

OBSERVATIONS ON EVOLUTIONARY RATES IN HYPHODONTY

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An examination of fossil horse teeth from the American Cenozoic faunas reveals a gradual increase in hypsodonty (the height of the crown of the cheek-teeth) from late Lower Miocene to Pleistocene time. This is illustrated in the equine (*Merychippus*, *Calippus*, *Pliohippus*, *Equus*) and hipparion (*Merychippus*, *Hipparion*, *Neohipparion*, *Nannippus*) groups of hypsodont horses. There is some increase in crown height in the other groups of horses but it is only slight or is associated with an increase in the dimensions of the tooth as a whole. Hypsodonty is displayed also in other families of North American plains animals (Castoridae, Heteromyidae, Geomyidae, Mylagaulidae, Rhinocerotidae, Camelidae, Antilocapridae, etc.) at that time, but for the most part it is less accentuated and not as well documented as in the Equidae. In this report attention is directed to a combination of phenomena closely associated with this evolutionary progression in the horses.

Simpson (1944, p. 16) states that—"hypsodonty is an important unit character on the criterion of selection value, but morphologically it is the resultant of two other characters which are correlated in one way and uncorrelated in another, and genetically it is undoubtedly controlled by at least two and probably many genes that simultaneously control other, quite distinct phenotypic characters." In this connection it may be useful to enumerate some of the features in the skulls and dentitions of Cenozoic horses that seem to have direct bearing on the inception and evolution of hypsodonty in the Equinae. Development of the crochet

and the hypostyle as employed in the closure of the pre- and postfossettes was essential in the formation of a basic pattern for an effective triturating surface. From this basic pattern, then, in certain Lower Miocene species of *Parahippus*, the teeth in a succession of species and genera evolved into structurally sound hypsodont teeth. An additional strengthening factor was the deposition of cement which filled the inflections and fossettes and even reinforced the outer surface of the tooth. Other important considerations in this evolutionary process would be the gene or genes controlling an increase in the depth of the facial and the mandibular regions to accommodate higher crowned teeth, and those controlling the deposition of enamel and dentine.

Origin and evolution in Tertiary mammals, particularly in the hypsodont horses, has usually been correlated with a change in diet. This dietary change probably involved a shift from browsing on softer herbaceous plants to grazing on harsh or siliceous grasses which acted as abrasive agents on the teeth. Only a few authors have mentioned sand mixed in the food of the grazers as an additional source of abrasive material. These changes in turn, are associated directly with increasing aridity on the Great Plains of the middle and late Tertiary. It is observed that the appearance of widespread sandy deposits, together with the appearance of bunch grass (*Stipidium*,¹ Elias, 1935), and increasing aridity, are contemporary with the development of hypsodonty. M.

¹ Referred to the living genus *Stipa*—spear grass by some botanists.

K. Elias (1935, p. 25) in his very useful paper, "Tertiary Grasses and other Prairie Vegetation from High Plains of North America," cites literature and supports the evidence for late Cretaceous and Cenozoic grasses. To quote: "Only the presence of *Arundo*, *Phragmites* and perhaps *Bambusa* in the late Cretaceous and Tertiary beds was considered as being established on sufficient fossil evidence. The living representatives of these grasses are tall water-loving species which dwell along the shores of ponds and streams. The association of their fossil relatives with the arboraceous vegetation permits no doubt that in the late Cretaceous and Tertiary times they grew in the same environment." It is difficult to believe that shorter grasses also were not in these associations as they are in similar environments today. If siliceous grasses were present in the early Cenozoic and their presence affected the teeth of those animals that fed upon them why did not hypsodonty arise in several groups of mammals at that time? As a matter of fact, there is very little if any relative increase in the height of crown in the Eocene and Oligocene horses. It is impossible, however, to prove that these animals were not browsers exclusively. In this event it might be assumed that the siliceous grasses would have no effect on their teeth, though the grasses may have been present. On the other hand is there any reason to conclude that they fed only on other kinds of plants? I think we can assume, with reason, that the grasses were not as dry nor as harsh in the early Tertiary as they were in the Miocene and Pliocene.

A review of the literature reveals that there was a predominance of shales and sandstones from the Puerco, Torrejon and Tiffany in New Mexico (Granger, 1917); and in beds of the same age in Wyoming, Jepsen (1930) reports mostly sombre clays, and sandstones. The Eocene (see Van Houten, 1945), though containing much volcanic detritus, also shows considerable sandstone, clay and

shale. Primarily clays occur in the Oligocene with intermittent deposition of sandy stream channels. Toward the close of the epoch a greater percentage of sandy deposits accumulated in the Great Plains area.

