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The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection

11. Equidae

by

Theodora D. Vlachou[*)] **& George D. Koufos**[*)]

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Abstract

More than 200 hipparionine remains have been unearthed recently from the Turolian localities of Samos. The material has been studied along with relevant specimens of the Forsyth Major collection in Lausanne (MGL) and B. Brown's collection at the American Museum of Natural History (AMNH). The morphological analyses and the morphometric description that have been done on skulls and metapodials let us define seven hipparion species: *Hipparion proboscideum*, *Hipparion brachypus*, *Hipparion prostylum*, *Hipparion dietrichi*, *Hipparion* cf. *forstenae*, *Hipparion* cf. *matthewi* and *Hipparion nikosi*. The seven species are arranged in three successive assemblages with clear chronological differences: *Hipparion prostylum* and *Hipparion proboscideum*, from MLN, Qx, Q6 and MYT, corresponding to the end of early Turolian - beginning of middle Turolian; *Hipparion dietrichi*, *Hipparion proboscideum*, *Hipparion brachypus*, *Hipparion* cf. *matthewi* and *Hipparion* cf. *forstenae* from Q4, MTLA, MTLB, Q1, corresponding to middle Turolian, and *Hipparion dietrichi*, *Hipparion nikosi*, *Hipparion* cf. *forstenae*, *Hipparion* sp. 1 and *Hipparion* sp. 2 from Q5, corresponding to the latest middle Turolian or the beginning of late Turolian.

The comparisons of the Samos hipparionine horses with other already known hipparionines from the Eastern Mediterranean region provide many similarities with the Western Asian forms, but also significant differences to those from Central Asia and Continental Greece. The phylogenetic relationships of the hipparion species are also discussed. The hipparionine species are part of already known lineages, having spread to Greece, the Black Sea region, Asia, Iran and probably China.

Keywords: Late Miocene, Samos, Greece, Mammalia, Equidae, Systematics.

Zusammenfassung

Mehr als 200 hipparionartige Reste sind bei den letzten Ausgrabungen in der turolischen Fundstelle Samos gefunden worden. Das Material wurde gemeinsam mit relevanten Stücken aus der Sammlung von Forsyth Major in Lausanne (MGL) und aus der Sammlung B. Brown im American Museum of Natural History (AMNH) bearbeitet. Die morphologische Analyse und die morphometrische Beschreibung der Schädel und Metapodien erbrachte folgendes Ergebnis: *Hipparion proboscideum*, *Hipparion brachypus*, *Hipparion prostylum*, *Hipparion dietrichi*, *Hipparion* cf. *forstenae*, *Hipparion* cf. *matthewi* und *Hipparion nikosi*. Diese sieben Arten können in drei aufeinanderfolgende Vergesellschaftungen mit klaren chronologischen Unterschieden verteilt werden: *Hipparion prostylum* und *Hipparion proboscideum* aus MLN, Qx, Q6 und MYT korrespondiert mit dem Ende des frühen Turolium bis zum beginnenden Mittelturolium. *Hipparion dietrichi*, *Hipparion proboscideum*, *Hipparion brachypus*, *Hipparion* cf. *matthewi* und *Hipparion* cf. *forstenae* aus Q4, MTLA, MTLB, Q1 gehören in das mittlere Turolium und *Hipparion dietrichi*, *Hipparion nikosi*, *Hipparion* cf. *forstenae*, *Hipparion* sp. 1 und *Hipparion* sp. 2 aus Q5 sind ins mittlere Turolium oder zu Anfang des späten Turoliums zu stellen.

Der Vergleich der hipparionen Pferde aus Samos mit bereits bekannten Hipparionen aus der östlichen Milltelmeer-Region zeigt eine große Ähnlichkeit mit Formen aus Kleinasien und signifikante Unterschiede zu Formen aus Zentralasien und dem kontinentalen Griechenland. Die phylogenetische Verwandtschaft der Hipparionen-Arten wird diskutiert. Diese Arten sind Teil der bereits bekannten Linien, die in Griechenland, der Schwarzmeer-Region, Asien, Iran und wahrscheinlich auch in China verbreitet sind.

Schlüsselworte: Obermiozän, Samos, Griechenland, Mammalia, Equidae, Systematik.

[*)] MSc. Theodora D. Vlachou & Prof. George D. Koufos, Aristotle University of Thessaloniki. Department of Geology. Laboratory of Geology and Palaeontology. GR-54124 Thessaloniki, Greece. e-mail: dovla@math.auth.gr, koufos@geo.auth.gr

1. Introduction

The fossil-rich mammal localities on Samos Island have been known since the second half of the 19th century (Forsyth Major, 1894). Between 1890 and 1970, more than 30.000 specimens have been collected from the Samos fossiliferous beds and have been dispersed to a large number of museums and institutes in Europe and America (Solounias, 1981). Notwithstanding, the lack of precise stratigraphic information from that field period renders the fossil sample useless in many cases. Exceptions are the Forsyth Major collection in Lausanne (MGL) and B. Brown's collection at the American Museum of Natural History (AMNH), which bear locality indications and upon which most of the Samos hipparion studies are based on.

In 1993, a palaeontological team from the Aristotle University of Thessaloniki started a new survey in the Mytilinii Basin on Samos, giving attention to the stratigraphic arrangement of the newly discovered fossil sites and their correlation with the old ones. Kostopoulos et al. (2003) give an updated chronology of the fossil-bearing horizons of the Mytilinii Formation, at the same time trying to relocate the old quarries and to correlate them with the new ones, analyzing all the available data. In this volume, this work was improved in some points, adding more data about the stratigraphy, the fossiliferous sites and the taxonomy (Table1).

The new hipparion collection comes from the localities Mytilinii-4 (MLN), Mytilinii-3 (MYT) and Mytilinii-1A, and 1B (MTLA, MTLB). MLN is placed at the very base of the main fossiliferous horizons of Mytilinii Fm (White beds of Weidmann et al., 1984) and it is directly correlated with B. Brown's Quarry-2 (Q2) (Kostopoulos, this volume; Kostopoulos et al., this volume-a), dated between 7.65-7.45 My (~7.5). MYT is placed in the lower part of the main fossiliferous beds of Mytilinii Fm (lower MBB of Weidmann et al., 1984), with an approximate age of ~7.3 My (Kostopoulos et al., 2003, Kostopoulos et al., this volume-a); the site is placed in the same stratigraphic horizon with Forsyth Major's 'Stefano' and Solounias's (1981) S3, 4, whereas B. Brown's Quarry 4 (Q4) is slightly younger (Kostopoulos et al., this volume-a). MTLA and MTLB, dated at ~7.1 My, are located in Adrianos ravine at the upper part of the main fossiliferous beds; Quarry-1 (Q1) of B. Brown, 'Adriano' of F. Major and 'Adrianos' of Melentis are correlated with MTLA/B (Kostopoulos et al., this volume-a). Three more sites from B. Brown's collection are of special interest; Qx is placed in the lower part of Mytilinii Fm., dated between 8.0-7.6 My (Kostopoulos et al., 2003); Q6 was usually correlated with Qx, but new data (Kostopoulos, this volume-a) indicates a position between MLN and MYT, i.e. at about 7.4 My; Q5 is the uppermost fossiliferous site of B. Brown, with an estimated age between 6.7-6.9 My. More details about the stratigraphy and the age of these horizons are given by Kostopoulos et al. (this volume-a) and Koufos et al. (this volume).

The present study focuses on the new *Hipparion* collection stored at the Museum of Natural History of Samos Island (NHMA) but with reference to the old *Hipparion* material (PMMS, AMNH, MGL, SI, MF). The ulterior purpose is the definition of the Samos *Hipparion* taxonomy at species level, their relationships with the already described forms from the surrounding area and finally their chrono-spatial distribution.

2. The Previous List of Samos Hipparionine Horses

When Forstén (1980b) posed the question *"How many hipparions are there in Samos?"*, she knew that many palaeontologists before her tried to answer this question, but she could not know that several years later, we are still dealing with this problem.

Three of the best known and most widely dispersed hipparionine horses of the Eastern Mediterranean region base their typical and original descriptions on material originating from Samos. Abel (1926) created the new species *H. matthewi* based on a skull associated with the mandible, housed at the Museum of the Hungarian Geological Survey. Studer (1911) described a large-sized skull under the new species name *H. proboscideum*. Wehrli (1941), relying on the length of cheek tooth row, facial morphology and limb proportions, described the new species *Hipparion dietrichi* and distinguished four hipparion species in the Samos fauna: *Hipparion proboscideum*, *Hipparion dietrichi* (new species) (type a), *Hipparion dietrichi* (type b, smaller than type a) and *Hipparion matthewi*.

Following Wehrli's systematics, Sondaar (1971) studied the skull morphology of the hipparions from the different fossil quarries of Samos and recognized four hipparion species, *Hipparion dietrichi*, *Hipparion matthewi*, *Hipparion proboscideum* and *Hipparion* sp., large-sized. Besides, he proposed a possible correlation of the available metapodials from the different quarries with the studied skulls and finally he pointed out three different hipparion assemblages due to chronological differences (Table 1).

Forstén (1980b, 1983), using the relation of POB to P2 - orbit distance and the metapodial proportions, increased the hipparion species to four at one site and to more than six in the whole Samos fauna (Table 1). With all details, she reached the following conclusions:

Q5: *Hipparion matthewi*, *Hipparion dietrichi* (represented only by metapodials) and *Hipparion* sp. (large-sized hipparion with POF far from the orbit).

Q1: *Hipparion* sp. (medium-sized hipparion with single POF placed close to the orbit), *Hipparion dietrichi/schlosseri*, *Hipparion brachypus*, *Hipparion proboscideum*

Q4: *Hipparion* cf. *dietrichi*, *Hipparion brachypus*

Q6: *Hipparion* sp. (medium size) and *Hipparion* sp. (large size)

Koufos & Melentis (1984) studied only the material collected from the lower level of Adrianos ravine (correlated with the new locality MTLA), stored at the Palaentological Museum of Mytilinii, Samos (PMMS). They listed four hipparion species: *Hipparion dietrichi*, *Hipparion proboscideum*, *Hipparion* sp. 1 (represented by a large-sized

PREVIOUS STUDIES						RECENT WORK						
	SOLOUNIAS 1981	SWISHER 1996	SONDAAR, 1971	FORSTEN, 1980 & FORSTEN 1989	BERNOR et al., 1996	KOSTOPOULOS et al., this volume		KOUFOS et al., this volume				**present study**
	localities	Age (Ma)						localities Age (My)			MN ZONES	
Main Bone Beds (MBB)	Q5		*H. matthewi, Hipparion sp.*	*H. matthewi, H. schlosseri-dietrich, H.* sp. large sized	*"Hippotherium" brachypus, "Hipparion" dietrichi, "Cremohipparion" matthewi, "Cremohipparion" aff. matthewi, "Cremohipparion" proboscideum*			Q5		6,9-6.7		***Hipparion* sp. I, *Hipparion* sp. II, *H. dietrichi, H. nikosi, H.* cf. *forstenae***
	Q1, A			*H. sp.* middle sized, *H. schlosseri-dietrichi, H. brachypus, H. proboscideum*		Mytilinii Fm	Upper	Q1, A	MTLB	7.1-7.0		***H. brachypus, H.* cf. *proboscideum, H. dietrichi, H.* cf. *forstenae, H.* cf. *matthewi***
									MTLA			
	Q3, S4, (Q4)		*H. dietrichi, H. proboscideum*					Q4, Q3				***H. brachypus, H. dietrichi, H.* cf. *matthewi***
									MYT			***H.* cf. *proboscideum, H. prostylum H. cf. forstenae, H.* cf. *matthewi***
								Q6				***H. cf. proboscideum H. prostylum***
White Bebs & Gravel Beds (WB & GB)	Q2			*H. schlosseri-dietrichi, Hipparion.* sp. large sized	*"Hippotherium" giganteum, "Cremohipparion" nikosi*			Q2, S4	MLN		MN11	***Hipparion* sp. I (aff. *H. proboscideum*, *Hipparion* sp II (aff. *H. prostylum*),**
Old Mill Beds (OMB)	Q6 Qx	8.28-8.38	*H. proboscideum*	*Hipparion.* sp. middle sized, *Hipparion.* sp. large sized *H. proboscideum*	*"Hipparion" gettyi. "Hipparion" prostylum, "Cremohipparion" mediterraneum*		base	Qx				***H. proboscideum***

Table 1: Old and recent works on the Samos hipparion collections.

mandible with a short rostral portion) and *Hipparion* sp. 2 (small-sized hipparion species with a moderately developed POF close to the orbit).

The last but not least answer to Forsten's question was that of BERNOR et al. (1996a). BERNOR et al. (1996a) attempted to correlate the Samos fauna with that from Pikermi and Maragheh. They concluded the definition of three super-specific taxonomic groups, and more or less twelve hipparion species. The Samos fauna, in particular, includes ten of them (Table 1).

Abbreviations:

Localities

AKK: Akkaşdağhi; DTK: Dytiko, Axios Valley Greece, GRE: Grebeniki; HD: Hadjidimovo; KTD: Kemiklitepe D, Turkey; KTA-B: Kemiklitepe A & B, Turkey; LMRG: Lower Maragheh level, Iran; MMRG: Middle Maragheh level, Iran; MLN: Mytilinii 4, Samos, Greece; MYT: Mytilinii 3, Samos, Greece; MTLA: Mytilinii 1A, Samos, Greece; MTLB: Mytilinii 1B, Samos, Greece; NKT: Nikiti 1, Macedonia, Greece; NIK: Nikiti 2, Macedonia, Greece; PIK: Pikermi, Greece; PNT: Pentalophos, Axios Valley, Greece; PXM: Prochoma, Axios Valley, Greece; Q1, 4, 6: Quarry 1, 4, 6, Samos, Greece; RPl: Ravin de la Pluie, Axios Valley, Greece; RZO: Ravin des Zouaves-5, Axios Valley, Greece; TAR: Taraklia; VTK: Vathylakkos-2, Axios Valley, Greece.

Institutes & Museums

AMNH: American Museum of Natural History, New York; BMNH: British Museum of Natural History, London; BSP: Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; NHMW: Naturhistorisches Museum, Wien; KUAC: Department of Geology and Mineralogy, Kyoto University. MF: Frankfurt; MGL: Lausanne; MNHM: Muséum National d'Histoire Naturelle, Paris; NHMB: Naturhistorisches Museum, Bern, Switzerland; PMMS: Palaeontological Museum of Mytilinii, Samos; SI: Geological Institute of the University, Münster.

Morphology

POF: preorbital fossa; POB: preorbital bar, Mx: measurement number x

3. Terminology

The term "group" is used to define an assemblage of species based on the phenetic similarity of the specimens. WOODBURNE & BERNOR (1980) divided Vallesian and Turolian hipparion forms of the Old World into four groups on the basis of important facial characteristics, with possibly superspecific taxonomic value. FORSTÉN (1983, 1999) gave other grouping hypotheses of the western Old World hipparions based either on the distance between the orbit and the preorbital fossa, or the snout proportions and the POF development, and she mentioned that both hipparion groupings may or may not coincide with the grouping done on the basis of teeth and limb morphology. Therefore she considered the Vallesian and Turolian hipparions as being a single genus, *Hipparion*, with multiple species grouped under specific morphologies.

BERNOR et al. (1996b, c), improving their first work on the superspecific hipparionine horses grouping, created possible lineages in each group, based on the apparent phylogenetic relationships of the species. Hence, regarding SE Europe and SW Asia, they recognized the *"Hippotherium" brachypus* - *"Hippotherium" giganteum* lineage, possibly derived from the *"Hippotherium" primigenium* s.s. lineage of the *"Hippotherium"* group, the *"Hipparion" prostylum* - *"Hipparion" dietrichi* lineage that would appear to be derived from *"Hippotherium" gettyi* of the *"Hipparion"* group and the *"Cremohipparion" macedonicum* - *"Cremohipparion" nikosi* and *"Cremohipparion" mediterraneum* - *"Cremohipparion" proboscideum* lineages, both probably derived from *"Hippotherium"*

WATABE (2004) attempted to group the hipparion species, taking into account facial features such as the POF complex morphology, the metapodial proportions and the snout morphology. The occlusal cheek teeth morphology, including the enamel plication and the protocone shape, is considered as being useful only for distinguishing morphotypes from a single locality. The proposed groups and the aforementioned possible lineages of this study slightly differ from those of

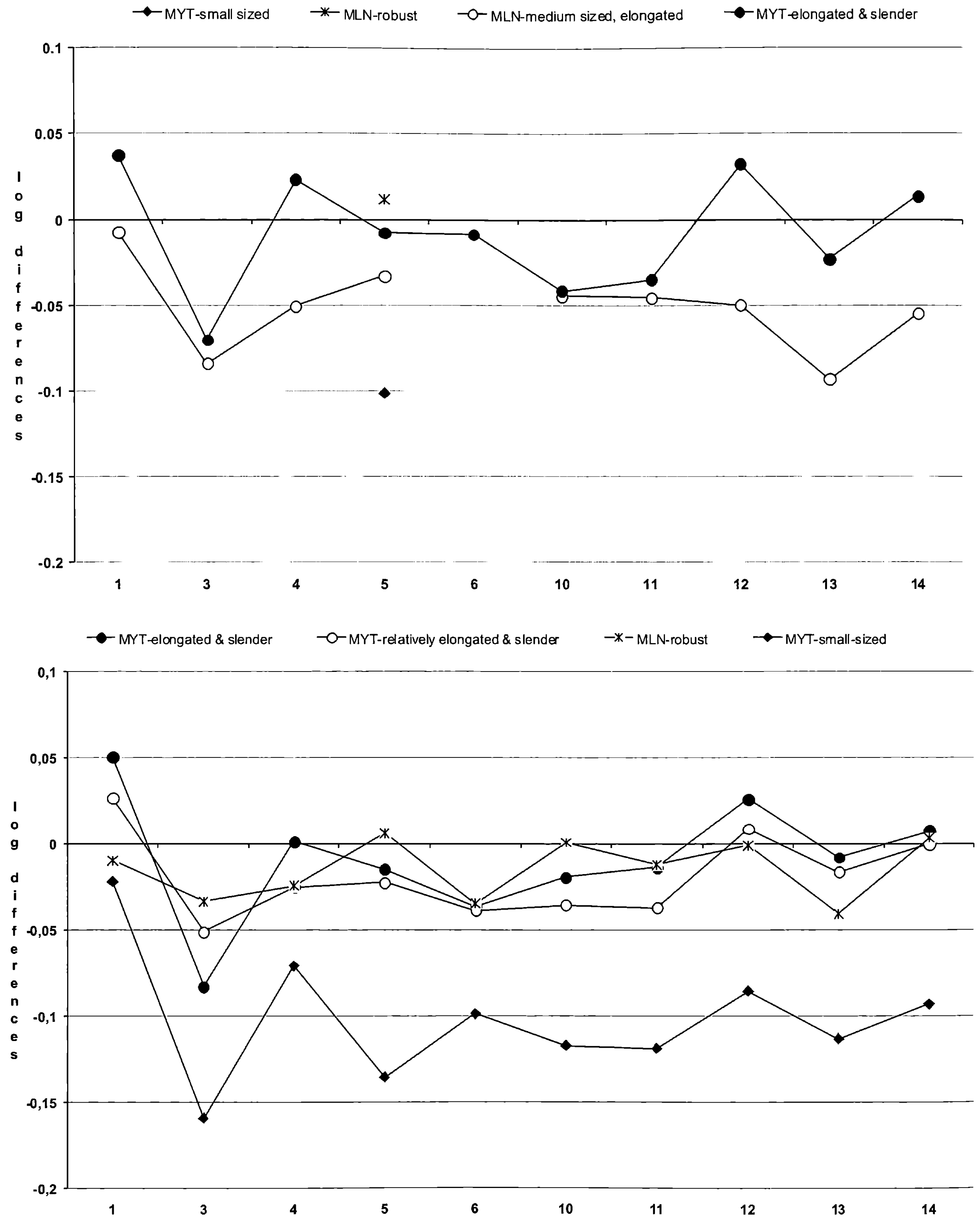

Figure 1: Logarithmic ratio diagram comparing the metacarpals (above) and metatarsals (below) from MLN and MYT with those from Höwenegg. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (BERNOR et al., 1997).

BERNOR et al. (1996b). Nevertheless, WATABE (2004) has a different opinion about the monophyletic origin of hipparionine horses and the superspecific values of the groups.

ZOUHRI & BENSALMIA (2005) corroborate the theory of the different hipparion genera proposed by BERNOR et al. (1996b). But, contrary to all the known theories about the hipparionine phylogeny, they regard the taxonomic value of some facial features, such as the narial opening depth and the presence of an anterior fossa, as meaningless. Hence, they created a series of synonyms, reducing the number of hipparion species in each group.

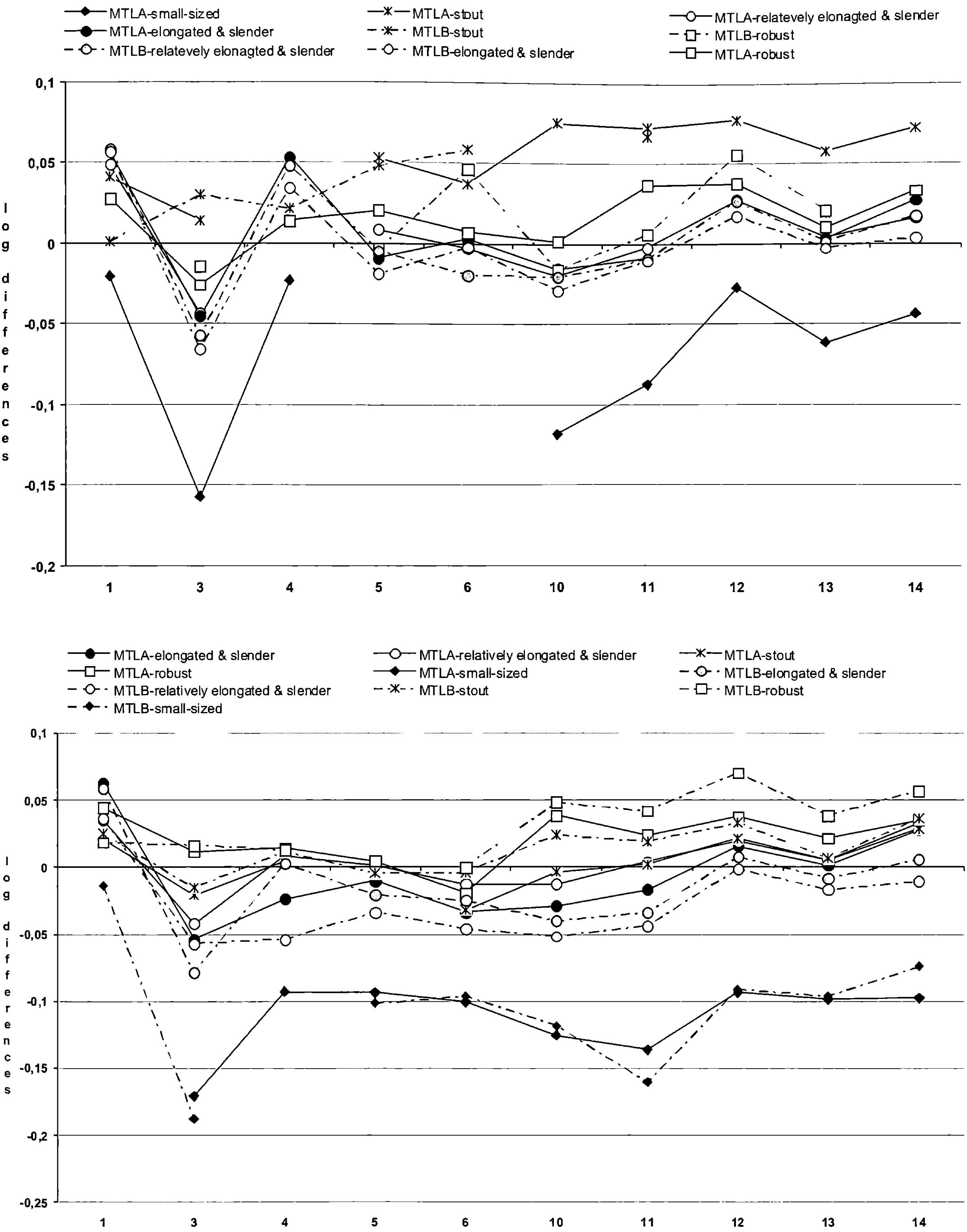

Figure 2: Logarithmic ratio diagram comparing the metacarpals (above) and metatarsals (below) from MTLA with those from Höwenegg. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (BERNOR et al., 1997).

4. Methodology

The newly collected hipparion material from Samos contains more than 200 specimens. Among them, there is a small number of complete and partially preserved skulls, several mandibles and a great number of postcranial remains. All specimens were measured according to the system proposed by EISENMANN et al. (1988) (Appendix-1). The given descriptions are based on the better-preserved specimens. The skull descriptions, in particular, rely more or less on the morphological characteristics proposed by BERNOR & LIPSCOMP (1995) (Appendix-2). The skeleton

Table 2: The minimum number of individuals (MNI) sorted by fossiliferous sites, morphological group and body mass.

Morphological Group	Body Mass (kg)	MLN	MYT	MTLA-B
H. macedonicum	100-130	—	4	2
H. dietrichi	150-220	3	8	29
H. brachypus *H. proboscideum*	200-350	2	3	17

pattern is mainly represented by the metapodial morphology exhibited in the log-ratio and scatter diagrams. Log ratio diagrams, as well as Box and Whiskers plots, were used to compare the Samos hipparion sample with other already known hipparion species of similar age and provenance. The log ratio diagrams usually provide differences among basic skeleton measurements. *H. primigenium* from Höwenegg (Bernor et al., 1997) has been used as a standard for comparison. The Box and Whiskers plots check the differences in basic measurements, especially when the compared samples are few in number and evaluate interspecific morphometric transitions, possibly related to phylogenetic changes. The approximate body mass estimation relies on the metapodial measurements and the methodology proposed by Scott (1990) and Eisenmann & Sondaar (1998).

5. Material Analyses

5.1. Skulls and Mandibles

Appendix-2 lists the morphologic diversity of the newly collected cranial remains. The morphological analysis of this table shows that there are four morphological hipparion groups in the Samos fauna:

***Hipparion primigenium* group**: it includes the large-sized skulls with elongated and relatively broad muzzle, short to deep narial opening, elongated preorbital bar, deep anteroposterior to slightly anteroventrally oriented preorbital fossa (POF) and highly plicated teeth with elliptical protocone. Representatives of this group were found in MYT and MTLA-B localities and we believe that they stand for the presence of the *Hipparion giganteum* - *Hipparion brachypus* lineage.

***Hipparion proboscideum* group**: it includes the large-sized skulls with elongated and narrow muzzle, short preorbital bar, deep and wide preorbital fossa, well defined canine fossa and highly plicated teeth with round or oval to elliptical protocone. Specimens with this morphology have been detected in the MTLA locality and probably represent the *Hipparion proboscideum* - *Hipparion mediterraneum* lineage.

***Hipparion dietrichi* group**: we believe that it is seperated in two sub-groups. Each is characterized by different skull morphology. The first is represented by medium- to large-sized skulls with broad muzzle, elongated preorbital bar, weakly to moderately developed preorbital fossa, short narial opening and moderately plicated teeth with elliptical to oval protocone. This morphology has been detected in specimens from MLN and MTLA-B and it seems to characterize the *Hipparion prostylum* - *Hipparion dietrichi* lineage. The second skull morphology is represented by small- to medium-sized skulls with elongated and narrow muzzle, long preorbital bar, shallow and elliptical-shaped anteroventrally oriented preorbital fossa, weakly defined canine fossa, deep narial opening and moderately plicated teeth with elliptical to oval protocone. This skull morphology has been found only in MTLA-B localities and, from a first point of view, is not related to any known lineage of the Eastern Mediterranean region. It is probably the morphology that Wehrli (1941) described under the species name *Hipparion dietrichi* - type b (see above Samos hipparion list) and what Vlachou & Koufos (2004) describe as *Hipparion* cf. *mediterraneum* in a preliminary list of the Turolian hipparion species from Greece. Similar skull morphology has also been detected in one specimen (NIK-714) from Nikiti 2, Northern Greece, where it is mentioned as *H. macedonicum* because no distinctions are detected among the small-sized metapodials from NIK and those described as *H. macedonicum* from Axios Valley (Vlachou & Koufos, 2002). Forstén & Garevski (1989) described a set of skulls from Titov Veles, FYR of Macedonia, under the name *H. verae*. *H. verae* shares several characteristics with the medium-sized hipparion from MTLA-B, but, at the same time, the former is more primitive in the short narial opening, the deeper POF and the occasional presence of the anterior fossa. *H. forstenae*, Zhegallo, 1971, from Shanxi (Loc. 30), China, differs

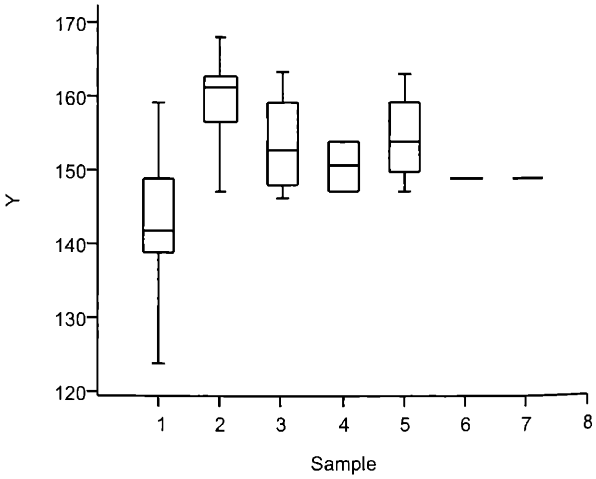

Figure 3: Box and Whiskers Plots on the length of maxillary cheek tooth row (M9) of "*H.*" *brachypus* and other relative forms. Samples: 1. Sinap forms; 2. *H. primigenium* Höwenegg; 3. NKT large-sized forms; 4. *H. brachypus* PIK; 5. *H. brachypus* HD; 6. *H. brachypus* Q4; 7. *H. brachypus* MTLB.

Table 3: The Samos hipparionine horses sorted by size, morphology and fossiliferous sites.

		MLN	MYT	MTLA	MTLB
H. dietrichi morphology	cranial remains	?	+	+	+
	postcranial elements	?	+	+	+
H. forstenae morphology	cranial remains	—	—	+	+
	postcranial elements	—	+	+	+
H. proboscideum morphology	cranial remains	—	+	+	
	postcranial elements	?	+	+	+
H. brachypus morphology	cranial remains	—	—	—	+
	postcranial elements	—	—	+	+
H. macedonicum morphology	cranial remains	—	—	+	
	postcranial elements	—	+	+	+
Development of Lineages	*H. prostylum - H. dietrichi* lineage	▬	▬	▬	▬
	H. verae - H. forstenae lineage		▬	▬	▬
	H. proboscideum - H. mediterraneum lineage	▬	▬	▬	▬
	H. giganteum - H. brachypus lineage			▬	▬
	H. macedonicum - H. nikosi lineage		▬	▬	▬

from the *H. verae* morphology in the retraction of the nasal notch above the posterior margin of P2 to the anterior half of P4 and the well-developed anterior fossa (Qiu, 1987). Bernor et al. (1990b), revising the Chinese hipparion species, described by Serve (1972) recognized in the *H. forstenae* facial morphology a subtriangular POF, which is anteroventrally oriented, medially shallow and has a slightly posterior pocketing, a distinct peripheral border outline, the anterior fossa being distinct but shallow and the nasal notch retracted to the posterior portion of P2, or anterior portion of P3. This set of characteristics is not far apart from those recognized in the small- to medium-sized hipparion from MTLA-B and possibly confirms the two hipparionine horses as closely related species, establishing, against one's better judgement, a *Hipparion verae - Hipparion forstenae* lineage.

***Hipparion macedonicum* group**: it includes the small-sized hipparions, formerly described under the species name of *H. matthewi* (Staesche & Sondaar, 1979). The skull includes a relatively elongated muzzle, short narial opening, moderately deep subtriangular POF, moderately to short POB and simple to moderately plicated teeth. Specimens with the above mentioned characteristics were found in MTLA-B and probably represent the *Hipparion macedonicum - Hipparion nikosi* lineage.

5.2. Postcranials

Specialization for a certain locomotor behaviour may strongly affect limb morphology. Metapodials, in particular, are highly adapted to a certain locomotor type. Therefore, their metric characteristics are quite useful in separating groups with similar locomotor behaviour. The skeleton size is also of great importance, because it reveals another animals functional behaviour of an animal, since it partly describes the relational position of a population in its ecosystem (ecological niche).

The log ratio diagrams for MCIII and MTIII indicate the presence of five skeleton patterns and three skeleton sizes in the Samos fauna (Figs. 1-2). The smaller size includes species ranging in weight from 100 to 130 kg in weight and the larger one from 200 to 350 kg. Both size groups, although continously present through time, from the MLN to MTLA-B fauna, have a low representation. On the contrary, the species of intermediate size (150-220 kg) seems to outclass them in the number of individuals, especially in the younger faunas (MTLA-B) (Table 2).

The analyses of the MLN sample indicate two hipparion species in this level. One is similar in size and skeleton pattern to *H. primigenium* from Höwenegg. The second is smaller and differs from the former in its metapodial morphology, having reduced midshaft width and a shallower, sharper defined distal articular surface (Figs. 1A, B).

In MYT, we recognized four types of skeletons, well-separated either by their size or by their morphology. The smaller hipparionine horse is characterized by elongated and slender metapodials (Fig. 1). Few specimens confirm the occurence of a large-sized hipparion. The scanty material does not allow further conclusions. It is possible, however, that it belongs to the same lineage as the robustly built hipparion from MLN. The medium-sized skeletons are grouped together in the log ratio diagram of Fig. 1. Two different morphologies of the proximal articular surface of the MCIII sample reveal two different taxa. One has a slightly larger size, a deeper articular surface and a more exaggerated protuberance for the musculus interosseus in the proximal part of MCIII than the other,

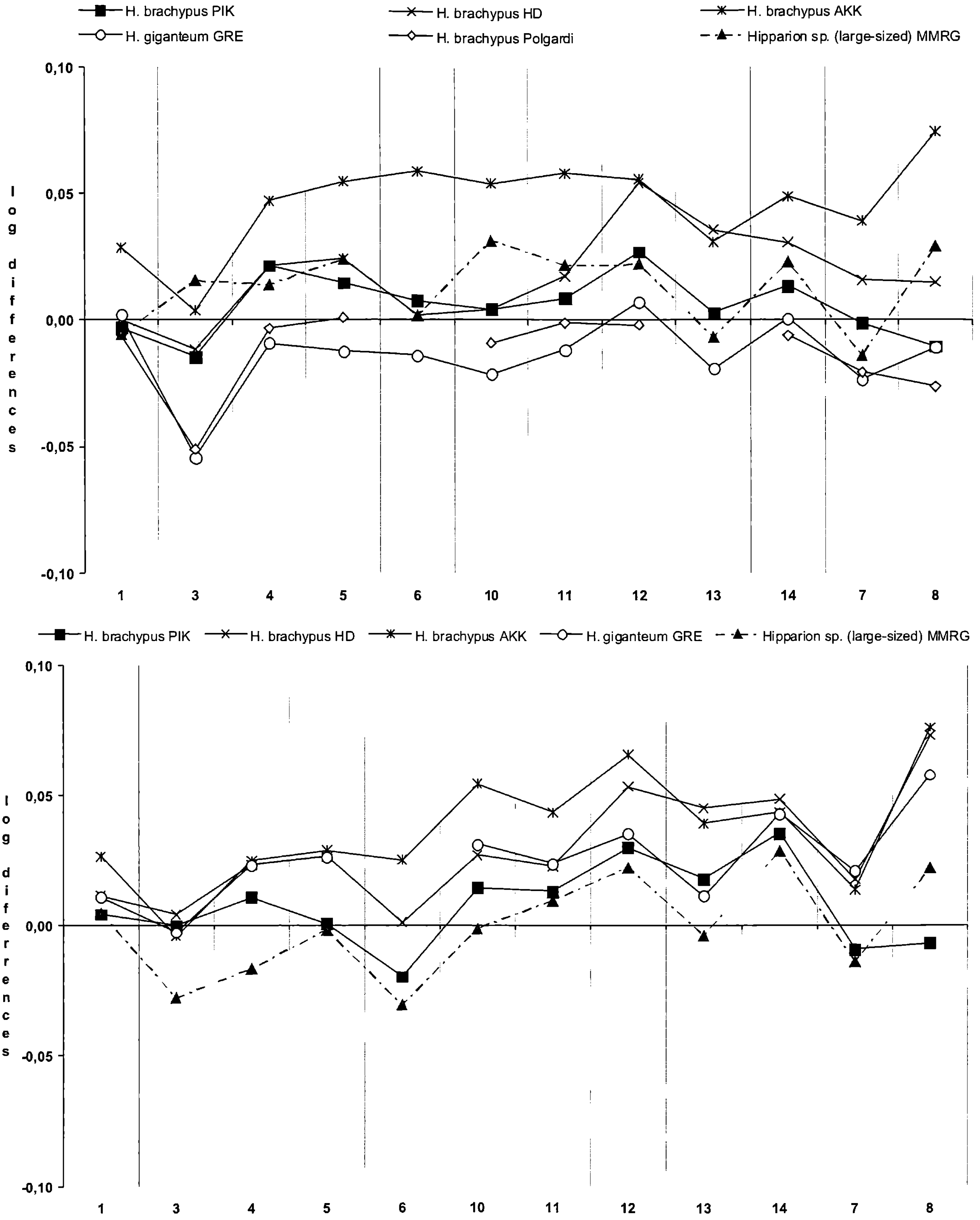

Figure 4: Logarithmic ratio diagram comparing the metacarpals (above) and metatarsals (below) of *H. brachypus* from PIK, HD, AKK and Polgardi with *Hipparion* sp. from MMRG and *H. giganteum* from Grebeniki. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

and probably a longer MTIII (Figs. 1A-B). From MYT to MTLA-B, one more large skeleton type is recorded. In other words, two large-sized metapodials have been recorded from MTLA-B localities. Both are robustly built, but one is more robust than the other (Fig. 2). The difference is better expressed in the MCIII morphology (Fig. 2A).

