Phylogeny of American horses of Blancan and Pleistocene age

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The genus *Equus*, as currently accepted, is polyphyletic in origin. *Equus*, subgenus *Dolichohippus*, including the living *E. grevyi*, of Africa, and the extinct *E. simplicidens*, of the Blancan age of North America, are descendent from *Dinohippus*, of Hemphillian age. *Asinus*, including the living Old World *Asinus (A.) asinus*, *Asinus (A.) somaliensis* and *Asinus (Hemionus) hemionus*, as well as the bulk of American Pleistocene horses, are descendent from Hemphillian *Astrohippus*. True *Equus (Equus)* may never have occured in the Pleistocene of North America, and was probably derived from a species of *Dinohippus* or *Equus (Dolichohippus)* that reached Asia in late Hemphillian or early Blancan time. A key character identifying Hemphillian and post-Hemphillian genera is the depth of the ectoflexid in the lower molar teeth. This criterion aids in the separation of groups of species into genera at almost 100 % level. A summary of Hemphillian, Blancan and Pleistocene horses is included.

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1. Introduction

Remains of horses are among the most common and easily recognized vertebrate fossils in North American late Tertiary sediments. The record of evolution in the group is so complete that it is often used as a classic example of the history of evolution of a living mammal, the domestic horse. However, the last step in the story is not clear, and no direct "ancestor" of the domestic horse or American Blancan and Pleistocene horses is generally recognized.

The study of fossil horse material of Hemphillian age, from Texas and Mexico, demonstrates that two different genera, *Dinohippus* and *Astrohippus*, show progressive evolution during Hemphillian time, and chronologically successive series of species of each genus lead to horses of Blancan age that are currently included in the genus *Equus*. Further, the two Hemphillian genera belong to lineages separated from each other since the Clarendonian age or earlier. The two lineages could have had a common ancestor not later than ten million years ago. Clearly "*Equus*" is a composite genus that requires separation into natural divisions.

Polyphyletic ancestory of *Equus* is not a new concept. STIRTON (1940), in his highly perceptive paper on the phylogeny of the Equidae, was driven to suggest polyphyletic origin of *Equus*. QUINN (1955) used a generic classification somewhat similar to that employed here, but the similarity is coincidental. QUINN's work, at least as it concerns the ancestry of Blancan and Pleistocene horses, seems to have been based on misconception and errors in identification (WEBB 1969:139). At present, most American workers have considered all Pleistocene and living horses to belong to *Equus* (SKINNER 1972).

The most helpful character used in identifying to genus the species of horses dealt with here is the nature of the ectoflexid (protoconid-hypoconid valley) in the lower molar teeth. The value of this character was recognized earlier, but was described and elaborated by SKINNER (1972:130) in the separation of *Equus (Dolichohippus)* from American Pleistocene horses. When this criterion is applied to Hemphillian, Blancan and Pleistocene horses, the species fall into natural groups that are easily recognized at almost 100 % level.

The ectoflexid is the median enamel fold on the outer margin of the lower cheek teeth, between the protoconid and hypoconid. In horse premolars, this fold is shallow and does not penetrate into the metaconid-metastylid isthmus. In the molars of some genera of horses, the ectoflexid is deep, penetrating well into the metaconid-metastylid isthmus, and usually is broad with a blunt or flat end. In other genera the ectoflexid of the molars is shallow, not penetrating into the isthmus, and usually slender with a more pointed end.

There is considerable variation in shape and depth of the ectoflexid, and the character must be used with caution. I have seen no premolars with a deep ectoflexid. Rarely molars, especially M1, of a species that typically has a deep ectoflexid will have the ectoflexid penetrating only slightly past the base of the isthmus, but such specimens usually have the fold broad and blunt-ended. Commonly, the moderately worn M1, less commonly M2, of a species that typically has a shallow ectoflexid will have the fold penetrating slightly past the base of the isthmus. However, with one possible exception, I have seen no M3's of species that typically have shallow ectoflexids with the fold penetrating well into the isthmus.

The shape of the linguaflexid (metaconid-metastylid valley) is a helpful character. Its value was recognized by STIRTON (1940) and was used by McGREW (1944) in separating *Equus* (*Dolichohippus*) from American Pleistocene horses. In some genera the linguaflexid is narrow and "V" shaped; in others it is broad and "U" shaped. In some genera this feature is highly variable and not entirely reliable. The shape of the linguaflexid is the result of several variables: curvature of the inner slopes of the metaconid and metastylid, divergence and angle of inclination of these cusps, and the presence or absence of an elongated isthmus connecting them (meta-isthmus of SKINNER 1972). The general shape of the linguaflexid is fairly consistent, however, and when used along with the ectoflexid is a valuable generic criterion.

