



Eurygnathohippus feibeli (Perissodactyla: Mammalia) from the Late Miocene of As Sahabi (Libya) and its Evolutionary and Biogeographic Significance

Raymond L. BERNOR, Noel T. BOAZ & Lorenzo ROOK

R.L. Bernor, College of Medicine, Department of Anatomy, Laboratory of Evolutionary Biology, Howard University, 20059 U.S.A.; rbernor@howard.edu; corresponding author

N.T. Boaz, International Institute for Human Evolutionary Research, Integrative Centers for Science and Medicine, Martinsville, VA 24112-2922 U.S.A., and Anthropology Program, School of World Studies, Virginia Commonwealth University, Richmond, VA 23284-2021 U.S.A.; ntboaz@vcu.edu

L. Rook, Dipartimento di Scienze della Terra, Università di Firenze, 50121 Firenze, Italy; lorenzo.rook@unifi.it

KEY WORDS - *Eurygnathohippus feibeli*, *Perissodactyla*, *Functional Morphology*, *As Sahabi*, *Lothagam*, *Africa*, *Late Miocene*.

ABSTRACT - *The discovery of a new hipparionine metacarpal III in 2010 has led to the recognition of the occurrence of the East African species Eurygnathohippus feibeli at Sahabi. Specimens of metacarpal III and metatarsal III previously referred to cf. Hipparion s.s. are reassigned herein to Eurygnathohippus feibeli. The occurrence of an East African hipparionine horse at Sahabi is congruent with findings of other Late Miocene ungulates and strengthens the biogeographic connections between the Sahabi and the Ethiopian Middle Awash and Kenyan Lothagam faunas. Taking into consideration the known biogeographic connections to eastern Mediterranean - Southwest Asia faunas, the Sahabi findings constitute a crucial crossroads fauna between Eurasia and Africa and reflect the maximum extension of Old World Pikermian faunas in the Late Miocene.*

RIASSUNTO - [Sulla presenza di *Eurygnathohippus feibeli* (Perissodactyla: Mammalia) nel Miocene Superiore di As Sahabi (Libya) e il suo significato biogeografico ed evolutivo] - *Il ritrovamento di un nuovo terzo metacarpale di un equide ipparionino avvenuto nella missione del 2010 ci ha permesso di riconoscere la presenza a Sahabi della specie ad affinità est africana Eurygnathohippus feibeli. Lo studio del nuovo materiale consente di attribuire anche i resti di metacarpale III e metatarsale III, in precedenza attribuiti a cf. Hipparion s.s., alla specie Eurygnathohippus feibeli. La presenza di un equide ipparionino con affinità est africana a Sahabi è congruente con la co-presenza di altri ungulati del Miocene Superiore nell'associazione faunistica ed è una conferma delle connessioni biogeografiche tra Sahabi e le associazioni faunistiche del Middle Awash (Etiopia) e di Lothagam (Kenya). Tenendo conto delle affinità biogeografiche che Sahabi mostra di possedere anche con le regioni del Mediterraneo orientale e dell'Asia sudoccidentale, la località libica si conferma come importante crocevia faunistico tra Eurasia e Africa nel Miocene terminale, e rappresenta la massima estensione geografica delle faune "pikermiane" nel Miocene Superiore.*

INTRODUCTION

As Sahabi is a celebrated Late Miocene vertebrate locality in northern Libya, located about 130 km south of Ajdabiya (at 30°00'26"N and 20°47'46"E; Fig. 1) along the road going south into the Libyan Sahara to Gialo and Kufra. In the 1920s and 1930s there was an active Italian army station with an airfield for small airplanes. Being on the road to various sites into the Libyan desert, As Sahabi was frequently crossed by caravans and explorers and was visited by eminent geologists such as A. Desio (1931) and G. Stefanini (1934). The discovery of the paleontological site and the recovery of abundant fossils at As Sahabi in early years is undoubtedly due to the efforts of C. Petrocchi (Rook, 2008). Italian soldiers and other Italian personnel assigned to the As Sahabi fort collected fossils as curiosities because they were so common around the military installation. In early 1934, a team of public health personnel realized the possible scientific importance of the fossil discoveries and reported them to the local authorities. Following these reports, Dr Carlo Petrocchi was charged to study these fossil remains and to survey the As Sahabi area. From 1934 to 1939 Petrocchi conducted several seasons of field survey and excavation, and undertook intensive laboratory work for

the preparation of collected material (Petrocchi, 1934, 1941, 1943). Continuing his work at As Sahabi proved to be difficult. After the initial enthusiasm, Petrocchi was left without sufficient support to continue his work at As Sahabi; no geologist or paleontologist was assigned to collaborate with him. The activity of these years resulted in the assembly of a large fossil collection including about 1000 specimens that were stored in Benghazi. Later, in 1939 when Petrocchi was named director of the Libyan Museum of Natural History, the Sahabi fossil material was transferred to Tripoli. At the beginning of 1940, Petrocchi was asked to organize a paleontological exhibition in Naples and the circumstances of the Italian participation in the 2nd World War made it impossible for Petrocchi to come back to Tripoli. He was obliged to remain in Italy, where he was able to continue working on the Sahabi material that was "temporarily" transferred to Italy (Petrocchi, 1951, 1954, 1956; Esu & Kotsakis, 1980; Rook & Martínez-Navarro, 2004; Sardella & Werdelin, 2007; Delfino, 2008a,b; Delfino & Rook, 2008).

From the middle 1970's to early 1980's a multidisciplinary research team, the International Sahabi Research Project (ISRP) developed intensive investigations in the area (Boaz et al., 1979, 1987). In 2004, the efforts of several institutions (among others

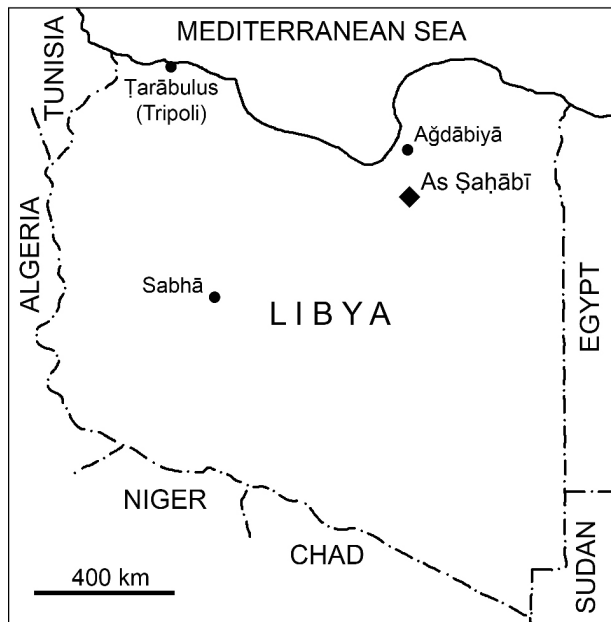


Fig. 1 - Location map of the As Sahabi site.

the Benghazi -formerly Garyounis- University, Benghazi, and the International Institute for Human Evolutionary Research, based in Martinsville, Virginia) formally re-organized Sahabi (and Jabal Zaltan) research into a renewed research initiative named the East Libya Neogene Research Project (ELNRP) (Boaz et al., 2008b). Thus far, the two international research initiatives (ISRP and ELNRP) have recovered over 5500 fossil vertebrates from 94 vertebrate localities of Late Miocene age (MN13 correlative; Boaz et al., 2008a).

