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***Hipparion pomeli* n.sp. from the late Pliocene of Ahl al Oughlam, Morocco, and a revision of the relationships of Pliocene and Pleistocene African hipparions.**

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Abstract

This paper addresses three points: 1. the description of a new species (*H. pomeli* n.sp.) of Late Pliocene hipparion from Morocco; 2. preliminary notes on hipparion skulls from Langebaanweg E Quarry (*H. hendeyi* n.sp.) and Chad Kossoum Bougoudi; 3. a new interpretation of African hipparion relations. The Appendix presents practical techniques allowing the estimation of adult dimensions in juvenile skulls and correlations between two mandibular and skull dimensions.

H. pomeli was a medium-size species related to, but smaller than, *H. hasumense* from East Africa. The distance vomer-basion was small and there was no reduction of the third incisors. The lower cheek teeth were caballine, moderately hypsodont, with moderate ectostylids. The limb proportions were cursorial. *H. pomeli* differed from the true 'Eurygnathohippus' (*H. afarensis* and *H. cornelianum*) by the basi-cranial proportions and the lack of reduction of the third incisors.

H. hendeyi had an extremely short vomer-basion distance, a short distance between the orbit and the POF, primitive teeth, and slender limb bones. It cannot be derived from *H. africanum* nor from *H. turkanense*. The greatest resemblances are with (the much smaller) *H. moldavicum* of Taraklia and *H. giganteum* of Grebeniki. The tentative reconstruction of *H. feibeli*'s skull indicates a possible relation with *H. hendeyi*.

The very large skull from Kossoum Bougoudi, Chad, resembles-but is much larger than, the Chinese *H. dermatorhinum*; its dimensions are compatible with the European *H. crassum* and the Mongolian *H. tchicoicum*.

It is proposed that more than two migrations gave rise to the various African species of hipparions.

Keywords: Equidae, Mammalia, Hipparion, phylogeny, Africa, Morocco

INTRODUCTION

Pliocene and Pleistocene hipparions are relatively well documented in East Africa but till now, they were very now poorly known in the Maghreb. The late Pliocene hipparion of Ahl al Oughlam is the first represented by skull, teeth and limb bones.

Ahl al Oughlam is a karst and fissure filling near Casablanca that has yielded a very rich fauna of micro- and macromammals (Raynal *et al.* 1990, 2001; Geraads 1993, 1995, 1996, 1997, 2002, 2004a, 2004b, 2006; Alemseged & Geraads 1998; Geraads & Amani 1998; Geraads *et al.* 1998; Geraads & Metz-Muller 1999) together with some fishes, reptiles (Bailon, 2000) and lots of birds (Mourer-Chauviré & Geraads, *in press*). The sediments are not stratified, and the faunal sample is homogeneous, showing that the filling of the fissures was virtually instantaneous. Biochronological comparisons with East Africa suggest an age of ca. 2.5 Ma, thus roughly contemporaneous with Omo Shungura Member D, or the gap in the Koobi Fora succession.

Abbreviations : AaO = Ahl al Oughlam; Hadar DD = Hadar Formation, Denen Dora member; Hadar KH = Hadar Formation, Kada Hadar member; Hadar SH = Hadar Formation, Sidi Hakoma member;
POF = pre-orbital fossa. L = length; W = width; MC III: third metacarpal, PH I: first phalanx of the third digit, PH II: second phalanx of the third digit, PH III: third phalanx of the third digit, MT III: third metatarsal.
Measurements are in mm.

SYSTEMATIC PALEONTOLOGY

Family Equidae Gray, 1821

Genus *Hipparion* De Christol, 1832

Hipparion pomeli n.sp.

Holotype. AaO-3647, skull, virtually complete but transversely crushed.

Type locality. Ahl al Oughlam, Casablanca, Morocco. About 2.5 Ma.

Diagnosis. A *Hipparion* of medium size; basion to vomer distance short; muzzle moderately long and wide; faint POF 50mm in front of the orbit. Incisor arcade rounded. Cheek-teeth large, moderately hypsodont; lower cheek-teeth caballoid, with moderate ectostylid but sometimes an accessory one.

Derivatio nominis: in acknowledgment of Auguste Pomel's prominent contributions to the paleomammalogy of North Africa.

Description

Skull. AaO-3647 (Figure 1A) is the skull of an adult male (canines 12mm long; all teeth erupted but not very worn). It is entire but distorted by lateral crushing. Most of the interesting information can nevertheless be noted. The size is medium, the basion to vomer distance is short, the muzzle moderately long and wide. There is a faint POF 50mm in front of the orbit. Comparisons are made with other hipparion skulls by ratio diagrams, taking the average *H. dietrichi* skull from Samos as reference; the corresponding data are given in Table 1. Some of the dimensions used in the ratio diagrams represent the supposed adult state, estimated from juvenile skulls (KNM ER 3539, Olduvai BK II-283). Some muzzle dimensions were also estimated from mandibles (AL 177-21, KNM ER 1626, Omo C, COR 679). Data and explanations are given in the Appendix.

Figures 2 and 3 are ratio diagrams comparing the Moroccan skull to other hipparions. In Africa, AaO-3647, although smaller, resembles AL-340-8 from the Denen Dora member of the Hadar Formation (Eisenmann 1976, Pl. 1). Bernor & Armour-Chelu (1997) referred the latter to *H. hasumense* (described on lower cheek teeth from locality 204, Tulu Bor member, East Turkana, Eisenmann 1983) and noted similarities with WW-1528-92 of Wembere Manonga. WW 1528-92, appears to have a longer muzzle but is otherwise quite similar. Other specimens that present some resemblances were found in the Denen Dora and Kada Hadar members of Hadar, and possibly in Member C of Shungura Formation. BKII-2845/6 of Olduvai, unfortunately distorted, seems also rather similar.

The next ratio diagrams (Figures 4 and 5) illustrate the pattern of a second group of late African hipparions. The main difference is in the shape and position of the posterior border of the vomer relatively to the basion and the posterior border of palate (measurements # 4 and # 3). The vomer-basion distance is much longer. As far as we know, such 'hypercaballine' proportions are unique. Moreover, in the adult type skull (AL 363-18) of *H. afarensis* from Hadar KH and in the juvenile skull KNM ER-3539, the vomer has an acute V-shaped posterior border and an acute median ridge (Eisenmann 1976, Pl. 2 and 3). In probable correlation with the long vomer-basion distance, the Postorbital line (# 24) looks longer relative to the Anteorbital line (# 23). In addition, the muzzle width (# 15) is very large when compared to the cheek teeth and muzzle lengths (# 9 and 1), reminding of *H. dietrichi* of Samos.

Scatter diagrams (Figures 6-7) illustrate the differences between the two groups. The corresponding data (including those that were not plotted) are given in Table 2.

Thus, in a very schematic way, at least two groups of skulls may be distinguished:

1. *H. hasumense* group: *H. hasumense* (Hadar AL 340-8 and Wembere Manonga WW 1528/92) and *H. pomeli* (AaO-3647 and Olduvai BK II-2845/6).

The muzzle is long and narrow; the basion to vomer distance is short; the cheek teeth are relatively large. We refer to *H. hasumense* the Hadar skulls and skull fragments AL 116-115, AL 155-6, AL 164-3, AL 241-18, possibly AL 142-18, and the mandibles AL 177-21 (the latter was first referred to *H. afarensis* by Eisenmann, but we presently agree with Bernor & Armour-Chelu 1999a that it belongs to the *H. hasumense* group); Omo 18-1968-363 and Omo 18-1969-90. Thus the group is documented, besides Ahl al Oughlam, in the Hadar Formation, SH2, DD, and KH 1-2 members; Wembere-Manonga Valley, Kilolei member; Shungura Formation member C; Olduvai BK II.

2. *H. afarensis* group: *H. afarensis* (Hadar AL 363-18, and probably AL 164-3) and *H. cornelianum* (East Turkana KNM ER-3539). The vomer has an acute V-shaped posterior border and an acute median ridge; the basion to vomer distance is long; the muzzle is short and wide; the cheek teeth are relatively small. These two species differ mostly by the degree of reduction of the third incisors. We refer to *H. cornelianum* the skull fragments Olduvai BK II-264, BK II-283, BK II-067/5465, and the mandibles or fragments of mandibles Hadar AL 59-9, East Turkana KNM ER-1626; Omo 118-1972-5; Olduvai no n° (Leakey 1965, pl.20), Olduvai 067/5344, Olduvai 1955-293; Cornelia Cor 679. This group is documented in the Hadar Formation, KH 2-3 member; East Turkana Formation, Burgi member; Shungura Formation, member F; Olduvai Bed II; Cornelia.

None of these skulls has a real POF, but some of them exhibit a more or less marked depression a few centimetres in front of the orbit. It may be clearly seen on the Olduvai skull illustrated by Hooijer (1975, Plate 7-1) and on AL 241-18 of Hadar.

In both groups the lower cheek teeth are caballine and with ectostylids.

Mandible. AaO-197 is a left mandible without symphyseal part (Figure 8B2). The cheek tooth series is 159mm long and the length of the ascending ramus behind the cheek series is 129mm. The heights are: ca 60mm in front of p2 and 70mm below p4.

