The Przewalski Horse: Morphology, Habitat and Taxonomy

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ABSTRACT

The pure-bred Przewalski Horse has differs in several clear-cut features of external and cranial morphology from domestic horses, and has a relatively restricted range of variation. Its former distribution and typical habitat are discussed. It seems to have been the eastern vicariant of a formerly widespread Eurasian species of wild horse, which may or may not have been the ancestor of the domestic horse (Although Przewalski's Horse was not itself that ancestor).

INTRODUCTION

Przewalski's Horse, the last living form of wild horse, now survives only in captivity, as far as is known. The success of its captive breeding has led to projects to reintroduce it into the wild.

Unfortunately, one of the two major blood-lines of Przewalski’s horse, the Prague line (B-line), is known to have a Mongol pony as one of its ancestors; while the Munich line (A-line) is not known to have any domestic ancestry, there are fears (Volf, 1970) that generations of captive breeding have "domesticated" it, and selective breeding to ensure maintenance of the "typical" conformation may prove desirable.

But what is "typical"? Was there not, throughout its recent history, always the possibility of wild horses crossing with local domestic stock? This paper will examine the question from a morphological standpoint, at the same time as trying to put Przewalski's Horse into perspective among recent wild horses.

MORPHOLOGY

External Characters
Because of the problem of the Mongol Pony ancestry, and possible
cchanges over generations of captive breeding, Mazak & Dobroruka (1967)
found it necessary to reconstruct the characters of Przewalski's horse as a
basis for future selection in the Prague line. Their sources included
descriptions, photographs and measurements, from 10 authors, of horses
shot or captured in the wild, beginning with the type description by
Poliakov in 1881. Where no other data were available, they used the first-
generation captive-born offspring of the Hagenbeck imports, and their own
observations of preserved material and the appearance of the last
Przewalski's Horse to be captured in the wild, Orlitsa III, caught in 1947.
Contrary to fears expressed by cynics from Lydekker (1912) onward, the
result was the discovery of a consistent type, homogeneous to the extent
that all wild taxa are homogeneous. The validity of the standards laid down
by these authors was corroborated by observations and measurements on
the subadult stallion Bars, offspring of Orlitsa by a stallion of the Munich
line (A-line) (Mazak, 1966).

Heck (1970) illustrated his own criteria for recognition of pure-bred
Przewalskis from those with some domestic ancestry. The basis of his
argument is not stated, but presumably relates to the the characteristics
seen in the reputedly pure-bred Munich line (A-line) as contrasted with
those which recur in the Prague line (B-line), which is known to contain
some Mongol Pony ancestry. It is interesting that, briefly, his results
generally agree with those of Mazak & Dobroruka.
Still further detailed information was given by Mohr (1959, and the 1971
English edition), who paid special attention to age changes; and by
Heptner (1961), who was anxious to establish criteria for detection of
domestic admixture as an approach to the problem of "purity" in European
wild horses. The conclusions of these authors are the basis for the
description which follows.

Stature

The stature is recorded for 10 first- or second-generation horses, more
than three years old, born in Askania Nova before the Second World War.
Six males were 138-146 cm high at withers; four females, 134-140 cm. There
was no difference between first- and second-generation individuals. Only
one record from the wild exists: a male shot by Grum-Grshimailo was
claimed to be 146.8 cm, though the method of measurement was not
stated. These figures, collected by Mazak & Dobroruka (1967), must be
regarded as more reliable than those given by Bannikov (1958), Sokolov
(1959), Mohr (1959) and Heptner et al. (1961), all of whom give values going
down to 124 or even 120 cm (sources not given, but certainly including
some not-fully-mature specimens, under three years old), and none of
whom take possible sexual dimorphism into account.
Weight

Three first- and second-generation males in Askania Nova, all five years old or more, weighed 278-297.2 kg; a three-year-old male weighed 260 kg. Two females, five and eight years old, weighed 244 and 280 kg (Mazak & Dobroruka, 1967).

Body conformation

Typically, Przewalski’s horse has a low-slung robust build with a remarkably thick, rather short neck; the withers are not prominent; the limbs are comparatively short but slender (Mazak & Dobroruka, 1967). Heck (1970) considers that the croup in the pure-bred Przewalski’s horse should be narrow, and the thick neck is not held upright like a deer (“nicht hirschartig aufrecht getragen”). The legs he describes as short, very sturdy, and strong-boned, and that long fine-boned legs are a sign of domestic ancestry; this may be true, but Mazak & Dobroruka’s discussion shows that the ”stockiness” can be overstated.

Head form

The muzzle is short and high and the lower margin of the jaw is straight, so that the profile line of the jaw meets the dorsal profile line of the head at an angle of some 16°-18°30’ (21° in a subadult), compared to about 25-32° in a domestic horse; the upper lip protrudes somewhat beyond the lower lip (Mazak & Dobroruka, 1967). Volf (1970) has, as described below, documented some differences in the ventral profile of the mandible between wild-caught and captive-born specimens; for the moment it need only be noted that any changes that have occurred do not close the gap between Przewalski’s horse and domestic horses.