Parastylids are usually lacking in the permanent teeth of American horses of post-Hemphillian age, other than hipparions. Their presence in all lower teeth except M3 of a species of horse from the Pleistocene of Mexico is unique.

Upper cheek teeth of post-Clarendonian horses possess few characters, other than of the

protocones, of taxonomic value at the generic level. In the hipparions the protocones, except on P2, are isolated lakes, separated from the protoselene almost to the base of the tooth. In *Dinohippus*, and its descendant, *Equus* (*Dolichohippus*), the protocones in the upper part of the crowns of the teeth are usually angular, but appear more rounded when worn. In these genera there is no true rounded anterior heel on the protocone and the bulk of the cusp, except for a pointed spur, usually lies posterior to the commissure. In other genera the protocone has an anterior heel, giving the cusp a rounded end that extends anterior to the commissure. In some forms of Pleistocene and Recent horses, the commissure is attached to almost the middle of the protocone.

Critical diagnostic characters of Hemphillian and later horses are summarized as follows:

Hemphillian in age

1. Protocone isolated except in P2

    a. Ectoflexid of molars penetrating into isthmus: *Nannippus*
    b. Ectoflexid of molars not penetrating into isthmus: *Neohipparion*

2. Protocone connected to protoselene in all teeth

    a. Ectoflexid of molars penetrating into isthmus: *Dinohippus*
    b. Ectoflexid of molars not penetrating into isthmus: *Astrohippus*

Blancan in age

1. Protocone isolated except in P2: *Nannippus*

2. Protocone connected to protoselene

    a. Ectoflexid of molars penetrating into isthmus: *Equus* (*Dolichohippus*)
    b. Ectoflexid of molars not penetrating into isthmus: *Asinus*

Pleistocene in age

1. Ectoflexid of molars penetrating into isthmus

    a. Linguaflexids broadly "U" shaped, parastylids lacking: *Equus* (*Equus*) (Old World)
    b. Linguaflexids "V" shaped, parastylids present except on M3: *Equus* (*Parastylidequus*)

2. Ectoflexids of molars not entering isthmus: *Asinus* (several subgenera)

The very character, depth of ectoflexid, that serves to separate the two genera of hipparions, *Nannippus* from *Neohipparion*, also serves to

separate *Dinohippus* from *Astrohippus*. Surely this is coincidental. Hipparions have the protocone isolated, except in P2, and were derived from primitive *Merychippus*. *Astrohippus* and *Dinohippus* have the protocones connected to the protoselene, and probably were derived from some early *Pliohippus*. For a more extended discussion of the Clarendonian genera see WEBB (1969). Nevertheless the value of the ectoflexid as a generic character is obvious.

Study of evolution of species within genera of horses is made difficult by the relatively great amount of variation found in the enamel patterns of the cheek teeth. The basic pattern of cusps, folds connecting cusps, and enamel structures thrust up from the cingulum, is genetically fixed and relatively stable. However, the enamel-forming organs of the cheek teeth must have a complicated shape, corresponding to the enamel pattern of the individual tooth. Pressures exerted on the tooth germ's enamel-forming organ, by accident, ontogeny and senility, may distort it and cause minor distortion of the basic, genetically fixed, patterns.

Some important diagnostic characters are present only in the upper third or less of the crown of the tooth. These are often the progressive, evolving features (see also WEBB 1969: 134). With age, the enamelforming organ seems to shrink into a more simple, generalized pattern. Evolution in species of horses is best seen in lightly-worn teeth.

The evolutionary stage of the dentitions of Hemphillian and later horses is not uniform within populations. In almost any large series of specimens from a single locality, some atavistic specimens resemble older types, and some precocious individuals exhibit conditions found in later populations. The norm, and most specimens, lie between the two extremes. When material is adequate, as from the Coffee Ranch and Ocote local faunas, the trends of evolution are clear but identification to species of individual specimens is not always easy. To consider the atavistic, normal, and precocious forms to each represent different species will multiply the number of accepted species, and present a false interpretation of the conditions that actually existed. Thus MOOSER (1973) found teeth in the Ocote local fauna that resembled teeth of *Astrohippus stocki* Lance, from the older Yepomera local fauna of Chihuahua, and teeth that resembled the still older *A. ansae* (Matthew and Stirton), from the Coffee

Ranch local fauna of Texas. I think these specimens are atavistic, individual variants of *Astrohippus albidens* Mooser, a species with advanced characters that are the norm for the Ocote local fauna.

