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**The horse: its domestication, diffusion
and role in past communities**

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**Quaternary horses: possible candidates to
domestication**

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QUATERNARY HORSES: POSSIBLE CANDIDATES TO DOMESTICATION

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Ever recurring questions about modern horses are: how many species and/or subspecies there are? Are the "Tarpan" and the "Przewalski horse" the same "thing"? How closely related are they to the fossil Pleistocene wild horses? From what stock(s) do the domesticated horses spring?

The very recurrence of the questions is a proof that definitive answers are difficult to give. This paper is no exception and will only try to present some evidences relevant to the questions above.

Before that, two points must be recalled and stressed. Whatever was the "Tarpan", its presently available osteological remains are limited to one complete skeleton (St Petersburg: ZIN 521) and one isolated skull without mandible (Moscow: MGU 94 535). Other specimens labelled "Tarpans" are the result of tentative genetic "reconstructions" by crossing domestic horses and selecting what individuals appear in their exterior morphology more like to the extinct "Tarpans". The other point concerns the "Przewalski horses". There is every reason to believe that from the moment when they began to interest the international community, and been bought in numbers by zoological parks, the imported batches included not only wild "Przewalski horses" but also Mongolian domestic (and feral?) horses (Sokolov, 1967). As soon as arrived, in most zoological parks, these animals were crossed with domestic horses. In result, it is very doubtful whether any presently living animal can be considered as a genetically pure wild "Przewalski horse". Accordingly, the safest way to have an idea about the subject would be to study only the specimens collected before the "Przewalski rush", i.e. between 1878 and 1900. That is what I have tried to do when studying skulls. But associated skeletons are excessively rare, and eventually, I have decided to use all available limb bones. Thus my "Przewalski horse" skull sample is probably safe but possibly does not include enough information about the 'natural' variation of this taxon. On the reverse, the skeletal sample is not safe and certainly includes too much variation.

Fossil wild horses considered in this paper are nearly all from the Upper Pleistocene: Dalian, China (Zhou Xuexin *et al.*, 1990); Binagady, Azerbaidjan (possibly Late Middle Pleistocene: Vereshchagin & Baryshnikov, 1980); Selerikan (Lazarev, 1980; Vereshchagin & Baryshnikov, 1982), Kostenki and Ural (Kuzmina, 1980 and 1985), Russia; Mezin, Ukraina (Belan, 1985); Jaurens and Siréjol (Philippe *et al.*, 1980), Le Vieux Mounoi (Hameau, pers. comm.), Aven des Planes (Aujard-Catot *et al.*, 1979; Crégut, 1995), Le Quéroy (sondage, postglacial: Tournepiche, 1986 and in press). France: Fontainhas and Escoural, Portugal (Cardoso, 1996). The Holocene horses are mostly Eneolithic or of Bronze age: Swat, Pakistan (precise age unknown: Azzaroli, 1975); Sen-mut, Egypt (Boessneck, 1970); Dereivka and Kirovo, Ukraina (Bibikova, 1970); Roucadour (Ducos, 1957), La Balance (Helmer, 1979; Crégut, pers. comm.), France; Maccarese, Italy (Curci & Tagliacozzo, 1995); Central Europe (Müller, 1993).

SKULL: POSITION OF THE POSTERIOR BORDER OF THE VOMER

An important feature in equid craniometry is the distance of the posterior border of the Vomer to the Basion (Eisenmann, 1986, fig. 2). On figure 1 are plotted the Vomer-Basion distances relatively to the Basilar lengths for 19 "Przewalski horses" (Amsterdam ZM 981; Bern NM 93-75; Cambridge. Harvard MCZ 51088; Leiden RMNH 359; London BM 1907-5-15-1; Moscow MGU 1772, 110476, 115391, 133806; München ZMBS 1951-173; St. Petersburg ZIN 5213, 5214, 5218, 5230, 27031, 27089, 31877, 32578, 32050). 11 Arab horses, 5 "Tarpans" (ZIN 521; MGU 94 535, 96 872, 96 873; Bonn 76 629), 6 Kurgan horses (Odessa: archaeological collection K1P3; St. Petersburg: ZIN 18339-1, 2, 3, 4; CNIGR 1283-1); 3 Upper Pleistocene fossils from France, and one (age unknown) from Iraq (MCZ. Field collection 95).

