Hipparions and the Mio-Pliocene boundary

Véra Eisenmann  
Institut de Paléontologie  
Museum Nat. d’Histoire Naturelle, Paris

Paul Sondaar  
Instituut voor Aardwetenschappen  
Rijksuniversiteit te Utrecht


ABSTRACT — The review of classical Pliocene forms (groups of Hipparion crassum, H. fissurae, H. rocinantis) shows that they do not occur before the upper Ruscinián, MN 15 zone. The model of hipparion’s characterization of the Mio-Pliocene boundary based on Mongolian data does not seem valid. In the lower Ruscinián of Europe, hipparions which are so abundant during the Miocene have virtually disappeared probably because the environment was too warm and moist. In Africa, where the passage from Miocene to Pliocene was smoother, autochthonous forms persisted at the Mio-Pliocene boundary. In North America, this boundary is marked by the extinction of tridactyl horses and the development of monodactyl or functionally monodactyl (Nannippus) equids, probably in relation to aridization. There is no reason to consider that Eurasian cabaloid hipparions are closely related to the North American Neohipparion, their similarities are probably the result of parallelism. The relation between Eurasian and African cabaloid hipparions is still open to discussion: neither parallelism nor migration can be excluded.


INTRODUCTION

There is no general agreement on the exact age of the Mio-Pliocene boundary. It could be as old as 5.3 MY (Berggren et al., 1985) or as young as 4.84 MY (Zygelveld et al., 1986). The data on hipparions strictly contemporary with this boundary are very scanty. One interesting exception is the Kirgis Nur Formation in Western Mongolia which is said to contain the Mio-Pliocene boundary and in which hipparions are abundant (Devyatkin, 1970). Zhgallo (1978) and Pevzner et al. (1982) proposed an age for the Kirgis Nur Formation mostly based on biostratigraphical correlation between mongolian and west european rodents and hipparions. As far as hipparions are concerned in the model used by Zhgallo, Pevzner and coauthors, the beginning of the Pliocene is characterized by the immigration of Neohipparion from North America into Asia, and the first appearance of Hipparion crassum in Europe possibly immigrating from Asia.

This kind of correlation is wholly dependent on a solid characterization of the taxa that are used as the reference for the model, and a careful identification of the compared species. In this paper, we will first consider what are Hipparion crassum, Neohipparion, and the other new, typically Pliocene, hipparions, and what are their supposed ages of appearance. We will next look more closely at the Western Mongolian model to see if it is valid. Afterwards, we will consider what happened to the North American hipparions at the Miocene--Pliocene boundary.

HIPPARION CRASSUM

Described by Depéret (1890), Hipparion crassum is not a very well known species. The upper cheek teeth are very plicated; the lower cheek teeth have a classical pattern. The most characteristic point about it is the extreme shortness of the third metacarpals which evoke the mountain adapted equids of South America. Three metacarpals from Perpignan, the type locality, are also very flat (the anteroposterior diameters are small) and wide (especially the distal end). The articular facet for the hamatum is very well developed (Text-fig. 1b). Let us remark that, due to an error in the captions, the proximal end of MCIII labeled H. crassum in fig. 1b of Depéret actually belongs to an Equus caballus, the proximal end of the H. crassum MCIII
being represented in fig. 1c with the caption *E. caballus*. Another important character of *H. crassum* is the relative development of the distal articular width of the MCIII (Text-fig. 2). The main fauna of Perpignan is placed in zone MN 15 by Mein (1975). There would be no special reason to discuss *H. crassum* in a paper dealing with the Mio-Pliocene boundary if this species had not been mentioned at Alcoy, in Spain (Alberdi, 1974; Alberdi, 1986) and at Ptolemais, in Greece (Koufos, 1982).

Alcoy is considered to belong to the MN 13 zone, or to a transitional MN 13 - MN 14 zone (Alberdi, 1986). According to Alberdi (1974, p. 106), the hipparion material is not very rich (12 teeth, a proximal fragment of MCIII and two phalanges) and not homogeneous (*H. gromovae*, a Turolian species is also recognized at Alcoy). The main evidence for *H. crassum* would be the proximal part of a metacarpal (Alberdi, 1974, pl. 7, fig. 1). In our opinion, this specimen does not prove the presence of *H. crassum* at Alcoy because the most significative character of the species, the shortness of the bone, cannot be ascertained. Moreover, the Alcoy MCIII has a very un-hipparion like morphology of the articular facet for the hamatum, which we have not seen in *H. crassum* specimens, but which is common in *Equus* (Text-fig. 1c). Also, the facet for the hamatum is not very well developed. The determination of *H. crassum* at Alcoy on the basis of the remaining material is, in our opinion, uncertain.