Incisors. The upper, not very worn, incisors of the skull AaO-3647 are large (Figure 1A2). From I1 to I3 the mesio-distal diameters are ca. 18, 22, and 19mm. The incisive arcade is rounded and not very wide, because the I3 are placed behind the I2. Their position does not seem to result from postmortem deformation but from premaxillaries that are too small to accommodate large incisors. The maximal incisor arcade width (across the I2s) is 65mm. A prominent ridge is visible on the labial surface of the left I3. On the occlusal surface, it comes in contact with the distal border of I2.

Another complete set of not very worn upper incisors is AaO-2104. From I1 to I3 the maximal heights are 68, 64, and ca. 55mm; the mesio-distal diameters are 21, 21, and ca. 22mm; the labio-lingual diameters are 10, 11, and 9.5mm. There again, the I3s were placed behind the I2s as shown by a clear indentation along the distal buccal border of the I2s. At mid-crown, the diameters are 15*13 on I1, 16.5*14 on I2, and 15*11 on I3.

Even in *Equus*, the distinction between upper and lower incisors may be difficult, and it is even more so in hipparions. Most of the isolated incisors, often fragmentary, from AaO cannot be surely sorted. But it is clear that during their wear they did not remain wide (mesio-distally) and shallow (labio-lingually) for as long a time as those of *H. afarensis* s.l and *H. cornelianum*. On the other hand, when they are little worn, their width is much larger than in AL 155-6 (also little worn) from the Denen Dora member, and more like AL 177-21 (even less worn and also from Denen Dora). In the Shungura Formation, the more similar incisors are from unit C8 (Eisenmann 1985, Pl.1-1).

Permanent upper cheek teeth. Eight individuals are represented by complete series or associated teeth (Figure 1A3, 1B, 1C; Table 3). There are moreover 20 isolated cheek teeth (Table 4). The sample looks homogeneous. The teeth are moderately or very plicated, with plis caballins ranging in number from one to four. Protocones are lenticular or lingually concave (Eisenmann et al. 1988, Fig.5 C4, C6). In P3 and P4, the occlusal surface tends to be flat, while molars tend to have transversal ridges.

In Tunisia, the upper cheek teeth of Aïn Brimba are larger while those of Ichkeul are about the same size (Figure 9; Tables 5-6). In East Africa, the more similar sizes may be found in the skull of *H. afarensis* of the Kada Hadar and Sidi Hakoma members of Hadar, in Usno, and in member B of Shungura Formation. The Denen Dora teeth are often larger, while most of the Omo teeth are smaller.

A scatter diagram compares the hypsodonty of upper unworn or little worn M3s, plotting the height at the mesostyle versus length at mid-crown (Figure 10). Schematically, three groups may be distinguished: less hypsodont in Chad (Kollé and Toros Menalla), Ichkeul; middle hypsodont ranging in time from Omo A (4-3.5Ma) to Omo E (2.4-2.3Ma); very hypsodont from Omo C (3-2.5Ma) to Olduvai. Note that one of the two M3s of Omo C plots with middle hypsodont and the other with very hypsodont, indicating the possible presence of two species. The little worn M3 of AaO appears middle hypsodont. The Hypsodonty Index ($HI = \text{mesostyle height} * 100 / \text{length at mid-crown}$) is 221 to 235 in the less hypsodont group, 241 to 276 in the middle hypsodont, and 297 to 315 in the very hypsodont one.

Three groups appear again for unworn or little worn other upper cheek teeth (Figure 11). A very hypsodont group (HI = 318 to 340) comprises teeth from Olduvai, KBS, Omo F, Omo G, but also, very surprisingly, one tooth from Omo B. The middle hypsodont group (HI = 264 to 298) comprises specimens from Hadar DD and unknown levels, Omo C, Omo F, and Kossom Bougoudi, Chad. Aïn Brimba and Ichkeul plot with the less hypsodont group (HI = 243 to 257). Again, there is possible evidence for two species at the same time: at Hadar DD2, Omo F, and at Chad Kossom Bougoudi. There are no data for AaO.

Deciduous upper cheek teeth. They are moderately plicated but with large or bifid plis caballins (Figure 1D). Data are provided in Table 7.

Permanent lower cheek teeth. Four individuals are represented by complete series (Figure 8A-B; Table 8). There are also 12, mostly isolated, specimens (Table 9). The teeth are caballoid, with protostylids (plis or isolated) and ectostylids. Most ectostylids are not very large, although they are larger at the base of the crown. In two molars there are additional ectostylids, very small but reaching the occlusal surface at least ca. 3cm from the roots. The caballoid pattern of the lower cheek teeth indicates without any doubt that the AaO hipparion is an 'advanced' hipparion. What additional indications may be gathered from the presence of ectostylids ?

The development of ectostylids and its possible use for biostratigraphy has been discussed in detail for samples of Hadar, Omo, and East Turkana (Eisenmann 1977). Although there are no extensive analyses of the function of ectostylids, it seems likely that they do have some function, possibly in increasing the grinding ability. It is clear, however, that whatever their function, as long as ectostylids are not yet in wear, the plis caballinid appear as some kind of 'vicariants' of ectostylids, providing occlusal enamel at the very place occupied later by ectostylids. A good illustration is provided by the molar Omo C 40-68-3015 (Eisenmann 1985 Pl.2-17-18) and by several teeth from Aïn Brimba (Arambourg 1970, Pl XVII-11, 11a):

- On the occlusal surface of a little-worn m2, the pli caballinid is very well developed; the apex of a first ectostylid appears 12mm below the occlusal surface; the apex of a second ectostylid is visible 10mm below the first; at that level, the first ectostylid is about 5mm long; a few millimetres below, the second ectostylid is nearly as long as the first; if they were to fusion, the total ectostylid length would be of about 8-9mm.

- On the slightly more worn m1 of the same series, the first ectostylid is already beginning to wear, taking the place of the nearly absent pli caballinid; the apex of the second ectostylid is visible 32mm below the occlusal surface.

- On the unerupted p4, an ectostylid appears ca. 10mm below the occlusal surface; between the occlusal surface and the ectostylid there is a very developed pli caballinid.

Measurements of Aïn Brimba lower cheek teeth are given in Table 10.

At Ichkeul, the apex of the ectostylid on an unworn premolar is about 9mm from the occlusal surface. The tooth was sectioned at 2cm from the occlusal surface. At this level, the length is 28mm, the width is 14.7mm, the double knot is 14.7mm long, the postfossette 12.2, the ectostylid 3mm. The rest of the tooth is broken.

The growth of teeth proceeding from apex to roots, the distance between the apex of the tooth and the apex of the ectostylid(s) should be more meaningful in terms of evolution than the height of the ectostylid from the base of the crown. In the Omo C5-8 little worn m2 (Eisenmann 1985, Pl.2-18) the first ectostylid appears more 'evolved' - i.e. closer to the occlusal surface, than in the m2 of Aïn Brimba while in an unworn p4 of the Kilolei Member of Wembere-Manonga Valley (Bernor & Armour-Chelu 1997), the distance is the same as in the p4 of Aïn Brimba. Naturally in different species the development of ectostylids may be different: from the Ibole Member of Wembere-Manonga Valley (Bernor & Armour-Chelu 1997), the ectostylid of one m2 (large species) is at more than 37.6mm from the occlusal surface, while in another m2 (small species), the distance is only 13mm. But in the m2 of the large species of Kilolei member, the ectostylid has grown to less than 13.9mm from the occlusal surface.

In Omo member F, the first ectostylid at least is already formed at the apex of the crown (Eisenmann 1985 Pl.2-5). Three or even four ectostylids appear on sectioned teeth from Omo G (Eisenmann 1985 Pl.2-9). Their fusion results in a peculiar, inflated and trifold ectostylid, at times almost fused with the pli caballinid (Eisenmann 1985 Pl.2-12-15). This seems to be the ultimate degree of ectostylid evolution. A trifold pattern is already present in some teeth of the Denen Dora member of Hadar (AL 183-41). It may also be seen at Koobi Fora (KNM ER 2766 SU-, Burgi and KBS).

At AaO, there are no unworn lower p3-m2 so that we do not know if ectostylids were already developed at the apex of the crown. There is no evidence of the peculiar trifold pattern of Omo G; the ectostylids are not very large but a second ectostylid may occur (AaO-4072). In East Africa, the pattern would be consistent with an age older than 3Ma.

Deciduous lower cheek teeth. Most teeth are in the very first stages of wear (Figure 8C; Table 11). Protostylids are always present and may sometimes be isolated. Ectostylids are not very large. They appear about 10mm below the top of the tooth. Secondary ectostylids appear about 5mm lower. It

may be noted that the double knots of dp2 grow in the same way as the ectostylids, i.e. by fusion with a secondary enamel pillar a few millimetres below the top of the crown.

Size Index, variability of limb bones, and sexual dimorphism. Obviously, the size of a specimen can be qualified by comparisons with the same kind of specimens. But how to compare the size of a talus to the size of a second phalanx ? And how to determine if the overall size of animals found at one locality was larger or smaller than at another ? The Variability Size Index (VSI) is a way to address these questions. Devised by archeozoologists (Uerpmann 1982, Meadow 1999), the VSI is one of the size index scaling techniques. A sample including all the bones of a taxon is chosen as reference. Mean and standard deviation are calculated for each measurement of this sample. The comparisons are done using the following formula : $VSI \text{ (variability size index)} = 25(x-m)/s$ where s is the standard deviation of the mean (m) of the reference measurements to which another measurement (x) is being compared. The obtained values are plotted on a histogram graduated in one, two, three, or more standard deviations from the reference. As phrased by Meadow (1986), 'Using this formula, the standard dimension is set at zero; a measurement one standard deviation larger than the standard (reference) dimension will be plotted at 25, one standard deviation smaller at -25, etc'. It is recommended to use the same kind of dimensions (widths, or depths, or lengths) for all the bones. We have tried to find if this technique could bring some interesting information in the present study.

