Equidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey

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ABSTRACT
Akkaşdağı is a new vertebrate locality from Central Anatolia, Turkey, dated to middle Turolian (MN 12). Rich bone pockets are included in the upper horizon of a tuff layer dated to 7.1 Ma. *Hipparion* remains are particularly abundant. On the basis of skeletons, four different species were recognized in Akkaşdağı hipparions sample: 1) *H. dietrichi*, medium- to large-sized with long and slender limb bones; 2) *H. moldavicum*, small- to medium-sized with long and slender limb bones; 3) *H. brachypus*, large-sized with short and robust limb bones; and 4) *H.* cf. *longipes*, very large-sized form with very long and slender limb bones. The phylogenetic relationship of the Akkaşdağı hipparions with other Eurasian late Miocene hipparions is discussed, and we also analyse biostratigraphic and palaeobiogeographic distribution of the determined species in correlation with the available biochronologic, radiometric and magnetostratigraphic data.

KEY WORDS
Mammalia,
Equidae,
Hipparion,
late Miocene,
Akkaşdağı,
Central Anatolia,
Turkey,
biochronology,
biostratigraphy.

RÉSUMÉ
Equidae (Mammalia, Perissodactyla) du Miocène supérieur d'Akkaşdağı, Turquie.
Akkaşdağı est un nouveau gisement de vertébrés en Anatolie Centrale, Turquie, daté du Turolien moyen (MN 12). Des poches fossilifères sont incluses dans la partie supérieure d'un tuf daté de 7,1 Ma. Les restes d'*Hipparion* sont particulièrement abondants. Quatre espèces d'*Hipparion* sont identifiées sur la base du matériel crânien et postcrânien : 1) *H. dietrichi* de taille moyenne à grande avec des os de membres allongés et graciles ; 2) *H. moldavicum* de taille petite à moyenne avec des os de membres allongés

MOTS CLÉS
Mammalia,
Equidae,
Hipparion,
Miocène supérieur,
Akkaşdağı,
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biostratigraphie.

et graciles ; 3) *H. brachypus* de grande taille avec des membres courts et robustes ; et 4) *H.* cf. *longipes*, le plus grand des hipparions d'Akkaşdağı, avec des membres très allongés et graciles. Le riche matériel d'Akkaşdağı a permis de revoir les rapports phylétiques de ces espèces avec d'autres espèces miocènes d'Eurasie. La distribution spatiale et temporelle des ces espèces est discutée en correlation avec les donnés biochronologiques, radiométriques et magnétostratigraphiques.

INTRODUCTION

The locality of Akkaşdağı is situated in the southern part of the Çankırı-Çorum Basin, 125 km SE of Ankara. The first information about the fossils of the area are provided by F. Ozansoy and M. Ayan in the 1960's. During the 1970's, Heintz collected some fossils stored now in the Muséum national d'Histoire naturelle of Paris (Sen *et al.* 1998b). A more detailed study of the area started at 1995 by geologists from Ankara University. The latest research at Akkaşdağı was undertaken by a team led by Sevket Sen in 2000. The main bulk of the Akkaşdağı material was collected during the field seasons of 2000-2001.

The fossil-bearing horizon is exposed along an erosional tuff surface, in pockets, at the southwestern slopes of the hill Akkaşdağı, at an altitude of 950 m covering a distance more than 2 km. There is no clear lithification or graded bedding in the tuffs which are dated at 7.1 Ma by Ar/Ar (Karadenizli *et al.* 2005). During the field campaigns more than 10 pockets have been excavated. The material collected from each pocket is labelled separately using the first two letters of the locality (AK) followed by the pocket number (or the letter K when the material is issued from old collections or surface findings) (e.g., AK1, AK2, AKK, etc.) and stored in the Natural History Museum of Ankara. More information about the locality and the stratigraphy of the basin is given by Kazancı *et al.* (2005).

The Akkaşdağı fauna is very rich in hipparion's remains. More than 2000 specimens have been found, representing 72% of the collected specimens. The hipparion sample includes several complete and partial skulls, mandibles, postcranials, isolated teeth, and several maxillary or mandibular fragments with milk teeth. The milk dentition, isolated teeth, carpals and tarsals (except astragalus and calcaneum) are not included in this study. All the rest of the material has been studied and compared. The *Hipparion* sample of Akkaşdağı includes four species. In the present article the Akkaşdağı hipparions will be described and compared with other Eurasian late Miocene hipparions, their biostratigraphy and biogeography will also be discussed.

MATERIAL AND METHODS

The main problem in studying such a rich hipparion sample is the correlation between the postcranial and cranial material and their assignment to a species. Concerning the skulls the recognition is easier as the morphological differences between the various species are clear and certain. On the other hand, the separation of the postcranials in species is a quite difficult process, especially when more than two species are included in the sample. There are no clear anatomic differences between the postcranials of various *Hipparion* species preventing in this way their determination. Their distinction is usually based on their proportions; but, if the different species have similar size and if there is an overlap in the metapodial proportions, the species recognition becomes impossible.

Moreover, the absence of complete skeletons associated with skulls makes difficult and arbitrary the correlation of the cranial and postcranial material.

In the studied hipparion collection the skulls, mandibles, maxillae and mandibular fragments have been separated according to their morphological features and dental characters. The description of the cranial remains is based on the methodology given by Bernor *et al.* (1990). As regards to the postcranials, the numerous specimens and the presence of transitional sized forms between the different postcranial morphotypes make the distinction difficult. Hence, for their classification and taxonomy we used scatter diagrams, logarithmic ratio diagrams, as well as principal component and cluster analysis (SPSS: Statistical Package of Social Sciences; PAST: Palaeontological Statististical Program). The material was measured according to the system proposed by Eisenmann *et al.* (1988).

The elaboration of the measurements, using scatter diagrams and Principal Component Analysis (PCA), showed that, based on the size and proportions of the third metapodials, four morphotypes could be distinguished: 1) medium- to large-sized, long and slender; 2) small- to medium-sized, long and slender; 3) large-sized, short and robust; and 4) large-sized, very long and slender metapodials The metacarpal is considered as a quite characteristic bone for species distinction, and for this reason it is used here as an example (Fig. 1). The dendrogram that comes from the hierarchical cluster analyses of the metacarpals, after the principal component analyses and using the algorithm of the Ward's method (Fig. 2B) confirms the metapodial morphotypes recognized here above.

Relying on the facial morphology, the snout proportions and the dental characters, four types of skull could be recognized. The first one is characterized by large size, elongated muzzle, deep narial opening, triangular deep preorbital fossa anteroposteriorly oriented, placed far from the orbit and facial crest, highly plicated teeth and elliptical protocone. The other type is also large with short and broad muzzle, short narial opening, weak preorbital fossa, strongly anteroventraly oriented, placed far from the orbit and facial crest, moderate enamel plication and elliptical protocone. The third one has small to medium size, short and narrow muzzle, short narial opening, preorbital fossa subtriangular to oval, moderately deep, placed relatively close to the orbit but far above the facial crest; the maxillary teeth have moderate enamel plication and rounded protocone. A fourth cranial morphotype is based on maxillary remains and it is characterized by large size, highly plicated teeth, elliptical protocone with spur and very elongated and narrow P2.

The correspondence of the postcranials to the cranial remains is usually arbitrary. However, bibliography in connection to the recognized morphotypes leads us to the following assumptions:

1) the large-sized skull with the subtriangular deep preorbital fossa corresponds to the large-sized, short and robust limbs;

2) the large-sized skull with the faint preorbital fossa corresponds to the medium- to large-sized, long and slender limbs;

3) the small-sized skull with the subtriangular to oval and moderately deep preorbital fossa corresponds better to the medium- to small-sized, long and slender limbs; and

4) the large-sized form with very plicated maxillary teeth and elongated P2 corresponds to the large-sized, very elongated and slender limbs.

Apart from the taxonomic conclusions, the principal component and the cluster analysis also provide important information, concerning the relations between the variables (= measurements). Checking the normality and the correlation of the variables we observe that all the variables, except V1 and V2, are linearly correlated each other (Fig. 2B). Even if V1 and V2 are linearly correlated, their correlation with all the other variables is not linear (Fig. 2B). This could mean that, except the metacarpal length, the other changes in a single variable seem to depend on ontogenetic growth of the animal, while the length of the bone is possibly more dependent on phylogenetic changes and/or on ecological adaptations.

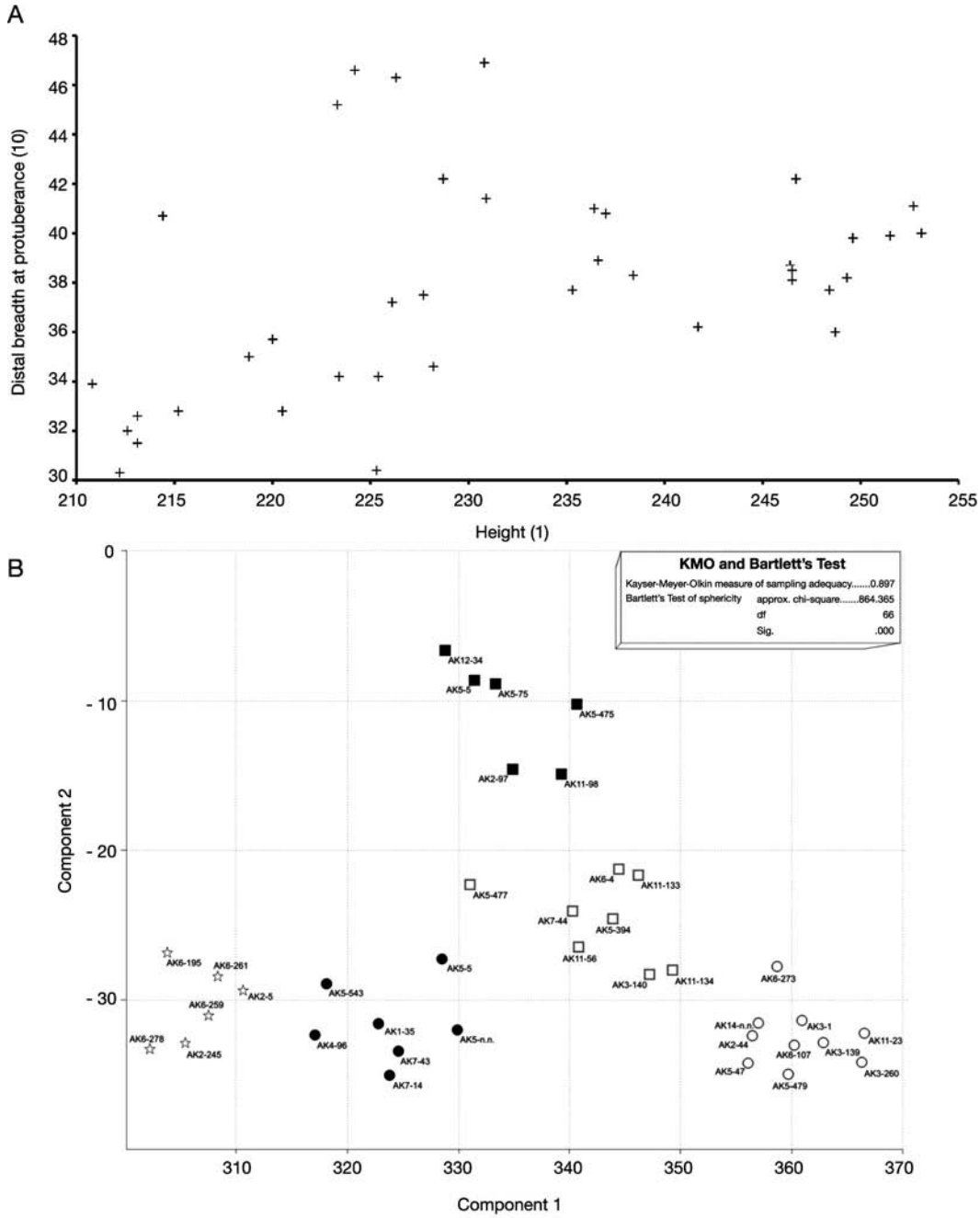

FIG. 1. — Distinction of the third metacarpals of the Akkaşdağı hipparions by X/Y scatter diagrams (**A**), and Principal Component Analysis (PCA) (**B**). The total variance is given in Appendix 1.

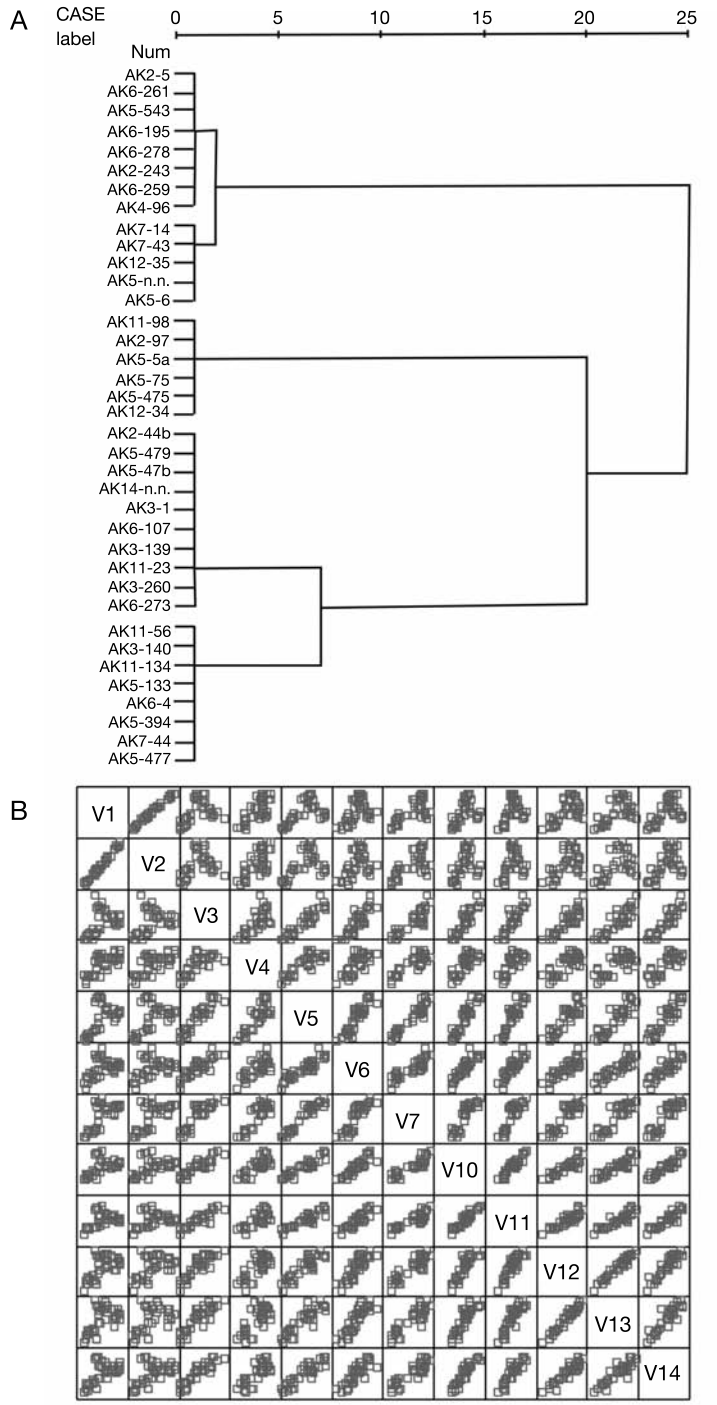

FIG. 2. — **A**, the clusters of the Akkaşdağı *Hipparion* metacarpals using Ward's algorithm; **B**, linear correlation of the variables (measurements of the Akkaşdağı *Hipparion* metacarpals).

ABBREVIATIONS

AK (A, B, K, 1-14)	Akkaşdağı collection;
AMNH	American Museum of Natural History, New York;
BMNH	Natural History Museum, London;
DTK	Dytiko1, Axios Valley, Greece;
KTA,B,D	Kemiklitepe A,B,D, Turkey;
MNHN	Muséum national d'Histoire naturelle, Paris;
MTA-MA	Maden Tetkik ve Arama Museum [Geological Survey], Ankara;
dex	right;
m	measurement;
n.n.	no number;
sin	left.

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus *Hipparion* de Christol, 1832

Hipparion brachypus Hensel, 1862

LOCALITY. — Akkaşdağı, near Keskin, Turkey.

AGE. — Middle Turolian, MN 12 (late Miocene).

MATERIAL. — Skull associated with the mandible, AKK-147; hemimandible with i1-m2 dex, AK6-23; mandible with p2-m1 dex and sin, AK3-57; mandibular fragment with p2-m3 sin, AK3-175; mandibular fragment with p2-p4 dex, AK11-138; mandibular fragment with p3-m3 sin, AK4-245; mandibular fragment with p4-m1 dex, AK4-127; mandibular fragment with p2-p3, dp4-m2 dex, AK7-80; 2 mandibular fragments with p2-m3 dex, AK5a-329, AK2-107; mandibular fragment with p3-m2 sin, AK12-9; 7 distal parts of humerus, AK3-10, 257, AK5-465, 536, AK12-26, 28, 29; radius, AK6-233; radius+carpals+McII+McIII+McIV, AK11-98a-l; 2 distal parts of radius, AK2-391, AK5-341; 2 McII+McIII+McIV, AK4-5, AK12-34; 4 McIII, AK2-97, AK4-149, AK5-75, 475; 2 proximal parts of McIII, AK4-151, AK5-395; distal part of McIII, AK3-6; 7 distal parts of tibia, AK2-20, AK4-154, 217, AK5-557, AK6-15, AK7-48, AK11-46; 10 astragali, AK2-26, 27, AK3-269, AK4-17, 29, AK5-13, 100, 472, AK10-14, AK11-54; 2 calcanei, AK5-174, AKK-172; MtII+MtIII+MtIV, AK11-37a-c; 8 third metatarsals, AK3-87, 276, AK4-95, AK5-158, 480, 564, AK7-135, AK11-135; 4 distal parts of MtIII, 279, 282, AK4-169, 219; 3 first phalanges, AK2-425, AK3-288, AK4-13; 4 second phalanges AK5-n.n., 119, 163, 416; 4 third phalanges, AK5-166, 171, AK6-43, 162.

DESCRIPTION

Skull and dentition

The studied skull belongs to a relatively young individual, preserving the dP4. The P2 and P3 are just rised without any attrition, while the M3 is almost inside the bone (Fig. 3). The skull is very long and relatively narrow. The muzzle is very elongated and relatively broad. The narial opening is deep and narrow. Its posterior border is situated far from the orbit, above the middle of the P2 (Fig. 3A). The preorbital fossa is subtriangular, large and deep, anteroposteriorly oriented with a deep posterior pocketing, and placed far from the orbit. The anterior rim is not well expressed, and is placed approximately above the anterior part of the P2. The posterior one is situated above the anterior border of the M2. The ventral rim is straight, parallel to the toothrow and at the same line with the lower border of the orbit. The infraorbital foramen is situated slightly inferior to the anteroventral border of the fossa (Fig. 3A). The orbit is rounded and its anterior border is situated above the posterior part of the M3. The facial crest is quite strong; it is developed far from the alveoli and the ventral rim of the preorbital fossa (POF), while its anterior border is situated above the anterior half of the dP4. The palate is elongated, wide and shallow. The index m2 × 100/m13 is 202. The correspondence index for *H. brachypus* of Pikermi is 221.5 on average, while in *H. mediterraneum* from Pikermi with shorter palate it is 183 on average (Koufos 1987a). The choanae, although they are damaged, seem to be wide with their anterior border situated at the level of the contact between M1 and M2. The upper toothrow is almost complete including the dP1, P2-3-dP4-M1-2 and it seems to be quite long. The P2, 3 are unworn and their enamel morphology is not visible. The dP4 is quadrangular with moderate enamel plication in the fossettes. The protocone is elliptical and isolated. The hypocone is elliptical with relatively shallow distal hypoconal groove. The pli caballin is single and short. The M1 is worn enough to see its morphology. The enamel plication is rich (more than 17 plis) with deep plis. The protocone is large and elliptical, and the pli caballin is

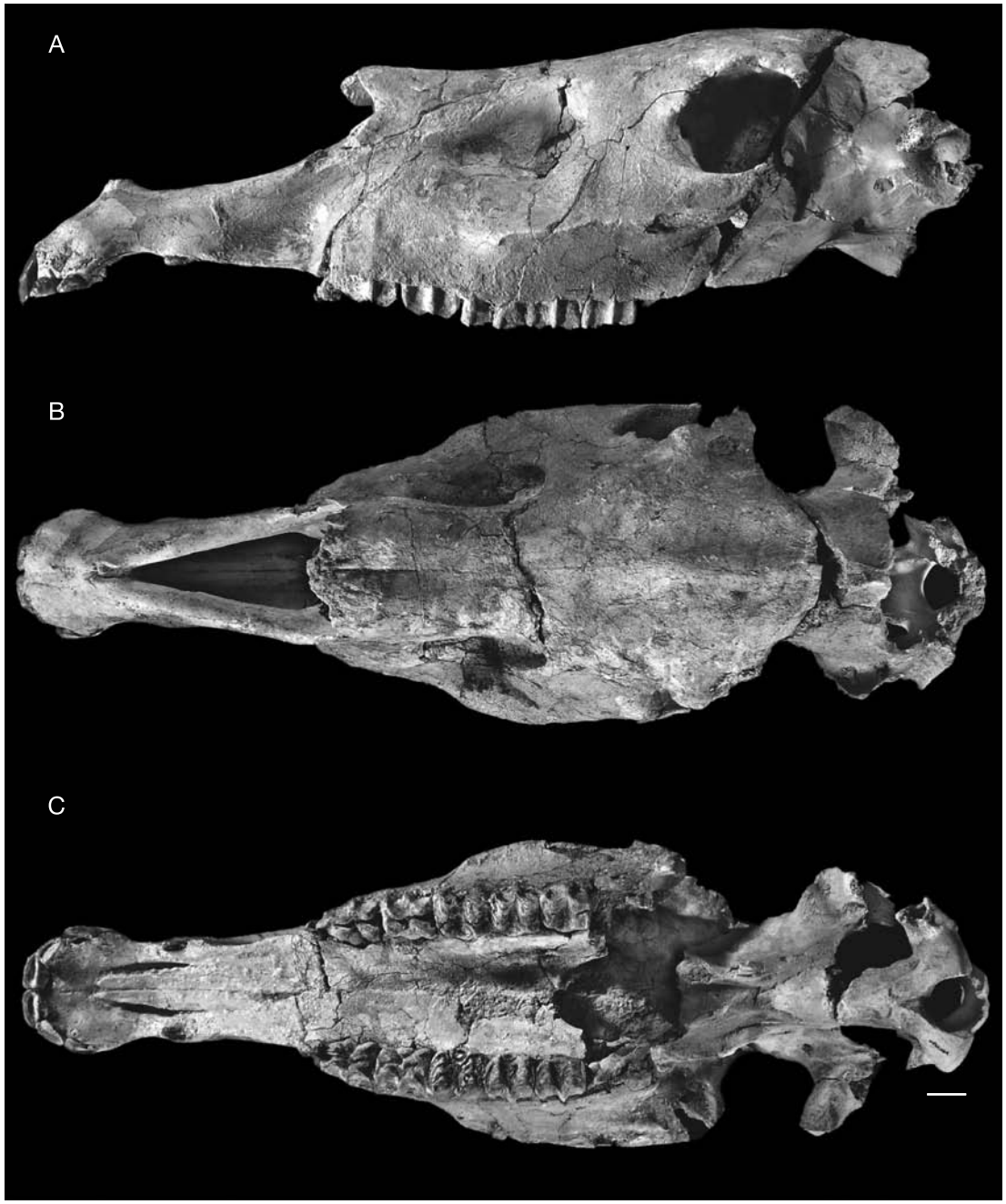

FIG. 3. — *Hipparion brachypus*, Akkaşdağı, Turkey, skull AKK-147; **A**, lateral view; **B**, dorsal view; **C**, occlusal view. Scale bar: 2 cm.

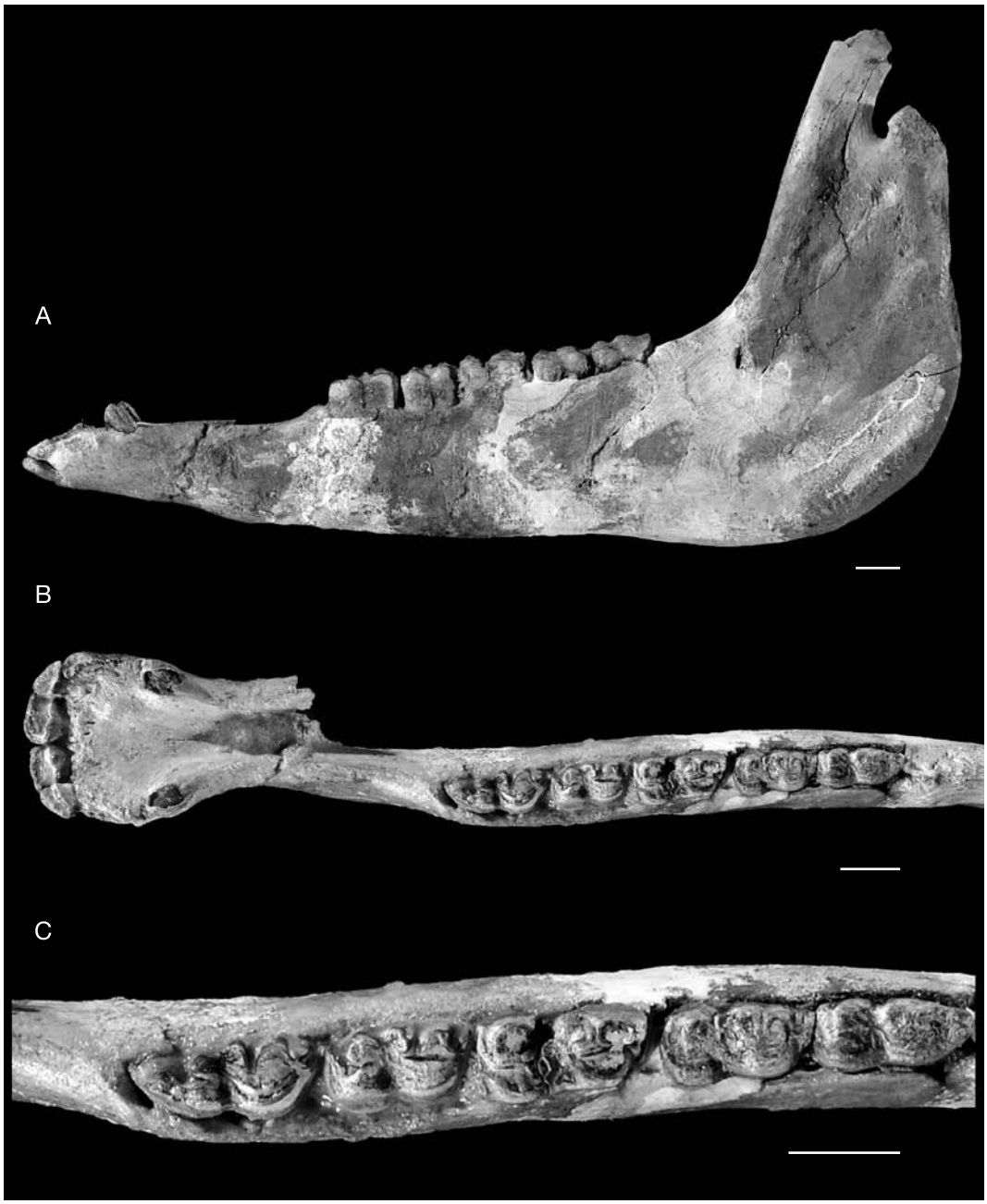

FIG. 4. — *Hipparion brachypus*, Akkaşdağı, Turkey, mandible AKK-147; **A**, lateral view; **B**, dorsal view; **C**, left toothrow, occlusal view. Scale bars: 2 cm.

double. The distal hypoconal groove is deep while the lingual hypoconal groove is absent.
The mandible is elongated and high with long and relatively narrow snout (Fig. 4A, B). The index m2 × 100/m7 is 259 for AKK-147 versus 254 for *H. brachypus* of Pikermi, 213 for *H. mediterraneum* of Pikermi with shorter snout, and 167 for *H. dietrichi* of Prochoma (Axios Valley, Greece) with short and wide snout (Koufos 1987a, b). The horizontal ramus is relatively short. The symphysis is relatively short and narrow. The toothrow is elongated and the teeth are large and wide (Fig. 4C). The parastylid is well developed and closed. The metaconid is rounded, the metastylid is elliptical to rounded and the entoconid elliptical. The ectoflexid is shallow in the premolars, reaching the middle of the tooth while in the molars it is long and narrow reaching the linguaflexid. The last is shallow and V-shaped in the premolars, while in the molars it is U-shaped. A pli caballinid is sometimes present (AK6-23). It is stressing that the specimen AK6-23 seems to have short muzzle but the dental size and morphology, as well as the toothrow length are similar to the studied forms.

Postcranials
The metapodials are short and robust (Fig. 5). The mean index Length McIII × 100/Length radius is 78.4 indicating a relatively short metacarpal. The absence of complete tibia cannot allow the calculation of the corresponding index for MtIII. The robusticity index (m11 × 100/m1) is 18.7 for McIII and 16.2 for MtIII indicating robust metapodials. The keel index (Sen *et al.* 1978) is 121.1 for McIII and 128.4 for MtIII indicating that the keel is not very prominent. For comparison, *H. primigenium* with short and robust metapodials has the following indices respectively: McIII: 15.3 and 122.8; MtIII: 17.1 and 115.7 (data from Bernor *et al.* 1997).

COMPARISONS
The large-sized skull from Akkaşdağı shares the same morphological pattern with *H. brachypus*, *H. giganteum* (Gromova 1952) and *H. gettyi* (Bernor 1985). All are known from the Turolian of the Eastern Mediterranean region and a comparison with these species is useful to determine the studied material.
Hipparion brachypus is known from Pikermi and it is characterized by large size, elongated skull with relatively wide muzzle and deep narial opening. The preorbital fossa is oval, anteroposteriorly oriented, well marked, frequently deeply posteriorly pocketed and situated far from the orbit. The upper cheek teeth are highly plicated (Koufos 1987a).
The skull morphology of the large-sized hipparion from Akkaşdağı (AKK-147) is similar to that of *H. brachypus* from Pikermi. The unworn teeth lack morphology, but the little worn M1 indicates rich enamel plication with deep plis, like in *H. brachypus*. Figure 6 contrasts the proportions of the large-sized skull (AKK-147) with *H. brachypus* specimens from Pikermi and Hadjidimovo (Bulgaria) and indicates that the three skull forms are almost identical. Comparatively to *H. brachypus* from Pikermi, the muzzle of AKK-147 is longer and the facial height larger (measurements 1, 25 in Fig. 6). However, AKK-147 belongs to a young individual (M3 is almost inside the bone) and consequently both measurements are probably unreliable. Additionally, the facial height depends strongly upon the preservation of the skull, and a slight deformation leads to different values. The premolar length (measurement 7 in Fig. 6) is also longer, but this is possibly due to the low attrition of the teeth. Not much more can be said for the contrast between AKK-147 and *H. brachypus* from Hadjidimovo except that the later one appears to have narrower snout (Hristova *et al.* 2003) (measurements 14, 15 in Fig. 6).
The skull morphology of *H. gettyi* and *H. giganteum* is also very close to that of *H. brachypus* and to the Akkaşdağı skull AKK-147. *Hipparion gettyi* is known from the Lower Maragha. The type specimen (KNHM RLB 8401) is a medium-sized skull with deep preorbital fossa (POF), triangular-shaped, posteriorly pocketed, anteroposteriorly oriented and placed far from the orbit and facial crest. The slender snout and the remarkably short facial length (measurements 1, 31 in Fig. 6)

FIG. 5. — *Hipparion brachypus*, Akkaşdağı, Turkey; **A**, third metacarpals, AK5-75, AK5-5a, AK11-98k; **B**, third metatarsals, AK11-371, AK11-37b. Scale bars: 2 cm.

