In: Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire.
Vol. II: Palaeobiology. - *CIFEG Occas. Publ.*, 1994/29, Orléans, CIFEG, pp. 289-307

EQUIDAE OF THE ALBERTINE RIFT VALLEY, UGANDA

Véra EISENMANN *

* URA 12 du CNRS, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, 8 rue Buffon, F-75005 PARIS

VERSION ABRÉGÉE FRANÇAISE

La Formation de Kakara située à la base du Miocène supérieur (Pickford *et al.*, 1993) a livré des dents d'hipparion de taille exceptionnellement grande, très plissées, avec des plis caballins multiples. Les diagrammes de dispersion (Fig. 1, 2, 3) montrent qu'elles sont plus grandes que celles d'*H. koenigswaldi* du Vallésien de Nombrevilla (Espagne), et celles d'*H. primigenium* du Miocène supérieur (Vallésien) de Beglia (Tunisie) et de Ngorora, Nakali et Samburu (Kenya). Ces dents sont rapportées à une nouvelle espèce : *Hipparion macrodon* (Pl. I : fig. 1; Pl. II : fig. 1). Au total, on peut supposer la présence de trois espèces d'hipparions en Afrique orientale au Miocène supérieur ancien : *H. macrodon* (Kakara), *H.* cf. *primigenium* (Samburu, Nakali, Ngorora) à dents plus petites, et *H.* aff. *africanum* (Samburu) à dents encore plus petites.

C'est de la Formation de Nkondo que provient le meilleur échantillon actuellement connu de dents d'hipparion de la fin du Miocène en Afrique de l'Est. Deux espèces de taille différente sont représentées : *H. turkanense* (Pl. I : fig. 2 à 5; Pl. II : fig. 3 à 16) et *H.* cf. *sitifense*, de taille plus petite (Pl. I : fig. 6 à 10; Pl. II : fig. 17). Chez les deux espèces, les dents jugales inférieures sont caballoïdes et dépourvues d'ectostylides. D'après les dimensions dentaires (Fig. 5, 6), *H. turkanense*, décrit à Lothagam 1 par Hooijer et Maglio (1973, 1974) est également présent à Mpesida, Lukeino, Ekora, Nyaburogo et Warwire. Le crâne (Lothagam 1) est dépourvu de fosse préorbitaire et les os des membres sont grands. *H.* cf. *sitifense*, dont la relation avec *H. sitifense* d'Afrique du Nord n'est pas établie, est représenté à Ekora par un crâne pourvu d'une fosse préorbitaire éloignée de l'orbite. Ce crâne a été précédemment rapporté par Hooijer à *H. primigenium* mais les dimensions dentaires sont celles d'*H.* cf. *sitifense* (Fig. 5). Si on en juge par les dents (Fig. 5, 7) et les métapodes, cette espèce est aussi présente à Lothagam, Lukeino et Sahabi. Les métacarpes (Fig. 4) sont aussi sveltes ou plus sveltes que chez *H. mediterraneum* de Pikermi. Leurs diamètres antéro-postérieurs proximaux sont plus forts et leurs extrémités distales plus "évoluées" : la largeur articulaire est plus grande que la largeur sus-articulaire. *H.* cf. *sitifense* est probablement aussi présent dans les Formations de Nyaburogo et Warwire.

L'absence d'ectostylides et l'aspect imparfaitement "caballin" de la double boucle sur les dents jugales inférieures distinguent les hipparions des formations de Nkondo, Nyaburogo et Warwire des hipparions africains plus évolués qu'on appelle stylohipparions. Il semble qu'il n'y a pas non plus d'ectostylides sur les dents récoltées à Mpesida, Ekora et Laetoli, presque jamais à Lothagam. On observe parfois des ectostylides à Lukeino, presque toujours à Chemeron (peut-être seulement dans les niveaux supérieurs) et toujours à Kanapoi. Le développement des ectostylides semble donc s'être produit quelque part entre 6 et 4 Ma, mais sans doute pas dans toutes les populations : les ectostylides sont absents sur les dents de Laetoli (plus de 3,7 Ma) et dans la Baard's Quarry de Langebaanweg (2 Ma environ). En Afrique de l'Est, les doubles boucles primitives "hipparioniennes" sont remplacées par les doubles boucles caballoïdes au cours du laps de temps qui sépare Samburu (9 Ma environ) et Mpesida (6,5 Ma environ). Toutefois le dessin "caballin" caractéristique ne se répand que vers la fin du Pliocène. En Eurasie, ce dessin (non accompagné d'ectostylides) apparaît dans les zones MN 15 - MN 16 en Espagne (Villaroya), Géorgie (Kvabebi), Russie (Beregovaya) et Mongolie (Chamar). Comme en Afrique, il existe auparavant des formes "caballoïdes" moins typiques, par exemple dans les niveaux 37-40 de Kirgis Nur (Mongolie), à Venta del Moro (Espagne) ou même dans le Turolien inférieur de l'Iraq. Toutefois, ces hipparions n'ont pas le pli caballinide aussi développé que les formes africaines.

Dans notre échantillon de l'Ouganda, des dents de stylohipparions sont peu nombreuses. Elles apparaissent à partir de 3 Ma environ dans la formation de Kyeoro puis celle d'Hohwa (Pl. II : fig. 20). Le groupe des stylohipparions est encore mal connu. D'après les dimensions des dents et des os des membres, il comprend certainement plus d'une espèce. Outre l'hypsodontie, la forme caballine de la double boucle et la présence d'ectostylides, certains stylohipparions au moins présentent un vomer particulier (membre de Kada Hadar de la Formation d'Hadar en Ethiopie et zone à *Notochoerus scotti* de la Formation de Koobi Fora au Kenya) et une symphyse mandibulaire longue, large, aplatie, avec des troisièmes incisives réduites (Cornelia Beds en Afrique du Sud, Bed II d'Olduvai en Tanzanie). Toutefois nous ne savons pas comment ces caractères sont liés entre eux, ni quand ils se développent. Il existe ainsi une symphyse mandibulaire de Garba IVD, à Melka Kunturé en Ethiopie, vieille d'environ 1,4 Ma, sur laquelle les troisièmes incisives ne sont pas réduites. D'autre part, une symphyse de Laetoli en Tanzanie est déjà évoluée dans ce sens alors que les dents jugales inférieures du même site sont dépourvues d'ectostylides.

Le genre *Equus* apparaît en Afrique de l'Est dans le membre G de la Formation de Shungura, il y a moins de 2,3 Ma. Les os des membres suggèrent la présence de trois espèces, dont *E. numidicus* ?, de taille moyenne, est la plus fréquente. C'est à cette espèce qu'on peut rapporter la dent jugale inférieure de Kaiso site B et la dent jugale supérieure de Kaiso 3.

I. INTRODUCTION

The anatomical features diagnostic for African hipparions and the most convenient systematic framework have been discussed at length in previous papers (Eisenmann, 1979, 1983). But it seems useful to stress three points about what use can be made of the cheek teeth - the most frequently recovered material. 1. Hypsodonty is certainly an important character, but its intraspecific variation has never been assessed in equids (not even in *Equus*). Admittedly, the Pleistocene hipparions have higher crowns than those of the Vallesian, but we do not know the details of this evolution. 2. The information yielded by the upper cheek teeth is exceedingly difficult to use: the possible ranges of variation for the overall size as well as of the length and width of the protocone are poorly known because there are few good samples for comparisons; the degree of plication seems more related to ecological conditions than to geological age. 3. The lower cheek teeth are more diagnostic: the oldest forms have classical hipparionine double knots without ectostylids, the youngest have caballine double knots with ectostylids. However, the caballine morph and the ectostylids are not linked, and the caballine morph seems to appear earlier than the ectostylids. The caballine morph is not a quantifiable character and it evolves from "more or less caballine" to "quite caballine" type. There is always a certain amount of subjective impression at work, complicated by the necessity to make allowance for stages of wear. Thus the appearance of the caballine morphology is difficult to date exactly. The appearance of ectostylids is also difficult to date because they may be hidden in the cement, specially if they are very short, and because we do not know if they are absolutely constant in a population (Eisenmann, 1977). Nevertheless, lower cheek teeth of African hipparions may be used to date a site, while the upper cheek teeth are not so reliable.

Thus, *H. albertense* (Hopwood, 1926) based on the vestibular half of a high-crowned upper molar from Kaiso Village should rather, in my opinion, be considered as a *nomen vanum*, the more so because no lower cheek tooth was found at the same site (Cooke & Coryndon, 1970).

The occurrence of *Equus* teeth on its own gives a good indication of the maximum age of a site since monodactyl Equidae do not seem to be found earlier than about 2.5 Ma in Europe nor in Africa (Eisenmann, 1992). But teeth of that period exhibit a uniform, primitive, "stenonine" morphology that does not help to distinguish species. When collected, third metapodials are much more diagnostic.

II. MATERIAL AND METHODS

Most of the Equidae fossils from Uganda studied here belong to the genus *Hipparion*: among 83 specimens only 2 or 3 can be referred to *Equus*. Nearly all specimens are cheek teeth, entire or fragmentary. Limb bones are represented only by two tali. The fossils were collected at different localities belonging to different formations (Tab. I) the age of which ranges between about 10 and 2.3 Ma (Pickford *et al.*, 1993). Teeth and bones were measured and observed according to the recommendations of the "New York International Hipparion Conference" (Eisenmann *et al.*, 1988).

III. SYSTEMATIC DESCRIPTIONS

1. KAKARA FORMATION

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Hipparion* de Christol, 1832
***Hipparion macrodon* nov. sp.**

Holotype: associated right $P^2P^3P^4$ and M^3, NY 256'90 (Pl. I: fig. 1).

Type locality: Locality NY 75, Kakara Formation of the Kisegi-Nyabusosi region, Toro, Western Rift Valley, Uganda.

