CORMOHIPPARION AND *HIPPARION* (MAMMALIA, PERISSODACTYLA, EQUIDAE) FROM THE LATE NEOGENE OF FLORIDA

Richard C. Hulbert, Jr.

This public document was promulgated at an annual cost of $3626.50 or $3.627 per copy. It makes available to libraries, scholars, and all interested persons the results of researches in the natural sciences, emphasizing the circum-Caribbean region.

Publication date: October 20, 1988   Price: $3.75

CORMOHIPPARION AND HIPPARION (MAMMALIA, PERISSODACTYLA, EQUIDAE) FROM THE LATE NEOGENE OF FLORIDA

Richard C. Hulbert, Jr.*

ABSTRACT

Five species of *Cormohipparion* are recognized from the late middle Miocene to late Pliocene (late Barstovian through Blancan) of Florida. A small sample of isolated teeth collected from a late Barstovian horizon of the lower Bone Valley Formation, south-central Florida, represents *Cormohipparion* sp., cf. *C. sphenodus*. In the Clarendonian, a larger species of *Cormohipparion*, cf. *C. occidentale*, is represented by three isolated teeth, also from an older horizon of the Bone Valley Formation. The very late Clarendonian Love Site produced numerous dentitions of two species of *Cormohipparion*, one small-sized and one medium-sized, here referred to *C. ingenuum* and *C. plicatile*, respectively. The completeness of the referred material allows for new phylogenetic interpretations concerning these previously poorly known species described by Joseph Leidy over a century ago on isolated teeth. The first appearance of *C. ingenuum* was in the early Clarendonian of Texas and Florida, and it persisted in Florida until the late early Hemphillian, a duration of about five million years. It is also recorded from the early Hemphillian Gracias Fauna of Honduras. *C. ingenuum* is not the senior synonym of *Nannippus lenticularis* (Cope), as proposed by some authors, as the two share few characters but size. *C. plicatile* is limited to the late Clarendonian-early Hemphillian of Florida, but is usually the more common of the two at sites where both occur. The range of *C. emsliei* is extended to the early Hemphillian (ca. 7 Ma), based on its presence at the Moss Acres Racetrack Site. It persisted through the Blancan (to about 2.0 Ma), and is the youngest known representative of the genus in North America. These three species form a monophyletic group, *Cormohipparion (Notiocradohipparion)* n. subgen., united by their relatively very elongated muzzles. This clade was apparently limited to the Gulf Coastal Plain and Central America. Three major trends observed in Florida *Cormohipparion* over this ten million year period are increasing hypsodonty, increasing enamel complexity (in fossette plications, pli caballins, styles, and pli caballinids), and decreasing depth of the dorsal preorbital fossa.

Hipparion is rarely recorded from the late Miocene of Florida. Referable samples include those from the lower Bone Valley Formation (?Clarendonian), the Love Site, the Moss Acres Racetrack Site, and the Withlacoochee River 4A local fauna (late early Hemphillian). The latter two are among the youngest records of *Hipparion* from North America. They are all tentatively referred to the medium-sized species, *Hipparion tehonense*.

* The author is a Postdoctoral Research Fellow at the Florida State Museum, University of Florida, Gainesville FL 32611.

Cladistic analysis based on 58 dental and cranial characters suggests the following phylogenetic hypotheses: (1) the Tribe Hipparionini is monophyletic and contains a minimum of six North American genera and several species of uncertain generic affiliation; (2) *Hipparion*, *Merychippus* s.s., *Nannippus*, *Cormohipparion*, and Old World hipparionines form one monophyletic clade, the *Hipparion*-genus group; (3) *Neohipparion*, *Pseudhipparion*, and *"Merychippus" coloradense* form a second clade, the *Neohipparion*-genus group, which is the sister taxon of the *Hipparion*-genus group; (4) *"Merychippus" goorisi* (MacFadden and Skinner) is the sister taxon to *Nannippus* + *Cormohipparion*, but its uniquely derived facial region prevents it from being ancestral to either genus; and (5) *Cormohipparion* from Florida (*Notiocradohipparion*) is the sister taxon to *C. occidentale* + Old World *"Cormohipparion"* (i.e. Group 1 hipparionines).

RESUMEN

Se reconocen cinco especies de *Cormohipparion* del Mioceno medio tardío al Plioceno tardío (Barstoviano tardío al Blancano) de Florida. Una pequeña muestra de dientes aislados recogidos del horizonte Barstoviano tardío de la formación Bon Valley inferior, centro-sur de Florida, representa *Cormohipparion* sp., cf. *C. sphenodus*. En el Clarendoniano, una especie mayor de *Cormohipparion*, cf. *C. occidentale*, se representa por tres dientes aislados, también de un horizonte antiguo de la formación Bone Valley. El sitio Love, Clarendoniano muy tardío, produjo mucho material de dos especies de *Cormohipparion*, una pequeña y una mediana, se asignan aqui a *C. ingenuum* u *C. plicatile*, respectivamente. El material excelente permite nuevas interpretaciones filogenéticas de estas especies descritas por Joseph Leidy hace más de un siglo a base de dientes aislados, y hasta ahora poco conocidas. La primera ocurrencia de *C. ingenuum* fue en el Clarendoniano temprano de Texas y Florida, y la especie perduró en Florida hasta el Hemphilliano temprano tardío, una duración de aproximadamente cinco millones de años. También se conoce de la fauna Gracias Hemphilliano temprano de Honduras. *Cormohipparion ingenuum* no es sinónimo mayor de *Nannippus lenticularis* (Cope), como han sugerido algunos autores, pues las dos comparten pocas características fuera del tamaño. *Cormohipparion plicatile* se limita al Clarendoniano tardío Hemphilliano temprano de Florida, pero es la más frecuente en sitios donde se encuentran las dos. La ocurrencia de *C. emsliei* se extiende al Hemphilliano temprano (aprox. 7 Ma), basado en su presencia en el sitio Moss Acres Racetrack. Perduró por el Blancano (a aprox. 2.0 Ma), y es el representativo mas joven del género conocido en Norte América. Estas tres especies forman un grupo monofilético, *Cormohipparion* (*Notiocradohipparion*) subgénero nuevo, unidos por sus hocicos relativamente muy largos. Este grupo aparentemente se limitó a la planicie costera del golfo y América Central. Tres tendencias importantes observadas en *Cormohipparion* de Florida durante diez millones de años son aumento en hipsodontia, aumento en complejidad del esmalte dental, y reducción en la profundidad de la fosa preorbital dorsal.

Hipparion se ha encontrado poco en el Mioceno tardío de Florida. Muestras incluyen las de la formación Bone Valley inferior (Clarendoniano?), el sitio Love, el sitio Moss Acres Racetrack, y la fauna local del Rio Withlacoochee 4A (Hemphilliano tardió temprano). Las dos últimas se cuentan entre los encuentros mas jóvenes de *Hipparion* en Norte América. Todas se asignan tentativamente a la especie mediana, *Hipparion tehonense*.

Análisis cladístico basado en 58 características dentales y craniales sugiere las sigientes hipótesis: (1) la tribu Hipparionini es monofilética y contiene por lo menos seis géneros norteamericanos y varias especies de posición genérica incierta; (2) *Hipparion*, *Merychippus* s.s., *Nannippus*, *Cormohipparion*, y los hipparioninos del viejo mundo forman un grupo monofilético, el grupo de *Hipparion*; (3) *Neohipparion*, *Pseudhipparion*, y *"Merychippus" goorisi* (MacFadden y Skinner) forman el taxon hermano del grupo *Hipparion*;   (4) *"Merychippus" goorisi* (MacFadden y Skinner) es el taxon hermano de *Nannippus* + *Cormohipparion*, pero por la estructura única de su cara no puede ser antecesor de ninguno de ellos; y (5) *Cormohipparion* de Florida (*Notiocradohipparion*) es el taxon hermano de *C. occidentale* + *"Cormohipparion"* del viejo mundo (o sea hipparioninos de grupo 1).

TABLE OF CONTENTS

INTRODUCTION

This is one of several recently completed or planned studies describing fossil equids from the Late Neogene of the Gulf Coastal Plain of the southeastern United States. Previous studies have dealt with *Dinohippus* and *Astrohippus* (MacFadden 1986), *Pseudhipparion* (Webb and Hulbert 1986), *Neohipparion* (Hulbert 1987b), *Calippus* and *Protohippus* (Hulbert 1988a), and a new species of *Cormohipparion* (Hulbert 1988b). Future work will include studies of *Nannippus* (Hulbert in prep.) and post-cranial elements. Together, they will provide a modern revision of the Late Neogene Equinae from this important faunal province, as well as complementing and supplementing ongoing research on equids from other regions of North America. These studies will also aid intracontinental biostratigraphic correlation with radiometrically dated faunas from the western United States, and will allow greater understanding of equid evolution and paleoecology during a critical period of their history in North America.

Hippotherium ingenuum, the first equid and second fossil vertebrate species described from Florida, was named by Leidy (1885) based on two unassociated upper molars from Mixson's Bone Bed (Figs. 1, 2). During the subsequent century, opinions concerning the generic allocation of Leidy's taxon have varied considerably, and a number of equid populations from outside of Florida have been referred to it. Since Stirton (1940), it has most often been included in *Nannippus*. *Hippotherium plicatile*, also named by Leidy (1887), was based on an isolated tooth from the same locality and has had a similar complicated taxonomic history. Despite two periods of re-excavation at Mixson's Bone Bed, during the early 1910s by the Florida Geological Survey and the late 1930s and early 1940s by field crews financed by Childs Frick, additional topotypic material remained undescribed until very recently (MacFadden 1984). Compared to other sites in Florida of comparable age, equids were not especially diverse or common at Mixson's, and the limited amount of topotypic material hindered systematic study of these two species.

Three recently discovered sites in particular have proved crucial in unraveling the phylogenetic affinities of Leidy's species. The Love Site, located north of the town of Archer, Florida (about 18 km northwest of Mixson's; Fig. 2), was discovered in 1974 and excavated by field crews of the Florida State Museum until June 1981. Equids, with a minimum of over 300 individuals, were among the most common mammalian taxa recovered from the Love Site (Webb et al. 1981; Hulbert 1982). This study confirms that large numbers of upper and lower dentitions from the Love Site are referable to Leidy's two species, as was first noted by Jackson (1978), and later by MacFadden (1984).
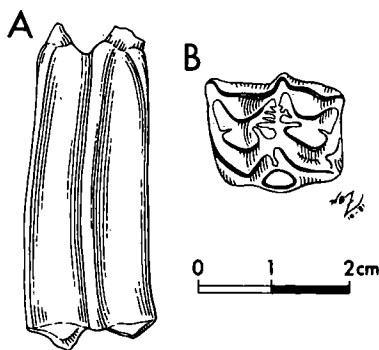
FIGURE 1. Lateral (A) and occlusal (B) views of USNM 3306, the holotype left upper molar of *Cormohipparion ingenuum* Leidy (1885) from Mixson's Bone Bed, Levy County, Florida. This species was the first equid to be described from Florida, and only the second fossil mammal species to be named from the state. This study will demonstrate the validity of Leidy's species, and determine its phylogenetic position among North American hipparionines.
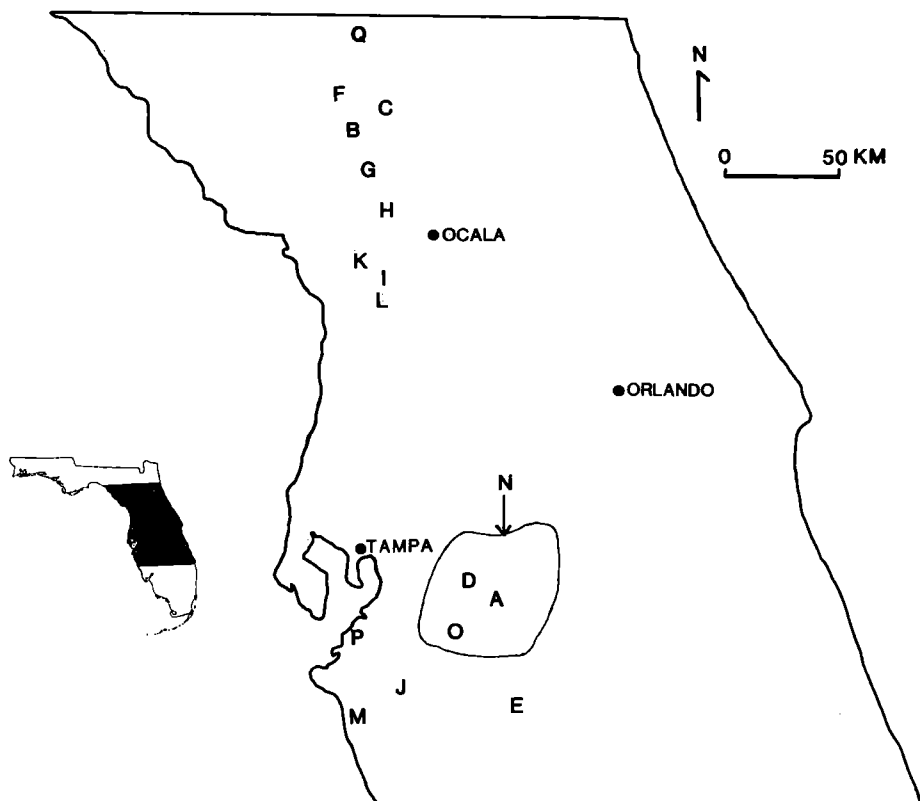
FIGURE 2. Map of northern and central peninsular Florida (between 27° and 30° N) depicting approximate locations of fossil sites frequently mentioned in the text. A. Phosphoria Mine and Hookers Prairie Mine (including Agricola Road Site), Polk County. B. Love Site, Alachua County. C. Coffrin Creek, Gainesville Creek, and VA Hospital Site, Alachua County. D. Nichols Mine, Polk County. E. Peace River near Gardner, Hardee County. F. McGehee Farm Site, and Haile Sites 5B, 6A, 15A, and 19A, Alachua County. G. Mixson's Bone Bed, Levy County. H. Moss Acres Racetrack Site, Marion County. I. Withlacoochee River Sites 4A and 4X, Marion County. J. Manatee Dam Site, Manatee County. K & L. Dunnellon Phosphate Mine sites, Marion and Citrus counties. M. Lockwood Meadows and Macasphalt Shell Pit, Sarasota County. N. Bone Valley Region (within general outline), Polk and adjacent counties; O. Fort Green and Four Corners Mines, Polk, Hardee, and Hillsborough counties. P. Leisey Shell Pit 1C, Hillsborough County, and Port Manatee Site, Manatee County. Q. Pareners Branch Site, Alachua County.

Their absence in the preliminary faunal list of Webb et al. (1981) is inexplicable. The Moss Acres Racetrack Site, located about 15 km southeast of Mixson's, is a late early Hemphillian locality notable for the presence of skulls and associated skeletons (Hulbert 1987b; 1988a). It was discovered in 1984 and is still being worked. It has produced the two most complete mandibles described in this study. The Agricola Road Site contained the greatest concentration of terrestrial vertebrate specimens yet recovered from a

single quarry in the Bone Valley Formation, Polk County (Fig. 2). Discovered in 1987, it produced a rich record of early Clarendonian mammals from a period previously very poorly known in Florida. Specimens from these three sites, along with others from less productive localities, permit a detailed morphological and statistical reevaluation that demonstrates that both of Leidy's species should be referred to the recently described genus *Cormohipparion*.

The purposes of this study are: (1) to describe in stratigraphic sequence all material from Florida referable to *Cormohipparion* or *Hipparion* (in conjunction with Hulbert 1988b); (2) to compare this material with contemporaneous records from the Texas Gulf Coastal Plain and the Great Plains; (3) to determine if material from other regions of North America is referable to species described from Florida; and (4) to analyze the phylogenetic relationships of the Florida taxa, along with those from the Great Plains and the western United States, revising to some extent the results of MacFadden (1984).

Throughout this study, *Cormohipparion* and *Hipparion* are used following the definitions of Skinner, MacFadden and co-workers (e.g. Skinner and MacFadden 1977; Woodburne et al. 1981; MacFadden 1984). These definitions result from a hypothesized phylogeny in which two separate clades of North American hipparionines are recognized as sister groups of two distinct clades of Old World hipparionines. Implicit in this hypothesis is that there were at least two separate immigrations into Asia of New World hipparionines. Other workers have proposed alternate phylogenies; while generally agreeing with Woodburne et al. (1981) that "*Cormohipparion*" is the probable sister group of an early immigrant wave into Asia, they suggest instead that Old World hipparionines are essentially monophyletic (e.g. Bernor et al. 1980; Forstén 1968, 1984; Bernor and Hussain 1985; Bernor 1985). Among these workers, there is no current agreement as to whether this monophyletic clade includes just one genus, or several genera. This in turn has nomenclatural ramifications on New World taxa (cf. Bernor and Hussain 1985:39). For example, if New World *Cormohipparion* (*sensu* MacFadden 1984) is "ancestral" to Old World *Hipparion* s.s., then *Cormohipparion* could be considered a junior synonym of *Hipparion*, and New World *Hipparion* (*sensu* MacFadden 1980, 1984) would belong in another (unnamed) genus. Or, if Old World hipparionines are divided among several genera, there is still the possibility that *Hippotherium* and/or *Sivalhippus* are senior synonyms of *Cormohipparion* (Bernor and Hussain 1985). Only a complete phylogenetic analysis of Old World hipparionines, which has yet to be done, can resolve these nomenclatural problems. It is also uncertain which of the Eurasian genus-level names that have gone unused for about 80 years, such as *Hippotherium*, should be considered *nomina oblita*. As the scope of this report concerns taxa with no direct involvement with these unresolved questions, I

have elected to consistently use one of several possible nomenclatural alternatives. A much less satisfactory approach would be to group these taxa into a single genus (*Hipparion* s.l.), and ignore their phylogenetic interrelationships.

ACKNOWLEDGMENTS

ABBREVIATIONS

AMNH - Department of Vertebrate Paleontology, American Museum of Natural History, New York.
F:AM - Frick Collection, housed with the AMNH collection.
PPM - Panhandle-Plains Historical Museum, Canyon, Texas.
TMM - Texas Memorial Museum, University of Texas, Austin.
UCMP - University of California Museum of Paleontology, Berkeley.
UF - Vertebrate Paleontology Collection, Florida State Museum, University of Florida, Gainesville.
UF/FGS - Florida Geological Survey Collection, now housed with UF collection.
UNSM - University of Nebraska State Museum, Lincoln.
USNM - National Museum of Natural History, Smithsonian Institution, Washington, D.C.
R, L - right, left.
I/i - upper/lower incisor.
C/c - upper/lower canine.
P/p - upper/lower premolar (e.g. P4 is an upper fourth premolar).
M/m - upper/lower molar (e.g. m2 is a lower second molar).
D/d - upper/lower deciduous tooth (e.g. dp2 is a deciduous lower second premolar).
P34, p34, DP34, dp34, M12, m12 - collective terms for indistinguishable isolated teeth (e.g. P34 refers to upper third and fourth premolars).
DPOF - dorsal preorbital fossa (= lacrimal or nasomaxillary fossa).
assoc. - associated.

Ma - Mega-anna, millions of years before present on the radioisotopic time scale.

x - sample mean.

s - sample standard deviation.

r - sample correlation coefficient.

n - sample size.

CV - sample coefficient of variation expressed as a percentage.

OR - observed range of a sample.

s.s. - *sensu stricto*

s.l. - *sensu lato*

l.f. - local fauna

Abbreviations of measurements (see also Fig. 3). Those in uppercase refer to upper dentitions; lowercase to lowers.

APL - maximum anteroposterior length, excluding the ectoloph and hypocone.

BAPL - anteroposterior length at the base of the crown.

TRW - transverse width from mesostyle to lingual-most part of the protocone.

PRL - maximum length of the protocone, excluding spur and connection to protoselene.

PRW - maximum width of the protocone perpendicular to PRL.

MSCH - crown height measured from the occlusal surface to the base of the crown along the mesostyle.

UTRL - upper toothrow length from the anterior-most projection of the P2 to the posterior-most part of the M3.

UDL - upper diastema length, measured between the alveoli of the I3 and the P2 (excludes DP1 if present).

apl - maximum anteroposterior length from the paralophid to the hypoconulid.

bapl - anteroposterior length at the base of the crown.

atw - transverse width from the protoconid to the metaconid.

ptw - transverse width from the hypoconid to the metastylid.

entl - anteroposterior length of the entoflexid.

mml - length from the anterior-most point of the metaconid to the posterior-most point of the metastylid.

mcch - crown height measured from the occlusal surface to the base of the crown along the metaconid.

ltrl - lower toothrow length measured from the anterior-most part of the p2 to the posterior-most point of the m3.

ldl - lower diastema length measured between the alveoli of the i3 and p2 (excluding dp1 if present).

MATERIALS AND METHODS

Samples of equid crania, mandibles, and isolated teeth representing *Hipparion* and *Cormohipparion* from the five major Late Neogene localities or faunas of Florida (Agricola Road, Love, McGehee Farm, Mixson's, and Upper Bone Valley; Fig. 2) were examined and analyzed quantitatively. Specimens from other, less productive sites were also studied, and often measured, but were not subjected to statistical analysis because of small sample sizes. As in previous studies (Webb and Hulbert 1986; Hulbert 1987b, 1988a), lack of relatively complete cranial material, and a near complete absence of associated post-cranial elements necessitated a heavy reliance on dental characters to study this group of Gulf Coastal Plain equids. Important comparative material examined included samples of *C. sphenodus* from the Barstovian of Colorado and Nebraska (in the F:AM and AMNH collections); *C. occidentale* from the Clarendon Fauna of Donley County, Texas (PPM and F:AM), the Lapara Creek Fauna of Bee County, Texas (TMM), and the Xmas-Kat Channel Quarries of north-central Nebraska (F:AM); *H. tehonense* from the Tejon Hills Fauna, San Joaquin Valley, California (UCMP), the Lapara Creek Fauna (TMM), and the Clarendon Fauna (PPM and F:AM); and *H. forcei* from the Black
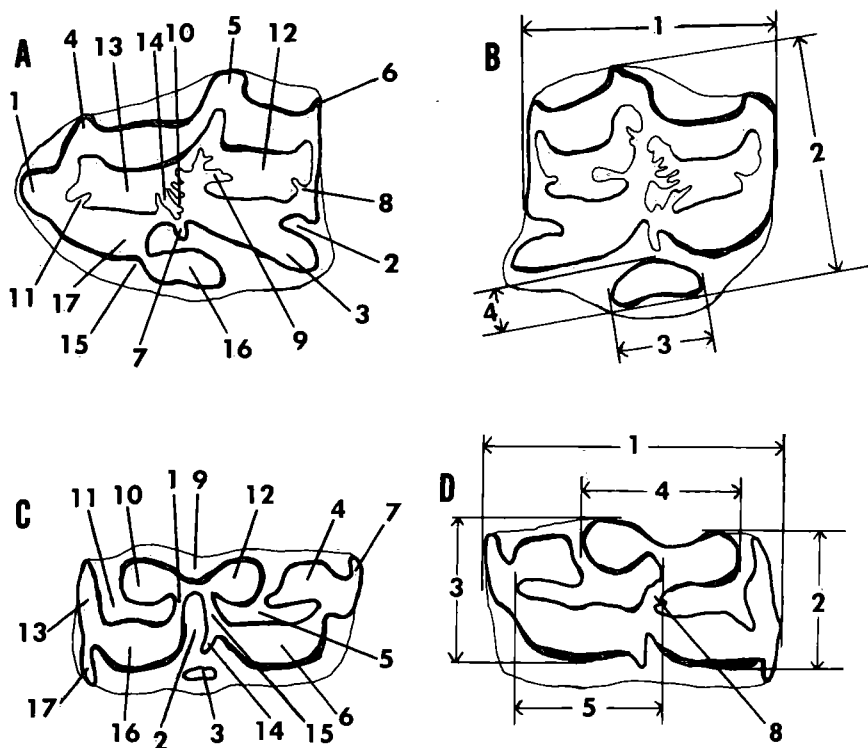
FIGURE 3. Schematic occlusal views of upper and lower cheekteeth of equids demonstrating nomenclature and measurements used in this study. A. Upper left second premolar (anterior to left, labial up): 1, anterostyle (found on P2s and DP2s only); 2, hypoconal groove; 3, hypocone; 4, parastyle; 5, mesostyle; 6, metastyle; 7, pli caballin; 8, pli hypostyle; 9, pli postfossette; 10, pli prefossette; 11, pli protoloph; 12, postfossette; 13, prefossette; 14, prefossette loop; 15, preprotoconal groove; 16, protocone; 17, protoselene. B. Upper right third or fourth premolar (P34) showing the four measurements made on the occlusal surfaces of upper cheekteeth: 1, APL, maximum anterior-posterior length, excluding the ectoloph and hypocone; 2, TRW, transverse width from mesostyle to lingual-most part of protocone; 3, PRL, maximum protocone length, excluding spur or connection to protoselene (if present); 4, PRW, protocone width perpendicular to PRL. C. Lower left molar (anterior to left, lingual up): 1, antisthmus; 2, ectoflexid; 3, ectostylid (generally found only on deciduous teeth in North American taxa); 4, entoconid; 5, entoflexid; 6, hypoconid; 7, hypoconulid; 9, linguaflexid; 10, metaconid; 11, metaflexid; 12, metastylid; 13, paralophid; 14, pli caballinid; 15, postisthmus; 16, protoconid; 17, protostylid. D. Lower right third or fourth premolar (p34) showing the five measurements made on the occlusal surface of lower cheekteeth: 1, apl, maximum anterior-posterior length, excluding protostylid; 2, atw, anterior width from metaconid to protoconid; 3, ptw, posterior width from metastylid to hypoconid; 4, mml, metaconid-metastylid length; 5, entl, length of entoflexid; 8, isthmus, the combined antisthmus and postisthmus when the ectoflexid is shallow.

Hawk Ranch 1.f., Contra Costa County, California (UCMP), and the Cambridge Fauna (Ft-40), Frontier County, Nebraska (UNSM).

Six characters were measured on each upper cheektooth, and seven on each lower tooth, following the procedures described by Hulbert (1987b, 1988a) and illustrated in Figure 3. Each measurement was taken to the nearest 0.1 mm with dial calipers. Plication counts of fossettes follow the procedures of MacFadden (1984). Standard equid dental terminology (e.g. Stirton 1941; MacFadden 1984, fig. 4) is generally followed (Fig. 3A, 3C). The term "ectostylid," widely used in the literature of Old World hipparionines, is employed rather than Stirton's (1941) "protostylid." The latter term is used instead to refer to the structure called the parastylid by Stirton (1941). The rudimentary first upper cheektooth is referred to as the DP1, as it erupts with the deciduous rather than the permanent premolar series (Skinner and Taylor 1967). "Hipparionine" collectively refers to the genera *Neohipparion, Pseudhipparion, Merychippus* s.s., *Nannippus, Hipparion, Cormohipparion,* and Old World derivatives. Definitions of North American Land Mammal Ages follow Tedford et al. (1988).

SYSTEMATIC PALEONTOLOGY
ORDER PERISSODACTYLA OWEN, 1848
FAMILY EQUIDAE GRAY, 1821
SUBFAMILY EQUINAE STEINMANN AND DÖDERLEIN, 1890
TRIBE HIPPARIONINI QUINN, 1955
GENUS *Cormohipparion* SKINNER AND MACFADDEN, 1977

Type Species.-- *Cormohipparion occidentale* (Leidy), 1856.

Included Subgenera.-- *C. (Cormohipparion)* and *C. (Notiocrado-hipparion)* n. subgen.

Included North American Species.-- *C. occidentale* (Leidy), 1856; *C. sphenodus* (Cope), 1889; *C. ingenuum* (Leidy), 1885; *C. plicatile* (Leidy), 1887; and *C. emsliei* Hulbert, 1988.

Revised Generic Diagnosis.-- Medium- to large-sized hipparionine equids. Prominent, oval or tear-drop shaped, pocketed, generally deep DPOF with well developed, usually continuous anterior rim; other margins also well defined; positioned far anteriorly from orbit; advanced lineages in both Old and New World independently reduce DPOF. Cheekteeth hypsodont, well cemented. Upper cheekteeth generally with large DP1 retained with adult dentition; protocone isolated (except P2) until late wear, usually oval or elongate-oval in shape. Protocone spur absent or rudimentary. P2 anterostyle well developed and P2 much longer than other cheekteeth. Pli caballin prominent, often bifurcated, multiple, or both; fossettes moderately to very complicated, with persistent plis protoloph and hypostyle, and well developed prefossette loop; styles strong, parastyle frequently grooved. Lower cheekteeth have large, well separated, oval or angular metaconids and metastylids; usually well developed protostylids (absent on p2); plicated paralophids and isthmuses frequent; pli caballinids variably developed, become more prominent and persistent in

younger species. Paraconid of p2 relatively expanded. Ectostylids prominent on dp2-dp4.

Chronologic and Geographic Distribution in North America.-- Late Barstovian through early Hemphillian of West Coast, Great Basin, and Great Plains; late Barstovian through late Blancan of Gulf Coastal Plain; early Hemphillian of Central America.

Discussion.-- In his recent review, MacFadden (1984) recognized three North American species of *Cormohipparion*, *C. goorisi*, *C. sphenodus*, and *C. occidentale*. *C. ingenuum* was placed in *Nannippus*, and *C. plicatile*, while recognized as a distinct species, could not be referred unambiguously to any genus by MacFadden. More recently (Hulbert 1987a, 1988c; see also below), I determined that "*Merychippus*" *goorisi* was the sister taxon to both *Nannippus* and *Cormohipparion*, and excluded it from the latter genus. The three species described from Florida (*C. ingenuum*, *C. plicatile*, and *C. emsliei*) are referred to a new subgenus of *Cormohipparion*, described below.

Cormohipparion sphenodus (COPE), 1889

Hippotherium sphenodus COPE 1889:449-450.
Merychippus sphenodus (Cope), GIDLEY 1907:908; OSBORN 1918:112-114; STIRTON 1940:181; GALBREATH 1953:105.
Cormohipparion sphenodus (Cope), WOODBURNE et al. 1981:503-514; MACFADDEN 1984:156-162.

Type Specimens.-- AMNH 8281, a R P2, lectotype; a L P34 (also AMNH 8281) is the paratype (see discussion in Woodburne et al. 1981).

Type Locality and Horizon.-- Pawnee Creek Formation, Pawnee Buttes, Logan or Weld County, Colorado. Late Barstovian (about 13 to 14 Ma).

Revised Distribution.-- Late Barstovian through early Clarendonian (about 11 to 15 Ma) of California, New Mexico, Colorado, South Dakota, Nebraska, and Texas. Possibly also late Barstovian of Florida (see below).

Revised Diagnosis.-- Medium-sized and moderately hypsodont hipparionine with a UTRL of about 126 mm. Unworn MSCH of P2 about 30 to 35 mm. DPOF moderately pocketed. Protocones oval with poorly developed anterior spur in early wear-stages. Fossettes only moderately complex (for the genus), especially the opposing borders of the prefossette and postfossette. Pli caballinids moderately developed in premolars and poorly developed or absent in molars. (Slightly modified after MacFadden [1984:156]; note that his "M1MSTHT" should read "P2MSTHT".)
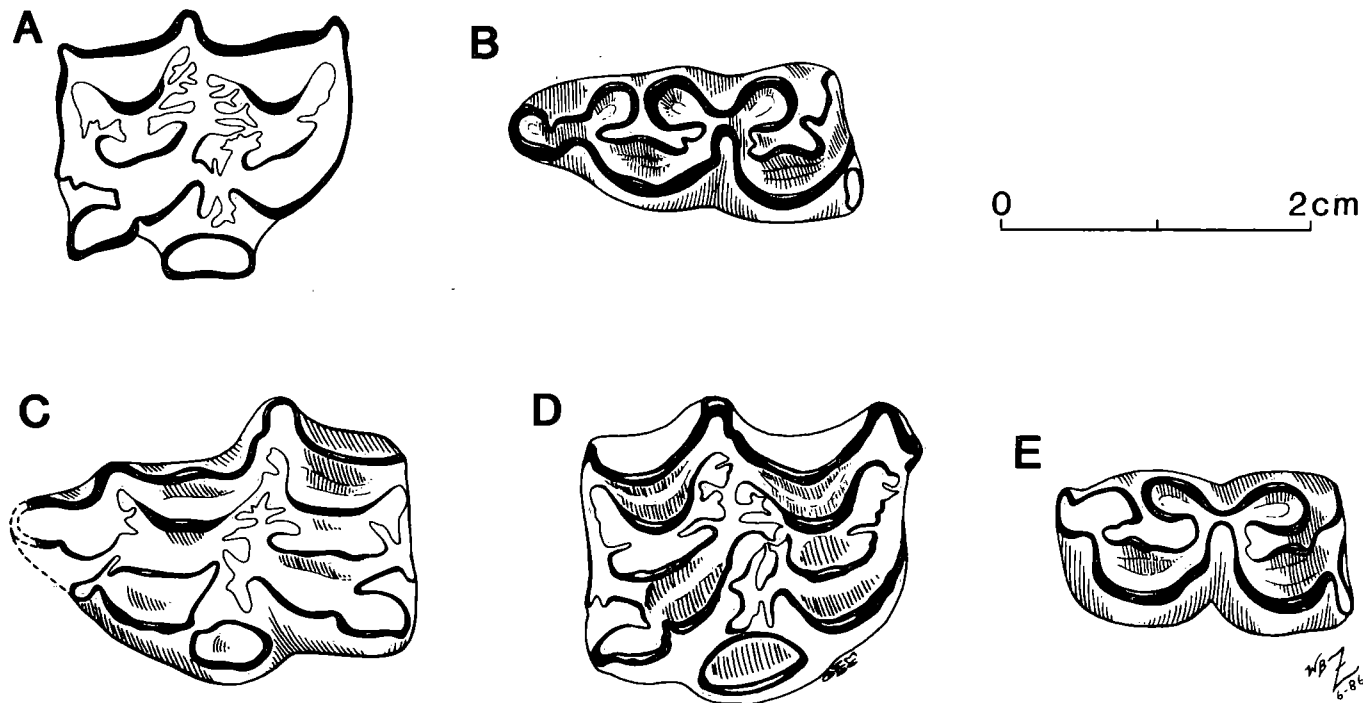
FIGURE 4. Occlusal views of upper and lower cheekteeth referred to *Cormohipparion* from lower horizons of the Bone Valley Formation, Polk County, Florida. A-B. *Cormohipparion* sp., cf. *C. sphenodus*, Red Zone (late Barstovian), Phosphoria Mine. A. UF 28432, sectioned R M12. B. UF 28447, R m3. C-E. *Cormohipparion ingenuum* , Gray Zone (early Clarendonian), Phosphoria Mine. C. UF 28683, L P2. D. UF 28556, R P34. E. UF 28569, R m12.

Cormohipparion sp., cf. *C. sphenodus*
Fig. 4A-4B; Tables 1-2

        Referred Specimens.-- Phosphoria Mine (Red Zone), Polk Co., FL: UF 28432, 28433 2 R M12; UF 28434 L M12; UF 28435 L M3; UF 28436 L P34; UF 28459 L p2; UF 28458 R p34; UF 28460, 28475, 28476 3 L p34; UF 28453 R m12; UF 28446, 28447 2 R m3.
        Description and Discussion.-- In the mid-1970s, J. S. Waldrop and associates excavated from the banks of a dragline cut in the Phosphoria Mine a large sample of pre-Hemphillian terrestrial vertebrates from the Bone Valley District of south-central Florida. Two of the fossiliferous horizons, informally termed the Red and Gray Zones, contained late Barstovian and early Clarendonian vertebrates, respectively (Webb and Hulbert 1986). Both produced a medium-sized hipparionine referable to *Cormohipparion*. Although comparisons are limited by the small sample sizes, the specimens from the overlying Gray Zone are slightly more hypsodont and complex than Red Zone specimens. As the samples are too limited for statistical analysis, Tables 1 and 2 present measurements taken on relatively complete specimens. The population of *Cormohipparion* from the Gray Zone of the Phosphoria Mine matches the more numerous sample from the Agricola Road Site from the nearby Hookers Prairie Mine. They are both referred to *C. ingenuum*, and described below. Those from the Red Zone compare favorably in occlusal dimensions and crown height instead with data presented by Woodburne et al. (1981) for *C. sphenodus*. Additionally, the sample corresponds in almost every detail of enamel morphology of *C. sphenodus* as described and illustrated by Woodburne et al. (1981) and MacFadden (1984). The protocone is oval or elongate-oval with a rudimentary spur in early wear; it is isolated from the protoloph in all specimens (Fig. 4A). The hypocone is oriented posterolingually and has a constricted connection to the metaloph. The posterior half of the prefossette and the anterior half of the postfossette are moderately complex, but less so than typical younger samples of *Cormohipparion* from Florida. In early wear-stages, the lower premolars have moderately developed pli caballinids, shallow ectoflexids, and numerous enamel plications. In later wear-stages (e.g. UF 28460), the ectoflexid penetrates the isthmus past the level of the base of the entoflexid. The protostylid, which comes into wear about 10 mm below the unworn occlusal surface, is at first isolated (Fig. 4B), but later connects with the protoconid and is a prominent feature. This is also typical for all younger species of *Cormohipparion*. A definite species referral is precluded by the limited nature of the sample. Instead of *C. sphenodus*, these teeth could possibly represent the common ancestor of *C. plicatile* and *C. ingenuum*. However, much more

complete material would be needed to conclusively demonstrate this hypothesis.

The Red Zone equid assemblage includes *Cormohipparion* sp., cf. *C. sphenodus*, *Merychippus* sp. near *M. califomicus*, *Calippus proplacidus* (= *C. francisi*, see Hulbert 1988a), and *Pliohippus* sp. (Table 10). A late Barstovian age is indicated, but larger and more complete samples are required for a more precise age determination. Approximate equivalents among western faunas are the Cold Spring Fauna of Texas and the Devil's Gulch Fauna of Nebraska (Webb and Hulbert 1986).

SUBGENUS *Cormohipparion* (*Cormohipparion*) SKINNER AND MACFADDEN, 1977
Cormohipparion (*Cormohipparion*) *occidentale* (LEIDY), 1856
Tables 1, 5-7

Hipparion occidentale LEIDY 1856:59; OSBORN 1918:176.
Hippotherium occidentale (Leidy), COPE 1886:359; COPE 1889:434 (in part).
Neohipparion dolichops GIDLEY 1906:148; STIRTON 1940:182.
Neohipparion occidentale (Leidy), GIDLEY 1907:877; STIRTON 1940:182; GREGORY 1942: 414 (in part) ; FORSTÉN 1975:65 (in part).
Cormohipparion occidentale (Leidy), SKINNER and MACFADDEN 1977:917; MACFADDEN 1984:162.

Type Specimen.-- Academy of Natural Sciences, Philadelphia, Number 11287, four R and one L associated upper cheekteeth.

Type Locality and Horizon.-- Exact locality unknown, Little White River Region, South Dakota, see discussion in Skinner and Taylor (1967). Probably Ogallala Group; middle Clarendonian, about 10 Ma.

Distribution.-- Latest Barstovian to early Hemphillian in the Great Plains (about 6.0 to 12.0 Ma). Clarendonian and early Hemphillian of the Great Basin, Columbia Plateau, and California. Clarendonian of the Texas Gulf Coastal Plain, and possibly Florida.

Referred Gulf Coastal Plain Specimens.-- Lapara Creek Fauna, Farish Ranch Site, Bee Co., TX: TMM 31081-844 crushed skull with R & L P2-M3. Other specimens as listed by Forstén (1975:66-67), except those referred to *Neohipparion affine* by Hulbert (1987b).

Specimens provisionally referred to this species from Florida are: Phosphoria Mine (possibly Gray Zone), Polk County: UF 28607 R P34. Hookers Prairie Mine, Polk County: UF 102552 L P34; 102553 R M12.

Diagnosis.-- Largest North American species of *Cormohipparion*, with toothrow lengths of 133-150 mm in middle wear-stages. Unworn MSCH of M12 54-60 mm. Deep, continuously well rimmed, keyhole-shaped DPOF.

