

Pleistocene Mammals of Europe

Björn Kurtén



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Order Perissodactyla

THE Perissodactyla or odd-toed ungulates comprise the horse, tapir and rhinoceros families. The order passed its apogee long ago; several other perissodactyl families existed in the Tertiary but later became extinct. In the European Pleistocene only the modern families were represented.

The name odd-toed ungulates does not necessarily mean that the number of toes is odd, though this is the rule in most groups. It means that the axis of the foot always coincides with the third or central toe, which is the strongest. In the even-toed ungulates the axis passes between the third and fourth toes, which are equally strong.

The earliest Perissodactyla appeared in the Eocene.

Family Tapiridae, Tapirs

The Tapir family was widely distributed in North America and the Old World in the Tertiary. It is very close to the original perissodactyls of the Early Eocene and so is a primitive group, unspecialized except for the development of a short proboscis. In the Pleistocene tapirs invaded South America; then the northern tapirs became extinct, so that only South America and the East Indies are now inhabited by tapirs. In Europe the family became extinct at the close of the Villafranchian.

The Auvergne Tapir, *Tapirus arvernensis* Croizet & Jobert. This small species of tapir was common in the Astian but has also been found in the beginning of the Villafranchian (Etouaires; Vialette; also in Germany). It was absent in the middle Villafranchian but returned toward the end of the stage and is recorded at Val d'Arno and A-Tegehlen. The species does not differ much from living tapirs.

Tapirs are forest animals and partly aquatic; they live on water

vegetation but also browse on forest trees, pulling down branches and twigs with the help of the short trunk. In fleeing from a predator the tapir will go for the densest thicket available, which it easily penetrates protected by its tough skin but which will stop most carnivores. Tapirs are usually solitary in habits [83].

Family Rhinocerotidae, Rhinoceroses

The rhinoceroses form an important element in the Pleistocene fauna of Europe. Large, robust bones and teeth are more likely to be preserved than small ones; as a result, the rhinos have a good fossil record. Many species are known and show an interesting range of adaptations to various environments from tundra to forest.

Almost all the Ice Age rhinos of Europe belong to the group of the present-day Sumatra rhinoceros, the genus *Dicerorhinus*. These animals have two nose horns, the one in front being the longest. They also have a somewhat more hairy skin than other living rhinos, which have nearly no hair at all. The dicerorhine rhinos were common in Eurasia in the late Tertiary and the Pleistocene forms were obviously direct derivatives of the Pliocene ones.

The only exception is the Giant 'Unicorn', which however was mostly distributed in eastern Europe. It belongs to a group of its own among the rhinoceroses, with a long, separate record.

Christol's Rhinoceros, *Dicerorhinus megarhinus* Christol. This is the typical rhinoceros of the Astian in Europe but it survived into the earliest Villafranchian (Etouaires; Vialette) in a progressive form, trending towards the daughter species *D. etruscus*. In the Astian form the nasal bone does not connect with the upper jaw in front, or in other words there was no ossification of the septum between the nares, which was entirely cartilaginous. As the nasal bones carry the horns, they would be liable to breakage with the impact of a heavy charge. Accordingly there is a tendency to ossification of the nasal cartilages in the early Villafranchian specimens, especially in the males with their heavier horns; such an arrangement would reduce the risk of breakage by transferring part of the strain on to the bones of the upper jaw. This trend continued in the Etruscan rhinoceros, in which a firm base was formed for the horn-bearing nasal bones.

Like its successor, Christol's rhinoceros was a comparatively small, gracefully built form [278].

The Etruscan Rhinoceros, *Dicerorhinus etruscus* Falconer. This species was the sole representative of the rhinoceros family during most of the Villafranchian in Europe; it has been recorded, for instance, at Villaroya, Pardines, Saint-Vallier, Senèze, Olivola, Val d'Arno, Erpfingen and A-Tegelen. It remained common in the early Middle Pleistocene, where it occurs both in forest faunas (Mauer; Forest Bed) and steppe faunas (Süssenborn; Mosbach) up to the 2-Mindel. At that time, however, a more highly specialized competitor entered the stage in the shape of Merck's rhinoceros. Shortly after the immigration of this species and of the steppe rhinoceros slightly later, the Etruscan rhinoceros died out.

