A contribution to the evolutionary history of Ethiopian hipparionine horses (Mammalia, Equidae): morphometric evidence from the postcranial skeleton

Raymond L. BERNOR
College of Medicine, Department of Anatomy,
Laboratory of Evolutionary Biology, Howard University, 520 W St. NW,
Washington D.C. 20059 (USA)
rbernor@howard.edu

Robert S. SCOTT
Department of Anthropology, University of Arkansas,
Fayetteville, AR 72701 (USA)
rscott@uark.edu

Yohannes HAILE-SELASSIE
Cleveland Museum of Natural History, 1 Wade Oval Drive,
Cleveland, OH 44106 (USA)
yhailese@cmnh.org

Bernor R. L., Scott R. S. & Haile-Selassie Y. 2005. — A contribution to the evolutionary history of Ethiopian hipparionine horses (Mammalia, Equidae): morphometric evidence from the postcranial skeleton. *Geodiversitas* 27 (1) : 133-158.

ABSTRACT

A morphometric analysis of third metapodials and first phalanges of Middle Awash and Hadar hipparions dating from the 6.0-3.0 Ma interval was conducted using two methods. Morphological comparisons using standard metrics were made using: 1) log10 ratio diagrams; 2) size independent variables developed with reference to scaling trends for hipparions in general. Results of these analyses suggest that hipparion diversity during this temporal interval was relatively low. A single dominant gracile lineage of *Eurygnathohippus* Van Hoepen, 1930, most plausibly derived from the Lothagam (Kenya) species *Eurygnathohippus feibeli* (Bernor & Harris, 2003), would appear to have persisted throughout this interval and is marked by increases in size with measured change in metapodial and phalangeal morphology. A rarer, more robust form is found in the Ethiopian sample at 4.0 Ma and is morphometrically similar to *Eurygnathohippus turkanense* Hooijer & Maglio, 1973 from late Miocene horizons of Lothagam. Another smaller form, of uncertain systematic status, appears likely late in the Kada Hadar sequence, *c.* 3.0 Ma.

KEY WORDS
Mammalia,
Equidae,
hipparionine,
Ethiopia,
Middle Awash,
Hadar,
postcranials,
morphometrics,
evolution.

RÉSUMÉ

Contribution à l'histoire évolutive des chevaux hipparions éthiopiens (Mammalia, Equidae) : morphométrie du squelette postcrânien.

Par deux approches différentes, une analyse morphométrique est réalisée sur les troisièmes métapodes et les premières phalanges des « hipparions » provenant des niveaux datés de 6,0 à 3,0 Ma dans le Middle Awash et le Hadar. En utilisant les mesures traditionnelles, des comparaisons morphologiques sont faites par l'intermédiaire : 1) des diagrammes de ratios des mesures transformées en log 10 ; et 2) des variables indépendantes de taille étalonnées pour établir les tendances. Les résultats indiquent que la diversité des « hipparions » était relativement faible pour la période de temps considérée. Une seule lignée dominante, gracile, d'*Eurygnathohippus* Van Hoepen, 1930, probablement dérivée de l'espèce *Eurygnathohippus feibeli* (Bernor & Harris, 2003) de Lothagam (Kenya), semble avoir persisté à travers cette période. Cette lignée montre une augmentation de taille avec un changement modéré de la morphologie des métapodes et phalanges. Une forme plus rare et plus robuste, trouvée dans les niveaux éthiopiens datés à 4,0 Ma, est morphométriquement similaire à *Eurygnathohippus turkanense* Hooijer & Maglio, 1973 des niveaux datés du Miocène supérieur de Lothagam. Une forme plus petite, au statut systématique incertain, apparaît dans la séquence du Hadar *c.* 3,0 Ma.

MOTS CLÉS
Mammalia,
Equidae,
hipparion,
Éthiopie,
Middle Awash,
Hadar,
éléments postcrâniens,
morphométrie,
évolution.

INTRODUCTION

Hipparionine horses originated in North America *c.* 16 Ma and first entered the Old World between 11.1 and 10.7 Ma (Bernor *et al.* 2003). Recent evidence suggests that Sub-Saharan Africa participated in the so-called "Hipparion Datum" with the recognition that the Ethiopian locality of Chorora rivals the antiquity of other Eurasian "Datum" localities, and has a hipparion species there that is distinctly primitive (Geraads *et al.* 2003; Bernor *et al.* 2004). First occurring Old World hipparions are now recognized as being morphologically and morphometrically very similar to the North American genus *Cormohipparion* Skinner & MacFadden, 1977, and specifically, *C. occidentale* s.l. (Woodburne 1996). Evolutionary diversification of Old World hipparions would appear to have occurred already in the early Vallesian (MN 9), but certainly varied provincially in the tempo and mode of their evolution. Bernor *et al.* (2003) have demonstrated a "punctuated" diversification in later MN9 hipparions of Sinap, Turkey, whereas Central European hipparions exhibited relative stasis or low diversity through much of the Vallesian (Bernor *et al.* 1996; Bernor & Franzen 1997; Bernor & Armour-Chelu 1999a; Kaiser *et al.* 2003).

Whereas the Eurasian late Miocene hipparion record is rich and species diverse, that of Africa is relatively meager. Bernor & Armour-Chelu (1999b) have provided an extensive overview of the evolutionary history of African hipparions that will not be repeated here. It is sufficient to say that the late Miocene East African record is particularly poor and best represented skeletally in the 7-5 Ma interval at the Kenyan locality of Lothagam. Bernor & Harris (2003) demonstrated that Lothagam's Upper and Lower Nawata members include a derived lineage of hipparions that they refer to the genus *Eurygnathohippus* Van Hoepen, 1930. Two species are recognized, one larger with robustly built metapodials, *Eurygna-*

thohippus turkanense Hooijer & Maglio, 1973, and a smaller one with elongate, slender metapodials, *Eurygnathohippus feibeli* (Bernor & Harris, 2003). *Eurygnathohippus* is a genus belonging to a radicle of hipparionines termed the "*Sivalhippus* Complex" by Bernor & Hussain (1985). Bernor & Lipscomb (1991, 1995), Bernor & Armour-Chelu (1999a, b) and Bernor & Harris (2003) have argued that *Eurygnathohippus* is a vicariant, late Miocene-Pleistocene clade restricted to Africa and united by the occurrence of ectostylids on the permanent lower cheek teeth of all its species. Given the propensity of Old World hipparionines to extend their ranges over long geographic distances in relatively short intervals of time, it is remarkable that this clade would appear to be restricted to Africa for 7+ million years time.

We present here an analysis and interpretation of Ethiopian hipparion postcranial evolution for the 6.0-3.0 Ma interval based on samples collected by the Middle Awash and Hadar research projects. This work follows an earlier one by Bernor & Scott (2003) where the authors reevaluated the Sahabi, Libya (latest Miocene, *c.* 7-5.3 Ma) hipparion fauna undertaking a morphometric analysis of metacarpal IIIs, metatarsal IIIs and 1st phalanges III. In that work, the authors demonstrated that there were at least two species of hipparion, one with affinities to the predominantly eastern Mediterranean *Cremohipparion* aff. *matthewi* lineage and the other to the Indo-Pakistan-African "*Sivalhippus* Complex". Because the East African late Miocene-medial Pliocene equid record is limited, there are few papers discussing their evolutionary record (see Bernor & Armour-Chelu 1999b for a complete review). Most publications are site specific, and none pointedly addresses the postcranial component of that evolutionary process. We will follow Bernor & Scott (2003) in demonstrating what morphometric trajectories Ethiopian hipparions took in the 6.0-3.0 Ma interval.

The Middle Awash (see Fig. 1 for a map of localities) material was initially identified and analyzed by YHS and presented as part of his Ph.D. dissertation (Haile-Selassie 2001). Haile-Selassie (2001) recognized two species of *Eurygnathohippus* from the latest Miocene/earliest Pliocene Middle Awash horizons, including the larger *E. turkanense* and a smaller form, *Eurygnathohippus* sp.: the larger form is recognized only by cheek teeth, while the smaller form is recognized by mandibular and postcranial material. Haile-Selassie (2001) has recognized the difficulty of distinguishing the differences between these taxa by teeth alone. The Middle Awash chronology used here is based on work published by Renne *et al.* (1999) and WoldeGabriel *et al.* (2001).

The Hadar material has been collected from the 1970's onward by Dr. Donald Johanson and his collaborators, and is currently curated by the Institute of Human Origins (IHO), Arizona State University, Tempe, at the National Natural History Museum of Ethiopia (Addis Ababa). A small portion of this material was described by Eisenmann (1976), and since then the Hadar hipparions have only been mentioned in passing. Correlation of the Hadar localities to Hadar Formation members and submembers is taken from Gray (1980). Current Hadar chronology, based on single crystal argon dates, has recently been summarized by Kimbel *et al.* (1996). Accordingly, we correlate Hadar localites cited here as follows:

1) The Sidi Hakoma Member includes four submembers, ordered from base to top: SH1, SH2, SH3 and SH4. The base of SH1 is defined by the SHT (SH Tuff), 3.40 +/- 0.03 Ma. Upper SH3 includes the KMB Tuff dated 3.28 Ma +/- 0.04 Ma (C. Feibel pers. comm.).

2) The Sidi Hakoma Member is stratigraphically succeeded by the Denen Dora Member, which itself includes three submembers, DD1, DD2 and DD3. The base of the Denen Dora Member is defined by the TT-4 tuff dated 3.22 +/- 0.01 Ma.

3) The Denen Dora Member is stratigraphically succeeded by the Kada Hadar Member, which includes three submembers, KH1, KH2 and KH3. The base of the Kada Hadar Member is defined by the KHT, dated 3.18 +/- 0.01 Ma. The uppermost KH localities referred to here (from KH3), AL 361 and AL 363, are from a sand body placed between BKT-1 (undated) and

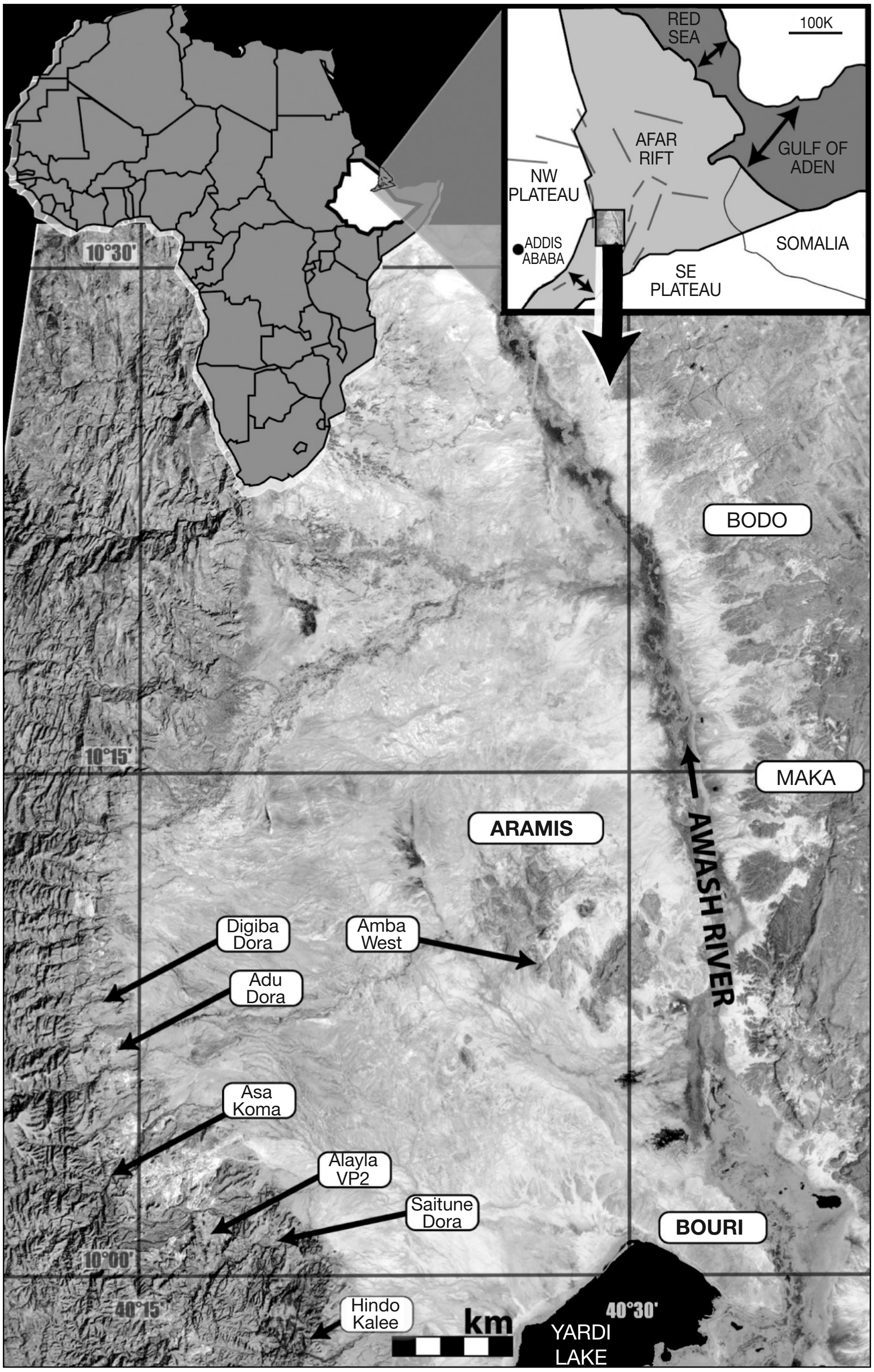


FIG. 1. — Map showing paleontological localities of the Middle Awash. Hadar and Galili are not plotted on this map and are about 50 km north of Bodo (Hadar) and 30 km southeast (Galili) of Yardi Lake, respectively. Modified after WoldeGabriel *et al.* 2001.