The lithostratigraphy of the Sahabi Formation was reported by de Heinzelin & El-Arnauti (1982, 1987) and includes four members, from lower to higher, named T, U, V, and Z. The aggregate thickness of the Sahabi Formation is between 41 m and 130 m depending on facies variations. Two units of Member U, U-1 and U-2, have yielded the bulk of the fossil vertebrates collected and excavated by the ISRP and ELNRP, whereas most of the earlier fossil collections made in the western exposures of the Sahabi Formation are from Member V (Boaz, 2008). Surface exposures have been subjected to continuing survey and recovery by members of the ELNRP, refining earlier studies (Muftah et al., 2008b; Shawaidhi & Al-Trabelci, 2008). Boreholes through the Sahabi Formation and into underlying formations have added some 165 m of additional stratigraphic depth and confirmed the Late Miocene age of marine sediments underlying the Sahabi Formation (NN10b-NN11b; Muftah et al., 2008a).

Fossil material referable to *Eurygnathohippus feibeli* is recognized here based on a newly discovered MCIII, 82P17A, collected by an ELNRP field team led by P. Pavlakis in 2010 from Unit U-1 in the Sahabi Formation (Fig. 2). This discovery has served to resolve referral of small postcranial bones and, specifically metacarpal III's (MCIII's) and metatarsal III's (MTIII's) from cf. *Hipparion* sp. s.s. (Bernor et al., 2008) to *Eurygnathohippus feibeli*. The Sahabi equid fauna includes at least 3 genus-level lineages of hipparionine horse, including

Sivalhippus, *Cremohipparion* and now *Eurygnathohippus*. *Cremohipparion* is a Eurasian lineage yet unreported from Sub-Saharan Africa (Bernor et al., 1996). *Sivalhippus* is abundantly known with several species from the Potwar Plateau of the Indian Subcontinent as well as the East African Late Miocene (Bernor et al., 2008, 2010). *Eurygnathohippus* is a distinctly African clade that was distributed across all latitudes of the continent by 2.5 Ma (Bernor et al., 2010). Thus far, *Eurygnathohippus feibeli*, and its close relative *Eurygnathohippus* aff. *feibeli* are known from the Late Miocene of Kenya (Bernor & Harris, 2003) and Ethiopia (Bernor et al., 2005, 2008), respectively. This work on Sahabi equids follows previous work by Bernor and others (Bernor, 1982; Bernor et al., 1987; Bernor & Scott, 2003; Bernor et al., 2009) that has progressed as the East Libya Neogene Research Project has retrieved more complete fossil horses.

The African deposits attributable to the later part of the Late Miocene are relatively rare (Hill, 1999). As a matter of fact, in recent years the effort of several research groups has extended our knowledge of this time interval thanks to the identification and exploitation of a number of sites in various countries, namely Kenya, Ethiopia and Chad. Lothagam is an important Late Miocene site located southwest of Lake Turkana (Kenya). The site contains deposits dated between 8 and 4 Ma and samples an incredibly diverse Late Miocene fauna (Leakey & Harris, 2003). The lowest fossiliferous unit is termed Nawata Formation (Feibel, 2003), chronologically constrained, based on radiometric and paleomagnetic studies, from about 9 Ma to about 5.5 Ma (McDougal & Feibel, 2003). The Nawata Formation is divided into 2 members (Upper member and Lower member), with a boundary at 6.54 Ma. The Nachukui Formation forms the upper part of the Lothagam sequence. The latter is much more extended than the Nawata Formation, either in terms of sediment thickness or time span (the youngest members of the Nachukui Formation overlapping the famous KBS Tuff dated 1.88 Ma). The basal member of the Nachukui Formation (Apak Member) is dated from 5.5 Ma to about 4 Ma (McDougal & Feibel, 2003). Based on the suid faunas, Cooke (1987) observed similarities between Sahabi and Lothagam, and proposed a correlation between the Sahabi and the Lothagam Upper Nawata and Apak members. Harris & Leakey (2003) concurred with Cooke in correlating Sahabi with the latest Miocene Lothagam Upper Nawata. Bernor & Rook (2008) found that the fauna that has the most species-level similarity to Sahabi is Baynunah, followed by Lothagam Nawata. This result suggests that Sahabi, Baynunah, and Lothagam Nawata closely overlap chronologically and shared broadly in their biogeographic relationships. The transition between MN12 and MN13 is a likely correlation for Sahabi and Baynunah, and corresponds broadly to Upper Nawata faunas of Kenya.

MATERIALS AND METHODS

The material studied here includes specimens from the Late Miocene of Africa, Iran and the Indian Subcontinent as appear in log10 ratio diagrams of Figures 4 and 5 herein. All measurements used for these statistical analyses follow

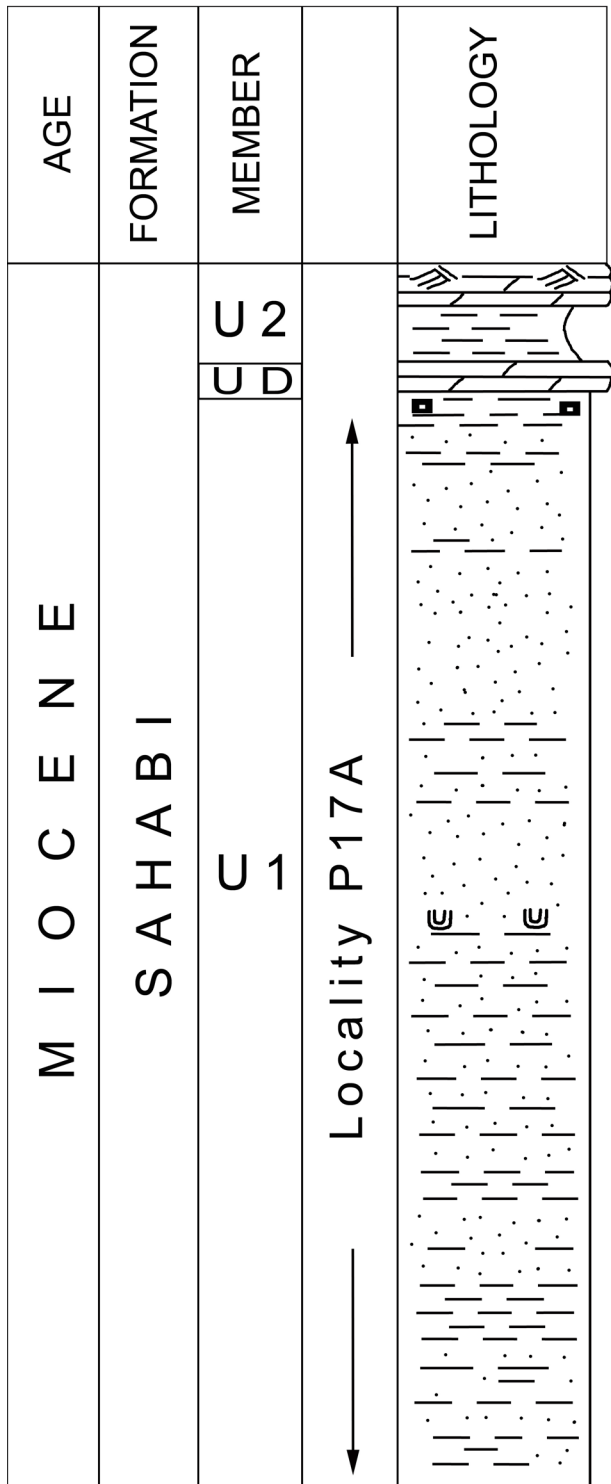


Fig. 2 - Stratigraphic section of paleontologic site P17A at As Sahabi. MCIII 82P17A (herein described) and other specimens are derived from Member U1.

