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The late Miocene mammalian fauna of Chorora, Awash basin, Ethiopia: systematics, biochronology and ⁴⁰K-⁴⁰Ar ages of the associated volcanics

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ABSTRACT

New whole-rock ⁴⁰K-⁴⁰Ar ages on lava flows bracketing the Chorora Fm, Ethiopia, confirm that its *Hipparion*-bearing sediments must be in the 10-11 Ma time-range. The large Mammal fauna includes 10 species. They point to an early age within the Late Miocene, although not unambiguously near its lower limit. It lends support to the isochronous hypothesis of the "*Hipparion* datum".

RESUME

De nouveaux âges ⁴⁰K-⁴⁰Ar, sur roche totale, des coulées qui encadrent la Formation de Chorora (Ethiopie) confirment que ses sédiments à *Hipparion* doivent se situer dans une fourchette de 10 à 11 Ma. La faune de grands Mammifères comprend 10 espèces. Elle indique un âge ancien dans le Miocène supérieur, quoique pas nécessairement près de sa limite inférieure. Elle tend à confirmer l'hypothèse du synchronisme de l'"*Hipparion* datum".

Key-words: Upper Miocene, Ethiopia, Mammal fauna, K-Ar dating

INTRODUCTION

The Chorora Formation was named by Sickenberg & Schönfeld (1975). It includes the oldest sediments of the Afar depression, which were deposited along its southwestern escarpment. At its type-locality (8°53'40" N, 40°18'40" E), it consists of diatomites, pumices, tuffs, clays, sands and gravel; its thickness there is about 30 meters. Kunz et al. (1975) bracketed the Formation between 9 and 10.5 M.y., but these dates were obtained on lavas about 30 km away and not directly associated with sediments of the type-locality.

Vertebrate fossils were first discovered by Sickenberg & Schönfeld in a sandy layer of the type-locality. Fragmentary fossils (most of them now kept in the Niedersächsisches

Landesmuseum für Bodenforschung, Hannover: NLfB) allowed them to list the following species: *Homotherium* sp., Suidae gen.indet., Hippopotamidae (gen et sp. (?)nov.), Giraffidae (Palaeotraginae ?), Bovidae gen.indet., *Mastodon* (s.l.) spec. of longirostrinae group, *Stephanorhinus* ex aff. *leakeyi* Hooijer, *Hipparion primigenium* Kaup sspec., *Testudo* spec.

Tiercelin et al (1979) discovered micromammals in the same level (some of them were described by Jaeger et al., 1980) and they also gave (1979, Fig.1A) a section of the upper part of the Chorora Formation at the type-locality and provided ^{40}K - ^{40}Ar ages, 10.7 ± 0.19 and 10.5 ± 0.24 My respectively, for the rhyolites that directly under- and overlie the sediments which include the fossiliferous layer:.

In 1996 and 1997, two field campaigns led by the senior author were specifically devoted to the collection of large and micromammals (all kept in the National Museum of Addis Ababa, NMAA). Some of the Rodents were described by Geraads (1998); others are currently under study. We also sampled the lava flows overlying the sediments (samples CH 12 and CH 13) and from the one underlying them (sample CH11). A simplified section is given in Fig.1.

The fossiliferous layer can be followed over several thousand square meters, but careful survey demonstrated that large fossils are very scarce, with no real concentration. Even in the most fossiliferous area, where large Mammals are associated with Rodents, several test-excavations demonstrated a very low density of fossils.

ISOTOPIC DATING (H.B.)

Ages determinations were carried out on three whole-rock lavas (CH 11, 12 and 13), using the conventional ^{40}K - ^{40}Ar method. For whole rock analyses, samples were crushed and sieved to 315-160 μm grain size and then cleaned with distilled water. This fraction was used (1) for argon extraction under high vacuum by HF heating prior to a purification cycle of the gaseous released sample on three titanium sponge furnaces and one Ti-Zr S.A.E.S getters, and (2) after reduction to a powder for potassium analysis by atomic absorption spectrometry.

