CALIPPUS AND *PROTOHIPPUS* (MAMMALIA,
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(BARSTOVIAN-EARLY HEMPHILLIAN OF THE
THE GULF COASTAL PLAIN

Richard C. Hulbert, Jr.

CALIPPUS AND *PROTOHIPPUS* (MAMMALIA, PERISSODACTYLA, EQUIDAE) FROM THE MIOCENE (BARSTOVIAN-EARLY HEMPHILLIAN) OF THE GULF COASTAL PLAIN

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ABSTRACT

Nine species of Calippus and four species of Protohippus are recognized from the late Miocene (late Barstovian to early Hemphillian, from about 14.0 ma to 6.0 ma) of the Gulf Coastal Plain. Two subgenera of Calippus are recognized: C. (Calippus) which includes four small species, C. proplacidus n. comb. (senior synonym of C. francisi), C. placidus, C. regulus and C. elachistus n. sp.; and C. (Grammohippus) n. subgen. which contains five medium-sized species: C. circulus n. comb., C. martini, C. cerasinus n. sp., C. hondurensis n. comb., and C. maccartyi n. sp. Protohippus is a valid genus, not synonymous with nor related to Merychippus sensu stricto, and not ancestral to Pliohippus, Dinohippus, or Equus. Four successive species of Protohippus are recognized from the Gulf Coastal Plain, P. vetus, P. perditus, P. supremus (senior synonym of P. simus), and P. gidleyi n. sp. Eight of these 13 species also ranged north into the Great Plains, and are useful in faunal and chronological correlations between the two regions. Phylogenetic analyses of cranial and dental characters suggest the following hypotheses: (1) Protohippus and Calippus are more closely related to each other than either is to any other equid genus, and the two form a monophyletic group, the Subtribe Protohippina Quinn new rank; (2) Protohippus and Calippus form the sister group to a second monophyletic radiation of hypsodont equids, the equines; and (3) the

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common ancestor shared by protohippines and equines was a relatively small, late Hemingfordian-early Barstovian taxon, dentally of primitive merychippine-grade. In these . clades, dental characters are more subject to parallelism than cranial characters, thus the latter are often more useful for deducing phylogenetic relationships.

RESUMEN

.Se reconocen nueve especies de Calippus y cuatro especies de Protohippus del Mioceno tardío (Barstoviano tardío hasta Hemphiliano temprano, de aprox. 14.0 ma a 6.0 ma) de la planicie costera del Golfo de México. Se reconocen dos subgéneros de Calippus: C. (Calippus) incluyendo cuatro especies de tamaño pequeño, C. proplacidus comb. n. (sinónimo mayor de C. francisi), C. placidus, C. regulus, y C. elachistus esp. n.; y C. (Grammohippus) subgén. n. que incluye cinco especies de tamaño mediano: C. circulus comb. n., C. martini, C. cerasinus esp. n., C. hondurensis comb. n., y C. maccartyi esp. n.   Protohippus es un género válido; no es sinónimo ni pariente cercano de Merychippus en el sentido estricto, ni es progenitor de Pliohippus, Dinohippus, ni Equus. Cuatro especies sucesivas de Protohippus se reconocen de la planicie costera del golfo, P. vetus, P. perditus, P. supremus (sinónimo mayor de P. simus), y P. gidleyi esp. n.   Ocho de estas trece especies se extendían al norte hasta los llanos centrales, y son útiles en correlaciones faunísticas y cronológicas entre las dos regiones. Análisis filogenéticos de características craneales y dentales sugieren las siguientes hipótesis: (1) Protohippus y Calippus son más afines entre sí que con cualquier otro género équido, y los dos forman un grupo monofilético, la subtribu Protohippina Quinn, rango nuevo; (2) Protohippus y Calippus forman el grupo hermano a una segunda línea monofilética de équidos hipsodontos, los equinos; y (3) el progenitor común de los protohipinos y equinos era un taxon de tamaño relativamente pequeño, del Hemingfordiano tardío o Barstoviano temprano, con dientes del grado merychipino primitivo. En estas líneas filogenéticas, las características dentales son más sujetas a paralelismo que las características craneales; por eso las últimas son frecuentemente más útiles para deducir relaciones filogenéticas.

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INTRODUCTION

This is one of several recently completed studies describing fossil equids from the Late Neogene (Barstovian, Clarendonian, and Hemphillian Land Mammal Ages) of the Gulf Coastal Plain of North America. Previous studies have dealt with *Dinohippus* and *Astrohippus* (MacFadden 1986), *Pseudhipparion* (Webb and Hulbert 1986), *Neohipparion* (Hulbert 1987b), *Cormohipparion* and *Hipparion* (Hulbert 1987c; Hulbert in press), and

Nannippus (Hulbert 1987a; in prep. A).   Together they provide modern revisions of these taxa from this important faunal province, aid in intracontinental biostratigraphic correlation of Gulf Coastal Plain faunas with radiometrically dated faunas from the western United States, and allow greater understanding of equid evolution and paleoecology during a critical period of their history in North America

Protohippus was first described by Leidy (1858) as a subgenus of *Equus*, but was later given generic status (Leidy 1869). The taxon was widely used until about 1930, with many species referred to it (see e.g. Gidley 1907). McGrew and Meade (1938), and later Stirton (1940), reduced it to the rank of subgenus, within an expanded, horizontal concept of *Merychippus*. In their revised classification of the Equidae, *M. (Protohippus)* was considered ancestral to all equine genera, just as *M. (Merychippus)* was thought to give rise (paraphyletically) to all hipparionines. It will be shown that this classification, which relied primarily on upper cheektooth morphology, is incorrect, based on a phylogenetic analysis that additionally includes cranial, incisor, and lower cheektooth characters. However, much of the classification of Gidley (1907) is not falsified by this analysis.

Calippus was first described by Matthew and Stirton (1930) as a subgenus of *Protohippus*, but was later considered a distinct genus by Stirton (1935; 1940) and subsequent authors. *Calippus* has often been thought to consist solely of dwarf species of equines, somewhat analogous to the position of *Nannippus* among hipparionines (Stirton 1940; Simpson 1951). Originally, however, Stirton and co-workers included larger species in *Calippus* (e.g. *C. martini* and *C. ansae*; Stirton 1935; Hesse 1936), a concept Stirton later abandoned. Study of previously undescribed specimens in the Frick Collection of the American Museum of Natural History, including complete skulls and mandibles of most species, indicates that *Calippus* is indeed a distinct genus characterized by several unique autapomorphies, that it includes both small and moderate-sized species, and that it is more closely related to *Protohippus* than any other equid genus.

The purpose of this study is to document the systematics and biochronology of Gulf Coastal Plain *Calippus* and *Protohippus*, including the recognition of four new species. A second study (Hulbert in prep. B) will examine populations from the Great Plains, and will include detailed descriptions of relatively complete cranial material collected by Morris Skinner and others for Childs Frick (and now housed in the AMNH). Some preliminary discussion of Great Plains material in this report is unavoidable, because: (1) some species are poorly known in the literature, and any referral to them must be justified by reference to types, topotypes, or specimens from near the type locality; (2) some populations from the Gulf Coastal Plain are referable to described Great Plains taxa, but these species need to be transferred to *Calippus* or *Protohippus* from another genus; or (3) specimens

of previously undescribed taxa are known from both geographic provinces, and because of better quality, that from the Great Plains is chosen to be the type, or contributes characters not observed in Gulf Coastal Plain material.

ACKNOWLEDGEMENTS

ABBREVIATIONS

AMNH - Department of Vertebrate Paleontology, American Museum of Natural History, New York.

ANSP - Academy of Natural Sciences, Philadelphia.

F:AM - Frick Collection, housed with AMNH collection.

MHNES - Museo de Historia Natural de El Salvador.

PPM - Panhandle-Plains Historical Museum, Canyon, Texas.

TAMU - Texas A & M University collection, now housed with TMM collection.

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.

WM - Walker Museum Collection, now housed at the Field Museum of Natural History, Chicago.

WT - West Texas State University Collection, housed in the PPM.

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.

s.s. - sensu stricto.

s.l. - sensu lato.

l.f. - local fauna.

ma - mega-anna, millions of years before present on the radioisotopic timescale.

FL - Florida.

NE - Nebraska.

TX - Texas.

x - sample mean.

s - sample standard deviation.

n - sample size.

V - sample coefficient of variation.

OR - observed range of a sample.

Abbreviations of dental measurements. Those in uppercase refer to upper dentitions; lowercase to lowers (measurements taken on occlusal surfaces are illustrated in Fig. 1).

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.
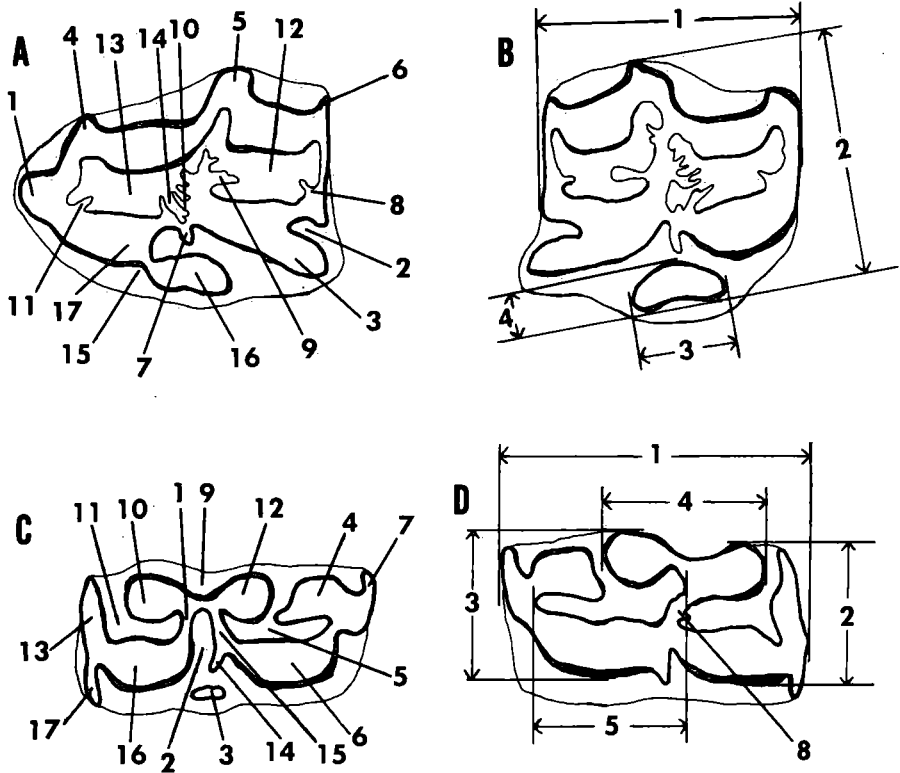
Figure 1. Schematic occlusal views of upper and lower cheekteeth of equids demonstrating nomenclature and measurements used in this study. A. Upper left second premolar (anterior to left, labial up): 1, anterostyle (found on P2s and DP2s only); 2, hypoconal groove; 3, hypocone; 4, parastyle; 5, mesostyle; 6, metastyle; 7, pli caballin; 8, pli hypostyle; 9, pli postfossette; 10, pli prefossette; 11, pli protoloph; 12, postfosette; 13, prefossette; 14, prefossette loop; 15, preprotoconal groove; 16, protocone; 17, protoselene. B. Upper right third or fourth premolar (P34) showing the four measurements taken on the occlusal surface of upper cheekteeth: 1, APL, maximum anteroposterior 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 connections to protoselene or hypocone (if present); 4, PRW, protocone width perpendicular to PRL. C. Lower left molar (m12, anterior to left, lingual up): 1, antisthmus; 2, ectoflexid; 3, ectostylid (generally found only on deciduous premolars); 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 taken on the occlusal surface of lower cheekteeth: 1, apl, maximum anteroposterior 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.

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 postcanine diastema length, measured between the alveoli of the C and the P2 (excludes DP1 if present).

ROC - radius of curvature of the mesostyle.

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 postcanine diastema length measured between the alveoli of the c and p2 (excluding dp1 if present).

MATERIALS AND METHODS

Gulf Coastal Plain terrestrial vertebrate faunas from both Texas and Florida range in age from the Arikareean to the Recent (Tedford and Hunter 1984); the taxa under study here are from the later half of the Miocene (about 14 to 6 ma). This study includes all material referable to *Calippus* and *Protohippus* from Florida housed in the UF, UF/FGS, F:AM, and USNM collections. Principal included faunas from Florida are (Fig. 2): (1) a number of sites from lower horizons in the Bone Valley Formation (Bradley and Agricola Faunas, late Barstovian and latest Barstovian-early Clarendonian, respectively; Bone Valley faunal names follow Webb and Hulbert 1986 and Waldrop and Webb in prep.); (2) the Archer Fauna, latest Clarendonian-early Hemphillian (includes the following sites or local faunas: Love Site, McGehee Farm, Pareners Branch Site, Coffrin Creek, Mixson's Bone Bed, and Haile 19A); (3) the Moss Acres Racetrack Site (early Hemphillian; Hulbert 1987b); (4) the Withlacoochee River UF locality 4A (late early

Hemphillian; Becker 1985); and (5) the Manatee County Dam Site (late early Hemphillian; Webb and Tessman 1968). Currently, no specimens referable to either *Calippus* or *Protohippus* can be undoubtably demonstrated to have originated from the classic latest Hemphillian (early Pliocene) upper Bone Valley Fauna.

Specimens of *Protohippus* and *Calippus* from the late Burkeville, Cold Spring, and Lapara Creek Faunas of the Texas Gulf Coastal Plain were also extensively studied. Quinn (1955) and Forsten (1975) have previously described the same material, and Tedford and Hunter (1984) have recently summarized the age and geological context of these faunas. When available, samples of cheekteeth from all faunas were measured to examine quantitative variation within and among taxa.
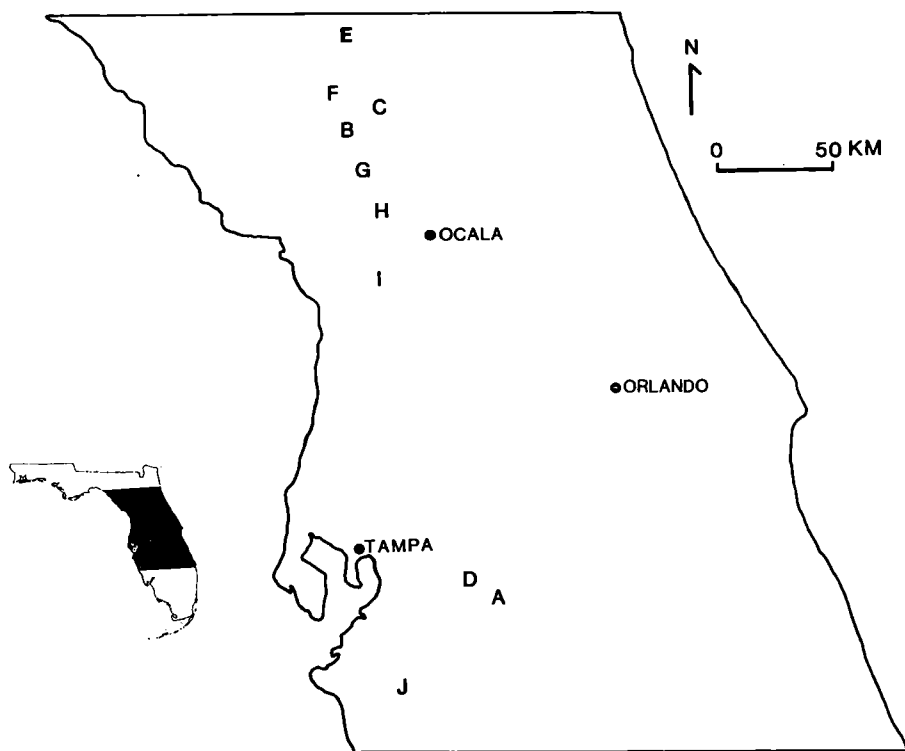
Figure 2. Map of northern and central peninsular Florida (between 27° and 30°N) depicting approximate locations of some of the fossil sites mentioned in the text. A: Phosphoria and Hookers Prairie Mines, Polk County. B: Love Site, Alachua County. C: Coffrin Creek and other Gainesville sites, Alachua County. D: Nichols Mine, Polk County. E: Pareners Branch Site, Alachua County. F: McGehee Farm and Haile sites, Alachua County. G: Mixson's Bone Bed, Levy County. H: Moss Acres Racetrack Site, Marion County. I: Withlacoochee River Site 4A, Marion-Citrus county line. J: Manatee County Dam Site, Manatee County.

As in previous studies (Hulbert 1987a; Hulbert 1987b; Webb and Hulbert 1986), comparative fossil material from other geographic areas, notably the Great Plains, was also examined. As noted above, this is not an exhaustive survey of *Calippus* and *Protohippus* from the Great Plains. Rather, large measurable samples were obtained from major faunas or localities (e.g. the Burge, Minnechaduza and Clarendon faunas) for statistical and morphological comparison with Gulf Coastal Plain specimens. Skulls are much more common from these faunas than those of the Gulf Coastal Plain; as will be documented below, use of cranial characters is essential for proper reconstruction of the phylogeny of protohippine equids. For the sake of completeness, cranial features are included in generic and specific diagnoses, even though they are based primarily on specimens from the Great Plains. During the course of this study, specimens of *Calippus*, *Protohippus*, and equines from the Great Plains were examined from the following collections: F:AM, AMNH, TMM, PPM, UNSM, and UCMP.

Methods employed are identical to those of Hulbert (1987b) and Webb and Hulbert (1986). Species assignments were determined by comparison with topotypic samples and those from large faunas, and are primarily based on qualitative dental and cranial features and quantitative analyses of cheekteeth. All measurements were taken to the nearest 0.1 mm with dial calipers on the occlusal surface (exclusive of cement, see Fig. 1), except for crown heights, and basal tooth lengths (BAPL and bapl) which were measured at the base of the crown. Radius of curvature was measured along the mesostyle following the methods of Skinner and Taylor (1967). Standard equid dental nomenclature is used (Fig. 1), and generally follows MacFadden (1984a, fig. 4) and Stirton (1941). Pli entoflexid refers to the posterolingual enamel projection from the isthmus into the entoflexid (=pli hypoconid of Quinn [1955]), a common (primitive) feature in protohippines. The following terms are used informally to collectively refer to monophyletic groups of equid genera: hipparionine, *Neohipparion*, *Pseudhipparion*, *Nannippus*, *Cormohipparion*, *Hipparion*, and Old World derivatives; protohippine, *Calippus*, and *Protohippus*; and equine, *Pliohippus*, *Astrohippus*, *Dinohippus*, *Equus*, *Onohippidium*, and *Hippidion*. The first tooth in the upper cheektooth series is referred to as the DP1; it erupts with the other deciduous teeth, is not replaced, and commonly remains with the permanent dentition (Skinner and Taylor 1967). A vestigial, single-rooted dp1 is sometimes found on juvenile rami of protohippines, but not in adult specimens. In species diagnoses, the range given for toothrow length refers to values of UTRL and ltrl commonly observed in mature individuals (and not that of extremely young adults or very old individuals, which typically have longer or shorter toothrow lengths, respectively). Also, "unworn molar crown height" refers to MSCH of M12 and mcch of m12; and not to either the M3 or m3. Durations and boundaries of North American Land Mammal Ages follow the

recommendations of Tedford and Hunter (1984) and Tedford et al. (in press).

SYSTEMATIC PALEONTOLOGY

ORDER PERISSODACTYLA OWEN, 1848
FAMILY EQUIDAE GRAY, 1821
SUBFAMILY EQUINAE STEINMANN AND DODERLEIN, 1890
TRIBE EQUINI QUINN, 1955 amended
SUBTRIBE PROTOHIPPINA QUINN, 1955 new rank

GENUS *Calippus* MATTHEW AND STIRTON, 1930

Type Species.— *Calippus (Calippus) placidus* (Leidy), 1858.
Included Subgenera.— *C. (Calippus)* and *C. (Grammohippus)* n. subgen.
Revised Generic Diagnosis.— Very small to medium-sized equids, with toothrow lengths less than 140 mm. DPOF long, relatively shallow, not pocketed; or absent. Malar fossa absent. Muzzle region greatly expanded (width 45% or greater than UTRL), with relatively large I12/i12. First and second incisors positioned in a straight row of four teeth, with the I3/i3 angled sharply posteriorly. Postcanine diastema relatively short. Cheekteeth moderate to extremely hypsodont. Upper cheekteeth with elongate or oval protocones broadly connected to protoselene (very rarely isolated in early wear), generally simple fossettes with plications absent or limited to early wear-stages, and single, unbranched pli caballins that fade with wear and are typically much stronger on premolars than molars. Lower cheekteeth typically with relatively non-persistent lingual flexids, shallow premolar ectoflexids, and lacking plications (except for pli entoflexids in early wear-stages) and pli caballinids. Deciduous lower premolars lack ectostylids.
Chronologic and Geographic Distribution.— Early late Barstovian through late early Hemphillian (about 14.5 to 6.0 ma), although most abundant and diverse during the Clarendonian. Widespread in North America east of the Rocky Mountains, ranging from Florida to Texas, north through the Great Plains to South Dakota, and south to Honduras.
Discussion.— The genus *Calippus* is here recognized by its unique, highly derived muzzle morphology (Figs. 3 and 4), which along with other cranial and dental characters distinguish it from all other equid genera. The failure of prior studies (e.g. Stirton 1940) to recognize this can be attributed to the rarity of complete specimens, i.e. associated premaxillae and maxillae or mandibles with symphyses. Only the Frick Collection contains a sufficient
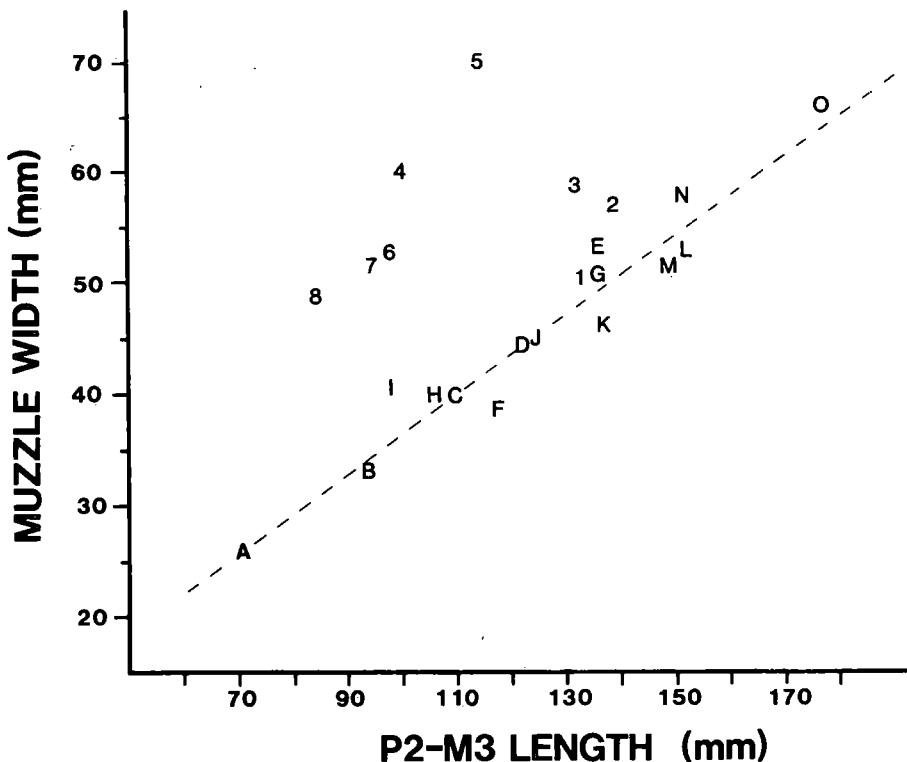
Figure 3. Relationship between upper toothrow length and muzzle width for various equid species. A-O are taxa judged to have normal (i.e. unexpanded) muzzles and are plotted to indicate baseline values for muzzle width relative to body size (here represented by toothrow length). A, Mesohippus barbouri; B, "Merychippus" primus; C, Merychippus insignis; D, Cormohipparion sphenodus; E, Cormohipparion occidentale; F, "Merychippus" republicanus; G, Neohipparion affine; H, Pseudhipparion retrusum; I, Pseudhipparion gratum; J, "Merychippus" isonesus; K, Pliohippus mirabilis; L, Pliohippus pernix; M, Dinohippus leidyanus; N, D. interpolatus; O. Equus grevyi. The least squares regression line fitted to these 15 points has an equation of y = 0.362x + 0.457, with a correlation coefficient of 0.967. The remaining eight points (1-8) are of taxa with relatively expanded muzzles: 1, Protohippus perditus; 2, Protohippus supremus; 3, Calippus (Grammohippus) martini; 4, C. (G.) maccartyi (muzzle width estimated from mandibular symphysis); 5, C. (G.) sp. from the Hemphillian of the Great Plains; 6, C. (Calippus) proplacidus; 7, C. (C.) placidus; and 8, C. (C.) regulus. Of these, the most primitive is P. perditus whose muzzle width falls within the observed range of normal equids. However, it is relatively expanded when compared to contemporary equines such as Pliohippus mirabilis (K). All points are mean values for each species, taken on mature (but not extremely heavily worn) individuals, and when available on equal numbers of each sex. Muzzle width measured across I3s, toothrow length from P2 to M3.
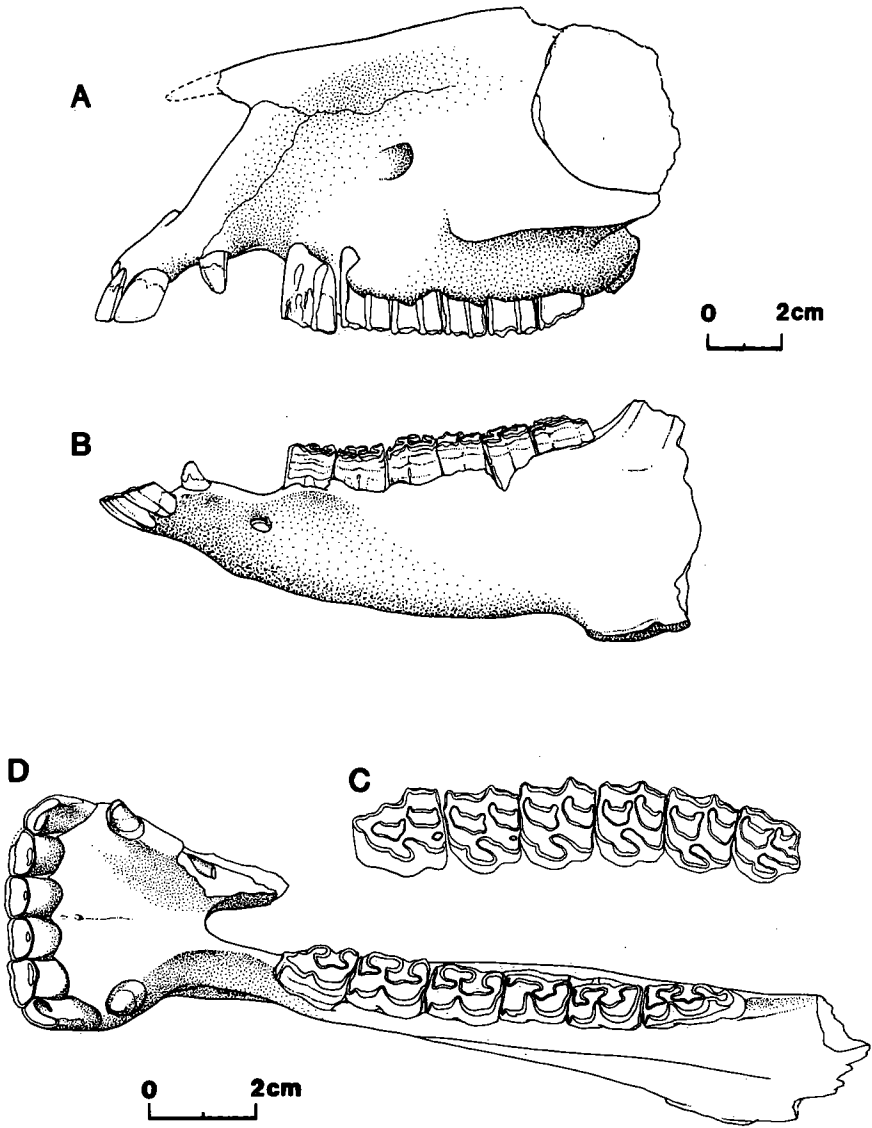
Figure 4. Calippus (Calippus) regulus from MacAdams Quarry, Donley County, Texas (Clarendon Fauna). A. F:AM 60430, left lateral view of skull. B. F:AM 114176, lateral view of left mandible and symphysis. C. F:AM 60430, occlusal view of left P2-M3. D. F:AM 114176, occlusal view of right and left i1-i3, c and left p2-m3. These specimens illustrate such typical Calippus features as shallow nasal notch; lack of malar fossa; shallow, unpocketed DPOF; simple fossettes; connected oval to elongated protocones; shallow premolar ectoflexids; very short post-canine diastema; large canines on males; broad muzzle; and linearly-arranged incisors.

number of relatively complete crania of most of the species of *Calippus* to allow recognition of the systematic importance of the anterior skull region.

Two monophyletic species-groups of *Calippus* are recognized: the smaller-sized taxa that traditionally comprise the genus, and a number of medium-sized species classically referred to *Astrohippus* or *Pliohippus*. Both groups lack malar fossae, a derived feature present in *Pliohippus* (MacFadden 1984b:275-277) and *Astrohippus* (Matthew and Stirton 1930:361; MacFadden 1984b:277). These two genera have normal (i.e. primitive) equid diastema lengths, incisor morphologies, and muzzle widths relative to their body size (Fig. 3). The two species-groups of *Calippus* are here formally recognized as subgenera, *C.* (*Calippus*) and *C.* (*Grammohippus*) n. subgen.

Quinn (1955) divided the Equinae into four tribes, Hipparionini, Equini, Calippini and Protohippini. Cladistic analysis (see phylogenetic section) suggests that only two of these tribes should be recognized, the Hipparionini (includes hipparionine genera listed above plus some merychippine-grade species of uncertain generic affiliation) and the Equini. The Equini is here considered to consist of all of the taxa originally included by Quinn (1955; *Equus* sensu lato and *Dinohippus*), as well as all genera he placed in the tribes Protohippini and Calippini (except *Pseudhipparion* = *Griphippus* which is a hipparionine, and *Hippodon* which is a *nomen dubium*). As demonstrated below, *Calippus* and *Protohippus* form a strictly monophyletic clade of hypsodont equids, here designated to constitute the Subtribe Protohippina Quinn new rank.

SUBGENUS *Calippus* (*Calippus*) MATTHEW AND STIRTON, 1930

Type Species.— *C.* (*C.*) *placidus* (Leidy), 1858.

Included Species.— *C.* (*C.*) *proplacidus* (Osborn), 1918 n. comb.; *C.* (*C.*) *regulus* Johnston, 1937; and *C.* (*C.*) *elachistus* n. sp.

Revised Subgeneric Diagnosis.— Relatively very small, hypsodont equids with UTRL and ltrl less than 105 mm. Elongate, elliptical protocones that connect immediately to the protoselene at onset of wear. Pli caballin single, relatively small or absent; absent or only present in very early wear-stages of molars; usually present through middle wear-stages of premolars. Upper cheekteeth relatively straight; styles reduced; shallow hypoconal groove closed by a hypostylar fold in early or middle wear-stages, lost or persists as an isolated fossette in advanced wear-stages. Protostylids present on p3-m3 and dp3-dp4. Muzzle width relatively very broad, exceeds 50% of UTRL.

Chronologic and Geographic Distribution.— Early late Barstovian to middle Clarendonian of Great Plains and Texas Gulf Coastal Plain; late Barstovian through early Hemphillian of Florida.

Discussion.— *C.* (*Calippus*) includes all species traditionally placed in *Calippus* (e.g. Stirton 1940; Quinn 1955; Webb 1969). They are among the smallest of advanced, hypsodont equids; being matched in size only by some species of *Pseudhipparion* (Webb and Hulbert 1986) and smaller individuals of *Nannippus minor*. The phylogeny of this group is therefore of interest, as decreases in body size are rare among equid lineages (Romer 1949; MacFadden 1987). In addition to smaller size, members of *C.* (*Calippus*) generally differ from those of *C.* (*Grammohippus*) n. subgen. in their straighter upper cheekteeth, simpler fossettes, weaker pli caballins, and well developed protostylids on lower cheekteeth (except p2).

Calippus (*Calippus*) *proplacidus* (OSBORN), 1918 **new combination**
Figs. 5, 6A-6B; Tables 1-3

Protohippus proplacidus OSBORN 1918:139-141 (in part).
Merychippus francisi HAY 1924:9; STIRTON 1940:181; HESSE 1943:168-169, 171.
Merychippus proplacidus (Osborn), STIRTON 1940:182; GALBREATH 1953:105.
Calippus francisi (Hay), QUINN 1955:27-30; WEBB 1969:82; FORSTEN 1975:41-44.

Type Specimen.— AMNH 9115B, palate with L DP1-DP2 and R DP1-DP4, M1 (unerupted) and assoc. L and R rami with dp2-dp4 (Osborn 1918, fig. 112).

Type Locality and Horizon.— Sand Canyon Fauna, Logan Co., Colorado. Ogallala Group (late Barstovian, about 12 to 13 ma).

Revised Distribution.— Late Barstovian of northeastern Colorado, Nebraska, and the Gulf Coastal Plain of Texas and Florida.

Referred Specimens.— Sand Canyon Fauna, Logan Co., Colorado: AMNH 9038, dp3 (one of three paratypes listed by Osborn 1918:140).

Devils Gulch Horse Quarry, Brown Co., NE (Skinner and Johnson 1984:282): F:AM 60443, 60439 2 skulls; 60438 assoc. skull and mandible; 60442, 60444, 60445, 60446 4 maxillae; 114088 assoc. R and L mandibles with deciduous dentition.

Cold Spring Fauna. Noble Farm Local Fauna, Grimes Co., TX: TAMU 3013 R DP34; 3014-3015 2 L P34; 2390 (holotype, *C. francisi*), 3016-3017 3 L
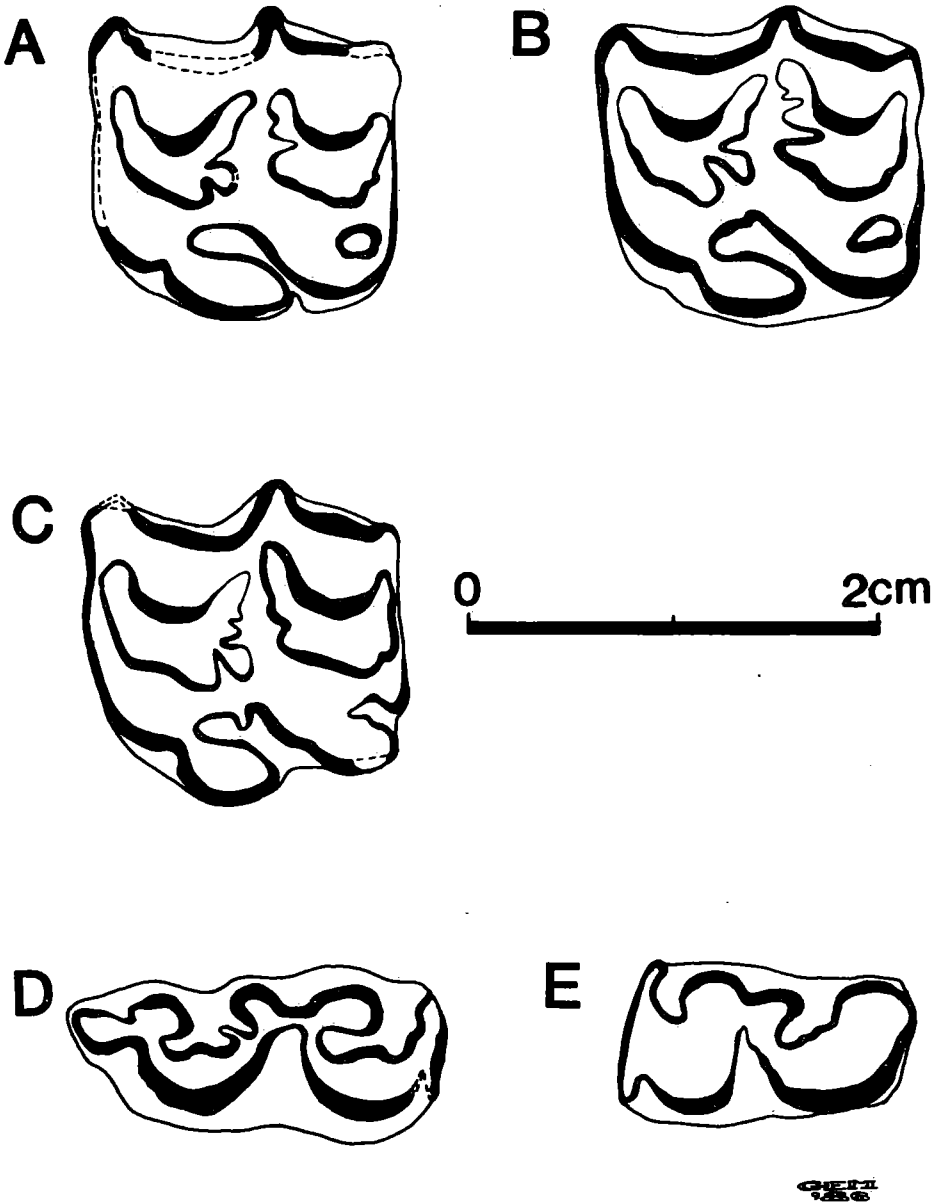
Figure 5. Occlusal views of cheekteeth of C. (Calippus) proplacidus from the Cold Spring Fauna, Texas (late Barstovian). A-B. Noble Farm site, Grimes County. A. TAMU 2390, L M12, holotype of C. francisi (Hay). B. TAMU 3016, L M12. C-E. Cold Spring local fauna, San Jacinto County. C. TMM 31219-309, L P34. D. TMM 31219-95, R m12. E. TMM 31219-302, L m12.

M12; 3018 L M3. Cold Spring Local Fauna, San Jacinto Co., TX: TMM 31219-143, -165 2 R P2; -307, -308 2 R P34; -309-313 5 L P34; -25, -314-318 6 R M12; -53, -67, -91, -319-323 8 L M12; -324, -325 2 L M3; -286 R mandible with m1-m3; -240 L mandible with p4-m3; -10 L mandible with p3,dp4,m1; -110 assoc. R m2-m3; TAMU 3005 R dp2; TMM 31219-290, -291 2 R p2; -283, -292-294 4 L p2; -202, -296 2 R p34; -52, -295, TAMU 3004 3 L p34; TMM 31219-11, -63, -95, -297-299 6 R m12; -122, -162, -300-302 5 L m12; -114, -196, -305, -306 4 R m3; -106, -303, -304 3 L m3. Sam Houston Local Fauna, San Jacinto Co., TX: TMM 31191-12, -29 2 L M12. Goodrich Local Fauna, Polk Co., TX: TMM 31183-63 and -49 assoc. palate with R and L DP1-M3 and R mandible with p2-m3. Chapel Hill Site, Washington Co., TX: TMM 31272-35 R M12.

Lower Agricola Fauna. Red Zone, Phosphoria Mine, Polk Co., FL: UF 28442, 28443, 28467, 28469-28471, 28474 2 deciduous and 5 permanent upper cheekteeth; UF 28452 L m12. TRO locality F7201, Kingsford Mine, Polk Co., FL: UF 55938 L P34.

Ashville Local Fauna, Jefferson Co., FL: UF/FGS V-6101, -6125 2 L P34; -6064 R M12; -6117 L M12; -6061 L m12.

Revised Diagnosis.— Small equid with toothrow lengths of about 95 to 102 mm and unworn molar crown heights about 40 mm. Larger than *C. regulus* or *C. elachistus*, and with better developed styles and fossette plications. Less hypsodont, shallower linguaflexids, and less elongated metaconids and metastylids than *C. placidus*.

Description.— *Calippus proplacidus* has many distinctive characters that it shares with other members of the subgenus, including relatively small size (Figs. 5, 7, and 8; Tables 1-3), weak pli caballin, simple fossettes, lack of a malar fossa, protostylids on lower cheekteeth, and ectostylids absent on dp2-dp4. The maximum length of the unworn DP1 of AMNH 9115B is 8.0 mm. Three specimens from the Devil's Gulch Horse Quarry have DP1 lengths of 8.1, 8.2 and 9.0 mm (F:AM 60439, 60443 and 60442, respectively), and a Cold Spring specimen (TMM 31183-63) has a DP1 length of 8.8 mm. The lower toothrow length (dp2-dp4) of the holotype is 59.8 mm. F:AM 114088, from the Devil's Gulch Horse Quarry, that is in the same very early wear-stage as AMNH 9115B, has a length of 59.1 mm. Toothrow lengths of juvenile rami of *C. regulus* are smaller; F:AM 114178 and F:AM 60428 from McAdams Quarry, Clarendon Fauna, measure 52.3 and 52.9 mm, and F:AM 60495 and F:AM 60496, from Lucht Quarry, Burge Fauna, 55.9 and 56.1 mm.

