INTRODUCTION TO HORSE EVOLUTION:
ANATOMICAL CHARACTERISTICS, CLASSIFICATION, AND THE STRATIGRAPHIC RECORD

The impetus for producing this educational article was a telephone conversation with a man whom I normally enjoy. He's a cowboy, and grew up on a ranch. He's a kind fellow who has done a good job with not only a lot of horses, but also his kids, who are likewise very fine people. He's a Christian – a commitment that I respect – and his children were not only raised in their church, but have gone on to attend Bible College. At the same time, this fellow knows that I'm a paleontologist interested in fossil horses. In our recent conversation, at one point he suddenly burst out, "I can't understand it! Belief in evolution is simply stupid!"

I was quite taken aback at his lack of respect for my point of view, because his attitude invalidates my experience and beliefs in a way that I would never impose in return – not to mention that it goes against nearly every piece of advice that St. Paul ever gave. What could possibly cause an otherwise reasonable man to make such a statement so vehemently to someone he knows it is going to offend? Why of course — because the fellow *cares* about me; he wants my soul to be saved, even at the cost of his own.

Dr. Deb's favorite image of "stupid paleontologists" (Moe, Larry, and Curly of the Three Stooges)

Why does he think my soul is in danger of damnation? Because he believes that the words he reads in the Bible are to be taken absolutely literally – no room for metaphorical interpretations, textual criticism, or alternative readings. To this guy, there is one translation of the Bible (I don't know which one) that is the true and accurate record of God's thoughts, desires, and commands: it is without error, and covers every conceivable situation. Such fundamentalism prevents him from being able to reconcile the huge time-span that geology and paleontology propose for the world, because what mention of that subject there is in Scripture indicates that the world was created less than 5,000 years ago. Fundamentalism has crippled his ability to accept any evidence that would indicate otherwise, and my beliefs scare him (for my sake), because he believes they are contrary to Scripture and therefore sinful. But to deny the existence of the (as you are about to see, *thousands)* of fossilized skeletons of horses and other animals known to science is simply foolish. Worse, to claim as some folks have that they have been "carved out of the rock" in an effort to deceive the public, is an irresponsible lie. And yet, this guy, so schooled in looking for the truth within Scripture, is inclined to believe exactly these lies and distortions. He even gave me a link to a website by a creationist with a Ph.D. degree (in Economics) that disseminates them!

Because the elders of his church tell him so, my cowboy friend does not believe that scientific results are reliable. However, I think the news media have also helped to destroy some peoples' faith in the reliability of science. Mis-teaching in the public schools hasn't helped, either – but the fault for all of this lies squarely at the doorstep of my own profession, which has failed to make or maintain an adequate public educational effort. Thus, evolutionist vs. creationist debates are still staged; in Kansas the legislature once again wants to ban the teaching of evolution in public schools; and the people of the United States have elected a string of conservative legislators and Presidents who, responding to strong lobbying by conservative and fundamentalist Christians, have nearly eliminated funding for paleontological research by Universities and Museums.

The concept that the public has of what evolution is and how it works simply does not match that which paleontologists hold. In fact, it hasn't matched for more than a century. When your High School biology teacher taught you that evolution means one animal changing into another animal over a long span of time – and the picture he conveyed was of *morphing* — he taught you badly; for there is no known mechanism for morphing among living things. When you go to your local Museum and you see an exhibit that shows a single series of horses gradually getting bigger through time – what I call an "inflate-a-horse" exhibit – this is a classic example of an exhibit that makes people think that one horse species has morphed into the next. It so far fails to convey the real story that it is almost a crime. Instead, change through time is *iterative* in nature, usually occurring one "click" at a time, like working a lock with a roller dial, or like solving a Rubik's Cube puzzle.

Evolution means "change through time". Charles Darwin said that it occurred as a result of predation, accident, and disease acting upon variability within a population of animals. This was sloganized by Thomas Huxley into the "survival of the fittest." But it needs to be remembered that that what Darwin was proposing was *one possible mechanism* by which animals in later generations might accumulate enough changes to be recognizable as a species different from their ancestor. Other mechanisms for change through time have also been proposed – the two most famous alternatives to Darwinism coming from Ernst Mayr and Stephen Jay Gould (see the separate Horse Evolution Bibliography PDF). My personal belief is that there is no incompatibility at all between believing that animals have changed or evolved through time, and that God created the universe. For paleontology says nothing at all about how the universe began; its only interest is in what has unfolded afterward. It is not paleontologists but fundamentalist creationists who arrogantly insist that they know *exactly how* God has nourished, or how He continues to nourish, this unfolding.

In the horse family, change through time is very well documented, based on literally thousands of fossil skeletons that have been unearthed and studied over the past two and a half centuries. Students who wish to understand the subject will want to pay attention to two areas in particular: logical systems for classifying living things, and age determination for the remains of animals that have been found within rock strata. In this article, I present the information on stratigraphy and age-determination primarily in pictorial form. The rules and procedures of taxonomy (the science of classifying living things) are explained below. The example used throughout is, of course, the horse – so here you will also get a complete classification of the horse along with many of the actual, technical reasons for that classification. I have also supplied many wonderful photos showing fossil specimens exhibited in museums around the world, so that this article functions as a virtual World Museum Tour.

This article and its sister-piece "The Evolution of the Horse: History and Techniques of Study" are upgrades and expansions of a 37-page article originally published in the expensive and difficult-to-find Elsevier *World Animal Science Encyclopedia* (Volume C, Horse Breeding and Management, J. Warren Evans, ed., 1992). The present upgrade has more than doubled the number of illustrations and color photos. I certainly hope that you find studying this material enjoyable and fascinating as well as enlightening!

Classification

Living things are classified on the basis of similarity in structure. This means that you must first notice the structure of whatever living thing you mean to study, noting particularly any features (taxonomists call them "characters") unique to that creature. Similarities shared by a range of organisms, or features unique to only one or a few of them, can then be tabulated.

Characters common to a large number of organisms are said to be primitive. "Primitive" in this sense does not imply crudeness, for all organisms living at all times must have a body plan that works very well in order to stay alive at all. Nor does the term "primitive" necessarily imply that the feature occurs early in time, for in fact most of the characters of most organisms now alive have been inherited unchanged through untold generations, over the span of millennia.

Because of this, characters which are unique to a given organism – characters which of necessity must be modifications, great or small, of earlier designs – have special significance in classification, for only such "derived" features can define the boundaries of taxonomic units — groups of related species. The logical system of classification, called cladistics, makes use of derived features shared by all members of a taxonomic unit to define that unit. Because derived features can only arise from pre-existing designs (those which are comparatively more widespread or more primitive), a cladistic logic-diagram also indicates the order (and often also, the geographic place) in which the descendants of any given lineage acquired derived features.

The science of classification formally began in the mid-18th century with the work of Swedish scientist Karl Linné. Linné (whose name is usually Latinized to Carolus Linnaeus) proposed the system of binomial nomenclature which is still used today. In this naming system, all species receive two names – the first signifying the genus to which the species belongs. When the second term, called the trivial, is paired with the genus name, the two terms taken together uniquely name and identify the species. The example most relevant to our interests would be:

Equus – the genus for horses, asses, onagers, quaggas, and zebras. The Latin word "equus" means "weighting all four feet equally".

caballus – the trivial term is a Latin word meaning "nag". Note that by itself, the trivial term does not identify the horse — or any other animal. There is, for example, at least one beetle and also one plant whose genus names are followed by the trivial "caballus". Thus, in order to be sure that we're discussing the living horse, we need to write:

Equus caballus – this binomial term is the scientific name, used in taxonomic classification, that uniquely identifies the horse.

Please note the importance of capitalization and italicization. In scientific writing, it is mandatory to capitalize the first letter of the genus name, and to not capitalize the first letter of the trivial. The genus name, which is OK to use alone, or the full binomial when it is used, must be italicized or in some other manner set off from the surrounding text (i.e., boldface or underline are OK too). While these rules are mandatory in any technical journal, good usage demands that they be followed in all publications (so for example, the better-edited newspapers and monthlies such as Equus Magazine scrupulously follow these rules).

The subspecies is the smallest taxonomic unit. In this article, you will learn that there are seven valid subspecies of the horse, *Equus caballus*. The Przewalski Horse or Mongolian Wild Horse is one of these seven. Its subspecific designation is written this way:
Equus caballus przewalskii

Occasionally, especially where there are a large number of species in a given genus, to designate a sub-genus. Thus, for the horse genus we might write:

Equus (Amerhippus) andium -- a fossil species known from various localities in western North America and South America.

If different subspecies of *Equus andium* were being discussed, for clarity we might have to write:

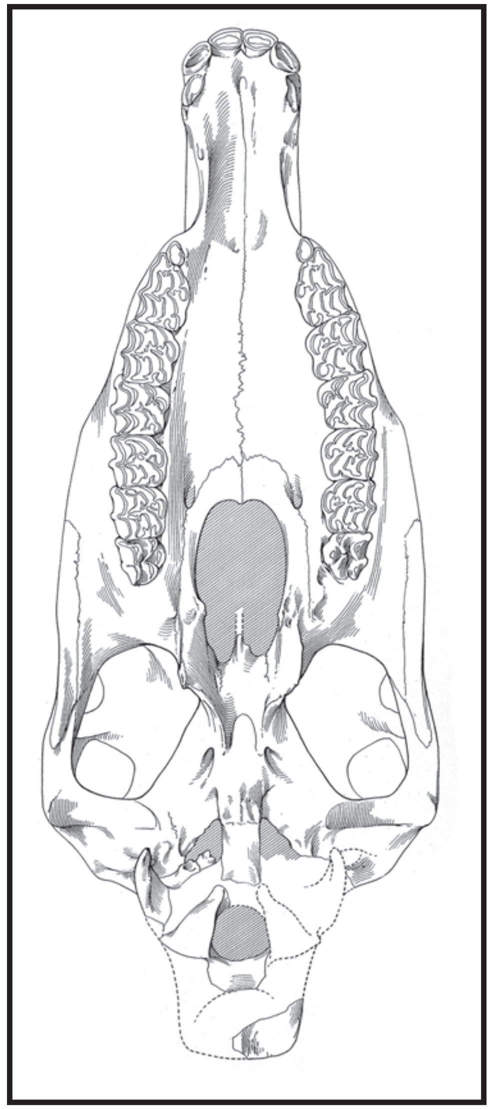
Equus (Amerhippus) andium andium
Equus (Amerhippus) andium wyomingensis

This makes a name consisting of four terms -- the maximum number of terms that may be used.

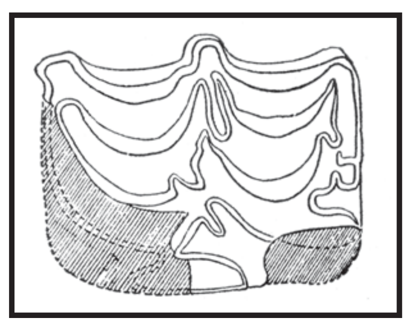
Naming Species: Importance of the Type Specimen

There are also important rules concerning the naming of species. The person who is the first to describe and publish, in an encyclopedia or peer-reviewed journal, any new species gets permanent credit for doing so. The most important rule of taxonomy is that the trivial term is permanently associated with a "type specimen." Ideally this would be a complete skeleton; practically in horse paleontology it is often a skull, a partial dentition, or even a single tooth. The type specimen must be housed in a Museum of Natural History or other permanent and professionally curated collection, it must bear a unique specimen number, and it must remain accessible in perpetuity for any scientist who wishes to examine it.

Once the type specimen has been designated and named, the real work concerning it begins. This consists of observation, discussion, and even controversy among all the paleontologists who have examined it. Because the trivial can never appear, and has no scientific meaning, unless it is assigned to and paired with a genus name, the original namer must assign it to some genus. But that by no means guarantees that's where it's going to stay! After examining the type, another scientist may feel justified in re-assigning the specimen to a different genus. These re-assignments may go on for



One of the best type specimens of horses, the nearly-complete AMNH no. 17724, *Dinohippus leidyanus* named by H.F. Osborn in 1918.

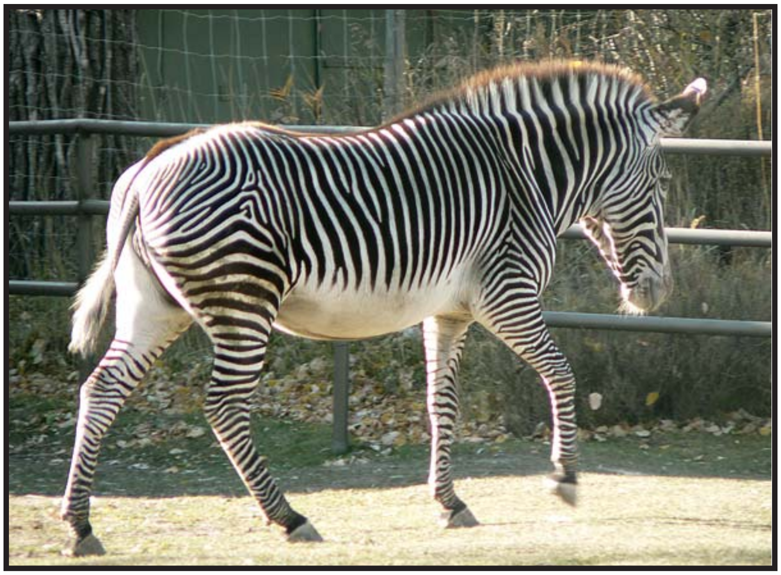


Probably the worst, most troublesome specimen ever selected to be a type: Cope's 1878 type of *Equus simplicidens*, which consists of a single broken tooth.

years – often because other discoveries, whether in the area of the geology and stratigraphy or as a result of further study of the skeletal material itself, help to put the type specimen into better perspective. There so many examples of this in the paleontological literature that I can only say, "let the student be forewarned". Here's a table containing a few examples; boldface indicates instances where the current expert opinion is that the original namer actually got it right!

Original Date & Namer	Original Assignment	Present Assignment
Erwin Hinckley Barbour, 1914	*Hypohippus matthewi*	*Megahippus matthewi*
Edward Drinker Cope, 1873	*Anchitherium cuneatum*	*Mesohippus cuneatus*
E.D. Cope, 1873	***Protohippus sejunctus***	***Protohippus sejunctus***
E.D. Cope, 1879	*Anchitherium praestans*	*Kalobatippus praestans*
E.D. Cope, 1889	*Hippotherium isonesum*	*Calippus isonesus*
E.D. Cope, 1889	*Hippotherium sphenodus*	*Griphippus sphenodus*
E.D. Cope, 1889	*Hippotherium retrusum*	*Calippus retrusus*
E.D. Cope, 1892	***Equus simplicidens***	***Equus simplicidens***
E.D. Cope, 1893	*Hippidium interpolatum*	*Dinohippus interpolatus*
E.D. Cope, 1893	*Protohippus lenticularis*	*Nannippus lenticulare*
E.D. Cope, 1893	*Equus eurystylus*	*Neohipparion eurystyle*
J.W. Gidley, 1903	***Neohipparion whitneyi***	***Neohipparion whitneyi***
J.W. Gidley, 1907	*Merychippus campestri*	*Pliohippus campestris*
Joseph Leidy, 1850	*Palaeotherium baridii*	*Mesohippus bairdii*
J. Leidy, 1856	*Hipparion occidentale*	*Cormohipparion occidentale*
J. Leidy, 1858	*Eohippus perditus*	*Pseudhipparion perditus*
J. Leidy, 1869	*Protohippus placidus*	*Calippus placidus*
J. Leidy, 1869	*Protohippus supremus*	*Pliohippus supremus*
J. Leidy, 1869	*Hipparion gratum*	*Griphippus gratus*
Othniel C. Marsh, 1874	***Pliohippus pernix***	***Pliohippus pernix***
Henry Fairfield Osborn, 1918	***Miohippus gidleyi***	***Miohippus gidleyi***
H.F. Osborn, 1918	*Merychippus republicanus*	*Pseudhipparion republicanum*
H.F. Osborn, 1918	*Pliohippus leidyanus*	*Dinohippus leidyanus*
O.A. Peterson, 1907	***Parahippus nebrascensis***	***Parahippus nebrascensis***
E.H. Sellards, 1916	*Hipparion minor*	*Nannippus minor*
William Berryman Scott, 1893	*Anchitherium equinum*	*Hypohippus equinus*

In all cases -- even where later research has proven the generic assignment incorrect -- the original namer continues in perpetuity to receive credit for naming and describing the type – his name is forever associated with it. So, for example, even though it was Morris Skinner and Bruce MacFadden who did the work and had the insight to re-assign the type specimen of *Hipparion occidentale* to *Cormohipparion,* the full correct citation for *"Cormohipparion occidentale"* is *Cormohipparion occidentale* (Leidy, 1856).



Animals are classified on the basis of similarity of structure. Structural differences between different living species can be seen from the outside, as with the Grevy's zebras *(Equus grevyi)*, versus these Persian onagers *(Equus onager).* Both photographed at the Calgary Zoo.

The Classification Hierarchy

Linnaeus' original system of classification was hierarchical. A hierarchical classification functions like bowls that stack one inside the other: into the biggest bowl go many organisms, which are themselves bundled into groups. Each of these groups, in turn, functions like a bowl which holds still smaller bowls, and so on until we reach the level of the genus, species, or subspecies.

