THE EVOLUTION OF THE HORSE:
History and Techniques of Study
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HISTORICAL INTRODUCTION

The story of the evolution of the horse family was codified so early in the history of the science of vertebrate paleontology, and has been repeated so often since that time by scientific popularizers, that the history of this family of mammals has, at least for the general public, become litany. This brief discussion breaks little new ground, but nevertheless much of what is presented here will be surprising to those to whom only a dated and standardized story is known.

The first fossil equid bones to come to the light of science were dug from the Montmartre gypsum within the city of Paris. They were sent to the Paris Conservatory to be studied by the famous Baron Georges Cuvier, who in 1825 illustrated and described the remains, which he called *Paleotherium.* Cuvier, considered the father of paleontology, was correct in considering the Eocene *Paleotherium* to be a browser related to the living tapir.

The Englishman Sir Richard Owen made the next significant contribution, when in 1839 he named and described the remains of *Hyracotherium*. Its small, relatively short-snouted skull and low-crowned, cusped teeth bear little resemblance to the high-crowned grinders of the modern horse; the fossil dentition looked to Owen "rather like that of the Hare or other timid Rodentia." The name Owen conferred upon the skull reflected his belief; *Hyracotherium* means "rabbit-like animal."

Owen's isolated find excited little attention at the time. He did not recognize *Hyracotherium* as the oldest member of the Family Equidae, because in 1839 there were very few fossil horse bones with which his material could be compared. Neither did he recognize it as an ancestor of *Equus,* for at the time, the concept of gradually-evolving lineages had not yet taken intellectual hold of the scientific community.

In 1839, twenty years had yet to elapse before publication of Darwin's "The Origin of Species". Its publication marked the beginning of a long intellectual confrontation between creationists, who believe with Louis Agassiz that "there is nothing like parental descent connecting...faunas of different ages. The link by which they are connected is of a higher and immaterial nature" (Agassiz and Gould, 1851) — and evolutionists such as T.H. Huxley (Fig. 2). Huxley, who called himself "Darwin's Bulldog" had been interested in fossils for a long time, but when in the 1870's abundant fossil horse material began to be excavated both in Europe and in the Americas, it provided him with ammunition in favor of the argument that species change or evolve through time.

The first fossils to be recognized as members of the horse lineage were found in Europe: the Eocene *Palaeotherium* (Cuvier, 1825), *Anchitherium* (Cuvier, 1825) of the Oligocene Epoch, and *Hipparion* (de Christol, 1832) of the Miocene. In 1872, Huxley began to popularize the idea that these forms, whose bones are contained in successive stratigraphic layers, constituted a lineage showing "parental descent." The small

19th-century vertebrate paleontologists whose work opened our knowledge of the history of the horse family. Fig. 1, above: V. Kovalevsky, who first described *Hyracotherium*; Fig. 2, below, T.H. Huxley, "Darwin's bulldog."

morphological differences between successive species which sum to great differences over long spans of time seemed to constitute a series showing gradual evolutionary change.

In 1873, the Russian paleontologist Vladimir Kovalevsky (Fig. 1) studied the existing British and European fossil horse remains and in 1876 was the first to recognize *Hyracotherium* as "a relative of the horse family", in a treatise in which he also strongly agreed with Huxley's ideas (Kovalevsky, 1873).

Meanwhile, the science of vertebrate paleontology had also taken root in North America. Even before Kovalevsky and Huxley began to publish concerning the ancestry of *Equus,* Joseph Leidy (Fig. 5) had issued a series of well-illustrated monographs (Leidy, 1856, 1857, 1858, 1859, 1869, 1870, 1873) in which he provided the first descriptions of many different North American genera of fossil horses, including the now-familiar *Pliohippus, Protohippus, Merychippus, Parahippus, Mesohippus,* and *Hypohippus* as well as forms resembling the European *Hipparion.*
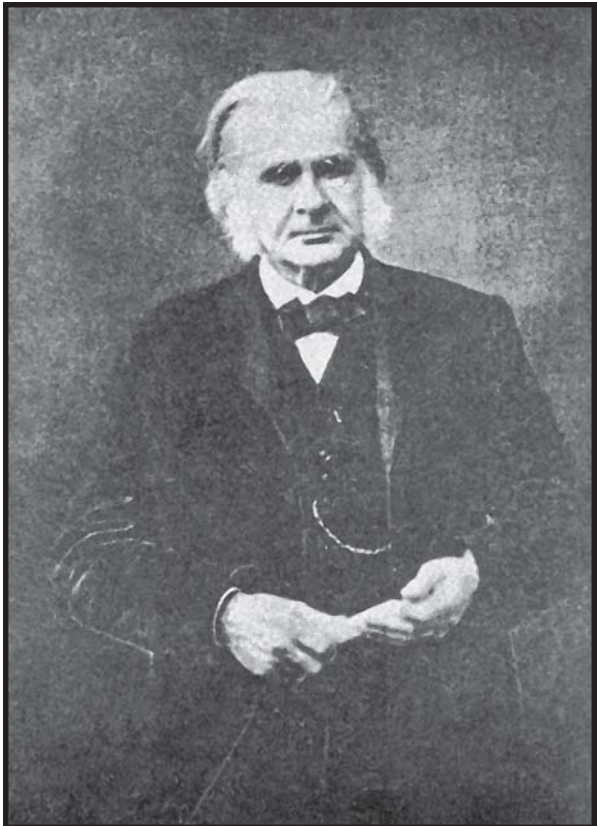
Most of these remains came from richly fossiliferous Tertiary strata in the newly-opened Great Plains region, west of the Mississippi River in the U.S.A. Although he recognized that these forms were equids, Leidy, a very cautious and careful scientist who was characteristically unwilling to go beyond his data, did not attempt to construct a phylogeny from this collection of fossils. In short, though Leidy accepted Darwin's idea that species change or evolve through time, he was not certain that the forms in his possession represented a series of rungs on an evolutionary ladder; they could just as easily represent terminal branches on an evolutionary bush. Complicating the problem of interpreting the family history of horses was a lack of reliable stratigraphic data. Leidy, who had not himself dug up the fossils he described, had doubts about the accuracy of stratigraphic determinations attached by collectors to the fossils that they sent to him. He simply had to hope that more fossils from less doubtful stratigraphic contexts would be discovered.
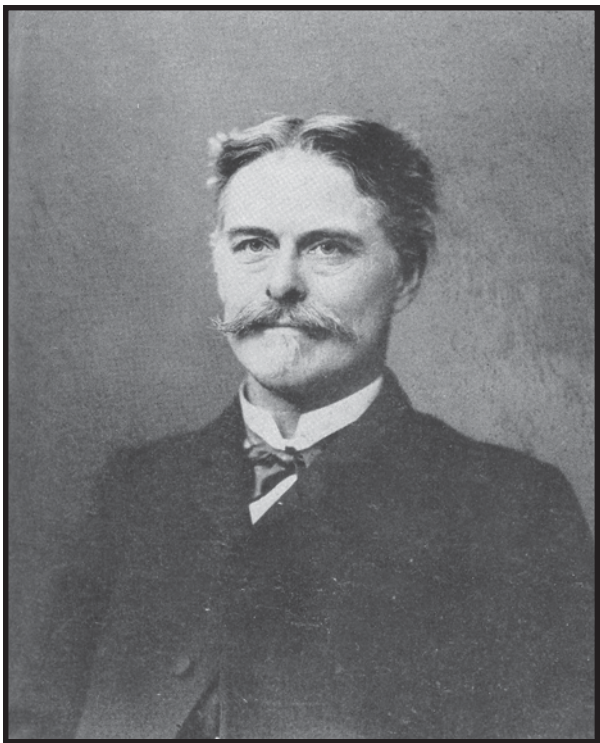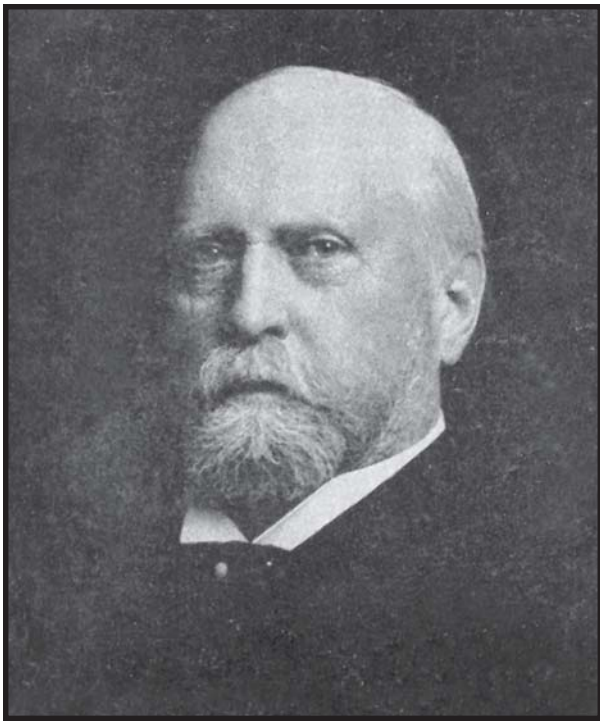
The two most important 19th-century paleon-tologists in America: Fig. 3, above, Othniel Charles Marsh; Fig. 4, below, Edward Drinker Cope. Marsh was on faculty at Yale; Cope, for much of his career, worked as an independent. He founded *The American Naturalist*, a science magazine still in exist-ence today. Cope and Marsh were bitter rivals.

He had not long to wait. Paleontologist O.C. Marsh of Yale University (Fig. 3) was also paying collectors to work in the western fossil beds, and already by 1871 they had begun to send him equid remains from Eocene and later strata (Schuchert and LeVene, 1940; Simpson, 1951). A Darwinist, Marsh early leaped to the conclusion that his collection of fossil horse remains, the largest and most complete in the world, represented an evolutionary ladder in which one species gradually evolved into the next later (and therefore "higher") form (Marsh, 1874). In addition, Marsh's (1874) conclusion that "the remains now known supply every important form" proved to be over-optimistic. However, the evidence was enough by 1873 to convince Huxley that the center of horse evolution throughout the Tertiary had been North America, not Europe.

Marsh's 1874 scheme was missing the first member of the horse family, now well-known as "Eohippus". This form, whose remains come from lower Eocene beds of New Mexico and Wyoming, had been named and described in 1873 by Marsh's bitter rival, Professor E.D. Cope (Fig. 4). It was also Cope who, a few years later, realized that Eohippus is synonymous with the European *Hyracotherium.* Despite the publication of this important fact, both scientists and journalists still continue to utilize Cope's well-coined name Eohippus, which means "dawn horse." (This usage is now considered to be correct only when the name is used as a vernacular term, without italicization. The correct technical term is *Hyracotherium*).

More than any other worker, it was Marsh who codified the story of the evolution of the horse. In 1874, he wrote:

"The large number of equine mammals now known from the Tertiary deposits of this country, and their regular distribution through the subdivisions of this formation, afford a good opportunity to ascertain the probable lineal descent of the modern horse. The American representative of the latter is the extinct Equus fraternus *Leidy, a species almost, if not entirely, identical with the old world* Equus caballus *Linn., to which our recent horse belongs.*
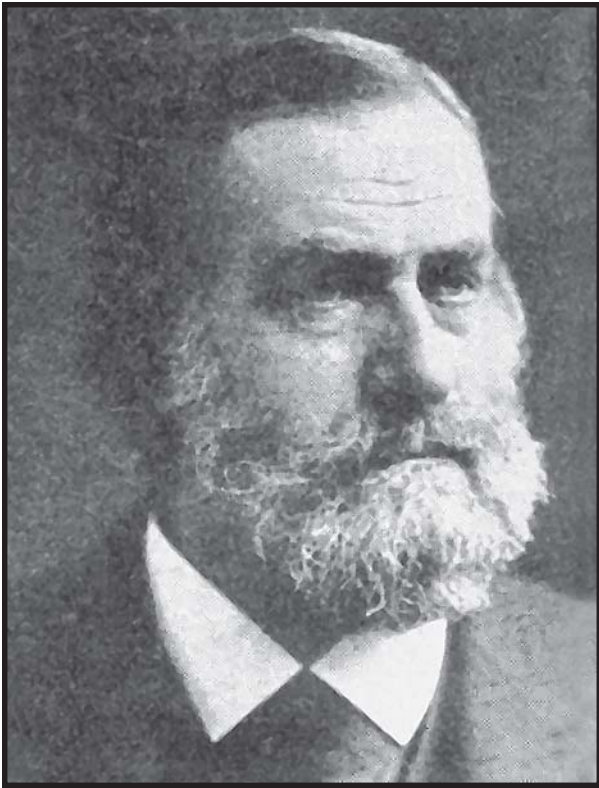
Fig. 5: Joseph T. Leidy, above, was a careful and conscientious early worker. Fig. 6: William Berryman Scott (below) wrote the first comprehensive textbook on American fossil mammals, including, importantly, the record from South America.

Huxley has traced successfully the later genealogy of the horse through European extinct forms, but the line in America was probably a more direct one, and the record is more complete. Taking, then, as the extremes of a series, Orohippus agilis *Marsh, from the Eocene and* Equus fraternus *Leidy, from the Quaternary, intermediate forms may be intercalated with considerable certainty from the thirty or more well marked species that lived in the intervening periods. The natural line of descent would seem to be through the following genera:* Orohippus, *of the Eocene;* Miohippus *and* Anchitherium, *of the [Oligocene and] Miocene;* Anchippus, Hipparion, Protohippus *and* Pliohippus, *of the [Miocene and] Pliocene; and* Equus...

"The most marked changes undergone by the successive equine genera are as follows: 1st, increase in size; 2d, increase in speed, through concentration of limb bones; 3d, elongation of head and neck, and modifications of skull. The increase in size is remarkable. The Eocene Orohippus *was about the size of a fox.* Miohippus *and* Anchitherium, *from the Miocene [Oligocene] were about as large as a sheep.* Hipparion *and* Pliohippus, *of the [Miocene and] Pliocene, equalled the ass in height; while the size of the Quaternary* Equus *was fully up to that of the modern horse...*

"The ancient Orohippus *had all four digits of the fore feet well developed. In* Miohippus ... *the fifth toe had disappeared, or is only represented by a rudiment, and the limb is supported by the second, third, and fourth, the middle one being the largest.* Hipparion ... *still has three digits, but the third is much stouter, and the outer ones have ceased to be of use, as they do not touch the ground. In* Equus, *the last of the series, the lateral hoofs are gone, and the digits themselves are represented only by the rudimentary splint bones. The middle, or third, digit supports the limb, and its size has increased accordingly."*

This passage has been quoted at length because of its strong influence on later workers, who have almost entirely focused upon the amplification and refinement of Marsh's themes concerning increase in size, decrease in

Fig. 7: Henry Fairfield Osborn, flamboyant director of the American Museum of Natural History and student of elephant paleontology. Osborn bridged the change of century from 19th to 20th. There was much to occupy him: the American Museum's collection of fossil mammals is unrivalled in the world. Expanding, curating, and researching such a collection takes money, and Osborn was highly successful in his efforts to solicit from wealthy families. Premier among these was Childs Frick, heir to the Carnegie Steel fortune, who himself was a graduate of the Berkeley program at the University of California under W.D. Matthew. Frick paid father-son collectors Charles and George Sternberg to scour the badlands of the Dakotas, Nebraska, Wyoming, and northern Texas for the remains of fossil mammals. Later, Frick's collector was the great Morris F. Skinner. Frick underwrote the building of a laboratory -- nine stories high and almost a city block square -- to house all the fossils in perpetuity at the AMNH. The Frick American Mammals collection is today a repository for priceless fossils, and a major source of data and knowledge for students of the horse.

the number of toes, and increase in the height and complexity of the grinding teeth. Exceptions to this pattern have been few, either in terms of the body part studied (for example, Edinger, 1948, and Edinger and Kitts, 1954, on the evolution of the equid brain; Bennett on the evolution of the axial skeleton, 1988) or the evolutionary mechanism invoked (for example, non-gradualism; Gould and Lewontin, 1979; Eldredge and Gould, 1972; Prothero and Shubin, 1989).

More subtle, and ultimately more damaging to our ability to understand what life was like in the past, is Marsh's tacit assumption that the horse fossils in his possession represented "lineal" descent and formed "a series". Although this concept has been the orthodox viewpoint (Bock, 1973; Gingerich, 1983; Matthew, 1926; Mayr, 1969; Simpson, 1945; Stirton, 1940), it is not the only possible evolutionary mechanism and it is probably not the correct one for the horse family, which, because of the abundance and diversity of fossil remains, must be regarded more as a bush than as a ladder (Gould, 1977, 1987; Hennig, 1966; Kavanaugh, 1972; Schaeffer et al. 1972). The mental image of an evolutionary ladder formed by species which, like rungs, succeed each other in time, gives rise to a number of significant conceptual distortions, the most frequently encountered of which are:

1) There is one "main line" of horse evolution, which begins with "Eohippus" *(Hyracotherium)* and ends with the one-toed *Equus*;

2) Different horse genera succeeded one another through time with little or no overlap, i.e., several different kinds of horses rarely coexisted;

3) One species gradually evolved into another, so that an "intermediate form" can be expected in every newly-discovered stratigraphic layer;

4) The reason that Eohippus and other early forms existed was in order to evolve into *Equus*, i.e., the existence of the presently living form was pre-directed or predestined.

All four of these ideas are false. Although they are frequently voiced by the media which feeds the public, they also represent scientific viewpoints which were current during this century, some until recently. Gould and Lewontin (1979) succinctly summarize the argument for non-gradualistic, non-linear evolution within the horse family:

"W.D. Matthew [one of the greatest students of fossil horses] slipped into a...biased assessment...[in a 1926 paper] because his designation of one pathway [in what is, in reality, an evolutionary bush] as a ladder forced an interpretation of all other [branches] as diversions....Yet we have recognized the bushiness of horse evolution from the very beginning. How else did Marsh forestall Huxley, but by convincing him that his European 'genealogy' of horses was only a stratigraphic sequence of discontinuous stages, falsely linking several side branches that had disappeared without issue?"

ENVIRONMENTAL FACTORS BEARING ON THE EVOLUTION OF GRAZING EQUIDS

The first principle of Darwinian evolution is the adaptation of the organism to the environment in which it lives. Throughout time, equids have been able either to adapt to the prevailing environment, or to migrate to a more suitable one. During the whole of the earlier half of the Tertiary, only two kinds of body morphology developed in the horse family: the scansorial browser form, typified by *Hyracotherium*, and the chalicothere-like browser form, typified by *Hypohippus* (Figs. 10, 11, 12, 13). Both of these morphs were already well established by the late Eocene. Late-occurring species possessing these bodily adaptations tend to be larger than earlier forms. Having

Fig. 8: William Diller Matthew, perhaps the greatest of all teachers of vertebrate paleontology. A careful and meticulous scientist, he was an excellent writer and -- best of all -- a brilliant synthesizer of ideas and principles. His 1939 book, "Climate and Evolution," still stands as a classic, and his papers are models for students to imitate. The greatest 20th-century vertebrate paleontologists were contemporaneous with Matthew, and were either his students or were influenced by him. Premier among these are George Gaylord Simpson, Edwin H. Colbert, and Alfred Sherwood Romer. Simpson's 1951 book "Horses" is a must-read for anyone interested in the history of the horse family.
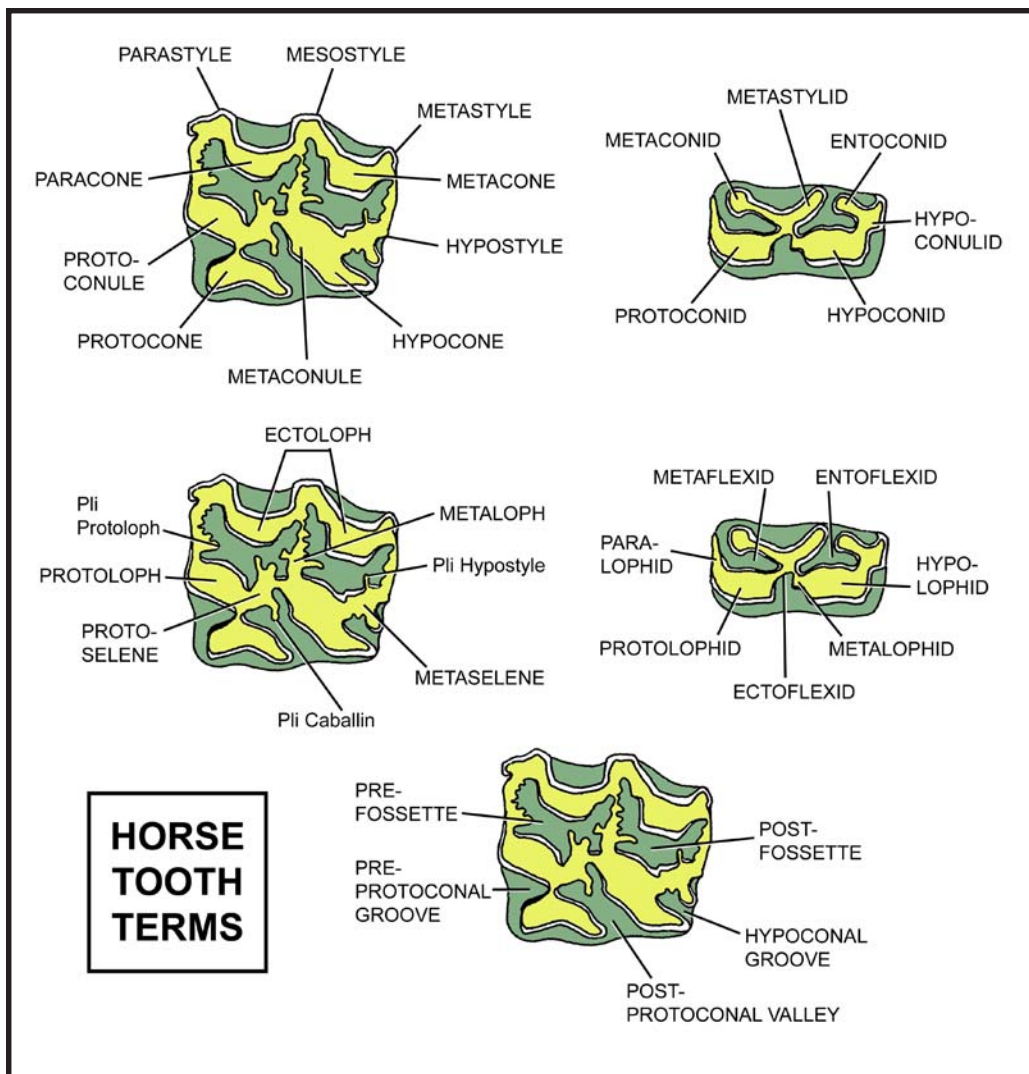
achieved a body morphology enabling them to survive and reproduce in a given environment, equid species have tended to retain successful forms through long periods of time (Prothero and Shubin, 1989). In response to the expansion of grasslands in the latter half of the Tertiary, one branch of the horse family acquired a third body design, suitable for life in open, unforested areas -- the grazer morphology (Fig. 14).