The series of skulls from the Devil's Gulch Horse Quarry allows description of the facial morphology of *C. proplacidus* (Hulbert in prep. B). The DPOF is usually large and shallow, with a moderate posterior rim. The fossa blends into the surrounding facial region anteriorly and ventrally. The preorbital bar is relatively narrow. The ventral portion of the face lacks a malar fossa.
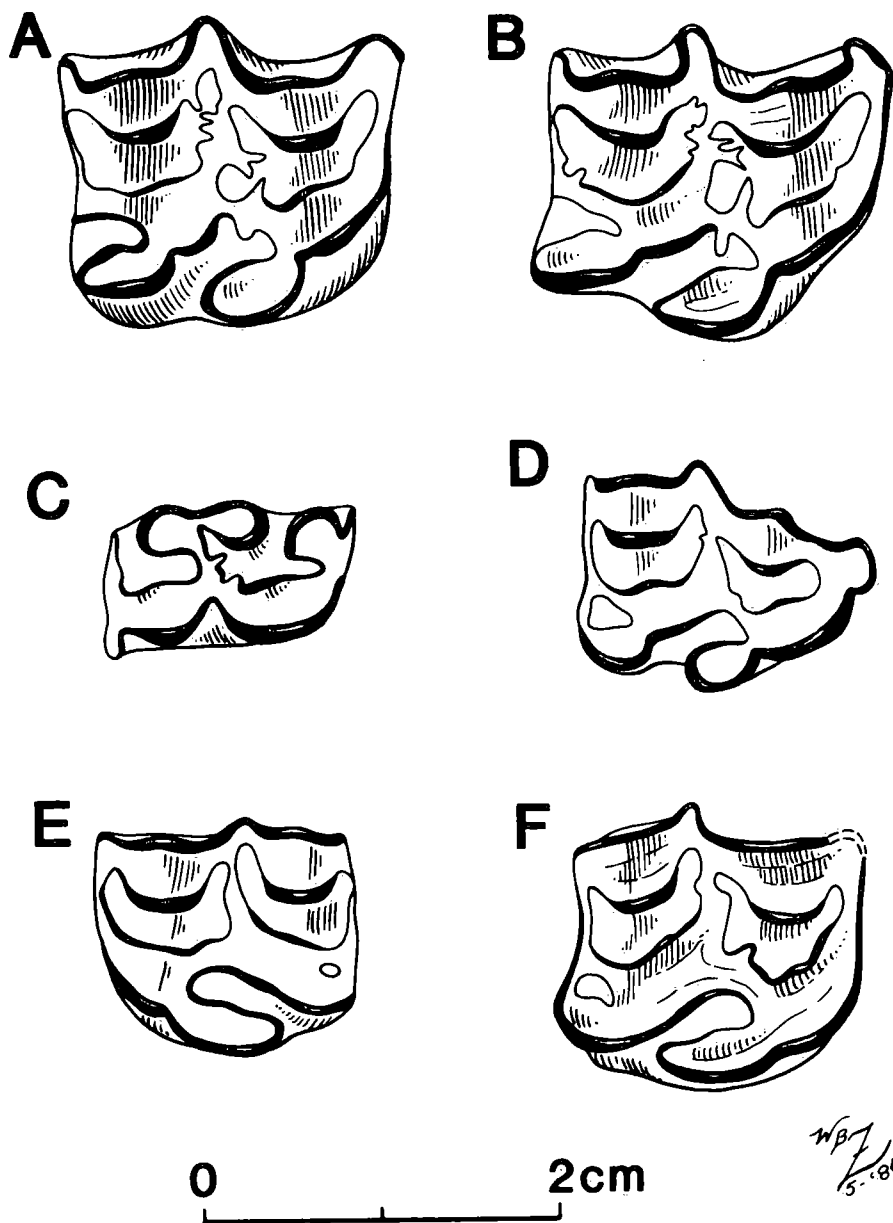
Figure 6. Occlusal views of cheekteeth of C. (Calippus) from lower horizons of the Bone Valley Formation, Polk County, Florida. A-B. C. proplacidus, Red Zone, Phosphoria Mine. A. UF 28469, R P34. B. UF 28442, R M12. C-F. Calippus sp. C. UF 61343, L p34, Kingsford Mine. D. UF 28421, R P2, Red Zone, Phosphoria Mine. E. UF 28680, L M12, Gray Zone, Phosphoria Mine. F. UF 93201, R P34, Gray Zone, Phosphoria Mine.

The cheekteeth of *C. proplacidus* (Tables 1-3; Fig. 5) have been previously well described by Quinn (1955) and Forsten (1975:42-43) as *C. francisi* for the Cold Spring sample. Specimens from Florida (Figs. 6A and 6B) and Nebraska generally conform to their observations. However, Forsten (1975:43) noted that her sample included teeth with up to 14 fossette plications, about twice the maximum I observed. Probably her sample was heterogeneous and included specimens of the similarly sized, but more complex, *Hipparion shirleyi*. Based on F:AM 60442, TMM 31183-63 and 31183-91, unworn or slightly worn MSCHs of *C. proplacidus* are about 29 mm for P2 and 35 to 40 mm for P3-M2. *C. proplacidus* is significantly much larger in occlusal dimensions than *C. regulus* or *C. elachistus*, but about the same size as *C. placidus* (Figs. 7-8; Tables 1-2). Upper cheekteeth are characterized by relatively strong (for the subgenus) styles, including small metastyles on some individuals (Figs. 5B-5C, 6A-6B). The protocone is usually connected to the protoselene at the onset of wear, although very slightly worn P34s may have isolated protocones with large spurs (e.g. UF 28443, F:AM 60445). The long axis of the protocone is oriented slightly anterolabial-posterolingually. The protocone occasionally connects to the hypocone in well worn molars. As described by Forsten (1975), the hypoconal groove is closed by a hypostylar fold, generally in the upper quarter of the crown, but may remain as an isolated lake until late wear before disappearing (Figs. 5A-5B). A few specimens (e.g. UF 28469) retain the primitive condition of an open hypoconal groove until moderate to late wear-stages. Fossette plications are relatively complex for a *Calippus*, with a single, small pli protoloph (that rapidly disappears with wear) and a somewhat more persistent single pli hypostyle. The internal fossette margins usually have one or two shallow plications that disappear by middle wear-stages.

Lower cheekteeth of *C. proplacidus* (Table 2) generally resemble others of the subgenus. The lingual flexids, especially the linguaflexid, are more poorly developed and less persistent than those of *C. placidus*, but somewhat more advanced than those of *C. regulus* (Figs. 5D-5E; Quinn 1955, plate 4.6). A strong pli entoflexid is observed in early wear-stages. Protostylids appear on the occlusal surface shortly after the onset of wear on the p3-m3.

Discussion.— Osborn (1918) based "*Merychippus*" *proplacidus* on a nearly unworn, associated upper and lower juvenile dentition, and listed it as a member of his Sand Canyon Fauna. Galbreath (1953) and Tedford et al. (in press) have discussed the biostratigraphy of Miocene deposits in northeastern Colorado. Tedford et al. (in press) concluded that the Sand Canyon Fauna is equivalent to both the Vim-Peetz and Kennesaw local faunas of Galbreath (1953), and that it dates from about 13 to 12 ma. They list among its chronologic equivalents local faunas in the Crookston Bridge and Devil's Gulch Members of the Valentine Formation in Nebraska, and the Cold Spring Fauna of southeastern Texas. As noted by Galbreath (1953),

Stirton (1940:182) proposed that *C. proplacidus* was a member of an older fauna in the Pawnee Creek Formation. Referral of morphologic equivalents from the Crookston Bridge Member (Webb 1969:82), Devil's Gulch Member, and the Cold Spring Fauna to *C. proplacidus* would appear to invalidate Stirton's suggestion. Osborn (1918:140) listed three paratypes for "*M.*" *proplacidus*, AMNH 9036, 9037 and 9038, and gave their locality data as "...also probably from Sand Canyon...". Of the three, only AMNH 9038 probably belongs with *C. proplacidus*. It is an unworn dp34 of similar size (apl = 21.6 mm) and morphology as the holotype (e.g. lacks an ectostylid, strong protostylid). AMNH 9036 is a partial associated, heavily worn upper and lower dentition that is referable to *Pseudhipparion*, cf. *P. retrusum*, because
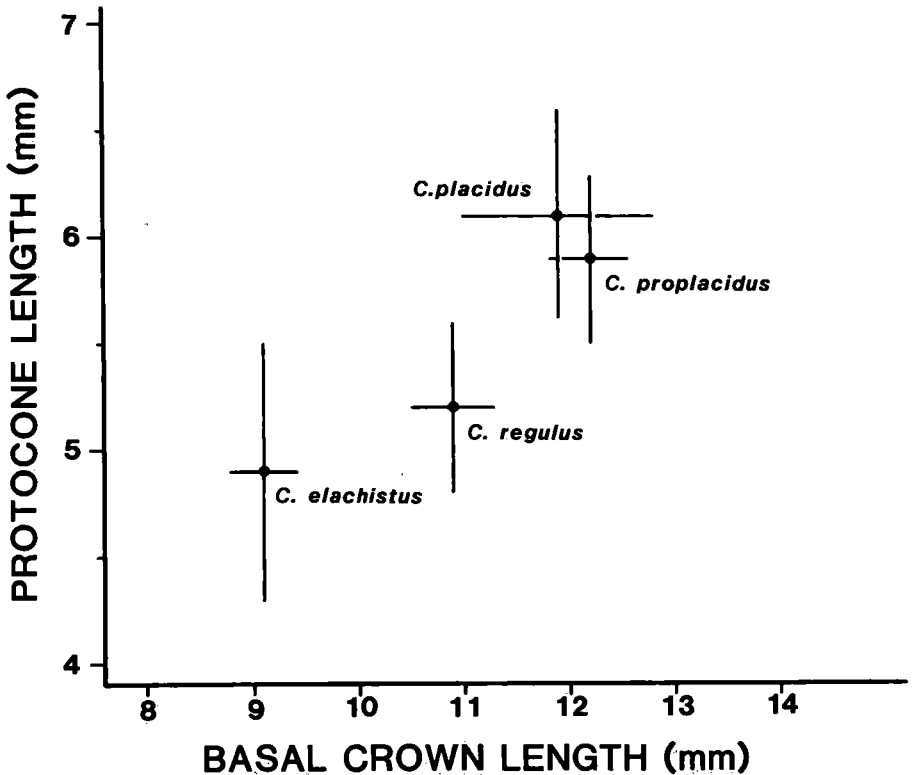
Figure 7. Bivariate plot of basal crown length (BAPL) versus protocone length (PRL) of combined samples of M1s and M2s for four species of C. (Calippus). One standard deviation is plotted on both sides of the mean value for the following populations: C. proplacidus, Cold Spring Fauna; C. placidus, Minnechaduza Fauna; C. regulus, Clarendon Fauna; C. elachistus, Archer Fauna (primarily Love Site). See Tables 1 and 4 for statistics.

despite the late wear-stage the specimen retains traces of pli caballins, the fossettes still bear some plications, and the linguaflexids are still moderately deep. AMNH 9037, an assemblage of seven associated right and left lower cheekteeth (plus incisors and fragments), while referable to *Calippus*, is too small to be included in *C. proplacidus*, but resembles primitive, late Barstovian representatives of *C. regulus* from the Devil's Gulch and Burge Faunas in size and morphology.

Merychippus francisi was described from an isolated upper molar (TAMU 2390, Fig. 5A) by Hay (1924) and subsequently referred to *Calippus* by Quinn (1955). The fauna from the type locality (Noble Farm, Grimes Co., Texas) includes *Gomphotherium* (Hesse 1943); thus its age is no older than late Barstovian (Tedford et al. in press). Other specimens referred and figured by Hay (1924) as *M. francisi*, including a P2 and a m3, probably do not represent the same species as the type. Hesse (1943), Quinn (1955), and Forsten (1975) described additional material of *C. francisi* from other sites in the Cold Spring Fauna, including some relatively complete dentitions. The Cold Spring population is morphologically indistinguishable from Great Plains samples of *C. proplacidus*, but on average smaller (Tables 1 and 2). Until larger samples of more complete material are recovered from the Gulf Coastal Plain, *C. proplacidus* must be regarded as the senior synonym of *C. francisi*. Forsten (1975:41-42) also referred a few isolated teeth from some Upper Burkeville Fauna sites (early late Barstovian) in the Texas Gulf Coastal Plains sequence to *C. proplacidus*. These are more primitive than referred Cold Spring or Devil's Gulch specimens; e.g. a slightly worn M1 (TMM 40070-26) has a MSCH of only 32.4 mm. The older material is inadequate to document specific identity with *C. proplacidus*, but is referable to *C. (Calippus)* and indicates that the two subgenera of *Calippus* had diverged by about 14 ma.

Specimens from Florida referable to *C. proplacidus* (Figs. 6A-6B; Table 3) have been collected *in situ* from the lower part of the Bone Valley Formation in the Phosphoria Mine. There they were found stratigraphically below another terrestrial vertebrate fauna (Waldrop and Webb in prep.). This younger fauna (the Gray Zone) correlates well with the Lapara Creek Fauna of Texas (early Clarendonian), and includes *Pseudhipparion curtivallum* (Webb and Hulbert 1986), *Cormohipparion sphenodus*, *Calippus martini* (see p. 260 below) and *Protohippus supremus*. The older fauna (the Red Zone) includes, besides *C. proplacidus*, *Cormohipparion sphenodus* (more primitive than Gray Zone specimens; Hulbert in press), *Calippus* sp. (see p. 247 below), "*Merychippus*" sp., and *Pliohippus* sp. near *P. mirabilis*. The Red Zone fauna is probably late Barstovian, and thus approximately contemporaneous with other known occurrences of *C. proplacidus*. The dimensions of the Red Zone specimens (Table 3) are similar to, or slightly smaller than, those from the Cold Spring Fauna, but are otherwise indistinguishable. A few isolated teeth
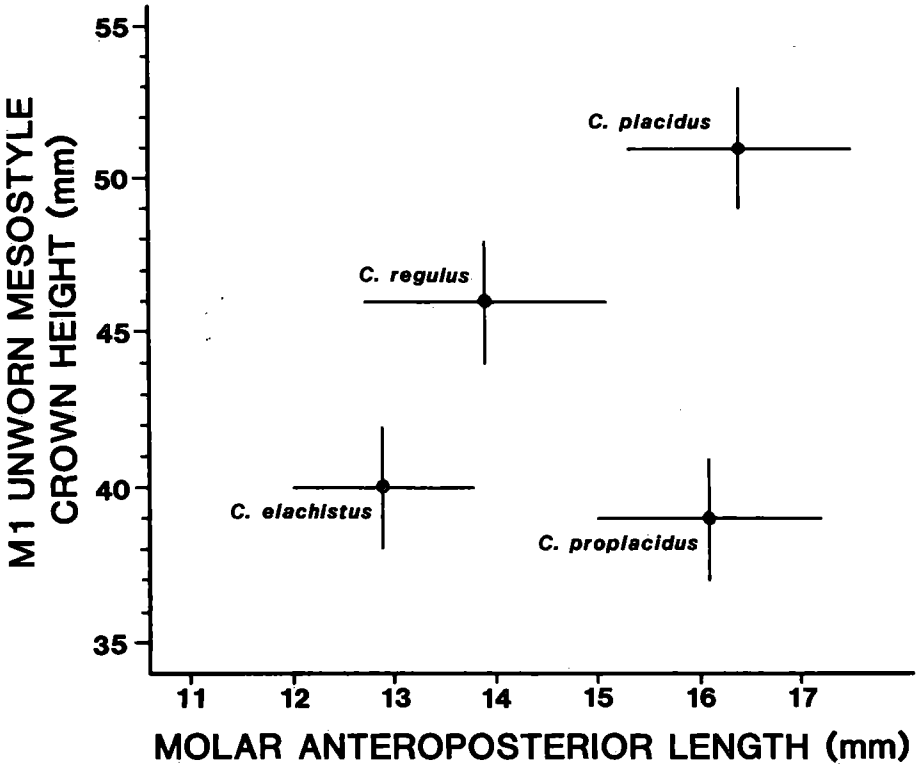
Figure 8. Bivariate plot of the occlusal anteroposterior length (APL) of M1s and M2s versus the estimated unworn molar crown height for the same four populations as in Figure 6. One standard deviation is plotted to the right and left of the mean for APL, while the unworn crown height is plotted plus and minus 2 mm to estimate the observed range of variation of this character.

from the Ashville local fauna (Olsen 1964) are also referable to *C. proplacidus*. Although poorly preserved, they appear to have better developed styles and are larger than *C. regulus*. Tedford and Hunter (1984) date the Ashville local fauna at about 12.5 to 13 ma, and regard it as chronologically equivalent to portions of the Cold Spring Fauna.

Calippus (Calippus) placidus (LEIDY), 1869
Fig. 9; Tables 1-2

Protohippus placidus LEIDY 1869:277-279 (in part); GIDLEY 1906:140-142
      (in part); GIDLEY 1907:887 (in part); OSBORN 1918:133-136.
Protohippus (Calippus) placidus Leidy, MATTHEW and STIRTON 1930:354.
Calippus placidus (Leidy), STIRTON 1940:188; QUINN 1955:39-40; WEBB
      1969:79-82 (in part).
Calippus optimus QUINN 1955:35-38.
Astrohippus curtivallis QUINN 1955:40-42 (in part).
Pliohippus (Astrohippus) martini (Hesse), GREEN 1956:161 (in part).
Calippus anatinus Quinn, WEBB 1969:82 (in part).

  Lectotype Specimen.— USNM 621, L P2 (Osborn 1918, fig. 106).
Selected from type series by Gidley (1907).
  Type Locality and Horizon.— Collected from deposits along "the
Niobrara River" (Leidy 1869:277). Presumably Minnechaduza Fauna (Ash
Hollow Formation) of northern Nebraska (see Webb 1969 and below).
  Revised Distribution.— Clarendonian (about 11.5 to 9.5 ma) of
northern and southern Great Plains, and Texas Gulf Coastal Plain.
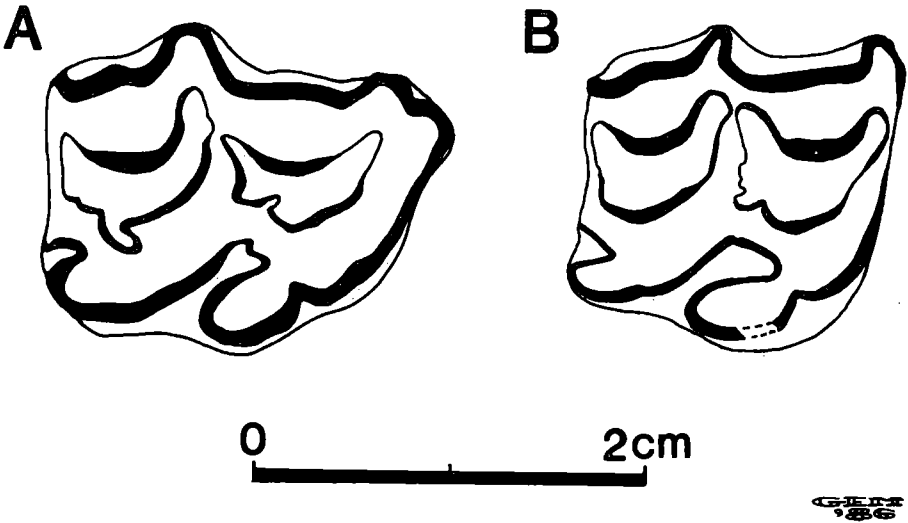
Figure 9. Occlusal views of upper cheekteeth of C. (Calippus) placidus from the Lapara Creek Fauna, Bee County, Texas (early Clarendonian). A. TMM 31081-75, R P2, Farish Ranch Site. B. TMM 31132-617, R M12, Bridge Estate Site.

Referred Gulf Coastal Plain Specimens.— Lapara Creek Fauna. Buckner Ranch, Bee Co., TX: TMM 30896-528, -530 assoc. palate with R and L P2-M3 and R mandible with p3-m3 (type, *C. optimus* Quinn); -200 assoc. R P4-M2; -187 DP2-M1; -479 R mandible with dp2-m1; -419 assoc. R DP2-DP4. George West Site, Live Oak Co., TX: TMM 30936-160 L P34; -353 L P34; -80 R P34. Bridge Estate Site, Bee Co., TX: TMM 31132-105 assoc. L P3-M2; -617 R M12. Farish Ranch Site, Bee Co., TX: TMM 31081-75 R P2; -1375 R M12; -1139 R M3. (Hulbert in prep. B documents relatively complete material of *C. placidus* from the northern and southern Great Plains.)

Revised Diagnosis.— Small equid with toothrow lengths of about 95 to 105 mm; unworn molar crown heights about 51 mm. DPOF long, oval and relatively deep (for a *Calippus*). Higher-crowned teeth than *C. proplacidus*. Larger than *C. regulus* and *C. elachistus*, with more complex fossettes, deeper linguaflexids, and a larger, moderate-sized DP1.

Description.— As described by Hulbert (in prep. B), *C. placidus* lacks a true malar fossa, as do all members of the genus, although a shallow depression on the malar bone is occasionally observed. Incisor morphology is typical for the genus, I12 and i12 in straight rows across a broad, squared-off muzzle. The width of the muzzle (measured across the I3s) is about 55% of the UTRL (Fig. 3).

Upper cheekteeth of *C. placidus* (Table 1) have, in early wear-stages, relatively large pli caballins on the premolars, but they are absent or small on the molars. Protocones are elongate, and connected to the protoselene (Fig. 9). The hypoconal groove remains open, or is present as an isolated lake through at least two-thirds of the total crown height. Fossette plications are shallow and primarily restricted to the posterior half of the prefossette (one to three) and the anterior half of the postfossette (one or two). Older individuals tend to lack all plications. Unworn MSCH is about 33 mm for P2s, 47 mm for P34s and 51 mm for M12s. Deciduous premolars have elongate, obliquely oriented protocones broadly connected to protoselene; open hypoconal grooves until late wear; simple fossettes; and small or absent pli caballins. The anterostyle of the DP2 is not large and is broadly connected to the rest of the tooth.

Lower cheekteeth of *C. placidus* (Table 2) show notable advancement from the primitive *Calippus*-grade, with relatively elongated metaconids and metastylids, increased depth and persistence of the lingual flexids, some flattening of the labial borders, and a minor reduction in depth of the ectoflexid in slightly worn molars (Quinn 1955, plate 6.1). No enamel plications except the protostylid are present in moderately worn teeth (pli entoflexid having disappeared). Lower deciduous premolars (e.g. TMM 30896-479; Quinn 1955, plate 6.3) also have moderately elongated, well separated metaconids and metastylids, and lack ectostylids.

Discussion.— *Calippus placidus* has had a very tortuous taxonomic history, due in part to an inadequate lectotype and no knowledge as to the stratigraphic horizon of the type series. Moderate to heavily worn teeth of *C. placidus* are not easily differentiated from equally worn specimens of *Pseudhipparion gratum* (Cope 1892; Quinn 1955; Webb 1969; Webb and Hulbert 1986), a similarly sized equid with which *C. placidus* coexisted in the Clarendonian of Nebraska and South Dakota. Leidy's (1869) type series of ten isolated teeth includes specimens referable to both taxa (e.g. Leidy 1869, plate 18, figs. 40, 43, and 44 are *C. placidus*; figs. 39, 41, 47, and 48 are *P. gratum*), and others which are indeterminant. Leidy (1869:279) himself recognized that some of the specimens listed above could represent *P. gratum*. Gidley (1906; 1907) attempted to better characterize *C. placidus* by referring specimens to it from Big Springs Canyon, South Dakota, as "neotypes." Unfortunately, as noted by Webb (1969), all of Gidley's material is referable to *Pseudhipparion*, not *Calippus*. When Matthew and Stirton (1930) named *Calippus*, with *Protohippus placidus* as the subgenotypic species, they stated that it originated from the Valentine Formation of Nebraska. Quinn (1955), while correctly recognizing its presence in the Clarendon and Lapara Creek Faunas, also stated that *C. placidus* was from the Valentine. Webb (1969), however, concluded that the type series was not from the Barstovian Valentine Formation, but from the overlying Ash Hollow Formation (his Minnechaduza Fauna), and referred five additional specimens to *C. placidus*. The evidence for this derives from the type series including *P. gratum*, an Ash Hollow Formation taxon, rather than *P. retrusum*, the corresponding Valentine Formation species (Webb 1969; Webb and Hulbert 1986). I agree with Webb (1969) that *C. placidus* occurs in the Cap Rock and the lower part of the Merritt Dam Members of the Ash Hollow Formation of Nebraska (Hulbert in prep. B). There it is found in lithosympatry with *Pseudhipparion gratum*, *Cormohipparion occidentale*, *Neohipparion affine*, *Hipparion tehonense*, *Nannippus* n. sp., *Calippus martini*, *Protohippus supremus*, and *Pliohippus pernix*; a typical, diverse middle Clarendonian equid assemblage. Webb (1969, fig. 20b) also referred specimens from the upper Merritt Dam Member (Xmas-Kat Quarry Zone) to *C. placidus*. These specimens are referable instead to *Pseudhipparion skinneri* (Webb and Hulbert 1986). The subgenus *C. (Calippus)* is apparently absent from the Xmas-Kat Fauna, and all younger faunas of the Great Plains.

Quinn (1955) recognized four small protohippine species in the Lapara Creek Fauna: *C. anatinus*; *C. optimus*; *C.* cf. *placidus*; and *Astrohippus curtivallis*. Webb (1969) later referred all four to a single taxon (*C. anatinus*). Following Forsten (1975), *C. anatinus* is here recognized as a junior synonym of *C. regulus* (see below). She noted that the remaining three taxa are distinctly larger than *C. regulus* and suggested that they were referable to *Pseudhipparion*. Webb and Hulbert (1986) concluded that the holotype of *A.*

curtivallis (TMM 30896-196) is indeed referable to *Pseudhipparion*, and it thus became the type of the Lapara Creek sample of *Pseudhipparion* (i.e. *P. curtivallum*). However, specimens recognized by Quinn (1955) as *C. optimus*, *C.* cf. *placidus* and the figured upper premolars of *A. curtivallis* are not referable to *Pseudhipparion*, but to *C. placidus* (see also Fig. 9). The numerous referred specimens now known from Nebraska indicate that the cheekteeth of *C. placidus* do resemble those of hipparionines in some features (e.g. its expanded metaconid-metastylid complex), thus perpetuating the confusion between it and *Pseudhipparion*. The two can be distinguished by the more rapidly connected protocone, the greater tendency in worn teeth for lost pli caballins and hypoconal grooves, and simpler fossettes in *C. placidus*. Cranially, the two are quite distinct, with *Calippus* having a much better developed DPOF, shorter diastema, and widened, squared-off muzzle.

Calippus (*Calippus*) *regulus* JOHNSTON, 1937
Fig. 4; Tables 4-5

Protohippus proplacidus OSBORN 1918:139-141 (in part).
Calippus sp., HESSE 1936:65.
Calippus regulus JOHNSTON 1937:905-907; STIRTON 1940:188; QUINN
        1955:27; WEBB 1969:81; FORSTEN 1975:44-48.
Calippus anatinus QUINN 1955:30-35; WEBB 1969:82 (in part).

Type Specimen.— WT 878, R maxilla with P2-M3.
Type Locality and Horizon.— Clarendon Fauna, Grant Lease Site, Donley Co., Texas (see Schultz 1977, fig. 6). Ogallala Formation or Group, middle Clarendonian (about 10.5 ma).
Revised Distribution.— Late Barstovian of northern Great Plains; early and middle Clarendonian of southern Great Plains; early Clarendonian of Texas Gulf Coastal Plain.
Referred Gulf Coastal Plain Specimens.— Lapara Creek Fauna. See Forsten (1975:44, 46) for listing of specimens.
Revised Diagnosis.— Very small, hypsodont equid with toothrow lengths generally between 75 and 85 mm and unworn molar crown heights of about 46 mm. Very short, broad rostrum. DPOF long, shallow, unrimmed and runs anteriorly to connect with buccinator fossa. Cheektooth enamel morphology more simple than *C. placidus* or *C. proplacidus*. Metaconid of p2 very reduced or absent. Linguaflexid very shallow, metaconid and metastylid broadly confluent on molars after slight wear.
Discussion.— *Calippus regulus* from the Texas Gulf Coastal Plain was accurately described and profusely illustrated by Quinn (1955) as a new

species, *C. anatinus*. I follow Forsten (1975) in considering *C. anatinus* a junior synonym of *C. regulus*. The differences in size (Fig. 10; Tables 4 and 5) and morphology of the Lapara Creek and Clarendon samples of this tiny horse are inconsequential. The extended descriptions of Lapara Creek specimens of *C. regulus* by Quinn (1955) and Forsten (1975) make further discussion of the material superfluous. Representative cranial and dental specimens from the type Clarendon Fauna are illustrated in Figure 4 for comparative purposes.

Calippus (Calippus) sp.
Figs. 6C-6F; Table 6

Referred Specimens.— Bradley Fauna. Kingsford Mine, Polk Co., FL: UF 61323 R M3; 61324 L M12; 61325, 61343 2 L p34; Nichols Mine (Mobil), Polk Co., FL: UF 23960, 23983, 50756 3 M12; 23979 R P34.

Early Agricola Fauna. Red Zone, Phosphoria Mine, Polk Co., FL: UF 28421 R P2; 28419, 28420 2 L M12; 28422 R M3; 28477 L p34.

Late Agricola Fauna. Gray Zone, Phosphoria Mine, Polk Co., FL: UF 28549 L P2; 28542, 28680 2 L M12; 28540 R M3; 28541 L M3; 28543, 28544 2 L m12. Hookers Prairie Mine, Polk Co., FL: UF 93201 R P34; 98491 L P34; 98492 R M12; 93202 R M3; 98285, 98490 2 L M3; 98286-98287 2 L p34; 98288 L p34; 98289 R m3.

Lower Bone Valley Formation (Bradley or Agricola Fauna). Four Corners Mine, Hillsborough Co., FL: UF 93210 R p2. Palmetto Mine, Polk Co., FL: UF 69656 L p34. Specific mine unknown, Polk Co., FL: UF 68993 L M12; 61505 L p34; 32031 L m3.

Ashville Local Fauna, Jefferson Co., FL: UF/FGS V-60086 R M12; -6087 R M3; -6110 L M12; -6111 L M3.

Discussion.— A limited sample of isolated teeth from the Bradley and Agricola Faunas (Waldrop and Webb in prep; Webb and Hulbert 1986) of the lower Bone Valley Formation, Florida, are clearly referable to *C. (Calippus)*. In enamel morphology they are extremely similar to *C. regulus*, in particular the very simple fossettes, reduced styles, and persistent isolated hypoconal lake in upper cheekteeth (Figs. 6D-6F), and well developed protostylids, large pli entoflexids in early wear-stages, relatively deep ectoflexids, and shallow linguaflexids in lower cheekteeth (Fig. 6C). They differ from *C. regulus* in their smaller size (Table 6; Fig. 10), relatively well developed p2 metaconid (UF 93210), and probably shorter unworn crown heights. Maximum unworn M12 MSCH for these specimens is estimated to have been no more than 40 mm, although the limited number of unworn or slightly worn teeth does not allow this parameter to be accurately predicted.
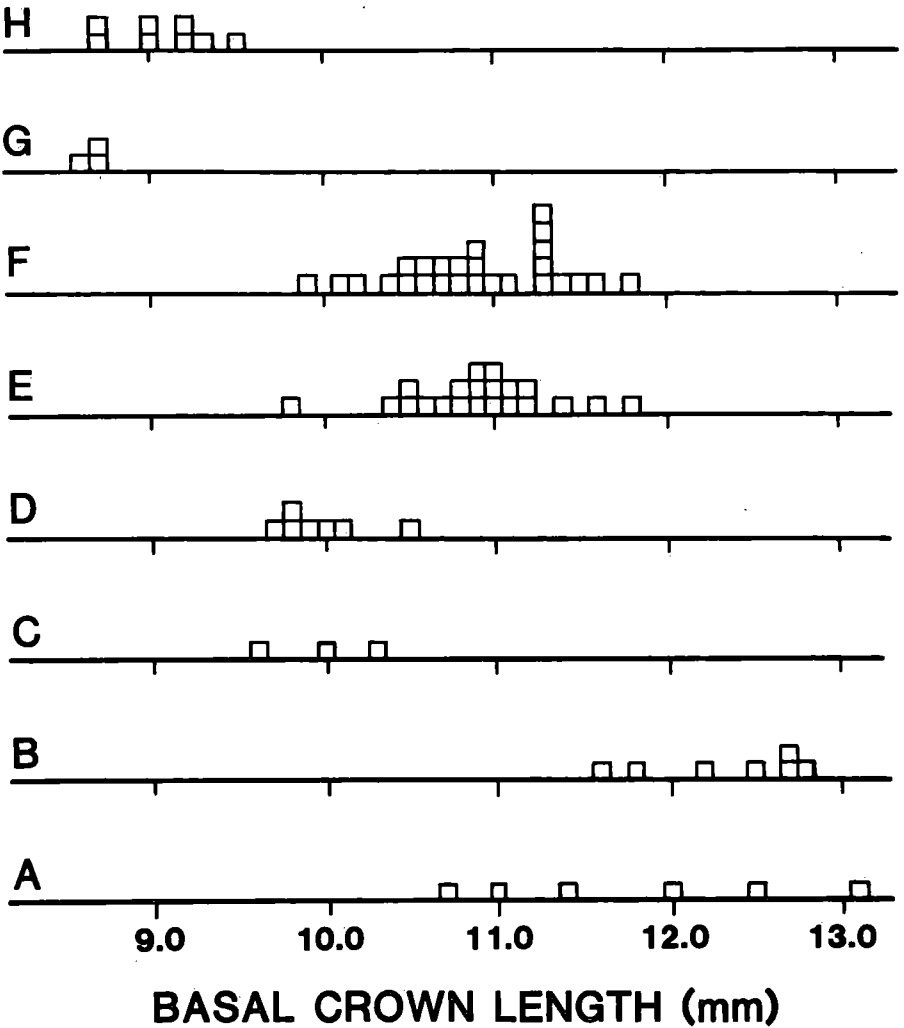
Figure 10. Histograms of basal crown lengths (BAPL) of combined samples of P3s and P4s (A-D), and of M1s and M2s (E-H) for four populations of <u>Calippus</u> (<u>Calippus</u>). A, E. <u>C. regulus</u>, Lapara Creek Fauna, Texas Gulf Coastal Plain. B, F. <u>C. regulus</u>, Clarendon Fauna, Texas Panhandle. C, G. <u>Calippus</u> sp., lower Bone Valley Formation, Central Florida. D, H. <u>C. elachistus</u> n. sp., Love Site, Central Florida. The two Texas populations of <u>C. regulus</u> are of approximately the same size, but are much larger than the samples from Florida. Each square represents one individual.

C. (Calippus) sp. is of similar size as younger samples from Florida (*C. elachistus*, Table 6 and Fig. 10), but differs considerably from them in enamel morphology.

C. (Calippus) sp. occurs at several distinct biostratigraphic zones (formally described by Waldrop and Webb in prep.) in the Bone Valley Formation. Further sampling may indicate the presence of more than one species and permit formal description. The oldest zone, the Bradley Fauna, is best known from limited exposures in the Nichols and Kingsford Mines and is late, but not latest, Barstovian (Waldrop and Webb in prep.; Webb and Crissinger 1983). Equids from this fauna include *C. (Calippus)* sp., *Pliohippus* cf. *mirabilis*, *Protohippus perditus* (see below), *"Merychippus"* sp. or spp., and *Pseudhipparion* sp. (Webb and Hulbert 1986). *C. (Calippus)* sp. is also found in both the Red and Gray Zones of Phosphoria Mine (early and late Agricola Fauna), latest Barstovian and early Clarendonian, respectively (see discussion of *C. proplacidus*). A fourth population is represented by several teeth from the late Barstovian Ashville l.f. of northern Florida (Olsen 1964).

Calippus (Calippus) elachistus **new species**
Figs. 11-13; Tables 4-5, 7

Calippus cf. *regulus*, WEBB et al. 1981:527.

Type Specimens.— Holotype, UF 32139, R mandibular fragment with m2-m3. Paratypes, UF 53431 R P2; 53448 L M2; 53585 R p34. All collected by FSM personnel between 1974 and 1981.

Type Locality and Horizon.— Love Site (NW 1/4, SW 1/4, NW 1/4 Sec. 9, T11S, R18E, Archer Quad.), 1.5 km N of Archer, Alachua Co., Florida (Webb et al. 1981). Fluvial sediments of the Alachua Formation, very late Clarendonian or about 9.0 ma.

Distribution.— Very late Clarendonian through early Hemphillian (about 6.2 to 9.0 ma) of central Florida.

Etymology.— *elachistos*, Greek for smallest or least.

Referred Specimens.— Love Site, Alachua Co., FL: UF 53618-53620 3 R DP2; 68839 R DP34; 96323 L DP34; 53430 R P2; 53432-53434 3 L P2; 53435-53436, 53578, 53580 4 R P34; 53437-53441, 53598 6 L P34; 53576-53577, 53579 3 R M12; 53442-53445, 53447, 53599 6 L M12; 53450, 53616-53617, 53575 4 L M3; 53601 assoc. L m1-m2; 59161, 92951-92952 3 R dp34; 92953 L dp34; 53581-53584, 96979 5 R p2; 64527, 96565 2 L p2; 53586-53591, 68951-68952 8 R p34; 53593-53597, 59163-59164, 68954-68955 9 L p34; 53603-53610, 59166, 68953, 68956 12 R m12; 59172, 68958 2 L m12; 53611-53614 4 R m3.

Haile 19A, Alachua Co., FL: UF 47320 R M12; 47325 L m3.

McGehee Farm, Alachua Co., FL: UF 45640 R M12; 45641 L M3; 18471 R p34; 17313 R m12; 7238 R m3.

Nichols Mine, Polk Co., FL: UF 92999 L M3; 23957 L m12.

Manatee County Dam Site, Manatee Co., FL: UF 11932 L M3; 95366 L m12.

Diagnosis.— Occlusal dimensions of cheekteeth much smaller than any other species of *Calippus* except *C. regulus*; slightly smaller occlusal dimensions in early to middle wear-stages and significantly smaller basal crown lengths than *C. regulus*. Protostylid reduced on p3-m3. Metaflexid and linguaflexid better developed and more persistent with wear than in *C. regulus*. Metastylid and hypoconulid not extremely elongated in early wear-stages on m1-m3. Ectoflexid reduced in depth on permanent and deciduous cheekteeth, generally not penetrating isthmus, except in heavily worn molars. Pli entoflexid absent on molars. Fossettes simple, without plications except in earliest wear-stages. Styles weak, but slightly stronger than those of *C. regulus*. Pli caballin absent or vestigial. Hypoconal groove closed with onset of wear, persists as a lake until middle wear-stages on premolars; disappears in very early wear-stages of molars.
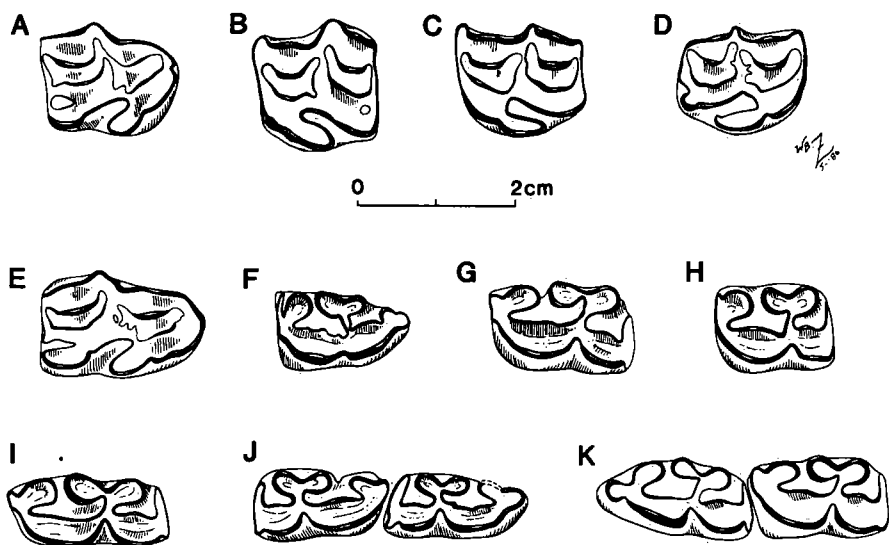
Figure 11. Occlusal views of upper and lower cheekteeth of C̲. (Calippus) elachistus n. sp. from the Love Site, Alachua County, Florida (latest Clarendonian). A. UF 53431, R P2 (paratype). B. UF 53436, L P34. C. UF 53448, L M12 (paratype). D. UF 53576, R M12. E. UF 53620, R DP2. F. UF 53584, R p2. G. UF 68951, R p34. H. UF 53585, R p34 (paratype). I. UF 92952, R dp34. J. UF 53601 probably associated L m1 and m2. K. UF 32139, R m2-m3 (holotype).

