

Climate and the evolution of *Equus* (Perissodactyla, Equidae) in the Plio-Pleistocene of Eurasia

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Abstract. The evolution of *Equus* in Eurasia correlates with global climatic change. Three main evolutionary events stand out: the arrival and dispersal in Eurasia of the genus *Equus* in the late Pliocene, the replacement of the stenonid (= zebroid) subgroup of *Equus* by the caballoid one in the early mid-Pleistocene, and body-size decrease in the late Pleistocene. These events seem to have been universal for Eurasia and all three appear to have been climatically induced. Their direct association with speciation is not clear.

Key words: climate, evolution, *Equus*.

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I. INTRODUCTION

The temperature and the distribution and amount of rainfall affect the vegetation and thus the herbivores dependent on the vegetation. Evolutionary events (changes in morphology, distribution, number, and diversity) in herbivores are often associated with climatic change (VRBA 1992, but see SCHOPF 1984).

In the Plio-Pleistocene of Eurasia, horses of the genus *Equus* experienced three main evolutionary events having to do with their distribution, diversity, and morphology. These events, which correlated with climatic change, were the immigration of *Equus* from North America, the replacement of dominant subgroups within *Equus*, and body-size decrease. Speciation in the genus was not concentrated in pulses coincident with times of extreme climates or climatic change, and thus appears to have been opportunistic rather than climatically induced.

The immigration of *Equus* into Eurasia in the late Pliocene, ca 2.5 Ma ago, and subsequently into Africa, opened up new territories for colonization and was followed by speciation, partitioning of the ecological niche, and the frequent sympatry of different taxa. This increase in diversity resulted from the adaptive filling-up of suitable space and available subniches. Later, in the mid-Pleistocene, the caballoid or true horses replaced the early immigrant, stenonid, forms, but this event was followed by the extinction of the stenonids rather than by speciation. The caballoid horses, in contrast to the stenonids, were ecologically broadly adapted and seldom occurred in sympatry with one another; their broad adaptations and wide geographic distribution may not have allowed for specific differentiation. The Late Pleistocene body-size decrease in the caballoids was a gradual process, evidently tracking climatic change, but without speciation.

II. ARRIVAL AND DISPERSAL

Since the early Miocene, a land connection between northeastern Eurasia and northwestern North America intermittently formed in the Bering area. This connection (called Beringia or Beringida) was used by mammals, including equids on at least three, possibly four or five, occasions, as a dispersal route between the continents. The direction of equid dispersal was predominantly from the east to the west, i. e., from taxonomic high to low diversity, in accordance with MACARTHUR & WILSON's (1967) equilibrium theory. However, surprisingly few equid genera of the many once extant in North America used this connection for dispersal. This may indicate that the land bridge was seldom present and/or it was mostly unsuitable for equids.

The last equid genus to disperse via the Bering land bridge was *Equus*, at present comprising horse, zebras, and asses. The early arrival and subsequent dispersal in the Old World of *Equus*, represented by zebra-like or stenorid forms, has been dated at ca 2.5 Ma ago (LINDSAY et al. 1980). Oxygen isotope ratios in fossil foraminiferal shells (THUNELL & WILLIAMS 1983), palynology (ZAGWIJN 1986; ZAGWIJN & SUC 1984), and fossil mammalian communities (SHER 1986) strongly indicate a pronounced global climatic change at that time. The climate became colder and drier (BONNEFILLE 1981; LEONE 1985). The earliest tundra communities in Beringia are from that time (SHER 1986), as are the earliest tundra-like open vegetations in the Netherlands (VAN DEN HAMMEN et al. 1971; ZAGWIJN 1986). In the Mediterranean area strong seasonality with summer drought developed (SUC 1984). These climatic changes were evidently associated with an early Arctic glaciation and ice-rafting in the Arctic Ocean (SHACKLETON et al. 1984; REA & SCHRADER 1985). The resulting world-wide drop in sea level (STIPP et al. 1967; AZZAROLI et al. 1988) may have exposed the Bering land bridge and furnished the physical means for dispersal.

Following the opening up of the Bering bridge several mammalian genera, such as *Lepus*, *Synaptomys*, *Spermophilus*, and *Tremarctos*, as well as *Equus*, took part in faunal exchange between Eurasia and North America (REPENNING 1980; HOFFMANN 1980; LINDSAY et al. 1980, 1984). It is not known how many different species of *Equus* arrived in Eurasia, nor how many subsequently dispersed from Eurasia to Africa, but the number may have been low, judging by the relative morphological homogeneity of the Old World species which soon evolved. The arrival of stenorid *Equus* in the Old World was followed by speciation and diversification mainly in body size and limb proportions, resulting in frequent sympatry of two (seldom more) species of different size. Diversification in the genus seems to have been due to colonization of new and unoccupied areas and partitioning of the ecological niche. The Old World hipparions, still extant at that time, do not seem to have been serious competitors. In Eurasia the hipparions became extinct soon after the arrival of *Equus*, while in Africa they lived on in sympatry with *Equus* for some 1.5 Ma years.