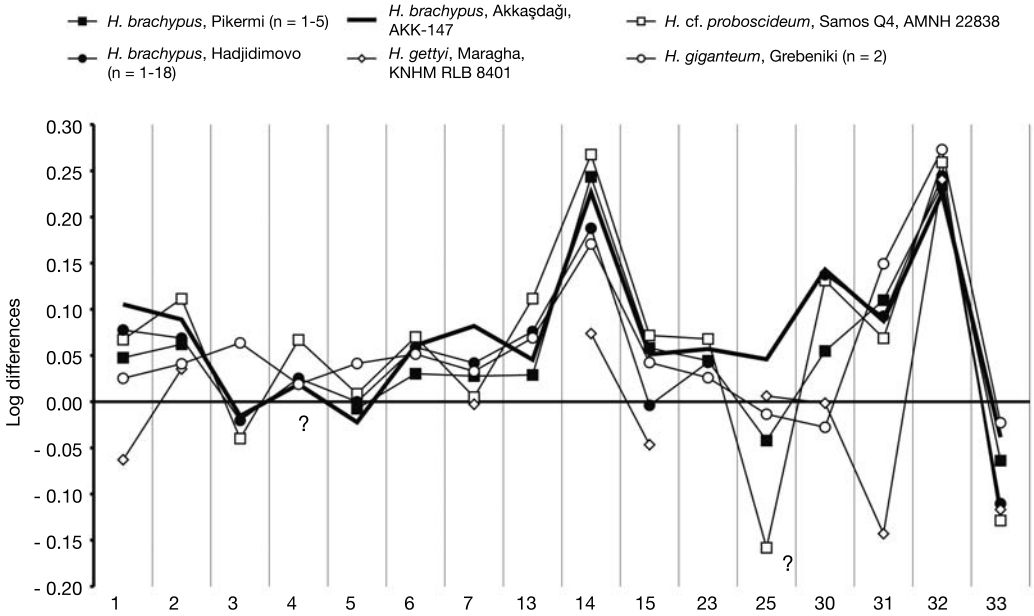

FIG. 6. — Logarithmic ratio diagram comparing the skull of *Hipparion brachypus* from Akkaşdağı with *H. brachypus*, *H.* cf. *proboscideum*, *H. gettyi and H. giganteum* from various localities. Standard *H. mediterraneum*, Pikermi, n = 1-9 (Koufos 1987a).

distinguish this species from *H. brachypus* and AKK-147 (Fig. 6). Additionally, the premolar length is significantly shorter reinforcing the idea about a medium-sized form, smaller than that of *H. brachypus* and AKK-147. The upper cheek teeth seem to be less plicated and the plis are not so deep. On the other hand, *H. giganteum* from Grebeniki proportionally resembles the studied form, but the facial region seems to be shorter. Gromova (1952) described *H. giganteum* as a large-sized hipparion with single, elliptical and deep POF, strongly posteriorly pocketed and placed far from the orbit and facial crest. There is no canine fossa, but in its place there is an elongated groove, connecting the preorbital fossa with the buccinator one. The last character is also observable in some slightly deformed specimens of *H. brachypus* from Pikermi and Hadjidimovo, rendering this character unreliable for species determination.

A large-sized skull (AMNH 22838) from Samos Q4 was described by Sondaar (1971) as *H.* cf. *proboscideum*. This skull has a single deep and not extended preorbital fossa (Sondaar 1971), being in that different from the type skull of *H. proboscideum* that is characterized by double and extremely deep preorbital fossa. This is probably the reason why Sondaar (1971: 431) wrote: "AMNH 22838 […] with considerable doubt referred to *H. proboscideum*". The morphology of the preorbital fossa is similar to that of the Akkaşdağı skull. Furthermore, the proportions of this skull are very close to those of *H. brachypus* from Pikermi and Hadjidimovo (Fig. 6). The distance vomer-basion (measurement 4 in Fig. 6), however, seems to be slightly longer than that of *H. brachypus*. This measurement is estimated for the studied skull, and for this reason it is given with a question mark. The comparatively shorter premolar length of AMNH 22838 is possibly due to the relatively advanced stage of wear, while the facial height is doubtfully measured as the skull is dorsoventraly compresed, hence the question mark. Recently, a partly preserved skull (MTLB-30) with strong morhological similarities to *H. brachypus*, was found in "Mytilinii-B" (MTLB),

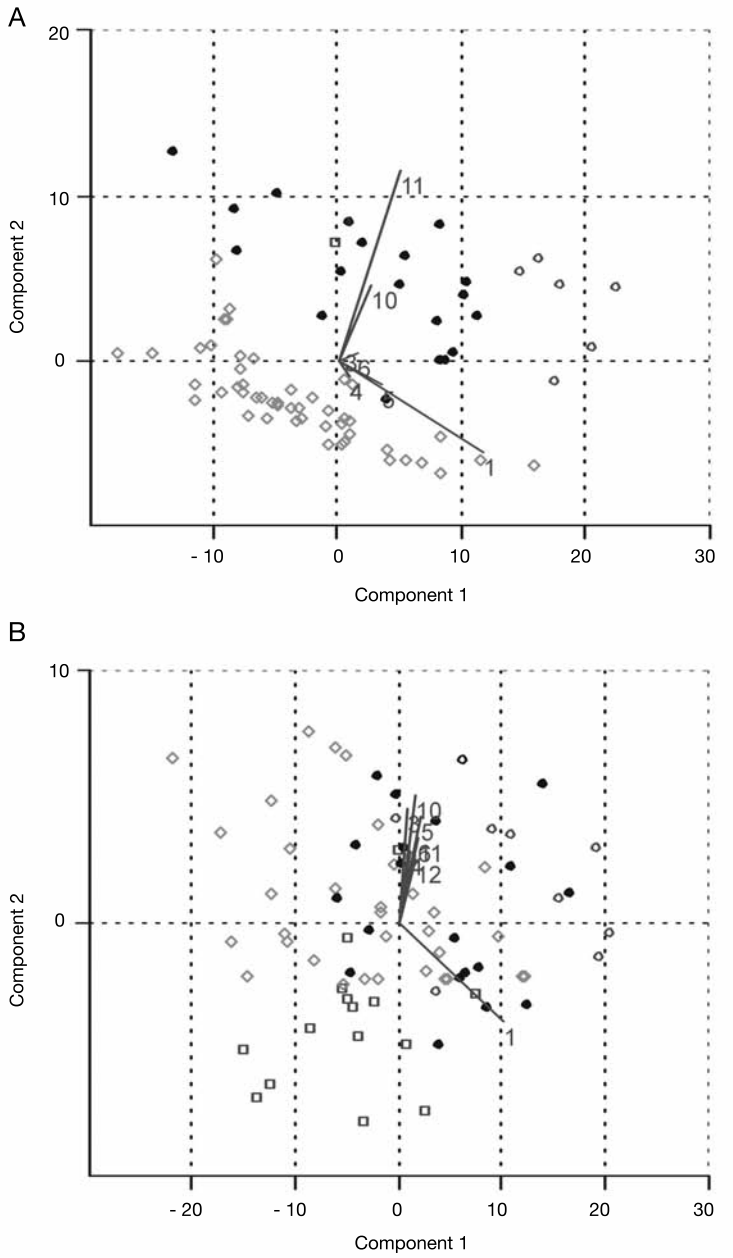

FIG. 7. — PCA plots giving the relations of the metacarpal (**A**) and metatarsal (**B**) of *Hipparion brachypus* from Akkaşdağı with other similar forms from various localities. ○, *H. brachypus* (Akkaşdağı); ●, *H. brachypus* (Hadjidimovo); □, *H. brachypus* (Pikermi); ◇, robust form (Maragha).

Samos locality. Several specimens from Samos with morphology similar to that of *H. brachypus* exist in the collections of some European museums (Weimar, Lausanne, München). These observations suggest the possible presence of *H. brachypus* in the Samos fauna, dated to about 7.5 Ma (Q4) to 7.1 Ma (MTLB), being in agreement with the age (7.1 Ma) of the Akkaşdağı locality (Kostopoulos *et al.* 2003; Karadenizli *et al.* 2005).

The metapodials of the studied form appear to be similar to those of *H. brachypus* from Pikermi, but they are larger. This difference is well reflected in the PCA of MCIII and MTIII (Fig. 7). The robusticity index of MCIII and MTIII (m11 × 100/m1) is 18.7 and 16.2 versus 17.9 and 16 for *H. brachypus* from Pikermi respectively, indicating that the Akkaşdağı sample proportionally resembles *H. brachypus* from Pikermi.

The metacarpal of *H. brachypus* from Hadjidimovo is similar to the Pikermi one, but it differs in having stronger distal articular facet as on the Akkaşdağı metacarpal (m11, m12, m13, m14 in Fig. 8). The metacarpal from Samos Q4 referred to "*H.* cf. *proboscideum*" (Sondaar 1971) is generally larger than that from Pikermi, and close to the Akkaşdağı sample in its length, the mid-shaft width and the depth of the distal articular keel. On the other hand, they sharply differ in their reduced mid-shaft depth, proximal and distal articular dimensions (Fig. 8). The sample from Samos Q1 differs from Akkaşdağı one in being slightly shorter and in having narrower proximal articular depth (m6) and narrower distal supra-articular and articular breadth (m10, m11). Since the large-sized skull from Samos Q4 (AMNH 22838) is closer to *H. brachypus*, there is a great possibility for the metacarpals from Q4 to belong to the same species. Similarly, the large-sized form from Kemiklitepe A-B, that had been referred as *Hipparion* sp. with affinities to *H. proboscideum* (Koufos & Kostopoulos 1994), must also belong to *H. brachypus* since its metacarpals are similar to "*H.* cf. *proboscideum*" from Q4 (Fig. 8). The metacarpals from Polgardi and Grebeniki, referred to *H. brachypus* by Eisenmann (1995), are basically similar each other and significantly smaller than all *H. brachypus* samples (Fig. 8).

On the contrary, the metatarsal of *H. brachypus giganteum* (Eisenmann 1995) from Grebeniki (Ukraine) is closer to *H. brachypus* group (Fig. 9). It tracks closely the third metatarsal from Hadjidimovo and both differ from Pikermi in having larger proximal and distal articular dimensions (Fig. 9). The Akkaşdağı metatarsal is striking by its larger size comparatively to that of Pikermi and diverges from Hadjidimovo and Grebeniki samples in having deeper proximal articular facet and larger distal articular dimensions (m10, m11, m12 in Fig. 9). The metatarsal of "*H.* cf. *proboscideum*" from Samos Q4 provides similar results as the metacarpal, being closer to the Akkaşdağı one, but more robust (Fig. 9). The sample from Kemiklitepe A-B (Turkey) includes two incomplete metatarsals, KTA-577 (proximal part) and KTA-579 (distal part) both described as *Hipparion* sp. (Koufos & Kostopoulos 1994). The distal part seems to be closer to the Akkaşdağı metatarsal, but slightly larger (probably due to the scanty material), while the proximal part is better compared to *H. mediterraneum*, the smaller hipparion form of KTA-B locality (Fig. 9). Therefore, contrary to the initial suggestion, the two metatarsals from KTA-B possibly belong to *H. brachypus* (KTA-579) and to *H. mediterraneum* (KTA-577).

The astragalus dimensions of the Akkaşdağı form are also larger than those of Pikermi confirming once more the size difference between the two samples. The significantly larger tuber calcaneum (measurements C4, C5 in Fig. 10), compared to *H. brachypus* from Pikermi, and the larger dimensions of the distal part of the calcaneum (measurements C6, C7 in Fig. 10), which is possibly correlated to the size and body weight of the animal (Vlachou & Koufos 2002), reinforce the size superiority of the studied form.

The correlation of the first and second phalanx of the Akkaşdağı sample to those of *H. brachypus* from Pikermi and *Hipparion* sp. from KTA-B is depicted in Figure 11. The first phalanx of the studied form compared to *H. brachypus* from Pikermi is longer, its diaphysis narrower, its supra

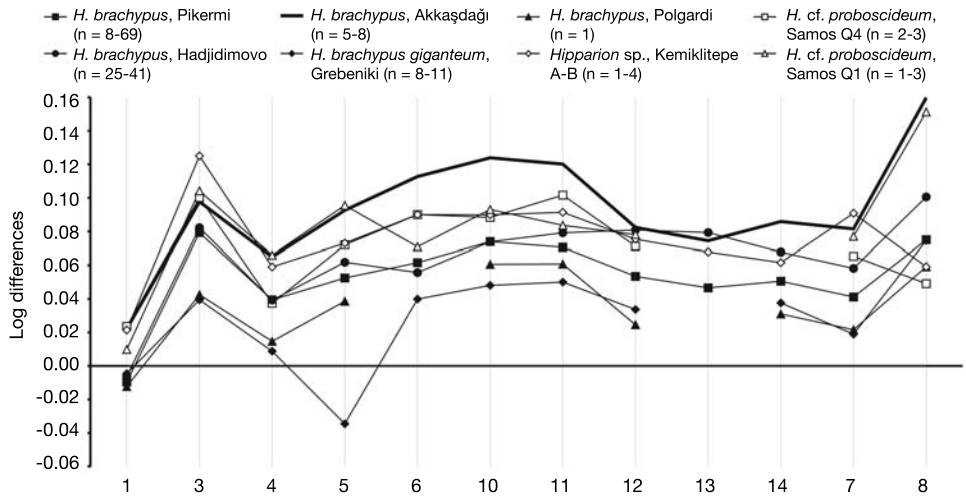

FIG. 8. — Logarithmic ratio diagram comparing the third metacarpal of *Hipparion brachypus* from Akkaşdağı with *H. brachypus*, *H.* cf. *proboscideum* and *H.* sp. from various localities. Standard *H. mediterraneum*, Pikermi, n = 12-39 (Koufos 1987a).

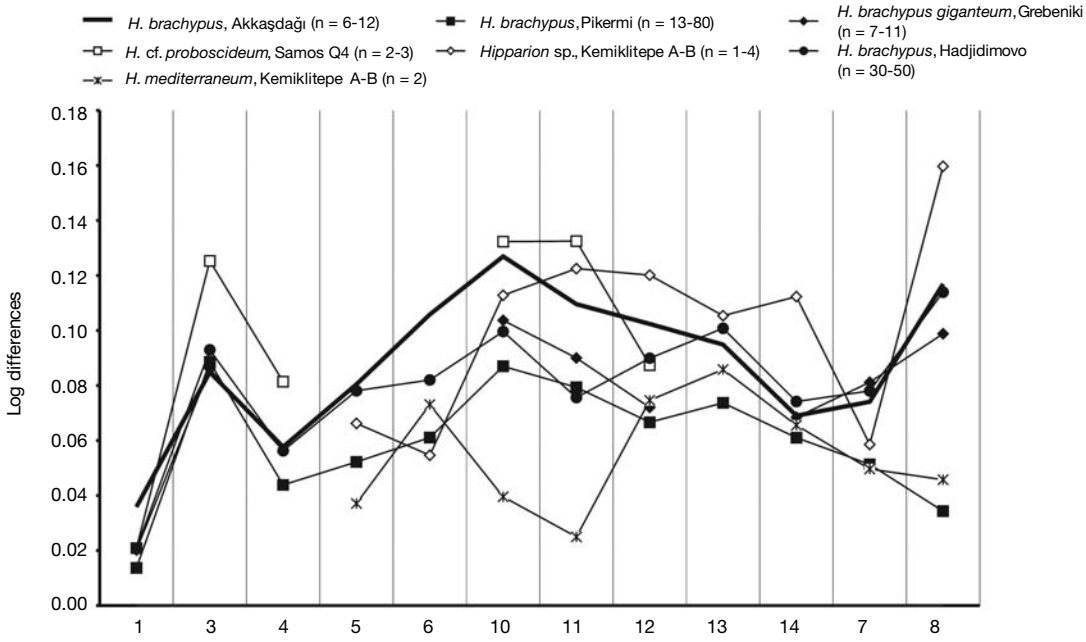

FIG. 9. — Logarithmic ratio diagram comparing the third metatarsal of *Hipparion brachypus* from Akkaşdağı with *H. brachypus*, *H.* cf. *proboscideum* from various localities and *H. mediterraneum* and *H.* sp. from Kemiklitepe A-B. Standard *H. mediterraneum*, Pikermi, n = 11-65 (Koufos 1987a).

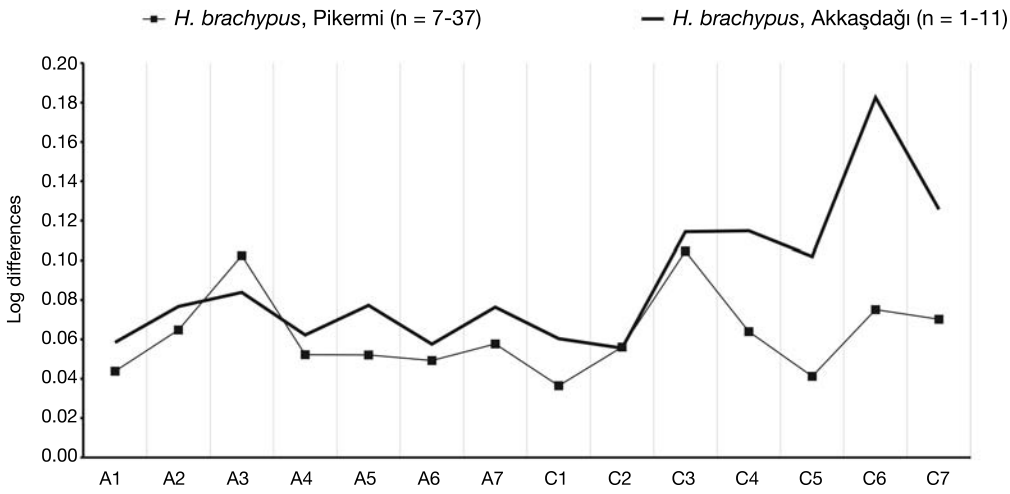

FIG. 10. — Logarithmic ratio diagram comparing the astragalus and calcaneum of *Hipparion brachypus* from Akkaşdağı with *H. brachypus* from Pikermi. Standard *H. mediterraneum*, Pikermi, n = 6-27 (Koufos 1987a).

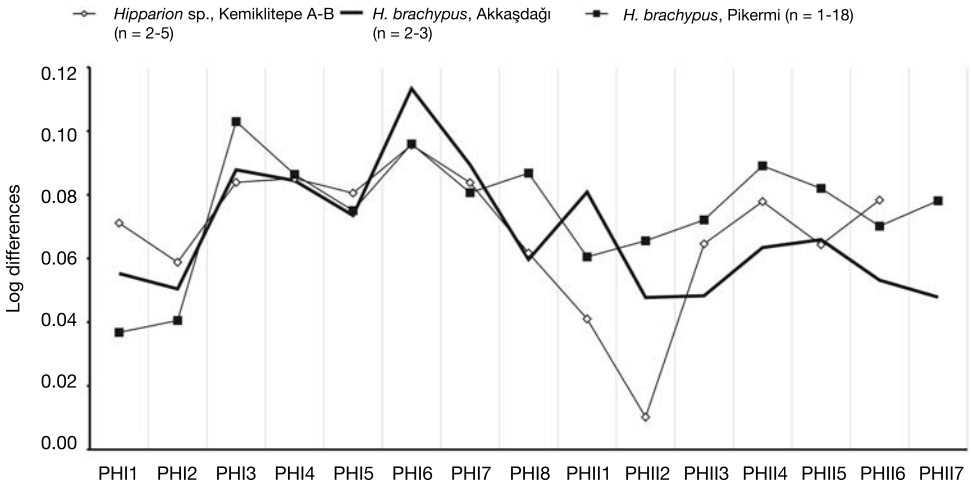

FIG. 11. — Logarithmic ratio diagram comparing the first and second phalanges of *Hipparion brachypus* from Akkaşdağı with *H. brachypus* from Pikermi and *H.* sp. from Kemiklitepe A-B. Standard *H. mediterraneum*, Pikermi, n = 2-8 (Koufos 1987a).

articular width larger, and its distal articular depth smaller (Fig. 11). Compared to *Hipparion* sp. from KTA-B the first phalanx from Akkaşdağı is shorter, and it has larger supra articular width (Fig. 11). The two samples, however, seem to be close to each other and could belong to the same species. The second phalanx of the studied species is slightly longer and more slender than that of *H. brachypus* from Pikermi (Fig. 11), while the second phalanx of *Hipparion* sp. from Kemiklitepe has closer proportions to the Akkaşdağı sample, but it has significantly shorter anterior length (measurement PHII2 in Fig. 11).

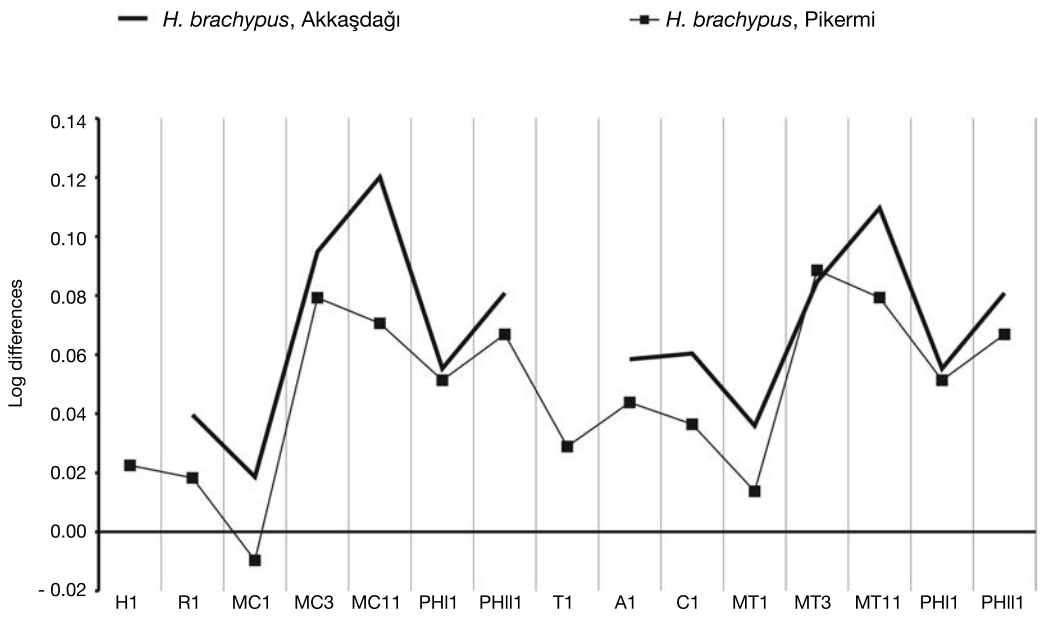

FIG. 12. — Logarithmic ratio diagram comparing the front and hind legs of *Hipparion brachypus* from Akkaşdağı with *H. brachypus* from Pikermi. Standard *H. mediterraneum*, Pikermi (Koufos 1987a).

The front and hind leg of the studied hipparion are compared in Figure 12. The Akkaşdağı form is generally slightly larger than *H. brachypus* from Pikermi with significantly broader distal epiphysis in the metapodials. This fact correlated to the slightly larger skull (Fig. 3) indicates that the Akkaşdağı form is larger than the typical *H. brachypus* from Pikermi although its proportions as well as the skull and dental morphology are similar. Consequently, the Akkaşdağı form can be determined as *H. brachypus*. The similarity of some large-sized forms from Samos Q4 (Greece) and Kemiklitepe (Turkey) with the Akkaşdağı *H. brachypus* indicates that this species must also be present in these localities.

Hipparion cf. *longipes* Gromova, 1952

LOCALITY. — Akkaşdağı, Keskin, Turkey.

AGE. — Middle Turolian, MN 12 (late Miocene).

MATERIAL. — Left maxilla with P2-M3, AK7-69; right maxilla with P2-M3, AK7-70; 19 distal parts of humerus, AK2-16, 101, 232, AK3-91, 148, 226, AK5-177, 391, 464, AK5-83, AK6-21, AK7-2, 3, 47, 89, AK11-3, 50, 51, 111; radius+ulna, AK2-234; 2 radii, AK3-259, AK11-122; 2 proximal parts of radius+ulna, AK3-214a-b, AK5-221; proximal part of radius, AK5-84; 9 third metacarpals, AK2-393, AK3-1, 139, 260, AK5-478, 479, AK6-107, 273, AK14-n.n.; 2 McII+McIII+McIV, AK2-244a-c, 24; proximal part of McIII+carpals, AK5-220; proximal part of McII+McIII+McIV, AK4-98; distal part of tibia+tarsals+MtII+MtIII+MtIV, AK11-99a-i; 17 distal parts of tibia, AK2-19, 262, AK3-7, 157, 268, AK5-400, 402, 470, 471, 555, AK6-183, 221, 256, AK12-43, 44, 45, AKK-274; astragalus+calcaneum, AK2-103; 30 astragali, AK2-103, 25, 264, AK3-20, 21, 103, 104, 228, 270, AK4-25, 28, 30, 32, 156, AK5-99, 169, 170, 175, 403, 582, 583, 580, AK6-12, 112, 149, 214, 215, AK7-137, AKK-167, 170; 5 calcanei, AK4-157, AK5-65, 178, 130, 131; 2 MtII+MtIII+MtIV, AK11-136, 137; 12 third metatarsals, AK2-1, 3, 242, 400, AK3-86, 88, AK4-165, AK5-72, 73, 153, AK14-4, 11; 7 proximal parts of MtIII, AK2-6, AK3-3, AK4-1, 11, 35, 166, AK7-1; 4 distal parts of MtIII, AK3-141, AK5-156, AK11-43, AK13-16; PhI+PhII, AK4-103; 2 first phalanges, AK5-587, AK5-115; 5 second phalanges, AK3-163, AK4-16, 178, AK6-277, AKK-188; 4 third phalanges, AK5-418, AK7-97, 113, AK11-120; part of a third phalanx, AK6-49.

Description

Dentition

The upper toothrow is long with elongated and narrow teeth which are little worn; the M3 is just erupted and unworn (Fig. 13). The P2 has elongated anterostyle, bended lingually; the fossettes are closed. In the P3, 4 the mesiolabial part of the postfossette is still in touch with the mesostyle's enamel but this is due to the early wearing stage. The enamel plication is rich with deep and narrow plis; the mean plication number is 21.0 for the premolars and 20.5 for the molars. Both studied maxillae are at the first wearing stage, and this means that the enamel plication number will increase somewhat in the second wearing stage. The protocone is elliptical and flattened lingually, especially in the premolars. In the P2 it bears a "spur". The pli caballin is strong, double in the premolars and simple in the molars. The hypocone is elongated and angular with deep and open distal hypoconal groove, while a slight lingual hypoconal groove is also present, especially in the premolars.

Postcranials

The postcranials of this hipparion are large and slender. The metapodials are very elongated and slender (Fig. 14). The metacarpal is relatively long with narrow epiphyses. The index Length McIII × 100/Length radius is 80, and the robusticity index is 14.7, both indicating a slender metacarpal form. The keel index (m12 × 100/m13) of the studied metacarpal is 122.8 indicating a relatively prominent keel (not well prominent). Similarly the metatarsal is very long and slender. The robusticity index is 13.5 confirming its slenderness, and the keel index (m12 × 100/m13) is 126.9 indicating also a relatively prominent keel.

Fig. 13. — *Hipparion* cf. *longipes*, Akkaşdağı, Turkey, right upper toothrow, AK7-70, occlusal view. Scale bar: 2 cm.

Comparisons

A large-sized hipparion from Pavlodar (Kazakhstan) having very long and slender metapodials was described under the name *H. longipes* by Gromova (1952). The type collection of *H. longipes* includes only isolated teeth (Gromova 1952). Two maxillary fragments from Akkaşdağı can belong to this species. Their toothrow length varies between 162.5 and 169.0 mm, while in *H. brachypus* Pikermi it varies between 147.0 and 168.3 mm with a mean value of 154.86 mm (Koufos 1987a). Such a large-sized hipparion with very long and slender metapodials is

FIG. 14. — *Hipparion* cf. *longipes*, Akkaşdağı, Turkey; **A**, third metacarpals, AK6-273, AK3-260, AK11-23; **B**, third metatarsals, AK5-153, AK2-3, AK3-86. Scale bars: 2 cm.

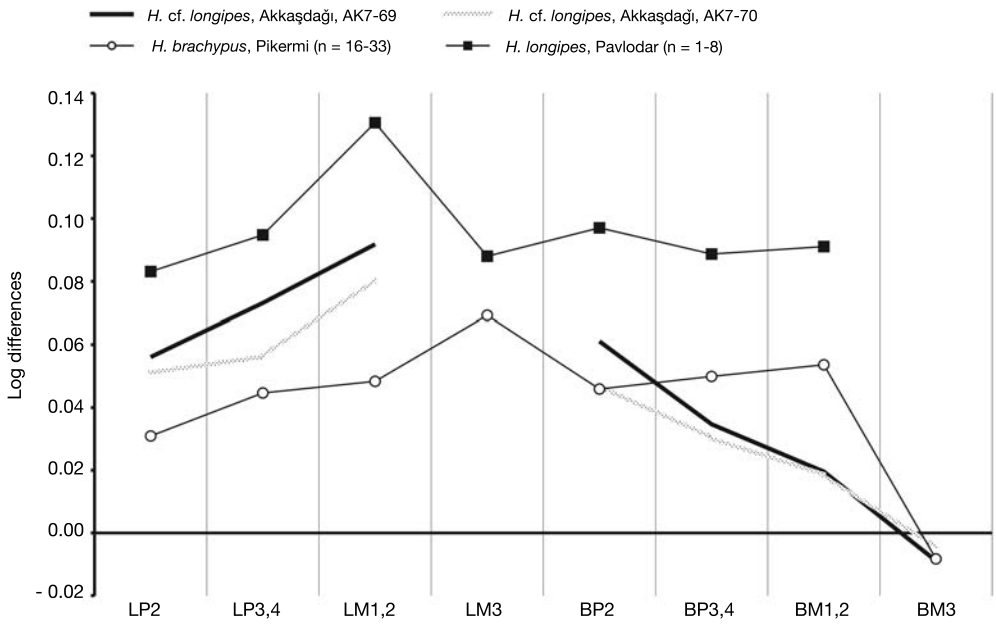

FIG. 15. — Logarithmic ratio diagram comparing the dimensions of the upper teeth of *Hipparion* cf. *longipes* from Akkaşdağı with *H. longipes*, *H.* cf. *longipes* and *H. brachypus* from various localities. Standard *H. mediterraneum*, Pikermi, n = 10-32 (Koufos 1987a).

unknown in the Turolian of Eastern Mediterranean region.