Description.— The known sample of *Calippus elachistus* is almost exclusively isolated cheekteeth, and its facial and incisor morphology are therefore unknown. The holotype, UF 32139, consists of a mandibular fragment with a moderately worn m2 and slightly worn m3 (Figs. 11K, 12; Table 7). No distinctive portion of the ramus, e.g. its ventral border, remains with the specimen. As lower dental morphology changes so drastically with wear in *Calippus*, the holotype is best compared with similarly worn specimens of other species (e.g. Fig. 4D, *C. regulus*). In UF 32139, the ectoflexid does not penetrate the isthmus on either the m2 or m3 (as it does in F:AM 114176). The rounded metastylids are well separated from the metaconids, however, by relatively deep, V-shaped linguaflexids and anterolingual projections of the entoflexid (Fig. 11K). The labial borders of the metaflexid and entoflexid are relatively flat, with little or no tendency to be curved. The protostylids are small, and do not extend labially beyond the protoconid.

Based on the topotypic sample, the upper cheekteeth of *C. elachistus* most closely resemble those of *C. regulus* with their small size (Figs. 7-8; Table 4) and simple fossettes. Upper premolars have moderately well developed
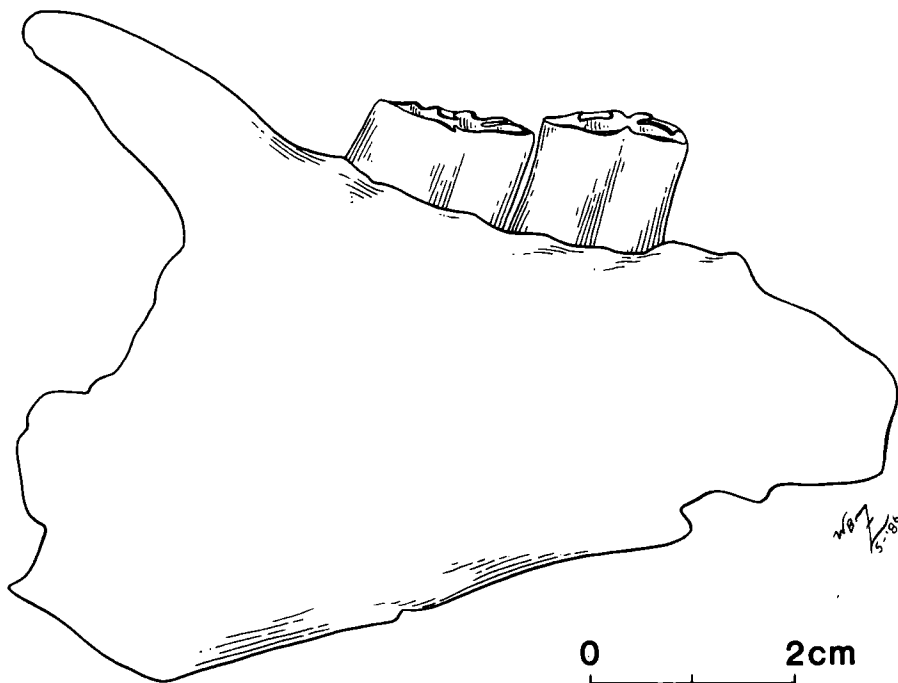
Figure 12. Lateral view of UF 32139, right mandibular fragment. Holotype of C. (Calippus) elachistus n. sp.; from the Love Site, Alachua County, Florida. See Fig. 11K for occlusal view of m2-m3.

parastyles and mesostyles, and some have very slight metastyles. In this, they more closely resemble *C. placidus* than *C. regulus*. A weak pli caballin may be present, but only in early wear-stages. The protocone varies in shape from oval to very elongated (Figs. 11A-11D, 13A), and is broadly connected to the protoselene. The preprotoconal groove is shallow or absent. The hypoconal groove is open in earliest wear-stages, usually becomes an isolated lake rather quickly, and disappears during late wear-stages. For example, UF 53441 retains an open hypoconal groove with an MSCH of about 29 mm, the heavily worn UF 53435 (MSCH = 17.9 mm) still retains its hypoconal lake, although UF 53439 (MSCH = 19.0 mm) does not. Neither a pli protoloph nor pli hypostyle are observed in even the least worn P34. In early wear-stages, the posterior half of the prefossette may have one to three shallow plications, and a moderately developed prefossette loop can be present. The anterior half of the postfossette bears at most a single, shallow plication. With moderate wear (i.e. MSCH of 25 mm or less), all plications are obliterated. In the P2, the anterostyle is generally not well separated from the ectoloph, and is not well developed. Three DP2s from the Love Site are referred to *C. elachistus* rather than the similarly sized *Pseudhipparion skinneri* (Webb and Hulbert 1986). These DP2s have poorly developed anterostyles (Fig. 11E), while a DP2 referred to *P. skinneri* (UF 90263) has a well developed anterostyle. The DP2 fossette borders are more complexly plicated than their permanent counterparts (Fig. 11E), and the hypoconal groove persists as a lake until late wear. All three DP2s have appression facets for a DP1, as does UF 53433, a P2.

Upper molars are slightly smaller than the premolars, with more delicate styles, pli caballin absent, simpler fossettes, and more elongate protocone. The hypoconal groove is generally very shallow and disappears with relatively little wear (Fig. 11C). Occasionally, as in UF 53443, the hypoconal groove is as deep as in premolars. In very early wear (e.g. UF 53576 or UF 53577), the internal fossette margins may bear several very shallow plications; they are shallower than those on comparably worn premolars and are lost with wear more rapidly. Unworn or slightly worn MSCH for the M12 is about 40 mm.

The p2 is represented by nine specimens from the Love Site. Their metaconids are stronger than in *C. regulus* (contrast Fig. 11F with 4D), although it varies from a small angular structure projecting anteriorly from the metastylid, to being rounded and almost equal in size to the metastylid. The ectoflexid is very shallow and does not penetrate the isthmus (Fig. 11F). The hypoconulid is well separated from the entoconid by a deep, U-shaped flexid until middle wear. The other lingual flexids are deep and well developed. In early wear a small pli entoflexid and pli caballinid may be present. The p34 are well represented in the topotypic sample. The metastylid is rounded to slightly elongate-oval, subequal in size to the rounded metaconid (Figs. 11G-11H). The two are well separated throughout
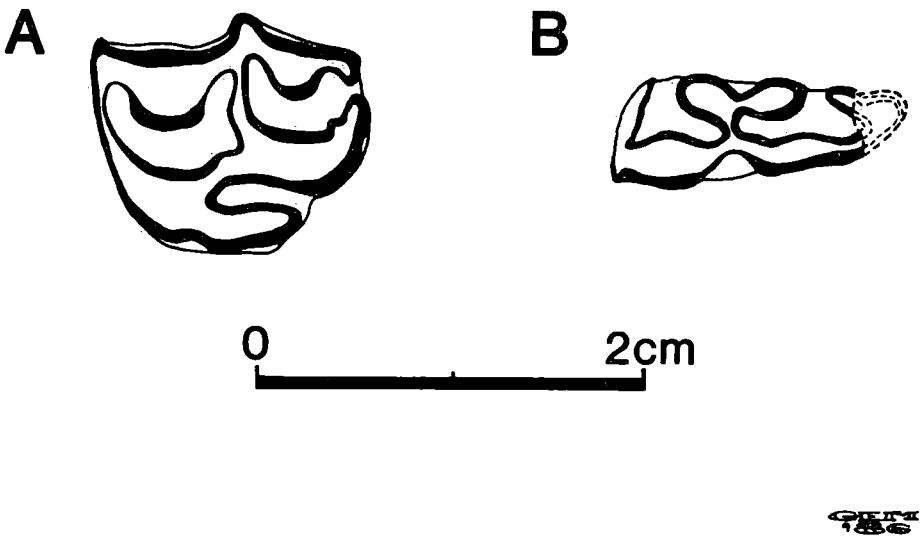
Figure 13. Occlusal views of cheekteeth of C. (Calippus) elachistus n. sp. from the Manatee County Dam Site, Florida (late early Hemphillian, see Webb and Tessman, 1968). A. UF 11932, L M3, sectioned about 10 mm above unworn occlusal surface. B. UF 95366, partial L m12. These are the youngest known specimens of the subgenus C. (Calippus), about 6 to 6.5 ma.

most of the crown by the deep lingual flexids. The linguaflexid is broadly U-shaped, and much better developed than in *C. regulus*. The ectoflexid is shallow and never penetrates the isthmus. The protostylid is small, much less prominent than in other members of the subgenus. Pli entoflexids are not observed, but the sample does not include any very slightly worn p34s. Several dp34s are referred to *C. elachistus*. Compared to those of *C. regulus*, they have shallower ectoflexids that just barely penetrate the isthmus, and shallower, broader V-shaped linguaflexids. The entoflexid is especially elongated, but unplicated (Fig. 11I). The protostylids are reduced, but stronger than in the p34. Lower molars are especially notable for their reduced ectoflexids, which only occasionally penetrate the isthmus, and persistent lingual flexids (Figs. 11J-11K, 13B). The metaflexid, which is rapidly reduced with wear in *C. regulus* (e.g. the m1 in Fig. 4D, note that F:AM 114176 is a relatively young adult), is more persistent in *C. elachistus* and not markedly reduced in depth until crown height is less than 15 mm. The linguaflexid is also much better developed than in the molars of *C. regulus* and persists throughout the entire crown. The metaconid and

metastylid are of approximately the same size and are oval. The metastylid and hypoconulid are not extremely elongated in very early wear, as is characteristic of *C. regulus* and *C. placidus*. The protostylid is present, but reduced or vestigial. Unworn or slightly worn mcchs are about 30 mm for the p2 (UF 96979), 35 mm for p34, and 40 mm for m12 (UF 59166).

Discussion.— *Calippus elachistus* is known from five localities in central Florida. The majority of known specimens are from the Love Site, the type locality, and are latest Clarendonian (Webb et al. 1981). Two nearby and slightly younger (early Hemphillian) localities also contain specimens referable to *C. elachistus*, McGehee Farm and Haile 19A. A Hemphillian age for these two sites is based on the presence of megalonychid sloths (Hirschfeld and Webb 1968), and more advanced canids than those of the Love Site; however, all three share many faunal elements, including equids, and are very close in age. Similar-aged taxa are rarely recovered from the Bone Valley Formation, most terrestrial specimens are either older or younger. However, a well worn lower molar from the Bone Valley, UF 23957, is definitely referable to *C. elachistus* rather than the older sample described above as *C. (Calippus)* sp. Especially notable in this specimen are its persistent entoflexid and linguaflexid and the relatively shallow ectoflexid, all derived character states found in *C. elachistus*.

Calippus elachistus is the youngest known member of the subgenus *C. (Calippus)*. Although based on only a few specimens, *C. elachistus* apparently persisted into the late early Hemphillian (about 6 to 6.5 ma) of Florida (Fig. 13) without significant morphological change. The late early Hemphillian age of the Manatee County Dam Site was determined by vertebrate biostratigraphic correlation and interpretation of its low elevation relative to known global sealevel fluctuations (Webb and Tessman 1968; Tedford et al. in press).

SUBGENUS *Calippus (Grammohippus)* new subgenus

Type Species.— *Calippus (Grammohippus) martini* Hesse, 1936.

Included Species.— *C. (G.) circulus* (Quinn), 1955 n. comb.; *C. (G.) cerasinus* n. sp.; *C. (G.) hondurensis* (Olson and McGrew), 1941 n. comb.; and *C. (G.) maccartyi* n. sp.

Etymology.— *grammodes*, Greek for linear and *hippos*, Greek for horse. In reference to the linearly arranged incisors of the genus.

Chronologic and Geographic Distribution.— Clarendonian and early Hemphillian of northern and southern Great Plains and Florida. Late

Barstovian and Clarendonian of Texas Gulf Coastal Plain. Hemphillian of Central America and Mexico.

Diagnosis.— Small- to medium-sized hypsodont equids with toothrow lengths between 100 and 135 mm. Protocone oval or elongate-oval, connected to protoselene (only rarely isolated in very early wear-stages). Pli caballin single, large in premolars, variable in molars. Relatively simple fossettes, with moderately developed plications limited to the upper half of the crown. Hypoconal groove generally remains open longer than in *C. (Calippus)*; variably persistent and occasionally forms a lake; usually completely lost in latter wear-stages; lost earlier with wear in premolars than molars. Large parastyles and mesostyles; moderately well developed metastyles often present. Upper cheekteeth moderately curved, much more so than in *C. (Calippus)*, although less than in *Pliohippus*. Protostylids vestigial or absent on permanent lower cheekteeth; if present moderately developed only on the lower third (or less) of the crown. DPOF long, narrow, shallow, unpocketed, poorly rimmed posteriorly; probably absent in some younger species. Rostrum short, relatively broad; muzzle width varies from 45% to greater than 60% of the UTRL.

Discussion.— Members of the subgenus *Grammohippus* are easily distinguished from those of *C. (Calippus)* by their greater size, stronger styles, more curved upper cheekteeth, and rudimentary or absent protostylids. Specimens here assigned to *Grammohippus* have been variously placed in *Pliohippus*, *Astrohippus*, or *Protohippus*. While these four taxa can be easily differentiated by their facial fossae morphology, and *Grammohippus* has the unique *Calippus* incisor arrangement, isolated cheekteeth and some toothrow series cannot always be unequivocally assigned to a genus. In general, *Pliohippus* upper cheekteeth differ from those of *Grammohippus* by being larger, more curved, having more rapid closure and loss of the hypoconal groove, simpler fossettes, and much more frequent connection between the protocone and hypocone. *Protohippus* upper cheekteeth tend to be larger, have better developed pli caballins and prefossette loops, and often have isolated protocones in early wear-stages. *Astrohippus* upper cheekteeth are less curved, have simpler fossettes, more rudimentary pli caballins, and more rapid loss of the hypoconal groove. The lower cheekteeth of all four share many plesiomorphic characters. Discrimination among genera is further complicated by frequent parallel evolution of certain characters, especially those related to the elongation of the metaconid-metastylid complex and greater development of the lingual flexids (see discussion below).

Five species are referred to *Grammohippus*, ranging in age from late Barstovian to early Hemphillian. While this subgenus evidently diverged from *C. (Calippus)* sometime in the early Barstovian, no records exist prior to the late Barstovian (Cold Spring Fauna). However, it is unlikely that early specimens of *Grammohippus* would be readily distinguished from *Protohippus*

or *Pliohippus*, unless very complete cranial material was available. *"Protohippus" castilli* was described by Cope (1885) from the Tehuichila Fauna, Hidalgo, Mexico, possibly of late Hemphillian age (based on supposed co-occurrence with *Agriotherium*; Miller and Carranza-Casteneda 1984). The occlusal dimensions of the holotype (AMNH 8344) fall well outside the observed range of *C. (G.) hondurensis*, but it otherwise resembles that species in its enamel morphology, especially the relatively small protocone. *"Protohippus" castilli* thus may represent a late surviving member of *C. (Grammohippus)*. However, a sample of five upper and three lower cheekteeth from the Corinto Fauna, El Salvador (MHNES 70-26, -31, -179, -181 and -183 = UF 57488-54791, casts; Webb and Perrigo 1984, fig. 12B) compare favorably with the type of *"P." castilli* in size as well as morphology. Their large size and deep ectoflexids suggest referral instead to a equine genus (larger samples are needed for a more precise identification). That the morphology of AMNH 8344 compares so very favorably with both protohippine and equine species emphasizes that isolated cheekteeth are unreliable indicators of phylogenetic relationships among these horses. Additionally, there are several late early Hemphillian records of *Calippus* from the Great Plains mentioned by Tedford et al. (in press). These are currently under study by M. R. Voorhies and M. F. Skinner, and probably are also referable to *C. (Grammohippus)*.

Calippus (Grammohippus) circulus (QUINN), 1955 new combination
Fig. 14; Table 10

Merychippus perditus (Leidy), HESSE 1943:171 (in part).
Pliohippus circulus QUINN 1955:22-24 (in part).
Merychippus circulus (Quinn), FORSTEN 1975:32-35 (in part).

Type Specimen.— TMM 31191-10, assoc. R p4-m3.

Type Locality and Horizon.— Sam Houston Local Fauna (Hesse 1943:171), San Jacinto County, Texas; Cold Spring Fauna, Fleming Formation, late Barstovian (about 13.0 ma).

Revised Distribution.— Known only from the middle late Barstovian (about 13.5 to 12.5 ma) of the eastern Texas Gulf Coastal Plain.

Referred Specimens.— Cold Spring Fauna. Cold Spring Local Fauna (Hesse 1943:170), San Jacinto Co., TX: TMM 31219-327 R P2; -160 R P34; TAMU 3027 R M12; TMM 31219-326 L m3. Noble Farm Local Fauna (Hesse 1943:167), TAMU locality No. 19, Grimes Co., TX: TAMU 3019, 3020 2 L M12; 3021 R M3; 3022 R m12; 3023-3024 2 L m12; 3025 R m3; 3026 L m3.

Revised Diagnosis.— Cheekteeth with least unworn crown height of known species of the subgenus; unworn molar MSCH about 40 mm. Smaller than *C. martini*, with less complex fossettes, poorly developed pli caballins on premolars, and variable, often strong protostylids.

Description.— *Calippus circulus* is at present known only from a few isolated teeth; its generic referral is thus somewhat problematic until more complete material is discovered. A P2, TMM 31219-327, is moderately worn (Fig. 14A; Table 10) and the anterior third is broken off. The well connected protocone is round to slightly oval with a small preprotoconal groove (Fig. 14A). The fossettes are very simple with only a trace of a pli prefossette, and there is neither a pli caballin nor hypoconal groove remaining at this wear-stage. The moderately worn P34, TMM 31219-160, is very typically calippine, with a connected, elongate-oval protocone, small pli caballin, simple fossettes, well developed parastyle, and a slight metastyle (Fig. 14B). The tooth is moderately curved (ROC = 40 mm). M12 are represented by three specimens. TAMU 3027 is just barely worn, but has an MSCH of only 38 mm. The other two specimens are heavily worn. The protocone is elongate-oval, broadly connected to the protoselene, and with a shallow but persistent preprotoconal groove. Fossettes are simple; the pli caballin is vestigial, and the hypoconal grooves close without forming a lake.

The associated lower series that constitutes the holotype was illustrated and exhaustively described by Quinn (1955:23-24). The referred lowers
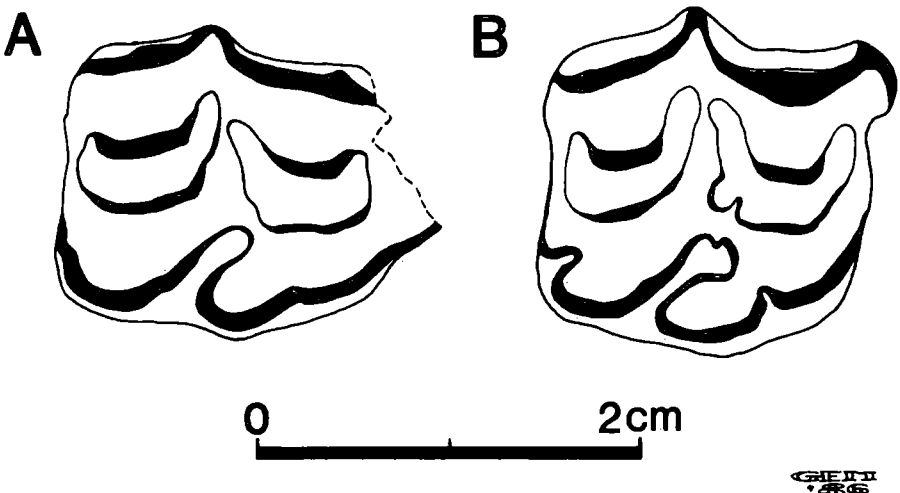
Figure 14. Occlusal views of upper cheekteeth of Calippus (Grammohippus) circulus from the Cold Spring local fauna, San Jacinto County, Texas (late Barstovian). A. TMM 31219-327, R P2. B. TMM 31219-160, R P34.

match the type in size and general enamel morphology, although many of the molars have stronger protostylids. They can be well developed on the lower third of the crown and present to near the top of the unworn crown. On others, including the type series and most of the referred m3s, the protostylid is much weaker, and is at best moderately developed only near the base of the crown. Smaller and less high crowned than *C. martini*, the lowers otherwise resemble that better known taxon. The metaconid-metastylid complex is relatively unexpanded, and the lingual flexids shallow, short, and nonpersistent.

Discussion.— Quinn (1955) described *Calippus circulus* as a primitive member of *Pliohippus* based on two specimens, the type lower series and a juvenile upper dentition (TMM 31219-165). The latter includes the right and
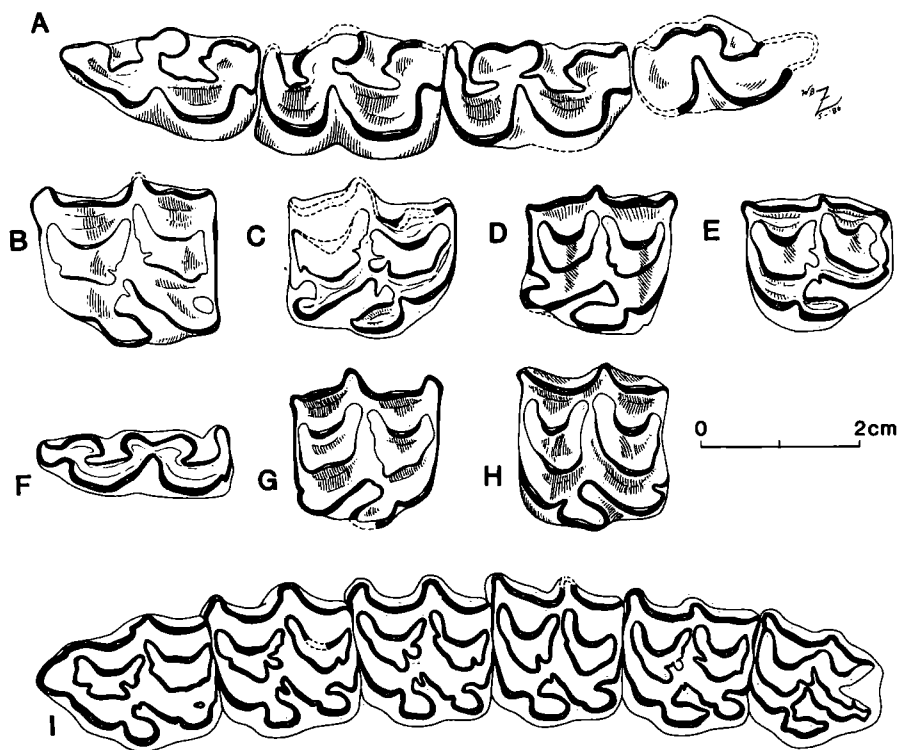
Figure 15. Occlusal views of upper and lower cheekteeth of medium-sized species of Calippus (Grammohippus) from Florida and Honduras. A-F. Calippus martini, Agricola Fauna (early Clarendonian), Polk County, Florida. A. UF 55806, associated L p2-m1. B. UF 28552, L P34. C. UF 98292, R P34. D. UF 98498, R M12. E. UF 98300, L M3. F. UF 98303, R dp34. G. UF 9506, R P34, Calippus sp. cf. C. hondurensis, McGehee Farm, Alachua County (very early Hemphillian). H-I. Calippus hondurensis. H. F:AM 113643, L M12, Mixson's Bone Bed, Levy County, Florida (early Hemphillian). I. F:AM 27029, associated L P2-M3, Rancho Lobo, Gracias Fauna, Lempira, Honduras (early Hemphillian).

left DP2-DP4, the right M1-M2 (Quinn 1955, plate 3.5-3.7), and the left M2-M3. The upper molars of TMM 31219-165 have strong pli caballins, moderately complex fossettes, and isolated protocones in early wear-stages, all of which suggest a referral to *Protohippus* rather than *Pliohippus* or *Calippus*. They are also larger than other upper cheekteeth from the Cold Spring Fauna which appear to be those of a primitive, moderate-sized member of *C. (Grammohippus)*. The latter are judged to better correspond to the type lowers of *C. circulus.* The total sample is quite limited, and more complete specimens would enable a confirmation of the association of upper and lower teeth proposed here. In the absence of cranial material, the referral to *Calippus* rather than *Pliohippus* is based on the moderate size (contemporary populations of *P. mirabilis* in Nebraska are much larger), the strong styles, and the moderately developed protostylids of the Cold Spring sample. Forsten (1975) grouped Quinn's (1955) *Pliohippus circulus* and *Eoequus wilsoni* into a single taxon *(Merychippus circulus)*. Most of the larger protohippine specimens from the Cold Spring Fauna do pertain to a single species, although I follow Hesse (1943) in referring them to *Protohippus perditus* (see below). The few specimens here referred to *C. circulus* differ from those of *P. perditus* by being smaller, much shorter crowned, having simpler fossettes, rapidly connected protocones, less elongate lingual flexids, and weaker protostylids. *C. circulus* is at present recognized only from the Texas Gulf Coastal Plain.

Calippus (Grammohippus) martini HESSE, 1936
Figs. 15A-15F; Tables 8-10

Protohippus perditus Leidy, GIDLEY 1906:136-139 (in part); GIDLEY
      1907:882-883 (in part); QUINN 1955:19-20 (in part).
Callippus martini HESSE 1936:52-54.
Pliohippus (Astrohippus) martini (Hesse), STIRTON 1940:190, 192;
      FORSTEN 1975:48-53 (in part).
Pliohippus sp., GREGORY 1942:412-413.
Protohippus martini (Hesse), QUINN 1955:21-22.
Equus laparensis QUINN 1955:58-61 (in part).
Equus sp., QUINN 1955:61-62.
Astrohippus martini (Hesse), WEBB 1969:95-96; SCHULTZ 1977:48.
Astrohippus sellardsi (Quinn), WEBB 1969:96 (in part).

Type Specimen.— UCMP 32814, assoc. L P2-M3.

Type Locality and Horizon.— Cragin Quarry (UCMP V-3516), Beaver Co., Oklahoma; Ogallala Formation, middle Clarendonian (about 10.0 to 11.5 ma).

Revised Distribution.— Early to middle Clarendonian of the northern and southern Great Plains; early Clarendonian of the Gulf Coastal Plain of Texas and Florida.

Referred Gulf Coastal Plain Specimens.— Lapara Creek Fauna. Buckner Ranch Site, Bee Co., TX: TMM 30896-127 assoc. R P2-M3; -195 assoc. L P2-P4 (holotype *E. laparensis*); -188 palate with R DP2-DP4 and L DP2-M1; -569 crushed skull with R P4-M3; -418 assoc. R P4-M1; -533 L p2; -545 assoc. R p2-p4 and L p2-m3; -207 R mandible with dp2-m1; -501 L mandible with dp2-dp4; -535 L dp2; -420E R p34. Farish Ranch Site, Bee Co., TX: TMM 31081-169 R M12; -1244 L M12; -1253B L p34. Bridge Estate Site, Bee Co., TX: TMM 31132-190C, -366B 2 R P34; -190B L P34; -169, -334B, -366A 3 R M12; -430 assoc. R p3-p4; -343 assoc. L p4-m3; -357 L dp34; -445 L dp2; -445B R dp34; -498 R p34; -13A, -285A, -400, -569 4 L m12. Medio Creek, Site No. 19, Bee Co., TX: TMM 31170-73 R P34; -74B R dp34; -74A R m12; -13A L m12.

Late Agricola Fauna. Gray Zone, Phosphoria Mine, Polk Co., FL: UF 28552, 93326 2 L P34; 28551 R M12; 28579 L m3; 55886 assoc. L p2-m1. Brewster Haynsworth Mine, Polk Co., FL: UF 24375 R M3 (Berta and Galiano 1984, fig. 2). Fort Green Mine, Polk Co., FL: UF 57358 R p34; 55888 L p34; 52409 R m12. Hookers Prairie Mine, Polk Co., FL: UF 98290 L P2; 98292-98293, 98495-98496 4 R P34; 98291, 98499-98500 3 LP34; 98294-98295, 98498 3 R M12; 98296-98298 3 L M12; 98497 R M3; 98299-98302 4 L M3; 98303 R dp34; 98304, 98493 2 L dp34; 98305 R p34; 98306-98307 2 L p34; 98308-98310 3 R m12; 98311, 98494 2 L m3.

Revised Diagnosis.— Largest described species of *Calippus*, with toothrow lengths of 125 to 140 mm and unworn molar crown height of about 57 mm. Metastylid poorly separated from metaconid by relatively shallow and rapidly retracting linguaflexid and entoflexid. Muzzle width about 45% of toothrow length.

Description.— Crania preserving the phylogenetically important facial and incisor regions of *Calippus martini* are known only from the Great Plains and are described by Hulbert (in prep. B). The following descriptions of Gulf Coastal Plain specimens are of necessity limited to dental characters (see also Quinn 1955, plates 2.5, 3.1, 14.1 and 14.4).

Upper cheekteeth of *C. martini* (Tables 8, 10; Figs. 15B-15E) have large parastyles and mesostyles. Protocones are oval (elongate-oval in early wear), have rounded or pointed posterior ends, and are of moderate length relative to tooth size. The protoconal connection is narrow and constricted by a deep preprotoconal groove in early wear-stages (Fig. 15C); it is more open in later wear-stages (Fig. 15B). The protocone is oriented in an oblique, anterolabial-

posterolingual direction, more so in premolars than molars. A long, single pli caballin is evident in moderate to slightly worn premolars; smaller or absent with greater wear. Pli caballins are typically small or absent on molars and infrequently well developed (Figs. 15D-15E). Fossette plications are usually simple and shallow, but better developed than those of *C. (Calippus)*. Premolars in early wear-stages usually have two to four plications on each of the internal fossette borders, sometimes bifurcated, and with moderate development of a prefossette loop. Pli protoloph and pli hypostyle are either single and shallow, or, more frequently, absent. P34 with MSCH of 18 mm and less typically have lost all plications. The fossettes of the molars are even simpler, and most plications are lost very early in ontogeny. The hypoconal groove closes to form a lake about in middle wear-stages, but the crown height at which this occurs varies. Well worn molars (i.e. those with less than half of their original crown height) generally lack all fossette plications, pli caballins, and a hypoconal groove. The protocone rarely connects to the hypocone, and then only in very heavily worn molars. Deciduous premolars are as similar in fossette complexity and pli caballin development as the permanent premolars. The hypoconal groove, however, remains open longer, until late wear-stages. A moderate-sized DP1 (about 10 mm long) is present and remains with the permanent dentition. Unworn or slightly worn MSCHs are about 45 mm for the P2, 52 mm for the P34, and 57 mm for the M12.

The lower cheekteeth of *C. martini* display the primitive protohippine pattern (Fig. 15A). The premolars have smaller, more lingually situated metastylids than metaconids. Therefore, posterior width is typically greater than atw (Table 9), although the difference is much less in older individuals. In early wear-stages, the linguaflexid and a well developed anterolingual extension of the entoflexid "pinch off" the metastylid from the metaconid (Fig. 15A). With wear, both contract, thus broadening the connection between them. The metaflexid rapidly retreats with wear, creating a broad confluence between the protoconid, metaconid, and protolophid (Fig. 15A). The ectoflexid is relatively shallow on the p2, not penetrating the isthmus. In the p34, its depth is variable; in early wear-stages it generally slightly penetrates the isthmus, to a point deeper than the level of the base of the entoflexid. In later wear-stages, it may retreat. Molars are much narrower than premolars, with relatively short metaconid-metastylid complexes (Table 9), and with the isthmus completely divided by the deep ectoflexid. The lingual flexids are shallow and rapidly contract with wear. Plications are uncommon; a small pli caballinid is rarely observed in slightly worn premolars, and a pli entoflexid is somewhat more common in both slightly worn molars and premolars. Usually a weakly developed protostylid is present only on the lower 15 to 25 mm of the crown of the p3-m3, thus reaching the occlusal surface only in older individuals. Lower deciduous premolars in early wear resemble the permanent premolars with shallow

ectoflexids and lingually placed metastylids. The dp2 has a well developed paraconid and an angular metaconid that is relatively large for a protohippine. With wear, the ectoflexids deepen and the dp2-dp4 take on a more molariform appearance, although with more expanded metaconids and metastylids (Fig. 15F). Protostylids are moderately developed on the lower two-thirds of the crown (e.g. TMM 30896-207; see also Hesse 1936, fig. 2). Ectostylids are absent. A small, vestigial dp1 may be present with the juvenile dentition, but it is lost with the eruption of the p2, and its alveolus is reabsorbed.

Discussion.— As can be judged from the synopsis of usage, the nomenclatural history of *Calippus martini* is complex. Some of the confusion originated with Hesse's (1936) description. He failed to list any measurements taken on the holotype, and the type figure (Hesse 1936, fig. 1) is not natural size as stated in the caption, but reduced by about 20%. This created a misconception in some that the species is considerably smaller than it really is. Measurements of the holotype are listed in Table 10. The remainder of the confusion can be traced to Stirton's (1940) transfer of *C. martini* to *Pliohippus* (*Astrohippus*).

Stirton (1940) described *Astrohippus* as a new subgenus of *Pliohippus*, with "*Protohippus*" *ansae* as the subgenotype. Stirton (1940) hypothesized that *A. ansae* was ancestral to *Equus*, and that "*A.*" *martini* was ancestral to *A. ansae*. "*A.*" *martini* was in turn thought to be descended from "*Merychippus*" *perditus*. While subsequent work has documented that *Dinohippus*, and not *Astrohippus*, is the sister group of *Equus* (Lance 1950; Bennett 1980; MacFadden 1984b), most authors have followed Stirton (1940) in considering *martini* as a member of *Astrohippus*. Quinn (1955) is a notable exception, as his systematic approach was vertical rather than the horizontal definitions of Stirton (1940). All the characters of the cheekteeth that Stirton (1940) used to unite *C. martini* and *A. ansae* are either primitive or are judged to have evolved in parallel (see phylogenetic section, below). He needed a late Miocene link between *Merychippus* s.l. and *A. ansae*, so that there would be a complete North American phylogenetic sequence of species from *Hyracotherium* to *Equus*. *C. martini* was inserted into this sequence based on its moderate size, appropriate age, and suitable cheektooth morphology. However, the derived *Calippus* muzzle morphology prevents *C. martini* from being ancestral to *A. ansae* or *Equus*. Furthermore, the well-developed malar fossa of *Astrohippus* (lacking in *C. martini*) is a shared derived character with *Pliohippus*.

Quinn (1955) recognized a total of eight medium to large-sized protohippine and equine taxa in the Lapara Creek Fauna (*Protohippus perditus, Equus* sp., *E. laparensis, Hippotigris sellardsi, H. parastylus, Pliohippus supremus, Dinohippus subvenus,* and *Asinus* sp.). Webb (1969) recognized the first four as a single taxon, which he referred to as *Astrohippus sellardsi*, and

the other four as *Pliohippus supremus*. Forsten (1975) also recognized just two taxa, but in a different combination. She referred to *Pliohippus (Astrohippus) martini* the first six listed taxa, and only the latter two to *P. (Pliohippus)* cf. *P. supremus*. Based on relatively complete skulls and mandibles, contemporary faunas from the Great Plains (e.g. Clarendon and Minnechaduza) contain at least three medium- to large-sized protohippines and equines: *Calippus martini*, *Protohippus supremus*, and *Pliohippus pernix*. *Dinohippus* may also be present, as Tedford et al. (in press) recognize it as early as the late Barstovian, but it is not as yet clearly documented in Clarendonian faunas. As previously indicated, *Calippus*, *Protohippus*, and *Pliohippus* are often difficult, or even impossible, to distinguish on the basis of isolated cheekteeth, which make up the bulk of the Lapara Creek sample. However, some of the more complete specimens can be relatively confidently referred to each of the three taxa found in the more northern faunas (Fig. 16).

Forsten (1975:52) noted that her sample of "*P.*" *martini* varied considerably in morphology, and that two morphs could be distinguished: a smaller population with hypoconal lakes, weaker (often absent) pli caballins, poorer styles, and weak or absent protostylids; and a larger population with stronger styles, pli caballin persistent and large in premolars and present in molars, and large, well developed protostylids. She also noted that some of the deciduous lower premolars lacked ectostylids (protostylids of her terminology) and others had them (Forsten 1975:51). She included these two populations in a single species because their range in size greatly overlapped and they had other characters in common. Samples from the Clarendon and Minnechaduza Faunas indicate that these are among the consistent dental differences that distinguish *C. martini* and *Protohippus supremus*, respectively. While the two are clearly distinct based on muzzle and facial characters, they are of about the same size, and overall their cheekteeth greatly resemble one another.

A sample of about 40 isolated teeth from a lower horizon in the Bone Valley Formation of south-central Florida is referable to *C. martini*. Its morphology and size (Table 10; Figs. 15A-15F) agree with the other referred samples. These specimens are larger than younger individuals of *C. (Grammohippus)* from Florida. *C. martini* is an important biochronologic indicator in the Bone Valley. Its presence in the Phosphoria and Hookers Prairie mines indicates a Clarendonian age for the associated fauna. An M3 of *C. martini* (UF 24375) also suggests that the type of *Pliocyon robustus* Berta and Galiano (1984) is Clarendonian, as the two specimens were found in close proximity in undisturbed sediments.
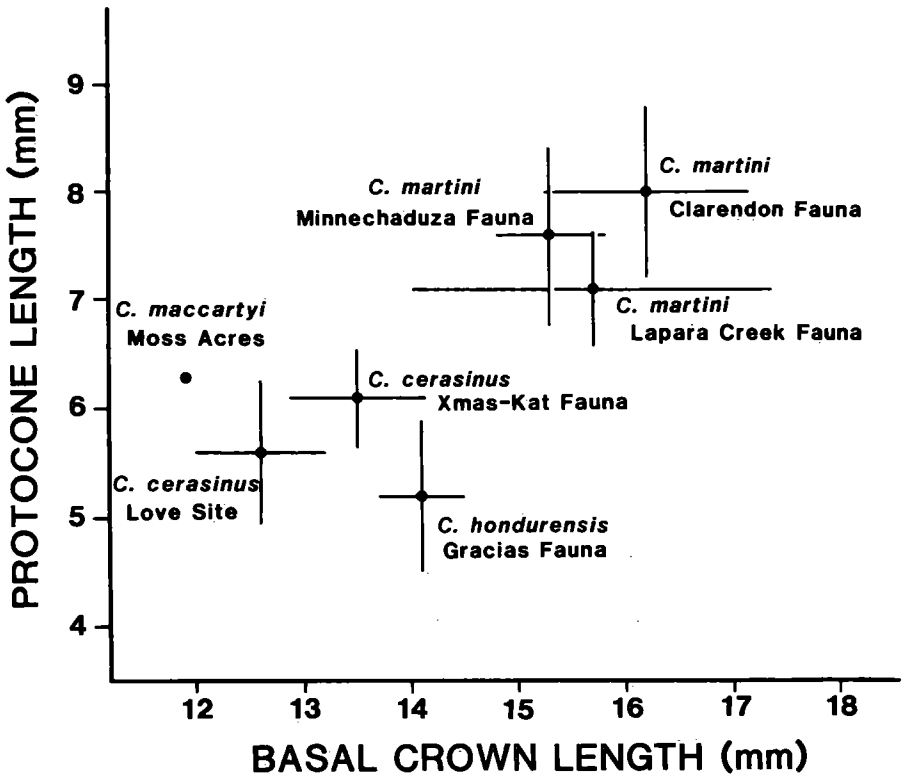
Figure 16. Bivariate plot of basal crown length (BAPL) versus protocone length (PRL) of combined samples of M1s and M2s for four species of Calippus (Grammohippus). One standard deviation is plotted on both sides of the mean value for the following populations: C. martini, Minnechaduza, Lapara Creek and Clarendon Faunas; C. cerasinus, Love Site and Xmas-Kat Fauna; C. hondurensis, Gracias Fauna. Also plotted are the values for UF 90299, a molar of C. maccartyi from the Moss Acres Racetrack Site. See Tables 8 and 11 for statistics.

Calippus (Grammohippus) cerasinus new species
Figs. 17-19; Tables 10-12

Astrohippus martini (Hesse), WEBB et al. 1981:527.

Type Specimen.— F:AM 114100, partial adult skull containing left maxilla with P2-M3, and portions of the left facial region, orbit, and braincase.

Type Locality and Horizon.— *Leptarctus* Quarry (NE 1/4, NE 1/4 sec. 28, T34N, R25W, Sparks Quad.), Cherry Co., Nebraska; Xmas-Kat Faunal Zone. Upper Merritt Dam Member, Ash Hollow Formation, Ogallala Group. From channel deposits incised into the Cap Rock Member (Skinner and Johnson 1984). Very late Clarendonian.

Etymology.— *cerasinus*, Greek meaning of or related to cherries. In reference to the county which produced the holotype and thousands of other vertebrate fossils.

Distribution.— Very late Clarendonian (about 9.0 to 10.0 ma) of Nebraska and Florida.