In the accounts that follow I have depended, for Hemphillian evolutionary trends, on three chronologically successive local faunas: the Coffee Ranch (type Hemphillian) of Texas, the Yepomera, of Chihuahua, Mexico, and the Ocote, of Guanajuato, Mexico. Adequate materials of the first and last of these faunas are available to me, and the horses of the Yepomera local fauna have been well described and illustrated (LANCE 1950). Doubtless material from elsewhere would supplement the present work but that of the three faunas listed seems sufficient.

As used here, the Clarendonian Land Mammal Age belongs in the latest Miocene epoch, Hemphillian in the early Pliocene, Blancan in the late Pliocene, and Irvingtonian and Rancholabrean in the early and late Pleistocene, respectively.

2. Evolution in American Post-Clarendonian horses

Neohipparion Gidley, 1903. — Horses of this genus are surprisingly advanced in dental characters in the Coffee Ranch local fauna. There is no appreciable increase in size, and only moderate increase in hypsodonty, through later Hemphillian time. *Neohipparion* was abundant at Yepomera and Ocote, and two species are reported from each local fauna. The Ocote forms may represent the climax of the genus, for it did not survive the Hemphillian. It left no descendants and needs no detailed discussion here.

Nannippus Matthew, 1925. — *Nannippus* seems to be poorly represented in Clarendonian faunas, and does not become prominent until the Hemphillian, after the equally small and superficially similar *Pseudhipparion* had become extinct. Two lineages were present in Hemphillian time. Diminutive forms include *Nannippus minor* (Sellards), of Florida, *N.* cf. *minor*, of Yepomera (LANCE 1950), and *N. aztecus* Mooser, from Ocote. The species are quite similar and little evolutionary advance is apparent in material seen. Ancestral forms may eventually

be found in early Hemphillian sites in Mexico. The line may have extended through the Blancan but dentitions suitable for identification are lacking.

A separate and better known line of larger species extends from the Hemphillian *Nannippus lenticularis* (Cope) through *N. beckensis* Dalquest and Donovan, of the early Blancan to *N. phlegon*, of the Blanco local fauna (for more detailed account see DALQUEST & DONOVAN 1973). The larger *Nannippus* seem to be rare in Hemphillian faunas of Mexico. None were reported by Lance from Yepomera, and Mooser found only two teeth (*N. hesperides* Mooser) at Ocote.

Nannippus has been reported from numerous early and late Blancan sites in the United States. Most of the material consists of isolated and often fragmentary teeth, inadequate for specific identification. This material suggests a radiation of species during Blancan time, and additional species may need to be recognized.

Nannippus apparently did not extend into the Pleistocene. HIBBARD (1970) reported the genus from some Pleistocene faunas, but HIBBARD & DALQUEST (1973) considered the same faunas to be late Blancan. *Nannippus* is absent from the earliest Irvingtonian faunas, such as the Holloman local fauna of Oklahoma and the Gilliland local fauna of Texas. The extinction of *Nannippus* marked the end of the hipparions in America.

Dinohippus Quinn, 1955. — The large horse of the Hemphillian may have evolved from *Pliohippus pachyops* (Cope), according to WEBB (1969). During Hemphillian time, progressive evolution may be detected in the protocones of the upper teeth. In *Dinohippus interpolatus* (Cope) the protocones tend to be rounded, there is rarely an anterior spur, and the body of the cusp lies posterior to the commissure. In *D. mexicanus* Lance, from Chihuahua, the protocone usually has a deep lingual groove and is angular in shape. In *D. ocotensis* Mooser, from Guanajuato, the protocone is angular, deeply grooved on the lingual surface, and a small, angular spur often projects anterior to the commissure. The crowns of the upper teeth tend to be less curved lingually in *D. ocotensis*, and teeth with only slight curvature are more common than in earlier faunas, but variation in the amount of curvature is great in all three series.

The lower dentitions of the three species vary individually but I see no consistent evolutionary advances in the series. As a group, they share some unique features among Hemphillian horses. In the upper part of the crown, the entoflexid usually is deeply wrinkled, the metaconid-metastylid isthmus often has bead-like or angular bulges, and even the metaflexid may have a wrinkled floor.

