

Equus: an evolution without lineages?

VÉRA EISENMANN

UMR 8569 CNRS, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle,
8 rue Buffon, F-75005 Paris, France
vera@mnhn.fr

The story of equids is still tantalizing and frustrating after 150 years of study, during which time it has attracted scientists and fed their debates. The fossil material is rich enough to raise hopes, but not rich enough to fulfil them. The variety and abundance of data exercises such constraints on interpretations that they rarely remain simple and conclusive.

Like the taxa themselves, ideas about equid evolution have their FAD's and LAD's, and like equid taxa, it is not easy to precisely identify these dates. It seems that OWEN (1861) was the first to consider that *Hipparion* "might be" the transitional form between *Paloplotherium* and *Anchitherium*, on one hand, and the modern horse on the other. However, OWEN favoured repeated creations and thus did not accept this interpretation. T.H. HUXLEY (1870) did, and even though he was conscious of the dangers of mistaking "uncles and nephews for fathers and sons", he thought that the pedigree of the horses was a clear case of true linear evolution. The theory of the direct descent of *Equus* from *Hipparion*, first rejected by PAVLOVA (1888), remained a controversial matter for about 50 years. In 1932, HOEPEN considered that zebras descended from *Hipparion* and asses from zebras. The concept of a linear evolution was, however, soon replaced by the more complex tree representation (SIMPSON 1951) and its more recent cladogram variants (EVANDER 1989). Gradualists and punctualists alike accept this representation because some evolutionary trends seem obvious enough to justify discrete branches or, in other words, lineages.

There is no question that such a generalised tree is a good representation of an overall evolutionary model, nor that ancestor-descendant links exist. However, looking at evolution over 60 million years gives a picture that is not necessarily reproduced when zooming-in on a

shorter period. According to PROTHERO & SHUBIN (1989), "the evolution of Oligocene horses is characterised by multiple speciation events" and not by orthogenesis "of a single continuous lineage." At a scale of about two million years, the relations between fossil *Equus* species appear more like a net than a ramification. I shall try to illustrate this by focusing on several epochs, beginning with modern *Equus* and going backwards in time.

In modern times, the genus (or subgenus) *Equus* is represented by two species (*E. grevyi* and *E. zebra*) and four specific groups: Caballines (*E. caballus* and *E. przewalskii*), Plains zebras (*E. burchelli* and *E. quagga*), Hemionines (*E. hemionus* and *E. kiang*) and Asinines (*E. africanus* and *E. asinus*).

During the Late Pleistocene, there is good evidence for one additional species within the Plains zebra group, *E. capensis* from South Africa (THACKERAY 1992); at least two more within the Asinines, *E. melkiensis* (BAGTACHE et al. 1984) from North Africa and *E. lauracensis* (ASTRE 1948) from France; another Hemionine, *E. hydruntinus* (BURKE et al. 2003); and at least two of unknown affinities, *E. graziosii* from Italy (AZZAROLI 1966) and *E. valeriani* from Uzbekistan (EISENMANN et al. 2002). Caballines include at least three morphs: the ubiquitous heavy horse (known by such names as *gallicus*, *germanicus*, *latipes*, *uralensis*, *lenensis*, *lambei*), the giant horse of San Sidero, Italy, and the southern light horse, *E. antunesi*, of Italy and Portugal (CARDOSO & EISENMANN 1989). There is also a Caballine, *E. algericus*, from North Africa (BAGTACHE et al. 1984).

Between ca. 500 ka B.P. and the Late Pleistocene, there occur giant Caballines with varying morphologies (Mosbach and La Caune de l'Arago), in addition to some smaller ones (Lunel-Viel). The earliest *E. hydruntinus* is pos-

sibly represented at Lunel-Viel, France (BONIFAY 1991). In Africa there is evidence for a small *Equus* at Rabat, Morocco (ENNOUCHI 1953), possibly related to the small and poorly known South African *E. lylei* (BRINK 1994). In South Africa, *E. capensis* is well represented (EISENMANN 2000).

At about 700 ka B.P. (GERAADS et al. 1986), *Equus mauritanicus*, a Plains zebra, is well documented from Algeria (EISENMANN 1979, 1980, 1981). Evidence of Caballines is rare for that period or earlier (FORSTÉN 1988), at least in Europe. Instead, throughout the Old World, there is evidence of several morphs that may be referred to as *E. suessenbornensis* sensu lato (FORSTÉN 1986). In addition to the type-site Süßenborn (MUSIL 1969), these have been found at Akhalkalaki, Georgia (VEKUA 1986), North-eastern Siberia (*E. verae*, SHER 1971, and *E. colimensis*, LAZAREV 1980), Old Crow, Yukon (HARRINGTON 1989; MORLAN 1996) and probably at Cueva Victoria and Cullar de Baza, Spain (ALBERDI & RUIZ BUSTOS 1989). Moreover, at Süßenborn there is at least one Hemionine (*E. marxi*) and a small species of uncertain affinity, *E. altidens* (FORSTÉN 1990).