In the original description of the type material from Pavlodar, Gromova (1952) noted that the upper teeth of *H. longipes* are characterized by their large size, short and wide protocone and moderate enamel plication. In the revision of the Pavlodar material, Forstén (1997) noted that the upper teeth are moderately hypsodont, the protocone is apparently flattened lingually and often preserves a "spur", the plication number is medium to high (22.7 ± 1.5 plis) and the hypocone has occasionally a hypostylar foramen. The Akkaşdağı sample has similar morphology and dimensions to those of *H. longipes*. In Figure 15 the dental dimensions of the studied specimens are compared with *H. longipes* from Pavlodar (measurements from Gromova 1952 and Forstén 1997), as well as with the large-sized *H. brachypus* from Pikermi (Koufos 1987a). There are no significant differences in the dental size between the studied material, *H. brachypus* from Pikermi and *H. longipes* from Pavlodar. The Akkaşdağı form has possibly narrower teeth, but we wonder if this is due to the wearing stage or to the way of measuring. However, the teeth length is close to the maximum values for *H. brachypus* and closer to *H. longipes*.

The metapodials of *H. longipes* from Pavlodar are long and slender (Gromova 1952). The index Length McIII × 100/Length radius is 80 in Akkaşdağı sample, while the robusticity index is 14.7 for McIII and 13.5 for MtIII, suggesting elongated and slender metapodials. The corresponding index for *H. longipes* of Pavlodar varies between 14.5 and 14.9 for McIII and 12.5 and 12.9 for MtIII (Gromova 1952; Eisenmann & Sondaar 1998). Comparatively to *H. longipes* from Pavlodar, the metacarpals from Akkaşdağı are slightly shorter with reduced mid-shaft depth and pronounced supra-articular width (measurements 1, 4, 10 in Fig. 16). It is worth mentioning here that the Pavlodar sample is poor (one to two specimens) to appreciate the variation of these characters. One proximal part of metacarpal belonging to a large-sized and slender form is

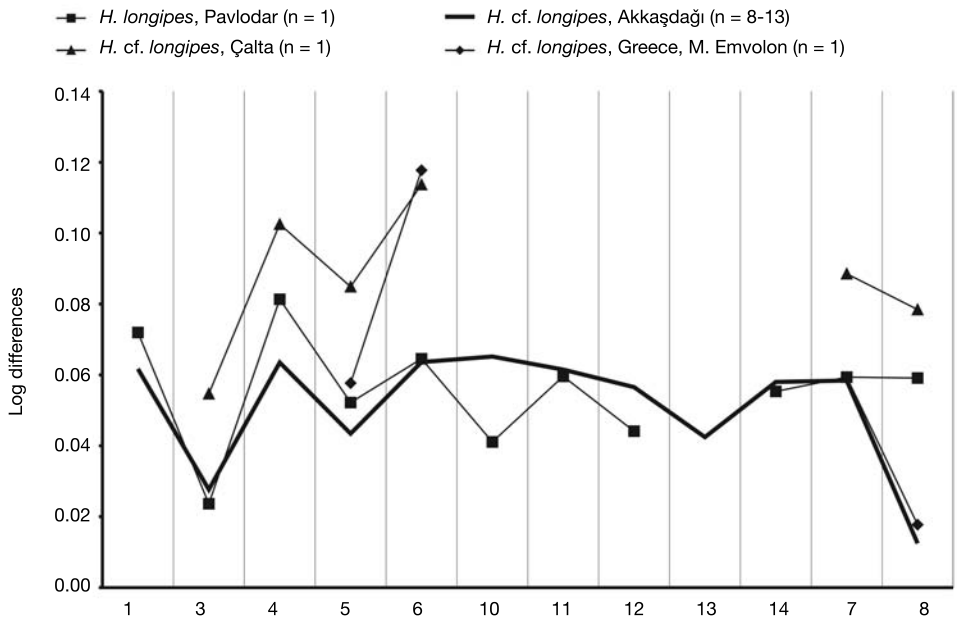

FIG. 16. — Logarithmic ratio diagram comparing the third metacarpal of *Hipparion* cf. *longipes* from Akkaşdağı with *H. longipes* and *H.* cf. *longipes* from various localities. Standard *H. mediterraneum*, Pikermi, n = 12-39 (Koufos 1987a).

known from the Pliocene (MN 15) locality of Çalta, Turkey. It was first referred to *H. longipes* (Heintz *et al.* 1975) and later to *H.* cf. *longipes* (Eisenmann & Sondaar 1998). This partial metacarpal seems to be larger than the typical *H. longipes* of Pavlodar and those from Akkaşdağı (Fig. 16). The proximal part of a metacarpal from Megalo Emvolon (MN 15) (Macedonia, Greece) was referred to as *H. gracile* (Arambourg & Piveteau 1929). It is a large-sized form with proximal articular width similar to that of the typical *H. longipes* from Pavlodar, but the proximal articular depth is significantly larger, and similar in that to *H.* cf. *longipes* from Çalta (Koufos *et al.* 1991). The Akkaşdağı metatarsal is closer to the typical *H. longipes* from Pavlodar and to *H.* cf. *longipes* from Çalta, but it is shorter and its distal articular depth quite smaller (Fig. 17).

The astragalus and calcaneum are also compared with those of *H. longipes*. The dimensions of the astragalus are generally smaller than those of the typical *H. longipes*, while those of calcaneum seem to be similar (Fig. 18).

The similarity of the studied form with *H. longipes* from Pavlodar is also observable on the logarithmic ratio diagram that compares the first and second phalanges of the Akkaşdağı form to those of *H. longipes*. The first phalanx is similar in size to *H. longipes* from Pavlodar, but it is significantly shorter than that of Çalta (Turkey) and Megalo Emvolon, Greece (Fig. 19). Moreover, the Megalo Emvolon first phalanx seems to be more slender than that of Pavlodar, Çalta and Akkaşdağı (Fig. 19). These differences are due either to the age differences between the localities or to the differences between the phalanges of front and hind leg. The second phalanx of the studied form is also very close to *H. longipes* from Pavlodar (Fig. 19). The Çalta material is again larger than that of the Akkaşdağı and Pavlodar samples (Fig. 19).

A comparison of both legs of the Akkaşdağı material with *H. longipes* from the type locality of

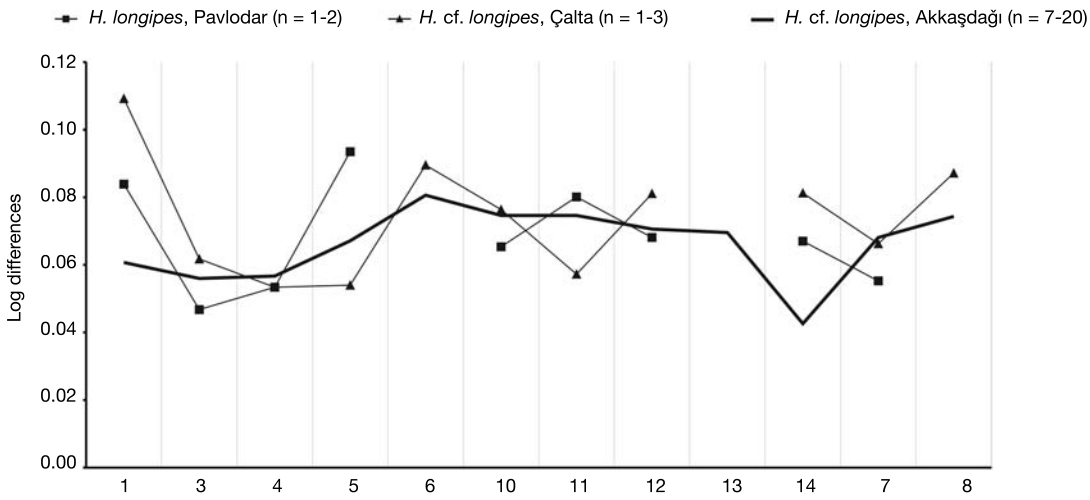

FIG. 17. — Logarithmic ratio diagram comparing the third metatarsal of *Hipparion* cf. *longipes* from Akkaşdağı with *H. longipes* and *H.* cf. *longipes* from various localities. Standard *H. mediterraneum*, Pikermi, n = 11-65 (Koufos 1987a).

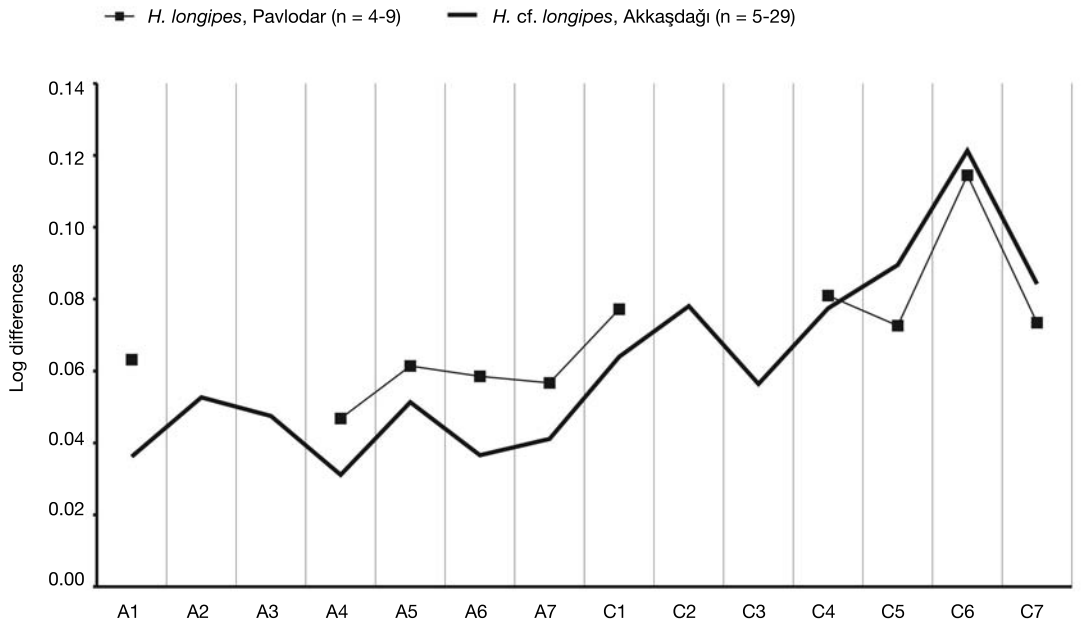

FIG. 18. — Logarithmic ratio diagram comparing the astragalus and calcaneum of *Hipparion* cf. *longipes* from Akkaşdağı with *H. longipes* from Pavlodar. Standard *H. mediterraneum*, Pikermi, n = 6-27 (Koufos 1987a).

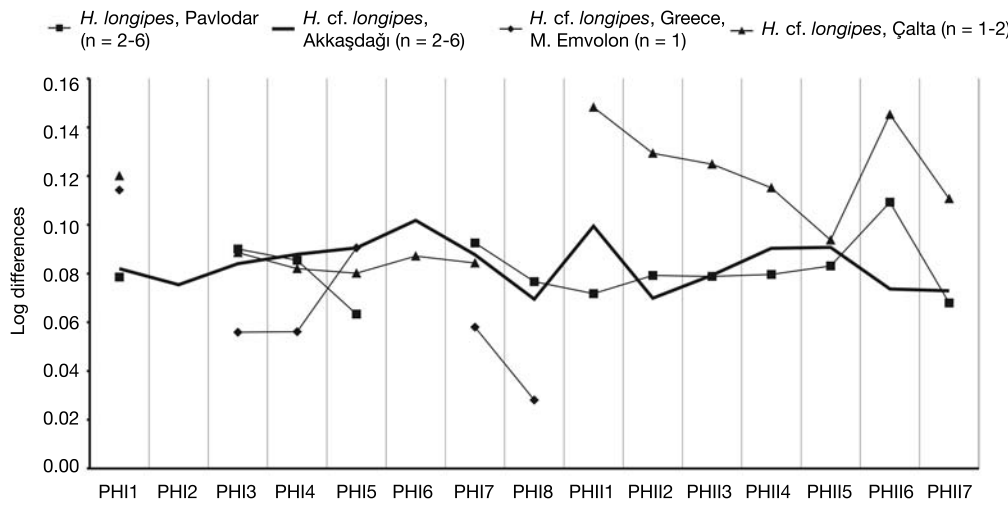

Fig. 19. — Logarithmic ratio diagram comparing the first and second phalanges of *Hipparion* cf. *longipes* from Akkaşdağı with *H. longipes* and *H.* cf. *longipes* from various localities. Standard *H. mediterraneum*, Pikermi, n = 2-8 (Koufos 1987a).

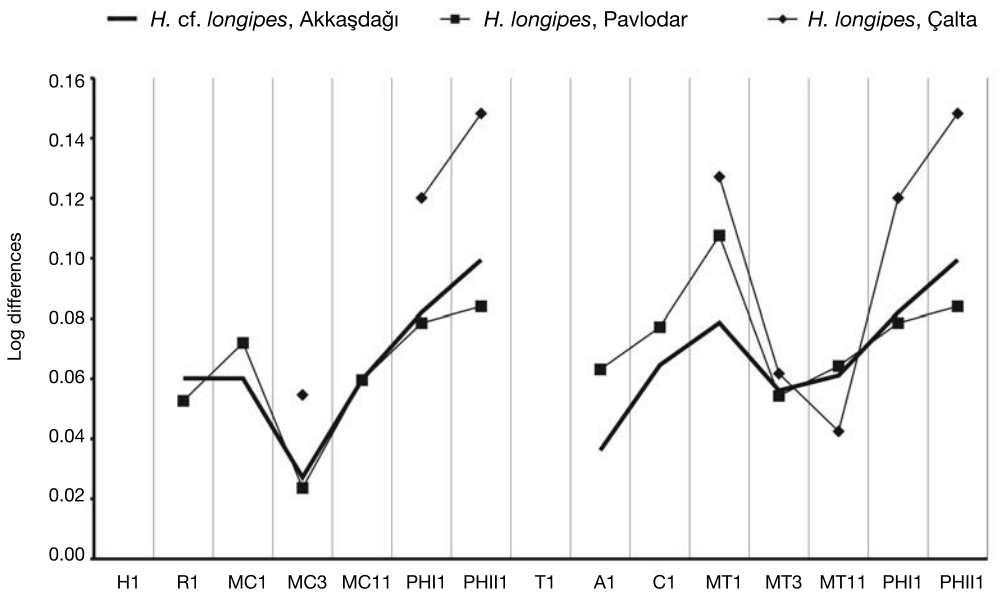

Fig. 20. — Logarithmic ratio diagram comparing the front and hind legs of *Hipparion* cf. *longipes* from Akkaşdağı with *H. longipes* from Çalta and Pavlodar. Standard *H. mediterraneum*, Pikermi, n = 3-61 (Koufos 1987a).

Pavlodar, as well as from Çalta, is given in Figure 20. It is quite clear from the diagram that the Akkaşdağı form is closely related to the type form; their lines are parallel and very close to each other, indicating a similar size. The small differences are possibly due to the scanty material from both localities. On the other hand the Çalta form is significantly larger than the Akkaşdağı form with relatively narrower metatarsal (measurements 3, 11 in Fig. 20). This size difference is possibly due to the younger age of the Çalta material (Sen *et al*. 1998a).

Taking into account all the above mentioned data, the very large and slender form from Akkaşdağı is morphologically and proportionally close to *H. longipes* from Pavlodar. However, the unknown skull morphology and the limited dental morphology of *H. longipes*, as well as the poor material from its type locality cannot allow a certain determination for the studied material. Thus, it is referred to as *Hipparion* cf. *longipes*. However, if the presence of *H. longipes* in the Akkaşdağı fauna is a fact, it could mean that: 1) *H. longipes* appeared in Asia earlier than in its type locality Pavlodar which is correlated to late Turolian (MN 13), and survived in Greece and Turkey during Ruscinian; 2) the Turolian *H. longipes* (Pavlodar, Akkaşdağı) is smaller in size than the Ruscinian one from Çalta and Megalo Emvolon indicating an evolutionary size increase. However, the poor material referred to *H. longipes*, and especially the absence of skull, do not allow to testify the previous thoughts about the origin and dispersal of this species.

Hipparion dietrichi Wehrli, 1941

LOCALITY. — Akkaşdağı, Keskin, Turkey.

AGE. — Middle Turolian, MN 12 (late Miocene).

MATERIAL. — Skull, AK3-211; anterior part of the skull with I1-M3 dex and sin, AK2-499; anterior part of the skull with the muzzle and P2-M3 dex and sin, AK3-234; maxilla with P2-M3, AK6-136; maxilla with P2-M3, dex and sin, AK5-n.n.; maxilla with P3-M3, AK11-83; maxilla with dP4-M2 dex and P3-dP4-M2 sin, AK2-498; right maxillary fragment with P2-M3, AK2-46; right maxillary fragment with P3-M3, AK2-172; right maxillary fragment with P4-M2, AK2-175; right maxillary fragment with P3-M2, AK2-173; right maxillary fragment with P2-P3, AK4-59; left maxillary fragment with P4-M3, AK3-170; left maxillary fragment with P2-M1, AK5-510; right maxillary fragment with P3-M3, AK7-71; maxillary fragment with P4-M3 sin, AK6-137; maxillary fragment with P3-M2 sin, AK14-19; 2 maxillary fragments with M2-M3 dex, AK14-18, AK7-115; 4 mandibles, AK2-177, 51, AK4-129, AK5-530; left and right mandibular fragment with p2-m3, AK2-357, 358; mandibular fragment with p2-m1 sin, AK2-119; mandibular fragment with p2-m3 sin, AK5-33; mandibular fragment with m1-m3 sin, AK5-645; mandibular fragment with c-m1 dex and m1-m2 sin, AK6-129; 5 distal parts of humerus, AK2-327, AK3-92, AK6-19, 268, AK7-114; humerus+radius, AK6-222; 2 radii, AK5-467, AK7-49; 4 proximal parts of radius, AK3-n.n., AK5-8a, AK5b-102, AK6-103; 5 distal parts of radius, AK2-392, AK3-215, AK4-249, AK6-147, AK11-115; 5 third metacarpals, AK3-140, AK5-394, 476, 477, AK6-4; 3 McII+McIII+McIV, AK11-56a-c, 133, 134; 3 proximal parts of McIII, AK3-4, 264, AK11-20; 3 distal parts of McIII, AK2-8, AK5-219, AK7-44; distal part of tibia+astragalus+tarsals+MtII+MtIII+MtIV, AK11-5-13; distal part of tibia+astragalus+calcaneum+navicular, AK6-263a-c; distal part of tibia+astragalus+calcaneum, AK6- 264a-b; 14 distal parts of tibia, AK3-146, AK4-2, 34, AK5-554, 556, 558, 559, AK7-92, AK11-12, 38, 41, 44, 128, AK12-46; astragalus+tarsals+MtII+MtIII+MtIV, AK6-181; astragalus+calcaneum, AK5-10a-b, AK11-15; astragalus+tarsals, AK2-28a-b; 20 astragali, AK3-19, 153, AK4-14, 101, AK5-98, 168, 173, 404, 581, 584, AK6-10, 111, 113, 148, 220, 314, AK7-11, 50, 136, 137; 9 calcanei, AK2-30, AK2-32, 272, AK4-31, AK5-12, 405, 473, n.n., AK7-112; 8 partial calcanei, AK-2-29, 32, AK3-18, AK4-27, AK5-111, AK11-15, 16, 33; 2 MtII+MtIII+MtIV, AK5-563, AK11-42a-c; 12 third metatarsals, AK2-96, 401, AK5-158, 408, 409, 481, 482, 485, AK5b-n.n., AK6-108, 181, 270; 7 proximal parts of MtIII, AK2-7, AK3-2, 277, AK5-566, AK6-109, AK12-50, 51; 6 distal parts of MtIII, AK2-9, AK3-85, AK5-157, AK6-8, AK10-15, AK11-25; PhI+PhII, AK6-274a-b; 7 first phalanges, AK5-116, 162, 415, 588, AK6-119, 265, AKK-149; distal part of first phalanx, AK6-45; 7 second phalanges, AK2-33, AK5-118, 419, 589, AK5a-121, AK6-159, 266; 3 third phalanges, AK4-15, AK5-496, AK11-119; part of a third phalanx, AK5-165.

DESCRIPTION

Skull and dentition

The studied form corresponds to the medium- to large-sized hipparion of Akkaşdağı. Contrary to the abundance and good preservation state of the postcranials, the cranial and mandibular remains are fragmentary. All available skulls

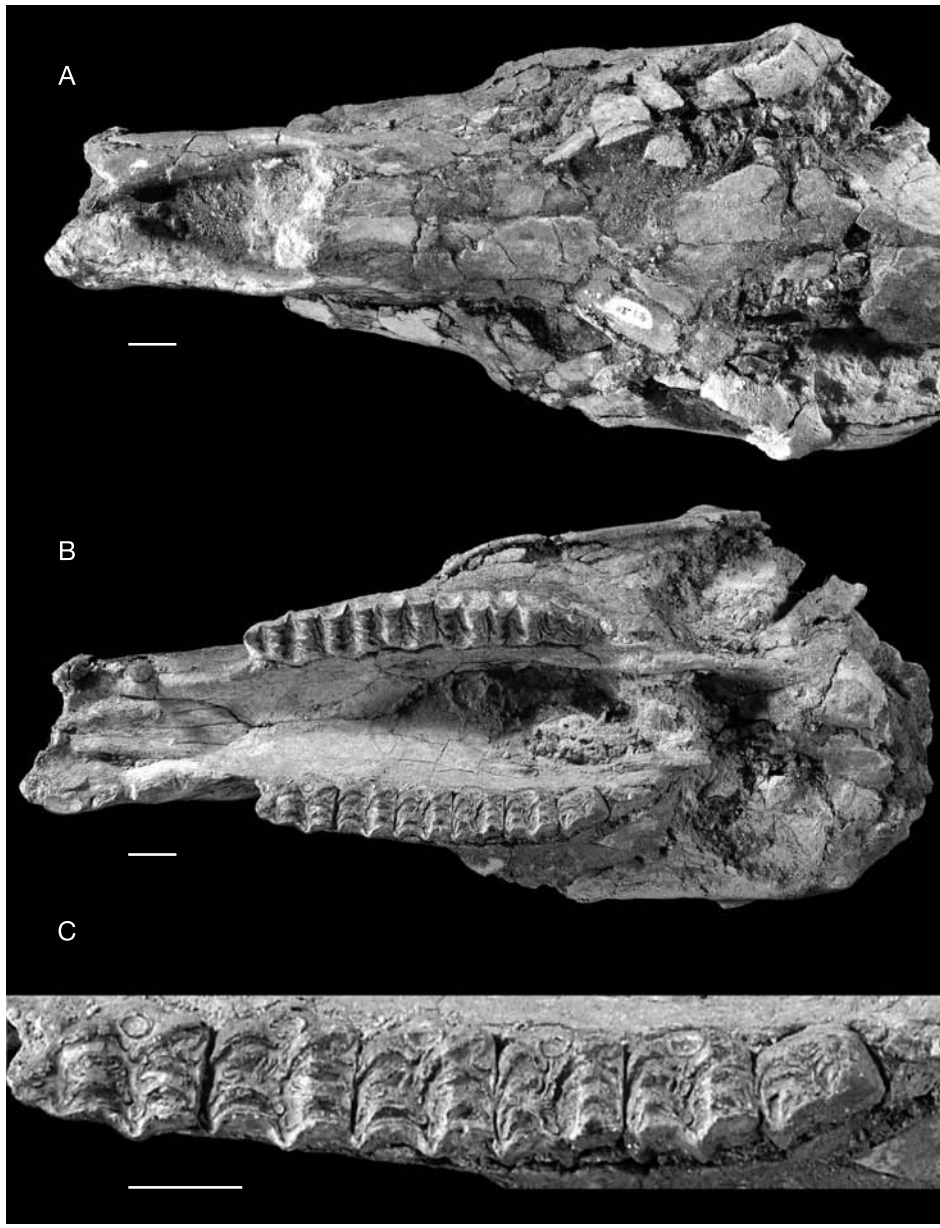

FIG. 21. — *Hipparion dietrichi*, Akkaşdağı, Turkey, skull, AK3-211; **A**, dorsal view; **B**, ventral view; **C**, right toothrow, occlusal view. Scale bars: 2 cm.

lack the braincase, and in most of them the muzzle is broken. The most complete skulls are AK3-211, AK2-499 and AK3-234 (Figs 21-23), preserving either the facial region with the preorbital fossa or the muzzle. The AK3-211 is so badly preserved and dorsoventrally compressed that its morphological characters cannot be safely used. Consequently, the description is mainly based on the last two skulls, AK2-499 and AK3-234.

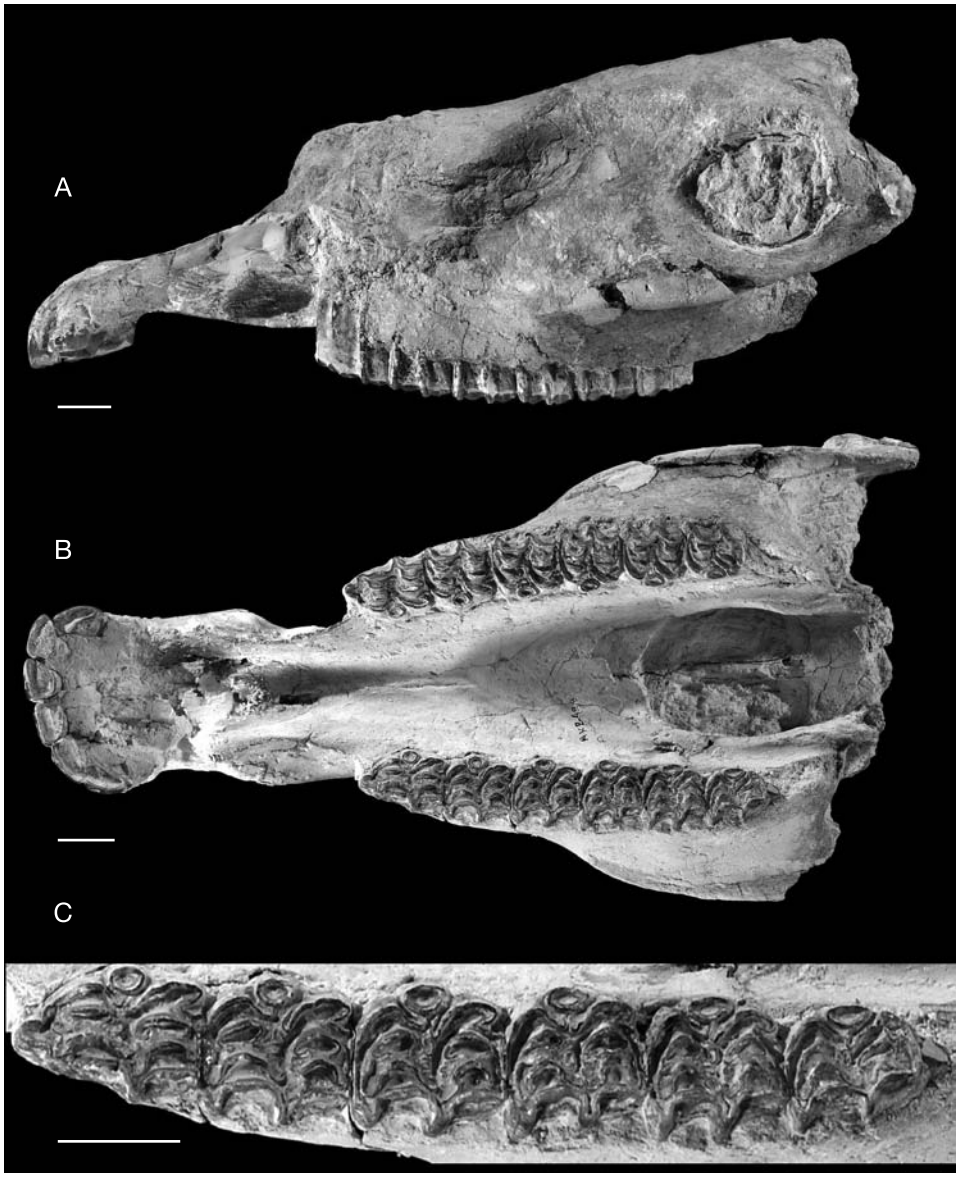

FIG. 22. — *Hipparion dietrichi*, Akkaşdağı, Turkey, skull AK2-499; **A**, lateral view; **B**, ventral view; **C**, right toothrow, occlusal view. Scale bars: 2 cm.

The skull is medium- to large-sized with a very short, wide, U-shaped and deep muzzle. The narial opening is short and its posterior border is situated just above or in front of the P2. The palate is narrow, elongated and quite deep; the index m2 × 100/m13 is 136.4. The preorbital fossa is anteroventrally oriented, relatively narrow and elliptical, moderately deep (no more than 15 mm) with a well marked but no pocketed posterior rim and a faint anterior rim. It is situated far from the orbit and its posterior end is situated quite higher to the orbit (Fig. 22A). The lacrymal

FIG. 23. — *Hipparion dietrichi*, Akkaşdağı, Turkey, skull AK3-234; **A**, dorsal view; **B**, ventral view. Scale bar: 2 cm.

seems to be large but does not invade the preorbital bar. The crista facialis is well developed and its anterior end is placed close to the maxilla, situated above and between the contact of the P4 and M1. The infraorbital foramen is situated above the posterior border of the P2 and just inferior to the anteroventral rim of the preorbital fossa. The orbit is oval-shaped and its anterior border is situated well behind the M3.

The upper cheek teeth are relatively short and wide (Figs 21C; 23C). The P2 is elongated and it has a moderately developed anterostyle directed forward. The fossettes are free and isolated. The emamel plication is moderate with deep and rela-

FIG. 24. — *Hipparion dietrichi*, Akkaşdağı, Turkey, mandible AK5-530; **A**, ventral view; **B**, lateral view; **C**, left toothrow, occlusal view. Scale bars: 2 cm.

tively wide plis in the moderately worn teeth. The plication number is 12-27 in the P3,4 and 7-19 in the M1,2. The protocone is rounded in the premolars and elliptical in the molars. The pli caballin is long and usually simple to multiple in the premolars, while it is small and simple in the molars. The hypocone is elliptical with well developed and deep distal hypoconal sinus and lingual hypoconal sinus in M3 where it tends to be isolated.