Referred Specimens.— Xmas-Kat Fauna, Cherry Co., NE. *Leptarctus* Quarry: F:AM 114124 L P2; F:AM 114125-114126 2 R P34; F:AM 114127 L P34; F:AM 114128 R M12; F:AM 114129-114132, 114241 5 L M12; F:AM 114133 L M3; F:AM 114134 R p34; Xmas Quarry: F:AM 114096 R mandible with i2,c,p2-m2; F:AM 114097 L male mandible and symphysis with L i3,c,p2-
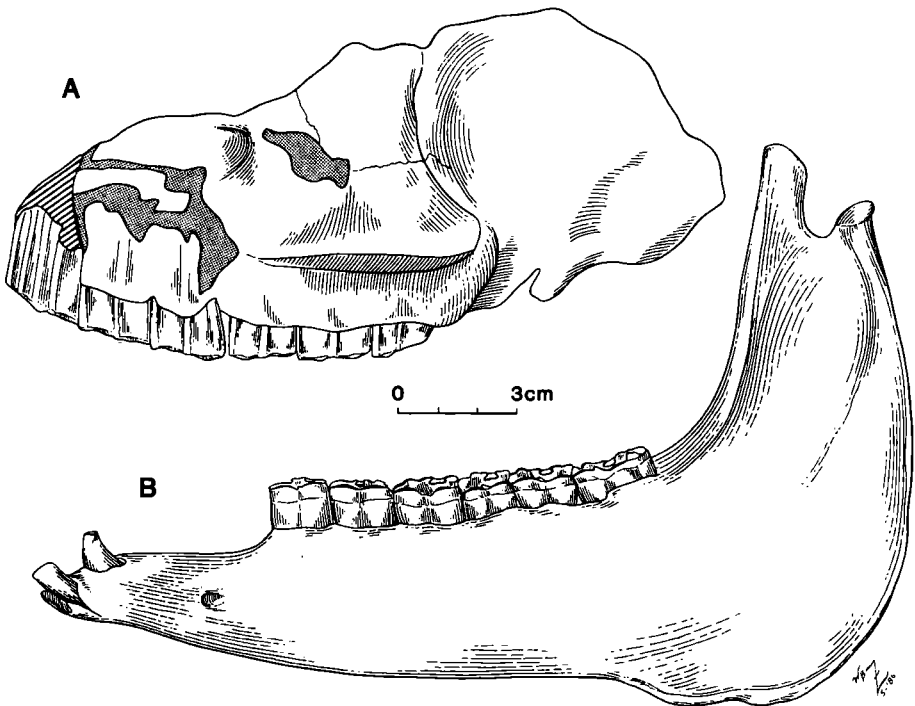
Figure 17. Lateral views of holotype and referred mandible of Calippus (Grammohippus) cerasinus n. sp., Merrit Dam Member, Ash Hollow Formation, Cherry County, Nebraska (very late Clarendonian). A. F:AM 114100, partial skull, Leptarctus Quarry, holotype (see Fig. 18A for occlusal view of cheekteeth). B. F:AM 114097, left mandible, Xmas Quarry (see Fig. 19F for occlusal view of this specimen).

m3 and R i2-i3,c; F:AM 114099 assoc. R mandible with p2-m2 and L mandible with p2-m1; West Line Kat Quarry: F:AM 114117 L P2; F:AM 114242 R P34; F:AM 114102 114118 2 R M12; F:AM 114103-114104 2 L M12; F:AM 114101 L mandible with p2-m3; F:AM 114119 R p34; F:AM 114120 R m12; Quarter Kat Quarry: F:AM 114122 R M12; F:AM 114240 L M12; F:AM 114238 R m12; Kat Quarry: F:AM 114115 L mandible with p2-m1; Connection Kat Quarry: F:AM 114123 L m12; East Kat Quarry: F:AM 114105 L P34; F:AM 114121 L p34; Wade Quarry: F:AM 114160 R mandible with m1-m3. Precise locality and stratigraphic data for these sites are listed in Skinner and Johnson (1984).

Love Site, Alachua Co., FL: UF 32268 assoc. R P4-M3 and L M1-M3; 32281 assoc. R M1-M2; 32286 assoc. R DP2-DP4; 60315 assoc. R and L M1; 65238-65239, 90266 3 R DP2; 65240-65241 2 L DP2; 65242, 92993 2 L DP34; 35974, 60251-60267 18 R P2; 36144, 60234-60246, 60248-60250 16 L P2; 60268-60275, 60277-60287, 60314, 60328, 60351-60352 23 R P34; 60288-60291, 60293-60294, 60297-60300, 60302-60306, 60308-60313, 60359 22 L P34; 60276, 60316-60327, 60329-60350, 92957 36 R M12; 60292, 60296, 60301, 60307, 60353-60358, 60360-60368 20 L M12; 60380-60394 15 R M3; 60369-60379 11 L M3; 32143 R mandibular fragment with p3; 32141 R mandible with dp2-dp3; 32194 R mandible with p3-m2; 32201 R mandible with p3-m3; 32206 L mandible with p3-m3; 32215 L mandible with p2-p3; 96548 R pd2; 96549-96554 6 L dp2; 65246-65247, 92956, 96547 4 R dp34; 65243-65245, 92954-92955, 96545-96546, 96977-96978 9 L dp34; 59178-59184, 64528, 65248, 69804, 96557-96559 13 R p2; 59176-59177, 64508, 96555-96556, 96976 6 L p2; 59185-59200, 68786 17 R p34; 59951-59956, 59958-59969 18 L p34; 59990-59999, 60207-60218 22 R m12; 59970-59989 20 L m12; 60219-60225, 68784-68785 9 R m3; 60226-60233 8 L m3.

Haysand Road, Gainesville, Alachua Co., FL: UF 17233 L P34.

Pareners Branch Site, Alachua Co., FL: UF 98489 R P34.

Nichols Mine, Polk Co., FL: UF 24648 R m12; 24634 R m3.

Swift Mine, Polk Co., FL: UF 18922 L M1.

Diagnosis.— Smaller than *C. martini* and with less high-crowned cheekteeth. Unworn molar crown height about 50 mm; toothrow lengths of 105 to 110 mm in moderate wear. Moderately curved upper cheekteeth with strong styles; anterolabial-posterolingually oriented, elongate-oval protocones with rounded lingual borders and shallow preprotoconal grooves; hypoconal groove variable in depth, persistently open in molars, closed to form lake and then lost with wear in premolars; pli caballin vestigial in premolars, absent in molars.   Protocone relatively and absolutely longer than that of *C. hondurensis*. Lower cheekteeth with small metastyles relative to metaconids, generally with deeper ectoflexids than *C. hondurensis*, and with more poorly developed protostylids.

Description.— The holotype, F:AM 114100 (Figs. 17A, 18A; Table 10), is a partial skull of a young adult. The M3 is in the process of erupting and its posterior half is as yet unworn. The ventral half of the facial region is slightly crushed, but nearly complete. The malar region lacks a distinct fossa, but contains a slight oval depression equadistant between the anterior margin of the orbit and the IOF. This depression resembles those sometimes found in crania of *C. martini* and may have been caused or accentuated by the crushing. The malar crest is not expanded (as it is in *Pseudhipparion*), and extends anteriorly just dorsal to the M1 mesostyle. The IOF is located about 43 mm anterior from the orbit and 38 mm dorsal to the alveolar border above the M1 parastyle. F:AM 114100 is broken dorsally 5 mm above the IOF, so the condition of the DPOF is unknown. The anterior-most point of the lacrimal is present (about 32.5 mm in front of the orbit) and does not form part of the DPOF (Fig. 17A).

The upper cheekteeth are moderately curved, with ROC of P34s between 45 and 50 mm, and for M12s, between 38 and 45 mm. The styles are moderately strong, and the P3 through M2 generally have a moderate metastyle (Figs. 18A-18E). The protocone is elongate-oval with a pointed posterior end. The protocone connects to the protoselene at the onset of wear, and, in early wear-stages, the connection is constricted by a moderate preprotoconal groove and the postprotoconal valley. By mid-wear (e.g. the M1 of the holotype), the preprotoconal groove becomes shallow and the protoconal connection widens; further wear accentuates this. The relative PRL is similar to that of *C. martini*, averaging about 33 to 35% of APL in P3-M2, and the protocone is similarly oriented in an oblique, anterolabial-posterolingual direction (Fig. 18B). The pli caballin is small and nonpersistent in the premolars and absent in molars. Fossette plications are also similar in number as those of *C. martini*, but are slightly less persistent with wear, as in *C. hondurensis*. Single, shallow pli protolophs and pli hypostyles are variable in early wear-stages, only rarely observed in older individuals. In premolars, the posterior half of the prefossette is the most complex, with from one to four shallow plications in early wear-stages (Fig. 18A); generally zero or one by mid-wear; and unplicated in later wear-stages (Fig. 18D). The anterior half of the postfossette bears at most two shallow plications in early wear (more commonly one or none), these are lost by middle wear-stages. In molars, the pli protoloph and pli hypostyle are rarer and, if present, less persistent. The inner borders of the fossettes generally have one plication each in early wear-stages; these are shallow and nonpersistent. The hypoconal groove closes almost at the onset of wear on the P2-P4, forming a lake. This persists for about the upper third of the crown and is then lost at MSCHs of about 30 mm. In the M12, the Xmas-Kat Fauna sample generally retain open hypoconal grooves until late wear-stages. Two individuals (F:AM 114102 and 114130), however, have lost the
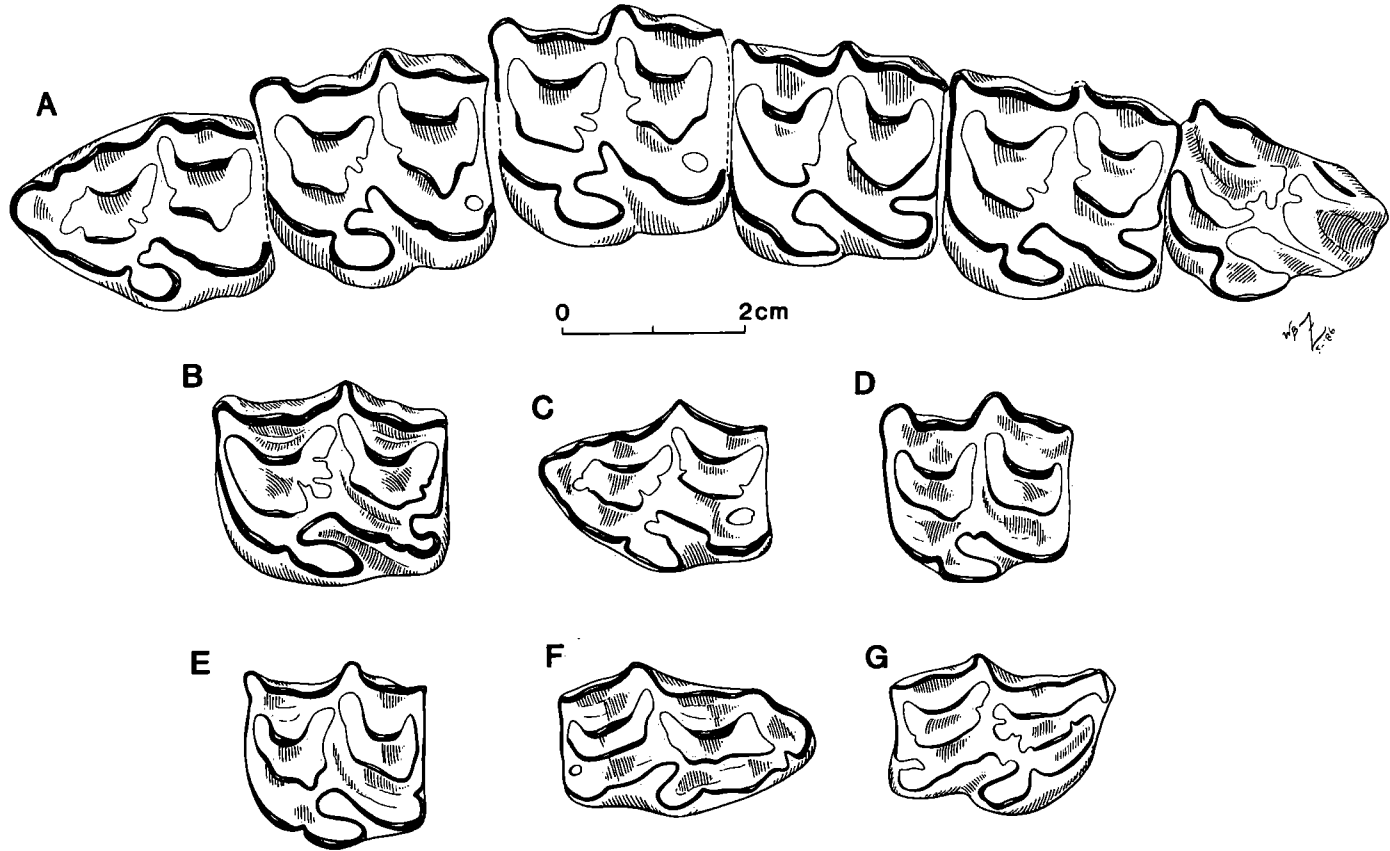
Figure 18. Occlusal views of upper cheekteeth of Calippus (Grammohippus) cerasinus n. sp. from the late Clarendonian of Nebraska and Florida. A. F:AM 114100, L P2-M3, holotype, Leptarctus Quarry, Cherry County, Nebraska. B. F:AM 114239, L M12, Quarter Kat Quarry, Cherry County, Nebraska. C-G. Love Site, Alachua County, Florida. C. UF 60240, L P2. D. UF 60309, L P34. E. UF 60292, L M12. F. UF 65238, R DP2. G. UF 32286 R DP34.

hypoconal groove at crown heights of 40.0 and 31.0 mm, respectively. The Love Site sample of M12s tends to lose the hypoconal groove much earlier on average, generally at MSCHs of 32 to 35 mm, although in some it may persist to an MSCH of 26 mm or less (e.g. UF 60344). In both faunas, the groove of the M12 rarely forms an isolated hypoconal lake (only one example from the Love Site sample of about 50 molars); the structure just becomes increasingly shallow until it disappears. Unworn or slightly worn MSCHs are about 36 mm for the P2, 47 mm for the P34, and 50 mm for the M12.

Deciduous upper premolars (Figs. 18F-18G) have rudimentary pli caballins in early wear, that are soon lost. Protocone shape and orientation, styles, and fossette complexity resemble those of the permanent premolars. The hypoconal groove is open in very early wear-stages, closes to form a lake, and is lost in late wear-stages.

Lower cheekteeth (Fig. 19) are on average smaller than those of *C. martini* (Tables 9, 10, 12) but similar in morphology. The premolars in early wear have the metastylid well separated from the metaconid by the linguaflexid and an anterolingual projection of the entoflexid (Fig. 19E). The metastylid is notably smaller than the metaconid and is positioned more lingually. The ectoflexid on the p2 is shallow and does not penetrate the isthmus; on the p34, it generally partially penetrates the isthmus, deeper than the labial borders of the metaflexid and entoflexid. With wear, the flexids retract, broadening the dentine confluence of the conids. By latest wear-stages (Fig. 19F, p3), the metaflexid and linguaflexid are particularly shallow. The molars in earliest wear-stages have relatively more expanded metaconids and metastylids than in *C. martini*. The lingual flexids are shallower and less well developed than those of the premolars, particularly the entoflexid. The isthmus is completely divided by a deep ectoflexid that, until it begins to retract in late wear, separates the metaconid and metastylid. Typical of *Calippus*, the lingual flexids retreat with wear (contrast Figs. 19B, 19C, and m1 of 19F). Protostylids, if present, are restricted to the lower part of the crown and are weak. In the Love Site sample, more than 90% of the p3-m3 bear not even the slightest trace of a protostylid. Plications are rare, and generally limited to minor pli entoflexids in early wear-stages. The dp2 has a persistently shallow ectoflexid, lacks a pli caballinid or isthmus plications, and has a well developed metaconid. The dp34 (Fig. 19D) differ from those of *C. martini* by having deep ectoflexids and linguaflexids in early wear-stages. Protostylids are more vestigial than in *C. martini* and ectostylids are absent. Unworn or slightly worn mcch are about 30 mm for p2, 45 mm for p34, and 48 mm for m12.

The incisors and muzzle region of *C. cerasinus* are at present best known from mandibular symphyses (e.g. F:AM 114097, Figs. 17B, 19F). They are very similar to those of *C. martini* and *C. hondurensis*. The occlusal surface of the R and L i12 form a straight line, the i12 are large relative to other equids,
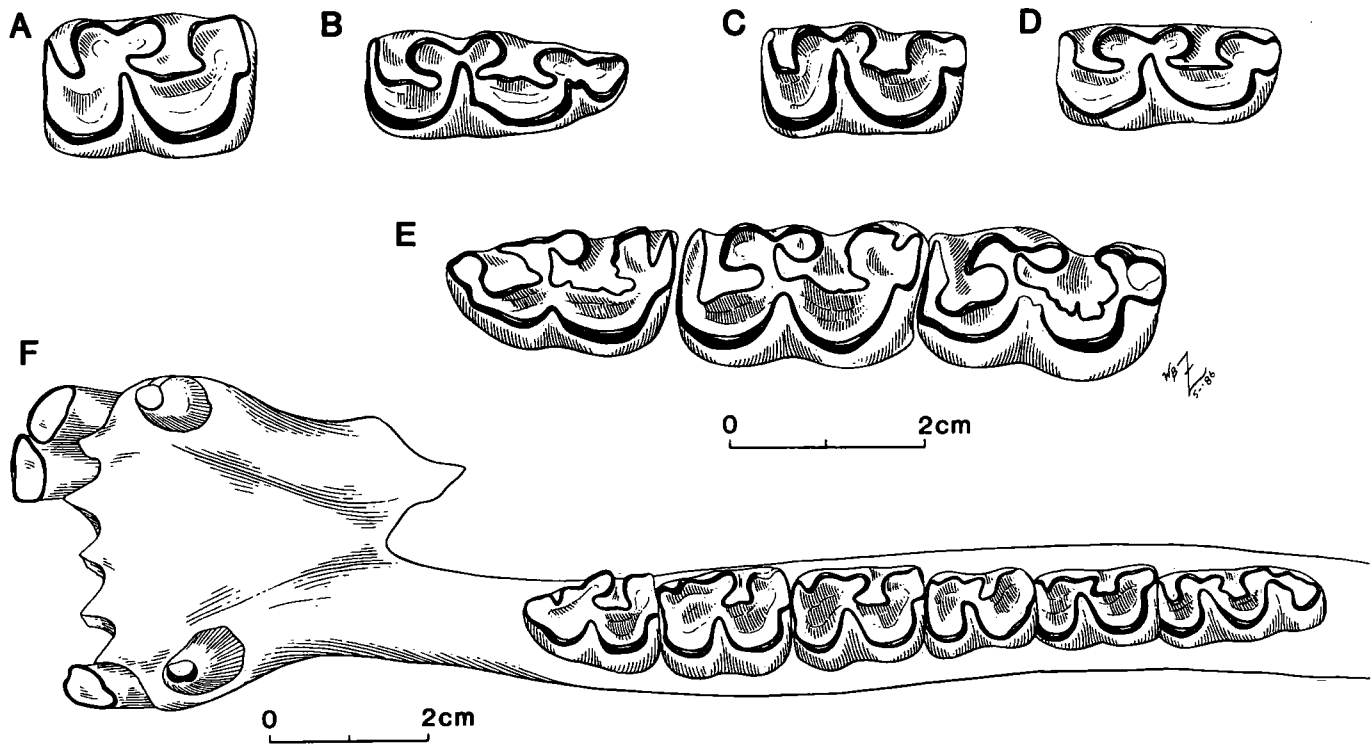
Figure 19. Occlusal views of lower cheekteeth of <u>Calippus</u> (<u>Grammohippus</u>) <u>cerasinus</u> n. sp. from the late Clarendonian of Nebraska and Florida. A-E. Love Site, Alachua County, Florida. A. UF 59956, L p34. B. UF 59971, L m12. C. UF 59973, L m12. D. UF 65243, L dp34. E. UF 32215, associated L p2-p4 (slight wear). F. F:AM 114097, left mandible and symphysis with L i3, c, p2-m3 and R i2-i3, c; Xmas Quarry, Cherry County, Nebraska; moderately heavily worn male.

and the male lower canines are especially massive and conical. The muzzle width appears to have been at least 50% of the UTRL.

Discussion.— *Calippus cerasinus* is closely related to *C. hondurensis*. The two are inseparable on the basis of size (Fig. 16; Tables 11-12), and differ only in details of cheektooth morphology and crown height. The most important of these are length, morphology and orientation of the protocone, the formation of a hypoconal lake on the P34, the strength of the pli caballin, the depth of the ectoflexid on p3-m3, and the relative size and separation of the metaconid and metastylid on p34. The unworn crown height of *C. hondurensis* cheekteeth are about 10% greater than those of *C. cerasinus*.

C. cerasinus is at present recognized from two faunas that are quite separated from one another geographically, but that seem very close biochronologically (see also Webb et al. 1981; Webb and Hulbert 1986; Tedford et al. in press). Much of the apparent size differences between the two populations (Fig. 16; Tables 11 and 12) are related to differences in age distributions. The Xmas-Kat sample (especially the uppers) proportionally includes many more younger individuals, which accounts for its greater means for many of the characters. The basal lengths of molars and premolars indicate that the Xmas-Kat population was actually only about 5 to 8% larger than that of the Love Site. This minor size difference is not considered sufficient to separate the two as distinct species. At present three equid species are recognized from both the Xmas-Kat Fauna and the Love Site, *Neohipparion trampasense* (MacFadden 1984a; Hulbert 1987b), *Pseudhipparion skinneri* (Webb and Hulbert 1986), and *C. cerasinus*. These three would appear to be excellent indicators of the latest Clarendonian or earliest Hemphillian. In Nebraska, both directly underlying strata (containing the early to middle Clarendonian Minnechaduza Fauna) and younger strata (that containing the early Hemphillian Cambridge Fauna) either have different species of the same genera or, in the case of *Pseudhipparion*, the Xmas-Kat record is its youngest appearance in the region. In Florida, earliest Hemphillian faunas generally contain the same equid species as the Love Site (with the exception of *C. cerasinus*, which is replaced by *C. hondurensis*), but there is a major re-organization in the late early Hemphillian.

Calippus (Grammohippus) hondurensis (OLSON AND MCGREW), 1941
new combination
Figs. 15H-15I; Tables 10-12

Pliohippus sp., FRICK 1933:528.
Pliohippus hondurensis OLSON and MCGREW 1941:1232-1235; WEBB and
    PERRIGO 1984:245, 247-249 (in part).

Type Specimen.— WM 1769, palate with R P2-M3 and L P2-P4.

Type Locality and Horizon.— Rancho Lobo, 6 km NW of Gracias, Department of Lempira, Honduras. Gracias Formation, early Hemphillian.

Revised Distribution.— Early Hemphillian (about 7.0 to 9.0 ma) of Honduras, Mexico and Florida.

Referred Specimens.— Gracias Fauna. Rancho Lobo, Honduras [in addition to those listed by Olson and McGrew 1941]: F:AM 27029 L maxilla with P2-M3; 27028 L maxilla with P2-M2; 27021 assoc. R and L DP2-DP4; 27030-27032, 27040 4 mandibular fragments with teeth; UF 17754 assoc. R P3-M1; UF 17755 assoc. L M1-M3; UF 92339 L P2; 92340, 92344 2 R P34; 92341 R M3; 92342-92343 2 L M3; 92326 assoc. R p2-m3; 17758 R p2; 92327-92333 7 R p34; 92347-92348 2 L p34; 92334, 92345-92346 3 R m12; 17782, 92338 2 L m12; 92335-92337 3 L m3; 92349 L mandibular fragment with m3; Saddle Locality, Honduras (see Webb and Perrigo 1984, fig. 3 for location of UF sites in the Gracias Formation of Honduras): UF 92351 L M12; 92350 R p34; 17745 L m12; New Year Locality, Honduras: 17774, 92358-92360 4 R P34; 92355-92357 3 L P34; 92361-92364 4 R M12; 92365-92366 2 R M3; 92352-92354, 92367 4 L M3; 92370 R p2; 92372 L p2; 92368-92369 2 R p34; 92373-92374 2 L p34; 92371 R m12; 92375 L m12; El Carrizal Locality, Honduras: UF 92376-92377 2 L P34; 92378-92379 2 R P34; 18017 L m12.

Tehuichila Fauna, Hildalgo, Mexico: AMNH 8343 L P34.

Mixson's Bone Bed, Levy Co., FL: F:AM 113641 L P2; 113642-443643, 113645 3 L M12; 113646 R P4; 113648 R M3.

Revised Diagnosis.— Smaller than *C. martini* or *"Protohippus" castilli*, with moderately worn toothrow lengths of about 101 to 112 mm. Unworn molar crown height about 55 mm. Protocone small, oval, with persistent preprotoconal groove and flattened lingual border. Hypoconal groove shallow; persistently open until late wear-stages in molars; closed earlier in premolars, without hypoconal lakes on P34. Molars with pli caballins in early wear. Ectoflexid generally shallower than in *C. cerasinus*, rarely penetrating isthmus in p2-p4. Large metastylid on p34. Protostylids variably developed.

Description.— The facial region of *C. hondurensis* is unknown. The most complete cranial material includes the holotype and F:AM 27029, both of which preserve only the ventral-most portion of the face. The anterior portion of the malar crest is well preserved on F:AM 27029. As in *C. cerasinus*, it is uninflated. Its anterior-most part is directly dorsal to the M1 parastyle.

The cheekteeth of *C. hondurensis* were admirably described by Olson and McGrew (1941). Of particular note was their attention to ontogenetic variation in enamel morphology. A slight drawback was their failure to distinguish between molars and premolars in their discussion of upper cheekteeth, as they did with the lowers. The following discussion will highlight those features of *C. hondurensis* that differ from those of other

members of *C.* (*Grammohippus*), that allow Florida specimens to be referred to this Central American taxon, and that allow it to be placed in *Calippus* rather than *Pliohippus*.

As noted by Olson and McGrew (1941) in their diagnosis, a characteristic feature of *C. hondurensis* is its relatively short protocones (Table 11; Figs. 15H-15I). For the Honduras sample, the P34 protocone length averages 26% of the APL; the M1 protocone, 31%. Those of the premolars in particular are much smaller than those of *C. martini* or *C. cerasinus*, which average between 32 and 36% of the APL. Other important features are the persistently deep preprotoconal groove and the flattened lingual border of the protocone (Fig. 15I). The difference in the preprotoconal groove between *C. hondurensis* and *C. cerasinus* is best judged by comparing similarly worn teeth, e.g. Figs. 15H and 18D. In *C. hondurensis*, the premolars in early wear-stages have moderately well developed pli caballins, and the molars have small ones; these along with the fossette plications are lost by middle wear-stages. A hypoconal lake is formed only on the P2 in the available F:AM and UF samples. In the P34, the well developed hypoconal groove in early wear becomes progressively shallower with wear, and is generally lost at MSCHs of about 28 mm. The hypoconal groove generally persists in the molars until late wear-stages, although it can be lost in teeth with MSCHs as great as 30 mm. Unworn or slightly worn MSCHs for P34 are about 51 mm and about 55 mm for the M12.

Lower cheekteeth (Table 12) differ notably from those of *C. cerasinus* in the greater relative size of the metastylid (especially on slightly worn premolars), the shallower ectoflexids, and the deeper and more expanded linguaflexids at similar wear-stages. Protostylids are variably developed, but are generally present on the p3-m3. They usually begin to be expressed on the occlusal surface when crown heights reach from 20 to 30 mm and can be moderately well developed (e.g. F:AM 27031), although not to the degree of *Protohippus* or *C.* (*Calippus*).

The incisor region is best preserved on WM 1771 (Olson and McGrew 1941, plate 2B). The symphysial region is similar to, but relatively even more massive than that of *C. cerasinus* (e.g. F:AM 114097), and the male canines are equally massive and conical. The enlarged symphysis and short diastema are characteristic of *Calippus*.

Discussion.— Olson and McGrew (1941) assigned their new species to the genus *Pliohippus*, but failed to note any distinctive (i.e. derived) characters that it shared with that taxon. In a brief section discussing relationships, they excluded *Nannippus* because of its isolated protocones and "*Protohippus*" *placidus* because of its straighter upper cheekteeth and (supposed) less complex fossettes. *Pliohippus* upper cheekteeth differ from those of "*P.*" *hondurensis* in having rapidly closed hypoconal grooves, very frequent connection of the protocones and hypocones (Skinner et al. 1977),

and are more curved. Connected protocones and hypocones are only rarely observed in *Calippus* (*Grammohippus*) populations (< 5% of observed molars). *Pliohippus* lower cheekteeth lost the protostylid in the late Barstovian. "*Pliohippus*" *hondurensis* dentally is most similar to *C. martini* and *C. cerasinus*. The few known incisor arcades associated with cheekteeth of "*P.*" *hondurensis*, especially WM 1771, show *Calippus*-like features. "*P.*" *hondurensis* is therefore transferred to *C.* (*Grammohippus*).

The topotypic sample of *C. hondurensis* was derived from fluvial sediments in Honduras. The first major collection was made by Blick in 1929, and later briefly mentioned by Frick (1933) in his description of the proboscideans. Olson and McGrew (1941) and Webb and Perrigo (1984) reported the presence of *C. hondurensis* not only at Rancho Lobo, but at a number of other localities within the Gracias Formation. As noted above, specimens from El Salvador referred to *C. hondurensis* by Webb and Perrigo (1984) are much larger than topotypes, and have much deeper ectoflexids. They do not represent *C. hondurensis*, but rather some member of the equine clade. Generic identification of the sample will require more complete specimens. AMNH 8344, a premolar from the Tehuichila locality, is indistinguishable from topotypes of *C. hondurensis*.

Olson and McGrew (1941) concluded that the age of the Gracias Fauna was Clarendonian, primarily based on the stage of evolution of the equids. McGrew (1944) later suggested a younger age, possibly Hemphillian, based on the presence of *Osteoborus cynoides*. Webb and Perrigo (1984) reviewed the Gracias Fauna, and confirmed its age as early Hemphillian. The other common equid in the Gracias Fauna is *Cormohipparion ingenuum* (not *C. plicatile* as referred by Webb and Perrigo 1984; see Hulbert 1987a), which was originally described from the early Hemphillian Mixson's Bone Bed locality in Levy County, Florida (Leidy 1885).

A limited sample of six upper and two lower cheekteeth from Mixson's Bone Bed apparently represent a population of *C.* (*Grammohippus*) referable to *C. hondurensis* rather than *C. cerasinus*. Important features observed in the sample (Fig. 15H; Table 10) are short protocones with flattened labial borders; deep, persistent preprotoconal grooves; and strong pli caballins on premolars. The presence of *C. hondurensis* at Mixson's would seem to confirm a Hemphillian age for the Gracias Fauna.

Calippus (Grammohippus) sp., cf. C. hondurensis
Fig. 15G; Table 10

Referred Specimens.— McGehee Farm, Alachua Co., FL: UF 17259 L DP34; 9506, 17236A 2 R P34; 17236B L P34; 18323, 16624 2 L M12; 17237 L M3; 18940 R p34; 17242 R m12.

Haile 19A, Alachua Co., FL: UF 45948/47489 assoc. R P2-P4 and L P2-M3; 47322, 65733 2 partial upper cheekteeth.

Coffrin Creek, Alachua Co., FL: UF 17238 L P34; 58553 L p34.

Discussion.— This limited sample of cheekteeth is definitely referable to C. (Grammohippus), but is morphologically intermediate between C. cerasinus and C. hondurensis. Most of the specimens are either heavily worn or broken, thus hindering specific identification. UF 18323 (Fig. 15G) is one of the best preserved specimens, and of the sample it most resembles C. cerasinus in its protocone morphology. Others do have better developed and more persistent preprotoconal grooves, as is characteristic of C. hondurensis. The lingual border of the protocone varies from rounded as in UF 18323 to slightly flattened as in UF 17236, 17238, and 17259. The protocone orientation is less oblique than in C. cerasinus but more than in C. hondurensis. On both UF 52963 and 58553, the metastylid is relatively large, resembling that in C. hondurensis rather than the smaller metastylid of C. cerasinus. This sample was referred to "Pliohippus" hondurensis by Waldrop (1971), who was the first to recognize the close relationship between the Central American and Florida samples (although see also Webb 1969:29). The McGehee, Coffrin Creek, and Haile 19A populations probably represent a slightly older sample within an evolving chronospecies of Calippus (Grammohippus) than that of Mixson's, but larger, more complete samples are needed before they can be referred to a species with a high degree of confidence.

The three principal north-central Florida localities of the Archer Fauna (the Love Site, McGehee Farm and Mixson's Bone Bed) otherwise share a common equid fauna at the species level, except for some absences at Mixson's. While other mammalian taxa are similarly shared (e.g. camelids, dromomerycids), others differ (see above). The degree of evolution of C. (Grammohippus) suggests the relative ages for the three sites are, from oldest to youngest, Love, McGehee, and Mixson's.

Calippus (Grammohippus) maccartyi new species
Figs. 20-21; Table 10

Pliohippus cf. *hondurensis* Olson and McGrew, BECKER 1985:29.

Type Specimen.— UF 69951 badly crushed anterior half of skull of adult male with R and L I1-I3, C, P2 and L P3-M3; assoc. mandibular symphysis and lower cheekteeth, R and L i1-i3, c, p2 and L p4-m2. Skull and mandible were found in near occlusion and certainly represent a single individual. Collected by R. McCarty on 5 March 1985.

Type Locality and Horizon.— Moss Acres Racetrack Site (NW 1/4, NE 1/4 sec. 11, T14S, R19E, Morriston Quad.), 5.8 km E of Morriston, Marion Co., Florida. From a massive clay deposit, Alachua Formation, late(?) early Hemphillian.

Etymology.— Named for Russell McCarty of the Florida State Museum, who collected and prepared the holotype and several topotypes. Formation of the species name follows Recommendation 21a of the International Code of Zoological Nomenclature.

Distribution.— Early, probably late early, Hemphillian (about 6.5 to 7.5 ma) of north-central Florida.

Referred Specimens.— Moss Acres Racetrack Site, Marion Co., FL: UF 65249 L DP34; 95407 R P2; 90299 L M12; 95397 R p34; 97275 L p34; 90287 R m12; 90298 3 lower cheektooth fragments.

Withlacoochee River UF locality 4A, Marion-Citrus Co. border, FL: UF 45537 L P2; 17240 R P34; 45540 L P34; 45535-45536 2 R M12; 45538 L M3; 53460, 53487 2 R p34; 53463 R m12; 61348 R m3.

Diagnosis.— Small species of *C.* (*Grammohippus*) with toothrow lengths of about 100 mm. Preprotoconal groove deep, persistent. Protocones elongate, not short as in *C. hondurensis*; lingual borders rounded to slightly flattened; oriented slightly obliquely. Hypoconal groove open until mid-wear; forms lakes on P2-P4. Pli caballin small, single; fades with wear; vestigial or absent in molars. Plications simple but persistent, not lost until heavy wear. Upper cheekteeth not as curved as other species of *Grammohippus*. Lower cheekteeth with widely expanded metaconids and metastylids; lingual flexids more persistent than other species; variable protostylids; enamel plications in early wear-stages. Ectoflexid shallow on p2-p4, only moderately deep on m1-m3. Muzzle width about 60% of UTRL.

Description.— *Calippus maccartyi* is as yet known only from a small number of specimens, but its dental morphology (especially the lowers) indicates the presence of a distinct species of *Grammohippus*. The holotype (UF 69951) is one of the five known Tertiary equid specimens from Florida with associated upper and lower dentitions. The other four (two individuals
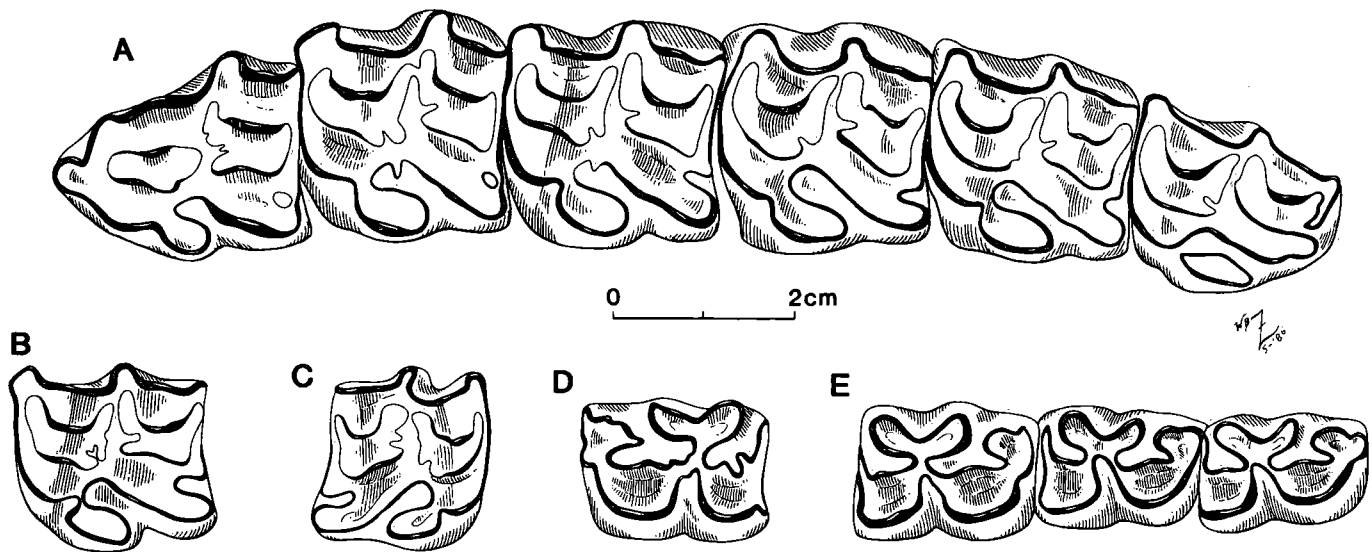
Figure 20. Occlusal views of upper and lower cheekteeth of Calippus (Grammohippus) maccartyi n. sp. from the early Hemphillian of Florida. A-B, E. Moss Acres Racetrack Site, Marion County. C-D. Withlacoochee River UF Locality 4A, Marion-Citrus County line. A. UF 69951, L P2-M3; holotype, teeth restored to their natural relative positions. B. UF 90299, L M12. C. UF 45536, R M12. D. UF 53462, R p34. E. UF 69951, L p4-m2, holotype (same individual as teeth figured in 20A).

of *Nannippus* and two of *Cormohipparion*) are also from the newly discovered
Moss Acres Racetrack Site. UF 69951 consists of the anterior (pre-orbital)
half of a skull, but it has been crushed laterally such that no facial characters
can be recognized. The specimen does suggest that any fossae were shallow
at best. The premaxillary region is the least damaged part of the cranium, but
it is still cracked and distorted. The teeth that are present, however, are very
well preserved, except for the left I3, which has the top 10 mm of its crown
broken off. Much of the mandibular symphysis is preserved intact and
undistorted. The incisors display the characteristic *Calippus* morphology (Fig.
21): i12 are aligned in a straight row; the i3 was originally positioned at a
sharp angle to them, but with wear its occlusal surface has become aligned
with that of the i12. The width across the i3s of UF 69951 is 58.4 mm. Due
to the post-mortem crushing, this value is probably within 2 mm of the true
width and is probably too small (as the teeth are compressed laterally). The
diastema between the i3 and c is short (4.6 mm). The left c is 7.5 mm long
and 6.1 mm wide.

Upper cheekteeth of *C. maccartyi* (Table 10; Figs. 20A-20C) are smaller
than average-sized individuals of *C. cerasinus* or *C. hondurensis*, but fall within
their observed ranges. UF 69951 is an adult, with the occlusal surface of the
M3 fully worn, and an M1 MSCH of about 27 mm. The P2 of UF 69951
seems relatively more heavily worn, perhaps pathologically, when compared
to the other teeth. The P2 protocone is short and rounded, with a broad
connection to the protoselene. It has no pli caballin, and the hypoconal
groove is a small lake on the left side, while the right side has lost all trace of
it. Fossette plications are limited to a vestigial pli prefossette and a single,
modest pli postfossette. The metastyle is still relatively prominent. On the
less worn UF 95407, there is a small pli caballin, a deep hypoconal groove
that is in the process of being closed off by a labial projection from the
hypocone, and an oval, very obliquely oriented protocone. The fossettes are
also simple, although the single pli prefossette and pli postfossette are deeper
than in UF 69951. On the P3 and P4, the protocone is large, more elongate-
oval in shape, oriented anterolabial-posterolingually, and with a slightly
flattened lingual border (Fig. 20A). The preprotoconal groove is moderately
deep, so that the protoconal connection is notably constricted. A single,
small pli caballin is present on both the P3 and P4 of the type. The more
heavily worn premolars from the referred Withlacoochee 4A sample lack pli
caballins, but still have moderate preprotoconal grooves. The P4 of UF
69951 retains an open hypoconal groove, while the P3 has an isolated lake.
The preprotoconal grooves of the M1 and M2 are shallower than those of the
premolars, thus broadening the protoconal connection, and the protocone is
less obliquely oriented (Fig. 20A). The type M1 and M2 both lack a pli
caballin, but the less worn UF 90299 has a very small one. The hypoconal
groove closes on molars variably during ontogeny; it would close on UF

90299 at an MSCH of about 20 mm, but would be present until late wear on UF 45535. On both M3s the hypoconal groove opens directly into the postfossette, a not uncommon condition in equid M3s. The M3 of UF 69951 also has an isolated protocone, a feature not observed in a sample of 25 specimens of *C. cerasinus* from the Love Site. An isolated protocone is rarely observed in M3s of *C. martini*. Molars in early wear-stages (as exemplified by UF 90299) have very deep preprotoconal grooves.