Argon isotopic composition was then analysed in a 180° stainless steel mass spectrometer with a 6 cm radius equipped with a 642 E Keithley ultra-sensitive ionic currents amplifier and reader, using isotopic dilution utilising the technique fully described in Bellon et al. (1981): an Al foil target containing a known volume of ^{38}Ar , buried as

positive ions under 30 KeV energy was added to each sample at the time of weighing, so that isotope dilution and homogenisation were achieved during the fusion of the sample.

Taking account of the "zero time" regressed ionic currents (for each isotope, i.e ^{36}Ar , ^{38}Ar and ^{40}Ar), age calculations were performed using the constants recommended by Steiger & Jäger (1977) with a one σ error calculated according to Mahood & Drake (1982).

Duplicate results are presented in table 1 together with the most characteristic parameters of the measurements i.e the ^{40}ArR (radiogenic argon 40), the percentage of ^{40}ArR versus the sum of ^{40}ArR and atmospheric ^{40}Ar and the amount of ^{36}Ar isotope of only atmospheric origin, but uncorrected from low blank values, typically less than 3.10^{-10} cm^3 for ^{36}Ar).

Within the limits of 1σ errors the ages for CH 12 and CH 13 are similar. Thus a mean age of 10 ± 0.30 Ma may be proposed for the emplacement of the rhyolitic upper flows that are slightly discordant upon the Chorora upper member, which includes the fossiliferous sedimentary strata. The lower flow (CH 11) has a significantly quite older age of 11 ± 0.45 Ma, that allows us to postulate this date for the upper limit of the age of the Chorora lower member.

The above new results confirm those by Tiercelin et al. (1979), but introduce a slightly larger period between the two volcanic sequences, which includes a quiescent episode during which the deposition of a conglomeratic sequence containing small sized volcanic pebbles occurred. The most probable age for the fossil-bearing level is at 10.5 ± 0.5 Ma, thus placing it in the Early Tortonian according to the 1994 geological time scale (Odin, 1994).

SYSTEMATIC STUDY OF THE MAMMALIAN FAUNA (D.G. & Z.A.)

Order Proboscidea

Family Elephantidae

Genus *Stegotrabelodon* PETROCCHI, 1941 ?

Stegotrabelodon n.sp.?

The specimen, an almost complete right lower M/3 (AL1000-1, National Museum, Addis Ababa; pl.1, fig.2) has already been briefly described by Coppens & Tassy (in Tiercelin et al., 1979); they pointed out its similarities with *Stegotrabelodon*.

Assuming that only a fragment of the first lophid is missing, it has 6 lophids plus a talonid. The structure of each lophid is that of an evolved tetralophodont gomphothere,

such as the one from Eppelsheim figured by Tobien (1980, fig.10), but there are several differences. Each lophid is more plate-like (an impression strengthened by a thick cement cover), less antero-posteriorly thick, and the main cusps are not so much larger than the mesoconelets. They are higher, however. There are strong posterior pretrite central conules, set against the main tubercles, on all first five lophids, and accessory posterior posttrite central conules on the 1st lophid, and vestigial ones on the other lophids.

Nothing is known of the tusks, and the placement of this tooth in the Amebelodontinae cannot be completely ruled out (Tassy, 1983, 1986, has suggested that *Tetralophodon*-like European molars might belong to this sub-family, and *Amebelodon* has been described from the late Miocene of Sahabi, Libya, by Gaziry, 1987), but we believe that it is much more likely that this tooth is intermediate between gomphotheres and elephantids.

It is more derived than the European Vallesian "*Stegotrabelodon*" *gigantorostris*, if this species really belongs here, as assumed by Tobien (1980). However, it is more primitive than other *Stegotrabelodon* from Africa, namely *S.syrcticus* from the late Miocene of Sahabi, Libya, *S.orbus* from the late Miocene of Lothagam, Kenya, or *S.schneideri* from the Pliocene of Menalla, Chad, by:

- the greater size and height of the main cusps relative to the mesoconelets, resulting in a less pillar-like appearance of all tubercles, and a less plate-like appearance of each lophid;
- the lower number of lophids.