1. VSI based on Höwenegg sample. The detailed description by Bernor et al. (1997) of the late Miocene Höwenegg sample affords the first basis of normal intraspecific variation for hipparions. Among the published measurements we have chosen to use only widths (Table 12), because they are more frequently available on fossils than lengths and depths, and because it is not recommended to use together different kind of measurements. For the tibial diaphysis width, we have used the median of Höwenegg (44.6) instead of the mean (42.6) and we supposed a standard deviation of 2 instead of 5.61 because they appear more consistent with the rest of the data: a minimal value of 32.4 and a corresponding standard deviation of 5.61 indicate either the inclusion of a juvenile specimen or a printing error; there is no reason why the standard variation would be more than 5 for the tibia width when it is comprised between 1.1 and 2.66 for other bone widths.

Equus bones do not evidence sexual dimorphism, at least not in a marked way. There is no evidence yet that it was otherwise in hipparions (Bernor et al. 1997). The distribution of metrical values within a monospecific adult (epiphyses perfectly fused) sample should be normal. In consequence, an "abnormal" variation or distribution may reflect a long time of deposition during which a given species could have changed, or a coexistence of different taxa, or sexual dimorphism.

The AaO histogram seems, on the whole, to follow a normal distribution, centered on a peak between 50 and 75, i.e. at two-three standard deviations from Höwenegg (Figure 12). But eight values plot between 175 and 250, evidencing the presence of surprising widths. All of them are proximal widths of MC III. The preserved six distal widths of the corresponding MC III plot between 50 and 150. Thus, the asymmetry of the histogram reflects only an anatomical difference between AaO and Höwenegg MC III: in the first, the proximal epiphyses of some MC III are relatively wider.

According to the coefficients of variation, the variability of AaO is compatible with the variability of some assumed monospecific samples of *Equus*, but compared to the best samples of *Equus* (Eisenmann et David 2002; Eisenmann 2002, 2004), and *Allohippus*, the size variability at AaO is larger. Indeed, the coefficients of variation of the tali are quite bigger than in the well represented extant *Equus grevyi* and bigger too than in the very large fossil sample of *Allohippus vireti* from Saint-Vallier (Table 13). Since the fossils of AaO are believed to have been deposited during a short period of time (see Introduction), and since there is no evidence for the coexistence of two species, we cannot exclude that some sexual dimorphism existed in *H. pomeli* but it does not appear clearly on the VSI histograms.

Although much poorer than AaO's, the Hadar DD sample is interesting because it includes a nearly complete skeleton: AL 155-6. On Figure 12, it is represented by white points. One of the largest values of AL 155-6 is, like in *H. pomeli*, the proximal MC III width (the two other are second and third phalanges widths). On the larger side of AL 155-6 plot two radii (AL 155-1 and 338-13), one distal MC III (AL 155-1), one proximal MC III (AL 116-33), and one second phalanx (Al 340-1). After consideration of the other dimensions (not included in our VSI), it appears that only the fragmentary MC III AL 155-1 (extreme point on Figure 12) belongs without any doubt to a larger hipparion.

The recurring very large deviations of MC III proximal widths from the Höwenegg standard suggests that this old hipparion is not quite appropriate as a basis of size comparison for much younger hipparions. We have therefore tried to use *H. pomeli* as standard for further size comparisons.

2. VSI based on *H. pomeli* sample.

Using this reference (Table 12), the AaO histogram is of course 'normal' (Fig. 13). The Koobi Fora hipparions are quite smaller: the white ellipses indicate KBS member specimens, the two black squares correspond to tali from Chari and 'TB-?'. The Olduvai Bed II sample appears to possibly include two species: a distal MC III (DC II 52/679) seems very large.

Figure 14 shows the size differences between members A-B and G of the Omo Shungura sequence: a very small hipparion appears in member F, possibly represented later in KBS member of Koobi Fora Formation.

Hipparions of Hadar (Figure 15) appear quite larger than those of Shungura (Figure 14). At DD, there is an impression of three size groups, the associated bones of AL 155-6 plotting with the smallest.

Using AaO as standard instead of Höwenegg (Figure 12), AL 155-6 acquires a normal distribution. The presence of an extremely large hipparion (AL 155-1) is confirmed.

3. Conclusions

- Although far from perfect, the use of *H. pomeli* as standard may be recommended for size comparisons of late African hipparions bones.
- There is no evidence of a marked sexual dimorphism in *H. pomeli*.
- The too frequent lack of association of bones, teeth, and skulls renders specific attribution of bones very awkward, but excepting the extremely large AL 155-1, the DD histogram is a good approximation to the size of *H. hasumense*. The latter was at least one standard deviation larger than *H. pomeli*.

Third metapodials. There are about 20 more or less complete adult MC IIIs and 35 MT IIIs, 15 of which are more or less entire (Table 14). In ratio diagrams, we use the minimal antero-posterior diameter of the medial condyle (# 13 VE) rather than of the lateral condyle (# 13 NY). The latter was introduced only at the New York conference (Eisenmann et al. 1988) and most of our equid material was measured before.

Some scatter diagrams (not figured) show two sizes and /or morphologies: more or less robust, with more or less large proximal articular surfaces or distal widths. The coefficients of variation, however, are compatible with a monospecific sample. Table 15 gives the dimensions of some small and/or slender specimens of third metapodials not included in the statistical tables. They are probably subadult metapodials (like AaO-3707 and AaO-196) or juvenile.

Metacarpals. Compared to *H. mediterraneum* from the late Miocene of Pikermi (reference for the Simpson ratio diagram, Figure 16), the AaO metacarpals are longer (# 1), more robust (# 3), wider at the level of supra-articular tuberosities (# 10), and have a more developed keel (# 12).

Comparisons with other African hipparions are illustrated in Figure 17. The closest resemblance is with the hipparion of Olduvai (mean of FLKN I 934, 7693, and SHK II 57/935), which is, however, more robust. From Koro Toro, Chad, one MC III (KT 96-17) is much more robust and has a more developed distal end; it falls outside the range of variation of AaO. The MC III from Ichkeul is longer than the average and seems slenderer, but since it is not well preserved, most of its dimensions are uncertain. A metacarpal from Melka Kunturé, Gomboré II, seems close to those of Olduvai but is also poorly preserved. Most metacarpals from Hadar (not illustrated) are overall larger or have relatively larger distal ends (in particular the single specimen from the upper level AL 361-1, Kada Hadar member).

The development of the keel is an important character: functionally, it limits the lateral mobility of the articulation between third metapodials and first phalanges and facilitates sagittal 'pendular' movements. It is however difficult to quantify. To do so, Staesche & Sondaar (1979) have introduced the keel index: maximal antero-posterior diameter of the keel divided by the minimal antero-posterior diameter near the keel (percentage). Bernor et al. (2005) have greatly refined the estimation of the keel development by taking also into account the size (scaling); in doing so, however, they were obliged to deal with relatively few specimens. We did no scaling - thus being able to use more specimens - and instead of calculating a percentage, we have considered the development of the keel as the difference between its maximal antero-posterior diameter and the minimal antero-posterior diameter of the medial condyle. When plotted versus the distal articular width of third metacarpals (Figure 18), it appears - naturally enough - that the protrusion of the keel is related to the size of the MC III. A main group includes most of African hipparions: the relative development of the keel is roughly the same from Langebaanweg E and Olduvai (small form: l,m,n) to Olduvai (large form: o to u), including AaO, Hadar SH (d,i,j,k) and KH (b). Outside this main group, plot Omo F (5) and Roccaneyra (6) where the protrusion is maximal and more pronounced than in dolichopodial hipparions (Venta del Moro, Maramena (1), Layna (2), Odessa (3), Sagajdak (4)). Minimal protrusion is found at Koro Toro, Chad (9) and in one specimen of Hadar DD2-3 (a). It is remarkable, by the way, that the keel seems relatively less developed in Hadar DD (c, e to h), and in particular less than in the contemporaneous Omo B (v,w). Mongolian (Shamar and Beregovaja) hipparions, whether more robust (*H. tchicoicum*) or more gracile (*H. houfenense*), plot with the main group. Not represented on Figure 18, *Hipparion crassum* (Perpignan), *H. crusafonti* (Villaroya), and most of *H. heintzi* (Çalta) also plot with the main group.

Thus, it seems that the development of the keel cannot be directly related to geological age, nor to size, or gracility. Very probably, it is more related to environmental conditions that may select better adaptation to running in open landscapes, but local population idiosyncrasies cannot be excluded. At all events, it seems risky to recognize lineages using the keel development.

Metatarsals. Compared to *H. mediterraneum* (reference for the Simpson ratio diagram, Figure 19), the AaO metatarsals are longer (# 1), more robust (# 3), proximally and distally deeper (# 6, # 12), and have much more developed distal widths (# 10 and 11). The single and incomplete MT III of Kvabebi (Vekua 1972; Alberdi & Gabunia 1985) is smaller but otherwise quite similar to the average of AaO; so are, to a lesser extent, the MT IIIs of Villaroya and Roccaneyra. No African

Plio-Pleistocene metatarsals resemble those of AaO, the less dissimilar being those from Olduvai and Koro Toro, Chad (Figure 20).

