

Hipparions and the Mio-Pliocene boundary

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ABSTRACT — *The review of classical Pliocene forms (groups of *Hipparion crassum*, *H. fissurae*, *H. rocinantis*) shows that they do not occur before the upper Ruscinian, 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 Ruscinian 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 Eurasiatic caballoid hipparions are closely related to the North American Neohipparion, their similarities are probably the result of parallelism. The relation between Eurasiatic and African caballoid hipparions is still open to discussion: neither parallelism nor migration can be excluded.*

RIASSUNTO — [Gli hipparion e il limite Mio-Pliocene] — *La revisione delle forme classiche del Pliocene (gruppi dell'*Hipparion crassum*, *H. fissurae*, *H. rocinantis*) mostra che essi non sono presenti prima del Rusciniiano superiore, zona MN 15. Non sembra valido il modello di definizione del limite Mio-Pliocene sulla base degli hipparion costruito sui dati della Mongolia. Nel Rusciniiano inferiore dell'Europa gli hipparion, così abbondanti durante il Miocene, sono praticamente spariti forse a causa dell'ambiente troppo caldo e umido. In Africa, dove il passaggio da Miocene a Pliocene è più graduale, forme autoctone persistono senza grandi cambiamenti. In Nord America il limite Mio-Pliocene è segnato dall'estinzione dei cavalli tridattili e dallo sviluppo di equidi monodattili o, come *Nannippus*, funzionalmente monodattili. Questi eventi sono probabilmente in relazione con un aumento dell'aridità. Non vi è motivo di credere che gli hipparion caballoidi eurasiatici siano strettamente imparentati con Neohipparion del Nord America: le loro somiglianze sono probabilmente dovute a parallelismi. Le relazioni fra gli hipparion caballoidi Eurasiatici e Africani sono ancora in discussione: non possono essere escluse né migrazioni né parallelismi.*

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 (Zydeveld *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). Zhegallo (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 Zhegallo, 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 con-

sider what are *H. 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 significant 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.

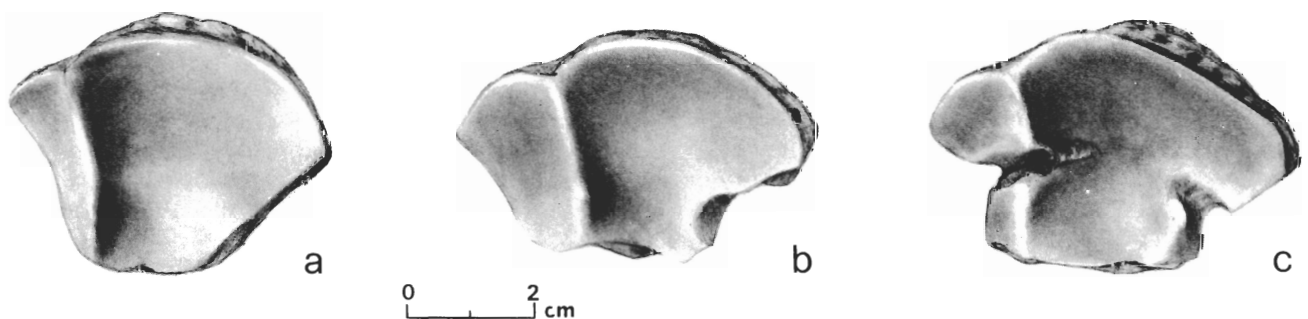
H. crassum was also described from the lignite deposits of the basin of Ptolemais (Koufos, 1982). Van de Weerd (1979) places the Ptolemais lignites in MN 14 zone. The presence of *Promimomys* together with *Hipparion* places the locality in a Ruscinian younger than Maritsa which is considered to belong to the base of MN 14 (De Bruijn, pers. comm.) The material is composed of a P¹-P³ series, and a few limb bones. The P² and P³ are not very plicated (about 6 plis on the P² and 8 on the P³). 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*.