The fossettes of the P3-M3 are similar. A pli hypostyle or pli protoloph are not observed, except during earliest wear-stages. The opposing inner fossette margins are closely appressed (Figs. 20A-20B), more so than in other species of *Grammohippus*. Fossette plications are shallow, unbranching and not numerous, but are retained until the MSCH reaches about 20 mm or less.
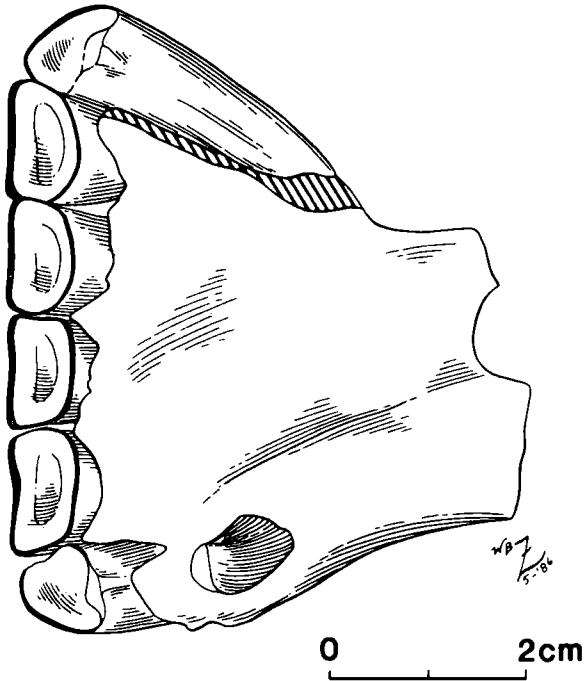
Figure 21. Occlusal view of mandibular symphysis of <u>Calippus</u> (<u>Grammohippus</u>) <u>maccartyi</u> n. sp.; UF 69951, holotype; from Moss Acres Racetrack Site, Marion County, Florida. Teeth present: R i1-i3; L i1-i3, c; R side of symphysis is broken and the i3 has been restored to near its original position.

With the limited sample, unworn crown heights are not directly observable. The specimen with the greatest MSCH (UF 45535, 40.2 mm) has formed roots and has a completely worn occlusal surface. Therefore, its unworn crown height would have been at least 5 to 10 mm greater. ROC of available specimens of *C. maccartyi* varies from 55 to 85 mm, much greater than that of *C. cerasinus* or *C. hondurensis* (their OR is 38-50 mm). The crowns are not as straight as those of *C. (Calippus)*, however.

The lower cheekteeth of *C. maccartyi* (Table 10; Figs. 20D-20E) are considerably advanced over other species of *Grammohippus*, with large, widely flairing metaconids and metastylids. They greatly resemble the basic enamel pattern observed in *Astrohippus*, as the metaconid, metastylid, and unpenetrated isthmus form a "Y" (Fig. 20D). In premolars (Figs. 20D-20E), the ectoflexid is shallow, the labial borders are rounded or only slightly flattened, and the lingual flexids are deep and persistent through much of the crown. The metaconid of the p2 is large and well developed. In earliest wear-stages, there may be plications extending posteriorly from the isthmus and/or protolophid on both premolars and molars. Molars resemble premolars more than in any other species of *Calippus*, but do differ in their deeper ectoflexids and narrower occlusal surfaces. On p3 to m3, the protostylid is a variably developed ridge that extends to near the top of the unworn crown, and that often becomes more prominent with wear (Fig. 20D). Even extremely worn molars (e.g. UF 53463) retain well developed lingual flexids.

Discussion.— *Calippus maccartyi* is recognized from only two early Hemphillian localities in north-central Florida. The combined presence of *Indarctos* and *Machairodus* at Withlacoochee 4A indicate a late early Hemphillian age (Becker 1985; Tedford et al. in press A). Neither is present at Moss Acres, but its fauna (Table 13) also indicates a younger age than either the Mixson's or McGehee local faunas. Those species that it does share with these two earlier Hemphillian faunas (e.g. *Cormohipparion ingenuum* and *C. plicatile*) are represented by morphologically more advanced individuals (Hulbert, in press B). Other taxa, e.g. *Nannippus minor* and *Aphelops mutilus*, are represented by more advanced species. Thus, the Moss Acres Racetrack Site is probably late early Hemphillian, but perhaps not as young as Withlacoochee 4A. *C. maccartyi* represents one of the youngest known species of *C. (Grammohippus)* and is the most derived in terms of dental evolution. The lower cheekteeth of *C. maccartyi* resemble those of *Astrohippus*; however, this is interpreted to represent parallelism and not an especially close phylogenetic relationship (see below). *Pseudhipparion simpsoni* is a third equid lineage that evolved a similar morphology (Webb and Hulbert 1986).

GENUS *Protohippus* LEIDY, 1858

Type Species.— *Protohippus perditus* (Leidy), 1858.

Included Species.— *P. vetus* Quinn, 1955; *P. supremus* Leidy, 1869; *P. gidleyi* n. sp.

Chronologic and Geographic Distribution.— Late Barstovian through early Hemphillian of Great Plains and Florida; Barstovian and early Clarendonian of Texas Gulf Coastal Plain; possibly Clarendonian of California.

Revised Diagnosis.— Medium- to large-sized, hypsodont, tridactyl equids with toothrow lengths generally between 125 and 145 mm in mature individuals. Malar fossa absent. DPOF large, teardrop-shaped, relatively shallow; distinctly rimmed dorsally and posteriorly in earlier populations, often with a small posterior pocket; less distinct in later populations, without a pocket. Lacrimal bone large, included in posterior region of DPOF. Diastema short; rostrum broad, but not to the degree of advanced species of *Calippus*; incisors form typical equine rounded arcade. Upper cheekteeth with large, elongate-oval protocones that are isolated from the protoselene to varying degrees during early wear-stages (most prevalent on P34 and M3); moderately large, single pli caballins on P34 (smaller and less persistent with wear on molars); simple but relatively persistent fossette plications; hypoconal groove generally remains open until at least middle wear; prominent parastyles on P34. Large protostylids on permanent and deciduous lower cheekteeth. Variably developed ectostylids on dp2-dp4.

Discussion.— Leidy (1858) first named *Protohippus* as a subgenus of *Equus*, but later (e.g. Leidy 1869) raised it to generic rank. It was commonly used in the latter half of the 19th Century; Leidy, Marsh, and Cope described a total of 11 species of *Protohippus* before 1900 (Gidley 1907). However, many of these were subsequently regarded as synonymous and/or belonging to other genera (Stirton 1940; Webb 1969), and only four species of *Protohippus* are here recognized as valid. In a series of papers based on an increasing number of relatively complete specimens with more accurate locality data, Gidley (1904; 1906; 1907) was able to redefine *Protohippus* and clearly distinguish it from *Pliohippus* and *Merychippus*. Gidley's (1907) concepts of *Pliohippus* and *Protohippus* were essentially followed by Osborn (1918) and Matthew (1926). McGrew and Stirton (e.g. McGrew 1938; McGrew and Meade 1938; Stirton 1940) proposed a horizontal reorganization of these taxa, in which a number of "primitive" species thought ancestral to a number of advanced genera were all placed in a single genus, *Merychippus*. *P. perditus* (the genotype) was one of these, thus *Protohippus* was synonymized with *Merychippus*, although retained as a subgenus. The chronologic age of a species played a major role in determining its generic

assignment in this scheme. They considered the boundary between the Miocene and Pliocene to fall between the Devil's Gulch and Burge Faunas, and all late Miocene non-anchitherine equids were placed in *Merychippus* sensu lato. The characters they used to define *Merychippus* are all primitive, and can no longer be considered valid reasons for taxonomic grouping. MacFadden and Skinner (e.g. MacFadden and Skinner 1981; MacFadden 1984a) have recognized pre-Burge equid populations with *Merychippus*-grade dentitions as members of advanced genera (*Hipparion* and *Cormohipparion*). A similar, vertical repartitioning of the taxa Stirton (1940) assigned to *Merychippus* (*Protohippus*) is therefore appropriate, and can be based on the stratigraphically controlled Frick collection of crania and associated dentitions. The phylogenetic relationships of *Protohippus* with other genera will be discussed at length below.

Quinn (1955:54) proposed the new genus *Eoequus* for a single specimen from the late Barstovian of the Texas Gulf Coastal Plain. As the name suggests, Quinn (1955:58) considered the new taxon to be directly ancestral to *Equus*. The holotype of *Eoequus wilsoni* is a young adult that is referred below to *Protohippus perditus*. *Eoequus* thus becomes a junior synonym of *Protohippus*.

Protohippus perditus (LEIDY), 1858
Fig. 22A; Tables 14-16

Equus (*Protohippus*) *perditus* LEIDY 1858:26-27.
Protohippus perditus (Leidy), LEIDY 1869:275-277; GIDLEY 1906:136-139
      (in part); GIDLEY 1907:882-883 (in part); OSBORN 1918:129-130;
      QUINN 1955:19-21 (in part); EVANDER 1978:41.
Protohippus or *Hippotherium profectus* COPE 1889:447.
Merychippus perditus (Leidy), COPE 1892:943; MCGREW and MEADE
      1938:200-202; STIRTON 1940:182; HESSE 1943:168-169;
      FORSTEN 1975:31.
Eoequus wilsoni QUINN 1955:54-58.
Merychippus circulus (Quinn), FORSTEN 1975:32-35 (in part).

Type Specimen.— USNM 619, a R maxillary fragment with P4-M3 (Leidy 1869, plate 17.1, 17.2).

Type Locality and Horizon.— From "the valley of the Niobrara River" (Leidy 1858:20) in Nebraska. Probably from the Valentine Formation (Devil's Gulch or Crookston Bridge Member?) or stratigraphic equivalent, late Barstovian.

Distribution.— Late, but not latest, Barstovian (about 12 to 14 ma) of the northern Great Plains and the Gulf Coastal Plain of Florida and Texas.

Referred Specimens.— Devil's Gulch Fauna, Devil's Gulch Horse Quarry, Brown Co., NE: F:AM 60350-60352, 60358, and 114067 5 skulls; F:AM 114091 mandible with dp2-m2. There are many additional, mostly uncatalogued, crania, mandibles, and teeth in the F:AM collection from this fauna. Material from the slightly older Crookston Bridge (Evander 1978) and Norden (Skinner and Johnson 1984) Faunas is also referable to *P. perditus*, and is principally housed in the UNSM and F:AM collections.

Cold Spring Fauna. Cold Spring Local Fauna, San Jacinto Co., TX: TMM 31219-165 assoc. R DP2-DP4,M1-M2 and L DP2-DP4,M2-M3; -230 partial skull with R DP3-DP4,M1-M2 and L DP1-DP4,M1-M2; -61, -328 2 L P2; -253 R P34; -329, -330 2 L P34; -331, TAMU 3030 2 R M12; TMM 31219-332 L M12; -333 R M3; -5 L M3; -203 assoc. R and L mandibles with dp2-dp4 (probably same individual as 31219-165); -43 R mandible with dp2-m1 (probably same individual as 31219-230); -204 R mandible with p4-m3; -337 L mandible with p2-m1; -138 L assoc. p4-m3; -168 assoc. (?) L p3-p4; TAMU 3027 R dp4; TMM 31219-334 R p2; -336 R p34; -335, TAMU 3028, 3029 3 L p34; TMM 31219-338-340 3 L m12. Noble Farm Local Fauna, Grimes Co., TX: TAMU 3031-3033 3 R P34; 3034 L M12; 3035 L mandible with dp2-m2; 3036 R p34. Chapel Hill, Washington Co., TX: TMM 31272-8 L M3. Goodrich Local Fauna, Polk Co., TX: TMM 31183-30, -37 and -66 assoc. skull with R and L P2-M3 and R and L mandibles with p2-m3 (holotype, *Eoequus wilsoni*; Quinn 1955, plates 10-13).

Bradley Fauna. Kingsford Mine (Paige No. 1 Dragline), Polk Co., FL: UF 61344 L M1.

Revised Diagnosis.— Slightly smaller and less hypsodont than *P. supremus*, with toothrow lengths of about 120 to 135 mm and unworn molar crown heights of about 47 mm. Relatively short postcanine diastema and large DP1. Shorter, more oval protocones than *P. supremus* or *P. gidleyi*; also shorter metaconid-metastylid complexes and entoflexid lengths.

Description.— The holotype of *Protohippus perditus* (Osborn 1918, Fig. 102) lacks precise locality data, and was recovered from a region where vertebrate fossils have been found ranging in age from the early Miocene to the Pleistocene. A large sample of upper dentitions from the Devil's Gulch Horse Quarry (DGHQ) closely match USNM 619 in size and morphology, and are here referred to *P. perditus* following unpublished work by Morris Skinner. This sample also includes associated mandibles and crania, thus permitting a more complete description of one of the earliest named North American equid species.

The cranial morphology of *P. perditus* is well preserved on several skulls from the DGHQ, especially F:AM 60350 and 60351. No malar fossa or depression is evident on these specimens, as well as USNM 619 or TMM
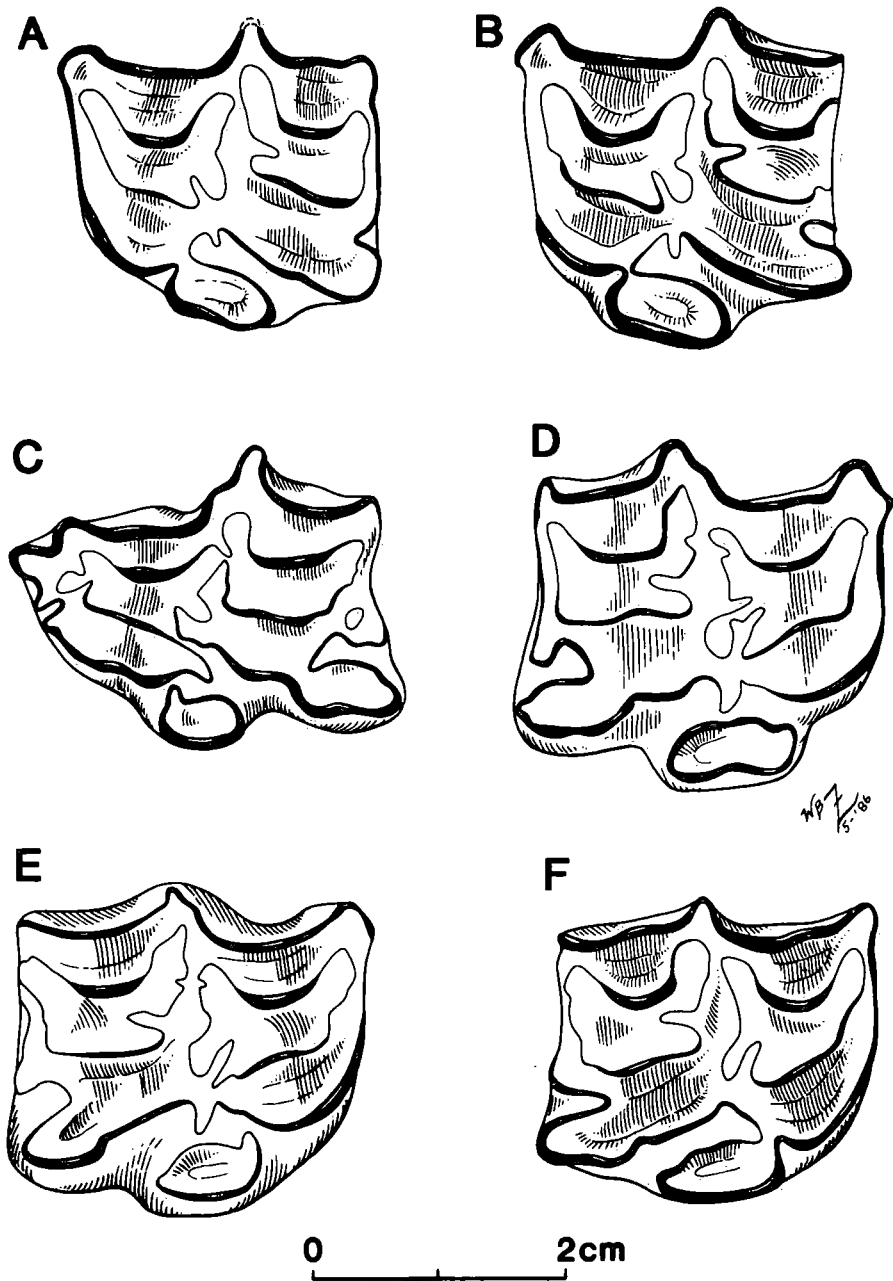
Figure 22. Occlusal views of upper cheekteeth of Protohippus from Florida. A. UF 61344, P. perditus, L P4, Kingsford Mine, Bradley Fauna (late Barstovian), Polk County. B. UF 28553, P. supremus, L P4, Grey Zone, Phosphoria Mine, Agricola Fauna (early Clarendonian), Polk County. C-F. P. gidleyi n. sp., Love Site, latest Clarendonian, Alachua County. C. UF 62482, L P2. D. UF 62497, R P34. E. UF 62500, R P34. F. UF 62540, R M12.

31183-30 (Quinn 1955, Plate 12).   The DPOF is large, oval or teardrop-shaped, and runs from above the anterior half of the M3 to the posterior half of the P3. Its greatest length is about 80 mm; its maximum height measured perpendicular to the latter and just posterior to the IOF is about 45 mm. The posterior and dorsal margins of the DPOF on the lacrimal and nasal bones are well rimmed, and there is a slight posterior pocket. The preorbital bar is relatively narrow (about 13.5 to 15.5 mm). The postcanine diastema is shorter than that of *P. supremus*, and the incisor region is only slightly expanded (Fig. 3; the muzzle width is about 38% of the UTRL). A relatively large DP1 (12 to 13 mm long) is retained with the adult dentition, functionally occludes with the p2, contains several distinct cones and lophs, and resembles those of *Pliohippus*.

The upper cheekteeth of *P. perditus* (Table 14; Fig. 22A) are characterized by oval (elongate-oval in early wear) protocones that are isolated from the protoselene in very early wear-stages (Quinn 1955, Plate 10.1), but which then rapidly connect. When isolated, the protocones have large anterolabial spurs. Protocones of the premolars are notably shorter than those of the molars.   In heavily worn molars, the protocone not uncommonly connects with the hypocone. Fossette plications are relatively simple and not as numerous as in *P. supremus* or *P. gidleyi*, nor is the prefossette loop so well formed. By moderate wear-stages, only a single pli prefossette and pli postfossette remain (Fig. 22A). The hypoconal groove remains open until moderate wear; it may simply fade with wear or persist as an isolated lake.   The pli caballin is generally less prominent than in *P. supremus* or *P. gidleyi* and is frequently absent in moderately worn teeth. The upper cheekteeth are moderately curved, with ROC usually about 45 to 55 mm.   Examples of measurable slightly worn or unworn teeth are rare. MSCHs for the slightly worn P2 and P3 of TMM 31183-30 are about 36 and 42 mm, respectively. The slightly worn M1 of TMM 31219-230 has an MSCH of 43.3 mm. Two very slightly worn molars from the DGHQ have MSCHs of 42 and 45 mm. Thus unworn MSCH of the M12 probably lies between 45 and 50 mm. The DP2-DP4 resemble the permanent cheekteeth, but the protocone is relatively much shorter, and the fossette plications are more numerous and persistent in early wear-stages (e.g. TMM 31219-165). Small pli caballins are present and the hypoconal groove remains open even in heavily worn DPs.

Lower cheekteeth (Table 15) are typically protohippine, with large protostylids on p3-m3 and dp34. The metastylid is equal or subequal to the metaconid in size. Permanent premolars in early wear most often have a long isthmus that connects to the metaconid, and the metastylid buds off the metaconid posteriorly and lingually. In some, the ectoflexid can be deep and penetrate the isthmus to varying depths (this morph is very common in the Cold Spring sample).   In the majority of observed premolars from the

DGHQ, the ectoflexid is shallow and does not, or only shallowly, penetrate the isthmus, however. The metaflexid contracts rapidly with wear (the primitive protohippine condition), as do the linguaflexid and entoflexid to a lesser degree. The p2 and dp2 have flattened anterior margins. Molars greatly resemble those of *Calippus martini*, except for the strong protostylids, slightly larger metastylids, and lesser mcch. The moderately well-cemented deciduous lower premolars are characterized by deep linguaflexids and ectoflexids that nearly divide the tooth. With wear, the linguaflexid retreats, along with the metaflexid, leaving a broad area of confluence between the metastylid, metaconid, and protoconid. Moderate wear exposes large ectostylids on the dp2-dp4, that rise about 5 to 6 mm above the base of the crown. Heavier wear reveals hypostylids that are especially well developed on the dp3.

Discussion.— *Protohippus perditus* has long been recognized as a characteristic member of the fauna from lower units of the Valentine Formation (McGrew and Meade 1938). However, Gidley's (1907) "neotype" of *P. perditus* (AMNH 10838) from the Clarendonian of South Dakota is instead referable to *Calippus martini* (Hulbert 1987a). The relatively complete referred material from the Valentine Formation allows a better understanding of *P. perditus* and aids the generic diagnosis. The referred specimens from the Gulf Coastal Plain, including the type of "*Eoequus*" *wilsoni* and UF 61344, resemble that from the DGHQ and USNM 619 in size, hypsodonty, and general dental morphology (Table 16; Fig. 22A), and indicate that the species was wide-spread during the late Barstovian.

Protohippus profectus was recovered along with the type of *Pseudhipparion retrusum* (Cope 1889), which suggests a late Barstovian age. It is synonymized with *P. perditus* rather than *P. supremus* because of its smaller size, weak fossette plications, and less well developed pli caballins. In the lower units of the Valentine Formation, *P. perditus* is found in lithosympatry with the slightly larger *Pliohippus mirabilis* (Leidy 1858). *P. mirabilis* differs from *P. perditus* in its very deep DPOF, its well developed malar fossa, and a number of dental characters outlined in Table 17. The two cannot be synonymous, as was proposed by Stirton (1940:182).

<div align="center">

Protohippus supremus LEIDY, 1869
Figs. 22B, 23; Tables 14-16

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Protohippus supremus LEIDY 1869:328 (in part).
Protohippus simus GIDLEY 1906:139-140; GIDLEY 1907:925-926;
        OSBORN 1918:136-138.

Pliohippus supremus (Leidy), GIDLEY 1907:889-890 (in part); OSBORN
    1918:150-151; STIRTON 1940:192; QUINN 1955:24-26 (in part);
    WEBB 1969:83-95 (in part); FORSTEN 1975:53.
Pliohippus simus (Gidley), MCGREW and MEADE 1938:201; STIRTON
    1940:192.
Hippotigris sellardsi QUINN 1955:46-48.
Hippotigris clarendonensis QUINN 1955, 49-50.
Hippotigris parastylus QUINN 1955:50-51.
Pliohippus martini (Hesse), FORSTEN 1975:48-53 (in part).
Pliohippus (Pliohippus) cf. *P. supremus* (Leidy), FORSTEN 1975:53-61 (in
    part).

Lectotype Specimen.— ANSP 11280.1, a slightly worn L P34. Selected
by Gidley (1907) from the syntypic series, he referred to it as a M1, but his
measurements clearly indicate which specimen he chose as the lectotype, as
later figured by Osborn (1918, Fig. 118.2).

Type Locality and Horizon.— Exact locality unknown, Little White
River region, South Dakota. Probably Clarendonian deposits of the Ogallala
Group.

Distribution.— Latest Barstovian and Clarendonian of northern Great
Plains (about 10.0 to 12.0 ma); Clarendonian of southern Great Plains, Gulf
Coastal Plain of Florida and Texas.

Referred Specimens.— Little White River region, SD: AMNH 980
partial skull with R I3, R and L DP1-M3 (type, *P. simus*); AMNH 10871 L
maxilla with P2-P4, M2-M3.

Burge Fauna. Burge Quarry, Cherry Co., NE: F:AM 60353 assoc. skull,
rami, and postcranial skeleton; 60356 skull with R and L DP1-M3; 108187,
114058-114063 7 maxillae or palates; 60357 assoc. skull, R and L rami;
Midway Quarry, Cherry Co., NE: F:AM 60354 assoc. skull, R and L rami.

Clarendon Fauna. MacAdams Quarry, Donley Co., TX: F:AM 111728
assoc. skull and rami. C. Risley Ranch Site, Donley Co., TX: TMM 255-29 R
mandible with p3-m3 (type, *H. clarendonensis*); TMM 255-17 L m12.

Lapara Creek Fauna. Bridge Estate Site, Bee Co., TX: TMM 31132-
284D R P34; -541, -542 2 R M12; -459 L mandible with p2-m3 (type, *H.
parastylus*); -335 assoc. p4,m2-m3; -237 L m12. Buckner Ranch Site, Bee Co.,
TX: TMM 30896-503 assoc. R and L P2-M3 (type, *H. sellardsi*); -206 and -
541 assoc. mandibles with R p3-m3 and L p2-m3; -240, -476 2 R mandibles
with dp2-m1; -420C, F assoc. L m2-m3; -447 R p34; -420G L p34. Farish
Ranch Site, Bee Co., TX: TMM 31081-1183 L p34; -664 R mandible with p2-
m3; -168E, F assoc. p4-m1; -1210 L p2.

Late Agricola Fauna. Gray Zone, Phosphoria Mine, Polk Co., FL: UF
28553 L P34. Nichols Mine, Polk Co., FL: UF 25125 R P4.

Revised Diagnosis.— Large *Protohippus* with toothrow lengths of about 130 to 145 mm and unworn molar crown heights of about 54 mm. Larger and more hypsodont than *P. perditus*, with a broader muzzle, smaller (on average) DP1, more elongate protocone, and more complex fossette plications. Hypoconal groove present until late wear-stages; forms lake on premolars. Protocones isolated from protoselene in early wear-stages of P3-M2, until moderate wear on M3; not as isolated as those of *P. gidleyi*. Metastylid large, well separated from metaconid by well developed, persistent lingual flexids especially on premolars.

Description.— Based on AMNH 9820 (holotype, *Protohippus simus*) and a number of crania from the Burge Member of the Valentine Formation, the facial region of *P. supremus* greatly resembles that of the genotypic species, *P. perditus*. No malar fossa is present. The DPOF is approximately the same size and in the same position as in *P. perditus*, but it is notably shallower and less well-rimmed (Osborn 1918, Plate 21.1). The Burge specimens retain a well defined posterior rim and a very slight pocket. Clarendonian specimens (e.g. AMNH 9820 and F:AM 111728) have an even shallower and less well defined DPOF without a posterior pocket, but are otherwise identical to the latest Barstovian (Burge) population. As noted by Gidley (1906) in his description of *P. simus*, the muzzle is very broad (about 45% of the UTRL), much greater than that of a similarly sized, typical equid (Fig. 3). The first two incisors are not linearly arranged, as in *Calippus*, but are slightly arcuate.

The upper cheekteeth of *P. supremus* (Tables 14, 16; Figs. 22B, 23) have very strong styles, including a well developed metastyle. The P2 has a shorter, rounder protocone than the other teeth; it is connected to the protoselene in all known specimens. The fossettes of the P2 tend to be simpler, and the hypoconal grooves close earlier than in the P34. The P34 have large, widely open parastyles and mesostyles, and small metastyles that are retained until late wear-stages. The protocone of the P34 is elongate; with wear it becomes shorter and wider. In early wear-stages, the protocone is isolated from the protoselene, but has a large labially directed spur. With wear, the spur connects with the protoselene (Fig. 23); this connection is at first greatly constricted by a deep preprotoconal groove, this condition persists until at least moderate wear-stages. The P34 protocone orientation is markedly oblique (Fig. 22B), and, in late wear-stages, the protocone does not connect with the hypocone. The P34 have a large, usually single (but occasionally branched) pli caballin that is reduced and lost at MSCHs of about 25 to 30 mm. The hypoconal groove remains open at least until moderate wear-stages; it closes to form a lake and disappears at a greater crown height than in the molars. Fossette plications are relatively complex and persistent for a protohippine, as only very greatly worn P34 totally lack plications (Fig. 23). A pli protoloph and pli hypostyle are uncommon, but occasionally found on slightly worn teeth. The posterior half of the prefossette almost always has
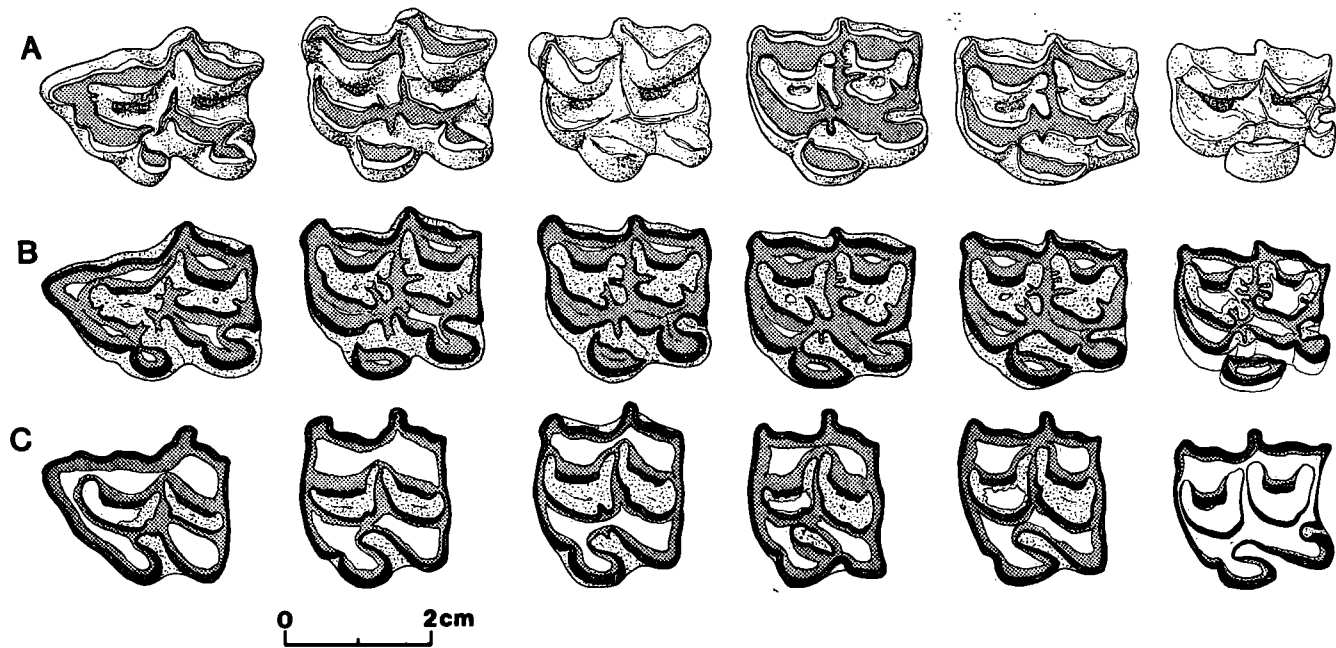
Figure 23. Cross-sectioned and occlusal views of left upper cheekteeth of Protohippus supremus, F:AM 108187, from the Burge Quarry, Valentine Formation, Brown County, Nebraska (very late Barstovian). A. Occlusal surface of teeth; P4 and M3 were beginning to erupt and are essentially unworn, P2-P3 and M2 very slightly worn; M1 slightly worn. B. Early maturity wear-stage. C. Near base of teeth. This specimen reflects the normal pattern of protocone attachment to the protoselene in the genus Protohippus. Note also the connection between the protocone and hypocone with very heavy wear on the M1.

two deep plications surrounding a large prefossette loop in moderate to slightly worn teeth, with a third accessory plication possible. The opposing side of the postfossette has a deep pli postfossette and an accessory plication. At moderate wear-stages, the accessory plications are lost, and only the deep folds remain. These are gradually lost only in very heavily worn P34s.

The molars exhibit basically the same pattern as the P34 (Fig. 23), although the pli caballin is smaller and lost earlier in wear, the hypoconal groove remains open until very late wear-stages (and does not form a lake), and the protocone orientation is not as oblique. In late wear-stages, the protocone of the M12 may unite with the hypocone (Fig. 23 and F:AM 111728), isolating the postprotoconal valley as a fossette. This occurs less frequently and typically only in much more deeply worn teeth than in *Pliohippus*. In terms of degree of isolation of the protocone, the M3 ranks highest, followed by the P34, then the M12, and finally the P2. Even moderately to heavily worn M3s can retain isolated protocones, for example the left M3 of AMNH 9820. This same pattern is observed, to an overall greater degree of isolation, in the younger species *P. gidleyi*. The deciduous premolars are similar to those of *P. perditus*, having more complex internal fossette borders with persistent plications and rounded protocones. The DP1 is retained with the adult dentition, but is relatively (and usually absolutely) smaller than that of *P. perditus* (x = 10.3 mm; OR = 9.2-11.1 mm; n = 5). P3-M2 are moderately curved, with ROC generally between 45 and 50 mm. Unworn upper cheekteeth that can unambiguously be assigned to *P. supremus* are rare, thus maximum MSCHs are estimated from slightly worn teeth, and should be considered minimum values. These estimates are about 38 mm for the P2 and about 55 mm for the P3-M2.

Lower cheekteeth of *P. supremus* (Table 15) are especially characterized by large protostylids that appear on the occlusal surface shortly after the onset of wear, and relatively large metastylids. In premolars, the metastylid is expanded equally with the metaconid. This, in conjunction with large, deep lingual flexids in early and moderate wear-stages gives the premolars a hipparionine-like appearance. The ectoflexid of the premolars is quite variable in its depth of penetration of the isthmus, but is most often shallow. The contraction of the lingual flexids is delayed relative to that observed in *P. perditus* and most species of *Calippus*. In general, the isthmus connects to the metaconid, or between the metaconid and metastylid, but occasionally to the metastylid as observed by Quinn (1955, Plate 9.5). The molars also have enlarged and expanded metaconids and metastylids, but are otherwise of typical protohippine morphology. Lower deciduous premolars are slightly larger, but similar to those of *P. perditus*, with low ectostylids and large protostylids on dp34. The dp2 has a flattened anterior border, and frequently a small protostylid. The anterior margin of the p2 is often similarly truncated in later wear-stages.

Discussion.— Leidy (1869) based *Protohippus supremus* on three isolated upper cheekteeth from different individuals. He figured two of the specimens (Leidy 1869, plate 27.3 and 27.4) and described the third as unworn. Gidley (1907:889), acting as first reviser, selected one of the figured specimens (ANSP 11280.1) as the lectotype, the tooth Leidy (1869) described in most detail and figured in Plate 27.4 (reillustrated by Osborn 1918, Fig. 118.2). Gidley's (1907) choice of a lectotype is critical, as the two principal syntypes apparently represent distinct species of different genera. The lectotype, here interpreted to represent *Protohippus*, is a premolar and not an M1, as was stated by Gidley (1907) and repeated by Osborn (1918). Quinn (1955:24) also recognized that it is a P34, but failed to properly grasp its phylogentic significance. The specimen has the following characters, which indicate that it is a premolar and not a molar: (1) parastyle open and very large (it is somewhat larger than indicated in the illustrations); (2) mesostyle widely open, not constricted; and (3) its angle of attrition is anterior (the method of Bode 1931). This determination is important, as the dimensions of ANSP 11280.1 (Table 16), while matching those of referred P34s, are much larger than average for molars. The paratype (ANSP 11280.2) is a true molar (probably a M2), despite its much greater APL than the lectotype. Besides size, the lectotype has six characters that indicate its referral to *Protohippus* rather than *Pliohippus*: (1) protocone isolated from protoselene; (2) very strong pli caballin that nearly touches the protocone; (3) very long prefossette loop that extends lingually farther than the main body of the prefossette; (4) deep hypoconal groove that would have remained open until late wear-stages; (5) large parastyle; and (6) radius of curvature of about 50 mm. All these are characteristic of premolars from the referred sample of *Protohippus supremus* and differ considerably from the conditions found in contemporary Clarendonian *Pliohippus* populations (pers. obs. and Skinner et al. 1977). The paratype is referable to *Pliohippus* based on its greater size, lower radius of curvature (40 mm), smaller prefossette loop, and the absence of a pli caballin. While Gidley (1907) did not clearly state which of the two he considered the type, the measurements he gives are those of the specimen that Osborn (1918) later stated was the lectotype. Because his purpose was to place Leidy's species in *Pliohippus*, Gidley's (1907) choice of a lectotype was ironically incorrect, as his study was otherwise the first to clearly enumerate the differences between *Protohippus* and *Pliohippus*, and he used characters that were ignored by later workers (e.g. Stirton 1940).

The lectotype of *P. supremus* matches in size, curvature, and morphology a well represented sample from the very late Barstovian and Clarendonian of Nebraska and South Dakota. Although similar in many features, it is more advanced than, and clearly distinct from, *P. perditus* (as was first recognized by Gidley 1906 in his description of *P. simus*). The important generic characters this referred sample shows are: lack of a malar fossa; large, shallow DPOF;

broadened muzzle; isolated protocones in early wear-stages; and well developed protostylids. The large series of associated dentitions in various wear-stages from the Burge Fauna indicate that the differences between the types of *P. supremus* and *P. simus* (both were collected from the Little White River region of South Dakota) result from differing degrees of wear, and that the two are not specifically distinct. Based on priority, the proper name is *P. supremus*.

Protohippus and *Pliohippus* lived contemporaneously, and apparently sympatrically, in Texas and the Great Plains from the late Barstovian to the early Hemphillian. Gidley (1907), primarily using cranial characters, recognized the differences between the two and allied *Calippus* (his *Protohippus placidus*) with *Protohippus*. Later studies (e.g. McGrew and Meade 1938; Stirton 1940) emphasized the use of upper cheekteeth to determine relationships (at the expense of cranial and lower cheektooth features), and contemporary populations of the two genera were frequently lumped into one species. For example, Stirton (1940) proposed that *P. perditus* and *Pliohippus mirabilis* were synonyms, and Webb's (1969) referred sample of "*Pliohippus*" *supremus* includes specimens of both *Protohippus* and *Pliohippus*. Table 17 contrasts the features of *Protohippus* and *Pliohippus* and is based on the large series of associated skulls and mandibles in the Frick collection.

Webb (1969) provided the most complete discussion of the relationships of *Pliohippus* s.l. (including *Protohippus* as recognized here) in what might be termed the post-Stirton (1940) period. Webb correctly concluded (in my opinion) that many of the previously named, large, Clarendonian species of *Pliohippus* were synonymous. Webb (1969:95) hypothesized that species of *Pliohippus* could be divided into two groups, one with a shallow "lacrimal" fossa and no malar fossa, the other with deep malar and lacrimal fossae. He bemoaned the lack of an adequate sample of skulls with which to test this hypothesis. The Frick collection, then unavailable to Webb for study, contains such a sample. Another factor then creating confusion was the common perception that *Pliohippus pachyops* from the Clarendon Fauna displayed a "*Protohippus*"-type face and a "*Pliohippus*"-type dentition, suggesting that the two could not be separated. The equine dental features of the type of *P. pachyops* include dp3 and dp4 with very reduced protostylids and no ectostylids, and the connected protocone on the slightly worn M1. Recently, the holotype of *P. pachyops* has been further prepared, and removal of matrix in the ventral preorbital region revealed the presence of a small but distinct malar fossa similar to the one found on the type of *Pliohippus fossulatus*, also from the Clarendon Fauna (D. Winkler, pers. comm.). *P. simus* cannot be synonymized with *P. pachyops*, as Webb (1969) suggested, because of both its cranial and dental morphology.

The results of this study indicate that Webb's (1969) preferred hypothesis about Clarendonian *Pliohippus* s.l. was correct in its essential point (i.e. there are two taxa clearly differentiated on the basis of facial fossae and other characters), but that the names he chose for the two (*Pliohippus supremus* and *Pliohippus pachyops*) were incorrect. Instead, the presence of two genera are indicated, *Pliohippus* s.s. and *Protohippus*. With the referral of *P. supremus* to *Protohippus*, the next available name for the large Clarendonian *Pliohippus* is *Pliohippus pernix* Marsh (1874), the genotypic species. A review of the systematics of *Pliohippus*, and the relationships of *Dinohippus* and *Pliohippus*, is clearly needed, as both are paraphyletic assemblages as currently perceived in the literature.