The scatter diagram of the keel development (not figured here) carries less information than for the third metacarpals. However, another feature seems interesting because it expresses approximately the position of the lateral digits: when they are placed more ventrally, the diaphysis is narrower and deeper (Figure 21). The deepest diaphyses are found in dolichopodial hipparions (Venta del Moro, Maramena (1), La Gloria (2)) but also in some specimens from Langebaanweg E and Olduvai. The widest and flattest diaphyses occur at Çalta (*H. heintzi*), Omo C (10), Hadar, and in *H. turkanense* (11). In Vallesian species, the diaphysis may be very wide and flat (Eppelsheim, 12), or much less (Esme Akçaköy). Not illustrated *H. cf. houfenense* of Shamar and Beregovaja and *H. cf. crusafonti* of Kvabebi plot with the intermediate group together with AaO.

Phalanges of the third digit: first phalanges. In most species of *Equus*, it is possible to discriminate anterior and posterior phalanges (Dive & Eisenmann 1991). The discrimination is more difficult in hipparion. Nevertheless, a scatter diagram of the proximal depth versus the distal articular width (Figure 22) gives good results: in samples of first phalanges associated with third metapodials (Höwenegg, Hadar, Shamar, Layna, Grebeniki) or determined by Gromova 1952 (*H. elegans* from Pavlodar, *H. moldavicum*) and Gabunia 1959 (Khadjibi, Chobruchi, Kuialnik), the proximal depth is relatively bigger when the phalanx is posterior. Moreover, within the same species, anterior first phalanges are usually slenderer. According to these criteria, we have at AaO four anterior, and three posterior, phalanges (Table 16). The best preserved anterior phalanx (AaO 1261, Figure 23B) is small and may belong to a not fully grown individual. On the ratio diagram (Figure 24) it compares well with a specimen from Olduvai M-14456c (possibly Bed I), which is however slenderer. Similar proportions are found in the much larger AL 161-1 (Hadar DD) and in the much smaller Omo 1974-263-573 (member C ?). The other anterior phalanges of AaO are larger and more robust.

One of the posterior PH I associated with a MT III and a second phalanx (AaO-196) is badly preserved and looks very small. It could fit with the anterior AaO-1261. On the ratio diagram (Figure 25) AaO-2838 resembles two Tanzanian phalanges (Olduvai SHKII 1957.1165 and Laetoli M 31934) and also AL 194-2 of Hadar (DD). Specimen AaO-2844 (Figure 23A) is more like AL 155-6 (Hadar DD).

Second phalanges. Second phalanges may be sorted into anterior or posterior by plotting the distal articular breadth versus the maximal length: posterior phalanges are relatively narrower. They are

also deeper at the proximal end. According to these characters, there are four anterior and five posterior phalanges at AaO. The sample appears monospecific (Table 17).

Third phalanges. It is easy to distinguish anterior from posterior third phalanges of the same individual, for example in Hadar AL 155-6 (Table 18), the anterior being wider at the sole and having wider and more shallow articular surfaces. But the intraspecific variation is very big and the assignment is often uncertain in unassociated bones. At AaO (Figure 23C-D), three third phalanges are certainly anterior and two are certainly posterior. The assignment of the rest is tentative.

Other limb bones. Compared to the extant *Equus grevyi* and the fossil *Allohippus vireti* the variation of the talus is large (Table 13; Figure 23E) but all attempts to split the sample were unsuccessful. Measurements of other limb bones are in Table 19.

Limb bone segments. In *Equus* and hipparion, the relative lengths of limb bones give useful information about the cursorial abilities; information on the ground (hard or heavy) is provided by the relative width of third phalanges (Eisenmann 1984, 1991, Eisenmann & Sondaar 1998). Schematically, third phalanges are narrow when the ground is hard; proximal limb bones are relatively short when species are cursorial. Till now there was no good data on monospecific whole (associated) skeletons of hipparions, so that in the past (Eisenmann & Sondaar 1998), ratio diagrams comparisons were made with the extant *E. hemionus onager*. But now we are able to use as reference the Höwenegg sample (Bernor et al. 1997 and personal data; Table 20). For humeri and femora, we use articular lengths, for the third phalanx, we use the solar width of the anterior phalanx, for all other bones, we use maximal lengths.

There is only one associated skeleton of African hipparion (AL 155-6 of the Denen Dora member of Hadar), presumably belonging to *H. hasumense*, and few samples rich enough for using reliable average dimensions. A ratio diagram (not illustrated) has shown no big differences between the proportions of the possibly juveniles and the other bones of AaO justifying the use of average dimensions. Figure 26 compares *H. hasumense* AL 155-6, *Hipparion heintzi* of Çalta, the sample of Langebaanweg E, and *H. pomeli*. The very short metapodials of *H. heintzi* are a good indication for a poor cursorial adaptation. In contrast, *H. hasumense* and *H. pomeli* were probably better runners. Moreover, at Höwenegg and Çalta, the femora and radii are of subequal length, while in *H. pomeli* (like in all extant *Equus*) the radius is much longer. The proportions of the Langebaanweg E hipparion are similar to those of *H. pomeli*.

The cursorial adaptations of *H. pomeli* from Ahl al Oughlam are in good agreement with the environment of the locality, where the abundance of alcelaphines and antilopines among bovids suggest an open landscape.

ADDITIONAL NOTES: *H. HENDEYI* N.SP. FROM LANGEBAANWEG E AND *H. AFF. CRASSUM* FROM KOSSOM BOUGOUDI, CHAD

Langebaanweg E

Hooijer (1976) referred to *H. cf. baardi* the material from Langebaanweg E Quarry, South Africa. Hendey (1978) quite correctly pointed that the hipparion of Quarry E was very different from *H. baardi* of Baard's Quarry and gave measurements of the lower cheek teeth. We propose to name this hipparion *H. hendeyi*, and choose as holotype the complete skull of an old female, L 22187, from Langebaanweg E, preserved at the Cape Town National Museum and figured by Hooijer (1976, pl.1). The skull (Table 1) has a very long vomer-palate distance, a very faint POF, and a long and narrow muzzle; the cheek teeth of the skull are too worn to provide information on their dimensions but according to Hendey's data the lower series was about 152mm long. On the whole, the skull resembles *H. giganteum* and *H. verae* of Grebeniki (Appendix Fig.5), *H. moldavicum* of Taraklia, and possibly *H. feibeli* from Ekora-Kanapoi (Figure 27). The cheek teeth of E Quarry are hipparionine, although some are hypsodont; the lower incisors are grooved (Hooijer 1976, Pl. 2-6; Pl. 8, fig.2). The MC IIIs have well developed keels (Figure 18) exceptional in a species which is not dolichopodial. Two MT IIIs (L 5899 and L 21827) have very wide diaphyses and do not fit with the rest of the sample (Figure 21).

Chad, Kossom Bougoudi 9

A fragment of skull, KB 9-97-13, dated to about 5Ma. (Brunet et al. 2000), is remarkable by its very large dimensions (Table 1). The POF is situated at about 40mm in front of the orbit. The fossa is very well delimited at its anterior and dorsal borders, but not much ventrally and posteriorly. The vomer-palate distance is long. The premolars and M1 are much worn; the less worn M2 and M3 are plicated.

This skull differs from *H. proboscideum* of Samos by the presence of only one POF instead of two (Koufos & Vlachou 2005), the long vomer-palate and P2-Orbit distances. On the whole, it resembles best *H. dermatorhinum* from China (data Bernor et al. 1990 and personal) and possibly *H. crassum* and *H. tchicoicum*, judging by the dimensions of the mandibles Pp 208 from Perpignan and Shamar 3381-53 (Table 2). *H. garedzicum magianense* of Sor, Tadjikistan (Zhegallo 1978) very probably belongs to the same group (Table 1, Fig. 28).

DISCUSSION

Like some other authors (Koufos & Vlachou 2005), we use *Hipparion* as a generic name for all Old World late Miocene equids without distinction of the numerous complexes to which they may belong. We prefer also not to give specific names to isolated limb bones or teeth.

Bernor & Armour-Chelu (1999a) have presented a comprehensive overview of hipparions in general and more particularly of African forms. According to them, there were only two founding populations in Africa. The first derived from the *Hippotherium* complex, which includes (among other species) the European *H. primigenium* and *H. giganteum*, the Chinese *H. dermatorhinum*, and the African *H. africanum*. The second founding population derives from the *Sivalhippus* complex, which includes among other species, the Siwaliks *S. perimense* and the Chinese *Plesiohipparion houfenense*, as well as the European *Pl. crassum* (Bernor & Armour-Chelu 1999b). Bernor & Armour-Chelu consider *S. perimense* as the sister group of *Eurygnathohippus* within which are placed *H. turkanense* and all the post-Miocene African hipparions.

In 2003, Bernor & Harris write that the POF of *Eurygnathohippus* aff. *feibeli* of Ekora "suggests relationships within the *Cormohipparion-Hipparion-Hippotherium* trichotomy while *Eurygnathohippus turkanense*'s reduced POF and limb proportions suggest an alliance between *E. turkanense* and *S. perimense*. The occurrence of ectostylids in Lothagam *E. turkanense* and *E. feibeli* suggests a phylogenetic relationship exclusive of Eurasian hipparions and inclusive with Plio-Pleistocene African hipparions".