According to Heck (1970), the interorbital distance should be relatively narrow, and the eyes project laterally. Too broad a forehead, and eyes that are too forward-looking, indicate domestic blood. Frechkop (1965) described the craniological basis for this feature, but found that some domestic ponies do not differ much, if at all, from Przewalski’s horse.

Cranial Characters

Frechkop (1965) was the first author to point out differences between the skulls of Przewalski’s horse and domestic horses. The orbit is oval and dorso-ventrally compressed in the Przewalski skull, but it is rounded in the domestic horse; the orbital rim is more prominent anteriorly, less so posteriorly, than in most (not all) domestic horses. The Przewalski skull has a higher nasal cavity than most domestic horses (a few pony breeds alone excepted), so that the facial angle is smaller, a difference which is
appreciable in the living animal (see previous section). In the mandible, the corpus is deeper and the ascending rami are shorter and more vertical (less convergent towards the jaw angles).

Azzaroli (1966) compared in detail the skulls of Przewalski horses with those of domestic horses. The Przewalski skull differs in the following three features: (1) the convexity of the braincase roof is less pronounced; (2) the narial opening is longer, its posterior end being above the distal margin of premolar 2 (P2), whereas in the domestic horse it is above the mesial lobe of P2; (3) the palate is longer, reaching the level of the distal lobes of the third molar (M3), while in domestic horses it reaches only the M2/3 boundary. An interesting finding was that the skulls of Upper Pleistocene horses from Europe (Italy, Germany and Russia) resemble the domestic horse, not Przewalski’s horse, as apparently does the skull of the Tarpan (see below).

According to Eisenmann (1982), craniometrically Przewalski’s horse belongs to a long-snouted group along with certain extinct North American species and the heavy horses among domestic breeds; European and Alaskan fossil horses, and pony breeds, are short-snouted. Forsten (1988) compared Przewalski skulls with those of tarpans and Late Pleistocene wild horses from Europe and Siberia, using log ratio diagrams. In comparison the Przewalski skull has a narrow snout and short, broad braincase.

Volf (1970) has, however, put some of these differences into perspective. Studying the mandibles of six Przewalski horses caught in the wild, six that were first- to third-generation captive-born, and 10 domestic horses (5 Mongol ponies, 5 Kladrub horses), he found that the captive-born Przewalski horses approach domestic horses somewhat compared to the wild-born ones. The height of the mandibular corpus decreases, leaving the mandibular angle much more prominent, and the toothrow shortens. Volf comments that this could be simple genetic plasticity, brought out by inappropriate feeding with its consequences for jaw mechanics; or it could reflect the need for stronger selection-to-type in the captive stock. A possible criticism of this study is that the ancestry of four of Volf’s captive-born specimens is not absolutely clear according to the studbook, but his point about the need for selection is well taken, and further studies need to be made.

Body colour

The foals caught by Hagenbeck were of two colour types: one pale grey-yellow, the other a bright yellowish red-brown. There has been considerable discussion over this: were there two subspecies, even two species, involved? Matschie (1903) thought so, and distinguished a new
species *Equus hagenbecki* from *E. przewalskii* (see below). Mohr (1959) argued against this; there is no evidence that the two morphs were from different geographic areas, indeed she quotes a record from Pallas that two colour types occurred within the same herd, and draws attention to a photograph of the two morphs in the same herd published by Bannikov (1954).

The head and neck are darker than the body, as Poliakov (1881) himself noted; this contrast is less marked in the dark morph than in the light one. The underparts are lighter than the flanks; Heck (1970) emphasises the manner in which this light tone extends upward behind the forelegs and in front of the hindlegs, creating with the brownish flanks a saddle effect. The distal segments of the limbs are also dark, even black, from the tarsus and carpus (or even higher) to the hooves; this tone is more expressed on the anterior than the posterior surfaces, at least on the forelimbs. Three to ten thin dark stripes are present on the carpus, and there are generally a few on the tarsus too.

A dark dorsal stripe, or "eel-mark", runs from the mane down the back and dorsal side of the tail to the tail-tuft. It is much clearer and darker in adults than in the young, and in summer than in winter. The type specimen, a juvenile in winter coat, had no noticeable dorsal stripe at all, a circumstance which was unfortunately used as a diagnostic character in the type description (Poliakov 1881)!

Across the shoulders, just in front of the end of the mane, there is at least a trace of a thick dark cross-stripe. It may be present on one side only. The muzzle tends to be light coloured, often actually white, but the lips and the margins of the nostrils are dark. The region round the eyes is also somewhat lighter than the general tone of the head.