standards published by Eisenmann et al. (1988) and Bernor et al. (1997). We undertook postcranial measurements with a digital caliper recording data to the nearest 0.1 that is the standard recognized for equid research. We utilize the Höwenegg skeletal sample log10 means for MCIII and MTIII (definitions below) to plot comparisons with selected and directly relevant species of Late Miocene-Pliocene hipparions following Bernor et al. (2003, 2005, 2008, 2010) and Bernor & Haile-Selassie (2009).

Institutional Abbreviations

AL: Afar Locality at Hadar, Ethiopia housed in the National Museum of Ethiopia, Addis Ababa; AMNH: American Museum of Natural History, New York; BMNH: London Museum of Natural History, London; BH: Bou Hanifia, Algeria, collections maintained by the Museum National d’Histoire Naturelle, Paris; KNM-LT: Lothagam Hill, Kenya Museums of Natural History, Ethiopia; MMTT: Maragheh, Iran collections maintained by Howard University, Washington D.C.; SAM: South African Museum of Natural History, Capetown.

Anatomical Abbreviations

MCIII: metacarpal of the third (central) digit; MTIII: metatarsal of the third (central) digit. M1-M38: refer to measurements as prescribed by Eisenmann et al. (1988) and Bernor et al. (1997). Specific measurement parameters are included in the figure legends.

Systematic Conventions

Hipparionine horses have an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following Old World genera: *Cormohipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion*, *Sivalhippus*, *Eurygnathohippus* (= senior synonym of “*Stylohipparion*”), *Proboscidipparion*, *Plesiohipparion*. Characterizations of these taxa have most recently been made by Bernor & Harris (2003), Bernor & Kaiser (2006), Woodburne (2007), Eisenmann & Geraads (2007), Bernor & White (2009), Bernor et al. (2010, 2011), and references cited therein.

GEOLOGICAL FRAMEWORK

The fossil specimens discussed here derive from eastern exposures of the Sahabi Formation from Member U1 (Fig. 2). This stratigraphic unit is poorly exposed in the western outcrops at As Sahabi, originally investigated by early Italian teams. Locality P17A is the point locality from which the new MCIII (82P17A) is recorded, and is contiguous to other equid-containing localities in the eastern exposures referenced below. These localities are precisely plotted in the locality and geological maps of Sahabi published in Boaz et al. (1987). Member U1 consists of sand bodies varying in thickness from 2 m to 25 m. They are locally fossiliferous, preserving vertebrate bones and teeth as light to dark brown fossils embedded in a remarkably loosely consolidated, clean, and white sand. Other sand units are coarser in grain size and more poorly sorted. Thin clay lenses are intercalated between sand units and occasionally contain clay balls. Locally

abundant silicified wood fossils co-occur with vertebrate remains. Member U1 was deposited under subaqueous conditions along the estuary of the large Eosahabi paleo-river (Griffin, 2011) and within associated tidal channels (de Heinzelin & El-Arnauti, 1987; Muftah et al., 2008b).

Biostratigraphic assessments of the age of the Sahabi Formation have varied from Early Pliocene to Late Miocene, confounded by the presence of endemic elements in the fauna, the amalgamation of taxa from different stratigraphic levels, and the sampling at Sahabi of a broad range of paleohabitats. A lack of radiometric geochronological control for the Sahabi Formation and an unclear temporal relationship of gypsiferous Formation P at Sahabi to the Messinian Event have also complicated assessments of the geochronological age of the Sahabi fauna. Renewed fieldwork at As Sahabi by the East Libya Neogene Research Project has clarified the geographical location and stratigraphic position of earlier collections from Sahabi, allowing a precise definition of a young faunal assemblage, from Sahabi Formation Member V, and older assemblages from Sahabi Formations Member U and T, respectively. These three formations also differ in their sedimentary depositional environments and the paleohabitats which they sample, with Formations U and V sampling primarily terrestrial habitats deposited under fresh water, and Formation T dominated by species, primarily sirenians (Bianucci et al., 2008), deposited under shallow marine conditions.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848

Suborder HIPPMORPHA Wood, 1937

Superfamily EQUOIDEA Hay, 1902

Family EQUIDAE Gray, 1821

Subfamily EQUINAE Steinmann & Doderlein, 1890

Genus *EURYGNATHOHIPPUS* Van Hoepen, 1930

Eurygnathohippus feibeli Bernor & Harris, 2003
(Figs 3a-b, d)

Holotype - KNM-LT-139, right forelimb including proximal radius, MCIII, 1PHIII and 2PHII.

Referred Specimens - In this manuscript we include the Lothagam type specimen of *Eurygnathohippus feibeli* and the following Sahabi specimens: 82P17A, MCIII (Fig. 3a); 25P26A, distal MCIII; 67P16A, MTIII (Fig. 3d); 6P108A, MTIII (proximal 3/4th); 1030A, fragmentary proximal epiphysis MTIII; 468P28A, MTIII (distal 2/3^{rds}); 10P30A, fragmentary proximal epiphysis MTIII; 11P85A, distal MTIII. Other As Sahabi postcranial previously referred to cf. *Hipparion* s.s. require further comparison to small Old World hipparionine clades.

Locality and Horizon - The Lothagam type specimen is from the Upper Nawata. Bernor & Harris (2003) reported several specimens from the Lower and Upper Nawata, Lothagam Hill, Kenya.

Emended diagnosis (modified from Bernor & Harris, 2003) - A small hipparionine equid with gracile limbs.

Metacarpal III is elongate and has a slender diaphysis. Anterior first phalanx III elongate with narrow midshaft width. Metatarsal III is likewise elongate and slender with medio-lateral narrow and cranio-caudally deep dimensions of the mid-shaft. Maxillary cheek teeth with thin parastyle and mesostyle; labiolingually moderately curved to straight, maximum crown height believed to be between 50 and 60 mm; mostly moderate complexity of the pre- and postfossettes; posterior wall of postfossette mostly separated from posterior wall of the tooth; pli caballin mostly single or poorly defined double; hypoglyph variable with wear; protocone tending to be elongate and compressed; protoconal spur usually absent but may appear as a small, vestigial structure; premolar and molar protocone placed lingually to hypocone. Mandibular cheek teeth having premolar metaconid/metastylid mostly rounded, molar metaconid/metastylid mostly rounded to elongate; metastylid spur absent; ectoflexid not separating metaconid/metastylid in premolars, variably separating metaconid/metastylid in molars; pli caballinid variably present/absent; when expressed, protostylid is most often presented as a posteriorly directed, open loop; ectostylids are variably expressed and when present are diminutive structures that do not rise high on the labial side of the tooth; premolar and molar linguaflexid shallow V-shape; preflexid and postflexid enamel margins generally with simple complexity; protoconid enamel band rounded.

