New interpretations of the systematics, biogeography and paleoecology of the Sahabi hipparions (latest Miocene) (Libya)

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ABSTRACT
Sahabi is a latest Miocene/earliest Pliocene vertebrate fauna from Libya. It includes a mixture of Eurasian and African vertebrates, and as such is important for biogeographic reconstruction and paleoecologic comparisons. We undertake a morphometric analysis of Sahabi hipparion metacarpal 3s, metatarsal 3s and 1st phalanges 3 in order to reevaluate and revise this assemblages' systematics, biogeographic relationships and paleoecologic setting. In so doing we recognize two hipparion taxa at Sahabi: a slender-limbed form adapted for open country cursoriality, "*Cremohipparion*" aff. *matthewi*; and a robust-limbed form, a likely woodland denizen with likely less cursorial capability, "*Hipparion*" sp. (*Sivalhippus* Complex). "*Cremohipparion*" aff. *matthewi* exhibits its closest affinity with the Samos and Maramena slender-limbed hipparions of the *Cremohipparion matthewi/nikosi* lineage. We believe that this lineage also likely includes the Indo-Pakistan hipparion, "*Cremohipparion*" *antelopinum*. This lineage provides evidence for a late Miocene hipparion biogeographic connection between Indo-Pakistan, Southwest Asia, the Eastern Mediterranean and North Africa. The large Sahabi form "*Hipparion*" sp. (*Sivalhippus* Complex) would appear to belong to a lineage whose late Miocene distribution was between Indo-Pakistan, North Africa and East Africa. The East African slender-limbed form *Eurygnathohippus feibeli* would appear to be convergent on the "*Cremohipparion*" small slender-limbed hipparion, having synapomorphies of the lower dentition with the *Eurygnathohippus* radicle of the "*Sivalhippus*" Complex.

KEY WORDS
Mammalia,
Equidae,
hipparion,
Sahabi,
Libya,
postcrania,
biogeography,
paleoecology.

RÉSUMÉ

Nouvelles interprétations sur la systématique, la biogéographie et la paléoécologie des hipparions de Sahabi (Miocène terminal) (Libye).

La localité de Sahabi en Libye a livré une faune de vertébrés d'âge miocène terminal à pliocène inférieur. Cette faune se compose d'un mélange d'éléments connus en Eurasie et en Afrique, elle revêt donc une importance tant pour la biogéographie que pour des comparaisons paléoécologiques. Nous proposons une analyse morphométrique pour le troisième métacarpien, le troisième métatarsien et la première phalange du doigt 3 pour l'hipparion de cette localité, afin d'évaluer et de réviser l'assemblage systématique, les relations biogéographiques et la paléoécologie de Sahabi. Ces études ont permis d'identifier deux hipparions dans cette localité. L'un, "*Cremohipparion*" aff. *matthewi*, possède des membres graciles et il est adapté à la course dans des paysages ouverts ; l'autre, "*Hipparion*" sp. (*Sivalhippus* Complex), est une forme plus robuste à l'adaptation cursoriale moindre qui peuplait des milieux plus denses. "*Cremohipparion*" aff. *matthewi* présente des affinités avec les hipparions à membres graciles de Samos et de Maramena, appartenant à la lignée *Cremohipparion matthewi*/*nikosi* qui inclut l'hipparion indo-pakistanais "*Cremohipparion*" *antelopinum*. Cette lignée indique aussi que des connexions biogéographiques ont été empruntées au Miocène terminal par les hipparions de diverses régions : Indo-Pakistan, Asie du sud-ouest, Méditerranée orientale et Afrique du Nord. À la même époque, "*Hipparion*" sp. (*Sivalhippus* Complex), la forme robuste de Sahabi, appartiendrait à une lignée dont la distribution paléogéographique comprenait la région indo-pakistanaise, l'Afrique du Nord et l'Est africain. *Eurygnathohippus feibeli*, la forme à membre gracile de l'Est africain, est proche de la forme comparable de Sahabi, elles partagent des synapomorphies définies sur la denture inférieure, que l'on connaît dans la lignée *Eurygnathohippus* du complexe « *Sivalhippus* ».

MOTS CLÉS
Mammalia,
Equidae,
hipparion,
Sahabi,
Libye,
éléments postcrâniens,
biogéographie,
paléoécologie.

INTRODUCTION

Fossil bones were first discovered in neighborhood of Qasr as-Sahabi in the late 1920's by Italian soldiers stationed at the local fort. The Italian geologist Desio first visited Sahabi in 1931 and 1932, and collected mollusks from which he inferred an early Miocene age for the site. Fossil collection and excavation continued under the direction of Carlo Petrocchi between 1934 and 1939 when systematic work was halted by World War II. Petrocchi's research led to the establishment of 62 fossiliferous localities (Petrocchi 1951). The repository/ies of most of the Italian fossil mammal collections is/are unknown, although it is more likely that they are stored in crates in the Tripoli museum than that they are still in Italy (Boaz N. T. 1987).

During World War II Sahabi was an area of active conflict and was heavily mined. Oil companies cleared these mines in the 1960's and 1970's. The latest research at Sahabi was undertaken by a group organized by Noel T. Boaz and Ali El-Arnauti in November, 1975. Four seasons followed under the aegis of the International Sahabi Research Project: June-July, 1977; June-September, 1978; February-March, 1979; June-July, 1980; December, 1980-March, 1981. There were further geological excursions and collecting trips by individual members of the project to Sahabi outside those dates. Sahabi's fauna, geologic context, zoogeography and paleoenvironmental context were ably reported in a 25-chapter-monograph (Boaz N. T. *et al.* 1987).

Heinzelin & El-Arnauti (1987) reported 141 localities documented by the International Sahabi Research Project. The geological horizons include, from base to top, formations M, P and the Sahabi Fm. (with members T, T.X, U-1, U-2, V and Z). The lowermost portion of the sequence is a marine transgression, while the middle and upper parts are more littoral, estuarine and lagoonal. All exposed formations and members contain bones, with the exception of Member Z. Sand channels in Member U-1 are especially rich in well preserved bones, and shark teeth and remains of aquatic reptiles are associated. Member U-2 is less rich; mammal, crocodile and turtle remains are still present. A whale skeleton was excavated in 1937. Locally, lower Member V contains land mammal remains in sand channels. Upper Member V is poorer, but there are still rolled crocodile bones (Boaz N. T. 1987).

Sahabi's vertebrate fauna has been variously interpreted as being latest Miocene or basal Pliocene age. The latest Miocene age is based on strong faunal similarities seen in the terrestrial mammals (Geraads 1982; Howell 1987). Heinzelin & El-Arnauti (1987) argued that the thick stratified gypsum deposits that underlie the continental vertebrate-bearing horizons correlated with the terminal Messinian event itself, making the latter earliest Pliocene age. Domning & Thomas (1987), Bernor *et al.* (1987) and Bernor & Pavlakis (1987) followed this interpretation. Lehman & Thomas (1987) judiciously suggested that the Sahabi mammal fauna rested at the Mio-Pliocene limit. In fact, all biochronologic interpretations published thusfar differ from one another by less than 1.0 Ma, and provide a robust biochronologic correlation. An age of *c.* 5.2 Ma, or slightly older, is a good probability age for the Sahabi fauna. There is little time depth apparent in the vertebrate-bearing fossil horizons (Heinzelin & El-Arnauti 1987).

Thomas *et al.* (1982) argued for a particularly strong biogeographic connection in the middle and late Turolian (*c.* 8-5.2 Ma) between the Eastern Mediterranean, North Africa and South Africa. Bernor & Pavlakis (1987) supported Bernor's (1978, 1983, 1984) earlier proposals for Eurasian and African faunal provinciality, but supported Thomas *et al.*'s (1982) claim of an Eastern Mediterranean-North African late Miocene biogeographic connection. Geraads (1998) presented an elegant factor analysis of Mio-Pliocene Eurasian and African rodent faunas and favored Agusti's (1989) earlier hypothesis that North Africa and Spain shared a biogeographic connection during the terminal Miocene.

Sahabi indeed shows a strong Western Eurasian faunal similarity, particularly with the Subparatethyan faunas of Bernor (1983, 1984; alternatively, the Graeco-Iranian faunas *sensu* Bonis *et al.* 1992 and Gentry 1999). Taxa shared with Eurasia that immigrated into North Africa prior to the Messinian Event include: several carnivores (Howell 1987), anthracotheres and amebelodonts (Gaziry 1987a-c), the rodent *Sayimys* (Munthe 1987), the bovids *Leptobos*, *Miotragocerus* and *Prostrepsiceros* (Lehman & Thomas 1987), the rhinoceros *Diceros* (= *Ceratotherium*) *neumayri* (Bernor *et al.* 1987; Heissig 1996), possibly a swan-sized anatid (Ballman 1987), and the short-necked giraffid *Samotherium* (Harris 1987). Sub-Saharan paleogeographic connections include: the bulk of the avian fauna (Ballman 1987), the crocodilian *Euthecodon* (Hecht 1987), suids (Cooke 1987; but also identified in Arabia by Bishop & Hill 1999), bovids (Lehman & Thomas 1987), equids (Bernor *et al.* 1987) and the hippo *Hexaprotodon* (Gaziry 1987c). Boaz N. T. (1987) has provided a good overview of this information. New information provided below bears on the biogeographic relationships of the hipparion fauna.

Whybrow & Hill (1999) have presented a 36-chapter-volume on the late Miocene faunas, geology and paleoenvironments of the Emirate of Abu Dhabi, United Arab Emirates. While it is beyond the scope of this paper to review the results of this book, suffice it to say that these faunas compare closely with that of Sahabi. However, it still appears that the principal reason why the Sahabi and Abu Dhabi faunas do not show closer homotaxis with Pikermi, Samos and Maragheh (Bernor *et al.* 1996) is because they are younger in age (*c.* < 7 Ma, and most likely ≤ 6 Ma). The Sahabi fauna as a whole supports a biogeographic connection with Subparatethyan Pikermian faunas and the hipparion data we present here further supports both the Pikermian connection as well as a Siwalik-East African connection.