Table I - List of fossil *Hipparion*

Formation	Localities	Age Ma	Numbers	Upper Cheek teeth	Lower Cheek teeth	Other	Determinations
Kakara	NY 2	10 Ma	NY 13-86	R P2			H. cf macrodon
Kakara	NY 32	10 Ma	NY 186-90	R M3, fragt			Hipparion sp
Kakara	NY 33	10 Ma	NY 135-87		L M2 associated		H. cf macrodon
Kakara	NY 33	10 Ma	NY 136-87		L M1 associated		H. cf macrodon
Kakara	NY 75	10 Ma	NY 256-90	R P3 + R P4			H. macrodon
Kakara	NY 75	10 Ma	NY 256-90	R P2			H. macrodon
Kakara	NY 75	10 Ma	NY 256-90	R M3			H. macrodon
Kakara	NY 75	10 Ma	NY 337-90		L P2		H. macrodon
Kakara	NY 75	10 Ma	NY 47-90	Fragt			Hipparion sp
Kakara	KI 6	10 Ma	KI 77-92		L P3 or P4		H. cf macrodon
Upper Oluka	NY 21	6 Ma	NY 20-87	L M3			H. cf sitifense
Upper Oluka	NY 21	6 Ma	NY 21-87	R M			H. cf sitifense
Lower Nyaburogo	NY 34	5 Ma	NY 144-87		R M		Hipparion sp
Warwire	WA 121	4.5	NK 364-89			I3 sup ?	Hipparion sp
Warwire	NK/WA 28	4.5	NK 897-89		R M3		H. turkanense
Warwire	NK/WA 28	4.5	NK 898-89		R P		H. turkanense
Warwire	NK/WA 28	4.5	NK 2612-89	R M ± unworn			H. cf sitifense
Warwire	NK/WA 92	4.5	NK 485-88		R M3		H. turkanense
Kyero	KY 1	3 Ma	KY 27-90	R vestibular half (M ?)			Stylohipparion sp ?
Kyero	KY 4	3 Ma	KY 67-90		R P2, fragt		Stylohipparion sp
Hohwa	HO 13	2.6 Ma	HO 26-89		L M3		Stylohipparion sp
Hohwa	HO 11	2.6 Ma	HO 11-90			R talus	Stylohipparion sp ?
Hohwa	HO 11	2.6 Ma	HO 13-90	L M1 or M2, unworn			Stylohipparion sp ?
Hohwa	HO 1	2.6 Ma	HO 39-90	R vestibular half (M ?)			Stylohipparion sp ?
Kaiso	Site A	Omo E-F (2.6)	KS 41-89		L M1 or M2, unworn		Stylohipparion sp ?
Kaiso	Site B	Omo G (2.3)	KS 82-90		R P3 or P4		Equus numidicus ?
Kaiso	KS 3	2.3 Ma	KS 1-86	R M			Equus numidicus ?
Behanga	NY 4	1.5	NY 414-87		R P3 or P4, unworn		Equus ? useless
Nkondo	NK 11	5.5 - 6.5	NK 58-86		L P		H. turkanense
Nkondo	NK 11	5.5 - 6.5	NK 79-86			L talus	H. cf sitifense
Nkondo	NK 14	5.5 - 6.5	NK 172-86	R P2 ? fragt			Hipparion sp
Nkondo	NK 16	5.5 - 6.5	NK 194-86	R P2, worn			H. turkanense
Nkondo	NK 17	5.5 - 6.5	NK 209-86	R M			H. turkanense
Nkondo	NK 19	5.5 - 6.5	NK 233-86		R P		H. turkanense
Nkondo	NK 25	5.5 - 6.5	NK 264-86		L M		H. turkanense
Nkondo	NK 29	5.5 - 6.5	NK 276-86	R M3			H. cf sitifense
Nkondo	NK 32	5.5 - 6.5	NK 315-86	R P2, worn			H. turkanense
Nkondo	NK 33	5.5 - 6.5	NK 333-86	1/2vest R P			H. turkanense
Nkondo	NK 34	5.5 - 6.5	NK 336-86		L P2		H. turkanense
Nkondo	NK 35	5.5 - 6.5	NK 345-86	R M			H. cf sitifense
Nkondo	NK 41	5.5 - 6.5	NK 392-86		R P		H. turkanense
Nkondo	NK 56	5.5 - 6.5	NK 540-86	R M			H. cf sitifense
Nkondo	NK 56	5.5 - 6.5	NK 541-86	R M			H. cf sitifense
Nkondo	NK 56	5.5 - 6.5	NK 542-86		R M entamée/sciée		H. turkanense
Nkondo	NK 57	5.5 - 6.5	NK 559-86	L P			H. cf sitifense
Nkondo	NK 34	5.5 - 6.5	NK 597-86		R P		H. turkanense
Nkondo	NK 34	5.5 - 6.5	NK 598-86		R M		H. turkanense
Nkondo	NK 68	5.5 - 6.5	NK 653-86	fragt L P			H. turkanense
Nkondo	NK 34	5.5 - 6.5	NK 154-88		R DP, 1/2 dist		H. turkanense
Nkondo	NK 41,45,46,47	5.5 - 6.5	NK 202-88		R P2		H. turkanense
Nkondo	NK 41,45,46,47	5.5 - 6.5	NK 203-88		L P		H. turkanense
Nkondo	NK 28	5.5 - 6.5	NK 512-88	R M			H. turkanense
Nkondo	NK 28	5.5 - 6.5	NK 513-88	L P			H. turkanense
Nkondo	NK 28	5.5 - 6.5	NK 514-88		L M		H. turkanense
Nkondo	NK 28	5.5 - 6.5	NK 515-88		L P		H. turkanense
Nkondo	NK 28	5.5 - 6.5	NK 517-88		R P		H. turkanense
Nkondo	NK 28	5.5 - 6.5	NK 546-88	R M			H. turkanense
Nkondo	NK 102	5.5 - 6.5	NK 613-88	R M			H. cf sitifense
Nkondo	NK 101	5.5 - 6.5	NK 656-88		R P		H. turkanense
Nkondo	NK 101	5.5 - 6.5	NK 657-88		R M3		H. turkanense
Nkondo	NK 115	5.5 - 6.5	NK 751-88	R P			H. cf sitifense
Nkondo	NK 115	5.5 - 6.5	NK 752-88		L M		H. turkanense
Nkondo	NK 115	5.5 - 6.5	NK 754-88	L M3			H. cf sitifense
Nkondo	NK 115	5.5 - 6.5	NK 756-88	R P2			H. turkanense
Nkondo	NK 34	5.5 - 6.5	NK 818-88	R M3			H. cf sitifense
Nkondo	NK 101	5.5 - 6.5	NK 215-89		L P		H. turkanense
Nkondo	NK 13	5.5 - 6.5	NK 310-89		R M		Rolled, uworn, useless
Nkondo	NK 123	5.5 - 6.5	NK 547-89		L M		H. turkanense
Nkondo	NK 123	5.5 - 6.5	NK 548-89	R M			H. cf sitifense
			NK 549-89	R M			H. cf sitifense
Nkondo	NK 115	5.5 - 6.5	NK 734-89		R P		H. turkanense
Nkondo	NK 115	5.5 - 6.5	NK 735-89		R M		H. turkanense
Nkondo	NK 115	5.5 - 6.5	NK 788-89	L P2			H. cf sitifense
Nkondo	NK 34	5.5 - 6.5	NK 959-89	R M3			H. cf sitifense
Nkondo	NK 34	5.5 - 6.5	NK 960-89	L M3			H. cf sitifense
Nkondo	NK 34	5.5 - 6.5	NK 962-89		R M		Broken, useless
Nkondo	NK 34	5.5 - 6.5	NK 963-89		R P		H. turkanense
Nkondo	NK 34	5.5 - 6.5	NK 964-89	R M			H. cf sitifense
Nkondo	NK 34	5.5 - 6.5	NK 965-89		L P		H. turkanense
Nkondo	NK 4	5.5 - 6.5	NK 1466-89			I sup ?	Hipparion sp.
Nkondo	NK 58	5.5 - 6.5	NK 1546-89		L P		H. turkanense
Nkondo	NK 115	5.5 - 6.5	NK 1984-89		R M		H. cf sitifense
Nkondo	NK 101	5.5 - 6.5	NK 2330-89	L M3			H. cf sitifense

Etymology: reference is made to the very large size of the teeth.

Age and geographic distribution: probably base of the Upper Miocene of Uganda (Pickford *et al.*, 1993).

Referred material: left P_2 NY 337'90 from the same locality (Pl. II: fig. 1).

Diagnosis

Upper premolars of very large size, larger than any of the known species of the genus *Hipparion*, very plicated, with multiple plis caballins. Protocone lenticular and pointed on upper P^3 and P^4, round and small on P^2. Ectoflexid deep on the unique lower P_2. Skull, mandible and limb bones unknown.

Description and comparisons of the upper cheek teeth (Tab. II)

Four characters are usually considered in descriptions and comparisons of *Hipparion* teeth: hypsodonty, size and shape of the protocone, degree of enamel plication, and size. Their diagnostic value and interpretation is however rendered difficult by the wide range of intraspecific and interspecific variations, and, in the case of hypsodonty, by the necessity to measure the height of unworn teeth.

We have no unworn teeth for *H. macrodon* and thus no indication about the hypsodonty. On the P^3 and P^4 the protocone is neither short and rounded as in *H. primigenium* of Eppelsheim, nor elongated and flattened as in some Pliocene and Pleistocene African forms. But this character on its own would not allow the description of a new species. Neither would the degree of plication, since very plicated teeth are found in the Vallesian as well as in the Pliocene and Pleistocene of Africa. Thus the description of *H. macrodon* relies heavily on its very large size. The comparison with good samples of upper cheek teeth of *Hipparion* shows however that the size is, in this case, a good diagnostic character.

Table II - Measurements (mm) of upper cheek teeth of hipparions from the Kakara Formation

		H. cf macrodon	Hipparion macrodon				H. sp.
		Kakara 2	Kakara 75	Kakara 75	Kakara 75	Kakara 75	Kakara 32
		P2	P2	P3	P4	M3	M3
		NY 13-86	NY 256-90	NY 256-90	NY 256-90	NY 256-90	NY 186-90
Wear stage		II	II	II	II	II	I-II
Height		30,0	34,0	33,0	42,0	40,0	48,0
	Occlusal	37,0		31,5	30,0		
Length	At 2cm					29,0	23,0
	At 1cm	36,0		30,0	29,0	30,0	23,0
	Occlusal	25,0	24,0	30,0	30,0		
Width	At 2cm					24,0	22,5
	At 1cm	25,8	23,0	30,0	31,0	24,0	22,5
Protocone L	Occlusal	10,0	7,5	10,0	11,5	9,5	8,0
Protocone W	Occlusal	5,0	5,0	4,0	5,7		
Plis Fossette		plicated	4,4,6,3	5,7,11,3	3,9,11,2	3,8,5,3	
Plis Caballin		1	1	4	3	2 or 3	1

Figures 1 to 3 compare the occlusal length of the crown and of the protocone of upper premolars (P^3 and P^4) belonging to different species or forms of Europe, North Africa, and East Africa. Only moderately worn teeth were taken into account.