5.3. Correlation between Skulls and Postcranials

Table 3 summarizes the results of the cranial and postcranial analyses. The correspondance of the cranial material with the postcranial material and the possible ecological preferences of the different hipparionine horses of Samos were a real puzzle for the authors. There

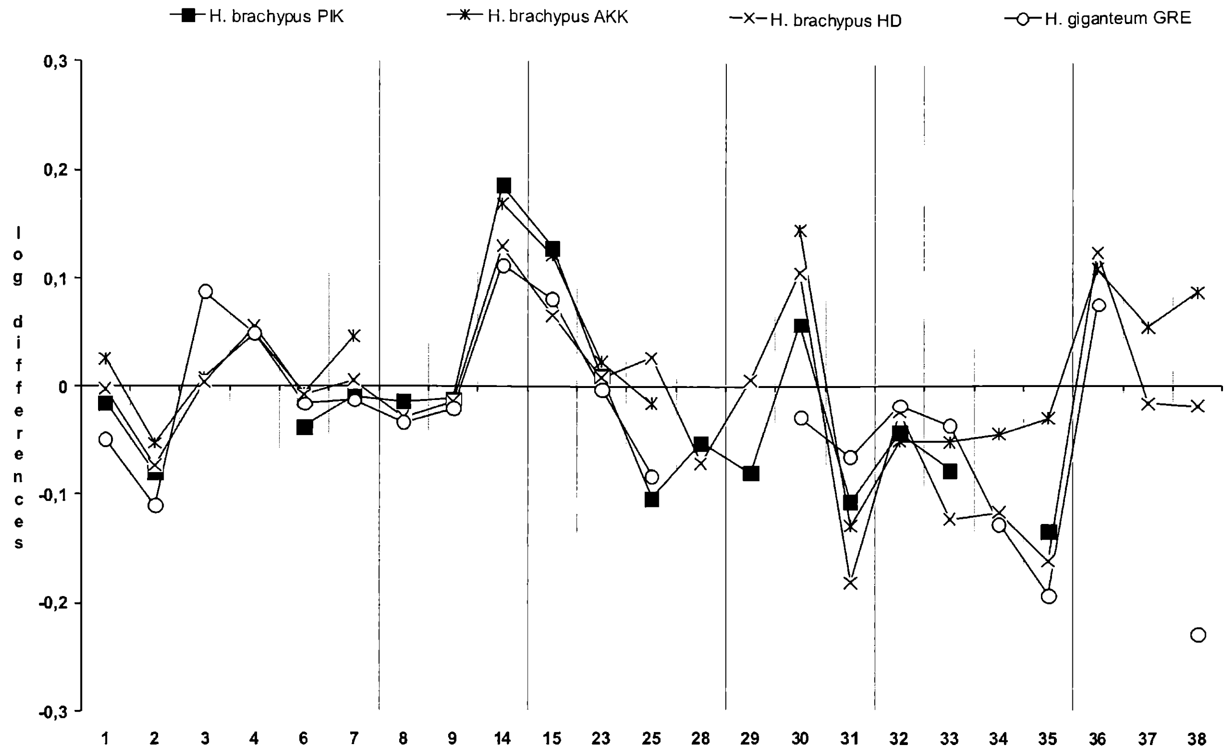

Figure 5: Logarithmic ratio diagram comparing the skull of *H. brachypus* from PIK, HD and AKK with *H. giganteum* from Grebeniki. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

are many theories dealing with morphologies favouring different palaeoecological conditions. The body size affects the physiological functions of an organism and is instrumental in the ecological niche definition (Alberdi et al., 1995). Janis (1990) supports the theory that the cheek tooth row length is closely related to skull length, and consequently, to the body size. Scott (1990) discussed how ontogeny influences tooth row length, and proposed the distal metapodial articular width for more accurate body mass estimations. Unlike to the distal articular width, the total metapodial length is possibly ecologically influenced. Elongated third metapodials are adapted to open landscape running forms (open habitats) while the stout ones are adapted to more close and wet habitats (Gregory, 1912; Gromova, 1952; Eisenmann, 1995; Scott, 2004). Additionaly, Janis & Erhardt (1988) concluded that the relative muzzle width is correlated with the dietary category. Therefore, the more selective feeders usually have narrow muzzles, whereas the grazing forms have wider muzzles. The above theories corroborate a huge number of papers with extensive discussions about different hipparion taxa and their possible skeleton patterns.

The *Hipparion giganteum* - *Hipparion brachypus* lineage includes large-sized forms, probably mixed feeders, with a robustly built skeleton (Koufos, 1987c; Bernor et al., 1996b, c; Eisenmann, 1995; Hristova et al., 2002; Scott, 2004; Koufos & Vlachou, 2005). Similar in size, but probably different in the skeleton pattern, is the *Hipparion proboscideum*-like morphological group (Koufos, 1987a; Koufos & Kostopoulos, 1994; Vlachou & Koufos, 2006). The *Hipparion prostylum* - *Hipparion dietrichi* lineage, as well as that of *Hipparion forstenae,* have a slenderly built skeleton, adapted to open habitats (Bernor et al., 1990a; Watabe & Nakaya, 1991a; Scott, 2004; Koufos & Vlachou, 2005; Qui, 1987). Lastly, the small hipparions of the *Hipparion macedonicum* - *Hipparion nikosi* lineage are characterized by a small size, a significantly slender skeleton morphology, but with a mixed diet, at least for *Hipparion macedonicum* (Koufos et al., 2006b)

The application of all this information to the Samos material analyses leads us to the following conclusions:

"Mytilinii 4" (MLN). The material is scanty and badly preserved, with few postcranials and two partly preserved mandibles (Appendix-1). Despite the limited specimens, two forms have been recognized. The small- to medium-sized mandible with the broad muzzle is possibly correlated to the elongated metapodials and belongs to the *H. prostylum* - *H. dietrichi* lineage. The larger form, with the short and broad metapodials, is in favour of the *H. proboscideum* - *H. mediterraneum* lineage (Table 3).

"Mytilinii 3" (MYT). From MLN to MYT, the number of specimens increases significantly (Appendix-1) and the equids are represented by four hipparion species. The smaller one, recognized by its elongated metapodials must belong to the *H. macedonicum* - *H. nikosi* lineage. The larger one is mainly recognized by a few maxillae with functional dP^1 and highly plicated teeth with an elliptical protocone. This morphology is better correlated to the large-sized postcranial elements and seems to belong to the *H. proboscideum - H. mediterraneum* lineage. The medium-sized slender skeleton with the exaggerated protuberance for the musculus interosseus on the upper articular surface of MCIII and the elongate MTIII probably corresponds to the *H. prostylum - H. dietrichi* lineage, while the slightly smaller slender skeleton with the somewhat shorter metapodials is probably correlated to the *H. forstenae* lineage (Table 3).

"Mytilinii-1A & B" (MTLA-B). We recognized five hipparion forms in the upper fossiliferous horizons. The small hipparion, which is represented by a skull, a few maxillae and several slender postcranials, clearly belongs to the *H. macedonicum - H. nikosi* lineage. The large-sized specimens should correspond to different hipparion lineages. The MTLA skull with the deep POF, the short POB and the well defined anterior fossa is probably correlated to the stout metapodials, recognized not only in MTLA, but also in MTLB, and represents the *H. proboscideum - H. mediterraneum* lineage. On the other, hand the MTLB skull with the single deep POF and the elongated POB, on the basis of the AKK sample, might correspond to the robust metapodials and seems to belong to the *H. giganteum - H. brachypus* lineage (Table 3). The hipparionine horse with the shallow POF, weak canine fossa, narrow muzzle, moderately deep narial opening and slender, but relatively short metatarsals, potentially represents the *H. forstenae* lineage. The fifth hipparion species from MTLA-B is characterized by a shallow POF, long POB, short narial opening, wide muzzle, elongated metapodials, and represents the *H. prostylum - H. dietrichi* lineage.

6. The *Hipparion giganteum – Hipparion brachypus* lineage

Representatives of this lineage have been found in MTLA and MTLB, both dated to middle Turolian, MN 12 (Koufos et al., this volume). The *H. giganteum   H. brachypus* lineage is widespread in Turolian, especially during MN 12, and it is widely accepted that it derives from a member of the Vallesian *H. primigenium* group. The last, in general, includes a large number of taxa related to the first hipparion immigrant from North America to the Old World (Bernor et al., 1990a, 1996a). The elongated muzzle, the deep and posteriorly pocketing POF, the long POB and the robust metapodials are some of the characteristics included in this group and to the discussed lineage. The body mass increases towards the more evolved forms and the nasal notch is retracted above the end of P^2-anterior part of P^3. The *H. giganteum - H. brachypus* lineage includes two species: *H. brachypus* and *H. giganteum. H. brachypus* is the most-recorded robust hipparion form in the Eastern Mediterranean and Western Asian faunas, dated to MN 12 (Koufos, 1987c; Bernor et al., 1996a, b; Hristova et al., 2002; Koufos & Vlachou, 2005; Forstén, 1983, 1999). *H. giganteum* is usually mentioned from the Black Sea region and ranges from 9.0 to 7.1 Ma (NOW) in time (Gromova, 1952).

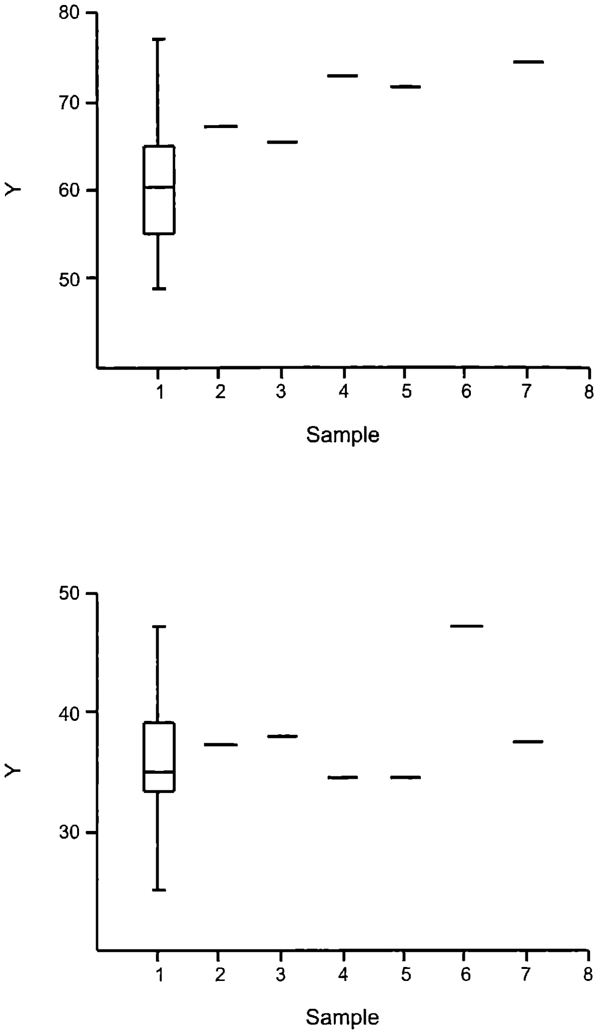

Figure 6: Box and Whiskers Plots on POF variables; (above) maximum length (M33) (below) maximum width (M35). Samples: 1. *H. brachypus*, HD; 2. *H. brachypus*, Q4; 3. *H. brachypus*, Q1; 4. *H. brachypus*, MTLB; 5. *H. brachypus*, AKK; 6. *H. brachypus*, PIK; 7. *H. giganteum* GRE

Hipparion brachypus (Hensel, 1862)

Holotype: A set of robust metapodials described by Hensel (1862).

Lectotype: Cast of a forelimb [made by Othenio Abel (1927], München.

Neotype: BMNH-M.11240 (MCIII), BMNH-M.11265 (MTIII); (Koufos, 1987).

Type Locality: Pikermi, Greece.

Age: Middle Turolian, MN 12 (Late Miocene)

Remarks: The type material includes some metapodials from Pikermi described by Hensel (1862). This material has been lost and instead of this Koufos (1987c) proposed the metacarpals BMNH-M.11240 as neotype (Pl. VII, 2a, b, Koufos, 1987c) and the metatarsal BMNH-M11265 (Pl. VII, 1a, b, Koufos 1987b) with a set of metapodials from the Gaudry collection (BMNH) as topotype. Further certain references to *H. brachypus* come from Samos (Forstén, 1999), Bulgaria (Hristova et al., 2002) and Turkey

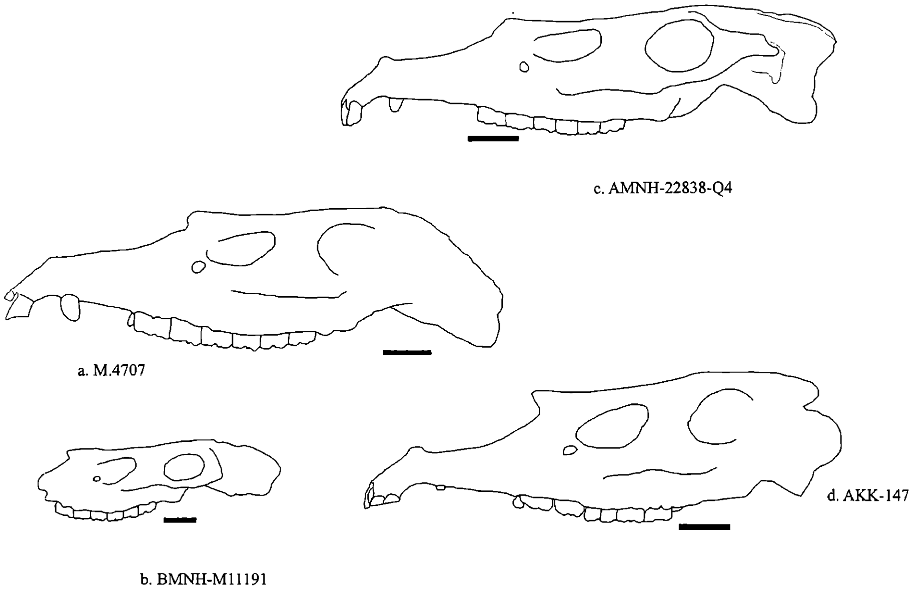

Figure 7: *H. brachypus* skulls, lateral view. Scale bar equals 5 cm.

a: Samos, unknown locality, SM4707; b: Pikermi, BMNH-M.11191; c: Samos, Q4, AMNH-22383; d: Akkaşdaği, AKK-147.

(Koufos & Vlachou, 2005). It possibly occurred in the Middle Maragheh (MMRG) (Bernor et al., 1996a) and in some localities of Central Europe (Scott, 2004).

The *H. brachypus* skull strongly resembles that of *H. primigenium*. Among the several characteristics proposed by Bernor & Lipscomb (1995), the narial opening is probably the only one that could distinguish the two forms. All the stratigraphically early hipparionine horses described by Bernor et al. (1996b) under the genus "*Hippotherium*" have a short narial opening with the nasal incision placed well anteriorly to P^2. *H. brachypus* is more evolved regarding this characterisitc, and the nasal incision ranges from the P^2 parastyle to the anterior border of P^3 (Bernor et al., 1996b; Forstén, 1983; Watabe, 2004; Vlachou, in prep.).

The skull of *H. brachypus* is large and the muzzle elongated. The well developed POF is the morphology that dominates the facial region. As in *H. primigenium*, it is placed far from the orbit and the border outline is strongly delineated posteroventrally, or around the entire periphery. The orientation varies from anteroposterior to anteroventral. Usually, it is elliptical to subtriangular-shaped, quite deep (more than 15 mm) and always pocketing posteriorly. The upper cheek tooth row does not really differ from that of *H. primigenium*. It retains a functional dP^1 and includes highly plicated teeth with an elliptical to oval, sometimes lingually flattened protocone, and usually a double pli caballin.

The tooth row length of *H. brachypus* from Pikermi, in particular, is longer than that of the Sinap forms, but similar to those of the NKT large-sized hipparions (Fig. 3). The lingually flattened protocone in the upper teeth and the maintenance of the lingual hypoconal groove in teeth of an early to moderate stage of wear confirm the cohesive relationship of *H. brachypus* from PIK with the primitive *Hippotherium* species.

The similar metapodial morphology might be considered as an extra evidence of this relationship. The MCIII of *H. brachypus* from PIK shares similar length with that of *H. primigenium*, but it slightly decreases in the midshaft width (M3) and increases in all the anteroposterior diameters (M4, M12, M14), (Fig. 4A). Likewise, the MTIII sample is similar to that of *H. primigenium* from Höwenegg, in the length and the midshaft dimensions, but at the same time seems to slightly decrease in the upper articular depth and to increase in all the lower articular dimensions (Fig. 4B).

Questionable remains indicate the presence of *H. brachypus* in Chalkoutsi (Attica, Greece and Halmyropotamos (Evia, Greece), but the scanty material prevents certain results (Koufos & Vlachou, 2005; Koufos, 2006).

Many authors have reported the presence of a large-sized hipparion with robust postcranials from the Bulgarian localities of Kalimantsi, Kromidovo and Hadjidimovo, underlining at the same time the similarities of this sample with that of *H. brachypus* from Pikermi (Nikolov, 1973; Forstén, 1978, Hristova et al., 2002; Spassov et al., 2006). However, *H. brachypus* was recognized with certainity only from Kalimantsi and Hadjidimovo (Hristova et al., 2003; Spassov et al., 2006).

The material list from Hadjidomovo includes several almost complete skulls and dozens of metapodials assigned to *H. brachypus*. The skulls are in their basic dimensions and morphology comparable to those from Pikermi (Fig. 5). However, some characteristics, such as the slightly deeper narial opening (the nasal notch retracted above the end of P2 or the anterior part of P3) (M31) and the less extended POF generally (M33-M34) with an usually anteroposterior orientation, might prove the Hadjidimovo sample to be more evolved than the Pikermi one.

Figure 4 compares the metapodials of *H. brachypus* from Hadjidimovo with those from various localities. The two samples, Hadjidimovo and Pikermi, are comparable in length (M1) and midshaft dimensions, but they really differ in the articular surfaces. The metacarpals from Hadjidimovo significantly increase in the distal articular depth (M12-M140 (Fig. 4A), while the metatarsals grow larger in more or less all dimensions of both articular surfaces, proximal and distal (M5-6, M11-14) (Fig. 4B). Hristova et al. (2002) ascribed these differences

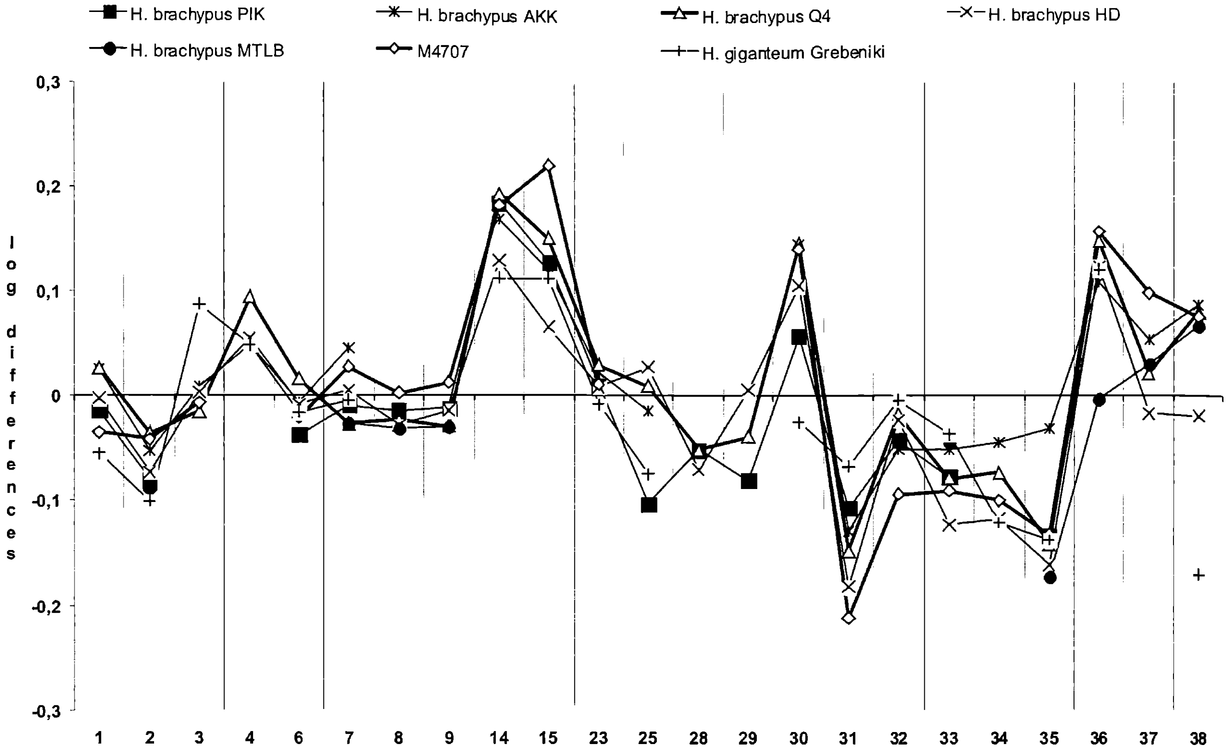

Figure 8: Logarithmic ratio diagram comparing the skull of *H. brachypus* from the Samos localities with that from PIK, HD and AKK, and *H. giganteum* from Grebeniki. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

to dissimilar palaeoecology between the two sites. It is worth mentioning that despite the occurrence of forms related to *H. primigenium* forms in the Black Sea area, as well as in Continental Greece during Turolian, neither *H. primigenium*-like forms nor *H. brachypus* have been reported from FYR of Macedonia till now (Forstén & Garevsky, 1989). The data from the Romanian localities is limited and the presence of a *H. primigenium*-like form has not been certified yet (Forstén, 1980a).

Material assigned to *H. brachypus* has also been described from the Easten Mediterranean region, C. Turkey and Iran. Forstén (1983) assigned a set of skulls from Q4 and Q1 (Samos) to *H. brachypus,* on the basis of the relation of orbit-preorbital fossa distance to P^2 - orbit distance, but she did not give extended descriptions and comparisons of related hipparion forms.

Koufos & Vlachou (2005) recognized this taxon in the Turkish locality of Akkaşdaği. The material list includes a completely preserved skull with the mandible and numerous postcranial elements. The skull belongs to a relatively young individual (dP^4 is barely preserved, P^2 and P^3 are unworn and M^3 is almost inside the maxillary bone). The relatively young age of the AKK skull cannot allow a certain comparison with the skulls from Pikermi and Hadjidimovo. The AKK sample seems to have a longer premolar length (M7) and larger POF (M33-35) (Fig. 5). The elongated premolar rows are probably due to their low attrition, while the POF dimensions hardly fall within the variability of the HD sample (Figs. 5, 6). The narial opening is deep and the nasal notch is located above the parastyle of P2. Taking into account that the skull is still undergoing ontogenetic change, we believe that the nasal notch could be retracted above the end of P2 or even further, demonstrating that this characterisitc is similar to the evolutionary stage of the HD sample, or younger.

The metapodial pattern is similar to that of *H. brachypus* from the Balkans (Fig. 4). But the size clearly separates the AKK sample from that of PIK and HD (Fig. 4) since almost all the MCIII and MTIII dimensions appear to be increased (Fig. 4). Tobien (in Bernor et al., 1996a, b) recognized a single robust metapodial potentially ascribed to *H. brachypus* in the material from the MMRG horizons (Iran). Watabe & Nakaya (1991b) list a medium- to large-sized robustly built hipparion from the lower and middle fossiliferous levels of Maragheh, which is similar to *H. brachypus* from Pikermi. Personal observations corroborate Watabe & Nakaya's opinion, but the presence of *H. brachypus* in the Maragheh fauna must remain questionable, as more material is necessary for certain results (Fig. 4).

Hipparion giganteum Gromova, 1952

Holotype: Skull, 1015 (University of Odessa)
Type Locality: Grebeniki, Ukraine.
Age: Vallesian/Turolian, MN 10/11 (Late Miocene).
Remarks: *H. giganteum* was created by Gromova (1952) to describe a set of skulls from Grebeniki (Ukraine). According to her diagnosis, the skull is large (total length 455 mm), with an elongated muzzle and short narial opening (the nasal notch is situated slightly anterior to P2). The POF is short in dorsoventral direction, well-marked and

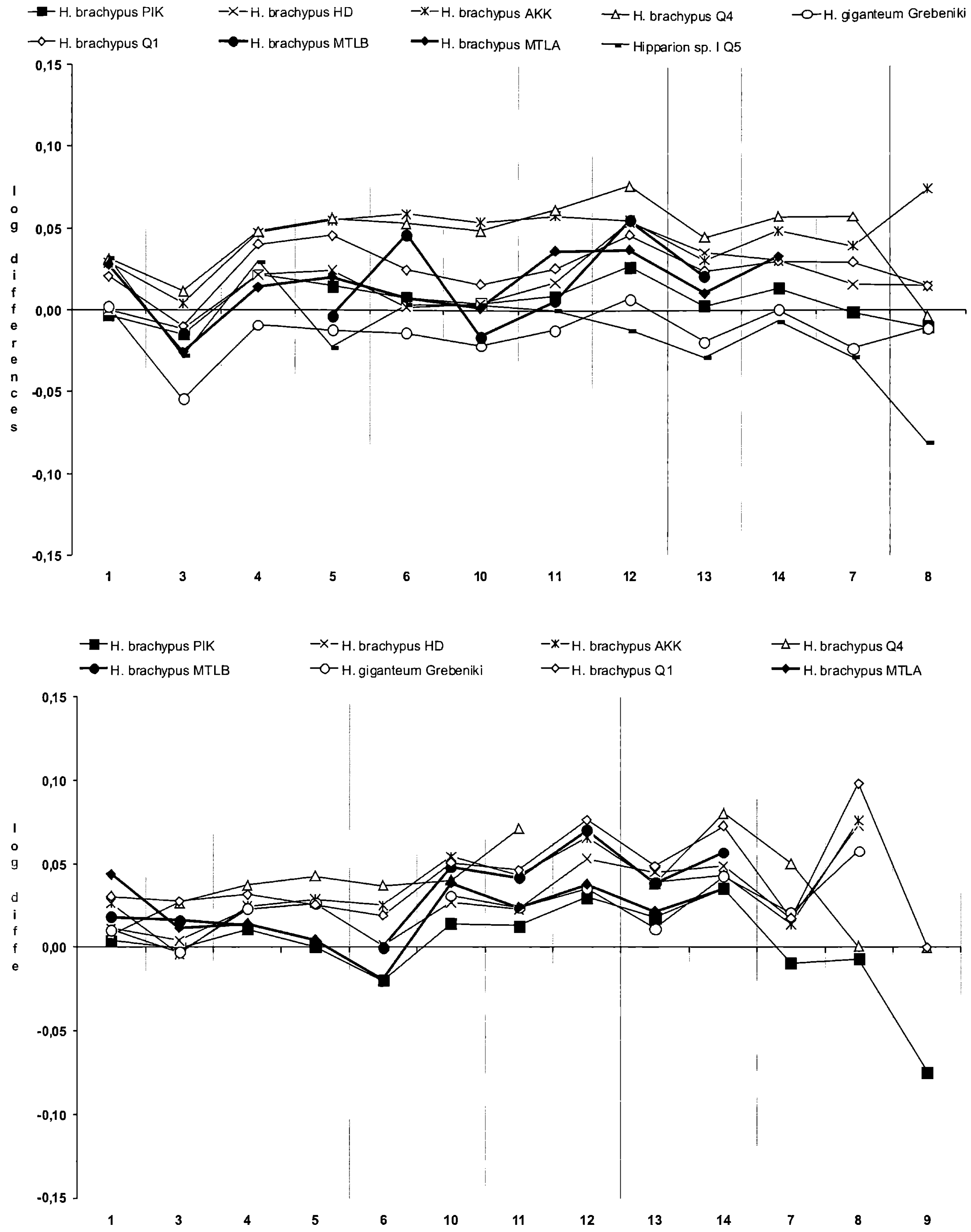

Figure 9: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H. brachypus* from Samos localities with those from PIK, HD and AKK and *H. giganteum* from Grebeniki. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

posteriorly pocketed, there is no anterior fossa, but in some specimens the POF is connected to the buccinator fossa through a long groove. Eisenmann (1995) referred the material of Grebeniki to *H. brachypus giganteum* downgrading the differences between *H. brachypus* and *H. giganteum* to subgenus level. Bernor et al. (1996b) believe that *H. giganteum* is certainly derived from the *H. primigenium* complex, and possibly from the characteristics exhibited by Pikermi horses assigned to *H. brachypus*. Another opinion proposed here is that *H. giganteum* derives from a Vallesian

H. primigenium-like form from the former USSR, such as *H. sarmaticum* from Kalfa or *H. sebastopolitanum* from Sebastopol. Zouhri & Bensalmia (2005) studied the two hipparion species's morphology and regard *H. giganteum* and *H. brachypus*, as synonyms of *H. primigenium*.

The type skull of *H. giganteum* seems to be comparable to *H. brachypus* in length and morphology, as well as to *H. primigenium* (Fig. 5). The similarities in the tooth row length and the dental morphology confirm the size similarity of these three hipparion forms and their possible phylogenetic relationships. The muzzle and facial morphology resembles that of *H. brachypus*. The groove which connects the POF with the buccinator fossa is occasionally present in the HD sample (e.g. XA-10037, XA-10095), but maybe it is less strongly marked. The short narial opening is the main characteristic that clearly distinguishes *H. giganteum* from *H. brachypus*, and at the same time, in our opinion, the morphological characteristic that places the Black Sea form closer to the *H. primigenium* group, maybe a step below *H. brachypus* from PIK and HD in the evolutionary scale.

The metapodials from Grebeniki assigned to *H.* "*brachypus giganteum*" by Eisenmann (1995) are generally robust. In comparison to the metapodials of *H. brachypus* from the Balkans, the MCIII appears to be reduced in size and is surprisingly more slender than that of *H. brachypus* from PIK and HD, because of its significantly reduced midshaft width (Fig. 4A). The MTIII sample has a similar midshaft width (M3) and distal articular depth (M12-14) as the PIK sample and a comparable length (M1), midshaft depth (M4) and upper and lower articular width to the HD sample (Fig. 4B).

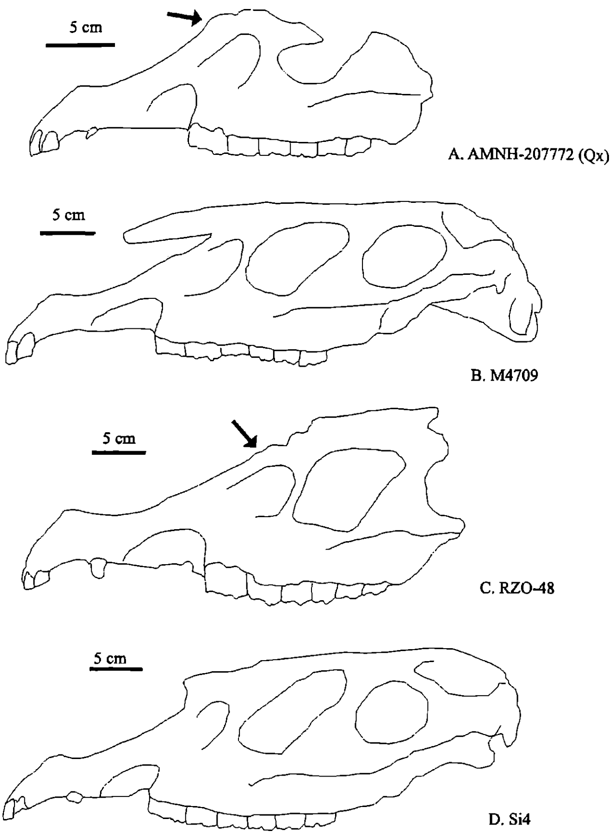

Figure 10: *H. proboscideum* skulls, lateral view, A: Qx, AMNH-20772, B: Unknown loc., M.4709, C: RZO-48, D. Q1, SI 4.

Systematics of the Material

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821

Genus *Hipparion* Christol, 1832

Hipparion brachypus **Hensel, 1862**
(Plate 1)

Synonymy:
H. cf. *proboscideum*, Q4, Sondaar, 1971

Localities: Mytilinii-1A, B, (MTLA, MTLB), Adrianos ravine, Mytilinii Basin, Samos, Greece; Quarry-1 (Q1), Adrianos ravine, Mytilinii Basin, Samos, Greece; Quarry-4 (Q4), Potamies ravine, Mytilinii Basin, Samos, Greece.

Age:
Middle Turolian, MN 12 (late Miocene).
Mytilinii-1A (MTLA, B), Quarry-1 (Q1): ~7.1Ma.
Quarry-4 (Q4): 7.3-7.1 Ma.

Material:
MTLA: MCIII, MTLA-402, 415; distal part of MCIII, MTLA-133, 454, 132; MTIII, MTLA-500, 354, 128, 57, 31; distal part of MTIII; MTLA-243;
MTLB: partly preserved skull MTLB-30; MCIII, MTLB-276; MTIII, MTLB-299; distal part MTIII, MTLB-26,
Q4: Skull, AMNH-22838; maxilla: AMNH-22832; MCIII, AMNH-20764F; MTIII, AMNH-20764A, 22841B, 22841Q
Q1: Skull, L S73; MCIII, AMNH-23012, 23012b; proximal part of MCIII, AMNH-23046c; MTIII, AMNH- 23044B, 23044A, 23044; proximal part of MTIII, AMNH-23044; distal part of MTIII, AMNH-23044, 20669B.
Unknown Locality: Skull, SM4707
Short Diagnosis: Large size, elongated and wide muzzle, deep narial opening; well-defined elliptical to subtriangular POF which is posteriorly pocketed, medially deep and situated far from the orbit; richly plicated upper teeth with usually elliptical protocone and double pli caballin; robust limb bones.

Description:
New material. The "*Hippotherium*" morphology is poorly represented in the newly collected material. Only one skull from MTLB and some postcranials from MTLA and MTLB can be attributed to this morphological group. Among the large-sized postcranials, only the metapodials can be correlated to this group. The rest of the specimens are referred to in the material list as *Hipparion* sp. (large-sized) (Appendix-1). The specimen MTLB-30 is a partly preserved skull lacking the muz-

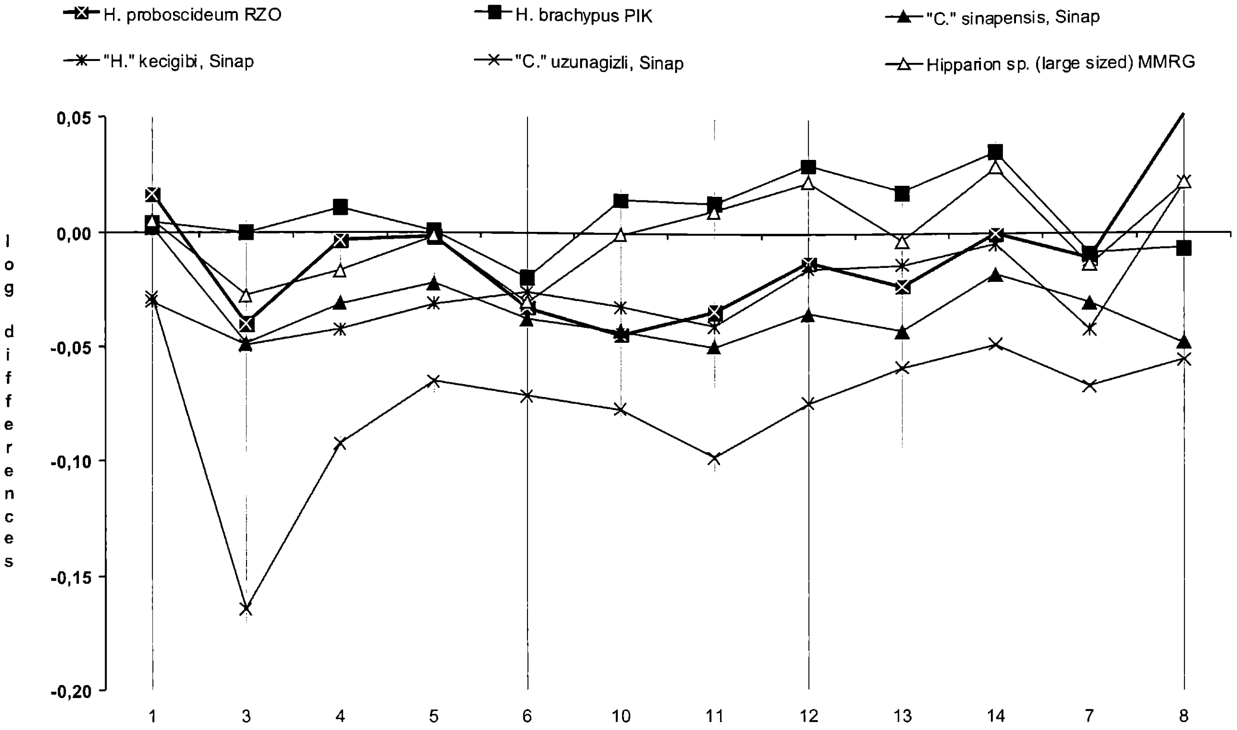

Figure 11: Logarithmic ratio diagram comparing the metatarsal of *H. proboscideum* from RZO with *H. brachypus* PIK, "*C*". *sinapensis*, "*H.*" *kecigibi*, "*C*" *uzunagizli* from Sinap and *Hipparion* sp. (large-sized) from MMRG. Standard: *H. primigenium*, Höwenegg, n = 16-24 (Bernor et al., 1997).

zle, part of the facial region and the opisthocranion. The POF is deep, with a strongly defined peripheral border and seems to be placed far from the orbit and the facial crest. It seems to have an elliptical shape and anteroposterior orientation. The upper cheek teeth are moderately plicated, the protocone is elliptical to oval, always isolated from the protoloph and the pli caballin is simple (Plate I-1b).

The metapodials, potentially corresponding with the above mentioned skull remains, are robust. The material is scanty and so the conclusions are limited. The robusticity index for MCIII is 16.7, on the basis of only one specimen from MTLA, and for MTIII, 14.1-15.9 on the basis of two specimens from MTLB. The values fall within the limits of *H. brachypus* and *H. primigenium* from various localities.

