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SAHABI *EURYGNATHOHIPPUS FEIBELI:* ITS SYSTEMATIC, STRATIGRAPHIC, CHRONOLOGIC AND BIOGEOGRAPHIC CONTEXTS

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Abstract. Sahabi, Libya is an important latest Miocene locality having yielded an extensive paleobotanical and vertebrate fauna. Amongst the fossil mammals there occurs an extensive, species diverse record of hipparionine horses. We develop here a complete record of Sahabi *Eurygnathohippus feibeli* now based on dental and postcranial material, in comparison to other equids from late Miocene equids from Europe, West Asia and Africa. We find that *E. feibeli* is the earliest recognized species of the predominantly African clade *Eurygnathohippus*, that its biogeographic range was Kenya, Ethiopia, Libya and Morocco, it ranged between 7.0 and 5.7 Ma and that it had deep-time evolutionary roots extending back to first occurring Old World hipparions. We further find that *Eurygnathohippus* was restricted to Africa until a more advanced member of the clade extended its range into the Indian Subcontinent during the late Pliocene, ca. 3.6-2.6 Ma.

Introduction

The genus *Eurygnathohippus* has been reported from the late Miocene – Pleistocene of Africa (Bernor & Harris 2003; Bernor & Kaiser 2006; Bernor et al. 2005, 2010; Cirilli et al. 2020). The genus' appearance in Eurasia is limited to the Indian late Pliocene (Jukar et al. 2019). The oldest recognized member of this genus - *Eurygnathohippus feibeli* - has been reported from Lothagam, Kenya (Bernor & Harris 2003), the late Miocene of the Middle Awash, Ethiopia (Bernor & Hailie Selassie 2009), and Sahabi, Libya (Bernor & Scott 2003; Bernor et al. 2008, 2012). Previous contributions to our understanding of *Eurygnathohippus feibeli* has largely been restricted to its derived postcranial skeleton, with the exception of the partial skull of *E. feibeli* from Ekora, Kenya (Bernor & Harris 2003). This contribution integrates additional postcrania and dental morphology into our recognition of *Eurygnathohippus feibeli* and engages a more comprehensive comparative analysis of postcrania with Western Eurasian and Africa localities yielding the genera *Cormohipparion, Hipparion* s.s., *Cremohipparion, Sivalhippus* and *Eurygnathohippus*. We recognize the basal evolutionary status of Central European *Hippotherium primigenium* (Bernor et al. 1997, 2017), Turk-

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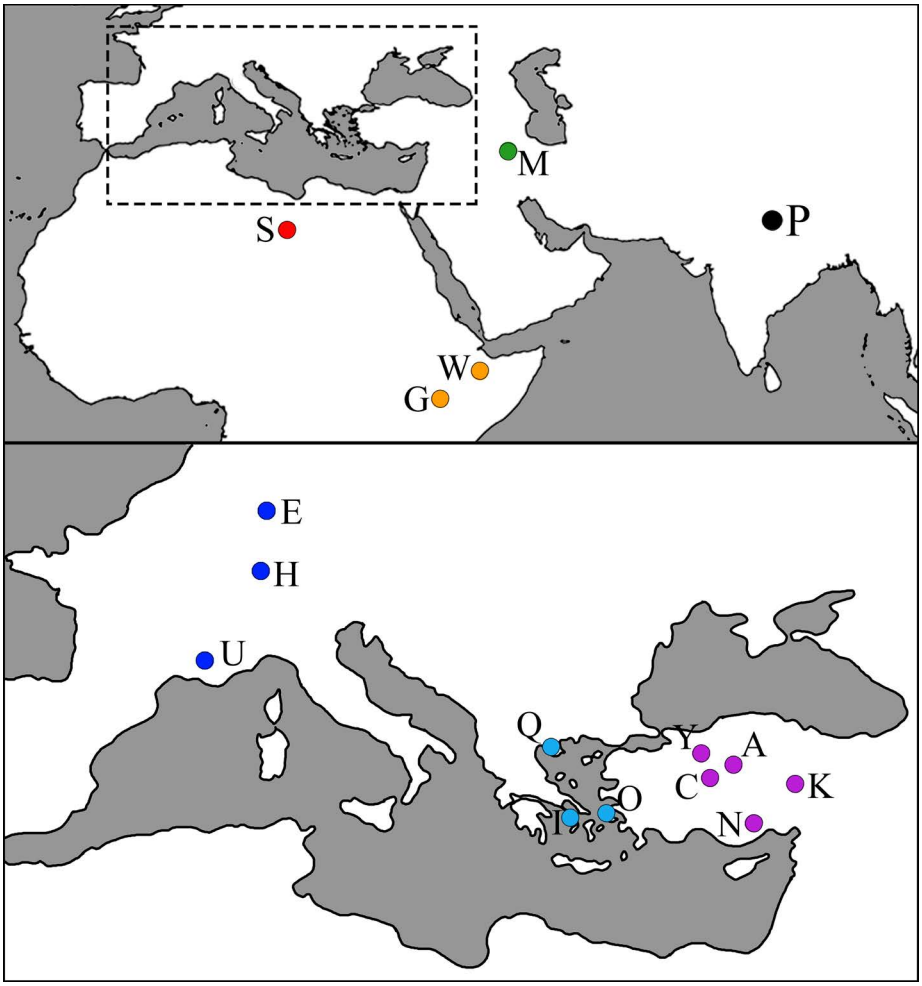

Fig. 1 - Geographical Locator Map: A) Akkasdagi; C) Calta; E) Eppelsheim; G) Lothagam; H) Hoewenegg; I) Pikermi; K) Kurutlu; U) Mt. Luberon; M) Maragheh; N) Sinap & Esme Acakoy; O) Samos; P) Potwar Plateau; Q) Saloniki; S) Sahabi; W) Awash; Y) Corak Yerler.

Locality	Country	Age Ma	Symbol
Akkasdagi	Turkey	7.1	A
Calta	Turkey	4.0	C
Eppelsheim	Germany	10.0	E
Lothagam	Kenya	7.0-5.0	G
Hoewenegg	Germany	10.3	H
Pikermi	Greece	8.0	I
Kurutlu	Turkey	late Miocene	K
Mt. Luberon	France	8.0-7.0	U
Maragheh	Iran	8.9-7.4	M
Sinap & Esme A.	Turkey	10.8-9.0	N
Samos	Greece	8.3-7.0	O
Potwar Plateau	Pakistan	10.8-7.0	P
Saloniki	Greece	8.0-7.0	Q
Sahabi	Libya	7.0-6.7	S
Awash	Ethiopia	6.0-5.6	W
Corak Yerler	Turkey	late Miocene	Y

Tab. 1 - Localities and ages analysed in Bivariate Plots.

ish *Cormohipparion sinapensis* (Bernor et al. 2003) and Algerian *"Cormohipparion" africanum* (Bernor & White 2009) in our statistical and morphological analyses and uncover morphological pathways in dental and postcranial anatomy of *Eurygnathohippus* and other hipparionine lineages. Figure 1 is a geographical locator map of the localities from which our sample is drawn. These include: the Potwar Plateau (P), Pakistan; Hoewenegg (H) and Eppelsheim (E), Germany; Mt. Luberon (U), France; Pikermi (I), Saloniki (Q) and Samos (O), Greece; Maragheh (M), Iran; Sinap and Esme Acakoy (N), Kurutlu (K), Corak Yerler (Y), Akkasdagi (A) and Calta (C), Turkey; Sahabi (S), Libya; Middle Awash (W), Ethiopia; Lothagam (G), Kenya. The symbols corresponding to localities (in parentheses) are included in Table 1.

Systematic Conventions

We follow characterizations and definitions for hipparionine horses recently provided in Bernor et al. (1996, 1997, 2010, 2016). Hipparion monographs by Gromova (1952) and Gabunia (1959) are cited after the French and English translations. The taxon Hipparion has been applied in a variety of ways by

different authors. We utilize the following definitions in this work:

Hipparionini - a tribe of Equidae with an isolated protocone on maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Cormohipparion*, *Neohipparion*, *Nannippus*, *Pseudhipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion*, *Sivalhippus*, *Baryhipparion, Shanxihippus, Eurygnathohippus* (= a senior synonym of *Stylohipparion*), *Proboscidipparion* and *Plesiohipparion*. These lineages have recently been reviewed by Qiu et al. (1988), Bernor & White (2009), Bernor et al. (2010, 2013, 2014), Armour-Chelu & Bernor (2011), Wolf et al. (2013), Bernor & Sun (2015), Bernor & Sen (2017).

Hipparion s.s. - the nomen is restricted to a specific lineage of hipparionine horses with the facial fossa positioned dorsally high on the face (MacFadden 1980, 1984; Woodburne & Bernor 1980; Woodburne et al. 1981; MacFadden & Woodburne 1982; Bernor 1985; Bernor & Hussain 1985; Bernor & Tobien 1989; Bernor et al. 1996, 2016; Woodburne 1989). Bernor's definition departs from some investigators in not recognizing North American species of *Hipparion* s.s. Bernor (1985).

"Hipparion" - several distinct and separate lineages of Old World hipparionine horses once considered to be referable to the genus *Hipparion* (re: Bernor et al. 1996; 2010). We emphasize here the need to avoid confusion of well defined hipparionine lineages with poorly characterized taxa of "Hipparion" sensu lato.

Hippotherium - a discrete genus of Western Eurasian hipparionine horses known from Central Europe, Italy, Greece, Turkey and Ukraine. Species belonging to this genus include *H. primigenium, H. intrans, H. microdon, H. kammerschmittae, H. malpassii, H. brachypus* and perhaps *H. giganteum* (re: Bernor et al. 2011).

Metric Procedures

Measurements are all given in millimeters and rounded to 0.1 mm. Measurement numbers (M1, M2, M3, etc.) refer to those published by Eisenmann et al. (1988) and Bernor et al. (1997) for the skulls and postcrania. Tooth measurement numbers refer to those published by Bernor et al. (1997) and Bernor & Harris (2003). Bernor & Armour-Chelu (1999), Bernor & Harris (2003), Bernor & Scott (2003), Bernor et al. (2004, 2005, 2010, 2013), Gilbert & Bernor (2008), Bernor & Haile Selassie (2009), and Bernor & White (2009) have compared African hipparions to an extensive series of Late Miocene-Pleistocene Eurasian and African assemblages. Bernor & Sun (2015) have recently reviewed cheek tooth ontological stages in Chinese *Plesiohipparion* and *Proboscidipparion.*

In various studies Eisenmann (see Eisenmann 1995 for a comprehensive summary) has used log10 ratio diagrams to evaluate differences in hipparion metapodial proportions as a basis for recognizing taxa and their evolutionary relationships. Bernor et al. (2003), Bernor & Harris (2003), Armour-Chelu & Bernor (2011) and Bernor et al. (2014, 2016) have used multiple statistical tests, including univariate, bivariate and multivariate statistics as well as log10 ratio diagrams, to evaluate and resolve the alpha systematics of hipparionine horses. Bernor et al. (2005) used log10 ratio diagrams together with multivariate statistics to evaluate metapodial and first phalangeal evidence for postcranial evolution in Ethiopian hipparions. We incorporate these previously used methodologies in this work. Our statistical analyses use the skeletal population from Hoewenegg (Hegau, southern Germany, 10.3 Ma; Bernor et al. 1997) for calculating 95% confidence ellipses used in bivariate plots, and log10 mean standard values for all log10 ratio diagrams for 1PHIII MCIII and MTIII.

Sahabi measurements were taken by R.L. Bernor and O. Cirilli. Comparative measurements were taken from Bernor's equid database which will be published on the NSF sponsored FuTRES website (https://futres.org/) in 2021. Analyses of the Sahabi and other African and Eurasian specimens (re: Table 1) include: hipparion bivariate plots of MCIII, MTIII and 1PHIII. All of these skeletal elements are clearly differentiated with the exception of 1PHIII. While anterior and posterior 1PHIII can be clearly differentiated in living *Equus*, the same cannot be said for all hipparions (see, e.g., Wolf et al. 2013). The Hoewenegg hipparion skeletons were found in articulation and thus the anterior versus the posterior 1PHIII are known. However, the statistical differences between these phalanges are minor at best in the Hoewenegg sample, which has led us to analyze all 1PHIII together. Some advanced African hipparions may in fact differ significantly in anterior versus posterior 1PHIII dimensions (Bernor et al. 2010). Table 2 provides a list of Sahabi *Eurygnathohippus feibeli* specimens, their species attributions, measurements, ages and stratigraphic provenience.