In figure 1 are plotted two teeth of *H. primigenium* of Eppelsheim (measured on a cast of Din 2849-1076, Darmstadt) and a sample of *H. koenigswaldi* (measured at Sabadell). Sondaar (1961, p. 267) described *H. koenigswaldi* (Vallesian of Nombrevilla, Spain) as a new species differing from *H. primigenium* by several characters, among which was the larger size of its teeth. Figure 1 shows that the P^3 and P^4 of *H. macrodon* from the Kakara Formation are even larger. In upper cheek teeth of *H. koenigswaldi*, the hypocone is bordered by two hypoconal grooves that are absent in *H. macrodon*. In *H. koenigswaldi* the pli caballin is usually double and symmetric, while in *H. macrodon* several plis caballins of different sizes are present. Moreover, in *H. macrodon* the fossettes of the P^2 are not confluent, whereas confluence was observed in 29 out of 33 P^2 of *H. koenigswaldi*.

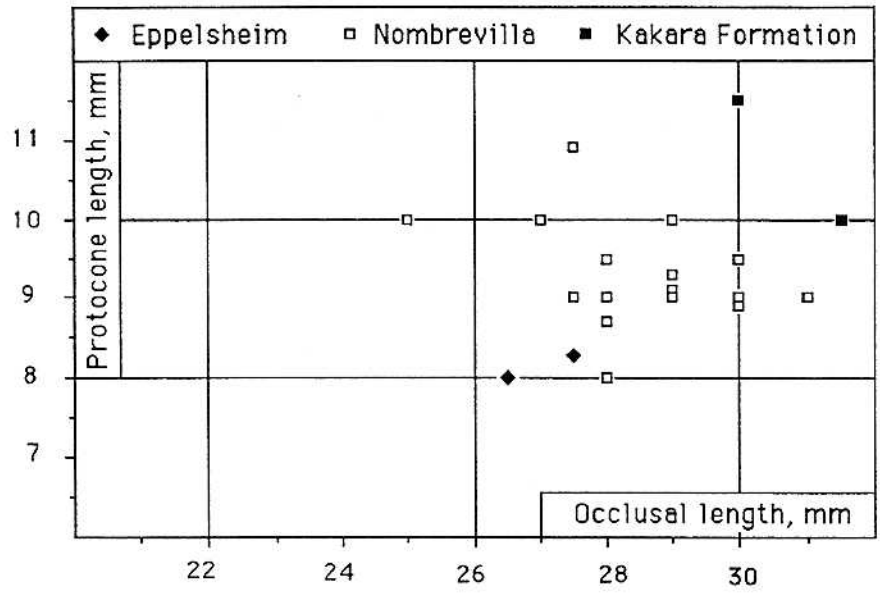


Figure 1 - Scatter diagram of P^3P^4 of hipparions from Eppelsheim (*H. primigenium*), Nombrevilla (*H. koenigswaldi*) and Kakara (*H. macrodon*).

Figure 2 compares the sample of *H. africanum* from Bou Hanifia, Algeria, one premolar (AMA 19) from Menacer, Algeria (collections of the Laboratoire de Paléontologie du M.N.H.N.) and two premolars from Beglia, Tunisia (33650 and 33653, University of Colorado Museum, kindly communicated by P. Robinson). The Menacer material has been referred to *H. africanum* by Arambourg (1959), and the Beglia fossils to *H. primigenium* by Forsten (1972). Although the morphology of the Menacer teeth is consistent with the Vallesian age supposed by Arambourg, a recent revision of the mammals (Thomas & Petter, 1986) suggests a Turolian age for Menacer. The Beglia *Hipparion* is Vallesian (Forsten, 1972). The age of the *Hipparion* level at Bou Hanifia (MN 9) is estimated at little more than 10.5 Ma (Sen, 1990), close to 10.85 by extrapolation based on the sedimentation rate. Whatever the exact ages of these hipparions, the dispersion diagram shows that *H. macrodon* premolars are much larger than any of these North African forms.

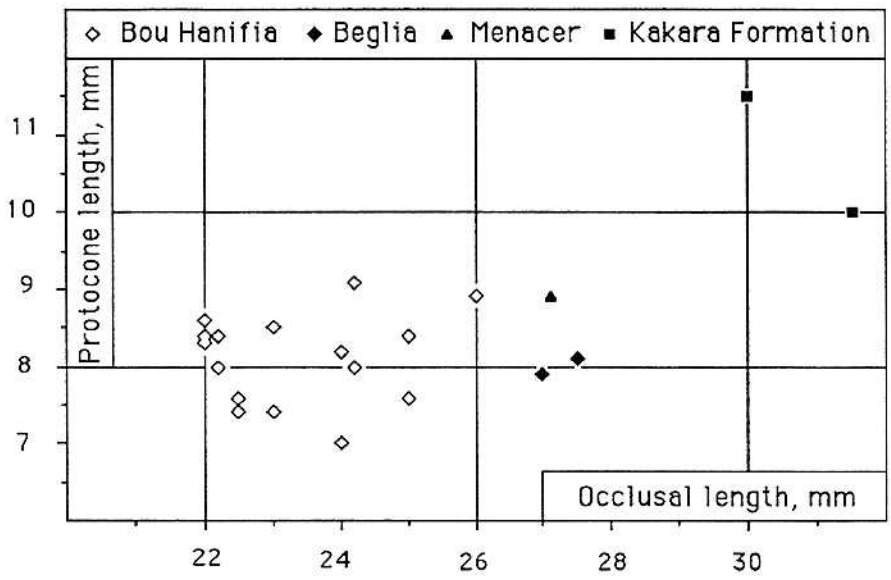


Figure 2 - Scatter diagram of P^3P^4 of *Hipparion* from Bou Hanifia (*H. africanum*), Beglia (*Hipparion* sp.), Menacer (*Hipparion* sp.), and Kakara (*H. macrodon*).

Figure 3 compares the measurements given by Nakaya and Watabe (1990) for the hipparions from Namurungule Formation (Samburu Hills, Kenya) which they refer to *H.* aff. *africanum*, with the measurements of one premolar from the Ngorora Formation, Kenya, given by Hooijer (1975) and referred by him to *H. primigenium*, two casts of premolars from Nakali, Kenya, referred to *H. africanum* by Aguirre and Alberdi (1974) and kindly provided by M.T. Alberdi, and the two premolars of *H. macrodon*. This scatter diagram suggests that two species with different sizes of cheek teeth are represented in the Samburu sample. The smaller teeth fall within the range of variation of *H. africanum* (see Fig. 2, 3). The scatter of the middle sized teeth does not include the *H. africanum* nor the H. *macrodon* premolars. The interpretation of the few premolars from Ngorora and Nakali is difficult. They may be considered as rather large

specimens belonging to the middle sized species of Samburu. Or they may represent the lower extreme of *H. macrodon* range of variation while the Kakara specimens would represent the upper extreme. At present, I prefer to assume that three hipparions are present in the Vallesian of East Africa: *H.* aff. *africanum* (small species of Samburu Hills), *H.* cf. *primigenium s. l.* (middle sized Hipparion of Samburu Hills, possibly present also at Nakali and Ngorora) and *H. macrodon* from locality 75 of the Kakara Formation.

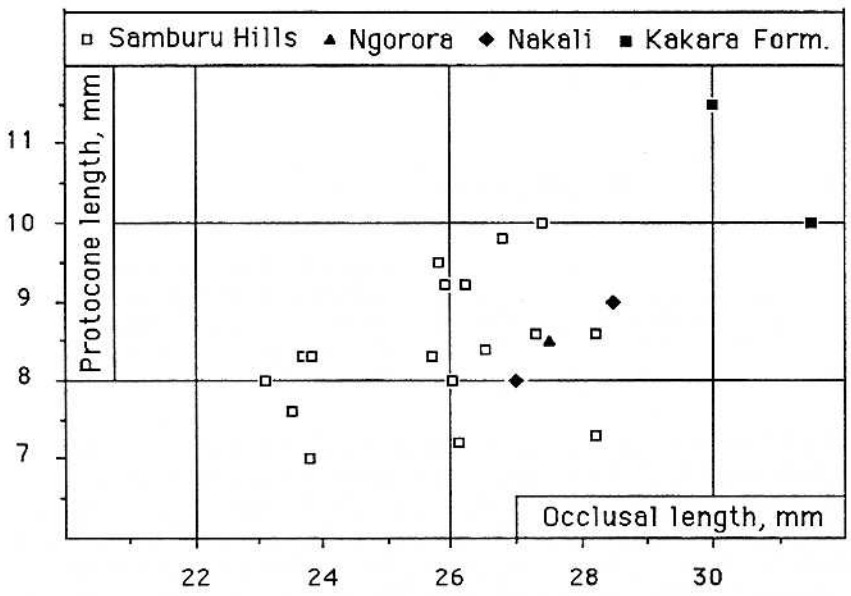


Figure 3 - Scatter diagram of P^3P^4 of *Hipparion* from Samburu Hills (*H.* aff. *africanum* = small species; *H.* cf. *primigenium* s.l. = middle sized species), Ngorora (*H.* cf. *primigenium* s.l.), Nakali (*H.* cf. *primigenium* s.l.), and Kakara (*H. macrodon*).

The age of the Samburu hipparions is estimated at 9 Ma (Nakaya & Watabe, 1990). *Hipparion* fossils of Ngorora come from the uppermost part of the formation (M. Pickford, pers. comm.) and from younger sites; their age is younger than 10 Ma (Hill *et al.*, 1986), and they probably belong in the MN 10 zone. Nakali is believed to be a little younger than 9 Ma (Hill, 1987).