Morphological change on a smaller scale can also be found within each of these three adaptive forms. Speciation, leading to rapid diversification of morphology over short intervals of time, is characteristic of the horse family. Horse remains, especially teeth, are durable; the organisms bearing them were mobile and thus

Fig. 9. The terminology that students of horse anatomy use to describe the parts or "characters" visible on the occlusal surfaces of horse teeth. Particular, small differences in the presence, shape and position of these characters are the defining criteria by which Equid species are classified and by which we discern to which bloodline each belongs.

You will need to be familiar with these terms as you study the cladogram and phylogram presented on pp. 8 and 11 of this report. Print out this page for handy reference.

horses, more than most other large mammals, spread their remains over wide areas. For these reasons, the horse family is most useful for biostratigraphic determinations throughout the terrigenous post-Paleocene strata of North America (Skinner and Johnson, 1984; Skinner et al. 1977; Tedford et al. 1987).

Due to episodic but continual northward displacement of the North American tectonic plate during the Tertiary Period, the climate of the continent became cooler and drier through a series of descending cycles (Durham, 1959). Paleocene floras of Alaska are tropical in character; by the end of the Oligocene, some 45 million years later, tropical floras were found only south of Texas, as they are today (Kummel, 1970). The "modernization" of floras which occurred at the beginning of the Miocene Epoch divides the Tertiary into an older portion, the Paleogene, and a younger division, the Neogene. Paleogene forests in the area of the conterminous United States were tropical or subtropical in character, dense, and nearly continuous except for openings created by large bodies of water. At the beginning of the Neogene, climatic conditions had deteriorated to a critical point at which a continuous forest cover of tropical character could no longer survive (Schwarzbach, 1963). Thereafter, forest cover became increasingly patchy and subject to latitudinal zonation, providing grasses the physical space in which to spread and diversify (Brooks, 1928; Wright, 1970). Neogene forests were largely subtemperate in character, although during the Pliocene a further climatic deterioration resulted in the development of both boreal and xeric floras (Chaney and Elias, 1936; Axelrod, 1937).
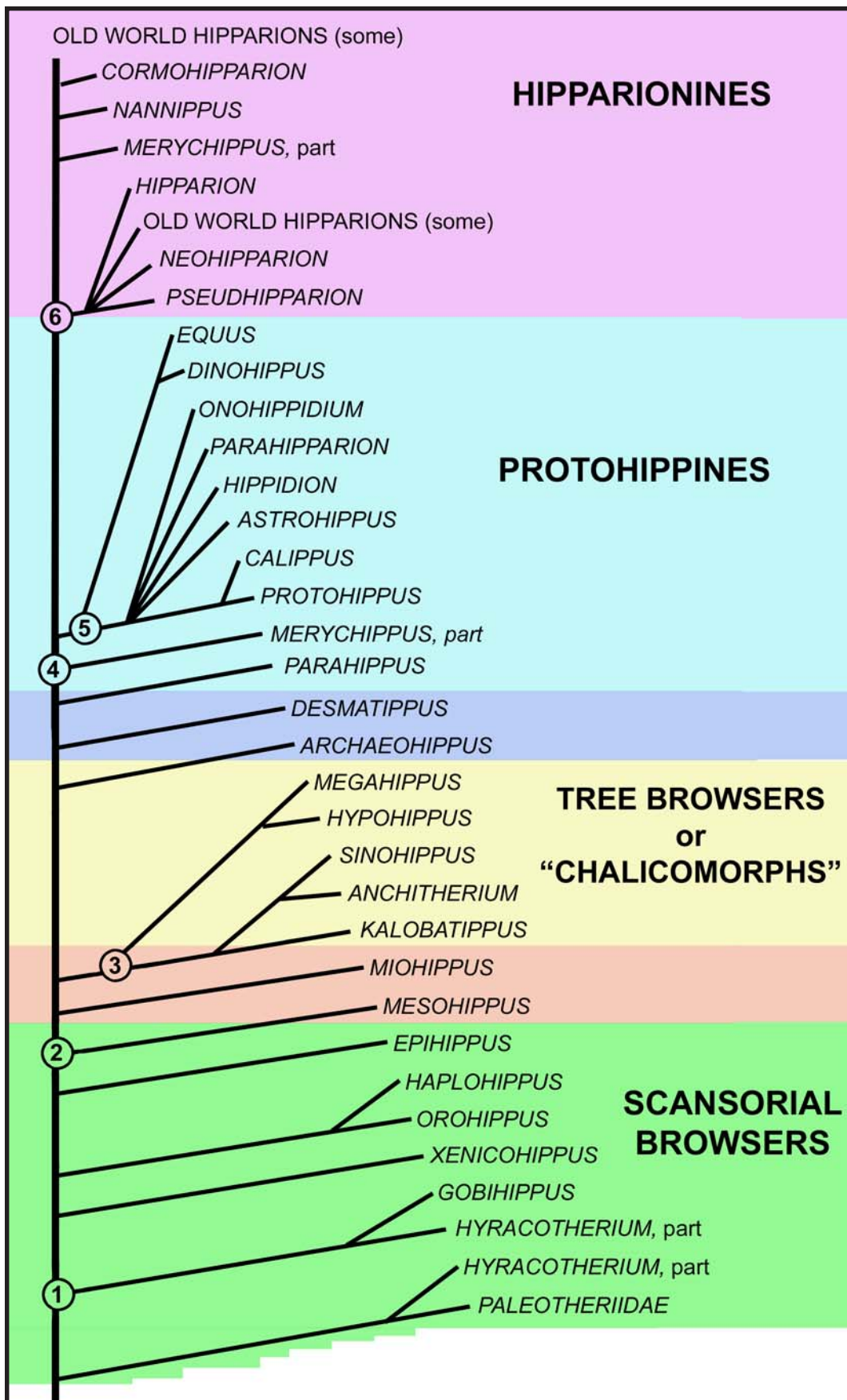
Fig. 10. Cladogram or "logic diagram" showing relationships among all the horse genera currently believed to be valid (after MacFadden, 1992). The original version of the paper you are now reading contained a cladogram made up by the author which contained fewer genera and that was based on less data. I am happy to improve this presentation by following Bruce's lead, and want to acknowledge especially his lifetime of work on the hipparionine horses. For further commentary on cladograms and Cladism, please see following page. To make following this part of the discussion easier, the reader is invited to print out this and the next few pages.

The main purpose of my original cladogram was not to attempt to revise the horse family, nor to propose into what subfamilies, infra-families, super-genera or whatnot other sorts of clades these organisms should be classified.

Rather, I have wanted to emphasize the fact that the structural similarities observable among different clades of Equids have strong and quite consistent implications as to what sort of lifestyle the animals were living. I have therefore overprinted the cladogram on the previous page with colored bands indicating the "adaptive groups" that I think Equids fall into.

MacFadden's cladogram differs little in this respect from my previous one. Because he has been able to include more horse genera, "transitional" forms appear in two places -- under the blue band *(Archaeohippus* and *Desmatippus),* and under the orange band *(Mesohippus* and *Miohippus).* Animals under the orange band take the scansorial browsers out of deep forest of tropical character. They are representative of the body morphologies that gave rise to both the "chalicomorphs" or tree-browsers, and to the ancestors of the grazers.

Animals under the blue band continue the "generalized" -- or you might as well say "mainstream" -- morphology of the orange band, and thus are representative of the body morphologies that gave rise to the first grazing Equid, *Parahippus.*

On P. 11 of this essay, I present the evolution of the horse family in the old-fashioned way, by means of what is called a phylogram. Phylograms differ from cladograms in that they make definite statements about ancestor-descendant relationships. Notice that in making a cladogram, the paleontologist temporarily pretends that she does not have any inkling about bloodlines. Cladograms therefore almost always make it appear that there are no ancestral forms; every organism comes out looking like a "side branch." The process of making a cladogram forces the scientist to think with cold logic, treating the remains of living things strictly as "specimens" -- they could as readily be clocks or any other inanimate object having lots of parts and thus amenable to a logical sorting process.

However, we do know that sexually reproducing, living things all actually have ancestors. The phylogram, therefore, is one possible interpretation of the information that is presented in the cladogram. It doesn't have to be, and may not be, truth as it actually happened; as a matter of fact, no one is likely ever to know that, because we weren't there to see the animals reproduce, determine whether there was panmixia in the population, see which individuals or herds were surviving best, etc.

The phylogram can do another couple of things that the cladogram shies away from: it indicates time sequence, with species from older strata near the bottom and those from younger strata near the top. It indicates which forms are "generalized" or "mainstream"; the logical rules for making cladograms tend to either make such animals look problematical, or force them to look like "side branches". The phylogram may also indicate degree of relationship, whereas the length of the sticks in a cladogram has no such meaning.

So, in this day and age when all students of paleontology (including myself) have been taught the methods of cladistics, the paleontologist who publishes a phylogram is really sticking her neck out. This is not the first time I've done that, nor will it be the last. To me, jumping off the cladogram is well worth doing because, in making definite statements about time sequence and bloodlines of inheritance, I make the latest and best results of scientific thought about horse evolution CLEAR to the reader -- for a phylogram is far easier to read and interpret than a cladogram. That may make me a worse scientist, but I know it makes me a better public educator. An understandable picture may help other people gain a lively interest in the long, diverse, and fascinating history of the horse family.

CHARACTERS AND "POLARITY"

On MacFadden's cladogram you will notice seven numbers and four question marks. The numbers occur at branching-points called "nodes". They indicate that "shared derived character states" occur for all the taxa above the node. "Shared derived character states" is Cladistic techno-speak for "structural features shared by all species in the group that are visible in the skeleton and teeth and that are different from the commonly-inherited primitive structure."

The question marks are also important. They imply that the researcher can see that fossil species differ in morphology, but cannot find a derived character to define each (by the rules of cladistics, no matter how many primitive characters you can see, you can't use them to define a taxon). Wherever there is either a question mark or the absence of a number at a node, you have license to re-arrange the cladogram -- for cladistic analysis depends strictly upon the discovery of derived characters. So for example, I have used this license to make the chart of bloodline descent (phylogram) on the next page.

The polarity of shared-derived characters reveals two things: first, trends within a given group -- the "direction" of evolution. Once polarity is known, it also reveals parallelism -- the tendency of terminal forms belonging to different clades to take up similar lifestyles and thus to develop or re-develop similar structures. Parallelism is common within the horse family and can be very confusing.

MacFadden's seven nodes are supported by the following derived characters (**boldface** terms for taxonomic groupings are in some cases mine rather than MacFadden's:

Node 1: Defines the **Family Equidae.** Foramen ovale absent or confluent with the middle lacerate foramen (see Fig. 21 this text). Optic foramen separated from other foraminae in the orbit (Fig. 20 this text). Post-protocrista (a tiny but distinct cusplet) present on the upper 3rd premolar.

Node 2: Defines the **Subfamily Anchitheriinae**. Upper cheek teeth from the 2nd premolar through the last molar are completely "squared up" or "molarized" to form a chewing battery. Fore and hind feet have three digits. Metacarpal of digit V present but reduced. Incisors with pitted crowns. Premaxilla bone long, and a relatively long diastema (toothless space or "bars") is present. Angle of lower jaw uniformly rounded, lacking posterior notch.

Node 3: Defines the **Tribe Chalicomorphini.** Large crown area on cheek teeth. Thick cingula on teeth (the "cingulum" is a rounded ridge at the base of the tooth crown that often bears cusplets). Loss of ribs between the styles on the cheek teeth (see Fig. 9 this paper). Large body size.

Node 4: Defines the **Subfamily Equinae.** Cement formed on deciduous and permanent cheek teeth. Pli caballin present on upper cheek teeth (Fig. 9 this text). Pli entoflexid present. Moderately deep ectoflexid on 2nd lower premolar (Fig. 9 this text). Relatively great degree of hypsodonty.

Node 5: Defines the **Tribe Equini.** Dorsal pre-orbital fossa (facial fossa or "DPOF") may be absent to moderately deep. If present, it has a shallow posterior pocket. The protocone of the 3rd and 4th upper premolars connects to the protoloph at least in early stages of wear. An enamel-rimmed "lake" forms from a deep re-entrant in the hypoconid of the lower 3rd and 4th premolars. Metastylid of lower cheek teeth much smaller and located more labially than the metaconid.

Node 6: Defines the **Tribe Hipparionini.** Well-developed and persistent pli caballin present on the molars of the upper jaw. Metacarpal V articulates primarily with metacarpal IV.

Node 7: Defines the genus *Equus.* DPOF shallow or absent. Very high crowned and relatively straight teeth. Complex enamel plications. Well-developed intermediate tubercle on distal humerus.
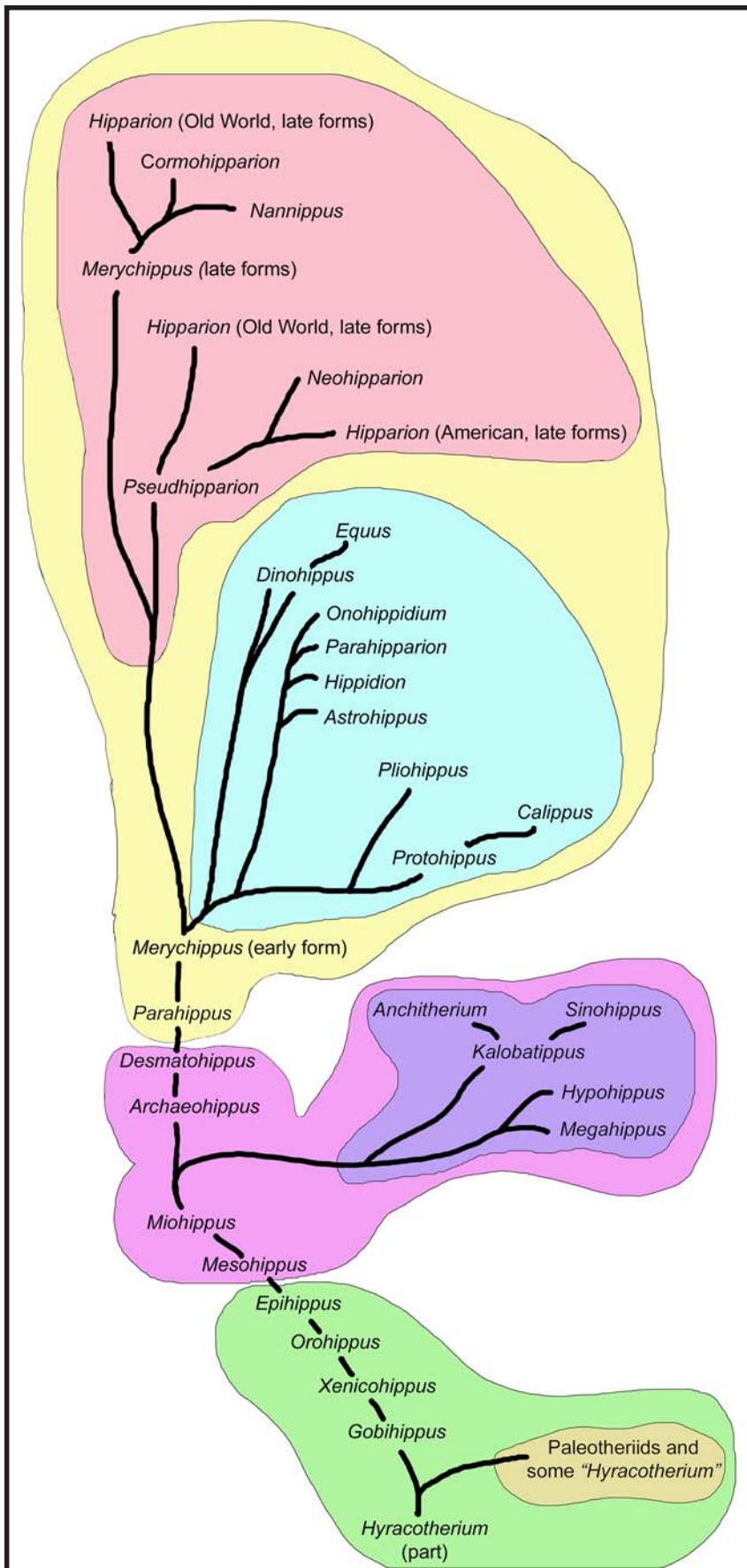
Fig. 11. A phylogram showing bloodline relationships within the Family Equidae.

Color code indicates the taxonomy: Green = Subfamily Hyracotheriinae. Brown = Tribe Paleotheriini. Purple = Subfamily Anchitheriinae (term used in the strict sense). Dark blue = Tribe Chalicomorphini. Yellow = Subfamily Equinae (the Equines, capital "E"). Light blue = Tribe Protohippini. Note that the living genus *Equus* is a member of this tribe. Rose = Tribe Hipparionini.

This diagram thus proposes the following classification:

Family Equidae
Subfamily Hyracotheriinae
    Tribe Hyracotheriini
    Tribe Paleotheriini
Subfamily Anchitheriinae
    Tribe Anchitheriini
    Tribe Chalicomorphini
Subfamily Equinae
    Tribe Merychippini
    Tribe Protohippini
    Tribe Hipparionini

This phylogram is entirely in agreement with all the data presented in MacFadden's 1992 cladogram, but I use my own terminology for subfamilies and tribes.

The student may understand from study of both the cladogram and the phylogram that the marriage between Linnaeus' system of binomial nomenclature and hierarchical classification, and any attempt to show relationships or descent, is and always of necessity will be an uneasy one.
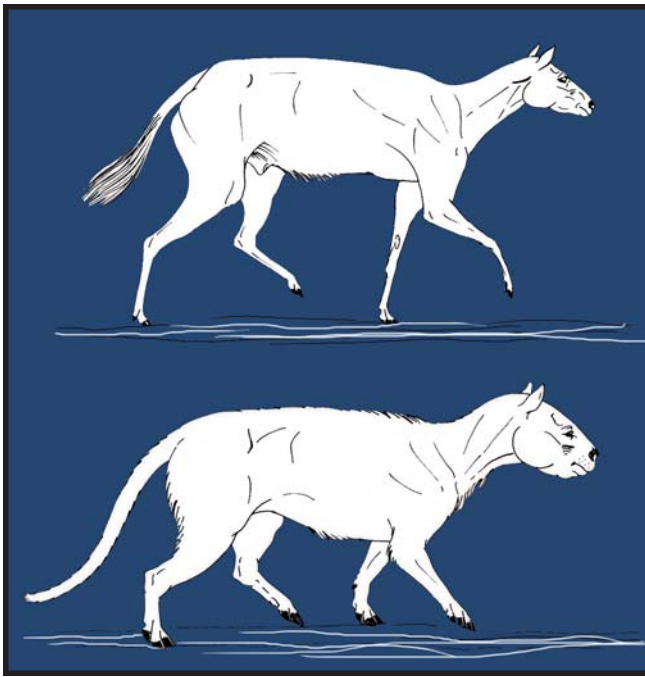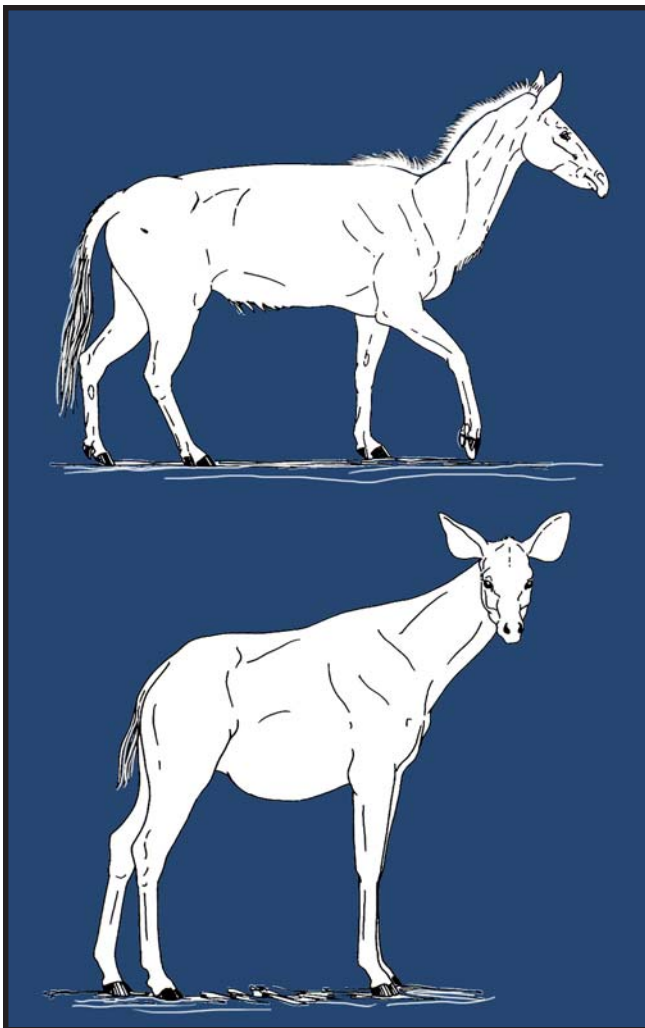
Fig. 12: Above: Scansorial body form exemplified by the Eocene fossil horse *Hyracotherium* and the Miocene Artiodactyl oreodont *Merycoidodon.*

Shortly after the beginning of the Neogene, with the advent of widespread grasslands, and in response to the evolution of taller, swifter, and more intelligent carnivores, one horse lineage developed the body structures necessary for it to masticate and digest grass and to run away from predators swiftly in a straight line. Some branches of this lineage remained small and light, resembling deer or small antelopes in form, some becoming dwarfs smaller than their first grazing ancestor. Other branches tended toward the stockiness characteristic of the living *Equus.* Most were tridactyl, but monodactyl forms developed more than once (Simpson, 1951; Voorhies, XXX). During the Miocene and Pliocene, many different grazing genera coexisted on the open savannas of North America, while browsing forms with the chalicomorph body design continued to exist in the remaining patches of forest (Bennett, 1984; Gidley, 1907; Merriam, 1913; Quinn, 1955; Scott, 1893; Webb, 1969).