The apparent terminal member of this group, *Dinohippus ocotensis*, has approached the zebra, *Equus* (*Dolichohippus*), so closely that its describer (MOOSER 1958) termed it a zebra and placed it in the genus *Hippotigris* (=*Dolichohippus*).
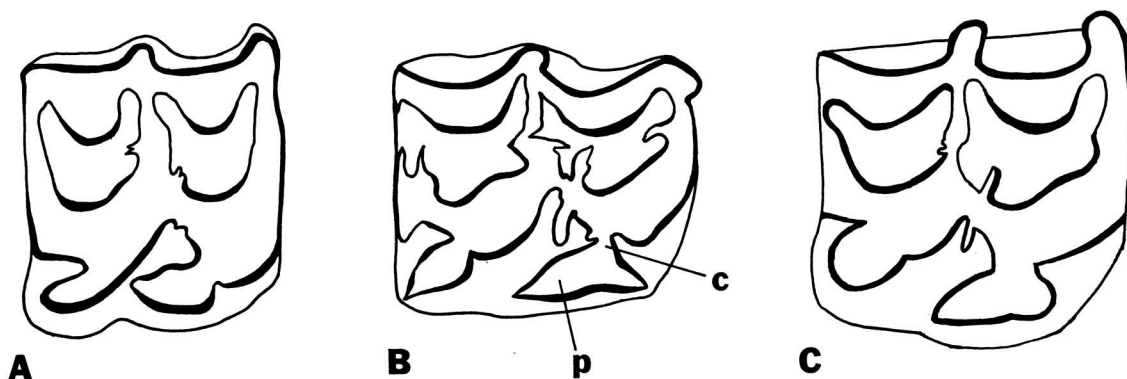

Fig. 1. Enamel patterns of upper first molars of horses. A = *Dinohippus interpolatus* (middle Hemphillian), B = *D. ocotensis* (late Hemphillian), C = *Equus* (*Dolichohippus*) *simplicidens* (Blancan). p = protocone; c = commisure. Teeth in Midwestern State University collection. Not to scale.

Equus (Dolichohippus) Heller, 1912. — For synonymy see SKINNER (1972:118). SKINNER (1972) has noted that the Blancan zebra, *Equus (Dolichohippus) simplicidens* Cope is so similar to the African grevy zebra, *E. (D.) grevyi* Oustalet, that only minor details serve to separate skulls of the two forms. I have here treated *Dolichohippus* as a subgenus of *Equus. Equus (Dolichohippus)* originated in America from *Dinohippus. Equus (Equus)* probably originated in the Old World from emigrant *Dinohippus*.

The dentition of *Dinohippus* grades from *D. interpolatus* through *D. ocotensis* to *Equus (Dolichohippus) simplicidens.* Dental characters of *Equus (Dolichohippus)* are essentially those of *Dinohippus*. An angular protocone without a rounded anterior heel is usually present only in the upper third or less of the crown of the upper teeth, and the wrinkled entoflexid of the lower teeth is most apparent in lightly worn teeth. The upper teeth are almost straight (but occasional individuals are as curved as those of most *Dinohippus*), and the limb bones of *E. simplicidens*, especially the metapodials, are stouter than those of *D. interpolatus*. No metapodials are available from Ocote, and the metapodials figured by LANCE (1950) apparently include more than one species.

The origin of *Equus (Dolichohippus)* from *Dinohippus* was demonstrated by LANCE (1950). This important paper, perhaps because it was in Spanish, has not been properly appreciated. Much of the evolutionary sequence listed above was clear to LANCE. Unfortunately the value of the ectoflexid was not recognized by him, nor was the nature of *Asinus cumminsi* appreciated. LANCE believed that all American Blancan horses were of the genus *Plesippus* (=*Dolichohippus*), and that, consequently, *Plesippus* must be intermediate between *Dinohippus* and the Pleistocene horses here placed in the genus *Asinus*. He was quite correct in deriving *Plesippus (Dolichohippus)* from *Dinohippus mexicanus; D. ocotensis* is merely a step farther along the way from *Dinohippus* to *Equus (Dolichohippus).* The American Pleistocene horses, however, cannot be derived from *E. (Dolichohippus).* In following a single-line phylogeny, LANCE rejected *Astrohippus* as an ancestor for the Pleistocene horses, a position postulated by STIRTON (1940).