Description - Our description here is confined to specimens of MCIII (Fig. 4) and MTIII (Fig. 5) of *Eurygnathohippus feibeli* from Sahabi, Libya and Lothagam, Kenya (Tab. 1). We compare these specimens to the Höwenegg (early Vallesian, MN9; Hegau District, Germany) log 10 mean and pertinent African and Eurasian hipparionine species. We employ log10 ratio diagram comparisons of these taxa to investigate alpha taxonomy, phylogeny and convergent evolution in derived, elongate distal limbed Old World hipparionine taxa.

Figure 4A compares Lothagam *Eurygnathohippus feibeli* KNM-LT139A to As Sahabi *Eurygnathohippus feibeli*, 82P17A to other African hipparions including *Eurygnathohippus hooijeri* from Langebaanweg, South Africa (ca. 5.0 Ma; Bernor & Kaiser, 2006), "*Cormohipparion*" *africanum* from Bou Hanifia, Algeria (ca. 10.5 Ma; Bernor & White, 2009) and *Eurygnathohippus hasumense* from Hadar, Ethiopia (3.2 Ma; Bernor et al., 2010). This log10 ratio exhibits virtual identity of the log10 ratio profiles of Sahabi and Lothagam *Eurygnathohippus feibeli*. The Lothagam specimen has slightly elevated size of the proximal articular width (M5) and distal articular dimensions (M13 and M14). In comparison to the primitive and older taxon "*Cormohipparion*" *africanum*, *Eurygnathohippus feibeli* MCIII has: greater length (M1), a narrower midshaft (M3) and proportionally similar cranio-caudal depth (M4), similar proximal articular width (M5; in Lothagam, not so much in Sahabi), virtually identical proximal articular depth (M6), similar distal articular dimensions (M10-M14) except for Lothagam *Eurygnathohippus feibeli* which has comparatively elevated dimensions for M13 and M14. Langebaanweg *Eurygnathohippus hooijeri* overall has very similar proportions to *Eurygnathohippus feibeli* and "*Cormohipparion*" *africanum*, but is larger



Fig. 3 - *Eurygnathohippus feibeli* and *Hippotherium primigenium* metapodials. a-c) MCIII in cranial view: *Eurygnathohippus feibeli* (a: 82P17A from Sahabi; b: cast of KNM-LT139A from Lothagam) compared to *Hippotherium primigenium* from Höwenegg (c). d-e) MTIII in cranial view: *Eurygnathohippus feibeli* 67P16A from Sahabi (d) compared to *Hippotherium primigenium* from Höwenegg (e). Scale bar 10 cm.

with elevated dimensions of mid-shaft cranio-caudal depth (M4) and distal sagittal keel (M12). Together, *Eurygnathohippus feibeli* and “*Cormohipparion*” *africanum* exhibit proportionally narrower midshafts (M3) with contrasting deep midshafts (M4) compared to *Hippotherium primigenium*. This contrast in mid-shaft proportions already evident in first occurring Old World *Cormohipparion sinapensis* was termed the “Esme Acakoy Effect” believed to be due to *Cormohipparion*’s greater adaptation to open country running than *Hippotherium primigenium* (Bernor et al., 2003). Hadar *Eurygnathohippus hasumense* contrasts sharply from these other hipparions in its overall larger more robust build. It shows a marked increase in all dimensions and of particular significance is the very elevated dimension of the distal mid-sagittal keel (M12).

Figure 4B compares the Bou Hanifia, Lothagam and Sahabi MCIII’s discussed above to an MCIII from the type collection of *Cremohipparion antelopinum*. In all regards *Cremohipparion antelopinum* compares closely to these taxa and contrasts similarly to *Eurygnathohippus hasumense*. This similarity reflects a likely phylogenetic

signal and the close relatedness of Old World *Cormohipparion* and primitive members of the slender-limbed *Cremohipparion* and *Eurygnathohippus* clades.

Figure 5A plots Langebaanweg, Bou Hanifia, Hadar and Sahabi MTIII’s of the same taxa cited above. 67P16A is distinct from “*Cormohipparion*” *africanum* and *Eurygnathohippus hooijeri* in its narrow medio-lateral midshaft dimension (M3) that contrasts strikingly from its very deep cranio-caudal midshaft dimension (M4). “*Cormohipparion*” *africanum* and *Eurygnathohippus hooijeri* are very similar in their log₁₀ ratio profiles with the latter consistently being larger in all dimensions from the former. All three of these taxa contrast sharply in their elongate-slender (M1, M3) and deep midshaft (M4) dimensions with *Hippotherium primigenium*. Hadar *Eurygnathohippus hasumense* has, as expected, dimensions similar to the MCIII and contrasts strikingly in its large and robust size from the other hipparions under consideration herein.

Figure 5B contrasts Sahabi *Eurygnathohippus feibeli* MTIII with *Cremohipparion antelopinum* from the type BMNH collection and the AMNH collection derived from

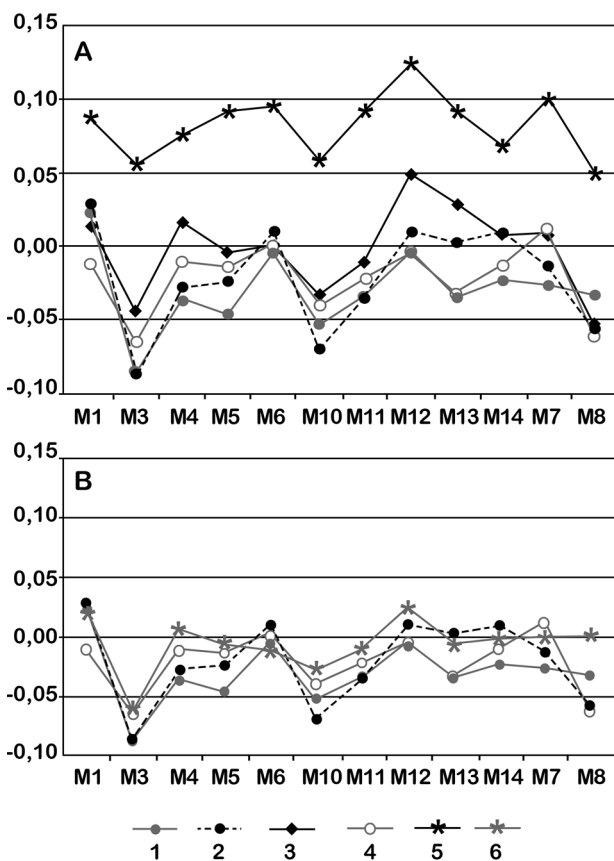


Fig. 4 - Metacarpus III log₁₀ ratio diagrams (Höwenegg sample as standard). A) compares *Eurygnathohippus feibeli* to African Hipparionines; B) compares *Eurygnathohippus feibeli*, "*Cormohipparion*" *africanum* and *Cremohipparion antelopinum*. 1) *Eurygnathohippus feibeli* from Sahabi, Libya (82P17A); 2) *Eurygnathohippus feibeli* from Lothagam, Kenya (KNM-LT139A); 3) *Eurygnathohippus hooijeri* from Langebaanweg, South Africa (mean); 4) "*Cormohipparion*" *africanum* from Bou Hanifia, Algeria (mean); 5) *Eurygnathohippus hasumense* from Hadar, Ethiopia (AL-155-6BB); 6) *Cremohipparion antelopinum* from the Dhok Pathan (BMNH2650).

the Dhok Pathan (ca. 8 Ma; MacFadden & Woodburne, 1982; Bernor & Hussain, 1985). Overall, these proportions are similar, with AMNH19669 being most similar to Sahabi *Eurygnathohippus feibeli*. Sahabi *Eurygnathohippus feibeli* would appear to be distinct from the other specimens in its reduced supraarticular (M10) dimension. Also, the Paratype *Cremohipparion antelopinum* BMNH specimens, from an unknown provenience in the Indian Subcontinent, are very similar to one another in their greater maximum length (M1) dimensions but overall close log₁₀ profile to the AMNH and Sahabi specimens.