BKT-2 (2.92 +/- 0.03 Ma). Feibel (pers. comm.) believes that these localities are approximately correlative with the Kaena Subchron, 3.02 Ma. A disconformity occurs less than 10 m above BKT-2. The horizons above the disconformity are substantially younger and calibrated near the top of the section by BKT-3, 2.33 Ma (Kimbel *et al.* 1996).

We will not erect new taxa in this contribution. Potential naming of any new Ethiopian hipparion taxa must first take into consideration complete skeletal assemblages that are analysed and characterized compared to other relevant assemblages. It is our intention that this work serves as a contribution to the postcranial background of East African latest Miocene-medial Pliocene hipparion evolution.

METHODS

Table 1 (Appendix) lists the Ethiopian localities that we analyse here along with those Eurasian and African localities we use for statistical comparison. Table 2 (Appendix) provides a list of Hadar localities and their stratigraphic provenance following Gray (1980). We analyse the morphology of metacarpal IIIs (hereafter MCIIIs), metatarsal IIIs (MTIIIs; MCIIIs and MTIIIs collectively will be referred to as MPIIIs) and 1st phalanges IIIs (1PHIIIs), using standard equid measurements published by Eisenmann *et al.* (1988) and Bernor *et al.* (1997). In all our analyses, we use the Höwenegg sample as our analytical standard for the postcranial skeleton. This population is composed of 14 articulated skeletons (many of which are complete) and is "biologically uniform", including only a single primitive species, *Hippotherium primigenium* Meyer, 1833 (Bernor *et al.* 1997). This sample has been found to be particularly useful for statistical comparisons of postcranial elements. Indeed, the possibilities for broad comparative study of hipparion metapodials are greatly expanded by the extraordinary preservation of and body of scholarship on hipparions from Höwenegg (Bernor *et al.* 1997; Scott 2004).

Two morphometric approaches are adopted here. Traditionally, log10 ratio diagrams have been used as a descriptive tool in discussions of hipparion morphology (e.g., Eisenmann 1995). We apply this approach here to MPIIIs and 1PHIIIs. Log10 ratio diagrams graphically illustrate deviations from a comparative standard (in this study the Höwenegg population sample) and are a useful descriptive heuristic. Profiles shown in ratio diagrams represent absolute deviations from a morphometric standard.

A limitation of log10 ratio diagrams is that they do not account for morphological differences that might result from allometric scaling. Therefore, a second approach is also used here to make comparisons concerning key morphological components after correcting for the effects of scaling. Accordingly, we have produced bivariate plots of key measurements versus a proxy size variable and of size independent variables summarizing key morphological components. These plots summarize differences in shape relative to body size.

Previous principal components analyses of late Miocene hipparion samples from Sümeg (Hungary; Bernor *et al.* 1999), Sinap (Turkey; Bernor *et al.* 2003), Sahabi (Libya; Bernor & Scott 2003), Dorn Dürkheim (Germany; Kaiser *et al.* 2003), and Akkasdagi (Turkey; Scott & Maga in press) have demonstrated the importance of variables relating to relative elongation and slenderness for understanding MCIII, MTIII and 1PHIII morphology. Staesche & Sondaar (1979) have also suggested that the development of the sagittal keel is a similarly important component of MPIII morphology (see also Kaiser *et al.* 2003). Thus, we have focused on bivariate plots concerning the scaling of MPIII length, slenderness and MCIII sagittal keel development. We have also plotted size independent variables detailing these features relative to a scaling trend for the large sample of hipparion MPIIIs of Scott (2004).

Body mass estimates or some proxy measure are necessary to describe the scaling of key morphological axes. The regression formulae of Scott (1990) are available for body mass estimation but typically yield divergent estimates for MCIIIs and MTIIIs making them of limited utility for studies addressing both MCIIIs and MTIIIs. Gordon (2002, 2003, 2004; see also Jungers *et al.* 1995) argued that geometric mean size variables termed Global Size Variables (GSVs) are more stable measures of general body size than body mass estimates and can be measured without prediction errors. A GSV of non-length metapodial dimensions (Metapodial Global Size Variable, or MGSV) is used here to investigate the scaling of MPIIIs. This MGSV is precisely analogous to the geometric mean of nine non-length metapodial dimensions used by Bernor & Scott (2003) which they termed "GEOMEAN Size". MGSV is calculated as follows:

$\mathrm{MGSV} = (\mathrm{M3} \times \mathrm{M4} \times \mathrm{M5} \times \mathrm{M6} \times \mathrm{M10} \times \mathrm{M11} \times \mathrm{M12} \times \mathrm{M13} \times \mathrm{M14})^{(1/9)}$

A similar size variable for 1PHIIIs was calculated as follows:

$\mathrm{PGSV} = (\mathrm{M3} \times \mathrm{M4} \times \mathrm{M5} \times \mathrm{M6})^{(1/4)}$

In order to generate shape variables that are not correlated with body size (or size independent variables), and to summarize differences in MPIII length, slenderness, and sagittal keel development that are not the result of scaling, M1, M3, M12, and M13 were first divided by MGSV and the resulting ratios were logged. These ratios were tested for a correlation with the log of MGSV using the entire hipparionine sample described by Scott (2004) in SAS (SAS Institute, Cary, NC). In each case a significant correlation was found ($p > 0.05$) and the residual of the logged ratios was computed. This residual is identical to the residual of the logged measurement versus the log of MGSV. The prefix "si" was added to resulting size independent variables (siM1, siM3, siM12, siM13). The result was four variables uncorrelated with MGSV that summarized: 1) MPIII length relative to body size (= siM1); 2) MPIII slenderness relative to body size (= siM3); and 3) development of the sagittal keel relative to body size (= siM12 and siM13).

For 1PHIIIs, the log transformed variables M1 (maximum length) and M3 (minimum mid-shaft width) were plotted versus 1PHIII PGSV. These plots also include least squares regressions for the Höwenegg sample of these variables versus PGSV and follow Bernor *et al.* (2003) closely.

ABBREVIATIONS AND CONVENTIONS

AMNH	American Museum of Natural History, New York;
AL	Afar locality, designated for Hadar localities;
AS	Ankara, Sinap;
BMNH	Natural History Museum, London (former British Museum of Natural History, London);
CrmedPikK87	*Cremohipparion mediterraneum*, Pikermi, from Koufos (1987);
ISP	International Sahabi Project, directed by Drs. Noel T. Boaz and Ali El Arnuati;
KNM-LT	National Museums of Kenya, Lothagam specimens;
MA	Middle Awash localities designated by an abbreviation followed by VP-Number of Locality-Specimen number (example: JAB-VP-1-1; see Appendix, Table 3);
MNHN	Muséum national d'Histoire naturelle, Paris;
Ho STD	Höwenegg standard.

Measurements are in millimeters (mm) (all measurements as defined by Eisenmann *et al.* [1988] and Bernor *et al.* [1997] and rounded to 0.1 mm).

MCIII	metacarpal III;
MTIII	metatarsal III;
MPIII	metapodial III;
1PHIII	1st phalanx III.

The nomen *Hipparion* has been used in a variety of ways by different authors. We follow characterizations and definitions for hipparionine horses recently provided in Bernor *et al.* (1996, 1997). Anatomical descriptions have been adapted from Nickel *et al.* (1986). Getty (1982) was also consulted for morphological identification and comparison. Hipparion monographs by Gromova (1952) and Gabunia (1959) are cited after the French translations.

ANALYSIS

We analyze here MCIIIs, MTIIIs and 1PHIIIs from the Ethiopian latest Miocene-medial Pliocene in comparison to Eurasian localities. We present our analyses by element in the following order: MCIII, MTIII and 1PHIII. We follow Bernor *et al.* (1997) in not distinguishing between anterior and posterior 1PHIIIs except when the association is secure. This methodology is based on the Höwenegg sample which showed negligible morphological and metrical differences between the fore and hind 1PHIIIs.

Table 1 (Appendix) lists the hipparion localities, their geographic location, age and specimen identifier. Table 2 (Appendix) further breaks down the Hadar specimens by locality and stratigraphic position. Table 3 (Appendix) contains measurements of all Ethiopian skeletal materials analyzed in this contribution. The measurements follow the methods illustrated in Eisenmann *et al.* (1988) and Bernor *et al.* (1997).

LOG10 RATIO DIAGRAMS

Figure 2A is a log10 ratio diagram of mostly complete MCIIIs from lower MN 9 of Sinap (AS93/604), Pakistan (AMNH 19761 and AMNH 19685) and Lothagam (KNM-LT22871). Bernor *et al.* (2003) and Bernor & Scott (2003) have demonstrated that AS93/604 is the most primitive Old World hipparion yet known and referable to the North American genus *Cormohipparion*, *C. sinapensis* Bernor, Scott, Fortelius, Kappelman & Sen, 2003. Therefore, this plot shows the relative length and width deviations away from the Höwenegg sample and the first occurring (and primitive) Old World hipparion sample represented by AS93/604. Compared to the Höwenegg sample, the Sinap specimen has a similar relative maximum length (M1), more slender mid-shaft width (M3), similar mid-shaft depth (M4), lesser proximal articular width (M5) and depth (M6), distal supra-articular width (M10), distal articular width (M11), distal sagittal keel (M12) and cranial-caudal dimensions of the distal articular surface (M13, lateral and M14, medial). The most characteristic feature of the primitive Sinap MCIII is the sharply lower M3 versus M4 dimension: relative to the Höwenegg hipparion, the primitive morphology seems to be a relatively narrow mid-shaft width compared to mid-shaft depth. The AMNH specimens plotted here are referable to *Sivalhippus perimense* (*sensu* Bernor & Hussain 1985), and exhibit the following characteristics compared to the Höwenegg sample: similar length (M1); M3 similar or slightly elevated, M4-M14, more strongly elevated in their relative size. Clearly, *Sivalhippus perimense* had a greater body mass than the *Hippotherium primigenium*. The single Lothagam MCIII is referable to *Eurygnathohippus turkanense* Hooijer & Maglio, 1973 (Bernor & Harris 2003) and exhibits a log10 ratio size pattern closely similar to *Sivalhippus perimense*. *Eurygnathohippus turkanense* is in fact slightly more robustly built than *Sivalhippus perimense* Pilgrim, 1910 in most of its dimensions. An interesting additional observation is that all hipparions under consideration in Figure 2A have a very similar relative length, and we believe that this is a primitive feature for Old World hipparionine horses.

Figure 2B plots more gracile morphs from Bou Hanifia, Pikermi, Sahabi Lothagam and Amba West (5.2 Ma) compared to Sinap AS93/604A. There is an extensive overlap between *C. sinapensis* (AS93/604A), "*Hippotherium*" *africanum* Arambourg, 1959 (MNHN 95), *Eurygnathohippus feibeli* (KNM-LT139A) and *Cremohipparion mediterraneum* on most data points and overall trajectory of the log10 plot. An exception to this is the strong lengthening of *E. feibeli* maximum length (M1), also noted by Bernor & Scott (2003). The single Sahabi MCIII, ISP27P25B, is shorter than the rest of the sample, with a strong deviation in its mid-shaft width (M3) and distal articular width (M11). As cited by Bernor & Scott (2003: fig. 1A, B), these aspects of the Sahabi hipparion compare closely with the gracile hipparions from Samos and this is the reason that the authors referred the Sahabi form to the genus *Cremohipparion*. We further plot in this figure the oldest complete MCIII from the Middle Awash sequence, AMW-VP-1-15 (Amba West; 5.2 Ma; Haile-Selassie 2003). The Amba West individual overlaps Lothagam *E. feibeli* in maximum length (M1), is closely similar to it in mid-shaft width (M3) and mid-shaft depth (M4), has greater dimensions for the proximal articular facet (M5 and M6) and distal articular (M10 and M11) dimensions, while overlapping it for their distal sagittal keel dimensions (M12, M13 and M14). In effect, the Amba West specimen is closest in its morphology to *E. feibeli*, being derived in its