Interhemispheric migration of equid species was periodically possible throughout the Tertiary, depending upon plate tectonic conditions. During the early Eocene, *Hyracotherium* spread from North America to Europe via a Greenland bridge (Cooper, 1932; Simpson, 1951). In Europe, it gave rise to several species of the genus, as well as to the first of the chalicothere-like equid genera, *Paleotherium* (Barbour, 1914; Deperet, 1917; Filhol, 1888; Remy, 1965, 1972a; Savage et al., 1965; Simpson, 1952).

The various descendants of *Hyracotherium* had died out in the Old World by the early Oligocene, and rather surprisingly since an intercontinental connection between Alaska and Asia was in existence at that time, no horse remains have been found in Oligocene

Fig. 13: Left: The high-in-front body form good for browsing trees and tall bushes. In the text, this is called "chalicomorph" body form. Here it is exemplified by the Miocene fossil horse *Hypohippus* and the living artiodactyl giraffid *Okapi.*
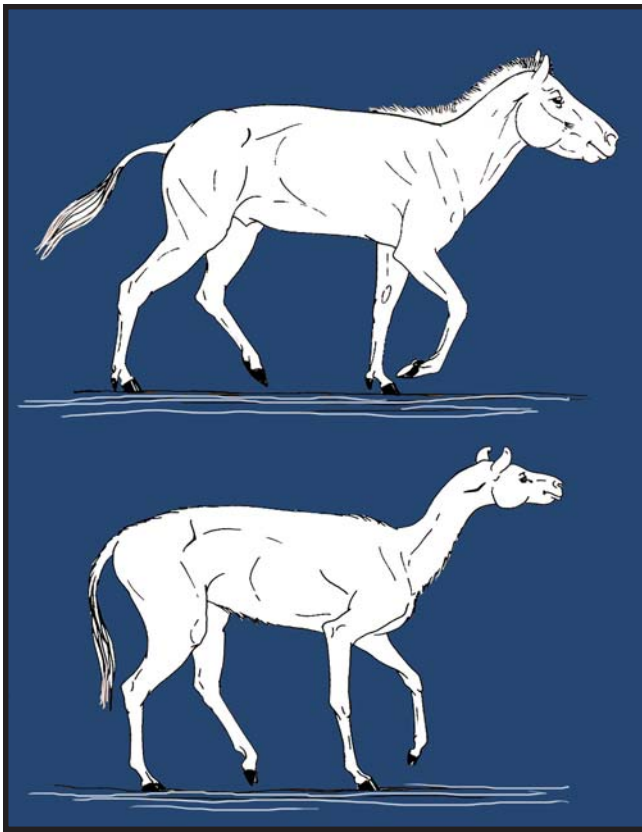
Fig. 14: Grazer body form exemplified by the Miocene equid *Neohipparion* and the Miocene artiodactyl camelid *Poebrotherium.*

rocks there (Simpson, 1951). In the middle Oligocene, all interhemispheric connections were severed, but by late Oligocene time the Beringian land route was again open and the North American chalicomorph browser *Anchitherium* used it to travel westward (Cope, 1873; Matthew, 1915). In Eurasia its descendants diversified into several different genera represented by many species. They may also have been the first equids to inhabit Africa (Churcher and Richardson, 1978). In North America, *Kalobatippus* continued the chalicomorph line.

The genus *Hipparion* was the next, in the early Miocene, to migrate from North America to Eurasia via Beringia. Remains of many species of *Hipparion* are found in great abundance all over Eurasia, from China to Spain (Bernor and Hussain, 1985; Crusafont and Sondaar, 1971; Falconer and Cautley, 1845-1849; Forsten, 1968; Hussain, 1971; Koenigswald, 1970; Matthew, 1929; MacFadden, 1980; Pirlot, 1956; Sefve, 1927; Woodburne, MacFadden, and Skinner, 1981). The genus persisted longest in Africa, finally dying out there in the early Pleistocene, the last three-toed horses in the world (Patterson and Pascual, 1972; Churcher and Richardson, 1978).

By that time, the last interhemispheric migrant of the equid family had also reached Africa: the heavy-bodied, monodactyl genus *Equus*. Because the fossil record of the Pliocene and Pleistocene is more complete than that of earlier Tertiary epochs, and because more precise dates can be assigned to individual fossils, we can document the separate trans-Beringian migrations of several different species of *Equus*, and what is more, of back-migrations from Eurasia to North America (Bennett, 1980; Matthew, 1915). A more complete fossil record would probably reveal an equally complex history of parallel migrations for the genera *Hyracotherium, Anchitherium,* and *Hipparion.*

COMPETITION AND PREDATION AS FACTORS IN THE EVOLUTION OF GRAZING EQUIDS

Until the evolution of the grassland-adapted Camelidae in the middle Oligocene, the Perissodactyls (horses, tapirs, rhinoceroses, chalicotheres, and their relatives) had been the most diverse and numerous order of hoofed mammals. After the middle Oligocene, the Artiodactyl order (containing swine, oreodonts, camels, cervids, bovids, and their relatives) gradually became ascendant. Today the Artiodactyla are by far the dominant order, while the Perissodactyla are nearly extinct (Romer, 1966).

After the end of the Oligocene, when equids entered the grassland biome, they competed very successfully with the Artiodactyl ungulates, as proved by the rapid diversification and large numbers of fossil equids which lived
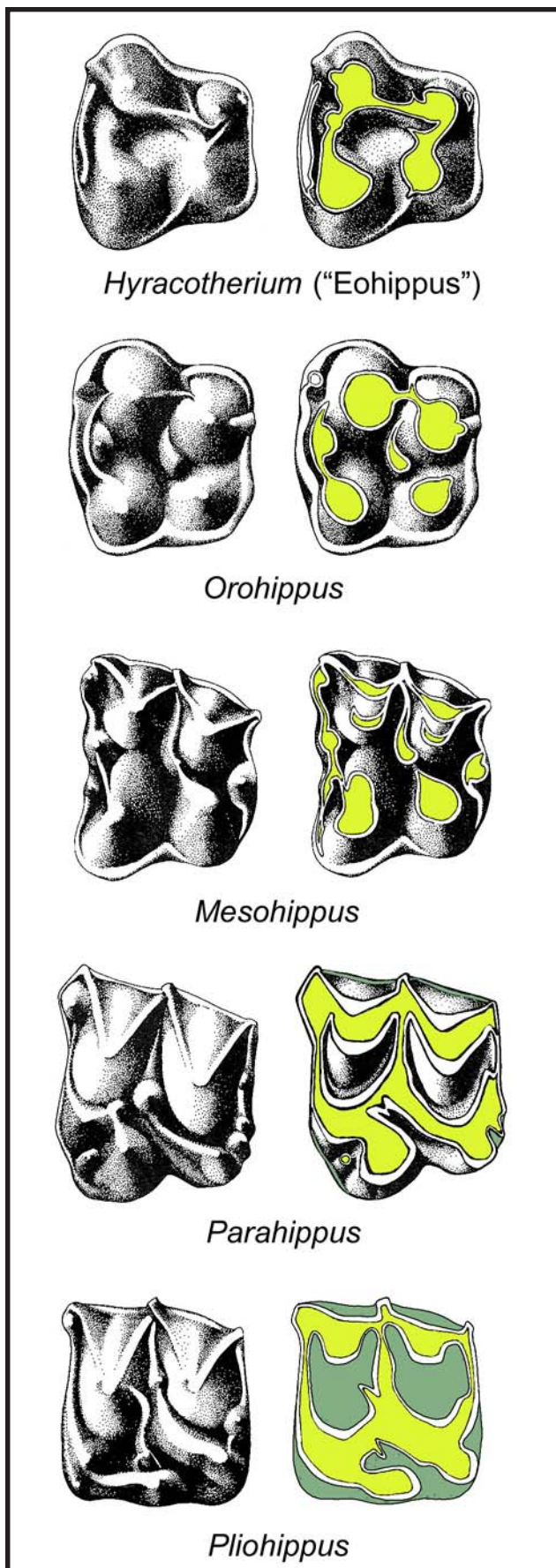
during the Miocene. What is of greater interest is the effect that the head-start of the Camelidae probably had on the development of effective predation on browsing equines.

Throughout the Tertiary, the brains of carnivores tended to be smaller and less complex in structure than those of their ungulate prey. Likewise, carnivores have consistently retained primitive skeletal structures. These two facts conspired, during the earlier half of the Tertiary, to produce a relatively stable balance between predator and prey, in which *advances always came first in the prey species*. The evolution of more intelligent or swifter prey thus induced the development of smarter and swifter predators. Equid populations which did not "keep up" with increases either in intelligence or locomotor capability were eventually consumed by the better-designed predators capable of catching them (Scott, 1913).

Early camelid populations were well equipped to outstrip existing predators, but within a few million years, before the end of the Oligocene, species of both the Aeluroid (cat-like) and the Arctoid (dog-like) carnivores existed which were capable of catching and killing camels by employing a "rush" from cover out into the open (Scott, 1913). The

Hyracotherium ("Eohippus")

Orohippus

Mesohippus

Parahippus

Pliohippus

Fig. 15: Two main factors affect the pattern that a researcher will see on the occlusal surface of an equid tooth: the structure of the tooth, and the degree of wear. This figure compares the first upper molar in five equids, showing the structural changes from bunodont teeth having discrete, cone-shape cusps (top) to hypsodont teeth in which the cusps have coalesced to form lophs (bottom). Newly-erupted teeth (lefthand column) are, of course, completely covered with enamel in somewhat the same manner as icing coats a cupcake. In this diagram, black stipple pattern indicates an unbroken enamel "icing". As the tooth is abraded, the enamel wears away to expose the dentine within (yellow). Hypsodont teeth have enamel-rimmed "lakes" filled with cementum (green), a reinforcing material that also enwraps the outer surface of the tooth.
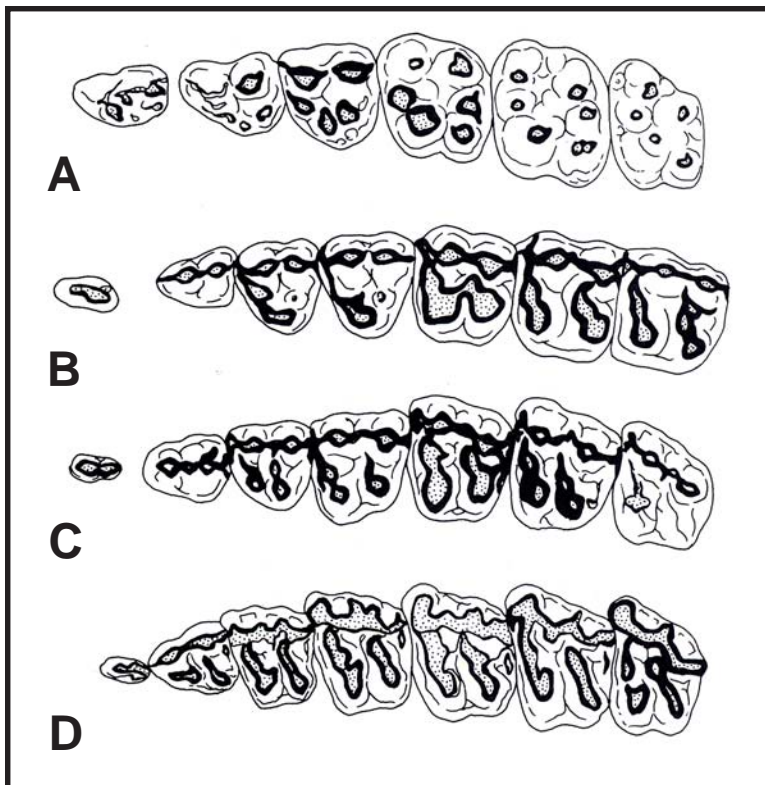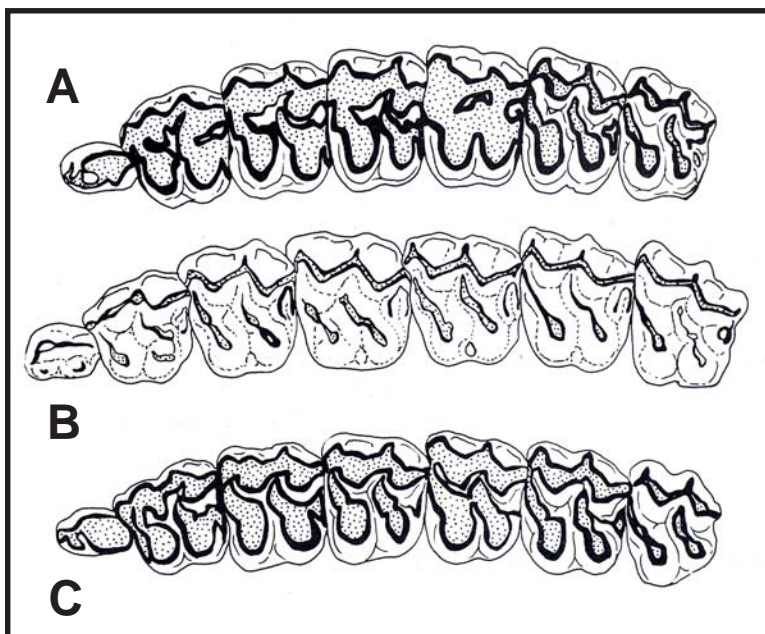
Fig. 16: Left: Left superior cheek dentitions of a condylarth and browsing equids, occlusal view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. Black indicates exposed surface of worn enamel, stipple indicates dentine. A, *Phenacodus*, a condylarth, after Simpson. B, *Hyracotherium,* after Simpson. C, *Orohippus,* after Simpson. D, *Epihippus,* after Simpson. Note bunodont, brachydont structure, and absence of connection between metaloph and ectoloph.

Fig. 17: Below: Left superior cheek dentitions of dentally advanced browsing equids, occlusal view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. A, *Mesohippus,* after Osborn. B, *Miohippus,* after Prothero and Shubin, nearly unworn. C, *Miohippus,* after Osborn, worn condition. Note brachydont, lophodont structure and absence of connection between metaloph and ectoloph. The hypoconule is large in these forms, as is the first premolar.

Oligocene also marked the first development of saber-form canines in the Felidae (Romer, 1966).

During the late Oligocene, equids were still peeping out from the forest eaves. Because of the early invasion of the grasslands by the camelids, carnivores existed which were easily capable of catching any forest-adapted equid foolish enough to stray out into the open. Besides the lure of nutritious grass as an abundant food source, the camelid-induced efficiency of predation within the forest during the late Oligocene acted to select the swiftest equids and to accelerate the divergence of the lineage of grazing equids from their forest-dwelling relatives (Scott, 1913).

STRUCTURAL ADAPTATIONS NECESSARY FOR MAMMALIAN GRAZING

The first adaptation required for a mammal to make use of grass as a food source is the ability to digest it. The oreodonts (Fig. 12) and camels (Fig. 14) were the first to evolve ruminant digestion, still the most efficient
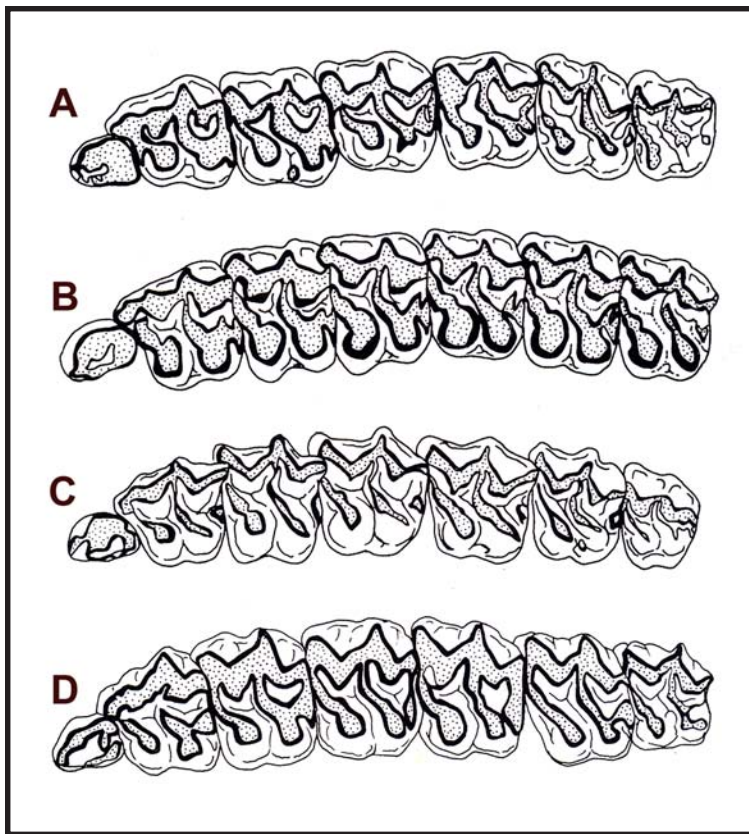
Fig. 18: Left superior cheek dentitions of chalicomorph equids, occlusal view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. A, European *Anchitherium,* after Osborn. B, *Kalobatippus* after Osborn. C, *Hypohippus* (nearly unworn condition), after Osborn. D, *Megahippus* after Osborn. Note the sub-hypsodont, lophodont structure and the presence of a connection between metaloph and ectoloph. With wear, a posterior fossette -- an enamel-rimmed lake -- forms on many teeth.

means by which mammals can extract energy from grass. By contrast, horses possess a caecal digestion. Despite the co-adaptation of horses with particular gut flora and fauna which are also necessary for grass digestion in ruminants, and despite considerable expansion of the equid caecum, horses have an essentially primitive digestive system which remains inefficient compared to that of ruminants.

After the acquisition of a semi-ruminant digestion by species in the oreodont and camel families, the next evolutionary development was of teeth suited to the efficient mastication of grass. Because blades of grass contain abundant tiny spicules of biogenic silica, and are also often coated with environmental grit, chewing grass quickly wears out low-crowned bunodont teeth (Fig. 15). The lifespan of an individual in nature is limited by the length of time its teeth remain sound and useful. To increase this span of time in spite of an abrasive diet, the teeth of all grazing mammals possess one or more of the following structural features:

   1) High crowns — the teeth are tall from root to crown ("hypsodonty" = high-crowned teeth; "hypselophodonty" = ever-growing teeth)(see Fig. 35 for insight as to development of both hypsodonty and lophodonty in equid teeth);

   2) Increased number of cusps;

   3) Interconnection of the cusps to produce a more complex pattern of enamel exposed on the tooth crown (Figs. 9, 35);