Figure 5C compares Sahabi *Eurygnathohippus feibeli* to Upper Maragheh *Hipparion campbelli* MTIII. All three of these postcrania are similar in their elongate (M1), very slender (M3) and deep (M4) midshafts. *Eurygnathohippus feibeli* contrasts with *Hipparion campbelli* in its proportionally deeper midshaft and greater distal articular dimensions (M11-M14) that are similar to the Höwenegg hipparion sample. Also noteworthy is that the *Hipparion campbelli* specimens have very similar or smaller proximal articular widths (M5) but proportionally

elevated proximal articular depths (M6) compared to *Eurygnathohippus feibeli*. *Hipparion campbelli* would appear to have evolved along a similar morphologic trajectory of hyper-gracility, was slightly more lightly built than *Eurygnathohippus feibeli*, and evolved very deep proximal articular surface (M6).

DISCUSSION

Our analysis and description of Sahabi MCIII's and MTIII's provide evidence that *Eurygnathohippus feibeli* had a geographic range that extended in the Late Miocene from East Africa to North Africa. The apparent extension of this small clade of *Eurygnathohippus* occurred at a time when open country woodlands expanded across Eurasia and Africa in the medial and Late Miocene (Bernor, 1984; Bernor et al., 1996; Eronen et al., 2009). We have also demonstrated here that hipparionine distal limb lengthening can be rigorously characterized in African species of the "*Cormohipparion*" *africanum* - *Eurygnathohippus* evolutionary succession, but at the same time is highly convergent with other Eurasian hipparionine clades, *Hipparion* s.s. and *Cremohipparion* spp.

We can determine that *Hipparion* s.s., *Cremohipparion* spp. and *Eurygnathohippus* sp. are different clades from a number of morphological characters of other bones and morphological complexes. *Hipparion* s.s. evolves a facial morphology that primitively has a preorbital fossa with a long preorbital bar (*Hipparion prostylum*) to a face lacking any preorbital fossa (*Hipparion hippidioidus*, *Hipparion dietrichi* and *Hipparion campbelli*). *Cremohipparion* spp. is a clade of hipparionines ranging from China to Europe, North Africa and the Siwaliks in the Late Miocene (Bernor et al., 1996). *Cremohipparion* spp. vary from having large preorbital fossae placed close to the orbit (short preorbital bar; *Cremohipparion moldavicum*), to taxa with 3 distinct fossae (preorbital, caninus and buccinator; *Cremohipparion mediterraneum*, *Cremohipparion proboscideum*, *Cremohipparion forstenae* and *Cremohipparion licenti*) very strongly developed, to taxa that express 3 fossae, but reduce their depth and peripheral outline (*Cremohipparion forstenae* and *Cremohipparion antelopinum*; Bernor et al., 1996). As such, the *Cremohipparion* clade is distinct from *Hipparion* s.s. and *Eurygnathohippus*. Late Miocene *Eurygnathohippus feibeli* is not known from skull material. However, Bernor & Harris (2003) and Bernor et al. (2010; Fig. 35.10) have reported that a skull of *Eurygnathohippus feibeli* has been discovered at the Early Pliocene of Ekora, Kenya. The Ekora skull is a juvenile of a relatively small horse with a large preorbital fossa set far from the orbit (long preorbital bar). The primitive facial morphology combined with relatively complex maxillary teeth and short maximum crown height (< 60 mm) of an unerupted M10 led Hooijer & Maglio (1974) to refer this specimen to "*Hipparion*" *primigenium*. In fact, its size and morphology have suggested a better referral to *Eurygnathohippus feibeli* by Bernor & Harris (2003). Also, *Eurygnathohippus* variably expresses ectostylids on worn permanent cheek teeth, a character not known for *Cremohipparion* or *Hipparion* s.s. Ectostylids evolve in

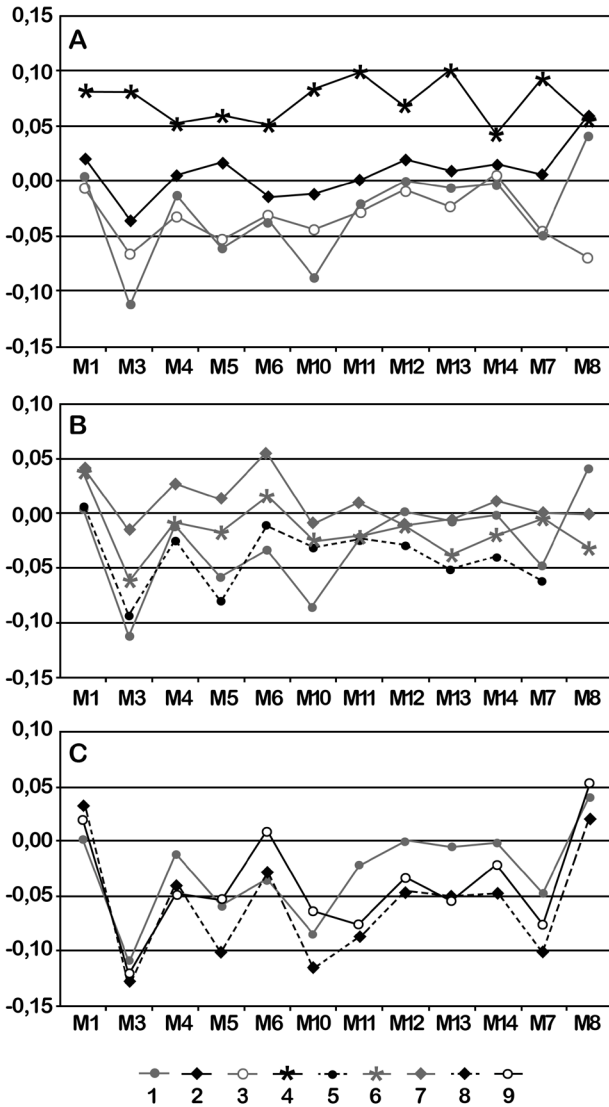


Fig. 5 - Metatarsus III log10 ratio diagrams (Höweneegg sample as standard). *Eurygnathohippus feibeli* from Sahabi is compared to: A) key African Hipparionine Horses; B) *Cremohipparion antelopinum* from the Dhok Pathan; C) *Hipparion campbelli* from Upper Maragheh. 1) *Eurygnathohippus feibeli* from Sahabi, Libya (67P16A); 2) *Eurygnathohippus hooijeri* (Langebaanweg, sample mean); 3) “*Cormohipparion*” *africanum* (Bou Hanifia, sample mean); 4) *Eurygnathohippus hasumense* (Hadar, AL1556AZ); 5) *Cremohipparion antelopinum* (Dhok Pathan, AMNH19669); 6) *Cremohipparion antelopinum* (Dhok Pathan, BMNHM16681); 7) *Cremohipparion antelopinum* (Dhok Pathan, BMNHM17865); 8) *Hipparion campbelli* (Upper Maragheh, MMTT 13/1153); 9) *Hipparion campbelli* (Upper Maragheh, MMTT 13/1622).