A number of nominal species of the subgenus *Dolichohippus* have been described but SKINNER (1972) seemingly considers all of the names to be synonyms of *E. simplicidens* of the early Blancan. The Blancan was a long period of time, and it seems likely that some of the described species, at least, should be valid. *Equus (Dolichohippus)* usually occurs in the same Blancan faunas that contain *Nannippus.* Like *Nannippus*, it may not to have lived into the Pleistocene. However, some of the many specimens of "medium-sized Pleistocene horses" presently preserved in collections may prove to be zebras.

Equus (Dolichohippus) must have reached the Old World in Blancan time to give rise to the modern grevy zebra.

Equus (Parastylidequus) Mooser and Dalquest, 1975. — The subgenus *Parastylidequus* (misspelled *Parastilidequus* in publication) was established for *E. parastylidens* Mooser, an enigmatic species known from two fragmentary lower jaws from the middle Pleistocene of the State of Aguascalientes, Mexico. The basic characters of the dentition of the species are zebrine; the ectoflexid of the lower molars is deep and wide, can be matched, almost detail for detail, by lower jaws of the African lowland zebra, *E. (Pseudoquagga) burchelli* Gray. It seems unlikely that the Mexican and African species are closely related. Horses with parastylids on the lower molars are unknown in Pleistocene deposits of the United States. If the African and American populations were never connected, the similarity of the species must be the result of convergent evolution on two continents.

No probable ancestor of *Equus parastylidens* is known from Hemphillian faunas. However, the P3 of the holotype lower jaw of *Dinohippus ocotensis*, from Guanajuato, has a tiny parastylid. There are no parastylids on the other teeth. Parastylids are common on the teeth of some Clarendonian horses (e.g. *Pliohippus pernix* Marsh). I have seen no parastylids on the teeth of Pleistocene horses from the United States, nor has M. F. Skinner (personal comm.) found parastylids on teeth of such fossils in the American Museum of Natural History. However, D. A. Hooijer (personal comm.) has called my attention to a tiny parastylid indicated on the M3 of a lower dentition of a large horse from the State of Mexico, illustrated by HIBBARD (1955:67). The only known lower M3 of *E. parastylidens* lacks a parastylid.

No upper teeth have been referred to *Equus parastylidens*. I have left the species in the genus
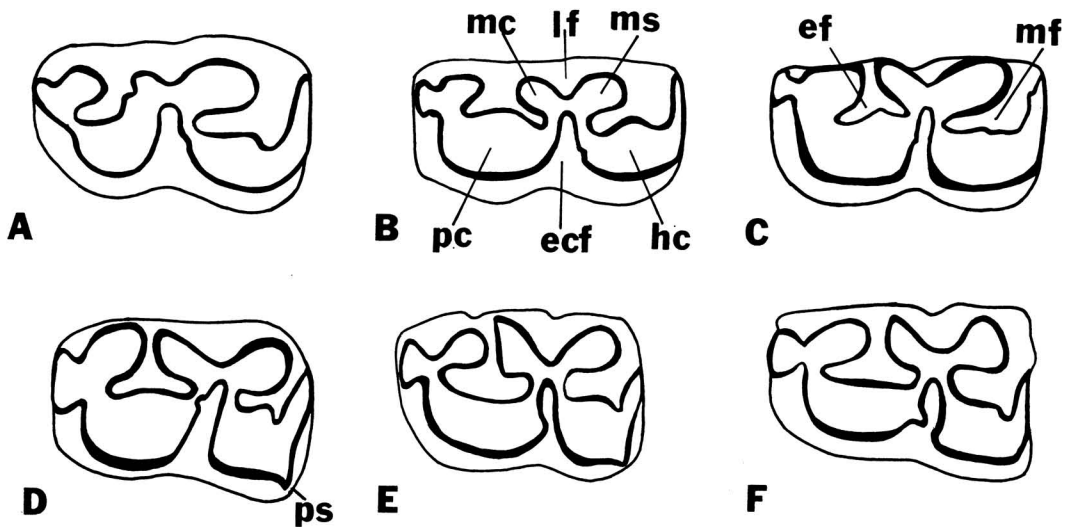
Fig. 2. Enamel patterns of lower second molars of horses. A = *Dinohippus interpolatus* (middle Hemphillian), B = *D. ocotensis* (late Hemphillian, moderately worn), C = *Equus (Dolichohippus simplicidens* (Blancan), D. = *E. (Parastylidequus) parastylidens* (Pleistocene), E = *E. (Pseudoquagga) burchelli* (recent), F = *E. (E.) caballus* (recent). ecf = ectoflexid, ef = entoflexid, hc = hypoconid, lf = linguaflexid, mc = metaconid, mf = metaflexid, ms = metastylid, pc = prtotoconid, ps = parastylid. C from jaw in Texas Tech University collection, others from jaws in Midwestern State University collection. Not to scale.