The mandible (Figs 24; 25) has a wide snout. The index m2 × 100/m7 is 221.8 indicating a short snout. The symphysis is relatively elongated and deep. The cup seems to be large and wide

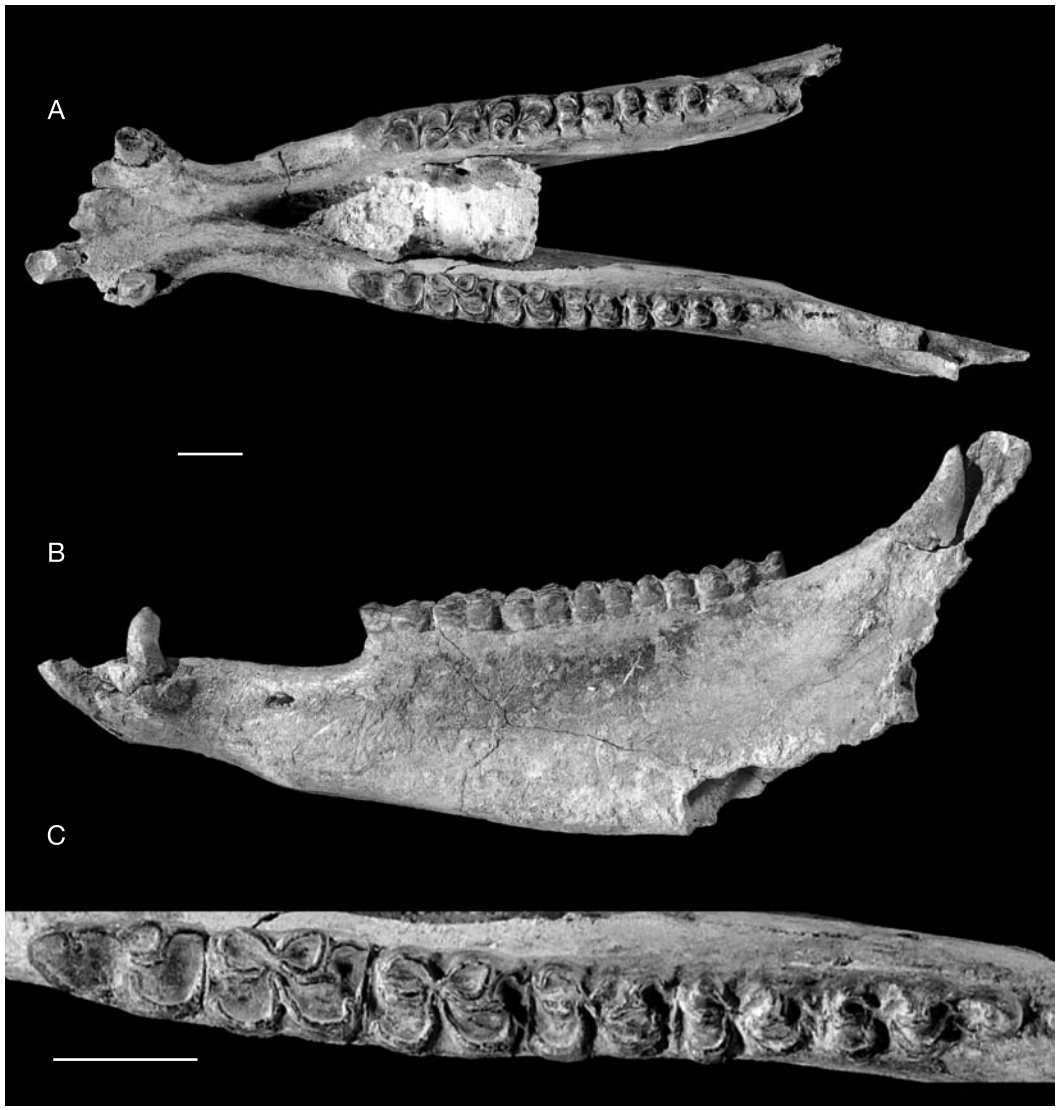

FIG. 25. — *Hipparion dietrichi*, Akkaşdağı, Turkey, mandible AK2-177; **A**, dorsal view; **B**, lateral view; **C**, left toothrow, occlusal view. Scale bars: 2 cm.

and the insisors are moderately curved. The horizontal ramus has moderate height. The premolars are relatively short and wide having a robust aspect (Figs 24C; 25C). The metaconid and metastylid are elliptical. The enamel at the flexid's borders is plicated or crenulated. The entoconid is elliptical in all teeth. The ectoflexid is moderately deep in the premolars, separating the pre- and post-flexid, and very deep in the molars touching the lingualflexid. The latter is open, U-shaped and shallow. The pli caballinid is simple in the premolars and simple or absent in the molars. The hypoconulid is well developed especially in the less worn teeth.

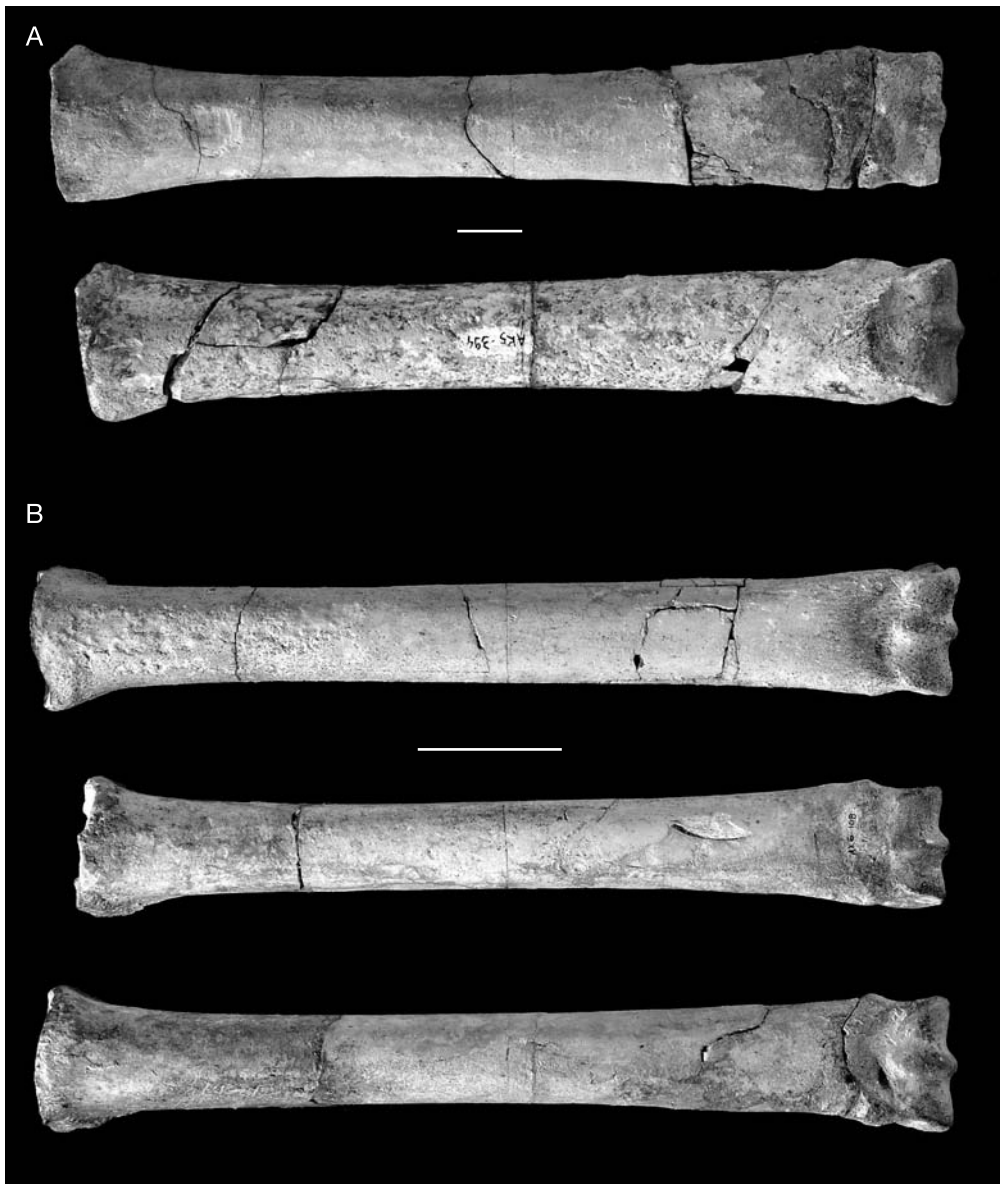

FIG. 26. — *Hipparion dietrichi*, Akkaşdağı, Turkey; **A**, third metacarpals, AK5-394, AK3-140; **B**, third metatarsals, AK5-409, AK5-408, AK6-108. Scale bars: 2 cm.

Postcranials

The metapodials are relatively long and slender (Fig. 26). The index Length McIII × 100/Length radius is 75.5 indicating a relatively long metacarpal. The robusticity index (m11 × 100/m1) is 16.0 for McIII and 14.3 for MtIII respectively, indicating long and relatively robust metapodials. The facet for cuneiforme II is always present. The keel index (m12 × 100/m13) is 120.4 for McIII and 128.4 for MtIII, indicating a well developed keel.

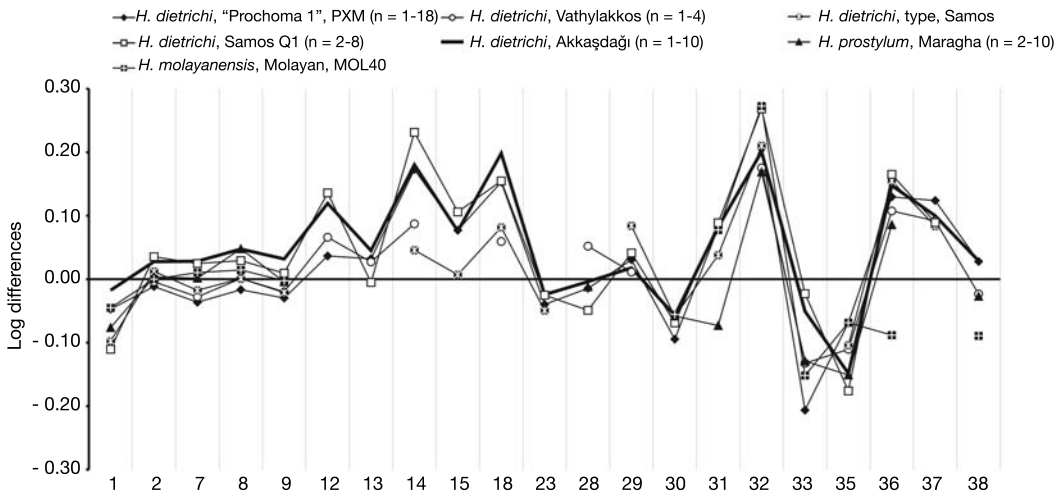

FIG. 27. — Logarithmic ratio diagram comparing the skull of *Hipparion dietrichi* from Akkaşdağı with other similar forms from various localities. Standard *H. mediterraneum*, Pikermi, n = 1-9 (Koufos 1987a).

COMPARISONS

H. dietrichi is the best known Old World hipparion and, according to Bernor *et al.* (1996a), belongs to "*Hipparion* s.s.-group" that derives from an Old World form belonging to the "*Hippotherium* Complex". It was originally described from Samos (locality unknown) as *Hemihipparion dietrichi* (Wehrli, 1941). Later, it was transferred to the genus *Hipparion* and for a long time it was considered as a local species of Samos. The main features that characterize the type specimen of *H. dietrichi* are: medium to large size, short and broad muzzle, short narial opening (above or in front of P2), oval-shaped and relatively shallow preorbital fossa situated quite far from the orbit and far above the facial crest, moderately plicated upper teeth, oval-shaped protocone and elongated and relatively slender metapodials (Sondaar 1971).

A set of skulls from Samos Q1 and Q4, stored in the AMNH, have been described as *H. dietrichi* by Sondaar (1971: pl. IIb). Some skulls from Adrianos ravine, stored in the Natural History Museum of Aegean, Samos, were also referred to *H. dietrichi* by Koufos & Melentis (1984). Later on, the species was recognized in the Turolian localities of "Ravin des Zouaves-5" (RZO), "Prochoma 1" (PXM), "Vathylakkos 1,2,3" (VLO, VTK, VAT) of the Axios Valley and in the locality "Nikiti 2" (NIK) of Chalkidiki, Greece (Koufos 1987b, c, 1988a; Vlachou & Koufos 2002). All these skulls share more or less the morphology of the type specimen. The Akkaşdağı skulls seem to be closely related to the sample of *H. dietrichi*, as they have several morphological affinities and metrical similarities (Figs 22; 27). Comparing the Akkaşdağı form to *H. dietrichi* from various localities, it has longer muzzle (measurement 1) and narrower preorbital fossa (measurement 35). Overall, the dimensions of the studied sample track those of *H. dietrichi* from Q1 and the larger toothrow length suggest a larger body mass compared to the rest of the sample (Fig. 27).

Another species closely related to *H. dietrichi* is *H. prostylum* which was also referred by Bernor *et al.* (1996a) to "*Hipparion* s.s.-group". *Hipparion prostylum* was originally described from Mont Lubéron by Gervais in 1849, and it was also mentioned from Pikermi, Thessaloniki and Middle Maragha (Bernor 1985; Watabe & Nakaya 1991b) but Koufos did not recognize this taxon neither in Pikermi nor in Axios Valley (Koufos 1987b). Two badly preserved skulls from Mont Lubéron are stored in the BMNH. One of them, BMNH 26617,

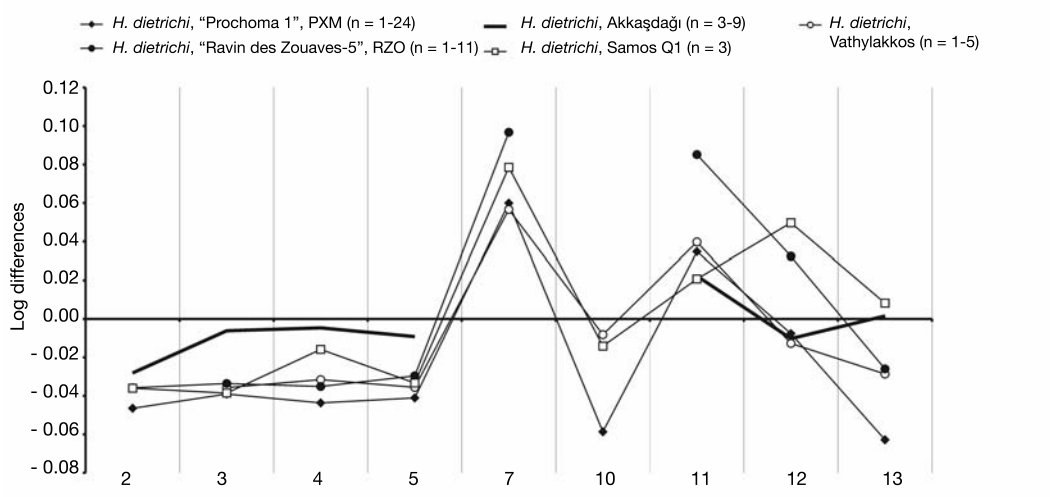

FIG. 28. — Logarithmic ratio diagram comparing the mandible of *Hipparion dietrichi* from Akkaşdağı with other similar forms from various localities. Standard *H. mediterraneum*, Pikermi, n = 2-24 (Koufos 1987a).

has an oval preorbital fossa, anteroposteriorly oriented and its anterior rim is well defined. The preorbital bar is long. The posterior border of the narial opening is situated above P2, while the muzzle is short (measurement 1 is 105 mm). These characters are common in *H. dietrichi* and, comparing the skull of *H. prostylum* from Maragha either to the type skull of *H. dietrichi* or to the skulls of *H. dietrichi* from Axios Valley and Samos, no more differences are observed except the well marked peripheral outline of the preorbital fossa and the short cheek teeth length; in other words, the Maragha *H. prostylum* seems to be very close to *H. dietrichi* (Fig. 27; Appendix 2: Table 20). The studied hipparion from Akkaşdağı shares some characters with both Axios and Maragha samples (Appendix 2: Table 20). In more details, the cheek teeth length is longer than that of *H. prostylum* and closer to that of *H. dietrichi* (measurement 31 in Fig. 27). Furthermore, the length of the preorbital fossa is comparable to that of *H. dietrichi* from Q1, but the width and the general morphology of the fossa is similar to that of *H. prostylum* from Maragha (measurements 33, 34 in Fig. 27). Among the above mentioned forms, there are no clear differences in the upper teeth morphology. Taking into account all the above mentioned, either *H. prostylum* from Maragha and *H. dietrichi* are closely related forms or they are synonyms and, the small differences in the preorbital fossa morphology are due to intraspecific variation.

Another hipparion species having similarities to the above mentioned forms is *H. molayanensis* from Molayan, Afghanistan (Zouhri 1992). Its snout is short, but not as broad as in *H. dietrichi* and the Akkaşdağı form (Appendix 2: Table 20). The nasal notch is situated above the anterior part of P2. The skull proportions almost follow those of *H. dietrichi* and the Akkaşdağı form (Fig. 27). The preorbital fossa resembles that of *H. dietrichi* in being shallow, oval-shaped, situated far from the orbit and occasionally well defined posteriorly. Besides these similarities, *H. molayanensis* seems to have more oval fossa, situated closer to the facial crest and to the maxilla (measurements 34, 36, 38 in Fig. 27) and, from this point of view, *H. molayanensis* is closer to *H. mediterraneum* from DTK. The dental morphology is similar to that of *H. dietrichi*, *H. prostylum* from Maragha and the Akkaşdağı form (Appendix 2: Table 20). The mandibles from Akkaşdağı are also very similar to that of *H. dietrichi* from the various localities (Fig. 28). However, the toothrow of the Akkaşdağı form is

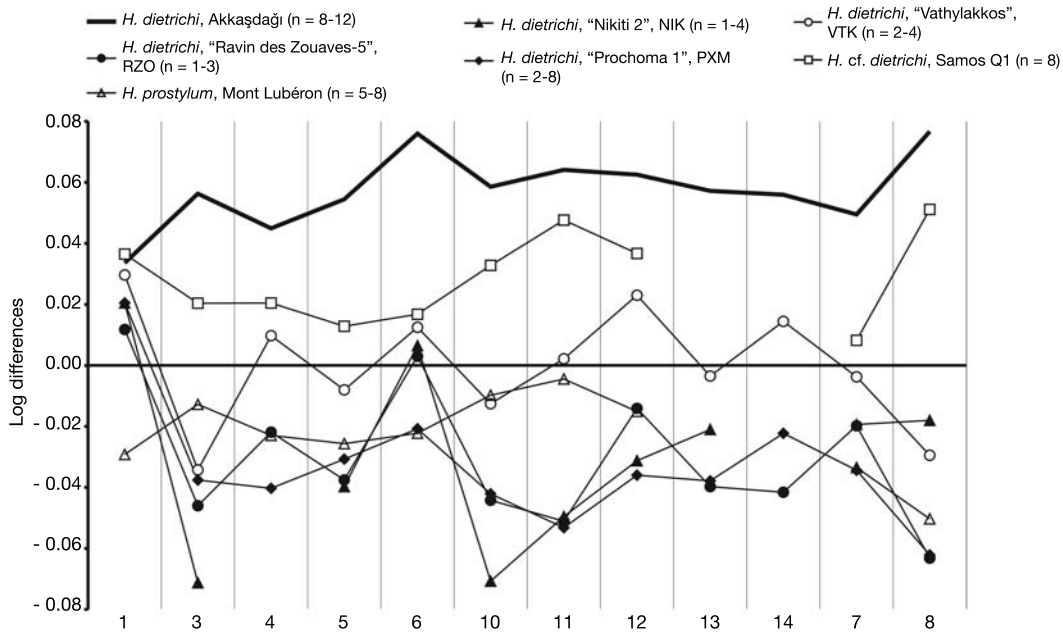

FIG. 29. — Logarithmic ratio diagram comparing the third metacarpal of *Hipparion dietrichi* from Akkaşdağı with *H. dietrichi* from various localities. Standard *H. mediterraneum*, Pikermi, n = 12-39 (Koufos 1987a).

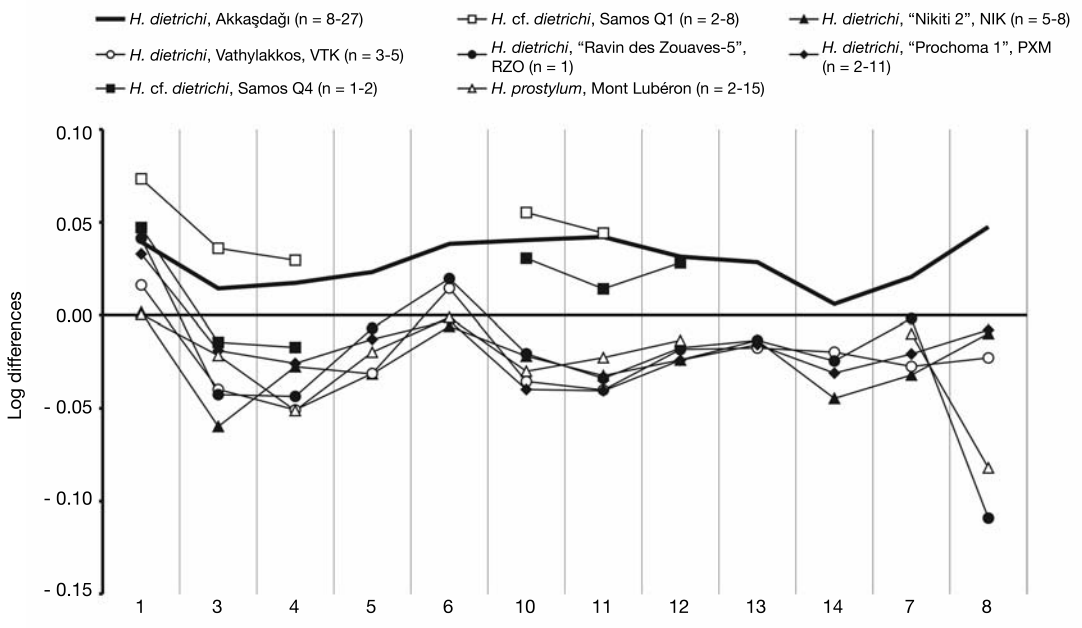

FIG. 30. — Logarithmic ratio diagram comparing the third metatarsal of *Hipparion dietrichi* from Akkaşdağı with *H. dietrichi* from various localities. Standard *H. mediterraneum*, Pikermi, n = 11-65 (Koufos 1987a).

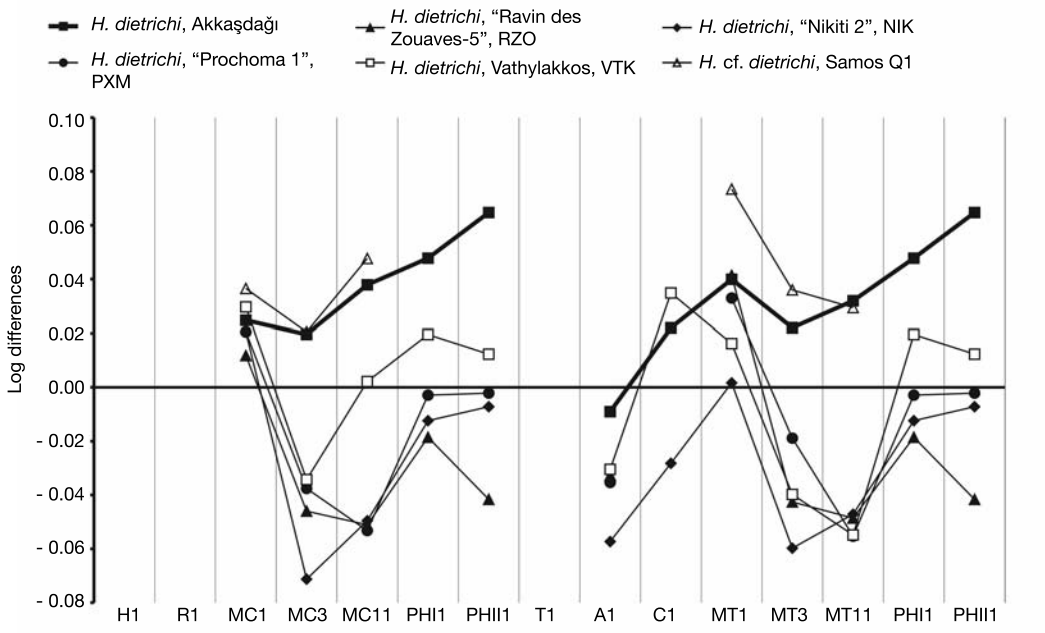

FIG. 31. — Logarithmic ratio diagram comparing the front and hind legs of *Hipparion dietrichi* from Akkaşdağı with other forms from various localities. Standard *H. mediterraneum*, Pikermi (Koufos 1987a).

longer than in all the other samples, except *H. dietrichi* from Samos Q1 (measurements 3, 4, 5 in Fig. 28).

The metacarpal of the Akkaşdağı form is long and slender, and in this feature it differs from *H. dietrichi* from Northern Greece. In comparison to that from Samos Q1, despite their similar length, it is more robust (Fig. 29). Generally, the metacarpal from Akkaşdağı has a different pattern than that of *H. dietrichi* in having mid-shaft width larger than the depth (measurements 3, 4 in Fig. 29). In this character, the Akkaşdağı sample resembles better *H. prostylum*, but the latter is quite smaller. Unlike metacarpals, the metatarsals from Akkaşdağı provide great similarities in size with *H. dietrichi* from Samos Q1 and in general terms similar morphological pattern to the *H. dietrichi* sample (Fig. 30). The metatarsal from Mont Lubéron, possibly referred to *H. prostylum*, is quite smaller than the Akkaşdağı sample and comparable to *H. dietrichi* from Axios Valley (Fig. 30).

Our knowledge about the size and morphology of the *Hipparion* limb bones from Central Asia and former USSR is limited either because the material is mixed or because the number of specimens is poor and not well determined. Well studied samples of *H. dietrichi* are known from Northern Greece (Axios Valley, Chalkidiki) where the species is frequent (Koufos 1987b, c, 1988a; Vlachou & Koufos 2002). In this area, the chronology of the localities is well established, and the presence of two or three species in each locality with clear size differentiation (small-medium-large) make the correlation of the limb bones with the skull more certain. So, in these localities the metapodials referred to *H. dietrichi* are long and slender.

Direct postcranial associations from Samos are unknown. Sondaar (1971) refers some metapodials to *H. dietrichi*, although he points out that "in the American Museum material it was not possible to find indicators for correlating the bones with the skull", i.e. his correlation is arbitrary and temporal. The comparison of *H. dietrichi* from Northern Greece and Samos suggests that although the cranial morphology is homogenous,

there is an increase in the size (more robust metapodials, larger toothrow) towards the East. The comparison of the front and hind limb bones of *H. dietrichi* from various localities (Fig. 31) confirms these results. It is quite clear that the Axios Valley forms are smaller than the Akkaşdağı and Samos ones, the latter being smaller than that of Akkaşdağı. The presence in Akkaşdağı of a skull similar to that of *H. dietrichi* from Samos Q1,4 and postcranials also similar to those of *H. dietrichi*, as referred by Sondaar (1971), confirms the determination of the Akkaşdağı sample as *H. dietrichi*. The available data about the postcranial skeleton of *H. prostylum* and *H. molayanensis* are not precise enough for an accurate comparison. The material of *H. prostylum* from Maragha belongs to old collections, which are mixed and they cannot be correlated to the stratigraphy. However, according to Watabe & Nakaya (1991a), *H. prostylum* has possibly large, elongated and probably robust metapodials, as well as large tarsals. Concerning *H. molayanensis*, despite the fact that all the material was collected from the same locality, we are suspicious about the homogeneity of the postcranial remains, since the presence of another species is not excluded. However, the several similarities between the skulls of *H. dietrichi*, *H. prostylum* and *H. molayanensis* prove a kind of relation between them. The poor information about their postcranial skeleton, the lack of personal observations and a direct comparison between the samples do not permit us to testify their relationship. The three species could be synonyms, representing a widespread form with some local adaptations, or they possibly belong to the same lineage representing forms derived from one another; both assumptions need further study.

Hipparion moldavicum Gromova, 1952

LOCALITY. — Akkaşdağı, Keskin, Turkey.

AGE. — Middle Turolian, MN 12 (late Miocene).

MATERIAL. — Complete skull associated with the mandible, AK7-155; complete skull, AK2-501; 2 partial skulls, AK2-500, AK6-226; maxillary fragment with P3-M3 sin, AK5-509; maxillary fragment with P2-M3 dex, AK2-174; maxillary fragment with P3-M3 sin, AK2-504; maxillary fragment with P2-M2 sin, AK12-1; maxillary fragment with P4-M3 dex, AK6-237; maxillary fragment with P3-M2 dex, AK6-325; 2 mandibles with p2-m3 dex and sin, AK2-178, AK5-644; 2 mandibular fragments with p2-m3 dex, AK6-187, AK2-53a; mandibular fragment with p3-m3 sin, AK4-229; mandibular fragment with p2-p4 dex, AK11-86; mandibular fragment with p2-m2 dex, AK2-52; mandibular fragment with p3-m3 dex and p4-m3 sin, AK2-53b; mandibular fragment with p3-m2 dex, AK5-287; mandibular fragment with p3-m1 sin, AK5-300; mandibular fragment with p4-m1 sin, AK5-298; mandibular fragment with m1-m3 dex, AK5-288; mandibular fragment with m1-m3 sin, AK2-171a-b; mandibular fragment with p4-m3 sin, AK2-n.n.; distal part of humerus+radiocubitus +carpals+McIII, AK6-261; 6 distal parts of humerus, AK2-233, AK3-217, AK4-146, AK5-539, AK6-20, AK12-30; 4 distal parts of radius, AK3-97, AK6-230, AK11-113, AK11/12-9; 2 McII+McIII+McIV, AK6-248a-c, 259a-c; 13 third metacarpals, AK2-5, 243, AK4-96, AK5-6a-c (with laterals), AK5-76, 155, 543, n.n., AK6-195, 278, AK7-44, 43, AK12-35; 5 distal parts of McIII, AK2-8, AK3-144, AK5-179, AK6-9, 278; 5 proximal parts of McIII, AK3-262, AK4-97, 152, AK5-155, 546; distal part of tibia+astragalus+ tarsals+MtIII, AK6-179; distal part of tibia+astragalus+calcaneum+tarsals+MtIII, AK6-267a-i; 4 tibiae, AK3-8, AK5-551, AK6-16, 184; 26 distal parts of tibia, AK2-17, 18, 21, 117, 261, AK3-147, 154, AK4-104, 220, 250, AK5-161, 187, 399, 401, 469, 560, 562, 561, AK6-114, 161, 186, AK11-100a, 126, AK12-42, 47, AK14-6; 7 astragali, AK2-415, AK4-155, AK5-167, AK6-11, 53, 79, AK7-53; 4 partial astragali, AK2-263, AK10-13, AK11-129, AKK-275; 9 calcanei, AK2-31, 265, AK4-100, AK5-11, AK6-225, AK7-93, 111, 159, AK11-55; 5 partial calcanei, AK2-266, AK5-101, 224, AK5-104, AK11-132; 2 MtIII+tarsals, AK5-154, AK6-180; MtII+MtIII+ MtIV, AK11-117; 16 third metatarsals, AK2-2, 4, 269, 399, AK3-n.n., 142, AK4-162, 163, AK5-18, 565, 545, AK6-7, AK7-45, 46, AK12-48, 49; 11 proximal parts of MtIII, AK2-271, AK3-5, AK5-17, 80, 79, 150, 483, 485, AK6-185, 217, AK11-40; 6 distal parts of MtIII, AK4-164, 168, AK5-77, AK6-14, 246, AK11-39; distal part of MtIII+PhI+PhII+PhIII, AK6-262a-d; 4 first phalanges, AK5-114, AK6-198, AK7-133, AKK-279; 4 second phalanges, AK5-16, 120, 338, 339; 3 third phalanges, AK3-291, AK4-179, AK7-114; part of a third phalanx, AK5-122.

