Ascent and decline of monodactyl equids: a case for prehistoric overkill

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Monodactyly developed independently in at least four distinct equid lineages: *Astrohippus*, *Pliohippus*, the two closely related genera *Hippidion* and *Onohippidium* and the lineage represented by *Protohippus*, *Dinohippus* and *Equus*. While *Astrohippus* and *Pliohippus* did not survive past the Hemphillian (late Miocene to earliest Pliocene), *Hippidion* and *Onohippidium* survived until the end of the Pleistocene or beginning of the Holocene, and *Equus* survives today with six species in the Old World. In spite of a remarkable uniformity in body structure this genus dispersed over five continents and gave rise to a rich evolutionary radiation, adapting to a variety of habitats and diverse, even extreme climates. Six lineages differentiated within it between the late Pliocene and the early Pleistocene. One of these, represented by *Equus stenonis* and its descendants, six to eight species in all, became extinct during the middle Pleistocene, with a possible survival into the late Pleistocene in the Indian peninsula. The other five lineages survived until the end of the Pleistocene, when they were represented by no less than 27 species. This should be considered a minimum estimate: several poorly known species are not considered here. There were never critical periods of mass extinction and many species disappeared through evolutionary change, resulting in the radiation of the final Pleistocene. The South American genera *Hippidion* and *Onohippidium* also dispersed widely and survived into the final Pleistocene or early Holocene with an unknown, but probably restricted number of species. In view of their remarkable capacity of adaptation, the dramatic decline of equids in number of species, and in the case of Eurasia in number of individuals of the surviving species, can hardly have been caused by climatic factors alone and is believed to be largely the result of prehistoric overkill.

1. Monodactyl equids in the fossil record

In the history of equids, monodactyly was the end of an evolutionary process which started in the early Eocene with digitigrade, tetradactyl hands and tridactyl feet, continued in the Oligocene with still digitigrade, entirely tridactyl limbs, passed through tridactyl unguligrade limbs, in which the weight rested on the hoof and the lateral digits had only a supporting function in fast running and jumping, then, after a short phase in which the lateral digits were reduced to

functionless rudiments, the process ended in the extremely simplified monodactyl limb, marvellously adapted to fast running sustained over long distances. This was obtained with the development of the interosseus tendon and of the sesamoidean ligaments (Camp & Smith 1942). Achievement of this adaptation was presumably the main reason why monodactyl equids everywhere superseded tridactyl equids and dispersed on five continents, adapting to the most varied environments and displaying an unprecedented capacity for expansion.

Monodactyly developed independently in at least four lineages of equids. One of these is represented by the small, slender-limbed *Astrohippus* Stirton, 1940, which has been reported from late Miocene and earliest Pliocene (late Hemphillian) sites in the southern United States and Mexico. The second lineage is represented by the well-known North American *Pliohippus* Marsh 1874, characterized by a complicated system of facial pits. This genus was confined to the Miocene and possibly the earliest Pliocene; it seems, however, that not all its species became monodactyl (Matthew & Stirton 1930, Azzaroli 1988). The third lineage is represented by the mainly South American genera *Hippidion* Owen, 1870 and *Onohippidium* Moreno, 1891. These were animals with peculiarly specialized skulls and some species were of very stocky build, with short and massive limbs. They were widespread in the Pleistocene of South America, where they became extinct at the end of the Pleistocene or at the beginning of the Holocene (Borrero 1984, Alberdi et al. 1986). Their older history is poorly known but they were clearly derived from some North American species more or less closely related to *Pliohippus*. *Onohippidium galushai* MacFadden & Skinner, 1979 is the most primitive representative of its genus and has been recorded from the late Hemphillian of Arizona. A jaw from the late Pliocene of California was tentatively referred to *Hippidion* (MacFadden & Skinner 1979). These authors referred the fossil to the early Irvingtonian but its age, older than the Oldovai palaeomagnetic subchron, places it in the late Blancan (see Lundelius et al. 1987:21 for discussion of the Blancan/Irvingtonian boundary). Details of the transition from tridactyly to monodactyly in these lineages are not known.

Both *Astrohippus* and the *Hippidion-Onohippidium* group are represented by a small number of species. *Pliohippus* is more diversified but the structure of the limbs is known in only a few of its species.

The fourth lineage of monodactyl equids had a much more varied history and is represented by the North American *Dinohippus* Quinn, 1955 and its descendant *Equus* L., which evolved from the former around the transition from Hemphillian to Blancan (early Pliocene) and subsequently gave rise to a rich evolutionary radiation. In the Americas *Equus* survived until the end of the Pleistocene or the Holocene, in the Old World it survives to the present. The origin of monodactyly in this lineage is better known, although not all the phases of the process are documented. It appears at any rate that the process took place around 10 m.y. (Voorhies, pers. comm.).