More higher crowned cheekteeth than *C. sphenodus* or *C. ingenuum*. More complexly plicated fossettes than *C. sphenodus*, *C. plicatile*, and *C. ingenuum* (on average, at comparable wear-stages). Ectostylids on dp34 oval and larger than those of other North American species.

Description.-- TMM 31081-844 is notable as the only cranial material of *Cormohipparion* known from the Gulf Coastal Plain preserving the entire preorbital region. The DPOF (on the better preserved right side) is teardrop shaped, about 60 mm long, and has a maximum dorsoventral height of about 30 mm. The anterior border is located above the P3, and the posterior border is above the M1-M2 contact. The pocketed, well rimmed fossa is located well anterior to the orbit with a preorbital bar length of about 57 mm (due to crushing and reconstruction with plaster this measurement is a rough estimate). For all important features, the facial region of TMM 31081-844 falls within the range of variation expressed by the large Hans Johnson Quarry sample of *C. occidentale* from the late Clarendonian of Nebraska (Skinner and MacFadden 1977). The size and complexity of the cheekteeth of TMM 31081-844 are equivalent to the dental features of the Lapara Creek sample of *C. occidentale* described in detail by Forstén (1975). MacFadden (1984a, fig. 134) was the first to illustrate a specimen of *C. occidentale* from this fauna, TMM 31081-619, a right maxillary fragment with P2-M1.

In the upper cheekteeth, Gulf Coastal Plain specimens of *Cormohipparion occidentale* display the following important features that reflect their close relationship with other referred samples of the species (notably those from the Clarendon and Xmas-Kat Faunas). Premolars are slightly longer and much wider than the molars, with well developed styles. In early wear, the parastyles of the P34 are slightly grooved. The fossettes are richly plicated; typically in premolars the anterior half of the prefossette has a deep, persistent, generally unbranched pli protoloph and zero to three smaller, less persistent accessory plications. The posterior half of the prefossette and the anterior half of the postfossette are of approximately equal complexity, with numerous (usually four or five, up to eight) plications apiece, several of which are usually deep and bifurcated. The pli hypostyle is usually deep, unbranched, and persistent; it is often (33% of examined specimens) accompanied by one or two additional small plications. In the M12, the fossettes are typically only slightly less complex, but the folds are not as deep and have fewer bifurcations. Both the pli protoloph and pli hypostyle are well developed, persistent, and have occasional accessory plications. Pli caballins are prominent, often multiple (60% of specimens examined) in P34, generally single in P2 and M1-M3. Protocones vary greatly in length, but are usually elongate-oval, and slightly longer than twice their width, very rarely with spur, except on P2. Protocones are isolated until very late wear-stages, again except for the P2 which generally connects the protocone during the moderate wear-stage. When compared with the Clarendon and Xmas-Kat populations of *C. occidentale*, the southern

samples show slight differences in size (they are on average about 5% smaller), hypsodonty (unworn M12 MSCH is about 50-54 mm in the Lapara Creek sample, about 60 mm in the Clarendon and Xmas-Kat samples), and plication frequency. The Xmas-Kat sample is significantly more complicated than either of the two Texas populations. For example, pli caballins are multiple or bifurcated in 88% of the P34s (n = 66) and 55% of the M12s (n = 75). In complexity of fossette plications, the Xmas-Kat Quarries population of *Cormohipparion* is exceeded among North American hipparionines only by the late Hemphillian sample of *C. emsliei* (Table 7).

In the lower cheekteeth, the Lapara Creek sample is characterized by rounded to slightly flattened labial protoconid and hypoconid borders (but not to the degree of *Neo. affine*); large, oval, subequal metaconids and metastylids; and relatively large protostylids that are often isolated from the protoconid during early wear. Pli caballinids are variably developed on the p2-p4; prominent in early wear-stages, retreating with wear until disappearing during late middle wear-stages. They are at best rudimentary on the m1-m3, and then only appearing in very early wear-stages. Lower cheekteeth are frequently plicated (Table 5); these are best expressed during early and early moderate wear-stages. The ectoflexids on the premolars generally penetrate to a level about equal to the base of the metaflexid, although there are some with deeper and some with shallower ectoflexids. In the molars, ectoflexids are deep and completely divide the isthmus. Deciduous lower premolars have wider and deeper ectoflexids than permanent premolars, rudimentary pli caballinids, and relatively large, tall ectostylids that soon appear on the occlusal surface after the onset of wear (e.g. TMM 31081-456, 31081-7).

Discussion.-- Leidy described this species on five associated upper cheekteeth. Although of uncertain stratigraphic provenience (Skinner and Taylor, 1967), the holotype displays a number of characters than unites it with referred populations from the Lapara Creek, Clarendon, and Xmas-Kat Faunas (and others listed by MacFadden 1984a:163). These include size (Table 1, relatively large), elongated protocones without spurs, well developed pli caballins that tend toward branching on the premolars, and complex fossette plications (Table 7). Prior to the naming of *Cormohipparion* by Skinner and MacFadden (1977), the species *occidentale* was routinely referred to the genus *Neohipparion* (e.g. Stirton 1940). While there are similarities between *C. occidentale* and *N. affine* (the type species of *Neohipparion*), especially in protocone shape and overall size, there are major differences in DPOF depth and degree of rimming, relative position of the DPOF and lacrimal bone, fossette complexity, shape of the labial borders of the protoconid and hypoconid, and the development of the ectostylid in deciduous premolars (Skinner and MacFadden 1977; Skinner et al. 1977; MacFadden 1984a; Hulbert 1987b). These serve not only to distingiush the two as distinct species, but support a phylogenetic hypothesis that they represent separate

genera. With the recognition of a separate subgenus within *Cormohipparion* (named below), the clade containing the genoholotype *C. occidentale* automatically becomes the nominate subgenus *C. (Cormohipparion)*. Based on the phylogenetic analysis presented below, that clade does not include any North American species besides *C. occidentale*, but does contain some Old World hipparionines. *C. sphenodus* is not a member of either recognized subgenus. Instead of naming a third, monotypic subgenus for it, I prefer to consider *C. sphenodus* a plesion of subgeneric rank.

MacFadden (1984:90) synonymized *Neohipparion affine* and *N. dolichops*. The latter species was named by Gidley (1906) on a maxilla (AMNH 10865) and complete mandible (AMNH 10832) from Big Spring Canyon, South Dakota. Numerous topotypes were described by Gregory (1942) as *"N."* *occidentale*. Based on the dental differences described above, these specimens suggest that *N. dolichops* should be synonymized with *C. occidentale* rather than *N. affine*, as these two species are presently used. This synonymy is of more interest than it first appears. As the holotype of *C. occidentale* lacks stratigraphic and locality data, and consists only of upper cheekteeth, some workers at the 1981 AMNH Hipparionine Systematics Symposium suggested that it might be an inadequate type. If true, then Gidley's *"N."* *dolichops* would be the next available name for this widespread species.

Although widespread and very abundant throughout the western half of the United States during the Clarendonian, *C. occidentale* is as yet only provisionally recognized from Florida, on the basis of but three isolated teeth. These specimens clearly document the presence in Florida of a relatively large species of *Cormohipparion* in the middle Miocene. The occlusal dimensions of the three teeth (Table 1) fall within the OR of both *C. plicatile* and *C. occidentale*. Based on biogeographic grounds, a reference to the former would seem more likely. However, several features indicate closer affinities with the latter, including multiple plis protoloph on UF 28607 and UF 102552, very complex and deep internal fossette plications on all three (considering their advanced wear-stages, this is especially important), and the elongate protocones with flattened lingual borders. The protocone of UF 28607 is not as elongate as the others, but it does have a flattened lingual border, and its length (6.9) falls within the OR of PRL for the Lapara Creek sample of *C. occidentale* (6.0-9.8 mm). The PRL of UF 102553 (8.8 mm) is well outside the OR for *C. plicatile* (Table 3), which is based on a very large sample size. Therefore, pending recovery of additional, more complete samples, a tentative reference to *C. occidentale* appears to be the most appropriate referral for these specimens. The age of these specimens cannot be determined exactly, but it is almost surely pre-late Hemphillian. None was collected *in situ* with other taxa in a biostratigraphic context, nor were teeth referable to *C. occidentale* recovered from the rich, early Clarendonian Agricola Road Site. Their age is most likely early Clarendonian, as terrestrial and marine

vertebrates of that age are frequently recovered from the Hookers Prairie and Phosphoria mines in the Bone Valley Region.

SUBGENUS *Cormohipparion* (*Notiocradohipparion*) **new subgenus**

Type Species.-- *Cormohipparion* (*Notiocradohipparion*) *ingenuum* (Leidy), 1885.

Included Species.-- *C.* (*N.*) *ingenuum* (Leidy), 1885; *C.* (*N.*) *plicatile* (Leidy), 1887; *C.* (*N.*) *emsliei* Hulbert, 1988.

Etymology.-- *notio*, Greek for southern, *krado*, Greek for branch, and *hipparion*, Greek for small horse. In reference to both the phylogenetic and geographic position of the subgenus.

Chronologic and Geographic Distribution.-- Early Clarendonian through late Blancan of Florida; early Clarendonian of south Texas; early Hemphillian of Honduras; late Hemphillian of Louisiana.

Diagnosis.-- Relatively small- to moderate-sized *Cormohipparion* (UTRL and ltrl between 112 and 135 in moderate wear-stages), distinguished from all other North American *Cormohipparion* by an extremely elongated muzzle. Lower diastema length equals 70% or greater of ltrl. Ectostylids absent from permanent lower cheekteeth.

Discussion.-- These three species comprise a monophyletic clade that persisted for at least 9 million years (ca. 2 to 11 Ma). As presently recognized, the subgenus was limited to regions bordering the Gulf of Mexico: Florida, Louisiana, Texas, and Honduras. However, its range could have extended much further in the eastern United States, as late Miocene deposits are very poorly known throughout that region.

Cormohipparion (*Notiocradohipparion*) *ingenuum* (LEIDY), 1885
Figs. 1, 4C-4E, 5-10; Tables 1-7

Hippotherium ingenuum LEIDY 1885:33.
Hippotherium gratum (Leidy), COPE 1889:445 (in part); LEIDY and LUCAS 1896:49-50 (in part).
Hipparion gratum Leidy, HAY 1902:620 (in part).
Hipparion ingenuum (Leidy), GIDLEY 1907:902; SELLARDS 1916:94, 97 (in part); OSBORN 1918:191; WEBB and TESSMAN 1968:807.
Hipparion (*Nannippus*) *ingenuum* (Leidy), MATTHEW and STIRTON 1930:354; SIMPSON 1930:187-188 (in part).
Hipparion plicatile (Leidy), SIMPSON 1930:187-188 (in part); WEBB and PERRIGO 1984:243-245 (in part).
Nannippus ingenuus (Leidy), STIRTON 1940:186; QUINN 1955:75 (in part); JACKSON 1978:53; MACFADDEN 1984:126-133 (in part).

Nannippus nr. *N. ingenuum* (Leidy), HIRSCHFELD and WEBB 1968:249
Nannippus cf. *N. ingenuum* (Leidy), FORSTÉN 1975:61-65 (in part).
Hippotherium plicatile Leidy, MACFADDEN 1984:170-174 (in part).
Cormohipparion n. sp., BECKER 1985:30.
Cormohipparion ingenuum (Leidy), HULBERT 1988a:274, 280; HULBERT 1988b:454.
Probably *Neohipparion montezuma* (Leidy), OLSON and MCGREW 1940:1236 (in part).

Type Specimen.-- USNM 3306, a L upper molar, probably an M1 (Fig. 1). See MacFadden (1984:127-128) for a discussion of the type status and locality.

Type Locality and Horizon.-- Mixson's Bone Bed (NE 1/4, SW 1/4 Sec. 29, T12S, R19E, Williston 7.5' Quadrangle), Levy County, Florida. Alachua Formation, early Hemphillian, about 8.5 Ma.

Revised Distribution.-- Early Clarendonian through early Hemphillian (about 6.0 to 11.0 Ma) of central Florida. Early Clarendonian of the Texas Gulf Coastal Plain. Early Hemphillian of Honduras.

Referred Gulf Coastal Plain Specimens.-- John Dye Farm Site, Goliad Co., TX: TMM 31204-1 assoc. R P2-M3.

Farish Ranch Site, Bee Co., TX: TMM 31081-501 R mandible with p2-p4.

Hookers Prairie Mine, Polk Co., FL: UF 102554 L DP34.

Agricola Road Site, Hookers Prairie Mine, Polk Co., FL: UF 98101 assoc. R P4-M2 and L P2-M1; 98102 assoc. R & L P4-M3; 98103 assoc. R M1-M2 and L DP4-M2; 98104 assoc. R & L P4-M1; 98105 assoc. R M3 and L M2-M3; 98106 assoc. R P4 and L P3, M1; 98107 R DP34; 107760 L DP34; 98108, 98109 2 R P2; 98110 L P2; 98111, 98112, 107564 3 R P34; 98113-98116, 107565, 107654 6 L P34; 98117-98119, 107613 4 R M12; 98121, 107614, 107660, 107759 4 L M12; 98123, 98124, 107758 3 L M3; 98125 assoc. R p2-p4 and L p3; 98126 assoc. R p2-m3 and L p2, p4-m3; 98127 assoc. R p2-p4 and L p4; 98128 assoc. R p2-p4; 98129 assoc. L p2-p4; 98130 assoc. R & L dp3-dp4; 98131 assoc. L p2-m3; 98132 L mandibular fragment with m1-m2; 98133 assoc. L p3-p4; 98134, 98135 2 assoc. R & L m2; 98136 assoc. R dp4-m1; 98137 L pd2; 107761, 107762 2 R dp34; 98138 L dp34; 98139 R p2; 98140, 98141, 107577, 107612, 107655, 107763 6 R p34; 98159-98161, 102119, 107566, 107620 6 L p34; 98142-98144, 98146-98155, 107578, 107764 15 R m12; 98162-98166, 107621, 107765, 107766 8 L m12; 98156-98158 3 R m3; 107567 L m3.

Gray Zone, Phosphoria Mine, Polk Co., FL: UF 28683 L P2; 28556 R P34; 28558, 28613 2 R M12; 28557 R M3; 28583 R dp34; 28567, 28617, 28619 3 L p34; 28568, 28569 2 R m12; 28618 L m12.

Silver City Mine, Polk Co., FL: UF 65706 L P34.

Love Site, Alachua Co., FL: UF 32300 partial skull with L I3, R and L C,P2-M3; 32254 assoc. R maxilla with P2,P4-M3 and L maxilla with P2-M3; 35953 assoc. R DP2-DP4; 35947 assoc. R DP2-DP3; 32278, 32295, 36122 3 assoc. L DP2- DP4; 53409 assoc. R and L M2; 53410 assoc. R and L M1; 35901, 35906, 35907, 35910-35912, 35916-35919, 35932, 35933, 35936, 35943,

35949, 35955, 35959, 96757 18 R DP2; 36077, 36079, 36083, 36085, 36086, 36089, 36092, 36098, 36107, 36110, 36111, 36113, 36116, 36118, 36135, 69822, 96758, 96759 18 L DP2; 96724-96756, 96880 34 R DP34; 69823, 69824, 96686-96723 40 L DP34; 35966, 35971-35973, 35975, 35979-35980, 35990, 35996, 36011, 36017-36023, 36026-36027, 36029-36030, 36039, 36042-36043, 36045-36046, 36050, 36052, 36055, 36058, 36061-36062, 36067, 36261-36262, 36264-36265, 36267-36268, 60396 39 R P2; 36138-36142, 36148, 36150, 36154, 36160-36161, 36163-36164, 36167, 36170, 36172, 36175, 36178-36179, 36187, 36191, 36196-36198, 36203-36204, 36207-36208, 36215-36216, 36224, 36230-36231, 36234, 36240, 36242, 36245-36246, 36252, 36259, 36271, 69808 43 L P2; 53350, 53392, 53393, 53397, 53399-53405, 62433-62437, 62439-62446, 62418, 62426, 62297 27 R P34; 53176, 53406-53408, 62325, 62377, 62449-62453, 62455, 62457-62459, 62461-62464, 62466-62470 24 L P34; 53333, 53341, 53343, 53386-53391, 53394-53396, 53426, 62304, 62414-62417, 62419-62425, 62427-62432 31 R M12; 53375, 53380-53385, 62390-62407, 62409-62413, 96376, 96925 32 L M12; 96341-96358 18 R M3; 96359-96374 16 L M3; 32120, 32133 2 R mandibles with dp2-dp4; 32150 L mandible with dp2-dp4; 32191 assoc. R mandible with p2-m3 and L mandible with p3-m3; 32172, 36286 2 R mandibles with p2-m3; 32169 R mandible with p2-m2; 96946 R mandible with p2-m1; 32155, 32189 2 R mandibles with p3-m3; 32101, 32154, 32297 3 L mandibles with p2-m3; 32108, 32170, 32198 3 L mandibles with p3-m3; 32117, 32124, 32132, 32138, 32171, 32181, 32241, 32289, 36280, 36284, 60395 11 partial R mandibles; 32103, 32112, 32115, 32128, 32158 5 partial L mandibles; 90199, 90200 2 assoc. R dp2-dp3; 90198 assoc. L dp2-dp3; 32294 assoc. L dp2-dp4; 32200, 36286 2 assoc. R p2-m3; 35894 assoc. R m1-m3; 90201-90209 9 R dp2; 90210-90214 5 L dp2; 90236-90261 26 R dp34; 90215-90235 21 L dp34; 50357, 50363, 50366, 50367, 64807-64842, 64923-64925, 64932, 64933, 92968 16 R p2; 50371, 64800, 64801, 64803-64806, 64922, 64938, 64939, 69817, 92967 12 L p2; 50438, 50538, 50542, 64752-64778, 64987, 65025 32 R p34; 50418, 50457, 50459, 50519, 50526, 64779-64799 26 L p34; 64814-64859, 65174, 65175 48 R m12; 64860-64901, 65169-65173 47 L m12; 50617, 96507, 96508, 103769-103780 15 R m3; 50625, 103781-103800 21 L m3..

Coffrin Creek, Alachua Co., FL: UF 57107 R m12.

Gainesville Creek, Alachua Co., FL: UF 18527 R P34; 18333 L M12; 7448 R M3; 7444, 17177 2 L p34; 7445, 58562 2 L m12.

VA Hospital Site, Alachua Co., FL: UF 17224 L M12; 53562 R M12;

Pareners Branch Site, Alachua Co., FL: UF 53568 L M12.

McGehee Farm, Alachua Co., FL: UF 17209 R P34; 7246 L P34; 9557, 45613 2 L M12; 17218, 17219, 53549 3 R M3; 11825 L dp34; 17165 L p2; 17194 L p34; 17140C, 45626 2 R m12; 9775, 17101 2 L m12.

Haile 19A, Alachua Co., FL: UF 65727, 107894 2 L M12; 47323 R p2; 64751 R p34; 107892, 107893 2 R m3.

Mixson's Bone Bed, Levy Co., FL: F:AM 107875 assoc. R P2,P4-M3 and L P2-M3 (MacFadden 1984, fig. 141); F:AM 113623, 113624, 113638, USNM 3306 4 L M12; USNM 3305 L M3.

"Stream Matrix" Horizon, Nichols Mine, Polk Co., FL: UF 24624, 53561 2 L M12; 24650 R dp34; 24632 L p2.

Four Corners Mine, Polk Co., FL: UF 102621 R m12.

Leisey 1C, Hillsborough Co., FL: UF 107529 L p34; 107530 R m12.

Port Manatee Site, Manatee County, FL: UF 107543 L P34; 107542 R m3.

Peace River, near Gardner, Hardee Co., FL: UF 55950 R m12.

Joshua Creek, DeSoto County, FL: UF 17225 L M12.

Withlacoochee River UF locality 4A, Marion-Citrus county line, FL: UF 17204 L maxilla with P2-M3; 45517, 53518, 53519 3 L P2; 17200, 53516 R P34; 45530 R M12; 19622, 53512 2 L M3; 53459, 53482, 53492 3 L p34.

Withlacoochee River UF locality 4X, Marion-Citrus county line, FL: UF 18329 L P34.

Dunnellon Phosphate Mining Region, Marion Co., FL: UF/FGS V-1479 R M12; UF/FGS V-1483, V-1485 2 L M12.

Revised Diagnosis.-- Small-sized *Cormohipparion* with toothrow lengths of 112-123 mm in middle wear-stages. Unworn MSCH of P2 about 37 mm and M12 about 49 mm. Smaller than *C. sphenodus*, *C. occidentale*, or *C. plicatile*. Less unworn crown height than *C. occidentale*, *C. plicatile*, or *C. emsliei*. Ventral border of DPOF less distinctly rimmed than *C. occidentale* or *C. plicatile*, but fossa better developed than in *C. emsliei*. Lower permanent and deciduous second premolars with an enamel fold projecting from the metaconid (or less frequently the paraconid) that in late wear-stages often closes off the metaflexid into an isolated fossettid. Relatively poorly developed pli caballinid on p2-p4, usually absent on m1-m3.

Description.-- Cranial material completely exhibiting the facial region is unknown for *C. ingenuum*. Only two referable specimens (UF 32300 from the Love Site and UF 17204 from the Withlacoochee River 4A locality) preserve portions of the face; each includes only the ventral-most part of the DPOF. On the more complete specimen (UF 17204, Fig. 5A), the ventral portion of the DPOF consists of a moderately deep impression (at least 11 mm) with an unrimmed, sloping ventral border located about 33 mm above the alveolar border of the P4. The border is located just posterior to the infraorbital foramen. On UF 32300, the ventral-most part of the DPOF is located about 37 mm dorsal to the alveolar border of the P3.

Summary statistics of measurements on upper and lower cheekteeth are listed in Tables 3 and 4. The following dental descriptions are based on the largest quarry sample of the species, that from the Love Site, although they generally apply to all referred populations. Chronoclinal differences with older and younger samples are noted in the discussion section. Frequencies (in
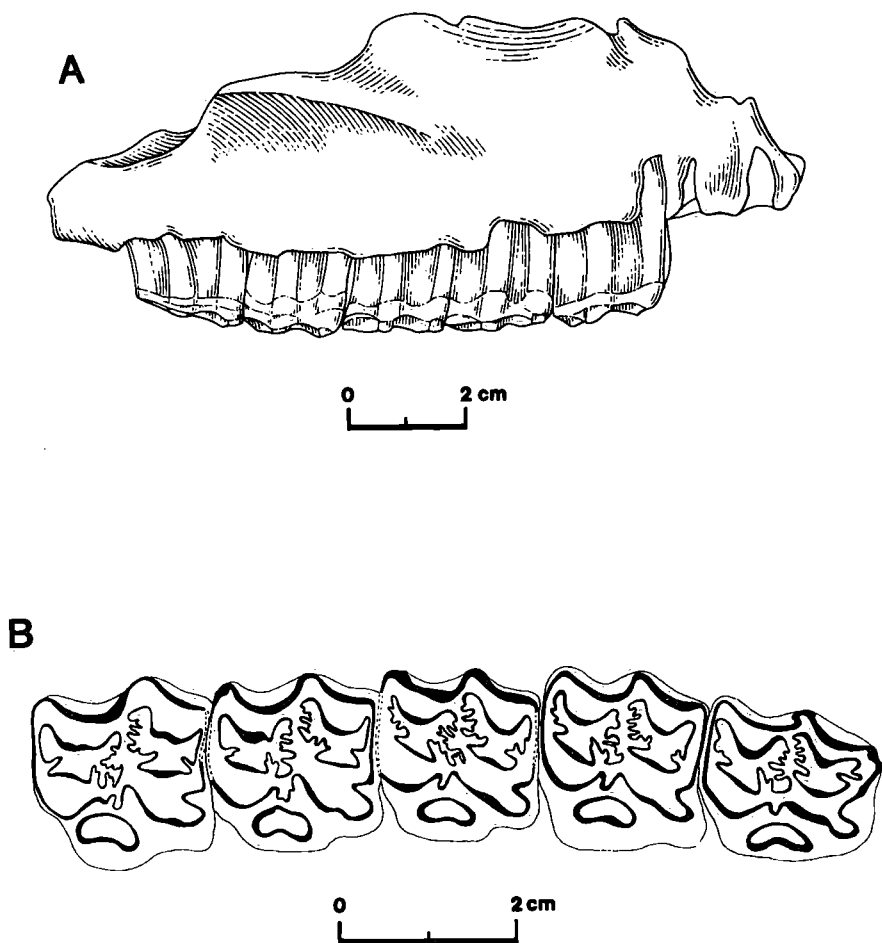
FIGURE 5. Lateral and occlusal views of *Cormohipparion ingenuum* from the Withlacoochee River Site 4A (late early Hemphillian), Marion County, Florida. A. UF 17204, lateral view of right maxilla showing poorly defined ventral margin of dorsal preorbital fossa. B. UF 17204, occlusal view of R P3-M3 (reversed).
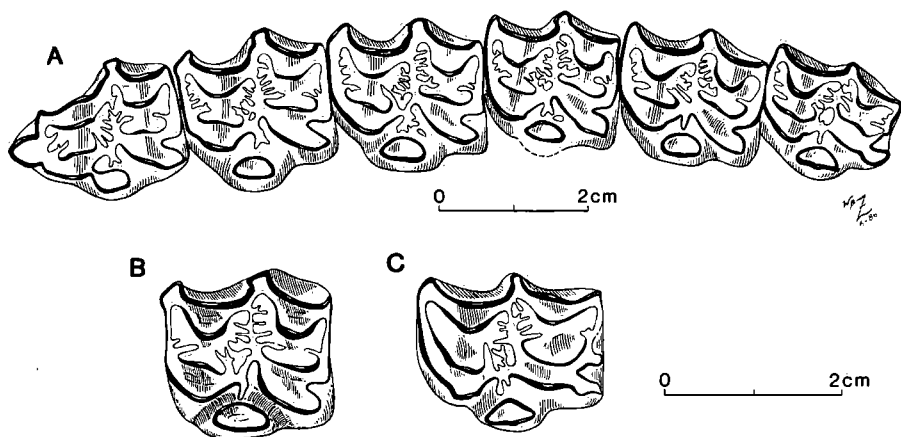
FIGURE 6. Occlusal views of upper cheekteeth of *Cormohipparion ingenuum* from Florida. A. UF 32300, assoc. L P2-M3, Love Site (late Clarendonian), Alachua County. B. UF 18329, L P34, Withlacoochee River Site 4X (late early Hemphillian), Marion County. C. F:AM 113624, slightly worn L M12, Mixson's Bone Bed (early Hemphillian), Levy County.

percent) given for character states pertain only to the Love Site sample. As is typical for *Cormohipparion*, the P2 is the longest upper cheektooth, with a well developed anterostyle (Figs. 4C, 6A, 9A). Upper premolars are characterized by elongate-oval protocones, often with straight or concave lingual borders, that are isolated until late wear (except P2), grooved parastyles for the upper third of the crown, well developed pli caballins and complex fossette borders (Figs. 4D, 5B, 6A, 6B). In the Love Site sample, half (26 of 52 observed specimens) of all P34s contain bifurcated or multiple pli caballins; this includes almost all specimens in early and moderate wear-stages. Most (75%, n = 51) of the P34s have a single, deep, unbranched pli protoloph on the anterior half of the prefossette; the remainder have an additional one to three smaller plications labial to it. The pli protoloph is lost only in very late wear-stages. The posterior half of the prefossette is richly plicated, the large prefossette loop is secondarily plicated with deep folds in early wear, and there are usually four to six total infoldings of varying depth and complexity. The anterior half of the postfossette is somewhat less complex, generally with between two and five folds (96% of observed specimens); the pli postfossette is usually bifurcated, as are one or two of the other plications in early wear-stages. A single, unbranched pli hypostyle is found on most of the P34 (92%, n = 50); it is rarely absent or with accessory folds. The hypoconal groove remains open throughout wear. Unworn or slightly worn MSCH of P2s range from 36 to 38

mm; examples of unworn or slightly worn P34s are rare, but their MSCHs are about 45 mm.

Upper molars are noticeably smaller in occlusal area than P34 (Tables 1, 3), with less well developed styles and generally with shorter, more oval protocones (Fig. 6A, 6C). The lingual border of the protocone is usually convex or straight; occasionally concave, especially in early wear-stages. Pli caballins, while well developed, are more likely to be single (76%, n = 55, Love Site sample) than branched or multiple (18%), but are retained until very late wear-stages (Figs. 5B, 9H). The anterior half of the prefossette most often has a single pli protoloph (56%, n = 55), while 27% also have small accessory plications. The posterior half of the prefossette consists of only a moderately developed (relative to that of the P34) prefossette loop and generally four to six plications. These are smaller and shallower than their counterparts on the P34, and have a greater tendency to disappear with wear (Fig. 9H). The anterior half of the postfossette most often has between three and five plications, and the pli postfossette is often bifurcated in early and moderate wear. The posterior half of the postfossette generally (84%, n = 50) has a single, shallow pli hypostyle (Figs. 6A, 9E-9G). Unworn MSCH of M12 varies from 47 to 51 mm.

Upper deciduous premolars resemble their permanent counterparts in many respects. The fossettes are richly plicated, with persistent pli protoloph and pli hypostyle, the pli caballin is multiple in early and moderate wear-stages, and the lingual border of the protocone is usually straight. The hypoconal groove is deep and persistently open. The styles are very well developed. The protocone often bears a spur in early wear-stages, this is soon lost in the DP34, but connects the protocone with the protoloph in moderate wear-stages of the DP2. They are difficult to distinguish from DPs of *Neohipparion trampasense*, but differ in that the DP2 parastyle is not recurved, and the fossettes are transversely wider. Unworn MSCH of the DP2 is 17-19 mm, that of the DP34 is 20-22 mm.

Only one mandible of *Cormohipparion ingenuum* with a complete symphysis is known (UF 32170, Table 4), as most rami are broken between the canine and the p2. The diastema length (82.3 mm) of UF 32170 is relatively long (73% of ltrl), a synapomorphy of the members of the subgenus *Notiocradohipparion*. Three other Love Site rami referred to *C. ingenuum* (UF 32154, 32172, and 32198) have nearly complete symphyses, but are broken such that the ldl can not be measured. They all are proportioned similar to UF 32170, indicating that the diastema length of the latter specimen is not unusually large for the species.

Lower cheekteeth of *C. ingenuum* demonstrate many phylogenetically important features. They generally resemble lower dentitions of other species of *Cormohipparion*, except for their smaller size (Tables 2, 4, 5). Lower premolars are characterized by: rounded labial borders; large metaconids and

metastylids equal in size and well separated from each other, especially by an anterolingual extension of the entoflexid; ectoflexids that generally partially penetrate the isthmus; and well developed protostylids (Figs. 7, 8, 10A, 10B). As is typical in *Cormohipparion*, the ectoflexid depth is shallower on the p2 than the p34 (Fig. 7A); infrequently, most commonly in p4s, the isthmus may be deeply divided. In early wear-stages, isthmus and paralophid plications are common, and a small pli caballinid is usually present (Table 5, Figs. 8B, 10B). With wear, the ectoflexid deepens, and the plications and pli caballinid fade (Fig. 7B). Protostylids are slightly less prominent than in *C. plicatile*. As is usual in *Cormohipparion*, they first appear as isolated structures, but quickly connect to the protoconid. On most p2s (and dp2s), there is an anterolabial plication that emanates from the metaconid (Figs. 7A, 8A). Infrequently, the plication originates instead from the paraconid, and projects posteriorly, or both plications can be present (e.g. Figs. 8B, 10A). The plication first appears on the occlusal surface during early to middle wear-stages, although the crown height at which it becomes exposed varies. In later wear-stages, it commonly connects the metaconid and paraconid, isolating a portion of the metaflexid as a fossettid (Figs. 7B, 8A, 8C). While similar plications are occasionally found on p2s of other species of *Cormohipparion* and other genera, in no other sample is its appearance so frequent (except for *C. emsliei*). Unworn mcch of p2 is about 35 mm, and 43-47 mm for the p34.

The lower molars of *Cormohipparion ingenuum* are similar in morphology to those described below for *C. plicatile*, but have shorter unworn crown heights and are much smaller (Tables 2, 4; Figs. 4E, 7, 10A-10E). Pli caballinids are very rare and if present occur only in slightly worn individuals (m1 in Fig. 10C). Plications on the isthmus and paralophid are common (Table 5), especially in slightly worn teeth. Unworn or slightly worn m12 mcch is about 50 mm.

Lower deciduous premolars of *Cormohipparion ingenuum* have relatively shallow ectoflexids; elongated metaconids, metastylids, and entoconids; and moderately developed pli caballinids in early wear. With wear, however, the ectoflexids deepen, the metaconids and metastylids become more oval, and the pli caballinids are lost or become rudimentary (Fig. 10C). In late wear-stages, relatively small, generally elongate-oval ectostylids appear on the occlusal surface (Figs. 8A, 10C). They are not as prominent as in *C. emsliei, C. occidentale*, or *C. plicatile*, and can be especially rudimentary on the dp2. Unworn dp34 mcch is about 21-23 mm.

Discussion.-- Four major topics are presented in this section: (1) a review of previous phylogenetic hypotheses regarding *"Hippotherium" ingenuum* Leidy; (2) a demonstration that the holotype of *"H." ingenuum* contains sufficient characters to unambiguously associate it with one, and only one, species; (3) a discussion of the phylogenetic relationships of this species; and (4) a description of the geographic distribution and chronoclinal variation
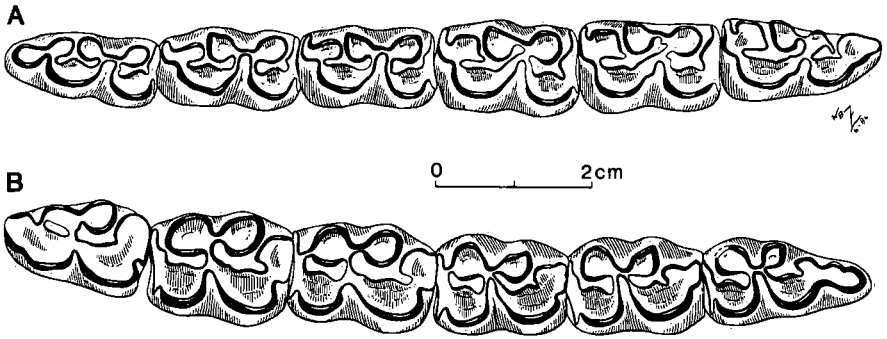
FIGURE 7. Occlusal views of lower cheektooth series of *Cormohipparion ingenuum* from the Love Site (late Clarendonian), Alachua County, Florida. A. UF 32172, moderately worn R p2-m3. B. UF 32101, heavily worn L p2-m3. Note the metaconid plication on the p2.
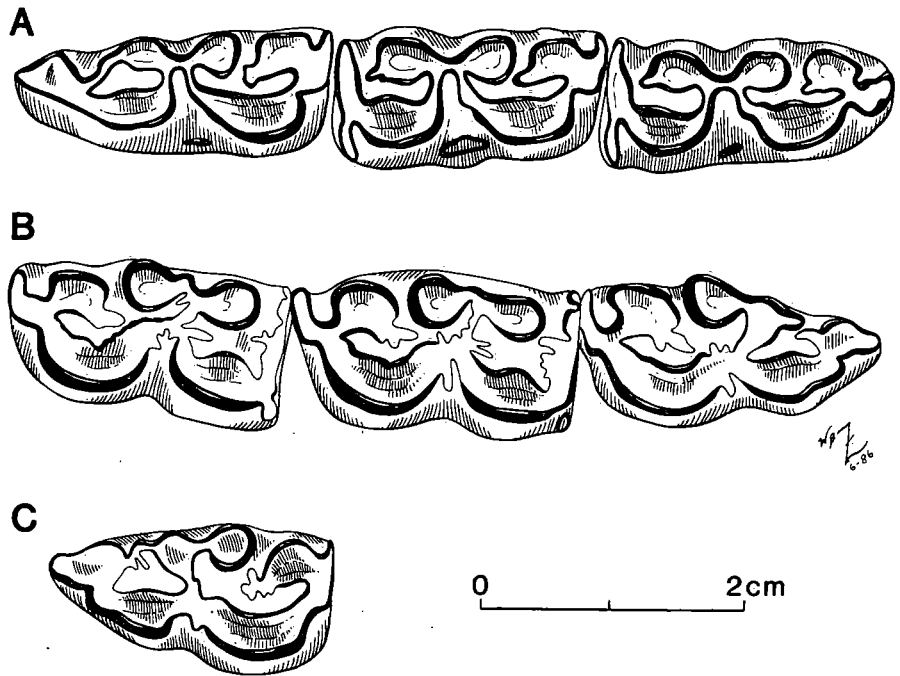
FIGURE 8. Occlusal views of lower cheekteeth of *Cormohipparion ingenuum* from Florida. A-B. Love Site (late Clarendonian), Alachua County. A. UF 32294, moderately worn assoc. L dp2-dp4. B. UF 32171, slightly worn assoc. R p2-p4. C. UF 24632, L p2, "Stream Matrix" Horizon, Nichols Mine (probably late Clarendonian), Polk County.
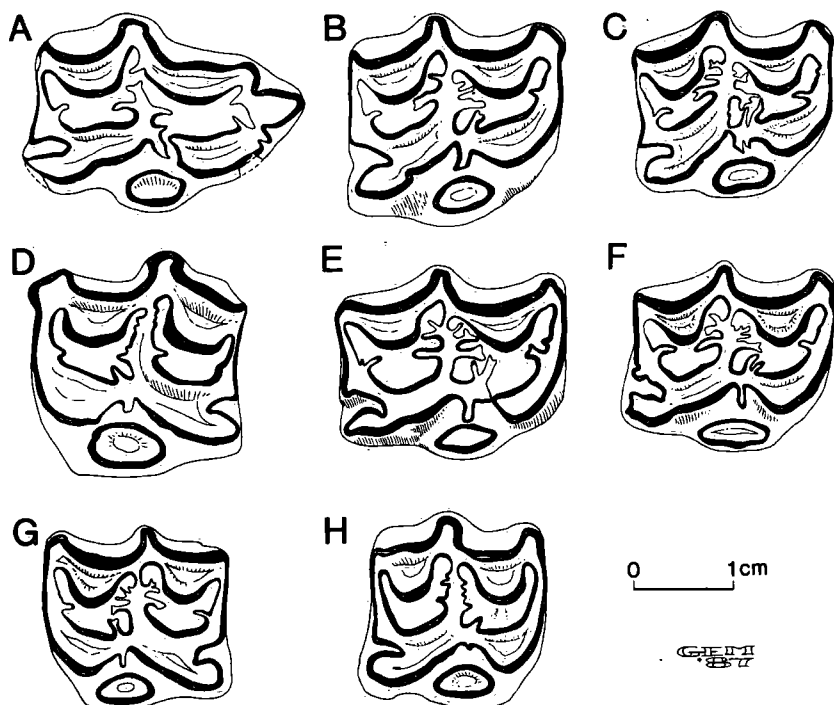
FIGURE 9. Occlusal views of upper cheekteeth of *Cormohipparion ingenuum* from the Agricola Road Site, Hookers Prairie Mine (early Clarendonian), Polk County, Florida. A. UF 98108, R P2. B. UF 98106, R P4. C. UF 107564, R P34. D. UF 98101, L P4, late wear-stage. E. UF 98117, R M12, early wear-stage. F. UF 98118, R M12. G. UF 98121, L M12. H. UF 98102, R M2, late wear-stage.

observed in the referred populations of this taxon. The generic affinities of *"H."* *ingenuum* have remained enigmatic primarily due to the paucity of topotypic material. This has led to a number of equid populations from the western United States being incorrectly considered conspecific with it. The newly referred samples described here for the first time give an accurate representation of the size and variation of its upper and lower cheekteeth and at least a partial indication of its facial morphology. These combine to suggest a new generic assignment for *"H."* *ingenuum* and to falsify all previous hypotheses.