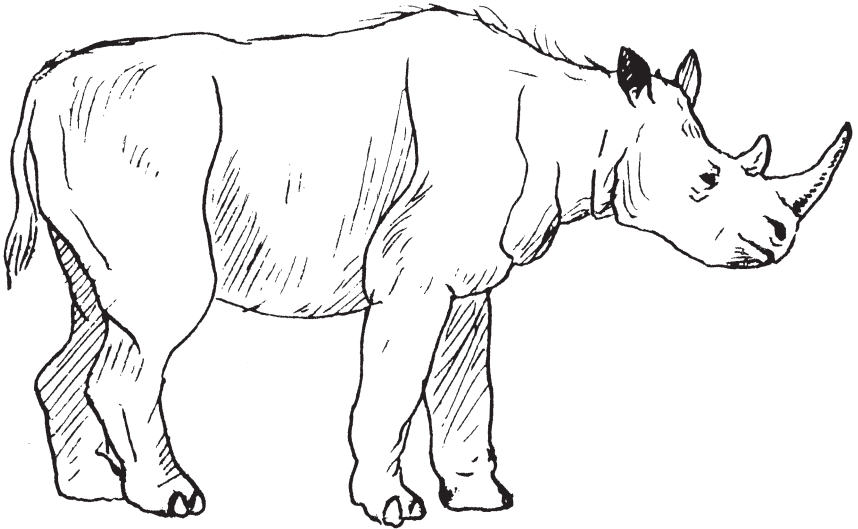


Figure 58. Restoration of Etruscan Rhinoceros, *Dicerorhinus etruscus*, based on a skeleton from Senèze.

The reasons for the extinction may probably be sought in the incomplete specialization of the Etruscan rhinoceros. It was a relatively small form, about the size of the smallest living species, and judging from the angle between the occipital plane and the skull base, the head was carried in an almost horizontal position. It has been shown that the leaf-eating rhinos of the present day habitually carry their heads slightly tilted upward and in their skulls the occipital plane is inclined forward in relation to the skull base. The African black rhinoceros, which eats grass as well as leaves, carries its head horizontally, while the white rhinoceros, an exclusively grazing form, habitually hangs

its head. The Etruscan rhinoceros in this respect most closely resembles the black rhinoceros and is likely to have had a similarly unspecialized diet including leaves as well as grass. Savanna and bush steppe would seem to have been the most congenial environments of this form, but it is also found in faunas dominated by woodland species.

There are complete skeletons of this species, for instance from Senèze (Basel). The head-and-body length was somewhat less than 2.5 m., the shoulder height about 1.5 m.; the animal was unusually long-legged for a rhinoceros and probably rather fleet of foot [6; 127; 242; 278].

Merck's Rhinoceros, *Dicerorhinus kirchbergensis* Jäger (*Rhinoceros mercki* Jäger). This species is the constant companion of the straight-tusked elephant in most interglacial faunas from the D-Holsteinian to the F-Eemian. Its first appearance, however, comes somewhat unexpectedly in the 2-Mindel (Mosbach 2), where it is found in a steppe association; it is, however, rare. In England Merck's rhinoceros was particularly abundant during the D-Holsteinian (Swanscombe; Clacton), while the steppe rhinoceros was scarce. At E-Ilford, on the other hand, the steppe rhinoceros was common and Merck's rhinoceros rare. Finally, in the F-Eemian the species was completely absent in England, while *D. hemitoechus* held sway.

In central Europe on the other hand Merck's rhinoceros was common in the F-Eemian and became extinct only at the end of the interglacial. In Spain the species persisted during the first part of 4-Würm I.

The ecological successor of the Etruscan rhinoceros, *D. kirchbergensis* resembles its forerunner in many respects; the skull has the same general shape. But Merck's rhinoceros was considerably larger, which may have given it an advantage in the competition. Like the Villafranchian species, Merck's rhinoceros probably inhabited woodland, parkland and occasionally savanna environments but it does not appear in extreme steppe milieus apart from the very beginning of its history; such environments were taken over by the steppe rhinoceros and the woolly rhinoceros. Unfortunately, no complete skeleton of this species has been found to date.

D. kirchbergensis may have evolved from extra-European representatives of the Etruscan stock. A Chinese Villafranchian member of the genus *Dicerorhinus* is closely allied to Merck's rhinoceros and may well be its ancestor. Merck's rhinoceros had a great range in Asia

(southern Siberia), which may also suggest an Asiatic origin [6; 262; 316].