This continued in the Lower Miocene with the widespread deposition of sands and sandy silt in the Arikareean formations of Nebraska, South Dakota, Wyoming and Colorado. These formations must have been much more widely distributed, but subsequent erosion and deposition either removed or covered most of the deposits. Sand grains in the later Miocene and Pliocene average larger and these sandy flood plain and stream channel deposits predominate particularly in this region where they form most of the later Tertiary blanket.

Toward the close of the Arikareean the first records of bunch-grass appear. Elias discovered the siliceous husks of a small *Stipidium* in the late Lower Miocene Harrison beds of western Nebraska. This appears to be the first appearance of these grasses in the American Cenozoic.

Contemporary with these Harrison grasses we note the formation of cement on the teeth and a tendency toward heightening of the crown in some species of *Parahippus* in the late Lower Miocene. In these horses, is seen the basic dental structure for the development and evolutionary progression in the cheek-teeth of successive races of hypsodont horses from the Lower Miocene to the Pleistocene. Certainly there is not a better example of evolution in Cenozoic Mammalia and it is questioned whether a better succession occurs in any other group of organisms (figures 1-2).

The Lower Miocene evidently marked the beginning of plains conditions with a gradual change through moist to dry temperate climates in the later Pliocene. That these plains were exactly like the prairies of the Great Plains region as we know it today is quite unlikely, but they were considerably different from those in Eo-

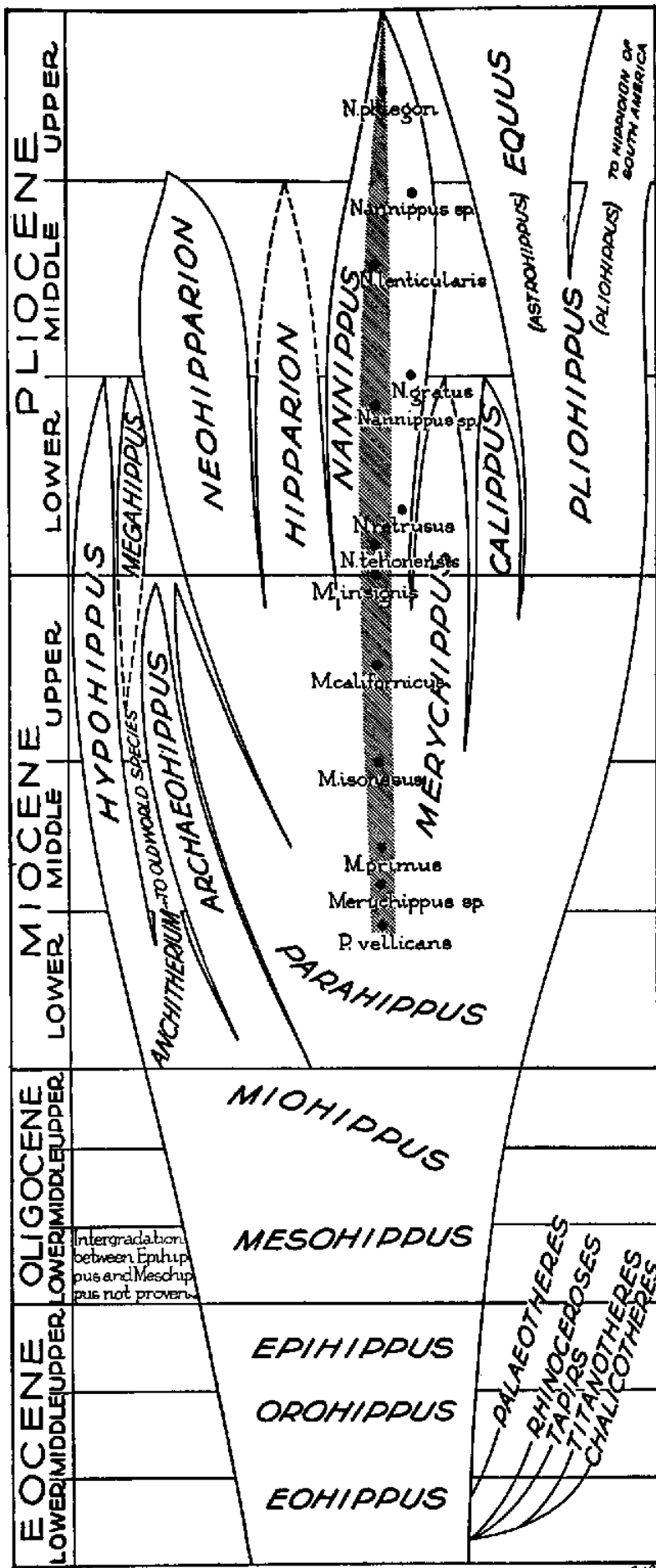


FIG. 1. A phylogeny of North American Equidae illustrating phyletic position of the *Parahippus vellicans* (Hay) to *Nannippus phlegon* (Hay) line of descent.