In his initial, brief descriptions of *"Hippotherium"* *ingenuum* and *"H."* *plicatile*, Leidy (1885; 1887) made no attempt to compare them with other taxa, except for *"H."* *venustum*, an inadequately known species from South Carolina. The holotype of the latter is lost, and it is best regarded as a *nomen dubium* (MacFadden 1984:126). Cope (1889) synonymized *"H."* *ingenuum* with *"H."*
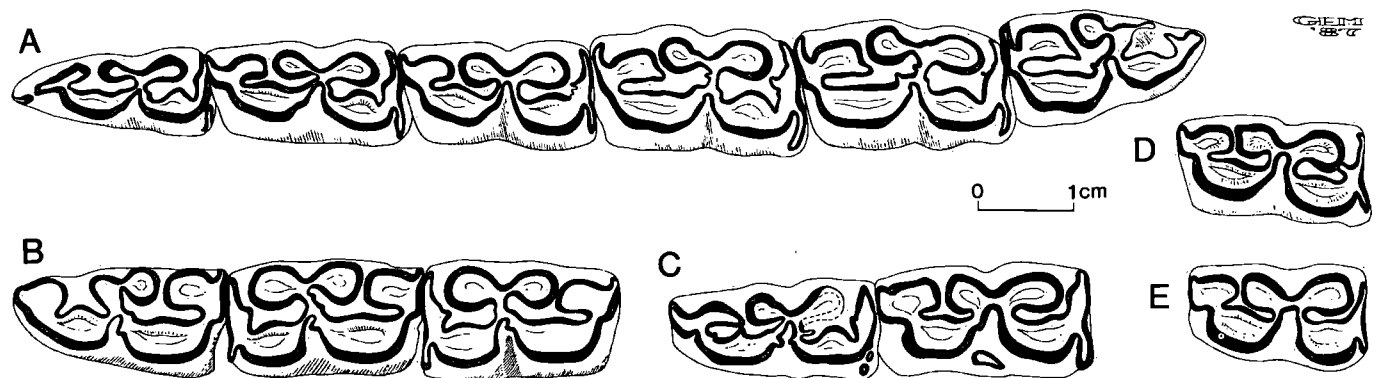
FIGURE 10. Occlusal views of lower cheekteeth of *Cormohipparion ingenuum* from the Agricola Road Site, Hookers Prairie Mine (early Clarendonian), Polk County, Florida. A. UF 98126, associated R p2-m3. B. UF 98129, associated L p2-p4. C. UF 98136/98145, probably associated R dp4-m1. D. 98146, R m12. E. UF 98154, R m12.

gratum without comment, and Lucas (*in* Leidy and Lucas 1896) and Hay (1902) followed this synonymy. *Pseudhipparion gratum* is now known to differ greatly from "*H.*" *ingenuum* in size, facial morpholgy, and enamel pattern (Webb 1969a; Webb and Hulbert 1986). Leidy's (1885) referral of *ingenuum* to the genus *Hippotherium* reflected no particular phylogenetic significance. During this period, all hipparionine and many merychippine species were placed in *Hippotherium*, a name then considered valid for most if not all Eurasian and North American hipparionines (e.g. Cope 1889). Starting about 1900, *Hipparion* replaced *Hippotherium* as the commonly used genus for hipparionine equids (e.g. Hay 1902).

Gidley (1907) resurrected Leidy's species from Cope's synonymy, and it has subsequently been considered a valid species. Gidley's use of the binomen "*Hipparion*" *ingenuum* did have phylogenetic significance, however, as he felt that "*H.*" *ingenuum* (along with "*H.*" *plicatile* and "*H.*" *venustum*) "...belong to an American branch of the *Hipparion* group of the Old World" (Gidley 1907:906). Gidley's separation of hipparionines into two genera, *Neohipparion* (for New World species) and *Hipparion* (primarily for Old World species), was not accepted by his contemporaries Matthew and Osborn (see e.g. Osborn 1918:173), who continued to refer all hipparionines to a single, broadly defined genus. Matthew (1924) concluded that the Miocene hipparionines named by Leidy from Florida and South Carolina (including "*H.*" *ingenuum*) were not especially related to Old World species, a view also endorsed by Simpson (1930). Matthew and Stirton (1930:354) and Simpson (1930:188) placed "*H.*" *ingenuum* in Matthew's (1926) subgenus *Nannippus*. Stirton (1940) raised *Nannippus* to the status of genus, and included "*H.*" *ingenuum* in his listing of species of *Nannippus*. None of these authors stated any specific reasons for this referral, but presumably it was based on the relatively small size of the holotype (Table 1). Most subsequent references to the species have been to "*Nannippus*" *ingenuus* (e.g. Quinn 1955; Forstén 1975; MacFadden 1984).

Large samples of Clarendonian and early Hemphillian equids are now known from Florida. Four species of medium- to large-sized hipparionines (UTRL between 115 and 140 mm) are present; as the oldest available name, *Cormohipparion ingenuum* should apply to one of them. Two, although of similar size as the holotype of *C. ingenuum*, are distinguished from it primarily on qualitative grounds. One, referred to *Neohipparion trampasense* by MacFadden (1984) and Hulbert (1987b), differs in its more elongated protocone, narrower fossettes, and stronger metastyle. *Hipparion* sp., cf. *H. tehonense*, described below, differs in its rounded lingual protocone margin, simpler fossettes, and weaker pli caballin. The holotype of *C. ingenuum* (and that of *C. plicatile*) falls within the observed range of enamel morphology of the two remaining populations, which are very similar to each other and are distinguished primarily by size. That the two do in fact represent distinct species is emphasized by differences in DPOF morphology, diastema length, p2
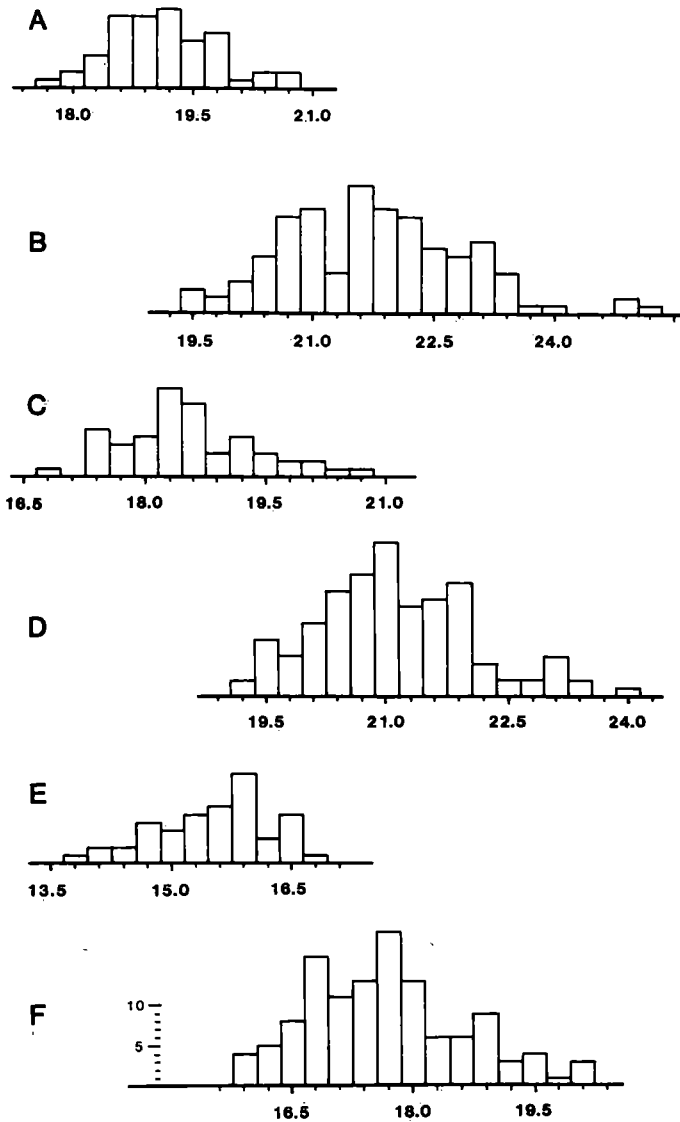
FIGURE 11. Histograms of the distribution of occlusal anteroposterior length (APL), transverse width (TRW), and basal crown length (BAPL) for combined Florida samples of upper third and fourth premolars (P34) of *Cormohipparion ingenuum* (A, C, and E) and *C. plicatile* (B, D, and F). Analized samples exclude very slightly worn and very heavily worn individuals. A-B. P34 APL; n = 53 for *C. ingenuum*, n = 121 for *C. plicatile* (similarly, the first value given in the following for sample size is that of *C. ingenuum*, the second *C. plicatile*). C-D. P34 TRW; n = 53, 123. E-F. P34 BAPL; n = 48, 121. Distributions are interpretted as being primarily bimodal with varying degrees of overlap between the two species. All measurements in millimeters.

morphology, and unworn crown height.   However, the only significant difference between isolated, worn upper cheekteeth is size.

   For *Cormohipparion ingenuum* and *C. plicatile* to both be valid, distinct species, it is necessary to show: (1) that two different-sized populations of *Cormohipparion* exist at Mixson's Bone Bed and other nearby localities; (2) that the holotype of *C. ingenuum* uniquely matches upper cheekteeth of the smaller-sized population in size and morphology; and (3) that the holotype of *C. plicatile* matches upper cheekteeth of the larger-sized population. If only a single population exists, or if the two match with the same population, then *C. plicatile* must be considered a junior synonym of the older name, *C. ingenuum*. If one (or both) can be shown to be specifically undiagnostic by falling within the observed range of variation of more than a single species, then it should be considered a *nomen dubium*. Leidy and all subsequent authors have correctly identified the type of *C. ingenuum* (USNM 3306, Fig. 1) as a true molar. However, since its initial description, the holotype tooth of *C. plicatile* (USNM 3292) has also been described as a "molar" (Leidy 1887:310; Osborn 1918:192; MacFadden 1984:170). Leidy used the term to refer to both true molars and premolars. Leidy and Lucas (1896:50) described USNM 3292 as a molar, "...probably the third...," presumably a reference to a P4. There are several features of the specimen that indicate that it is indeed a premolar, and not a molar.   These include the relatively large and widely open parastyle and mesostyle, and the complex pli caballin.   Most importantly, the mesostyle angles anteriorly in labial view when the occlusal surface is face down, a distinguishing characteristic of P34s and not M12s (Bode 1931).   That the holotype of *C. plicatile* is a premolar is important, because the size difference between the holotypes of *C. plicatile* and *C. ingenuum* (Table 1) might merely reflect the typical significant size differences between P34s and M12s of *Cormohipparion*.   The range in size and CV of the combined sample are greater than that observed in other single-species quarry or faunal populations (Table 6), strongly suggesting the presence of more than a single species. Frequency distributions of occlusal and basal crown dimensions (Figs. 11, 12) are bimodal, but do indicate an appreciable amount of overlap between the two populations. Much of the apparent overlap in APL is lessened when the data are adjusted for crown height. The Mahalanobis distances between the two populations are significantly different (at $p < 0.01$) for both of the separately analyzed samples of P34 and M12. The holotype of *C. ingenuum* clearly clusters with the molars of the smaller-sized population both in univariate and multivariate analyses (Tables 1, 3; Figs. 11-13), indicating that the smaller sample should be referred to the older name. The holotype of *C. plicatile*, while within the range of only the larger-sized population for TRW and BAPL (Tables 1, 3; Fig. 11D, 11F), has a relatively small APL (19.7 mm) that is within the observed range of both populations (Table 3; Fig. 11B). Linear discriminant analysis separates the two species with very little overlap
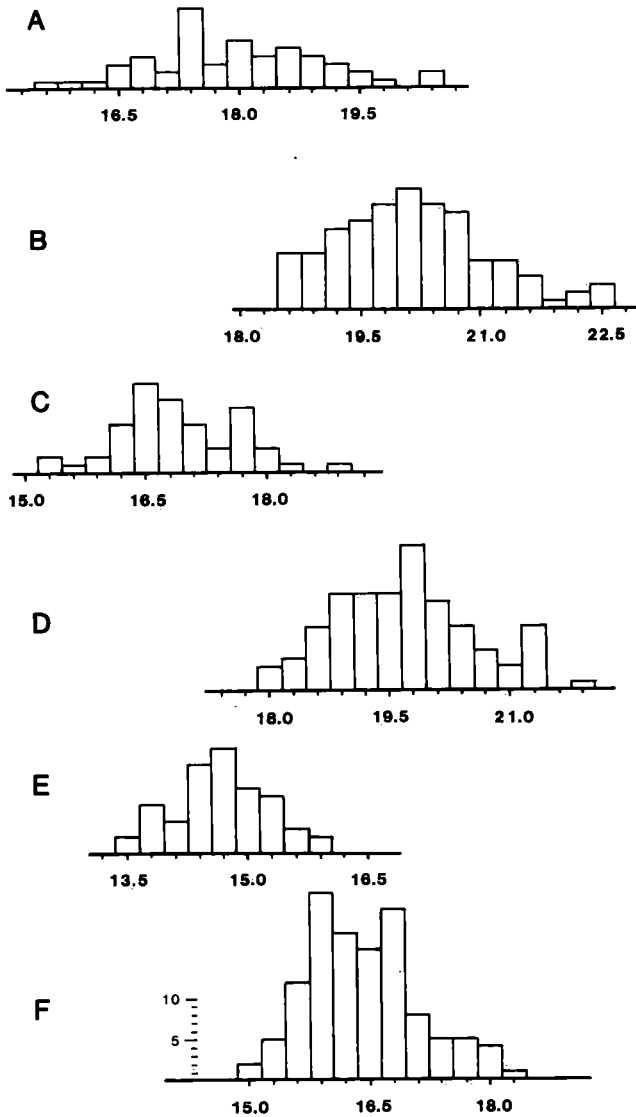
FIGURE 12. Histograms depicting the distribution of occlusal anteroposterior length (APL), transverse width (TRW), and basal crown length (BAPL) for combined Florida samples of first and second molars (M12) of *Cormohipparion ingenuum* (A, C, and E) and *C. plicatile* (B, D, and F). Analized samples exclude very slightly worn and very heavily worn individuals. A-B. M12 APL; n = 52, 110. C-D. M12 TRW; n = 53, 105. E-F. M12 BAPL; n = 56, 120. Distributions are interpretted as being primarily bimodal with varying degrees of overlap between the two species. All measurements in millimeters.
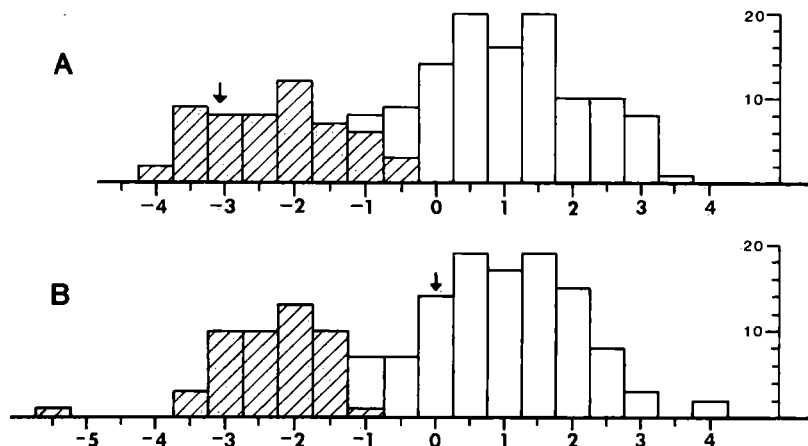
FIGURE 13. Results of canonical discriminant analysis between *Cormohipparion ingenuum* (shaded) and *C. plicatile* (not shaded) using four variables, APL, BAPL, TRW, and PRL. Variables standardized to $x = 0$ and $s = 1$ before analysis. Separate analyses performed for a sample of combined upper first and second molars (A) and a sample of upper third and fourth premolars (B). Sample sizes are, for *C. ingenuum*, 48 premolars and 55 molars; for *C. plicatile*, 110 premolars and 107 molars. Histograms show distribution of canonical scores; actual results produced no overlap for the premolars, and only three molars were "misidentified" (i.e. discriminant analysis would assign them to the other species). The holotypes of both species were included in the analysis (their scores indicated by arrows), and each fell within the OR of its respective population. The results are consistent with there being two morphospecies of *Cormohipparion* present in the late Miocene of Florida.

and places USNM 3292 with the larger sample (Fig. 13). Thus, the link between USNM 3292 and the larger-sized population, while somewhat more uncertain than that of the type of *C. ingenuum* and the smaller-sized population, is reasonable. Also, the best matches for the peculiar fossette morphology of USNM 3292 are found in the larger-sized population (e.g. UF 17211, Fig. 16B). The conditions for validation of both *C. ingenuum* and *C. plicatile* set forth above are thus apparently met, although the holotype of *C. plicatile* is atypical for certain characters relative to the majority of specimens referred to that species. These are judged to reflect individual variation rather than species-level differences.

Qualitative analyses of the dental material described above indicate that *"Hippotherium" ingenuum* is more closely related to *C. sphenodus* and *C. occidentale* (excluding other species from Florida) than to species from any other hipparionine genus from North America, and that it can be referred to *Cormohipparion sensu* MacFadden (1984). *C. ingenuum* shares the following features with *C. sphenodus* and *C. occidentale* which in combination serve to distinguish them from other North American hipparionine genera: high, well developed ectostylids on deciduous lower premolars; lower permanent

premolars with moderately reduced ectoflexid depth and moderate pli caballinids in early wear-stages; high frequency of plicated isthmuses and paralophids; strong protostylids on p3-m3 and dp34; p2 and P2 much longer than p34 and P34 with expanded paraconids and anterostyles, respectively; oval or elongate-oval protocones isolated until late wear-stages; and highly complex and intricately plicated fossettes and pli caballins until at least middle wear-stages. While some of these character states evolved independently in other hipparionine genera, in combination they support the referral of *ingenuum* to *Cormohipparion* (see also phylogenetic section below). This assignment can be tested with the discovery of more complete material, especially well preserved skulls.

References to *C. ingenuum* outside of Florida have been relatively infrequent. Quinn (1955:73) listed both *Nannippus tehonensis* and *N. ingenuum* [sic] as occurring in the Lapara Creek Fauna of the Texas Gulf Coastal Plain. Forstén (1975) later referred the entire sample of medium-sized hipparionines from both the Lapara Creek and Clarendon faunas to *Nannippus* cf. *ingenuum*. She gave no specific reasons for her referral, and presented no comparisons with material from Florida. MacFadden (1980; 1984) referred the same population from the Clarendon Fauna to *H. tehonense*, and a portion of the Lapara Creek sample is also referable to this species of *Hipparion*. Most of the other specimens from the Lapara Creek Fauna included in "*Nannippus* cf. *ingenuum*" by Forstén (1975) are referable instead to *Nannippus* s.s. (Hulbert 1987a). Only two specimens from Texas appear to represent *C. ingenuum*, TMM 31204-1 and 31081-501. Although other Lapara Creek specimens might belong to this taxon, they are isolated teeth that are best regarded as specifically and generically indeterminant. It is worth noting that this is a rare (perhaps unique) instance of Quinn (1955) underestimating the taxonomic diversity of a group of Gulf Coastal Plain equids.

MacFadden (1984:132) synonymized "*Nannippus*" *ingenuus* and *N. lenticularis* (a late Hemphillian species particularly well known from the Coffee Ranch, Edson, and Uptegrove localities of the Great Plains) "...based on overall similarity in size, crown height, and dental pattern... ." This synonymy, if valid, would extend the range of *C. ingenuum* north of the Gulf Coastal Plain to Nebraska. However, examination of large numbers of individuals of both taxa fails to substantiate MacFadden's synonymy. While of similar size ("*H.*" *ingenuum* is slightly larger on average, but observed ranges of tooth length and width overlap), there are numerous important differences between the two. In *C. ingenuum*, a moderately developed DPOF is located posterior to the infraorbital foramen. In *N. lenticularis*, the posterior cheek region does not contain a fossa, but according to MacFadden (1984:130) there is a small fossa located anterior to the infraorbital foramen. This observation is based on a single specimen, F:AM 113731. I believe that this feature is an artifact of the preservation and/or preparation of this particular specimen, and that most of

what has been interpreted as a fossa is the exposed inner wall of a maxillary sinus. In any event, the facial regions of the two are different, even with our presently inadequate knowledge of the cranial features of both species. Significant dental differences between the two taxa are:

1. Unworn crown height of upper and lower third and fourth premolars of *C. ingenuum* is about 45 mm, of first and second molars about 50 mm. In *N. lenticularis*, unworn P34 crown height is about 50 mm, and 57 mm for M12.

2. In *C. ingenuum*, the P2 and p2 are much longer than the other premolars, with well developed anterostyles and paraconids, respectively. In *N. lenticularis*, they are relatively short, with poorly developed anterostyles and paraconids. The former is characteristic of *Cormohipparion* and *Neohipparion*, the latter condition is found in *Nannippus* and *H. tehonense*. A reduced anterostyle is a derived character state for hipparionines (see below).

3. In *C. ingenuum*, pli caballins are well developed, frequently bifurcated or multiple, and persistent throughout wear. In *N. lenticularis*, pli caballins are at best moderately developed, not branched or multiple, and are often absent or lost with wear (e.g. F:AM 111731, MacFadden 1984, Fig. 98D).

4. In *C. ingenuum*, fossette plications are very complex, often deep and bifurcating. In *N. lenticularis*, fossette plications are shallow and usually simple, with a much greater tendency for the pli hypostyle to be absent.

5. In *C. ingenuum*, the lingual border of the protocone is often straight or concave, especially in premolars. In *N. lenticularis*, it is nearly always convex. The protocone also tends to connect to the protoselene much earlier in the premolars of *N. lenticularis*, at MSCHs as great as 25 mm.

6. In *C. ingenuum*, the protostylid is prominent and is isolated from the protoconid only for a short period of wear. In *N. lenticularis*, the protostylid is small, usually remains isolated from the protoconid until very late wear-stages, and is occasionally absent (see also Dalquest 1983).

7. In *C. ingenuum*, the metaconid of the p2 and dp2 typically have an anterolabial plication that closes off the metaflexid. In samples of *N. lenticularis*, such structures are absent or very rare.

There are additional, minor, differences between the cheekteeth of the two taxa, but those listed (plus their respective cranial morphologies) suffice to indicate that they belong in separate species (and genera). MacFadden (pers. comm.) has suggested that the differences listed above represent chronoclinal variation, but in my opinion they are of greater magnitude than those observed between early and late populations of any other equid species with a long, well

documented chronologic range (e.g. *Neohipparion trampasense* or *C. occidentale*). Typically in those cases, younger populations show more advanced features than those observed in more rudimentary form in the older population. Samples of intermediate age are of intermediate grade. With regard to C. *ingenuum* and *N. lenticularis*, some of the features of the younger taxon (those numbered 3, 4, 5, and 7) are more primitive than those of the older. Others (2 and 6), which are derived in the younger population, are not observed in any rudimentary or incipient form in the older samples. *N. lenticularis* is best considered a distinct, valid species.

Cormohipparion ingenuum is known from three periods of time: early Clarendonian (ca. 10-11 Ma, Lapara Creek and late Agricola Faunas); latest Clarendonian-early Hemphillian (ca. 8-9 Ma, Love Site, McGehee Farm, Haile 19A, Mixson's, i.e. the Archer Fauna of Webb and Hulbert 1986); and late early Hemphillian (ca. 6-7 Ma, e.g. Port Manatee, Withlacoochee River 4A, 4X, and Dunnellon sites). The Honduran sample (see below) may date from either of the two latter periods. As might be expected in such a long-ranging taxon, some morphological differences exist between populations from different eras. Unlike those described above, the differences are minor, and more primitive states are observed only in older populations. Unfortunately, the youngest samples are the most poorly known; their small sample sizes prevent detailed analysis and permit only specific identification. However, detailed comparisons can be made between the cheekteeth of the oldest and intermediate populations.

The sample of *Cormohipparion ingenuum* from the Agricola Fauna (material from Hookers Prairie, Phosphoria, and Silver City mines in referred specimens listing) is clearly intermediate in size between C. *ingenuum* and C. *plicatile* from the Archer Fauna (Tables 1-4, Figs. 9, 10). This is the case for mean P34 and M12 APL, TRW, and BAPL. The sample of P2s from the older fauna is too small for reliable analysis. Mean p2, p34, and m12 apl and bapl are also intermediate between average values for C. *ingenuum* and C. *plicatile* from the Love Site (Table 4), but are all nearer the means for C. *ingenuum*. Mean atw and ptw, however, are not statistically different from the Love Site sample of C. *ingenuum* for all lower cheekteeth. That the Agricola Fauna sample belongs to C. *ingenuum* and not C. *plicatile* nor their common ancestor is suggested by two characters. The shape of the lingual border of the protocone varies, but in 4 of 7 premolars and 8 of 12 molars it is straight or concave (Fig. 9C, 9D, 9F-9H). In the sample of p2s, 4 of 7 display a plicated metaconid on the occlusal surface (Fig. 10A), a much greater frequency than that state is observed in C. *plicatile*. Flattened labial protocone borders and plicated p2 metaconids are derived character states uniting C. *ingenuum* and C. *emsliei* (see below). Thus their appearance in the Agricola Fauna sample, although in lesser frequencies than observed in younger populations, suggests phylogenetic affinity with the C. *ingenuum-C. emsliei* clade. With their

toothrow lengths of 112-130 mm, *C. ingenuum* and *C. emsliei* are also smaller than their sister taxa in *Cormohipparion*, that have average toothrow lengths greater than 130 mm. The Agricola Fauna sample referred to *C. ingenuum* has toothrow lengths of about 120-125 mm (Table 4). This moderate size is most parsimoniously regarded as another synapomorphy uniting it with *C. ingenuum*. In a lineage decreasing in size with time, older populations will not unexpectedly be larger than younger ones. In a more simplistic but less parsimonious scenario, the Agricola Fauna sample could represent the common ancestor of *C. ingenuum* and *C. plicatile*. But this would require three reversals in the *C. plicatile* lineage to reacquire its primitive size, protocone shape, and p2 metaconid morphology. A more likely phylogenetic hypothesis suggests instead that the cladogenetic event that resulted in *C. ingenuum* and *C. plicatile* occurred prior to the early Clarendonian, and that there is a chronologic gap in the first appearance of *C. plicatile* of at least 2 million years. The preceding has emphasized the differences between the older and younger populations of *C. ingenuum*, rather than their similarities (Figs. 5-10). As an example of the latter, the Agricola Fauna sample includes several examples of unworn or slightly worn P34s, M12s, p34s, and m12s. These demonstrate identical values for unworn MSCH and mcch as specimens from the Love Site, about 45 mm for P34 and p34, 50 mm for M12 and m12.

Webb and Perrigo (1984) referred a sample of teeth from the Gracias Formation of Honduras to "*Hipparion*" *plicatile*. As they noted, in many respects this sample does compare favorably with *Cormohipparion plicatile* as defined in this study. However, the size of the specimens, as listed by Webb and Perrigo (1984:244), clearly indicates a referral instead to the smaller *C. ingenuum* (Tables 1, 2). The north-central Florida and Central American samples are remarkably similar, considering the geographic distance separating them. One difference is a slightly better developed pli caballinid in the Honduran sample. It is more persistent on some of the p2-p4 than is typical for the Florida sample, and even occurs on some molars. It is not nearly so well developed as in *C. emsliei*, however, nor does the Honduran sample have the derived stylar features and extreme fossette complexity observed in the Pliocene species from Florida (Hulbert 1988b). The relatively advanced nature of the Honduran sample of *C. ingenuum* emphasizes Webb and Perrigo's (1984) conclusion that the age of the Gracias Fauna is early Hemphillian rather than late Clarendonian. The other major study of the Gracias Fauna (Olson and McGrew 1940) also recognized a hipparionine, which was referred to *Neohipparion montezuma*. The heavily worn molar they figured (plate 2E) may indeed represent *Neohipparion*, as its PRL (8 mm) falls outside the OR of *C. ingenuum* (Table 3). The more abundant UF sample from this fauna does not contain any specimens referable to *Neohipparion*.

As noted by Simpson (1930), *Cormohipparion ingenuum* is commonly found in Florida; however, typically it is less abundant than its congener, *C.*

plicatile. For example, the Love Site sample consists of a minimum number of 62 individuals of *C. ingenuum* and 83 of *C. plicatile* (MacFadden and Hulbert in press). Its biostratigraphic range in Florida as recognized here extends from the early Clarendonian to the late early Hemphillian. Simpson (1930, fig. 20C) illustrated a molar labelled as *C. ingenuum* that is instead *Nannippus minor* (UF/FGS V-1426). The specimen is less complete than represented in the figure and slightly smaller. The slightly worn molar he figured as *C. plicatile* (Simpson 1930, fig. 20B) is referable to *C. ingenuum* instead. Diagnostic features of this specimen (UF/FGS V-1485) are its narrow protocone with a flattened lingual border and its small TRW. *C. ingenuum* has often been recognized from the late Hemphillian Upper Bone Valley Fauna of Florida (Sellards 1916; Simpson 1930; Webb and Tessman 1968; Webb 1969b), either as "*Hipparion*" *ingenuum* or "*Nannippus*" *ingenuus*. Most of these records are referable to the more advanced species, *C. emsliei*. Others are either generically indeterminant or referable to *N. minor*. Both *C. plicatile* and *C. ingenuum* are recognized from the Bone Valley Formation (see referred specimens listing and Figs. 4C-4E, 8C, 9, 10), but are interpreted as being derived from older horizons than that which produces *C. emsliei*. Based on the joint occurrence with *C. plicatile* (see below), *Pseudhipparion skinneri* (Webb and Hulbert 1986), *Neohipparion trampasense*, and *Calippus cerasinus* (Hulbert 1988a), the Nichols Mine "Stream Matrix" Horizon records are either late Clarendonian or early Hemphillian. The early Clarendonian age of the late Agricola Fauna specimens discussed above is based on their co-occurrence with *Pseudhipparion curtivallum*, *Nannippus* n. sp., *Calippus martini*, *Protohippus supremus*, and *Hypohippus* sp., cf. *H. affinis* (Hulbert 1988a).

Cormohipparion (Notiocradohipparion) plicatile (LEIDY), 1887
Figs. 14-19; Tables 1-7

Hippotherium plicatile LEIDY 1887:310; COPE 1889:444; LEIDY and LUCAS 1896:50; MACFADDEN 1984:170-174 (in part, not fig. 141).
Hipparion plicatile (Leidy), HAY 1902:620; GIDLEY 1907:905; HAY 1916:41-42; OSBORN 1918:192; SIMPSON 1930:187-188 (in part); HIRSCHFELD and WEBB 1968:249; JACKSON 1978:53; WEBB and PERRIGO 1984:243-245 (in part).
Hipparion sp., SIMPSON 1930:176.
?*Hipparion plicatile* (Leidy), STIRTON 1940:184.
Neohipparion cf. *leptode* Merriam, HULBERT 1982:159 (in part).
Cormohipparion plicatile (Leidy), HULBERT 1988a:274, 280; HULBERT 1988b:454.

Type Specimen.-- USNM 3292, a R upper cheektooth, probably a P4 (MacFadden 1984, fig. 140).
Type Locality and Horizon.-- Mixson's Bone Bed, Levy County, Florida. Alachua Formation, early Hemphillian.

Distribution.-- Very late Clarendonian through early Hemphillian (about 6.0 to 9.0 Ma) of central Florida.

Referred Specimens.-- Coffrin Creek, Alachua Co., FL: UF 17129 RP2; 17178A L p2; 17178B R p34; UF 58552 R m12; 17223 R m3.

Gainesville Creek, Alachua Co., FL: UF 7441 LP34; 7437 L m3.

Love Site, Alachua Co., FL: UF 32257 partial skull with R and L I2-I3,P3 and R P4; 32260 assoc. R maxilla with P4-M2 and L maxilla with P4-M3; 32250 R maxilla with P4-M3; 32255 L maxilla with DP2-M1; 35891 L maxilla with P4-M1; 32267 assoc. R DP2-DP4; 96622 assoc. R DP3-DP4; 27993, 32262, 32263 3 assoc. R and L P2-M3; 32283 assoc. R P2,P4-M1 and L M1-M2; 32270 assoc. R P2-M1,M3 and L M1-M3; 32265 assoc. R and L P2-M2; 32264 assoc. R P3-P4,M2-M3 and L P4-M3; 27316 assoc. R P2-M3 (MacFadden 1984, fig. 144); 36289 assoc. R M1-M2 and L P4; 32276, 32295 2 assoc. L DP2-DP4; 96619-96621 3 assoc. L DP3-DP4; 96618 assoc. L DP3-DP4 and R DP3; 32285 assoc. L DP2-M1; 32266, 96933 2 assoc. L P2-M2; 53284 assoc. L P3-P4; 35902-35905, 35920-35922, 35926, 35927, 35929, 35940, 35944, 35946, 35948, 35952, 35954, 35957, 35960, 35961, 96623, 96937 21 R DP2; 36078, 36081, 36084, 36087, 36088, 36090, 36096, 36097, 36100, 36103, 36105, 36112, 36114, 36115, 36119, 36121, 36128-36130, 36132, 36137, 96881 22 L DP2; 96624-96649, 96935, 96936 28 R DP34; 69812, 96650-96685 37 L DP34; 35967, 35970, 35976-35978, 35984-35985, 35988-35989, 35994, 36000-36002, 36005-36006, 36008, 36010, 36015, 36031-36035, 36037, 36040, 36044, 36047, 36051, 36063, 36068-36071, 36263, 36266, 36269 37 R P2; 36143, 36147, 36151, 36153, 36156, 36158-36159, 36162, 36165-36166, 36169, 36171, 36177, 36181-36182, 36184-36186, 36188, 36190, 36193-36194, 36201, 36205, 36209, 36211, 36218-36219, 36223, 36225-36227, 36237, 36243-36244, 36247, 36250, 36253, 36255 40 L P2; 50641, 50643-50644, 53287-53289, 53291-53294, 53296, 53298-53299, 53301, 53423-53424, 62326-62350, 62438, 62447, 69810 44 R P34; 53302-53328, 53373, 53422, 62306-62324, 62381, 62384, 69809 50 L P34; 50642, 50645, 50647-50648, 53329-53332, 53334-53340, 53344-53349, 53351-53353, 53416, 53417, 62351-62365, 69811 42 R M12; 53154-53156, 53354-53360, 53362-53367, 53369-53371, 53374, 53377-53379, 53418-53421, 62367-62376, 62378-62380, 62382-62383, 62385-62389, 62408 48 L M12; 96388-96402 15 R M3; 96403-96428 26 L M3; 32119 R mandible with dp2-dp3; 32157 assoc. R and L mandibles with p2-p3,dp4,m1-m2; 32180 assoc. mandibles with R m2-m3 and L p3-m3; 27317 R mandible with p2-m3 (MacFadden 1984, fig. 145); 32104, 32174 2 R mandibles with p2-m2; 32212 R mandible with p2-m1; 32116 R mandible with p2,p4-m3; 32190 R mandible with p3-m3; 32144, 35893 2 R mandibles with p4-m3; 32107, 32199 2 L mandibles with p2-m3; 32111, 32118, 32160 3 L mandibles with dp2-dp4; 32123, 32163 2 L mandibles with p2-m2; 32113, 32151 2 L mandibles with p2-m1; 32198, 32245 2 L mandibles with p3-m3; 32165 L mandible with p4-m3; 32182, 32105, 36282, 32134, 36285, 36280 6 partial R mandibles; 32197, 32195, 32137, 36287, 35892, 32102 6 partial L mandibles; 35895 assoc. R dp2-dp4 and L

dp3-dp4; 32286, 90154 2 assoc. R dp2-dp4; 90160 assoc. R dp2-dp3; 90155, 90156 2 assoc. R dp3-dp4; 32196 assoc. R p2-m3 and L p2-m2; 32293 assoc. L p4,m2-m3 and R p3-p4; 32146 assoc. R p2-m3; 32225 assoc. R p2-p4; 32239 assoc. R p3-m3; 32203, 32229 2 assoc. R p4-m3; 32181, 32223 2 assoc. R m1-m3; 32232, 32221 2 assoc. R m2-m3; 90158 assoc. R dp3 and L dp2-dp4; 90159 assoc. L dp2-dp3; 32227 assoc. L m1-m2 and R m2; 65167 assoc. L m1-m3; 90162-90179 18 R dp2; 69813, 69814, 90121-90159 41 R dp34; 90180-90197 18 L dp2; 90071-90120 50 L dp34; 50355, 50356, 50358-50362, 50364, 50365, 50369, 64926-64927, 64929-64931, 64934-64936 19 R p2; 50370, 50372, 50374-50379, 64937, 64940-64943, 64466 14 L p2; 50461-50479, 50544, 50635, 50639, 64981-64986, 64988-65025, 65027 67 R p34; 50447-50455, 50460, 50458, 50640, 32226, 64944-64946, 64948-64980, 65166 50 L p34; 50420-50437, 50439-50445, 65076-65109, 65028-65050, 69816 83 R m12; 50400-54017, 54019, 65113-65131, 65133-65165, 69818, 90262 73 L m12; 50380-50389 10 R m3; 50390-50399 10 L m3.

"Stream Matrix" Horizon, Nichols Mine, Polk Co., FL: UF 24638 R P2; 23986, 24636 2 R P34; 28837 L M12; 24626, 24655 2 R dp34; 24628, 24631 2 R p34; 24625 R m12; 24642 L m12.

Fort Green Mine, Polk and Hardee Cos., FL: UF 47473 R M1; 102095 R dp3; 53924 R p34.

Four Corners Mine, Hillsborough Co., FL: UF 102620 R P34; 102022 R M3.

Unknown mine near Mulberry, Polk Co., FL: AMNH 22482 mandible with p3-m3.

Peace River, near Gardner, Hardee Co., FL: UF/FGS V-4889, UF 55948 2 R M12; UF/FGS V-1482 L p34; UF 55951 R m12; 55952 L m12.

McGehee Farm, Alachua Co., FL: UF 17220 L maxilla with DP34; 17221 L PD34; 17121 L P2; 17099, 17124, 17208, 19237, 19428, 45616 6 R P34; 17206, 17210, 17212, 45614, 53548 5 L P34; 9605, 9611, 17213, 3 R M12; 17090, 17207, 17214, 17125, 45612 5 L M12; 45615 R M3; 7234 assoc. R mandible with p2-m2 and L mandible with p2-p4; 9541 assoc. R dp2-dp3; 12050 R dp2; 7240 L dp34; 45619, 45620 2 R p2; 17167, 45627, 53454 3 R p34; 17196, 17197, 45623, 53452 4 L p34; 7243, 9606, 16837, 17140A, 17173, 17192A, 18707, 45624, 45625, 53451 10 R m12; 17100, 17139, 17140B, 17169A, 17169B, 17172, 17175, 17192B, 17193-17195, 45618 12 L m12; 45631 R m3.

Pareners Branch Site, Alachua Co., FL: UF 53564 L P34; 55492 L M3.

Haile 5B, Alachua Co., FL: UF 17226 L P34.

Haile 6A, Alachua Co., FL: UF 102551 R p2.

Haile 19A, Alachua Co., FL: UF 47319, 103729 2 R M12; 103730 RM3; 103731 R dp34; 103732 R m12; 58387 L m12; 103733 L m3.

Cummer Mine No. 8, Alachua Co., FL: UF/FGS V-1408 L p34.

Mixson's Bone Bed, Levy Co., FL: UF/FGS V-1428 R P2; USNM 3292 R P34 (holotype); F:AM 111730 assoc. R P2-M2 and L P3-M3 (MacFadden

1984, fig. 142); 107876 badly crushed skull with R and L DP2-M1; 113620 assoc. L P2-M2 and R M1; 113621 assoc. R P2-P3,M2-M3 and L P3,M2-M3; 113625-113629, 113638 6 upper cheekteeth; 107874 assoc. R and L mandibles with i3,c1,p2-p3,dp4,m1-m2 and R i2 (MacFadden 1984, fig. 143); 113630 assoc. R p2-p3 and L p2; 113634 assoc. L m2-m3; USNM 3309 R p2; F:AM 113640 L p2; 113636 R p34; 113631, 113632 2 L p34; 113633, 113635 2 L m12.

Moss Acres Racetrack Site, Marion Co., FL: UF 93000 assoc. juvenile crushed skull with R and L DP2-M1, R and L mandibles with dp2-m1, and various post-cranial elements; 96386 assoc. R M1-M3 and L M3; 69968 R M12; 69967 assoc. male R and L mandibles with i1-i3,c,p2-m3; 103754 assoc. R and L mandibles with R i1, dp2-dp4,m1-m2 and L di2-di3,dp2-dp4,m1-m2.