*H. crassum* was also described from the lignite deposits of the basin of Ptolemais (Koufos, 1982). Van de Weerd (1979) places the Ptolemais lignites in MN 14 zone. The presence of *Promimomys* together with *Hipparion* places the locality in a Ruscinian younger than Maritsa which is considered to belong to the base of MN 14 (De Bruijn, pers. comm.) The material is composed of a P⁴-P⁵ series, and a few limb bones. The P⁴ and P⁵ are not very plicated (about 6 plis on the P⁴ and 8 on the P⁵). Judging from Koufos illustration, the MCIII is large (about 228 mm in maximal length) but not very robust; the proximal end is much deeper than in *H. crassum* (Text-fig. 2); moreover the supra-articular distal width is very large, much larger than the distal articular width (Koufos, 1982, table 1). Another distal end of MCIII (conserved at Utrecht) has the same proportions. All these differences do not permit us to identify the Ptolemais hipparion with the typical *H. crassum*.

At Kirgis Nur, in levels 51-55, was found an hipparion referred to *H. sefiei*, and said to be close to *H. crassum*. The levels of Kirgis Nur containing *H. sefiei* are supposed to belong to the MN 14 zone (Pevzner & Vangenheim, 1986, fig. 3). The upper cheek teeth of this *H. sefiei* are rather large and plicated, as in *H. crassum*. But, according to fig. 53 given by Zhegallo (1978, p. 86), the MCIII does not look very much like the specimens from Perpignan. The Kirgis Nur MCIII is much more slender (Text-fig. 2), its distal articular end is not very developed, and the facet for the hamatum is rather small. It is always possible to consider that some phylectic relation existed between *H. crassum* and *H. sefiei* but the similarities are not so strong that they warrant a tight correlation between Kirgis Nur and Perpignan.

Thus, in none of the sites discussed above (Alcoy, Ptolemais, Kirgis Nur) can we be sure of the presence of *H. crassum*. One could even be tempted to consider *H. crassum* as a local hyperspecialized form, if a larger but morphologically very close hipparion had not been found at Çalta in Turkey, (Sen, Sondaar & Staesche, 1978, p. 378). The material from Çalta has been kindly shown to us by Sen. Çalta is referred to the Upper Ruscinian (Sen & Bruijn 1977, p. 224) and can be placed in MN 15 zone.

The same kind of large and robust Pliocene hipparion with very plicated teeth has been found at Malusteni and Iaras-Cariera in Romania (Samson 1975, p. 192-197). Both sites are Pliocene, Iaras being the younger. Pevzner & Vangenheim (1986, p. 14) suggest a lower MN 16 position for Malusteni because it belongs.
to the *Viviparus bifasciatus* mollusque zone, deposited during the Gilbert chron. In fact some recent chronological hypotheses place the MN 16 zone into the Gauss chron (De Giuli *et al*., 1983; Torre, 1987). Anyway, it may be that Pevzner and Vangenheim place Malusteni in such a high zone because they believe that *Equus* is present in the Malusteni-Beresti levels, which in our opinion is very doubtful. The teeth referred to *Equus simplonensis* (Samson, 1975, fig. 25) clearly belong to an *Equus caballus*, whose arrival in Europe at the beginning of MN 16 or earlier is most improbable. The first caballine horses do not exist anywhere, not even in North America, earlier than about 1 MY ago. The polyphyletic, pre-Pliocene, origin of this caballine horse suggested by Samson does not seem very likely either. Anyway, the measurements of MTIII given by Samson (1975, tabl. 8) show that *H. maultenense* from Malusteni is not very different from *H. crassum* from Perpignan, although slightly longer (Text-fig. 3); Samson himself noted the similarities between the two forms. The younger MTIII from Iaras referred to *H. cf. maultenense* is much more robust and looks more like the Calta hipparion.

As already noted by Zhgallo (1978, p. 90), to the same *H. crassum* group belongs *H. tbicoicum* from Chamar and Beregovaja (Mongolia and Transbaikalia). The Formation of Tchikoisk is younger than the Kirgis Nur Formation and could be about 3 to 4 MY old.