EVOLUTION IN HORSES

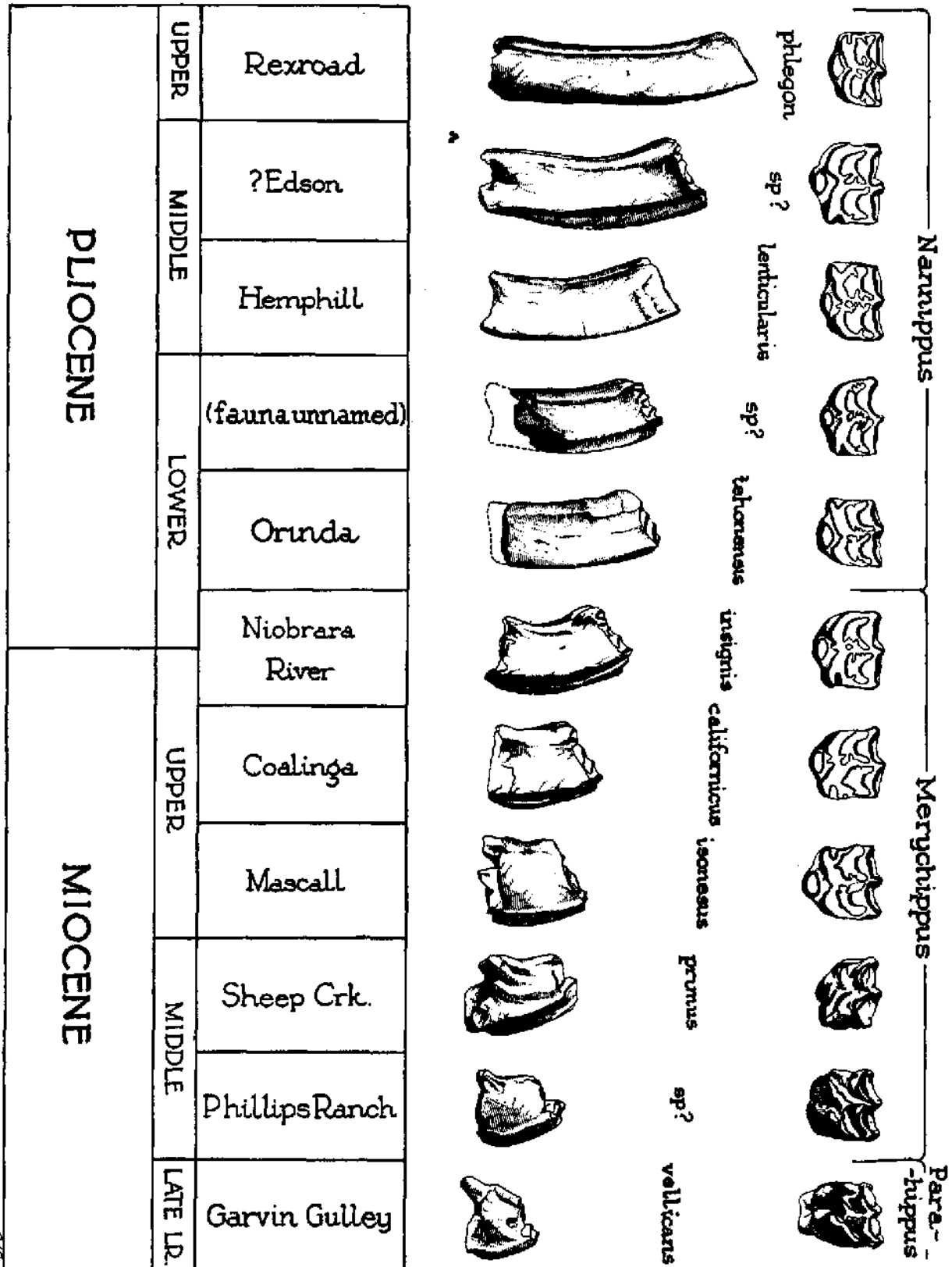


FIG. 2. Progressive hypsodonty as illustrated by unworn or slightly worn isolated horse cheek-teeth. The *Nannippus* sp. in the unnamed fauna from California is not well known and it might be questioned as to the position of this tooth in the late Clarendonian stage. Some of our research may clarify this problem in the next few years. The *Nannippus* sp. from the ?Edson fauna apparently is not in the direct line leading from *N. lenticularis* (Cope) to *N. phlegon* (Hay), but it does represent the stage of hypsodonty intermediate between those species. *N. retrusus* (Cope) and *N. gratus* (Leidy) are on a side line that evidently did not extend into Middle Pliocene time.