Withlacoochee River Site 4X, Marion Co., FL: UF 53525 L M12.

Dunnellon Phosphate Company mine, Marion Co., FL: USNM 8265 R maxilla with P2-P4 (Hay 1916, plate 2.8).

Dunnellon Phosphate Company, Plant No. 5, near Hernando, Citrus Co., FL: UF/FGS V-1400 R M12.

Port Manatee Site, Manatee Co., FL: UF 107541 R m3.

Revised Diagnosis.-- Medium-sized *Cormohipparion* with toothrow lengths of 128-140 mm in middle wear-stages. Unworn MSCH of P2 about 40 mm and M12 about 58 mm. On average, smaller than *C. occidentale*, generally with less complicated fossettes, less elongate protocones, and relatively more elongated diastema. More hypsodont and more complex enamel plications than *C. sphenodus*. Larger and higher crowned cheek teeth than *C. ingenuum*; larger than *C. emsliei* with simpler fossette plications and weaker pli caballinids.

Description.-- All cranial material referable to *Cormohipparion plicatile* lacks uncrushed or complete pre-orbital regions. Four specimens (UF 32257, 32255, 35891, 32250) from the Love Site and UF 93000 from Moss Acres preserve parts of the facial region, but none contains the entire DPOF. The specimen with the most complete DPOF, UF 32250, is an uncrushed, partial maxilla with well worn but diagnostic P3-M2 (Fig. 14B). It contains the ventral base and rim of a deep (at least 15 mm) DPOF located 46 mm dorsal to the toothrow (Fig. 14A). The three other Love Site specimens also preserve small portions of a fossa. These crania differ considerably from Love Site specimens assigned to *Neohipparion trampasense*, in which the DPOF is reduced to a slight depression (MacFadden 1984; Hulbert 1987b). The badly crushed skull of UF 93000 preserves only the dorsal portion of both DPOFs. They were evidentially less well-rimmed dorsally than those of *C. occidentale*, and probably shallower. Another extremely crushed skull of *C. plicatile*, F:AM 107876 from Mixson's Bone Bed, was noted by MacFadden (1984:174) as not possessing a deep DPOF. F:AM 107876 is crushed and fragmented to such a
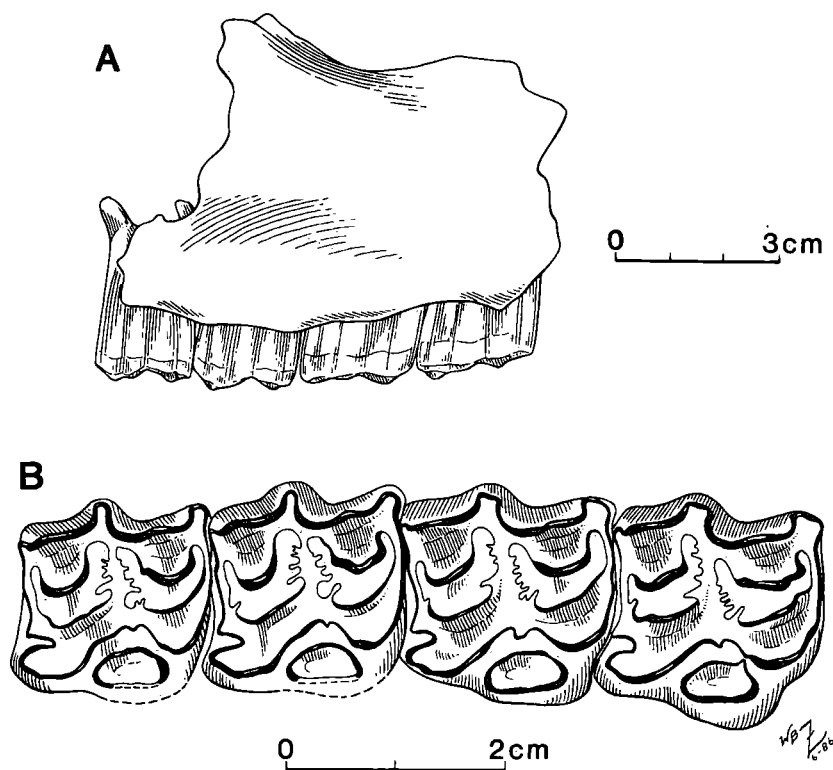
FIGURE 14. Lateral (A) and occlusal (B) views of UF 32250, *Cormohipparion plicatile*, Love Site (late Clarendonian), Alachua County, Florida. Lateral view shows the well defined ventral margin of the DPOF. Occlusal pattern of R P3-M2 represents the late wear-stage for this species.

degree that not even the orbits are discernible. Until discovery of uncrushed, more complete cranial material, the facial region of *C. plicatile* and the exact morphology of its DPOF must remain poorly documented. The Love Site and Moss Acres Racetrack Site specimens demonstrate the presence of a moderate to deep DPOF, but not its complete morphology.

The following dental descriptions are based primarily on the abundant Love Site sample, with added comparisons from other localities. Statistics of cheektooth dimensions of *C. plicatile* are presented in Tables 3 and 4. Upper cheekteeth of *C. plicatile* are characterized by oval protocones with convex lingual borders, richly plicated internal fossette borders (especially in early wear), moderately deep hypoconal grooves open to near the base of the crown, and strong styles. The P2 has a well developed anterostyle, and is by far the longest tooth in the toothrow (Fig. 15A, 15B). The oval protocone of the P2

generally remains isolated from the protoselene until mid-wear. Many P2s with MSCHs of 20 to 25 mm retain isolated protocones. Unworn MSCH of the P2 is about 38 to 42 mm. Fossette plications resemble those of the P34, except that the anterior half of the prefossette usually has two or three small folds. The pli caballin is generally single, although often bifurcated. The P34 (Figs. 14B, 15, 16B) are much larger in occlusal area than the M12, with larger and more widely opened parastyles and mesostyles. The parastyles are often slightly grooved, and metastyles are occasionally developed, but not as prominently as in *C. emsliei* or *Neohipparion eurystyle*. In very early wear, the protocone of the P34 is elongate, occasionally with a rudimentary spur, but with wear the spur (if present) vanishes and the protocone rapidly becomes more oval. This change is produced by an increase in protocone width, as protocone length is uncorrelated with crown height ($r = 0.05$, $n = 132$), while protocone width has a significant negative correlation with crown height ($r = -0.64$, $n = 130$, $p < 0.001$). Protocone length is generally less than twice its width, a feature useful in distinguishing *C. plicatile* from its slightly smaller contemporary, *Neohipparion trampasense*. The main axis of the protocone runs in a more direct anterior-posterior direction than that of *N. trampasense*. The protocone of the P34 does not connect to the protoselene until very late wear-stages (MSCH of 15 mm or less). Fossette and pli caballin complexity also vary considerably with crown height. In early wear, the well developed pli caballin is usually multiple, branched, or both (Fig. 15A). With wear, it decreases in length and complexity, usually becoming single by late mid-wear (MSCH of 15 to 30 mm), and lost or rudimentary only in very late wear (Fig. 14B). In the Love Site sample, the anterior half of the P34 prefossette most often is not plicated (60% of examined specimens, $n = 112$), or has a single, small pli protoloph (32%; Fig. 15A, 15B). The latter condition occurs most frequently in the less worn teeth. The posterior half of the prefossette in early to moderate wear is richly plicated, with four to nine folds, of which several are often deep and bifurcating. The anterior half of the postfossette is only slightly less complex, generally with a deep, often branched pli postfossette and two to five accessory plications. In moderate to late wear-stages, these internal fossette plications become shallower and less numerous (e.g. Fig. 14B), although even very heavily worn teeth usually retain at least two or three folds. The posterior half of the postfossette has a single (59%, $n = 110$), relatively shallow and small pli hypostyle, or lacks all plications (39% of observed specimens). Early Hemphillian samples of P34s of *C. plicatile*, while of similar proportions to the Love Site sample (Tables 1, 3), are on average more complexly plicated (Fig. 16B, 16D). For example, of 16 observed P34s, seven (44%) had a single pli protoloph, eight (50%) had a pli protoloph plus one or two accessory plications, and only one lacked all plications on the anterior half of the prefossette (the character state found in the majority of the Love Site sample). Unworn P34 MSCH varies from 50 to 55 mm.
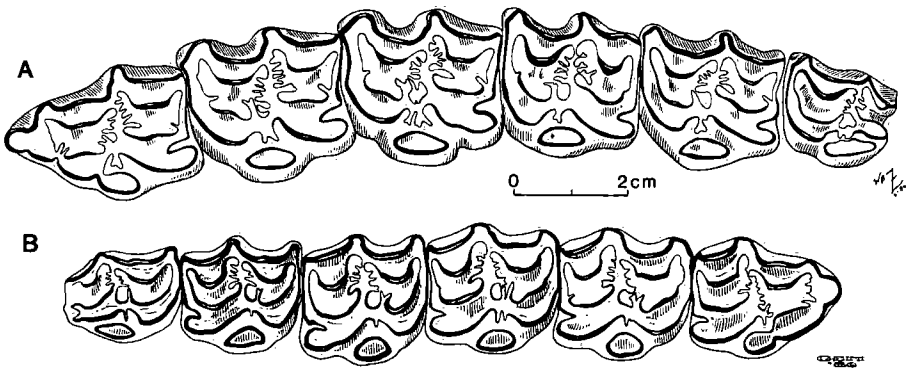
FIGURE 15. Occlusal views of representative upper toothrows of *Cormohipparion plicatile* from the Love Site (late Clarendonian), Alachua County, Florida. A. UF 32262, L P2-M3, an average-sized individual, early wear-stage. B. UF 32270, R P2-M3, a relatively small individual, early wear-stage.
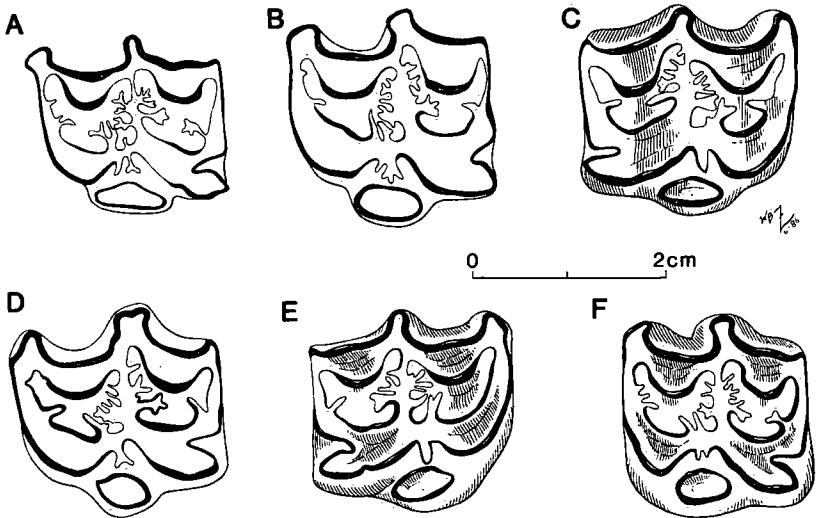
FIGURE 16. Occlusal views of upper cheekteeth of *Cormohipparion plicatile* from the early Hemphillian of Florida. A. UF 93000, L M1, sectioned to show moderate wear-stage, Moss Acres Racetrack Site (late early Hemphillian), Marion County. B-C. McGehee Farm Site (early Hemphillian), Alachua County, Florida. B. UF 17210, sectioned L P34; this individual more closely matches the enamel pattern of the holotype than any other subsequently found specimen. C. UF 9605, R M12. D-F. Mixson's Bone Bed (early Hemphillian), Levy County. D. F:AM 113620, sectioned L P3. E. F:AM 113620, R M1, same individual as in Figure 16D. F. F:AM 113629, heavily worn L M12.

In mid-wear, M12 of *C. plicatile* have nearly square occlusal surfaces, with length slightly exceeding width on average (Table 3). However, since length is positively correlated with crown height (r = 0.77, n = 124), and width is negatively correlated with crown height (r = -0.50, n = 123), the ratio of length to width changes greatly through ontogeny. The M12 protocone is slightly smaller than that of the P34 (Table 3), but similar in morphology and degree of isolation from the protoselene. The pli caballin is only rarely double (6% of observed Love Site specimens, n = 121), but it persists until late wear, when it gradually disappears in extremely worn teeth (almost always after MSCH is less than 20 mm). In the Love Site sample, the anterior half of the prefossette of the M12 generally lacks plications (81%, n = 120; Figs. 14B, 15). A single, relatively shallow pli protoloph is occasionally found in early wear-stages, and it rarely has accessory plications. The posterior half of the prefossette most often has from three to five, rarely bifurcated plications, and a well developed prefossette loop. The anterior half of the postfossette generally has between two and four plications (86% of Love Site sample, n = 121), usually consisting of a relatively deep, unbifurcated pli postfossette and several labial accessory plications. The posterior half of the postfossette in early wear often has a single pli hypostyle; it is usually lost by mid-wear. As with the P34, M12 of *C. plicatile* from the early Hemphillian localities (Mixson's, McGehee, Moss Acres) are on average more complicated than the Love Site population (Fig. 16A, 16C), although of the same general size (Table 3). For example, a third of the pooled sample of M12 from the younger sites have multiple pli caballins (Fig. 16A, 16F). Also, fossette plications are more numerous and tend to persist longer throughout wear. Unworn MSCH of M12 are about 56-59 mm for the Love Site sample. Based on UF 96386 from Moss Acres (Table 1), Hemphillian *C. plicatile* had increased its unworn crown height by about 8%.

Deciduous upper premolars of *C. plicatile* have very large parastyles, generally multiple pli caballins, and oval protocones. The degree of fossette complexity is intermediate between that of the P34 and the M12. Protoconal spurs are not uncommon, and the hypoconal groove frequently has a pli dihypostyle. No specimens are available to indicate the relative size of the DP1, but it was apparently lost in some mature individuals (e.g. USNM 8265).

The referred Love Site sample includes numerous associated lower dentitions and partial mandibles referred to *Cormohipparion plicatile* (as well as several hundred isolated lower cheekteeth), but none is complete; i.e. there are no mandibles that include symphyseal regions, and only one with an ascending ramus. However, UF 69967, from the Moss Acres Racetrack Site, has a relatively complete symphysis (Fig. 17). In this adult male individual (m1 mcch = 35.3 mm), the incisors form a normal equine arcade about 55 mm in width (across the i3s) and are slightly procumbent. The i1s have only small traces of the infundibula remaining, and the i3s do not have enclosed infundibula. The symphyseal region is extremely elongated, with an ld1 of
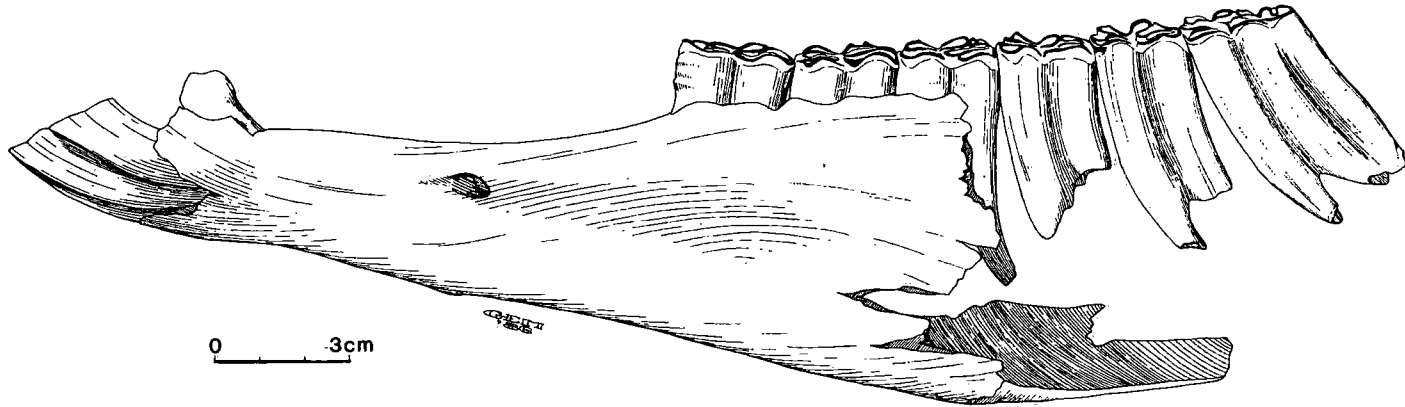
FIGURE 17. Left lateral view of UF 69967, left mandibular ramus and symphysis of *Cormohipparion plicatile* from the Moss Acres Racetrack Site (late early Hemphillian), Marion County, Florida. Occlusal view of the cheekteeth of this specimen shown in Figure 18C. Note the extremely elongated diastema, characteristic of the subgenus *Notiocradohipparion*.

about 107 mm (Fig. 17; Table 4).   Adequate samples of associated lower
dentitions of *C. plicatile* are available to allow comparisons with other Miocene
hipparionines. The lower premolars of *C. plicatile* are very wide relative to
length, as contrasted with the molars, or with the premolars of *Neohipparion
trampasense*.   The p2-p4 have large, oval metaconids, metastylids and
entoconids (Figs. 18, 19B, 19D). In very early wear-stages, the ectoflexid is
very shallow, the isthmus is often plicated, and a pli caballinid is variably
developed (Fig. 19B). If present, the pli caballinid reduces in size with wear
until it gradually vanishes, usually by moderate wear-stages. Plications from
the isthmus and paralophid are common (Table 5) and generally persist until
at least mid-wear. The protostylid first comes into wear after the first 12-15
mm of the crown are worn away, and is at first isolated from the protoconid
(e.g. the p3 in Fig. 18A, 18B). It quickly becomes attached and is a prominent
feature. The labial borders of the protoconid and hypoconid are rounded or
only very slightly flattened. Ectoflexid depth varies, but most commonly only
penetrates the isthmus to about the level of the base of the entoflexid, or
slightly deeper, even in heavily worn teeth (Fig. 19D). As in other species of
Cormohipparion, occasionally the p4, and more rarely the p3, can have deep
ectoflexids. Unworn mcch of p2 is about 40 mm, and 51-54 mm for the p34.

The lower molars of *Cormohipparion plicatile* (Figs. 18, 19A, Table 4)
closely resemble those of *C. occidentale* and *C. ingenuum* in overall enamel
morphology. Although initially shallow, the ectoflexid deepens rapidly with
wear, so that even molars with crown heights exceeding 50 mm have
completely divided isthmuses.   The metaconid and metastylid are well
separated from each other by the deep ectoflexid and a broad, 'U'-shaped
linguaflexid. The metaconid is generally oval, while the metastylid is typically
more angular (Fig. 18B, 18C). The bases of the metaflexids and entoflexids are
not flat, due to rounded lingual projections from the protoconid and
hypoconid. Pli caballinids are rare in molars (Table 5), always small, and
confined to early wear-stages. Rudimentary thickenings of the enamel at the
position in the ectoflexid from where pli caballinids would originate are not
infrequent in early and moderate wear-stages, however. The antisthmus
generally has a single plication in early wear-stages (Fig. 18), but plications are
less common from the paralophid and postisthmus than in the premolars
(Table 5). Slightly worn to unworn mcch of m12 varies between 56 and 60 mm,
while that of the m3 is about 53-56 mm.

Lower deciduous premolars of *Cormohipparion plicatile* (Table 2; Fig.
19C) have more elongated metaconids and metastylids than do the p2-p4, large
protostylids on the dp34, and somewhat variable ectoflexid depths.   The
ectoflexids may be shallow, especially in early wear-stages, and sometimes do
not penetrate the isthmus; but generally they deepen with wear on the dp34.
The dp2 ectoflexid tends to remain shallow. As is typical for the genus,
ectostylids are well developed, especially on the dp3. This structure rises
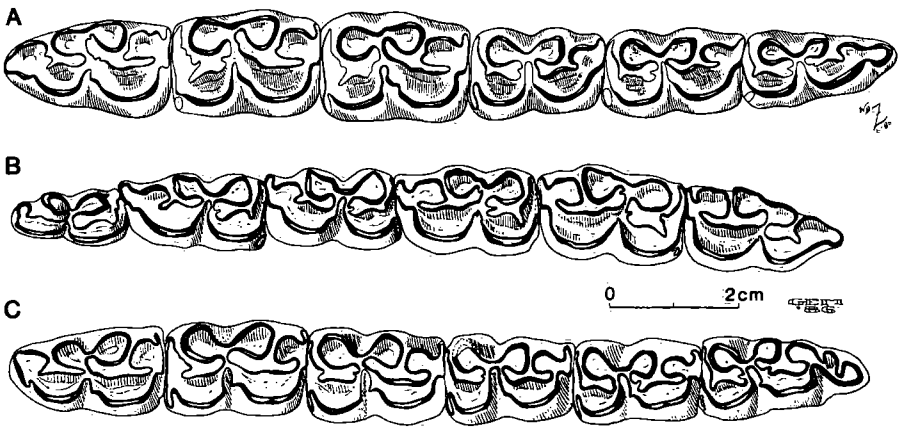
FIGURE 18. Occlusal views of lower cheecktooth series of *Cormohipparion plicatile* from Florida. A. UF 32107, L p2-m3, Love Site (late Clarendonian), Alachua County. B. UF 32196, R p2-m3, Love Site. C. UF 69967, L p2-m3, Moss Acres Racetrack Site (late early Hemphillian), Marion County.
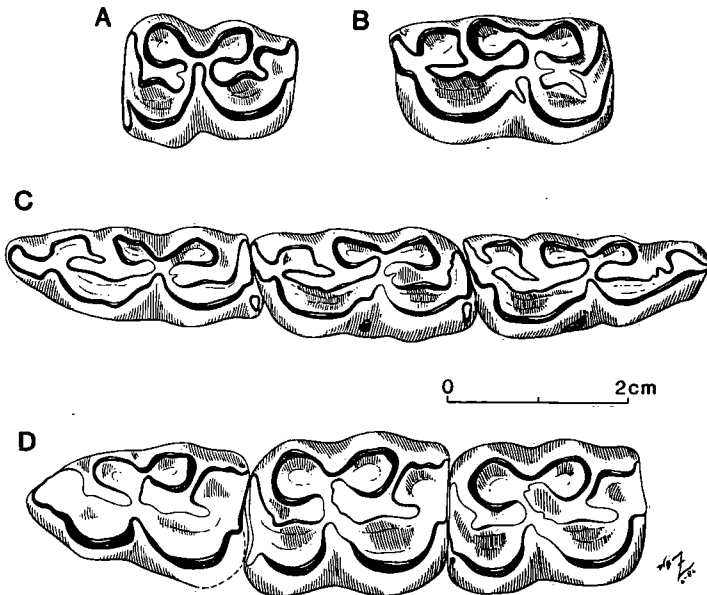
FIGURE 19. Occlusal views of lower cheekteeth of *Cormohipparion plicatile* from Florida. A. F:AM 113635, L m12, Mixson's Bone Bed (early Hemphillian), Levy County. B-C. Love Site (late Clarendonian), Alachua County. B. UF 50639, slightly worn p34. C. UF 90154, slightly worn assoc. R dp2-dp4. D. UF 7234, heavily worn assoc. L p2-p4, McGehee Farm Site (early Hemphillian), Alachua County.

variably from 8 to 17 mm above the base of the tooth, producing an isolated, dentine-filled lake on the occlusal surface when the tooth is sufficiently worn (Fig. 19C). Pli caballinids are either absent, or, in early wear-stages, rudimentary. Metaconid crown height of unworn dp34s is about 26 mm.

Discussion.-- As demonstrated in the discussion section for *Cormohipparion ingenuum*, the holotype of "*Hippotherium*" *plicatile* is specifically diagnostic, and the name should be applied to the larger of the late Miocene species of *Cormohipparion* from Florida. The early taxonomic history of *C. plicatile* resembles that of *C. ingenuum*. It was originally placed in the genus *Hippotherium* and later transferred to *Hipparion* s.l. Gidley (1907) hypothesized a close phylogenetic relationship with Old World hipparionines, but this was not followed by Matthew (1924) or Simpson (1930). When Stirton (1940) separated North American *Hipparion* s.l. into three genera, *Hipparion* s.s., *Nannippus*, and *Neohipparion*, and referred to Leidy's species as "?*Hipparion plicatile*," he again raised the possibility that it was more closely related to Old World taxa than North American hipparionines (most of which he assigned to either *Neohipparion* or *Nannippus*). More recently, "*H.*" *plicatile* has appeared in some faunal lists (e.g. Hirschfeld and Webb 1968; Webb and Perrigo 1984), but it was not again analyzed phylogenetically until MacFadden (1984). MacFadden (1984:170-174) concluded that the species, while valid, was generically indeterminant. The major problem with all prior studies of the generic affinities of "*Hippotherium*" *plicatile* was the limited amount of available topotypic and referable material. This obstacle has been eliminated by the McGehee Farm, Moss Acres, and Love Site samples. These referred samples suggest assignment of the species to the genus *Cormohipparion*, based on the same suite of characters as listed above for *C. ingenuum* (pp. 261-262). The phylogenetic relationships of *C. plicatile* are discussed at length below. The referral to *Cormohipparion* vindicates the observations of Gidley and Stirton that *C. plicatile* is more closely related to Old World hipparionines than most North American hipparionines.

Leidy's name "*plicatile*" suggested that the species had exceptionally complex fossette borders (as indeed is shown by the somewhat atypical holotype). This has been further emphasized by MacFadden (1984:170-171). However, these observations were based on small sample sizes, and, in some cases, included specimens I refer to *Cormohipparion ingenuum*. Indeed, *C. plicatile* has fewer fossette plications on average than any other advanced species of North American *Cormohipparion* (Table 7; Figs. 20 and 21). It might also be noted that the complexity of the holotype of *C. plicatile* results more from extreme bifurcating of plications, and not an unusually high value of total plications (12) for the species. Although the median differences (Table 7) are slight, Figures 20 and 21 reveal a quite different pattern of fossette plications between *C. plicatile* and *C. occidentale*. The multimodal distribution for *C. occidentale* is not the result of combining samples from different
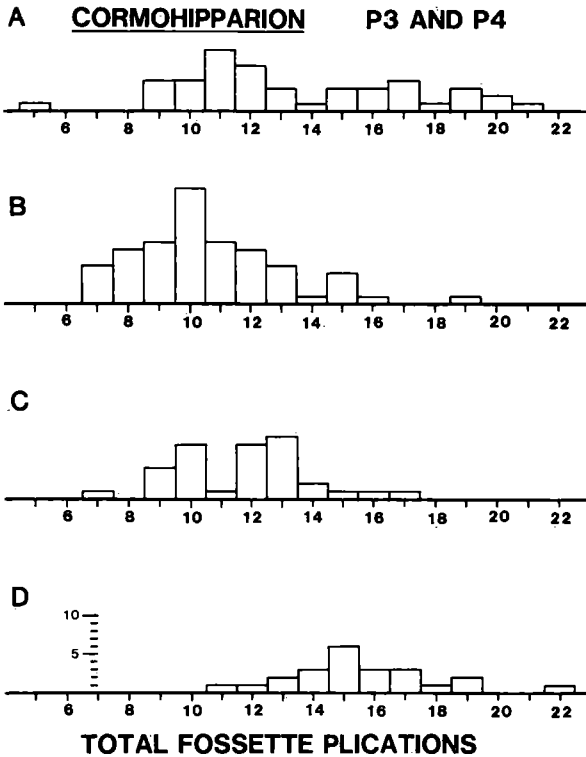
FIGURE 20. Histograms of total number of fossette plications on the P3 and P4 of four species of *Cormohipparion*. A. *C. occidentale*, combined sample from Clarendonian and early Hemphillian of Texas and Nebraska, n = 44. B. *C. plicatile*, combined sample from Florida sites, n = 62. C. *C. ingenuum*, combined sample from Florida sites, n = 33. D. *C. emsliei*, combined sample from Bone Valley and Macasphalt Shell Pit sites, n = 23. Samples include only specimens with MSCH between 50 and 90% of unworn crown height for each particular species.

localities. Similar multimodal distributions were produced using a sample drawn from a restricted geographic and chronologic population (Fig. 22). Much of the difference between *C. plicatile* and *C. occidentale* results from variation of plications on the anterior half of the prefossette. Slightly worn uppers of *C. occidentale* typically have four to six plications on the anterior half of the prefossette. More moderately worn teeth most often have only one or two. The decrease does not proceed linearly with wear, but tends to follow a step-wise pattern. This, combined with a perhaps more linear decrease in plications on other regions of the fossettes, produces the multimodal
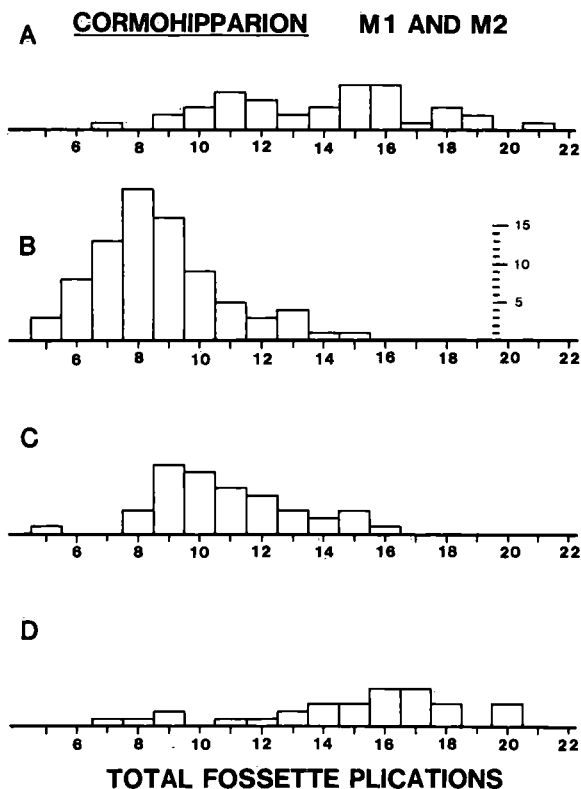
FIGURE 21. Histograms of total number of fossette plications on the M1 and M2 of four species of *Cormohipparion*. A. *C. occidentale*, combined sample from Clarendonian and early Hemphillian of Texas and Nebraska, n = 39. B. *C. plicatile*, combined sample from Florida sites, n = 85. C. *C. ingenuum*, combined sample from Florida sites, n = 41. D. *C. emsliei*, combined sample from Bone Valley and Macasphalt Shell Pit sites, n = 29. Samples include only specimens with MSCH between 50 and 90% of unworn crown height for each particular species.

distributions in Figures 20A, 21A, and 22. There are three distinct peaks in fossette complexity within the moderate wear-stages of *C. occidentale*. These are an early phase with a mode of 18, 19, or 20 (here termed fossette-group A); an intermediate group (B) with a mode of 15 to 17; and a final group (C) with a mode of 11 to 13. In *C. plicatile*, three important differences are observed: (1) the number of plications on the anterior half of the prefossette is much less variable, being almost always 0, 1, or more rarely 2; (2) the modal values are less (by 2 or 3); and (3) group C is reached much earlier in ontogeny, such that

TOTAL FOSSETTE PLICATIONS
Cormohipparion occidentale
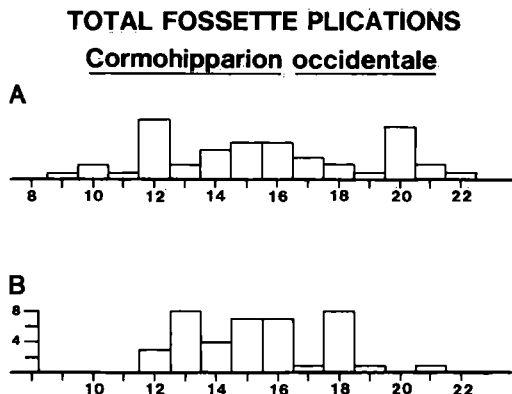
FIGURE 22. Histograms of total number of fossette plications of the P3 and P4 (A, n = 43) and of the M1 and M2 (B, n = 40) of *Cormohipparion occidentale* from the Xmas-Kat Quarries Fauna, Cherry County, Nebraska (late Clarendonian). Sample analyzed as those in Figures 20 and 21, but the Xmas-Kat sample consists primarily of skulls. Therefore, crown height cannot be directly measured on most of these specimens. To make the sample comparable to those in Figures 20 and 21, values of APL were used to exclude slightly worn or excessively worn specimens. The Xmas-Kat specimens, although slightly more complex on average, display the same multimodal pattern as the combined sample of *C. occidentale* in Figures 20 and 21.

groups A and B are either not observed (group A for molars, Fig. 21B) or are very rare. Generally, the first two fossette-groups are ephemerally expressed during earliest wear-stages, in the first 10% of the crown. The result is a distribution that appears more normal than that of *C. occidentale*, and only slightly skewed to the left. The pattern in *C. plicatile* is judged to represent the primitive condition, as the general trend in the genus is to increase plication number and duration, and because *C. sphenodus* appears to have a similar pattern (although limited available sample sizes prevent further analysis of that species). The fossette border morphology of *C. occidentale* could evolve from one like *C. plicatile* by slightly increasing the median plication number (per fossette-group), and, more importantly, substantially delaying the average crown height at which fossette-group A transforms into B, and likewise B into C.

Fossette plications in *Cormohipparion ingenuum* more resemble those of *C. plicatile* than *C. occidentale* in frequency distributions (Figs. 20, 21), although it has slightly more fossette plications on average than does *C. plicatile* (Table 7). The distribution of total fossette plications for the P3 and P4 (Fig. 20C) is obscured by the small sample size, and no obvious modal value for fossette-group C is apparent. It could be either 10, 12, or 13. However, the

distribution of fossette plications of the M1 and M2 is more revealing (Fig. 21C). Two modes are apparent, that of group C at 9, and group B at 15. Like *C. plicatile, C. ingenuum* represents the primitive *Cormohipparion* pattern for ontogenetic variation in fossette complexity.

Cormohipparion plicatile is known from at least 19 localities in Florida (see referred specimens list, Table 10, and Fig. 2) that range in age from latest Clarendonian (ca. 9.0 Ma) through the later part of the early Hemphillian (ca. 6.0 Ma). The oldest well-dated population of *C. plicatile* is that from the Love Site, latest Clarendonian (Webb et al. 1981). The Bone Valley records from the Nichols, Fort Green, and Four Corners mines are most likely of a similar, late Clarendonian-early Hemphillian age. Vertebrates of this age are usually very rare in the Bone Valley, but are sometimes recovered from these particular mines. As phylogenetic analysis suggests that *C. plicatile* is the sister taxon to *C. ingenuum* + *C. emsliei*, its first appearance should be close to that of *C. ingenuum* (i.e. early Clarendonian). However, it was not recovered *in situ* from the two most productive sites of that age, the Gray Zone in Phosphoria Mine and the Agricola Road Site in Hookers Prairie Mine. This absence is significant, as *C. plicatile* is usually more common than *C. ingenuum* when both are present (note the 3:1 ratio for referred Nichols Mine specimens).

The youngest specimens referred to *Cormohipparion plicatile* are those derived from the Moss Acres Racetrack Site, the Dunnellon phosphate-mining region and the Withlacoochee River Site 4X in Marion and Citrus counties in north-central Florida, and the Port Manatee Site in southern Florida (Fig. 2). At these sites, *C. plicatile* was recovered with *Nannippus minor* and *Neohipparion eurystyle* (Hulbert 1987a, 1987b). These two species are more advanced than those of the same genera present at the Love Site, McGehee Farm, and Mixson's Bone Bed (*Nannippus westoni* and *Neohipparion trampasense*, respectively). The concurrent range zone of *C. plicatile, C. ingenuum, N. minor,* and *N. eurystyle* in Florida is the late early Hemphillian, or between 6 and 7 Ma. The otherwise taxonomically most diverse fauna of this interval in Florida, the Withlacoochee River Site 4A (Webb 1969b; Becker 1985), lacks *C. plicatile*, however. Differences hypothesized to have resulted from anagenic evolution are observed when younger and older samples of *C. plicatile* are compared, especially in terms of plication complexity. The best represented of the relatively young referred samples, that from the Moss Acres Racetrack Site, includes upper and lower teeth (Figs. 16A, 18C). The upper molars of UF 69968, 93000, and 96386 are much more complex than average Love Site specimens, with multiple pli protolophs and pli caballins. The lower molars of UF 69967, 93000, and 103754 have stronger and more persistent pli caballinids than any specimen from the numerous Love Site sample. The Moss Acres sample does not appear to differ from older populations in terms of size, and is only slightly more hypsodont. The observed magnitude of intraspecific

evolution in *C. plicatile* is similar to that found in other equid chronospecies over similar intervals of time (e.g. *Neohipparion trampasense*).

Equid populations from outside of Florida have only occasionally been referred to *C. plicatile*. Webb (1969a) listed "*H.*" *plicatile* in the Clarendon Fauna, but gave no references or specimen numbers. Apparently he was referring to the same population later placed by MacFadden (1980, 1984) in *H. tehonense*. Webb and Perrigo (1984) recently referred to "*H.*" *plicatile* a sample of 50 cheekteeth from the Gracias Formation of Honduras. While morphologically similar to *C. plicatile*, as noted above, the smaller occlusal dimensions of this sample clearly indicate a referral to *C. ingenuum* (Tables 1, 2). Examination of equid specimens from the following major faunas or localities (in the F:AM, AMNH, PPM, UNSM, and UCMP collections) of late Clarendonian or early Hemphillian age has failed to indicate the presence of *C. plicatile* in western North America: Xmas-Kat Channels, Cole Highway Pit, Pratt Pit I, J. Swayze Quarry, Port of Entry Pit, Box T Quarry, Higgins Fauna, and the Cambridge Fauna. Most of these instead contain a large, advanced form of *C. occidentale*. Thus, at the present time, there are no known referable samples of *C. plicatile* outside of central Florida.

Cormohipparion (*Notiocradohipparion*) *emsliei* HULBERT, 1988
Fig. 23; Tables 1-5, 7

Hipparion ingenuum (Leidy), SELLARDS 1916:97 (in part).
Hipparion (*Nannippus*) *ingenuum* (Leidy), SIMPSON 1930:187-188 (in part, not fig. 20C).
Hipparion plicatile (Leidy), SIMPSON 1930:187-188 (in part).
Nannippus phlegon (Hay), ROBERTSON 1976:158-159 (in part, fig. 15); MACFADDEN and WALDROP 1980:7 (in part).
"*Hippotherium*" *plicatile*-like form, MACFADDEN 1986:471.
Neohipparion eurystyle (Cope), HULBERT 1987b:830 (in part).
Cormohipparion emsliei HULBERT 1988:454.

Type Specimen.-- UF 94700, partial skull including R maxilla with DP1-M3, partial L maxilla, and premaxillae with incisors (Hulbert 1988b, fig. 2A-2C).

Type Locality and Horizon.-- Macasphalt Shell Pit of APAC, Inc., Sarasota County, Florida (Fig. 2). The holotype and most of the original topotypes (UF 94696-94700) were collected *in situ* at UF Locality Macasphalt 1A, which is located in the S 1/2, NW 1/4, NE 1/4 Sec. 12, T36S, R18E, Bee Ridge 7.5' Quadrangle (incorrect coordinates were listed in Hulbert 1988b). Other topotypes (UF 94634-94637) were collected at UF Locality Macasphalt 1B, which is located about 100 m SSE of Macasphalt 1A. Unit 4 (of Petuch 1982), "Pinecrest" Beds, late Blancan.

Revised Distribution.-- Late early Hemphillian through late Blancan of central Florida (about 7.0 to 2.0 Ma); late Hemphillian of Louisiana.

Referred Specimens.-- In addition to those listed in Hulbert (1988b), the following specimens from Florida are referred to *C. emsliei*. See Manning and MacFadden (in press) for specimens from Louisiana.

Macasphalt Shell Pit 1A, Sarasota County, FL: UF 101450 R dp34; 100364 juvenile proximal phalanx of lateral digit.

Moss Acres Racetrack Site, Marion Co., FL: UF 95410 assoc. R M2 and L M2-M3; 97259 female assoc. R and L mandibles with i1-i3,p2-m3; 97260 assoc. juvenile, probably fetal, upper and lower toothrows with R DI1-DI2,DP2 and di1-di2,dp2-dp4, and L DI1-DI2,DP2-DP3 and dp2-dp4. UF 97260 was found closely associated with UF 97259.