The accompanying figures illustrate a hierarchical classification of the living horse, *Equus caballus*. Students of the horse need to be familiar with the meaning of such terms as Perissodactyl (vs. Artiodactyl), Equid vs. Equine, and Equine (capital "E") vs. equine (little "e"). All taxa (groupings) are defined in terms of structure; those for living organisms tend to emphasize features like hair thickness and color, ear and tail length, and metabolic characteristics. Those for fossil organisms almost exclusively relate to structural differences that can be observed on the teeth, skull, and skeleton.

For example, a fossil member of the Order Perissodactyla is identified as such because it possesses certain unique, derived features that are visible on the skeleton. Each of the "learning units" that accompany the classification section of this article (below, beginning on Page 8), is designed to familiarize you with the particular characteristics that define and characterize each taxonomic unit, whether Kingdom, Phylum, Class, Order, Family, Genus, or species.

How Species are Defined

The smallest unit recognized by the science of taxonomy is the subspecies. However, where horses are concerned, it is obvious that we often benefit from looking at still smaller units – for example, herds within a subspecies, and even the individual within the herd. The reason that taxonomic classification stops at the level of the subspecies is that this is the level where panmixia occurs.

"Panmixia" is a term relating to the genetics of populations. Remember that, in classifying animals, we do not look at their genes; instead, we look at the results of gene action which are manifested as the structural peculiarities of the visible body. Panmixia is the condition which occurs within a population of animals in which every breeding individual has an equal chance of mating with every other individual. When this is the case, any given gene has its best shot at showing up in the maximum number of individuals. “Gene flow” through a panmictic population is free of restrictions or bottlenecks. Subspecies are, by definition, panmictic populations.

A species, which may contain one or more than one subspecies, is a group of populations in which any individual is capable of breeding with any other individual to produce viable offspring that can themselves breed to produce viable offspring. In other words, a species is defined by reproduction and gene flow (which in turn creates a certain limited range of skeletal structures within that population). When a species is spread out over a lot of territory – and the horse at one time represented one of the best examples of such – inevitably there will be barriers to reproduction. For example, a mountain range may intervene between the easternmost and westernmost populations of a species. The difficulty in crossing the mountains will make it less likely that individuals from the eastern vs. western populations will meet and interbreed.

When there are barriers to panmixia, and when environmental conditions differ from one range to another, populations or herds inhabiting different regions will tend to become adapted to the particular conditions found in that region. This is, of course, not only because they tend to breed only with each other, but also because individuals less physically suited to a given regime of terrain, forage, and climate tend to reproduce less often and produce fewer offspring. They may also be more susceptible to predation, accident, and disease. Over time, the physical type they represent becomes rare and may become altogether extinct. This is how the gene pool of a population becomes characteristic of that population. We detect the range of different gene combinations within a given gene pool through its expression in the physical bodies of individuals.

When dealing with the fossil record, we are, of course, lucky to find preserved even one member of any population. It has been estimated that somewhere between 1% and 15% of the skeletons of all the mammals that ever lived were fossilized. Of this small number, only a tiny fraction are actually found, collected, studied, and reported. These statistics are often used as a kind of apology for any mistakes that paleontologists might make in interpreting the fossil record – we have to work from very partial data. However, the same statistic should also be used in reverse — as a measure of the number and diversity of animals that have lived on Earth. For example, the student may consider the fossil record of horses: in the five largest collections of fossil mammals in North America (the American Museum of Natural History in New York City, the National Museum of Natural History/Smithsonian Institution in Washington D.C., the University of Nebraska at Lincoln, the

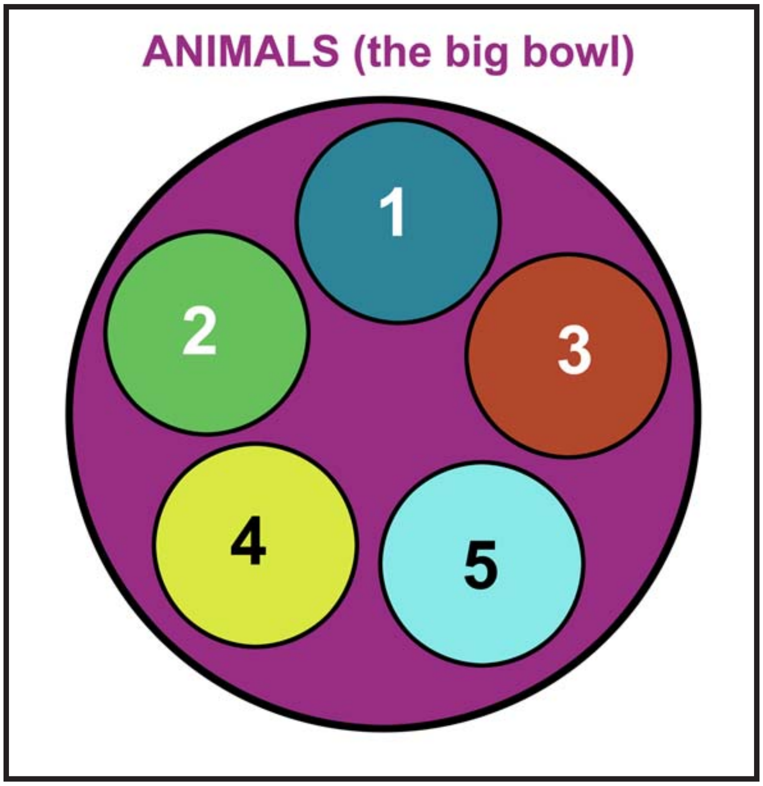
We are lucky whenever we find fossils. Above, the skull of a baby *Teleoceras* (an extinct rhino) from the famous Ashfall Quarry in Nebraska. Still in its protective plaster “field jacket”, this specimen will be cleaned, cataloged, and added to the permanently-curated study collection.

University of California at Berkeley, and the University of Florida at Gainesville) there are tens of thousands of horse bones and teeth sufficiently complete to permit identification at least to the level of genus. There are also numerous other, smaller collections: The University of Kansas at Lawrence, the University of Michigan at Ann Arbor, the Page LaBrea Tar Pit Museum in Los Angeles, the Los Angeles County Museum of Natural History, and the University of Colorado Museum at Denver, not to mention the National Museum of Mexico in Mexico City, the National Museum of Canada in Ottawa, and the Drumheller Museum in Alberta. If this is the case, it is simply awesome to contemplate the number of animals belonging to the horse lineage that have lived on Earth.

Where the Horse Family Fits in Classification

KINGDOM Animals

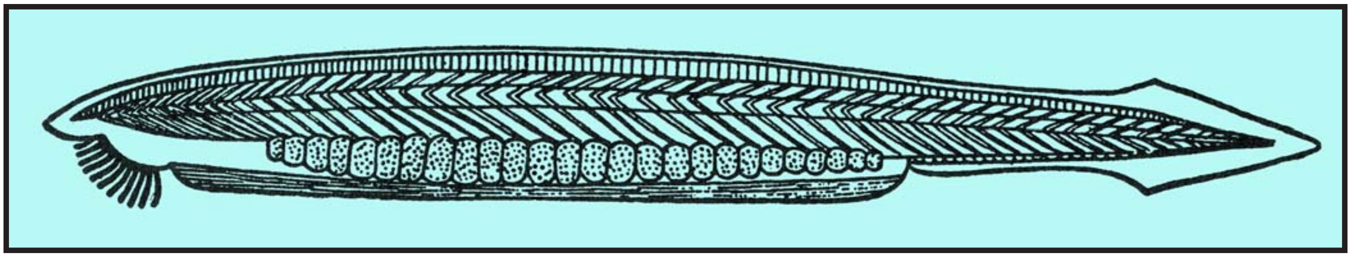
Animals are multi-cellular animals characterized by the power to move. Although as adults some become rooted by a stalk or pedicle (example: clams, crinoids, anemones), for at least part of their lives they are motile. The cells of animals are thin-walled, lacking stiff cellulose reinforcement.



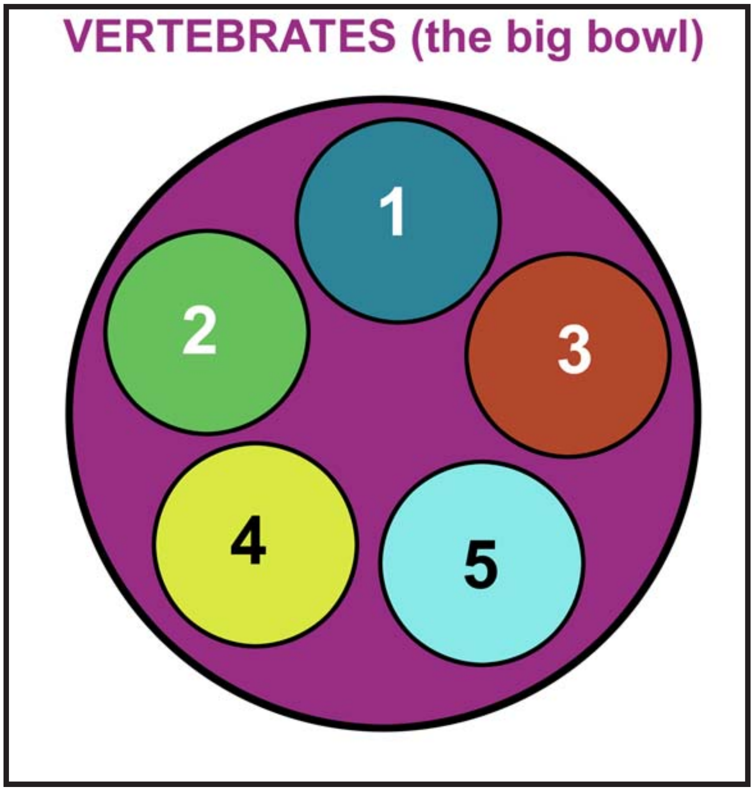
This diagram pictures an animal kingdom containing only five phyla. In reality, the Kingdom Animalia contains many more phyla than this -- those that can commonly be found as fossils include: Sponges, coelenterates (jellyfish, hydras and their relatives), flatworms, roundworms, ringed worms, mollusks, brachiopods, arthropods (crabs, insects, spiders, scorpions, trilobites and their relatives), echinoderms (starfish, sea cucumbers, sand dollars, crinoids, and their relatives), and chordates. Vertebrates, the animals with backbones, are a subphylum within the Chordata.

PHYLUM Chordates

Animals that have a stiff rod of cartilage extending along the dorsal part of the body. This rod, called a notochord, functions to protect the central nerve cord, which is also located dorsally. In most, the notochord is present only at an early embryonic stage, but in a few (the tunicates) it is present in early life, or (in *Amphioxus*) it persists throughout life. Chordates possess the full compliment of body systems, i.e. they have a complete digestive tube with a front opening (mouth) and rear opening (anus); central and peripheral nervous systems; segmented muscles; a heart that recirculates blood through a closed circulatory system. There is a brain and sense organs concentrated at the front end of the body, and the body itself is bilaterally symmetrical. The



Amphioxus -- a primitive chordate familiar to all students of evolutionary biology.
It is a chordate, but not a vertebrate.



Five Classes are recognized within the Vertebrate subphylum: fish, amphibians, reptiles, birds, and mammals. Any good high school or college biology textbook will contain information about the unique characteristics of each of these groups, and all students of the horse should be familiar with them.

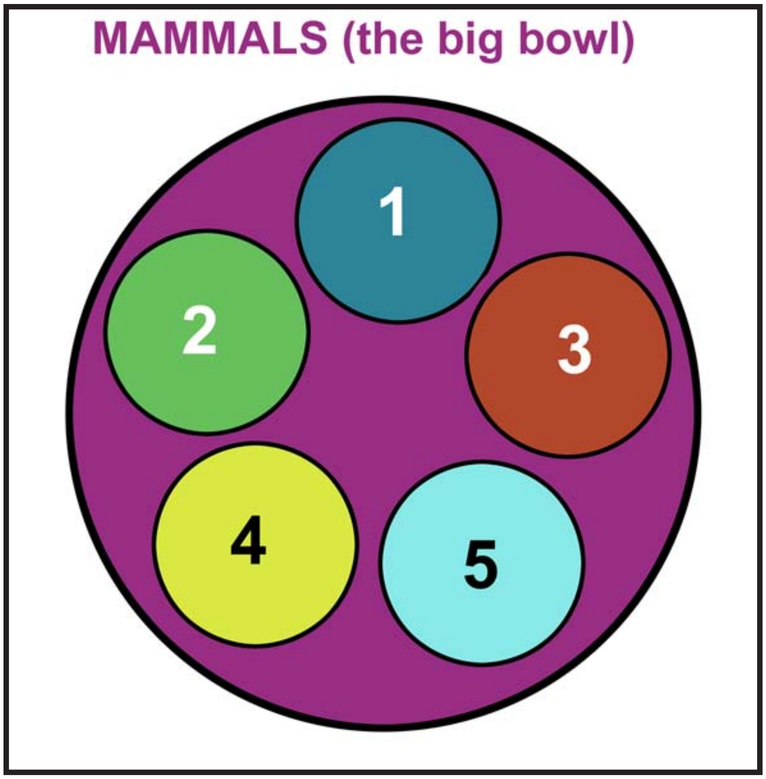
creature breathes by means of a long series of gills, and although there is a mouth opening, there are no jaws. The sense of "hearing" is diffuse, the whole body being sensitive to vibrations in the water; there are no ears.

SUBPHYLUM Vertebrates

Chordates in which the notochord becomes replaced during embryonic life by a chain of vertebrae which enclose and protect the dorsal nerve cord. Generally, there are additional parts as well – limbs — to compose an internal skeleton (endo-skeleton). In most vertebrates, the skeleton in the adult creature is bony, but in some specialized forms, such as sharks, the skeleton is cartilagenous. A skull, or at least the lower part of the skull (the palate area and basicranium) is present, and part of the gill series is modified to become jaws that articulate with the skull. A specialized, "concentrated" organ of hearing appears on the side of the head in the area of the jaw joint. The mouth possesses rows of hard teeth.

CLASS Mammals

Vertebrates which have fur, secrete milk for their young, and whose jaw joint is specifically formed by the articulation of the dentary element of the jaw with the squamosal part of the temporal bone of the skull. This latter is, of course, the criterion by which paleontologists distinguish mammals from near-mammals and non-mammals.



This diagram makes it look like there are only five orders of mammals. In actuality, there are two sub-classes of mammals, Prototherians and Eutherians. The orders of Prototherian mammals are the Monotremes (egg-laying mammals such as the Platypus and spiny echidna), and the Marsupials (pouched mammals such as the kangaroo, koala, wombat, and opossum).

The orders of Eutherian mammals are the Insectivores (shrews, moles and their relatives); Dermopterans (flying lemurs); Chiropterans (bats); Primates; Edentates (anteaters, sloths, armadillos); Pholidotans (pangolins); Lagomorphs (hares and rabbits); Rodents (mice, voles, agoutis, squirrels, porcupines, beavers, and their relatives); Mysticetes (baleen whales); Odontocetes (toothed whales); Carnivores; Tubulidentates (aardvarks); Proboscideans (elephants, mammoths, mastodons); Hyracoids (hyraxes); Sirenians (dugongs, manatees, and desmostylians); Artiodactyls (pigs, peccaries, hippos, camels, chevrotains, deer, giraffes, pronghorns, cattle, and their relatives); and Perissodactyls (horses, asses, half-asses, zebras, rhinos and tapirs).

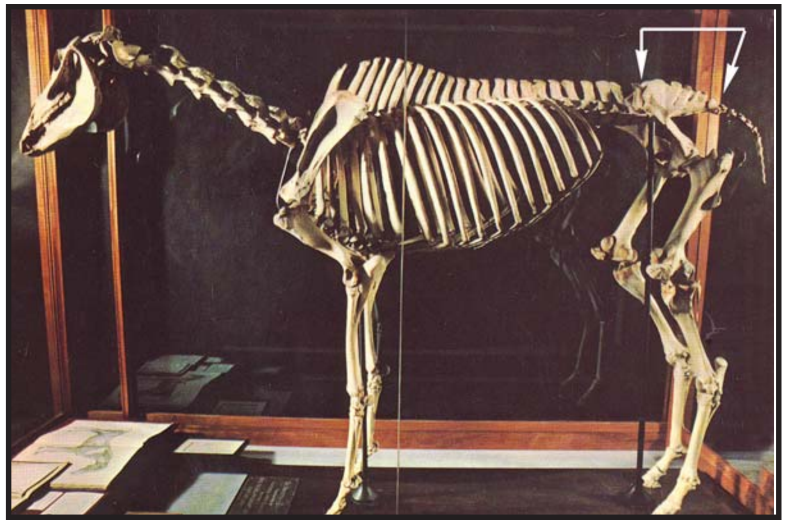
Generally speaking, mammals possess teeth of several different shapes – i.e., incisors, canines, premolars and molars; but some mammals lose all teeth or reduce them to vestiges (armadillos, pangolins, aardvarks, sloths), others modify them to fantastic new structures (baleen whales), and still others return to having teeth of uniform morphology (dolphins, killer whales). No matter how modified, however, mammals have only one row of teeth along the margins of the jaws, and they replace only the anterior part of the dental arcade only one time. The teeth develop in, and erupt through the gums out of, sockets called alveoli.