Mitochondrial-DNA studies show early (pre-2.5 Ma ago) branching-off from the latest common ancestor of the extant 26 species of *Equus* (GEORGE & RYDER 1986). This would locate origination of the extant lineages in North America and indicates separate dispersal of the ancestor of each species, including the common ancestor of *E. grevyi* OUSTALET and *E. burchelli* (GRAY). The two latter species differentiated ca 1.6 Ma ago, i. e., probably in the Old World. The extant three zebras could be derived from the early stenorid immigrants, but there are no clearly identifiable Old World fossil ancestors of the Asiatic and African asses until the middle and late Pleistocene respectively, nor of the caballoid horses until the early Pleistocene. These three lineages therefore appear to have arrived later, unless they did not leave an early fossil record or simply evolved their specific morphology late.

III. REPLACEMENT OF SUBGROUPS

Early *Equus* in Eurasia belonged to the stenorid (=zebroid) subgroup, which presently includes the zebras and asses. This subgroup is characterized by the relatively primitive enamel pattern of

its lower cheek teeth, but it is also molecularly and cytologically uniform (KAMINSKI 1979; FLINT et al. 1990). The second or caballoid subgroup, comprising extant domestic and Przewalski's horse, seems to have appeared later than the stenorid one, both in the North American and Eurasian fossil record, but the exact timing of its appearance is still controversial. Caballoids, characterized by the more derived enamel pattern of their cheek teeth, seem to appear for the first time in North America with *E. scotti* GIDLEY in the Irvingtonian and they are present in Europe at East Runton (UK) in the late Villafranchian, less than 1.8 Ma ago, possibly even earlier at Groserea and Berbesti-Slavesti (Romania; SAMSON 1975). It is not with certainty known whether New and Old World caballoids represent separate evolutionary lineages or dispersal between continents, but there is no evidence for a dispersal at 2 Ma ago of caballoid *Equus* from the Old to the New World as proposed by REPENNING (1985).

Even if present in Eurasia already in the Villafranchian, the caballoids are clearly in the minority among the equid fossils from that period, which are dominated by the stenorids. In the early mid-Pleistocene there was a sudden shift in the frequency of the subgroups, following the replacement of the stenorids by the caballoids (FORSTEN 1988). Caballoids are absent in the fossil-rich early fauna from Stranska Skala (Czechia; MUSIL 1971) and from Ahalkalaki (Georgia; VEKUA 1962), and are poorly represented at Süssenborn (Germany; FORSTEN 1986a). Both caballoid and stenorid horses are known from Tiraspol (Moldova; GROMOVA & DUBROVO 1971) and from almost all the Forest Bed localities (UK), with their various proportions of Villafranchian and post-Villafranchian faunas. Caballoids dominate in the main fauna of Mosbach (Germany), dated at ca 0.6 Ma ago (BRÜNING 1978, Abb. 6), and have since dominated in fossil samples from the middle and late Pleistocene of temperate and cool Eurasia. Stenorids have, following their arrival in the Old World, reigned in Africa. In the middle Pleistocene they still occurred in the southern parts of Eurasia, e. g., the Indian subcontinent (BADAM 1984), China (FORSTEN 1986b), and the Balkans (TSOUKALA 1989), evidently in climatically favorable areas or geographical dead-ends. The stenorid, so called "European Ass", *E. hydruntinus* REGALIA, became extinct as late as in the Neolithic/Copper Age and Asiatic wild asses, stenorids in a wide sense, are still extant. However, these species were never as dominant in Eurasian Pleistocene faunas as were the caballoids, except locally, e. g., *E. hydruntinus* on the Crimea (VERESHCHAGIN & BARYSHNIKOV 1980) and in the Caucasus (GADZIEV 1953, BARYSHNIKOV 1987). In addition they usually occurred together with caballoid horses.

What caused this rather dramatic shift in the dominance of different horse subgroups? The replacement of the stenorids by the caballoids does not seem to have been a competitive process. The stenorids in the Villafranchian were highly successful, judging from their wide geographic distribution and ubiquity in fossil faunas. They were also taxonomically diverse. However, they may have been ecologically specialized, often occurring in sympatry with one another, and relatively thermophilous, since their Pleistocene and present distribution is mainly in Africa south of the equator. The caballoids, on the other hand, were rare in the Villafranchian and their middle and late Pleistocene distribution comprised the Palearctic with its sharp oscillations between glacial and interglacial climates. I believe that the replacement was caused by a climatic change which favored the caballoids at the expense of the stenorids, and that we see here the replacement of a more ancient, thermophilous subgroup of *Equus* by a more modern, climatically versatile, one.