Paleoecologically, Sahabi has been reconstructed as having sampled wooded habitats along adjacent banks of a large river contrasted with semiarid conditions away from the river that probably became intensified during a well marked dry season (Boaz D. D. 1987). Dechamps (1987) and Dechamps & Maes (1987) identified fossil wood with traumatic rings that resulted from bush fires associated with dry seasons which may have been as long as 10 months. Savanna environments are interpreted to have been in place at Sahabi (Boaz N. T. 1987). Sahabi also supported wooded habitats with evidence of shrews and squirrels; however, gerbils constituted half of the micromammal fauna collected (Munthe 1987). The sediments (Geyter & Stoops 1987) and marine microfauna (Willems 1987) demonstrate the proximity of the sea, yet most of the water-adapted bird species (Ballman 1987), fish species (Gaudant 1987) and reptiles (Hecht 1987) are freshwater forms. Excluding water-tied fauna such as the birds, anthracotheres, hippopotamids, cetaceans, sirenians and most reptiles and fish, most of the remaining taxa suggest open-country habitats, including bovids, equids, giraffids and rhinocerotids. The carnivores and primates are clearly less diagnostic of habitat preference (Boaz N. T. 1987).

REASSESSMENT OF THE HIPPARION TAXA

Bernor *et al.* (1987) presented an assessment of Sahabi's perissodactyl fauna. In this presentation, the authors recognized two species of hipparion: "*Hipparion*" cf. *africanum* Arambourg, 1959 and "*Hipparion*" cf. ?*sitifense* Pomel, 1897; the former a larger, more robust-limbed form, and the latter a smaller, more slender-limbed form. The size and robusticity distinctions of these two different sized hipparions was amply illustrated in the metapodials (figs 4-6, 10), astragali (figs 7, 11), calcanea (figs 8, 12) and distal tibiae (fig. 9) of the sample (Bernor *et al.* 1987).

We present a reassessment of the systematics and evolutionary relationships of the Sahabi hipparions based on the metacarpal 3s, metatarsal 3s and 1st phalanges 3. Eisenmann (1995) has provided a cogent rationale for undertaking morphometric analyses on metapodials, and their use for evolutionary reconstructions. Bernor *et al.* (1997) published a detailed description of the Höwenegg hipparion skeletons (Höwenegg, Germany; 10.3 Ma [Swisher 1996; Woodburne *et al.* 1996]), and likewise found that the metapodials are very useful in this regard. Our analysis of metapodial morphology has expanded to include log10 ratio diagrams (following Eisenmann 1995 and previous work cited therein). This proved useful in the analysis of the Lothagam (late Miocene, Kenya) hipparions (Bernor & Harris 2003). In our study of the Sümeg (late Miocene, MN10, Hungary) hipparion, *Hippotherium suemegense* (Bernor *et al.* 1999), as well as the diverse MN9-MN13 hipparion fauna from Sinap (Turkey; Bernor *et al.* in press), Scott used a principal components analysis of the covariance matrix of multiple MC3 variables from a growing database of specimens including a broad range of sites to compare Hungarian and Central European specimens. A key result of this analysis was to clearly identify and confirm the importance of morphological axes relating to relative slenderness and elongation of MP3s. We have found (particularly with the Sinap hipparions) that when bivariate plots, ratio diagrams and PCAs are combined, they can produce a powerful morphometric heuristic that promotes functional anatomical interpretations and species discrimination. Multivariate analyses of a broad database of MP3s that include principal components analyses and discriminate analyses are in preparation. Here, we employ an amended version of earlier methodologies to focus specifically on a reassessment of the systematics, biogeography and paleoecology of the Sahabi hipparions.

TABLE 1. — Measurements on Sahabi Hipparion 1st phalanx and metapodial 3s.

Specimen No.	Taxon	Bone	Side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
ISP32P25B	Cmat	1ph3	rt	61.2	56.7	24.3	35.9	27.9	30.2	32.2	17.2	13.8	42.7	45.6	14.6	12.9	
ISP25P26A	Cmat	mc3	rt										34.4	35.0	26.9	22.4	23.6
ISP27P25B	Cmat	mc3	lt	193.3	188.1	20.7	17.6	31.9	24.2	30.2	8.8		29.6	30.9	23.7	20.2	21.0
ISP33P15A	Cmat	mc3	rt										30.0	28.9	26.1	20.8	23.6
ISP11P85A	Cmat	mt3	rt										34.3	34.2		23.3	26.4
ISP1P25B	Cmat	mt3	lt	242.8	237.9	20.5	21.6						29.6	28.4	27.1	20.6	24.1
ISP31P25A	Cmat	mt3	rt										29.8	28.3	26.4	21.4	22.8
ISP468P28A	Cmat	mt3	rt			24.4	24.1						31.5	32.4	28.4	21.6	25.2
ISP59P16A	Cmat	mt3	lt										31.8	30.3	28.0	23.8	25.5
ISP67P16A	Cmat	mt3	rt	245.6	240.2	23.9	27.6	37.0	31.2	35.3	11.2	5.6	32.9	35.8		25.0	26.9
ISP6P108A	Cmat	mt3	rt			25.3	23.8	36.6	30.8	34.2	11.1	7.0					
ISP2P111A	Hsp	1ph3	lt	68.2	60.2	35.4	46.6	34.0	38.0	39.5	24.4	18.2	43.6	44.8	16.5	15.2	
ISP17P33A	Hsp	mc3	rt										41.1				
ISP10P30A	Hsp	mt3	rt					37.7	30.2	36.0	10.8	5.1					
ISP35P17A	Hsp	mt3	rt			28.6	30.2						42.9	39.9			27.6
ISP3P11B	Hsp	mt3	lt										41.8	39.8	34.2	26.5	29.9
ISP6P34A	Hsp	mt3	rt										43.8	38.5	32.7	25.4	29.2
ISP77P16A	Hsp	mt3	rt										45.9	43.5			29.3

METHODS

Table 1 here lists the Sahabi metapodial and phalangeal material used in this study. Table 2 provides a list of hipparion localities we use in our comparison. We analyse the morphology of metacarpal 3s (hereafter MC3s), metatarsal 3s (MT3s) and 1st phalanges 3s (1P3s), using standard equid measurements published by Eisenmann *et al.* (1988) and Bernor *et al.* (1997). While we use morphometrics here for taxonomic description and evolutionary reconstruction, we wish to state that the shapes and proportions we discern here could well be subject to homoplasy. However, this is not extraordinary for the hipparion skeleton, because we know of no anatomical component in hipparion (skull, dental or postcranial) that has been demonstrated to be homoplasy-free.

In all our analyses we use the Höwenegg sample as our analytical standard. This population is “biologically uniform”, including only a single primitive species, *Hippotherium primigenium* (Bernor *et al.* 1997), and is particularly useful for postcranial comparisons.

Previous principal components analyses of Sümeg (Bernor *et al.* 1999), Sinap (Bernor *et al.* in press) and Dorn Dürkheim (Kaiser *et al.* in press) have demonstrated the importance of variables relating to relative length and slenderness in understanding MP3 morphology. Accordingly, bivariate plots are used to investigate the scaling of MP3 length and slenderness and to place the Sahabi specimens in comparative context with other African specimens, *Cremohipparion mediterraneum* from Pikermi, specimens from Samos, the Siwaliks of Pakistan, and primitive forms from Sinap, Turkey. A similar analysis was also undertaken for 1P3s.

The issue of scaling complicates the description of morphological groups because only rarely can comparisons be made among specimens of strictly comparable body sizes. Therefore, 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 MT3s and MC3s making them of limited utility for studies addressing both MT3s and MC3s. Here we follow Jungers *et al.* (1995) and construct a proxy size variable (GEOMEAN size) based on the geometric mean of nine non-length measurements available for a large array of MP3s: M3, M4, M5, M6, M10, M11, M12, M13, and M14. A similar size

TABLE 2. — List of localities cited.

Locality	Country	Age
Bou Hanifia	Algeria	9.5 Ma
Lothagam	Kenya	7.5-5.2 Ma
Middle Sinap	Turkey	10.7-9.5 Ma
Pikermi	Greece	*c.* 8 Ma.
Samos	Greece	*c.* 8-7 Ma
Maramena	Greece	*c.* 5.2 Ma
Sahabi	Libya	*c.* 5.2 Ma
Siwaliks	Indo-Pakistan	10.7-5 Ma.
Höwenegg	Germany	10.3 Ma.

variable was computed for 1P3s: the geometric mean of M3, M4, M5, and M6.

Least squares regressions for MP3s from Höwenegg were performed for the log transformed variable M1 (maximal length) and the log transformed ratio of M4 to M3 versus log transformed GEOMEAN size. These regression models were used to derive predicted values for M1 and M4:M3 ratio for all other specimens in the analysis. The deviations of the observed values for M1 and M4:M3 from the predicted values for M1 and M4:M3 provide measures of elongation and slenderness respectively expressed relative to size and the Höwenegg sample. Positive deviations indicate relatively long or slender MP3s while negative deviations indicate relatively short and broad MP3s. These measures of elongation and slenderness thus express the same morphological axes uncovered previously using PCA (i.e. Sümeg hipparion; Bernor *et al.* 1999). One advantage of these measures is a more direct presentation of the original metrics and increased consistency with log ratio diagrams. Both log ratio diagrams and plots of the deviation measures described herein make direct use of the Höwenegg sample as a comparative standard. We have plotted the deviation measure of M4:M3 ratio versus the deviation measure of M1. This separates short, broad MP3s and elongate, slender MP3s and shows all specimens relative to the Höwenegg standard. Furthermore these results are parallel to PCA results rendered in prior analyses. Since these axes are defined relative to the Höwenegg sample, MC3s and MT3s may be shown in tandem on the same plot. In several cases, plotting specimens required extrapolating outside the GEOMEAN size range of the Höwenegg sample. This practice lacks the robusticity of statistical significance but is heuristic in making clear comparisons with the Höwenegg standard.

