

Mitochondrial-DNA time-table and the evolution of *Equus*: comparison of molecular and paleontological evidence

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A mitochondrial-DNA-based timetable for the branching of the extant species of the genus *Equus* (Perissodactyla, Equidae) is compared with the record of dated fossils of that genus. Agreement and discrepancies between the two timetables are identified and discussed.

1. Introduction

George & Ryder (1986), on the basis of mitochondrial-DNA and cytological and molecular studies (eg. Clegg 1974, Ryder & al. 1978, Kaminski 1979), give a timetable for the presumed phylogenetic branching of the extant species of the genus *Equus* (horses, zebras, and asses) (Fig. 1). There is partial agreement between their time-table and the equid fossil record (Fig. 1), the latter based on morphological analysis of dated fossil finds, but there are also considerable discrepancies. Since the fossil record is incomplete and since species, even species groups, are difficult to identify among the fossils, discrepancies are to be expected. Therefore agreement between the molecular timetable and the fossil record is particularly interesting. The molecular timetable acts as a welcome control for presumed evolutionary events and may help us to spot inconsistencies in the fossil record. The fossil record, on the other hand, may help to

identify variations in the DNA substitution rates through time, and in the rate of morphological change of lineages.

2. Present taxonomic situation

There are 6 (according to some students even 7–8) extant species of the genus *Equus*:

Three zebras: Grevy's, *E. grevyi* Oustalet; Mountain, *E. zebra* L; and Plains, *E. burchelli* (Gray) (including *E. quagga* Boddaert, see Lowenstein & Ryder 1985, Higuchi et al. 1987).

Two asses: the African ass, *E. asinus* L. (including the wild and the domestic ass); and the Asiatic wild ass, *E. hemionus* Pallas. Groves & Mazak (1967) also consider the kiang, *E. kiang* Moorcroft, and Bennett (1980) considers the onager, *E. onager* Boddaert, as separate species.

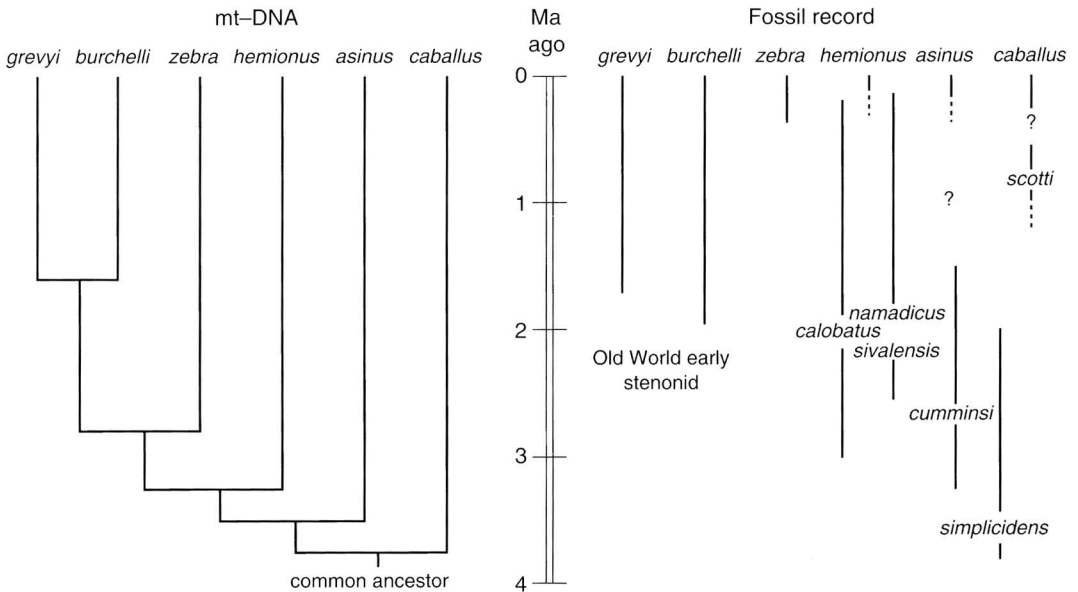


Fig. 1. Extant species of *Equus*. Tree based on mt-DNA cleavage maps (George & Ryder 1986:fig. 4b), and fossil record. Continuous line depicts known fossil record, stippled line referred fossils.