SPEC_ID	SPECIES	SEX	BONE	SIDE	AGE	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	LOC	UNIT
ISP16P61A	*Eu. feibeli*	3	1ph2	rt.	7,1	25,4	18,3	12,4		13,2	11,6									P61A	U1
ISP18P10A	*Eu. feibeli*	3	1ph2	rt.	7,1	27,9	16,2	11,4	8,1	11,2	10,9									P10A	U1
ISP32P25B	*Eu. feibeli*	3	1ph3	lt.	7,1	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		P25B	U1
ISP1P87A	*Eu. feibeli*	3	1ph4	rt.	7,1	29,7	15,0	10,1	8,3	12,7	11,5									P87A	U1
ISP63P36A	*Eu. feibeli*	3	1ph4	lt.	7,1	28,0	17,1	11,2	7,8	12,2	10,9									P36A	U1
ISPP60A	*Eu. feibeli*	3	1ph4	rt.	7,1	26,6	15,9	10,9	6,6	12,1	10,4									P60A	U1
ISP121P16A	*Eu. feibeli*	3	2ph3	lt.	7,1	36,9	29,5	28,9	35,9	26,4	32,9									P16A	U1
ISP293P16A	*Eu. feibeli*	3	3ph3	lt.	7,1	47,4	47,6			25,8	32,8									P16A	U1
ISP5P109A	*Eu. feibeli*	3	astragalus	rt.	7,1	42,1	38,5	28,9	35,9	26,1	32,9	34,1								P109A	U2
ISP470P28A	*Eu. feibeli*	3	astragalus	lt.	7,1	48,7	48,3	27,2	50,4	38,4	27,0	39,5								P28A	U1
ISP48P25A	*Eu. feibeli*	3	astragalus	lt.	7,1	48,1	45,5	24,3	45,3	36,7	27,5	36,8								P25A	U1
ISP55P28A	*Eu. feibeli*	3	astragalus	rt.	7,1	48,5	47,2	23,5	45,9	37,3	26,4	37,9								P28A	U1
ISP5P103A	*Eu. feibeli*	3	astragalus	rt.	7,1	46,4	43,9	22,9	45,7	35,5	26,2	35,1								P103A	U1
ISP40P16A	*Eu. feibeli*	3	calcaneum	rt.	7,1			20,3			39,3									P16A	U1
ISP54P16A	*Eu. feibeli*	3	calcaneum	rt.	7,1	99,0	61,9	20,1	26,1	42,2	41,2	42,6								P16A	U1
ISP90P28A	*Eu. feibeli*	3	calcaneum	rt.	7,1	99,5	62,0		27,5	39,2		41,5								P28A	U1
ISP38P25A	*Eu. feibeli*	3	cuboideum	lt.	7,1	26,1	33,7	23,2												P25A	U1
ISP12P34A	*Eu. feibeli*	3	cuneiforme	rt.	7,1	9,4	36,4	28,8												P34A	U1
ISP20P99A	*Eu. feibeli*	3	cuneiforme	rt	7,1	10,3	37,3	31,5												P99A	U1
ISP24P10B	*Eu. feibeli*	3	magnum	rt.	7,1	15,0	30,2	27,2												P10B	T/U1
ISP600P34A	*Eu. feibeli*	3	magnum	rt.	7,1	16,2	36,2													P34A	U1
ISP74P109A	*Eu. feibeli*	3	magnum	rt.	7,1	14,8	32,4													P109A	U2
ISP116P28B	*Eu. feibeli*	3	mandible	lt.	7,1											53,5	40,2			P28B	U1
ISP147P28B	*Eu. feibeli*	3	mandible	lt	7,1				77,9											P28B	U1
ISP28P25A	*Eu. feibeli*	3	mandsymph		7,1														26,7	P25A	U1
ISP82P17A	*Eu. feibeli*	3	mciii	rt.	7,1	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	P17A	U1
ISP25P26A	*Eu. feibeli*	3	mciii	lt.	7,1										34,4	35,0	26,9	22,4	23,6	P26A	U1
ISP112P24A	*Eu. feibeli*	3	mtii	lt.	7,1			9,5	15,8											P24A	U1
ISP16P24A	*Eu. feibeli*	3	mtii	rt.	7,1			12,8												P24A	U1
ISP24P24A	*Eu. feibeli*	3	mtii	lt.	7,1					7,9	16,3									P24A	U1
ISP25P25A	*Eu. feibeli*	3	mtii	lt.	7,1					9,1	17,5									P25A	U1
ISP11P85A	*Eu. feibeli*	3	mtiii	lt.	7,1										34,3	34,2		23,3	26,4	P85A	U1
ISP67P16A	*Eu. feibeli*	3	mtiii	lt	7,1	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	P16A	U1
ISP59P16A	*Eu. feibeli*	3	mtiii	rt.	7,1										31,8	30,3	28,0	23,8	25,5	P16A	U1
ISP468P28A	*Eu. feibeli*	3	mtiii	rt.	7,1			24,4	24,1						31,5	32,4	28,4	21,6	25,2	P28A	U1
ISP10P30A	*Eu. feibeli*	3	mtiii	lt.	7,1					37,7	30,2	36,0	10,8	5,1						P30A	U1
ISP6P108A	*Eu. feibeli*	3	mtiii	lt.	7,1			25,3	23,8	36,6	30,8	34,2	11,1	7,0						P108A	U1
ISP17P24A	*Eu. feibeli*	3	mtiv	rt.	7,1					8,9	15,6									P24A	U1
ISP64P99A	*Eu. feibeli*	3	mtiv	lt.	7,1			15,9	21,8											P99A	U1
ISP42P99A	*Eu. feibeli*	3	naviculare	rt.	7,1	10,6	38,1	29,4												P99A	U1
ISP83P6A	*Eu. feibeli*	3	naviculare	lt.	7,1	10,9	36,6	28,5												P6A	U1
ISP13P26A	*Eu. feibeli*	3	tibia	rt.	7,1			39,6	26,4			60,7	41,0							P26A	U1
ISP237P16A	*Eu. feibeli*	3	tibia	rt.	7,1							60,1	41,2							P16A	U1
ISP57P61A	*Eu. feibeli*	3	tibia	lt.	7,1			36,1	22,8			55,2	35,8							P61A	U1
ISP3P34B	*Eu. feibeli*	3	tmm1	rt.	7,1	26,4		15,0	7,3	10,3	15,9	13,7	11,2	10,8	55,8					P34B	U1
ISP86P24	*Eu. feibeli*	3	tmm1	rt.	7,1	23,1	20,2	12,8	8,7	10,2	12,1	11,9		9,3	40,6					P24	U1
ISP32P28	*Eu. feibeli*	3	tmm1	lt.	7,1	24,7	19,2	10,9	8,0	9,3	11,3	10,9	9,7	8,4	39,9					P286	U1
ISP71P103A	*Eu. feibeli*	3	tmm1	rt.	7,1	26,9		14,0	9,0	11,0	11,6		9,8	8,7	39,6					P103A	U1
ISP216P65A	*Eu. feibeli*	3	tmm1	rt.	7,1	25,2	23,7	14,2	7,8	10,5	14,3	15,5	14,0	11,8	30,7					P65A	U1
ISP16P22A	*Eu. feibeli*	3	tmm1	lt.	7,1	23,0	20,7	13,3	6,3	8,8	13,7	14,7	12,9	11,4	27,0					P22A	U1
ISP195P16A	*Eu. feibeli*	3	tmm1	rt.	7,1	22,5	21,2	14,9	8,5	5,8		12,8	14,8	15,2	16,6					P16A	U1
ISP81P103A	*Eu. feibeli*	3	tmm2	rt.	7,1	24,9	19,9	11,3	7,3	10,1	12,2	11,5	9,9	9,1	43,6					P103A	U1
ISP77P17A	*Eu. feibeli*	3	tmm3	lt.	7,1	24,9	26,1	11,8	7,2	9,8	9,9	9,9	10,4	9,3	43,5					P17A	U1
ISP65P103A	*Eu. feibeli*	3	tmp4	lt.	7,1	27,1	23,4	14,5	9,9	11,1	14,4	14,1	11,8	11,5	44,8					P103A	U1
ISP183P16A	*Eu. feibeli*	3	tmp4	rt.	7,1	25,3	23,0	13,2	9,2	15,3		12,1		12,1	40,8					P16A	U1
ISP84P24	*Eu. feibeli*	3	tmp4	rt.	7,1	22,6	21,9	15,8	9,0		14,4	12,6			35,8					P24A	U1
ISP76P17A	*Eu. feibeli*	3	txM1	lt.	7,1	25,2	20,7	21,2	24,9		5,0	6,0	5,0	4,0	6,6	4,5				P17A	U1
ISP52P103A	*Eu. feibeli*	3	txM1	rt.	7,1	21,4	20,9	19,2	20,3	20,2	3,0		5,0	5,0	6,6	3,9				P103A	U1
ISP212P34A	*Eu. feibeli*	3	txM3	lt.	7,1	25,1	23,4	18,6	20,5	30,1	1,0	6,0	2,0	1,0	7,0	4,9				P34A	U1
ISP16P108A	*Eu. feibeli*	3	txM3	lt.	7,1	21,8	20,8	19,3	20,4	32,1	4,0	4,0	3,0	2,0	5,9	3,5				P108A	U1
ISP63P109A	*Eu. feibeli*	3	txM3	rt.	7,1	20,3	19,6	16,7	17,8	22,2	3,0	5,0	5,0	4,0	5,3	3,3				P109A	U2
ISP75P17A	*Eu. feibeli*	3	txP2	lt.	7,1	30,0	31,5	24,3	21,6	27,3	6,0	6,0	5,0		7,8	4,8				P17A	U1
ISP26P10A	*Eu. feibeli*	3	txP2	lt.	7,1	35,4	30,2	22,8	21,0	32,0	4,0	4,0	4,0	3,0		4,4				P10A	U1
ISP2P204A	*Eu. feibeli*	3	txP2	rt.	7,1	26,2	23,9	23,2	20,7	27,4	4,0	5,0	3,0	1,0	7,0	4,9				P204A	U1
ISP120P65A	*Eu. feibeli*	3	txP2	lt.	7,1	34,2	31,0	23,3	20,2	24,3	5,0	5,0	3,0	3,0	6,3	4,1				P65A	U1
ISP4P16B	*Eu. feibeli*	3	txP3	rt.	7,1	24,4	25,4	25,8	25,2	28,3	5,0	5,0			7,9	4,9				P16B	U1
ISP40P103A	*Eu. feibeli*	3	txP3	lt.	7,1	24,3	20,2	26,3	24,0	23,2	4,0	7,0	3,0	2,0	7,6	4,9				P103A	U1
ISP39P49A	*Eu. feibeli*	3	txP3	lt.	7,1	25,5		18,1			5,0	8,0	4,0	4,0	7,0	4,8				P49A	U1
ISP85P24A	*Eu. feibeli*	3	txP4	lt.	7,1	24,4	20,1	21,4	20,0	43,2	2,0	4,0	4,0	2,0	7,3	4,2				P24A	U1
ISP35P99A	*Eu. feibeli*	3	txP4	rt.	7,1			26,7	24,8	41,3	2,0	8,0	5,0		7,1	4,2				P99A	U1
ISP78P17A	*Eu. feibeli*	3	txP4	lt.	7,1	23,8		21,3			3,0	5,0	5,0	5,0	6,9	4,7				P17A	U1
ISP1P85A	*Eu. feibeli*	3	txP4	lt.	7,1	24,8	19,5	21,9	21,0	43,0	3,0	6,0	3,0	1,0	6,5	3,2				P85A	U1
ISP130P16A	*Eu. feibeli*	3	txP4	lt.	7,1					41,5	3,0	6,0	4,0	1,0						P16A	U1

Tab. 2 - Measurements of *Eurygnathohippus feibeli.*

Abbreviations

In this manuscript we use the abbreviation Ma for mega-annum in the geochronologic time scale. Ages in m.y. are based on radioisotopic or magnetostratigraphic analyses. North Africa localities may be referred to the MN biochronologic time scale (Rook et al. 2019). Western Eurasia Vallesian, Turolian, and Ruscinian intervals of the European land mammal age sequence are commonly termed units (sensu Fahlbusch 1991).

Measurement Table Abbreviations. Sex: M = male; F = female; ? = unknown. Sex can be defined by the size of a canine tooth, male being large, female being small. Side: lt. = left; rt. = right. Cranial: IOF = infraorbital foramen; POB = preorbital bar; POF = preorbital fossa. Postcranial: 1PHIII = first phalanx III (central digit) of either the anterior or posterior limb, which are difficult to distinguish in most hipparion species; MCIII = metacarpal III; MTIII = metatarsal III; MPIII = metapodial III. M1-M38 refers to measurements as described by Eisenmann et al. (1988) and Bernor et al. (1997). Statistical plots include abbreviations by locality (Locality Symbols are included in Table 1).

Museum Collections Abbreviations. We sample the following museum and institutional vertebrate collections for this study: AMNH – American Museum of Natural History, New York; ISP – International Sahabi Project Collection in Museum of Vertebrate Paleontology, University of Benghazi, Libya; MMTT – Muze Melli Tarikh Tabeie, Tehran; MNHN – Museum National d'Histoire Naturelle, Paris; NHMW – Naturhistorisches Museum, Wien; MCZR – Museo Civico di Zoologia, Rome.

Sahabi Stratigraphy and Chronology

Sahabi is a latest Miocene locality in northern Libya, well known for its celebrated vertebrate fossil fauna. In the 1920s and 1930s there was at Sahabi an Italian army station and, being on the road to various sites into the Libyan Desert, the area was frequently crossed by caravans and explorers and was visited by eminent geologists and palaeontologists (Rook 2008). After several decades of no field activity at Sahabi, multidisciplinary research teams undertook extensive investigations in the area from the middle 1970's to early 1980's, and later on since early 2000's (Boaz et al. 1979, 1987, 2008).