Equus because its characters indicate that a species of *Dinohippus* was its ancestor. The subgenus is retained.

Equus (Equus) Linnaeus 1758. — Included here are the domestic horse and Przewalski's horse, of the Old World. These horses resemble zebras in having a deep ectoflexid in the lower molars, but differ in having broadly "U" shaped linguaflexids.

A number of Pleistocene fossils from the United States have been referred to *Equus caballus* Linnaeus. I can find no consistent characters in the upper cheek teeth to separate *Equus* from *Asinus*, and believe that all Pleistocene records of *E. caballus* based on upper teeth or dentitions must be rejected. With two exceptions, all specimens or figures of specimens of lower jaws that have been referred to *E. caballus* that I have examined, and are identifiable, show the characters of *Asinus*, not *Equus*.

The holotype skull and lower jaws of *Equus (Equus) laurentius* Hay is definitely *Equus*. MATTHEW (1926:180) stated that the holotype was the skull of a recent horse. Later speculation has done nothing to resolve the problem. I now believe MATTHEW was correct; at best the Pleistocene origin of the specimen is suspect.

A lower jaw from a Pleistocene deposit in Aguascalientes, Mexico, was referred to *Equus caballus* (MOOSER & DALQUEST 1975). In this specimen the ectoflexids are broad and relatively deep in all three molars. They enter into the metaconid-metastylid isthmus, but not deeply so. This is a common but not the extreme condition in *E. (E.) caballus* and *E. (Dolichohippus)*. It is also the condition sometimes seen in the M1, rarely the M2, of aberrant specimens of *Asinus*. I now think that this fossil represents an extreme variant of *Asinus excelsus* (Leidy) that is unique in having an M3 like the M3 of true *Equus*. Linguaflexids are broadly "U" shaped.

No probable ancestor of *Equus (Equus)* is apparent in the American Hemphillian or Blancan horses. Probably true *Equus* never did occur in the New World. Presumably it originated in Asia from immigrant *Dinohippus* or *Equus Dolichohippus)*.

Astrohippus Stirton, 1940. — WEBB (1969) recognized *Astrohippus* in pre-Clarendonian faunas, but the genus is not well-known until the Hemphillian. In this genus alone, among Hemphillian horses with the protocone connected, the ectoflexid of the lower molars is

shallow and does not enter into the isthmus. In the upper cheek teeth, the protocones bear rounded anterior heels, so that the commissure appears to be attached relatively far back. In the lower teeth, metaconids and metastylids are well separated, often, especially in the premolars, on an elongated isthmus. The isthmus, floor of the entoflexid and floor of the metaflexid, are not wrinkled.

Evolution in *Astrohippus* in the Pliocene is illustrated in the series from *A. ansae* (Matthew and Stirton), of the Cɔffee Ranch, through *A. stocki* Lance, from Yepomera, to *A. albidens* Mooser, from Guanajuato. Progressive changes include: crowns of teeth increasingly hyposodont; crowns of upper teeth increasingly straight (only slightly curved in *A. albidens*); metastylids in lower teeth more distinctly pinched.

Astrohippus is represented at the Coffee Ranch by jaw fragments and about one hundred isolated teeth and by more than one thousand teeth from Ocote. The variation in dimensions of crowns of the upper teeth in both series is great. I attribute this primarily to sexual dimorphism, with male dentitions larger than those of females.

The enamel pattern of the upper cheek teeth of Hemphillian *Astrohippus* exhibits a "habit" that has seldom been mentioned. The hypoconal groove is obsolete, usually completely lacking. Most teeth of *A. ansae* have no hypoconal groove, even in the early stages of wear. Nearly all the upper teeth illustrated by LANCE (1950: 14), from Yepomera, lack the hypoconal groove; the exception is a single tooth just coming into wear. The hypoconal groove is present in a large proportion of the teeth from Ocote. The groove is seen most often in slightly worn teeth, but is also present in well worn teeth. Sometimes it is present almost to the base of the crown. The groove is a feature once present in ancestral forms, almost lost in mid-Hemphillian species, but being reestablished in late Hemphillian populations.