   4) Alternation on the crown of bands of materials of differentdegreesof hardness, to produce differential wear and thus to develop self-sharpening crests for the comminution of long fibers (Figs. 9, 35);
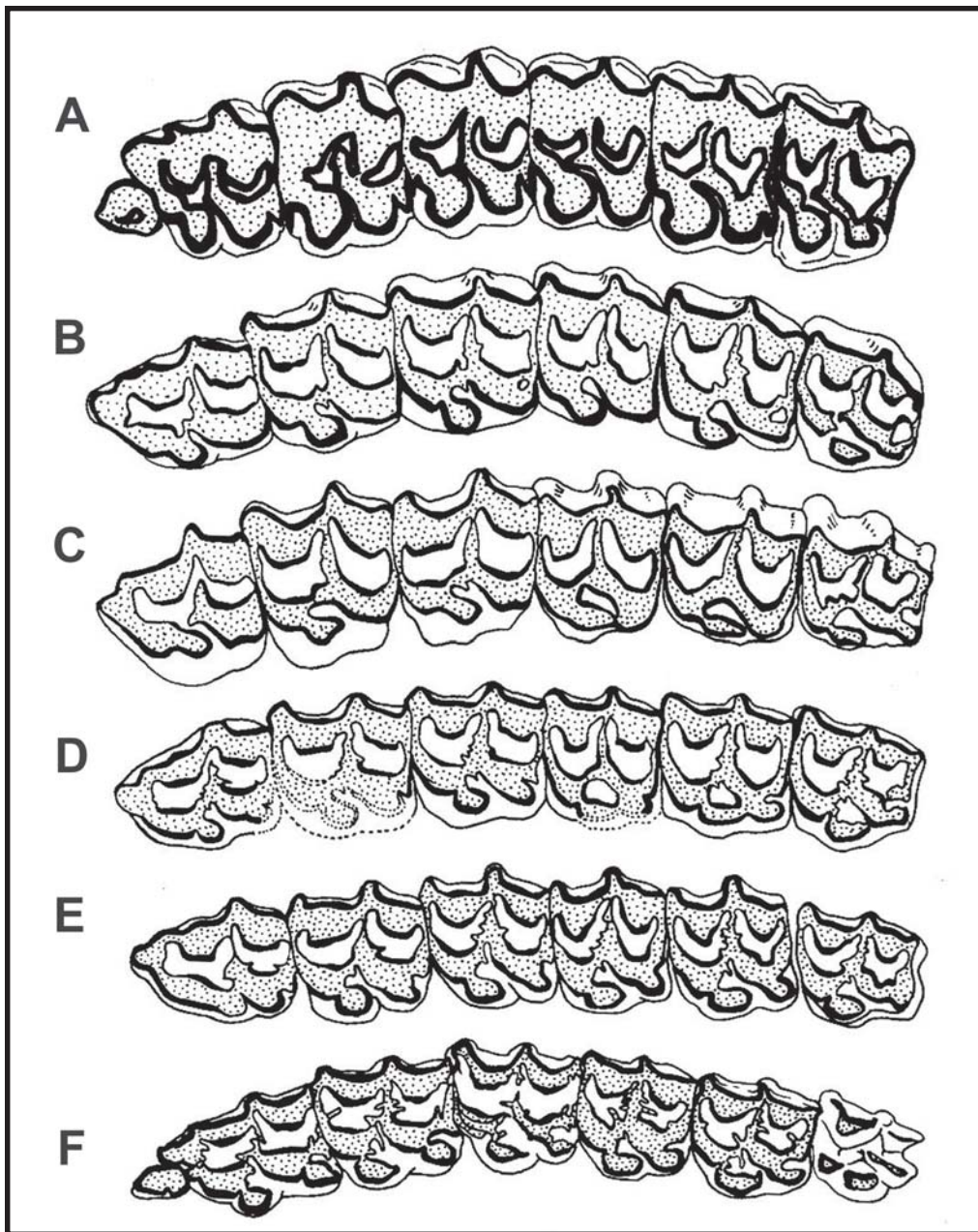
Fig. 19: Left superior cheek dentitions of grazing equids of the protohippine clade, occlusal view. These forms (A-E) usually possess large fossettes, relatively unplicated enamel, and connected protocones. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. Cementum is present on these teeth, and is shown in white surrounding the exterior enamel and filling or partially filling the fossettes. A, *Parahippus*, after Osborn. B, *Protohippus* after Osborn (this specimen called "Merychippus" by Osborn). C, *Protohippus,* after Osborn. D, *Pliohippus* after Osborn. E, *Onohippidium* after Hoffstetter. F, *Dinohippus* after Osborn. Both an anterior and a posterior fossette are present in grazing equids because the crochet of the metaloph has expanded anteriorly to become confluent with the protoloph. This is seen clearly in A. Note the fully hypsodont, lophodont structure.
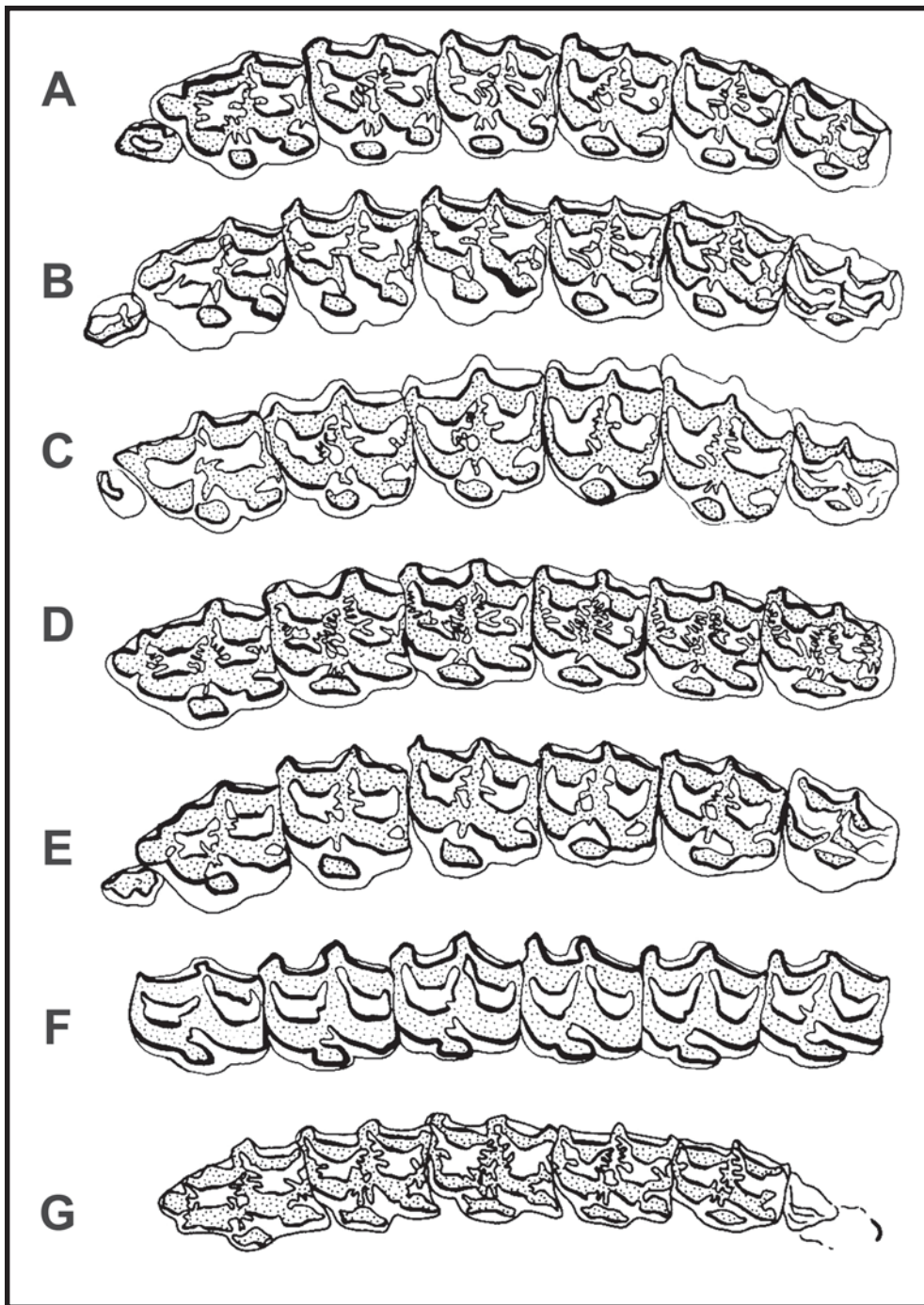
Fig 20: Left superior cheek dentitions of grazing equids of the hipparionine clade, occlusal view. These forms (all but F) usually possess highly plicated enamel and disconnected protocones. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. Cementum is present on these teeth, and is shown in white surrounding the exterior enamel and filling or partially filling the fossettes. A, *Hipparion* after Osborn (this specimen called "Merychippus" by him). B, European *Hipparion* after MacFadden. C, *Nannippus* after Osborn. D, *Cormohipparion* after Skinner and MacFadden. E, *Pseudhipparion* after Webb and Hulbert. F, *Astrohippus* after Matthew and Stirton. G, *Neohipparion* after Bennett. Note the deep hypoconal groove (hcg) and strong style development of most forms. Protocone may connect "backwards" (to metaloph) in *Pseudhipparion*.

5) Increased size of individual grinders;

6) Formation of the grinders into a uniform series or "battery" (Figs. 16-20 and 23-25).

Changes in tooth structure, especially the acquisition of hypsodont or hypselodont teeth, require concomitant changes in skull morphology in order to accommodate the tall teeth. In all hypsodont mammals, the rostrum above and the jaws below become deeper as the teeth become longer. Horses in particular have tended to lengthen their battery of high-crowned grinders; as the tooth row became longer, so also did the rostrum and jaws. The forward displacement of the rostrum also prevented the roots of the most posterior molar from impinging upon the orbit (Figs. 26-29).

STRUCTURAL ADAPTATIONS NECESSARY FOR
FLEEING PREDATORS IN OPEN ENVIRONMENTS

The first postcranial skeletal component to undergo adaptive change from a browsing to a grazing mode of life was the vertebral column (Slijper, 1946). Morphological changes in the shape of the equid occiput, ear region, and basicranium are the direct result of modifications in the length and shape of the neck vertebrae. Increase in neck length was related to the ability of the chalicomorph browser to stretch its snout upward, and to the ability of the grazer to put its nose to the ground. Changes in articular shape, and thus movement capability, affected all axial skeletal components. These changes, which produced a spine in grazers much more rigid (Getty, 1975) than in browsers, were related to the necessity for rapid escape along a straight trajectory. In all equids living before the end of the Oligocene Epoch, escape from predators had been via a rabbit-like series of dodges, highly adaptive when the organism fled through undergrowth, but much less effective in a grassland setting.

Telescoping of distal limb elements and simplification of limb construction put the final touch to the equid commitment to the lifestyle of a grassland ungulate (Ewart, 1894; Matthew, 1926; Simpson, 1951). The fact that size increase is an inconsistent trend within the Equidae has already been mentioned, but needs to be emphasized again in the context of limb length. *Equid limbs did not become steadily longer through time.* Relative to proximal limb elements, the distal limb elements of scansorial browsers lengthened very little from the Eocene through the middle Miocene, when browsing equids became extinct. *Mesohippus* is about twice as tall as Eohippus, but its "cannon bones" are no more than twice as long. In short, in skeletal morphology, *Mesohippus* and *Miohippus* are little more than scaled-up versions of their ancestor *Hyracotherium.* (In chalicomorph browsers, body size increased markedly as did the proportional length of the forelimbs).

After horses aquired the digestive, dental, and axial body structures for life in the open came an explosion in distal limb length (and the development of large body mass in a few lineages). Telescoping of the distal limb elements conferred upon grazing horses the appropriate leverage for long-distance cruising while at the same time depriving them of the jump-start "first gear" capabilities of their scansorial ancestors. At the same time, the grazer carpus and tarsus were strengthened and simplified, and movement upon the distal joints became restricted to narrow planes. Distal limb elements, both bony and muscular, were reduced in number, producing lightweight, streamlined legs.

EVOLUTION IN THE EQUID SKULL

The transition from condylarth ancestors *(Phenacodus)*
and the establishment of the Equidae

The skull in phenacodontid condylarths is sturdy, short, broad, and deep (Fig. 26). The face is bent downward on the basicranium, and because of this, the orbit is located relatively high. The ear region is relatively open and the jaw loosely articulated. On the ventral basicranium, the middle lacerate foramen and the foramen ovale form two separate openings (Kitts, 1954)(Fig. 22). The broad-based occiput slopes back sharply toward the neck. Anteriorly, the optic foramen of the orbit is isolated from other nearby foraminae (MacFadden, 1976)(Fig. 21). In the snout, the nasal opening is high and broad, and, just as in many modern carnivores, the nasal bones do not project far forward. The lower jaws are relatively thin and the left and right jaws come together anteriorly to form a sharp "V".

In the transition to *Hyracotherium* and the establishment of the equid family, the basicranium became shorter, thus compressing the ear region and jaw articulation. The jaw articulation no longer permitted much fore-aft movement, and side-to-side chewing movement has since been characteristic of the Equidae (Kitts, 1956, 1957; Radinsky, 1966).

In the basicranium, the foramen ovale and middle lacerate foraminae are confluent (Kitts, 1954, 1956; Edinger and Kitts, 1954; MacFadden, 1976)(Fig.7). The position of the optic foramen within the orbit is lower and more posterior than in phenacodontids (Edinger, 1948; Simpson, 1952; Savage et al., 1966; MacFadden, 1976)(Fig. 8).

The rostrum in *Hyracotherium* is shallower and slightly longer than in *Phenacodus.* The snout in browsing equids is bent down on the basicranium much less than in phenacodontid co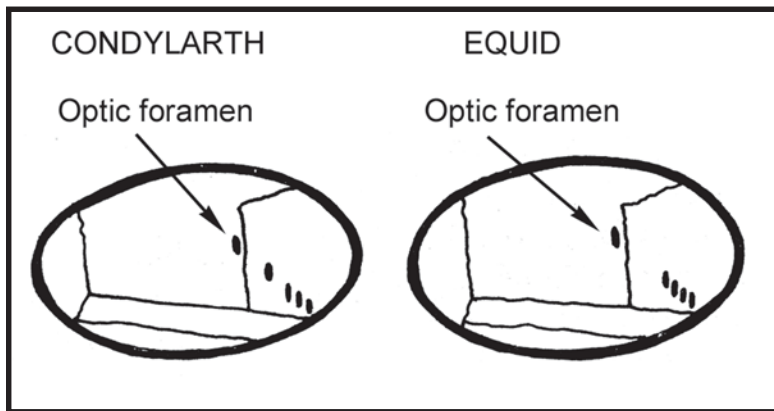ndylarths, and the equid orbit is therefore located lower on the face. In the scansorial browsing equids, including *Hyracotherium, Orohippus, Mesohippus* and *Miohippus*, the nasal bones are relatively long, typically extending as far forward as the central incisors. In the first three of these genera, the nasal notch does not reach as far back as P2/ (Figs. 26, 30). The chalicomorph browsers were the first to modify this nasal conformation.

The lower jaw in *Hyracotherium* is sturdier and deeper throughout than that of phenacodontids, and anteriorly the root area for lower incisors is more robust. The left and right jawbones do not meet in a "V" but flare out to form a spoon-shaped region shaped to accommodate broad, shovel-shaped lower incisors (Simpson, 1951). In side view, the anterior third of the jaw is bent upward, ensuring that the upper and lower incisors meet squarely to form "nippers." Posteriorly, the areas of the jaw for the attachment of the pterygoid and masseteric chewing muscles are larger than in phenacodontid condylarths, while that for the temporalis muscle is smaller (Radinsky, 1966; Smith and Savage, 1959)(Fig. 13).

Fig. 21: Configuration of the orbital foraminae in Equids vs. condylarths. The heavy oval represents the orbit of the skull (after Kitts, 1954).

Shortening of the basicranium in *Hyracotherium* also changed the orientation of the occipital plate from back-sloping to forward-sloping. The narrow occiput in browsing equids is surmounted by a strong lambdoidal crest, which provides attachment for the anterior neck musculature. The neural crest of the axis vertebra and the "wings" of the atlas are also very large in *Hyracotherium* and *Orohippus.* This morphology of the upper neck and occipital region indicates that backward-directed, rooting movements of the snout were an important adaptation in these browsers (Martin and Bennett, 1977).
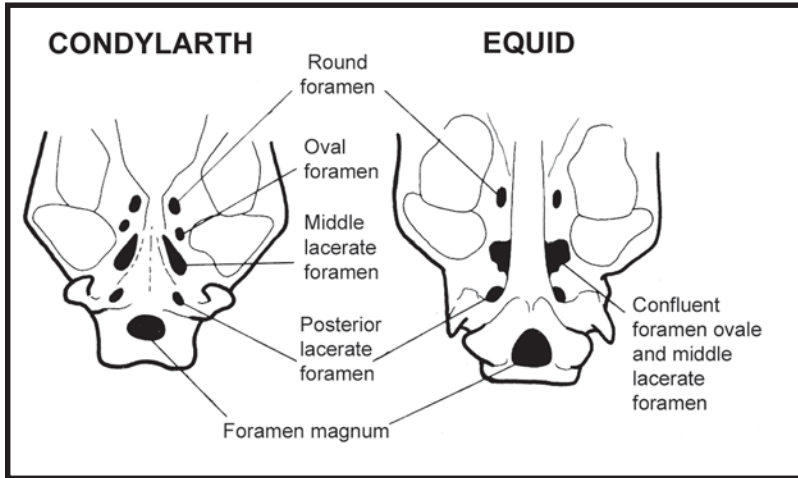
Fig. 22: Basicranium in condylarths vs. Equids

The skull in chalicomorph browsers

The scansorial browser lineage gave rise during the Eocene in Europe (Deperet, 1917; Filhol, 1888; Remy, 1965, 1972a; Savage et al., 1965) and during the Oligocene in North America (Stirton, 1940; Merriam, 1913; McGrew, 1971; Osborn, 1918) to chalicomorph browsers. While scansorial browsers remained small and light, some European genera possessing this body morphology are large — one species of *Palaeotherium* stood three feet high at the withers (Simpson, 1951).

Chalicomorph skulls were also larger and longer-snouted than those of their scansorial relatives (Fig. 27). The maxilla bone, which supports the upper dentition, is long and heavy. The lower jaw is longer than in scansorial browsers, and its anterior end is bent upward more, so that the broad, rounded incisors meet squarely. The front of the jaws is broad and spout-like. The tongue in the chalicomorphs was probably longer and more cylindrical in shape than in other equids, similar to that of a giraffe.

The chalicomorph browsers quickly acquired several other skull adaptations which grazing equids achieved later and in lesser degree. The first is vertical enlargement of the occiput, surmounted by a narrow, pointed lambdoidal crest. The atlas and axis vertebrae are long. At the same time, the areas for muscle origin on the atlas and axis vertebrae are smaller than in *Hyracotherium*. This formation of the occipital region hints at upper neck mobility, especially the ability to twist the skull on the neck.

The second adaptation is shortening of the nasal bones and retraction of the nasal notch. In *Palaeotherium*, the tip of the nasals extends forward to the level of the first premolar; the nasal notch is retracted nearly to the orbit. In the North American *Megahippus*, the retractions are more modest, to the level of the canine and third premolar, respectively. In *Hypohippus*, the retractions are slighter still, but are still greater than in any equid except the late grazers such as *Pliohippus* and *Equus* (Figs. 27, 28, 30). We are used to the soft, mobile nostrils and semi-prehensile upper lip of living equines. Retraction of the nasal bones in mammals usually signals the presence of a proboscis, in the development of which a semi-prehensile upper lip is the first stage.

Related to the development of a proboscis is the presence of deep facial pits or fossae. Pits are not present on the long, high expanse of rostrum of *Equus,* but deep fossae are present in the skull of the living tapir lateral to the nasal opening, and on the maxilla in the area above and behind the upper canines. The parallel lips of the fossae provide a condensed area of attachment for the many strong muscles which move the tapir's snout and
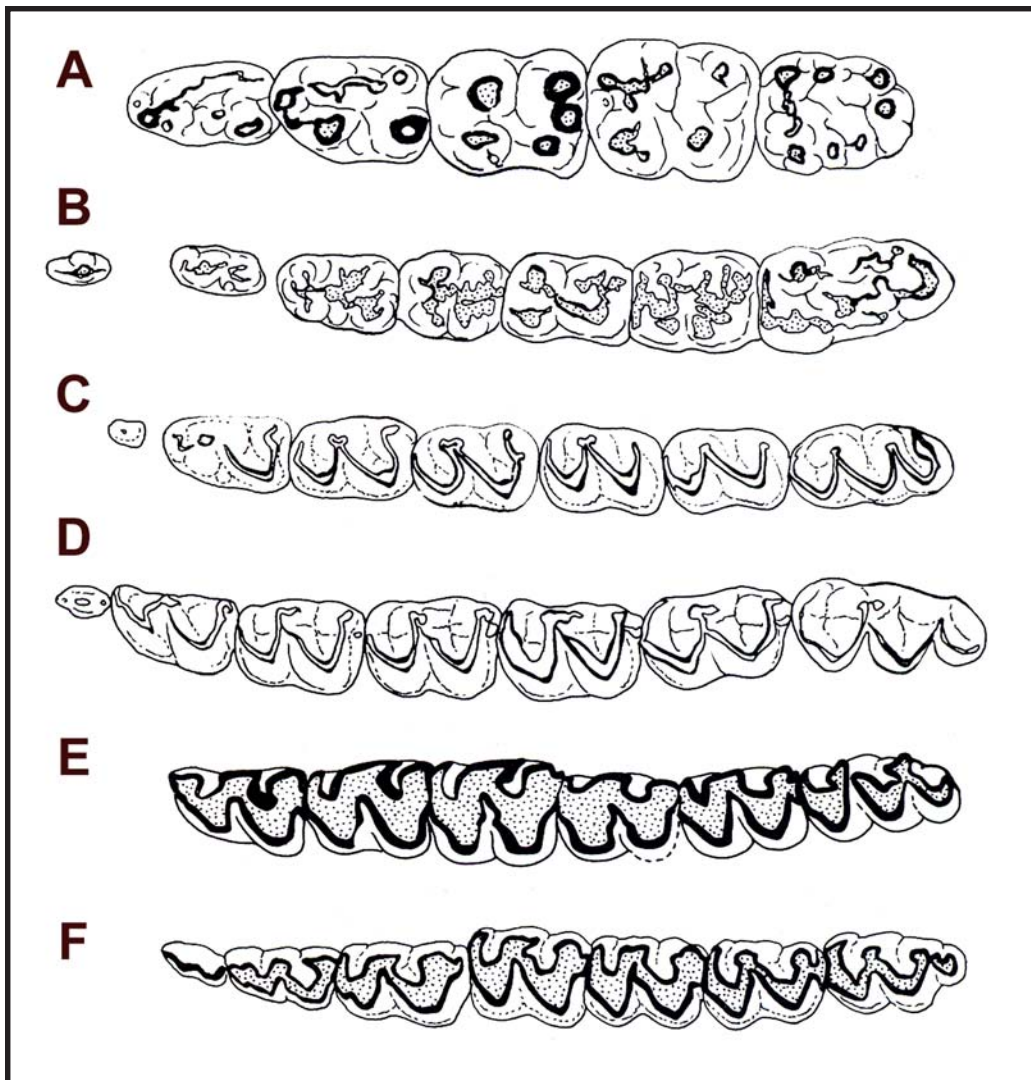
Fig. 23: Left inferior cheek dentitions of a condylarth and scansorial and chalicomorph browsers, occlusal view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. A, *Phenacodus,* a condylarth, after Simpson. B, *Hyracotherium* after Simpson. C, *Mesohippus* after Osborn. D, *Miohippus* after Prothero and Shubin. E, *Kalobatippus* after Osborn. F, *Megahippus* after Osborn. Note bunodont structure in A, buno-lophodont structure in B, lophodont structure in C-F. In scansorial browsers (B-D), metaconid and metastylid are tiny and little separated. In chalicomorph browsers, these two cusps are larger but still little differentiated. The ectoflexid penetrates deeply in all.

