The Early Pliocene *Plesiohipparion* and *Proboscidipparion* (Equidae, Hipparionini) from Çalta, Turkey (Ruscinian Age, *c.* 4.0 Ma)

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ABSTRACT

The Early Pliocene locality of Çalta, Turkey (Ruscinian Age, *c.* 4.0 Ma) has two species of advanced hipparionine horses that we refer to *Plesiohipparion* cf. *longipes* (Gromova, 1952) and *Proboscidipparion heintzi* (Eisenmann & Sondaar, 1998). Our study follows an extensive treatment of the entire mammalian fauna in 1998 and in particular an important and comprehensive work on the hipparions by Eisenmann & Sondaar in 1998. We undertake herein a morphologic and metric analysis of skulls, mandibles, dentitions and postcranial elements to segregate all elements into these two taxa. Our analysis follows and concurs with Eisenmann & Sondaar's work except for the generic attributions here which are original. Beyond the basic empirical work here, we strike comparisons to other Old World hipparion lineages and find that these two hipparion taxa compare closely, at the genus level, to Asian *Plesiohipparion* Qiu, Huang & Guo, 1987 and *Proboscidipparion* Sefve, 1927. Our comparisons further elucidate that *Plesiohipparion* had undertaken a range extension into Anatolia by 7.1 Ma where it is present at the locality of Akkaşdağı. Our work suggests that *Proboscidipparion* extended its range from China into Anatolia in the Early Pliocene. Reevaluation of the entire Çalta mammalian fauna suggests that Anatolia was a dynamic biogeographic region in the Early Pliocene including endemic forms, Late Miocene Eurasian holdovers and Asian and African immigrant taxa. Turkey was in fact a Eurasian cross-roads region of active intercontinental mammalian migrations in the Early Pliocene.

KEY WORDS
Equidae,
hipparionines,
Pliocene,
paleobiogeography,
Çalta,
Turkey.

RÉSUMÉ

Plesiohipparion *and* Proboscidipparion *(Equidae, Hipparionini) du Pliocène inférieur de Çalta, Turquie (Ruscinien,* c. *4.0 Ma).*

Le gisement de Çalta se situe en Anatolie centrale en Turquie et il est corrélé au Pliocène inférieur (Ruscinien, *c.* 4,0 Ma). Il a livré deux espèces d'hipparions à caractères dérivés que nous appelons *Plesiohipparion* cf. *longipes* (Gromova, 1952) et *Proboscidipparion heintzi* (Eisenmann & Sondaar, 1998). La faune de Çalta a fait l'objet d'une étude intégrale en 1998 et, dans ce contexte, Eisenmann & Sondaar ont décrit en détail les hipparions de ce site. Nous proposons ici une analyse morphologique et biométrique de crânes, mandibules, dentitions et éléments postcrâniens appartenant à ces deux taxons. Notre analyse est en accord avec le travail de Eisenmann & Sondaar, sauf pour les attributions génériques qui sont ici reconsidérées. Au-delà du travail empirique de base, nous avons effectué des comparaisons avec d'autres lignées d'hipparions de l'Ancien Monde et constaté que ces deux taxons se comparent étroitement, au niveau générique, avec les hipparions asiatiques que sont *Plesiohipparion* Qiu, Huang & Guo, 1987 et *Proboscidipparion* Sefve, 1927. Nos comparaisons montrent en outre que l'extension géographique de *Plesiohipparion* jusqu'en Anatolie est déjà ancienne, puisqu'il existe déjà dans la localité d'Akkaşdağı qui date de 7,1 Ma. En revanche, notre travail suggère que l'extension de *Proboscidipparion* de Chine en Anatolie est apparemment plus tardive, probablement au début du Pliocène. La réévaluation de l'ensemble de la faune mammalienne de Çalta suggère que l'Anatolie était une région biogéographique dynamique au début du Pliocène, et abritait, à côté de quelques formes endémiques, des survivants eurasiennes du Miocène supérieur et des taxons immigrants asiatiques et même peut-être africains. La Turquie était en fait une région de carrefour très actif au début du Pliocène pour les migrations intercontinentales de mammifères.

MOTS CLÉS
Equidae,
hipparionines,
Pliocène,
paléobiogeographie,
Çalta,
Turquie.

INTRODUCTION

The hipparionine remains studied in this paper come from the locality of Çalta, which is situated about 50 km NW of Ankara in Central Anatolia, Turkey (Fig. 1). Its coordinates are 40°14'21.8"N and 32°32'39.0"E. The material was collected in 1972 by a French-Turkish team, and the hipparionines were initially studied by Heintz *et al.* (1975) and Eisenmann & Sondaar (1998). These authors recognized two species, *Hipparion* cf. *longipes* Gromova, 1952 and *Hipparion heintzi* Eisenmann & Sondaar, 1998. For its ecomorphological adaptations, Sen *et al.* (1978) noted the extreme specialization in limb proportions of the second species.The present study provides an update of their systematic status based on an extensive comparison of their metrical and morphological features with similar forms in Eurasia and Africa, aiming to enlighten their bearing to the evolutionary history of related Old World hipparionines and their dispersal history.

The Çalta locality yielded a rich and diverse vertebrate assemblage including amphibians, reptiles, small and large mammals. A monogroph on this fauna, edited by one of us in 1998 in *Geodiversitas*, provides a rather complete view of its diversity.

Central Anatolia, where the locality is situated, is at present a 1000-1500 m high plateau surrounded by the Pontides and Taurides mountain chains that are part of the Alpine system. This plateau was uplifted due to the collision of the Afro-Arabian and Eurasian plates, and it is squeezed between the two subduction-accretion suture zones formed by the closure of northern and southern branches of the Neotethys ocean. After the closure of the northern branch of the Neotethys, in Late Cretaceous-Early Eocene, several foreland basins developed in Anatolia, the largest of them being the Tuzgölü Basin. These initially marine basins were transformed to continental basins by the final collision event in Late-Oligocene-Early Miocene, which resulted in the closure of southern branch of Neotethys. Subsequently this region developed thick accumulations of terrestrial deposits (Görür *et al.* 1998).

The Çalta area is situated in the northwestern part of the large Tuzgölü Basin. In this area, the substratum of Neogene deposits is composed of chaotically associated schist, calc-schist, quartzite, phyllite and Jurassic limestones, unconformably overlain by Eocene conglomerates and nummulitic limestones (Rojay & Karaca 2008). The Mio-Pliocene deposits cover unconformably this basement and develop over 1000 m thick terrestrial sedimentary infill. These deposits partly interfinger with volcanics of the Galatean Volcanic Province, which covers large areas to the north-northwest. The oldest sedimentary unit, the Pazar Formation, does not outcrop in the Çalta area but occupies large areas to the east. It is mainly composed of clastics at the base and, cherts and limestones at the top of the sequence representing a fresh water lake environment (Karaca 2004). It is overlain by a basaltic lava flow dated to 15.2 ± 0.3 Ma (Lunkka *et al.* 2003). This formation is unconformably covered by the Sinap Formation that crops out in large areas in that part of the basin. It was subject of detailed stratigraphic, sedimentological and paleontological research. It is mainly composed of floodplain deposits. Lunkka *et al.* (2003) divided this formation into several members, the youngest of them being the Çalta Member (Fig. 1). Lunkka *et al.* (1998) studied in detail stratigraphy and sedimentology of Çalta Member in its type section across the Çalta vertebrate locality. It is composed

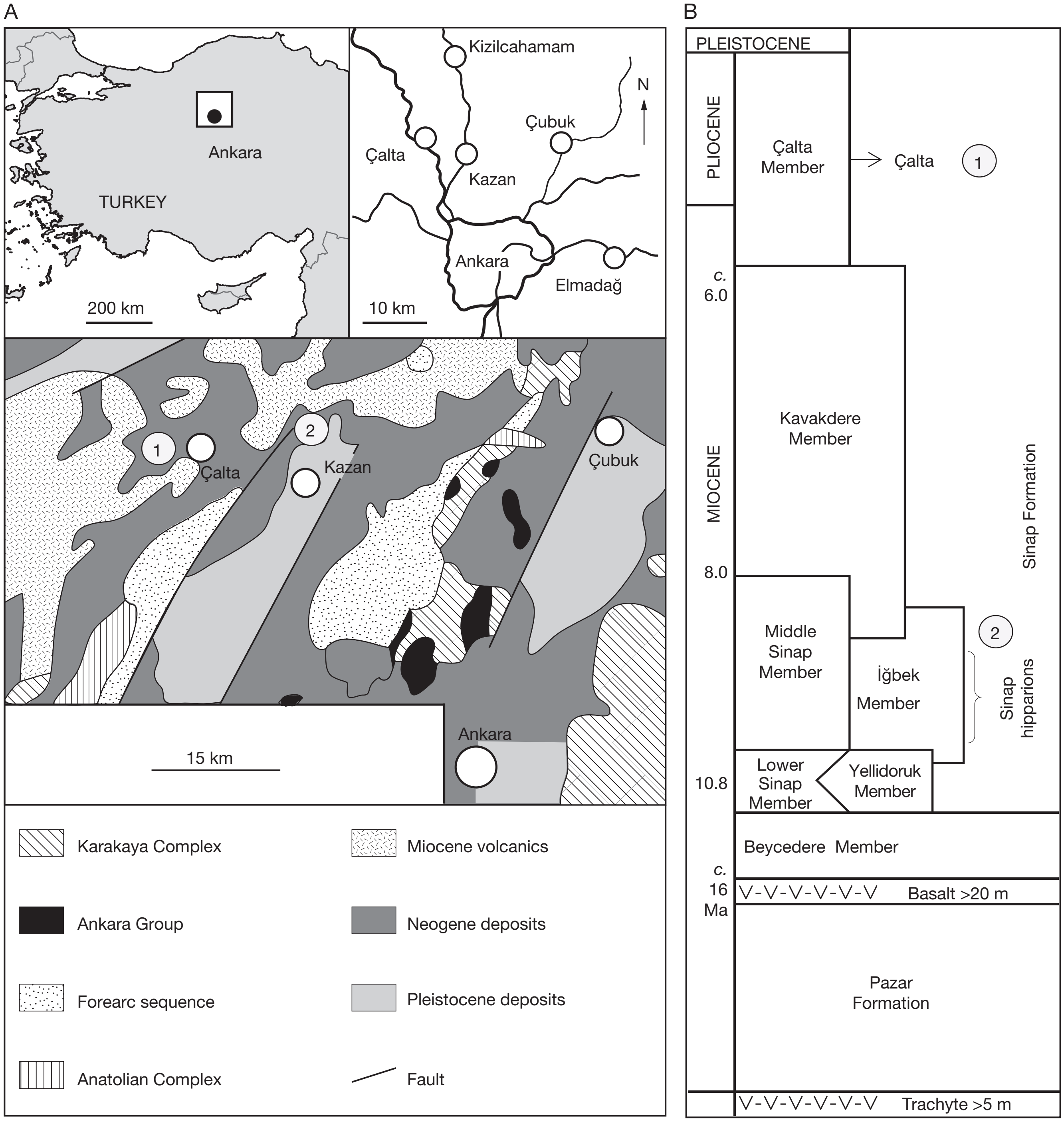

Fig. 1. — **A**, Simplified geology map of the Kazan-Çalta area (modified from Lunkka *et al.* 1998); **B**, stratigraphy of the Sinap Formation as estalished by Lunkka *et al.* (2003), on which the stratigraphic position of Çalta (**1**) and the Middle Sinap Member hipparion localities (**2**) are indicated.

of massive mudstones interbedded with rather thin layers of gravel conglomerates and sandstones, which mainly occur in the lower part of the section. Conglomerates and sandstones are led down as channel and overbank deposits, while the massive mudstones are interpreted as deposits of floodplain environment. The Çalta vertebrate locality is included in the upper part of the section in massive mudstones.

This locality yielded a mammalian assemblage rather diversified with four species of insectivores (*Asoriculus gibberodon* (Petenyi, 1864), *Mafia csarnotense* Reumer, 1984, Soricidae indet., *Erinaceus* sp.), one ochotonid (*Ochotonoma anatolica* Sen, 1998), nine rodents (*Centralomys magnus* (Sen, 1977), *Occitanomys* sp., *Orientalomys galaticus* (Sen, 1975), *Apodemus dominans* Kretzoi, 1959, *Mesocricetus* cf. *primitivus* de Bruijn, Dawson & Mein, 1970, *Pseudomeriones tchaltaensis* Sen, 1977, *Mimomys davakosi* van de Weerd, 1979, *Pliospalax macoveii* (Simionescu, 1930), *Dryomimus eliomyoides* Kretzoi, 1959), five carnivores (*Vulpes galaticus* Ginsburg, 1998, *Nyctereutes* *donnezani* (Deperet, 1890), *Chasmaporthetes kani anatolicus* Ginsburg, 1998, *Lynx issiodorensis* (Croizet & Jobert, 1828), *Machairodus giganteus* (Wagner, 1848)), one rhinocerotid (*Dicerorhinus megarhinus* (de Christol, 1834)), two hipparionines (*Plesiohipparion* cf. *longipes* (Gromova, 1952), *Proboscidipparion heintzi* (Eisenmann & Sondaar, 1998)), one suid (*Sus arvernensis minor* Deperet, 1890), one cervid (*Cervus* cf. *perrieri* Croizet & Jobert, 1828), one giraffid (*G.* cf. *jumae* Leakey, 1965) and five species of bovids (*Gazella emilii* Bouvrain, 1998, *Tchaltacerus longicornis* Bouvrain, 1998, Bovidae indet. cf. *Koufotragus bailloudi* (Arambourg & Piveteau, 1929), *Gazellospira* sp., Hippotragini indet.). It is mainly composed of elements with European and Asiatic affinities. The age of this fauna is deduced from the stage of evolution of some key taxa that are strictly limited to the Pliocene such as *Asoriculus, Mafia*, *Mesocricetus*, *Mimomys, Dryomimus, Vulpes, Dicerorhinus*, *Sus* and *Giraffa* or appear at most during the Latest Miocene such as *Centralomys*, *Nyctereutes* and *Chasmaportetes* (Sen *et al.* 1998). The occurrence of the primitive arvicolid *Mimomys* together with many other Pliocene species suggests a correlation to the mammalian biozone MN15, and more probably to the lower part of this biozone, with an absolute age *c.* 4 Ma. Since the outcome of the Çalta monograph in 1998, this correlation received a general agreement of paleontologists.

ABBREVIATIONS

Ma	mega-annum in the geochronologic time scale. Ages in m.y. usually based on radioisotopic analyses or magnetostratigraphic analyses. North Africa: localities may be referred to the MN biochronologic time scale. Western Eurasia: Vallesian, Turolian, and Ruscinian; intervals of the European land mammal age sequence, commonly termed units (sensu Fahlbusch 1991).

Measurements

Sex

Sex can be defined by the size of a canine tooth, male being large, female being small.

M	male;
F	female;
?	unknown.