Hilzheimer (1909) went even further than Matschie, and recognized three different subspecies: *Equus equiferus equiferus* from Baitak Bogdo, with light muzzle and black limbs; *Equus equiferus typicus* from Zagan Nor, with dark muzzle and black mane; and *Equus equiferus hagenbecki* from the Urungu River, with light limbs and muzzle and red-brown mane. Volf (1974) found no evidence that these differences were geographic; he suggested, however, that captive breeding in some stocks has tended to make the type more homogeneous.

White or dark marks on the face and elsewhere are expected to be more frequent in cross-bred horses, but are not necessarily indicative of domestic ancestry, according to Mohr (1959), who described and pictured an apparently pure-bred (A-line) stallion with a white star between the eyes. While the iris of the eye is generally brown, a few blue-eyed individuals are known (Lee Boyd, personal communication).
Mane and Tail

The mane, dark brown to black, begins between the ears and reaches the withers; there is no forelock. The mane is upright, or falls slightly to one side, especially in older animals; it never, however, hangs like a domestic horse. In winter, whitish hairs some two-thirds the length of the dark mane-hairs border the mane on either side. The hairs forming the mane are 16-20 cm long (Mazak & Dobroruka, 1967).

Perhaps the most striking difference from domestic horses is that in Przewalski's horse the dock is short-haired: that is to say, the proximal half of the tail is free of the long "horse-hairs" which form the tuft; it is nearly always a lighter shade of the dorsal colour of the body. The dorsal stripe continues down the tail-dock. On the sides the hairs get longer and darker distally, grading into the long dark tuft hairs. The long tail hairs reach to the level of the fetlocks.

Body hair

The natal coat is yellowish and curly; it is shed within the first few weeks of life. The mane of the newborn foal is short and curly, and does not begin to grow in adult fashion until some six months of age.

The hair in winter is markedly longer than in summer. On the cheeks and posterior half of the lower jaw it forms a "beard" 5-8 cm long in winter (Mazak & Dobroruka 1967), which almost disappears in summer. The mane may hang to the side more in winter than in summer, but a hanging mane may indicate poor health, or a delay in moulting.

The timing of the spring moult seems to depend on ambient temperature. In 1958 the Prague Zoo horses began to shed between April 2nd and 22nd in different individuals, in 1959 a month earlier (March 10th-28th), and in 1960 in between (March 21st-April 5th); in all cases the mean daily temperature was of the order of 5 to 7°C at the beginning of the moult (Mazak 1962). The moult takes 48-69 days in adults, with a slight tendency for it to last longer in older animals; and even up to 87 days in foals in their first moult. The sides of the face, a spot behind the ear, and a spot on the upper haunch are the first areas to moult; further flank spots are then shed, followed by the forehead and midface, the upper third of the neck, and the remainder of the neck and the flanks, in that order. The belly, lower limb segments, angle of the jaw, and throat retain their winter hair longest (Mazak 1962). Domestic horses moult in more diffuse and irregular fashion.

Postcranial Skeleton
Stecher (1961) found that 15 out of 21 Przewalski’s horse skeletons had 18 thoracic vertebrae, the rest 19; 11 had five lumbars, the remainder six; 17 had five sacrals, 3 had four. These figures differ somewhat from those of domestic horse, which generally have 18 thoracics like the Przewalski horse, but six lumbar (89/94 skeletons).

Forsten’s (1988) comparison of postcranial measurements with those of Upper Pleistocene horses refutes the idea of any consistent differences apart from size (the Przewalski Horse is smaller). The skeleton of a tarpan had shorter, broader phalanges than the Przewalski series.

**DISTRIBUTION AND HABITAT**

Bannikov (1958) has recorded all that is known of the distribution and habitat of Przewalski’s horse in recent times. Przewalski himself met with wild horses only in Dzungaria; he had earlier reported them from Tsaidam and Lop Nor, but subsequently admitted that this was in error. Pevzoff described its range as from the Manas river in the west to the latitude of the eastern border of the Tien Shan range (about 95°E), in saxaul (*Haloxylon*) steppe. Grum-Grzhimailo found them in the Gashun district, north of the Gutchan Mountains. Clemenz met with them south and southeast of the Baitak-Bogdo Mts.; Bannikov himself saw one in Ulan Bator which had been captured on the northern slope of the Baitak Bogdo. Bannikov summarises the turn-of-the-century distribution as limited in the north by the Urungu and the High Altai, extending to 46°N, 90°E; in the southwest by the Tien Shan, down to 44°N; and extending east to 95°E. Most of this range is in the northern part of Xinjiang (i.e. Dzungaria); only its eastern edge extends into Mongolia itself.