Four Corners Mine, Hillsborough Co., FL: UF 102601-102603 3 L M12; 102600 R M12; 102604-102606 3 R M3; 102607 L p34.

Gardinier Mine, Polk Co., FL: UF 100224 R P34; 100225 L M12; 91155 R dp2; 103705 R p2; 101964 L p2; 100226, 103676 2 R p34; 10027 L p34; 100228 R m12.

Phosphoria Mine, Polk Co., FL: UF 102586 L P34; 102587 L dp3; 102588 L p34; 102589 L m12.

Fort Green Mine, Polk and Hardee Cos., FL: UF 102642 R M12; 102641 L p34; 102640 R m12.

Hookers Prairie Mine, Polk Co., FL: UF 102577 R M12.

New Wales Mine, Polk Co., FL: UF 96257 R M3.

Amax Mine, Polk Co., FL: UF 93236 L m1.

Mineco Mine, Polk Co., FL: UF 91204 R p34.

Bone Valley Region, specific mine or locality unknown, Polk Co., FL: UF 92929 R P34; 93216 R p34.

Diagnosis.-- Small- to medium-sized, moderately hypsodont species of *Cormohipparion*, with estimated toothrow lengths of mature individuals 115-132 mm; unworn M12 MSCH about 57 mm. Smaller, on average, than *C. occidentale* and *C. plicatile*; larger than "*Merychippus*" *goorisi* and all species of *Nannippus*; size similar to *C. sphenodus* and *C. ingenuum*. Protocone relatively small, elongate-oval, with flattened or concave lingual borders (rounder on P2), and isolated until late wear except on P2. On average, more complex fossette plications and better developed pli caballinid than any other North American species of *Cormohipparion*. Parastyle of P3 and P4 usually grooved; occasionally also M1 and M2; metastyle present, often relatively prominent. Ectoflexid shallow, not penetrating isthmus on p2-p4; metaconid and metastylid of dp2-dp4 and p2-p4 with lingual groove in early wear-stages; metaconid and paraconid of dp2 and p2 frequently connected in moderate wear-stages, isolating metaflexid as a fossettid.

Discussion.-- A complete description of this species is presented in Hulbert (1988b). One of the more remarkable aspects of this recently

described species is its fossette complexity. On average, *C. emsliei* has the most complexly plicated fossette borders of any North American species of *Cormohipparion* (Table 7; Figs. 20, 21). As is the case with *C. occidentale*, much of the increase resulted from the persistent retention of multiple plications on the anterior half of the prefossette. *C. emsliei* apparently proceeded even further than *C. occidentale* in delaying wear-induced fossette simplification. Thus, fossette-group C only rarely appears before the first 50% of the crown is worn away (Figs. 20D, 21D), and the majority of specimens retain group B levels of complexity through the moderate wear-stage. Lower cheekteeth of this species are also relatively complex, with high frequencies of plications (Table 5).

The three Moss Acres specimens listed above fall within the observed size ranges of both *Cormohipparion ingenuum* and *C. emsliei*. They are referred to the latter because of the multiple pli protoloph and well developed styles of UF 95410 (including strong metastyle and constrict mesostyle); the well developed pli caballinids (Fig. 23B) that are present even on the heavily worn molars of UF 97259; angular metastylids; and very high ectostylids on UF 97260. The mandibular symphysis of UF 97259 is the relatively most elongated of any observed North American hipparionine (Table 4; Fig. 23A), the ldl being almost as long as the ltrl. No canines, nor alveoli for canines, are present on this specimen, indicating that it was a female. UF 97260, which was discovered less than a meter from UF 97259, appears to represent a fetal individual, as the deciduous teeth are not fully erupted, are poorly cemented, and show no sign of wear. The lowers of UF 97260 differ from the late Hemphillian and Blancan dps referred to *C. emsliei* in their lack of well developed grooves on the metaconid and metastylid. Faint grooves are only present on the dp2 metastylid and the dp3 metaconid. The Moss Acres sample is significantly older than those previously referred to *C. emsliei*, by about 3 myr. The overall fauna (see Hulbert 1988a, table 13) indicates an early, probably late early, Hemphillian age. The primary indicator taxa for this interval, *Machairodus* and *Indarctos* (Tedford et al. 1988), have not yet been recovered at Moss Acres. Both are present at the Withlacoochee River Site 4A, whose fauna otherwise greatly resembles that of Moss Acres. For example, both contain *Nannippus minor*, *Neohipparion eurystyle*, *Calippus maccartyi*, *Aphelops mutilus*, and *Enhydritherium*. The *Neohipparion* and *Nannippus* at Moss Acres both appear to be of a more primitive grade of evolution than specimens from Withlacoochee River Site 4A; previously, this led me to suggest a slightly older age for the former locality (Hulbert 1987a, 1987b). However, the *Cormohipparion* from Withlacoochee River Site 4A demonstrates none of the advanced features of *C. emsliei*, and instead resembles *C. ingenuum* (Fig. 5A, 5B). Thus, it now seems best to consider the two sites approximately contemporaneous until other aspects of the faunas are thoroughly studied. I previously (Hulbert 1987b:830) identified UF 95410 as *N. eurystyle*, based on its
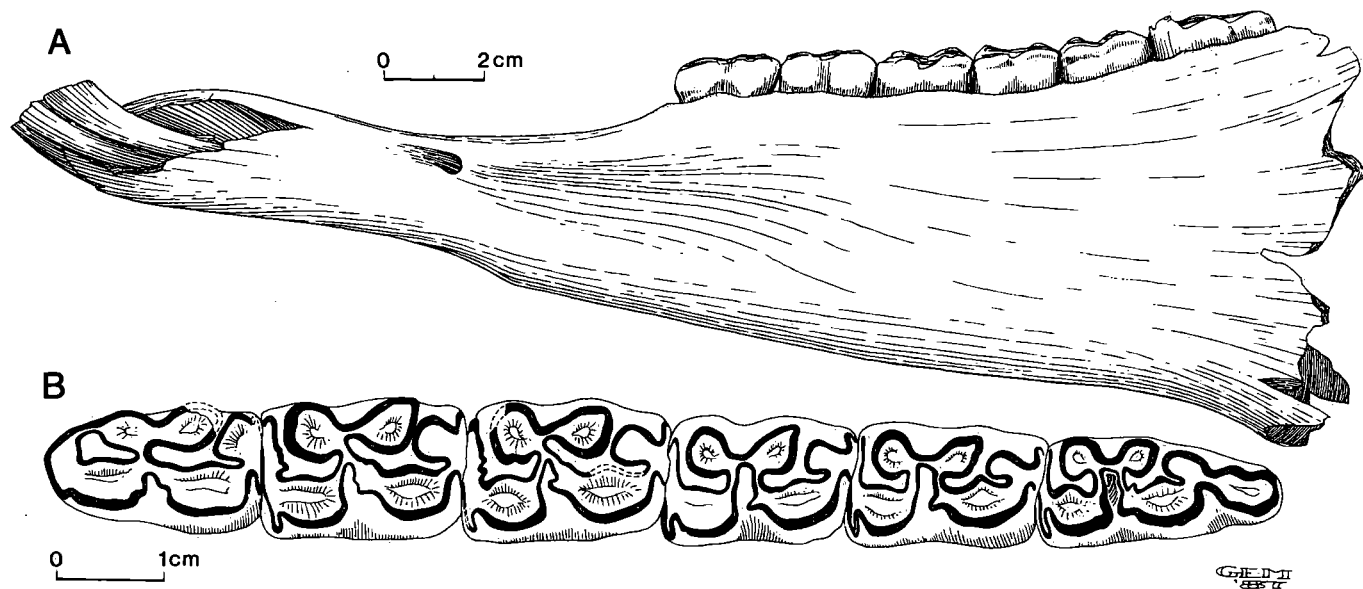
FIGURE 23. Lateral (A) and occlusal (B) views of UF 97259, mandibular ramus referred to *Cormohipparion emsliei* from the Moss Acres Racetrack Site (early Hemphillian), Marion County, Florida. Note the extremely elongated diastema. The angular metastylids and presence of pli caballinids in the late wear-stage are diagnostic of *C. emsliei*, and not *C. ingenuum*.

strong styles. The relatively short protocones (Table 1) and wide fossettes signify stronger affinities with *C. emsliei* than with *Neohipparion*. This does not alter the conclusion that *Neohipparion* from Moss Acres is best identified as *N. eurystyle* rather than *N. trampasense*, although its morphology is in many aspects intermediate between the two.

Hulbert (1988b) hypothesized that *Cormohipparion emsliei* represented a relictual population limited to the Gulf Coastal Plain, possibly even to peninsular Florida. However, late Hemphillian-Blancan localities to the south and east of the Great Plains are extremely rare (except in Florida), so that the seemingly very restricted range of *C. emsliei* originally presented in Hulbert (1988b) is primarily based on negative evidence. The mammalian faunas from two of the most notable Hemphillian localities from the southeast excluding Florida, the Mobile l.f. and the Lee Creek Mine (Tedford and Hunter 1984), unfortunately remain undescribed. Manning and MacFadden (in press) describe a recently recovered small sample of two pre-Pleistocene equids from eastern Louisiana. These are referred to *Nannippus minor* and *C. emsliei*. The referred sample of the latter, although limited to a few specimens, includes a very diagnostic p2, and in all respects falls within the OR of the Bone Valley population of *C. emsliei* (Manning and MacFadden in press). The Louisiana sample thus falsifies the restrictive hypothesis that *C. emsliei* was limited to Florida, but not the more general hypothesis that the species was restricted to mesic coastal environments.

GENUS *Hipparion* DE CHRISTOL, 1832
Hipparion sp., cf. *H. tehonense* (MERRIAM), 1916
Fig. 24; Tables 1-2

Referred Specimens.-- Hookers Prairie Mine, Polk Co, FL: UF 93203 R p34.

Phosphoria Mine, Polk Co., FL: UF 50753 R p34.

Four Corners Mine, Hillsborough Co., FL: UF 102599 R P34; 102622 L M12.

Love Site, Alachua Co., FL: UF 53405 R P34; 53375, 62165 2 L P34; 32125 L mandible with p2-m2; 96526 R p34; 64917, 64918 2 R m12; 96527 L m3.

Moss Acres Racetrack Site, Marion Co., FL: UF 95396 R M3; 95388 L m2.

Withlacoochee River Site 4A, Marion-Citrus county line, FL: UF 17205 assoc. L maxilla with P2-M1 and R P2-M3; UF 53414 assoc. L P3-P4; UF 53517 R P2; UF 17198 L P2; UF 53510, 53515 2 R M12; UF 17201, 19620 2 L M12; UF 17203, 53511 2 R M3; UF 19621, 53513 2 L M3; UF 17300 assoc. R and L

mandibles with p2-m3; UF 20868 L mandible with p2-m3; UF 21027 L mandible with p2-m3 (probably same individual as UF 17205); UF 17305 R p2; UF 53464, 53484-53486 4 R p34; UF 53483 L p34; UF 53470-53472, 53474 4 R m12; UF 53466-53469 4 L m12; UF 53475 R m3.

Dunnellon Phosphate Mining Region, Marion Co., FL: UF/FGS V-1406 R P2; V-1491 R p34.

Description and Discussion.-- UF 50753 and 93203 (Fig. 24A) are referred to *Hipparion* rather than *Cormohipparion* based on their poorly developed protostylids, lack of pli caballinids, and moderate size. Their size (Table 2) falls within the OR for *H. tehonense* lower premolars, and they closely resemble referred specimens of that taxon (e.g. MacFadden 1984, figs. 38-39). Both were recovered from mining spoil piles, and thus their original stratigraphic position is unknown. Terrestrial vertebrates older than late Hemphillian are relatively common in phosphatic sediments being processed in the region where these two specimens were collected, including the Clarendonian Gray Zone fauna recovered *in situ* from the Phosphoria Mine and the Agricola Road Site in the Hookers Prairie Mine. This older, Clarendonian, horizon is the most likely source for UF 50753 and 93203. If they have been correctly identified, the absence of *Hipparion* from these two localities, where about 300 early Clarendonian equid teeth have collected, is puzzling.

The Withlacoochee River 4A l.f. consists of a moderately diverse suite of late early Hemphillian vertebrates (Webb 1969b; Becker 1985). An important factor in the age determination is the co-occurrence of *Indarctos* and *Machairodus* (see above). The Withlacoochee River 4A l.f. includes a minimum of six species of equids (Table 10), of which two are common. They are *Nannippus minor* and the population here referred to *Hipparion*. The latter are referred to *Hipparion* based on the presence of a moderately deep DPOF (Fig. 24B); upper cheekteeth with rounded to slightly oval protocones with anterior spurs in early wear-stages that connect to the protoselene relatively early in ontogeny, fossettes with relatively simple and shallow plications, relatively poorly developed pli caballins (especially on molars), hypoconal grooves open to the base of the crown, and broad, unconstricted connections of the hypocone and the metaloph (Fig. 24C); and lower cheekteeth with relatively deep ectoflexids, poorly developed protostylids, and weak plications (Fig. 24D). This combination of dental and facial characters excludes the population from all hipparionine genera except *Hipparion*.

In contrast to the situation at the Withlacoochee River Site 4A, *Hipparion* is the rarest recognized taxon at the Love Site and Moss Acres. The upper cheekteeth from these two sites referred to *Hipparion* are within the size range of *Cormohipparion ingenuum* and *Neohipparion trampasense* (Table 1), but differ in their shorter, oval protocones, relatively simple fossette plications, and weak pli caballin. The lowers resemble those of *Hipparion* from
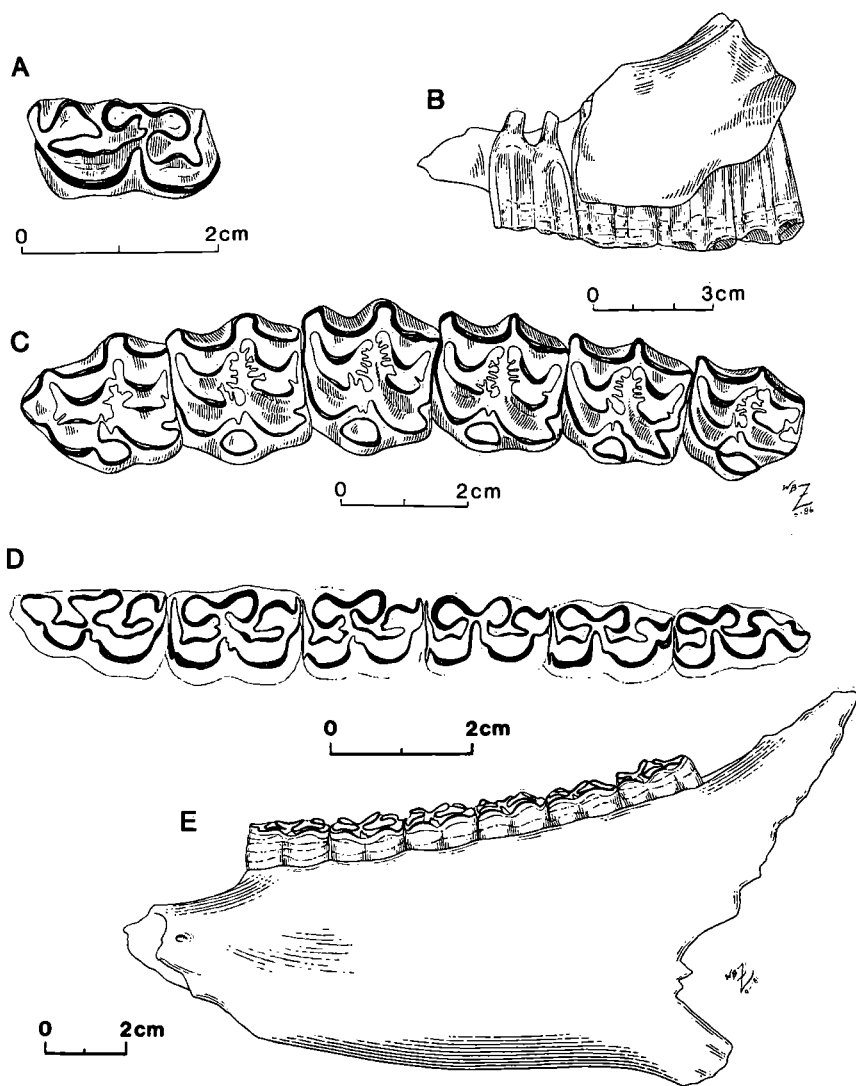
FIGURE 24. *Hipparion* sp., cf. *H. tehonense* from Florida. A. UF 93203, occlusal view of R p34, Hookers Prairie Mine (?early Clarendonian), Polk County. B-E. Withlacoochee River Site 4A (late early Hemphillian), Marion County. B. UF 17205, left maxilla in lateral view. C. UF 17205, occlusal view of L P2-M1 and assoc. R (reversed) M2-M3. D. UF 21027, occlusal view of L p2-m3. E. UF 21027, lateral view of L mandible. UF 17205 and 21027 probably represent the same individual.

Withlacoochee River Site 4A, with deep ectoflexids (including the p2 of UF 32125), no pli caballinids, and no isthmus plications.

When compared to the two recognized advanced species of *Hipparion* from western North America, *H. tehonense* and *H. forcei* (MacFadden 1984), the referred specimens from Florida compare more favorably in size and many features with *H. tehonense*. *H. forcei*, including the early Hemphillian populations referred to by MacFadden (1984), is about 15% larger than *H. tehonense*. UF 17205 also compares favorably with *H. tehonense* in the location and depth of the DPOF. The anterostyle of the P2 is poorly developed and not well separated from the rest of the tooth as in *H. tehonense* (Fig. 24C). A major difference is that the Florida samples are smaller. The Withlacoochee River Site 4A population lacks retention of the DP1 with the permanent dentition, has on average more complex and persistent fossette plications, has slightly higher unworn crown heights (by about 5-7 mm), and, on average, better developed plications on the lower cheekteeth. These are not considered sufficient to designate a new species. Rather, they are trends typically observed in evolving equid chronospecies. Early Hemphillian *H. forcei* from Nebraska shows several of the same differences when compared with Clarendonian populations from California, and the magnitude of change is comparable to that in other species with long chronologic ranges (e.g. *C. occidentale, C. plicatile, Neohipparion trampasense*).

PHYLOGENETIC RELATIONSHIPS

Several recent studies have proposed differing hypotheses regarding the phylogenetic relationships of hipparionine horses. MacFadden (1984) presented cladograms of species for each genus separately; he assumed that hipparionines were a polyphyletic assemblage with each genus having a separate merychippine sister taxon. Forstén's (1984) analysis suggested instead that the group was monophyletic, and that *Pseudhipparion* was also a true hipparionine (following Webb 1969). Later studies (Webb and Hulbert 1986; Hulbert 1987b) confirmed these two points, but demonstrated that Forstén's (1984) arrangement of hipparionine genera was probably incorrect. They hypothesized instead that *Neohipparion* and *Pseudhipparion* (plus "*Merychippus*" *coloradense*) formed a strictly monophyletic group, and that it was the sister taxon to other hipparionines. This hypothesis has yet to be falsified by analyses including greater numbers of characters and taxa, and employing the parsimony criterion and a computer program, PAUP (Swofford 1985), to generate cladograms (Hulbert 1988c; Hulbert and MacFadden in prep.; this study). However, the use of a broader suite of outgroups has demonstrated that the earlier analyses of Webb and Hulbert (1986) and
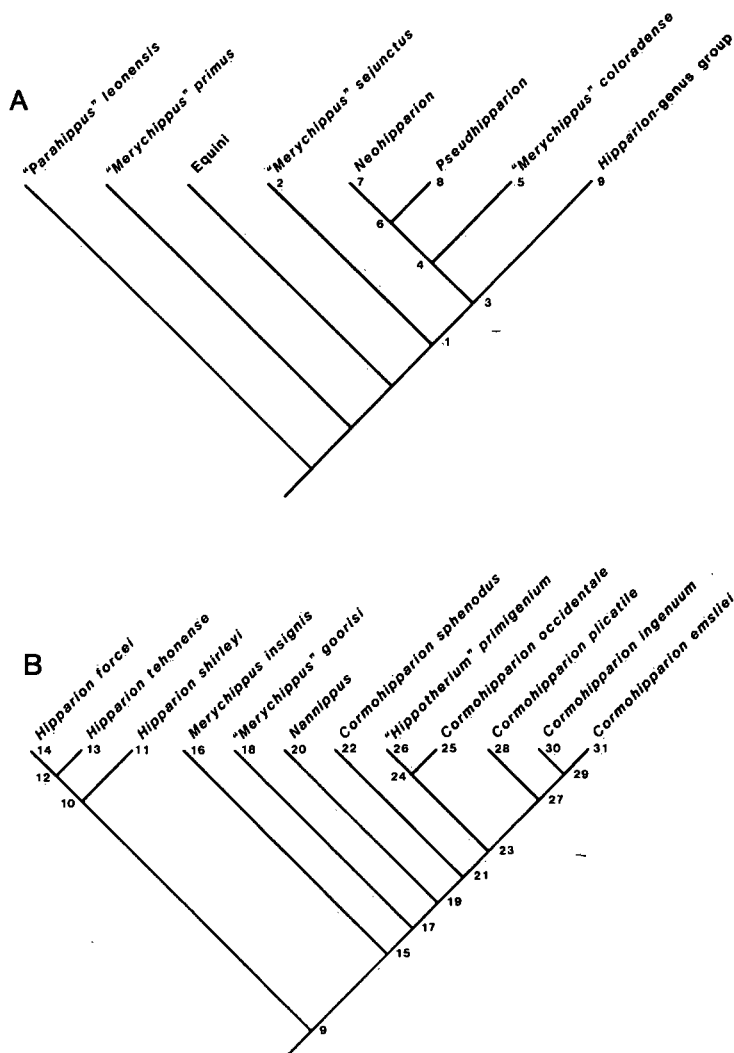
Hulbert (1987b) erred in the choice of *Merychippus insignis* as an outgroup for all hipparionines. This resulted only in an incorrect determination of polarity for several character states, and did not affect the relative phylogenetic positions of the in-group taxa. The most notable of the former was that the shallow DPOF observed in *Neohipparion* and *Pseudhipparion* was thought to have been derived from a primitively much deeper fossa. The computer-generated analyses suggest instead that a relatively shallow DPOF is the shared primitive condition in the Hipparionini and Equini, based on its development in "*M.*" *primus* and "*Parahippus*" *leonensis* (Hulbert 1988c). *Merychippus* s.s.

FIGURE 25. Most parsimonious cladogram depicting phylogenetic relationships among hipparionine equids relative to three outgroups, *"Parahippus" leonensis*, *"Merychippus" primus*, and the Equini. The cladogram was produced by the computer program PAUP based on an analysis of 58 cranial and dental characters (Tables 8, 9). A. Hypothesized relationships of *"Merychippus" sejunctus*, members of the *Neohipparion*-genus group, and the *Hipparion*-genus group. B. Hypothesized relationships among members of the *Hipparion*-genus group. The cladogram is supported by the following list of synapomorphies. Numbers referring to characters and character states are those of Table 8. The character state to the left of the hyphen is the ancestral state, to the right the derived state. Node 1 (Hipparionini): 31 (1-2); 33 (2-3); 48 (0-1); 52 (0-1); 55 (0-1). Node 2 (*"M." sejunctus*): 12 (0-1); 27 (2-1); 40 (1-0). Node 3: 27 (2-4); 28 (2-4); 35 (1-2); 70 (3-4). Node 4 (*Neohipparion*-genus group): 20 (1-3); 23 (1-2); 31 (2-1); 43 (0-1); 48 (1-2); 52 (1-2); 63 (0-1); 71 (2-4). Node 5 (*"M." coloradense*): 16 (2-3); 70 (4-5). Node 6: 2 (2-1); 5 (1-0); 7 (0-1); 10 (0-1); 23 (2-3); 34 (0-1); 62 (1-2); 63 (1-2). Node 7 (*Neohipparion*): 19 (0-1); 24 (0-1); 25 (0-1); 26 (0-1); 27 (4-6); 28 (4-6); 29 (1-0); 38 (2-0); 39 (2-0); 40 (1-0); 46 (1-0); 54 (1-2); 60 (0-1); 61 (0-1); 65 (0-1); 71 (4-7). Node 8 (*Pseudhipparion*): 1 (0-1); 7 (1-2); 28 (4-3); 29 (1-2); 41 (0-1); 70 (4-3). Node 9 (*Hipparion*-genus group): 3 (0-1); 6 (0-1); 7 (0-1); 33 (3-4); 38 (2-1); 39 (2-1). Node 10 (*Hipparion*): 1 (0-1); 7 (1-2); 16 (2-3); 23 (1-2); 35 (1-0); 71 (2-3). Node 11 (*H. shirleyi*): 3 (1-0); 70 (4-3). Node 12: 9 (0-1); 10 (0-1); 20 (1-3); 22 (0-1); 25 (0-2); 26 (0-1); 29 (1-0); 38 (1-0); 39 (1-0); 40 (1-0); 43 (0-1); 71 (3-5). Node 13 (*H. tehonense*): no known autapomorphies. Node 14 (*H. forcei*): 63 (0-1), 70 (4-5); 71 (5-6). Node 15: 30 (2-3); 32 (0-1); 48 (1-2). Node 16 (*M. insignis*): 6 (1-0); 16 (2-1); 41 (0-1); 71 (2-3). Node 17: 2 (2-4); 3 (1-2); 4 (0-1); 27 (4-5); 28 (4-5); 33 (4-5); 38 (1-0); 39 (1-0); 40 (1-0); 52 (1-2). Node 18 (*"M." goorisi*): 9 (0-1); 10 (0-1). Node 19: 7 (1-2); 20 (1-3); 23 (1-2); 25 (0-1); 26 (0-1); 29 (1-0); 43 (0-1); 46 (1-2); 53 (0-1); 58 (0-1); 60 (0-1); 62 (1-2); 63 (0-1); 71 (2-5). Node 20 (*Nannippus*): 19 (0-2); 22 (0-1); 70 (4-3). Node 21 (*Cormohipparion* s.l.): 25 (1-2); 49 (0-1); 58 (1-2); 59 (0-1); 70 (4-5). Node 22 (*C. sphenodus*): no known autapomorphies. Node 23: 10 (0-1); 16 (2-3); 25 (2-3); 61 (0-1); 71 (5-6). Node 24: 32 (1-2); 33 (5-6); 70 (5-6). Node 25 (*C. occidentale*): 23 (2-3); 24 (0-1); 71 (6-8). Node 26 (*"Hippotherium" primigenium*): 70 (6-7); and others, see text. Node 27 (*Notiocradohipparion*): 16 (3-4). Node 28 (*C. plicatile*): 71 (6-8). Node 29: 2 (4-3); 6 (1-0); 24 (0-2); 50 (0-1); 70 (5-4). Node 30 (*C. ingenuum*): no known autapomorphies. Node 31 (*C. emsliei*): 2 (3-1); 4 (1-0); 32 (1-2); 33 (5-6); 49 (1-2); 54 (1-2); 60 (1-2); 61 (1-2); 63 (1-2); 64 (0-1); 68 (0-1).

(including *M. insignis, M. brevidontus*, and a few other species) is more closely related to *Nannippus* and *Cormohipparion* than to other hipparionine genera (see below), and is a member of the tribe Hipparionini as broadly redefined by Hulbert (1988c). The purpose of this section is to demonstrate and discuss: (1) the composition and synapomorphic character states of the Hipparionini; (2) the relative phylogenetic relationships of the six North American hipparionine genera, as well as several hipparionine species not assigned to any of these genera; (3) the phylogenetic relationships of species that make up the

clades *Hipparion* and *Cormohipparion*; and (4) the possible relationships between the latter and certain Old World hipparionines.

This analysis is based on the distribution of 58 characters among 19 taxa. All of the 71 cranial and dental characters described by Hulbert and MacFadden (in prep.) were used except for those that are primitive in each of the 19 taxa under consideration. The remaining 58 characters and their observed states are listed in Table 8. In order to facilitate comparison with Hulbert and MacFadden (in prep.) and future analyses, the same numbering scheme is used here to refer to characters as in these studies. As postcranial elements associated with skulls are unknown for the vast majority of taxa being studied, no attempt was made to use any of the 26 postcranial characters selected by Hulbert and MacFadden (in prep.) as having phylogenetic utility. The 19 taxa analyzed here include seven of the merychippine-grade species also studied by Hulbert and MacFadden (in prep.; "*Parahippus*" *leonensis*, "*Merychippus*" *primus*, "*M.*" *sejunctus*, "*M.*" *coloradense*, "*M.*" *goorisi*, *M. insignis*, and *Hipparion shirleyi*), the two other North American species of Hipparion (H. tehonense and H. forcei), the five species of North American *Cormohipparion* (*C. sphenodus, C. occidentale, C. plicatile, C. ingenuum*, and *C. emsliei*), the oldest Eurasian hipparionine ("*Hippotherium*" *primigenium*), the three other hipparione genera (*Pseudhipparion, Nannippus*, and *Neohipparion*), and the tribe Equini. Character states for the latter four supraspecific taxa are those determined to be primitive for the clade based on previous analyses (Webb and Hulbert 1986; Hulbert 1987a, 1987b, 1988a, 1988c; Hulbert and MacFadden in prep.). Character states for "*Hippotherium*" *primigenium* were taken from published descriptions, especially those of Forstén (1968, 1972, 1978), Woodburne and Bernor (1980), and Bernor and Hussain (1985).

Cladograms were generated from the character matrix (Table 9) for these 19 taxa on an 80286/80287-based microcomputer by the PAUP program (version 2.4; Swofford 1985). PAUP uses a number of user-defined options to produce one or more equally most parsimonious cladograms ("trees"). "*P.*" *leonensis* was used as the outgroup to determine character state polarities. A single, most parsimonious tree (Fig. 25) was generated with the SWAP = GLOBAL and MULPARS options (Swofford 1985), and equally weighted characters (default option). Using the WEIGHTS = SCALE option, which attempts to lessen the influence of multistate characters on binary characters, resulted in two most parsimonious trees of equal length. One was the same as that produced with equally weighted characters, the other differed only in the relative positions of two species of *Cormohipparion* (the relative merits of this alternative cladogram are discussed below). Swofford (1985) noted that several equally long pathways of character state transformation can exist within the same tree (these can be obtained by the CSPOSS option). The reconstruction of character state transformation events shown in Figure 25

presents what is considered the evolutionarily most likely route in those instances when there are two or more possibilities. For example, character 20 (amount of cement on deciduous cheekteeth) may have evolved by two different pathways of equal length. Well cemented DPs may have evolved independently three times (at Nodes 4, 12, and 19 in Fig. 25); or may have appeared at Node 3, reversed to being poorly cemented at Node 9, and then re-evolved at Node 19. In this case, as in others, parallelism is arbitrarily judged to be more likely than a reversal. The one character whose most parsimonious evolutionary pathway is not shown in Figure 25 is unworn crown height (character 71). Shorter unworn crown heights evolved four times, according to the most parsimonious arrangement. As even one such instance is unlikely, a slightly less parsimonious pathway involving more parallel increases in unworn crown height is shown in Figure 25. This route takes 23 steps, 2 more than the most parsimonious arrangement.

The taxa united at Node 1 (Fig. 25A) form the tribe Hipparionini. It is defined so as to be the sister taxon of the Equini. *"Merychippus" primus* is the closest known sister taxon to the Equini + Hipparionini. Synapomorphies uniting the Hipparionini are strong pli caballins on molars, more persistent fossette plications, stronger protostylids, persistently well separated metaconids and metastylids, and articulation of the fifth metacarpal primarily with the fourth metacarpal (rather than with the unciform). The importance of the latter character was first noted by Sondaar (1968:33). Members of the Hipparionini not shown in Figure 25 are *"M."* isonensus and *"M."* tertius. Together they and *"M."* sejunctus may form a monophyletic group (Hulbert 1988c), but the most parsimonious arrangement is for *"M."* sejunctus to form the nearest sister taxon to the group united at Node 3 in Figure 25A (Hulbert and MacFadden in prep.). Synapomorphies uniting the taxa at Node 3 include more isolated protocones, well developed metastyles, and increased size.

The taxa united at Node 3 comprise two monophyletic clades, those united at Nodes 4 and 9, respectively. Hulbert (1988c) suggested the informal designations *Neohipparion*-genus group for the former, and *Hipparion*-genus group for the latter. These informal group names (a convention of Wiley 1981) are of subtribal rank. Webb and Hulbert (1986) and Hulbert (1987b) have presented phylogenetic analyses of the 14 known species that comprise the *Neohipparion*-genus group. Although *M. insignis* was incorrectly used as an outgroup in those studies, its replacement with *"Parahippus" leonensis* and use of PAUP did not substantially alter their results (Hulbert 1987a). The *Neohipparion*-genus group is united by numerous synapomorphies including well cemented deciduous premolars, elongate-oval protocones, weaker molar pli caballins, strong metastyles, straighter upper cheekteeth, stronger protostylids, shallower p34 ectoflexids, and higher crowned cheekteeth. Synapomorphies for *Pseudhipparion* and *Neohipparion* are listed in Figure 25. This basic dichotomy within the Hipparionini of the *Neohipparion*-genus group

and *Hipparion*-genus group was first recognized by Gidley (1907), on the basis of many of the same characers, in his division of hipparionines into two genera, *Neohipparion* and *Hipparion*. Unfortunately, this insightful observation was overlooked by most later workers.

The *Hipparion*-genus group, united at Node 9 of Figure 25, is made up of four genera found in, if not confined to, North America (*Hipparion*, *Merychippus* s.s., *Nannippus*, and *Cormohipparion*), and "*Merychippus*" *goorisi*, which is a plesion of generic rank. All Old World hipparionines also belong in this group, despite recent referrals of some to *Neohipparion* (e.g. Forstén 1984). Hulbert (1987b, see also Flynn and Bernor 1987) hypothesized that *Neohipparion* is a strictly North American group, as originally proposed by Gidley (1903), and resemblances with Old World taxa result from parallelism. As noted in the introduction, the exact phylogenetic affinities of Old World hipparionines with North American members of the *Hipparion*-genus group is still under debate. One Old World species, "*Hippotherium*" *primigenium*, was included in the analysis, to suggest at least one possible tie between North American and Eurasian hipparionines. Synapomorphies uniting the *Hipparion*-genus group are: a pocketed DPOF with distinct ventral rim; moderately long preorbital bar; increased fossette complexity; and more open hypoconal grooves. The three North American species of *Hipparion* form the sister group (at Node 10) to the remainder of the genus group. They are united by their deeper nasal notch, long preorbital bar, long muzzle, elongate-oval protocones, poorly developed or absent metastyles, and increased unworn crown height. MacFadden's (1984) cladogram of these three species is identical to the most parsimonious arrangement calculated by PAUP, although there are some differences in character interpretation between the two studies. MacFadden's (1984:177) only synapomorphy for the clade was its "...diagnostic configuration of the DPOF... ." Based on the analysis presented in Figure 25, most of the features of the DPOF in these three species are plesiomorphic for the *Hipparion*-genus group, the exception being the relatively long preorbital bar. Other characters of the cranium and dentition serve to unite the group. It should be emphasized that the protocone shape, although slightly more elongated than the primitive hipparionine condition, is less elongated in these species than in other taxa for which the character (23) is similarly coded, such as "*M.*" *coloradense* or *Cormohipparion sphenodus*. This clade retained relatively more oval protocones into the Clarendonian than any other hipparionine genus. *H. shirleyi* is the sister taxon of *H. forcei* and *H. tehonense*, as was shown by MacFadden (1984). He (fig. 27) considered the size of *H. shirleyi* primitive; this analysis suggests the most parsimonious arrangement is for the small size of this species to be derived. *H. forcei* and *H. tehonense* share numerous synapomorphies (Node 12, Figure 25B), including reduced lacrimal bone, thickly cemented deciduous premolars, reduced P2 anterostyle, reduced protoconal spur, more open hypoconal grooves that do not form lakes, and

straighter upper cheekteeth. *H. tehonense* lacks any autapomorphies relative to *H. forcei*, but the latter is larger, has higher crowned teeth, and shallower p34 ectoflexids relative to the former.

At Node 15, *Merychippus*, *Nannippus*, *Cormohipparion*, and "*M.*" *goorisi* share the following derived character states relative to *Hipparion* and their common ancestor with the *Neohipparion*-genus group (Node 3): frequently multiple pli caballins on premolars, persistently plicated external fossette borders (pli protoloph and pli hypostyle), and well developed protostylids on dp34. The placement of *Merychippus* this "high" in the cladogram runs contrary to the usual concept of the genus; i.e. a group of mesodont, mid-Miocene equids ancestral to all hypsodont genera. *Merychippus* is used here in a very restricted sense, to include only the type species (*M. insignis*) and those species with which it forms a monophyletic clade. Moreover, the position of *M. insignis* in Figure 25B is actually not very different from that proposed by Stirton (1940), who regarded it as ancestral to both *Nannippus* and *Hipparion*. To him the latter included taxa now regarded as *Cormohipparion* or *Cormohipparion*-derivatives. Derived characters of *M. insignis* relative to Node 15 include weakened ventral rim of DPOF, shortened muzzle, hypoconal lake on molars, and increased crown height. The latter is not characteristic of more primitive members of *Merychippus* s.s., such as *M. brevidontus*.

United at Node 17 are "*M.*" *goorisi*, *Nannippus*, and *Cormohipparion*. They share a very deep, well pocketed DPOF with a well defined anterior margin, protocones isolated to late wear-stages (except on P2), complex fossette plications, hypoconal groove open to base of crown, and well developed protostylids on p3-m3. It has been frequently stated in the literature than "*M.*" *goorisi* only shares derived facial character states with *Cormohipparion*, but that its dentition is of merychippine grade (e.g. MacFadden 1984). However, as demonstrated by this list of synapomorphies, and despite its low crown height and thin cement, the cheekteeth of "*M.*" *goorisi* are advanced in several respects. MacFadden (1984:185) suggested that "*M.*" *goorisi* was directly ancestral to *Cormohipparion sphenodus*, despite possession of a possible autapomorphy, a very deeply pocketed DPOF. Evander (1985) noted that the fossa of the holotype of "*M.*" *goorisi* (F:AM 73900) had the most deeply pocketed DPOF of the topotypic sample, and that there was considerable variation for the expression of this character. Therefore, I do not consider the degree of pocketing in this species to be derived beyond that observed in other species of *Cormohipparion*. The face of "*M.*" *goorisi* does have derived characters; the lacrimal bone is reduced and does not form part of the DPOF. As the preorbital bar is only moderately long (i.e. the DPOF is close to the orbit), the jugal forms the posteroventral half of the DPOF (a unique feature among North American hipparionines, because others with reduced lacrimals also have long preorbital bars such that only the maxilla and nasal form the DPOF). This derived facial morphology makes it unlikely for

"*M.*" *goorisi* to have been ancestral to *C. sphenodus* (or any other known species) and also differentiates it from *M. insignis* (*contra* Evander 1986).

As suggested by Hulbert (1987a, 1988c), *Nannippus* and *Cormohipparion* are sister taxa, united at Node 19 of Figure 25B. The character states reported for *Nannippus* (Table 9) are those of an undescribed, but well represented species from the Clarendonian of Nebraska, Texas, and Florida (Hulbert 1987a, in prep.). Several maxillae and partial skulls in the Frick Collection (e.g. F:AM 117046) clearly demonstrate the facial morphology of this taxon, which closely resembles that of *C. sphenodus*. These samples, plus a large number of teeth of a very late Clarendonian *Nannippus* from the Love Site form a chronomorphocline for many dental character states that bridges the differences between *Cormohipparion* and typical Hemphillian *Nannippus*. At Node 19, *Nannippus* and *Cormohipparion* share a very long preorbital bar, thickly cemented deciduous premolars, elongate-oval protocones, reduced protoconal spur, straighter upper cheekteeth, strong ectostylids on dp2-dp4, isolated protostylids in early wear-stages, plicated isthmuses, small pli caballinids on slightly worn p2-p4, shallower premolar ectoflexids, and increased unworn crown height. Species of *Nannippus* share the following derived characters (Node 20), very reduced or lost DP1, reduced P2/DP2 anterostyle, and decreased size.