Old material. Two complete skulls from Q4 and Q1, one more skull (SM4707) stored at the Senckenberg Museum in Frankfurt and originating from an unknown locality of Samos, and a few postcranial remains from both localities are attributed to the *H. giganteum* - *H. brachypus* lineage. All studied skulls belong to male individuals of different ages and they are characterized by an elongated and relatively wide muzzle. The narial opening is deep; the nasal notch in the skull AMNH-22838 from Q4 is situated above the mesostyle of P^2, while in the skulls LS73 from Q1 and SM4707, the nasal notch is retracted above the anterior part of P^3. The POF is placed far from the orbit and the facial crest is deep, anteroposteriorly oriented and, especially in the specimen SM4707, deeply posteriorly pocketed. The POF varies from tear-shaped (Q4) to subtriangular (SM4707), (Fig. 7). The upper cheek teeth are richly plicated, with an elliptical protocone and double pli caballin. In the less worn teeth, the lingual hypoconal groove is generally present and the dP1 is still in function (SM4707).

The metapodials correlated to this skull morphology are quite robust. The robusticity index is 18.8-16.8 for the MCIII and 16.8-16.3 for the MTIII, without proven differences among the different quarries, because of the small number of specimens, but slightly larger compared to the newly collected sample, quite close to the PIK and HD samples and better comparable to the AKK sample.

Comparisons:

The occlusal cheek teeth length indicates that the large-sized form from MTLB is comparable in body size to *H. brachypus* from PIK and HD, and possibly slightly smaller than that from AKK (Figs. 3, 8). In MTLB-30, the teeth are quite worn and the enamel plication becomes simple. Unlike the PIK and HD samples, the teeth from MTLB have an oval protocone, always isolated, the plication number is 8 in M1 and the pli caballin is weak, simple and occasionally absent. The plication number is counted 10-18 for the PIK sample and is slightly increased in the HD sample, varying from 15-21. The *H. brachypus* from AKK have more than 17 plis in the M1 (Koufos & Vlachou, 2005), while *H. giganteum* from Grebeniki is characterized by almost 10.5 plis in the moderately worn $M^{1,2}$ (Gromova, 1952).

The facial region resembles that of *H. brachypus* in the deep, elliptical POF, which is placed far from the orbit

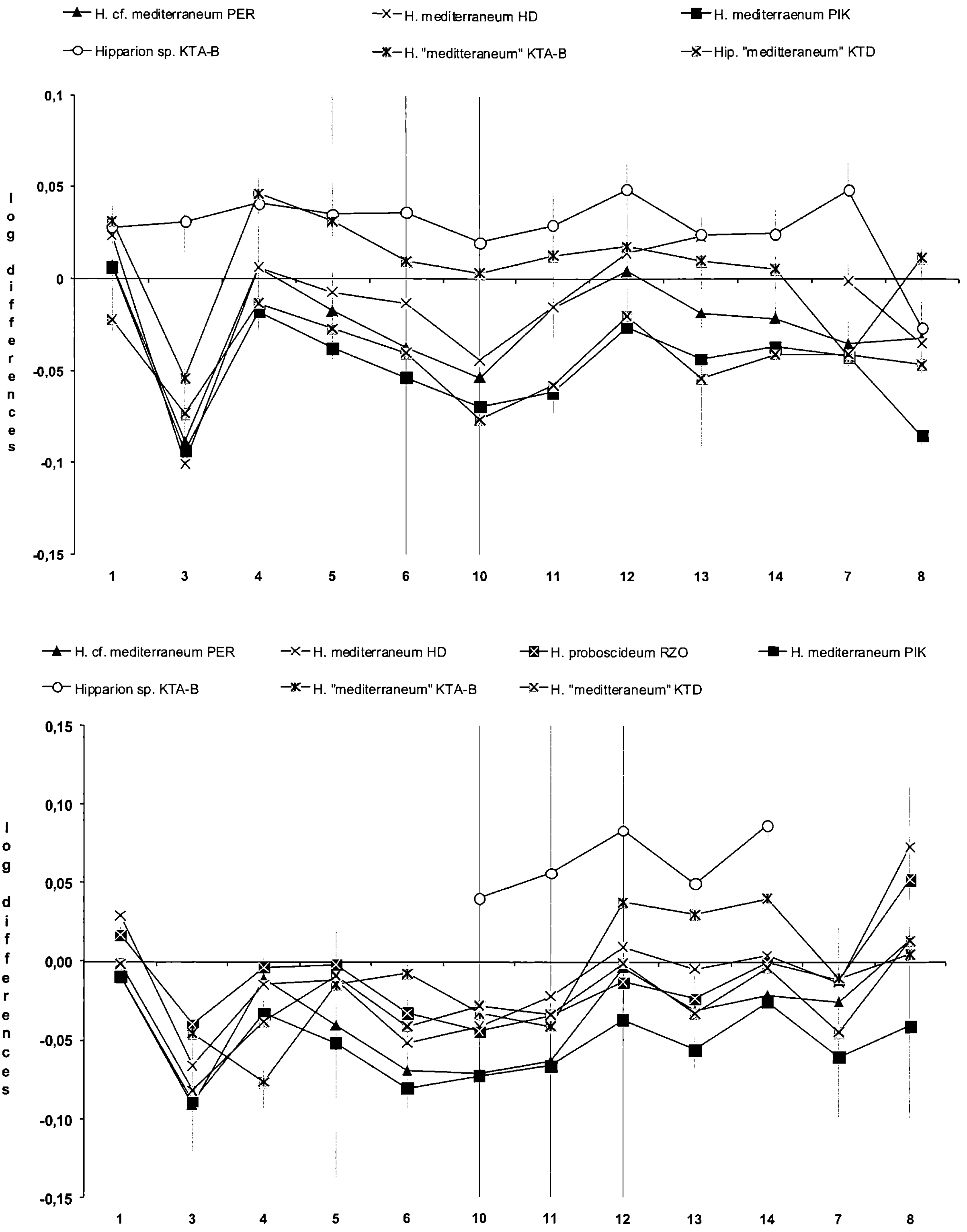

Figure 12: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H. mediterraneum* from various localities with *H. proboscideum* from RZO and *Hipparion* sp. (large-sized) from KTA-B. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

and the facial crest. The POF dimensions (M33, M35) fall within the range of the HD sample; they more resemble the AKK sample, and partly *H. giganteum* from GRE (Fig. 6). However, the deep narial opening that virtually could confirm the attribution of the MTLB skull either to *H. brachypus* or to *H. giganteum* is missing. Sondaar (1971) described the skull from Q4 (AMNH-22838) as *H.* cf. *proboscideum* (Fig. 7). A few years later, Forstén (1980b) attributed the before mentioned skull to *H. brachypus* and finally to *H.* cf. *brachypus* (Forstén, 1999). She further

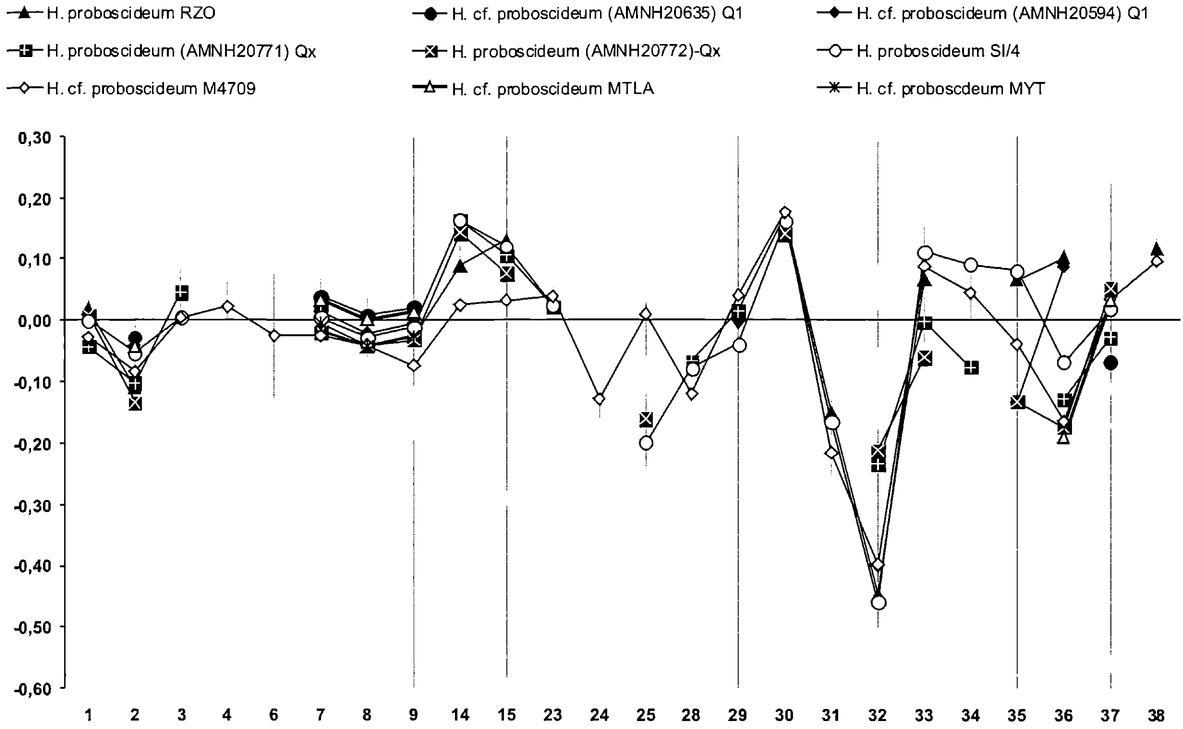

Figure 13: Logarithmic ratio diagram comparing the skull of *H. proboscideum* from Samos localities with that from RZO. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

assigned the following specimens to this taxon: Geological Museum, Lausanne (LM 73, 148, 175, Andriano locality); Naturhistorisches Museum, Vienna (VM 1911, V118); Senckenberg Museum, Frankfurt am Main (SM4707) (Fig. 16); American Museum of Natural History (possibly AMNH-22912 & 22922, Q5) (Forstén, 1999).

The dimensions of the Q4 skull resemble those of *H. brachypus* from PIK, HD, AKK very closely, as well as that from MTLB. On the other hand, the Q4 skull clearly differs from *H. giganteum* from GRE in the shorter narial opening (M30) and the more elongated cheek tooth row (M31) (Fig. 8). The POF complex morphology, despite some small size differences, is similar in all the above listed samples. The narial opening is more comparable to *H. brachypus* from HD and AKK, since the nasal notch is similarly retracted above the second half of P2. The cheek teeth length is shorter than that of *H. brachypus* from AKK, but identical to the PIK, HD and MTLB samples (Figs. 3, 8). Among the dental characteristics, the elliptical protocone, the double pli caballin and the occasional presence of the lingual hypocone groove suggest that the Q4 skull is close to *H. brachypus* from HD and PIK.

The skull SM4707 shares several morphological similarities with the S73 (Fig. 7). Both skulls differ from the Q4 and MTLB samples in the subtriangular and deeply posteriorly pocketed POF, the retraction of the nasal notch above the anterior part of P^3, the elliptical protocone and the lingual hypoconal groove in the upper cheek teeth. Additionally, the increased tooth row lengh of the former skull SM4707 potentially indicates an increased body mass (M9, Fig. 8). However, this assumption is not confirmed by the total skull length (M6, Fig. 8). The retraction of the nasal notch from the posterior half of P2 in the Q4 skull to the anterior part of P3 in SM4707 and S73 is generally regarded as an evolved morphology, allowing the correlation of SM4707 with the upper level of the fossiliferous Samos sequence, Q1-Andrianos.

The SM4707 cranial dimensions are closely allied to those of the *H. brachypus* skull from AKK (Fig. 7); it mainly differs in the shorter and broader muzzle (M1, M15), the shorter POB (M32) and the narrower POF (M35) (Fig. 8). The narial opening, as described above, is deeper, but taking the relatively younger ontogenetic age of the AKK skull into account, it is difficult to certify the exact position of the nasal notch. A position at the end of P2, or even more at the anterior part of P3, are equally possible assessments. Likewise, the upper dental morphology is poorly defined. If it is observable, the plication is similar to the Q4 skull, while the protocone and the lingual hypoconal groove show the same development as that of SM4707 and S73, reinforcing the similaries of SM4707 with *H. brachypus* from AKK and the association of the skull with the upper Samos fossiliferous horizons. Their age, about 7.1 Ma, fits in quite well with that of the AKK locality, 7.0±0.1Ma (Koufos et al., this volume; Karadenizli et al., 2005).

The metapodial comparisons confirm the similarities among the above described skulls, but due to the small number of specimens, no further conclusions can be provided, especially about size differences.

Fig. 9A compares the morphology of MCIII samples from Q4, MTLA, B and Q1 with that of *H. brachypus*

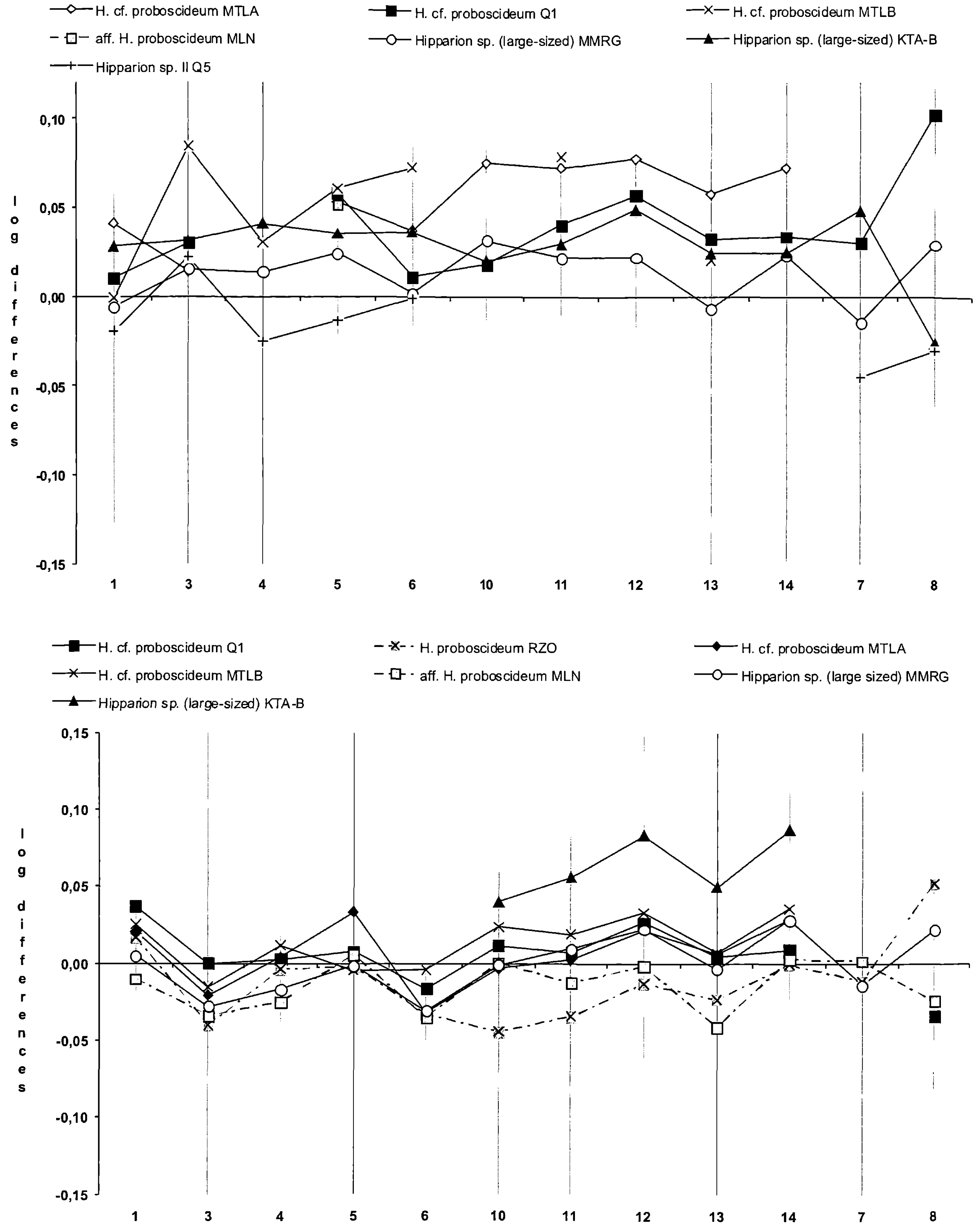

Figure 14: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H. proboscideum* from Samos with *H. proboscideum* from RZO and *Hipparion* sp. (large-sized) from KTA-B and *Hipparion* sp. (large-sized) from MMRG. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

from various localities and *H. giganteum* from Grebeniki. It is obvious that the MCIII sample of *H. giganteum* is notably separated from all the other listed samples by its smaller size and the significantly decreased midshaft width (M3). The Samos MCIII samples generally have quite similar proportions across all measurements, but exhibit a noticeable size variability. The MCIII from Q4 more or less follows the dimensions of *H. brachypus* from AKK, and it is generally larger than that from PIK and HD (Fig. 9A). The MCIII specimens from Q1 provide a similar morphological pattern to the above mentioned samples, Q4 and AKK. Nevertheless their decreased measurements seem to place the size pattern of the Q1 sample somewhere between that of *H. brachypus* from AKK and that of the Balkans (Fig. 9A). In spite of the similar length (M1) of the MCIII from MTLA to those from Q4, Q1 and AKK it shares the rest of its measurements with that of *H. brachypus* from PIK and HD and only the distal articular dimensions (M11-14) are allied to those of the Q1 and AKK sample (Fig. 9A). Finally, the single and partly preserved MCIII from MTLB shares measurements either with the Q4 and AKK (M6, M12-13) samples or with the PIK, HD and MTLA samples (M5, M10-11) (Fig. 9A). The observed size variability among the different localities is probably due to statistical errors because of the small number of specimens. It is neither supported from the chronological data (e.g. Q4 is not isochronous to AKK) nor from the cranial measurements, which are strongly correlated to the body mass, such as the total skull length, and the upper cheek teeth length (see above, skull comparisons).

The comparison of the MTIII samples reinforces the last similarities. In Fig. 9B the Q4, Q1 and MTLB samples match, and they are separated from the *H. brachypus* samples of PIK and HD, as well as from that of *H. giganteum,* by their general increase of the midshaft width, the proximal articular depth (M6) and the distal articular surface (M10-14) (Fig. 9B). The *H. brachypus* sample from AKK appears to have similar size patterns to the Samos specimens, but differs from them in the slightly increased total length (M1) and the reduced midshaft width (M3) (Fig. 9B).

In conclusion, the presence of *H. brachypus* in the Samos fauna is fully supported by cranial and postcranial remains from Q4 and Q1. The sample from MTLA and MTLB is not large enough to confirm the presence of the taxon in these localities. However, the skull from MTLB, with morphologigal affinities to the *"Hippotherium"* group, the similarities among the robust skeleton pattern from Q4 and MTLA-B and, lastly, the recent correlation of the old quarry Q1 to the new localities MTLA-B (KOSTOPOULOS et al., this volume-a), support the attribution of the robust large-sized skeleton to *H. brachypus.* If the MCIII size variability is regarded as a statistical error, the Samos samples have no significant differences to each other, although the skull from Q1 is more evolved than that from Q4 in the retraction of the narial opening. Based on the same characteristics, the PIK and HD samples are close to the Q4 evolutionary stage. The majority of the metapodial data, however, supports a reduced size pattern for *H. brachypus* from the Balkans in relation to the Eastern forms of the taxon. Moreover, the MCIII of *H. brachypus* from PIK and HD seems to be slightly shorter than that of the Samos samples. Both last differences potentially reflect different palaeoecological conditions between the two areas. FORTELIUS et al. (2002), based on the mean hypsodonty of large mammal plant-eaters, suggested gradually more open habitats in Western and Central Asia, in relation to the Balkans and Black Sea area, during the Turolian interval (8-5 Ma). The same assumption is also supported by the ecomorphological approach on the metapodial of the hipparionine horse from AKK (SCOTT & MAGA, 2005). The whole cranial morphology of *H. brachypus* from AKK fits in better with that of the Q1 sample. The MCIII morphological patterns make this hypothesis potentially reliable, but the MTIII from AKK is more elongated and more slender than that of Samos and most likely suggests a younger age.

The presence of *H. brachypus* in Q5 (FORSTÉN, 1980b) is not supported by cranial remains. There are two robust metacarpals providing morphological affinities with the MTLA *H. brachypus* sample, but it seems to have decreased distal articular dimensions (Fig. 9A). They could possibly be assigned to the *"Hippotherium"* morphological group, but the number of specimens is too small for further conclusions.

7. The *Hipparion proboscideum – Hipparion mediterraneum* Lineage

It was first recognized from MLN and further appeared in the localities MTLA-B (MN11-12) of Samos. The lineage is included in the morphological group which is described as *H. proboscideum* here, and as the *"Cremohipparion"* genus by BERNOR et al. (1996b, c) and ZOUHRI & BELSANMIA (2005) or as the *H. mediterraneum* group by WATABE (2004). The short POB, coupled with the hypertrophied POF, which is placed very close to the facial crest, and the moderately developed anterior fossa, define the *Hipparion proboscideum - Hipparion mediterraneum* lineage. The unique cranial morphology of the taxa included in this lineage is sufficient for their distinction.

It is believed that the ancestor of the *Hipparion proboscideum - Hipparion mediterraneum* lineage belongs to the *H. primigenium* complex. BERNOR et al. (1996b) consider *Hipparion mediterraneum* as the primitive hipparion form in the *Hipparion mediterraneum - Hipparion proboscideum* lineage, but VLACHOU & KOUFOS (2004) claim that the FAD of *H. proboscideum* and the relative age of the PIK fauna cannot support this relationship. We include two species in this lineage, *Hipparion proboscideum* and *Hipparion mediterraneum.*

Hipparion proboscideum STUDER, 1911

Holotype: Skull, coll. No 46, Naturhistorisches Museum, Berne, Switzerland

Type Locality: Unknown, Samos

Age: Turolian, MN 11-13 (Late Miocene).

Remarks: According to the recent available faunal data from various localities, the oldest occurrence of *Hipparion proboscideum*, and probably of this morphological group, is recorded in the locality RZO (Axios Valley, Macedonia, Greece), dated to early Turolian, MN 11 at ~8.2 Ma (KOUFOS, 1987a; SEN et al., 2000) or in the Samos Qx fauna, dated to early Turolian, MN 11 at 8.0-7.6 Ma (SONDAAR, 1971; KOSTOPOULOS et al., 2003). *Hipparion mediterraneum* seems to be included in younger faunas and its oldest occurrence is that from PER (Thessaly, Greece), dated to middle Turolian at 7.3-7.1 Ma (Vlachou & Koufos, 2006; Koufos et al., 2006).

The taxon has a significant geographic range. Apart from the type locality of Samos, *Hipparion proboscideum* has been reported from Northern Greece, FYR of Macedonia, Romania and maybe from Turkey (Sondaar, 1971; Forstén, 1980a; Koufos, 1987a; Forstén & Garevski, 1989; Koufos & Kostopoulos, 1994). The absence of this taxon from the Bulgarian and Black Sea Turolian faunas remains questionable.

The type specimen of *Hipparion proboscideum* is characterized by an elongated and narrow muzzle, a deep narial opening, possibly above P4, short POB, extremely deep and strongly defined POF, moderately developed anterior (or canine) fossa, which is separated from the posterior one by a sharp and narrow bar.

The skulls from Samos Qx, which are ascribed to *Hipparion proboscideum,* include all the above described characteristics. The nasal notch, although not well defined, seems to be placed above the parastyle of P^2 (Vlachou & Koufos, 2006), (Fig. 10-A). The RZO skull, dated close to that from Qx, confirms the previous facial morphology, but its narial opening is reduced in comparison to the type specimen, since the nasal notch is placed above the mesostyle of P^3 (Vlachou & Koufos, 2006), (Fig. 10-C). A skull from an unknown locality of Samos, housed at the Senckenberg Museum, Frankfurt (M4709), shares the same facial morphology with the RZO skull and the narial opening development (Vlachou & Koufos, 2006) (Fig. 10-B). The several morphological affinities among the type skull and the skulls assigned to *Hipparion proboscideum* on the one hand, and the great difference in their nasal notch position on the other, make us somewhat suspicious of the real depth of the narial opening in the type specimen. The *Hipparion proboscideum* skulls provide inconsistency in the nasal notch position, ranging from the P^2 parastyle to the P^3 mesostyle. This variety is probably related to the chronological differences of the samples. In other words, regarding the RZO fauna as being slightly older than that of Qx (Koufos et al., this volume), we should accept a decrease in the depth of the narial opening in the younger forms. The tooth row length varies from 140.1-159.2 mm in the Qx sample and is 150 mm in RZO. The dP^1 is occasionally retained and the teeth are highly plicated, with an elliptical to oval protocone and usually a single pli caballin.

Postcranial elements, possibly corresponding to the *Hipparion proboscideum* skull morphology, have been found only in the RZO material. There are three hipparion forms in the RZO fauna, clearly distinguished by their size and skeleton morphological skeleton pattern. The single large-sized metatarsal, assigned to *Hipparion proboscideum* by Koufos (1987a), although robust, is more slender than that of *H. primigenium* from Höwenegg and *H. brachypus* from PIK, and as slender as that of the primitive hipparion forms from Sinap (Bernor et al., 2003) (Fig. 11). The skulls from Q1 housed at AMNH and assigned to *Hipparion proboscideum* by Sondaar (1971), rarely preserve the entire facial region. The only preserved morphology is a deep, posteriorly pocketed and strongly defined POF, situated close to the orbit and even closer to the facial crest. The presence of the anterior fossa is assumed by the bar, which is well marked just in front of the POF. The SI/4 skull, which is housed at the Geological Institute of the University of Münster and mentioned from Samos Q1, strongly resembles *Hipparion proboscideum* from the older localities RZO and Qx, but it also differs from them in the less pronounced bar between the anterior and posterior fossa and the less perimetrically marked anterior fossa (Fig. 10-D). The tooth row length varies from 167-154 mm for the Q1 sample, and the dental occlusal morphology is comparable to that of the older specimens.

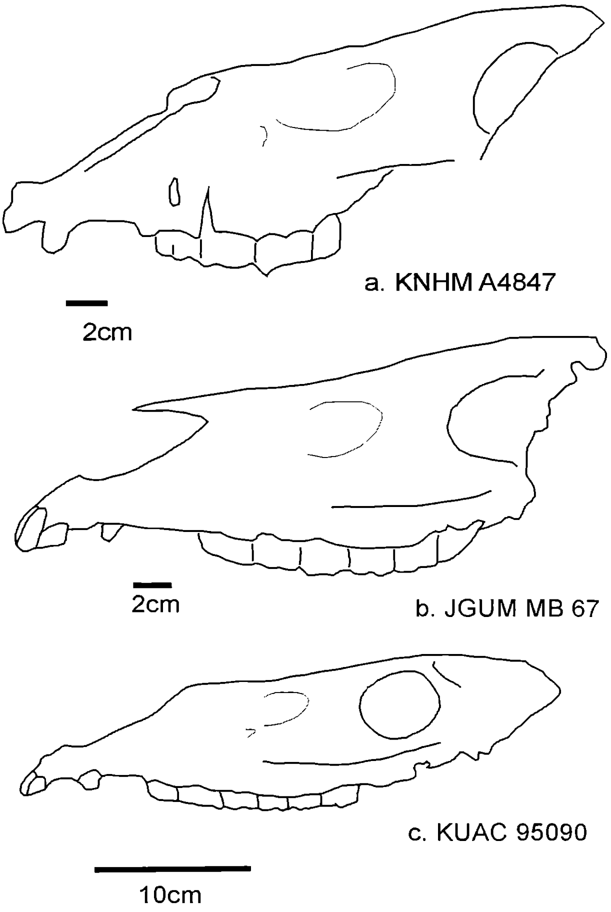

Figure 15: *Hipparion prostylum* skulls, lateral view, a: NHMW A4847, b: JGUM MB57, c: KUAC 95090.

Sondaar (1971) described some metapodials from Samos Q1 and Q4 as *Hipparion* cf. *proboscideum.* The new data from Q1 and Q4 localities asserts the presence of two large-sized hipparion taxa in both localities and consequently the mean values that Sondaar (1971) proposed for the metapodials of *Hipparion* cf. *proboscideum* must be reviewed.

Forstén (1980a) described a skull of *Hipparion proboscideum* from Romania (UB118). The distance P^2 - orbit (~178 mm) plots with the *Hipparion proboscideum* sample from Samos. The POB is short (~25 mm), and the tooth row length is 154 mm. Only the posterior, very deep portion

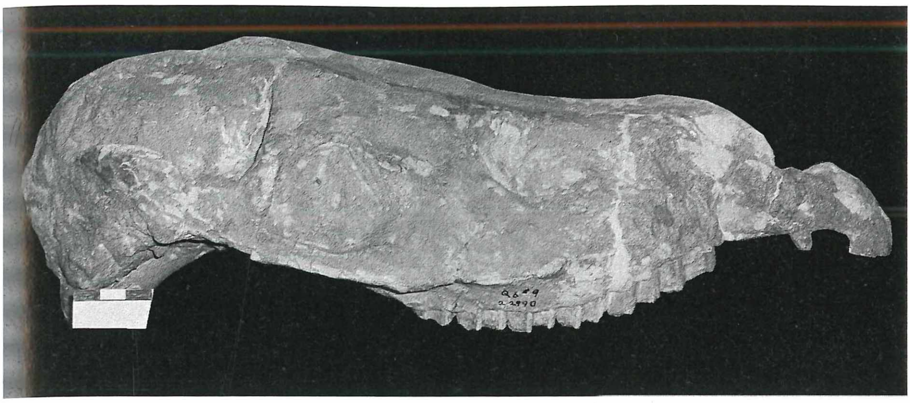

Figure 16: *Hipparion prostylum*, Samos-Q6, Greece. Skull AMNH-22990, lateral view.

of the fossa is visible (Forstén, 1983; Watabe, 2004). There are no corresponding metapodials.

Forstén & Garevski (1989) also mention *Hipparion proboscideum* from Titov Veles (FYR of Macedonia), dated to Turolian, from 8.2 to 5.3 My (NOW, 2008). According to these authors, the Titov Veles sample resembles the Samos material, even though the skulls are slightly smaller than those from Samos Q1. The facial region shares the typical facial characteristics of *Hipparion proboscideum*, and the narial opening ranges from the metacone of P^2 to the mesostyle of P^3 in depth, reinforcing the aforementioned assumption about the increased variability of the narial opening depth and its change through time. Forstén & Garevski (1989) further proposed short and massive metapodials for *Hipparion proboscideum*, slightly smaller than those from Samos. The mean values are: proximal breadth: 44.8 mm and 42.9 mm for MTIII and MCIII, respectively; distal metapodial breadth between 39.3-40.2 mm.

Koufos & Kostopoulos (1994) attributed a set of large-sized metapodials from KTA-B, Turkey, to *Hipparion* sp. with affinities to *Hipparion proboscideum*. The MCIII sample shares with the *Hipparion mediterraneum* samples a more or less similar total length, but the rest of the measurements seem to be significantly larger, providing a completely different morphological pattern than that of *Hipparion mediterraneum* and *Hipparion proboscideum* from the Balkans (Fig. 12A). This size superiority of the KTA-B against the last samples is also confirmed by the single and partly preserved MTIII (Fig. 12B).

Hipparion mediterraneum Roth & Wagner, 1855

Lectotype: Skull (Fig. 1 in Wagner, 1848)
Neotype: MNHN-259, (Bernor et al., 1996b), Museum of Natural History, Paris.
Type Locality: Pikermi, Greece.
Age: Middle Turolian, MN 12 (Late Miocene).
Remarks: It is a medium to large-sized form quite similar to *Hipparion proboscideum* in the facial and dental morphology, but with small differences in their skeleton patterns. Vlachou & Koufos (2006) believed that *Hipparion mediterraneum* derives directly from *Hipparion proboscideum*, probably reducing the depth of the narial opening and minimizing the anterior fossa development. The nasal notch of *Hipparion mediterraneum* skulls from PER, PIK and HD is retracted above P2 and the anterior fossa is weakly developed, almost invisible when the skull is deformed or crushed (Vlachou & Koufos, 2006; Bernor et al., 1996b). We have already detected this morphology in *Hipparion proboscideum* from Q1 (Fig. 10-D), which is younger than Qx on the basis of the magnetostratigraphic record (Kostopoulos et al., 2003; Koufos et al., this volume).

The metapodials that probably correspond to *Hipparion mediterraneum* are less robust than those of *Hipparion proboscideum* from RZO (Koufos, 1987a). The metatarsal of *Hipparion mediterraneum* from various localities in comparison to that of *Hipparion proboscideum* from RZO, has a more slender morphology, but the similar general size pattern also suggests similarities in the body mass (Fig. 12B).

Koufos & Kostopoulos (1994) assigned some cranial and postcranial remains from KTD and KTA-B localities of Turkey to *Hipparion mediterraneum*. *Hipparion mediterraneum* is generally absent in Western and Central Asia during Turolian. The MCIII from KTD differs from that of *Hipparion mediterraneum* from PER, PIK and HD only in the shorter total length and the slightly increased midshaft width (M1, M3, Fig. 12A). The MTIII dimensions fall into the ranges of variation of *Hipparion mediterraneum* from the various localities, and they closely resemble the dimensions of *Hipparion proboscideum* from RZO (Fig. 12B). The KTA-B MCIII sample has morphological similarities with the *Hipparion mediterraneum* sample and differs from that of KTD, increasing in all of its measurements especially in the total length, the midshaft depth and the dimensions of the proximal and distal articular surfaces (M1, M4-14) (Fig. 12A). The MTIII sample exhibits metrical affinities with *Hipparion mediterraneum* from HD and *Hipparion proboscideum* from RZO, but seems to have an increased midshaft (M6) and distal articular depth (M12-14) (Fig. 12B). Instead of the general similarity between the metapodial morphological pattern of the KTA-B sample and that of *Hipparion mediterraneum*, the corresponding skull from KTA-B includes a set of facial features which are different from those of *Hipparion mediterraneum*, and closer to the *Hipparion dietrichi*-like morphology. So, the presence of *Hipparion mediterraneum* in KTA-B and KTD faunas is not strongly supported and

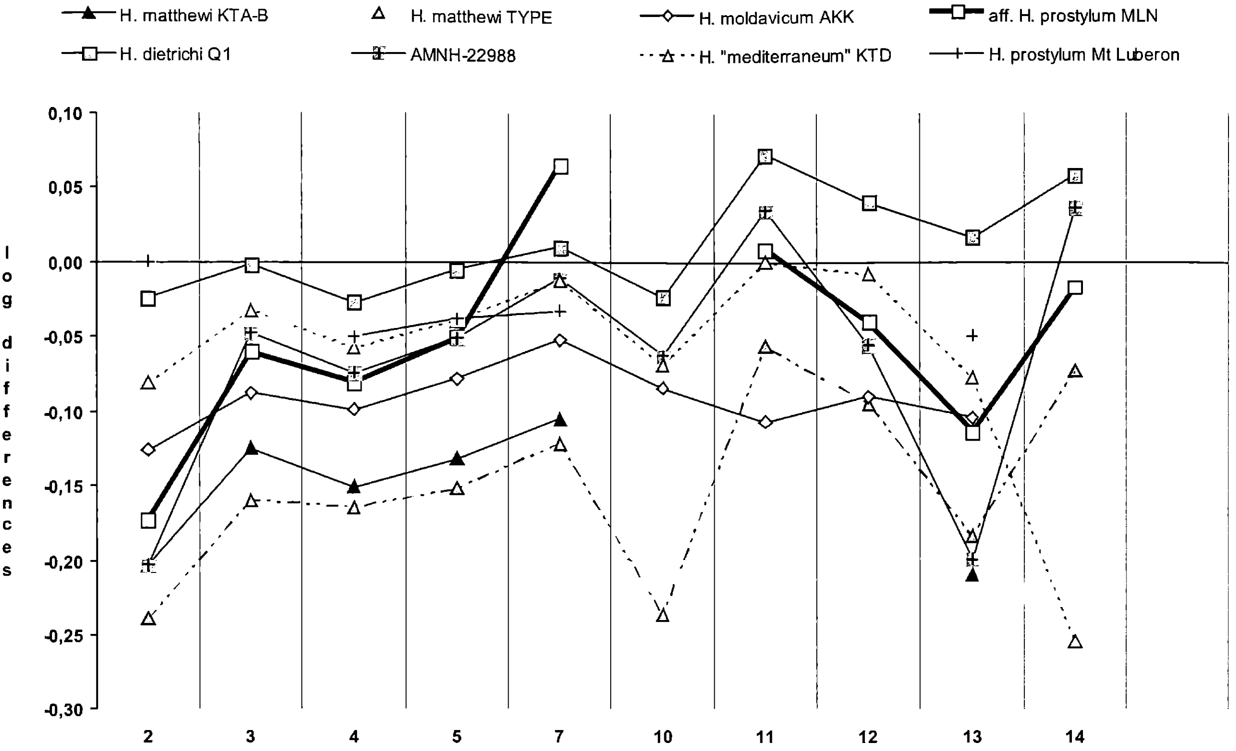

Figure 17: Logarithmic ratio diagram comparing the mandible of aff. *Hipparion prostylum* from MLN with *H. prostylum* from Q6, KTD and Mont Luberon; *H. dietrichi* from Q1; *H. moldavicum* from AKK and *H. matthewi* from KTA-B and Samos type specimen. Standard: *H. primigenium*, Höwenegg, n = 6-11 (Bernor et al., 1997).

might be discussed and compared with the species included in the *Hipparion prostylum* - *Hipparion dietrichi* lineage. Koufos (1988b) also lists *Hipparion mediterraneum* from the DTK locality of Axios Valley, Greece. Similarly to the KTA-B remarks, the metapodial sample resembles that of *Hipparion mediterraneum* from PIK, but the skull morphology is strongly reminiscent of the morphology of the *Hipparion prostylum* - *Hipparion dietrichi* lineage.

