean values (because of extreme sexual dimorphism, CANAPL and CANTRNW are excluded). Abbreviations for characters are given in the text.

Bernor, 1980; MacFadden, unpub. work on Pikermi hipparions). A particularly attractive project of this nature for future study is the large quarry sample of hipparion from the early Vallesian Höwenegg site in the Hegau region of West Germany (Tobien, 1959).

The present paper is predicated on the hypothesis that North American hipparions can be diagnosed at the generic level by a suite of character complexes of which different configurations in the DPOF is of prime importance. It is now necessary to discuss the distribution and polarity of facial fossae within the equids, with particular reference to hipparions. Morphological and biostratigraphical data are presented here to hypothesize, respectively, relative relatedness and then the calibration of phylogeny following the procedures advocated by workers such as Schaffer, Hecht, and Eldredge (1972).

The hipparions themselves do not constitute a monophyletic group because they appear to have been derived from (or are most closely related to) at least two taxa within the merychippine (or perhaps even "parahippine") complex. In addition, the phylogenetic interrelationships of all other Miocene "premerychippine" horses are markedly polyphyletic (for example *Miohippus*, see Stirton, 1940) or are too poorly known to be helpful in the present discussion. However, it does appear that *Mesohippus* and all other more derived (post-Eocene, excluding the aberrant *Haplohippus*) horses can be united as a monophyletic group based on the presence of three or fewer digits in the manus and pes (or, stated differently, less than four digits in the pes) and molarization of the second, third, and fourth premolars (MacFadden, 1976).

Within the monophyletic taxon that includes *Mesohippus* and all descendants of all species of this genus, it is necessary to know

the distribution of dorsal and ventral preorbital fossae (not including the buccinator). From a survey of taxa of this group, it appears that the absence of facial fossae is rare and limited to, for example, some species of *Mesohippus* (see illustrations in Osborn, 1918), *Nannippus* (MacFadden and Waldrop, 1980), certain species of *Neohipparion,* some Old World hipparions (Hooijer and Maglio, 1973, 1974; Hooijer, 1975), and *Equus.* On the other hand, the presence of some combination of dorsal and malar preorbital fossae is extremely widespread including many species of *Miohippus, Parahippus, Archaeohippus, Merychippus* (*sensu lato*), *Cormohipparion, Hipparion* (*sensu lato*), *Pliohippus, Dinohippus,* and *Onohippidium* (for example, see illustrations in Osborn, 1918; Skinner and MacFadden, 1977; MacFadden and Skinner, 1982). Invoking the principle of commonality (the most widespread character state is primitive), within the monophyletic group defined above, the presence of some combination of facial fossae is relatively primitive, whereas the absence of facial fossae is relatively derived. The polarity of equid facial fossae character states theoretically proceeds from well-developed fossae (most primitive) to reduced fossae to fossae absent (most derived). Bennett (1980) independently reached the same conclusion as to the polarity of facial fossa in her study of late Cenozoic horses (including *Equus*). The present analysis of facial fossa polarity is possibly oversimplified depending on whether or not the development of these structures represents one monophyletically related event or two or more acquisitions of similar structures.

Biochronological data for hipparions also appear to corroborate the morphocline polarity for facial fossae presented above (as a colleague once commented, "the chronocline approximates the morphocline"). In some cases, there appears to be a trend toward reduction in the development of facial fossae in ancestral-descendant sequences, for example, in the species of *Neohipparion.* For Old World hipparions, Woodburne and Bernor (1980) and Bernor, Woodburne, and Van Couvering (1980) present an example of what is interpreted as morphological transformation of facial fossae in the sedimentary sequence at Maragheh, Iran. (This observation is of course predicated on the assumption that evolution *in situ* without immigration of species into the region studied.) The hipparions in the lower units have relatively well-developed dorsal preorbital fossae and there appears to be a transition to apparently descendant hipparions with dorsal preorbital fossae that are poorly developed or lost. Another clear example of reduction in facial fossae as interpreted by biochronological evidence is the transformation from *Pliohippus* to *Dinohippus* to *Equus* (see, e.g., Bennett, 1980).

In other cases within monophyletic taxa, the development of facial fossa is relatively constant. A good example of this is represented by the *Cormohipparion* species, i.e., *C. goorisi, C. sphenodus,* and *C. occidentale.* In the transformation series represented by these species, the DPOF is well developed and unreduced.

In summary, facial fossae are taxonomically valid character complexes. In hipparions, as well as other hypsodont horses, the presence of the DPOF is interpreted to represent the primitive condition. Reduction, or loss (i.e., absence) of this fossa is interpreted to represent the derived condition. The configuration of the DPOF as well as other characters can be used to diagnose the North American genera *Hipparion, Neohipparion, Nannippus,* and *Cormohipparion* (fig. 8).

MORPHOMETRICS AND QUANTITATIVE VARIATION OF HIPPARION CHEEK TEETH

A basic premise of most studies on fossil horses is that cheek tooth dentitions are of prime importance in taxonomy. One of the most vexing problems related to this premise is the amount of variation associated with each of the commonly used characters. In the last several decades numerous workers have presented studies of dental variation in horses

(e.g., Bader, 1956 for *Parahippus*; Downs, 1961 for *Merychippus*; and Forstén, 1970 for *Mesohippus*). During the present study a suite of measured, counted, and coded characters were evaluated for available samples of upper dentitions and teeth of each species discussed in this report. The types of characters are extensively described above (in Dental Nomenclature, Mensuration, and Statistics); and that section provides an integral and necessary foundation for the discussion that follows here. In this section I (1) investigate types of character variation in a large quarry sample (using the MacAdams Quarry *Hipparion tehonense* as a case study); (2) compare results from this quarry sample to other recognized species, and (3) evaluate the relative taxonomic utility of different dental characters. This section is followed by a discussion of the sources of variation in the dental pattern of hipparion horses.

A CASE STUDY: MacAdams *Hipparion tehonense*. As was also the case for the cranial study described above, the large sample of *Hipparion tehonense* from the early Clarendonian MacAdams Quarry in Donley County in the Texas Panhandle provided an excellent opportunity to study variation and character utility in the upper cheek tooth dentition. (Because of the frequent lack of definite association, lower dentitions are not included in the morphometric analysis both in this case study as well as throughout this report.) Specimens of *H. tehonense* were selected from MacAdams Quarry because they possessed complete dentitions or because they were also used in the corresponding cranial study (for a possible cross check). For the 40 individuals measured, the population age structure and sex is presented in figure 13. As might be expected, the distribution of individuals in wear classes and numbers of each sex are similar to those analyzed in the cranial study (compare with fig. 10). This age distribution is of particular importance because it shows that the subsequent analysis of the upper dentition will not be biased by an overabundance of specimens in either the young or old age classes (i.e., the MacAdams *Hipparion tehonense* seems to represent a catastrophic assemblage). In the MacAdams Quarry almost all the specimens were collected and labeled as being from either the "yellow sand" or

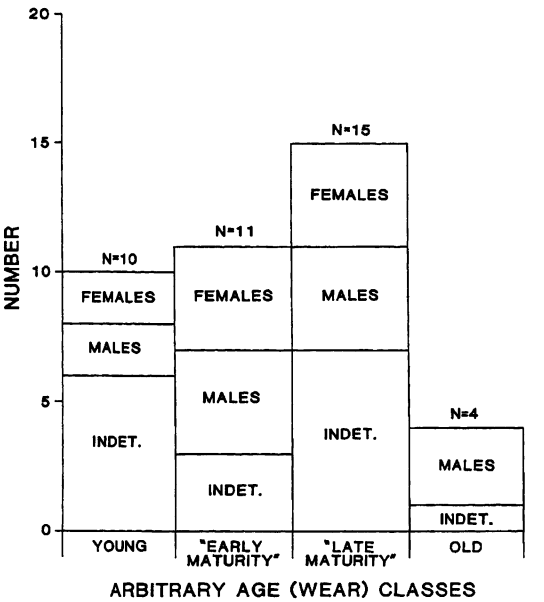


FIG. 13. Population age structure and distribution of sexes for the upper dental sample (N = 40) of MacAdams *Hipparion tehonense*. See discussion of arbitrary age (wear) classes in text.

"gray sand." Therefore, the first step in the use of specimens from both of these microstratigraphic units as a combined "population" was to test for significant differences for all measured characters. The results of ANOVA indicate that there is no significant difference in the sample statistics for specimens collected from the yellow sand (N = 31), gray sand (N = 6), or of indeterminate provenance within the quarry (N = 3).

The next step was to test for characters of the cheek tooth dentition that may be sexually dimorphic. For specimens in which the canine was preserved, the sex was unambiguously determined (using the two characters CANAPL and CANTRNW, see fig. 11). For each of the measured and counted characters,[4] the *t*-tests were used to test the null hypothesis of no significant difference. The results of this analysis (presented in table 5)

[4] Both *t*-tests and ANOVA are sensitive to significant departures from normality. Coded characters (e.g., presence or absence) are oftentimes not normally distributed and are therefore excluded from these statistical tests.

TABLE 5

Upper Dental Characters and Tests for Sexual Dimorphism for *Hipparion tehonense* from the Early Clarendonian MacAdams Quarry of Donley County, Texas Panhandle[a]

	Males					Females					*t*-test	
Character	N	$\bar{x}$	*s*	*V* (%)	OR	N	$\bar{x}$	*s*	*V* (%)	OR	*t*	?Null[b]
P2APL	12	24.60	1.64	6.67	21.5–27.6	10	24.90	1.71	6.87	22.0–27.3	0.42	Accepted
P2TRNW	11	19.06	1.52	7.97	17.1–21.4	10	18.97	1.40	7.66	15.8–20.1	1.24	Accepted
P2PRTL	8	5.66	0.67	11.84	4.9–7.0	9	5.47	0.39	7.13	4.7–5.9	0.75	Accepted
P2PRTW	11	4.38	0.49	11.19	3.7–5.2	10	3.94	0.50	12.69	2.7–4.5	2.04	Accepted[c]
P2MSPL	11	14.94	1.34	8.97	12.9–18.0	7	15.06	0.97	6.44	13.6–16.3	0.20	Accepted
P2MSTHT	9	25.74	7.00	27.20	14.6–36.7	10	29.24	6.52	22.30	17.1–37.5	1.13	Accepted
P2TOTPLI	12	3.75	2.09	55.73	1–7	8	3.50	2.27	64.86	0–7	0.24	Accepted
M1APL	13	18.29	1.13	6.18	16.0–20.4	10	19.13	0.92	4.81	17.7–20.6	1.92	Accepted[c]
M1ECTL	13	18.35	1.42	7.74	15.7–20.9	10	19.42	1.62	8.34	16.9–22.4	1.68	Accepted
M1TRNW	13	19.53	0.68	3.48	18.6–20.7	10	19.28	0.84	4.36	18.0–20.5	0.79	Accepted
M1PRTL	13	6.16	0.74	12.01	4.9–7.5	10	6.29	0.77	12.24	5.2–7.7	0.40	Accepted
M1PRTW	13	3.75	0.45	12.00	3.1–4.7	10	3.87	0.32	8.27	3.5–4.7	0.74	Accepted
M1MSPL	12	15.04	0.66	4.39	13.8–16.0	10	15.45	0.87	5.63	13.6–16.7	1.25	Accepted
M1MSTHT	0	—	—	—	—	2	32.30	17.54	54.30	19.9–44.7	—	—
M1TOTPLI	11	5.82	3.22	55.33	0–11	9	5.44	2.96	54.41	2–9	0.26	Accepted

[a] See abbreviations above.

[b] Test of null hypothesis; accepted indicates no significant difference at $P \leq 0.05$.

[c] Accepted at $P \leq 0.1$.

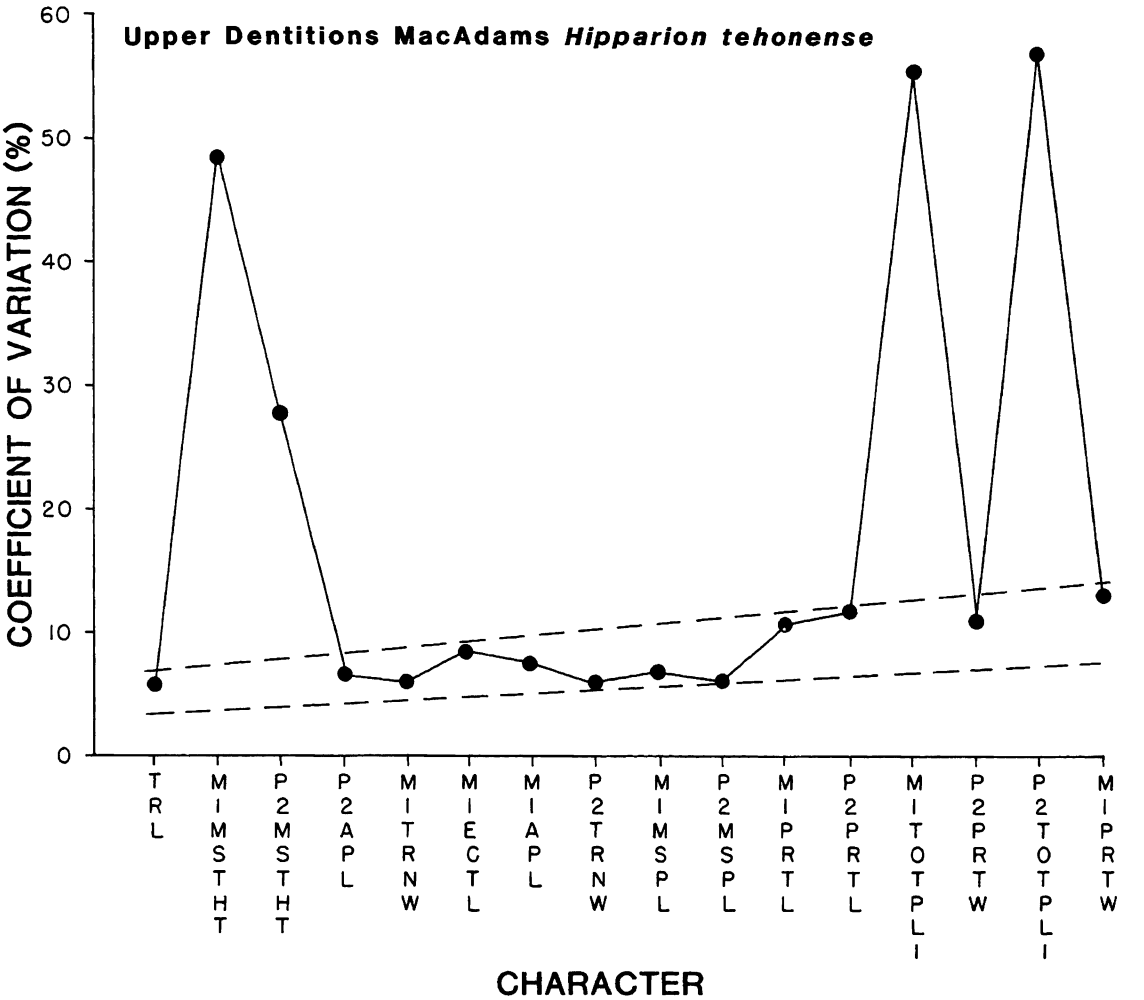


FIG. 14. Variability profiles for measured and counted upper dental characters of MacAdams *Hipparion tehonense*. For figures 14–17, the dashed lines show a trend (or "drift," *sensu* Yablokov, 1974) for most of the measured characters (i.e., excluding the highly variable M1MSTHT, P2MSTHT, M1TOTPLI, P2TOTPLI) towards increased *V*s for characters with smaller mean values. Also see discussion in text.

indicate that none of these characters are sexually dimorphic.

In order to investigate possible ontogenetic differences in the same 16 dental characters, the null hypothesis was tested using Model I ANOVA. Each specimen was placed into one of four arbitrary age classes (also described above) based on relative wear. The results (table 6) indicate that several important measured and counted dental characters exhibit significant ontogenetic differences. These characters are P2APL, P2MSTHT, P2TOTPLI, M1APL, M1ECTL, M1PRTW, M1MSTHT, and M1TOTPLI. Furthermore, even if "young" and "old" individuals are removed and a *t*-test is performed between those of "early maturity" and "advanced maturity," significant differences are still exhibited for these same characters. These data suggest that for measured and counted dental characters taken from a pooled sample (containing the spectrum of ontogenetic varia-

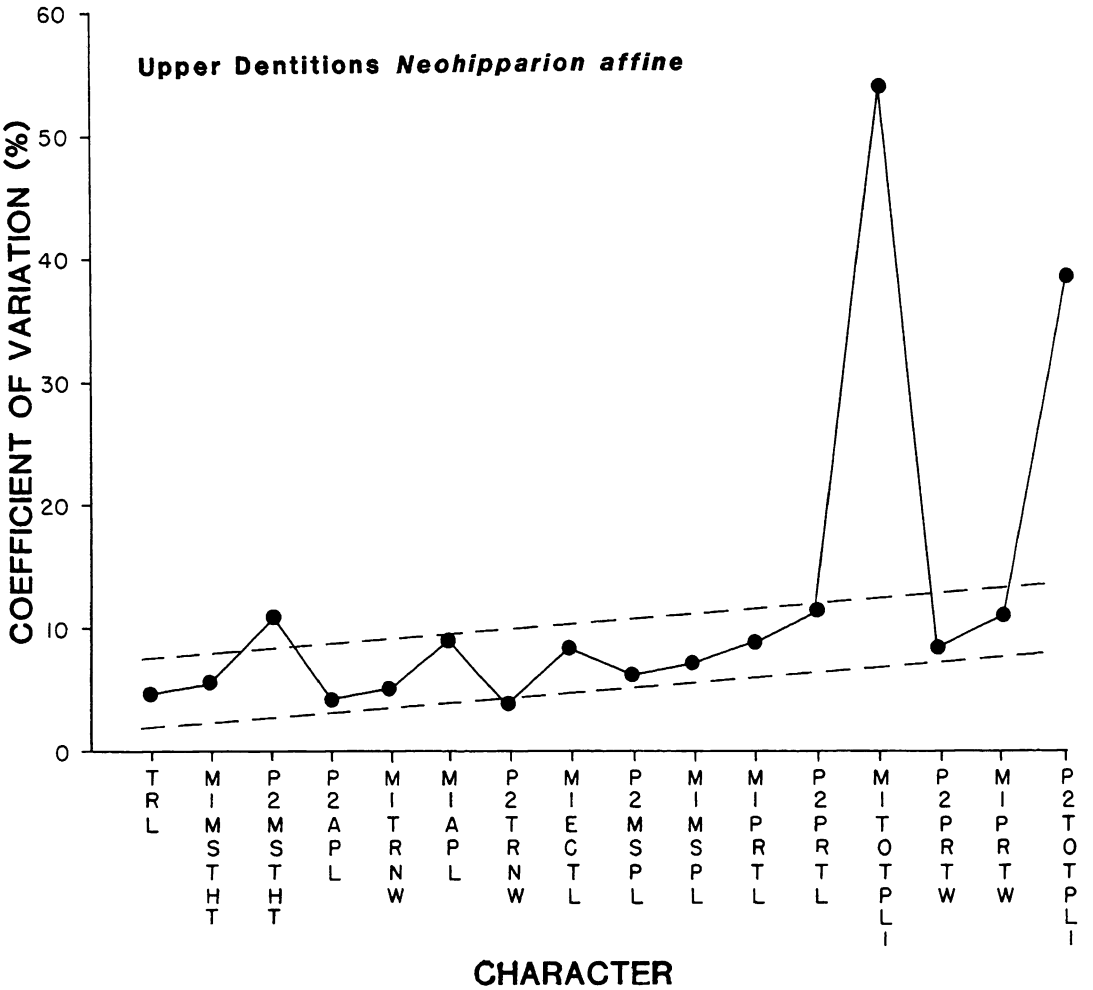


FIG. 15. Variability profiles for measured and counted upper dental characters of the pooled (i.e., specimens from numerous localities) sample of *Neohipparion affine*. Also see explanation in caption of figure 14.

tion), one must critically assess each character to evaluate its taxonomic utility (see also further discussion below).

Based on these same measured and counted characters, a variability profile (Yablokov, 1974; Sokal and Braumann, 1980; see above) was constructed for the MacAdams *Hipparion tehonense* (fig. 14). This profile indicates the relative *V* for each character. The following characters appear to have high *V*s (i.e., ≥ 10.0): M1MSTHT, P2MSTHT, M1PRTL, P2PRTL, M1TOTPLI, P2PRTW, P2TOTPLI, and M1PRTW. This pattern is consistent with those of other hipparion species. The taxonomic implications of these data will be discussed below.

DENTAL VARIATION IN OTHER HIPPARION SPECIES: Variability profiles were constructed for one species of each of the other genera of North American hipparions (i.e., *Neohipparion affine, Nannippus minor,* and *Cormohipparion occidentale,* figs. 15–17). The original data used to construct these profiles are tabulated below in the relevant section that describes each of these species (see Systematic Paleontology). These three additional species

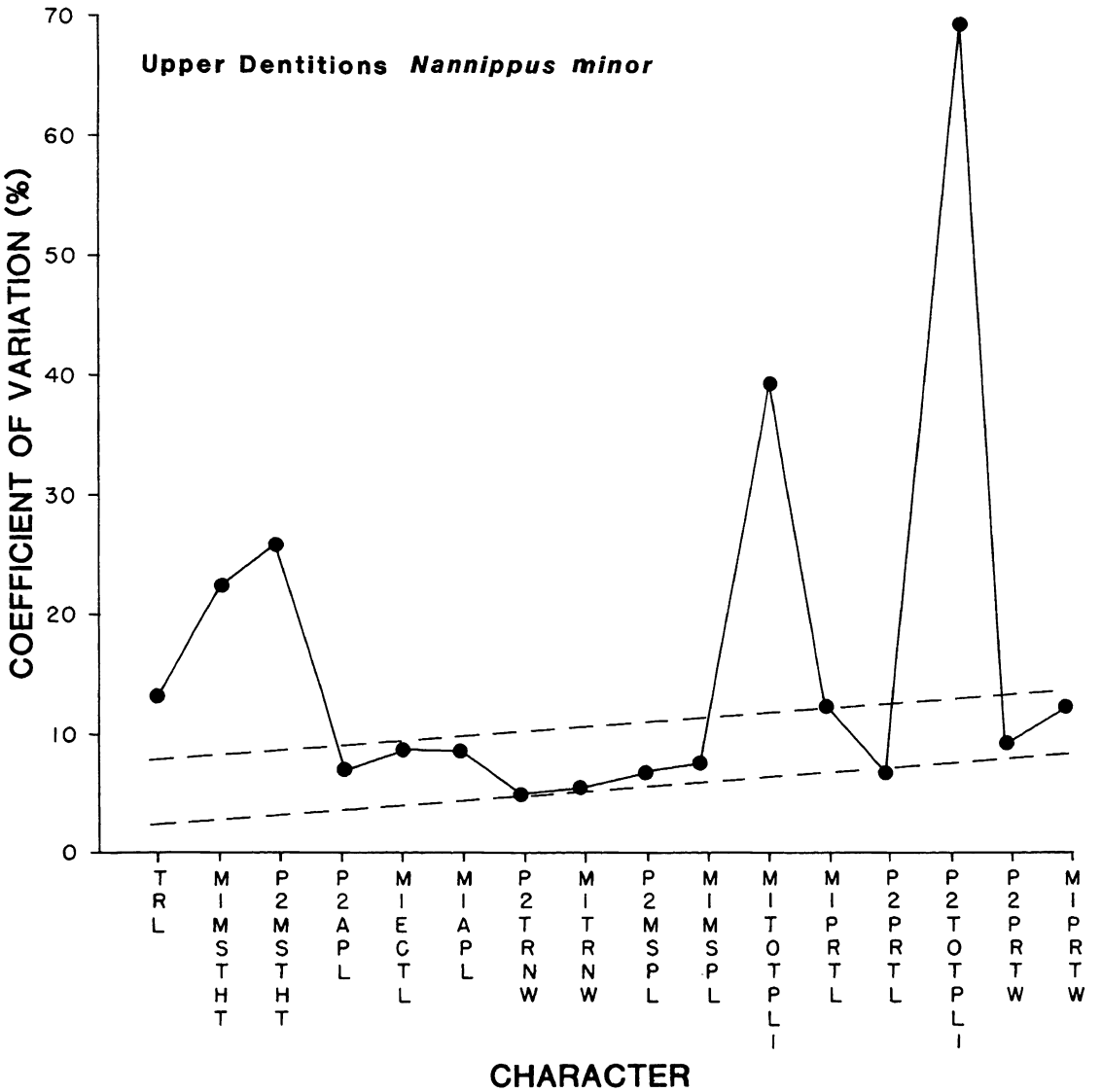


FIG. 16. Variability profiles for measured and counted upper dental characters of the pooled (i.e., specimens from numerous localities) sample of *Nannippus minor*. Also see explanation in caption of figure 14.

were chosen because they are represented by relatively large sample sizes (respectively, N = 22, N = 72, N = 23). The patterns described here from the variability profiles seem also to be representative of the data obtained for the remaining North American hipparion species.

It is evident from these three variability profiles and that of *Hipparion tehonense* that several general patterns emerge from the data: (1) The *V*s for P2MSTHT, M1MSTHT, M1TOTPLI, and P2TOTPLI are characteristically high (the low values of P2MSTHT and M1MSTHT for *Neohipparion affine* are a result of a small sample for those characters). (2) The remaining 12 characters show *V*s that are "acceptable" (i.e., <10.0).[5] (3)

[5] Simpson, Roe, and Lewontin (1960, p. 91) stated

TABLE 6

ANOVA for Measured and Counted Upper Dental Characters of *Hipparion tehonense* from MacAdams Quarry as a Test for Significant Differences Based on Ontogeny

Character	Source of Variation	Sum of Squares	Degrees of Freedom	Mean of Squares	F-value	?Null Hypothesis[a]
P2APL	Between groups	25.2249	3	8.4083	4.72	Rejected
	Within groups	53.4902	30	1.7830		
	Total	78.7151	33			
P2TRNW	Between groups	12.7687	3	4.2562	3.18	Accepted
	Within groups	38.8737	29	1.3405		
	Total	51.6424	32			
P2PRTL	Between groups	3.0718	3	1.0239	2.86	Accepted
	Within groups	8.5953	24	0.3581		
	Total	11.6671	27			
P2PRTW	Between groups	1.7627	3	0.5876	3.71	Accepted
	Within groups	4.4373	28	0.1585		
	Total	6.2000	31			
P2MSPL	Between groups	4.9787	3	1.6596	1.77	Accepted
	Within groups	20.6324	22	0.9378		
	Total	25.6111	25			
P2MSTHT	Between groups	799.1687	3	266.3894	16.91	Rejected
	Within groups	409.6028	26	15.7540		
	Total	1208.7715	29			
P2TOTPLI	Between groups	82.0182	3	27.3394	18.66	Rejected
	Within groups	42.0423	29	1.4497		
	Total	124.0605	32			
M1APL	Between groups	43.8717	3	14.6239	17.42	Rejected
	Within groups	28.5432	34	0.8395		
	Total	72.4149	37			
M1ECTL	Between groups	56.7420	3	18.9140	18.74	Rejected
	Within groups	34.3136	34	1.0092		
	Total	91.0556	37			
M1TRNW	Between groups	1.0038	3	0.3346	0.27	Accepted
	Within groups	40.7491	33	1.2348		
	Total	41.7529	36			
M1PRTL	Between groups	1.1142	3	0.3714	0.73	Accepted
	Within groups	17.2829	34	0.5083		
	Total	18.3971	37			
M1PRTW	Between groups	2.9057	3	0.9686	5.96	Rejected
	Within groups	5.2018	32	0.1626		
	Total	8.1075	35			
M1MSPL	Between groups	7.1135	3	2.3712	2.58	Accepted
	Within groups	29.3539	32	0.9173		
	Total	36.4674	35			
M1MSTHT	Between groups	704.9023	1	704.9023	388.91	Rejected
	Within groups	3.6250	2	1.8125		
	Total	708.5273	3			
M1TOTPLI	Between groups	145.7644	3	48.5881	10.20	Rejected
	Within groups	138.1143	29	4.7626		
	Total	283.8784	32			
TRL	Between groups	256.9382	3	85.6461	3.77	Accepted
	Within groups	613.1407	27	22.7089		
	Total	870.0789	30			

[a] $P \leq 0.01$; accepted indicates no significant difference among four arbitrary wear classes; rejected indicates significant difference (also see discussion in text).

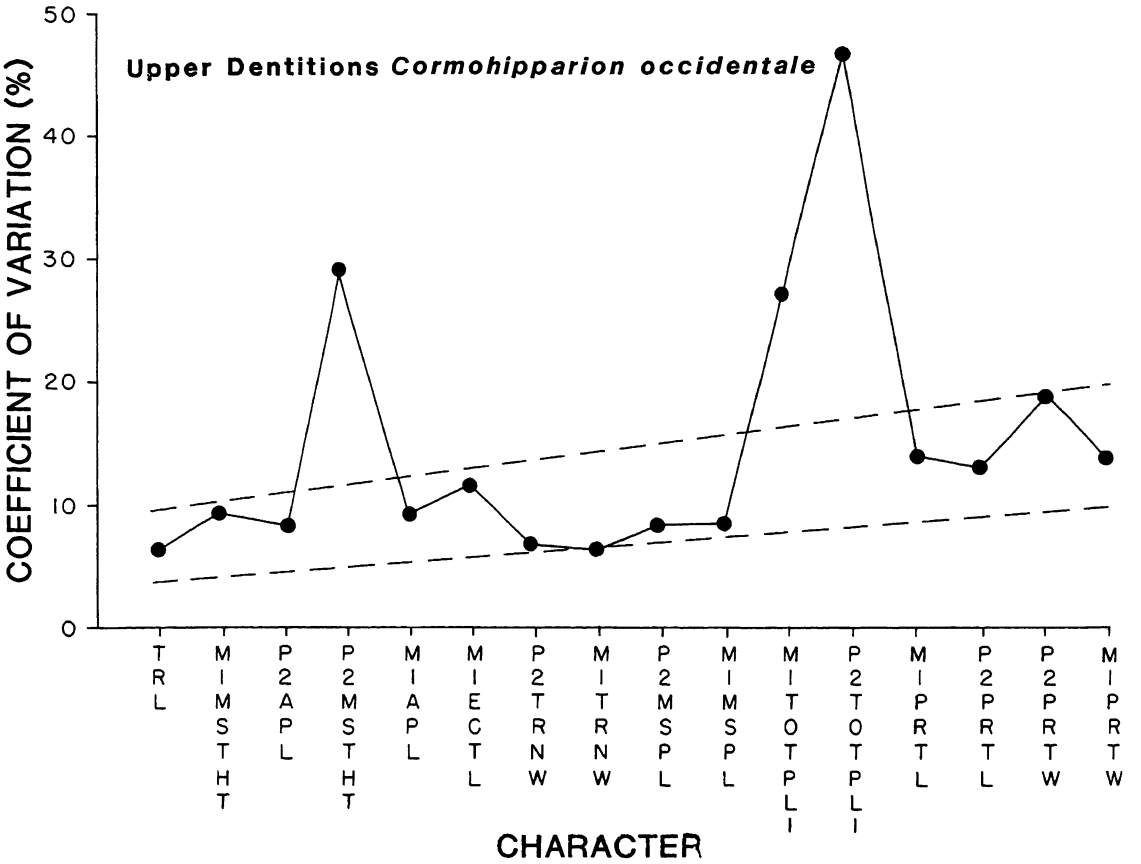


FIG. 17. Variability profiles for measured and counted upper dental characters of the pooled (i.e., specimens from numerous localities) sample of *Cormohipparion occidentale*. Also see explanation in caption of figure 14.

None of these characters show extremely low *V*s (i.e., much less than 4). (4) The amount of character variation for *N. affine, N. minor,* and *C. occidentale,* all of which represent "pooled" species samples (i.e., from different localities), does not seem to be any greater than that represented by the single sample of *Hipparion tehonense* from MacAdams Quarry. (5) If the "anomalously" high characters (P2MSTHT, M1MSTHT, M1TOTPLI, and P2TOTPLI) are excluded from consideration, then the other 12 characters indicate a variability "drift" (see Yablokov, 1974), or increase in *V*s (dashed lines in figs. 14–17) corresponding to decreasingly smaller character means (this was also observed for the cranial characters of *H. tehonense* presented above).

TAXONOMIC UTILITY OF UPPER CHEEK TOOTH CHARACTERS: The preceding discussion has identified differences in variation of measured characters of the upper cheek tooth

that: "Discernment of the meaning of a value of *V* is largely a matter of experience. Its interpretation on functional zoological grounds depends on nonnumerical biological knowledge. We have compared hundreds of *V*'s for linear dimensions of anatomical elements of mammals. As a matter of observation, the great majority of them lie between 4 and 10, and 5 and 6 are good average values. Much lower values usually indicate that the sample was not adequate to show the variability. Much higher values usually indicate that the sample was not pure, for instance, that it included animals of decidedly different ages or of different minor taxonomic divisions."

dentition that probably can serve as a general model for all North American hipparion species. Before these characters are discussed, we will first evaluate the taxonomic utility of the counted and coded characters (see Methods section for a complete listing and description of these).

When this study was originally designed, a suite of coded dental (and cranial) characters was established, i.e., P2PRTSPR, P2PRTSHP, and P2PLSHP. The variables for these are arbitrary coded characters based on qualitative decisions, e.g., rudimentary or absent, present, well developed, etc. During the data-gathering phase, it was realized that decisions had to be made about specimens that exhibited an intermediate character state, e.g., a protocone that was intermediate between being "rounded" or "oval." These decisions ultimately led to a large degree of arbitrariness that rendered these characters of questionable taxonomic significance. During the data analysis stage, it was confirmed that these types of coded characters are not normally distributed and, as such, they cannot be subjected to standard parametric tests or multivariate analyses. However, I do not advocate deletion of these or other coded characters from any subsequent analysis because: (1) they are very valuable reference guides to qualitatively assess certain characters during the writing of descriptions (sometimes many months or even years after the specimen may have been examined in other institutions); and (2) these kinds of characters may prove valuable in other taxonomic studies, e.g., a Wagner Tree analysis.

Many workers have relied heavily upon plication counts in the fossettes of the upper cheek teeth in their taxonomic analyses. If the results of the present analysis are applicable to other studies of hipparions and other hypsodont horses, then plication counts are so variable that they are rendered of little quantitative significance, e.g., they should not be used as characters in statistical analyses. Perhaps the only use of plication counts is in general qualitative statements, such as "*Cormohipparion occidentale* has relatively complicated fossette borders."

For the measured characters in a limited sample in which there are not enough individuals to separate ontogenetic stages, based on the present study, the best characters to assess size are TRL, P2TRNW, and M1TRNW. If there is a large enough sample so that different ontogenetic groupings can be made, then size statistics can be obtained from P2APL, M1APL, and M1ECTL. Protocone size is best assessed by P2PRTL and M1PRTL; however these characters, as well as P2PRTW and M1PRTW, can be significantly affected by ontogeny. P2MSPL and M1MSPL are convenient measures of the length and development of the pli caballin; however these characters were not extensively used below as general size statistics. Based on this study it seems that there is no significant difference between corresponding measured characters of P^2 and M^1, i.e., P2APL versus M1APL.

Crown heights, i.e., P2MSTHT and M1MSTHT are extremely important characters in hypsodont horse taxonomy. However it is clear that these characters are extremely sensitive to ontogenetic variation during wear. Because of these factors, when using P2MSTHT and M1MSTHT, some reference must be made at all times to the particular ontogenetic stage. Furthermore, it must be made clear which tooth is being used for comparison of mesostyle crown heights. In the present study, it was found that for a given species little-worn P2MSTHTs are characteristically smaller than little-worn M1MSTHTs (although not used for comparative purposes here, it was noted that the little-worn mesostyle crown heights of P^4 and M^2 exceed those of either P2MSTHT or M1MSTHT).

In summary, from analyses of a large quarry sample of *Hipparion tehonense* and pooled samples (i.e., from different localities) of *Neohipparion affine, Nannippus minor,* and *Cormohipparion occidentale,* the following generalizations can be made with regard to the upper cheek tooth dentitions: (1) Characters of upper cheek teeth are not sexually dimorphic to any significant degree (although for a possible exception to this hypothesis, see the discussion below for *Cormohipparion occidentale* from Hans Johnson Quarry, north-central Nebraska). (2) Many dental characters are significantly affected by ontogenetic differences. (3) For most measured characters (except P2MSTHT and M1MSTHT), *V* falls

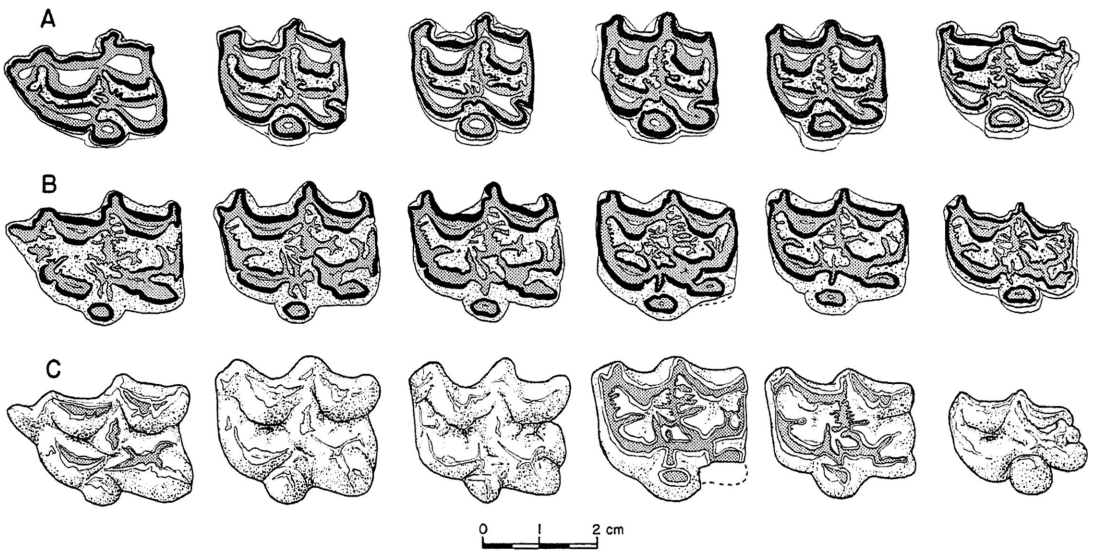


FIG. 18. Cross-sectioned and occlusal views of left upper cheek tooth dentition of *Cormohipparion occidentale,* F:AM 71801, from Xmas Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska. This figure illustrates individual variation of the dental pattern in a single individual. A. Near base of tooth. B. Approximate middle of tooth. C. Occlusal surface of tooth.

within "acceptable" or "good" limits (i.e., *ca.* 4.0 to 10.0). (4) Plication counts are too variable to be used in rigorous comparisons or quantitative analyses. (5) Coded characters are of dubious significance because of their arbitrariness and non-parametric properties. (6) Variability profiles show "drift" (*sensu* Yablokov, 1974) similar to other studies of mammals. Perhaps a final observation should be that dental characters are no "better" than cranial characters; in fact the former seems to be more strongly affected by ontogeny.

SOURCES OF DENTAL VARIATION IN HIPPARION CHEEK TEETH

> Nearly all species of fossil horses have been, and no doubt will continue to be, described with much reliance on the "elusive" traits of enamel pattern, along with size and proportions. If one assumes that the tooth samples . . . represent uniform stages of wear, and consequently similar age groupings, it is necessary to determine the variability of these traits, and, thus establish a standard for comparison in similar studies (Downs, 1961, p. 9).

It has been common for workers to describe new species based on what now seems to be very fragmentary material. In many cases these species were known from one or a few isolated teeth of uncertain provenance with few, if any, topotypes. The characters used to diagnose these horses were oftentimes so minor that by present-day standards they seem absurd. More recent paleontological studies usually account for the variation of dental pattern by describing more complete samples. The present paper is predicated on the assumption that the species-level taxonomy of hipparions can be interpreted by dental *differentia,* and superspecific taxa (genera) are principally based on characters such as the development of the DPOF (see discussion above). Because dental characters are so important, the following discussion attempts to identify the range of qualitative variation in hipparion cheek tooth dental pattern and discuss the significance with respect to equid systematics and, in particular, hipparions. Dental variation recognized here include: (1) intraspecific variation related to differential wear stages in individuals, quarry samples, and separate geographic and temporal sam-

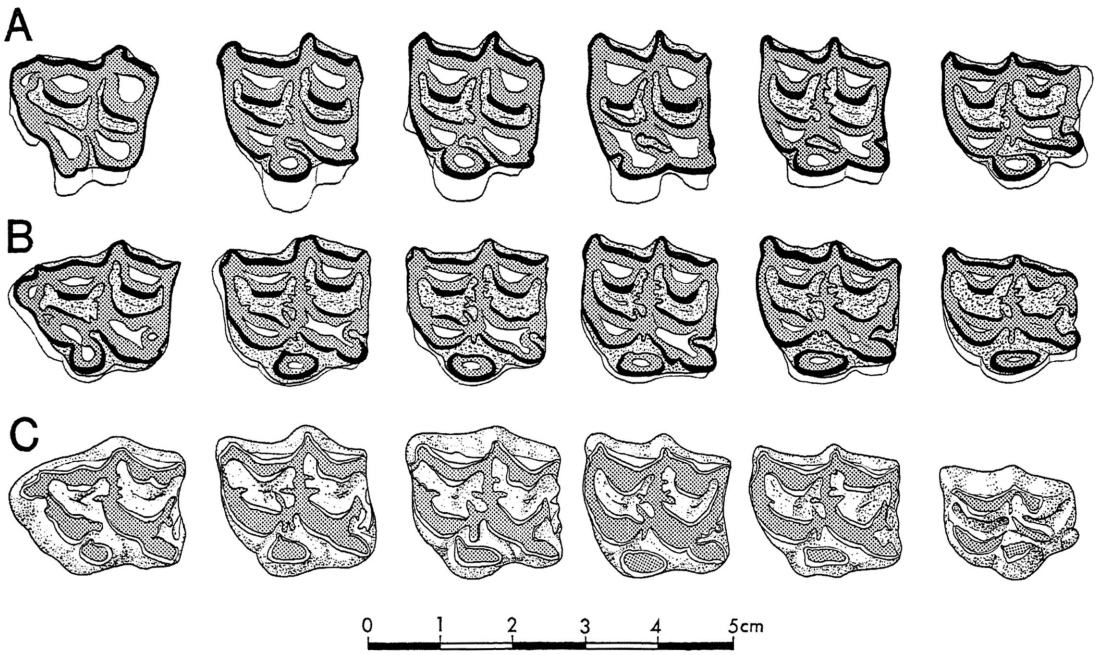


FIG. 19. Cross-sectioned and occlusal views of left upper cheek tooth dentition of *Neohipparion coloradense,* UNSM 42447, from the Crookston Bridge Member, Valentine Formation, Valentinian of Cherry County, north-central Nebraska. This figure illustrates variation of the dental pattern in a single individual. A. Near base of tooth. B. Approximate middle of tooth. C. Occlusal surface of tooth.

ples; and (2) superspecific variation, i.e., either within genera or among genera.

1. INTRASPECIFIC VARIATION: This type of variation is best exemplified in a single tooth or tooth row of an individual, within a quarry sample of a "population," or among geographically and temporally separated "populations" within a species. Figures 18 and 19 represent individual variation in dental pattern within an individual of, respectively, *Cormohipparion occidentale,* F:AM 71801, from the late Clarendonian Xmas Quarry of north-central Nebraska and *Neohipparion coloradense,* UNSM 42447, from locality Cr-117 from the Valentinian of north-central Nebraska. Occlusal cross-sections at the middle and base of the crown represent the dental pattern at, respectively, maturity and old age. Near the middle of each tooth the protocone is characteristically (for hipparions) isolated, the pli caballin is prominent (a single or double loop), the hypoconal groove is shallow, and the plications on the pre- and postfossette borders are relatively complex. In some hipparions, the protocone in P^2 frequently becomes connected to the protoloph in earlier wear stages than in other teeth. In advanced wear stages the protocone frequently becomes connected to the protoloph (e.g., figs. 18A, 19A) in P^2, the pli caballin is poorly developed, the hypoconal groove is shallow or absent, and the plications on the pre- and postfossettes are poorly developed. The vertical variation in dental pattern seen in these cross-sectioned cheek teeth of a single individual is similar to: (1) The ontogenetic variation seen in individuals of different wear stages from what is interpreted to be one species from a single quarry, e.g., *Neohipparion trampasense* from the late Clarendonian Love Bone Bed of north-central Florida (fig. 20). (2) The ontogenetic variation within what is interpreted to be one species from different horizons and localities, e.g., *Cormohipparion sphenodus* (fig. 21).

Anteroposterior variation is also exhibited

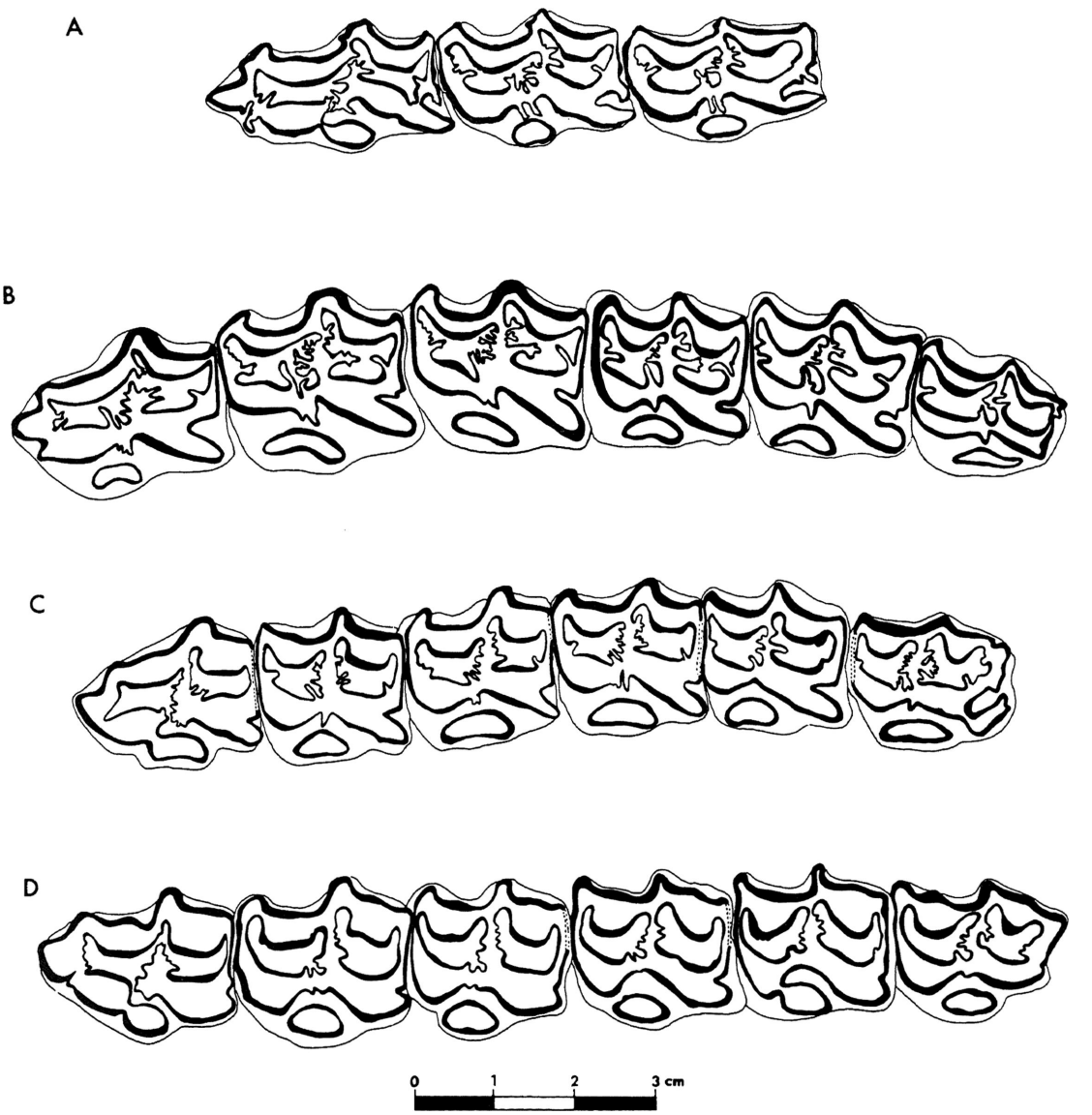


FIG. 20. Variation in the upper cheek teeth of a "population" quarry sample of *Neohipparion trampasense* from the Love Bone Bed, Alachua Formation, late Clarendonian of Alachua County, north-central Florida. A. UF 27990, left dP^2–dP^4. B. UF 27991, left P^2–M^3 in early mature wear. C. UF 27992, left P^2–M^3 in late mature wear. D. UF 27993, left P^2–M^3 in advanced wear.

within a single tooth row at any given wear stage. This is exemplified by the upper cheek tooth rows of *Cormohipparion sphenodus* (fig. 21).

In the upper cheek teeth of any of these examples, the cross-sectional area of the premolars is greater than the molars. The protocones can vary from oval with well-rounded borders to angular in shape as well as being isolated or connected to the protoloph. The pli caballin can vary from a poorly developed single spur to a well-developed elongated double spur. The complexity of enamel plications on the pre- and postfossettes are also

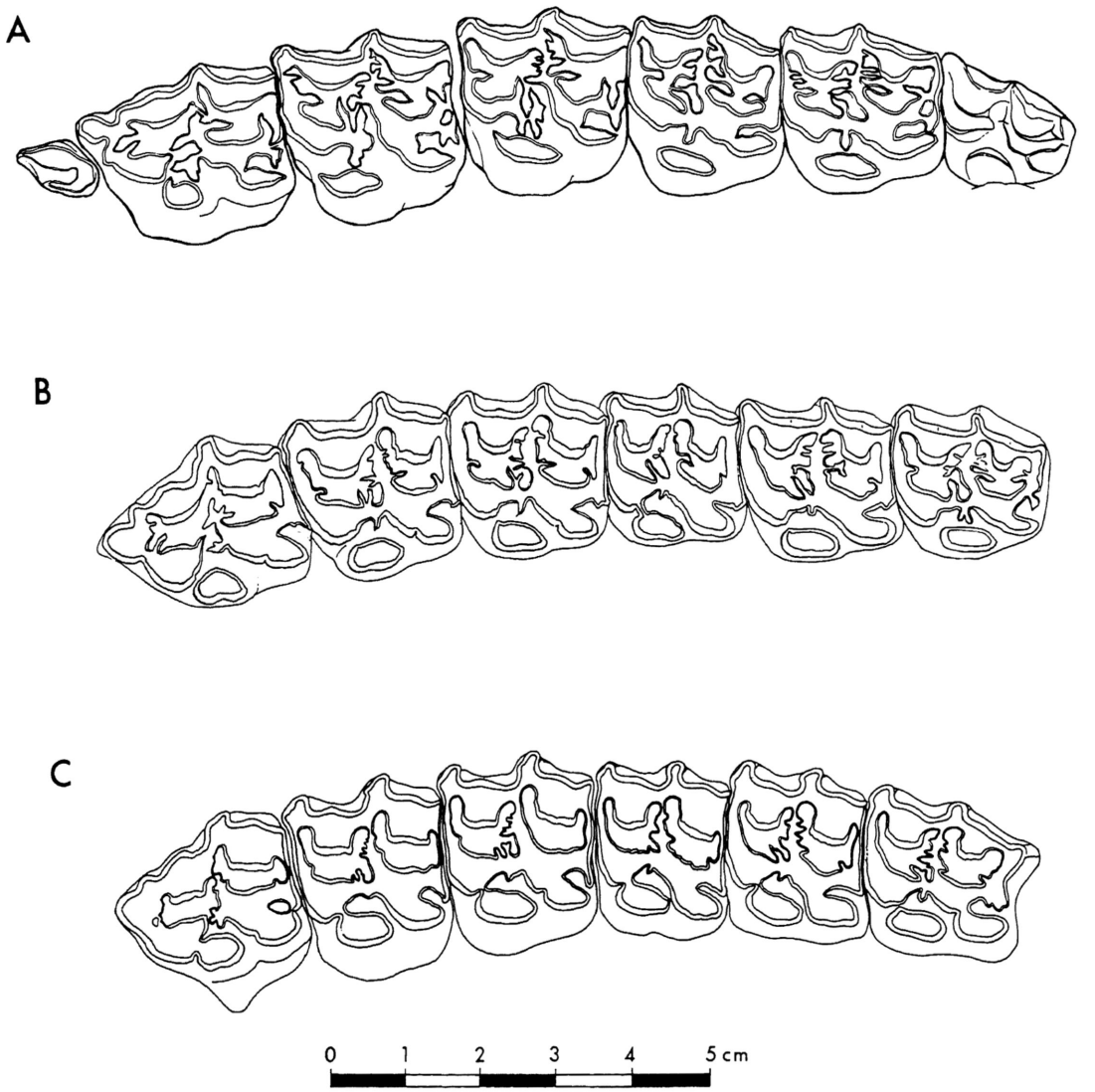


FIG. 21. Ontogenetic and geographic variation in the upper cheek tooth dentition of *Cormohipparion sphenodus*. A. F:AM 71888, right P^1–M^3 (reversed), mature wear stage, from Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, Valentinian of Brown County, north-central Nebraska. B. F:AM 108234, left P^2–M^3, advanced maturity wear stage, from Conical Hill Quarry, Ojo Caliente Sandstone Member of the Tesuque Formation, Santa Fe Group, Clarendonian of Rio Arriba County, north-central New Mexico. C. UNSM 1352 (=AMNH 105229), advanced wear stage, from Railway Quarry "A," Crookston Bridge Member of the Valentine Formation, Valentinian of Cherry County, north-central Nebraska.

variable in number as well as length of elongation.

The cause of ontogenetic variation is a complex integration of factors. In any hipparion sample this variation can result from one or more of the following: (1) The morphogenesis and subsequent ontogenetic wear of the dental pattern varies vertically within the cheek tooth crown. (2) The premolars as a group vary from the molars. This phenom-

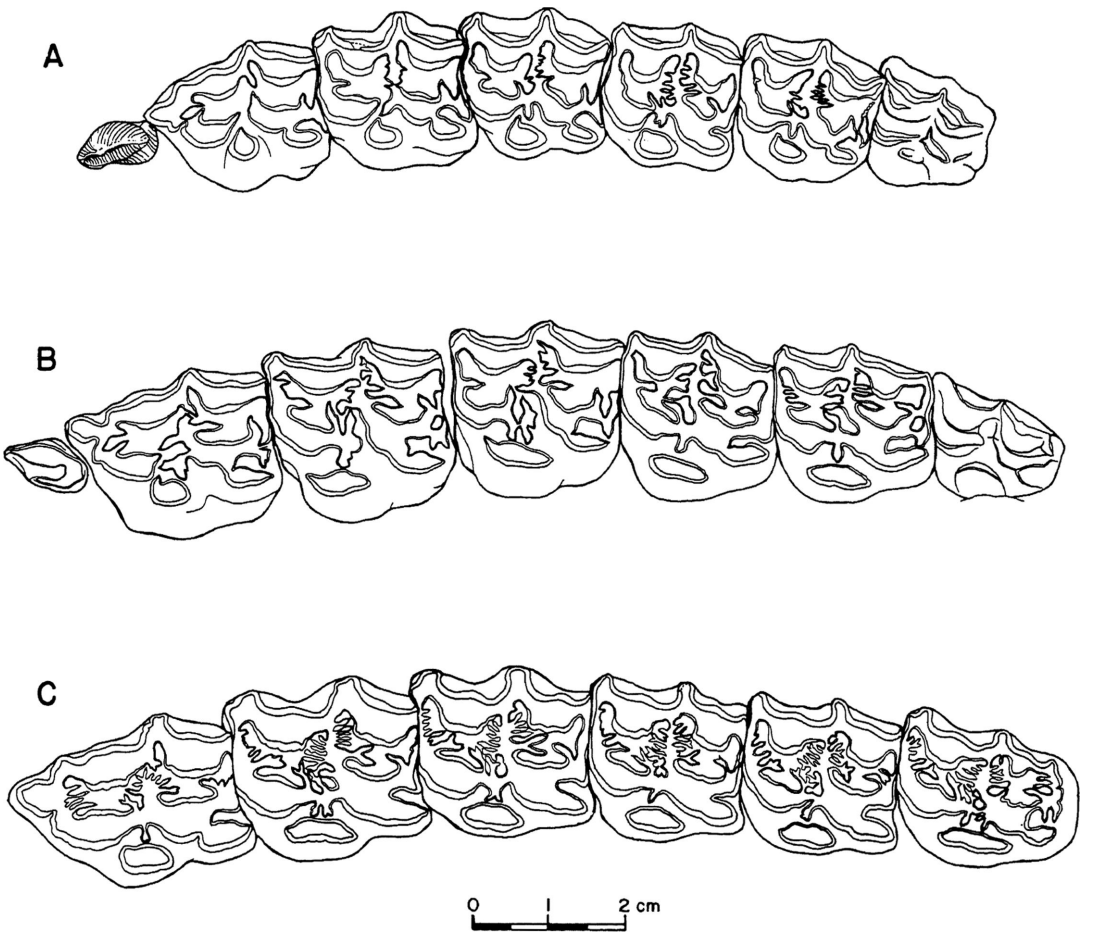


FIG. 22. Variation in upper cheek tooth dental pattern in three species of *Cormohipparion.* A. F:AM 73940, holotype of *C. goorisi,* from Trinity River Pit I, Fleming Formation, early Barstovian, of San Jacinto County, Texas Gulf Coastal Plain. B. F:AM 71888, *C. sphenodus,* from Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, Valentinian of Brown County, north-central Nebraska. C. *C. occidentale,* F:AM 71800, from Xmas Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska.

enon is related to different "morphogenetic pathways" or as Butler (1952) asserted, different embryonic molar fields for the two separate sets of teeth. (3) Within a tooth row, the individual teeth begin to wear sequentially: Both upper and lower M1 and M2 erupt at the time of advanced wear in the deciduous premolars and M3 erupts at about the time of replacement of the deciduous premolars with the permanent premolars. This complex eruption sequence results in a spectrum of dental pattern variability due to differential wear on each of the cheek teeth.

2. SUPERSPECIFIC VARIATION: This category of dental variation can be seen both within species of the same genus, or among the different genera. This distinction may reflect personal taxonomic preference depending upon the group studied. For this category, dental variation is exemplified in upper and lower cheek teeth of temporally and phylogenetically successive species of *Cormohipparion,* i.e., *C. goorisi* from the early Barstovian of Texas, *C. sphenodus* from the Valentinian of Nebraska, and *C. occidentale* from the late Clarendonian of Nebraska (figs.

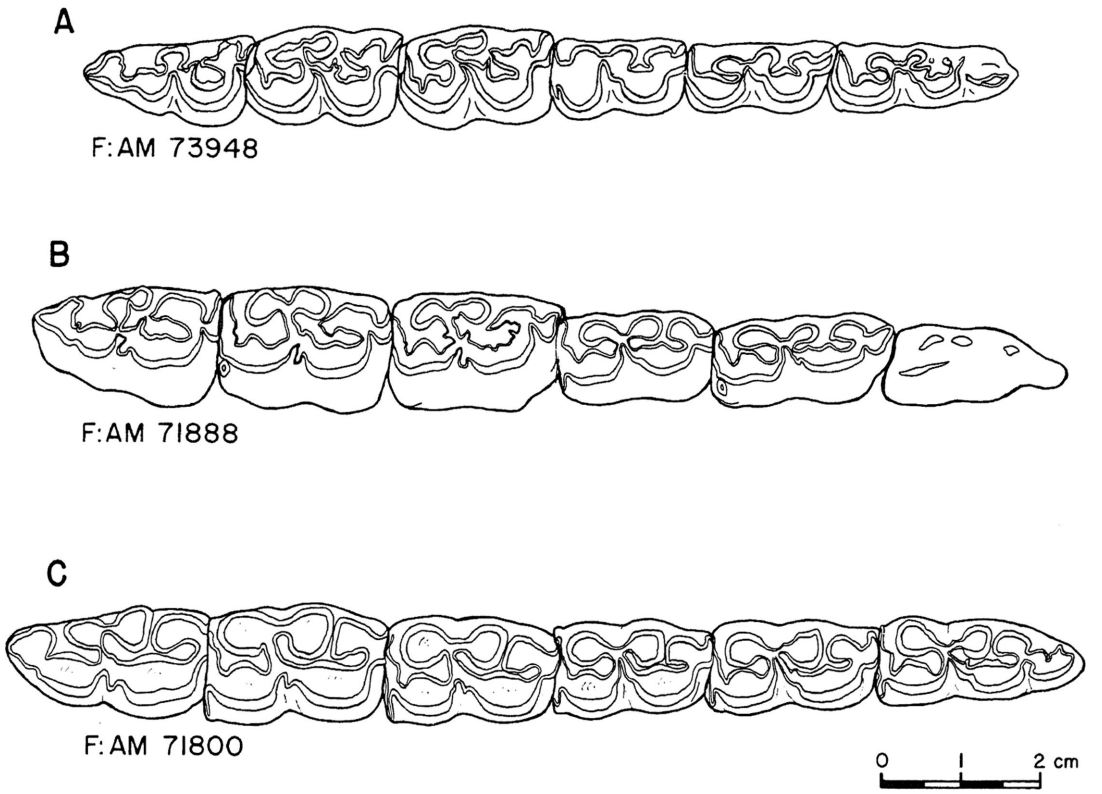


FIG. 23. Variation in lower cheek tooth dentitions in three species of *Cormohipparion*. A. F:AM 73948, *C. goorisi,* from Trinity River Pit I, Fleming Formation, early Barstovian of San Jacinto County, Texas Gulf Coastal Plain. B. F:AM 71888, *C. sphenodus,* from Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, Valentinian of Brown County, north-central Nebraska. C. F:AM 71800, *C. occidentale,* from Xmas Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska.

22, 23). Examples from within or among other hipparion genera could also be added but would not be fundamentally different in demonstrating superspecific variation.

The *Cormohipparion* dentitions illustrated in figures 22 and 23 are all in middle wear stage and show differences in dental pattern among species. There is an increase in crown height and occlusal cross-sectional area. In the upper cheek teeth, the protocone varies from rounded with an anterior spur in *C. goorisi,* to oval and elongated and sometimes with angular borders in *C. sphenodus* and *C. occidentale.* The pre- and postfossette borders are relatively simple in *C. goorisi,* slightly more complicated in *C. sphenodus,* and very complicated in *C. occidentale.* In the lower cheek teeth, the ectoflexid is relatively deep in *C. goorisi* and is relatively more shallow with a concomitant development of the pli caballinid in *C. sphenodus* and *C. occidentale.*

In summary, this section identifies examples of intra- and interspecific variation observed in fossil horses. As a result of this complexity, it is clear that caution must be exhibited when describing horse dentitions, particularly in the case of new taxa. The dental pattern should be examined both quantitatively and qualitatively to identify taxonomically useful characters. All intraspecific descriptions should be based on as large a sample as possible, take into account the range of ontogenetic and, if recognizable, sexual variation,[6] and also, where relevant, make comparisons with superspecific variation.

[6] The statistical study of *Hipparion tehonense* from

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758
ORDER PERISSODACTYLA OWEN, 1848
FAMILY EQUIDAE GRAY, 1821
HIPPARION DE CHRISTOL, 1832

INCLUDED NORTH AMERICAN SPECIES

Hipparion shirleyi, new species.
Hipparion tehonense (Merriam), 1916a.
Hipparion forcei Richey, 1948.

TYPE SPECIMEN AND LOCALITY: The concept of the genus *Hipparion sensu stricto* (see MacFadden, 1980) is based on the species *H. prostylum* de Christol, 1832 from Mt. Léberon, of late Turolian age, in the province of Vaucluse, southern France. There is some confusion about the exact type specimen (see History of Investigations above). De Christol (1832) did not name any species associated with this genus. Gervais (1849) described *Hipparion* material from Vaucluse in southern France. In that report he names the species *H. prostylum, H. mesostylum,* and *H. diplostylum* based on differences in lower dental pattern (from his illustration, it seems that Gervais based the last two of these names on deciduous dentitions). Later Gervais (1859) synonymized all three of these species as *H. prostylum.* In these studies, no holotype was formally designated although through inference from Gervais's descriptions it could be said that the right ramus with P_2–M_2 (1849, pl. 19, fig. 6) of *H. prostylum* should serve as the type. Sondaar (1974) states that the holotype is the fragmentary palate with P^4–M^2 described by Gervais (1849) and probably housed in the Musée Requien, Avignon. In a sense, Sondaar acted as "first revisor" and designated the genoholotype of *Hipparion.* However, it is not clear whether or not this specimen is lost. If so, then a neotype needs to be designated. The question of the genoholotype is presently unresolved.

GENERIC DIAGNOSIS: Based on the configuration of DPOF and other characters, MacFadden (1980, pp. 618–619) presented the following revised generic diagnosis for *Hipparion sensu stricto*:

> Medium-sized, mesocephalic, and moderately hypsodont tridactyl horses. Nasal notch moderately developed and extends posteriorly to a position anterior to, or lying over, P^2. Intraorbital foramen lies over P^3. Preorbital facial fossa lies dorsal to P^3–M^1 on the nasal and maxillary bones well forward of the anterior rim of the orbit. The posterior portion of the fossa is usually developed on the nasal and maxillary bones, anterior to the lacrimal. Anteriorly the fossa is poorly defined and is confluent with the facial region. Posteriorly the fossa is moderately pocketed and has a well-developed and continuous rim. There is no ventral fossa associated with the malar crest as is the case in some other horses. In the upper cheek teeth, the protocones vary from rounded to oval to lenticulate. There is a tendency for the protocone to be connected to the protoloph in earlier wear stages than some other hipparions e.g., *Neohipparion.* The hypoconal groove is moderately developed and is distinct to the base of the tooth. In the lower cheek teeth there is a progressive deepening of the ectoflexids posteriorly. The metaconids and metastylids are widely separated. The parastylid (also termed ectoparastylid or protostylid) is often developed and is either connected to the protoconid or is isolated. In both the upper and lower cheek teeth the enamel plications vary from simple to moderately developed.

Based on the present study, for the North American species of *Hipparion sensu stricto* the mean TRL ranges from 105.35 mm to 133.50 mm; the unworn or little-worn M1MSTHT ranges from *ca.* 25 mm to 50 mm.

Hipparion sensu stricto is set apart from hipparion (and other) horses based on the diagnostic configuration of the DPOF. In addition, *Hipparion sensu stricto* can also be differentiated from species of *Neohipparion, Nannippus,* and *Cormohipparion occidentale* based on a combination of size and dental characters (see table 1 and tables for each

MacAdams Quarry did not indicate any significant difference in cheek tooth dentition between the sexes and this result is probably applicable to many other hipparion samples or species. For a possible exception, see discussion (in Systematic Paleontology) for *Cormohipparion occidentale* where there may be sexual dimorphism in the number of plications in the upper cheek tooth fossettes.

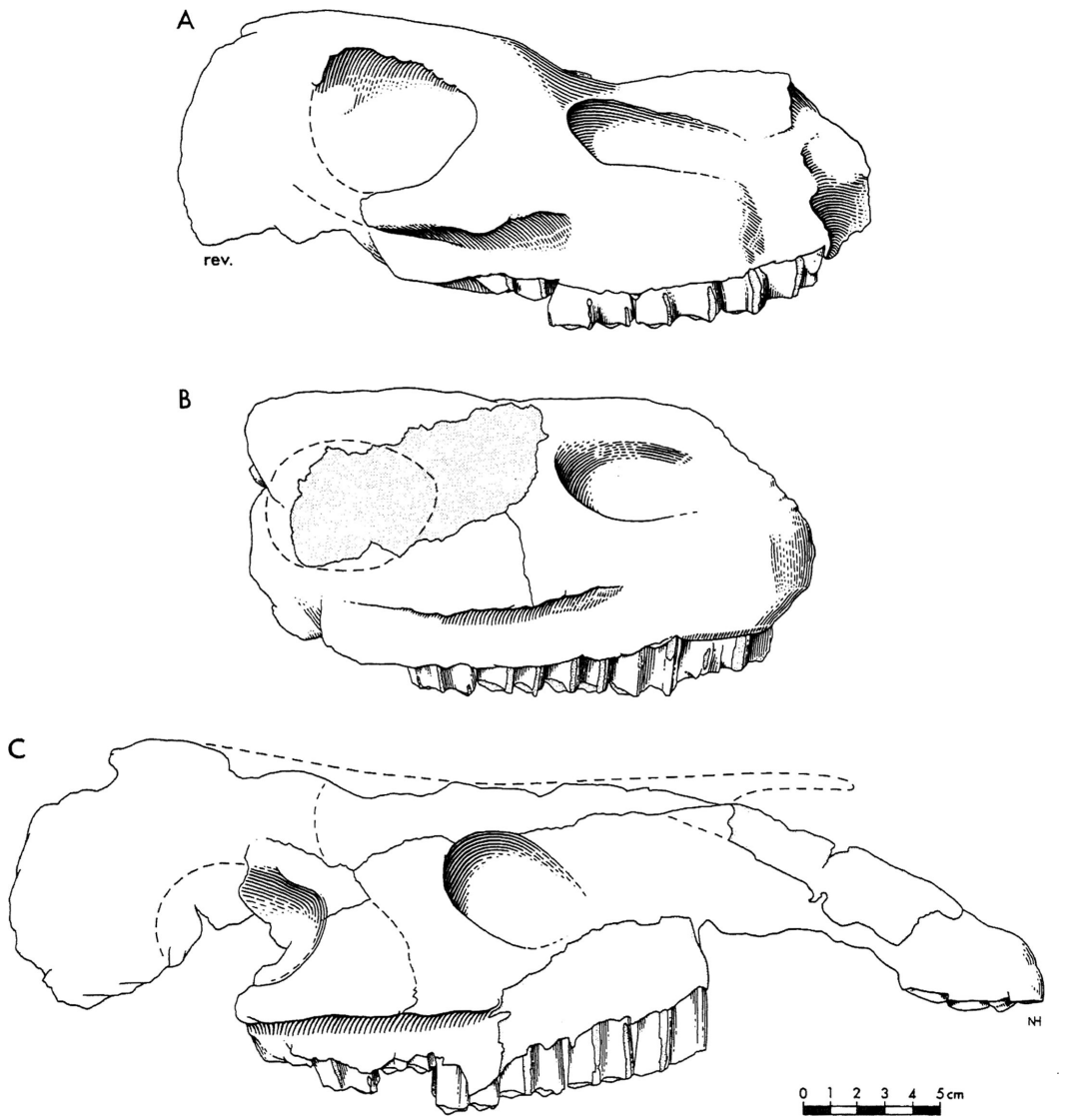


FIG. 24. Skulls of *Hipparion prostylum* from the late Turolian of Mt. Léberon, France, showing details of the preorbital region. A. NMNHP "unnumbered." B. NMNHP Lub. 156. C. BMNH M26617.

species below). (*C. goorisi* and *C. sphenodus* are not easily differentiated from *Hipparion sensu stricto* on characters other than the configuration of the DPOF.) The North American species of *Hipparion sensu stricto* do not attain the very large size exhibited in *C. occidentale* or advanced *Neohipparion.* All *Hipparion sensu stricto* differ from *Neohipparion* in dental characters. In contrast to *Neohipparion, Hipparion sensu stricto* exhibits smaller protocones, deeper ectoflexids, and well-developed pli caballinids. All *Hipparion sensu stricto* usually differ from *Nannippus* in greater size and less hypsodont dentitions. In contrast to *Nannippus,* all species of *Hipparion sensu stricto* usually have a more complex enamel pattern in the upper cheek teeth; in addition, the lower cheek teeth of

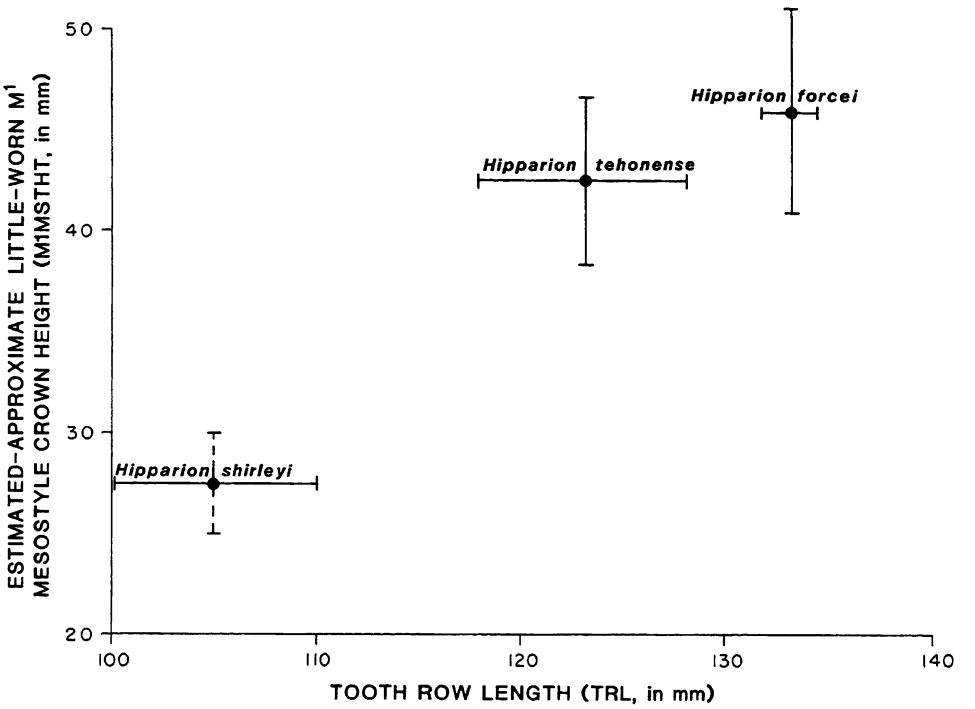


FIG. 25. Bivariate plot of TRL versus estimated-approximate little-worn M1MSTHT for three recognized species of North American *Hipparion sensu stricto.* Plot gives general comparison of size versus crown height. For TRL, one standard deviation (*s*) is plotted on both sides of the mean. Values for M1MSTHT are taken from available specimens in early wear (i.e., juveniles). When only small samples are available, mean values and standard deviations are estimated (the latter assuming a *V* of less than 10 and indicated by dashed lines). As discussed in text, M1MSTHT is greatly affected by wear and therefore can only be considered approximate. Data used to construct this graph are tabulated for each species in relevant sections below.