Primitively, the limbs of mammals terminate in five digits of about equal length arranged in a fan shape. From this original design many modifications have been tried, including loss of some digits, lengthening or shortening of one or more digits, fusion of digits to form a single stout digit, change from claws to either fingernails or hoofs, or change of the whole limb from a paw into a flipper or a wing.

With few exceptions, mammals have exactly 7 cervical vertebrae (whales and dolphins, and also giant ground sloths, have less than 7 vertebrae).

Each half of the mandible (the jawbone) in mammals is made up of but one, single element, the dentary bone (in reptiles, amphibians, fish, and birds the mandible is formed either of more than one bony element, or is formed from a different bone than the dentary)(see illustrations, next page).

The pelvis of mammals is likewise relatively simple, each half being composed of only three elements, the ischium, ilium, and pubis (the pelvis in other vertebrates tends to have additional elements). Importantly, mammals possess a sacrum composed of five or more vertebrae which fuse to make a rod above the pelvis. Birds and frogs also show fusions in this area, but they are far more extensive and serve to prevent flexion of the pelvis on the lumbar vertebrae. In mammals, up-and-down flexion of the spine is a crucial and characteristic element of locomotion, in contrast to the characteristically side-to-side, sinusoidal motions of the vertebral chain in reptiles, amphibians, and fishes (you can tell a fish from a whale or dolphin by the orientation of its tail fins: the fish's tail fin is vertical, because in order to swim, he "wags his tail" from side to side. Marine mammals, by contrast, have their flukes oriented horizontally, because the main swimming motion is "humping" or up-and-down action of the tail).

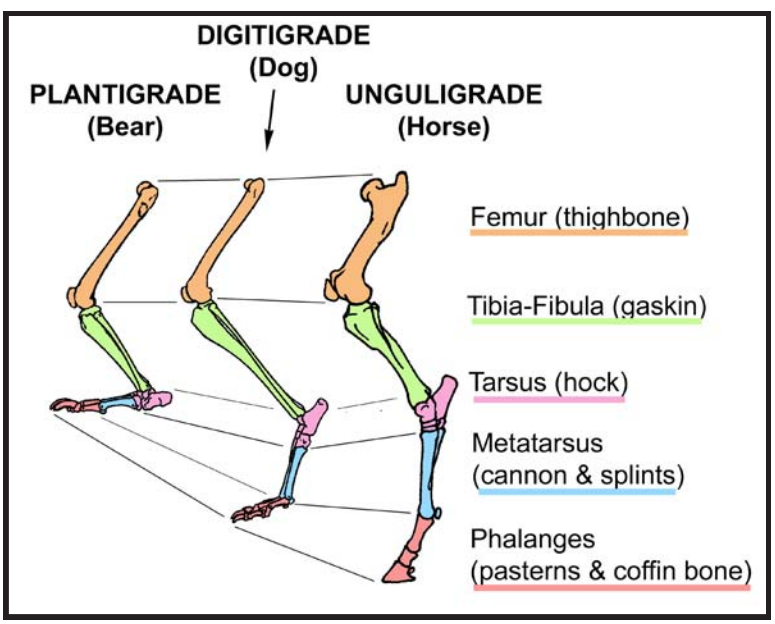


The skeleton of the famous Thoroughbred racehorse "Eclipse" on exhibit at the British Museum of Natural History in London. White arrows indicate the sacrum in Eclipse's vertebral chain.

Every student of the horse should be able to name and know the characteristics of all five of the classes of vertebrates: mammals, birds, reptiles, amphibians, and fishes. By contrasting mammals with the other four, we derive a richer picture of the unique nature of all mammals, and of the horse in particular.

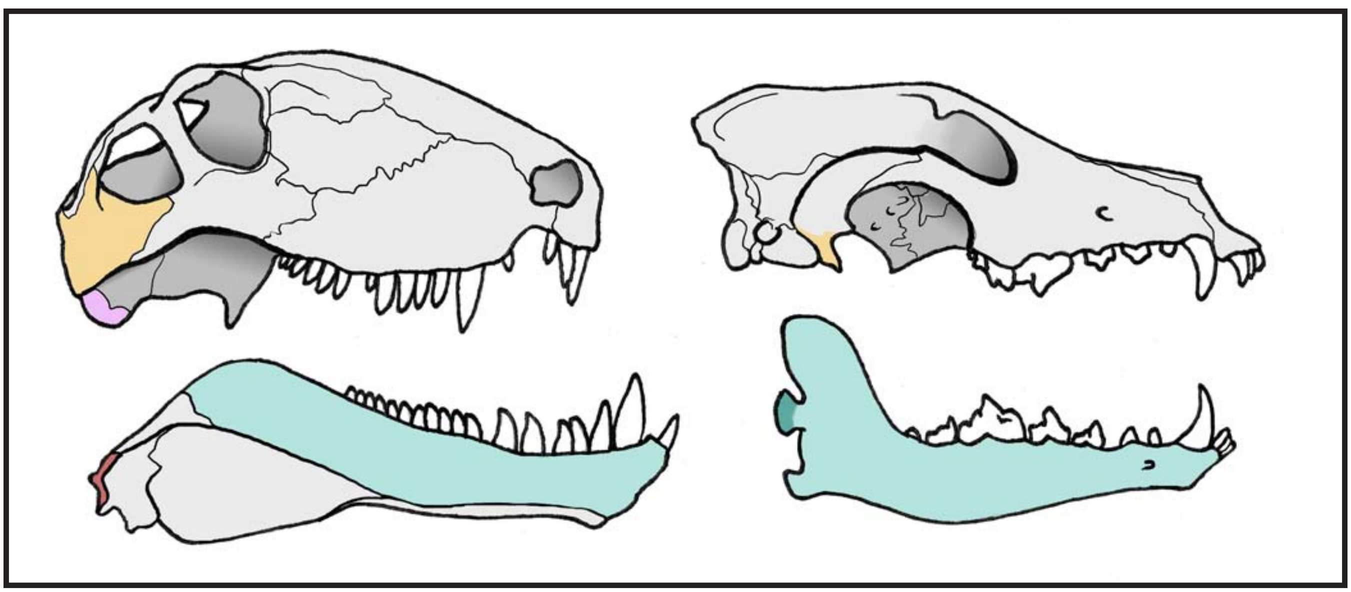
ORDER Perissodactyla

Herbivorous or omnivorous mammals that retain a caecal digestive system. Perissodactyls have single, obliquely-ridged tibial tarsal bones (astragali), in contrast to the other major order of herbivorous mammals, the Artiodactyla, which have double, parallel-ridged astragali.

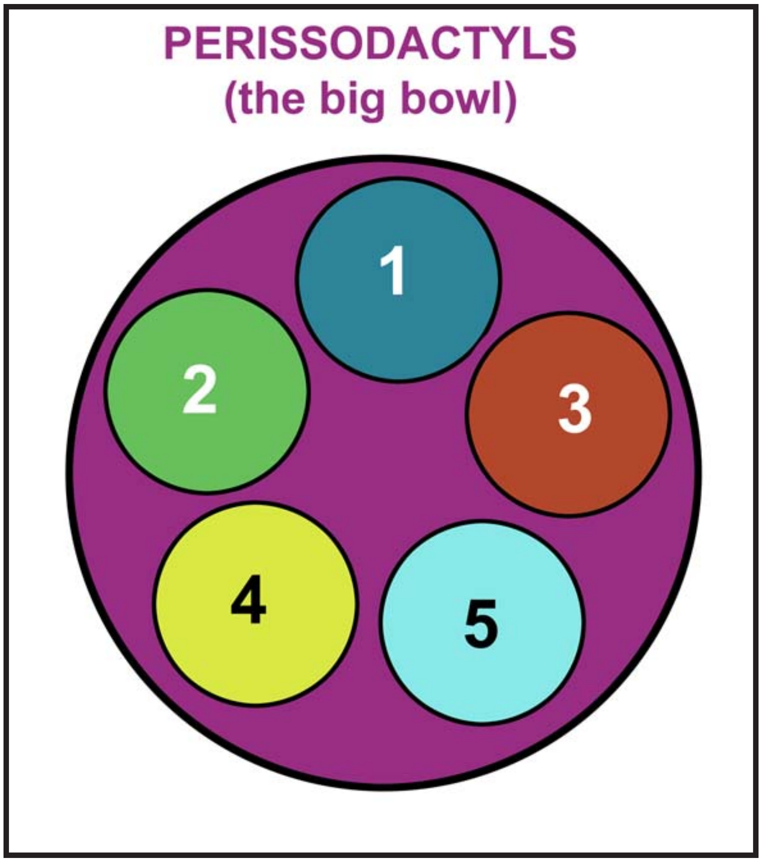


The "gradies" -- limb posture in mammals. People and bears are plantigrade, because we walk with the sole of our foot against the ground, and touch the ground with the calcaneus or fibular tarsal bone with each step. Dogs, "Eohippus", rhinos, chalicotheres, and brontotheres are digitigrade, because they walk with the palmar side of the knuckle joint and the undersides of the toes bearing most of the weight. Horses and Tapirs, along with most Artiodactyls, are unguligrade, because they stand upon a hoof and bear weight upon the broadened distal surface of the terminal phalanges.

The white arrow points to the jaw joint of this skull of a Przewalski Horse *(Equus caballus przewalskii)*. A vertebrate is classified as a mammal if the jawbone is made up of a single element (the dentary), which articulates with the squamous portion of the temporal bone of the skull (the “squamosal bone”).



The jaw joint in a mammal, such as the dog shown at right, is made up of the articulation of the dentary bone (blue) with part of the squamosal element of the skull above (yellow). The jaw construction of a reptile *(Dimetrodon)* is shown at left. Blue shows the dentary element of the jaw (below) and yellow the squamosal element of the skull (above); they do not articulate. Moreover, the jaw of the reptile is made of many bony elements, as shown by the multiple suture lines. The reptile jaw articulation is composed of the quadrate bone (above, pink) and the articular bone (below, red). In mammals, the entire jawbone is formed out of the dentary (blue; dark blue shows the actual articular surface)(After Romer, 1971).



There are five major groups within the Perissodactyl Order: Equids, Tapiroids, Rhinoceroses, Chalicotheres, and Brontotheres. The characteristics of each of these groups are explained in the text.

The term "Perissodactyl" comes from Greek words meaning "digits arranged around *(peri-)* a central toe *(-dactyl)"* – and this is indeed the foot-symmetry of all animals belonging to this Order. The central digit, designated by Roman numeral III, is the largest and bears most of the limb's weight, even when the animal retains three, four, or five toes. This too is in contrast to the Artiodactyla, in which the main part of the weight is shared by closely-appressed or fused digits III and IV.

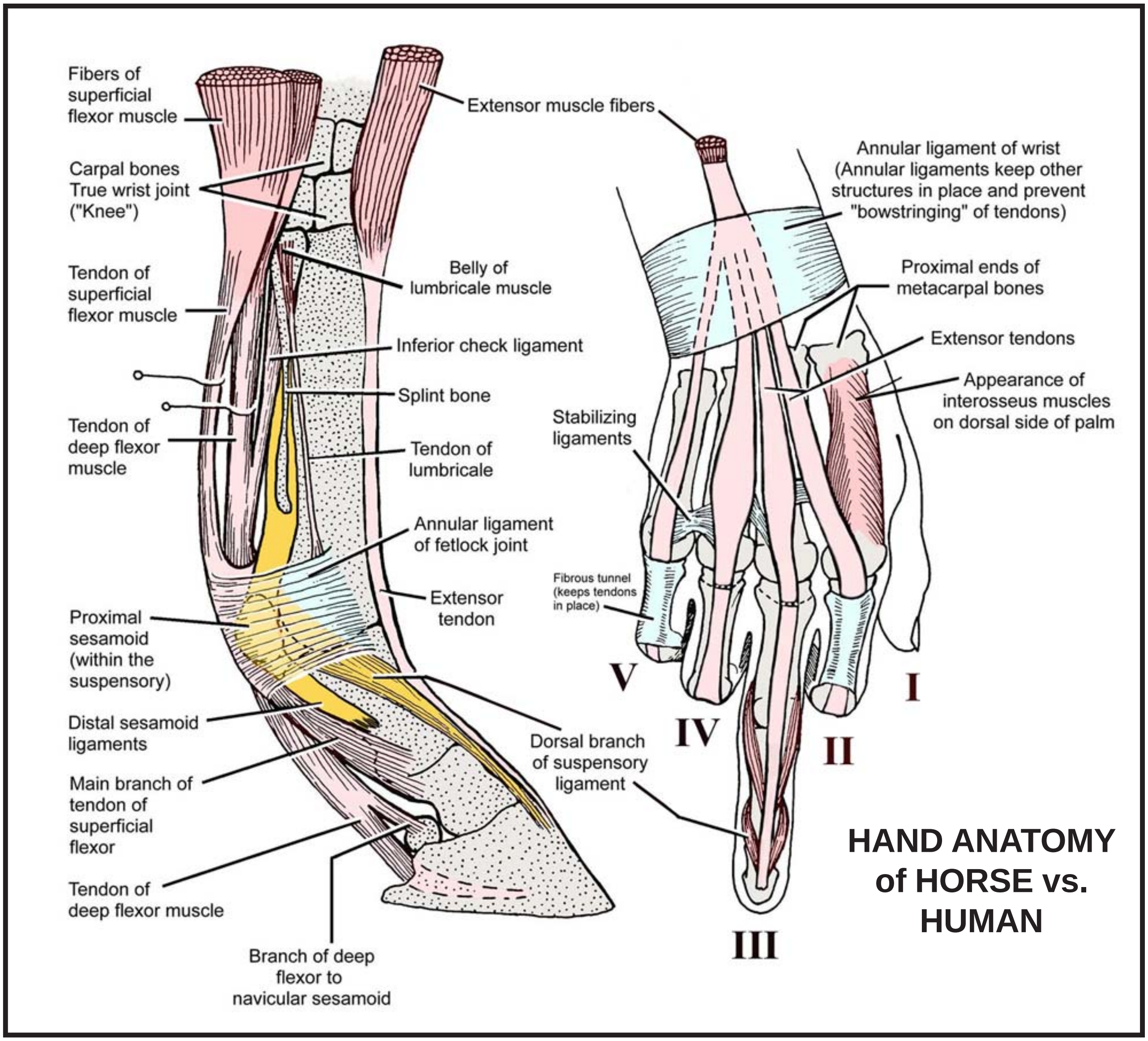
There is a strong tendency to flatten the radius and to closely appress it to the ulna, so as to inhibit or prevent supination of the manus (turning the forefoot inward or upward). In the hind limb, the tibia becomes reduced in size and loses its articulation below with the tarsus. A deep pair of grooves on the distal end of the tibia, which are obliquely oriented to match the ridges on the astragalus, forms a strong, tight, and stable articulation and likewise prevents the hind foot from turning inward.

All Perissodactyls have 18 thoracic vertebrae (and thus 18 pairs of ribs), although the number of lumbar vertebrae may be as high as 8.

Perissodactyls have bunodont (cusped) or lophodont (ridged) teeth. In the upper dentition, the teeth have the cusps or ridges are so arranged that when the tooth is somewhat worn, they make a shape that looks like the Greek letter "pi". Worn lower teeth look like the small letter "m".

The tooth formula in Perissodactyls is usually as follows: in each half of either the upper or lower jaws, there are: 3 incisors, 1 canine, 4 premolars, and 3 molars. Normally, the tooth formula is written this way: I3C1P4M3. This contrasts with the more advanced Artiodactyls such as sheep, cattle, and camels, which possess no upper incisors -- although some Chalicotheres (which are perissodactyls) also lack upper incisors.

The jaw condyle is lozenge-shaped and transversely oriented. It articulates with a glenoid fossa (formed in the squamous part of the temporal bone of the skull) which is saddle-shaped, shallow, and open to the front. The chewing motion is rotatory, with the lower jaw being moved first downward, then laterally, and finally obliquely up-and-across. The lateral component of the chewing motion is more prominent in hypsodont forms -- the grazing horses and rhinos -- than in browsing forms, which tend to retain large cusps on the teeth that block full lateral excursion.



The manus or hand of the horse and human compared. The "hand" includes all parts of the limb beyond the wrist. The true wrist or carpus of the horse is commonly called the "knee", which can confuse matters. Anatomically, everything below the horse's "knee" in the forelimb is its manus; the palm of its hand is, therefore, where we find the tendons. It is the same in the hind limb; since the "hock" is the true ankle or tarsus, everything below that is the horse's hind foot, and the sole of the foot is where we find the tendons.

The horse is an ungulate animal and has an unguligrade limb posture, in which it stands on the tip of the most distal bone of digit III. The most distal bone of the limb in a horse is commonly called the "coffin bone", but its proper anatomical name is the distal phalanx or third phalanx ("phalanx" is sometimes spelled phalange, and the plural of phalanx is phalanges).

Any given digit includes all bones from the wrist or carpus down. Traditionally, the digits are designated by Roman numerals, and primitively in mammals there are five of them. The horse has enlarged digit III, vestigialized digits II and IV so that they are thin and have no functional phalanges, and has entirely lost digits I and V. The horse's fore "cannon bone" is the enlarged metacarpal of digit III.