Systematics of the Material

Hipparion proboscideum Studer, 1911

(Plates 2-4)

Localities: Mytilinii-1A, B, (MTLA, MTLB), Adrianos ravine, Mytilinii Basin, Samos, Greece; Mytilinii-3 (MYT), Potamies ravine, Mytilinii Basin, Samos, Greece; Mytilinii-4 (MLN), Potamies ravine, Mytilinii Basin, Samos, Greece; Quarry-1 (Q1), Adrianos ravine, Mytilinii Basin, Samos, Greece; Quarry-x (Qx), near Mytilinii village, Mytilinii Basin, Samos, Greece.

Age: Middle Turolian, MN 12 (late Miocene).
Mytilinii-1A, B (MTLA, B), Quarry-1 (Q1): ~7.1Ma.
Mytilinii-3 (MYT): ~7.3 Ma.
Mytilinii-4 (MLN): ~7.5 Ma.
Quarry-4 (Q4): 7.3-7.1 Ma.

Material:
MLN: Proximal part of MCIII, MLN-4; MTIII, MLN-1, 3, 36;
MYT: Maxillae, MYT-4, 91, 22, 45;
MTLA: Partial skull, MTLA-328; maxilla with P2-M3 (sin, dex), MTLA-414; MCIII, MTLA-508; proximal part of MCIII, MTLA-130, 163; distal part of MCIII, MTLA-134; MTIII, MTLA-89, 416, 126, 346, 56;
MTLB: MCIII, MTLB-7, MTIII, MTLB-217, proximal part MTIII, MTLB-184, 262, 145, 218, 310, distal part of MTIII, MTLB-65, 215, nn.
Unknown Locality: Skull, SM 4709; Qx: Partial skull, AMNH-20771, 20772; Q1: Skull, SI/4, partial skull AMNH-20594, AMNH-20635, AMNH-20594, MCIII, 23045; MTIII, AMNH-23044D, 23043E, 20764A 22841B, 22841Q; proximal parts of MTIII, AMNH-20667.

Short Diagnosis: Large size, elongated and relatively wide muzzle, deep narial opening; unusual double, strongly defined POF, situated close to the orbit, medially deep, posteriorly pocketed and rhomboid to subtriangular-shaped, moderately developed anterior fossa; moderately plicated teeth, usually with elliptical to oval protocone, double pli caballin; robust limb bones.

Description:

New material: The skulls MTLA-328 and MTLA-414 belong to adult individuals and both preserve only the maxillae and a small part of their facial region. It is certain that the POF is deeply posteriorly pocketed, medially deep and developed very close to the facial region (Plate 2). Moreover, just in front of the POF, there are traces of the anterior fossa. The teeth of both specimens are little to moderately worn and highly plicated. The protocone is elliptical to oval

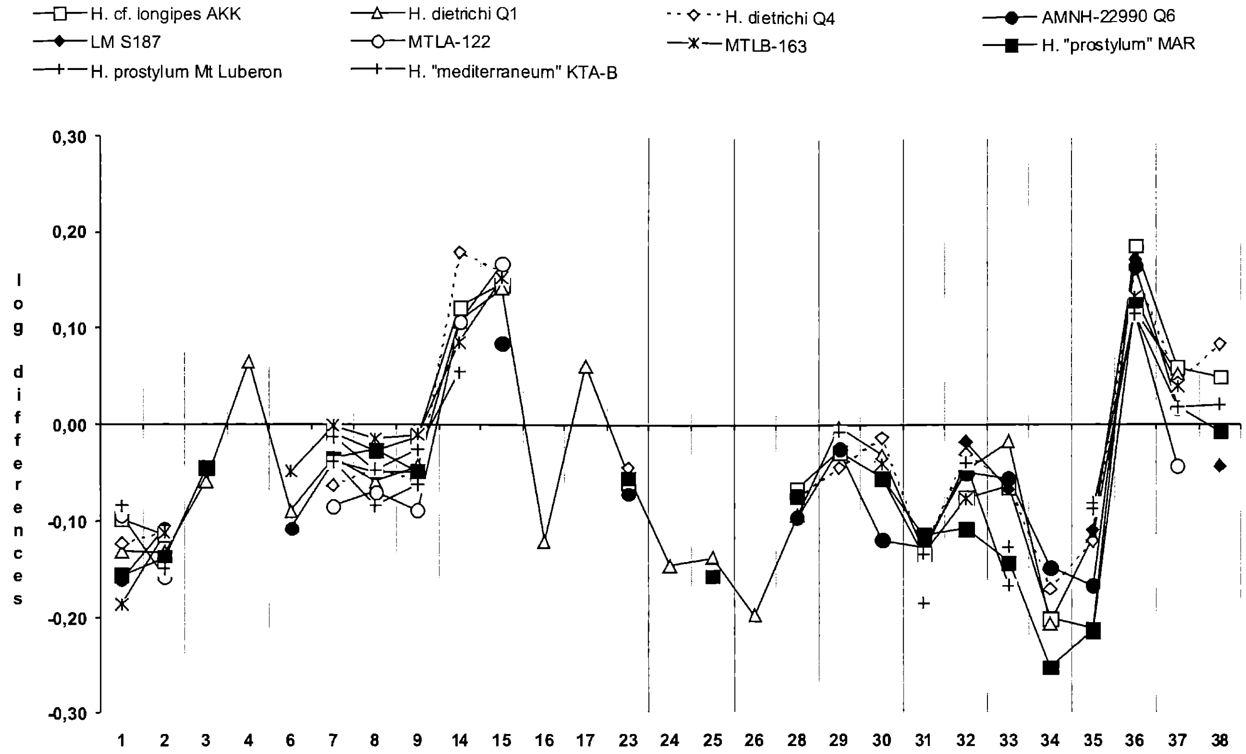

Figure 18: Logarithmic ratio diagram comparing the skull of *H. dietrichi* from different Samos localities with the *H. dietrichi* type specimen and the AKK sample as well as with *H. prostylum* from Q6, MMRG and Mont Luberon. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

and the pli caballin is often single. The tooth row length ranges from 157.0-164.3 mm. The same dental morphology more or less characterizes some partly preserved maxillae from MYT. Most of the maxillae (MYT-4, 91, 22) have moderately worn teeth and differ from those of the MTLA sample in their often double pli caballin (Plate II-1, 2). The only maxilla with little worn teeth (MYT-45) retains dP1 and the protocone is more lenticular.

The postcranial remains attributed to the *Hipparion proboscideum* morphology are robust and they have been recorded from the MLN, MTLA and MTLB fossiliferous sites. The robusticity index of the metapodials is 18.2-20.3 for the metacarpals and 15.5-14.9 for the metatarsals.

Old material: The skulls from Samos Q1 and Qx have already been discussed and assigned to *Hipparion proboscideum* above. We briefly mention the extremely developed POF, predominant in the face, the well-developed anterior fossa and the deep narial opening, probably reduced in time from the level of P3 mesostyle to P2 parastyle. The muzzle is elongated and narrow. The upper cheek teeth are highly plicated, the protocone shows an elliptical to oval shape in the Q1 sample and is oval to round in the primitive forms from Qx. The pli cabalin is usually single. The dp1 is occasionally present and the lingual hypoconal groove is usually retained in M3, except in the specimen AMNH-20635 from Samos Q1, where it occurs in more teeth. The metapodials assigned to *Hipparion proboscideum* in this article are stout, and the robusticity index is 18.6 for MCIII and 15.7-13.5 for MTIII from Samos Q1. Despite the small number of specimens, the values are similar to those of the MLN, MTLA and MTLB samples, as well as to that of *Hipparion proboscideum* from RZO, and slightly increased compared to *Hipparion mediterraneum* from PIK, PER and HD. It is striking that postcranials from Qx have not been reported.

Comparison

The scanty and partially preserved newly collected material provides extended comparisons among the specimens from MTLA, MYT, *Hipparion proboscideum* and *Hipparion mediterraneum* from various localities. The cranial comparisons concern the upper tooth row features and the POF position. In MTLA-328, as in *Hipparion proboscideum*, the POF seems to be deep, posteriorly pocketed, and the ventral rim is very close to the facial crest (M36, Fig. 13). The tooth row length and the dental occlusal morphology from the MTLA and MYT samples are comparable to that of *Hipparion proboscideum* from Samos and Axios Valley (M9, Fig. 13).

The metapodial comparisons provide more interesting results. Fig. 14 compares the metapodials assigned to the *Hipparion proboscideum - Hipparion mediterraneum* lineage from MTLA, MTLB and MLN with *Hipparion proboscideum* from various localities. The sample from MTLA and MTLB is, in morphology and size, comparable with that from Samos Q1, while the MLN sample is closer to *Hipparion proboscideum* from RZO in size, but the morphological pattern resembles that from the Samos upper fossiliferous horizons (Fig. 14). The differences among them could be explained by the small sample. Both metacarpals and metatarsals from Q1, MTLA and MTLB

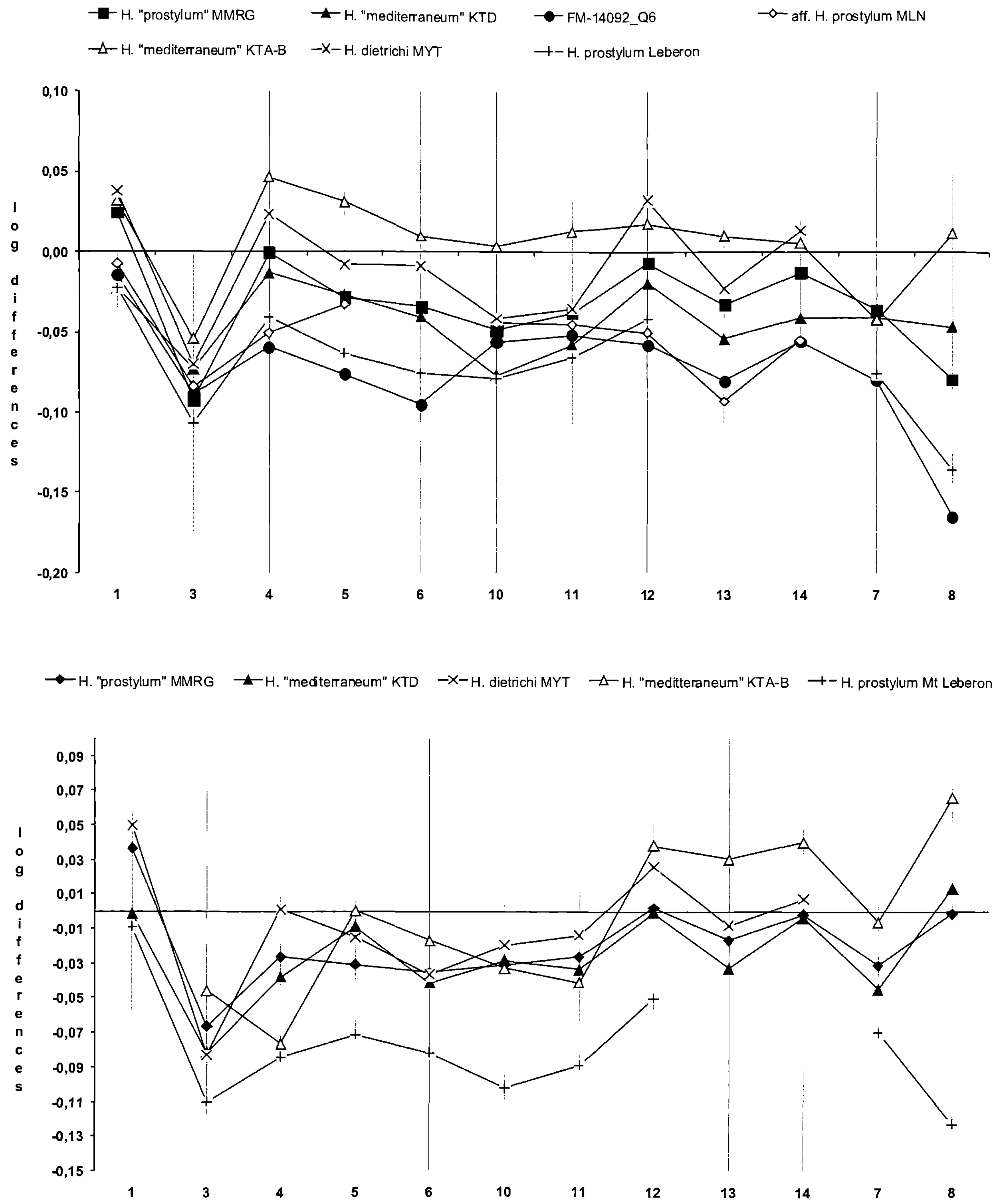

Figure 19: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of aff. *Hipparion prostylum* from MLN with those of *H. prostylum* from Q6, MYT, MMRG, KTA-B and KTD. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

are clearly distinguished from the *Hipparion proboscideum* RZO sample, being larger and more robust. The proximal upper articular width of the MCIII from MLN falls into the range of the MTLA, MTLB and Q1 samples (Fig. 14A). On the contrary, the MTIII resembles the proportions of the MTLA, MTLB and Q1 samples, but it seems to be smaller in size and at the same time comparable to the RZO specimen in the midshaft width (M3), the proximal articular dimensions (M5,6) and the distal articular depth (M12-14) (Fig. 14B).

Most of the data supports the presence of *Hipparion proboscideum* in the MLN, MTLA-B localities. Regarding the RZO fauna as the oldest among the MLN, MTLA-MTLB-Q1 faunas (Koufos et al., this volume;

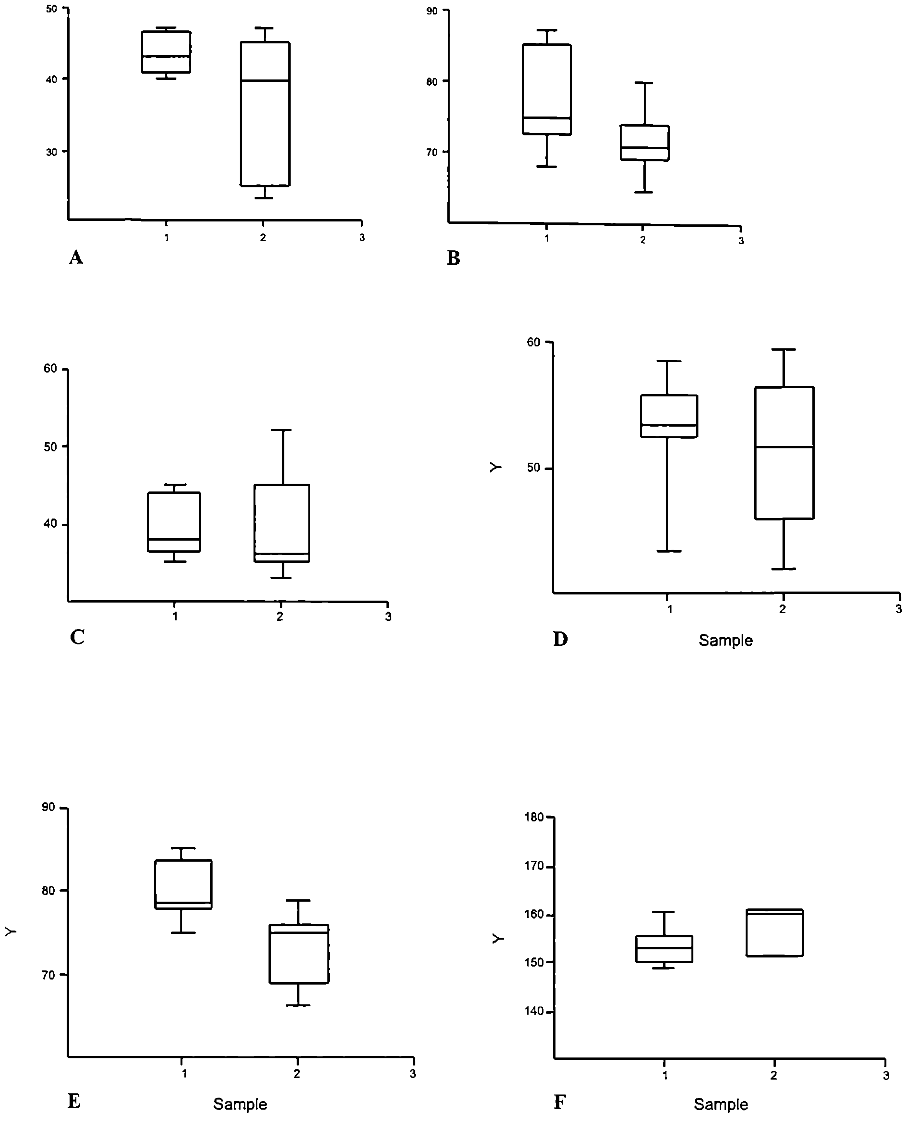

Figure 20: Box and Whiskers Plots on the skull variables; A. POB (M32); B. POF maximum length (M33); C. POF maximum width (M35); D. (M37); E. (M38); F. P^2 - Orbit distance.

Samples: 1. *H. prostylum*, MMRG and KTA-B; 2. *H. dietrichi*, Samos localities.

Sen et al., 2000), the most primitive form of *Hipparion proboscideum* should be considered as a hipparion of relatively slender build, which progressively evolved to a more robust form.

The metapodials from the Turkish locality of KTA-B, assigned to *Hipparion* sp. (with affinities to *Hipparion proboscideum*) show great similarities with the samples from MTLA, MTLB and Q1. The metacarpal from KTA-B is allied to the Q1 sample in more details, despite small differences in the dimensions of the upper articular surface (M5-6), (Fig. 14A). The metatarsal, on the other hand, appears to be slightly larger than that from MTLA, MTLB and Q1 but keeps the general morphological pattern (M10-14) (Fig. 14B). The small number of specimens could explain such differences. The faunal list from KTA-B supports a slighty older age than that of MTLA-B and Q1, possibly similar to the MYT fauna (Koufos et al., this volume). Besides, the MYT material includes a large-sized *Hipparion* with affinities to *Hipparion proboscideum*. Combining the above observations, the presence of *Hipparion proboscideum* in the KTA-B and MYT localities is quite possible and reliable. The comparison of the large-sized metapodials from MMRG (Iran) with those of *Hipparion proboscideum* from Samos and KTA-B provides another approach for the taxonomy of the large-sized hipparion from MMRG. Bernor et al. (1996a) support the presence of *Hipparion brachypus* in the MMRG fauna, but the Figure 14 provides great similarities between the MMRG metapodial sample and that of *Hipparion proboscideum*. The metacarpal from MMRG is slightly smaller than that of *Hipparion proboscideum* from Q1 and KTA-B but the morphological pattern is almost the same (Fig. 14A). Similarly, the metatarsal closely follows the measurements of *Hipparion proboscideum* from MLN (Fig. 14B). The first record of *Hipparion proboscideum* in general is that from RZO at ~8.2 My, while that of *Hipparion brachypus* is from Q4 between 7.3-7.1 My. The proposed age of 8.0-8.2 My for MMRG (Bernor et al., 1996a), although older than that of ~7.5 My for MLN, seems to be in favour of the presence of *Hipparion proboscideum*, rather than of *Hipparion brachypus,* in the MMRG fauna.

Only one metacarpal from Q5 retains the morphological pattern of the *Hipparion proboscideum* lineage from the upper fossiliferous levels of Mytilinii Fm., and seems to differ from that by having a reduced midshaft depth and maybe a reduced proximal articular width (M4-5, M7) (Fig. 14A).

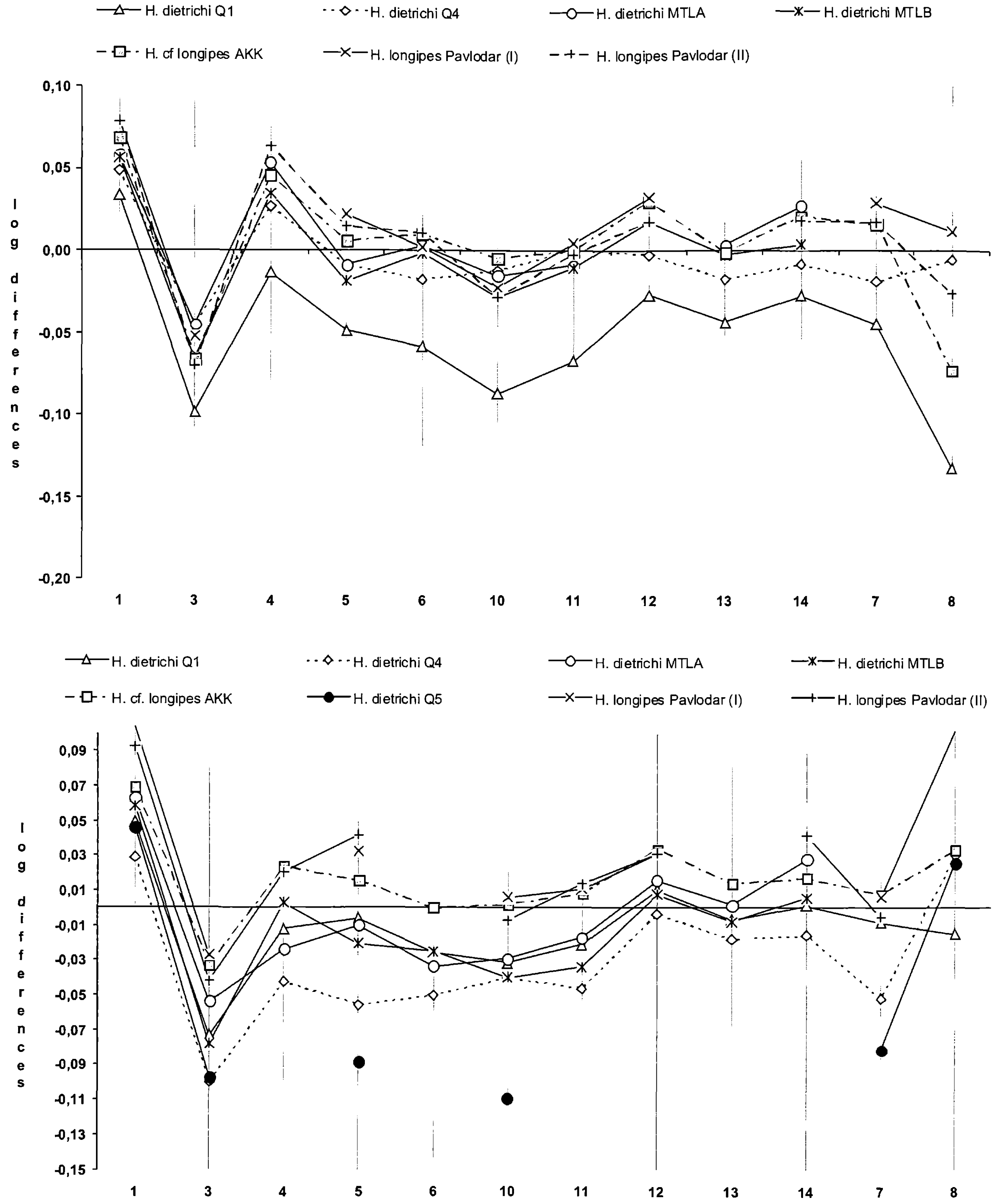

Figure 21: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H. dietrichi* from Samos with *H. longipes* from Pavlodar and AKK. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

Therefore, the occurrence of *Hipparion proboscideum* in the uppermost fossiliferous horizon of the Mytilinii Basin is possible, but not well-supported.

Taking all the data about the *Hipparion proboscideum* morphology into account, the available material of the large-sized hipparion from MTLA-B and Q1, with the double fossa on the facial region of the skull, suggests similarities to *Hipparion proboscideum* from RZO and Qx, and it should be assigned to it. But because of the different skeleton pattern, it should rather be assigned to *Hipparion* cf. *proboscideum*, similarly to the scanty sample from MYT. The sample from MLN, also because of the small number of specimens, is better referred to as aff. *Hipparion proboscideum*.

Hipparion proboscideum could possibly derive from a member of the *H. primigenium* group, with relatively slender metapodials and a deep narial opening. *H. gettyi* morphology includes both last features (Bernor, 1985; Bernor et al., 1996b) and it could potentially announce the *Hipparion proboscideum* morphology, increasing the facial length, the maxillary width and reducing the POB.

The relatively slender *Hipparion proboscideum* from RZO indicates a connection between Continental Greece and W. Asia via Samos at the beginning of MN 11. The NIK fauna, which is slightly older than that of RZO, dated to the lowermost Turolian (Koufos, 2006), does not include *Hipparion proboscideum,* but the presence of a large-sized form comparable to *Hipparion proboscideum* cannot be excluded (Vlachou & Koufos, 2002). All data, in our opinion, shows that *Hipparion proboscideum* from the Balkans possibly adapted to new ecological conditions and evolved to *Hipparion mediterraneum,* mainly reducing the midshaft width (M3) and the articlular dimensions (M5-6, M11-14) of the metapodials, as well as the development of the anterior fossa. The next attested record of *Hipparion proboscideum* morphology in the Balkans is that of *Hipparion* cf. *mediterraneum* from the PER fauna, dated to MN 12 at ~7.3-7.1My (Vlachou & Koufos, 2006; Koufos et al., 2006) and the last in the PIK and HD faunas, both dated to middle Turolian (MN 12) (Koufos, 1987c; Hristova et al., 2002, 2003). The PER form is considered as an intermediate form between *Hipparion proboscideum* from RZO and *Hipparion mediterraneum* from PIK and HD (Vlachou & Koufos, 2006). In Samos, W. Turkey and Iran, *Hipparion proboscideum* probably evolved to more robust forms, though keeping the well-defined anterior fossa.

8. The *Hipparion prostylum - Hipparion dietrichi* Lineage

It is the most completely represented lineage, since it has records from all studied localities of Samos (MN 11-MN 12). Bernor et al. (1996b), as well as Zouhri & Bensalmia (2005) assign the lineage to the genus *"Hipparion"* Forstén (1983) includes *H. dietrichi*, *H. prostylum* and *H. urmiense* in the Turolian hipparions with long POB, while Watabe (2004) recognized two clusters in the *H. prostylum* group, *H. prostylum*, Gervais 1849 and *H. hippidiodus*, Sefve 1927. The *H. prostylum* group corresponds to the *H. dietrichi* group in this paper, while that of *H. hippidiodus* includes forms with a vestigial POF, for instance *H. hippidiodus*, *H. platygenys*, Gromova, 1952, *H. urmiense*, Gabunia, 1959 and *H. molayanense*, Zouhri, 1992. Even if we do not know much about their skeleton pattern, we believe that it is quite possible that they belong to the *"Hipparion"* group, although their relationship to the *Hipparion prostylum - Hipparion dietrichi* lineage is uncertain and needs further study.

The *Hipparion prostylum - Hipparion dietrichi* lineage is represented by at least one taxon in the majority of the most well known Turolian Old World localities. The records increase from Western Europe (France) to the East (Greece, Turkey, Iran, Afghanistan) and from early MN 11 (Greece) to middle MN 12 (Iran) Turolian. Bernor (1985) believes that *"Hipparion" prostylum* appears to be the oldest member of the *"Hipparion"* group, because it is the most widely dispersed hipparion of the group and has some morphological characteristics which converge backwards to the *"Hippotherium"* group.

The *Hipparion prostylum Hipparion dietrichi* lineage contains the following species:

Hipparion prostylum Gervais, 1849

Holotype: Partly preserved and deformed skull, BMNH-M.33603.

Type Locality: Mont Luberon or Cucuron, Rhône Valley, France.

Age: Turolian (MN 12) (NOW, 2008)

Remarks: *H. prostylum* was the fist record of the *"Hipparion"* group in Western Europe. The species was first created to describe the material from Mont Luberon, France (Gervais, 1849), while Christol (1832) created the genus *Hipparion* based on this. It has a medium size, a short and wide muzzle, a short narial opening, long POB, an oval, anteroposteriorly oriented, moderately deep, slightly pocketed POF with a well-defined peripheral rim outline; moderately to richly plicated upper cheek teeth, a double pli caballin and an elliptical protocone (pers. observation). It possibly has a slender skeleton.

Further occurrences of *Hipparion prostylum* were listed from the Middle Maragheh, Samos, Pikermi, and the Thessaloniki-MNHN collection (Bernor, 1985; Bernor et al., 1996a, b; Watabe, 2004; Zouhri & Moussa, 2005). The skulls referred to *Hipparion "prostylum"* from Maragheh illustrate a significant range in the POF complex morphology and it are partly comparable to that of *Hipparion prostylum* from Mont Luberon. The ancestor of *H. prostylum* is still under discussion. Bernor (1985) cites *Hipparion gettyi* as the potential ancestor of *Hipparion "prostylum"* from Maragheh but this assumption is not widely accepted (Watabe & Nakaya, 1991b; Vlachou, in prep.).

Bernor (1985) assumes that the material from Maragheh, stored at MNHN, comes from the middle fossiliferous horizons of the Maragheh sequence (MMRG), which is the most well-studied of all the Maragheh vertebrate localities. He supposed that the sample is not chronologically biased, although more than one palaeontological expedition has worked there and the collected material has no precise stratigraphic control (Bernor et al., 1996a). The *Hipparion "prostylum"* sample shows, as mentioned above, significant variability in its facial morphology. The POF is always placed far from the orbit and the facial crest, but it varies from oval, well-marked all around, moderately deep, posteriorly pocketed and anteroposteriorly oriented (AMNH-22807) to elliptical, poorly marked, sometimes without anterior rim, shallow, well-marked posteriorly, but not pocketed and anteroventrally oriented (KUAC 95090, MNHN 359) (Fig. 15). The first described POF morphology is reminiscent of the *Hipparion prostylum* morphology, while the second, which is probably more evolved, is similar

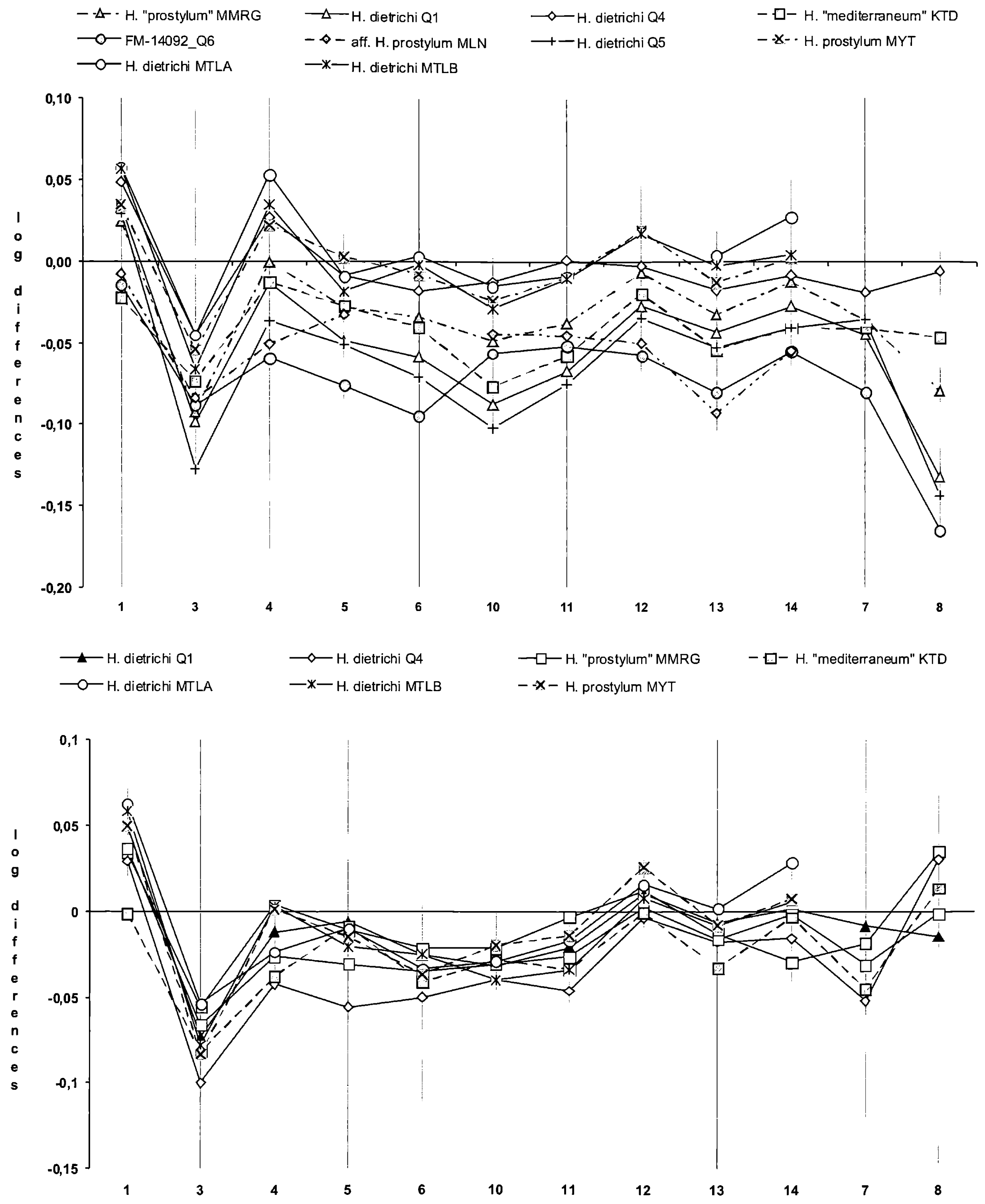

Figure 22: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H. dietrichi* from Samos with *H. prostylum* from MLN, MYT, Q6, MMRG and *H. "mediterraneum"* from KTD. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

to that of *Hipparion dietrichi*. Vlachou & Koufos (2006) assume that the extended morphological limits could thus be explained, considering that either the Maragheh material comes from different stratigraphic levels, covering a time span more than 8.0-8.2 My (Bernor et al., 1996a), or that this time span represents a transitional zone from *Hipparion prostylum* to *Hipparion dietrichi* and thus both morphologies are present. Both approaches sound logical, but the first one seems to be more credible. *Hipparion prostylum* was also listed from the Old Mill Beds, Samos, as well as from the Thessaloniki-MNHN Arambourg collection (Bernor et al., 1996a; Watabe, 2004; Zouhri & Moussa, 2000). Samos Qx and Q6 belong to the Old Mill beds, dated to early Turolian (MN 11) (Table 1).

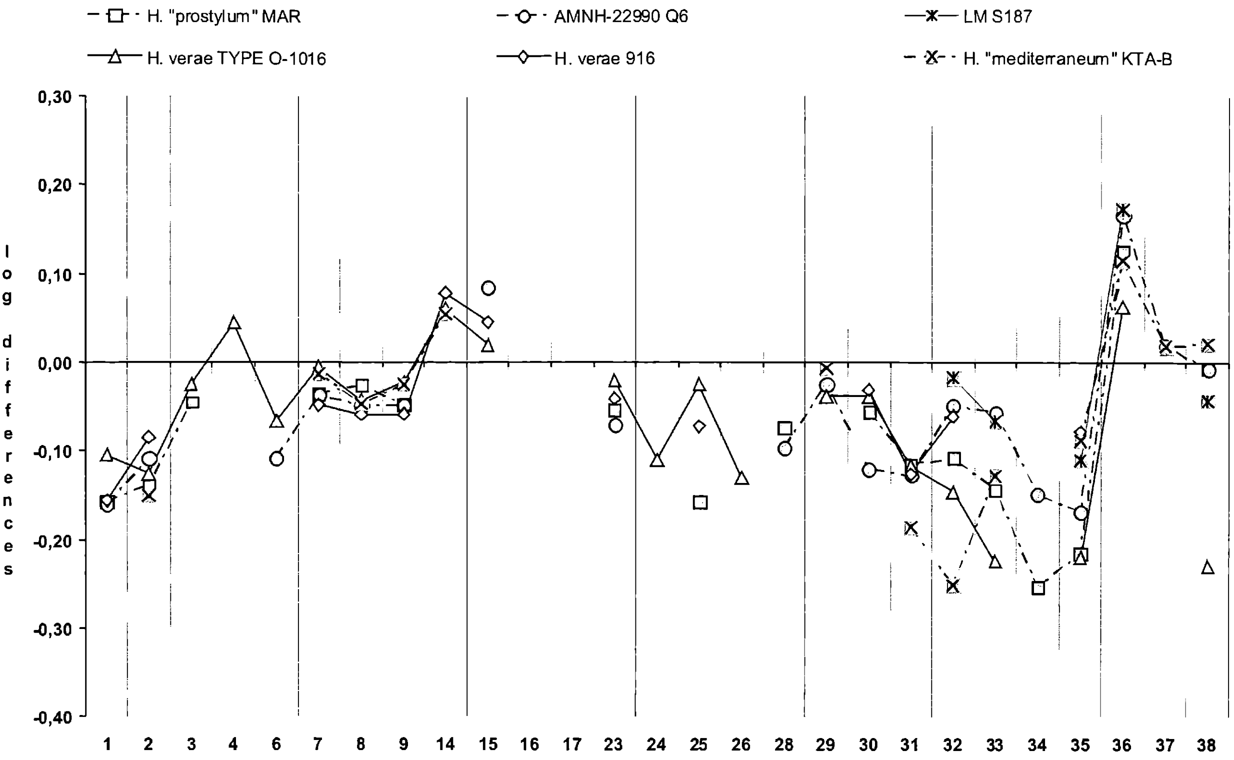

Figure 23: Logarithmic ratio diagram comparing the skull of *H. prostylum* from different Samos localities with *H. verae* from Grebeniki. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

Indeed, the occurrence of *Hipparion prostylum* at that time is possible, but there are no reported specimens. Watabe (2004) mentioned *Hipparion prostylum* from Thessaloniki, MNHN collection, while Zouhri & Moussa (2000) recognized *Hipparion dietrichi* in the same collection, but soon after that, Zouhri & Bensalmia (2005) regarded *Hipparion dietrichi* as synonymous with *Hipparion prostylum*. Previous studies of material coming from Axios Valley (Greece) and other neighbouring localities of a similar age (e.g. NIK, PER), or even younger (PIK), by the first or/ and the second author, rule out the occurrence of *Hipparion prostylum* in Continental Greece during early-middle Turolian, MN 11-MN 12 (Koufos, 1987a, 1987b, 1987c, 1988a, 1999, 2006; Bonis & Koufos, 1999; Vlachou & Koufos, 2002, 2004, 2006).

