CONTRIBUTIONS TO PALÆONTOLOGY

V

TOOTH CHARACTERS OF PROTOHIPPINE HORSES WITH SPECIAL REFERENCE TO SPECIES FROM THE MERYCHIPPUS ZONE, CALIFORNIA

By Francis D. Bode

With two plates and six text-figures

[Preprinted from Carnegie Institution of Washington Publication No. 453, pages 39 to 63, December 20, 1934]

Daich Graduate School of the Geological Sciences
California Institute of Technology
Pasadena, California

Contribution No. 146

CONTRIBUTIONS TO PALÆONTOLOGY

V

TOOTH CHARACTERS OF PROTOHIPPINE HORSES WITH SPECIAL REFERENCE TO SPECIES FROM THE MERYCHIPPUS ZONE, CALIFORNIA

By Francis D. Bode

With two plates and six text-figures

[Issued December 20, 1934]

CONTENTS

	Page
Introduction	41
Description of Material	42
Merychippus brevidontus n. sp	42
Merychippus californicus Merriam	43
Variation in Cheek-tooth Characters of Fossil Horses and its Stratigraphic Significance	47
Superior Cheek-teeth	49
Inferior Cheek-teeth	56
Consideration of Single Characters	48
Views of Other Authors	59
Conclusions	61

TOOTH CHARACTERS OF PROTOHIPPINE HORSES WITH SPECIAL REFERENCE TO SPECIES FROM THE MERYCHIPPUS ZONE, CALIFORNIA

INTRODUCTION

The critical review of equine tooth characters attempted in this paper is the result of a study of the protohippine horses obtained from the Merychippus Zone of the north Coalinga district, California. During the conduct of extensive excavations in this zone since 1928 by the California Institute, more than two thousand teeth of the genus *Merychippus* have been collected. In addition to the types represented by the equine material, a number of associated land mammals have been secured. The faunal list, which includes some fifteen species, suggests that this locality occupies a stratigraphic position approximately late middle Miocene in age.

The variation displayed in the dental characters of the merychippine material from the Merychippus Zone necessitated comparisons with cheek-teeth of Equidæ from practically all of the Miocene formations furnishing vertebrate remains in the Pacific Coast and Great Basin Provinces. A comprehensive study of these collections clearly demonstrates that many of the cheek-tooth characters employed in the description of type specimens of fossil horses are variable to an extent which renders them unreliable in a determination of species. The variation of these characters within a large collection also indicates that it is possible for teeth referable to a particular species to have a wider stratigraphic range than has been hitherto appreciated. The conclusion is reached that the presence of a species has less value in reaching an age determination of the strata in which it occurs than evidence furnished by an association of several species.

Indebtedness is acknowledged to the Museum of Paleontology, University of California, for a generous loan of fossil material, including type specimens, from the Barstow and Mascall formations. The writer takes this opportunity to thank Dr. Chester Stock for advice given during the course of the investigation. The illustrations have been prepared by John L. Ridgway. The enamel patterns of cheek-teeth reproduced in the text were accurately outlined on photographs of the specimens. The photographic prints were then treated in a bleaching solution, which obliterated the photograph but did not affect the ink outline.

DESCRIPTION OF MATERIAL

Merychippus brevidontus n. sp.

Type specimen—P3, No. 1414, Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Plate 1, figs. 3-3b.)

Paratypes—P4, No. 1413; M2, No. 1408; M1, No. 1422; Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Plate 1, figs. 6-8.)

Referred specimens—Series of upper and lower cheek-teeth, Nos. 1409-1412, 1415-1421, 1423-1432, Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Plate 1, figs. 4-4b, 5-5b, and Plate 2, figs. 4-12.)

Specific characters—Crowns of cheek-teeth fully hypsodont but extremely short relative to size of cross-sections. Enamel pattern of upper and lower cheek-teeth highly complex with complexity continuing almost to base of crown.

This species is represented in the collections by approximately seventy-five upper and lower cheek-teeth. The species is found also in formations of middle Miocene age at Virgin Valley, Nevada, and Skull Spring, eastern Oregon.

The principal character is the great complexity of the enamel pattern, associated with fully hypsodont but relatively short crowns. In unworn teeth the average height of crown is 20.5 mm. The maximum measurement was 23.4 mm. and the minimum 18.7. The cross-sectional area is comparable in size to that seen in the type of *Merychippus isonesus* Cope. As many as seventeen enamel folds have been observed on the borders of the fossettes. The pli-caballin is sometimes tripartite, is never absent and rarely single. At the juncture of the protoloph and the metacone, the prefossette is sometimes incompletely enclosed on relatively unworn teeth. In such instances the lingual end of the protoconule shows a curious increase in number and in arrangement of plications. The protocone usually possesses a spur extending toward the protoconule. The hypocone is flattened and elongate. The long axis of this cusp is oriented usually in an anteroposterior direction. The cusp is often twice as long as the protocone and is frequently not connected with the metaconule.

The average height of crown of the inferior cheek-teeth is 21.3 mm. The number and type of plications of the enamel walls are unique for a tooth of this size, the complexity frequently approaching that seen in lower teeth referred to *Hipparion mohavense* Merriam. The metaconid-metastylid column usually occupies well over one-third of the anteroposterior width of the crown and remains separate throughout the wear of the tooth. The entoconid extends far across the lingual valley and frequently touches the metaconid. The internal walls of the protoconid and hypoconid usually carry several plate-like projections or crenulations of enamel. The teeth are well cemented.

The type of *Merychippus sphenodus* Cope presents a similar type of enamel pattern, but exhibits a much higher crown. *M. brevidontus* differs from *M. seversus* Cope (fig. 2, e to i) in complexity of the enamel pattern, shortness of crown and in larger cross-sectional area of crown. Teeth of *M. seversus* are considerably higher crowned. The type of *M. relictus* Cope is also smaller in cross-section than in the Californian form and the enamel pattern is characterized by its simplicity. Moreover, unworn teeth referable to *M. relictus* (fig. 2b and 2d) have a height of crown comparable to that in *M. isonesus* Cope. *M. westoni* Simpson and *M. gunteri* Simpson approach the small Coalinga species in shortness of crown. However, the teeth in the Florida species seem to possess a much simpler enamel pattern. *M. brevidontus* is distinguished from *M. isonesus* (fig. 3a to 3m) by its shorter crown and more complex enamel pattern. In his description of the Miocene horses from the Sheep

Creek and lower Snake Creek horizons of western Nebraska, Matthew [1] refers to a collection of very short-crowned teeth. Although not certain of their affinities, Matthew regarded them as belonging to a form distinct from the *M. paniensis* group. Nearly all of these specimens are unworn teeth and a comparison of the enamel pattern with that of *M. brevidontus* is consequently difficult. The size of crown comes close to that of *M. brevidontus*. It is possible that these forms are sufficiently similar as to be specifically related. It is interesting to note that, as in the case of the large collection from the north Coalinga horizon, those from the Sheep Creek and lower Snake Creek horizons contain, along with a large number of normal-sized teeth of *Merychippus*, a few very short-crowned teeth whose characters do not grade into the larger and highly variable group. It may be mentioned that up to the present time these small forms have always been found in association with a progressive species of *Parahippus*.