The Sahabi Formation was named and described by de Heinzelin & El-Arnauti (1987) as one of three formations with an aggregate stratigraphic thickness of over 60 meters outcropping over an area of some 50 by 30 km (1500 sq. km.). They interpreted Formation P, a gypsum-rich layer underlying the Sahabi Formation to be of Late Miocene (Messinian) age. Formation P in turn overlies the marine limestone of Formation M of presumed Middle Miocene age (de Heinzelin & El-Arnauti 1987). Correlating Formation P with the Messinian Salinity Event placed the vertebrate fossil-bearing deposits above the Mio-Pliocene boundary. El-Shawaihdi et al. (2016) utilized extensive results from additional fieldwork, core drilling, and laboratory analyses to revise the Sahabi stratigraphy (Fig. 2). The major effect of this revision was to define the upper and lower limits of the Sahabi Formation. The unconformity above Unit U2 is now correlated with the Messinian-aged down-cutting of the Eosahabi River, yielding a minimum age of the top of Upper Member of the Sahabi Formation of 5.3 ma. Sediments of the Qarat Weddah Formation, formerly named Member V of the Sahabi Formation, represents the transgressive infilling of the Eosahabi Channel during the re-filling of the Mediterranean Basin at the end of the Miocene.

The former Formation P is now recognized as a gypsiferous lagoonal deposit comprising the Lower Member of the Sahabi Formation, within the Messinian Stage beginning at 7.2 Ma but not coterminous with the Messinian Salinity Crisis at the end of the stage, 5.3 Ma. Formation P overlies the marine limestone of Formation M, now reliably correlated with the Benghazi Formation and dated to the Tortonian Stage (11.6 – 7.2 Ma; Muftah et al. 2008). El-Shawaihdi et al. (2014) dated the Benghazi Formation at Sahabi to between 9.6 and 9.0 Ma based on the $^{87}Sr/^{86}Sr$ isotope analyses of unaltered marine invertebrate fossils plotted against the marine strontium isotopic curve. Calcareous nannofossils recovered from cores into the Benghazi Formation drilled at Sahabi correlate to biozone NN10b-NN11a and confirm its Late Miocene (Tortonian) age. Beyer (2008) reported a K-Ar date of sedimentary glauconite from the Benghazi Formation (former Formation M) at Locality P53 which yielded an age of between 7.7 – 7.5 Ma, but he noted that that these sediments may well have been redeposited and not representative of the deposit's actual age.

The fossiliferous Upper Member of the Sahabi Formation is a package of interbedded layers of sand and clay laid down by a large, slow-moving Eosahabi River and its related lagoonal and estuarine facies near the paleo-Gulf of Sirt (Boaz 2008). The vertebrate fossil assemblage is surface -collected within mapped localities with secure spatial and stratigraphic control. The Sahabi fossil equid sample derives almost exclusively from one sedimentary unit, Unit U1 of the Upper Member of the Sahabi Formation. Beyer (2008) reported a

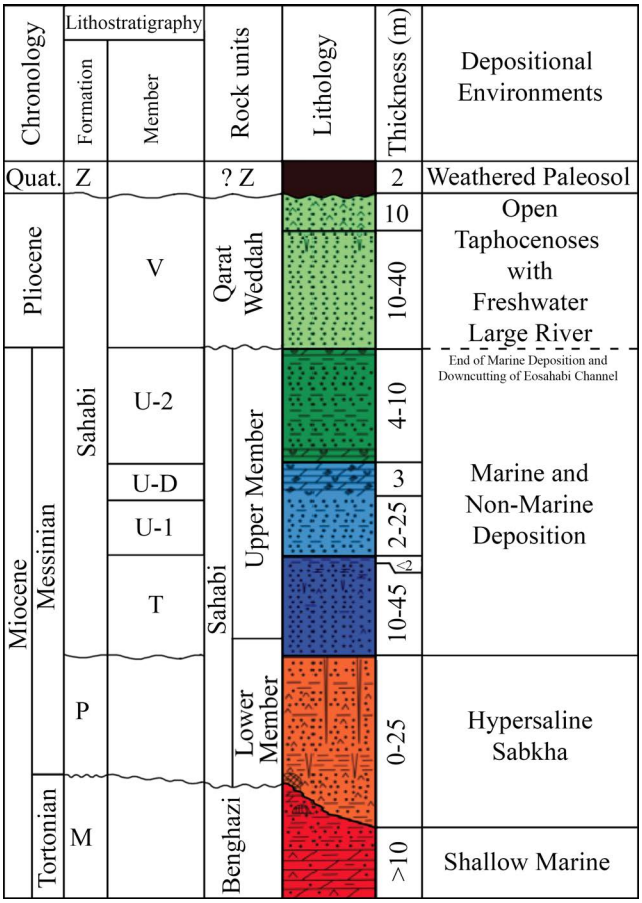

Fig. 2 - Sahabi chronological interpretation and stratigraphic column (not to scale) with synopsis of formational subdivision (Heinzelin & El-Arnauti 1987; Muftah et al. 2020), rock units (El-Shawaihdi et al. 2016), and depositional environments (El-Shawaihdi et al. 2016).

magnetized clayey bed in Unit U1 at Locality P28 that he interpreted as a tuffite and near which he obtained preliminary paleomagnetic results. Muftah et al. (2013) reported detailed microstratigraphic and mineralogical analyses of this unit at two Sahabi localities which yielded no minerals of volcanic origin, datable by isotopic analyses, but rather felsic minerals consistent with a sedimentary origin from Precambrian rocks in northeastern Chad. Boaz et al. (2008) differentiated the U1 mammalian fauna as correlative with the Messinian age while that collected by Italian expeditions in the 1930's was likely collected from the younger U-2 unit covered in part by Qarat Weddah Formation (formerly Unit V) and Formation Z (Fig. 2). Boaz et al. (2008) estimated Sahabi U1's fauna as being ca. 6.8 ma. This age is consistent with a biostratigraphic age review and biogeographic comparison of late Miocene and Eurasian faunas (Bernor & Rook 2008; Pandolfi & Rook 2019). The age of Sahabi *Eurygnathohippus feibeli* is therefore estimated to be 6.8 Ma (Boaz et al. 2008) and agrees well with the chronologic range of *E. feibeli* from Morocco, Ethiopia and Kenya.

Statistical Analysis

Bivariate Plots

Bivariate plots will include two parallel sets of plots: one of our entire analytical sample; a second of the Sahabi (S), Middle Awash (W) and Lothagam (G) specimens plotted: all localities with *Eurygnathohippus feibeli*. We analyze 1PHIII, MCIII and MTIII below. The bivariate plots on bones have a 95% ellipse representing the Hoewenegg population standard of *Hippotherium primigenium*. The array of comparative Hipparion measurements is intended to be heuristic for demonstrating the range of variation in size and proportion of the element/sample combination being plotted.

Figure 3 plots 1PHIII dimensions of maximum length (M1) versus distal articular width (M7). Most of the sample falls within the Hoewenegg 95% confidence ellipse (Fig. 3A). There are larger specimens above the ellipse from Pakistan (P), Saloniki (Q) and Middle Awash (W). A large specimen with the widest distal articular dimension is from Calta (C) and is referable to *Proboscidipparion heintzi* (Bernor & Sen 2017). Smaller specimens are derived from Sinap and Esme Acakoy (N), Samos (O), and Mt. Luberon (U). These are likely small members of the *Cremohipparion* clade (Bernor et al. 2016). Figure 3B plots specimens from Lothagam (G), Sahabi (S) and Middle Awash (W), all within or on the upper border of the Hoewenegg ellipse.

Figure 4 plots MCIII maximum length (M1) versus distal articular width (M11). Figure 4A plots many specimens within the Hoewenegg ellipse including Sinap and Esme Acakoy (N), Maragheh (M), Pikermi (I), Samos (O) and Eppelsheim (E). Above the ellipse there are a great number of specimens from Akkasdagi (A), the longest ones representing cf. *Plesiohipparion longipes* (Koufos & Vlachou 2005). There are elongate specimens from Maragheh (M) referable to cf. *Cremohipparion moldavicum* (Bernor et al. 1996), Samos (O) and Pikermi (I) referable to *Cremohipparion* sp. Specimens to the left of the ellipse include specimens from Saloniki (Q) referable

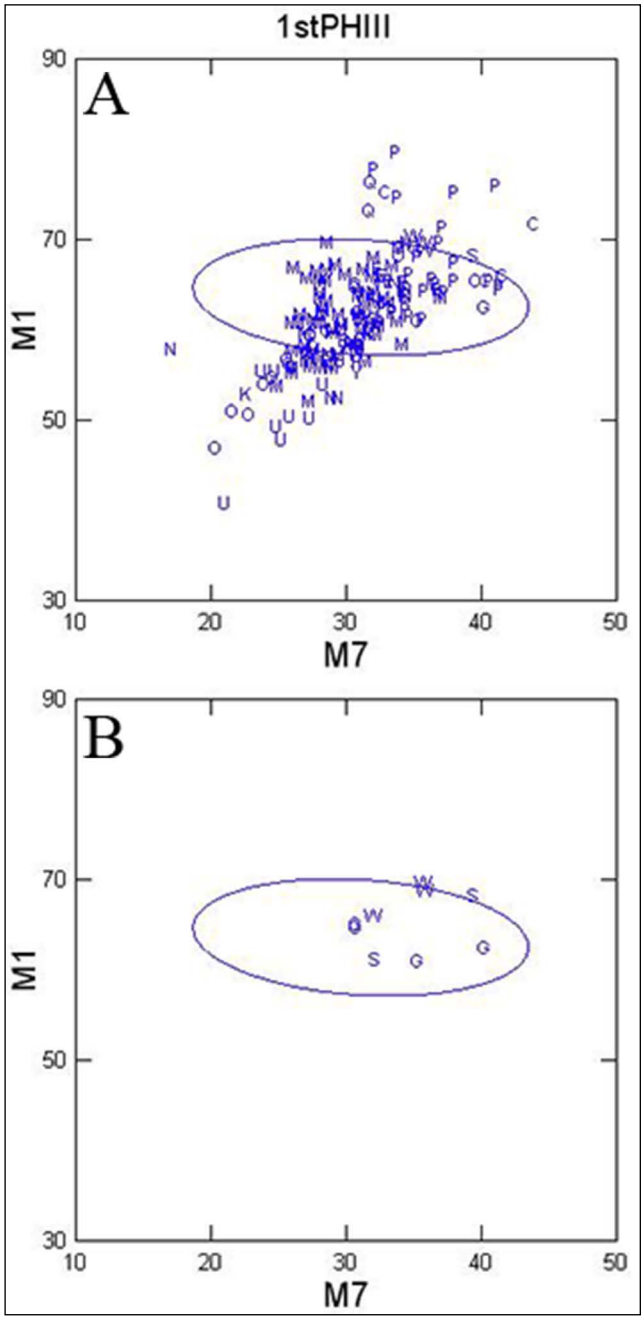

Fig. 3 - 1PHIII maximum length (M1) versus distal articular width (M7); A) entire sample; B) Lothagam (G), Sahabi (S) and Middle Awash (W) only.

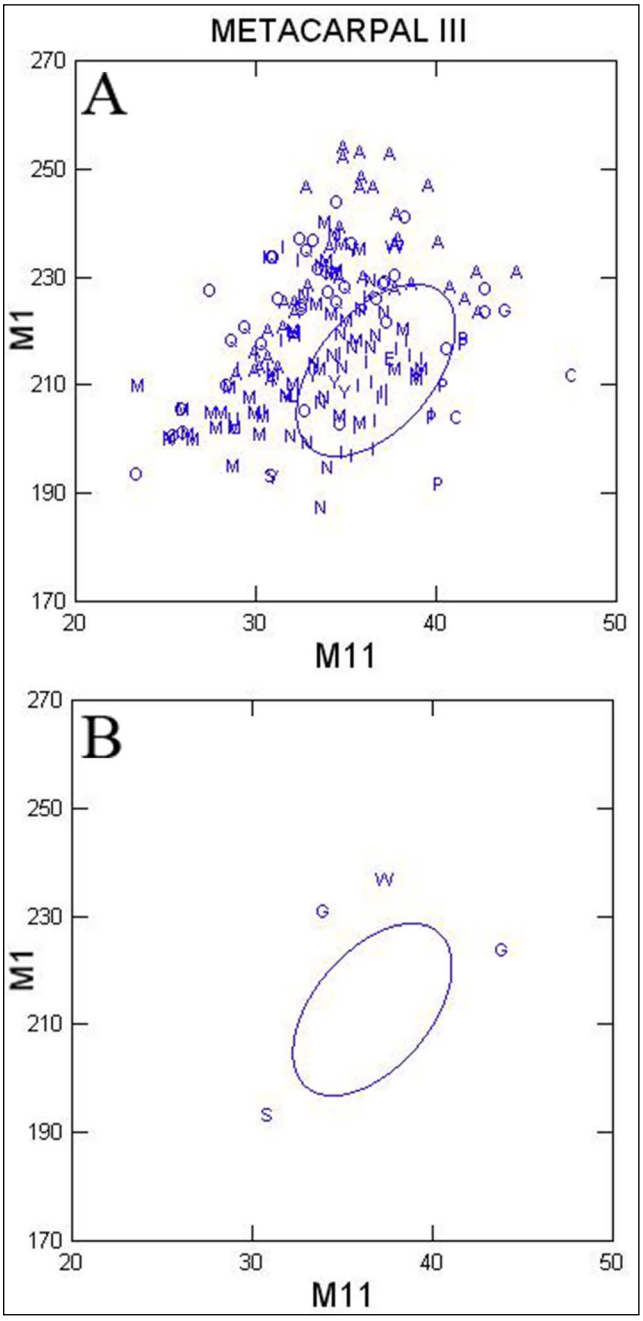

Fig. 4 - MCIII maximum length (M1) versus distal articular width (M11). A) entire sample; B) Lothagam (G), Sahabi (S) and Middle Awash (W) only.

to cf. *Hipparion prostylum* (Bernor et al. 2016), Maragheh (M) cf. *Hipparion* spp., Pikermi (I) and Akkasdagi (A) likely representing smaller, slender limbed *Cremohipparion* spp. Below the ellipse and to the left the smallest specimens are derived from Samos (O) and Maragheh (M) (cf. *Cremohipparion* aff. *matthewi*), Sinap (N), Sahabi (S) (cf. *Cremohipparion*) and Pakistan (P) ("Hipparion" sp.). Figure 4B plots two specimens above the Hoewenegg ellipse and to the left: Middle Awash (W) and Lothgam (G) likely referable to cf. *Eurygnathohippus feibeli*. The one specimen to the right of the upper portion of the ellipse from Lothagam is referable to cf. *Sivalhippus turkanensis*. The one specimen below the ellipse from Sahabi is referable to cf. *Cremohipparion* small.