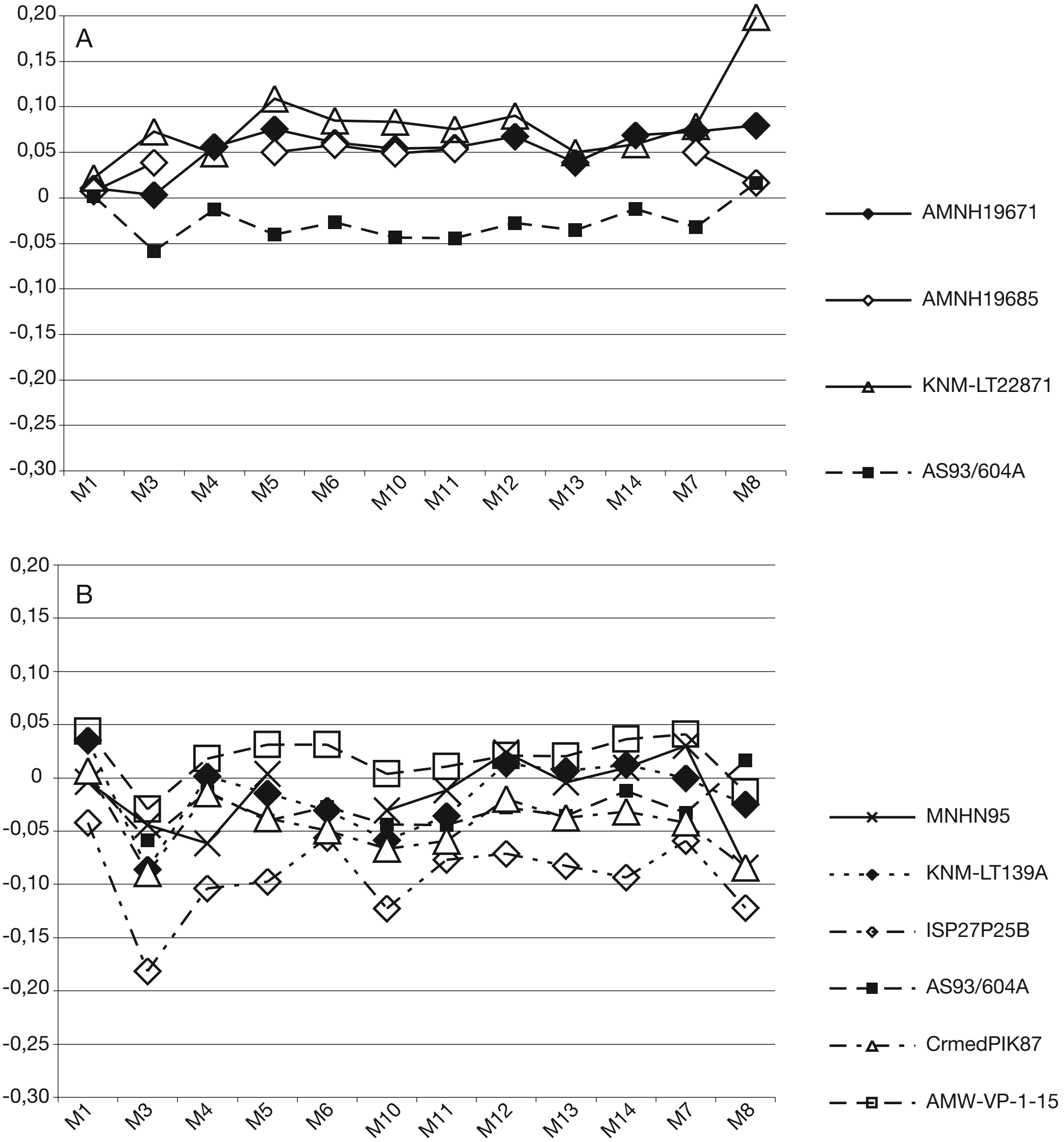
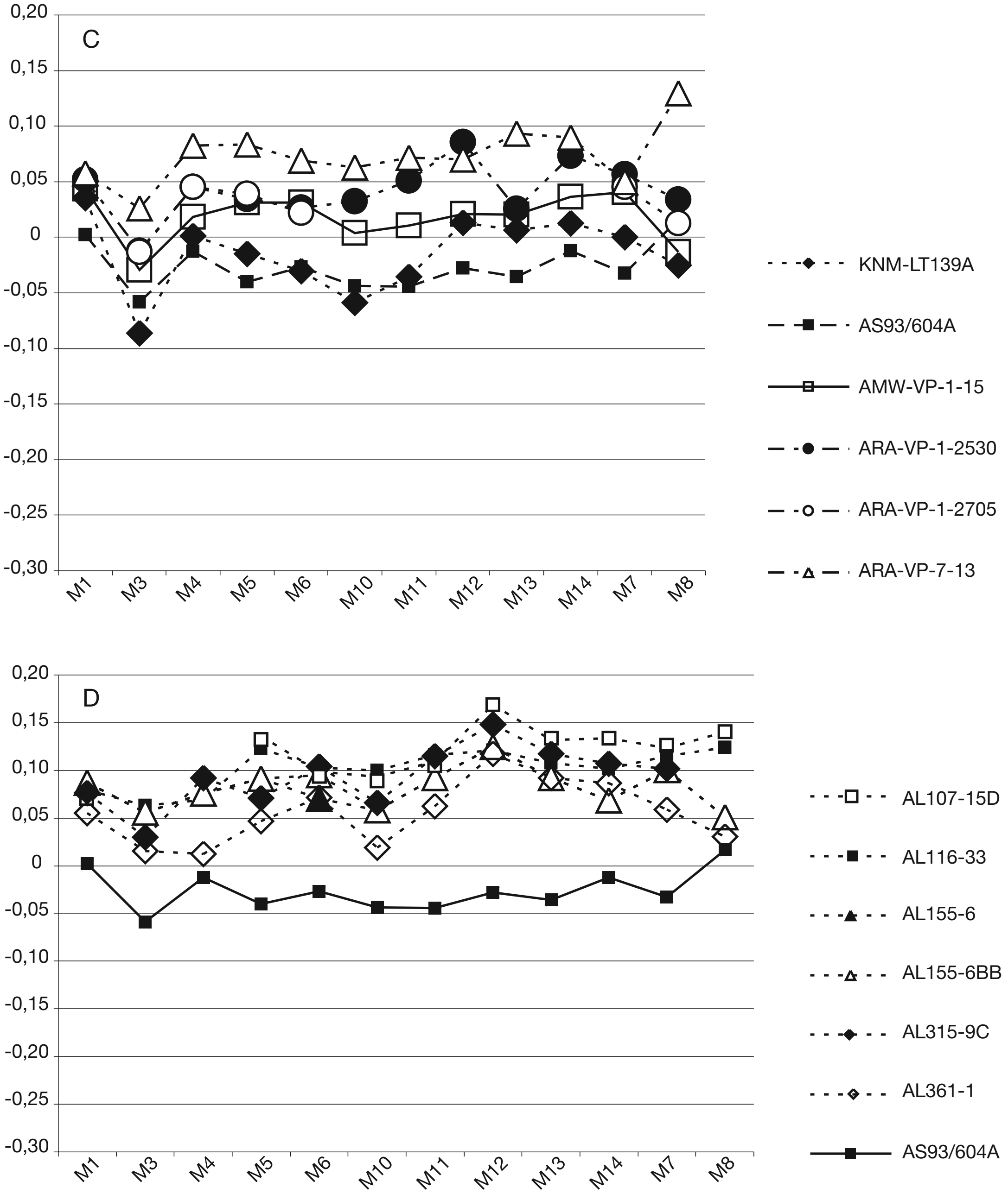


FIG. 2. — **A**, MCIII log10 ratio, robust taxa of the *Sivalhippus* Complex, compared to Sinap *Cormohipparion sinapensis*, Ho STD; **B**, MCIII log10 ratio, gracile taxa, Bou Hanifia, Pikermi, Sahabi, Lothagam and Amba West compared to Sinap, Ho STD; **C**, MCIII log10 ratio, Middle Awash, Lothagam *E. feibeli*, compared to Sinap, Ho STD; **D**, MCIII log10 ratio, Hadar compared to Sinap, Ho STD.

slightly greater robusticity, but does not have a greater relative length. It has elevated dimensions of the mid-shaft width (M3), proximal (M5, M6) and distal articular (M10, M11) dimensions compared to Sahabi and Samos small species of the *Cremohipparion* lineage.

Figure 2C plots the entire Middle Awash sample in comparison to *C. sinapensis* and Lothagam *E. feibeli*. *Eurygnathohippus feibeli* clearly exhibits its distinctive derivation compared to Sinap *Cormohipparion sinapensis* in its increased relative length (M1) and distal articular dimensions



(M12, M13 and M14). The increased dimension of the distal sagittal keel is particularly important in that it likely indicates that the locking mechanism of the MCIII-1PHIII joint was more developed (Eisenmann 1995). The differences cited above between *E. feibeli* and the Amba West MCIII are continued and augmented by the three Aramis specimens: ARA-VP-1-2530 (4.4 Ma), ARA-VP-1-2705 (4.4 Ma) and ARA-VP-7-13 (4.2 Ma). It is interesting that the marginally youngest specimen, ARA-VP-7-13, has the greatest dimensions for M3-M11 and M13. Once again, the trajectories and dimensions for all the Ethiopian MCIIIs are most similar to one another, and at the same time continue the morphometric trends of increased length and increased relative size of the distal articular surface developed in *E. feibeli* away from the primitive morphology.

Figure 2D plots all of the complete Hadar MCIII material. Of this material, one specimen is from the Sidi Hakoma Member (AL107-15D, SH2u, 3s), four are from the Denen Dora unit (AL116-33, AL155-6, AL155-6BB and AL315-9C from DD2-3) and one from the upper Kada Hadar (AL361-1, KH3s; Gray 1980). All of the specimens show similar proportions throughout, and the Sidi Hakoma and Denen Dora specimens generally exhibit increased relative size over all other hipparions considered here. Interestingly, the youngest specimen from Kada Hadar (AL361-1) exhibits the smallest dimensions for maximum length (M1), midshaft width and depth (M3 and M4), proximal articular width (M5) and distal articular dimensions (M11 and M12). The Hadar hipparions exhibit trends in MCIII evolution that were apparent with *E. feibeli* and the Middle Awash hipparions: maximum length (M1) continued to increase, proximal (M5 and M6) and distal (M10, M11 and M12) articular dimensions have increased. The single most striking increase in dimension is distal sagittal keel (M12), which is strikingly elevated. Again, we propose that this increased dimension of M12 reflects enhanced locking of the MTIII-1PHIII joint and likely increased functional monodactyly.

Figure 3A plots the robust taxa in our MTIII sample compared to the Höwenegg standard and Sinap *Cormohipparion sinapensis* (AS93/827A), including specimens from: Pakistan (AMNH 26953 and AMNH 29811, *Sivalhippus perimense*) and Lothagam (KNM-LT25470, *E. turkanense*). The Pakistan and Lothagam specimens exhibit very similar proportions: they have fundamentally the same maximum length dimensions as the standard and *C. sinapensis*; they further exhibit elevated dimensions for all other measurements except AMNH 29811 which has a small M13 dimension of the distal articular facet. These individuals clearly had a heavier body mass than *H. primigenium* and *C. sinapensis*.

Figure 3B plots MTIIIs of the gracile taxa from Bou Hanifia (MNHN numbers, *H. africanum*), Pikermi (CrmedPikK87, mean values following Koufos 1987) and Sahabi (ISP numbers, *Cremohipparion* aff. *matthewi*) compared to Sinap. All specimens have relative maximum lengths similar to the Höwenegg and Sinap specimens. All specimens further exhibit sharply reduced mid-shaft width reduction compared to Höwenegg, and except for two specimens of *H. africanum* (MNHN 9214 and MNHN 923), mid-shaft depth (M4) is relatively much greater than mid-shaft width. Pikermi *C. mediterraneum* Roth & Wagner, 1854 tracks Sinap *C. sinapensis* remarkably closely in all measurements, being mostly reduced in its overall size. The same applies generally for *H. africanum.* One Sahabi specimen, ISP67P16A, likewise is similar to Pikermi, having a more slender mid-shaft dimension, but ISP1P25B shows a sharp reduction in midshaft dimensions (M3 and M4) and distal supra-articular (M10) and articular (M11) dimensions, while maintaining relatively greater distal articular dimensions M12, M13 and M14. It is possible that there are two different species of small hipparions represented by these two specimens.

Figure 3C plots Lothagam *E. turkanense* (KNM-LT2547), Middle Awash (GAL-VP-6-5A, 4.0 Ma and HIN-VP-1-3, 4.0 Ma) and Hadar (AL151-47 and AL155-6AZ, both originating from the Denen Dora Member, *c.* 3.2 Ma) with Sinap *C. sinapensis* and Höwenegg as bases of comparison. The Lothagam, Middle Awash and Hadar forms are remarkable for their elevated values in most measurements. Lothagam *E. turkanense* and the two Middle Awash specimens retain the same relative length as *H. primigenium* and *C. sinapensis*, while the Hadar specimens exhibit a strong increase in the maximum length dimension (M1). Whereas the Middle Awash and Lothagam forms exhibit relatively greater mid-shaft depth dimensions (M4) than mid-shaft width dimen-

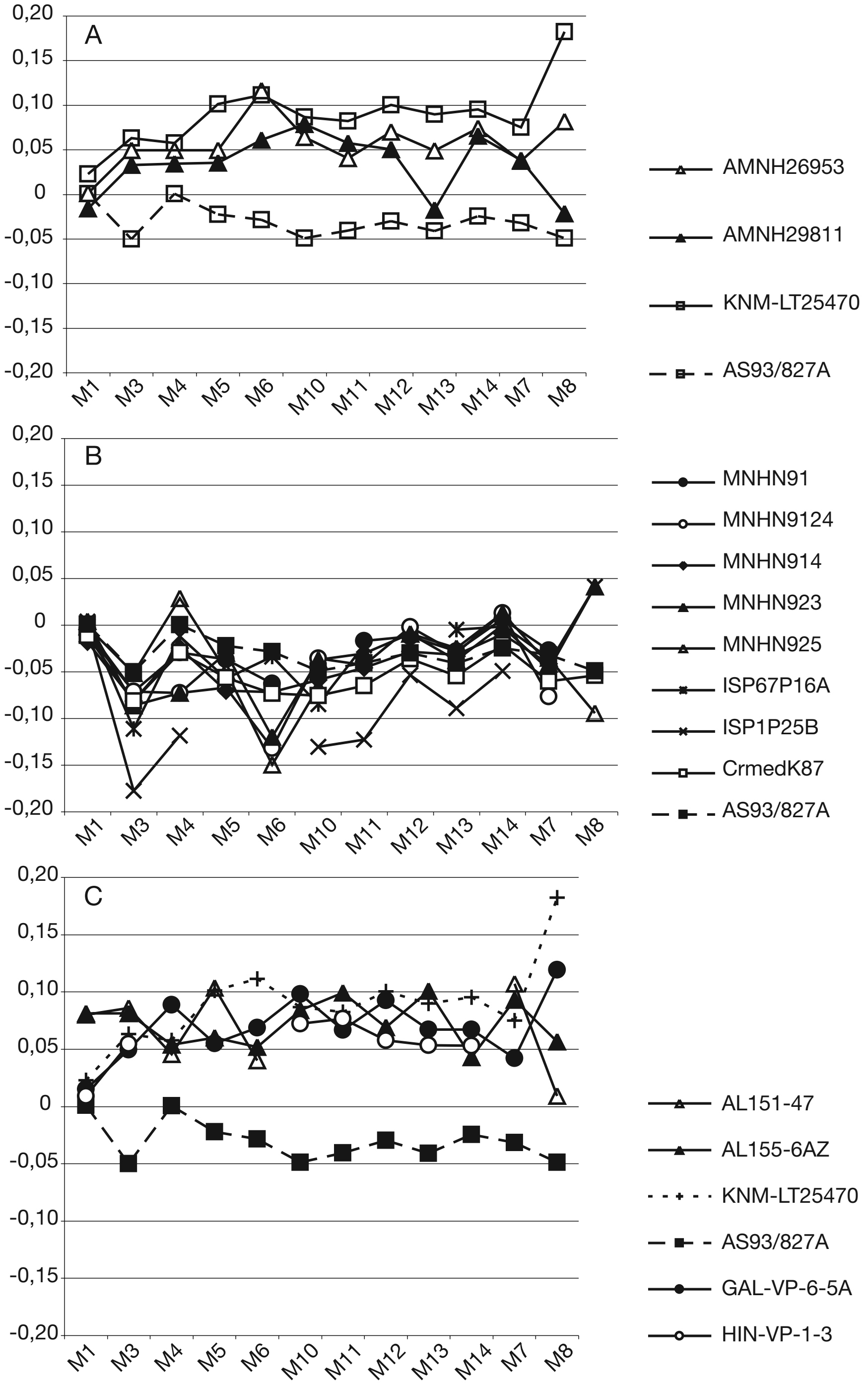


FIG. 3. — **A**, MTIII log10 ratio, robust taxa of the *Sivalhippus* Complex, compared to *Cormohipparion sinapensis*, Ho STD; **B**, MTIII log10 ratio, gracile taxa, Bou Hanifia, Pikermi and Sahabi compared to Sinap, Ho STD; **C**, MTIII log10 ratio, Lothagam, Middle Awash and Hadar *Eurygnathohippus* spp., compared to Sinap, Ho STD.