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upper lip. Morphologically similar fossae are also present somewhere on the rostrum of every chalicomorph equid. Among scansorial browsers, a deep facial pit first appears in species of *Miohippus* in conjunction with the retraction of the nasal notch to the level of P2/ (Forsten, 1983; Osborn, 1918; Prothero and Shubin, 1989). The chalicomorph browsers trace their origin to these forms of *Miohippus.*

Changes in skull morphology in grazing equids

Many changes in the skull morphology of grazers are related to the development of hypsodonty. Premier among these is the lengthening and deepening of the rostrum. The rostrum in *Parahippus* is "pulled out" from under the orbit like a drawer, so that only the roots of the third molar reside beneath the orbit (Fig. 28). In later forms,
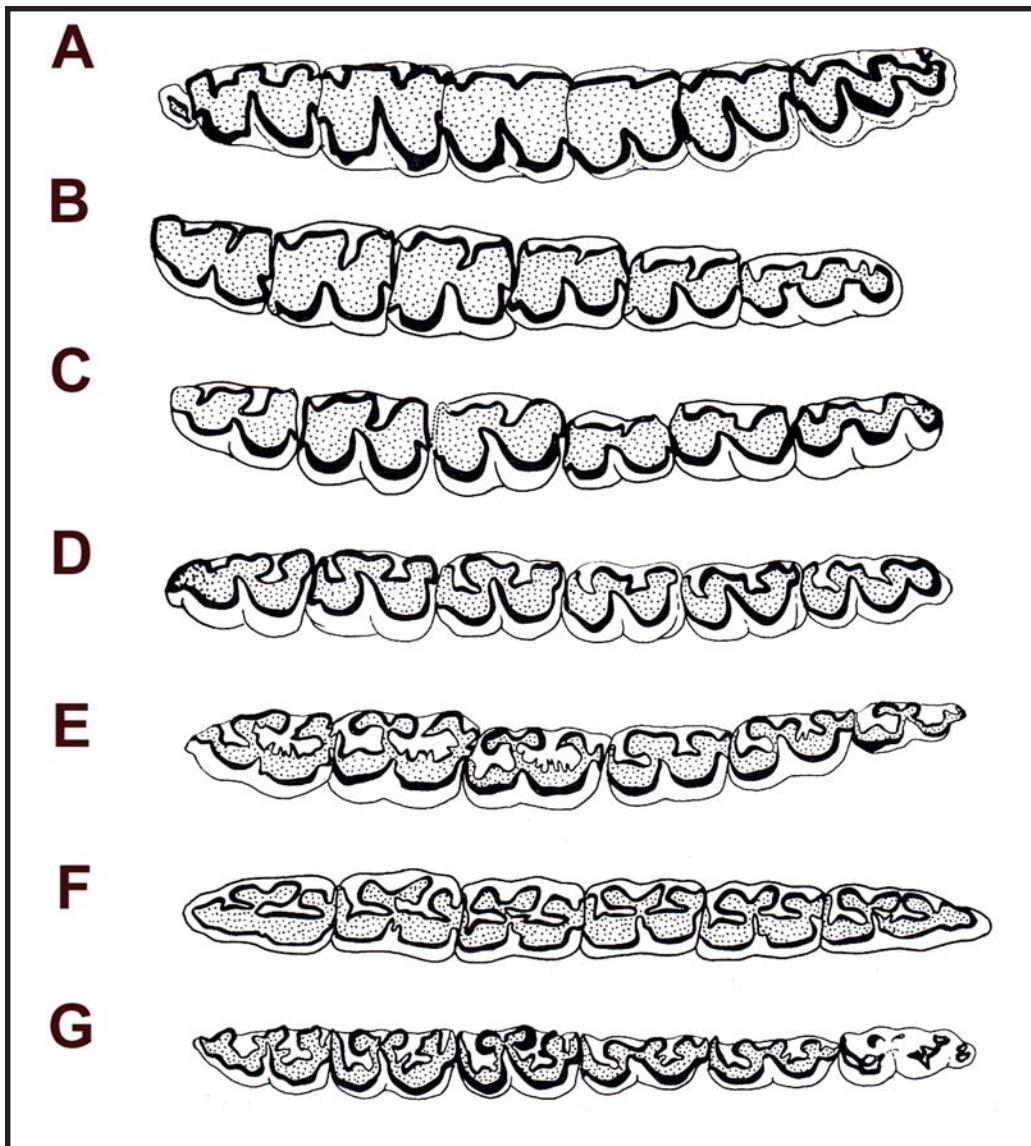
Fig. 24: Left inferior cheek dentitions of grazing equids, occlusal view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. Cementum surrounds the external enamel in these forms. A-F show grazers belonging to the protohippine clade. A, *Parahippus,* after Osborn. B, *Protohippus* after Osborn (called by him "Merychippus"). C, *Pliohippus* after Osborn. D, *Onohippidion* after Hoffstetter. E, *Dinohippus* after Osborn. F, *Equus* after Hoffstetter. G, *Hipparion* after MacFadden; this is a hipparionine for comparison. In all except E, F, and G, the metaconid and metastylid remain relatively small and undifferentiated. The entoconid is likewise simple; plications are at a minimum, there is no pli caballinid, and the ectoflexid penetrates nearly to the external border of the tooth. Inferior cheek teeth of E and F are comparable to those of hipparionines (G).
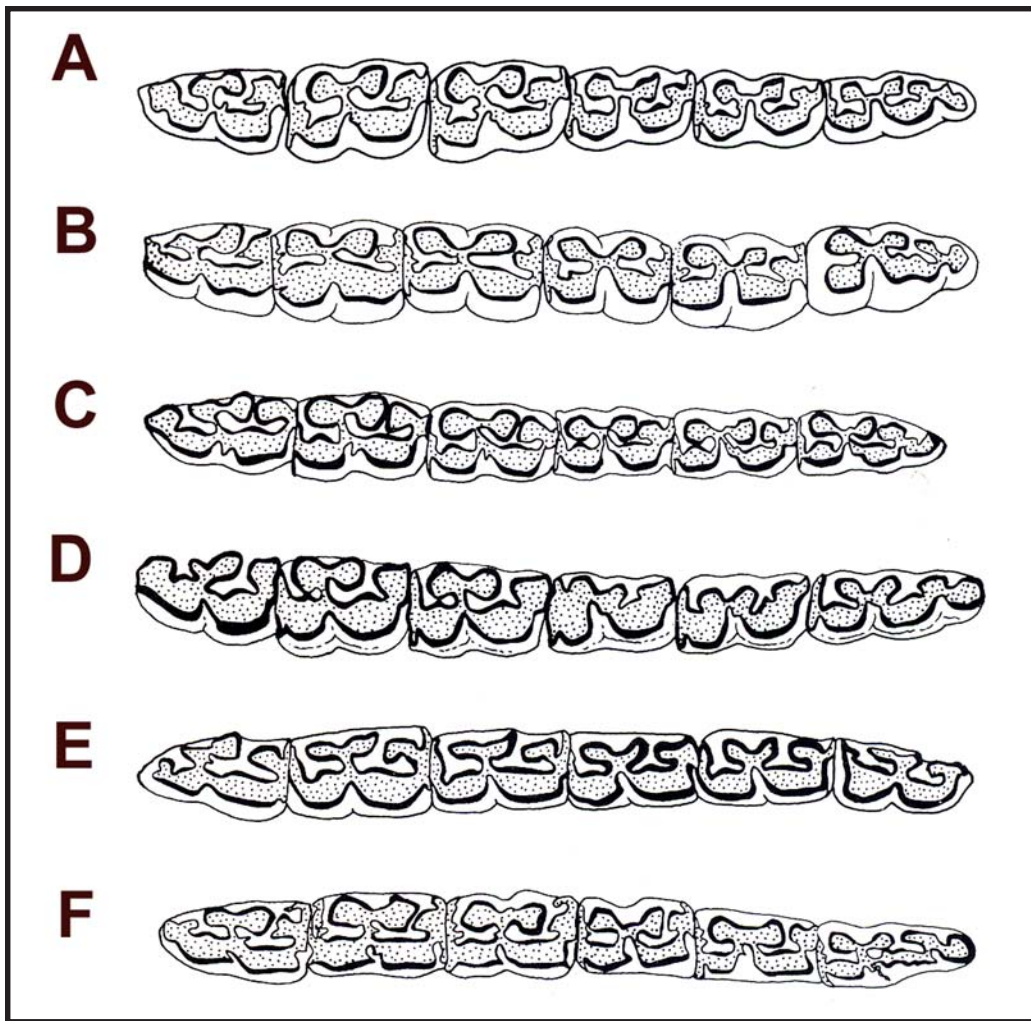
Fig. 25: Left inferior cheek dentitions of grazing equids of the hipparionine clade, occlusal view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. Cementum (white) surrounds the external enamel in these forms. A, *Hipparion* after MacFadden. B, *Nannippus* after MacFadden. C, *Cormohipparion* after Skinner and MacFadden. D, *Pseudhipparion* after Webb and Hulbert. E, *Astrohippus* after Matthew and Stirton. F, *Neohipparion* after Bennett. Anteroposterior attenuation and "squaring up" of the corners of the teeth is characteristic of this clade. The metaconid and metastylid are large and well-differentiated, the entoconid is bipartate and plicated, a protostylid is characteristic as are plications of the enamel.

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even the third molar is displaced anterior to the orbit. At the same time, in order to accommodate tall teeth, both the rostrum and the jaws are deep, producing the characteristically wedge-shaped skull of grazing equids (Figs. 28, 29).

The jaws are deepest behind the tooth battery, especially the region for attachment of the masseter musculature, indicating strengthening and a shift in jaw leverage which displaced the point of greatest crushing force farther forward (Smith and Savage, 1959). All grazing equids possess a postorbital bar. The development of this rear orbital buttress is likewise related to a forward shift and increase in bulk of the temporal musculature (Figs. 30 - 32).

Grazers once again lengthened the basicranium, reversing the trend in scansorial browsers. However, they kept the ancestral straight alignment of rostrum and basicranium; in some late forms, the face is even bent *upward* on the basicranium, an adaptation which raises the orbits relative to the plane of the forehead. Lengthening of the basicranium opened the temporal region and made the occiput more vertical, but did not open the jaw articulation as in chalicomorphs; it remained in grazers a precisely-articulated mechanism for lateral mastication. These changes produced a skull in which there is an unusually large amount of space between the back of the jaw joint and the front of the auditory bulla (Bennett, 1980).

Deep retraction of the nasal notch never developed in some grazer lineages, notably *Pseudhipparion* and *Neohipparion*. However, in some *Hipparion* species and in *Pliohippus*, the notches are typically even deeper than in North American chalicomorph browsers. Predictably these species, like the chalicomorphs, have well-developed facial fossae.

EVOLUTION OF THE EQUID DENTITION

The transition from condylarth ancestors *(Phenacodus)* and the establishment of the Equidae:

Phenacodus possessed small, prognathous, subconical incisors; as in many carnivores, the lower incisors are particularly small. Also as in a carnivore, the canines are robust, conical stabbers, while the anterior premolars are narrow and triangular, suitable for slicing meat or fruit. The posterior premolars and the molars in the upper jaw were formed like the teeth of a pig or a bear: broad and bearing many separate, conical cusps, good for crushing a varied diet of meat, insects, fruit, or vegetable material (Figs. 16, 23). The cheek teeth of the lower jaw are narrower than those above, but their crowns are formed in such a way that their cusps interlock precisely with those of the upper teeth when the jaws closed. *Phenacodus* must have looked much like an opossum when it chewed; the teeth worked best when the jaws simply opened and shut, but both back-and-forth and side-to-side movements were also possible. No diastema was present; the teeth formed a uniform row from incisors to molars (Matthew, 1897, 1937; Radinsky, 1966).

The dentition of *Hyracotherium* indicates a dietary shift away from insectivory or carnivory and toward specialization on a leafy diet. Leaves are a tougher and more fibrous fare than meat or fruit, and equid teeth are structured for efficient nipping, chopping, and crushing. In Perissodactyls, food is frequently plucked or torn off with the lips as much as nipped off by means of the incisors.Characteristically, food is manipulated with the tongue. The tongue curls around the food and helps to orient the fibers until they are parallel. Then the tongue bearing the food is withdrawn to place the fibers along the cheek tooth battery, where side-to-side mastication acts to chop and crush the herbage (Baker and Easley, 1999).

The incisors of *Hyracotherium,* especially the lower ones, are larger and stouter than those of phenacodontids. The incisors are aligned close together to form a battery. They are shovel-shaped, with a flat terminus for nipping, not pointed as in condylarths and carnivores.

Sexual dimorphism in canine size is also characteristic of equids. In supposed male *Hyracotherium* and *Orohippus,* the superior canine is little shorter than in *Phenacodus,* but it is more slender and is flattened from side to side. In supposed females of these genera, the superior canine is smaller than in males. Large, sharp superior canines are frequently found in males of extant solitary, forest-dwelling browsers; they indicate fierce and bloody seasonal competition between males for mates, and the absence of the social adaptations for herding (Vaughan, 1972).
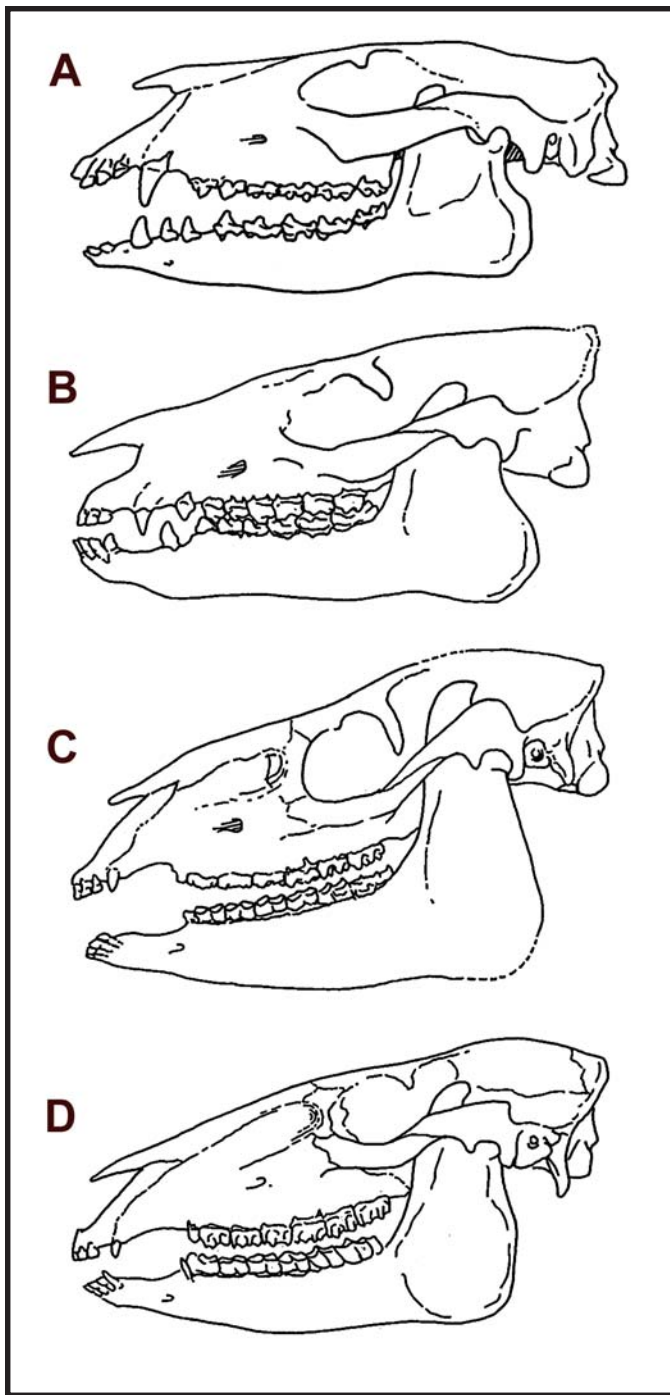
Fig. 26: Skulls of browsing equids, left lateral view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. A, *Phenacodus* after Scott. B, *Hyracotherium* after material housed in the U.S.N.M. C, *Mesohippus* after Osborn. D, *Miohippus* after Prothero and Shubin. Note the small incisors, shallow muzzle and jaw, relatively slight retraction of nasal notch, and relatively forward position of the orbit in these forms.

The canine of the lower jaw in *Hyracotherium* is, however, small and is pushed far forward to abut the incisors. This and the condensation of the incisors produces a long diastema or toothless space in the lower jaw between the canine and the first premolar (Figs. 23). In the upper jaw, two short diastemata appear, one between the last incisor and the canine, and the other between the canine and first premolar (Granger, 1908; Kitts, 1956; Radinsky, 1966)(Fig. 16).

While the lower canine in the scansorial browsers functions as an extra lower incisor, the first lower premolar is enlarged and conical. In *Hyracotherium, Orohippus,* and *Haplohippus* this tooth mimics a canine (Stirton, 1940; McGrew, 1971). The first upper premolar is also caniniform in these genera. In *Epihippus,* the first premolars are reduced in size and are single-rooted (Cooper, 1932; Granger, 1908). This simplification of the first premolar teeth, achieved before the end of the Eocene, carries through the rest of the evolution of the family. In grazing equids, these unicuspid teeth are often reduced to tiny pegs (the so-called "wolf teeth" of Baker and Easley, 1999).

The two posterior premolars and the three molars of each jaw quadrant form the cheek tooth battery proper in browsers. The cusps on all these teeth are more aligned than in *Phenacodus*, permitting efficient side-to-side mastication. They are also less separate; the outer three cusps of each superior tooth are united by enamel ridges which form the outer margin of each upper cheek tooth into a blade called the ectoloph (Fig. 9). Another ridge (the protoloph) connects the protocone to the ectoloph, and a shorter third ridge (the metaloph) parallels the protoloph. These three ridges form the shape of the Greek letter "PI." All subsequent dental changes in equids are built upon this basic pattern (Fortelius, 1985; Stirton, 1941).

Both the posterior premolars and the molars of the upper jaw in equids are broader and squarer than in most phenacodontid condylarths. The premolars of the lower jaw, however, retain a narrow, pointed

shape. The inferior molars in *Hyracotherium* are much narrower than in *Phenacodus* (Fig. 23). The cusps of the lower molars, like those of the upper ones, are aligned to permit efficient side-to-side chewing (Radinsky, 1966).

Further dental evolution
within the scansorial browser lineage

While the design of skull and skeleton changed very little from the Eocene until the extinction of this lineage at the end of the Oligocene, changes in tooth construction continued and indicated still further commitment to a wholly herbivorous diet.

In this lineage, the upper incisors acquired a second, partial, internal enamel band, making them more durable. The space between the enamel bands was filled with softer dentine; within the internal circlet is a hollow space, the "dental mark" of horse dealers.

The premolars in the scansorial browser lineage gradually became "squared up" or "molarized" (Figs. 23 -25). This was accomplished in equids through enlargement of the interior pair of cusps (the protocone and the hypocone, Fig. 9) on each upper cheek tooth (Butler, 1952). In *Hyracotherium*, the two anterior premolars of the upper jaw are formed as narrow cutting blades, much as in a carnivore. The occlusal surface of the two posterior premolars is triangular in shape. In *Orohippus*, the second upper premolar is subtriangular, while the fourth is four-cusped and square. In *Epihippus*, the second premolar is subquadrate, and both the third and fourth premolars are molarized. In *Mesohippus*, all the premolars are
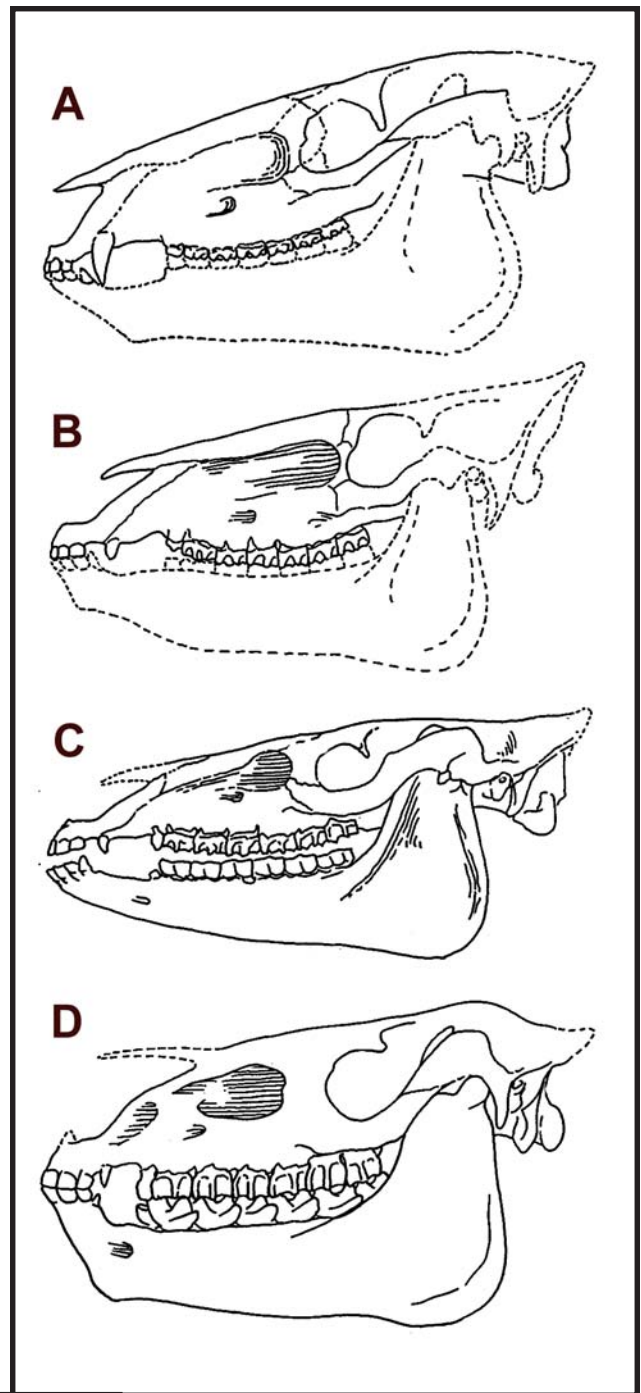

Fig. 27: Skulls of chalicomorph equids, right lateral view. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. A, *Anchitherium,* after Osborn (who called this specimen "Miohippus"). B, *Kalobatippus,* after Osborn. C, *Hypohippus,* after Osborn. D, *Megahippus* after material housed in the U.S.N.M. Note the relatively deep nasal retraction, deep facial fossae, tendency for large canines, and upturned lower incisors and jaw symphysis.

molarized except the first, which throughout equid evolution remains a unicuspid tooth.

Through time in this lineage, the height and width of all three lophs of the "PI" became greater. In *Hyracotherium* three tiny cusps are present along the outer margin of the upper cheek teeth which alternate with the paracone and metacone. In *Orohippus* these cusps are little larger, but in *Epihippus* they are tall and closely appressed to the ectoloph, forming rodlike buttresses called styles. The addition of styles forms the ectoloph into a "W" shape, thus folding more hard enamel into the same small area (Kitts, 1957; Radinsky, 1966)(Fig. 16).

The hypostyle, a tiny cusplet in *Orohippus,* is in *Mesohippus* and *Miohippus* large and connected to the ectoloph by a ridge of enamel, forming a crest along the rear margin of the tooth which parallels the protoloph and metaloph in front of it (Prothero and Shubin, 1989). However, in these forms, a connection between the upper end of the metaloph and the ectoloph is never achieved. A posterior fossette is therefore never present in these forms. This feature differentiates the teeth of scansorial browsers from those of the chalicomorph browsers and the grazers.