A few forms similar to the Chorora one are known in the late Miocene of East Africa. In the Namurungule Formation, Nakaya et al. (1984) described a *Tetralophodon* sp. with some plate-like tendency of the lophs, and posttrite conules on most lophs, but its M/3 is unknown. From the Kakara Fm of Uganda, probably of early Upper Miocene age, Tassy (1994) described an "Elephantidae, forme primitive, gen.et sp.incertae sedis", which has only 5 lophs on M3/, almost no pretrite conule, and more plate-like appearance of the lophs. These last two characters are more derived than at Chorora, and on the whole, the *Stegotrabelodon* from Chorora is a good intermediate between these two forms.

We believe that the central position that the Chorora specimen seems to occupy between the tetralophodonts and true elephantids warrants a specific distinction, but since too many proboscidean taxa have been based upon isolated teeth, we refrain from naming a new species.

Order Artiodactyla
Family Hippopotamidae

Genus *Kenyapotamus* PICKFORD, 1983

cf *Kenyapotamus* sp. ?

We refer a single tooth (NLfB) to this taxon. It is an anterior upper premolar of a bunodont ungulate. The root is 8-shaped in section, suggesting incipient division. The crown is single-cusped, high, lingually recurved, with high anterior (?) cingulum, where the tooth is more worn. There is a posterior interstitial wear facet. This tooth belongs to an hippopotamoid animal in which the premolars were close together, without diastemas, because the large anterior wear facet must have been made by a lower P/1. It is not unlike the P1/ of a hippo of medium size (but this tooth is rarely preserved in the collections), but it is also very similar to the P1/ from Ngeringerowa referred by Pickford (1983) to *Kenyapotamus coryndoni*. There are, however, some differences: the crown is higher, the cingulum is not continuous but higher anteriorly. We tentatively refer this tooth to *Kenyapotamus*, a genus known from the early upper Miocene of Ngeringerowa, Ngorora, Nakali, Namurungule and Beglia (Pickford, 1990).

It is most unfortunate that this identification cannot be more positive, because *Kenyapotamus* is a good biostratigraphic marker, being replaced in the latest Miocene by true hippos (Pickford, 1983).

Family Giraffidae

Gen. et sp. indet. (Sivatheriini ?)

An incomplete upper molar, CHO1-14 (NMAA), lacking the labial wall, is similar in size and morphology to the "cf *Samotherium* sp" from Nakali (Aguirre & Leakey, 1974, fig.5), but we refrain from referring it to this genus because the mesostyle of the Nakali tooth looks stronger than in Eurasian *Samotherium* (as noted by Gentry, 1997: 110), and because the occurrence of this genus in Africa has never been satisfactorily demonstrated. The Chorora tooth is not very brachyodont, and its hypocone is U-shaped, a derived character contrasting with Giraffini and "*Palaeotragus germaini*" from Bou Hanifia (Arambourg, 1959), in which taxa it remains V-shaped.

A left calcaneum (pl.1, fig.3) is long and slender, with a concave posterior border. It is more like that of the Vallesian sivatheriine *Decennatherium* from Spain (Crusafont, 1952, pl.29, fig.4; Morales & Soria, 1981, fig.22) than like that of *Samotherium*.

The Chorora giraffid is certainly different from both Ngorora taxa, referred to *Palaeotragus primaevus* by Hamilton (1978), and to a larger species, close to *Giraffa*, by Gentry (1997: 110), but it might be identical with the larger taxon of the Namurungule Fm (Nakaya et al., 1984).

Family Bovidae

Gen et sp indet. 1

The most common bovid is represented by 6 teeth and a few limb-bones (NMAA). Upper teeth (fig.2) have moderate styles and ribs, the molars have a weak median pillar, a small central enamel island, a strong posterior accessory crest and V-shaped internal valleys. Lower molars have rather flat lingual walls, no goat fold, a small basal pillar on one of them but none on the other, and labial lobes rounded near the base but more angular higher up.

Literature suggests that a sharp break separates East African bovid faunas of the late Middle / early Upper Miocene from those of the late Upper Miocene. From Fort Ternan (Gentry, 1970) and Ngorora (Thomas, 1981), the most common bovids are boselaphines and species of uncertain tribal affiliation, looking like contemporaneous forms of Eurasia. They are unlike the Chorora larger bovid. In the late Miocene of Mpesida and Lukeino (Thomas, 1980) and Manonga (Gentry, 1997) modern tribes are first recorded: Alcelaphini, Reduncini, Tragelaphini.