Still more recently, Zouhri & Bensalmia (2005) made a thorough revision of Old World hipparions. They recognize four genera: *Hippotherium*, *Cremohipparion* (including *Cr. moldavicum* as a synonym of *Cr. mediterraneum*), *Hipparion*, and *Proboscidipparion*. The later is subdivided into three subgenera: *Proboscidipparion*, *Plesiohipparion*, and *Eurygnathohippus*. They rightly point that *H. crassum* cannot be considered as a *Plesiohipparion* because of the primitive pattern of its lower cheek teeth, and rightly exclude *H. turkanense* from *Eurygnathohippus* because it has neither the typical lower cheek teeth nor the reduction of the third incisors of *Eurygnathohippus*.

1. Discussion of Bernor & Armour-Chelu (1999a) and Bernor & Harris (2003) opinions.

Our first point of disagreement concerns the definition of *Eurygnathohippus*. All late hipparions - not only African - exhibit a lot of apomorphies. But synapomorphies are not so evident.

a. The grooved lower incisors are not a synapomorphy of all African late hipparions since they are present in *H. moldavicum* (Chobruchi), *H. giganteum* (Grebeniki), *H. crassum* (Perpignan), and *H. houfenense*. On the other hand, the incisors of AL 155-6 (Denen Dora of Hadar) are not grooved, while they are grooved in AL 177-21 of the same member, and in AL 59-9B of the earlier Sidi Hakoma member. Both grooved and not grooved incisors are represented in Omo member C.

b. The cheek teeth of late hipparions present many apomorphies. Most are probable homoplasies related to grazing hard food. Such are the hypsodonty, the elongated and narrow protocones, the angular double knots, the development of protostylids, the straightening of the vestibular enamel ridges, and the development of vestibular enamel structures between protoconid and hypoconid. As already pointed (and partly illustrated) by Forstén (1997a and b), the latter are similar on the whole, but different in detail. In *H. huangheense* from China (FAM 11820), a posterior pointed extension of the protoconid may be a functional equivalent of the pli caballinid/ectostylid complex. In *H. crusafonti* from Villaroya the pointed extension of the protoconid is present but less marked than in *H. huangheense*. In *H. cf. crusafonti* of Kvabebi there are very well developed plis caballinid (but no extension of the protoconid); moreover, there are well developed plis protostylids on dp2 (Figure 29).

The only cheek tooth synapomorphy of African late hipparions would be the development of ectostylids as functional equivalents of plis caballinid or protoconid extensions. But ectostylids are quite visible on the occlusal surface of the molars of BMNH 26211 from Bhandar Bone Bed of Dhok Pathan (Forstén 1997b, Fig. 16A). On the other hand, they are not developed at Laetoli, and Baard's Quarry of Langebaanweg and not expressed in *H. turkanense* of Lothagam Lower Nawata, appearing only in the Upper Nawata member.

c. In our opinion, the major point is the structure of the vomer and the basi-cranial 'caballine' proportions (vomer distances from the palate and the basion). They constitute solid synapomorphies for *H. afarensis* and the *H. cornelianum* of East Turkana. The Chinese *H. houfenense* s.s. (type skull THP 10508) possibly had the same kind of vomer, because of its apparently long basion-vomer distance (Qiu, pers. comm.) but we are not certain of that since the skull is badly preserved. In *H. huangheense* (FAM 11820) the structure of the vomer and the basi-cranial proportions are uncertain because of incomplete preparation. In *H. crusafonti* of Villaroya, the basi-cranial proportions are not known. In *H. cf. crusafonti* of Kvabebi, the distance from vomer to palate seems short but the morphology of the vomer and the distance between vomer and basion are unknown. When we studied the skull of *Sivalhippus perimense*, the basicranium was not fully prepared, so that information on this important point is again lacking. It is quite clear,

however, that *H. turkanense* did not possess any of the basi-cranial characters shared by *H. afarense* and *H. cornelianum*.

d. Short, squarish, and broad arcades, without reduction of I3, are not uncommon in hipparions. The best example is the very well known Greek *H. dietrichi*, but similar morphologies may be found also in *H. prostylum* of Lubéron, and even in China (AMNH 35 B 255). This kind of structure is obviously related to grazing (Eisenmann 1998) and may well have developed in parallel in more than one lineage. But the extreme pattern with loss of the third incisors and a broad, square incisival arcade was achieved only by very late African hipparions (Cornelia and Olduvai, possibly East Turkana Burgi member) and seems to be the second synapomorphy. Indeed, it is this pattern that was first used to define '*Eurygnathohippus*'. *Eurygnathohippus*-like symphyses and ectostylids are not necessarily associated: ectostylids are present in *H. pomeli*, but there is no reduction of the third incisors and the incisival arcade is rounded.

In *H. houfenense* s.s. (THP 10508 and THP 10733. Qiu pers. com. and Qiu et al. 1988), the muzzle is long and narrow. *H. huangheense* (FAM 11820) is larger, and its muzzle is wider. *H. crusafonti* of Villaroya seems close to the latter species. *H. cf. crusafonti* of Kvabebi is smaller, with a short but not very wide muzzle (Figure 30). *S. perimense* and *H. turkanense* have rounded and rather narrow arcades.

To summarize, in our opinion the name of *Eurygnathohippus* should be applied only to hipparions that present a derived basicranium, i.e. pointed vomer and long basion-vomer distance. *H. hasumense* s.l. (normal posterior border of vomer situated at subequal distances from basion and palate) is probably a sister group to *Eurygnathohippus*. Their origins are presently unknown.

Our second point of disagreement concerns the derivation of several African hipparions from *H. turkanense*.

Both *H. hendeyi* and *H. feibeli* differ from *H. turkanense* by their slender limb bones. Moreover, *H. hendeyi* (Figure 27) strongly differs from *H. turkanense* by its very short basion-vomer and orbit-POF distances (Figure 30, # 4 and O-POF).

Hipparion sp. of Chad Kossom Bougoudi (Figure 28) differs from *H. turkanense* by the presence of a POF, relatively close to the orbit (but not as much as in *H. hendeyi*).

The derivation of *H. hasumense* from *H. turkanense* would imply a notable reorganization of the skull (Figure 33), beside the acquisition of ectostylids. Such an evolution is possible but still hypothetical.

2. Discussion of Zouhri & Bensalmia (2005) opinions.

Our main disagreement concerns *Eurygnathohippus*. The amended diagnosis of Zouhri & Bensalmia comprises: large size, lack of POF, short naso-incisival notch, long and narrow muzzle, caballine basi-cranium, very hypsodont teeth, constant ectostylids associated to caballoid patterns in lower cheek teeth. Thus defined, *Eurygnathohippus* comprises three species: *E. libycum*, *E. cornelianum*, and *E. afarense* (including *E. hasumense* as a synonym). Zouhri & Bensalmia refer the AaO hipparion to *E. libycum*. We think that this diagnosis is incorrect:

a. The large size is not a good character: hipparions of Shungura F member and Koobi Fora KBS member, although presumably belonging inside *Eurygnathohippus* sensu Zouhri & Bensalmia, were small (Figures 13, 14).

b. The degree of indentation of the naso-incisival incisure is defined by three points: prosthion, apex of the incisure, and anteriormost point of the orbit. Length of naso-incisival notch (# 30) is the distance between the first two; cheek length (# 31) is the distance between the last two. The naso-incisival notch is short when it is smaller than the cheek length ($\# 30 < \# 31$). This is observed in *H. cornelianum* of Koobi Fora (Appendix Table 2) and *H. hasumense* of Olduvai Bed II (Table 1). The naso-incisival notch is long in *H. hasumense* of Hadar; the two lengths are equal in *H. pomeli* (Table 1). In consequence, the length of naso-incisival notch is not a good character for a diagnosis of *Eurygnathohippus*.

c. Figure 6 shows that the muzzle is long and narrow in *H. hasumense*, but quite shorter and wider in *H. cornelianum*. Thus a 'long and narrow muzzle' cannot be mentioned in a diagnosis of *Eurygnathohippus*.

d. As pointed above, the basi-cranium of our *Eurygnathohippus* is 'hypercaballine' with a remarkably long basion-vomer distance. Moreover, the morphology of the vomer posterior border is quite peculiar in *H. afarense* and *H. cornelianum*. This is absolutely not the case of *H. pomeli* of AaO (Fig.2 # 4).

e. 'Very hypsodont teeth' is a vague definition. As shown on Figure 10 and 11, many teeth referred to *Eurygnathohippus* by Zouhri & Bensalmia are only moderately hypsodont, or even not hypsodont when compared to other African hipparions.

Thus, we disagree as to the validity of the genus *Eurygnathohippus* as defined by Zouhri & Bensalmia (2005), since the various species referred by them to this genus display too many and too important differences.

Another point is the inclusion of the AaO Hipparion in the species *H. libycum*. This species is based upon two lower premolars from Algeria, of which we hereby select the one better illustrated by Pomel (1897, Pl.1, fig.5-7) as lectotype (not holotype as stated by Zouhri & Bensalmia). Given the difficulties in Hipparion systematics, it is clear that this material does not

allow for confident referral of any other specimen to the same species. Therefore, to avoid mixing of several unrelated species within the same species name, the name *Hipparion libyicum* should be restricted to the type.