A number of species and specimens from beyond the type region are referable to *Protohippus supremus*. "*Hippotigris*" *clarendonensis* Quinn from the Clarendon Fauna resembles *P. supremus* rather than *Calippus martini* or *Pliohippus pernix* with its large metastylids, well developed lingual flexids and protostylids, and reduced ectoflexid depth on m1-m3. F:AM 111728, which was illustrated by MacFadden (1984a, figs. 66 and 69) as *Neohipparion affine*, is another Clarendon specimen of *P. supremus*. Based on examination of the F:AM, TMM, and PPM collections, *Protohippus* is rare in the Clarendon Fauna, while *C. martini* and *P. pernix* are common. Similarly, *P. supremus* is rare in the Minnechaduza Fauna, although it is common in the Burge. As the decline coincided with the appearance of *C. martini*, competition with that species may have played a role in its drastic reduction in abundance. *P. supremus* is also present, but again rare relative to *C. martini* and *P. pernix*, in the Lapara Creek Fauna. Quinn (1955) named two species of *Hippotigris* from the Lapara Creek Fauna, *H. sellardsi* and *H. parastylus*, that are referable to *P. supremus*. The three figured upper teeth (Quinn 1955, plate 4.1-4.3) are also referable to *P. supremus*, although the lowers called "*Pliohippus*" *supremus* (plate 4.4) are instead referable to *P. pernix*. Two specimens from Florida, UF 28553 (Fig. 22B; Table 16) and UF 24125 also represent *P. supremus*. Although moderately worn, UF 28553 still retains a well developed prefossette loop and a pli caballin, the hypoconal groove is open, and the protoconal connection is tightly constricted. The slightly worn UF 24125 (MSCH = 48.5 mm) has an isolated protocone with a large spur, and a large prefossette loop. It has an ROC of 65 mm, unusually high for the species. The rare nature of *P. supremus* in the Agricola Fauna is again associated with the presence of *Calippus martini*.

Protohippus gidleyi new species
Figs. 22C-22F, 24-25; Tables 14-16

Dinohippus or *Pliohippus* sp., HIRSCHFELD and WEBB, 1968:247, 249.
cf. *Pliohippus* sp., WEBB et al., 1981:527.

Type Specimens.— Holotype, UF 62473, assoc. R P2-M3 and L P2-M1.
Paratype, UF 32173, R mandible with p2-m3, missing symphysis and most of
ascending ramus.

Type Locality and Horizon.— Love Site (NW 1/4, SW 1/4, NW 1/4 sec.
9, T11S, R18E, Archer Quad.), 1.5 km N of Archer, Alachua Co., Florida
(Webb et al. 1981); fluvial sediments of the Alachua Formation, very late
Clarendonian, or about 9.0 ma.

Etymology.— Named in honor of James W. Gidley, an outstanding
scholar of mammalian systematics and evolution; especially for his
contributions to the study of *Protohippus*.

Distribution.— Very late Clarendonian to early Hemphillian of Florida
(about 6.5 to 9.0 ma); early Hemphillian of Nebraska.

Referred Specimens.— Love Site, Alachua Co., FL: UF 32261 R maxilla
with P2,P3-M3; 32298/32299 assoc. R P3-M3 and L P2-M3; 32269 assoc. R
P2-P3,M1,M3 and L P4-M3; 67703 assoc. R M1-M3; 60875 assoc. R M1-M2;
32279 assoc. L P4-M3; 65237, 69821 2 R DP2; 36044, 36095, 36101, 36123,
96882 5 L DP2; 65231-65232, 68849-68850, 92958-92959, 96893-96900 14 R
DP34; 65233-65236, 92960, 96883-96892 15 L DP34; 36031, 36057, 60245,
62471-62472, 62474-62475 7 R P2; 36146, 36225, 36236, 62476-62477, 62479-
62482, 92992 10 L P2; 61350, 62493-62502, 62504-62510, 62537 19 R P34;
61349, 62483-62491, 62513-62521 19 L P34; 62536, 62539-62540, 62542-
62550 12 R M12; 62522-62532, 62534-62535 13 L M12; 68822-68824, 68826-
68831 9 R M3; 68832-68838 7 L M3; 32207 R mandible with p3-m3; 32167,
32209 2 L mandibles with p3-m3; 32242 L mandible with p4-m2; 32205 assoc.
R dp2-dp3; 64402 assoc. L dp2-dp4; 67704 assoc. R p3-m3; 67747 assoc. R
p4-m3; 32129, 32135, 32140, 32220, 32243, 32288, 36279, 67729, 67746,
68776, 68782, 68787 12 partial mandibles or assoc. lower dentitions; 69802,
90267, 96538 3 R dp2; 90187, 90268-90269, 96537, 96917 5 L dp2; 90278-
90279, 96539 3 R dp34; 90270-90277, 96540-96544 13 L dp34; 36290-36296,
96953-96956 11 R p2; 36297-36300, 67701-67702, 92961, 96331, 96950-96952
11 L p2; 67705-67723, 96957-96959 22 R p34; 67724-67728, 67730-67745,
67748, 96960-96961 24 L p34; 67779-67800, 68781, 96964-96966 26 R m12;
67749-67778, 92962, 96962-96963 33 L m12; 68770-68779, 92991, 96533 12 R
m3; 68758-68769, 96523, 96534 14 L m3.

McGehee Farm, Alachua Co., FL: UF 45634 R M12; 17138 R p2; 19238 R p34; 16633, 45622 2 R m12; 7239 L m12; 45630 R m3.

Haile 19A, Alachua Co., FL: UF 52963 L p34.

Pareners Branch Site, Alachua Co., FL: UF 98488 R P2.

Mixson's Bone Bed, Levy Co., FL: F:AM 113639 assoc. R P4 and L P2-M3.

Withlacoochee River Site 4A, Marion-Citrus Cos. boundary, FL: UF 45521 assoc. R and L DP2-DP4,M1.

Cambridge Fauna, UNSM loc. Ft-40, Frontier Co., NE: UNSM 90641 skull; 2634 R maxilla with P2-M3; 4024, 4072-4075, 4078-4079, 4082, 4251 9 isolated upper cheekteeth; 2635 assoc. R mandible with p2-m2 and L mandible with p2-m3; 2951, 4046-4047, 4049-4050, 4052, 4054, 4056-4058, 4062-4065, 4067, 4237 16 isolated lower cheekteeth.

Diagnosis.— *Protohippus* intermediate in size between *P. perditus* and *P. supremus*, with toothrow lengths of 125 to 135 mm. Unworn molar crown height about 58 mm. Protocones of P3 and P4 generally isolated for uppermost 20% of crown, then connected to protoselene at MSCHs of 30 to 40 mm. M3 protocone also often isolated until moderate wear-stages, but may connect earlier. P2, M1, and M2 protocones generally isolated only in very early wear-stages. Protocone of P3-M2 large, elongate; on M12 connected to hypocone in latest wear-stages. Anterostyle of P2 reduced. Lower cheekteeth similar to those of *P. supremus* but with more expanded metaconid-metastylid complex, more persistent lingual flexids, and less prominent protostylids. Paraconid of p2 and dp2 less flattened than in *P. supremus*. Ectostylid of dp2-dp4 rudimentary.

Description.— The holotype, UF 62473 (Fig. 24A; Table 16), consists of an associated assemblage of upper cheekteeth of a young adult. The M3 had only partially erupted, as its posterior half is not yet fully worn. The specimen evidently represents an individual whose remains were scattered by currents, as the teeth were recovered from several contiguous quadrants and were not recognized as being associated in the field. That they represent a single individual is evidenced by similarity of preservation, their identical wear-stage, and the goodness of fit between them. The P2 (Fig. 24A) resembles others in the referred sample of moderate wear with its rounded protocone, well developed preprotoconal groove, lack of a pli caballin, deep hypoconal groove, simple fossettes, and relatively short anterostyle. The P34 have larger styles, moderate pli caballins, deep hypoconal grooves, and oval-elongate protocones with constricted protoconal connections and pointed posterior ends. The protocone of the right P4 is still isolated (Fig. 24A), but its spur is within 1 mm of the protoselene, and it would no doubt have connected after slightly more wear. The M1 and M2 of UF 62473 differ from the P34 only slightly in size (Table 16), but do not have pli caballins, their protocones are more broadly connected and less obliquely oriented, have weaker styles, and
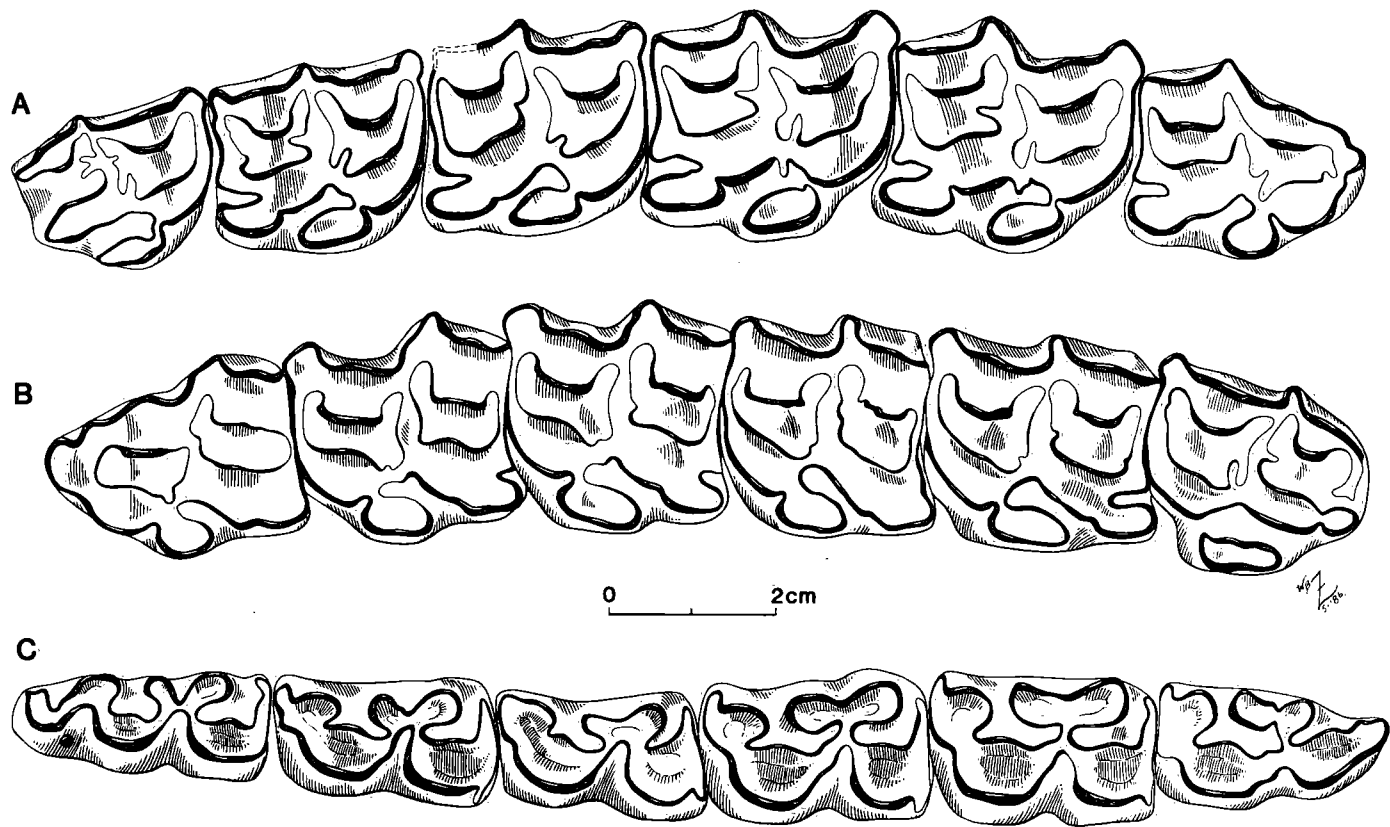
Figure 24. Occlusal views of upper and lower cheekteeth of _Protohippus gidleyi_ n. sp. from the Love Site, latest Clarendonian, Alachua County, Florida. A. UF 62473, associated R P2-M3, holotype, early moderate wear-stage. B. UF 32298, associated L P2-M3, late moderate wear-stage. C. UF 32173, associated R p2-m3, paratype, moderate wear-stage.

smaller prefossette loops. The protocone of the M3 is connected to the protoselene by a very narrow isthmus; most M3s of similar MSCH in the topotypic sample have isolated protocones.

Upper cheekteeth of *P. gidleyi* (Figs. 22C-22E, 24A-24B; Tables 14, 16) resemble those of *P. supremus* in most regards. They are only moderately curved, with ROC of molars between 50 and 60 mm. The P2 in early wear
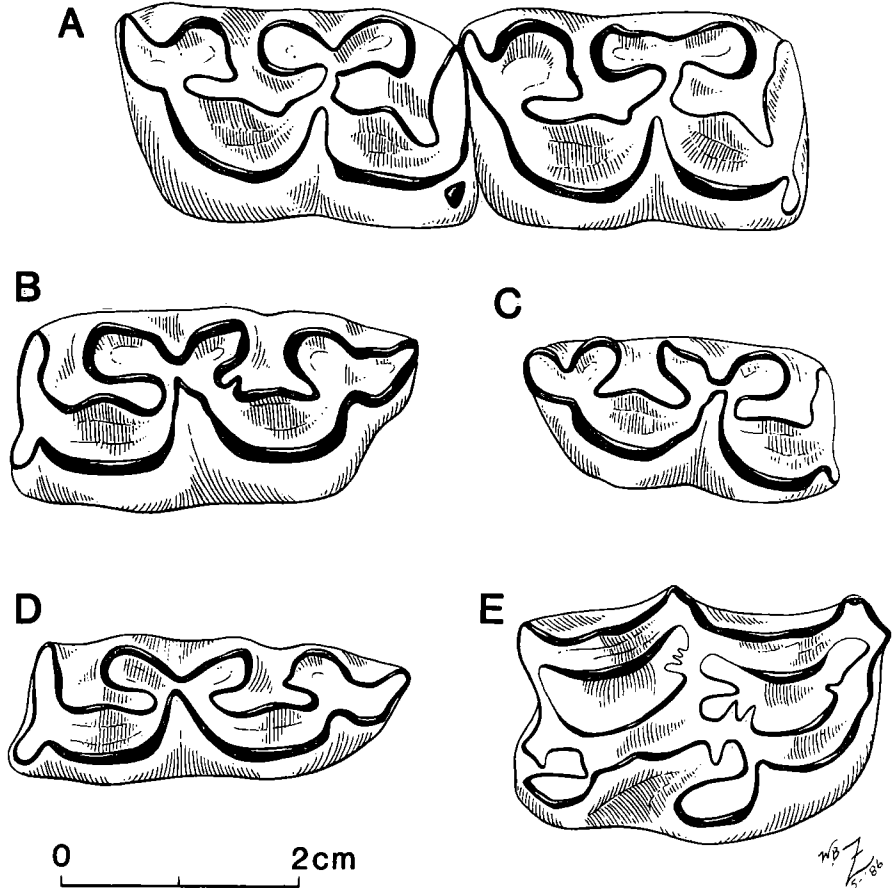
Figure 25. Occlusal views of upper and lower cheekteeth of Protohippus gidleyi n. sp. from the Love Site, latest Clarendonian, Alachua County, Florida. A. UF 67704, associated R p3-p4, early wear-stage. B. UF 67769, L m12, early wear-stage. C. UF 45622, R m12, early moderate wear-stage. D. UF 90274, L dp34. E. UF 65232, R DP34.

(Fig. 22C) has a rounded, isolated protocone with a spur, and the postprotoconal valley is often confluent with the prefossette (e.g. UF 62481, 62482). A strong metastyle is usually present, but it tends to fade with wear, as does the pseudoparastyle. The anterostyle is often weak, giving the P2 a more blunt appearance, rather than its usual triangular form. The prefossette and postfossette are confluent in over half the sample of P2s from the Love Site, although they are separate in almost all of the heavily worn specimens (Fig. 24B). In early wear, the P2 can have well plicated fossettes (e.g. UF 62476), but these soon fade with wear, leaving at most a single pli prefossette and pli postfossette. Pli caballins are rarely present, and almost always weaker than those of the P34. With wear, the protoconal connection widens, the fossettes lose all plications and become more narrow, and with heavy wear the hypoconal groove is lost. The P34 (Figs. 22D-22E) have strong styles, including metastyles, deep hypoconal grooves that persist until about 45% of the crown is worn (Fig. 26), and moderately complex fossettes. The hypoconal grooves are almost always lost without forming a lake. A single, generally small pli protoloph or pli hypostyle is occasionally present in the upper quarter of the crown. In early wear-stages, the posterior half of the prefossette may have up to four (two or three are more common) plications, and the anterior half of the postfossette usually bears one or two. The prefossette loop is well developed, but is usually not as long as in *P. supremus*. Moderate to heavily worn P34s generally retain one or two plis prefossette and a single, deep pli postfossette. These too tend to be lost as MSCHs reach 21 mm and less. This is also the period when the pli caballin is usually lost. The protocones tend to be long, often with flattened to slightly concave lingual borders. The MSCH at which the protocone attaches to the protoselene is variable (Fig. 26), but usually between 30 and 40 mm. Prior to connecting, the protocone bears a large, anterolabial spur (Fig. 22E). After the connection, the preprotoconal groove remains deep until latest wear-stages (Fig. 24B).

The M12 tend to be of about the same APL as the P34, but somewhat narrower (Table 14). As is typical for protohippines, the fossette plications are less numerous and are lost at earlier wear-stages than the P34, and pli caballins are found in only the earliest wear-stages (Figs. 22F, 24A). The protocone is connected rapidly with wear, is oriented much less obliquely than in the P34, and becomes connected to the hypocone with heavy wear. The protoconal connection remains constricted throughout much of the crown, with a deep preprotoconal groove. Metastyles are much less prominent than on the P34. The hypoconal groove remains open until the MSCH reaches 20 mm or less. Unworn or slightly worn MSCHs are about 39 mm for P2, 50 mm for P34, and 58 mm for the M12.

Deciduous upper premolars are narrower counterparts to their permanent successors (Fig. 25E). The DP2 has a short protocone and a poor

pli caballin.   The DP34 have elongate protocones, generally strong pli caballins, well developed styles, and moderately simple fossettes.   The hypoconal groove is deep and a pli dihypostyle is usually present.

Lower cheekteeth of *P. gidleyi* (Tables 15-16; Figs. 24C, 25A-25D) especially resemble those of *P. supremus*, the principal difference being that the younger species tends to exhibit advanced features, such as elongated metaconids and metastylids, through a greater percentage of the crown. The paratype, UF 32173, is a typical example of a moderately worn individual (Fig. 24C). Deep lingual flexids are retained on all but the m1, which is starting to lose the metaflexid and shorten the metastylid. The lower premolars retain expanded metaconids and metastylids and relatively deep lingual flexids even at crown heights of less than 20 mm. In very early wear-stages, the bases of the metaflexid and entoflexid may bear several plications (Fig. 25B), but these are soon lost with wear.   The p34 ectoflexid is a broad "V," generally penetrating into the isthmus to a depth about that of the base of the entoflexid (Fig. 25A). The ectoflexid of the p2 is shallower, not penetrating the isthmus, and the paraconid is usually angular in moderate to early wear-stages, becoming more blunt with heavy wear as in *P. supremus.* In the molars, the ectoflexid almost always separates the isthmus. In early wear-stages, the deep, "V"-shaped linguaflexid and the ectoflexid nearly completely separate the metaconid and metastylid, except for a narrow commissure (Fig. 25C). With wear, both retreat, so that there is greater dentine confluence between the metaconid and metastylid (Fig. 24C). In early to moderate wear-stages the metastylid is nearly as large as the metaconid, but tends to be angular while the latter is more rounded. Only in later wear-stages is the metastylid noticeably smaller and less lingually placed than the metaconid. Moderate protostylids appear on the occlusal surface shortly after the onset of wear on the p3-m3, and may at first be isolated from the protoconid (e.g. the m2 of UF 67704); they are stronger in p34 than m1-m3, but vary with age. The labial borders of the protoconid and hypoconid are rounded. Lower deciduous premolars are like those of *P. supremus* (Fig. 25D), but have more rudimentary ectostylids.   The strong protostylids, however, serve to distinguish them from the dp2-dp4 of *Pliohippus.* As in the permanent teeth, the protostylid is often isolated from the protoconid in early wear-stages (e.g. UF 64402).

Cranial features of *P. gidleyi* are known only from UNSM 9064, a nearly complete skull from the referred Nebraskan population. The dentition of UNSM 9064 is extremely worn and nondiagnostic (except to indicate that it is a protohippine or equine).   The broadened muzzle and short diastema distinguish it from *Dinohippus*, the only other large equine in the fauna. It is larger and with a less broadened and robust muzzle than in advanced species of *C. (Grammohippus).* The facial region of UNSM 9064 has been distorted by crushing, and the depressions in the malar region are of post-depositional
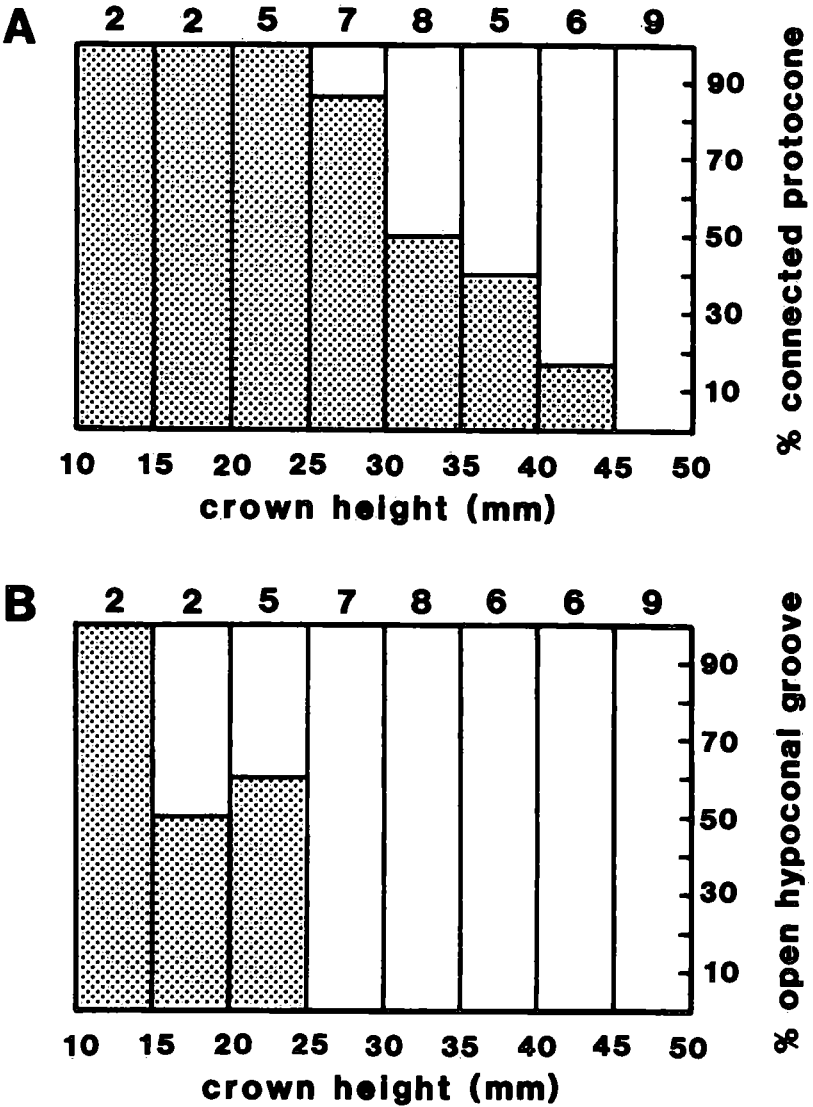
Figure 26. Histograms indicating at what wear-stage the protocone connects to the protoselene, and the hypoconal groove becomes closed in upper third and fourth premolars of the Love Site population of <u>Protohippus</u> <u>gidleyi</u> n. sp. A. Percentage of specimens in each 5 mm wear-class with (shaded) and without (unshaded) connected protocones. All specimens with less than 50% of original crownheight have connected protocones. B. Percentage of specimens with open hypoconal grooves (unshaded) and those that have lost the hypoconal groove (shaded). Numbers above each wear-class indicate the sample size for each group.

origin. The dorsal facial region of the somewhat better preserved right side indicates the presence of a faint DPOF located very anterior to the orbit, dorsal to the M2 to P3, and about 50 mm long. It is not distinctly rimmed or pocketed. Small alveoli indicate that a DP1 was retained with the permanent dentition.

Discussion.— *Protohippus gidleyi* is the youngest and most derived species of *Protohippus*. Unworn crown heights of its cheekteeth are about 5% greater than those of *P. supremus*. Its lower cheekteeth have the most expanded metaconids and metastylids of any protohippine, and elongated metaflexids and entoflexids remain deep until very late wear-stages. The most interesting trend evident in *P. gidleyi* is the tendency for increased isolation of the protocone from the protoselene. Possession of isolated protocones is generally considered structurally inferior to the connected condition (Stirton 1941). The trend in *Protohippus* for increased protocone isolation, along with the successful radiation of the hipparionines, suggests that this hypothesis is incorrect.

The topotypic sample of *P. gidleyi* contains a number of upper and lower dentitions, along with many isolated cheekteeth, thus allowing a good estimate of individual and ontogenetic dental variation. Several early Hemphillian sites from Florida contain a few teeth that cannot be distinguished from the Love Site sample of *P. gidleyi*. UF 45521, a juvenile individual from the late early Hemphillian, is only provisionally referred to *P. gidleyi*. The protocone of the M1 is relatively small, and the fossettes are somewhat more plicated than in the topotypic population. A well represented sample from the late early Hemphillian of Nebraska suggests that the latter feature may be a chronoclinal trend within *P. gidleyi*. This sample is important, as it includes the only known skull of *P. gidleyi*. It demonstrates notable differences in muzzle and fossae morphology from *Dinohippus*, *Pliohippus*, and *Calippus* and corroborates the dental evidence that the species belongs in *Protohippus*. The minor differences between the Love Site and Ft-40 populations are best explained by geographical variation and chronoclinal evolution. For example, the protocone of the M12 tends to be more isolated in the younger sample, surely a continuation of the trend observed throughout the entire genus.

PHYLOGENY OF *CALIPPUS* AND *PROTOHIPPUS*, AND THEIR RELATIONSHIPS WITH OTHER EQUID GENERA

Protohippus and *Calippus* are here hypothesized to form a monophyletic clade based on several shared derived cranial and dental character states. As with all attempts to examine the interrelationships of hypsodont equid

genera, this analysis is hampered by a vast number of poorly known, late Hemingfordian and Barstovian species that lie at the base of the Miocene radiation of the Equinae. These species are all traditionally referred to the genus *Merychippus*. Problems associated with many of these primitive species are lack of adequate cranial material, poor sample sizes of cheekteeth, paucity of associated upper and lower dentitions, and inadequate stratigraphic data for type specimens. The following, therefore, is a *preliminary* assessment of phylogenetic relationships among protohippine and equine genera.

Using the character states presented in Table 18, hypotheses of evolutionary relatedness of protohippines with other equid taxa were formulated using standard cladistic methods. Character state polarity was primarily determined by the outgroup method, i.e. the character state found in one or more taxa considered the probable sister group(s) of the taxa being studied is assumed to be primitive. Four outgroups were used: "*Parahippus*" *leonensis*; "*Merychippus*" *gunteri*; "*M.*" *primus*; and the Hipparionini. "*P.*" *leonensis* is especially well represented from the early Hemingfordian Thomas Farm Site (Simpson 1932; Bader 1956; Forsten 1975; Hulbert 1984), and has long been considered closely related or ancestral to later equids (Stirton 1940; Downs 1956). The late Hemingfordian "*M.*" *gunteri* is at present known only from isolated teeth, partial toothrows, and a limited sample of post-cranial elements (Simpson 1932); dentally it is among the least progressive of species commonly referred to "*Merychippus*" (e.g. Stirton 1940). "*M.*" *primus* is known from a large series of skulls, mandibles, and post-cranial elements from the late Hemingfordian Sheep Creek Fauna (Osborn 1918; Matthew 1924; Skinner et al. 1977; Evander 1985), but detailed descriptions of them have never been published. The Hipparionini are a monophyletic clade (Forsten 1982; Hulbert 1987b) of at least six genera. The character states listed for the Hipparionini represent the primitive states for the tribe as determined by a separate phylogenetic analysis.

Figure 27 demonstrates the cladistic relationships of the protohippines and equines using cranial and dental characters (Table 18). Both form reasonably well defined, monophyletic clades, as each are united by synapomorphies of the dentition and by cranial characters. There are three shared derived character states that join these two clades (at Node 1, Fig. 27): protocones that connect to the protoselene in very early wear-stages; relatively simple internal fossette margins; and molar metaconids positioned notably more lingually than the metastylids. The interrelationships of equines (*Astrohippus, Pliohippus, Equus,* etc.) are currently under study by B. MacFadden. They are here treated as a single, monophyletic taxon (although this may be disproven with further investigation) that forms the sister group of the protohippines. Provisionally, they are derived with respect to *Calippus, Protohippus,* and their common outgroups by their possession (at Node 2, Fig. 27) of: well developed malar fossae (secondarily lost in some); moderately
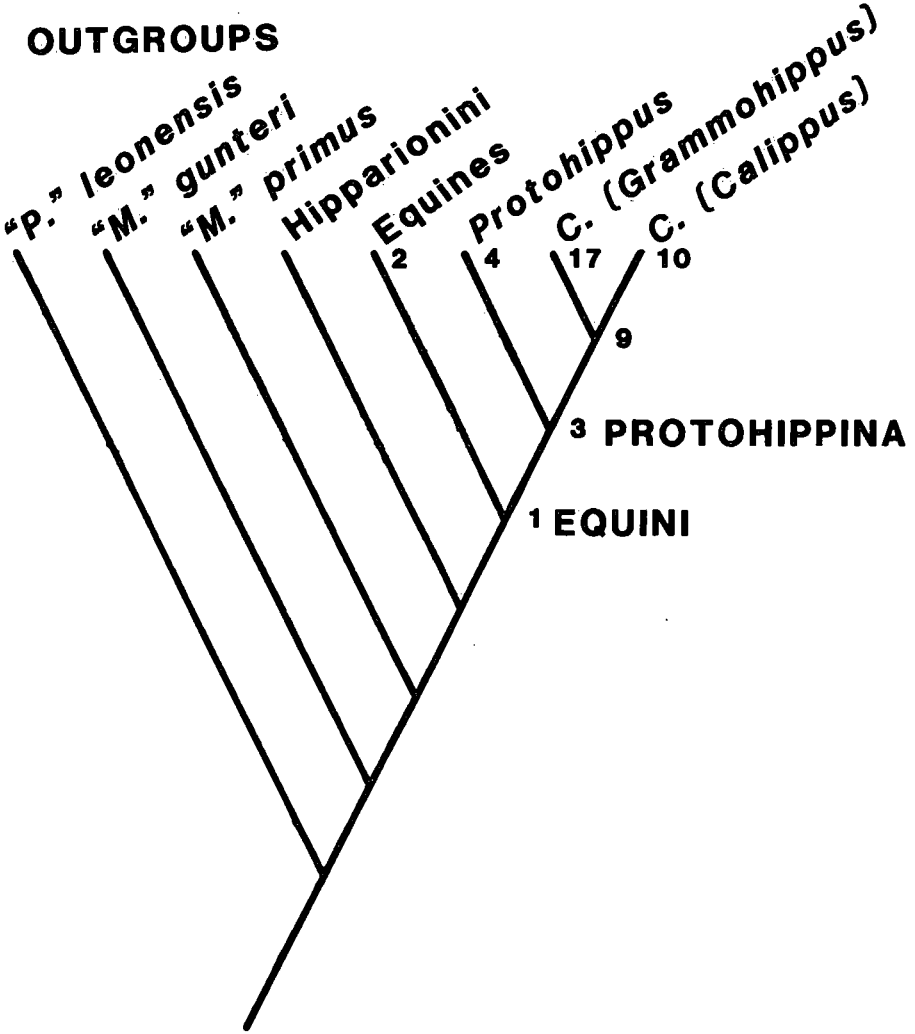
Figure 27. Cladogram expressing hypothesized evolutionary relationships among protohippine and equine equids based on distribution of character states listed in Table 18. Numbers at the nodes on the cladogram refer to groups of shared derived character states discussed in the text.

deep DPOF (also secondarily reduced in some taxa); elongated muzzles; very simple internal fossette margins; and reduced or absent lateral phalanges.

As shown in Figure 27, Node 3, *Calippus* and *Protohippus* are sister taxa and share the following derived character states: relatively broad muzzle; elongate-oval protocones; markedly oblique premolar protocone orientation; well developed protostylid on p3-m3; metaconid and metastylid well separated in early wear-stages; shallow premolar ectoflexids; and increased unworn crown height. *Protohippus* is principally defined by the retention of many primitive character states, but it does have four autapomorphies (Fig. 27, Node 4), increased size (UTRL $\geq$ 120 mm), a very broad DPOF, an inflated malar region lacking depression or fossa, and enlarged metastylids of approximately the same size as metaconids. The condition of the malar region is actually a reversal to the state observed in *"Parahippus" leonensis* and *"M." primus*.

The four recognized species of *Protohippus* may represent a single, anagenetically evolving lineage, as there is only minor evidence for cladogenesis, and they do not overlap in time (see below). *Protohippus vetus* was described by Quinn (1955) on an upper dentition of a young adult and a single lower molar, both from the early late Barstovian Burkeville l.f. of the Texas Gulf Coastal Plain. A few additional specimens from the same fauna were described by Forsten (1975) as *Merychippus vetus*. As cranial material of this taxon is unknown, its relationships must be determined solely on the basis of its cheekteeth. It is of moderate size (UTRL about 120 mm), slightly smaller than *P. perditus* or *Calippus martini*, and larger than *C. proplacidus* or *C. cerasinus*. It has relatively well developed protostylids and elongate-oval protocones, both derived character states shared with *Calippus* and *Protohippus*. In early wear-stages, its protocones are isolated with prominent spurs (Quinn 1955, plate 1.14); with wear, they rapidly connect with the protoselenes. Its upper and lower deciduous cheekteeth are relatively low crowned and poorly cemented, with well developed protostylids, ectostylids, and parastyles. The size, unworn molar crown height (about 35 mm), and morphology of the cheekteeth of *"P." vetus* are those expected in the most primitive species of *Protohippus*. At Node 5 (Fig. 28), *P. perditus*, *P. supremus*, and *P. gidleyi* are derived relative to *P. vetus* by their strong premolar pli caballin, larger protostylids, increased unworn crown height, and increased size (UTRL $\geq$ 130 mm). No derived character states relative to *P. supremus* and *P. gidleyi* were found for *P. perditus*. *P. supremus* and *P. gidleyi* share a number of derived character states at Node 6 (Fig. 28), including increased crown height, increased degree of protoconal isolation, reduced DP1, metaconid and metastylid more expanded and more persistently well separated, reduced depth of DPOF, and a more greatly broadened muzzle. Based on this analysis, *P. supremus* is derived with respect to *P. gidleyi* only by its greater size and perhaps by a better developed prefossette loop (Node 7).

P. gidleyi has a number of autapomorphies, notably its shallower DPOF, very long preorbital bar, more isolated protocones, reduced anterostyle on P2, and reduced ectostylids on dp2-dp4 (Node 8).

Within the eight million year record of *Protohippus* (about 6 to 14 ma), a number of trends are evident. First, there are those commonly found in many equine genera, such as increasing crown height, reducing DPOF depth, decreasing the size of the DP1, and increasing the length, depth, and persistence of the lingual flexids. Second, a trend also seen in the two subgenera of *Calippus*, is an increase in the relative breadth of the anterior muzzle region and mandibular symphysis. Finally, a trend observed in no other protohippine or equine lineage, but which is characteristic of hipparionines, is the increasing degree of isolation of the protocone from the protoselene. The youngest known population of *Protohippus*, from the Ft-40 locality in Nebraska, is the most derived sample in terms of an isolated protocone.

A number of derived character states are shared by the species of *Calippus* (Fig. 28, Node 9), especially the very short post-canine diastema, very broad muzzle, and flattened, non-arcuate incisor margin. Synapomorphies of the cheektooth series include the immediate connection of the protocone to the protoselene, relatively rapid closure of the hypoconal groove, very shallow p2 ectoflexid, and loss of the ectostylid on the dp2-dp4. These dental characters are not sufficient to define the genus, as several were independently attained by some equine taxa. As in hipparionines (Skinner and MacFadden 1977; MacFadden 1984a), cranial features appear to be more useful than dental characters in distinguishing genera (or groups of genera), and less subject to parallelism (although it certainly is not absent). The two recognized subgenera of *Calippus* are each defined by a number of synapomorphies. The two probably diverged by the late early Barstovian. The oldest specimens probably referable to *Calippus* are from the Eubanks Fauna, Pawnee Creek Formation of northeastern Colorado, about 15 ma (Tedford et al. in press). Osborn's (1918) "*M.*" *proparvalus* may represent this taxon, although both the holotype and paratype are too worn to be very diagnostic. In size, it is intermediate between the larger species of *C. (Calippus)* (e.g. *C. placidus*) and the smaller species of *C. (Grammohippus)* (e.g. *C. circulus* or *C. cerasinus*).

Members of the subgenus *C. (Calippus)* share the following derived character states (Fig. 28, Node 10): small size (UTRL ≤ 105 mm); relatively straight upper cheekteeth; strong protostylid on p3-m3; relatively enlarged metastylid; and shallow ectoflexids on the p2-p4. *C. proplacidus* and *C. placidus* are derived with respect to *C. regulus* and *C. elachistus* by possessing strong premolar pli caballins and deeper and more persistent metaflexids and entoflexids (Node 11). As noted above, the latter is a commonly observed trend in advanced equids. *C. placidus* is derived relative to *C. proplacidus* by

its greater unworn crown height, more elongated metaconids and metastylids, better developed lingual flexids, shallower ectoflexids, and some flattening of the labial borders of the protoconid and hypoconid (Node 12).   No autapomorphies are known that distinguish *C. proplacidus* relative to *C. placidus*, and it may have given rise to the latter through anagenesis.   *C. regulus*, *C. elachistus*, and *Calippus* sp. are derived relative to *C. proplacidus* and *C. placidus* (Fig. 28, Node 13) by their much smaller size (UTRL $\leq$ 85 mm), very simple fossettes, reduced DPOF, reduced size (or loss) of DP1, closure of hypoconal groove in early wear-stages, and very great muzzle width relative to UTRL. *C. regulus* has the following autapomorphies: very reduced styles; and p2 metaconid very small or absent (Node 14).   *C. elachistus* and *Calippus* sp. from the late Barstovian through early Clarendonian of Florida share their derived very small basal crown lengths (Node 15). *C. elachistus* is derived relative to *Calippus* sp. and *C. regulus* by its absent or vestigial pli caballins, loss of pli entoflexids, unexpanded metaconids and hypoconids in early wear, reduced protostylids, and shallower ectoflexids on both molars and premolars (Node 16).

   Members of the subgenus *Grammohippus* share the following derived character states: relatively stronger and more persistent metastyles; and deeper and more persistent preprotoconal grooves (Fig. 28, Node 17).   *C.*
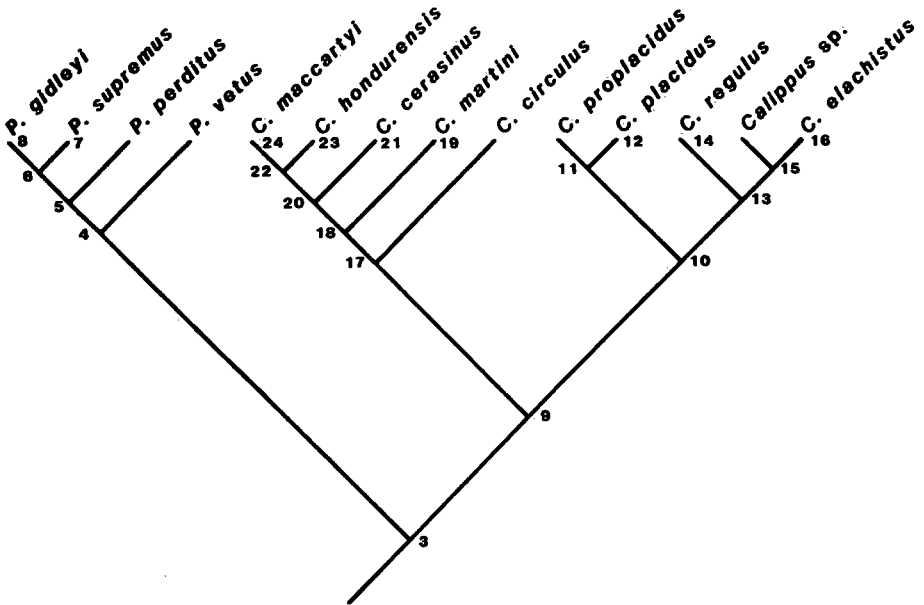
Figure 28.   Cladogram of hypothesized evolutionary relationships among species of Protohippus and Calippus. Numbers at the nodes on the cladogram refer to groups of shared derived character states discussed in the text.

circulus is at present recognized only on the basis of primitive characters. The remaining four species of *C. (Grammohippus)* share increased unworn crown height and reduced protostylids (Node 18). *C. martini* is derived relative to other species of *C. (Grammohippus)* in its more persistent fossette plications, stronger pli caballin on P2-P4, and much greater size and unworn crown height (Node 19). *C. cerasinus, C. hondurensis,* and *C. maccartyi* share the following derived characters, reduced DPOF, relatively greater muzzle width, and increased relative metaconid-metastylid length (Node 20). *C. cerasinus* is derived relative to *C. hondurensis* and *C. maccartyi* in its reduced pli caballins and protostylids, and its rapid closure of the hypoconal groove on the P2-P4 (Node 21). *C. hondurensis* and *C. maccartyi* are derived with respect to *C. cerasinus* by having a more persistent preprotoconal groove, more flattened lingual protocone border, shallower ectoflexid on p2-p4, and increased metastylid size relative to the metaconid (Node 22). *C. hondurensis* has the following autapomorphies: relatively short protocones with very flattened lingual borders; hypoconal groove closes on P2-P4 without forming lakes; and the protocone orientation is less oblique (Node 23). *C. maccartyi* has the following autapomorphies: less curved upper cheekteeth; fossettes very closely appressed; expanded metaconids and metastylids; and shallow ectoflexids on molars as well as premolars (Node 24).