The dental characters of *Astrohippus* are clearly those expected in the ancestor of the American Pleistocene horses (*Asinus*). *Astrohippus* resembles *Asinus*, and differs from *Equus* (*Dolichohippus*), in just those characters by which *Dinohippus* resembles *Equus* (*Dolichohippus*) and differs from *Asinus:* shallow ectoflexid in the lower molars, unwrinkled entoflexids, pinched metastylids, crowns of upper teeth nearly straight, rounded

anterior heel on protocones, etc.

STIRTON (1940) recognized the similarity of *Astrohippus* to the Pleistocene horses. Unfortunately he did not realize the importance of the ectoɾexid in separation of genera. STIRTON, like LANCE ten years later, thought all Blancan horses were like *Equus* (*Dolichohippus*) *simplicidens* (of the 7 species of "Upper Pliocene *Equus*" listed by Stirton, only *Asinus cumminsii* is not a zebra, and the nature of *A. cumminsii* was not known in 1940). The concept of monophyletic origin of the Pleistocene horses demanded that Blancan "*Plesippus*" be intermediate between Hemphillian and Pleistocene horses. Since they were morphologically unsuited to this position, STIRTON remarked: "There is some indication of polyphyletic origin of the genus *Equus*, namely from different species of the subgenus *Astrohippus*, and the origin of some species from such forms as *Pliohippus* (*Pliohippus*) *coalingensis* (Merriam) is possible."

Asinus cumminsii (Cope), 1893. — This species was long thought to be closely related to or synonomous with *Equus* (*Dolichohippus*) *simplicidens*. The two species were described in the same paper. from the early Blancan Blanco Formation of Texas. HIBBARD (1944:716) first appreciated that *A. cumminsii* was not a zebra. His illustrations clearly show the differences that separate *Asinus* from *Equus* (*Dolichohippus*), though Hibbard did not remark on the differences at that time.

Asinus cumminsii remains poorly known. The lower jaw fragment with P3-M3, illustrated by HIBBARD, from Seward County, Kansas (University of Kansas Museum of Paleontology no. 6021) appears to be the most informative specimen available. A series of three associated lower teeth (Texas Memorial Museum no. 31166-3, probably P3 and M1-M2) from the Blanco Formation of Texas, the type locality, are like the specimen from Kansas. A few isolated upper and lower teeth are also available from The Blanco, and one from the Early Blancan Beck Ranch local fauna of Texas. All of these teeth are much worn. The lower jaw figured by STRAIN (1966) is from the late Blancan Hudspeth local fauna of Texas.

The upper cheek teeth of *Astrohippus albidens* and *Asinus cumminsii* share the following basic characters: crowns moderately to slightly curved; protocones with distinct anterior heel, apparent even in the worn teeth of *A. cumminsii*;

hypoconal groove often absent (lacking in all available specimens of *A. cumminsii*), fossettes simple. The lack of the hypoconal groove and simple fossettes in *A. cumminsii* may or may not be the result of excessive wear. No unworn upper teeth are available.

Lower teeth of *Astrohippus albidens* and *Asinus cumminsii* share the following basic features: ectoflexid shallow; linguaflexid sharply "V" shaped; metaconid rounded but metastylid pinched.

Major differences between *Astrohippus albidens* and *Asinus cumminsii* include the larger size of *A. cumminsii*, metaconids and metastylids more widely separated and swollen, and larger entoconid. All of these are quantitative in nature. *Astrohippus albidens* could be the direct ancestor of *Asinus cumminsii* but more likely ancestors may yet be discovered in late Hemphillian faunas of Mexico or the United States. It is my impression that *A. albidens* is less similar to *A. cumminsii* than *Dinohippus ocotensis* is similar to *Equus (Dolichohippus) simplicidens*. Nevertheless it seems clear that *A. cumminsii* is closely related to *A. albidens* and probably descendant from a species of *Astrohippus*.

By earliest Pleistocene (Irvingtonian) time, several very distinct species of *Asinus* were in existence. The paucity of specimens of *Asinus* in Blancan faunas of the United States suggests that most of this radiation may have occurred elsewhere, perhaps on the Mexican plateau.

Asinus Gray, 1824. — Among the Old World horses, the donkey, *Asinus (Asinus) asinus* (Linnaeus), the wild ass, *A. (A.) somaliensis* Frisch, and the onager, *A. (Hemionus) hemionus* (Pallas), resemble the American Pleistocene horses in basic details, and are doubtless descendent from American species that reached Asia in the early Pleistocene. The oldest generic name available is *Asinus*. I am grateful to M. F. Skinner (personal communication) for pointing out that *Asinus* dates from Gray, 1824, rather than Frisch 1775 or other pre-1824 authors.