The deviation plots cited above describe metapodial shape relative to the apparent scaling of the Höwenegg sample but do not make specific body size comparisons. A histogram for GEOMEAN size (our proxy size variable) based on MT3s from all sites in the analysis was generated to provide a simple tool for assessing likely differences in body size. An overlay of the Höwenegg MC3 GEOMEAN size distribution and ISP27P25B (the complete MC3 from Sahabi) places ISP27P25B in the general size context of specimens from all sites included in the analysis.

For 1P3s, the log transformed variables M1 (maximum length) and M3 (minimum mid-shaft width) were plotted versus 1P3 GEOMEAN size. These plots also include least squares regressions for the Höwenegg sample of these variables versus GEOMEAN size.

ABBREVIATIONS AND CONVENTIONS

AMNH	American Museum of Natural History, New York;
AMPG and MA	Maramena specimens collected by Professor Norbert Schmidt-Kittler, Mainz, Germany;
AS	Ankara, Sinap;
BMNH	The Natural History Museum, London (former British Museum of Natural History, London);
HmedPikK87	"*Hipparion*" *mediterraneum*, Pikermi, from Koufos (1987);
ISP	International Sahabi Project, directed by Drs. Noel T. Boaz and Ali El-Arnauti;
KNM-BN	National Museums of Kenya, Baringo Basin specimens;
KNM-LT	National Museums of Kenya, Lothagam specimens;
MNHN	Muséum national d'Histoire naturelle, Paris.

The taxon *Hipparion* has been applied in a variety of ways by different authors. We follow definitions recently provided in Bernor *et al.* (1996, 1997).

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).

MC3	metacarpal 3;
MP3	metapodial 3;
MT3	metatarsal 3;
1P3	1st phalanx 3.

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) were cited after the French translations.

ANALYSIS

We analyse here MC3s, MT3s and 1P3s from a number of localities in Africa, the eastern Mediterranean and southwest Asia, and Indo-Pakistan. These are listed in Table 1. We present our analyses by element in the following order: MC3, MT3 and 1P3. We follow Bernor *et al.* (1997) in not distinguishing between anterior and posterior 1P3s. This is based on the Höwenegg sample which showed no morphological or metrical differences between the fore and hind 1P3s.

METAPODIALS 3

Figure 1A is a log10 ratio diagram of mostly complete MC3s from lower MN9 of Sinap (AS93/604), MN10 of Bou Hanifia (MNHN 926, 928 and 95), latest Miocene of Lothagam (KNM-LT139A and 22871) and Sahabi (ISP27P25B). The most primitive hipparion rendered here is the Sinap specimen. Compared to the Höwenegg hipparion, the most distinct difference is the relatively narrow mid-shaft width measurement, M3, compared to the cranio-caudal mid-shaft dimension, M4. We believe that the Sinap specimen represents the morphology of first occurring Old World hipparion, and is closest to its likely North American ancestral group, *Cormohipparion occidentale* s.l. (Bernor *et al.* in press). The three Bou Hanifia (Arambourg 1959) specimens are very closely comparable to the Sinap specimen, and in this characteristic we think it is primitive compared to the Höwenegg hipparion. Likewise, the Lothagam small form (KNM-LT139A), *Eurygnathohippus feibeli* (Bernor & Harris, 2003) shares the morphology of the Sinap and Bou Hanifia forms. The largest form, KNM-LT22871, is referable to the heavily built form *Eurygnathohippus turkanense* (Bernor & Harris, 2003). As with the Höwenegg hipparion, *E. turkanense* has a weak M3-M4 dimension contrast. Sahabi has a single individual represented here, ISP27P25B, which is relatively elongate and very narrow. It shows its strongest derivation in mid-shaft dimension (M3) and has an even stronger M3-M4 contrast.

Figure 1B contrasts the Höwenegg and Sinap hipparion with specimens from Samos, Greece (all AMNH numbers) and the mean measurements for "*Hipparion*" *mediterraneum* from Pikermi (HmedPikK87). The log10 ratio plots of the Sinap and Pikermi forms are virtually identical to one another. The Samos "slender-limbed form" is quite variable, but generally exhibits the proportions of the Sahabi "slender-limbed form" (Fig. 1A). Variability in the Samos hipparion can most likely be attributed to some degree of time averaging between the quarries sampled (Solounias 1981).

Figure 1C is a plot of Sinap and Indo-Pakistan MC3s. The most heavily built specimen is AMNH19671 which is a portion of a complete limb that has been attributed to "*Sivalhippus*" *perimense* (*sensu* Bernor & Hussain 1985). AMNH19685 and AMNH29819 are two other MC3s that are nearly identical to AMNH19671 in all its measurements. These specimens of "*Sivalhippus*" *perimense* have the same proportions, but are not quite as robust as *Eurygnathohippus turkanense* (Fig. 1B). "*Sivalhippus*" *perimense* and *Eurygnathohippus turkanense* are believed to share a close evolutionary relationship (Bernor & Lipscomb 1991, 1995; Bernor & Harris 2003).

Figure 1C reveals another, more slenderly built specimen, BMNHM2650, that is part of the type collection of "*Hipparion*" *antelopinum.* This is a distinctly more slenderly built form. It has a morphology that is strikingly similar in its proportions to the Sinap form, having somewhat elevated measurements throughout, but especially M12, distal sagittal keel. It is therefore like the other more primitive hipparion from Bou

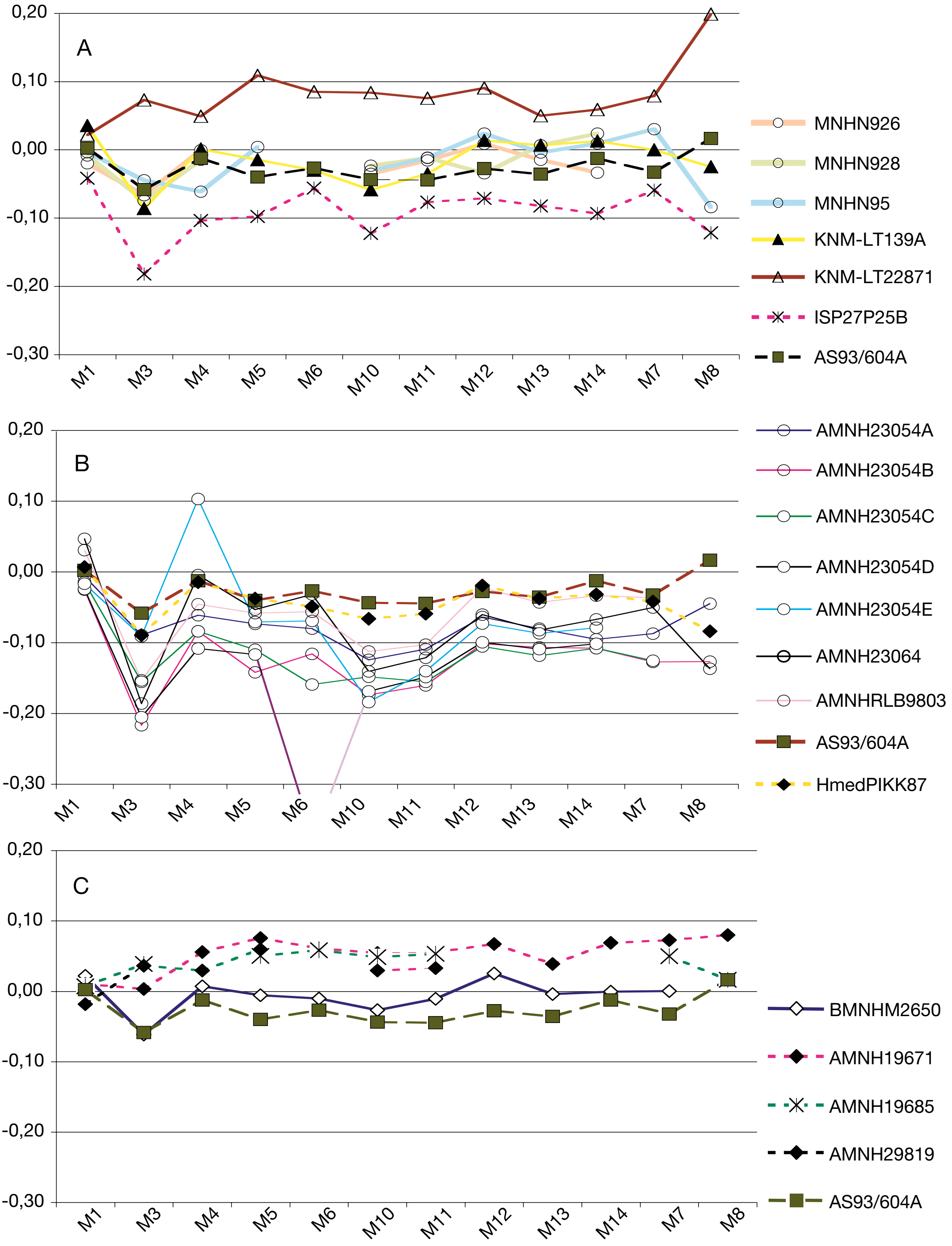


FIG. 1. — Metacarpal 3 log10 ratio diagrams; **A**, Bou Hanifia, Lothagam, Sahabi, Sinap, Höwenegg standard; **B**, Samos, Pikermi and Sinap, Höwenegg standard; **C**, Indo-Pakistan and Sinap, Höwenegg standard.

Hanifia and Lothagam ("*Hipparion*" *africanum* and *Eurygnathohippus feibeli*, Fig. 1A) and Pikermi ("*H.*" *mediterraneum*; Fig. 1B).

Figure 2 shows log10 ratio plots of the MT3. Figure 2A includes the African localities related to Sinap and the Höwenegg standard. It can be seen here that the Sinap species, represented by AS93/332 and AS93/827A, exhibits very little intra-population variability, and is for the most part as long as, but more slenderly built than, the Höwenegg horse. The closest population here to Sinap is, again, Bou Hanifia (all MNHN numbers). Bou Hanifia however has three specimens with markedly reduced M6 (proximal articular surface cranio-caudal depth) compared to both Höwenegg and Sinap. There is a very slender limbed form from Sahabi represented by two specimens, ISP1P25B and ISP67P16A.