CONCLUSIONS

In our interpretation, during the last 7Ma, there were in Africa at least five kinds of hipparions:

- *H. turkanense* of Lower Nawata (Bernor & Harris 2003) has normal basi-cranial proportions (Figure 33). A very faint POF is placed very far from the orbit. Resemblances between the skull of *H. turkanense* and that of *S. perimense* (AMNH 19761, formerly named *Cormohipparion antelopinum*) do exist and have been illustrated by ratio diagrams a long time ago (Eisenmann 1982, fig. 5). It is quite possible that *H. turkanense* derives from *S. perimense* from which it seems to differ mainly by the lack of, or a very faintly marked, POF. But we lack information on *S. perimense* basicranial proportions. Unfortunately, we have not at our disposal photographs of the Lower and Upper Nawata cheek teeth except the very worn series of the type skull of *H. turkanense*.

- *H. hendeyi* and *H. feibeli* ?. Two European skulls are similar to that of *H. hendeyi* (Figure 27). They belong to the quite smaller *H. moldavicum* of Taraklia, and to *H. giganteum* of Grebeniki. They have short basion-vomer distances and narrow muzzles; the POF of *H. hendeyi*, however, is placed closer to the orbit than in *H. giganteum* and not as close as in *H. moldavicum*. The upper cheek teeth have small and rounded protocones; the lower cheek teeth are hipparionine (Hendey 1978). *H. hendeyi* cannot be derived from *H. africanum* because of its very short naso-incisival notch (Figure 32). It may have derived from another immigrant. The skulls from Ekora and Kanam, possibly referable to *H. feibeli* but poorly known, may be akin.

- *Hipparion* sp. of Kossom Bougoudi (Figure 28). It is represented by one of the largest skulls of hipparion. Unfortunately, the teeth are much worn. We do not know whether the Chad skull derived from the *Hippotherium* complex of Bernor & Armour-Chelu (1999a) because of its resemblances with *H. dermatorhinum*, or from the *Sivalhippus* complex (Bernor & Armour-Chelu 1999b) because of its resemblances with *H. crassum* s.l.

- *H. hasumense* group (Figures 2 and 3). This group displays several apomorphies: short cheek, deep naso-incisival notch, caballine double knots, isolated ectostylids and protostylids. Vomer and basi-cranial proportions are normal. The muzzle is long and narrow. We recognize it at Wembere Manonga, Hadar, Ahl al Oughlam (*H. pomeli*), and possibly Olduvai (complete but badly preserved skull BK II 2845/6).

- *H. afarensis* and *H. cornelianum* (Figures 4 and 5). As already noted, the structure of the vomer is unique: the acutely pointed vomerian incisure is associated with 'hypercaballine' basi-cranial proportions. The muzzle is short and wide. Other apomorphies are like in *H. hasumense*.

It is quite probable that *H. afarensis* was the ancestor of the true *Eurygnathohippus* for two reasons: 1) the skulls AL 363-18 of *H. afarensis* and KNM ER 3539 of *H. cornelianum* are quite similar; 2) KNM ER 3539 is about 1-2 years old by *Equus* standards (Klingel & Klingel 1966); at that age the permanent I1 (contra Bernor & Armour-Chelu 1999a) are erupting and they can perfectly be seen on this skull because the DI1 are lost; an unerupted right I2 may be seen for the same reason, and there is no room for an I3 other than a very reduced one (Figure 31).

Bernor & Armour-Chelu (1999a) believe that the preceding forms may derive from *H. turkanense* which they consider as an *Eurygnathohippus*, sister group to *S. perimense*. In our opinion, the derivation of *Eurygnathohippus* from *H. turkanense* is, for the moment, an assumption based more on the belief that there were no other immigrations of hipparions into Africa than on osteological evidence.

If the Pliocene African hipparions are not descended from *H. turkanense*, they must have an Eurasian origin, and have immigrated into Africa around the Mio-Pliocene boundary (Figure 34). This period documents indeed a major turnover in African mammalian faunas, mostly by local evolution from local forms. However, there are also some newcomers. In North Africa, the Messinian crisis prompted some faunal exchanges across the Gibraltar straits; they are best known for rodents, but probably involve also canids, and it is likely that a better knowledge of North African Mio-Pliocene large Mammals would increase the list. Other taxa of Eurasian origin, arriving in Africa at this time are the Camelidae, first known from the early Pliocene of Chad, and perhaps *Giraffa* and some carnivores: the ursid *Agriotherium*, the hunting hyena *Chasmaporthetes*, and the mustelid *Plesiogulo*. The list is not long, but definitely demonstrates that North-South migrations were possible at that time. The presence at Kossoum Bougoudi, Chad, of a huge hipparion with a very developed fossa could also result from a migration, possibly of a kind of *H. crassum*.

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TABLE CAPTIONS

Table 1. Measurements in mm of hipparion skulls. n: number of specimens; approximate data between brackets.

Table 2. Measurements in mm of hipparion skulls. Numbers refer to the measurements defined in Table 1. Approximate data between brackets. Asterisks indicate skull estimations from mandibular data (see Appendix). Data for Manonga WW 1528/92 are according to Bernor & Armour-Chelu 1997.

Table 3. Permanent upper cheek series or associated teeth from Ahl al Oughlam. Measurements in mm, approximate values between brackets.

Table 4. Other permanent upper cheek teeth from Ahl al Oughlam. Asterisks for dimensions at mid-crown height.

Table 5. Permanent upper cheek teeth from Ain Brimba.

Table 6. Permanent upper cheek teeth from Ichkeul.

Table 7. Deciduous upper cheek teeth from Ahl al Oughlam.

Table 8. Permanent lower cheek series or associated teeth from Ahl al Oughlam. Measurements in mm, approximate between brackets. L: length. W: width.

Table 9. Other permanent lower cheek teeth from Ahl al Oughlam.

Table 10. Permanent lower cheek teeth of Ain Brimba. #: very small.

Table 11. Deciduous lower cheek teeth from Ahl al Oughlam. E1 and E2: first and second ectostylid. DK: Double Knot.

Table 12. Statistics of Höwenegg limb bones widths from Bernor et al. 1997. x: mean, s: standard deviation, n: number of specimens, min: minimal observed value, max: maximal observed value. Tibia diaphysis, supposed: values used in this paper (see text).

Table 13. Statistics for tali of the AaO sample, for the extant *E. grevyi*, and for the fossil *Allohippus vireti*. Abbreviations as for Table 12, plus v: coefficient of variation ($v=100*s/x$). 1: maximal length, 2: maximal diameter of the medial condyle, 3: maximal breadth, 4: breadth of the trochlea at the apex of each condyle, 5: distal articular breadth, distal articular depth, 7: maximal medial depth.

Table 14. Statistics for third metacarpals and metatarsals from Ahl al Oughlam. Abbreviations as in Table 13.

Table 15. Metapodials from Ahl al Oughlam. Measurements as in Table 14.

Table 16. First phalanges of the third digit (PH I). W: width.

Table 17. Second phalanges of the third digit (PH II).

Table 18. Third phalanges of the third digit (PH III).

Table 19. Measurements of limb bones from Ahl al Oughlam.

Table 20. Articular lengths (in mm) of Humerus (H), Femur (F); maximal lengths of Radius (R), Tibia (T), third metacarpal (MC), third metatarsal (MT), first anterior and posterior phalanges of the third digit (PH IA and PH IP); solar width of third anterior phalanx of the third digit (PH IIIA). For Höwenegg, data from Bernor et al. 1997 and personal.

FIGURE CAPTIONS

Figure 1. *Hipparion pomeli* n.sp. from Ahl al Oughlam. A: holotype skull AaO-3647; A1: dorso-lateral view; A2: occlusal view of upper incisors; A3: cheek-teeth. B: upper cheek-teeth AaO-2048 (reversed from the right side). C: upper cheek-teeth AaO-198 (M2 and M3 reversed from the right side). D: upper milk premolars AaO-4073. Scale-bar = 15 cm for Figure A1, 7.5 cm for Figure A2, 5 cm for all others.

Figure 2. Ratio diagrams comparing the holotype skull of *Hipparion pomeli* (AaO-3647) to *H. hasumense* s.l. of Wembere Manonga Kilolei WW 1528/92 (Data Bernor & Armour-Chelu 1997), and *H. hasumense* of Hadar DD AL 340-8. Data in Tables 1 and 2.

Figure 3. Ratio diagrams comparing the Moroccan skull (AaO 3647) to *H. hasumense* s.l. of Hadar SH (AL 142-18), DD (AL 116-115, AL 155-6, AL 241-18, AL 177-21), Shungura C (18-1968-363 and 18-1969-90), and Olduvai BK II 2845/6. Data in Table 2.

Figure 4. Ratio diagrams illustrating the pattern of *H. afarensis* type skull and *H. afarensis* s.l. from East Turkana Burgi (KNM ER 3539) and *Notochoerus scotti* Zone (KNM ER 1626). Data in Table 1, Appendix Table 2, and Appendix Text.

Figure 5. Ratio diagrams illustrating the pattern of other *H. afarensis* s.l. skulls from Olduvai Bed II (BK II 264, 283, 5344) and unknown (BM 5465), and Cornelia. Data in Table 2, Appendix Table 2, and Appendix Text.