The true horse, *E. caballus* L. (including the domestic and Przewalski's horse, *E. przewalskii* Poljakov).

With the use of dental morphology, the extant and fossil species of *Equus* may be separated into two main groups, the stenonid (zebroid) and the cabaloid (true) horses (Boule 1899, Hopwood 1936, McGrew 1944). The most important morphological traits differentiating these groups are in the lower cheek teeth: the morphology of the metaconid-metastylid loops of the double knot and the shape of the entoflexid (linguaflexid of Skinner 1972) separating them; in the stenonids the entoflexid is V-shaped, in the cabaloids it is U-shaped (Fig. 2). However, the double knot and the shape of the entoflexid are variable characters (eg. in old stenonid molars the entoflexid may be U-shaped, while in the young cabaloid premolar it may be V-shaped), but they are useful for a rough discrimination among the fossils of the two equid groups.

Within the two main equid groups, subgroups (sometimes formally recognized as subgenera) are often separated on additional morphological criteria. Thus the asses are sometimes subdivided

into geographically distinct, generic/subgeneric, entities (*Asinus*, *Hemionus*) and separated from the zebras, which in their turn are subdivided (*Dolichohippus*, *Hippotigris*, *Zebra*). However, among fossil *Equus*, which are mainly represented by their teeth, increasingly minute subdivisions are difficult to identify objectively. In this paper I will use, maybe simplistically, the dichotomous grouping of *Equus* into stenonids and cabaloids, since this grouping finds support in protein and cytological studies, which unite the extant stenonids, i.e. zebras and asses, but separate them from the extant cabaloids, i.e. domestic and Przewalski's horse (Ryder et al. 1978, Kaminski 1979, George & Ryder 1986 fig. 4c, Flint et al. 1990).

3. Origin and dispersal

Lindsay et al. (1980) believe the genus *Equus*, with the species *E. simplicidens* (Cope), to occur for the first time in the Hagerman fauna, early to middle Blancan of Idaho. The age of the Hagerman Horse Quarry fauna is less than 3.3 Ma (Kurtén & Anderson 1980:14). *Equus* cf.

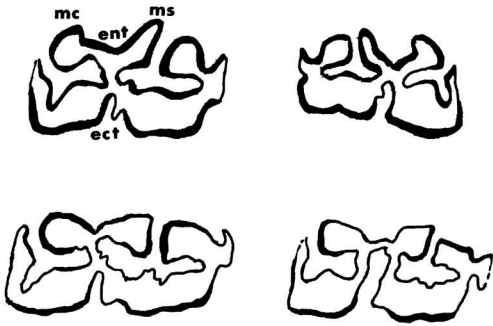


Fig. 2. Cabaloid (top) and stenoid (bottom) lower cheek teeth (premolar left, molar right). mc = metaconid; ms = metastylid; ent = entoflexid; ect = ectoflexid.

simplicidens from the Ringold Formation, Washington (Gustavson 1978), is older than the occurrence at Hagerman; Lindsay et al. (1984) dated the fauna described by Gustavson (1978) between 3.4–3.8 Ma. In the still older Concha Fauna, New Mexico (earliest Blancan, aged appr. 4.2 Ma), there occurred a horse which either represented an advanced *Pliohippus* (so-called *Dinohippus*, considered a direct ancestor of *Equus*) or an early *Equus* (Lindsay et al. 1984). The age of the Ringold and Concha faunas are very close to 3.9 Ma, the age proposed by George & Ryder (1986) for the common ancestor of all extant *Equus*. mtDNA does not indicate a polyphyletic origin of *Equus*, as suggested by McGrew (1944) and Dalquest (1978, 1988) on dental morphology. *Equus simplicidens* could thus be the ancestor of later *Equus*.

Early fossil *Equus* belonged dentally to the stenoid group. Some early stenonids had a primitively short protocone in their upper cheek teeth, while others, with an advanced, long protocone, already dentally resembled the extant stenonids. In limb proportions these horses soon became differentiated, some becoming exceedingly slenderly built with long distal members of their limbs. They also became diverse in body size. Following this morphological and, evidently, ecological differentiation, sympatry of two or more species occurred.