The Steppe Rhinoceros, *Dicerorhinus hemitoechus* Falconer. This species appears to be represented as early as at Val d'Arno but is not found again until the D-Holsteinian, when it invaded Europe; from that time on it occurs in the interglacials with a frequency inversely related to that of Merck's rhinoceros. The steppe rhinoceros carried its head in a hanging position like the present-day white rhinoceros of Africa and its high tooth crowns are adapted to deal with the abrasive grasses of the steppe. It may therefore be taken as an indicator of open grasslands, but it does not seem to have developed any special adaptation to cold so that it was unable to colonize the tundra biotope; its main habitat lay in temperate areas. However, a head with preserved skin and hair of a rhinoceros found in frozen earth at a tributary of the Jana River in Siberia in 1877 is stated to belong to *D. hemitoechus*. Presumably this indicates survival well into 4-Würm.

The steppe rhinoceros is closely related to the Etruscan rhinoceros and may represent an offshoot from early representatives of that group [16; 262; 316].

The Woolly Rhinoceros, *Coelodonta antiquitatis* Blumenbach (*Rhinoceros tichorhinus* Cuvier). The woolly rhinoceros was a highly specialized derivative of the *Dicerorhinus* stock, which invaded Europe in the 3-Riss and remained a typical member of the cold fauna there until the end of the 4-Würm. It apparently evolved in northeast Asia, where predecessors of this species dating from the Early Pleistocene have been found. Discovery of frozen remains in Siberia, and especially the find of a remarkably well preserved cadaver in deposits impregnated with salt and petroleum at Starunia in Galicia, have given detailed information on the appearance in the flesh of this animal; there is a complete stuffed specimen in the Museum of Kraków. The woolly rhinoceros also figures in Stone Age paintings and engravings.

This rhino had a thick, woolly coat as a protection against the Arctic cold. A fairly well-developed pelage may well have been a common character of all the dicerorhine rhinoceroses but *Coelodonta* was probably unusually endowed in this respect. The ossification of the nasal septum was extreme also; and in addition the nasals grew down in front to fuse with the upper jaws – the resulting odd appearance of the rostrum has led French palaeontologists to name it 'the rhino of the closed nares'. The strengthening of the horn base corresponded to

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the development of two powerful, elongated nasal horns. The cheek teeth were very high-crowned, even more so than in the steppe rhinoceros. Not only the head but also the neck was carried low in this species, thus showing extreme grass-eating specialization.



Figure 59. Restoration of Woolly Rhinoceros, *Coelodonta antiquitatis*, based on stuffed specimen from Starunia; original in the Zoological Museum, Kraków.

The woolly rhinoceros is perhaps mostly thought of as an extreme tundra form, but unmistakable specimens of this species have also been discovered in completely different surroundings. In Spain, for instance, *C. antiquitatis* occurs at Cueva del Toll, north of Barcelona, in deposits from the interstadial 4-Würm I-II; pollen analysis of the same deposit indicates a dry, temperate climate with extensive grasslands and a few broad-leaved trees; there is no possibility whatever that this could be a 'cold' steppe [259].

The Giant 'Unicorn', *Elasmotherium sibiricum* Fischer. The homeland of this species was the steppes of southern Russia, but a few stray finds indicate that it made a temporary incursion in central Europe in the Middle Pleistocene. This species is the terminal form of an evolutionary line that has its roots far down in the Tertiary; we have glimpses of it in the Miocene of Spain, the Pliocene of China and the Pleistocene of Russia.

It was a truly gigantic animal, far larger than any living rhinoceros. It had no nose horn, but instead an immense horn on the forehead: it grew to a length of two metres. This animal was thus a veritable unicorn. Its great, prismatic cheek teeth with their complicated enamel pattern are as highly specialized as those of the horses and show a wonderful adaptation to grazing habits. Knowledge of the postcranial skeleton is incomplete [42].