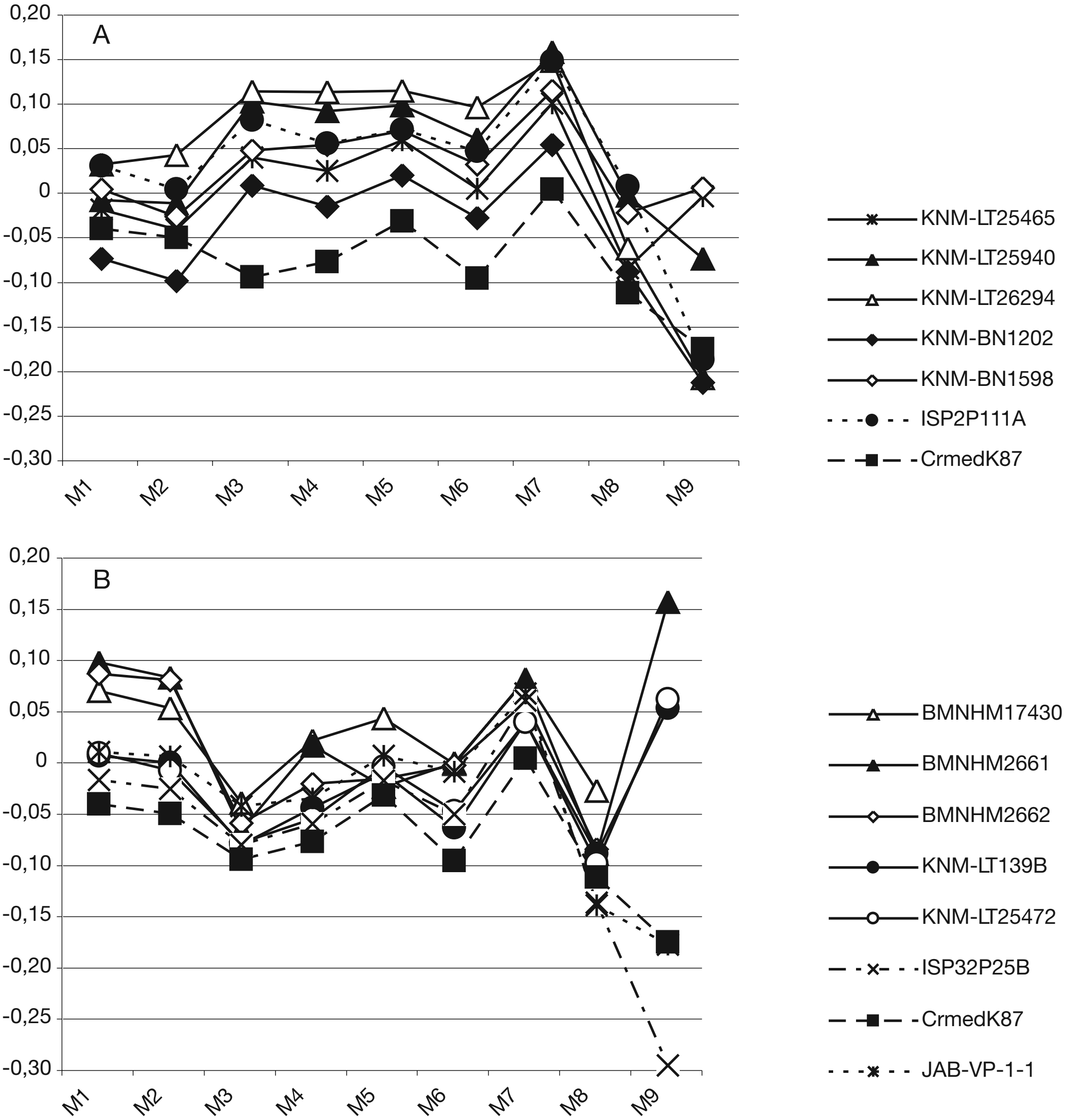
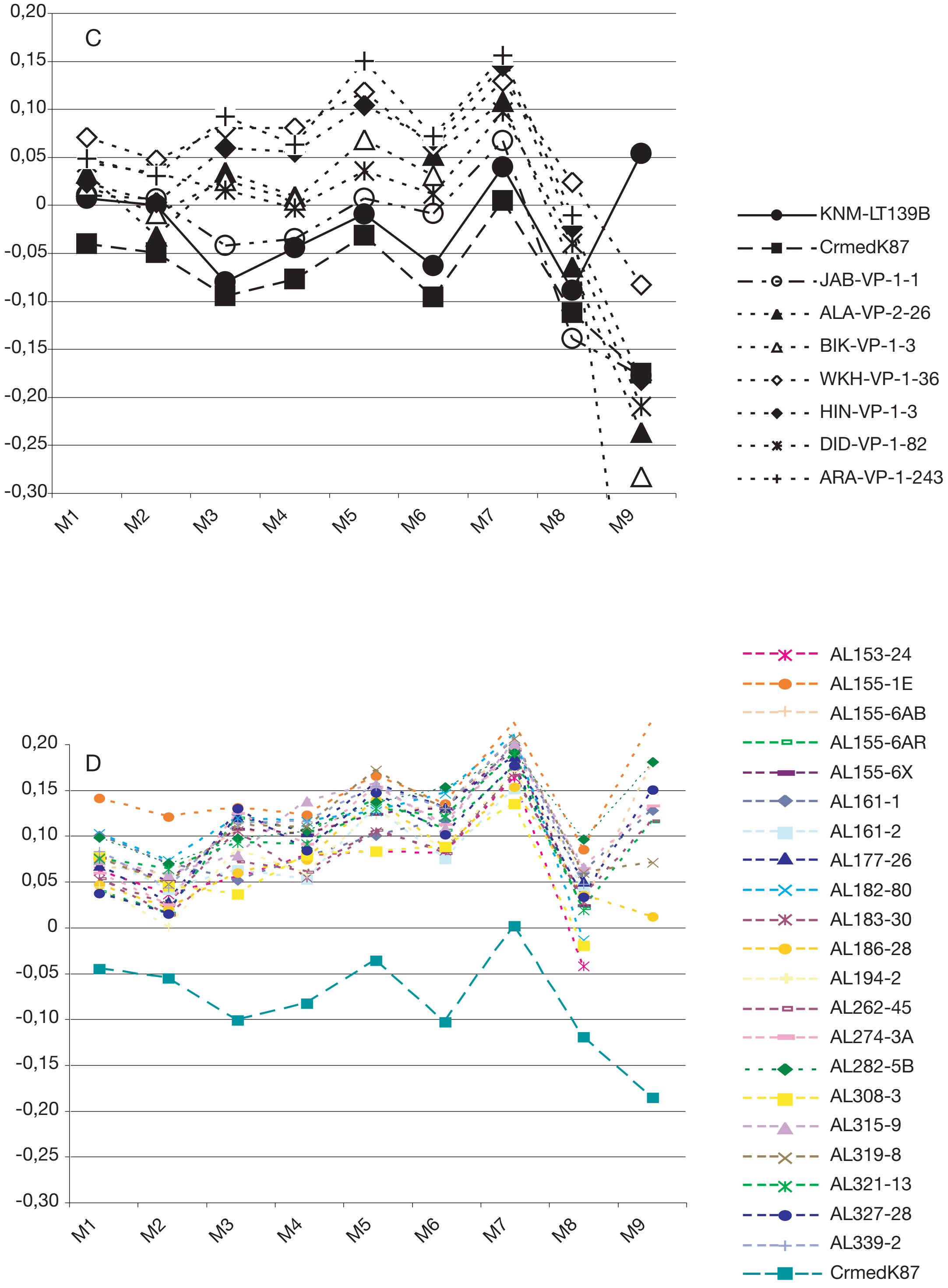


FIG. 4. — **A**, 1PHIII log10 ratio, robust taxa from Ngorora, Lothagam and Sahabi compared to Pikermi, Ho STD; **B**, 1PHIII log10 ratio of slender taxa from Indo-Pakistan, Lothagam, Sahabi, Pikermi and the Middle Awash, Ho STD; **C**, 1PHIII log10 ratio, Middle Awash, Lothagam *Eurygnathohippus feibeli* compared to Pikermi, Ho STD; **D**, 1PHIII log10 ratio, Hadar compared to Pikermi, Ho STD.

sions (M3), the converse is true in the two Hadar dimensions: M3 is elevated compared to M4. The greatest proximal articular surface depth dimension (M6) is found in *E. turkanense,* again reflecting the large body mass of this individual. In summary, this plot shows that Ethiopian hipparions exhibit a trend toward increased body size and lengthening of the MTIII during the 4.0-3.2 Ma temporal interval.

Figure 4A plots late Miocene 1PHIIIs from the Baringo Basin (KNM-BN numbers), Lothagam (KNM-LT numbers), Sahabi (ISP2P211A) and Pikermi (CrmedPikK87). All of the African specimens are similar in their log10 trajectories, and


C
0,20
0,15
0,10
0,05
0
-0,05
-0,10
-0,15
-0,20
-0,25
-0,30
M1
M2
M3
M4
M5
M6
M7
M8
M9
KNM-LT139B
CrmedK87
JAB-VP-1-1
ALA-VP-2-26
BIK-VP-1-3
WKH-VP-1-36
HIN-VP-1-3
DID-VP-1-82
ARA-VP-1-243
D
0,20
0,15
0,10
0,05
0
-0,05
-0,10
-0,15
-0,20
-0,25
-0,30
M1
M2
M3
M4
M5
M6
M7
M8
M9
AL153-24
AL155-1E
AL155-6AB
AL155-6AR
AL155-6X
AL161-1
AL161-2
AL177-26
AL182-80
AL183-30
AL186-28
AL194-2
AL262-45
AL274-3A
AL282-5B
AL308-3
AL315-9
AL319-8
AL321-13
AL327-28
AL339-2
CrmedK87

deviate from Pikermi mostly in their mid-shaft (M3), proximal articular surface width (M4) and depth (M5) and distal articular width (M7) dimensions. The African specimens mostly deviate away from the Pikermi specimen in the mid-shaft dimension (M3), they are more robustly built, and, save for a single Baringo Basin specimen (KNM-BN1202), all are relatively more robustly built than the *H. primigenium* standard. One Lothagam specimen (KNM-LT25456), is smaller than the other two Lothagam specimens, and plots between the two Baringo Basin specimens (KNM-BN1202 and KNM-BN1598). Bernor & Harris (2003: 402, fig. 9.14) noted the distinctly smaller and less robust size of this specimen and asserted that it represented a third, intermediate sized taxon in the Lothagam Nawata Formation fauna. They referred this taxon to *Hippotherium* cf. *primigenium* because of its relatively primitive morphology. The other two Lothagam specimens, KNM-LT25940 and KNM-LT26294, are referable to *E. turkanense,* and these in turn are virtually identical in their proportions to a large specimen from Sahabi (ISP2P111A; Bernor & Scott 2003).

Figure 4B plots 1PHIIIs of the more slenderly built taxa from Indo-Pakistan (BMNH numbers), Lothagam (KNM-LT numbers), Sahabi (ISP), Pikermi (Crmed) and Jara-Borkana (JAB), Middle Awash. All of these specimens have relatively slender mid-shaft (M3) dimensions compared to *H. primigenium.* All specimens except the *C. mediterraneum* sample from Pikermi have elevated distal articular width (M7) dimensions compared to Höwenegg. The Indo-Pakistan specimens are remarkable for being the most elongate-slender specimens of the sample. Lothagam specimen KNM-LT139B is the type specimen of *Eurygnathohippus feibeli*. This specimen compares very closely with the other Lothagam specimen, KNM-LT25472 and the oldest 1PHIII currently known from the Middle Awash sequence, JAB-VP-1-1 (6 Ma). JAB-VP-1-1 deviates from the *E. feibeli* trajectory only in its distal supra-articular width (M7) dimension, which is not metrically significant at the species level. The Sahabi specimen ISP32P25B is intermediate in its morphology between Sinap *C. sinapensis* and the Lothagam and Middle Awash specimens.

Figure 4C plots 1PHIIIs from the Middle Awash (6-4 Ma, numbers with VP in them) compared to the type specimen of *E. feibeli* from Lothagam and *C. mediterraneum* from Pikermi. This plot again demonstrates how similar JAB-VP-1-1 is to the type of *E. feibeli*. The Middle Awash specimens exhibit a general trend for increase in proximal (M4, width; M5, depth) and distal (M7, width) articular dimensions through time: JAB (6.0 Ma), ALA and BIK (5.7 Ma), DID (5.2 Ma), WKH (4.9 Ma) and ARA (4.4 Ma). A break appears within the Middle Awash series for these dimensions between DID-VP-1-82 and WKH-VP-1-36 specimens (between 5.2 and 4.9 Ma).