Figure 1 shows that the studied "Przewalski horse" skulls have relatively shorter Vomer-Basion distances than "Tarpans", Arab horses, wild fossil horses and subfossil domestic horses.

THIRD METACARPAL

Limb bones in general cannot be expected to give as much information as skulls. Breadths in relation to maximal length are however used to distinguish "robust" and "slender" forms possibly correlated to climatic conditions (Gromova, 1949, p. 46). In addition, equid metapodials are often considered "primitive" or "evolved" depending on the proportions of their distal breadths (supra-articular and articular) and the relative antero-posterior development (= depth) of the distal keel (Gromova, 1949, p. 9-14). Whatever the interpretation of the metapodial characters, I believe that the depths, not only of the distal end, but of the proximal end and of the diaphysis as well are also informative.

Maximal length, proximal, diaphyseal, and distal breadths and depths (Eisenmann, 1986, fig. 39) were used to compare third metacarpals of Upper Pleistocene fossil horses, the unique specimen of "Tarpan" (ZIN 521), and modern "Przewalski" horses in a broad sense (see above). The data for the small horse from Dalian, China (*E. przewalskyi sinensis*) were taken from Zhou Xuexin *et al.*, 1990; the rest are personal.

A principal components analysis was run on a correlation matrix of 8 variables for 163 third metacarpals, using "Statview". The first vector (79 % of the original variance) is defined by all the variables, strongly correlated: it is a size factor. The second vector (7 % of the variance) is defined mostly by diaphyseal depth on one side, and proximal and distal breadths on the other. French Pleistocene horses (Jaurens, Solutré) and the Tarpan have wide metacarpals, Przewalski horses have deep diaphyses; Pleistocene horses from Portugal, Ukraine (Dereivka), Russia (Kostenki), Azerbaidjan (Binagady), and China (Dalian) are intermediate (fig. 2).

Another principal components analysis was run on the indices of breadths and depths relatively to the maximal lengths. The variance proportion is increased for the second value (10 % of original variance) and lessened for the first (72 % of the variance) but there is still a first 'size' vector and an opposition between depth of diaphysis, and distal breadths on the second vector. On the graph representing the individuals, most Chinese specimens are close to horses from Azerbaidjan and Portugal (fig. 3).

While the overlap is such that discrimination would be difficult, it is yet evident that "Przewalski horse" metacarpals differ from Pleistocene fossil metacarpals and also from the "Tarpan".

RELATIVE LENGTHS OF THE THIRD METATARSAL AND THE FIRST POSTERIOR PHALANX

Gregory (1912) and Osborn (1929) have already shown that relative lengths of limb segments are indicative of locomotion aptitudes: cursorial animals (Gazellas) have relatively short proximal segments, the reverse is the case of graviportal animals (Elephants). Inside

more restricted taxonomic ranges, differences are naturally smaller, more difficult to explain in a functional way, but they do exist (Eisenmann & Guérin, 1984; Eisenmann, 1984; Eisenmann, in press). Among horses, the relative lengths of third metapodials and first phalanges may be quite different; the point was illustrated by ratio diagrams in a previous work (Eisenmann, 1991). During the last years, I was able to collect more data, and in particular to measure myself several fossil samples from Ukraine and Russia.

Figures 4 and 5 are scatter diagrams of the lengths of third metatarsals and first posterior phalanges of different horses. When associated bones are available, points represent individuals; in other cases, they represent means (table 1).

All Upper Pleistocene horses but those of Portugal have relatively longer first phalanges than Przewalski horses and the Tarpan (fig. 4). According to the data published by Müller (1993), most Bronze age horses fall inside the range of variation of Przewalski horses. So does the horse Katelai T40, Pakistan, described by Azzaroli (1975). Other Holocene horses (Bibikova, 1970; Boessneck, 1970; Ducos, 1957; Curci & Tagliacozzo, 1995) have relatively longer first phalanges (fig. 5).