About 1 million years ago, the Mongolian *E. nalaikhaensis* (EISENMANN & KUZNETSOVA in press) exhibits a mosaic of characters in its skull, teeth and limb bones, reminiscent of Hemionines, Grevy's zebras and Asinines. This strange association is not so surprising if considered in parallel with current biomolecular interpretations (OAKENFULL et al. 2000). Taking, as a starting point, the age of *E. mauritanicus* (the first clear Plains zebra) at 700 ka, it seems that *E. africanus* and *E. grevyi* differentiated a short time before (820 ka and 770 ka B.P., respectively) and *E. zebra* slightly later (670 ka B.P.), although the precise timing and order of differentiation are uncertain. Hemionines would have been differentiating at around 1.07 Ma B.P. and Caballines still earlier, at about 2 Ma B.P. (according to OAKENFULL et al. 2000, "the common ancestor of the extant equids was a species that probably existed around 2 mya and was not one of the first *Equus* to have emerged in the New World ca 3.7 mya"). In practical terms, this means that ca. 1 Ma B.P., all *Equus* species that were not caballine were able to express Hemionine, ass and zebra characters, but these were not combined in the specific ways familiar to us. *Equus* may thus be compared to a kaleidoscope, able to produce different pictures while always retaining the same crystals.

Another important point is the apparent cra-

nological gap between *Plesippus* and *Allohippus*, on the one hand, and *Equus*, on the other. One basicranial character distinguishes them perfectly (EISENMANN & BAYLAC 2000), whereas teeth and limb bones may look absolutely alike. In practice, this means that, in the absence of well-preserved skulls, there is no way to tell whether Early Pleistocene species should be attributed to *Equus* or *Allohippus*. Accordingly, there is no sense in proposing lineages between, for example, *E. (Allohippus) stenonis*, *E. (?) granatensis*, *E. (?) altidens* and *E. (Equus) hydruntinus*. Moreover, "lineages" leading, for example, from *Plesippus* or *Allohippus* to *Equus grevyi* are certainly wrong (FORSTÉN & EISENMANN 1995).

This lack of traceable *Equus* lineages appears strange by comparison with other large mammals. Several explanations are possible. The first is that inside a specific group like the Caballines, there is no unidirectional trend for any given character. There are instead fluctuations in size (EISENMANN & DAVID 2002), in protocone length, in more-or-less cursorial adaptations and so on. Admittedly, the 500 ka old horse from Mosbach 2 (MAUL et al. 2000) is different from most younger horses. However, there is no reason to describe it as more primitive or less adapted. It was recently demonstrated that, in virtually contemporaneous Magdalenian sites (encompassing a few thousands years), the anatomical features of horses differ between the Paris Basin and the Swiss Plateau (BIGNON 2003). On a longer time span, anatomical features will also "change" naturally, but as yet they have never been observed to "evolve". The same is probably true for other *Equus* species or specific groups other than Caballines.

The second possible explanation is that the differentiation of most modern species took place less than 1 million years ago, on an area encompassing at least Asia, Europe and Africa (North America is very probably the cradle of Caballines, and possibly of Hemionines, but there is no sound evidence for a North American origin for modern asses or zebras). Compared with these temporal and geographical ranges, the information at hand is sparse.

The third possible reason may be related to the methodology employed in the study of *Equus*, which relies on extensive comparisons of numerous skull, teeth and limb bone characters. CUVIER, the founder of comparative anatomy, brilliantly demonstrated the law of correlation between characters when he dissected

the fossil marsupial from Montmartre. Indeed, this law is the very basis of palaeontological reconstructions of complex organisms. On the other hand, the scale of observation and the kaleidoscope pattern interfere. In the relatively recent past, there are known puzzling combinations of characters (and possibly others which have not yet been identified) that would not have been evident if fewer characters had been studied.