Figure 4D plots the Hadar 1PHIIIs compared to Pikermi *C. mediterraneum*. The pattern at Hadar is remarkable from two standpoints: it is homogeneous and it overlaps extensively with the 4.9-4.0 Ma Middle Awash specimens with limited elevated levels for maximum length (M1) and distal articular width (M7). It would appear from the 1PHIII values, that there is a single dominant morphology for this element between 4.9 and 3.0 Ma in Ethiopia.

BIVARIATE SHAPE AND SCALING ANALYSES

Figure 5A plots siM3 versus siM1 of MCIIIs from Amba West, Aramis and Hadar. All of these individuals are both relatively elongate and slender. They all plot in the lower right quadrant and contrast sharply with the Höwenegg sample of (comparatively speaking) relatively short and broad MCIIIs. What is also striking about these specimens is that despite ranging in age from 5.2-3.0 Ma, they are all similar in shape and display variability similar to that demarcated by the Höwenegg 95% confidence ellipse. This consistency in MCIII elongation and slenderness suggests that all specimens may well be accommodated within a single lineage. This is significant in light of the fact that previous principal components analysis has identified these shape variables as those that express the most variability between hipparionine species (Scott & Maga in press).

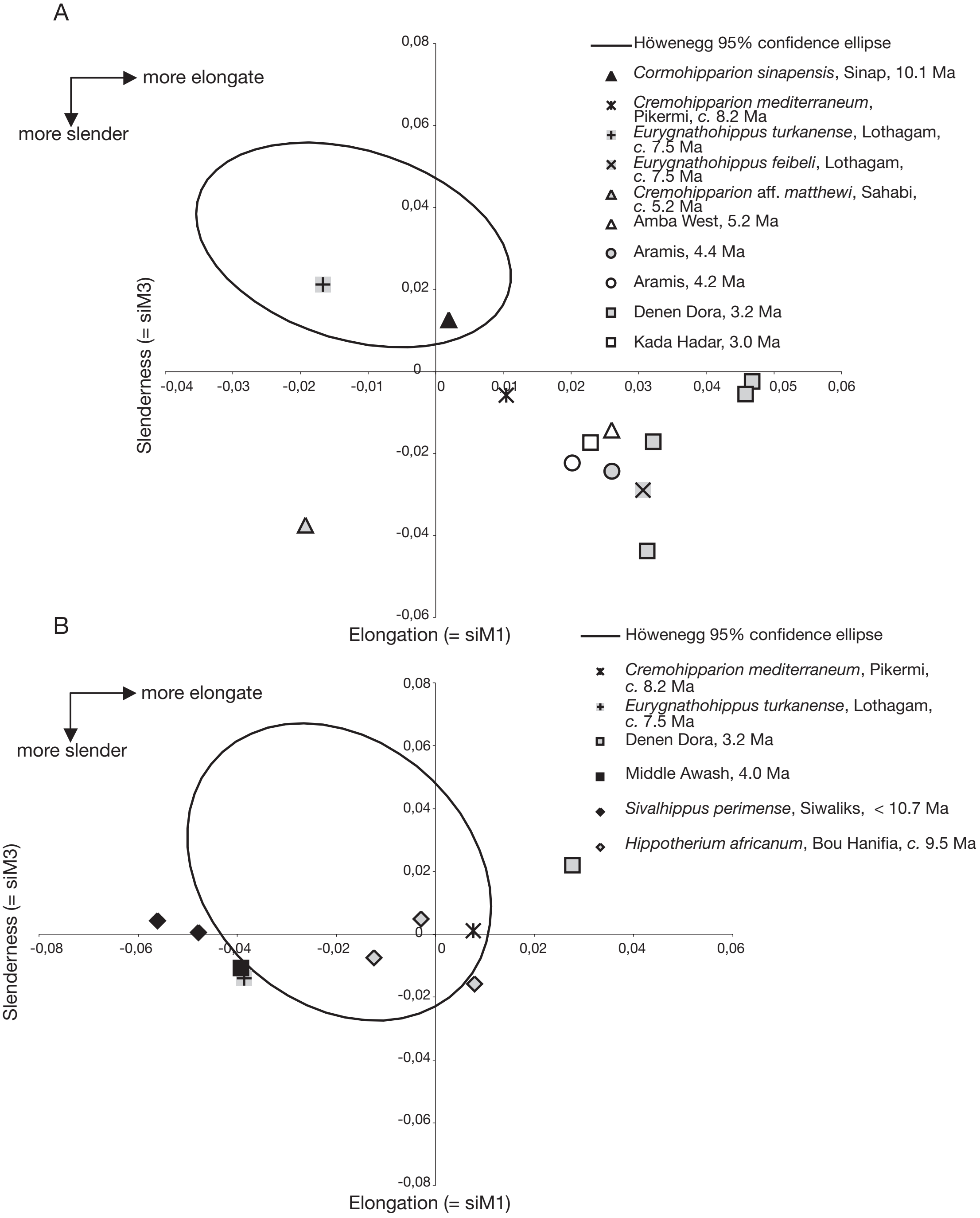


FIG. 5. — Plot of siM3 and siM1; **A**, MCIIIs; **B**, MTIIIs.

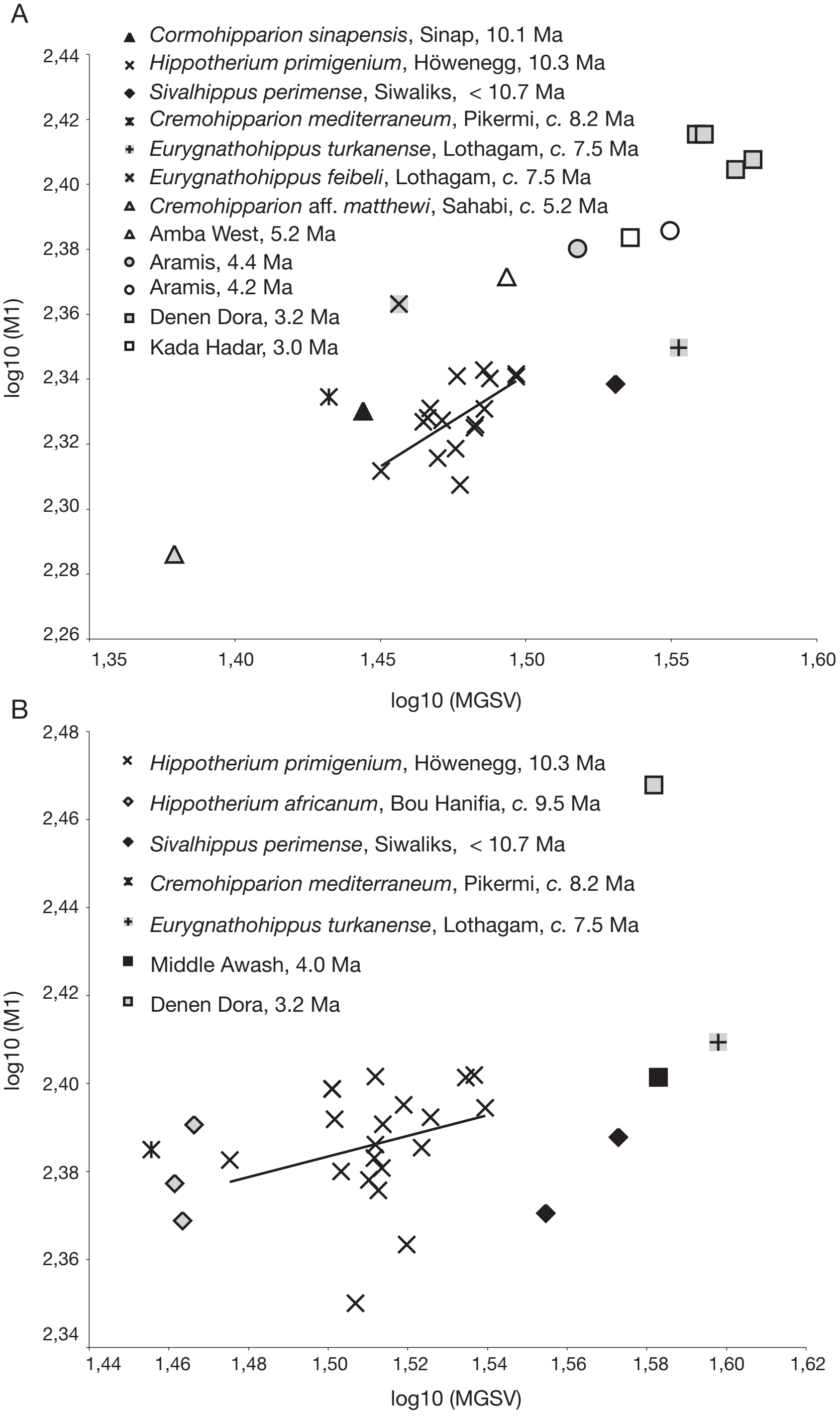


FIG. 6. — Plot of logged MPIII length (M1) and MGSV; **A**, MCIIIs; **B**, MTIIIs.

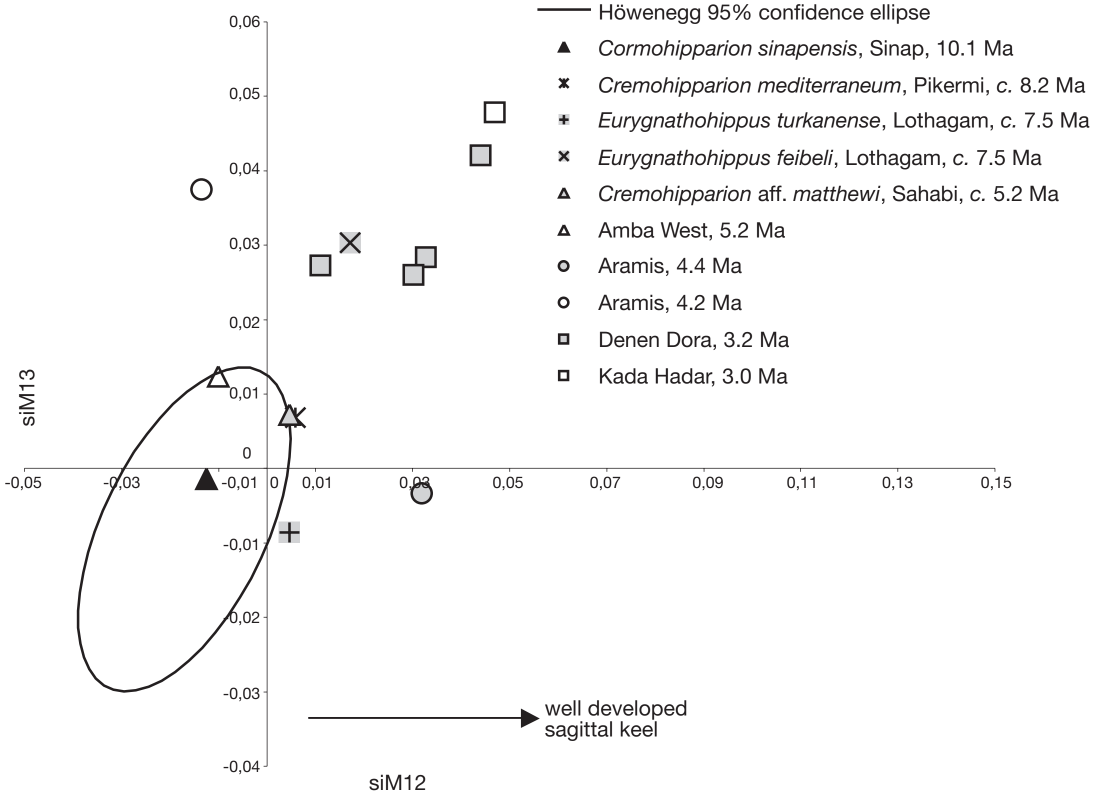


FIG. 7. — Plot of siM13 and siM12 for MCIIIs.

Eurygnathohippus feibeli appears to compare most favorably with the Ethiopian MCIIIs in terms of shape. All are elongate compared to the Höwenegg standard, *Eurygnathohippus turkanense*, *Cormohipparion sinapensis* and *Cremohipparion mediterraneum*. The Sahabi MCIII and the specimen of *Sivalhippus perimense* from the Siwaliks are short like the Ethiopian specimens.

Figure 5B plots relative elongation and relative slenderness for MTIIIs. The one MTIII available from the Denen Dora Member is clearly relatively elongate compared to the Höwenegg standard much the same way that the Denen Dora MCIIIs were shown to be. MTIIIs of "*Hippotherium*" *africanum* from Bou Hanifia are comparable to the most slender and elongate of the Höwenegg MTIIIs. The robust forms, *Eurygnathohippus turkanense*, *Sivalhippus perimense*, and GAL-VP-6-5A (Middle Awash 4.0 Ma) have relatively shortened MTIIIs and plot to the left of the Höwenegg 95% confidence ellipse. GAL-VP-6-5A (4.0 Ma) appears to belong to a lineage separate from AL155-6AZ from the Denen Dora and the elongate and slender MCIIIs comparable to *Eurygnathohippus feibeli*.