The faunal break is perhaps not so sharp, however, because a rather wide time-gap separates both groups of localities, because there may be phyletic links between both groups of taxa (Gentry, 1978: 307), and because the appearance of modern tribes is much more firmly documented at the later site of Lukeino than at Mpesida.

The Chorora bovid has similarities with tragelaphines, but such an identification would be too speculative. It differs from Recent and putative late Miocene specimens of this tribe by its broad upper molars with V-shaped internal valleys. Precise identification, however, is hindered by the almost complete lack of horn-cores in Africa during most of the upper Miocene. There are indications of the occurrence of several other still poorly known taxa, at Bou Hanifia (Arambourg, 1959) or Djebel Krechem (Geraads, 1987) in North Africa, in the Namurungule Fm of Kenya (Nakaya et al., 1984) and the African bovid fauna in the Upper Miocene might be more diverse than usually assumed.

Gen. et sp. indet. 2, cf Neotragini

A single M3/, CHO1-23 (10.0 x 8.4; NMAA), documents a very small bovid, whose size and morphology match the Neotragini. The styles and pillars are very weak, and the external walls are flattened while the internal lobes are keeled.

Very small antelopes referred to Neotragini are known from Mpesida (Thomas, 1980) and perhaps even from the Middle Miocene of Ngorora (Thomas, 1981).

Order Perissodactyla

Family Chalicotheriidae

Subfamily Schizotheriinae

Genus *Ancylotherium* Gaudry, 1863

Ancylotherium sp cf *A.tugenense* (Pickford, 1979)

A first phalanx (CHO1-10; NMAA; fig.3: 4) belongs to a large chalicotheriid. The proximo-dorsal orientation of the proximal facet and the weak convexity of the distal one are unlike Chalicotheriinae, in which they are respectively more fully dorsal and strongly convex, and there is no doubt that this phalanx belongs to a schizotheriine. It is strongly asymmetrical and stout, but since it is not a duplex, usually found in digit II in *Ancylotherium*, we refer it to digit IV. It differs from that of *A.pentelici* (Schaub, 1943, fig.32, 35) by its flat palmar face, which is almost straight in lateral view, as in the African Plio-Pleistocene species *A.hennigi* (Dietrich, 1942, pl.IV, fig.33).

The earliest mention of the Schizotheriinae in Africa is at Mpesida, from where Pickford (1979) described a few remains of the manus and pes that he assigned to a new genus and species, *Chemositia tugenensis*. As pointed out by Coombs (1989), the generic name is probably not necessary, since the supposedly articular facets of the palmar face, the main characteristic of the genus, cannot possibly be articular. We will retain the specific name, however, because there is no evidence that the Mpesida schizotheriine is identical with *Ancylotherium hennigi*, defined at Laetoli, and the earliest mention of which is at Lukeino (Pickford, 1979).

Another schizotheriine was described from the Namurungule Fm (Nakaya et al., 1984); it was said to be distinct from "*Chemositia*" by its smaller size, but nothing is known of sexual dimorphism and differences between anterior and posterior phalanxes in East African forms. We believe that more evidence is needed before the occurrence in Africa of a second schizotheriine genus, besides *Ancylotherium*, can be accepted.

In any case, the Chorora phalanx confirms the occurrence of this sub-family in the upper Miocene of this continent.

Family Rhinocerotidae

Dicerotini indet.

The material includes 3 upper premolars (NMAA and NLfB; fig.3: 1-3), a lower premolar, a trapezoid and a cuneiform (NLfB). The labial wall of the upper premolars was apparently rather flat, a little wavy, without marked pillar. The protoloph is not pinched lingually, and is broadly connected to the metaloph, even on the P2/, which is less worn than the other premolars. On P2/, the bridges connecting the internal tubercles to the external ones are narrow; the post-fossette is enclosed by the posterior cingulum, and an "ante-fossette", anterior to the protoloph, is enclosed by the high anterior cingulum, as in *Paradiceros* Hooijer, 1968, from the late Middle Miocene of Fort Ternan and Beni Mellal (Guérin, 1976).