**Text-fig. 2** - Ratio diagrams of *H. crassum* MCIII from the type locality (France) and of *H. sp. MCIII* from Ptolemais (Greece), and Kirgis Nur (Mongolia); 1) maximal length, 3 and 4) width and depth at mid-diaphysis; 5 and 6) proximal articular width and depth; 7 and 10) distal widths, supra-articular and articular, 12) depth of the distal keel; 13 and 14) minimal and maximal depths of the medial condyle; 7) width of the facet for the magnum, 8) width of the facet for the hamatum, (see Eisenmann & Beckenche, 1986).

**Text-fig. 3** - Ratio diagrams of *H. crassum* and *H. cf. crassum* MTIII from the type locality (France), Chamar and Beregovaja (Mongolia and Transbaikalia), Iaras-Cariera and Malusteni (România). Same measurements as in Text-fig. 2 but: 7) width of the facet for the large cuneiform, and 8) width of the facet for the small cuneiform.
(Zhegallo, 1978, p. 138; Pevzner et al., 1982, fig. 3). Although *H. tchicoicum* (Text-fig. 3) is more slender, the similarities between its MIII, measured by one of us, and those of Çalta are striking.

To summarize, *H. crassum* and a closely related form are undoubtedly present at Perpignan (France) and Çalta (Turkey) and can be considered as characteristic of zone MN 15. Related forms, possibly younger, are very probably present in Romania and Mongolia. There is no solid evidence for any earlier presence of *H. crassum*, at the Mio-Pliocene transition at Alcoy (Spain) nor in the lower Ruscian of Ptolemais (Greece), or Kirgis Nur (Mongolia).

**HIPPARION FISSURAE** (Text-fig. 4)

*H. fissurae* from Layna, Spain, (Crusafont & Sondaar, 1971) is a middle sized rather hypsodont hipparion, with long and very slender metapodials. The lower cheek teeth have a classical hippocarnine pattern (Alberdi, 1972, fig. 113). Layna belongs in the zone MN 15 (Mein, 1975).

Metapodials as slender as those of *H. fissurae* are very rare. *H. longipes* from Pavlodar has metapodials of about the same size and the same slenderness (Text-fig. 4), but the indifferent state of preservation of *H. fissurae* does not allow precise comparisons. Pavlodar is believed to belong to Magnetic Chron 6 and is placed in MN zone 12 by Pevzner and Vangenheim (1984, p. 76, tabl. 3).

Heintz, Ginsburg and Sen (1974) have referred to *H. longipes* a larger but also very slender MT III from Çalta (MN zone 15). Another MIII, from Karaburun, Macedonia (Greece), certainly belongs to the same taxon; Karaburun is believed to belong to zone MN 14 or MN 15 (Sondaar & de Brujin, 1979, p. 1123).

Thus, the characteristic dolichopodial Pliocene hipparions are not found at the Mio-Pliocene boundary, but mostly in MN 15 zone, with the possible exception of La Gloria 4, Teruel basin, Spain, (base of MN 14) where a *Promimomys* and a slender hipparion were found together (Mein, pers. comm.).

**THE NEOHIPPARION PROBLEM**

If correlations are to be made between New and Old World “neohipparions” on the basis of possible migrations (Zhegallo, 1978; Forstén 1984a), it seems quite important to determine what sort of “neohipparions” have migrated, and when they did so. And, most important of all, to make sure that the alleged similarities between New World and Old World “neohipparions” did not result from parallel evolution. Therefore we will try to define and compare precisely some morphologies observed in Old World and New World “neohipparions”.

1. **OLD WORLD NEOHIPPARIONS IN GENERAL, AND EURASIAN FORMS**

When the name *Neohipparion* is used to define an Old World species, it usually implies a large, derived form of tridactyl horse, with caballoid lower cheek teeth. At all events caballoid cheek teeth do characterize the Eurasian species *H. boujenense*, *H. rocinantis*, or *H. crusafonti* and several African species. The term “caballoid” is used to describe the shape of the double knot (Eisenmann, 1977, fig. 1) where a broad lingual valley separates pointed metaconids and metastylids. Apart from this point, the lower teeth of these hipparions are characterized by rounded protoconids and hypoconids, moderately developed pis caballinid, and
in most of the cases, a deep vestibular groove on the molars (Text-fig. 5c). However, during the evolution of the African forms, the vestibular groove tends to become more shallow, first on the M₁, later on the M₂ and M₃ as well (Eisenmann, 1977, p. 75). As far as Eurasian forms are concerned, there can be no question about their very close relation because there is no denying the extraordinarily similar although original, pattern of their cheek teeth. Old World “neohippopartians” are easily recognizable when lower cheek teeth are known.