Hipparion cf. *macrodon*

Left P_3 or P_4 KI 77'92 from locality KI 6; two associated lower left molars NY 135'87 from locality NY 33; a right P^2 NY 13'86 from locality NY 2. Kakara Formation.

The P_3 or P_4 from locality KI 6 (Pl. II: fig. 2; Tab. III) is not perfectly preserved but has approximately the same size as two lower premolars from Ngorora (Hooijer, 1975), two from Nakali (casts of 69-66 and 69-180), and one from Samburu (SH 196, Nakaya & Watabe, 1990, Pl. II, fig. 9). The double knot is typically hipparionine, but the protostylid is lacking while it is present on all the other mentioned premolars. The two lower molars from locality NY 33 also belong to a large form (Tab. III); the double knot is hipparionine. There are no ectostylids but a protostylid pli is present on the M_2. The vestibular groove is shallow in the premolar and deep in the molars.

The lower cheek teeth of hipparions seem to have a larger range of size variability than the upper cheek teeth. Correlation of upper and lower cheek teeth is not easy. Besides, I lack good samples that could be used as a reference of intraspecific variation. Presently I do not know if the large teeth enumerated above belong to one or more species, nor if they belong to *H. macrodon*.

Table III - Measurements (mm) of lower cheek teeth of hipparions from the Kakara Formation

		H. macrodon	H. cf macrodon		
		Kakara 75	Kakara 6	Kakara 33	Kakara 33
		NY 337-90	KI 77-92	NY 136-87	NY 135-87
		P2	P	M1	M2
Wear stage		2 - 3	2	2	2
Height		31,0	45,0	47,0	45,0
	Length	33,5	26,0	25,5	25,0
	Ante Foss	8,5	8,0	8,0	7,0
Occlusal	Double K	14,5	15,0	14,0	14,0
	Post Foss	15,0	12,0	10,5	10,5
	Width	15,0	14,0	11,5	12,5
At	Length		26,0	25,5	24,0
2 cm	Width		18,0	13,0	14,5
At	Length	31,0	25,0	25,5	23,5
1 cm	Width	14,0	18,0	13,0	14,5
Protostylid		0	?	?	pli
Pli Caballinid		0	0	?	0

2. NKONDO FORMATION

Hipparion turkanense and *Hipparion* cf. *sitifense*

The scanty material certainly belonging, and possibly belonging, to *H. sitifense* was figured and discussed in detail previously (Eisenmann, 1980). The type material is lost; the material collected later at the same locality of Saint Arnaud is limited to a badly preserved lower cheek tooth and a distal fragment of MT III, of unknown age. At present, we only know that *H. sitifense* was a primitive form, with rather short and curved crowns and a rounded protocone (Pomel, 1897, Pl. I), smaller than *H. africanum*, but not very much so.

The type of *Hipparion turkanense* described by Hooijer and Maglio (1973, 1974) is a skull from Lothagam 1, lacking the preorbital fossa, with very worn teeth. No mandible is associated with the skull, but lower cheek teeth also collected at Lothagam and referred to *H. turkanense* have more or less caballine double knots and no ectostylids. Beside *H. turkanense*, Hooijer & Maglio (1974) recognized at Lothagam the presence of a smaller hipparion, *H.* cf. *sitifense*. The lower cheek teeth have a rather caballoid pattern and no ectostylids. One exception is KNM LT 143 (Hooijer & Maglio, p. 18) referred for this reason to *H. primigenium*. I do not think that the occurrence of an ectostylid is a sufficient reason to refer a tooth to *H. primigenium*, especially if the double knot is not primitive. Neither do I think that the small hipparion of East Africa is necessarily related to the North African *H. sitifense*. But since there is not enough material to correctly describe the small East African species, it may still be referred as *H.* cf. *sitifense* for the sake of commodity.

From about the same level as the skull of *H. turkanense*, there is a third metacarpal referred by Hooijer and Maglio (1974) to *H.* cf. *sitifense*. The problem of the correlation between skull size and metapodial size has been addressed previously for the genus *Equus* (Eisenmann & Karchoud, 1982). Breadths of metapodials correlate well with the skull basilar length. Although the samples are naturally far from good in the case of *Hipparion*, it still seems that the distal articular breadth is closely related to the basilar length of the skull. Judging from the distal articular breadth (35 mm) of the Lothagam MC III, the corresponding skull should have a basilar length of about 425 mm. The basilar length of *H. turkanense* is 465 mm and the distal articular breadth of the corresponding metapodials should be about 40 mm. Thus the Lothagam MC III indeed belongs to *H.* cf. *sitifense* and not to *H. turkanense*.

The lower part of Lothagam, from where come the discussed specimens, is older than 3.8 Ma (Brown *et al.*, 1985). According to Hill (1987), the fauna of Lothagam 1 is equivalent to that of Lukeino, *i.e.* approximately between 6.2 and 5.6 Ma (Hill & Ward, 1988).

At Lukeino (Hooijer, 1975) there is also evidence of two hipparions, referred to *H. turkanense* and *H.* cf. *sitifense*. The lower cheek teeth are rather caballine and without ectostylids. Both fragments of MC III referred to the small species fit well (Fig. 4) with the *H.* cf. *sitifense* MC III from Lothagam. The Lukeino Formation lies between about 6.2 and 5.6 Ma (Hill & Ward, 1988).

At Sahabi (Libya) there are also two hipparions differing in size. Bernor *et al.* (1987) have referred their remains to *H.* cf. *africanum* and to *H.* cf. *?sitifense*. In the larger *Hipparion*, the distal articular breadth ranges from 38.4 to 43.5 mm. This is too big for *H. africanum* metapodials (34.5-37), but would fit well with the *H. turkanense* skull. Although the measurements given by Bernor *et al.* (1987) are difficult to use because of misprints, it seems that the large upper cheek teeth are too large for *H. africanum* and fit better with those of *H. turkanense*. Another interesting resemblance exists between the MC III of the Lothagam and Sahabi small *Hipparion* (Fig. 4). Unfortunately Bernor *et al.* (1987) do not illustrate nor discuss the pattern of the lower cheek teeth so that we do not know if they are of the caballoid or the primitive sort. According to Hill & Ward (1988) the Sahabi units are younger than the beginning of the Pliocene.

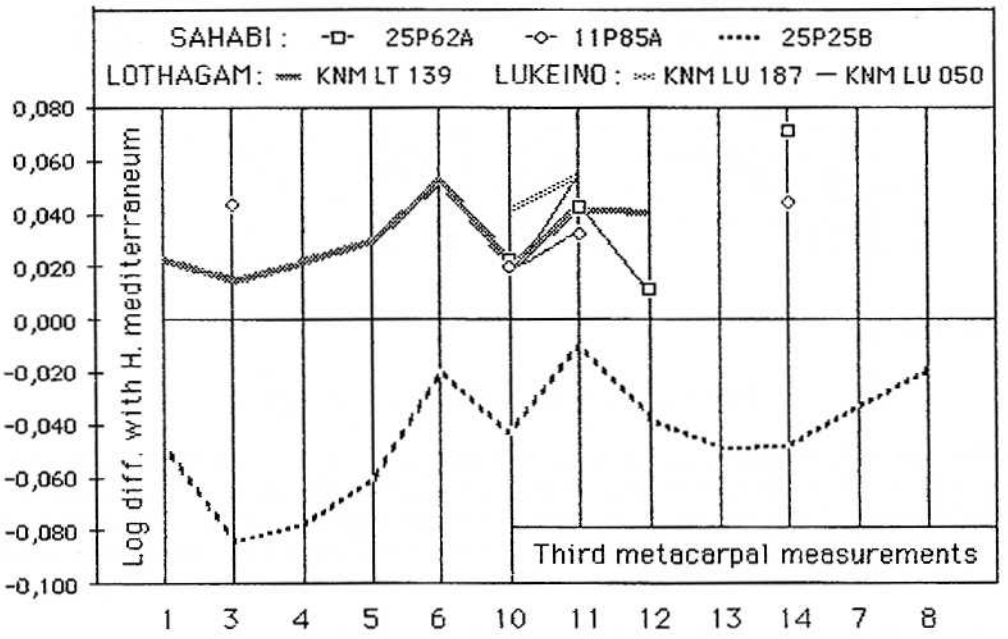


Figure 4 - Ratio diagram of *Hipparion* cf. *sitifense* third metacarpals from Lothagam, Lukeino and Sahabi.
1 = maximal length, 3 = mid-diaphysis width, 4 = mid-diaphysis depth, 5 = proximal articular width, 6 = proximal articular depth, 10 = distal supra-articular width, 11 = distal articular width, 12 = maximal distal depth (keel), 13 = minimal depth of the medial condyle, 14 = maximal depth of the medial condyle, 7 = maximal diameter of the articular facet for the magnum, 8 = diameter of the anterior facet for the unciform.

At Ekora, under the Kanapoi basalt (Hooijer & Maglio, 1974, Fig. 2), was found a juvenile skull KNM EK-4 with a preorbital fossa far from the orbit. Hooijer and Maglio (1974) stressed its resemblances to the Bou Hanifia *H. africanum* skulls. Following Forsten (1968) they put *H. africanum* into synonymy with *H. primigenium* and accordingly referred the Ekora skull to the European Vallesian species. They referred to the same species a large lower caballine premolar, without ectostylid, while a small molar which was also caballine without ectostylid was referred to *H.* cf. *sitifense*. However, it is interesting to remark that the M1 of the juvenile skull fits in the cluster of *H.* cf. *sitifense* molars (Fig. 5), as does the small lower molar KNM EK-6 (Fig. 7) whereas the large premolar KNM EK-7 fits with the *H. turkanense* teeth (Fig. 6). If my interpretation is right, we again have at Ekora the association of *H. turkanense* (KNM EK-7) and of *H.* cf. *sitifense* (skull and KNM EK-6). The Kanapoi basalt probably belongs either to the Mammoth or the Kaena event, but the faunal collections from Kanapoi and Ekora could be considerably older (Brown *et al.*, 1985).