These dental features allow a clear distinction from *Brachypotherium* and *Chilotheridium*, while the large size distinguish these teeth from those of *Paradiceros* or "*Dicerorhinus*" *leakeyi* Hooijer, 1966, of the African Middle Miocene. In this latter species, to which Sickenberg & Schönfeld (1975) had referred the Chorora rhino, the premolars are also more trapezoid. In turn, no significant feature allow them to be distinguished from the Dicerotini, present in Africa from the late Middle Miocene onwards, and common in the upper Miocene. The cuneiform is less broadened than that of *Ceratotherium*, but a generic identification would be speculative.

Family Equidae

Hipparion sp cf *H.primigenium*

Hipparion is the most common large Mammal, but it is represented only by isolated teeth (NMAA, NLfB). Upper cheek teeth (fig.4: 1-4) are of medium size. The number of plications on the best preserved specimen is high, and it was apparently also high on the other, eroded specimens. The "pli caballin" consists of 4 or 5 folds. The protocone is flattened, and all upper teeth have a sharply demarcated hypocone, which is even isolated on M3/.

Lower teeth (fig.4: 5-7) have no ectostylid, but bear a protostylid. The double knot is rather symmetrical, with well rounded metaconid and metastylid, separated by a wide notch with a flat lingual bottom.

A single tooth, CHO1-5 (fig.4: 7), has no protostylid at the occlusal surface, and a very deep labial groove although it is undoubtedly a premolar. We prefer to explain these differences by the late wear stage of this tooth than by a taxonomic difference, although its large size and deep groove recall *H.macrodon* Eisenmann, 1994, from Uganda.

Measurements

	P ² no N°	P ² CHO1-1	M ¹ CHO1-2	M ¹⁻² no N°	M ¹⁻² CHO1-4	M ³ CHO1-3	P ₃₋₄ no N°	P ₃₋₄ CHO1-5	M ₁₋₂ CHO1-8	M ₃ CHO1-7
Length	35	31+	25.2	28.5	-	25	27.8	29.2	25	27.4
Width	25.5	25	26.1	-	-	21.5	15	15	-	-
L protocone	8.5	7.5	8.5	-	8.3	8.6				
L double-knot							15.6	14.9	13.8	11.7
Number of folds	28?		32							

The Chorora *Hipparion* shares many features with *H.africanum* Arambourg, 1959, from Bou Hanifia (flattened protocone, demarcated hypocone, hipparionid double knot), but it can be distinguished by its slightly larger size and stronger plication. These characters are found in the upper Miocene African hipparions that Eisenmann referred to *H.primigenium* (1980) or to *H. cf primigenium* s.l. (1994). They are known from Ngorora (Eisenmann, 1980; Hooijer, 1975), Nakali (Aguirre & Leakey, 1974; Aguirre & Alberdi, 1974), and Namurungule (Nakaya et al., 1984). They are smaller than *H.macrodon*, larger than the *H.cf sitifense* from East Africa, and morphologically clearly different from *H.turkanense* from the late Miocene (Hooijer & Maglio, 1974, pl.2). However, we will follow Eisenmann (1994) in keeping them in open nomenclature, because their relationships with the true European *H.primigenium* remain unclear.

Order Carnivora

Family Viverridae

Genus *Herpestides* Beaumont, 1967 ?

Herpestides ? afarensis n.sp.

Holotype: CHO1-24, incomplete left mandible, National Museum, Addis Ababa. Fig.5.

Diagnosis: A species of *Herpestides* similar to, but smaller than, *H.aequatorialis* Schmidt-Kittler, 1987, from Rusinga, with a relatively shorter P/4.

Derivatio nominis: from the Afar region.

The holotype is the mandible of a very small Carnivore, with P/3-M/1 and the alveoli of P/2. It is broken in front of P/2, at the level of the mental foramen, and just

behind M/1, so that the size of M/2 is unknown. The mandibular corpus is relatively slender, of regular height, with a convex lower border, except below P/3, behind the symphysis, where it is concave. The premolars are long, not at all crowded, with even a clear diastema between P/3 and P/4. The length of P/3 is more than 2/3 that of M/1.