A comparison to the Greek localities (Fig. 2B), Samos, Pikermi and Maramena (Sondaar & Eisenmann 1995) again shows the closest relationship to Sinap is shared by "*Hipparion*" *mediterraneum* from Pikermi. Samos has the most slender medio-lateral dimensions (M3, M5, M10, M11) and is in general, the most gracile hipparion in this figure. It is closely matched in this feature by the slender limbed form from Maramena which is potentially conspecific with a Samos slender limbed form.

Indo-Pakistan has both robustly built forms (Fig. 2C) and more slenderly-built forms (Fig. 2D). The two AMNH specimens, AMNH26953 and AMNH29811 (Fig. 2C) have a similar morphology to the Lothagam form, *Eurygnathohippus turkanense* (KNM-LT25470, Fig. 2A). AMNH 29824 is generally similar, except it has smaller dimensions of M4 and M6 than these two previously mentioned specimens. We believe that these three specimens are referable to "*Sivalhippus*" *perimense* (*sensu* Bernor & Hussain 1985).

The Indo-Pakistan slender forms (Fig. 2D) show a remarkable shape similarity, again to the Sinap primitive specimens. Both the AMNH (AMNH19667 and AMNH19669) and BMNH (BMNH16681 and BMNHM17865) have specimens of this form that we believe are referable to "*Hipparion*" *antelopinum*. There is some variability between the AMNH and BMNH specimen, especially in proximal articular measurements, but still the consistency in shape is remarkable especially since these were collected at distinctly different times by different expeditions. The BMNH specimens have absolutely no provenance, while Barry (pers. comm.) has a general idea that these specimens may have been collected from the Dhok Pathan Formation.

Deviation measures of M1 and M4:M3 ratio further describe relative elongation and slenderness of MP3s. Figure 3 compares these measures for the Sahabi MC3, ISP27P25B, and a composite MT3 based on the mean values for two MT3s from Sahabi, ISP67P16A (missing M12) and ISP1P25B (missing M5 and M6) with the Höwenegg sample and specimens attributed to a primitive hipparion from low in the Sinap Formation MN9 sequence. Figure 3A also includes specimens from Bou Hanifia and Lothagam. Figure 3B adds specimens from Samos, Greece, the mean measurements for "*Hipparion*" *mediterraneum* from Pikermi (also from Koufos 1987), and the mean measurements for "*Hipparion*" *brachypus* from Pikermi (from Koufos 1987). Figure 3C includes the addition of specimens from the Siwaliks.

The two cases for Sahabi plot close together with large positive deviations from the Höwenegg sample for both M1 (maximum length) and M4 (mid-shaft craniocaudal depth):M3 (mid-shaft mediolateral width) ratio. The deviation for the M4:M3 ratio is outside the Höwenegg range for both cases. The M1 deviation for the Sahabi MC3 specimen ISP27P25B lies just within the Höwenegg range and the composite Sahabi MT3 is just outside the Höwenegg range. Figure 4 demonstrates the small size of ISP27P25B. These data suggest a diminutive hipparion species with elongate slender metapodials represented by ISP27P25B, ISP67P16A and ISP1P25B.

In Figure 3, the specimens from Samos, the mean measurements for "*Hipparion*" *mediterraneum* from Pikermi (from Koufos 1987), specimens from the Siwaliks of "*Hipparion*" *antelopinum*,

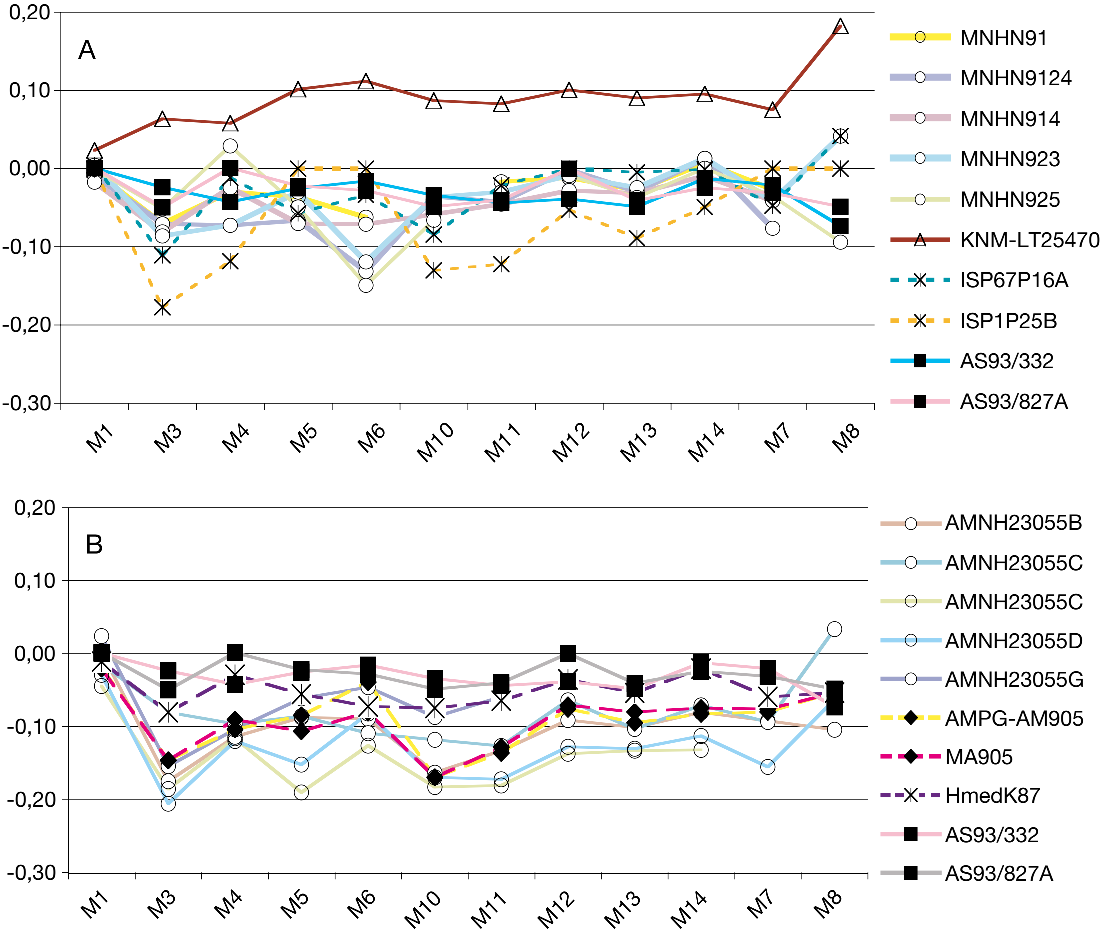
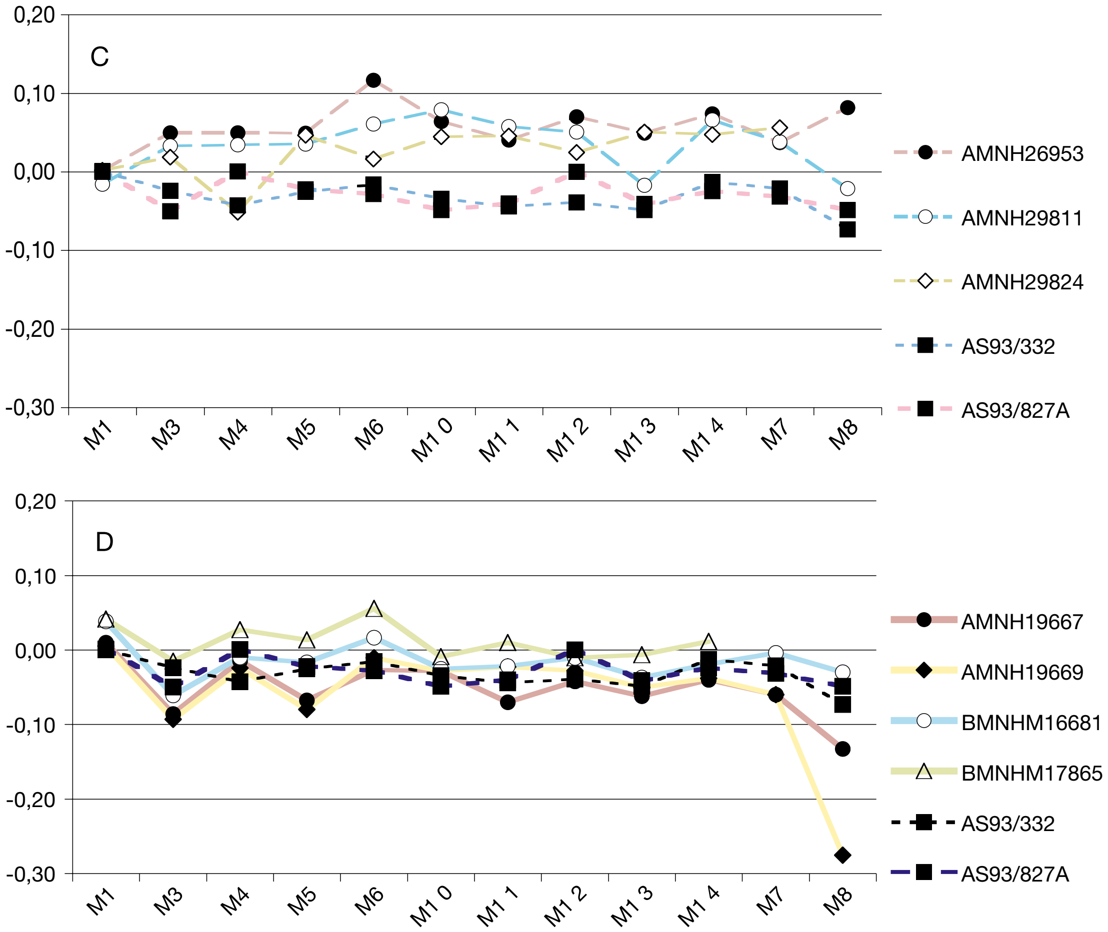


FIG. 2. — Metatarsal 3 log10 ratio diagram; **A**, Bou Hanifia, Lothagam, Sahabi, Sinap, Höwenegg standard; **B**, Samos, Pikermi, Maramena and Sinap, Höwenegg standard; **C**, Indo-Pakistan robust forms and Sinap, Höwenegg standard; **D**, Indo-Pakistan slender forms and Sinap, Höwenegg standard.

one MC3 from Lothagam, and the primitive Sinap specimens all have elevated deviations for M4:M3 ratio and M1. Together they form a morphological group that is distinguished from the Höwenegg sample by relatively elongate and slender metapodials. The Sinap specimens that have been interpreted as being primitive are mainly distinguished by their greater relative length. The deviations for the M4:M3 ratio describe a range of variation in slenderness that indicates some overlap with the Höwenegg sample. It appears likely that the Sinap form was less extreme in terms of relative slenderness and elongation of MP3s than specimens from Samos, "*Hipparion*" *mediterraneum* from Pikermi (from Koufos 1987), and "*Hipparion*" *antelopinum* from Indo-Pakistan. The single Lothagam MC3 specimen attributed to *Eurygnathohippus feibeli* appears to be among the most extreme in terms of relative elongation.