The most important dental development in the scansorial browsers first appears in *Mesohippus* and is further developed in *Miohippus:* the crochet, a widening in the upper third of the metaloph produced by enlargement of the metaconule (Figs. 9, 17, 19). In some *Miohippus,* the crochet meets and unites with the middle of the protoloph, forming an enamel-lined ring (infundibulum or fossette) in the anterior half of the tooth. This morphology was inherited by *Parahippus,* and widening and
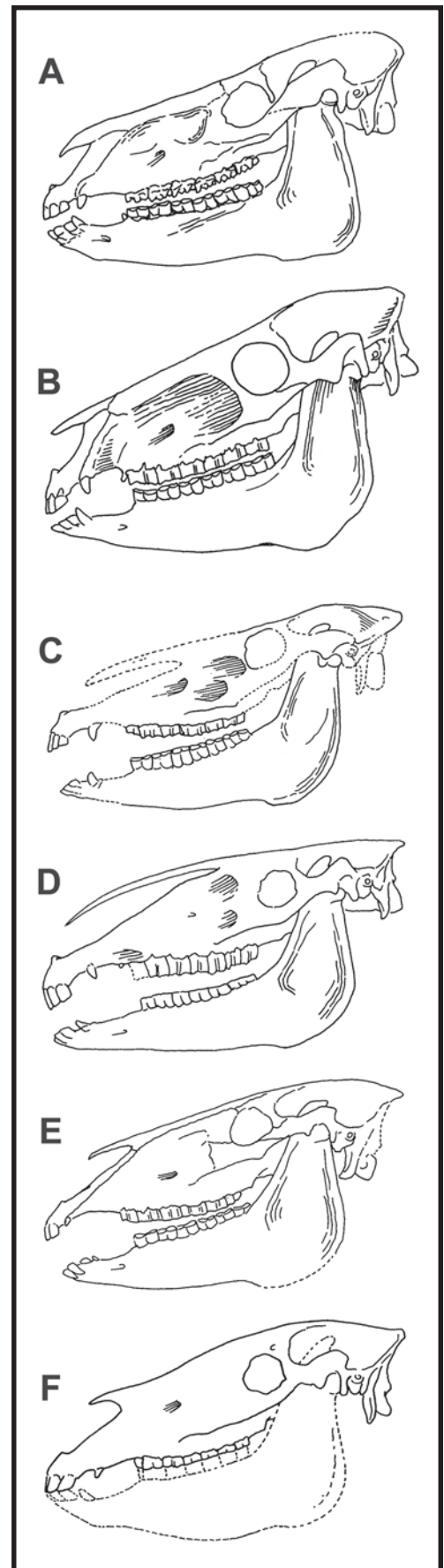

Fig. 28: Skulls of grazing equids belonging to the protohippine clade, right lateral view. When a facial fossa is present (B-D), it is large, deep and bipartate and incorporates the facial foramen. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. A, *Parahippus* after Osborn. B, *Protohippus* after Osborn (who calls this specimen "Merychippus"). C, *Pliohippus,* corrected after Osborn. D, *Hippidium* after Hoffstetter. E, *Dinohippus* after Osborn. F, *Equus* after Hoffstetter. The facial fossa is shallow or absent in E and F. All forms show relatively deep retraction of the nasal notch, presence of a postorbital bar, deep jaw, long face, orbit positioned behind cheek tooth rows.

elaboration of the crochet area is characteristic of its descendants, the grazing equids (Figs. 19, 20).

The dentition in chalicomorph browsers

These forms early specialized in eating the drier, tougher vegetation of the forest understory and shrubs, rather than the more succulent plants and dropped fruits of the forest floor eaten by the scansorial equids. The paleothere *Plagiolophus* of the European Eocene possessed moderately high-crowned, broad, curved, strongly ridged, completely cement-covered teeth — adaptations like those seen in rhinoceroses for eating tough vegetation, and not to be achieved for another forty million years by the descendants of scansorial browsers, the grazing equids (Remy, 1972a,b). In all chalicomorph equids, the upper teeth are broad and the protocone and hypocone are bulbous (Fig. 18).

The browser *Miohippus* was the first equid in which a connection between the metaloph and the ectoloph was established (Cope 1878, 1879; Osborn, 1918; Prothero and Shubin, 1989)(Fig. 17, 19). A large hypoloph is also present in this form and its descendants, *Anchitherium and Kalobatippus* (Fig. 18). With very little wear, these three lophs unite to form an enamel-rimmed fossette in the posterior half of each upper cheek tooth. The crochet, however, does not enlarge in North American chalicomorph browsers, and thus an anterior fossette is never present.
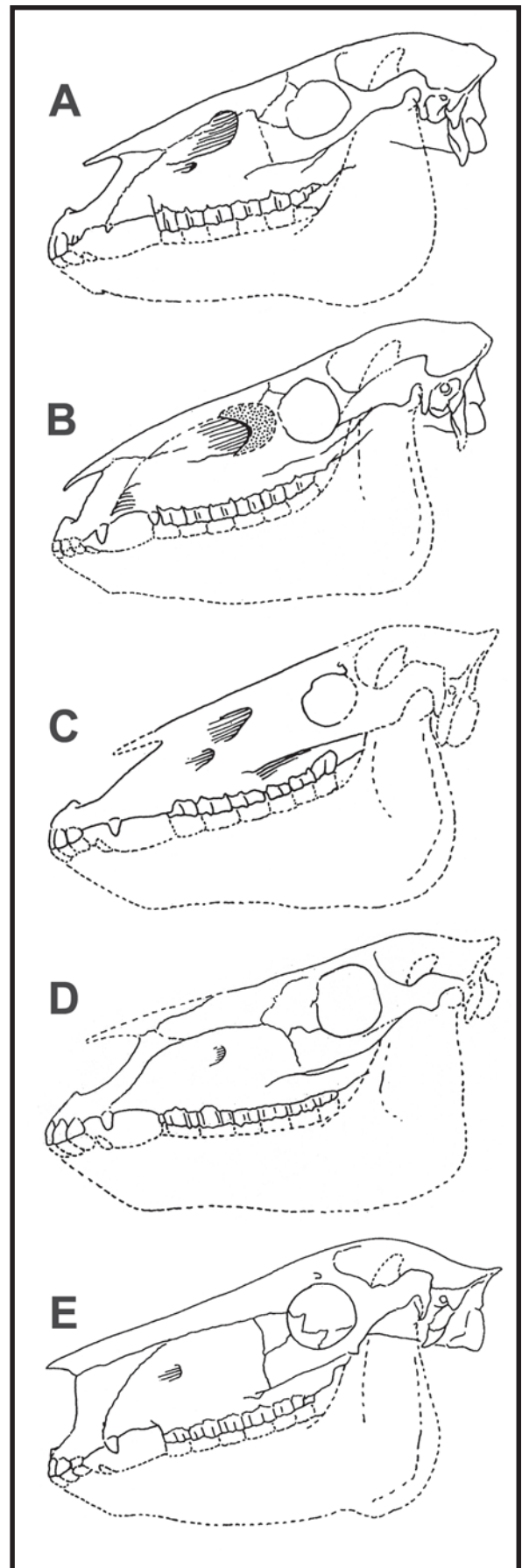

Fig. 29: Skulls of grazing equids belonging to the hipparionine clade, right lateral view. When a facial fossa is present (A-C), it is deep and may be pocketed (B) or rimmed, and excludes the facial foramen. All are drawn to approximately equal anteroposterior length to facilitate proportional comparisons. A, *Hipparion* after MacFadden. B, *Cormohipparion* after Skinner and MacFadden. C, *Nannippus* after Osborn. D, *Pseudhipparion* after Webb and Hulbert. E, *Neohipparion* after Bennett.

Hypohippus sp.

Mesohippus bairdi

Hyracotherium sp.

Changes in dental morphology in grazing equids

The shift from eating leaves to eating grass imposed the necessity on *Parahippus* and its descendants of developing high-crowned teeth (Kovacs, 1971). *Parahippus* and the tiny *Archaeohippus,* which dwelled along the forest margin and which were probably still not wholly committed to grazing, were not hypsodont (Gidley, 1906; Peterson, 1907; Webb, 1969). Early hipparionines and protohippines have more definitely high-crowned teeth. The greatest degree of hypsodonty developed in the late Miocene and Pliocene hipparionines *Nannippus* (Johnston, 1938; Matthew and Stirton, 1930) and in the Miocene *Pseudhipparion*; one species of the latter actually developed hypselodont, or incipiently ever-growing cheek teeth, like some rodents (Webb and Hulbert, 1986). This extreme of specialization is found in the most gracile, antelope-like equids, late forms whose paleoecological context indicates that they inhabited dry grasslands.

A cementum covering develops along with hypsodonty, to provide structural support for what would otherwise be a tooth composed of a bundle of tall, parallel cusps and crests — a structure like a cobweb-covered pipe-organ (Fig. 35). The cementum coats the outside surface of the tooth, and fills in between the "pipes" (White, 1959) (Fig. 9).
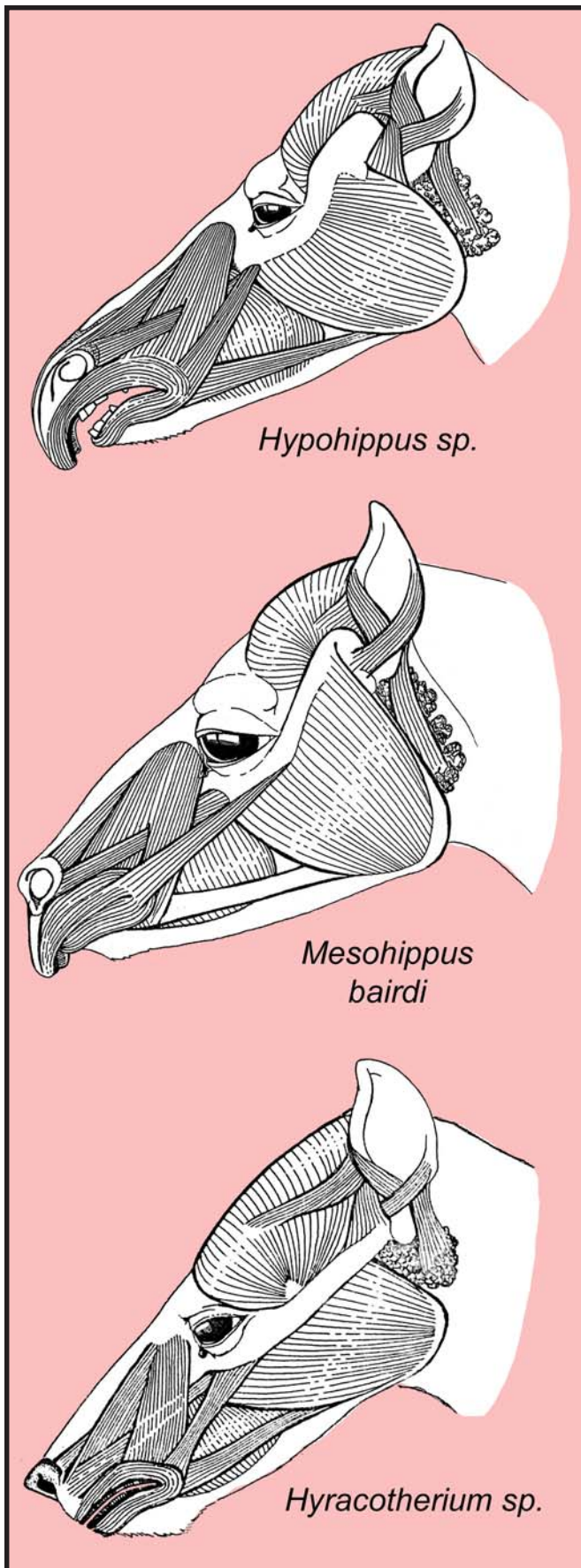
Fig. 30: Restorations by the author of the facial musculature and appearance of the lips and nostrils in *Hyracotherium, Mesohippus,* and *Hypohippus.* Note the rhinarium ("leather" nose) retained by *Hyracotherium;* this is to be expected in animals that have little or no retraction of the nasal notch. By contrast, *Hypohippus* shows great retraction of the nasal notch along with deep facial fossae, which I believe existed to expand the area of attachment for muscles to move an upper lip expanded to form a small, strong, highly prehensile proboscis.
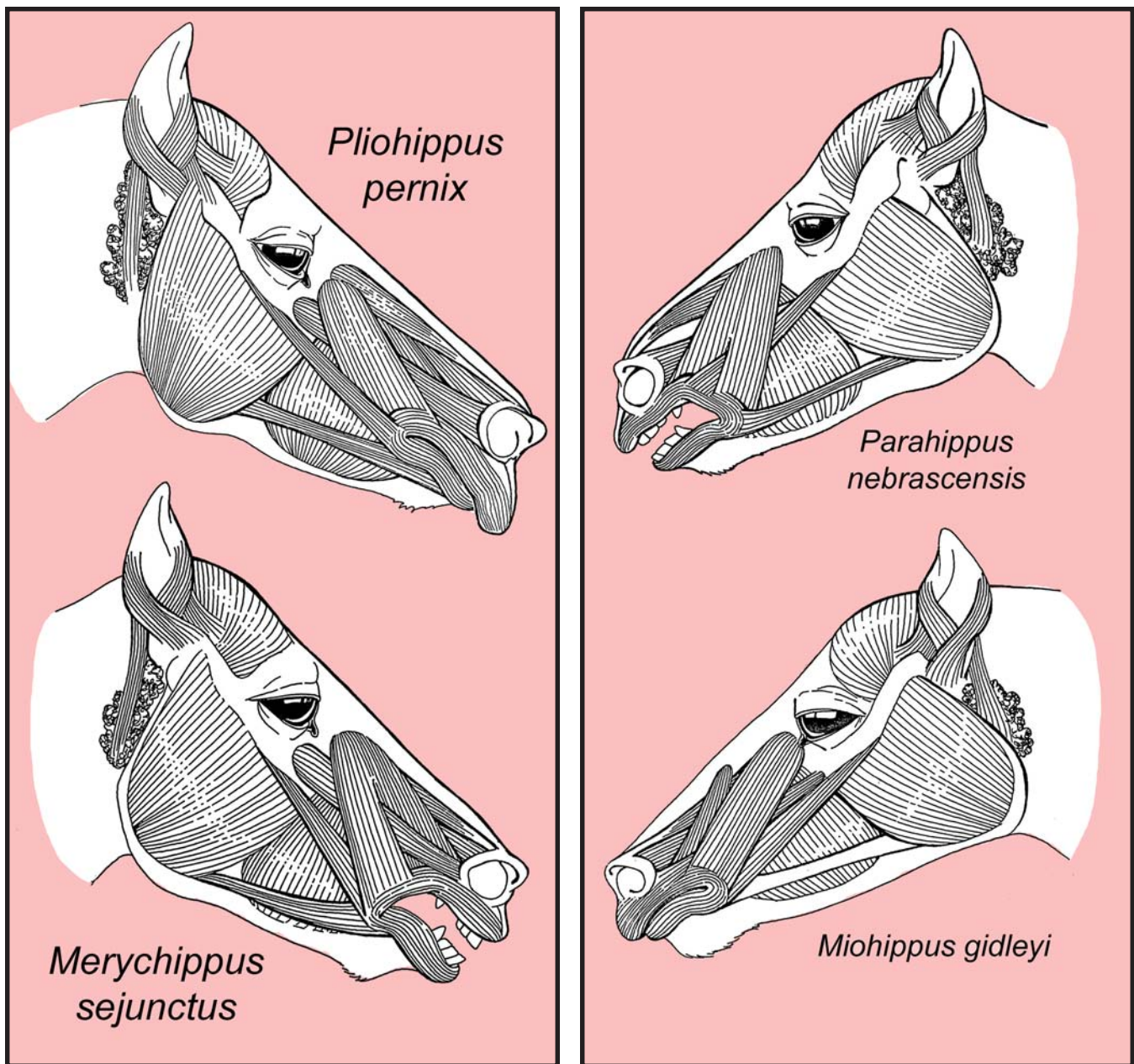
Fig. 31: Reconstructions of the facial musculature of Tertiary equids by the author. Fig. 28 (right): *Miohippus gidleyi* and *Parahippus nebrascensis*; these are equids transitional from the scansorial browsers to the protohippine grazers. Fig. 32 (left): *Merychippus sejunctus* and *Pliohippus pernix*, grazing equids of the protohippine group. Only *Pliohippus* has deep facial fossae, and I have therefore visualized it as having a short, strong, mobile, and prehensile upper lip.

In scansorial browsers, the widest superior tooth is the second molar. In chalicomorph browsers, with different jaw form and leverage and concomitantly greater crushing power, the widest tooth is the fourth premolar. Grazers also shift the point of the widest tooth forward to deal with their tough and fibrous diet; in *Parahippus* it is the first molar, and in later forms it moves to the fourth premolar (Granger, 1908).

Multiplication of the number of parallel enamel bands, to form a tooth composed of alternating bands of enamel, dentine, and cementum, is a feature of grazer dentitions (Figs. 9, 19, 20). This trend affected not only the cheek
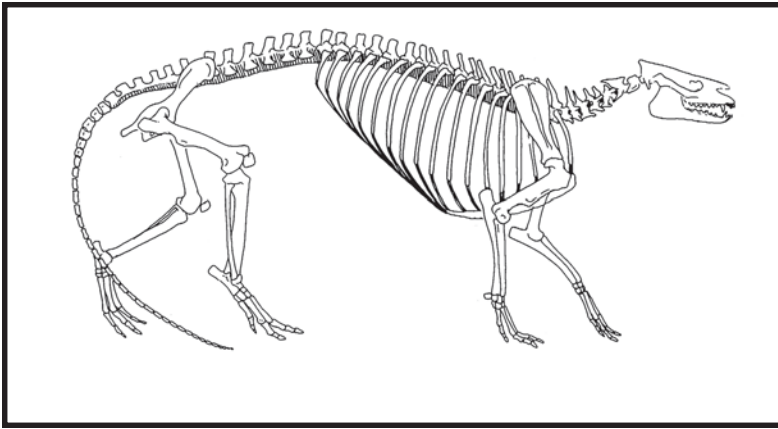
Fig. 33: The skeleton of equid ancestor, the phenacodontid condylarth *Phenacodus* (corrected after Scott, 1913).
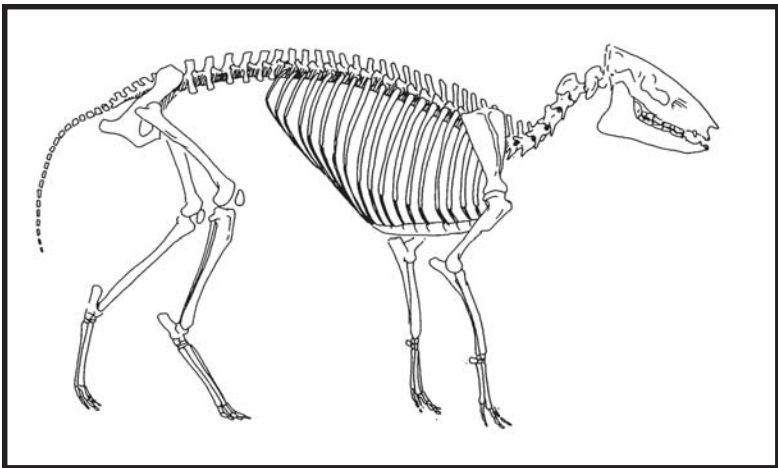

Fig. 34: Skeleton of *Hyracotherium* ("Eohippus")(corrected after a photo of an AMNH mount). By comparing with *Phenacodus,* you can see what a tremendous amount of structural change occurred in the transition from condylarth ancestors to equids.

teeth, but the incisors as well. In the lower incisor teeth of *Parahippus*, a "mark" forms from a partial second band of enamel to match the "mark" already present in its upper incisors. In some later forms, the partial inner enamel bands of the upper and lower incisors coalesce with the outer bands to form a complete circlet in the partially-worn tooth, as in the living *Equus.*

In the cheek teeth, while late scansorial browsers develop an anterior fossette, and chalicomorph browsers develop a posterior one, grazers develop both. A connection is present in *Parahippus* between the metaloph and the ectoloph; at the same time, the crochet is broad and these two connections serve to establish the borders of both an anterior and a posterior fossette (Fig. 19, 20).

Fossettes having been formed, the grazers promptly go on to acquire pleats and wrinkles in their enamel lining, thus packing still more enamel reentrants into the chewing surface of each tooth. Two deep pleats early establish themselves in each fossette; these are present in all grazers (Figs. 19, 20). This is the maximum complexity achieved by most protohippines, in which the upper teeth are characteristically large, square, curving, and not exceedingly hypsodont. In the hipparionine and pseudhipparionine lineages, secondary and even tertiary wrinkling of the pleats is characteristic. A pleat, called the pli caballin, also develops in the lower rim of the crochet and is likewise bifurcated and wrinkled in later forms (Bennett, 1984; Forsten, 1973; Gidley, 1903; MacFadden, 1984, 1985; Skinner and MacFadden, 1977)(Fig. 9). Teeth of forms in these clades are characteristically small or medium-sized, square, straight, and may be very hypsodont.

Another major dental change established with the origin of grazing equids involved a complete overhaul of the morphology of the lower cheek teeth. In scansorial browsers, these have essentially the same form: that of a rounded letter "m". The cusps of the inner wall of the tooth — metaconid, metastylid, and entoconid — remain small (in chalicomorphs the metaconid and metastylid draw widely apart). The ectoflexid, the inner apex of the "m", penetrates all the way to the outer wall of the tooth (Fig. 23 - 25).
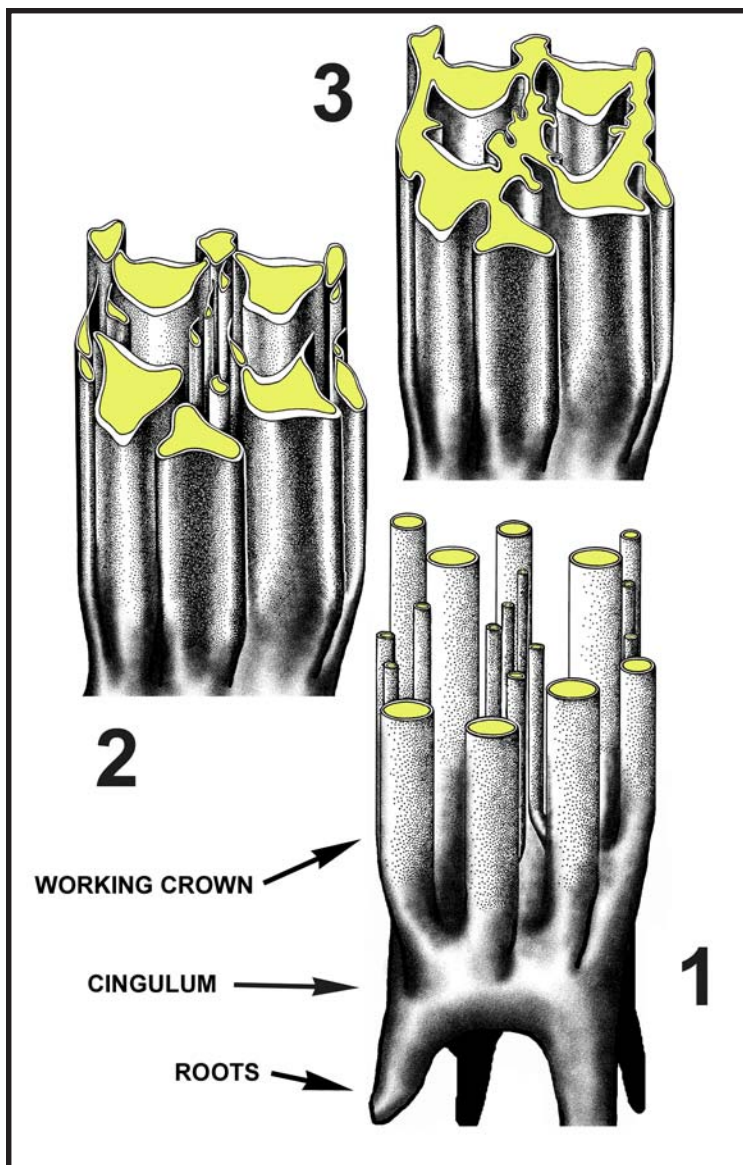
Fig. 35: Here is a gift intended for all students of vertebrate paleontology: a visualization of how the cusps in hypsodont horse teeth became coalesced to form lophs. I want to emphasize that this diagram is dangerous: please DO NOT interpret it as an evolutionary sequence -- this diagram actually shows "morphing" and it is NOT intended to show the actual sequence of structural changes that occurred from scansorial browsing equids with brachydont, bunodont teeth to grazers with hypsodont, lophodont teeth. Rather, what these pictures show is simply what connections between the original cusp positions (represented by the "organpipes" in view 1) there would have to be to produce the tooth of *Equus caballus* (view 3). From this drawing, it is easy to see how more wrinkling of the enamel structure would produce the kind of teeth we see in the hipparionines.