Side

lt.	left;
rt.	right.

Element abbreviations

CALC	calcaneum;
AST	astragalus;
MCIII	metacarpal III;
MCIV	metacarpal IV;
MTIII	metatarsal III;
MPIII	metapodial III;
1PHIII	1st phalanx III
2PHIII	2nd phalanx III (central digit) of either the anterior or posterior limb, which are difficult to distinguish in hipparion.
I, C, P, M	maxillary tooth (uppercase);
i, c, p, m	mandibular tooth (lower case).

Statistical plots

M1-M38 refers to measurements as described by Eisenmann *et al.* (1988) and Bernor *et al.* (1997). Statistical plots include abbreviations by locality. Color symbols have been added to the Figures to clarify their readings. These abbreviations and symbols are as follows:

▲	(a)	Akkaşdağı, Turkey;
◆	(b)	Sahabi, Libya;
⬢	(c)	China, *Plesiohipparion* spp.;
▲	(e)	Ethiopia;
■	(g)	Germany;
+	(k)	Pikermi;
▼	(l)	Langebaanweg;
■	(m)	Maragheh;
▣	(n)	Sinap;
▼	(p)	Pakistan;
⌂	(t)	Tanzania;
◈	(w)	Perpignan;
⊖	(y)	Kenya;
☀	(Z)	Çalta, *Proboscidipparion*;
☀	(z)	Çalta, *Plesiohipparion*.

Taxonomic abbreviations

Taxonomic abbreviations used in Log10 plots (from R.L. Bernor database unless otherwise indicated):

AS93/332	*Cormohipparion sinapensis* Bernor, Scott, Fortelius, Kappelman & Sen, 2003 from Sinap, Turkey (MN9, 10.5 Ma);
Csin	*Cormohipparion sinapensis* from Esme-Akçaköy, Turkey (MN9, 10.5 Ma);
Cafr	"*Cormohipparion*" *africanum* (Arambourg, 1959) from Bou Hanifia, Algeria (MN9, 10.5 Ma);
Crmed_MEAN	Mean measurements of *Cremohipparion mediterraneum* (Roth & Wagner, 1854) from Pikermi, Greece (MN11, *c.* 8.0 Ma; Koufos 1987);
Crant_MEAN	Mean measurements of *Cremohipparion antelopinum* (Falconer & Cautley, 1849) from the Late Miocene of Indo-Pakistan (Late Miocene age);
Hcamp	*Hipparion campbelli* Bernor, 1985 from Late Miocene of Maragheh, Iran (MN12, *c.* 7.9 Ma);
Hbralg_S_MEAN	Mean measurements of *Hippotherium brachypus* (Hensel, 1862) large population from Samos, Greece (MN12, *c.* 8-7 Ma);
HbraP_MEAN	Mean measurements of *Hippotherium brachypus* type assemblage from Pikermi, Greece (MN 11, *c.* 8.0 Ma.; Koufos 1987);
HpriDS	*Hippotherium primigenium* von Meyer, 1829 from Dinotheriensande, Germany (MN9, 10.5 Ma);
Euafa	*Eurygnathohippus afarense* Eisenmann, 1976 from Hadar, Ethiopia (*c.* 3.4-2.9 Ma);
EufeiL	Type *Eurygnathohippus feibeli* (Bernor & Harris, 2003) from Upper Nawata, Lothagam Hill, Kenya (*c.* 6.0 Ma);
EufeiS	*Eurygnathohippus feibeli* from Sahabi, Libya;
Euhoo_MEAN	*Eurygnathohippus hooijeri* Bernor & Kaiser, 2006 from Langebaanweg, South Africa (*c.* 5.0 Ma);
Euwold	*Eurygnathohippus woldegabrieli* Bernor, Gilbert, Semprebon, Simpson & Semaw, 2013 from Aramis, Ethiopia (*c.* 4.4 Ma);
Pl_C _MEAN	Mean measurements of *Plesiohipparion* spp. China (6-2.5 Ma);
Pllong_MEAN_A	*Plesiohipparion longipes* from Akkaşdağı, Turkey (*c.* 7.1 Ma; Koufos & Vlachou 2005 and Scott & Maga 2005);
Prhein	*Proboscidipparion heintzi* from Çalta, Turkey (4.0 Ma);
PrheinT	*Proboscidipparion heintzi*, type specimen, Çalta, Turkey (4.0 Ma).

Sper_MEAN	Mean measurements of *Sivalhippus perimensis* Pilgrim, 1910 from the Siwaliks, Indo-Pakistan (*c.* 8.5-7.5 Ma);
Stur	*Sivalhippus turkanensis* (Hooijer & Maglio, 1973) from Lower Nawata, Lothagam Hill, Kenya (*c.* 6.5 Ma).

Museum collections

AMNH	American Museum of Natural History, New York (AMNH numbers);
BMNH	Natural History Museum, London, England (BMNH numbers);
MNHN	Muséum national d'Histoire naturelle, Paris (MNHN.F numbers);
THP	Tianjin Museum of Natural History, Tianjin, China (THP numbers).

Systematic conventions

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

Hipparionine

A taxonomic 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* Skinner & MacFadden, 1977, *Neohipparion* Gidley, 1903, *Nannippus* Matthew, 1926, *Pseudhipparion* Ameghino, 1904, *Hippotherium* von Meyer, 1829, *Cremohipparion* Qiu, Huang & Guo, 1987, *Hipparion* Christol, 1832, "*Sivalhippus*" Bernor & Hussain, 1985, *Eurygnathohippus* van Hoepen, 1930 (senior synonym of "*Stylohipparion*"), *Proboscidipparion* Sefve, 1927, *Plesiohipparion* Qiu, Huang and Guo, 1987. These lineages have recently been reviewed by Qiu *et al.* (1987), Bernor & White (2009), Bernor *et al.* (2010, 2013, 2014), Armour-Chelu & Bernor (2011), Wolf *et al.* (2013), Bernor & Sun (2015) and Bernor *et al.* (2015a, b).

Hipparion *s.s.*

This 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 *et al.* 1987, 1989; Woodburne 2007). The posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne & Bernor 1980). Bernor's definition departs from some investigators in not recognizing North American species of Hipparion s.s. Bernor (1985), Bernor (in Bernor *et al.* 1989) have argued that any morphologic similarity between North American "Hipparion" and Old World *Hipparion* s.s. is due to homoplasy. Bernor *et al.* (2016) have recognized Old World *Hipparion* s.s. to include *Hipparion prostylum* Christol, 1832*, Hipparion dietrichi* Wehrli, 1941 and *Hipparion campbelli* based on the combination of cranial and postcranial characters. Chinese *Hipparion hippidiodus* Sefve, 1927 may be another member of this clade *sensu stricto*.

"Hipparion"

Several distinct and separate lineages of Old World hipparionine horses once considered to be referable to the genus *Hipparion* (Bernor *et al.* 2011). 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 and the Ukraine. Species belonging to this genus include *H. primigenium*, *H. intrans* Kretzoi, 1983, *H. microdon* Kormos, 1914, *H. kammerschmittae* Kaiser, Bernor, Scott, Franzen & Solounias, 2003, *H. malpassii* Bernor, Kaiser, Nelson & Rook, 2011, *H. brachypus* and perhaps *H. giganteum* Gromova, 1952 (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). 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 log 10 ratio diagrams to evaluate differences in hipparion metapodial proportions as a basis for recognizing taxa and their evolutionary relationships. Bernor *et al.* (2003) and Bernor & Harris (2003) have used multiple statistical tests, including univariate, bivariate and multivariate statistics as well as log 10 ratio diagrams to evaluate and resolve the alpha systematics of hipparionine horses. Bernor *et al.* (2005) used log 10 ratio diagrams together with multivariate statistics to evaluate metapodial and first phalangeal evidence for postcranial evolution in Ethiopian hipparions. Bernor *et al.* (2016) have used log 10 ratios combined with bivariate plots to integrate postcranial with cranial morphology to characterize multiple species of Maragheh, Iran hipparions. We incorporate these previously used methodologies in this work. Our statistical analysis uses the skeletal population from Höwenegg (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 (MCIIIs, MTIIIs and 1PHIIIs).

Table 1. — Measurements of the cranial and postcranial specimens of hipparionine horses from Çalta, Turkey. Taxon abbreviations: ***P. h.***, *Proboscidipparion heintzi* (Eisenmann & Sondaar, 1998); ***P.* cf. *l.***, *Plesiohipparion* cf. *longipes* (Gromova, 1952). Specimen numbers come from MNHN.F Collection.

Specimen number	Taxon	Bone	Side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18
ACA336	*P. h.*	skull	3	–	108.0	105.7	–	–	–	104.8	–	–	55.0	31.0	37.6	71.6	–	–	–	–	–
ACA336	*P. h.*	txdP1	lt.	13.7	–	9.9	–	9.4	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA336	*P. h.*	txdP2	rt.	44.0	–	24.5	–	13.9	4.0	5.0	3.0	0.0	6.7	5.5	–	–	–	–	–	–	–
ACA336	*P. h.*	txdP3	rt.	33.4	–	23.7	–	14.4	0.0	6.0	1.0	1.0	6.4	5.4	–	–	–	–	–	–	–
ACA336	*P. h.*	txdP4	rt.	31.8	–	23.7	–	14.5	4.0	3.0	2.0	2.0	6.2	4.8	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP1	lt.	14.1	–	8.3	–	7.9	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP2	lt.	43.1	–	24.6	–	12.8	4.0	4.0	3.0	2.0	8.2	6.3	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP3	lt.	30.5	–	24.4	–	11.8	3.0	4.0	1.0	0.0	6.8	5.8	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP4	lt.	31.5	–	23.7	–	12.3	3.0	4.0	2.0	0.0	8.0	5.4	–	–	–	–	–	–	–
ACA337B	*P. h.*	txM1	lt.	31.3	–	24.5	–	17.0	–	–	–	–	8.0	4.5	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmdp2	lt.	37.3	34.4	16.7	11.2	14.6	15.2	–	14.1	14.7	14.3	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmdp3	lt.	28.1	28.3	17.9	11.0	14.2	15.3	–	15.0	14.2	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmdp4	lt.	28.5	29.6	18.5	11.0	12.7	14.6	–	13.2	12.3	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmm1	lt.	30.2	26.0	16.7	9.8	12.9	12.3	–	11.8	10.2	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	mand	lt.	406.0	101.0	96.3	–	–	120.4	–	228.6	223.4	–	75.1	58.6	82.6	40.5	–	–	–	–
ACA122	*P. h.*	p1ph3	lt.	65.3	58.5	33.9	45.8	34.9	38.6	39.6	23.1	17.7	39.7	43.8	17.8	16.8	–	–	–	–	–
ACA123	*P. h.*	p1ph3	lt.	67.2	59.9	34.8	47.2	35.0	39.1	–	20.9	23.8	–	–	–	–	–	–	–	–	–
ACA77	*H.* sp.	–	rt.	65.9	57.8	32.4	45.1	33.4	38.3	41.6	22.1	18.5	47.7	45.9	11.5	14.4	–	–	–	–	–
ACA106	*P. h.*	a1ph3	rt.	71.7	64.6	35.9	49.7	35.1	44.2	43.9	23.3	21.9	45.1	47.4	17.3	17.4	–	–	–	–	–
ACA78	*P. h.*	a1ph3	lt.	65.4	55.8	34.9	47.3	32.9	40.0	40.3	21.4	16.7	38.4	39.7	13.8	18.3	–	–	–	–	–
ACA76	*P. h.*	a1ph3	lt.	67.9	63.7	36.0	50.5	34.7	40.9	>38	23.5	18.7	45.0	–	17.6	–	–	–	–	–	–
ACA82	*P.* cf. *l.*	1ph3	lt.	75.1	65.8	28.8	38.8	33.6	32.9	32.9	–	20.2	49.0	50.0	17.2	16.4	–	–	–	–	–
ACA124	*P.* cf. *l.*	1ph3	lt.	–	–	–	40.9	31.1	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA81	*P. h.*	2ph3	lt.	47.9	38.2	44.1	51.1	31.5	50.4	–	–	–	–	–	–	–	–	–	–	–	–
ACA260	*P. h.*	2ph3	rt.	47.3	37.9	42.6	51.4	30.9	44.3	–	–	–	–	–	–	–	–	–	–	–	–
ACA173	*P. h.*	–	lt.	42.6	36.2	39.3	46.6	29.6	42.9	–	–	–	–	–	–	–	–	–	–	–	–
ACA86	*P. h.*	–	lt.	43.8	32.9	39.4	–	28.5	38.4	–	–	–	–	–	–	–	–	–	–	–	–
ACA83	*P. h.*	–	lt.	43.4	34.3	38.7	–	28.1	41.1	–	–	–	–	–	–	–	–	–	–	–	–
ACA84	*P.* cf. *l.*	–	lt.	48.1	36.7	36.6	42.4	28.6	41.8	–	–	–	–	–	–	–	–	–	–	–	–
ACA87	*P.* cf. *l.*	–	lt.	56.6	53.7	59.2	44.2	25.1	40.2	–	–	–	–	–	–	–	–	–	–	–	–
ACA89	*P. h.*	p3ph3	lt.	61.7	64.7	64.5	46.4	27.8	38.3	–	–	–	–	–	–	–	–	–	–	–	–
ACA126	*P. h.*	p3ph3	3	63.9	64.4	65.3	48.2	25.1	36.5	–	–	–	–	–	–	–	–	–	–	–	–
ACA112	*P. h.*	p3ph3	3	58.2	59.7	75.0	52.0	25.1	37.2	–	–	–	–	–	–	–	–	–	–	–	–
ACA251	*P. h.*	a3ph3	lt.	56.6	56.6	70.2	49.8	26.6	36.2	–	–	–	–	–	–	–	–	–	–	–	–
ACA66	*P. h.*	ast	rt.	57.1	56.4	28.0	62.3	49.4	46.8		–	–	–	–	–	–	–	–	–	–	–
ACA150	*P. h.*	calc	rt.	113.1	80.5	24.7	35.9	51.2	57.5	51.5	–	–	–	–	–	–	–	–	–	–	–
ACA61B	*P. h.*	ast	rt.	61.2	60.8	28.5	60.6	49.4	36.2	51.4	–	–	–	–	–	–	–	–	–	–	–
ACA61A	*P. h.*	calc	rt.	–	–	21.4	–	–	56.3	46.5	–	–	–	–	–	–	–	–	–	–	–
ACA73	*P. h.*	calc	lt.	–	–	23.4	–	–	–	54.2	–	–	–	–	–	–	–	–	–	–	–
ACA65	*P. h.*	ast	rt.	63.5	62.3	30.3	63.0	49.8	37.7	52.1	–	–	–	–	–	–	–	–	–	–	–
ACA64	*P. h.*	ast	rt.	62.7	65.4	29.2	65.4	50.1	38.5	65.0	–	–	–	–	–	–	–	–	–	–	–
ACA67	*P. h.*	calc	rt.	–	–	24.1	–	–	64.5	53.2	–	–	–	–	–	–	–	–	–	–	–
ACA92	*P.* cf. *l.*	ast	rt.	64.2	59.8	26.6	54.9	47.4	37.1	59.7	–	–	–	–	–	–	–	–	–	–	–
ACA63	*P.* cf. *l.*	ast	rt.	61.4	62.6	26.5	59.1	49.3	39.0	51.6	–	–	–	–	–	–	–	–	–	–	–
ACA259	*P.* cf. *l.*	ast	lt.	64.3	63.0	28.9	54.2	45.9	37.0	53.0	–	–	–	–	–	–	–	–	–	–	–
ACA112C	*P. h.*	mtiii	rt.	–	–	31.2	27.5	48.1	40.1	44.5	11.0	6.9	–	–	–	–	–	–	–	–	–
ACA55	*P.* cf. *l.*	mtiii	rt.	–	–	22.9	24.7	41.3	32.9	39.4	9.9	3.9	–	–	–	–	–	–	–	–	–
ACA209	*P.* cf. *l.*	mtiii	rt.	–	–	28.9	27.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA214	*P.* cf. *l.*	mtiii	rt.	319.5	313.0	30.1	29.9	40.2	36.9	41.6	10.0	7.1	39.8	36.0	34.4	27.3	30.9	–	–	–	–
ACA257B	*P. h.*	mciii	rt.	204.1	193.2	32.2	–	48.4	33.6	41.9	14.7	–	–	41.2	36.9	27.8	31.2	–	–	–	–
ACA56	*P.* cf. *l.*	mciii	rt.	–	–	28.6	26.7	44.0	27.3	39.2	11.8	6.3	–	–	–	–	–	–	–	–	–
ACA49A	*P.h.* type	mciii	rt.	211.6	195.7	34.1	26.6	50.2	33.6	42.2	15.7	6.9	49.2	47.5	35.1	28.6	29.1	–	–	–	–