Eurygnathohippus spp. to become large in their mesio-distal and labio-lingual dimensions and rise high on the labial side of the crown. Late Pliocene-Pleistocene members of the clade have crown heights approaching 90 mm. In their earliest stage-of-evolution, Late Miocene *Eurygnathohippus* variably express small ectostylids that do not rise high on the labial side of the crown (Bernor & Harris, 2003; Bernor & Haile-Selassie, 2009).

Our investigation of *Eurygnathohippus feibeli* postcrania together with previous study of Kenyan (Bernor & Harris, 2003), Ethiopian (Bernor et al., 2008, 2009) and North African (Bernor & White, 2009) and South African (Bernor & Kaiser, 2006) *Eurygnathohippus* have suggested that it is a distinct clade of African hipparions. Early Late Miocene North African “*Cormohipparion*” *africanum* from Bou Hanifia, Algeria would appear to be closely related to Chorora, Ethiopia (ca. 10.5 Ma., Bernor et al., 2004) and Samburu Hills, Kenya (ca. 9.5 Ma) “*Cormohipparion*” aff. *africanum*. Likewise, Langebaanweg *Eurygnathohippus hooijeri* (Bernor & Kaiser, 2006) would appear to be closely related, particularly in the postcrania, to “*Cormohipparion*” *africanum*, exhibiting a slight increase in overall size but a great increase in cheek tooth height (80 mm maximum). *Eurygnathohippus hooijeri* retained a distinct preorbital fossa high on the face with essentially primitive proportions of the distal limb elements. *Eurygnathohippus feibeli* is very close in its distal limb proportions to *Eurygnathohippus hooijeri* but has slenderly built limbs and proportionally greater length. Bernor et al. (2005) suggested that *Eurygnathohippus feibeli*-*Eurygnathohippus hasumense* was an evolutionary clade that evolved between 6 and 3 Ma. This clade initially diverged as *Eurygnathohippus feibeli* with reduced size and slender distal limb proportions, and then became progressively larger with lengthening of the MCIIIs and MTIIIs, but also increasing robustness of these elements and the 1PHIII’s. This clades’ lengthening of the metapodial III’s and 1PHIII’s with narrow medio-lateral and deep cranio-caudal midshafts mark an increase in open country running (Bernor et al., 2003, 2005). The progressive increase in crown height reflects an increase dependence on grazing C4 grass (Bernor et al., 2008; White et al., 2009).

The hipparionine specimens from Sahabi described here add a significant dimension to our understanding of the “open country” component of this diverse Late Miocene vertebrate fauna, which derives overall from paleobiocenoses ranging from terrestrial to riverine, to estuarine to marine. The fossil mammal fauna as a whole

Specimen ID	Taxon	Bone	side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
KNM-LT139A	<i>Eurygnathohippus feibeli</i> (type)	MCIII	R	230.8	221.8	25.8	22.4	38.6	25.7	34.6	11.0	5.8	34.3	34.0	28.8	24.8	26.8
ISP82P17A	<i>Eurygnathohippus feibeli</i>	MCIII	R	224.8	217.9	25.8	19.2	35.9	25.8	33.1	33.1	10.4	34.8	34.1	27.7	22.6	24.5
ISP67P16A	<i>Eurygnathohippus feibeli</i>	MTIII	L	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	<i>Eurygnathohippus cf. feibeli</i>	MTIII	-			25.3	23.8	36.6	30.8	34.2	11.1	7.0					
ISP468P28A	<i>Eurygnathohippus cf. feibeli</i>	MTIII	R			24.4	24.1						31.5	32.4	28.4	21.6	25.2

Tab. 1 - Measurement of Lothagam (type specimen) and Sahabi *Eurygnathohippus feibeli* metapodials. Codes M1 to M14 indicate standard measurements (Eisenmann et al., 1988; Bernor et al., 1997). See text for institutional abbreviations.

has been variously characterized as an anthracothere-dominated endemic fauna, a relictual fauna largely bypassed by Late Miocene turnover-pulse, and a “crossroads fauna” between Africa and Asia as well as between regions of Africa (see Boaz, 2008; Boaz et al., 2008a; Bernor & Rook, 2008; Marra et al., 2011). From our analysis the record of *Eurygnathohippus feibeli* at As Sahabi offers strong support for the lattermost characterization of the open country terrestrial component of this important fauna.

CONCLUSIONS

The Sahabi mammal fauna has previously been demonstrated to have close biogeographic relationship with the East African localities of the Middle Awash, Ethiopia and Lothagam, Kenya (Bernor & Rook, 2008; Bernor et al., 2009; Haile-Selassie et al., 2009). Bernor et al. (2008) argued that there were three lineages of hipparion represented at Sahabi, *Cremohipparion*, *Sivalhippus* and cf. *Hipparion* s.s. The MCIII's and MTIII's of Sahabi cf. *Hipparion* s.s. are now confidently referred to *Eurygnathohippus feibeli*. The other postcranial elements of As Sahabi cf. *Hipparion* s.s. could prove to be referable to *Eurygnathohippus feibeli*, but because of size and proportion convergence cannot out of hand be reassigned from cf. *Hipparion* s.s. It is sufficient now to demonstrate a lineage-based biogeographic connection between the Libyan, Ethiopian and Kenyan latest Miocene. The Sahabi taxon *Sivalhippus* sp. may likewise prove to be closely related to the Lothagam equid *Sivalhippus turkanense*.

ACKNOWLEDGEMENTS

The East Libya Neogene Research Project is an international collaboration governed by signed agreement between Benghazi University and the International Institute for Human Evolution (N.T. Boaz, International Director, and Ahmed Muftah and Moftah Shawaihi, Libyan Co-Directors). We thank the National Science Foundation (grant number EAR-125009) for supporting the hipparion research (awards to RLB) and the Revealing Hominid Origins Initiative (NSF grant BCS-0321893) to F.C. Howell and T.D. White for supporting Bernor, Boaz and Rook on their respective research projects and, specifically, for research leading to this publication.