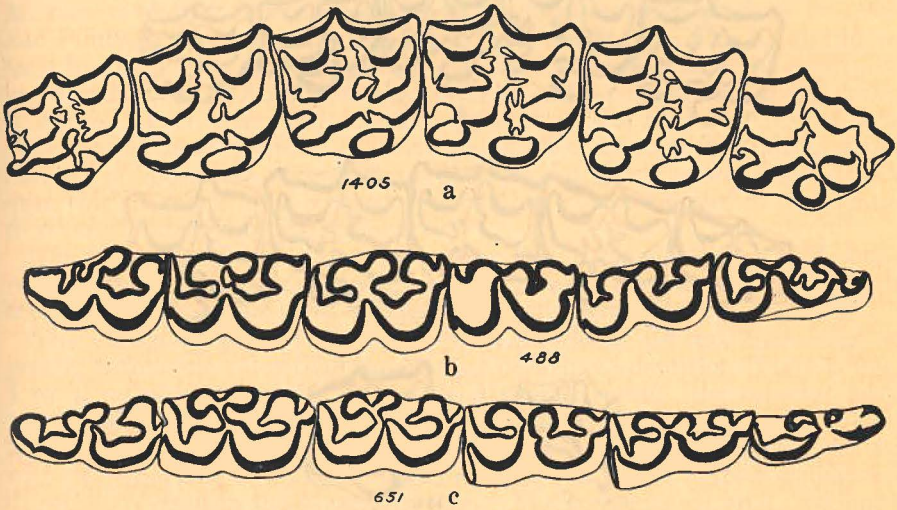


FIG. 1—*Merychippus californicus* Merriam. Referred specimens. a, composite upper cheek-tooth series, No. 1405; b, c, individual lower cheek-tooth series, Nos. 488 and 651; x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California. (Specimens show average grouping of characters seen in teeth from the Merychippus Zone.)

Merychippus californicus Merriam

Type specimen—M1, No. 21247, Univ. Calif. Coll. Vert. Pale., Merychippus Zone, north Coalinga district, California.

Referred specimens—A composite series of upper cheek-teeth, P2-M3, No. 1405; mandibles with all cheek-teeth present, Nos. 488 and 651, Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Fig. 1-1c.)

The material from the Merychippus Zone consists almost entirely of scattered teeth and fragments of limb elements. In the entire collection no associated upper cheek-teeth are present. Three more or less complete mandibles were collected during the progress of the excavations. The limb bones have suffered considerably from abrasion, presumably during transportation in water. Skeletal materials are so fragmentary and are usually so well worn that they possess little taxonomic value.

[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, 159, 1924.

The amount of variation (figs. 3 to 6) seen in over two thousand teeth referable to this species makes it impossible to find any one character sufficiently unique to afford a constant distinction between *Merychippus californicus* and many of the specific forms belonging to this genus. Some of the teeth in the collection are specifically inseparable from specimens of *M. sumani* Merriam (fig. 5) from the Barstow. Others can not be distinguished from the type of *M. isonesus* (figs. 3 and 4). In like manner, selections can be made of teeth whose characters approach those of most of the described species of *Merychippus*. Only when the collection is regarded as a whole can differences be recognized.

For the superior dentition, referred specimen No. 1405 (fig. 1a) Calif. Inst. Tech. Coll. is seen to be considerably more typical of the group than is the

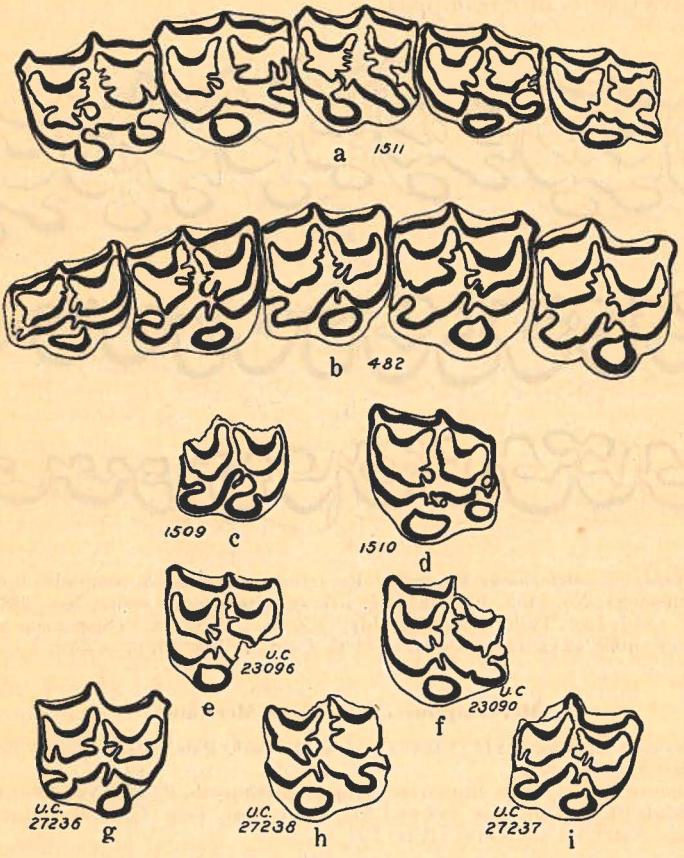


FIG. 2—a, *Merychippus primus* Matthew, composite upper cheek-tooth series of referred specimens showing extent of variation of enamel patterns, Sheep Creek middle Miocene, western Nebraska. b, *Merychippus relictus* (Cope), referred specimen, upper cheek-tooth series of one individual shows type of pattern of small teeth that may be referred to this species, Skull Spring middle Miocene, eastern Oregon. c, d, *Merychippus relictus* (Cope), referred specimens, Skull Spring middle Miocene, eastern Oregon. e to i, *Merychippus seversus* (Cope), referred specimens showing types of variation of enamel pattern of small teeth referable to this species. Mascall middle Miocene, eastern Oregon; x 1. (Specimen numbers designated "U. C." from Univ. Calif. Coll.; without designation, from Calif. Inst. Tech. Coll.)

type specimen described by Merriam.[1] However, it should be noted that some of the *Merychippus* teeth in the collections of the University of California from the Barstow Miocene, closely approach No. 1405. As is shown in this specimen, the union of protoconule with metaloph, to enclose the prefossette, is incompletely established in the premolars, and the lingual end of the protoconule is greatly plicated. These characters are present in approximately 70 per cent of all premolars of *M. californicus* from the Merychippus Zone, whose crowns have been less than half removed by wear. The prefossette is nearly always found completely enclosed in well-worn premolars and is always so in molars. Frequency of occurrence of an open prefossette in the premolars is apparently the most distinctive character found in the permanent teeth from the Merychippus Zone. It should be noted, however, that an open prefossette has been observed in a number of equine species and genera, among which may be mentioned: Specimens referred to *M. isonesus* from the Skull Spring locality in eastern Oregon; *M. sumani* and *M. intermontanus* from the Barstow; *Hipparion mohavense* and *Pliohippus tantalus* from the Ricardo of the Mojave Desert; and in at least five additional species found in the Great Plains region. The relatively small collections at hand from the several localities mentioned above make it impossible to determine accurately the incidence of occurrence of this character in these species. The material studied seems to indicate that the number of specimens with open prefossette is proportionately less. However, this character must be used with caution when employed in the identification of a merychippine species.

The lower cheek-teeth from the Merychippus Zone, exclusive of those referred to *M. brevidontus*, present no characters which serve to distinguish them from comparable teeth of most species of *Merychippus*.

The deciduous teeth of *Merychippus californicus* possess characters of greater taxonomic value than those of the permanent dentition (Plate 2, figs. 1 to 3). Compared to *M. isonesus* and similar species, the superior milk teeth in *M. californicus* are higher crowned, well cemented and the protocone and hypocone are cylindrical rather than conical. The hypocone is oriented with principal axis in an anteroposterior direction rather than in a diagonal direction, as seen in the Mascall species. The crescents are well developed and the fossettes completely formed, so that the Coalinga milk teeth resemble those of the permanent dentition. In *M. isonesus*, the deciduous premolars have a "*Parahippus*-like" appearance. The principal difference between the teeth from the Merychippus Zone and those from the Barstow is largely one of size, the latter being as a rule considerably larger. In size alone, the Coalinga specimens are more nearly comparable to those of *M. isonesus*, while the milk teeth from the Barstow are similar to corresponding teeth of *Protohippus*.

The inferior milk teeth from the Merychippus Zone are sometimes more than twice as high-crowned as average specimens from the Mascall. These teeth carry a thin deposit of cement along the lingual side. The external valley is well filled with cement. Compared to corresponding teeth from the Barstow, the Coalinga specimens are smaller, shorter crowned, but equally as well cemented.

It may appear from the foregoing description that the specific status of *Merychippus californicus* is questioned. Since some of the teeth are similar in character to the type of *M. isonesus*, it might be concluded that the Coalinga horse represents that species. On the other hand, an equal number

[1] J. C. Merriam, Trans. Amer. Philos. Soc., n. s., vol. 22, pt. 3, 9, 1915.