Measurements:

P/3 : 3.1 x 1.4 ; P/4 : 4.0 x 1.6 ; M/1 : 4.6 x 2.2

P/3 looks somewhat eroded, but was certainly low, and simple.

P/4 is also rather low, but much more complex, with a strong anterior lobe, a strong accessory cuspid on the posterior edge of the main cuspid, and a thick posterior cingular transverse ridge.

M/1 is well worn; it has a long, forwardly salient paraconid, separated by a shallow valley from a strong metaconid which is clearly more posterior than the protoconid. The talonid is rather long but much narrower than the trigonid. It is basin-shaped with a ridge-like labial hypoconid, and a lengthened entoconid extending along the lingual border, but not reaching the metaconid. There is no distinct hypoconulid.

In spite of its very small size and of some similarities of its M/1 with African mustelids such as *Ictonyx*, this mandible is clearly viverrid by its long and low premolars, and especially its complex P/4 with well demarcated anterior lobe. The only Recent genus showing some resemblance to the Chorora species is *Viverra*, but its trigonid is not so widely opened lingually, its paraconid is shorter, and its metaconid smaller. These characters are already present in *V.chinjiensis* PILGRIM, 1932 from the Siwaliks. The earlier *V.modica* from France (Beaumont, 1973) has an M/1 with stronger metaconid, and more distinct talonid tubercles; the greatest differences with Chorora are found at La Grive, only slightly older than Chorora, showing that the evolutionary trends of this species are quite different from the East African ones. Viverrids are much less common than mustelids in the late Neogene of Eurasia and Africa, but are not rare in the lower Miocene of Kenya (Schmidt-Kittler, 1987). Among them, *Leptoplesictis rangwai* Schmidt-Kittler, 1987, from Rusinga, is about the same size as the Chorora species, but the metaconid of M/1 is much smaller. On the contrary, *Herpestides aequatorialis* Schmidt-Kittler, 1987, also from Rusinga, is very similar, in its available features, to the Chorora species:

- short diastema between P/3 and P/4;
- open trigonid on M/1, with long paraconid and posteriorly set metaconid;
- relatively narrow talonid, with two bordering ridges. However, the talonid is longer at Chorora than at Rusinga

We believe that the *Chorora* species can be included in the same genus as the Rusinga one, but it can be doubted whether this is really an *Herpestides*. Beaumont (1967) had insisted upon the variability of the carnassial talonid in the type-species of the genus, *H. antiquus* from the Aquitanian of France, but the morphology of the East African forms is unusual in France, and they might belong to a clade of their own.

Family Felidae

Genus *Machairodus* KAUP, 1833

Machairodus aphanistus (KAUP, 1833)

A fragment of left mandible (NLFb; pl.1, fig.1) includes the anterior part of the corpus, with the canine base, and part of the incisor alveoli. The length of the diastema and the possible occurrence of a P/2 are unknown, but the incisors and canines were set much higher than the premolars and molar, because the upper and lower border of the corpus are strongly convergent posteriorly. The mental foramen opens in the depressed lateral face, behind the canine root. A rounded ridge outlines the antero-inferior edge, which is regularly curved. On the anterior face of the symphysis, a wide vascular opening opens into a shallow vertical groove. In front view, this anterior face is rectangular, much higher than broad, with a lateral edge parallel to the sagittal plane. The anterior border of the symphysis is weakly concave. The alveolar border is missing, but the bottom of the alveoli is visible. I/1 was probably very small, I/2 and I/3 were larger, and the root of the latter was close to the canine. The incisors were thus rather crowded, little protruding, and much smaller than the canine. The maximum diameter of the latter is slightly greater than its distance to the midline. Its posterior keel is crenulated, and unworn. A second keel is lingual at the base of the tooth. Between them, the surface is flat.

Measurements:

Basal diameters of the canine: 16.5 x 11.9

Estimated breadth of the symphysis, anteriorly: 45

Height " " 54+ (± 58)

A proximal MtIII fragment is felid and probably of the same species. The articular facet for MtIV is deeply bowl-shaped, as in modern felids, not flattened as in *Homoherium* (Ballésio, 1963; Geraads, 1997).