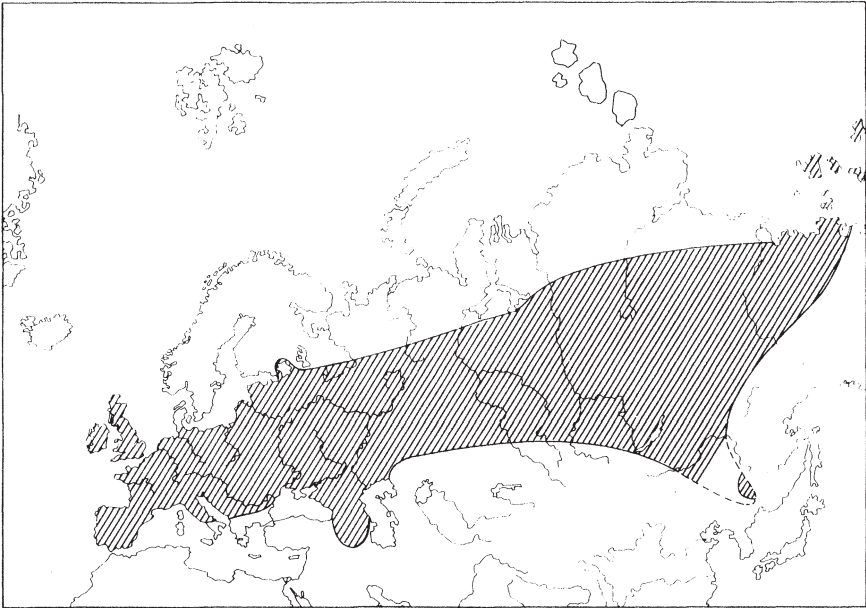


Figure 60. Distribution of Woolly Rhinoceros, *Coelodonta antiquitatis*, in the Pleistocene. After Trofimov.

Family Equidae, Horses

The history of the horse family in the Tertiary is often cited as a classical example of evolution demonstrated by palaeontology, though in fact several other mammalian families have as detailed a record. The earliest equid, the Eohippus or *Hyracotherium* of the Eocene epoch, was a small animal with four-toed fore-feet and three-toed hind feet and a very primitive dentition. These animals, which of course did not in the least resemble a modern horse, are linked to the latter by an unbroken evolutionary series spanning almost 50 million years. In addition various side branches of different types arose; some of them were the dominant horses of their day and could have made a case for