Hipparion dietrichi Wehrli, 1941

Holotype: Partly preserved skull, GIUM-SI/7, Münster
Type Locality: Samos, unknown locality
Age: Turolian (MN 11-13)
Remarks: The type specimen originates from Samos. It differs from *Hipparion prostylum* in having an elliptical to subtriangular POF, a less developed peripheral rim, reduced depth, unpocketed posterior rim and sometimes no anterior rim. The nasal notch is usually placed above the P2 anterostyle, or just in front of P2 (Sondaar, 1971; Bernor, 1985). On Samos, *Hipparion dietrichi* is known from Q4 and Q1 (Sondaar, 1971; Forstén, 1983; Vlachou, in prep). Apart from Samos, *Hipparion dietrichi* was also recognized from the Greek localities RZO, PXM, VTK, NIK and PER (Koufos, 1987a, 1987b, 1987c, 1988a, 1999, 2006; Vlachou & Koufos, 2002, 2004, 2006), as well as from FYR of Macedonia and Turkey (Forstén & Garevski, 1989; Koufos & Kostopoulos, 1994; Koufos & Vlachou, 2005) all dated from MN 11 to MN 12.

Hipparion "dietrichi" from Continental Greece, in spite of its morphological affinities with *Hipparion dietrichi* from Samos, is clearly distinguished from the last species by its smaller size and the more slender metapodials (Vlachou & Koufos, 2006) and it is probably a distinct taxon (Vlachou, in prep.). *Hipparion dietrichi* from Q4 is represented by a single skull and few postcranials, while the sample from Q1 includes numerous cranial and postcranial remains. The sample from Q1 shares the same morphology with that from Q4 (Sondaar, 1971). The skull morphology has the typical characteristics of *Hipparion dietrichi,* without significant differences among the specimens, and furthermore, it seems comparable to the advanced morphology of *Hipparion "prostylum"* from MMRG (Vlachou & Koufos, 2006). The metapodials assigned to *Hipparion dietrichi* are, similar to *Hipparion "prostylum"*, elongated and slender (Vlachou & Koufos, 2006).

Forstén & Garevski (1989), also stressing the morphological affinities between *Hipparion prostylum* and *Hipparion dietrichi*, described a set of cranial and postcranial remains from Titov Veles (FYR of Macedonia) under the name *Hipparion prosylum / Hipparion dietrichi*. Bernor (1985) pointed out that *Hipparion dietrichi* derives from *Hipparion prostylum,* and all remarks reinforce his assumption (Bernor, 1985, Vlachou & Koufos, 2006). The elongated and slender metapodials from AKK

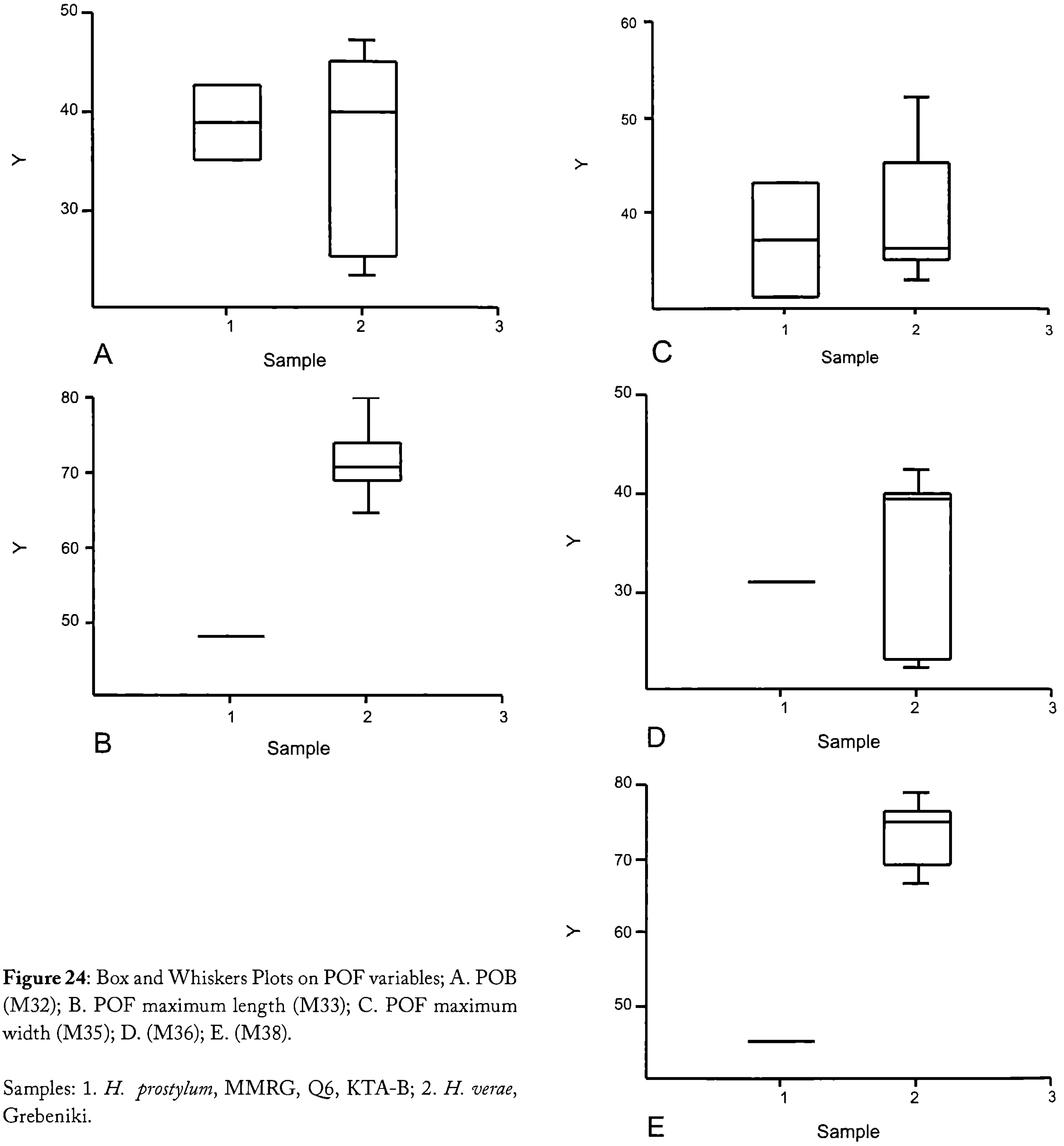

Figure 24: Box and Whiskers Plots on POF variables; A. POB (M32); B. POF maximum length (M33); C. POF maximum width (M35); D. (M36); E. (M38).

Samples: 1. *H. prostylum*, MMRG, Q6, KTA-B; 2. *H. verae*, Grebeniki.

(Turkey) were separated by Koufos & Vlachou (2005) into two groups, based mainly on their total length, since the rest of their measurements were similar. In addition, Vlachou (in prep.) states that the more elongated metacarpals, assigned to *Hipparion* cf. *longipes*, have a more pronounced protuberance for the musculus interosseus in the upper articular surface than that of the slightly shorter MCIII sample assigned to *Hipparion dietrichi*. *Hipparion dietrichi* morphology in the Akkaşdaği fauna was testified not only by the postcranials but also by cranial remains (Koufos & Vlachou, 2005). On the other hand, *Hipparion* cf. *longipes* is represented mainly by postcranials and the skull morphology is unknown (Vlachou & Koufos, 2005). During the study of the Samos material from MYT, MTLA and MTLB, two metapodial groups were recognized, both similarly elongated. One is possibly more slender than the other and, similar to the AKK sample, is characterized by a pronounced protuberance for the musculus interosseus in the upper articular surface of the metacarpal. We assigned the last morphology to the *Hipparion prostylum* - *Hipparion dietrichi* lineage and the other to the *Hipparion forstenae* lineage. According to these observations, we should reclassify the AKK skulls, already assigned to *Hipparion dietrichi* by Koufos & Vlachou (2005), as belonging to *Hipparion* cf. *longipes*, supposing that *Hipparion* cf. *longipes* derives from the *Hipparion dietrichi* morphology. At the same time, the postcranials assigned to *Hipparion dietrichi* should be ascribed to the *Hipparion forstenae* lineage. These re-classifications are adopted here and they are used in the following comparisons concerning the AKK sample.

Hipparion longipes Gromova, 1952

Holotype: MTIII, coll. PIN no 2413/5030
Type Locality: Pavlodar, Kazakhstan.
Age: Late Turolian, MN 13 (Late Miocene, NOW, 2007).
Remarks: Few things are known about the typical morphology of *H. longipes*. The upper teeth of *H. longipes* from Pavlodar are characterized by a large size, a short and wide protocone and moderate enamel plication. Forstén (1997) further noted that the protocone is apparently lingually flattened. The metapodials are extremely elongated and quite slender (Gromova, 1952).

The sample assigned to *H.* cf. *longipes* from AKK is characterized by very elongated metapodials similar to those from Pavlodar (Koufos & Vlachou, 2005) while the recent re-classification of the AKK material connects the *H.* cf. *longipes* sample directly with the *H. dietrichi* morphology.

Systematics of the Material

Hipparion prostylum Gervais, 1849
(Plate 5)

Synonyms:
H. dietrichi, Q6 (Forstén, 1983)
H. mediterraneum, KTA-B, KTD (Koufos & Kostopoulos, 1994)

Localities: Mytilinii-4 (MLN), Potamies ravine, Mytilinii Basin, Samos, Greece; Quarry-6 (Q6), Tholoremma, Mytilinii Basin, Samos, Greece.
Age: Early/Middle Turolian, MN 11/12 (late Miocene).
Mytilinii-4 (MLN): ~7.5 Ma.
Quarry-6 (Q6): ~7.4 Ma.
Material:
MLN: Partial mandible with P_2-P_4 dex and P_2-P_3 sin, MLN-20; mandibular fragment with P_2-M_3 dex, MLN 16, MCIII, MLN-2, 17, 37; distal part of MCIII, MLN-55
Q6: Skull, AMNH-22990, mandible, AMNH-22989; MCIII, FM-14092
MYT: Partial maxillae, MYT-92, 94, 95; MCIII, MYT-32; proximal part of MCIII, MYT-34, 76, 112; MTIII, MYT-35, 53, 62, 96; proximal part of MTIII, MYT-59, 70
Unknown Locality: Partial skull, MGL-LM S187
Short Diagnosis: Medium size, short and broad muzzle, shallow narial opening; well-defined POF, placed far from the orbit, medially deep, slightly posteriorly pocketed and oval-shaped; moderately plicated upper teeth with usually elliptical to oval protocone and single to double pli caballin; slender limb bones.

Description:
New material: In MLN, the *Hipparion prostylum* - *Hipparion dietrichi* lineage is represented only by a partially preserved mandible (MLN-20) and a mandibular fragment (MLN-16). The mandible MLN-20 belongs to an adult, middle aged male individual, while the MLN-16 belongs to a younger adult individual. The muzzle is short (85.5 mm) and seems to be wide, between 50-60 mm. The tooth row length of the younger adult is 143.3 mm. The metaconid is rounded; the metastylid is angular, while the ectoflexid is moderately deep in P_4 and quite deep in the molars. The pli caballinid is weakly developed, the pre- and post-flexids are slightly crenellated in the younger aged individuals, while the protostylid is preserved only in P_3 (Plate 5). The MYT partly preserved maxillae have medium to large-sized upper teeth, moderately plicated with an oval to round protocone and a single pli caballin. The metapodias are slender and relatively elongated.
Old material: The skull AMNH-22990 from Q6 belongs to a semi-aged, adult male individual of medium size. The muzzle is short and wide. The nasal notch is placed just in front of P2. The POF is well-defined as a moderately deep depression, oval-shaped, almost anteroventrally oriented and slightly posteriorly pocketed. It is placed far from the orbit and the facial crest (Fig. 16). The occlusal length of the cheek teeth row is 142 mm and the P2 - orbit distance is 151.1 mm. Both measurements are comparable to those of *Hipparion "prostylum"* from middle Maragheh. The teeth are moderately worn and moderately to richly plicated. The plication count of P4 and M1 is 22 to 16. The protocone is elliptical and the pli caballin double in the premolars, and usually single in molars.

The mandible resembles that from MLN in the morphology as well as in the dimensions (Appendix 1, Fig. 17), while the metacarpal that possibly corresponds to the AMNH-22990 morphology is moderately elongated and slender.

The skull from the Geological Museum of Lausanne preserves only the facial region. The POF complex morphology is comparable to that of AMNH-22990. The maxillae preserve only the M^2-M^3, which are moderately plicated with an elliptical protocone.

Comparisons:
Both skulls from the old material (AMNH, MGL) are morphologically close to the primitive morphology of *Hipparion "prostylum"* from Maragheh, but they seem to have a less pronounced POF, or in other words, a less strengthened peripheral rim. The skull measurements, in both specimens, are quite close to those of *Hipparion prostylum* from Mont Luberon and Maragheh but differ from the latter in having a shorter narial opening (M30), a slightly longer POB (M32) and furthermore, a larger POF (M33-35) (Fig. 18). With regard to the *Hipparion* cf. *longipes* sample from AKK, the Samos specimens have a shorter and less broad muzzle (M1, M15), a shorter tooth row length (M9), a shorter narial opening (M30), a longer POB (M32), an increased POF width (M35) and a shorter distance between the most posterior point of the POF and the alveolar border (M38) (Fig. 18). The last decreasing measurement (M38), when compared to the distance between the infraforamen and the alveolar border (M37), shows that the POF of the Samos sample is more anteroposteriorly oriented than that of *H.* cf. *longipes* from AKK (Fig. 18). It is worth noting that the nasal notch position in AMNH-22990 falls into the variability of *Hipparion "prostylum"* from MMRG and *Hipparion* cf.

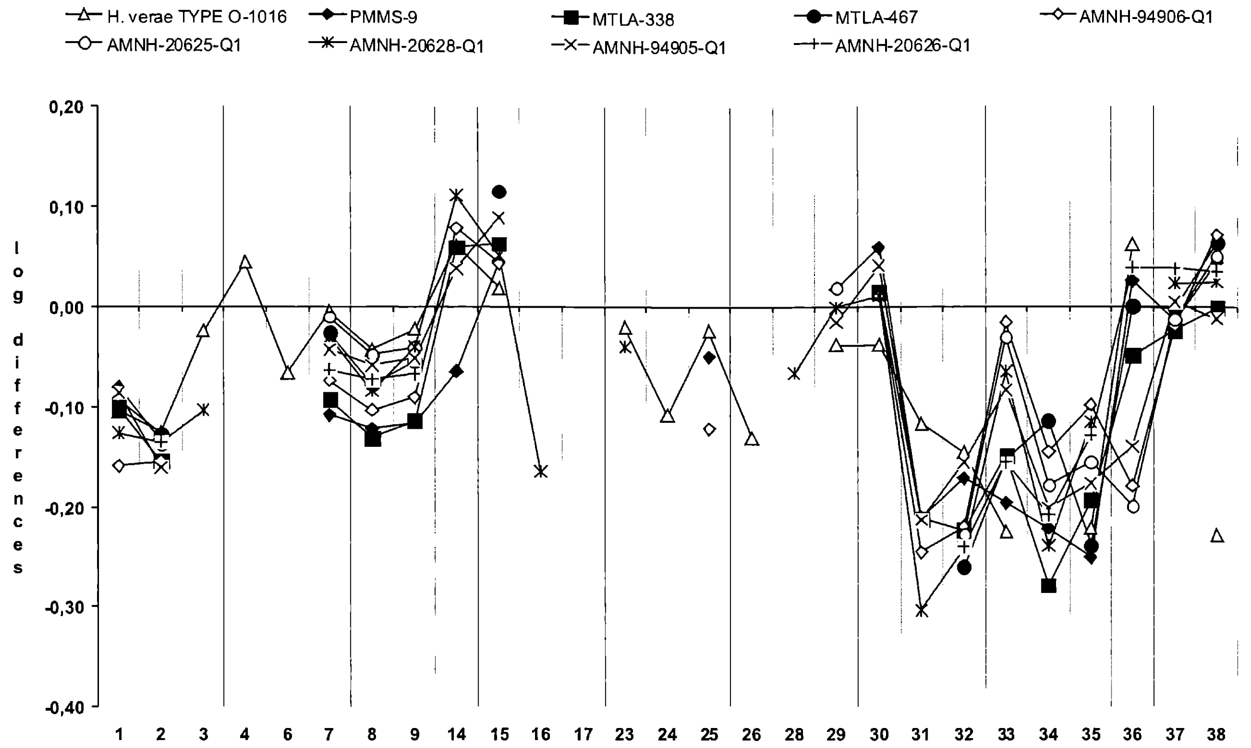

Figure 25: Logarithmic ratio diagram comparing the skull of *H.* cf. *forstenae* from Samos with that of *H. verae* (type specimen) from Grebeniki. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

longipes from AKK. More precisely, in AMNH-22990 it is placed just in front of P^2, while in *Hipparion "prostylum"* from Maragheh and *Hipparion* cf. *longipes* from AKK, it is retracted from just in front of P^2 (MAR-465, AK3-234) to the P^2 parastyle (MAR-359, AK2-499) (Watabe & Nakaya, 1991; Koufos & Vlachou, 2005).

The mandible AMNH-22989 and those from MLN show similarities with *Hipparion moldavicum* from AKK, but they differ in the shorter and broader muzzle and in the sharply increased height of the mandibular ramus at P_4-M_1 level (M11) (Fig. 17). The lower teeth occlusal morphology does not really differ, except maybe the more crenellated pre- and post-flexid in the MLN and Q6 sample. Unfortunately, there is no mandibular data of *Hipparion "prostylum"* from MMRG or postcranial remains from the medium-sized hipparion from Q6 for further comparisons.

From the fossiliferous levels of the Kemiklitepe locality (KTA-B, KTD), Koufos & Kostopoulos (1994) assigned a set of medium-sized hipparion bones to *Hipparion "mediterraneum"*. Further study of the Kemiklitepe material reveals that these specimens are similar to the Q6 and MLN samples and better comparable to *Hipparion "prostylum"* from the MMRG level (Vlachou, in prep.). The mandible from KTD shows metrical and morphological affinities with *Hipparion prostylum* from Mont Luberon and, excluding the somewhat increased muzzle length (M2), is similar to the specimens from Q6 and MLN in the relatively wide muzzle (M7), the angular metastylid, the presence of the protostylid in $P_{3,4}$ and the occasionally weakly developed pli caballin (Fig. 17). Similarly, the skull KTA-B-586 from Kemiklitepe, assigned to *Hipparion "mediterraneum"* by Koufos & Kostopoulos (1994), includes all the morphological characteristics of the Q6 skull. The POF is shallow, elliptical to subtriangular in form, moderately far from the orbit. The nasal notch is situated just in front of P2. The tooth row length and most of the available metric characteristics fall into the limits of the described specimens (Fig. 18).

The metacarpal sample from MLN is almost identical to the Q6 and Mont Luberon samples (Fig. 19). All differ from the KTD sample by the reduced midshaft depth (M4) and the shorter proximal and distal articular depth (M6, M12-14), but their general morphology is almost the same. The samples from MMRG, MYT and KTA-B reveal a more evolved morphological pattern than those from MLN and Q6, having a similar midshaft width (M3) and the rest of the measurements (M1, M6-14) are increased (Fig. 19). Similarly, the metatarsal sample from KTD and *H. prostylum* from Mont Luberon confirm the advanced character of the MYT, MMRG and possibly KTA-B samples, reinforcing the younger character of the last three faunas. In conclusion, the Q6 sample shows great similarities to the *Hipparion prostylum* sample from Mont Luberon and it should be described under the same species name. Concerning the MLN sample, although closely related to *Hipparion prostylum,* the data is not enough to confirm the species in this stratigraphic level and we prefer to ascribe the sample to aff. *Hipparion prostylum.* On the basis of cranial and postcranial morphology, *Hipparion "mediterraneum"* from Kemiklitepe (KTD, KTA-B) should be synomymized with *Hipparion prostylum.* MYT, KTA-B and MMRG skeleton patterns show a better adaptation

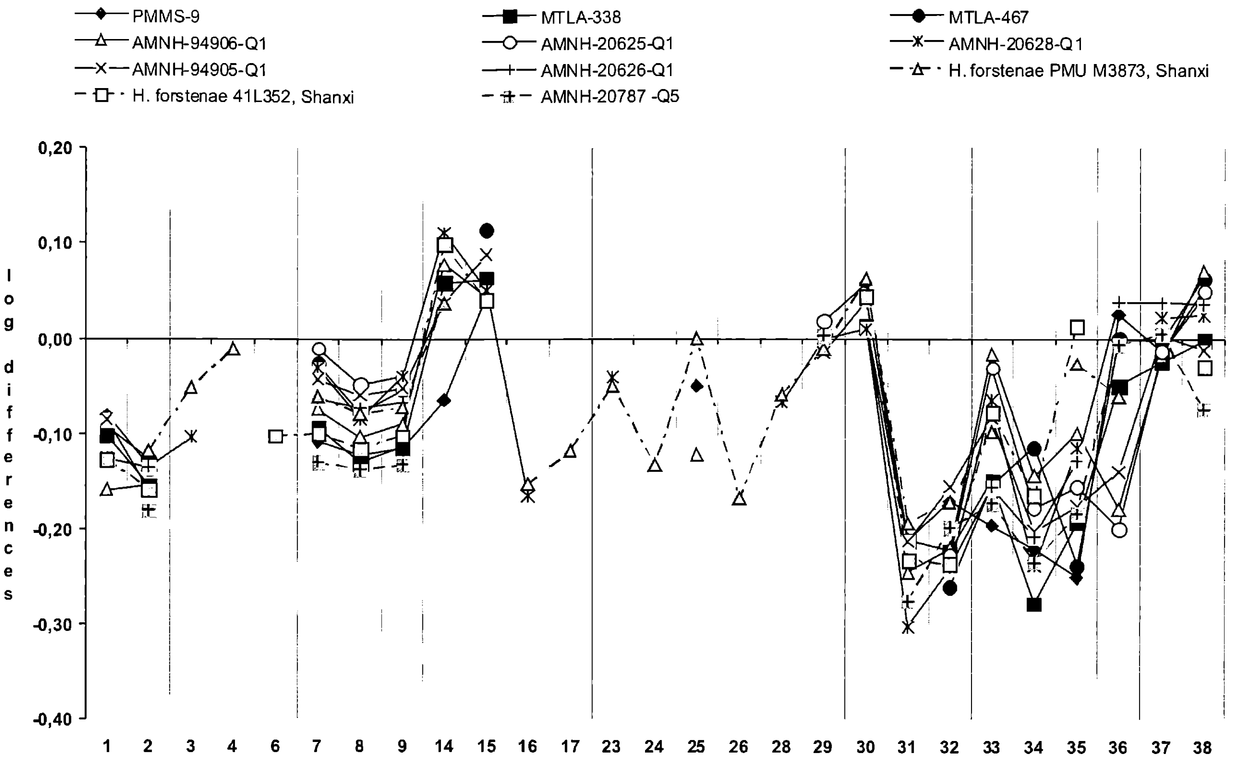

Figure 26: Logarithmic ratio diagram comparing the skull of *H.* cf. *forstenae* from Samos with that of *H. forstenae* from Shanxi, China. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

for running than the skeleton of *Hipparion prostylum* from Mont Luberon, KTD, MLN and Q6, indicating the appearance of the *Hipparion dietrichi* morphology. The MYT sample lacks cranial elements, and the postcranial remains could be ascribed either to *Hipparion prostylum* or to *Hipparion dietrichi*. But we prefer although to list the MYT sample under the species *Hipparion prostylum*, because the MYT fauna is older than that of Q4 and MTLA-B and better correllated to that of KTA-B (Bonis, et al. 1994; Kostopoulos et al., this volume).

Hipparion dietrichi Wehrli, 1941
(Plates 6-8)

Localities: Mytilinii-1A, B, C (MTLA, MTLB, MTLC), Adrianos ravine, Mytilinii Basin, Samos, Greece; Quarry-1 (Q1), Adrianos ravine, Mytilinii Basin, Samos, Greece; Quarry-4 (Q4), Potamies ravine, Mytilinii Basin, Samos, Greece.

Age: Middle Turolian, MN 12 (Late Miocene).

Mytilinii-1A, B, C (MTLA, B, C), Quarry-1 (Q1): ~7.1 Ma. Quarry-4 (Q4): 7.3-7.1 Ma.

Material:

MTLA: Partial skull, MTLA-122; MCIII, MTLA-264, 259; proximal part of MCIII, MTLA-302, 391,458; distal part of MCIII, MTLA-136; MTIII, MTLA-314, 296, 205, 318, 439; proximal part of MCIII, 30, 60, 303, 498; distal part of MCIII, 58, 276, 404, 435, 504

MTLB: Partial skull, MTLB-163; mandible, MTLB-323; MCIII, MTLB-272, 275, 298; proximal part of MCIII, MTLB-351; distal part of MCIII, MTLB-88, 202; MTIII, MTLB-274; proximal part of MTIII, MTLB-144, 166, 318; distal part of MTIII, MTB-277, 300

Q4: Skull, AMNH-22860; partial mandible AMNH-22836; MCIII, AMNH-20764d, 20764g, 20764; MTIII, AMNH-20764C, 20764, 22841; proximal part of MTIII, AMNH-20764., 20764

Q1: Skull, AMNH-20596, 20997A; partial skulls, AMNH-20608, 20692, 20559A, 20598A, 20598, 22787, 94907; mandible, AMNH-20635, 20603; MCIII, AMNH-94483, 23046, RBL0202, RBL0201, 20665Q, 23046H, 23046D; proximal part of MCIII, AMNH-Bx35-B15; MTIII, AMNH-20658A, 23043B, 23043C, 23043A, 23012.

Unknown Locality: Partial skull, GIUM-SI/7; partial skull: MGL-LM-S191.

Short Diagnosis: Medium-large size, short and broad muzzle, short narial opening; long POB; shallow POF far above the facial crest, anteroventrally oriented, well-defined but weakly marked peripheral outline; moderately plicated teeth, elliptical to oval protocone, single pli caballin; elongated and slender limb bones.

Description:

New material: The description is based mainly on a badly preserved skull from MTLB and a partially preserved skull from MTLA. Both belong to male adult individuals. The skull MTLB-163 is dorsoventrally compressed and strongly crushed, while the MTLA-122 lacks the opisthocranion and the upper part of the facial region (Pl. 7). The muzzle is short and wide and the nasal notch is placed just above the anterior part of P2. The POF is

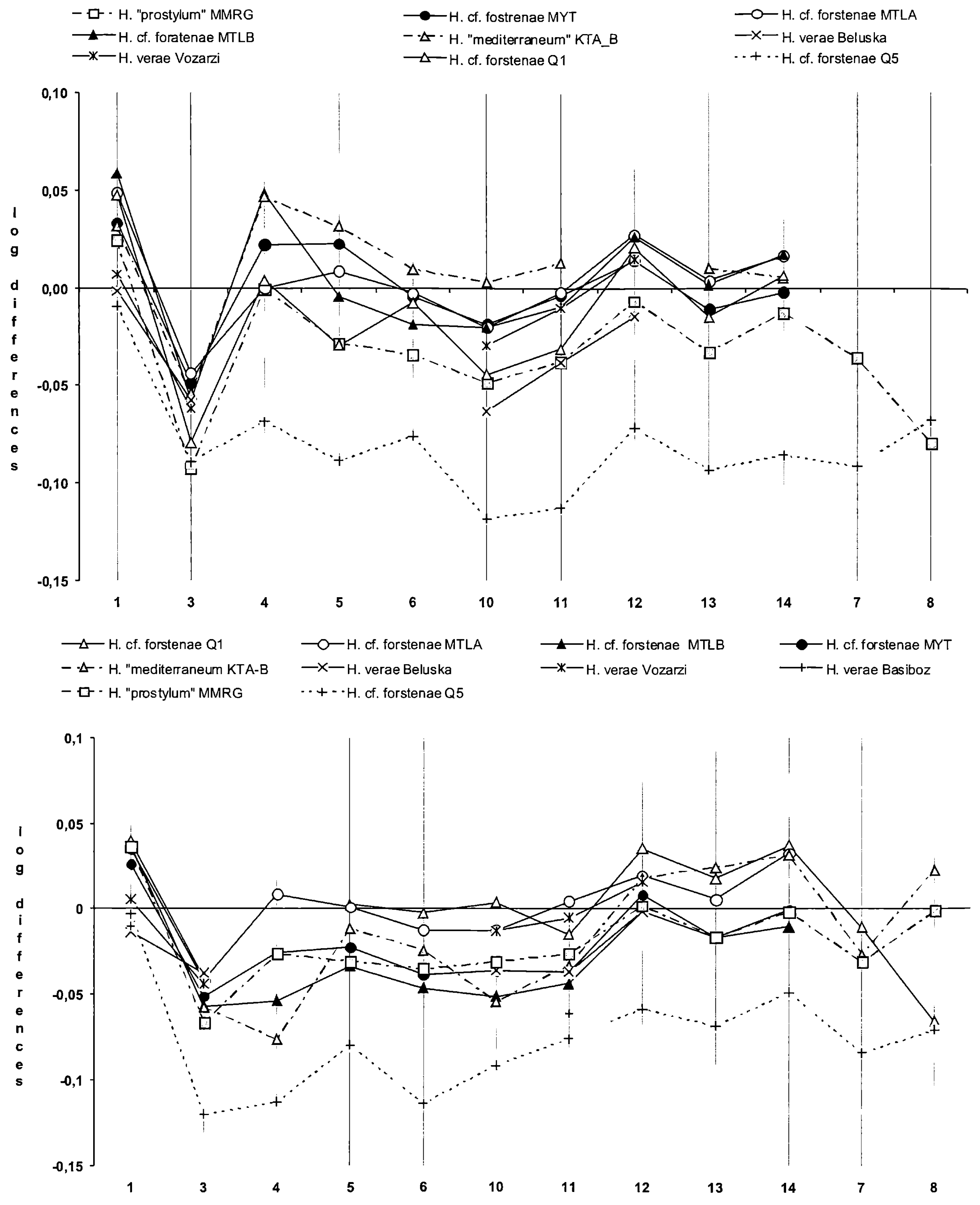

Figure 27: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H.* cf. *forstenae* from Samos with *H. prostylum* from MMRG and *H. verae* from Basiboz and Beluska, Titov Veles. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

certainly placed far from the orbit and the facial crest, and seems to be shallow and elliptical in shape. The tooth row length changes with wear and varies from 130.0 to 155.6 mm. The teeth are moderately plicated (~16 plis in P^4 and 11 in M^1), the protocone is elliptical and the pli caballin is single, even in the more heavily worn teeth. The metapodials are elongated and slender. The robusticity index varies from 14.0 to 16.3 for MCIII and from 12.2 to 13.8 for MTIII. It is worth mentioning that the protuberance for the musculus interosseus is significantly exaggerated in the proximal part of MCIII.

Old material: Three almost complete skulls and nine partially preserved skulls have been attributed to *Hipparion dietrichi* by Sondaar (1971) and Forstén (1983). The muzzle is short and broad. The muzzle length varies from 87-112.5 mm, while the breadth ranges from 61.5-69.6 mm. The narial opening is short. The nasal notch is retracted above the anterior part of P^2 to far in front of P^2. The POF is always placed far from the orbit and the facial crest and varies from elliptical to subtriangular-shaped. It is usually shallow, extended from the anterior part of M^2 to the P^3 mesostyle, and the peripheral rim is well- to slightly marked. The posterior rim is generally unpocketed, while the anterior one is sometimes absent. The POF usually has an anteroventral orientation and the infraforamen is situated below the anteroventral part of the fossa, usually above the end of P^3.

The tooth row length changes from 132.7-149.0 mm with wear. The teeth are moderately plicated, the protocone is often oval with lingual flattening, the pli caballin is single, and present even in more heavily worn teeth.

The metapodials we assigned to *Hipparion dietrichi* are also elongated and slender, with the protuberance for the musculus interosseus significantly exaggerated. The robusticity index, similar to the newly collected material, varies from 13.1 to 16.5 for MCIII and 12.3 to 14.1 for MTIII.

Comparisons

The attribution of the old collected skulls to *Hipparion dietrichi* is taken for granted. The sample shares the same basic morphology with the typical *Hipparion dietrichi*, the nasal notch in vertical line in front of P^2, the short and wide muzzle and the weakly developed POF. Fig. 18 compares the measurements of *Hipparion dietrichi*, *Hipparion prostylum* and *Hipparion* cf. *longipes* from Samos, MMRG, Mont Luberon and Akkaşdaği (AKK). The measurements of the newly collected material are very close to those of *Hipparion dietrichi* from Q1, Q4 and *Hipparion* cf. *longipes* from AKK (Fig. 18). The *Hipparion prostylum* samples are similar to *Hipparion dietrichi* and *Hipparion* cf. *longipes* in the muzzle morphology, tooth row length (M7-9), facial and cheek length (M23, M31), but they are distinguished from them by the POF-related measurements. Despite the similar P2 - Orbit distance, *Hipparion prostylum* seems to have a longer POB (M32), a more elongated fossa (M33-35) while the most posterior point of the fossa is always placed further from alveolar border (M38) (Figs. 18, 20). So, considering *Hipparion "prostylum"* from MMRG and Q6, *Hipparion dietrichi* from Samos (Q4, Q1, MTLA-B) and *Hipparion* cf. *longipes* from AKK as members of the same lineage, the last two species could derive from the first, increasing the range of the POB length (M32), slightly decreasing the POF length (M33) and changing the POF orientation from anteroposterior in *Hipparion prostylum* to anteroventral in *Hipparion dietrichi* and *Hipparion* cf. *longipes* (M37) (Fig. 20). In addition, the POF depth in *Hipparion dietrichi* is decreased, the peripheral rim is often slightly marked, while the posterior rim is never pocketed (Vlachou, in prep.).

The metapodials from MTLA and MTLB follow the morphological pattern of those from Q1 and Q4 very closely (Fig. 21). The Q4 MCIII sample seems to be more primitive than those of Q1, MTLA and MTLB, in the weakly increased midshaft width in relation to the midshaft depth (Fig. 21A). However, the number of specimens from Q4 is too small (2 specimens) to support this conclusion.

Regarding the postcranials of *Hipparion dietrichi* and *Hipparion prostylum,* the MCIII sample of *Hipparion dietrichi* follows the measurements of *Hipparion prostylum* from MYT, KTA-B and MMRG, but it is longer and more developed in anteroposterior direction than the samples from MLN, Q6 and KTD (Fig. 22A). Similar to MCIII, the MTIII sample shows that *Hipparion prostylum* from MYT, KTA-B and MMRG is almost identical to that of *Hipparion dietrichi* from Q4 and Q1, while the sample from KTD is distinguished from *Hipparion dietrichi* by the shorter total length (M1) (Fig. 22B).

The metapodials of *Hipparion* cf. *longipes* from AKK and *Hipparion longipes* from Pavlodar are morphologically comparable to those of *Hipparion dietrichi* from the different Samos fossiliferous levels, but they differ in all cases in the increased total length, especially in MTIII (Fig. 21B).

In conclusion, the mentioned specimens from MTLA and MTLB resemble *Hipparion dietrichi* from Q4 and Q1 and must be assigned to this taxon. *Hipparion dietrichi* possibly derives from *Hipparion prostylum,* reducing the POF depth, changing its orientation to anteroposterior and increasing the total metapodial length.

In the Q5 fauna, although younger than that of AKK (Koufos et al., this volume), the presence of *Hipparion longipes* is not supported. Instead, the partly preserved skull with a short and wide muzzle (AMNH - no number) and elongated and slender metacarpals, smaller than those from MTLA, MTLB and Q1 (Fig. 21A), make the presence of *Hipparion dietrichi* in the Q5 fauna questionable. *Hipparion longipes* is possibly the most evolved member of the *Hipparion prostylum* - *Hipparion dietrichi* lineage and is restricted to Northern and Central Asia. However, the data is not enough for certain conclusions. The Pavlodar sample lacks cranial specimens, while the conclusions coming from the AKK sample were mainly based on suggestions, rather than on certain records.

9. The *Hipparion verae – Hipparion forstenae* Lineage

It is a newly described lineage with representatives from MYT, MLTA-B localities, dated to middle Turolian (MN 12). The morphology of this lineage differs from that one described under the *Hipparion prostylum* - *Hipparion dietrichi* lineage in the presence of the anterior fossa, the elongated muzzle and the deeper narial opening. Zouhri & Bensalmia (2005) generally include this morphology in "*Cremohipparion*", Watabe (2004) believes that despite the similarities with the *H. prostylum* group, it fits better into the *Hipparion mediterraneum* group, while Forstén (1983), based on its morphology and size, places it closer to *Hipparion macedonicum* and *Hipparion matthewi*. There are short and dubious references on the morphology of the

Hipparion verae - Hipparion forstenae lineage from the ex-USSR region (Gromova, 1952) and Turkey (Forstén & Kaya, 1984), but it certainly occurred in the faunas from Titov Veles, FYR of Macedonia (MN 11-12) (Forstén & Garevski, 1989; NOW, 2008) and Shanxi, China (MN 12) (Qiu, 1987; Bernor et al., 1990b; Deng, 2006). The *Hipparion verae - Hipparion forstenae* lineage includes the following species:

Hipparion verae Gabunia, 1979

Type Species: Skull, OGU 1016, University of Odessa.
Type Locality: Grebeniki, Moldavia.
Age: Early Turolian, MN 11 (Late Miocene).
Remarks: The species was originally described from Grebeniki as *Hipparion gromovae* (Gabunia, 1959), but as the name was given to a Spanish hipparionine species, Gabunia (1979) proposed the new name *Hipparion verae*. The species is of medium size, has a long muzzle, a nasal notch placed in front of the P^2 to P^2 mesostyle and a POF placed variably far from the orbit (about 25-50 mm); it is shallow, rounded-oval, sometimes triangular in shape, with a narrow slight posterior pocket, usually well-defined all around, with an occasional anterior fossa (Forstén & Garevski, 1989; Forstén, 1999; Watabe, 2004). The skulls assigned to *Hipparion verae* from Titov Veles (probably dated to early - middle Turolian, MN 11-12) are medium-sized and the nasal notch is situated at a level just anterior of P^2. The POF, which is situated close or far from the orbit, is egg- or round to triangular-shaped, rather deep, with a slight posterior pocket or lacking it (Forstén & Garevski, 1989). In some specimens, the POF ends at the infraorbital foramen or spills past P^2. In other forms there is a weakly developed anterior fossa (Forstén & Garevski, 1989).