*H. rocinantis* was described from La Puebla de Almoradier, Spain, on the basis of a small sample. It comes from an uncertain level, which has been successively considered as Turolian or possibly Ruscician (Alberdi, 1974, p. 100 and 120), Ruscian (Alberdi & Gabunia, 1985), and Lower Villafranchian, MN zone 16a, (Alberdi, 1986). The M₁ figured by Alberdi (1974, pl. 6, fig. 5) has a rather deep vestibular groove.

*H. crusafonti* was described on the basis of much better material from Villaroya (Villalta, 1952). Because the teeth are similar *H. crusafonti* has been put into synonymy with *H. rocinantis*, from which it may differ only at a subspecific level (Alberdi, 1974, p. 101). At any rate, on the M₁ of the series figured by Villalta (1952, pl. 19, fig. 3), the vestibular groove is shallower than on the specimen from La Puebla de Almoradier. This could provide evidence of a younger age for Villaroya. Villaroya is believed to belong in the MN 16a zone, Lower Villafranchian. (Alberdi, 1986).

To the same species can be referred the hippoparion of Roccaseyre although the metapodials were probably slightly smaller. The teeth are unknown. If all the material comes indeed from the same place, Roccaseyre would probably be the youngest site of all, because at Roccaseyre, lower cheek teeth of *Equus stenonis* are associated with *H. crusafonti* metapodials (Eisenmann & Brunet, 1973).

To *H. crusafonti* were referred fossils from Kvabei, a Georgian site in the USSR (Vekua, 1952). The lower cheek teeth of the figured series (Vekua, 1952, fig. 2) are quite caballoid. They differ from those of Villaroya by the shallow vestibular grooves on all their molars and by the higher frequency of isolated protostylics. The M₁₁ has a wider but less deep diaphysis than at Villaroya and Roccaseyre. It is likely that the Kvabei fossils represent a species more derived than *H. crusafonti* from Villaroya, although both sites are placed in the MN 16 zone (Pevzner & Vangenheim, 1986; Alberdi, 1986).

Caballoid lower cheek teeth were also described from China and Mongolia under the name of *H. boufenense*. A skull with the associated lower jaw was collected at Loc. 26, Yushe Basin, Shansi (Qiu *et al.*, 1980). The vestibular grooves are deep on the M₁ and M₂, but shallow on the M₃; protostylics are well developed but not isolated (perhaps because the teeth are rather worn). Judging from the morphology of the teeth (Text-fig. 5c), this hippoparion is less derived than the one from Kvabei, and approximately at the same stage as the one from Villaroya. According to Forstén (1984b) typical *Neohipparion boufenense* are upper Ruscian-lower Villafranchian.

The teeth from Kirgis Nur levels 37-40 and 51-55 (Zhegallo, 1978, fig. 75) referred to *H. boufenense* are caballoid but are primitive in the depth of the vestibular groove on the molars. Protostylics are not isolated. As has already been mentioned, Kirgis Nur levels 37-40 are supposed to belong to the base of MN zone 14 (Pevzner & Vangenheim, 1986, fig. 3). We will discuss that assumption later.

Zhegallo (1978, fig. 74) refers some material from the younger sites of Chamar and Beregovaja to a more evolved form of *H. boufenense*. Lower cheek teeth and metapodials (which he kindly showed to one of us and allowed to measure) are very different from the previously discussed species. The metatarsals look rather like those from Roccaseyre but they are much larger and have wider proximal ends. The lower cheek teeth are caballoid with rather flattened protoconids and hypoconids, complicated plis caballiniid and tend to have shallow vestibular grooves on the molars.

Could all these forms, or some of them, be related to the North American neohippopartians?

2. NEW WORLD NEOHIPPARIONS

The diagnosis of *Neohipparion* given by Forstén (1984a, p. 169) mentions in first place the caballoid lower cheek teeth. The genotype, *Neohipparion whitneyi*, synonymised with *N. affine* by MacFadden (1984, p. 75) is a Clarendonian species which disappears around 8.5 MY (MacFadden, 1984, p. 186), at the beginning of the Hemphillian. From fig. 47 of MacFadden (1984), it may be seen that its lower cheek teeth are not caballoid (Text-fig. 5a).