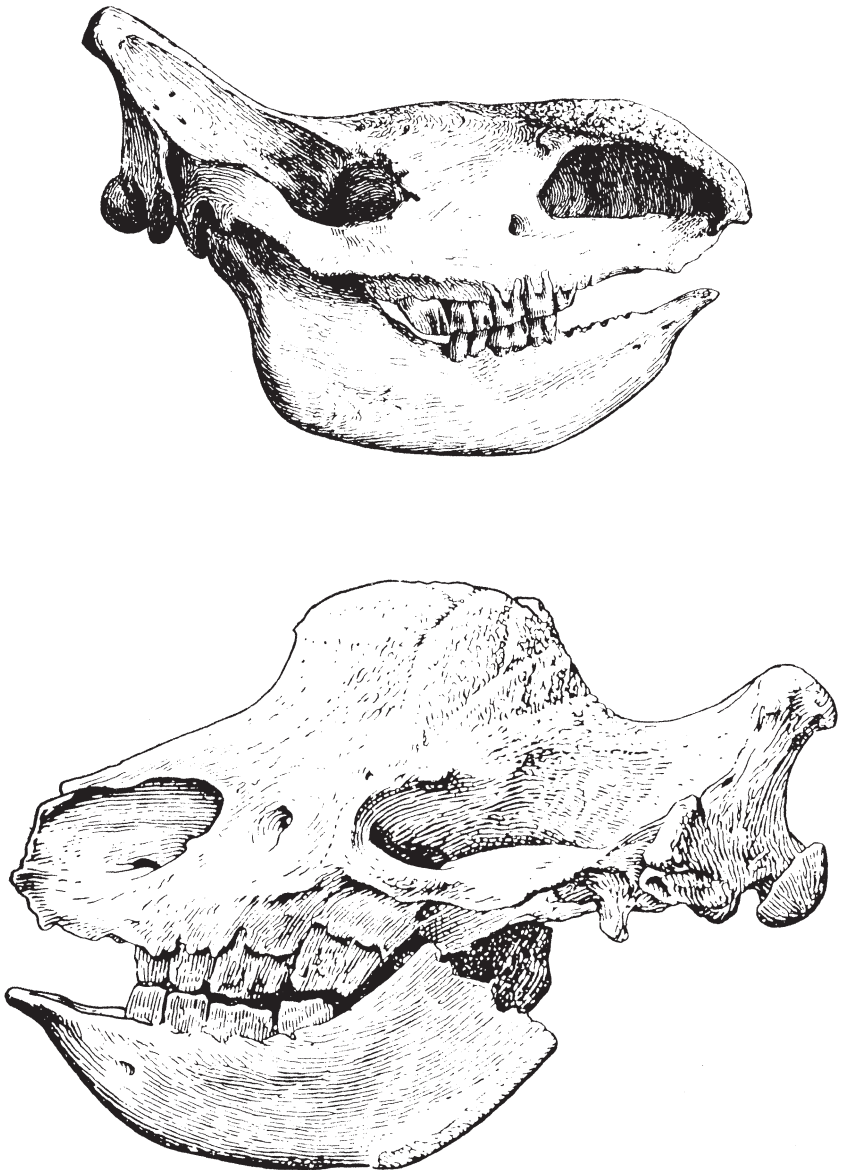


Figure 61. Skull and mandible of Woolly Rhinoceros, *Coelodonta antiquitatis* (above) and Giant 'Unicorn', *Elasmotherium sibiricum* (below), both one-fifteenth natural size. Pleistocene, U S S R.

regarding our one-toed horse as an evolutionary side-branch. One of these earlier types of dominant horses, the three-toed *Hipparion*, survived in the Early Pleistocene of Europe. Otherwise one-toed horses of modern type are predominant in the Pleistocene and their migration from North America across the Bering Bridge constitutes one of the main faunal markers inaugurating the Pleistocene.

Crusafont's hipparion, *Hipparion crusafonti* Villalta. With this species the line of three-toed horses expired in Europe after having been a dominant faunal element for some 10 million years. The genus *Hipparion* originated in North America, which was the centre of equine evolution throughout the Tertiary. The invasion of *Hipparion* in the Old World is usually taken as the event marking the beginning of the Pliocene, so that this genus is one of the most important index fossils of its time. The Pliocene hipparions were usually small, about the size of a pony but lighter in build, and there were even one or two dwarf species of gazelle-like proportions in Spain. One line tended to gradual size increase and this trend culminated in the Villafranchian *H. crusafonti* which was almost as large as a modern horse. Its immediate ancestor seems to be the Pliocene *H. rocinantis* Hernandez-Pacheco, a fairly large form that lived in Spain. In China, too, a large hipparion was present in Villafranchian times.

The hipparions differ from *Equus* in that all four feet still have three functional toes instead of one. In the modern horses the middle toe is very strong and linked to the lower part of the leg by a powerful system of ligaments which give it a spring-like action. The middle toe had the same function in the hipparions but was more slenderly built; when galloping or trotting, the side toes would touch the ground and assist the main toe in taking up the impact.

This system apparently functioned well enough, especially in small, lightly built forms such as most of the hipparions. In a large form it must have been less efficient than the one-toed arrangement, which may be one of the reasons why the invading *Equus* rapidly eclipsed its three-toed competitors. In Europe the competition between one-toed and three-toed horses was enacted in the early Villafranchian; in Africa, however, hipparions survived to a much later date.

The external appearance of the hipparions probably would have been that of a slim, delicately built horse. *Hipparion crusafonti* occurs in great numbers at Villaroya. A somewhat smaller form of *Hipparion* is present at Perrier (Roccaneyra, Pardines) but very rare. In

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Pardines times *Equus* invaded Europe, and *Hipparion* apparently became extinct almost immediately [108; 298].