By the early 1950s, Przewalski’s horses appear to have been restricted to the Baitan Bogdo, and as far east as the Takhin-Shara-Nuru ridge. Photographs of what were identified as wild horses, in the distance, taken by Kaszab in 1966, were considered to be *Equus hemionus* by Volf (1967), but Kaszab himself (1968) strenuously defended his original identification and was supported by Bokonyi (1974). Even if these animals actually were wild horses, none - not even tracks - have been seen since. It seems therefore that Przewalski’s horse is extinct in the wild: hunted for meat, and excluded from their pastures and watering points by domestic stock. The region it was known to inhabit is not sandy or rocky desert, but better described as semi-desert, at some 1000 to 1400 metres altitude. Vegetation in some regions is surprisingly dense, consisting of saxaul (*Haloxylon ammodendron*), wormwood (*Artemisia incana*), tamarisk (*Salicornia herbacea*) and various grasses; elsewhere it is very sparse, with only isolated tufts of the salt-grass *Salsola* breaking the flat desertscape. It is this latter habitat which is shared with Kulan (*Equus hemionus*). Wild horses however were not as nearly independent of water, although they
were said to be capable of digging into the sand for water with their hooves.

In this area, mean January temperature is -15 to -18°C, plunging to a minimum of -35°C, and mean July temperature +2° to +25°C, reaching a maximum of +40°C; annual rainfall is not above 400mm (Bannikov 1964). The same habitat supports, even today, other large ungulates notably Kulan (*Equus hemionus hemionus* and *E.h.luteus*), Saiga (*Saiga tatarica mongolica*), Goitred gazelle (*Gazella subgutturosa hillieriana*), Mongolian gazelle (*Procapra gutturosa*), Wild Camel (*Camelus ferus*) and, in the desert ranges, Argali (*Ovis ammon darwini*). The main predator is the wolf (*Canis lupus*), but small cats (*Felis silvestris chutucha, Otocolobus manul*) occur. Desert hares (*Lepus spp.*) and rodents constitute the remaining terrestrial mammal fauna.

**TAXONOMY**

The Przewalski Horse

Mohr (1959) gives the following local names for Przewalski's Horse, as collected by various authors: *Take* (*Tachi, Takke, Tekke*), *Statur* or *Dzurlkadu* (Mongol), *Surtake* (*Surtaken, Syrtach*) or *Kertag* (*Kurtach*) (Kirghiz), *Jauwat* or *Takky* (Turfan). There seems to be some dispute about these names. Falz-Fein, according to Mohr, gives the Mongol (sic) word for horse as *Tach*, while *Syr* means desert and *Kur* means mountain: hence *Syrtach* and *Kurtach*, which would be the light and dark colour morphs respectively.

Przewalski's wild horse was mentioned in literature and even known to the scientific world long before it was described taxonomically. Bokonyi (1974) cites a description of a wild horse hunt, in what would now be Ganssu, by Genghis Khan in 1226, and of a wild horse captured at Takhyn-nus (central Mongolia) by order of Chechen Khan and presented to the Emperor of Manchuria in 1637. Mohr (1959) draws attention to the observation of wild horses in the region east of the Ob, about 45°N, 85-90°E, by John Bell in 1719-1722. Przewalski's horse was certainly among the *Equiferi* mentioned by Pallas (1811: see below).

An intriguing interlude between these old mentions and the scientific description of *Equus przewalskii* is the Yo-to-tze. Smith (1841), after recording information received from various sources about wild horses in Central Asia (among which certainly is Przewalski's horse), described (pp.304-7) and pictured (Pl.17) an equine called *Asinus equuleus*, the Yo-to-tze, which had been drawn by the editor, Lizars, at the request of Sir Joseph Banks, who had obtained from Earl Rivers information that there was "an undescribed species of diminutive horse brought from the Chinese frontier north-east of Calcutta, and was then to be seen in a livery stable
near Park Lane”. It was a male, slightly under three feet high although nearly four years old (by its teeth), rather slenderly built, with a "coarse abundant mane, larger than the ass, but still standing upright"; the tail was long-haired nearly to the root (and, indeed, the plate does show a horsehair-free basal portion to the tail); there were chestnuts on the forelegs only; it was a "yellowish red clay colour", with black mane and tail hair and dorsal stripe, a vague shoulder-cross, knee- and hock-stripe, and black fetlocks, the rest of the lower limbs being brown. Smith states that he had "hesitated long" over whether it was not really a horse rather than an ass. The plate, by error labelled *Asinus hippagrurus*, corresponds more or less to the description except that the mane is unexpectedly short. Lydekker (1912) was the first to draw attention to the reputed locality, Chinese Tatary (=Mongolia), and to the close fit of this description to Przewalski's horse; only because the muzzle was not described (nor figured) as white he considers it "impure". He is surely right that this was the first Przewalski horse to be described in a scientific work; only the residual uncertainty that remains where there is no type specimen prevents the name *equuleus* from becoming the senior synonym for *przewalskii*. Poliakov (1881) described *Equus przewalskii* from a subadult (15-month-old) specimen forwarded to him by the Polish cavalry officer N.M.Przewalski, who in turn had obtained it from A.K.Tikhonov in 1878. It had been killed by Kirghiz hunters not, as at first thought, in the Lob Nor district but in eastern Dzungaria (see Mohr, 1959:4, 71-2). Matschie (1903) proposed to restrict the type locality to Zagan Nor and Baitak-Bogdo, but there is no evidence to support this action; Harper's (1940) proposal of Gashun Oasis (44°30'N, 90°E) seems more acceptable, based as it is on other known early collecting localities. Matschie's *Equus hagenbecki*, described on the supposition that the light and dark morphs are actually distinct species, was from Ebi Spring, Njursaul and the Urungu River district; Lydekker (1912) ascribes it to "an admixture of blood" but, as we have seen above, there is no evidence that it is other than a simple polymorphism.