Figure 5A plots data on MTIII maximum length (M1) versus distal articular width (M11). Again, there is a great density of specimens plotting within the ellipse from Maragheh (M), Pikermi (I), Samos (O), Pakistan (P), and Sinap and Esme

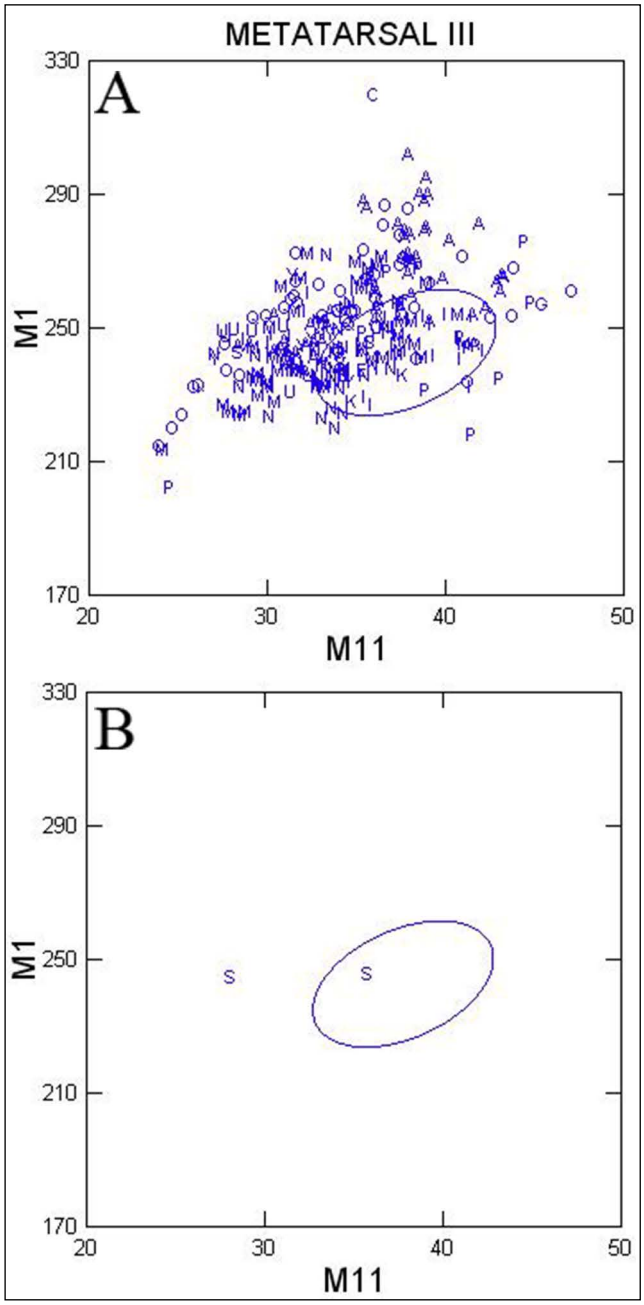

Fig. 5 - MTIII maximum length (M1) versus distal articular width (M11). A) entire sample; B) Sahabi (S) only.

Acakoy (N). There are many specimens above the ellipse from Akkasdagi (A) which include cf. *Plesiohipparion longipes* and Samos (O) that likely include large species of *Cremohipparion ?proboscideum*. The longest MTIII is from Calta (C), and has been referred to *Plesiohipparion* cf. *longipes* by Bernor & Sen (2017). To the left of the ellipse are slender hipparions from Maragheh (M), Saloniki (Q), and Mt. Luberon (U) which include a mixture of *Hipparion* cf. *prostylum, Cremohipparion moldavicum*, and *Cremohipparion matthewi*. To the right of the ellipse are specimens of large *Sivalhippus* sp. from Pakistan (P), *Sivalhippus turkanensis* from Lothagam (G) and large cf. *Hippotherium brachypus* from Samos (O). The smallest specimens referable to cf. *Cremohipparion matthewi* are found from Samos (O) and Maragheh (M). The small specimen from Pakistan (P) is referable to "*Hipparion*" sp. Figure 5B includes two MTIII specimens from Sahabi (S), one within the ellipse referable to cf. "*Hipparion"* large and one to the left of the ellipse that is referable to *Eurygnathohippus feibeli*.

Log10 Ratio Analyses

Figure 6A and B are log10 ratio diagrams of 1PHIII. Figure 6A compares Sahabi specimens with specimens from Lothagam, Pikermi, Sinap, Langebaanweg and Tizi N'Tadderht specimens. Bernor et al. (2003) recognized a primitive species of *Cormohipparion sinapensis* from the oldest hipparion bearing horizons at Sinap and Esme Acakoy, Turkey (CsinMean). The *Cormohipparion sinapensis* log10 ratio exhibits an elongate shaft (M1) and slender (M3) and relatively deep midshaft (M4), narrow proximal articular depth (M6) compared to the Hoewenegg standard. The trajectory of Sinap *Cormohipparion sinapensis* 1PHIII is shared with *Cremohipparion matthewi* (Cr.matt), Lothagam *Eurygnathohippus feibeli*, Pikermi *Cremohipparion mediterraneum* and Sahabi specimen ISP32P25B referable to cf. *Eurygnathohippus feibeli*. Three larger specimens include Lothagam Mean, the Sahabi MCZR-PV2010.0037 referable to cf. *Sivalhippus turkanensis,* and the Langebaanweg Mean of *Eurygnathohippus hooijeri* (Bernor and Kaiser 2006). Figure 6B replots Lothagam cf. *Sivalhippus turkanensis* Mean, Sinap *Cormohipparion sinapensis,* European *Cremohipparion matthewi* MEAN, Lothagam *Eurygnathohippus feibeli* and the Middle Awash late Miocene sample (ALA, BIK, JAB, KAR, DID, ALA) data. JAB-VP1-1 is the oldest 1PHIII in the Middle Awash sample and plots very closely with *C. sinapensis* and *Eurygnathohippus feibeli* from Lothagam. The remaining Middle Awash specimens, ALA-VP-2-26, KAR-VP-4/3, BIK-VP-1-3 and DID-VP-1-82 vary slightly from Lothagam *Eurygnathohippus feibeli* and JAB-VP-1-1 being slightly more robust and KAR-VP-4/3 is the longest 1PHIII in the sample.

Figure 7A and B are log10 ratio diagrams of MCIII. Figure 7A includes two primitive MC-III samples: *Cormohipparion sinapensis* (Csin) from

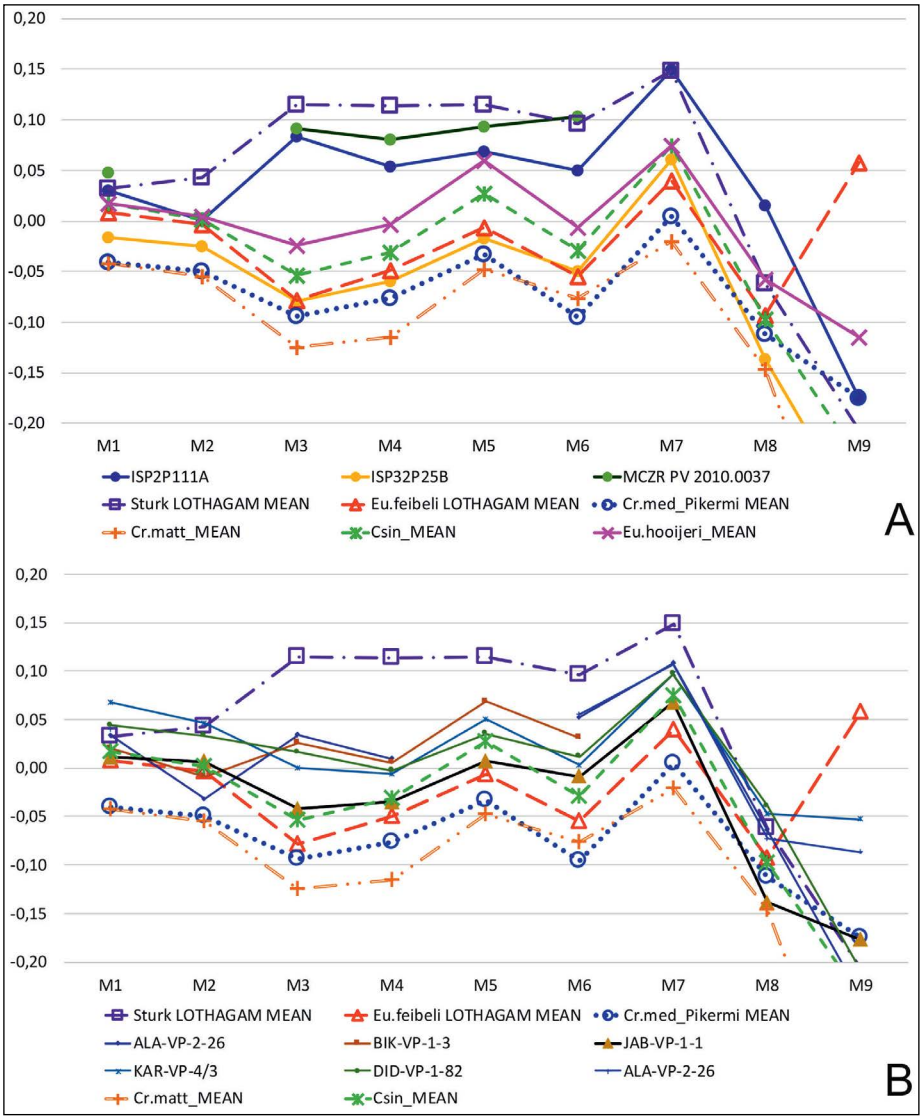

Fig. 6 - 1PHIII log10 ratio Diagrams. A) 1PHIII Sahabi and other Late Miocene European and African Hipparions log10 ratio compared to Ho. Log10 MEAN, Sahabi is ISP2P111A and ISP32P25B and MCZRPV2010.0037; Lothagam is Sturk (*Sivalhippus turkanensis*), Eu. feibeli is Lothagam mean of *Eurygnathohippus feibeli,* Cr.med is Pikermi *Cremohipparion mediterraneum* Mean measurements; Cr.matt_Mean is Mean measurements on *Cremohipparion matthewi*, Csin_Mean is mean measurements on Sinap & Esme Acakoy *Cormohipparion sinapensis,* Eu.hooijeri_MEAN is the mean measurements on Langebaaneweg *Eurygnathohippus hooijeri.* B) 1PHIII Lothagam, European and Middle Awash log10 ratio compared to Ho. log10 MEAN, Sturk Lothagam Mean, Eu.feibeli Lothagam Mean, Cr.med_Pikermi Mean, Middle Awash localities including ALA, BIK, JAB, KAR, DID, ALA (all between 6 and 5.4 Ma), Cr.matt_MEAN and Csin_Mean.

Sinap and Esme Acakoy and *"Cormohipparion" africanum* (Cafr, MNHN1951-9-5Type) from Bou Hanifia, Algeria (Bernor & White 2009). The log10 proportions of these two taxa are virtually identical and exhibit narrowing of the midshaft (M3) with relatively deeper keel (M4) characteristic of the earliest Old World hipparions, and distinction from Central European *Hippotherium primigenium*. Lothagam *Eurygnathohippus feibeli* (Eu. feiLothMean), Langebaanweg *Eurygnathohippus hooijeri* and Pikermi *Cremohipparion mediterraneum* all are remarkably similar to the primitive Old World *Cormohipparion* condition. Sahabi IPS82P17A and ISP25P26A are also similar to Lothagam and the other primitive taxa and referable to cf. *Eurygnathohippus feibeli.* Sahabi IPS27P25B is very similar to Samos *Cremohipparion matthewi* and is extremely slender in its midshaft but generally has the same log10 trajectory as the primitive *Cormohipparion* but with much exaggerated midshaft slenderness (M3) and more slender build but elongate (M1). In Figure 7B Middle Awash AMW-VP-1-15 and AME-VP- 1/175 are very similar to the primitive *Cormohipparion sinapensis* MCIII log10 trajectory except for a slightly elevated distal suprarticular tubercle diameter (M10) permitting a referral to cf. *Eurygnathohippus feibeli.* Lothagam *Sivalhippus turkanensis* is substantially larger and more robustly built.