Another possible reference to the *Hipparion forstenae* morphological group comes from Bazalethi (Georgia) (MN 13). Among the specimens assigned to *Hipparion garedzicum* from Bazalethi, there is a skull (B-51) which is distinguished by its long muzzle and the double fossa in its facial region (Forstén, 1999; Watabe, 2004).

The specimens referred to *Hipparion verae* have notably extended morphological limits and could be grouped under more than one species name. A revision of the hipparion species from the Black Sea region, on the basis of the hipparion morphotypes that have been recorded in Eastern Mediterranean region, could be helpful to better understand the evolution of hipparionine horses and their dispersal.

Hipparion forstenae Zhegallo, 1971

Type species: PMU M3873, Palaeontological Museum of Upsala University
Type locality: Loc. 30, Baode Country, Shanxi province, China.
Age: Baodean, MN 12 (Late Miocene).
Remarks: The species includes specimens from Chinese localities dated to middle Turolian, MN 12. It mainly differs from *H. verae* in the retraction of the nasal notch above the position from the posterior margin of P^2 to the anterior half of P^4. It has a medium-sized skull with a basilar length of about 400 mm. The POB is moderately long, ranging from 30-37 mm. The POF is occasionally pocketed, and its deepest point measures 20 mm from the facial surface (Qiu, 1987). It is elliptical to subtriangular-shaped, anteroventrally oriented, with a distinct peripheral outline. Above P^2-P^3, there always is a shallow, but well-marked anterior fossa. The tooth row length varies from 130-150 mm and the teeth are moderately plicated with a single pli caballin and a rounded to elongated protocone (Bernor et al., 1990b).

Systematics of the Material

Hipparion cf. *forstenae*
(Plates 8-10)

Synonyms:
H. cf. *matthewi*, Forstén & Kaya, 1995
cf. *H. mediterraneum*, Forstén, 1999
cf. *H. mediterraneum*, Vlachou & Koufos, 2004
H. dietrichi (pars), Koufos & Vlachou, 2005

Localities: Mytilinii-1A, B, (MTLA, MTLB), Adrianos ravine, Mytilinii Basin, Samos, Greece; Mytilinii-3 (MYT), Potamies ravine, Mytilinii Basin, Samos, Greece; Quarry-1 (Q1), Adrianos ravine, Mytilinii Basin, Samos, Greece.
Age: Middle Turolian, MN 12 (late Miocene).
Mytilinii-1A, B (MTLA, B), Quarry-1 (Q1): ~7.1Ma.
Mytilinii-3 (MYT): ~7.3 Ma
Material:
MYT: MCIII, MYT-8, 17, 97; proximal part of MCIII, MYT-126; MTIII, MYT-30, 124, 125; proximal part of MTIII, MYT-8.
MTLA: Partial skull: MTLA-338, 467, PMMS-9; MCIII, MTLA-96, 204, 305; proximal part of MCIII, MTLA-164, 226, 359; distal part of MCIII, MTLA-275, 355; MTIII, MTLA-274, 323, 230; proximal part of MTIII, MTLA-131, 393, 127, 333, 472; distal part of MTIII, MTLA-332, 180.
MTLB: maxillae: MTLB-31, 167; MCIII, 13, 117; proximal part of MCIII, MTLB-132; distal part of MCIII, MTLB-25; MTIII, MTLB-112, 247, 113, 188, 246; proximal part of MTIII, MTLB-348, 263, 114; distal part of MTIII, MTLB-50
Q1: Almost complete skull, AMNH-20628; partly preserved skull, AMNH-20626, 94906, 20625, 94905, MCIII, AMNH-23046, 23046F, 23046O; proximal part of MCIII, AMNH-20669B, MTIII, AMNH-20687A
Short diagnosis: Medium size; elongated and narrow muzzle; moderately deep narial opening; POB varies from long to moderately developed; shallow POF, elliptical to subtriangular-shaped with weakly marked peripheral rims; no posterior pocket; weakly developed anterior fossa; teeth moderately plicated with oval protocone and single pli caballin; elongated metapodials.

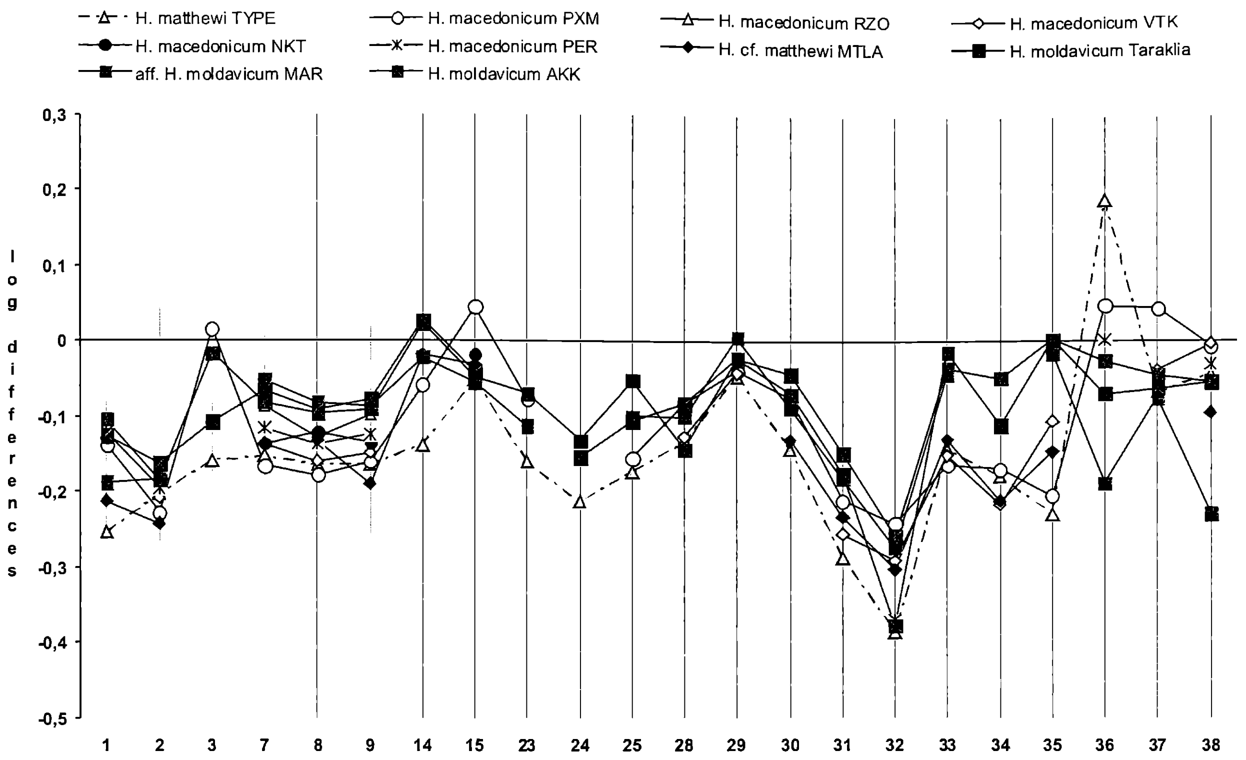

Figure 28: Logarithmic ratio diagram comparing the skull of the *H. matthewi* type specimen with that of *H. macedonicum* from Continental Greece and Samos localities and *H. moldavicum* from MMRG and AKK. Standard: *H. primigenium*, Höwenegg, n = 1-9 (Bernor et al., 1997).

Description:

New material: Three skulls from MTLA and two maxillae from MTLB share the cranial characteristics of the *Hipparion forstenae* morphological group. The muzzle is elongated and narrow. The length varies from 110.8-116.3 mm and the width from 52-61.2. The relative index (muzzle length) x 100/(muzzle breadth) is estimated from 184.6-223.6 slightly smaller than that of *H. brachypus* from HD and PIK (196.8-239.8), *Hipparion proboscideum* from RZO and Qx (228.3-245.5) and much more smaller than that of *Hipparion* cf. *mediterraneum* from PER (255.6). The nasal notch is placed between the P2 parastyle and the P2 mesostyle. The most posterior end of the POF measures 26.9-33 mm distance from the orbit (POB), while its ventral rim is 20.5-29.5 mm away from the facial crest (M36). The POF has an elliptical (MTLA-467) to subtriangular shape (MTLA-338) and extends from the anterior part of M^3 to the M1-P4 level. The peripheral outline is not strongly marked. The posterior rim is slightly pocketed to unpocketed and the anterior rim usually weakly developed. The POF depth is shallow, comparable to that of the *Hipparion dietrichi* POF. In front of the POF, above P3-P2, an anterior fossa is formed. It is well-defined, although not well marked peripherically, and it is not connected to the buccinator fossa. The tooth row length varies from 121.7-141 mm. The teeth are simply plicated (15-10 plis on P4, M1), the protocone is elliptical to oval, and the pli caballin is well-developed and single.

The postcranials corresponding to this morphology are slender and actually not very different from those of *Hipparion dietrichi*. The MCIII is well-distinguished from the latter species by the lack of the pronounced protuberance for the musculus interosseus in its upper part. The robusticity index is 14.8-16.3 and 11.4-14.2 for MCIII and MTIII respectively.

Old material: There are five skulls from Q1 which share the same morphology with those from MTLA and MTLB. They slightly differ from the MTLA ones in the further retraction of the nasal notch above the end of P^2 to the anterior part of P^3. The tooth row length varies from 129.3-145 mm and the teeth are also comparable with the MTLA and MTLB samples in their morphology. The skeleton is slender and the robusticity index was calculated to 14-14.8 and 13.7 for MCIII and MTIII respectively.

Comparisons

We readily admit that the *Hipparion verae* - *Hipparion forstenae* lineage shares several characteristics with the "*Hipparion*" group. But it is risky to conclude that the *Hipparion verae* - *Hipparion forstenae* lineage derives from the "*Hipparion*" group, because the lineage morphology also shows similarities with the "*Cremohipparion*" group, especially with what Watabe (2004) described as the *H. mediterraneum* group. However, in our personal judgement, the *Hipparion verae* - *Hipparion forstenae* lineage is morphologically closer to the "*Hipparion*" morphological group.

Fig. 23 depicts the cranial metrical comparison between *Hipparion verae* from Grebeniki and *Hipparion prostylum* samples from various localities. The two samples are similar in muzzle morphology (M1, M15), total skull

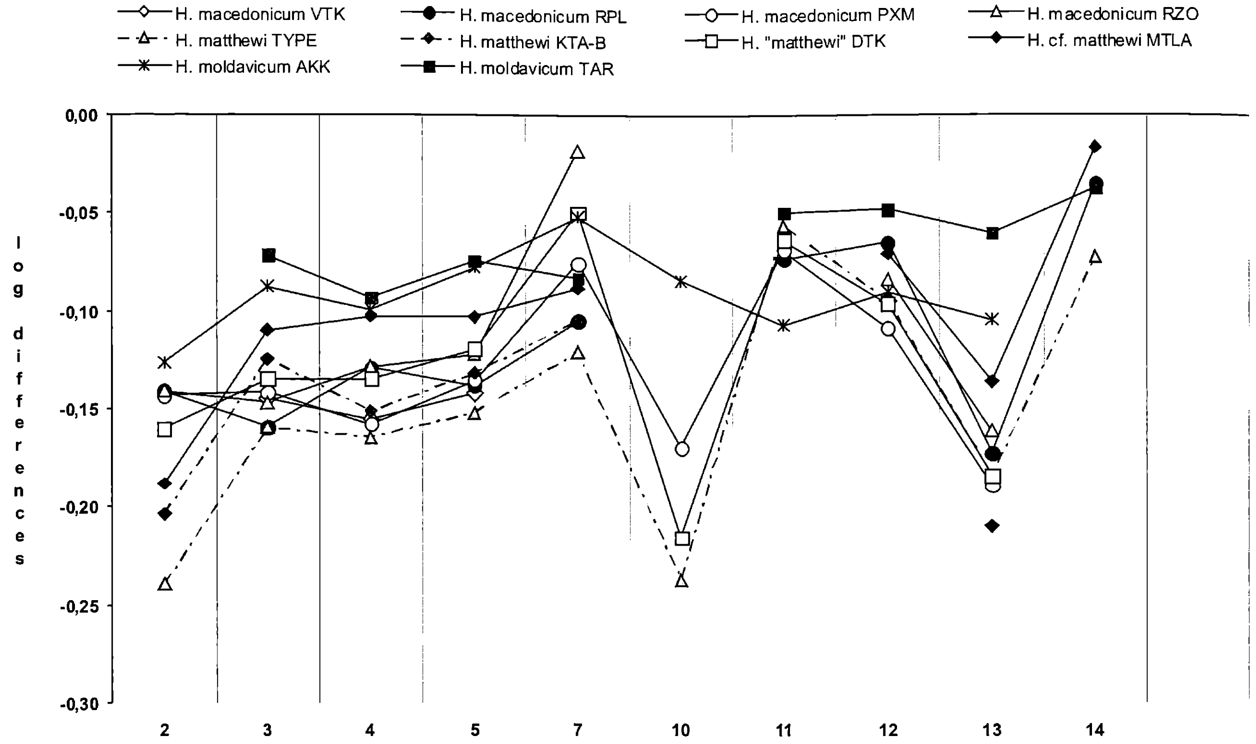

Figure 29: Logarithmic ratio diagram comparing the mandible of the *H. matthewi* type specimen with that of *H. macedonicum* from Continental Greece and Samos localities, *H. matthewi* from KTA-B and DTK, *H. moldavicum* from TAR and AKK. Standard: *H. primigenium*, Höwenegg, n = 6-11 (Bernor et al., 1997).

length (M6), tooth row length (M9), anterior ocular length (M23), narial depth (M30) and cheek length (M31). The POF complex morphology shows the expected increased variability. Both, *Hipparion verae* and *Hipparion prostylum*, have a POF which is neither especially deep, nor strongly marked. But the POF of the *Hipparion verae* sample is significantly shorter (M33) than that of *H. prostylum* and in addition its most posterior point is placed closer to the facial crest (M38) (Figs. 23, 24).

We have scanty metrical informations about *Hipparion verae* from FYR of Macedonia. It seems that the tooth row length varies, similar to that of the *Hipparion prostylum* sample and *Hipparion verae* from Grebeniki, between 127-158 mm and the POB from 25-50 mm (Forstén & Garevski, 1989).

The specimens from MTLA are mainly distinguished from those of *Hipparion verae* by the less pronounced POF rim, the absence of a posterior pocket in general and the retraction of the nasal notch above the P^2 parastyle to the P^2 mesostyle. Regardless of the affinities in muzzle morphology, the specimens from MTLA show an enlarged narial opening (M30) in relation to that of *Hipparion verae,* and a decreased cheek teeth length (M31) (Fig. 25). The POF from the MTLA sample differs significantly in length and width, but the most posterior point is placed further away from the alveolar border (M38) than that of *Hipparion verae*, probably indicating a change in the POF orientation from the anteroposterior oriented POF of *Hipparion verae* to anteroventrally in the MTLA sample. Similar changes in POF orientation have already been pointed out in the *Hipparion prostylum* - *Hipparion dietrichi* lineage. The specimens from Q1 differ from the MTLA sample in the weakly enlarged narial opening and the further retraction of the nasal notch above the end of P^2, but it is closer to the MTLA sample morphology rather than to *Hipparion verae* (Fig. 25).

The skull 109/XXI-78 from Gülpinar (Turkey) was assigned to *Hipparion* cf. *matthewi* by Forstén & Kaya (1995). Although it is characterized by the presence of a canine fossa, a deep narial opening (nasal notch above P^2-P^3), the upper tooth row length is too large for *H. matthewi* (Forstén & Kaya, 1995). Taking all the above mentioned morphologies into account, the skull from Gülpinar is better correlated with the Q1 and MTLA sample and must be referred to the same species. Further evidence of this resemblance is the orbit-preorbital fossa distance, which is almost 34.0 mm in the Gülpinar skull, versus 27-33 mm and 28.1-34.2 mm for the MTLA and Q1 skulls, respectively, and the upper cheek teeth length, which varies from 129.3 to 145 mm in the Q1 and MTLA specimens and 140.0 mm in 109/XXI-78.

The Chinese species, *Hipparion forstenae*, shares all the characteristics of the preorbital fossa and narial opening with the skulls from MTLA-B and Q1. Fig 26 suggests that *Hipparion forstenae* skull measurements follow those of MTLA and Q1, except the POF width, which is somewhat increased. The most posterior end of the POF of *Hipparion forstenae* is placed far from the alveolar border, similar to the MTLA and Q1 samples. The skull AMNH-20787 from the Q5 locality exhibits several affinities with *Hip-*

parion forstenae, MTLA and Q1 specimens. The narial opening is not preserved, but the POF is subtriangular, medially shallow, weakly marked all around the rim and placed 31 mm away from the orbit. The anterior fossa is well-formed and, compared to the MTLA and Q1 samples, shallow. The cheek teeth are worn, not far from a middle stage of wear, and the fossettes are weakly plicated, the protocone is elliptical and the pli caballin weakly developed to absent. The skull measurements almost fit to those of the Samos sample (MTLA & Q1) and differ from *Hipparion forstenae* mainly in the significant reduction of the POF width (M35) (Fig. 26).

The metapodials corresponding to the above mentioned samples are slender and similar to those of *Hipparion prostylum*. It is possibly one more indication of the *Hipparion forstenae* lineage derivation. Fig. 27 shows that the MYT, MTLA-B, Q1 and Titov Veles samples are distinguished into two groups. The two groups have comparable lower articular dimensions and midshaft width, but they differ in the total metapodial length. The shorter metapodials belong to the *Hipparion verae* sample from Titov Veles, while the more elongated ones belong to the species represented by the new and old collected specimens from Samos, as well as to those from AKK.

Considering *Hipparion verae* from Grebeniki, the skull from Gülpinar and *Hipparion forstenae* from Shanxi, there is no published data to compare the metapodial morphology, and consequently, its relation to the above cited samples. This notwithstanding, QIU (1987) ascribes to all Chinese hipparion species slender postcranial elements, while FORSTÉN & KAYA (1995) associated the skull 109/XXI-78 also with slender metapodials, which, when plotted on width to length, fall either into the upper range or just outside the range for the slenderly built *Hipparion* "*matthewi*" from Q5 (FORSTÉN & KAYA, 1995, Fig. 4-5).

In conclusion, and keeping in mind that the enlarged narial opening, which is represented by the retraction of the nasal notch from the level in front of P2 in *Hipparion verae* to the posterior end of P^2 in *Hipparion forstenae*, when coupled to the decrease of the strength of the POF outline, to the change in the POF orientation from anteroposterior to anteroventral, and the probably increased metapodial length, might imply a transition to a more evolved species. Consequently, the taxon represented by the described skulls from MTLA, MTLB, Q1, as well as that from Q5, is more evolved than *Hipparion verae* from Grebeniki and Titov Veles in the enlarged narial opening, the POF morphology and metapodial length, it can probably be assigned to *Hipparion forstenae* from Shanxi. Retaining, however, some doubts about the skeleton morphology of *Hipparion forstenae,* it is attributed to *Hipparion* cf. *forstenae*. The MYT sample, although it includes only postcranial elements, shows similarities in size and morphology to those from MTLA, MTLB and Q1 and can also be assigned to *Hipparion* cf. *forstenae*. Finally, the skull and the metapodials from Gülpinar preserve all the characteristics of the Samos specimens and could be assigned to the same species.

10. The *Hipparion macedonicum – Hipparion nikosi* Lineage

It is an easily recognized lineage, because it includes small-sized hipparionine species. It has representatives from the MYT and MTLA-B localities. The morphology of this hipparion cluster is included in the "*Cremohipparion*" genus by BERNOR et al. (1996b) and ZOUHRI & BENSALMIA (2005), or to the *Hipparion mediterraneum* group by WATABE (2004) and FORSTÉN (1983). BERNOR et al. (1996b, c) recognized two distinct lineages in the "*Cremohipparion*" assemblage, the "*Cremohipparion*" *macedonicum* - "*Cremohipparion*" *nikosi* lineage and the "*Cremohipparion*" *moldavicum* - "*Cremohipparion*" *mediterraneum* - "*Cremohipparion*" *proboscideum*" lineage, both having their origin in the "*Hippotherium*" group. According to BERNOR et al. (1996c), the "*Cremohipparion*" *macedonicum* - "*Cremohipparion*" *nikosi* lineage possibly is an early distinction from the "*Cremohipparion*" *moldavicum* morphology, which in turn follows a distinct evolutionary process, resulting in small-sized forms. In the formerly mentioned evolutionary process, the evolved species are the following:

Hipparion moldavicum (GROMOVA, 1952)

Type Species: Partial skull PIN 1256/3639 Palaeontological Institute of Science Academy, USSR
Type Locality: Taraklia, Ukraine.
Age: Early - middle Turolian, MN 11-12 (Late Miocene).
Remarks: It is considered as the most primitive member of this evolutionary lineage (BERNOR et al. 1996a, c). It was created by GROMOVA (1952) and is characterized by its medium size (skull length almost 379 mm), elongated muzzle, short tooth row (121-141 mm) and single elongated and deep POF, which is placed moderately far from the orbit (20-28 mm) (GROMOVA, 1952). The narial opening is short (nasal notch in front of P2), and the upper cheek teeth have an oval protocone and moderate enamel plication. The metapodials are slender (GROMOVA, 1952). The species has also been described from Novo-Elizavetovka (NOVOEL) (GROMOVA, 1952), Cherevichnoe (CHERE) (FORSTÉN & KRAKHMALNAYA, 1997) and Novaya Emetovka-2 (NOVAEM) (KRAKHMALNAYA & FORSTÉN, 1998).

The first record of *Hipparion moldavicum* from the Black Sea area was that from middle Maragheh (MMRG) (BERNOR, 1985). In the original species description BERNOR (1985) added the subtriangular, anteroposterior oriented, dorsoventrally deep and high, all around well-expressed POF. Furthermore, he mentioned that the POF is sometimes egg- or pear-shaped, posteriorly pocketed with an often distinct anterior rim. The Akkaşdaği area, Central Turkey, is another region occupied by the species during middle Turolian, MN 12. The *Hipparion moldavicum* sample from Akkaşdaği is more or less similar to those from Maragheh and Taraklia (KOUFOS & VLACHOU, 2005). The earliest appearance of the species is probably that from MMRG (8-8.2 My) and the youngest that from the Black Sea area, probably from Cherevichnoe, dated to late Turolian (MN 13) (FORSTÉN & KRAKHMALNAYA, 1997).

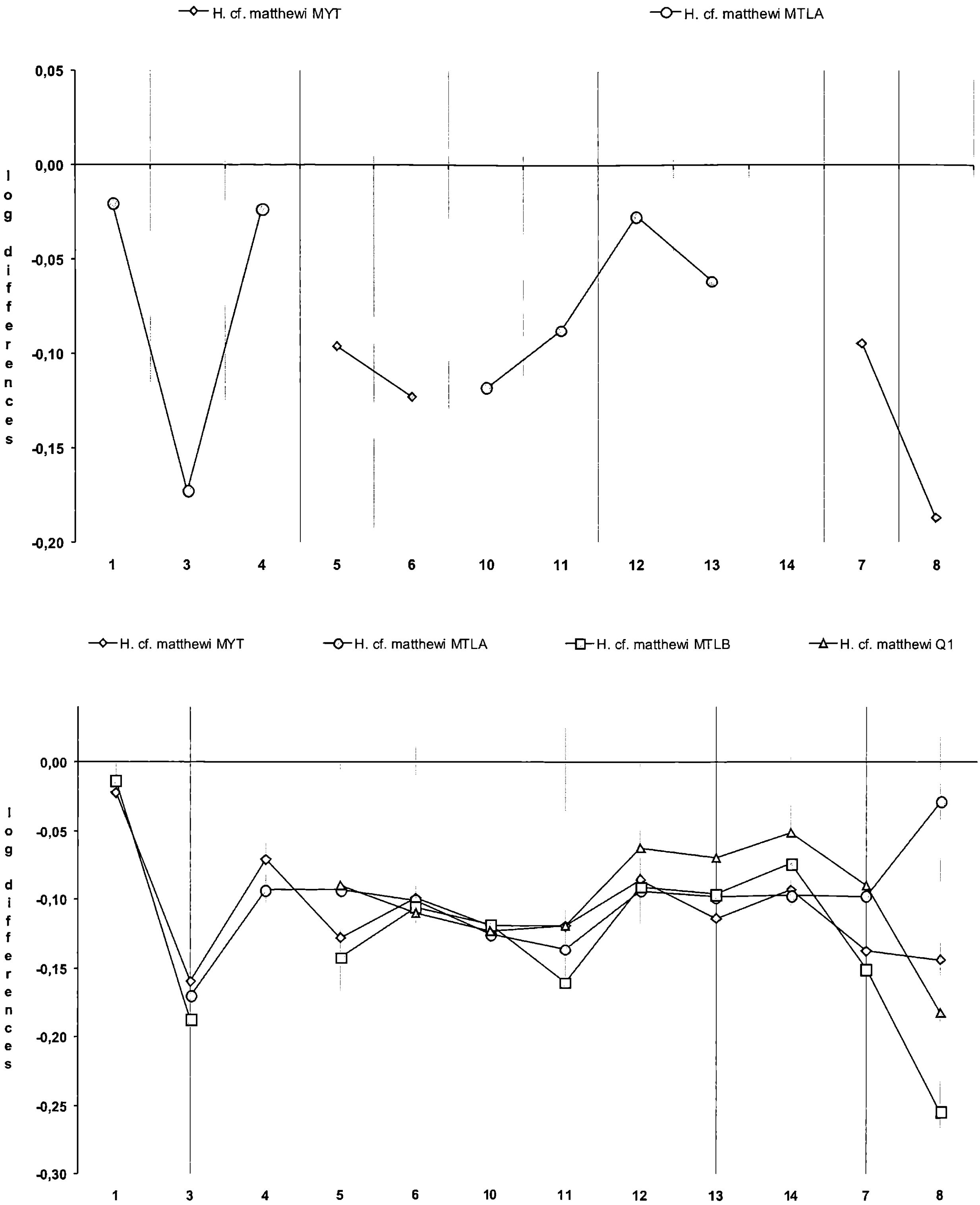

Figure 30: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H.* cf. *matthewi* from different Samos localities. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (Bernor et al., 1997).

Hipparion macedonicum KOUFOS, 1984

Type Species: Mandibular fragment, RPl-21; Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, Greece.
Type Locality: Ravin de la Pluie (RPl), Axios Valley, Northern Greece.
Age: Vallesian - Turolian, MN 9-12 (Late Miocene).

Remarks: *Hipparion macedonicum*, although more evolved in the facial morphology than *Hipparion moldavicum*, has older records. The first taxon appearance is the Vallesian (MN 10) localities of Axios Valley, "Pentalophos-1" (PNT) (MN 9/10) and "Ravin de la Pluie" (RPl) (MN 10) (Koufos, 1984, 2000b). Further occurrences of *Hipparion macedonicum* are those from the Turolian localities of Axios Valley (RZO, PXM, VTK) and the neighbouring area (NKT, NIK, PER) (Koufos, 1987a, b, 1988a, 2000a; Vlachou & Koufos, 2006). Outside of Greece, it is only known by some isolated teeth and a few postcranial remains from Montredon, France (MN 10) (Eisenmann, 1988). The *Hipparion macedonicum* morphology is clearly distinct from that of *Hipparion moldavicum* and it is more evolved, being smaller in size, with a noticeably less pronounced and always subtriangular POF and significantly smaller and more slender metapodials (Vlachou & Koufos, 2006).

Hipparion matthewi Abel, 1926

Type Species: Complete skull associated with the mandible, OK/557, Hungarian Geological Survey.
Type Locality: Samos, unknown locality.
Age: Middle - ?late Turolian, MN 12-?13 (Late Miocene).

Hipparion nikosi Bernor & Tobien, 1989

Type Species: Partial skull, BSPM 1899 VII31b, Bayerische Staatssammlung für Pälaontologie und Historische Geologie, München, Germany.
Type Locality: Samos, unknown locality.
Age: ?Middle - Late Turolian, MN ?12-13 (Late Miocene).
Remarks: *Hipparion matthewi* originates from Samos, but the type locality is unknown (Sondaar, 1971). It only differs from *Hipparion macedonicum* in having a slightly smaller size and a narrower muzzle (Vlachou & Koufos, 2006).

Hipparion matthewi is restricted to the Eastern Mediterranean region. It has been described from Greece, Samos, Q5 (Sondaar, 1971) and Axios Valley, DTK (Koufos, 1988b), from FYR of Macedonia, Titov Veles (Forstén & Garevsky, 1989) and from Turkey, Kemiklitepe A-B (Koufos & Kostopoulos, 1994) and Sazak (Kaya, 1993), covering the time span from middle to late Turolian (MN 12 - MN 13).

Sondaar (1971) assigned seven skulls from Q5 and several metapodials to *Hipparion "matthewi"* The skulls are comparable in size and POF complex morphology to the type skull of *Hipparion matthewi,* but they clearly differ from it in the absence of the POF anterior rim and the retraction of the nasal notch above the anterior aspect of P^3 to P^3-P^4 level.

Bernor & Tobien (1989), describing the skull BSPM-1899 VII31b from Samos (unknown locality), created the new species *Hipparion nikosi,* considering that the difference between the typical *Hipparion matthewi* and the BSP 1899 VII31b specimen is the position of the nasal notch (most anterior of P^2 and the mesostyle of P^4, respectively). At the same time, they assigned the small-sized skulls from Q5 to a hipparion form with an intermediate morphology between the typical *Hipparion matthewi* and *Hipparion nikosi*. Vlachou & Koufos (2006) concur that the skull morpholgy of the Q5 sample is closer related to *H. nikosi* and that it should be integrated into this species.

In the Balkans, *Hipparion matthewi* was recognized from the Titov Veles area (FYR of Macedonia) (Forstén & Garevski, 1989) and the Axios Valley locality DTK, Greece (Koufos, 1988b). In FYR of Macedonia, the small-sized hipparion was represented by several skulls and numerous postcranial elements. The skulls resemble the type of *Hipparion matthewi* in the narrow and short muzzle, the subtriangular and shallow POF, which is placed 22.5-35 mm away from the orbit (Forstén & Garevski, 1989:fig. 1) and in the occlusal teeth morphology. They are distinguished from it by the enlarged narial opening. In most cases, the nasal notch is situated above P^2-P^3 (Forstén & Garevski, 1989). The metapodials are slender and elongated, similar to the sample from Q5, as well as to the *Hipparion macedonicum* samples from the various localities of Greece (Forstén & Garevski, 1989). All the above characteristics place the small-sized hipparion from Titov Veles close to the small-sized hipparion from Q5, and consequently to *Hipparion nikosi*.

Hipparion matthewi from DTK is represented by a partly preserved skull and few postcranial remains. The short narial opening (nasal notch in front of P2) place the DTK sample very close to the typical *Hipparion matthewi* morphology. On the other hand, the wide and relatively elongated muzzle also links the DTK skull with *Hipparion macedonicum.*

Hipparion matthewi from Sazar is represented by a juvenile mandibular fragment and a set of tarsals, astragalus and calcaneum, similar in size to *Hipparion macedonicum* from RZO (Kaya, 1993). In KTA-B the species is represented by a few mandibular fragments and some more postcranial remains (Koufos & Kostopoulos, 1994). The mandible resembles the mandible of the type specimen of *Hipparion matthewi* in size and morphology (Vlachou & Koufos, 2006). The skull is missing from KTA-B and the postcranials can be ascribed to *Hipparion macedonicum,* not only by their size, but also by their morphology (Vlachou & Koufos, 2006). Hence, the KTA-B material could be referred either to *Hipparion matthewi* or to *Hipparion macedonicum*.

For a long time, all the small-sized hipparions of the Eastern Mediterranean were referred to *Hipparion matthewi*. *Hipparion matthewi* is known only by a single skull. But the skull morphology is overlapping with the morphology of *Hipparion macedonicum,* and the two species could be synonymous. But the solely known specimen of *Hipparion matthewi* and the absence of certain stratigraphic data for the type specimen of *H. matthewi*, make the synonymy somewhat dubious, and for this reason we prefer to keep *Hipparion matthewi* as a separate species at the moment, until being able to collect new material from Samos for reliable results.

Systematics of the Material

Hipparion cf. *matthewi*

(Plates 11, 12)

Localities: Mytilinii-1A, B (MTLA, MTLB), Adrianos ravine, Mytilinii Basin, Samos, Greece; Mytilinii-3 (MYT), Potamies ravine, Mytilinii Basin, Samos, Greece; Quarry-1 (Q1), Adrianos ravine, Mytilinii Basin, Samos, Greece.

Age: Middle Turolian, MN 12 (late Miocene).
Mytilinii-1A, B (MTLA, B), Quarry-1 (Q1): ~7.1 Ma.
Mytilinii-3 (MYT): ~7.3 Ma.

Material:

MYT: Distal part of humerus MYT-33, 109, 107; proximal part of radius, MYT-116, 106; distal part of radius MYT-105; proximal part of MCIII, MYT-98; tibia, MYT-50, distal part of tibia, MYT-127, 104, 10; astragalus, MYT-113; calcaneum, MYT-119; MTIII, MYT-52, 54, proximal part of MTIII, MYT 99, 9; distal part of MTIII MYT-36.

MTLA: Partial skull, MTLA-422; maxillary fragment withP2-M3 (dex), MTLA-326, mandible, MTLA-77; distal part of radius, MTLA-432, 430, 436, MCIII, MTLA-32, distal part of MCIII, MTLA-32; tibia, MTLA-105; distal part of tibia, MTLA-257; astragalus, MTLA-397, PMM-29; MTIII, MTLA-30; proximal part of MTIII, MTLA-225, 505; distal part of MTIII, MTLA-380.

MTLB: Distal part of humerus MTLB-nn; distal part of radius, MTLB-147; tibia, MTLB-314; proximal part of tibia, MTLB-255; distal part of tibia, MTLB-29, 282; MTIII, MTLB-263; PHI+PHII, MTLB-379.

Q1: MCIII, AMNH-20665Q, MTIII, 20663A, 23043D; proximal part of MTIII, AMNH-94483; distal part of MTIII, AMNH-Bx35-BI5.

Short diagnosis: Small size, tooth row length no more than 125 mm; relatively elongated and wide muzzle; nasal notch in front of P2; subtriangular, shallow POF, moderately marked all around, posteriorly unpocketed; POB short; cheek teeth simply plicated, elliptical protocone, simple to double pli caballin; elongated and slender metapodials.

Description:

New material: MTLA-422 is the only preserved skull among the small-sized newly collected material from Samos, and consequently the skull description is based on it. The skull lacks the opisthocranion and the facial region is slightly deformed. The muzzle is short and narrow, the nasal notch is situated just in front of P^2 and the POB is short. The POF, although slightly deformed, seems to be shallow subtriangular in shape, moderately marked all around and posteriorly unpocketed. The cheek teeth are in the last stage of wear and the occlusal surface is completely worn. The maxillae MTLA-326 belongs to an adult semi-aged individual and completes the description of the small-sized hipparion concerning the occlusal cheek teeth morphology. The teeth are simply plicated (10 plis in M^1), the protocone is elliptical in form and the pli caballin is single. The mandible (MTLA-77) has been correlated to the small-sized skull and is characterized by a rounded metaconid and an elliptical to angular metastylid. There is no pli caballinid, the ectoflexid is shallow in the premolars, deeper in molars and the protostylid is often moderately developed in the premolar and the first molar. The small hipparion of MYT and MTLB is represented by postcranial elements only, which are similar to those of MTLA. All are similarly slender and the metapodials seem elongated. The small number of specimens does not allow an extended morphological comparison. The robusticity index is 11.5-12.5 for the MTIII and falls into the range of variation of *Hipparion macedonicum* from Continental Greece, which is 10.9-12.8.

Old material: The small-sized hipparion is the lesser represented species in Q1, and there are postcranial remains only. The metapodials are fragmentary and similar in size to those from MTLA and MTLB.

Comparisons

The skull MTLA-422 resembles the type of *Hipparion matthewi* in size and morphology, as well as *Hipparion macedonicum*. The muzzle is shorter and narrower than that of the *Hipparion macedonicum* sample and comparable to the *Hipparion matthewi* morphology. The rest of the available measurements are similar to the samples of both species (Fig. 28).

The POF depth is reduced compared to that of *Hipparion moldavicum*, while the nasal notch is placed just in front of P^2, excluding the Q5 small-sized hipparion, *Hipparion nikosi*, from the possibly attributed species. The tooth row length is very close to that of *Hipparion matthewi* and *Hipparion macedonicum*, but smaller than that of *Hipparion moldavicum* (Fig. 28). The occlusal surface morphology is more or less comparable to all above cited taxa, *Hipparion matthewi*, *Hipparion macedonicum* and *Hipparion moldavicum* (Vlachou, in prep).

In Fig. 29, which compares the mandibles of *Hipparion matthewi*, *Hipparion macedonicum* and *Hipparion moldavicum* from various localities with the MTLA specimen, the last specimen closely resembles the morphology of *Hipparion matthewi* and *Hipparion macedonicum*, but it apparently has a somewhat increased size, although it is always smaller than *Hipparion moldavicum* (Fig. 29). The muzzle length is similar to that of *Hipparion matthewi*, but the index M2/M7 is equally comparable to both *Hipparion matthewi* and *Hipparion macedonicum*. The short symphysis (M13) also distinguishes the MTLA specimen from the *Hipparion moldavicum* sample (Fig. 29).

The metapodials from MYT, MTLA, MTLB and Q1 are slender and elongated, without significant differences which enforce the distinction of the sample into different hipparion species (Fig. 30). Among the four samples, the MYT sample seems to have the most primitive morphology in the reduced total MTIII length, the slightly increased midshaft width, the smaller distal articular width and the somewhat increased distal articular depth (Fig. 30B).