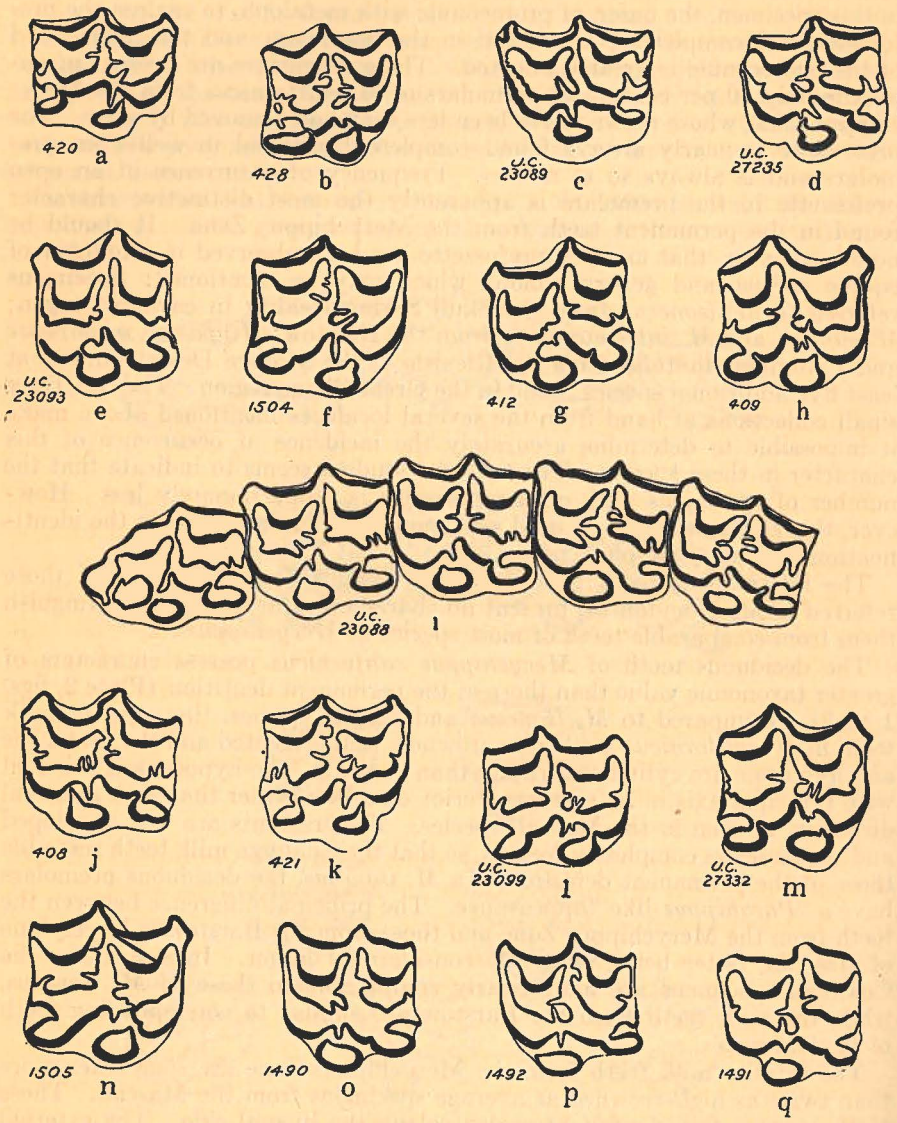


FIG. 3—a to m, *Merychippus isonesus* (Cope), referred specimens from Mascall middle Miocene of eastern Oregon showing some types of variation of enamel pattern; n to q, *Merychippus californicus* Merriam, referred specimens from Merychippus Zone showing types of enamel patterns similar to *M. isonesus;* x 1. (Specimen numbers designated "U. C." from Univ. Calif. Coll.; without designation, from Calif. Inst. Tech. Coll.)

of teeth from the Merychippus Zone have characters which approach those of the type of *M. sumani*. Specimens are available which approximate those of additional species belonging to *Merychippus*. Arbitrary assignment of the entire group to a described species other than *M. californicus* involves a procedure of little or no value, since such reference may be made with equal right to any one of a number of types. On the other hand, the collection may well be regarded as comprising teeth of several distinct, merychippine species. Were such a view adopted, however, a number of teeth would of necessity be recognized as possessing intermediate structural features and could consequently be regarded as characteristic of additional specific types. Rather than adopt a procedure which would become extremely unwieldy, it appears more desirable to retain within the *Merychippus californicus* group all these variant forms, with the referred specimen, No. 1405 (fig. 1a), presenting the average grouping of characters seen in teeth from the north Coalinga Zone. The latter is distinct from all other type specimens of merychippine species. No. 1405 may be regarded as typifying in its characters the species *Merychippus californicus*.

VARIATION IN CHEEK-TOOTH CHARACTERS OF FOSSIL HORSES AND ITS STRATIGRAPHIC SIGNIFICANCE

Since characters of the teeth of fossil horses are of considerable importance, not only in a determination of species but also in making a determination of the stratigraphic position of fossil material, it is important to acquire information concerning the variation and reliability of dental characters in these forms. The material from the Merychippus Zone offers opportunity to study the variation of cheek-tooth characters as exhibited in a large number of individuals, all referable to a single species. An attempt has been made, therefore, to determine the extent to which each character varies and to indicate the limits within which these characters can be safely used in their application to stratigraphy.

The collections from the Merychippus Zone were obtained at Locality 108, Calif. Inst. Tech. Vert. Pale., in a zone of sandstones and conglomerates approximately three feet in thickness. Deposition of the sedimentary beds probably required a relatively short period of geologic time. The fossil remains represent presumably a cross-section of the Equidæ, as this group existed during the unit of time recorded in the accumulation of the deposits of the Merychippus Zone. The small amount of time which elapsed during this deposition makes the possibility rather remote that the variation in tooth characters is due to progressive evolutionary changes within this merychippine species. Actual counts made of particular teeth in the cheek-tooth series indicate the presence of nearly two hundred individuals in the collections.

In approaching the study, a list was compiled of the cheek-tooth characters used by all known authors in describing species of the Equidæ with hypsodont teeth. This list shows that attempts have been made to employ more than fifty different peculiarities of tooth

structure in the definition of species. The variation of each of these characters and its relation to the variation of all other characters was then observed in more than two thousand teeth from locality 108. In addition, comparisons were made with teeth from practically all Tertiary vertebrate horizons of the Pacific Coast and Great Basin Provinces.

It is not the purpose in the following discussion to invalidate a large number of described equine species. Nor is the account to be construed as an attempt to destroy the value of horse teeth as stratigraphic markers. Rather is it to be regarded as an effort to point out the degree to which characters of teeth of fossil horses vary, and to suggest methods by which such characters can be more accurately and reliably defined for stratigraphic purposes, especially with reference to the limits within which geologic age assignments may be made.

CONSIDERATION OF SINGLE CHARACTERS

As previously demonstrated by Gidley,[1] the factors responsible for differences in the enamel pattern of cheek-teeth may be divided into two groups: (1) Stage of wear of an individual tooth, and (2) individual variation.

As a single tooth is worn to the base of the crown, various changes in the enamel pattern and in the diametral ratios take place. The maximum complexity of the enamel pattern occurs when approximately the first one-fifth of the crown has been removed by wear. From this stage onward the complication of the enamel folds gradually decreases, the simplest pattern appearing at the base of the crown. The enamel pattern in both superior and inferior cheek-teeth, whose crowns have been worn almost to the base, is very simple. In such instances, it is practically impossible to reach more than an approximate determination of the type. Where the evolutionary stage represented by such a tooth is transitional between two genera, an assignment to either genus is questionable.