Figure 8 includes MTIII log10 comparisons of primitive hipparions in comparison to Sahabi, European and African specimens following the description of 1PHIII and MCIII above. Figure 8A shows once again that *Cormohipparion sinapensis* and *"Cormohipparion" africanum* have slender and relatively deep midshafts compared to the Hoewenegg standard, the so-called "Esme Acakoy Effect" of Bernor et al. (2003). *Cremohipparion mediterraneum* and Sahabi ISP67P16A cf. *Eurygnathohippus feibeli*

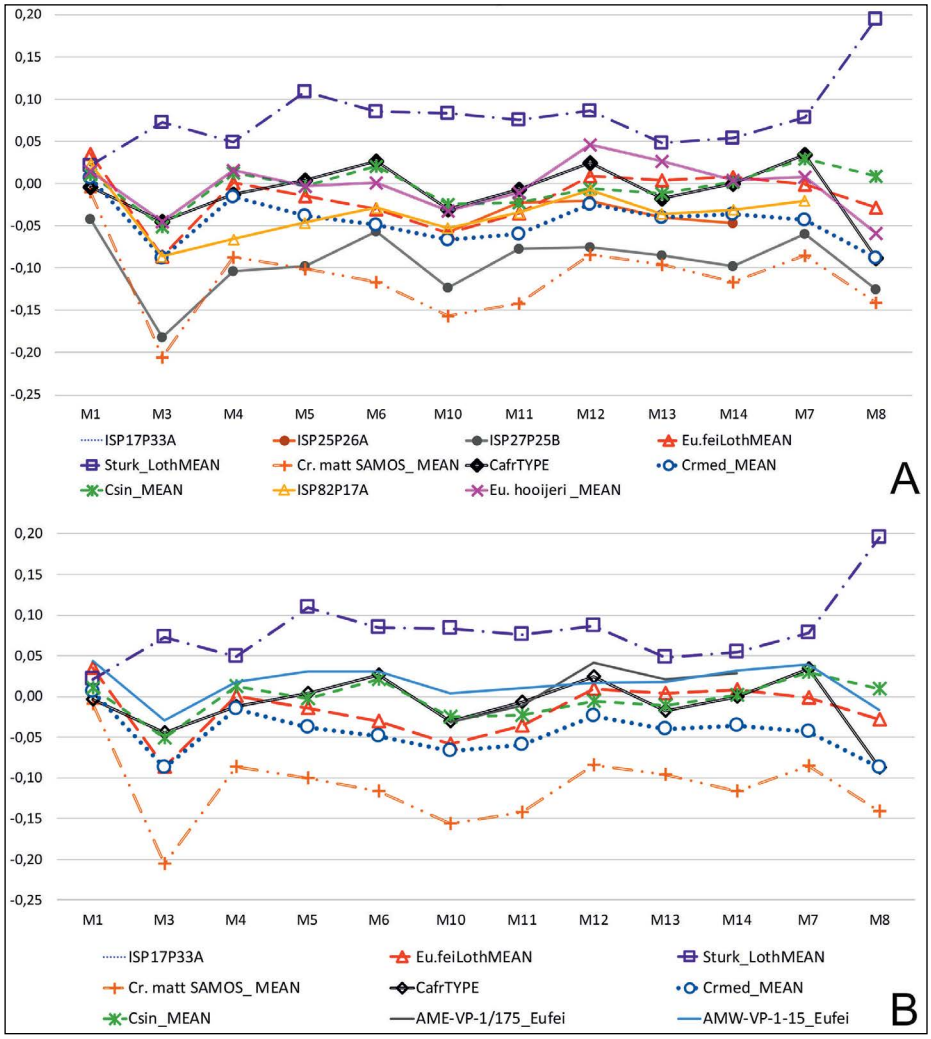

Fig. 7 - MCIII log10 ratio Diagrams.
A) Metacarpal III Sahabi, Lothagam, European and African Hipparions, log10 ratio, Ho Std. – abbreviations as in Figure 6A.
B) Metacarpal III Sahabi, Lothagam, European, Middle Awash and African Hipparions, log10 ratio, Ho. Std. AME and AMW Middle Awash Localities, the remaining as in Figure 5A.

likewise exhibit the same general trajectory with the Sahabi specimen having a narrower mid-shaft. Langebaanweg *Eurygnathohippus hooijeri* is larger than these specimens but has a similar overall trajectory as the primitive *Cormohipparion*. Lothagam *Sivalhippus turkanensis* contrasts sharply in its heavier build with elevated midshaft (M3 and M4), proximal articular (M5 and M6) and greater distal supraarticular (M10) diameter. Sahabi also has a partial distal MTIII, ISP6P34A that compares closely with Lothagam Stur and is referable to cf. *Sivalhippus turkanensis*. Also, Samos *Cremohipparion matthewi* again shows extreme slender dimensions with greatly reduced midshaft (M3 and M4) proximal articular (M5 and M6) and distal articular (M10 and M11) dimensions. Figure 8B illustrates that the partial Lothagam *Eurygnathohippus feibeli* is similar to primitive *Cormohipparion* and *Cremohipparion mediterraneum*. The Middle Awash preserves no complete MTIIIs from the 6.0-5.6 Ma interval.

Systematics

Order **Perissodactyla** Owen, 1848
Suborder **Hippomorpha** Wood, 1937
Superfamily Equoidea Hay, 1902
Family Equidae Gray, 1821
Subfamily Equinae Steinmann & Döderlein, 1890
Tribe Hipparionini Quinn, 1955
Genus *Eurygnathohippus* Van Hoepen, 1930
Type- Species: *Eurygnathohippus feibeli* Bernor & Harris, 2003

Etymology: Named in Honor of Professor Craig Feibel.
Age: Late Miocene of Africa, ca. 7-5.7 Ma.

Eurygnathohippus feibeli Bernor & Harris, 2003

Synonymy:
Hipparion turkanense Hooijer & Maglio, 1973: 311
Hipparion turkanense Hooijer & Maglio, 1974: 8
Not: *Hipparion turkanense* Hooijer, 1975: 19-22
Hipparion sp. cf. *sitifense* (Pomel, 1897) Tobien, 1982
"Hipparion" cf. *sitifense* Bernor et al., 1987
Eurygnathohippus turkanense Leakey et al., 1996: 561

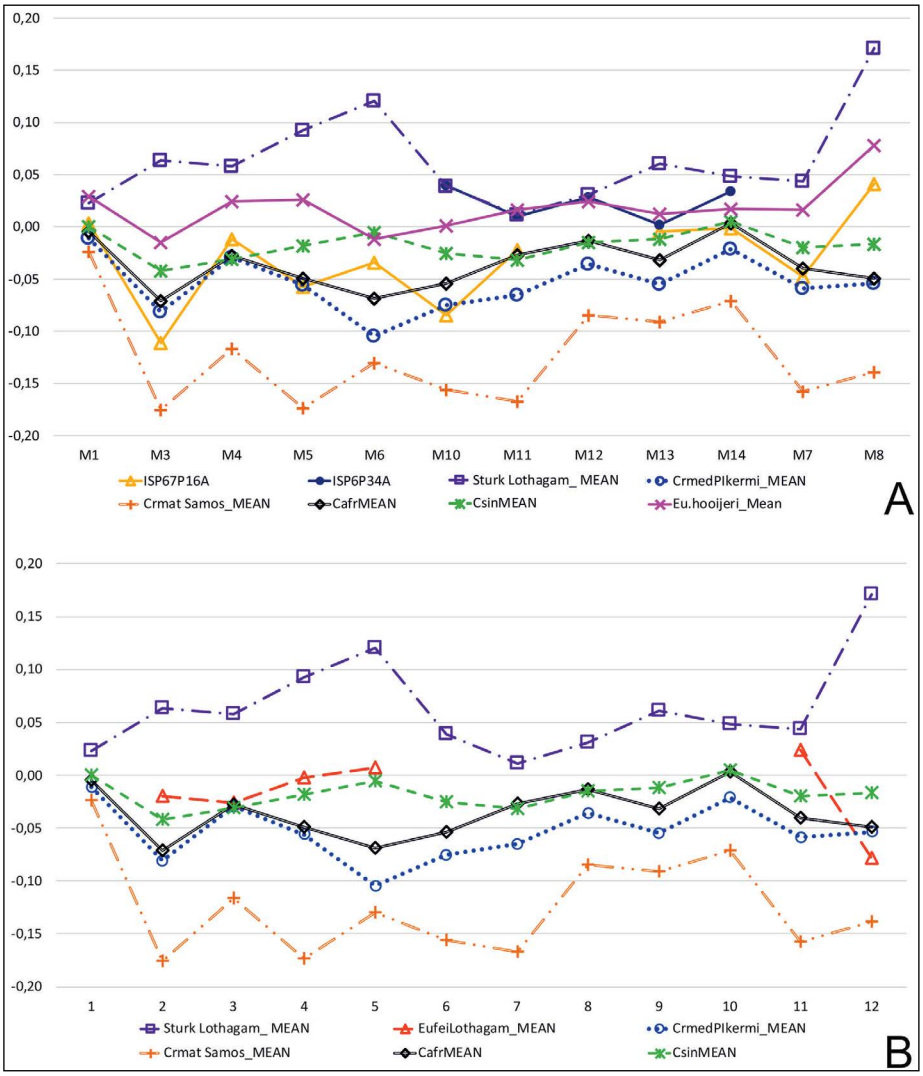

Fig. 8 - MTIII log10 ratio Diagrams. A) Metatarsal III Sahabi, European and African Hipparions, log10 ratio, Ho Std. – abbreviations as in Figure 6A. B) Metatarsal III Lothagam, European, and African Hipparions, log10 ratio, Ho. Std. Localities, as in Figure 6A.

Type Specimen: KNM-LT139, partial anterior foot.

Type Locality: Lothagam Upper Nawata.

Diagnosis (modified from Bernor & Harris 2003): * indicates primitive characters for Old World hipparions; ** indicates autapomorphies for *Eurygnathohippus*.

A medium sized hipparion with primitive facial morphology including long preorbital bar and medially deep preorbital fossa*. Maxillary cheek teeth with elongate P2 anterostyle*; mesostyle is usually very narrow and blade like in early to middle wear becoming rounded later in wear**; pre- and postfossettes are complexly plicated in middle wear*; protocone is rounded and lingually flattened in early wear becoming oval in middle wear and more rounded in late wear*; pli caballins are double to single*; hypoglyphs are moderately deep to deep*. Mandibular cheek teeth with elongate metaconids in early to middle wear becoming rounded in later wear**; metastylids are square shaped in early to middle wear becoming rounded in late wear*; linguaflexids are shallow and broad in early wear becoming deeper V- to U shape later in wear*; pre- and postflexids are complex in early to middle wear becoming simple later in wear*; pli caballinids are single to absent*; ectostylids variably occur and sometimes rise high on the labial side of the crown*; protostylids are expressed in middle to late wear and when they occur they are open loops extending far labially*. Postcrania are medium sized; metapodials are elongate slender**; 1PHIIIs are elongate**.

Description

Dentition

There are 15 maxillary cheek teeth referred to *Eurygnathohippus feibeli* in the Sahabi sample, all derived from the U1 unit (Table 2).

There are three txP2, ISP26P10A (left side; height = 32.0 mm), ISP75P17A (left side; height = 27.3 mm) and ISP120P65A (left side; height = 24.3 mm). ISP26P10A (Fig. 9A, labial and B, occlusal) has the highest crown. The occlusal surface is complete except for the mesio-lingual and distolingual portions and has: anterostyle elongate; mesostyle V-shaped labially; pre- and postfossettes coming into wear and being moderately heavily plicated and separated by a narrow groove; pli caballin is weakly bifid; protocone ovate in shape and hypoglyph moderately deeply incised. ISP75P17A (Fig. 9C, labial and D, occlusal) is slightly more worn, with mesial-labial surface broken not preserving the anterostyle;

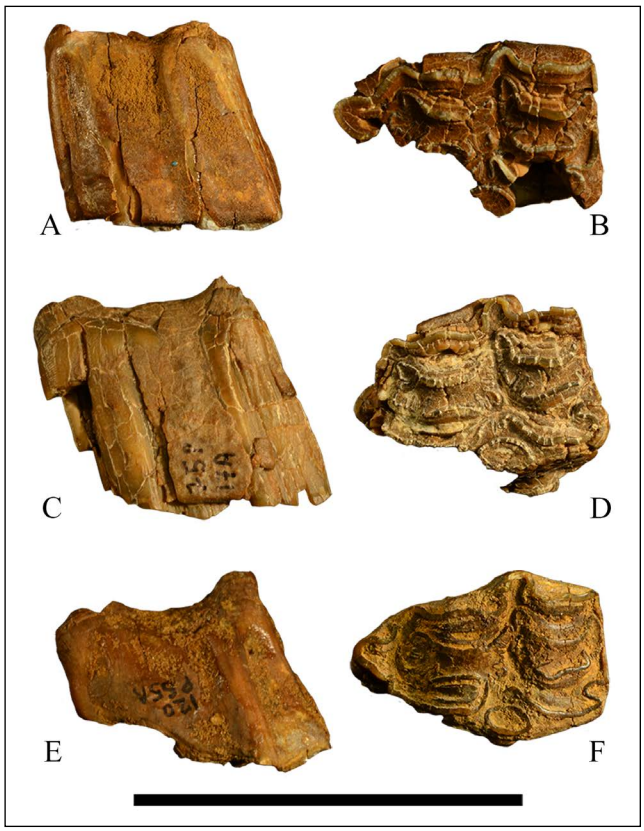

Fig. 9 - Sahabi *Eurygnathohippus feibeli* P2; ISP26P10A: A) labial, B) occlusal; ISP75P17A: C) labial, D) occlusal; ISP120P65A: E) labial, F) occlusal. Scale bar 5 cm.