cene and in early Oligocene time. Thus apparently by another elevation of the region to the west, an environment was established in the Great Plains that became the most important recorded center of dispersal and evolution for plains mammals in the world. A combination of phenomena existing in this environment was so effective in wearing down cheek-teeth that there seem to have arisen definite protective modifications in the organism. These modifications were the increase in activity of the odontoblasts and ameloblasts to lay down more dentine and enamel while the tooth was still in the formative stage. Just how such changes arose as heritable modifications and resulted in the progressive development of higher crowned teeth or hypsodonty is certainly not clear from the fossil record.

Bunch grasses, possibly both long and short, became widespread in the Great Plains area shortly after their first appearance. The siliceous husks are found abundantly in the sandy stream deposits. A certain amount of silica and the dry harsh condition of grass in the later summer and autumn had its effect in the wearing down of teeth, but it is felt that this was only secondary in effect to sand as a foreign substance mixed with the grass. In this region a close inspection will reveal much sand adhering to grass or lodged in between the blades and stems where it was splashed after thunder showers or blown by winds. Thus it is possible for these sand grains to be taken into the mouth with the food where it acts as an effective abrasive agent.

It is a well known fact that horses grazing on the sandy plains pastures dis-

play heavily worn teeth, and those in the less sandy pastures to the east show teeth with much less wear. Ranchers in western Kansas and Nebraska tell of serious sickness among their horses resulting from grazing too long in sandy wheat fields where so much sand is blown into the young wheat. Local veterinarians attribute the ailment to too much sand being lodged in the stomach.

Hypsodonty in later Cenozoic horse teeth is also closely correlated with root closure or time of fusion of the basal dentinal plate with the upper part or crown of the tooth. My information on this is not as complete as one might wish but I have been able to observe a slight retardation in root closure and continuation of vertical growth in the cheek-teeth of species from the succeeding ages from Middle Miocene to Pleistocene. This is shown when the time of root closure is compared with the amount of occlusal wear on the tooth (figures 3-7).



FIG. 3. Deciduous lower cheek-teeth of *Mesohippus* displaying only slight wear at the time M_1 is erupting.

The formation of enamel, as laid down by the ectodermal ameloblasts, begins at the crown of each tooth, spreads down over the sides and into the fossettes. The first centers of enamel formation are over each cusp or high point; these coalesce as growth continues. At the same time

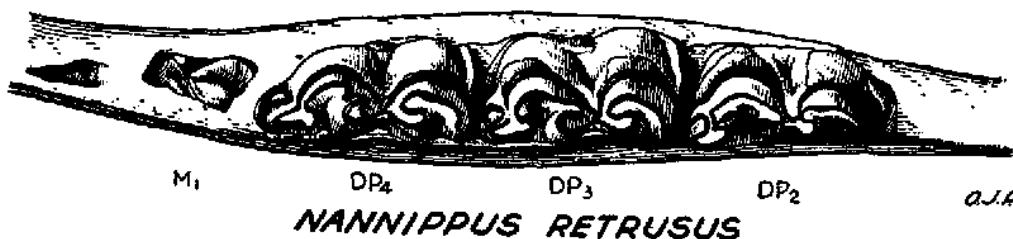


FIG. 4. Deciduous lower cheek-teeth of *Nannippus* displaying considerable wear at the time M_1 is erupting.