According to this particular feature, the Tarpan is like a Przewalski horse. Neither of them is similar to the usual Upper Pleistocene horse from France, Ukraine, or Russia.

DISCUSSION AND CONCLUSION

During the Upper Pleistocene, caballine horses may be found from 75°N (Lazarev, 1980) to 35°N (Bagtache et al., 1984), and from 130°E (Kuzmina, 1990) to 10°W (Cardoso, 1996). But from this wide range (fig. 6), only a few fossils isolated in space and time are known. Did they belong to the same species?

Members of a single species are supposed to be recognized, not according to their likeness, but according to their ability to produce fertile offspring (one may wonder how we can guess whether crossing of wild Siberian and Algerian horses would have produced fertile hybrids!). It looks, however, that even using genetic criteria in extant animals, the answer is not a plain yes or no. In spite of numerous biological studies, the degree of genetic distance between Przewalski and domestic horses is not clear (Ryder, 1994). In practice, taxonomists must use morphological likeness as indicator of genetic proximity, specially if they deal with fossils.

Comparative osteology shows that a number of characters appear to vary among the taxa more or less easily recognizable as 'caballine'. Most of the variants are supposed to be adaptative: overall size is bigger in cold climates; it decreases in unfavorable conditions; cold reduces the size of extremities (including the muzzle): the muzzle is long when limbs are long; bones are gracile in dry climate; teeth and protocones are larger when food is abrasive; distal segments are longer in cursorial forms (but also when the snow cover is deep); third phalanges are wider when the ground is soft.

If all these variants are so pregnant with signification and if the corresponding characters are so plastic, they will tell us a lot about environment but nothing about genetic relations. Size may well be reduced by underfeeding in freshly domesticated European horses, or in wild Siberian horses at the turn of the Holocene. Short muzzles will traduce cold conditions in modern Mongolian horses as well as in magdalenian horses of Europe. Conversely, nothing precludes a direct ancestor from being quite dissimilar from its descendants, provided that the environment has changed in the meanwhile. And the environment does change all the time during the Quaternary... Thus, if we want to guess something about genetic closeness, we should look for inert and neutral characters, not to be influenced by ecological changes because they are not functional.

Actually, caution against 'evident' morpho-functional interpretations comes from those

who did look in detail at relation between form and function in modern animals (Lauder, 1995). We have no real proof that the characters listed above in horses are really so simply related to functional adaptations (Forsten, 1981, 1993). They may be, however, so they are not 'safe'. The three characters discussed in this paper are the safest I have yet found, because they have not (yet) been functionally explained. Among the three, the relative position of the vomer seems the safest, because it is the harder to provide with an adaptative significance.

The relative position of the vomer is one of the classical features distinguishing donkey skulls from horse skulls : the distance between the vomer and the occipital opening is shorter in donkeys. It is also very short in the first pliocene Equus (Forsten & Eisenmann, 1995). As indicated by the ethymology of their name, Hemiones (including kiangs) are considered as morphologically intermediate between donkeys and horses. For this particular feature however, large kiangs plot together with small Przewalski horses. When a character apparently inert and neutral, endowed with such a good taxonomical reputation, turns out to cluster together two species (kiang and Przewalski horses) and separate taxa evidently much more closely related (Przewalski and other horses), there is clearly something wrong ! On what ground are we to look for phylogenetical relations if we cannot use functional characters because they are too much influenced by environment, nor neutral characters because they do not seem as reliable as they should be ?

Actually, no phylogenetical or taxonomical pattern emerge at all from the distribution of reputedly adaptative as well as supposedly non adaptative characters among caballine horses during the Quaternary. There is instead a reticular pattern, a mosaic of characters that are combined at different places and times in different ways. The names we use, even when they are written in latin, have no real taxonomical value, because they do not traduce any understanding of the objects to which they apply; they just point to a particular combination of visible characters.

On the other hand, if we are not able to understand why characters are different, nor why they are combined in different ways, different combinations still do exist. Przewalski horses do not combine the same characters as the Upper Pleistocene horses of Europe. Therefore, statements identifying Upper Pleistocene and Przewalski horses are not true, unless they mean to tell that all horses are horses. The less we understand, the more exact we should be in our statements.