The cladistic arrangement of species of *Cormohipparion* in Figure 25B differs greatly from that of MacFadden (1984). "*M.*" *goorisi* is not considered a member of *Cormohipparion*, as to include it would render the genus paraphyletic. Three species not considered by MacFadden (1984) as belonging in *Cormohipparion* form a monophyletic group that branches off between *C. sphenodus* and *C. occidentale* on the cladogram. Also, he suggested that "Old World *Cormohipparion*" was more closely related to *C. sphenodus* than to *C. occidentale*, but did not list any shared derived characters to demonstrate this (MacFadden 1984, fig. 149A). This study suggests instead that *C. occidentale* and "Old World *Cormohipparion*" share eight derived character states not observed in *C. sphenodus*, five of these with *C. (Notiocradohipparion)* at Node 23, and three at Node 24. Apomorphic character states that unite all *Cormohipparion* s.l. at Node 21 include a very reduced or absent protoconal spur, shallower ectoflexids on dp2-dp4, persistent isthmus plications, plicated paralophids, and increased size. *C. sphenodus* has no known autapomorphies, and may, as suggested by Woodburne et al. (1981), be directly ancestral to all or some of the remaining species of the genus. At Node 23, these five species are united by lacrimal excluded from DPOF (this state unknown for *Notiocradohipparion* spp.), more elongated muzzle, protoconal spur usually absent, pli caballinid present on slightly worn molars, and increased unworn crown height. The three shared-derived character states of *C. occidentale* and "*Hippotherium*" *primigenium* are multiple plis protoloph common, persistently very complex internal fossettes, and increased size (Node 24).

Autapomorphies for *C. occidentale* (Node 25) include elongated protocone with flattened lingual borders, and increased unworn crown height. Also apparently derived for *C. occidentale* is the very narrow anterior portion of the DPOF (MacFadden 1984). Relative to *C. occidentale*, *"H."* *primigenium* is derived by its larger size, and the dorsoventrally high, anteroventrally-oriented DPOF (Woodburne et al. 1981; Bernor and Hussain 1985). Also, a variable but significant fraction (10 to 50%) of p3-m2 have ectostylids in *"H."* *primigenium* (Forstén 1978:300-301), a character almost never observed in permanent teeth of North American hipparionines. Most of the differences and similarities in cranial morphology between *C. sphenodus*, *C. occidentale*, and *"H." primigenium* listed above were previously discussed by Bernor and Hussain (1985).

The three remaining species, *C. plicatile*, *C. ingenuum*, and *C. emsliei*, form a monophyletic group united at Node 27, herein designated the new subgenus *Notiocradohipparion*. They share but one synapomorphy, a very elongated muzzle region. The length of the lower diastema (ldl) is equal to or greater than 70% of the lower toothrow length (ltrl); in *C. occidentale* the ldl is less than 65% of the trl. Obviously, a clade based on a single synapomorphy is not well supported. As these three species are still poorly known with regards to cranial and postcranial characters, recovery of more complete specimens will test the hypothesis of their monophyly. *C. plicatile* forms the sister taxon to *C. ingenuum* + *C. emsliei*; relative to them its only autapomorphy is increased unworn crown height. Its size and enamel morphology are judged to reflect the primitive conditions for the clade, as does what is known of the morphology of its DPOF. *C. ingenuum* and *C. emsliei* share (Node 29) a shallower DPOF without a distinct ventral rim, protocone lingual borders often flat or concave, p2/dp2 metaconid with anterior plication that connects to paralophid, and decreased size. *C. ingenuum* has no known autapomorphies relative to *C. emsliei*. *C. emsliei* has numerous autapomorphies, including an apparently very shallow DPOF without a distinct anterior margin, increased fossette complexity, shallower ectoflexids, strong and persistent pli caballinids, and elongated, angular metaconids and metastylids.

The cladogram and hypothesized relationships discussed above form the most parsimonious arrangement of these taxa when all characters are equally weighted. As previously noted, PAUP has an option (WEIGHT = SCALE) that scales each character with regards to its number of possible states. For a character with only two states (0 and 1), the transformation 0—>1 or 1—>0 counts as 1.0 step (the same as with equally weighted characters). For a character with three states (0, 1, and 2), single step transformations, e.g. 0—>1, 1—>2, or 1—>0, each count as 0.5 steps. In the case of four states, single step transformations count as 0.333 steps; or in the general case of n states, each single step counts as 1/(n-1), such that the complete transformation from 0—>(n-1) always equals 1.0. The purpose of this option is to prevent

characters with many states from having undue influence on the cladogram (Swofford 1985). With this option in effect for the data set in Table 9, PAUP produced two equally most parsimonious cladograms. One of these was that produced with the default equally weighting option and shown in Figure 25. The second cladogram differed slightly in that it united *C. ingenuum* and *C. emsliei* with *C. occidentale* as a monophyletic group, whose closest sister taxon was "*H.*" *primigenium*. There are several reasons for considering this alternative arrangement less likely than the one previously discussed. It unites *C. ingenuum*, *C. emsliei*, *C. occidentale*, and "*H.*" *primigenium* by their more complexly plicated fossettes (characters 32 and 33), and increased size (the same three characters that unite Node 24 in Fig. 25B). *C. occidentale*, *C. ingenuum*, and *C. emsliei* are united only by a flattened lingual border of the protocone (24). *C. ingenuum* and *C. emsliei* are united by the same characters as listed for Node 29 in Figure 25B, except that the decrease in size is of greater magnitude. *C. ingenuum* is derived relative to *C. emsliei* by simplifying its fossettes, i.e. *C. ingenuum* does not really possess any of the three characters that are supposed to unite this clade, so it must reverse all three back to the primitive condition. The alternate tree also requires parallel acquisition of the very elongated muzzle in *C. plicatile* and *C. ingenuum* + *C. emsliei*. This combination of parallelisms and reversals seems less likely than that required for the other tree.

Another reason for considering the alternate hypothesis less likely is the chronologic distribution of the taxa involved. Although biostratigraphic records should not be used to construct phylogenies (Novacek and Norell 1982), they can be used, along with biogeographic distributions, to choose among phylogenies of equal length. This is especially valid when the fossil record is relatively complete, as is the case for late Miocene horses. In the alternative phylogeny, both *C. emsliei* and *C. ingenuum* possess derived character states relative to one another, thus as sister taxa their time of first appearance should be about the same. In the first cladogram (Fig. 25), *C. ingenuum* has no autapomorphies relative to *C. emsliei*. Thus it may have given rise to *C. emsliei* through anagenesis (if their observed ranges do not overlap in time), or through cladogenesis with the parent species not going extinct during speciation (if there is overlap in their temporal ranges, as appears to be the case based on the Moss Acres Racetrack Site record). The chronological ranges of these two species, as currently known, favors the latter scenario. *C. ingenuum* is first known in the early Clarendonian, 4 myr prior to the first appearance of *C. emsliei* at Moss Acres. The alternative cladogram also implies a much older (late Barstovian) origination for *C. plicatile* than is reflected in the fossil record (late Clarendonian). Therefore, I consider the cladogram in Figure 25 to represent the most likely hypothesis of relationships among the species of the *Hipparion*-genus group, based on the distribution of cranial and dental character states.

BIOCHRONOLOGY AND BIOGEOGRAPHY

The chronological and geographical distribution of the five recognized species of *Cormohipparion*, the three species of *Hipparion*, and *"Merychippus" goorisi* are outlined in Figure 26. The oldest known species of *Hipparion*, *"H." shirleyi*, and *"Merychippus" goorisi* are both at present known only from the Barstovian of the Texas Gulf Coastal Plain. However, as noted by MacFadden (1984), additional specimens may exist in other regions, but would be difficult to separate from other merychippines without very complete material. MacFadden (1984:154-155) extended the chronologic range of *"M." goorisi* beyond that of the type locality into the late Barstovian, with reference to specimens from the Cold Springs Fauna. He specifically referred TMM 31242-71 to *"M." goorisi*, and stated that it came from the "Cold Springs L. F." (p. 155). However, this specimen is from the Point Blank local fauna, stratigraphically the lowest among the local faunas that make up the Burkeville Fauna (early Barstovian; Tedford et al. 1988), and is the holotype of *Protohippus vetus* Quinn (1955). If MacFadden's (1984) reference is followed, then *"M." goorisi* must become a junior synonym of *P. vetus*. However, the two are distinctly different in fossette complexity, degree of protocone attachment, and crown height and are not specifically identical. The status and phylogenetic position of *Protohippus vetus* was further discussed by Hulbert (1988a). I do not recognize *"M." goorisi* from the Cold Springs Fauna; rather that fauna contains a relatively primitive population of *C. sphenodus*.

The late Barstovian-early Clarendonian taxon *C. sphenodus* is widely distributed, from California to Florida, and apparently represents the ancestral stock for the remaining members of the genus (Woodburne et al. 1981; MacFadden 1984). Bernor and Hussain (1985) discount *C. sphenodus* as being "directly" ancestral to Old World hipparionines, because it is too primitive, and noted the variation in DPOF morphology in specimens referred to *C. sphenodus*. Further analysis may show that *C. sphenodus* as presently used is a grade, with two separate clades, one closer to *Notiocradohipparion*, and one to *C. occidentale*, respectively. The southern and eastern *C. sphenodus*-derived lineage is represented by *C. plicatile*, *C. ingenuum*, and *C. emsliei*, which together comprise the subgenus *Notiocradohipparion*. *C. plicatile* as known is restricted to the late Clarendonian and early Hemphillian of peninsular Florida. *C. ingenuum* is also known from Central America; probably this represents an immigration event southward along the Gulf Coastal Plain from Texas. *C. emsliei* is the youngest surviving species of *Cormohipparion* in North America (Fig. 26) and is as yet known only from localities along the Gulf Coastal Plain in Florida (Hulbert 1988b) and Louisiana (Manning and MacFadden in press). It is possible that all three had much larger ranges in southeastern North America, and that their apparently limited distribution is
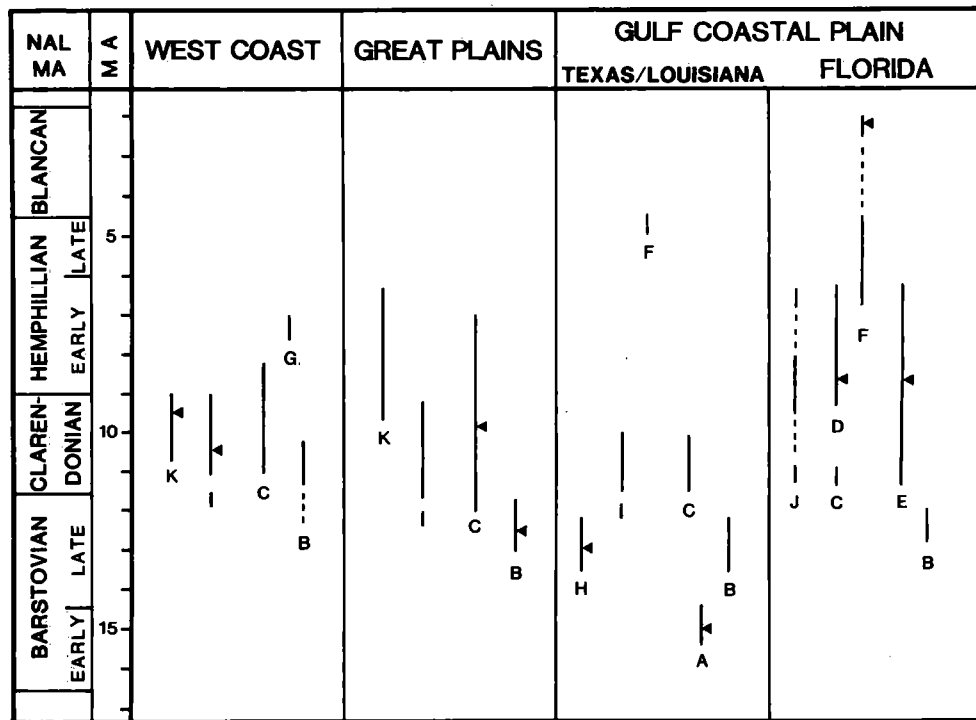
FIGURE 26. Biogeographic and chronologic distributions of North American species of *Cormohipparion* and *Hipparion*, exclusive of Central America. Triangles point to the approximate chronologic position of the type locality for each species; dashed lines fill stratigraphic gaps. A. *"Merychippus" goorisi*. B. *C. sphenodus*. C. *C. occidentale*. D. *C. plicatile*. E. *C. ingenuum*. F. *C. emsliei*. G. *Cormohipparion* sp., Rattlesnake Formation, Oregon. H. *Hipparion shirleyi*. I. *H. tehonense*. J. *Hipparion* sp., cf. *H. tehonense*. K. *H. forcei*. Identifications of *C. sphenodus* and *C. occidentale* in Florida are tentative (see text). Other than the present study, references include Hulbert (1988b), MacFadden (1984), Manning and MacFadden (in press), and personal observations of the TMM, F:AM and UCMP collections.

more a reflection of a biased fossil record. For example, the absence of *Cormohipparion* in the late Clarendonian and Hemphillian of the Texas Gulf Coastal Plain (Fig. 26) probably just reflects the total lack of faunas of the appropriate age. In the Great Plains, *Cormohipparion* is not observed in any late Hemphillian (6.0 to 4.5 Ma) or younger localities. The Upper Bone Valley Formation sample and those from the Florida Blancan mark the last North American appearance of what was once one of the dominant equid genera of the late Miocene. Its absence in western late Hemphillian and Blancan faunas is probably real, as sites of this age are fairly well known.

In general, *Cormohipparion* is much poorer in terms of biostratigraphic utility for correlation of Gulf Coastal Plain and Great Plains localities than *Pseudhipparion, Neohipparion, Calippus,* or *Protohippus*. This is because of the long temporal durations of species' ranges (Fig. 26, Table 10) and limited geographic distribution. They are of more use for correlation within the circum-Gulf of Mexico region, e.g. *C. ingenuum* in Honduras, and especially within the state of Florida.

The genus *Hipparion* (*sensu* MacFadden 1984) ranges from the late Barstovian to early Hemphillian in North America. The record of *Hipparion* east of the Rocky Mountains is scattered, and it is typically rare, the Clarendon Fauna being a notable exception. In faunas from California, however, the genus is more common. Relative to its contemporaries, *Hipparion* was not a diverse group. Besides *H. shirleyi*, only two other chronospecies are recognized; both range from the Clarendonian to the late early Hemphillian. The sample of *Hipparion*, cf. *H. tehonense*, in Florida ranges from the early Clarendonian to late early Hemphillian. Records from the Moss Acres Ranch Site and the Withlacoochee River 4A l.f. are two of the youngest for the genus. MacFadden (1984) referred a similarly aged population from Nebraska to *H. forcei*. *Hipparion* is also a poor biostratigraphic indicator in Florida, because of its rarity and long chronologic range.

Table 10 summarizes the distribution of equid species in Florida from the late Barstovian to the end of the Blancan, the interval for which *Cormohipparion* is known to have been present. The late early Hemphillian (6-7 Ma) was the period of maximum species richness for the *Hipparion*-genus group in Florida, with six contemporary species. Only two of these lineages persisted into the late Hemphillian, *C. emsliei* and *Nannippus minor*. This mid-Hemphillian extinction event (at about 6.0 Ma) includes the last appearance in North America of four equid genera, *Hipparion, Calippus, Protohippus,* and *Pliohippus* (Hulbert 1987a, 1988a), in what marks a major event in the decline of the Clarendonian Chronofauna (Webb 1977, 1984).

CONCLUSIONS

Of the five recognized North American species of *Cormohipparion* and three of *Hipparion*, all appear in Gulf Coastal Plain faunas except *H. forcei*. "*Merychippus*" *goorisi* and *H. shirleyi* are both small, primitive species known from the Barstovian Fleming Formation of southeast Texas, but are as yet unknown from Florida. The ubiquitous late Barstovian-early Clarendonian *C. sphenodus* is provisionally recognized for the first time in eastern North America. Limited samples of isolated teeth are found in the lower of two superposed faunas in the Bone Valley Formation of south-central Florida. *C. occidentale*, well known from the latest Barstovian, Clarendonian, and early Hemphillian of the Great Plains and California, is also provisionally recognized for the first time in Florida, from a limited suite of isolated teeth. The nearest well-documented occurrence is in the Lapara Creek Fauna of southern Texas (Forstén 1975).

Two previously enigmatic hipparionine species described a century ago by Joseph Leidy from Mixson's Bone Bed, Levy County, Florida, are both referred to *Cormohipparion*. This is based on newly recovered and more complete material from the Love, McGehee Farm, and Moss Acres Racetrack sites. Referred material of *C. ingenuum* ranges in age from early Clarendonian to late early Hemphillian (about 11.0 to 6.0 Ma), and demonstrates minor amounts of chronoclinal evolution, most notably in increasing enamel complexity. The range of *C. plicatile* is limited to the late Claredonian-early Hemphillian (9.0-6.0 Ma), but it is typically more abundant than *C. ingenuum* and shows a greater degree of chronoclinal change. *C. plicatile* is not recognized as yet from localities outside of peninsular Florida. The population of medium-sized hipparionines from the Lapara Creek Fauna is for the most part not referable to *C. ingenuum*, as was suggested by Quinn (1955) and Forstén (1975), but instead to *H. tehonense* and to an undescribed species of *Nannippus*. Only two Texas specimens are referred to *C. ingenuum*. *C. ingenuum* and *C. plicatile* differ principally in size and crown height. The *Cormohipparion* population from the Gracias Formation of Honduras, referred to *C. plicatile* by Webb and Perrigo (1984), is notably smaller than Florida samples of that species, but well within the observed range of *C. ingenuum*. *C. ingenuum* is not the senior synonym of *Nannippus lenticularis* (Cope), as was proposed by MacFadden (1984). Although of similar size, the two taxa differ in facial morphology, crown height, and in numerous details of the dentition.

Cormohipparion is not observed in late Hemphillian faunas of the west, as it disappears there along with many other members of the Clarendonian Chronofauna. However, the genus persisted in Florida until near the end of the Blancan. The upper Bone Valley Formation and two late Blancan faunas

from Florida contain a small to moderate-sized and distinctively complexly plicated species, *C. emsliei* (Hulbert 1988b). *C. emsliei* apparently is descended from *C. ingenuum*, but their observed ranges overlap in the late early Hemphillian, based on a new record from the Moss Acres Racetrack Site. Many dental features that appeared in the *C. ingenuum-C. emsliei* lineage parallel those observed in *Neohipparion*, but occur about four million years later. In terms of its degree of hypsodonty, *C. emsliei* is much more primitive than contemporary species of *Pseudhipparion, Neohipparion, Nannippus, Astrohippus,* and *Dinohippus*, and reflects a Clarendonian grade of evolution (Hulbert 1988b). However, its fossettes have on average more plications than any other North American hipparionine.

Hipparion tehonense is recognized (at least provisionally) in Florida, from an early Clarendonian horizon in the Bone Valley Formation, from the late Clarendonian Love Site, and from the early Hemphillian Moss Acres and Withlacoochee River 4A sites. The latter two represent the youngest records of the species. These referred specimens are morphologically similar to the topotypic sample from California, but are on average smaller.

LITERATURE CITED

Becker, J. 1985. Fossil herons (Aves: Ardeidae) of the late Miocene and early Pliocene of Florida. J. Vert. Paleon. 5:24-31.
Bernor, R.L. 1985. Systematic and evolutionary relationships of the hipparionine horses from Maragheh, Iran (late Miocene, Turolian Age). Palaeovertebrata 15(4): 173-269.
___, and S.T. Hussain. 1985. An assessment of the systematic, phylogenetic and biogeographic relationships of Siwalik hipparionine horses. J. Vert. Paleon. 5:32-87.
___, M.O. Woodburne, and J.A. Van Couvering. 1980. A contribution to the chronology of some Old World faunas based on hipparionine horses. Geobios 13:705-739.
Bode, F.D. 1931. Characters useful in determining the position of individual teeth in the permanent cheektooth series of merychippine horses. J. Mamm. 12:118-129.
Christol, J. de. 1832. [untitled]. Annales des Sciences et de l'industrie du Midi de la France 1:180-181.
Cope, E.D. 1886. On two new species of three-toed horses form the upper Miocene, with notes on the fauna of the *Ticholeptus* beds. Proc. Amer. Phil. Soc. 23:357-361.
___. 1889. A review of the North American species of *Hippotherium*. Proc. Amer. Phil. Soc. 26:429-458.
Dalquest, W.W. 1983. Mammals of the Coffee Ranch local fauna, Hemphillian of Texas. Texas Mem. Mus., Pearce-Sellards Ser. (38):1-41.
Evander, R.L. 1985. Middle Miocene horses of North America. Ph.D. diss., Columbia Univ., 433 p.
___. 1986. The taxonomic status of *Merychippus insignis* Leidy. J. Paleon. 60(6): 1277-1280.
Forstén, A. 1968. Revision of the Palearctic *Hipparion*. Acta Zool. Fennica 119:1-119.
___. 1972. *Hipparion primigenium* from southern Tunisia. Notes Serv. Geol. 35, Trav. Geol. Tunisienne 5:7-28
___. 1975. The fossil horses of the Texas Gulf Coastal Plain: A revision. Texas Mem. Mus., Pierce-Sellards Ser. (22):1-86.
___. 1978. *Hipparion primigenium* (v. Meyer, 1829), an early three-toed horse. Ann. Zool. Fennici 15:298-313.

_____. 1982. The status of the genus *Cormohipparion* Skinner and MacFadden (Mammalia, Equidae). J. Paleon. 56:1332-1335.

_____. 1984. Supraspecific groups of Old World hipparions (Mammalia, Equidae). Paläon. Zeit. 58:165-171.

Galbreath, E.C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas Paleon. Contrib., Vertebrata 4:1-120.

Gidley, J.W. 1903. A new three-toed horse. Bull. Amer. Mus. Nat. Hist. 19:465-476.

_____. 1906. New or little known mammals from the Miocene of South Dakota. Part IV. Bull. Amer. Mus. Nat. Hist. 22(8):135-153.

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

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

Gregory, J.T. 1942. Pliocene vertebrates from Big Spring Canyon, South Dakota. Bull. Dept. Geol. Sci., Univ. California 26(4):307-446.

Hay, O.P. 1902. Bibliography and catalogue of fossil Vertebrata of North America. Bull. U. S. Geol. Surv. 179:1-868.

_____. 1916. Descriptions of some Floridian fossil vertebrates, belonging mostly to the Pleistocene. Ann. Rept. Florida Geol. Sur. 8:39-76.

Hirschfeld, S.E., and S.D. Webb. 1968. Plio-Pleistocene megalonychid sloths of North America. Bull. Florida State Mus., Biol. Sci. 12(5):213-296.

Hulbert, R.C. 1982. Population dynamics of the three-toed horse *Neohipparion* from the late Miocene of Florida. Paleobiology 8:159-167.

_____. 1987a. Phylogenetic systematics, biochronology, and paleobiology of Late Neogene horses (Family Equidae) from the Gulf Coastal Plain and the Great Plains. Ph.D. diss., Univ. Florida, 570 p.

_____. 1987b. Late Neogene *Neohipparion* (Mammalia, Equidae) from the Gulf Coastal Plain of Florida and Texas. J. Paleon. 61(4):809-830.

_____. 1988a. *Calippus* and *Protohippus* (Mammalia, Perissodactyla, Equidae) from the Miocene (Barstovian-early Hemphillian) of the Gulf Coastal Plain. Bull. Florida State Mus., Biol. Sci. 32(3):221-340.

_____. 1988b. A new *Cormohipparion* (Mammalia, Equidae) from the Pliocene (latest Hemphillian and Blancan) of Florida. J. Vert. Paleon. 7(4):451-468.

_____. 1988c. Phylogenetic interrelationships and evolution of North American Late Neogene Equidae. *In* D.R. Prothero, R. Schoch, and J.L. Franzen (eds.). The evolution of perissodactyls. Courier Forschung-Institute, Senckenberg.

_____. in prep. *Nannippus* (Mammalia, Equidae) from the late Miocene and earliest Pliocene of the Gulf Coastal Plain and the Great Plains, and the origin of the genus.

_____, and B.J. MacFadden. in prep. Morphological transformation and cladogenesis at the base of the adaptive radiation of Miocene hypsodont horses.

Jackson, D.R. 1978. Evolution and fossil record of the chicken turtle *Deirochelys*, with a re-evaluation of the genus. Tulane Stud. Zool. Bot. 20:35-55.

Leidy, J. 1856. Notice of some remains of extinct Mammalia, recently discovered by Dr. F. V. Hayden in the bad lands of Nebraska. Proc. Acad. Nat. Sci. Philadelphia 8:59-60.

_____. 1884. Vertebrate fossils from Florida. Proc. Acad. Nat. Sci. Philadelphia 36:118-119.

_____. 1885. *Rhinoceras* and *Hippotherium* from Florida. Proc. Acad. Nat. Sci. Philadelphia 37:32-33.

_____. 1887. Fossil bones from Florida. Proc. Acad. Nat. Sci. Philadelphia 39:309-310.

_____, and F.A. Lucas. 1896. Fossil vertebrates from the Alachua Clays of Florida. Trans. Wagner Free Inst. Sci. Philadelphia 4:1-61.

MacFadden, B.J. 1980. The Miocene horse *Hipparion* from North America and from the type locality in southern France. Palaeontology 23:617-635.

_____. 1984. Systematics and phylogeny of *Hipparion*, *Neohipparion*, *Nannippus*, and *Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. Bull. Amer. Mus. Nat. Hist. 179:1-196.

_____. 1986. Late Hemphillian monodactyl horses (Mammalia, Equidae) from the Bone Valley Formation of central Florida. J. Paleon. 60:466-475.

____, and R.C. Hulbert. in press.   Body-size estimates and size distribution of ungulates (Mammalia) from the late Miocene Love Bone Bed of Florida. *In* J. Damuth and B.J. MacFadden (eds.). Body Size in Mammalian Paleobiology. Cambridge Univ. Press, New York.

____, and M.F. Skinner. 1981.   Earliest Holarctic hipparion, *Cormohipparion goorisi* n. sp. (Mammalia, Equidae), from the Barstovian (medial Miocene) Texas Gulf Coastal Plain. J. Paleon. 55(3):619-627.

____, and J.S. Waldrop. 1980. *Nannippus phlegon* (Mammalia, Equidae) from the Pliocene (Blancan) of Florida. Bull. Florida State Mus., Biol. Sci., 25(1):1-37.

Manning, E., and B.J. MacFadden. in press. Pliocene three-toed horses from Louisiana, with comments on the Citronelle Formation. Tulane Stud. Geol. Paleon.

Matthew, W.D. 1924. Third contribution to the Snake Creek Fauna. Bull. Amer. Mus. Nat. Hist. 50:59-210.

Merriam, J.C. 1916. Mammalian remains from the Chanac Formation of the Tejon Hills, California. Bull. Dept. Geol., Univ. California 10:111-127.

Novacek, M.J., and M.A. Norell. 1982. Fossils, phylogeny, and taxonomic rates of evolution. Syst. Zool. 31(4): 366-375.

Olson, E.C., and P.O. McGrew. 1940. Mammalian fauna from the Pliocene of Honduras. Bull. Geol. Soc. Amer. 52:1219-1244.

Osborn, H.F. 1918. Equidae of the Oligocene, Miocene, and Pliocene of North America. Iconographic type revision. Mem. Amer. Mus. Nat. Hist., n. ser. 2:1-331.

Owen, R. 1848. Description of teeth and portions of jaws of two extinct anthracotheroid quadrapeds....with an attempt to develope Cuvier's idea of the classification of pachyderms by the number of their toes. Quart. J. Geol. Soc. London 4:104-141.

Petuch, E.J. 1982. Notes on the molluscan paleoecology of the Pinecrest Beds at Sarasota, Florida with the description of *Pyruella*, a stratigraphically important new genus (Gastropoda: Melongenidae). Proc. Acad. Nat. Sci. Philadelphia 134:12-30.

Quinn, J.H. 1955. Miocene Equidae of the Texas Gulf Coastal Plain. Bur. Econ. Geol., Univ. Texas Publ. (5516):1-102.

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

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

Simpson, G.G. 1930. Tertiary land mammals from Florida. Bull. Amer. Mus. Nat. Hist. 59:149-211.

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

____, and B.E. Taylor. 1967. A revision of the geology and paleontology of the Bijou Hills, South Dakota. Amer. Mus. Novitates (2300):1-53.

____, S.M. Skinner, and R.J. Gooris. 1977. Stratigraphy and biostratigraphy of Late Cenozoic deposits in central Sioux County, western Nebraska. Bull. Amer. Mus. Nat. Hist. 158(5): 263-371.

Sondaar, P.Y. 1968. The osteology of the manus of fossil and Recent Equidae. Verh. Koninkl. Nederl. Akad. Wetensch., Natuurkund. 25:1-76.

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

____. 1941. Development of characters in horse teeth and the dental nomenclature. J. Mamm. 22:434-446.

Swofford, D.L. 1985. PAUP, Phylogenetic Analysis Using Parsimony. Users Manual Version 2.4. Illinois Nat. Hist. Surv., Champaign, 70 p.

Tedford, R.H., and M.E. Hunter. 1984. Miocene marine-nonmarine correlations, Atlantic and Gulf Coastal Plains, North America. Palaeogeogr., Palaeoclimat., Palaeoecol. 47: 129-151.

Tedford, R. H., T. Galusha, M.F. Skinner, B.E. Taylor, R.W. Fields, J.R. Macdonald, J.M. Rensberger, S.D. Webb, and D.P. Whistler. 1988. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene Epochs), North America. Pp. 153-210 *in* M.O. Woodburne (ed.). Cenozoic Mammals of North America: Geochronology and Biostratigraphy. Univ. California Press, Berkeley.

Webb, S.D. 1969a.   The Burge and Minnechaduza Clarendonian mammalian faunas of north-central Nebraska. Univ. California Publ. Geol. Sci. 78:1-191.
_____. 1969b. The Pliocene Canidae of Florida. Bull. Florida State Mus., Biol. Sci. 14(4):273-308.
_____. 1977. A history of savanna vertebrates in the New World. Part 1: North America. Ann. Rev. Ecol. Syst. 8:355-380.
_____. 1984. On two kinds of rapid faunal turnover. Pp. 417-436 in W.A. Berggren and J.A. Van Couvering (eds.). Catastrophes and Earth History. Princeton Univ. Press, Princeton, New Jersey.
_____, and R.C. Hulbert. 1986.   Systematics and evolution of Pseudhipparion (Mammalia, Equidae) from the Late Neogene of the Gulf Coastal Plain and the Great Plains. Pp. 237-285 in K.M. Flanagan and J.A. Lillegraven (eds.). Vertebrates, Phylogeny, and Philosophy. Univ. Wyoming Contrib. Geol., Spec. Pap. 3.
_____, and S.C. Perrigo. 1984.   Late Cenozoic vertebrates from Honduras and El Salvador. J. Vert. Paleon. 4:237-254.
_____, and N. Tessman. 1968. A Pliocene vertebrate fauna from low elevation in Manatee County, Florida. Amer. J. Sci. 266:777-811.
_____, B.J. MacFadden, and J.A. Baskin. 1981. Geology and paleontology of the Love Bone Bed from the late Miocene of Florida. Amer. J. Sci. 281:513-544.
Wiley, E.O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York, 439 p.
Woodburne, M.O., and R.L. Bernor. 1980.   On supraspecific groups of some Old World hipparionine horses. J. Paleon. 54:1319-1348.
_____, B.J. MacFadden, and M.F. Skinner. 1981. The North American "Hipparion" Datum, and implications for the Neogene of the Old World. Geobios 14:1-32.

TABLE 1. Measurements of selected upper cheekteeth of *Cormohipparion* and *Hippparion* from Florida and Honduras. Florida locality abbreviations: ARS, Agricola Road Site; COC, Coffrin Creek; DUN, Dunnellon Phosphate Mines; FGM, Fort Green Mine; 4CM, Four Corners Mine; GRD, Gardinier Mine; GZP, Gray Zone, Phosphoria Mine; H5B, Haile 5B; H19, Haile 19A; HPM, Hookers Prairie Mine; LOV, Love Site; MAR, Moss Acres Racetrack Site; MGF, McGehee Farm; MIX, Mixson's Bone Bed; PHM, Phosphoria Mine; PTM, Port Manatee Site; RZP, Red Zone, Phosphoria Mine; SCM, Silver City Mine; SMN, "Stream Matrix" Horizon, Nichols Mine; W4A, Withlacoochee River Site 4A; W4X, Withlacoochee River Site 4X. Honduran locality abbreviation: GFH, Gracias Fauna. See Table 3 for univariate statistics. Measurements defined in text and in Figure 3. An "a" before a value indicates that it is an approximation from a broken or waterworn specimen. All measurements in millimeters.

	Loc	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	Comment
				Cormohipparion sp., cf. *C. sphenodus*						
UF 28434	RZP	M1	R	a19	18.8	8.2	3.5	15.5	29.7	
UF 28432	RZP	M12	R	19.8	18.4	6.6	3.9	--	a31	
UF 28433	RZP	M12	R	—	a20	8.4	—	a16	a43	
UF 28435	RZP	M3	L	18.7	15.4	7.3	3.0	17.6	38.2	
				Cormohipparion sp. cf. *C. occidentale*						
UF 28607	GZP	P34	R	23.4	22.1	7.0	4.1	18.7	37.4	
UF 102552	HPM	P34	L	22.9	21.8	8.8	3.5	17.6	a29	
UF 102553	HPM	M12	R	22.6	23.5	8.7	a4	18.6	33.8	
				Cormohipparion ingenuum						
UF 36107	LOV	DP2	L	30.8	18.4	5.2	4.0	27.1	9.8	
UF 35953	LOV	DP2	R	29.3	17.8	4.9	3.2	26.6	11.7	
UF 36122	LOV	DP2	L	30.5	17.0	5.3	3.4	28.2	12.7	
UF 35932	LOV	DP2	R	30.9	18.1	5.8	3.4	27.7	14.0	
UF 35947	LOV	DP2	R	30.9	17.0	5.3	3.5	27.0	14.5	
UF 35953	LOV	DP3	R	23.8	17.9	4.7	3.6	20.1	12.1	
UF 36122	LOV	DP3	L	23.7	16.4	5.4	3.0	--	12.6	

Table 1 Continued.

	Loc	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	Comment
				Cormohipparion ingenuum (continued)						
UF 35947	LOV	DP3	R	23.2	17.2	5.2	3.3	20.1	14.5	
UF 36122	LOV	DP4	L	24.2	14.8	5.7	2.8	21.1	13.9	
UF 35953	LOV	DP4	R	24.5	15.8	5.0	2.8	20.2	15.5	
UF 102554	HPM	DP34	L	22.2	15.0	4.6	2.9	19.1	15.0	
UF 98107	ARS	DP34	R	21.6	15.4	3.4	2.9	19.1	12.5	
UF 96691	LOV	DP34	L	23.3	17.5	5.8	3.4	20.0	9.0	
UF 96751	LOV	DP34	R	22.5	17.2	6.3	3.6	19.3	11.7	
UF 96740	LOV	DP34	R	22.9	16.3	6.7	2.9	20.2	16.1	
UF 98101	ARS	P2	L	--	19.7	7.0	4.8	--	13.6	
UF 98108	ARS	P2	R	26.3	18.8	6.2	3.8	21.5	28.1	
UF 28683	GZP	P2	L	a27	18.6	5.5	3.6	20.9	28.2	
UF 36203	LOV	P2	L	24.4	18.0	5.5	3.5	19.5	19.1	
UF 32300	LOV	P2	L	26.0	18.5	5.3	3.8	--	26.1	
UF 36161	LOV	P2	L	25.5	17.2	6.4	3.4	20.3	28.8	
UF 36020	LOV	P2	R	24.2	18.2	6.0	3.6	18.0	29.2	
UF 36150	LOV	P2	L	26.6	15.8	5.9	4.0	19.8	35.7	
F:AM 107875	MIX	P2	L	25.5	18.3	6.4	3.7	20.6	20.4	
UF 46323	GFH	P2	L	23.6	16.8	5.3	3.4	--	35.7	
UF 98101	ARS	P3	L	20.6	21.2	7.5	4.5	16.4	16.9	
UF 98106	ARS	P3	L	21.8	19.9	6.3	4.1	16.5	28.2	
UF 32300	LOV	P3	L	20.4	20.7	5.9	3.5	--	--	
F:AM 107875	MIX	P3	L	19.7	19.5	6.8	3.8	--	24.2	
UF 17204	W4A	P3	R	18.7	18.3	6.7	3.7	--	--	
UF 98101	ARS	P4	L	20.1	21.2	7.7	4.6	15.9	17.4	
UF 98102	ARS	P4	L	18.2	19.7	6.9	3.7	16.8	15.2	
UF 98106	ARS	P4	R	21.5	20.2	6.4	3.9	16.4	30.8	
UF 32300	LOV	P4	L	19.8	19.5	6.1	3.6	--	--	
F:AM 107875	MIX	P4	L	19.5	19.2	7.0	3.7	16.7	27.4	
UF 17204	W4A	P4	R	18.0	17.4	6.8	3.6	--	--	

UF 18329	W4X	P4	L	19.1	18.6	7.1	3.7	16.3	33.8	
UF 18034	GFH	P4	R	19.6	19.0	7.3	3.4	15.6	41.2	
UF 65706	SCM	P34	L	21.4	--	7.9	3.1	16.5	a30	
UF 28555	GZP	P34	L	a20.5	19.1	7.3	3.8	--	35.4	
UF 28556	GZP	P34	R	21.2	19.8	7.0	4.1	16.4	36.5	
UF 107564	ARS	P34	R	19.7	18.1	6.5	3.1	15.4	23.2	
UF 62464	LOV	P34	L	18.8	17.8	6.4	3.6	16.6	19.1	
UF 53404	LOV	P34	R	18.9	18.4	6.8	3.4	14.7	27.3	
UF 53401	LOV	P34	R	19.5	18.3	7.1	3.7	15.6	27.5	
UF 53400	LOV	P34	R	19.6	18.6	8.0	3.8	14.9	35.5	
UF 62434	LOV	P34	R	21.5	17.3	7.9	3.5	16.0	42.6	
UF 7246	MGF	P34	L	19.5	18.6	6.9	3.5	16.4	23.4	
UF 17200	W4A	P34	R	19.3	18.4	5.1	3.6	15.8	21.3	
UF 107543	PTM	P34	L	19.8	a18	5.3	3.3	a15.5	a34	
UF 46321	GFH	P34	L	17.8	17.9	5.9	3.7	14.6	15.6	
UF 98102	ARS	M1	R	18.1	18.4	7.2	4.0	16.2	12.5	
UF 98101	ARS	M1	R	18.7	19.8	7.2	4.2	15.1	15.2	
UF 98106	ARS	M1	L	19.4	18.9	5.9	3.7	15.5	28.7	
UF 98104	ARS	M1	L	21.4	17.8	6.8	3.2	14.5	43.8	
UF 32300	LOV	M1	L	18.1	17.8	5.5	3.1	--	--	
F:AM 107875	MIX	M1	L	18.4	17.9	7.0	3.6	15.9	27.3	
UF 17204	W4A	M1	R	16.8	16.8	6.7	3.4	--	--	
UF 98102	ARS	M2	R	17.3	18.1	6.4	3.3	16.1	19.8	
UF 32300	LOV	M2	L	18.6	17.2	5.6	3.3	--	30.9	
F:AM 107875	MIX	M2	L	18.4	17.6	7.4	3.2	15.6	31.2	
UF 17204	W4A	M2	R	17.2	16.6	6.8	3.5	--	--	
UF 98117	ARS	M12	R	22.5	18.9	6.5	3.1	15.3	47.8	
UF 98118	ARS	M12	R	19.9	18.0	7.3	3.2	16.5	38.2	
UF 98121	ARS	M12	L	18.1	17.4	6.0	3.2	14.6	33.9	
UF 62392	LOV	M12	L	20.1	17.0	6.4	3.4	14.8	49.1	
UF 62414	LOV	M12	R	19.1	16.0	7.2	3.2	15.1	45.8	
UF 62424	LOV	M12	R	20.4	17.7	6.1	3.1	15.1	38.0	
UF 53394	LOV	M12	R	18.1	16.8	5.2	3.3	14.6	25.8	
UF 62410	LOV	M12	L	17.8	18.9	7.0	4.2	14.6	20.1	
UF 45613	MGF	M12	L	19.1	18.1	6.5	3.0	--	--	
UF 107894	H19	M12	L	17.5	a15.5	5.6	--	14.4	29.1	
USNM 3306	MIX	M12	L	18.5	15.8	5.1	2.9	14.5	40.6	Holotype

Table 1 Continued.