All lower dentitions of the donkey and wild ass that I have seen or seen figured have sharply "V" shaped linguaflexids and this may be a subgeneric character. In the subgenus *Hemionus* Stehlin and Graziosi, 1955, the limbs are long and slender, and the linguaflexids of the lower teeth are not as sharply "V" shaped.

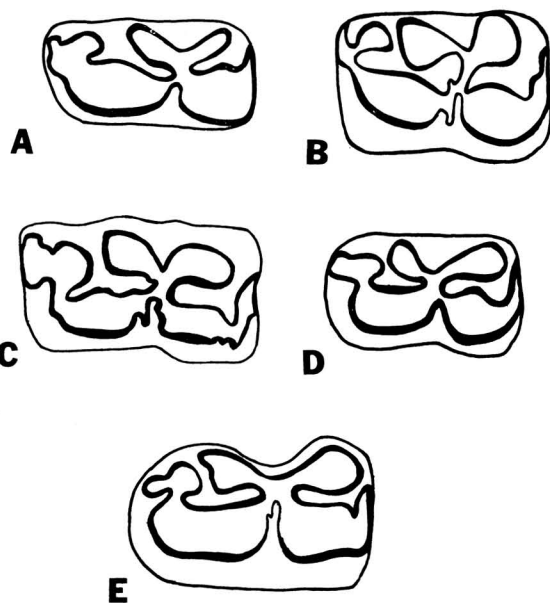Some American Pleistocene horses may eventually be referred to the subgenus *Asinus*

Fig. 3. Enamel patterns of lower second molars of horses. A = *Astrohippus albidens* (late (Hemphillian), B = *Asinus (A.) cumminsii* (Blancan), C = *A. (A.) asinus* (recent), D = *A. (Hemionus) tau* (Pleistocene), E = *A. (Amerhippus) conversidens* (Pleistocene). B from Hibbard (1944), others from jaws in Midwestern State University collection. Not to scale.

but none of the lower jaws that I have seen are referable here. In the Blancan *Asinus (Asinus)* · *cumminsii* (Cope) the linguaflexids are uniformly and sharply "V" shaped. Resemblance of lower dentitions of the little Blancan horse to the donkey is very close, and *A. cumminsii* probably belongs in the subgenus *Asinus*.

The American Pleistocene horses remain a confused group of nominal species that probably includes a relatively small number of biological species. To some extent, separation of the nominal species onto subgenera is practical, especially when type specimens are adequate or identifiable fossils can reasonably be referred to named species. The status of many of the nominal species of medium-sized Pleistocene *Asinus* may never be determined.

The subgenus *Hemionus* includes, in addition to the Recent Old World species, the stiltlegged horses of the American Pleistocene: *Asinus calobatus* (Troxell), *Asinus tau* (Owen), probably *Asinus altidens* (Quinn), and perhaps others.

Stocky-legged horses with elongated protocones on the molars may be referable to the

subgenus *Amerhippus* Hoffstetter, 1950 (M. F. Skinner, personal communication). SKINNER has noted (1972:118) that the absence of infundibula on the lower incisors, a character used by Hoffstetter, is not valid at the subgeneric level. Probably a number of species of American Pleistocene horses should be placed in the subgenus *Amerhippus*, including *Asinus conversidens* (Owen) and *A. scotti* (Gildey).

Pleistocene horses with short, broad, protocones on the molars perhaps belong in still another subgenus. This group is typified by *Asinus occidentalis* (Leidy). SAVAGE (1951:246) noted that this species was described from three upper teeth from California (one from Tuolumne County and two from Kern County) and that the Kern County specimens may belong to a zebra, *Equus* (*Dolichohippus*). SAVAGE implied that Kern County is the type locality of *A. occidentalis*. This is incorrect. GIDLEY (1901) selected the Tuolumne County tooth as the lectotype because it was the only one figured by Leidy. This action must stand (Article 73, International Rules of Zoological Nomenclature). The well-known horse of the Rancho La Brea has teeth like the lectotype of *Asinus occidentalis*, and I see no reason not to use the name for the Rancho La Brea horse.

Tomolabis Cope, 1892, type species *Equus fraternus* Leidy, was listed by SKINNER (1972: 118) and may represent still another subgenus of American Pleistocene *Asinus*.

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