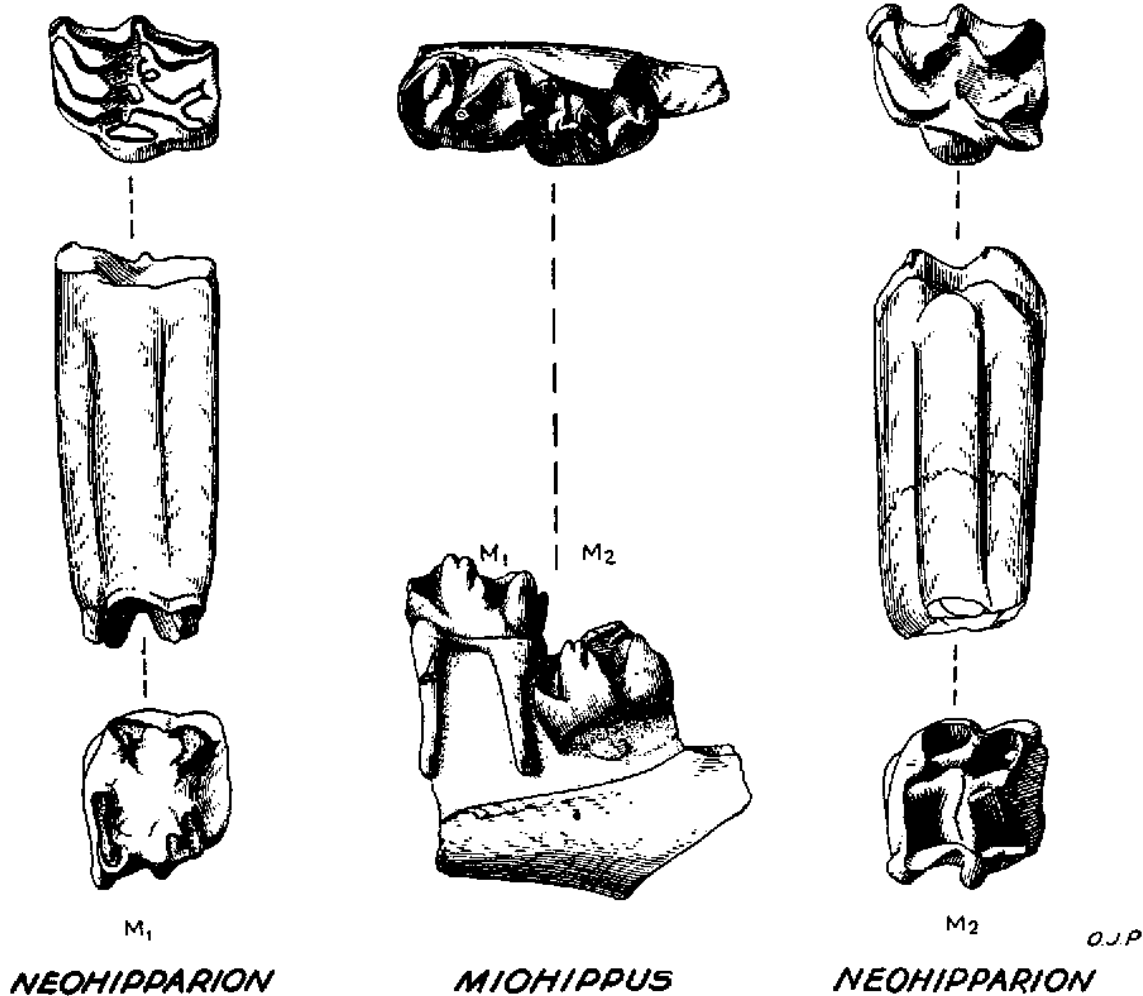


FIG. 5.

FIG. 6.

FIG. 7.

FIG. 5. *Neohipparion occidentale* (Leidy). M₁ slightly worn and showing basal dental plate fused with crown.

FIG. 6. *Miohippus* sp., John Day of Oregon, showing roots fused on M₁ before the enamel is worn through to expose dentine; the roots have not formed on M₂ as the tooth starts eruption.

FIG. 7. *Neohipparion occidentale* (Leidy). M₂ unworn and without basal dental plate, but bottoms of fossettes are closed.

in the dental papilla the mesodermal odontoblasts are forming dentine. The odontoblasts apparently persist throughout the life of the individual and continue to produce dentine so that the root canals become nearly, and in some individuals, completely obliterated. The full height of crown in a tooth is formed in *Miohippus* before the top of the crown erupts through the gums and the fusion of the roots to the crown is completed very soon after eruption, but in *Nannippus*, *Neohipparion* and *Pliohippus* the tooth not only erupts but displays some wear before the basal dental plate becomes fused with the crown and the height of crown is fixed. (See figures 5 and 7.) In *Equus* this

fusion is more retarded than in the Lower and Middle Pliocene genera (figure 8).

The identification of species has been based on a multitude of characters in the cheek-teeth, i.e., crown height, shape of protocone, complication or simplification of fossette borders, prominence of styles, occlusal dimensions, isolation of hypocoanal groove, degree of connection of protocone to protoselene, flatness of ectoloph, bifurcation of plicaballin, etc., not to mention similar characters in the mandibular teeth as well as other features in the skull and feet. It was found that a character constant in the identification of one species or group might be variable in another.