The Sahabi cases plot in the midst of the Greek samples (Pikermi, Samos and Maramena). "*Hipparion*" *antelopinum* is quite similar to these in terms of slenderness but appears slightly more elongate. The Samos sample appears variable, but it is to the Samos specimens that the Sahabi cases



compare most closely in terms of overall size (see Fig. 4). "*Hipparion*" *mediterraneum* (Pikermi) and "*Hipparion*" *antelopinum* (Indo-Pakistan) appear to have been similar in body size and somewhat larger than forms from Sahabi and Samos. With MC3s relatively more slender and elongate than MT3s, Samos MC3s and MT3s do not appear to be strictly comparable. The variability we report here in Samos small hipparion specimens is likely due to the relatively long chronologic interval from which they are sampled and their taxonomic heterogeneity.

The Pikermi species "*Hipparion*" *brachypus* compares closely in terms of relative elongation and slenderness (Fig. 3B), as well as overall size, to the Höwenegg *Hippotherium primigenium* sample. The three Bou Hanifia specimens (Fig. 3A) overlap with the Sinap and Höwenegg samples in terms of relative elongation and slenderness, and compare closely with the Sinap specimens in terms of their size (Fig. 4). Specimens from Maramena are smaller but compare well with Bou Hanifia in terms of their relative elongation. The large-bodied forms from Lothagam (*Eurygnathohippus turkanense*) and Indo-Pakistan ("*Sivalhippus*" *perimense*) are very robust, and relatively short when compared to other MP3s in our analyzed sample.

Based on Figure 3 of MP3s in this analysis we are able to arrange the taxa we have considered here in order of increasing relative elongation and slenderness (i.e. increasing gracility) as follows: "*Sivalhippus*" Complex specimens (*Eurygnathohippus turkanense* (Lothagam) and "*Sivalhippus*"

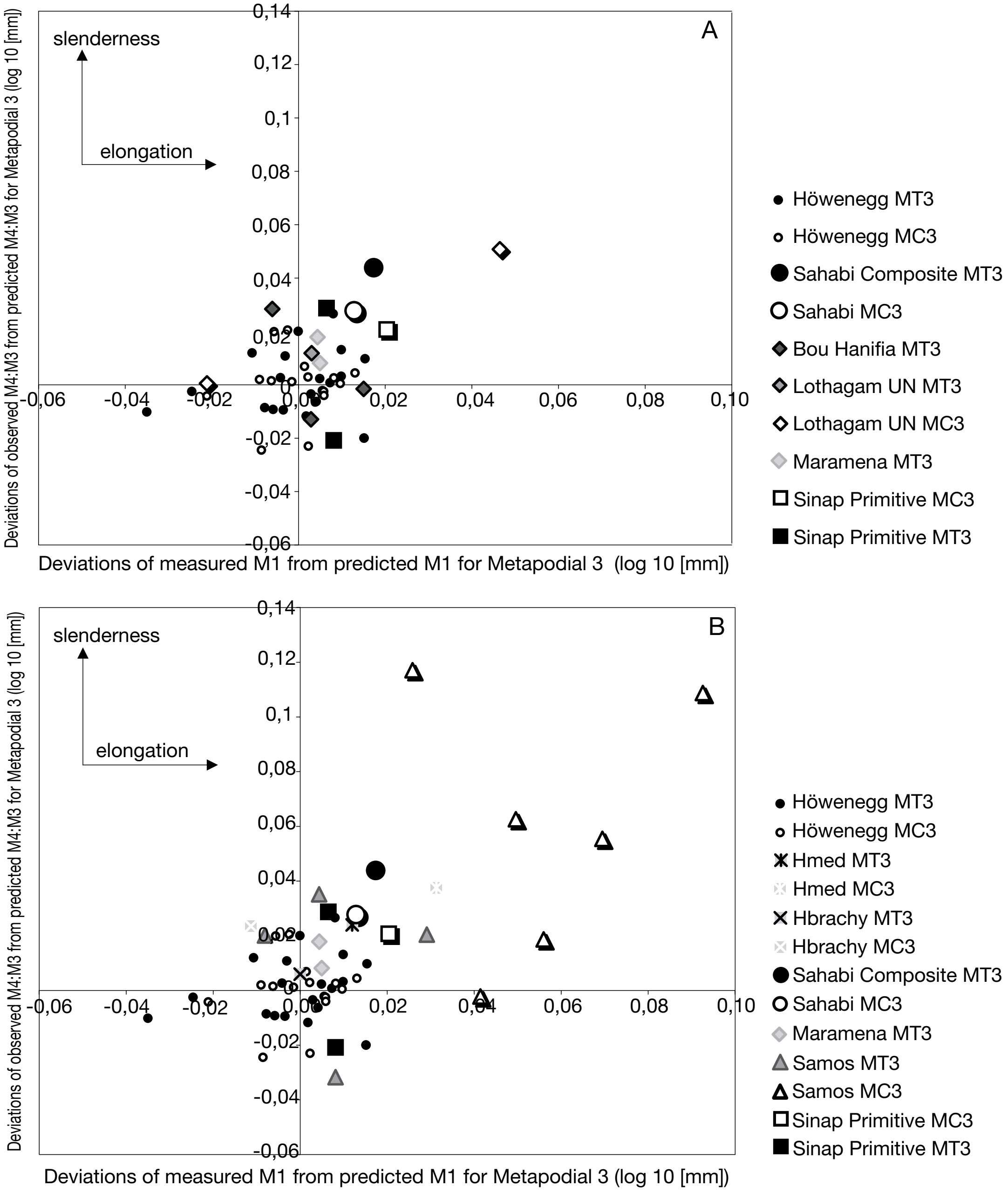
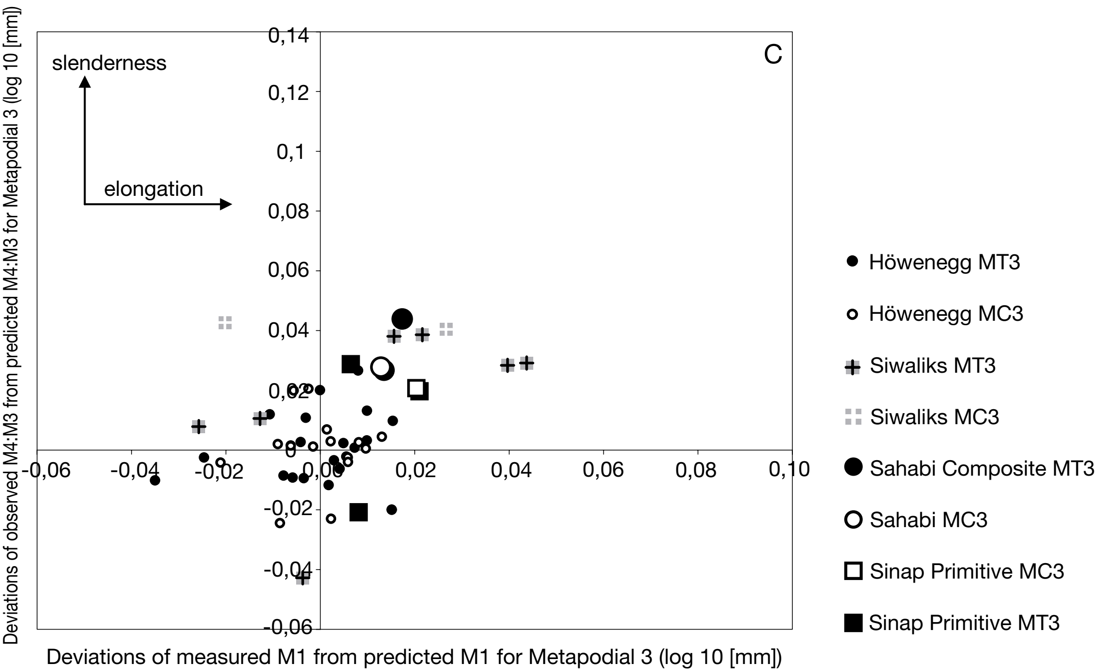


FIG. 3. — Plots of relative MP3 slenderness versus relative MP3 length; **A**, African and Sinap specimens shown in conjunction with the Höwenegg sample; **B**, Sahabi, Sinap and Greek specimens shown in conjunction with the Höwenegg sample; **C**, Sahabi, Sinap and Siwalik specimens shown in conjunction with the Höwenegg sample. Absolute deviations of the observed ratio of M4:M3 (midshaft depth:midshaft width) and observed M1 from predicted values based on least squares regressions against GEOMEAN size for the Höwenegg sample are shown. The M4:M3 deviations are plotted versus M1 deviations. GEOMEAN size is the geometric mean of nine non-length measurements and acts as a proxy variable for generalized body size. Deviations of observed M4:M3 from predicted values describe slenderness relative to a Höwenegg-based scaling model. Deviations of observed M1 from predicted values describe MP3 elongation relative to a Höwenegg-based scaling model. All MC3s are plotted with unfilled symbols (white centers) and all MT3s are plotted with filled symbols. Points for *Cremohipparion mediterraneum* and *Hipparion brachypus* are based on the mean values reported by Koufos (1987). All values are log transformed.



perimense (Siwaliks)); to *Hippotherium primigenium* (Höwenegg) and "*Hipparion*" *brachypus* (Pikermi); to "*Hipparion*" *africanum* (Bou Hanifia) and "*Cremohipparion* aff. *matthewi*" (Maramena); to *Cormohipparion* sp. (Sinap); to *Cremohipparion* aff. "*matthewi*" (Samos and Sahabi) and "*Hipparion*" *mediterraneum* (Pikermi); to "*Hipparion*" *antelopinum* (Siwaliks) and *Eurygnathohippus feibeli* (Lothagam). This ranking could change with the addition of improved associated limb data.