Caballoid cheek teeth begin to occur only in early Hemphillian “neohippopartians”. So that, as so often happens in paleontology, the question arises as to what extent the limits of a taxon may be stretched in order to include, not only the typical forms, but also their possible descendants or ancestors.

Anyway the Hemphillian “neohippopartians” may, or may not, be the descendants of *N. whitneyi*, but it is among them that the “caballoid” type develops. It achieves its most evolved and original pattern in the late Hemphillian forms, referred to *N. eurystyle* (MacFadden, 1984, fig. 83; Stirton, 1955, fig. 5). The late Hemphillian Yepomera locality has been dated to 4.8 MY (Berggren *et al.*, 1985, p. 249).

Are these New World caballoid teeth similar to Old
World ones? The lingual valley is indeed very broad and the metaconids and metastylids show a tendency to be pointed, but in other characters, these lower cheek teeth are quite different from most of the Old World ones (Text-fig. 5b). The protoconids and hypoconids tend to have straight vestibular walls (instead of rounded ones), the plis caballinid tend to be extraordinary developed and complicated, and the vestibular grooves are shallow even in the molaris. Although “caballoid” and “evolved”, the New World “neohipparians” do not seem at all identical to the Old World “caballoid” and “evolved” H. bouchenense or H. rocicnantis. Even the early Hemphilidian N. leptode (MacFadden, 1984, fig. 77) is too “evolved” to have given rise to Old World “neohipparians”. The only Old World hipparion looking a little like a North American Neohipparion is the “late H. bouchenense” from Chamar and Beregovaja (Zhegallo, 1978, fig. 74) but even there, the morphology is not quite similar. Besides, as we will see later, neohipparians had disappeared from North America by the probable time of Chamar and Beregovaja.

All the derived characters displayed by neohipparians appear time and time again among equids. The very names of “caballoid” double knot and “pli caballiniid” refer to characters distinguishing Equus caballus from other species of the genus. In Equus caballus also, the protoconids and hypoconids tend to acquire flattened vestibular walls. African Plio-Pleistocene stylohipparions tend to develop large and complicated ectostylids which may be considered as equivalents of the large and complicated plis caballinids of neohipparians; they also acquire (but much later) shallow vestibular grooves on the molaris.

To summarize the caballoid New World neohipparians cannot be considered as the group from which the caballoid Old World hippiparions originated. Not-yet-caballoid New World neohipparians could be ancestral to them but their not-yet-derived morphology would make them very hard to recognize; it would therefore be unwise to use them for precise correlations. A parallel development of derived characters in New World neohipparians and in Old World hippiparions, as considered by MacFadden (1984, p. 188) seems at the moment to be the most reasonable hypothesis.

3. AFRICAN CABALLOID HIPPARIONS

African derived caballoid hippiparions are often referred to by the name “stylohipparions” because of the particular development of isolated and sometimes very large and complicated ectostylids on their permanent lower cheek teeth. But the development of ectostylids and the caballoid shape are not linked: clearly caballoid teeth without ectostylids do exist.

If African caballoid hippiparions result from an eurasian migration, a matter of interest is to discover when caballine lower cheek teeth appeared in Africa? It is not easy to answer this question because of the lack of material, contradictory evidences, and uncertainties about the ages of relevant sites. The Quartzose Sand and the Pelletal Phosphorite Members of the Varswater Formation (Langebaanweg E Quarry) are especially interesting because they have deposited during the early Pliocene transgression (Hendey, 1981) but no clear answer is to be found there: some lower cheek teeth look caballoid while the morphology is not so clear in others. Another interesting site is Lothagam. The hipparion skull found there is a nearly exact replica of a Pakistani skull from Dhok Pathan (Eisenmann, 1982, fig. 5). But there are only a few lower teeth, some of which have a rather caballoid morphology, but not

![Text-fig 5 - Lower left cheek teeth series of equids. 5a: Neohippoparion affine (Clarendonian, redrawn from MacFadden, 1984, fig. 47); 5b: Neohippoparion eurystyle (Late Hemphilidian, redrawn from MacFadden, 1984, fig. 80); 5c: Hippoparion bouchenense (Lower Villafranchian, loc. 26, Yushe Basin, Shansi).]
clearly so. Furthermore, the Lothagam fauna may be representative of a relatively long span of time (Hendy, 1981). Thus, Africa does differ from Eurasia, where there is usually no problem to recognize if a lower cheek tooth is caballine or not.