Equus is believed to have dispersed to Eurasia 2.5–3.0 Ma ago (Lindsay et al. 1980, Azzaroli

1983). Early *Equus* in the Old World morphologically represented the stenonids, with dental characters still close to those of *E. simplicidens* and even recalling those of ancestral *Pliohippus* (*Dinohippus*). In the Old World, as had already happened in the New World, *Equus* became morphologically and taxonomically diverse, resulting in frequent sympatry of mostly two species (Forstén 1988b and references therein).

4. Origin of the zebras

Early stenoid *Equus* in the Old World may have been the ancestor of the zebras; the dispersal date 2.6/2.5–3.0 Ma ago corresponds to the date 2.8 Ma ago, which mtDNA indicates to be the age of the latest common ancestor of the extant zebras (George & Ryder 1986). From Eurasia the stenonids dispersed to Africa and appeared for the first time in the Omo beds, Member G of the Shungura Formation, Ethiopia, appr. 2 Ma ago (Hooijer 1976, Eisenmann 1976). Eisenmann (1985) distinguished two species of *Equus* in Member G, one of which is *E. burchelli*. In the slightly younger Member L of the Shungura Formation, she identified *E. grevyi*. Churcher (1981) calls this horse *E. oldowayensis* Hopwood, considered ancestral to *E. grevyi*. These finds indicate differentiation probably within Africa, of these still extant species, in agreement with George & Ryder's (1986) proposed age of approx. 1.6 Ma for this event. *Equus zebra*, the cytologically most distinct of the extant zebras (Ryder et al. 1978), has been identified among the fossils in Africa only since the middle Pleistocene (Churcher & Richardson 1978), but must have had a considerably longer, separate evolutionary history. This species branched off from the common zebra ancestor during the pre-African period of *Equus* evolution (between 2 and 2.6–3.0 Ma ago), which indicates separate dispersal from Eurasia to Africa of the ancestor of *grevyi-burchelli* on the one hand and of ancestral *E. zebra* on the other. However, among the many described taxa of fossil stenonids in Eurasia it is not possible to discriminate morphological precursors of recent species. Evidently morphological change was not simultaneous with the mtDNA substitution; in fact, the morphology characteriz-

ing the extant species may be of a relatively recent date.

5. Origin of the asses

The fossil record of the asses is difficult to fit in with the mtDNA timetable. African and Asiatic asses are, karyologically, more closely related to each other than to other stenonids (Ryder et al. 1978), but are sufficiently dissimilar to have had long, separate evolutionary histories. Thus their cytological and molecular differences do not support the suggestion, by Van Bemmelen (1972) and Davis (1980), that African and Asiatic asses are demes of a single species complex. Among extant *Equus* the asses are molecularly more closely related to zebras than to true horses (Clegg 1974, Kaminski 1979, George & Ryder 1986), but differ sufficiently from either group in their mtDNA to have branched off from the common *Equus* ancestor as early as 3.4–3.9 Ma ago (George & Ryder 1986). In dental morphology the asses either resemble the zebras (the African ass and some Asiatic asses) or the true horses (some Asiatic asses). Cranially and skeletally they resemble true horses (Eisenmann 1980, Harris & Porter 1980). Among the fossils their hard parts are usually recognized as being asinine from their small size, their slender limb proportions and their dental morphology, particularly the often shallow ectoflexid in the lower molars. However, Hibbard (1953) noted that dental morphology does not make it possible to discriminate asses and zebras among early fossil *Equus*. This is confirmed by Pleistocene large stenonids in California (*E. bautistensis* Frick and *E. occidentalis* Leidy) and China (*E.* sp. from Choukoudien locations 1–13) with “asinine” shallow ectoflexids in the lower molars, but massive limbs. Ecologically extant asses are adapted to areas that are, at least seasonally, extremely arid.

The fossil record of the asses is ambiguous. *Equus cummingsi* (Cope), allegedly from the mid-Blancan (aged 4.2–3.2 Ma; Savage & Russell 1983:360, Lundelius et al. 1987: fig. 7.3) and early Pleistocene (< 1.8 Ma ago) of Kansas and Texas, has been identified as an early ass on the basis of its dental morphology (Hibbard 1956,

Quinn 1957, Dalquest 1978, 1988). However, the best preserved dental material referred to *E. cummingsi*, e.g. from the late Blancan of Red Light, Texas (Akersten 1972), and lower Pleistocene of Arkalon, Kansas (Hibbard 1944), is associated with limb bones of the stilt-legged horse *E. calobatus* Troxell (see also Hibbard 1953:121). *Equus cummingsi* from the late Blancan type-locality of Blanco, Texas, is poorly represented by fossils (Dalquest 1975), but even if it were an ancestral ass it would not furnish morphological support for an early branching off of the asses, since the age of Blanco is only approx. 2 Ma (Lundelius et al. 1987: fig. 7.3).