The maximum anteroposterior diameter in all cheek-teeth is situated near the summit of the crown in an unworn tooth. This diameter decreases gradually with wear. The transverse diameter gradually increases toward the base, usually becoming greater than the anteroposterior diameter in well-worn teeth. Ratios involving the use of these two diameters change materially with age. It follows therefore that the diameters and proportional ratios of a molar-premolar series may also vary with age. A large number of observations seems to indicate that the rate of change of these diameters and ratios is variable. Consequently, comparisons based upon these characters have little value. For purposes of comparison, only teeth that have attained

[1] J. W. Gidley, Bull. Amer. Mus. Nat. Hist., vol. 14, art. 9, 1901.

the same stage of wear should be used and comparisons should be limited preferably to teeth in early stages of wear. In the following discussion of the variation of cheek-tooth characters, observations have been limited to teeth whose crowns have been less than one-third removed by wear.

Among the numerous cheek-tooth characters employed by various authors, it appears especially desirable to discuss the following points.

Superior Cheek-teeth

Protocone—The shape, orientation and position of the protocone have been frequently used as specific characters. In the collections from the Merychippus Zone this cusp, while usually separate to the base of the crown, may also be found connected with the protoconule at any stage of wear. The cusp may be round or greatly flattened. When elliptical in cross-section, the orientation of the long axis may be in any direction. A spur or process extending toward the protoconule varies in size and is frequently absent. The enamel wall of this cusp is seen to be either inflated or indented. Its position with reference to other parts of the occlusal surface is variable. In addition, all characters vary with the wear of the tooth. In *Merychippus,* as in succeeding genera, separation of the protocone seems to be linked with the complexity of the enamel pattern. A protocone connected with protoconule at an early stage of wear is to be found more often in teeth whose enamel pattern is simple. A discrete protocone, on the other hand, is frequently found associated with more complex types of enamel patterns. This association exists throughout the geologic history of the genus *Merychippus* and appears to indicate that the major tooth characters, which distinguish *Hipparion* and *Pliohippus,* were foreshadowed long before the period when these genera appeared. A discrete protocone is of value in distinguishing *Hipparion* from *Pliohippus* or *Protohippus.* Its use in separating a primitive *Hipparion* from a progressive merychippine form, whose characters are approaching those of the former genus is of no value. A spur on the protocone is more characteristic of *Merychippus* than of *Hipparion,* but this character must be used with caution, since it has been observed in a few teeth referred to *Hipparion* and is frequently absent in *Merychippus.* Moreover, in those merychippine forms regarded as ancestral to *Hipparion,* and in *Hipparion* as well, a progressive tendency is noted toward enlargement of protocone in an anteroposterior direction and development of this cusp at the expense of the hypocone. Consequently, the latter cusp is displaced more and more toward the rear of the tooth. While the protocone may be employed on occasion to distinguish *Merychippus* and *Hipparion,* the numerous exceptions which have been noted obviate the possibility of general application.

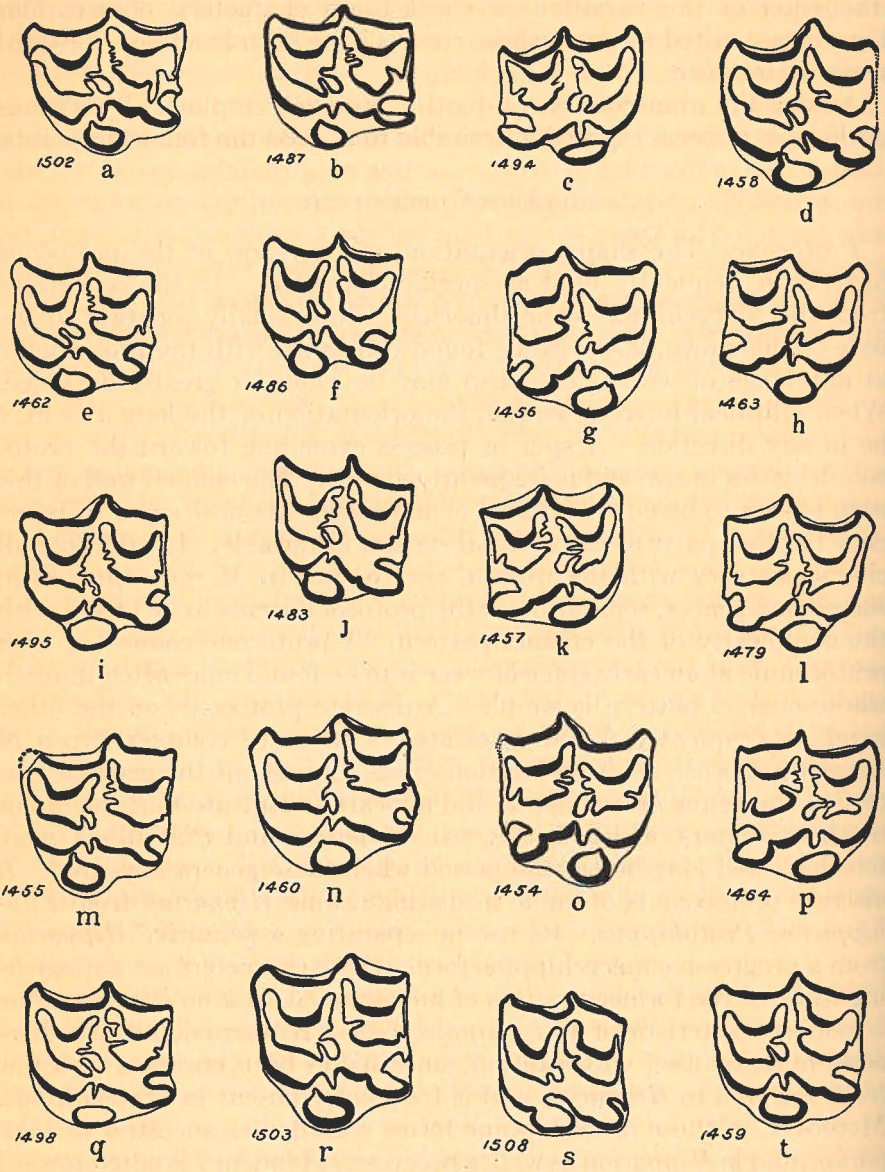


FIG. 4—*Merychippus californicus* Merriam. a to t, referred specimens showing variations of enamel patterns similar to *M. isonesus;* x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California.

In *Protohippus* and in *Pliohippus* the protocone is always connected with the protoloph. In *Protohippus* the protocone is nearly equal to the hypocone in size and is sometimes connected with that cusp. The distinction between *Protohippus* and *Merychippus* as based on this cusp is usually fairly well marked; although in species situated near the border line between the two genera, the distinction is by no means so clearly defined. In *Pliohippus* the protocone also tends to become larger, but unlike that in *Hipparion* this cusp remains connected with the protoloph and develops progressively toward the anterior side of the tooth. The forward extension of the protocone on the anterior side of the isthmus clearly distinguishes *Equus* from *Pliohippus*. A study of material referable to *Plesippus* indicates that the use of the characters of this cusp in the definition of the latter genus is open to question.

The protocone presents by far the most characteristic structure of the occlusal surface. In fact, cheek-tooth characters of most of the genera are built around this cusp. While it is of great value in distinguishing the major lines of evolution in the Equidæ, its variations, as exhibited by the collection from the Merychippus Zone and by those from other Tertiary localities, are quite diverse within individual genera. Its use as a specific character is negligible and its value from the standpoint of stratigraphy is limited to two time stages for each genus, in that the progressive and primitive forms of a genus may be distinguished by the modification of the protocone. In intermediate stages the extent of variation would probably always include types comparable to the end stages as well.

Hypocone—In the material from north Coalinga, the hypocone is seen to vary in much the same manner as the protocone. It is sometimes found separate from the metaloph at a late stage of wear. It assumes a variety of shapes from round to flat. The position of the hypocone, relative to the other cusps, varies to a noticeable degree. In size, this cusp is usually, though not always, smaller than the protocone. The relative size of these two cusps is of little value as a distinctive character, however, since the hypocone is usually smaller than the protocone throughout the history of the Equidæ. In *Hipparion* the hypocone is pushed backward with development of the protocone. With the exception of the modification of the cusp in this genus, no evolutionary changes of stratigraphic value seem to have occurred.