Hipparion sensu stricto usually exhibit well-developed protostylids and relatively deep ectoflexids in both the premolars and molars. In contrast to *C. occidentale* and most species of *Neohipparion,* all species of *Hipparion sensu stricto* have less elongated protocones.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Based on the revised interpretation of *Hipparion sensu stricto,* MacFadden (1980) asserted that this genus was more common in North America than had been previously recognized (e.g., Gidley, 1907; Osborn, 1918; Stirton, 1940). In the present report, *Hipparion sensu stricto* is recognized from faunas of late Barstovian age from the Texas Gulf Coastal Plain, numerous sites of Valentinian and Clarendonian age in the midcontinent (Nebraska, Colorado, and South Dakota), the Great Basin (Nevada), and California, and last occurs in the early Hemphillian faunas of the Great Plains. In Neogene sediments of the Old World this genus was widespread during the Turolian to early Villafranchian (see discussion below).

DISCUSSION: An important consideration for hipparion systematics is what type of facial morphology is represented in the topotypic material of *Hipparion prostylum* from Mt. Léberon. Based on examinations of the Paris (NMNHP) and London (BMNH) collections from this locality, MacFadden (1980) described the configuration of the DPOF for *H. prostylum* (fig. 24). The genus *Hipparion sensu stricto,* as perceived by MacFadden (1980), is characterized by a DPOF that anteriorly is poorly defined and posteriorly is moderately pocketed with a well developed and continuous rim. This is also similar in

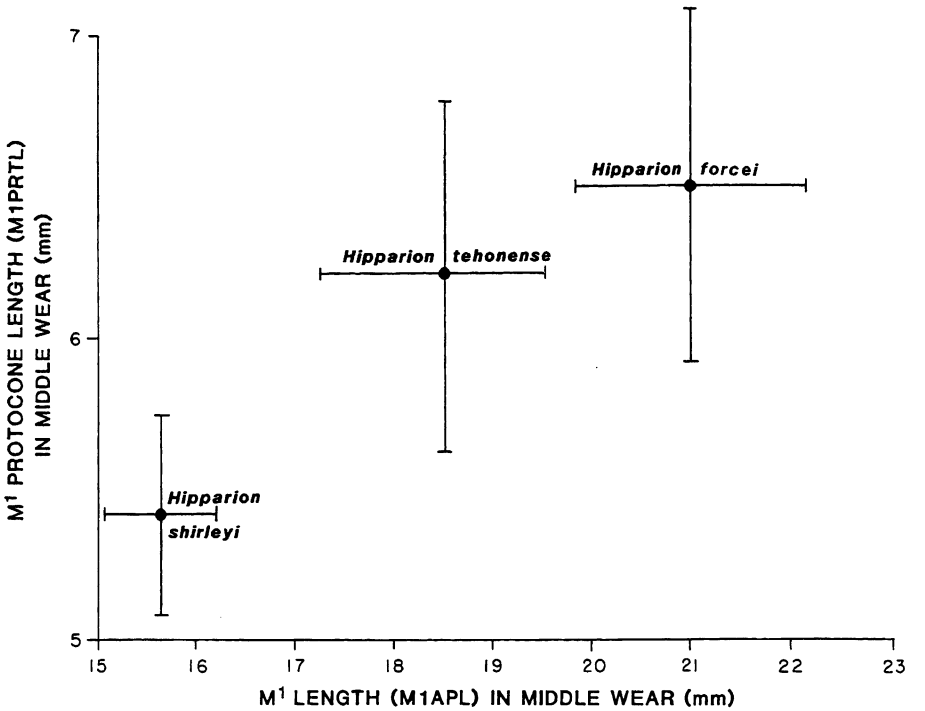


FIG. 26. Bivariate plot of M1APL versus M1PRTL for each of three recognized species of North American *Hipparion sensu stricto.* Plot gives an indication of relative increase in protocone size. Because of significant ontogenetic differences in these characters, only "middle age" (=early maturity and advanced maturity combined) specimens are used here. For each value, one standard deviation (*s*) is plotted on both sides of the mean. Data used to construct this graph are tabulated for each species in relevant sections below.

concept to "Group 3" hipparions of Woodburne and Bernor (1980).

The North American species of *Hipparion sensu stricto* form a monophyletic genus separate from other hipparions. For the three species of *Hipparion sensu stricto,* selected measured characters that give an indication of size versus hypsodonty (TRL vs. M1MSTHT) and increase in relative size of the protocone (M1APL vs. M1PRTL) are presented in figures 25 and 26. The data used to construct these graphs are tabulated for each species below. The important character polarities and distributions are presented in figure 27 and table 7. These characters are used below to assess phylogenetic interrelationships of *H. shirleyi, H. tehonense,* and *H. forcei* and to indicate the possible phylogenetic position of Old World *Hipparion sensu stricto.*

Earlier workers such as Gidley (1907), Osborn (1918), and Stirton (1939, 1940) state that *Hipparion* was rare in the New World and it was represented by a few species from California and Florida. Their interpretations were based on the fact that these hipparions were purported to have relatively small protocones like many of the Old World species of *Hipparion.* With the revised concept of *Hipparion* (MacFadden, 1980) it appears that this genus was widespread in North America. It is also conceivable that other occurrences of New World *Hipparion sensu stricto* will be recorded in the future as additional well-preserved cranial and dental material is discovered.

There was a generic-level continuity of *Hipparion sensu stricto* throughout much of North America and the Old World during the Clarendonian and early Hemphillian and

TABLE 7

Selected Important Morphological Character Distributions and Temporal and Spatial Data for the Three North American Species of *Hipparion sensu stricto* and the Merychippines (outgroup)[a]

Morphocline Character[b] (see fig. 27)	Merychippines[c] (outgroup)	*Hipparion shirleyi*, new species	*Hipparion tehonense*	*Hipparion forcei*
1. Size (relative to all hipparions)	Small to medium	Small	Medium	Medium
2. Mean upper cheek tooth row length P^2–M^3 (TRL)	—	105.35 mm	123.38 mm	133.50 mm
3. Hypsodonty	Brachydont to mesodont	Mesodont	Hypsodont	Hypsodont
4. Estimated-approximate M^1 crown height (M1MSTHT) for little-worn specimens	—	25–30 mm	40–45 mm	42–50 mm
5. Dorsal preorbital fossa (DPOF)	Highly variable in different species, usually present	Présent and diagnostic of genus *Hipparion sensu stricto* (see table 1)	Present and diagnostic of genus *Hipparion sensu stricto* (see table 1)	Present and diagnostic of genus *Hipparion sensu stricto* (see table 1)
6. Protocone size and shape	Small and rounded to oval, usually connected to protoloph	Small and rounded to oval	Usually oval, rounded borders	Usually oval, rounded borders
7. Anterior spur of protocone	Relatively well developed	Relatively well developed	Usually poorly developed, rudimentary or absent	Usually poorly developed, rudimentary or absent
DISTRIBUTIONAL DATA[d]				
Known biochronological range (teilchron)	—	Barstovian	Clarendonian	Late Clarendonian to early Hemphillian
Known biogeographic occurrence(s)	—	Texas Gulf Coastal Plain	California, Nevada, Great Plains, Texas Panhandle	California, Nevada, Great Plains

[a] This table accompanies figure 27 (numbered characters).

[b] Descriptions of dental characters are representative of early and medial wear stages.

[c] Included as outgroup comparison for qualitative characters only. Quantitative characters (measurements) and temporal and spatial data are variable depending upon species and therefore not available. See discussion of the problems associated with this polyphyletic operational taxonomic unit in introductory sections.

[d] These data are not used in figure 27 and therefore they are not numbered sequentially as are the morphocline characters.

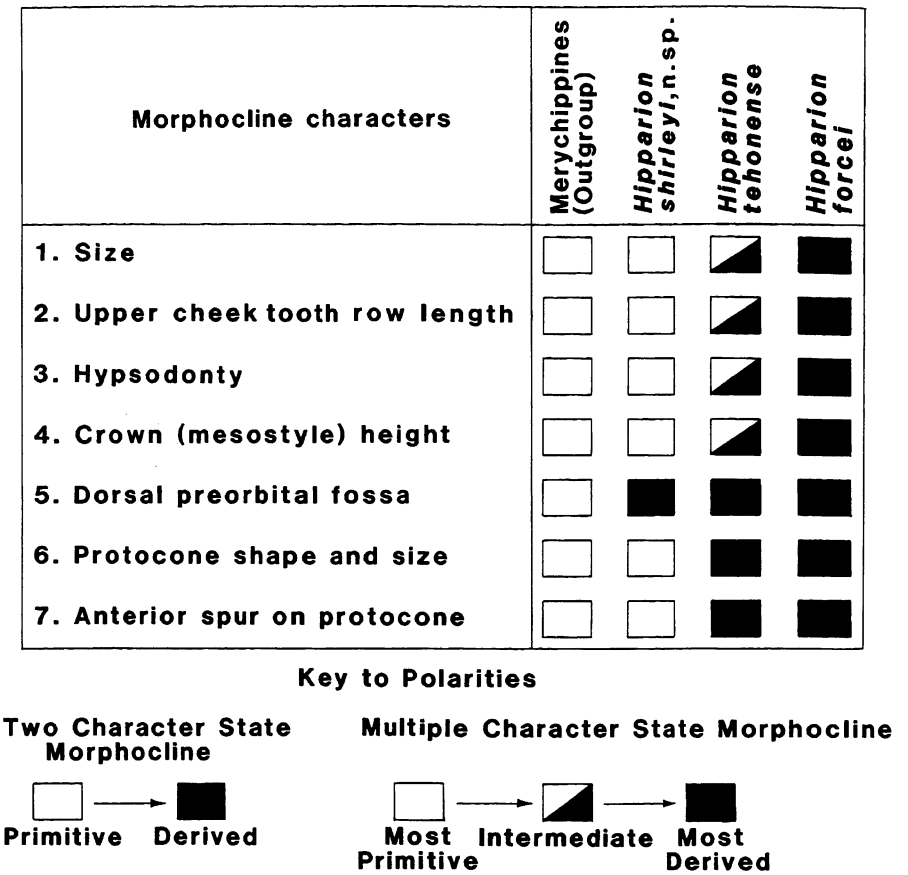


FIG. 27. Graphical representation of selected important character distributions and morphocline polarities in the four North American species of *Hipparion sensu stricto* and merychippines (outgroup). Numbered characters correspond to those in table 7. Also see text for discussion.

roughly equivalent Turolian ages (late Miocene). Woodburne and Bernor (1980) have examined collections from numerous Old World localities and they conclude that, so far as is known, *Hipparion sensu stricto* was apparently not represented in the Vallesian. The ramifications of these systematic interpretations for the concept of the "Hipparion Datum" are discussed below.

Hipparion shirleyi, new species
Figures 25–31, 146, 150; Tables 2, 7–11

PREVIOUS REFERENCES

"ancestral Hipparions" Quinn, 1952.
Merychippus? Quinn, 1955.
Probably, in part, *Merychippus* sp. near *Hipparion* Forstén, 1975.

TYPE SPECIMEN AND LOCALITY: F:AM 73950, skull, mandible, and nearly complete associated postcranial skeleton (see discussion below) from Wright Farm, 8 miles south of Livingston, Polk County, Texas Gulf Coastal Plain, Fleming Formation, Barstovian (medial Miocene) age (figs. 28, 29, and possibly 30, see below).

ETYMOLOGY: Named in honor of Shirley M. Skinner, former Scientific Assistant in the Frick Laboratory at the American Museum of Natural History. This is in recognition of her contributions to the study of Cenozoic mammals of North America.

DIAGNOSIS: Small hipparion; size similar to, or slightly smaller than, *Cormohipparion goorisi* from the same region and smaller than

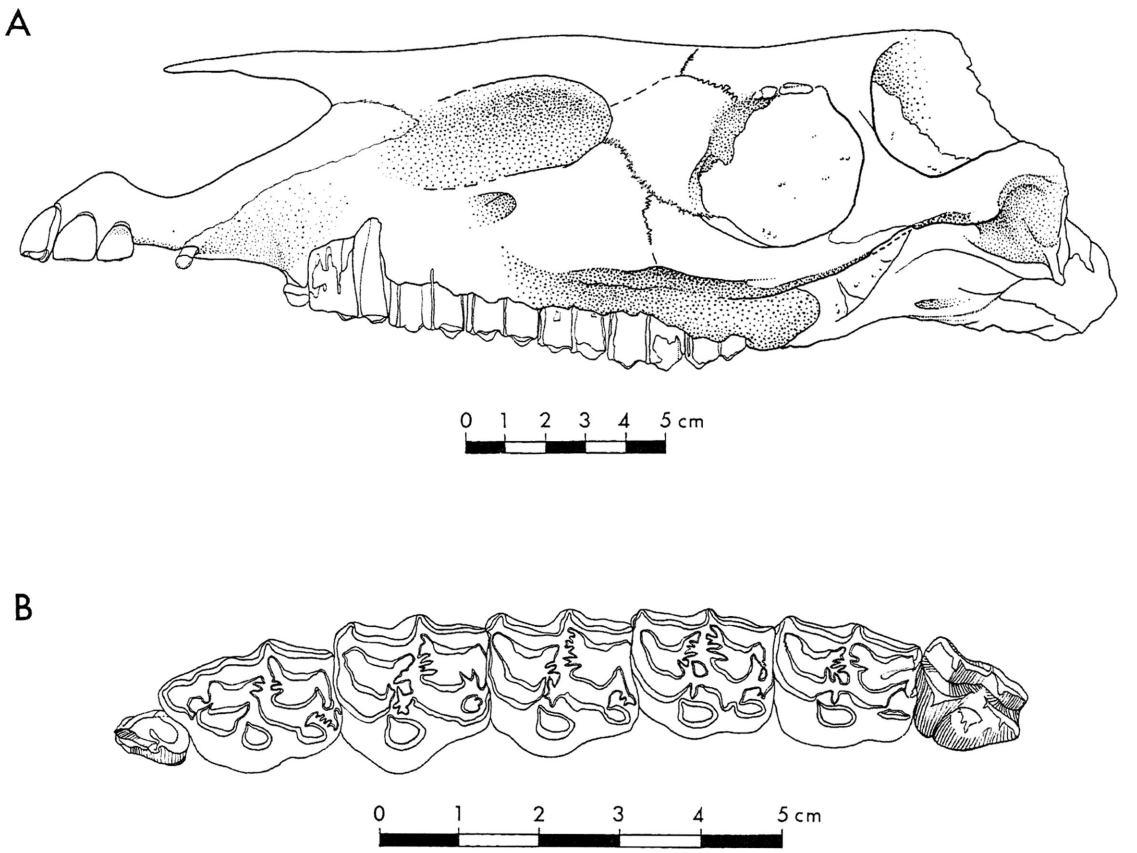


FIG. 28. *Hipparion shirleyi,* new species, F:AM 73950, holotype, female in mature wear stage from Wright Farm, Fleming Formation, late Barstovian of Polk County, Texas Gulf Coastal Plain. A. Left lateral view of skull with some restoration due to crushing. B. Occlusal view of left upper cheek teeth, P^1–M^3. Also see figure 29.

Hipparion tehonense from the Texas Panhandle. Cheek tooth row and occlusal cross-sectional area significantly smaller than *Hipparion tehonense.* Mean TRL 105.35 mm. DPOF characteristic of *Hipparion sensu stricto*: Posteriorly, fossa is moderately deep dorsoventrally with well-defined posterior rim. Wide PRB, i.e., posterior margin of the fossa is far anterior to the orbital margin in contrast to *Neohipparion* and *Cormohipparion.* Lacrimal bone does not touch posterior margin of the fossa. In contrast to *Cormohipparion,* anterior margin of DPOF poorly defined and blends into anterior region of the face; posterior pocket very poorly developed or absent. No malar fossa. Relatively deep nasal notch.

Teeth mesodont, i.e., intermediate between brachydont and hypsodont. Unworn or little-worn M1MSTHT *ca.* 25–30 mm. Protocone small, rounded, with a prominent anterior spur. Fossette borders moderately plicated. Deep hypoconal groove with constricted connection between hypocone and metaloph. Mandible shallow. Ectoflexids deep. Protostylids vary in development from prominent to absent. Tridactyl manus and pes.

Hipparion shirleyi differs from merychippines and other hipparion genera in the distinctive development of the DPOF. *Hipparion shirleyi* is smaller, shorter crowned, has a relatively smaller protocone, and a more persistent anterior protoconal spur than either

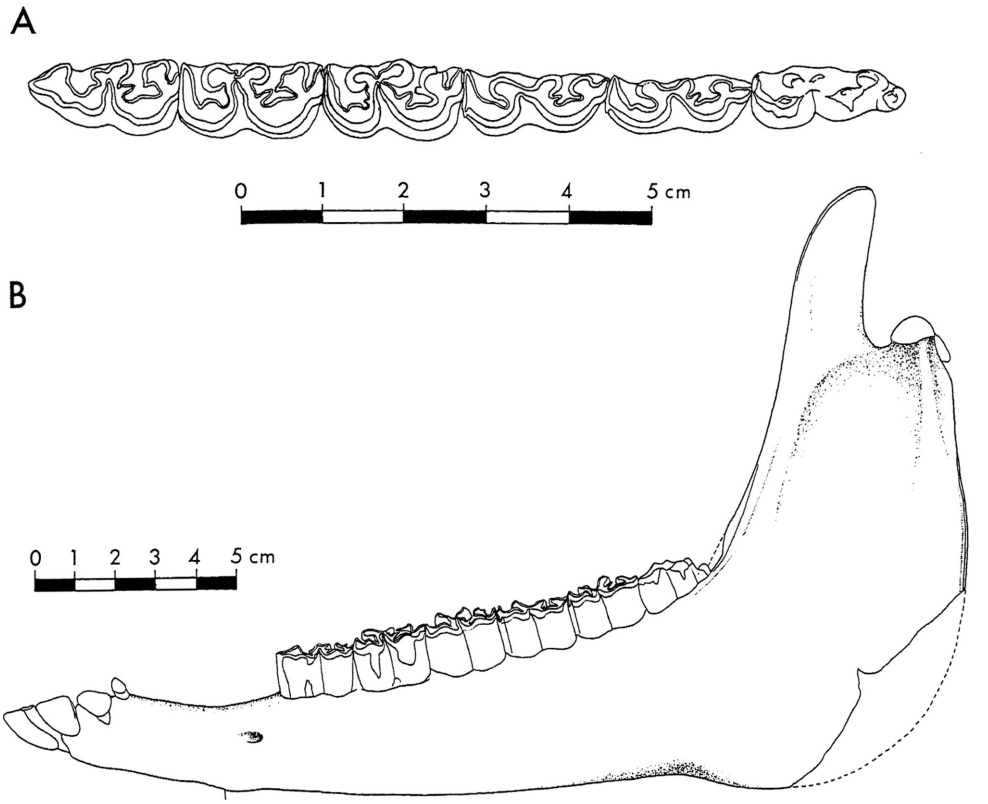


FIG. 29. *Hipparion shirleyi,* new species, F:AM 73950, holotype, female, in mature wear stage from Wright Farm, Fleming Formation, late Barstovian of Polk County, Texas Gulf Coastal Plain. A. Occlusal view of left lower cheek teeth, P_2–M_3. B. Left lateral view of mandible. Also see figure 28.

H. tehonense or *H. forcei. Hipparion shirleyi* also seems to have a slight posterior pocket of the DPOF that is not seen in either *H. tehonense* or *H. forcei.*

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Based on specimens in the Frick collection, *Hipparion shirleyi* is recognized from two counties within the Fleming Formation of the Texas Gulf Coastal Plain: (1) Wright Farm (Frick field notes indicate that the Smith and Winham localities are from the same general area), which is the type locality (see above), 8 miles south of Livingston, Polk County, collected by C. Riley and associates of the Frick Laboratory in 1938; and (2) McMurry pits 1 and 2, 2 miles north of Cold Springs and ½ mile northeast of Maxie Hill, from east side of wash, San Jacinto County, collected by N. Z. Ward and associates of the Frick Laboratory during the 1950s. These occurrences are of medial Miocene, or late Barstovian age, equivalent to the better-known Cold Spring Fauna of this region (see Hesse, 1943; Quinn, 1955; Patton, 1969; Forstén, 1975). Based on faunal correlations to other sites in North America with associated radiometric control, these Texas Gulf Coastal occurrences are about 13–14 myBP (Tedford et al., in press).

REFERRED MATERIAL: The following specimens are referred to *Hipparion shirleyi* because of the presence of associated skulls and dentitions that demonstrate diagnostic characters of this species. Other less complete specimens from the same localities may also be referable to *H. shirleyi,* however, it cannot be positively determined that they do not represent another morphologically similar equid. In addition, it is also probable that *H. shirleyi* occurs at other localities within the

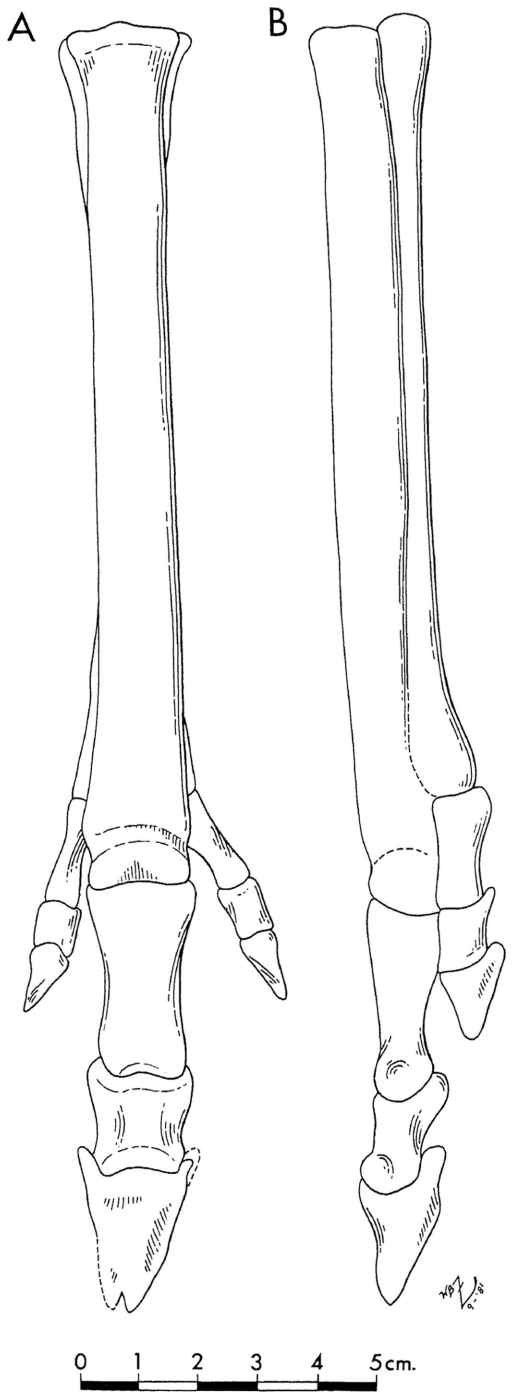


FIG. 30. Right lower pes of *Hipparion shirleyi*, new species, from the type locality. This specimen is either from the holotype, F:AM 93950 (figs. 28, 29), or the topotype, F:AM 99384. Because both specimens represent two disarticulated individuals collected from the same block, it is not possible to determine which postcranial elements belong with which skulls. A. Dorsal view. B. Lateral view.

Texas Gulf Coastal Plain and beyond this region; however, with isolated teeth or incomplete dentitions, it is not possible to confidently refer other samples to this species.

Wright Farm (type locality): F:AM 73950, holotype (see above), female with dentition in mature wear stage; F:AM 99384, female skull, mandible, and partial associated skeleton, advanced wear stage. These two specimens were collected in the same block with two partial associated skeletons. The two pairs of lower jaws can be easily matched to the two skulls because of extreme differences in dental wear stages of the two individuals. Although it is not certain from the field sketches exactly which skull belongs with which of the skeletal parts, it is clear that the block represents two individuals of the same species in only slightly disassociated death-poses (with flexed articulated limbs).

McMurry Pit 1: F:AM 73951, virtually complete crushed skull with right I^3, P^2–M^3, left P^1–M^3; F:AM 99386, male, skull fragment with right and left C, P^1–M^3; F:AM 99391, maxillary fragment with right M^1–M^3; F:AM 99392, maxillary fragment with left M^1–M^3; F:AM 99394, maxillary fragment with left P^4–M^3; F:AM 99395, maxillary fragment with right M^1 and M^2; F:AM 99385, mandible with right and left P_2–M_3; F:AM 99393, mandible with right and left P_3–M_3; F:AM 99390, left ramus with symphysial region, left P_2–M_3; F:AM 99388, left ramus with P_2–M_3; F:AM 99389, jaw fragment with P_3–M_3.

McMurry Pit 2: F:AM 99382, palate with right and left P_2–M_3; F:AM 99383, left P_4–M_3.

DESCRIPTION: *Hipparion shirleyi* is a small and mesodont hipparion (tables 7–10). The skull is generally similar in size to *Cormohipparion goorisi* from the Texas Gulf Coastal Plain (MacFadden and Skinner, 1981) and significantly smaller than *Hipparion tehonense* from the Texas Panhandle (*sensu*

TABLE 8
Selected Upper Dental Measurements and Univariate Statistics for *Hipparion shirleyi*, New Species[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	4	20.83	1.24	5.95	19.0–21.6	2	20.30	1.84	9.06	19.0–21.6
P2TRNW	4	15.45	0.55	3.56	14.9–16.1	2	15.90	0.28	1.76	15.7–16.1
P2PRTL	4	4.30	0.48	11.23	3.6–4.7	2	4.60	0.14	3.04	4.5–4.7
P2PRTW	4	3.63	0.37	10.41	3.1–4.0	2	3.85	0.21	5.45	3.7–4.0
P2TOTPLI	4	7.25	2.50	34.48	6–11	2	2.00	0	—	—
M1APL	7	16.32	1.27	7.82	14.6–18.5	5	15.66	0.60	3.83	14.6–16.1
M1ECTL	7	16.83	1.13	6.72	14.9–18.3	5	16.42	1.04	6.33	14.9–17.4
M1TRNW	7	16.59	1.12	6.75	15.1–17.9	5	16.60	1.05	6.32	15.1–17.9
M1PRTL	7	5.30	0.46	8.58	4.8–5.9	5	5.38	0.52	9.66	4.8–5.9
M1PRTW	7	3.26	0.26	8.10	2.9–3.6	5	3.34	0.27	8.08	2.9–3.6
M1TOTPLI	7	9.43	2.64	27.97	6–13	5	8.60	2.70	31.39	6–13
TRL	4	105.35	5.15	4.89	97.8–109.3	2	102.20	6.22	6.09	97.8–106.6

[a] Abbreviations are presented on pp. 21 and 22; see text for specimens examined.
[b] Juvenile and old wear (age) classes removed.

MacFadden, 1980). In length of the cheek tooth row, *H. shirleyi* is smaller than both *C. goorisi* and *H. tehonense*. The nasal notch is retracted to a position that lies dorsal to P^1 (figs. 28, 31) and is deep relative to some other hipparions, e.g., *C. goorisi* in which the nasal notch lies above the canine. The premaxillary bone extends posteriorly to the anterior margin of the DPOF. The precanine diastema is shorter than the postcanine diastema. The infraorbital foramen lies dorsal to either P^3 or P^4. There is a robust malar crest. The buccinator fossa extends posterodorsally to the anterior margin of the DPOF.

The DPOF is diagnostic of the genus *Hipparion*. There is a relatively wide PRB (table

TABLE 9
Crown (Mesostyle) Height (from Occlusal Surface to Base of Enamel Crown in Millimeters) for Selected Upper Cheek Teeth[a] of *Hipparion shirleyi*, New Species, from the Texas Gulf Coastal Plain

Specimen	Tooth	Height
F:AM 73950, holotype	Right M^3	>22.7
	Left P^2	19.0
F:AM 99384[b]	Right P^2	9.7
	Left P^2	9.1
F:AM 99386	Right P^2	24.6[c]
	Right M^3	>27.1
	Left M^3	29.2
F:AM 99394[b]	Left M^1	11.5[c]
F AM 99392	Left M^3	>12.9
F:AM 99391	Left M^1	13.0[c]
F:AM 99395	Right M^2	18.7[c]

[a] These teeth were selected because the roots were exposed in the maxilla.
[b] Very worn dentition of old individual.
[c] Measurement approximate.

TABLE 10
Measurements (in Millimeters) of Dorsal Preorbital Fossa of *Hipparion shirleyi*, New Species, from the Texas Gulf Coastal Plain[a]

Specimen	Anterior-posterior Length (APLDPOF)	Dorso-ventral Depth (DVDPTH)	Preorbital Bar Length (PRB)
F:AM 73950, holotype			
Right side	Crushed	Crushed	35.4
Left side	58.1	30.8	32.4
F:AM 99384			
Right side	43.0	24.6	25.6
Left side	37.6	26.5	23.1
F:AM 75951			
Right side	—	—	—
Left side	52.8	Crushed	>21.5[b]

[a] Due to crushing and reconstruction of specimens, all measurements are probably precise to ±5 mm.
[b] Measurements approximate due to breakage or estimation of limit of structure (e.g., the rim or anterior extent of dorsal preorbital fossa).

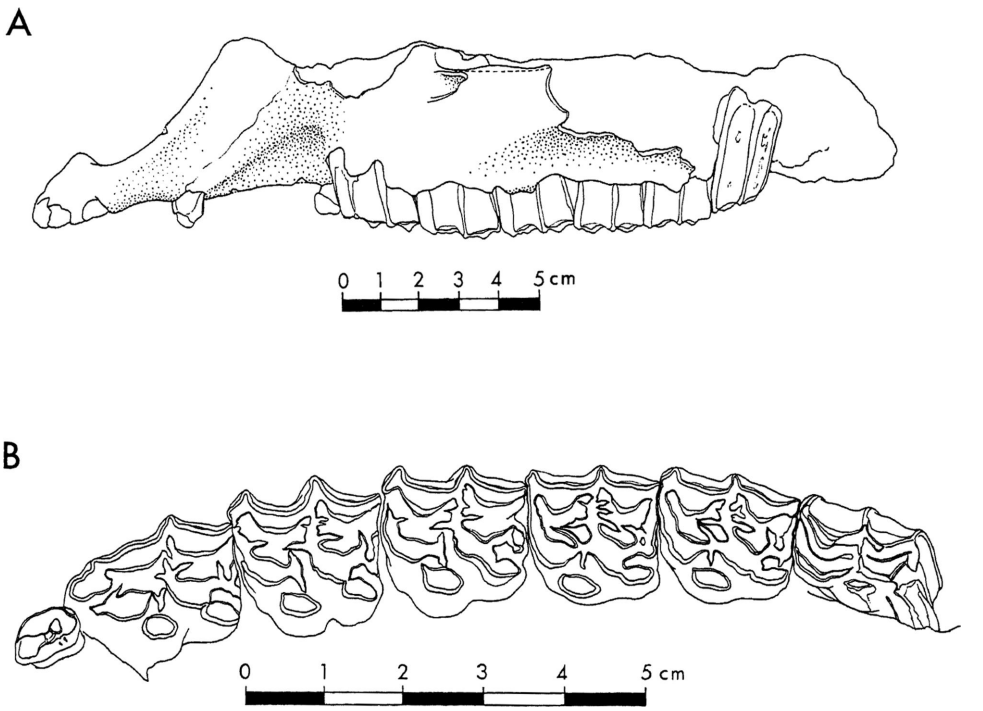


FIG. 31. *Hipparion shirleyi,* new species, F:AM 99386, male in mature wear stage, from McMurry Pit 1, Fleming Formation, late Barstovian of San Jacinto County, Texas Gulf Coastal Plain. A. Left lateral view of symphysial and maxillary regions. B. Occlusal view of left upper cheek teeth, P^1–M^3.

10) in contrast to *C. goorisi.* The posterior portion of this fossa is shallow relative to the deep pocket seen in *C. goorisi.* However, this pocket is anteriorposteriorly deeper in *H. shirleyi* than in *H. tehonense.* The posterior, median-dorsal, and median-ventral rims of the fossa are well defined. The anterior part of the fossa is poorly defined with no rim. It smooths out onto the cheek into the posterodorsal part of the buccinator fossa. The lacrimal bone is rhomboidal in outline. It extends from the anterodorsal margin of the orbit to the posterior portion of the DPOF. Ventrally, the maxillary-jugal suture extends from the malar crest to the lacrimal bone. Dorsally, the nasofrontal suture connects with the lacrimal bone approximately midway between the DPOF and the orbital margin.

The upper incisors have cement-filled infundibula (cups) not recessed below the occulusal surface. In occlusal view, the incisor series is rounded rather than linear as seen in some other equids (e.g., *Calippus*). The canines show marked sexual dimorphism as is characteristic of most fossil equids. The dP^1 is large, retained throughout ontogeny, and comes into wear in mature individuals.

The morphology of the cheek teeth is principally described here as exhibited in middle wear stage (figs. 28, 29, 31). The absolute crown height of the cheek teeth (table 5) is similar to, or perhaps slightly greater than,[7] *C. goorisi* and smaller than *Hipparion tehonense.* The P^2 has an anteriorly placed and moderately developed anterostyle. The protocone is small, oval, and has a well-developed anterior spur. The protocone remains isolated from the protoloph until late wear stages. The hypocone is oval with a constriction at the connection to the metaloph. A deep hypoconal groove persists until late wear stages. The anterior border of the prefossette

[7] Because of the small sample sizes for these two species, a definite distinction between crown heights cannot be made.

TABLE 11
Measurements (in Millimeters) of Metapodials of *Hipparion shirleyi*, New Species, F:AM 93950 (Holotype) and F:AM 99384, from Type Locality, Wright Farm, Texas Gulf Coastal Plain[a]

Element	Length	Width Distal Trochlea
Right MT III[b]	167.8	18.5
Left MT III	166.3	18.8
Right MT III	165.8	18.2
Left MC III	148.0	20.2
Left MC III	147.2	21.6

[a] Specimen numbers cannot be determined because of dissociation of skeletal parts.
[b] Illustrated in figure 30.

(pli protoloph) is usually simple with no plications. A pli protoconule usually is developed on the posterointernal margin of the prefossette. Multiple pli postfossettes are developed on the anterior margin of the postfossettes. The pli hypostyle usually consists of a single loop. The pli caballin is well developed and usually consists of a single or double loop.

The depth of the mandible is shallow as expected in species with a mesodont dentition (fig. 29). In occlusal view, the lower incisor series is rounded. The lower incisors have cement-filled infundibula (cups) not recessed below the occlusal surface. The canine is closely positioned to the I_3 forming a small precanine diastema. The postcanine diastema is elongate. The mental foramen lies in the posterior half of the postcanine diastema. P_1 is absent in mature and advanced wear stages (no juvenile mandibles are represented in the hypodigm of this species). The protostylid varies greatly from well developed to absent. This structure is usually better developed in the molars than the premolars. The metaconids and metastylids are rounded and not widely separated. On the anterior toe of the metaflexid (posterior enamel of postisthmus) there usually is a single plication. The entoconids and hypoconulids are rounded. The entoconid is usually slightly larger than the hypoconulid. In size and many characters of the lower dental pattern, *Hipparion shirleyi* resembles *Cormohipparion goorisi.*

The block from the type locality, Wright Farm, has associated postcranial elements. The metapodials are small and relatively slender for hipparions, approximately the size of *Nannippus minor* (fig. 30, table 11). The lateral digits are relatively well developed and indicate tridactyly. The terminal lateral phalanges extend distally on the manus and pes to a position lateral to the distal tip of the first medial (III) phalanx.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: In many characters, *Hipparion shirleyi* is not far removed from merychippines in relative primitiveness in contrast to *H. tehonense* and *H. forcei* (fig. 27, table 7). *H. shirleyi* retains a primitive merychippine-like rounded to oval protocone that has a distinct, persistent, anterior spur. These are primitive in contrast to the character states seen in *H. tehonense* and *H. forcei* where there is a trend toward increase in size and hypsodonty, as well as a more oval or elongate protocone that loses the rudimentary connection to the protoloph during earlier wear stages. The polarities of these character states are interpreted from comparison with the merychippine outgroup.

Despite the decidedly primitive nature of *H. shirleyi,* the DPOF clearly indicates its shared-derived affinity with *H. tehonense, H. forcei,* and Old World species of the genus *Hipparion.* All these species are united by the diagnostic development of a DPOF that: (1) is located relatively far forward on the face (i.e., with a relatively wide PRB), (2) is well-defined posteriorly, and (3) is relatively poorly defined anteriorly (in contrast to *Cormohipparion*) and smooths out onto the adjoining facial region.

Hipparion shirleyi is only known from the Barstovian of the Texas Gulf Coastal Plain. These occurrences are limited to localities with well-preserved or fragmentary cranial material. As with *Cormohipparion goorisi,* because of their very primitive characters in contrast to other hipparions, these two species actually may have been more common or widespread; however, they are not easily recognized from only dental material. In these instances, they are probably identified in collections as *Merychippus* based on primitive character states.

TABLE 12
Synopsis of Collections Examined for *Hipparion tehonense* Used for Descriptions and Comparisons in this Report

Locality or Area	Collection	Geology and Geography	Age	Comments
Tejon Hills	UCMP, LACM	Chanac Formation, southern Tejon Hills, California	Early Clarendonian	Type area
San Francisco Bay Region, San Joaquin Valley	UCMP	Orinda Formation, northern and central California	Early Clarendonian	
Mohave Desert	UCMP, LACM, UCR	Ricardo Formation, southern California	Clarendonian	
Western Nevada	UCMP	Upper Aldrich Station and Coal Valley formations, Lyon and Mineral counties	Clarendonian	
Texas Panhandle	AMNH, F:AM, PPM, TMM	Clarendon Beds, Donley County	Clarendonian	Large quarry sample (from MacAdams, see analysis in text)
Northern Great Plains	AMNH, F:AM, UNSM	Valentine and Ash Hollow formations, Brown and Cherry counties, Nebraska; adjacent South Dakota	Valentinian to late Clarendonian	
Sebastian Place	F:AM	Ogallala Group, Decatur County, Kansas	Probably late Clarendonian	

Hipparion tehonense (Merriam), 1916a
Figures 8, 10–14, 25–27, 32–39, 146, 150; Tables 2–7, 12, 13

TYPE SPECIMEN AND LOCALITY: UCMP 21780, right upper M^1?, described by Merriam (1916a, p. 119, fig. 1), Chanac ("Santa Margarita") Formation, South Tejon Hills, early Clarendonian of southern California.

DIAGNOSIS: Generic characters same as for other species of the genus *Hipparion sensu stricto,* in particular, the DPOF is well developed posteriorly, but anteriorly becomes poorly defined. Wide PRB. Deep nasal notch that lies dorsal to P^2. Larger and more hypsodont than *H. shirleyi.* Smaller and less hypsodont than *H. forcei.* Mean TRL 123.38 mm. Unworn or little-worn M1MSTHT *ca.* 40–45 mm. Protocone oval with rounded borders. Differs from merychippines and *H. shirleyi* in lack of a persistent, distinct anterior spur on protocone. Protocone less elongate than usually developed in *Neohipparion.*

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Clarendonian of California, Nevada, Texas Panhandle, Kansas, Nebraska, and South Dakota (see table 12).

DESCRIPTION: The skull of *Hipparion tehonense* is known from numerous specimens from Texas and the Great Plains (figs. 32–34). *Hipparion tehonense* is larger and more hypsodont (table 13) than *H. shirleyi* and slightly smaller and usually less hypsodont than *H. forcei.*

Specimens of *H. tehonense* from the Frick MacAdams Quarry of the Texas Panhandle (fig. 32, also see *H. "lenticulare"* in Osborn, 1918, pl. 32B) show a relatively deep nasal notch that lies dorsal to P^2 in contrast to the late Clarendonian North American species

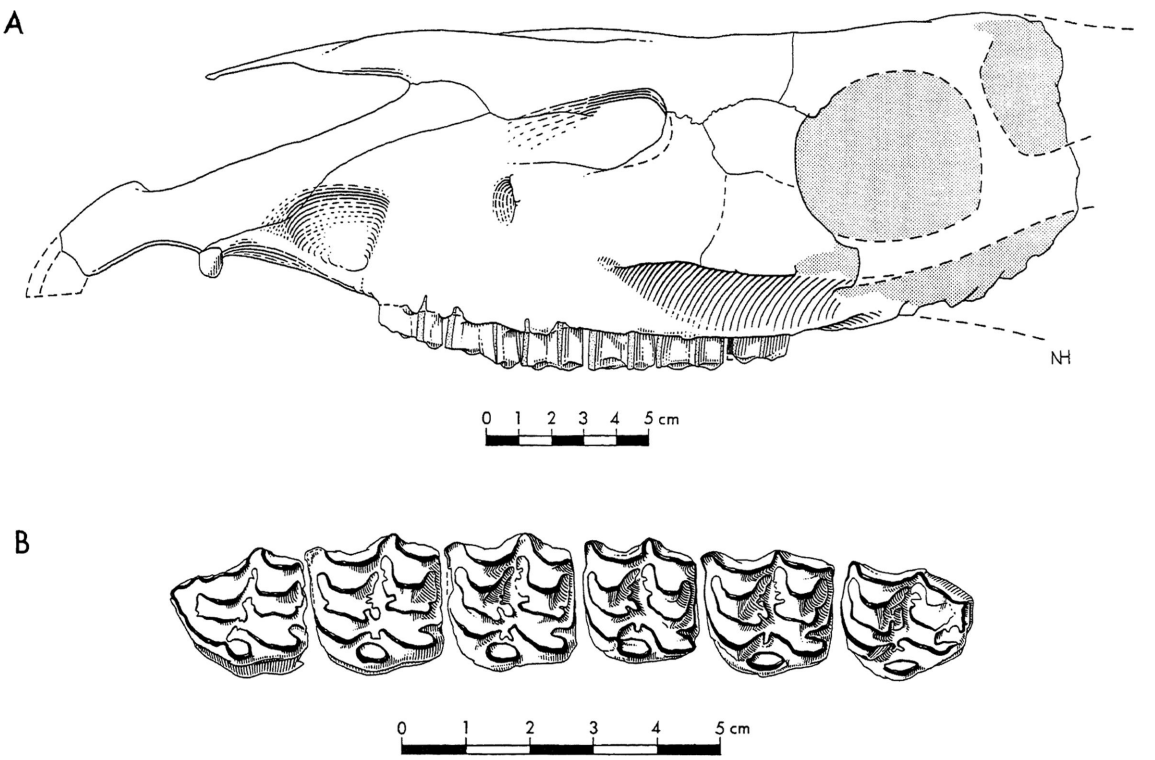


FIG. 32. *Hipparion tehonense,* F:AM 74478, from MacAdams Quarry, Clarendon Beds, Ogallala Group, early Clarendonian of Donley County, Texas Panhandle. A. Left lateral view of skull. B. Occlusal view of left P^2–M^3.

TABLE 13
Selected Upper Dental Measurements and Univariate Statistics for *Hipparion tehonense*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	43	24.36	1.54	6.32	21.5–27.6	29	24.33	1.61	6.62	21.6–27.3
P2TRNW	42	18.39	1.43	7.78	13.6–21.4	28	18.58	1.14	6.14	16.9–21.3
P2PRTL	37	5.67	0.65	11.37	4.3–7.5	25	5.49	0.51	9.29	4.3–6.7
P2PRTW	40	4.16	0.43	10.30	2.7–5.2	27	4.14	0.31	7.49	3.5–4.9
P2TOTPLI	39	3.41	1.92	56.17	0–7	28	3.32	1.66	50.00	0–7
M1APL	49	18.79	1.43	7.61	16.0–22.8	33	18.53	0.97	5.23	16.9–21.2
M1ECTL	49	18.81	1.57	8.33	15.7–22.4	33	18.47	1.09	5.90	16.3–21.0
M1TRNW	47	19.10	1.91	6.24	15.3–21.0	31	19.18	0.98	5.10	17.5–21.1
M1PRTL	49	6.28	0.66	10.44	4.9–7.9	33	6.27	0.64	10.08	5.2–7.9
M1PRTW	47	3.73	0.46	12.20	2.2–4.7	31	3.77	0.38	10.08	3.1–4.7
M1TOTPLI	44	5.59	2.78	49.75	0–12	31	5.45	2.53	46.42	1–11
TRL	36	123.38	5.85	4.74	110.2–134.6	26	122.58	6.04	4.93	110.2–134.6
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	35	27.43	6.62	24.13	12.4–37.5	9	33.82	3.32	9.82	28.5–37.5
M1MSTHT	9	32.78	10.52	32.11	18.9–47.2	4	42.38	4.25	10.03	38.7–47.2

[a] Abbreviations are presented on pp. 21 and 22; see table 12 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

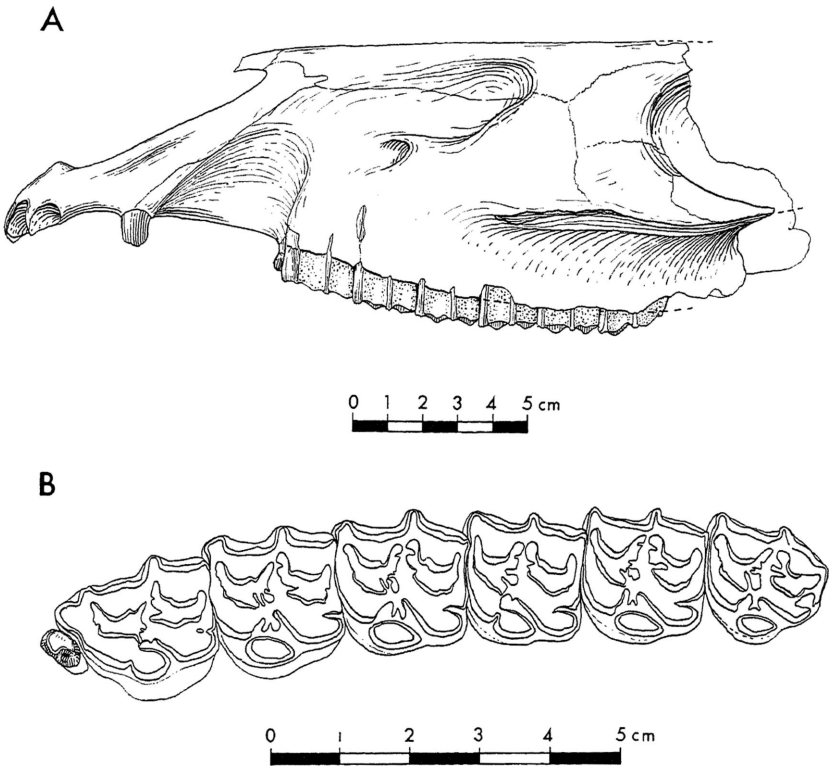


FIG. 33. *Hipparion tehonense,* F:AM 107664, from Trail Side Kat Quarry Channel, Ash Hollow Formation, late Clarendonian of north-central Nebraska. A. Left lateral view of skull. B. Occlusal view of left P^1–M^3.

H. forcei. The dentition is characteristic of the genus. In the upper cheek teeth (figs. 32–36) the protocones are rounded to oval and advanced over the character state seen in *H. shirleyi* in which the protcone has a more persistent anterior spur and is rounded. The protocones in most samples of *H. tehonense* are much less elongate and do not have angular borders in contrast to *Neohipparion* and advanced species of *Cormohipparion.*

The mandible is of moderate depth (fig. 37). In the lower cheek teeth the ectoflexids are usually deep in the premolars and shallower in the molars (figs. 38, 39). The pli caballinid is usually poorly developed, rudimentary, or absent. The enamel plications of *H. tehonense* are simple to moderate in contrast to, e.g., *Neohipparion eurystyle* and *Cormohipparion occidentale.*

CHARACTER ANALYSIS AND GENERAL DISCUSSION: *Hipparion tehonense* is clearly a member of the genus *Hipparion* based on the development of the diagnostic DPOF. *Hipparion tehonense* is the primitive sister species of *H. forcei.* In contrast to merychippines and *H. shirleyi, H. tehonense* is of larger size, more hypsodont, and has a more derived protocone (see description, figs. 26, 27, table 7). These character states are interpreted to be derived over the condition seen in *H. shirleyi* based on outgroup comparisons. In contrast to *H. forcei, H. tehonense* is primitive in size, crown height, shape of protocone, and complexity of enamel plications. In summary, *H. tehonense* exhibits numerous character states that are of intermediate polarity in a morphocline that proceeds from *H. shirleyi* to *H. tehonense* to *H. forcei.*

Dentitions of *Hipparion tehonense* have been recognized from California since the early part of this century (see fig. 35). Based on similar dental patterns and stage of hyp-

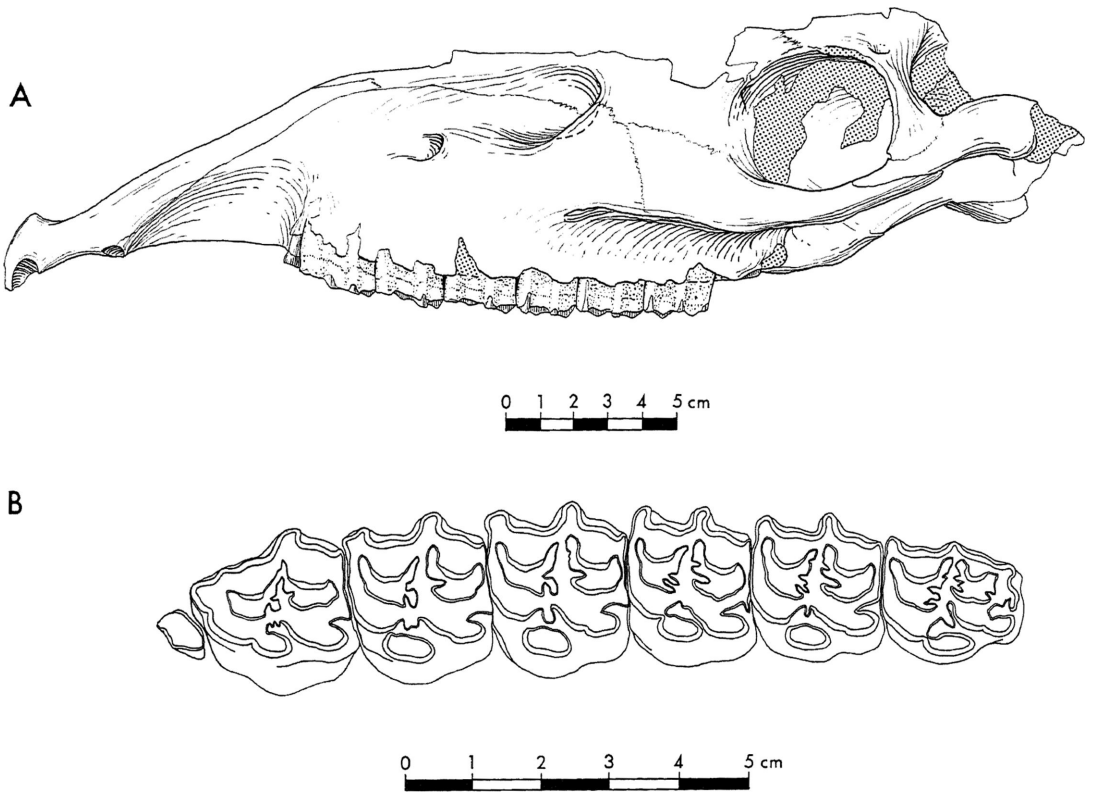


FIG. 34. *Hipparion tehonense,* F:AM 107663, from Rosebud Agency Quarry, Ash Hollow Formation, late Clarendonian of south-central South Dakota. A. Left lateral view of skull. B. Occlusal view of left P^1–M^3.

sodonty, MacFadden (1980) referred a large sample from MacAdams Quarry in the Texas Panhandle and additional material from the Great Plains of Nebraska and adjacent South Dakota to *H. tehonense.* The sample of this species from the midcontinent is represented by numerous (i.e., over 100 from MacAdams) skulls that show the characters of the preorbital cheek region of *Hipparion, sensu stricto* (also see discussion above). In addition, recent examination of the UCMP collections suggests that *H. tehonense* also oc-

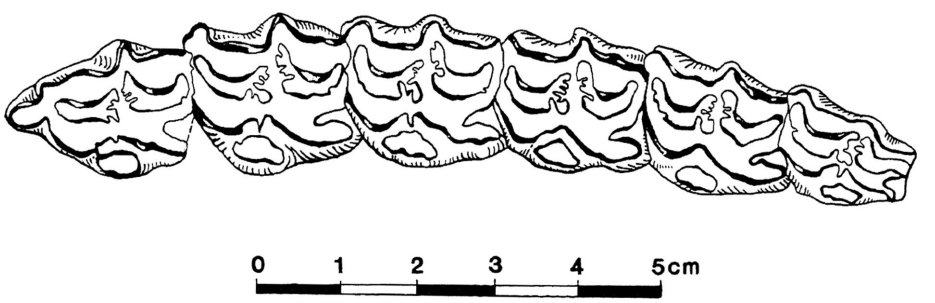


FIG. 35. Occlusal view of right (reversed) P^2–M^3 of *Hipparion tehonense,* LACM (CIT) 303/2598, from Tejon Hills, early Clarendonian of Kern County, California (also see Drescher, 1942).

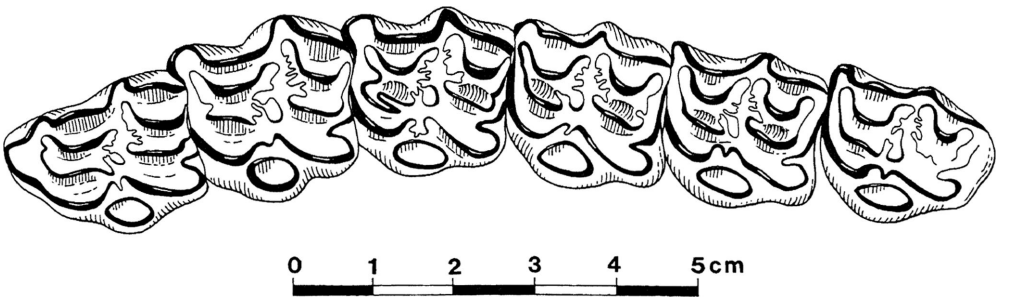


FIG. 36. Occlusal view of left P^2–M^3 of *Hipparion tehonense,* F:AM 103849, from the Frick Sebastin Place locality, Ogallala Group, late Clarendonian of Decatur County, northwestern Kansas.

curs at some localities in western Nevada. This species seems to have been biogeographically widespread in the midcontinent and Pacific Coast and Great Basin provinces during the Clarendonian.

The nomenclature of the Clarendon sample of *Hipparion tehonense* from Donley County, Texas, is confused in the literature (also see discussion below for *Nannippus ingenuus*). Gidley (1907) and Osborn (1918) referred the Clarendonian hipparion to ?*Hipparion lenticularis* and *H. lenticulare,* respectively. The species "*H. lenticularis*" (=*Nannippus ingenuus* of this report) from the late Hemphillian of Texas and *H. tehonense* are remarkably similar in dental pattern. These two species differ in that "*H. lenticularis*" is noticeably more hypsodont than *H. tehonense.* The Clarendon hipparion is referred to *H. tehonense* based on numerous

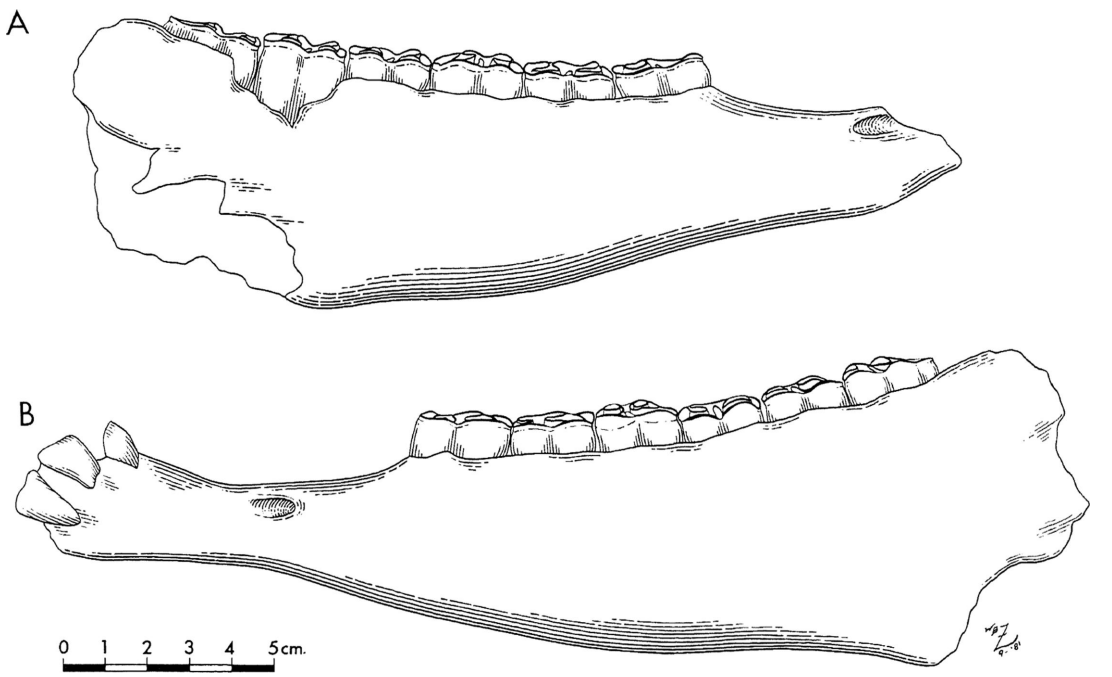


FIG. 37. Lateral views of *Hipparion tehonense* showing postcanine diastema and depth of ramus, from MacAdams Quarry, Clarendon Beds, Ogallala Group, early Clarendonian of Donley County, Texas Panhandle. A. F:AM 105440, right side with P_2–M_3. B. F:AM 105441, left side with I_2, I_3, C, P_2–M_3. Also see figure 38.

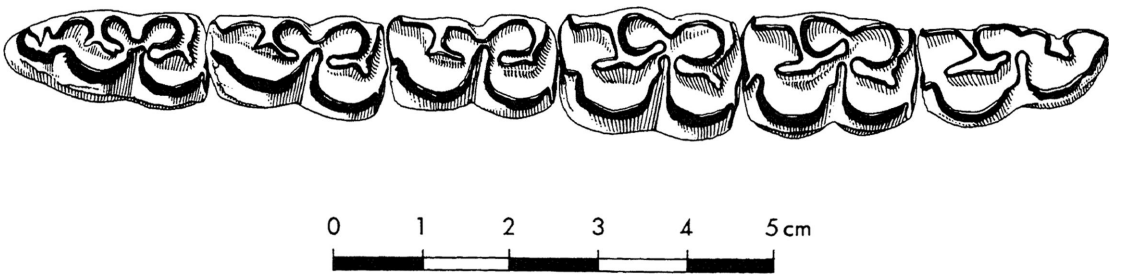


FIG. 38. Occlusal view of P_2–M_3 of *Hipparion tehonense*, F:AM 105440, from MacAdams Quarry, Clarendon Beds, Ogallala Group, early Clarendonian of Donley County, Texas Panhandle. Also see figure 37A.

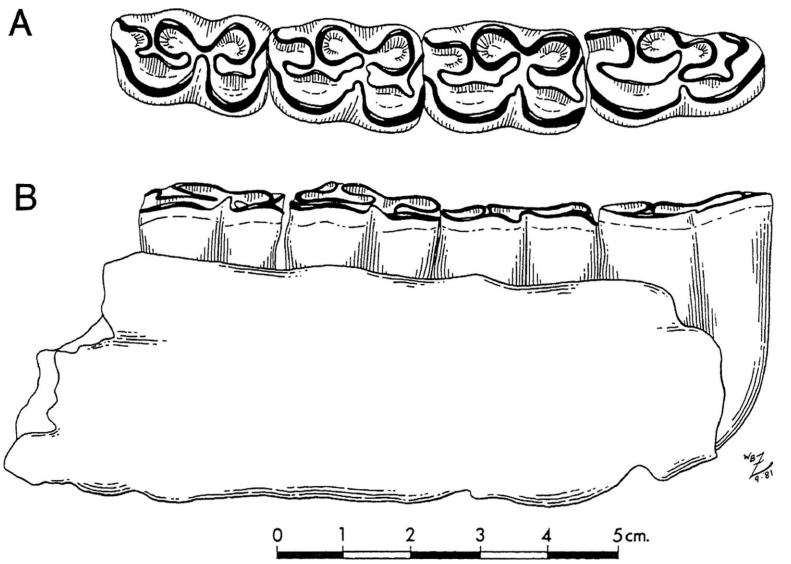


FIG. 39. *Hipparion tehonense*, F:AM 103856, from the Frick Sebastin Place locality, Ogallala Group, late Clarendonian of Decatur County, northwestern Kansas. A. Occlusal view of right P_2–M_1. B. Lateral view.

similarities in size, hypsodonty, and dental pattern as exhibited by this species from the California samples (MacFadden, 1980).

Hipparion forcei Richey, 1948

Figures 25–27, 40–45, 146, 150;
Tables 2, 7, 14, 15

TYPE SPECIMEN AND LOCALITY: UCMP 33051, P^3, from Green Valley Formation, Black Hawk Ranch Quarry (UCMP locality V-3310), Mount Diablo area, from strata of late Clarendonian age, Contra Costa County, California.

DIAGNOSIS: DPOF same as for other species of the genus. Larger and more hypsodont than *H. shirleyi*. Larger and probably slightly more hypsodont than *H. tehonense*. Mean TRL 133.50 mm. Unworn or little-worn M1MSTHT *ca.* 42–50 mm. Enamel plications on fossette borders moderate. Protocone lacking well-developed anterior spur except during early wear. Protocone relatively less elongate and enamel plications less complex than, e.g., *Cormohipparion occidentale* or *Neohipparion eurystyle*.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Previously reported from beds of late

TABLE 14
Synopsis of Collections Examined for *Hipparion forcei* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Black Hawk Ranch, V-3310	UCMP	Green Valley Formation, Mt. Diablo, Contra Costa County, California	Late Clarendonian	Type locality
Numerous, Ricardo	UCMP, LACM, UCR	Ricardo Formation, Kern County, California	Early to late Clarendonian	
Olcott Quarry Hipparion affine Channel	F:AM	Olcott Formation, Sioux County, Nebraska	Late Clarendonian	
Box T., Pit I	F:AM	Ogallala Group, Lipscomb County, Oklahoma	Early Hemphillian	
Ft-40	UNSM	Ogallala Group, Frontier County, Nebraska	Early Hemphillian	

Clarendonian age in California (type locality) and Great Plains (e.g., north-central Nebraska and adjacent South Dakota, see MacFadden, 1980). *Hipparion forcei* also possibly occurs in the Clarendonian of western Nevada (as represented in the UCMP collections) and the Hemphillian of Nebraska and Texas Panhandle (table 14).

DESCRIPTION: Richey (1948) presented a thorough diagnosis and description of this

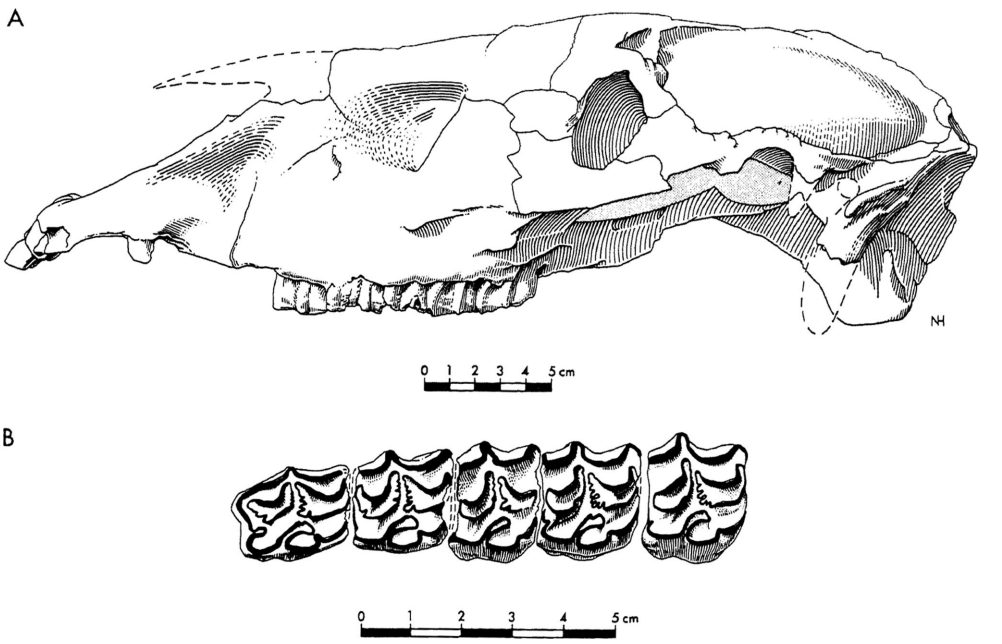


FIG. 40. *Hipparion forcei,* UCMP 34511 (drawn from cast, UF 27656) from Black Hawk Ranch Quarry, Green Valley Formation, Mount Diablo area, late Clarendonian of Contra Costa County, San Francisco Bay region, northern California. A. Left lateral view of skull. Morphology of DPOF is distorted (it is dorsoventrally deeper) because this specimen is crushed. B. Occlusal view of right P^3–M^3 in very late wear stage.

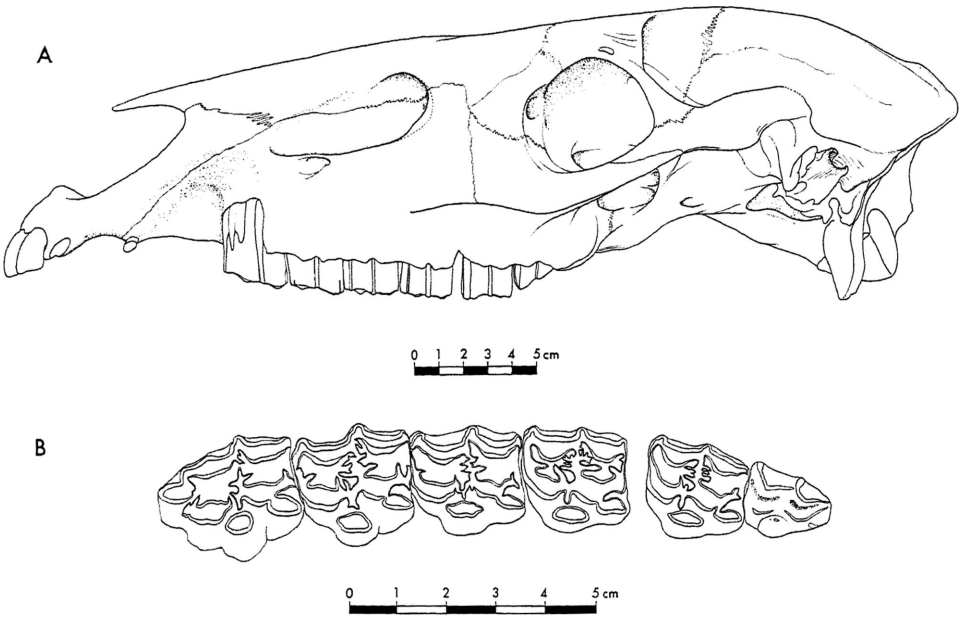


FIG. 41. *Hipparion forcei,* F:AM 71887, from Olcott Quarry, Hipparion Channel, Olcott Hill, late Clarendonian of Sioux County, northwestern Nebraska. A. Left lateral view of skull. B. Occlusal view of left P^2–M^3.

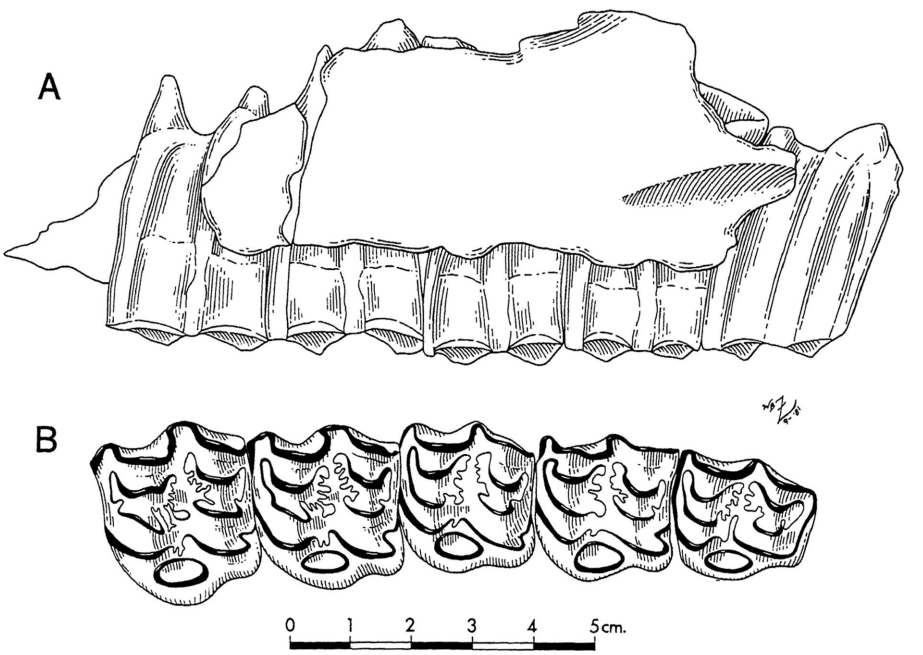


FIG. 42. Upper cheek tooth dentition of *Hipparion forcei,* UNSM 2648, from the UNSM Ft-40 locality, Cambridge L.F., Ash Hollow Formation, Ogallala Group, early Hemphillian of Frontier County, south-central Nebraska. A. Lateral view of left maxillary fragment with P^3–M^3. B. Occlusal view.

TABLE 15
Selected Upper Dental Measurements and Univariate Statistics for *Hipparion forcei*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	7	27.84	1.38	4.98	25.0–29.1	5	27.66	1.64	5.93	25.0–29.1
P2TRNW	7	19.54	0.76	3.92	18.6–20.8	5	19.60	0.89	4.54	18.6–20.8
P2PRTL	7	5.99	0.51	8.49	5.5–6.9	5	6.02	0.61	10.13	5.5–6.9
P2PRTW	7	4.19	0.44	10.63	3.5–4.9	5	4.18	0.22	5.26	3.8–4.4
P2TOTPLI	7	8.29	3.99	48.13	3–16	5	9.80	3.56	36.33	7–16
M1APL	14	20.94	1.75	8.38	17.1–24.4	11	20.96	1.15	5.49	19.3–22.5
M1ECTL	11	21.05	2.21	10.52	16.6–24.6	8	21.16	1.53	7.23	19.6–23.5
M1TRNW	13	20.06	1.24	6.17	17.1–22.0	10	20.18	0.79	3.91	19.0–21.9
M1PRTL	12	6.64	6.47	9.75	5.9–7.8	9	6.59	0.64	9.71	5.9–7.8
M1PRTW	12	3.94	0.46	11.72	3.1–4.8	9	4.00	0.27	6.75	3.6–4.4
M1TOTPLI	12	10.25	3.28	31.99	2–14	9	11.11	2.21	19.89	8–14
TRL	2	133.50	1.13	0.80	132.7–134.3	1	132.70	—	—	—
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	6	35.03	8.04	22.96	21.6–45.1	2	41.15	5.59	13.58	37.2–45.1
M1MSTHT	10	38.30	6.89	17.98	27.2–50.0	2	46.35	5.16	11.13	42.7–50.0

[a] Abbreviations are presented on pp. 21 and 22; see table 14 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

species based on abundant material from Black Hawk Ranch of the San Francisco Bay region (see Discussion below). A skull of *H. forcei* from the type locality is presented in figure 40. This specimen is distorted from postmortem crushing; however, it preserves important morphological characters such as the preorbital region. In addition, the present description is based on abundant material from numerous other North American localities (e.g., figs. 41, 42). The DPOF is situated relatively far anterior to the orbit, i.e., there is a wide PRB. This is characteristic of *Hipparion sensu stricto* (and Woodburne and Bernor's, 1980, Group 3) from both North America and the Old World. *Hipparion forcei* is larger than *H. tehonense* (e.g., figs. 25, 26; tables 13, 15). The protocones are rounded to oval. As in some other *Hipparion sensu stricto,* there is a tendency for the protocone to connect to the protoloph in P^2 during relatively early wear stages. In contrast to the complexity in *C. occidentale,* in *H. forcei* the pli protoloph and pli hypostyle usually consist of single loops. The pli protoconule, pli prefossette, and pli postfossette consist of multiple loops. The pli caballin consists of either a single or double loop.