	Loc	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	Comment

Cormohipparion ingenuum (continued)

	Loc	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	Comment
F:AM 113623	MIX	M12	L	19.1	16.6	5.4	3.3	14.1	35.2	
F:AM 113624	MIX	M12	L	21.1	17.4	6.1	3.5	14.4	40.1	
F:AM 113638	MIX	M12	L	20.4	16.3	4.7	3.3	14.3	39.4	
UF 45530	W4A	M12	R	17.3	17.8	7.0	3.5	15.0	33.6	
UF 28557	GZP	M3	R	17.8	14.0	5.4	3.1	16.9	29.8	

Cormohipparion plicatile

	Loc	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	Comment
UF 36119	LOV	DP2	L	32.5	19.4	5.4	4.0	29.0	9.6	
UF 35929	LOV	DP2	R	31.6	18.8	5.9	4.3	--	10.2	
UF 35928	LOV	DP2	R	31.8	18.4	5.5	3.2	28.5	12.3	
UF 35931	LOV	DP2	R	32.2	18.7	4.8	3.5	29.5	14.0	
UF 36102	LOV	DP2	L	32.6	17.6	5.6	3.5	28.9	17.9	
UF 96621	LOV	DP3	L	24.6	19.0	5.5	4.5	--	a6	
UF 69920	LOV	DP3	L	24.4	20.3	5.8	4.5	--	a7	
UF 96622	LOV	DP3	R	24.5	19.7	5.6	4.7	22.5	10.5	
UF 35928	LOV	DP3	R	25.0	17.9	5.6	3.3	21.4	13.2	
UF 35931	LOV	DP3	R	25.2	18.9	5.6	3.6	21.5	13.9	
UF 96621	LOV	DP4	L	24.9	18.9	6.6	4.8	--	9.2	
UF 69920	LOV	DP4	L	25.8	19.0	6.7	4.4	--	12.3	
UF 96622	LOV	DP4	R	24.6	18.4	6.5	4.2	21.8	13.0	
UF 35928	LOV	DP4	R	25.9	16.3	5.9	3.0	20.9	16.2	
UF 35931	LOV	DP4	R	26.6	16.3	6.0	3.3	21.3	17.5	
UF 36244	LOV	P2	L	25.3	20.4	6.0	4.1	21.3	15.8	
UF 32266	LOV	P2	L	26.5	18.6	5.7	3.6	21.8	24.5	
UF 32270	LOV	P2	R	25.2	19.5	5.8	3.8	21.6	26.1	
UF 32263	LOV	P2	R	26.3	17.3	6.1	3.4	21.3	27.8	
UF 32262	LOV	P2	L	28.4	19.2	6.2	3.7	--	28.3	
UF 27316	LOV	P2	R	26.5	19.0	6.2	3.8	24.0	29.9	

UF 35988	LOV	P2	R	30.6	19.9	6.6	4.3	21.9	32.0
UF 36159	LOV	P2	L	28.3	19.0	5.7	3.7	22.5	38.7
UF 32265	LOV	P2	R	28.7	17.5	5.7	3.9	21.4	39.8
UF 35978	LOV	P2	R	27.8	18.7	5.5	3.9	20.9	40.7
UF 17121	MGF	P2	L	26.6	20.4	6.7	4.1	22.2	16.2
UF/FGS V-1428	MIX	P2	R	27.1	19.7	6.0	3.7	22.1	35.0
F:AM 111730	MIX	P2	R	26.8	20.7	6.5	3.9	21.7	--
F:AM 113620	MIX	P2	L	25.6	20.0	5.6	3.9	22.4	24.0
F:AM 113621	MIX	P2	R	29.3	19.7	6.3	3.7	21.4	34.4
UF 32270	LOV	P3	R	22.0	21.3	6.3	4.0	17.2	32.2
UF 32263	LOV	P3	R	21.4	19.3	6.5	3.5	16.8	32.9
UF 32250	LOV	P3	L	20.6	20.0	8.0	4.5	--	--
UF 32266	LOV	P3	L	21.5	20.3	6.1	3.6	17.7	23.0
UF 27316	LOV	P3	R	22.2	20.8	6.5	3.7	18.5	23.1
UF 32264	LOV	P3	R	22.2	21.2	6.9	4.1	--	19.4
UF 32262	LOV	P3	L	23.2	21.7	7.7	3.9	18.0	32.2
F:AM 111730	MIX	P3	R	22.6	22.1	6.6	3.9	--	--
F:AM 113620	MIX	P3	L	21.8	21.8	6.2	4.0	17.7	32.0
F:AM 113621	MIX	P3	R	22.1	20.8	6.2	3.4	17.3	30.5
USNM 8265	DUN	P3	R	22.7	23.2	7.6	4.1	--	--
UF 32264	LOV	P4	R	20.6	20.5	7.1	3.8	18.2	22.4
UF 32250	LOV	P4	L	20.1	19.7	8.3	4.2	--	--
UF 27316	LOV	P4	R	21.0	20.5	7.1	4.0	17.7	28.0
UF 32266	LOV	P4	L	20.4	20.4	7.1	3.9	17.1	28.1
UF 32270	LOV	P4	R	21.5	20.7	7.0	3.8	16.6	35.7
UF 32263	LOV	P4	R	20.9	19.4	6.6	3.5	16.7	36.7
UF 32262	LOV	P4	L	23.0	21.7	8.2	3.7	16.8	39.9
F:AM 111730	MIX	P4	R	22.5	22.0	7.4	4.0	17.4	--
F:AM 113620	MIX	P4	L	21.5	21.2	6.1	4.0	17.0	37.5
F:AM 113621	MIX	P4	L	23.0	21.2	7.0	3.6	17.5	40.4
UNSM 8265	DUN	P4	R	21.0	23.4	7.6	4.4	--	26.3
UF 62327	LOV	P34	R	20.4	19.6	6.6	3.0	16.1	29.7
UF 53289	LOV	P34	R	24.2	20.3	8.3	3.7	19.8	45.1
UF 53302	LOV	P34	L	23.6	21.5	7.1	3.8	18.1	51.2
UF 17206	MGF	P34	L	23.5	22.0	7.1	3.7	18.0	34.1
UF 17208	MGF	P34	R	22.0	22.0	6.1	4.4	18.8	20.8
UF 17212	MGF	P34	L	21.5	22.7	8.1	4.9	18.8	18.8

Table 1 Continued.

	Loc	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	Comment
					Cormohipparion plicatile (continued)					
UF 17124	MGF	P34	R	23.9	21.1	7.2	3.7	--	37.4	
UF 17226	H5B	P34	L	22.5	21.9	7.6	4.2	17.0	29.6	
UF 102620	4CM	P34	R	21.8	21.9	8.0	3.9	--	31.3	
USNM 3292	MIX	P34	R	19.7	21.1	6.9	3.8	17.1	29.7	Holotype
F:AM 113626	MIX	P34	L	--	20.9	6.5	4.0	16.6	29.5	
F:AM 113627	MIX	P34	R	20.6	20.6	6.4	3.9	17.5	25.2	
F:AM 113628	MIX	P34	L	21.8	21.5	6.2	4.2	18.8	22.6	
UF 32264	LOV	M1	R	19.2	19.5	6.9	3.9	15.5	21.4	
UF 32266	LOV	M1	L	19.4	20.4	6.6	3.9	15.8	25.9	
UF 27316	LOV	M1	R	18.7	20.6	6.1	3.9	15.9	28.2	
UF 32263	LOV	M1	R	20.4	18.1	6.8	3.5	15.8	36.0	
UF 32270	LOV	M1	R	20.0	19.8	6.4	3.6	15.8	36.9	
UF 32262	LOV	M1	L	21.1	20.5	7.4	3.5	15.6	39.2	
UF 32265	LOV	M1	R	21.5	18.4	6.6	3.2	15.1	52.0	
F:AM 111730	MIX	M1	L	20.3	19.0	7.4	3.7	--	48.1	
F:AM 107876	MIX	M1	L	18.8	19.4	5.6	3.8	--	--	
F:AM 113620	MIX	M1	R	20.9	19.6	7.3	3.5	16.0	43.5	
UF 96386	MAR	M1	R	22.6	21.2	9.2	3.6	15.9	51.8	
UF 32264	LOV	M2	R	19.4	18.8	6.9	3.8	16.4	24.9	
UF 32266	LOV	M2	L	18.9	18.7	6.5	3.6	16.2	29.5	
UF 27316	LOV	M2	R	18.5	18.6	6.2	3.5	16.2	30.4	
UF 32263	LOV	M2	R	19.7	17.5	6.9	3.5	16.0	38.1	
UF 32270	LOV	M2	L	19.3	18.5	6.4	3.5	15.8	41.1	
UF 32262	LOV	M2	L	21.5	19.5	7.5	3.5	16.9	43.9	
F:AM 111730	MIX	M2	R	20.2	19.1	7.0	3.8	--	--	
F:AM 113620	MIX	M2	L	19.6	19.0	6.1	3.4	16.5	--	
F:AM 113621	MIX	M2	L	22.0	17.1	8.4	2.8	16.4	50.0	
F:AM 113637	MIX	M2	R	18.5	18.9	6.4	3.4	15.8	32.0	
UF 96386	MAR	M2	R	23.4	20.1	9.9	4.2	18.5	61.4	

UF 53349	LOV	M12	R	19.9	21.4	7.3	4.5	16.9	17.6
UF 53338	LOV	M12	R	20.8	19.8	7.7	3.4	18.2	38.0
UF 53334	LOV	M12	R	20.3	19.1	7.4	3.6	16.7	45.0
UF 53332	LOV	M12	R	23.0	18.8	6.3	3.2	17.2	51.2
UF 50647	LOV	M12	R	22.4	16.9	6.4	2.6	15.9	56.5
UF 50648	LOV	M12	R	23.3	15.5	6.9	2.8	16.2	59.3
UF 9605	MGF	M12	R	21.5	20.8	7.1	3.6	17.1	49.3
UF 9611	MGF	M12	R	21.0	19.9	6.1	3.6	16.8	45.6
UF 17214	MGF	M12	R	21.4	20.4	7.1	3.5	17.3	38.1
UF 17090	MGF	M12	L	20.5	20.2	5.9	3.6	--	--
UF 47319	H19	M12	R	20.6	a20	6.6	3.7	15.7	31.1
F:AM 113629	MIX	M12	L	20.0	20.1	6.4	4.0	17.7	25.3
UF/FGS 1400	DUN	M12	R	20.3	19.9	6.4	3.9	--	30.2

Cormohipparion emsliei

UF 102022	4CM	M3	R	23.5	19.3	7.9	4.1	21.4	30.5
UF 95410	MAR	M2	L	19.2	19.1	7.5	3.6	15.8	a38
UF 102600	4CM	M12	R	17.1	16.6	7.0	3.1	15.2	26.5
UF 102601	4CM	M12	L	20.8	16.3	7.1	2.9	16.0	52.9
UF 95410	MAR	M3	L	20.2	15.1	8.9	3.1	--	a42

Hipparion sp., cf. *H. tehonense*

UF 17198	W4A	P2	L	22.0	16.7	5.3	3.0	16.6	22.6
UF 17205	W4A	P2	R	22.5	18.6	4.8	3.9	17.0	24.2
UF 17205	W4A	P3	R	18.5	19.1	5.3	3.8	15.4	25.5
UF 17205	W4A	P4	R	18.6	19.8	5.8	3.9	13.9	32.0
UF 102599	4CM	P34	R	21.3	19.2	5.6	3.3	--	40.0
UF 62165	LOV	P34	L	19.1	17.3	5.0	3.5	15.5	17.1
UF 53375	LOV	P34	L	18.8	18.2	5.5	3.3	15.4	30.5
UF 17205	W4A	M1	R	17.1	18.3	5.1	3.5	14.3	34.8
UF 102622	4CM	M2	L	17.5	16.1	5.2	3.4	13.2	a42
UF 17205	W4A	M2	R	17.0	17.8	5.0	3.4	14.3	38.5

TABLE 2. Measurements of selected lower cheekteeth of *Cormohipparion* and *Hippparion* from Florida, Texas, and Honduras. See Table 4 for univariate statistics. Format and abbreviations as in Table 1. Additional locality abbreviations: BNV, Bone Valley Region, specific mine unknown; H6A, Haile 6A; L1C, Leisey Shell Pit 1C; LCF, Lapara Creek Fauna, Texas; Measurements defined in text and in Figure 3.

	Loc	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch	Comment
					Cormohipparion sp., cf. *C. sphenodus*							
UF 28459	RZP	p2	L	20.7	7.5	9.3	7.7	9.5	18.0	25.9	slight wear
UF 28458	RZP	p34	R	19.3	8.5	--	--	9.4	--	31.9	
UF 28460	RZP	p34	L	18.7	--	10.0	10.5	9.3	16.2	28.2	
UF 28446	RZP	m3	R	22.8	9.0	7.8	10.5	6.8	--	29.9	
UF 28447	RZP	m3	R	22.8	8.7	8.2	10.1	7.1	--	a29	
					Cormohipparion ingenuum							
UF 90209	LOV	dp2	R	28.2	7.1	9.3	9.8	11.5	24.0	9.0	
UF 32294	LOV	dp2	L	26.4	8.1	9.3	10.2	8.6	22.7	9.7	
UF 32133	LOV	dp2	R	27.5	6.6	8.1	10.1	11.3	23.6	11.5	
UF 90200	LOV	dp2	R	26.6	7.3	9.1	10.9	11.3	23.0	11.8	
UF 98130	ARS	dp3	L	24.9	9.5	9.4	13.0	10.8	22.3	13.9	
UF 32294	LOV	dp3	L	23.2	9.5	9.4	11.7	8.8	20.2	9.4	
UF 90200	LOV	dp3	R	24.2	8.9	8.8	11.7	10.1	20.6	13.7	
UF 32133	LOV	dp3	R	22.7	7.3	8.2	10.6	10.5	20.9	14.5	
UF 98136	ARS	dp4	R	22.4	9.7	9.1	12.3	6.2	20.3	a8	
UF 98130	ARS	dp4	L	27.4	8.2	7.7	12.5	9.8	22.1	18.7	
UF 32294	LOV	dp4	L	24.2	9.2	8.7	12.0	8.0	20.6	12.4	
UF 90223	LOV	dp4	L	26.8	8.4	7.9	11.8	9.8	19.7	19.1	
UF 18126	GFH	dp4	L	24.0	7.9	8.4	11.2	9.4	19.1	a18	
UF 98138	ARS	dp34	L	24.7	8.6	8.5	11.8	7.3	20.4	12.9	
UF 90249	LOV	dp34	R	22.7	10.8	10.1	12.2	7.4	21.4	5.7	
UF 90222	LOV	dp34	L	22.2	9.1	9.2	11.5	9.5	19.1	11.2	
UF 90237	LOV	dp34	R	23.5	8.9	8.7	11.6	9.3	21.7	13.5	

TMM 31081-501	LCF	p2	R	22.1	8.5	10.4	8.2	8.7	--	--
UF 98125	ARS	p2	R	21.4	9.5	11.0	10.0	8.3	18.5	16.7
UF 98126	ARS	p2	L	21.0	7.7	11.1	7.2	10.2	18.4	24.6
UF 98128	ARS	p2	R	22.1	8.0	10.4	8.5	9.9	18.3	24.1
UF 98129	ARS	p2	L	22.5	8.4	10.3	7.6	9.4	19.1	17.9
UF 24632	SMN	p2	L	22.9	8.8	10.8	8.4	10.1	18.8	21.0
UF 64925	LOV	p2	R	24.1	9.4	10.8	10.1	10.2	17.7	29.9
UF 64813	LOV	p2	L	21.0	9.2	11.9	8.6	8.6	16.9	24.8
UF 64801	LOV	p2	L	22.6	8.3	9.9	8.4	9.3	18.5	24.4
UF 64800	LOV	p2	L	20.2	7.8	10.3	7.5	8.5	17.0	24.3
UF 64808	LOV	p2	R	20.8	7.9	10.1	8.8	9.9	18.3	20.0
UF 64811	LOV	p2	R	20.7	7.9	10.4	8.5	8.5	17.8	14.9
UF 47323	H19	p2	R	22.0	8.6	9.6	8.2	10.1	--	a25
UF 18036	GFH	p2	L	19.9	8.3	10.1	9.2	8.4	16.8	24.3
TMM 31081-501	LCF	p3	R	20.3	10.9	11.1	11.8	9.2	--	--
UF 98125	ARS	p3	R	20.8	12.1	11.6	13.5	10.0	18.0	21.5
UF 98126	ARS	p3	R	22.8	10.5	11.2	13.1	10.8	18.1	34.8
UF 98128	ARS	p3	R	22.4	10.8	11.2	13.3	9.9	17.6	31.3
UF 98129	ARS	p3	L	20.9	11.0	10.9	12.1	10.1	17.4	23.3
TMM 31081-501	LCF	p4	R	20.7	11.0	10.4	10.4	8.1	--	a32
UF 98125	ARS	p4	R	20.4	12.2	10.7	13.1	9.8	17.2	23.3
UF 98126	ARS	p4	R	21.9	10.6	10.5	12.1	10.0	17.6	40.0
UF 98128	ARS	p4	R	21.4	10.1	10.1	11.4	9.8	16.5	36.8
UF 98129	ARS	p4	L	20.5	11.0	10.0	11.9	9.7	17.6	28.7
UF 28567	GZP	p34	L	20.0	7.9	8.4	9.2	9.7	16.8	40.7
UF 28617	GZP	p34	L	19.9	10.3	--	11.0	9.8	--	a35
UF 107620	ARS	p34	L	20.1	10.0	10.7	11.0	9.9	16.5	32.6
UF 24631	SMN	p34	R	--	11.4	11.4	13.0	9.9	--	a36
UF 24646	SMN	p34	L	17.7	10.5	9.6	10.6	7.9	15.0	13.8
UF 64752	LOV	p34	R	21.3	10.0	10.4	11.2	10.2	16.3	38.4
UF 64774	LOV	p34	R	19.0	9.5	8.9	10.0	8.5	14.4	37.6
UF 64780	LOV	p34	L	21.0	10.5	11.0	11.8	9.7	15.8	33.0
UF 50457	LOV	p34	L	20.3	10.4	10.9	12.1	9.8	17.6	29.7
UF 64791	LOV	p34	L	18.4	11.6	10.5	11.5	9.1	15.7	20.6
UF 64768	LOV	p34	R	18.7	11.9	10.9	11.4	8.2	16.2	13.6
UF 107529	L1C	p34	L	18.0	10.6	10.5	10.7	8.7	--	a33
UF 98126	ARS	m1	L	20.8	9.3	8.2	12.1	7.2	--	a34

Table 2. Continued

	Loc	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch	Comment
					Cormohipparion ingenuum (continued)						
UF 98131	ARS	m1	L	19.3	9.2	8.5	11.8	6.9	16.2	25.6	
UF 18036	GFH	m1	L	18.3	9.5	9.3	11.2	6.8	—	a35	
UF 98126	ARS	m2	L	21.0	8.7	8.1	11.3	7.9	—	40.1	
UF 98131	ARS	m2	L	19.4	8.8	—	10.7	7.7	16.3	33.3	
UF 18036	GFH	m2	L	18.2	9.0	8.9	10.9	7.0	15.1	a39	
UF 28568	GZP	m12	R	22.1	7.5	6.6	10.1	9.3	16.7	42.6	
UF 28569	GZP	m12	R	19.3	8.9	8.5	11.6	6.7	15.4	a30	
UF 28618	GZP	m12	L	22.6	8.3	8.2	10.2	8.9	16.3	40.9	
UF 98164	ARS	m12	L	21.0	7.8	7.2	9.9	7.7	16.6	a42	
UF 98162	ARS	m12	L	20.8	9.2	9.0	11.2	7.9	15.3	37.1	
UF 107621	ARS	m12	L	21.9	6.8	7.2	9.9	7.9	15.7	39.9	
UF 98150	ARS	m12	R	18.9	9.7	8.5	11.0	8.3	16.2	25.5	
UF 28857	SMN	m12	L	18.6	9.7	9.0	10.9	6.1	15.7	25.1	
UF 64820	LOV	m12	R	21.6	7.7	7.1	9.6	7.9	15.7	46.6	
UF 64818	LOV	m12	R	21.0	8.0	7.2	10.0	7.7	15.5	41.5	
UF 64878	LOV	m12	L	17.8	8.8	8.2	10.6	7.7	14.5	36.2	
UF 64899	LOV	m12	L	19.1	8.6	7.7	10.4	6.6	16.3	28.9	
UF 64876	LOV	m12	L	18.1	10.0	9.1	10.9	6.1	15.3	23.0	
UF 64901	LOV	m12	L	17.3	10.0	8.5	9.7	4.5	15.2	13.3	
UF 102621	4CM	m12	R	18.9	8.9	8.9	10.8	7.7	—	43.0	
UF 18035	GFH	m12	L	19.5	9.2	8.9	10.9	8.1	15.1	a39	
UF 103791	LOV	m3	L	21.2	9.0	8.2	9.3	5.4	20.9	12.6	
UF 69819	LOV	m3	L	22.1	8.3	8.1	10.3	6.6	22.4	a25	
UF 103790	LOV	m3	L	21.6	9.1	8.2	10.4	7.0	21.2	29.6	
UF 103772	LOV	m3	R	22.0	8.4	7.7	10.3	6.0	20.3	33.4	
UF 107893	H19	m3	R	21.7	8.5	7.8	10.0	7.2	21.3	a42	
UF 107542	PTM	m3	R	20.4	8.4	7.6	10.3	5.6	—	a35	

Cormohipparion plicatile

UF 35895	LOV	dp2	R	27.5	9.1	10.3	12.6	11.0	24.1	8.7
UF 90178	LOV	dp2	R	28.2	8.3	10.0	11.5	11.0	24.3	8.7
UF 90157	LOV	dp2	R	28.7	8.7	9.8	12.0	11.4	24.3	12.0
UF 32286	LOV	dp2	L	28.4	8.7	10.6	12.0	11.2	25.3	12.1
UF 90154	LOV	dp2	R	29.1	8.0	9.9	11.6	11.6	25.5	13.1
UF 103754	MAR	dp2	R	25.8	9.5	10.5	13.1	8.7	24.7	5.6
UF 93000	MAR	dp2	L	27.6	8.4	8.9	12.9	11.5	24.3	10.4
UF 90158	LOV	dp3	L	23.2	11.7	11.0	13.4	7.7	22.0	a4
UF 35895	LOV	dp3	R	24.3	11.2	10.5	13.3	9.0	21.5	10.5
UF 90155	LOV	dp3	R	25.8	10.9	10.5	14.7	9.9	23.0	10.5
UF 90156	LOV	dp3	R	25.6	9.8	9.5	11.9	10.5	22.9	13.6
UF 32286	LOV	dp3	L	25.6	9.9	10.2	13.1	10.3	22.7	14.4
UF 90154	LOV	dp3	R	26.1	9.8	10.0	12.8	11.6	23.3	14.5
UF 24655	SMN	dp3	R	25.4	9.5	9.0	12.6	10.5	22.7	15.7
UF 103754	MAR	dp3	R	22.7	11.8	10.2	14.3	8.1	21.9	a6
UF 93000	MAR	dp3	L	23.3	9.3	8.4	13.6	11.7	20.9	13.7
UF 90158	LOV	dp4	L	24.6	10.9	10.0	13.8	6.7	22.6	8.6
UF 90155	LOV	dp4	R	29.5	10.2	9.8	15.1	9.1	23.5	13.9
UF 35895	LOV	dp4	R	27.7	10.0	8.7	13.8	9.4	22.1	15.2
UF 90156	LOV	dp4	R	28.1	8.6	8.3	11.7	9.9	22.6	16.8
UF 32286	LOV	dp4	L	28.5	8.8	9.1	13.0	9.5	23.4	18.6
UF 90154	LOV	dp4	R	28.6	8.7	9.0	12.7	10.6	23.2	20.0
UF 102095	FGM	dp4	R	26.9	8.9	8.5	12.5	8.9	23.4	18.7
UF 103754	MAR	dp4	R	23.7	10.2	9.7	13.7	8.5	21.8	a10
UF 93000	MAR	dp4	L	26.0	8.5	8.1	14.2	10.1	—	17.0
UF 24650	SMN	dp34	R	23.1	9.7	9.3	12.8	9.5	20.5	11.6
UF 24626	SMN	dp34	R	21.7	12.9	11.7	13.1	6.7	—	a5
UF 50379	LOV	p2	L	22.9	9.4	11.4	10.1	6.1	20.9	11.9
UF 64942	LOV	p2	L	23.2	9.5	11.6	10.5	10.1	20.8	19.8
UF 50366	LOV	p2	R	23.3	8.1	10.0	9.8	9.6	19.8	21.4
UF 50373	LOV	p2	L	23.1	8.0	9.6	8.6	10.5	19.3	28.0
UF 32196	LOV	p2	L	27.1	9.9	12.1	11.1	11.5	21.0	31.0
UF 50374	LOV	p2	L	24.6	8.9	10.8	10.7	10.9	20.0	34.7
UF 102551	H6A	p2	R	22.2	10.1	12.5	11.0	6.8	19.7	13.7
UF 7234	MGF	p2	L	22.7	9.6	12.2	10.8	7.6	—	17.0

Table 2 Continued

	Loc	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch	Comment
					Cormohipparion plicatile (continued)						
USNM 3309	MIX	p2	R	24.6	8.5	11.0	9.2	10.3	19.5	32.7	
F:AM 113630	MIX	p2	R	23.0	8.6	12.5	10.7	9.8	19.5	23.9	
F:AM 113640	MIX	p2	L	24.9	8.6	10.3	10.1	11.5	18.8	31.8	
UF 6997	MAR	p2	R	23.6	10.4	11.9	12.6	10.6	20.8	a22.5	
UF 32225	LOV	p3	R	24.5	12.0	12.8	13.9	10.6	19.0	43.3	
UF 35892	LOV	p3	L	22.2	12.2	12.2	13.5	10.1	--	28.7	
UF 7234	MGF	p3	L	21.0	13.4	13.5	13.7	10.0	--	--	
F:AM 113630	MIX	p3	R	21.4	12.5	12.4	13.1	10.1	18.2	26.1	
UF 69967	MAR	p3	R	21.8	12.6	11.7	14.5	10.5	18.7	26.3	
UF 32225	LOV	p4	R	23.9	11.1	10.8	12.5	9.9	18.8	52.9	
UF 32133	LOV	p4	L	22.8	11.7	12.0	13.0	10.4	17.7	41.6	
UF32244	LOV	p4	L	22.1	13.3	12.1	13.6	10.1	18.1	22.7	
UF 7234	MGF	p4	L	20.4	13.0	12.4	12.7	10.0	--	--	
UF 69967	MAR	p4	R	21.8	12.4	10.9	13.6	10.8	18.6	34.6	
UF 50458	LOV	p34	L	22.2	13.8	13.0	14.1	9.2	19.0	20.9	
UF 50460	LOV	p34	L	21.7	11.3	12.1	13.3	10.5	19.2	28.0	
UF 50455	LOV	p34	L	21.8	12.3	12.9	13.5	10.7	18.3	34.5	
UF 50469	LOV	p34	R	24.0	12.3	12.4	14.6	10.6	18.7	40.2	
UF 50448	LOV	p34	L	24.8	11.3	11.4	12.6	12.0	19.2	47.4	
UF 50463	LOV	p34	R	23.5	10.8	10.2	11.9	10.6	18.1	51.0	
UF 53924	FGM	p34	R	20.5	13.6	--	13.3	8.6	16.4	22.5	
UF 53507	BNV	p34	L	22.1	11.1	10.1	11.5	10.3	--	a35	
UF 45623	MGF	p34	L	22.1	11.6	11.6	11.9	10.8	--	--	
F:AM 113631	MIX	p34	L	24.1	11.1	10.9	12.1	10.8	17.3	41.6	
F:AM 113632	MIX	p34	L	21.2	12.6	11.7	13.1	9.5	17.7	30.0	
F:AM 113636	MIX	p34	R	19.4	12.3	11.7	12.7	8.0	17.8	18.9	
UF 32219	LOV	m1	L	23.9	11.0	9.8	14.3	9.1	18.6	41.8	
UF 32223	LOV	m1	R	26.3	9.1	8.6	12.1	9.9	16.9	55.6	
UF 7234	MGF	m1	R	18.4	11.8	10.0	11.1	8.0	--	a27	

F:AM 107874	MIX	m1	R	22.5	9.1	8.6	11.5	7.0	--	48.8
UF 69967	MAR	m1	R	20.2	10.9	9.6	12.1	8.2	17.6	32.9
UF 103754	MAR	m1	R	23.5	9.1	7.5	11.1	10.1	--	59.9
UF 32203	LOV	m2	R	21.2	11.2	10.0	12.9	8.1	17.9	41.9
UF 32146	LOV	m2	R	22.9	10.2	9.2	12.6	8.0	17.6	45.8
UF 32219	LOV	m2	L	25.1	8.9	8.3	12.8	9.3	19.5	50.1
UF 32221	LOV	m2	R	23.7	9.5	8.0	11.5	9.2	17.9	53.4
F:AM 113634	MIX	m2	L	21.8	9.1	7.5	10.1	7.2	--	48.3
F:AM 107874	MIX	m2	R	21.1	8.1	7.1	10.1	7.8	16.9	54.9
UF 69967	MAR	m2	R	21.1	10.7	9.4	12.0	8.4	18.2	35.8
UF 103754	MAR	m2	L	--	7.0	6.3	--	--	--	63.0
UF 24625	SMN	m12	R	18.9	10.7	9.5	11.6	6.3	16.1	30.1
UF 24642	SMN	m12	L	19.2	10.2	9.8	12.5	6.9	15.4	38.4
UF 50435	LOV	m12	R	19.1	11.2	10.0	11.7	6.3	17.4	19.1
UF 50578	LOV	m12	R	19.7	11.2	9.5	12.0	6.4	17.6	26.0
UF 50415	LOV	m12	L	20.9	11.1	10.4	12.1	7.8	16.9	37.0
UF 50406	LOV	m12	L	23.4	10.9	10.5	13.5	8.3	18.3	46.4
UF 50424	LOV	m12	R	24.3	8.9	7.5	11.9	10.1	17.6	57.7
UF 58387	H19	m12	L	21.0	a10.2	--	12.4	9.1	--	--
UF 103732	H19	m12	R	20.6	11.6	10.5	12.8	7.2	17.1	28.9
UF 50386	LOV	m3	R	23.1	10.1	8.5	11.0	6.1	22.7	23.5
UF 50394	LOV	m3	L	25.3	10.5	9.8	11.4	7.4	25.1	29.2
UF 50382	LOV	m3	R	25.6	10.3	9.0	12.7	6.4	25.2	35.7
UF 50384	LOV	m3	R	22.1	9.4	8.4	10.2	6.3	22.7	35.8
UF 50381	LOV	m3	R	24.5	9.2	8.1	10.7	8.2	24.9	42.3
UF 103733	H19	m3	L	23.1	9.4	8.4	10.6	6.8	--	48.6
UF 69967	MAR	m3	R	26.3	10.1	8.7	11.3	8.8	25.8	39.3

Cormohipparion emsliei

UF 97259	MAR	p2	L	20.9	9.3	11.0	11.8	9.7	--	a8
UF 101964	GRD	p2	L	19.5	7.4	8.8	7.0	8.8	16.0	27.6
UF 97259	MAR	p3	R	18.8	13.0	12.0	12.3	9.5	--	--
UF 97259	MAR	p4	L	19.4	12.4	10.9	11.9	10.4	--	--
UF 102607	4CM	p34	L	17.9	11.2	11.4	11.2	9.6	16.8	a17
UF 102641	FGM	p34	L	20.2	10.9	11.0	12.0	9.8	--	a35
UF 100226	GRD	p34	R	18.3	9.6	8.9	10.9	9.5	14.2	a36

very slight wear

Table 2 Continued

	Loc	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch	Comment
					Cormohipparion emsliei (continued)						
UF 102588	PHM	p34	L	19.7	9.7	10.6	10.4	9.8	16.0	40.0	
UF 97259	MAR	m1	L	17.6	10.7	10.0	10.8	6.8	--	--	
UF 97259	MAR	m2	L	18.7	10.7	8.8	10.8	7.1	--	--	
UF 102589	PHM	m12	L	19.0	8.6	9.1	11.1	7.0	16.0	40.3	
UF 97259	MAR	m3	L	23.2	9.6	8.1	9.6	6.0	--	--	
					Hipparion sp., cf. *H. tehonense*						
UF 17300	W4A	p2	R	19.0	7.3	8.7	8.0	8.5	--	--	
UF 21027	W4A	p2	L	20.3	7.9	10.0	7.4	8.1	--	--	
UF 17300	W4A	p3	R	19.0	9.3	9.1	9.2	7.6	--	39.2	
UF 21027	W4A	p3	L	18.0	10.5	11.0	10.6	9.2	--	--	
UF 93203	HPM	p34	R	19.9	9.3	9.6	9.6	9.9	15.7	30.0	
UF 50753	PHM	p34	R	19.7	8.8	9.1	9.6	8.2	14.0	31.7	
UF 96526	LOV	p34	R	19.1	9.8	10.0	10.1	8.2	--	29.5	
UF 17300	W4A	m1	R	19.9	9.1	8.1	10.4	7.0	--	43.9	
UF 21027	W4A	m1	L	17.2	9.6	9.0	10.7	6.0	--	--	
UF 20868	W4A	m2	L	21.7	8.0	7.1	10.1	7.8	--	--	
UF 64917	LOV	m12	R	20.3	7.4	7.1	9.7	6.9	--	34.9	
UF 64918	LOV	m12	R	18.3	8.0	7.1	9.3	6.6	14.1	29.9	
UF 95388	MAS	m12	L	20.6	7.9	7.5	9.3	7.2	--	a50	

TABLE 3. Univariate statistics for upper cheekteeth of *Cormohipparion plicatile*, *C. ingenuum*, and *C. emsliei* from Florida. Measurements and their abbreviations defined in text and Figure 3. All measurements in millimeters. The first line in each entry gives x, s, and n; the second line, OR and CV. Faunal abbreviations: LOVE, Love Site, Alachua County, late Clarendonian; HEMP, combined sample from various early Hemphillian localities including McGehee Farm, Mixson's Bone Bed, Moss Acres Racetrack Site, and Withlacoochee River 4A and 4X; ARS, Agricola Road Site, Polk County, early Clarendonian; and UBV, combined sample from the Upper Bone Valley Fauna, Polk and adjacent counties, latest Hemphillian. Dental abbreviations: P2, sample of upper second premolars; P34, combined sample of upper third and fourth premolars; M12, combined sample of upper first and second molars.

TAXON	*C. plicatile*	*C. plicatile*	*C. ingenuum*	*C. ingenuum*	*C. ingenuum*	*C. emsliei*
FAUNA	LOVE	HEMP	ARS	LOVE	HEMP	UBV
			P2			
APL	26.7, 1.26, 55	27.1, 1.36, 4	26.7, 4.95, 2	24.5, 1.24, 43	25.2, 0.42, 2	23.7, 2.14, 5
	23.5-30.6, 4.73	25.6-29.3, 5.03	26.3-27.0, 1.86	22.1-26.9, 5.06	24.9-25.5, 1.68	21.8-27.3, 9.00
BAPL	21.8, 0.79, 54	22.0, 0.40, 5	21.2, 4.24, 2	19.8, 0.91, 42	20.6, −, 1	20.2, 2.21, 4
	20.4-24.0, 3.59	21.4-22.4, 1.84	20.9-21.5, 2.00	18.0-21.2, 4.60		17.6-22.7, 10.95
TRW	19.6, 0.94, 57	20.6, 1.17, 6	19.0, 0.59, 3	17.3, 0.74, 44	17.8, 0.44, 3	18.1, 1.39, 8
	17.3-21.5, 4.79	19.7-22.8, 5.70	18.6-19.7, 3.08	14.9-18.8, 4.27	17.5-18.3, 2.45	16.5-19.8, 7.70
PRL	6.1, 0.53, 58	6.5, 0.68, 6	6.4, 0.68, 4	5.9, 0.55, 43	6.9, 0.61, 3	5.7, 0.55, 11
	5.0-7.2, 8.66	5.6-7.6, 10.60	5.5-7.0, 10.59	4.6-7.5, 9.37	6.4-7.6, 8.81	4.9-6.6, 9.71
PRW	4.1, 0.52, 57	4.0, 0.30, 6	3.9, 0.60, 4	3.6, 0.32, 42	3.4, 0.23, 3	3.3, 0.32, 10
	3.4-5.6, 12.76	3.7-4.5, 7.59	3.5-4.8, 15.30	3.0-4.8, 8.87	3.3-3.7, 6.73	2.8-3.7, 9.83
			P34			
APL	21.8, 1.19, 112	22.1, 1.08, 18	20.7, 1.21, 9	19.2, 0.73, 49	18.8, 1.58, 9	18.9, 1.40, 23
	19.4-25.3, 5.46	19.7-23.9, 4.88	18.2-21.8, 5.83	17.8-21.5, 3.82	15.0-20.5, 8.44	17.0-22.1, 7.39

Table 3 continued

TAXON	*C. plicatile*	*C. plicatile*	*C. ingenuum*	*C. ingenuum*	*C. ingenuum*	*C. emsliei*
FAUNA	LOVE	HEMP	ARS	LOVE	HEMP	UBV
BAPL	17.6, 0.98, 107	17.6, 0.72, 14	16.3, 0.44, 8	15.5, 0.70, 46	15.8, 1.12, 4	15.5, 1.01, 15
	15.9-20.0, 5.56	16.6-18.8, 4.09	15.4-16.8, 2.68	13.9-16.6, 4.52	14.2-16.7, 7.07	14.2-17.9, 6.53
TRW	21.0, 0.99, 112	21.5, 0.96, 19	19.9, 1.00, 8	18.5, 0.85, 49	17.4, 2.02, 9	18.2, 1.29, 24
	18.6-24.1, 4.70	19.8-23.4, 4.46	18.1-21.2, 5.02	16.9-20.7, 4.58	14.0-19.5, 11.6	16.2-20.9, 7.06
PRL	7.4, 0.80, 116	6.9, 0.70, 19	6.9, 0.71, 9	6.7, 0.69, 50	6.4, 0.92, 9	6.0, 0.80, 24
	5.9-9.2, 10.80	6.1-8.5, 10.04	5.8-7.9, 10.25	5.0-8.7, 10.24	4.8-7.5, 14.49	4.8-8.8, 13.33
PRW	4.1, 0.47, 114	3.9, 0.36, 19	3.8, 0.58, 9	3.6, 0.37, 49	3.5, 0.30, 9	3.3, 0.29, 22
	3.0-5.2, 11.41	3.4-4.9, 9.23	3.1-4.6, 15.20	3.1-4.7, 10.17	2.9-3.8, 8.53	2.8-3.9, 8.73
			M12			
APL	20.5, 1.36, 115	20.5, 1.51, 18	19.3, 1.54, 11	18.3, 1.28, 54	18.6, 1.27, 12	19.2, 1.09, 24
	18.2-25.4, 6.61	17.6-23.9, 7.38	17.3-22.5, 7.96	15.6-20.8, 7.00	16.8-21.1, 6.85	17.5-21.5, 5.66
BAPL	16.4, 0.69, 108	16.5, 0.69, 11	15.6, 0.70, 10	14.6, 0.57, 47	14.9, 0.70, 8	15.7, 1.01, 17
	15.1-18.2, 4.20	15.4-17.7, 4.20	14.5-16.5, 4.48	13.5-15.8, 3.90	14.1-15.9, 4.67	13.9-17.1, 6.41
TRW	19.4, 1.22, 113	19.4, 0.94, 18	18.1, 0.89, 11	16.7, 0.94, 54	17.0, 0.86, 12	17.2, 1.18, 22
	15.4-22.0, 6.29	17.1-20.8, 4.82	16.4-19.8, 4.93	13.8-18.9, 5.65	15.6-18.1, 5.03	15.3-20.1, 6.87
PRL	6.9, 0.62, 121	6.7, 0.68, 18	6.5, 0.58, 10	6.5, 0.58, 55	6.3, 0.83, 12	6.4, 0.64, 23
	5.7-8.3, 8.99	5.6-8.4, 6.26	5.8-7.3, 8.85	5.2-7.5, 8.84	4.7-7.4, 13.33	5.2-7.5, 9.96
PRW	3.8, 0.56, 120	3.6, 0.41, 18	3.4, 0.44, 11	3.4, 0.39, 54	3.3, 0.27, 12	3.2, 0.31, 23
	2.6-5.2, 14.76	2.8-4.9, 11.37	2.8-4.2, 13.00	2.3-4.3, 11.45	2.9-3.7, 8.11	2.4-3.7, 9.72

TABLE 4. Univariate statistics for lower cheekteeth and mandibles of *Cormohipparion plicatile*, *C. ingenuum*, and *C. emsliei* from Florida. Measurements and their abbreviations defined in text and Figure 2. Format as in Table 3, except that the mandible of *C. emsliei* is from the Moss Acres Racetrack Site, not the Bone Valley. Dental abbreviations: p2, sample of lower second premolars; p34, combined sample of lower third and fourth premolars; m12, combined sample of lower first and second molars.