In *Calippus,* as with *Protohippus,* a number of evolutionary trends are evident, including some that are observed proceeding independently in both subgenera. For example, in both there is a trend towards increased muzzle width relative to UTRL, and both evolve species with very shallow ectoflexids (*C. elachistus* and *C. maccartyi*). Another trend, also evident to varying degrees in all protohippine and equine genera, is for younger taxa to have increasingly better developed lingual flexids, which remain stronger through ever increasing percentages of ontogeny. This trend is apparently related to two other commonly observed trends, increased protocone length on upper cheekteeth, and increased metaconid-metastylid length on the lowers. In the two subgenera of *Calippus,* these trends are maximized by *C. placidus* and *C. maccartyi*. A functional rationale for these widespread trends was proposed by Rensberger et al. (1985), who concluded that changes in diet (to a preponderance of grasses) and jaw movements during chewing led to selection for maximizing anteroposteriorly-directed enamel edges in Miocene equids. Clearly, no species of *Calippus* or *Protohippus* approached *Neohipparion eurystyle* or *Equus* in attaining a cheektooth morphology of most efficient grade. However, comparisons of endmembers within each lineage reveals considerable evolutionary change proceeding in a similar direction.

Protohippine, equine, and hipparionine equids display a great deal of parallelism in a variety of dental characters. Many of these can be explained by one of two mechanisms. The first is loss of vestigial or functionally

unimportant characters (cf. Hecht and Edwards 1976). An example of this is the ectostylid, a remnant of the once prominent labial cingulum on the lower cheekteeth of equids. It was better developed and phylogenetically retained longer in the deciduous series, except in some Old World hipparionines. Ectostylids of the dp2-dp4 are judged to have been independently lost or substantially reduced at least six times within North American Equinae: in *Neohipparion* (retained by sister group *Pseudhipparion*); *Pseudhipparion simpsoni* (retained by sister group *P. skinneri*); *Nannippus minor* + *N. peninsulatus* (retained by sister group *"Merychippus" westoni*); *Calippus* (retained by sister group *Protohippus*); *P. gidleyi* (retained by sister group *P. supremus*); and *Equus* + *Astrohippus* + *Pliohippus* (retained by sister group *"P." carrizoensis*). The loss occurs at a variety of taxonomic levels. Other character states, such as loss of the protostylid or pli caballin, follow similar patterns.

The second mechanism assumes that similar structures, under similar selection regimes, will often produce parallel results, especially in closely related taxa (Gosliner and Ghiselin 1984). Equid cheektooth trends that probably fall under this category are increased protocone length (usually coupled with increased metaconid-metastylid length), increased length of the metaflexid and entoflexid, and flattening of the labial borders of the protoconid and hypoconid, i.e. those characters related to the evolution of greater grinding efficiency in the model proposed by Rensberger et al. (1985). The common trends of increasing crown height and/or enamel complexity are related to increasing or maintaining constant potential longevity as diet and/or body size change (Van Valen 1960; Hulbert 1982).

Given the high degree of parallel acquisition of apomorphies among the Equinae, it is obvious that phylogenetic hypotheses solely using the criterion of parsimony may prove incorrect (Gosliner and Ghiselin 1984). They suggest the use of outgroups not only to determine character state polarity, but also to check whether or not a given character is likely to exhibit parallelism. For example, the widely expanded metaconids and metastylids, the shallow ectoflexids, and elongated protocones (all apomorphic within protohippines and equines) might suggest a close relationship between *C. maccartyi* and *Astrohippus ansae*. However, both the ingroup (in this case protohippines and equines) and the closest outgroup (hipparionines) have taxa with primitive and derived states for these characters, implying that they are subject to parallelism. No taxon of the outgroup has widely expanded muzzles with linearly arranged incisors. It follows that this character is less subject to parallelism and more likely to give the correct interpretation of evolutionary history (see Gosliner and Ghiselin 1984 for further discussion).

DWARFING EQUID LINEAGES AND *CALIPPUS*

Calippus is commonly cited along with *Archaeohippus* and *Nannippus* as classical examples of dwarfing lineages, i.e. progressive size decreases through successive ancestral-descendant species pairs (e.g. Romer 1949; Simpson 1951). It should be noted that *Nannippus* in the traditional sense (Stirton 1940) is now considered to consist of two separate, not closely related genera, *Nannippus* s.s. and *Pseudhipparion* (Webb 1969). As usual, Quinn (1955:66) defied "prevailing wisdom" and suggested instead that small forms of the later Tertiary were the direct descendants of even smaller species of *"Hippodon"* (i.e. primitive merychippines) and *Archaeohippus*. Thus, he hypothesized that *Nannippus, Calippus,* and *Griphippus* (*=Pseudhipparion*) were not dwarf forms, and that they displayed either continual size *increases* through time, although at more moderate rates than larger genera, or that they remained at a relatively constant size. Recent phylogenetic analyses of *Nannippus* (MacFadden 1984a; Hulbert 1987a), *Pseudhipparion* (Webb and Hulbert 1986), and *Calippus* (this study) allow a reexamination of these so-called dwarfing lineages.

Only in the case of *Nannippus* does Quinn's (1955) hypothesis not completely fail. Species of *Nannippus* display relatively little or no size differences (and certainly no long-term trends) during its observed range from the early Clarendonian through the Blancan (MacFadden 1985; Hulbert 1987a), and its terminal end-member is of similar size as the common ancestor shared by *Nannippus* and *Cormohipparion*. Webb and Hulbert (1986) documented a trend towards decreased size in successive Gulf Coastal Plain populations of *Pseudhipparion,* which culminated in the late Hemphillian. There were, however, apparently side lineages that also attained very small sizes much earlier (late Barstovian), so size patterns in *Pseudhipparion* are not simple orthogenetic trends. There is also a significant geographic component to body size in *Pseudhipparion*. After removing geographic effects, Webb and Hulbert (1986) found that the size of *Pseudhipparion* (based on basal molar length) decreased at a rate of 0.07 darwins from the early Clarendonian to the latest Hemphillian.

As recognized in this study, a group of species within *C. (Calippus)* also appear to represent a dwarfing lineage. The smallest taxon is *C. elachistus* (M12 BAPL x = 9.1 mm). *C. elachistus* and *C. regulus* share a common ancestor whose size (at minimum) would be about that of *C. regulus* (M12 BAPL x = 11.0 mm). They in turn share a common ancestor with *C. proplacidus* and *C. placidus* whose size (at minimum) would be about that of *C. placidus* (M12 BAPL x = 11.9 mm). Finally, these four species share a common ancestor with the subgenus *Grammohippus*. This ancestor would probably have been of similar size as smaller members of *Grammohippus,*

such as *C. cerasinus*; they are very similar in size to the oldest known
specimens of *Calippus*, "*Merychippus*" *proparvalus*. *C. cerasinus* has a mean
molar BAPL of 12.6 mm. Using Haldane's (1949) equation for measuring
rates of morphological evolution, a change from 12.6 to 9.1 mm over a period
of six million years (15 to 9 ma) is equivalent to -0.054 darwins, a rate of size
decrease slightly less than in *Pseudhipparion*. However, the mode of size
decrease in this lineage of *Calippus* was neither constant nor gradual. Late
Barstovian (ca. 12.5 ma) *Calippus* from Florida, the probable ancestral
population of *C. elachistus*, had already attained the same very small size as its
descendant (Fig. 10). Therefore, the decrease actually took place within a
maximum interval of about 2.5 million years (thus at a very rapid minimum
rate of -0.13 darwins), followed by a 5.5 million year period of stasis (in terms
of tooth size; morphological features and crown height were changing).
Based on regression equations relating equid body size to tooth dimensions
(MacFadden 1987), an adult *C. elachistus* would have weighed between 40
and 50 kg.

BIOCHRONOLOGY AND BIOGEOGRAPHY

Calippus and *Protohippus* played an integral role in the extremely diverse
equid community of the late Miocene (Fig. 29). For example, of the seven
genera and nine species of hypsodont equids in the Clarendon Fauna, three
are species of *Calippus* and one of *Protohippus*. The Love Site equid fauna
also consists of seven genera and nine species, of which two are *Calippus* and
one *Protohippus*. Neither genus is ever one of the most numerous species in a
fauna, but, if present, they are often relatively common. As they are relatively
speciose, rapidly evolving, and typically common, *Protohippus* and especially
Calippus are useful biochronologic indicators. Species of *Protohippus* and
Calippus are frequently encountered across wide areas of North America east
of the Rocky Mountains. However, they are notably absent in contemporary
West Coast faunas with the possible exception of "*Protohippus*" *tehonense*
Merriam (1915). It is not well enough known to be confidently referred to
either the protohippines or equines.

Calippus and *Protohippus* are extremely useful in the correlation
between Gulf Coast and Great Plains faunas (Fig. 29). In the late Barstovian,
P. perditus and *C. proplacidus* are recognized from the lower Valentine
Formation in Nebraska and the Pawnee Creek Formation of Colorado, the
Cold Spring Fauna of southeastern Texas, and lower horizons of the Bone
Valley Formation of Florida. In the early Clarendonian, *P. supremus* and *C.
martini* are known from the northern and southern Great Plains, and the
Gulf Coastal Plain of Texas and Florida. Also, *C. placidus* and *C. regulus*

ranged from southern Texas north to South Dakota and Colorado, respectively, although contemporary populations of small *Calippus* from Florida were distinct by this time. *C. cerasinus* is known from contemporary very late Clarendonian faunas of Nebraska and Florida, while the slightly more advanced early Hemphillian species *C. hondurensis* ranges from Florida to Central America. Its presence in the Gracias Fauna of Honduras, along with *Cormohipparion ingenuum* (Hulbert in press B), *Osteoborus cynoides* (McGrew 1944), and *Teleoceras* cf. *fossiger* (Webb and Perrigo 1984) indicate an early Hemphillian age and suggest strong faunal ties with more northernly sites. *P. gidleyi*, known from the latest Clarendonian to the end of the early Hemphillian in Florida, is also recorded in the late early Hemphillian of the Great Plains. The latest definite records for *Calippus* and *Protohippus* are late early Hemphillian (Ft-40, Withlacoochee River 4A, and Manatee County Dam sites), although the enigmatic *"Protohippus" castilli* from Mexico may represent an even younger population (see above).

The extinction of *Protohippus* and *Calippus* at the end of the early Hemphillian (Fig. 29, at about 6 ma) occurred at a time of major reduction in equid diversity. Two other genera (*Hipparion* and *Pliohippus*) also went extinct at this time, other lineages suffered significant declines in abundance or diversity, and others survived only in Florida, apparently going extinct on the Great Plains at this time (e.g. *Cormohipparion*, Hulbert 1987c). Exclusive of Florida, most late Hemphillian equid faunas are dominated by either *Dinohippus* or *Astrohippus* (or both), and other taxa are rare. The decline in equid diversity is apparently related to a major shift in climate, which in turn led to the conversion of the ungulate-rich, savanna-mosaic Clarendonian Chronofauna into a less species-rich, grassland community (Shotwell 1961; Webb 1977). The dramatic decline, while continual throughout the Hemphillian, is not constant. The periods of high faunal turnover, which have been chosen by Tedford et al. (in press) to demarcate the end of the early Hemphillian (about 6 ma) and the late Hemphillian (about 4.5 ma), witnessed by far the greatest number of extinctions of equid taxa (Hulbert 1987a).

SUMMARY

Calippus and *Protohippus* form a monophyletic clade characterized by short diastema, broadened muzzle, shallow DPOF, and a lack of a malar fossa. *Protohippus* is thus ancestral to neither *Pliohippus* nor *Equus*, as is commonly purported (e.g. Stirton 1940; Simpson 1951; Shotwell 1961), nor is it synonymous with *Merychippus* (*contra* McGrew and Meade 1938). Quinn (1955:22) reached similar conclusions, but his positive contributions have

been overlooked because of his oversplitting of clades and other incorrect phylogenetic interpretations. The common ancestor shared by *Calippus*, *Protohippus*, and equines would have been a small, primitive, subhypsodont *"Merychippus"* sp., dentally similar to *"M." primus*. A number of taxa commonly referred to *Pliohippus* are here transferred to either *Protohippus* (e.g. *P. supremus*) or *Calippus* (e.g. *C. martini*, *C. hondurensis*). Many dental characters evolved in parallel in various lineages of protohippines and equines, and classification schemes that relied too heavily on characters of the cheekteeth (e.g. Stirton 1940) are shown to be incorrect. In these taxa, facial characters and those of the muzzle region are judged to be more stable, less subject to parallelism, and better indicators of phylogenetic interrelationships (especially between genera).
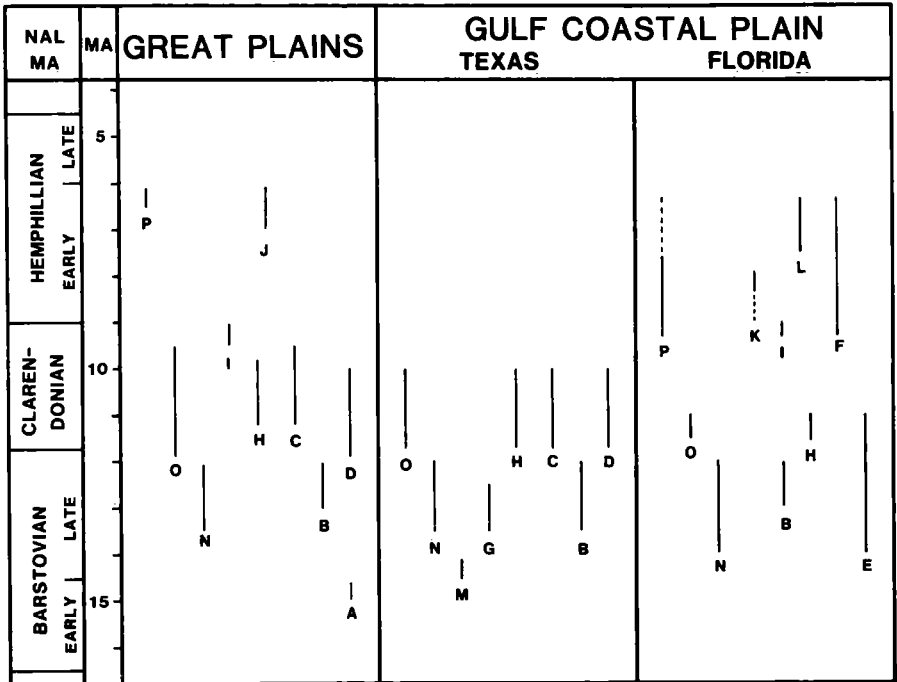
Figure 29. Chronologic and geographic distributions of protohippine species in the late Miocene. A, "Merychippus" proparvalus; B, Calippus proplacidus; C, C. placidus; D, C. regulus; E, Calippus sp.; F, C. elachistus; G, C. circulus; H, C. martini; I, C. cerasinus; J, C. (Grammohippus) n. sp. from Nebraska and Texas K, C. hondurensis; L, C. maccartyi, M, Protohippus vetus; N, P. perditus; O, P. supremus; P, P. gidleyi. Dotted lines indicate uncertain specific identification.

Four species of *Protohippus* are recognized: *P. vetus*, early late Barstovian; *P. perditus*, late Barstovian; *P. supremus* (senior synonym of *P. simus*), very late Barstovian and Clarendonian; and *P. gidleyi* n. sp., latest Clarendonian and early Hemphillian. The lectotype of *P. supremus* is referable to *Protohippus* rather than *Pliohippus*; thus the name cannot be the senior synonym of a number of described Clarendonian species of *Pliohippus* (as was suggested by Webb 1969). *Protohippus* is unique among equine and protohippine genera for increasing the duration of isolated protocones in its upper cheekteeth. *P. gidleyi* is the most derived in this respect.

Two subgenera of *Calippus* are recognized: *Calippus* and *Grammohippus* n. subgen. They share a unique adaptation of the muzzle region in which the premaxillae and mandibular symphyses are broadly expanded and massive, and the first and second incisors are arranged in a straight line rather than the normal equine arcade. The nominate subgenus includes four named small species: *C. proplacidus* (senior synonym of *C. francisi*), late Barstovian; *C. placidus*, Clarendonian; *C. regulus*, late Barstovian-middle Clarendonian; and *C. elachistus* n. sp., latest Clarendonian-early Hemphillian. In addition, there is a very small taxon from the late Barstovian and early Clarendonian of Florida that cannot be referred to any of these species, but that is too inadequately known to be described as new. A few isolated teeth indicate the presence of the subgenus in the early late Barstovian of the Texas Gulf Coastal Plain (Burkeville l.f.), but are likewise too poorly known to be named as a new species. *C. regulus* and *C. elachistus* are among the smallest known hypsodont equids, with toothrow lengths of less than 80 mm. The mass of *C. elachistus* is estimated to have been as little as 45 kg. The rate of size decrease in this lineage of *Calippus* is characterized by both periods of rapid change (-0.13 darwins) and periods of relative stasis. However, the latter period did witness considerable evolution in enamel morphology and some increase in crown height.

Species of *Grammohippus* previously have been assigned to *Pliohippus* or *Astrohippus*. They differ from species of those genera in their absence of a malar fossa, shortened diastema, and broadened muzzle. Five species are formally recognized: *C. (G.) circulus*, late Barstovian; *C. (G.) martini*, Clarendonian; *C. (G.) cerasinus* n. sp., latest Clarendonian; *C. (G.) hondurensis*, early Hemphillian; and *C. (G.) maccartyi* n. sp., late early Hemphillian. There is an additional undescribed late early Hemphillian taxon from the Great Plains. Species referred to *Grammohippus* are of moderate size (toothrow lengths of 100 to 130 mm). *Calippus* and *Grammohippus* diverged in the early Barstovian; "*Merychippus*" *proparvalus* is of similar size and morphology as their hypothetical common ancestor.

Many species of *Calippus* and *Protohippus* are extremely useful in biostratigraphic correlation between late Miocene faunas from Nebraska, Texas, and Florida, e.g. *P. perditus, P. supremus, C. martini,* and *C. proplacidus.*

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TABLE 1. Standard univariate statistics for upper cheekteeth of *Calippus* (*Calippus*) *proplacidus* from the Devil's Gulch Member, Valentine Formation, Brown County, Nebraska (late Barstovian), and from the Cold Spring Fauna, Fleming Formation, San Jacinto and Grimes counties, Texas (late Barstovian), and for *C.* (*C.*) *placidus* from the Minnechaduza Fauna, Ash Hollow Formation, Brown and Cherry counties, Nebraska, and Todd County, South Dakota (middle Clarendonian), and from the Clarendon Fauna, Donley County, Texas (middle Clarendonian). The first line for each entry gives the x, s and n. The second line gives OR and V. All measurements in millimeters.

Species	*C. proplacidus*	*C. proplacidus*	*C. placidus*	*C. placidus*
Fauna	Devil's Gulch	Cold Spring	Minnechaduza	Clarendon

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<tr><th colspan="5" style="text-align:center">P2</th></tr>
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<tbody>
<tr><td>APL</td><td>19.8,0.35,4
19.4-20.2,1.77</td><td>18.4,0.64,2
17.9−18.8,3.47</td><td>20.5,1.34,11
17.6-22.7,6.56</td><td>20.3,1.18,4
18.7-21.3,5.83</td></tr>
<tr><td>BAPL</td><td>15.8, -- ,1</td><td>-----</td><td>16.2,1.12,5
15.2-18.1,6.92</td><td>-----</td></tr>
<tr><td>TRW</td><td>15.9,1.27,4
14.1-17.0,7.98</td><td>14.7,0.42,2
14.4−15.0,2.89</td><td>16.2,1.23,12
14.1-18.1,7.57</td><td>16.5,1.32,4
14.9-18.1,7.98</td></tr>
<tr><td>PRL</td><td>4.7,0.47,4
4.2-5.3,9.94</td><td>4.9,0.28,2
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4.4-6.4,11.83</td><td>5.1,0.36,4
4.8-5.6,7.01</td></tr>
<tr><td>PRW</td><td>3.6,0.38,4
3.1-4.0,10.41</td><td>2.9,0.14,2
2.8-3.0,4.88</td><td>3.6,0.30,12
3.1-4.0,8.16</td><td>3.6,0.27,4
3.4-4.0,7.52</td></tr>
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<tr><td>APL</td><td>17.5,1.17,15
16.0-19.4,6.72</td><td>16.4,0.67,9
15.4-17.5,4.08</td><td>17.1,1.06,18
15.3-19.0,6.21</td><td>16.7,0.57,10
15.9-17.8,3.42</td></tr>
<tr><td>BAPL</td><td>14.3, -- ,1</td><td>13.1,0.49,6
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10.9-13.6,9.00</td><td>-----</td></tr>
<tr><td>TRW</td><td>17.9,0.67,15
16.3-18.7,3.73</td><td>16.6,0.74,9
15.0-17.8,4.47</td><td>17.8,0.87,18
16.5-19.8,4.89</td><td>18.2,1.22,9
16.7-19.9,6.73</td></tr>
<tr><td>PRL</td><td>6.0,0.84,15
4.8-7.7,13.99</td><td>6.1,0.75,9
5.2-7.1,12.31</td><td>6.2,0.54,18
5.1-7.2,8.74</td><td>6.3,0.65,10
5.5-7.5,10.36</td></tr>
<tr><td>PRW</td><td>3.5,0.34,15
3.1-4.1,9.84</td><td>3.3,0.30,9
3.0-4.0,9.12</td><td>3.9,0.40,18
3.4-4.8,10.21</td><td>3.8,0.30,10
3.2-4.1,7.91</td></tr>
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<tbody>
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14.9-18.6,6.90</td><td>16.1,1.08,14
14.8-18.2,6.67</td><td>16.5,1.08,17
14.9-18.3,6.56</td><td>15.8,1.02,10
13.8-17.1,6.45</td></tr>
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13.5-16.1,4.72</td><td>15.6,1.48,18
11.7-16.9,9.48</td><td>16.3,1.35,11
14.2-18.3,8.23</td></tr>
<tr><td>PRL</td><td>6.1,0.63,14
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5.0-6.7,7.15</td><td>6.1,0.62,18
4.9-7.4,10.17</td><td>6.4,0.80,11
5.5-7.9,12.34</td></tr>
<tr><td>PRW</td><td>3.2,0.29,14
2.8-3.6,8.76</td><td>3.1,0.30,17
2.5-3.6,9.61</td><td>3.3,0.24,17
3.0-3.7,7.36</td><td>3.5,0.22,11
3.0-3.8,6.23</td></tr>
</tbody>
</table>

TABLE 2. Standard univariate statistics for lower cheekteeth of *Calippus* (*Calippus*) *proplacidus* from the Devil's Gulch Member, Valentine Formation, Brown County, Nebraska (late Barstovian), and from the Cold Spring Fauna, Fleming Formation, Grimes and San Jacinto counties, Texas (late Barstovian), and for *C.* (*C.*) *placidus* from the Clarendon Fauna, Donley County, Texas (middle Clarendonian). Format as in Table 1.

Species	*C. proplacidus*	*C. proplacidus*	*C. placidus*
Fauna	Devil's Gulch	Cold Spring	Clarendon
		p2	
apl	17.2,0.34,4 16.7-17.5,1.98	16.2,1.16,6 14.5-17.6,7.19	16.8,1.15,5 14.9-17.9,6.84
bapl	-----	13.3,0.87,4 12.4-14.4,6.54	-----
atw	7.3,0.17,4 7.1-7.5,2.39	6.2,0.29,6 5.7-6.5,4.72	7.3,0.54,5 6.5-7.8,7.36
ptw	9.5,0.34,5 9.1-10.0,3.57	8.4,0.33,5 8.0-8.6,3.93	9.1,0.66,5 8.0-9.6,7.28
mml	5.1,0.62,4 4.4-5.9,12.07	4.4,0.76,6 4.0-5.7,17.23	6.1,0.34,5 5.7-6.4,5.59
entl	6.8,0.96,5 5.3-7.8,13.97	5.6,0.78,6 4.8-6.7,13.97	8.0,0.60,5 7.4-8.8,7.54
		p34	
apl	17.3,1.31,12 15.7-19.6,7.56	16.7,0.45,7 16.1-17.3,2.71	17.4,0.90,9 15.4-18.8,5.20
bapl	-----	13.9,0.50,4 13.3-14.5,3.61	-----
atw	10.0,0.68,12 9.3-11.1,6.79	8.8,0.63,7 8.1-9.9,7.12	9.6,1.26,9 7.7-11.1,13.16
ptw	10.1,0.70,12 8.7-11.0,6.96	9.3,0.93,7 8.0-10.3,9.98	9.3,0.83,9 8.1-10.6,8.91
mml	8.6,0.68,12 7.6-9.7,7.91	7.8,0.45,7 7.1-8.5,5.71	8.7,0.39,9 8.0-9.2,4.47
entl	6.7,0.87,12 5.2-7.9,12.97	7.0,0.31,7 6.5-7.4,4.40	8.0,0.75,9 6.3-9.0,9.47
		m12	
apl	16.7,1.53,14 14.7-19.9,9.16	16.2,1.43,10 14.3-18.4,8.79	16.7,1.34,10 14.7-18.7,8.03
bapl	-----	12.6,0.61,7 11.5-13.3,4.81	-----
atw	8.1,0.34,14 7.5-8.6,4.18	7.0,0.52,10 6.0-7.6,7.41	8.6,0.62,10 7.7-9.5,7.19
ptw	6.6,0.35,14 6.2-7.4,5.34	6.2,0.23,11 5.7-6.5,3.63	7.2,0.60,10 6.3-8.0,8.29

Table 2 continued

Species	C. proplacidus	C. proplacidus	C. placidus
Fauna	Devil's Gulch	Cold Spring	Clarendon
mml	7.3,0.42,14 6.5-7.9,5.72	6.7,0.49,10 6.2-7.4,7.38	7.5,0.65,10 6.7-8.6,8.65
entl	4.2,1.16,14 2.2-6.4,27.42	4.0,0.73,11 2.8-4.8,18.24	6.8,1.33,10 4.1-8.2,19.40

TABLE 3. Measurements of specimens of *Calippus* (*Calippus*) *proplacidus* from lower horizons of the Bone Valley Formation, Polk County, Florida. An "a" before a value indicates that it is an approximation from a broken or waterworn specimen. All measurements in millimeters.

	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	
UF 28469	P34	R	15.0	14.9	4.9	3.1	10.8	32.4	
UF 55938	P34	L	14.6	13.9	4.6	3.4	10.5	a31	
UF 28442	M12	R	15.4	14.8	5.8	3.1	11.4	33.0	
UF 28471	M12	R	15.4	12.9	5.6	3.1	10.1	a33	
			apl	atw	ptw	mml	entl	bapl	mcch
UF 28452	m12	L	16.0	6.9	6.4	6.9	6.0	--	32.3

TABLE 4. Standard univariate statistics for upper cheekteeth of *Calippus* (*Calippus*) *regulus* from the Clarendon Fauna, Donley County, Texas (middle Clarendonian), and from the Lapara Creek Fauna, Bee and Live Oak counties, Texas (early Clarendonian), and of *C.* (*Calippus*) *elachistus* n. sp. from the Archer Fauna, Alachua County, Florida (latest Clarendonian-early Hemphillian). Format as in Table 1.

Species	*C. regulus*	*C. regulus*	*C. elachistus*
Fauna	Clarendon	Lapara Creek	Archer

		P2	
APL	17.1,0.75,25	16.1,1.08,5	14.5,1.12,4
	15.8-18.7,4.38	14.5-17.4,6.67	13.1-15.8,7.70
BAPL	14.6,0.83,9	14.1,0.85,5	10.9,0.36,4
	12.9-15.7,5.72	12.8-14.8,6.00	10.1-11.5,6.73
TRW	13.1,0.52,25	12.6,0.59,5	13.1,0.36,4
	12.2-14.3,4.00	11.9-13.5,4.70	12.7-13.7,2.77
PRL	3.9,0.44,25	3.8,0.37,5	3.9,0.47,4
	3.3-4.8,11.19	3.2-4.1,9.70	3.4-4.5,11.88
PRW	3.2,0.33,25	3.1,0.30,5	2.9,0.29,4
	2.6-3.9,10.37	2.9-3.6,9.45	2.5-3.3,9.80

		P34	
APL	14.7,0.99,44	13.3,0.39,6	13.4,0.31,6
	12.6-16.7,6.58	12.8-13.8,2.91	13.0-13.8,2.28
BAPL	12.3,0.48,7	11.8,0.92,6	9.9,0.43,5
	11.6-12.8,3.85	10.7-13.1,7.80	9.3-10.5,4.38
TRW	14.7,0.84,43	14.4,0.55,7	14.3,0.48,6
	12.0-16.1,5.72	13.8-15.4,3.83	13.7-14.9,3.32
PRL	5.3,0.42,45	5.0,0.29,7	4.9,0.60,6
	4.1-6.5,7.94	4.5-5.4,5.89	4.1-5.7,12.24
PRW	3.3,0.26,44	3.2,0.13,7	3.2,0.27,6
	2.6-3.7,7.99	3.0-3.4,4.03	2.8-3.5,8.63

		M12	
APL	13.9,1.21,64	14.2,1.46,21	12.9,0.89,7
	11.1-16.3,8.69	11.7-16.9,10.28	11.8-14.0,6.91
BAPL	10.9,0.48,26	10.9,0.42,21	9.1,0.30,7
	9.9-11.8,4.40	9.8-11.8,3.88	8.7-9.5,3.33
TRW	13.6,0.88,64	12.8,0.65,22	12.2,0.89,8
	10.6-15.5,6.44	11.3-14.1,5.06	11.1-13.9,7.28
PRL	5.5,0.42,64	5.2,0.40,22	4.9,0.61,6
	4.6-6.3,7.61	4.2-5.8,7.62	3.9-5.6,12.58
PRW	3.1,0.28,64	2.9,0.29,22	2.7,0.21,6
	2.4-3.7,9.18	2.5-3.4,10.28	2.4-2.9,7.83

TABLE 5. Standard univariate statistics for lower cheekteeth of *Calippus* (*Calippus*) *regulus* from the Clarendon Fauna, Donley County, Texas (middle Clarendonian), and from the Lapara Creek Fauna, Bee and Live Oak counties, Texas (early Clarendonian), and of *C.* (*Calippus*) *elachistus* n. sp. from the Archer Fauna, Alachua and Polk counties, Florida (latest Clarendonian-early Hemphillian). Format as in Table 1.

Species	*C. regulus*	*C. regulus*	*C. elachistus*
Fauna	Clarendon	Lapara Creek	Archer
		p2	
apl	14.1,0.61,10	13.8,0.47,10	13.5,0.83,4
	13.2-14.8,4.35	12.8-14.2,3.39	12.6-14.5,6.14
bapl	11.9,0.21,3	11.7,0.66,6	9.7,0.81,4
	11.7-12.1,1.75	10.7-12.4,5.66	9.2-10.9,8.29
atw	6.3,0.45,10	6.0,0.14,10	6.2,0.54,4
	5.6-6.9,7.19	5.8-6.3,2.28	5.8-7.0,8.74
ptw	8.1,0.51,10	7.6,0.34,10	7.7,0.21,4
	7.5-9.2,6.27	7.2-8.1,4.44	7.5-8.0,2.67
mml	4.5,0.53,10	4.2,0.71,10	5.8,0.08,4
	3.3-5.1,11.71	3.4-5.6,16.89	5.7-5.9,1.41
entl	6.4,0.56,10	6.0,0.49,10	6.3,0.36,4
	5.1-7.3,8.89	5.0-6.7,8.13	6.0-6.8,5.73
		p34	
apl	14.9,0.86,25	14.3,0.74,16	13.9,1.08,16
	12.9-16.7,5.89	12.9-15.4,5.18	11.7-15.6,7.81
bapl	12.0,0.55,10	11.6,0.62,10	9.9,0.43,13
	11.0-12.7,4.56	10.5-12.4,5.30	8.9-10.5,4.33
atw	8.5,0.62,25	8.2,0.70,17	8.3,0.47,16
	7.2-10.2,7.31	7.0-9.3,8.57	7.4-9.2,5.70
ptw	8.6,0.70,25	8.4,0.68,17	8.4,0.36,16
	7.2-9.5,8.20	7.0-9.5,8.09	7.5-8.9,4.26
mml	6.8,0.42,25	6.6,0.48,17	7.4,0.45,16
	5.8-7.6,6.09	5.7-7.4,7.23	6.5-8.0,6.15
entl	6.6,0.57,25	6.4,0.81,17	7.1,0.65,16
	5.1-7.8,8.61	4.9-7.6,12.58	5.8-8.3,9.15
		m12	
apl	14.5,1.30,21	14.1,1.41,20	13.5,1.26,13
	12.0-17.2,8.97	11.1-16.1,9.97	11.5-15.0,9.37
bapl	11.4,0.67,5	11.2,0.58,14	9.2,0.50,10
	10.7-12.4,5.85	10.1-12.5,5.15	8.4-10.3,5.45
atw	6.9,0.48,21	6.9,0.73,20	7.1,0.45,13
	5.9-7.8,6.91	6.0-9.5,10.47	6.5-7.7,6.27
ptw	5.9,0.43,21	6.1,0.75,20	6.7,0.46,13
	5.1-6.7,7.19	5.1-8.6,12.25	6.2-7.6,6.88

Table 5 continued

Species	C. regulus	C. regulus	C. elachistus
Fauna	Clarendon	Lapara Creek	Archer
mml	5.8,0.53,21	5.7,0.52,20	6.1,0.51,14
	5.2-7.3,9.11	4.9-6.6,9.12	5.2-7.1,8.33
entl	4.9,0.81,21	4.9,1.05,20	6.0,0.96,13
	4.0-6.5,16.45	2.5-7.1,21.38	3.9-7.1,15.82

TABLE 6. Measurements of upper and lower cheekteeth of *Calippus (Calippus)* sp. from lower horizons of the Bone Valley Formation, Polk and Hillsborough counties, Florida. Specimens from three superposed faunas: A, Bradley Fauna, late Barstovian; B, Early Agricola Fauna, latest Barstovian; and C, Late Agricola Fauna, early Clarendonian. Format as in Table 3.

	Tooth	Side	Fauna	APL	TRW	PRL	PRW	BAPL	MSCH	
UF 23979	P34	R	A	12.8	13.4	4.3	3.0	9.6	20.3	
UF 61324	M12	L	A	9.8	--	4.3	2.5	--	--	
UF 23983	M12	L	A	13.0	--	5.0	2.5	--	a30	
UF 50756	M12	L	A	11.9	11.9	4.9	2.7	8.6	25.0	
UF 61323	M3	R	A	11.2	9.2	4.3	2.2	10.8	19.6	
UF 28421	P2	R	B	14.3	11.1	3.7	2.7	12.9	17.1	
UF 28549	P2	L	C	16.0	13.6	4.1	3.4	13.4	17.2	
UF 93201	P34	R	C	14.0	13.9	5.4	3.0	10.3	23.2	
UF 98491	P34	R	C	12.9	--	5.3	3.1	9.9	a18	
UF 28542	M12	L	C	10.1	11.0	4.2	2.8	8.6	10.4	
UF 28680	M12	L	C	12.4	11.7	5.5	2.5	8.2	29.3	
UF 93202	M3	R	C	12.1	10.3	5.0	2.0	12.8	22.3	
UF 68993	M12	L	?	--	10.5	4.5	2.2	--	a18	
				apl	atw	ptw	mml	entl	bapl	mcch
UF 61325	p34	L	A	13.1	7.4	7.8	5.6	6.3	--	--
UF 61343	p34	L	A	12.6	7.0	7.3	6.2	6.3	--	--
UF 23955	m12	L	A	13.9	5.9	6.1	5.7	6.4	--	--
UF 98287	p34	R	C	11.8	7.4	7.5	5.9	5.2	9.4	13.8
UF 98289	m3	R	C	15.9	5.7	5.2	5.3	5.6	16.0	23.3
UF 93210	p2	R	?	12.9	5.9	7.8	5.4	6.3	9.8	17.2
UF 61505	p34	L	?	12.5	7.4	7.6	6.0	6.8	9.9	26.2

TABLE 7. Measurements of upper and lower cheekteeth of *Calippus* (*Calippus*) *elachistus* n. sp. from the Archer Fauna, Alachua and Bone Valley Formations, Alachua and Polk counties, Florida. Format as in Table 3.

	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH		Comments
UF 53430	P2	R	15.8	12.7	4.5	3.3	11.5	20.3		
UF 53431	P2	R	14.8	13.0	4.3	2.9	10.1	23.4		paratype
UF 53432	P2	L	14.4	13.7	3.6	3.0	11.5	17.2		
UF 53435	P34	R	13.3	13.9	4.5	2.8	10.5	18.1		
UF 53436	P34	R	13.0	14.3	4.9	3.2	9.8	21.1		
UF 53441	P34	L	13.5	13.7	5.4	2.9	9.7	29.1		
UF 53445	M12	L	12.0	12.1	4.4	2.4	8.7	10.0		
UF 53448	M12	L	13.5	12.3	5.1	2.7	9.5	25.6		paratype
UF 53577	M12	R	14.0	12.0	5.2	2.7	8.7	34.0		
UF 53576	M12	R	13.8	11.2	5.6	2.4	--	a32		
			apl	atw	ptw	mml	entl	bapl	mcch	
UF 32139	m2	R	13.5	7.6	7.6	6.3	6.3	--	26.8	holotype
UF 32139	m3	R	14.4	6.7	6.9	6.1	6.1	--	--	holotype
UF 53582	p2	R	13.8	6.0	7.5	5.8	6.8	9.6	21.1	
UF 53584	p2	R	14.5	7.0	8.0	5.8	6.2	10.9	24.0	
UF 53585	p34	R	12.7	8.1	8.3	6.7	6.8	9.5	17.4	paratype
UF 53590	p34	R	14.1	8.6	8.9	7.8	6.8	10.0	22.1	
UF 68951	p34	R	15.6	8.7	8.3	7.8	8.3	10.3	32.6	
UF 53604	m12	R	12.4	7.7	6.6	5.8	5.6	9.0	15.8	
UF 53607	m12	R	15.0	6.5	6.4	6.2	6.3	9.2	32.7	
UF 23957	m12	L	11.1	6.2	5.7	4.9	4.8	9.3	14.	

TABLE 8. Standard univariate statistics for upper cheekteeth of *Calippus (Grammohippus) martini* from the Clarendon Fauna, Donley County, Texas (middle Clarendonian), from the Minnechaduza Fauna, Brown and Cherry counties, Nebraska, and Todd County, South Dakota (middle Clarendonian), and from the Lapara Creek Fauna, Bee and Live Oak counties, Texas (early Clarendonian). Format as in Table 1.

Fauna	Clarendon	Minnechaduza	Lapara Creek
		P2	
APL	25.4,1.17,19	24.5,1.10,3	24.7,0.62,3
	23.6-27.6,4.60	23.4-25.6,3.66	24.2-25.4,2.53
BAPL	21.3,1.57,12	21.3,0.78,2	20.2, -- ,1
	17.5-22.8,7.41	20.7-21.8,3.66	
TRW	19.9,1.07,18	19.3,1.40,3	18.8,0.35,3
	17.7-22.1,5.40	18.3-20.9,7.25	18.5-19.2,1.87
PRL	5.9,0.41,19	5.6,0.40,3	5.7,0.28,2
	5.3-6.9,7.03	5.2-6.0,7.14	5.5-5.9,4.96
PRW	4.5,0.48,19	4.3,0.10,3	3.8,0.12,3
	3.1-5.2,10.68	4.2-4.4,2.33	3.7-3.9,3.04
		P34	
APL	21.9,1.47,37	21.5,0.65,11	20.9,0.66,5
	18.6-24.6,6.71	20.4-22.5,3.01	20.2-22.0,3.17
BAPL	16.4,0.87,21	16.2,0.58,7	16.1,0.52,3
	15.2-18.9,5.34	15.2-16.9,3.60	15.5-16.4,3.23
TRW	22.1,1.22,37	21.7,1.15,10	21.1,1.19,6
	20.1-24.5,5.51	20.0-23.8,5.29	19.0-22.4,5.66
PRL	7.5,0.91,37	6.9,0.51,10	7.2,0.59,7
	6.1-9.4,12.10	6.1-7.5,7.35	6.1-7.8,7.75
PRW	4.4,0.38,37	4.4,0.38,10	4.0,0.20,7
	3.7-5.4,8.57	3.9-5.0,8.66	3.7-4.3,5.11
		M12	
APL	21.2,1.58,42	20.6,1.28,13	20.1,0.64,5
	17.5-23.6,7.42	18.9-23.0,6.22	19.4-21.0,3.17
BAPL	16.2,0.91,23	15.3,0.50,8	15.7,1.67,4
	15.0-18.0,5.62	14.7-15.9,3.28	13.5-17.3,10.64
TRW	20.5,1.82,44	20.7,1.45,13	19.5,1.79,5
	15.8-24.1,8.89	17.4-22.8,7.01	16.6-21.2,9.17
PRL	8.0,0.80,44	7.6,0.82,13	7.1,0.49,5
	5.6-10.0,10.01	5.7-8.5,10.74	6.3-7.6,6.86
PRW	4.0,0.41,44	4.1,0.33,13	3.7,0.31,5
	3.3-5.0,10.15	3.5-4.5,8.05	3.2-4.0,8.46

TABLE 9. Standard univariate statistics for lower cheekteeth of *Calippus (Grammohippus) martini* from the Clarendon Fauna, Donley County, Texas (middle Clarendonian), from the Minnechaduza Fauna, Brown and Cherry counties, Nebraska, and Todd County, South Dakota (middle Clarendonian), and from the Lapara Creek Fauna, Bee and Live Oak counties, Texas (early Clarendonian). Format as in Table 1.