The most complete lower cheek tooth of *H. forcei* is represented by UCMP 124928 (fig. 43) from the Dove Springs L.F. of the Ricardo area of southern California (the topotypic material from Black Hawk Ranch consists almost entirely of isolated teeth). Another relatively well-preserved lower cheek tooth dentition of *H. forcei* is illustrated in figure 44. The protostylid is variously developed; it ranges from absent to a moderately well-developed anteroexternal projection. The ectoflexids are moderately deep in the premolars and very deep (so as to divide the isthmus) in the molars. The pli caballinid is poorly developed, rudimentary, or absent. The enamel borders are relatively simple with few plications.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: *Hipparion forcei* is clearly a member of the genus *Hipparion* based on the diagnostic configuration of the DPOF. *Hipparion forcei* shows several characters that are derived relative to *H. tehonense, H. shirleyi,* and merychippines. In contrast to merychippines and the primitive North American species of *Hipparion, H. forcei* is of larger size and has higher crowns. Richey (1948) stated that an important character of *H. for-*

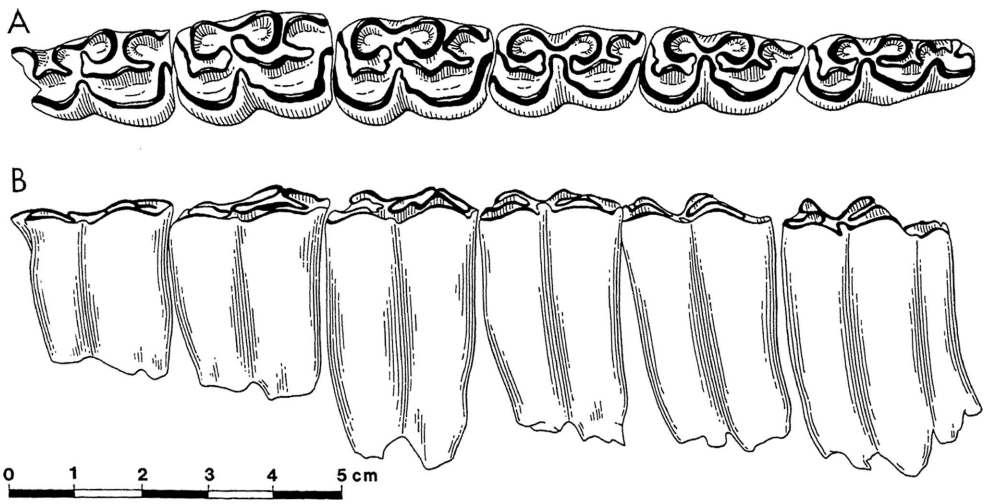


FIG. 43. Lower cheek tooth dentition of *Hipparion forcei,* UCMP 124928 from upper Ricardo Formation, Dove Springs L.F., UCMP locality V5803, late Clarendonian of Kern County, southern California. A. Occlusal view of left P^2–M^3. B. Lateral view.

cei was the very small protocone, comparable in relative size to Old World *Hipparion.* In the present study it is concluded that in samples referred to *H. forcei,* the protocone varies in size from small and rounded to oval, but not significantly smaller in relative size to *H. tehonense.* In addition, Richey (1948) also discussed the connection of the protocone to the protoloph in P^2 during relatively early wear as a diagnostic character of *H. forcei.* During the present study it was determined that the tendency for a connected protocone in P^2 is common in North American species of *Hipparion sensu stricto.* Therefore, it is concluded that this character is of dubious taxonomic significance in the diagnosis of *H. forcei.* Nevertheless, the other dental characters related to size and hypsodonty do demonstrate the validity of *H. forcei. Hipparion forcei* represents the most derived member of North American *Hipparion sensu stricto.*

Some previously undescribed early Hemphillian collections of *H. forcei* show characters diagnostic of, or closest to, this species. These samples include specimens from the UNSM FT-40 locality, e.g., UNSM 2648 (upper cheek teeth, fig. 42) and UNSM 2646 (lower cheek teeth, fig. 44), and probably F:AM specimens from Box T locality in the Texas Panhandle, e.g., F:AM 108534 (skull, fig. 45) and F:AM 99396 (mandible). Although the protocones seem slightly more elongate in some of these samples than to-

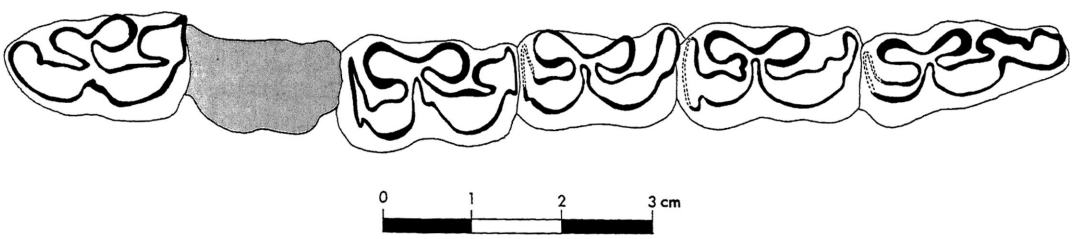


FIG. 44. Occlusal view of *Hipparion forcei,* UNSM 2646, left P_2, P_4–M_3, from UNSM Ft-40 locality, Cambridge L.F., Ash Hollow Formation, Ogallala Group, early Hemphillian of Frontier County, south-central Nebraska.

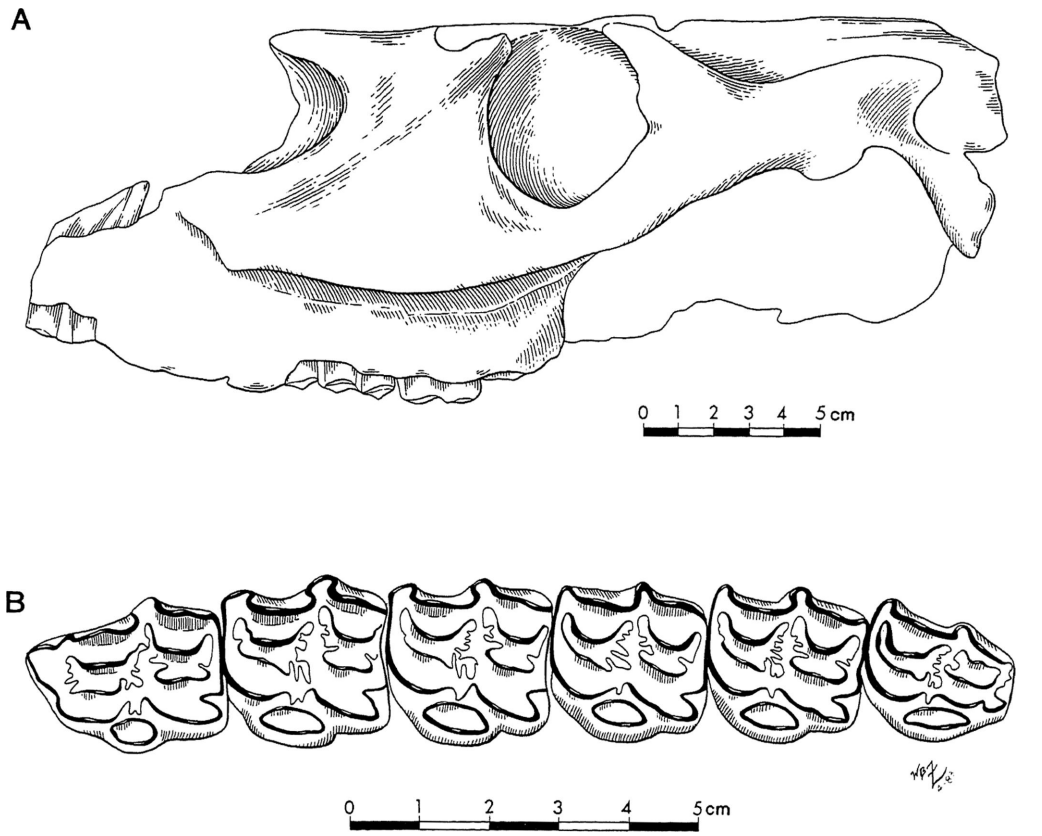


FIG. 45. *Hipparion forcei,* F:AM 108534, from the Frick Box T locality (Pit I), Ogallala Group, early Hemphillian of Lipscomb County, Texas Panhandle. A. Left lateral view of skull. Position of sutures is unavailable. B. Occlusal view of left P^2–M^3.

potypic *H. forcei* from Black Hawk Ranch, they are referable to this species based on size and complexity of enamel plications (particularly in the fossette borders). These new occurrences are of early Hemphillian age and, therefore, extend the known range of *H. forcei.*

NEOHIPPARION GIDLEY, 1903

INCLUDED SPECIES

Neohipparion coloradense (Osborn), 1918.
Neohipparion affine (Leidy), 1869.
Neohipparion trampasense (Edwards), 1982.
Neohipparion leptode Merriam, 1915a.
Neohipparion eurystyle (Cope), 1893.
Neohipparion gidleyi Merriam, 1915a.

TYPE SPECIMEN AND LOCALITY: The genus *Neohipparion* is based on a virtually complete skeleton, AMNH 9815, that Gidley (1903) named *N. whitneyi,* collected by the AMNH Whitney expedition of 1902 from the "Upper Miocene" late Clarendonian beds, Little White River, near Rosebud Indian Agency, South Dakota (Gidley, 1903; Osborn, 1918; see figs. 5, 46).

REVISED GENERIC DIAGNOSIS: Medium to large-size. Moderately to very hypsodont. Mean TRL 127.30 mm to *ca.* 150.00 mm. Unworn or little-worn M1MSTHT range between *ca.* 35 to 71 mm. DPOF poorly developed (shallow) or absent. Anterior portion of DPOF, if present, is developed on the nasal and maxillary bones and fades into the surrounding facial region. Posterior portion of the DPOF if present, is developed on the nasal, maxillary, and sometimes lacrimal bones. Also, if present, posterior portion of the

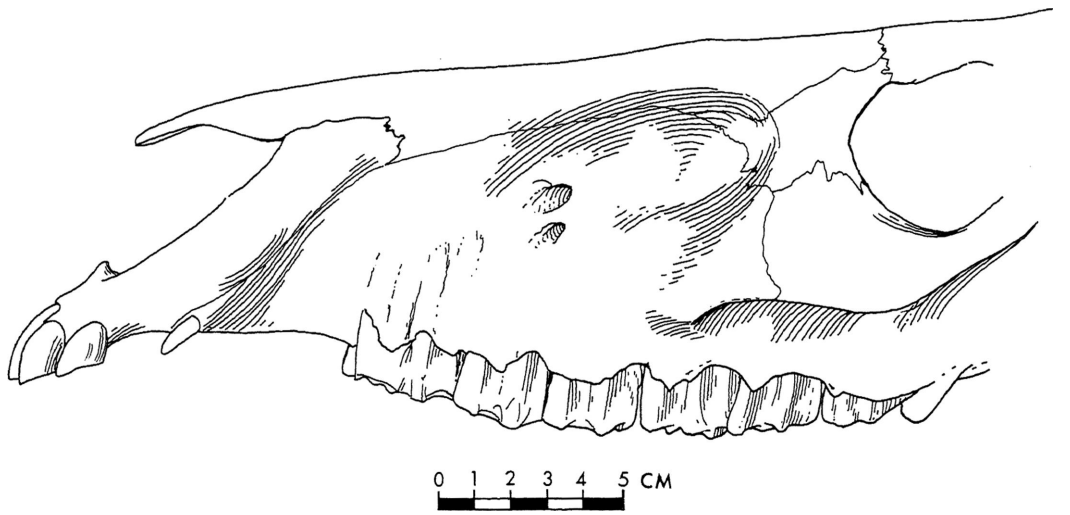


FIG. 46. Left lateral view of skull of *Neohipparion affine,* AMNH 9815 (genoholotype of *Neohipparion whitneyi*), from Little White River, Clarendonian of South Dakota. Redrawn from Osborn (1918, pl. 32, fig. 1). See figure 47 of this report for illustrations of the cheek tooth dentition.

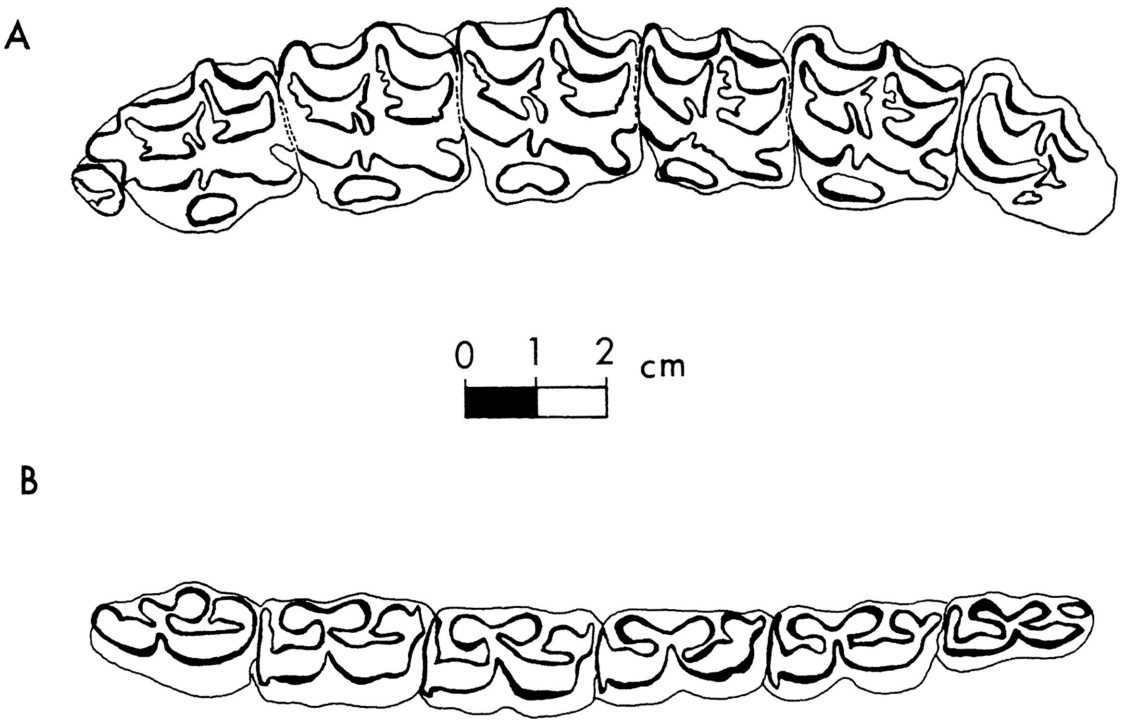


FIG. 47. Occlusal views of *Neohipparion affine,* AMNH 9815, from Little White River, Clarendonian of South Dakota (also see fig. 46). A. Left P^2–M^3. B. Right (reversed) P_2–M_3. Redrawn from Osborn (1918, p. 181, fig. 144).

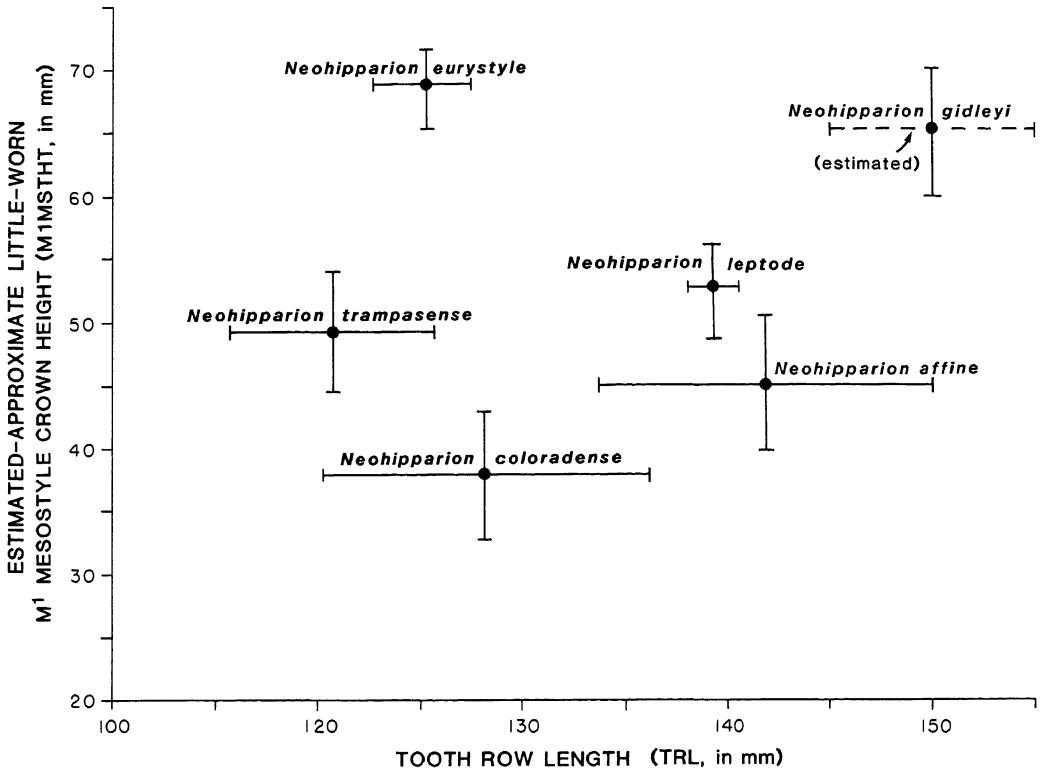


FIG. 48. Bivariate plot of TRL versus estimated-approximate little-worn M1MSTHT for the six recognized species of *Neohipparion*. TRL for *Neohipparion gidleyi* is estimated because of the lack of available specimens that preserve this character. For each value, one standard deviation (*s*, either actual or estimated) is plotted on both sides of the mean. Also see figure 25 for further explanation.

DPOF is very shallow and it usually lacks a well-developed rim or pocket (except in the dorsal and posterior margins in primitive forms). In the upper cheek teeth, protocones very elongate. In the lower cheek teeth of some species, e.g., *N. eurystyle,* there are well-developed pli hypoconids, pli caballinids, isthmuses, and elongate entoconids and hypolophids. The degree of enamel plications varies from simple to complex. Metapodials moderate to very long.

Neohipparion differs from most Holarctic species of *Hipparion sensu stricto* in numerous dental characters, e.g., relatively elongated protocones and (except for *N. coloradense* and some *N. affine*) extreme development of the pli caballinid. *Neohipparion* differs from most Old World species and all North American species of *Hipparion sensu stricto* in the morphology of the DPOF. *Neohipparion* differs from *Nannippus* in larger size, numerous dental characters, e.g., more elongate protocones and complex enamel plications, and, except for primitive species, the development of the DPOF. *Neohipparion* differs from *Cormohipparion* in numerous dental characters, e.g., development of the pli caballinid and ectoflexid, and morphology of the DPOF.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Valentinian of Nebraska, early Clarendonian of Nebraska and Texas, and widespread in Central America and North America during the late Clarendonian to late Hemphillian. Probably unknown from the Old World (although see discussion of Zhegallo, 1978, below).

DISCUSSION: The genus *Neohipparion* is recognized here by its medium to large-size along with characters of the preorbital facial

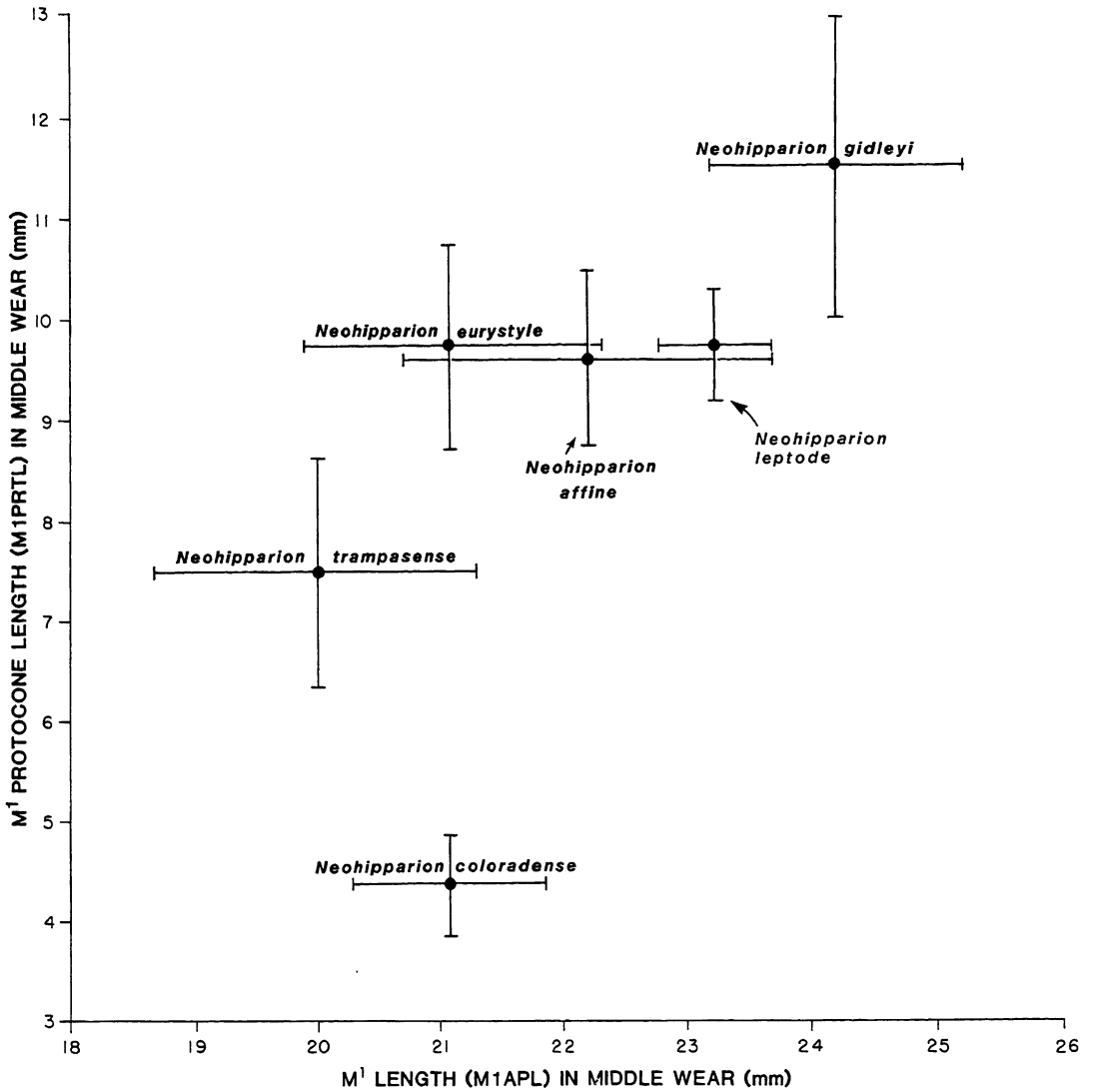


FIG. 49. Bivariate plot of M1APL versus M1PRTL for six recognized species of *Neohipparion*. For each value, one standard deviation (*s*) is plotted on both sides of the mean. Also see figure 26 for further explanation.

morphology and dentitions. For the six species of *Neohipparion*, selected measured characters that give an indication of size versus hyposodonty (TRL vs. M1MSTHT) and increase in relative size of protocone (M1APL vs. M1PRTL) are presented in figures 48 and 49. The data used to construct these graphs are tabulated for each species below. *Neohipparion* ranges in size from moderate to very large, rivaling that developed in large late Cenozoic horses such as *Dinohippus* and *Equus*. The DPOF of *Neohipparion* is poorly developed in primitive species and trends toward reduction or absence in advanced species. The characters represented by the species of *Neohipparion* form a morphocline proceeding from the most primitive *N. coloradense* ultimately to *N. gidleyi*. Figure 50 and table 16 represent the important character polarities and distributions among the

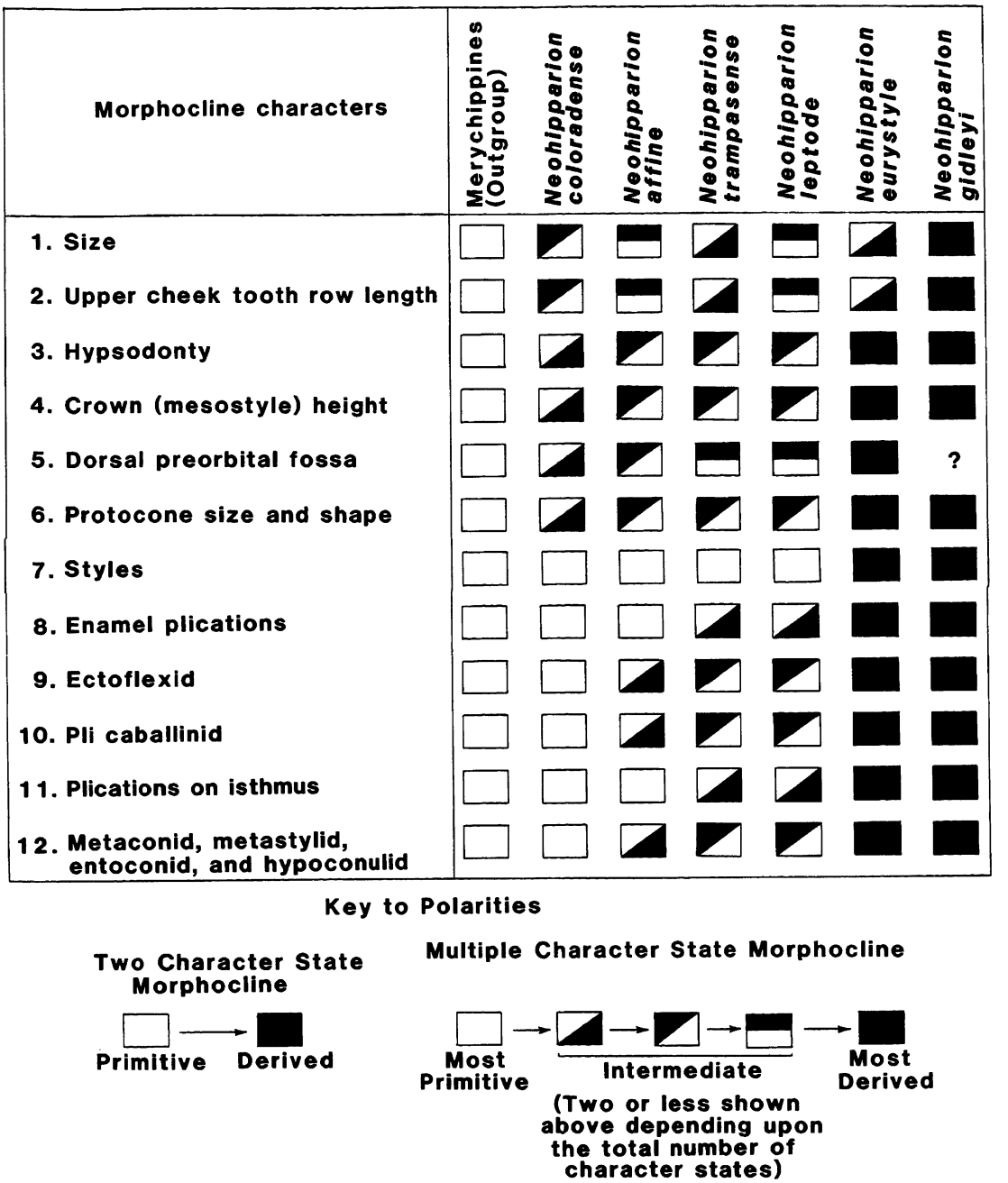


FIG. 50. Graphical representation of selected important character distributions and morphocline polarities in the six species of *Neohipparion* and merychippines (outgroup). Numbered characters correspond to those in table 16. Also see text for discussion.

merychippine outgroup and the species of *Neohipparion*.

The revised definition of *Neohipparion* as presented here is actually very similar to the early concept of this genus. Gidley (1907, p. 869), in a broadened description of *Neohip-*

TABLE 16

Selected Important Morphological Character Distributions and Temporal and Spatial Data for the Six Species of *Neohipparion* and the Merychippines (Outgroup)[a]

Morphocline Character[b] (see fig. 50)	Merychippines[c] (outgroup)	*Neohipparion coloradense*	*Neohipparion affine*	*Neohipparion trampasense*	*Neohipparion leptode*	*Neohipparion eurystyle*	*Neohipparion gidleyi*
1. Size (relative to all hipparions)	Small to medium	Medium	Large	Medium	Large	Medium	Very large
2. Mean upper cheek tooth row length, P^2–M^3 (TRL)	—	127.31 mm	142.47 mm	121.36 mm	140.95 mm	125.62 mm	*Ca.* 150 mm
3. Hypsodonty	Brachyodont to mesodont	Hypsodont	Hypsodont	Hypsodont	Hypsodont	Very hypsodont	Very hypsodont
4. Estimated-approximate mesostyle crown height (M1MSTHT) for little-worn specimens	—	35–43 mm	42–50 mm	46–53 mm	48–56 mm	65–71 mm	60–70 mm
5. Dorsal preorbital fossa (DPOF)	Highly variable depending upon species	Present with relatively well-defined posterior rim	Present but shallow and poorly defined	Relatively reduced	Relatively reduced	Virtually absent	Condition unknown
6. Protocone size and shape	Small and rounded to oval, usually	Oval, sometimes slightly elongate	Elongate	Elongate	Elongate	Very elongate, oftentimes with angular borders	Very elongate, oftentimes with angular borders
7. Parastyles, mesostyles	Rounded	Rounded	Rounded	Rounded	Usually rounded	Flattened and expanded	Flattened and expanded
8. Enamel plications on fossette borders	Highly variable in different species	Simple	Simple	Moderate	Moderate	Moderate to complex	Moderate to complex

TABLE 16—(*Continued*)

Morphocline Character[b] (see fig. 50)	Merychippines[c] (outgroup)	*Neohipparion coloradense*	*Neohipparion affine*	*Neohipparion trampasense*	*Neohipparion leptode*	*Neohipparion eurystyle*	*Neohipparion gidleyi*
9. Ectoflexid	Usually deep	Relatively deep	Deep	Usually shallow in premolars, deeper in molars	Usually shallow in premolars, deeper in molars	Shallow to very shallow	Shallow to very shallow
10. Pli caballinid	Variable depending upon species, but relatively poorly developed	Poorly developed, rudimentary, or absent	Poorly developed, rudimentary, or absent	Moderate to well developed, particularly in premolars	Moderate to well developed, particularly in premolars	Well developed to very well developed in both premolars and molars	Well developed to very well developed in both premolars and molars
11. Plications on isthmus	Absent	Absent	Absent	Sometimes developed	Sometimes developed	Frequently developed	Frequently developed
12. Metaconids, metastylids, entoconids and hypoconulids	Separated, rounded borders, not greatly expanded	Separated, rounded borders, not greatly expanded	Separated, rounded borders, moderately expanded	Separated, rounded to angular borders, expanded	Separated, rounded to angular borders, expanded	Widely separated, rounded to very angular borders widely expanded	Widely separated, rounded to very angular borders, widely expanded
DISTRIBUTIONAL DATA[d]							
Known biochronological range (teilchron)	—	Early Barstovian to Clarendonian	Valentinian to late Clarendonian	Late Clarendonian, probably early Hemphillian	Early Hemphillian	Hemphillian (mostly late Hemphillian)	Hemphillian (mostly late Hemphillian)
Known biogeographic occurrences	—	Great Plains, New Mexico	Great Plains	California, Nebraska, and Florida	Nevada and Great Plains	Cosmopolitan, Central and North America	California, New Mexico, Oklahoma, and Mexico

[a] This table accompanies figure 50 (numbered characters).

[b] Descriptions of dental characters are representative of early and medial wear stages.

[c] Included as outgroup comparison for qualitative characters only. Qualitative characters (measurements) and temporal and spatial data are variable depending upon species and these are not available.

[d] These data are not used in figure 50 and are therefore not numbered sequentially as are the morphocline characters.

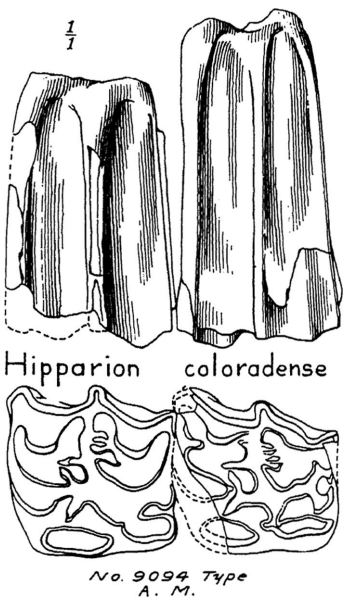


FIG. 51. *Neohipparion coloradense,* AMNH 9094, holotype M^1 and M^2, from Sand Canyon area, upper Pawnee Creek Beds, Ogallala Group, late Barstovian of Logan County, northeastern Colorado (taken from Osborn, 1918, p. 183, fig. 146). A. Lateral view. B. Occlusal view.

parion, characterized it as follows: "Enamel foldings of fossette borders comparatively simple; protocone comparatively large, and laterally compressed; lachrymal fossa shallow, borders not sharply defined; malar fossa shallow or wanting . . . ." It is interesting that Gidley recognized the importance of the DPOF in this diagnosis. Since Gidley's early work (1903, 1907), the concept of the genus has been emended principally using dental and metapodial characters (e.g., Stirton, 1940).

Stirton (1940, p. 183) stated that: "*Neohipparion* is descended from species of *Merychippus* closely related to *M.* (*M.*) *eohipparion* Osborn and *M.* (*M.*) *republicanus* Osborn. Some undescribed specimens in the Niobrara River fauna seem to be even nearer to the immediate ancestry than the above-named species." Pending a revision of *Merychippus sensu lato* it is difficult to determine what are the exact phylogenetic interrelationships of the species within this generic complex, as well as descendant species in other genera. With regard to Stirton's comments (above), based on the current systematics presented here, neither *M. eohipparion* nor *M. republicanus* seem close to the ancestry of *Neohipparion. Merychippus eohipparion,* the type of which (AMNH 9402) consists of a complete juvenile mandible and associated skeleton, lack any diagnostic characters (i.e., it could be either *Neohipparion* or *Cormohipparion*). The type of *M. republicanus,*

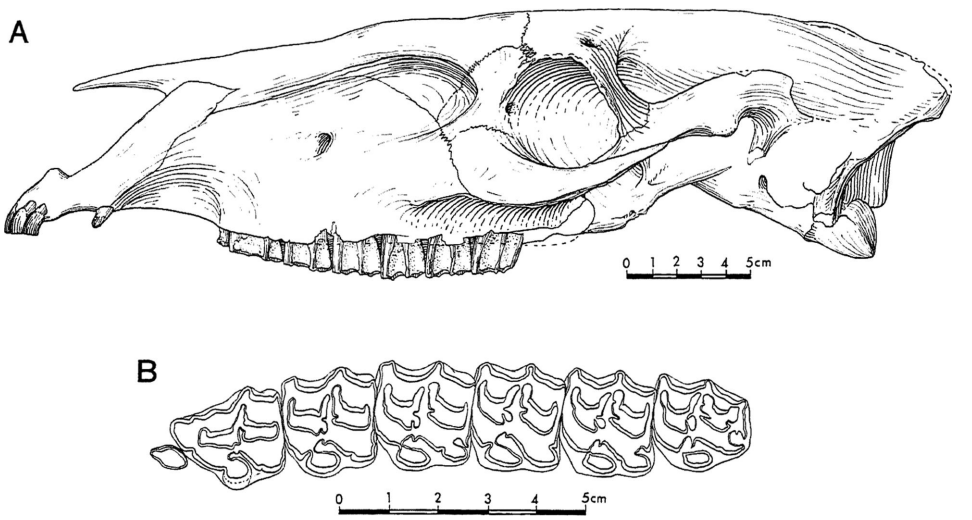


FIG. 52. *Neohipparion coloradense,* F:AM 69506, from the late Barstovian of northeastern Colorado. A. Left lateral view of skull. B. Occlusal view of left P^1–M^3 in late wear. Also see figure 58.

TABLE 17
Synopsis of Collections Examined for *Neohipparion coloradense* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Numerous, including Euhl Pit, Pawnee Buttes, Sand Canyon	F:AM	Ogallala Group, Weld and Logan counties, Colorado	Barstovian-early Clarendonian	Probable type area, see text for discussion
Paleo Channel Quarry	F:AM	Valentine Formation (Burge Member equivalent), Sheridan County, Nebraska	Late Valentinian	
Boulder Quarry	F:AM	Olcott Formation, Sioux County	Early Barstovian	
Several (unnamed)	F:AM	Chama el Rito and Pojoaque members, Tesuque Formation, Santa Fe Group, Rio Arriba County, New Mexico	Late Barstovian-early Clarendonian (Tedford, 1981)	
Unnamed	F:AM	Santa Fe Group, northern Ceja del Rio Puerco area, Sandoval County, New Mexico	Late Barstovian-early Clarendonian	
Cr-117, West Valentine Quarry; Quinn Mastodon Quarry	UNSM, F:AM	Crookston Bridge and Burge members, Valentine Formation; Cherry County, Nebraska	Valentinian	Only examined cast of UNSM 42447 from Cr-117 locality

AMNH 8347, displays characters such as small size and relatively smooth facial region (lacking even the posterior rim and narrow PRB of primitive *Neohipparion*) that would also seem to remove this species from the direct ancestry of *Neohipparion.* In addition, it is impossible to determine the exact affinities of Stirton's *M.* cf. *republicanus,* which he based on the isolated dentitions (see Stirton, 1940, fig. 24). For this form, the moderately elongated protocone, complex enamel plications, and size suggest closer affinities with some other species of *Neohipparion* (*sensu* this report), or more probably, *Cormohipparion* near C. *sphenodus.*

Workers such as Gidley (1903, 1907) and Stirton (1940) have stated that *Neohipparion* was the common medium to large hipparion in North America and that *Hipparion sensu stricto* was very rare in North America (restricted to a few species in Florida and California). With the revised generic concepts presented here it is agreed that *Neohipparion* was common in North American Miocene deposits, but so too were the other medium to large genera *Hipparion sensu stricto* and *Cormohipparion.*

Few paleontologists have asked the question if *Neohipparion* was common, or even present, in the Old World. If so, how would this affect the concept of the "Hipparion Datum" (see below)? There are several examples that can be cited of Old World hipparions that have a DPOF that is either poorly developed or absent. Hooijer and Maglio (1973, 1974) and Hooijer (1975) describe skulls of the African *Hipparion turkanense* and *H. ethiopicum* with *Neohipparion*-like configu-

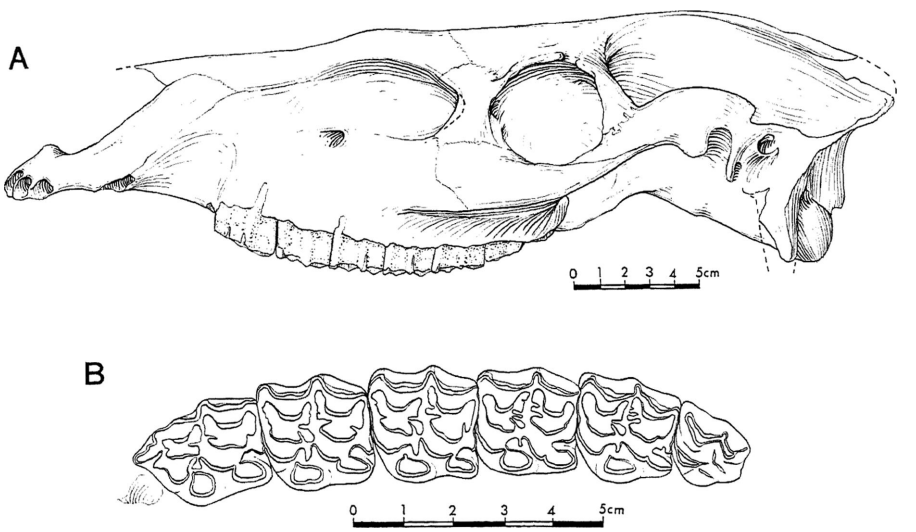


FIG. 53. *Neohipparion coloradense,* F:AM 69508, from Paleo Quarry, upper Valentine Formation, late Valentinian of Sheridan County, western Nebraska. A. Left lateral view of skull. B. Occlusal view of left P^1–M^3.

rations of facial fossae. Zhegallo (1978) also infers close affinities with New and Old world hipparions by referring to the large late Neogene Old World species as *Hipparion* (subgenus *Neohipparion*) *houfenense* (also see below). At present it is difficult to decide if similar configurations of the DPOF in North American *Neohipparion* and Old World hipparions indicate phylogenetic affinity (and Holarctic dispersal) or parallel evolution. This question remains unsolved and awaits further studies of the phylogenetic interrelationships of North American and Old World hipparion horses.

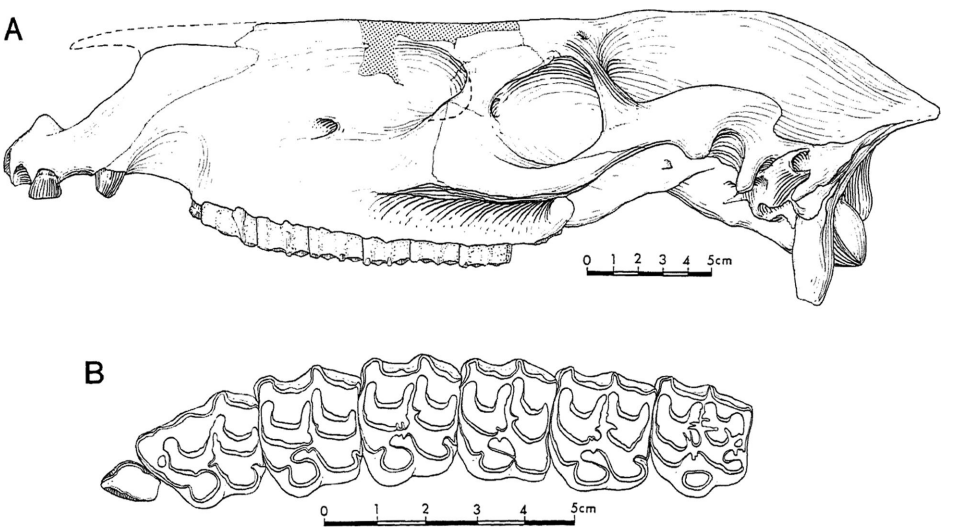


FIG. 54. *Neohipparion coloradense,* F:AM 69511, from Boulder Quarry, Olcott Formation, early Barstovian of Sioux County, northwestern Nebraska. A. Left lateral view of skull. B. Occlusal view of left P^1–M^3. Also see figure 59.

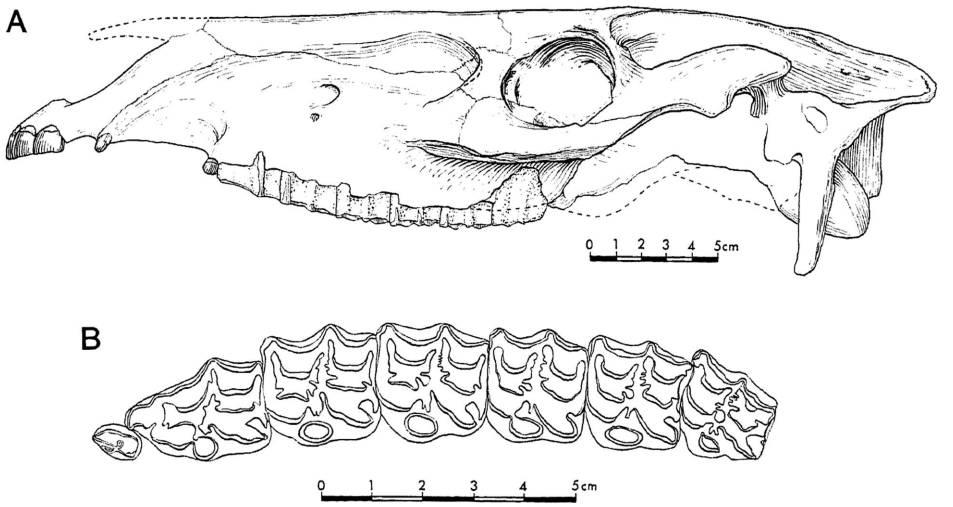


FIG. 55. *Neohipparion coloradense,* UNSM 1159, from locality Cr-117, Crookston Bridge Member of the Valentine Formation, medial Valentinian of Cherry County, north-central Nebraska. A. Lateral view of skull (composite restoration from both sides and UNSM 42450). B. Occlusal view of left P^1–M^3. Also see figure 60.

Neohipparion coloradense (Osborn), 1918
Figures 19, 48–62, 147, 150; Tables 2, 16–18

TYPE SPECIMEN AND LOCALITY: AMNH 9094, two isolated upper molars (probably M^1 and M^2, fig. 51) and associated postcranial elements from the Sand Canyon L.F., Ogallala Group (Ash Hollow equivalent), late Barstovian of Logan County, Colorado.

REVISED DIAGNOSIS: Medium-sized hipparion. Large DPOF with very narrow PRB,

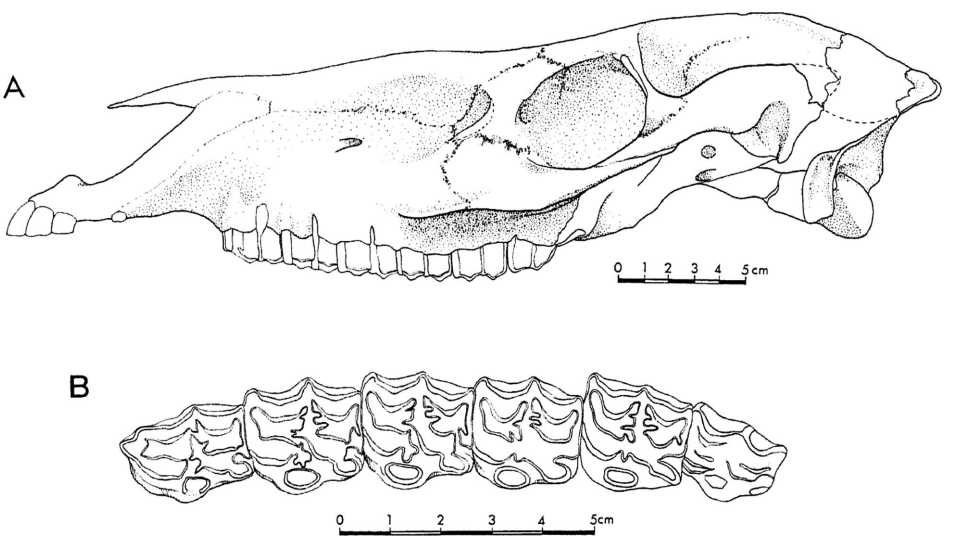


FIG. 56. *Neohipparion coloradense,* F:AM 69500, from the Chama El Rito Member of the Sante Fe Group, late Barstovian or early Clarendonian of Rio Arriba County, north-central New Mexico. A. Left lateral view of skull. B. Occlusal view of left P^2–M^3. Also see figure 61.

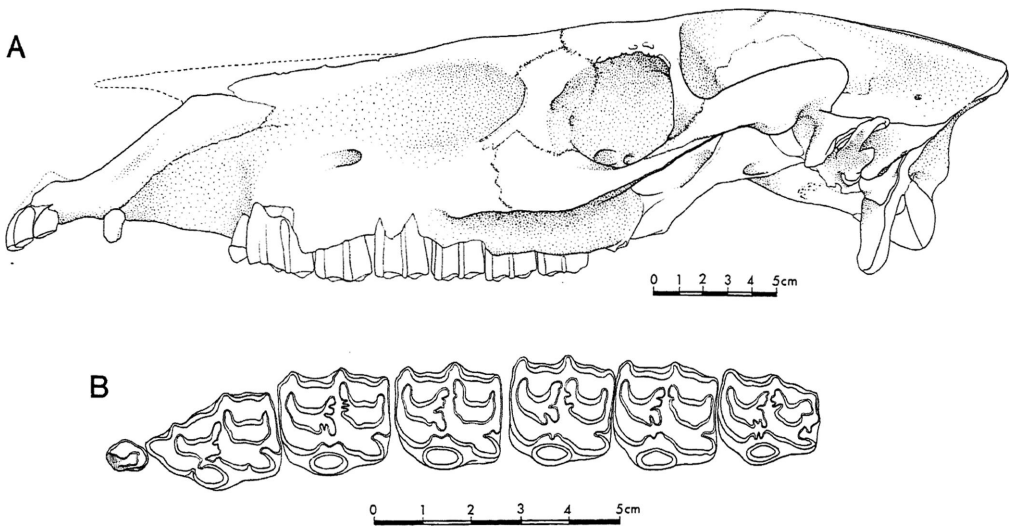


FIG. 57. *Neohipparion coloradense,* F:AM 69503, from the Cerro del Rio Puerco, Sante Fe Group, late Barstovian or early Clarendonian of the northern Albuquerque basin, Sandoval County, northern New Mexico. A. Left lateral view of skull. B. Occlusal view of left P^1–M^3. Also see figure 62.

well-defined posterior border, shallow posterior pocket, anteroventral margin poorly defined and confluent with adjoining facial region. Anterior part of lacrimal bone within posterior part of DPOF. Nasal notch lies dorsal to postcanine diastema.

Mean TRL 127.31 mm. Teeth hypsodont. Unworn or little-worn crown M1MSTHT *ca.*

TABLE 18
Selected Upper Dental Measurements and Univariate Statistics for *Neohipparion coloradense*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	12	25.13	1.96	7.80	22.4–29.1	5	25.80	0.74	2.87	24.6–26.5
P2TRNW	14	20.04	1.75	8.71	17.6–23.5	5	19.24	0.61	3.17	18.4–19.9
P2PRTL	13	6.44	0.76	11.75	5.2–7.6	6	6.48	0.62	9.57	6.0–7.6
P2PRTW	11	4.68	0.81	17.24	3.5–6.4	6	4.47	0.45	10.07	3.6–4.8
P2TOTPLI	13	1.08	0.86	80.07	0–2	6	1.67	0.52	31.14	1–2
M1APL	17	19.99	1.99	9.95	17.0–24.4	8	21.08	0.86	4.08	19.3–22.3
M1ECTL	14	20.16	1.64	8.14	16.7–22.4	6	20.82	0.80	3.84	19.9–21.8
M1TRNW	16	21.95	1.69	7.69	18.7–26.3	7	22.23	0.50	2.25	21.4–22.9
M1PRTL	14	7.86	0.95	12.08	6.5–9.9	7	8.19	1.11	13.55	6.8–9.9
M1PRTW	15	4.32	0.40	9.27	3.5–4.9	8	4.33	0.45	10.39	3.5–4.9
M1TOTPLI	17	3.24	2.44	75.34	0–7	8	3.5	2.45	70.00	0–7
TRL	13	127.31	7.01	5.51	116.0–136.2	5	132.68	3.45	2.60	127.5–135.7
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	8	21.65	1.99	48.22	14.9–27.8	1	27.8	—	—	—
M1MSTHT	5	28.76	11.11	38.64	12.6–43.0	1	43.0	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 17 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

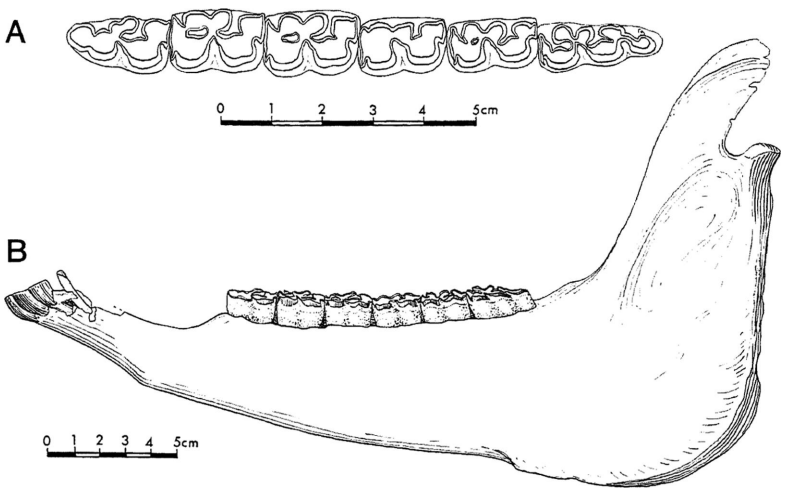


FIG. 58. *Neohipparion coloradense,* F:AM 69506, from the late Barstovian of northeastern Colorado. A. Occlusal view of left P_2–M_3. B. Lateral view of left ramus. Also see figure 52.

35–43 mm. Anterior protoconal spur oftentimes to sometimes present in early wear. Oval to moderately elongated protocones, fossette borders simple, particularly in the pli protoloph and pli hypostyle. Relatively deep ectoflexids. Poorly developed pli caballinids.

Neohipparion coloradense differs from other hipparion (and all other) horse genera in the diagnostic generic characters. *N. coloradense* is the most primitive sister species within the genus. It differs from all other *Neohipparion* species in characters such as a more distinct DPOF, smaller crown heights, and the tendency to retain the anterior protoconal spur during early wear.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Valentinian to Clarendonian of Nebraska, Barstovian of Colorado, Barstovian-Clarendonian of New Mexico (see table 17).

DESCRIPTION: *Neohipparion coloradense* is

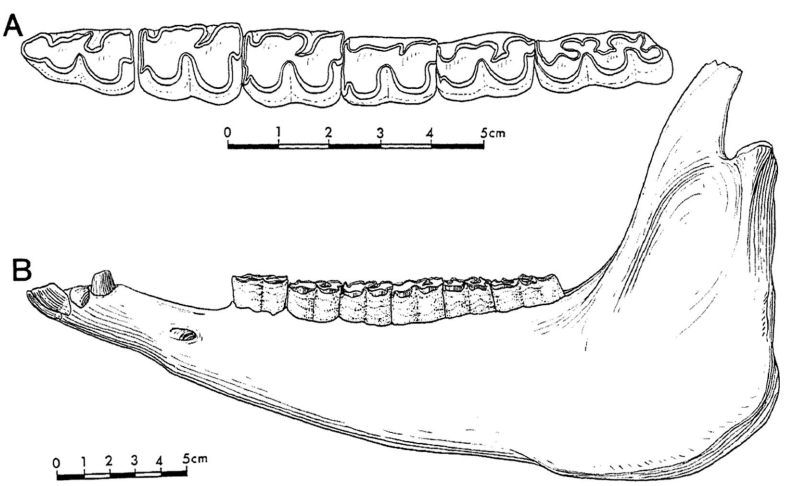


FIG. 59. *Neohipparion coloradense,* F:AM 69511, from Boulder Quarry, Olcott Formation, early Barstovian of Sioux County, northwestern Nebraska. A. Occlusal view of right (reversed) P_2–M_3. B. Lateral view of right ramus (reversed). Also see figure 54.

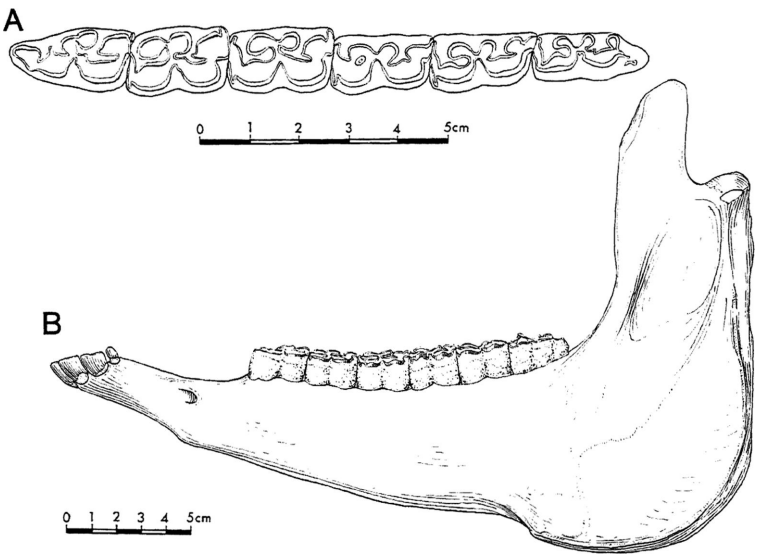


FIG. 60. *Neohipparion coloradense,* UNSM 1159, from locality Cr-117, Crookston Bridge Member of the Valentine Formation, medial Valentinian of Cherry County, north-central Nebraska. A. Occlusal view of left P_2–M_3. B. Lateral view of left ramus. Also see figure 55.

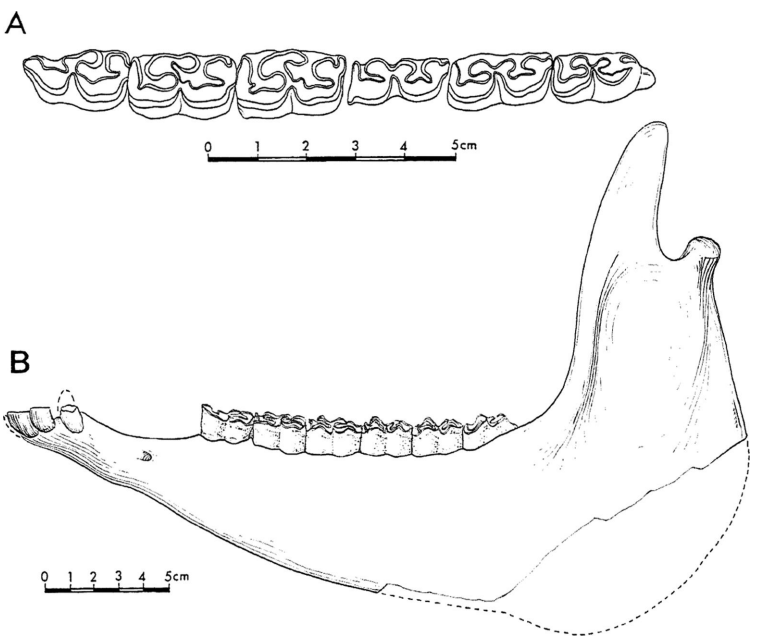


FIG. 61. *Neohipparion coloradense,* F:AM 69500, from the Chama El Rito Member of the Tesuque Formation, Santa Fe Group, late Barstovian or early Clarendonian of Rio Arriba County, New Mexico. A. Occlusal view of left P_2–M_3. B. Lateral view of left ramus. Also see figure 56.

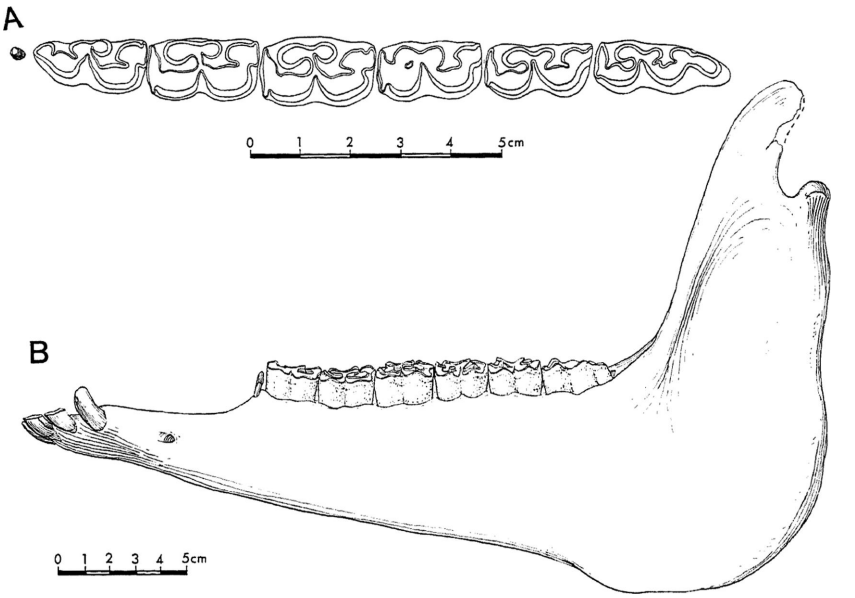


FIG. 62. *Neohipparion coloradense*, F:AM 69503 from the Cerro del Rio Puerco, Santa Fe Group, late Barstovian or early Clarendonian of the northern Albuquerque basin, Sandoval County, northern New Mexico. A. Occlusal view of left P_1–M_3. B. Lateral view of ramus (drawn from combination of both sides).

a medium-sized hipparion with relatively hypsodont teeth (figs. 52–57, table 18). The premaxillary bone extends posteriorly to position dorsal to P^2. The DPOF is poorly developed anteriorly; posteriorly it has a distinct and well-developed rim with a small posterior pocket. The posterior rim of the DPOF is situated dorsal to M^2 close to the anterior edge of the orbit, i.e., there is a very narrow PRB. The lacrimal bone is incorporated into the posterior part of the DPOF.

In the upper cheek tooth row the protocones are oval; they are relatively less elongated than in the other species of *Neohipparion* (fig. 49). The anterior protoconal spur frequently is present in early wear stages. In the prefossette, the pli protoconule usually is absent or consists of a single loop; the pli protoconule consists of a single loop, and the pli prefossette consists of one or more loops. In the postfossette, the pli postfossette usually consists of two or three loops; the pli hypostyle is absent or consists of a single loop. The pli caballin usually consists of a single loop.

Because the lower dental series has many primitive characters, it is best described from specimens that are definitely associated with skulls (figs. 58–62). The mandible is moderately deep. The ectoflexids are very deep in both the premolar and molar series. The pli caballinid is usually absent. The metaconids, metastylids, entoconids, and hypoconulids have rounded borders but, in contrast to most other hipparions, these parts are relatively unexpanded. The enamel is usually not plicated. The protostylids are well developed in P_3–M_3.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: As is also the case with the other most primitive species of the three other North American hipparion genera, *Neohipparion coloradense* exhibits many characters that are not far removed from the primitive merychippine grade of organization. (This is particularly true for the numerous primitive character states of the dental pattern.) In terms of crown height, *N. coloradense* is slightly more advanced than the other most primitive sister species of hipparions discussed in this

TABLE 19
Synopsis of Collections Examined for *Neohipparion affine* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comment
Several (see text and Osborn, 1918)	AMNH, USNM	Ash Hollow Formation and equivalents, northern Nebraska and southern South Dakota	Clarendonian	Type specimens of *N. affine, N. whitneyi* and *N. dolichops*
MacAdams Quarry, Locality 17; Quarries 1 and 7	F:AM, PPM	Clarendon Beds, Ogallala Group, Donley County, Texas	Clarendonian	
Numerous	F:AM	Ash Hollow Formation, Brown and Cherry counties, north-central Nebraska	Valentinian-Late Clarendonian	
Mo-101, Upper Miller Quarry	UNSM	Ash Hollow Formation, Morrill County, Nebraska	Late Clarendonian	

report. However, the configuration of the DPOF and its position on the face is a derived character complex that is shared with other members of the genus *Neohipparion* (fig. 50, table 16).

Because the early collection of many "merychippine grade" types from northeastern Colorado lack detailed provenance data, and because the lithostratigraphic nomenclature is ambiguous, the exact type locality can only be inferred for "*Hipparion*" *coloradense* (see Galbreath, 1953, for a discussion of the geology, faunas, and history of investigations in this region). Nevertheless, the type of "*Hipparion*" *coloradense* probably comes from the Sand Canyon L.F. from Logan County. The Frick sample referred to here as *N. coloradense* from Euhl Pit comes from approximately contemporaneous sediments of the Pawnee Creek Formation in adjacent Weld County (Tedford, personal commun., 1982). Therefore, this large quarry sample can be used as a reference for the morphology of this species in the region in which the type was collected. In addition to the Colorado specimens of *N. coloradense,* large samples are also represented in the Frick Collection from Nebraska and New Mexico. The total sample is referred here to *N. coloradense* based on similarities in both the dentitions and associated postcranial elements (the type also includes some of the latter). In both the type and referred samples, the protocones are oval to slightly elongated, the fossette borders are of similar complexity, the pli caballin usually consists of a single well-developed fold, and the crown heights and postcranial elements are of similar proportions.

The oldest occurrence of *N. coloradense,* which is also the first occurrence of the genus, is from the early Barstovian Boulder Quarry in Sioux County, Nebraska. As such, this species is roughly contemporaneous with the most primitive species of *Hipparion* and *Cormohipparion,* i.e., *H. shirleyi* and *C. goorisi. N. coloradense* apparently becomes very widespread in the midcontinent during the late Barstovian and probably persists into the early Clarendonian. During the Valentinian of Nebraska, *N. coloradense* coexists with its more advanced sister species, *N. affine.*

Neohipparion affine (Leidy), 1869
Figures 8, 15, 47–50, 63–69, 147, 150; Tables 2, 16, 19, 20

JUNIOR SYNONYMS

Neohipparion whitneyi Gidley, 1903, pp. 467–476 (no figure).

Neohipparion dolichops Gidley, 1906, pp. 148–149, fig. 14.

TYPE SPECIMEN AND LOCALITY: USNM 584, a series of five upper molars, from the Niobrara River near Fort Niobrara, deposits of

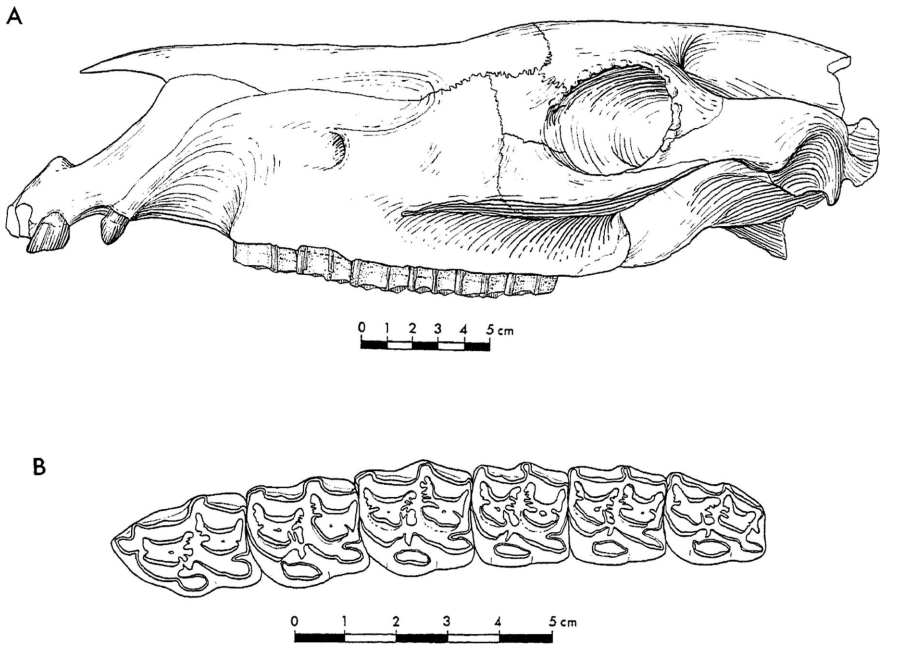


FIG. 63. *Neohipparion affine*, UNSM 42449, from UNSM locality Mo-101, Upper Miller Quarry, Ogallala Group, late Clarendonian of Morrill County, western Nebraska. A. Left lateral view of skull. B. Occlusal view of left P^2–M^3.

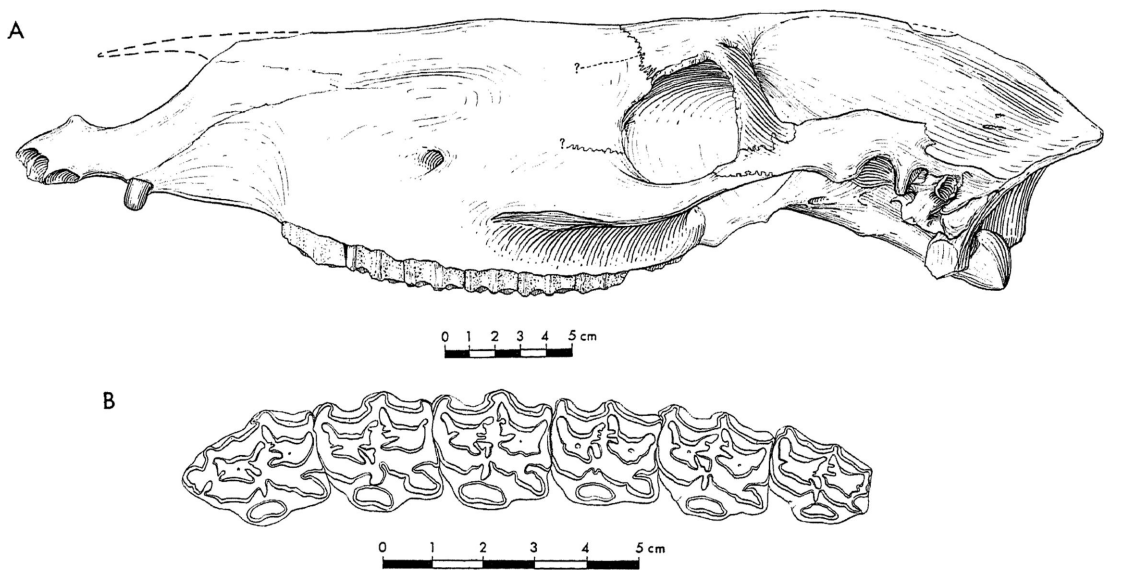


FIG. 64. *Neohipparion affine*, F:AM 108644, from Leptarctus Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska. A. Left lateral view of skull. Development of lacrimal bone is uncertain due to poor preservation. B. Occlusal view of left P^2–M^3.

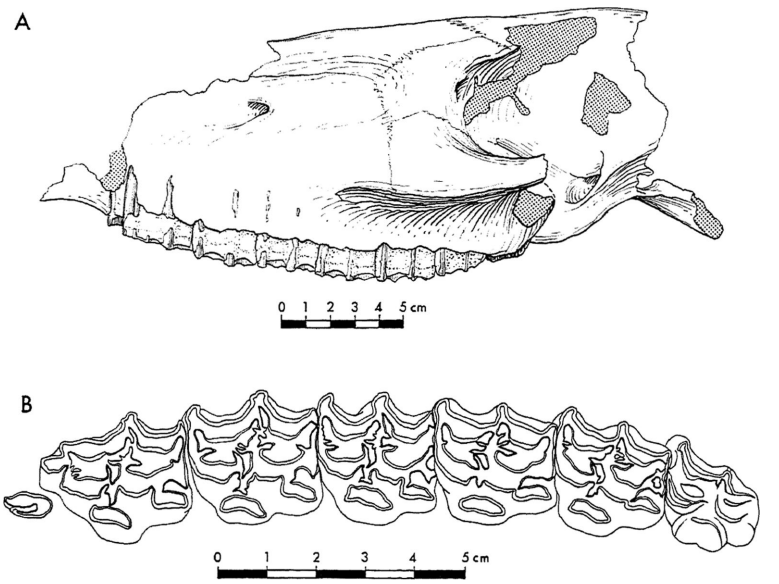


FIG. 65. *Neohipparion affine,* UNSM 42438, from UNSM locality Mo-101, Upper Miller Quarry, Ogallala Group, late Clarendonian of Morrill County, western Nebraska. A. Left lateral view of skull. B. Occlusal view of left P^1–M^3.

late Clarendonian age from Nebraska (see Osborn, 1918, p. 178, fig. 141).

REVISED DIAGNOSIS: Same as for generic diagnosis with the following specific characters: DPOF poorly developed and fades onto the surrounding cheek region. Posteriorly, DPOF relatively shallow, not pocketed, and not rimmed. Posterior extent of this fossa developed on the nasal and maxillary bones or on the lacrimal bone. Mean TRL 142.47 mm. Cheek tooth dentition moderately hypsodont. Unworn or little-worn M1MSTHT *ca.* 42–50 mm. Protocone elongate. Ectoflexids relatively deep.

Neohipparion affine differs from other hipparions (and all other horse genera) in the diagnostic generic characters (see above). In particular, *N. affine* differs from the merychippine outgroup and *N. coloradense* in its greater size, increased hypsodonty, and numerous dental characters, such as fully isolated and elongated protocones and expansion of conids and stylids. *N. affine* differs from *N. trampasense* in its larger size and more primitive dental pattern; from *N. leptode* in a more primitive dental pattern; *N. eurystyle* in lower crown height, larger size, and more primitive dental pattern; and from *N. gidleyi* in lower crown height, smaller size, and more primitive dental pattern.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Valentinian of Nebraska and adjacent South Dakota, early Clarendonian of the Texas Panhandle, and late Clarendonian of the Texas Panhandle, Nebraska, and South Dakota (table 19).

DESCRIPTION: *Neohipparion affine* is a large hipparion with relatively hypsodont cheek teeth (figs. 46, 47, 63–67; table 20). The nasal notch is shallow, i.e., retracted to a position just posterodorsal to the canine. The premaxillary bone extends posteriorly to a position over P^2. The buccinator fossa is not confluent with the DPOF. The DPOF is poorly developed in contrast to *Cormohipparion* and *Hipparion* and better developed than *Nannippus peninsulatus.* In *N. affine* the DPOF is usually developed on the nasal and maxillary bones, but sometimes the posterior border is also developed on the lacrimal bone (see, for example, holotype of *Neohipparion "whitneyi"* Gidley, 1903, AMNH 9815; also see fig. 46 of this report). The anterior border of the DPOF is poorly defined and extends

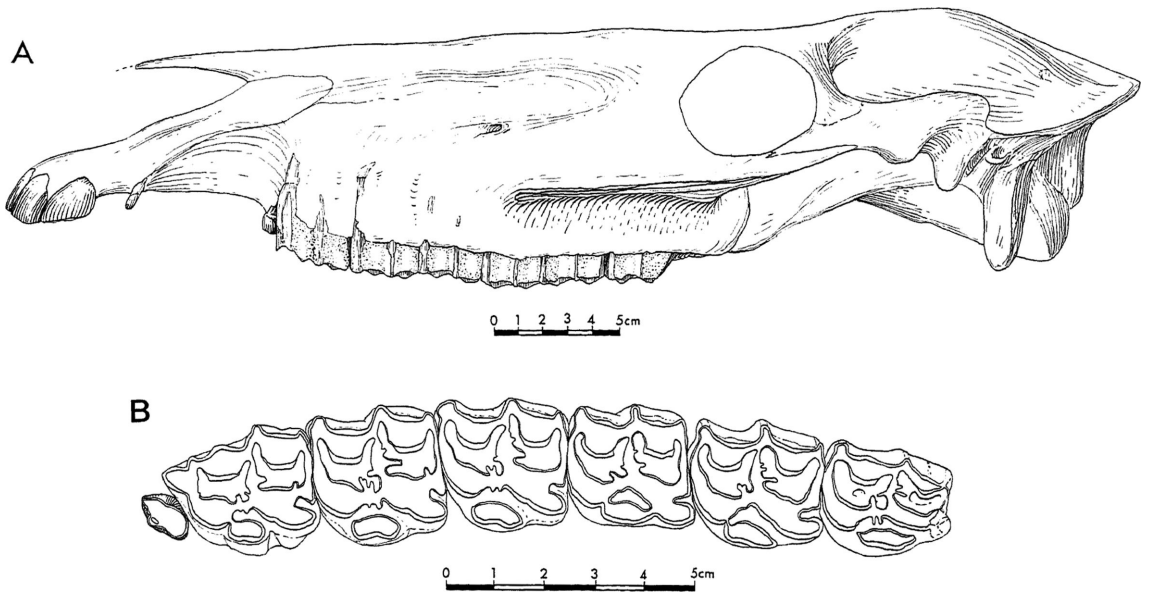


FIG. 66. *Neohipparion affine,* F:AM 111728, from MacAdams Quarry, Clarendon Beds, Ogallala Group, early Clarendonian of Donley County, Texas Panhandle. A. Lateral view of skull (composite restoration from both sides). Position of sutures on cheek region is indeterminate. B. Occlusal view of right (reversed) P^1–M^3.

smoothly onto the surrounding facial region. The posterior border is shallow and never rimmed or pocketed as in *Cormohipparion.* The infraorbital foramen lies over P^4.

In the upper cheek teeth the protocones are characteristic of *Neohipparion* (figs. 46, 63–68). These structures are very elongate in contrast to, e.g., North American *Hipparion sensu stricto.* The anterior and posterior margins of the protocone vary (with geographic sample and wear) from rounded to angular. The plications on the fossette borders are simple to moderately well developed, but less so than, e.g., *N. leptode* or *Cormohipparion occidentale.* In the prefossette, the pli protoloph consists of one loop or is absent. The pli protoconule usually consists of a single loop. The pli prefossette usually consists of multiple loops. In the postfossette, the pli hypostyle is absent, rudimentary, or consists of a single loop. The pli postfossette usually consists of multiple loops.