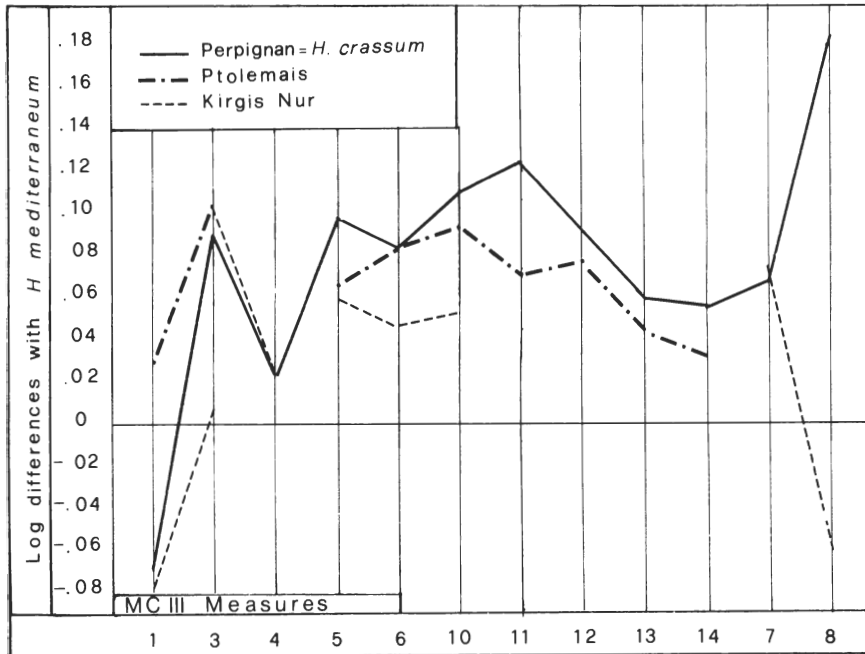
At Kirgis Nur, in levels 51-55, was found an hipparion referred to *H. sefvei*, and said to be close to *H. crassum*. The levels of Kirgis Nur containing *H. sefvei* are supposed to belong to the MN 14 zone (Pevzner & Vangenheim, 1986, fig. 3). The upper cheek teeth of this *H. sefvei* are rather large and plicated, as in *H. crassum*. But, according to fig. 53 given by Zhegalov (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 phyletic relation existed between *H. crassum* and *H. sefvei* 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



Text-fig. 1 - Proximal views of equid left MC III. 1a: *Hipparion mediterraneum* (Pikermi); 1b: *Hipparion crassum* (Perpignan), 1c: *Equus caballus* (from Deperet, 1890, fig. 1)

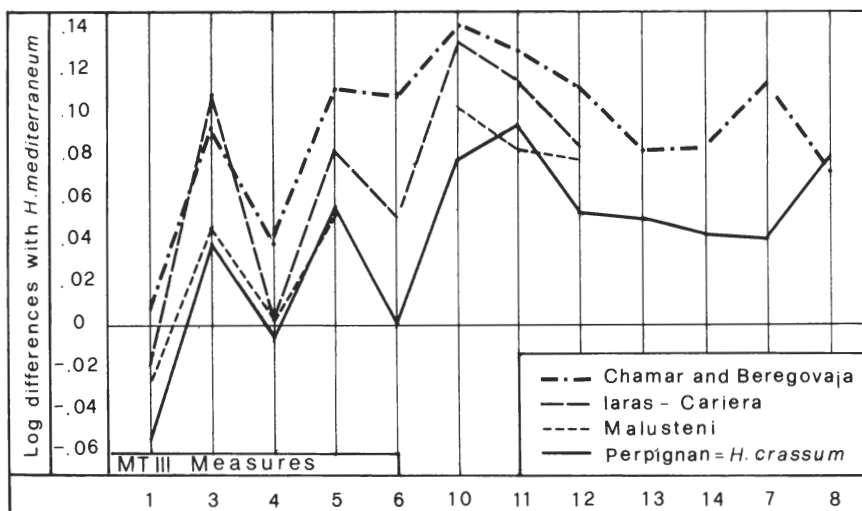


Text-fig. 2 - Ratio diagrams of *H. crassum* MCIII from the type locality (France) and of *H. sp.* MCIII from Ptolemais (Greece), and Kirgis Nur (Mongolia); 1) maximal length, 3 and 4) width and depth at mid-diaphysis; 5 and 6) proximal articular width and depth; 10 and 11) distal widths, supra-articular 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 & Beckonche, 1986).