Hypostyle and Pli-Caballin—These features of the occlusal surface are merely reflections of the complication of the enamel pattern. In a tooth in which the enamel pattern is simple, the pli-caballin is single or absent. Intricate enamel patterns are associated with a pli-caballin, which may be double or tri-partite. In like manner, the number of plications in the area designated as the hypostyle seems to be a func-

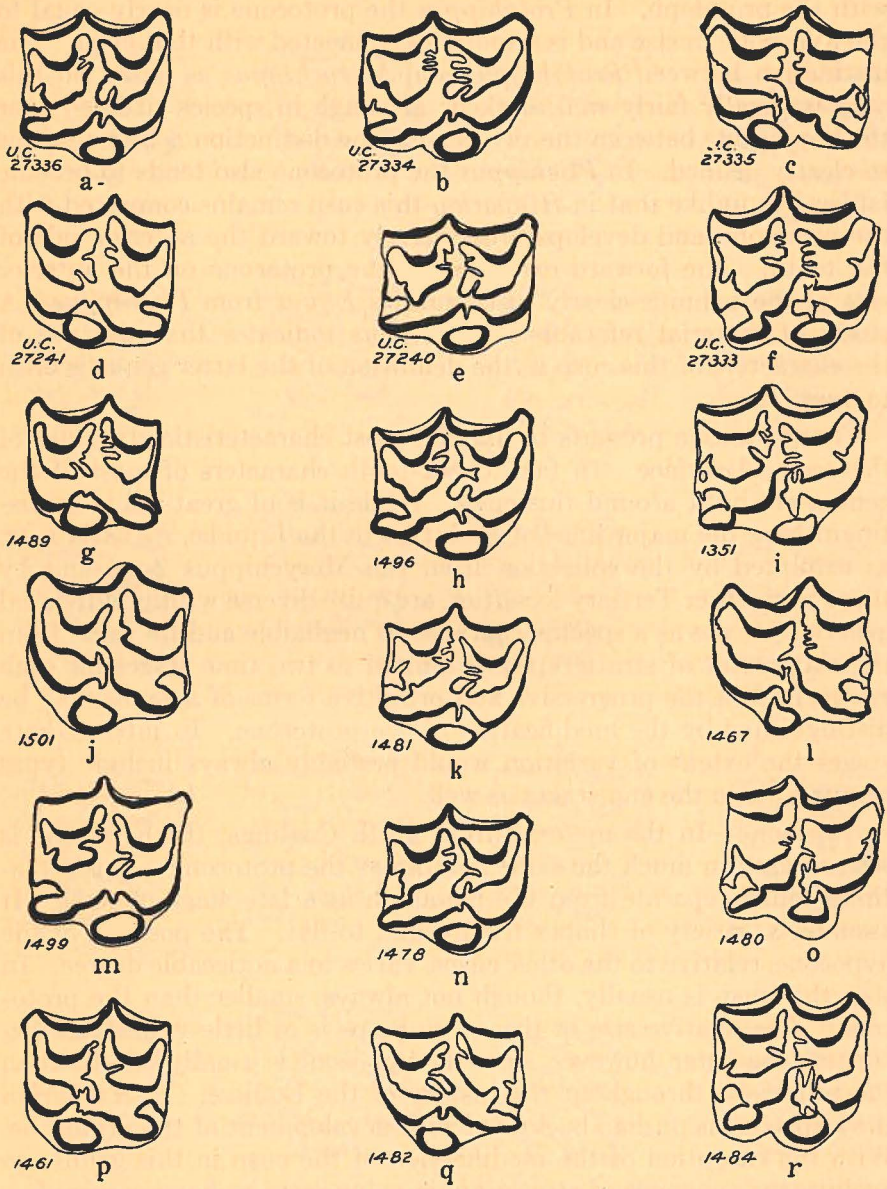


FIG. 5—a to f, *Merychippus sumani* Merriam, referred specimens showing examples of variation of enamel pattern. Univ. Calif. Coll., Barstow upper Miocene, California; g to r, *Merychippus californicus* Merriam, referred specimens showing types of enamel patterns similar to *M. sumani;* x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California.

tion of the intricacies of the enamel walls of the fossettes. Considered alone, these characters have little value in the distinction of a species. They may be regarded as of same importance as the complication of the enamel walls of the fossettes.

Fossettes—Expansion or contraction of the fossettes and position of the external lobes has been found to be so variable in the materials studied as to suggest that these characters are completely unreliable for diagnostic purposes. Degree of complexity of the enamel walls of the fossettes appears to possess some general value. Such terms as highly, moderately or simply plicated borders are satisfactory when the description is based on the average grouping of occlusal characters as seen in a large group of specimens. Complexity of the enamel, when described in this manner, along with height and curvature of crown and appearance of protocone, furnish features of value in assigning specimens to their respective species. Complexity of the fossette borders is of value only if the crown is not too greatly worn. Moreover, comparisons of individual peculiarities are of no value since the number, shape and arrangement of the plications of the enamel walls are subject to a wide range of variation. In *Hipparion* the enamel pattern varies from moderately to highly complex. Some of the patterns exhibited by teeth referred to *Equus* may also show considerable complexity. In *Pliohipus* and in *Protohippus* the types of patterns are moderate to simple. All three stages of complexity are found in *Merychippus.*

External Styles—The strength of the external styles as displayed in teeth of a particular species is variable. Ratios indicating the relation of width of these styles to anteroposterior diameter of the entire tooth have been obtained for Tertiary horses from several horizons. These ratios and their range of variation were found to be similar in every collection furnishing materials for measurements. The strength of the styles, in relation to size of tooth, remains approximately the same in all genera.

Cement—An examination of teeth from numerous localities, representing stratigraphic stages from middle Miocene to Recent, indicates that the amount of cement present on a tooth has little value, even as a generic character for horses with hypsodont teeth. Some of the merychippine teeth from the Mascall carry as much cement in proportion to their size as do the large teeth of *Equus.*

Shape of Occlusal Surface—This is an unreliable character. As has been stated before, this surface is usually elongated in anteroposterior direction in relatively unworn teeth, and in worn teeth the greatest width is usually in transverse direction. The surface in moderately worn teeth is nearly square, but the shape varies considerably with the individual and with age. The variation of this character in teeth,

which have reached practically the same stage of wear, is also considerable. A quantitative idea of this variation may be obtained from the ratios of the anteroposterior diameters to the transverse diameters. This ratio was calculated for more than three hundred first and second molars from the Merychippus Zone. The amount of wear to which each of these teeth had been subjected is approximately the same. The ratio varies from 1.40 to 0.85 and is sufficient to include most of the members of the Equidæ. Measurements of the last two premolars indicate that the shape of the occlusal surface in these teeth varies in a manner identical with that of the molars. The shape of M3 and P2 varies in still greater measure. This character has sometimes been used for specific distinctions. The variation is not due to extreme differences in anteroposterior diameters of the teeth, when compared to the rest of the series. Position of these teeth in the maxillary is variable and is rarely parallel to that of other cheek-teeth in an anteroposterior-vertical plane. Consequently, the occlusal surface is worn obliquely to the vertical axis of the tooth and the area of the surface is thus subject to a greater range of variation than that of intermediate teeth, whose position in the maxillary is more nearly constant.

Curvature of Crown—The extent of curvature of the crown is of value in distinguishing genera. Comparison of this character should be limited to unworn or slightly worn teeth. The original curvature can not be determined accurately for a tooth that has been more than half worn. In *Merychippus,* as indicated by the collections studied, the crowns of cheek-teeth are curved to varying degrees and are rarely straight. In *Hipparion* the teeth are straight to only slightly curved. This character is of particular value in distinguishing primitive forms of *Hipparion* from progressive types of *Merychippus* which possess teeth that are otherwise similar. However, caution must be exercised, for teeth from large collections of merychippine materials are sometimes, though infrequently, straight. In *Protohippus* and in the earlier forms of *Pliohippus* the crowns are curved. Greatest curvature of crown is seen in some species of *Pliohippus.* This character possesses no special value in distinguishing these two genera from *Merychippus.* Advanced forms of *Pliohippus* may not always be distinguishable from *Plesippus* and *Equus* by this single character.