The Mursi Formation (Omo, Ethiopia) is older than 4 Ma (Brown *et al.*, 1985). From this unit comes a fragment of a large MC III and a P_2 without ectostylid referred by Hooijer (1975) to *H. turkanense*.

The Usno Formation is younger than 4.1 Ma (Brown *et al.*, 1985). The lower cheek teeth have ectostylids (Hooijer, 1975). With the exception of the sample from Laetoli (Hooijer, 1979) and one molar from Shungura Member B (Eisenmann, 1985), ectostylids are always present on P_3 to M_3 from younger sites of East Africa, whether the teeth are large or small.

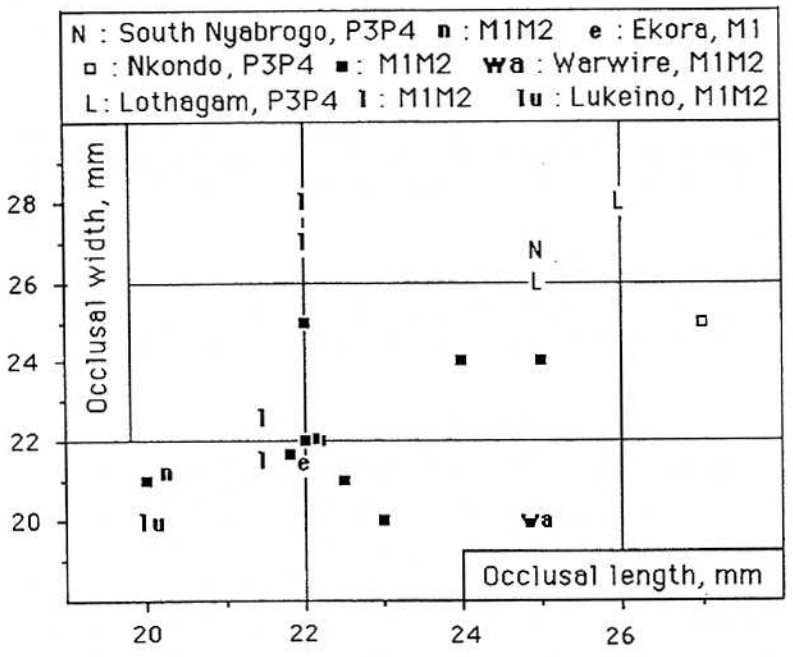


Figure 5 - Scatter diagram of upper cheek teeth of hipparions (*H. turkanense* and *H.* cf. *sitifense*) from Nkondo, Nyaburogo, Warwire, Lothagam, Lukeino, and Ekora.

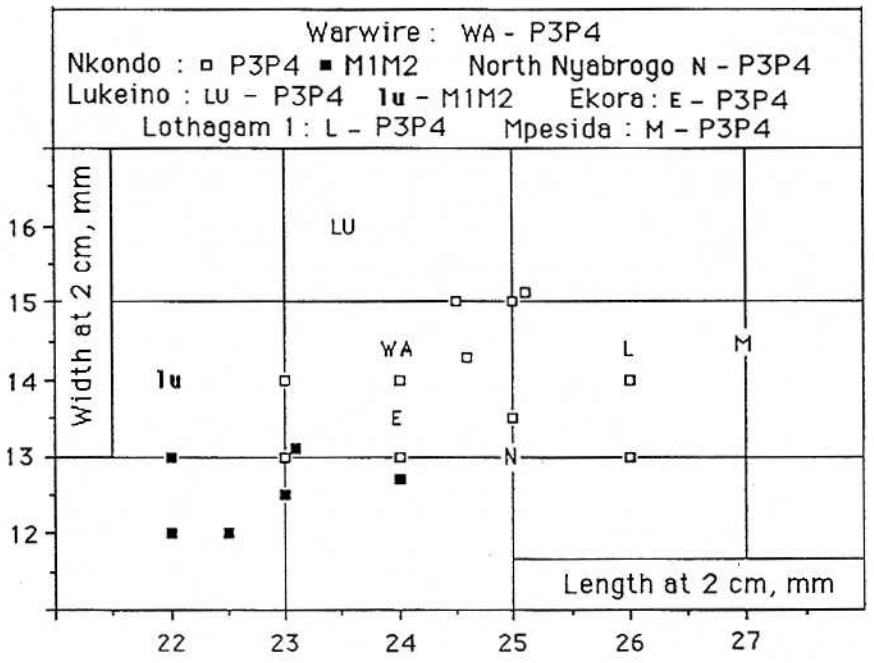


Figure 6 - Scatter diagram of lower cheek teeth of *Hipparion turkanense*.

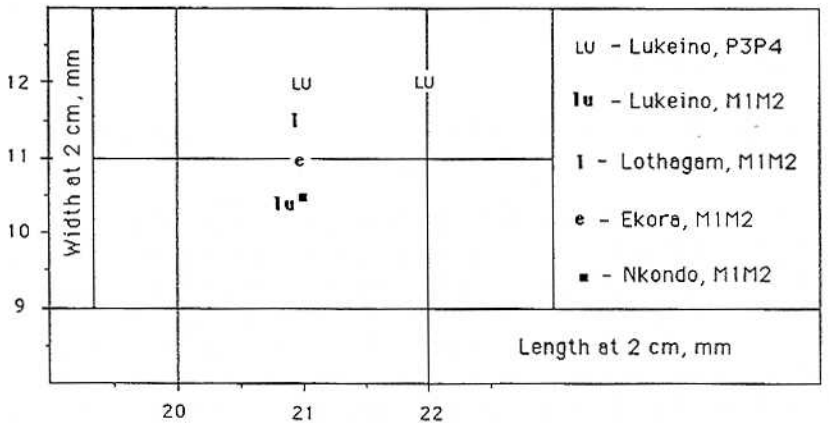


Figure 7 - Scatter diagram of lower cheek teeth of *Hipparion* cf. *sitifense*.

A. Nkondo upper cheek teeth (Pl. I: fig. 2 to 10; Tab. IV)

Judging from the dimensions of the upper cheek teeth (Tab. IV), there are also two hipparions in the Nkondo Formation. On the scatter diagram (Fig. 5) a cluster of large teeth (P^3P^4 and M^1M^2 from Nkondo and Lothagam) appears separated from a cluster of smaller teeth (M^1M^2 from Nkondo, Lothagam, Lukeino and Ekora). The two clusters probably represent *H. turkanense* and *H.* cf. *sitifense*.

There is nothing much to say about their morphology. Both in the large and the small teeth the plications are moderate (Tab. IV), and the protocone is rather elongated. One molar from Chemeron (Hooijer, 1975, Pl. III: fig. 4) and one from Lukeino (Hooijer, 1975, Pl. VI: fig. 6) look respectively rather like the Nkondo molars NK 546'88 (Pl. I: fig. 3) and NK 541'86 (Pl. I: fig. 8).

Table IV - Measurements (mm) of upper cheek teeth of hipparions from the Nkondo and Upper Oluka Formations

		Nkondo 14	Nkondo 16	Nkondo 32	Nkondo 115	Nkondo 115	Nkondo 33	Nkondo 28	Nkondo 17	Nkondo 35
		P2	P2	P2	P2	P2	P	P	M ?	M
		NK 172-86	NK 194-86	NK 315-86	NK 756-88	NK 788-89	NK 333-86	NK 513-88	NK 209-86	NK 345-86
Height		30	[20]	[16]	57	48	54	49	36	31
	Occlusal		30,5		38,0		27,0	27,0	25,0	22,2
Length	At 2cm		30,5		35,5		25,0	26,5	23,0	22,0
	At 1cm		30,5				24,0	26,0	23,0	21,5
	Occlusal	23,0	24,0	24,0		22,2		25,0	24,0	22,0
Width	At 2cm		24,0	24,0	25,0	22,2		25,0	25,0	23,0
	At 1cm		24,0	24,0				24,0	25,0	23,0
Protocone L	Occlusal	8,0	9,1	9,5		7,5		9,2	9,0	6,5
Protocone W	Occlusal	5,1	5,5	5,5		3,5		4,2	4,8	4,0
Plis Fossette		4,2,5,1	4,4,2,1	1,8,3,2		3,2,3,1	8,13,8,2	8,10,4,1	5,7,7,2	2,8,6,3
Plis Caballin		1	2	0		1		2	2	1
		Nkondo 56	Nkondo 56	Nkondo 57	Nkondo 28	Nkondo 28	Nkondo 102	Nkondo 115	Nkondo 123	Nkondo 123
		M	M	M	M	M	M	M	M	M
		NK 540-86	NK 541-86	NK 559-86	NK 512-88	NK 546-88	NK 613-88	NK 751-88	NK 548-89	NK 549-89
Height		48	57	58	38	58	47	53	38	21
	Occlusal	22,5	22,1	25,0	22,0	24,0	22,2	26,0	20,0	21,0
Length	At 2cm	22,2	21,0	22,0	22,0	22,0	21,8	23,0	20,0	21,0
	At 1cm	22,0	21,0	21,5	21,5	21,0	21,7		20,0	20,0
	Occlusal	21,0	22,0		25,0	24,0	21,0		21,0	
Width	At 2cm	23,0	22,0	22,0	25,7	24,0	21,7	20,0	21,5	
	At 1cm	23,0	22,0	23,0	26,0		21,5		22,0	
Protocone L	Occlusal	7,3	6,9	8,5	9,0	9,0	7,5	8,0	8,0	7,7
Protocone W	Occlusal	4,2	4,0	3,0	4,5	4,5	4,0	5,0	4,0	5,0
Plis Fossette		7,9,9,2	3,13,9,3		5,13,7,3	4,7,5,4	1,6,4,1	2,7,3,1	4,9,6,2	1,10,6,0
Plis Caballin		1		1	1	1	1	1	1	1
		Nkondo 34	Nkondo 29	Nkondo 115	Nkondo 34	Nkondo 34	Nkondo 34	Nkondo 101	Oluka NY 21	Oluka NY 21
		M	M3	M3	M3	M3	M3	M3	M	M3
		NK 964-89	NK 276-86	NK 754-88	NK 818-88	NK 959-89	NK 960-89	NK 2330-89	NY 21-87	NY 20-87
Height		58	50	51	53	40	57	51	31	29
	Mid-crown		22,0	23,5	22,0	24,0	22,5	23,5	20,2	21,0
Length	At 2cm		22,5	25,0	22,0	24,0	23,0	24,0		21,0
	At 1cm		23,0	25,0	22,0	23,0	24,0	24,0	21,0	20,0
	Mid-crown		19,0	20,7	20,0	22,5	20,2	21,7	21,0	19,0
Width	At 2cm		20,0	21,0		22,0	20,5	21,7		19,0
	At 1cm		20,0	21,0		23,0	21,0	21,5	21,0	18,7
Protocone L	Occlusal	7,1	8,0	10,0	8,5	9,0		7,5	6,9	7,0
Protocone W	Occlusal	4	2,7	3,5	3,8	3,7		4,0	4,0	4,0
Plis Fossette			3,6,5,1	1,5,3,1		4,8,6,1		6,10,5,3	2,7,5,2	2,7,6,1
Plis Caballin		1	1	1	1	2		1	1	1

B. Nkondo lower cheek teeth (Pl. II: fig. 3 to 17; Tab. V, VI)

By size, most of the lower cheek teeth from the Nkondo Formation are referable to *H. turkanense* (Fig. 6); one M_1 or M_2 is close to *H.* cf. *sitifense* from Lothagam, Lukeino, and Ekora (Fig. 7).