What is sure is that cabaloid lower cheek teeth are constant from about 3-4 MY up (Kubi Algi Formation; Koobi Fora Formation below the Hasuma Tuff; Laetoli; Hadar Formation; Kanapoi; Ekora; Chemeron). Therefore, the appearance of cabaloid cheek teeth is broadly contemporarily in Eurasia and Africa. It is sure also that skulls of evolved African hipparions (H. afarensis, *H. cornelianum*) look like the skull of *H. boufenense* (Eisenmann, 1981; 1982) but there is no clear evidence for a brusque invasion of cabaloid forms replacing or coexisting with, more primitive ones. Actually, the very fact that it is difficult to define some teeth as cabaloid or not, may be evidence for an African parallel evolution of the cabaloid trend.

THE WESTERN MONGOLIAN MODEL

1. BIOSTRATIGRAPHY

The Western Mongolian Kirgis Nur Formation is very interesting because it may contain the Mio-Pliocene boundary and because it is rather rich in *Hipparion* fossils. An extensive geological description of Kirgis Nur and other Western Mongolian Neogene formations was done by Devyatkin (1970).

The hipparions were studied by Zhegallo (1978) in his monograph on “The Hipparions of Central Asia”. Zhegallo has placed the boundary between the Pontian and Kimmerian, i.e. the boundary between the upper Miocene (Turolian) and lower Pliocene (Ruscinian), at level 37. Levels situated below are characterized by the association of different subspecies of *Hipparion theobaldi* with *Hipparion elegans*. The upper levels are characterized by the first appearance of *Neohippoparion boufenense*, the evolution of *H. theobaldi platyodus* into *H. sefvei*, and of *H. elegans* into *H. parvum*. *H. theobaldi platyodus* is considered as the possible ancestor for the European *H. crassum*, and the most primitive form of *N. boufenense*, as the possible ancestor for the European *N. rocinantis*. In 1978, Zhegallo had no way other than paleontology to date the Kirgis-Nur Formation. Therefore, when he proposed an age of 5 to 6 MY for the Mio-Pliocene boundary, it was because of the supposed equivalent ages of Alcoy (first *H. crassum*) and La Puebla de Almoradí (first *H. rocinantis*) suggested by Alberdi (1974, p. 120). Let us note however the difference between what seems to occur in Europe, from what happens in the Kirgis Nur formation where the “rocinantis-like” *N. boufenense* appears more than 15 meters below the “crassum-like” *H. sefvei* (Zhegallo, 1978, p. 15, fig. 10).

A subsequent paper (Pevzner et al., 1982) discuss the age and correlations of the Kirgis Nur Formation using biostratigraphical and paleomagnetic data. Pevzner and his co-authors accept the same age (upper Turolian or lower Ruscinian) for Alcoy and La Puebla de Almoradí (again basing themselves on the work of Alberdi, 1974). Both sites should be close to the end of the Messinian and, therefore, about 5.2 MY old. Since *H. sefvei* and *N. boufenense* are considered as equivalents of *H. crassum* (Alcoy) and *N. rocinantis* (La Puebla de Almoradí), the upper part of the Kirgis-Nur Formation which contains the most primitive forms of *H. sefvei* and *N. boufenense* cannot be younger than 5.2 MY. The Ruscinian age of the upper levels is confirmed by the appearance of *Orientatalomys* sp. and *Microtodon atavus* at level 37 (Pevzner et al., 1982, p. 13, fig. 1). Five meters below, in levels 20-24 was found an *Occitanomys* close to *O. adroveri*, indicating an uppermost Turolian age. The first *H. sefvei*, in levels 51-55, falls inside a positive magnetic period which the authors suppose immediately underlies the Gilbert Chron. The first *N. boufenense*, in levels 37-40 also falls inside a positive magnetic period, probably the same one although a negative episode is found between the first *H. sefvei* and the first *N. boufenense* levels.