FIRST PHALANGES 3

Bernor *et al.* (1997) found no significant morphological differences in the Höwenegg anterior 1st phalanges 3 and the corresponding posterior 1st phalanges 3. We therefore do not distinguish these here, but we use our statistics on the Höwenegg anterior 1st phalanges 3 as well as Koufos' (1987) statistics on the Pikermi anterior 1st phalanges 3 as standards of comparison.

Figure 5A is a log10 ratio plot of the Lothagam robust form *Eurygnathohippus turkanense* (KNM-LT25940 and KNM-LT26294), the Sahabi robust form (ISP2P111A), and intermediate form from Lothagam (KNM-LT25465), and two specimens from Ngorora (KNM-BN1202 and KNM-BN1598). The Lothagam robust species and the Sahabi robust species are virtually identical in their maximum length (M1) and several width measurements: M3 (minimal width), M6 (distal tuberosity width) and M7 (distal articular breadth). The Ngorora species has very similar proportions to the robust forms from Sahabi and Lothagam, but falls in the same size bracket as the intermediate species from Lothagam (Bernor & Harris 2003). In fact, the Lothagam intermediate species and the Ngorora species may share a close taxonomic identity. The Lothagam intermediate species and the Ngorora species have a different shape than the Höwenegg hipparion, but deviate the least from it when compared to the other robust species.

Figure 5B includes 1st phalanges 3 from Lothagam (KNM-LT139b and KNM-LT25472), Sahabi (ISP34P25B) and Pikermi (HmedPikK87). These specimens all have a remarkably similar morphology to one another, and differ most significantly in minimum width (M3), proximal articular width (M4) and distal

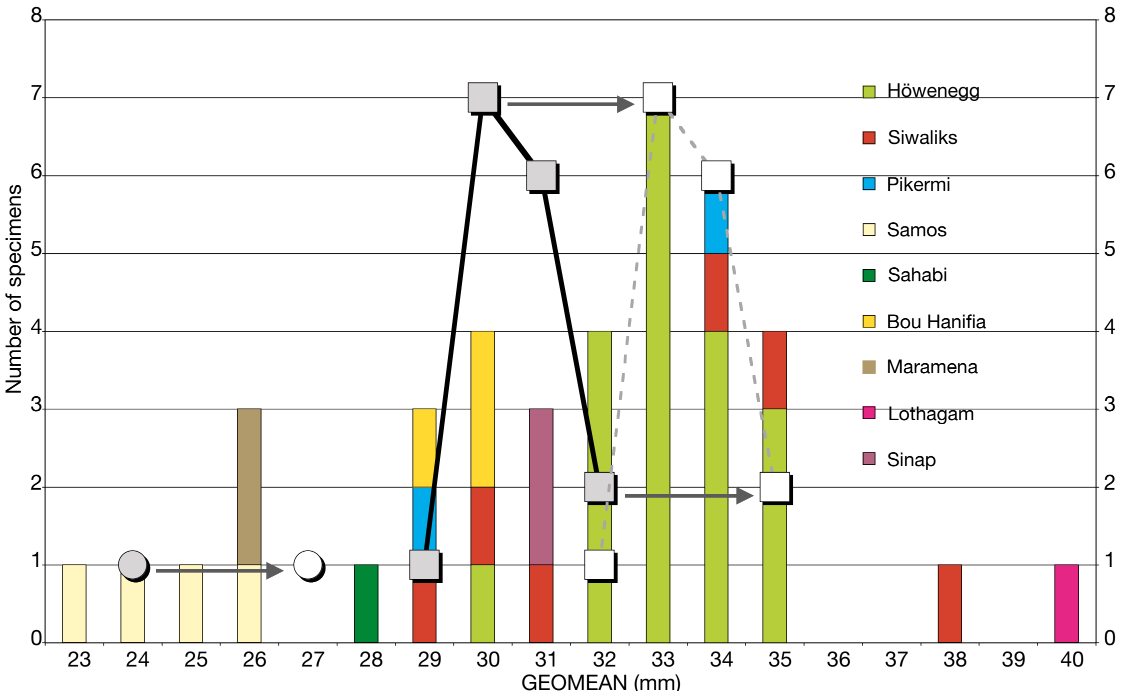


FIG. 4. — Histogram for GEOMEAN size of MT3s included in this study. GEOMEAN size is the geometric mean of nine non-length measurements and acts as a proxy variable for generalized body size. GEOMEAN size for the Sahabi MC3 and for the Höwenegg MC3 distribution is shown as an overlay. Arrows show an adjustment of the MC3 data aligning the Höwenegg MC3 and MT3 distributions.

articular width (M6) from all the specimens cited in Figure 3A. Given Pikermi's close metapodial proportions to the Sinap hipparion, we suspect that the proportions exhibited here may approximate the ancestral condition of Old World hipparions, with the Lothagam and Sahabi species showing some lengthening over the Pikermi species.

Figure 5C is a log10 ratio plot of 1st phalanges from Indo-Pakistan (BMNHM17430, BMNHM2661 and BMNHM2662) and Pikermi (HmedPikK87). The Indo-Pakistan suite is part of the type series of *Hipparion antelopinum* maintained by the BMNH. *Hipparion antelopinum* exhibits a dramatic increase in both maximum length (M1) and anterior length (M2) measurements, while minimal width (M3) remains the same as in the slender African forms (Fig. 3B).

Figure 6 compares phalangeal length (M1) and breadth (M3) to a phalangeal measure of size (the geometric mean of M3 [minimum mid-shaft width], M4 [proximal articular width], M5 [proximal articular craniocaudal depth], and M6 [distal width at the tuberosities]). Most variation in phalanx morphology is associated with M1 when compared to general size. Two Sahabi forms are evident: 1) a form with elongate slender 1P3s which is likely the same as the Sahabi form with long and slender metapodials; and 2) a second form with large short, robust 1st phalanges 3. The second form plots near two specimens from Lothagam of *Eurygnathohippus turkanense* (KNM-LT25940 and KNM-LT26294). As noted already, *Hipparion antelopinum* has very elongate and slender 1P3s and is clearly distinguishable from all other taxa on this basis.

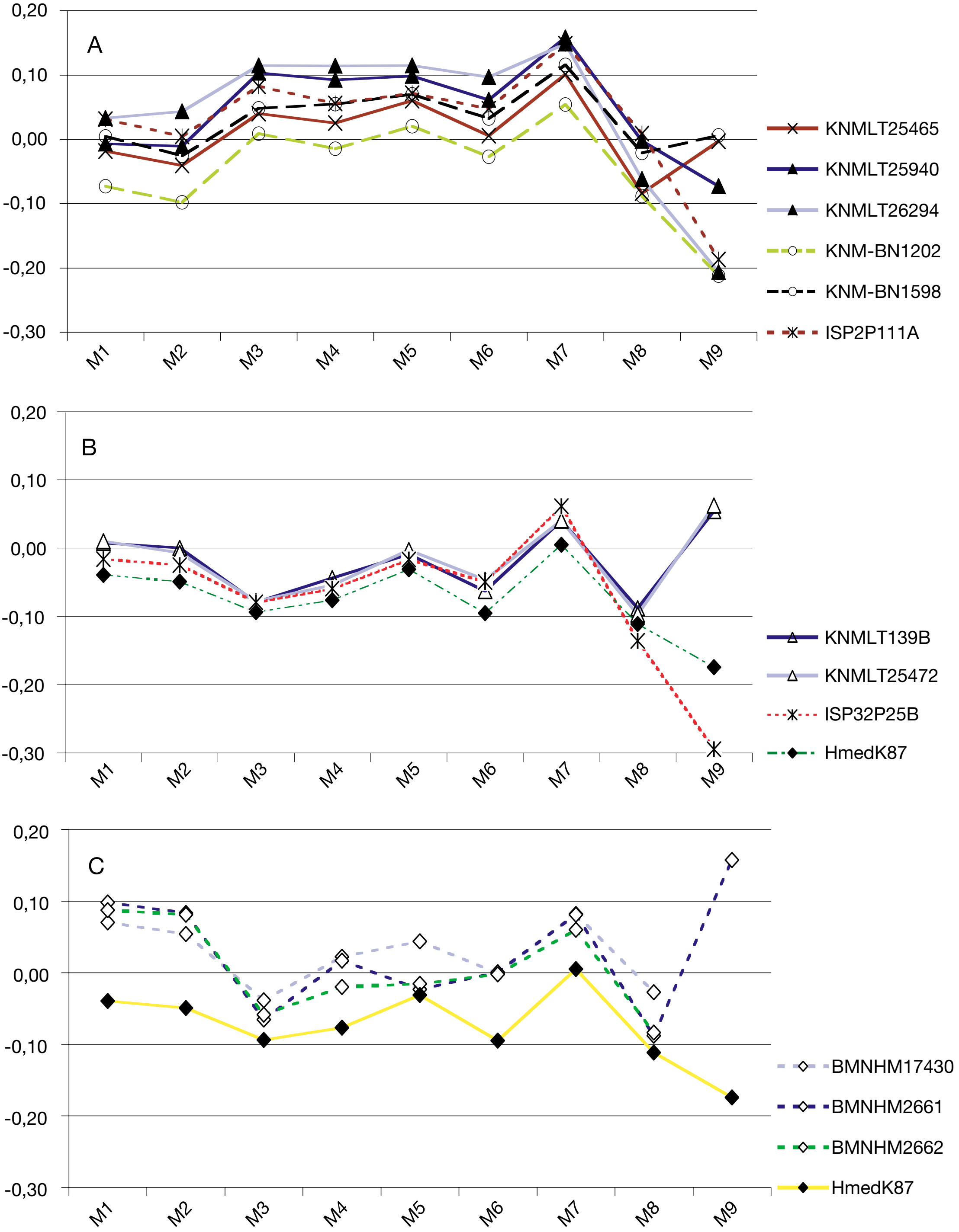


FIG. 5. — First phalanx 3 log ratio diagrams; **A**, Ngorora, Lothagam, Sahabi robust and intermediate forms, Höwenegg standard; **B**, Lothagam, Sahabi and Pikermi slender forms, Höwenegg standard; **C**, Indo-Pakistan and Pikermi, Höwenegg standard.