Figure 6. Scatter diagram of muzzle lengths and widths in *H. dietrichi* of Samos (Table 2), *H. hasumense* s.l. a: AL 340-8, Hadar DD; b: AaO 3647, Ahl al Oughlam; c: WW 1528/92,

Wembere Manonga, Kilolei; d: AL 177-21, Hadar DD; e: Olduvai BK II 2845/6; and *H. cornelianum* f. KNM ER 1626, East Turkana *Notochoerus scotti* zone; g: KNM ER 3539, East Turkana Burgi.

Figure 7. Scatter diagram of P2-M3 lengths and muzzle widths in *H. dietrichi* of Samos (Table 2), *H. hasumense* s.l. a: AL 155-6, Hadar DD; b: AaO 3647, Ahl al Oughlam; c: WW 1528/92, Wembere Manonga, Kilolei; d: AL 340-8, Hadar DD; e: 18-198-363 & 18-1969-90, Omo C; and *H. afarensis* s.l. f: KNM ER 1626, East Turkana *Notochoerus scotti* zone; g: AL 363-18, Hadar KH; h: KNM ER 3539, East Turkana Burgi.

Figure 8. *Hipparion pomeli* n.sp. from Ahl al Oughlam. A: lower cheek teeth AaO-2993. B: mandible AaO-197; B1: cheek-teeth, B2: lateral view. C: lower milk premolars AaO-4070. D: four metatarsals, from left to right: AaO-3694, AaO-3353; AaO-3700, AaO-2825. E: three metacarpals, AaO-4267, AaO-3307, AaO-2112. Scale bar = 20 cm for Figure B2, 10 cm for Figures D-E, 5 cm for all others.

Figure 9. Scatter diagram of P3-4 and M1-2 lengths and widths of Ahl al Oughlam, Ichkeul, and Ain Brimba.

Figure 10. Scatter diagram of unworn or little worn M3 lengths and heights in various African hipparions. HI: Hypsodonty Index. 1: TM 47-101-11, HI=220.8; 2: KL 20-98-11, HI=235; 3: Ichkeul, HI=224; 4: 1968-1005-38, HI=276.2; 5: 4094, FS 751, HI=260.9; 6: L 768-1, HI=254.2; 7: AaO 1433, HI=258.3; 8: 1969-108-81, HI=262.5; 9: L 1-61, HI=252; 10: ER 2922, HI=250; 11: AL 58-10, HI=240.7; 12: ER 1263, HI=305; 13: L 724-3, HI=315; 14: L 675-2, HI= 304.8; 15: Average of Hooijer 1975, HI=296.7.

Figure 11. Scatter diagram of unworn or little worn P3-4 and M1-2 lengths and heights in various African hipparions. HI: Hypsodonty Index. 1a: KB3 98-93, HI=257.1; 1b: KB4 96-13, HI=254.2; 1c: KB3 97-136, HI=277.6; 2: TM 47 101-1C, HI= 247.8; 3a: AL 155-6, HI=264.3; 3b: AL 305-5, HI=274.5; 4: AL 58-10E, HI=251; 5: 1950-1-21, HI=252; 6: 1958-14-191, HI=254.5; 7: KT33 96-1, HI=242.9; 8a: L 253-3a, HI=297.8; 8b: 1972-14-108, HI= 285.7; 8c: L 398-1182, HI= 321.7; 9: L 767-1, HI= 295.7; 10a: AL 239-68, HI= 285.7; 10b: AL 288-19, HI=286.8; 11a: F 513-33, HI=340; 11b: L 616-62, HI=338.1; 11c: L 627-89, HI= 333.3; 12a: ER 2263, HI=320.9; 12b: ER

2073, HI=318.2; 12c: ER 1231, HI=347.6; 13: A 581, HI=325.6; 14: 1692, HI=337.8; 15: 1973-1958-212, HI= 340.4.

Figure 12. Variation Size Indices for AaO and Hadar DD hipparion samples, using Höwenegg as standard. n: number of widths. White points for AL 155-6 associated limb bones.

Figure 13. Variation Size Indices using AaO as standard for Olduvai Bed I, Bed II, and Koobi Fora. White ellipses for KBS member specimens.

Figure 14. Variation Size Indices using AaO as standard for Shungura Formation (Omo).

Figure 15. Variation Size Indices using AaO as standard for Hadar Formation. White ellipses for AL 155-6 associated bones.

Figure 16. Ratio diagrams for AaO third metacarpals maximal, average (x), and minimal values. Measurements as in Table 14.

Figure 17. Ratio diagrams comparing average AaO third metacarpal to metacarpals of Chad, Ichkeul, Olduvai (FLKNI 934 and 7693, SHKII 57/935), and Melka Kunturé. Measurements as in Table 14.

Figure 18. Scatter diagram (mm) of third metacarpal keel development versus distal articular width. Hadar: a. 116-33, DD2-3; b. 361-1, KH; c. 99-38, unknown; d. 327-14A, SH2; e. 115-6BB, DD2; f. 150-1, DD; g. 212-3, DD2-3; h. 315-9C, DD2-3; i. B 236-7, SH2-3; j. B 147-20, SH2-3; k. 107-15, SH2-3. Olduvai: l. 1963/2750, subadult, BK II; m. M 16985, unknown; n. 57/576, subadult ?, SHK II; o. 59/366, LGK; p. F 345, unknown; q. 7963, FLKN I; r. F 811, S4 1941; s. 933, FLKN I; t. 57/935, SHK II; u. 1952/307, BK II. Omo B: v. 3004-41; w. 3005-41. Omo D: x. 73-2626.

Figure 19. Ratio diagrams for AaO third metatarsals maximal, average (x), and minimal values. Measurements as in Table 14.

Figure 20. Ratio diagrams comparing average AaO third metatarsal to metatarsals of Olduvai (BKII 1953-435, 1953-135, 1963-620; unknown 807 and 1-6), Chad KT13 (96-21, 39, 489), Roccaneyra (1948-13-11), Villaroya, and Kvabebi (KV 1082). Measurements as in Table 14.

Figure 21. Scatter diagram (mm) of third metatarsal diaphysis depth versus diaphysis width.

Figure 22. Scatter diagram (mm) of first phalanges of the third digit proximal depth versus distal articular width. Ant: anterior phalanges, Post: posterior phalanges. Data in Table 16.

Figure 23. *Hipparion pomeli* n.sp. from Ahl al Oughlam. A-D: phalanges in 1: dorsal, 2: palmar/plantar, and C: proximal views. A: first phalanx AaO-2844, B: first phalanx AaO-1261, C: third phalanx AaO-1520, D: third phalanx AaO-2122. E: astragalus in 1: dorsal, 2: plantar, and 3: medial views; from left to right AaO-3336, AaO-3456, AaO-193, AaO-1530, AaO-4438. F: femur AaO-1503 in dorsal view. Scale bar = 20 cm for Figure F, 10 cm for all others.

Figure 24. Ratio diagrams comparing first anterior phalanges of the third digit. Data in Table 16.

Figure 25. Ratio diagrams comparing first posterior phalanges of the third digit. Data in Table 16.

Figure 26. Ratio diagrams comparing limb bone segments in hipparions. Data in Table 20.

Figure 27. Ratio diagrams comparing the skulls of Langebaanweg E, Ekora-Kanam, *H. giganteum* of Grebeniki and *H. moldavicum* of Taraklia. Data in Table 1 and Appendix Table 2.

Figure 28. Ratio diagrams comparing the skulls of Chad Kossom Bougoudi, *H. dermatorhinum*, and *H. crassum*. Data Bernor et al. 1990 and personal for *H. dermatorhinum*. Other data in Tables 1 and 2.

Figure 29. *Hipparion* cf. *crusafonti*, Kvabebi. A: dp2, B: m2-m3.

Figure 30. Ratio diagrams comparing the skulls of *H. houfenense* s.l., Villaroya, and Kvabebi. Data in Table 1.

Figure 31. Muzzle KNM-ER 3539; A: dorsal view, B: ventral view.

Figure 32. Ratio diagrams comparing the skulls of *H. turkanense*, *H. hendeyi*, and *H. africanum*. Data Bernor & Harris 2003 for *H. turkanense*. Other data in Table 1.

Figure 33. Ratio diagrams comparing the skulls of *H. turkanense* LT 136 and *H. hasumense* of Wembere Manonga WW 1528/92 (Data Bernor & Armour-Chelu 1997) and AL 340-8 of Hadar.

Figure 34. Schematic chronology of some hipparion-bearing late Cenozoic Old World localities.

Appendix

JUVENILE SKULLS

Well preserved skulls are rare. It is very frustrating when they belong to juvenile animals, and thus cannot be directly compared to adults. It may, however, be possible to "extrapolate" the juvenile dimensions to adult ones. We have tried to do so by applying what we know about the skull growth of extant *Equus* species.

Four species were considered: Grevy's zebra, Plains zebras, Hemiones, and Przewalski's horses. Comparison was made between average adult skulls and juvenile skulls of different ages by calculating the % rate of "growth" of the later. Appendix Table 1 gives the percentages of growth of the dimensions used in our ratio diagrams. The choice of dimensions was made to adapt to the more or less complete fossil material. Thus, some are simple measurements while others are sums of segments. Most were defined in Eisenmann et al. 1988. Appendix Figure 1 illustrates the values of the percentages of growth in the considered extant species.