There are a number of important general trends among Perissodactyls:

(1) They tend to go for body-size increase as a way to avoid or inhibit predation. They increase not only in height but in bulk – even to extremes, such in Baluchitheres, which stood an unbelievable eighteen feet high at the shoulder, and were the largest land mammals ever to exist.

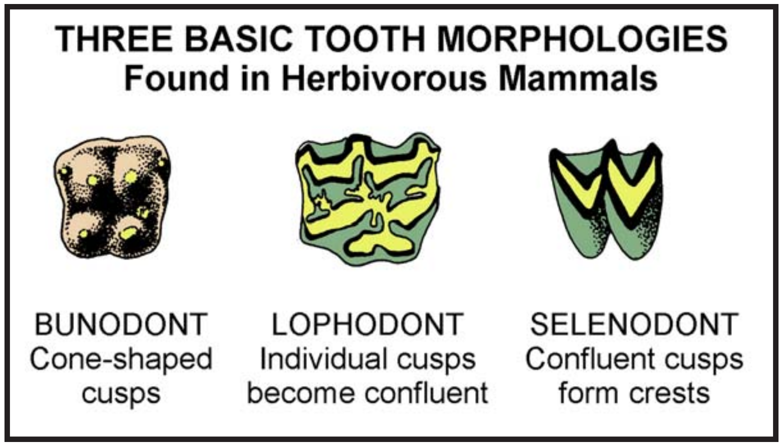
(2) They tend to lose digits. All of them lose digit I (the thumb) early on; many also lose digit V (the pinkie). Thus, the normal condition in Perissodactyls is to have three or four toes per foot. By contrast, the normal condition in Artiodactyls is to have either four or two toes per foot.

(3) None of them are plantigrade.

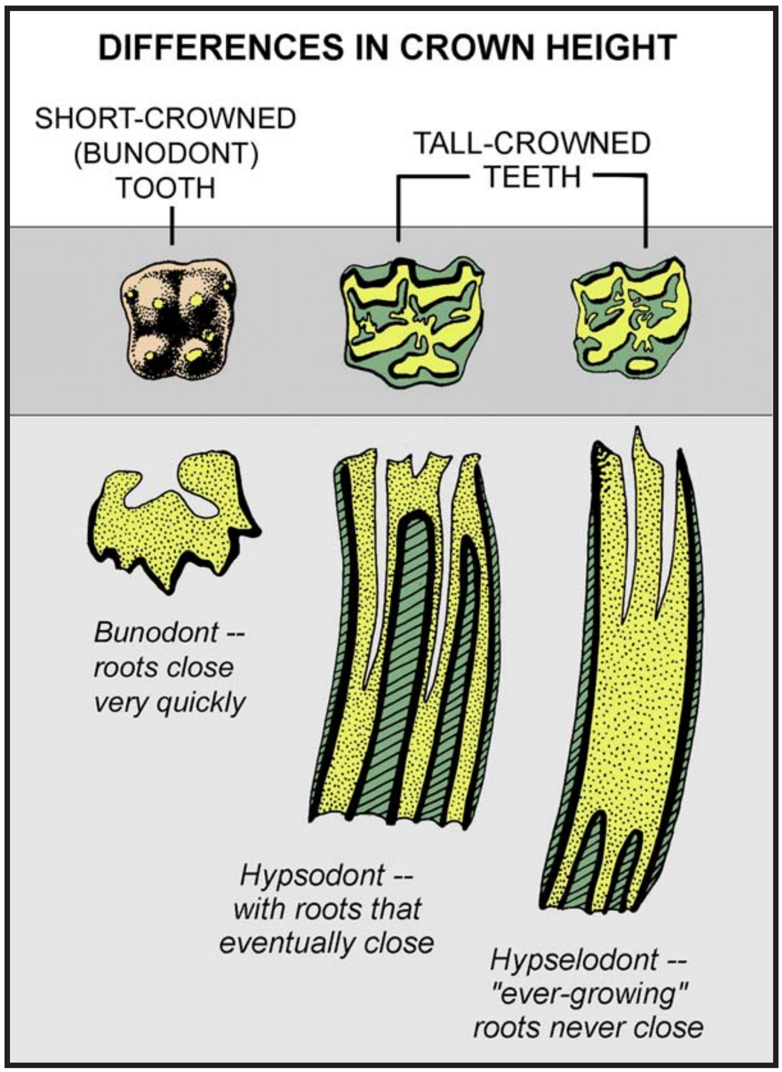
(4) As a strategy to make the teeth last longer in eating a tough, abrasive herbaceous diet, they tend to increase the crown-height of the teeth, becoming either hypsodont (high-crowned) or sub-hypsodont.

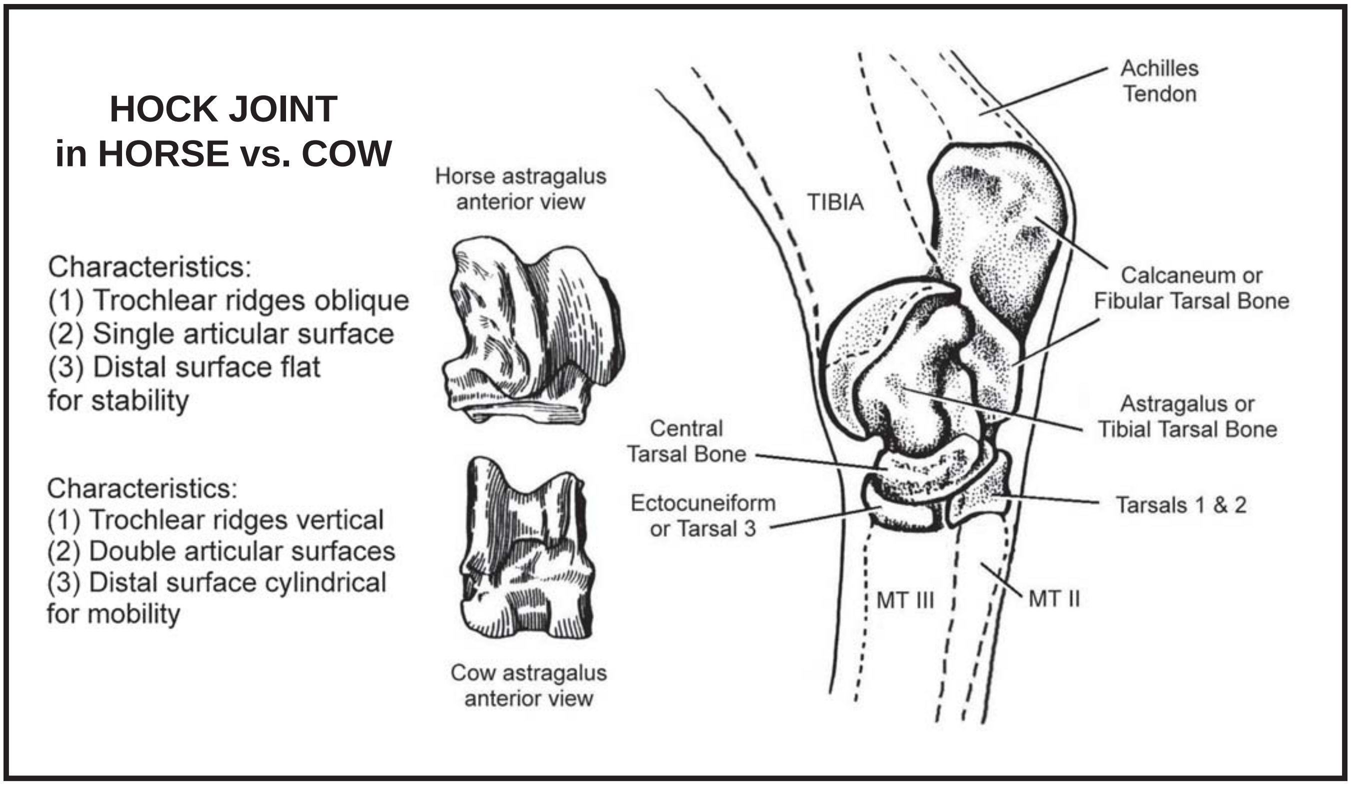
Hyracotherium ("Eohippus") has bunodont teeth. *Equus* has hypsodont teeth. The fossil genus Pseudhipparion developed hypselodont or "ever-growing" cheek teeth, in which the roots never closed. Keeping the roots open means maintaining the blood supply, so that the cells that make new tooth material may be kept alive.

Horse teeth are made up of three hard materials: enamel, dentine, and cementum. In both diagrams on this page, tan = enamel; yellow = dentine; green = cementum. In bunodont teeth, enamel coats the tooth as icing coats a cupcake. With wear, the enamel "icing" becomes thin and finally breaks through, exposing the dentine which makes up the bulk of the tooth.



Early members of the horse family, such as *Hyracotherium* ("Eohippus"), have bunodont teeth; so do we humans. Grazing-adapted equids, including the living horse *Equus* caballus, have lophodont teeth. Certain artiodactyls ("cloven-hoofed animals"), such as sheep and camels, have selenodont teeth.





The key bone of the hock is the tibial tarsal or astragalus bone. In horses and other perissodactyls, the ridges or trochleae that articulate with grooves on the lower end of the tibial bone are oblique. In cattle and other artiodactyls, the ridges are vertical, and there is both an upper and a lower set of them.

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(5) As a further strategy to increase the life of the teeth and thus the potential lifespan of the animal, they tend to increase the complexity of the teeth – which translates in lophodont teeth to increased length of the enamel bands exposed on the tooth crown.

(6) They tend to reduce the size of the first premolar tooth (P1 in both upper and lower dentitions), while increasing the size of the molars and the other premolars. There is a strong tendency to form the “cheek teeth” into a battery of uniform or near-uniform size.

(7) They tend to develop a long anterior skull with one or more toothless spaces between the cheek battery to the rear and the incisors in front.

(8) They tend to have nasal or frontal horns.

(9) They almost universally have a short trunk or proboscis, or at least a soft, strong, flexible, semi-prehensile upper lip.

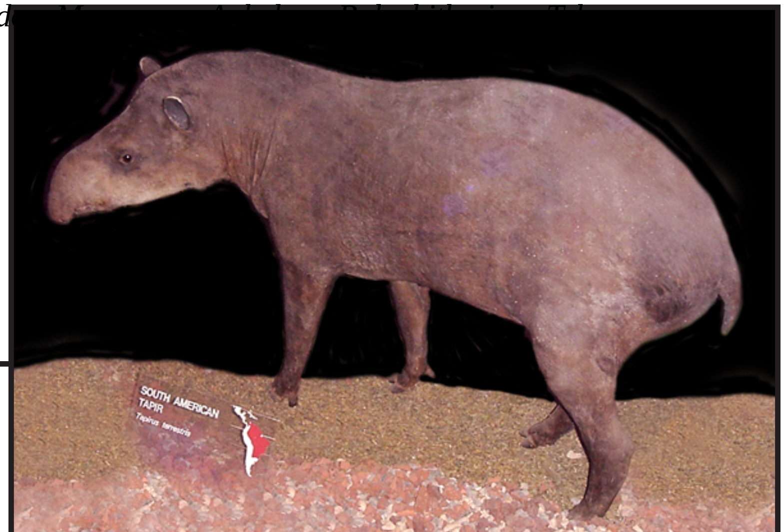
All interested students of the horse will want to take every opportunity to look at the mounted skeletons of Perissodactyls which they will find in Museums of Natural History. Throughout time, there have been five major Families of Perissodactyls, to wit:

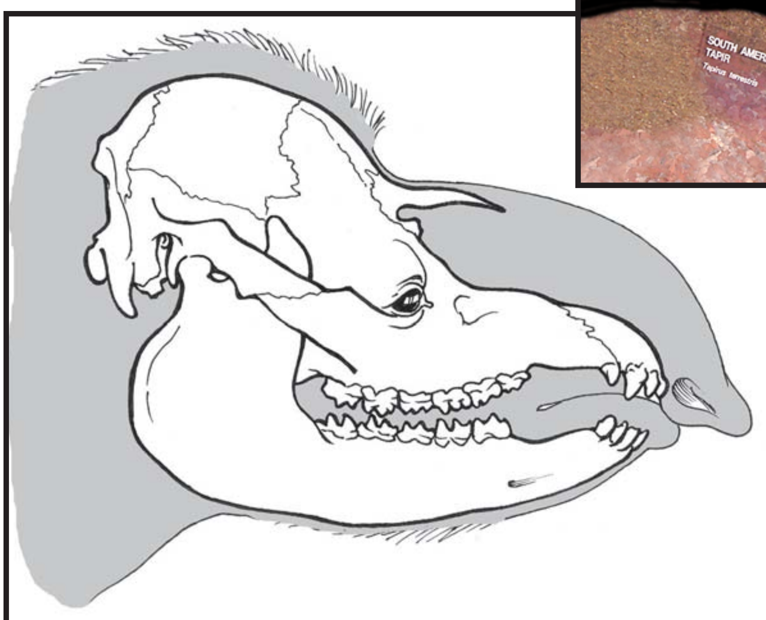
Equids – *Hyracotherium, Paleotherium, Parahippus, Griphippus, Astrohippus, Cormohipparion, Neohipparion, Hipparion, Onohippidion, Calippus, Anchitherium, Nannippus, Megahippus* and many other fossil genera besides the still-surviving *Equus.*

Tapiroids – The tapir genus *Tapirus* still survives, but the group was once much more common, including such forms as *Homogalax, Helaletes, Hyrachyus, Chasmotherium, Lophiodon, Paleotapirus, and Protapirus*. Tapirs are round-backed, moderately heavy-bodied animals with pronounced retraction of the nasal notch and development of a short proboscis. They live in forests or along the forest edge, eating a mixed diet of leaves, fallen fruit, and insects.

Rhinocerotoids – The still-surviving genera *Ceratotherium, Dicerorhinus, Diceros,* and *Rhinoceros* plus their fossil relatives, including *Hyracodon, Amynod*

THE TAPIR GALLERY





Above: Taxidermy mount of the living South American tapir, to show the body form of the animal. It stands about two feet high at the shoulder, and has four functional toes on each limb. Notice the short, highly-prehensile proboscis or trunk that serves the animal as a finger.

Right: Skull of a tapir, showing the very high degree of retraction of the nasal notch. The bone that sticks out over the animal's eye like an awning is the shortened nasal bone. The drawing (above) relates the shape of the animal's mouth and fleshy trunk to the underlying skull.

THE RHINO GALLERY

Left: skull of the still-extant (but highly endangered) African black rhino, *Diceros bicornis*. Note the stout nasal bones that, in life, supported a pair of large horns. The teeth are sub-hypsodont. Below: mounted skeleton and skull of the fossil rhino *Aphelops* from the Pliocene of Nebraska. Note the thinner and more fragile nasal bones in this species; though it was fully as big as the black rhino, it was probably hornless. Rhinos have the second incisors of the lower jaw enlarged to form tusks.

Elasmotherium, and many more. Rhinoceroses are moderately to extremely large animals with a thick, tough, largely hairless hide. They characteristically have long, scoop-shaped heads and one or more horns (made of compressed fibers similar to hoof horn) upon their nose. Some diet mostly upon leaves and twigs, while others prefer grass.

Chalicotheres – An odd and wholly-extinct group uniquely characterized by long, heavy forelegs with claws. Chalicotheres are the only Perissodactyls that retain and even enhance the ability to supinate the manus. They are thought to have dieted primarily upon leaves and twigs, using their clawed forelimbs, slope-backed build, spout-shaped mouth and long rounded tongue to grasp branches and stip them of leaves. The best-known genus is *Moropus.*

Brontotheres – These animals may be likened to rhinos that have imitated Arnold Schwarzenegger: they are generally larger than rhinos and far more massive through the shoulders and chest. Instead of having one or two conical horns mounted “in line” on their nose, they possess a flattened, saddle-shaped horn of bony construction mounted

ANOTHER INTERESTING EXTINCT RHINO

Right: *Teleoceras*, a rhino with hippo-like body morphology. This species, which was contemporaneous with *Aphelops* in North America, occupied a completely different ecological niche. While *Aphelops* preferred the forest margin and dieted mainly upon leaves and twigs, *Teleoceras* lived in and near rivers and ponds. Very short-legged, it avoided predators by submerging itself in water by day. At night it would come out and feed upon grass growing near the water. The grass-eating habits of this rhino are reflected in the structure of its teeth, which are more hypsodont than those of almost any other rhino. Top: mounted skeleton; middle, skull in right lateral view; bottom, left forefoot showing the short toes and broadened “coffin bones”.