The only other name given to a Mongolian wild horse is *Equus caballus gutsenensis* Skorkowski, 1946. This name was given to the supposed "pure component" of the Przewalski horse, as part of an elaborate attempt to get back to the original pure-blooded subspecies of *Equus caballus*, all domestic breeds and even wild stock being, it was supposed, cross-bred (see below). The type of *gutsenensis* was a skull from Gutchen (=the Gashun oasis or the Gutchan Mts).

**European and western Asian wild horses**

The mouse-grey Tarpan of western Russia, Ukraine, Poland and northern Germany has been endlessly discussed in the literature, both from a taxonomic standpoint and with regard to its nomenclature. Herodotus
(Book 4:51-2) mentioned wild white horses living around the great lake in Scythia which forms the source of the Hypanis (=the River Bug) (de Selincourt, 1954); the Bug does not today originate in a lake, but alterations of river courses are not unknown historically, and the upper course of the river is in the same general area as the Pripyat Marshes, in the region of the Poland/Byelorussia/Ukraine border. Smith (1841) cited Schneebergius as saying that the wild horses of Prussia were "mouse-coloured", with a dark dorsal stripe; he also, interestingly, gave two Roman sources for them in North Africa (one described them as "whitish ashy grey", the other as rufous - but were these really wild horses, as opposed to wild asses?). Lydekker (1912) and Bokonyi (1974) have conveniently summarised some of the other historical sources, as early as Roman times (when wild horses occurred as far west as Spain). Von Heberstein, between 1517 and 1528, saw cream-coloured wild horses in Lithuania. On the other hand Albertus Magnus in the early 13th century described those in Prussia as being "cinereus" (ashy), with a dark dorsal stripe; despite the claim of Bokonyi (1974), this does not sound like the "creamy" description of von Heberstein but, as we shall see, a seasonal colour change seems likely.

The first detailed description of European wild horses was provided by Gmelin (1774), who encountered them in 1769 in the region of Bobrovsk, near Voronesh. They were, he said, "hardly as large as the smallest Russian" [pony]; they had very thick heads, pointed ears, short frizzly mane, and "tail-hair shorter" than in domestic horses (perhaps referring to short hair on the dock?). They were mouse-coloured, with white or ashy-grey belly, and the limbs black from the knees and hocks down. The hair was very long and thick. Gmelin and the peasants assisting him killed a stallion and two mares, together with a Russian mare that had run wild with the herd, and captured the hybrid she had produced as well as a pure-bred foal.

Pallas (1811) described the Russian wild horse as a variety of Equus caballus under the name Equiferus; a name not intended in a scientific sense, but as a simple descriptive term in a book written in Latin, despite its adoption by later nineteenth-century and early twentieth-century authors as a scientific name (discussed in Mohr, 1959). In fact, he mentioned wild horses between the Dnieper and the Altai, but did not distinguish clearly between the western and eastern ones, though he mentions their colour as being reddish or pale grey - most subsequent commentators have felt at liberty to interpret this as meaning that the western ones were the grey ones, as the reddish ones would be satisfactorily accounted for by the Przewalski horse.

Smith (1841) provided a wealth of interesting information on wild horses, admittedly second-hand from Tatars and Cossacks whom he had interviewed in 1814, but in the main quite consistent with other evidence.
Referring to true wild horses as tarpan and tarpani, to distinguish them from feral horses \textit{(takja or muzin)}, Smith's informants told him that the purest wild horses were found on the Karakorum, south of the Aral Sea, on the Syr Darya, near Kusneh (presumably the Kuznetsk-Alatau region of the Dzungarian border, not Kuznetsk on the western Kazakhstan border), and east into the Gobi; while in Russia there were mixed herds near settlements. Like Pallas, Smith referred to a variety of colours: tan, "isabella" (yellowish-grey), or mouse, with a whitish "surcoat" (frosting?). Then, curiously, Smith went on to describe as a genuine wild horse (whether on the same authority or no, it is difficult to say) "the white woolly animal of the Kara Koom and the high table land of Pamere", 14 hands high, with large head, thick muzzle, short ragged mane, a "beard", "grisly white, somewhat darker in summer". On pp.262 and following, what seems to be the same horse is mentioned again, and figured (pl.4), as "The White or Grey stock" from the Pamir Plateau, the steppes north of the Black Sea, Armenia and Cilicia; but the horse under description this time would seem to be domestic. One of the irritating things about this potentially fascinating work is the way it appears, almost throughout, to have been written hurriedly, and seems forever on the verge of exactitude without ever really achieving it.