It seems that *Dinohippus* was derived from some still unidentified species of *Protohippus* Leidy, 1858. *Dinohippus leidyanus* (Osborn, 1918) is common in the Coffee Ranch fauna of Texas, dated around 6 m.y. B.P. (Lindsay et al. 1984), at Wikieup, Arizona, dated around 5.5 m.y. (MacFadden et al. 1979) and at other sites which have not been dated more precisely: Snake Creek, Nebraska; Edson, Kansas. This form is monodactyl: the lateral metapodials extend the full length of the central metapodial but bear no articular facets for the phalanges at their distal ends (Azzaroli 1988). The transition from *Protohippus* to *Dinohippus* was gradual and no clear-cut division may be traced between these two genera.

The late Clarendonian (10 m.y. B.P.) Poison Ivy Quarry of Nebraska, discovered some years ago by M. R. Voorhies, offers an unique example of fossilization (Voorhies & Thomasson 1979): an ash flow suddenly killed large herds of herbivores, mainly rhinoceroses and equids, and many skeletons were preserved articulated and practically intact. There are several species of equids, of medium or small size. Among them a species of *Protohippus* is noteworthy: some specimens have tridactyl limbs, with rudimentary lateral digits which had lost any function; in others the lateral digits have disappeared completely and the lateral metapodials bear no distal articular facets. The lateral digits disappeared by

fluctuation after they had become functionless rudiments (M. R. Voorhies, pers. comm., 1984).

2. The early history of *Equus*

Bennett (1980) assumed that the species currently grouped in the genus *Equus* were derived from two distinct species of *Dinohippus,* which were not named. Dalquest (1988) went even further towards a diphyletic origin in assuming that zebras and true horses ("zebrine" and "caballine" equids) were derived from *Dinohippus*, while hemiones and asses ("asinine" equids) descended from *Astrohippus.* These interpretations do not seem to be supported by evidence. The record of equids in the early Pliocene of North America is discontinuous but rich and has so far provided no trace of more than one species of *Equus.* The very rich early Blancan faunas of Hagerman, Idaho, and Broadwater, Nebraska, contain only one species, *Equus simplicidens* Cope 1892. Individual variation in size is broad but continuous in these samples and anatomical features of skulls, teeth and limbs, well preserved in the Hagerman fauna, are uniform (Azzaroli & Voorhies, in press).

Equus simplicidens is primitive in its features: large size, strongly deflected braincase, large preorbital and buccinator pits, deep longitudinal furrow on the median nasal feature, posterior palatine foramina placed rostrally to the last molars, retention of the first (milk?) premolar in the maxilla, short protocones in the upper cheek teeth, very irregularly developed volar ridge on the distal portion of the central metapodials above the keel. Matthew (1924) proposed the new genus name *Plesippus* for this species, but Skinner (1972) restored it to the genus *Equus*, subgenus *Dolichohippus* Heller, 1912 because of its cranial and dental similarities to the type species of this subgenus, the living *Equus grevyi* Oustalet, 1882.

During the early Blancan the diversity of *Equus* remained low. It was only in the later Blancan, starting from approximately 3 m.y. B.P., that signs of differentiation began to appear. In 1893 Cope described *Equus cumminsii* from the late Blancan of Mt. Blanco, Texas. This species was based on a single, damaged tooth which is obviously inadequate for a diagnosis: its only

distinguishing features being the small size and the rather simple enamel pattern. In 1921 Frick reported on other teeth of small size, named *Pliohippus francescana* (sic) *minor,* from the late Blancan of the San Timoteo Badlands, California. Hibbard (1944) referred to *Equus cumminsii* an incomplete tooth row from the Meade Formation, Kansas, and Strain (1966) described as *Asinus cumminsii* a ramus from the late Blancan Hudspeth local fauna of Texas. In the collection of the Palaeontological Department of the University of California at Berkeley there is a cast of a well preserved palate of small size from Cita Canyon, Texas (UCMP 64604/V-371). The cheek teeth are primitive, with a simple enamel pattern and short protocones; the first premolars have disappeared.

These specimens provide evidence of the occurrence of one or more small-sized species of *Equus* in the late Blancan, but none is adequate for specific identification. There is evidence, on the other hand, that at least two small sized species lived at this time in North America. One was characterized by slender, elongated limbs (AMNH 116503, 116504, from Eleven Miles Wash, Duncan Area, Arizona). The second had much shorter limbs with more normal proportions (AMNH 116501, Safford Area, Dry Mountains locality, San Simon drainage system, Arizona; see Azzaroli & Voorhies, in press).