The lower cheek teeth of *Neohipparion affine* are of similar pattern and size to *Cormohipparion.* Therefore, the lower dentition of *N. affine* is best described from specimens with associated skulls and jaws such as AMNH 9815 (fig. 47B) or F:AM 111728 (fig. 69). The ectoflexids are relatively deep. The pli caballinid is usually rudimentary or poorly developed in the premolars and absent in the molars. The isthmus is characteristically distinct. Plications are usually rudimentary or absent on the isthmus. Anteriorly in the lower cheek teeth there are well-developed protostylids. The enamel borders are usually not plicated.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: *Neohipparion affine* exhibits the diagnostic characters that ally this species with this genus (see generic discussion above). With respect to character polarities, *N. affine* represents an intermediate species within the genus. In contrast to merychippines and *N. coloradense, N. affine* is larger and more hypsodont (fig. 50, table 16). In the dentition, *N. affine* is advanced over merychippines and *N. coloradense* in character states such as the more elongated protocones and more expanded conids and stylids. The DPOF of *N. affine* is reduced (derived) relative to the condition in *N. coloradense.* With regard to size

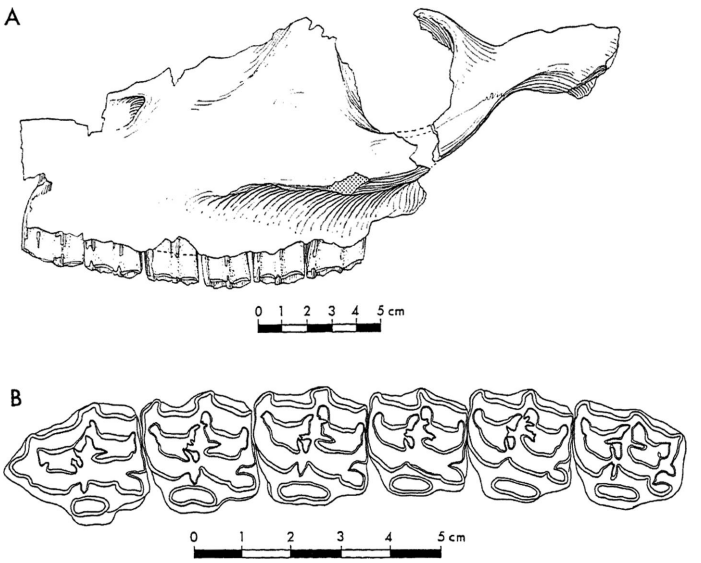


FIG. 67. *Neohipparion affine*, F:AM 111729, from MacAdams Quarry, Clarendon Beds, Ogallala Group, early Clarendonian of Donley County, Texas Panhandle. A. Left lateral view of skull. Position of sutures on cheek region is indeterminate. B. Occlusal view of P^2–M^3.

N. affine exceeds the other species of *Neohipparion* except *N. gidleyi* (figs. 48, 49). *N. affine* has shorter crowns than either *N. eurystyle* or *N. gidleyi*. The dental pattern of *N. affine* is more primitive than *N. trampasense, N. leptode, N. eurystyle* and *N. gidleyi*. Based on these morphoclines it is apparent that there are several conflicting character polarities for

TABLE 20
Selected Upper Dental Measurements and Univariate Statistics for *Neohipparion affine*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	17	28.44	1.08	3.81	26.8–30.4	15	28.61	1.03	3.60	27.4–30.4
P2TRNW	19	21.99	1.03	4.69	19.6–23.5	16	22.10	1.07	4.84	19.6–23.5
P2PRTL	19	7.80	1.05	13.41	5.9–9.8	16	7.90	1.02	12.91	6.1–9.8
P2PRTW	19	4.24	0.35	8.18	3.6–4.9	16	4.21	0.36	8.55	3.6–4.9
P2TOTPLI	17	4.24	1.64	38.73	1–7	15	4.33	1.63	37.64	1–7
M1APL	21	22.07	1.98	8.98	18.3–25.9	18	22.22	1.93	8.69	19.9–25.9
M1ECTL	22	21.99	1.76	7.99	18.6–25.5	19	23.04	1.67	7.25	19.7–25.5
M1TRNW	22	22.30	1.17	5.24	20.5–24.8	19	22.33	1.20	5.37	20.5–24.8
M1PRTL	22	9.54	0.82	8.62	8.3–10.9	19	9.62	0.86	8.94	8.3–10.9
M1PRTW	22	4.18	0.44	10.6	3.2–5.1	19	4.11	0.41	9.98	3.2–4.9
M1TOTPLI	19	4.74	2.56	53.98	0–11	16	5.00	2.39	47.80	2–11
TRL	13	142.47	7.03	4.93	132.6–154.5	10	143.97	7.10	4.93	136.0–154.5
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	8	34.05	3.77	11.06	28.8–39.0	1	39.0	—	—	—
M1MSTHT	3	43.70	2.43	5.55	41.7–46.4	0	—	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 19 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

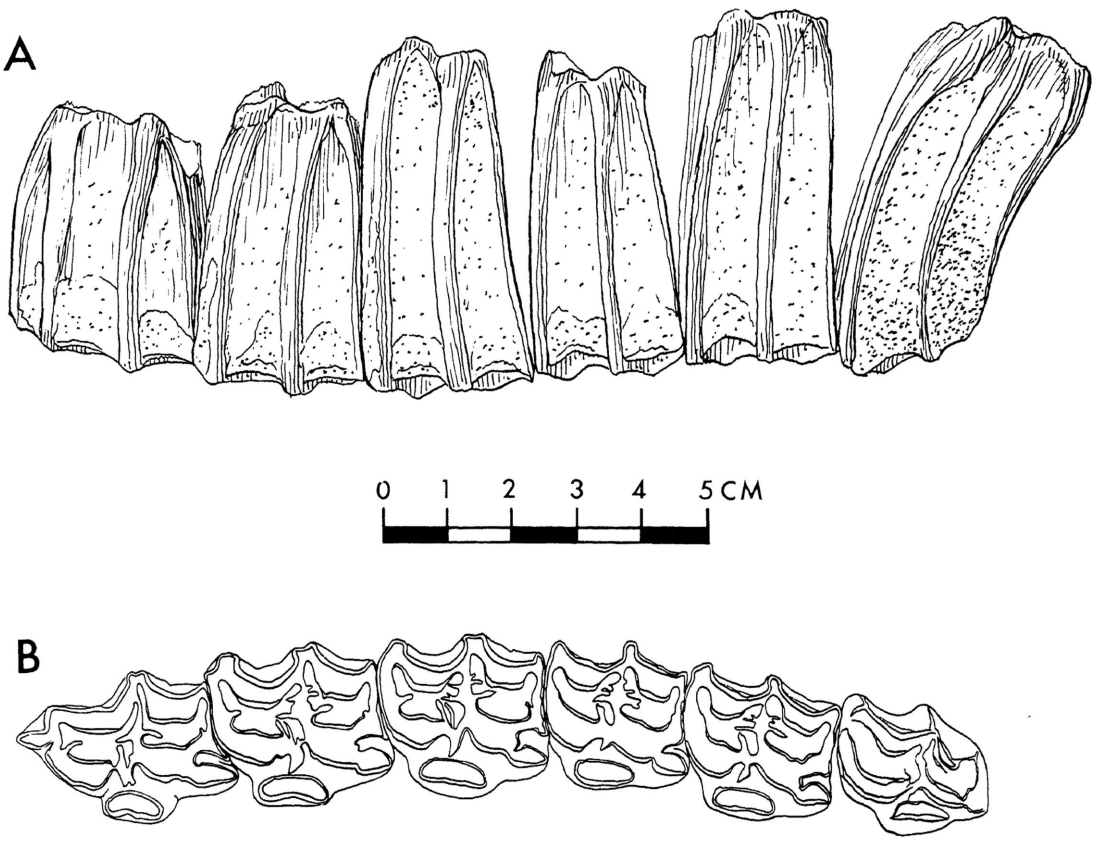


FIG. 68. *Neohipparion affine,* F:AM 108236, from Eli Ash Pit, Caprock Member of the lower Ash Hollow Formation, early Clarendonian of Cherry County, north-central Nebraska. A. Lateral (external view) of left P^2–M^3 showing crown height. B. Occlusal view.

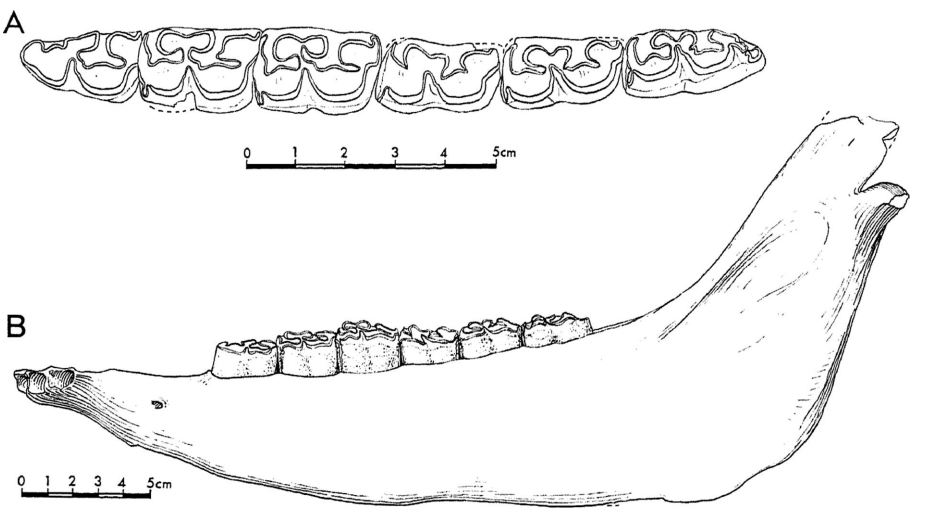


FIG. 69. *Neohipparion affine,* F:AM 111728, from MacAdams Quarry, Clarendon Beds, Ogallala Group, early Clarendonian of Donley County, Texas Panhandle. A. Occlusal view of left P_2–M_3. B. Lateral (external) view of left ramus.

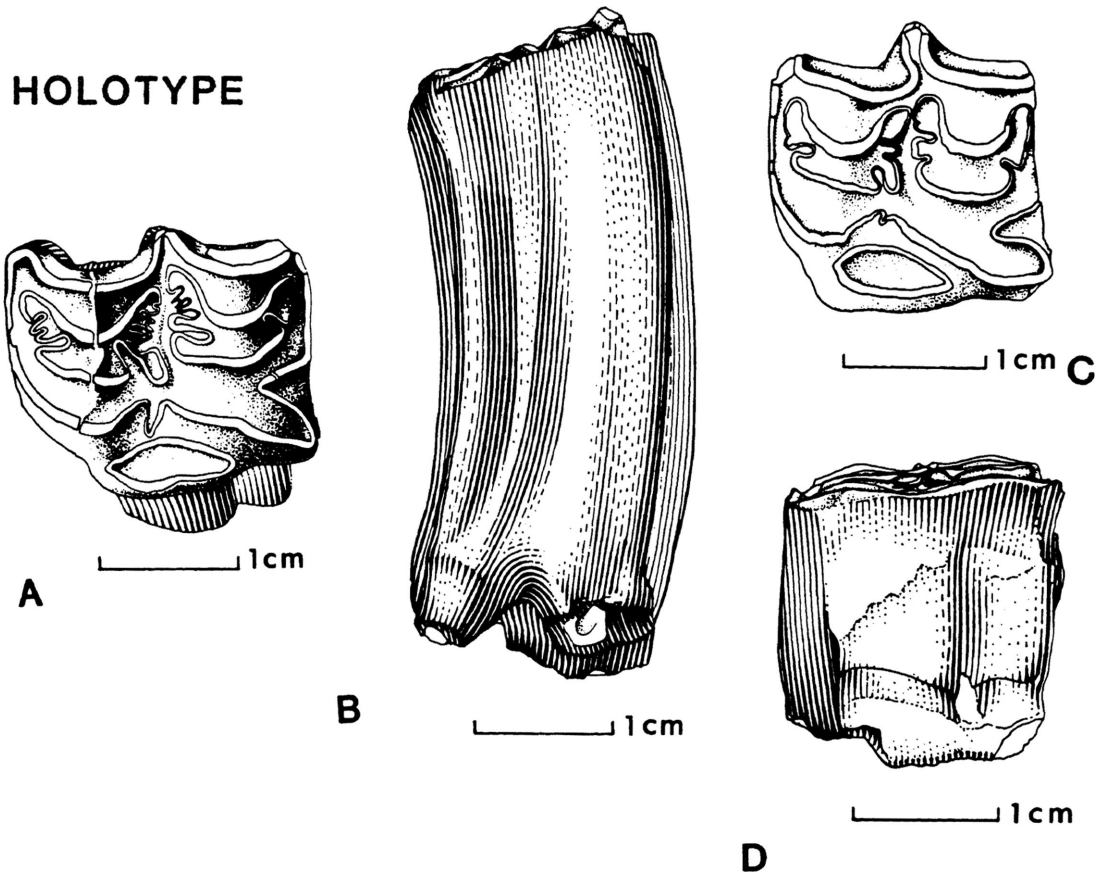


FIG. 70. *Neohipparion trampasense* from the Kendall-Mallory L.F., UCMP locality V6107, late Clarendonian of Contra Costa County, San Francisco Bay region of northern California. (A) Occlusal and (B) posterior views of holotype, UCMP 58234, left M^2. (C) Occlusal and (D) lingual views of UCMP 125678, well-worn left P^4. ©1982 and reproduced (slightly modified) with permission of the Journal of Vertebrate Paleontology.

the genus *Neohipparion* (fig. 50). The phylogenetic implications of this character analysis is discussed below. The earliest occurrence of *N. affine* is from the Crookston Bridge Member of the Valentine Formation (represented by a crushed skull, UNSM 53998). During the Barstovian and early Clarendonian (also Valentinian) both *N. affine* and *N. coloradense* occur contemporaneously in the Great Plains region. The Valentinian *N. affine* is probably, at least in part, what Stirton (1940) referred to as *Merychippus* cf. *republicanus*. Stirton's concept of *M.* cf. *republicanus* is based on specimens from Nebraska. However, the type of *M. republicanus* is a small skull, AMNH 8347, which probably is not related to *Neohipparion*.

Several workers such as McGrew (1938), Stirton (1940), Gregory (1942), and Webb (1969) concluded that the late Clarendonian species *N. whitneyi, N. dolichops, N. affine,* and "*N.*" *occidentale* are synonymous. Skinner and MacFadden (1977) demonstrated that "*N.*" *occidentale* is a member of *Cormohipparion* based on well-preserved skulls and dentitions. After removing *C. occidentale* from this late Clarendonian *Neohipparion* complex, the recommendation of previous workers is followed here, i.e., *N. whitneyi* and *N. dolichops* are junior synonyms of *N. affine*.

TABLE 21
Synopsis of Collections Examined for *Neohipparion trampasense* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comment
Kendall-Mallory L.F., V6107, V6318	UCMP	Contra Costa Group (undifferentiated), Bolinger Canyon, Contra Costa County, California	Late Clarendonian	Type locality
Hans Johnson Quarry	F:AM	Ash Hollow Formation, Cherry County, north-central Nebraska	Late Clarendonian	Only one specimen definitely referable to this species from Hans Johnson Quarry, F:AM 111727
Love Bone Bed	UF	Alachua Formation, Alachua County, Florida	Late Clarendonian	
McGehee	UF	Alachua Formation, Alachua County, Florida	Early Hemphillian	Probably referable to this species (Hulbert, personal commun., 1983)

In addition, known cranial material for *N. affine* (*sensu lato*) demonstrates a morphological continuity that justifies this synonymy.

Neohipparion trampasense (Edwards), 1982, New Combination
Figures 20, 48–50, 70–75, 147, 150; Tables 2, 16, 21, 22

TYPE SPECIMEN AND LOCALITY: UCMP 58234, LM^2 from locality V6107, Bolinger Canyon, Kendall-Mallory L.F., Contra Costa County, California (see Edwards, 1982; also fig. 70).

REVISED DIAGNOSIS: Same as for genus with the following specific characters: DPOF rudimentary or absent. Medium-sized hipparion (small for *Neohipparion*). Mean TRL 121.36 mm. Teeth moderately hypsodont. Unworn or little-worn M1MSTHT *ca.* 46–53 mm. Elongated protocones oftentimes with angular borders. Fossette borders relatively plicated. In the lower cheek teeth, pli caballinids and isthmuses well developed in premolars; pli caballinids rudimentary to absent and ectoflexids deep in molars. Isthmuses frequently plicated.

Neophipparion trampasense differs from other hipparion (and all other) horse genera in the diagnostic generic characters. It differs from the merychippine outgroup and *N. coloradense* in more hypsodont teeth and more advanced dental pattern (e.g., elongated protocones more complex fossette borders, shallower ectoflexids, and, in the premolars, better developed pli caballinids). *N. trampasense* differs from *N. affine, N. leptode* and *N. gidleyi* in its smaller size. It differs from *N. eurystyle* and *N. gidleyi* in crown height and a less complex dental pattern (the generic extremes are represented by the latter two species, see below).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Late Clarendonian of California, Nebraska, and Florida; probably early Hemphillian of Florida (table 21).

DESCRIPTION: *Neohipparion trampasense* is a medium-sized hipparion (table 22). Partial skulls referred to this species are only known from the Love Bone Bed L.F. of Florida (e.g., fig. 71). There is a very slight depression that lies above M^1 that probably represents the posteriormost portion of a rudimentary DPOF. The remainder of the cheek region that lies between this depression and the anterior margin of the orbit is smooth. The lacrimal bone lies far posterior to the rudimentary DPOF. There also is a very faint depression anterior to the orbit (in the position of the malar fossa).

In the upper cheek teeth the protocones are relatively elongated (figs. 70–73). The pli caballin usually consists of two loops in the

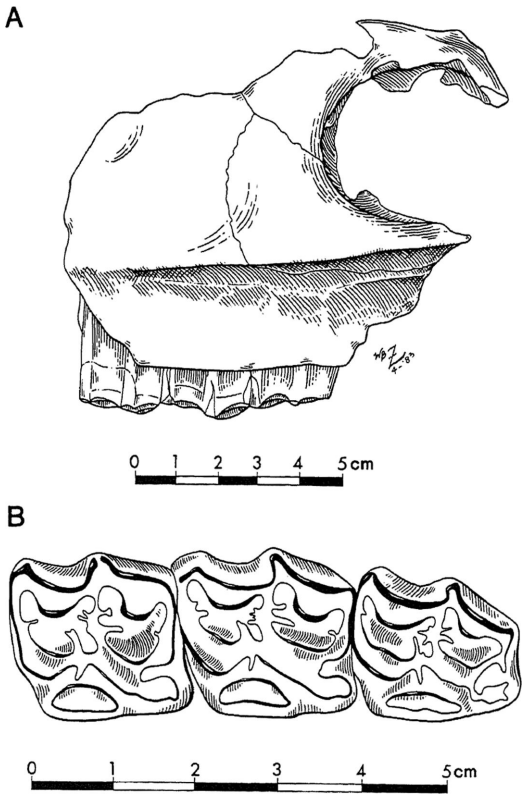


FIG. 71. *Neohipparion trampasense,* UF 32251, from Love Bone Bed, Alachua Formation, late Clarendonian of Alachua County, north-central Florida. A. Lateral view of right (reversed) preorbital region. B. Occlusal view of right (reversed) M^1–M^3.

premolars and one loop in the molars. In the prefossette, the pli protoloph usually consists of one to multiple loops (it is not usually absent except during examples of later wear), the pli protoconule consists of a very large loop, and the pli prefossette usually consists of multiple loops. The pli postfossette usually consists of multiple loops and the pli hypostyle usually consists of a single loop.

In the lower cheek teeth the conids, stylids, and hypoconulids are expanded like more advanced species of *Neohipparion* (figs. 74, 75). In the premolars, the ectoflexids are shallow or rudimentary and the pli caballinids are very well developed. The isthmus is usually plicated on both the anterior and posterior margins. As with some other hipparions (e.g., advanced *Neohipparion* and *Cormohipparion occidentale*) the molar series in *N. trampasense* exhibit a generally more primitive morphology than that of the premolar series. In the molars the ectoflexid is usually relatively deep (although for an exception see fig. 75) which results in the division of the isthmus into the antero-isthmus and postero-isthmus. The protostylid is well developed. Frequently there are plications developed on these isthmuses.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: *Neohipparion trampasense* represents an intermediate member of a morphocline consisting of the species of this genus. As is also the case for *N. eurystyle,* but

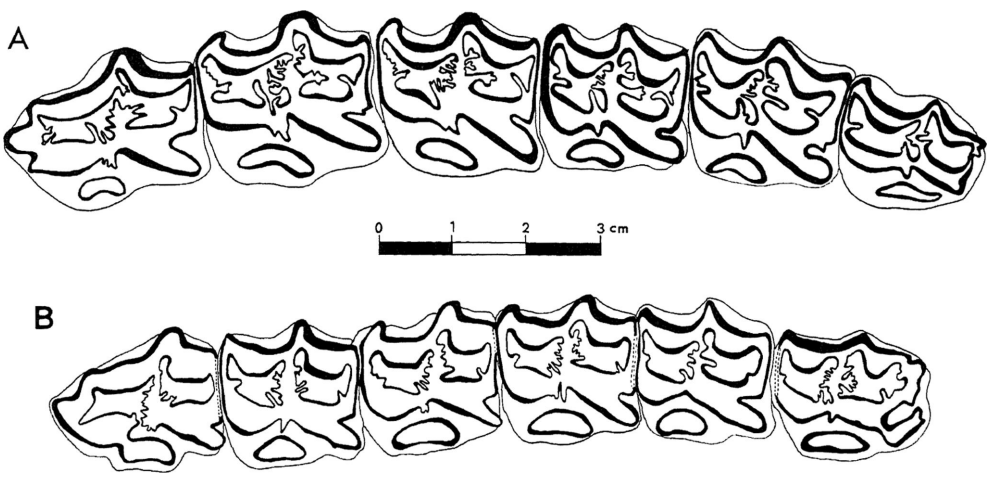


FIG. 72. Left occlusal views of P^2-M^3 of *Neohipparion trampasense* from Love Bone Bed, Alachua Formation, late Clarendonian of Alachua County, north-central Florida. A. UF 27991. B. UF 27992.

TABLE 22
Selected Upper Dental Measurements and Univariate Statistics for *Neohipparion trampasense*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	9	24.92	1.87	7.49	21.5–26.6	6	24.70	2.05	8.30	21.5–26.5
P2TRNW	8	17.80	0.87	4.89	16.8–19.0	6	18.05	0.87	4.82	16.8–19.0
P2PRTL	8	7.10	0.66	9.31	5.9–7.7	6	7.25	0.53	7.31	6.5–7.7
P2PRTW	8	3.63	0.27	7.48	3.3–4.0	6	3.67	0.28	7.63	3.3–4.0
P2TOTPLI	7	7.86	3.44	43.74	3–12	6	8.67	2.94	33.91	4–12
M1APL	17	20.35	1.84	9.04	16.9–23.4	10	20.02	1.64	8.19	17.9–22.8
M1ECTL	17	20.54	1.93	9.40	17.7–23.4	10	19.99	1.79	8.95	18.2–22.8
M1TRNW	17	17.25	1.83	10.63	12.5–19.4	10	17.73	1.30	7.33	14.4–19.0
M1PRTL	17	7.62	1.00	13.10	5.0–9.1	10	7.53	1.14	15.14	5.0–9.1
M1PRTW	16	3.29	0.32	9.68	2.9–3.9	10	3.29	0.31	9.42	2.9–3.7
M1TOTPLI	16	9.25	2.54	27.49	4–14	10	10.50	1.96	18.67	8–14
TRL	5	121.36	5.72	4.71	115.6–129.3	4	122.50	5.91	4.82	115.6–129.3
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	8	28.83	7.77	26.94	15.3–39.5	2	35.85	5.16	14.39	32.2–39.5
M1MSTHT	12	39.93	9.53	23.86	18.0–52.2	4	49.18	4.20	8.54	43.0–52.2

[a] Abbreviations are presented on pp. 21 and 22; see table 21 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

in contrast to *N. affine, N. leptode,* and *N. gidleyi, N. trampasense* retains a relatively small size. In the dental pattern (particularly in the lower cheek teeth), *N. trampasense* is advanced over primitive merychippines, *N. coloradense,* and *N. affine. N. trampasense* shares several derived dental characters with *N. leptode, N. eurystyle,* and *N. gidleyi,* e.g., development of the pli caballinids and shallow ectoflexids.

Edwards (1982) originally described the species *Hipparion trampasense* from late Clarendonian deposits of Bolinger Canyon in northern California. During the present study, the topotypic sample was examined and measured. Based on the advanced *Neohipparion* characters discussed above, this recently named species is recognized here as *N. trampasense* (it is too advanced in the dental pattern to be included in *Hipparion, Nannippus,* or *Cormohipparion*). One mandible from the late Clarendonian of Nebraska, F:AM 111727 (fig. 75), as well as the large sample from the late Clarendonian Love Bone Bed of Florida, display many of the *differentia* of the topotypic sample and are therefore referred to this species. In addition, because the Bolinger Canyon sample does not contain any cranial specimens, the Love site material (see fig. 71) is important because it demonstrates the cheek morphology of this species and therefore corroborates allocation to the genus *Neohipparion.* Work in progress (Hulbert, personal commun., 1983) indicates that specimens referable to this species are probably represented at the early Hemphillian McGehee L.F. from north-central Florida. In summary, *N. trampasense* was a geographically widespread, although not particularly common, species of *Neohipparion.* It probably co-occurred in sediments in the same region as *N. affine* (as well as other species of hipparions). The present study corroborates Edward's (1982) suggestion that *N. trampasense* seems to have been close to the basal stock from which the advanced Hemphillian *Neohipparion* species were derived.

Neohipparion leptode Merriam, 1915a

Figures 48–50, 76, 77, 147, 150;
Tables 2, 16, 23, 24

TYPE SPECIMEN AND LOCALITY: UCMP 19414, an isolated lower molar, from Thou-

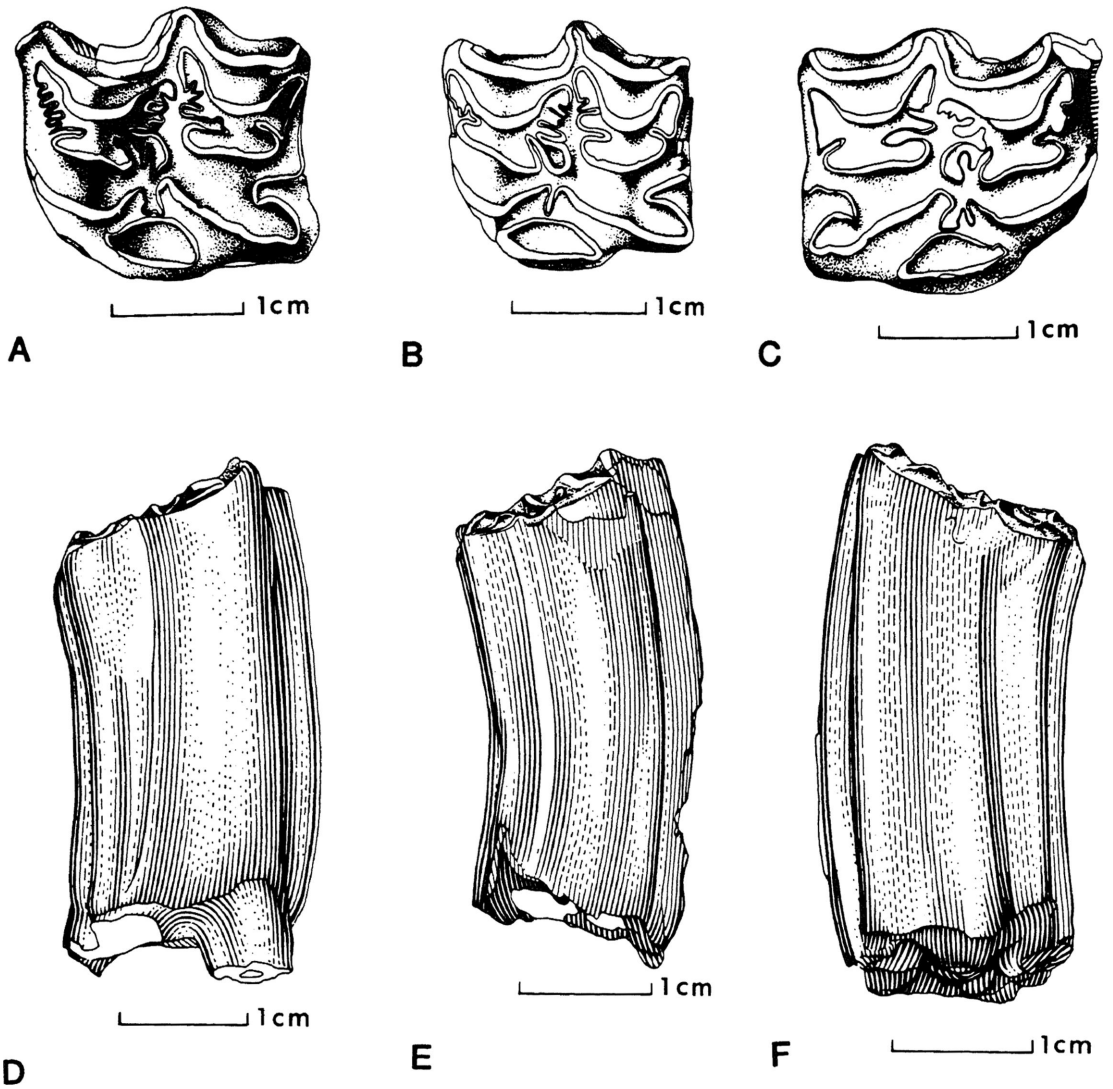


FIG. 73. *Neohipparion trampasense* from the Kendall-Mallory L.F., UCMP locality V6107, late Clarendonian of the San Francisco Bay region, Contra Costa County, northern California. (A) Occlusal and (D) posterior views of UCMP 71201, left P^4. (B) Occlusal and (E) posterior views of UCMP 112199, left M^2. (C) Occlusal and (F) posterior views of UCMP 58235, right P^3. ©1982 and reproduced (slightly modified) with permission of the Journal of Vertebrate Paleontology.

sand Creek (UCMP locality 1101), early Hemphillian of Humboldt County, Nevada (see Merriam, 1915a, p. 4, fig. 3).

REVISED DIAGNOSIS: Same as for the genus with the following specific characters: DPOF rudimentary or absent. Large hipparion. Mean TRL 140.95 mm. Teeth relatively hypsodont. Unworn or little-worn M1MSTHT *ca.* 46–55 mm. More elongate protocones than *N. affine* but less elongate than *N. eurystyle*. Fossette borders moderately complicated. Pli caballinids well developed in the premolars but less well developed in the molars. Metaconids, metastylids, entoconids, and hypoconulids moderately expanded with rounded or angular enamel borders.

Neohipparion leptode differs from other hipparion (and all other) horse genera in the

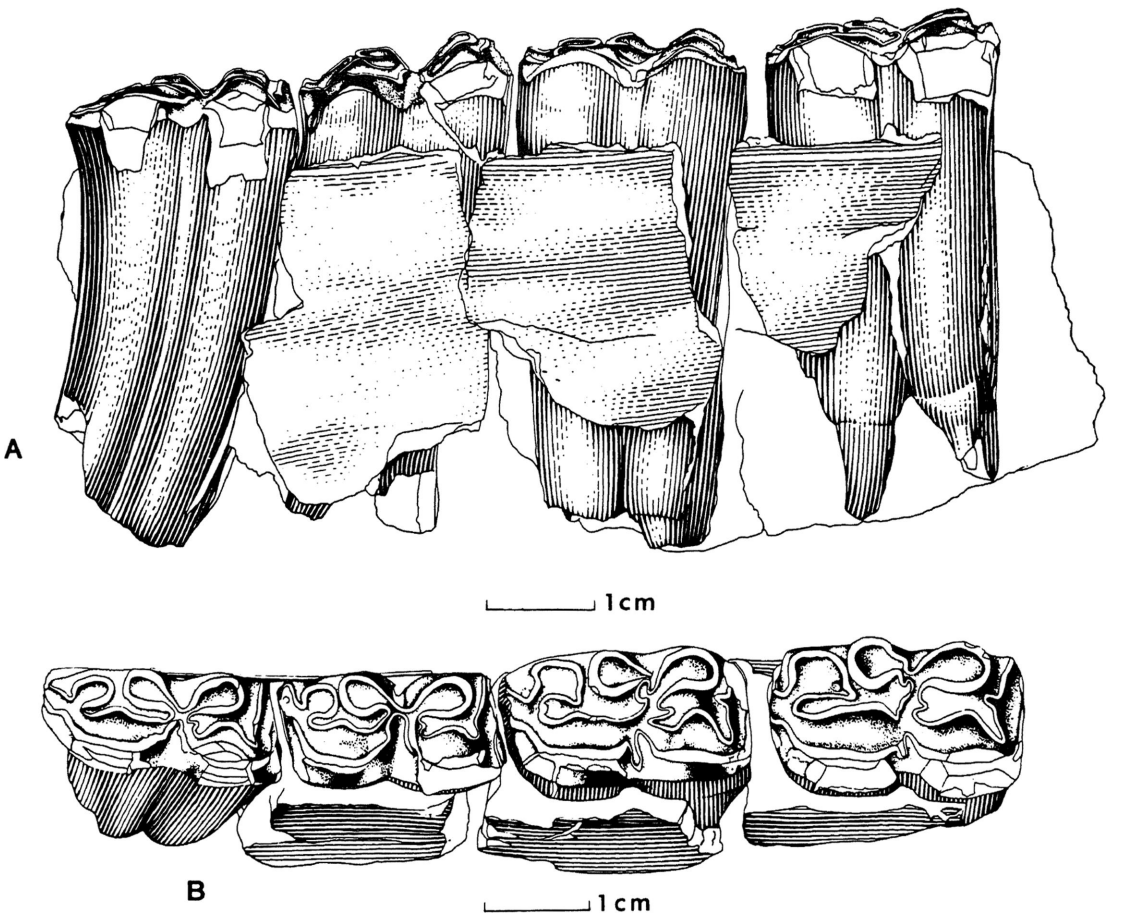


FIG. 74. *Neohipparion trampasense,* UCMP 58244, from the Kendall-Mallory L.F., UCMP locality V6107, late Clarendonian of the San Francisco Bay region, Contra Costa County, northern California. (A) Lateral (external) view of partial right ramus with P_2–M_2. (B) Occlusal view. ©1982 and reproduced (slightly modified) with permission of the Journal of Vertebrate Paleontology.

diagnostic generic characters. It differs from the merychippine outgroup, *N. coloradense,* and *N. affine* in the relatively reduced DPOF, slightly larger size and hypsodonty, and numerous dental characters, e.g., increased relative size (elongation) of protocones, development of pli caballinids (particularly in the premolars), conids and stylids, and shallower ectoflexids. *N. leptode* differs from *N. trampasense* principally in its larger size. *N. leptode* differs from *N. eurystyle* in its larger size and probably shorter crowns (less hypsodont), less elongated and less angular protocones, and, particularly in the molars, less well-developed pli caballinids and slightly deeper ectoflexids. Although *N. leptode* is of similar size to *N. gidleyi,* the former species is not as advanced in characters of the dental pattern.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Several localities of Hemphillian age including Ogallala Group of western Oklahoma and Kansas, and the Thousand Creek Beds of Nevada (table 23).

DESCRIPTION: This species is best represented in the LACM (CIT) collection described by Stock (1951), although good specimens referred to this species are also housed in other collections (table 23).

Neohipparion leptode is a large hipparion,

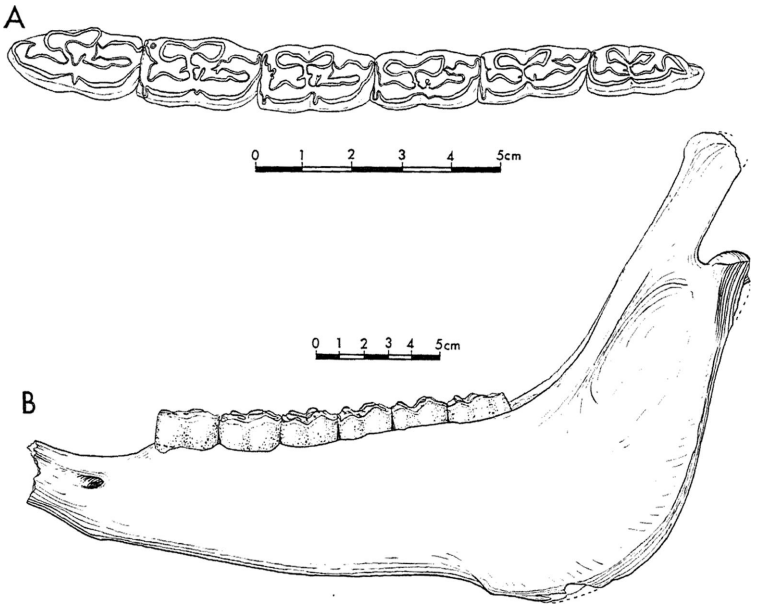


FIG. 75. *Neohipparion trampasense,* F:AM 111727, from Hans Johnson Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska. A. Occlusal view of left P_2–M_3. B. Lateral view of left ramus.

similar in size to *N. affine* (fig. 76, table 24). The nasal notch is retracted to a position above the postcanine diastema just anterior to P^2. In the cranial material from Thousand Creek, e.g., LACM (CIT) 54 (also UCMP 27126, not illustrated here), the DPOF consists of a very faint depression (fig. 76) similar to structures in available cranial material of *N. trampasense* and *N. eurystyle.* In LACM (CIT) 54 this depression may be accentuated

TABLE 23
Synopsis of Collections Examined for *Neohipparion leptode* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Thousand Creek, UCMP 1101	LACM (CIT), UCMP	Thousand Creek Beds, Humboldt County, western Nevada	Early Hemphillian	Type locality
Arens Quarry	F:AM	Ogallala Group, Norton County, northern Kansas	Hemphillian	
Capps-Neu Quarry	WTSU	Ogallala Group, Ellis County, Oklahoma	Early Hemphillian	Well-preserved skull, WTSU-V-6675; Capps-Neu Quarry equivalent to Port of Entry pit and Arnett locality (Schultz, personal commun., 1981)

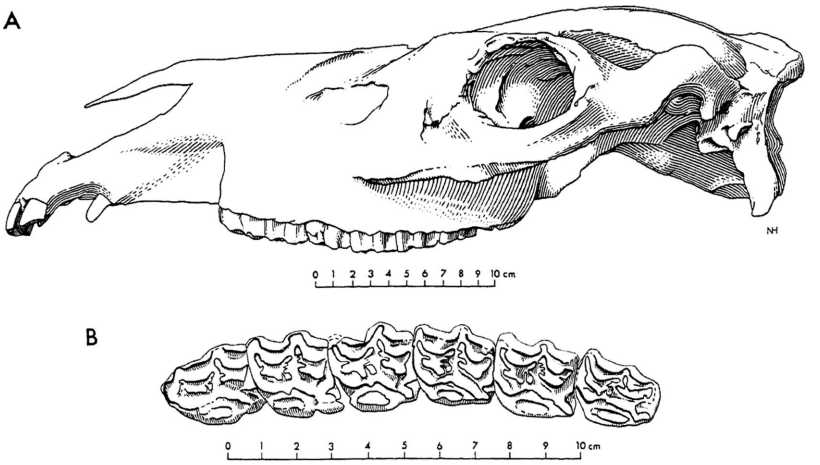


FIG. 76. *Neohipparion leptode,* LACM (CIT) 54, from the Thousand Creek L.F., Thousand Creek Beds, early Hemphillian of Humboldt County, northwestern Nevada. A. Left lateral view of skull. B. Occlusal view of P^2–M^3. Also see Stock (1951).

by dorsoventral crushing. The DPOF is situated relatively anterior to the orbit (right PRB = *ca.* 55 mm, left PRB = 46 mm). As is also seen in *N. trampasense* (fig. 71), LACM (CIT) 54 (and also noted by Stock, 1951 in his description of this specimen) appears to have a very small, rounded, and poorly developed pit just anterior to the orbit and dorsal to the malar crest (in the position of the malar fossa in other horses such as *Pliohippus* and *Astrohippus*). In both *N. trampasense* and *N. leptode* this pit is much smaller in anteriorposterior length than in the other horses with a malar fossa, i.e., it is a faint pit rather

TABLE 24
Selected Upper Dental Measurements and Univariate Statistics for *Neohipparion leptode*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	4	28.70	1.12	3.89	27.2–29.8	3	27.93	0.75	2.69	27.2–28.7
P2TRNW	3	21.23	0.46	2.15	20.7–21.5	3	21.23	0.46	2.15	20.7–21.5
P2PRTL	4	9.35	0.58	6.21	8.7–10.1	3	9.10	0.36	3.96	8.7–9.4
P2PRTW	3	4.03	0.25	6.20	3.8–4.3	3	4.03	0.25	6.20	3.8–4.3
P2TOTPLI	3	6.67	2.08	31.21	5–9	3	6.67	2.08	31.21	5–9
M1APL	6	23.87	1.44	6.05	22.7–26.7	4	23.18	0.37	1.59	22.7–23.6
M1ECTL	5	20.66	1.75	8.49	17.8–20.2	3	21.77	0.35	1.61	21.4–22.1
M1TRNW	6	23.57	1.22	5.16	22.8–25.9	4	23.15	0.52	2.25	22.8–23.9
M1PRTL	6	9.70	0.66	6.81	9.0–10.7	4	9.63	0.47	4.90	9.3–10.3
M1PRTW	5	3.96	0.36	9.09	3.5–4.5	3	4.10	0.35	8.53	3.9–4.5
M1TOTPLI	4	8.75	2.36	27.00	7–12	3	9.33	2.52	27.00	7–12
TRL	2	140.95	0.07	0.05	140.9–141.0	2	140.95	0.07	0.05	140.9–141.0
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	2	40.40	6.36	15.75	35.9–44.9	1	44.9	—	—	—
M1MSTHT	3	54.0	2.84	5.26	50.8–56.0	1	56.2	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 23 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

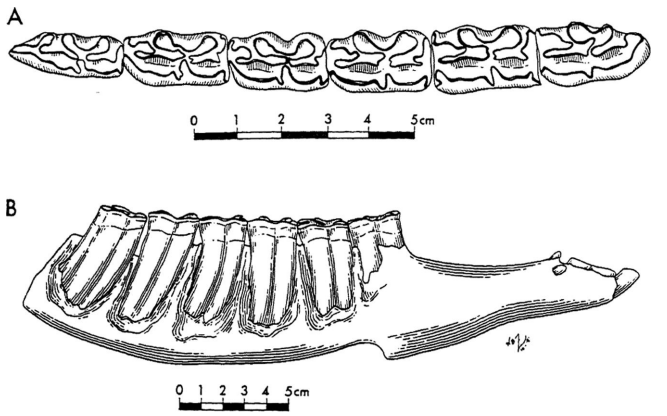


FIG. 77. *Neohipparion leptode,* UCMP 27126, from the Thousand Creek L.F., Thousand Creek Beds, early Hemphillian of Humboldt County, northwestern Nevada. A. Occlusal view of right P_2–M_3. B. Right lateral view of mandible with bone removed to show crown height of lower cheek teeth.

than an elongate depression. To a certain extent in LACM (CIT) 54, this feature might be accentuated by crushing, but it does appear as a distinct depression (a similar structure is also found in skulls of *N. eurystyle,* see below). This ventral "pit" is not represented in other specimens referred to *N. leptode,* e.g., from Oklahoma. In LACM (CIT) 54 the extent of the lacrimal bone on the facial region cannot be determined.

In the upper dentition the protocone is elongate, but relatively less so than *N. eurystyle.* The anterior borders of the prefossettes and posterior borders of the postfossettes are less plicated than the posterior borders of the prefossettes and anterior borders of the postfossettes. The fossette borders are sometimes more plicated than *N. affine* and usually less plicated than *N. eurystyle* or *N. gidleyi.* The pli caballin usually consists of a single or double loop.

In the mandible, the postcanine diastema is moderately elongate (fig. 77). The canine is nearly appressed to I_3, forming a very short precanine diastema. In the lower cheek tooth dentition the ectoflexids, particularly in the premolars, are shallower than *N. affine* and deeper than *N. eurystyle* and *N. gidleyi.* The protostylids are well developed, usually the pli caballinid is moderately to strongly developed. The enamel borders are not usually plicated except on, or just internal to, the isthmus, where there sometimes are developed rudimentary secondary loops. However, these loops are not so well developed as in *N. eurystyle* or *N. gidleyi.*

Well-preserved and abundant postcranial remains are usually not found associated with topotypic material for hipparion species. For *N. leptode* it is fortunate that there are a few virtually complete skeletons, i.e., LACM (CIT) 54, LACM (CIT) 63, and a partial skeleton UCMP 27126, from Thousand Creek. The postcranial skeletons demonstrate that there is little reduction in the length of the lateral metapodials and the medial metapodials were elongate and moderately stout (also see Stock, 1951).

CHARACTER ANALYSIS AND GENERAL DISCUSSION: Merriam (1915a) described *N. leptode* based principally on dentitions. Knowledge of this species was greatly increased with discovery of the fine sample from Thousand Creek described by Stock (1945, 1951) as well as well-preserved cranial and dental material from the other localities mentioned above (table 23).

In many characters *N. leptode* represents an intermediate member of a morphocline for the genus *Neophipparion* (fig. 50, table 16). Of particular importance, the virtual absence of a DPOF, well-developed pli caballinids (particularly in the premolars), and prominent plicated isthmuses are derived characters relative to *N. coloradense* and *N. affine. N. leptode* is larger than *N. trampas-*

ense but otherwise these two species are generally similar, particularly in the dental pattern. In contrast to *N. eurystyle, N. leptode* is larger, less hypsodont, and has slightly less elongated protocones, deeper ectoflexids in the molars, less well-developed pli caballinids and plications on the isthmuses, and less expanded conids and lophids. These same dental characters can also be used to differentiate *N. leptode* and *N. gidleyi*; however, *N. leptode* is smaller than *N. gidleyi.*

Neohipparion eurystyle (Cope), 1893
Figures 48–50, 78–84, 147, 150;
Tables 2, 16, 25, 26

JUNIOR SYNONYMS

Probably *Neohipparion molle* Merriam, 1915a, pp. 2–3, fig. 2.
Probably *Hipparion phosphorum* Simpson, 1930, pp. 187, 189, fig. 20A.
Neohipparion floresi Stirton, 1955, pp. 886–902, text-figs. 1–5, 6A, 6B (=*Hesperohipparion floresi* Dalquest, 1981).
Neohipparion arellanoi Stirton, 1955, pp. 886–902, text-figs. 6C–6H, 7 (=*Hesperohipparion arellanoi* Dalquest, 1981).
In part *Neohipparion otomii* Mooser, 1960, pp. 376–388, figs. 1–15 (=*Hesperohipparion otomii* Dalquest, 1981).
Neohipparion monias Mooser, 1964, pp. 393–396, fig. 1 (=*Hesperohipparion monias* Dalquest, 1981).
Hesperohipparion stirtoni Dalquest, 1981, pp. 502–512, figs. 1–3.

TYPE SPECIMEN AND LOCALITY: Holotype, TMM 40289-1, from Palo Duro Canyon (see Osborn, 1918, p. 186, fig. 149) in the Texas Panhandle. Based on Cope's (1893) locality description for the holotype, Schultz (1977, p. 84) stated that the type locality is "at the lower end of Lake Tanglewood in Randall County—probably the Currie Ranch Local Fauna site." Schultz (1977) lists the age of the Currie Ranch L.F. as latest Hemphillian. In addition to the holotype, Cope (1893, p. 43) discusses four other isolated lower cheek teeth from the late Hemphillian Goodnight L.F. that also characterized "*Equus eurystylus.*" Osborn (1918, p. 186, fig. 149) designated these four specimens paratypes of Cope's type series and illustrated two of them. Although modern taxonomic methodology de-emphasizes the significance of paratypes, from an historical perspective these specimens have been considered part of the syntypic series by workers such as Osborn (1918), even though they are from a different locality than the holotype.

REVISED DIAGNOSIS: Very hypsodont medium-sized hipparion. Mean TRL 125.63 mm. Unworn or little-worn M1MSTHT *ca.* 65–71 mm. DPOF absent. Protocone anteriorposteriorly very elongate and usually with angular anterior and posterior borders. Cheek teeth relatively straight transversely. Prominent expanded and flattened parastyles and mesostyles (particularly in the premolars). Fossettes in upper cheek teeth moderately to very plicated. Pli caballin frequently consists of multiple loops. Very shallow ectoflexids, well-developed pli caballinids (often with multiple secondary accessory folds), widely separated metaconids and metastylids, elongated entoconids and hypoconulids, and prominent isthmuses.

Neohipparion eurystyle differs from all other horse genera in the diagnostic generic characters listed above. There also are numerous dental characters that set *N. eurystyle* apart from all other species of *Neohipparion* except *N. gidleyi.* These include characters such as the combination of isolated and very elongated protocones, expanded and flattened styles, very shallow ectoflexids, well-developed pli caballinids and plications on the isthmuses, and expanded conids and stylids frequently with angular enamel borders. *N. eurystyle* is separated from *N. gidleyi* based principally on its smaller size

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Early Hemphillian of the Great Plains; cosmopolitan in Central and North America during the late Hemphillian (table 25).

DESCRIPTION: Despite the cosmopolitan distribution of *Neohipparion eurystyle,* skulls with well-developed preorbital regions are very rare and they have not previously been described in the literature. The only sample examined during the present study in which the preorbital region is preserved comes from the Yepómera L.F. of Chihuahua, Mexico. (Stirton, 1955, named two new species from this area, but for reasons discussed below, these are considered junior synonyms of *N. eurystyle.*) The best preserved skulls of *N.*

TABLE 25
Synopsis of Collections Examined for *Neohipparion eurystyle* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Numerous	F:AM, TMM, PPM, UNSM	Ogallala Group, Texas Panhandle, Kansas and Nebraska	Hemphillian	Includes probable type localities from Texas Panhandle of *N. eurystyle, N. stirtoni,* and *Hesperohipparion*
Yepómera	LACM (CIT)	Unnamed unit, Chihuahua, Mexico	Late Hemphillian	Includes topotypic samples of *N. arellanoi* and *N. floresi*
Rancho El Ocote	TMM (previously Mooser's private collection)	Unnamed unit, Guanajuato, Mexico	Late Hemphillian	Includes topotypic sample of *N. otomii* and *N. monias*
Numerous	UCMP	Green Valley, Mulholland, and Pinole formations and correlative units, Contra Costa County, San Francisco Bay region and north Coalinga region, San Joaquin Valley, California	?Late Clarendonian, Hemphillian	Includes type locality of *N. molle*
Numerous	UF, USNM	Bone Valley Formation, Polk and adjacent Hillsborough counties, central Florida	Late Hemphillian	Includes type locality of *Hipparion phosporum*
Numerous (e.g., Ft-40)	UNSM	Ogallala Group, Frontier and other counties, Nebraska	Hemphillian	

eurystyle from Yepómera are exemplified by LACM (CIT) 3331 (fig. 78), one of Stirton's paratypes of *N. floresi,* from CIT locality 275, and LACM (CIT) 3330, one of Stirton's paratypes of *N. arellanoi* from CIT locality 276. The preorbital facial region is smooth with no trace of the DPOF. (There is a small depression on the anterior portion of the maxillary bone dorsal to the malar crest. As mentioned above, a similar circular pit is also preserved in *N. leptode,* LACM (CIT) 54, from Thousand Creek.) The lacrimal bone is rhomboidal-shaped and encompasses the anterodorsal margin of the orbit. The anterior tip of this bone extends about 25 mm anterior to the orbital margin in LACM (CIT) 3331.

The cheek teeth of *N. eurystyle* are of moderate size with extremely elongated crowns (figs. 78–82, table 26). There seems to be an increase in crown height (*ca.* 10 mm) between relatively little-worn specimens of this species from the early late Hemphillian (e.g., Coffee Ranch L.F. and equivalent) sites to the latest Hemphillian (e.g., the upper Bone Valley of Florida, Christian Ranch L.F. of the Texas Panhandle, and Yepómera L.F. of Mexico) sites. In the latest Hemphillian representatives of *N. eurystyle,* the absolute M1MSTHT in certain specimens exceeds 70 mm, which

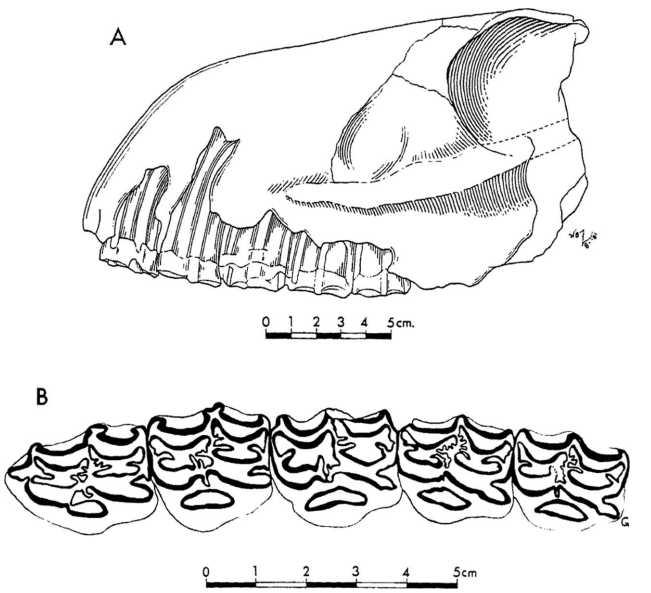


FIG. 78. *Neohipparion eurystyle* ("paratype" of *Neohipparion floresi* Stirton 1955), LACM (CIT) 275/3331, from the Yepómera L.F., late Hemphillian of Chihuahua, northern Mexico. A. Left lateral view of partial skull with details of preorbital region. B. Occlusal view of P^2–M^2.

surpasses all other North American hipparions (except *N. gidleyi*) and rivals that of primitive *Equus*, e.g., *E.* (*Dolichohippus*) *simplicidens*.

In the upper cheek teeth, the protocones are very elongate and usually have oval or angular anterior and posterior borders. The shape of the protocones usually differs from most other hipparions where this structure is less angular. The parastyles and mesostyles are characteristically anteriorposteriorly expanded and mediolaterally flattened. The fossette borders are moderately to very plicated. The pli caballin usually consists of single or multiple loops.

In the lower teeth there are very shallow ectoflexids in both the premolars and molars (figs. 83, 84). The pli caballinid is very well developed and consists of single or multiple loops. The parastylids and protostylids are very expanded. There is a well-developed isthmus that is usually plicated. In contrast to most other hipparions (1) the metaconids and metastylids are flattened and expanded,

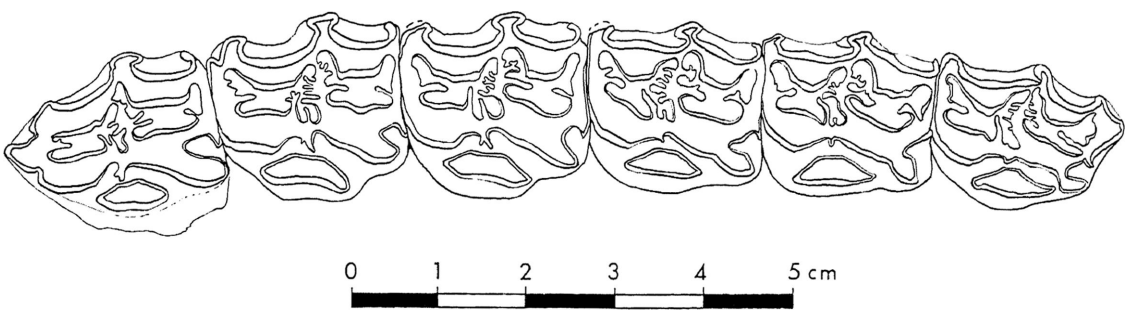


FIG. 79. Occlusal view of left P^2–M^3 of *Neohipparion eurystyle*, F:AM 107884, from the Channing area, Ogallala Group, late Hemphillian of Hartley County, Texas Panhandle.

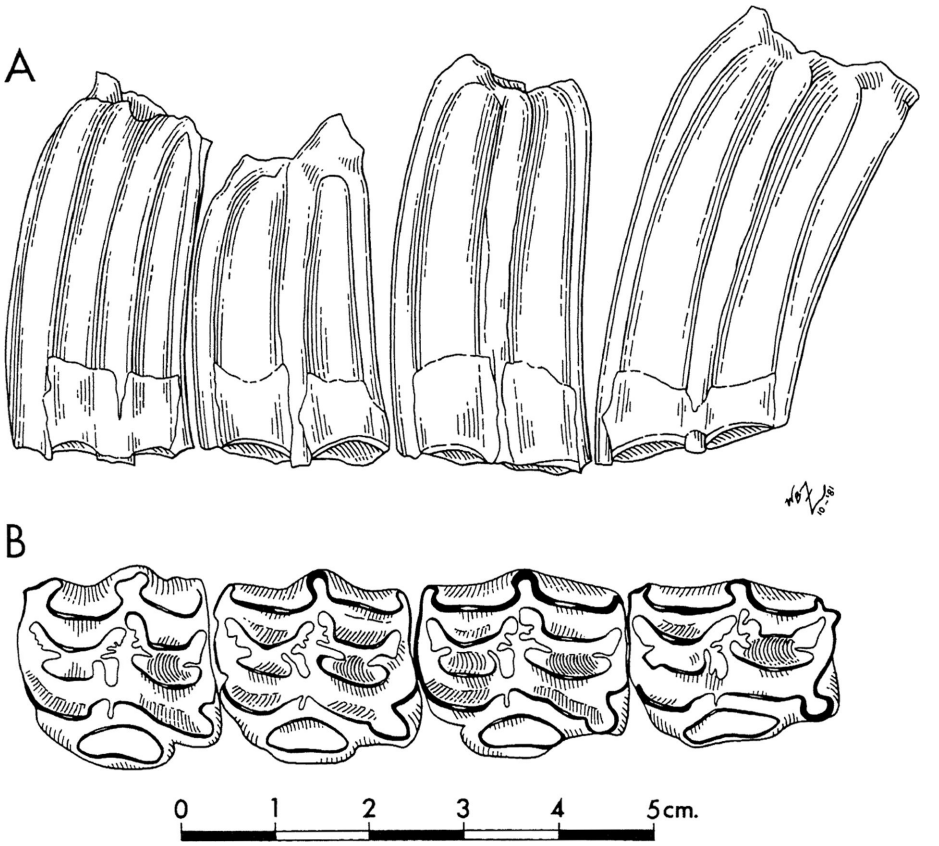


FIG. 80. *Neohipparion eurystyle,* UF 18318, left P^3–M^2, from Payne Creek Mine, upper Bone Valley Formation, late Hemphillian of Polk County, central Florida. A. Lateral view. B. Occlusal view.

and (2) the entoconids are larger than the hypoconulids and both of these structures have angular rather than rounded borders.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: The characters of the facial region and dental pattern of *N. eurystyle* clearly indicate that this species is a member of the genus *Neohipparion.* Many of the dental characters described here set *N. eurystyle* apart from its primitive sister species *N. coloradense, N. trampasense,* and *N. leptode,* particularly in the slightly greater absolute crown height and the lower cheek tooth pattern. The premolars of *N. trampasense* and *N. leptode* exhibit many of the lower cheek tooth characters of *N. eurystyle,* but the molars are usually more primitive, e.g., the presence of deep ectoflexids and poorly developed pli caballinids. *N. eurystyle* is the penultimate member of a morphocline for this genus.

Based on several characters, *Neohipparion eurystyle* is one of the most derived North American hipparions (although, in certain other characters such as relative hypsodonty and relative limb elongation, *Nannippus peninsulatus* is at least as derived). In absolute mesostyle crown height for little-worn upper cheek teeth, *N. eurystyle* approaches primitive species of *Equus.* In his original description, Cope (1893) described this new species as *Equus eurystylus.* The extreme development of the pli caballinids and isthmuses and very shallow ectoflexids has been acquired several times during horse evolution, including *N. eurystyle* and *N. gidleyi,* Pleistocene *Hipparion* from Africa (Eisenmann, 1977),

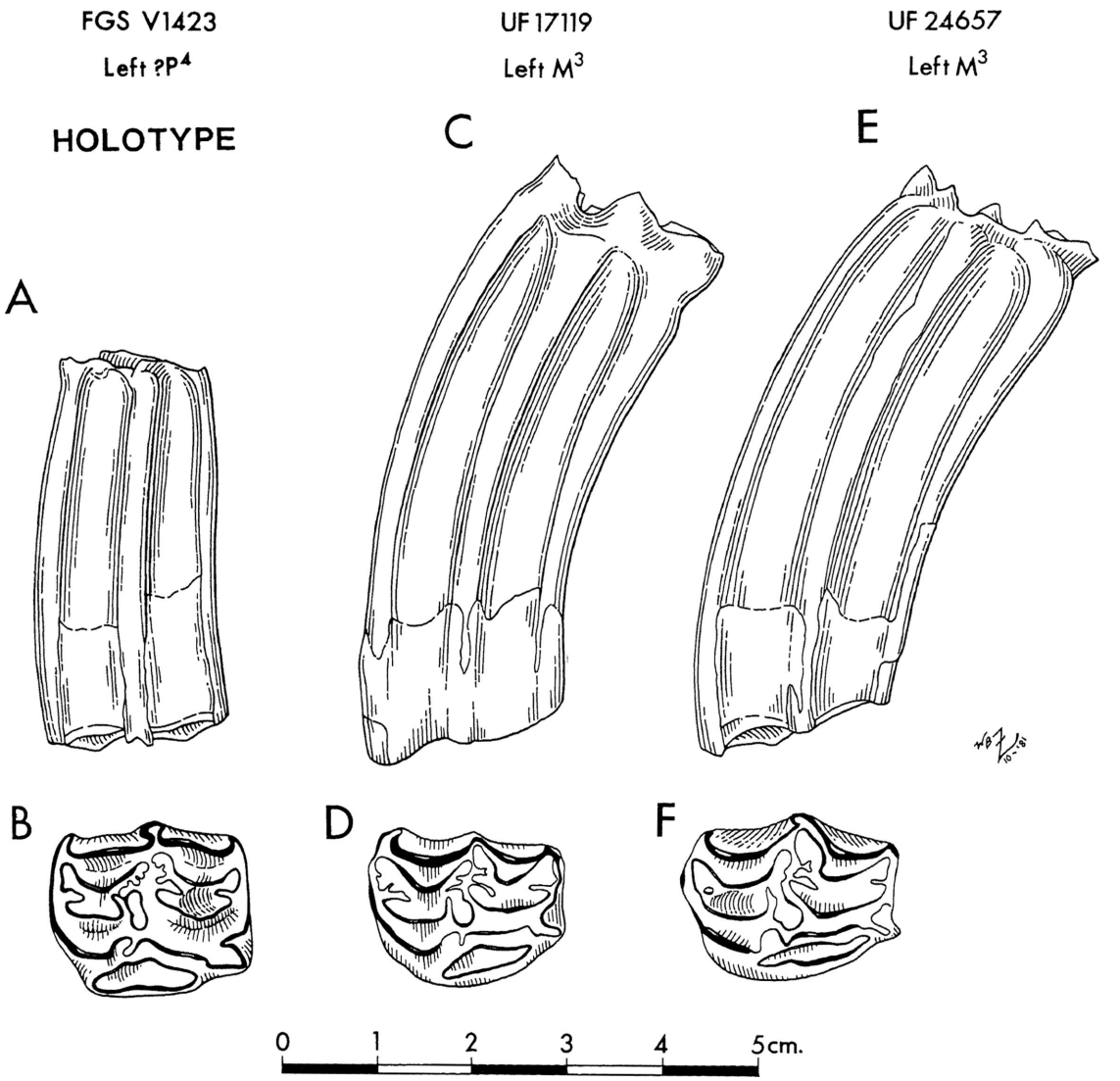


FIG. 81. Isolated upper cheek teeth of *Neohipparion eurystyle* from the Bone Valley Formation, late Hemphillian of central Florida. FGS V1423 (holotype of *Hipparion phosphorum* Simpson, 1930), left ?P^4, from Amalgamated Phosphate Mine, near Brewster, lateral (A) and occlusal (B) views. UF 17119, left M^3, from Kingsford Mine, lateral (C) and occlusal (D) views. UF 24657, left M^3, from Fort Green Mine, lateral (E) and occlusal (F) views.

and caballine *Equus*. These dental characters increase the amount of enamel that is exposed on the occlusal surface of the teeth and together provide a more resistant surface against wear during mastication.

In this report, seven other species names are considered probable junior synonyms of the oldest name, "*Equus*" *eurystylus* Cope, 1893.

Merriam (1915a) named the species *Neohipparion molle* based on an isolated left upper molar, UCMP 21370, from Mack Pumping Station 3 (UCMP locality 2076), Etchegoin Formation (or Jacalitos Formation

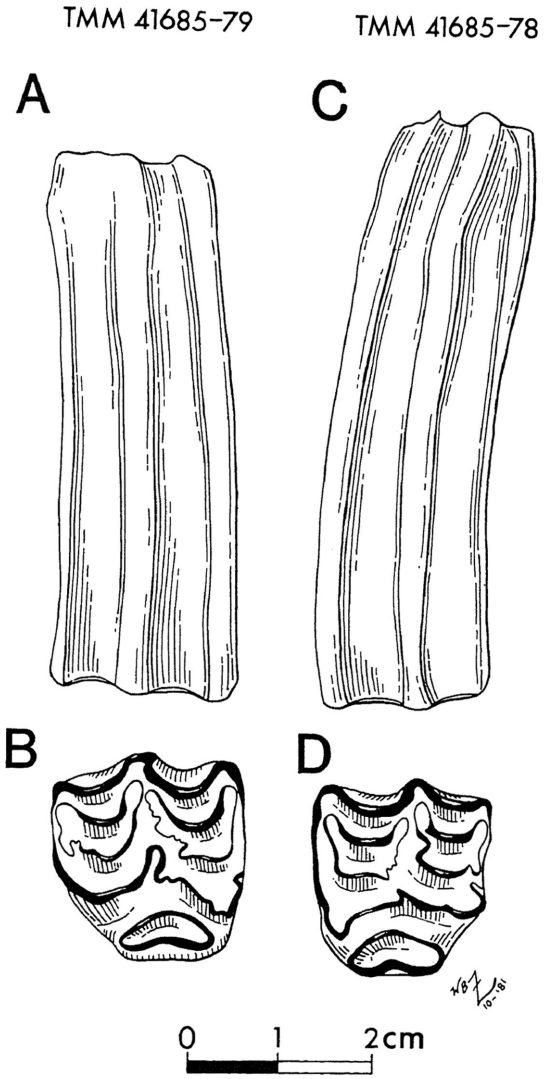


FIG. 82. *Neohipparion eurystyle,* isolated left upper cheek teeth, from the Rancho El Ocote L.F., late Hemphillian of Guanajuato, southern Mexico (originally named *Neohipparion monias* by Mooser, 1964). TMM 41685-79 (=Mooser's F.O. 887, paratype), lateral (A) and occlusal (B) views. TMM 41685-78 (=Mooser's F.O. 886, holotype), lateral (C) and occlusal (D) views.

fide Merriam, 1915a), north Coalinga region, San Joaquin Valley, California. The only published material of *N. molle* from the type locality is represented by the holotype (see illustrations in Merriam, 1915a, p. 2, fig. 2 and Osborn, 1918, p. 196, fig. 160). Specimens from other localities in California have also been referred dubiously to *Hipparion* cf. *molle* (e.g., Merriam, 1916a; Drescher, 1941). The type is medium-sized and relatively hypsodont (Merriam, 1915a, fig. 2). The protocone is elongate with angular anterior and posterior borders. The pli caballin consists of a single loop. The fossette borders are moderately plicated. In the prefossette, the pli protoloph is absent and the pli protoconule and pli prefossette consist of multiple loops. In the postfossette, the pli postfossette and pli hypostyle both consist of single loops. The hypoconal groove is well developed.

Neohipparion molle has numerous characters that probably ally this "species" with advanced *Neohipparion,* i.e., elongate protocones, moderately complicated fossette borders (in contrast to, e.g., *C. occidentale*), and high crowns. The type specimen was collected along with other remains including *Pliohippus coalingensis,* which suggests a late Hemphillian age. Tedford et al. (in press) referred *N. molle* to the *N. eurystyle* group. *N. molle* is considered here a junior synonym of *N. eurystyle.*

Simpson (1930) named the species *Hipparion phosphorum* which was collected from the American Cyanamid Company mine near Brewster in the central Florida phosphate district of southwestern Polk County. Although there are older and poorly known units at the base of the Bone Valley Formation (e.g., MacFadden, 1982; MacFadden and Webb, 1982), the type of *H. phosphorum,* FGS V-1423, is probably of late Hemphillian age based on the biochronology of other land mammals collected from that mine. Simpson (1930) recognized that this species was close to the *Neohipparion affine* "group" based on the elongate protocone. The type of "*H.*" *phosphorum* (fig. 81A, 81B) compares very favorably in size, hypsodonty (although it is fairly worn), flattened mesostyle, and angular borders of the protocone with the UF specimens of *N. eurystyle* from the late Hemphillian Bone Valley Formation as well as specimens of this species from other localities in Central and North America. Therefore, "*Hipparion*" *phosphorum* should be considered a junior synonym of *N. eurystyle* rather than a distinct species.

Stirton (1940) recommended that several

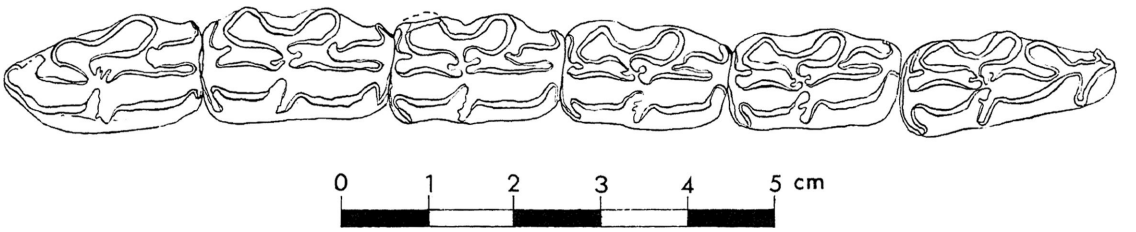


FIG. 83. Occlusal view of *Neohipparion eurystyle,* F:AM 107885, left P_2–M_3, from the Channing area, Ogallala Group, late Hemphillian of Hartley County, Texas Panhandle.

species of advanced *Neohipparion* be included in the *N. eurystyle* group. Since that time, many references have been to the *N. eurystyle* or *N. affine* "groups." Stirton (1955) named two new species of the *N. eurystyle* group, *N. floresi* and *N. arellanoi,* from the late Hemphillian Yepómera L.F. of Chihuahua, Mexico. In that paper Stirton presented an exhaustive description of the many (mostly qualitative) dental characters that differentiated *N. arellanoi, N. floresi,* and *N. eurystyle.* The two Yepómera species do not coexist at any of the collecting sites (Stirton, 1955). However, Stirton believed that the geological evidence offered (1955, p. 886) "no basis for a time difference between the assemblages from these localities." However, in a recent study of these collections and renewed field work, Lindsay (in press) separated the Yepómera "fauna" into two distinct local faunas because of what he believed to be significant ecological or time differences. Based on examination of the LACM collection and the revised interpretation about the possible temporal differences represented by the Yepómera sites, it is concluded that the two "species" *N. floresi* and *N. arellanoi* are: (1) probably local populations of the same species, and (3) are considered here to be junior synonyms of *N. eurystyle.*

Mooser (1960, 1964) named two additional new species of the *N. eurystyle* group, *N. otomii*[8] and *N. monias,* from the late Hemphillian Ocote L.F. of Guanajuato, Mexico. Based on examination of the topotypic material of these Mexican species of the *N. eurystyle* group in the TMM (formerly in Mooser's private collection, now TMM 41865-47 through 79) and LACM (CIT) collections, it appears that: (1) Mooser mixed distinctly smaller and larger forms in his concept of *N. otomii.* The lectotype, TMM 41685-47 (fig. 84) is relatively small and seems to fall within the range of *N. eurystyle.* The larger forms are probably best referred to *N. gidleyi* (see below). (2) The only specimens from the Mexican localities of possibly questionable

[8] Mooser (1960, p. 376) listed seven numbered specimens that comprised the holotype of *Neohipparion otomii.* Silva-Barcenas (1969, p. 11) selected Mooser's F.O. 10 (=MSU 11378, =TMM 41685-47), consisting of a left ramus with P_2–M_3 (fig. 84) as the lectotype of the species.

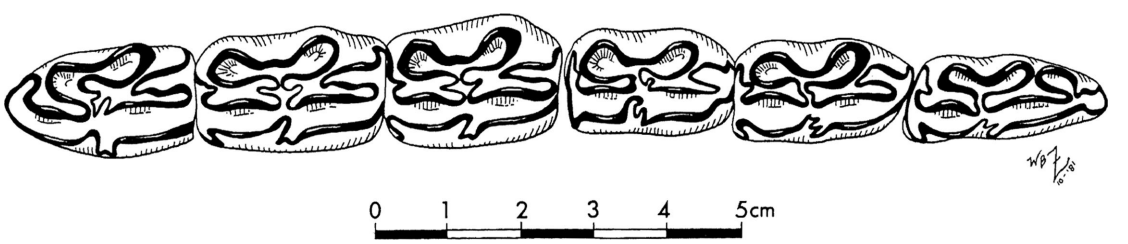


FIG. 84. Occlusal view of right (reversed) lower cheek tooth dentition, P_2–M_3, of *Neohipparion eurystyle,* TMM 41685-47 (lectotype of "*Neohipparion otomii,*" =MSU 11378 =Mooser's F.O. 10) from Rancho El Ocote L.F., late Hemphillian of Guanajuato, central Mexico.

TABLE 26
Selected Upper Dental Measurements and Univariate Statistics for *Neohipparion eurystyle*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	13	25.21	2.42	9.64	21.6–29.8	12	25.51	2.27	8.90	22.2–29.8
P2TRNW	12	18.73	0.58	3.08	18.1–19.7	11	18.77	0.58	3.09	18.1–19.7
P2PRTL	12	8.44	1.61	19.01	7.2–12.9	11	8.53	1.65	19.34	7.2–12.9
P2PRTW	11	3.74	0.27	7.31	3.1–4.2	10	3.72	0.28	7.53	3.1–4.2
P2TOTPLI	10	10.00	3.43	34.32	6–10	9	10.11	3.62	35.81	6–18
M1APL	13	21.19	1.70	8.04	19.3–24.4	10	20.94	1.60	7.64	19.3–24.3
M1ECTL	13	20.59	1.46	7.10	18.2–23.5	10	20.30	1.34	6.60	18.2–23.0
M1TRNW	13	18.40	0.94	5.12	16.9–19.7	10	18.52	0.92	4.97	17.3–19.7
M1PRTL	13	9.73	0.92	9.41	8.2–11.0	10	9.65	0.92	9.53	8.2–11.0
M1PRTW	13	3.93	0.30	7.66	3.6–4.5	10	3.97	0.32	8.06	3.6–4.5
M1TOTPLI	10	10.20	2.04	20.04	8–14	8	10.00	2.20	22.00	8–14
TRL	4	125.63	3.40	2.70	121.0–129.1	4	125.63	3.40	2.71	121.0–129.1
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	10	33.86	5.28	15.58	26.8–41.3	0	—	—	—	—
M1MSTHT	7	47.59	14.90	31.31	31.4–71.2	1	71.20	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 25 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

affinities are those of *N. "monias"* (fig. 82). These specimens, with a rudimentary pli caballin and simple enamel, may represent extreme individual variants. However, in the present report these compare most closely with the concept of *N. eurystyle* (*sensu stricto*).