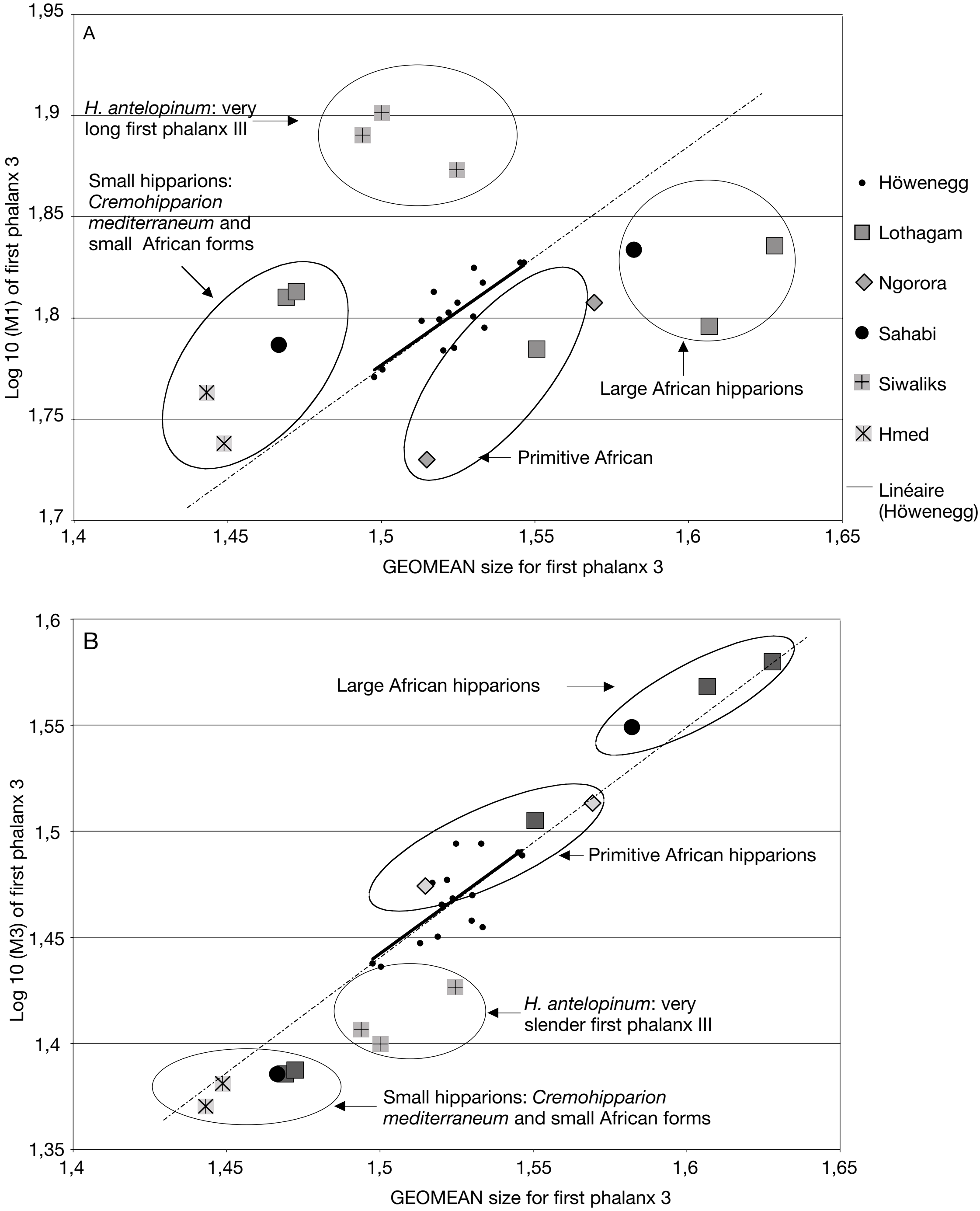


FIG. 6. — **A**, plot of M1 (length) versus GEOMEAN size for 1st phalanx 3, the thick line represents the least squares regression for the Höwenegg sample and the dashed extension of this line is a linear extrapolation outside of the Höwenegg sample; **B**, plot of M3 (mid-shaft width) versus GEOMEAN size for 1st phalanx 3, the thick line represents the least squares regression for the Höwenegg sample and the dashed extension of this line is a linear extrapolation outside of the Höwenegg sample.

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
Suborder HIPPOMORPHA Wood, 1937
Superfamily EQUOIDEA (Gray, 1821) Hay, 1902
Family EQUIDAE Gray, 1821
Subfamily EQUINAE (Gray, 1821)
Steinmann & Döderlein, 1890
Genus *Cremohipparion* Qiu,
Weilong & Zhiui, 1988

"*Cremohipparion*" aff. *matthewi*

REFERRED SPECIMEN. — 1P3: ISP32P25B (Fig. 7A); MC3: ISP25P26A, ISP27P25B (Fig. 8), ISP33P15A; MT3: ISP11P85A, ISP1P25B, ISP31P25A, ISP468P28A, ISP59P16A, ISP67P16A, ISP6P108A.

AGE. — Latest Miocene, late Turolian (MN13).

GEOGRAPHIC RANGE. — Greece and North Africa.

REMARKS

Pomel (1897) applied the nomen *Hipparion sitifense* to a small hipparion from Saint-Arnaud Cemetery, Algeria. As cited by Bernor & Harris (2003), this nomen has been applied to a number of African small hipparion samples. However, as they have pointed out, this is inappropriate since there was no type ever nominated for this nomen and, according to Eisenmann (pers. comm.), the type assemblage cannot be located. As far as we are aware, there are no other fossil materials available from this site. Furthermore, there are several lineages of smaller hipparion from the Eurasian and African Late Neogene that disallow reasonably certain assignment of any Late Neogene hipparion assemblage to "*Hipparion*" *sitifense*. We believe, given this set of circumstances, that it is not scientifically sound to assign any smaller hipparion sample to *Hipparion sitifense* and suggest that it be considered a *nomen dubium*.

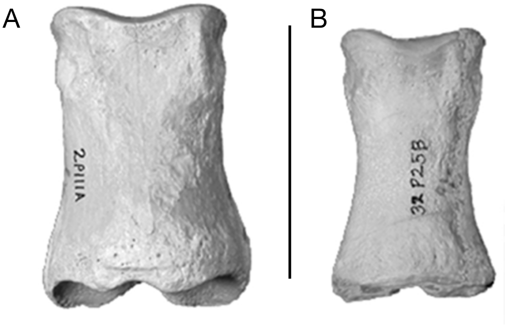


FIG. 7. — First phalanx 3 in cranial view; **A**, ISP2P111A, "*Hipparion*" sp. ("*Sivalhippus*" Complex); **B**, ISP32P25B, *Cremohipparion* aff. *matthewi*; both from Sahabi. Scale bar: 5 cm.

Bernor *et al.* (1987: figs 4-6) figured a series of Sahabi metapodials and phalanges. In so doing, they referred an MC3, 27P25B (fig. 4a), an MT3, 1P25B (fig. 5A) to "*Hipparion*" cf. *sitifense*, and yet another MT3, 67P16A (fig. 6) to "*Hipparion*" cf. *africanum*. We believe that all three of these specimens are best interpreted as being derived from the same species and refer them here to "*Cremohipparion*" aff. *matthewi* (see Table 1; Fig. 8). We likewise refer the 1P3 ISP32P25B (Bernor *et al.* 1987: fig. 5A) to "*Cremohipparion*" aff. *matthewi* (Fig. 7).

We have demonstrated here that these postcrania exhibit the greatest similarity to the Samos small equids belonging to the "*Cremohipparion*" lineage (Bernor & Tobien 1989; Bernor *et al.* 1989; Bernor *et al.* 1996). The *Cremohipparion* lineage includes a complex of hipparions with an eastern Mediterranean, southwest Asian and Chinese geographic range. Whereas the Chinese lineages are known from late Miocene-early Pliocene aged horizons (Qiu *et al.* 1987), the eastern Mediterranean-southwest Asian radicle is known only from late Miocene aged horizons. There are two small equid species reported from Samos: *Cremohipparion matthewi* and *Cremohipparion nikosi* (Bernor & Tobien 1989). Evidence presented here based on MP3 and 1P3 morphology suggests a similar morphologic pattern between slender elongate distal limb element hipparions from Pikermi, Samos, Sahabi and Indo-Pakistan. This may indicate homoplasy between these taxa, or an actual phylogenetic relationship between them. If there is a phylogenetic relationship between these equids, then there is a specific taxonomic conflict that requires discussion.