Although the evidence is meagre, it may tentatively be assumed that the slender-limbed species represents the stem group of hemiones and asses, including the North American species *Equus semiplicatus* Cope, 1893 (*calobatus* Troxell, 1915) and *Equus francisci* Hay, 1915 while the short-limbed species may represent the stem of the subgenus *Amerhippus* Hoffstetter,1950, with *Equus fraternus* Leidy 1860, and *Equus conversidens* Owen, 1863 in the United States and Mexico and several species in South America. (The generic, or subgeneric name *Tomolabis* Cope, 1892, with type species *E. fraternus*, has priority over *Amerhippus;* but it was not used by later authors and in 1950 was already a "nomen oblitum").

3. First dispersal to the Old World

Well before the end of the Pliocene *Equus* had reached the Old World. Its arrival in India was

dated to 2.5 m.y. by Lindsay et al. (1980; see also Azzaroli & Napoleone 1982); its arrival in western Europe dates from the same time or slightly earlier (Lindsay et al. 1980; Alberdi et al. 1983; Leone 1985; Bonadonna & Alberdi 1987; Azzaroli et al. 1988).

Equus livenzovensis Baigusheva, 1978 is represented in Southern Russia by several dentitions and postcranial bones but only by two damaged skulls; more fragmentary remains from Western Europe may be referred to this species. *Equus livenzovensis* is closely similar to *Equus simplicidens* but of larger size (Baigusheva 1978; Azzaroli 1990). The Northern Chinese *Equus sanmeniensis* Teilhard & Piveteau, 1930, from the (?) late Pliocene of Nihowan, is of large size and is primitive in skull features; it seems however to be more derived than *Equus simplicidens* in its dentition. The small-sized *Equus teilhardi* Eisenmann, 1975 is probably of the same age as *Equus sanmeniensis* and may be related to it, but is poorly known.

In East Africa *Equus koobiforensis* Eisenmann, 1983 is related to *Equus simplicidens* and *Equus sanmeniensis* but seems more derived in its open facial angle; its age is late Pliocene, around 2 m.y. (Eisenmann 1983). The late Pliocene to early Pleistocene *Equus oldowayensis* Hopwood, 1937 may possibly be conspecific with *Equus koobiforensis*; its remains were recently redescribed by Churcher & Hooijer (1980) but the skull is not known. This is also the case with the maghrebian *Equus numidicus* Pomel, 1897 (Arambourg 1970). The living *Equus grevyi* represents a terminal branch of this lineage, which may be considered the central stem of the genus *Equus*.

The origin of the African subgenus *Hippotigris* Hamilton Smith, 1841, with the middle Pleistocene *Equus mauritanicus* Pomel, 1897 from the Maghreb, the recently extinct *Equus quagga* Gmelin, 1788 from South Africa and the living *Equus zebra* L., 1758 and *Equus burchelli* Gray, 1825 is still obscure. It may be assumed that these species were derived from the primitive *E. koobiforensis* or some related species, from which they differ markedly in skull structure; *Equus quagga* is the most widely divergent in the characters of its skull and dentition.

4. The aberrant "stenonid" lineage

Shortly after the first dispersal event into the Old World, other lineages began to split from the central stem. *Equus stenonis* Cocchi, 1867 is a common species in the late Pliocene and early Pleistocene of Europe and its range extended as far as China (Azzaroli 1965, 1982, 1987, 1990). Several authors, among these Gromova (1949), Samson (1975), and Prat (1980), placed *Equus stenonis* in the subgenus *Allohippus* Kretzoi, 1938. This author gave no description nor definition of his new subgenus and only defined as subgenotype *Equus plicidens* Owen, 1844, a taxon based on poorly diagnostic teeth which certainly do not belong to *Equus stenonis*. The lack of definition and the fact that *Equus plicidens* is indeterminate invalidates Kretzoi's name. Gromova gave a new definition of *Allohippus* based on her "*Equus stenonis* var. *major* Boule" and Samson (1975) argued that the subgenus name is therefore valid and its author is not Kretzoi 1938 but Gromova 1949. Here the taxonomic procedure becomes entangled and rules of nomenclature have been ignored. There is: a) a case of homonymy; b) change of subgenotype; c) the additional complication that Boule's *Equus major* is indeterminate (Viret 1954) and Gromova's "*Equus stenonis* var. *major*" is actually *Equus livenzovensis* (Azzaroli 1990); d) a second case of homonymy between *Equus stenonis* race *major* Boule 1893, and the name *Equus major,* apparently used to designate different taxa, by De Kay (1842), Cope (1878) and Leidy (1899). In conclusion, the names *Allohippus* and *major* are not available and should be cancelled from future literature as "nomina dubia". It is preferable on the other hand not to introduce new names in an already crowded literature and place *stenonis* in *Dolichohippus* because of its undoubtedly primitive features. It represents, however, the branching off of a lineage distinct from the central stem represented by *Equus simplicidens, sanmeniensis, koobiforensis* and *grevyi*.