Transverse Diameter—In observations on the value of tooth characters, Gidley[1] pointed out that following the early stages of wear the transverse diameter was only slightly variable. This opinion is somewhat substantiated by measurements made on teeth from the Merychippus Zone. The range in width as measured in millimeters is from 19.6 to 14.2, a difference of 5.4. However, it should be pointed out that most of the species of *Merychippus* fall within these limits. In

[1] J. W. Gidley, *op. cit.,* 105-106, 1901.

addition, some teeth referred to *Parahippus, Protohippus, Pliohippus* and *Hipparion* give similar diameters. While the variation as measured in millimeters is not particularly large, the increase in this diameter during the evolution of the later equines was so gradual and slight as to render this character of little distinctive value as a time indicator.

Height of Crown—Measurements of the height of crown of unworn teeth were made on more than five hundred specimens from the Merychippus Zone. Similar measurements were made also on teeth refer-

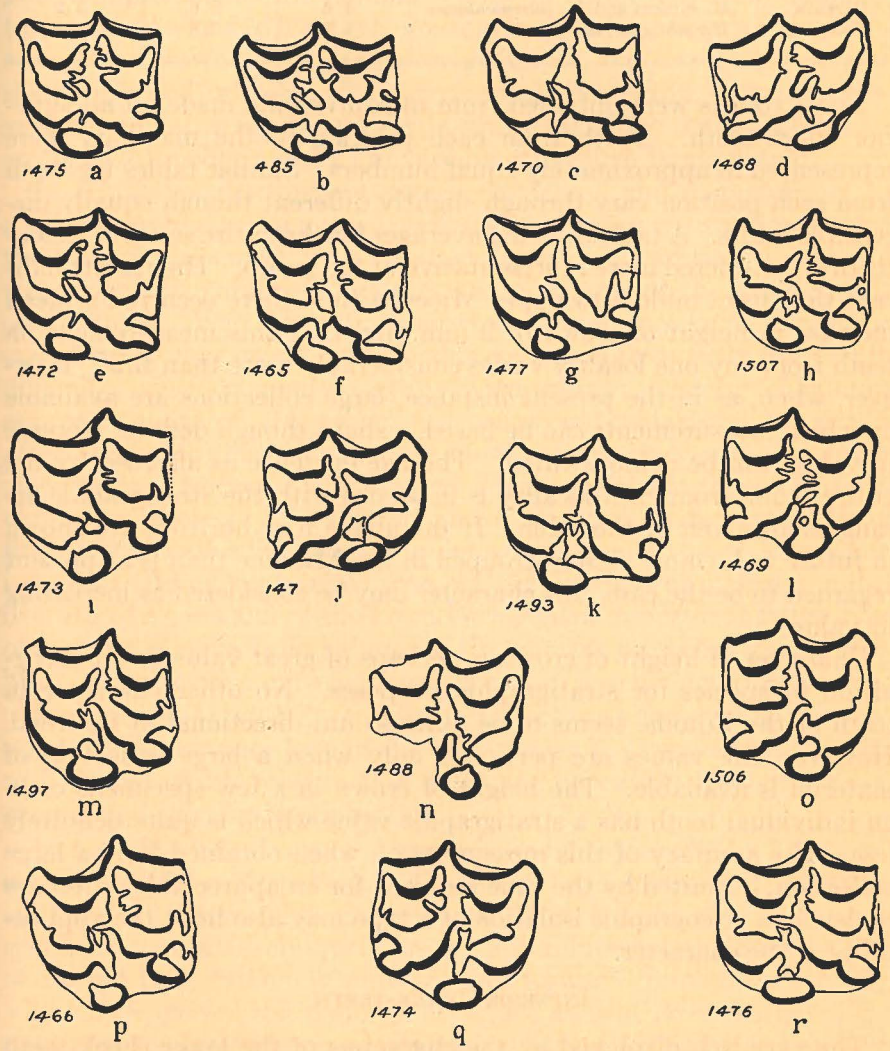


FIG. 6—*Merychippus californicus* Merriam. a to r, referred specimens showing examples of variation of enamel patterns; x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California.

able to *Merychippus isonesus* from the Mascall and Skull Spring localities in eastern Oregon, *M. sumani* and *M. intermontanus* from the Barstow, and on teeth of a merychippine form from an upper Miocene locality near Tonopah, Nevada. The following table gives the results of these measurements in centimeters.

Horizon	Species	Maximum	Mean	Minimum
Mascall	*M. isonesus*	3.4	2.9	2.6
Coalinga	*M. californicus*	4.2	3.4	2.9
Barstow	*M. sumani* and *M. intermontanus*	4.6	3.6	3.2
Tonopah	*Merychippus*, sp.	4.7	3.8	3.3

These results were obtained from measurements made on all superior cheek-teeth. Teeth from each position in the maxillary were represented in approximately equal numbers. Similar tables for teeth from each position vary through slightly different though equally discernible limits. A table showing averages for the entire series of cheek-teeth is considered more representative of the group. The results indicate that from middle to upper Miocene time there occurred a mean increase in height of crown of 9 mm. and that this measurement on teeth from any one locality varies considerably more than this. However, when, as in the present instance, large collections are available on which measurements can be based, a slight though definite increase in values can be demonstrated. The age evidence as afforded by the entire fauna from each locality is in accord with the stratigraphic arrangement given in the table. If the above four horizons are shown in future to be more closely grouped in the Miocene than is at present regarded to be the case, this character may be considered as increasing in value.

Character of height of crown is perhaps of great value in the recognition of species for stratigraphic purposes. No other character in teeth of the Equidæ seems to be quite so uni-directional in its trend. However, the values are pertinent only when a large collection of material is available. The height of crown in a few specimens or in an individual tooth has a stratigraphic value which is quite definitely less. The accuracy of this measurement, when obtained from a large collection, is limited by the time required for an appreciable difference to develop. Geographic isolation of a type may also limit the applicability of the character.

Inferior Cheek-teeth

The variation displayed by the characters of the lower cheek-teeth is similar to that seen in the superior dentition. The inferior dentition presents no character whose value is comparable to that of the

protocone or of the curvature of the crown of an upper cheek-tooth. Age assignments on the basis of characters exhibited by lower cheek-teeth are less satisfactory than for upper teeth. The relationships of forms based on lower cheek-teeth frequently depends upon an association of these teeth with the upper dentition. Only the more frequently used characters will be discussed. As in the case of the superior dentition, observations have been limited to teeth whose crowns have been less than one-third removed by wear.

Metaconid-metastylid column—In the collection of teeth from the Merychippus Zone this column varies in anteroposterior diameter from over one-half to less than one-fourth of the anteroposterior diameter of the crown. The groove or gutter on the inner wall may be sharply incised or open. The groove may be narrow or wide transversely and varies in size and shape with wear of the tooth. The characters of this column in $P\underline{2}$ are variable to a much larger extent.

In *Hipparion* the gutter between metaconid and metastylid is, as a rule, broadly open and displays a greater tendency to widen toward the base of the crown than in other genera. In advanced forms of *Hipparion* this column sometimes occupies most of the internal side of the tooth. The distinction between similar species of *Hipparion* and *Merychippus* on the basis of this column is frequently made with difficulty, since in many teeth of *Merychippus,* whose characters approach those of *Hipparion,* the metaconid-metastylid column is often similar to that found in the more progressive genus. In specimens whose structural features are transitional from those of *Merychippus* to those of *Protohippus* and *Pliohippus,* this character is of little help in affording a generic determination. It is of interest to note that Gidley [1] concluded from an examination of a large number of teeth of *Equus* and of the Loup Fork genera of horses that the type of metaconid-metastylid column in these forms presented great variability and possessed extreme unreliability in specific determination.

Posterior Lobe of $M\underline{3}$—In all the collections studied, the development of the posterior lobe of the third molar has been found variable to a degree which renders this character unreliable for purposes of generic and specific determination.