The taxonomic conflict has its origins with Woodburne & Bernor's (1980) initial discrimination of Old World hipparion superspecific

FIG. 8. — MC3s in cranial view; **A**, Höwenegg, *Hippotherium primigenium* A skeleton (cast; Hegau, Germany); **B**, ISP27P25B, *Cremohipparion* aff. *matthewi* (Sahabi); **C**, LT139, *Eurygnathohippus feibeli* (Lothagam, Lower Nawata, Kenya); Scale bar: 10 cm.

groups. In recognizing their four superspecific groups, Woodburne & Bernor (1980) clearly distinguished a medium sized lineage with a small preorbital fossa placed dorsally high on the face (their Group 3, or *Hipparion* s.s.), another medium-large size lineage with a very large, dorsoventrally deep preorbital fossa set close to the orbit, accompanied by well defined buccinator and intermediate fossae (their Group 2; *Cremohipparion* of Bernor & Tobien 1989), and a third small lineage whose preorbital fossa (POF) was most similar to Group 2 hipparions, but simply smaller (their Group 4). Bernor *et al.* (1980) gave a biochronologic ranking of these three groups and demonstrated that groups 2 and 3 were in fact species rich and biogeographically long ranging (Bernor *et al.* 1980: 729, fig. 8).

Qiu *et al.* (1987) recognized the subgenus "*Hipparion*" (*Cremohipparion*) for the Chinese species "*Hipparion*" (*Cremohipparion*) *forstenae* and "*Hipparion*" (*Cremohipparion*) *licenti*, and these hipparions retain the same three POFs that are known to occur in Woodburne & Bernor's Group 2 hipparions. Moreover, all Group 2 hipparions have the synapomorphy of a short preorbital bar (POB) with the lacrimal invading the posterior aspect of the POF. Bernor & Tobien (1989) raised Qiu *et al.*'s (1987) subgenus "*H.*" (*Cremohipparion*) to generic rank and recognized the small Samos horse, *Cremohipparion matthewi*, as a member of this clade. Bernor & Tobien (1989) nominated a new Samos small species, *Cremohipparion nikosi*, based on its more retracted nasals. Bernor & Tobien (1989) recognized that these two small taxa are similar to *Cremohipparion moldavicum* in their lack of an intermediate (= caninus) fossa, common across all other known members of the clade. Neither of the two Samos small species of *Cremohipparion* have directly associated postcrania, but the proxy association of elongate slender MP3s with these small "skull species" is a time honored one (Sondaar 1971).

The realization that the MP3s and 1P3s of the type series of *Hipparion antelopinum* are morphometrically similar to the small Samos *Cremohipparion* thus presents a taxonomic conflict. The type specimen of *Hipparion antelopinum* Falconer & Cautley, 1849 is a sub-adult right maxilla fragment with P2-M3 (BMNHM 2647), derived from the Middle Siwaliks Dhok Pathan District. In this BMNH material there is additionally a juvenile left maxilla fragment with dP2-4 and P2 (BMNHM2646), an adult skull fragment with P4-M3 (BMNH16170) and the MP3s and the 1P3s we have analysed here. According to Bernor & Hussain (1985), these skull fragments are sufficient to say that the preorbital fossa was dorsoventrally restricted. The previous contention that the preorbital fossa was placed "well anterior to the orbit" was inferred (Bernor & Hussain 1985: 60, left column, 1st paragraph, lines 6, 7). It is certainly a possibility that the Indo-Pakistan taxon "*Hipparion antelopinum*" has a short POB with lacrimal invading, and therefore could have this key *Cremohipparion* synapomorphy. It is further possible that *Cremohipparion matthewi* and *Cremohipparion nikosi* (Greece) and "*Cremohipparion*" *antelopi-*

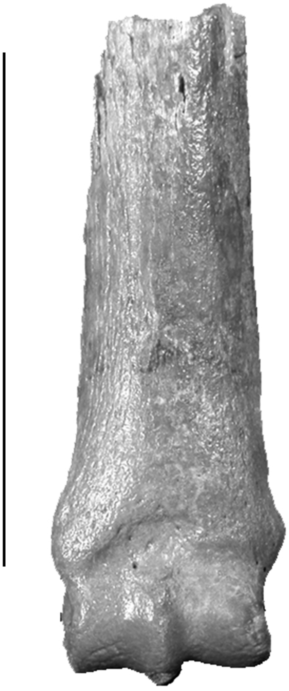


FIG. 9. — MT3 in cranial view, ISP6P34A, "*Hipparion*" sp. ("*Sivalhippus*" Complex) Sahabi. Scale bar: 10 cm.

num (Indo-Pakistan) share an evolutionary relationship with the Sahabi form "*Cremohipparion*" aff. *matthewi*.

"*Hipparion*" sp. (*Sivalhippus* Complex)

REFERRED SPECIMENS. — 1P3: ISP2P111A (Fig. 7B); MC3: ISP17P33A; MT3: ISP10P30A, ISP35P17A, ISP3P11B, ISP6P34A (Fig. 9), ISP77P16A.

AGE. — Latest Miocene, late Turolian (MN13).

GEOGRAPHIC RANGE. — N Africa and possibly Indo-Pakistan and E Africa.

REMARKS

The Sahabi large MP3 and 1P3 material was believed by Bernor *et al.* (1987) to be referable to "*Hipparion*" cf. *africanum*. Eisenmann (1994: 296) noted that the Sahabi large hipparion was too big to be referred to "*H.*" *africanum.* We agree. Our analysis here shows that the size and proportions of this Sahabi material establishes it as a member of the "*Sivalhippus*" Complex. Bernor & Lipscomb (1991, 1995) and later Bernor *et al.* (1996) established that the "*Sivalhippus*" Complex is a clade that occurs from the late Miocene to Pleistocene of Eurasia and Africa and included the genera: *Plesiohipparion*, *Proboscidipparion*, *Eurygnathohippus* and "*Sivalhippus*". The phylogenetic relationship of "*Sivalhippus*" *perimense* and *Eurygnathohippus turkanense* has been established to be a particularly close one on the basis of cranial, dental and postcranial anatomy (Bernor & Lipscomb 1991, 1995; Bernor & Harris 2003, and the analysis presented here).

The presence of a primitive member of the "*Sivalhippus*" Complex lineage in Indo-Pakistan, "*Sivalhippus*" *perimense* (*sensu* Bernor & Hussain 1985), has led to the assumption that this clade arose in the Indian Subcontinent and subsequently extended its range into Africa and East Asia in the late Miocene and Europe at the base of the Pliocene (Bernor *et al.* 1989). An alternative interpretation of this hypothesis is that "*Sivalhippus*" *perimense* and *Eurygnathohippus turkanense* (Lothagam, Lower Nawata; Bernor & Harris 2003) are two closely related clades that shared an earlier pan Indo-Pakistan-East Africa biogeographic connection. We believe that the Sahabi robust-limbed form "*Hipparion*" sp. (*Sivalhippus* Complex) is a member of one of these clades. If the Sahabi form proves to have ectostylids on the lower permanent dentition, it would best be referred to *Eurygnathohippus.* If it proves to lack ectostylids, as is the case with the Indo-Pakistan form, then it would be best referred to "*Sivalhippus*".

An interesting feature of our analysis is the finding that the Ngorora (*c.* 9 Ma) hipparion 1P3s are somewhat smaller, but have the same proportions as these robust members of the "*Sivalhippus*" Complex. In turn, the Ngorora 1P3s perfectly bracket the rare, so-called intermediate form from the Lower Nawata, Lothagam (Kenya; Bernor & Harris 2003). Neither of these forms have yielded any evidence of ectostylids on the lower permanent cheek teeth. However, this may well be due to poor sampling. These observations support a pan Indo-Pakistan-North and

East African biogeographic connection of this hipparion clade early in the late Miocene (Gentry 1999).

CONCLUSIONS

Our analysis suggests that the Sahabi small hipparion is most likely related to an eastern Mediterranean-southwest Asian-south Asian "*Cremohipparion*" *matthewi-antelopinum* lineage. This lineage underwent reduced body size accompanied by lengthening of the distal limb elements (namely, MP3s and 1P3s). The combination of reduced body size and limb elongation suggests that these hipparions were adapted to open country running. "*Cremohipparion*" *antelopinum* would appear to be similar in its MC3 and MT3 morphology to Sahabi, but derived in its elongate 1P3. The Samos "*Cremohipparion*" *matthewi-nikosi* sample has relatively elongate MC3s compared to Sahabi and Indo-Pakistan MC3s, but similar MT3s and 1P3s. The distal limb proportion differences between these various taxa could be due either to homoplasy or vicariant biogeography. We presently favor the vicariant hypothesis.

The Lothagam small hipparion, *Eurygnathohippus feibeli*, was apparently not a member of the "*Cremohipparion*" lineage (Bernor & Harris 2003). The Lothagam Nawata slender MC3 is both absolutely and relatively longer than that of the Sahabi slender-limbed form, and the presence of ectostylids on the permanent cheek tooth dentition is a character that has not been observed in Eurasian hipparions (except rarely in very worn Dinotheriensandes *Hippotherium primigenium*).

The Sahabi robust limbed form exhibits close size and proportional comparisons with the Indo-Pakistan species "*Sivalhippus*" *perimense* and *Eurygnathohippus turkanense*. Moreover, this robust morphology would appear to have its foundations in the older Ngorora (Kenya) hipparion as well as the late occurring Nawata Lothagam intermediate hipparion (Bernor & Harris 2003).

We believe that the Sahabi large, heavy limbed form was adapted to a more closed habitat setting where cursorial behavior was not held at a premium. The Sahabi small, elongate-slender limbed form was likely adapted to more open country habitats where cursoriality would confer a selective advantage.

Our analyses of Sahabi MC3s, MT3s and 1P3s confirm Eisenmann's (1995) assertion that postcranial morphometrics offer a powerful analytical tool for analyzing equid postcranial functional anatomy and systematic relationships. Based on our own, independent studies here, as well as elsewhere (Bernor *et al.* 1999, in press; Bernor & Harris 2003) we actively advocate incorporating multiple tests of morphometric postcranial analyses in any equid systematic study.

Acknowledgements
We would like to thank Prof. George Koufos for providing us his raw measurements on Pikermi postcrania, Prof. Sevket Sen for encouraging us to submit this paper to *Geodiversitas*, and Prof. Noel T. Boaz for likewise encouraging us to continue our research on the Sahabi equid collections. This research was supported by NSF grant EAR-0125009 to R. L. Bernor (PI) and NSF grant BCS-0112659 to J. Kappelman (PI) and R. S. Scott.

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