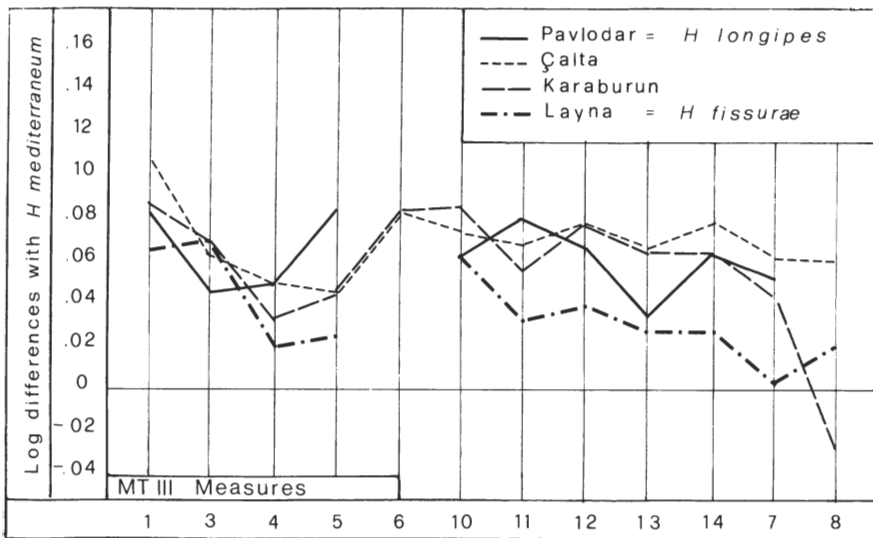
to the *Viviparus bifarcinatus* mollusque zone, deposited during the Gilbert chron. In fact some recent chronological hypotheses place the MN 16 zone into the Gauss chron (De Giuli *et al.*, 1983; Torre, 1987). Anyway, it may be that Pevzner and Vangenheim place Malusteni in such a high zone because they believe that *Equus* is present in the Malusteni-Beresti levels, which in our opinion is very doubtful. The teeth referred to *Equus simionescui* (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. malustenense* 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. malustenense* is much more robust and looks more like the Çalta hipparion.

As already noted by Zhegallo (1978, p. 90), to the same *H. crassum* group belongs *H. tchicoicum* 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. 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 (Romania). 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.



Text-fig. 4 - Ratio diagrams of MTIII of *H. fissurae* from the type locality (Spain), *H. longipes* from the type locality (USSR), and of *H. cf. longipes* from Çalta (Turkey) and Karaburun (Greece). Same measurements as in Text-fig. 3.

(Zhegallo, 1978, p. 138; Pevzner *et al.*, 1982, fig. 3). Although *H. tchicoicum* (Text-fig. 3) is more slender, the similarities between its MTIII, 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 Ruscinian 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 hipparionine 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 MTIII, from Karaburun, Macedonia (Greece), certainly belongs to the same taxon; Karaburun is believed to belong to zone MN 14 or MN 15 (Sondaar & de Bruijn, 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 EURASIATIC 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 Eurasiatic species *H. boufenense*, *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 plis 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 M_3 , later on the M_1 and M_2 as well (Eisenmann, 1977, p. 75). As far as Eurasiatic 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 "neohipparions" 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 Ruscinian (Alberdi, 1974, p. 100 and 120), Ruscinian (Alberdi & Gabunia, 1985), and Lower Villafranchian, MN zone 16a, (Alberdi, 1986). The M_3 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 M_3 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 hipparion of Roccaneyra although the metapodials were probably slightly smaller. The teeth are unknown. If all the material comes indeed from the same place, Roccaneyra would probably be the youngest site of all, because at Roccaneyra, lower cheek teeth of *Equus stenonis* are associated with *H. crusafonti* metapodials (Eisenmann & Brunet, 1973).

To *H. crusafonti* were referred fossils from Kvabebi, 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 protostylids. The MTIII has a wider but less deep diaphysis than at Villaroya and Roccaneyra. It is likely that the Kvabebi 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 M_1 and M_2 but shallow on the M_3 ; protostylids are well developed but

not isolated (perhaps because the teeth are rather worn). Judging from the morphology of the teeth (Text-fig. 5c), this hipparion is less derived than the one from Kvabebi, and approximately at the same stage as the one from Villaroya. According to Forstén (1984b) typical *Neohipparion boufenense* are upper Ruscinian-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. Protostylids 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 Roccaneyra but they are much larger and have wider proximal ends. The lower cheek teeth are caballoid with rather flattened protoconids and hypoconids, complicated plis caballinid and tend to have shallow vestibular grooves on the molars.