STATISTICAL ANALYSIS

Bivariate plots

Table 1 provides measurements of the Çalta specimens used in this analysis. These measurements were taken by R.L. Bernor. Comparative measurements were taken from Bernor's unpublished equid database. Höwenegg, Germany (10.3 Ma) is used as the population standard for calculating 95% ellipses. In addition, we include the following hipparion samples in the analysis:

- Akkaşdağı, Turkey (symbol "a"; 7.1 Ma; MN 12);
- Sahabi, Libya (symbol "b"; *c.* 7.5-7.0 Ma; MN 12 and 13);
- Yushe and Nihowan, China specimens of *Plesiohipparion* (symbol "C"; 6-2.5 Ma.);
- Middle Awash and Gona, Ethiopia (symbol "e"; 6-1 Ma);
- Eppelsheim, Germany (symbol "g"; *c.* 10.3-10.0 Ma);
- Pikermi, Greece (symbol "k"; *c.* 8 Ma);
- Sinap (symbol "n"; *c.* 10.7-9.9 Ma);
- Siwalik Hills, Pakistan (symbol "p"; *c.* 10.7-6.9 Ma);
- Late Miocene-Pleistocene of Tanzania (symbol "t"; *c.* 7-1 Ma);

TABLE 1. — Continuation.

Specimen number	Taxon	Bone	Side	M19	M20	M21	M22	M23	M24	M25	M26	M27	M28	M29	M30	M31	M32	M33	M34	M35	M36	M37	M38
ACA336	*P. h.*	skull	3	–	–	–	–	–	–	–	–	–	54.5	48.3	–	–	–	–	–	–	–	57.9	–
ACA336	*P. h.*	txdP1	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA336	*P. h.*	txdP2	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA336	*P. h.*	txdP3	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA336	*P. h.*	txdP4	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP1	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP2	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337B	*P. h.*	txdP4	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337B	*P. h.*	txM1	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmdp2	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmdp3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmdp4	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	tmm1	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA337A	*P. h.*	mand	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA122	*P. h.*	p1ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA123	*P. h.*	p1ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA77	*H.* sp.	–	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA106	*P. h.*	a1ph3	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA78	*P. h.*	a1ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA76	*P. h.*	a1ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA82	*P.* cf. *l.*	1ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA124	*P.* cf. *l.*	1ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA81	*P. h.*	2ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA260	*P. h.*	2ph3	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA173	*P. h.*	–	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA86	*P. h.*	–	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA83	*P. h.*	–	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA84	*P.* cf. *l.*	–	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA87	*P.* cf. *l.*	–	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA89	*P. h.*	p3ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA126	*P. h.*	p3ph3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA112	*P. h.*	p3ph3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA251	*P. h.*	a3ph3	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA66	*P. h.*	ast	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA150	*P. h.*	calc	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA61B	*P. h.*	ast	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA61A	*P. h.*	calc	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA73	*P. h.*	calc	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA65	*P. h.*	ast	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA64	*P. h.*	ast	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA67	*P. h.*	calc	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA92	*P.* cf. *l.*	ast	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA63	*P.* cf. *l.*	ast	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA259	*P.* cf. *l.*	ast	lt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA112C	*P. h.*	mtiii	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA55	*P.* cf. *l.*	mtiii	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA209	*P.* cf. *l.*	mtiii	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA214	*P.* cf. *l.*	mtiii	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA257B	*P. h.*	mciii	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA56	*P.* cf. *l.*	mciii	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ACA49A	*P. h.* type	mciii	rt.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

- Perpignan, France (symbol “w”; *c.* 4-3 Ma);
- Late Miocene-Pliocene of Kenya (symbol “k”; *c.* 8-2.5 Ma);
- Çalta, Turkey (symbol “Z” for *Proboscidipparion heintzi* and “z” for *Plesiohipparion longipes*; *c.* 4 Ma).

These measurements were taken from Bernor’s equid measurement database.

Analyses of the Çalta hipparions include bivariate plots of CALC, AST, MCIII, MTIII, 1PHIII and 2PHIII. Analysis of dP2 was recently done by Wolf & Bernor (2013) and Bernor *et al.* (2015a). 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. The Höwenegg *Hippotherium primigenium* skeletons were found in articulation and thus the anterior versus a posterior 1PHIII are known. However, the statistical differences between these phalanges are minor at best, which has led us to analyze all 1PHIII together. Some advanced African hipparions may in fact differ significantly in anterior versus posterior 1PHIII dimensions, but this has not been adequately demonstrated

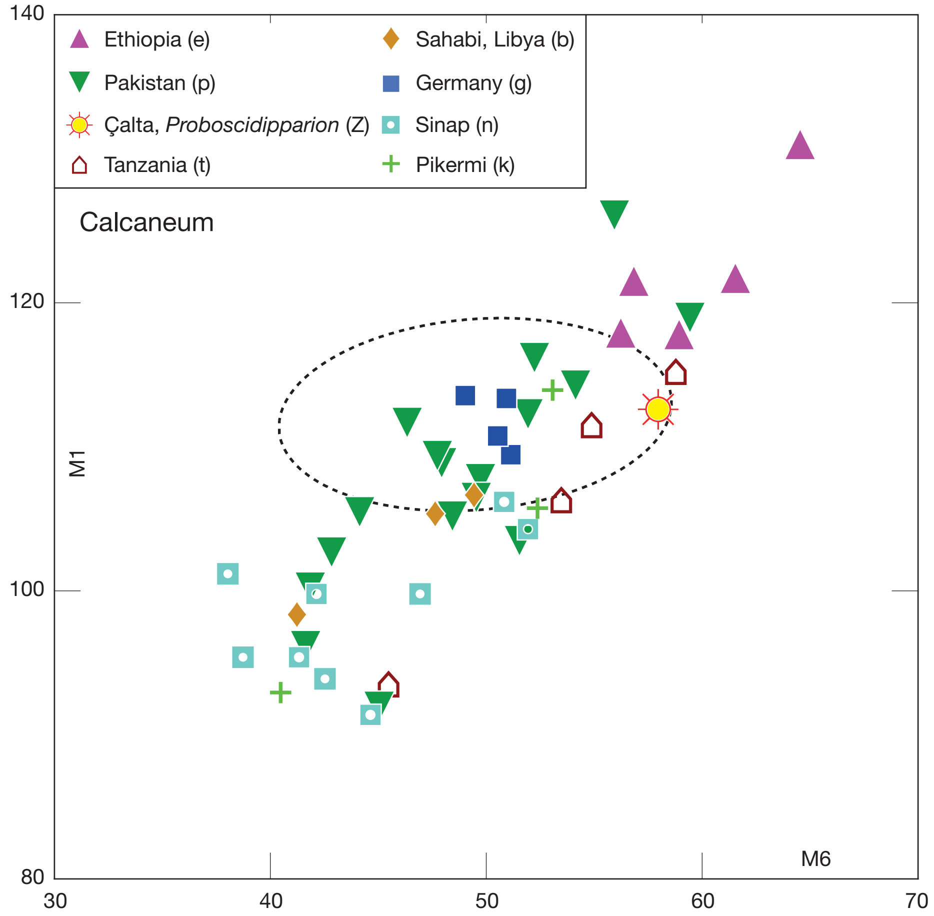

FIG. 2. — Bivariate plot of calcaneum maximum length (M1) versus distal maximal width (M6).

across individual lineages. Bivariate plots will include two parallel sets of plots when needed: one of our entire sample; a second of the Çalta specimens alone to highlight their plot points clearly.

Calcaneum maximum length (M1) versus distal maximal width (M6) (Fig. 2)

A number of localities have specimens plotting within the Höwenegg ellipse, including (Fig. 2): Eppelsheim (g; *Hippotherium primigenium*), Pakistan (p; *Sivalhippus*), Sahabi (b, *Sivalhippus*), Tanzania (t; *Eurygnathohippus* sp.) and to the far right of the ellipse Çalta *Proboscidipparion heintzi*. Larger specimens found above the ellipse include 5 specimens from Ethiopia (e, *Eurygnathohippus* sp.), 2 from Pakistan (p; *Sivalhippus*) and 1 from Tanzania (t; *Eurygnathohippus* sp.). Small calcanea plotting below the ellipse including several from Sinap, Turkey (n; *Cormohipparion sinapensis* and "*Hipparion*" spp.), a small taxon from Sahabi (b; cf. *Eurygnathohippus feibeli*), Tanzania (t; *Eurygnathohippus* sp.) and Pakistan (p; ?*Cremohipparion* sp.).

Astragali maximum length (M1) versus distal articular width (M5) (Fig. 3)

Figure 3A exhibits the rich sample of astragali that we have from our composite sample. The largest specimens plotting above the Höwenegg ellipse are of *Eurygnathohippus* spp. from Ethiopia (e) and Tanzania (t), *Sivalhippus* from Pakistan (p). The smallest specimens, falling below the ellipse are again from Pakistan (p), Sinap (n), Pikermi (k), Sahabi (b), Kenya (y) and Tanzania (t). Many specimens are densely plotted within the Höwenegg ellipse. Çalta (Fig. 3B) has a number of specimens plotting within the upper border and above the upper border of the Höwenegg ellipse. There are two specimens attributed to *Plesiohipparion longipes* (z) immediately above the ellipse and one inside the upper border of the ellipse. There are two specimens attributed to *Proboscidipparion heintzi* plotted above the upper border of the ellipse and two just inside the upper border of the ellipse. In that there is no meaningful statistical separation between specimens attributed to *Plesiohipparion longipes* and *Proboscidipparion heintzi*, we refrain from formally recognizing these taxa based on astragali bivariate plots herein. Figure 3A and 3B demonstrates that astragalus size is a better estimate of body mass than taxonomy.

MCIII maximum length (M1) versus distal articular width (M11) (Fig. 4)

Figure 4A exhibits the great dispersion of plotted points for our sample reflecting the great diversity in MCIII size and proportions. Within the Höwenegg ellipse there are several specimens of primitive hipparions from Sinap, Turkey (n;

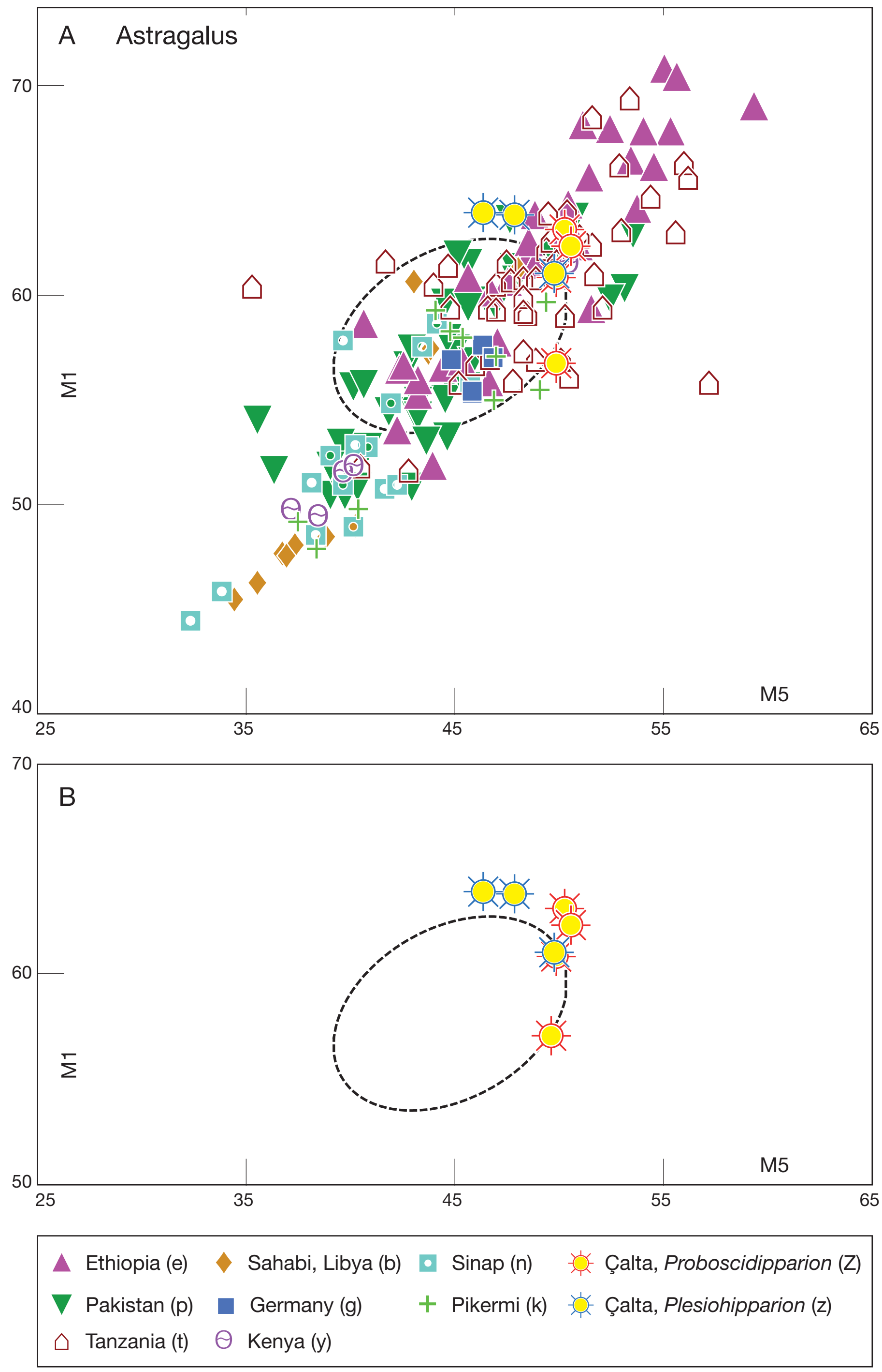

FIG. 3. — **A**, Bivariate plot of astragalus maximum length (M1) versus distal articular width (M5); **B**, bivariate plot of astragalus maximum length (M1) versus distal articular width (M5) for Çalta *Plesiohipparion* Qiu, Huang & Guo, 1987 and *Proboscidipparion* Sefve, 1927 only.