Figure 6A plots log10 M1 versus MGSV and shows variability in size and MCIII length. It is clear that *Eurygnathohippus feibeli* and the Ethiopian MCIIIs share a different scaling trajectory of length versus size than that for *Eurygnathohippus turkanense*, *Sivalhippus perimense*, and the Höwenegg hipparion. It also appears that the elongate and slender MCIIIs of Amba West, Aramis and Hadar vary considerably in size and that this variability may be due to evolutionary changes through time. Amba West is similar in

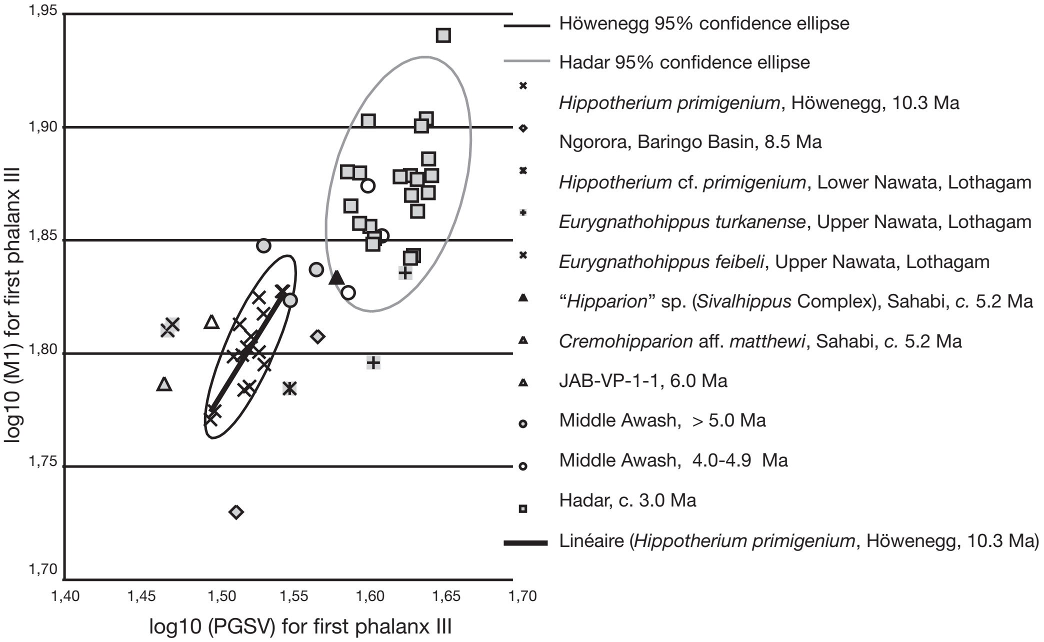


FIG. 8. — Plot of logged 1PHIII length (M1) and PGSV.

size to the largest of the Höwenegg hipparions and larger than the Lothagam type specimen of *Eurygnathohippus feibeli*. The two Aramis MCIIIs are younger (4.4 and 4.2 Ma) and show an increase in size. The Denen Dora MCIIIs are younger yet and again show a substantial size increase. This increasing size trajectory appears to reverse itself at 3.0 Ma, with AL361-1 from KH being comparable in its size to the Aramis MCIIIs (as measured by MGSV).

Figure 6B plots log10 M1 versus MGSV and shows variability in size and MTIII length. As with Figure 6A, the most striking contrast in this plot is the relatively great length of the single Denen Dora MTIII compared to relatively shorter lengths for *Eurygnathohippus turkanense*, GAL-VP-6-5A (*E.* aff. *turkanense*) and *Sivalhippus perimense*. These observations serve to reinforce our conclusions about the relationships of these taxa.

Figure 7 plots siM13 versus siM12 and expresses the development of the sagittal keel and the extent of reduction in minimal distal depth relative to size. The two Aramis specimens appear variable with respect to these dimensions but the Amba West and Hadar specimens share with *Eurygnathohippus feibeli* values for siM12 and siM13 that are clearly elevated compared to the Höwenegg standard (Fig. 7). The fact that both of these values are elevated contrasts with the prediction that the development of the sagittal keel (M12) is likely to be accompanied by a reduction in minimal distal depth (M13) (Eisenmann 1995). In the case of *Eurygnathohippus feibeli*, the Amba West and Hadar MCIIIs, the expansion of the sagittal keel (M12) relative to body size appears accompanied by a similar expansion in the minimal distal depth (M13) relative to body size.

Figure 8 plots 1PHIII length versus PGSV, the geometric mean based size proxy. The Hadar 1PHIIIs plot below an extrapolation of the trendline for the Höwenegg sample suggesting that with increased body mass the Hadar 1PHIIIs have become more robust. The Hadar 1PHIIIs appear somewhat more variable than those from Höwenegg and the Hadar 95% confidence ellipse

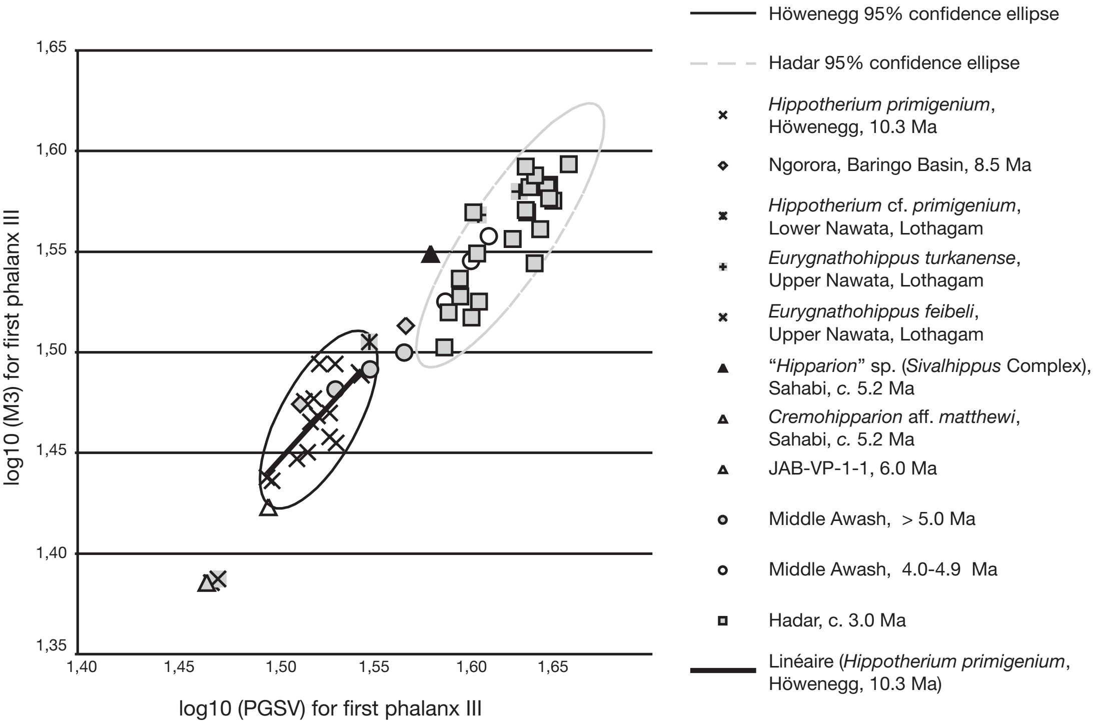


FIG. 9. — Plot of logged 1PHIII breadth (M3) and PGSV.

is somewhat more extended. However, it is difficult to split the Hadar 1PHIIIs into multiple groups and it is our opinion that the variability present here for the Hadar 1PHIIIs likely represents intraspecific variation.

The three Middle Awash 1PHIIIs that date to between 4.9 and 4.0 Ma plot within the Hadar 95% confidence ellipses for M1 versus PGSV (Fig. 8) and M3 versus PGSV (Fig. 9). This suggests that by the early Pliocene, Middle Awash hipparions had gained a size and length comparable to later Hadar forms. One of the Middle Awash 1PHIIIs, HIN-VP-1-3, plots at the very bottom edge of Hadar 95% confidence ellipses for M1 versus PGSV (Fig. 8, open circle). This specimen is associated with a distal MTIII which appears more robust and is possibly referable to the same taxon as equivalent aged GAL-VP-6-5A (= *E.* aff. *turkanense*).

Three older Middle Awash specimens are smaller than the Hadar 1PHIIIs and could represent a smaller member of the same lineage as the Hadar 1PHIIIs. The 6.0 Ma 1PHIII, JAB-VP-1-1, is smaller still and compares closely with *Eurygnathohippus feibeli* from Lothagam.

In general, the 1PHIIIs present a picture generally congruent with that suggested by the MPIIIs. The pattern appears to be one of increasing size and constant morphology in a single dominant lineage beginning with *Eurygnathohippus feibeli* from the Upper Nawata of Lothagam and reaching a much larger body size by 3.4 Ma with the Hadar hipparion.

DISCUSSION

Our analysis of 6.0-3.0 Ma Ethiopian MPIIIs and 1PHIIIs supports earlier assertions (Bernor & Lipscomb 1991, 1995; Bernor & Armour-Chelu 1999a, b; Bernor *et al.* 1996; Bernor & Harris 2003) that East African hipparionine horses belonged to a distinct lineage, *Eurygnathohippus*. We have identified the presence of the Lothagam small hipparion, *Eurygnathohippus feibeli*, in the Middle Awash sequence based on the 1PHIII from Jara-Borkana, *c.* 6.0 Ma. The *Eurygnathohippus feibeli* lineage would appear to be represented at Amba West by a complete MCIII (AMW-VP-1-15) that is somewhat larger in size, but overall has a similar shape to the KNM-LT139B (type, *E. feibeli*). It is apparent from our analysis that early-middle Pliocene samples from Ethiopia (5.2-3.0 Ma) are currently best interpreted as being members of a time-successive lineage derived from species more akin to *Eurygnathohippus feibeli* than the robust-limbed *Eurygnathohippus turkanense* lineage. The exceptions to this observation are the two relatively massively built, short MTIIIs from the Middle Awash 4.0 Ma interval: GAL-VP-6-5A and HIN-VP-1-3 (partial MTIII, but with associated 1PHIII). While it cannot be conclusively demonstrated by MTIIIs alone, it may be that these 4 Ma metapodials represent a late occurrence of the *Eurygnathohippus turkanense* lineage (= *E.* aff. *turkanense*).

Between 5.2 and 3.4 Ma there may well be species-step(s) of the more slender-limbed assemblage. Discrimination of one or more species steps in this interval of the Middle Awash sample will need to closely consider skull, mandibular and dental morphologies. Our analysis suggests that the Hadar hipparions, with their elongate MPIIIs and associated large 1PHIIIs, are most likely derived from the earlier slender-limbed lineage. This hypothesis will require congruent data from the cranial, mandibular and dental data.

Eisenmann (1976, 1983) recognized two species of hipparion from Hadar, "*Hipparion*" sp. and "*Hipparion*" *afarense* (our quotes, = *Eurygnathohippus*). The type *Eurygnathohippus afarense* (Eisenmann, 1976) is a partial skull, AL363-18, from the Kada Hadar Member (KH3, *c.* 3.0 Ma). Most of the Hadar hipparion material occurs below this level, and indeed the bulk of our sample here comes from richer Sidi Hakoma (SH1-4) and Denen Dora Members (DD1-3). Eisenmann (1976) has reported a virtually perfectly preserved skull, AL340-8 from DD2 (Gray 1980) that is distinguished from *E. afarense* by its narrower incisor arcade.

Eisenmann (1983) recognized "*Hipparion*" (= *Eurygnathohippus*) *hasumense* based on a p4-m2 cheek tooth row (type, KNM-ER 2776) from zones B and C of the Kubi Algi Formation. She has included in the hypodigm of *E. hasumense* cheek teeth of common morphology from the Chemeron Formation (Kenya) and the Denen Dora Member of the Hadar Formation. Included in this hypodigm was the partial skeleton, including cheek teeth, of AL155-6 from DD2. The AL155 postcrania analyzed here are of the same skeleton, and therefore the referral of *E. hasumense* is a direct one.

Denen Dora 2 has also produced a beautifully preserved skull of "*Hipparion*" (= *Eurygnathohippus*) sp., AL340-8 (Eisenmann 1976: pl. 1A-C). In their study of the Manonga Valley (Tanzania) hipparions, Bernor & Armour-Chelu (1997) found a close morphological correspondence between the Beredi 3 Member hipparion partial skull, WM1528/92, and AL340-8, and referred them both to *Eurygnathohippus hasumense*. These lines of evidence suggest that the Denen Dora hipparion is likely referred to a distinct species, *E. hasumense,* and that by Kada Hadar 3 times this species may have been succeeded (or co-occurred) with a new species, *Eurygnathohippus afarense*. Eisenmann (1976: pl. 5A) has referred a DD2 mandible, AL177-21, also to *E. afarense* based on its enlarged incisors, but it is unclear to us why this mandible cannot be referred to *E. hasumense*. There is no reason that we find from the Denen Dora hipparion postcrania to assert that there is more than a single hipparion species in the DD member.

Our analysis of the Hadar MPIIIs and 1PHIIIs suggest species-level homogeneity at Hadar up until KH3 where the MCIII, AL361-1, exhibits size reduction compared to all other Hadar hipparions. We cannot directly relate this morphology with the type *E. afarense* skull, nevertheless there are clearly distinct MCIII and skull morphologies in KH3 compared to the lower Hadar stratigraphic units. Whether the mandible

AL177-21 is best referred to *E. hasumense* or *E. afarense* should be the subject of future study.

CONCLUSIONS

Our work follows Bernor & Scott's (2003) study and comparison of Sahabi hipparion MPIIIs and 1PHIIIs to other Eurasian and African hipparions. That study concluded that the Sahabi hipparion fauna included the eastern Mediterranean small, cursorial horse lineage "*Cremohipparion*" aff. *matthewi* and a member of the South Asian-sub-Saharan "*Sivalhippus*" Complex. The authors were unable to establish that Sahabi fauna includes a member of the *Eurygnathohippus* clade, because not a single Sahabi hipparion adult mandibular cheek tooth preserves an ectostylid, a synapomorphy for *Eurygnathohippus*. This could be due to sampling, and/or the fact that ectostylids are poorly developed and variable in late Miocene African hipparions. Nevertheless, we currently have no data verifying that *Eurygnathohippus* occurred at Sahabi.