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Origin of the data	Localities	MT III Length	n	PHIP Length	n
Personal	Selerikan	246.0	*	80.0	*
Personal	Siréjol	270.1	13	85.1	12
Personal	Jauréns	267.9	18	83.2	24
Personal	Fontainhas	270.0	1	79.0	3
Personal	Escoural	279.0	1	77.0	1
Personal	Kostenki, n°32641	272.0	*	85.5	*
Personal	Kostenki	284.3	24	89.2	13
Personal	Óural, Bezymiany	265.3	4	83.1	7
Personal	Vieux Mounci	270.0	*	86.0	*
Personal	Planes	266.0	1	84.0	2
Personal	Planes, n°833	268.0	*	84.0	*
Personal	Mezin	268.8	5	86.5	13
Tournepicche, pers. comm.	Quéroy Sondage	264.5	12	83.4	8
Personal	Balançé	270.0	1	89.0	1
Ducos, 1957	Raucadour	245.0	1	79.5	14
Bibikova, 1970	Kirovo	267.3	3	86.3	43
Curci & Tagliacozzo, 1995	Maccarese	268.3	*	84.0	*
Boessneck, 1970	Sen-mut	270.0	*	83.0	*
Azzaroli, 1975	Katelai n°T40	253.0	*	74.0	*

Tab. 1. Maximal lengths in millimetres of third metatarsals (MT III) and first posterior phalanges (PHIP) of fossil horses. The values are average when there is more than a one specimen. An asterisk indicates associated bones of the same individual; when the bones are not associated, the number of specimens is given in the column 'n'. In the left column are listed the references for other author's published measurements.

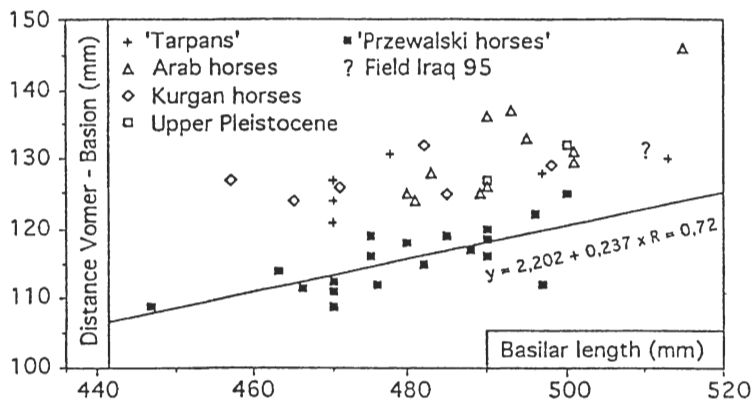


Fig. 1. Horses skulls. Scatter diagram and regression line for basilar length and vomer-basion distance in 19 Przewalski horses (old collections). Other horses seem to have relatively longer vomer-basion distances.