REFERENCES

- Bernor R.L. (1982). A Preliminary Assessment of the Mammalian Biochronology and Zoogeographic Relationships of Sahabi, Libya. *Garyounis Scientific Bulletin*, Special Issue, 4: 133-142.
- Bernor R.L. (1984). A zoogeographic theater and biochronologic play: the time/biofacies phenomena of Eurasian and African Miocene mammal provinces. *Paleobiologie Continentale*, 14: 121-142.
- Bernor R.L., Armour-Chelu M., Gilbert H., Kaiser T. & Schulz E. (2010). Equidae. In Werdelin L. & Sanders B. (eds), *Cenozoic Mammals of Africa*. University of California Press, Berkeley: 685-721.
- Bernor R.L. & Haile Selassie Y. (2009). Equidae. In Haile-Selassie Y. & Woldegabriel G. (eds), *Ardipithecus kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley: 397-428.
- Bernor R.L., Haile Selassie Y. & Rook L. (2009). Paleobiogeography. In Haile-Selassie Y. & Woldegabriel G. (eds), *Ardipithecus kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley: 549-563.
- Bernor R.L. & Harris J. (2003). Systematics and Evolutionary Biology of the Late Miocene and Early Pliocene Hipparionine Horses from Lothagam, Kenya. In Leakey M. & Harris J. (eds), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York: 387-438.
- Bernor R.L., Heissig K. & Tobien H. (1987). Early Pliocene Perissodactyla from Sahabi, Libya. In Boaz N.T., El-Arnauti A., Gaziry A.W., de Heinzelin J. & Boaz D.D. (eds), *Neogene Paleontology and Geology of Sahabi*, Alan R. Liss, New York: 233-254.
- 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: 32-87.
- Bernor R.L. & Kaiser T.M. (2006). Systematics and Paleoecology of the Earliest Pliocene Equid, *Eurygnathohippus hooijeri* n. sp. from Langebaanweg, South Africa. *Mitteilungen aus dem Hamburischen Zoologischen Museum und Institut*, 103: 147-183.
- Bernor R.L., Kaiser T.M. & Nelson S.V. (2004). The oldest Ethiopian hipparion (Equinae, Perissodactyla) from Chorora: systematics, paleodiet and paleoclimate. *Courier Forschungsinstitut Senckenberg*, 246: 213-226.
- Bernor R.L., Kaiser T.M., Nelson S.V. & Rook L. (2011). Systematics and Paleobiology of *Hippotherium malpassii* n. sp. (Equidae, Mammalia) from the latest Miocene of Baccinello V3 (Tuscany, Italy). *Bollettino della Società Paleontologica Italiana*, 50: 175-208.
- Bernor R.L., Kaiser T.M. & Wolf D. (2008). Revisiting Sahabi Equid Species Diversity, Biogeographic Patterns and Diet Preferences. *Garyounis Scientific Bulletin*, Special Issue, 5: 159-167.
- 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. & Mittman H.W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 307-338.
- Bernor R.L. & Rook L. (2008). A current view of Sahabi large mammal biogeographic relationships. *Garyounis Scientific Bulletin*, Special Issue, 5: 283-290.
- Bernor R.L. & Scott R.S. (2003). New Interpretations of the Systematics, Biogeography and Paleoecology of the Sahabi Hipparions (latest Miocene), Libya. *Geodiversitas*, 25: 297-319.
- 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., Scott R.S. & Haile-Selassie Y. (2005). A Contribution to the Evolutionary History of Ethiopian Hipparionine Horses: Morphometric Evidence from the Postcranial Skeleton. *Geodiversitas*, 27: 133-158.
- 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. & White T.D. (2009). Systematics and Biogeography of “*Cormohipparion*” *africanum*, Early Vallesian (MN 9, ca. 10.5 Ma) of Bou Hanifia, Algeria. In Barry Albright L. III (ed), *Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne*. *Bulletin, Museum of Northern Arizona*, 65: 635-658.
- Bianucci G., Carone G., Domning D.P., Landini W., Rook L. & Sorbi S. (2008). Peri-Messinian dwarfing in Mediterranean *Metaxytherium* (Mammalia: Sirenia): evidence of habitat