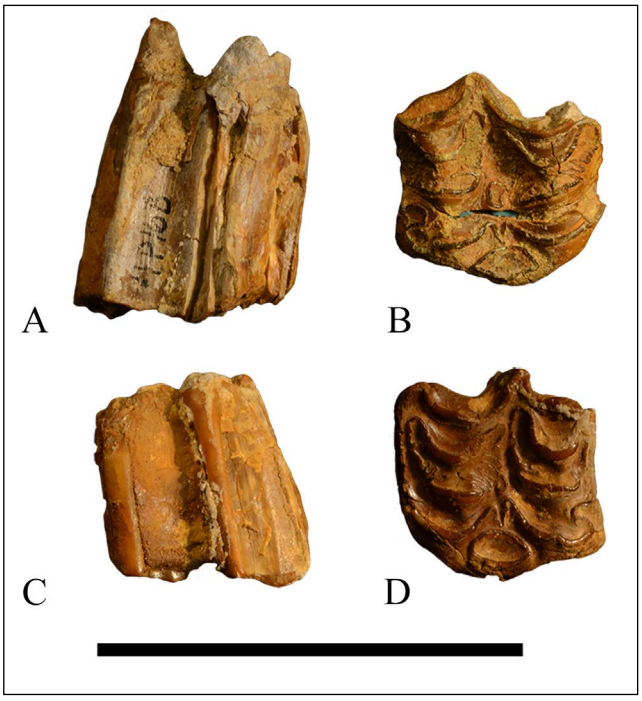

Fig. 10 - Sahabi *Eurygnathohippus feibeli* P3; ISP4P16B: A), labial, B) occlusal; ISP40P103A: C) labial, D) occlusal. Scale bar 5 cm.

mesostyle is rounded and pre- and postfossettes are separated with moderately heavily complex plications as in ISP26P10A; pli caballin is strongly bifid and protocone ovate; hypoglyph is as in ISP26P10A being moderately deeply incised. ISP120P65A is a left P2 that is the most worn P2 (Fig. 9E, labial and 9F, occlusal). The anterostyle is elongate; mesostyle is rounded, the pre- and postfossetes are complexly plicated, but this individual has the opposing borders of pre- and postfossettes touching; pli caballin is multiple; protocone is ovate and hypoglyph is moderately deeply incised.

There are three txP3, ISP4P16B (right side; height = 28.3 mm), ISP40P103A (left side; height = 23.2 mm) and ISP39P49A (left side; height unknown). ISP4P16B (Fig. 10A, labial and 10B, occlusal) has mesial border clearly leaning mesially with a fragmentary labial margin; occlusal surface has mesostyle narrowly rounded; pre- and postfossettes have complex margins; pli caballin is single; protocone is ovate and hypoglyph is moderately deeply incised. ISP40P103A (Fig. 10C, labial and 10D, occlusal) is in a late stage of wear and exhibits pre- and postfossettes well worn with reduction of plis except the distal border of the prefossette which remains complex; mesostyle is pointed; pli caballin is single, protocone is oval; hypoglyph is moderately deeply incised.

There are five txP4, ISP85P24A (left side; height = 43.2 mm), ISP1P85A (left side; height = 43.0 mm), ISP130P16A (left side; height = 41.5 mm), ISP35P99A (right side; height = 41.3 mm), ISP78P17A (left side; height unknown). ISP-85P24A (Fig. 11A, labial and 11B, occlusal) is the highest crowned P4 (43.2 mm) in our sample and has a straight mesial wall and missing enamel on the mesial-buccal and mesial-lingual surfaces; mesostyle is very slender and blade like in buccal view (Fig. 11A). Occlusally, the mesostyle is very slender and pointed; pre- and postfossettes are coming into wear with only prefossette distal margin showing faint plis; pli caballin is faintly bifid; protocone is rounded labially with lingual margin broken; hypoglyph is deeply incised. This specimen is in an early stage-of-wear and suggests a maximum unworn crown height of less than 50 mm. ISP1P85A (Fig. 11C, labial and 11D, occlusal) is slightly more worn than ISP85P24A with the occlusal surface exhibiting more clearly differentiated fossettes; prefossette is well preserved with complexity on the

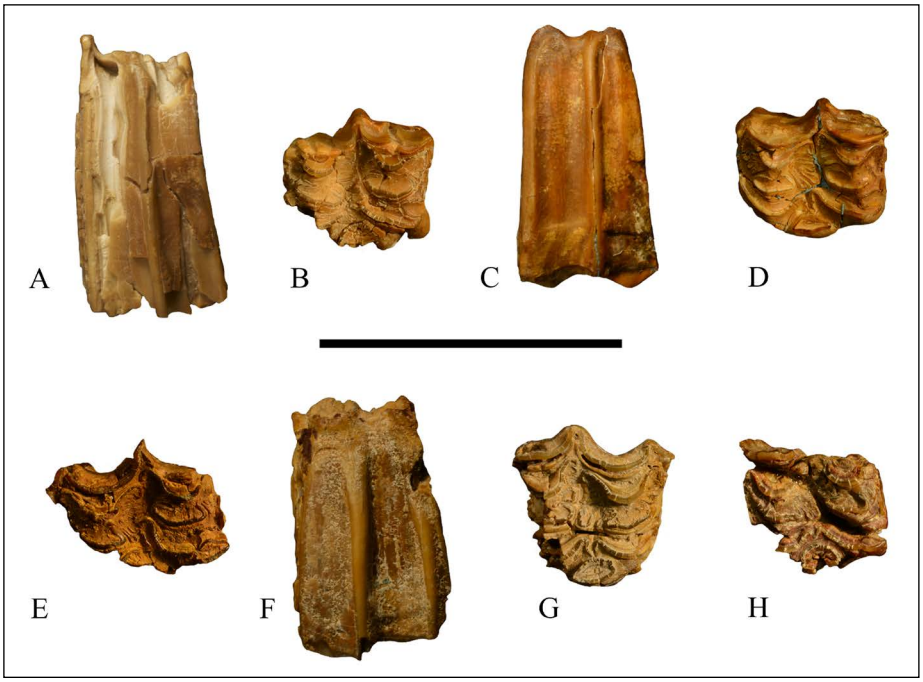

Fig. 11 - Sahabi *Eurygnathohippus feibeli* P4; ISP85P24A: A) labial, B) occlusal; ISP1P85A: C) labial, D) occlusal; ISP130P16A: E) occlusal; ISP35P99A: F) labial, G) occlusal; ISP78P17A: H) occlusal. Scale bar 5 cm.

mesial margin and long, complex plications distally; postfossette is in early wear with modest plications on the mesial margin and no plications yet appearing on the distal margin; pli caballin is long and single; protocone is elongate-oval and distinctly flattened lingually; hypoglyph is deeply incised. ISP130P16A is slightly more worn yet (Fig. 11E, occlusal view) and has lingual margin damaged; mesostyle is again very pointed and blade-like; opposing margins of pre- and postfossettes are closely opposed and touching each other; prefossette is heavily plicated on both mesial and distal margins; pli caballin is not developed; protocone is missing; hypoglyph is very deeply incised. ISP35P99A (Fig. 11F, labial and 11G, occlusal) has virtually the same crown height of ISP130P16A with better preserved labial margin showing a blade-like mesostyle until near the base of the tooth where it widens mesodistally; occlusally the mesostyle is pointed and slightly less blade-like than in previously described specimens; pre- and postfossettes are very closely opposed; prefossette is well preserved and complex; postfossette has only the mesial border preserved and moderately complex; pli caballin is single; protocone is ovate; hypoglyph is broken. ISP78P17A (Fig. 11H, occlusal view) is the most worn txP4 with all peripheral margins damaged; pre- and postfossette are complex preserving short, albeit complex plications; pli caballin is single; protocone is oval; hypoglyph is deeply incised.

There are 2 txM1, ISP52P103A (right side; height = 20.2 mm) and ISP76P108A (left side; height unknown due to breakage of base). ISP52P103A (Fig. 12A) is in late wear and in occlusal view has a rounded mesostyle; fossettes retain complex, albeit short plications; pli caballin is weakly double, protocone is oval shape with flattened lingual margin and hypoglyph is deeply incised. ISP76P108A is a middle stage-of-wear specimen lacking the base and not measurable for height; mesostyle is pointed labially and blade-like; fossettes are complexly plicated and linked at their intersecting labial limit; pli caballin is single, protocone ovate; hypoglyph deeply incised.

There are three txM3, ISP16P108A (left side; height = 32.1 mm), ISP63P109A (right side; height = 22.2 mm) and ISP212P34A (left side; height = 30.1 mm). ISP16P108A (Fig. 13A) does not have mesostyle preserved; prefossette has complex mar-

Fig. 12 - Sahabi *Eurygnathohippus feibeli* M1; ISP25P103A: occlusal view (labial view not available). Scale bar 5 cm.

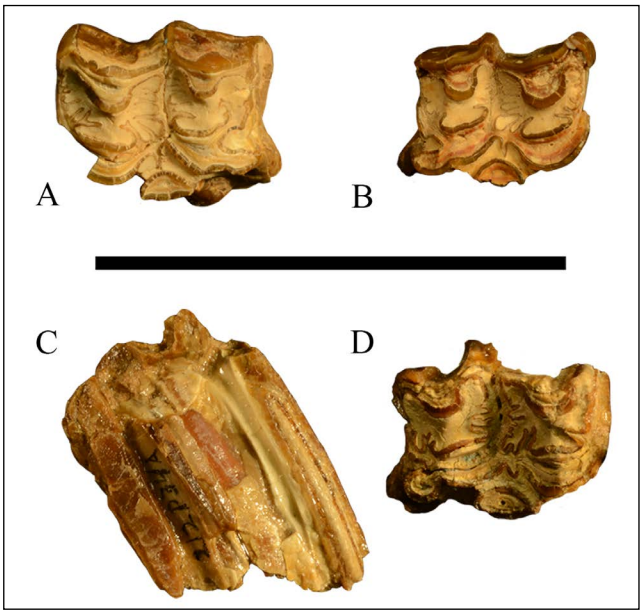

Fig. 13 - Sahabi *Eurygnathohippus feibeli* M3, ISP16P108A: A) occlusal; ISP63P109A, B) occlusal; ISP212P34A: C) labial, D) occlusal. Scale bar 5 cm.

gins, postfossette is less complex, and in particular the distal margin; pli caballin is single; protocone is lingually flattened and labially rounded; hypoglyph is deeply incised. ISP63P109A (Fig. 13B) is in a late stage-of-wear but preserves blade-like mesostyle; complex prefossette, simpler postfossette; single pli caballin, ovate protocone, deeply incised hypoglyph. ISP212P34A (Fig. 13C and D) is leaning steeply distally (Fig. 13C); mesostyle is narrowly rounded labially; fossettes have complex opposing margins with a distinct accessory enamel ridge separating them; mesial border of prefossette and distal border of the postfossette are relatively simpler in their amplitude; pli caballin is simple; protocone is ovate and hypoglyph is deeply incised.

There are 11 mandibular cheek teeth referred to *Eurygnathohippus feibeli* in the Sahabi sample, all derived from the U1 unit (Table 2).

There are three tmp4, ISP65P103A (left side; height = 44.8 mm), ISP84P24 (left side; height = 35.8 mm) and ISP183P16A (right side; height = 40.8 mm). ISP65P103A (Fig. 14A and B) has a vertically straight mesial wall (Fig. 14A); in occlusal view metaconid is elongate, metastylid is round and linguaflexid is shallow and broad; preflexid and postflexid have complex margins; ectoflexid is shallow with a distinct pli caballinid; there is no protostylid nor ectostylid apparent. ISP84P24 (Fig. 14C and D) is straight walled mesially (Fig. 14D);

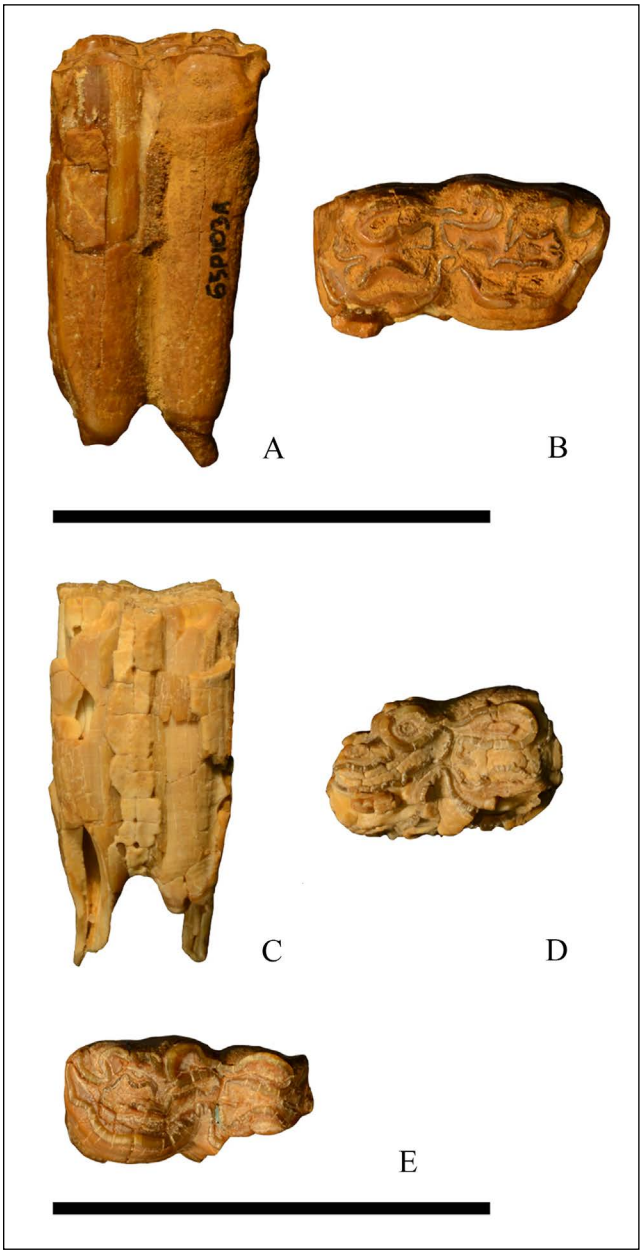

Fig. 14 - Sahabi *Eurygnathohippus feibeli* p4, ISP65P103A: A) labial, B) occlusal; ISP84P24: C) labial, D) occlusal; ISP183P16A: E) occlusal. Scale bar 5 cm.

metaconid is rounded whereas metastylid is oblong; there is a small metastylid spur; pre- and postflexid have simple margins, ectoflexid is shallow with a very small bifid pli caballinid and distinct, but small, compressed ectostylid. ISP183P16A (Fig. 14E) has metaconid and metastylid as in ISP84P24; preflexid and postflexid are slightly plicated; ectoflexid has multiple pli caballinds and complex margin distally.