In Beringia the stenorids were replaced by caballoids in the Akanian fauna, ca 0.7 Ma ago (SHER 1986). This date is significant. A shift from low to high amplitude glacial cycles has variously been dated at 0.9 Ma ago (THUNELL & WILLIAMS 1983) or 0.74 Ma ago (RUDDIMAN & RAYMO 1988). Loess became frequent and abundant in Europe after 0.97-0.90 Ma ago (KUKLA 1977; COOKE 1981). Authors agree that the climate became colder, with stronger oscillations between glacials and interglacials. This shift to a consistently colder climate is believed to have been caused by uplifting of the Tibetan Plateau and by the formation of a permanent Arctic Ocean pack-ice cover (HUNKINS et al. 1971; BARRY 1983; REA & SCHRADER 1985; RUDDIMAN & RAYMO 1988).

This climatic change and its concomitant environmental change seem to have been the deciding factors in the replacement of the stenonids by the caballoids as the dominant equids in Eurasia.

IV. BODY SIZE DECREASE

Many mammalian species underwent body-size decrease in the late Pleistocene to Holocene (0.08 Ma ago to Recent). Size decrease is usually believed to have been caused by climatic warming in the Holocene in accordance with BERGMAN's Rule, although EDWARDS (1967) believed that man, by hunting mainly large individuals, selected for small body size and thus caused size decrease in his prey. However, in Eurasia the horses became smaller long before the Holocene warming (FORSTEN 1991). In addition, in the middle Pleistocene, when the horses tended to be large, they were particularly large during the temperate periods. Temperate or warm climates as such do not seem to have caused size decrease in the horses.

If Pleistocene glaciations became increasingly rigorous with time, body-size decrease in the late Pleistocene horses may have been an economizing adaptation to such worsened conditions. It is also possible that glaciations created "island conditions" by splitting up previously continuous horse populations. Such island conditions may have led to body size decrease. A small-bodied herbivore needs less, although higher-quality, food than a large one, and may better be able to track resource fluctuations (GLASSER 1983; MCKINNEY 1990). A small-bodied animal may be a better colonizer and may have faster maturation and generation turn-over, favorable in an unstable environment. The small horses of the late Pleistocene were certainly ecologically ubiquitous, as shown by their wide geographic distribution and their frequency in faunas of different climatic type, but maturation was no faster than in other extant species of *Equus*, judging on the basis of Przewalski's horse, until recently a wild, small horse. The gestation period in Przewalski's horse is rather short, however (MACDONALD 1984).

V. COMPARISONS WITH OTHER CONTINENTS

Are there discernible evolutionary events at the same time in African, South and North American equids, which could be traced to similar causes? In South America the record shows some interesting parallels to that in Eurasia. In Argentina, the earliest horses, of the genus *Hippidion*, arrived in the Uquian (3.4-2.47 Ma ago) with the opening-up of the Panamanian land bridge (TONNI et al. 1992, Fig. 8). The hippidions represent a side-branch of the monodactyl horses, derived directly from the earliest monodactyl, but dentally primitive, genus *Pliohippus*. In a later wave of immigrants in the Lujanian (0.7 Ma ago and younger) the genus *Equus* (?*Amerhippus*) arrived (TONNI et al. 1992, Fig. 8), evidently without replacing the hippidions, however. SICKENBERG (1962) showed that throughout the Pleistocene South American *Equus* underwent body-size decrease. Extinction, which in contrast to the Eurasian horses struck those in South America at the end of the Pleistocene, can be seen as an ultimate event, possibly caused by climatic warming and spread of unsuitable environments, although the influence of man cannot be ignored.

In Africa, stenonid *Equus* appeared 2-2.5 Ma ago during a period of aridity (VRBA 1992). The stenonids were not replaced by caballoids, which never dispersed south of the Sahara, except much later with the aid of man. However, the native hipparions, three-toed horses of long standing in Africa, became extinct about 0.6 Ma ago after having lived in sympatry with *Equus* for some 1.5 Ma.

In North America, the homeland of *Equus*, the three important dates 2.5, 0.9-0.7, and <0.08 Ma ago, have as far as known no particular significance in horse evolution.

VI. CONCLUSIONS

Three main evolutionary events in the genus *Equus* in Eurasia, i. e., arrival, replacement of subgroups, and body size decrease, are correlated with climatic change. This seems true for horse evolution also in South America, but less so in Africa and North America. Speciation in *Equus* is difficult to correlate with global climate and appears to have depended on local factors. There are no recognizable speciation pulses at appr. 2.5, 0.9-0.6, or < 0.08 Ma ago.

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