DESCRIPTION

Skull and dentition

The description of the skull morphology of the small-sized hipparion from Akkaşdağı is mainly based on the specimen AK2-501, while addition-

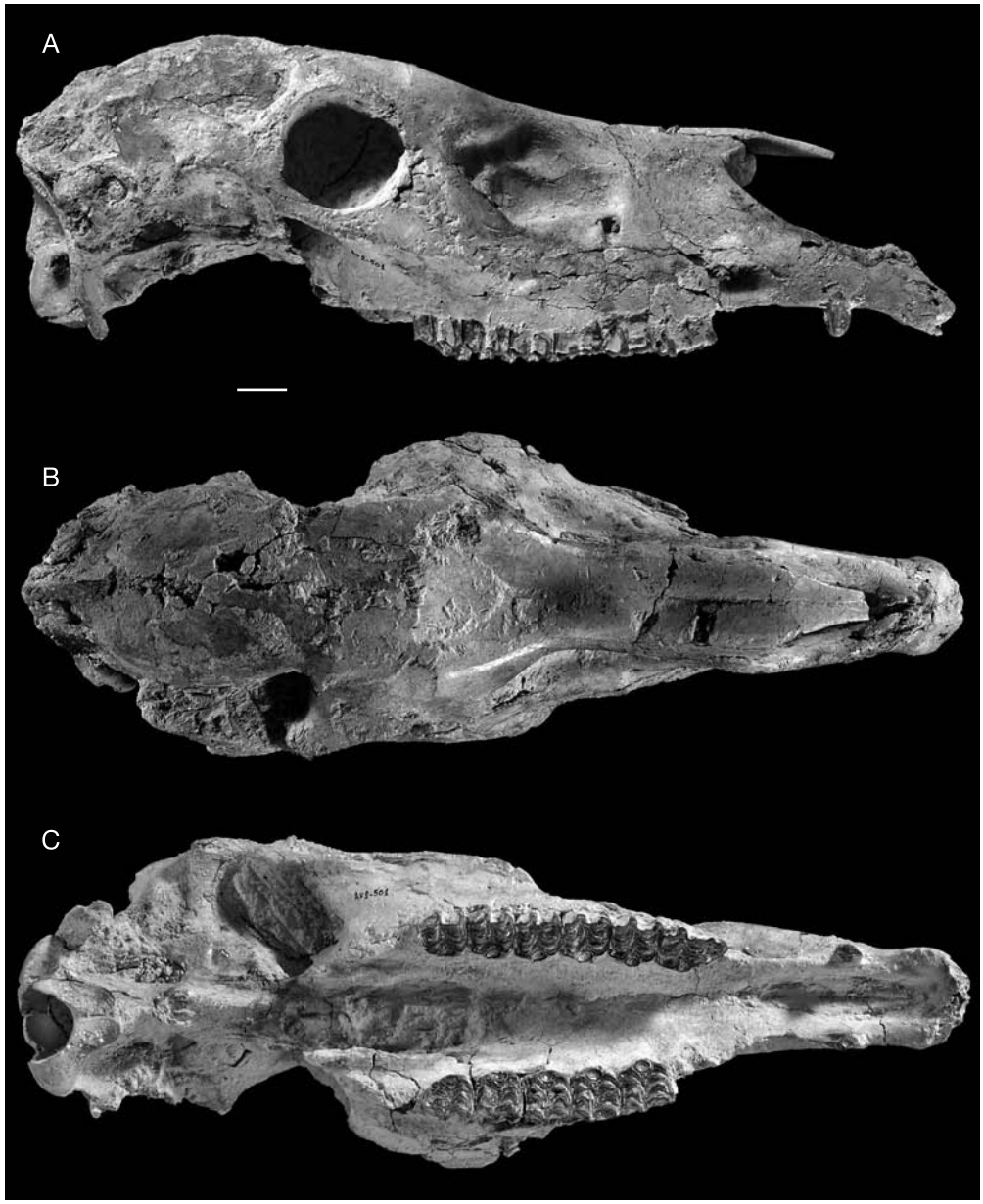

FIG. 32. — *Hipparion moldavicum*, Akkaşdağı, Turkey, skull AK2-501; **A**, lateral view; **B**, dorsal view; **C**, ventral view. Scale bar: 2 cm.

al information is taken from the specimens AK2-500 and AK6-226. The skull AK2-501 is almost complete, well preserved but slightly compressed laterally (Fig. 32). It lacks the left zygomatic arch, part of the left orbit and the incisors. The other two specimens AK2-500 and AK6-226 are partial skulls lacking the muzzle and the posterior part of the skull. The first one is slightly deformed tilting to the right, and the second one is crushed (Fig. 33A, B).

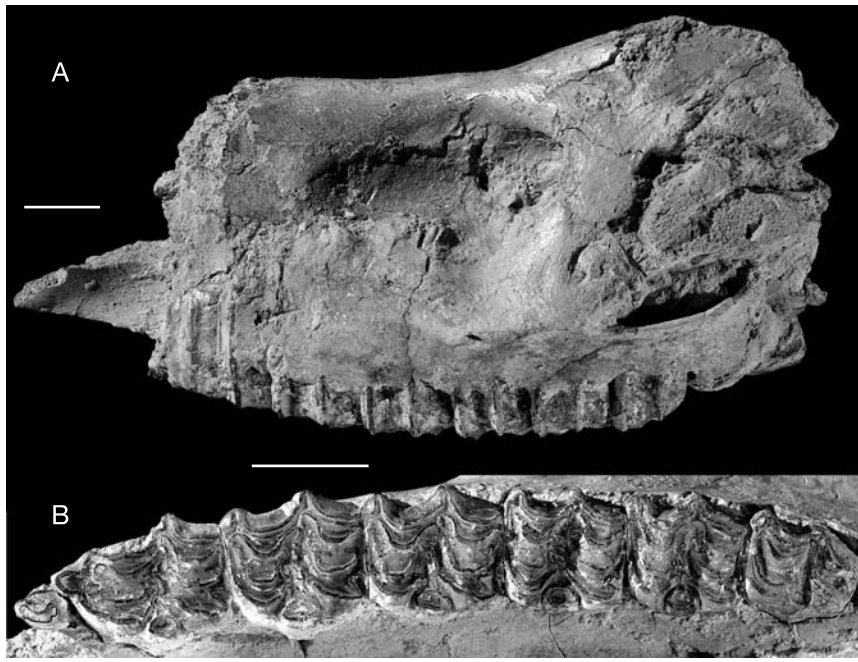

FIG. 33. — *Hipparion moldavicum*, Akkaşdağı, Turkey, skull AK6-226; **A**, lateral view; **B**, left toothrow, occlusal view. Scale bars: 2 cm.

The small-sized hipparion from Akkaşdağı has a narrow and elongated skull (Fig. 32). Its length is 375 mm and the breadth between the anterior borders of the facial crests is approximately 130 mm (AK2-501). The muzzle is narrow and short (the index m15 × 100/m1 in AK2-501 is 318.2). The narial opening is narrow and elliptical-shaped. The nasal notch is situated above or in front of P2 and it is placed far from the orbit (138 mm in AK2-501). The anterior border of the nasals is situated above the canines. The preorbital fossa is large, oval, anteroposteriorly oriented (Figs 32A; 33A); its maximum depth is observed medially and varies between 15 and 18 mm (AK2-501, AK2-500 and AK2-226). Both anterior and posterior rims are well expressed and situated above P3 and M2 or M3 respectively. The posterior rim is slightly pocketed, especially in the specimen AK6-226 (Fig. 33B). The peripheral rim is also well expressed but, in its lower part, the continuity is interrupted by a pit variable in size (Figs 32A; 33A). The upper part of the fossa is rugose with pits more or less expressed (Fig. 32A). The distance orbit-preorbital fossa is short and varies between 16 and 23.5 mm. The lacrymal suture approaches but does not touch the posterior rim of the fossa. The infra-orbital foramen is situated above the posterior half of P2 and just inferior to the anteroventral rim (AK2-501) or above the anterior border of P2 and just superior to the anteroventral rim (AK6-226). The zygomatic arch is developed very close to the parietal (AK2-501). The crista facialis is strongly projected. Its anterior border is situated above the end of P4 or at the middle of M1 and close to the maxilla (distance crista facialis-alveolar level = 17.8-23.3mm). The palate is long, narrow and deep. The index m2 × 100/m13 varies from 176.5 (AK2-500) to 196 (AK2-501). The choanae are relatively wide and their anterior border is situated at the contact between M2 and M3.

The toothrow is almost straight and short comparatively to the skull length (Fig. 34). The length of the toothrow varies from 127.3 mm in the old individuals to 140.2 mm in the young

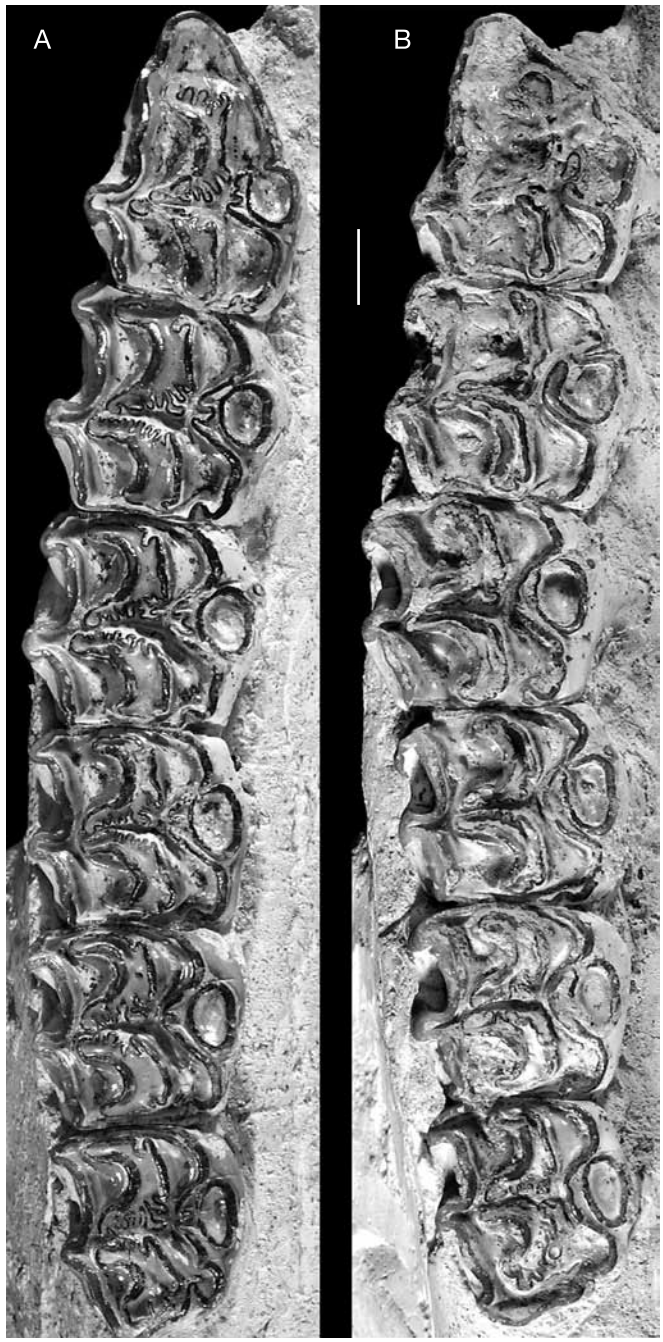

FIG. 34. — *Hipparion moldavicum*, Akkaşdağı, Turkey; **A**, right toothrow, AK2-501; **B**, right toothrow, AK7-155. Scale bar: 1 cm.

adults. The toothrow AK2-500 retains the dP1 (Fig. 33A). The teeth are small (Fig. 34). The anterostyle of P2 is rounded, short and projected mesially. The length of the anterostyle reduces as the wear increases. The fossettes are closed with moderate enamel plication at their borders. The plis are narrow and shallow depending on the wear stage. The plication number is 10-29 in the premolars and 9-23 in the molars. The protocone is large comparatively to the tooth size and, in the more worn dentitions, it is oval to rounded and connected to the protoloph, while in the young to adult individuals it is more elliptical and always free. The pli caballin is well developed in the premolars but weak in the molars. It is multiple in the less worn teeth (AK2-500) while in the more worn dentitions it is double to single in the premolars and single to absent in the molars. The hypocone is elliptical-rounded with deep distal hypoconal groove while a lingual hypoconal groove is rarely present in M3 (AK2-501).

Among the cranial remains of the small-sized hipparion there is a complete skull in association with the mandible, AK7-155 (Fig. 35), that shows several similarities with the above described skulls; however, it differs mainly in the shape of the preorbital fossa, the morphology of the occipital and possibly in the skull width. The preorbital fossa of AK7-155 is triangular-shaped, moderately pocketed posteriorly while the anterior rim is not well expressed (Fig. 35A). The maximum depth (> 15 mm) is observed at its posterior part, and the pits are absent. Comparatively to AK2-501, the occipital condyles are narrower, less curved, their backside is less flat and they are strongly projected backwards (Figs 36; 35; 32). In spite of the above mentioned differences, the skull AK7-155 is similar in size and dental morphology (length, tooth size, enamel morphology), the position of the nasal notch and the proportions of the muzzle. Both skulls must be old male individuals as their canines are strong. Therefore, the differences we noted can be considered neither as sexual dimorphism nor as ontogenetic growth differences. Among the Taraklia (type locality) material of *H. moldavicum* there are two skulls, nos. 1256/2963 and 1256/3639, that, despite their different fossa morphology, are ascribed to the same species (Gromova 1952: pls I, III). Unfortunately, no information is available about the width of the Taraklia skulls and their occipital morphology. In comparison with the Taraklia material, we believe that AK7-155 must be incorporated in the small hipparions group together with AK2-501, AK2-500 and AK6-226.

Mandible

The mandible has a relatively long and narrow snout with shallow and narrow cup (Figs 37; 38). The index m2 × 100/m7 is 208 (186 for AK7-155). The horizontal ramus has a medium depth, and the symphysis is narrow and close to the premolars (AK2-178, AK5-644). The symphysis in AK7-155 is narrow but more robust, and it is placed more distant to the premolars. The toothrow is short with small teeth (Figs 37C; 38D). The parastylid is well developed in the P3, 4. The metaconid and metastylid are triangular to elliptical in the premolars and rounded in the molars. The ectoflexid is deep reaching the preflexid in the premolars and very deep in the molars where it touchs the linguaflexid. The linguaflexid is shallow and open in the premolars while it is V-shaped in the molars.

Postcranials

The metapodials are relatively long and slender (Fig. 39). The index McIII or MtIII Length × 100/Radius or Tibia Length is on average 85.0 and 76.5 respectively indicating long metapodials. The robusticity index (m11 × 100/m1) is 14.4 for McIII and 13.4 for MtIII. The keel index (m12 × 100/m13) is 123.8 for McIII and 125.7 for MtIII. In the third metatarsal the articular facet for cuneiforme II is usually absent.

COMPARISONS

The species *H. moldavicum* was erected by Gromova (1952) based on the material from Taraklia (Moldavia). According to her diagnosis, it is a medium-sized hipparion with long muzzle, high frontal, short toothrow, single elongated and deep preorbital fossa situated close to the orbit,

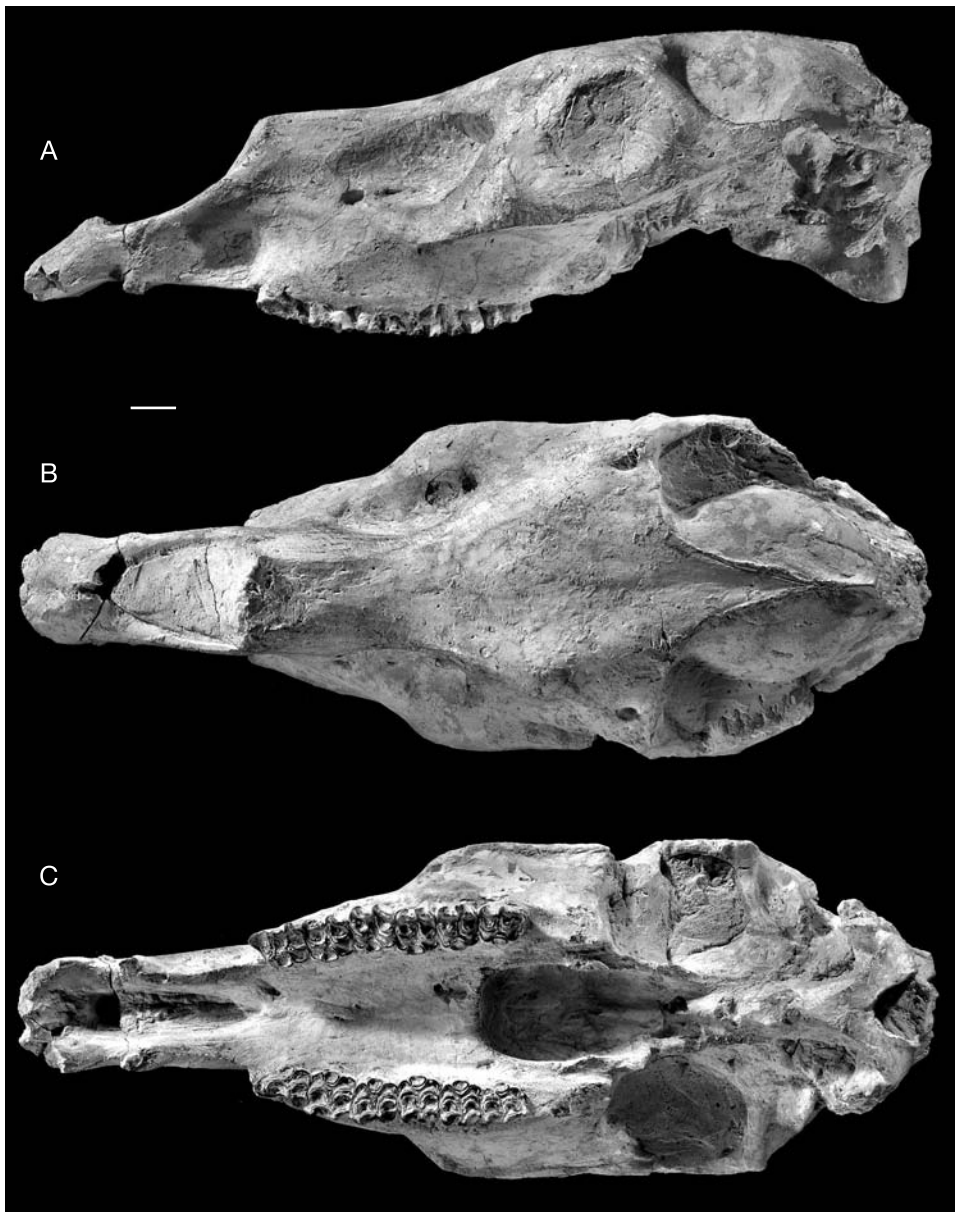

FIG. 35. — *Hipparion moldavicum*, Akkaşdağı, Turkey, skull AK7-155; **A**, lateral view; **B**, dorsal view; **C**, ventral view. Scale bar: 2 cm.

moderately developed nasal opening whose posterior border is situated above the anterior border of P2. The upper teeth have an oval ("court et large") protocone and moderate enamel plication, while the lower teeth have a deep ectoflexid. The metapodials have a moderate length and they are slender. Later on, *H. moldavicum* was synonymized with *H. mediterraneum* (Forstén 1978) but recently it was recognized as an independent species (Bernor 1985; Krakhmalnaya 1996; Forstén & Krakhmalnaya 1997). Bernor (1985) in an emended diagnosis for *H. moldavicum*, in

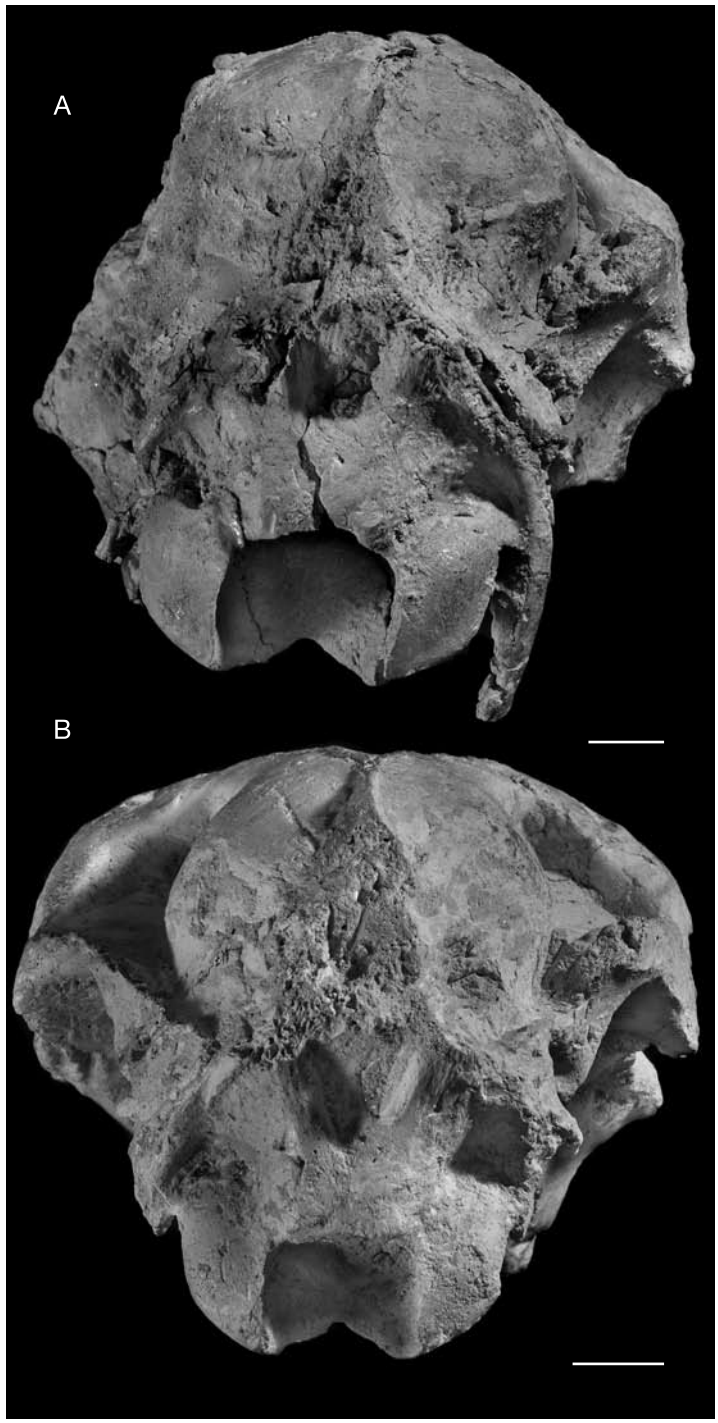

FIG. 36. — *Hipparion moldavicum*, Akkaşdağı, Turkey, occipital region; **A**, skull AK2-501; **B**, skull, AK7-155. Scale bars: 2 cm.

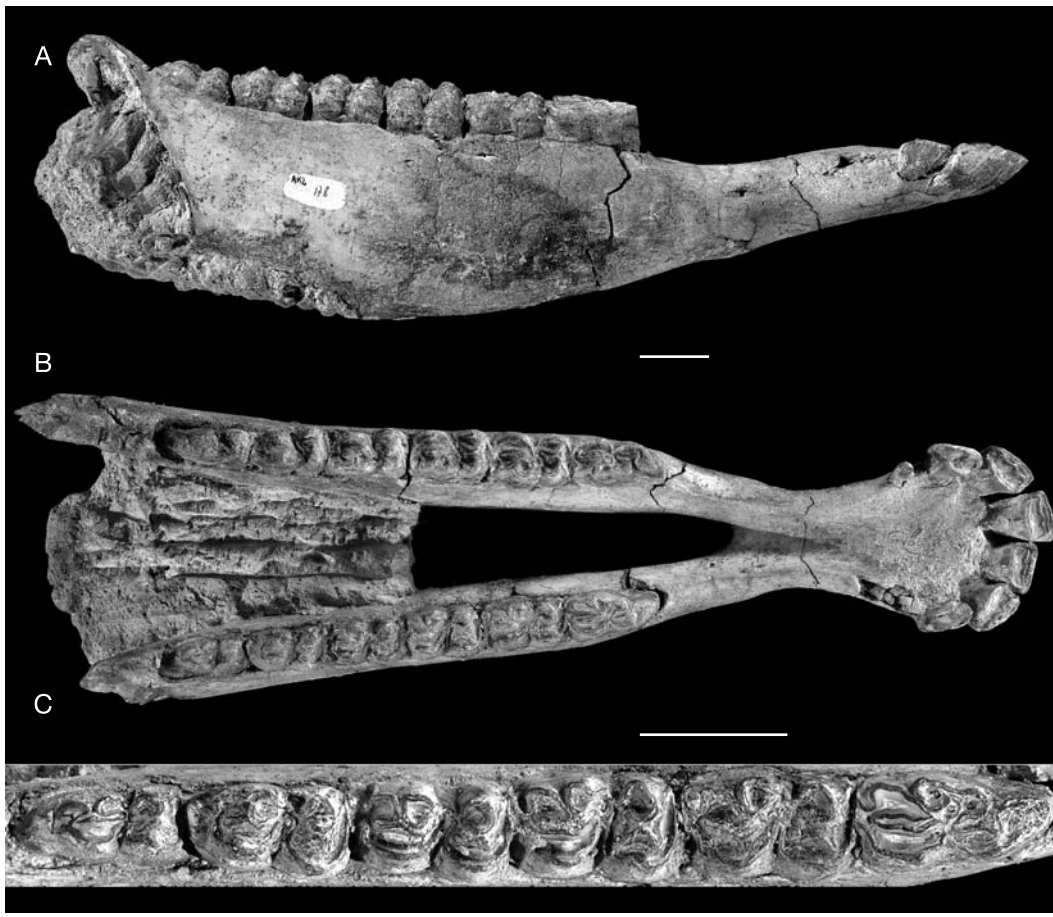

FIG. 37. — *Hipparion moldavicum*, Akkaşdağı, Turkey, mandible AK2-178; **A**, lateral view; **B**, dorsal view; **C**, right toothrow, occlusal view. Scale bars: 2 cm.

addition to the characters given by Gromova (1952), mentioned that the preorbital fossa is subtriangular, anteroposteriorly oriented, dorsoventrally deep, slightly posterior pocketing, with distinct anterior rim, well expressed peripheral outline and short preorbital bar. The upper teeth have moderately plicated enamel, the protocone is generally rounded, and the P2 anterostyle is usually long but it can be short and rounded.

The small-sized skulls from Akkaşdağı fit morphologically to the description that Gromova (1952) gave for *H. moldavicum* from Taraklia and, in general terms, share the characters that Bernor *et al*. (1996a) attributed to "*Cremohipparion* group". However, contrary to "*Cremohipparion* group", the studied skulls retain the dp1, and the lacrymal suture approaches but seems to not invade the posterior part of the preorbital fossa.

The logarithmic ratio diagram in Figure 40A compares the skull proportions of the Akkaşdağı sample with *H. moldavicum* from various localities. On the whole, the Akkaşdağı skull proportions track quite close those of the type sample of *H. moldavicum* from Taraklia. The samples have similar skull length, but they strongly differ in the position of the vomerine notch that seems to be placed closer to choanae in the Akkaşdağı skulls. This

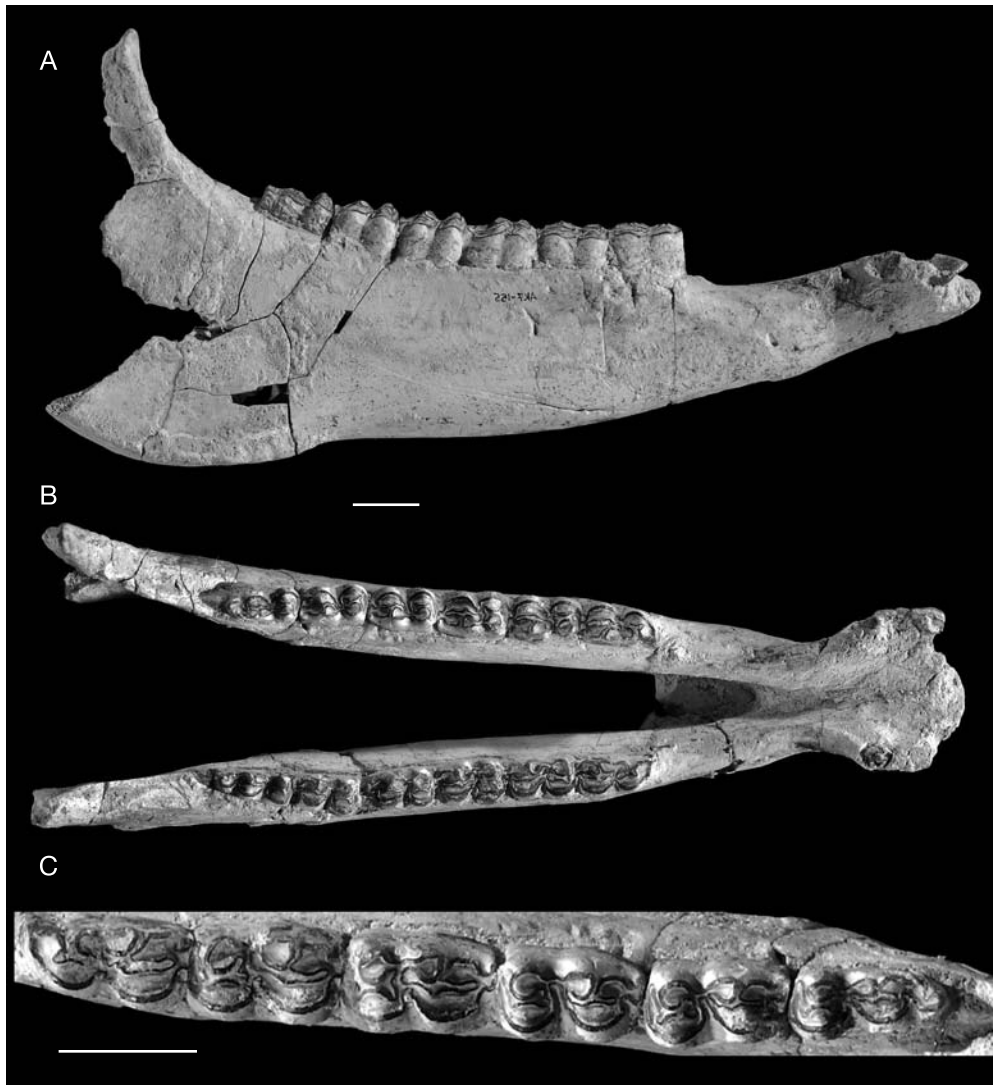

FIG. 38. — *Hipparion moldavicum*, Akkaşdağı, Turkey, mandible AK7-155; **A**, lateral view; **B**, dorsal view; **C**, left toothrow, occlusal view. Scale bars: 2 cm.

causes the increase of the basion-vomerine length against choanae-vomerine length (measurements 3, 4 in Fig. 40A). The position of the vomerine notch is somewhat questionable especially if the skull is crushed or deformed, such damages may change the proportion of the choanae-vomerine and vomerine-basion lengths. Consequently, we consider that the significance of these measurements is somewhat doubtful. However, the Akkaşdağı sample differs from *H. moldavicum* from Taraklia in having slightly shorter and narrower muzzle (measurements 1, 15), greater skull height in front of P2 (measurement 25), larger anteroposterior orbit diameter, apparently shorter distance between preorbital fossa and orbit (measurement 32), and the infraforamen placed closer to the posterior edge of the preorbital fossa (measurement 34 in Fig. 40A).

FIG. 39. — *Hipparion moldavicum*, Akkaşdağı, Turkey; **A**, third metacarpals, AK2-243, AK6-259b, AK6-248b; **B**, third metatarsals, AK6-7, AK12-48. Scale bars: 2 cm.