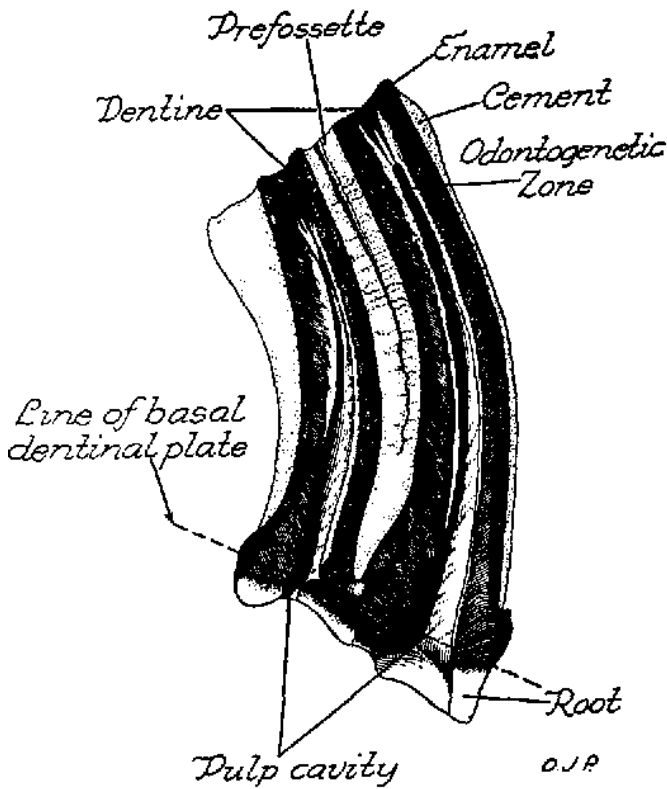


FIG. 8. *Nannippus retrusus* (Cope). P⁴ with vertical section through paracone, prefossette, and protoselene.

The specimens illustrated in the phyletic sequence, *Parahippus*—*Merychippus*—*Nannippus*, are hand-picked but they represent my estimate of an average crown height for the species in successive faunas. It is true that there is much variation in crown height in these species, in some samples, even overlapping in range the species from preceding and the following ages. Though there are large series of isolated teeth from some faunal assemblages, it is difficult to find a tooth displaying the full crown height for a species. Teeth assume different proportions and different features in their occlusal patterns at different stages of wear, but a student familiar with the phyletic sequence in horses and also with first hand information on large series of teeth from given faunas can make an accurate estimation of crown height. Thus in identifying specimens these facts must be considered. For these reasons I have found it exceedingly difficult to compile satisfactory measurements on crown height in relation to coronal dimensions. The

conclusions in this report, then, are based on my judgment of similarities and differences in specimens of North American late Cenozoic mammals as based on my experience in curating and identifying specimens.

The oldest known beavers from the Oligocene of Europe and North America are hypsodont though not as high crowned as in the later genera. The best evidence available on intergradational evolution in this family is in the North American genera—*Monosaulax* Upper Miocene, *Eucastor* Lower Pliocene, *Dipoides* Middle Pliocene, *Procastoroides* Upper Pliocene, and *Castoroides* Pleistocene (subfamily Castoroidinae). Fortunately for correlation purposes, intergradation of the generic characters occurs at the time of the designated boundaries between the named geologic ages. There was a gradual increase in the height of crown in the cheek-teeth of these beavers which may have been linked genetically with a breaking through of the fossettes and inflections to the outside of the tooth as well as a lengthening of lateral grooves on the sides of the teeth. Evolution of the tooth was relatively constant in the succeeding genera but there was an acceleration in hypsodontology in the late Pliocene and Pleistocene (figure 9).

Since there does not seem to be a continued acceleration between the Blancan and Pleistocene equivalent to that between the Hemphillian and Blancan time we may be confronted here with a distinct break in our faunal records at the close of the Middle Pliocene, which future collecting will clarify.² Therefore, though there is a distinct difference in the rate of evolution in hypsodontology with the oncoming of widespread glacial conditions it may not be as great as it appears from the evidence available.

The ecological conditions under which the castoroid beavers lived is not known, but a few inferences can be made. It is

² I have seen some evidence of faunas of this age from the Panhandle of Texas.