Independently from the present study, Carranza-Castañeda and Ferrusquia-Villafranca (1979) presented an analysis of the two previously named species of *Neohipparion*, *N. otomii* Mooser, 1960, and *N. monias* Mooser, 1964, from the late Hemphillian Rancho El Ocote L.F. from Guanajuato in central Mexico. Based on a detailed analysis of the quantitative and qualitative characters, they concluded that Mooser's two species of *Neohipparion* from Ocote are junior synonyms of *N. floresi* from Yepómera. In this section, I go a step further and synonymize both of the samples of Mexican *Neohipparion*, i.e., from Ocote and Guanajuato, with *N. eurystyle* and *N. gidleyi*.

Dalquest (1981) named a new genus, *Hesperohipparion*, from the Hemphillian of North America. This genus is diagnosed solely on dental characters as follows (p. 506):

> Hipparions with the protocones of the upper cheek teeth isolated, except that the protocone of P^2 is sometimes connected to the protoloph in very early or very late stages of wear; protocones much antero-posteriorly elongated, usually with pointed ends and sinuous, concave or straight lingual borders, but not convex lingual margins; lower cheek teeth very high-crowned and upper part of crown anteroposteriorly expanded; metaconid and metastylid almost prostrate in early stages of wear, with long axes of cusps parallel to long axis of tooth, and widely separated by long, shallow linguaflexid, median lingual spur often present in center of linguaflexid, pli caballinid strongly developed and plicated. In more advanced stages of wear, metaconid and metastylid column converging. In lower part of crown, tooth shorter anteroposteriorly, metaconids and metastylids shorter and rounder, and linguaflexids shorter and broadly "U" shaped. Ectoflexids of premolars shallow, with metaconid and metastylid appearing to be elevated on the isthmus; ectoflexids of molars shallow, not penetrating between metaconid and metastylid at any stage of wear; parastylids moderately to strongly developed but not isolated in cementum.

Within the genus *Hesperohipparion*, Dalquest recognized six species: *Equus eu-*

TABLE 27
Synopsis of Collections Examined for *Neohipparion gidleyi* Used for Descriptions and Comparisons in This Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Petaluma	UCMP	Petaluma Formation, Sonoma County, northern California	Late Hemphillian	Type area
Port of Entry Pit, Box T, Guymon	F:AM	Ogallala Group, Ellis and Texas counties, Oklahoma	Early to late Hemphillian	
Lyden Quarry	F:AM	"Chamita Formation" (referred), Santa Fe Group, Rio Arriba County, New Mexico	Hemphillian	
Rancho El Ocote	TMM	Unnamed deposits, Guanajuato, Mexico	Late Hemphillian	Type locality of *N. otomii*

rystylus Cope, 1893; *Neohipparion floresi* Stirton, 1955; *Neohipparion arellanoi* Stirton, 1955; *Neohipparion otomii* Mooser, 1960; *Neohipparion monias* Mooser, 1964, and *Hesperohipparion stirtoni,* a new species from the late Hemphillian Coffee Ranch L.F. of the Texas Panhandle, the latter of which Matthew and Stirton (1930) called *Hipparion (Neohipparion) eurystyle.*

There are several reasons why this new genus is not justified. In the generic diagnosis the characters used as *differentia* are either primitive for hipparions, primitive for the genus *Neohipparion,* or merely can be used to unite seven "species" with either *N. eurystyle* or *N. gidleyi.* Other considerations that reflect the present author's stance include: (1) the problem that the cranial morphology was not considered in the diagnosis of this genus, (2) the *V*s for dental characters analyzed here (tables 26 and 28) suggest two coherent taxa, and (3) the genus *Neohipparion* would be rendered paraphyletic. With regard to the species allocated to *Hesperohipparion,* the arguments on dental variability discussed above apply to the previously named species later included in Dalquest's genus as well as his "species" *Hesperohipparion stirtoni.*

In summary, there appears to be no reason to retain the concept of the *Neohipparion eurystyle* "group," i.e., a species complex for these very similar late Hemphillian forms. Previous interpretations about dental variation and distinct species are probably attributable to intraspecific "populational" or geographic variation. Therefore, as diagnosed in the present report, *N. eurystyle* represents a single species of *Neohipparion* that was rare in the early Hemphillian but cosmopolitan during the late Hemphillian throughout Central and North America.

Neohipparion gidleyi Merriam, 1915a
Figures 48–50, 85–88, 147, 150;
Tables 2, 16, 27, 28

JUNIOR SYNONYM

In part *Neohipparion otomii* Mooser, 1960, pp. 376–388, figs. 1–15 (=*Hesperohipparion otomii* Dalquest, 1981).

TYPE SPECIMEN: UCMP 21382, LM^3, from locality 1036, Lawler Ranch, 6 miles east of Petaluma, late Hemphillian, Contra Costa County, California (fig. 85).

DIAGNOSIS: Largest North American hipparion. Estimated mean TRL *ca.* 150 mm. Very hypsodont. Unworn or little-worn M1MSTHT *ca.* 60–70 mm. Very elongated protocones. Elongated and flattened parastyles and mesostyles. Well-developed pli caballins. In lowers, very expanded conids and stylids. Very well-developed pli caballinids, shallow ectoflexids, and well-developed plications on the isthmuses.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Early Hemphillian of Oklahoma, late Hemphillian of California, Texas, New Mexico, and Mexico (table 27).

DESCRIPTION AND DISCUSSION: This species of the "*Neohipparion eurystyle* group" was based on well-worn isolated teeth from Pet-

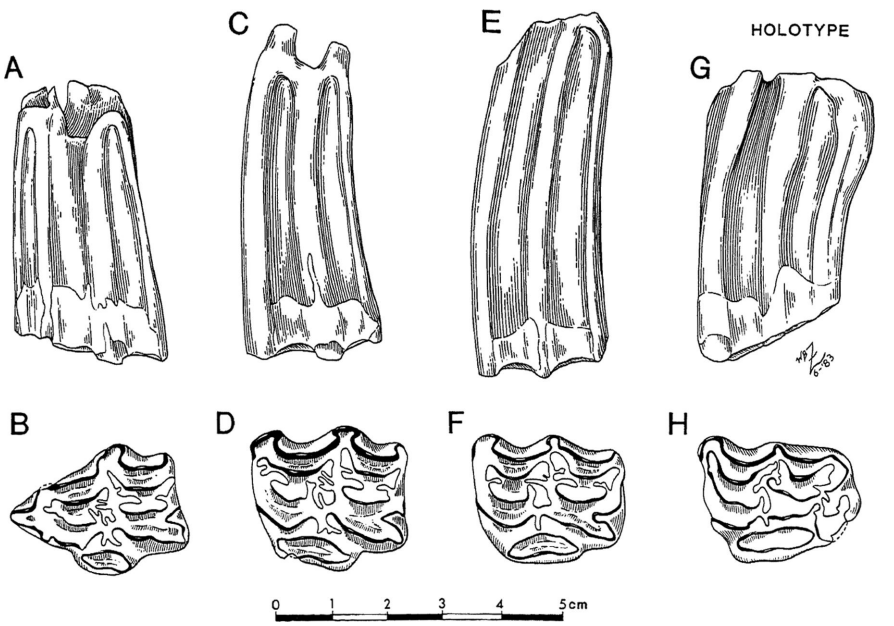


FIG. 85. Isolated upper cheek teeth of *Neohipparion gidleyi* from selected late Hemphillian localities. From left to right: F:AM 111740, left P^2, lateral (A) and occlusal (B) views. F:AM 111737, left P^4, lateral (C) and occlusal (D) views. F:AM 111738, left M^2, lateral (E) and occlusal (F) views. F:AM 111737, 111738, and 111740 are from the Optima (Guymon) L.F., Ogallala Group, Texas County, Oklahoma Panhandle. UCMP 21382, left M^3, holotype, lateral (G) and occlusal (H) views, from Lawler Ranch, UCMP locality 1036, San Francisco Bay region, northern California.

aluma. Despite their advanced wear stage, these teeth are much too large and hypsodont to fit into the concept of *N. eurystyle* or *N. leptode*. The topotypic sample of lower cheek teeth (also see Stirton, 1939, 1952) are, except for their large size, non-diagnostic because of their late wear stage.

During the present study some F:AM specimens were examined that are clearly of advanced *Neohipparion* affinities (figs. 85–87). These and some other late Hemphillian specimens are too large to be referred to *N. eurystyle* (figs. 48, 49; table 28). In addition, the dental pattern seems advanced as represented by (1) the elongated protocones, parastyles, and mesostyles in the upper cheek teeth, and (2) the extremely elongated pli caballinids, plicated isthmuses, and greatly expanded conids and stylids in the lower cheek teeth (e.g., fig. 88). Based on this suite of characters, these specimens are morphologically most similar to what is known for *N. gidleyi*. Although there are no complete upper cheek tooth dentitions, it is estimated (by correlation to P2TRNW and M1TRNW) that the TRL for *N. gidleyi* is *ca.* 150 mm (fig. 48). Unfortunately, there are no known specimens that preserve the morphology of the preorbital region. However, given the advanced features of this species based on dentitions, it is predicted that *N. gidleyi* would lack a DPOF.

Within the genus *Neohipparion, N. gidleyi* exhibits numerous derived character states including its very large size, elongate crowns, and advanced dental pattern (fig. 50; table 16). As such, this is the most derived species within the genus.

Mooser (1960) described the new species *N. otomii* from the late Hemphillian Rancho El Ocote L.F. in Guanajuato, Mexico (fig. 87). Mooser was impressed with the very elongated crowns (some mesostyle heights in excess of 70 mm) and advanced dental pattern. However, within his sample he seems to have mixed one smaller and one larger form. As

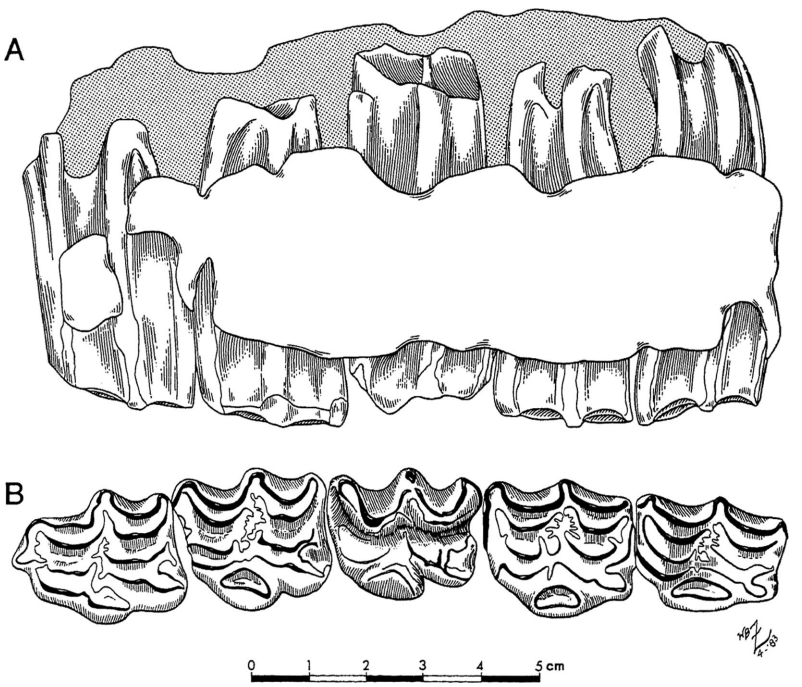


FIG. 86. *Neohipparion gidleyi,* F:AM 111735, right (reversed) upper cheek tooth dentition, P^2–M^2, from Lyden Quarry, upper Santa Fe Group ("Chamita Formation," see MacFadden, 1977, p. 796), late Hemphillian of Rio Arriba County, north-central New Mexico. A. Lateral view. B. Occlusal view.

TABLE 28
Selected Upper Dental Measurements and Univariate Statistics for *Neohipparion gidleyi*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V (%)	OR	N	$\bar{x}$	s	V (%)	OR
P2APL	4	28.43	1.87	6.57	27.2–31.2	3	28.73	2.16	7.52	27.2–31.2
P2TRNW	4	21.23	1.66	7.83	19.8–23.2	3	21.67	1.72	7.94	19.8–23.2
P2PRTL	4	9.18	1.74	18.95	7.7–11.5	3	9.67	1.76	18.20	8.0–11.5
P2PRTW	4	4.13	0.13	3.05	4.0–4.3	3	4.07	0.06	1.47	4.0–4.1
P2TOTPLI	3	8.00	1.00	12.50	7–9	3	8.00	1.00	12.50	7–9
M1APL	8	24.25	1.20	4.99	22.8–26.0	6	24.22	1.26	5.20	22.8–26.0
M1ECTL	8	24.11	1.60	6.62	22.4–27.0	6	24.30	1.72	7.08	22.4–27.0
M1TRNW	8	19.43	2.48	12.77	16.8–24.0	6	19.63	2.61	13.35	17.4–24.4
M1PRTL	8	10.93	1.79	16.36	8.4–13.8	6	11.58	1.51	13.03	9.7–13.8
M1PRTW	8	3.93	0.64	16.21	3.0–5.0	6	4.05	0.61	15.06	3.5–5.0
M1TOTPLI	7	8.57	3.16	36.81	3–12	5	8.00	3.67	45.88	3–12
TRL	0	—	—	—	—	0	—	—	—	—
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	4	46.38	4.06	8.76	43.1–52.3	1	52.3	—	—	—
M1MSTHT	7	60.63	4.78	7.88	51.7–64.6	2	64.25	0.50	0.78	63.9–64.6

[a] Abbreviations are presented on pp. 21 and 22; see table 27 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

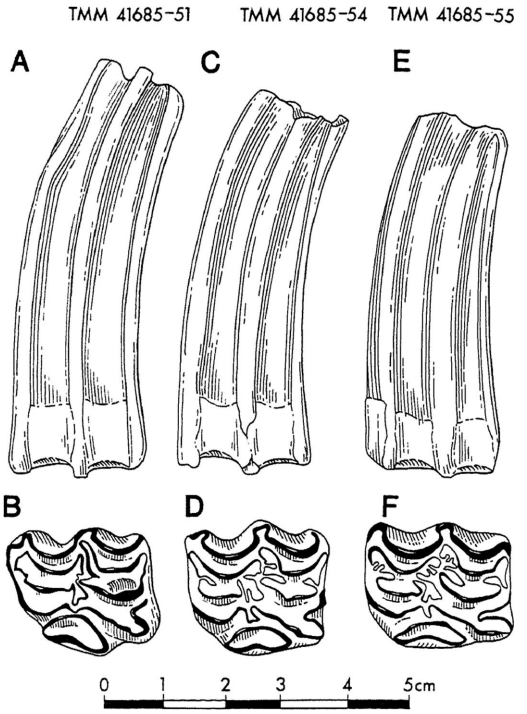


FIG. 87. *Neohipparion gidleyi,* isolated left upper cheek teeth, from the Rancho El Ocote L.F., late Hemphillian of Guanajuato, central Mexico (originally named *Neohipparion otomii*). Lateral (A) and occlusal (B) views of TMM 41685-51 (=Mooser's F.O. 26). Lateral (C) and occlusal (D) views of TMM 41685-54 (=Mooser's F.O. 31). Lateral (E) and occlusal (F) views of TMM 41685-55 (=Mooser's F.O. 31).

mentioned above, the smaller form is referred to *N. eurystyle.* Based on examination of this collection (now in the TMM), it is clear that the larger form of *N. otomii* fits within the concept presented here for *N. gidleyi.*

Stirton (1952) stated that the California *N. gidleyi* indicates a late Hemphillian age. The midcontinental occurrences reported here extend the range of this species into the early Hemphillian. Therefore, *N. gidleyi* coexists during the early Hemphillian with both *N. leptode* and *N. eurystyle* and during the late Hemphillian with *N. eurystyle.* Although *N. gidleyi* was widespread, from the known occurrences it was neither as common nor as cosmopolitan as the ubiquitous *N. eurystyle.*

NANNIPPUS MATTHEW, 1926

INCLUDED SPECIES

Nannippus minor (Sellards), 1916.
Nannippus ingenuus (Leidy), 1885.
Nannippus beckensis Dalquest and Donovan, 1973.
Nannippus peninsulatus (Cope), 1885.

TYPE SPECIES: *Nannippus peninsulatus* (Cope), 1885, senior synonym of *N. phlegon* (Hay), 1899, see discussion of type specimen and locality below.

DIAGNOSIS: Small, hypsodont, and gracile hipparion. Mean TRL ranges from 82.25 to 115.90 mm. Unworn or little-worn M1MSTHT *ca.* 37–66 mm. Cheek teeth hypsodont to very hypsodont. Relatively elongate rostrum and postcanine diastema. DPOF absent. Upper cheek teeth with oval protocones and moderately complex enamel plications on fossette borders. Lower cheek teeth with relatively deep ectoflexids, pli caballinids rudimentary or absent, widely separated metaconids and metastylids, protostylids poorly developed or absent, and P_2 with relatively small anterior projection of the paralophid. Very elongate and relatively slender metapodials relative to body size.

Nannippus differs from all other horses in a combination of the lack of DPOF (e.g., fig. 89), small size, relative hypsodonty as well as numerous dental characters. *Nannippus* also possibly differs from other horses in the lack of trapezium in the manus (see Discussion below).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Late Clarendonian through late Blancan of Central and North America. Although this genus was apparently restricted in its range from late Clarendonian to the late Hemphillian, *Nannippus* was cosmoplitan in Central America and southern North America during the Blancan (table 29).

DISCUSSION: In characters of the facial region, size, dental pattern, and possibly the manus and pes, *Nannippus* can be differentiated from all other horses. Cranial material, which is known for *N. ingenuus, N. beckensis,* and *N. peninsulatus,* indicates that this genus is characterized by a facial region in which the DPOF is rudimentary or absent (e.g., fig. 89). Therefore, *Nannippus* differs from *Hipparion, Cormohipparion,* and prim-

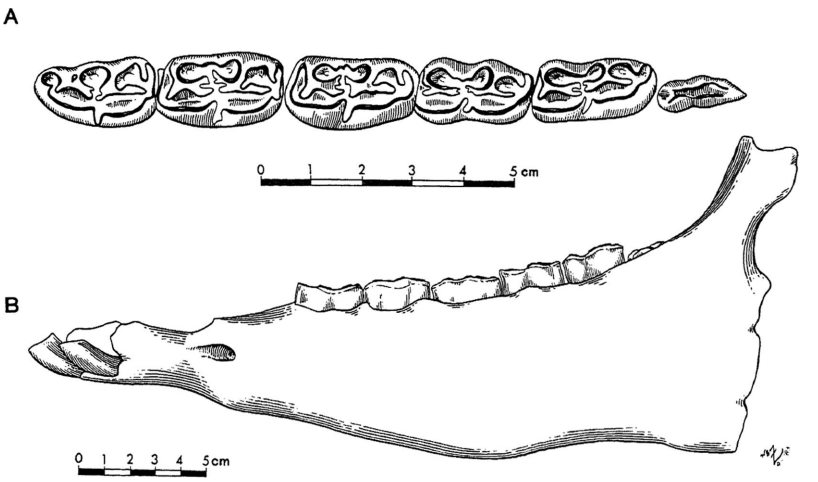


FIG. 88. *Neohipparion gidley,* F:AM 111741, from Port of Entry Pit, Ogallala Group, early Hemphillian of Ellis County, Oklahoma. A. Occlusal view of P_2–M_2 (M_3 not completely erupted). B. Composite lateral view of mandible.

itive species of *Neohipparion* based on the virtual lack of a DPOF. *Nannippus* differs from all other hipparions based on its very small size, relatively hyposodont teeth, and relatively elongated and gracile metapodials. For the four species of *Nannippus,* selected measured characters that give an indication of size versus hypsodonty (TRL versus M1MSTHT) and increase in relative size of the protocone (M1APL versus M1PRTL) are presented in figures 90 and 91. As is discussed below, there also are unique combinations of

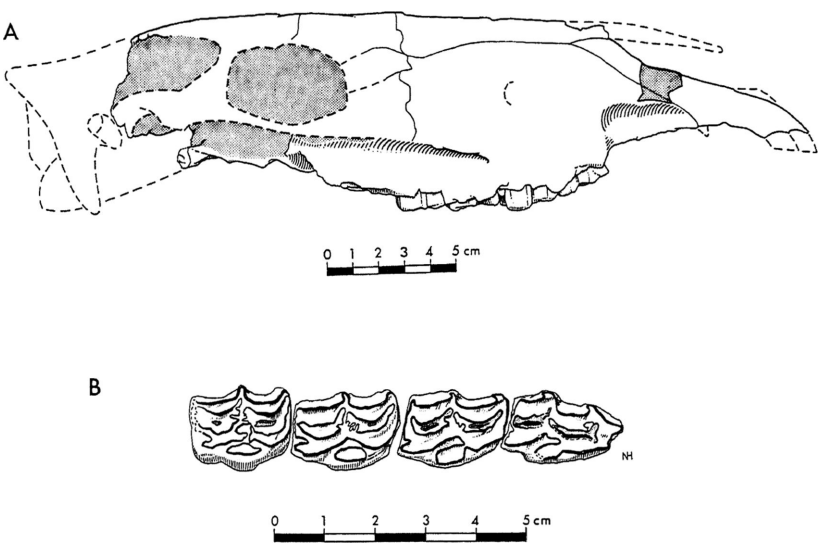


FIG. 89. Representative skull morphology of *Nannippus.* This specimen, AMNH 104708, is of *N. peninsulatus* from Mt. Blanco, Crayfish Draw, Blanco Beds, late Blancan of Crosby County, Texas Panhandle. A. Right lateral view of skull. B. Occlusal view of right dP^2–dP^4, M^1. Note that the wear on the deciduous dentition, with characters such as the connected protocones, is not diagnostic for this genus and species.

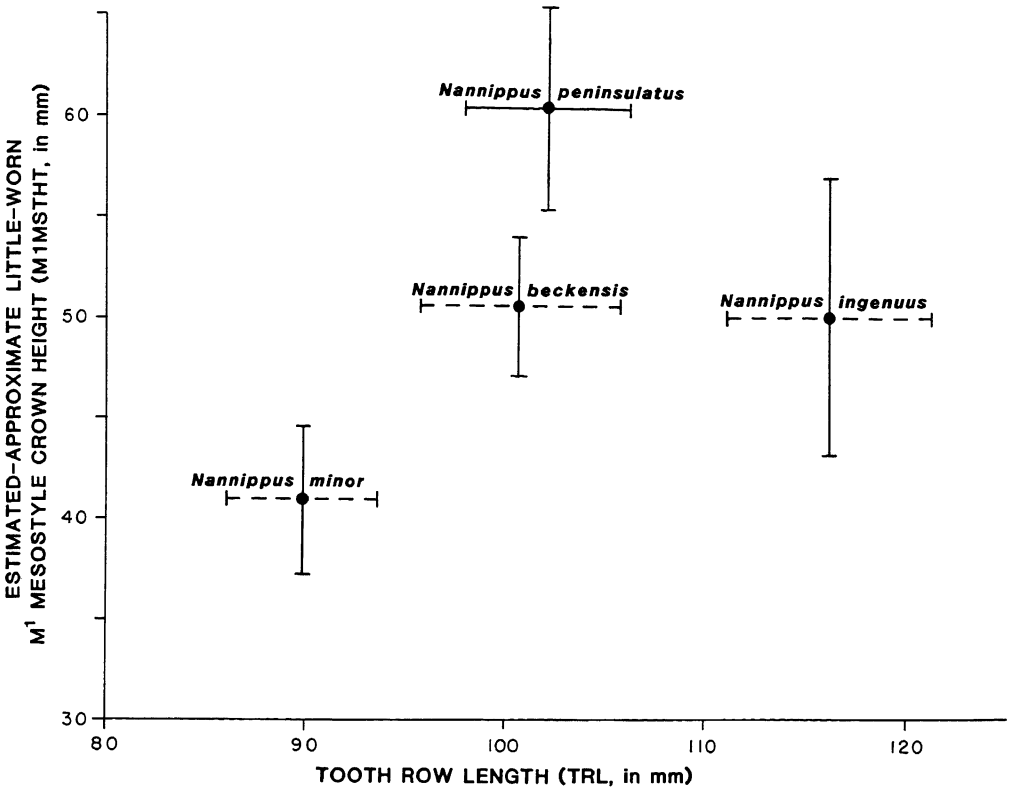


FIG. 90. Bivariate plot of TRL versus estimated-approximate little-worn M1MSTHT for the four recognized species of *Nannippus*. TRL for *N. minor, N. beckensis,* and *N. ingenuus* are estimated because of small sample size. For each value, one standard deviation (*s,* either actual or estimated) is plotted on both sides of the mean. Also see figure 25 for further explanation.

dental characters that distinguish individual species from other hipparions (and other horses).

In addition to the diagnostic characters for *Nannippus* listed here, Matthew (1926) also stated that this genus could be differentiated by the absence of the rudimentary fifth digit and trapezium. Matthew apparently based this judgment on his knowledge of what has been commonly thought to be the genotypic species *N. "phlegon,"* probably as represented by the fine sample collected during the AMNH 1924 expedition to Mt. Blanco. In a detailed analysis of the manus of fossil and extant horses, Sondaar (1968) confirms the lack of the trapezium in *Nannippus* as a diagnostic generic character. From the museum collections that Sondaar studied (as listed in his paper), he probably based this judgment on material of *N. "phlegon"* and *N. minor.* Therefore, the presence or absence of both the trapezium as well as the rudimentary fifth digit is not known in the two other species of *Nannippus,* i.e., *N. ingenuus* and *N. beckensis.* During the present study, there were no relevant postcranial elements in these last two species of *Nannippus* in which the states of these characters could be determined. Therefore, the absence of the rudimentary fifth digit and trapezium are considered here as questionable generic characters.

In the present report four species of the genus *Nannippus* are considered valid; *N. minor, N. ingenuus, N. peninsulatus,* and *N. beckensis.* In many characters of the dental pattern, these species form a morphocline that seems to proceed from *N. minor* to *N. ingenuus* to *N. beckensis* to *N. peninsulatus.* In

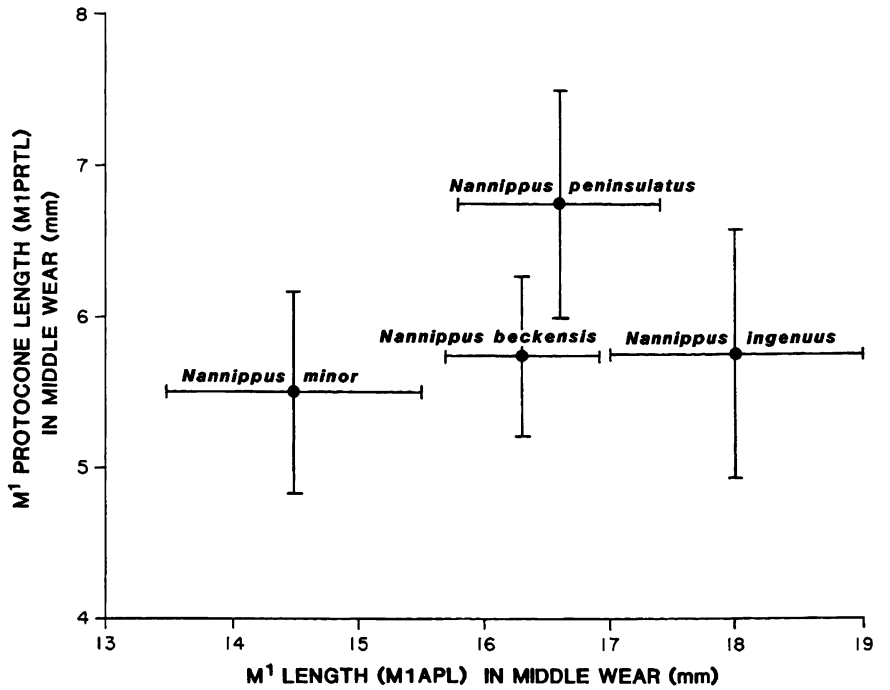


FIG. 91. Bivariate plot of M1APL versus M1PRTL for the four recognized species of *Nannippus*. For each value, one standard deviation (*s*) is plotted on both sides of the mean. Also see figure 26 for further explanation.

certain characters related to size and hypsodonty, there is not a simple progression among the species. In fact, in some of these characters, *N. beckensis* seems to be uniquely derived (autopomorphic). The character distributions and morphocline polarities for the merychippine outgroup and the species of *Nannippus* are presented in figure 92 and table 29.

Matthew (1926) proposed *Nannippus* as a subgenus of *Hipparion*. Matthew's concept of *Nannippus* included tiny and gracile North American forms and *N. "phlegon"* was central to the concept of this subgenus. In the present report, this well-known species is determined to be a junior synonym of *Nannippus peninsulatus* (Cope), 1885, the latter of which is, therefore, the genotypic species. Since Matthew's original description, *Nannippus* has been elevated to full generic status (e.g., Stirton, 1940). Numerous species of tiny North American hipparions have at one time or another been assigned to the genus *Nannippus*. Many of these share closer relationships to other genera of hipparions as well as to other small fossil horses (e.g., *Pseudhipparion*). Morris F. Skinner (in Skinner and Hibbard, 1972, p. 117), one of the foremost students of the Equidae, has 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*." Sondaar (1968, p. 69) noted that: "After considering the material from Blanco on which the genus was based (stored in the American Museum), it becomes clear that this genus is so specialized that we must restrict the generic name *Nannippus* to a much smaller group [of species]. There are small *Hipparion*-like animals which do not belong to the genus *Nannippus*, for example the species *lenticulare* [*ingenuus*], which do not have the generic characters." Also, the biostratigraphic utility of *Nannippus* is obscured with a broader, polyphyletic, interpretation.

Nannippus was a highly cursorial antelope-

TABLE 29

Selected Important Morphological Character Distributions and Temporal and Spatial Data for the Four Species of *Nannippus* and the Merychippines (Outgroup)[a]

Morphocline Character[b] (See fig. 92)	Merychippines[c] (outgroup)	*Nannippus minor*	*Nannippus ingenuus*	*Nannippus beckensis*	*Nannippus peninsulatus*
1. Size (relative to all hipparions)	Small to medium	Very small	Small	Small	Small
2. Mean upper cheek tooth row length, P^2–M^3 (TRL)	—	*ca.* 90 mm	*ca.* 116 mm	*ca.* 102 mm	101.55
3. Hypsodonty	Brachyodont to mesodont	Hypsodont	Very hypsodont	Very hypsodont	Extremely hypsodont
4. Estimated-approximate mesostyle crown height (M1MSTHT) for little-worn specimens	—	37–45 mm	43–57 mm	47–53 mm	55–66 mm
5. Occlusal cross-sectional area of cheek teeth	Small to medium	Tiny	Small	Small	Small
6. Dorsal preorbital fossa (DPOF)	Highly variable in different species, usually present	Not known	Small, poorly developed, far anterior of orbit	Absent	Absent
7. Rostrum and postcanine diastema	Short to moderate	Elongate	Elongate	Elongate	Elongate
8. Anterostyle on P^2, paraconid on P_2	Moderate	Reduced	Reduced	Reduced	Reduced
9. Protocone	Small and rounded to oval	Oval with rounded borders	Oval with rounded borders	Oval with rounded borders	Oval to elongate, usually with rounded borders
10. Protosylid	Variable depending upon species, usually less well developed than in hipparions	Usually present and relatively well developed	Reduced in frequency of development	Further reduced in frequency of development	Virtually absent

TABLE 29—(*Continued*)

Morphocline Character[b] (See fig. 92)	Merychippines[c] (outgroup)	*Nannippus minor*	*Nannippus ingenuus*	*Nannippus beckensis*	*Nannippus peninsulatus*
11. Ectoflexid (relative to all hipparions)	Usually deep	Moderately deep	Moderately deep	Moderately deep	Moderately deep
12. Pli caballinid	Variable depending upon species, but relatively poorly developed	Moderately developed to rudimentary	Moderately developed to rudimentary	Moderately developed to rudimentary	Moderately developed to rudimentary
13. Metapodials (relative to all hipparions) as represented by MC III and MT III	Variable depending upon species, but relatively short to moderately elongate	Gracile and relatively short	Gracile and moderately elongate	Gracile and moderately elongate	Gracile and very elongate
14. Trapezium and MC V	Present	Absent	Character state unknown	Character state unknown	Absent
DISTRIBUTIONAL DATA[d]					
Known biochronological range (teilchron)	—	Late Clarendonian to early Blancan	Hemphillian	Early Blancan	Blancan
Known biogeographic occurrence(s)	—	Southeastern United States (principally Florida), Texas, Mexico	Great Plains, Florida	Beck Ranch, Texas	Widespread in southern North America and Mexico

[a] This table accompanies figure 92 (numbered characters).

[b] Description of dental characters are representative of early and medial wear stages.

[c] Included as outgroup comparison for qualitative characters only. Quantitative characters (measurements) and temporal and spatial data are variable depending upon species and these are not available.

[d] These data are not used in figure 92 and are therefore not numbered sequentially as are the morphocline characters.

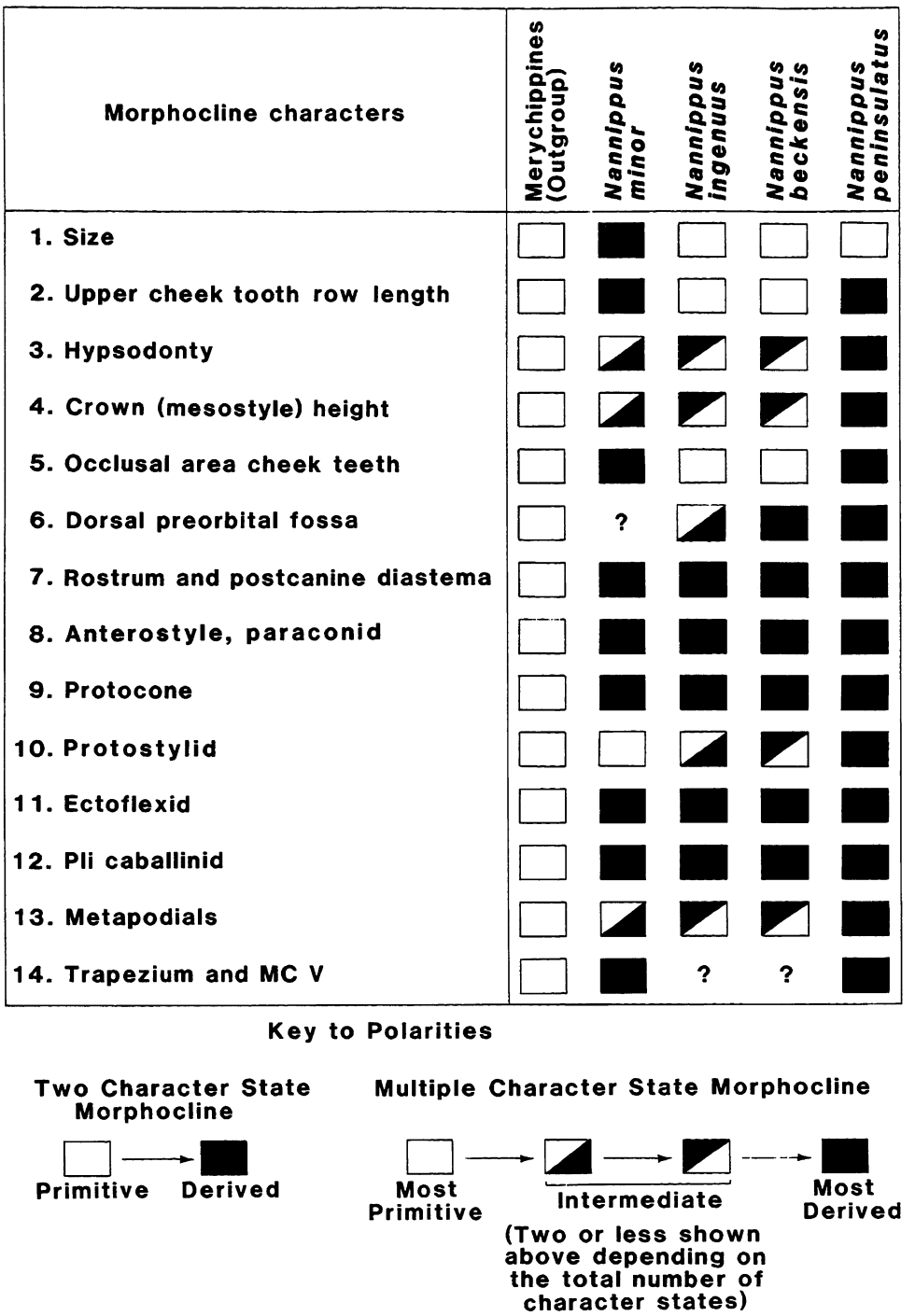


FIG. 92. Graphical representation of selected important character distributions and morphocline polarities in the four species of *Nannippus* and merychippines (outgroup). The numbered characters correspond to those in table 29. Also see text for discussion.

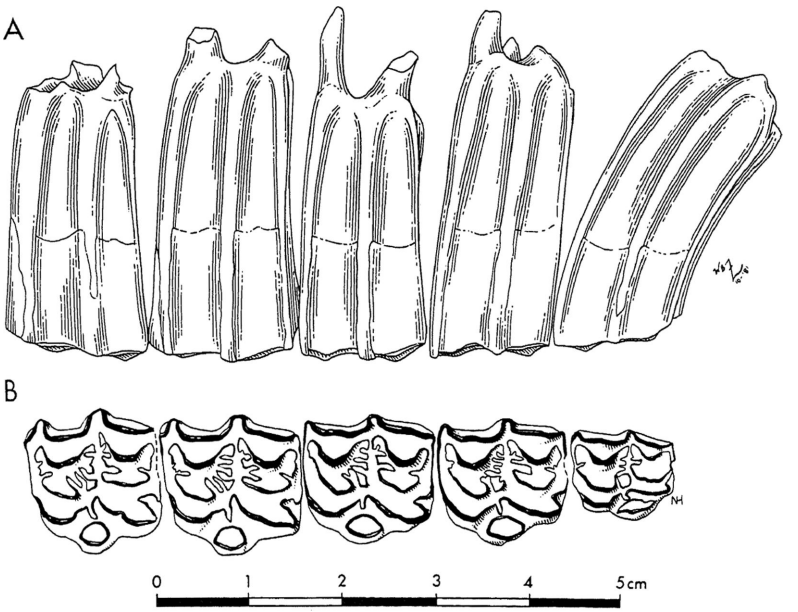


FIG. 93. *Nannippus minor,* UF 17570, neotype, left P^3–M^3, from Palmetto Mine, upper Bone Valley Formation, late Hemphillian of Polk County, central Florida. A. Lateral view. B. Occlusal view. The remainder of the neotype, which consists of the right M^2 and M^3, is not illustrated here.

like horse. Sondaar (1968) stated that *Nannippus* (particularly *N. "phlegon"*) had greatly reduced lateral metapodials and was functionally monodactyl. In some characters *Nannippus* exceeds *Equus* in the high degree of cursorial adaptation.

Nannippus minor (Sellards), 1916
Figures 16, 90–96, 105, 148, 150;
Tables 2, 29–31

SYNONYMS

Hipparion venustum Leidy, 1859, *nomina dubium et oblitum.*

Nannippus aztecus Mooser, 1968, pp. 1, 7–12, figs. 8–11, table 3.

Possibly *Nannippus hesperides* Mooser, 1968, pp. 1, 10–12, fig. 13.

TYPE SPECIMEN AND LOCALITY: Holotype, FGS 5867, isolated upper molar from the Amalgamated Phosphate Company pit near Brewster, Polk County, Florida. The holotype of *N. minor* has been lost since about the 1920s (Skinner and Hibbard, 1972). MacFadden and Waldrop (1980) designated a neotype, 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. 93).

REVISED DIAGNOSIS: Same as for genus with the following specific characters: Very small and moderately hypsodont. Estimated mean TRL *ca.* 90 mm. Unworn or little-worn M1MSTHT *ca.* 37–45 mm. Occlusal cross-sectional area of cheek teeth very small. Protostylids relatively well developed. Metapodials tiny and moderately elongated.

Nannippus minor differs from *N. ingenuus* and *N. beckensis* in its smaller size and smaller cross-sectional area of the cheek teeth. *N. minor* differs from *N. ingenuus, N. beckensis,* and *N. peninsulatus* in shorter crowns (less hypsodont), and greater frequency of protostylid development.

GEOGRAPHIC AND STATIGRAPHIC DISTRIBUTION: Late Clarendonian to late Hemphillian of Central and southern North America (table 30).

DESCRIPTION: *N. minor* is very small, which is one striking character of the genus *Nannippus.* The cheek teeth are hypsodont (e.g., fig. 93), but significantly less so than, e.g., *N.*

TABLE 30
Synopsis of Collections Examined for *Nannippus minor* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Numerous	UF, USNM	Alachua Formation, Alachua County, Bone Valley Formation, Polk and Hillsborough counties, central Florida	Late Clarendonian to late Hemphillian	Includes type "locality" (see text)
Yepómera	LACM (CIT) UALP	Unnamed unit, Chihuahua, Mexico	Late Hemphillian	
Rancho El Ocote	TMM	Unnamed unit, Guanajuato, Mexico	Late Hemphillian	Type locality for *N. aztecus*
Coffee Ranch	MSU	Ogallala Group, Hemphill County, Texas Panhandle	Late Hemphillian	Very rare at this locality

peninsulatus. The crown (mesostyle) height of *N. minor* for little-worn upper cheek teeth is usually between *ca.* 37–45 mm and almost always less than 50 mm (Waldrop, 1971; MacFadden and Waldrop, 1980; table 31). No skulls of *N. minor* are known and therefore the facial region cannot be characterized.

The cheek tooth row length is the smallest of all North American hipparions. The estimated TRL of *ca.* 90 mm is based on one available specimen in middle wear (TMM 41685-81, fig. 94B; TMM 41685-80, fig. 94A is too worn to be representative).

The cheek teeth are slightly curved in the transverse plane. As is characteristic of *Nannippus*, P^2 has a reduced anterostyle relative to other hipparions. The protocones are rounded to oval and small relative to the

TABLE 31
Selected Upper Dental Measurements and Univariate Statistics for *Nannippus minor*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V (%)	OR	N	$\bar{x}$	s	V (%)	OR
P2APL	22	16.75	1.04	6.23	15.0–19.4	18	17.01	0.95	5.58	15.7–19.4
P2TRNW	22	14.39	0.71	4.94	12.7–15.8	18	14.46	0.76	5.26	12.7–15.8
P2PRTL	22	4.66	0.30	6.52	4.1–5.2	18	4.65	0.31	6.67	4.1–5.2
P2PRTW	22	3.32	0.33	9.87	2.8–4.0	18	3.23	0.26	8.05	2.8–3.7
P2TOTPLI	22	4.23	2.93	69.23	1–10	18	4.72	3.01	21.19	1–10
M1APL	52	14.42	1.19	8.24	10.9–17.3	29	14.47	0.95	6.56	12.9–17.3
M1ECTL	50	14.49	1.20	8.35	10.7–17.5	28	14.53	0.91	6.26	12.9–17.1
M1TRNW	50	14.01	0.75	5.34	12.5–15.6	27	14.13	0.63	4.46	12.9–15.4
M1PRTL	51	5.46	0.68	12.21	3.7–6.8	28	5.48	0.69	12.59	3.7–6.8
M1PRTW	50	3.27	0.43	13.07	2.3–3.8	28	3.28	0.42	12.80	2.3–3.8
M1TOTPLI	51	6.73	2.65	39.35	0–14	29	7.10	2.23	31.41	3–14
TRL	2	82.25	11.24	13.67	74.3–90.2	1	90.2	—	—	—
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	20	26.58	6.70	25.23	13.1–39.0	0	—	—	—	—
M1MSTHT	49	28.37	6.26	22.05	13.9–44.5	6	38.37	5.49	14.31	36.9–44.5

[a] Abbreviations are presented on pp. 21 and 22; see table 30 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

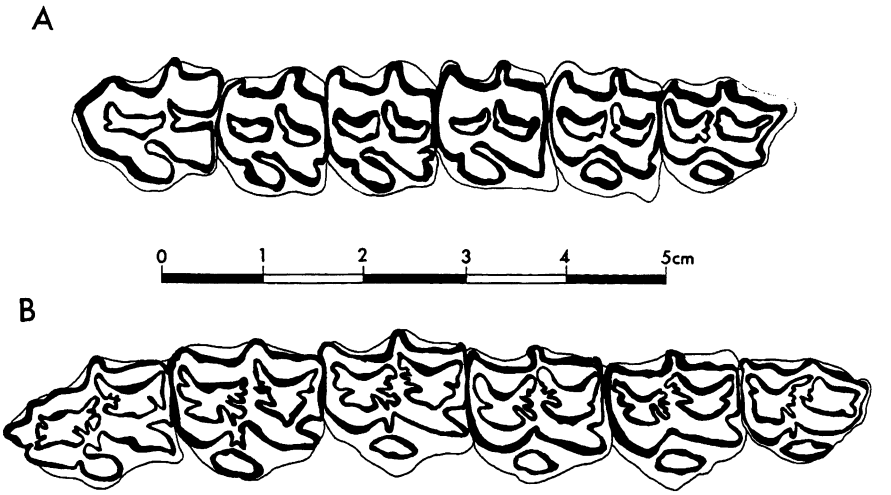


FIG. 94. Occlusal views of *Nannippus minor* (=*N. aztecus* of Mooser, 1968) from the Rancho El Ocote L.F., late Hemphillian of Guanajuato, central Mexico. A. TMM 41685-80 (=holotype of *N. aztecus* =MSU 11125), right (reversed) P^2–M^3 in very late wear stage. B. TMM 41685-81 (=MSU 11126), right (reversed) P^2–M^3 in middle wear stage.

cross-sectional area of the tooth. The pli caballin usually consists of a single fold or is absent. The pre- and postfossette borders are moderately plicated.

The lower cheek teeth are slightly curved in the transverse plane and relatively curved anteriorposteriorly. Moderately to well-worn lower cheek teeth are relatively wide transversely, giving them a relatively square, rather than rectangular, appearance as in some other hipparions (fig. 95). Corresponding with the small anterostyle in P^2, there is a relatively small paraconid in P_2. The protostylids are usually relatively well developed and occur in a relatively high proportion of teeth (fig. 95 is not representative of the development of this character state). The ectoflexids are relatively deep and the pli caballinids are either rudimentary or absent. The enamel borders are usually not plicated. As represented by the large sample of postcranial elements from Yepómera at the LACM (also see Lance, 1950; Lamina III), *N. minor* has tiny metapodials. These are slender and indicate affinities with *Nannippus,* however, the metapodials are significantly shorter than the other species, e.g., in contrast to the extreme development in *N. peninsulatus.*

CHARACTER ANALYSIS AND GENERAL DISCUSSION: Although *N. minor* is one of the few North American hipparion species for which the skull is unknown,[9] several derived characters indicate affinities with the genus *Nannippus.* These characters include very small size, moderate hypsodonty, poorly developed anterostyle on P^2 and correspondingly small paraconid on P_2, and gracile metapodials. If a skull of *N. minor* were discovered, it is predicted that this species would have a long rostrum (postcanine diastema), and a DPOF that is either very poorly developed or absent.

Based on the presence of numerous primitive character states, *Nannippus minor* is set apart as the most primitive sister species of the genus. In characters such as hypsodonty and reduction of the protostylid, a simple morphocline proceeds from *N. minor* to *N. ingenuus* to *N. beckensis* to *N. peninsulatus* (see fig. 92, table 29). In other characters such

[9] Based on correspondence during the 1960s between Morris F. Skinner and John J. Stephens, then of the Department of Geology and Orton Museum at Ohio State University, there supposedly exists a skull probably referable to *Nannippus minor* collected from Chihuahua, Mexico. If so, this would represent the only specimen that preserves the preorbital region. Unfortunately, at the time of the present study, this specimen was not available for examination.

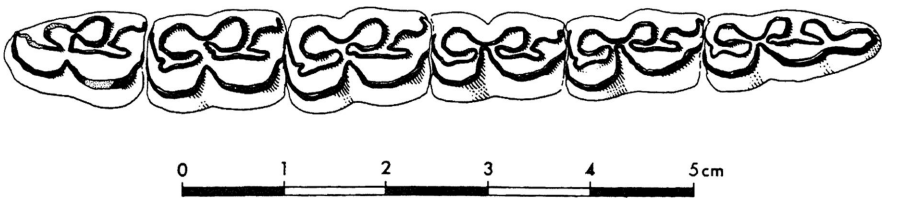


FIG. 95. Occlusal view of left P_2–M_3 of *Nannippus minor*, TRO 567 (private collection of John S. Waldrop, Lake Wales, Florida) from Palmetto Mine, upper Bone Valley Formation, late Hemphillian of Polk County, central Florida.

as size, the exact transformations of states do not indicate simple morphoclines; *N. minor* is relatively tiny, but there is no clear unidirectional trend with regard to *N. ingenuus, N. beckensis,* and *N. peninsulatus* (figs. 90, 91). *Nannippus minor* is the smallest of the North American hipparions. There is no other hipparion that approaches the diminutive stature of *N. minor.* Even the smallest Old World species "*Hipparion*" *matthewi,* which is best known from Samos, appears to be larger (see Sondaar, 1971).

Leidy (1859) proposed the name *Hipparion venustum* for two isolated upper molars from "Post-Pliocene" beds along the Ashley River, South Carolina. These specimens are illustrated in Osborn (1918, p. 200, fig. 165). The paratype has very plicated fossette borders and a small protocone; it appears to be similar to, although smaller than, "*Hippotherium*" *plicatile.* The type, which is now lost, was small, relatively hypsodont, with moderately plicated fossette borders; it appears to be the same taxon as *Nannippus minor.* Inasmuch as the paratype represents a different taxon, it cannot be designated as the neotype for *N. minor.* The smaller "type" has to stand as the name-bearer, but because it is lost, "*Hipparion venustum*" is here considered a *nomen vanum.* In addition, because its synonym *Nannippus minor* Sellards (1916) has been in common usage for over a half-century "*Hipparion venustum*" is also considered a *nomen oblitum.*

Mooser (1968) named two species of *Nannippus, N. aztecus* and *N. hesperides,* from the late Hemphillian Ocote L.F. of Guanajuato, Mexico. Based on Mooser's descriptions and examination of the topotypic sample now deposited in the TMM (TMM 41685-5 and TMM 41685-80 through 87; also see fig. 94A), it appears that *N. aztecus* is a junior synonym of *N. minor. Nannippus hesperides* is discussed below under *N. peninsulatus.*

Akersten (1972) reports the presence of *Nannippus* cf. *minor* from the Blancan Red Light L.F. of Hudspeth County, western Texas. If this occurrence were correct, it would extend the range of *N. minor*-like forms into the Blancan. Akersten's referral to this species is based on two isolated, poorly preserved upper cheek teeth (both catalogued as TMM 40866-1). Based on mesostyle crown height, general size, and dental pattern, the teeth are better referred to *N. peninsulatus.*

Nannippus minor is morphologically and temporally the most primitive species of the genus *Nannippus.* With a range from late Clarendonian to latest Hemphillian, or about 10 to 4 m.y., *N. minor* is the most long-lived North American hipparion species. The oldest-known occurrence is from the Love Bone Bed L.F. of Florida. In this and contemporaneous localities *N. minor* can be confused with *Pseudhipparion.* However, *N. minor* has a well-developed hypoconal groove and more complicated fossettes than *Pseudhipparion* (fig. 96). Despite the fact that relatively well-developed dental material is available for *N. minor,* with lack of relevant crania the origin of *N. minor* and hence this genus remains enigmatic. It is not clear whether *N. minor* is most closely related to some other hipparion or to a species within the merychippine complex (see further discussion below).

Nannippus ingenuus (Leidy), 1885
Figures 90–92, 97–102, 105, 148, 150;
Tables 2, 29, 32, 33

JUNIOR SYNONYM

Protohippus lenticularis Cope, 1893, pp. 41–42, plate 12, figs. 1, 2, 2a.

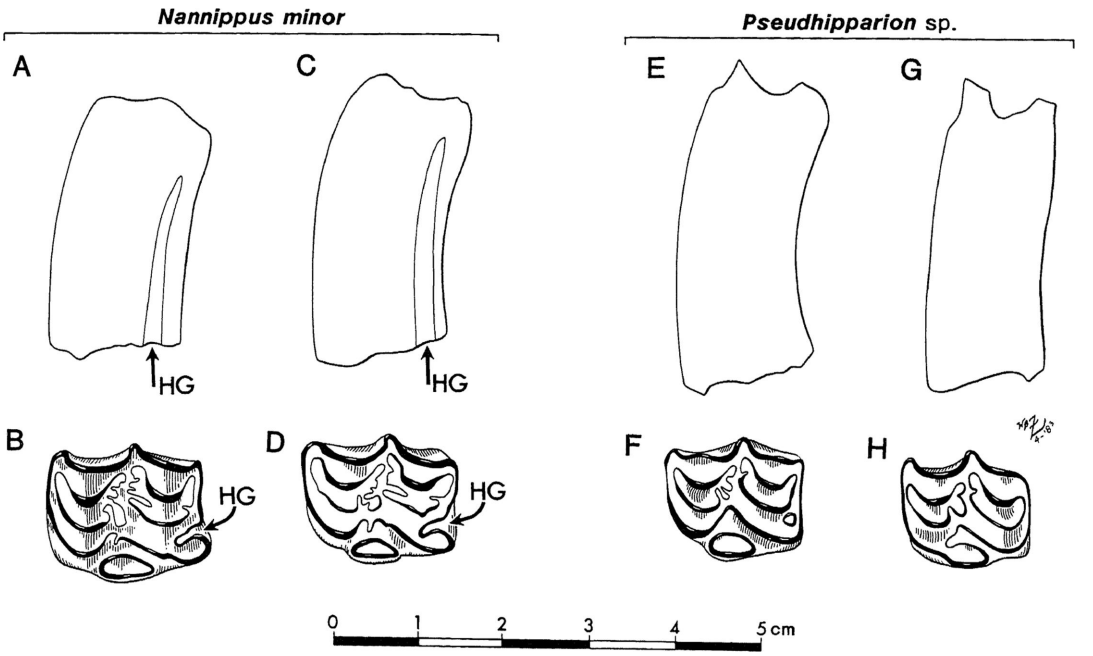


FIG. 96. Comparison of isolated right (reversed) upper cheek tooth (M^2) pattern in middle wear for *Nannippus minor* and *Pseudhipparion* sp. from Love Bone Bed, Alachua Formation, late Clarendonian of Alachua County, north-central Florida. UF 50351, *Nannippus minor,* lateral (A) and occlusal (B) views. UF 50352, *Nannippus minor,* lateral (C) and occlusal (D) views. UF 50353, *Pseudhipparion* sp., lateral (E) and occlusal (F) views. UF 50354, *Pseudhipparion* sp., lateral (G) and occlusal (H) views. HG is abbreviation for hypoconal groove.

SELECTED SYNOPSIS OF USAGE
(See discussion below):

Hippotherium ingenuum Leidy, 1885, pp. 32–33.
Hippotherium gratum Leidy and Lucas, 1896, pp. 49, 50, pl. 19, figs. 9, 10.
?*Hipparion lenticularis* Gidley, 1907, pp. 915–917.
Hipparion lenticulare Osborn, 1918, pp. 184–185, figs. 147, 148, 148a, pl. 32, fig. 2, pl. 33, figs. 5–7.
Hipparion ingenuum, Osborn, 1918, p. 191, fig. 154.
Hipparion ingenuum, Simpson, 1930, pp. 176, 180, 183, 184, 187, 188, fig. 20.
Hipparion (*Nannippus*) *lenticulare* Matthew and Stirton, 1930, pp. 363–364, pls. 57, 58.
Nannippus lenticularis Stirton, 1940, p. 186.
Nannippus ingenuus Stirton, 1940, p. 186.
Nannippus lenticularis Dalquest and Donovan, 1973, pp. 38, 44.

TYPE SPECIMEN AND LOCALITY: USNM 3306, isolated left $?M^1$ in moderate wear, probably from Mixson's Bone Bed, town of Williston, Levy County, early Hemphillian of north-central Florida (fig. 97, see discussion below). There is some confusion as to the type status for this species. It is clear from Leidy's (1885) original description that

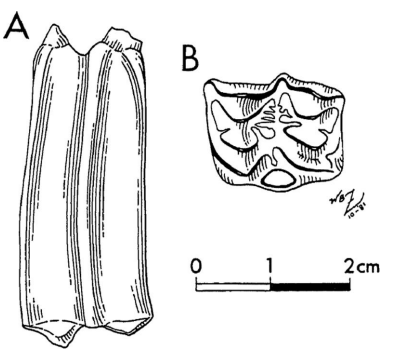


FIG. 97. *Nannippus ingenuus,* USNM 3306, left $?M^1$, holotype, probably from Mixson's Bone Bed, early Hemphillian of Levy County, north-central Florida (see discussion in text). A. Lateral view. B. Occlusal view.

TABLE 32
Synopsis of Collections Examined for *Nannippus ingenuus* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Mixson's Bone Bed or "near Archer"	USNM, F:AM, UF	Alachua Formation, Levy or Alachua counties, Florida	Probably Hemphillian	Type locality, see discussion in text
Edson Quarry and North Quarry, Maxwell Ranch	F:AM	Ogallala Group, Sherman County, Kansas	Late Hemphillian	Site of only known specimens that preserve crania
Miami (Coffee Ranch) and Guymon (Optima) quarries	F:AM, UCMP, PPM	Ogallala Group, Hemphill and Texas counties, Texas and Oklahoma panhandles (respectively)	Late Hemphillian	
Uptegrove, Cn-10	UNSM	Ogallala Group, Cheyenne County, Nebraska	Hemphillian	

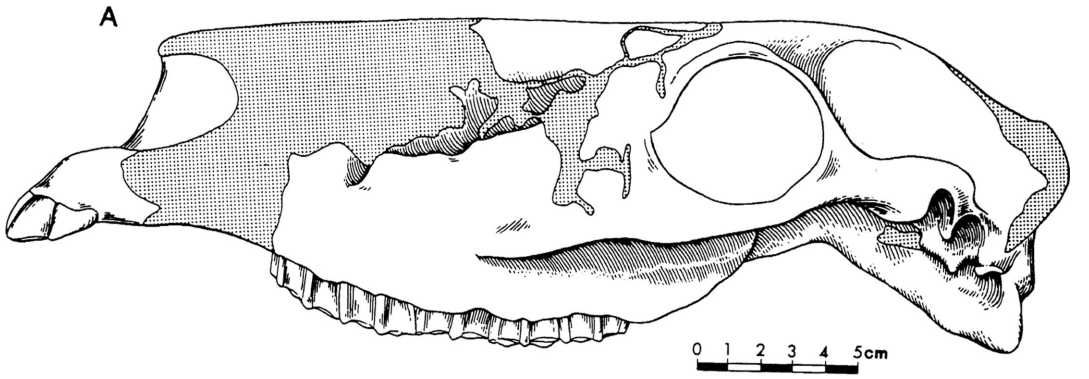
USNM 3306 is the type specimen. However, Osborn (1918, p. 191) states that the type includes: "Two superior molar teeth of the left side." Osborn (1918, fig. 154) illustrates both of these, i.e., USNM 3305 and 3306 (although they were both incorrectly listed as USNM 3306 in his description). Nevertheless, Leidy's (1885) original description does not mention a second specimen. Therefore, the isolated left upper cheek tooth (?M^1), USNM 3306, is clearly the holotype and the second specimen (USNM 3305, a left M^3) is not part of the type concept as originally conceived by Leidy. In addition, there is some confusion about the type locality. The inscription on the holotype, USNM 3306, reads: "Pres [*sic*] to Dr. Leidy from J. C. Neal Archer Fla. March 4, 1885." As discussed in Leidy and Lucas (1896), Dr. Neal's collection contains specimens that could have come from several localities in Levy and Alachua counties. Based on examination of the state and preservation and color of USNM 3306, and as Simpson (1930) also noted, the holotype was probably collected from Mixson's Bone Bed in Williston.

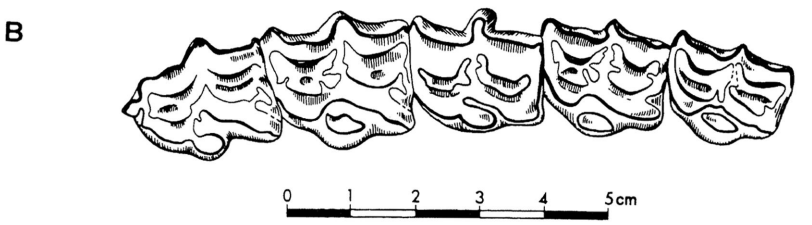
REVISED DIAGNOSIS: So far as is known, same as for genus with the following specific characters: Medium-sized and relatively hypsodont hipparion. Estimated mean TRL *ca.* 116 mm. Unworn or little-worn M1MSTHT *ca.* 43–57 mm. DPOF faint and very far anterior of orbit. Protocone rounded to oval. Fossette borders simple to moderately plicated. Ectoflexids relatively deep. Pli caballinids poorly developed, rudimentary, or absent. Protostylids moderately developed. Metapodials gracile and moderately elongated.

Nannippus ingenuus differs from *N. minor* in its significantly larger size, particularly in occlusal cross-sectional area of cheek teeth, and less frequency of well-developed protostylids. *Nannippus ingenuus* differs from *N. beckensis* in (1) slightly larger size, (2) the better and more frequently developed protostylids, and (3) in the upper cheek teeth, less well-developed styles. *Nannippus ingenuus*

→

FIG. 98. *Nannippus ingenuus* from the Ogallala Group, late Hemphillian of Sherman County, northwestern Kansas. F:AM 113731, right (reversed) lateral view of partial skull and probably associated premaxillary, F:AM 113732 (A) and occlusal view (B) of right (reversed) P^2, P^3, dP^4, M^1, and M^2 from North Quarry on the Marshall Ranch. F:AM 111731, from Edson Quarry, left lateral view of partial skull (C) and occlusal view of left P^2–M^3 (D).


A
0 1 2 3 4 5cm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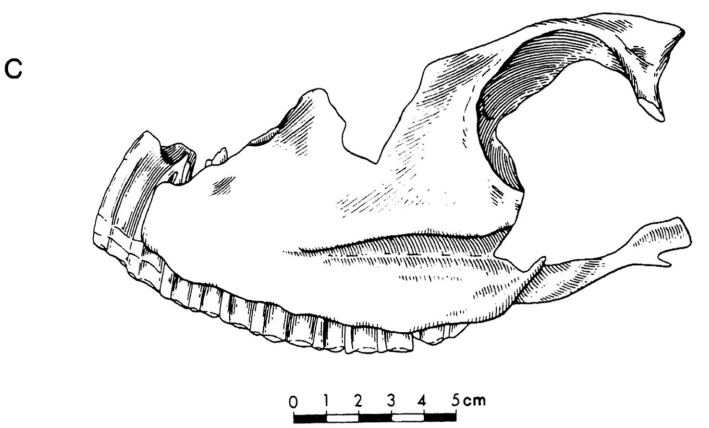
C
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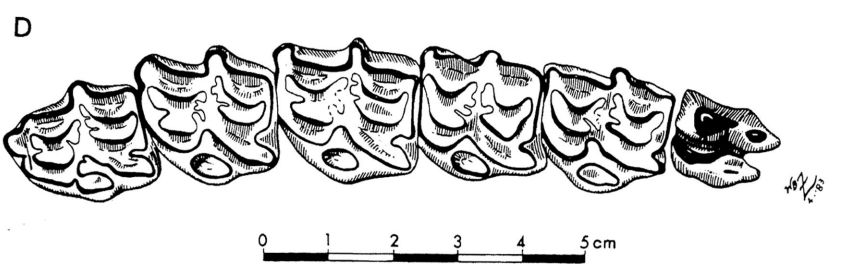
D
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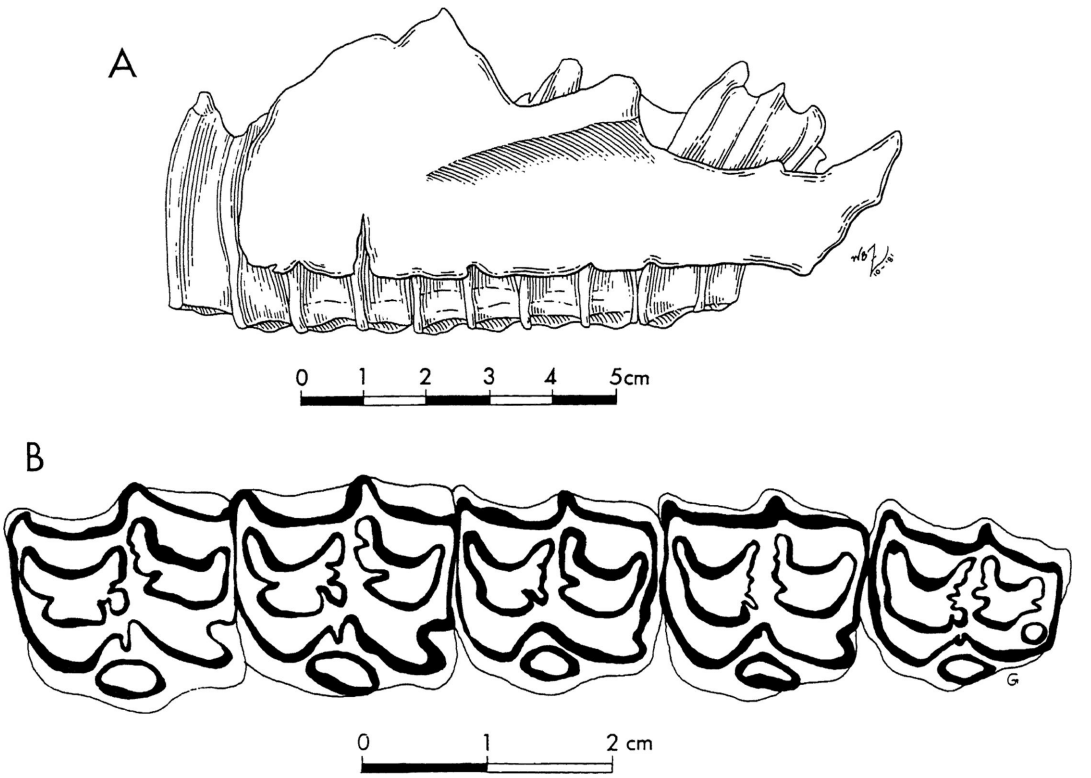

FIG. 99. *Nannippus ingenuus,* UNSM 61447, from UNSM Uptegrove locality Cn-101, Ogallala Group, late Hemphillian of Cheyenne County, western Nebraska. A. Right (reversed) lateral view of maxillary fragment with P^3–M^3. B. Occlusal view.

differs from *N. peninsulatus* in its larger size, shorter crown (mesostyle) heights, better and more frequently developed protostylids, and less well-developed styles.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Early Hemphillian of Florida and Nebraska; late Hemphillian from the Great Plains of Texas, Oklahoma, Kansas, and Nebraska (table 32).

DESCRIPTION: The skull of *Nannippus ingenuus* is known from two specimens, F:AM 111731 and a composite of two probably associated specimens, F:AM 113731 and 113732 (fig. 98). In the posterior cheek region, the face is smooth (with no trace of a DPOF as is developed in, e.g., *Cormohipparion* or *Hipparion*). In the anteriormost cheek region there is a small, poorly developed "DPOF" that lies above P^2–P^4. The IOF is situated in the posterior portion of the DPOF over P^4. The lacrimal bone is triangular shaped and it extends anteriorly to a position that lies approximately above M^1–M^2. The upper symphysial dentition of *N. ingenuus* is not known. The upper cheek tooth dentition is mostly represented by isolated teeth. In addition to the skulls (fig. 98), the best preserved dentition of *N. ingenuus* examined during this study consists of a maxillary fragment with right P^3–M^3, UNSM 61447 (fig. 99), from the late Hemphillian Uptegrove locality (Cn-101), Cheyenne County of western Nebraska. The upper cheek teeth are medium-sized, relatively hypsodont, and slightly curved in the transverse plane (fig. 100, table 33). The protocones are rounded to oval. The fossette borders are simple to moderately plicated. The pli protolophs and pli hypostyles are absent or consist of a single loop. The pli protoconules, pli prefossettes, and pli postfossettes consist of multiple loops. The pli caballinid usually is

rudimentary, poorly developed, or consists of a single loop.

The mandible and lower dentition are represented by UNSM 2641, UCMP 30239 (Matthew and Stirton, 1930, pl. 57), and several other specimens in the UCMP collection, e.g., UCMP 30238 (figs. 101, 102). The canine is nearly appressed to I_3. The postcanine diastema is dorsoventrally slender and anteriorposteriorly relatively elongate as in *N. beckensis* and *N. peninsulatus*. The paraconid in P_2 is small (and similar to other species of *Nannippus*). The protostylids, when present, vary from a well-developed projection of the paralophid to an isolated conid (also see Dalquest and Donovan, 1973). The ectoflexids are relatively deep with pli caballinids that are rudimentary or absent. The metapodials are less elongate than, e.g., *Neohipparion eurystyle* from the Coffee Ranch L. F. (Matthew and Stirton, 1930, pl. 55) and *Nannippus peninsulatus* from localities in Texas, Arizona, and Florida.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: *Nannippus ingenuus* clearly possesses the generic characters based on a combination of its poorly developed DPOF, very

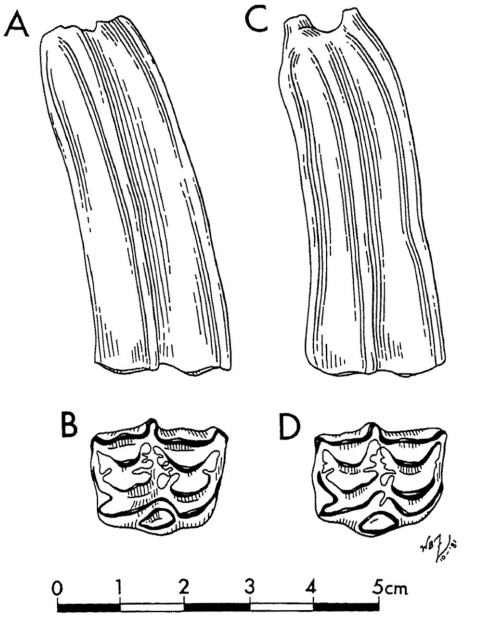

FIG. 100. Isolated upper cheek teeth of *Nannippus ingenuus*, UCMP 30843 (both specimens), right M^2, from the Coffee Ranch (=Frick Miami) L.F., Ogallala Group, late Hemphillian of Hemphill County, Texas Panhandle, lateral (A, C) and occlusal (B, D) views.

TABLE 33
Selected Upper Dental Measurements and Univariate Statistics for *Nannippus ingenuus*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V (%)	OR	N	$\bar{x}$	s	V (%)	OR
P2APL	9	22.68	1.66	7.32	19.9–24.9	5	22.46	1.11	4.94	21.2–23.9
P2TRNW	9	17.08	1.19	6.96	15.2–18.3	5	16.98	1.14	6.71	15.7–18.0
P2PRTL	9	5.84	0.52	8.81	5.1–6.9	5	5.70	0.24	4.21	5.4–5.9
P2PRTW	9	3.60	0.52	14.37	2.7–4.2	5	3.56	0.44	12.36	2.9–3.9
P2TOTPLI	8	6.25	2.49	39.89	1–9	5	7.40	1.52	20.54	6–9
M1APL	15	18.23	1.58	8.49	15.3–21.1	8	17.99	1.03	5.73	17.4–20.4
M1ECTL	15	18.72	1.61	8.61	15.6–21.3	8	18.44	1.16	6.29	17.1–20.9
M1TRNW	15	16.99	1.52	8.94	13.9–19.1	8	16.72	1.22	7.30	15.1–18.5
M1PRTL	15	6.00	1.08	17.95	4.6–8.1	8	5.74	0.86	14.98	4.6–7.2
M1PRTW	13	3.45	0.45	13.12	2.5–4.2	8	3.36	0.29	8.63	2.9–3.7
M1TOTPLI	12	5.50	2.43	44.20	2–10	8	6.25	2.32	37.12	2–10
TRL	1	115.90	—	—	—	0	—	—	—	—
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	8	29.06	7.15	24.60	15.9–40.5	2	38.05	3.46	9.09	35.6–40.5
M1MSTHT	12	43.51	8.05	18.49	28.8–56.1	3	49.87	7.00	14.04	41.9–55.0

[a] Abbreviations are presented on pp. 21 and 22; see table 32 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

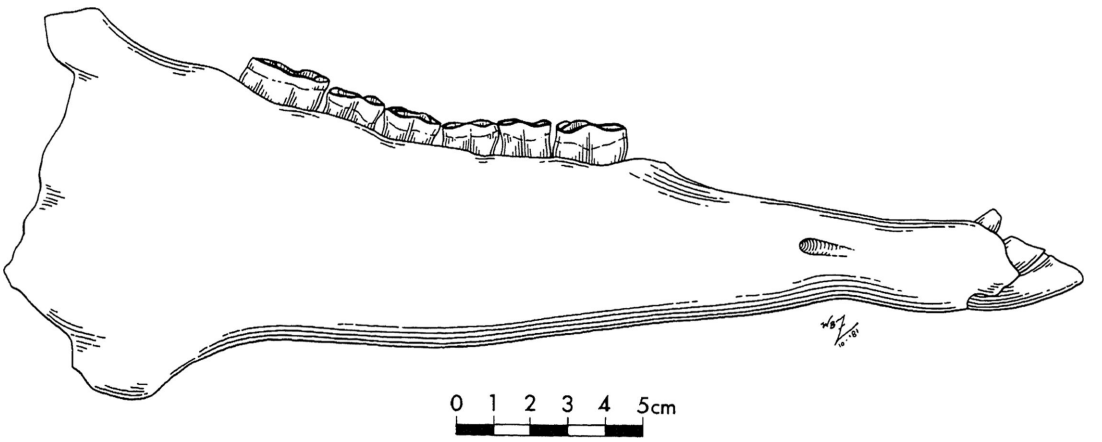

FIG. 101. Right lateral view of ramus and symphysis of *Nannippus ingenuus,* UNSM 2641, from the Ft-40 locality, Cambridge L.F., early Hemphillian of Frontier County, south-central Nebraska.

small size, elongate rostrum, and numerous dental characters, e.g., relative size and shape of the protocone, moderately plicated fossette borders, poorly (or less frequently) developed pli caballins, pli caballinids, and protostylids.