There are seven tmm1s, ISP3P34B (right side; height 55.8 mm; highest crowned cheek tooth in the sample); ISP86P24 (right side; height = 40.6 mm); ISP32P28 (left side; height = 39.6 mm), ISP71P103A

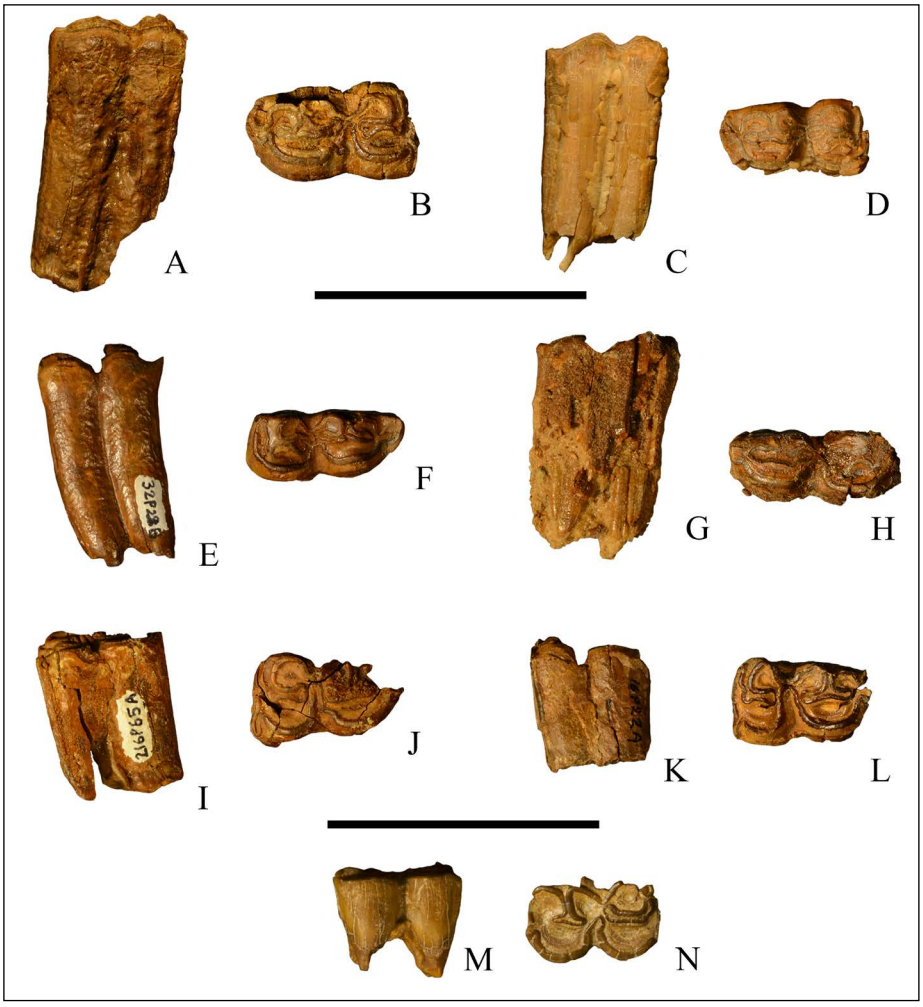

Fig. 15 - Sahabi *Eurygnathohippus feibeli* m1, ISP3P34B: A) labial, B) occlusal; ISP86P24: C) labial, D) occlusal; ISP32P28: E) labial, F) occlusal; ISP-71P103A: G) labial, H) occlusal; ISP216P65A: I) labial, J) occlusal; ISP16P22A: K) labial, L) occlusal; ISP-195P16A: M) labial, N) occlusal. Scale bar 5 cm.

(right side; height = 39.6 mm), ISP216P65A (right side; 30.7 mm); ISP16P22A (left side; height = 27.0 mm), ISP195P16A (right side; height = 16.6 mm). ISP3P34B (Fig. 15A and B) is very high crowned. Occlusally, metaconid is round, metastylid is square; linguaflexid is a shallow U-shape with no metastylid spur; pre- and posflexids have simple margins; ectoflexid is deep separating metaconid and metastylid; there is a distinct small ectostylid expressed both labially (Fig. 15A) and occlusally (Fig. 15B). ISP86P24 (Fig. 15C and D) has metaconid elongate and metastylid rounded; linguaflexid is a shallow U-shape; ectoflexid is deep with a distinct, albeit small pli caballinid. ISP32P28 (Fig. 15E and F) has rounded metaconid and metastylid; linguaflexid is a deep V-shape with no metastyid spur; pre- and postflexids have simple margins; ectoflexid is deep lacking a pli caballinid; there is no ectostylid. ISP-71P103A (Fig. 15G and H) is not well preserved; it preserves an elongate metaconid and squared metastylid; linguaflexid is a deep V-shape; pre- and postflexids have simple margins; ectoflexid is deep; there is no pli caballinid but there is a tiny rounded ectostylid near the labial border. ISP216P65A (Fig. 15I and J) is poorly preserved; metaconid is round and metastylid square with an oblique crack running through it; pre- and postflexids are simple; linguaflexid is a deep V-shape; there is an elongate open protostylid extending far labially; ectoflexid is very elongate extending into the isthmus between metaconid and metastylid; there is no apparent pli caballinid or ectostylid. ISP16P22A (Fig. 15K and L) is as in ISP216P65A, remarkable again is the expression of a buccally open protostylid extending far labially. ISP195P16A (Fig. 15M and N) is in a very late wear stage. The labial view (Fig. 15M) has a distinct ectostylid confined to the base of the crown; occlusally metaconid is rounded; metastylid is square; pre- and postflexid are sharply reduced in size with simple margins; ectoflexid penetrates the isthmus between metaconid and metastylid; there is no ectostylid, pli caballinid or protostylid preserved.

There is single tmm2, ISP81P103A (right side; height = 43.6 mm; Fig. 16A and B). The metaconid

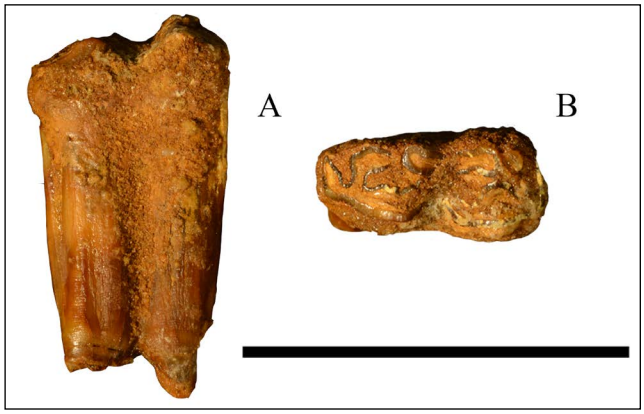

Fig. 16 - Sahabi *Eurygnathohippus feibeli* m2, ISP81P103A: A) labial, B) occlusal. Scale bar 5 cm.

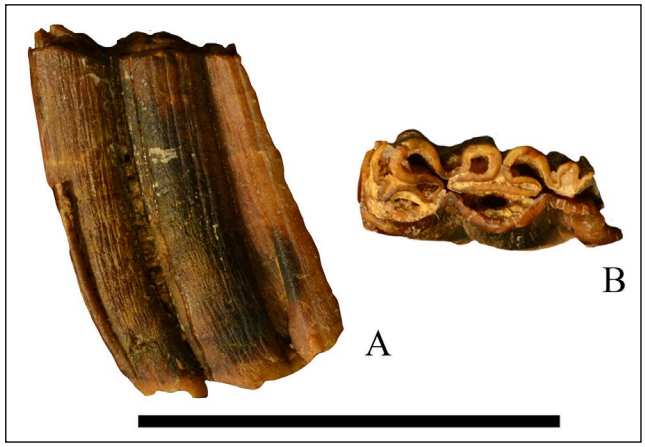

Fig. 17 - Sahabi *Eurygnathohippus feibeli* m3, ISP77P17A: A) labial view, B) occlusal view. Scale bar 5 cm.

is extremely elongate extending far mesially; metastylid is rounded; linguaflexid is shallow; preflexid is poorly defined while postflexid is irregular shape and complex; ectoflexid, pli caballinid and ectostylid are not observable; there is no protostylid.

There is one tmm3, ISP77P17A (left side; height = 43.5 mm; Fig. 17A and B). The labial view shows that all cementum is lacking and that there is a strong protostylid on the mesio-labial border (Fig. 17A); occlusally metaconid and metastylid are round; linguaflexid is a deep U-shape; pre- and postflexid have simple margins; ectoflexid is deep; pli caballinid and ectostylid are not present; protostylid does not ascend to occlusal level.

Postcranial

Bernor et al. (2012) identified a Sahabi MCIII (82P17A, Fig. 3a) that is identical to the type specimen of *Eurygnathohippus feibeli* from Lothagam, Kenya. Bernor et al. (2012) further identified a complete MTIII of *E. feibeli* from Sahabi (67P16A) that was of appropriate length and proportions to be recognized as a member of this taxon. Table 2 lists an extensive suite of postcrania which we now refer to *E. feibeli* based on their comparable size, and in the case of MPIIIs their size and elongate-slender proportions.

Figures 5A and 5B provide log10 ratio diagrams comparing Lothagam *E. feibeli* to a suite of European, West Asian and African 1PHIIIs. Sahabi *E. feibeli* (ISP32P25B) plots very close to the type Lothagam and Middle Awash (JAB-VP-1-1; 6.0 Ma; Bernor & Hailie Selassie 2009) *E. feibeli* as do Pikermi *Cremohipparion mediterraneum* and the primitive Old World Sinap (Turkey) *Cormohipparion sinapensis*. It is apparent that the 1PHIII proportions are shared primitively between *Cormohipparion sinapensis, Cremohipparion mediterraneum* and *Eurygnathohippus feibeli.*

The type specimen of Lothagam MCIII exhibits a close length and proportion comparison with specimens from Sahabi (ISP82P17A), Pikermi (Crmed MEAN), Sinap (Csin_MEAN), and Middle Awash (AME-VP-1/175_Eufei and AMW-VP-1-15_Eufei) and Langebaanweg (Eu.hooijeri_MEAN) (Figs. 7A and B). As with the 1PHIII, the MCIIIs of Lothagam and Sahabi *Eurygnathohippus feibeli* reflect primitive elongate-slender proportions shared with *Eurygnathohippus hooijeri, Cormohipparion sinapensis* and *Cremohipparion mediterraneum.*

Sahabi MTIII *Eurygnathohippus feibeli* (ISP-67P16A) compares most closely with Bou Hanifia (Algeria, 10.5 Ma) *Cormohipparion africanum* and Pikermi *Cremohipparion mediterraneum.* Sinap *Cormohipparion sinapensis* has a similar length to *E. feibeli* but not as narrow a midshaft width (M3). Langebaaneweg *Eurygnathohippus hooijeri* is larger and does not have as exaggerated ratio between midshaft width (M3) and midshaft depth (M4). It is apparent that *Cormohipparion sinapensis, "Cormohipparion" africanum, Cremohipparion mediterraneum* exhibit similar trends to *Eurygnahohippus feibeli* in length and slenderization of MTIII but were not as far advanced, while a larger horse, Langebaanweg *Eurygnathohippus hooijeri* likewise shares similar log10 proportions. Our analyses of 1PHIII, MCIII and MTIII show that *Eurygnathohippus feibeli* is derived from a primitive postcranial pattern likely stemming from the most primitive Old World hipparions related to *Cormohipparion sinapensis*.

Discussion

ISP63P109A, an astragalus and an M3, and ISP74P109A, a magnum are the only skeletal elements that are derived from unit U2; the remaining 70 specimens are derived from unit U1. Sahabi's current correlation suggest that these fossils are circa 6.8 Ma and approximately correlative with *Eurygnathohippus feibeli*'s type locality, Lothagam. Our combined study of the postcrania (1PHIII, MCIII and MTIII) with the dental remains of Sahabi *Eurygnathohippus feibeli* suggests that this clade has a deep time origin.