Fauna	Clarendon	Minnechaduza	Lapara Creek
		p2	
apl	21.0,0.71,10	19.7,1.01,7	20.3,1.30,5
	19.8-21.8,3.36	18.4-21.3,5.10	18.8-21.9,6.41
bapl	17.4,0.73,10	-----	18.2,0.36,3
	16.7-19.1,4.18		17.9-18.6,1.98
atw	8.6,0.85,10	8.4,0.45,7	8.3,3.94,5
	7.5-10.1,9.89	7.8-9.1,5.33	7.7-8.8,4.74
ptw	11.2,0.65,10	10.8,0.28,7	10.3,0.51,5
	10.1-12.1,5.82	10.3-11.1,2.61	9.7-10.8,4.98
mml	7.2,0.87,10	7.3,0.72,7	6.9,1.34,5
	5.7-8.7,12.14	6.2-8.1,9.83	4.6-8.0,19.37
entl	8.5,0.54,10	5.7,1.78,7	8.4,2.32,5
	7.5-9.2,6.40	3.3-8.1,31.50	4.8-10.7,27.63
		p34	
apl	21.8,0.90,17	19.1,1.55,9	19.2,0.32,3
	20.2-23.7,4.12	16.9-21.0,8.08	19.0-19.6,1.67
bapl	16.6,0.58,15	-----	16.4,0.99,2
	15.7-18.0,3.49		15.7-17.1,6.04
atw	11.4,0.80,17	11.6,0.92,9	11.3,1.32,3
	10.2-13.0,7.05	10.1-12.5,7.93	9.9-12.5,11.66
ptw	12.1,1.00,16	11.5,0.59,9	11.9,0.38,3
	10.4-13.9,8.23	10.8-12.4,5.09	11.5-12.2,3.18
mml	9.7,0.63,17	8.4,0.58,9	9.4,1.65,3
	8.6-11.2,6.48	7.3-9.0,6.86	8.3-11.3,17.58
entl	8.8,0.85,17	6.2,2.62,9	7.3,1.32,3
	7.2-10.2,9.69	3.2-9.6,42.21	6.1-8.7,18.09
		m12	
apl	22.3,1.95,29	18.0,2.39,11	21.4,1.80,5
	18.4-27.3,8.73	15.5-21.6,13.27	18.9-23.7,8.39
bapl	16.3,0.79,29	-----	16.6,1.38,5
	15.2-17.9,4.85		15.6-18.9,8.29
atw	9.4,0.78,28	9.3,0.99,11	9.1,0.77,5
	8.1-11.5,8.29	7.8-11.3,10.56	8.4-10.0,8.50
ptw	8.9,1.00,29	7.7,0.51,11	8.6,0.65,5
	7.3-12.6,11.25	6.8-8.4,6.57	7.8-9.6,7.58
mml	8.5,0.70,29	6.7,1.08,11	8.9,1.28,5
	7.3-10.0,8.25	4.3-8.2,15.95	7.8-11.1,14.37
entl	5.9,0.95,29	4.1,1.72,11	6.2,2.02,5
	4.3-8.1,15.95	1.2-6.2,42.20	4.2-9.6,32.52

TABLE 10. Measurements of selected upper and lower cheekteeth of *Calippus* (*Grammohippus*) from Florida, Oklahoma, Nebraska, and Mexico. Locality abbreviations: CR, Cragin Quarry, Beaver County, Oklahoma; LQ, Leptarctus Quarry, Cherry County, Nebraska; QK, Quarter Kat Quarry; CS, Cold Spring Fauna, Texas; AG, Agricola Fauna; LOV, Love Site; CC, Coffrin Creek; HS, Haysand Road; MG, McGehee Farm; MIX, Mixson's Bone Bed; H19, Haile 19A; MAR, Moss Acres Racetrack Site; W4A, Withlacoochee River 4A; and TEL, Teluichila Fauna, Hildago, Mexico. Format as in Table 3.

	Tooth	Side	Loc	APL	TRW	PRL	PRW	BAPL	MSCH	Comments
					Calippus circulus					
TMM 31219-327	P2	R	CS	--	15.9	4.7	4.0	--	18.6	
TMM 31219-160	P34	R	CS	18.2	18.0	6.1	3.8	14.7	25.3	
					Calippus martini					
UCMP 32814	P2	L	CR	25.6	20.9	6.0	4.2	--	--	holotype
UCMP 32814	P3	L	CR	21.1	22.9	6.6	4.4	--	--	"
UCMP 32814	P4	L	CR	21.9	23.8	7.5	4.6	--	--	"
UCMP 32814	M1	L	CR	19.1	22.8	6.6	4.2	--	38.8	"
UCMP 32814	M2	L	CR	19.5	20.6	7.6	4.5	--	43.2	"
UF 98290	P2	L	AG	22.3	a18	5.3	3.4	19.3	26.4	
UF 98292	P34	R	AG	21.7	--	7.3	4.1	15.4	a45	
UF 98293	P34	R	AG	18.4	20.7	5.8	4.3	14.9	23.8	
UF 98495	P34	R	AG	19.1	19.3	6.2	3.6	13.8	25.1	
UF 98496	P34	R	AG	19.5	a20	6.7	4.4	14.3	36.6	
UF 98500	P34	L	AG	19.4	21.4	5.7	4.3	15.4	28.4	
UF 28552	P34	L	AG	19.0	18.5	6.2	4.0	15.1	30.1	
UF 28551	M1	R	AG	19.7	19.8	6.5	4.0	14.5	32.0	
UF 98294	M12	R	AG	17.6	20.5	6.8	3.9	14.5	22.3	
UF 98498	M12	R	AG	18.1	18.3	7.4	3.8	13.7	34.9	
UF 98296	M12	L	AG	22.5	19.3	9.4	4.2	15.5	39.9	
					Calippus cerasinus					
F:AM 114100	P2	L	LQ	a22	16.2	4.4	3.3	--	27.9	holotype
F:AM 114100	P3	L	LQ	18.7	18.6	5.7	3.7	--	--	"
F:AM 114100	P4	L	LQ	18.7	19.1	6.1	3.8	--	a34	"
F:AM 114100	M1	L	LQ	17.8	18.4	5.6	3.4	--	30.8	"
F:AM 114100	M2	L	LQ	18.5	17.2	5.7	3.3	--	--	"
F:AM 114124	P2	L	LQ	21.8	17.6	4.5	4.0	18.0	24.6	
F:AM 114125	P34	R	LQ	19.6	18.9	7.6	3.9	13.0	44.4	
F:AM 114130	M12	L	LQ	17.2	19.1	5.5	3.6	13.2	31.0	
F:AM 114139	M12	L	QK	20.8	17.1	7.0	3.7	13.8	48.6	
UF 60244	P2	L	LOV	21.0	16.5	4.2	3.6	16.0	23.6	
UF 60240	P2	L	LOV	22.8	16.9	5.8	3.9	17.3	32.4	
UF 60304	P34	L	LOV	16.7	19.6	5.9	3.9	12.5	23.4	
UF 60309	P34	L	LOV	18.0	19.1	6.2	3.5	13.4	22.1	
UF 60269	P34	R	LOV	18.6	18.4	6.8	4.0	13.1	37.3	
UF 60292	M12	L	LOV	16.9	17.7	6.2	3.1	12.7	33.6	
UF 60324	M12	R	LOV	16.5	18.0	5.6	3.1	12.5	21.2	
UF 60331	M12	R	LOV	18.3	16.9	6.5	3.6	12.0	35.8	
UF 17233	P34	L	HS	16.7	16.9	5.7	2.9	a12	33.1	
					Calippus sp. cf. *C. hondurensis*					
UF 9506	P34	R	MG	16.6	17.5	5.3	--	12.4	27.0	
UF 17236A	P34	R	MG	16.4	18.7	5.1	3.0	--	a23	
UF 17236B	P34	L	MG	18.1	--	5.4	3.3	--	a38	
UF 47489	P4	R	H19	16.6	19.6	4.6	4.8	14.0	12.0	
UF 17238	P34	L	CC	16.0	17.8	5.5	3.5	--	15.1	

TABLE 10 continued

	Tooth	Side	Loc	APL	TRW	PRL	PRW	BAPL	MSCH	Comments
					Calippus hondurensis					
F:AM 113643	M12	L	MIX	16.6	18.2	5.7	3.5	14.1	24.7	
F:AM 113642	M12	L	MIX	17.8	18.3	5.7	3.6	13.6	31.2	
F:AM 113645	M12	L	MIX	18.5	16.7	5.1	3.7	13.9	32.7	
F:AM 113641	P2	L	MIX	--	17.7	5.2	--	--	32.1	
AMNH 8343	P34	L	TEL	17.7	18.2	5.5	3.5	14.2	35.3	
					Calippus maccartyi					
UF 69951	P2	R	MAR	21.2	17.0	4.3	3.1	16.6	18.2	holotype
UF 69951	P3	L	MAR	15.4	18.2	5.9	3.8	--	24.7	"
UF 69951	P4	L	MAR	15.8	17.3	6.1	3.7	--	30.9	"
UF 69951	M1	L	MAR	15.2	16.6	6.2	3.5	--	26.9	"
UF 69951	M2	L	MAR	15.4	15.6	6.2	3.5	--	--	"
UF 90299	M12	L	MAR	17.1	17.0	6.3	3.4	11.9	37.6	
UF 95407	P2	R	MAR	20.1	16.2	4.3	3.7	--	30.6	
UF 45536	M12	R	W4A	16.3	16.7	5.5	3.4	11.8	a25	
				apl	atw	ptw	mml	entl	bapl	mcch
					Calippus martini					
UF 55886	p2	L	AG	20.6	7.9	10.0	5.8	6.7	15.7	23.9
UF 55886	p3	L	AG	19.3	--	--	--	7.8	--	a27
UF 55886	p4	L	AG	20.4	10.6	--	7.9	7.5	--	37.6
UF 57358	p34	R	AG	18.3	11.9	11.6	8.4	4.6	14.8	18.8
UF 98305	p34	R	AG	19.6	--	12.5	8.7	6.9	14.3	a26
UF 98306	p34	L	AG	20.0	11.3	--	8.8	8.1	--	a30
UF 98307	p34	L	AG	18.6	12.9	11.5	7.6	3.4	14.6	a13
UF 55888	m12	L	AG	15.5	--	10.4	7.0	5.3	13.4	15.3
UF 98303	dp4	R	AG	25.0	8.0	8.2	10.0	6.3	20.7	14.2
UF 98304	dp4	L	AG	25.4	8.5	8.2	10.5	4.9	21.1	13.6
					Calippus cerasinus					
UF 32215	p2	L	LOV	18.8	7.7	9.5	6.2	7.2	--	--
UF 32215	p3	L	LOV	19.9	10.8	10.4	8.3	8.4	--	--
UF 59956	p34	L	LOV	18.0	10.8	11.0	8.5	7.5	13.8	26.7
UF 59187	p34	R	LOV	16.8	11.2	10.5	6.7	5.7	13.5	25.9
UF 59973	m12	L	LOV	18.0	9.1	8.9	7.9	4.8	13.3	33.6
UF 60207	m12	R	LOV	17.5	8.4	8.1	6.6	4.7	12.9	32.2
UF 59984	m12	L	LOV	16.0	8.5	7.7	6.2	4.0	13.0	17.2
					Calippus sp. cf. C. hondurensis					
UF 18940	p34	R	MG	15.0	9.7	10.5	6.6	5.3	--	a13
UF 58553	p34	L	CC	16.3	11.6	11.2	7.5	5.9	14.2	16.9
					Calippus maccartyi					
UF 69951	p2	L	MAR	16.6	8.1	9.4	7.9	7.8	--	a19	holotype
UF 69951	p3	L	MAR	16.2	10.5	10.3	9.5	7.9	12.4	30.5	"
UF 69951	m1	L	MAR	15.0	9.8	8.2	8.4	5.8	12.8	24.7	"
UF 69951	m2	L	MAR	15.4	9.4	8.3	8.2	6.6	--	--	"
UF 95397	p34	R	MAR	18.0	8.9	9.2	10.0	9.2	--	a37	
UF 97275	p34	L	MAR	16.6	9.7	11.5	9.9	9.0	12.3	27.3	
UF 90287	m12	R	MAR	--	8.9	--	8.1	--	--	35.1	
UF 53460	p34	R	W4A	17.1	11.5	11.1	9.3	8.1	--	a26	

TABLE 11. Standard univariate statistics for upper cheekteeth of *Calippus* (*Grammohippus*) *cerasinus* n. sp. from the Xmas-Kat Fauna, upper Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska (latest Clarendonian), and from the Love Site, Alachua Formation, Alachua County, Florida (latest Clarendonian), and of *C.* (*G.*) *hondurensis* from the Gracias Fauna, Department of Lempira, Honduras. Format as in Table 1.

Species	*C. cerasinus*	*C. cerasinus*	*C. hondurensis*
Fauna	Xmas-Kat	Love	Gracias

	P2		
APL	23.1,1.78,2	20.0,1.52,26	22.2,0.75,3
	21.8-24.3,7.65	17.8-22.9,7.60	21.5-23.0,3.38
BAPL	18.3,0.35,2	16.3,0.80,25	18.8, -- ,1
	18.0-18.5,1.94	14.5-18.1,4.91	
TRW	16.7,0.76,3	16.4,0.78,28	16.0,0.42,3
	16.2-17.6,4.53	14.7-17.9,4.79	15.7-16.5,2.60
PRL	4.4,0.15,3	4.5,0.39,26	4.3,0.12,3
	4.2-4.5,3.50	3.9-5.8,8.62	4.2-4.4,2.71
PRW	3.6,0.35,3	3.6,0.27,25	3.7,0.10,3
	3.3-4.0,9.76	3.1-4.1,7.32	3.6-3.8,2.70

	P34		
APL	18.8,0.64,6	17.1,1.07,35	17.9,0.75,10
	17.8-19.6,3.41	14.7-19.1,6.27	16.6-19.2,4.18
BAPL	13.8,0.80,3	12.7,0.56,29	14.9,0.40,6
	13.0-14.6,5.81	11.7-14.4,4.37	14.2-15.3,2.69
TRW	18.8,0.52,6	18.2,0.89,34	18.5,0.89,12
	18.0-19.5,2.77	16.6-19.8,4.90	16.1-19.3,4.81
PRL	6.5,0.86,6	5.7,0.68,33	4.7,0.34,12
	5.7-7.6,13.40	4.4−7.3,11.84	4.2-5.5,7.20
PRW	3.9,0.18,6	3.6,0.27,32	3.7,0.38,12
	3.7-4.2,4.53	3.0-4.2,7.53	2.9-4.4,10.18

	M12		
APL	19.0,0.94,13	16.4,1.23,46	16.9,0.73,7
	17.2-20.8,4.96	13.8-19.4,7.50	15.9-17.9,4.32
BAPL	13.5,0.63,10	12.6,0.60,45	14.1,0.40,3
	12.5-14.0,4.70	11.6-14.1,4.77	13.7-14.5,2.84
TRW	17.4,1.41,13	17.2,1.05,48	17.5,1.02,7
	14.0-19.1,8.11	13.3-19.3,6.07	16.0-18.5,5.84
PRL	6.1,0.44,12	5.6,0.67,47	5.2,0.69,7
	5.5-6.8,7.18	4.3-7.7,11.80	4.2-6.0,13.17
PRW	3.6,0.27,12	3.5,0.34,47	3.5,0.41,7
	3.1-4.1,7.63	3.0-4.7,9.89	3.2-4.3,11.51

TABLE 12. Standard univariate statistics for lower cheekteeth of *Calippus* (*Grammohippus*) *cerasinus* n. sp. from the Xmas-Kat Fauna, upper Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska (latest Clarendonian) and from the Love Site, Alachua Formation, Alachua County, Florida (latest Clarendonian), and of *C.* (*G.*) *hondurensis* from the Gracias Fauna, Department of Lempira, Honduras. Format as in Table 1.

Species	*C. cerasinus*	*C. cerasinus*	*C. hondurensis*
Fauna	Xmas-Kat	Love	Gracias

		p2	
apl	18.3,0.60,5 17.5-18.9,3.28	16.8,0.92,8 15.8-18.7,5.45	20.5,0.85,3 19.6-21.3,4.17
bapl	-----	13.2,0.17,4 13.0-13.3,1.32	15.5,0.07,2 15.4-15.5,0.46
atw	7.5,0.85,5 6.2-8.4,11.40	7.8,0.35,8 7.2-8.3,4.47	7.6,0.25,3 7.3-7.8,3.33
ptw	10.0,1.08,5 8.5-11.2,10.73	10.2,0.46,7 9.5-10.7,4.48	10.5,0.12,3 10.4-10.6,1.10
mml	6.6,0.71,5 5.4-7.3,10.81	6.8,0.59,8 5.8-7.8,8.72	7.8,0.36,3 7.4-8.1,4.62
entl	6.1,1.80,5 3.5-7.8,29.55	5.7,1.06,8 3.9-7.3,18.55	7.7,0.32,3 7.3-7.9,4.19

		p34	
apl	18.7,1.25,9 16.6-19.9,6.69	17.3,1.35,35 15.0-19.8,7.80	17.8,0.82,11 16.6-19.1,4.60
bapl	-----	13.4,0.35,22 12.7-14.2,2.63	14.5,0.94,5 13.6—16.0,6.52
atw	10.2,0.97,9 8.9-11.4,9.44	10.5,0.72,36 8.7-11.6,6.82	10.4,0.89,11 8.1-11.1,8.53
ptw	10.9,0.80,9 9.8-11.7,7.36	10.6,0.84,37 7.8-11.8,7.91	10.8,1.00,11 8.3-11.8,9.32
mml	8.5,0.71,9 7.5-9.4,8.31	7.8,0.68,36 6.6-9.2,8.66	8.9,0.43,11 8.0-9.6,4.80
entl	7.3,1.61,9 4.3-9.3,21.89	6.4,1.39,36 3.9-8.9,21.62	6.3,1.29,10 3.9-8.0,20.45

		m12	
apl	17.3,2.01,10 13.7-20.5,11.61	17.2,2.24,35 14.2-22.4,12.97	15.7,1.40,12 14.3-19.3,8.92
bapl	13.4,0.35,2 13.1-13.6,2.65	12.6,0.59,27 11.5-13.8,4.69	13.0,0.21,5 12.8-13.3,1.59
atw	8.5,0.99,11 7.1-10.5,11.60	8.3,0.66,38 7.0-9.9,7.89	8.5,0.32,12 8.0-9.1,3.82

Table 12 continued

Species	C. cerasinus	C. cerasinus	C. hondurensis
Fauna	Xmas-Kat	Love	Gracias
ptw	7.5,0.51,11	7.8,0.60,38	7.3,0.51,12
	6.6-8.1,6.75	6.7-9.0,7.65	6.6-8.2,7.04
mml	6.9,0.58,11	6.7,0.86,36	6.6,0.73,12
	5.6-7.5,8.31	4.9-8.5,12.72	5.8-8.3,11.12
entl	4.1,0.72,11	4.5,0.94,38	3.3,0.47,11
	2.7-5.0,17.66	2.8-6.7,20.92	2.6-4.3,14.23

TABLE 13. Preliminary list of the vertebrate fauna from the Moss Acres Racetrack Site, Alachua Formation, Marion County, Florida (early Hemphillian, about 6.5 to 7.5 ma).

Class Osteichthyes
  Order Lepisosteiformes
    Family Lepisosteidae
      Lepisosteus sp.
Class Reptilia
  Order Crocodilia
    Family Alligatoridae
      Alligator mississippiensis
  Order Chelonia
    Family Trionychidae
      Trionyx ferox
    Family Emydidae
      Pseudemys sp.
Class Mammalia
  Order Edentata
    Family Megalonychidae
      Pliometanastes protistus
  Order Carnivora
    Family Canidae, gen. indet.
    Family Mustelidae
      Enhydritherium sp.
  Order Proboscidea
    Family Gomphotheriidae
      Amebelodon sp., near *A. fricki*

Order Perissodactyla
  Family Equidae
    Calippus maccartyi n. sp.
    Dinohippus sp.
    Neohipparion eurystyle
    Cormohipparion plicatile
    Cormohipparion ingenuum
    Hipparion sp., cf. *H. tehonense*
    Nannippus minor
    very small equid, gen. indet.
  Family Rhinocerotidae
    Aphelops mutilus
Order Artiodactyla
  Family Tayassuidae, gen. indet.
  Family Camelidae
    cf. *Procamelus*
    Aepycamelus sp.
    "Hemiauchenia" minima
  Family Dromomerycidae
    Pediomeryx n. sp. (?)
  Family Gelocidae, gen. indet.

TABLE 14. Standard univariate statistics for upper cheekteeth of three species of *Protohippus*: *P. perditus* from the Devil's Gulch Member, Valentine Formation, Brown County, Nebraska (late Barstovian); *P. supremus*, combined sample from the Burge Fauna, Valentine Formation and the Minnechaduza Fauna, Ash Hollow Formation, Brown and Cherry counties, Nebraska (latest Barstovian-middle Clarendonian); *P. gidley* n. sp. from the Archer Fauna, Alachua Formation, Alachua County, Florida (latest Clarendonian-early Hemphillian); and *P. gidleyi* n. sp. from the Cambridge Fauna (UNSM loc. Ft-40), Frontier County, Nebraska (late early Hemphillian). Format as in Table 1.

Species	*P. perditus*	*P. supremus*	*P. gidleyi*	*P. gidleyi*
Fauna	Devil's Gulch	Burge/Minn.	Archer	Cambridge
P2				
APL	25.9,1.25,5	27.5,1.02,13	25.1,1.02,13	27.3,0.64,2
	23.9-27.2,4.82	25.1-28.6,3.72	23.5-27.0,4.05	26.8-27.7,2.34
BAPL	19.2, -- ,1	22.4,0.83,4	20.3,1.07,13	-----
		21.6-23.5,3.68	18.7-22.0,5.26	
TRW	19.3,1.21,5	21.7,1.06,13	19.7,0.81,11	22.2,1.41,2
	17.9-20.8,6.27	19.7-22.8,4.86	18.2-20.7,4.10	21.2-23.2,6.37
PRL	5.5,0.53,5	6.0,0.44,13	5.6,0.27,13	6.3,0.42,2
	4.9-6.3,9.71	5.2-6.8,7.33	5.1-6.0,4.73	6.0-6.6,6.73
PRW	4.7,0.53,5	5.0,0.44,13	4.1,0.23,11	5.3,0.85,2
	4.0-5.3,11.36	4.3-6.1,8.88	3.7-4.5,5.56	4.7-5.9,16.01
P34				
APL	21.3,1.90,9	23.7,1.32,33	22.4,1.50,37	22.2,2.24,5
	18.6-24.9,8.93	20.9-26.0,5.56	19.0-25.2,6.67	18.9-24.9,10.10
BAPL	-----	19.2,1.02,12	16.3,0.70,36	17.7, -- ,1
		17.0-20.6,5.33	15.1-18.0,4.31	
TRW	22.6,0.44,9	24.3,1.12,33	22.3,0.98,37	23.3,1.07,5
	22.1-23.2,1.95	20.8-25.9,4.60	20.3-24.1,4.42	22.6-25.2,4.60
PRL	7.3,0.73,9	7.8,0.89,33	8.1,0.97,38	8.8,1.45,5
	6.0-8.5,10.04	6.3-10.7,11.42	6.4-9.9,12.02	7.0-10.2,16.45
PRW	4.6,0.55,9	4.8,0.24,32	4.5,0.29,38	5.1,0.54,5
	3.6-5.5,11.99	4.5-5.4,5.03	3.9-5.4,6.40	4.5-6.0,10.53
M12				
APL	20.1,1.77,11	23.0,1.87,42	21.0,1.35,32	22.4,2.72,11
	16.9-23.1,8.83	20.0-27.3,8.14	17.4-23.2,6.43	18.1-26.8,12.13
BAPL	15.0, -- ,1	18.5,0.70,16	15.5,0.88,30	18.4,0.74,6
		17.3-19.9,3.79	13.9-17.8,5.70	17.8-19.7,4.02
TRW	21.5,0.80,11	22.5,1.46,44	20.5,1.06,32	22.3,1.00,11
	19.9-22.8,3.72	18.0-24.7,6.50	18.5-22.5,5.18	20.3-23.5,4.47
PRL	8.0,0.84,11	8.7,0.99,43	8.0,0.81,33	8.2,1.31,11
	6.7-9.2,10.56	7.1-10.5,11.31	6.5-10.0,10.08	6.6-10.6,13.79
PRW	4.5,0.49,11	4.5,0.49,43	4.2,0.32,32	4.9,0.36,11
	3.6-5.2,10.84	3.2-5.5,10.80	3.7-4.8,7.44	4.4-5.3,7.29

TABLE 15. Standard univariate statistics for lower cheekteeth of three species of *Protohippus*: *P. perditus* from the Devil's Gulch Member, Valentine Formation, Brown County, Nebraska (late Barstovian); *P. supremus*, combined sample from the Burge Fauna, Valentine Formation and the Minnechaduza Fauna, Ash Hollow Formation, Brown and Cherry counties, Nebraska (latest Barstovian-middle Clarendonian); *P. gidley* n. sp. from the Archer Fauna, Alachua Formation, Alachua County, Florida (latest Clarendonian-early Hemphillian); and *P. gidleyi* n. sp. from the Cambridge Fauna (UNSM loc. Ft-40), Frontier County, Nebraska (late early Hemphillian). Format as in Table 1.

Species	*P. perditus*	*P. supremus*	*P. gidleyi*	*P. gidleyi*
Fauna	Devil's Gulch	Burge/Minn.	Archer	Cambridge
p2				
apl	21.5,0.84,19	23.2,1.14,8	22.0,1.05,12	23.4,1.61,6
	19.9-22.9,3.92	21.8-24.7,4.93	20.7-24.4,4.79	20.7-25.5,6.87
bapl	-----	-----	18.1,0.87,9	19.5,0.72,5
			16.5-19.4,4.79	18.7-20.6,3.68
atw	8.8,0.87,19	9.0 0.79,8	9.2,0.46,11	9.8,0.19,6
	6.9-10.4,9.94	8.1-10.4,8.78	8.4-9.7,5.01	9.5-10.0,1.92
ptw	11.3,0.91,19	11.8,0.49,8	11.8,0.77,12	12.5,0.60,6
	9.0-12.8,8.01	11.1-12.4,4.12	10.3-12.7,6.56	12.0-13.5,4.79
mml	6.1,0.90,19	6.9,0.91,8	8.4,0.62,12	9.6,1.18,6
	4.3-7.7,14.76	5.5-8.2,13.18	6.8-9.3,7.41	8.2-11.4,12.32
entl	6.9,1.45,19	8.2,1.56,8	9.2,1.26,12	10.2,1.86,6
	4.1-8.9,21.22	5.8-10.0,19.04	6.5-11.7,13.65	6.6-11.5,18.19
p34				
apl	22.1,1.06,31	23.6,1.41,25	21.5,1.19,47	23.3,0.77,9
	20.2-24.9,4.81	20.8-25.7,5.98	19.1-24.7,5.54	21.8-24.5,3.29
bapl	-----	19.5,0.52,9	16.7,0.70,30	19.2,1.13,7
		18.8-20.3,2.67	15.4-18.2,4.18	17.7-21.1,5.90
atw	12.0,1.12,31	12.5,0.92,25	12.6,0.63,47	13.2,0.61,9
	9.5-14.7,9.36	10.8-14.4,7.38	11.1-14.0,5.01	12.3-14.0,4.60
ptw	12.6,1.02,31	13.3,0.71,25	12.1,0.64,46	13.2,0.67,9
	10.2-14.4,8.10	12.2-14.9,5.38	10.8-13.8,5.28	12.0-13.9,5.12
mml	10.1,0.47,31	10.7,0.55,25	11.1,0.55,47	12.5,0.65,9
	9.0-11.2,4.61	9.7-12.0,5.07	10.0-12.4,4.91	11.7-13.4,5.15
entl	7.7,1.68,31	9.4,1.78,25	8.5,1.17,47	10.6,0.28,9
	4.3-10.5,21.89	5.4-12.6,18.87	3.7-10.0,13.79	8.2-12.3,12.00
m12				
apl	20.8,1.90,38	23.0,2.23,23	21.0,2.03,64	23.1,1.99,11
	17.1-25.8,9.11	19.0-26.4,9.71	17.4-27.2,9.69	19.0-25.9,8.60
bapl	-----	19.1,0.25,5	15.9,0.52,44	18.6,0.79,6
		18.7-19.3,1.30	15.0-16.9,3.30	17.2-19.5,4.25
atw	10.0,1.00,38	10.2,0.82,23	10.6,0.58,64	10.8,1.01,10
	7.9-12.4,9.96	8.2-11.3,8.04	8.6-11.6,5.45	9.1-12.6,9.39

Table 15 continued

Species	*P. perditus*	*P. supremus*	*P. gidleyi*	*P. gidleyi*
Fauna	Devil's Gulch	Burge/Minn.	Archer	Cambridge
ptw	8.5,0.70,38	8.6,0.47,23	8.7,0.54,65	9.0,0.59,10
	6.9-9.9,8.23	7.8-9.5,5.41	6.9-9.8,6.22	8.0-9.9,6.54
mml	8.6,0.54,37	9.4,0.63,23	9.3,0.79,66	10.5,0.84,11
	7.7-10.5,6.26	8.2-10.6,6.65	7.8-11.7,8.50	9.0-11.7,8.01
entl	4.4,1.27,38	5.5,1.22,23	6.4,1.25,65	7.8,1.31,11
	1.0-7.0,29.18	3.5-8.3,22.18	2.2-9.7,19.47	5.2-9.4,16.77

TABLE 16. Measurements of selected upper and lower cheekteeth of *Protohippus* from South Dakota, Texas, and Florida. Locality and faunal abbreviations: BR, Bradley Fauna; CS, Cold Spring Fauna; AG, Agricola Fauna; LOV, Love Site; MG, McGehee Farm; MIX, Mixson's Bone Bed; H19, Haile 19A; LWR, Little White River region, South Dakota. Format as in Table 3.

	Tooth	Side	Loc	APL	TRW	PRL	PRW	BAPL	MSCH	Comments
						Protohippus peridtus				
UF 61349	P4	L	BR	20.6	a22	7.7	4.5	16.3	32.9	
TMM 31219-253	P34	R	CS	21.1	22.7	6.9	4.2	15.7	22.5	
TMM 31219-329	P34	L	CS	20.4	22.9	8.0	4.2	15.5	23.5	
TAMU 3032	P34	R	CS	20.9	a22	6.6	3.5	16.6	31.3	
TAMU 3033	P34	R	CS	20.2	21.4	6.4	3.9	16.8	22.9	
TMM 31183-30	M1	R	CS	22.0	21.2	7.6	3.9	--	--	
TMM 31219-165	M1	R	CS	20.9	19.8	6.5	3.3	15.5	35.9	
TMM 31219-331	M12	R	CS	19.0	20.5	6.5	4.3	--	15.6	
						Protohippus supremus				
ANSP 11280.1	P34	L	LWR	24.4	25.0	8.8	4.9	17.0	48.4	lectotype
UF 28553	P34	L	AG	20.2	22.9	8.6	4.9	17.3	33.9	
						Protohippus gidleyi				
UF 62473	P2	R	LOV	23.5	20.1	5.6	4.4	18.7	28.6	holotype
UF 62473	P3	R	LOV	23.6	22.2	7.7	4.0	17.0	34.7	"
UF 62473	P4	R	LOV	24.1	21.8	8.0	4.5	16.7	40.6	"
UF 62473	M1	R	LOV	21.9	20.3	7.4	4.2	16.3	40.5	"
UF 62473	M2	R	LOV	21.8	18.5	8.4	4.1	15.1	44.0	"
UF 62482	P2	L	LOV	24.5	20.7	5.7	4.1	20.0	35.1	
UF 62500	P34	R	LOV	22.9	21.0	7.3	4.2	--	45.5	
UF 62497	P34	R	LOV	24.4	23.1	8.9	4.2	16.9	35.3	
UF 62540	M12	R	LOV	21.5	20.0	8.5	4.2	14.8	46.5	
UF 45634	M12	R	MG	20.4	21.1	8.3	4.6	15.8	27.4	

				apl	atw	ptw	mml	entl	bapl	mcch
UF 52963	p34	L	H19	19.3	--	13.3	9.8	7.9	--	25.7
UF 45622	m12	R	MG	22.1	9.8	8.4	9.7	6.9	--	--
UF 32173	p2	R	LOV	21.6	8.6	10.3	8.4	8.4	--	--
UF 32173	p3	R	LOV	21.2	11.8	11.4	11.2	8.6	--	--
UF 32173	p4	R	LOV	21.1	12.3	11.2	10.9	9.4	--	--
UF 32173	m1	R	LOV	19.1	9.7	7.7	7.8	5.4	--	--
UF 32173	m2	R	LOV	20.8	10.2	8.5	9.1	6.2	--	--
UF 32173	m3	R	LOV	23.7	8.7	7.7	8.4	5.1	--	--
UF 67704	p3	R	LOV	23.4	12.1	12.0	11.5	9.3	16.5	37.2
UF 67704	p4	R	LOV	23.1	11.7	11.1	11.0	9.5	16.5	47.8
UF 67704	m1	R	LOV	22.7	10.6	8.7	10.0	7.6	16.0	39.5
UF 67704	m2	R	LOV	23.2	10.1	8.5	10.1	6.8	16.4	45.2
UF 67769	m12	L	LOV	26.2	10.2	9.2	10.9	7.2	15.4	51.1

TABLE 17. Comparison of cranial character states of *Protohippus* and *Pliohippus*.

Character	Protohippus perditus	Protohippus supremus	Pliohippus mirabilis	Pliohippus pernix
Malar fossa	absent	absent	present, often pocketed	present, variably deep
DPOF	large, shallow, small pocket	large, very shallow	large, deep, well pocketed	large, deep, pocketed
Muzzle width	slightly enlarged	enlarged	normal	normal
Protocone connection	occasionally isolated in early wear	often isolated with spur	rarely isolated and only in earliest wear—stages	very rapidly connected; very rarely isolated
Protocone shape	oval	oval to elongate—oval	rounded to oval	oval or elongate-oval
Fossette complexity	simple to moderate	moderate and persistent	very simple	very simple
Pli caballin	moderate	strong	small, not persistent	small, not persistent
Radius of curvature	45-50 mm	50-55 mm	35-40 mm	35-40 mm
Hypoconal groove	closed with moderate wear	closed after heavy wear	closed with slight wear	closed with slight wear
M12 MSCH	45 mm	55 mm	53 mm	58 mm
protostylid (p3-m3)	large, appears early	large, appears early	rudimentary or absent	generally absent
protostylid (dp34)	large	large	rudimentary	rudimentary
ectostylid (dp2—dp4)	present	present	absent	absent
metastylid size relative to metaconid	slightly smaller	equal	smaller	smaller
Referred samples	Devil's Gulch, Crookston Bridge, Norden, Cold Spring and Bradley Faunas	Burge, Minnechaduza, Clarendon, Lapara Creek and Agricola Faunas	Devil's Gulch, Crookston Bridge and Bradley Faunas	Burge, Minnechaduza, Big Spring Canyon, Snake Creek, Clarendon and Lapara Creek Faunas

TABLE 18. Character state matrix for protohippines and equines used for phylogenetic reconstruction. For supra-specific taxa, the given character state is the one observed in its primitive members. A "?" indicates that a particular character state is unknown. Character states printed in normal typeface are judged to be primitive, those in boldface derived, those in boldface and underlined further derived, and those in italics secondarily primitive. The first four listed taxa were used as outgroups in the analysis.

	General Size	Side Toes	Postcanine Diastema	Muzzle Width	Incisor Arcade
"Parahippus" leonensis	small	present	moderate	narrow	arcuate
"Merychippus" gunteri	small	present	?	?	?
"Merychippus" primus	small	present	moderate	narrow	arcuate
Hipparionini	**moderate**	present	moderate	narrow	arcuate
Protohippus	**moderate**	present	**short**	**broad**	arcuate
C. (Calippus)	*small*	?	**very short**	**very broad**	**linear**
C. (Grammohippus)	**moderate**	?	**very short**	**very broad**	**linear**
Dinohippus	**moderate to large**	**absent**	**long**	narrow	arcuate
Pliohippus	**large**	**reduced**	**long**	narrow	arcuate
Astrohippus	**moderate**	**absent**	**long**	narrow	arcuate

	Malar Region	DPOF Pocketed	DPOF Depth	Preorbital Bar Length	Molar Crown Height
"Parahippus" leonensis	inflated	no	shallow	very narrow	ca. 18 mm
"Merychippus" gunteri	?	?	?	?	ca. 27 mm
"Merychippus" primus	inflated	no	shallow	narrow	ca. 28 mm
Hipparionini	**variable depression**	**variable**	**moderate to deep**	narrow	ca. 30 mm
Protohippus	*inflated*	**yes**	shallow	**moderate**	ca. 35 mm
C. (Calippus)	**variable depression**	no	shallow	**moderate**	ca. 38 mm

Table 18 continued

	Malar Region	DPOF Pocketed	DPOF Depth	Preorbital Bar Length	Molar Crown Height
C. (*Grammohippus*)	variable depression	no	shallow	moderate	ca. 40 mm
Dinohippus	variable, ? fossa	no	moderate	moderate	ca. 60 mm
Pliohippus	deep fossa	yes	very deep	moderate	ca. 50 mm
Astrohippus	deep fossa	no	moderate	narrow	ca. 60 mm

	Protocone Shape	Protocone Connection	Protocone Orientation	Fossette Plications	Cheektooth Curvature
"Parahippus" leonensis	round	in mid-wear	straight	moderate	very curved
"Merychippus" gunteri	round	in mid-wear	straight	moderate	very curved
"Merychippus" primus	round to oval	in mid-wear	straight	moderate	very curved
Hipparionini	round to oval	in mid-wear wear	straight	moderate, persistent	moderate
Protohippus	elongate-oval	in early wear	oblique	simple	moderate
C. (*Calippus*)	elongate	very early	oblique	simple	straight
C. (*Grammohippus*)	elongate-oval	very early	oblique	simple	moderate
Dinohippus	oval	very early	straight	simple	very curved
Pliohippus	round to oval	very early	straight	very simple	very curved
Astrohippus	oval	very early	straight	very simple	straight

	Cement on DPs & dps	Cement on P2-M3	Ectostylid (dps)	Ectoflexid Depth on Premolars
"Parahippus" leonensis	none	weak	present	deep
"Merychippus" gunteri	none or very weak	weak to moderate	present	deep

Table 18 continued

	Cement on DPs & dps	Cement on P2-M3	Ectostylid (dps)	Ectoflexid Depth on Premolars
"Merychippus" primus	weak	moderate	present	deep
Hipparionini	weak	**heavy**	present	deep
Protohippus	**moderate**	**heavy**	present	usuallly shallow
C. (Calippus)	**moderate**	**heavy**	**absent**	shallow
C. (Grammohippus)	**moderate**	**heavy**	**absent**	shallow
Dinohippus	**heavy**	**heavy**	**absent**	moderately deep
Pliohippus	moderate	**heavy**	**absent**	deep
Astrohippus	**heavy**	**heavy**	**absent**	shallow

	Protostylid (dp34)	Protostylid (p3-m3)	Pli Entoflexid	Metaconid, -stylid Separation
"Parahippus" leonensis	present	low, weak	absent	very poor
"Merychippus" gunteri	present	low, weak	**present**	very poor
"Merychippus" primus	present	low, weak	**present**	poor
Hipparionini	**strong**	moderate	**present**	**persistently very good**
Protohippus	**strong**	**strong**	**present**	good in early wear only
C. (Calippus)	**strong**	**strong**	**present**	good in early wear only
C. (Grammohippus)	**moderate**	**variably strong**	**present**	good in early wear only
Dinohippus	present	*absent*	**present**	**good**
Pliohippus	weak	*absent*	**present**	poor
Astrohippus	present	*absent*	*absent*	**very good**

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