The first step in creating this visualization was to strip the tooth of all cementum; next was to locate the cusps. All that then remained was to "morph" or stretch the cusps (view 2). Wherever cusps got close enough to touch, the enamel coating separating them disintegrated, allowing them to become confluent. Confluency of cusps creates lophs. Enjoy.

In *Parahippus,* the metastylid and entoconid are larger than in any scansorial browser; the lower teeth resemble those of chalicomorph browsers. In early *Hipparion* and *Protohippus*, the metaconid enlarges and the entoconid becomes bipartate and angular. The ectoflexid penetrates almost to the outer margin of the tooth, but is otherwise unelaborated. Few protohippines go beyond this degree of cusp development. They tend to have thick, heavy enamel on the ectoflexid and a heavy coating of cementum (Fig. 19).

Hipparionines possess much more complex inferior cheek teeth. The metaconid and metastylid loops are well-inflated and often widely separated (Skinner and MacFadden, 1977). The entoconid, hypoconulid, and paralophid are large, angular, and elaborated by plications. The thin enamel of the tooth's outer margin is squared at the anterior and posterior corners of the tooth. The ectoflexid in some forms even fails to penetrate to the inner enamel border, isolating the metaconid and metastylid on a stem or "isthmus" (this is very well shown in Fig. 9, but also in Fig. 25).
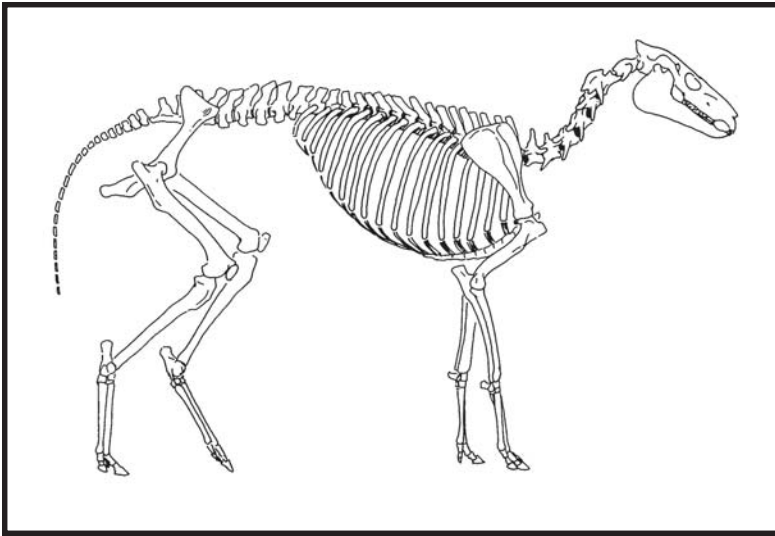
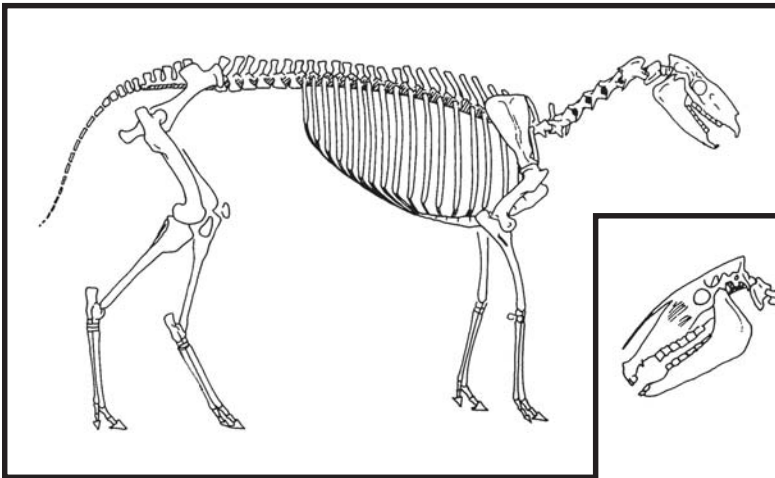Fig. 36: Above: Skeleton of *Mesohippus*, after an AMNH mount.

The superior teeth of hipparionines are smaller, narrower, more hypsodont, straighter, and less heavily covered in cementum than those of protohippines. Styles are more prominent. Species in both these lineages usually show secondary plications of the fossette borders and of the pli caballin. Some hipparionines carry the tendency for great hypsodonty and for plication of the fossette borders to an extreme; most of these were small or even dwarf forms. *Pseudhipparion* is distinguished by possession of a "bridging" protocone which, at least at some levels of tooth wear, connects not only forward to the protoloph but also establishes a rearward connection to the metaloph (Cope,1889; Gidley, 1907; Webb, 1969).

Fig. 37: Above: *Parahippus*, corrected after a USNM mount.
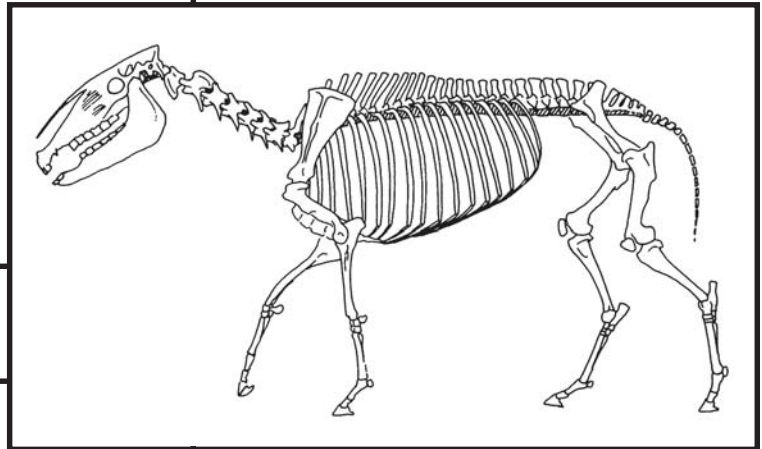
Fig. 39: Above: *Hippidion,* the horse with the "diving board snout", after Hoffstetter. Deep retraction of the nasal notch creates the "diving board".
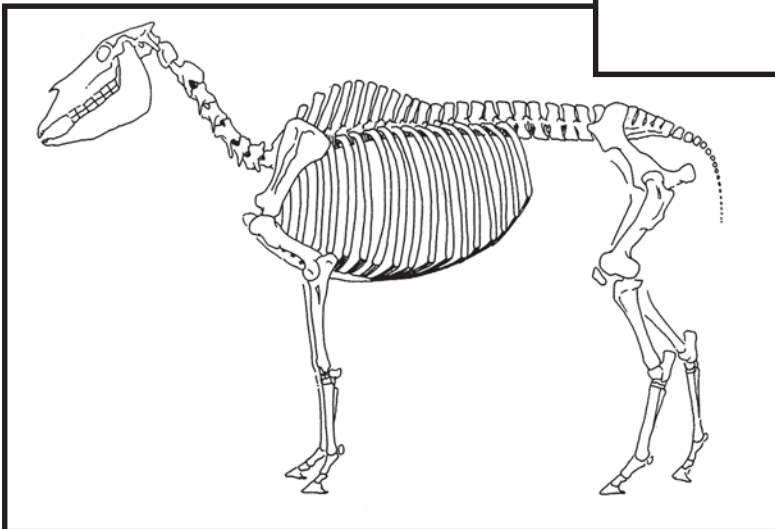
These images allow you to trace changes from the latest and largest of the scansorial browsers, *Mesohippus*, to the first grazer, *Parahippus*. Later grazers are *Equus* and the South American *Hippidion.* All skeletons are reduced to about the same width to make it easy to see their proportions.

Fig. 38: Above: *Equus scotti,* after an AMNH mount.

Fig. 40: Skeleton of an American species of *Hipparion*, after an AMNH mount.

Fig. 41: Skeleton of *Neohipparion,* after after an AMNH mount. These two skeletons represent hipparionine horses.

EVOLUTION OF THE AXIAL SKELETON IN EQUIDS

The story of horse evolution as it is usually presented concerns changes in the skull, teeth, and feet, but the unifying factor has been the horse's back. Trends in the evolution of the axial skeleton in any mammal have not been widely discussed in the literature (Slijper, 1946) and the following brief overview can only provide an introduction to this fascinating area of study. Osteological evidence for the evolution of some important soft tissue structures in equids will also be mentioned.

The transition from condylarth ancestors *(Tetraclaeonodon, Phenacodus)* and the establishment of the Equidae

In all non-ungulates, the axial skeleton has much greater poetntial for flexibility than in ungulates. The lumbar, and to a lesser extent, the thoracic vertebrae of ungulates lose whole classes of movement ability which are present in condylarths and carnivores (Kitts, 1956, 1957).

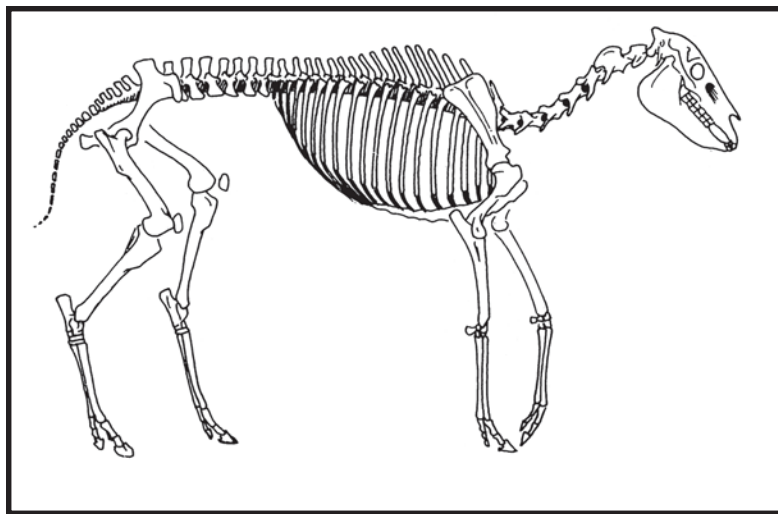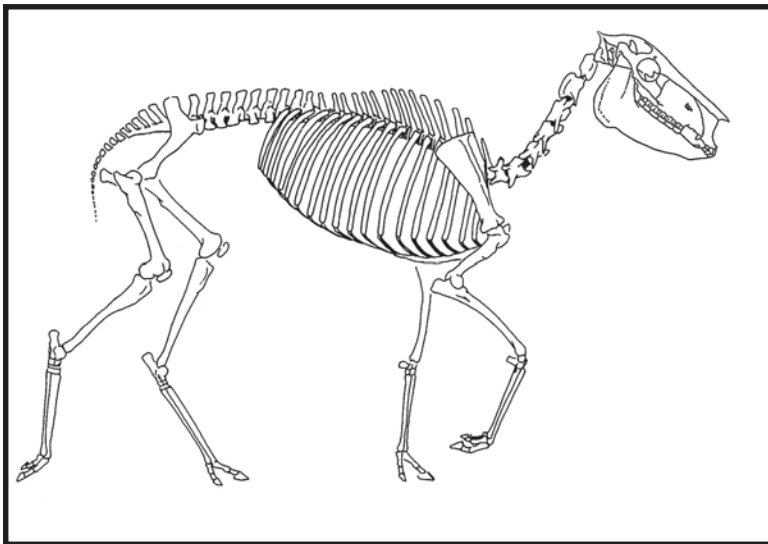In *Phenacodus*, the lumbar span is long and the individual vertebrae are large and heavy (Fig. 33). The obliquely-oriented accessory processes permit rotatory movement of the ribcage and loin, and it is safe to conclude on the basis of this fact that condylarths, like similarly-constructed living carnivores, utilized a rotatory gallop (Hildebrand, 1974).

Anteriorly, the neck in *Phenacodus* is short. The neural flange of the axis and the wings of the atlas are small. Each of the poterior five neck vertebrae sprouts a spike-like dorsal process, indeicating the absence of either a crest or a lamellar sheet associated with the long dorsal ligaments of the neck. It is likely that in *Phenacodus* the deepest layer of the hypaxial neck musculature had not yet been converted to non-contractile "yellow ligament" tissue (Getty, 1975).
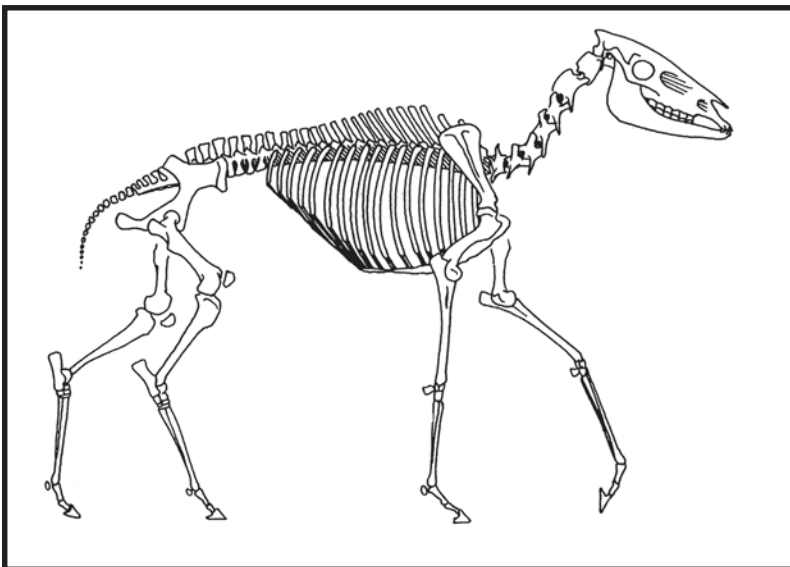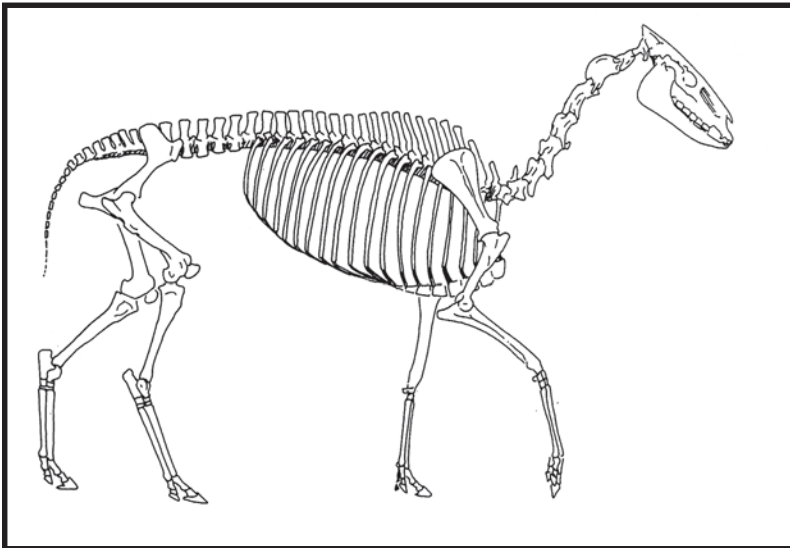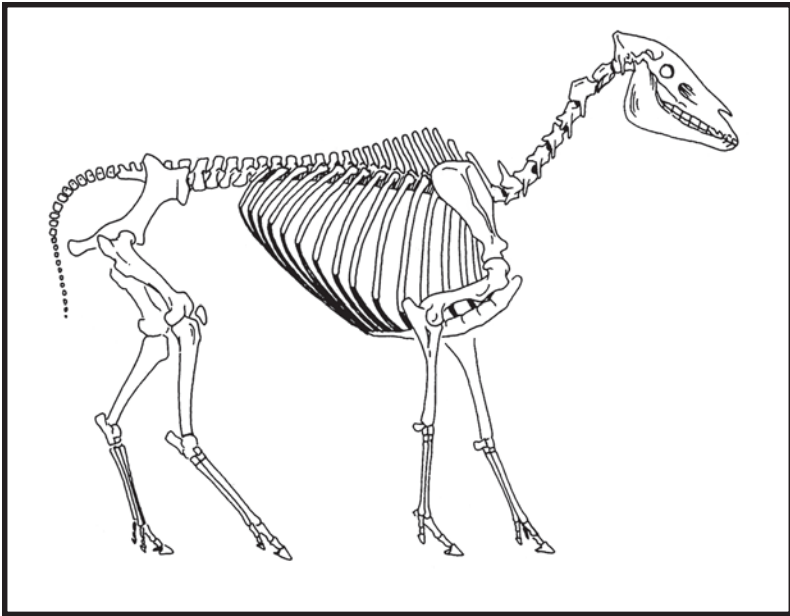
Fig. 42, top left: Skeleton of an anchithere, probably *Anchitherium,* after de Gaudry (he refers to this skeleton as *"Hipparion").* Fig. 43, Middle: *Hypohippus,* after an AMNH mount. Fig. 44, Bottom: *Pliohippus,* corrected after an AMNH mount. These horses all show Okapi-like body morphology, i.e. with long neck, high withers, long forelimbs. They all have steep molar table angles and retain relatively simple tooth construction; *Hypohippus* has teeth like a rhino. They all have deep facial fossae coupled with considerable retraction of the nasal notch, and that to me indicates the presence of a longer, stronger, more prehensile upper lip than in *Equus,* amounting to a short proboscis. Tooth morphology causes us to classify these animals in different clades, but what is interesting to me is the apparent persistent tendency among equids to re-develop tooth and body style suitable for browsing rather than grazing.

Dorsal processes in the "withers" region are spike-like and no taller than those of the lumbar span. The absence of withers is also related to the absence of a crested neck. In phenacodontid condylarths, there are up to 18 thoracic vertebrae, as there are in all perissodactyls, but there may be as many as eight lumbar vertebrae.

The sacrum in *Phenacodus* was short and curving; no intertransverse articulations between the lumbars, or between the sacrum and lumbars, are present. The tail is loong enough to have touched the ground and the individual vertebrae are relatively heavy (Cope, 1887; Matthew, 1937).

In *Hyracotherium* great changes have taken place. The lumbar vertebrae are smaller and the span more condensed (both through loss of vertebrae, to establish the normal number for equids at six, and through making the individual lumbars smaller) than in phenacodontid condylarths. The lumbar articular processes are more vertical and more tightly articulated than in either modern cats or in *Phenacodus* (Kitts, 1956); thus, at the very beginning of equid history, the ability to rotate the pelvis on the lumbar span was lost. For this reason, equids have always used a transverse gallop (Hildebrand, 1974).

The neck of *Hyracotherium* is short, like that of its ancestors. However, two important internal changes were established in it. The first is the relatively great increase in size of the neural crest on the axis and the "wings" of the atlas. In *Orohippus* and all other scansorial browsers, the cervical transverse processes are also unusually large (Kitts, 1957). In combination with changes in the occipital region of the skull, these indicate that the short epaxial musculature of the anterior neck was strong, and that the snout could be raised forcefully for rooting. The second change is the loss of dorsal spines on C3 through C5, and the reduction of the spines on C6 and C7, indicating the conversion of the deepest layer of neck musculature from contractile to acontractile tissue (Getty, 1975).

Dorsal arches in the "withers" region remained low in *Hyracotherium* (though Cope's 1887 restoration erroneously shows tall withers, and this restoration is still reproduced in many books, for example, Simpson, 1951, plates XVIII and XXXII). Tall "withers" never developed in any scansorial browser; these animals all possessed a muscular, tubular neck like a dog's, completely lacking a crest.

The sacrum in equids is longer than in condylarths, and in *Hyracotherium* it articulates more tightly with the last lumbar, though intertransverse articulations are lacking in all scansorial browsers. The tail is shorter than in condylarths and much more slender, but its root has not been drawn up above long ischia as in grazers.

The axial skeleton in chalicomorph browsers

Chalicomorphs are structured to enable the snout to treach as far as possible upwards to grasp leafy vegetation. With this understanding, it is not surprising that chalicomorph browsers were the first equids to acquire large body size, long front limbs and a long neck. In addition, they possess deep nasal notches, deep facial fossae and spout-shaped jaws, all indicating the presence of a long tongue and at least a short proboscis.

The chalicomorphs have definite, though low, withers; the cervical division of the rhomboideus muscles, which roots along the crest of the neck, and which functions to raise the head or throw it back, must have been strong in these forms. The neural crest of the axis and the "wings" of the atlas are small, the occiput is high and narrow, the odontoid process of the axis is long, and the occipital condyles are prominent. These features indicate that the upper part of the neck was flexible and could twist and rotate easily.

An important change also occurred at the root of the neck: like camels as well as the grazing equids, the chalicomorphs re-shaped the first thoracic vertebra to look like one of the neck bones. Functionally, this gave the chalicomorphs another neck joint, which increased not only the length of the neck but its total flexibility.

As in scansorial browsers, the freespan of the back is well arched, and the lumbar span, while shorter thanin condylarths or cats, is longer than in grazing equids. The sacrum is longer than in scansorial browsers and

simlilar to that in grazers, except that it lacks intertransverse articular surfaces. The tail is fairly long and its root low, as in *Hyracotherium.*

The axial skeleton in grazing equids

Parahippus was the first equid genus to abandon the old scansorial method of fleeing predators by rapid acceleration followed by dodging through undergorwth. This mode of escape is of little use to large non-burrowing animals living in an open environment. Modifications took place in the grazer axial skeleton at this time which committed them to straight-line flight; to less rapid acceleration; to less flexibility in turns; and to the ability to maintain a relatively high cruising speed over a distance of more than one mile. These equids no longer jumped or dodged away from predators, and due to their increased size they could no longer hide under bushes. Instead, they outran predators by outlasting them in a protracted chase.