Entoconid—The shape of the entoconid has been used by Merriam [2] in distinguishing *Merychippus, Pliohippus,* and *Hipparion.* Merriam states: "In general the entoconid of *Merychippus* and *Pliohippus* species is truncated obliquely on the anterointernal angle by a plane or curved face, extending outward and forward from the inner side, while in *Hipparion* this region is expanded and the cross-section of the entoconid tends to take on a rectangular outline, instead of the approx-

[1] J. W. Gidley, *op. cit.,* 105, 1901.
[2] J. C. Merriam, Univ. Calif. Publ. Bull. Dept. Geol., vol. 10, 131-132, 1916.

imately triangular section seen in *Merychippus,* or the triangular to imperfectly rectangular but anteroposteriorly short section seen in *Pliohippus.*" In teeth from the Merychippus Zone, this cusp varies in outline from triangular to completely rectangular. A study of teeth referred to the above three genera indicates that this cusp has no value in specific determination and that it must be employed with care in distinguishing genera. Merriam's use of this character applies to distinctions between advanced forms of *Hipparion* and *Pliohippus* on the one hand and the primitive and intermediate stages of *Merychippus* on the other.

Entostylid—The posterior extension of the entostylid in molar teeth is variable. In general, it is greatest in unworn teeth and decreases with wear. This cusp is larger in molars than in premolars, but presents no peculiarities of taxonomic value.

Protoconid and Hypoconid—The external walls of these cusps are curved to varying degrees in the material from north Coalinga. In *Equus* the outer walls of the protoconid and hypoconid are flattened in contradistinction to the curved or convex walls of *Pliohippus.* An examination of teeth from localities assigned to the upper Pliocene and lower Pleistocene has convinced the writer that this character must be used with care in distinguishing *Plesippus* from either *Pliohippus* or *Equus.*

Cement—An examination of hundreds of specimens indicates that the amount of cement present on a lower tooth has no diagnostic value.

Supplementary Folds—The antero-external fold may be present or absent in the material from the Merychippus Zone. When present, the strength of this style varies considerably with the individual as well as with the extent of wear of the tooth. An antero-external fold of the enamel wall is frequently present in lower teeth of *Hipparion.* Its occurrence seems to be rather rare in *Pliohippus.* However, it has been observed in a series of lower teeth referred to *Plesippus shoshonensis* Gidley from the Idaho Pliocene. Presence of a fold or one or more plications of the enamel walls of the valley between protoconid and hypoconid has been observed in *Merychippus, Hipparion, Plesippus* and *Equus.* Its presence in so many genera would seem to invalidate its use as a specific character.

Occlusal Surface—The shape of the occlusal surface varies in a manner similar to that of upper cheek-teeth. Anteroposterior-transverse ratios obtained in the first and second molars at approximately the same stage of wear of the crowns vary from 1.70 to 2.10. In greatly worn teeth this ratio may have a value approximating 1.00. The extremes of this ratio are sufficiently removed to include most of the Equidæ.

Enamel Pattern—As in superior cheek-teeth, the complexity of the enamel pattern is well marked in *Hipparion* and in advanced forms of *Merychippus*, approaching the former genus. The extent of plication of the enamel walls of the lower cheek-teeth possesses a value for determination similar to that seen in the superior dentition.

Height of Crown—As in the superior dentition, this character is probably of great value in the distinction of species. The statements made for the superior dentition apply equally as well to the lower cheek-teeth. A table based upon measurements of lower teeth gives the following values in centimeters:

Horizon	Species	Maximum	Mean	Minimum
Mascall	*M. isonesus*	3.9	3.0	2.7
Coalinga	*M. californicus*	4.4	3.4	2.6
Barstow	*M. sumani* and *M. intermontanus*	4.4	3.5	2.8
Tonopah	*Merychippus*, sp.	4.8	3.6	3.1

VIEWS OF OTHER AUTHORS

The variation in tooth characters as observed by the writer is not unusual. Thus, Simpson,[1] in a study of the Miocene Vertebrate Faunas of Florida, found the characters of *Parahippus* grading into those of *Merychippus*. Gidley,[2] in a study of the genus *Equus* and of the Loup Fork genera, after determining the presence of considerable variation in characters of the cheek-teeth, concluded that many of the species of *Equus* ought not to be regarded as valid forms. To quote from Gidley:

"An application of the foregoing principles of the variability of tooth characters to the specific definitions of Owen, Leidy and Cope shows the unreliability of most of the characters they have employed. Thus, the degree of complexity of the enamel folding is seen to be greatly affected by both age and individual variability—a fact which must be correctly understood before this character can be of even subordinate value as a specific determinant; the other characters given by these authors have been shown to be so affected by age or individual variability, or both, that no dependence can be placed upon them; . . ."

A wide range of variation was found by Matthew[3] in the *Merychippus* material from the Sheep Creek and Lower Snake Creek horizons in western Nebraska. Matthew met this difficulty by assigning over ninety per cent of the material to one species:

"Within the material that I have referred to *M. paniensis* there is a wide range of variation, in size, length of crown and other proportional characters,

[1] G. G. Simpson, Florida State Geol. Surv., Bull. 10, 21-27, 1932.
[2] J. W. Gidley, *op. cit.*, 105, 1901.
[3] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, 159, 1924.

in the degree of union of the protocone, the development of the hypostyle, thickness of external styles, complication of the enamel on the lake borders, etc."

In commenting on the inadvisability of making a large number of species from the material he remarks:

"The thousands of isolated teeth or other fragmentary specimens would clearly show that there are no constant or uniformly associated distinctions between such 'species'."

Again, Matthew and Stirton [1] in their description of the Pliocene Equidæ from Texas state in regard to the variation of tooth characters in *Pliohippus* that:

"There is considerable variation in the size of the teeth, and some variation in height and curvature of the crown of the upper molars, in form and size of protocone, heaviness of mesostyle, tendency to union between protocone and hypocone, width of cement lakes and the development of the enamel inflections along their borders, and in probably all tooth-characters that have been used by all authors to distinguish species in the genus."

Merriam [2] in discussing the relationships of *Hipparion mohavense* from the Ricardo beds of the Mojave Desert, California, points out that:

"With the collections now available, few if any diagnostic characters in form or pattern of the Ricardo teeth designated as *H. mohavense* appear which may be considered as certainly separating them from the Chinese *H. richthofeni.*"

Then, with regard to the relationships of *Hipparion richthofeni* to the European species, *H. gracile,* Merriam [3] states that:

". . . some of the characters which have been used to separate *H. richthofeni* from *H. gracile* seem to disappear with the study of large collections."

Again, Merriam [4] in his report on the horses of Rancho La Brea states that the variation within this group is sufficient to include some of the teeth of several Pleistocene species and of *Equus caballus.* With regard to the value of tooth characters he states:

"While it is doubtless true that good specific differences appear in the enamel pattern of the cheek-teeth, it is certain that such characters must be used with caution. The final determination of the value of these characters must depend upon examination of considerable series of individuals of nearly the same age."

In his description of the merychippine forms from the Barstow of the Mojave Desert, Merriam described three species with the expectation that additional material would present characters more clearly demarcating the species.

[1] W. D. Matthew and R. A. Stirton, Univ. Cal. Publ., Bull. Dept. Geol., vol. 19, 358-359, 1930.
[2] J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 11, 557, 1919.
[3] J. C. Merriam, *ibid.*
[4] J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 7, 413, 1913.

A somewhat different result was reached by Sefve[1] in his description of the Hipparions from North China. On account of the wide variation exhibited, he describes as few species as possible and expresses the opinion that additional material will serve to divide his original groups into a larger number of more clearly demarcated species.

"Man muss auch hierbei darauf Rücksicht nehmen, dass die Variation in Wirklichkeit beträchtlich grosser gewesen ist als die Zahl der Arten erscheinen lässt. Wie aus meinen Artbeschreibungen hoffentlich hervorgeht, ist die Variation auch innerhalf der Arten sehr gross. Ich habe absichtlich so wenig Arten als möglich aufgestellt. Neue und vollständigere Funde werden warscheinlich zeigen, dass viele von den jetzt vorhandenen Variation, die ich bis auf weiteres nur als solche innerhalf der Art rechne, in Wirklichkeit verschiedene Arten repräsentieren."