Equus stenonis is derived in the great elongation of its snout and of the narial opening, which extends caudally above the P^3 or even as far as the commissure between P^3 and P^4 (Azzaroli 1965, 1982). It retains the preorbital pits, which are

somewhat smaller than in *Equus simplicidens* and *Equus livenzovensis*, and the furrow along the nasal suture, while its dentition, though still primitive, occasionally displays some derived features, such as elongated protocones in the upper cheek teeth and shallow ectoflexids in the lower molars. It is represented by several subspecies. The late Pliocene subspecies are distinguished by rather short, sometimes massive limbs: *Equus stenonis vireti* Prat, 1964, *Equus stenonis senezensis* Prat, 1964 and *Equus stenonis guthi* Boeuf, 1986 in France, *Equus stenonis pamirensis* (Sharapov, 1986) (originally *Hippotigris pamirensis)* in Central Asia. The nominal subspecies, from the late Villafranchian (early Pleistocene) of central Italy, was characterized by more slender and elongated limbs (Azzaroli 1965, De Giuli 1972). A similar, or identical subspecies was recorded from the early Pleistocene of Spain (Alferez 1978). The characteristic skull features of *Equus stenonis* also occur in the Indian species *Equus sivalensis* Falconer & Cautley, 1849 and *Equus namadicus* Falconer & Cautley 1849. These are represented by a few skulls, a limited number of limb bones and several minor fragments and isolated teeth. The skulls only differ from *Equus stenonis* in the more progressive features of their dentition: consistently elongated protocones and shallow ectoflexids, and *Equus sivalensis* also in its smaller size (Azzaroli 1982); their exact age is not known. The oldest record of *Equus* in the Indian subcontinent has been dated around 2.5 m.y. (see above); the age of the skulls is not exactly known and the specific identities of the oldest Indian representatives of this genus are indeterminate. Around 2 m.y. ago, about the same time as in Europe, equids with the typical skull specializations of *Equus stenonis* and with similar dentitions made their appearance in North America (Azzaroli & Voorhies in prep.). One or more species with these features but with more elongated snouts and larger body size also occur slightly later, around the Pliocene/Pleistocene (Blancan/Irvingtonian) transition, in various places of the southern United States. They were not studied in detail by Azzaroli & Voorhies (in prep.) as they were being studied by other palaeontologists, and it is hoped that their results will soon be published. This "stenonid" lineage seems

to have become extinct in North America in the early Irvingtonian. It lasted longer in Eurasia: *Equus stenonis* survived till the end of the Villafranchian, more or less 1 m.y. B.P.; during the Villafranchian it seems to have given origin on one side to the small *Equus stehlini* Azzaroli 1965 (Azzaroli 1982, Privat Defaus 1985) and on the other to the gigantic *Equus bressanus* Viret, 1954 (Azzaroli 1984, 1990); it ended in the early middle Pleistocene (Galerian) of Europe with *Equus sussenbornensis* Wüst, l901 and in the Olyorian of North Eastern Asia with its close relative *Equus verae* Sher, 1971. With these two early middle Pleistocene species the "stenonid" lineage came to an end in Europe and in Central and Northern Asia. The date of its extinction in the Indian subcontinent is not known, but Badam (1979) recorded *Equus namadicus* from middle Palaeolithic sites in peninsular India.

5. *Equus idahoensis* and the heavy-structured species

A third lineage differentiated near the close of the Pliocene in North America. Its oldest representative is *Equus idahoensis* Merriam, 1918. This was a sturdy animal of large size. The teeth were large but still primitive in their enamel pattern and are distinguished by a thick cementum cover. The skull is massive, with thick bones, particularly so the premaxillaries and the mandibular rami; the snout is broad. The upper profile of the face is straight from the forehead to the nose, and this distinguishes *Equus idahoensis* from all other Pliocene and early Pleistocene species, in which the profile is wavy. The narial notch is shallow and there is a small, but well marked preorbital pit.

Equus idahoensis was presumably the ancestor of some middle and late Pleistocene species characterized by an equally heavy structure of the skull and by stout limbs: *Equus excelsus* Leidy, 1858, *Equus occidentalis* (in the sense of Merriam 1913). These two species may be grouped in the subgenus *Allozebra* Trumler 1961, with type species *Equus excelsus*. The somewhat aberrant *Equus pacificus* Leidy 1868 has been chosen as the type of the new subgenus *Hes-*

perohippus by Hibbard (1955) and seems also to be related to this lineage; it is distinguished by a strongly deflected brancase and occiput. *Allozebra* and *Hesperohippus* have been recorded only from North America.