Dalquest (1978) believed that asses were definitely present in North America by the earliest Pleistocene Irvingtonian about 1.8 Ma ago. These were the stilt-legged horses, e.g. *E. calobatus* and *E. taulfrancisi* Owen/Hay, but probably not *E. conversidens* Owen (Dalquest & Hughes 1965, Lundelius & Stevens 1970, Dalquest 1979). They share the shallow ectoflexid with the asses (Skinner 1972), but are even more extreme, thus more derived, in metapodial slenderness than are the Asiatic wild asses, with which they have been combined in a single subgenus (Skinner 1972). In the Old World, Churcher (1982) described a single MT III from Olduvai Gorge, Tanzania (aged 1.5–1.7 Ma), as the earliest known, true African ass. Eisenmann (1976) referred to asinine teeth from Koobi Fora, Kenya, later identified as *E.* cf. *tabeti* Arambourg (Eisenmann 1983). *Equus tabeti*, although possessing slender limb bones, had much larger bones than the single MT III from Olduvai and its teeth are not particularly asinine (Eisenmann 1981). Slenderly built, but generally quite large, Eurasian and African stenonids have often been referred to as “asses”, “asinine”, or “hemionine”, but their dental morphology (mostly deep ectoflexid in the lower molars, for instance) seems to exclude affinity with the extant asses, to which they may have corresponded ecologically. These “asses” often occurred sympatrically with larger and heavier horses.

The ancestry and dispersal in the Old World of the extant asses is still far from clear. mtDNA indicates separation of the ass lineage from the *Equus* common ancestor long before the first dispersal of *Equus* in the Old World. Were the

asses late immigrants from North America when they suddenly appeared in the Old World: the earliest Asiatic wild asses in the late middle or late Pleistocene of Asia, the African ass only in the late Pleistocene of ?India, the Levant, and North Africa? Or are they autochthonous Old World elements? mtDNA supports the former alternative, while the lack of fossils, particularly of African ass-like horses, in eastern and Central Asia seems to exclude their dispersal from the east through Asia and rather supports an autochthonous Old World origin.

The Indian subcontinent could have been a possible evolutionary (later dispersal) center of the asses if the extant asses evolved there from an early immigrant stenorid/asslike ancestor. In the late Pliocene and the Pleistocene there existed stenorid horses, e.g. *E. namadicus* Falc. & Cautl. and *E. sivalensia* Falc. & Cautl. which did have both dental and limb characters resembling those of the asses, that is, fairly small and slender bones and a shallow ectoflexid in the lower molars. The Indian fossil horses are not sufficiently well known for us to draw any conclusions as to their possible association with the extant asses. The late Pleistocene, allegedly African, asses from India (Lydekker 1886, Murty 1974, Badam 1977) should be restudied.

6. Origin of the caballoids

True or caballoid horses are believed to have appeared for the first time in the North American fossil record in the late Blancan (Red Light fauna, Texas, Akersten 1972; Grandview fauna, Idaho, Winans 1989) with *E. cf. scotti* Gidley; these faunas are dated approx. 2 Ma ago (Kurtén & Anderson 1980, Savage & Russell 1983), and 2.5 Ma ago (Lundelius & al. 1987: fig. 7.3). In the Red Light fauna the referred lower premolar (Akersten 1972: fig. 15G) is stenorid and the referred metacarpals (Akersten 1972: table 12) are those of a stilt-legged horse, much longer and more slender than those of the truly caballoid *E. scotti* from Rock Creek, Texas (Lundelius 1984: fig. 11). The Red Light fauna does not appear to include a caballoid horse. Metapodials from Grandview also differ from those of *E. scotti* (Winans 1989: figs. 14, 6C & D) and the teeth

are clearly stenorid (Shotwell 1970: fig. 41). Like Red Light, Grandview seems to lack a caballoid horse.