In a more recent paper, Pevzner & Vangenheim (1986, p. 10) again propose an age of 5.5 to 5.6 MY for the lower limit of the “Ruscinian” in the Kirgis Nur Formation. In their opinion, the Ruscinian is characterized (as far as hipparions are concerned) by the immigration of *Neohippoparion* into the Old World, and of *H. crassum* into Europe. Levels 37-40 of Kirgis Nur, where the first *N. boufenense* are found, are considered as contemporaneous with Alcoy, where the first *H. crassum* was found.

2. DISCUSSION

As far as hipparions are concerned, the model proposed by Pevzner & Vangenheim (1986) implies: 1) the presence of *H. crassum* at Alcoy; 2) a close similarity between *H. crassum* and *H. sefvei*; 3) the contemporaneity between Alcoy (first *H. crassum*) and La Puebla de Almoradí (first *H. rocinantis*); 4) a close similarity between the North American neohippparions and the earliest *H. boufenense* from Kirgis Nur; 5) a close similarity between *H. boufenense* and *H. rocinantis* from Europe. As far as rodents are concerned, the model implies: 1) a Ruscinian age for *Orientatalomys* and 2) a Turolian age the “adroveri-like” *Occitanomys*.

A careful examination of these basic assumptions shows that most of them are not reliable: 1) the presence of *H. crassum* is not proven at Alcoy, nor even in
the lower Ruscinian MN 14; 2) the similarity between *H. crassum* and *H. sevex* from Kirgis Nur is not very close; 3) the contemporaneity of Alcoy and La Puebla de Almoradier is doubtful, since the last site is presently placed in zone MN 16, while the first may be as old as MN 13-MN 14; 4) there is no really close similarity between North American neohippnians and the *H. bounfenense* from levels 37-40 of Kirgis Nur. Point 5 is probably true: there does seem to exist a close similarity between the Kirgis Nur *H. bounfenense* and the European *H. rocinantis*.

For the rodents, we must point out that "adroveri-like" *Occitanomyx* have been found not only in Turolian but also in Ruscinian sites (Sen & Heintz, 1977; Agusti, 1986; Aguilar, De Bruijn, Mein; comm. pers.). If the Kirgis Nur levels 37-40 contain the same kind of *Occitanomyx* they could still be as young as the upper Ruscinian.

### Table

<table>
<thead>
<tr>
<th>MN</th>
<th>MY</th>
<th>AFRICA</th>
<th>EURASIA</th>
<th>AMERICA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>1</td>
<td></td>
<td>EQUS</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* "ERASSUM" GROUP  △ SLENDER GROUP  ■ CABALLOID GROUP

---

Text-fig. 6 - Mio Pliocene tridactyl horses from the New and Old Worlds. Asterisks: *H. crassum* and *H. cf. crassum*. White triangles: *H. longipes*, *H. fissurae*, and *H. cf. fissurae*. Black quadrates: Caballoid tridactyl horses. KB = Karaburun; Langeb. E = Langebaanweg E. Monodactyl horses (*Equus*) and functionally monodactyl horses (*Nannippus*) have also been represented. *E. c.* = *Equus caballus*.

The good record of fossil Mammals in the late Hemphillian of North America shows faunal changes and extinctions. Webb (1984) correlates them with the termination of a glacial cycle at the end of the Messinian. Unlike the Mediterranean, where a moist climate may be reconstructed in the early Pliocene (Zagwijn & Suc, 1983, p. 111), in contemporaneous North America mammal faunas we see better adaptation to arid conditions. The faunal turnover can be traced very well in North American fossil horses.

**NORTH AMERICAN HIPPARIONS**

The tridactyl horses are not only decimated in quantity but also in diversity. In the early Hemphillian, about 8.5 MY ago, there are about 5 genera of tridactyl horses. At the end of the Hemphillian in Yepomera, Chihuahua, Mexico, dated at 4.8 MY (May & Repenning, 1982) only one of these 5 genera is left. On the other hand, there appears a very small hipparion-like
horse: Nannippus. The sudden appearance of this genus in the late Hemphillian is clouded by the practice of assigning some small isolated molars of Clarendonian and early Hemphillian age without diagnostic characters to Nannippus. This is the case for the upper cheek teeth referred to Nannippus retrusus by Stirton (1940, figs. 34-35) and the upper cheek teeth referred to Nannippus minor by MacFadden (1984, fig. 96).