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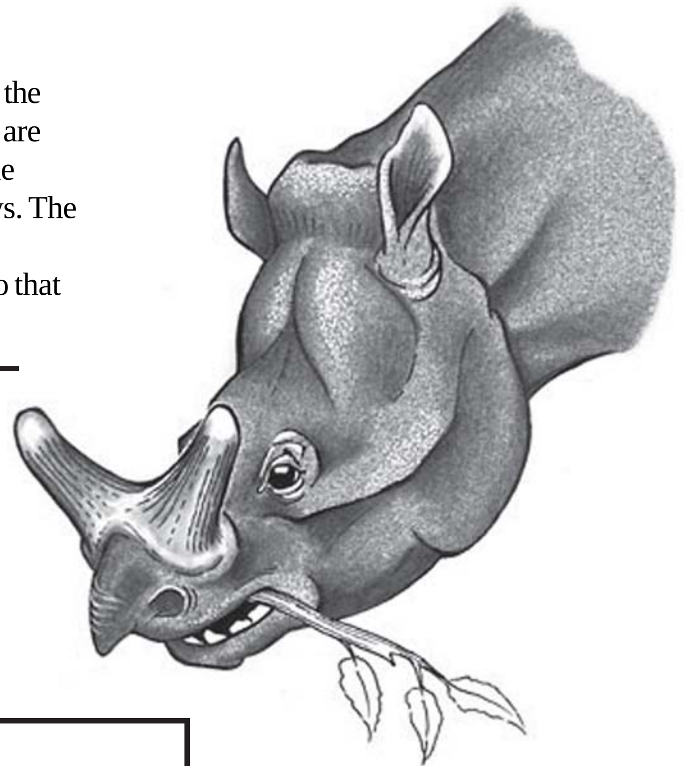
crosswise. Now wholly extinct, the group’s best-known members are *Brontops, Brontotherium, Titanotherium, Manteoceras,* and *Paleosyops.*

FAMILY Equidae

Equids are perissodactyls that tend to retain lightweight bodies, and that typically have a cursorial (running) mode of locomotion. While *Hyracotherium,* the earliest member of this family, retains four toes on the forefoot, and while *Equus* and some other late members of the family have only one functional digit per foot, the norm is for there to be three functional digits on each limb. This contrasts with the Artiodactyls, in which the norm is for there to be two functional digits per limb.

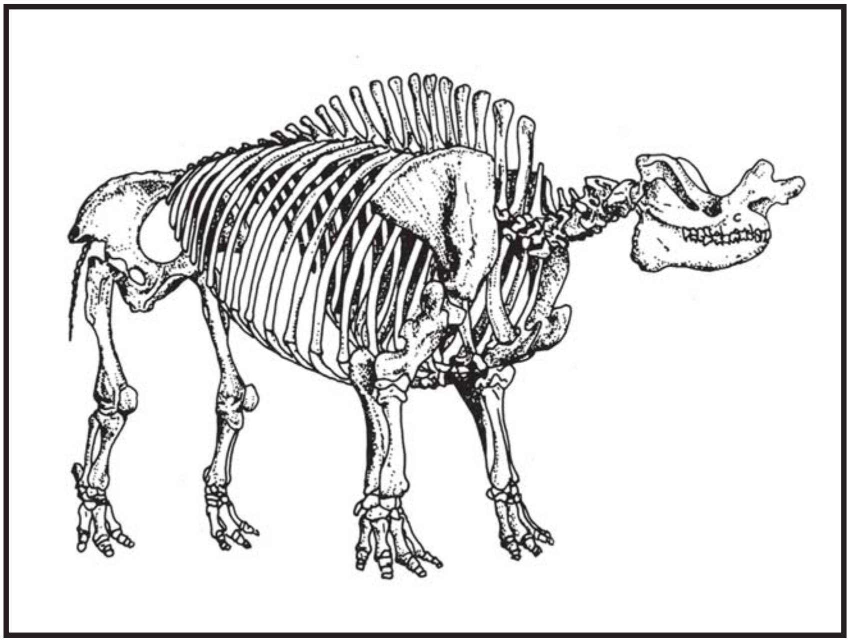
The general tendency among Equids is to lengthen the distal elements of the limbs, i.e. those bones below the carpus and tarsus.

They also strengthen and stabilize the distal limb joints: the carpal and tarsal bones articulate closely together, and are formed as block-like rather than rounded elements. The carpal bones are arranged into proximal and distal rows. The distal row tightly articulates with, and is firmly tied by ligaments to, the top of the metacarpal bones below, so that



TITANOTHERES

These perissodactyls had their main proliferation during the Oligocene epoch, then died out. To the right is my restoration of the living appearance of a Titanothere's head. Note the low-crowned teeth and the fact that there is no diastema (toothless interval or "bars"); the anterior premolars are large and the tooth row is continuous from the incisors and canines back to the cheek teeth. Titanotheres were browsers, dieting on leaves and twigs; they could not eat grass, even if there had been any. The mounted skeleton below is of the huge *Brontops*, which stood some eight feet high at the shoulder. To acquire large body size is a dandy way to avoid predation.



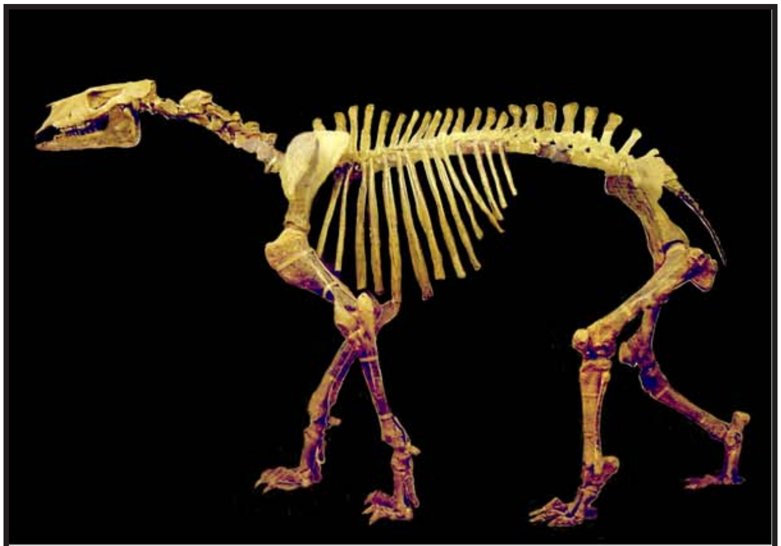
when the carpus folds only two joints open: that between the proximal carpal row and the distal end of the radius and ulna, and that between the two carpal rows.

Equids reduce the number of lumbar vertebrae to six, while enlarging the sacrum and retaining 18 thoracic and 7 cervical vertebrae.

Dentally, Equids are unique among herbivores in not only possessing, but uniformly enlarging the upper incisors. They typically possess a strong set of incisors not only in the upper but in the lower jaws, and are thus the only mammals whose dental functioning depends upon a "three point" balance, i.e. when the jaws are closed and centered, pressure is shared by the incisors, cheek teeth, and the jaw joint.

CHALICOTHERES

The oddest of all perissodactyls are the chalicotheres (pronounced “calico-theres”). They are the only perissodactyls that do not have hoofs; instead, they have large claws mounted on broad, rather mobile paws. Their long forelimbs and sloping body-build helped them to reach up into the branches of trees to pull down bunches of tasty leaves. Notice the somewhat horse-like head, and, again unique among all perissodactyls, the absence of upper incisors. So amazed were the bone-hunters who first discovered the remains of this animal that they were convinced they must have found the bones of two different species mixed together. Only when un-doubted, articulated remains came to light was there proof that this unusual animal was, indeed, “for real”. The skeleton of *Moropus* is on exhibit at the University of Nebraska State Museum in Lincoln. Top: the skeleton; middle, skull in left lateral view; bottom, the left forefoot, to show the clawed digits.



SUBFAMILY Equinae

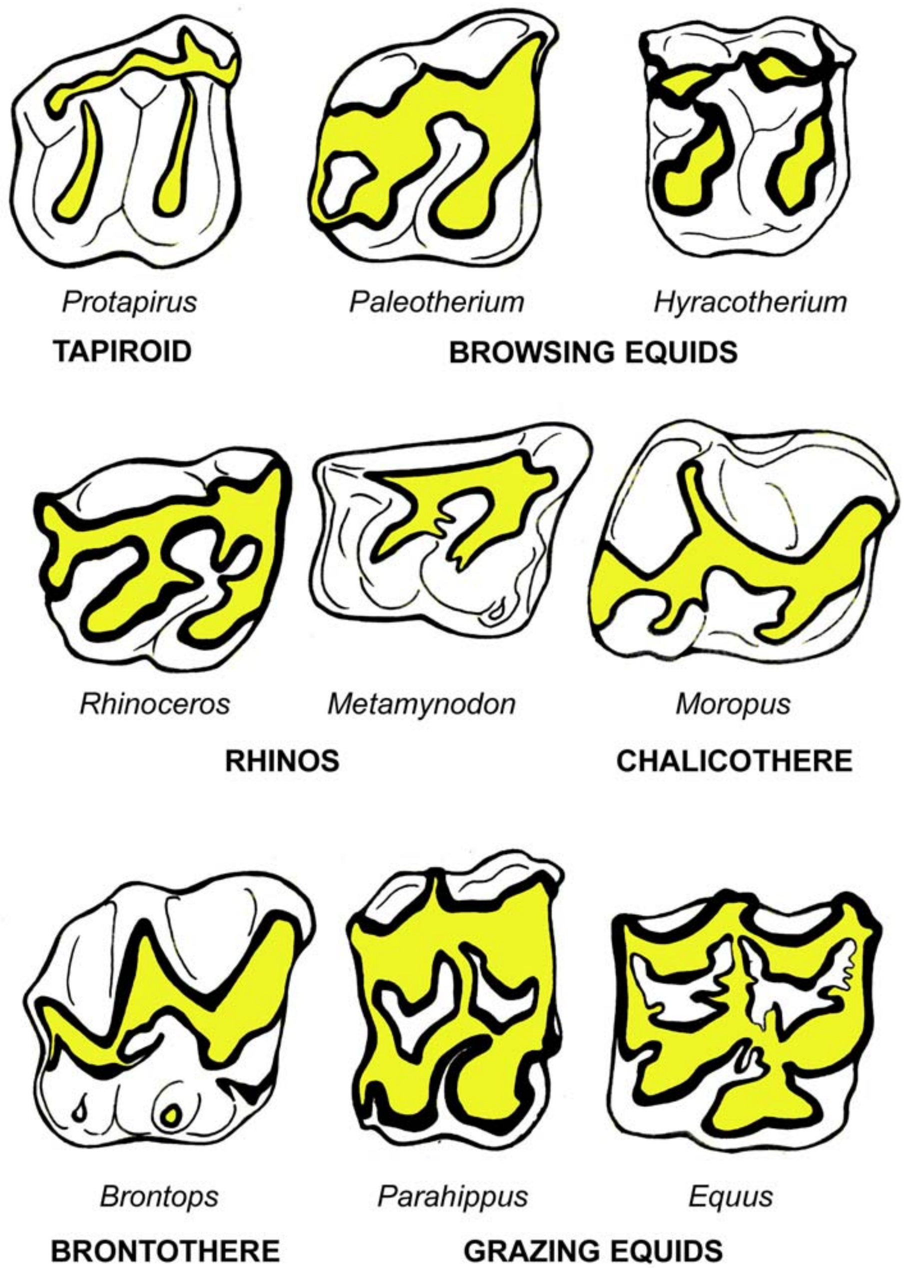
(Please note that the taxonomist’s use of the word “Equine” – capital “E” – differs from the way your veterinarian uses the word “equine” – little “e”. In veterinary parlance, “equine” means any of the living horse-like animals, i.e. not only domestic horses but Przewalski horses, zebras, onagers, or asses. These are also Equines – but the Equinae also includes a large number of extinct forms known from the fossil record).

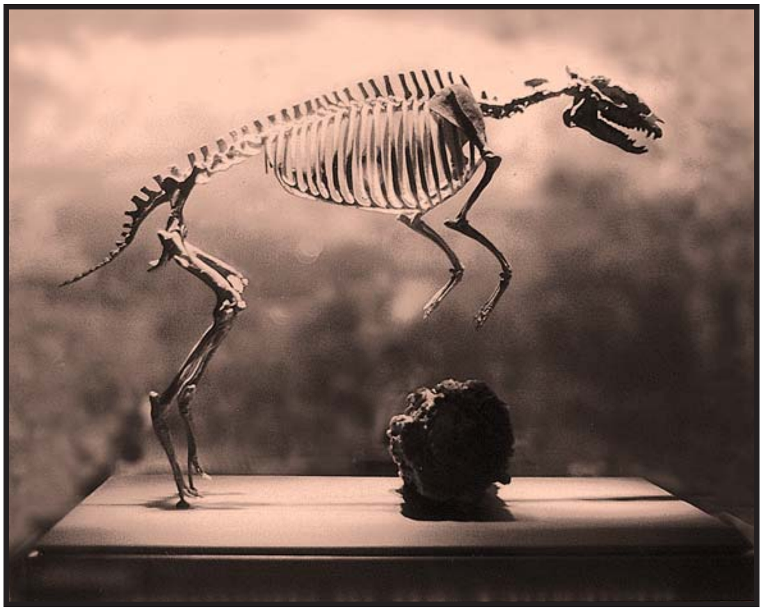
Equines are Equids adapted for eating grass. Thus, they have hypsodont teeth with cementum, a bone-like material, to support and strengthen each tooth. They have stout, wedge-shaped skulls in which both the maxilla and dentary are deep to accommodate the tall-crowned teeth.

The shape of the teeth is important in perissodactyl classification. While all perissodactyls build their teeth on the basic Greek letter “P” design, each order varies it in a characteristic way.

These drawings show the chewing or “occlusal” surfaces of one representative cheek tooth from a variety of perissodactyls. All the teeth show early to moderate wear. This means that the “icing” of enamel which was originally continuous over the surface of the tooth when it first erupted, has been worn through to expose the dentine (yellow) that composes the body of the tooth within. In all examples, the cut edge of the enamel is shown as a heavy black line. Notice that only the grazing equids have two fossettes or fully-rimmed circlets on the crown. These are filled with cementum (not shown).

Fourth Premolar teeth in Various Perissodactyls, to show variations on the π design. All teeth reduced to same width





A marvellous mount of the skeleton of *Hyracotherium* ("Eohippus") on display at the U.S. National Museum of Natural History/ Smithsonian Institution in Washington, D.C. The fossil horse is jumping over a fossil log! *Hyracotherium* is considered to be the earliest member of the horse family, Equidae.

The superior teeth of Equines have two fossettes. Each fossette is filled, or largely filled, with cementum.

Except for the first premolar, which is greatly reduced in size, the premolar and molar teeth of equines are large, square in cross-sectional shape, and tightly appressed to each other to form "cheek batteries" for the efficient grinding of grass blades.

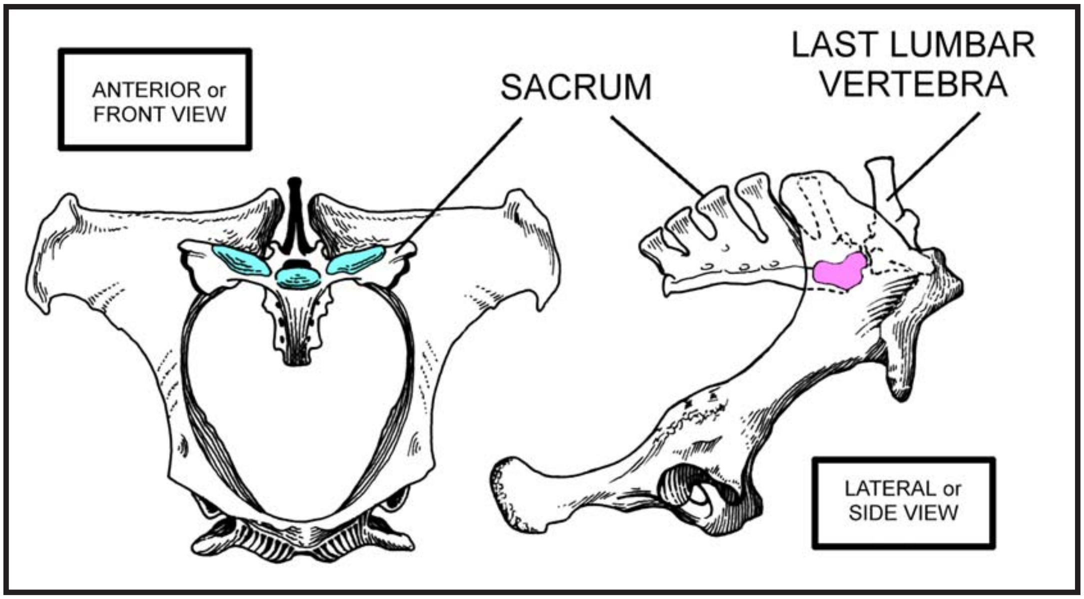
There is a strong tendency among equines to retract the nasal notch, i.e. to "undercut" the nasal bone, even to an extreme degree (vis., *Hippidium* and *Onohippidion).* In such forms, deep pits or "facial fossae" tend to be present on the face, the complex as a whole indicating the presence of a small trunk or a strongly prehensile upper lip longer than that in the living horse. Where there is little or no retraction of the nasal notch *(Neohipparion, Nannippus),* the face will be smooth, lacking facial fossae. Forms that have smooth faces tend to have the most complex and most highly hypsodont teeth.

Equines are universally unguligrade, having hoofs rather than claws and never locomoting with the hock, carpus, or "ankles" (the joint between the distal end of the cannon bone and the pasterns) touching the ground. Generally speaking, they are are tall and have proportionally long distal limb elements. They are adapted for straight-line flight over firm substrates in open terrain.