Some cranial remains from Maragha have been originally described by Bernor (1985) as *H*. aff. *moldavicum*. Later, Watabe & Nakaya (1991b) assigned the small-sized hipparion from Maragha to *H*. *moldavicum* studying some new material stored in the University of Kyoto (Japan) and part of the old Maragha collection stored in the BMNH. Apart from the diagnostic characters that Gromova (1952) and Bernor (1985) gave for the species, they additionally noted that the lacrymal

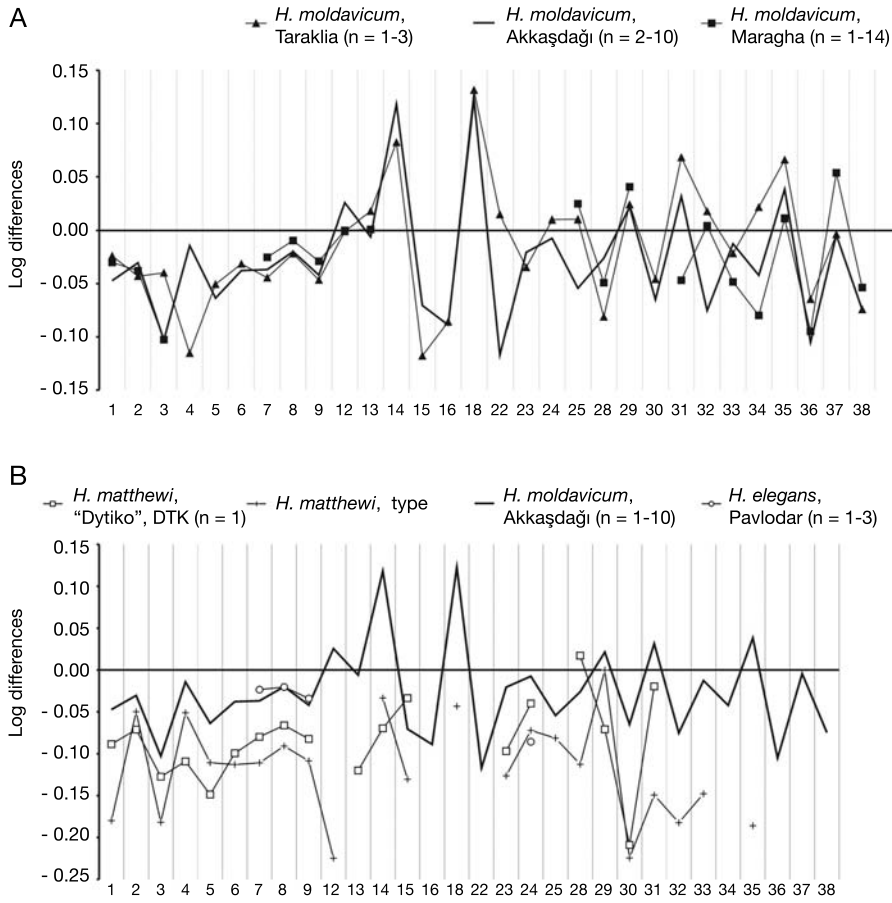

FIG. 40. — Logarithmic ratio diagram comparing the skull of *Hipparion moldavicum* from Akkaşdağı with *H. matthewi*, *H. elegans* (**B**) and *H. moldavicum* (**A**) from various localities. Standard *H. mediterraneum*, Pikermi, n = 1-9 (Koufos 1987a).

suture does not invade, but touch the posterior edge of the preorbital fossa, the preorbital fossa is anteroventraly oriented, the anterior rim is weakly to clearly expressed, the enamel plication number in M1 varies from 12 to 21, and the pli caballin is multiple to single depending on the stage of wear. The Akkaşdağı sample also fits with this description, and the cranial dimensions of the two samples are more or less similar. The differences are mainly detected in the facial region (Fig. 40A). Comparatively to the Akkaşdağı sample, *H. moldavicum* from Maragha has significantly shorter cheek teeth (m31), longer preorbital bar (m32) and smaller preorbital fossa (m33, m35), while the infraorbital foramen is placed further from the alveoli (measurement 37). Moreover, in the Maragha sample, the muzzle is longer and the teeth larger. The Figure 41 focuses our study, with a set of box and whiskers plots, on these crucial variables. The upper tooth dimensions (m7-9) are ploted in Figure 41A-C. The medial quartile of the Akkaşdağı sample (1) in all related plots is virtually identical to that of the Maragha sample (2). Hence, the teeth differences that appeared in the ratio diagram (measurements 7, 8, 9 in Fig. 40A) are not certain differences but they are due to the small size of the sample. In fact, the Akkaşdağı sample overlaps in its interquartile with the Maragha sample.

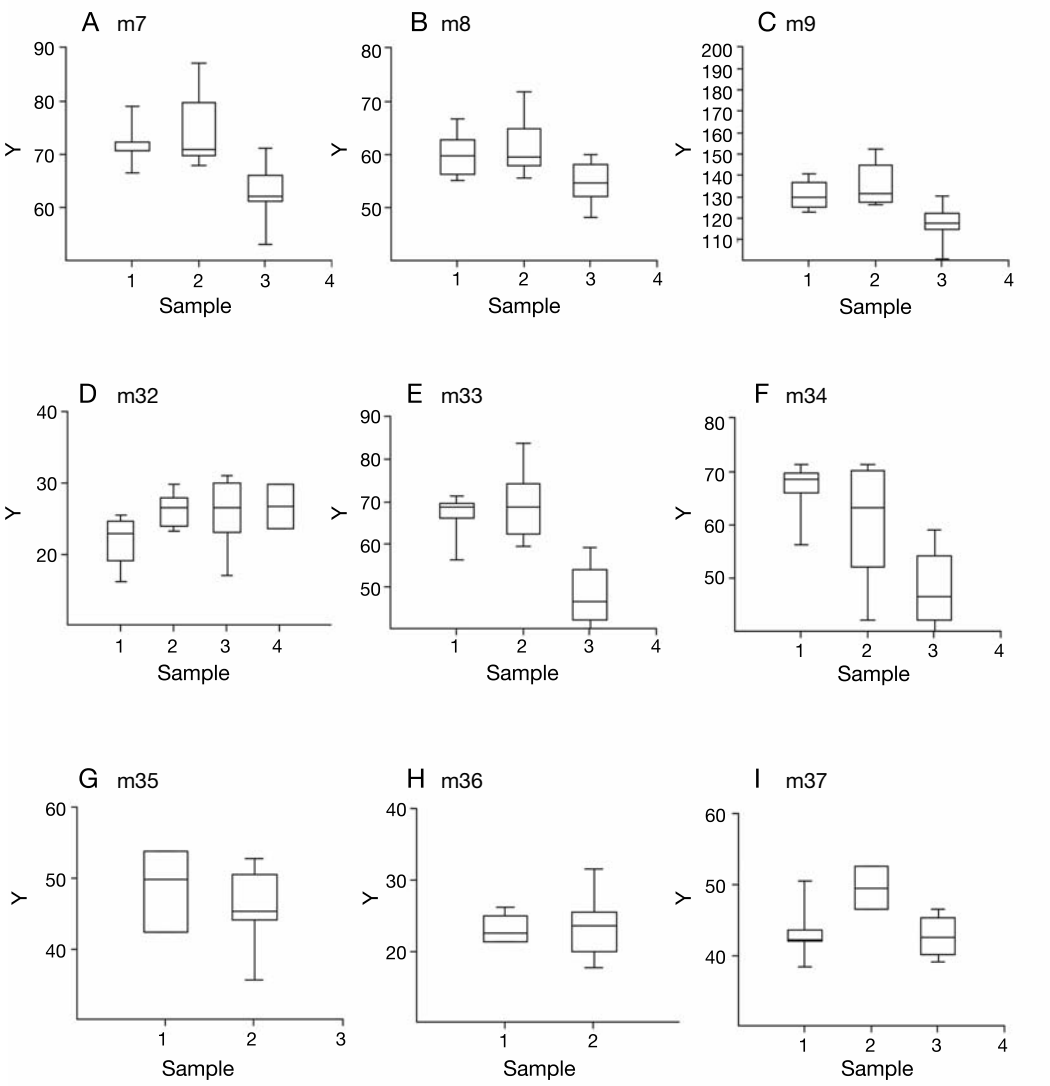

FIG. 41. — Box and Whiskers plots on skull variables; **A**, premolar length; **B**, molar length; **C**, length of the upper maxillary teeth; **D**, length of the preorbital bar; **E**, maximum length of the preorbital fossa; **F**, distance between the back of the preorbital fossa and the infraorbital foramen; **G**, height of the preorbital fossa: perpendicular to its maximal length; **H**, distance between the preorbital fossa and the facial crest; **I**, height of back of the infraorbital foramen above the alveolar border. Samples: **1**, *Hipparion moldavicum*, Akkaşdağı; **2**, *H. moldavicum*, Maragha; **3**, *H. matthewi*, Samos; **4**, *H. moldavicum*, Taraklia.

Concerning the length of the preorbital bar (m32) (Fig. 41D), the Akkaşdağı sample (1) has a slightly lower medial and lower quartile boundary than the Maragha (2) and Taraklia (4) samples. The size of the preorbital fossa at Akkaşdağı (m33, m35) does not really differ from that of the Maragha sample. In Figure 41E and G, the Akkaşdağı (1) interquartile range overlaps with Maragha (2). Similar observations are also true for the m34 and m36 (Fig. 41F, H), while the plot for the m37 shows that Maragha (2) compared to Akkaşdağı has a higher median and interquartile range.

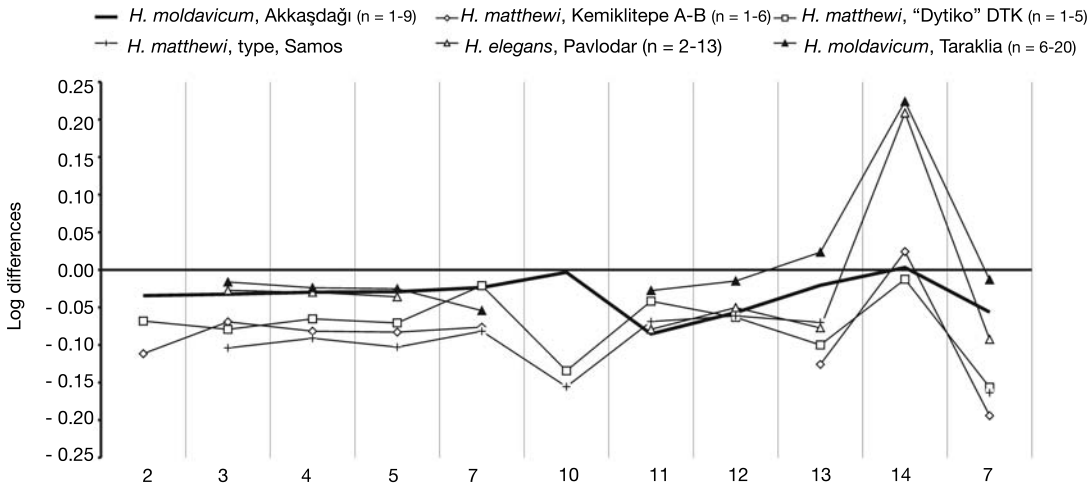

FIG. 42. — Logarithmic ratio diagram comparing the mandible of *Hipparion moldavicum* with other similar forms from various localities. Standard *H. mediterraneum*, Pikermi, n = 2-24 (Koufos 1987a).

H. matthewi is another small-sized hipparion known from various localities in Greece, Turkey, Bulgaria and former Yugoslavia. The type specimen has been found in an unknown locality of Samos while, according to Sondaar (1971), the species is very common in Q5 (Samos). The Akkaşdağı skulls are quite similar morphologically to the type of *H. matthewi*. The small size, the structure of the preorbital fossa, the muzzle morphology and the short narial opening are some of the common features between the two samples. However, *H. matthewi* from Q5 and especially the type skull are significantly smaller than the Akkaşdağı skulls, as shown in the ratio diagram (Fig. 40B). Box and Wiskhers plots (Fig. 41) confirm the size difference of the two samples (1, 4) and show that besides the similarities in the preorbital fossa morphology, the interquartile ranges of the corresponding measurements of *H. matthewi* (sample 4) are below the Akkaşdağı ones (sample 1).

Hipparion elegans is closed to *H. matthewi*, *H. moldavicum* and to the studied form. It was erected by Gromova (1952) as a new species from Pavlodar (Kazakhstan), morphologically similar to *H. moldavicum*. *Hipparion elegans* differs from *H. moldavicum* in having a smaller size, and quite deep preorbital fossa with very pronounced peripheral rim (Fig. 40B). All these characters also distinguish it from the Akkaşdağı sample.

Hipparion mediterraneum, *H. proboscideum* and *H. forstenae* are also clearly different from the Akkaşdağı sample firstly because of their differences in size and secondly because of their facial morphology. They are all larger in size and characterized by a deep, anteroventrally oriented preorbital fossa, which is separated from the buccinator fossa by a canine fossa.

The mandible of the studied form is very close to *H. moldavicum* from Taraklia (Fig. 42), confirming the similarity of the two samples. *Hipparion matthewi* is smaller, while *H. elegans* is closed to *H. moldavicum* and to the Akkaşdağı form.

Concerning the metapodials, the Akkaşdağı sample is also more similar to *H. moldavicum* than to *H. matthewi* and to *H. elegans*. Figure 43A shows that the metacarpals from Akkaşdağı have rather larger dimensions compared to *H. matthewi* from various localities and *H. elegans*. The proportions of the Akkaşdağı sample follow closely those of *H. moldavicum* from Taraklia, Tudorovo and Novaya Elisavetovka even though the metacarpal in the former sample is longer than the later ones (Fig. 43B). *Hipparion moldavicum* from Novaya

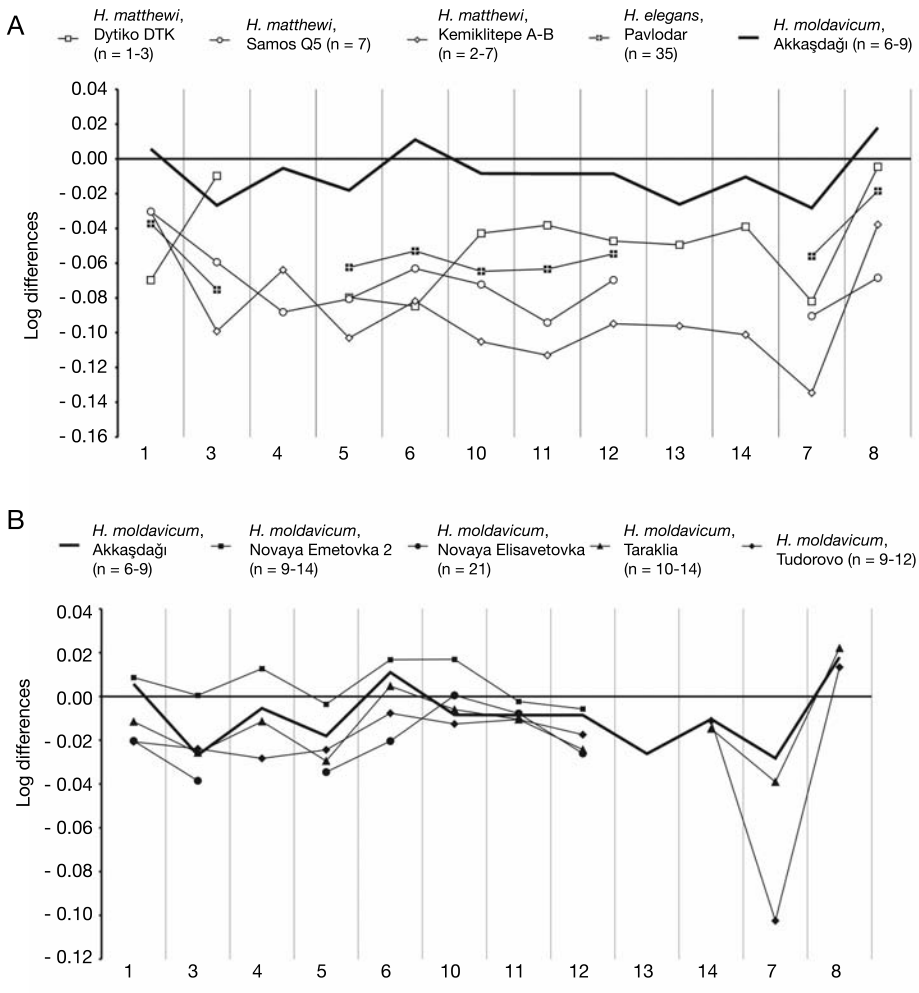

FIG. 43. — Logarithmic ratio diagram comparing the third metacarpal of *Hipparion moldavicum* from Akkaşdağı with other similar forms (**A**), and with *H. moldavicum* from various localities (**B**). Standard *H. mediterraneum*, Pikermi, n = 12-39 (Koufos 1987a).

Emetovka 2 is the exception of the previous ascertainment since its metacarpal is as long as that of Akkaşdağı sample, but the rest of the dimensions are larger and closer to *H. mediterraneum* from Pikermi (Fig. 43B). The mean robusticity index (m11 × 100/m1) is 14.4 in the Akkaşdağı material versus 14.5-15.3 in *H. moldavicum* from the various localities, 12.8 for *H. matthewi* from Samos Q5, 12.3 for *H. matthewi* from Kemiklitepe A-B (Turkey), 16.0 for *H. matthewi* from Dytiko (Axios Valley, Greece) and 14.0 for *H. elegans* confirming in general terms the previous assumptions.

The metatarsals from Akkaşdağı are also very close to those of *H. moldavicum* from Taraklia, Tudorovo and Novaya Elisavetovka (Fig. 44A). The robusticity index (m11 × 100/m1) is 13.4 for the Akkaşdağı sample versus 12.8-13.6 for *H. moldavicum* from various localities, 11.2-12.4 for *H. matthewi* and 12.0 for *H. elegans*. The logarithmic ratio diagram (Fig. 44A) shows that the Novaya Emetovka 2 form has slightly

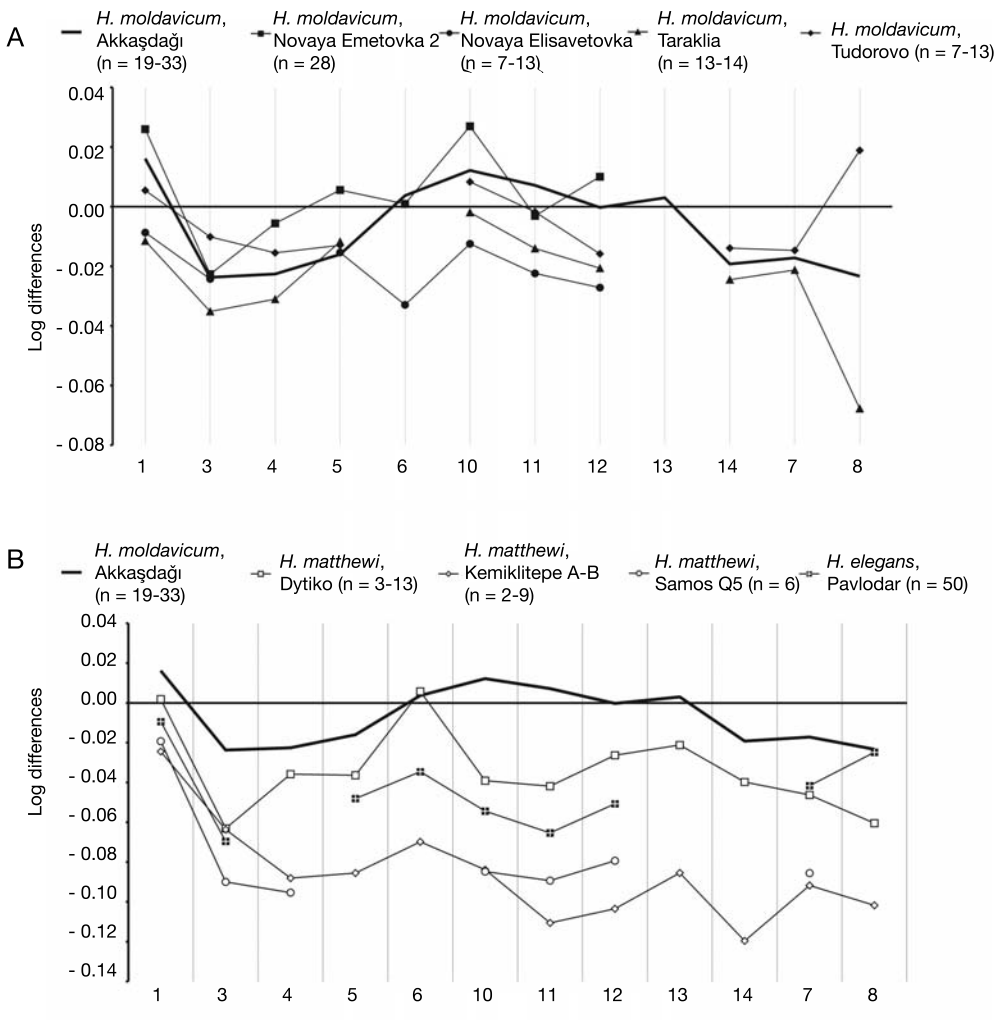

FIG. 44. — Logarithmic ratio diagram comparing the third metatarsal of *Hipparion moldavicum* from Akkaşdağı with *H. moldavicum* (**A**) and other similar forms (**B**) from various localities. Standard *H. mediterraneum*, Pikermi, n = 11-65 (Koufos 1987a).

longer metatarsal with deeper mid-shaft diaphysis (measurement 4), wider proximal articular surface (measurement 5) and larger suprarticular width (measurement 10) in comparison to the Akkaşdağı form and the other *H. moldavicum* samples. On the other hand, the metatarsals of *H. moldavicum* from Taraklia and Novaya Elisavetovka appear to be shorter with strongly reduced distal articular dimensions, shallower proximal articular surface and especially, when the Akkaşdağı sample compared to the Taraklia sample, they further differ in having more robust diaphysis. The metatarsal of *H. mediterraneum* from Pikermi is clearly distinguished from that of the studied sample in being significantly shorter with a quite robust diaphysis, larger proximal articular width and larger distal maximal depth of the medial condyle (measurements 3, 4, 5, 14 in Fig. 44B). Contrary to *H. mediterraneum*, *H. matthewi* and *H. elegans* have long and slender metatarsal as in the Akkaşdağı sample. They differ, although, from

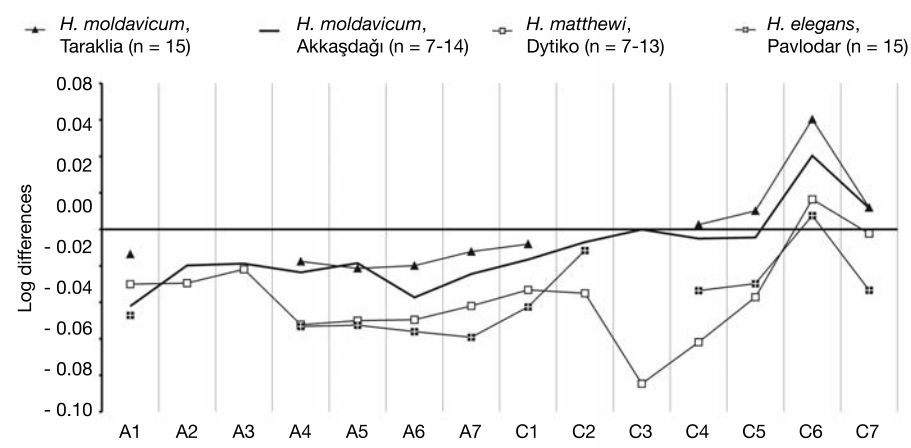

FIG. 45. — Logarithmic ratio diagram comparing the astragalus and calcaneum of *Hipparion moldavicum* from Akkaşdağı with other forms from various localities. Standard *H. mediterraneum*, Pikermi, n = 6-27 (Koufos 1987a).

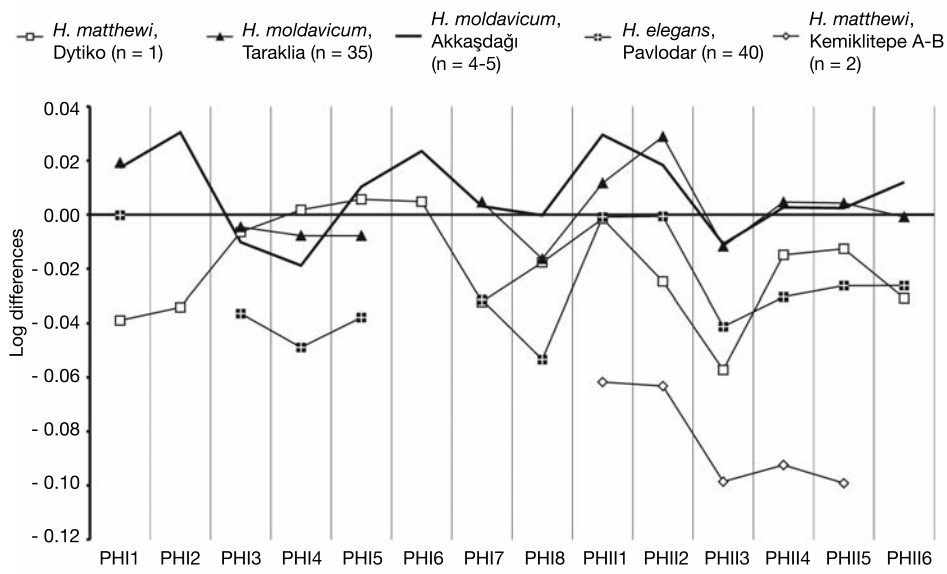

FIG. 46. — Logarithmic ratio diagram comparing the first and second phalanges of *Hipparion moldavicum* from Akkaşdağı with other forms from various localities. Standard *H. mediterraneum*, Pikermi, n = 2-8 (Koufos 1987a).

the Akkaşdağı metatarsal in having strongly smaller dimensions (Fig. 44B).

The astragalus and calcaneum from Akkaşdağı are also very close to *H. moldavicum* from Taraklia, despite the smaller height for astragalus (Fig. 45). In comparison to *H. mediterraneum* from Pikermi, the astragalus is larger, but the calcaneum is similar in size. However, *H. moldavicum* and the Akkaşdağı form have calcaneum with significantly broader distal articular surface than in *H. mediterraneum* (measurement C6 in Fig. 45). Similarly to the metapodials, *H. matthewi* and

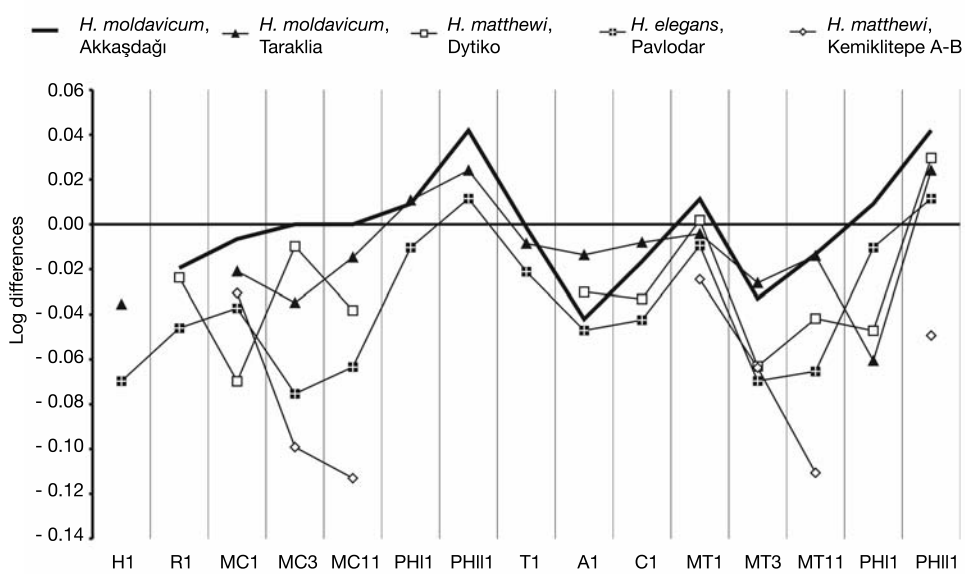

FIG. 47. — Logarithmic ratio diagram comparing the front and hind legs of *Hipparion moldavicum* from Akkaşdağı with other forms from various localities. Standard *H. mediterraneum*, Pikermi, n = 3-61 (Koufos 1987a).

H. elegans differ from the Akkaşdağı sample by their smaller tarsal bones (Fig. 45).

The comparison of the phalanges adds nothing more to the previous observations. The first and second phalanx of the Akkaşdağı small-sized form have more or less similar dimensions to those of *H. moldavicum*, and they are larger compared to *H. matthewi* and *H. elegans* (Fig. 46). Both phalanges from Akkaşdağı differ from that of *H. mediterraneum* in being longer, more slender but with larger distal articular dimensions (measurements 1, 3, 6 in Fig. 46).

In summary, the morphological and metrical comparisons suggest that the small-sized Akkaşdağı hipparion is closely related to *H. moldavicum* from Taraklia while it is larger than *H. matthewi* and *H. elegans* and smaller than *H. mediterraneum* from Pikermi (Fig. 47).

DISCUSSION

The hipparions are the most abundant group in the Akkaşdağı collection representing 72% of the large mammalian remains. They are followed by bovids and rhinos. The systematic study of the equid material indicates the presence of four hipparion species: 1) *H. dietrichi*, medium- to large-sized form with long and slender limb bones; 2) *H. moldavicum*, small- to medium-sized form with long and slender limb bones; 3) *H. brachypus*, large-sized form with short and robust limb bones; and 4) *H.* cf. *longipes*, very large-sized form with very long and slender limb bones.