On the question of "impurity" in wild horses, Pruski (1959) and Heptner et al. (1961) have some remarks. Because of the intensity of competition which pure-bred wild horses would offer, domestic horses would have a rather low probability of survival and breeding if they ran wild, and any cross-breds they produced would again be subjected to strong competition. In fact the influence of a wild stock on local domestic breeds is likely to have been much more significant than the reverse. Only in the last stages, when the wild horses were disappearing, would domestic genes begin to predominate.

As agriculture and stock-breeding gradually took over the steppes, the tarpans disappeared. But Heptner et al. (1961) argue that even the last survivors remained fairly true to their basic colour and conformation. The last survivor died in 1918 in captivity near Poltava. This last individual, known as the Dubrowka or Taurian tarpan, was described (Heptner 1955) as being 140-145 cm high, with a big head, small ears and short neck; "field-mouse-grey" with a broad dorsal stripe and an ill-defined shoulder-cross; the mane, tail and shanks black; and a thick mane, semi-erect but falling somewhat to both sides of the neck; the forehead broad, vaulted, the profile straight. The only other tarpan to be described in the literature was the Shatilovski or Cherson tarpan, caught in 1866 on the Zagradoff steppes, north of Crimea. The Cherson tarpan, which was gelded and lived for 20 years in Moscow Zoo, was dark mouse colour with the shanks black; the mane hung down on the left side, and unlike a Przewalski’s horse had a
forelock. (The tendency of the mane to fall to the side, and the development of a forelock, are discussed by Heptner (1961)).

The skull of another tarpan, killed on Rachmanov steppe in 1854, was studied by Gorgas (1966) who measured its cranial capacity. The finding that its cranial capacity was small, like domestic horses, while that of Przewalski's horse is larger, was widely interpreted to mean that the tarpan was not a genuinely wild horse at all, but feral (because brain reduction is widely acknowledged as a consequence of domestication). Against this may be urged both the reputed homogeneity of tarpans, as already discussed; and the finding that some subspecies of a given species may be naturally smaller-brained than others (and so, in a way, more "domesticable" - see Hemmer, 1983).

In general, Heptner et al. (1961) distinguish what they call *Equus przewalskii gmelini*, the South Russian steppe tarpan, as having been dark grey with a black mane and tail, black dorsal stripe, and black lower limb segments; the young rusty-tinged; the winter coat long, dense, slightly wavy, and "dirtier looking" than the summer coat, evidently fading to ash-colour during winter; the facial skeleton rather short, molar teeth small, and frontal profile slightly concave. It lived as far east as the Ural River, or more probably only to the Volga, and west perhaps to Romania.

It was Antonius (1912) who gave the name *Equus gmelini* to the tarpan, although he considered that it was not the only wild horse of Europe: "*Equus ferus Pallas*" (on which name see above), the Przewalski horse, had lived in Europe during the Upper Palaeolithic, as had "*Equus gracilis Ewart*", a supposed pony-like species for which there is in fact no hard evidence, and six (!) other species for some of which there is fossil evidence (mainly, in fact, Middle Pleistocene), for others not. But there is no doubt that the name *gmelini* is antedated by more than a century: Boddaert (1785:159) founded a species *Equus ferus* largely on Gmelin's description, and it is this reference, rather than Pallas (see above), which is the original technical usage of the name. The earliest name for the Tarpan is therefore *Equus ferus* Boddaert, and *Equus gmelini* Antonius is a junior objective synonym.

Nobis (1971), apparently not realising that *gmelini* is an objective synonym of *ferus*, used both names, for different horses, associating them with different fossil samples: *Equus ferus ferus* from Mezin, and *Equus ferus gmelini* from Sungir.

A further name that seems likely to apply to the Steppe Tarpan is *Equus scythicus* Radulesco & Samson. This was founded upon teeth of latest Pleistocene age from Dobrogaea, Romania, but some domestic horses were also referred to the species (see Radulesco & Samson, 1962).
In addition to the Steppe Tarpan, Heptner et al. (1961) also distinguish a Forest Tarpan, *Equus przewalskii silvaticus* Vetulani. This would be smaller than the steppe form, and of a weaker build, and the colour fading was more intense in winter. It lived in western and southwestern Byelorussia, Lithuania, Poland, and Germany. The last representatives survived in the Bialowieza Forest until about 1814, when they were all caught and either tamed or killed (Pruski, 1959). The name *silvaticus* Vetulani is actually long antedated by *Equus sylvestris* Brincken, 1826, a name applied to wild horses which had lived "40 years previously" in Bialowieza Forest, which were described simply as "graufarbig, mit einem Aalstrich über den Ruecken" (gray coloured, with an eel-stripe down the back).