Both Nannippus and Neobipparion have extremely hypsodont cheek teeth. The locomotion of the tridactyl Nannippus was very specialized and it was probably functionally monodactyl (Sondaar, 1968). In contrast, Neobipparion metapodials show a slightly developed sagittal keel usual in geologically older, tridactyl, forms. Out of 50 MCIII from Yepomera loc 275 present in the Los Angeles County Museum, 43 are from the monodactyl genera Astrobius and Dinobippus, 6 are from Neobipparion and 1 from Nannippus. These numbers demonstrate the dominance of monodactyl horses. The hypsodont teeth suggest that the four genera were feeding on the same type of vegetation but they must have occupied different habitats. The functional tridactyl locomotion of Neobipparion would have been more effective on soft sandy or muddy soil (Sondaar, 1968).

In the Blancan fauna which may be well correlated with the Pliocene, Neobipparion is no longer present. Nannippus is represented by a species somewhat larger than N. minor from the late Hemphillian. Thus, at about the Mio-Pliocene boundary, took place the extinction of the last true North American tridactyl horse, Neobipparion. This represented the end of more than 10 MY in the history of a very successful group in North America. Nannippus survived until the end of the Blancan (MacFadden, 1984, p. 186).

CONCLUSIONS

In Text-figure 6 we have tried to give a general view of what we know about the hipparions discussed in this paper.

Clearly, hipparions safely referable to the lower Ruscinian (zone MN 14) are dramatically rare in Europe. They are so poorly known, that even when a few good fossils exist (Ptolemais), their correlation is impossible because no other similar forms have been described. In South Africa, a possibly endemic form is known at Langebaanweg E. At an older level, a correlation may be possible between the Lothagam Hipparion turkenense and a form from Dhok Pathan, Pakistan. In Asia, hipparions may exist around the Mio-Pliocene boundary but we do not have enough data to characterize and correlate them. It is only in North America that the history of hipparions at the Mio-Pliocene boundary is quite clear: tridactyl Neobipparion disappear; functionally monodactyl Nannippus develops.

Pliocene hipparions again become relatively abundant and frequent during zone MN 15 (upper Ruscinian). The detailed study of the metapodials allows good correlations between the very massive forms of the H. crassum group (small size at Perpignan and Malusteni; large size at Ibaras, huge size at Çalta and Changar). Correlations are also possible between the very slender and very large hipparions of Çalta and Karaburun, and possibly the smaller but very slender form of Layna. The third group is even easier to recognize because both metapodials and lower cheek teeth are very characteristic: it is the group of caballoid hipparions represented in Asia and Europe. This group does not seem to be related to the North American nehipparions. Its relation with the African cabaloid group is not yet clear. Many characters considered as synapomorphic may have resulted from parallel evolution.

If we try to relate what is known of these Mio-Pliocene hipparions with environmental changes, it appears that these were not identical everywhere. In North America an aridization led to the development of monodactyl horses and the extinction of the tridactyl forms. In Europe, the warm and moist conditions at the base of the Pliocene were probably not favorable to hipparions so it seems that they have all but disappeared. In Africa, hipparion fossils at that time are also very rare an exception being the South African site of Langebaanweg. But Africa differs from Europe and North America by a relatively "smooth transition between the Miocene and the Pliocene faunas" (Cooke, 1982, p. 20) which would account for the survival of hipparions at a time when they seem to vanish from Europe.

REFERENCES

—, 1974, El genero Hipparion en Espana: Trabajos sobre Neogene- Cuaternario: 146 pp., 26 figs., 7 pls, 56 tab.
Crusafont, M. & Sondaar, P.Y., 1971, Une nouvelle espèce d'Hip-


— & Vancenheim, E.A., 1984, Sootnoshenie kontinenal'nnoj shkaly pozdnego miotsena zapadnoj Evropy so stratigrafijskimi shkalamis srednezemnomor'ja i vostochnogo paratateta: Izves-

(tia A.N. SSSR, serija geologicheskaja, (5): 69-78, 4 tab.


—, 1955, Two new species of the equid genus Neophippotam from the middle Pliocene, Chihuahua, Mexico: J. of Paleontology, 29 (5): 886-902, 7 figs., 4 tab.


(mscript received March 31, 1988 accepted April 30, 1988)

Vera EISEN Mann

UA 12 du CNRS, Institut de Paléontologie 8 rue Buffon 8, 75005 Paris, France

Paul Y. Sondaar

Institutit van Aardwetenhsappen

Budaelpaas 4, 3508 TA Utrecht, Nederland