Samples of adult skulls were chosen to correspond as much as possible to the available (always poor) juvenile samples. For instance, only adult *E. burchelli* from Etosha Pan were used because the best sample of juvenile skulls comes from Etosha Pan. For adult skulls, means were calculated on ca. 60 *E. grevyi* (but cheek and naso-incisival notch lengths are known only in 5 specimens), and ca. 60 hemiones (excluding hemippes, kiangs, and Mongolian hemiones), 22 to 31 *E. przewalskii*, and 15 *E. burchelli*. Juvenile samples vary from one age group to another.

The studied juvenile skulls (Appendix Table 2) are: KNM ER 3539 from East Turkana, BM 5465, and BK II 283 from Olduvai (*H. cornelianum*); KNM EK 4 from Ekora and BM 15906 from Kanam West (*H. feibeli* ?).

One-two years. Juvenile samples consist of 9 *E. grevyi*, 9-10 *E. burchelli*, 6-11 *E. hemionus*, and 7-13 *E. przewalskii*.

Naturally, the highest percentages concern the "growth" of the cheek teeth, since there are only three decidual teeth instead of six adult. The smallest percentages concern the growth in length of the muzzle. Obviously, skulls of different species grow in different ways. In *E. grevyi* the muzzle width grows less than in other species while the length of the Naso-Incisival notch seems to increase more. On the whole, however, the concordance seems good enough to justify tentative reconstructions of juvenile skulls.

A perfectly preserved juvenile skull (KNM ER 3539) was found under the KBS Tuff in East Turkana. It was illustrated in Eisenmann (1976, Plate 3). The M1 begin to wear, the M2 are not erupted. In *Equus*, that would indicate an age comprised between one and two years. The following ratio diagram (Appendix Figure 2) compares dimensions of the juvenile skull with tentative reconstructions of its adult state according to the *Equus* species growth. It shows that most of predicted adult dimensions are similar but notable interspecific differences concern the muzzle width.

The use of *Equus* skulls as basis for a reconstruction of an *Hipparion* skull may appear rash and untestable. We can, however, somehow 'test' the extrapolation of KNM ER 3539 by comparing it with the adult skull of *H. afarensis* AL 363-18 (Eisenmann, 1976, Plate 2). The obvious resemblances on the next ratio diagram (Appendix Figure 3) make our reconstruction credible. The adult skull ER 3539, when adult, would probably have looked like *H. afarensis*, possibly slightly smaller and with longer teeth and palate. The muzzle would have been at least 70.4mm wide (according to the *E. grevyi* model), possibly as wide as, but no more than, 91.7mm (*E. przewalskii* model), more probably about the calculated average (81mm) which is close to the actual width of *H. afarensis* (80mm).

About one year. Juvenile samples consist of 1 *E. grevyi*, 6 *E. burchelli*, 2-5 *E. hemionus*, and 5 *E. przewalskii*.

The juvenile skulls KNM EK 4 from Ekora and BM 15906 from Kanam West are about one year old (unerupted M1). They both have a POF and have also the same dimensions of the deciduous series. We suppose that they belong to the same species. The various possibilities of adult state are represented in Appendix Figure 4. Their overall concordance justifies the use of an average adult state (Appendix Figure 5).

One of us has already pointed that the Ekora skull may well belong to the small hipparion of Lothagam (Eisenmann 1995). If so, our reconstruction gives an idea about the adult skull of *H. feibeli* (Bernor et Harris 2003). According to our results, *H. feibeli* skull resembles most *H. verae* and *H. giganteum* of Grebeniki (as seen on the ratio diagram Appendix Figure 5), and *H. hendeyi* (Figure 24).

From Olduvai, there is another fragmentary skull about one year old, BM 067/5465. Although perhaps slightly younger than KNM ER 3539, it has larger dimensions. Otherwise it does not seem very different. Unfortunately the vomer-basion distance is uncertain. Two alternatives were used (Appendix Figure 6). It appears that BM 5465 had relatively smaller teeth than KNM ER 3539 but probably belonged also to *H. cornelianum*.

About three years. Juvenile samples consist of 1-15 *E. grevyi*, 4-7 *E. burchelli*, 5-10 *E. hemionus*, and 3-8 *E. przewalskii*.

A fragmentary juvenile skull from Olduvai Bed II, BK II 283, was illustrated by Hooijer (1975, Plates 9-10). P4 and M3 are erupting, which would point in *Equus* to an age of around 3 years. The skull is particularly interesting because it has well preserved frontals. The reconstructions based on our modern models differ but slightly. Like in BM 5465, the teeth are relatively small. We refer it also to *H. cornelianum* (Appendix Figure 6).

The real (juvenile) and extrapolated "adult" values are in Appendix Table 2.

SKULL-MANDIBLE

Another question concerns the relation between mandible and skull dimensions, in particular muzzle lengths and widths.

Muzzle lengths. We have calculated the regression line for skull versus mandible dimensions in 83 modern horses (Appendix Figure 7). The correlation R² is 0.88. The skull muzzle length = (0.963 * mandible muzzle length) + 15.8. The Hadar skull of *H. hasumense* AL 340-8 is associated to a mandible. The mandible muzzle length is about 130mm, the skull muzzle length is about 140mm. The muzzle length of the mandible AL 177-21 (also from DD) is the same; according to the regression, the skull muzzle length would have been 141.2mm i.e. close to the actual length in AL 340-8. For the mandible of *H. cornelianum* KNM ER 1626 (muzzle length 115mm), the corresponding skull dimension would have been 126.7mm. For the mandibles of *H. crassum* Pp 208 and of *H. tchicoicum* (muzzle lengths 144 and 136mm), the corresponding skull dimensions would have been 154.8 and 147mm.

The regression of mandible versus skull dimensions is: mandible muzzle length = (0.910 * skull muzzle length) + 1.022.

Muzzle widths. We have calculated the regression lines for skull versus mandible dimensions and of mandible versus skull dimensions in modern equids with broad muzzles to match the broad muzzled African hipparions. The sample comprises 32 horses and 29 kiangs (Appendix Figure 8). The correlation R² is 0.80.

- The skull muzzle width = (0.729 * mandible muzzle width) + 21.823.

- The mandible muzzle breadth = (1.097 * skull muzzle width) - 11.959.

On the first scatter diagram (Appendix Figure 8) are plotted the real values for the associated skull and mandible AL 340-8 of *H. hasumense* and the values estimated from the mandible and from the skull. The real AL 340-8 plots far from the regression line, with an actual skull muzzle 57mm wide instead of the calculated 61.2mm. This is probably because it is very old and slightly crushed (Eisenmann, 1976, Plate 1).

On the same diagram are plotted the values for *H. hendeyi* of Langebaanweg E. The skull L 22187 is old, and its muzzle width is 57mm, giving 50.6mm for an estimated width of the mandibular muzzle. On the normal mandible L 20553 the muzzle width is 56mm giving 62.7mm as the probably normal skull width.

On Appendix Figure 9 are plotted the estimations for the skull muzzle widths of AL 177-21 (62.7mm), Omo 18-1968-363, KNM ER 1626 (73.6mm), 324 (64.1mm), and 1221 (67mm), Olduvai 067/5344, Melka Kunturé Garba IVD 6767, and Cornelia COR 679 (74mm).

On Appendix Figure 10 are plotted the estimations for the mandibular muzzle widths of AL 155-6 (53.9mm), AL 363-18 (64.8mm), AL 142-18 (68.1mm), Olduvai BK II 2845/6 (56mm) and BK II 264 (71.4mm), WW 1528/92, AaO 3647 (53.9mm), Lothagam LT 136 (54.7mm), KNM ER 3539, and Kanam BM 15906.

Not plotted estimations for *H. crassum* and *H. tchicoicum* are in Table 2.

APPENDIX TABLE CAPTIONS

Appendix Table 1. Percentage of growth of extant *Equus* species.

Appendix Table 2. Measurements in mm of juvenile hipparion skulls.

APPENDIX FIGURE CAPTIONS

Appendix Figure 1. Percentage of growth of extant *Equus* species. Measurements defined in Appendix table 1.

Appendix Figure 2. Ratio diagram of *H. cornelianum* juvenile skull from Koobi Fora, Burgi and its adult dimensions according to the growth of extant *Equus* skulls.

Appendix Figure 3. Ratio diagram of *H. cornelianum* skull supposed adult dimensions compared to the adult *H. afarensis*.

Appendix Figure 4. Ratio diagram of *H. feibeli* ? juvenile skulls from Ekora and Kanam and its adult dimensions according to the growth of extant *Equus* skulls.

Appendix Figure 5. Ratio diagram of *H. feibeli* ? skull supposed adult dimensions compared to the adults *H. verae* and *H. giganteum* of Grebeniki.

Appendix Figure 6. Ratio diagram of supposed adult dimensions of *H. cornelianum* from Koobi Fora, Burgi and Olduvai Bed II.

Appendix Figure 7. Scatter diagram and regression of the skull muzzle length on the mandibular muzzle length.

Appendix Figure 8. Scatter diagram and regression of the skull muzzle width on the mandibular muzzle width.

Appendix Figure 9. Scatter diagram and regression of other skull muzzle widths on other mandibular muzzle widths.

Appendix Figure 10. Scatter diagram and regression of the mandibular muzzle width on the skull muzzle width.