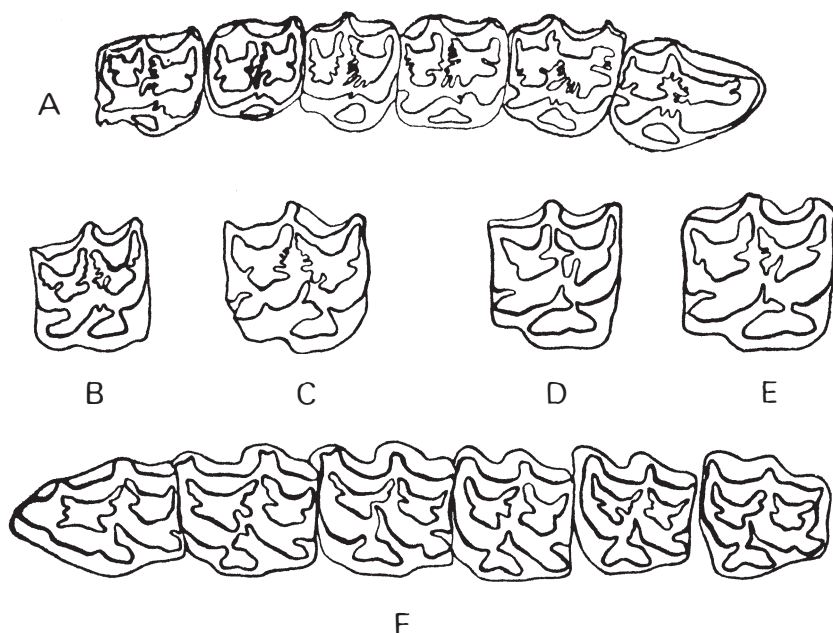


Figure 62. Upper cheek teeth of Equidae. A, tooth series in Crusafont's *Hipparion*, *Hipparion crusafonti*, Villafranchian, Villaroya; B-C, isolated teeth of European Zebra, *Equus stenonis*, Villafranchian; D-E, isolated teeth of Wild Horse, *E. przewalskii*, Recent; F, tooth series in European Wild Ass, *E. hydruntinus*, Late Pleistocene, Grotta Romanelli. About one-half natural size. A after Villalta; B-F after Gromova.

Zebrine Horses, *Equus stenonis* Cocchi and *E. süssenbornensis* Wüst. The earliest *Equus* to enter the Old World seem to have been zebra-like as regards their dentition, at any rate; whether they were striped like modern zebras is, of course, unknown. But in Europe the zebra-like *Equus stenonis* appears at a later date, in the middle Villafranchian of Saint-Vallier, at a time when the 'caballine' robustus horse (*E. bressanus*) was already present. *Equus stenonis* was abundant in the later half of the Villafranchian (Senèze; Olivola; Val d'Arno; Doveholes; Tegelen) and finally was replaced by, or evolved into, the Süssenborn zebra. Exactly where in the time scale the boundary between the two species should be drawn is not clear at present. At any rate it

may be concluded that the zebras in Europe ranged in time from the middle Villafranchian to 1-Günz II.

The European zebras were relatively small, lightly built forms. A complete skeleton of *E. stenonis* (at Basel) indicates a shoulder height of about 140 cm.; the specimen comes from Senèze. The earliest immigrants of this species in Europe were considerably larger, like the Villafranchian zebrine horses found in India (*E. sivalensis* Falconer & Cautley) and China (*E. sanmeniensis* Teilhard & Piveteau) are probably closely related to the European zebra; they are about the same size or slightly larger. This group may be directly derived from the North American Pliocene genus *Plesippus*. However, the early Villafranchian zebras soon gave rise to caballine and asinine horses, which later on were to crowd out the zebras throughout Eurasia; zebras now survive only in Africa [17; 87; 302].

Caballine Horses, *Equus bressanus* Viret (*E. robustus* Pomel), *E. mosbachensis* Reichenau, *E. germanicus* Nehring, *E. przewalskii* Poliakov and perhaps other species. The systematics of the 'true' or caballine horses in Europe during the Ice Age are somewhat chaotic. A great number of species have been proposed, but it is most improbable that all or even a majority of them will turn out to be valid. However, as Stehlin [265] says, it is '*plus facile de reconnaître la faute que d'y remédier*'. In brief, the following seems to be the main outline of the history of the caballine horse in Europe.

The first invaders in Europe of the genus *Equus* were of caballine type and belonged to the species *E. bressanus*, the so-called robustus horse, which appeared at Pardines; later on it lived side by side with the zebrine *E. stenonis* (Senèze). Other localities include Erpfingen, Chagny, Norwich Crag, A-Tegelen. This great horse is easy to distinguish from the zebrine horse because of its enormous size, rivalling that of the biggest living carthorses. The caballine horse type must have evolved at an early stage from the first zebrine invaders in the Old World.

A slightly smaller form, which has been called *E. mosbachensis*, occurs in the C-Cromerian and 2-Mindel (Mosbach; Mauer; Forest Bed; Koneprusy, etc.). Material from 1-Günz times (Episcopia; Nagyarsányhegy; Hundsheim; Gombasek; Jockgrim, etc.) is sometimes referred to the robustus horse and sometimes to the Mosbach horse (or species of their own).

The tendency to size reduction continues later on in the Pleistocene.