Ectostylids are not visible on teeth from the Nkondo Formation which has yielded the richest sample known from this period (the dark spot on NK 1546'89, Pl. II: fig. 5, is not an ectostylid). Ectostylids are also absent in the Nyaburogo and Warwire Formations (see below). Following the publications by Hooijer, there are no ectostylids at Mpesida, Ekora, and Laetoli, and almost never at Lothagam. Ectostylids are present in some teeth from Lukeino, nearly all teeth from Chemeron (possibly from the younger levels mentioned by Hill & Ward, 1988), and all teeth from Kanapoi. These data would be consistent with the development of ectostylids somewhere between 6 and 4 Ma. The total lack of ectostylids in the Nkondo sample could either indicate an age older than Lukeino and Lothagam, or could suggest that

ectostylids failed to develop in some quite "caballine" populations, whatever their age, as seems to be the case with Laetoli (older than 3.7 Ma) and Baard's Quarry at Langebaanweg (about 2 Ma according to Hendey, 1978).

Table V - Measurements (mm) of lower cheek teeth of hipparions from the Nkondo Formation

		Nkondo 34	41,45,46,47	Nkondo 11	Nkondo 19	Nkondo 41	Nkondo 34	41,45,46,47	Nkondo 28	Nkondo 28
		P2	P2	P	P	P	P	P	P	P
		NK 336-86	NK 202-88	NK 58-86	NK 233-86	NK 392-86	NK 597-86	NK 203-88	NK 515-88	NK 517-88
Wear stage		2 - 3	2	2	2	1	1	1	2	3
Height		31	35	43	44	54	64	61	[52]	25
	Length	29,0	28,0	25,0	24,0	26,0	26,0	26,0	[27]	25,0
	Ante Foss	8,0	9,0	8,5	8,0	9,0	10,0	10,0	9,0	9,0
Occlusal	Double K	13,0	11,0	14,5	15,0	14,0	14,9	12,8	15,6	15,0
	Post Foss	12,0	12,8	12,7	11,8	12,0	12,7	12,0	13,5	13,0
	Width	12,1	13,5	13,2	14,0	12,0	12,0	12,5	13,8	13,0
At	Length	28,5	26,5	24,0	23,0	23,0	25,0	24,6		25,0
2 cm	Width	13,5	13,0	13,0	14,0	13,0	15,0	14,3	14,0	15,0
At	Length		26,0	24,0	22,0	22,0	24,0	24,6		24,5
1 cm	Width		12,8	14,0	13,0	13,0	15,0	15,0	14,2	14,0
Protostylid		0	0	2	2		2	2		0
Pli Caballinid		+	small	++	+	++	++	+++	2	small
		Nkondo 101	Nkondo 115	Nkondo 34	Nkondo 34	Nkondo 58	Nkondo 25	Nkondo 56	Nkondo 34	Nkondo 28
		P	P	P	P	P	M	M	M	M
		NK 215-89	NK 734-89	NK 963-89	NK 965-89	NK 1546-89	NK 264-86	NK 542-86	NK 598-86	NK 514-88
Wear stage		2	3	3	0 - 1	2	2	1	1	2
Height		35	24	27	65	50	49	65	60	45
	Length	25,1	25,0	26,0	28,0	24,5	24,0	26,0	25,2	25,0
	Ante Foss	7,0	9,0	9,0		8,0	7,5	9,3	8,3	
Occlusal	Double K	15,0	15,0	15,5		15,0	14,0	14,2	16,0	
	Post Foss	11,5	14,0	13,0		12,0	10,0	10,0	11,8	11,8
	Width	14,0	13,5	14,0	13,3	13,0	11,6	12,5	11,0	
At	Length	24,5			26,0	24,0	23,0	22,5	22,0	23,0
2 cm	Width	15,0			13,0	14,0	12,5	12,0	13,0	13,0
At	Length	24,5	24,5	25,0	25,5	24,0		21,7	21,0	22,0
1 cm	Width	14,5	14,5	14,5	12,7	14,0	12,5	12,0	13,2	13,0
Protostylid		+	pli	pli		3	1	1	0	?
Pli Caballinid		+	small	small		+	++	++++	++	++

Table VI - Measurements (mm) of lower cheek teeth of hipparions from the Nkondo, Warwire, Nyaburogo and Hohwa Formations

		Nkondo 115	Nkondo 115	Nkondo 115	Nkondo 101	Nyaburogo 34
		M	M	M	M3	M
		NK 752-88	NK 735-89	NK 1984-89	NK 657-88	NY 144-87
Wear stage		2	3	3	2	2
Height		38	25	30	47	45
	Length	27,0	22,0	21,0	26,0	22,0
	Ante Foss	7,5	6,1	7,0	7,0	6,5
Occlusal	Double K	14,0	13,5	11,8	12,0	13,0
	Post Foss	11,0	10,0	9,5	10,5	10,0
	Width	11,5	12,0	10,5	10,0	11,5
At	Length	24,0			27,3	21,0
2 cm	Width	12,7			12,0	13,0
At	Length		21,5	20,5	28,0	20,0
1 cm	Width	12,0	13,0	11,0	11,5	13,0
Protostylid		1	pli	pli	1	1
Pli Caballinid		++	0	small	+	0
		NK/WA 28	NK/WA 92	NK/WA 28	Hohwa 13	
		P	M3	M3	M3	
		NK 898-89	NK 485-88	NK 897-89	HO 26-89	
Wear stage		1	1 - 2	2 - 3	2	
Height		65	55	31	47	
	Length	27,5	27,5	30,0	24,0	
	Ante Foss		8,5	9,0	6,5	
Occlusal	Double K		13,0	13,0	11,3	
	Post Foss		11,0	10,0	9,5	
	Width	13,0	10,0	11,0	9,5	
At	Length	24,0	28,0		25,0	
2 cm	Width	14,5	12,0		11,0	
At	Length	24,0	29,0	31,0		
1 cm	Width	14,5	12,0	11,0		
Protostylid				0	Ectostylid	
Pli Caballinid				+	+	

In Africa the replacement of hipparionine double knots by caballoid ones took place between Samburu (about 9 Ma, Nakaya & Watabe, 1990) and Mpesida (about 6.5 Ma, Hill & Ward, 1988). All Nkondo lower cheek teeth may be classified as caballoid, although the metastylids are not as triangular and pointed as they are in the younger Plio-Pleistocene typically caballine forms. In Eurasia, the characteristically caballine double knot appears in MN 15 - MN 16 zones (Mein, 1990) at Villaroya (Spain), Kvabebi (Georgia), Beregovaja (Russia), and Shamar (Mongolia). As in Africa, this typical caballine double knot is preceded by less pronounced incipiently caballoid patterns, for instance at Kirgis Nur levels 37-40 (Zhegallo, 1978, fig. 50) or Venta del Moro (Alberdi, 1972, fig. 114-112), or even in the Early Turolian of Iraq (Thomas *et al.*, 1980, Pl. I: fig. 1). But the Eurasian caballoid forms usually do not have a pli caballinid as much developed as in Africa.

Taking all the characters together, morphologies close to that of Nkondo lower cheek teeth are found at Mpesida, Lothagam, and even Laetoli, *i.e.* between 6.4 and 3.7 Ma.

C. Talus

The left talus NK 79'86, though badly preserved, may be referred to *H.* cf. *sitifense*: its height of 55 mm and distal articular width of about 42 mm are close to those of two small astragali from Lothagam referred to this species, and are smaller than those of an astragalus referred to *H. turkanense* or *H. primigenium* by Hooijer and Maglio (1974).

3. Lower Nyaburogo, Warwire, Kyeoro, Hohwa Formations

***H. turkanense, H.* cf. *sitifense, Stylohipparion* sp.**

It seems convenient to establish a distinction between "hipparions" without ectostylids, and "stylohipparions", even if the later derive from the former. In our sample from Uganda, hipparions are found up to the Warwire Formation, and are referred to *H.* cf. *sitifense* or *H. turkanense*. Stylohipparions appear for the first time at Kyeoro and are informally referred to *Stylohipparion* sp.

The taxonomy of stylohipparions is far from clear. Judging from the size of teeth and limb bones, there are certainly more than one species. Beside having high crowns, ectostylids and caballine lower cheek teeth, some stylohipparions exhibit two very original characters: a peculiar vomerine ridge (Kada Hadar Member of the Hadar Formation, Ethiopia; *Notochoerus scotti* zone of Koobi Fora, Kenya) and a flat, long, and broad mandibular symphysis with reduced third incisors ("*Eurygnathohippus*" of the Cornelia Beds of South Africa; Olduvai Bed II, Tanzania). We do not know however if, and how, all these characters are linked, nor when they developed. For example, there is a mandibular symphysis from Garba IVD, Melka Kunture, Ethiopia, probably about 1.4 Ma old, in which the third incisors are not reduced and the symphysis is not long nor flat. Whereas one mandibular symphysis from Vogelfluss (= Laetoli), Tanzania, seems to be on the way to "*Eurygnathohippus*" although the lower cheek teeth from Laetoli have no ectostylids.