The type locality of *E. scotti*, Rock Creek, is Irvingtonian and has been dated variously from approx. 1.9 Ma ago (Kurtén & Anderson 1980, Savage & Russell 1983) to only 0.75 Ma ago (Lundelius 1984 and in litt. 1989). The latter date would fit the early occurrence of the caballoids in the Old World, but neither date fits the much older 3.4–3.9 Ma which George & Ryder (1986) propose as the branching-off date of the true horses from their common *Equus* ancestor. Both in the New and in the Old World, the known fossil horses from the period 3.4–3.9 to approx. 1.8 Ma ago belong morphologically to the stenorid group. In the caballoids, as in *E. zebra*, the mtDNA change must have occurred much earlier than the change in morphology, i. e. chiefly modernization of the enamel pattern of the cheek teeth, which sets true horses apart from the dentally more primitive stenorids and allows for their identification among the fossils. In any case the proposed early branching-off date, and the known fossil record (or rather, lack of an early record in Eurasia) seem to exclude an Old World origin of the caballoids.

Almost all the dates given for the early occurrence of caballoid horses in the fossil record of North America (early Pleistocene Irvingtonian, approx. 1.8–0.3 Ma ago) are older than those of their early occurrence in the Eurasian fossil record; closest to the latter is the date of 0.75 Ma ago (Lundelius 1984 and in litt. 1989) for the age of Rock Creek, Texas, and its typical, caballoid, *E. scotti*. In Eurasia, caballoids first appeared in the Galerian, which is early middle Pleistocene (1–0.4 Ma ago; Azzaroli 1983), but they seem to have become common only towards the middle or end of that period. By that time they had almost completely replaced the stenorids, which preceded them. The appearance of the caballoids in Eurasia was sudden and there are no known transitional forms between stenorids and caballoids. Dalquest (1978), on the other hand, does not acknowledge the presence of caballoids (subgenus *Equus* (*Equus*) in his terminology) in the New World, but refers New World caballoids (*scotti*, *niobrarenensis*, *caballus*, *lambei*, etc.) to a subgenus *Amerhippus*. At our present state of

knowledge, New World caballoids cannot be differentiated from those in the Old World. The early branching-off time indicated by mtDNA supports an origin of the caballoids in the New World, and the fossil record suggests an even rather late dispersal to the Old World.

There are no known fossil caballoids older than 1.8 Ma, with a notable exception: Berești. The mtDNA timetable and the evolution and dispersal of the genus *Equus*, as revealed by the fossil record, makes the occurrence of horses of this genus at Berești and Malușteni, Romania (Simionescu 1930, 1932, Samson 1975), unlikely. These two contemporaneous localities, with a typical lower middle Pliocene (Ruscinian) fauna, but allegedly including *Equus* (a caballoid at Berești, a stenorid at Malușteni; Samson 1975), have been dated 3.8 Ma ago and 3.6–4.0 Ma ago (Samson 1975:174, Andreescu et al. 1987:117). These dates are close to the date 3.4–3.8 Ma ago for the earliest known fossil *Equus* in North America and to the mtDNA based age 3.9 Ma ago for the presumed earliest common *Equus* ancestor. They are slightly older than the date 3.4–3.9 Ma ago for the mtDNA based, presumed splitting-off of the true horses from ancestral *Equus*, more than 1 Ma older than the early dispersal of stenorid *Equus* at 2.6/2.5–3.0 Ma ago, 2 Ma older than the oldest known morphological caballoid of less than 1.8 Ma ago, and almost 3 Ma older than the Gálerian dispersal of caballoid *Equus*. The *Equus* fossils at Berești and Malușteni seem, therefore, to be younger than the rest of the fauna at these sites.

If the first occurrence of the caballoids in the fossil record is difficult to fit in with the proposed ancient date of their branching-off from the ancestral *Equus* on the basis of mtDNA, so is the proposed differentiation of the various breeds of domestic horse difficult to fit in with the fossil record. mtDNA indicates that the separation of lineages within this single species took place a very long time ago. According to George & Ryder (1986), the ancestor of the Arabian breed branched off from the common ancestor of all domestic breeds and Przewalski's horse more than 200 000 years ago, i.e. in the middle Pleistocene. A possible morphological fossil ancestor of the extant caballoids appeared only in the late Pleistocene, 80 000–12 000 years ago.

This was a caballoid of rather small stature, the “loess horse” of the northern Palearctic (Forstén 1988a).