6. The "caballine" lineage, or true horses

The straight profile of the skull of *Equus idahoensis* also points to some relationship with *Equus caballus* L. 1758 (some authors contend that the Linnean name was based on domesticated animals and prefer to use the name *Equus ferus*, proposed by Pallas to designate the wild form), and its relative *Equus niobrarensis* Hay, 1913, which, however, are of more slender build both in their skulls and their limbs. *Equus niobrarensis* is even more slender than *Equus caballus* in skull structure and differs in several details of the dentition. *Equus lambei* Hay, 1917 seems to be only a small-sized subspecies of *Equus niobrarensis*. These species may be grouped under the nominal subgenus *Equus* L.

The oldest fossil of *Equus caballus* in North America is probably a mandible from the early Irvingtonian Red Cloud Formation of Southern Nebraska (Azzaroli & Voorhies, in press). This formation underlies the Sappa Formation (Lexique Stratigraphique International, 1967), which has been dated 1.1–1.2 m.y. by Repenning (1987). *Equus caballus* is also represented by some fragmental skulls and jaws from late Irvingtonian and Rancholabrean sites of California and is very common in the late Pleistocene or Holocene of Alaska.

Equus caballus dispersed from North America into the Old World, where it is well represented by several subspecies ranging from Galerian and Olyorian to Holocene and present times. The oldest record in Eurasia dates from 0.9 m.y. in the Lakhuti 2 local fauna of Tadjikistan (Azzaroli et al. 1988).

Equus algericus Bagtache, Hadjouis & Eisenmann, 1984, from the late Palaeolithic of Algeria, may also be ascribed to the subgenus *Equus*. Its diagnosis was based on teeth and limb bones which are inadequate to define the species but conclusively testify to the occurrence of "caballines" in the late Pleistocene of the Maghreb.

7. Hemiones and asses

Hemiones and asses (subgenera *Hemionus* Stehlin & Graziosi, 1935 and *Asinus* Frisch, 1775) may possibly trace their origin to some small-sized, slender-limbed species of the late Blancan of North America (see above). The Irvingtonian and Rancholabrean *Equus semiplicatus* Cope, 1895 and *Equus francisci* Hay, 1915 may be referred to *Hemionus*, although they differ from Old World hemiones in their more laterally oriented orbits (Azzaroli & Voorhies, in prep.).

The history of asses and hemiones in the Old World is still imperfectly known. In the early middle Pleistocene (Galerian) hemiones are represented by the still poorly known *Equus altidens* Von Reichenau 1915. The oldest record of this species is from Lakhuti 1 local fauna of Tadjikistan, dated about 1.0 m.y. (Azzaroli et al. 1988).

Asses have less extremely slender limbs than hemiones and are also distinguished by small teeth, particularly so the incisors (Stehlin & Graziosi 1935). They are now confined to Africa, with *Equus asinus* L., 1758 (*Equus africanus* Fitzinger, 1857 for those who prefer names based on wild animals), but lived also in Syria in the late Pleistocene (Ducos 1986). Churcher (1982) recorded a metatarsal referred to an ass from the middle of Bed II, Olduvai Gorge, Tanzania, dated between 1.5 and 1.7 m.y., that is, considerably older than *Equus altidens* from Lakhuti 1, so that the origin of Old World asses still requires investigation. The Algerian *Equus tabeti* Arambourg, 1970, from Ain Hanech, is represented by teeth and limb bones with the typical features of asses. Its age has not been exactly determined but seems to fall in the early Middle Pleistocene.

Equus melkiensis Bagtache, Hadjouis & Eisenmann, 1984 is another ass-like species based on teeth and limb bones from the late Palaeolithic of Algeria. Its relationships are poorly understood. *Equus graziosii* Azzaroli, 1966, from the late Pleistocene of central Italy, is better known. It is represented by a skull, several jaws and some postcranial bones (Azzaroli 1979). It shows definite asinine features in the skull, in the jaw and in the scapula, and the radius is slender; it differs, however from living asses in some details of the skull and of the lower dentition.

The position of *Equus hydruntinus* Regàlia, 1904, a widespread species in the late Palaeolithic of southern Europe, is more uncertain. The skull is not known, and this is doubtless the main cause of uncertainty. Stehlin & Graziosi (1935) referred this species to the subgenus *Hemionus*; other authors on the other hand consider it a "zebrine" because of its dental features. The present writer favours the view of Stehlin & Graziosi and is inclined to see in *Equus hydruntinus* a possible descendant of a rather primitive variety of *Equus altidens* from the early Middle Pleistocene of Venta Micena in Southern Spain, described under the name of *Equus stenonis granatensis* by Marin (1987), but the question is still open. The name *Equus stenonis senezensis* var. *granatensis* was proposed by Ruiz Bustos (1976).