Equines characteristically develop joints between the "wings" of the sacrum and the transverse processes of the last lumbar vertebra. They also have articulations between the transverse processes of the last several lumbar vertebrae. Moreover, the joints between the accessory articular processes in the lumbar vertebrae of equines are vertically-oriented, and they are shaped to articulate like dovetail joints. These "inter-transverse" and "dovetail" articulations almost totally inhibit rotation and lateral flexion among the lumbar and lumbo-sacral joints, while promoting up-and-down coiling of the lumbo-sacral joint and loin-span. This is in sharp contrast to Artiodactyls, which retain long, relatively loosely-articulated lumbars which permit twisting and a greater degree of lateral flexion.

TRIBE Protohippini

Protohippine equines are distinguished by possessing high-crowned teeth that are nevertheless comparatively simple in structure (the genus *Equus* has the most complex teeth within the Protohippine lineage).



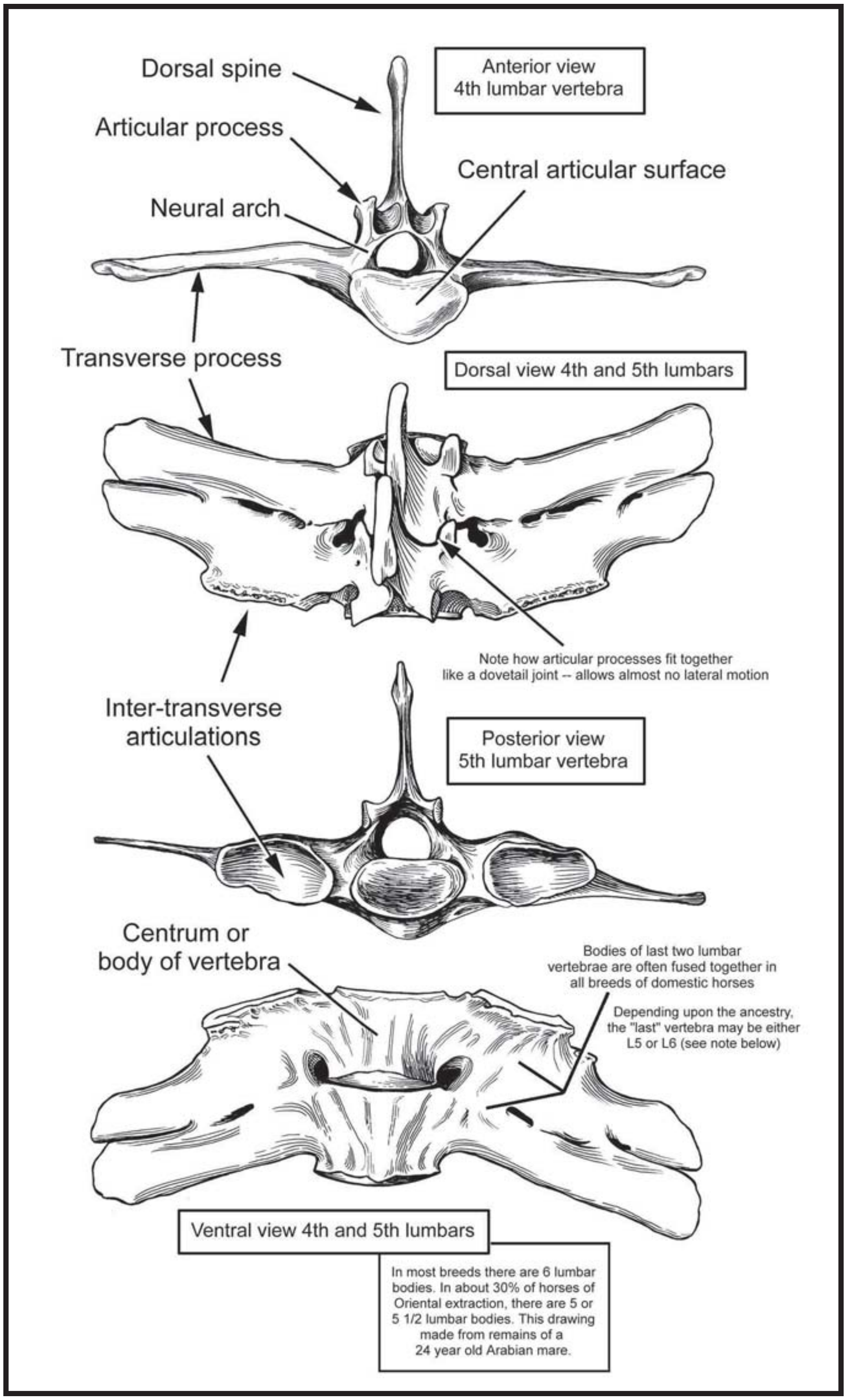
The front end of the sacrum bone in the horse bears three surfaces (blue) for articulation with the back end of the last lumbar vertebra. The central one is the "central articular surface", while the lateral ones are inter-transverse articulations. Together, these make up the sacro-lumbar joint. Purple color shows a nearby joint often confused with it: the sacro-sciatic joint, by which the sacrum is articulated to the pelvis. See next page for images of inter-transverse articulations between lumbar vertebrae.

An important distinguishing characteristic of the Protohippine dentition which is easy to see is that the protocone loop of enamel is joined to the hypoloph, not set off (as it is in Hipparionines) as a separate circlet.

Two kinds of skull and skeletal structure may be found within the Protohippini: one is the "normal" or mesomorphic build we associate with the genus *Equus*. These animals have flat or slightly-rounded backs, nasal notches only moderately retracted, moderately prehensile upper lips, and smooth faces. The other type re-echoes the "chalicomorph" or "okapi-like" body design in having forelimbs longer than hind limbs, a sloping back, deeply-retracted nasal notch, and deep facial fossae for the attachment of the muscles to move a long, strongly prehensile upper lip or short trunk. *Pliohippus* is an outstanding example of this, and study of *Pliohippus* should remind students never to fall back into the old 19th-century "evolutionary progression", proposed by O.C. Marsh, that supposedly led from *Protohippus* through *Pliohippus* to *Equus*. *Equus* is the descendant of *Protohippus* and *Dinohippus*, both flat-backed and smooth-faced genera, not *Pliohippus*.

Not surprisingly, to go along with the two different body-styles found within the Protohippini, there are two sorts of dentition. *Equus* and earlier members of its direct lineage have relatively straight teeth, with the angles of the "tables" or occlusal surfaces of the cheek batteries set at from 7 to 10 degrees of slope. *Pliohippus* and other "okapi-like" forms have upper teeth with a lot of curve to them, and thus table angles ranging from 10 to 25 degrees of slope. These teeth have exceptionally heavy outer styles and buttresses, and very simple lower teeth; such a design is less for dealing with grass than with "chop", i.e. twigs, leaves, and bark rather than grass. The supposition is that *Pliohippus* and similar forms were eating a diet similar to a deer's.

The other Equine Tribe is the Hipparionini. Students of the horse should take every opportunity, by visiting Museums of Natural History, to familiarize themselves with these animals. Hipparionines are typically small, narrow-bodied, lightweight, agile and dainty. While Protohippines tend to be large and heavy, Hipparionines are



Inter-transverse joints between lumbar vertebrae in a domestic horse mare. In some cases, one or more of the last several lumbar bones not only articulate but fuse together.

relatively small, some even becoming dwarfs no larger than the African dik-dik. All Hipparionines have extremely hypsodont teeth with highly complex structure, good for processing dry forage. These animals were, evidently, filling the ecological niche now exclusively occupied by antelopes.

GENUS *Equus*

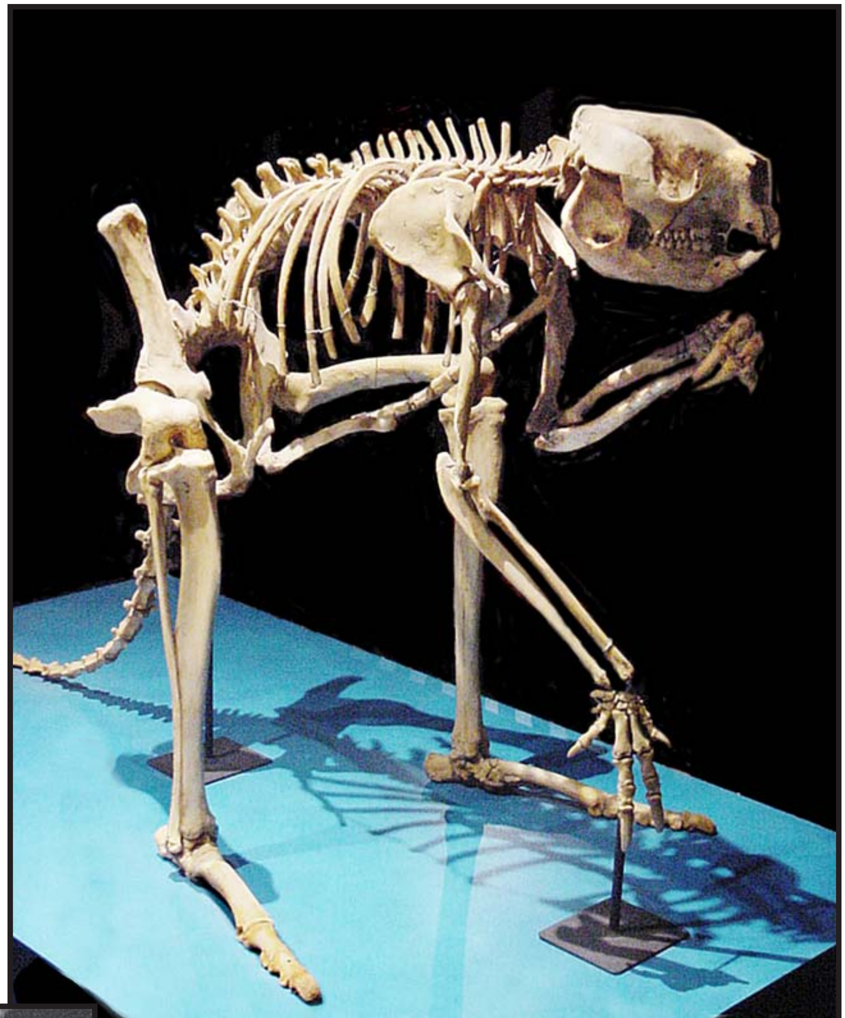
Members of the genus *Equus* have but one functional toe per foot.

It should be noted that *Equus* is not the only horse genus to become monodactyl; for example, there is a species of *Neohipparion* from the Ashfall Quarry in northern Nebraska that achieved this condition long before either *Equus* (or its direct ancestor *Dinohippus)* came into existence. Nevertheless, monodactyly is a derived character shared by all members of *Equus*, and is thus a diagnostic feature of the genus.

As previously stated, *Equus* has highly hypsodont teeth which have complex, more wrinkled enamel structure than other members of its lineage.

Once again, however, *Equus* does not have the most high-crowned teeth known among Equids: Hipparionines have teeth which are equally or more high-crowned than *Equus,* and there is even one species of *Nannippus* known from Florida which actually develops hypselodont teeth in which the roots never close and the tooth is “ever-growing”. Nor does *Equus* have the most complex enamel structure; that honor belongs to *Cormohipparion, Neohipparion,* and some of the European species of *Hipparion*.

Students of the horse should, by visiting a Museum of Natural History, study the remains of all the fossil horses. There are many more genera than the old "hippuses" ladder-of-descent litany tends to include, and, although I repeatedly admonish students to visit their local Museum, I forewarn you that many of the exhibits you see there are likely to be sadly out of date (this is because since the Carter Administration, and much more seriously since the Reagan Administration, federal funding for Museums and for all forms of so-called "esoteric" research has been cut to the bone. This is not the only reason, but it is an important one, why the author herself does not work in a Museum). So, when you visit the Museum you may see a "horse evolution exhibit" that still features the hackneyed and incorrect series that typically starts with "Eohippus" *(Hyracotherium)*, and then proceeds



Above: The living horse, *Equus caballus*, not only is not the only monodactyl horse -- horses are not the only monodactyl animals. The skeleton of this extinct short-faced kangaroo *Procoptodon* is on exhibit at the Museum of Natural History in Adelaide, South Australia. I'm amused by this exhibit; the animal seems to be having a good laugh at the presumptuousness of horses (quite in the Ozzie style).

Left: Photograph sent to me a number of years ago by a horse owner. This foal, born from a completely normal mare, has a super-numerary digit. For several reasons, this is an example of abnormal development of the fetus rather than a "throwback condition". First, the small digit appears on only the medial side of one limb -- thus there are not three toes, but two. Second, the bones of which it is composed are not articulated with the corresponding metapodial bone (medial "splint" bone) above. Extra digits like this one occur due to errors in cell division that occur early in fetal development.

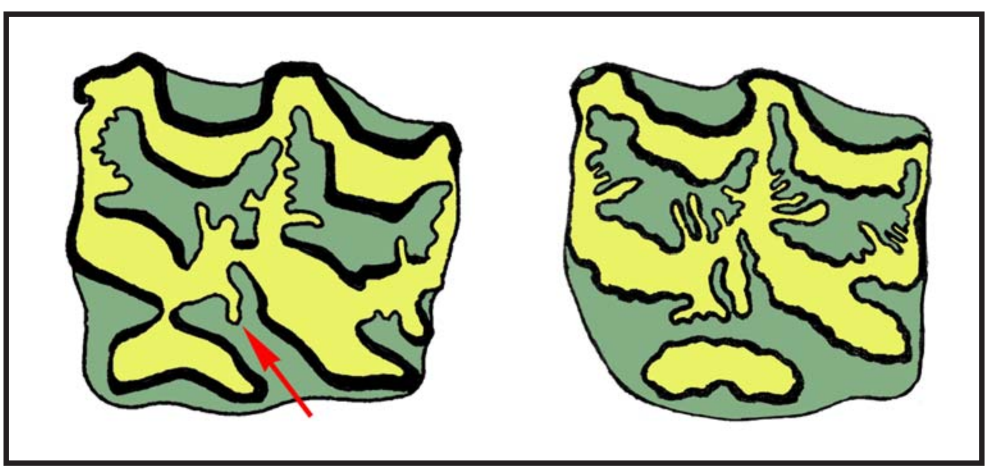
through *Orohippus*, *Mesohippus*, *Miohippus*, *Merychippus*, and *Pliohippus,* finally to terminate with *Equus*. But you may know that paleontologists are currently aware also of the following genera (in alphabetical order):

Anchitherium	*Gobihippus*	*Neohipparion*
Archaeohippus	*Griphippus*	*Onohippidion*
Astrohippus	*Haplohippus*	*Palaeotherium*
Calippus	*Hipparion*	*Parahipparion*
Cormohipparion	*Hippidium*	*Parahippus*
Cremohipparion	*Hypohippus*	*Protohippus*
Desmatippus	*Kalobatippus*	*Pseudhipparion*
Dinohippus	*Megahippus*	*Sinohippus*
Epihippus	*Nannippus*	*Xenicohippus*

SPECIES *Equus caballus*

Equus caballus is the heaviest and one of the tallest species in its genus, and it also happens to be one of the largest and heaviest of all equids. It has the broadest and deepest skull and the stoutest limbs. The upper cheek teeth are large, usually with long, bipartate protocones that look somewhat like a Dutch shoe (below). In general, the enamel plications visible upon the working surfaces of the upper teeth are quite complex; a pli caballin is typically present. The inferior cheek teeth show a "U"-shaped enamel re-entrant (the ectoflexid). The incisor teeth are large and all of them, even the lateral incisors, possess both infundibulae ("cups") and dental marks ("stars"), which can both, at a certain stage of wear, simultaneously be present in a given tooth. Although the incisor row is broad, it is not as broad as in some fossil genera, e.g. for example *Calippus*, nicknamed by paleontologists the "lawn mower horse" (see photo, next page).

There is little inflation of the frontal sinuses in most animals, so that they have straight faces and flat foreheads. One very useful characteristic (if one has a complete or nearly-complete skull to identify) is that the temporal bone of the skull forms a broad triangle behind the ear region in this species, broadly separating the postglenoid and paramastoid processes. This is a reflection of the fact that the occiput slopes backwards rather than being tucked under. The practical result is that you can tell the skull of a horse from that of an ass, mule, zebra, or onager by standing it up on end. The horse skull will balance; skulls of the mule and of the other species will fall forward.



The prize for having the most complicated enamel pattern in a horse tooth goes not to *Equus* (left) but rather to *Cormohipparion* (right) and its close relatives in the hipparionine clade, *Neohipparion* and *Hipparion.* The pli caballin is marked by the red arrow.