In spite of its fragmentary condition, it is clear that this mandible is close to *Machairodus aphanistus*, defined at Eppelsheim, and mostly known from the Vallesian, although it perhaps survived into the Turolian (Montoya & Monparler, 1996). It is more primitive than the Turolian *M. giganteus* (Beaumont, 1975, 1978; Bonis, 1994). The large

size of the canine relative to the incisors, the narrowness of the front teeth are indeed diagnostic features of the former species.

Machairodus is rare in Africa, and most of its representatives are late Miocene or early Pliocene in age: Sahabi (Howell, 1987); Wadi Natrun (Stromer, 1913); Aïn Brimba (Petter & Howell, 1987); Langebaanweg (Hendey, 1974). The mandibular symphysis is known in some of these forms only. At Langebaanweg, "I/3 was appreciably larger than I/1 and I/2 were much smaller than I/3" (Hendey, 1974: 157), which suggests that I/3 was much larger than at Chorora. At Wadi Natrun (Stromer, 1913, pl.9, fig.4) and at Sahabi (Howell, 1987: "substantial symphyseal flange") there is a mental apophysis, and the canine is reduced, two character states more derived than at Chorora. The symphysis is unfortunately unknown in the only "Vallesian" form, from Bled Douarah in Tunisia, *M. robinsoni* Kurtén, 1976.

THE CHORORA MAMMAL FAUNA AND ITS PALEOECOLOGY

The updated list of the Chorora large mammals is the following:

Stegotrabelodon n.sp. ?

cf *Kenyapotamus* sp. ?

Giraffidae gen. et sp. indet., cf Sivatheriini

Bovidae gen. et sp. indet. 1

Bovidae gen. et sp. indet. 2, cf Neotragini

Ancylotherium cf *tugenense*

Dicerotini indet.

Hipparion cf *primigenium*

Herpestides ? *afarensis* n.sp.

Machairodus aphanistus

The most common Mammal, *Hipparion*, was certainly an open-country form. giraffids, bovids and rhinos may point to the same environment, although none of them is very hypsodont. Browsing forms might be altogether absent: *Kenyapotamus* was perhaps a grazer like the hippos, and *Ancylotherium* had relatively hypsodont teeth, despite its clawed fingers purportedly used to hook tree branches. All this would suggest an open savannah-like environment, but the faunal list is certainly not complete.

BIOCHRONOLOGY

Late Miocene faunas of East Africa can be sorted into two main sets (VI and VII of Pickford), roughly equivalent to the Vallesian and Turolian of Western Europe. To the early set belong the upper part of the Ngorora Fm, Nakali, the Namurungule Fm, and probably the Kakara Fm of Uganda (and, in North Africa, Bou Hanifia, Beglia and Jebel Krechem); to the later one Mpesida, Lukeino, Lothagam and Manonga.

Although the Chorora large Mammal fauna is fragmentary, there is substantial evidence that it belongs to the early set:

- *Stegotrabelodon* ? n.sp. is more primitive than the more elephantoid *S.orbus* and *S.libycus*;
- *Kenyapotamus* (assuming that the identification is correct) is unknown in the later set;
- the *Hipparion* is much more similar to *H.cf primigenium* than to the late Miocene *H.turkanense*;
- *Herpestides* was previously known only in the Early and Middle Miocene;
- *Machairodus aphanistus* is quite rare in the Turolian.

The main argument against a very early age within the Late Miocene is the evolutionary stage of *Stegotrabelodon*, which looks more derived than more typical *Tetraolophodon* from Tunisia (Geraads, 1987) and Namurungule, the later being well dated at ± 9.5 Ma. (Sawada et al., 1998). The difference is not great, however, and could be explained, in any case, by the persistence of *Tetraolophodon*, alongside primitive *Stegotrabelodon*. The large Mammals of Chorora would perhaps suggest an age somewhat more recent than that provided by absolute dating, which correlates with the earliest Vallesian of Europe, but there is no definite evidence of this discrepancy, and the Chorora fauna ranks among the early *Hipparion* faunas of the Old World, briefly summarised below.