In comparison to the *Hipparion macedonicum*, *Hipparion matthewi* and *Hipparion moldavicum* metapodial samples, the studied specimens group better with *Hipparion macedonicum* from Continental Greece and *Hipparion matthewi* from KTA-B. The MCIII sample from MYT, MTLA and Q1, despite the size similarities with *Hipparion moldavicum* from various localities, resembles the pattern of the *Hipparion macedonicum* and *Hipparion matthewi* samples,

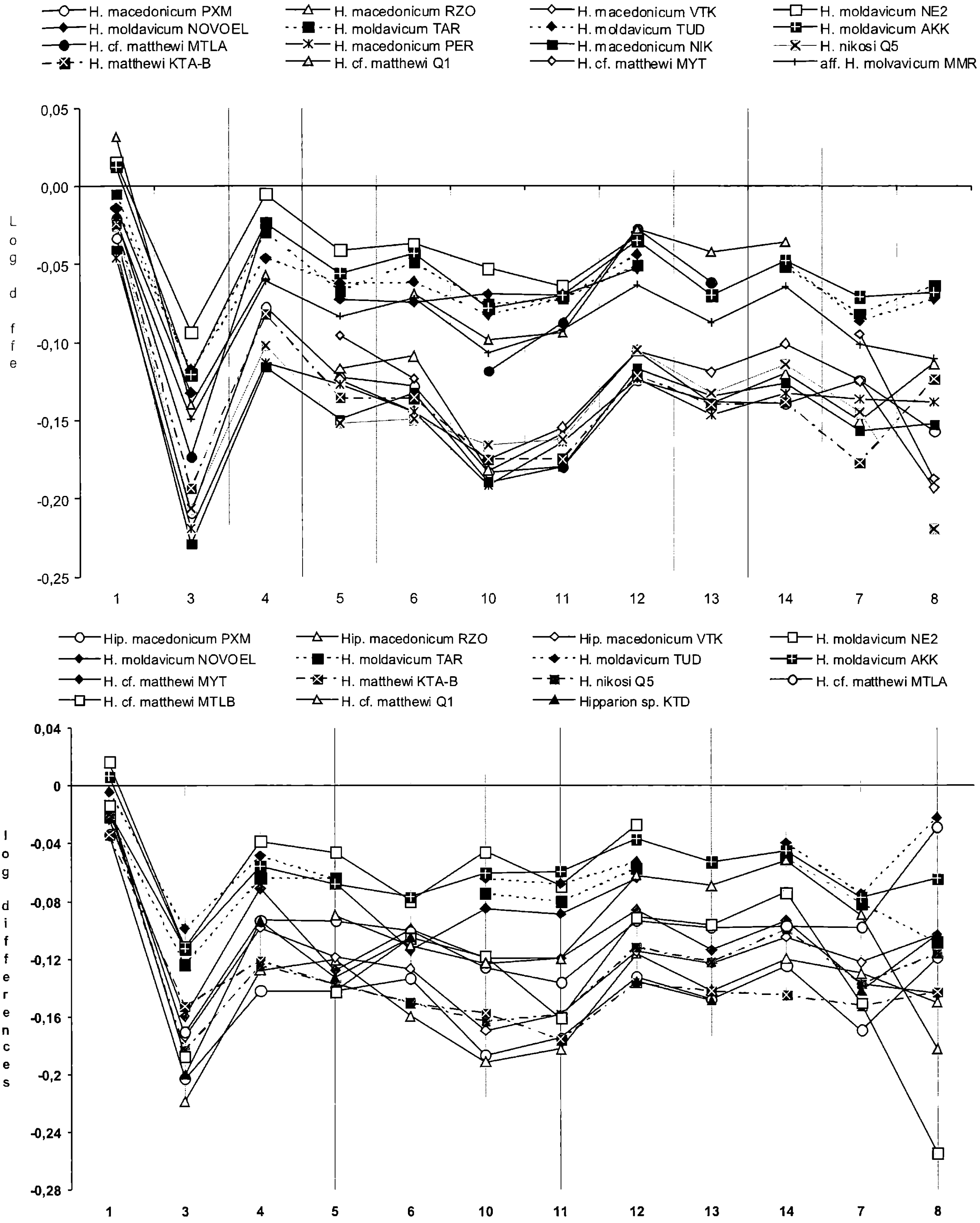

Figure 31: Logarithmic ratio diagram comparing the metacarpal (above) and metatarsal (below) of *H.* cf. *matthewi* from different Samos localities with *H. macedonicum* from Greece, *H. moldavicum* from TAR, NOVOEL, TUD, AKK and MMRG and *H. nikosi* from Q5. Standard: *H. primigenium*, Höwenegg, MCIII, n = 10-16; MTIII, n = 16-24 (BERNOR et al., 1997).

in which the length (M1) is increased in relation to the midshaft width (M3) (Fig. 31A). The MTIII sample from the Samos localities is smaller than that of *Hipparion moldavicum*, although larger than *H. macedonicum*, but similar to the MCIII morphology, it is more slender than *H. moldavicum* (Fig. 31B). The small-sized metatarsal from the KTD referred to as *Hipparion* sp. is included in the size and the morphology of the *Hipparion matthewi* and *Hipparion macedonicum* samples. Actually, it is similar to the MYT and *Hipparion macedonicum* samples, but it is also comparable to *Hipparion matthewi* from KTA-B in the general morphology, as well as in the proximal articular width (M5) and the distal articular depth (M12-14) (Fig. 31B). The result of the above comparisons is that the small hipparion from MYT, MTLA, MTLB and Q1 is comparable to *Hipparion matthewi* from KTA-B and probably from KTD but also very close to the Turolian *Hipparion macedonicum* morphology.

All the data supports the presence of a small-sized hipparion better ascribed to *Hipparion matthewi* in the middle Turolian horizons of Samos. At the uppermost stratigraphic level, the species probably evolved in the retraction of the nasal notch above P^3, and was finally replaced by *Hipparion nikosi* during late Turolian. The disadvantage of this approach are the doubts about the skeletal morphology and the origin of the typical *Hipparion matthewi*. For this reason, the MYT, MTLA, MTLB, Q1 small-sized hipparion is referred to as *Hipparion* cf. *matthewi*.

11. Biochronology

Based on all available taxonomic data, as well as on the stratigraphic distribution of the hipparionine horses on Samos and in the Eastern Mediterranean region, the occurring hipparion lineages provide the following information:

The *Hipparion giganteum* - *Hipparion brachypus* lineage

The primitive member of this lineage, *Hipparion giganteum*, originated from the Black Sea area and, up to now, has not been depicted either in the Samos fauna or in the surrounding area. *Hipparion brachypus* is the predominant species in the Eastern Mediterranean region, and its first record is that from Q4, dated between 7.3-7.1 Ma (Koufos et al., this volume). *Hipparion brachypus* has also been recorded from AKK (Koufos & Vlachou, 2005) with certainity, while its presence in the Maragheh fauna is questionable (Vlachou, in prep). The species has also been found in the Balkans (PIK and HD) and despite the morphological affinities to the eastern form, it is smaller-sized.

The *Hipparion proboscideum* - *Hipparion mediterraneum* lineage

Hipparion proboscideum appeared in the Samos fauna in the Qx locality, dated to 7.6-8.0 Ma (Koufos et al., this volume) and exists up to the upper fossil level (MTLA-B, Q1), dated to ~7.1 Ma. The most primitive form of *Hipparion proboscideum* is that from RZO, dated approximately to 8.2 Ma (Koufos, 1987; Sen et al., 2000). *Hipparion proboscideum* evolved in Continental Greece and developed the *Hipparion mediterraneum* morphology, traced in Perivolaki (PER) during middle Turolian, at 7.3-7.1 Ma (Koufos et al., 2006). On Samos, *Hipparion proboscideum* possibly evolved to a more robust skeleton build, but without significant changes in the facial morphology. Outside of Greece, *Hipparion proboscideum* is recorded from KTD (MN 11) and KTA-B (MN 12) (Turkey) and probably from Titov Veles (FYR of Macedonia), middle Maragheh level (Iran) as well as from Romania (Vlachou, in prep.), but not from the peri-Pontic region.

The *Hipparion prostylum* - *Hipparion dietrichi* lineage

It is the most common lineage in all Eastern Mediterranean localities. The primitive morphology of this lineage is described from the lower levels of the Samos faunal succession, MLN and Q6. *Hipparion prostylum* might also have occurred in the Kemiklitepe fauna, KTA-B, KTD (MN 11) and MMRG (MN 11) (Bernor at al., 1996a). During middle Turolian and soon after 7.3 Ma (Q4) it seems to be replaced by *Hipparion dietrichi*, which existed until late Turolian (level of Q5). *Hipparion dietrichi* morphology was also found in AKK, but possibly with a more evolved skeleton pattern, and was described as *Hipparion* cf. *longipes*. A similar morphology has been described from Pavlodar (MN 12/13), also was described as *Hipparion* cf. *longipes*.

The *Hipparion verae* - *Hipparion forstenae* lineage

Hipparion forstenae is the only member of the lineage recognized in the Samos fauna. It is possibly higher evolved than *Hipparion verae* in the deeper narial opening and the less pronounced POF on the facial region. The first certain record of this lineage in the Samos fauna is that of *Hipparion* cf. *forstenae* from MTLA and Q1. In MYT, the species is only represented by postcranial remains. Its skull morphology is unknown, but judging from the metapodial morphology, is more evolved than that of *Hipparion verae*. The species might also be present in AKK (MN 12) and Gülpinar (MN 12).

The *Hipparion macedonicum* - *Hipparion nikosi* lineage

Up to now, the small-sized hipparions from Samos were referred to as *Hipparion matthewi*. We cannot refute the presence of *Hipparion matthewi* in the Samos fauna, but it is also difficult to prove, because of the scanty available material. At the moment, we believe that it is better to ascribe the small-sized hipparions from Samos to *Hipparion* cf. *matthewi*. More material would help us understand the morphology of *Hipparion matthewi* and besides, its relationship to *Hipparion macedonicum*.

According to the present data, the first appearance of *Hipparion* cf. *matthewi* in the Samos fauna is at MYT, dated to ~7.3 My. The number of specimens increases in the younger localities MTLA, MTLB and Q1. We also have the impression that its size is also increasing with time, but the available material is not enough to confirm it. During late Turolian, *Hipparion* cf. *matthewi* is possibly replaced by the more evolved *Hipparion nikosi*, concerning the depth of the narial opening and the smaller size. The *Hipparion matthewi* morphology was also traced in the KTD and KTA-B localities. The territory defined by the Maragheh and Akkaşdaği localities seems to be occupied by the species *Hipparion moldavicum*. The phylogenetic relationship of *Hipparion moldavicum* and *Hipparion macedonicum* needs further study. We believe that the data does not support the theory that *H. macedonicum* is related to *H. moldavicum*. *Hipparion "minus"* from Sebastopol (MN 10), *Hipparion macedonicum* from PNT and RPl, Axios Valley, Creece (MN 9-10), as well as *Hipparion macedonicum* from Montredon, France (MN

10), are the earliest appearances of *Hipparion macedonicum*. Instead of *Hipparion macedonicum*, *Hipparion moldavicum* is recorded from the Black Sea region, MMRG and AKK, while an earlier stratigraphic appearance is that from MMRG (8.0-8.2 Ma) (MN 11) (BERNOR et al., 1996a). If we consider that *Hipparion moldavicum* derives from the *Hipparion primigenium* early stratigraphic group, and that *Hipparion macedonicum* is older than *Hipparion moldavicum*, then the morphology of the former species must include several primitive characteristics. This is not the case and makes us suspicious about the origin of *Hipparion macedonicum*. Two hipparion morphologies co-exist in Eurasia during Vallesian, the *Hipparion primigenium* and the *Hipparion macedonicum* morphology. The features of *Hipparion moldavicum* support a possible origin from the *Hipparion primigenium* morphology, while those of *Hipparion matthewi* and *Hipparion nikosi* derive from *Hipparion macedonicum*.

In our opinion, the two morphologies, *H. primigenium* and H. macedonicum, maybe do not converge backwards to the same *Cremohipparion* species. It is quite possible that more than one species migrated from Northern America to Eurasia. However, this issue needs more discussion and is beyond the aim of this paper.

12. Conclusions

The study of the new hipparion material from Samos and its correlation with the data from the old collections allow the recognition of the seven following taxa (table 1):

Q5: *H. nikosi*, *Hipparion* sp. I (large-sized), *Hipparion* sp. II (large-sized), ?*H. dietrichi*, *H.* cf. *forstenae*
Q1, MTLA & MTLB: *Hipparion* cf. *matthewi*, *Hipparion* cf. *proboscideum*, *Hipparion brachypus*, *Hipparion dietrichi*, *Hipparion* cf. *forstenae*
Q4: *Hipparion* cf. *matthewi*, *Hipparion brachypus*, *Hipparion dietrichi*
MYT: *Hipparion* cf. *matthewi*, *Hipparion* cf. *proboscideum*, *Hipparion* cf. *forstenae*, *Hipparion prostylum*
Q6: *Hipparion prostylum*, *Hipparion* sp. (aff. *Hipparion proboscideum*)
MLN: *Hipparion* sp. (aff. *H. prostylum*), *Hipparion* sp. (aff. *Hipparion proboscideum*)
Qx: *Hipparion proboscideum*

The aforementioned species are arranged in three successive assemblages:

- *Hipparion prostylum* and *Hipparion* cf. *proboscideum*, described from MLN, Qx, Q6 and MYT, corresponding to the end of early Turolian - beginning of middle Turolian.
- *Hipparion dietrichi*, *Hipparion* cf. *proboscideum*, *Hipparion brachypus*, *Hipparion* cf. *matthewi* and *Hipparion* cf. *forstenae*, from Q4, MTLA, MTLB, Q1, corresponding to middle Turolian, and
- *Hipparion dietrichi*, *Hipparion* sp. I, *Hipparion* sp. II., *Hipparion nikosi* and *Hipparion* cf. *forstenae* from Q5, corresponding to the middle - late Turolian. The proposed taxonomic and biostratigraphic resolution is partly different from previous approaches especially in the recognition of *Hipparion* cf. *forstenae* instead of *Hipparion mediterraneum* or *Hipparion dietrichi* type B and indicates a clear evolution of the Samos hipparion assemblage over time, evidently defined by environmental changes. The Samos hipparion assemblages, despite the differences, are better correlated to those from Turkey and Iran. At the same time, they clearly differ from those of Continental Greece in the biodiversity. No locality in Continental Greece includes more than three hipparion species. Furthermore, the taxa appeared in both areas, and even the morphological similarities provide us with differences in the body mass and the skeleton pattern.

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Appendix

Distribution of characteristics in the Samos *Hipparion* skulls and mandibles:

1. **Size**: A. small, B. moderate, C. large
2. **Relation of the lacrimal to the preorbital fossa**: A. lacrimal large, rectangularly shaped, invades medial wall and posterior aspect of preorbital fossa; B. lacrimal reduced in size, slightly invades or touches posterior border of preorbital fossa; C. preorbital bar (POB) long, with the anterior edge of the lacrimal placed more than half the distance from the anterior orbital to the posterior rim of the fossa; D. POB reduced slightly in length, but with the anterior edge of the lacrimal placed more than ½ the distance from the anterior orbital rim to the posterior rim of the fossa; E. POB reduced slightly in length, but with the anterior edge of the lacrimal placed almost at ½ the distance from the anterior orbital rim to the posterior rim of the fossa; F. POB very long, with the anterior edge of the lacrimal placed less than ½ the distance from the anterior rim to the posterior rim of the fossa; G. POB absent.
3. **Muzzle morphology**: A. short (<100 mm) and broad; B. short (<100 mm) and narrow, C. elongated (>100 mm) and broad; D. elongated and narrow;
4. **POB**: A. short, B. moderate, C. long
5. **Preorbital fossa shape**: A. large ovoid shape; B. subtriangular shaped; C. rounded structure D. subquadrangular shaped; E. vestigial but with a C-shaped or egg-shaped outline; F. elongate; G. absent.
6. **POF orientation**: A. ANT/VENTR = anteroventrally; B. ANT/POST = anteroposterior; C. intermediate position
7. **Fossa posterior pocketing**: A. deeply pocketed, greater than 15mm in deepest place; B. pocketing reduced, moderate to slight depth, less than 15 mm; C. not pocketed, but with a posterior rim; D. absent, no rim, but a remnant depression.
8. **Fossa medial depth**: A. deep, greater than 15 mm in deepest place; B. moderate depth, 10-15 mm in deepest place; C. shallow depth, less than 10 mm in deepest place; D. absent.
9. **Preorbital fossa medial wall morphology**: A. without internal pits, b. with internal pits
10. **Fossa peripheral border ouline**: A. strong, strongly delineated around entire periphery; B. moderately delineated around periphery; C. weakly defined around periphery; D. absent with a remnant depression; E. absent, no remnant depression.
11. **Ventral rim - facial crest distance**: A. long; B. moderate; C. short.
12. **Anterior rim morphology**: A. present; B. absent; C. vestigial
13. **Placement of infraorbital foramen**: A. placed distinctly ventral to approximately ½ the distance between the preorbital fossa's most anterior and most posterior extent; B. inferior to, or encroaching upon anteroventral border of the preorbital fossa; A+ placed distinctly ventral at more than ½ the distance between the preorbital fossa's most anterior and most posterior extent; C. in front and out of the POF.
14. **Caninus (intermediate) fossa**: A. absent; B. present
15. **Nasal notch position**: A. at posterior border of canine or slightly posterior to canine border; B. approximately half the distance between canine and P^2; C. at or near the anterior border of P^2; D. above P^2; E. above P^3; F. above P^4; G. above M^1; H. posterior to M^1.
    choane position
16. **Presence of dP1**: A. persistent and functional; B. reduced and non-functional; C. absent
17. **Curvature of maxillary cheek teeth**: A. very curved; B. moderately curved; C. straight
18. **Maximum cheek tooth crown height**: A. < 30 mm; B. 30-40 mm; C. 40-60 mm; D. 60-75 mm; E. 75+ mm maximum crown height
19. **Maxillary cheek tooth fossette ornamentation**: A. complex with several deeply amplified plications; B.

moderately complex with fewer, more shortly amplified, thinly banded plications; C. simple complexity with few, shortly amplified plications; D. generally no plis; E. very complex.

20. **Posterior wall of postfossette**: A. may not be distinct; B. always distinct
21. **Pli caballin morphology**: A. double, B. single or occasionally poorly defined double; C. complex; D. plis not well formed.
22. **Hypocone lingual groove**: A. deep, may occasionally isolate hypocone; B. moderately deep; C. shallow; D. only in M^3; E. absent.
23. **Protocone shape**: A. round q-shape; B. oval q-shape; C. oval; D. elongate-oval; E. lingually flattened-labially rounded; F. compressed or ovate; G. rounded; H. triangular; I. triangular elongate; J. lenticular; K. triangular with rounded corners.
24. **Isolation of protocone**: A. connected to protoloph; B. isolated from protoloph; C. isolated from protoloph except P2.
25. **Protoconal spur**: A. elongate, strongly present; B. reduced, but usually present; C. very rare to absent.
26. **Premolar protocone/hypocone alignment**: A. anteroposteriorly aligned; B. protocone more lingually placed
27. **Molar protocone/hypocone alignment**: A. anteroposteriorly aligned; B. protocone more lingually placed
28. **P2 anterostyle**: A. elongated; B. short and rounded
29. **P2 paraconid**: A. elongated; B. short and rounded
30. **Mandibular incisor morphology**: A. not grooved; B. grooved
31. **Mandibular incisor curvature**: A. curved; B. straight
32. **I3 lateral aspect**: A. elongate, not constricted labiolingually; B. very elongate, distally labiolingually constricted; C. atrophied
33. **Premolar metaconid**: A. rounded; B. elongated; C. angular on distal surface; D. irregular-shaped; E. squarely shaped; F. pointed
34. **Molar metaconid**: A. rounded; B. elongated; C. angular on distal surface; D. irregular-shaped; E. squarely shaped; F. pointed
35. **Premolar metastylid**: A. rounded; B. elongated; C. angular on proximal surface; D. irregular-shaped; E. squarely shaped; F. pointed
36. **Molar metastylid**: A. rounded; B. elongated; C. angular on proximal surface; D. irregular-shaped; E. squarely shaped; F. pointed
37. **Premolar ectoflexid**: A. does not separate metaconid and metastylid; B. separates metaconid and metastylid; C. converges with preflexid and postflexid to abut against metaconid and metastylid.
38. **Molar ectoflexid**: A. does not separate metaconid and metastylid; B. separates metaconid and metastylid; C. converges with preflexid and postflexid to abut against metaconid and metastylid.
39. **Pli caballinid P**: A. complex; B. rudimentary or single, C. absent.
40. **Pli caballinid M**: A. complex; B. rudimentary or single; C. absent.
41. **Protostylid**: A. a small poorly developed loop; B. a loop; C. a small, pointed projection continuous with the buccal cingulum; D. a strong projection continuous with the buccal cingulum; E. absent on occlusal surface, but may be on side of crown buried in cement
42. **Ectostylid**: A. present; B. absent, (px) = only in px
43. **Premolar linguaflexid**: A. shallow; B. deeper, V-shaped; C. shallow U-shaped; D. deep, broad U-shaped; E. very broad and deep.
44. **Molar linguaflexid**: A. shallow; B. deeper, V-shaped; C. shallow U-shaped; D. deep, broad U-shaped; E. very broad and deep.
45. **Preflexid morphology**: A. simple margins; B. complex margins; C. very complex
46. **Postflexid morphology**: A. simple margins; B. complex margins; C. very complex
47. **Postflexid invades metaconid/metastylid junction by most anterior postion bending sharply lingually**: A. no; B. yes

CHARACTER STATE DISTIBUTION OF SAMOS HIPPARIONINE SKULLS (NEW & OLD COLLECTIONS) & MLN MANDIBLE

	MORPHOLOGICAL CHARACTERS	MTLB-30	AMNH-22838	MTLA-422	MTLA-326	AMNH-22860	AMNH-20559A	AMNH-20598	AMNH-20596	AMNH-22787	AMNH-20997	AMNH-94907	AMNH-20598A	AMNH-20692	AMNH-20608	Q5 no number	AMNH-22832	MTLA-122	MTLB-31	MTLB-163	MTLB-167	MYT-4	MYT-22	MYT-92	MYT-94	MYT-91	AMNH-22990	AMNH-22987	MYT-45	MTLA-328	MTLA-414	M-4709	AMNH-20594	AMNH-20635	AMNH-20771	AMNH-20772	AMNH-22888	AMNH-22936	AMNH-22907A	AMNH-22908	AMNH-94906	AMNH-20625	AMNH-20628	AMNH-94905	AMNH-22787	AMNH-20626	MTLA-467	MTLA338	PMMS-9	MLN-20	AMNH-22988-Q6
1	Size	C	C	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	C	C	C	C	C	C	C	A	A	A	A	A	A	A	A	A	B	B	B	B	B	?
2	Relation of the lacrimal to the preorbital fossa		E	B		E	E		E	E	E			E						D							E			A		A	A		B		B	B						B	C	D	E	E	E	A	
3	Muzzle morphology		C	B		C	C	A	A		A			C						A							A					D			D	D		D	D	D	D		D	D			D	D	D		
4	POB	C	C	B		C	C	C	C	C	C	C		C						C							C					A	A		B	A	B	B	B	B	B	B	B	B	B	B	B	B	B		
5	POF shape	F	F	B		F	B	F	F	F	F	F		B						F							A					D				D	B	B	B	A	F	F	F	F	A	A	F	F	F		
6	POF orientation	B	B	B		A	A	A	A	A	A	C		C						A							C					A						B	B	B	A	A	A	A	B	C	A	A	A		
7	Fossa posterior pocketing	B	B	B		C	D	D	D	C	C	C		D						C							B					B						C	C	C	D	C	C	C	D	D	D	D	D		
8	Fossa medial depth	A	A	A		C	C	C	C	C	C	C		C						C							B					A						B	B	B	B	B	B	B	B	C	C	C	C		
9	Preorbital fossa medial wall morphology	A	A	C		B	B	B	B	B	B	B		B						A							A					A						C	C	C	A	A	A	A	C	B	A	A	A		
10	Fossa peripheral border ouline	A	A	A		C	C	C	C	C	C	C		C						C							B					A						B	B	B	C	C	B	B	B	C	C	C	C		
11	Ventral rim-facial crest distance	A	A	C		A	A	A	A	A	A	A		A						A							A					C						B	B	C	B	B	B	B	B	B	A	A	A		
12	Anterior rim morphology	A	A	B		C	C	C	C	C	A	C	A	C						B							A					A							C	C	A	A	A	A	A	A	A	A	A		
13	Placement of infraorbital foramen		C	B		B	B	B	B	B	B	B	B	B						B							B					B							B	B	B	B	B	B	B	B	C	C	C		
14	Caninus fossa	A	A	A		A	A	A	A	A	A	A	A	A	A					A							A					B							A	A	B	B	B	B	B	B	B	B	B		
15	Nasal notch position		D	C		C	C	C	C	C	C		C	C	C					C							C					E							E	E	E		E	E	E		D	D	D		
16	Presence of p1		C	C		C	C	C	C		C		C	C	B					C							C					C							C	C	C			B	C		B	C	C		
17	Curvature of maxillary cheek teeth																																																		
18	Maximum cheek tooth crown height																																																		
19	Maxillary cheek tooth fossette ornamentation	B	B		C	B			B	B	B	C		B	B	D	B		B	B		B	B	B	B	B	B		B	A	A	D	A	A																	
20	Posterior wall of postfossette	B	B		B	B			B	B	B	B		B	B	B	B		B	B		B	B	B	B	B	B		B	B	B	B	B	B																	
21	Pli caballin morphology	B	A		B	E			E	E	E	E		E	A	E	E		E	E		A	A	A	A	A	A		B	A	A	D	A	A																	
22	Hypocone lingual groove	D	D		D	D			D	D	D	D		D		D	E		E	D	D	D	D	D	D	D	D		D	D	D	E	D	D																	
23	Protocone shape	G	D		G	D	J	J	D	D	D	E	D	D	J	D	E		E	D	D	D	D	D	D	D	D	D	C	C	C	E	E	C	J									J							
24	Isolation of protocone	B	C		B	C	B	B	B	B	D	B	C	C	B	C	C		B		B	B	B	B	B	B	C	C	B	B	B	C	B	B	B									B							
25	Protoconal spur	C	C		C	C	C	C	C	C	C		C	C	C	C	C		C	C	C	C	C	C	C	C	C	C	B	C	C	C	C	C	C									C							
26	Premolar protocone/hypocone alignment	B	B		B	B	B	B	B	B	B		B	B	B	B	B		B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B										B							
27	Molar protocone/hypocone alignment	B	B			B	B	B	B	B	B		B	B	B	B	B		B	B	B	B	B	B	B	B	B		B	B	B	A	B	B										B							
28	P2 anterostyle	B	B		B	C	C	C	C		C		C	C	C	B	B		A	B	B	B	B	B	B	B	C		A	A	A	A	C	C										B							
29	P2 paraconid																																																		
30	Mandibular incisor morphology																																																		?B
31	Mandibular incisor curvature																																																		?B
32	I3 lateral aspect																																																		A
33	Premolar metaconid																																																		A
34	Molar metaconid																																																		A
35	Premolar metastylid																																																		C
36	Molar metastylid																																																		C
37	Premolar ectoflexid																																																		A
38	Molar ectoflexid																																																		C
39	Pli caballinid P																																																		B
40	Pli caballinid M																																																		B
41	Protostylid																																																	E	D(M/1)
42	Ectostylid																																																	A (p3)	B
43	Premolar linguaflexid																																																	B	B
44	Molar linguaflexid																																																		C
45	Preflexid morphology																																																	A	A
46	Postflexid morphology	?	?	?	?		?			?		?	?		?	?	?		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		?	?	?		?	?	?	?	?	?	?	?	?	?	A	A

PLATE 1

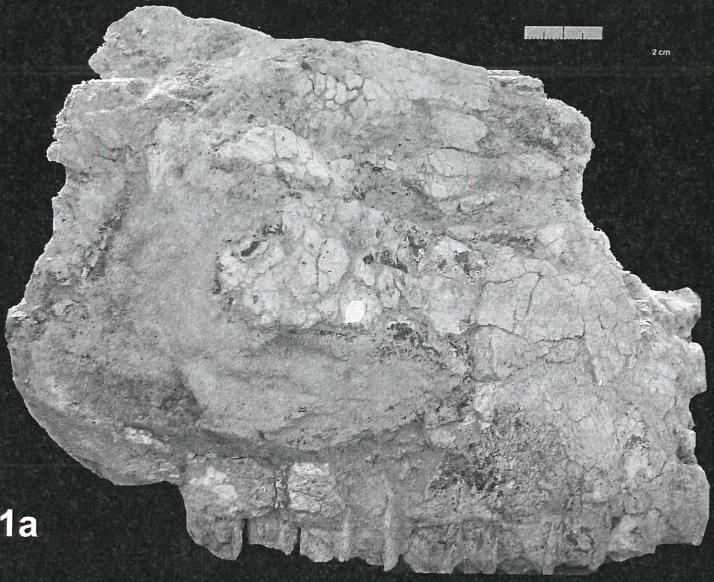
***Hipparion brachypus*, Mytilinii-1A-B (MTLA-B), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Partial skull, MTLB-30; a. lateral and b. occlusal view.

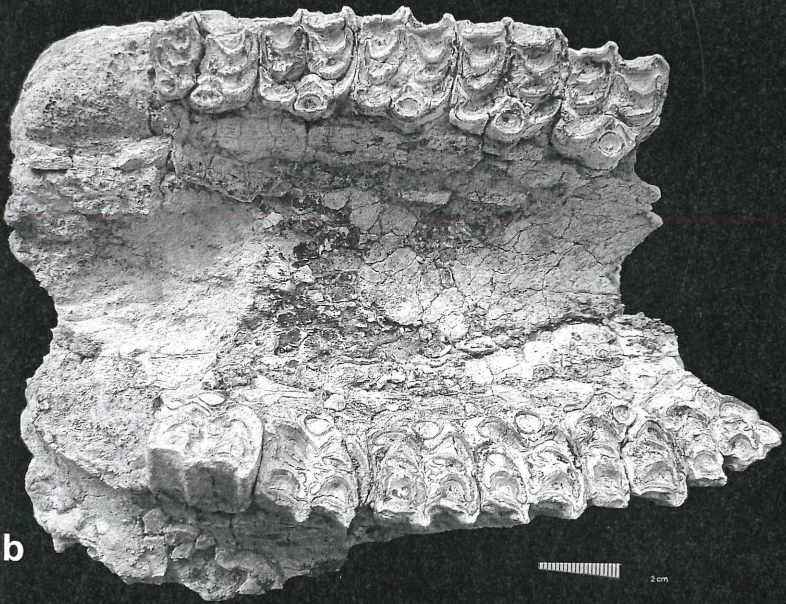
Fig. 2. Metatarsal, MTLA-500; a. anterior view, b. posterior view.

Fig. 3. Metacarpal, MTLA-402; a. anterior view, b. posterior view.

PLATE 1

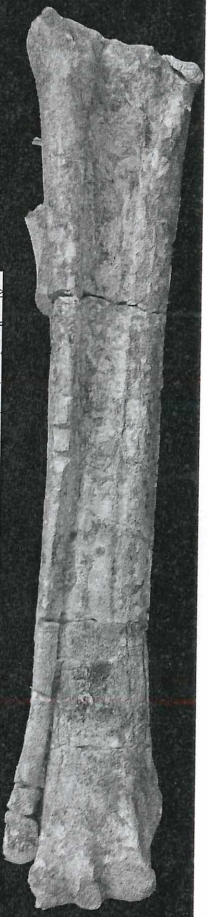


1a

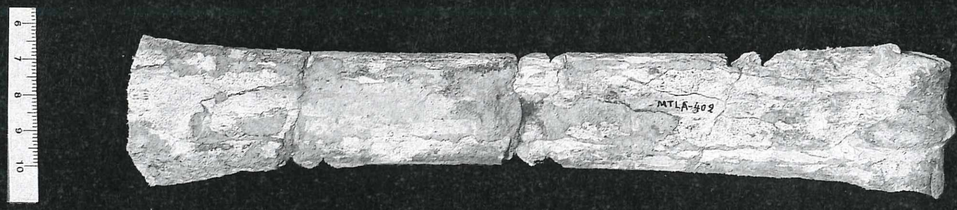


1b

2a



2b



3a

3b

PLATE 2

Hipparion cf. *proboscideum*, Mytilinii-1A, 3 (MTLA, MYT), Samos, Greece, Middle Turolian (MN 12).

Fig. 1. Partial skull, MTLA-328; a. lateral, b. occlusal view and c. left tooth row.

Fig. 2. Maxilla with both tooth rows, MYT-45: occlusal view.

PLATE 2

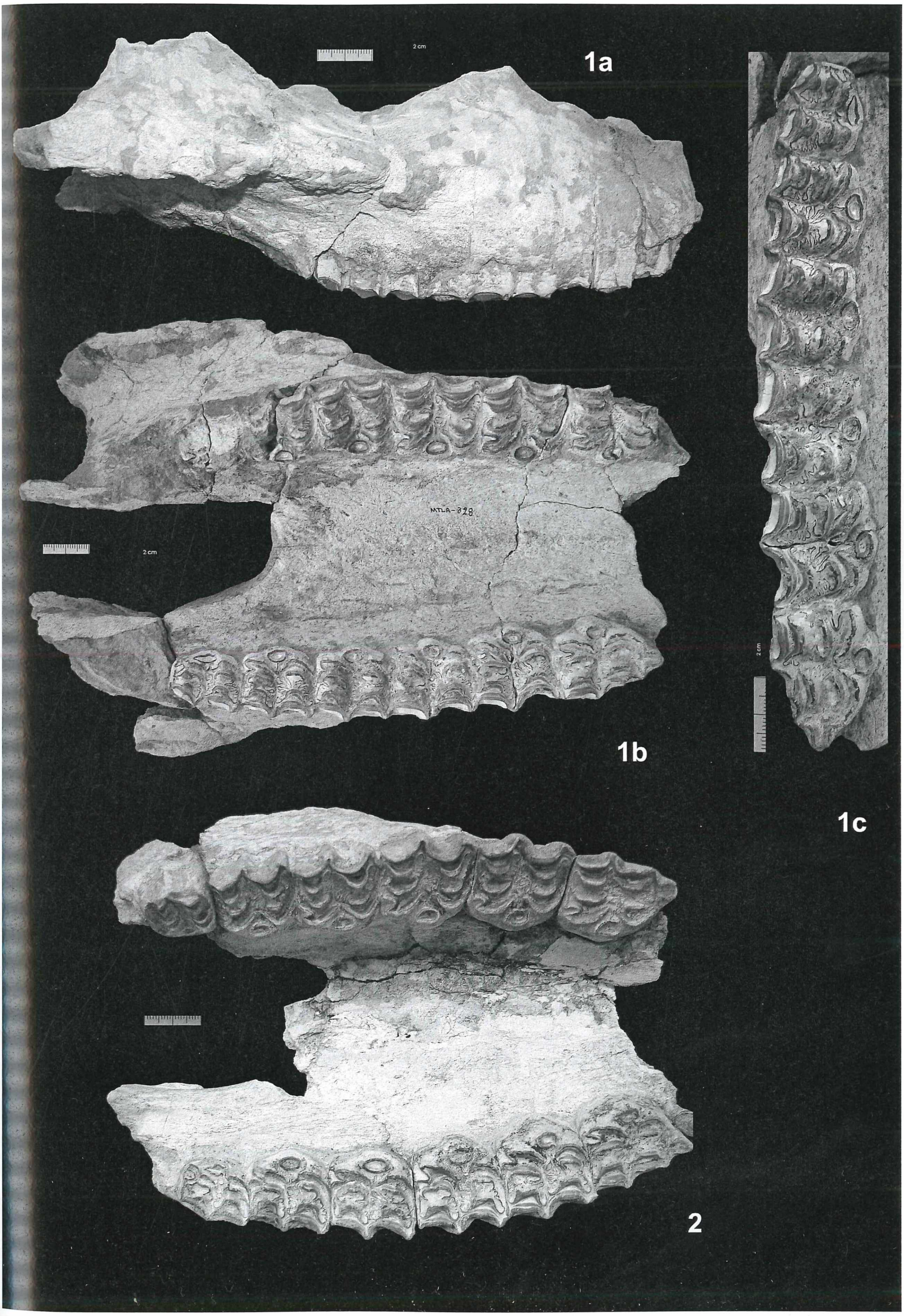


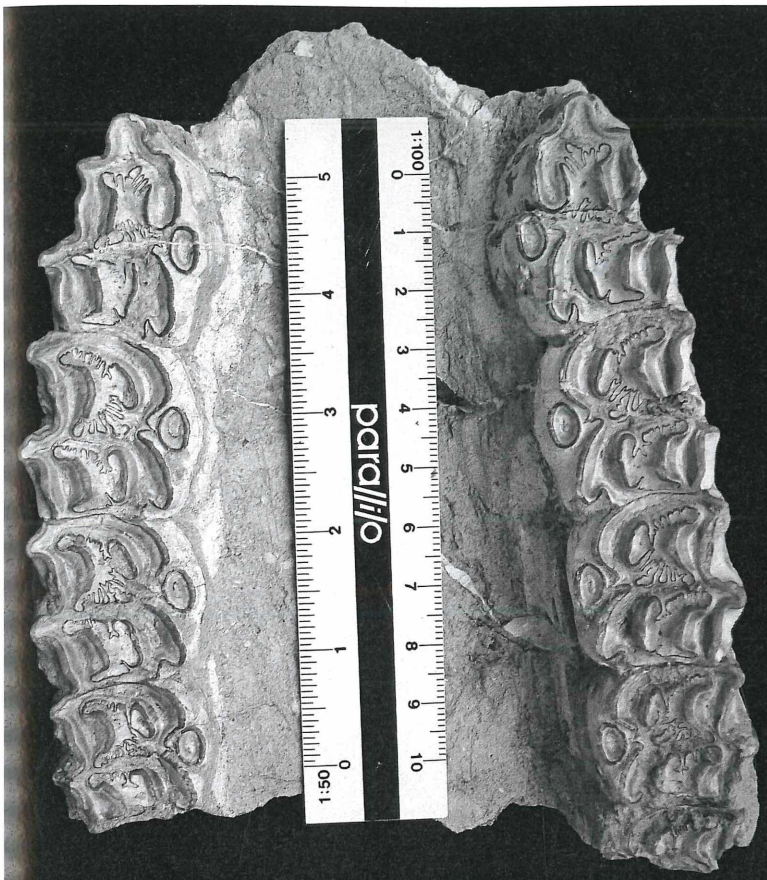
PLATE 3

***Hipparion* cf. *proboscideum*, "Adrianos" (Mytilinii 1A, MTLA), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Maxilla with P2-M1 dex and sin PMMS-5 a. occlusal view and b. right tooth row.