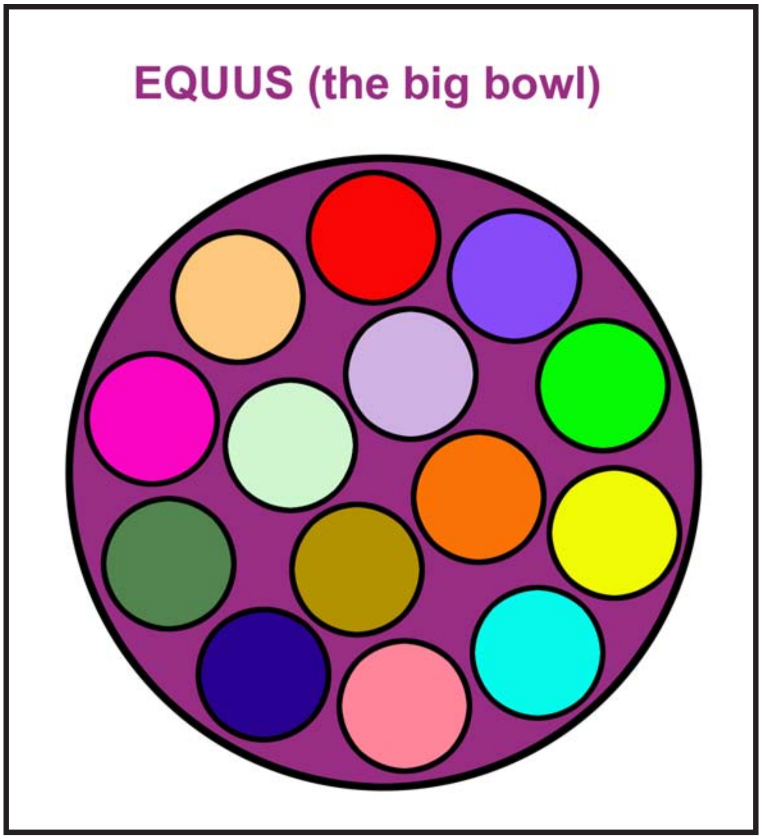
Living Species of *Equus*

Students of the horse should help themselves to put the horse into context by comparing it with the other eight living (or recently extinct) species in the genus *Equus*. You should realize at this point how closely related to the horse these animals are; the tragedy is that all of them are now on the brink of extinction (and the horse itself has been, since 1947, extinct in the wild). Since most of these very interesting animals can be seen in zoos, you should familiarize yourself with what they look like:

Equus zebra – the "true zebra". There are two subspecies, the Hartmann's zebra *(E. zebra hartmanni)*, and the Cape Mountain zebra *(E. zebra zebra)*. This species is distinguished by its donkey-like

Above: Palate view of the skull of a "lawnmower" *Calippus* recovered from late Tertiary strata. The bars are very short and the muzzle is extraordinarily wide.

Below: Four *Equus* skulls from the Roman-era diggings at Vindolanda, near Hadrian's Wall in the north of England. The "stand-up" test reveals that the three individuals on the left are horses, while the one on the right is a mule. Horse skulls stand up because the occipital plate makes a right angle (or even an oblique angle) with the top of the braincase, whereas the back of the ass skull is tucked under.



There are thirteen living (or recently extinct) species in the genus *Equus*. They fall into four groups: horses, asses, zebras, and half-asses. Yes, folks, there really is such a thing as a "half-ass" -- they are dziggetais, onagers, and kiangs, exotic creatures that live in far-sundered and remote places of the world. See text for more.

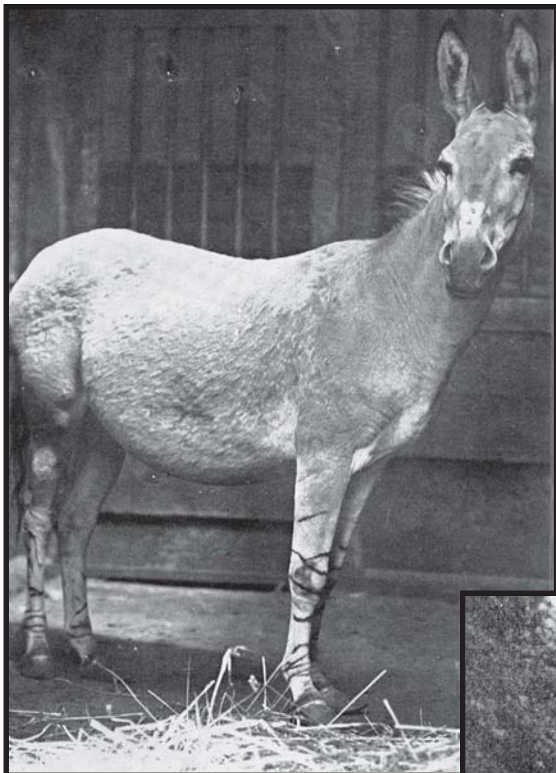
The British Museum Quagga mount

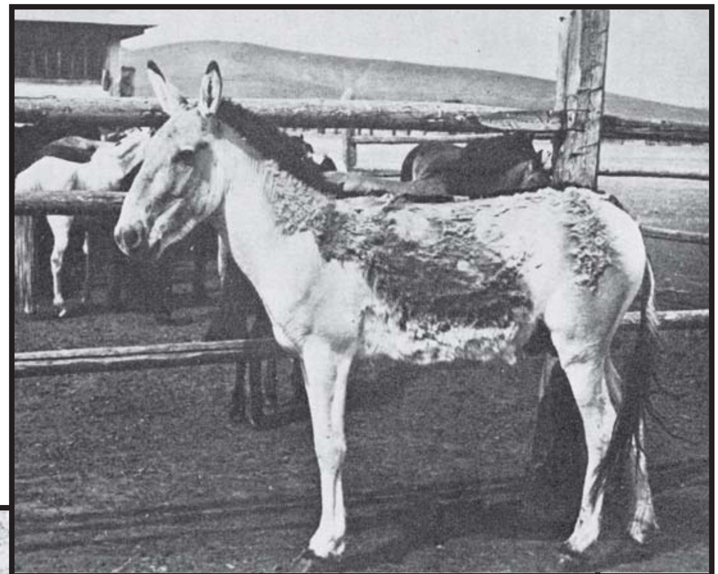
body size and form, pointed rather than rounded ears, and by the fact that there is a flap of skin or dewlap on the underside of the throat. The stripes never extend all the way under the belly, and that area of the body as well as the inner sides of the thighs and the area around the rump, is of a white or ivory color. There is a thin dorsal stripe; over the croup, there is a distinctive "grid iron" pattern of short stripes.

Equus burchelli – the Bontequagga, Plains zebra, or common zebra. This animal has a pony-like body form and an undulating facial profile. It completely lacks infundibulae in the lateral incisors. Its stripes are broad, although some forms may have thin, faint stripes lying in the white zones between stripes. The dorsal stripe is thin; body stripes extend all the way around under the belly. There is a great deal of variation in stripe width and, to some extent, in pattern, some forms having fewer, broader stripes and more white on the body, while some are melanistic and can be nearly black. There is also a maneless form. The ears are rounded and not as long as in the true zebra. This is the commonest zebra to be seen in zoos, and may often be seen in the circus. It is the zebra most commonly broken to ride and drive, and the most commonly used to get zebra-horse mules. It remains the most populous zebra species in the wild (although still endangered).

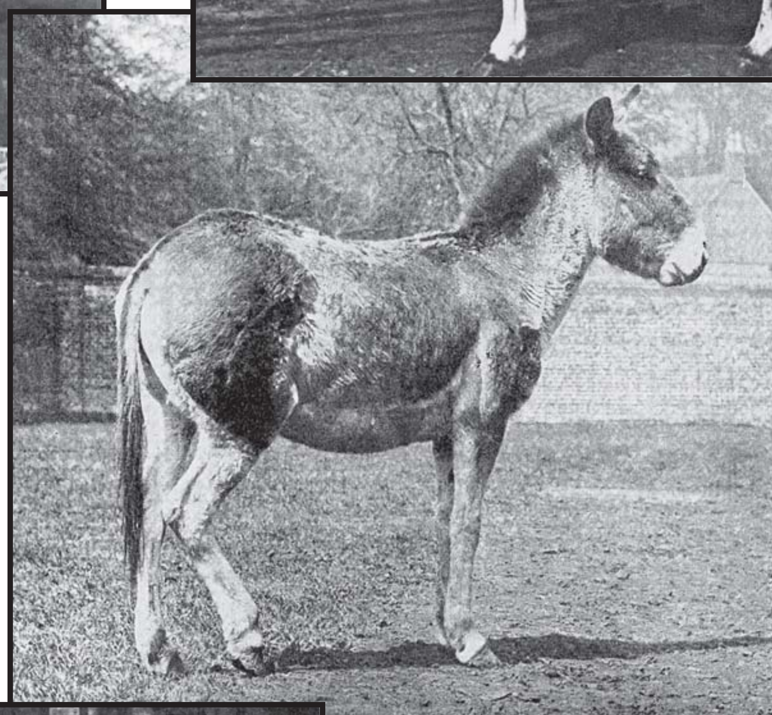
One member of the genus *Equus* that has been problematical and caused controversy is the Quagga, which once roamed the plains of South Africa in vast numbers but is now extinct. Its teeth are like those of *Equus caballus,* but amino-acid assay of an old hide showed it to be more similar to *Equus burchelli.*

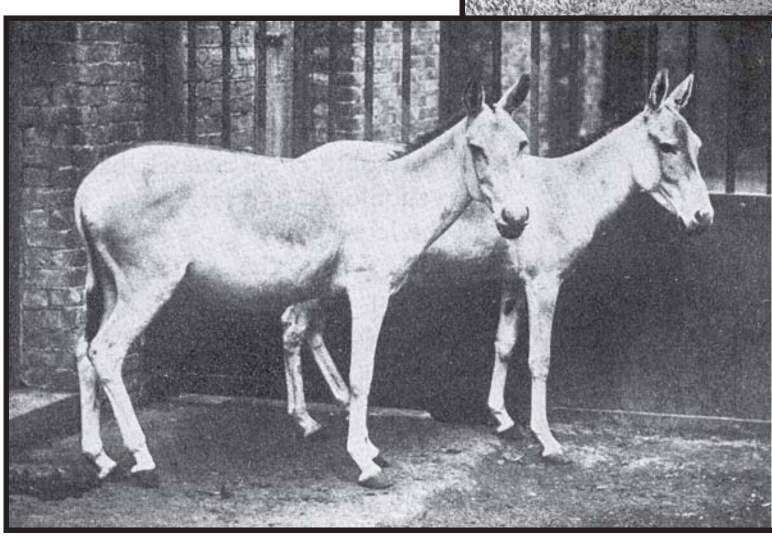
ASSES AND HALF-ASSES





Above: Somali wild ass, *Equus asinus somaliensis.* This animal, like its close relatives the Nubian and Syrian wild asses, is now probably extinct in the wild. Above right: A Mongolian Dziggetai, *Equus hemionus hemionus.* This animal, rarely photographed, inhabits the most barren and harsh parts of the Gobi Desert.

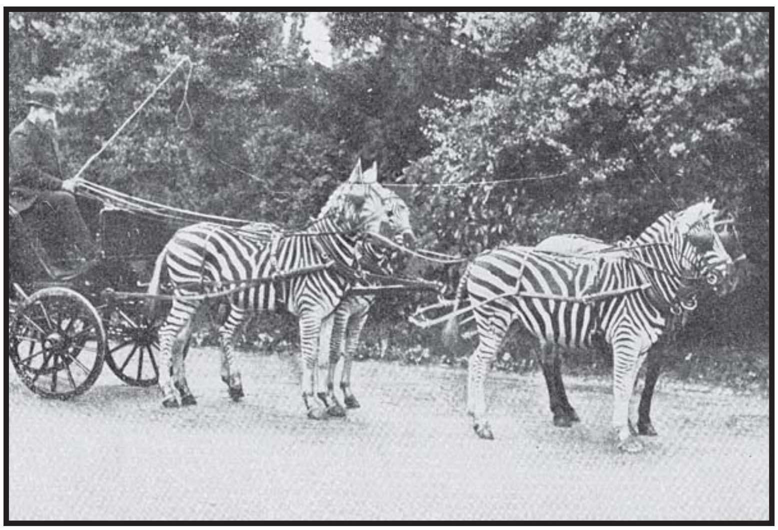




Above: Tibetan kiang, *Equus hemionus kiang,* a stallion photographed at the old Catskill Game Park in upstate New York. This animal, which in the wild lives on high-altitude plateaus in the Himalayan Mountains, has a more contrasting pelage than other half-asses. Left: a pair of *Equus hemionus onager* mares, khurs from Baluchistan or Pakistan. The most gracile of the half-asses, they also have the lightest-colored coats.

Equus grevyi – the narrow-striped zebra, Abyssinian zebra, or Grevy's zebra. This animal is the oldest of all African equids, its fossil record there extending back at least five million years. It is tall, sometimes reaching over 15 hands in height, and has fairly prominent withers. Its stripes are narrow and numerous, and there is a broad and continuous dorsal stripe. The stripes do not extent all the way under the belly; the pelage there is of a white or ivory color. The ears are long and have broad, saucer-shaped tips. The skull is long and narrow, and the facial profile may be either straight or slightly undulating. It has the simplest enamel pattern on its teeth of any *Equus*; in the lower teeth, the ectoflexid re-entrant reaches all the way across the teeth, as in its fossil ancestor *Equus stenonis*.

Equus onager – the Indian and west-Asian Onager, Onaigre, Khur, or Kulan. One of three so-called "hemione" (meaning "half like an ass") species, the Onager is an orange-colored animal with a buffy to white underbelly. It has ears longer than those of a horse but shorter than those of an ass; they are pointed like those of the horse and ass, rather than being rounded like those of zebras. Onagers and other half-asses are distinguished by having proportionally long, narrow cannon bones, short wedge-shaped heads, and lower cheek teeth in which the ectoflexid re-entrant does not penetrate all the way across the tooth.



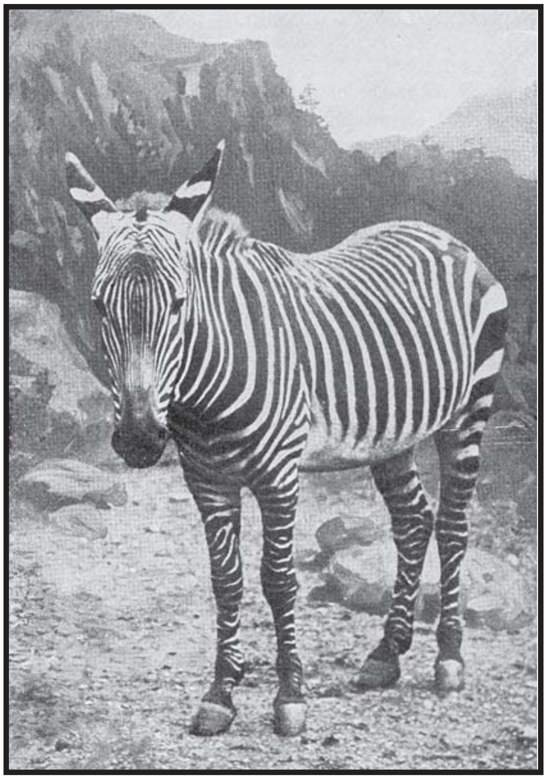
Sir William Rothschild with his team of Burchell zebras. Note the dark-colored domestic pony before, left; a steadying influence was evidently required. Nonetheless, in my files I have photos of every species of zebra being driven, ridden both aside and astride, and even being jumped. All equines have brains that people can communicate with.

Equus hemionus – the Dzhungarian (Chinese and Mongolian) hemione, Chiggetai or Dziggetai. This is the tallest and most gracile of the half-asses, and also the rarest to be seen in Western zoos. Its coat is a dusty-gray color and the back and belly contrast less than in the onager and kiang.

Equus kiang – the Tibetan Kiang. This is hemione has the shortest, stoutest limbs and overall the stoutest build. Its pelage is a rich blackish-brown, standing in sharp contrast to the nearly-white fur of the underbelly and the inner flanks.

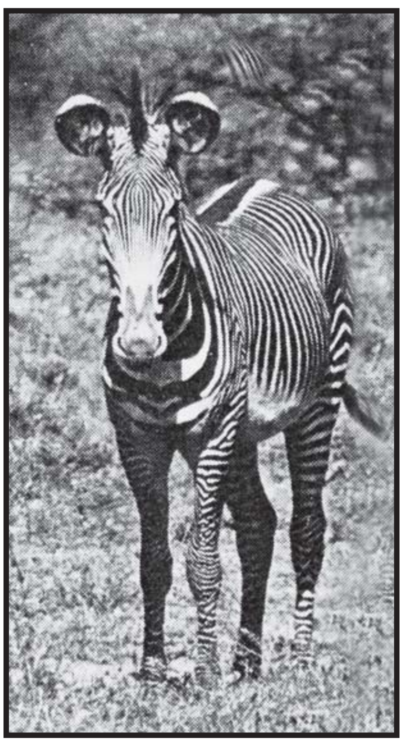
Equus asinus – the ass. Besides the domestic donkey, there were once wild donkeys in the Arabian Peninsula, and until the recent series of civil wars in Somalia, there was a population surviving there also.