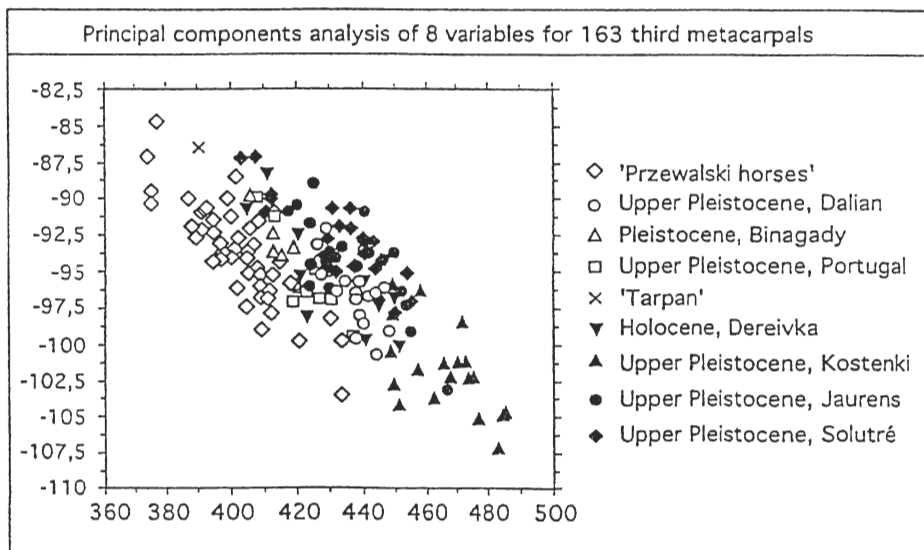


Fig. 2. Horse metacarpals. Principal components analysis on a correlation matrix of 8 variables (maximal length, proximal articular breadth and depth, diaphyseal breadth and depth, distal articular maximal breadth and depth, and distal supra-articular maximal breadth). The largest specimens (19 specimens from the Upper Pleistocene of Kostenki) are in the lower-right corner. the smallest (including the tarpan ZIN 521) at the opposite. "Przewalski horses" (50 specimens from various origins) tend to have deep diaphyses; French Upper Pleistocene horses (Jaurens, n=21; Solutré, n=23) tend to have broad proximal and distal ends.

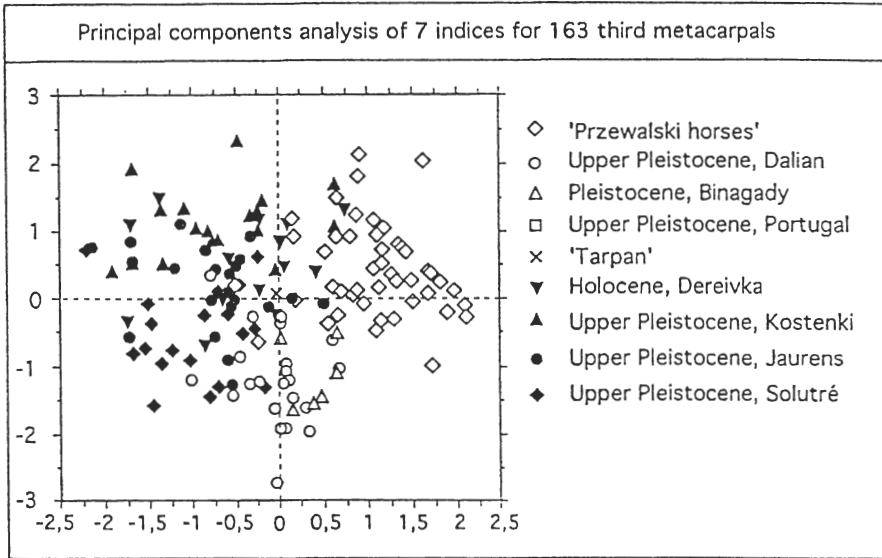


Fig. 3. Horse metacarpals. Principal components analysis of 7 indices (proximal articular breadth and depth, diaphyseal breadth and depth, distal articular maximal breadth and depth, and distal supra-articular maximal breadth, all divided by the maximal length). Relatively deep metacarpals are on the right side; relatively broad metacarpals are on the left.

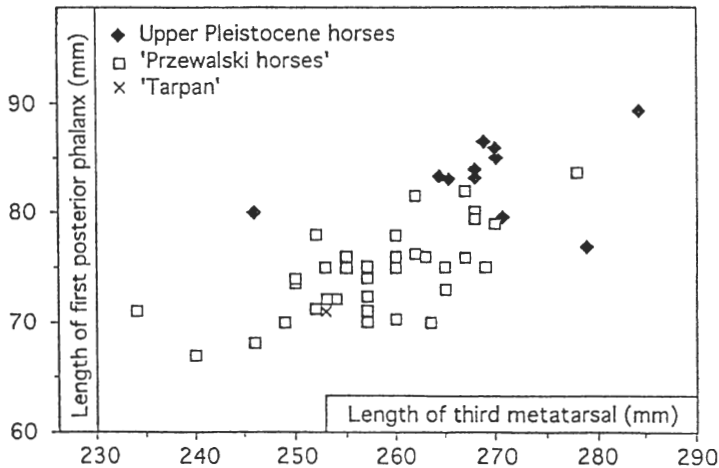


Fig. 4. Distal segments of the posterior leg: scatter diagram of the maximal lengths of the third metatarsal and of the first posterior phalanx. "Przewalski horses" and the Tarpan have relatively short phalanges; so do the Upper Pleistocene horses from Portugal. Other Pleistocene horses have longer phalanges (table 1).