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

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 "neohipparions". 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 "neohipparions" 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 extraordinarily developed and complicated, and the vestibular grooves are shallow even in the molars. Although "caballoid" and "evolved", the New World "neohipparions" do not seem at all identical to the Old World "caballoid" and "evolved" *H. boufenense* or *H. roci-nantis*. Even the early Hemphillian *N. leptode* (MacFadden, 1984, fig. 77) is too "evolved" to have given rise to Old World "neohipparions". The only Old World hipparion looking a little like a North American Neohipparion is the "late *H. boufenense*" from Chamar and Beregovaja (Zhegallo, 1978, fig. 74) but even there, the morphology is not quite similar. Besides, as we will see later, neohipparions had disappeared from North America by the probable time of Chamar and Beregovaja.

All the derived characters displayed by neohipparions appear time and time again among equids. The very names of "caballoid" double knot and "pli caballinid" 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 neohipparions; they also acquire (but much later) shallow vestibular grooves on the molars.

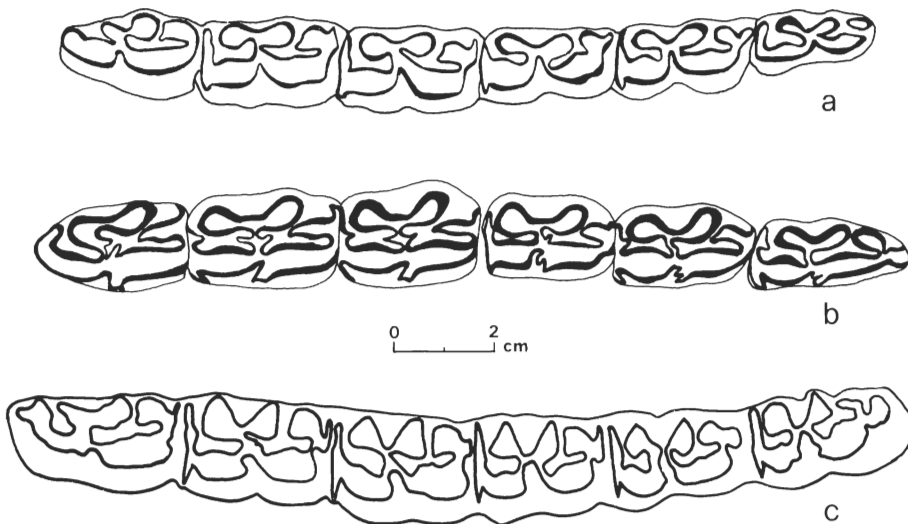
To summarize the caballoid New World neohipparions cannot be considered as the group from which

the caballoid Old World hipparions originated. Not-yet-caballoid New World neohipparions 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 neohipparions and in Old World hipparions, as considered by MacFadden (1984, p. 188) seems at the moment to be the most reasonable hypothesis.

3. AFRICAN CABALLOID HIPPARIONS

African derived caballoid hipparions 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 hipparions 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: *Neohipparion affine* (Clarendonian, redrawn from MacFadden, 1984, fig. 47); 5b: *Neohipparion eurystyle* (Late Hemphillian, redrawn from MacFadden, 1984, fig. 84); 5c: *Hipparion boufenense* (Lower Villafranchian, loc. 26, Yushe Basin, Shansi).

clearly so. Furthermore, the Lothagam fauna may be representative of a relatively long span of time (Hendey, 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 caballoid 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 caballoid cheek teeth is broadly contemporary 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 caballoid forms replacing or coexisting with, more primitive ones. Actually, the very fact that it is difficult to define some teeth as caballoid or not, may be evidence for an African parallel evolution of the caballoid 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 *Neohipparion 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 Almoradier (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).