Another slender-limbed, ass-like equid, of smaller size than *Equus hydruntinus*, was recorded from the late Middle Pleistocene of Lunel Viel cave in Southern France by Bonifay (1973), who referred it to *Equus hydruntinus*. An incomplete skull shows asinine features.

8. The subgenus *Amerhippus* and the dispersal to South America

A different lineage is represented by the subgenus *Amerhippus* Hoffstetter, l950 (type species *Equus andium* Wagner-Branco, 1883). This subgenus is restricted to the Western Hemisphere and is characterized by the consistent lack of cups in the lower incisors. This feature is, however, not unique to *Amerhippus*: it also occurs in *Equus occidentalis*, in some subspecies of the living African *Equus burchelli* and, at least occasionally, in *Equus francisci*, *Equus stehlini* and *Equus teilhardi*.

Peculiar features of *Amerhippus* are the bulging forehead, the strongly deflected braincase, a massive head, short limbs and generally moderate size. The vomer is known only in some South American species and inserts in the palatal roof well in front of the palatines (Hoffstetter 1952). Some South American species have rather stout limbs.

Amerhippus is represented in North America by *Equus fraternus* Leidy, 1860 and *Equus*

conversidens Owen, 1869. The former is known from the Irvingtonian to the Ranchilabrean, with a range from Florida to Southern Canada; the latter is known from the Rancholabrean of the Southern United States and Mexico.

Amerhippus was the only subgenus that crossed the Panamanian bridge and reached South America, where it dispersed widely in the plains and in the highlands, as far as southern Chile. It survived until the end of the Pleistocene or the beginning of the Holocene (Alberdi et al. 1986). Seven species have been described from the southern continent, only five of which are represented by cranial remains. They differ in size and proportions but are rather uniform in their features (MacFadden & Azzaroli 1987).

9. Radiation, expansion and decline of *Equus*

The list of species given in the preceding pages is not complete. Many more species have been proposed. A large proportion of them is the result of exceedingly "splitting" attitudes and fall into synonymy, or are of subspecific rank and were not mentioned in the present paper; some North American species of the *Equus stenonis* lineage are currently under study by other authors and have been mentioned briefly; still others were based on poorly diagnostic material and are "nomina dubia". It is in any case apparent that the main diversification of the genus *Equus* started between 3.0 and 2.5 m.y. B.P. and flourished richly in the Quaternary. There are probably over 40 valid species, and no less than 27 lived in the late Pleistocene or early Holocene. Only six of them survive today, all in the Old World; a seventh, the quagga, was exterminated in recent times. This rich radiation followed by an abrupt, dramatic decline calls for meditation. The question is linked with the well-known issue of the late Quaternary decline of game animals, or medium to large sized mammals in general. Two major lines of thought have been proposed: extinctions caused by overhunting by prehistoric (mainly late Palaeolithic) man versus extinctions cause by more ordinary, or "natural" (mainly climatic) causes. Opinions have of course been divided but characteristically in Martin & Wright (1967) the majority of authors favoured

the former alternative, while in Martin & Klein (1984) there was a shift to the other side, although the theory of prehistoric overkill still had passionate supporters (Martin 1984, McDonald 1984). The case ended in an "open verdict" (Marshall 1984).

In some cases the two theories have been presented as if they were mutually exclusive, which is not necessarily true. The two causes may have acted jointly to bring about what was undoubtedly one of the most dramatic events of the closing Pleistocene, and perhaps the fundamental question should rather be centered on which of the causes was prevalent. The cause of extinction is not necessarily the same for all kinds of mammals, nor for all continents. So, for instance, the extinction of North American tapirs, confined to warm rain forests, may well have been caused by the onset of a too dry, too cold, or too strongly seasonal climate. The same argument however does not hold for more adaptable animals, such as camels, equids, and possibly also ground sloths and glyptodonts, which expanded so widely in North America, and does not warrant generalizations concerning their extinction. The recent book by Martin & Klein (1984) is a collection of valuable papers but there are some problems with the sections on Europe. It is regrettable that there are no recent synthetic studies on the Quaternary faunas of this continent and P. Martin (1984) had to base his analysis on an outdated synthesis by Kurtén (1968). The subject was approached on broad terms, such as extinction versus survival, at the ordinal or family level. Many relevant facts thus escaped attention. Equids survived and are not listed among extinct taxa but it was overlooked that *Equus hydruntinus,* very common in the late Palaeolithic of southern Europe, declined dramatically in number at the end of the Palaeolithic. In the Neolithic its distribution was fragmented in restricted areas, mostly in eastern Europe: Crimea, Dobrudja, Hungary, Slovenia (Samson & Radulasco 1966). The last survivors of *Equus hydruntinus* have been reported from Copper age settlements of southern Spain (Uerpmann 1976, quoted by Nobis) and southern Dobrudja (dated 3900–3400 B.P.: Nobis 1986).