Eurygnathohippus variably expresses ectostylids on the lower cheek teeth by the end of the late Miocene, as exemplified by the Lower Nawata Lothagam hipparions, *c.* 6.5+ Ma (Bernor & Harris 2003). The latest Miocene/earliest Pliocene Middle Awash hipparions exhibit the same essential morphology of ectostylid development (Haile-Selassie 2001). This information, coupled with the current Sahabi data, suggests to us that *Eurygnathohippus* is a vicariant lineage of the *Sivalhippus* Complex restricted to sub-Saharan Africa. Evidence of *Eurygnathohippus* has not been reported from a single Eurasian locality. Other members of the *Sivalhippus* Complex are known beginning in the late Miocene from Indo-Pakistan and China (Qiu *et al.* 1987; Bernor *et al.* 1996; Bernor & Armour-Chelu 1999a). *Sivalhippus* Complex taxa including *Plesiohipparion* Qiu, Weilong & Zhihui, 1987 and *Proboscidipparion* Sefve, 1927 were well established in China by the early Pliocene, and some of these species extended their range into Europe during the early Pliocene (Bernor *et al.* 1989). The analysis of MPIIIs and 1PHIIIs supports the hypothesis of *Eurygnathohippus* endemic evolution in Africa. The current available postcranial data suggests that there was a single, predominant lineage living between 6.0 and 3.0 Ma in the environs of the Awash River Valley. Our analysis suggests that *Eurygnathohippus feibeli* occurred in the oldest, 6.0 Ma levels. Our interpretation is that a form closely related to *E. feibeli*, *E.* aff. *feibeli*, was present at Amba West (5.2 Ma). The abundant Hadar postcrania support the occurrence of *Eurygnathohippus hasumense* in the Denen Dora Member and probably the Sidi Hakoma Member, as well as correlative horizons in Kenya and Tanzania. Less certain, but intriguing, is the possible late survival of the *Eurygnathohippus turkanense* (here, *E.* aff. *turkanense*) lineage at the Middle Awash localities of Hindo Kalee and Galili, *c.* 4.0 Ma. Equally intriguing is the occurrence of derived skull and metapodial morphologies in the KH3 horizons at Hadar, *c.* 3.0 Ma.

Overall, the Ethiopian latest Miocene-medial Pliocene hipparion assemblages exhibit low species diversity compared to the late Miocene of Eurasia. Many unanswered questions remain concerning African hipparion evolution, not the least of which is whether or not the Ethiopian record directly and completely reflects this group's evolution throughout the rift South Africa, or whether there is provinciality across this great latitudinal expanse.

Acknowledgements

We would like to thank Prof. George Koufos (Aristotle University of Thessaloniki) for providing us his raw measurements on Pikermi postcrania. We would like to thank Prof. Tim White for his invitation to Bernor to pursue research on Middle Awash materials. We thank Craig Feibel and Paul Renne for updating us on Hadar stratigraphy and chronology. We further thank Maria Teresa Alberdi (Museo National de Ciencias Naturales, Madrid), David DeGusta (Stanford University) and Nikos Solounias (New York College of Osteopathic Medicine) for reviewing and providing many useful suggestions for improving this manuscript. This research was supported by NSF grant EAR-0125009 to R. L. Bernor (PI), NSF grant BCS-0112659 to J. Kappelman (PI) and R. S. Scott (Co-PI), a Homer Lindsey Bruce Fellowship from the University of Texas at Austin to R. S. Scott, NSF grants SBR-9318698, SBR-9512534, SBR-9714432 and BCS-9910344 to Tim White and NSF grant BCS-0321893 to F. Clark Howell and Tim White.

REFERENCES

BERNOR R. L. & HUSSAIN S. T. 1985. — An assessment of the systematic, phylogenetic and biogeographic relationships of Siwalik hipparionine horses. *Journal of Vertebrate Paleontology* 5 (1): 32-87.

BERNOR R. L. & LIPSCOMB D. 1991. — The systematic position of "*Plesiohipparion*" aff. *huangheense* (Equidae, Hipparionini) from Gülyazi, Turkey. *Mitteilungen Bayerischen Staatslammlung für Paläontologie und historische Geologie* 31: 107-123.

BERNOR R. L. & LIPSCOMB D. 1995. — A consideration of Old World hipparionine horse phylogeny and global abiotic processes, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven: 164-177.

BERNOR R. L. & ARMOUR-CHELU M. 1997. — Later Neogene Hipparions from the Manonga Valley, Tanzania, *in* HARRISON T. (ed.), *Neogene Paleontology of the Manonga Valley, Tanzania*. Topics in Geobiology Series. Plenum Press, New York: 219-264.

BERNOR R. L. & FRANZEN J. 1997. — The hipparionine horses from the Turolian Age (Late Miocene) locality of Dorn Dürkheim, Germany. *Courier Forschungsinstitut Senckenberg*: 117-185.

BERNOR R. L. & ARMOUR-CHELU M. 1999a. — 18. Family Equidae. *Volker Fahlbusch Memorial Volume*, *Münchner Geowissenschaftliche Abhandlungen* 1999: 193-202.

BERNOR R. L. & ARMOUR-CHELU M. 1999b. — Toward an evolutionary history of African hipparionine horses, *in* BROMMAGE T. & SCHRENK F. (eds), *African Biogeography, Climate Change and Early Hominid Evolution*. Wenner-Gren Foundation Conference, Livingstonia Beach Hotel, Salima, Malawi, Oxford: 189-215.

BERNOR R. L. & HARRIS J. M. 2003. — Systematics and evolutionary biology of the Late Miocene and Early Pliocene hipparionine horses from Lothagam, Kenya, *in* HARRIS J. M. & LEAKEY M. (eds), *Lothagam – The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York: 387-438.

BERNOR R. L. & SCOTT R. S. 2003. — New interpretations of the systematics, biogeography and paleoecology of the Sahabi hipparions (latest Miocene) (Libya). *Geodiversitas* 25 (2): 297-319.

BERNOR R. L., TOBIEN H. & WOODBURNE M. O. 1989. — Patterns of Old World hipparionine evolutionary diversification, *in* LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), NATO Advanced Research Workshop, Schloss Reisensberg, Germany, *European Neogene Mammal Chronology*. Plenum Press, New York: 263-319.

BERNOR R. L., KOUFOS G. D., WOODBURNE M. O. & FORTELIUS M. 1996. — The evolutionary history and biochronology of European and Southwestern Asian late Miocene and Pliocene hipparionine horses, *in* BERNOR R. L., FAHLBUSCH V. & MITTMANN H.-W. (eds), *The Evolution of Western Eurasian Later Neogene Faunas*. Columbia University Press, New York: 307-338.

BERNOR R. L., TOBIEN H., HAYEK L.-A. & MITTMANN H.-W. 1997. — The Höwenegg hipparionine horses: systematics, stratigraphy, taphonomy and paleoenvironmental context. *Andrias* 10: 1-230.

BERNOR R. L., KAISER T., KORDOS L. & SCOTT R. 1999. — Stratigraphic context, systematic position and paleoecology of *Hippotherium sumegense* Kretzoi, 1984 from MN10 (Late Vallesian) of the Pannonian Basin. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 39: 1-35.

BERNOR R. L., SCOTT R. S., FORTELIUS M., KAPPELMAN J. & SEN S. 2003. — Systematics and evolution of the Late Miocene hipparions from Sinap, Turkey, *in* FORTELIUS M., KAPPELMAN J., SEN S. & BERNOR R. L. (eds), *The Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York: 220-281.

BERNOR R. L., KAISER T. & NELSON S. 2004. — The oldest Ethiopian hipparion (Equinae, Perissodactyla) from Chorora: systematics, paleodiet and paleoclimate. *Courier Forschungsinstitut Senckenberg* 246: 213-226.

EISENMANN V. 1976. — Nouveaux crânes d'hipparions (Mammalia, Perissodactyla) Plio-Pléistocene d'Afrique orientale (Éthiopie et Kenya) : *Hipparion* sp., *Hipparion* cf. *ethiopicum* et *Hipparion afarense* nov. sp. *Geobios* 9 (5): 577-605.

EISENMANN V. 1983. — Family Equidae, *in* HARRIS J. M. (ed.), *Koobi Fora Research Project Vol. 2, The Fossil Ungulates: Proboscidea, Perissodactyla and Suidae*. Clarendon, Oxford: 156-214.

EISENMANN V. 1995. — What metapodial morphometry has to say about some Miocene hipparions, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and Evolution,* *with Emphasis on Human Origins*. Yale University Press, New Haven: 148-163.

EISENMANN V., ALBERDI M.-T., GIULI C. DE & STAESCHE U. 1988. — Studying fossil horses. Volume I: Methodology, *in* WOODBURNE M. O. & SONDAAR P. Y. (eds), *Collected Papers after the "New York International Hipparion Conference, 1981"*. Brill, Leiden: 1-71.

GABUNIA L. 1959. — *Histoire du genre* Hipparion. Académie des Sciences de Géorgie, Institut de Paléobiologie, Moscow, 570 p.

GERAADS D., ALEMSEGED Z. & BELLON H. 2003. — The late Miocene mammalian fauna of Chorora, Awash basin, Ethiopia: systematics, biochronology and the ^{40}K-^{40}Ar ages of the associated volcanics. *Tertiary Research* 21 (1-4): 113-122.

GETTY R. 1982. — *The Anatomy of Domestic Animals*. Saunders, Philadelphia, 1211 p.

GORDON A. D. 2002. — Increasing population sample sizes using global skeletal size variables. *American Journal of Physical Anthropology*. Suppl. 34: 77.

GORDON A. D. 2003. — Size matters – Does body mass? *American Journal of Physical Anthropology*. Suppl. 36: 102.

GORDON A. D. 2004. — *Evolution of Body Size and Sexual Size Dimorphism in the Order Primates: Rensch's Rule, Quantitative Genetics, and Phylogenetic Effects*. Ph.D. Dissertation, University of Texas, Austin, USA, 347 p.

GRAY B. T. 1980. — *Environmental Reconstruction of the Hadar Formation*. Ph.D. Dissertation, Case Western Reserve University, Cleveland, Ohio, USA, 431 p.

GROMOVA V. 1952. — *Le genre* Hipparion. BRGM, CEDP, Paris, 288 p.

HAILE-SELASSIE Y. 2001. — *Late Miocene Mammalian Fauna from the Middle Awash Valley, Ethiopia*. Ph.D. Dissertation. University of California, Berkeley, Califorania, USA, 425 p.

JUNGERS W. L., FALSETTI A. B. & WALL C. E. 1995. — Shape, relative size, and size-adjustments in morphometrics. *Yearbook of Physical Anthropology* 38: 137-161.

KAISER T. M., BERNOR R. L., SCOTT R. S., FRANZEN J. & SOLOUNIAS N. 2003. — New interpretations of the systematics and palaeoecology of the Dorn Dürkheim 1 Hipparions (Late Miocene, Turolian Age [MN11]) Rheinhessen, German. *Senckenbergiana Lethaea* 83 (1/2): 103-133.

KIMBEL W. H., WALTER R. C., JOHANSON D. C., REED K. E., ARONSON J. L., ASSEFA Z., MAREAN C. W., ECK G. G., BOBE R., HOVERS E., RAK Y., VONDRA C., YEMANE T., YORK D., CHEN Y., EVENSEN N. M. & SMITH P. E. 1996. — Late Pliocene *Homo* and Oldowan tolls from the Hadar Formation (Kada Hadar Member), Ethiopia. *Journal of Human Evolution* 31: 549-561.

KOUFOS G. D. 1987. — Study of the Pikermi hipparions. Part I: Generalities and taxonomy; Part II: Comparison of odontograms. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4^{e} série, 9, 1987, section C, 2: 197-252 and 3: 327-363.

QIU Z., WEILONG H. & ZHIHUI G. 1987. — Chinese hipparionines from the Yushe Basin. *Palaeontologica Sinica*, series C, 175 (25): 1-250.

NICKEL R., SCHUMMER A. & SEIFERLE E. 1986. — *The Anatomy of the Domestic Animals* 1. *The Locomotor System*. Schumberg, Berlin, 499 p.

RENNE P. R., WOLDEGABRIEL W. K., HART G., HEIKEN G. & WHITE T. D. 1999. — Chronostratigraphy of the Miocene-Pliocene Sagntole Formation, Central Awash Complex, Ethiopia. *Bulletin of the Geological Society of America* 111 (6): 869-885.

SCOTT K. M. 1990. — Postcranial dimensions of ungulates as predictors of body mass, *in* DAMUTH J. & MACFADDEN B. J. (eds), *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press, Cambridge: 301-336.

SCOTT R. S. 2004. — *The Comparative Paleoecology of Late Miocene Eurasian Hominoids*. Ph.D. Dissertation, The University of Texas, Austin, Texas, USA, 457 p.

SCOTT R. S. & MAGA M. in press. — Paleoecology of the Akkasdagi hipparions. *Geodiversitas*.

STAESCHE U. & SONDAAR P. Y. 1979. — *Hipparion* aus dem Vallesium und Turolium (Jungtertiäär) der Turkei. *Geologische Jahrbuch B*. 33: 35-79.

WOLDEGABRIEL G., HAILE-SELASSIE Y., RENNE P., HART W. K., AMBROSE S. H., ASFAW B., HEIKEN G. & WHITE T. 2001. — Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412: 175-178.

WOODBURNE M. O. 1996. — Reappraisal of the *Cormohipparion* from the Valentine Formation, Nebraska. *American Museum of Natural History Novitates* 3163: 1-56.

Submitted on 25 March 2004;
accepted on 13 October 2004.

APPENDIX

TABLE 1. — List of localities used in this study.