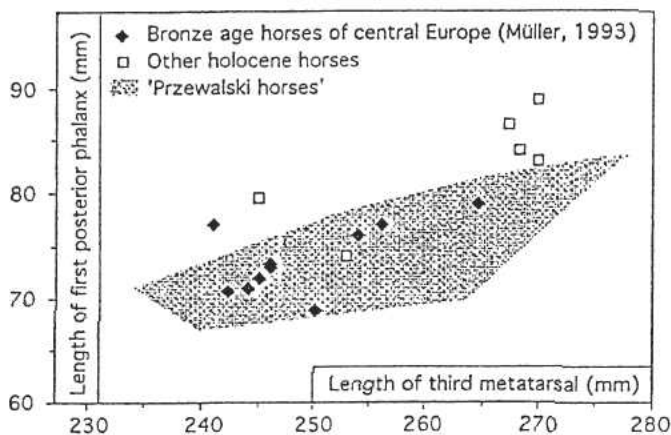


Fig. 5. Distal segments of the posterior leg. Most of Bronze age horses of Central Europe (Müller, 1993) fall inside the range of variation of "Przewalski - Tarpan". Most other Holocene horses fall outside (table 1). Exceptions are: the first horse from Siersleben (Si 1, Müller, 1993), and the skeleton T40 from Katelai (Azzaroli, 1975).

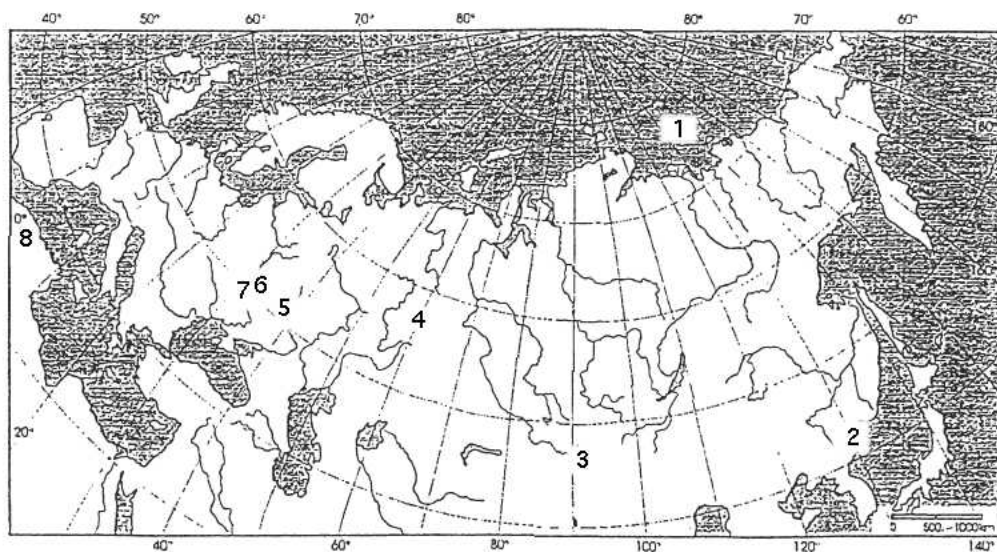


Fig. 6. Location of some Upper Pleistocene and Holocene horses. 1: Kotelný island ("*E. lenensis*"). 2. Ussuriisk ("*E. dalianensis*"). 3. Dzungaria ("*E. przewalskii*"). 4. Ural ("*E. uralensis*"). 5. Kostenki ("*E. latipes*"). 6. Mezin ("*E. latipes*"). 7. Dereivka. 8. Allobroges ("*E. algericus*"). 9. Fontainhas ("*E. antunesi*").