- ALBERDI, M.-T. & RUIZ-BUSTOS, A. (1989): Taxonomia y Biostratigrafía de Equidae (Mammalia, Perissodactyla) en la Cuenca de Guadix-Baza (Granada). In: M.-T. ALBERDI & F.P. BONADONNA (eds.), Geología y Paleontología de la Cuenca de Guadix-Baza, Trabajos sobre el Neogeno. – Cuaternario, **11**: 239-270; Madrid.
- BAGTACHE, B., HADJOUIS, D. & EISENMANN, V. (1984): Présence d'un *Equus* caballin (*E. algericus* n. sp.) et d'une autre espèce nouvelle d' *Equus* (*E. melkiensis* n. sp.) dans l'Atérien des Allobroges, Algérie. – Compt. Rend. Acad. Sci., II **298** 14: 609-612; Paris.
- BIGNON, O. (2003): Diversité et exploitation des équidés au Tardiglaciaire en Europe occidentale. Implications pour les stratégies de subsistance et les modes de vie au Magdalénien et à l'Azilien ancien du Bassin de Paris. – PhD thesis: 856 pp., annexes: 719-856; Université Paris X - Nanterre.
- BONIFAY, M.-F. (1991): *Equus hydruntinus* Regalia *minor* n. ssp. from the caves of Lunel-Viel (Hérault, France). In: R.H. MEADOW & H.-P. UERPMMANN (eds.), Equids in the ancient world, vol. II. – Tübinger Atlas des Vorderen Orients, Reihe A (Naturwissenschaften), Beih. **19** 2: 178-216; Wiesbaden (Dr. Ludwig Reichert Verlag).
- BRINK, J.S. (1994): An ass, *Equus (Asinus)* sp., from the late Quaternary mammalian assemblages of Florisbad and Vlakkraal, central southern Africa. – Suid-Afrikaanse Tydskrif vir Wetenskap, **90**: 497-500; Pretoria.
- BURKE, A., EISENMANN, V. & AMBLER, G. (2003): The systematic position of *Equus hydruntinus*, an extinct species of Pleistocene equid. – Quatern. Res., **59**: 459-469; Washington.
- CARDOSO, J.L. & EISENMANN, V. (1989): *Equus caballus antunesi*, nouvelle sous-espèce quaternaire du Portugal. – Palaeovertebrata, **19** 2: 47-72; Montpellier.
- EISENMANN, V. (1979): Les métapodes d' *Equus* sensu lato (Mammalia, Perissodactyla). – Géobios, **12** 6: 863-886; Villeurbanne.
- EISENMANN, V. (1980): Les Chevaux (*Equus* sensu lato) fossiles et actuels: crânes et dents jugales supérieures. – Cahier de Paléontologie. 186 pp.; Paris (Editions du CNRS).
- EISENMANN, V. (1981): Etude des dents jugales inférieures des *Equus* actuels et fossiles. – Palaeovertebrata, **10** 3-4: 127-226; Montpellier.
- EISENMANN, V. (2000): *Equus capensis* (Mammalia, Perissodactyla) from Elandsfontein. – Palaeont. Africana, **36**: 91-96; Johannesburg.
- EISENMANN, V. & BAYLAC, M. (2000): Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls: a morphometric definition of the subgenus *Equus*. – Zool. Script., **29** 2: 89-100; Oxford.
- EISENMANN, V. & DAVID F. (2002): Evolution de la taille des Chevaux d'Arcy-sur-Cure et de quelques autres Chevaux quaternaires. In: B. SCHMIDER (ed.), L'Aurignacien de la Grotte du Renne. XXXIV^{ème} supplément à Gallia Préhistoire.: 97-102; Paris (CNRS Editions).
- EISENMANN, V. & HELMER, D. & SAÑA SEGUI, M. (2002): The big *Equus* from the Geometric Kebaran of Umm El Tlel, Syria: *Equus valeriani*, *Equus capensis*, or *Equus caballus*? In: H. BUITENHUIS, A.M. CHOYKE, M. MASHKOUR & A.H. AL-SHYIAB (eds.), Proceedings of the fifth international symposium on the archaeozoology of southwestern Asia and adjacent areas. Archaeozoology of the New East, V. – ARC-Pulicaties, **62**: 62-73; Groningen.
- EISENMANN, V. & KUZNETSOVA, T. (in press): Early Pleistocene equids (Mammalia, Perissodactyla) of Nalaikha (Mongolia) and the emergence of modern *Equus*. – Geodiversitas; Paris.
- ENNOUCHI, E. (1953): Ossements fossiles découverts dans les fondations d'une maison à Rabat. – Compt. Rend. séan. mens. Soci. Sci. Nat. Maroc, **1**: 14-16; Rabat.
- EVANDER, R.L. (1989): Phylogeny of the family Equidae. In: D.R. PROTHERO & R.M. SCHOCH (eds.), The Evolution of Perissodactyls.: 109-127; New York, Oxford (Clarendon Press, Oxford University Press).
- FORSTÉN, A. (1986): A review of the Süssenborn horses and the origin of *Equus hydruntinus* Regalia. – Quartärpaläontologie, **6**: 43-52; Berlin.
- FORSTÉN, A. (1988): Middle Pleistocene replacement of stenorid horses by caballoid horses – Ecological implications. – Palaeogeogr., Palaeoclimat., Palaeoecol., **65**: 23-33, 2 tabs; Amsterdam.
- FORSTÉN, A. (1990): Old World "Asses". - Quartärpaläontologie, **8**: 71-78; Berlin.
- FORSTEN, A. & EISENMANN, V. (1995): *Equus (Plesippus) simplicidens* (COPE), not *Dolichohippus*. – Mammalia, **59** 1: 85-89; Paris.
- GERAADS, D., HUBLIN, J.-J., JAEGER, J.-J., TONG, H., SEN, S. & TOUREAU, P. (1986): The Pleistocene hominid site of Ternifine, Algeria: new results on the environment, age, and human industries. – Quatern. Res., **25**: 380-386; Washington.
- HARRINGTON, C.R. (1989): Pleistocene vertebrate localities in the Yukon. In: L.D. CARTER, T.D. HAMILTON &