It should be kept in mind, however, that *Equus hydruntinus*, as well as other small-sized, ass- or hemione-like equids are represented in Europe and Asia by highly fragmental remains, so that their specific identity is not always beyond doubt. *Equus caballus*, the horse, even more common than the former throughout Europe, was driven to the verge of extinction and survived as a relict in a few restricted areas; the decline in number of individuals may be grossly evaluated between 80 and 90 % if not more. The evidence derived from equids is thus gravely underestimated. Other cases are similar. The genus *Ursus* was not extirpated, nor was the family Ursidae, but their most common representative in southern Europe, the cave bear, became extinct. Wisent and aurochs were also severely decimated. Martin (1984) and Vereshchagin (1984) brought appalling evidence of overkill of the woolly mammoth in Russia. This is a species that ranged from the tundra to the Mediterranean and seems to have been highly adaptable to climate and environment. The same argument applies to the woolly rhinoceros.

For equids, it may be pointed out that in spite of their remarkable uniformity in anatomical features, they cover a widely diversified range of adaptations (Azzaroli 1979, Groves 1986). Horses lived in the Holocene in the Siberian tundra and in the high latitudes of Alaska, as well as in the temperate belt and in southern Europe, all of which cover a variety of climates and environments. Hemiones inhabit flat deserts and can stand the cold winters of Central Asia and Tibet. Asses prefer more rugged landscapes and can thrive in the extremely hot and arid Danakil desert. Zebras prefer rich parklands and savannahs, or uplands as in the case of the mountain zebra, or tropical bush as the zebra of Grévy. Leaving aside glaciated areas, high mountains and dense rain forests, it may be said that equids occupied a wide range of ecological niches until the end of the Pleistocene. The fact that they crossed the forested Panamanian bridge and expanded in the highlands and in the plains of South America, dispersig as far as the high latitudes of southern Chile, is illuminating.

The expansion of the genus *Equus* was an almost unique case, equalled perhaps only by *Felis* among mammals. As mentioned above, in addition to *Equus* the monodactyl equids *Hippidion* and *Onohippidium* also expanded widely in South America and survived until the arrival of Palaeolithic man.
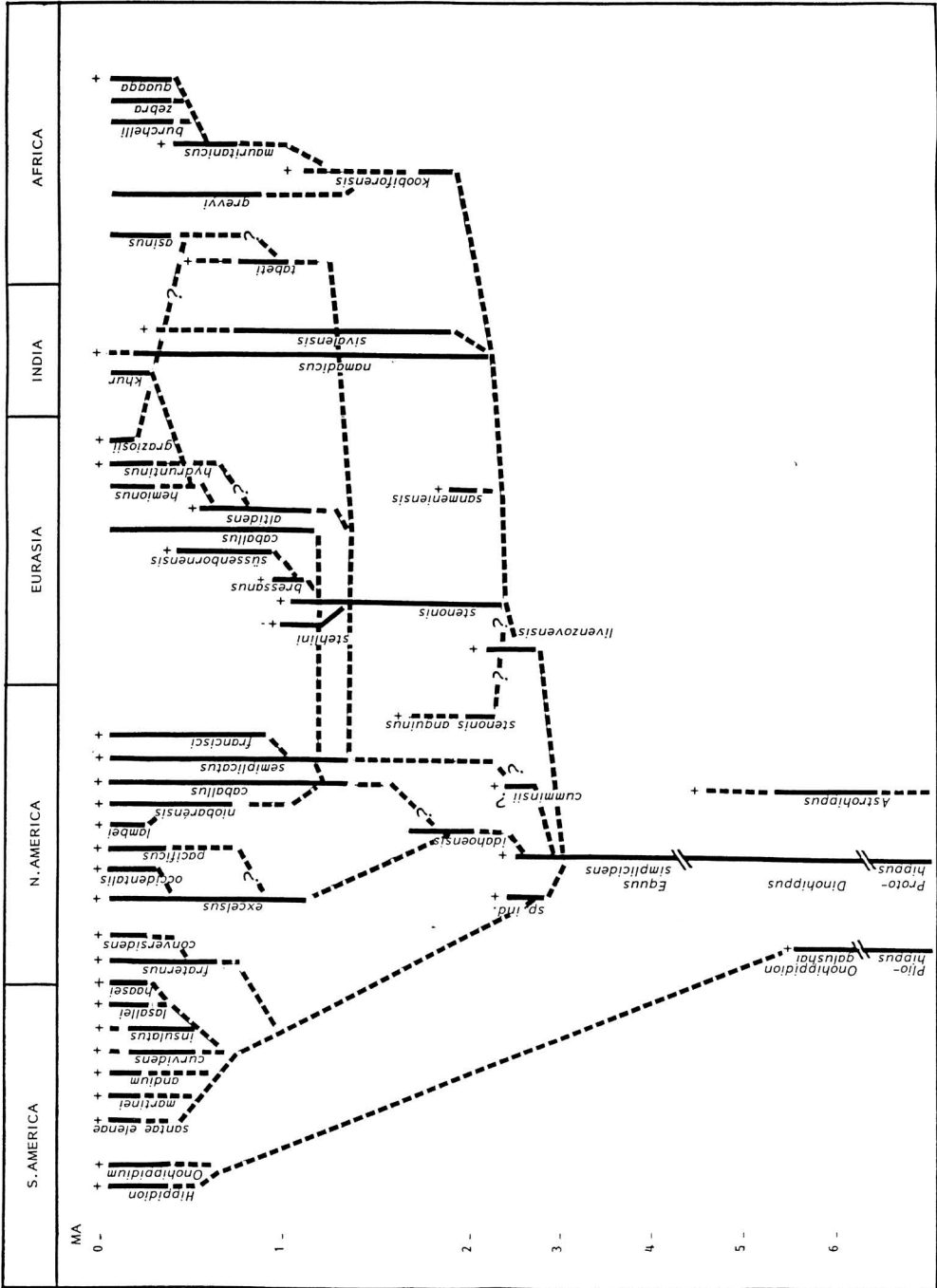
Fig. 1. Evolutionary tree of monodactyl equids.