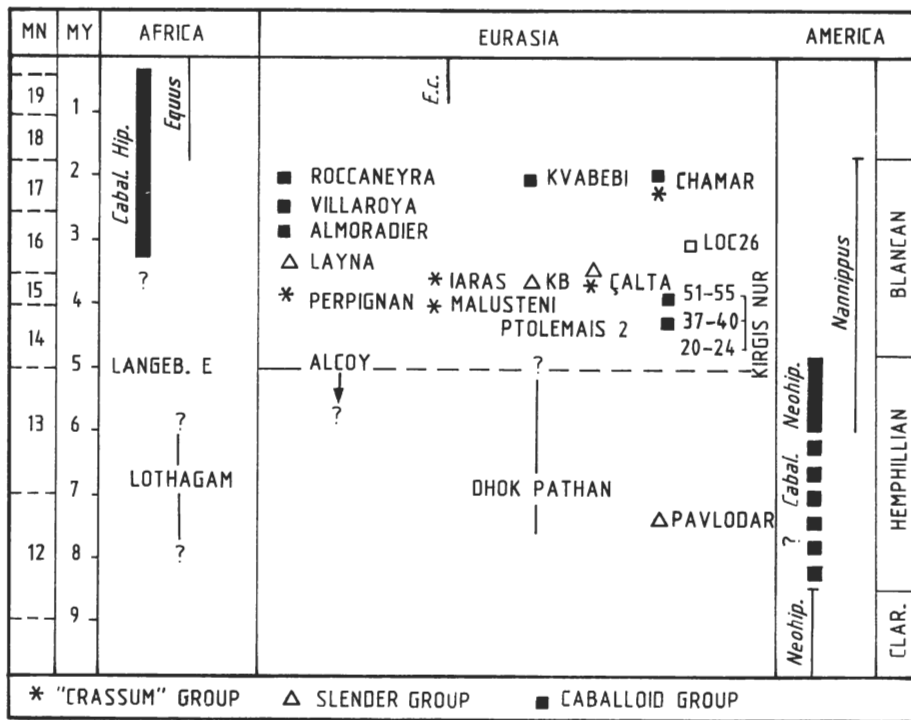
A subsequent paper (Pevzner *et al.*, 1982) discuss the age and correlations of the Kirgis Nur Formation using biostratigraphical and paleomagnetic data. Pevzner and his co-authors accept the same age (upper Turolian or lower Ruscinian) for Alcoy and La Puebla de Almoradier (again basing themselves on 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 Almoradier), 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 *Orientalomys* 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 *Neohipparion* 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 Almoradier (first *H. rocinantis*); 4) a close similarity between the North American neohipparions 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 *Orientalomys* 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



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: Cabaloid 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 lower Ruscinian MN 14; 2) the similarity between *H. crassum* and *H. sefvei* 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 neohipparions and the *H. houfenense* 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. houfenense* and the European *H. rocinantis*.

For the rodents, we must point out that "adroverilike" *Occitanomys* 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 *Occitanomys* they could still be as young as the upper Ruscinian.

3. CONCLUSIONS

The Mio-Pliocene boundary model based on correlations between Mongolian and European hipparions proposed by Pevzner & Vangenheim cannot be accepted but the correlations between European *H. rocinantis* and Mongolian early *H. houfenense* may be reliable. If we suppose that the levels 20-24 of Kirgis Nur (where an *Occitanomys* close to *O. adroveri* has been found) belong to the MN 14 zone, the upper levels of Kirgis Nur could belong to zone MN 15. Taking in

account the general Pliocene hipparion distribution pattern (Text-fig. 6), the presence of primitive cabaloid forms at that time in Mongolia would not be as strange as their supposed appearance at the base of MN 14 zone.

In that case, the Mio-Pliocene boundary could be situated somewhere near the base of the Kirgis Nur formation. Unfortunately, we have presently not enough data to try to correlate the fossils of those levels with any other hipparions.

NORTH AMERICAN HIPPARIONS

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.

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 *Neohipparion* have extremely hypsodont cheek teeth. The locomotion of the tridactyl *Nannippus* was very specialized and it was probably functionally monodactyl (Sondaar, 1968). In contrast, *Neohipparion* 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 *Astrohippus* and *Dinohippus*, 6 are from *Neohipparion* 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 *Neohipparion* 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, *Neohipparion* 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, *Neohipparion*. 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 turkanense* 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 *Neohipparion* 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 Iaras, huge size at Çalta and Chamar). 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 neohipparions. Its relation with the African caballoid 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.

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