Equus quagga – the South African Quagga. This animal became extinct in 1904, having once roamed the plains of South Africa in countless numbers. It was exterminated by the Afrikaaners as the buffalo were nearly exterminated by Anglo-Americans. The animal had a body form similar to that of a Burchell's zebra, but was typically striped only over the neck and anterior body. The legs and often the "blanket area" over the croup were white or buffy. My own analysis of quagga skulls – there are only five known to science – indicates that these animals deserve to be recognized as a separate species more similar to a horse than to a zebra. However, amino-acid assay tests performed on preserved quagga hides indicate that quaggas are zebras. Until I see the results from a DNA test performed with modern techniques, I am remain inclined to believe what the



Left: One of the rarest animals in the world, the Cape Mountain Zebra or True Zebra, *Equus zebra zebra.* This remarkable photograph, taken in 1902, captures the animal in its native habitat in southwestern Africa.

morphological analysis tells me, for unlike any zebra, the lateral incisors of quaggas possess full infundibulae – just like a horse. Along with the horse, the onager and the ass were both brought into domestication at least 4,000 years ago. In addition, all three species of zebra have in historical times been captured, tamed, ridden, driven, and trained for performance in the circus. Mules as normally bred in Europe and the Americas are the product of a human-planned cross between a jack ass and a mare (i.e. *E. caballus* X *E. asinus*), but there are other ways to get mules: African farmers frequently make use of zebra semen to get mules from mares, because they have much greater immunity to African parasites and stand the climate better (horses never occurred in sub-Sarharan Africa until people began bringing them there in the 16th century). Zebra-horse mules are called by various names such as “zebrules” or “zorses”.



The Grevy’s zebra has narrower and more numerous stripes than other zebras. Its big, round ears contrast with the narrow, ass-like ears of the Mountain zebra above. The Grevy’s long head is a holdover from its ancestor, *Equus stenonis.*

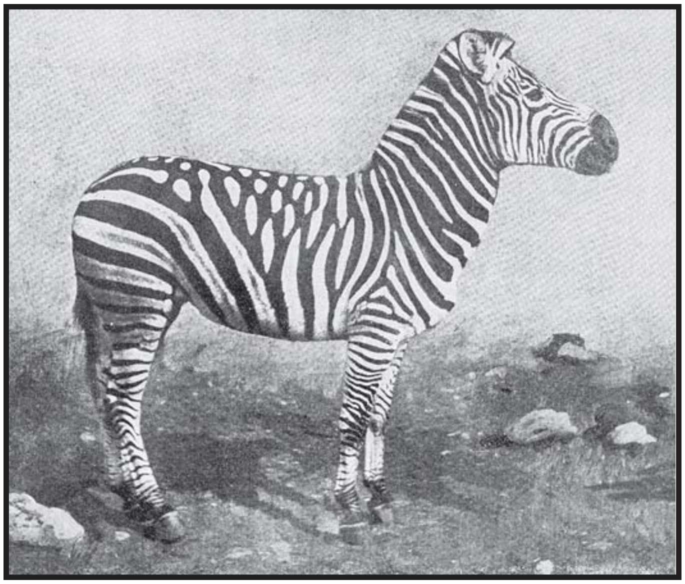
Fossil Species of *Equus*

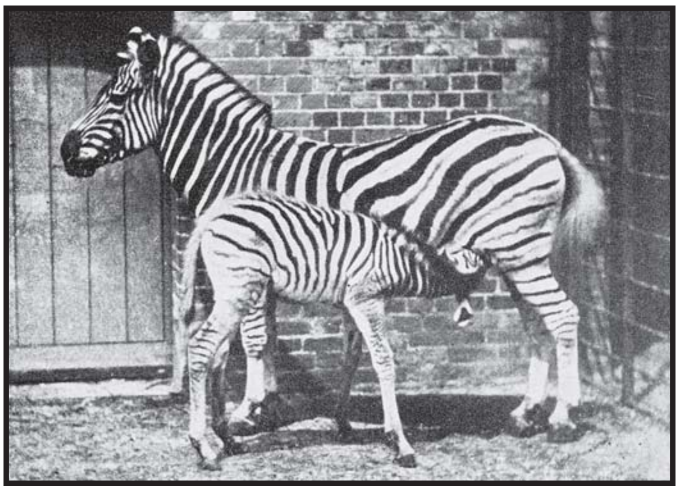
As if the abundance and diversity of living members of the genus *Equus* were not enough, we also have an extensive record of this animal in the Northern Hemisphere beginning with its origin at the end of the Tertiary Period. The genus immediately ancestral to *Equus* is *Dinohippus.* This animal is similar to *Equus* in every respect – so much so that I cannot find any characteristics to distinguish them. I continue to use the term *Dinohippus*, therefore, merely as a way of distinguishing certain species that lived in North America during the Hemphillian and Blancan Land Mammal Ages, between 7 and 5.5 million years ago. (This is a good example of the sometimes uneasy marriage between the logic trees generated by cladistic analysis and the older method of drawing “phylogenetic trees” showing the descent of a species through time. Properly, some day, it will probably be necessary to re-classify *Dinohippus* by making it a sub-genus, and then we will write, for the best-known species in the genus, “*Equus (Dinohippus) interpolatus”*).

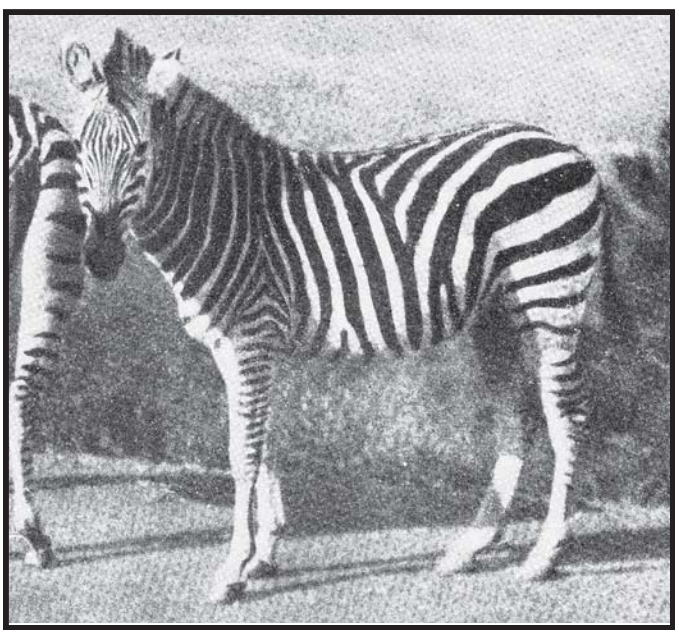
Dinohippus gave rise to a species, *Equus francescana*, that migrated from California across the Bering Land Bridge during the earliest phase of the Pleistocene when sea-level was lowered. Fossils of this species found in the Old World are called *Equus stenonis,* and in this form it spread throughout that continent and into Europe and Africa. In Europe, it gave rise to such species as *Equus sussenbornensis*, the ancestor of *Equus mosbachensis,* and *Equus bressanus* – the latter being the probable ancestor of asses. In western Asia and north Africa, *Equus stenonis*appears to have given rise to *Equus hydruntinus,* another ass-like form, and *Equus teilhardi,* which is probably an onager. In Africa, it ultimately gave rise to *Equus grevyi*.

In North America, *Equus francescana* gave rise to *Equus simplicidens*. *Equus francisi,* an onager-like species, also appears very early; it may be derived from *E. francescana* or from the back-migration of a Eurasian form. Likewise, *E. simplicidens* is a form which in many respects parallels *Equus grevyi*, having a very long head, big body, stout legs, and a relatively simple dental pattern. The "stilt-legged" *Equus francisi,* on the other hand, is not only longer in the shanks but smaller and lighter-bodied, with a more complex enamel pattern in the teeth.

From *Equus francescana,* and also possibly from forms back-migrating from the Old World, there came an enormous proliferation of North American species of the genus *Equus*. There really are quite a few of these, but those of you wishing to read the techical literature should be forewarned that paleontologists eager to make

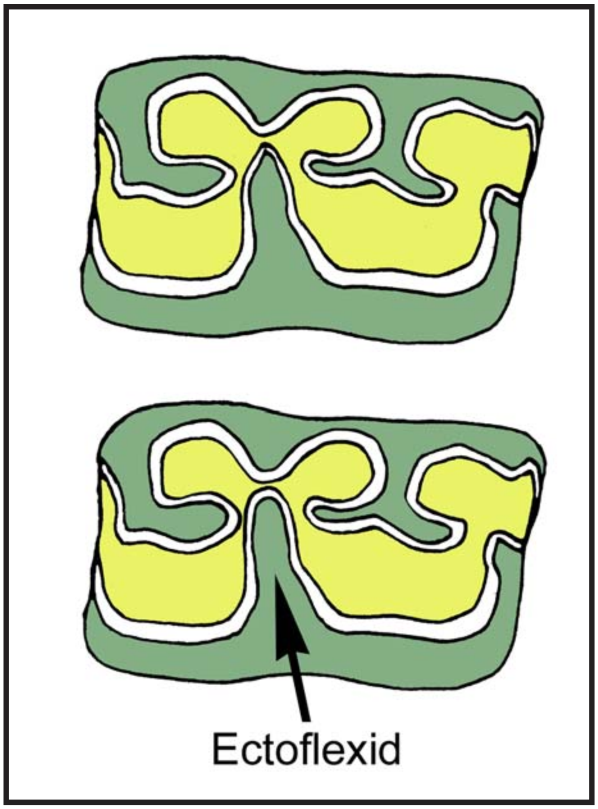






BONTEQUAGGAS

Three pelage variants of the Bontequagga or Common zebra, *Equus burchelli:* Top, Chapmann's zebra; middle, the Damaraland form with its distinctive "inter-striping"; bottom, Grant's zebra. These animals inhabit the savanna grasslands of sub-Saharan Africa along with lions, elands, elephants and giraffes.



Left: What are paleontologists looking at when they examine characters in fossil horse remains? Often, very small, subtle things -- because evolution mostly proceeds "one click at a time." This diagram shows the occlusal surface of the first lower molar tooth in two, very closely related fossil species of the genus *Equus:* above, the European *Equus stenonis;* below, the North American *Equus simplicidens*. The European species typically has a "V"-shaped ectoflexid loop, while this enamel re-entrant in the American species is "U"-shaped.

their mark in this fertile field of investigation have, over the past two centuries, almost hopelessly muddled matters by naming hundreds of species, most of which must be regarded, for a variety of reasons, as invalid "duplicates". I therefore discuss here only those species that I think are really unique and valid.

Bloodlines of the genus *Equus* continue through three Land Mammal Ages: the Blancan, which is the tail-end of the Tertiary; the Irvingtonian, which is the earlier part of the Pleistocene; and the Rancholabrean, which is the later part. In each of these time periods, *Equus* species can be classified into either "stout-legged" (horse or zebra-like) or "stilt-legged" (onager-like) forms. (Ass-like forms are difficult to distinguish, and apparently rare, in the fossil record from the New World):

Blancan

Stout-legged forms: long head, relatively simple teeth, large size

Equus francescana
Equus simplicidens (old names for this form that you might still see in a museum exhibit are *Plesippus, Equus shoshonensis).* This form is commonly exhibited because a large number of skeletons have been recovered from the famous Hagerman Quarry near Hagerman, Idaho. There is a complete skeleton of this species on exhibit in a small Museum run by the National Park Service in Hagerman, and at some seasons you can also take a bus tour to view the actual quarry itself. *Equus simplicidens* skeletons are also on exhibit at the U.S. National Museum of Natural History/Smithsonian Institution in Washington, D.C.).

Stilt-legged form: shorter head with broader snout, relatively complex tooth structure, smaller size
Equus francisi (first appearance)

Typically **Irvingtonian** (though some range from late Blancan up into the Rancholabrean):

Stout-legged forms:
Equus niobrarensis
Equus hatcheri
Equus scotti (See skeleton on exhibit at the American Museum of Natural History in New York City).

Stilt-legged forms:
Equus francisi (later occurrences)
Equus arellanoi
Equus calobatus
Equus zoytalis

Typically **Rancholabrean** (though some originate in the Irvingtonian):

Stout-legged forms:
Equus caballus
Equus occidentalis (See a complete skeleton and many skulls of this form on exhibit at the Page La Brea Tar Pit Museum in Los Angeles, California, and at the U.S. National Museum of Natural History/ Smithsonian Institution in Washington, D.C.)
Equus amerhippus
Equus excelsus (See a complete skeleton of this form on exhibit at the Nebraska State Museum of Natural History in Morrill Hall on the campus of the University of Nebraska at Lincoln).

Stilt-legged forms:
Equus altidens
Equus quinni
Equus conversidens (See a complete skeleton of this form on exhibit at the American Museum of Natural History in New York City).

Subspecies of *Equus caballus*

In a recent publication (Mammalian Species of the American Society of Mammalogists, 1999), my co-author Robert Hoffmann and I recognize seven subspecies within the species *Equus caballus*.

The first item to take care of under this heading are all the synonyms for *Equus caballus* – "duplicate names" proposed, as previously mentioned, by paleontologists eager to name horse types. Here is a list of published synonyms of *Equus caballus* with their namer and the publication date; you can see that this tendency for the proliferation of names goes right back almost to the beginning of the science:

Equus ferus (Boddaert, 1785)
Equus sylvestris (Brincken, 1828)
Equus przewalskii (Polyakov, 1881)
Equus mosbachensis (Reichenau, 1903)
Equus hagenbecki (Matschie, 1903)
Equus gmelini (Antonius, 1912)
Equus laurentius (Hay, 1913)
Equus niobrarensis alaskae (Hay, 1913)
Equus abeli (Antonius, 1914)
Equus mexicanus (Hibbard, 1957)
Equus midlandensis (Quinn, 1957)
Equus algericus (Bagtache, Hadjonis and Eisenmann, 1984)

Dr. Hoffmann and I recognize seven subspecies within the species. These are forms that we distinguish on the basis of their morphology as well as their mapped geographic occurrence. The seven valid subspecies are:

Equus caballus alaskae – the Lamut or Alaskan wild horse. Became extinct about 10,000 years ago, near the end of the Pleistocene. Once ranged in northeastern Asia and across the Bering Land Bridge into Alaska.

Equus caballus mexicanus – the American peri-glacial horse. Became extinct at the end of the Pleistocene. Once ranged from the glacial margin west of the Mississippi, south into northern Mexico.

Neither of these forms were ever domesticated, as they were already extinct by the time horse domestication began.

Equus caballus przewalskii – the Przewalski horse or Mongolian wild horse. Its last known range was a narrow strip in the Gobi Desert, but it once ranged broadly across Russia and Siberia from the Ural Mountains to northeastern Asia. You may frequently see this animal in zoos. It became extinct in the wild in 1947, but survives in zoos and preserves today, all living animals being the descendants of only 13 wild-caught ancestors. The Przewalski horse has contributed in a minor way to a restricted number of Asian breeds in Mongolia, northern China, and eastern Tibet. It is, as I have explained in both the “Mammalian Species” and “Origin of the Mustang” papers posted in our Knowledge Base, most definitely NOT the ancestor of the domestic horse.

Equus caballus ferus – the Tarpan. This animal became extinct in 1913, a herd being kept up until that time in the Bialovesh Forest Preserve in Poland. Once ranged from eastern Poland east to the Ural Mountains. This form was the first wild horse to be domesticated. Its characteristics are preserved within several Russian, eastern European, and west Asian breeds including the Konik, Hucul, and Akhal-Teke and related Turkmenian breeds. Through these in turn, Tarpan characteristics have been incorporated into the Thoroughbred.
Equus caballus pumpelli – the Afro-Turkic horse. This is the immediate ancestor of our “Oriental” breeds, including the Arabian, Old Hittite, Persian, Bashkir, Lokai, Marwari, and Barb.

Equus caballus mosbachensis – the Central European horse. The most ancient and primitive form of *Equus caballus*, the Mosbach horse is the immediate ancestor of the Warmblood breeds, including the Latvian, Grönigen, Friesian, Cleveland Bay, and all the German Warmbloods and their derivatives now bred in Sweden, Denmark, and the Low Countries.

Equus caballus caballus – the West European horse. This is the cold-and-wet adapted subspecies, the form that has the stoutest, most rounded body, the shortest ears, the broadest and deepest head, the shortest legs, the broadest feet, and the thickest fur, mane, and tail. It is native to those parts of Europe that lie west of the Rhine and Rhone rivers, from Norway and Sweden in the north through the Low Countries, the British Isles, western France, and Spain. *E. c. caballus* is the immediate ancestor of all the draft breeds, such as the Belgian, Clydesdale, Brabant, and Suffolk Punch and their derivatives now bred in other countries, such as Russia and the Americas. It is also the immediate ancestor of all the pony breeds, large and small, including the Fjord, Shetland, Exmoor, Dartmoor, Mehrens, Galician and Asturian. Ponies and draft horses all derive from a single ancestry, the overall size of a given form being concordant with the area of land upon which the form developed, i.e. Continental forms are the largest, those occurring on the main British island next biggest, and those occurring on offshore islands like Man, the Shetlands, and the Orkneys being the smallest.

Here we reach the end of our taxonomic tour, with the smallest recognizable and differentiable grouping in the horse family, the subspecies. For more information, please feel free to download the "Mammalian Species" paper on *Equus caballus* by Deb Bennett and Robert S. Hoffmann, as well as "Evolution of the Horse: History and Techniques of Study".

FOR BIBLIOGRAPHY LISTINGS, SEE SEPARATE PDF UNDER THE TITLE "Horse Evolution References"