The freespan of the grazer's back is *relatively* rigid. It is to be compared in function to a diving board – a mechanism perfectly designed for the storage and elastic release of energy (Bennett, 2005). The vertebral movement of grazing equids is characteristically sinusoidal and springy and, although there are also spring-mechanisms in the limbs, the root of this energy resides in the axial body. Artiodactyls such as cattle and antelopes also have spring-mechanisms in the limbs, but because they lack equid back design, they move much more stiffly than horses.

The definitive locomotory movement of the grazing equid is to coil its loins. Parahippus was the first equid to develop intertransverse articulations between the sacrum and last lumbar vertebra, and the first in which the lumbar articular processes are vertically oriented and tightly interlocking. These adaptations prevent rotation and largely inhibit lateral flexion of the loins, while promoting loin-coiling through flexion of the lumbosacral and inter-lumbar joints. This structural adaptation established itself concomitantly with the marked telescoping the limbs which also characterizes grazing equids (Bennett, 2005).

Intertransverse articulations likewise imply the presence of a reciprocating apparatus in the hind limb (Bennett, 2003). This is corroborated by the increased length of the ischium in grazers, which affords increased leverage to the hamstring musculature. Along with this increase came the enlar4gement and forward displacement of the first two tail vertebrae, which become functionally part of the sacrum. On these vertebrae are rooted, most unusually for any mammal, the upper heads of the hamstring muscles. These two modifications are important mechanical components of the hindlimb reciprocating apparatus because the semitendinosus muscle, in particular, is a key component of that system (Bennett, 2003, 2005).

The sacrum in grazers is stoutly constructed, but tapers sharply to the rear because the tail vertebrae are smaller, and the tail itself shorter, than in browsers. Dorsal spines of the sacrum slope sharply rearward, while those of the lumbar vertebrae slope sharply forward. This arrangement also implis the presence of the hindlimb reciprocating apparatus which, for efficient functioning, depends on stretching the ligaments which are rooted on the opposite-sloping spines and which span the V-shaped gap they form (Bennett, 2005). In many species, the lumbar spines are also somewhat tall, forming a kind of "second withers" to make the energy transfer from thrusting hindquarters to oscillating back even more efficient.

Improtant changes also occurred in the necks of grazers. As in chalicomorph browsers, the neck became longer and more flexible. Likewise, in grazers the first thoracic vertebra was "stolen" and made functionally part of the neck.

In grazers, the withers find their greatest development (Figs. 38 - 44). In all three grazer lineages, they increased in height steadily from *Parahippus* onward, and reach their greatest development among living wild equines, in the Grevy's zebra *(Equus grevyi)* and in the Przewalski horse *(Equus caballus)*. Tall withers imply the presence of a crest. Likewise, in grazers, all vestiges of dorsal processes are lost on all neck vertebrae, indicating the presence of both funicular and lamellar parts of the ligamentum nuchae.

EVOLUTION OF THE APPENDICULAR SKELETON IN EQUIDS

The transition from condylarth ancestors and the establishment of the Equidae

The limbs of Eocene carnivores such as *Sinopa* are short and relatively slender. They terminate in broad feet with five toes each. In life, the end of each digit was tipped with a sharp claw. The carnivore's limbs were flexible, capable of gripping a tree limb or scooping up food, much like a modern raccoon. Like a raccoon, when *Sinopa* walked, both its palm and the sole of its foot touched the ground.

In phenacodontid condylarths, the long bones supporting the palm (metacarpals) and the sole of the foot (metatarsals) are proportionally long, implying a change from the ancient plantigrade to a digitigrade posture, in which the heels of the feet and hands are elevated during walking. Mammals with digitigrade forefeet (such as modern cats) bear weight upon the front edge of the palm, along an arc formed by the bases of the fingers. Weight in the hind feet is likewise borne along the front edge of the sole of the foot. Small and medium-sized difitigrade mammals have toe pads, fibroelastic cushions that support the weight-bearing arc and also the tip of each digit.

The internal design of the feet of *Phenacodus* is also different from that in Sinopa. The central three structural elements (digits II, III, and IV) are large, while the lateral digits (I and V, thumb and little finger) are noticeably smaller, especially in the hind foot. The feet are more condensed, with the digits fanning out much less thanin primitive carnivores. Unlike carnivores, each toe in *Phenacodus* terminated not in a claw but in a blunt hooflet (Fig. 47).

In other details, however, the feet of phenacodontid condylarths remained primitive. The block-like mammalian wrist bones (carpals) form in two rows, one above the other. In phenacodontids, the bones of the lower row are aligned directly below those in the upper row, forming a "serial carpal". The ankle bone (tarsal) that articulates with the tibia above (the tibial tarsal or astragalus), bears a convex facet for articulation with the navicular bone below. In this feature too, *Phenacodus* is primitive (Radinsky, 1966; Kitts, 1956, 1957; MacFadden, 1976; Simpson, 1952).

The limbs of *Hyracotherium* are somewhat longer than those of *Phenacodus*, especially the hind limbs, which in the early equids
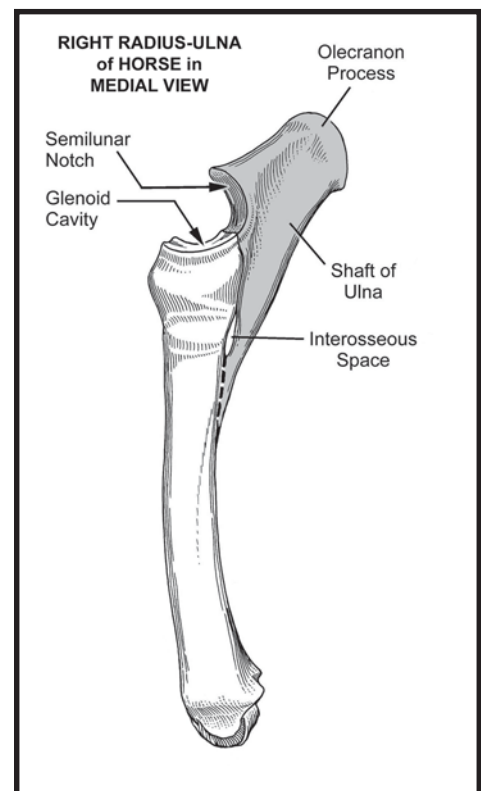
Fig. 48. The radius-ulna of the living horse, *Equus caballus.* In all Equines, the ulna (gray tone) is reduced and fused to the shaft of the radius.

were about 40% longer than the forelimbs. In life, *Hyracotherium* must have had a rump-high, semi-hopping gait, somewhat like that of a rabbit.

There were also more subtle changes in bone shapes and articulations within the feet. In *Hyracotherium,* the metacarpal and metatarsal bones are about twice as long, and more slender, than those in *Phenacodus.* The first and fifth digits of the hind foot, and the first digit of the forefoot, are absent. The metacarpals and metatarsals are more compressed and form a narrower wrist and ankle than in *Phenacodus.* The ankle is stabilized for the efficient delivery of impulsion by the development of a unique, convex, saddle-shaped navicular facet on the bottom surface of the astragalus (Cope, 1881, 1887; see Schaeffer, 1947 to compare different astragalar development in the other major order of ungulates, the Artiodactyla). Ridges on the tibial articular surface of this bone are also more prominent than in phenacodontid condylarths. The forefoot is also strengthened by the development of an "alternating""carpus (Fig. 45), in which the upper row of carpals interlocks with the lower row (Radinsky, 1966). These changes are significant in the development of the rapid acceleration, bounding gait, and sharp turns characteristic of the scansorial mode of locomotion.

In *Miohippus,* the last-surviving scansorial browser, a further strengthening of the ankle ("hock") region took place. In
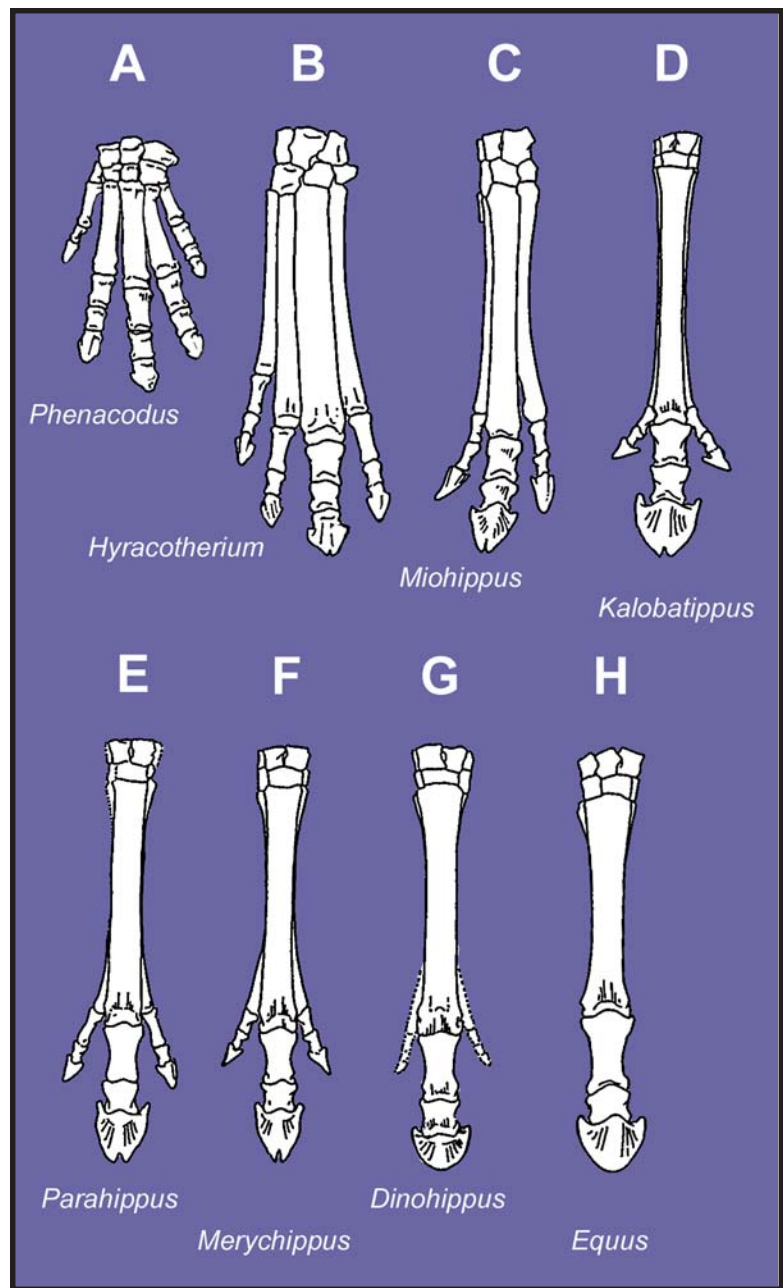

Fig. 45: Bones of the distal forelimb in representative Equids and *Phenacodus*. All except *Phenacodus* reduced to about the same length to make comparing the proportions easier.

eaqrlier equids, the top of the third metatarsal contacts the inner (ectocuneiform) tarsal bone. In *Mesohippus,* a more compact and tightly interlocking structure develops in which metatarsal III contacts both the ectocuneiform and the outer (cuboid) tarsal (Simpson, 1951; Prothero and Shubin, 1987). This ankle structure was inherited by *Parahipus* and all grazers, but is not present in the chalicomorph browsers, which derive separately from Eocene and Oligocene ancestors.

While some early Oligocene species of *Mesohippus* retained four digits on each forefoot, the twig-like digit V was soon lost (MacFadden, 1976). All descendants of *Mesohippus (Miohippus* and the grazers) possess no more than three digits per forefoot (Fig. 45).

The appendicular skeleton in chalicomorph browsers

Chalicomorph browsers have unique conformation. In later scansorial browsers, the *whole limb* is pro-portionally lengthened, not just the distal elements. Thus even *Miohippus* still stands rump-high. In chalicomorphs, the metacarpal bones, in particular, are lengthened to produce the first equids to stand "high in front" (Fig. 43). All the distal elements are lengthened, while scapula, humerus and femur keep about the same proportions they had in *Mesohippus.* The phalanges in the larger chalicomorphs tend to be broader and heavier than in other equids, but do not bear the prominent ridges and deep grooves for stabilizing the limb for straight-line flight seen in grazers (Gidley, 1903; Troxell, 1916; Osborn, 1918; Sondaar, 1968; McGrew, 1971)(Figs. 45, 46).

The appendicular skeleton in grazing equids

Long, slender distal limb elements are consistently present in grazers, while the scapula, humerus and femur are proportionally shorter than in browsers. The metapodials and phalanges of digits II and IV of each foot are much more slender than those of digit III; nevertheless, the lateral digits were necessary and useful elements (Hussain, 1975; Sondaar, 1968). In reviewing the history of the equidae, it is plain that to be three-toed is the *normal* condition; if any forms are aberrant, they are the few which completely lost the phalanges of the side toes to become monodactyl (Simpson, 1951; Voorhies, pers. comm.).

The fore-aft movement of limb elements in grazers must be vibration-free. The diostal parts of the limbs must not turn or twist
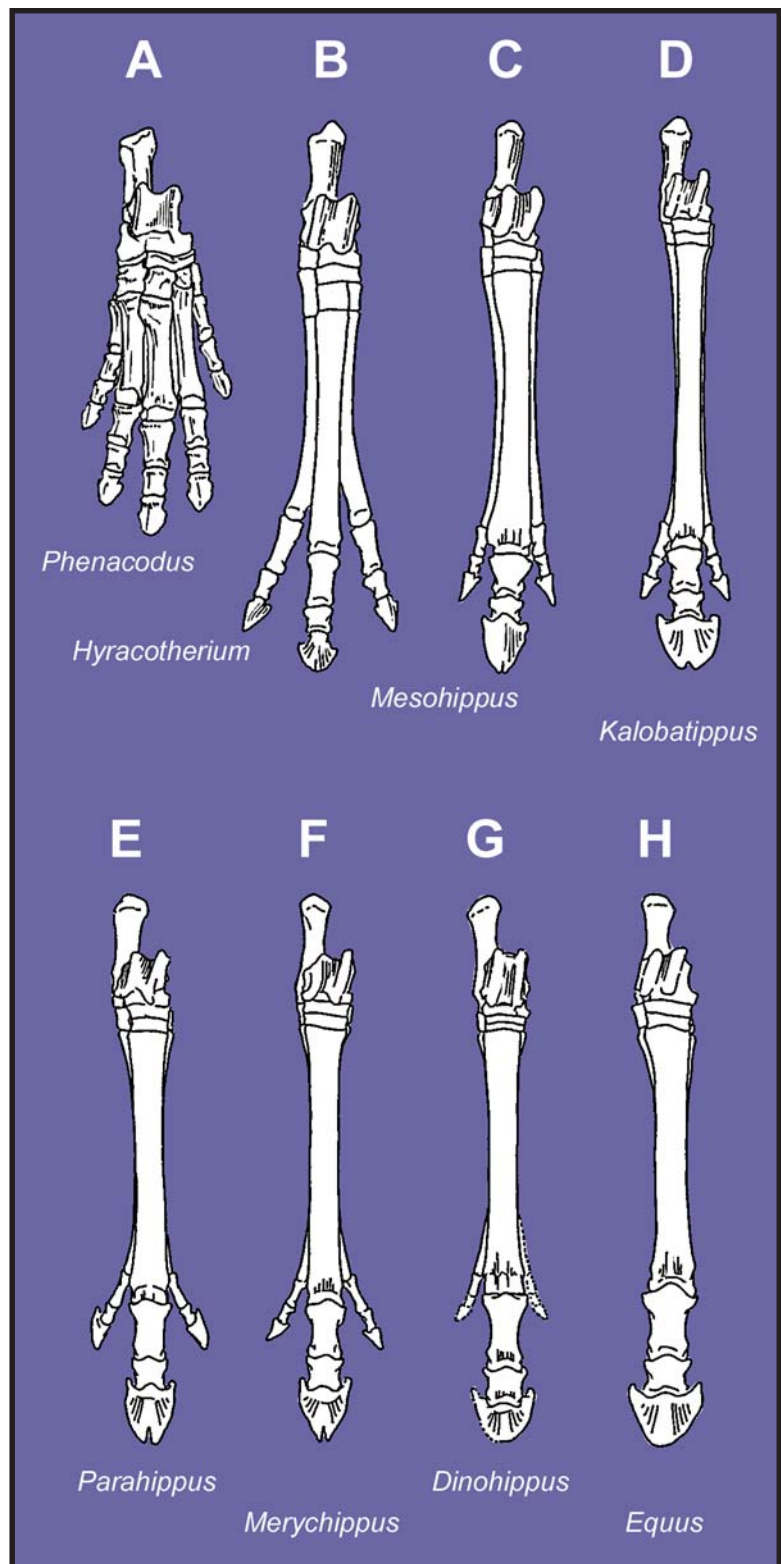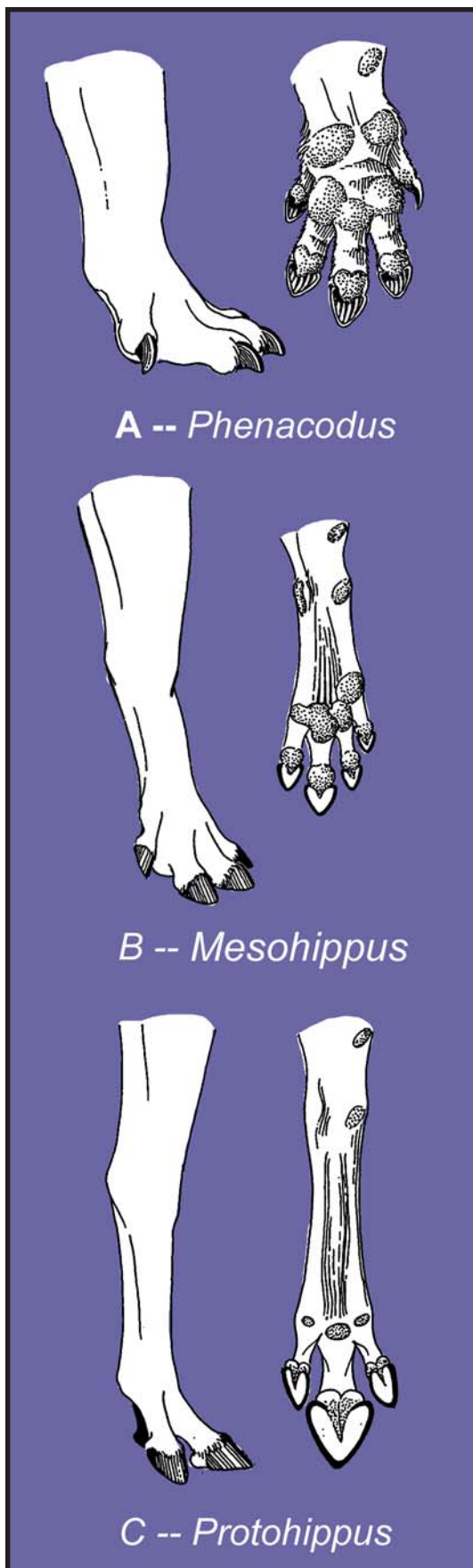

Fig. 46: Bones of the distal hind limb in representative Equids and *Phenacodus.* All except *Phenacodus* reduced to about the same length to make comparing the proportions easier.

A -- Phenacodus

B -- Mesohippus

C -- Protohippus

during flight; the hoofs must meet the ground faceing squarely to the front. A mammal can rotate its wrist to turn its palm upward (supination of the manus) if the head of the radius is rounded, and if its shaft is separate from that of the ulna. In scansorial browsers, the shafts of the radius and ulna, although closely appressed, are separate. Supination is inhibited in these forms by the development of a process on the lateral side of the upper end of the radius, which extends the articular surface for the humerus laterally and which acts to stop rotation of the radius (Radinsky, 1966). In grazers, this process is lost but the shaft of the ulna fuses to that of the radius, completely preventing supination (Fig. 48).

Unique to grazers is a system of prominent ridges and deep gtrooves developed on the lower ends of the metapodials and on both ends of the two upper phalanges (i.e. on the distal end of the "cannon bone" and on the "long pastern" and "short pastern"). The ridges and grooves are oriented in a fore-aft direction and act to limit joint flexion and extension to a narrow plane (Gidley, 1903).

In scansorial browsers, and probably also in chalicomorphs, large toe pads were present. In grazers, external toe pads are lost. The sole of the foot is thick and hard, to protect it from pounding on hard ground, while the ancient central toe pad persists as the frog and digital cushion. The digital cushion develops in the same place as the old toe pad, below and behind the last toe-bone, but in grazers it is incorporated within the horny walls of the hoof, protected by them and by the tough sole below (Simpson, 1951)(Fig. 47).

In many ways, the living *Equus* is not very representative of skeletal trends in grazers. *Equus* and the closely related south American genera *Hippidion* and *Onohippidium* (Hoffstetter, 1950) are the product of selection under glacial and subglacial

Fig. 47: Restorations by the author of the appearance of the forepaw in *Phenacodus* and the distal forelimb in two Equids. *Phenacodus* retains the primitive clawed manus with five functional digits. In this *Mesohippus* (from the Chadronian Land Mammal Age) there are still four digits in the forefoot, but one is very small and probably non-functional. The *Protohippus* shows the normal condition for Equids -- the configuration that is most common throughout the family: three functional digits, each toe tipped by a hooflet.

conditions; they are the large-headed, stocky-bodied, short-legged "Neanderthal" forms of their family. Most other grazers were much more deer-like in propotions; many were gracile creatures no bigger than goats or small antelopes. Even the relatively sotcky *Protohippus* and *Hipparion* were hardly taller than a shetland pony. No horse taller than fifteen hands, two inches (62 inches, 150 cm at the withers) ever existed in nature; larger specimens are the product of selective breeding of domestic stock carried out over the last 500 years. For these reasons, our sense of scale and proportion tends to be warped where it concerns horses, and we must take care that this does not bias our view of the fossil record. In view of the steady decline in numbers and diversity not only of equids, but of all Perissodactyls since the end of the Miocene, we are fortunate indeed that the horse, an archaic and uniquely adapted mammal, still lives in the world that we also inhabit.

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