From the lower part of the Nyaburogo Formation (around 5 Ma), comes a lower molar: NY 144'87. The length is rather small for *H. turkanense*, but the width is rather large for *H.* cf. *sitifense* (Tab. VI). There is no ectostylid. Cooke and Coryndon (1970) have described a few teeth from South and North Nyabrogo (*sic.*). The lower teeth (Cooke & Coryndon, 1970, fig. 5, J and K) do not show ectostylids and seem to belong to species of different sizes, possibly *H. turkanense* (Pl. II: fig. 18; Fig. 6) and *H.* cf. *sitifense*. The same impression is given by the upper cheek teeth: the P^3 and P^4 (Cooke & Coryndon, 1970, Fig. 5, D, E and F; this paper, Pl. I: fig. 13, 14) could belong to *H. turkanense*, while the molar M 33030 (Pl. I: fig. 15) is appreciably smaller (Fig. 5).

From the Warwire Formation (around 4.5 Ma), there is a lower premolar, NK 898'89, without ectostylid, which by its size (Tab. VI) may belong to *H. turkanense*. Two M_3, without ectostylids, possibly belong to the same species (Pl. II: fig. 19). An unworn upper molar, NK 2612'89, may belong to *H.* cf. *sitifense*.

At Kyeoro (about 3 Ma) there is a fragment of P_2 with an ectostylid. There is also a fragmentary upper molar, KY 27'90 (Tab. VII; Pl. I: fig. 11).

From the Hohwa Formation (around 2.6 Ma), there is a small unworn upper molar (HO 13'90), a small lower M_3 with an ectostylid (Pl. II: fig. 20), a talus too weathered to be measured, and a fragment of upper molar.

From Kaiso site A (also around 2.3 Ma), there is an unworn lower tooth of hipparion. No specimen can be compared with the Kaiso Village teeth, referred to "*H. albertense*" which may actually belong to different sized species, since the M^3 looks much larger than the type molar (Pl. I: fig. 16, 17).

Table VII - Measurements (mm) of upper cheek teeth of hipparions from the Warwire, Kyeoro and Hohwa Formations

		Warwire 28	Kyeoro 1	Hohwa 11
		NK 2612-89	KY 27-90	HO 13-90
		M	M	M
Wear stage		1	2	1
Height		65	52	64
	Occlusal	25,5	23,0	23,5
Length	At 2cm	21,0	22,5	22,0
	At 1cm	21,0	21,5	21,0
	Occlusal	20,0		
Width	At 2cm	23,0		22,0
	At 1cm	23,7		
Protocone L	Occlusal	9,0		9,5
Protocone W	Occlusal	3,8		
Plis Fossette			5,10,5,2	
Plis Caballin		1		

***Equus* sp.**

The earliest known *Equus* in East Africa are those of the Shungura Formation, Member G, which is younger than 2.3 Ma (Brown *et al.*, 1985). According to the limb bone sizes, I have supposed the existence of three species (Eisenmann, 1985): one very large, referred to *E.* cf. *stenonis vireti*, one large species referred to *E. numidicus* ?, and one smaller, referred to *E.* cf. *burchelli boehmi*. Most of the fossils were previously referred to *E. numidicus* ?. Later on, I had the opportunity to measure an entire MC III, number L7-3, from G5, smaller and slenderer than *E. numidicus* from Aïn Boucherit, and *E. numidicus* ? from Shungura G. It may represent another trend toward an "asininoid" morphology (incipient in *E. numidicus*), or it may just be an unusual *E. numidicus* ?. The small specimens previously referred to *E.* cf. *burchelli boehmi* may actually belong to this form.

From Kaiso site B, about the same age as Shungura G, there is a P_3 or P_4, KS 82'90. The height is 42 mm, the occlusal length more than 27 mm, the occlusal width is 17 mm. The lengths of the preflexid, double knot, and postflexid are respectively 9.5 mm, 18 mm and 14.5 mm. Length and width at 2 cm from the roots are 28 mm and 16 mm. Naturally the double knot is stenonine and the vestibular groove is shallow; there is a small pli caballinid. The dimensions are slightly smaller than in most premolars from Shungura G, but the Kaiso specimen may still be referred to *E. numidicus* ?.

From Kaiso 3, about 2.3 Ma, an upper molar, KS 1'86, is 56 mm high; the occlusal length is 26.5 mm and the protocone is 10.9 mm long; there is no pli caballin and 6 plis fossettes. This molar may also be referred to *E. numidicus* ? of Shungura G.

IV. CONCLUSIONS

From the Kakara Formation come a few *Hipparion* teeth of an exceptionally large size, not matched by any other species. They are referred to the new species *Hipparion macrodon*.

The Nkondo Formation hipparion teeth form the best sample presently known for the uppermost Miocene of East Africa. Two species are represented: *H. turkanense* and *H.* cf. *sitifense*. Both have caballoid – but not quite caballine – lower cheek teeth, without ectostylids. Judging from the teeth, *H. turkanense*, described by Hooijer from Lothagam 1,

seems to be present at Mpesida, Lukeino, Ekora, Nyaburogo, and Warwire. From the Lothagam material, it appears that *E. turkanense* had a skull without a preorbital fossa, and large limb bones. *H.* cf. *sitifense*, whose relation with the North African *H. sitifense* is not established, is represented at Ekora by a skull with a preorbital fossa, formerly referred by Hooijer to *H. primigenium*. Judging by the teeth and the metapodials, it is also present at Lothagam, Lukeino, and Sahabi. The metacarpals are as slender or slenderer than in *H. mediterraneum* from Pikermi; they have a deeper proximal end and a more "evolved" distal end, where the articular width is larger than the supra-articular one. *H.* cf. *sitifense* is also probably present at Nyaburogo and Warwire.

The younger, Pliocene fossils (Kyeoro, Hohwa, Kaiso site B, Kaiso 3) are poorly represented. Hipparions have ecto-stylids. The few *Equus* teeth may belong to *E. numidicus* ? found in Shungura Member G.

BIBLIOGRAPHY

AGUIRRE, E., & ALBERDI, M.T., 1974 - Hipparion remains from the Northern part of the Rift Valley (Kenya). - Proc. Koninkl. Nederl. Akad. Wetensch., ser. B, 77 (2) : 146-157.

ALBERDI, M.-T., 1972 - El genero *Hipparion* en España. - Vol. 1 : 368 p.; Vol. 2 : 235 tabl., 79 fig., 47 pl., Madrid.

ARAMBOURG, C., 1959 - Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. - Publ. Serv. Carte Géol. Algérie, n.s., Paléontologie, 4 : 161 p.

BERNOR, R.L., HEISSIG, K., & TOBIEN, H., 1987 - Early Pliocene Perissodactyla from Sahabi, Libya. - *In*: N.T. Boaz, A. El-Arnauti, A.W. Gaziry, J. de Heinzelin & D.D. Dechant-Boaz (eds), Neogene Paleontology and Geology of Sahabi, New York, Alan R. Liss Inc., 233-254.

BROWN, F.H., McDOUGALL, I., DAVIES, T., & MAIER, R., 1985 - An integrated Plio-Pleistocene chronology for the Turkana Basin. - *In*: E. Delson (ed.), Ancestors: the hard evidence, New York, Alan R. Liss Inc., 82-90

COOKE, H.B.S., & CORYNDON, S.C., 1970 - Pleistocene Mammals from the Kaiso Formation and other related deposits in Uganda. - Fossil. Vertebr. Afr., 2, 107-224.

EISENMANN, V., 1976 - Nouveaux crânes d'Hipparions (Mammalia, Perissodactyla) plio-pléistocènes d'Afrique orientale (Ethiopie et Kenya) : *Hipparion* sp., *Hipparion* cf. *ethiopicum* et *Hipparion afarense* nov. sp. - Geobios, 9 (5) : 577-605.

EISENMANN, V., 1977 - Les Hipparions africains : valeur et signification de quelques caractères des jugales inférieures. - Bull. Mus. natn. Hist. nat. Paris, 3^{e} sér., 438, Sci. Terre 60 : 69-87.

EISENMANN, V., 1979 - Le genre *Hipparion* et son intérêt biostratigraphique en Afrique. - Bull. Soc. géol. Fr., 7^{e} sér., XXI, 3 : 277-281.

EISENMANN, V., 1980 - Caractères spécifiques et problèmes taxonomiques relatifs à certains Hipparions africains. - *In*: R.E. Leakey & B.A. Ogot (eds.), Actes du 8^{e} Congrès Panafricain de Préhistoire et des Etudes du Quaternaire, Nairobi, 1977, 77-81.

EISENMANN, V., 1983 - Family Equidae. - *In*: J.M. Harris (ed.), Koobi Fora Research Project, Vol. 2, The fossil Ungulates: Proboscidea, Perissodactyla and Suidae, Oxford, Clarendon Press, 156-214.

EISENMANN, V., 1985 - Les Equidés des gisements de la vallée de l'Omo en Ethiopie (collections françaises). - *In*: Les Faunes plio-pléistocènes de la basse vallée de l'Omo (Ethiopie), T. 1 : Périssodactyles-Artiodactyles (Bovidae). - Cah. Paléontol., (Trav. Paléontol. est-afr.), CNRS, Paris : 13-55.

EISENMANN, V., 1992 - Origins, dispersals, and migrations of *Equus* (Mammalia, Perissodactyla). - Courier Forsch.-Inst. Senckenberg, 153 : 161-170.

EISENMANN, V., ALBERDI, M.-T., DE GIULI, C., & STAESCHE, U., 1988 - *In*: M. Woodburne & P. Sondaar (eds), Studying fossil horses, Collected papers after the "New York International Hipparion Conference, 1981"; Vol. I: Methodology, Leiden, Brill, 71 p.

EISENMANN, V., & KARCHOUD, A., 1982 - Analyses multidimensionnelles des métapodes d'*Equus*. - Bull. Mus. natn. Hist. nat. Paris, 4^{e} sér., 4, 1-2, C : 75-103.

FORSTEN, A.M., 1968 - Revision of the Palearctic *Hipparion*. - Acta Zoologica Fennica, 119, 134 p.