Bernor *et al.* 2003), the robust Pikermi species *Hippotherium brachypus* (k) and similar Maragheh form aff. *Hippotherium brachypus* (m; Bernor *et al.* 2016), *Sivalhippus* (p; Wolf *et al.* 2013) and *Eurygnathohippus* from Tanzania (t). There are many specimens that have longer MCIIIs and are above the ellipse of African *Eurygnathohippus* (e, t); Chinese *Plesiohipparion houfenense* (C), a cluster of Akkaşdağı *Plesiohipparion longipes* and several specimens of Ethiopian *Eurygnathohippus* plot far above the Höwenegg ellipse having extremely long MCIIIs. Çalta has two specimens of *Proboscidipparion heintzi* MCIIIs that are the length of the Höwenegg population, with one being much wider and similar to a Tanzanian specimen of *Sivalhippus turkanensis* Bernor & Harris, 2013 (Fig. 4B). Specimens that plot just outside the right border of the ellipse include *Sivalhippus* (p), Kenyan *Eurygnathohippus* (y) and Pikermi *Hippotherium brachypus*

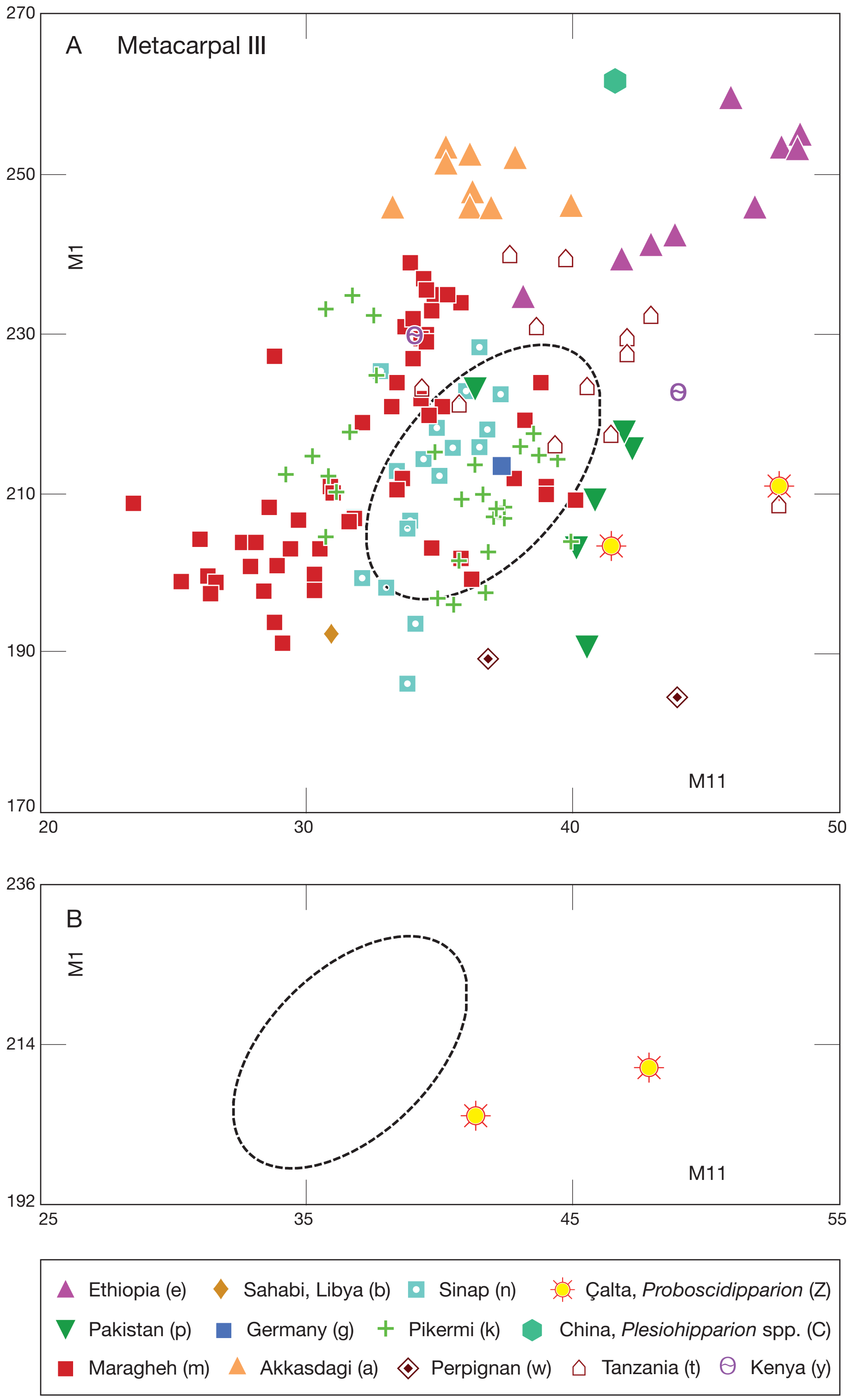

Fig. 4. — **A**, Bivariate plot of MCIII maximum length (M1) versus distal articular width (M11); **B**, bivariate plot of MCIII maximum length (M1) versus distal articular width (M11) for Çalta *Proboscidipparion* Sefve, 1927 only.

(k). Slender-elongate specimens plotting to the left of the Höwenegg ellipse include a large sample of *Cremohipparion moldavicum* Gromova, 1952 and *Cremohipparion matthewi* Kormos, 1911 from Maragheh (m) and two specimens of "Hipparion" from Sinap (n). Maragheh (m), Sahabi (b), Sinap (n), Siwaliks (p) and Perpignan (w) have hipparion specimens that are short, plotting below the Höwenegg ellipse. Figure 4B clearly exhibits the two specimens of Çalta *Proboscidipparion heintzi* (Z) that plot to the right of the ellipse, in one case very far to the right.

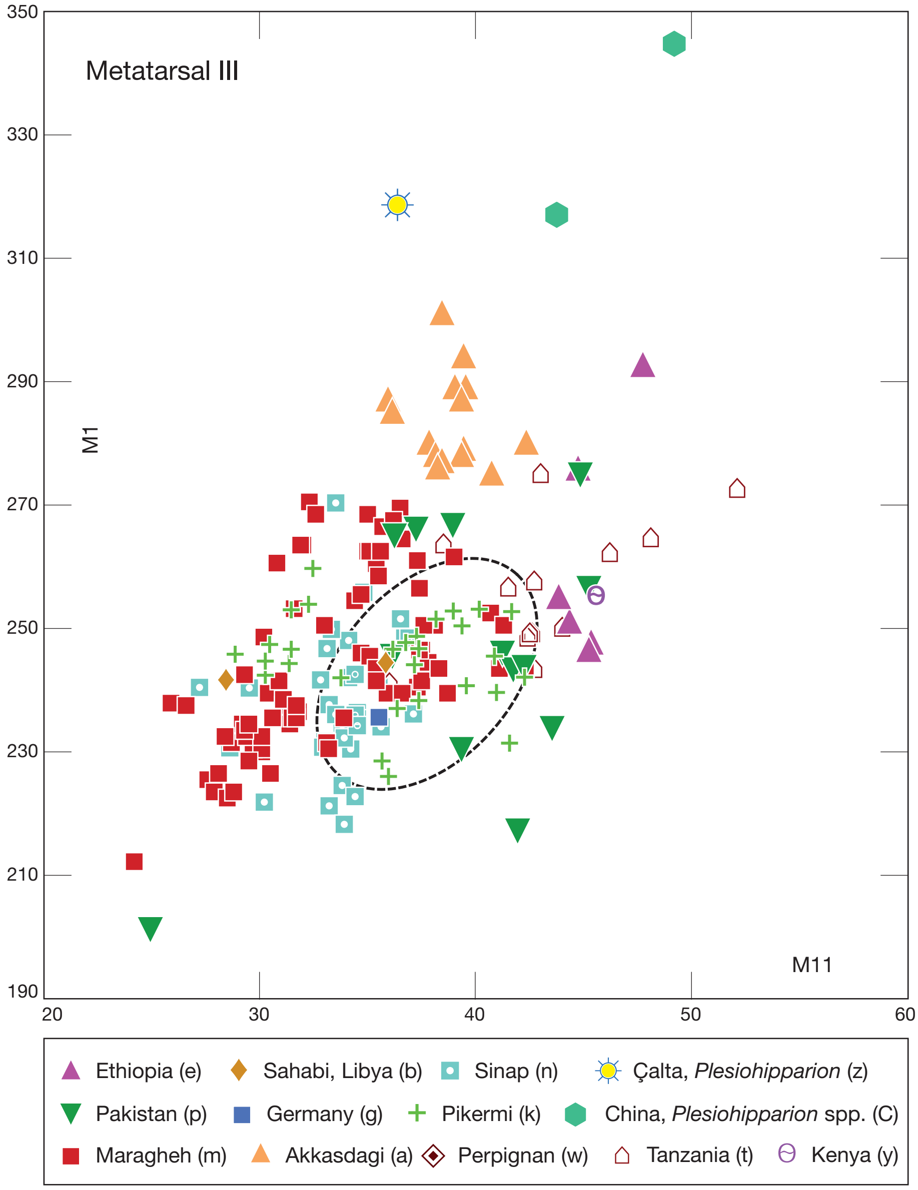

FIG. 5. — Bivariate plot of MTIII maximum length (M1) versus distal articular width (M11).

MTIII maximum length (M1) versus distal articular width (M11) (Fig. 5)

Figure 5 exhibits a great dispersion of plotted points. Chinese *Plesiohipparion houfenense* Qiu, Huang & Guo, 1987 (C) and Çalta *Plesiohipparion* cf. *longipes* (z) plot very far above the Höwenegg ellipse and have amongst the longest MTIIIs known for Old World hipparions. As with the MCIII plot, there is a cluster of several specimens of *Plesiohipparion* cf. *longipes* from Akkaşdağı plotting well above the Höwenegg being shorter than the Çalta specimen of *Plesiohipparion* cf. *longipes*. There is a great density of hipparion specimens that plot within the Höwenegg ellipse. The most abundant are primitive Sinap hipparions (n), Pikermi *Hippotherium brachypus* (k), Pakistan *Sivalhippus* (p) and Tanzania *Eurygnathohippus* (t). Eastern African *Eurygnathohippus* (e, Ethiopia; t, Tanzania; y, Kenya) have several specimens that are larger (longer and some wider) than the Höwenegg hipparion and plot above the Höwenegg ellipse. There are also a great number of more slender forms plotting to the left of the ellipse, but below the Akkaşdağı (a) cluster from Maragheh (m) that Bernor *et al.* (2016) identifies as being *Cremohipparion moldavicum* (longer specimens) and *Cremohipparion matthewi* (shorter specimens), *Cremohipparion mediterraneum* from Pikermi (k), Pakistan *Cremohipparion antelopinum* (p), Sahabi (b) and slender limbed Sinap hipparions (n).

1PHIII maximum length (M1) versus proximal articular width (M4) (Fig. 6)

Figure 6A exhibits a great dispersion of plotted points particularly above the Höwenegg ellipse. A number of specimens plot within the Höwenegg ellipse, including African *Eurygnathohippus* spp. (e, t and y), Pakistan *Sivalhippus* spp.

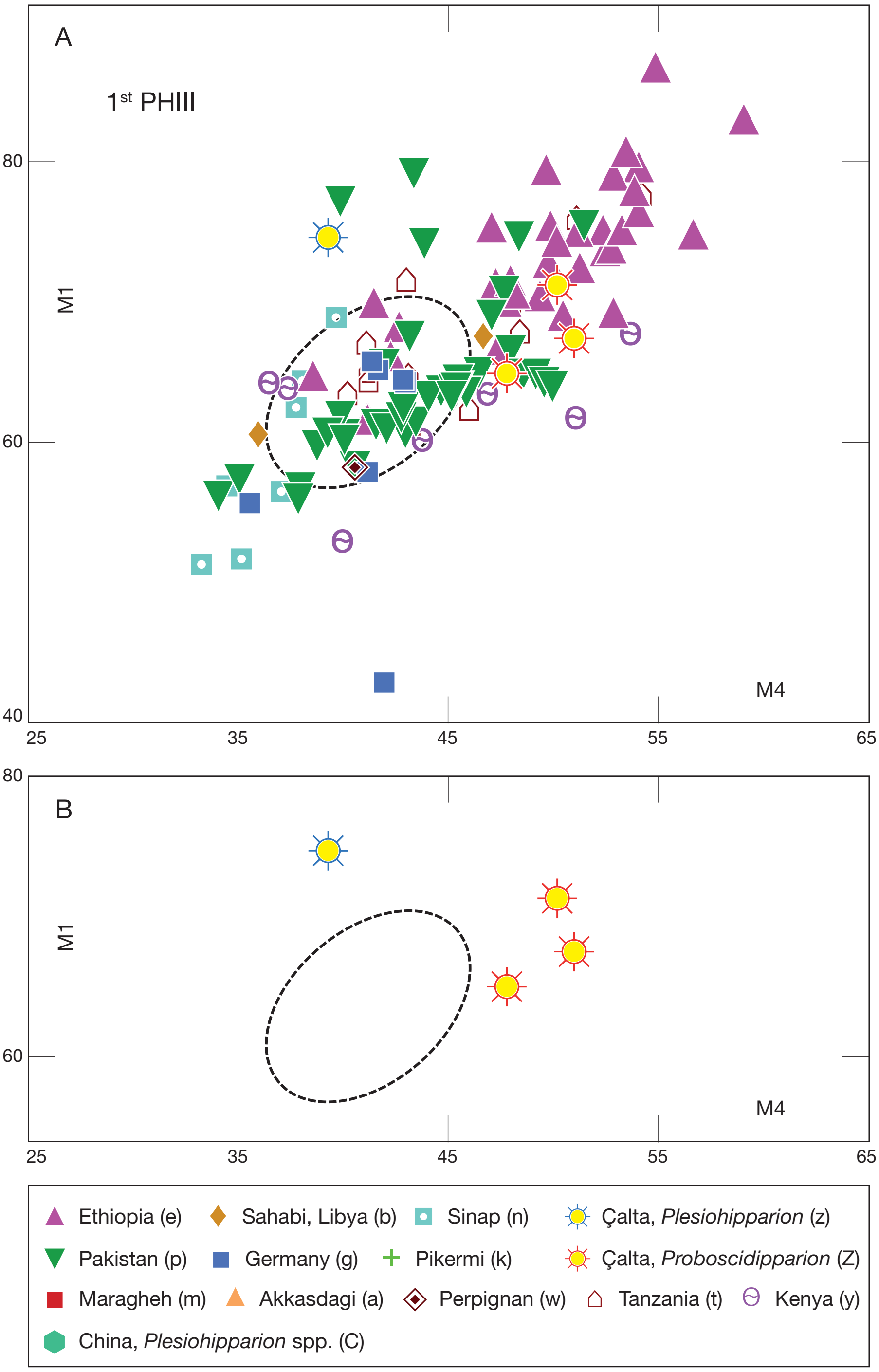

FIG. 6. — **A**, Bivariate plot of 1PHIII maximum length (M1) versus proximal articular width (M4); **B**, bivariate plot of 1PHIII maximum length (M1) versus proximal articular width (M4) for Çalta *Plesiohipparion* Qiu, Huang & Guo, 1987 and *Proboscidipparion* Sefve, 1927 only.