Based on morphocline analyses (fig. 92; table 29) of numerous characters, particularly of the dentition, *N. ingenuus* represents a phylogenetically intermediate species within the genus *Nannippus. Nannippus ingenuus* is more derived than *N. minor* in its increased crown height and decreased frequency and poorer development of the protostylids. *Nannippus ingenuus* is primitive relative to *N. peninsulatus* in slightly to much smaller crown heights, as well as more frequently and better developed protostylids. *Nannippus ingenuus* is larger than *N. beckensis.* In addition, Dalquest and Donovan (1973) stated that the styles in the upper cheek teeth are less well developed in *N. ingenuus* than either *N. beckensis* or *N. peninsulatus.* I cannot comment on the taxonomic utility of this character distinction because within hipparions it appears to be conservative and was not surveyed during the present study. However, following Dalquest and Donovan (1973), the relative development of the upper molar styles is possibly a character that can be used to differentiate between *N. ingenuus* on the one hand and *N. beckensis* and *N. peninsulatus* on the other hand.

Cope's (1893) species *Protohippus lenticularis,* which is well known in the literature (as either *Hipparion lenticulare* or *Nannippus lenticularis*), is here considered a junior synonym of *N. ingenuus.* This is based on the overall similarity in size, crown height, and dental pattern of the two named "species." The similarities between these "species" has also been previously noted elsewhere in the literature (e.g., Simpson, 1930). The name "*Hipparion*" *lenticularis* has one of the most

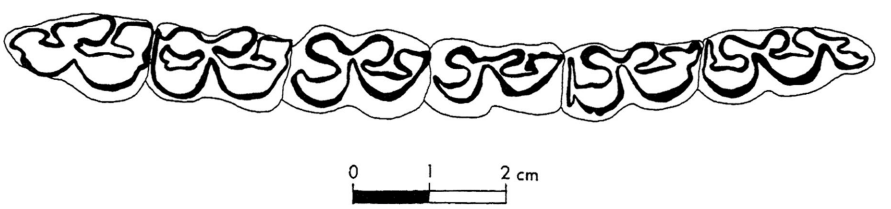

FIG. 102. Lower dentition, right (reversed) P_2–M_3 of *Nannippus ingenuus,* UCMP 30238 from the Coffee Ranch L.F., Ogallala Group, late Hemphillian of Hemphill County, Texas Panhandle.

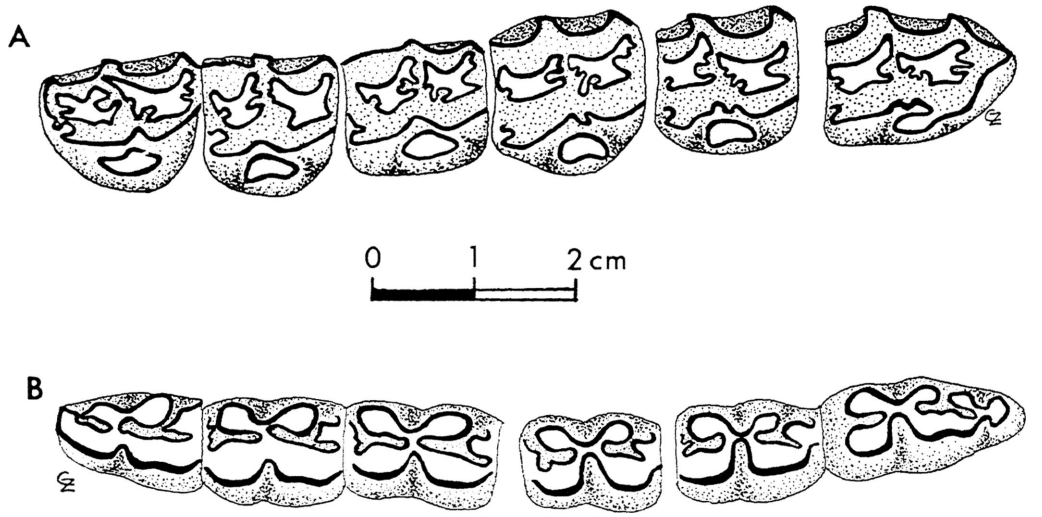

FIG. 103. Cheek tooth dentitions of *Nannippus beckensis* from Beck Ranch, Blancan of Scurry County, Texas. A. MSU 8362 (=TMM 41878-4), holotype, right P^2–M^3. B. MSU 8378, left P_2–M_3. Illustrations from Dalquest and Donovan (1973, p. 38, text-figs. 4a and 4b). ©1973 and reproduced (slightly modified) with permission of the Society of Economic Paleontologists and Mineralogists, Tulsa, Oklahoma.

confused histories of all fossil horse species. The history of usage of this species name is briefly summarized here because it relates to the concept of the Clarendonian *Hipparion, H. tehonense,* from Donley County in the Texas Panhandle as well as to *N. ingenuus.* Cope (1893) named *Protohippus lenticularis* based on an isolated molar from the late Hemphillian Goodnight L.F. in the Texas Panhandle. Gidley (1907) doubtfully referred better-preserved specimens, including the well-known skull AMNH 10584, from the early Clarendonian deposits of Donley County in the Texas Panhandle to ?*Hipparion lenticularis.* Osborn (1918) designated AMNH 10584 as the neotype of *H. lenticulare* [*sic*], although this was unwarranted since the type was not lost. Nevertheless, the usage of this species expanded to include early Clarendonian and late Hemphillian forms from the Texas Panhandle. Matthew and Stirton (1930) implicitly referred the Clarendon specimens, particularly AMNH 10584, to *H. lenticulare* although they recognized significant differences between this sample and that of *H. lenticulare* from the late Hemphillian Coffee Ranch L.F. (see their synonymy and discussion on pp. 363–365). MacFadden (1980) referred the Clarendonian hipparion to *Hipparion tehonense.* As also discussed above, it is recommended here that the concept of the well-known name *Hipparion* or *Nannippus lenticularis* should (1) exclude the present concept of *H. tehonense* from Donley County (and elsewhere), and (2) be considered a junior synonym of *Nannippus ingenuus.*

As recognized here, *Nannippus ingenuus* ranges throughout the Hemphillian. Its early Hemphillian occurrences include Mixson's Bone Bed of Florida and the Cambridge L.F. (Ft-40 locality) of Nebraska. Late Hemphillian occurrences include Coffee Ranch (=Frick Miami) and equivalent age localities in the Texas and Oklahoma panhandles (e.g., the Frick Guymon sites). This species also occurs in late Hemphillian localities such as Axtell in Randall County in the Texas Panhandle (also see "*Nannippus* cf. *lenticulare*" in Johnston and Savage, 1955).

Nannippus beckensis
Dalquest and Donovan, 1973
Figures 90–92, 103–105, 148, 150;
Tables 2, 29, 34

TYPE SPECIMEN AND LOCALITY: MSU 8362 (now TMM 41452-1), crushed partial skull

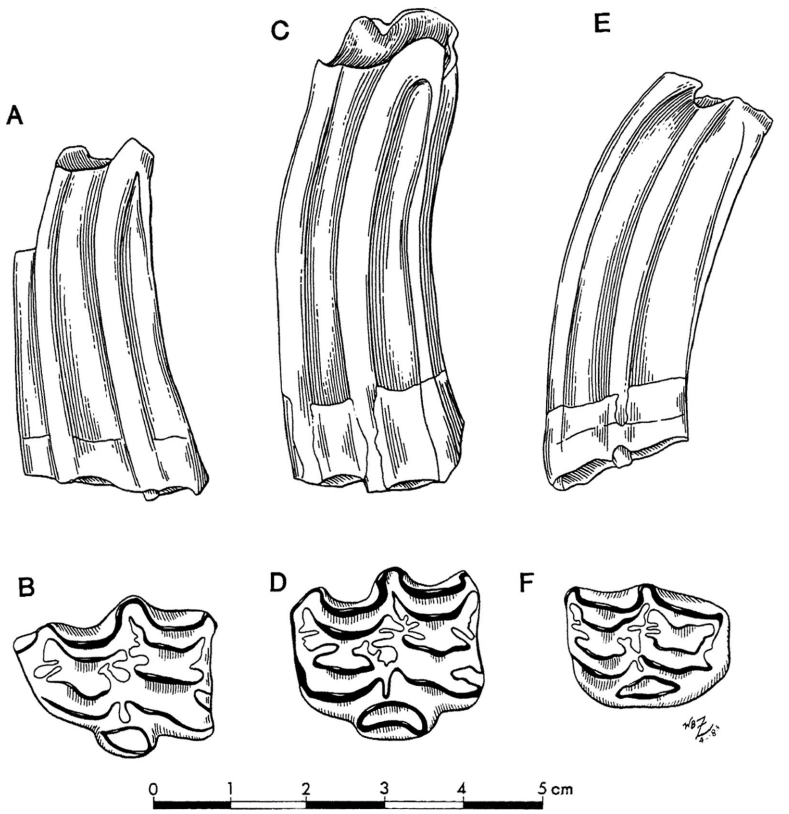

FIG. 104. Isolated upper cheek teeth of *Nannippus beckensis* in approximately "middle" wear. MSU 8566, left P^2, lateral (A) and occlusal (B) views. MSU 8353, left P^3 or P^4, lateral (C) and occlusal (D) views. MSU 8557, right (reversed) M^3, lateral (E) and occlusal (F) views.

with right and left P^2–M^3 (fig. 103), from the Beck Ranch L.F., early Blancan, Scurry Co., central Texas (Dalquest and Donovan, 1973; Dalquest, 1978).

DIAGNOSIS: Same as for genus with the following specific characters: Medium-sized and moderately hypsodont hipparion. Mean TRL *ca.* 102 mm. Unworn or little-worn M1MSTHT *ca.* 47–53 mm. DPOF absent. Protocone oval with rounded borders. Fossette borders relatively simple to moderately plicated. Protostylids usually absent. Ectoflexids moderate to deep. Pli caballinids poorly developed, rudimentary, or absent.

Nannippus beckensis differs from other species of this genus in the following characters: Intermediate in crown height between *N. minor* and *N. peninsulatus*. Cross-sectional area of cheek teeth larger than *N. minor*. Smaller than *N. ingenuus*.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: *N. beckensis* is only known from the type locality.

DESCRIPTION: The skull of *N. beckensis* is represented by the holotype, MU 8362. Although it is badly crushed and fragmented, the smooth facial region indicates that the DPOF is absent, consistent with the genus *Nannippus*. Due to the extremely poor state of preservation of this skull, an illustration is not presented here. *N. beckensis* is a medium-sized and moderately hypsodont hipparion (figs. 103, 104; table 34).

The upper cheek teeth are only slightly curved in the transverse plane and moderately curved anteriorly. The anterostyle is not

TABLE 34
Selected Upper Dental Measurements and Univariate Statistics for *Nannippus beckensis*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	5	20.66	1.51	7.33	19.0–22.5	4	20.20	1.28	6.34	19.0–21.5
P2TRNW	5	16.32	1.01	6.21	15.1–17.4	4	16.53	1.04	6.29	15.1–17.4
P2PRTL	5	5.96	0.52	8.69	5.5–6.8	4	5.75	0.25	4.35	5.5–6.1
P2PRTW	4	3.35	0.17	5.17	3.2–3.6	4	3.35	0.17	5.17	3.2–3.6
P2TOTPLI	3	5.33	1.16	21.65	4–6	3	5.33	1.16	21.65	4–6
M1APL	8	16.28	0.64	3.94	15.0–17.1	8	16.28	0.64	3.94	15.0–17.1
M1ECTL	8	15.74	0.70	4.47	14.6–16.7	8	15.74	0.70	4.47	14.6–16.7
M1TRNW	8	15.51	0.83	5.38	14.3–17.2	8	15.51	0.83	5.38	14.3–17.2
M1PRTL	8	5.75	0.47	8.21	5.1–6.5	8	5.75	0.47	8.21	5.1–6.5
M1PRTW	8	3.40	0.15	4.44	3.1–3.6	8	3.40	0.15	4.44	3.1–3.6
M1TOTPLI	7	7.14	1.07	14.97	6–9	7	7.14	1.07	14.97	6–9
TRL	1	101.0	—	—	—	1	101.0	—	—	—
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	5	34.34	8.26	24.06	25.4–43.1	1	36.30	—	—	—
M1MSTHT	9	35.84	4.61	12.85	26.5–51.8	2	50.40	1.98	3.93	49.0–51.8

[a] Abbreviations are presented on pp. 21 and 22.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

greatly expanded on P^2. The protocones are oval with rounded borders. The pli caballin usually consists of a single loop, is rudimentary, or is absent. The fossette borders are moderately plicated.

There is a long postcanine diastema that is characteristic of the genus *Nannippus*. Moderately to well-worn lower cheek teeth are relatively wide transversely, giving a relatively square appearance (fig. 103). In P_2 the paraconid is not well developed. The protostylids are usually absent. The ectoflexids are relatively deep and the pli caballinids are poorly developed, rudimentary, or absent. The enamel is usually simple with no plications. The metapodials of *N. beckensis* are moderately elongate and gracile (Dalquest and Donovan, 1973).

CHARACTER ANALYSIS AND GENERAL DISCUSSION: *Nannippus beckensis* is clearly a member of the genus based on combination of characters including the smooth preorbital region, elongate rostrum, and relatively small size. Although there are not many diagnostic specific characters, *N. beckensis* seems to be distinct based on a combination of crown height, size (figs. 90, 91; table 34), and following Dalquest and Donovan (1973, see discussion above for *N. ingenuus*), reduction in the frequency and development of the protostylids (and possibly pli caballinids) and relative development of upper cheek tooth styles.

Based on the present analysis and the conclusions of Dalquest and Donovan (1973) and MacFadden and Waldrop (1980), a morphocline analysis (fig. 92, table 29) of principally dental characters (and excluding size) indicates that the primitive to derived sequence of species proceeds from *N. minor* to *N. ingenuus* to *N. beckensis* to *N. peninsulatus*. These dental characters such as increased crown height, relative development of the styles, and reduction of the protostylid show congruent morphocline polarities. In size, as represented by, e.g., the occlusal cross-sectional area, *N. beckensis* does not conform to a simple morphocline with the other species of the genus; *N. beckensis*, and *N. peninsulatus* are small hipparions; however, these are significantly larger than the tiny species *N. minor*, and smaller than *N. ingenuus* (figs. 90, 91). A comparison of occlusal cross-sectional areas and little-worn crown heights suggest that these four species are distinct (fig. 105)

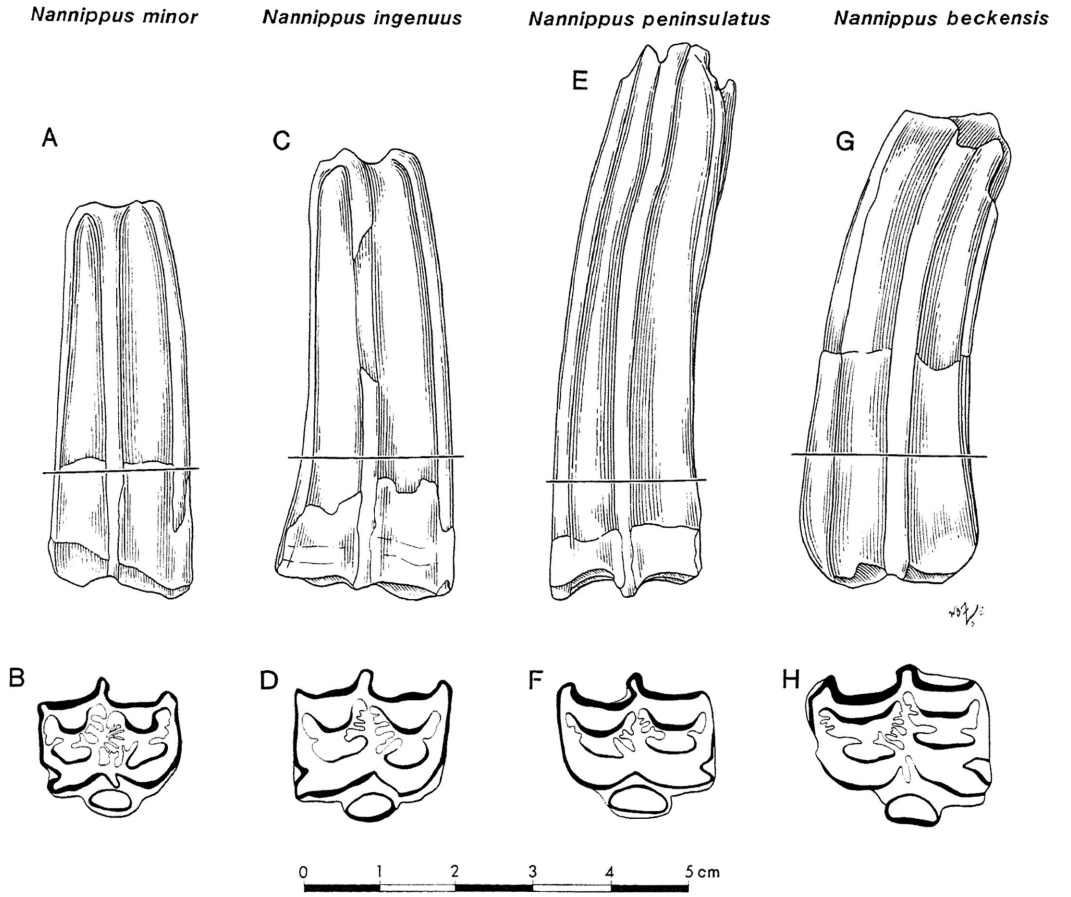

FIG. 105. Comparison of isolated M^1 of four species of *Nannippus* recognized in this report. These specimens were chosen because they each are in early wear. Therefore, the crown heights are near the maximum. In order to illustrate a representative occlusal pattern, each specimen was sectioned about 15 mm down (measuring from the mesostyle) the tooth (as indicated by line in each illustration). From left to right: *Nannippus minor,* UF 17253 from Palmetto Mine, upper Bone Valley Formation, late Hemphillian of Polk County, central Florida. Lateral (A) and sectioned (B) views. *Nannippus ingenuus,* MSU 3337 from Coffee Ranch, late Hemphillian of Hemphill County, Texas Panhandle, lateral (C) and sectioned (D) views. *Nannippus peninsulatus,* UA 47-7/2525, from the Blancan of Arizona, lateral (E) and sectioned (F) views. *Nannippus beckensis,* MSU 8592 from Beck Ranch, early Blancan of Scurry County, Texas, lateral (G) and sectioned (H) views.

although they may actually be morphologically intergradational.

Nannippus beckensis is only known from the early Blancan Beck Ranch L.F. The fact that this species is not known from other localities could be a result of either (1) that its spatial distribution was truly restricted to the southern Great Plains, or (2) that this species seems rare because of the paucity of early Blancan sites elsewhere in Central America and North America.

Nannippus peninsulatus (Cope), 1885

Figures 8, 89–91, 106–116, 148, 150;
Tables 2, 29, 35, 36

JUNIOR SYNONYMS

Equus phlegon Hay, 1899, p. 345.

Hipparion cragini Hay, 1917, pp. 40, 42–43, pl. 1, figs. 6, 7.
Probably *Nannippus hesperides* Mooser, 1968, pp. 10–12, fig. 13.

SELECTED SYNOPSIS OF USAGE
(See Discussion below):

Hippotherium peninsulatum Cope, 1885, pp. 1208–1209, pl. 37, fig. 5.
Equus minutus Cope, 1893, p. 67, pl. 20, fig. 8.
Equus phlegon Hay, 1899 (replacement name for *Equus minutus*), p. 345.
Protohippus phlegon Gidley, 1901, p. 127, figs. 18, 19.
Merychippus phlegon Hay, 1902, p. 617.
Hipparion peninsulatum Hay, 1902, p. 620.
Hipparion cragini Hay, 1917, pp. 40, 42–43, pl. 1, figs. 6, 7.
Hipparion peninsulatum Osborn, 1918, p. 198, fig. 163.

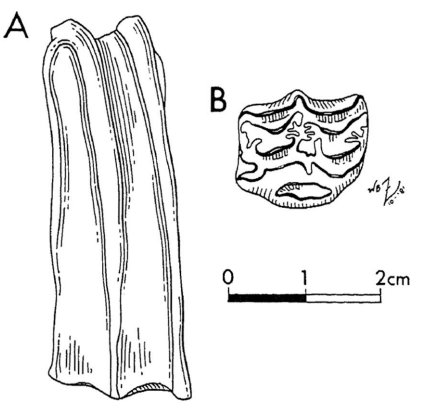

FIG. 106. *Nannippus peninsulatus*, AMNH 8345, holotype right ?M^2, from the late Miocene or Pliocene "Loup Fork" shales of Tehuichula, Mexico. Lateral (A) and occlusal (B) views, natural size.

TABLE 35
Synopsis of Collections Examined for *Nannippus peninsulatus* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Mt. Blanco	AMNH, TMM	Blanco Beds, Crayfish Draw Crosby County, Texas Panhandle	Late Blancan	Type locality of *N. phlegon*
Cita Canyon	JWT	"Blanco Beds," Randall County, Texas Panhandle	Late Blancan	
Numerous	F:AM, UALP	St. David and correlative units, San Pedro Valley, Cochise and Graham counties, Arizona; Long Pine Formation, Brown County, Nebraska	Late Blancan	
Haile XVA, Santa Fe River, Sarasota, Port Charlotte	UF	Several units, Alachua, Columbia, Sarasota and Charlotte counties, Florida	Late Blancan	
Mexico, Port Charlotte	USNM	"Loup Fork" shales, Tehuichila, Mexico; Charlotte County, Florida	Blancan	Type "locality" of *N. peninsulatus* (Mexico)
Miñaca Mesa (CIT loc. 105)	LACM (CIT)	Chihuahua, Mexico	Blancan	
Rancho El Ocote	TMM	Unnamed unit, Guanajuato, Mexico	Probably early Blancan (see Miller and Carranza-Castañeda, in press	Type locality of *N. hesperides*

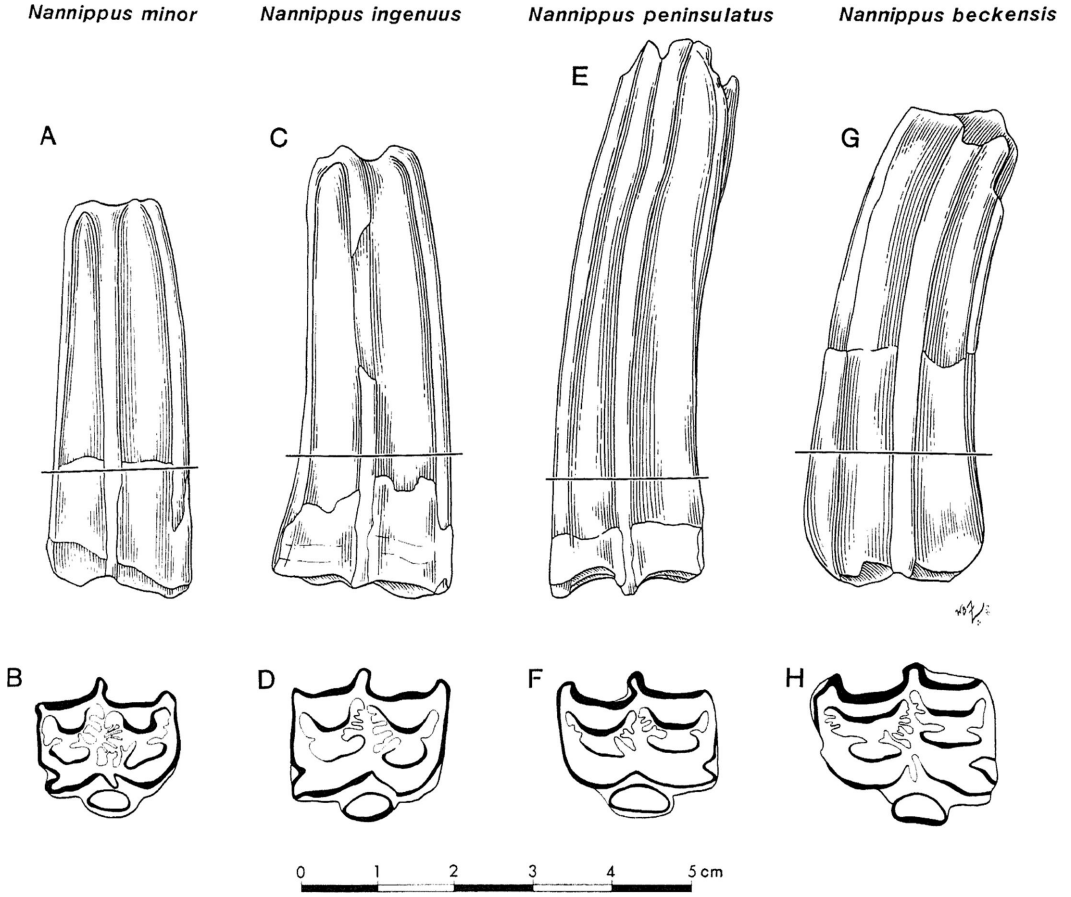

FIG. 105. Comparison of isolated M^1 of four species of *Nannippus* recognized in this report. These specimens were chosen because they each are in early wear. Therefore, the crown heights are near the maximum. In order to illustrate a representative occlusal pattern, each specimen was sectioned about 15 mm down (measuring from the mesostyle) the tooth (as indicated by line in each illustration). From left to right: *Nannippus minor,* UF 17253 from Palmetto Mine, upper Bone Valley Formation, late Hemphillian of Polk County, central Florida. Lateral (A) and sectioned (B) views. *Nannippus ingenuus,* MSU 3337 from Coffee Ranch, late Hemphillian of Hemphill County, Texas Panhandle, lateral (C) and sectioned (D) views. *Nannippus peninsulatus,* UA 47-7/2525, from the Blancan of Arizona, lateral (E) and sectioned (F) views. *Nannippus beckensis,* MSU 8592 from Beck Ranch, early Blancan of Scurry County, Texas, lateral (G) and sectioned (H) views.

although they may actually be morphologically intergradational.

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Nannippus peninsulatus (Cope), 1885
Figures 8, 89–91, 106–116, 148, 150;
Tables 2, 29, 35, 36

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Protohippus phlegon Gidley, 1901, p. 127, figs. 18, 19.
Merychippus phlegon Hay, 1902, p. 617.
Hipparion peninsulatum Hay, 1902, p. 620.
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Hipparion peninsulatum Osborn, 1918, p. 198, fig. 163.

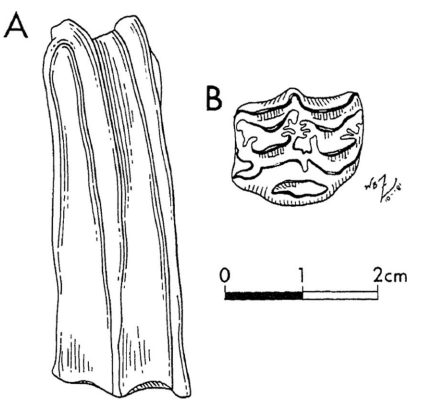

FIG. 106. *Nannippus peninsulatus,* AMNH 8345, holotype right ?M^2, from the late Miocene or Pliocene "Loup Fork" shales of Tehuichula, Mexico. Lateral (A) and occlusal (B) views, natural size.

TABLE 35
Synopsis of Collections Examined for *Nannippus peninsulatus* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Mt. Blanco	AMNH, TMM	Blanco Beds, Crayfish Draw Crosby County, Texas Panhandle	Late Blancan	Type locality of *N. phlegon*
Cita Canyon	JWT	"Blanco Beds," Randall County, Texas Panhandle	Late Blancan	
Numerous	F:AM, UALP	St. David and correlative units, San Pedro Valley, Cochise and Graham counties, Arizona; Long Pine Formation, Brown County, Nebraska	Late Blancan	
Haile XVA, Santa Fe River, Sarasota, Port Charlotte	UF	Several units, Alachua, Columbia, Sarasota and Charlotte counties, Florida	Late Blancan	
Mexico, Port Charlotte	USNM	"Loup Fork" shales, Tehuichila, Mexico; Charlotte County, Florida	Blancan	Type "locality" of *N. peninsulatus* (Mexico)
Miñaca Mesa (CIT loc. 105)	LACM (CIT)	Chihuahua, Mexico	Blancan	
Rancho El Ocote	TMM	Unnamed unit, Guanajuato, Mexico	Probably early Blancan (see Miller and Carranza-Castañeda, in press	Type locality of *N. hesperides*

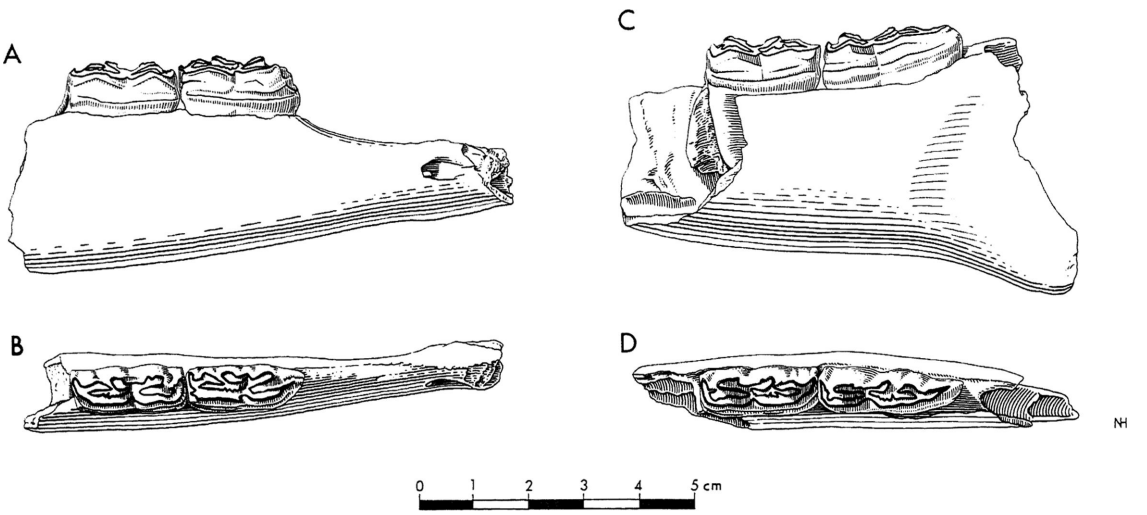

FIG. 109. Deciduous lower cheek tooth dentitions of *Nannippus peninsulatus* from the Santa Fe River 4A site, late Blancan of Columbia County, north-central Florida. UF 21319, lateral (A) and occlusal (B) views of right ramus with dP_2–dP_3. UF 21320, lateral (C) and occlusal (D) views of left ramus with dP_3–dP_4. Because of similar provenance, preservation, and stage of wear, these two specimens are almost certainly from the same individual.

ous dentition of *N. peninsulatus* is represented by the palates JWT 771 (fig. 107) and AMNH 104709 (fig. 108). MacFadden and Waldrop (1980) also described the deciduous dentition of this species as represented by the sample from Florida. The upper and lower deciduous dentitions from the Texas Panhandle have a much thicker covering of cement than in the Florida sample. In the upper deciduous dentition of *N. peninsulatus,* the cross-sectional area of each tooth is more rectangular than in the corresponding permanent premolar. The larger occlusal area of the deciduous dentition relative to the permanent premolar series is characteristic of most horses. In dP^2, the anterostyle seems slightly better developed than in the permanent P^2 of *N. peninsulatus.* The protocones in dP^2–dP^4 are oval and elongated. There is a tendency for the protocone of dP^2 to become connected to the protoloph in earlier wear stages than in the dP^3 and dP^4. The fossette borders are moderately plicated, perhaps slightly more so than in the permanent cheek teeth. The pli caballin varies from a single loop to rudimentary or absent. The hypoconal groove varies from shallow to moderately developed.

The lower deciduous dentition of *Nannippus peninsulatus* is represented by specimens such as AMNH 104710 (fig. 108) from Mt. Blanco and UF 21319 and UF 21320 from Sante Fe River 4A, Florida (fig. 109). In dP^2 the paraconid is poorly developed. The ectoflexid varies from shallow to moderate. The pli caballinid is poorly developed, rudimentary, or absent. In AMNH 104710 there are well-developed protostylids in dP^3 and dP^4, which are not characteristic of the adult dentitions. The isthmuses are not subdivided by the ectoflexids and there are few enamel plications. In AMNH 104710 from Mt. Blanco and illustrations of *N. peninsulatus* from Kansas (Hibbard 1956, p. 159, fig. 2E) the enamel borders are not plicated, whereas in the UF specimens there are plications, particularly on the metaconids and metastylids and the internal borders of the protoconids and hypoconids.

There are no upper permanent dental series known from either Mt. Blanco or Florida; however, complete specimens of this kind are represented by JWT 534 from Cita Canyon (fig. 110) and F:AM 107877 from the San Pedro Valley (fig. 111). Isolated specimens are known from numerous localities, e.g., the

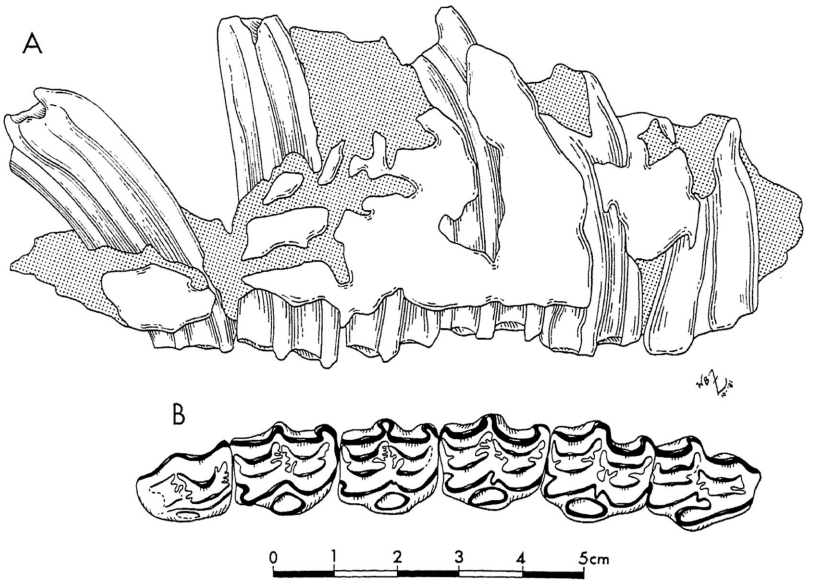

FIG. 110. Right upper cheek tooth dentition, P^2–M^3, of *Nannippus peninsulatus*, JWT 534, from Cita Canyon, late Blancan of Randall County, Texas Panhandle. A. Lateral view. B. Occlusal view.

Santa Fe River 4A site from Florida (fig. 112). The upper molars are very high crowned (table 36), moderately curved in the anterior-posterior plane, and slightly curved in the transverse plane. On the ectoloph of P^2 there is a poorly developed anterostyle. In P^2 there is a tendency for the protocone to become connected to the protoloph during relatively early wear stages. The protocones are oval, bean-shaped, or elongated with rounded or

TABLE 36
Selected Upper Dental Measurements and Univariate Statistics for *Nannippus peninsulatus*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V (%)	OR	N	$\bar{x}$	s	V (%)	OR
P2APL	10	19.96	1.55	7.78	18.1–23.4	7	20.17	1.70	8.43	18.1–23.4
P2TRNW	9	15.51	0.71	4.56	14.4–16.5	7	15.61	0.78	4.97	14.4–16.5
P2PRTL	8	6.64	0.92	13.92	5.5–7.9	7	6.71	0.97	14.46	5.5–7.9
P2PRTW	8	3.49	0.66	18.86	2.8–4.7	7	3.51	0.71	20.23	2.8–4.7
P2TOTPLI	9	4.11	2.37	57.62	2–8	7	4.71	2.36	50.11	2–8
M1APL	24	16.77	1.15	6.83	15.1–19.9	17	16.58	0.74	4.46	15.4–18.3
M1ECTL	24	16.73	1.04	6.22	14.9–18.9	17	16.67	0.82	4.92	15.3–18.1
M1TRNW	23	15.31	0.84	5.49	13.1–17.2	16	15.37	0.77	5.01	14.3–17.2
M1PRTL	24	6.87	1.02	14.86	5.1–9.4	17	6.77	0.80	11.82	5.8–8.5
M1PRTW	21	3.56	0.42	11.71	2.9–4.8	15	3.60	0.45	12.50	2.9–4.8
M1TOTPLI	22	6.36	1.97	30.88	3–11	17	6.59	2.00	30.35	4–11
TRL	2	101.55	3.61	3.55	99.0–104.1	2	101.55	3.61	3.55	99.0–104.1
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	6	30.28	9.26	30.59	19.3–39.2	0	—	—	—	—
M1MSTHT	25	44.70	9.09	20.33	25.7–66.3	4	56.33	8.63	15.32	45.6–66.3

[a] Abbreviations are presented on pp. 21 and 22; see table 35 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

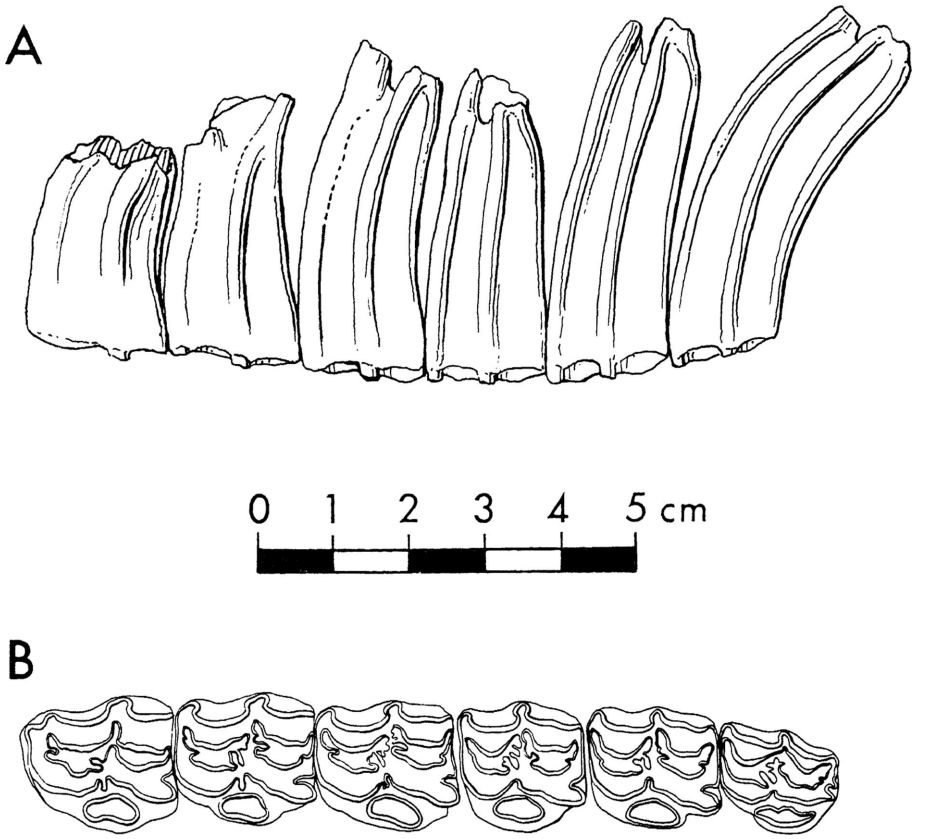

FIG. 111. Right (reversed) upper cheek tooth dentition, P^2–M^3, of *Nannippus peninsulatus*, F:AM 107877, from the San Pedro Valley, St. David Formation, late Blancan of Cochise County, southeastern Arizona. A. Lateral view. B. Occlusal view.

angular borders. In the prefossette, the pli protoloph and pli protoconule usually consist of a single loop and the pli prefossette consists of multiple loops. In the postfossette, the pli postfossette consists of multiple loops and the pli hypostyle consists of a single loop. The pli caballin usually consists of a single loop, is rudimentary, or is absent.

As represented by specimens such as UF 22631 (=F:AM 104712) and JWT 550, the mandible has an elongate symphysis (figs. 113, 114). The incisor arcade is transversely curved and relatively procumbent (or spatulate) in the anteriorposterior plane. The postcanine diastema is elongate and characteristic of *Nannippus*. The mental foramen lies approximately midway between C and P_2. P_1 is absent. As is also characteristic of *Nannippus*, the P_2 has a poorly developed paraconid (figs. 113–115). There are moderately developed parastylids. The protostylids are characteristically absent (figs. 113–116). The ectoflexids are moderately deep in the premolars and very deep in the molars. The pli caballinids are usually rudimentary or absent. The isthmuses are not plicated and they are sometimes subdivided by deep ectoflexids, particularly in the molars. The enamel patterns in the permanent lower cheek teeth are characteristically very simple with no plications.

The metapodials of *N. peninsulatus* are gracile and extremely elongated. Matthew (1926) stated that *Nannippus* (based on his observations of *N. "phlegon"*) lacked the trapezium and rudimentary metacarpal V (see discussion for the genus above).

CHARACTER ANALYSIS AND GENERAL DISCUSSION: The comparisons during the

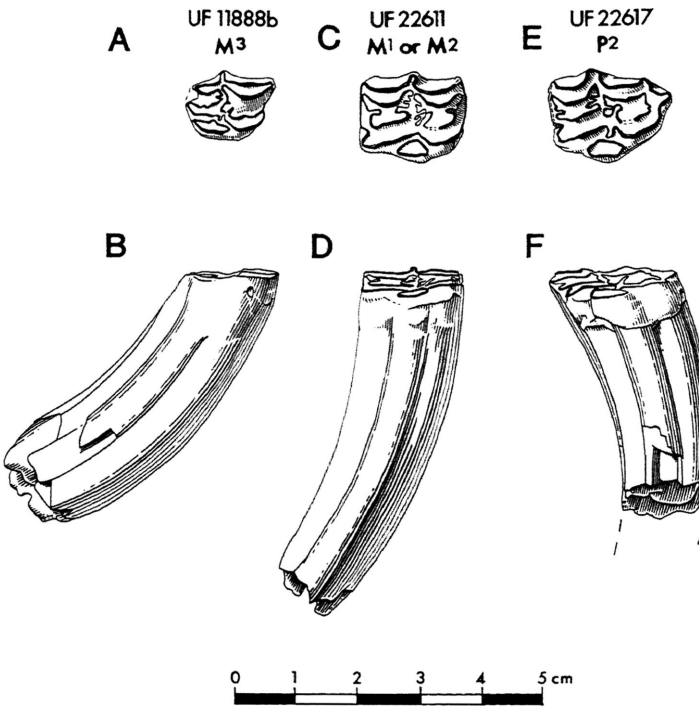

FIG. 112. Isolated upper cheek teeth of *Nannippus peninsulatus* from the Santa Fe river sites, late Blancan of Columbia County, north-central Florida. From left to right; UF 11888b, occlusal (A) and lingual (B) views; UF 22611, occlusal (C) and lingual (D) views; and UF 22617, occlusal (E) and lingual (F) views.

present study revealed that the holotype of "*Hippotherium*" *peninsulatum* Cope, 1885, AMNH 8345 (fig. 106) is indistinguishable from the well-known species *Nannippus phlegon* (Hay) 1899. AMNH 8345 is small and very hypsodont. Measurements for this specimen are as follows: M1APL = 17.1 mm; M1TRNW = 14.9 mm; M1MSTHT = 52.3 mm. This tooth is slightly curved in the transverse plane. The protocone is elongate with angular anterior and posterior margins. In the prefossette, the pli protoloph, pli protoconule, and pli prefossette consist of multiple loops. In the postfossette, the pli postfossette and pli hypostyle consist of multiple and single loops, respectively. The pli caballin consists of a single loop. There is a well-developed hypoconal groove. Based on the characters of size, crown height (in moderate, not early, wear), and dental pattern represented by the holotype, it is concluded that "*Hippotherium*" *peninsulatum* is morphologically indistinguishable from *Nannippus phlegon*. It is not an altogether new idea to ally "*Hippotherium*" *peninsulatum* with the genus *Nannippus*. For example, Stirton (1940) lists this species as *Nannippus peninsulatus* (although as distinct from *N. phlegon*). The morphological evidence from the present study conclusively supports going one step further and synonymizing these two names. Based on the chronology of authorship *Nannippus peninsulatus* becomes the senior synonym.

Nannippus peninsulatus obviously exhibits the generic characters such as smooth preorbital region without fossae, elongate rostrum, small size, high crowns, and the numerous dental characters described above. *N. peninsulatus* is clearly set apart from the other three species of *Nannippus* in the derived characters including the most elongate crowns and metapodials and almost complete absence of the protostylid (fig. 92, table 29).

In addition to the synonymy for the two names presented above, two other species

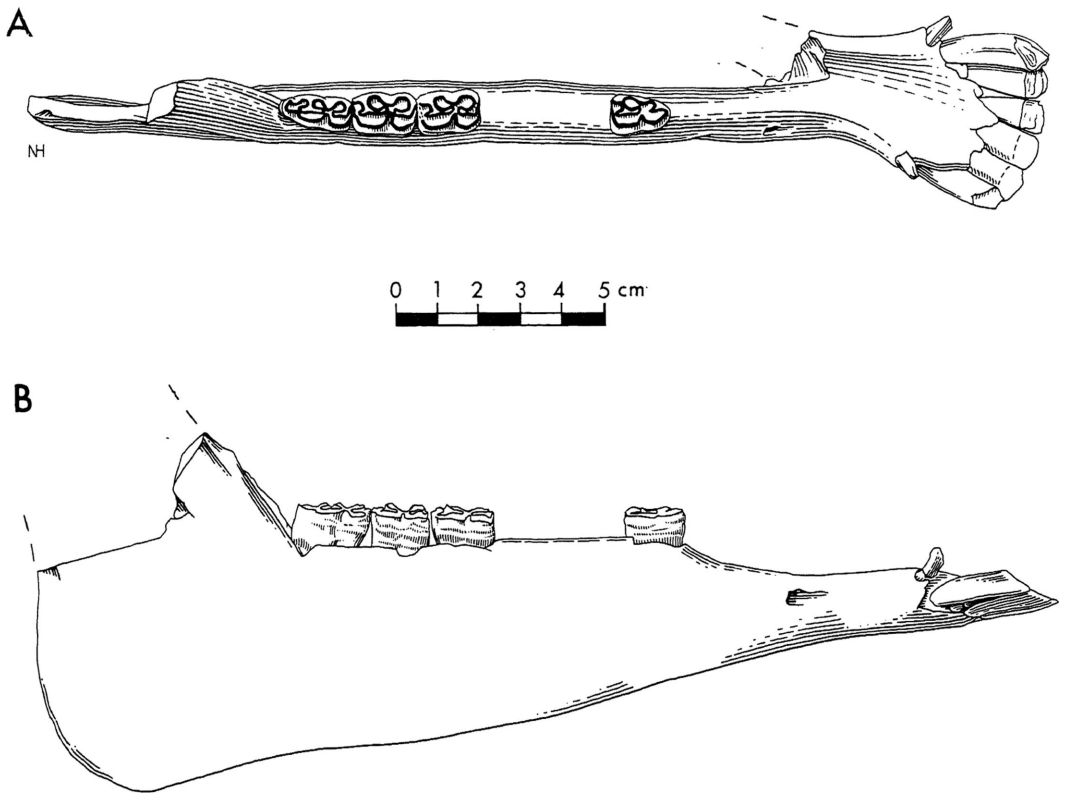

FIG. 113. Right mandibular ramus with symphysial dentition, P_2, M_1–M_3 of *Nannippus peninsulatus*, UF 22631 (=F:AM 104712, both are casts of RHB 1964, private collection of Roy H. Burgess, Venice, Florida) and Port Charlotte, Blancan of Charlotte County, southern Florida. A. Occlusal view. B. Lateral view.

names are considered here as junior synonyms of *Nannippus peninsulatus* (Cope), 1885. Hay (1917) named the new species of tiny and very hypsodont hipparion, *Hipparion cragini,* from the late Blancan Stump Arroyo Member of the Crooked Creek Formation, Clark County, Kansas (also see Hibbard, 1956). Hibbard (1956), although not directly stating so, implied that "*Hipparion*" *cragini* is a junior synonym of *N. phlegon.* During the present study, a cast of the holotype, a moderately worn P^4 or M^1 (FMNH PM 539, the original is housed in the Colorado College Museum, Colorado Springs), of *Nannippus cragini* (Hay), 1917, was examined. There are no diagnostic dental differences represented by the hypodigm of "*Hipparion*" *cragini.* Therefore "*Hipparion*" *cragini* is also considered here as a junior synonym of *N. peninsulatus.*

Mooser (1968) described two new species of *Nannippus* from the latest Hemphillian Rancho El Ocote L.F. of Chihuahua, Mexico. The smaller form, *N. aztecus,* is here synonymized with *N. minor.* The larger form, *N. hesperides,* was originally based on one left upper ($?M^1$) molar (now TMM 41685-10) and a paratype consisting of one right lower molar. Although the hypodigm of *N. hesperides* is small, examination of this material shows that it is clearly larger and morphologically distinct from *N. "aztecus."* Selected characteristic measurements for TMM 41685-10 are as follows: M1APL = 18.3 mm; M1TRNW = 13.6 mm; M1MSTHT = 56.8 mm.[10] In crown (mesostyle) height and oc-

[10] The occlusal surface of this tooth has been sawed off to expose the dental pattern. Therefore, the M1MSTHT is less than the actual value.

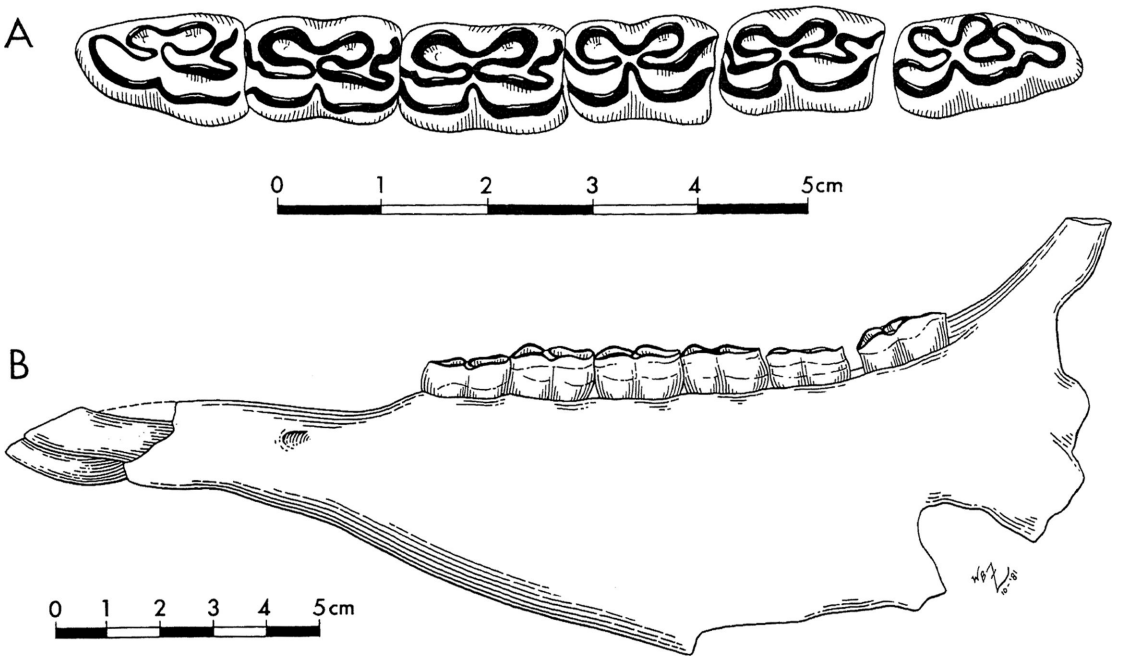

FIG. 114. Left ramus with P_2–M_3 of *Nannippus peninsulatus,* JWT 550, from Cita Canyon, late Blancan of Randall County, Texas Panhandle. A. Occlusal view. B. Lateral view.

clusal cross-sectional area and dental pattern, the upper molar is similar to other characteristic samples referred to here as *N. peninsulatus* (MacFadden and Waldrop, 1980, p. 9). The lower molar is well worn but in occlusal cross-sectional area it too is of appropriate size for *N. peninsulatus.* These teeth seem to be less square in occlusal cross-sectional area than *N. beckensis.* In dental pattern, *N. hesperides* is identical to *N. peninsulatus.* Therefore, *N. hesperides* is also considered a junior synonym of *N. peninsulatus.* The other horses from the Rancho El Ocote L.F. have been given new species names by Mooser (1960, 1964, 1968). Based on examination of the TMM and UF specimens from the Rancho El Ocote L.F., it appears that Mooser's *Neohipparion otomii* and *Neohipparion monias* are junior synonyms of *Neohipparion eurystyle* (see above) and *Astrohippus albidens* is a junior synonym of *A. stockii.* There also are *Dinohippus* specimens from the Rancho El Ocote L.F. in the TMM and UF collections that are referable to *D. mexicanus.* If these taxa were definitely associated with *N.* "*hesperides*" at Rancho El

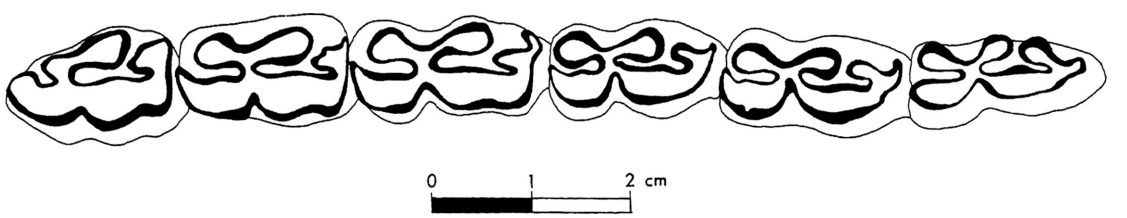

FIG. 115. Occlusal view of right cheek tooth dentition with P_2–M_3 (reversed) of *Nannippus peninsulatus,* AMNH 20081, from Mt. Blanco, Crayfish Draw, Blanco Beds, late Blancan of Crosby County, Texas Panhandle.

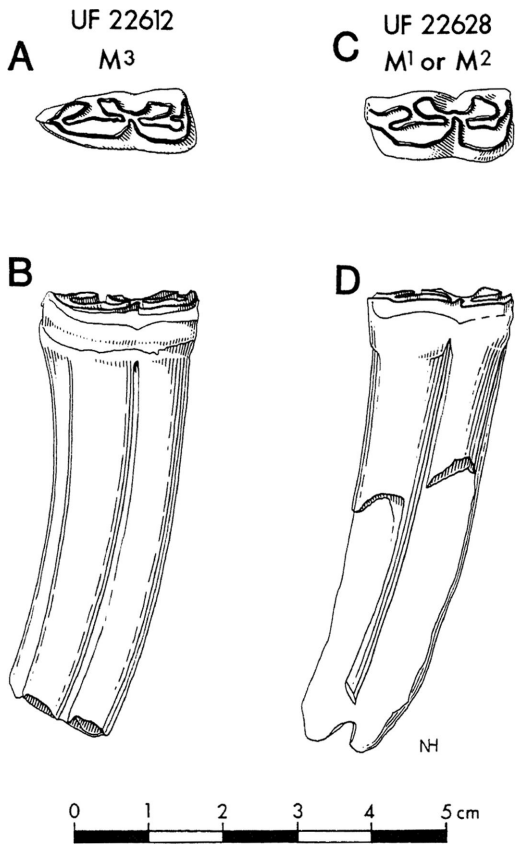

FIG. 116. Isolated right lower cheek teeth of *Nannippus peninsulatus* from the Santa Fe River sites, late Blancan of Columbia County, north-central Florida. UF 22612, occlusal (A) and lateral (B) views. UF 22628, occlusal (C) and lateral (B) views.

Ocote, then a late Hemphillian age would be assignable to this locality. However in renewed biostratigraphic investigations at this site, Miller and Carranza-Castañeda (in press) state that *N. peninsulatus* is restricted to the poorly fossiliferous sandy clay unit (also containing *Equus*) of Blancan age that uncomformably overlies the principal late Hemphillian concentration (which apparently lacks *N. peninsulatus*). Therefore, Mooser's earlier faunal descriptions probably represent temporally mixed samples. As such, and with the uncertain provenance data for the type locality of "*Hippotherium*" *peninsulatum,* this species seems restricted to the Blancan.

The tiny antelope-like hipparion *Nannippus peninsulatus* is an evolutionary curiosity because it is an extreme in the spectrum of horse evolution. *Nannippus peninsulatus* was highly cursorial and functionally monodactyl. Sondaar (1968) remarked that in several aspects this species (which he called *Nannippus phlegon*) was even more cursorial in its adaptations than *Equus. Nannippus peninsulatus* was very widespread in southern North America and Central America during the Blancan but is not represented at more northern sites (e.g., Hagerman of Idaho). The lack of specimens of *N. peninsulatus* at the northern sites probably reflects areas outside the actual range of this species as a result of a climatic filtering mechanism.

CORMOHIPPARION
SKINNER AND MACFADDEN, 1977

INCLUDED SPECIES

Cormohipparion goorisi MacFadden and Skinner, 1981.
Cormohipparion sphenodus (Cope), 1889.
Cormohipparion occidentale (Leidy), 1856.

TYPE SPECIES: *Cormohipparion occidentale* (Leidy), 1856, see discussion of the type specimen and locality below.

REVISED GENERIC DIAGNOSIS: Medium to large and mesodont to hypsodont hipparion. Mean TRL ranges from 116.83 to 138.00 mm. Unworn or little-worn M1MSTHT *ca.* 22–43 mm. Prominent DPOF with a relatively well-developed and usually continuous anterior rim. Posteriorly, this fossa also has a well-developed and pocketed rim. In general outline, this fossa is oval or teardrop in shape and situated far forward on cheek resulting in a very wide PRB. Anterior margin of the lacrimal bone usually is posterior to the posterior margin of the DPOF. Protocones rounded with anterior spur, oval, or elongate (with angular margins). Fossette borders moderately to very plicated. Protostylids usually present and moderately developed. Ectoflexids moderate to deep and pli caballinids moderate to absent.

All species of *Cormohipparion* differ from all other horses in the diagnostic development of the DPOF. All species of *Cormohipparion* differ from *Nannippus* in larger size. In addition, *C. occidentale* differs from all

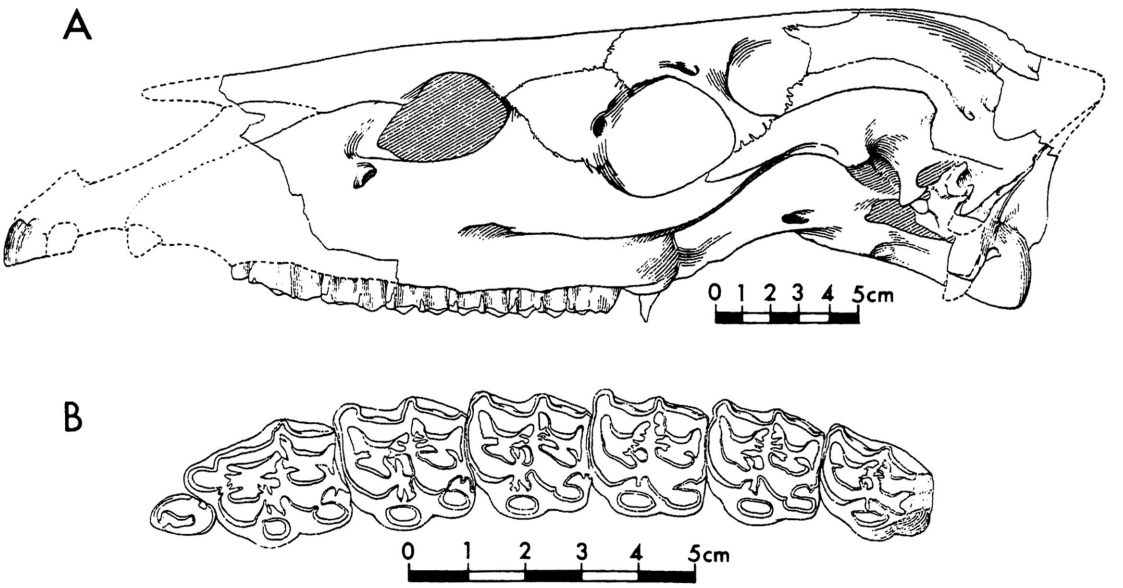

FIG. 117. Representative skull morphology of the genus *Cormohipparion*. This specimen of *C. sphenodus*, PU 12291, is from upper Pawnee Creek Beds, Ogallala Group, Sand Canyon area, late Barstovian of Logan County, northeastern Colorado. A. Right lateral view (partially reversed). B. Occlusal view of left P^1–M^3. Figure modified from Osborn (1918, plate 12).

other horses in a combination of size, hypsodonty, and dental pattern, i.e., elongate protocones and very complex enamel plications. (*Cormohipparion goorisi* and *C. sphenodus* do not have diagnostic characters of size and dental pattern that would allow unambiguous specific recognition.)

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: As recognized principally from cranial morphology, the following represent the known occurrences of the genus *Cormohipparion*: early Barstovian of the Texas Gulf Coast; widespread in the Great Plains and Rio Grande regions during the Valentinian and Clarendonian with occurrences from South Dakota, Nebraska, Texas, and New Mexico; although probably rare, may occur in the early Hemphillian of the Great Plains (table 37). *Cormohipparion* also occurs during the Miocene and Pliocene (Vallesian to ?Ruscinian or possibly Villafranchian) in the Old World (see below).

DISCUSSION: Skinner and MacFadden (1977) proposed the genus *Cormohipparion* based on abundant and well-preserved cranial material in the Frick Collection from numerous sites in the Great Plains and Rio Grande Valley of New Mexico. The configuration of the DPOF is the most striking diagnostic character of this genus (fig. 117). Skinner and MacFadden (1977) analyzed quarry samples of *Cormohipparion* and demonstrated that, despite claims to the contrary (see, e.g., Forstén, 1982b and response by MacFadden and Skinner, 1982), the configuration of the DPOF is not profoundly influenced by sexual dimorphism and ontogenetic variation (also see analysis of MacAdams *Hipparion tehonense* above). The most advanced species of this genus, *C. occidentale*, also has diagnostic dental characters including the combination of size, hypsodonty, elongated protocone, and very complex enamel plications on the fossette borders. The other two species, *C. goorisi* and *C. sphenodus*, are difficult to diagnose without relevant material that preserves the preorbital region. For the three species of *Cormohipparion*, selected measured characters that give an indication of differences in size versus hypsodonty (TRL vs. M1MSTHT) and increase in relative size of the protocone

TABLE 37

Selected Important Morphological Character Distributions and Temporal and Spatial Data for the Three North American Species of *Cormohipparion* and the Merychippines (Outgroup)[a]

Morphocline[b] Character (see fig. 120)	Merychippines[c] (outgroup)	*Cormohipparion goorisi*	*Cormohipparion sphenodus*	*Cormohipparion occidentale*
1. Size (relative to all hipparions)	Small to medium	Medium	Medium	Large
2. Mean upper cheek tooth row length, P^2–M^3 (TRL)	—	116.83 mm	126.48 mm	138.00 mm
3. Hypsodonty	Brachyodont to mesodont	Mesodont	Hypsodont	Hypsodont
4. Estimated-approximate M^1 mesostyle crown height (M1MSTHT) for little-worn specimens	—	22–28 mm	30–35 mm	37–43 mm
5. Dorsal preorbital fossa (DPOF)	Highly variable depending upon species, usually present	As for genus	As for genus	As for genus
6. Posterior pocket of dorsal preorbital fossa (DPOF)	Usually absent	Very deep	Moderately deep	Moderately deep
7. Protocone size and shape (relative to all hipparions)	Small and rounded to oval, usually connected to protoloph	Small, rounded to oval with anterior spur, rounded borders	Medium, oval and elongate, anterior spur absent, rounded or angular borders	Large, very elongate, anterior spur absent, rounded or angular borders
8. Enamel plications on fossette borders (relative to all hipparions)	Highly variable in different species	Simple	Moderate	Extremely complex
9. Pli caballin	Variable depending upon species, but relatively poorly developed	Single or double loop	Single or double loop	Single, double, or more complicated series of loops
10. Protostylid	Usually poorly developed	Poorly developed, rudimentary or absent	Moderately to well developed, sometimes isolated from paralophid	Moderately to well developed, sometimes isolated from paralophid

TABLE 37—(*Continued*)

Morphocline[b] Character (see fig. 120)	Merychippines[c] (outgroup)	*Cormohipparion goorisi*	*Cormohipparion sphenodus*	*Cormohipparion occidentale*
11. Ectoflexid	Usually deep	Deep	Moderate in premolars, deep in molars	Moderate in premolars, deep in molars
12. Pli caballinid	Variable depending upon species, but relatively poorly developed	Poorly developed, rudimentary or absent	Usually well-developed single loop in premolars, rudimentary or absent in molars	Usually well-developed single loop in premolars, rudimentary or absent in molars
13. Metaconid, metastylid, entoconid, hypoconulid	Separated, rounded borders, not greatly expanded	Separated, rounded borders, not greatly expanded	Separated, relatively distinct, relatively expanded with rounded borders	Separated, relatively distinct, relatively expanded with rounded borders
DISTRIBUTIONAL DATA[d]				
Known biochronological range (teilchron)	—	Barstovian	Late Barstovian-early Clarendonian (also Valentinian)	Clarendonian, probably early Hemphillian
Known biogeographic occurrences	—	Texas Gulf Coastal Plain	Great Plains, Texas, Rio Grande Graben, California	Great Plains, Texas, Rio Grande Graben, California

[a] This table accompanies figure 120 (numbered characters).

[b] Descriptions of dental characters are representative of early and medial wear stages.

[c] Included as outgroup comparison for qualitative characters only. Quantitative characters (measurements) and temporal and spatial data are variable depending upon species and these are not available.

[d] These data are not used in figure 120 and are therefore not numbered sequentially as are the morphocline characters.

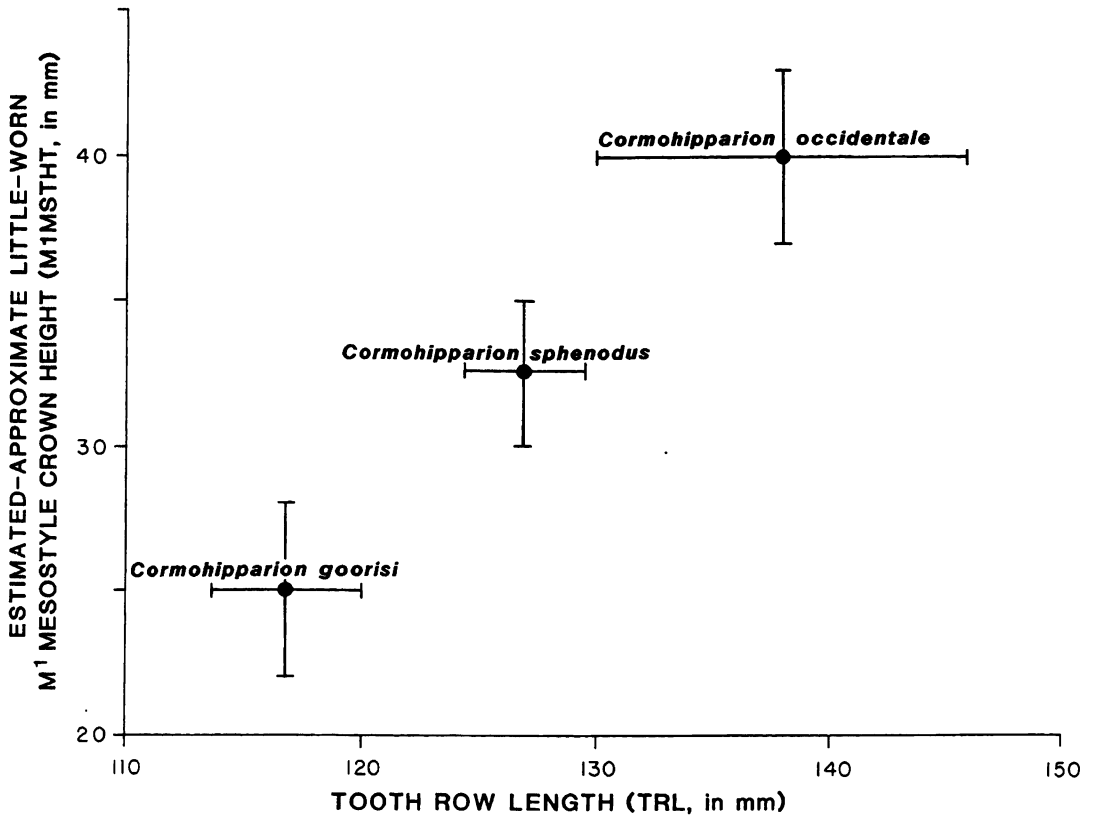

FIG. 118. Bivariate plot of TRL versus estimated-approximate little-worn M1MSTHT for the three recognized species of *Cormohipparion* from North America. For each value, one standard deviation (*s*, either actual or estimated) is plotted on both sides of the mean. Also see figure 25 for further explanation.

(M1APL vs. M1PRTL) are presented in figures 118 and 119.

The analysis of selected important characters and morphocline polarities is presented in figure 120 and table 37. It is clear from this analysis that within the monophyletic genus *Cormohipparion,* the North American species form a primitive to derived sequence that proceeds from *C. goorisi* to *C. sphenodus* to *C. occidentale.*

Recent work has shown that *Cormohipparion* was also fairly widespread in the Old World during the Neogene (e.g., Skinner and MacFadden, 1977; MacFadden and Bakr, 1979; Woodburne and Bernor, 1980; Woodburne, MacFadden, and Skinner, 1981; MacFadden and Woodburne, 1982). This section is devoted to the three North American species. The interrelationships of these species with respect to those of the Old World is discussed in the phylogenetic and paleobiogeographic sections below.

Cormohipparion goorisi
MacFadden and Skinner, 1981
Figures 22, 23, 118–123, 149, 150;
Tables 2, 37–39

SYNOPSIS OF USAGE

"Ancestral Hipparions" Quinn, 1952, pp. 5, 6.
?*Merychippus* Quinn, 1955, pp. 63–64, fig. 3.
Merychippus near *Hipparion* Forstén, 1975, pp. 35–40, tables 14, 32, fig. 4.
Hipparion sp. MacFadden and Skinner, 1977, pp. 532–533, 1 fig.
Cormohipparion goorisi, new species, MacFadden and Skinner, 1981, pp. 619–627, text-figs. 1–3.

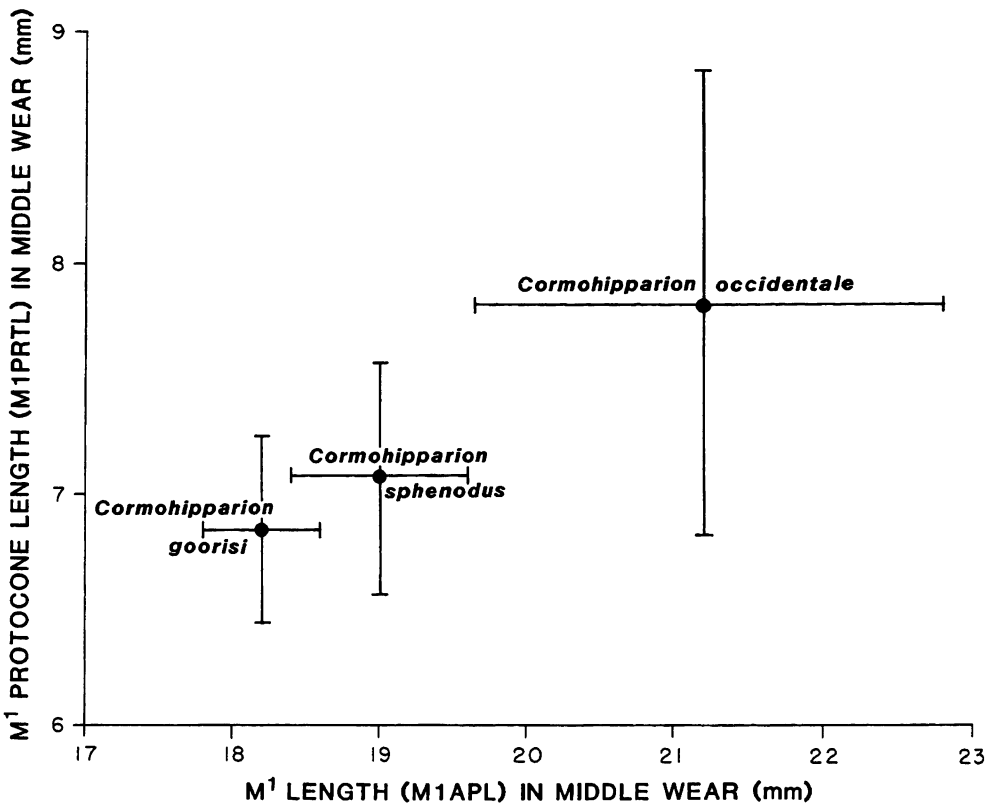

FIG. 119. Bivariate plot of little-worn M1APL versus little-worn M1PRTL for the three recognized species of *Cormohipparion* from North America. For each value, one standard deviation (*s*) is plotted on both sides of the mean. Also see figure 26 for further explanation.

TYPE SPECIMEN AND LOCALITY: Holotype, F:AM 73940, well-preserved skull with alveoli for incisors, right and left canines and P^2–M^3 (fig. 121), from Trinity River Pit I (equivalent to the Moscow L.F. of Hesse, 1943), Fleming Formation, Burkeville Fauna, early Barstovian, San Jacinto County, Texas Gulf Coastal Plain (MacFadden and Skinner, 1981).

REVISED DIAGNOSIS: Same as for genus with the following specific characters: medium-sized and mesodont hipparion. Mean TRL 116.83 mm. Unworn or little-worn M1MSTHT *ca.* 22–28 mm. Very deep (*ca.* 10 mm or greater) posterior pocket of DPOF that extends almost to the anterior margin of the orbit. DPOF positioned far forward of orbit resulting in a wide PRB. Anterior margin of the lacrimal bone does not touch the posterior rim of the DPOF. Protocones rounded with prominent anterior spur (particularly during early wear stages). Fossette borders moderately plicated. Pli caballin consists of single or double loops. Protostylids absent or rudimentary. Deep ectoflexids. Pli caballinids rudimentary or absent.

Cormohipparion goorisi differs from all other horse genera in the diagnostic generic characters (see above). *Cormohipparion goorisi* differs from both *C. sphenodus* and *C. occidentale* in being smaller in size and having less hypsodont cheek teeth, rounded protocones with rudimentary anterior spurs, simpler enamel plications, less well-developed protostylids, and deeper ectoflexids.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: So far as is known Barstovian of the Texas Gulf Coastal Plain (table 38).