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Horses from the D-Holsteinian, 3-Riss, F-Eemian and 4-Würm I seem however to vary only moderately in average size and may perhaps be regarded as a single species, although several names have been proposed (besides *E. germanicus*, which has already been mentioned, *E. steinheimensis* Reichenau and *E. taubachensis* Freudenberg belong here). These horses were inferior to the Mosbach horse in size but were still quite powerful.



Figure 63. Wild Horse, *Equus przewalskii*. A group of five horses and one bison. Wall painting, Lascaux, Dordogne. The small head, erect mane, short legs and hanging belly are typical of this form. After Laming.

Finally, in 4-Würm II the modern species *E. przewalskii* makes its appearance. It seems to be this rather small form that was depicted by the Stone Age artists, for instance in the cave paintings of Lascaux. This was also the form hunted at the famous site of Solutré.

The record suggests that the change in size was comparatively sudden in some instances, which would indicate replacement by immigration; this is the case in the *germanicus-przewalskii* shift. On the other hand a gradual transition *in situ* may also be possible, for instance in the *bressanus-mosbachensis* sequence.

Przewalski's horse is the stock from which the domestic horse has been derived and local races both in the east and in the west were probably tamed. The horse does not appear to be among the earliest domestic animals. In Europe the wild form became extinct long ago, but a small population survives in the Gobi desert in Asia. Before its recent decimation the population formed large herds led by an experienced stallion; the same holds for the European tarpan or wild horse of Russia and Poland, which became extinct in 1918.

The extinction of the tarpan is due to human activity, but the history of the equid family contains several examples of inexplicable extinctions. As late as the end of the Ice Age the plains of North and South America swarmed with horses and yet they all died out in the Postglacial and had passed completely from living memory among the American Indians. Reintroduced by Europeans, horses thrived and

soon multiplied into enormous feral herds on the prairie and the pampa. Why then did their forerunners become extinct? In England, horse is missing in the F-Eemian interglacial faunas; perhaps it became extinct when the island had become separated from the continent by the high stand of the interglacial sea. The problem is made still more intriguing by the absence of man in England at the same time [18; 87; 187; 192; 265; 271; 302].

The European Wild Ass, *Equus hydruntinus* Regalia. This species is somewhat intermediate between the Asiatic wild asses (*E. hemionus*) and the true donkeys; for while its slender limb bones resemble those of the Asiatic asses, the lightly built 'microdont' teeth are of the same type as in the African form. The earliest evidence of this group in Europe comes from the late Villafranchian; Val d'Arno has yielded a jaw of the same type and an incomplete find (part of a shoulder blade) from Senèze may belong to the same form. These are now regarded as a distinct, Villafranchian form, *E. stehlini* Azzaroli. Finds from the earlier Middle Pleistocene are scarce (a member of the subgenus *Asinus* is reported, e.g. from Bad Frankenhausen and Koneprusy, 2-Mindel), but in the D-Holsteinian and 3-Riss finds are common enough (Lunel-Viel; Châtillon-Saint-Jean; Achenheim, etc.) and in the Late Pleistocene there are numerous records from caves and open-air sites in western, central, southern and eastern Europe. The species became extinct at the end of the 4-Würm.

Reports of donkey (*E. asinus* Linné) from Pleistocene deposits in Europe may be due to misidentification of *E. hydruntinus*, which as we have seen had donkey-like teeth. However, a donkey-like form has recently been described from the Late Pleistocene of Val di Chiana, Italy, under the name *E. graziosii* [18]. *E. asinus* has been recorded from the Pleistocene of Africa; domestic forms appear in the Neolithic of the Near East [17].

The Asiatic Wild Ass or Kulan, *Equus hemionus* Pallas. This species has been reported at several localities in Europe including Achenheim (3-Riss) and various cave deposits from 4-Würm. However, records based on limb bones may represent *E. hydruntinus*, while some records based on teeth may represent the small Przewalski horse [243]. Finally, however, Dietrich [66] found both teeth and limb bones in the 4-Würm I-II interstadial Rixdorf Horizon of Berlin and was able to substantiate the presence of kulan.

The present-day kulan has a rather wide distribution in northern

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Asia, where it inhabits the steppes preferably in the neighbourhood of rivers and lakes. Whether the herds are normally led by a stallion (as in the case of wild horses) or an old mare (as with donkeys) is not clear; information is conflicting.

A related but smaller species, the Onager (*E. onager* Pallas), which originally inhabited the steppes and deserts from Palestine to northern India but is now very rare, appears never to have ranged into Europe.