and Eppelsheim *Hippotherium primigenium* (g); these specimens retain the primitive Old World hipparion length (M1) versus proximal width (M4) dimensions. There are a great number of *Eurygnathohippus* specimens that plot above the ellipse, particularly from Ethiopia (e), but also Tanzania (t) and Kenya (y). There are two specimens from Pakistan that have similar dimensions to Çalta *Plesiohipparion* cf. *longipes* (z) that are likely referable to another elongate distal-limbed species, *Cremohipparion antelopinum*. There are specimens of "Hipparion" incertae sedis from Sinap (n), Pakistan (p), Kenya (y) and Eppelsheim, Germany (g) that have smaller 1PHIIIs that plot below the ellipse. Figure 6B shows the three plotted points for Çalta *Proboscidipparion heintzi* (Z) well to the right of the Höwenegg ellipse and the single *Plesiohipparion* cf. *longipes* (z) plotted point above and to the left of the Höwenegg ellipse.

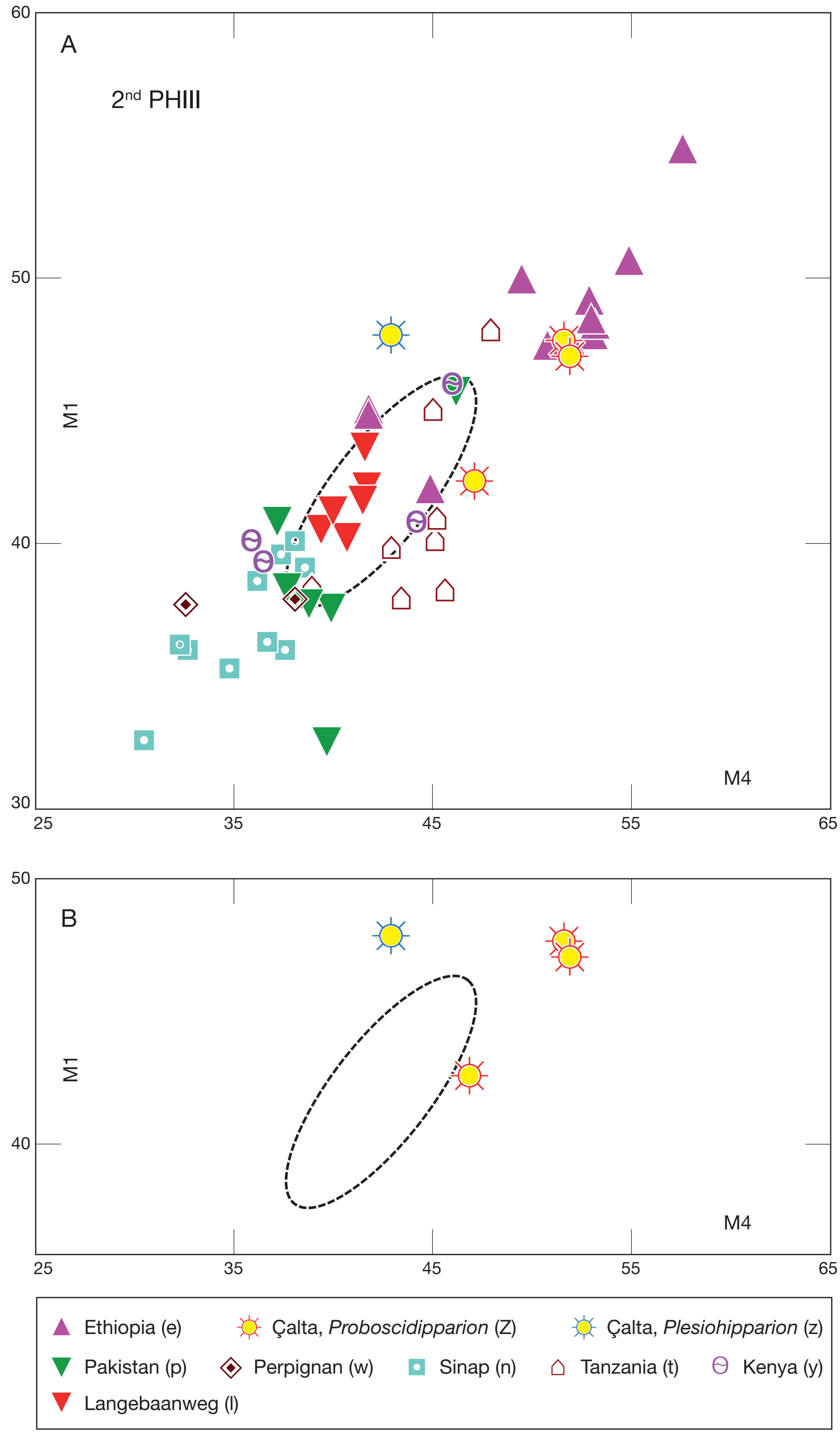

FIG. 7. — **A**, Bivariate plot of 2PHIII maximum length (M1) versus proximal articular width (M4); **B**, Bivariate plot of 2PHIII maximum length (M1) versus proximal articular width (M4) for Çalta *Plesiohipparion* Qiu, Huang & Guo, 1987 and *Proboscidipparion* Sefve, 1927 only.

2PHIII maximum length (M1)
versus proximal articular width (M4) (Fig. 7)

Specimens that plot within the Höwenegg ellipse include East African *Eurygnathohippus* (e, t and y), Sinap (n) “Hipparion” and Pakistan *Sivalhippus* (p). Specimens from Sinap (n), Perpignan (w) and Pakistan (p) plot below the ellipse. The longest 2PHIIIs are of Ethiopian (e) *Eurygnathohippus*. Figure 7B exhibits the three specimens of *Proboscidipparion* *heintzi* that plot to the right and above the Höwenegg ellipse and *Plesiohipparion longipes* that plots above and to the left of the Höwenegg ellipse.

Log10 ratio analysis

We provide herein log10 ratio analyses of MCIII, MTIII and 1PHIII of the Çalta hipparions in comparison to a broad series of Eurasian and African hipparion lineages that we segregate into primitive, slender-limbed, and robust-limbed lineages in meaningful combinations. These lineages range in age from basal Late Miocene through the Pliocene. We use the pristine Höwenegg sample of 14 *Hippotherium primigenium* skeletons, calculated as the mean for each measurement, as our standard for these log10 analyses.

Log10 analyses of MCIIIs (Fig. 8)

Figure 8A plots hipparions with primitive MCIII proportions, compared to the Höwenegg standard. Csin, Cafr, HpriDS and Euhoo are very similar in their length (M1), midshaft width (M3) and midshaft depth (M4) deviating from the Ho standard in their narrower midshaft width proportion; these are believed to represent the primitive proportions for Old World Hipparions. Bernor *et al.* (2003) distinguished this trait as the "Esme Akçaköy Effect". HpriDS has a slightly elevated proportion for proximal articular depth (M6), distal supra-articular width (M10) and distal articular width (M11, very slight). Euhoo has an expanded distal keel (M12) and slight elevation of distal articular depth (M13). Csin has smaller dimensions of proximal articular width (M5) and depth (M6), while Csin and Cafr have reduced proximal articular depth dimensions (M6).

Figure 8B plots the robust lineages in our sample. Stur has the longest length (M1) and widest midshaft (M3) dimensions and is closest in its proportions to PrheinT from Çalta. PrheinT has similar length (M1) and midsaft width (M3) of Sper and Prhein, but has elevated midshaft depth (M4) as well as proximal articular (M5 and M6) and distal (M10, M11, M12) dimensions. All four taxa plotted here have similar distal articular dimensions M13 and M14. All of these taxa are close in length to the Höwenegg hipparion, but have elevated dimensions of the proximal and distal articulations. Moreover, the strong contrast between narrow midshaft (M3) and deep midshaft (M4), or the "Esme Akçaköy Effect" is minimized in these taxa and deviated entirely from in PrheinT; PrheinT has a very deep midshaft.

Figure 8C includes slender limbed lineages of which there are 3 groupings. The smallest and most gracile are the EufeiL, EufeiS and Crmed taxa; EufeiL (Kenya) and EufeiS (Libya) are strongly convergent with Eurasian Crmed with elongate, slender limbs and sharply contrasting narrow midshaft dimensions (M3) accompanied by deeper midshaft depth dimensions. Plong_MEAN_A is characterized by very elongate MCIII (M1), with very sharply contrasting midshaft width (M3) versus midshaft depth (M4). Proximal articular dimensions (M5 and M6), distal articular dimensions (M10-M14) track the Höwenegg standard very closely and are essentially the same size. Çalta *Plesiohipparion* cf. *longipes* (Plong_C) is a fragmentary MCIII shaft and only has M3-M6 being measureable. The third grouping is the larger Pliocene Ethiopian lineages, Euafa and Euwold which overlap Pllong_Mean_A in length, track each other in their overall dimensions, have very similar midshaft depth (M4) and proximal articular width (M5) dimensions and then are somewhat larger in M6-M14 dimensions than the rest of our MCIII sample. Overall, Euwold, Euafa and Pllong_Mean_A track one another closely as larger, elongate-slender built hipparions. Euafa exhibits the most minimal M3-M4 contrast (the "Esme Akçaköy Effect").

Log10 analyses of MTIIIs (Fig. 9)

Figure 9A presents the smaller, slender limbed lineages Crmed, Crant and Eufei as well as primitive *Eurygnathohippus* species Euhoo in comparison to Sinap *Cormohipparion sinapensis* (Csin). Crmed, Crant and Eufei are strikingly similar in their elongate slender morphology and striking contrast of narrow midshaft width (M3) and relatively great midshaft depth (M4). These taxa have accentuated the "Esme Akçaköy Effect" beyond the primitive condition seen in Csin (Bernor *et al.* 2003). The most slender limbed form Eufei has the most accentuated M3 to M4 ratio. Crant has lengthened (M1) substantially, while retaining proportions virtually identical to Csin. Euhoo tracks Eufei particularly closely being larger bodied overall.

Figure 9B provides log10 ratios for the robustly built hipparions. HbraP tracks the Höwenegg population standard most closely. HpriDS also tracks the Höwenegg standard closely. Sper also has similar proportinos to the Höwenegg population standard with increased proximal articular width (M5) and distal width (M10 and M11) and midsagittal keel (M12) dimensions. Stur is the most robustly built taxon of our assemblage with heightened values for all proportions. Of these four taxa, none exhibit the strong contrast between M3 and M4 found in more slender-limbed forms and in fact these are reversed for HbraP and Stur. Stur and HbraP exhibit cranio-caudal (M4) flattening of the shaft.

Figure 9C provides log10 ratios for African Euafa, Çalta Plong_C, Akkaşdağı Plong_A_Mean and Chinese Phou. Plong_C and Plong_A track very closely for most points with the Çalta form having more elongated MTIII's. Both Plong_C and Plong_A also track Chinese Plhou_Mean well with Pl_hou being a larger species. Euafa is a large form also but without the striking contrast between midshaft width (M3) and midshaft depth (M4) seen in the *Plesiohipparion* taxa.

Log10 analysis of 1PH3's (Fig. 10)

Figure 10A provides log10 ratios of slender limbed *Cremohipparion* spp. (Crmed and Crant) and *Hipparion* s.s. (Hcamp). All hipparions have relatively slender midshafts (M3). Crmed and Hcamp have narrow proximal (M4) and distal (M6) articular widths while Crant is similar to the Höwenegg standard in these dimensions. Crant is extraordinary for its great lengthening of 1PHIII (M1 and M2) and has an elevated value for distal articular width (M7). There is no provenance for the Crant specimens and it is not at all out of the question that these BMNH specimens could belong to a lineage other than *Cremohipparion*. Comparisons with Chinese *Plesiohipparion* would be interesting to have.