In the two Americas, human settlements with associated bones of horses or other game animals are few, an this fact has been interpreted in opposite ways. Some authors see it as evidence against the influence of man in the destruction of the megafauna; others, in particular P. Martin (1984) and McDonald (1984), advanced the original and now well-known "Blitzkrieg" hypothesis to explain at the same time the sudden extinctions and the scarcity of archaeological documents.

It is an established fact that the dates of the last occurrences of equids in North America are mostly around 10 000–8 000 years B.P. (Mead & Metzer 1984), which is also the time when Palaeolithic hunters were most active. In Europe human settlements with remains of game animals are common and several of them testify to the large number of animals killed, for example, the appalling case of Solutré for horses (Prat 1968).

During the Pliocene and Pleistocene the history of the genus *Equus* was characterized by more or less continuous diversification. Only the lineage of *Equus stenonis* and its descendants became extinct, probably in the early Irvingtonian in North America; in Eurasia it survived the great end-Villafranchian faunal crisis (Azzaroli 1983), with *E. sussenbornensis* in Europe and *E. verae* in Siberia, and became extinct in the Galerian resp. Olyorian, shortly after the immigration of "caballines" and hemiones from the New World. It survived into the late Pleistocene in peninsular India, where *E. namadicus* was reported from middle Palaeolithic sites (Badam 1979). The other lineages all survived, some until the end of the Pleistocene, others to the present (Fig. 1). The increase in number of species in the late Pleistocene may perhaps be an artifact due to a better record, but there is no sign of large scale extinctions, nor of periods of crisis. The demise of the *E. stenonis* group took place at different times in the various areas and was compensated by the appearance of other species, except in the Indian peninsula. Its extinction may have been the result of interspecific competition.

There is no detailed record of the time ranges of individual species in North America. The study by Azzaroli & Voorhies (in prep.) was primarily dedicated to the diagnosis of species and their mutual relationships. Nevertheless some broad conlusions may be drawn. In a study of the causes of extinctions, the knowledge of the patterns of association between man and animals, and of the exact dates of the extinctions, is of primary interest, but the problem may also be approached from other viewpoints. In particular, in the case of equids, their extraordinary capacity of adaptation and of expansion, which implies power to withstand competition from other animals and to survive in case of unfavourable, or not completely favourable environments. A deterioration of climate, be it a fall in average temperature or the onset of high seasonal excursions, can hardly have been the cause of the disappearance of highly adaptable and mobile animals that had dispersed over plains and uplands, from the equatorial belt to beyond the arctic circle.

Horses, and equids in general, were always highly vulnerable to efficient hunters because of their preference for open areas. Forest animals, like aurochs, bison, deer and wild boar found an easy shelter in the enormous expanses of forests that followed the Pleistocene deglaciation in the middle latitudes. But these forests had reduced the habitat of equids and exposed them as an easy prey to hunters. It is significant that in South America the equids, once widespread in a variety of landscapes and climates, became extinct, while tapirs, much more exacting in terms of environment, survived in the rain forests.

To conclude, the sudden, dramatic decline of equids at the close of the Pleistocene, and their total extinction in the Western Hemisphere, cannot have been caused by climatic causes or alterations of the environment, which could at most have restricted their habitat. Their fate was only a part, although a spectacular one, of the first ecological disaster caused by man.

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