7. Conclusions

Although in some cases, mtDNA of the species of the genus *Equus* (zebras, asses, and true horses) gives slightly high branching-off dates compared with the fossil record, in other cases the two timetables are in fairly close agreement, e.g. on the age of ancestral *Equus* (appr. 3.9 Ma), the age of the common zebra ancestor (appr. 2.8 Ma), and the date of the differentiation of the zebra species *grevyi* and *burchelli* (appr. 1.6 Ma) (Fig. 1). Because of the difficulty in specifically identifying extant equids among the fossils, it is impossible to distinguish among the late Pliocene stenorids in Eurasia, early *E. zebra*, which presumably branched off from the common zebra ancestor approx. 2.8 Ma ago (George & Ryder 1986). However, the most puzzling discrepancy between the fossil record and the mtDNA timetable, is the lack of morphologically distinguishable true horses or caballoids in the fossil record until less than 1.8 Ma ago, in spite of their presumed early branching-off (appr. 3.4–3.9 Ma ago) from the common *Equus* ancestor. Either caballoids were so rare that their teeth have not been found in fossil faunas from the time interval between 3.4–3.9 and approx. 1.8 Ma ago, or else they were “disguised” for a long time by a stenorid dental morphology. The proposed mid-Pleistocene date of origin of the domestic breeds of *E. caballus* also seems too old, in view of the lack of a recognizable fossil ancestor at that time. This discrepancy may be accounted for by the presence of several mtDNA lineages as polymorphisms in the as yet unknown mid-Pleistocene ancestor.

Interestingly, the zebra lineage, which morphologically is the primordial lineage within the genus *Equus*, seems to provide the best fit between the mtDNA timetable and the fossil record. If, as has been maintained, *E. cummingsi* from the Pliocene–early Pleistocene is an ass within the African ass lineage, and the contemporaneous stilt-legged horses of North America belong in the Asiatic ass lineage, they would partly furnish

fossil evidence for the presumed early branching-off of these equids. However, they would not fill the gap in the Asiatic fossil record, thus leaving open the question of the direction of ass dispersal.

Substitutions of mtDNA are known to happen at considerably different rates in different, even related, lineages (Ovenden et al. 1987, Avise et al. 1988, Koop et al. 1989). Could this also be the case with the different lineages of *Equus*? The zebra lineage may represent the "normal" substitution rate, while caballoids may have different, faster, rates, giving an impression of apparently ancient branching. In fact, the branching rate calculated on the basis of mtDNA substitutions appears to give twice as high ages for the branching of the caballoids as does the fossil record. The rate of molecular evolution is negatively correlated with generation time and population size (Templeton 1935); variations in rates among related lineages are believed to be due to differences in these factors and in the repair rate of substitutions, which is for the most part unknown. Guthrie (1984) characterized *Equus* as having slow maturation, infrequent reproduction, but long life-expectancy. The males have family groups or harems, or they are territorial (Klingel 1974); caballoids may shift from one type of behaviour to the other depending on the environment (Rubenstein 1981). While slow maturation would tend to slow down evolution, small population size and social organization would speed it up (Bush et al. 1977, Templeton 1985).

On the other hand, agreement between the mtDNA timetable and the fossil record is a question of the morphological expression of a molecular change and how soon this is realized. It is possible that in the caballoids the realization of the typical morphology was delayed compared with that of the zebras and asses. The caballoids are dentally and ecologically the most derived among the extant equids. Their stratigraphic and their geographic distribution indicate that they are adapted to the temperate and cold conditions of the middle-late Pleistocene and Holocene Holarctic. They seem to have a wider ecological niche than the stonions, which they replaced (Forstén 1988b), although this may be a result of the fact that their environment was more unstable and less productive than that of the stonions. Morphologically recognizable caballoids first

occurred when the periodically cold conditions began, and in the Old World they became dominant in the equid fauna at the time of the first "great", or Mindelian/Elsterian, glaciation some 600 000 years ago. This indicates that their morphology is somehow correlated with the ecological conditions which made themselves felt at that time and which have reigned since.

The morphology of *E. zebra*, *E. asinus*, and *E. hemionus* may also be of recent date, extending back only to the middle Pleistocene. Evidently the Pleistocene, with its sharp climatic changes, was a period when several of the extant species of *Equus* evolved their modern morphology.

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