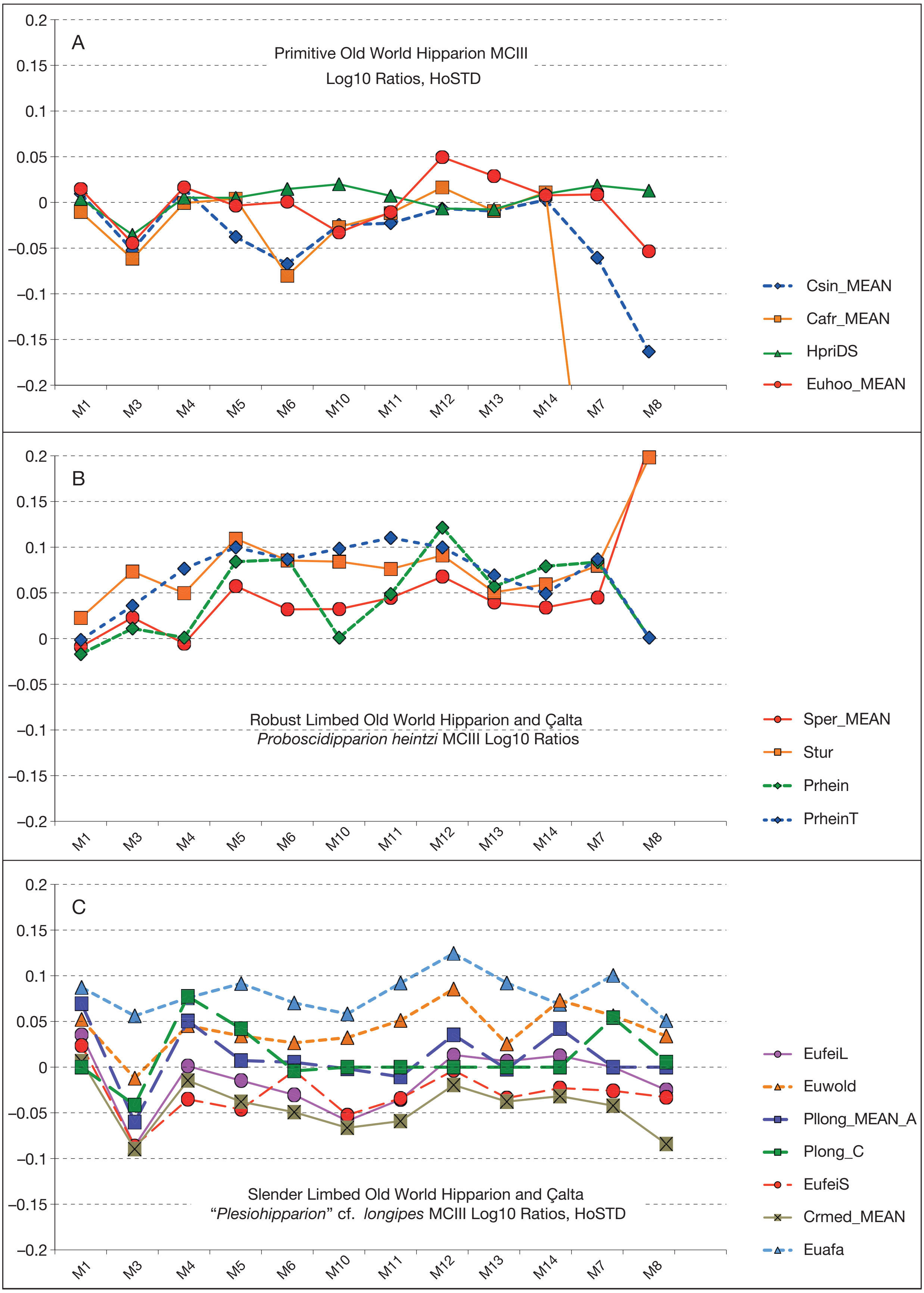

FIG. 8. — Log10 ratio diagram of MCIII: **A**, primitive Old World Hipparion; **B**, robust limbed Old World Hipparion and Çalta *Proboscidipparion heintzi* (Eisenmann & Sondaar, 1998); **C**, slender limbed Old World Hipparion and Çalta *Plesiohipparion* cf. *longipes* (Gromova, 1952).

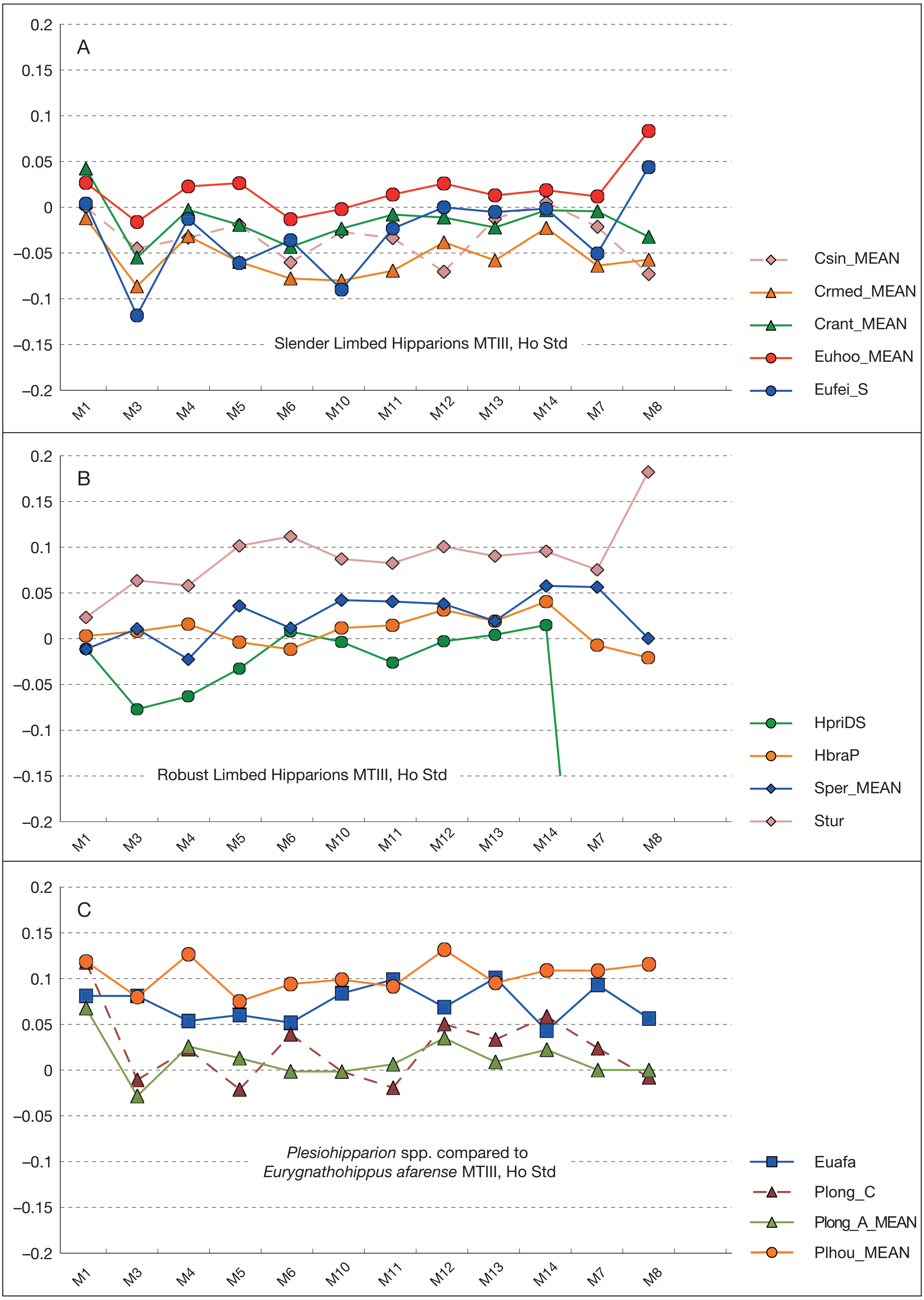

Fig. 9. — Log10 ratio diagram of MTIII: **A**, slender limbed Hipparions; **B**, robust limbed Hipparions; **C**, *Plesiohipparion* spp. compared to *Eurygnathohippus afarense* Eisenmann, 1976.

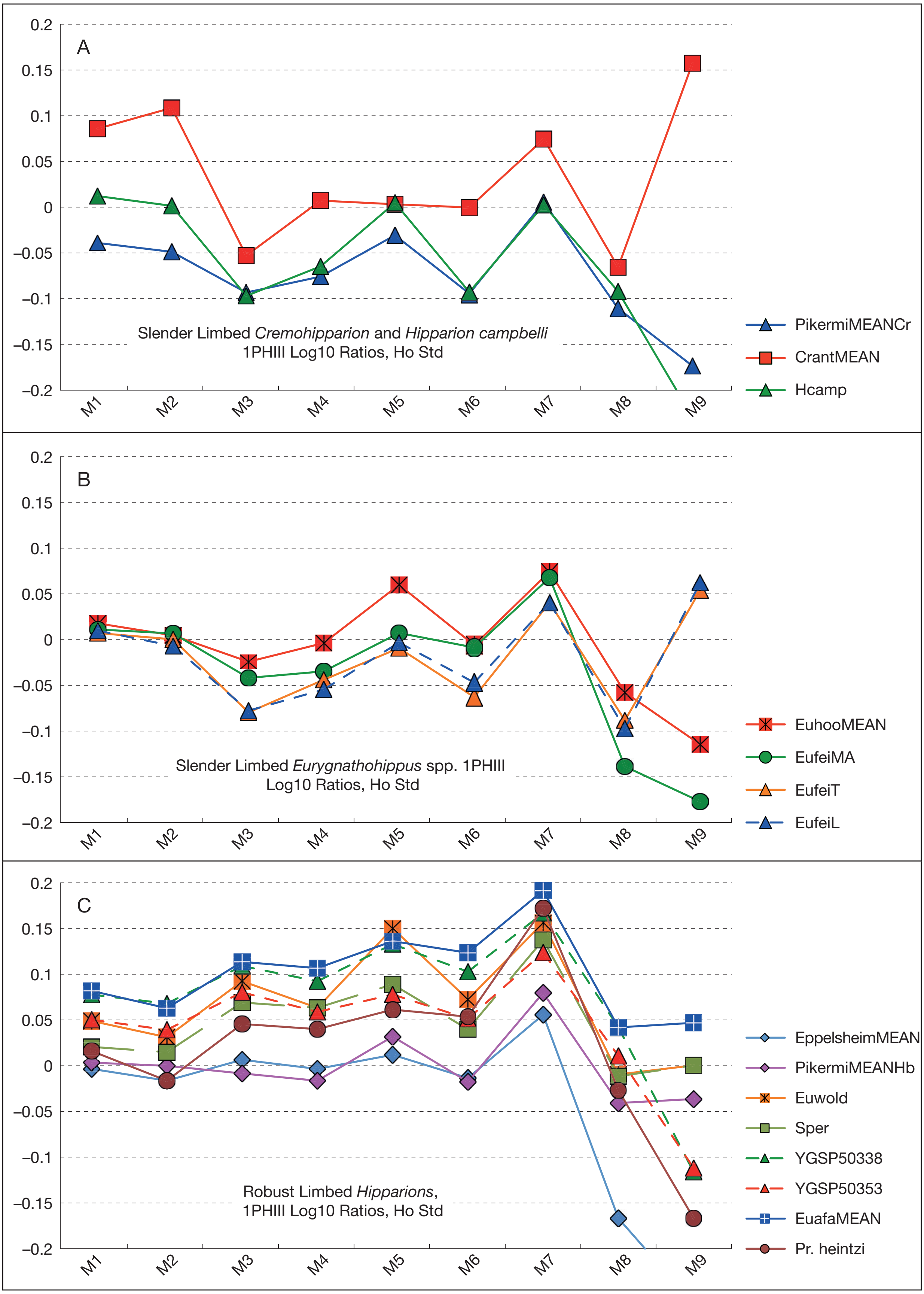

FIG. 10. — Log10 ratio diagram of 1PHIII: **A**, slender limbed *Cremohipparion* Qiu, Huang & Guo, 1987 and *Hipparion campbelli* Bernor, 1985, 1PHIII Log10 Ratios, Ho Std; **B**, slender limbed *Eurygnathohippus* 1PHIII; **C**, robust limbed Hipparions.

Figure 10B provides log10 ratios for slender limbed *Eurygnathohippus* spp.: Euhoo, EufeiMA, EufeiT and EufeiL. These taxa all have similar log10 ratios with Euhoo being the largest form, particularly in proximal articular width (M4) and proximal articular depth (M5). EufeiMA, EufeiT and EufeiL are very similar to one another and have narrow midshaft widths (M3), narrow proximal articular widths (M4) and relatively wide distal articular widths (M7) and narrow distal articular depths (M8).

Figure 10C provides log10 ratios for robust limbed Old World Hipparions and Çalta *Proboscidipparion heintzi* compared to the Höwenegg population standard. *Proboscidipparion heintzi* for the most part plots in the center of the chart, having elevated dimensions for M3-M7. *Proboscidipparion heintzi* generally tracks Indopakistan *Sivalhippus perimensis* following Wolf *et al.* 2013 (Sper), *Sivalhippus anwari* (San; YGSP50338 and YGP50353) and African EuwoldT and Euafa very closely having similar proportions for M1-M8. *Hippotherium* populations HpriDS and HbraP are very similar to the Höwenegg population standard, having flat projectories and being less robustly built than Sper, Euwold, Euafa and *Proboscidipparion heintzi. Proboscidipparion heintzi* 1PHIII plots very similarly to other large *Sivalhippus* Complex taxa: Sper, San, Euwold and Euafa).

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Suborder HIPPOMORPHA Wood, 1937
Family Equidae Gray, 1821
Tribe Hipparionini Quinn, 1955

Genus *Proboscidipparion* Sefve, 1927

Type species. — *Proboscidipparion sinense* Sefve, 1927 by original designation.

Proboscidipparion heintzi Eisenmann & Sondaar, 1998

Holotype. — Right MCIII of the central digit (MNHN.F.ACA49A), associated with the entire MCII (ACA149C) and the entire proximal portion of the MCIV (ACA49B). Collections are maintained at the Laboratoire de Paléontologie, MNHN, Paris.

Paratype. — 1PHIII (MNHN.F.ACA125; Eisenmann & Sondaar 1998: fig. 16C).

Type Locality. — Çalta, Turkey.

Age. — Early Ruscinian, MN15, *c.* 4.0 Ma.

Distribution. — Turkey.

Diagnosis (modified from Eisenmann & Sondaar 1998 with augmentation). — Skull as known from a juvenile individual large, lacking preorbital fossa with nasals retracted posterior to infraorbital foramen and directly above parastyle of dP3 (as conserved on the right side of MNHN.F.ACA336) with a broad narial opening. Deciduous cheek teeth with large dP1 retained into subadulthood; dP2 with very elongate anterostyle; fossette plications well developed; protocones short, oval to rounded; mandibular i1 very large being mesio-distally expanded. Metapodials very robustly built being relatively short and broad. 1PHIIIs robust, being long relative to metapodials, radii and tibiae. 3PHIIIs are extremely wide, and flat. MCVs are fused with MCIV's.

Description

The hypodigm for Çalta *Proboscidipparion heintzi* is listed in Table 1. The juvenile skull MNHN.F.ACA336 (Fig. 11A) is well preserved and virtually complete except for the premaxilla and the right side of the cranium. The narial opening, as seen in oblique view (Fig. 11B), is very wide. The dP1 is large and wide and retracted posterior to the infraorbital foramen and level of dP3 parastyle, suggesting that the premaxilla supported a mobile snout not unlike that of a tapir. The dP1 is rotated so as to have the mesial extent directed mesiolabially and distal extent oriented distolingually. The dP2 has anterostyle extended mesially; mesial and distal borders of the prefossette are strongly plicated, with the postfossette having a complex mesial border but simpler posterior border; the anterolingual enamel band is likewise complex, while the distolingual enamel band is simple; pli caballin is double with plis broadly separated; hypoglyph is very shallow; protocone is oval shaped and lacking a pli. The dP3 has the mesial border of prefossette worn with obliterated plis, while the posterior border is complex; mesial and distal borders of the postfossettes are likewise worn and not preserving the original plication frequency; pli caballin is complex with multiple folds; hypoglyph is moderately deeply incised; protocone is short and round. The dP4 is in relatively early wear and preserves moderately complex plications of the prefossette and lesser plication of the postfossette likely due to the early stage-of-wear; pli caballin would appear to be complex; hypoglyph is deeply incised; protocone is short, rounded with a flattened lingual border. The M1 is just emerging from its crypt.