- J.P. GALLOWAY (eds.), Late Cenozoic History of the Interior Basins of Alaska and the Yukon. – U.S. Geol. Surv. Circular, **1026**: 93-98; Washington.
- HOEPEN, E.C.N. VAN (1932): Die Stamlyn van die Sebras. – Paleontologiese Navorsing van die Nasionale Museum: 25-37; Bloemfontein (Museum Bloemfontein).
- HUXLEY, T.H. (1870): Address delivered at the anniversary meeting of the Geological Society of London, on the 18th February, 1870. – Proc. Geol. Soc. London.: 16-38; London (Taylor & Francis).
- LAZAREV, P.A. (1980): Antropogenovye Ioshadi Yakutii. – 190 pp.; Moscow (Nauka). (in Russian)
- MAUL, L.C., REKOVETS, L. HEINRICH, W.-D., KELLER, T. & STORCH, G. (2000): *Arvicola mosbachensis* (SCHMIDTGEN 1911) of Mosbach 2: a basic sample for the early evolution of the genus and a reference for further biostratigraphical studies. In: G. STORCH & K. WEDDIGE (eds.), Advances in Vertebrate Palaeontology. – Senckenb. Iethaea, **80** 1: 129-147; Frankfurt a. M.
- MORLAN, R.E. (1996): Late and middle Pleistocene vertebrate fossils from Old Crow Basin, Locality CRH 15, northern Yukon Territory. In: K. M. STEWART & K. L. SEYMOUR (eds.), Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals. Tributes to the Career of C.S. (Rufus) Churcher: 483-521; Toronto (University of Toronto Press).
- MUSIL, R. (1969): Die Equidenreste aus dem Pleistozän von Süßenborn bei Weimar. – Paläont. Abh., A **3** 3-4: 317-364, pls. XXXVII-XLV; Berlin (Akademie Verlag).
- OAKENFULL, E. A., LIM, H. N. & RYDER, O. A. (2000): A survey of equid mitochondrial DNA: Implications for the evolution, genetic diversity and conservation of *Equus*. – Conserv. Genetics, **1**: 341-355; Durham.
- OWEN, R. (1861): Palaeontology or a systematic summary of extinct animals. – 463 pp.; Edinburgh (Adam & Charles Black).
- PAVLOW, M. (1888): Etudes sur l'Histoire paléontologique des Ongulés. II. Le développement des Equidés. – Bull. Soc. Imp. Natural. Moscou, **1**: 1-80; Moscou.
- PROTHERO, D. R & SHUBIN, N. (1989): The evolution of Oligocene horses In: D. R. PROTHERO & R. M. SCHOCH (eds.), The Evolution of Perissodactyls.: 142-175; New York, Oxford (Clarendon Press, Oxford University Press).
- SHER, A.V. (1971): Mlekopitayushchie i stratigrafia Pleistotsena krainego severo-vostoka SSSR i severnoi Ameriki. – 310 pp.; Moskva (Nauka). (in Russian)
- SIMPSON, G.G. (1951): Horses. – 247 pp.; New York (Oxford University Press).
- THACKERAY, F. (1992): Isotopic analysis of equid teeth from Wonderwerk Cave, northern Cape Province, South Africa. – Palaeogeogr., Palaeoclimat., Palaeoecol., **99**: 141-150; Amsterdam.
- VEKUA, A.K. (1986): The Lower Pleistocene Mammalian Fauna of Akhalkalaki (Southern Georgia, USSR). – Palaeontogr. Ital., **74**: 63-96; Pisa.