Vetulani (1936) described how, from the 1920s on, he collected koniks from the vicinity of Bialowieza, which were known to incorporate tarpan blood from as recently as about 1820, and after a period of selective breeding reintroduced them to the wild. The males averaged 129.4 cm high, the females 128.0; they varied in colour from brown to black or isabel, and he selected them, in accordance with Brincken (1826), to be grey at least in summer - but it has been found that the coat grows white in winter (except for the distal limb segments, dorsal stripe, mane and tail), as does that of the primitive Hutsul breed of the Carpathians according to Bokonyi (1974). The white horses of Herodotus and von Heberstein can doubtless be understood in this light. The mane is erect in foals only, and falls to the side in adults. Volf (1979) has most recently described their appearance and behaviour.

**Any Other Wild Horses?**

Skorkowski (1946, 1961) was convinced that the wild horses known to us and to history are all mixtures between six originally pure types. Przewalski’s horse, tarpan, even ten out of fifteen fossil horse skulls which he examined - all are "mixed". Before dismissing these views peremptorily, we should remember that in the first half of the century this sort of analysis was widespread in a sister science: anthropologists, dismayed at the great variability within human races, and the wide overlap between them in measurable characters, hypothesized the former existence of "pure races" which had, during prehistory, inconsiderately intermingled. All that Skorkowski did was to apply the same principles to hippology (and refuse to modify them as time went on).

There are also those who believe that there were not merely different subspecies of *Equus ferus*, but different full species of wild horses, which all formed part of the ancestry of the domestic horse. This model has most recently been summarised by Kapitzke (1973), based on the work of Ebhardt, who never published his conclusions fully. There were four such species, according to this model: the Urpony (surviving in its purest form...
in the Exmoor Pony; the Tundrapony; the Ramshead-horse (best represented by the Sorraia Horse today); and the Ur-thoroughbred. Trumler (1961) allocates scientific names to the four types. The Przewalski horse is (mainly) a Tundrapony; the Tarpan was a mixture of types three and four. As with Skorkowski's model, so with Kapitzke's: even known wild horses are deemed not to be pure-bred representatives of one type or the other; again, fossil material that can be definitively allocated to one or the other is rather scarce, but the different types can, it is claimed, be recognised in European Upper Palaeolithic rock-art - leaving no room for stylistic variation or artistic license, of course. Thus, the Urpony is represented at Lascaux, Les Combarelles and Le Portel; the Tundrapony at Niaux, La Madeleine and, again, Les Combarelles; the Ramshead-horse at Spanish sites and Tassili; the Ur-thoroughbred at Fezzan. (It should be noted that Groves (1986) questioned the existence of wild horses in North Africa at all; but while his paper was in press, evidence at last became available finally resolving this much-discussed question (Bagtache et al., 1984): a true wild horse really did live in North Africa).

On this question of the accuracy of Upper Palaeolithic representations, Ucko and Rosenfeld (1967) urge caution. There are numerous hypotheses of the meaning of this prehistoric art - art for art's sake, sympathetic magic, mythological illustration, sacred decorations for religious sanctuaries - and it covers an immense period of time, and extended over vast areas of Europe and Africa. Surely not all, perhaps not even most, animal depictions are meant to be photographic? Yet hippologists, in particular, have tended to treat them as if they were: Blanchard (1964), for example, sees nearly 20 different species in European cave art! Even Mohr (1959), though realising that there are drawbacks to treating the paintings realistically, suggests on the basis of the Pech-Merle spotted horses (illustrated by Ucko & Rosenfeld, 1967:60, and again, among 22 horse depictions on a double page spread, 1967:154-5) that dapple-grey morphs existed at that time. There are perhaps just a few things that one can say about the latest Pleistocene horses of Europe on the basis of Upper Palaeolithic art: that most, at least, had upright manes and grew "beards" on the jaw-line, and that there were some with light muzzles, light underparts, and dark legs. Some of the most realistically depicted horses, such as the truly brilliant drawing from Niaux (Mohr, 1959:22), show all these features and are irresistibly reminiscent of Przewalski's horse, which means only that there was (among others?) a kind of wild horse in western Europe at that time which was of that general type.