Locality	Country	Specimen prefix	Age
Comparative localities			
Sahabi	Libya	ISP	*c.* 5.2 Ma
Lothagam	Kenya	KMN-LT	7.5-5.2 Ma
Samos	Greece	AMNH	*c.* 8-7 Ma
Pikermi	Greece	CrmedPik	*c.* 8 Ma
Baringo Basin	Baringo Basin	BN	*c.* 9 Ma
Bou Hanifia	Algeria	MNHN	9.5 Ma
Middle Sinap	Turkey	AS	10.7-9.5 Ma
Siwaliks	Indo-Pakistan	AMNH/BMNH	10.7-5 Ma
Höwenegg	Germany		10.3 Ma
Ethiopian localities	**Project collection**		
Hadar	Hadar	AL	3.4-3.0 Ma
Galili	Middle Awash	GAL	4.0 Ma
Hindo Kalee	Middle Awash	HIN	4.0 Ma
Aramis	Middle Awash	ARA	4.4-4.2 Ma
Worku Hassan	Middle Awash	WKH	4.90
Amba West	Middle Awash	AMW	5.20
Digiba Dora	Middle Awash	DID	5.20
Bikirmali Koma	Middle Awash	BIK	5.70
Alayla	Middle Awash	ALA	5.70
Jara-Borkana	Middle Awash	JAB	6.0+ Ma

TABLE 2. — Stratigraphic provenance of Hadar MCIIIs, MTIIIs and 1PHIIIs (after Gray 1980). Abbreviations: **DD**, Denen Dora Member (**1**-**3**, submembers); **KH**, Kada Hadar Member (**1**-**3**, submembers); **SH**, Sidi Hakoma Member (**1**-**4**, submembers).

Hadar locality	Stratigraphic position	Hadar locality	Stratigraphic position
AL53	SH3u	AL230	SH2u, 3s
AL58	SH4, (DD1), 2	AL233	SH4
AL107	SH2, 3	AL236	SH2, 3s
AL116	DD2, 3s, 3u	AL251	SH1
AL122	DD2, 3s	AL262	SH4, DD1
AL133	DD2, 3s	AL274	indet.
AL147	SH2u, 3s	AL282	DD2, 3s (3u, KH1)
AL148	SH1, 2s	AL295	DD2, 3s
AL150	DD1, 2, 3s	AL305	DD2, 3s
AL151	DD1, 2, 3s	AL308	DD2
AL153	DD2, 3s	AL315	DD2, 3s
AL154	DD2, 3s	AL319	SH4, (DD1)
AL155	DD2	AL321	DD2, 3s
AL158	DD2, 2s, 3s	AL327	SH2u
AL161	DD2, 3s	AL332	SH4, DD1, 2
AL162	DD3u, (KH1)	AL333W	DD2, 3s
AL165	SH2u	AL339	DD1, 2
AL166	SH1, 2s	AL342	DD2
AL177	DD2, 3s	AL352	SH4
AL182	DD2, (3s)	AL355	SH4
AL183	DD2, (3s)	AL358	DD1, 2
AL186	DD3s, 3u	AL361	KH3s
AL194	DD1	AL369	KH2
AL196	DD3s, 3u	AL400	SH2
AL212	DD2, 3s	AL429	?

TABLE 3. — Measurements (in mm) on Middle Awash and Hadar MCIIIs, MTIIIs and 1PHIIIs. Abbreviations: **lt**, left; **rt**, right.

Spec. id.	Side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
MCIII															
AMW-VP-1-15	lt	235.3	228.2	29.4	23.3	42.9	29.6	38.0	11.3	9.9	39.6	37.8	29.3	25.6	28.3
ARA-VP-1-2530	rt	240.0	232.4	30.6	24.8	43.2	29.3	39.4	12.6	6.9	42.3	41.5	34.0	25.9	30.8
ARA-VP-1-2705	rt			30.5	24.8	43.7	29.0	38.4	12.0	6.6					
ARA-VP-3-22	lt			30.1	27.9	43.9	31.2	39.4	11.7	6.9					
ARA-VP-7-13	lt	243.0	237.0	33.4	27.0	48.4	32.3	38.8	15.7		45.4	43.5	32.8	30.3	32.0
ARA-VP-14-131	rt					44.8	32.3	40.1	12.4	7.9					
ARA-VP-14-13	rt					45.0	32.9	40.5	12.9	7.7					
AL107-15D	rt	254.0	242.5			54.6	34.6	46.0	16.1	9.9	48.7	47.5	41.2	33.1	35.4
AL116-128	rt			38.3	31.0						51.0	44.9	38.3	29.7	33.1
AL116-149	lt										52.6	47.5	36.1	33.1	30.5
AL116-33	rt	255.6	247.3	36.4	26.2	53.0	34.9	45.1	15.5	6.8	49.4	48.2	36.9	31.3	32.9
AL122-32	lt										44.8	42.0	38.9	30.9	31.1
AL133-25	?														
AL147-18	lt										55.7	48.5	42.7	35.9	30.8
AL147-19	lt										45.2	42.4	37.7	29.9	28.8
AL147-20	rt										51.2	44.7			
AL150-1	lt										47.9	46.5	39.1	31.4	33.4
AL155-1D	lt										57.5	59.9	41.6	36.2	35.7
AL155-6	rt	260.2	251.3	35.8	26.6	49.3	32.4	43.6	13.1	8.4	44.9	45.6	37.2	30.2	30.5
AL155-6BB	lt	260.2	251.3	35.8	26.6	49.3	34.3	43.6	13.1	8.4	44.9	45.6	37.2	30.2	30.5
AL155-6BC	rt		251.5	36.1	28.2					7.9	43.7	45.8	37.7	30.1	31.6
AL158-11	rt										46.3	46.4	39.2	32.6	30.8
AL158-111	rt										46.6	46.6	39.1	32.7	31.0
AL165-27	lt										49.0	45.8	39.4	33.6	30.4
AL212-3	rt										47.7	47.2	39.0	32.3	30.7
AL230-2	rt			36.1	27.7						52.9	45.6	42.0	36.1	34.1
AL233-1	rt					46.0	32.4	44.8	10.8	7.4					
AL236-7	lt			34.0	28.0						47.2	45.0	40.4	33.9	32.8
AL251-64	rt										44.5	42.4	39.0	29.7	31.8
AL251-65	rt										50.8	46.0	42.4	36.7	33.3
AL295-6	rt										51.1	47.4	39.2	32.9	30.6
AL315-9C	rt	253.8	244.0	33.7	27.6	47.0	35.0	43.7		7.0	45.7	48.1	39.3	32.0	33.3
AL327-14A	lt										47.0	45.0	40.2	31.3	30.3
AL327-27	lt										55.9	47.4	41.0	35.0	32.6
AL332-22	rt										47.0	43.2	38.9	30.8	32.1
AL332-22	lt										47.3	42.8	38.4	32.4	31.5
AL342-6A	rt										51.8	48.2	40.4	33.1	31.6
AL352-1	lt										47.8	45.1	39.2	34.2	31.8
AL355-1	?														
AL361-1	lt	241.8	232.0	32.6	23.0	44.5	32.5	39.6	12.5	9.3	41.0	42.6	36.6	30.2	31.8
AL400-6A	lt										50.7	46.7	36.9	29.0	29.6
AL429-1	lt					52.6	34.9	45.2	15.7	7.9					
AL429-1	rt					52.6	34.9	45.2	15.7	7.9					
AL53-3	lt										48.0		39.5	31.6	34.6
AL58-9	lt										47.1	45.0	37.5	29.8	28.6
AL58-9	rt										46.5	45.1	36.2		29.5
MTIII															
ALA-VP-2-26	lt										41.6	38.3	34.8	27.9	30.6
ALA-VP-2-26	lt										41.5	39.4	34.9		
GAL-VP-6-5A	lt	252.0	245.0	34.6	34.8	47.9	39.5	43.4	13.4	8.5	50.1	43.9	37.9	29.5	31.5
HIN-VP-1-3	rt	248.6	244.5	35.0							47.2	44.9	35.0	28.6	30.5
AL147-18	lt			37.9	39.8		42.1		8.6						
AL148-101	rt			36.7	34.6						50.8	46.6	42.2	35.7	30.6
AL151-47	lt	292.9	286.0	37.6	31.5	53.6	37.0	50.4	10.4	6.8					
AL155-6AZ	rt	293.6	285.6	37.2	32.1	48.5	38.0	48.8	11.6	6.0	48.5	47.3	35.9	31.9	29.8
AL158-10	rt					56.0	47.1								

Spec. id.	Side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
AL161-22	lt										53.2	51.1	41.8	36.0	34.6
AL166-7	lt										49.8	44.8		33.6	27.9
AL182-79A/B	rt					48.5	40.3	46.6	13.3	9.1	48.7	46.9	38.7	29.3	33.7
AL196-1	lt										48.3	46.4	40.8	34.6	30.6
AL233-7	lt										44.6	44.1	39.9	35.5	32.6
AL251-10	lt					52.3	39.1	48.3	10.6	8.8					
AL262-4A	lt										50.0	46.6	43.9	35.6	33.5
AL305-12	rt			34.8	33.3						52.4	45.3	40.2	32.9	30.3
AL327-13B	lt										52.8	47.1	40.8	36.0	32.1
AL332-61	lt										48.5	42.0	40.8	31.7	31.2
AL333W-503	rt										54.9	50.4	44.8	39.3	33.1
AL342-5	rt										56.1	47.1	42.7	36.1	33.0
AL355-2	rt			35.1	33.2	52.6	43.8	51.8	9.8	7.5					
AL358-15A	lt					52.2	43.4	48.5	14.0	9.7					
AL358-18	?										54.0	48.7	41.7	35.1	32.6
AL369-3	lt					53.1	43.8	48.6	11.3	7.7					
AL369-3	rt					51.9	45.4	48.5	11.1	6.4					
AL53-47	rt										54.4	49.2	43.7	33.8	37.8
1PHIII															
JAB-VP-1-1	rt	65.2	61.0	26.5	38.0	29.5	33.2	32.7	17.1	18.1	48.5	47.0	13.4	12.1	
ALA-VP-2-26	rt	68.7	55.8	31.6	42.1		38.2	35.9	20.3	15.8	50.0	52.2	21.2	19.0	
BIK-VP-1-3	lt	66.6	58.9	31.0	41.7	34.0	36.4			14.2	45.6	51.6	16.2	16.4	
WKH-VP-1-36	lt	74.8	67.0	35.1	49.6	38.1	39.0	37.7	24.9	22.5	45.2	48.5	20.6	19.1	
HIN-VP-1-3	lt	67.1	60.5	33.5	46.8	36.9	39.6	39.1	22.3	17.9	42.1	42.2	18.2	17.0	
DID-VP-1-82	lt	70.4	64.9	30.3	40.9	31.5	34.8	35.0	21.5	16.8	49.7	49.2	14.7	16.1	
ARA-VP-1-243	rt	71.1	64.5	36.1	47.6	41.0	40.0	40.1	23.0	7.4	43.4	46.4	17.6	17.8	
AL153-24	lt	73.3	65.5	33.1	49.2	35.1	40.7	40.4	21.6		51.4	52.5	17.6	14.2	
AL155-1E	rt	87.2	78.8	39.2	54.3	42.1	45.9	46.1	28.6	45.0	59.2	59.5	18.7	14.3	
AL155-6AB	lt	74.1	68.6	37.1	51.9	38.4	45.7	43.4	25.0	40.7	51.2	51.7	16.8	16.3	
AL155-6AR	lt	69.7	62.6	38.2	52.3	39.7	43.1	41.4	24.8	35.3	43.3	41.9	19.8	18.9	
AL155-6X	rt	75.6	67.6	37.2	51.8	38.4	45.4	43.2	25.0		49.9	52.6	20.3	14.2	
AL161-1	rt	79.9	70.6	32.9	49.1	36.4	44.1	43.7	27.0	36.3	54.9	55.3	19.3	17.1	
AL161-2	rt	75.8	66.3	33.7	46.5	39.0	40.2	39.3	26.2		47.7	49.3	20.9	18.3	
AL162-7	rt		61.5	34.5			37.7	39.3	23.5		39.4		20.6	17.1	
AL177-26	lt	74.3	64.3	38.3	52.2	41.2	45.5	42.5	26.5		46.3	45.5	20.9	23.1	
AL182-80	rt	80.1	71.0	38.2	53.5	38.6	47.0	44.8	23.0		54.7	55.8	20.1	19.2	
AL183-30	lt	71.8	63.8	37.1	46.7	36.8	41.0	40.8	25.2		43.6	47.8	16.7	15.8	
AL186-28	rt	70.9	63.3	33.5	48.8	39.7	41.4	39.5	25.6	28.1	43.5	43.9	23.1	20.1	
AL194-2	lt	70.5	60.5	35.4	47.2	38.8	41.1	41.0	27.1		45.0	45.7	17.4	16.7	
AL262-45	lt	72.0	62.4	34.4	47.4	36.9	40.8	40.6	25.5	35.4	44.3	50.6	19.8	18.0	
AL274-3A	lt	72.9	63.9	38.7	50.7	40.9	43.7	43.3	27.3	36.7	43.4	47.0	22.4	19.6	
AL282-5B	lt	79.5	70.5	36.4	52.3	39.5	47.8	42.9	29.3	40.8	56.5	51.5	17.4	18.2	
AL308-3	rt	75.9	66.8	31.8	49.3	35.1	41.4	37.9	22.7		53.5	51.7	18.2	16.8	
AL315-9	rt	75.3	68.6	35.0	56.1	41.2	43.3	43.9	27.4		46.6	51.0	19.9	20.3	
AL319-8	rt	75.6	67.1	37.6	52.7	42.6	45.3	44.4	27.0	32.0	48.4	46.4	23.0	21.3	
AL321-13	lt	75.5	69.6	36.0	50.6	38.9	44.5	42.8	24.7		49.1	52.4	21.3	16.7	
AL321-7	lt	83.5	75.0	38.8	58.5	42.7			28.3	38.2		61.0		17.1	
AL327-28	rt	69.5	62.5	39.1	49.9	40.4	42.6	41.6	25.5	38.1	43.0	40.5	24.5	23.2	
AL327-29	rt					38.6									
AL339-2	rt	76.9	66.5	37.7	53.5	41.0	45.4	44.5	26.3		49.3	47.0	21.1	20.3	
AL342-6B	lt	82.5	72.9				48.6	45.7	27.6		55.7	55.2	20.3	21.2	