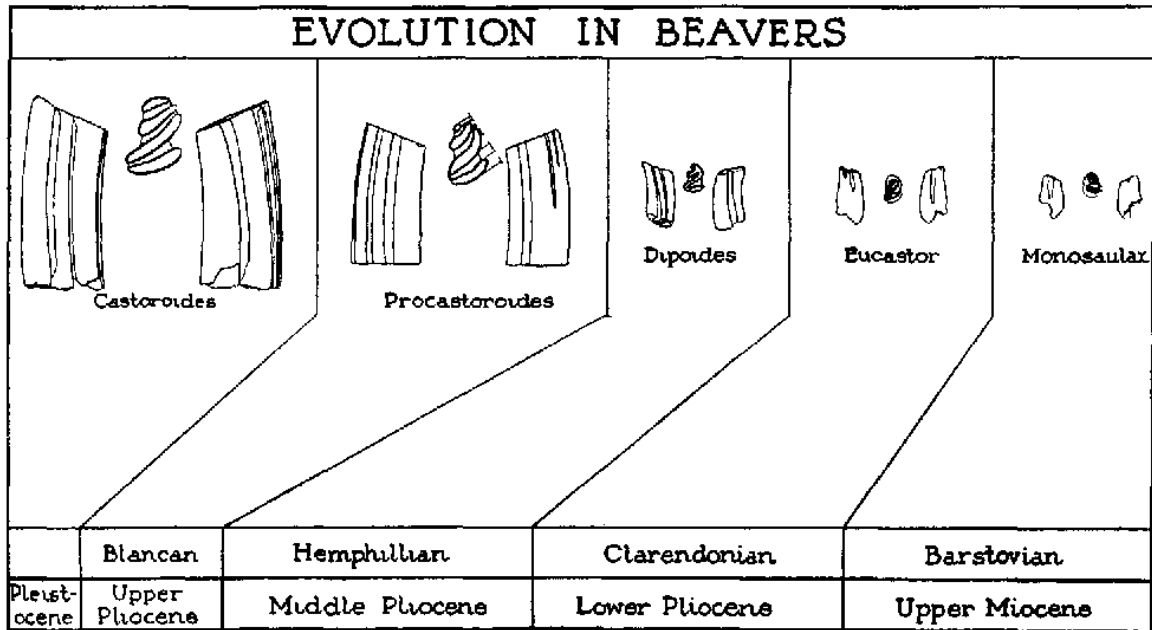


FIG. 9. Progressive hypsodonty as illustrated by slightly worn fourth lower premolars (P_4). The base of the *Procastoroides* tooth is semidiagrammatic.

likely they were water-loving animals since their remains are found so abundantly in stream channel deposits. The cause of their death in great numbers at any given time might be attributed in part to occasional severe droughts and disease. Possibly members of this subfamily were more like the muskrats in their habits and depended on green grasses and reeds for their livelihood. Thus in long periods of severe drought many of their special requirements would be eliminated, effecting heavy mortality. Scattered bones and teeth of the dead animals which had accumulated along the bank of dried up water courses could have been picked up by subsequent floods, then deposited in eddies or potholes in the stream. The ecology of these beavers, if this is an approach to a true picture of their environment and habits, is somewhat different from that of the contemporaneous nannippine horses, since the beavers were stream border and marsh dwellers, whereas the horses were open grassland types that frequented streams and waterholes when thirst impelled them. Nevertheless the same selective values may have operated in both phyletic lines. Abrasive sands would be as prevalent along stream

borders and in adjacent swampy areas as in the open grassland. It is interesting to observe then, though hypsodonty was initiated earlier in the castoroid beavers than in the merychippine-nannippine horses, the rate of evolution was comparable in both lines; and in both there was an acceleration in the late Pliocene. Evolution in the cheek-teeth of American castoroidine beavers differed from that in horses in that the loss of roots in the Middle Pliocene *Dipoides* and in the subsequent genera in that line of descent did not occur in the horses.

The rate of hypsodont evolution in antilocaprids (*Merycodus-Antilocapra*), contemporaries of the beavers and horses, was slower but only slightly accelerated in the late Middle and Upper Pliocene. Hypsodonty in the camels with higher crowned teeth (*Paratylopus-Oxydactylus-Procamelus-Camelops*) is about intermediate in rate between that in the antilocaprids on the one hand and the horses on the other. But evolutionary rates in camels and antilocaprids cannot be accurately determined until the phyletic relationships of the genera in these families are better known. This is also true in the Heteromyidae, Geomyidae,

Mylagaulidae and Rhinocerotidae, though in the rhinos it is much slower than in any of the other families mentioned here.

Another phyletic line of horses (*Merychippus*—*Pliohippus*—*Equus*) displays progressive hypsodonty of an equivalent rate to that seen in the nannippine horses with the difference that the occlusal dimensions were actually and relatively larger and there was not as noticeable an acceleration in the Upper Pliocene. It should be noted that in making these observations occlusal dimensions in relation to crown height were constantly kept in mind. It is apparent then from a study of late Cenozoic mammals that there are different rates of evolution in progressive hypsodonty in the different orders, in the families of an order, in the genera of a family, and in the species of a genus. I have seen no evidence for macromutations.

Though populations of antilocaprids, of camels, of nannippine and other hypsodont horses in all probability occupied the same grassland areas it is not logical to assume that they occupied the same ecological niches in their environment. This together with certain physiological factors may account for the different rates of evolution displayed in given characters in different lines of descent. Even in the *Merychippus*—*Nannippus* line there is indication of distinct lines diverging from the main stem, in some of these (*N. retrusus* (Cope)—*N. gratus* (Leidy)) hypsodonty was still progressive but in others (*M. brevidontus* Bode) it showed no progression or was greatly retarded.