EARLY HIPPARION FAUNAS OF THE OLD WORLD

There has been a continuous debate over recent years, on the date of immigration of *Hipparion* into the Old World. Long taken as close to 12 Ma., this arrival is now considered to be somewhat younger, but no agreement has been reached as to its isochrony (i.e., *Hipparion* reached all areas of the Old World within a short time) or diachrony. Reliable dating of *Hipparion* faunas older than 10 Ma. are extremely rare, and most of them point to a "First Appearance Datum" of ca. 10.5 Ma.:

- for Höwenegg, Swisher (1996) proposed an age of 10.3 Ma., based upon single-crystal ^{40}Ar - ^{39}Ar dating, but according to Woodburne et al. (1996) the *Hipparion* from Gaiselberg is more primitive, and therefore (according to these authors) older than that of Höwenegg;

- in Turkey, the magnetostratigraphic study of the Sinap Tepe section allowed Kappelman et al (1996) to estimate the *Hipparion* FAD at about 10.5 Ma.;
- in the Siwaliks, Woodburne et al. (1996) suggested a *Hipparion* FAD of ca. 10.4 Ma., mainly based upon magnetostratigraphy;
- in Tunisia, the Beglia Fm was supposed by Robinson & Black (1974) to cover the Middle / Upper Miocene boundary, thus precisely documenting the *Hipparion* FAD. It has been suggested, however (Geraads, 1989) that the whole Beglia Fm is of Upper Miocene age, and Woodburne et al. (1996) also reached the conclusion that its upper part is not of early "Vallesian" age;
- in Algeria, Sen (1990) assigned an age of more than 10.5 Ma. to the locality Bou Hanifia 1, which has yielded *Hipparion* (and the murid *Progonomys*). This date, based upon a magnetostratigraphic study, was considered as too old, again because of morphological features of the teeth, by Woodburne et al. (1996);
- in East Africa, besides Chorora, the first *Hipparion* seems to appear at Ngeringerowa, but the site is not precisely dated, and presumably later than the whole Ngorora Fm; the Namurungule Fm (Sawada et al., 1998) is probably slightly more recent.

All these results suggest approximate isochrony of the *Hipparion* FAD in wide areas of the Old World (most ages are within the 10.3 - 10.5 Ma range). A major discrepancy is the Spanish attempt to push back this FAD to 11.1 Ma., a proposal which is not entirely convincing because it is based upon stratigraphic and magnetostratigraphic correlation in which the key-section for FAD (Garcès et al., 1996, fig.3) is not continuous.

In sum, no positive data in the Old World point to a *Hipparion* FAD previous to about 10.6 Ma, but there are several datings, including Chorora, between 10.3 and 10.6 Ma. This accumulation of dates in a relatively narrow time-range tends to confirm the isochronous hypothesis, by failing to falsify it.

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CAPTION TO PLATE

- Fig.1 *Machairodus aphanistus*. Fragment of left mandible. NLfB. 1A: front view; 1B: lateral view. x 1.
- Fig.2 *Stegotetrabelodon* n.sp.? Lower right M₃ (stereo). NMAA. x 1/2.
- Fig.3 Sivatheriini ? indet. Calcaneum. NMAA. X 1/2.

CAPTIONS TO FIGURES

- FIG.1 Simplified stratigraphic column of the upper member of the Chorora Formation at the type-locality (from Tiercelin et al., 1979), showing the origin of the samples used for K-Ar dating.
- Fig.2 Bovid gen. et sp.indet.1. Upper teeth. x 2. NMAA. 1: left P⁴; 2: left P⁴; 3: left M^{2?}
- Fig.3 Perissodactyla. 1-3: Dicerotini indet. x 1. 1: left P^{3?}, NMAA; 2: right P^{4?}, NMAA; 3: right P², NLfB. 4: *Ancylotherium cf tugenense*, first phalanx of digit IV. x 2/3. NMAA.
- Fig.4 *Hipparion cf primigenium*. x 1. NMAA. 1-4: upper teeth. 5-7: lower teeth. 1, 3, 4: right teeth; 2, 5-7: left teeth.
- Fig.5 *Herpestides ? afarensis*. Left mandible with P₃-M₁. Holotype. NMAA. 1: lateral view. x 4. 2: M₁, lingual view, x 15. 3: M₁, occlusal view, x 15.