In the opinion of the writer, the addition of more material from the Barstow and Chinese horizons will serve mainly to fill the ranks of teeth, whose characters are intermediate, rather than to aid in more sharply defining the established species.

CONCLUSIONS

The variation of tooth-characters as exhibited by the hundreds of specimens studied by the writer from horizons distributed throughout the later half of the Tertiary and by studies of the descriptions of many authors, indicates that there are no hard and fast distinctions to be made between the various species and genera of the Equidæ. With the collections at hand at the California Institute, gradational series with almost no discernible break can be built up from *Parahippus* through intervening genera to *Equus* and *Hipparion*. The selection, from horizons closely related in time, to form these series does not need to conform necessarily to the exact stratigraphic sequence of the deposits determined by the entire fauna from each locality. The characters which distinguish a species or genus unquestionably grade into the diagnostic peculiarities of other succeeding and preceding species and genera. The vertical stratigraphic range of the characters peculiar to a single form seems usually to be greater than that of a single stratigraphic horizon as determined by the entire fauna. Every large collection studied from a single horizon contains, in addition to teeth unquestionably referable to the species peculiar to that horizon, specimens whose characters can be regarded as intermediate and in addition specimens whose characters would allow them to be referred to other species from either slightly higher or lower horizons. Due to the overlapping of characters of various species, individual teeth are found with characters which would permit their

[1] I. Sefve, Paleontologica Sinica, Series C, vol. 4, fascicle 2, 84, 1927.

assignment with equal right to any one of several species. When such a tooth is found, its stratigraphic value is defined by the total time range of the several species to which it might be assigned. In most cases this vertical range is considerably greater than the divisions of geologic time distinguished on the basis of a large and varied vertebrate fauna.

Refinements in application of the characters of cheek-teeth of fossil horses to stratigraphy do not lie in a radical revision of our present conception of a species. If the gradation of characters be taken as indicating synonymy, the results ultimately become absurd. The enlargement of the boundaries of a single species or genus merely serves to enlarge the stratigraphic range of that species or genus. From a purely taxonomic point of view, the inclusion of a large number of variants within a single species defeats the object of the description of these forms. The placing of a large number of variants within a single species fails not only to convey a satisfactory impression of the appearance of a collection, but also results in the establishment of an unwieldy group of taxonomic units for future workers to handle. The setting up of three species by Merriam in the case of the Barstow material has a value for future workers which is considerably greater than that which would arise if all of the forms were included under one species. Although characters intergrade and although the variation of any one character is for the most part independent of the variation of any other character, the illustration of several types representing several distinguishable averages is of considerable value. On the other hand, the division of a group into a number of poorly defined species increases the complexity of the problem.

The dividing lines between genera and species are not drawn at natural breaks, but frequently serve to emphasize the gaps in our knowledge of an evolutionary line. As more and more material becomes available, the boundary lines between individual groups become less and less distinct. While species within any one horizon may usually be clearly demarcated on the basis of frequency curves, the addition of material from horizons only slightly removed in time tends to run together the boundaries of such frequency curves. In such instances the maxima become closely crowded and are of little value. It should be recognized that the characters of some specimens will necessarily have to remain intermediate in nature and that they should be so defined.

For purposes of stratigraphy, the association of structural types comparable to various type specimens permits of greater accuracy in age determinations of sedimentary deposits. An examination of many collections discloses the fact that during a part of the interval of geologic time in which the characters distinguishing a type specimen

existed, these characters are associated with the gradually disappearing characters of a more primitive type, and that during another part of this time the characters of a more advanced type are appearing. The time required for one species to appear, reach its maximum development and disappear may be divided on the basis of the association of the central type with other advanced and primitive forms.

For the upper half of the Miocene of the Pacific Coast and Great Basin Provinces, the following associations appear to be of value and are in accord with the age determinations based on the evidence furnished by the entire fauna from each locality:

1. MASCALL—Associated with *Merychippus isonesus* are teeth referable to *M. relictus* and *M. seversus, Parahippus brevidens* and *P. avus.* Some of the more progressive teeth referred to *M. isonesus* are similar in aspect to teeth from the Merychippus Zone. *M. relictus* and *M. serversus* are small primitive types not found in the north Coalinga horizon. They would probably be found in horizons slightly earlier than the Mascall. The small species indicate an upward limit to which the Mascall might be assigned, while *M. isonesus* and "*M. californicus*-like" teeth suggest a lower limit. In addition, the merychippine milk-teeth from this horizon exhibit primitive conical cusps in contradistinction to the cylindrical shapes found in higher zones. The two species of *Parahippus* furnish further suggestions as to relative age of the assemblage. *P. avus,* though large, is a primitive form and has not been found in horizons higher than the Mascall. *P. brevidens* makes its first appearance in the Mascall and continues on into the time represented by the Merychippus Zone. The Skull Spring and Virgin Valley faunas occupy positions more nearly correlative with the Mascall.

2. MERYCHIPPUS ZONE—This horizon is characterized by the association of *Merychippus californicus* with teeth similar to the types of both *M. isonesus* and *M. sumani* and *Parahippus brevidens. M. isonesus* and *P. brevidens* reflect the time relationship which exists between the Merychippus Zone and Mascall. *M. sumani* indicates that the Barstow stage is not far removed.

3. BARSTOW—Teeth similar to the referred specimen of *Merychippus californicus,* No. 1405 Calif. Inst. Tech. Coll., from the Merychippus Zone, are present in the Barstow formation of the Mojave Desert and these now represent the most primitive type. *M. sumani* is abundant and is associated with *M. intermontanus,* a horse of which some of the tooth characters are similar to *Protohippus. M. intermontanus* furnishes an indication that the Barstow should be regarded as higher than the Merychippus Zone.

PLATE 1

Merychippus brevidontus n. sp.

FIGS. 1 to 8—Figs. 1 to 1c, referred specimen, P4, No. 1431; figs. 2 to 2c, referred specimen, M1, No. 1427; figs. 3 to 3b, type specimen, *P3, No. 1414;* figs. 4 to 4b, referred specimen, unworn M1, No. 1409; figs. 5 to 5b, referred specimen, P4, No. 1410; fig. 6, paratype, M1, No. 1422; fig. 7, paratype, P4, No. 1413; fig. 8, paratype, M2, No. 1408; x 1.

Calif. Inst. Tech. Coll. Merychippus Zone, California.


1


1a


1b


1c


2


2a


2b


2c


3


3a


3b


4


4a


4b


5


5a


5b


6


7


8

PLATE 2

Merychippus intermontanus Merriam

FIG. 1—Superior milk-tooth series (protocone region of Dp$\underline{3}$ restored by illustrator), No. 21640; x 1.

Univ. Calif. Coll. Barstow Upper Miocene, California.

Merychippus californicus Merriam

FIG. 2—Superior milk-tooth series, No. 1500; x 1.

Calif. Inst. Tech. Coll. Merychippus Zone, California.

Merychippus isonesus (Cope)

FIG. 3—Superior milk-tooth series, No. 544; x 1.

Calif. Inst. Tech. Coll., Locality 124. Skull Spring Middle Miocene, Oregon.

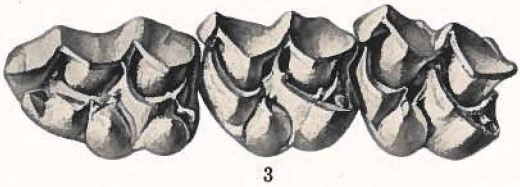
Merychippus brevidontus n. sp.

FIGS. 4 to 12—Referred specimens. Fig. 4, P$\underline{4}$, No. 1418; fig. 5, M$\underline{3}$, No. 1423; fig. 6, M$\underline{2}$, No. 1420; fig. 7, M$\underline{1}$, No. 1419; fig. 8, P$\underline{4}$, No. 1415; fig. 9, P$\underline{3}$, No. 1411; fig. 10, M$\underline{2}$, No. 1430; fig. 11, M$\overline{1}$, No. 1426; fig. 12, P$\overline{4}$, No. 1429; x 1.

Calif. Inst. Tech. Coll. Merychippus Zone, California.

1

2



3

4

5

6

7

8

9

10

11

12