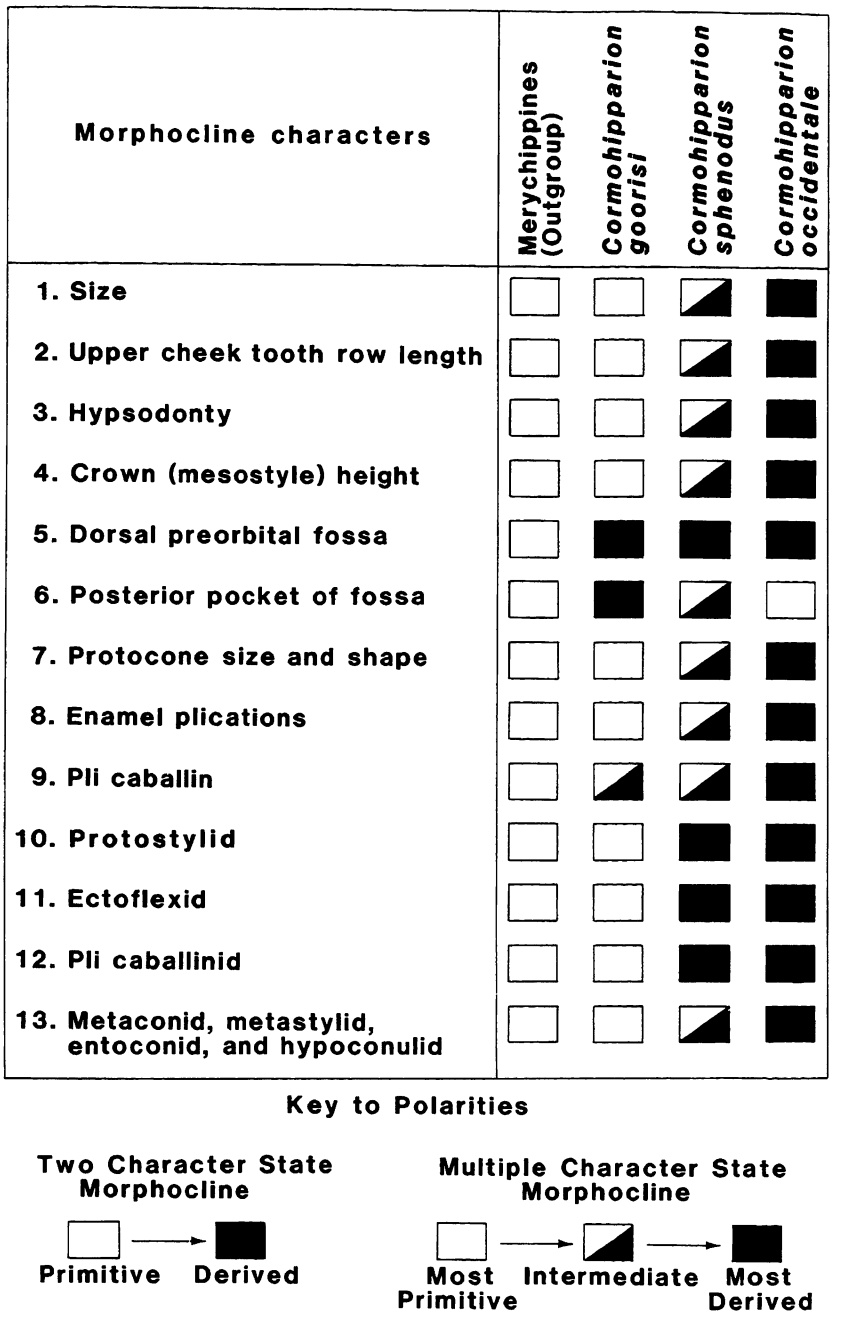

FIG. 120. Graphical representation of selected important character distributions and morphocline polarities in the three species of *Cormohipparion* and merychippines (outgroup). The numbered characters correspond to those in table 37. Also see text for discussion.

DESCRIPTION: *Cormohipparion goorisi* is a small and mesodont hipparion (figs. 121, 122; table 39). The description of cranial morphology is based on the holotype, F:AM 73940 (fig. 121), and five other specimens from the type locality (also see MacFadden

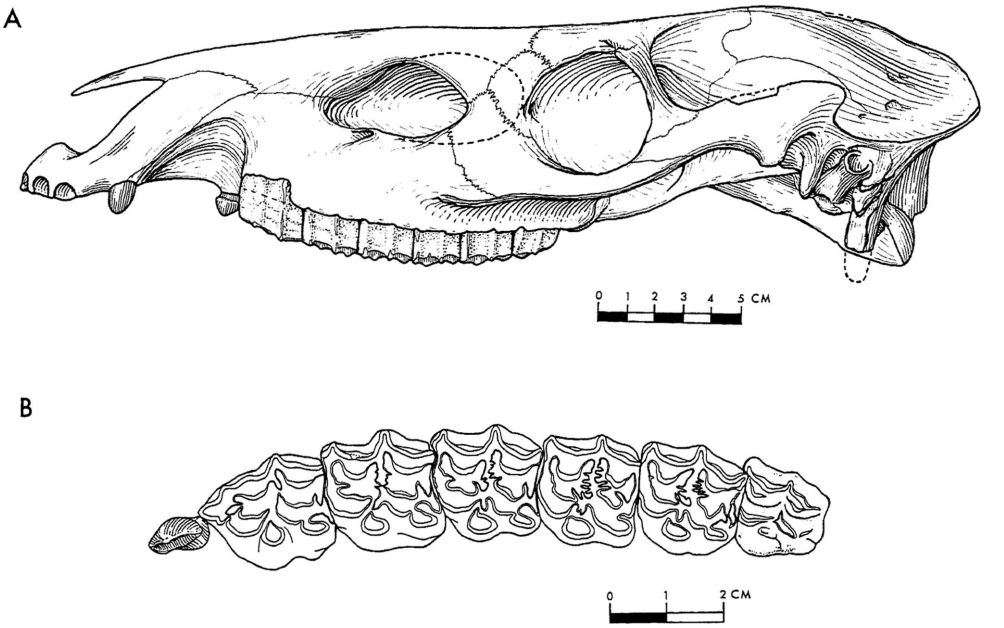

FIG. 121. *Cormohipparion goorisi,* F:AM 73940, holotype, from Trinity River Pit I, Fleming Formation, early Barstovian of San Jacinto County, Texas Gulf Coastal Plain. A. Left lateral view. B. Occlusal view of P^1–M^3.

and Skinner, 1981). The premaxilla extends posteriorly to a postion that lies dorsal to the anterior margin of the buccinator fossa. The postcanine diastema is moderately developed and much shorter (relative to the body size) than, for example, *Nannippus.* The infraorbital foramen lies over P^3 or P^4 at or near the anteriorventral margin of the DPOF. The DPOF is teardrop-shaped, has well-defined and continuous anterior and posterior rims, and is deeply pocketed. This fossa is well forward of the orbit resulting in a wide PRB. The anterior margin of the lacrimal bone does not touch the posterior rim of the DPOF.

The dP^1 is present and it appears not to be lost during ontogeny as is characteristic of more advanced horses. The upper cheek teeth are slightly curved. The protocone is rounded with an anterior spur that sometimes connects to the protoloph (figs. 121, 122). In the development of the protocone, *C. goorisi* is not far advanced over the condition of species such as *Merychippus insignis* (Skinner and Taylor, 1967). In the prefossette the pli protoloph and pli protoconule usually consist of single loops and the pli prefossette usually consists of multiple loops. The pli postfossette consists of multiple loops and the pli hypostyle usually consists of a single loop.

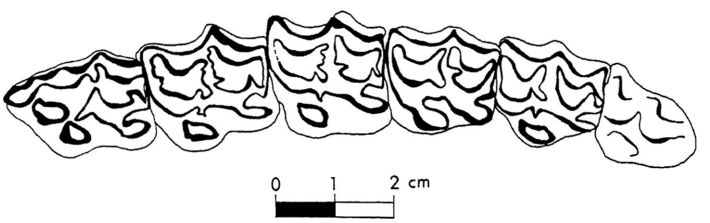

FIG. 122. Occlusal view of *Cormohipparion goorisi,* left P^2–M^3, TMM 31242-71, from the Burkeville Fauna, Fleming Formation, Barstovian of the Texas Gulf Coastal Plain.

TABLE 38
Synopsis of Collections Examined for *Cormohipparion goorisi* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Trinity River Pit I	F:AM	Fleming Formation, San Jacinto County, Texas Gulf Coastal Plain	Early Barstovian	Type locality
Burkeville and Cold Springs faunas	TMM	Fleming Formation, Texas Gulf Coastal Plain	Early to late Barstovian	

The pli caballins, if present, consist of single or sometimes double loops.

The lower cheek teeth have relatively deep ectoflexids and pli caballinids that are either rudimentary or absent (fig. 123). In contrast to most other hipparions the protostylids are usually rudimentary or absent in *C. goorisi*. The entoconids and hypoconulids are not very expanded and they have rounded enamel borders.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: Although primitive in many characters, *C. goorisi* is clearly referable to the genus based on the diagnostic configuration of the DPOF. In contrast to the two more advanced species of North American *Cormohipparion, C. goorisi* retains numerous primitive dental characters seen in merychippines. Within the genus, *C. goorisi* is set apart from both *C. sphenodus* and *C. occidentale* as the most primitive sister species based on the following primitive characters; small size, mesodont dentition, small and rounded protocones with anterior spurs (particularly in early wear), deep ectoflexids, pli caballinids rudimentary or absent, and not greatly expanded metaconids, metastylids, entoconids, and hypoconulids.

In a short note, Quinn (1952, p. 6) is the first to mention the presence of hipparions

TABLE 39
Selected Upper Dental Measurements and Univariate Statistics for *Cormohipparion goorisi*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	4	23.53	1.02	4.33	22.8–25.0	3	23.77	1.20	5.05	22.9–25.0
P2TRNW	4	18.35	1.54	8.38	16.3–19.8	3	19.03	0.87	4.57	18.1–19.8
P2PRTL	4	4.85	0.70	14.33	4.2–5.8	3	5.07	0.67	13.21	4.5–5.8
P2PRTW	4	4.28	0.56	13.01	3.7–4.8	3	4.47	0.49	10.96	3.9–4.8
P2TOTPLI	4	4.25	2.06	48.51	2–6	3	4.67	2.31	49.46	2–6
M1APL	6	17.87	0.62	3.46	17.0–18.5	4	18.20	0.41	2.25	17.6–18.5
M1ECTL	6	18.48	0.61	3.29	17.5–19.1	4	18.83	0.30	5.31	18.4–19.1
M1TRNW	6	19.88	1.45	7.32	18.1–21.6	4	20.63	1.13	4.85	19.0–21.6
M1PRTL	6	6.32	0.69	10.90	5.1–6.9	4	6.68	0.33	4.94	6.2–6.9
M1PRTW	6	4.03	0.39	9.62	3.5–4.4	4	4.08	0.33	8.09	3.7–4.4
M1TOTPLI	6	6.67	2.42	36.33	3–10	4	5.75	2.22	38.61	3–8
TRL	4	116.83	4.18	3.58	111.2–121.3	3	118.70	2.25	1.90	117.3–121.3
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	2	20.25	0.64	3.14	19.8–20.7	0	—	—	—	—
M1MSTHT	0	—	—	—	—	0	—	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 38 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

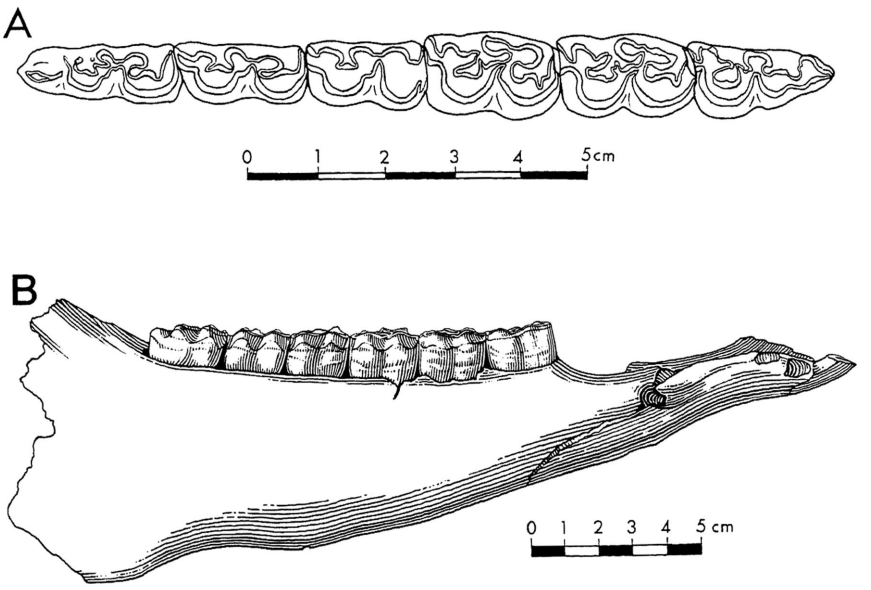

FIG. 123. Right ramus and dentition of *Cormohipparion goorisi*, F:AM 73948, with I_2, P_2–M_3 from Trinity River Pit I, Fleming Formation, early Barstovian of San Jacinto County, Texas Gulf Coastal Plain. A. Occlusal view. B. Lateral view.

from the Fleming Formation. Later, in the published version of his Ph.D. dissertation, Quinn (1955, p. 73) apparently referred to these horses as ?*Merychippus*. It is difficult to know which specimens he was referring to because they were neither listed nor described in the text as such. Forstén (1975), in a revision of the same material that Quinn studied, described one of the merychippine horses from the "Younger" Burkeville and Cold Springs Faunas as *Merychippus* sp. near *Hipparion*. This unnamed species was differentiated from the other merychippines in this fauna by numerous hipparion-like characters, particularly the isolated protocones (often with anterior spurs), deep hypoconal grooves, and moderately complex enamel plications on the fossette borders. Unfortunately, in Forstén's (1975) report there are no illustrations of either skulls or dentitions. In the relevant cranial material, i.e., TMM 31219-189 and TMM 31219-224, there are facial regions preserved, although important areas of the cheek are reconstructed or badly crushed. In these specimens the DPOF does not have a well-developed anterior rim or deep posterior pocket. Therefore, this sample is not referable to *Cormohipparion*. Some of the other specimens from these faunas, e.g., TMM 31242-71 (fig. 122), are referable to *C. goorisi* because they are identical in dental characters and similar in size to the topotypic sample from Trinity River Pit I.

MacFadden and Skinner (1981) only recognized *C. goorisi* from the type locality, i.e., the Trinity River Pit I, Fleming Formation, early Barstovian of the Texas Gulf Coast. During the present study, examination of the TMM collection revealed that specimens referable to *C. goorisi* also exist from the Cold Spring L.F. in the same region (e.g., TMM 31242-71, fig. 122). Therefore, the known range of this species is extended into the late Barstovian within the same geographic region. Due to the presence of numerous primitive merychippine-like dental characters, it is not surprising that *C. goorisi* is only recognized from the Barstovian localities in the Texas Gulf Coast. As is also the case with the primitive *Hipparion shirleyi*, *C. goorisi* pos-

TABLE 40
Synopsis of Collections Examined for *Cormohipparion sphenodus* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Sand Canyon	AMNH, F:AM, PU	Ogallala Group (Ash Hollow Equivalent), Logan County, Colorado	Late Barstovian	Type area, from PU collection only no. 12291 (skull, fig. 117) examined
Numerous	F:AM	Valentine Formation, Brown and Cherry counties, north-central Nebraska	Valentinian	
Conical Hill Quarry	F:AM	Ojo Caliente Sandstone, Tesque Formation, Santa Fe Group, Rio Arriba County, New Mexico	Clarendonian	
Numerous	UCMP	Orinda, San Pablo, and Santa Margarita formations, Contra Costa, San Joaquin, and Kern counties, California	Clarendonian ("Cerrotejonian")	
MacAdams Quarry	F:AM	Clarendon Beds, Donley County, Texas Panhandle	Early Clarendonian	
Numerous (Lapara Creek Fauna)	TMM	Goliad Formation, Bee and Goliad counties, Texas Gulf Coastal Plain	Early Clarendonian	

sibly occurs elsewhere; however, without preserved crania, it is difficult to recognize this species from outside of this region.

Cormohipparion sphenodus (Cope), 1889
Figures 8, 21, 22, 23, 117–120, 124–130, 149, 150; Tables 2, 37, 40, 41

TYPE SPECIMEN AND LOCALITY: AMNH (Cope Collection) 8281, right P^2 (holotype) and left P^3 (cotype) from the Pawnee Buttes of northeastern Colorado. These specimens were not collected from the same stratigraphic horizon. Osborn (1918, p. 112) states that: "The type of *M. sphenodus* is more progressive and appears to belong to a higher geologic level than the cotype." Osborn (1918, p. 112) designated a neotype of *M. sphenodus*, AMNH 1291. Later in this monograph (pl. 12) he indicates that PU 12291 (fig. 117), consisting of a well-preserved skull, is the neotype. Nevertheless, since the holotype was not lost, designation of a neotype or neotypes is unnecessary and Cope's original specimen stands as the name-bearer for this species.

REVISED DIAGNOSIS: Same as for genus with the following specific characters: Medium-sized and moderately hypsodont hipparion. Mean TRL 126.48 mm. Unworn or little-worn M1MSTHT *ca.* 30–35 mm. DPOF moderately pocketed (*ca.* 5 mm or less). Protocones oval and moderately complex. Protostylids moderately developed and sometimes isolated. Pli caballinids moderately developed in premolars and poorly developed in molars. Ectoflexids moderate in premolars and deep in molars.

Cormohipparion sphenodus differs from all other horse genera in the generic characters.

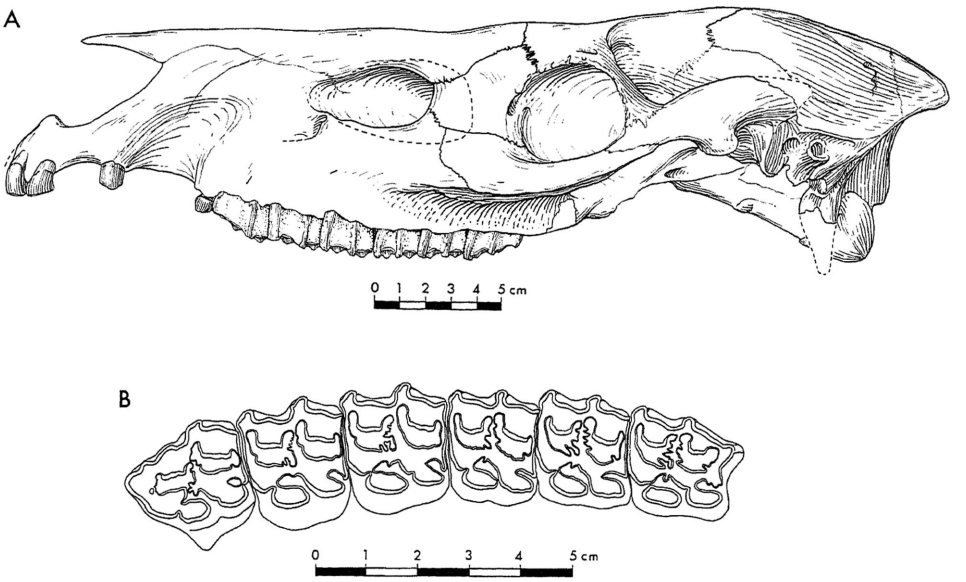

FIG. 124. *Cormohipparion sphenodus,* UNSM 1352 (= AMNH 105299, cast) from Railway Quarry A, Crookston Bridge Member of the Valentine Formation, Valentinian of Cherry County, north-central Nebraska. A. Left lateral view of skull. B. Occlusal view of left P^2–M^3.

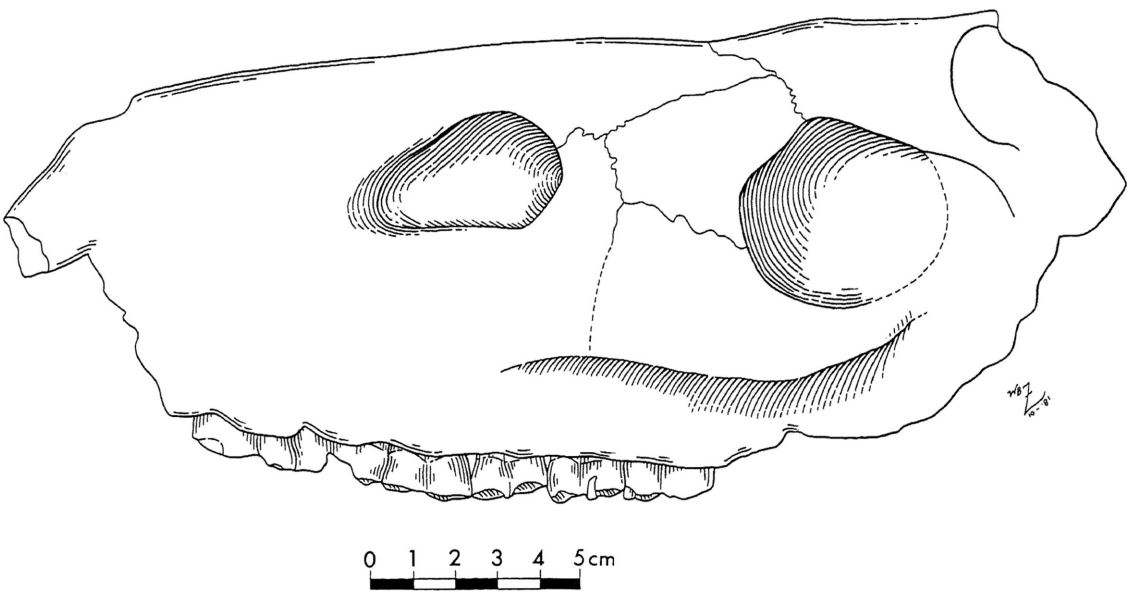

FIG. 125. Right (reversed) lateral view of skull of *Cormohipparion sphenodus,* UNSM 53999, from Verdigre Quarry, Valentine Formation, Valentinian of Knox County, northeastern Nebraska. Occlusal view of the cheek teeth is not shown here because they are in very late wear and the dental pattern is poorly represented.

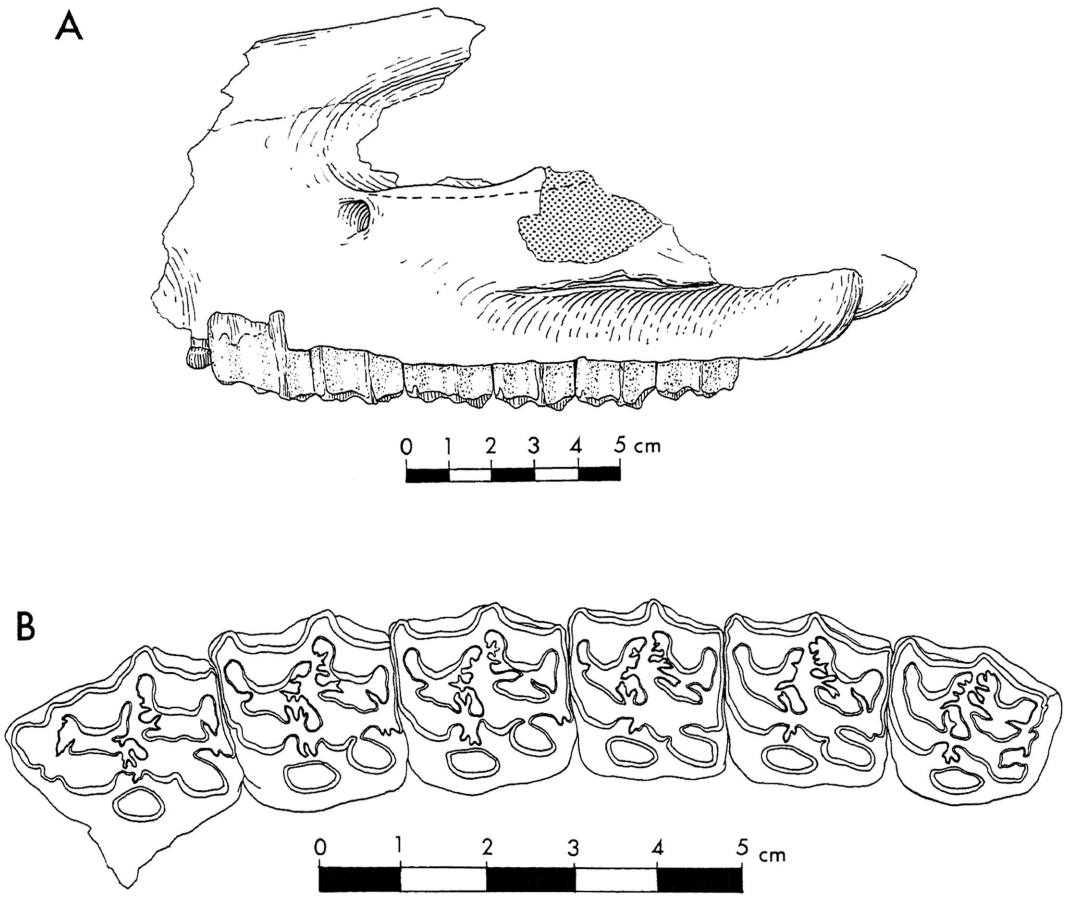

FIG. 126. *Cormohipparion sphenodus,* F:AM 71896, from Railroad Quarry A, Crookston Bridge Member of the Valentine Formation, Valentinian of Cherry County, north-central Nebraska. A. Combination left and right lateral view of skull fragment showing anterior region of DPOF. B. Occlusal view of left P^2–M^3.

Cormohipparion sphenodus differs from *C. goorisi* in increased size and crown height, shallower posterior pocket of the DPOF, more elongated protocone lacking rudimentary anterior spur, slightly more complex enamel plications on fossette borders, shallower ectoflexids and better developed pli caballinids (particularly in premolars), and more expanded metaconids, metastylids, entoconids, and hypoconulids. *Cormohipparion sphenodus* differs from *C. occidentale* in being smaller in size and having shorter crown height, less elongated protocones with more rounded borders, significantly simpler enamel plications on fossette borders, and less expanded and angular metaconids, metastylids, entoconids, and hypoconulids.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Late Barstovian to early Clarendonian (Valentinian) of northeastern Colorado (type locality), eastern and north-central Nebraska and adjacent South Dakota, Texas Gulf Coastal Plain and Texas Panhandle, north-central New Mexico, and San Francisco Bay region, San Joaquin County, and Kern County, California (table 40).

DESCRIPTION: The cranial morphology of *Cormohipparion sphenodus* is based on numerous well-preserved skulls in the Frick and UNSM collections, e.g., UNSM 1352 (fig.

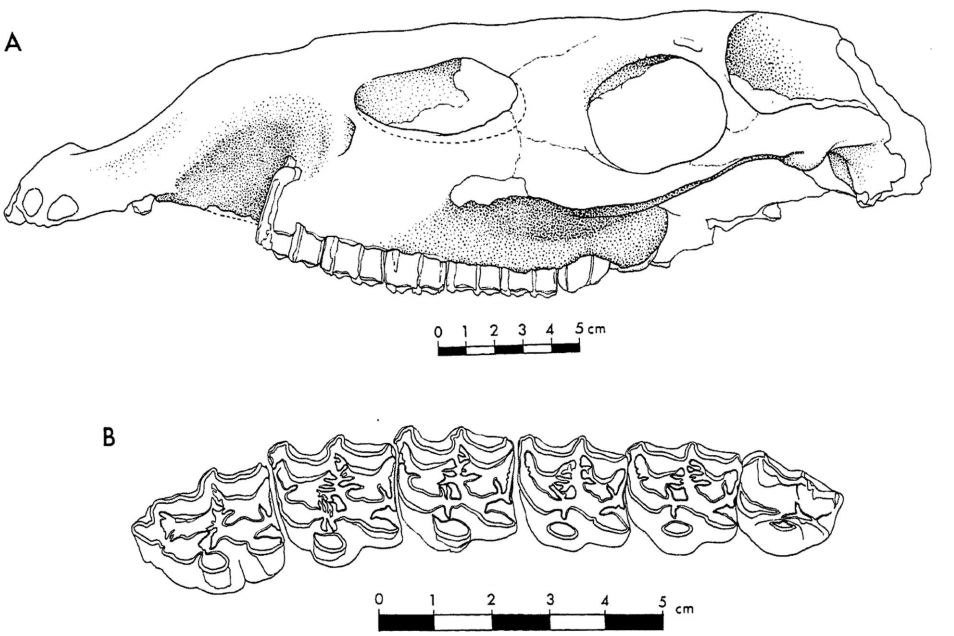

FIG. 127. *Cormohipparion sphenodus*, F:AM 108535, from MacAdams Quarry (loclocality 17), Clarendon Beds, Ogallala Group, early Clarendonian of Donley County, Texas Panhandle. A. Left lateral view of skull. B. Occlusal view of left P^2–M^3.

124), UNSM 53999 (fig. 125), F:AM 71896 (fig. 126), F:AM 108535 (fig. 127), F:AM 71899 (fig. 128), as well as a fine skull, PU 12291 (Osborn's 1918 "neotype," fig. 117).

Cormohipparion sphenodus is a medium-sized and moderately hypsodont hipparion (figs. 118, 119; table 41). The general morphology of the skull is similar to that of *C.*

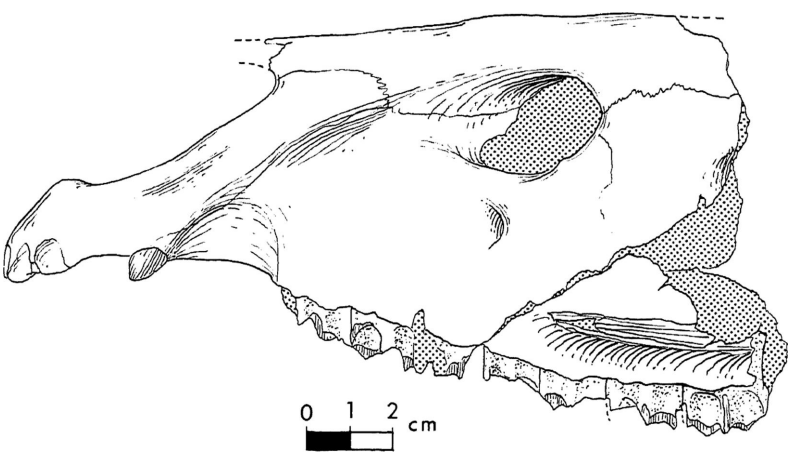

FIG. 128. Left lateral view of skull of *Cormohipparion sphenodus*, F:AM 71899, from the Ojo Caliente Member of the Tesuque Formation, Santa Fe Group, Clarendonian of Rio Arriba County, north-central New Mexico. Occlusal view of cheek teeth not shown here because they are in very late wear and dental pattern is poorly preserved.

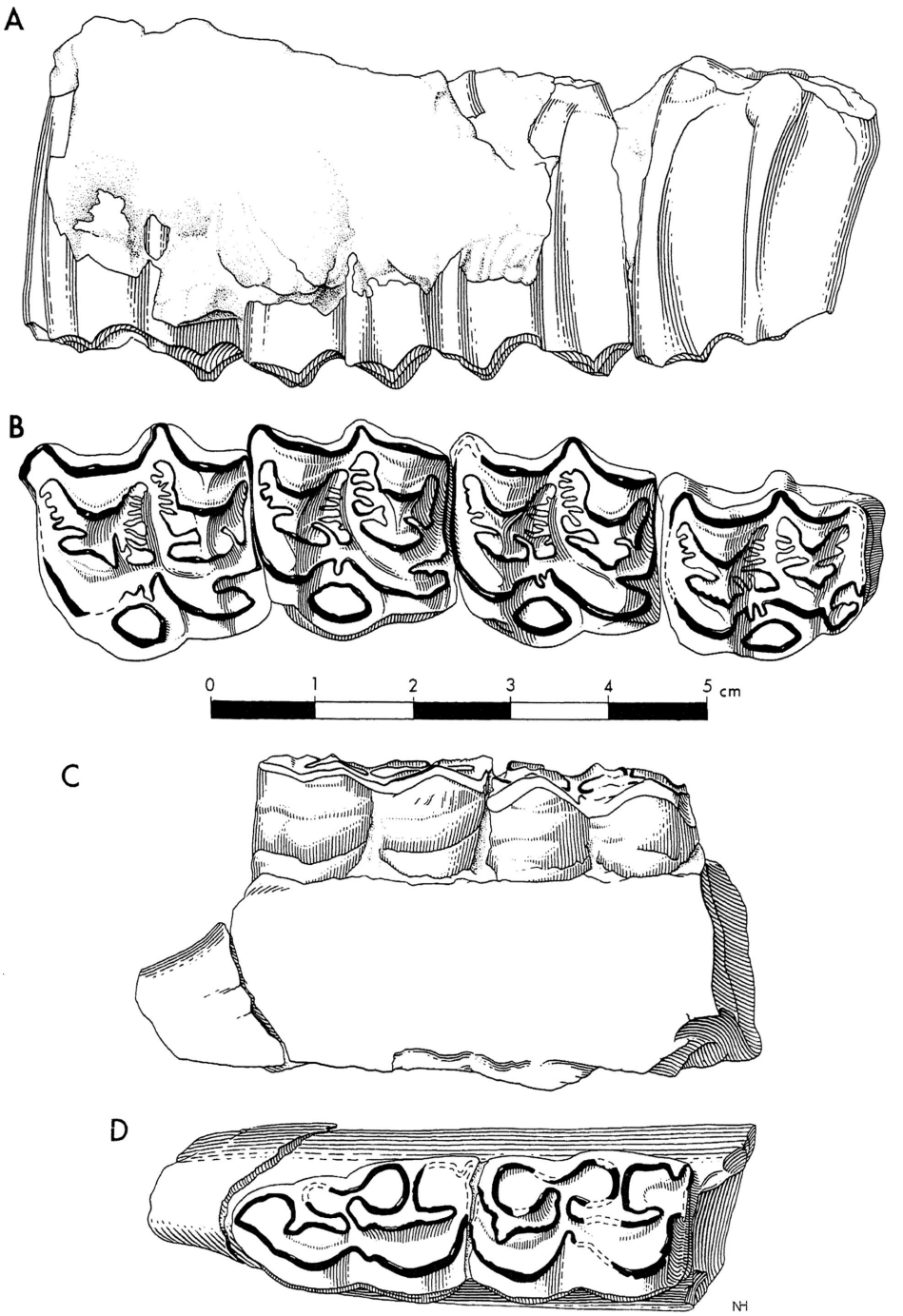

FIG. 129. *Cormohipparion sphenodus,* UCMP 62771, from UCMP locality V-6624, Caldecott Tunnel 3, Orinda Formation, Clarendonian of Contra Costa County, San Francisco Bay region, California. Left P^4–M^3, lateral (A) and occlusal (B) views. Left P_2–P_3, lateral (C) and occlusal (D) views.

TABLE 41
Selected Upper Dental Measurements and Univariate Statistics for *Cormohipparion sphenodus*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V (%)	OR	N	$\bar{x}$	s	V (%)	OR
P2APL	11	25.93	1.08	4.16	24.7–28.0	4	26.15	1.29	4.93	25.2–28.0
P2TRNW	11	19.15	1.03	5.39	16.6–20.8	4	19.50	0.32	1.64	19.2–19.9
P2PRTL	11	6.03	0.96	15.88	4.4–7.6	4	5.90	1.12	18.98	4.4–6.8
P2PRTW	11	4.26	0.30	7.06	3.9–4.8	4	4.23	0.26	6.15	4.0–4.5
P2TOTPLI	9	5.56	3.42	61.77	0–11	4	7.25	3.78	52.14	4–11
M1APL	12	19.46	1.45	7.49	17.2–22.0	6	19.00	0.58	3.05	17.9–19.4
M1ECTL	12	19.68	1.27	6.47	17.6–21.7	6	19.63	0.88	4.48	18.5–20.5
M1TRNW	12	20.20	0.90	4.46	18.3–21.5	6	20.37	0.54	2.65	19.3–20.8
M1PRTL	12	7.07	0.67	9.47	5.7–8.3	6	7.05	0.44	6.24	6.5–7.8
M1PRTW	12	3.97	0.48	12.08	3.3–4.6	6	4.12	0.51	12.38	3.5–4.6
M1TOTPLI	11	10.09	3.21	31.79	4–16	6	11.17	2.86	25.60	8–16
TRL	9	126.48	4.51	3.56	120.2–132.8	4	126.15	3.49	2.77	122.7–129.9
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	7	26.47	5.61	21.19	17.2–32.3	4	30.05	2.60	8.65	27.2–32.3
M1MSTHT	0	—	—	—	—	—	—	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 40 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

goorisi presented above. Of particular importance the DPOF is teardrop-shaped, has well-defined continuous anterior and posterior rims and, in contrast to *C. goorisi,* is only moderately pocketed. The DPOF is well-forward of the orbit resulting in a wide PRB. The anterior margin of the lacrimal bone usually does not touch the posterior rim of the fossa. In a juvenile specimen, F:AM 71894, the configuration of this fossa does not appear to be significantly different from adult specimens of *Cormohipparion.* The only difference appears to be that in the juvenile specimen the fossa lies over dP^2–dP^4 rather than P^3–M^1 as in adult specimens. Correspondingly, the infraorbital foramen, which is paired in F:AM 71894 and single in other specimens, lies dorsal to dP_2 at the anteriorventral margin of the DPOF.

DP^1 is present and it appears to be retained during ontogeny. The upper cheek teeth are slightly curved in the transverse plane. The protocone is elongate and oval-shaped with rounded or angular (usually during early wear stages) anterior and posterior borders (figs. 117, 121, 122, 124, 126, 127, 129). In contrast to *C. goorisi,* the anterior protocone spur is rudimentary or absent. In the prefossette, the pli protoloph consists of one or a few loops and the pli protoconule and pli prefos-

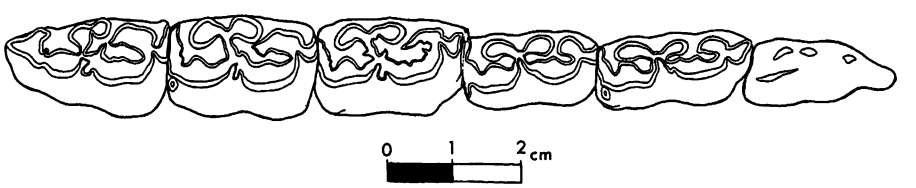

FIG. 130. Occlusal view of left P_2–M_3 of *Cormohipparion sphenodus,* F:AM 71888, from Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, Valentinian of Brown County, north-central Nebraska.

sette consist of numerous elongate loops. In the postfossette, the pli postfossette consists of numerous elongated loops and the pli hypostyle usually consists of one, or less frequently two, loops. The pli caballins, if present, consist of single or double loops.

In lower P_3–M_3 the protostylid is often developed; it is either connected to the protoconid-paralophid complex or it is an isolated column (figs. 129, 130). In the premolars the ectoflexids are shallow and there are moderately developed pli caballinids. In the molars the ectoflexids are deep (dividing the isthmuses) and the pli caballinids are rudimentary or absent. The internal enamel borders of the protoconids and hypoconids and anterior and posterior borders of the isthmuses are often plicated.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: In size, crown height, hypsodonty, and numerous dental characters cited above, *Cormohipparion sphenodus* has traditionally been included in the genus *Merychippus*. As is also the case in *C. goorisi*, the generic assignment of these species to *Cormohipparion* is principally based on the configuration of the DPOF, which is diagnostic for the genus (also see Woodburne, MacFadden, and Skinner, 1981). With regard to its position within the genus *Cormohipparion*, *C. sphenodus* is morphologically intermediate between the more primitive *C. goorisi* and the more advanced *C. occidentale* (fig. 120, table 37).

Cormohipparion sphenodus is well represented by cranial and dental material at numerous sites in the Great Plains and Rio Grande Graben (also see Woodburne, MacFadden, and Skinner, 1981). This species is also represented by dentitions from California (fig. 129). Based on examination of the TMM collections, there also probably are some specimens of this species from the Lapara Creek Fauna of the Texas Gulf Coastal Plain. Therefore, in contrast to the apparently restricted occurrence of *C. goorisi*, *C. sphenodus* was relatively widespread in midcontinental and western North America during the late Barstovian and early Clarendonian (Valentinian).

During the Vallesian and younger time intervals, *Cormohipparion* is well represented at many western Old World sites. In contrast, *Hipparion sensu stricto* does not appear to be common in the western Old World until the early Turolian. During the Vallesian, these Old World hipparions (predominantly *Cormohipparion* derivatives) are characterized dentally by relatively complex enamel plications on the fossette borders and small protocones in the upper cheek teeth in contrast to most contemporaneous (Clarendonian) hipparions in North America. The specimens of *C. sphenodus* from the Clarendonian of California have very plicated fossette borders and relatively small protocones (e.g., fig. 129). As such, this "population" is morphologically very close to certain Old World hipparions. These similarities led Woodburne, MacFadden, and Skinner (1981) to suggest that *Cormohipparion sphenodus* may have played an important role in the beginning of the so-called Hipparion Datum and subsequent radiation of derivative taxa in the Old World (see further discussion below).

Cormohipparion occidentale (Leidy), 1856

Figures 9, 17, 18, 22, 23, 118–120, 131–139, 149, 150; Tables 2, 37, 42, 43

JUNIOR SYNONYMS

Hipparion mohavense Merriam, 1913, p. 436, figs. 1–3.
Hipparion platystyle Merriam, 1915a, p. 5.
Hipparion mohavense callodonte Merriam, 1915b, pp. 53–55, figs. 5–7.

TYPE SPECIMEN AND LOCALITY: ANSP 11287, four left and one right upper cheek teeth probably from along the Little White River, late Clarendonian of South Dakota (for illustrations of the holotype, see Osborn, 1918, p. 177, fig. 140; Skinner and MacFadden, 1977, p. 919, text-fig. 4D). Skinner and Taylor (1967) discuss the type locality. *Cormohipparion occidentale* is the genotypic species for *Cormohipparion*.

REVISED DIAGNOSIS: Same as for genus with the following specific characters. Large and hypsodont North American hipparion. Mean TRL 138.00 mm. Unworn or little-worn M1MSTHT *ca.* 37–43 mm. DPOF with moderately developed (*ca.* 5 mm or less) posterior pocket. Protocones oval and relatively elongate. Fossette borders most plicated of

TABLE 42
Synopsis of Collections Examined for *Cormohipparion occidentale* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Little White River	ANSP	Ash Hollow equivalent, South Dakota	Late Clarendonian	Cast of type specimen examined
Numerous (e.g., Xmas Q. and Hans Johnson Quarry)	AMNH, F:AM	Burge Member of Valentine Formation, Ash Hollow Formation, Brown and Cherry counties, north-central Nebraska, and Bennett County, adjacent South Dakota	Valentinian-Clarendonian	Also see list of specimens in Skinner and MacFadden (1977)
Gidley Horse Quarry, Chamberlain's quarries	F:AM	Clarendon Beds, Ogallala Group, Donley County, Texas Panhandle	Clarendonian	
Numerous	F:AM	Santa Fe Group, Rio Arriba County, New Mexico	Late Clarendonian	
Numerous (Lapara Creek Fauna)	TMM	Goliad Formation, Bee and Goliad counties, Texas Gulf Coastal Plain	Early Clarendonian	
Numerous (Ricardo L.F.)	UCMP, LACM UCR	Ricardo Formation, Mohave Desert, Kern County, California	Late Clarendonian	Includes type area of *Hipparion mohavense* and *Hipparion mohavense callodonte*
Numerous (San Francisco Bay region)	UCMP	Orinda, Siesta, Green Valley formations and correlative units, San Francisco Bay area, Contra Costa County, California	Clarendonian	Includes type locality of "*Hipparion platystyle*"
Feltz Ranch	F:AM	Ogallala Group, Keith County, Nebraska	Hemphillian	Probably latest known record of genus and species; Bennett (personal commun., 1981) also has late representatives of *C. occidentale* in the Ogallala Group of Kansas

all North American hipparions. In the lower premolars, shallow ectoflexids and moderately developed pli caballinids. In the lower molars, deep ectoflexids and pli caballinids rudimentary or absent. Protostylids well developed and sometimes isolated. Elongate, expanded, and large metaconids, metastylids, entoconids, and hypoconulids with rounded or angular borders.

Cormohipparion occidentale is similar to

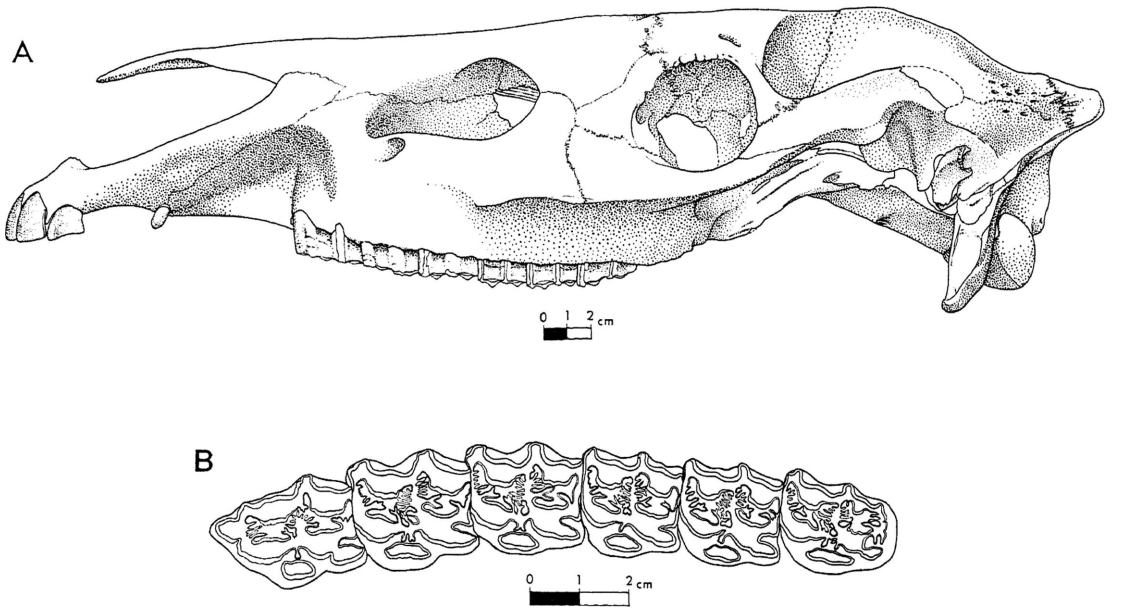

FIG. 131. *Cormohipparion occidentale,* F:AM 71800, from Xmas Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska. A. Lateral view of skull. B. Occlusal view of left P^2–M^3. Also see figure 135 for ramus and lower dentition.

Neohipparion affine and *N. leptode* in size. This species differs from other horse genera in the generic characters. *Cormohipparion occidentale* differs from both *C. goorisi* and *C. sphenodus* in larger size, higher crowns, more elongated protocones, significantly in-

TABLE 43
Selected Upper Dental Measurements and Univariate Statistics for *Cormohipparion occidentale*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V (%)	OR	N	$\bar{x}$	s	V (%)	OR
P2APL	16	28.45	2.14	7.52	24.7–31.9	12	28.21	2.32	3.54	24.7–31.9
P2TRNW	18	21.14	1.17	5.52	19.2–22.8	14	21.39	1.13	5.28	19.7–22.8
P2PRTL	16	6.76	0.91	13.42	5.1–8.5	13	6.85	0.91	13.28	5.1–8.5
P2PRTW	18	4.27	0.79	18.54	3.0–6.1	14	4.29	0.68	15.85	3.0–6.1
P2TOTPLI	17	9.18	4.22	45.95	0–17	14	9.86	3.68	37.32	3–17
M1APL	19	21.56	2.05	9.49	17.8–25.7	15	21.16	1.65	7.80	17.8–24.8
M1ECTL	17	21.37	2.32	10.88	17.6–27.2	14	21.05	1.76	8.36	17.6–24.9
M1TRNW	19	21.03	1.31	6.22	19.1–23.8	15	20.99	1.17	5.57	19.3–23.8
M1PRTL	19	7.70	1.13	14.80	5.5–9.6	15	7.47	1.08	14.46	5.5–9.6
M1PRTW	19	3.99	0.53	13.44	3.4–5.4	15	3.90	0.43	11.03	3.4–4.7
M1TOTPLI	19	12.42	3.42	27.54	7–19	15	12.27	3.47	28.28	7–19
TRL	13	138.00	8.52	6.18	125.1–151.0	10	136.39	6.88	5.04	125.1–149.7
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	12	27.92	8.34	29.87	10.9–35.5	1	35.5	—	—	—
M1MSTHT	5	35.82	3.51	9.81	30.2–39.1	1	39.1	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 42 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

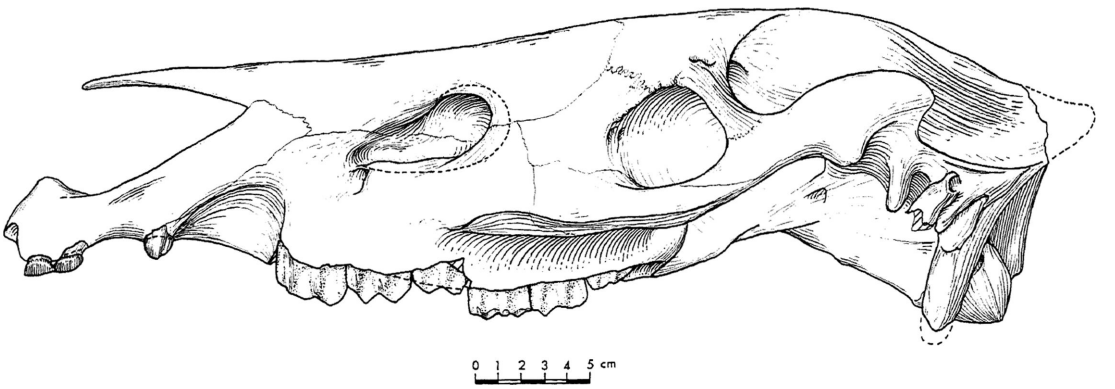

FIG. 132. Lateral view of skull of *Cormohipparion occidentale,* F:AM 71801, from Xmas Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, Nebraska. See figure 18 for occlusal views of sectioned left P^2–M^3.

creased complexity of enamel plications (particularly on fossette borders), and more expanded metaconids, metastylids, entoconids, and hypoconulids oftentimes with angular enamel borders.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Early Clarendonian of Texas, and San Francisco Bay region and Mohave Desert of California; late Valentinian of north-central Nebraska; late Clarendonian of Texas,

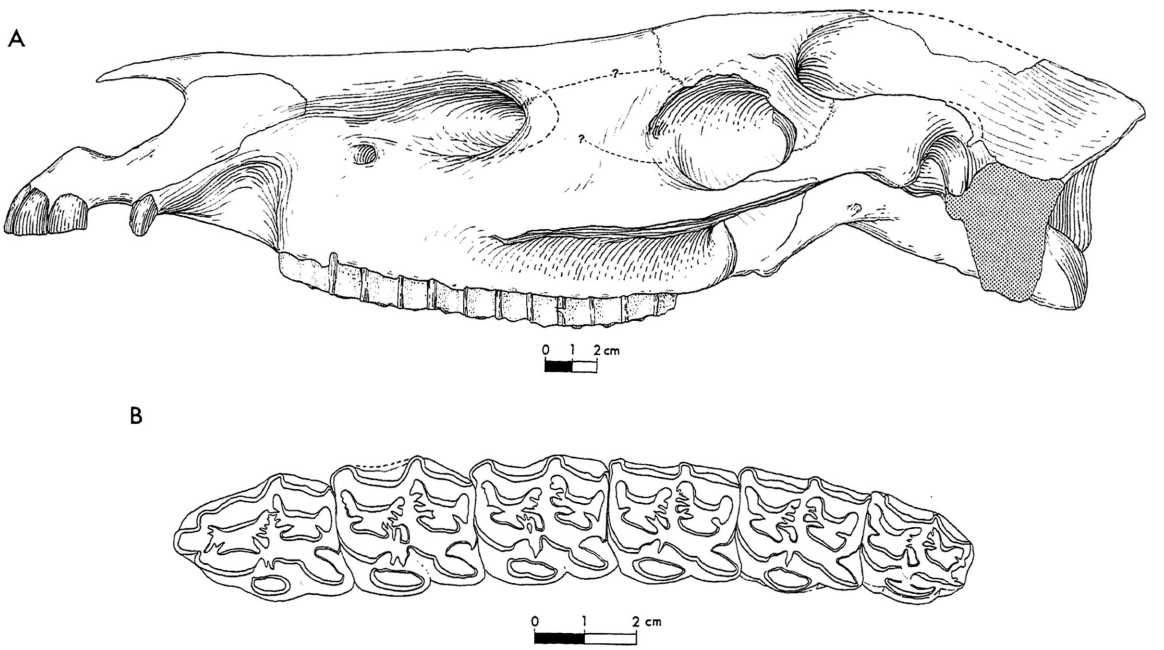

FIG. 133. *Cormohipparion occidentale,* F:AM 73909, from Gidley Horse Quarry, Clarendon Beds, Ogallala Group, late Clarendonian of Donley County, Texas Panhandle. A. Right (reversed) lateral view of skull. B. Occlusal view of right P^2–M^3 (reversed). Also see figure 136 for ramus and lower dentition.

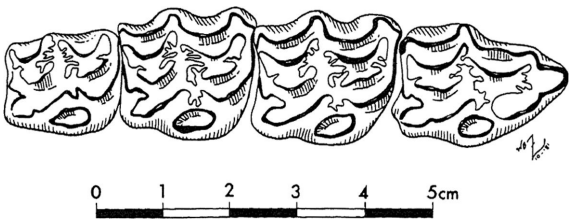

FIG. 134. Occlusal view of right P^2–M^1 of *Cormohipparion occidentale,* TMM 31081-619, from the Lapara Creek Fauna, Goliad Formation, early Clarendonian of the Texas Gulf Coastal Plain.

Nebraska and adjacent South Dakota, and north-central New Mexico; probable occurrences from the early Hemphillian of the Great Plains, e.g., Nebraska (table 42).

DESCRIPTION: This species is represented by large quarry samples from north-central Nebraska that allow assessment of the variability of the DPOF, as well as possible sexual dimorphism in size, canines, and dental pattern (also see discussion elsewhere in text). *Cormohipparion occidentale* is a very large and moderately hypsodont hipparion (figs. 90, 91; table 43). Skulls of *C. occidentale* are generally similar in morphology (although larger) to that of *C. goorisi* and *C. sphenodus* presented above. Of particular importance, the DPOF is teardrop-shaped, has well-defined continuous anterior and posterior rims, and is moderately pocketed (figs. 131–133). The fossa is well forward of the orbit resulting in a wide PRB. The anterior margin of the lacrimal bone usually does not touch, or barely touches, the posterior rim of the DPOF.

The upper cheek teeth are very slightly curved in the transverse plane. The cheek teeth are larger than *C. sphenodus.* The protocones are elongate and oval with rounded or angular borders (figs. 131–134). The pro-

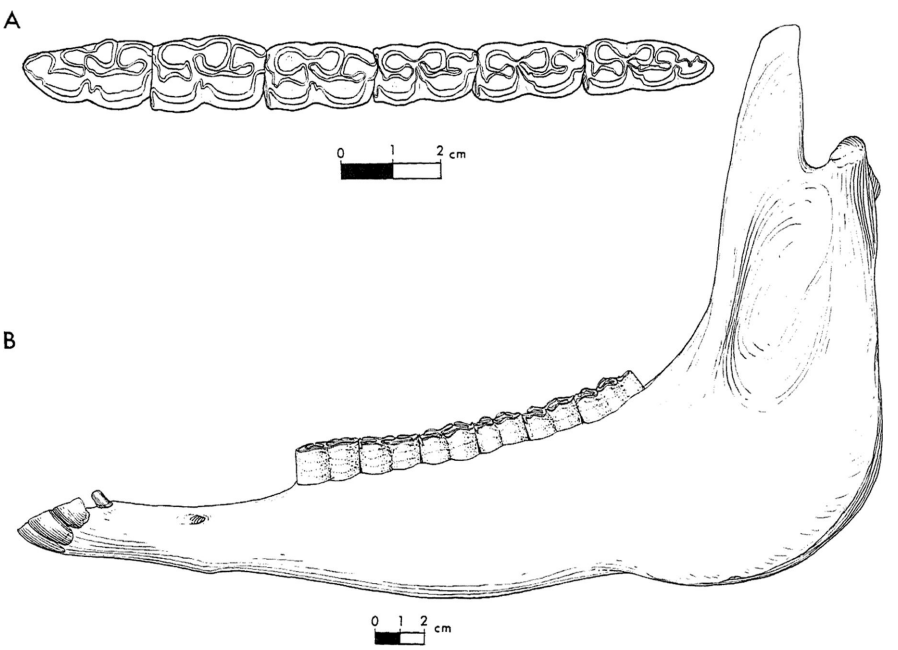

FIG. 135. *Cormohipparion occidentale,* F:AM 71800, from Xmas Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, Nebraska. A. Occlusal view of left P_2–M_3. B. Left lateral view of mandible. Also see figure 131 for skull and upper dentition.

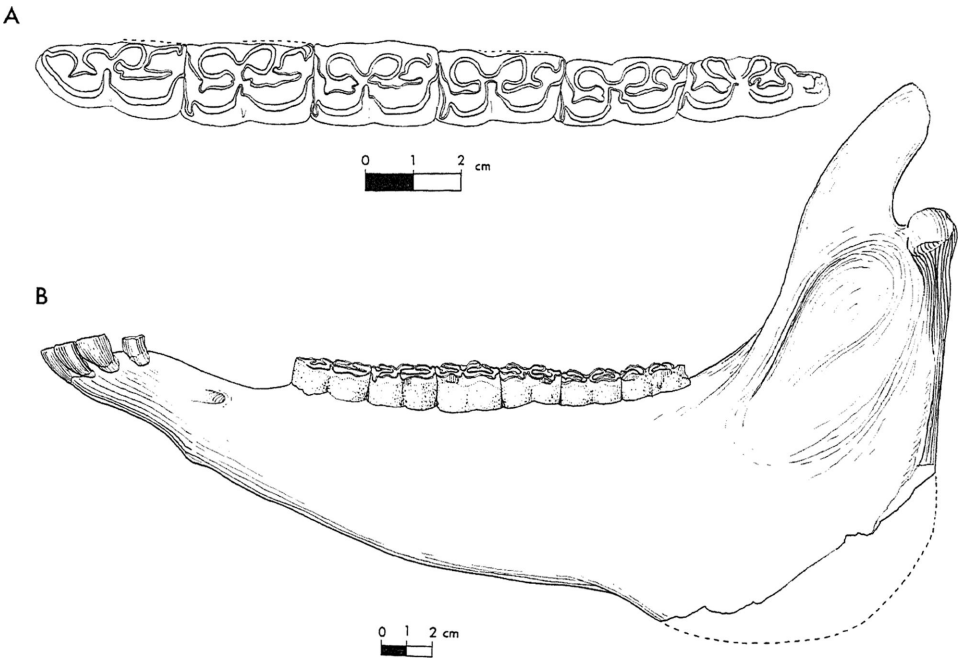

FIG. 136. *Cormohipparion occidentale,* F:AM 73909, from Gidley Horse Quarry, Clarendon Beds, Ogallala Group, late Clarendonian of Donley County, Texas Panhandle. A. Occlusal view of right (reversed) P_2–M_3. B. Right (reversed) lateral view of mandible. Also see Figure 133 for skull and upper dentition.

tocones in *C. occidentale* are usually not as elongate, nor have the very angular borders, as in *Neohipparion eurystyle.* The richly plicated fossette borders are striking in *C. occidentale* and similar in complexity to, for example, the large Siwalik species *Cormohipparion theobaldi* (*sensu* MacFadden and Woodburne, 1982). In the prefossettes and the postfossettes the enamel plications oftentimes consist of numerous primary and secondary loops. For example, there are sometimes (depending on individual and ontogenetic variation) ten or more plications in the pli prefossettes and pli postfossettes (i.e., mean P2TOTPLI = 9.18; mean M1TOTPLI = 12.42; see table 43). The pli caballins are usually well developed and consist of either single or double loops.

The mandible is moderately deep with a moderately elongate symphysis (figs. 135, 136). At the anteriorexternal border of P_3–M_3, the protostylids are usually well developed. They are either connected to the parastylid-protoconid complex or sometimes they are developed as isolated columns. In the premolars, the ectoflexids are shallow and there are moderately developed pli caballinids. In the molars, the ectoflexids are deep (dividing the isthmuses) and the pli caballinids are rudimentary or absent. The internal enamel borders of the protoconids and hypoconids and posterior borders of the isthmuses are sometimes plicated. The metaconids and metastylids are approximately equal in size, are very large, have rounded or angular enamel borders, and are widely separated. The entoconids and hypoconulids are expanded and the anterior borders of these parts frequently are in contact with the posterior border of the metastylids.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: *Cormohipparion occidentale* is the most advanced species within the genus. *Cormohipparion occidentale* is set apart from both *C. goorisi* and *C. sphenodus* because it possesses the following derived character states (see fig. 92, table 37); large size and high crowns, elongated protocones, very

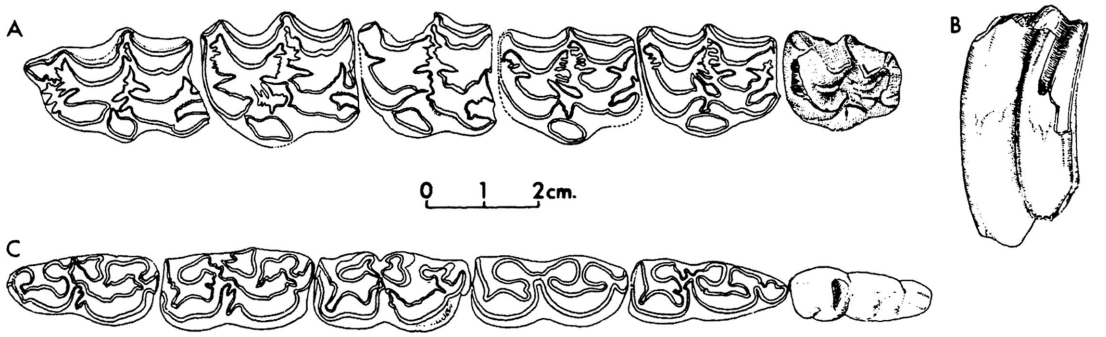

FIG. 137. Holotype of *Hipparion mohavense callodonte,* UCMP 21311, from the Ricardo Formation, probably Ricardo L.F. (*sensu stricto*), late Clarendonian of Kern County, southern California. A. Occlusal view of left P^2–M^3. B. External crown view of M^3. C. Occlusal view of left P_2–M_3. Taken from Merriam (1915b, p. 53, figs. 5–7).

complicated enamel plications on the fossette borders, and very expanded metaconids, metastylids, entoconids, and hypoconulids with angular borders.

"*Hipparion*" *occidentale* was the first North American hipparion to be described (Leidy, 1865; see table 2). Since that time this species has been frequently discussed in the literature. Several workers, such as Matthew (1924), Hesse (1935), McGrew (1938), Stirton (1940), and Webb (1969), have suggested that the "*Neohipparion occidentale* group" includes (with some variations depending on author) "*N.*" *occidentale, N. affine, N. whitneyi,* and *N. dolichops.* It seems justified to synonymize the last three species based on cranial and dental similarities, however, within the genus *Neohipparion.* "*N.*" *occidentale* is not related to those species based on cranial and dental morphology; this species belongs to the genus *Cormohipparion.*

During the early part of this century, Merriam proposed three names for hipparions collected from California. *Hipparion mohavense* (Merriam, 1913a) was based on several "associated" isolated upper cheek teeth (UCMP 19787, right P^3, M^1 and M^2) from the Ricardo L.F. of early Clarendonian age from the Mohave Desert, southern California. *Hipparion platystyle* (Merriam, 1915a) was based on an isolated P^2, UCMP 19380, from UCMP locality 708, Green Valley Formation of late Clarendonian age ("Montediablian") from the San Francisco Bay region (also see Stirton, 1939). *Hipparion mohavense callodonte* (Merriam, 1915b) was based on a well-preserved set of associated upper and lower cheek teeth (fig. 137) from the Ricardo L.F. of early Clarendonian age from the Mohave Desert, southern California. The characters that Merriam used to distinguish these three "species" are interpreted here to represent minor variations in the dental pattern. In each of these specimens and referred material, the following characters are exhibited: relatively large size, moderately hypsodont, moderately elongated protocones, richly plicated fossette borders, pli caballinids well developed in premolars and ectoflexids moderately deep. This complex of character states indicates that these three species names are morphologically indistinguishable from the senior name *C. occidentale.* It is unfortunate that there is no associated cranial material from the California samples. Further corroboration of the synonymy presented here would be the discovery of relevant material from California that showed the DPOF diagnostic of *Cormohipparion.*

In the analysis of the *Hipparion tehonense* sample from MacAdams Quarry presented above, it was shown that there is no significant difference in dental pattern of the muzzle dimensions and upper cheek teeth pattern that can be attributed to sexual dimorphism. Preliminary analysis made during the present study of the sample of *Cormohipparion oc-*

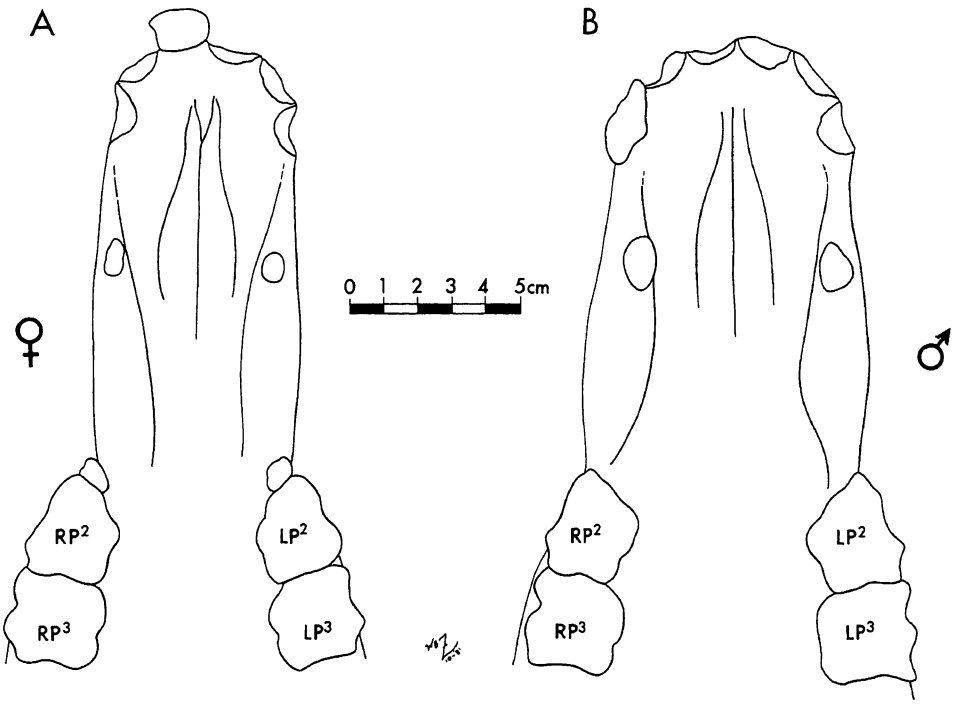

FIG. 138. Possible sexual dimorphism in relative robustness of the muzzle (postcanine diastema) of *Cormohipparion occidentale* from Hans Johnson Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska. A. F:AM 71858, ventral view of a female (as indicated from small canines) with a transversely narrow muzzle. B. F:AM 71860, ventral view of a male (as indicated from relatively large canines) with a transversely broad muzzle. The presence (absence) of P^1 in F:AM 71858 (F:AM 71860) does not appear to indicate sexual dimorphism. Diagrammatic with some restoration. Also see figure 139.

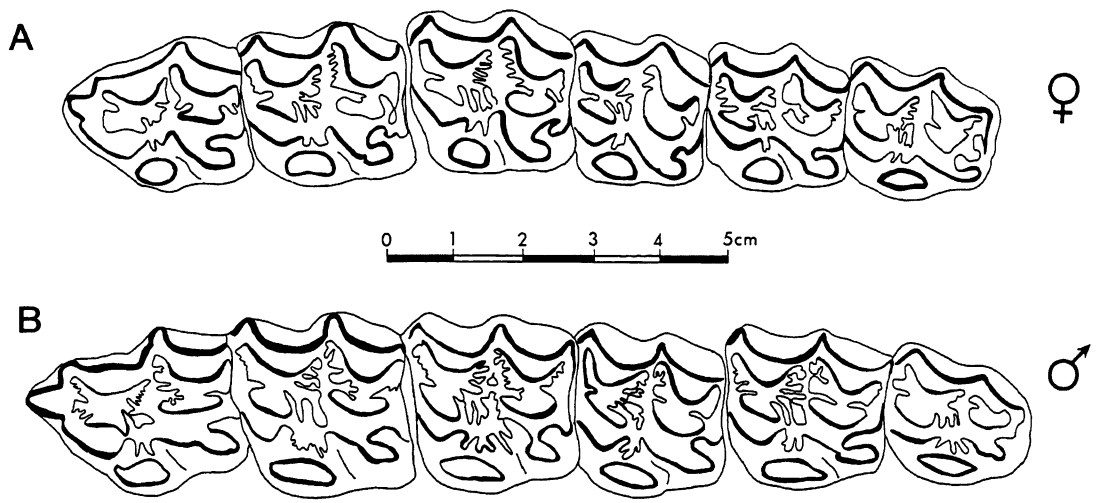

FIG. 139. Possible sexual dimorphism at similar ontogenetic (i.e., "advanced maturity") stages in the upper cheek tooth pattern of *Cormohipparion occidentale* from Hans Johnson Quarry, Ash Hollow Formation, late Clarendonian of Cherry County, north-central Nebraska. A. F:AM 71858, female. B. F:AM 71860, male. Also see figure 138.

cidentale from the late Clarendonian Hans Johnson Quarry of north-central Nebraska (also see fig. 9) may provide an exception to this rule. This quarry sample is presently under analysis by participants of the 1981 Hipparion Conference. Given the extreme range of variability observed (above) for plication counts and the limited number of individuals of *C. occidentale* from Hans Johnson Quarry, the hypothesis of sexual dimorphism presented here may be difficult to test with rigorous statistical methods. Nevertheless, in the males from this quarry, the muzzle seems generally broader than that of the females (fig. 138). The enamel plications on the fossette borders and protocones seem to be, respectively, relatively simple and oval in females and relatively complex and elongate in males at comparable ontogenetic stages, i.e., mature individuals with all teeth in wear ("advanced maturity," fig. 139, sexes are determined from canine size). Stated another way, males of *Cormohipparion occidentale* from Hans Johnson Quarry seem to show some phylogenetically advanced character states whereas females show the relatively primitive character states. This type of sexual dimorphism also may occur in Valentinian *C. occidentale* quarry samples from north-central Nebraska. In these "populations" certain male specimens trend towards the advanced dental characters seen in late Clarendonian *C. occidentale.*

With the revised and expanded concept of *Cormohipparion occidentale* presented here, this species was widespread in midcontinental and western North America during the Clarendonian. In addition, specimens from the Feltz Ranch L.F. (F:AM 104814 and Hesse, 1935, pl. 17) and northern Kansas (Bennett, personal commun., 1981) suggest that *C. occidentale* is probably represented in the early Hemphillian part of the Ogallala Group in the Great Plains.

Because of general overall dental pattern, particularly in the complex enamel plications of the fossette borders, it has been suggested that "*C.*" (or "*H.*") *occidentale* may be closely related to certain Old World hipparions (e.g., MacFadden and Bakr, 1979). However, as Woodburne, MacFadden, and Skinner (1982) point out, the very elongate protocone in *C. occidentale* is derived over the character state seen in most Old World hipparions. Thus *C. sphenodus,* with a smaller protocone, is probably a closer relative of certain Old World ("*Cormohipparion*-derived") hipparions than is *C. occidentale* (see further discussion below).

EQUIDAE ("HIPPARIONINE") INDETERMINATE

INCERTAE SEDIS

Hippotherium plicatile Leidy, 1887
Figures 140–145, 150; Tables 2, 44, 45

TYPE SPECIMEN AND LOCALITY: USNM 3292, isolated right upper molar, from Mixson's Bone Bed,[11] early Hemphillian of Levy County, north-central Florida (see Osborn, 1918, p. 192, fig. 155; also fig. 140 of this report).

COMMENT: As is presented below, the species name *Hippotherium plicatile* has a sufficient sample from the probable type locality. It does possess dental *differentia* that justify the recognition of this species. However, because of the lack of diagnostic cranial material or useful dental characters, this species cannot be unambiguously allocated to any one genus.

REVISED DIAGNOSIS: Medium-sized and moderately hypsodont hipparion. Mean TRL 125.50 mm. Unworn or little-worn M1MSTHT *ca.* 45–50 mm. Relatively small and rounded to oval protocones. Very complicated fossette borders. Ectoflexids moderate in premolars, deep in molars.

[11] It is generally assumed that Leidy's Alachua Clays collection was made only from Mixson's Bone Bed in the town of Williston in Levy County. However, Leidy and Lucas (1896) state that in addition to Mixson's plantation, specimens were also collected from several other localities in the vicinity of the town of Archer (some 18 km north of Williston). Due to the isolated nature of vertebrate-bearing deposits in this region, there is no reason to imply that specimens collected from these different localities are contemporaneous or necessarily represent the same taxon of horse.

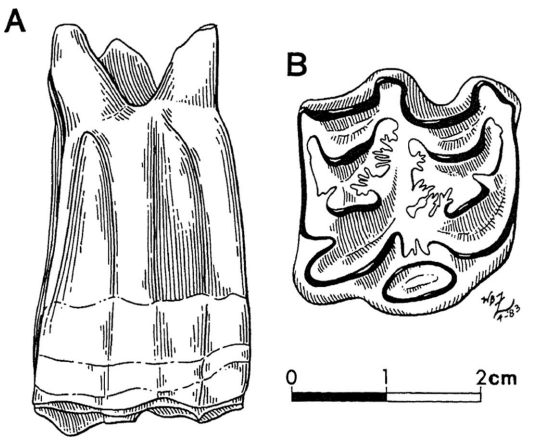

FIG. 140. *Hippotherium plicatile,* USNM 3292, holotype, right ?M^1, from Mixson's Bone Bed, early Hemphillian of Levy County, north-central Florida. A. Lateral view. B. Occlusal view.

Hippotherium plicatile differs from other hipparion (and all other) horse genera in the total combination of diagnostic dental characters, in particular its size, small protocones, and complicated fossette borders.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION: Known from the Hemphillian of Florida, Mixson's Bone Bed in Levy County (type locality). Probably also represented at the late Clarendonian Love Bone Bed L.F. of Alachua County, Florida (table 44). Possibly from the early Hemphillian McGehee Farm L.F. of Alachua County, Florida (Hulbert, personal commun., 1983).

DESCRIPTION: This species is medium-sized and moderately hypsodont (table 45). In the upper molars the protocone is usually small and similar in relative size to *H. tehonense, H. forcei,* and Old World hipparions (figs.