Hipparion dietrichi is well known in Eastern Mediterranean area (Fig. 48A). It seems to be quite abundant in the Turolian Samos fauna (Sondaar 1971). During our recent excavations in Samos localities, *H. dietrichi* was recorded in three sites, Mytilinii 1A, 1B and 2 (Koufos *et al.* 1997; Vlachou & Koufos 2004). The material is under study by the second author for her doctoral thesis. Recent magnetostratigraphic data from the sections including these sites suggest an age between 7.0 and 7.1 Ma for the first two localities and ≈ 7.5 Ma for the last one (Kostopoulos *et al.* 2003). The species is also well known from

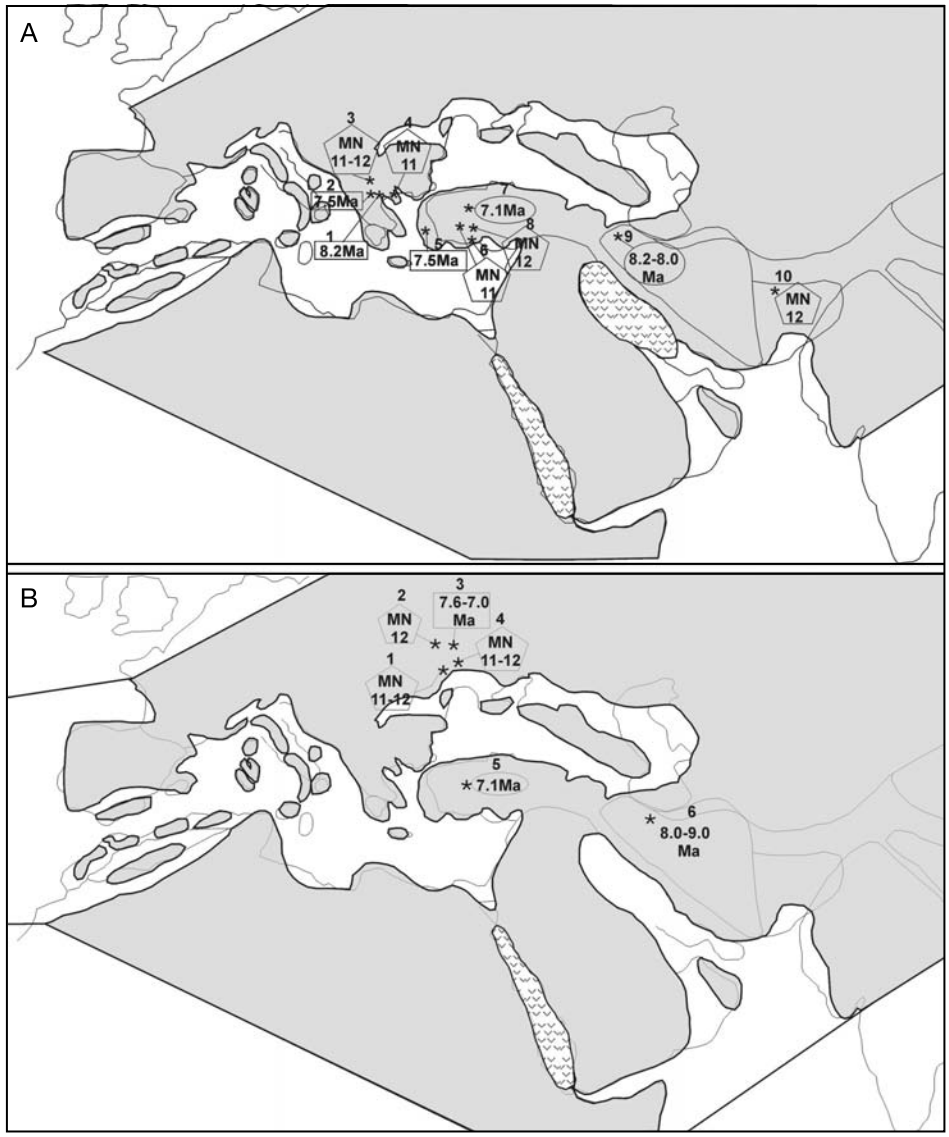

FIG. 48. — **A**, geographic distribution of the *Hipparion dietrichi* morphotype with the age of the localities, the palaeogeographic map is from Rögl (1999); **1**, "Ravin des Zouaves-5"; **2**, "Vathylakkos 1,2,3" and "Prochoma 1"; **3**, Titov Veles; **4**, "Nikiti 2"; **5**, Samos MTLA-B; **6**, Kayadibi and Garkın; **7**, Akkaşdağı; **8**, Kınık; **9**, Maragha; **10**, Molayan; **B**, geographic distribution of the *Hipparion moldavicum* morphotype with the age of the localities, the palaeogeographic map is from Rögl (1999); **1**, Taraklia; **2**, Tudorovo; **3**, Novaya Emetovka-2; **4**, Novaya Elisavetovka; **5**, Akkaşdağı; **6**, Maragha.

the Turolian localities of Axios Valley and from Chalkidiki peninsula (Macedonia, Greece) (Koufos 1990; Vlachou & Koufos 2002). The oldest known locality with *H. dietrichi* is "Ravin des Zouaves-5" (RZO) in Axios Valley, dated to early Turolian, MN 11 (Koufos 1987d; Bonis & Koufos 1999). Magnetostratigraphic data suggest for RZO an age about 8.2 Ma (Sen *et al.* 2000). The locality "Nikiti 2", (NIK) in Chalkidiki (Greece) includes *H. dietrichi*, and it is dated to

early Turolian, MN 11 (Vlachou & Koufos 2002). In Axios Valley, *H. dietrichi* is also known from the localities of "Prochoma 1" (PXM) and "Vathylakkos 1,2,3" (VLO, VTK, VAT) (Koufos 1987c, 1988b). They are dated to early MN 12 based on the presence of *Parapodemus schaubi* in the VTK fauna (Bonis & Koufos 1999; Koufos 2003) or, according to the magnetostratigraphy, at ≈ 7.5 Ma (Sen *et al.* 2000). The Axios Valley sample has similar cranial and dental morphology to that of Samos and Akkaşdağı, but it is clearly smaller in size.

The *H. dietrichi* morphotype is probably known in FYROM (Former Yugoslavian Republic of Macedonia) where it is referred as *H. prostylum-schlosseri-dietrichi* by Forstén & Garevski (1989). This complex name concerns a set of skulls and metapodials from various late Miocene localities of the area, and these skulls are similar to those of *H. prostylum* from Mont Lubéron and *H. schlosseri-dietrichi* from Samos (Forstén & Garevski 1989). These skulls share the typical morphology of *H. dietrichi* in having short and wide muzzle, short narial opening and weakly developed preorbital fossa that is placed far from the orbit and facial crest; the preorbital fossa is anteroposteriorly oriented and has variously defined posteroventral rim. Hence, *H. dietrichi* morphotype seems to be present in the Turolian of FYROM. The age of FYROM localities is not well stressed otherwise than the Turolian character of their faunas. In the NOW database (2003), the old collection from Titov-Veles is referred to middle Turolian.

The presence of *H. dietrichi* in Bulgaria is not supported by the available data. The Bulgarian hipparions are referred to various species (Bakalov & Nikolov 1962; Nikolov 1985). The recognition of hipparion species in these old collections needs a serious review and comparison with well documented Eurasian species for reliable systematic assignments. Contrary to this, the new collection from the Turolian locality of Hadjidimovo is studied in detail and includes three species: *H. brachypus*, *H. mediterraneum* and *H.* cf. *platygenys* (Spassov 2001; Hristova *et al.* 2002, 2003).

In Turkey *H. dietrichi* is poorly known. A medium-sized form from the Turolian localities of Kayabidi, Garkın and Kınık resembles *H. dietrichi* (Staesche & Sondaar 1979). The locality of Kayadibi is dated to early MN 11, Garkın to late MN 12 and Kınık to MN 12 (Koufos 2003). Its occurrence at Akkaşdağı is the first certain reference in Turkey. The Akkaşdağı form has the salient characters of *H. dietrichi*, it is clearly larger than the Axios Valley forms while it is similar in size to Samos *H. dietrichi*.

A medium-sized hipparion from Maragha (Iran) has been described as *H. prostylum* (Gervais 1849). Despite the differences in the length of the facial region and the fossa morphology, it seems to be quite close to *H. dietrichi* (see comparisons under *H. dietrichi*). The type material of *H. prostylum* is from Mont Lubéron (France), and in spite of the smaller size, the cranial morphology strongly reminds that of *H. dietrichi* from Samos and Axios. The species *H. molayanensis* (Zouhri 1992) from Molayan (Afghanistan) resembles *H. dietrichi* from Samos and Akkaşdağı (see comparisons under *H. dietrichi*) in its cranial morphology and size. Molayan yielded a typical Turolian fauna well compared with those of MN 12 (Sen 1998).

Taking into account the above remarks, the *H. dietrichi* morphotype is well known and widespread in Eastern Mediterranean during early and middle Turolian (Fig. 48A), and it is possibly present in Western Europe (Mont Lubéron). It is characterized by a moderate size, short and broad muzzle, weak preorbital fossa situated far from the orbit with poorly defined anterior rim and variable depth, moderate enamel plication, and elongated-slender metapodials.

The small-sized *H. moldavicum* is quite rare in Eastern Mediterranean area, unknown in the Balkans (Fig. 48B) but well known from the localities of the northern coasts of Black Sea. Its type locality, Taraklia (Moldavia), is considered as being between MN 12 and MN 13, while Novaya Elisavetovka is dated as being between MN 11 and MN 12 (NOW database 2003). *Hipparion moldavicum* is also known from the locality of Novaya Emetovka 2, Ukraine (Krakhmalnaya 1996), and is later referred as

H. aff. *moldavicum* (Krakhmalnaya & Forstén 1998). The locality is dated to late MN 12 (Krakhmalnaya 1996) or correlated by magnetostratistratigraphy either to the top of Chron C4 or to Chron C3B, suggesting an age between 7.6 and 7.0 Ma (Krakhmalnaya *et al*. 1993). A subspecies, *H. moldavicum tudorovense*, was reported from the locality of Tudorovo, Moldavia (Eisenmann 1995), dated to MN 12 (NOW database 2003). The presence of *H. moldavicum* in Akkaşdağı indicates that the species was also present in Asia Minor during MN 12. Recent study of the new hipparion collection from Samos showed that this small-sized hipparion must be also present in the locality "Mytilinii 1B" (Vlachou & Koufos 2004). The doubt is due to the lack of cranial remains although the comparison of the postcranial bones indicates the presence of a small- to medium-sized hipparion form similar to *H. moldavicum* from Akkaşdağı.

The presence of *H. moldavicum* is also recognized at the Middle horizons of Maragha, Iran (Bernor *et al*. 1996b; Watabe & Nakaya 1991b). The Middle Maragha fauna has an interpolated age between 8.2 and 8.0 Ma (Swisher III 1996). Therefore, *H. moldavicum* is widespread in the northern Black Sea area and southwest Asia during early-middle Turolian, MN 11-12 (Fig. 50). The absence of *H. moldavicum* in the Balkan Peninsula is an open question.

The short and robust metapodials from Pikermi have been described as *H. brachypus* by Hensel (1862), and for a long time this species was considered as restricted to Pikermi (Fig. 49A). Some large teeth with high enamel plication from Halmyropotamos (Evia, Greece) were referred to *H. koeningswaldi* (Melentis 1967); they possibly belong to *H. brachypus*. Some teeth from the neigbouring locality of Chalkoutsi are also similar to that of *H. brachypus* (Bonis & Koufos 1999). The Pikermi fauna has a questionable age as there are several opinions about its age (Bernor *et al*. 1996b). Based on the Gaudry's collection stored in the MNHN, Pikermi is dated to the uppermost middle Turolian. It is younger than Vathylakkos and Prochoma faunas as well as than Mytilinii 2, 3 of Samos (Mein 1990; Bonis & Koufos 1999; Koufos 2003). The Halmyropotamos fauna seems to be older than that of Pikermi and can be correlated to the lower MN 12 (Koufos 2003).

Recently, the species was recognized in the Bulgarian locality of Hadjidimovo, which is dated to MN 12, slightly older than Pikermi and maybe at the same level as Halmyropotamos (Spassov 2001; Koufos 2003). The size and the proportions of the Grebeniki large metapodials are close to *H. brachypus* from Pikermi, but they are slender (Figs 8; 9). The Grebeniki fauna is dated to MN 11-12 (NOW database 2003), and cannot be accurately correlated with the other localities. In Axios Valley (Macedonia, Greece) there is no certain evidence about the presence of *H. brachypus*. *Hipparion brachypus* from Akkaşdağı is the first certain record of the species in Asia, this indicates that *H. brachypus* was not restricted to the Balkan Peninsula (Fig. 49A). *Hipparion brachypus* is possibly present in the localities Kemiklitepe A-B (see comparisons under *H. brachypus*) while Tobien (1968) reports the possible presense of the species in the Middle Maragha fauna. All the available data for *H. brachypus* suggest that it is a middle Turolian (MN 12) species (Fig. 50).

The largest hipparion from Akkaşdağı belongs to the morphotype of *H. longipes*. It is characterized by long metapodials with robust epiphyses. The type locality of *H. longipes* is Pavlodar (Kazakhstan) (Fig. 49B). The Pavlodar fauna has been considered for a long time as Pontian (Russian terminology), but recent data suggest an age between 6.8 and 6.2 Ma (Forstén 1997). The MN 12/13 boundary is calibrated in Spain as being near the base of Chron A3An.2n (6.57 Ma) (Opdyke *et al*. 1997). If the age of the Pavlodar fauna is correct, it can be correlated to the uppermost MN 12 or to early MN 13. According to NOW database (2003), Pavlodar is referred to MN 13 or between 7.1 and 5.3 Ma based on the assumption that MN 12/13 boundary is dated to 7.1 Ma (Steininger *et al*. 1996). Some remains from late Ruscinian (MN 15) of Megalo Emvolon (Greece) and Çalta (Turkey) were referred to as *H. longipes*, *H*. aff. *longipes* or *H*. cf. *longipes*

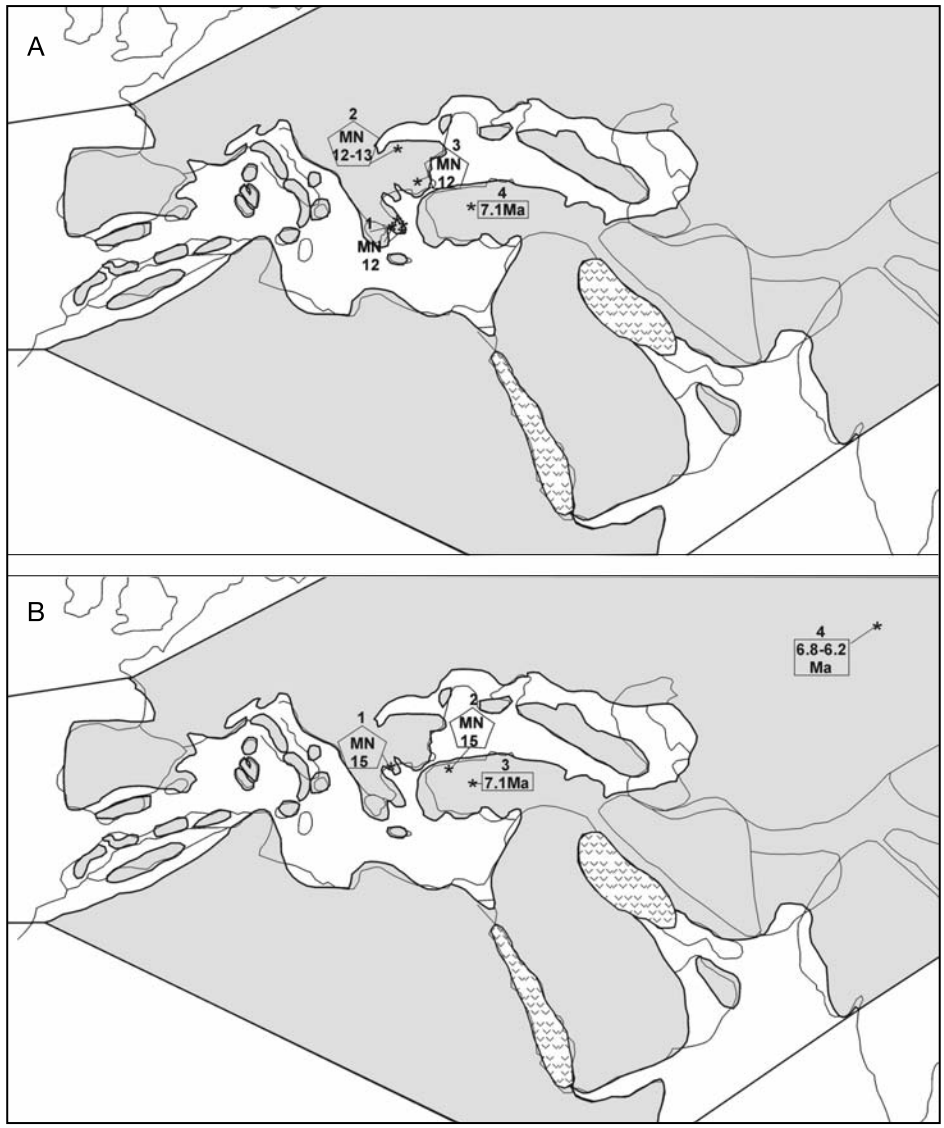

FIG. 49. — **A**, geographic distribution of the *Hipparion brachypus* morphotype with the age of the localities, the palaeogeographic map is from Rögl (1999); **1**, Pikermi, Chomateres, Chalkoutsi; **2**, Polgardi; **3**, Hadjidimovo; **4**, Akkaşdağı; **B**, geographic distribution of the *H. longipes* morphotype with the age of the localities, the palaeogeographic map is from Rögl (1999); **1**, Megalo Emvolon; **2**, Çalta; **3**, Akkaşdağı; **4**, Pavlodar.

(Koufos *et al*. 1991; Eisenmann & Sondaar 1998). Since *H. longipes* is unknown during the interval of latest Miocene-early Pliocene, Akkaşdağı represents probably the first appearance of the species in the Eastern Mediterranean area. In summary, the morphotype of *H. longipes* seems to appear at about 7.0 Ma (middle MN 12) in Asia and to survive in southeastern Europe during Ruscinian. Unfortunately, the available material of *H. longipes* from various localities is

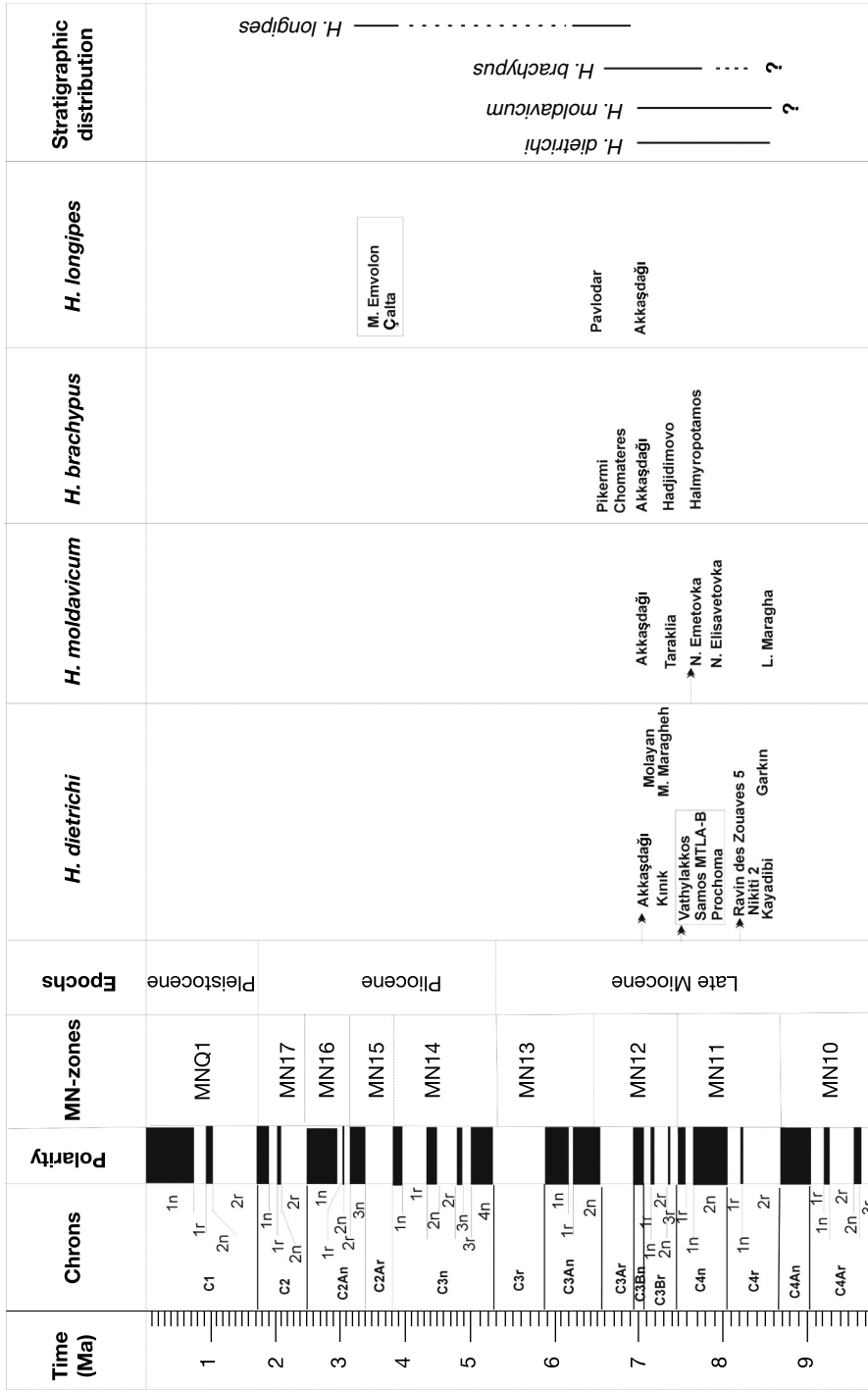

FIG. 50. — Stratigraphic distribution of the studied hipparions in Eastern Mediterranean.

poor and fragmentary (Akkaşdağı is the richest) and contains only postcranial remains. Consequently, it is difficult to certify the presence of the species either in the Akkaşdağı fauna or in other localities, and then to define the size range of the species for certain systematics and biostratigraphy.

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REFERENCES

ARAMBOURG C. & PIVETEAU J. 1929. — Les vertébrés du Pontien de Salonique. *Annales de Paléontologie* 18: 59-138.

BAKALOV P. & NIKOLOV I. 1962. — *The Fossils of Bulgaria. X. Tertiary Mammals*. Bulgarian Academy of Science, Sofia, 162 p.

BERNOR R. L. 1985. — Systematic and evolutionary relationships of the hipparionine horses from Maragha, Iran (late Miocene, Turolian age). *Palaeovertebrata* 15 (4): 173-269.

BERNOR R. L., TOBIEN H. & WOODBURNE M. O. 1990. — Patterns of Old World hipparionine evolutionary diversification and biogeographic extension, *in* LINDSAY E., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 263-338.

BERNOR R. L., KOUFOS G. D., WOODBURNE M. & FORTELIUS M. 1996a. — The evolutionary history and biochronology of European and southeastern Asian late Miocene and Pliocene hipparionine horses, *in* BERNOR R. L., FAHLBUSCH V. & MITTMAN H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 7-46.

BERNOR R. L., SOLOUNIAS N., SWISHER C. C. III & VAN COUVERING J. A. 1996b. — The correlation or the three classical "Pikermian" mammal faunas – Maragha, Samos and Pikermi – with the European MN Unit system, *in* BERNOR R. L., FAHLBUSCH V. & MITTMAN H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 137-154.

BERNOR R. L., TOBIEN H., HAYEK L.-A. & MITTMANN H.-W. 1997. — The Höwenegg hipparionine horses: systematics stratigraphy, taphonomy and paleoenvironmental context. *Andrias* 10: 1-230.

BONIS L. DE & KOUFOS G. D. 1999. — The Miocene large mammal succession in Greece, *in* AGUSTI J., ROOK L. & ANDREWS P. (eds), *Hominoid Evolution and Climatic Change in Europe,* vol. I: *The Evolution of the Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, New York: 205-237.

EISENMANN V. 1995. — What metapodial morphometry has to say about some Miocene hipparions, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Palaeoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven; London: 148-162.

EISENMANN V. & SONDAAR P. Y. 1998. — Pliocene vertebrate locality of Çalta, Ankara, Turkey. 7. *Hipparion*. *Geodiversitas* 20 (3): 409-439.

EISENMANN V., ALBERDI M. T., DE GIULI C. & STAESCHE U. 1988. — Methodology, *in* WOODBURNE M. & SONDAAR P. Y. (eds), *Studying Fossil Horses*. E. J. Brill, Leiden; New York, 71 p.

FORSTÉN A. M. 1978. — A review of the Bulgarian *Hipparion* (Mammalia, Perissodactyla). *Geobios* 11: 31-41.

FORSTÉN A. M. 1997. — A review of Central Asiatic hipparions (Perissodactyla, Equidae). *Acta Zoologica Fennica* 205: 1-26.

FORSTÉN A. M. & GAREVSKI R. 1989. — Hipparions (Mammalia, Perissodactyla) from Macedonia, Yugoslavia. *Geologica Macedonica* 3: 159-206.

FORSTÉN A. M. & KRAKHMALNAYA T. 1997. — The hipparions (Mammalia, Equidae) from the late Miocene of Cherevinchoe on the northern Black Sea coast, Ukraine. *Neues Jahrbuch für Geologie und Paläontologie, Monatschefte* H8: 489-499.

GERVAIS P. 1849. — Note sur la multiplicité des espèces d'*Hipparion* (genre de chevaux à trois digits) qui sont enfouis à Cucuron (Vaucluse). *Comptes Rendus de l'Académie des Sciences de Paris* D 29: 284-286.

GROMOVA V. 1952. — *Le genre* Hipparion. CEDP, Saint-Aubin 12, 288 p.

HEINTZ E., GINSBURG L. & SEN S. 1975. — *Hipparion longipes* Gromova du Pliocène de Çalta (Ankara, Turquie), le plus dolichopodial des hipparions. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* Amsterdam, B 78 (2): 77-82.

HENSEL R. 1862. — Über die Reste einiger Säugethierarten von Pikermi in der Münchener Sammlung. *Mber K. preus. Akademie Wissenschaften* 27: 560-569.

HRISTOVA L., KOVACHEV D. & SPASSOV N. 2002. — [The hipparions (Equidae, Mammalia) from the Upper Miocene locality Hadjidimovo, SW Bulgaria]. *Review of the Bulgarian Geological Society*, vol. 63, part 1-3: 89-98 (in Bulgarian).

HRISTOVA L., KOVACHEV D. & SPASSOV N. 2003. — *Hipparion brachypus* Hensel, 1862 from the late Miocene of Hadjidimovo, Southwestern Bulgaria. *Comptes Rendus de l'Académie bulgare des Sciences* 56 (2): 77-84.

KARADENIZLI L., SEYITOĞLU G., SEN S., ARNAUD N., KAZANCI N., SARAÇ G. & ALÇIÇEK C. 2005. — Mammal bearing late Miocene tuffs of the Akkaşdağı region; distribution, age, petrographical and geochemical characteristics, *in* SEN S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* 27 (4): 553-566 (this volume).

KAZANCI N., KARADENIZLI L., SEYITOĞLU G., SEN S., ALÇIÇEK M. C., VAROL B., SARAÇ G. & HAKYEMEZ Y. 2005. — Stratigraphy and sedimentology of Neogene mammal bearing deposits in the Akkaşdağı area, Turkey, *in* SEN S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* 27 (4): 527-551 (this volume).

KOSTOPOULOS D. S., SEN S. & KOUFOS G. D. 2003. — Magnetostratigraphy and revised chronology of the late Miocene mammal localities of Samos, Greece. *International Journal of Earth Sciences* 92: 779-794.

KOUFOS G. D. 1987a. — Study of the Pikermi hipparions. Part I: Generalities and taxonomy. *Bulletin du Muséum national d'Histoire naturelle Paris* 4e sér., 9, sect. C, 2: 197-252.

KOUFOS G. D. 1987b. — Study of the Pikermi hipparions. Part II: Comparisons and odontograms. *Bulletin du Muséum national d'Histoire naturelle Paris* 4e sér., 9, sect. C, 3: 327-363.

KOUFOS G. D. 1987c. — Study of the Turolian hipparions of the lower Axios Valley (Macedonia, Greece). 2. Locality "Prochoma-1" (PXM). *Paläontologische Zeitschrift* 61: 339-358.

KOUFOS G. D. 1987d. — Study of the Turolian hipparions of the lower Axios Valley (Macedonia, Greece). 1. Locality "Ravin des Zouaves-5" (RZO). *Geobios* 20: 293-312.

KOUFOS G. D. 1988a. — Study of the Turolian hipparions of the lower Axios Valley (Macedonia, Greece). 3. Localities of Dytiko. *Palaeovertebrata* 18: 187-239.

KOUFOS G. D. 1988b. — Study of the Turolian hipparions of the lower Axios Valley (Macedonia, Greece). 3. Localities of Vathylakkos. *Paleontologia i Evolucio* 22: 15-39

KOUFOS G. D. 1990. — The hipparions of the lower Axios Valley (Macedonia, Greece). Implications for the Neogene stratigraphy and the evolution of hipparions, *in* LINDSAY E., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 321-338.

KOUFOS G. D. 2003. — Late Miocene mammal events and biostratigraphy in the Eastern Meditarranean. *Deinsea* 10: 343-371.

KOUFOS G. D. & KOSTOPOULOS D. S. 1994. — The late Miocene mammal localities of Kemiklitepe (Turkey). 3. Equidae. *Bulletin du Muséum national d'Histoire naturelle Paris* 4e sér., 16, sect. C: 41-80.

KOUFOS G. D. & MELENTIS J. 1984. — The late Miocene (Turolian) mammalian fauna of Samos island (Greece). Study of the collection of Palaeontological Museum of Mytilinii, Samos. 2. Equidae. *Scientific Annals of the Faculty of Physics and Mathematics, University of Thessaloniki* 24: 47-78.

KOUFOS G. D., SYRIDES G. & KOLIADIMOU K. 1991. — A Pliocene primate from Macedonia. *Journal of Human Evolution* 21: 283-294.

KOUFOS G. D., SYRIDES G. E., KOSTOPOULOS D. S., KOLIADIMOU K. K., SYLVESTROU I. A., SEITANIDIS G. C. & VLACHOU T. D. 1997. — New excavations in the Neogene mammalian localities of Mytilinii, Samos island, Greece. *Geodiversitas* 19 (4): 877-885.

KRAKHMALNAYA T. 1996. — Gipparionovaya fauna drevnego meotica severnogo prichernomorya [= The hipparion-fauna of the early Maeotian of the Northern peri-Pontic region]. *Naukova Dumka*: 1-225 (in Russian).

KRAKHMALNAYA T. & FORSTÉN A. M. 1998. — The hipparions (Mammalia, Equidae) from the late Miocene of Novaya Emetovka-2, Odessa region, Ukraine. *Neues Jahrbuch für Geologie und Paläontologie, Monatschefte* H8: 449-462.

KRAKHMALNAYA T., SVETLITSKAYA V. & CHEPALYGA A. L. 1993. — New data on stratigraphy, magnetostratigraphy and mammal faunas of the late Miocene locality of Novaya Emetovka (Ukraine). *Newsletters on Stratigraphy* 29 (2): 77-89.

MEIN P. 1990. — Updating MN zones, *in* LINDSAY E. H., FALHBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 73-90.

MELENTIS J. K. 1967. — Die pikermifauna von Halmyropotamos (S. Eüboa/Griechenland). Teil I: Odontologie. *Annales géologiques des Pays helléniques* 19: 283-411.

NIKOLOV I. 1985. — Catalogue of the localities of Tertiary mammals in Bulgaria. *Palaeontology, Stratigraphy and Lithology* Sofia 21: 43-62.

NOW DATABASE 2003. — Neogene of the Old World. Database of fossil mammals: www.helsinki.fi/science/now

OPDYKE N. D., MEIN P., LINDSAY E., PEREZ GONZALEZ A., MOISSENET E. & NORTON V. L. 1997. — Continental deposits, magnetostratigraphy and vertebrate palaeontology, late Neogene of Eastern Spain. *Palaeogeography Palaeoclimatology Palaeoecology* 133: 129-148.

RÖGL F. 1999. — Circum-Mediterranean miocene palaeogeography, *in* RÖSSNER G. & HEISSIG K. (eds), *The Miocene Land Mammals of Europe*. Verlag Dr Friedrich Pfeil, München: 39-48.

SEN S. 1998. — The age of the Molayan mammal locality, Afghanistan. *Geobios* 31 (3): 385-391.

SEN S., SONDAAR P. Y. & STAESCHE U. 1978. — The biostratigraphical applications of the genus *Hipparion* with special reference to the Turkish representatives. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* Amsterdam, B 81: 370-385.

SEN S., BOUVRAIN G. & GERAADS D. 1998a. — Pliocene vertebrate locality of Çalta, Ankara, Turkey. 12. Palaeoecology, biogeography and biochronology. *Geodiversitas* 20 (3): 497-510.

SEN S., SEYITOĞLU G., KARADENIZLI L., KAZANCI N., VAROL B. & ARAZ H. 1998b. — Mammalian biochronology of Neogene deposits and its correlation with the lithostratigraphy in the Çankırı-Çorum Basin, central Anatolia, Turkey. *Eclogae Geologicae Helvetiae* 91: 307-320.