This non-progressive hypsodonty is further exemplified by *Merychippus* teeth described by J. T. Gregory (1942, pp. 225–228) in the Big Spring Canyon fauna.⁸ The primitive merychippines

⁸ Gregory considered these teeth as being close to *M. isonesus* (Cope) but I feel that they are even closer to *M. primus* (Osborn). This conclusion is based on the (a) attachment of protocone to protoselene, (b) crown height, (c) and dimensions of the teeth as a whole. There

represented by this Pliocene horse had started along the evolutionary lines of the other hypsodont horses (*Merychippus*—*Pliohippus*—*Equus*) but for some reason diverged from the hypsodont line in Hemingfordian time and evidently remained fixed in its dental characters until the late Clarendonian, when, in so far as we now know, they became extinct. Another kind of *Merychippus* (*Merychippus*—*Nannippus* line) in the Burge fauna, early Clarendonian, is more advanced than the more recent one from Big Spring Canyon. It had reached an early Barstovian evolutionary stage in hypsodonty and represents another unsuccessful divergent line.

The genus *Calippus* evolved to a degree where it became generically distinct from *Merychippus* in the late Miocene. The teeth were hypsodont but tended to decrease in size (*C. regulus* Johnston) and did not keep pace in progressive hypsodonty with *Nannippus* which also showed a decrease in occlusal dimensions. Present evidence indicates that it died out in the late Clarendonian or in early Hemphillian.

It should be noted that among contemporary horses the hypsodont ones are always more numerous. I assume that the hypsodont kinds occupied the open plains areas while the less progressive and lower crowned forms, at least in part, were ecologic competitors with anchitherine genera and possibly were semi-browsers.

Is there enough difference in the height of crown in the cheek-teeth of contemporaneous individuals in any given species of horse, or in succeeding generations of that species, or even in phyletic species from succeeding zones (i.e. stratigraphic zones of 1000–1,000,000 years duration, less than the time represented between any two successive faunas in figure 1) to make natural selection on the differ-

is no evidence that these teeth were secondarily deposited in the Big Spring Canyon sands and there is good reason to believe this horse was contemporary with that faunal assemblage.

ence in hypsodonty alone a determining factor in survival? I think not. After the group had continued to exist for perhaps three or four million years with the gene or genes involved in progressive hypsodonty linked with one or more genes controlling other factors of survival value, the degree of difference in hypsodonty in progressive forms could have become enough greater over the non-progressive forms, provided other factors were equal, that the animals with higher crowned teeth would have distinct advantage.

If hypsodonty alone was a determining factor in survival it is difficult to explain why the *Hipparion* line became extinct at the close of the Clarendonian in America and the *Neohipparion* line failed to survive beyond the Hemphillian. These horses were as progressive in their hypsodonty as their contemporaries in the *Nannippus* and *Pliohippus—Equus* lines which continued into the Blancan on the same continent and in the same areas.

There are a multitude of factors, it seems to me, that might play a role as important as hypsodonty in survival or longevity such as hardness of dentine and enamel, mechanical (see Camp and

Smith, 1942) and physical ability to secure food, to escape enemies, to produce and protect young, etc. All of these qualities must necessarily be related to a number of morphological and physiological variates, so many in fact, aside from their evaluation, that we cannot determine all of them even in living animals.

LITERATURE CITED

- CAMP, C. L., AND N. SMITH. 1942. Phylogeny and functions of the digital ligaments of the horse. *Mem. Univ. Calif.*, 13: 69-124.
- ELIAS, M. K. 1935. Tertiary grasses and other prairie vegetation from the high plains of North America. *Amer. Jour. Sci.*, 29: 24-33.
- GRANGER, W. 1917. Notes on Paleocene and lower Eocene mammal horizons of northern New Mexico and southern Colorado. *Bull. Amer. Mus. Nat. Hist.*, 37: 821-830.
- GREGORY, J. T. 1942. Pliocene vertebrates from Big Spring Canyon, South Dakota. *Univ. Calif. Publ. Bull. Dept. Geol. Sci.*, 26: 307-446.
- JEPSEN, G. L. 1930. Stratigraphy and paleontology of the Paleocene of northeastern Park county, Wyoming. *Proc. Amer. Philos. Soc.*, 69: 463-528.
- SIMPSON, G. G. 1944. Tempo and mode in evolution. *Columbia Univ. Press*, 1-237.
- VAN HOUTEN, F. B. 1945. Review of latest Paleocene and early Eocene mammalian faunas. *Jour. Pal.*, 19: 421-461.