Fig. 2. Mandible, PMMS- no number; a. occlusal view and b. left tooth row.

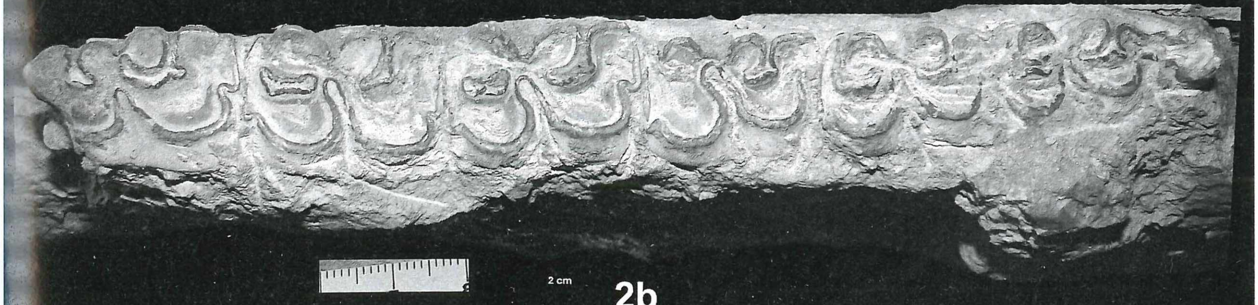
PLATE 3



1a

1b

2a



2b

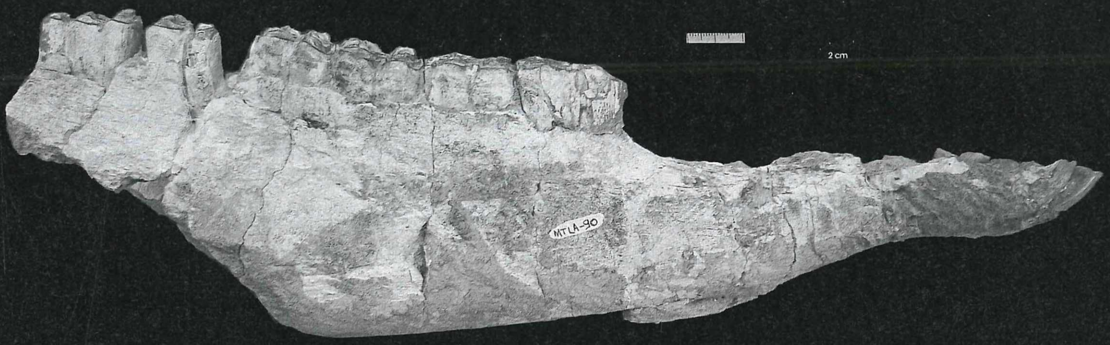
PLATE 4

***Hipparion* cf. *proboscideum*, Mytilinii-1A, B (MTLA, MTLB), Samos, Greece, Middle Turolian (MN 12).**

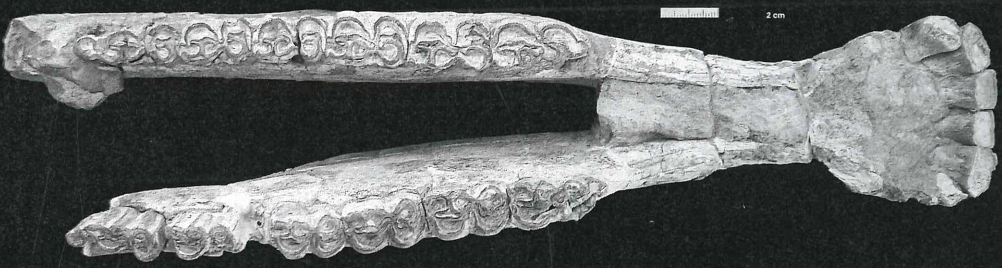
Fig. 1. Mandible, MTLA-90; a. lateral, b. occlusal view and c. left tooth row.

Fig. 2. Metacarpal, anterior view, a. MTLB-7; b. MTLA-508

PLATE 4



1a



1b

1c

2a

2b

PLATE 5

aff. *Hipparion prostylum*, Mytilinii-4 (MLN), Samos, Greece, Middle Turolian (MN 12).

Fig. 1. Mandible, MLN-20, a. lateral, b. occlusal view and c. right tooth row.

PLATE 5

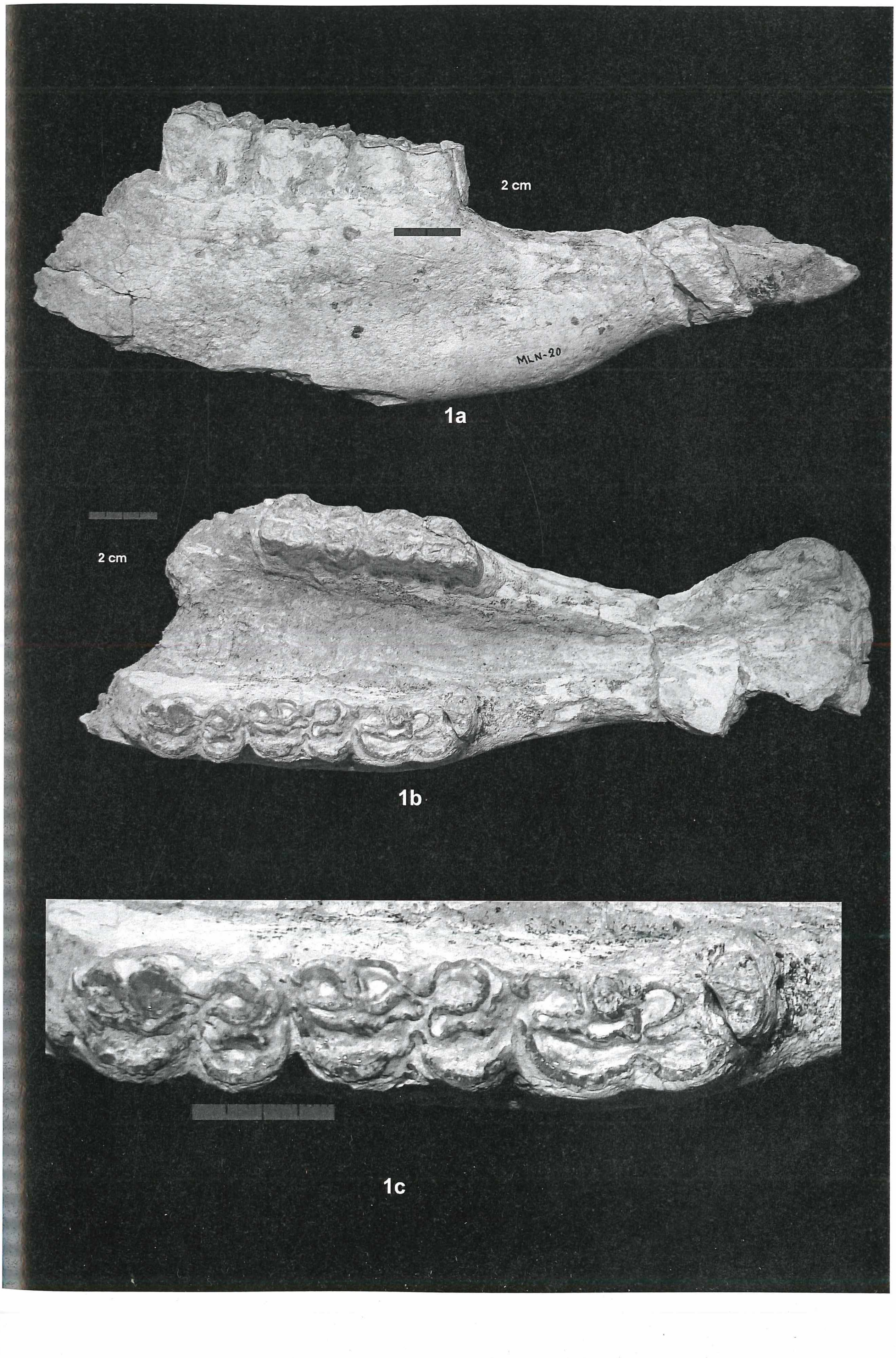


PLATE 6

***Hipparion dietrichi*, Mytilinii-1B (MTLB), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Skull, MTLB-163; a. right lateral, b. dorsal, c. occlusal view and d. upper tooth row.

PLATE 6

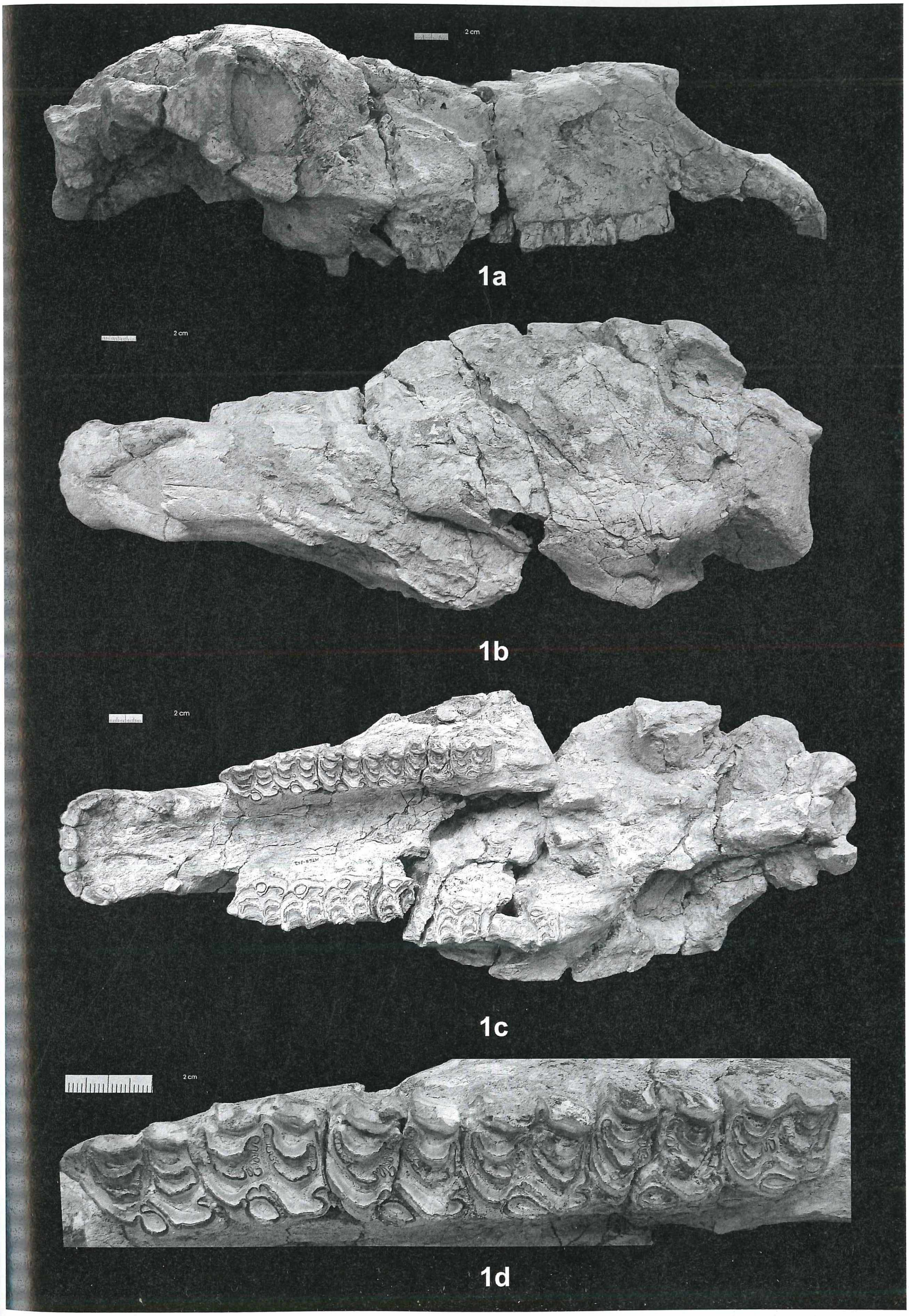


PLATE 7

***Hipparion dietrichi*, Mytilinii-1A (MTLA), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Partial skull, MTLA-122; a. lateral, b. dorsal and c. occlusal view.

PLATE 7

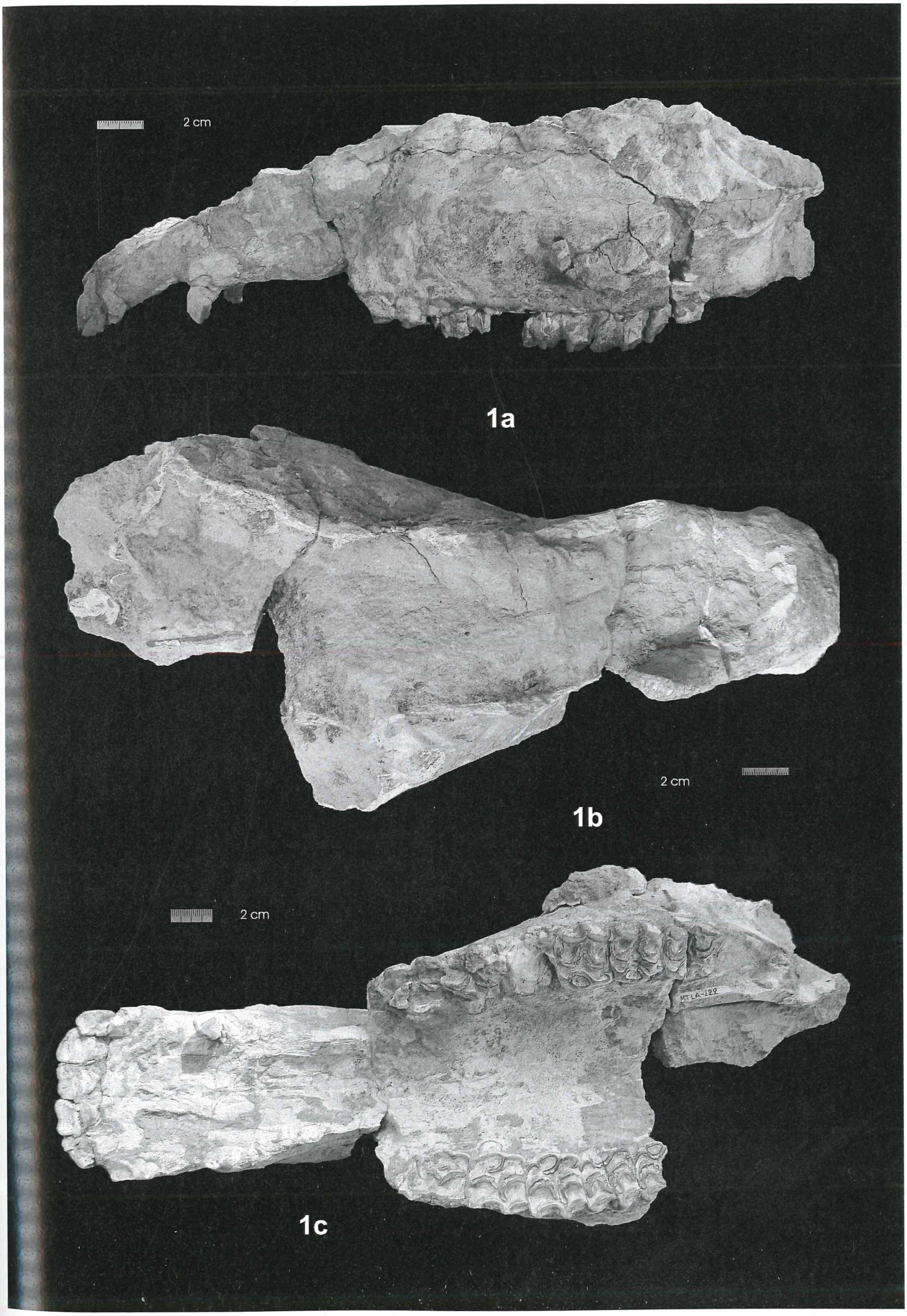


PLATE 8

***Hipparion* cf. *forstenae*, Mytilinii-1A (MTLA), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Skull, MTLA-338; a. lateral, b. dorsal, c. occlusal view and d. right tooth row.

PLATE 8

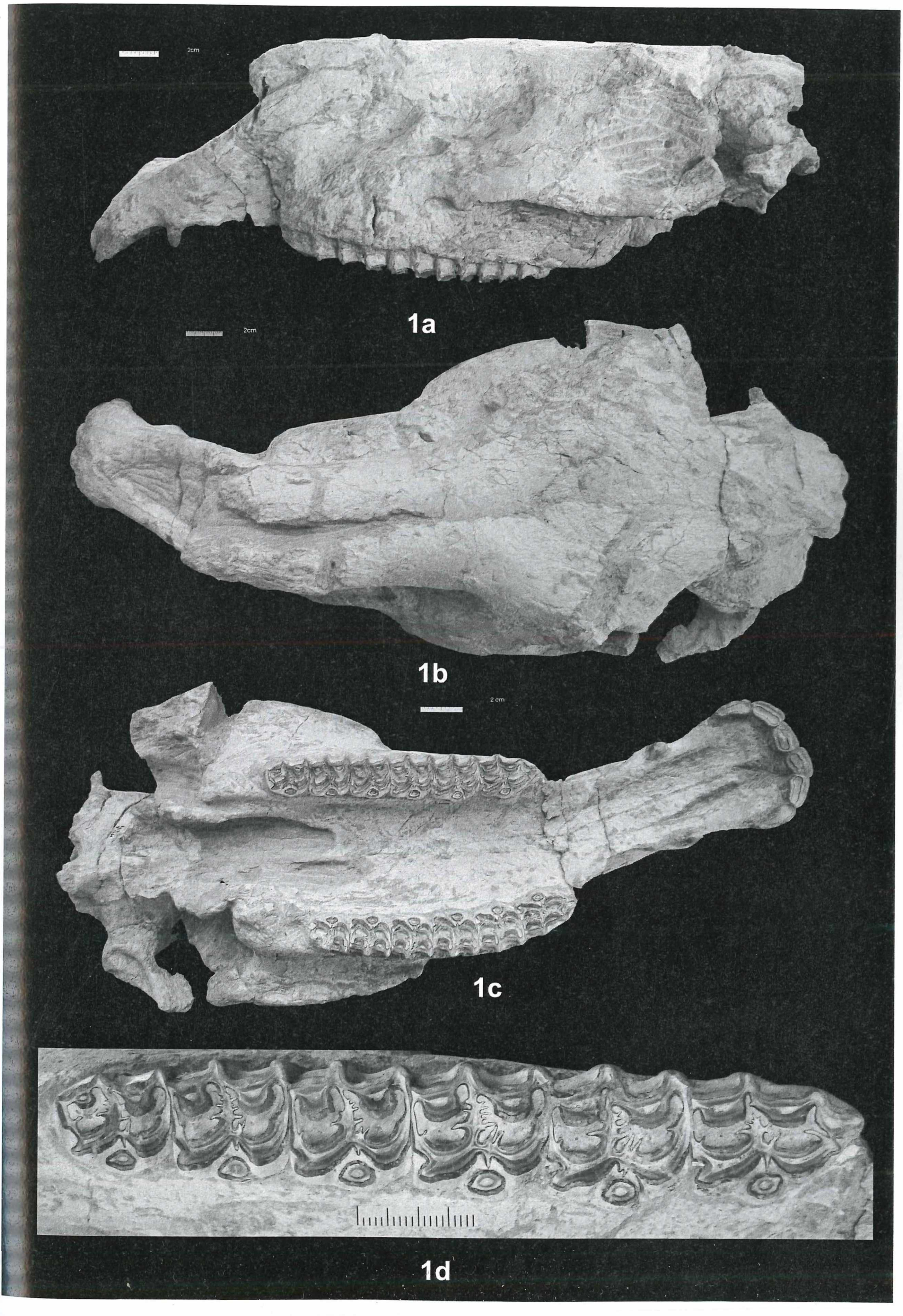
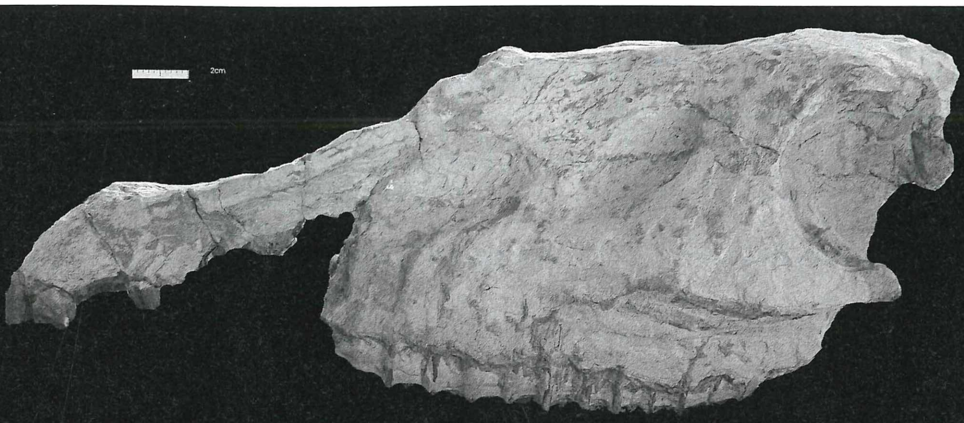


PLATE 9

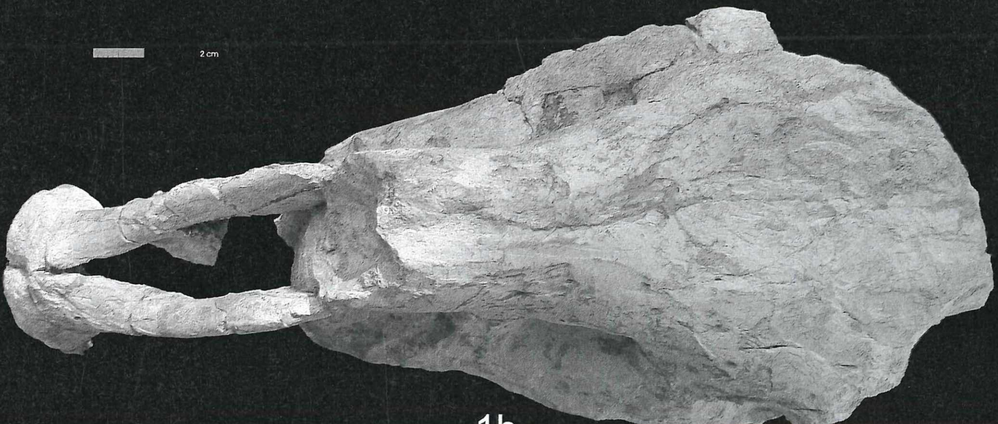
Hipparion cf. _forstenae_, Mytilinii-1A (MTLA), Samos, Greece, Middle Turolian (MN 12).

Fig. 1. Partial skull, MTLA-467; a. lateral, b. dorsal, c. occlusal view and d. left tooth row.

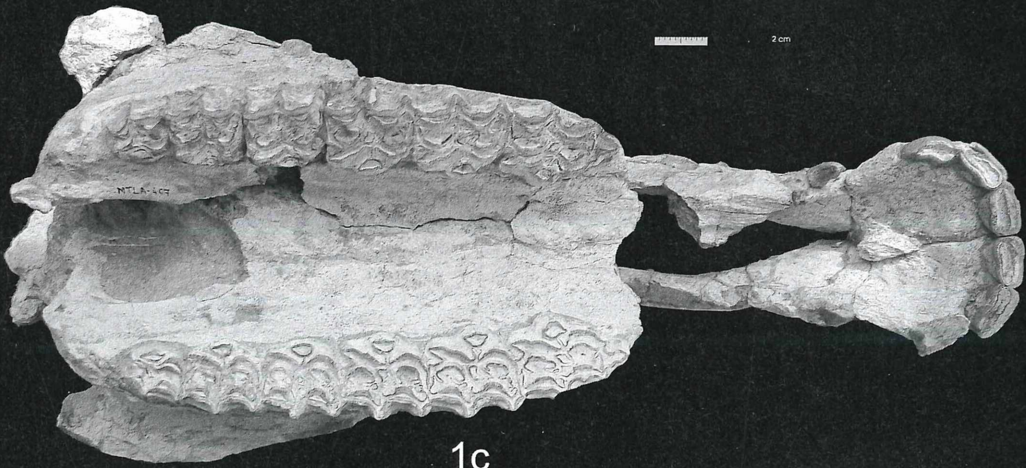
PLATE 9



1a



1b



1c

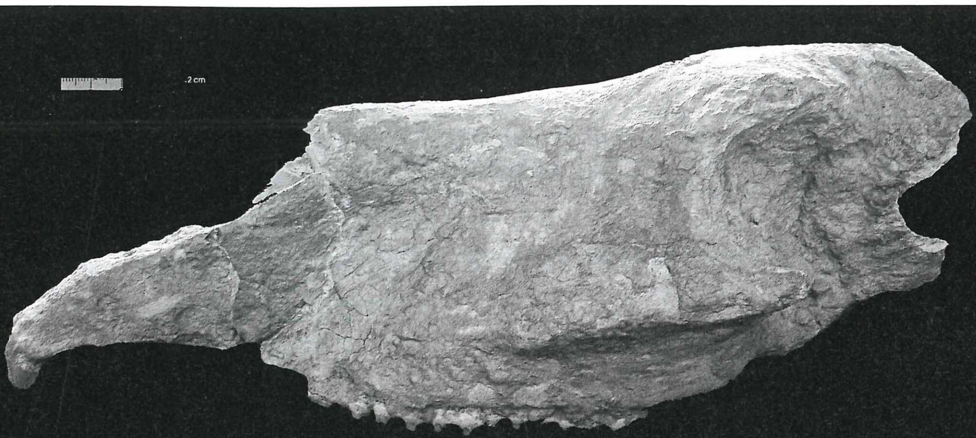
1d

PLATE 10

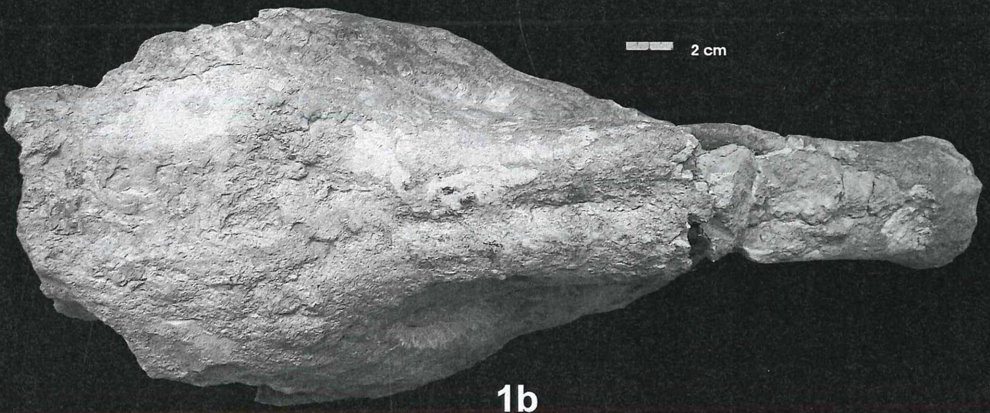
***Hipparion* cf. *forstenae*, ?Mytilinii-1A (?MTLA), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Partial skull, PMMS-9; a. lateral, b. dorsal, c. occlusal view and d. right tooth row.

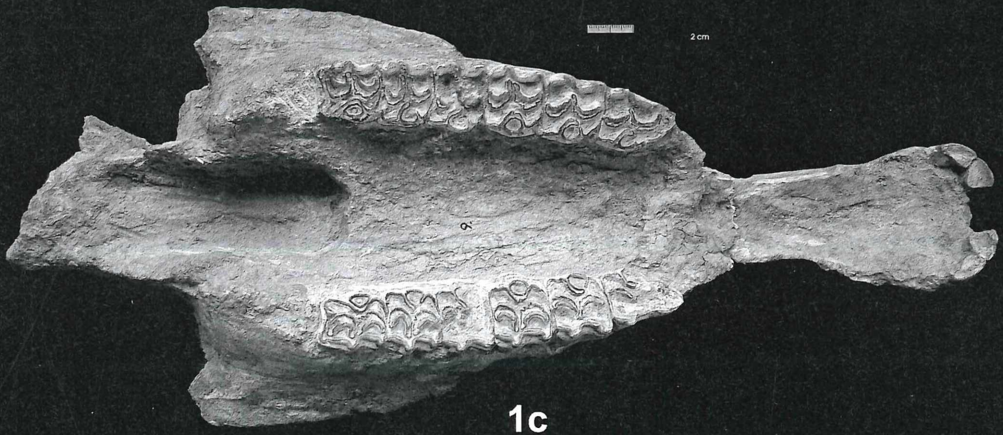
PLATE 10



1a



1b



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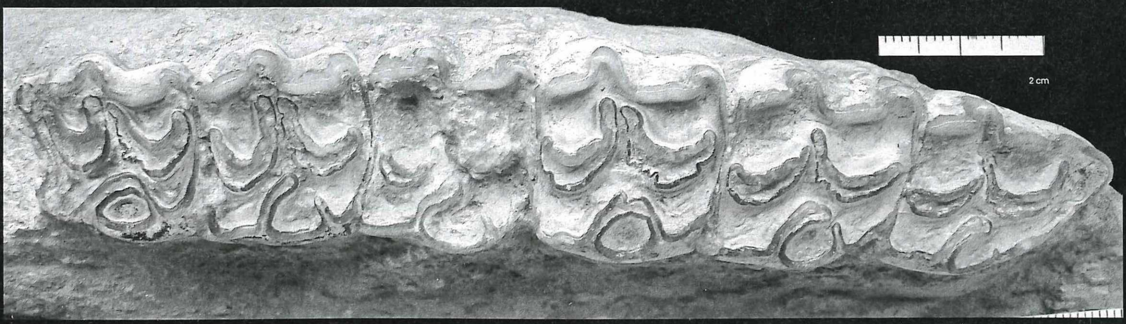


1d

PLATE 11

***Hipparion* cf. *matthewi*, Mytilinii-1A (MTLA), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Partial skull, MTLA-422; a. lateral, b. dorsal, c. occlusal view and d. left tooth row.

PLATE 11

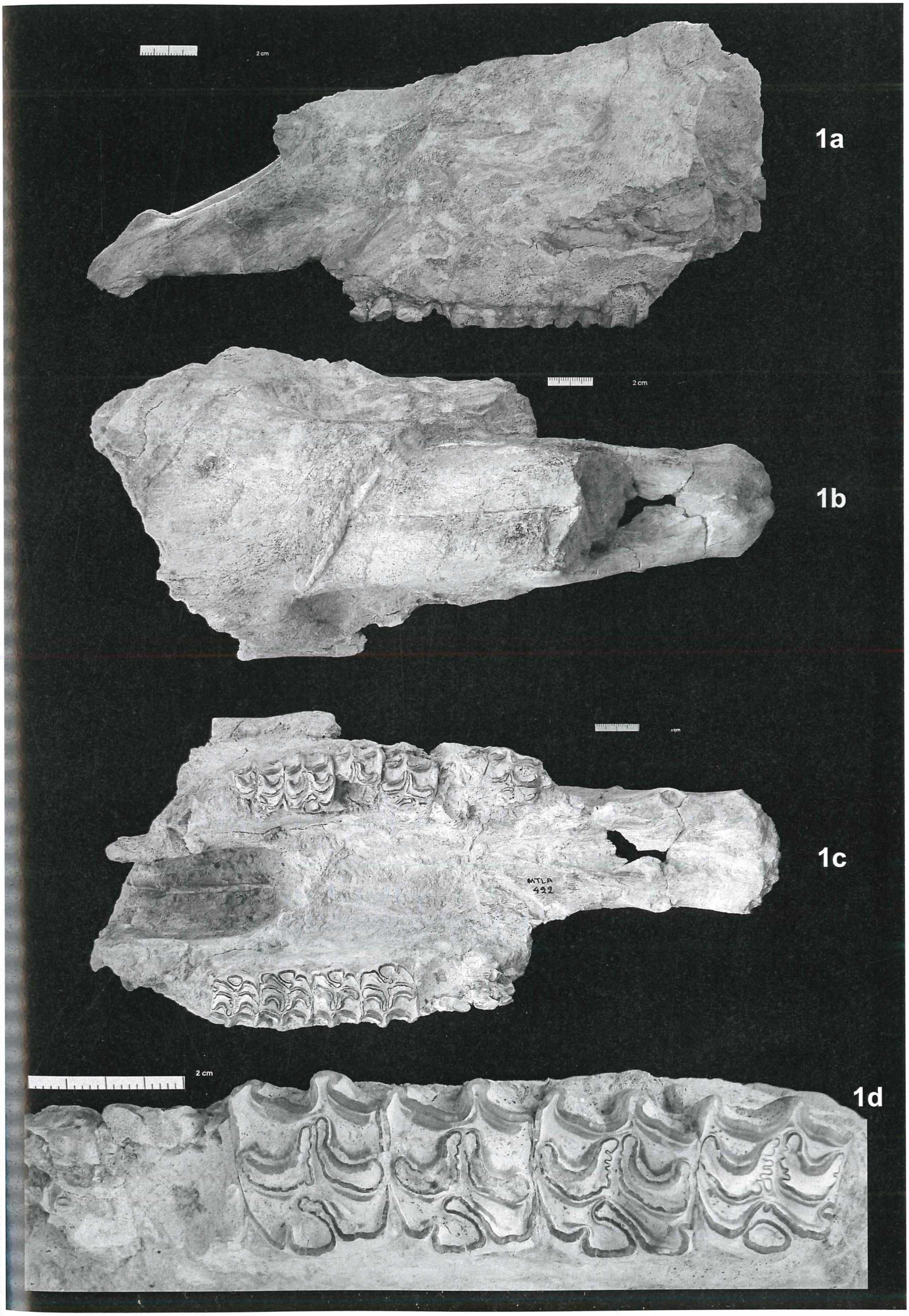


PLATE 12

***Hipparion* cf. *matthewi*, Mytilinii-1A, 2 (MTLA, MYT), Samos, Greece, Middle Turolian (MN 12).**

Fig. 1. Mandible, MTLA-77; a. lateral, b. occlusal view and c. left tooth row.

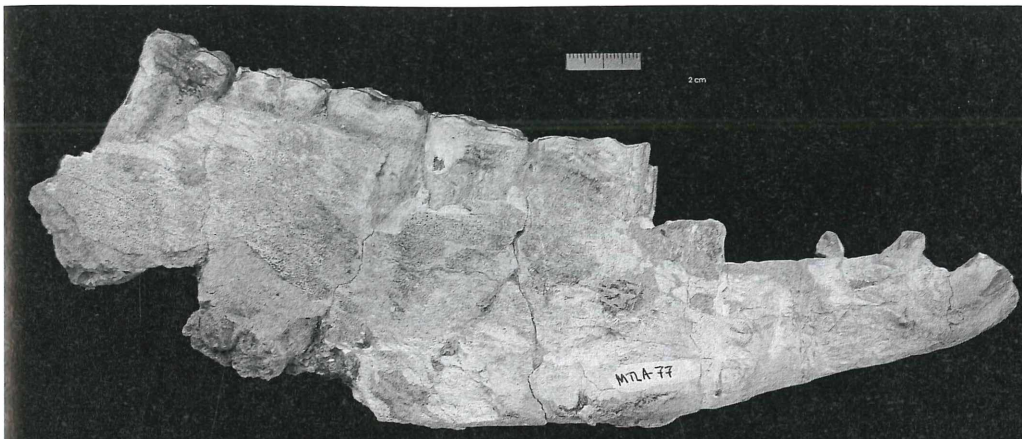
Fig. 2. Tibia, MYT-50; posterior view.

Fig. 3. Metacarpal, MTLA-32; anterior view.

Fig. 4. Metatarsal, MYT-52; anterior view.

Fig. 5. Metatarsal, MTLA-380; anterior view.

PLATE 12



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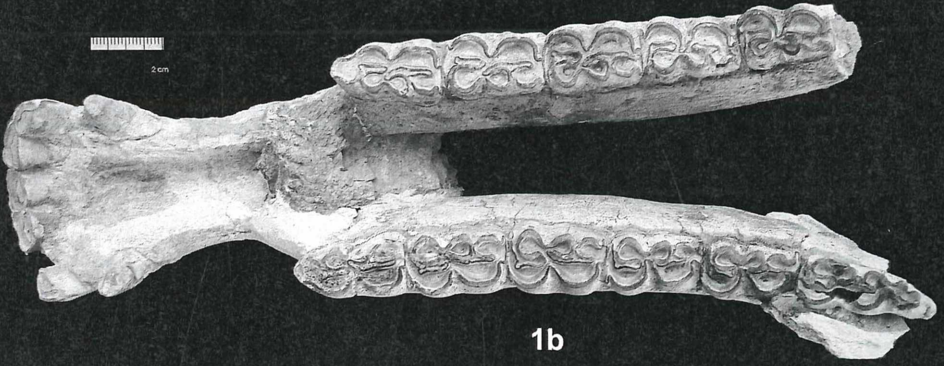

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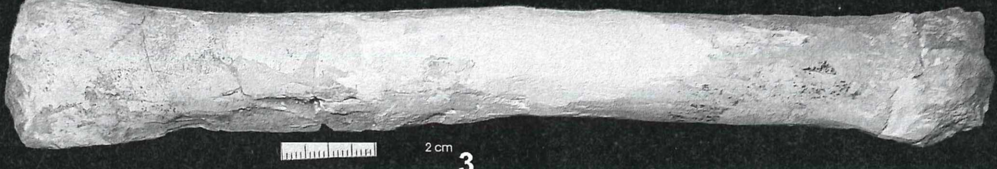
1c

2



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