TAXON	*C. plicatile*	*C. plicatile*	*C. ingenuum*	*C. ingenuum*	*C. ingenuum*	*C. emsliei*
FAUNA	LOVE	HEMP	ARS	LOVE	HEMP	UBV
			p2			
apl	23.7, 1.14, 39	23.8, 1.11, 4	21.9, 0.84, 6	21.5, 0.96, 19	22.0, −, 1	19.4, 1.46, 3
	22.0-27.1, 4.83	22.7-24.9, 4.67	21.0-23.2, 3.82	20.2-24.1, 4.48		18.1-21.0, 7.55
bapl	19.9, 0.92, 37	19.3, −, 1	18.6, 0.33, 5	18.0, 0.65, 19	------	16.2, 0.57, 2
	18.0-21.3, 4.62		18.3-19.1, 1.76	16.9-19.6, 3.64		15.8-16.6, 3.49
atw	9.3, 0.74, 39	8.8, 0.52, 4	8.3, 0.69, 6	8.6, 0.66, 21	8.4, −, 1	7.7, 0.78, 2
	7.5-10.4, 7.97	8.5-9.6, 5.88	7.7-9.5, 8.24	7.7-9.9, 7.70		7.1-8.2, 10.10
ptw	11.5, 0.91, 41	11.5, 1.03, 4	10.5, 0.55, 6	10.6, 0.86, 21	9.6, −, 1	9.2, 0.57, 2
	9.6-13.3, 7.91	10.3-12.5, 8.95	9.6-11.1, 5.22	9.0-12.6, 8.13		8.8-9.6, 6.15
mml	10.2, 1.13, 41	10.2, 0.74, 4	8.3, 0.98, 6	9.1, 0.99, 21	8.0, −, 1	8.6, 0.32.3
	7.0-12.5, 11.03	9.2-10.8, 7.20	7.2-10.0, 11.76	7.5-11.7, 10.87		8.4-9.0, 3.72
entl	9.8, 1.34, 41	9.8, 1.63, 4	9.5, 0.66, 6	8.7, 1.37, 21	10.1, −, 1	8.8, 1.54, 3
	6.1-12.0, 13.62	7.6-11.5, 16.64	8.3-10.2, 6.95	5.5-10.6, 15.85		7.0-9.8, 17.54
			p34			
apl	22.8, 1.34, 48	21.4, 1.34, 9	20.9, 0.98, 21	19.5, 1.13, 35	19.7, 0.76, 3	19.3, 1.36, 9
	19.2-25.6, 5.87	19.4-24.1, 6.28	18.8-22.8, 4.63	17.6-22.1, 5.81	19.2-20.6, 3.84	17.5-21.4, 7.08

Table 4 Continued.

TAXON	C. plicatile	C. plicatile	C. ingenuum	C. ingenuum	C. ingenuum	C. emsliei
FAUNA	LOVE	HEMP	ARS	LOVE	HEMP	UBV
bapl	18.7, 0.71, 49 17.0-20.6, 3.82	17.8, 0.37, 4 17.3-18.2, 2.08	17.4, 0.52, 14 16.5-18.1, 2.99	16.1, 0.74, 32 14.4-17.8, 4.60	16.2, 0.71, 2 15.7-16.7, 4.36	16.1, 1.07, 5 14.9-17.3, 6.69
atw	12.0, 0.98, 48 8.4-14.0, 8.14	12.3, 0.74, 8 11.1-13.4, 5.97	10.6, 1.03, 20 7.9-12.3, 9.66	10.9, 0.82, 34 9.5-12.5, 7.50	11.1, 0.21, 3 10.9-11.3, 1.88	9.9, 0.74, 9 8.6-11.1, 7.50
ptw	12.0, 1.01, 48 9.1-14.2, 8.45	12.0, 0.78, 8 10.9-13.5, 6.53	10.6, 0.76, 18 8.4-11.6, 7.21	10.6, 0.61, 35 8.9-11.8, 5.77	11.2, 0.46, 3 10.8-11.7, 4.09	9.5, 0.76, 10 8.6-10.9, 8.00
mml	13.1, 1.07, 48 9.9-15.3, 8.14	12.9, 0.68, 9 11.9-14.0, 5.24	11.9, 1.03, 22 9.2-13.5, 8.67	11.3, 0.59, 35 10.0-12.6, 5.23	12.1, 0.85, 3 11.5-13.1, 7.03	10.7, 0.95, 10 9.2-11.5, 8.92
entl	10.4, 1.02, 48 6.1-12.1, 9.88	10.1, 0.95, 9 8.0-11.2, 9.35	10.0, 0.66, 22 7.6-11.1, 6.67	9.1, 1.03, 35 6.1-10.8, 11.35	9.1, 1.50, 3 7.6-10.6, 16.50	9.3, 0.77, 10 8.1-10.6, 8.23
			m12			
apl	22.2, 2.03, 68 18.6-26.3, 9.15	21.3, 1.90, 15 18.4-24.4, 8.91	20.2, 1.47, 26 17.9-23.3, 7.25	19.5, 1.63, 43 17.0-23.5, 8.39	18.2, 1.82, 4 16.2-20.4, 10.02	19.1, 1.62, 18 15.9-22.0, 8.50
bapl	17.4, 0.90, 64 15.4-20.2, 5.15	17.8, 0.88, 8 16.9-19.4, 4.94	16.1, 0.56, 18 15.1-17.0, 3.50	15.3, 0.89, 41 13.2-17.1, 5.79	15.6, – , 1	15.5, 1.04, 8 14.1-16.5, 6.71
atw	10.2, 1.08, 68 8.1-12.6, 10.52	10.7, 1.72, 16 8.1-13.4, 16.14	8.9, 0.89, 24 6.8-10.5, 10.00	9.1, 1.07, 44 6.2-11.9, 11.81	9.9, 0.70, 5 9.4-11.1, 7.03	8.3, 0.65, 19 7.3-9.5, 7.80
ptw	9.3, 1.07, 68 6.4-11.4, 11.49	9.5, 1.50, 16 7.1-12.1, 15.78	8.2, 0.72, 22 6.6-9.1, 8.72	8.4, 0.84, 44 6.5-10.0, 9.96	9.0, 0.42, 5 8.6-9.7, 4.65	8.1, 0.81, 18 6.7-9.5, 10.01

mml	12.2, 0.83, 68 10.5-14.3, 6.78	12.1, 1.34, 16 10.1-14.2, 11.10	11.0, 0.83, 28 9.5-12.5, 7.53	10.7, 0.65, 44 9.0-12.1, 6.03	11.1, 0.69, 5 10.3-11.8, 6.18	10.4, 1.04, 19 8.7-12.0, 9.92
entl	8.0, 1.21, 68 5.5-10.1, 14.08	7.4, 1.21, 16 5.5-9.8, 16.29	7.6, 1.02, 28 5.1-9.4, 13.39	6.8, 1.08, 44 4.5-9.0, 15.80	6.5, 1.62, 5 4.3-7.2, 24.97	7.4, 0.89, 18 5.8-8.4, 12.04

MANDIBLE

p2-p4 L	69.4, 2.81, 9 64.9-74.2, 4.05	66.5, –, 1	63.3, 1.75, 4 62.0-65.7, 2.77	59.7, 2.26, 6 56.3-62.9, 3.78	—	58.3, --, 1
m1-m3 L	64.2, 1.91, 6 62.1-66.8, 2.97	66.4, –, 1	60.7, 1.98, 2 59.3-62.1, 3.26	57.3, 1.43, 8 55.0-59.7, 2.50	—	60.1, --, 1
p2-m3 L	133.0, 4.79, 3 129.6-138.5, 3.60	132.6, –, 1	124.2, 3.75, 2 121.5-126.8, 3.02	116.1, 0.61, 4 115.3-116.7, 0.53	—	117.7, --, 1
dp2-dp4 L	81.2, 1.43, 4 79.3-82.5, 1.76	76.1, --, 1	—	74.7, 1.43, 3 73.1-75.9, 1.91	—	—
ldl	—	106.9, --, 1	—	82.2, --, 1	—	112.2, --, 1

TABLE 5. Frequency of occurrence (in %) of different enamel plications in the lower cheekteeth of various populations of *Cormohipparion*. PARA, posterior plication on paralophid; ANTI, plication on antisthmus or anterior side of isthmus; PSTI, plication on postisthmus or posterior half of isthmus; PLCB, pli caballinid. The "Hemphillian" fauna for *C. ingenuum* and *C. plicatile* refers to a combined sample from Mixson's Bone Bed, McGehee Farm, Haile 19A, Coffrin Creek, and the Lower Bone Valley.

Species	Fauna	n	PARA	ANTI	PSTI	PLCB
p3 and p4 combined						
C. occidentale	Lapara Creek	24	49	33	50	58
C. occidentale	Clarendon	17	26	35	65	59
C. occidentale	Xmas-Kat	29	66	62	59	62
C. ingenuum	Agricola	23	61	22	35	56
C. ingenuum	Love Site	89	60	55	33	39
C. ingenuum	Hemphillian	6	50	50	33	50
C. plicatile	Love Site	130	41	50	20	28
C. plicatile	Hemphillian	15	53	73	40	47
C. emsliei	Bone Valley	20	85	75	25	100
m1 and m2 combined						
C. occidentale	Lapara Creek	16	30	63	38	12
C. occidentale	Clarendon	18	0	28	17	0
C. occidentale	Xmas-Kat	30	27	63	30	3
C. ingenuum	Agricola	29	24	21	7	10
C. ingenuum	Love Site	115	12	45	9	3
C. ingenuum	Hemphillian	12	9	18	0	9
C. plicatile	Love Site	165	12	52	2	7
C. plicatile	Hemphillian	30	17	67	13	3
C. emsliei	Bone Valley	27	33	78	22	56

TABLE 6. Comparison of variation in tooth length measured at the base of the crown (BAPL) of both single quarry and combined quarry (faunal) samples of hypsodont equid species. BAPL is statistically independent of crown height, and thus a better indicator of sample variation when comparing populations that may have different age structures than characters measured on the occlusal surface. Two measures of variation, CV (in %) and OR (in mm) are shown for combined samples of the upper third and fourth premolars (P34), and the upper first and second molars (M12). Numbers in parentheses following each species name are the sample sizes for the P34 and M12, respectively. Only populations with large sample sizes were chosen, except for *Cormohipparion occidentale*. It was included as it is the best available for a species congeneric with the two species of interest, *C. plicatile* and *C. ingenuum*. If the samples from the Love site of *C. plicatile* and *C. ingenuum* are combined (to create a single species), the observed variation is much greater than that observed in single quarry or even faunal samples of other species. This along with the bimodal distributions of measured characters (Figs. 11 and 12), and qualitative differences is justification for recognizing two species of *Cormohipparion* at the Love Site and other Florida localities. When treated separately, the variation each exhibits is equivalent to that observed in other quarry samples. References are Webb and Hulbert (1986), and Hulbert (1987a, 1987b, 1988a).

	Taxon	Quarry or Fauna	P34		M12	
			CV	OR	CV	OR
	Cormohipparion plicatile and *C. ingenuum* combined (153,155)	Love Site	7.91	6.1	6.65	4.7
Single quarry samples	*Cormohipparion plicatile* (107,108)	Love Site	5.56	4.1	4.20	3.1
	Cormohipparion ingenuum (46,47)	Love Site	4.52	2.7	3.90	2.3
	Neohipparion trampasense (124,138)	Love Site	5.04	4.0	4.66	3.2
	Pseudhipparion retrusum (24,19)	Burge Quarry	3.39	1.9	3.54	1.7
	Nannippus lenticularis (23,29)	Coffee Ranch	4.81	2.5	3.88	2.0
	Calippus cerasinus (29,45)	Love Site	4.37	2.7	4.77	2.5
	Protohippus gidleyi (36,30)	Love Site	4.31	2.9	5.70	3.9
	average		4.57	2.97	4.39	2.67
Faunal samples	*Cormohipparion occidentale* (9,6)	Xmas-Kat	4.63	2.6	5.84	3.1
	Neohipparion eurystyle (40,33)	Yepomera	5.71	3.3	4.84	3.8
	Pseudhipparion gratum (25,30)	Minnechaduza	4.26	2.4	3.67	1.7
	Pseudhipparion hessei (56,53)	Clarendon	5.03	2.8	6.64	3.5
	Nannippus minor (32,35)	Yepomera	3.51	1.8	3.84	1.8
	Calippus martini (21,23)	Clarendon	5.34	3.7	5.62	3.0
	Calippus regulus (25,41)	Clarendon	5.90	2.4	4.37	1.9
	average		4.91	2.71	4.97	2.69

TABLE 7. Median values for number of fossette plications of various species of *Cormohipparion*. Combined samples of upper third and fourth premolars, and first and second molars analized separately. Teeth included in the analysis only if their crown height fell between 50 and 90% of the maximum (i.e. unworn) possible for that particular species. Thus the samples exclude very slightly worn and heavily worn specimens. EXTPLI = sum of plications on the anterior half of the prefossette and the posterior half of the postfossette; INTPLI = sum of plications on the posterior half of the prefossette and the anterior half of the postfossette; TOTPLI = EXTPLI + INTPLI. Median values are given rather than means because fossette plication distributions are exceedingly variable and nonnormal.

	P3 and P4				M1 and M2			
	EXTPLI	INTPLI	TOTPLI	n	EXTPLI	INTPLI	TOTPLI	n
C. occidentale	3	10	12	44	4	9	14	39
C. plicatile	2	9	10	62	1	7	8	85
C. ingenuum	2	9	12	33	2	8	10	41
C. emsliei	4	11	15	23	5	10	16	29

TABLE 8.   Description of characters and character states used in phylogenetic analysis. Character numbers match those of Hulbert and MacFadden (in prep.).

1.   Depth of Nasal Notch. Two states are recognized: 0, notch shallow, dorsal to about the mid-point of the C-P2 diastema; 1, notch dorsal to anterior half of P2 or just anterior to the P2.

2.   Depth of DPOF. Five states are recognized: 0, fossa absent or very rudimentary; 1, depth very shallow, maximum depth less than 5 mm; 2, depth shallow, about 5-10 mm; 3, depth moderate, 10-15 mm; 4, depth deep, greater than 15 mm.

3.   DPOF Posterior Pocket. Three states are recognized: 0, DPOF without a pocket; 1, pocket shallow, not extensive; 2, deep, extensive pocket.

4.   DPOF Anterior Margin. Two states are recognized: 0, anterior margin of fossa confluent with face without a rim; 1, anterior margin well defined with a pronounced rim.

5.   DPOF Posterior Margin. Two states are recognized: 0, posterior margin of DPOF without a pronounced rim; 1, posterior margin with a pronounced rim.

6.   Distinct Ventral Rim on DPOF. Two states are recognized: 0, ventral rim of DPOF without distinct or pronounced margin; 1, ventral rim distinctly rimmed.

7.   Preorbital Bar Length. Three states are recognized: 0, narrow (less than 5 mm); 1, moderate (5 to 15 mm); 2, long (greater than 15 mm).

8.   DPOF Shape. Two states are recognized: 0, elongate-oval (length much greater than height); 1, oval (length less than 50% greater than height).

9.   Relative Size of the Lacrimal Bone. Two states are recognized: 0, relatively large; 1, relatively small.

10. Lacrimal in DPOF. Two states are recognized: 0, lacrimal makes up rear portion of the DPOF; 1, lacrimal not involved in the DPOF.

12. Malar fossa. Two states are recognized: 0, malar fossa absent; 1, malar fossa present.

13. Confluence of Malar and Dorsal Preorbital Fossae. Two states are recognized: 0, malar fossa and DPOF distinctly separated from one another; 1, malar fossa and DPOF merged with one another to form a single large fossa.

16. Muzzle Length. Character state is determined by comparing i3-p2 diastema length to toothrow length. Five states are recognized: 0, very short; 1, short; 2, moderate; 3, elongated; 4, very elongated.

19. Size of DP1. Three states are recognized: 0, DP1 large, present in adult dentitions; 1, DP1 small but functional and present in adult dentitions; 2, DP1 vestigial or absent in adult dentions.

20. Cement on Deciduous Premolars. Four states are recognized: 0, no cement present; 1, cement layer rudimentary, primarily on DP4 and dp4; 2, thin but extensive cement coating on all decidous cheekteeth; 3, thick coating of cement on all deciduous cheekteeth.

21. Cement on Permanent Cheekteeth. Three states are recognized: 0, thin layer of cement present; 1, moderate layer of cement present; 2, thick layer of cement present.

22. Anterostyle of P2 and DP2. Two states are recognized: 0, anterostyle well developed; 1, anterostyle reduced.

23. Protocone shape (P3-M2). Based on ratio of protocone length to width (L:W). Four states are recognized: 0, round (L:W less than 1.2); 1, oval (L:W 1.2-2.0); 2, elongate-oval (L:W 2.0-3.0); 3, elongate (L:W greater than 3.0).

24. Protocone Lingual Border. Three states are recognized: 0, protocone lingual border round or convex; 1, lingual border straight; 2, lingual border variably straight or concave.

Table 8 Continued

25. Protoconal Spur (P3-M3). Four states are recognized: 0, protoconal spur is large and persistent; 1, protoconal spur is large but present only in early wear-stages; 2, protoconal spur is reduced and present only in very early or early wear-stages; 3, protoconal spur absent or very rare.
26. Protoconal Spur Connection to Protoloph. Two states are recognized: 0, protoconal spur connects with protoloph; 1, protoconal spur does not connect with protoloph.
27. Timing of Protocone Connection to Protoloph on the P3 and P4. Seven states are recognized: 0, protocone connected to protoloph immediately after onset of occlusal wear; 1, connected during the very early wear-stage; 2, connected during the early wear-stage; 3, connected during the early moderate wear-stage; 4, connected during the late moderate wear-stage; 5, connected during the late wear-stage; 6, protocone isolated from protoloph to base of crown.
28. Timing of Protocone Connection to Protoloph on the M1 and M2. Same seven states as Character 27.
29. Protocone Connection to Hypocone on the M1 and M2. Three states are recognized: 0, protocone never connects to hypocone; 1, connection occurs only in late wear-stage; 2, connection occurs prior to late wear-stage.
30. Pli Caballin on P2-P4. Four states are recognized: 0, pli caballin absent or very rare; 1, pli caballin usually present but weak and nonpersistent; 2, pli caballin well developed, relatively persistent, usually single or unbranched; 3, pli caballin well developed, frequently branched or multiple.
31. Pli Caballin on M1-M3. Same four states as Character 30.
32. External Fossette Plications. Three states are recognized: 0, pli protoloph and pli hypostyle usually absent, or if present single and nonpersistent; 1, pli protoloph and/or pli hypostyle usually present, persistent, but single; 2, multiple pli protoloph and/or pli hypostyle present in early wear-stages.
33. Internal Fossette Plications. This character is based on the typical fossette morphology observed in early and moderate wear-stages. Seven states are recognized: 0, all internal fossette plications (pli prefossette, pli postfossette, etc.) absent, or very rare (if present simple and nonpersistent); 1, very simple internal fossette plications (pli prefossette and pli postfossette single or absent, prefossette loop not prominent); 2, simple but nonpersistent internal fossette plications (pli prefossette and pli postfossette usually multiple in early wear-stages, single in moderate wear-stages, absent in late wear-stages) that are relatively shallow and nonbranching; 3, simple but persistent internal fossette plications (as in 2 but with plications generally present in later wear-stages); 4, moderately complex internal fossette plications (usually 2 to 5 plications present on both sides in early and moderate wear-stages, with a limited amount of branching); 5, complex internal fossette plications (usually 3 to 7 plications present on both sides in early and moderate wear-stages, branching of plications common); 6, very complex internal fossette plications (usually 5 to 10 plications present on both sides in early and moderate wear-stages, branching of plications common).
34. Orientation of Protocone of P3 and P4. Two states are recognized: 0, long axis of protocone oriented in an approximately anteroposterior direction; 1, long axis of protocone obliquely oriented in an anterolingual-posterolabial direction.
35. Metastyle Development. Three states are recognized: 0, generally absent or very weak; 1, often present but not strong; 2, very well developed.
38. Timing of Hypoconal Groove Closure on P2-P4. Three states are recognized: 0, hypoconal groove open to near the base of the crown; 1, hypoconal groove closed in late wear-stages; 2, hypoconal groove closed in moderate wear-stages.
39. Timing of Hypoconal Groove Closure on M1-M2. Same three states as Character 38.

Table 8 Continued

40. Hypoconal Lake on P3-P4. Two states are recognized: 0, hypoconal groove does not form an isolated lake when it closes; 1, hypoconal groove does form a lake after closing.

41. Hypoconal Lake on M1-M2. Same two states as Character 40.

43. Curvature of Upper Cheekteeth. Based on the radius of curvature (ROC) measured along the mesostyle (Skinner and Taylor 1967). Three states are recognized: 0, strongly curved, ROC less than 40 mm; 1, moderately curved, ROC from 40 to 80 mm; 2, relatively straight, ROC greater than 80 mm.

45. Retention of the dp1. Three states are recognized: 0, dp1 relatively large, usually retained with permanent dentition; 1, dp1 reduced, variably present with adult dentition; 2, dp1 usually not present with permanent dentition.

46. Ectostylids on dp2-dp4. Three states are recognized: 0, absent or rudimentary; 1, moderate (less than 5 mm high); 2, strong.

48. Strength of Protostylids on dp3-dp4. Three states are recognized: 0, protostylids weak, may be present only near base of crown; 1, protostylids moderately well developed; 2, protostylids very well developed.

49. Depth of Ectoflexid on dp2-dp4. Three states are recognized: 0, ectoflexid deep, completely penetrates isthmus; 1, ectoflexid moderately deep, only partially penetrates isthmus; 2, ectoflexid shallow, does not penetrate isthmus.

50. dp2 and p2 metaconid. Two states are recognized: 0, metaconid without anterior plication, does not connect with paralophid except in late wear-stages; 1, metaconid with anterior plication, often connects with paralophid in moderate wear-stages isolating metaflexid as a fossettid.

52. Strength of Protostylids on p3-m3. Same three states as Character 48.

53. Protostylid Attachment. Three states are recognized: 0, protostylid always connected to protoconid; 1, protostylid initially isolated from protoconid, connects lower on the crown; 2, protostylid persistently isolated from the protoconid.

54. Expansion of Metaconid-Metastylid Complex. Three states are recognized: 0, metaconid-metastylid relatively small and unexpanded; 1, metaconid-metastylid expanded but not elongated; 2, metaconid-metastylid moderately elongated.

55. Separation of Metaconid and Metastylid on p3-m3. Three states are recognized: 0, metaconid and metastylid poorly separated from one another even in early wear-stages; 1, well separated from each other only in early wear-stages; 2, persistently well separated from each other.

56. Metaconid-Metastylid on p2. Two states are recognized: 0, single median lingual cuspid present, not separated in metaconid and metastylid; 1, separate metaconid and metastylid present on p2.

57. Development of Pli Entoflexid. Two states are recognized: 0, pli entoflexid absent or rudimentary; 1, pli entoflexid usually present, at least in early and very early wear-stages.

58. Development of Isthmus Plications. This character refers to plications other than the pli entoflexid. Three states are recognized: 0, isthmus plications absent or very rare; 1, isthmus plications frequent but nonpersistent; 2, isthmus plications frequent and persistent.

59. Development of Paralophid Plication. Two states are recognized: 0, paralophid without a plication into the metaflexid; 1, paralophid frequently plicated.

60. Pli Caballinid on p2-p4. Three states are recognized: 0, pli caballinid generally absent; 1, pli caballinid small, nonpersistent; 2, pli caballinid large, relatively persistent.

61. Pli Caballinid on m1-m3. Three states are recognized: 0, pli caballinid generally absent; 1, pli caballinid small, nonpersistent; 2, pli caballinid moderate, lasts until moderate wear-stages.

62. Ectoflexid Depth on p2. Same three states as Character 49.

63. Ectoflexid Depth on p3-p4. Same three states as Character 49.

Table 8 Continued

64. Ectoflexid Depth on m1-m3. Same three states as Character 49.
65. Labial Borders of Protoconid and Hypoconid. Two states are recognized: 0, labial borders rounded; 1, labial borders notably flattened.
67. Relative Size of the Metaconid and Metastylid on m1-m3. Two states are recognized: 0, metaconid and metastylid equal or subequal in size and position of their lingual borders; 1, metastylid notably smaller than metaconid, lingual border located more labially than that of metaconid (this state best observed in moderate and late wear-stages).
68. Shape of Metaconid-Metastylid Borders. Two states are recognized: 0, borders rounded or oval; 1, borders angular or pointed.
70. Toothrow Length. This character is used as an indicator of overall size, and reflects the mean upper or lower toothrow length in moderate wear-stage $\pm$ 5 mm. Eight states are recognized: 0, less than 85 mm; 1, about 90 mm; 2, about 100 mm; 3, about 110 mm; 4, about 120 mm; 5, about 130 mm; 6, about 140 mm; 7, about 150 mm or greater.
71. Unworn Molar Crown Height. This character is determined by unworn M1 mesostyle crown height or m1 metaconid crowm height, $\pm$ 2.5 mm. Nine states are recognized: 0, less than 20 mm; 1, about 25 mm; 2, about 30 mm; 3, about 35 mm; 4, about 40 mm; 5, about 45 mm; 6, about 50 mm; 7, about 55 mm; 8, about 60 mm, or greater.

TABLE 9. Character state matrix for merychippine and hipparionine equids in the PAUP analysis. Characters and character states are defined in Table 8. A "?" indicates a state that is unknown because of a lack of material; an "X" indicates a state that can not be defined, e.g. a descriptive character concerning a structure not present for a particular taxon. Both are treated identically as missing states by the PAUP program. Characters not listed here are found only in the primitive state for all taxa under consideration.

TAXON/CHARACTERS	1	2	3	4	5	6	7	8	9	10	12	13	16	19	20	21	22
"Parahippus" leonensis	0	1	0	0	0	0	0	0	0	0	0	X	1	0	0	0	0
"Merychippus" primus	0	1	0	0	0	0	0	0	0	0	0	X	1	1	1	1	0
Equini	0	3	1	0	1	0	1	0	0	0	0	X	2	0	1	2	0
"Merychippus" sejunctus	0	2	0	0	1	0	0	1	0	0	1	1	2	0	1	2	0
"Merychippus" coloradense	0	2	0	0	1	0	0	0	0	0	0	X	3	0	?	2	0
Neohipparion	0	1	0	0	0	0	1	0	0	1	0	X	2	1	3	2	0
Pseudhipparion	1	1	0	0	0	0	2	0	0	1	0	X	2	0	3	2	0
Hipparion shirleyi	1	2	0	0	1	1	2	0	0	0	0	X	3	0	1	2	0
Hipparion tehonense	1	2	1	0	1	1	2	0	1	1	0	X	3	0	3	2	1
Hipparion forcei	1	2	1	0	1	1	2	0	1	1	0	X	3	?	3	2	1
Merychippus insignis	0	2	1	0	1	0	1	0	0	0	0	X	1	0	1	2	0
"Merychippus" goorisi	0	4	2	1	1	1	1	0	1	1	0	X	2	0	1	2	0
Nannippus	?	4	2	1	1	1	?	0	0	0	0	X	?	2	3	2	1
Cormohipparion sphenodus	0	4	2	1	1	1	2	0	0	0	0	X	2	0	3	2	0
Cormohipparion occidentale	0	4	2	1	1	1	2	0	0	1	0	X	3	0	3	2	0
Cormohipparion plicatile	?	4	?	?	1	1	?	0	?	?	0	X	4	?	3	2	0
Cormohipparion ingenuum	?	3	?	?	1	0	?	0	?	?	0	X	4	?	3	2	0
Cormohipparion emsliei	?	1	?	0	?	0	?	0	?	?	0	X	4	0	3	2	0
"Hippotherium" primigenium	0	4	2	1	1	1	2	0	0	1	0	X	3	0	3	2	0

Table 9 Continued

TAXON/CHARACTERS	23	24	25	26	27	28	29	30	31	32	33	34	35	38	39	40	41
"Parahippus" leonensis	0	0	0	0	4	4	0	1	0	0	3	0	1	1	1	0	0
"Merychippus" primus	1	0	0	0	2	1	1	2	1	0	2	0	1	2	2	0	0
Equini	1	0	0	0	2	2	1	2	1	0	2	0	1	2	2	1	0
"Merychippus" sejunctus	1	0	0	0	3	2	1	2	2	0	2	0	1	2	2	0	0
"Merychippus" coloradense	2	0	0	0	4	4	1	2	1	0	3	0	2	2	2	1	0
Neohipparion	3	1	3	1	6	6	0	2	1	0	3	1	2	0	0	0	0
Pseudhipparion	3	0	0	0	4	3	2	2	1	0	3	1	2	2	2	1	1
Hipparion shirleyi	2	0	0	0	4	4	1	2	2	0	4	0	0	1	1	1	0
Hipparion tehonense	2	0	2	1	4	4	0	2	2	0	4	0	0	0	0	0	0
Hipparion forcei	2	0	2	1	4	4	0	2	2	0	4	0	0	0	0	0	0
Merychippus insignis	1	0	0	0	4	4	1	3	2	1	4	0	2	1	1	1	1
"Merychippus" goorisi	1	0	0	0	5	5	1	3	2	1	5	0	2	0	0	0	0
Nannippus	2	0	1	1	5	5	0	3	2	1	5	0	2	0	0	0	0
Cormohipparion sphenodus	2	0	2	1	5	5	0	3	2	2	6	0	2	0	0	0	0
Cormohipparion occidentale	3	1	3	1	5	5	0	3	2	2	6	0	2	0	0	0	0
Cormohipparion plicatile	2	0	3	1	5	5	0	3	2	1	5	0	2	0	0	0	0
Cormohipparion ingenuum	2	2	3	1	5	5	0	3	2	1	5	0	2	0	0	0	0
Cormohipparion emsliei	2	2	3	1	5	5	0	3	2	2	6	0	2	0	0	0	0
"Hippotherium" primigenium	2	0	3	1	5	5	0	3	2	2	6	0	2	0	0	0	0

Table 9 Continued

TAXON/CHARACTERS	43	45	46	48	49	50	52	53	54	55	56	57	58	59	60	61
"Parahippus" leonensis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
"Merychippus" primus	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0
Equini	0	2	1	0	0	0	0	0	1	1	1	1	0	0	0	0
"Merychippus" sejunctus	0	2	1	0	0	0	0	0	1	1	1	1	0	0	0	0
"Merychippus" coloradense	1	2	?	?	?	0	0	0	1	2	1	1	0	0	0	0
Neohipparion	1	2	0	2	?	0	2	0	2	2	1	1	0	0	1	1
Pseudhipparion	1	2	1	2	0	0	2	0	1	2	1	1	0	0	0	0
Hipparion shirleyi	0	2	1	1	0	0	1	0	1	2	1	1	0	0	0	0
Hipparion tehonense	1	2	1	1	0	0	1	0	1	2	1	1	0	0	0	0
Hipparion forcei	1	2	1	1	0	0	1	0	1	2	1	1	0	0	0	0
Merychippus insignis	0	2	1	2	0	0	1	0	1	2	1	1	0	0	0	0
"Merychippus" goorisi	0	2	1	2	0	0	2	0	1	2	1	1	0	0	0	0
Nannippus	1	2	2	2	0	0	2	1	1	2	1	1	1	0	1	0
Cormohipparion sphenodus	1	2	2	2	1	0	2	1	1	2	1	1	2	1	1	0
Cormohipparion occidentale	1	2	2	2	1	0	2	1	1	2	1	1	2	1	1	1
Cormohipparion plicatile	1	2	2	2	1	0	2	1	1	2	1	1	2	1	1	1
Cormohipparion ingenuum	1	2	2	2	1	1	2	1	1	2	1	1	2	1	1	1
Cormohipparion emsliei	1	2	2	2	2	1	2	1	2	2	1	1	2	1	2	2
"Hippotherium" primigenium	1	2	2	2	?	0	2	1	1	2	1	1	2	1	1	?

Table 9 Continued

TAXON/CHARACTERS	62	63	64	65	67	68	70	71
"Parahippus" leonensis	0	0	0	0	0	0	1	0
"Merychippus" primus	1	0	0	0	0	0	2	1
Equini	1	0	0	0	1	0	3	2
"Merychippus" sejunctus	1	0	0	0	0	0	3	2
"Merychippus" coloradense	1	1	0	0	0	0	5	4
Neohipparion	2	2	0	1	0	0	4	7
Pseudhipparion	2	2	0	0	0	0	3	4
Hipparion shirleyi	1	0	0	0	0	0	3	3
Hipparion tehonense	1	0	0	0	0	0	4	5
Hipparion forcei	1	1	0	0	0	0	5	6
Merychippus insignis	1	0	0	0	0	0	4	3
"Merychippus" goorisi	1	0	0	0	0	0	4	2
Nannippus	2	1	0	0	0	0	3	5
Cormohipparion sphenodus	2	1	0	0	0	0	5	5
Cormohipparion occidentale	2	1	0	0	0	0	6	8
Cormohipparion plicatile	2	1	0	0	0	0	5	8
Cormohipparion ingenuum	2	1	0	0	0	0	4	6
Cormohipparion emsliei	2	2	1	0	0	1	4	7
"Hippotherium" primigenium	2	1	0	0	0	0	7	6

TABLE 10. Distribution of late Barstovian, Clarendonian, Hemphillian, and Blancan equids in Florida. All sites containing three or more taxa are included. An "X" indicates that a particular species is present based on confidently identified referred material; a "C" represents a less certain identification; a "?" a problematical identification; a "-" the absence of that taxon based on presently available material; and a "T" indicates that the particular site is the type locality of the species in question. With the exception of Mixson's Bone Bed (USNM and F:AM collections), this table is based solely on material from the UF and UF/FGS collections, and on identifications made by the author. The latter do not agree in all instances with previously published identifications of other authors. The 26 localities or faunas represent six biochronological intervals, late Barstovian (ca. 12-14 Ma), early Clarendonian (ca. 11 Ma); latest Clarendonian-early Hemphillian (ca. 7.5-9 Ma), late early Hemphillian (ca. 7-6 Ma); late Hemphillian (ca. 4.5-5 Ma), and late Blancan (ca. 2-3 Ma). Key to localities (see also Fig. 2): late Barstovian, 1, Bradley Fauna, Kingsford and Nichols Mines; 2, Red Zone, Phosphoria Mine; early Clarendonian, 3, Grey Zone, Phosphoria Mine; 4, Agricola Road Site; 5, composite Agricola Fauna from Phosphoria, Hookers Prairie, and Silver City Mines; latest Clarendonian-early Hemphillian, 6, Love Site; 7, Pareners Branch Site; 8, "Stream Matrix" Horizon, Nichols Mine; 9, Coffrin Creek; 10, McGehee Farm Site; 11, Haile 5B; 12, Haile 19A; 13, Mixson's Bone Bed; late early Hemphillian, 14, Moss Acres Racetrack Site; 15, Withlacoochee River Site 4A; 16, Dunnellon Phosphate Mining District; 17, Leisey Shell Pit 1C; 18, Port Manatee Site; 19, Manatee County Dam Site; 20, Bradon River Site; 21, Lockwood Meadows Site; late Hemphillian, 22, TRO Quarry, Payne Creek Mine; 23, Rick's Pump Site, Gardinier Mine; 24, composite Upper Bone Valley Fauna; late Blancan, 25, Macasphalt Shell Pit; 26, Haile 15A.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Megahippus sp.	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypohippus affinis	-	-	-	C	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pliohippus mirabilis	X	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Astrohippus stockii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	X	-	-
Dinohippus sp.	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	C	-	-	X	-	-	-	-	-	-
Dinohippus mexicanus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-
Equus simplicidens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Equus advanced sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X
Protohippus perditus	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protohippus supremus	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protohippus gidleyi	-	-	-	-	-	T	X	-	-	X	-	-	X	-	C	-	-	-	-	-	-	-	-	-	-	-
Calippus proplacidus	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calippus sp.	X	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calippus elachistus	-	-	-	-	-	T	-	X	X	X	-	X	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Calippus martini	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calippus cerasinus	-	-	-	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 10 Continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Calippus hondurensis	-	-	-	-	-	-	-	-	C	C	?	C	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Calippus maccartyi	-	-	-	-	-	-	-	-	-	-	-	-	-	T	X	-	-	-	-	-	-	-	-	-	-	-
Neohipparion trampasense	-	-	-	-	-	X	X	X	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neohipparion eurystyle	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	X	X	X	X	X	-	X	X	-	-
Pseudhipparion sp.	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudhipparion curtivallum	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudhipparion skinneri	-	-	-	-	-	X	X	X	X	X	X	X	-	-	-	-	-	X	X	X	-	-	-	-	-	-
Pseudhipparion simpsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	X	X	X	-	-
Hipparion tehonense	-	-	-	-	C	C	-	-	-	-	-	-	-	C	C	C	-	C	-	-	-	-	-	-	-	-
Merychippus californicus	C	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nannippus n. sp.1	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nannippus n. sp.2	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nannippus n. sp.3	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	X	-	-	-	-	-	-	-	-
Nannippus westoni	-	-	-	-	-	X	-	X	-	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Nannippus minor	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	X	X	X	X	X	X	X	X	-	-
Nannippus peninsulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X
Cormohipparion sphenodus	?	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cormohipparion occidentale	-	-	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cormohipparion plicatile	-	-	-	-	-	X	X	X	X	X	X	X	T	X	-	X	-	X	-	-	-	-	-	-	-	-
Cormohipparion ingenuum	-	-	X	X	X	X	X	X	X	X	-	X	T	-	X	X	X	X	C	-	?	-	-	-	-	-
Cormohipparion emsliei	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	?	-	-	-	X	X	X	T	X

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES SERIES, may be in any field of biology. Manuscripts dealing with natural history or systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length--circa 35 to 200 pages (10,500-60,000 words). Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this the author(s) receive(s) 50 copies free, and he(they) may purchase additional separates at cost if ordered when page proof is returned. The author is also responsible for any charges incurred for alterations made by him on galley or page proofs. The Museum will send an invoice to the author for this amount upon completion of publication.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, 3rd Edition, 1972 (American Institute of Biological Sciences, Washington, D.C.).

Manuscripts must be submitted in duplicate and satisfy the following minimal requirements. Please submit duplicate copies of manuscripts. They must be double-spaced throughout, including tables, figure captions, and literature citations. Figure legends and tables should be typed on separate sheets. Also, please submit a copy of the complete text and tables on one or more 5¼" flexible diskettes.

All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. If the background of photographs (especially those of specimens) is not desired, amberlith should be cut out and used to cover the background. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lower case letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 9" x 14" (twice BULLETIN typepage size); illustrations should not be less than typepage width (4½"). With soft lead pencil on the back of each illustration, designate the top and identify each by author's name, manuscript title, and figure number.

All manuscripts not submitted in BULLETIN format will be returned to the author for retyping.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida State Museum
University of Florida
Gainesville FL 32611
U.S.A.