Bernor et al. (2017) reported a number of primitive dental characters in the Pannonian C hipparions from Atzelsdorf, Gaiselberg and Mariathal, Vienna Basin, Austria (11.4-11.0 Ma): relatively low crown height (the greatest recorded crown height for Sahabi *Eurygnathohippus feibeli* being 55.8 mm for ISP3P34B), oval protocones often with flattened lingual borders, frequent confluence of pre- and postfossette plications, presence of pli caballinids and ectostylids on mandibular p2-m1. Our survey of Sahabi *E. feibeli* cheek teeth reveal: a relatively low crown height (usually not greater than 50 mm), oval protocones with flattening occurring with some incidence, rare confluence of pre- and postfossettes and associated presence of pli caballinids and ectostylids in some mandibular cheek teeth. Co-occurrence of pli caballinids associated with ectostylids are characteristic of *Eurygnathohippus*. In fact, *Eurygnathohippus* species develop ectostylid height, length and width progressively through the Plio-Pleistocene and are almost exclusively restricted in their occurrence to the African late Miocene – Pleistocene, the last occurring there somewhat later than 1 Ma. *Eurygathohippus* only occurs outside of Africa in the Tatrot faunal zone of India, ca. 3.6-2.6 Ma (Jukar et al. 2019).

The suite of primitive maxillary and mandibular cheek tooth characters cited above were likely distributed through all first occurring Old World hipparions. Woodburne (2009) and Bernor et al. (2017) reported these characters for the Pannonian C hipparions, the oldest documented Old World hipparions. Bernor et al. (2017) were able to observe the crucial pli caballinid and ectostylid characters because, for the most part, Pannonian C hipparions lack cementum on their cheek tooth crown. Their Pannonian C hipparion ectostylids are "welded" to the labial side of the crown and rise only a fraction of the height of the crown terminating in a small pointed-to-rounded structure. Other older hipparion assemblages from Sinap, Turkey (Bernor et al. 2003) and the Siwaliks, Pakistan (Bernor & Hussain 2005; Wolf et al. 2013), Chorora, Ethiopia (Bernor et al. 2004) and Bou Hanifia, Algeria (Bernor & White 2009) have dentitions that are fully invested in cementum so that if ectostylids occur on the base of the crown, they are likely buried in cementum.

Our analyses of 1PHIII, MCIII and MTIII reveal that compared to the Hoewenegg Log10 standard, Sahabi, Lothagam and Middle Awash *Eurygnathohippus feibeli* exhibit elongate-slender proportions stemming from a plausible *Cormohipparion sinapensis* ancestry. For these three skeletal elements, elongate-slender proportions are similar between *Cormohipparion sinapensis, Cormohipparion africanum, Cremohipparion mediterraneum, Eurygnathohippus feibeli* and *Eurygnathohippus hooijeri*. The two *Cormohipparion* species, *C. sinapensis* and "*C*". *africanum* are remarkably similar in these postcranial proportions. *Cremohipparion mediterraneum, Eurygnathohippus feibeli* and *E. hooijeri* exhibit similarities amongst themselves. *Cremohipparion mediterraneum* and *Eurygnathohippus feibeli* exhibit similarities in size and 1PHIII, MCIII and MTIII proportions, especially the relationships between narrow midshaft (M3) and deep midshaft (M4) proportions of the metapodials. Bernor et al. (2003) and Scott et al. (2003) noted this M3-M4 proportion as the "Esme Acakoy Effect" and related it to increased cursoriality. Moreover, not to be overlooked the standing withers height of *Eurygnathohippus feibeli* has been estimated to have been 110 cm. (Mauricio Anton, in Bernor & Harris 2003: Fig. 9.8), slightly shorter than the standing mount of Hoewenegg *Hippotherium primigenium* (130-135 cm. Bernor et al. 1997: Figs. 5.2 and 5.3).

Eurygnathohippus feibeli is known to occur at Tizi N'Tadderht, Morocco, ca. 7 Ma (Cirilli et al. 2020) and Sahabi (Bernor et al. 2012). *Eurygnathohippus feibeli* was originally recognized in the Lower and Upper Nawata members of the Nawata Formation, Lothagam, Kenya with the Holotype, KNM-LT139 occurring in the Upper Nawata. The Lower Nawata member is dated 7.44 +/-0.05 Ma to 6.54 +/-0.04 Ma (McDougall & Feibel 2003). So, the oldest Nawata assemblage is marginally older than Sahabi and Tizi N'Tadderht, while the type specimen from the Upper Nawata is arguably marginally

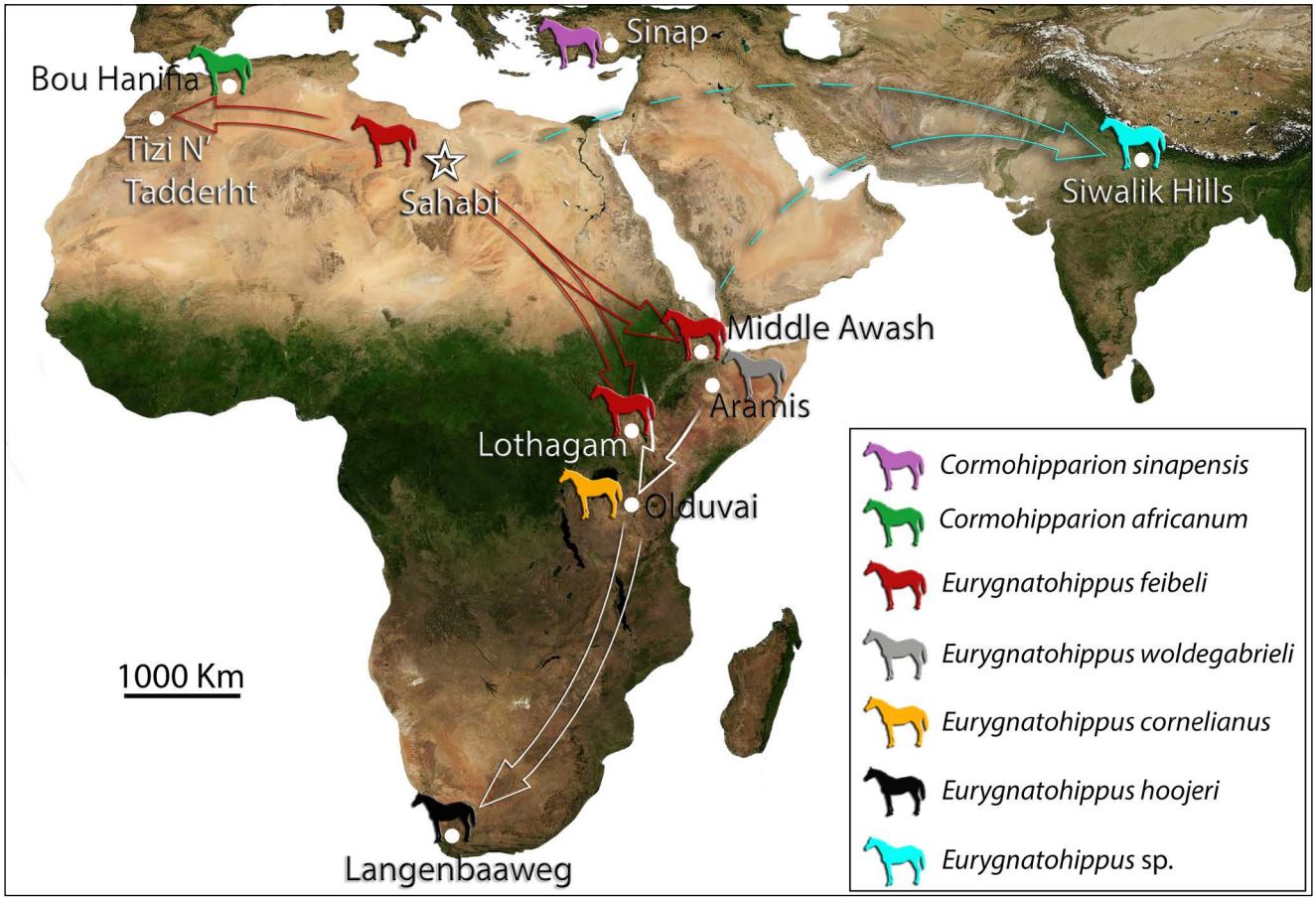

Fig. 18 - Biogeographic History of *Eurygnathohippus*. The genus arises from Old World *Cormohipparion* Datum of Sinap (Turkey) *Cormohipparion sinapensis* and Bou Hanifia (Algeria) *"Cormohipparion" africanum*. *Eurygnathohippus feibeli* earliest known occurrences from Lothagam (Kenya), Sahabi (Libya), and Tizi N'Tadderht (Morocco) with slightly younger recorded occurrence from JAB Middle Awash (Ethiopia); subsequent recorded succession in East and South Africa with *Eurygnathohippus woldegabrieli* from Aramis (Ethiopia), *Eurygnathohippus cornelianus* from Olduvai (Tanzania), and *Eurygnathohippus hoojeri* from Langenbaaweg (South Africa).

younger (<6.54 Ma). The oldest sediments in the Middle Awash are 6.0 Ma and a complete 1PHIII of *E. feibeli* occurs there at Jara-Borkana (JAB), 6.0 Ma. (WoldeGabriel et al. 2009). Bernor & Hailie Selassie (2009) have reported *Eurygnathohippus* aff. *feibeli* from younger Middle Awash levels dating 5.7-5.2 Ma. Mandibular cheek tooth pli caballinids and ecstostylids persist through the Middle Awash succession, but postcranial log10 proportions do shift later to larger size than *E. feibeli* in the section by 5.4-5.2 Ma.

The next recognized Ethiopian *Eurygnathohippus* species is *E. woldegabrieli* from the 4.4 Ma. locality of Aramis (Bernor et al. 2013). There are distinct trends in the evolution of the African *Eurygnathohippus* species *E. feibeli* – *E. woldegabrieli* – *E. hasumensis* – *E. cornelianus* which include: increase in size through *E. hasumensis*; increase in crown height; lengthening of MCIII and MTIII, increased height, length and width of ectostylids (Bernor et al. 2005; here, including *E. cornelianus*). *Eurygnathohippus cornelianus* first occurs at Olduvai Gorge (ca. 1.9 Ma) and is remarkable for the expansion of premaxillary and mandibular I1/i1 and I2/i2 with sharp reduction of I3/i3.

The origin, evolution and biogeography of the *Eurygnathohippus* clade has only recently become clarified. The oldest Old World hipparions have been reported from Pannonian C strata, Vienna Basin and are dated 11.4-11.0 Ma. Maxillary and mandibular cheek teeth of these hipparions exhibit a number of primitive characters discussed here, with some of these being found in *Eurygnathohippus*. Comparison of 1PHIII, MCIII and MTIII log10 proportions exhibits evolutionary trends stemming from Sinap, Turkey *Cormohipparion sinapensis* (10.8 Ma) and Bou Hanifia, Algeria *Cormohipparion africanum* (10.8 Ma) and evolving more slender, deep keeled MCIII and MTIII in *Cremohipparion mediterraneum* and *Eurygnathohippus feibeli*. In that *Cremohip-*

parion mediterraneum consistently lacks pli caballinids and ectostylids, it is derived compared to *Eurygnathohippus feibeli* and its descendants. The genus *Eurygnathohippus* is therefore validated now based on both dental and postcranial characters. Figure 18 illustrates the Late Miocene - Pliocene biogeographic record of *Eurygnathohippus*.

Conclusions

Eurygnathohippus is a distinct clade of hipparionine horses, with *Eurygnathohippus feibeli* having a known geographic range from Kenya, to Ethiopia, Libya and Morocco, and a chronologic range of approximately 7.0 – 5.7 Ma. *Eurygnathohippus feibeli* had primitive cheek tooth characters including occurrence of co-occurring ectostylids and pli caballinids on the mandibular cheek teeth; very narrow (knife-like) mesostyles with complex plications of the pre- and postfossettes in middle wear in the maxillary cheek teeth; and a maximum crown height of 56 mm. *Eurygnathohippus'* cheek tooth morphology is clearly derived from earliest occurring hipparions from the Pannonian C, Austria (Bernor et al. 2017) and its postcranial anatomy would appear to be derived from first occurring Old World *Cormohipparion sinapensis* from Sinap, Turkey (Bernor et al. 2003) and *"Cormohipparion" africanum* Bou Hanifia, Algeria (Bernor & White 2009). Moreover, the slender 1PHIIIs, MCIIIs and MTIIIs compare closely with Pikermi *Cremohipparion mediterraneum* and are divergent from primitive *Hippotherium primigenium*. The *Eurygnathohippus* clades' evolutionary radiation is restricted to Africa until the Pliocene when it extended its range into India during the Late Pliocene, ca. 3.6-2.6 Ma (Jukar et al. 2019). Whereas Zouhri and Bensalmia (2005) have recognized *Eurygnathohippus* at the subgeneric rank (*Proboscidipparion* (*Eurygnathohippus*)), we follow other authors recognizing *Eurygnathohippus* as a distinct clade of generic rank (Bernor & Harris 2003; Bernor & Hailie Selassie 2009; Bernor et al. 2010; Bernor et al. 2012; Cirilli et al. 2020).

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