FORSTEN, A.M., 1972 - *Hipparion primigenium* from Southern Tunisia. - Notes Serv. Géol. n° 35 & Trav. Géol. Tunis. n° 5, Formation Beglia, fasc. 1 : 7-28.

HENDEY, Q.B., 1978 - The age of the fossils from Baard's Quarry, Langebaanweg, South Africa. - Ann. S. Afr. Mus., 75 (1) : 1-24.

HILL, A., CURTIS, G., & DRAKE, R., 1986 - Sedimentary stratigraphy of the Tugen Hills, Baringo, Kenya. - *In*: L.E. Frostick, R.W. Renault, I. Reid & J.-J. Tiercelin (eds), Sedimentation in the African Rifts, Geol. Soc. Spec. Publ., 25 : 285-295.

HILL, A., 1987 - Causes of perceived faunal change in the later Neogene of East Africa. - J. Hum. Evol., 16 : 583-596.

HILL, A., & WARD, S., 1988 - Origin of the Hominidae: the record of African large hominoid evolution between 14 MY and 4 MY. - Yearb. Phys. Anthrop., 31 : 49-83.

HOOIJER, D.A., 1975 - Miocene to Pleistocene Hipparions of Kenya, Tanzania and Ethiopia. - Zool. Verh., 142 : 75 p.

HOOIJER, D.A., 1979 - Hipparions of the Laetolil Beds, Tanzania. - Zool. Mededel., Leiden, 54 (2) : 15-33.

HOOIJER, D.A., & MAGLIO, V.J., 1973 - The earliest hipparion south of Sahara, in the late Miocene of Kenya. - Proc. Koninkl. Nederl. Akad. Wetensch., B, 76 (4) : 311-315.

HOOIJER, D.A., & MAGLIO, V.J., 1974 - Hipparions from the late Miocene and Pliocene of Northwestern Kenya. - Zool. Verh., 134 : 34 p.

HOPWOOD, A.T., 1926 - Fossil Mammalia. - *In*: E.J. Wayland, The geology and palaeontology of the Kaiso Bone Beds. Occ. Pap. Geol. Surv. Uganda, 2 : 13-36.

MEIN, P., 1990 - Updating of MN zones. - *In*: E.H. Lindsay *et al.* (eds.), European Neogene Mammal Chronology. New York, Plenum Press : 73-90.

NAKAYA, H., & WATABE, M., 1990 - *Hipparion* from the Upper Miocene Namurungule Formation, Samburu Hills, Kenya: Phylogenetic significance of newly discovered skull. - Geobios, 23 (2) : 195-219.

PICKFORD, M., SENUT, B., & HADOTO, D., 1993 - Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire / Vol. I: Geology. - Orléans, CIFEG, CIFEG Occas. Publ., 24 : 1-190.

POMEL, A., 1897 - Homme, singe, carnassiers, équidés, suilliens, ovidés. Les Equidés. - Monographies Serv. carte géol. Algérie, n.s. Paléontologie : 1-44.

SEN, S., 1990 - *Hipparion* datum and its chronologic evidence in the Mediterranean area. - *In*: E.H. Lindsay *et al.* (eds.), European Neogene Mammal Chronology. New York, Plenum Press : 495-505.

SONDAAR, P.Y., 1961 - Les *Hipparion* de l'Aragon méridional. - Est. geol., Inst. Invest. "Lucas Mallada", 17 (3-4) : 209-305.

THOMAS, H., SEN, S., & LIGABUE, G., 1980 - La faune Miocène de la Formation Agha Jari du Jebel Hamrin (Iraq). - Proc. Koninkl. Nederl. Akad. van Wetensch., B, 83 (3) : 269-287.

THOMAS, H., & PETTER, G., 1986 - Révision de la faune de Mammifères du Miocène supérieur de Menacer (ex-Marceau), Algérie : Discussion sur l'âge du gisement. - Geobios, 19 (3) : 357-373.

ZHEGALLO, V.I., 1978 - Gippariony Tsentral'noj Azii. - Sovmestnaya Sovetsko-Mongol'skaya paleontologicheskaya Ekspeditsiya, Trudy, 7 : 152 p.

Plate I - Upper cheek teeth of hipparions

Figure 1 - *Hipparion macrodon* nov. sp. Holotype. Kakara Formation, locality NY 75. P^2, P^3, P^4 : NY 256'90.

Figure 2 - *Hipparion turkanense*. Nkondo Formation, locality NK 28. P^3 or P^4 : NK 513'88.

Figure 3 - *Hipparion turkanense*. Nkondo Formation, locality NK 28. M^1 or M^2 : NK 546'88.

Figure 4 - *Hipparion turkanense*. Nkondo Formation, locality NK 28. M^1 or M^2 : NK 512'88.

Figure 5 - *Hipparion turkanense*. Nkondo Formation, locality NK 17. M^1 or M^2 : NK 209'86.

Figure 6 - *Hipparion* cf. *sitifense*. Nkondo Formation, locality NK 102. M^1 or M^2 : NK 613'88.

Figure 7 - *Hipparion* cf. *sitifense*. Nkondo Formation, locality NK 56. M^1 or M^2 : NK 540'86.

Figure 8 - *Hipparion* cf. *sitifense*. Nkondo Formation, locality NK 56. M^1 or M^2 : NK 541'86.

Figure 9 - *Hipparion* cf. *sitifense*. Nkondo Formation, locality NK 123. M^1 or M^2 : NK 548'89.

Figure 10 - *Hipparion* cf. *sitifense*. Nkondo Formation, locality NK 34. M^3 : NK 959'89.

Figure 11 - *Stylohipparion* sp. ?. Kyeoro Formation, locality KY 1. M^1 or M^2 : KY 27'90.

Figure 12 - *Stylohipparion* sp. ?. Nyaweiga (*sic.*). M^1 or M^2 : British Museum, M 26315.

Figures 13 and 14 - *Hipparion turkanense*. South Nyabrogo (*sic.*). P^3 and P^4 : British Museum, M 26317 and 26316.

Figure 15 - *Hipparion* cf. *sitifense*. South Nyabrogo (*sic.*). M^1 or M^2 : British Museum, M 33030.

Figure 16 - *Hipparion* "*albertense*". Type. Kaiso Village. M^1 or M^2 : British Museum, M 12615.

Figure 17 - *Hipparion* "*albertense*". Type. Kaiso Village. M^3 : British Museum, M 26334.

1

2

3

4

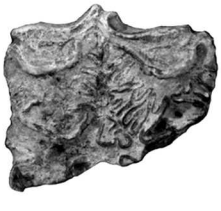
5

6

7

8

9



11

10

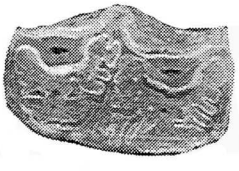
12

3 cm

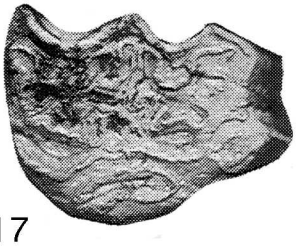
13

14

15



16



17

Plate II - Lower cheek teeth of hipparions

Figure 1 - *Hipparion macrodon* nov. sp. Kakara Formation, locality NY 75. P_2 : NY 256'90.

Figure 2 - *Hipparion* cf. *macrodon*. Kakara Formation, locality KI 6. P_3 or P_4 : KI 77'92.

Figure 3 - *Hipparion turkanense*. Nkondo Formation, locality NK 34. P_2 : NK 336'86.

Figure 4 - *Hipparion turkanense*. Nkondo Formation, locality NK 11. P_3 or P_4 : NK 58'86.

Figure 5 - *Hipparion turkanense*. Nkondo Formation, locality NK 58. P_3 or P_4 : NK 1546'89. There is no ectostylid!

Figure 6 - *Hipparion turkanense*. Nkondo Formation, locality NK 101. P_3 or P_4 : NK 215'89.

Figure 7 - *Hipparion turkanense*. Nkondo Formation, locality NK 34. P_3 or P_4 : NK 597'86.

Figure 8 - *Hipparion turkanense*. Nkondo Formation, locality NK 115. P_3 or P_4 : NK 734'89.

Figure 9 - *Hipparion turkanense*. Nkondo Formation, locality NK 28. P_3 or P_4 : NK 517'88.

Figure 10 - *Hipparion turkanense*. Nkondo Formation, locality NK 19. P_3 or P_4 : NK 233'86.

Figure 11 - *Hipparion turkanense*. Nkondo Formation, locality NK 56. P_3 or P_4 : NK 542'86.

Figure 12 - *Hipparion turkanense*. Nkondo Formation, locality NK 41 or NK 45, NK 46, NK 47. P_3 or P_4 : NK 203'88.

Figure 13 - *Hipparion turkanense*. Nkondo Formation, locality NK 28. P_3 or P_4 : NK 515'88.

Figure 14 - *Hipparion turkanense*. Nkondo Formation, locality NK 25. M_1 or M_2 : NK 264'86.

Figure 15 - *Hipparion turkanense*. Nkondo Formation, locality NK 115. M_1 or M_2 : NK 752'88.

Figure 16 - *Hipparion turkanense*. Nkondo Formation, locality NK 115. M_1 or M_2 : NK 735'89.

Figure 17 - *Hipparion* cf. *sitifense*. Nkondo Formation, locality NK 115. M_1 or M_2 : NK 1984'89.

Figure 18 - *Hipparion turkanense*. North Nyabrogo (sic). P_3 or P_4 : British Museum, M 26338.

Figure 19 - *Hipparion turkanense*. Warwire Formation, locality NK 92. M_3 : NK 485'88.

Figure 20 - *Stylohipparion* sp. Hohwa Formation, locality HO 13. M_3: HO 26'89.

1

2

3

4

5

6

7

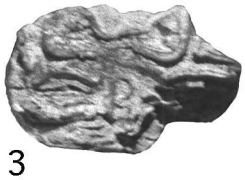
8

9

10

11

12



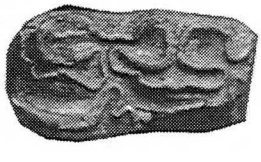
13

14

15

16

17



18

3 cm

19

20