- degradation related to Messinian Salinity Crisis. *Garyounis Scientific Bulletin*, Special Issue, 5: 145-157.
- Boaz N.T. (2008). A view of the south: Eo-Sahabi palaeoenvironments compared and implications for hominid origins in Neogene North Africa. *Garyounis Scientific Bulletin*, Special Issue, 5: 291-308.
- Boaz N.T., El-Arnauti A., Agustí J., Bernor R.L., Pavlakis P. & Rook L. (2008a). Temporal, lithostratigraphic, and biochronologic setting of the Sahabi Formation, North Central Libya. In Salem M.J., El-Arnauti A. & El Sogher Saleh A. (eds), *The Geology of East Libya*, 3: 233-246.
- Boaz N.T., El-Arnauti A., Gaziry A.W., de Heinzelin J. & Dechant Boaz D. (1987). Neogene Paleontology and Geology of Sahabi. Alan R. Liss, New York: pp. 1-401.
- Boaz N.T., El-Arnauti A. & Pavlakis P. (2008b). A brief history of As Sahabi Research and Collections. *Garyounis Scientific Bulletin*, Special Issue, 5: 1-11.
- Boaz N.T., Gaziry A.W. & El-Arnauti A. (1979). New fossil finds from the Libyan Upper Neogene site of Sahabi. *Nature*, 280: 137-140.
- Cooke H.B.S. (1987). Fossil Suidae from Sahabi, Libya. In Boaz N.T., El-Arnauti A., Gaziry A.W., de Heinzelin J. & Boaz D.D. (eds), *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss, New York: 255-266.
- de Heinzelin J. & El-Arnauti A. (1982). Stratigraphy and geological history of the Sahabi and related formations. *Garyounis Scientific Bulletin*, Special Issue, 4: 5-12.
- de Heinzelin J. & El-Arnauti A. (1987). The Sahabi Formation and related deposits. In Boaz N.T., El-Arnauti A., Gaziry A.W., de Heinzelin J. & Boaz D.D. (eds), *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss, New York: 1-21.
- Delfino M. (2008a). Late Neogene crocodylian faunas from Libya and the Mediterranean area. In Salem M.J., El-Arnauti A. & El Sogher Saleh A. (eds), *The Geology of East Libya*, 3: 291-296.
- Delfino M. (2008b). New remains of *Crocodylus checcchiai* Maccagno, 1947 (Crocodylia, Crocodylidae) from the Late Miocene of As Sahabi, Libya. *Garyounis Scientific Bulletin*, Special Issue, 5: 111-118.
- Delfino M. & Rook L. (2008). African crocodylians in the Late Neogene of Europe: a revision of *Crocodylus bambolii* Ristori, 1890. *Journal of Paleontology*, 82 (2): 336-343.
- Desio A. (1931). Osservazioni geologiche e geografiche compiute durante un viaggio nella Sirtica. *Bollettino della Reale Società Geografica Italiana*, ser. 6, 8: 275-299.
- Eisenmann V., Alberdi M.T., De Giuli C. & Staesche U. (1988). Volume I: Methodology. In Woodburne M. & Sondaar P. (eds), *Studying Fossil Horses*. Collected papers after the "New York International Hipparion Conference, 1981". Brill, Leiden: 1-71.
- Eisenmann V. & Geraads D. (2007). *Hipparion pomeli* sp. nov. from the late Pliocene of Ahl al Oughlam, Morocco, and a revision of the relationships of Pliocene and Pleistocene African hipparions. *Palaeontologia Africana*, 42: 51-98.
- Eronen J.T., Mirzaie M., Karne A., Micheels A., Bernor R.L. & Fortelius M. (2009). Distribution History and Climatic Controls of the Late Miocene Pliocene Chronofauna. *Proceedings of the National Academy of Sciences, USA*, 106 (29): 11867-11871.
- Esu D. & Kotsakis T. (1980). *Ichitherium arkesilai* sp. n. (Hyaenidae, Carnivora) del Terziario superiore di Sahabi (Cirenaica, Libia). *Rivista Italiana di Paleontologia e Stratigrafia*, 86: 241-250.
- Feibel C.S. (2003). Stratigraphy and depositional history of the Lothagam sequence. In Leakey M.G. & Harris J.M. (eds), *Lothagam: The dawn of humanity in eastern Africa*. Columbia University Press, New York: 17-30.
- Gray J.E. (1821). On the natural arrangement of vertebrate animals. *London Medical Repository*, 15 (1): 296-310.
- Griffin D.L. (2011). The late Neogene Sahabi rivers of the Sahara and the hamadas of the eastern Libya-Chad border area. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 309: 176-185.
- Haile Selassie Y., Bernor R.L., Rook L. & Vrba L. (2009). Biochronology. In Haile-Selassie Y. & Woldegabriel G. (eds), *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia*. University of California Press, Berkeley: 565-583.
- Harris J.M. & Leakey M.G. (2003). Lothagam Suidae. In Leakey M.G. & Harris J.M. (eds), *Lothagam: The dawn of humanity in eastern Africa*. Columbia University Press, New York: 485-521.
- Hay O.P. (1902). Bibliography and catalogue of the fossil Vertebrata of North America. *U.S. Geological Survey Bulletin*, 179: 1-868.
- Hill A. (1999). Late Miocene sub-Saharan African vertebrates, and their relation to the Baynunah fauna, Emirate of Abu Dhabi, United Arab Emirates. In Whybrow P.J. & Hill A. (eds), *Fossil Vertebrates of Arabia*. Yale University Press, New Haven: 420-429.
- Hooijer D.A. & Maglio V.J. (1974). Hipparions from the Late Miocene and Pliocene of northwestern Kenya. *Zoologische Verhandelingen*, 134: 1-34.
- Leakey M.G. & Harris J.M. (2003). Lothagam: The dawn of humanity in eastern Africa. Columbia University Press, New York: pp. 1-678.
- MacFadden B.J. & Woodburne M.O. (1982). Systematics of the Neogene Siwalik hipparions (Mammalia, Equidae) based on cranial and dental morphology. *Journal of Vertebrate Paleontology*, 2: 185-218.
- Marra A.C., Solounias N., Carone G. & Rook L. (2011). Palaeogeographic significance of the giraffid remains (Mammalia, Arctiodactyla) from Cessaniti (Late Miocene, Southern Italy). *Géobios*, 44: 189-197.
- McDougal I. & Feibel C.S. (2003). Numerical age control for the Miocene-Pliocene succession at Lothagam, a Hominoid-bearing sequence in the northern Kenya rift. In Leakey M.G. & Harris J.M. (eds), *Lothagam: The dawn of humanity in eastern Africa*. Columbia University Press, New York: 43-64.
- Muftah A.M., El-Mehaghag A.A. & Starkie S. (2008a). Biostratigraphical notes of the As Sahabi stratigraphic boreholes 1 and 2, Sirte Basin, Libya. *Garyounis Scientific Bulletin*, Special Issue, 5: 47-57.
- Muftah A.M., Salloum F.M., El-Shawaihi M.H. & Al-Faitouri M.S. (2008b). A contribution to the stratigraphy of formations of the As Sahabi area, Sirt Basin, Libya. *Garyounis Scientific Bulletin*, Special Issue, 5: 33-45.
- Owen R. (1848). Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds discovered in the Eocene deposits on the N. W. coast of the Isle of Wight. *Quarterly Journal of the Geological Society of London*, 4: 103-141.
- Petrocchi C. (1934). I ritrovamenti faunistici di as-Sahabi. *Rivista delle Colonie Italiane*, 7: 733-742.
- Petrocchi C. (1941). Il giacimento fossilifero di Sahabi. *Bollettino della Società Geologica Italiana*, 40: 107-114.
- Petrocchi C. (1943). Il giacimento fossilifero di Sahabi. Collezione scientifica e documentaria del Ministero dell'Africa Italiana, Verbania: 1-162.
- Petrocchi C. (1951). Notizie generali sul giacimento fossilifero di Sahabi. Storia degli scavi. *Rendiconti della Accademia Nazionale dei Quaranta*, 3: 8-31.
- Petrocchi C. (1954). I Proboscidi di Sahabi. *Rendiconti della Accademia Nazionale dei Quaranta*, 4/5: 1-76.
- Petrocchi C. (1956). I *Leptobos* di Sahabi. *Bollettino della Società Geologica Italiana*, 75: 1-36.
- Rook L. (2008). The discovery of Sahabi site: Ardito Desio or Carlo Petrocchi? *Garyounis Scientific Bulletin*, Special Issue, 5: 13-21.
- Rook L. & Martínez-Navarro B. (2004). *Viverra howelli* n. sp., a new viverrid (Carnivora, Mammalia) from the Baccinello-Cinigiano basin (latest Miocene, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 110: 719-723.
- Sardella R. & Werdelin L. (2007). *Amphimachairodus* (Felidae, Mammalia) from Sahabi (latest Miocene-earliest Pliocene, Libya), with a review of African Miocene Machairodontinae. *Rivista Italiana di Paleontologia e Stratigrafia*, 113: 67-77.
- Stefanini G. (1934). Sulla scoperta di resti fossili di vertebrati nella Sirtica orientale. *Bollettino Geografico del Governo della Tripolitana e della Cirenaica*, 5/6: 152-157.

- Shawaidhi M. & Al-Trabelci T. (2008). The Wadi Al-Farigh Member of the Sahabi Formation. *Garyounis Scientific Bulletin*, Special Issue, 5: 71-83.
- Steinmann G. & Döderlein L. (1890). Elemente der Paläontologie. Wilhelm Engelmann, Leipzig: pp. 1-848.
- Van Hoepen E.C.N. (1930). Fossiele Pferde van Cornelia. *Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein*, 2: 13-24.
- White T.D., Ambrose S.H., Suwa G., Su D.F., DeGusta D., Bernor R.L., Boisserie J.-R., Brunet M., Delson E., Frost S., Garcia N., Giaourtsakis I.X., Haile-Selassie Y., Howell F. C., Lehmann T., Likius A., Pehlevan C., Saegusa H., Semprebon G., Teaford M. & Vrba E. (2009). Macrovertebrate Paleontology and the Pliocene Habitat of *Ardipithecus ramidus*. *Science*, 326: 87-93.
- Wood H.E. (1937). Perissodactyl suborders. *Journal of Mammalogy*, 18(1): 1-106.
- Woodburne M.O. (2007). Phyletic diversification of the *Cormohipparion occidentale* Complex (Mammalia; Perissodactyla, Equidae), Late Miocene, North America, and the origin of the Old World *Hippotherium* Datum. *Bulletin of the American Museum of Natural History*, 306: 1-138.

Manuscript received 6 February 2012
Revised manuscript accepted 29 April 2012
Published online 27 June 2012
Editor Raffaele Sardella