Eisenmann & Sondaar (1998; MNHN.F.ACA337A) figured a juvenile right maxilla with dP1-4, M1 and M2 emerging from the crypt and M3 within its crypt (Fig. 12A) and an associated mandible with dp2-4 and m1-m2 (Fig. 12B). The maxillary deciduous cheek teeth are more worn than in ACA336 with resulting morphological differences. The dP1 is still retained but worn, with a similar orientation as ACA336. The dP2 still has an elongate anterostyle. All deciduous teeth have simpler plications of the fossettes; protocones are short and round; hypoglyphs are moderately deeply incised; M1 and M2 are too unworn to preserve occlusal details. The juvenile mandible (ACA337B) has rounded to elongate metaconids and metastylids ("caballine pattern" of Eisenmann & Sondaar 1998); pre- and postflexids have simple enamel margins; linguaflexid is shallow on dp2, V-shape on dp3-4 and m1; ectoflexid is progressively deeper on dp2 to m1, separating metaconid and metastylid on dp4 and m1. ACA337B includes a mandibular symphysis (Fig. 12C) that preserves a left i1 crown, in its crypt. This crown is extremely large in its mesiodistal dimension, and is only found in advanced members

FIG. 11. — MNHN.F.ACA336, juvenile skull: **A**, lateral view; **B**, oblique view of nasal opening; **C**, dP1-M1 occlusal view. Scale bars: A, B, 10 cm; C, 5 cm.

of the "*Sivalhippus* Complex", namely African Pleistocene *Eurygnathohippus cornelianus*.

Proboscidipparion heintzi is derived in its very robust, relatively short and wide MCIIIs (Figs 4A, B; 8B), as exemplified by the type specimen MNHN.F.ACA49A (Fig. 13A, B) exhibiting similarity in these dimensions to eastern African Lothagam, Late Miocene *Sivalhippus turkanensis* following Wolf *et al.* (2013). Çalta MCIII *Proboscidipparion heintzi* is extraordinary however in its combination of short and at the same time broad proximal, distal and midshaft dimensions. The *Proboscidipparion heintzi* MCIV (Fig. 13C) is not analysed and otherwise not very informative. Perpignan MCIII

Fig. 12. — MNHN.F.ACA337, juvenile maxilla and mandible: **A**, right dP1-M2 (in crypt), occlusal view; **B**, left dp2-m2 (in crypt); **C**, close up of very large i1 (in crypt). Scale bar: 5 cm.

(w; Fig. 4) is extraordinary in its own right having extremely short and wide dimensions; shorter than Çalta *Proboscidipparion heintzi.*

Çalta *Proboscidipparion heintzi* 1PHIII is short and robustly built (Figs 6B; 10C; 14A, B) comparing most closely with *Eurygnathohippus woldegabrieli*, *Eu. afarense* and *Proboscidipparion heintzi.* Eisenmann & Sondaar (1998: fig. 16) illustrated the contrasting 3PHIII morphologies of *Plesiohipparion* cf. *longipes* (MNHN.F.ACA87; Eisenmann & Sondaar [1998: fig. 16A] and *Proboscidipparion heintzi* (ACA89 and ACA125; Eisenmann & Sondaar [1998: fig. 16B, C]). Both our series of bivariate plots and log10 ratio diagrams for MCIII, MTIII and 1PHIII clearly show the strongly contrasting morphological proportions of Çalta *Plesiohipparion* aff. *longipes* and *Proboscidipparion heintzi.*

REMARKS

Sefve (1927) nominated the nomen *Proboscidipparion sinense* based on a complete skull and mandible from the Early Pleistocene of Langou, Mianchi County, Henan Province, China (Zdansky 1923; PMU M3925, Bernor *et al.* 1990: figs 17 and 18). Sefve (1927) recognized *Proboscidipparion sinense* unique in its very large size, and extraordinarily derived nasal and muzzle structure with characters that are absent in other known species of "Hipparion". *Proboscidipparion sinense* has deeply retracted nasals, a very elongate and narrow premaxilla and very strong plications of the upper cheek teeth (re: Bernor *et al.* 1990; Bernor & Sun 2015). Teilhard de Chardin & Piveteau (1930) described specimens of *Proboscidipparion* from Nihewan, Hebei but did not believe that a generic distinction was warranted (hence their *H. Proboscidipparion sinense*). *Proboscidipparion sinense* also cited as coming from Bajiazui in Qingyang, Gansu (Wang *et al.* 1966; Wang & Xue 1982), Banqiao in Heshui, Gansu (Zheng *et al.* 1975), Kehe in Ruicheng, Shanxi (Chia *et al.* 1962), Yangguo in Weinan, Shaanxi (Chi 1975), and Tuozidong in Nanjing-Jiangsu (Dong & Fang 2005). The age of *Proboscidipparion sinense* is Early Pleistocene (*c.* 2.6 Ma; Deng 2012).

Hipparion (*Proboscidipparion*) *pater* Matsumoto, 1927 was identified from the Gaozhuan Formation, Baihaicun based on a male skull (THP 14312) and nominated as a Lectotype by Qiu *et al.* (1987; pls. I and II). Another complete skull (THP20763) was reported from the Gaozhuang Formation Nihe, Yushe by Qiu *et al.* (1987: pl. II). Qiu *et al.* (1987: pl. IV; Fig. 15A-C) further reported a juvenile skull and mandible from the Gaozhuang Formation, Yushe, THP20847 which compares closely with the Çalta MNHN.F.ACA336 juvenile skull in maxillary, nasal and deciduous cheek tooth occlusal morphology.

Bernor *et al.* (1990), Bernor & Sun (2015) and Bernor *et al.* (2015a) have recognized *Proboscidipparion* as a distinct lineage of hipparion warranting generic rank. We include *Proboscidipparion heintzi* in this lineage because of its retracted nasals with broad narial opening, elongate dP2 anterostyle and exhibition of complex plication of the cheek teeth (as per Bernor & Sun 2015). The skull of *Proboscidipparion heintzi* compares most closely with Early Pliocene *Proboscidipparion pater* Qiu, Huang & Guo, 1987 in its nasal retraction and maxillary cheek tooth morphology (Qiu *et al.* 1987). Postcrania for Chinese *Proboscidipparion* species are not certainly known and may be confused with the elongate slender morphology of *Plesiohipparion* spp. It would appear that *Proboscidipparion* first evolved in the very Latest Miocene or earliest Pliocene of China and extended its range to Turkey in the Early Pliocene. Eisenmann & Sondaar (1998) estimated that *Proboscidipparion heintzi* was a large hipparion that weighed 300-360 kg when alive.

FIG. 13. — MNHN.F.ACA49A, type *Proboscidipparion heintzi* (Eisenmann & Sondaar, 1998), MCIII: **A**, cranial view; **B**, caudal view; **C**, MNHN.F.ACA49B, ACA140, type *Proboscidipparion heintzi* MCIV, lateral view. Scale bar: 5 cm.

Genus *Plesiohipparion* Qiu, Huang & Guo, 1987

TYPE SPECIES. — *Plesiohipparion houfenense* Teilhard de Chardin & Young, 1931.

Plesiohipparion* cf. *longipes (Gromova, 1952)
(Figs 4; 5; 16; 17)

DESCRIPTION

Eisenmann & Sondaar (1998) attributed a complete MTIII (MNHN.F.ACA214; Fig. 16A, B), a proximal fragment of MCIII (ACA56), one complete (ACA77) and one fragmentary (ACA124) 1PHIII, one complete 2PHIII (ACA82; Fig. 17), one complete 3PHIII (ACA87), one complete 3PHIII (ACA112) and three astragali (ACA250, ACA63 and ACA92) (Eisenmann & Sondaar 1998: figs 1-3, 15A, B, 16A, tables 1-3; Table 1) from Çalta. The phalanges were all believed to be from the posterior limb, but this is not certain. We further recognize 2 fragmentary MTIII (ACA209 and ACA55) and a single 1PHIII (ACA82; Fig. 17). The complete Çalta *Plesiohipparion* cf. *longipes* hypodigm, as we recognize it is listed in Table 1.

REMARKS

Gromova (1952) initially described "*Hipparion*" *longipes* from Pavlodar, Kazakhstan, which she believed was either Late Miocene or Pliocene (MN13 or 14). Gromova (1952) noted the exceptionally elongate metapodials as sufficient to recognize a valid taxon of hipparion. Vangenheim *et al.* (1993) characterized Pavlodar habitats as being dry. The most characteristic feature of the Çalta *Plesiohipparion* cf. *longipes* is the extremely elongate and slender morphology of MTIII

Fig. 14. — MNHN.F.ACA78, *Proboscidipparion heintzi* (Eisenmann & Sondaar, 1998), 1PHIII: **A**, cranial view; **B**, caudal view. Scale bar: 5 cm.

(Figs 5; 16) and 1PHIII (Figs 6; 17) well above the Höwenegg ellipse and rivaling Chinese *Plesiohipparion* (Figs 6; 8; 9; 10). In fact, *Plesiohipparion longipes* and *Plesiohipparion houfenense* have MCIII and MTIII length and width morphology greater than all Siwalik, Pikermi, and Sinap Late Miocene, and eastern African Pliocene hipparions in our sample; it is only paralleled by African Pliocene *Eurygnathohippus hasumense* Eisenmann, 1976 (Figs 8C; 9C). We believe that this extreme lengthening supports identity with Chinese *Plesiohipparion* taxa rather than *Hipparion* s.s., *Cremohipparion*, *Sivalhippus*. *Eurygnathohippus afarense* which clearly have different MCIII and MTIII proportions than our Chinese and Turkish *Plesiohipparion* sample (Figs 8C; 9C); the latter represents a separate lineage than *Eurygnathohippus* because of the persistence of large ectostylids on the permanent cheek teeth found particularly in Plio-Pleistocene members of the clade (such as *Eu. hasumense*; Bernor *et al.* 1996, 2015b; Bernor & Sun 2015).

Koufos & Vlachou (2005) referred extensive skeletal material from the MN12 locality of Akkaşdağı, Turkey (7.1 Ma; Karadenizli *et al.* 2005) to *Plesiohipparion* cf. *longipes*. The maxillary cheek teeth compare well with Chinese *Plesiohipparion houfenense*, particularly with regards to length of tooth row (P2-M3 = 162.5-169.0), the elongated P2 anterostyle bent lingually (not common, but does occur in *Plesiohipparion*), rich enamel plications, double pli caballins and the elliptical, lingually flattened protocones (Bernor & Sun 2015; Bernor *et al.* 2015b; Figs 6, 7, 8). Akkaşdağı MCIIIs (Figs 4; 8C) and MTIIIs (Figs 5; 9C) are elongate; MCIII ranging in maximum length from 246.4 to 254.0 mm (n = 11; mean = 249.7) and MTIII ranging in maximum length from 276.0 to 302.0 mm (n = 15; mean = 284.7) (Koufos & Vlachou 2005). The Çalta *Plesiohipparion* cf. *longipes* maximum length (= 319.5 mm) is greater than any Akkaşdağı specimen of this taxon, which is an advanced character for this clade. The Çalta MPIII lengthening rivals penecontemporaneous Chinese *Plesiohipparion houfenense.*

Scott & Maga (2005) undertook an ecomorphological approach on the Akkaşdağı hipparionine metapodials to investigate their likely habitat preferences. This study followed those of Bernor *et al.* (1997, 2003), Bernor & Scott (2003) and Scott *et al.* (2003) that hipparion metapodial morphology could predict habitat preferences. For both MCIII and MTIII, Scott & Maga (2005; Figs 4, 5) determined that Akkaşdağı *Plesiohipparion* cf. *longipes* was the most open country adapted of all four Akkaşdağı hipparions: *Hippotherium brachypus* (heavy-light cover), *Cremohipparion moldavicum* (heavy-light cover), *Hipparion dietrichi* (light cover-plains, but less open country than *Pl.* cf. *longipes*). Clearly, the very elongate metapodials in *Plesiohipparion* cf. *longipes* were the most adapted to open country cursoriality. The Çalta *Pleisohipparion* cf. *longipes* is advanced in having more elongate MPIIIs than the Akkaşdağı *Plesiohipparion* aff. *longipes* as well as other Akkaşdağı hipparion lineages.

Sen *et al.* (1978) used the keel development of hipparionine metapodials, including the robust hipparion from Çalta, as a biostratigraphic index. Eisenmann & Sondaar (1998) estimated that Çalta *Plesiohipparion* cf. *longipes* weighed 250-260 kg and that *Plesiohipparion longipes* from Pavlodar (type locality) weighed between 158-221 kg based on the metapodial proportions.

DISCUSSION

Eisenmann & Sondaar (1998) recognized two large hipparion species from Çalta that they assigned to *Hipparion heintzi* and *Hipparion* cf. *longipes.* They recognized that

FIG. 15. — THP 20847, Yushe Basin, China *Proboscidipparion pater* Qiu, Huang & Guo, 1987 juvenile skull and mandible: **A**, skull in right lateral view; **B**, occlusal view of palate; **C**, left mandible labial view; **D**, left mandible occlusal view. Scale bar: 5 cm.

Fig. 16. — MNHN.F.ACA214A, *Plesiohipparion* cf. *longipes* (Gromova, 1952), MTIII: **A**, cranial view; **B**, caudal view. Scale bar: 5 cm.

Hipparion heintzi was a robust limbed form particularly extraordinary for its short, robust metapodials and very wide distal phalanges III. *Hipparion* cf. *longipes* differed significantly in its elongate slender metapodial III's. Eisenmann & Sondaar (1998) found that *Hipparion heintzi* was relatively microdont and estimated its body mass to equal 300-350 kg and estimated that *Hipparion* cf. *longipes* was more lightly built with an estimated body mass of 250-260 kg. Eisenmann & Sondaar (1998: 428) deduced that *Hipparion heintzi,* with its robust limbs and broad 3PHIII was adapted to locomotion on soft soil and that the nasals of this taxon […]" may have borne nasal specialization like may be found in camels and saigas". We have recognized two distinct clades of Çalta hipparions herein, *Proboscidipparion sinense* and *Plesiohipparion* aff. *longipes.*

Sefve (1927) recognized *Proboscidipparion sinense* for a large skull with associated mandible (PMU M3925, Locality 39, Langou, Mianchi County, Henan Province; Bernor *et al.* 1990: figs 17, 18) from the Nihewanian, China. Teilhard de Chardin & Piveteau (1930) recognized *Proboscidipparion* from the Nihewan Basin of China. Qiu *et al.* (1987) recognized the clade status of this specimen but chose to hold it to the subgenus rank, *Hipparion* (*Proboscidipparion*) *sinense.* Qiu *et al.* (1987) diagnosed the subgenus *Proboscidipparion* as being: the largest of all hipparions, peculiar development of nasals (elongate and strongly retracted convergent on the living tapir), strong plication of the upper cheek teeth, cheek tooth relatively short compared to other hipparions. Qiu *et al.* (1987) further identified specimens of this genus from Hongya of the Nihewan Basin (Huang *et al.* 1974), the lower bed of the Nihewan Formation (Tang 1980), Heshui, Gansu (*Stegodon huanghoensis* Research Team 1975) and Kehe (Chia *et al.* 1962). Bernor *et al.* (1990) and Wolf *et al.* (2013) followed Sefve (1927) in recognizing the generic distinction of *Proboscidipparion* based on a phylogenetic analysis that revealed the genus' highly derived suite of cranial, facial and dental apomorphies which we follow. Deng (2012) described a well-preserved skull of *Proboscidipparion sinense* (his *Hipparion* (*Proboscidipparion*) *sinense*) from the basal Pleistocene (*c.* 2.6 Ma) Longdan locality, Dongxiang, Gansu Province, NW China and discussed some new details about this species. Wolf *et al.* (2013) further showed that *Proboscidipparion* has the distinct apomorphy of elongated dP2 while Bernor & Sun's (2015) study of section cheek teeth exhibit complex enamel plications in mid-adult wear and distinct nasal retraction with broad narial opening in juvenile crania (Bernor & Sun 2015).