That there were in fact other wild horses in latest Pleistocene and early Holocene times was convincingly argued by Lundholm (1949), who distinguished West European wild horses (France, Switzerland) from both Tarpan and Przewalski horse by the complex enamel of the cheekteeth, and by the fact that M3 was not longer than M2; and Swedish wild horses of
early postglacial times by a combination of skull characters, the enamel being simple. It is studies like these that do most to establish that there really were more than one taxon of wild horse in Eurasia in the last 20,000 years, although whether there was more than one distinct species, as opposed to just subspecies of \textit{E.ferus} is disputable: see Groves (1986) and Forsten (1988) for a summary of some evidence suggesting that there might have been two or more species in the late Pleistocene, but hardly three distinct genera, as proposed by Samson (1975)!

**Summary: taxonomy of recent wild horses**

The present "state of the art" is reviewed most recently by Groves (1986). The three postglacial wild horses for which there is osteological evidence are \textit{Equus ferus przewalskii}, the tarpan \textit{E.f.ferus} (of which Polish and Ukrainian representatives cannot, on present evidence, be distinguished from one another), and the unnamed Swedish form.

On the steppes east of the Volga, as Heptner (1955) argued, was a zone of intergradation where both grey (tarpan-like) and reddish (Przewalski-like) wild horses occurred. This is the evidence that the European Tarpan and Przewalski’s Horse were conspecific. (East of the Ural River, in Kazakhstan, wild horses were predominately of red type, so probably, according to Heptner, the true Przewalski’s horse.)

Tarpan skulls average very slightly longer than Przewalski’s in basal skull length, but slightly shorter in Vertex Length (upper length of skull), they have a less extended occipital crest, and the diastema is longer; the single complete Swedish skull is smaller than either, but again with a rather long diastema (Groves, 1986, Table 1). The Tarpan has on average smaller teeth than Przewalski’s horse; in the Swedish horse the teeth are smaller still (Groves, 1986, Table 2). Forsten (1988) found two tarpan skulls to have a longer, narrower braincase than those of Przewalski’s horse; Eisenmann (1982), though she studied no tarpans, noted a relatively short muzzle in various European late Pleistocene horses, which would seem to confirm Forsten’s finding from a different perspective.

In summary, then, I would recognize just two subspecies of wild horses in historic times, as follows:

1) \textit{Equus ferus ferus} Boddaert, 1785. The Tarpan. Synonyms: \textit{sylvestris} Brincken, 1826; \textit{gmelini} Antonius, 1912; \textit{silvaticus} Vetulani, 1928.

2) \textit{Equus ferus przewalskii} Poliakov, 1881. Przewalski’s Horse. Synonyms: hagenbecki Matschie, 1903; \textit{typicus} Hilzheimer, 1909; probably also \textit{equuleus} Smith, 1841.

**Wild Horses in Perspective**

The question of the relationship of modern horses to other equids has been reviewed by several authors (Azzaroli 1966, Bennett 1980, Groves &
Willoughby 1981, Groves 1986). There are problems with all of these models: whether true asses and hemiones form a clade, whether all zebras form a clade, and whether horses are (1) the most divergent of surviving equids or (2) the sister-group to hemiones and/or asses or (3) part of a clade including some or all zebras - these are still topics for lively debate. A further question, more perhaps a matter of taste than those listed above, is whether all living equids should be placed in a single genus, *Equus*, or should be split into several genera. Fortunately any of the possible answers to this last question would be effectively the same as far as horses are concerned, since *Equus caballus* is the type species of *Equus*. Is, then, *Equus ferus* to be maintained as a species separate from *Equus caballus*? Yes, for two reasons.

First, if domestic horses are not descended from the tarpan or any of its conspecifics, then the separation is warranted on taxonomic grounds. This is still an open question: a version of the multiple-origins theory may be correct, or domestic horses may be descended from some unknown ancestor, not the tarpan. Note that the chromosome difference (see Ryder, this volume) would seem to exclude Przewalski's horse from the ancestry of domestic horses, unless the mutation occurred almost at the moment of domestication (before breed diversification).

Even if domestic horses are descended from the tarpan, or from a wild ancestor conspecific with the latter, the question of whether wild horses are or are not *Equus caballus* becomes a non-question, to be decided on convenience alone, as discussed by Corbet & Clutton-Brock (1984), who advocate keeping them separate. Note that the chromosome characters which apparently rule out Przewalski's horse as the ancestor do not exclude the tarpan, since karyotyping of koniks and "bred-back tarpans", which are descended in part from the Bialowieza tarpans, has picked up no trace of heterogeneity. (As has been seen above, this is still an open question). Note, incidentally, that the chromosome difference does not require that Przewalski and Tarpan be separate species, as it is a simple Robertsonian one, which does not affect interferility and indeed is well-known between conspecifics in other mammalian groups; as we have seen, Heptner's (1955, 1961) evidence suggests there was in fact an intergrade zone between them.

REFERENCES CITED

Antonius, O. 1912. Was ist der "Tarpan"? Naturwissenschaftliche Wochenschrift, N.F. 11, no.33.