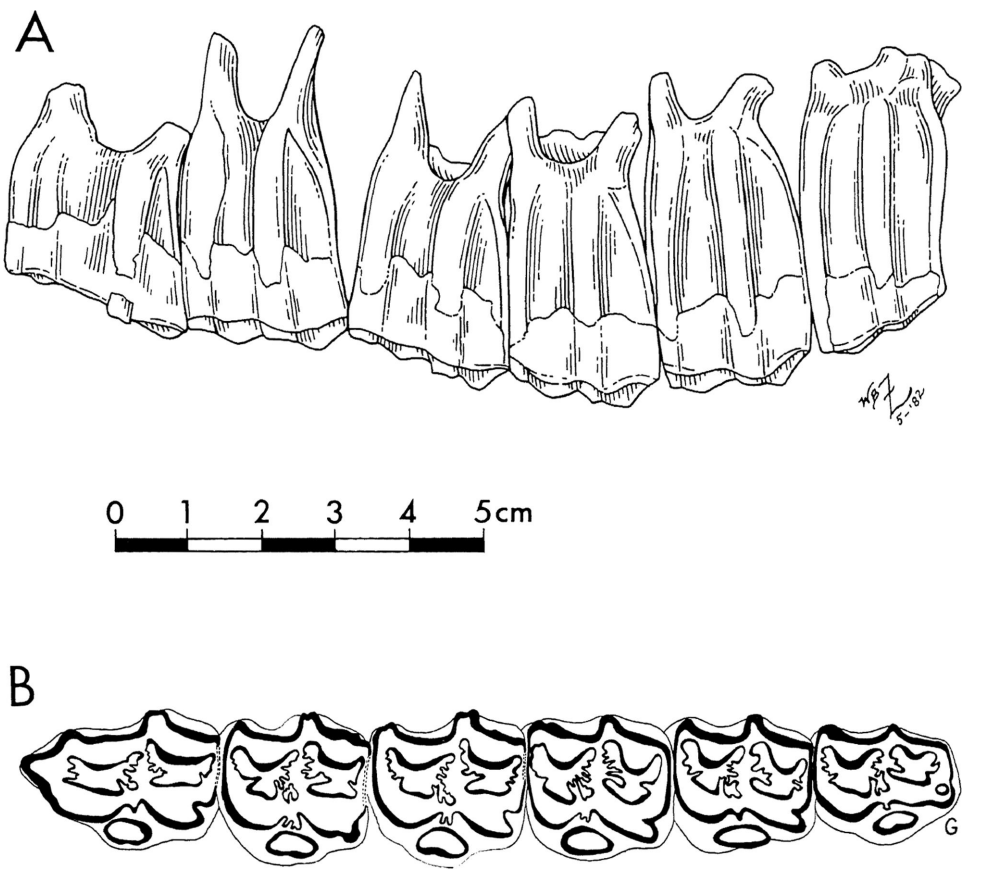

FIG. 141. Left P^2–M^3 of *Hippotherium plicatile,* F:AM 107875, from Mixson's Bone Bed. A. Lateral view. B. Occlusal view.

TABLE 44
Synopsis of Collections Examined for *Hippotherium plicatile* Used for Descriptions and Comparisons in this Report

Locality Name and Designation	Collection	Geology and Geography	Age	Comments
Mixson's Bone Bed	F:AM, UF, USNM	Alachua Formation, Levy County, Florida	Early Hemphillian	Only examined type specimen from USNM collection
Love Bone Bed	UF	Alachua Formation, Alachua County, Florida	Late Clarendonian	

141, 142). The anterior borders of the prefossettes and posterior borders of the postfossettes are moderately plicated. As the species name indicates, the posterior borders of the prefossettes and anterior borders of the postfossettes are very plicated and the pli caballins consist of one or multiple (usually from two to four) loops. As shown in a cross-sectioned upper tooth row from Mixson's Bone Bed, F:AM 111730 (fig. 142), the enamel plications persist to near the base of the cheek teeth.

A relatively complete mandible and associated dentition of *Hippotherium plicatile* is represented by F:AM 107874 from the type locality (fig. 143). The canine is appressed with I_3. There is an elongate postcanine diastema. The ectoflexids are shallow in the premolars and deep in the molars. The pli caballinid usually consists of a single loop in the premolars; it is rudimentary or absent in the molars. The isthmus is complete in the premolars and it is subdivided by the deep ectoflexids in the molars. Secondary plications are frequently developed, particularly in the premolars. The enamel borders of the protoconids and hypoconids usually are not very plicated in *Hippotherium plicatile.*

TABLE 45
Selected Upper Dental Measurements and Univariate Statistics for *Hippotherium plicatile*[a]

	All Wear (Age) Classes Combined					Middle Wear (Age) Classes[b]				
	N	$\bar{x}$	s	V(%)	OR	N	$\bar{x}$	s	V(%)	OR
P2APL	4	26.23	1.60	6.09	24.4–28.2	3	26.10	1.93	7.39	24.4–28.0
P2TRNW	4	18.95	1.35	7.14	17.7–20.6	3	18.40	0.96	5.22	17.7–19.5
P2PRTL	4	6.60	0.36	5.39	6.1–6.9	3	6.60	0.44	6.67	6.1–6.9
P2PRTW	4	3.83	0.15	3.92	3.7–4.0	3	3.80	0.17	4.47	3.7–4.0
P2TOTPLI	4	12.00	3.83	31.91	7–15	3	11.00	4.00	36.36	7–15
M1APL	3	20.17	0.95	4.69	19.1–20.9	2	19.80	0.99	5.00	19.1–20.5
M1ECTL	3	20.47	1.42	6.98	18.9–21.7	2	19.85	1.34	6.75	18.9–20.8
M1TRNW	3	19.03	0.60	3.17	18.4–19.6	2	19.00	0.85	4.47	18.4–19.6
M1PRTL	3	7.27	0.29	3.97	7.1–7.6	2	7.35	0.35	4.76	7.1–7.6
M1PRTW	3	3.70	0.27	7.15	3.4–3.9	2	3.85	0.07	1.82	3.8–3.9
M1TOTPLI	3	11.00	1.00	9.09	10–12	2	11.0	1.41	12.82	10–12
TRL	2	125.50	7.92	6.31	119.9–131.1	1	119.9	—	—	—
						Juvenile Wear (Age) Classes Only[c]				
P2MSTHT	3	25.40	7.32	28.81	20.4–33.8	0	—	—	—	—
M1MSTHT	3	39.27	10.64	27.10	27.2–47.3	1	47.3	—	—	—

[a] Abbreviations are presented on pp. 21 and 22; see table 44 for collections examined.
[b] Juvenile and old wear (age) classes removed.
[c] Approaches maximum mesostyle crown height.

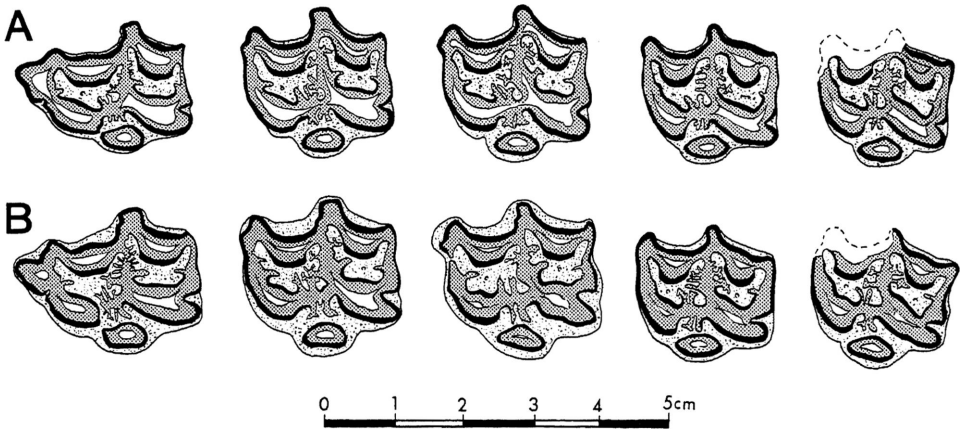

FIG. 142. Cross-sectional views of left P^2–M^3 of *Hippotherium plicatile*, F:AM 111730, from Mixson's Bone Bed. A. Near base of teeth. B. Near top of teeth.

CHARACTER ANALYSIS AND GENERAL DISCUSSION: The combination of size and dental characters indicate that *Hippotherium plicatile* is certainly a distinct species. In addition to the topotypic sample, other specimens from Florida sites (e.g., Love Bone Bed, figs. 144, 145) are referred to this species because of similarities in dental pattern. With regard to its dentition, the lower dental pattern is similar to the intermediate members (e.g., *Neohipparion trampasense*) of *Neohipparion*. In the upper cheek teeth, the small protocones are primitive for hipparions. The complex enamel plications, although derived for hipparions, do not indicate unambiguous affinities with any particular genus (although

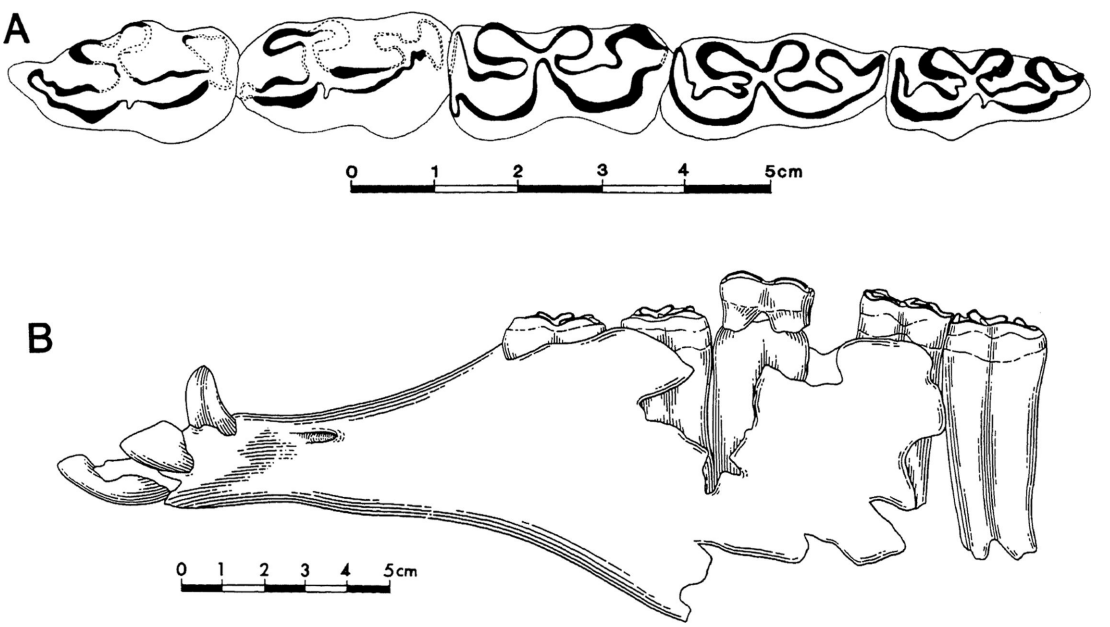

FIG. 143. Mandible with symphysial and cheek tooth (dP_2–dP_4, M_1, M_2) dentitions of *Hippotherium plicatile*, F:AM 107874, from Mixson's Bone Bed. A. Occlusal view. B. Lateral view.

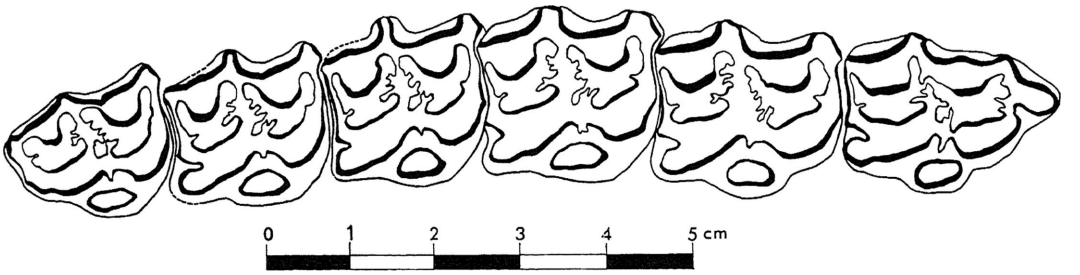

FIG. 144. Occlusal view of right P^2–M^3 of *Hippotherium plicatile,* UF 27136, from the Love Bone Bed, late Clarendonian of Alachua County, north-central Florida.

the superficial similarities in fossette plications would suggest affinities with either advanced *Neohipparion* or *Cormohipparion*). Unfortunately, well-preserved cranial material of *Hippotherium plicatile* is not available to indicate the development of the DPOF. There is one very crushed and fragmentary juvenile skull (F:AM 107876) that is referable to *Hippotherium plicatile* from Mixson's Bone Bed. The cheek region is fragmented but it suggests that the DPOF was either poorly developed or absent. For specimens referred to this species from other Florida sites, e.g., the Love Bone Bed, maxillary fragments indicate the presence of a ventral rim of the DPOF, which could suggest affinites with several hipparion groups (and is therefore non-diagnostic). It is also possible that the taxon from Mixson's Bone Bed, with suggestions of no DPOF, will turn out to be a different species from the one represented by the other Florida samples, e.g., Love Bone Bed, with the ventral rim of the DPOF (Hulbert, work in progress). If so, the similarities in dental pattern of this different sample would indicate parallel evolution. In summary, although *Hippotherium plicatile* possesses specific *differentia,* it does not show any derived characters that unambiguously ally it to any one hipparion genus. It is therefore relegated in this report to *incertae sedis.*

Despite its uncertain affinities, "*Hipparion*" *plicatile* has received much attention in the literature (e.g., Stirton, 1940). Because of the relatively small protocones, and, to a lesser extent, the complex enamel plications, this species has been considered very closely related to Old World *Hipparion.* This putative close affinity of "*Hipparion*" *plicatile* from Florida and Old World hipparions have perplexed biogeographers. For example, Joleaud (in Matthew, 1924, pp. 173–174) invoked a trans-Atlantic dispersal route between the New and Old worlds based on this paleontological evidence. With a more current knowledge of Cenozoic continental configurations as well as the problems involved in the taxonomic affinities of *Hippotherium plicatile,* this species now assumes a dubious role in elucidation of Holarctic intercontinental dispersal patterns during the late Miocene.

NOMINA DUBIA

Hippotherium sinclairi Wortman, 1882, p. 73.
Hippotherium montezuma Leidy, 1883, pp. 290–291, 1 fig.
Hippotherium rectidens Cope, 1886, pp. 360–361 (no figure).
Hipparion condoni Merriam, 1915a, pp. 6–8, figs. 4, 5.
Hipparion anthonyi Merriam, 1916b, pp. 129–133, figs. 1, 2.

COMMENT: The species names listed above have no *differentia* that allow them to be diagnosed at either or both the generic or specific levels. They all have general "hipparion characters" but their position within this polyphyletic group is indeterminate. Therefore, they are designated *nomina dubia.* The *nomen dubium* is preferred to *nomen vanum* (see recent discussion in Chorn and Whetstone, 1978).

These species are from the older literature. They are problematical because they were based on very fragmentary types with little or no additional topotypic or referred material or their precise stratigraphic prove-

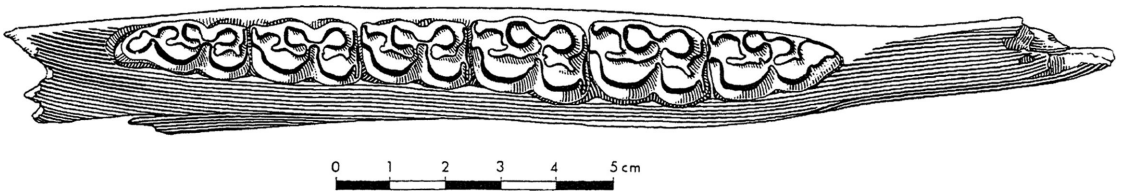

FIG. 145. Occlusal view of right ramus with P_2–M_3 of *Hippotherium plicatile,* UF 27317, from Love Bone Bed, late Clarendonian of Alachua County, north-central Florida.

nance is unknown so that the collection and recognition of subsequent and better-preserved topotypic material is impossible. With some of these *nomina dubia,* both problems apply. Figures of relevant specimens are not presented here because fine illustrations were compiled in Osborn (1918).

Hippotherium sinclari Wortman, 1882

TYPE SPECIMEN AND LOCALITY: AMNH (Cope Collection) 8178, left premolar, from Cottonwood Creek, Rattlesnake Formation, early Hemphillian of Oregon.

DESCRIPTION AND DISCUSSION: The holotype is moderately hypsodont and is of medium size. The protocone is elongate. The fossette borders are moderately plicated and the pli caballin consists of a single loop. Given these characters, this specimen could be referable to any of several of the more advanced North American hipparion species. With the uncertain exact provenance and lack of definitely associated topotypic material the affinities of this species name is uncertain.

Hippotherium montezuma Leidy, 1883

TYPE SPECIMEN AND LOCALITY: USNM 3304, right P^3 or P^4, collected from near Lacualtipan, Hidalgo, Mexico. The exact locality and age are uncertain, but Leidy (1883, p. 290) stated that the rocks from this locality are "probably of pliocene [*sic*] age, though they may be miocene [*sic*]." Osborn (1918, p. 197) lists the locality as ?Upper Miocene.

DESCRIPTION AND DISCUSSION: The holotype is illustrated in Osborn (1918, p. 197, fig. 162). It represents a medium-sized and relatively hypsodont hipparion. The tooth is slightly curved in the transverse plane. The protocone is relatively elongate and has angular anterior and posterior margins. The pli caballin consists of two well-developed loops. The hypoconal groove is moderately developed. The pli protoloph is absent. The pli prefossette and pli postfossette consist of multiple loops. The pli hypostyle is absent.

Based on generalized morphology of this single tooth without meaningful locality data, *Hippotherium montezuma* is rendered a *nomen dubium.* It does have some characters that are *Neohipparion*-like, but to use these when they could represent individual variation is absurd.

Since Leidy's (1883) original description, *Hippotherium montezuma* has been listed from a few other localities in Central America (Olson and McGrew, 1941; Ferrusquia-Villafranca, 1978). However, with the present status of the holotype, these samples can not be unambiguously referred to any single hipparion species.

Hippotherium rectidens Cope, 1886

TYPE SPECIMEN AND LOCALITY: AMNH (Cope Collection) 8346, right upper cheek tooth (?premolar) from the "Loup Fork shales" of Tehuichila, Mexico (possibly the same locality as *Nannipus peninsulatus*; see discussion in Miller and Carranza-Castañeda, in press). Cited as Hemphillian age (see faunal list in Ferrusquia-Villafranca, 1978), although the exact provenance is uncertain.

DESCRIPTION AND DISCUSSION: The type specimen is illustrated in Osborn (1918, p. 199, fig. 164). It represents a medium-sized and relatively hypsodont hipparion. The tooth is relatively straight. The protocone is elongated. The fossettes are moderately plicated.

Cope, 1886 (in Osborn, 1918, p. 199) presented the following characters for *Hippotherium rectidens*: "(1) Enamel folds similar to

those of the type of *H. peninsulatum* from the same locality; (2) including the subquadrate central loop [protocone], which is nearly cut off from the anterior lake [prefossette], tooth differing from *H. peninsulatum* in its larger size, presenting 6% more area of grinding surface; (3) shaft of tooth straight instead of being strongly curved; (4) crown owing to wear nearly square, while it is oblong in the type of *H. peninsulatum*; (5) two large loops extend inward toward the column instead of one, [*i.e.*, double pli caballin]."

The characters used by Cope (1886) to differentiate between *H. peninsulatum* and *H. rectidens* appear to represent minor variations in dental pattern that are of dubious taxonomic significance.

During the present study, the type specimens of these "species" were examined. In addition to the characters of the dental pattern that Cope recognized, there is a clear distinction in size; *Hippotherium rectidens* is larger than "*Hippotherium*" (=*Nannippus*) *peninsulatum. Hippotherium rectidens* has an elongate protocone, complexity of fossette borders, and overall size that seem to ally this form with a primitive species of *Neohipparion.* However, it is impossible to unambiguously determine from the characters represented in the holotype the exact affinities of this taxon. Therefore, *Hippotherium rectidens* is considered a *nomen dubium.*

Hipparion condoni Merriam, 1915a

TYPE SPECIMEN AND LOCALITY: UO 672, right P_4 and M_1, from the "Ellensberg Formation" of eastern Washington. The exact geographic location and stratigraphic provenance is unknown.

DESCRIPTION AND DISCUSSION: The original concept of *H. condoni* is based solely on the holotype and one other specimen, UO 668, which consists of a fragmentary symphysis and right I_3–I_1 and left I_1 and I_2 (Merriam, 1915a, p. 6, figs. 4, 5).

In the holotype, the paralophids are narrow and transversely elongate and the protostylids are well developed. The ectoflexid is shallow in P_4 and relatively deep in M_1. The pli caballinid is absent. The enamel is not plicated except for one loop on the posterior external margin of the paralophid in P_4.

The species name *H. condoni* has not been widely used in the literature. There are several comparisons to the holotype made by workers studying other species (e.g., Richey, 1948). The only additional material referred to *H.* cf. *condoni* was from the late Clarendonian Black Butte L.F. and early Hemphillian local faunas of the Juntura Basin in eastern Oregon. In this study, Shotwell (1963, p. 59) was keenly aware of the problems of hipparion taxonomy when, in reference to the Black Butte *H. condoni,* he stated that: "A cursory examination of the available material leads the worker to suggest that *Hipparion, Nannippus,* and *Neohipparion* are all present. However, careful study of associated material, which represents different stages of wear, and the comparison of homologous teeth, among the isolated specimens, leads to the conclusion that his material represents a single species of horse." Despite Shotwell's thorough analysis, there are no *differentia* that ally the Black Butte hipparion with the topotypic material of *Hipparion condoni.*

Hipparion condoni has characters that suggest affinities with some species of *Hipparion,* primitive *Neohipparion,* or *Cormohipparion.* However, because of the lack of diagnostic characters, meaningful provenance data, and associated topotypic material, the exact systematic position of *H. condoni* remains enigmatic. It is considered here as a *nomen dubium.*

Hipparion anthonyi Merriam, 1916b

TYPE SPECIMEN AND LOCALITY: UCMP 2235, right P^2, from three-quarters of a mile south of Ironside, Malheur County, eastern Oregon (Merriam, 1916b), early Hemphillian age.

DESCRIPTION AND DISCUSSION: The topotypic material of *H. anthonyi* from UCMP locality 3037 is very fragmentary. It includes the holotype, a right upper cheek tooth fragment, UCMP 22355 (illustrated in Merriam, 1916b, p. 132, fig. 1 and Osborn, 1918, p. 190, fig. 153), a right upper molar, UCMP 124923, and an incisor, UCMP 124924.

In the upper cheek teeth, the pli protoloph, pli protoconule, and pli prefossette consist of multiple loops. In UCMP 124923 the protocone is oval and the pli caballin consists of

three loops. In the lower tooth (the holotype) the ectoflexid is moderate in depth. The pli caballinid consists of three loops. The anterior projection of the paralophid is unexpanded. The anterior and posterior borders of the isthmus and internal border of the hypoconid are richly plicated.

Merriam (1916b) believed that the narrow transverse width and richly plicated enamel borders warranted the establishment of the species *Hipparion anthonyi*. Since the original description of this species, it has been virtually forgotten in the literature. It appears that the characters used by Merriam (1916b) to diagnose *H. anthonyi* represent minor dental variations of extremely doubtful significance. Based on the characters represented in the topotypic material, *H. anthonyi* seems similar to species such as *Cormohipparion sphenodus* or *C. occidentale*. However, there are neither sufficient diagnostic characters nor enough material to discriminate between these choices. Therefore, *Hipparion anthonyi* is here considered a *nomen dubium*.

PHYLOGENETIC INTERRELATIONSHIPS

In this section each genus with its constituent species of New World hipparions recognized above are discussed separately. A cladistic hypothesis is generated first by abstracting derived characters. The relevant character distributions and morphocline polarities for each genus are tabulated (tables 1, 7, 16, 29, 37) and illustrated (figs. 27, 50, 92, 120) above as well as discussed in the text. The second part of this section analyzes previous discussions in the literature of the phylogenetic interrelationships of relevant species (as recognized here) and then concludes with a revised phylogeny (a tree of ancestors and descendants with respect to absolute geological time) based on the systematic and chronological data presented above. A detailed discussion of the temporal and spatial distribution of the New World hipparions is presented in the next section entitled, Biochronology and Paleobiogeography.

Each of the four genera of North American hipparions recognized here are considered to constitute separate and distinct monophyletic taxa based principally on diagnostic configurations of the DPOF (fig. 8). In addition, this character complex is important in the recognition of the monophyly of each of these four groups (i.e., genera) of species: It is asserted here that for each genus, the diagnostic morphological structure of the preorbital region arose only once from a common ancestor.

HIPPARION

CLADISTICS (fig. 146A): As represented by dichotomy 1, all species of the monophyletic genus *Hipparion sensu stricto* are set apart from the merychippine outgroup (as well as all other horse genera) by the shared-derived and diagnostic configuration of the DPOF which is poorly defined anteriorly, is shallower than *Cormohipparion*, and is moderately well defined with a continuous rim posteriorly (fig. 8 et seq.; also see text above). *H. shirleyi*, which clearly displays this diagnostic fossa, is the most primitive sister species within this monophyletic genus. As represented by dichotomy 2, *Hipparion tehonense*, Old World *Hipparion sensu stricto*, and *H. forcei* are set apart from *H. shirleyi* by the shared-derived presence of numerous characters including (figs. 25–27, table 7); increased size, crown height, and hypsodonty, and oval or elongated protocones that essentially lack the anterior spur (particularly in middle to late wear stages).

Although not discussed in detail above, the "Old World *Hipparion sensu stricto*" is tentatively placed at point 3 in figure 146 as an arbitrary taxonomic unit. This taxon should not be interpreted as monophyletic. The detailed interrelationships of point 3 relative to points 2 and 4 must await a thorough analysis of the interrelationships of both the Old World and New World species of *Hipparion sensu stricto*.

As represented by dichotomy 4, *Hipparion forcei* is set apart as the most derived sister species by increased size, probably hypsodonty, and crown height (fig. 25, table 7).

PHYLOGENY (fig. 146B): There have only been a few discussions in the literature of the ancestral-descendant interrelationships of the

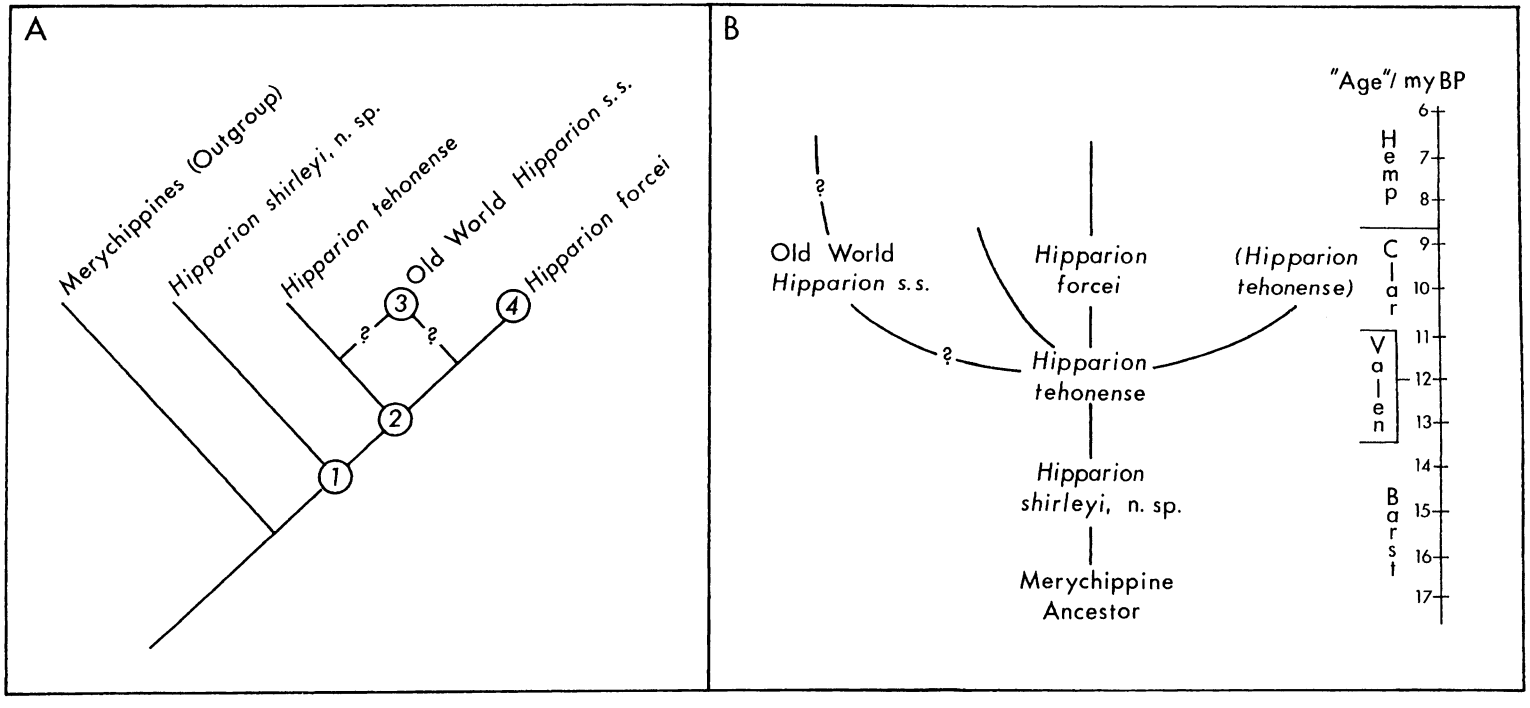

FIG. 146. Phylogenetic interrelationships of *Hipparion sensu stricto* with emphasis on the New World species. A. Cladogram. Shared-derived character states used to corroborate numbered points are as follows (also see fig. 27, table 7): (1) Diagnostic (for genus) configuration of DPOF. (2) Increased size, crown height, and hypsodonty; oval or elongated protocones lacking anterior spur. (3) An arbitrary taxonomic unit included here only to indicate possible phylogenetic position with respect to New World species. (4) Increased size, crown height, and probably hypsodonty. B. One possible phylogenetic tree. Also see discussion in text.

species of North American *Hipparion sensu stricto.* This stems from the fact that until recently, the species of North American *Hipparion sensu stricto* were: (1) considered to be very rare in North America, i.e., limited mostly to the Pacific Coast (e.g., Stirton, 1940), or (2) included in other genera (e.g., "*Nannippus*" *tehonense,* Webb, 1969). MacFadden (1980) identifies numerous occurrences in North America of *Hipparion sensu stricto* and, as did Webb (1969), recognizes an ancestral-descendant sequence between *H.* (or "*N.*") *tehonense* and *H.* (or "*N.*") *forcei.* With the addition of one more species, *H. shirleyi,* new species, the following is a suggested phylogeny for the genus *Hipparion* (fig. 146B): The earliest-known species of North American *Hipparion sensu stricto, H. shirleyi,* new species, arose from a merychippine ancestor (as yet unspecified) before the late Barstovian. Sometime during the late Barstovian or early Clarendonian (Valentinian), *H. shirleyi* gave rise to *H. tehonense. Hipparion forcei* was descended from *H. tehonense* during the Clarendonian. Old World species of *Hipparion sensu stricto* were descended from one or more North American species of this genus, i.e., *H. tehonense* or *H. forcei,* during the Clarendonian (or roughly equivalent Vallesian and early Turolian). So far as is known, the North American species of *Hipparion sensu stricto* became extinct before the end of the Clarendonian except for *H. forcei* which last occurs in early Hemphillian deposits (see, e.g., fig. 45). The paleobiogeographic consequences of the phylogenetic interrelationships of Old World and North American species of *Hipparion sensu stricto* will also be discussed below.

NEOHIPPARION

CLADISTICS (fig. 147A): As represented by dichotomy 1, all species of the monophyletic genus *Neohipparion* are set apart from the merychippine outgroup (as well as other hipparions) by the shared-derived and diagnostic configuration of a relatively poorly defined DPOF, which is described in detail above (fig. 8 et seq.; also see text). In addition, all species of *Neohipparion,* including the most primitive *N. coloradense,* are set apart from merychippines by increased size, crown height, hypsodonty, and relatively elongated protocones.

As represented by dichotomy 2, the sister species *N. affine, N. trampasense, N. leptode, N. eurystyle,* and *N. gidleyi* are set apart from *N. coloradense* by the shared-derived characters including a less well-developed DPOF, more hyposodont dentition, shallower ectoflexids, and better-developed pli caballinids (particularly in the premolars). As represented by point 3, *N. affine* is considered to have an autapomorphic (unique-derived) character state represented by a major size increase (figs. 48–50, table 16).

As represented by dichotomy 4, *N. trampasense, N. leptode, N. eurystyle* and *N. gidleyi* are set apart from their more primitive sister species particularly by shared-derived character states of the lower cheek tooth dentition, e.g., the shallow ectoflexids and better-developed pli caballinids in the premolars (fig. 50). In addition, the enamel plications and expansion of the conids and stylids are probably shared-developed character states for most of these species. As represented by point 5, although *N. leptode* is derived relative to *N. coloradense* and *N. affine,* the exact phylogenetic affinities of this species with respect to those united at dichotomy 4 are indeterminate: It is not clear whether *N. leptode* is more closely related to either *N. trampasense* on the one hand or *N. eurystyle* and *N. gidleyi* on the other hand. It also should be noted that in this cladistic hypothesis, *N. leptode* exhibits the autapomorphic character state of relatively large size.

As represented by point 6, *Neohipparion eurystyle* and *N. gidleyi* are set apart from the other species of this genus by the following derived character states: (1) in the upper cheek teeth, increased crown height and hypsodonty, greatly elongated protocones oftentimes with angular borders, expanded and flattened parastyles and mesostyles; and (2) in the entire lower cheek tooth row (i.e., both premolars and molars), very shallow ectoflexids, very well developed pli caballinids, well-developed plications on the isthmuses, and very expanded metaconids, metastylids, entoconids, and hypoconulids oftentimes with angular borders. *N. gidleyi* (point 7) is further set apart as the most derived species of the genus by a significant increase in size relative

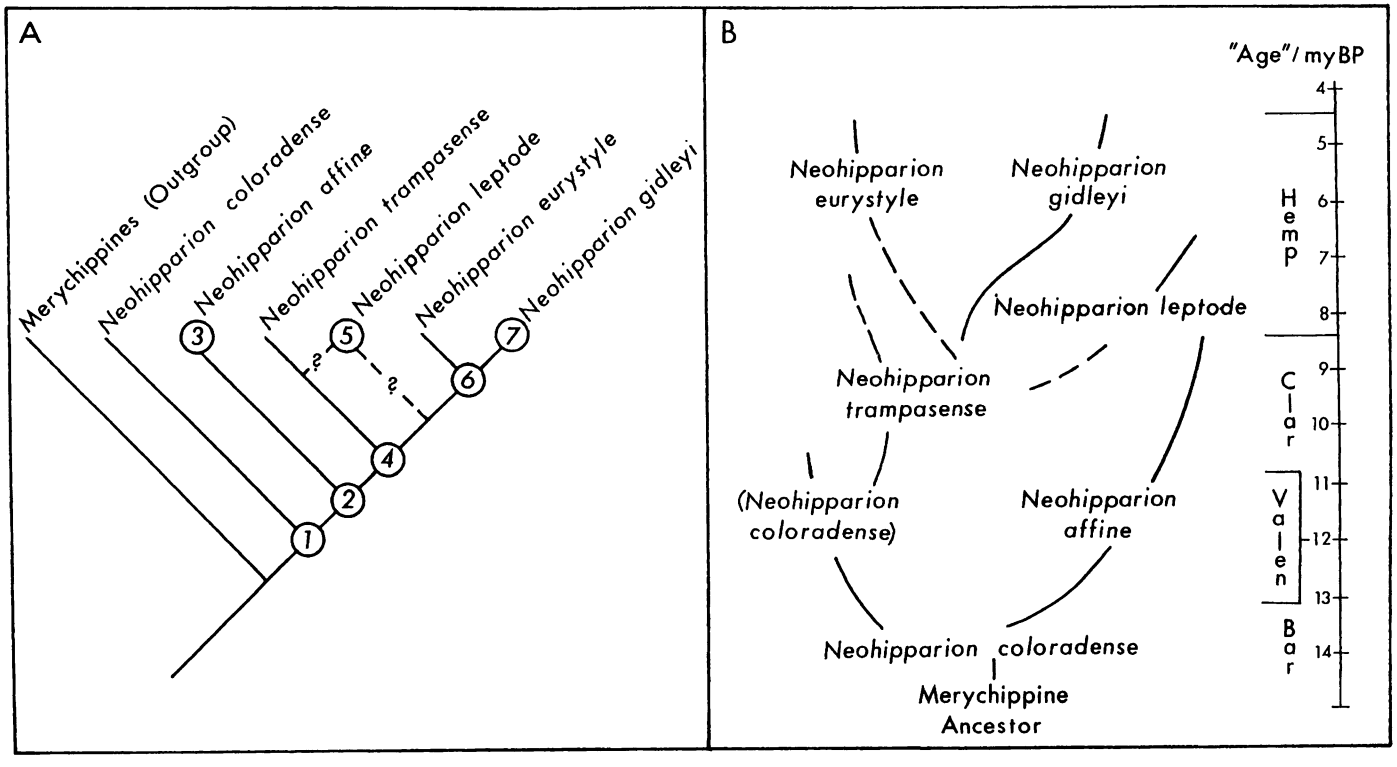

FIG. 147. Phylogenetic interrelationships of *Neohipparion*. A. Cladogram. Shared-derived character states used to corroborate numbered points are as follows (also see fig. 50, table 16): (1) Diagnostic (for genus) DPOF poorly developed, reduced, or absent; increased size, crown height, and hypsodonty; relatively elongated protocones. (2) Less well-developed DPOF; shallower ectoflexids and better developed pli caballinids (particularly in premolars). (3) Significant increase in size (autapomorphy). (4) Virtual absence of DPOF; relatively elongated protocones; in premolars, very shallow ectoflexids, well-developed pli caballinids and plications on isthmuses, and very expanded metaconids, metastylids, entoconids, and hypoconulids oftentimes with angular borders. (5) Increased size relative to *N. coloradense* and *N. trampasense* (autapomorphy). (6) Increased crown height and hypsodonty, very elongated protocones often with angular borders, expanded and flattened parastyles and mesostyles, complex enamel plications; in both premolars and molars, shallow ectoflexids, well-developed pli caballinids, expanded metaconids, metastylids, entoconids and hypoconulids; and plications on isthmuses. (7) Increased size (autapomorphy). B. One possible phylogenetic tree. Also see discussion in text.

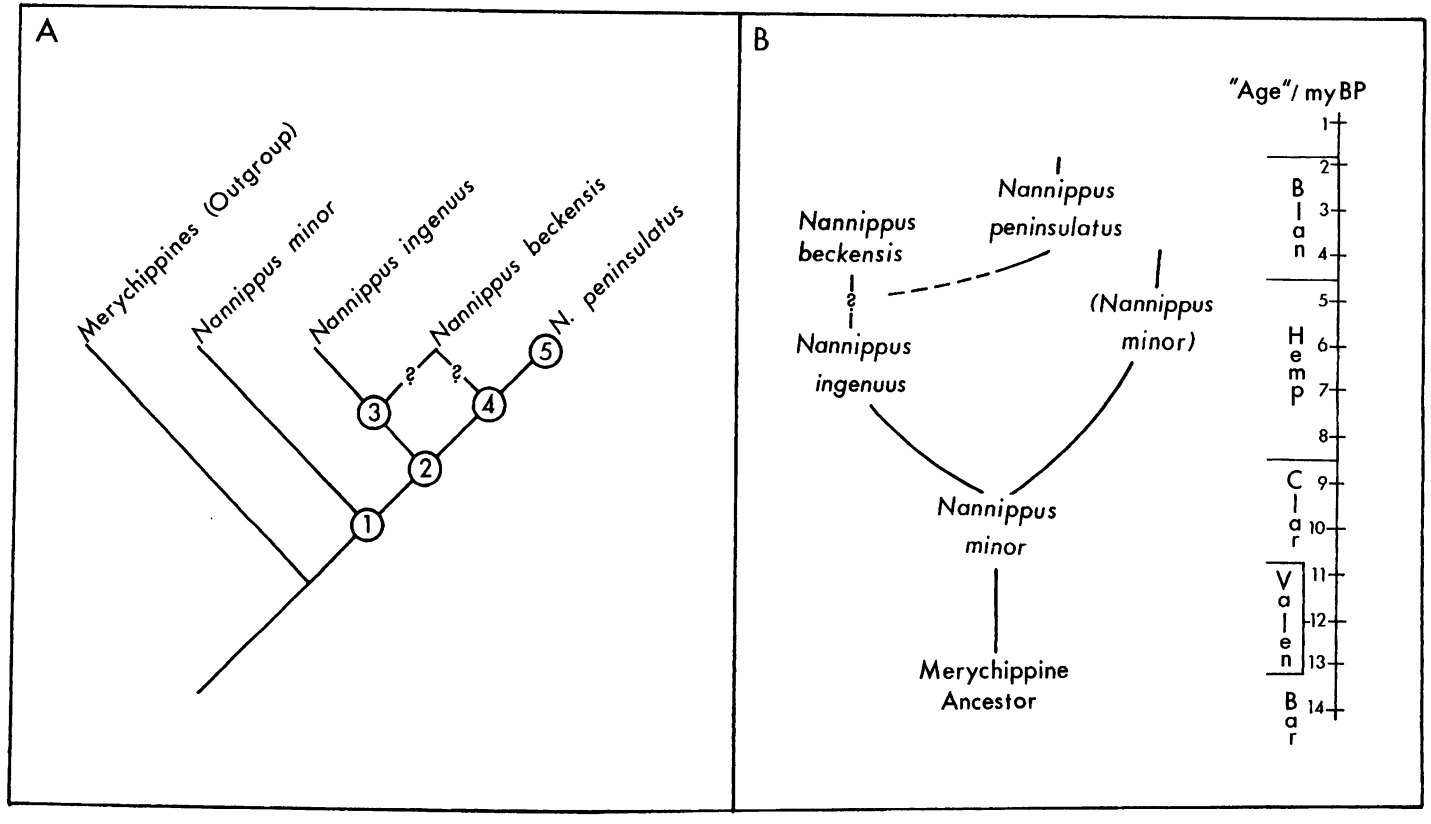

FIG. 148. Phylogenetic interrelationships of *Nannippus*. A. Cladogram. Shared-derived character states used to corroborate numbered points are as follows (also see fig. 92, table 29): (1) So far as known, DPOF reduced or absent; elongated rostrum and postcanine diastema; possibly small size; reduced anterostyles; increased crown height; relative size and shape of isolated protocones; reduced paraconids, development of protostylids, pli caballinids, and ectoflexids. Also possibly reduction and loss of trapezium and rudimentary MC V. (2) Increased crown height and hypsodonty; reduction in protostylids, increased size of metapodials. (3) If increase in size is considered derived for *Nannippus*, then the species *N. ingenuus* and *N. beckensis* are united at point 3. Otherwise, this point is uncorroborated. (4) Preferred hypothesis (instead of point 3); further reduction of protostylids and possibly better developed styles. (5) Longest crowns, virtual or complete absence of protostylids, very elongated metapodials. B. One possible phylogenetic tree. Also see discussion in text.

to *N. eurystyle* (figs. 48, 49). In addition, *N. eurystyle* seems advanced over most of the other more primitive species of *Neohipparion* (except perhaps *N. trampasense*) in that the former species almost completely lacks any DPOF. With regard to *N. gidleyi,* there are no specimens that preserve the facial region. However, if one were found, it is predicted that the DPOF would be similar to that of *N. eurystyle.*

PHYLOGENY (fig. 147B): *Neohipparion* was originally described (Gidley, 1903) to include most of the large species of North American hipparions that had formerly been included in either *Hippotherium* or *Hipparion sensu stricto.* Osborn (1918) did not recognize the existence of *Neohipparion* and included all North American species that usually have been associated with that genus in *Hipparion.* In the most complete phylogenetic discussion of *Neohipparion,* Stirton (1940, pp. 182–183; also see chart at end) suggests that many of the (stratigraphically) older species names are probably synonymous and illustrates an ancestral-descendant sequence of species that proceeds from *N. coloradense* to *N. occidentale* to *N. eurystyle* to *N. leptode* to *N. gidleyi.* Based on the present report, and in contrast to Stirton's phylogeny of *Neohipparion, N. occidentale* is transferred to the genus *Cormohipparion* and *N. eurystyle* is considered to be more derived than *N. leptode.* With regard to species named after Stirton's (1940) report, *N. eurystyle* is considered here the senior synonym of the many late Hemphillian species names (see Systematics above). Following the discussions of numerous workers (e.g., Matthew, 1924; Stirton, 1940; Gregory, 1942; Webb, 1969) and the present study, *N. affine* is considered the senior synonym of *N. whitneyi* and *N. dolichops.* Based on the present study, Edward's (1982) "*Hipparion*" *trampasense* is here considered a species of *Neohipparion.*

The following is suggested as one possible phylogeny for the species of *Neohipparion* based on the revisions presented in this report: The earliest-known species of *Neohipparion, N. coloradense,* arose from a merychippine ancestor (as yet unspecified) during the early Barstovian. *N. affine* was descended from *N. coloradense* during the late Barstovian (or Valentinian). *N. trampasense* was descended from *N. coloradense* during the Clarendonian. The exact origins of *N. leptode* are uncertain; it could have been descended from *N. trampasense* during the Clarendonian. So far as is known, *N. coloradense* and *N. affine* became extinct by the end of the Clarendonian. During the early Hemphillian, either *N. trampasense* or *N. leptode* gave rise to *N. gidleyi* and *N. eurystyle.* As is presently recognized, the species of *Neohipparion* do not seem to have given rise to any known Old World hipparions (although see discussion of Zhegallo, 1978 below). So far as is known, *N. trampasense, N. leptode, N. gidleyi,* and *N. eurystyle* all became extinct by the end of the Hemphillian.

NANNIPPUS

CLADISTICS (fig. 148A): As represented by dichotomy 1, the genus *Nannippus* is set apart from merychippines by the derived character states including: elongated rostrum and postcanine diastema, reduced anterostyles and paraconids, increased crown height, relative size and shape of protocones, development of the protostylids (in primitive species), and usually moderately developed pli caballinids and ectoflexids (also see figs. 90–92, table 29). By inference from what is known of *N. minor* and *N. peninsulatus, Nannippus* is probably also derived in the loss of the trapezium and rudimentary MC V (e.g., Matthew, 1926; Sondaar, 1969; see discussion above). Also by inference from what is known of *N. ingenuus, N. beckensis,* and *N. peninsulatus,* and in contrast to merychippines, *Nannippus* lacks the well-developed DPOF.

The polarities of several of the size-related characters for the species of *Nannippus* (e.g., overall size and upper cheek tooth row length) are not congruent with the absolute crown height and characters of the dental pattern, i.e., relative development of the protocones or protostylids (figs. 90–92, table 29). The size-related character complex (not including absolute crown height) is not used in the present cladistic analysis to interrelate the species of *Nannippus.*

Within the genus *Nannippus, N. minor* is the most primitive sister species. It possesses the derived characters diagnostic of the genus listed above. As represented by dichotomy 2,

N. ingenuus, N. beckensis and *N. peninsulatus* are set apart from *N. minor* by the shared-derived characters including increased size and crown height, and relative elongation of the metapodials (as represented by MC III and MT III).

Relative to outgroup comparisons, the small size of *N. minor* could be considered as either the primitive or derived character state, although within the genus *Nannippus* it seems derived. If size related characters had been chosen in this analysis as an indication of relative relatedness, then, depending on the outgroup comparison and as questionably represented by dichotomy 2, *N. ingenuus, N. beckensis* and *N. peninsulatus* could possibly show the derived character complex of increase in size relative to *N. minor.*

As represented by dichotomy 4, *N. beckensis* and *N. peninsulatus* are set apart from the more primitive species of *Nannippus* by the further reduction in the protostylid (relative to *N. ingenuus*) and, if Dalquest and Donovan (1973) are correct, better developed styles in the upper cheek teeth (see discussion of this character above). However, if these characters cited by Dalquest and Donovan (1973) are not valid in species recognition, then an unresolved trichotomy exists for *N. ingenuus, N. beckensis* and *N. peninsulatus* (and hence the questionable linkage between points 3 and 4 for *N. beckensis* in fig. 148A). As represented by point 5, *N. peninsulatus* is set apart as the most advanced species of the genus by the presence of the following derived character states; largest crowns, absence of protostylids, and very elongated metapodials (as represented by MC III and MT III).

PHYLOGENY (fig. 148B): There have been numerous discussions in the literature of the ancestral-descendant sequence of species within the genus *Nannippus.* Stirton (1940, see chart at end) depicts a direct sequence within this genus from *N. retrusus* to *N. gratus* to *N. lenticularis* to *N. phlegon.* Webb (1969) suggests a branching phylogeny for *Nannippus.* His ancestral species *N. tehonensis* gave rise to *N. forcei, N. ingenuus,* and *N. lenticularis. Nannippus ingenuus* then gives rise to both *N. minor* and *N. phlegon.* Stirton's (1940) *N. retrusus* and *N. gratus* are considered here to be only distantly related to the genus *Nannippus*; many subsequent workers (e.g., Webb, 1969) have placed these two species in *Pseudhipparion.* Based on the present study, Webb's (1969) *N. tehonensis* and *N. forcei* are transferred to *Hipparion sensu stricto, N. lenticularis* and *N. phlegon* are considered junior synonyms, respectively, of *N. ingenuus* and *N. peninsulatus,* and *N. montezumae* is considered a *nomen dubium.*

The following phylogeny is suggested for the genus *Nannippus*: *Nannippus minor* arose from some merychippine ancestor (as yet unspecified) before the late Clarendonian. During the late Clarendonian or early Hemphillian, *N. minor* gave rise to *N. ingenuus. Nannippus beckensis* arose from *N. ingenuus* during the latest Hemphillian or early Blancan. *N. peninsulatus* arose from either *N. ingenuus* or *N. beckensis* before the early Blancan. *Nannippus ingenuus* and *N. minor* became extinct at the end of the Hemphillian. So far as is known, *N. beckensis* and *N. peninsulatus* became extinct before the end of the Blancan (also see discussion in section below entitled Biochronology and Paleobiogeography).

CORMOHIPPARION

CLADISTICS (fig. 149A): As represented by dichotomy 1, all species and descendants (i.e., some Old World forms) of the monophyletic genus *Cormohipparion* are set apart from the merychippine outgroup by the shared-derived and diagnostic configuration of the DPOF, which has well-developed and continuous anterior and posterior rims and is moderately to deeply pocketed (fig. 8 et seq; also see text above). *Cormohipparion goorisi* is the most primitive sister species within the genus. It possesses the diagnostic DPOF; however (like *H. shirleyi*), it has few, if any, advanced dental character states relative to merychippines (figs. 118–120, table 37). As represented by point 2, the very deep posterior pocket may be interpreted as an autapomorphic character state relative to *C. sphenodus* and *C. occidentale.* The taxa represented by point 3 are set apart from *C. goorisi* by the following derived character states: increased size, hypsodonty, and crown height (figs. 118, 119); protocone usually oval

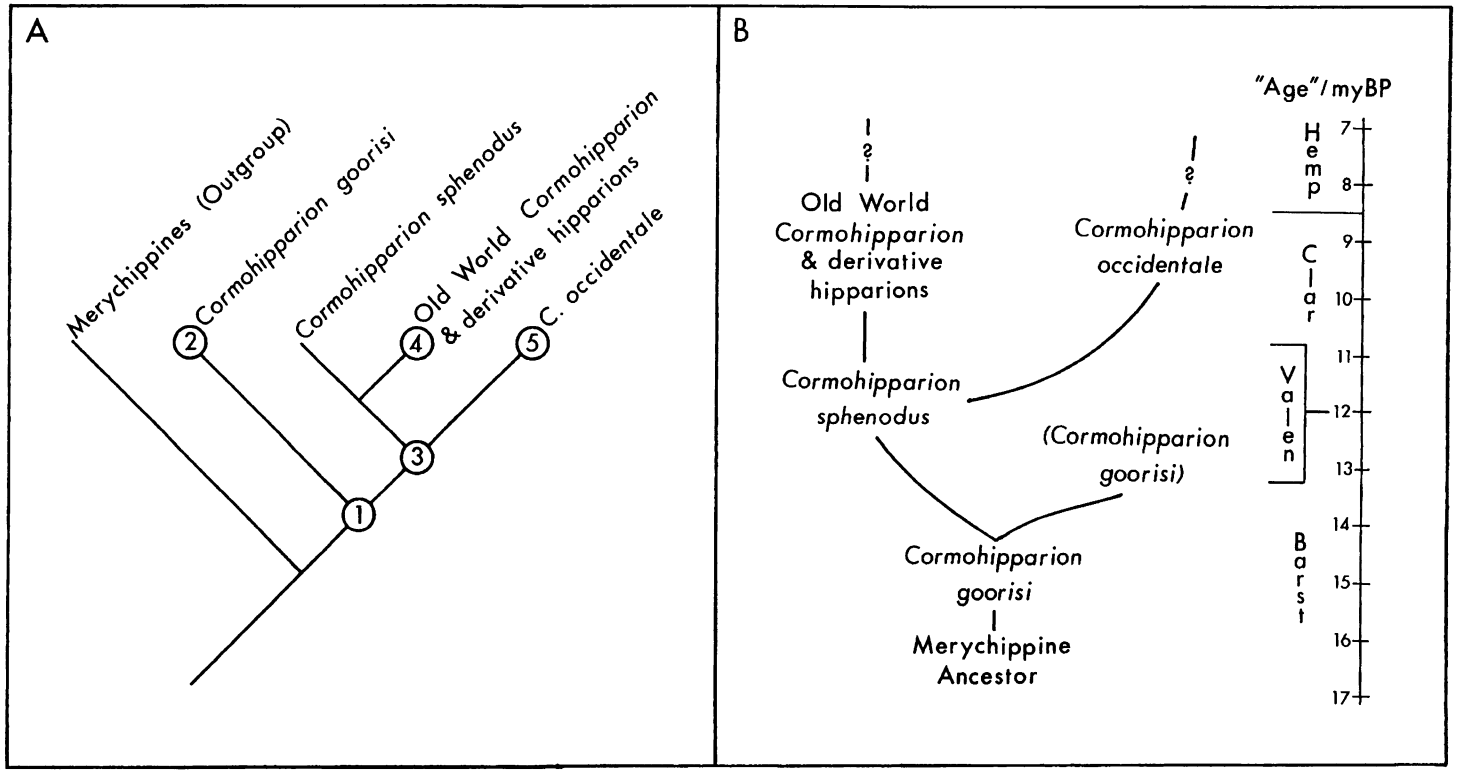

FIG. 149. Phylogenetic interrelationships of *Cormohipparion* with emphasis on the New World species. A. Cladogram. Shared-derived character states used to corroborate numbered points are (also see fig. 120, table 37): (1) Diagnostic (for genus) configuration of DPOF. (2) Very deep posterior pocket of DPOF (possible autapomorphy). (3) Increased size, hypsodonty, and crown height; oval protocones lacking prominent anterior spur; usually more complex enamel plications; better developed protostylids; ectoflexids shallower and pli caballinids slightly better developed (particularly in premolars); metaconids, metastylids, entoconids, and hypoconulids distinct and more expanded. (4) Arbitrary taxonomic unit included here only to indicate possible phylogenetic position with respect to New World species. (5) In contrast to *C. goorisi* and *C. sphenodus,* increase in size, crown height, and hypsodonty; very elongated protocones with angular borders; very elongated and expanded metaconids, metastylids, entoconids, and hypoconulids. B. One possible phylogenetic tree. Also see discussion in text.

without the prominent, persistent, anterior spur; enamel plications usually more complex; protostylids better developed; ectoflexids shallower and pli caballinids slightly better developed (particularly in premolars); and metaconids, metastylids, entoconids, and hypoconulids distinct and more expanded. Point 4, represented by the arbitrary taxonomic unit "Old World *Cormohipparion* and derivative hipparions" is placed here in order to indicate its phylogenetic position and the holophyly of the genus. Woodburne, MacFadden, and Skinner (1981) noted that *C. sphenodus* seems to be the closest sister species of many Old World Vallesian and later hipparions. As is also the case for Old World *Hipparion sensu stricto* discussed above, the arbitrary taxonomic unit represented at point 4 serves to indicate the position of certain Old World hipparions with respect to the species of *Cormohipparion.* However, the detailed interrelationships of Old World *Cormohipparion* and derivative hipparions is beyond the scope of the present paper and therefore will not be discussed here.

As represented by point 5, *C. occidentale* is set apart as the most derived species of the genus based on the following character states: In contrast to *C. goorisi* and *C. sphenodus, C. occidentale* is much larger in size, crown height, and hypsodonty (figs. 118, 119), and this species has very complex enamel plications (particularly on the fossette borders) and very elongated and expanded metaconids, metastylids, entoconids, and hypoconulids (fig. 120, table 37). In contrast to all other taxa within the monophyletic genus (i.e., the New World and Old World representatives) *C. occidentale* has very elongated protocones frequently with angular borders. (Some of the character states listed above that differentiate *C. occidentale* from *C. goorisi* and *C. sphenodus* may also, after further study, differentiate the former species from Old World *Cormohipparion* and derivative hipparions.)

PHYLOGENY (fig. 149B): The interrelationships of the three North American species of *Cormohipparion* have only recently been discussed in the literature because: (1) two of the constituent species have previously been included in other genera, usually as *Merychippus sphenodus* and *Hipparion* or *Neohipparion occidentale,* and the third, *C. goorisi,* was only recently named (MacFadden and Skinner, 1981); and (2) the genus itself is relatively new (Skinner and MacFadden, 1977). Based on the present revision (also see MacFadden and Skinner, 1981; Woodburne, MacFadden, and Skinner, 1981), one possible phylogeny for *Cormohipparion* is suggested as follows:

Cormohipparion goorisi arose from some merychippine species (as yet unspecified) probably during the early Barstovian (i.e., before the first-known occurrence of this species at *ca.* 15 myBP). *Cormohipparion goorisi* gave rise to *C. sphenodus* during the Barstovian (or roughly equivalent very early Valentinian). So far as is known, *C. goorisi* became extinct by the end of the Barstovian. *Cormohipparion sphenodus* probably gave rise to both Old World *Cormohipparion* and derivative hipparions as well as *C. occidentale* during the early Clarendonian (late Valentinian). So far as is known, *C. sphenodus* and *C. occidentale* became extinct by, respectively, the late Clarendonian and probably the "medial" Hemphillian (also see next section).

BIOCHRONOLOGY AND PALEOBIOGEOGRAPHY

In the New World, hipparionine horses have been recovered from early Barstovian to late Blancan deposits, i.e., from about 15½ to about 2 myBP. The concurrent range zonation of the relevant species, which will be central to this discussion, is presented in figure 150.

During the early Barstovian, about 15½ to 15 myBP, the earliest-known Holarctic hipparions are represented by *Cormohipparion goorisi* from the Fleming Formation of the Texas Gulf Coastal Plain and *Neohipparion coloradense* from the Great Plains (also see MacFadden and Skinner, 1977, 1981). These

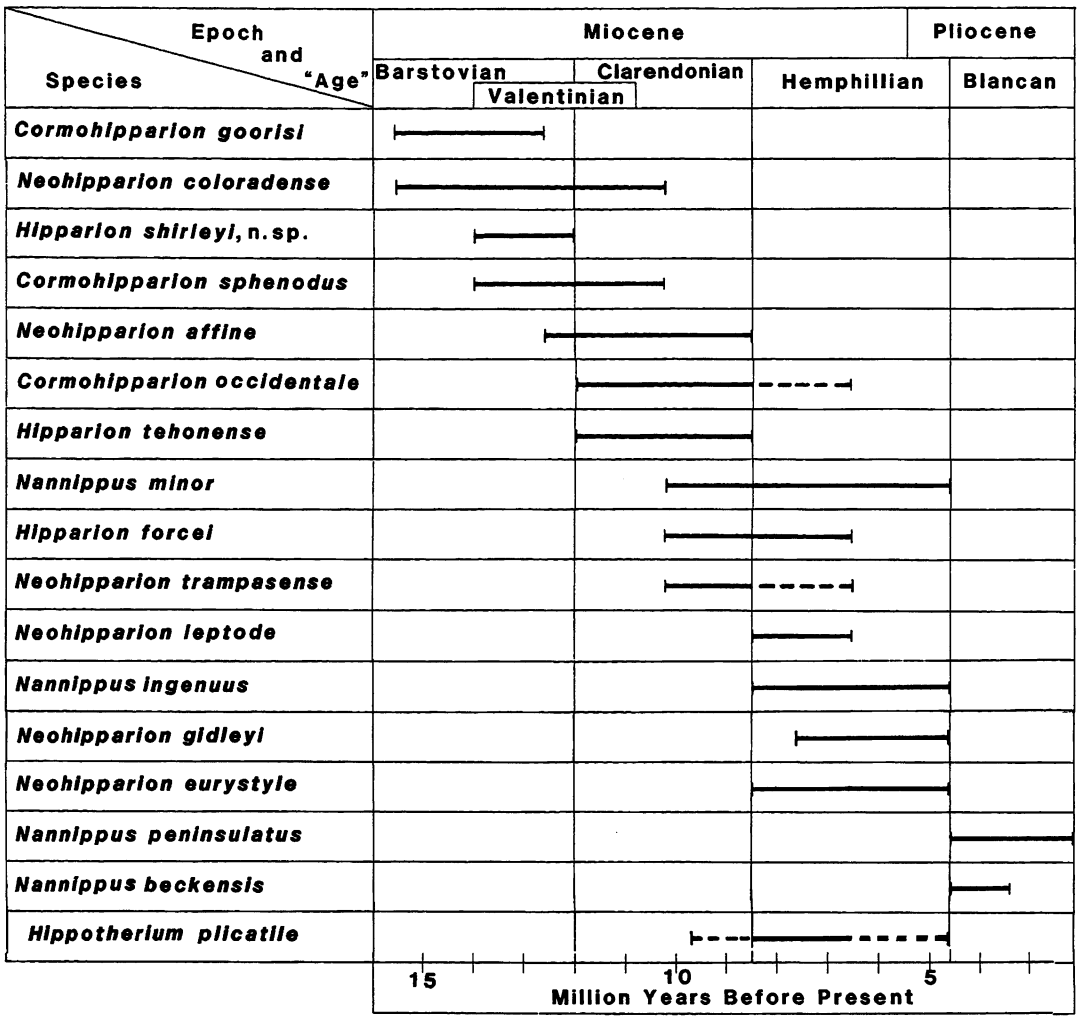

FIG. 150. Biochronological distribution of the New World species of *Hipparion sensu stricto, Neohipparion, Nannippus,* and *Cormohipparion.*

occurrences are significantly older than the first record of hipparions in the Old World at about 11 to 12 myBP. As has also been noted previously in the literature, with respect to species such as *C. goorisi,* the current interpretation of the so-called "Hipparion Datum" is polyphyletic and certainly diachronous (e.g., MacFadden and Skinner, 1977, 1981; Skinner and MacFadden, 1977; Woodburne, MacFadden, and Skinner, 1981; MacFadden and Woodburne, 1982). During the late Barstovian, at least two hipparions are probably represented in the Texas Gulf Coastal Plain (i.e., *C. goorisi* and *Hipparion shirleyi,* new species). It is difficult to determine if *C. goorisi* and *H. shirleyi* were actually restricted to the Texas Gulf Coastal Plain because recognition of these primitive species is difficult without well-preserved facial regions.

Also during the late Barstovian (or early Valentinian) three hipparions are represented at midcontinental sites: *N. coloradense, N. affine,* and *C. sphenodus.* During the early Clarendonian, hipparion diversity apparently increases with several new species that appear in the Gulf Coastal, midcontinental, and, for the first time (so far as is known), the

Pacific regions. *Cormohipparion occidentale* is first known from Burge Quarry, Lapara Creek, and equivalents. This species is common in post-Valentinian (late early Clarendonian) age deposits of the Great Plains. *Hipparion tehonense* appears to have been relatively widespread with numerous occurrences in the Great Plains and California. In addition to the first-known appearances of these new species, *Cormohipparion sphenodus* persists into the early Clarendonian as represented by occurrences in the Great Plains and Tesuque Formation of north-central New Mexico. So far as is known, both *N. coloradense* and *C. sphenodus* became extinct by the end of the early Clarendonian.

The height of hipparion diversity in North America occurred during the late Miocene, some 10 to 8 myBP. During the late Clarendonian, all four genera are represented by the following species: *Hipparion tehonense, H. forcei, Cormohipparion occidentale, Neohipparion affine, N. trampasense,* and *Nannippus minor.* In addition, "*Hippotherium*" *plicatile* may also be represented in Florida during the late Clarendonian. In general, during the late Clarendonian, the Pacific Coast region can be characterized by a predominance of the genus *Hipparion sensu stricto.* In the southeast, as exemplified by the Love Bone Bed L.F. of north-central Florida (Webb, MacFadden, and Baskin, 1981), *Neohipparion* (*N. trampasense*) and "*Hippotherium*" *plicatile* are common, whereas *Nannippus* and *Hipparion* are relatively rare. So far as is known, *Cormohipparion* was probably rare in Florida and the Texas Gulf Coastal Plain. During the late Clarendonian, the midcontinental sites are commonly represented by species of *Cormohipparion, Neohipparion,* and *Hipparion,* whereas *Nannippus* (*N. minor*) is very rare or absent.

As is also the case for other mammals of the "Clarendonian chronofauna," during the early Hemphillian hipparions were relatively diverse and known from throughout much of North America. This hipparion diversity is represented by *H. forcei, N. leptode, N. minor,* possibly *C. occidentale* (see discussion in systematics section above), and the probable first occurrence of *N. gidleyi* and *N. ingenuus.* Hipparions played a fundamental role as some of the dominant ungulates during the height of the Clarendonian chronofauna, which was a time of a diverse savanna community comparable to that of Africa today (Webb, 1977).

The hipparions of the Clarendonian chronofauna in North America are also relevant to an understanding of the origins of related forms in the Old World. Based on the phylogenetic analysis presented above, it appears that Old World hipparions were descended from species of two different genera of North American hipparions (i.e., *Hipparion sensu stricto* and *Cormohipparion*). Woodburne, MacFadden, and Skinner (1981) state that *Cormohipparion*-like species are dominant in the Vallesian and that the closest New World relative is *C. sphenodus.* Therefore, the so-called Hipparion Datum that defines the base of the Vallesian at about 12 to 11 myBP probably resulted from an immigrant species of *Cormohipparion. Hipparion sensu stricto* is unknown during the Vallesian and does not become common until the earliest Turolian (about 8 to 9 myBP). After this time, *Hipparion sensu stricto* is commonly represented in the Old World until the late Miocene. It appears that the presence of *Hipparion sensu stricto* in the Old World is a result of a second dispersal wave. (Although for a contrasting point of view, see Bernor, Woodburne, and Van Couvering, 1980.) Therefore, in contrast to the hypothesis of some workers (e.g., Forstén, 1968), Old World hipparions represent a distinctly polyphyletic assemblage resulting from more than one immigration event that occurred at different times during the late Neogene.

In an interesting report, Zhegallo (1978) presents a description of hipparions from central Asia. Although the exact interrelationships of the taxa represented in his report still need further comparisons with other Holarctic hipparions, some of Zhegallo's concepts have potentially important paleobiogeographic implications. Of particular relevance here, the extremely large late Neogene species "*Hipparion houfenense,*" which has previously been described from roughly coeval deposits in China (Teilhard and Young, 1931, also see fig. 151 for a well-preserved individual referable to this same species in the Frick Collection), is referred to the "subgenus" *Neohipparion.* Moreover, as depicted

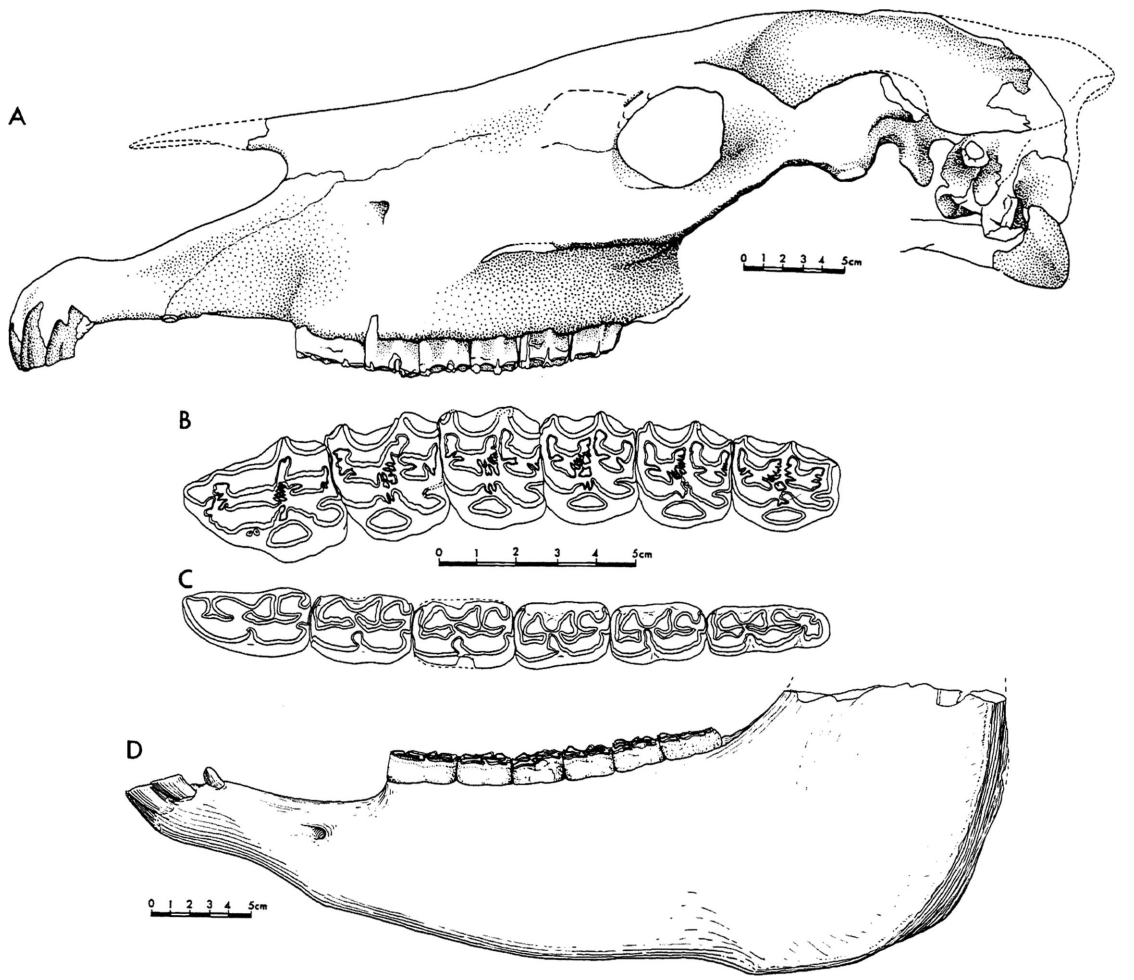

FIG. 151. "*Neohipparion*" *houfenense*, F:AM 111820, from Hsi Chwang, Ruscinian or Villafranchian of east Shansi, People's Republic of China. A. Left lateral view of skull. B. Occlusal view of left upper cheek teeth, P^2–M^3. C. Occlusal view of left lower cheek teeth, P_2–M_3. D. Lateral view of left ramus.

in Zhegallo (1978, fig. 79), it is suggested that "*Hipparion* (*Neohipparion*)" *houfenense* was derived from an immigrant species of *Neohipparion* that dispersed into the Old World about 6 myBP. It is indeed true that "*H.* (*N.*)" *houfenense* does share some morphological similarities with New World *Neohipparion,* including large size, lack of a DPOF, and very elongated protocones. However, it is also possible that these characters were developed independently in Old World Plio-Pleistocene hipparions (also see, e.g., Eisenmann, 1977, for a description of a similar morphology represented in African hipparions) from the North American radiation of *Neohipparion.* Nevertheless, until further comparisons can be made with relevant specimens, Zhegallo's (1978) suggestion of a close link between "*Hipparion* (*N.*)" *houfenense* and New World *Neohipparion* is an intriguing idea. If this hypothesis is corroborated in the future, it would further support the concept of multiple dispersal and entry of hipparions into the Old World.

Returning to North America, during the "medial" Hemphillian, about 7 to 6 myBP, there was a dramatic drop in hipparion diversity (fig. 150). During the late Hemphill-

ian, two hipparion genera, *Neohipparion* and *Nannippus,* are represented by the hypsodont species *Neohipparion gidleyi, Neohipparion eurystyle, Nannippus minor,* and *Nannippus ingenuus.* These Hemphillian hipparions were relatively widespread in Central America and North America. At the end of the Hemphillian, so far as is known, there was another drop in hipparion diversity with the extinction of *Neohipparion.* During the Blancan only the genus *Nannippus* is represented in North America by *N. beckensis* and *N. peninsulatus. Nannippus peninsulatus* was widespread in Neotropica during the Blancan with numerous occurrences reported in Central America and southern North America, but it was apparently rare or absent in northern North America.

It seems that the drop in diversity of North American hipparions is possibly related to the demise of the Clarendonian chronofauna. Possible explanations for this corresponding demise of North American hipparions during the late Miocene could include: (1) A change in climate which adversely affected ungulate diversity (Webb, 1977). (2) The advent of relatively hypsodont ungulates including the "pliohippine" (*sensu lato*) horses and advanced artiodactyls. It is reasonable to speculate that, if the second explanation cited here is valid, then the successful and cosmopolitan nature of advanced *Nannippus* species is related to the fact that they were highly cursorial and very hypsodont.

In summary, *Hipparion sensu stricto, Neohipparion, Nannippus,* and *Cormohipparion* constitute a polyphyletic assemblage of hypsodont and tridactyl horses that apparently arose from two or more distinct lineages within the merychippine complex. These "hipparions" were widespread in the New World during the Miocene and Pliocene. The oldest-known hipparion, *C. goorisi,* comes from about 15½ to 15 myBP sediments of the Texas Gulf Coastal Plain. There seems to have been at least two dispersals of different hipparion genera into the Old World. The earlier event, which defines the base of the Vallesian, involved *Cormohipparion*-like forms and the later one, which probably occurred some time during the latest Vallesian or earliest Turolian, involved *Hipparion sensu stricto.* There also could have been additional dispersals between the Old World and New World; however, these remain to be identified. In North America, the height of hipparion diversity occurred during the Clarendonian chronofauna. The last-known hipparion in the New World, *Nannipus peninsulatus,* became extinct about 2 myBP at the end of the Blancan.

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