Qiu *et al.* (1987) reported the stratigraphic range of the genus *Proboscidipparion* in China as being Gaozhuangian to early Zhoukoudianian (*c.* 5-1 Ma). Whereas *Proboscidipparion sinense* has an established range of 2.6 (Longdan juvenile skull) to 1 Ma, an earlier less derived form *Proboscidipparion pater* with less reflected nasals is known from the Yushe Basin. We follow Bernor & Sun (2015) herein recognizing that Çalta juvenile cranium MNHN.F.ACA336 (Fig. 11) and cheek teeth of ACA337 (Fig. 12) are similar to Yushe *Proboscidipparion pater* (THP20847; Fig. 15). Moreover, the Çalta *Proboscidipparion heintzi* is of similar age to Yushe *Pr. pater*, Early Pliocene. Postcrania of Chinese *Pr. pater* and *Pr. sinense* are not certainly known and may have been confused with sympatric occurring *Plesiohip-*

Fig. 17. — MNHN.F.ACA82, *Plesiohipparion* cf. *longipes* (Gromova, 1952), 1PHIII: **A**, cranial view; **B**, caudal view. Scale bar: 5 cm.

parion houfenense, *Pl. huangheense* and even *Pl. zandaense*. It is reasonably certain that *Proboscidipparion heintzi* is a *Proboscidipparion* based on its elongate dP2 and retracted nasals with broad narial opening and that, in fact it had robust distal limb elements, the most remarkable being the very broad 3PHIIIs.

Çalta *Plesiohipparion* cf. *longipes* exhibits broader Eurasian and perhaps African affinities. The genus *Plesiohipparion* is an advanced group of hipparionine horses that occur mostly in the Pliocene and Pleistocene of China (Teilhard de Chardin & Young 1931). Qiu *et al.* (1987) have reported *Plesiohipparion* from the late Baodean (?) to Nihewanian of Asia and Ruscinian to early Villafranchian of Europe including Spain (Hernández-Pacheco 1921; Villalta Comella 1950, 1952; Crusafont & Sondaar 1971). Li & Li (1990) reported a species of *Plesiohipparion, Pl. zandaense* from the Latest Miocene (*c.* 6 Ma?) of the Zanda Basin, southwest Tibet. Despite the Zanda Basin's proximity to the Indian subcontinent, there is no evidence that *Plesiohipparion* occurred in the Siwalik hills – our data found no support for *Plesiohipparion* occurring in the Siwaliks. Bernor & Lipscomb (1991) reported the occurrence of *Plesiohipparion* aff. *huangheense* from the Villafranchian locality of Gülyazi, Turkey and, because of the co-occurrence of *Equus* in the fauna, suggested an earliest Pleistocene correlation (*c.* 2.6 Ma).

Qiu *et al.* (1987) have credited Zhegallo (1978) with being the first to recognize the remarkable similarity in tooth morphology between Chinese "*Hipparion*" *houfenense* and Spanish "*Hipparion*" *rocinantis* and chose to hold *Plesiohipparion* at the subgenus rank, *Hipparion* (*Plesiohipparion*). Qiu *et al.* (1987) reaffirmed the striking similarity between "*H.*" *rocinantis crusafonti* (IPS H2268) from Villaroya and "*H.*" *houfenense.* Bernor & Lipscomb (1991, 1995) undertook a phylogenetic analysis of Old World hipparions and supported *Plesiohipparion* as a clade distinct from *Hipparion* s.s. Forsten (1968) and Aguirre & Alberdi (1974) observed that *Plesiohipparion* had metaconid/metastylid (= their double knot) morphology similar to African hipparions. Qiu *et al.* (1987) added that *Plesiohipparion* shared the following characters with African hipparions: lack of POF, shallow nasal notch, cheek teeth hypsodont (60-90 mm), triangular metaconid/metastylid, maxillary cheek teeth with elongate protocone (8-10 mm). Bernor *et al.* (2010) and Wolf *et al.* (2013) have suggested that *Plesiohipparion* has its evolutionary roots in the Siwalik Late Miocene *Sivalhippus* clade whereas Bernor *et al.* (2014) and Bernor & Sun (2015) have pointed out the plausible sister-taxon status of *Plesiohipparion* and *Eurygnathohippus*. Hulbert & Harrington (1999) reported partial skull of juvenile hipparion from Ellesmere Island, Canada attributed to *Plesiohipparion,* which represents its only known extension into North America.

Koufos & Vlachou (2005) reported the occurrence of *Hipparion* cf. *longipes* from the Late Miocene locality of Akkaşdağı, Turkey. The Akkaşdağı fauna is rich and well preserved within a volcanic tuff securely dated 7.1 Ma (Karadenizli *et al.* 2005). The Akkaşdağı equid fauna includes

TABLE 2. — Paleobiogeographic affinities of Çalta mammals (Turkey).

Çalta mammalian taxa	**Europe**	**Asia**	**Eurasia**	**Africa**	**Endemic**
Asoriculus gibberodon (Petenyi, 1864)	×	–	–	–	–
Mafia csarnotense Reumer, 1984	×	–	–	–	–
Erinaceus sp.	–	–	×	–	–
Centralomys magnus (Sen, 1977)	×	–	–	–	–
Occitanomys sp.	×	–	–	–	–
Orientalomys galaticus (Sen, 1975)	–	×	–	–	–
Apodemus dominans Kretzoi, 1959	–	–	×	–	–
Mesocricetus cf. *primitivus* de Bruijn, Dawson & Mein, 1970	–	–	–	–	×
Pseudomeriones tchaltaensis Sen, 1977	–	×	–	–	–
Mimomys davakosi van de Weerd, 1979	×	–	–	–	–
Pliospalax macoveii (Simionescu, 1930)	–	–	–	–	×
Dryomimus eliomyoides (Kretzoi, 1959)	×	–	–	–	–
Ochotonoma anatolica Sen, 1998	–	×	–	–	–
Vulpes galaticus Ginsburg, 1998	–	×	–	–	–
Nyctereutes donnezani (Deperet, 1890)	–	×	–	–	–
Chasmaporthetes kani anatolicus Ginsburg, 1998	–	×	–	–	–
Lynx issiodorensis (Croizet & Jobert, 1828)	×	–	–	–	–
Machairodus giganteus (Wagner, 1848)	–	×	–	–	–
Dicerorhinus megarhinus (de Christol, 1834)	×	–	–	–	–
Proboscidipparion heintzi (Eisenmann & Sondaar, 1998)	–	×	–	–	–
Plesiohipparion cf. *longipes* (Gromova, 1952)	–	×	–	–	–
Sus arvernensis minor Deperet, 1890	×	–	–	–	–
Cervus cf. *perrieri* Croizet & Jobert, 1828	×	–	–	–	–
Giraffa cf. *jumae* Leakey, 1965	–	–	–	×	–
Gazella emilii Bouvrain, 1998	–	×	–	–	–
Tchaltacerus longicornis Bouvrain, 1998	–	–	×	–	–
cf. *Koufotragus bailloudi* (Arambourg & Piveteau, 1929)	×	–	–	–	–
Gazellospira sp.	–	–	×	–	–
Hippotragini indet.	–	–	–	×	–

four species, three of which are typical Turolian age provincial species (*Hipparion dietrichi, Cremohipparion moldavicum* and *Hippotherium brachypus*) and *Hipparion* cf. *longipes.* In fact, Akkaşdağı *H.* cf. *longipes* right maxillary cheek tooth row AK7-70 (Koufos & Vlachou 2005: fig. 13) compares very closely with *Plesiohipparion houfenense* from the Yushe Basin, China (THP10733; Bernor & Sun 2015: fig. 7a, b) both in size and morphological characters. The Akkaşdağı MCIII and MTIII lengthening is greater than provincial Turolian slender-limbed taxa which is a character shared with Chinese *Plesiohipparion.* Thusfar, Akkaşdağı *Plesiohipparion* cf. *longipes* is the oldest known member of the *Plesiohipparion* clade.

Asian biogeographic affinities of Çalta hipparions are reinforced by the bulk Çalta fauna. This locality yielded 29 species of small and larges mammals (Sen *et al.* 1998). Among them two are endemic to the region, ten species have a large distribution all over Eurasia, eleven other are rather known as European, and four of them indicate stricly Asiatic affinities. (Table 2; Fig. 18). Indeed, all along the Neogene, mammalian faunas from Anatolia display large paleobiogeographic affinities, mainly with Europe and Asia, and scarcely with Africa.

Bernor *et al.* (2014, 2015a, b), Bernor & Sun (2015), Wolf & Bernor (2013) and Wolf *et al.* (2013) have most recently addressed the phylogenetic relationships of *Plesiohipparion* spp. and *Proboscidipparion* s.s. These taxa are related more broadly to the "*Sivalhippus* Complex" that include *Sivalhippus* spp., *Eurygnathohippus* spp., *Plesiohipparion* spp. and *Proboscidipparion* spp. The most primitive, and at the same time oldest member of this group is *Sivalhippus nagriensis* known from *c.* 10.5 Ma. There was a modest evolutionary radiation of *Sivalhippus* including *S. nagriensis, S. permiensis, S. theobaldi* and *S. anwari* in the Indian Subcontinent. *Sivalhippus* extended its range into eastern and perhaps northern Africa in the Late Miocene; it is represented by *S. turkanensis* at Lothagam Hill, Kenya by 6.5 and perhaps older. *Eurygnathohippus* is an African clade earliest represented in the Late Miocene of Kenya and Libya (*c.* 7-6 Ma) and underwent a Late Miocene-Pleistocene radiation that included *Eu. feibeli, Eu. hooijeri, Eu. woldegabrieli*, *Eu. hasumense, Eu. pomeli* and *Eu. cornelianus*, the last being the terminal taxon. *Eurygnathohippus* is unique among "*Sivalhippus* Complex" taxa in evolving persistently large, elongate and high crowned ectostylids on the permanent cheek teeth. Ectostylids very rarely occur on Siwalik *Sivalhippus* permanent cheek teeth and are otherwise absent on all other Old World hipparions. Nevertheless, Bernor & Sun (2015) and Bernor *et al.* (2015a, b), following other authors cited herein, have noted that there are several skull, maxillary and mandibular cheek tooth characters that are shared between Eurasian *Plesiohipparion* and African *Eurygnathohippus* and *Plesiohipparion.* We have added in this contribution further evidence of common lengthening of MCIII and MTIII shared by Eurasian *Plesiohipparion* and African *Eurygnathohippus.* It would appear that the ancestry of the *Plesiohipparion* – *Eurygnathohippus* clade extends deeper in time than 7.1 Ma and occurred at a time when many other hipparion lineages existed across Eurasia and Africa.

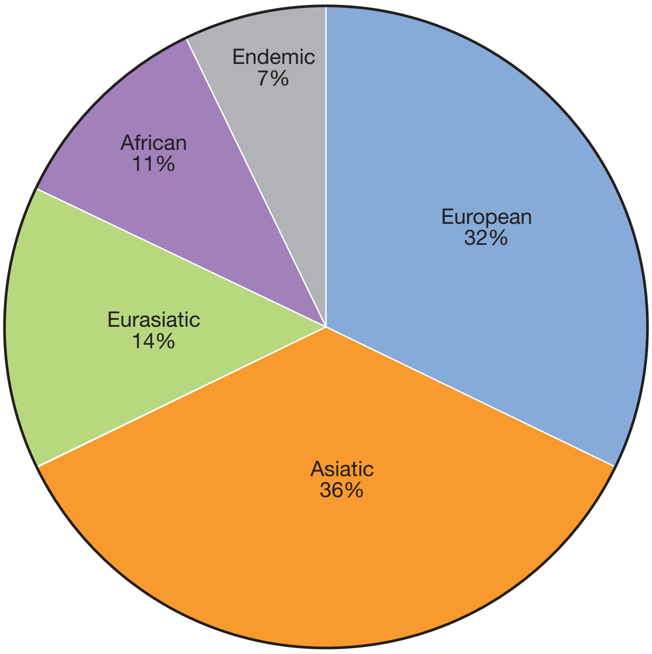

FIG. 18. — Paleobiogeographic affinities of mammalian taxa from Çalta (Turkey).

CONCLUSIONS

Çalta is a 4.0 Ma Turkish locality with two hipparion lineages represented, *Proboscidipparion heintzi* and *Plesiohipparion* cf. *longipes*. *Proboscidipparion heintzi* is a robust limbed form with massive MPIIIs, 1PHIIIs and very broad 3PHIIIs and a cranium with distinctly retracted nasals, no POF and elongate dP2. *Plesiohipparion* cf. *longipes* has very elongate-slender MPIIIs, elongate 1PHIII and cheek teeth that preserve a number of characters typical for *Plesiohipparion*, most similar to *Plesiohipparion houfenense* from China (Bernor *et al.* 2015b). The Çalta equid fauna is remarkable for the absence of typical later Turolian lineages *Hipparion dietrichi, Cremohipparion moldavicum,* and *Hippotherium brachypus* large form such as documented at Akkaşdağı, Turkey. These lineages became extinct at the end of the Miocene (Bernor *et al.* 1996) and the Çalta fauna documents their replacement in the Early Pliocene by the Chinese clades *Proboscidipparion* and *Plesiohipparion*. Whereas *Plesiohipparion* had a range that included China, Canada and Spain, *Proboscidipparion* was restricted to China and Çalta, Turkey. Perpignan, France has Early Pliocene "*Hipparion*" *crassum* which has an uncertain affinity with *Proboscidipparion heintzi*; the short MPIII and elongate symphysis may suggest a relationship, but more information is needed about "*H.*" *crassum*'s facial, nasal and cheek tooth morphology to assign it to *Proboscidipparion.*

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