SEN S., KOUFOS G. D., KONDOPOULOU D. & BONIS L. DE 2000. — Magnetostratigraphy of the late Miocene continental deposits of the lower Axios Valley, Macedonia, Greece, *in* KOUFOS G. D. & IOAKIM C. (eds), Mediterranean Neogene cyclostratigraphy in marine-continental deposits. *Bulletin of the Geological Society of Greece*, special publications 9: 97-206.

SONDAAR P. Y. 1971. — The Samos *Hipparion*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* Amsterdam, B 74: 417-441.

SPASSOV N. 2001. — The Turolian *Hipparion*-fauna and the character of the environment in the late Miocene of West Bulgaria. *Review of the Bulgarian Geological Society* 61: 47-60.

STAESCHE U. & SONDAAR P. Y. 1979. — *Hipparion* aus dem Vallesium und Turolium (Jungtertiär) der Turkei. *Geologische Jahrbuch* B 33: 35-79.

STEININGER F. F., BERGGREN W. A., KENT D. V., BERNOR R. L., SEN S. & AGUSTI J. 1996. — Circum-Mediterranean Neogene (Miocene and Pliocene) marine-continental chronologic correlations of European Mammal units, *in* BERNOR R. L., FAHLBUSCH V. & MITTMAN H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 307-338.

SWISHER C. C. III 1996. — New $^{40}Ar/^{39}Ar$ dates and their contribution towards a revised chronology for the late Miocene of Europe and West Asia, *in* BERNOR R. L., FAHLBUSCH V. & MITTMAN H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 64-77.

TOBIEN H. 1968. — Palaeontologische Ausgrabungen nach jungtertiaren Wirbeltieren auf der Insel Chios (Griechenland) und bei Maraghen (N. W. Iran). *Jahrbuch. Verein. "Fereunde der Universitat Mainz"*: 51-58.

VLACHOU T. & KOUFOS G. D. 2002. — The hipparions (Mammalia, Perissodactyla) from the Turolian locality "Nikiti-2" (NIK), Macedonia, N. Greece. *Annales de Paléontologie* 88: 215-263.

VLACHOU T. & KOUFOS G. D. 2004. — Study of the Turolian hipparions of Greece, *in* CHATZIPETROS A. A. & PAVLIDES S. B. (eds), *Proceedings of 5th International Symposium on Eastern Mediterranean Geology*, Thessaloniki, Greece, Vol. 1: 365-368.

WATABE M. & NAKAYA H. 1991a. — Phylogenetic significance of the postcranial skeletons of the hipparions from Maragha (late Miocene), Northwest Iran. *Memoirs of the Faculty of Sciences, Kyoto University*, ser. Geology and Mineralogy, LVI: 11-53.

WATABE M. & NAKAYA H. 1991b. — Cranial skeletons of *Hipparion* (Perissodactyla, Mammalia) from Maragha (Turolian, late Miocene), Northwest Iran. *Memoirs of the Faculty of Sciences, Kyoto University*, ser. Geology and Mineralogy, LVI: 55-125.

ZOUHRI S. 1992. — Hipparion molayanensis *n. sp. (Perisodactyla, Equidae) du Turolien de Molayan (Afghanistan). Description, comparaison et systématique*. Doctoral thesis, Université Paris VII, France, 148 p.

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APPENDIX 1

Total Variance of the Principal Component Analysis of the metacarpals from Akkaşdağı. Extraction method: Principal Component Analysis.

Component	Initial Eigenvalues			Extraction sums of squared loadings		
	Total	% of vicariance	Cumulative %	Total	% of vicariance	Cumulative %
1	9.593	79.943	79.943	9.593	79.943	79.943
2	1.490	12.420	92.363	1.490	12.420	92.363
3	0.302	2.518	94.881			
4	0.176	1.463	96.344			
5	0.129	1.076	97.420			
6	0.104	0.866	98.286			
7	0.07184	0.599	98.884			
8	0.05701	0.475	99.359			
9	0.03145	0.262	99.621			
10	0.02709	0.226	99.847			
11	0.01683	0.140	99.987			
12	0.001511	0.01259	100.000			

APPENDIX 2

TABLE 1. — Akkaşdağı hipparions, measurements of the skull (in mm); **1**, muzzle length: prosthion-middle of the line connecting the anterior borders of P2; **2**, palatal length: middle of the line connecting the anterior borders of P2-anterior border to choanae; **3**, length from anterior border of choanae to vomer; **4**, length vomer-basion; **5**, post-palatal length: basion-anterior border of choanae; **6**, basilar length: basion-prosthion; **7**, premolar length (alveolar); **8**, molar length (alveolar); **9**, tooth row length (alveolar); **10**, choanal length; **11**, minimal breadth of choanae; **12**, maximal breadth of choanae; **13**, palatal breadth between P4 and M1; **14**, minimal muzzle breadth; **15**, muzzle breadth: breadth between the posterior border of I3; **16**, maximal length of fossa temporalis; **17**, distance basion-foramen ethmoidalis; **18**, frontal breadth: between the most external points of the posterior borders of the orbits; **19**, zygomatic breadth: between the most external points of the zygomatic arcs; **20**, greatest breadth of the supra occipital crest; **21**, occipital breadth at paroccipital processes; **22**, occipital height: upper border of the occipital foramen-middle of the supra occipital crest; **23**, anterior ocular line: prosthion-most external point of the posterior border of the orbit; **24**, posterior ocular line: last point-middle of the supra occipital crest; **25**, facial height: height of the skull in front of P2; **26**, idem posterior of the orbits; **27**, height of meatus acusticus; **28**, anteroposterior diameter of the orbit; **29**, dorsoventral diameter of the orbit (perpendicular to 28); **30**, length of the naso-incisival notch: prosthion-posterior end of the narial opening; **31**, cheek length: posterior end of the narial opening-anterior border of the orbit; **32**, distance between the orbit and the preorbital fossa; **33**, maximal length of the preorbital fossa; **34**, distance between the back of the preorbital fossa and the infraorbital foramen; **35**, height of the preorbital fossa: perpendicular to its maximal length; **36**, distance between the preorbital fossa and the facial crest; **37**, height of back of the infraorbital foramen above the alveolar border; **38**, height of the back of the preorbital fossa above the alveolar border. Abbreviations: **s**, standard deviation (STDEV); **v**, variance coefficient (STDEV × 100 / mean).

	1	2	3	4	5	6	7	8	9	10
					Hipparion brachypus					
n	1	1	1	1	1	1	4	1	1	–
mean	148.5	130.1	110	94	190	70	92.275	75.7	162.5	–
min	–	–	–	–	–	–	90	–	–	–
max	–	–	–	–	–	–	95	–	–	–
s	–	–	–	–	–	–	2.42	–	–	–
v	–	–	–	–	–	–	2.62	–	–	–

	1	2	3	4	5	6	7	8	9	10
					Hipparion dietrichi					
n	2	2	–	–	–	–	8	9	7	1
mean	111.9	112.95	–	–	–	–	83.35	70.12	154.76	66.80
min	106.8	104.5	–	–	–	–	74.2	65.0	151.5	–
max	117.0	121.4	–	–	–	–	87.5	74.5	158.7	–
s	–	–	–	–	–	–	4.43	2.47	2.55	–
v	–	–	–	–	–	–	5.31	3.52	1.65	–
					Hipparion moldavicum					
n	1	2	1	1	1	1	4	10	3	1
mean	105	101	84.4	78.9	163	375	73.08	60.26	133.20	61.40
min	–	100.5	–	–	–	–	70.5	55.0	127.3	–
max	–	101.5	–	–	–	–	79.0	66.5	140.2	–
s	–	–	–	–	–	–	4.04	3.89	6.52	–
v	–	–	–	–	–	–	5.53	6.46	4.89	–

	11	12	13	14	15	16	17	18	19	20
					Hipparion brachypus					
n	–	–	1	1	1	–	–	–	–	–
mean	–	–	64.4	45.5	62	–	–	–	–	–
min	–	–	–	–	–	–	–	–	–	–
max	–	–	–	–	–	–	–	–	–	–
s	–	–	–	–	–	–	–	–	–	–
v	–	–	–	–	–	–	–	–	–	–
					Hipparion dietrichi					
n	–	1	3	3	2	–	–	1	–	–
mean	–	47.50	64.33	40.90	65.60	–	–	183.10	–	–
min	–	–	61.5	36.2	64.4	–	–	–	–	–
max	–	–	67.8	43.8	66.8	–	–	–	–	–
s	–	–	3.20	4.11	–	–	–	–	–	–
v	–	–	4.97	10.04	–	–	–	–	–	–
					Hipparion moldavicum					
n	–	2	4	1	1	2	–	–	–	–
mean	–	35.85	56.93	32.90	42.70	68.40	–	–	–	–
min	–	32.7	51.4	–	–	67.4	–	–	–	–
max	–	39.0	63.0	–	–	69.4	–	–	–	–
s	–	–	4.80	–	–	–	–	–	–	–
v	–	–	8.43	–	–	–	–	–	–	–

	21	22	23	24	25	26	27	28	29	30
					Hipparion brachypus					
n	–	–	1	–	1	–	–	–	–	1
mean	–	–	370.6	–	99.2?	–	–	–	–	191.1
min	–	–	–	–	–	–	–	–	–	–
max	–	–	–	–	–	–	–	–	–	–
s	–	–	–	–	–	–	–	–	–	–
v	–	–	–	–	–	–	–	–	–	–

	21	22	23	24	25	26	27	28	29	30
					Hipparion dietrichi					
n	–	–	2	–	–	–	–	2	2	1
mean	–	–	307.25	–	–	–	–	57.15	47.20	120.50
min	–	–	305.0	–	–	–	–	56.5	47.0	–
max	–	–	309.5	–	–	–	–	57.8	47.4	–
s	–	–	–	–	–	–	–	–	–	–
v	–	–	–	–	–	–	–	–	–	–
					Hipparion moldavicum					
n	1	1	–	1	1	–	–	1	1	1
mean	81.70	45.30	–	149.00	80.50	–	–	55.00	47.70	116.50
min	–	–	–	–	–	–	–	–	–	–
max	–	–	–	–	–	–	–	–	–	–
s	–	–	–	–	–	–	–	–	–	–
v	–	–	–	–	–	–	–	–	–	–

	31	32	33	34	35	36	37	38
				Hipparion brachypus				
n	1	1	1	1	1	1	1	1
mean	153.5	43.5	71.4	77.5	48	34.5	54.4	93
min	–	–	–	–	–	–	–	–
max	–	–	–	–	–	–	–	–
s	–	–	–	–	–	–	–	–
v	–	–	–	–	–	–	–	–
				Hipparion dietrichi				
n	1	3	1	1	2	1	1	2
mean	151.60	41.10	69.40	54.00	41.55	41.30	55.00	85.35
min	–	38.0	–	–	35.3	–	–	84.4
max	–	45.2	–	–	47.8	–	–	86.3
s	–	3.70	–	–	–	–	–	–
v	–	9.01	–	–	–	–	–	–
				Hipparion moldavicum				
n	1	3	4	4	2	3	4	3
mean	137.90	20.50	77.98	66.33	51.75	22.90	41.48	67.23
min	–	16.0	71.5	56.1	49.7	21.2	38.3	59.1
max	–	23.5	88.4	71.2	53.8	26.2	43.5	72.0
s	–	3.97	7.28	6.91	–	2.86	2.22	7.08
v	–	19.36	9.33	10.41	–	12.48	5.36	10.53

TABLE 2. — Akkaşdağı hipparions, measurements of the mandible (in mm); **1**, maximal length: posterior point of the articular condyle-anterior point situated between the two i1 (in projection); **2**, muzzle length: middle of the line connecting the anterior borders of p2 to a point situated between the two i1; **3**, premolar length (alveolar); **4**, molar length (alveolar); **5**, toothrow length (alveolar); **6**, distance from posterior end of m3-posterior border of the vertical ramus; **7**, muzzle breadth: breadth at the posterior borders of i3; **8**, height articular condyle-base of the horizontal ramus; **9**, height incisura mandibulae-base of the horizontal ramus; **10**, depth of the jaw behind m3; **11**, idem between p4 and m1; **12**, idem in front of p2; **13**, symphysial length; **14**, minimal breadth of the symphysis; **16**, length of the diastema p2-i3. Abbreviations: **s**, standard deviation (STDEV); **v**, variance coefficient (STDEV × 100 / mean).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16
Hipparion brachypus															
n	–	2	8	5	4	–	1	–	–	–	1	4	3	4	1
mean	–	120.45	83.09	73.38	153.45	–	18.70	–	–	–	72.10	47.38	83.33	20.48	91.50
min	–	110.9	76.5	70.5	150.0	–	–	–	–	–	–	45.0	82.0	17.2	–
max	–	130.0	89.0	75.3	160.0	–	–	–	–	–	–	49.5	85.0	24.0	–
s	–	–	4.96	1.93	4.46	–	–	–	–	–	–	2.21	1.53	2.89	–
v	–	–	5.97	2.63	2.91	–	–	–	–	–	–	4.67	1.83	14.10	–
Hipparion dietrichi															
n	–	2	10	10	8	–	1	–	–	–	3	8	2	5	4
mean	–	96.50	72.66	67.73	140.81	–	43.50	–	–	–	63.17	43.88	70.75	18.22	71.38
min	–	94.0	69.0	62.2	138.2	–	–	–	–	–	57.0	41.0	68.0	16.2	67.7
max	–	99.0	79.0	70.0	145.0	–	–	–	–	–	67.5	46.0	73.5	22.2	81.0
s	–	3.5	2.61	2.36	2.65	–	–	–	–	–	5.48	1.64	3.89	2.43	6.43
v	–	3.7	3.59	3.49	1.88	–	–	–	–	–	8.68	3.74	5.50	13.34	9.01
Hipparion moldavicum															
n	–	3	9	9	7	–	3	–	–	1	3	4	3	4	4
mean	–	95.10	68.40	63.92	134.49	–	45.73	–	–	85.20	49.30	39.40	67.23	17.63	75.55
min	–	93.0	61.5	58.3	128.8	–	42.2	–	–	–	45.0	35.6	63.5	16.5	74.7
max	–	97.3	74.6	70.0	142.1	–	50.0	–	–	–	54.4	42.0	72.1	18.5	77.0
s	–	2.15	4.45	3.89	5.18	–	3.95	–	–	–	4.75	2.97	4.41	1.03	1.02
v	–	2.26	6.50	6.08	3.85	–	8.64	–	–	–	9.64	7.53	6.56	5.85	1.35

TABLE 3. — *Hipparion brachypus*, Akkaşdağı, measurements of the upper teeth (in mm). Abbreviations: **Bo**, occlusal breadth; **EF**, enamel formula; **Lo**, occlusal length; **Lp**, protocone length; **s**, standard deviation (STDEV); **v**, variance coefficient (STDEV × 100 / mean); **Wp**, protocone width.

P2	**Lo**	**Bo**	**Lp**	**Wp**	**EF**	**M1**	**Lo**	**Bo**	**Lp**	**Wp**	**EF**
n	3	3	3	3	–	**n**	3	3	3	3	1
mean	32.87	23.40	7.07	4.43	–	**mean**	23.97	25.03	6.93	4.90	20.00
min	30.4	22.2	6.6	3.6	–	**min**	23.7	24.8	6.2	4.6	–
max	35.0	24.0	7.4	4.9	–	**max**	24.4	25.5	8.3	5.5	–
s	2.32	1.04	0.42	0.72	–	**s**	0.38	0.40	1.18	0.52	–
v	7.05	4.44	5.86	16.43	–	**v**	1.58	1.62	17.17	10.61	–
P3						**M2**					
n	3	3	3	3	–	**n**	2	2	2	2	1
mean	28.20	25.80	7.17	4.87	–	**mean**	24.40	23.50	7.40	5.10	18.00
min	27.6	24.3	6.3	4.6	–	**min**	23.6	23.0	6.5	4.8	–
max	29.0	26.6	8.6	5.0	–	**max**	25.2	24.0	8.3	5.4	–
s	0.72	1.30	1.25	0.23	–	**s**	–	–	1.27	0.42	–
v	2.50	5.04	17.36	4.71	–	**v**	–	–	17.20	8.31	–
P4						**M3**					
n	4	4	3	3	1	**n**	2	2	1	1	1
mean	27.10	24.80	7.43	5.03	26.00	**mean**	23.40	18.80	7.70	4.00	16.00
min	26.0	22.6	6.6	4.5	–	**min**	22.3	17.0	–	–	–
max	28.2	27.7	8.7	6.1	–	**max**	24.5	20.6	–	–	–
s	0.90	2.12	1.12	0.92	–	**s**	1.56	2.55	–	–	–
v	3.33	8.55	8.55	18.48	–	**v**	6.65	13.54	–	–	–

TABLE 4. — *Hipparion brachypus*, Akkaşdağı, measurements of the lower teeth (in mm). Abbreviations: **Bo ant**, anterior occlusal breadth; **Bo post**, posterior occlusal breadth; **EF**, enamel formula; **Lo**, occlusal length; **Lprfl**, preflexid length; **Lptfl**, postflexid length; **s**, standard deviation (STDEV); **v**, variance coefficient (STDEV × 100 / mean).

p2	Lo	Bo ant	Bo post	Lprfl	Lptfl	EF	m1	Lo	Bo ant	Bo post	Lprfl	Lptfl	EF
n	9	9	9	6	8	7	n	11	11	11	11	11	10
mean	29.91	11.00	12.70	7.88	12.84	2.57	mean	23.32	12.16	11.29	6.59	8.38	1.80
min	27.5	10.3	8.0	6.4	10.3	1.0	min	20.2	11.3	10.0	5.0	4.9	0.0
max	32.6	12.2	14.0	10.0	14.3	5.0	max	26.2	14.2	12.5	8.0	10.0	4.0
s	1.89	0.64	1.86	1.55	1.44	1.40	s	1.72	0.80	0.66	0.90	1.76	1.14
v	6.33	5.78	14.61	19.68	11.22	53.73	v	7.40	6.59	5.83	13.62	20.91	63.06
p3							m2						
n	11	11	11	10	10	10	n	8	8	8	8	8	6
mean	25.9	13.5	13.8	8.3	12.1	3.8	mean	23.9	11.4	10.3	7.2	8.8	1.8
min	24	9.7	11	7	7.2	1	min	21.7	9.7	8.9	6	5.2	1
max	28	16.2	15.8	9.6	13.7	7	max	28	12.5	11	7.9	11.7	4
s	1.282	1.570	1.131	0.881	2.237	1.619	s	2.139	0.995	0.727	0.731	1.868	1.169
v	4.95	11.63	8.196	10.614	18.488	42.605	v	8.95	8.728	7.058	10.153	21.227	64.944
p4							m3						
n	11	11	10	9	10	8	n	5	5	5	4	4	2
mean	25.2	13.1	13.5	7.3	11.4	2.6	mean	25.8	10.2	9.0	6.7	6.5	1.5
min	23.2	10.5	12.3	6.3	7.2	0	min	24.6	9	8	6.3	6.3	1
max	27.6	15	14.7	8.7	13.8	5	max	29.3	11.2	10.5	7.4	6.6	2
s	1.45	1.21	0.66	0.83	2.05	1.69	s	1.99	0.85	0.96	0.48	0.13	–
v	5.75	9.23	4.90	11.27	17.92	64.19	v	7.70	8.30	10.63	7.21	2.00	–

TABLE 5. — *Hipparion* cf. *longipes*, Akkaşdağı, measurements of the upper teeth (in mm). Abbreviations: see Table 3.

P2	Lo	Bo	Lp	Wp	EF	M1	Lo	Bo	Lp	Wp	EF
n	2	2	2	2	2	n	2	2	2	2	2
mean	34.8	24.6	8.3	4.1	20.5	mean	24.4	23.2	7.2	4.0	23.0
min	34.6	24.2	8.2	3.8	19	min	24	23	7	4	20
max	35	25	8.4	4.4	22	max	24.7	23.3	7.4	4	26
s	–	–	–	–	–	s	–	–	–	–	–
v	–	–	–	–	–	v	–	–	–	–	–
P3						M2					
n	2	2	2	2	2	n	2	2	2	2	2
mean	28.2	25.0	7.9	3.7	23.0	mean	26.0	20.9	7.0	3.7	18.0
min	27.5	24.7	7.7	3.4	20	min	25	20.8	7	3.5	17
max	28.8	25.3	8	4	26	max	27	21	7	3.8	19
s	–	–	–	–	–	s	–	–	–	–	–
v	–	–	–	–	–	v	–	–	–	–	–
P4						M3					
n	2	2	2	2	2	n	1	1	–	–	–
mean	25.9	24.55	9.15	3.65	19.5	mean	18.4	11.2	–	–	–
min	25.5	24.5	9	3.5	19	min	18.4	11.2	–	–	–
max	26.3	24.6	9.3	3.8	20	max	18.4	11.2	–	–	–
s	–	–	–	–	–	s	–	–	–	–	–
v	–	–	–	–	–	v	–	–	–	–	–

TABLE 6. — *Hipparion dietrichi*, Akkaşdağı, measurements of the upper teeth (in mm). Abbreviations: see Table 3.

P2	Lo	Bo	Lp	Wp	EF	M1	Lo	Bo	Lp	Wp	EF
n	10	11	12	11	12	n	21	20	22	21	21
mean	31.65	22.73	6.88	4.35	17.58	mean	22.60	22.42	6.97	4.36	17.00
min	28.5	20.6	5.8	3.0	11.0	min	20.0	19.9	5.2	3.7	7.0
max	33.7	23.5	8.2	5.1	24.0	max	25.3	24.5	8.5	5.1	25.0
s	1.95	0.90	0.76	0.70	3.26	s	1.39	1.38	0.82	0.42	5.04
v	6.16	3.99	11.09	16.35	18.52	v	6.13	6.16	11.79	9.48	29.65
P3						M2					
n	18	17	17	16	12	n	23	21	21	20	16
mean	25.79	23.95	6.97	4.59	20.50	mean	22.74	20.92	6.75	4.29	15.06
min	23.1	20.0	5.8	3.6	15.0	min	20.6	17.0	5.9	3.4	11.0
max	28.0	26.5	8.2	5.5	27.0	max	25.6	23.8	8.5	5.0	19.0
s	1.59	1.48	0.86	0.49	4.15	s	1.32	1.68	0.71	0.47	2.77
v	6.15	6.21	12.27	10.65	20.22	v	5.80	8.02	10.46	10.95	18.33
P4						M3					
n	20	19	19	19	18	n	15	15	14	14	10
mean	24.56	23.77	6.92	4.55	17.67	mean	21.21	16.15	7.01	3.71	14.70
min	22.5	21.3	5.1	3.8	12.0	min	18.5	11.2	6.1	2.4	1.0
max	26.8	26.0	8.0	5.5	29.0	max	24.0	20.3	8.5	4.6	23.0
s	1.02	1.21	0.78	0.47	4.80	s	1.92	2.90	0.69	0.65	7.48
v	4.16	5.09	11.29	10.40	27.13	v	9.03	17.93	9.89	17.43	50.91

TABLE 7. — *Hipparion dietrichi*, Akkaşdağı, measurements of the lower teeth (in mm). Abbreviations: see Table 4.

p2	Lo	Bo ant	Bo post	Lprfl	Lptfl	EF	m1	Lo	Bo ant	Bo post	Lprfl	Lptfl	EF
n	9	9	10	8	10	7	n	15	14	15	15	15	11
mean	26.02	10.02	12.05	6.93	10.14	1.14	mean	20.75	11.47	10.08	5.63	6.88	0.86
min	25.0	9.0	10.8	6.2	5.7	0.0	min	17.8	10.0	9.3	4.7	4.5	0.0
max	27.1	10.7	13.8	7.5	12.4	2.0	max	22.3	13.1	11.0	6.5	8.5	2.0
s	0.69	0.63	0.92	0.55	2.03	0.90	s	1.25	0.81	0.50	0.61	1.26	0.84
v	2.64	6.34	7.63	7.97	20.08	81.82	v	6.00	7.05	4.94	10.82	18.28	93.22
p3							m2						
n	10	11	10	11	11	11	n	12	11	12	12	12	9
mean	22.80	13.04	12.62	6.72	11.33	1.91	mean	20.49	10.61	9.36	5.58	6.22	0.78
min	21.7	11.5	10.2	5.8	9.0	0.0	min	18.5	9.0	8.0	4.0	4.7	0.0
max	24.3	14.8	14.6	7.4	12.5	4.0	max	22.0	11.8	10.7	6.9	8.0	3.0
s	0.76	1.15	1.34	0.51	1.12	1.22	s	0.98	0.85	0.84	0.74	1.16	1.09
v	3.34	8.82	10.61	7.55	9.87	64.26	v	4.78	8.06	8.97	13.30	18.69	136.63
p4							m3						
n	13	13	13	13	13	12	n	12	12	12	10	9	8
mean	22.58	12.35	11.82	6.45	9.81	1.42	mean	24.36	9.59	8.16	5.46	5.77	0.25
min	20.1	10.0	9.0	5.7	8.0	0.0	min	21.1	7.3	5.8	4.6	4.0	0.0
max	23.6	15.1	14.3	7.3	11.6	4.0	max	28.4	10.8	9.9	6.5	6.7	1.0
s	0.95	1.57	1.44	0.49	1.11	1.24	s	2.07	1.06	1.24	0.62	0.85	0.46
v	4.20	12.73	12.21	7.55	11.35	88.57	v	8.50	11.01	15.13	11.31	14.60	154.33

TABLE 8. — *Hipparion moldavicum*, Akkaşdağı, measurements of the upper teeth (in mm). Abbreviations: see Table 3.

P2	Lo	Bo	Lp	Wp	EF	M1	Lo	Bo	Lp	Wp	EF
n	7	7	7	6	6	n	15	15	15	15	13
mean	28.03	20.96	6.50	4.30	19.17	mean	18.69	20.20	7.05	4.75	13.31
min	24.9	20.2	6.0	3.9	12.0	min	16.1	19.0	5.8	3.8	1.0
max	31.5	21.7	7.1	5.2	26.0	max	21.6	21.2	8.2	5.4	23.0
s	2.19	0.53	0.45	0.49	5.49	s	1.48	0.57	0.54	0.48	6.34
v	7.83	2.51	6.94	18.24	28.60	v	7.91	2.83	7.68	10.04	47.69
P3						M2					
n	16	15	16	16	14	n	14	14	14	14	12
mean	22.04	21.72	6.71	4.93	15.36	mean	18.84	19.39	6.68	4.51	13.00
min	19.5	19.4	5.9	3.7	2.0	min	16.8	18.7	5.8	3.8	2.0
max	26.6	23.8	7.4	6.2	29.0	max	21.1	20.0	7.6	5.0	17.0
s	2.21	1.02	0.47	0.74	7.90	s	1.24	0.39	0.54	0.37	4.09
v	10.07	4.71	7.02	125.02	51.29	v	6.57	1.98	8.05	8.29	31.46
P4						M3					
n	15	14	15	15	13	n	10	10	10	10	10
mean	20.97	21.27	6.95	5.29	14.62	mean	20.51	16.86	6.48	3.75	10.70
min	19.0	20.1	5.5	3.7	3.0	min	18.9	12.3	4.6	2.3	0.0
max	23.6	22.3	8.1	9.7	25.0	max	21.6	19.2	7.6	4.4	20.0
s	1.38	0.68	0.74	1.42	6.08	s	0.92	2.34	1.02	0.71	6.52
v	6.57	3.17	10.78	26.87	41.62	v	4.51	13.83	15.72	18.74	60.90

TABLE 9. — *Hipparion moldavicum*, Akkaşdağı, measurements of the lower teeth (in mm). Abbreviations: see Table 4.

p2	Lo	Bo ant	Bo post	Lprfl	Lptfl	EF	m1	Lo	Bo ant	Bo post	Lprfl	Lptfl	EF
n	11	11	11	11	11	11	n	12	12	13	11	11	12
mean	24.58	9.56	11.73	6.16	10.15	0.64	mean	19.54	11.26	9.92	5.71	6.49	0.46
min	21.1	9.0	10.8	4.4	6.7	0.0	min	16.6	10.4	7.9	4.5	5.3	0.0
max	26.5	10.0	12.4	7.4	12.6	2.0	max	23.4	12.3	11.0	7.7	8.6	1.0
s	1.74	0.41	0.54	0.87	1.74	0.81	s	1.58	0.58	0.73	0.97	1.09	0.50
v	7.07	4.28	4.59	14.08	17.21	134.83	v	8.12	5.15	7.33	16.97	16.74	99.60
p3							m2						
n	14	14	14	14	14	13	n	11	11	12	11	10	10
mean	21.91	12.34	12.31	6.61	10.44	1.12	mean	19.57	10.49	8.96	5.84	6.03	0.45
min	19.8	11.7	11.0	6.0	5.7	0.0	min	17.3	9.8	7.3	4.7	3.5	0.0
max	23.3	13.0	13.4	7.9	12.0	3.0	max	22.0	11.6	10.2	11.0	8.0	2.0
s	1.02	0.37	0.54	0.53	1.99	0.92	s	1.16	0.49	0.74	1.76	1.40	0.69
v	4.64	2.97	4.37	7.99	19.14	83.27	v	5.91	4.66	8.19	30.38	23.28	137.00
p4							m3						
n	15	14	15	15	14	15	n	8	8	9	8	6	6
mean	21.17	12.23	11.56	6.53	9.73	0.73	mean	22.61	8.91	7.58	5.76	6.98	0.92
min	19.3	11.6	9.5	5.5	5.5	0.0	min	21.5	8.5	6.0	5.2	5.8	0.0
max	23.0	12.7	12.7	11.4	11.6	1.0	max	23.7	9.6	8.7	6.5	8.5	2.0
s	0.96	0.31	0.74	1.40	1.57	0.46	s	0.75	0.35	0.84	0.43	1.05	0.66
v	4.55	2.54	6.37	21.57	16.24	65.43	v	3.30	3.96	9.39	7.48	14.97	73.89

TABLE 10. — Akkaşdağı hipparions, measurements of the humerus (in mm); **1**, maximal length; **2**, internal length; **3**, minimal breadth of diaphysis; **4**, DAP of diaphysis at the level of 3; **5**, proximal breadth; **6**, proximal DAP at the level of the median tubercle; **7**, maximal breadth of the trochlea; **8**, distal maximal DAP; **9**, maximal trochlear height (medial); **10**, minimal trochlear height (in the middle); **11**, trochlear height at the sagittal crest near the condyle.

	1	2	3	4	5	6	7	8	9	10	11
						Hipparion brachypus					
n	–	–	–	–	–	–	8	7	8	8	8
mean	–	–	–	–	–	–	77.01	76.34	49.24	35.09	43.63
min	–	–	–	–	–	–	74.7	73.6	45.9	32.7	41.5
max	–	–	–	–	–	–	80.0	79.9	53.3	37.6	47.4
s	–	–	–	–	–	–	1.89	2.31	2.50	1.74	2.17
v	–	–	–	–	–	–	2.45	3.03	5.07	4.97	4.98
						Hipparion* cf. *longipes					
n	–	–	–	–	–	–	17	20	20	19	19
mean	–	–	–	–	–	–	69.94	72.88	47.11	34.87	42.91
min	–	–	–	–	–	–	65.5	68.8	43.9	31.7	39.6
max	–	–	–	–	–	–	72.2	77.4	50.3	37.1	46.3
s	–	–	–	–	–	–	1.87	2.36	1.68	1.72	1.77
v	–	–	–	–	–	–	2.67	3.23	3.57	4.92	4.13
						Hipparion dietrichi					
n	–	–	–	–	–	–	6	6	6	6	6
mean	–	–	–	–	–	–	62.35	65.22	41.52	31.68	38.48
min	–	–	–	–	–	–	60.8	62.4	39.3	27.3	36.6
max	–	–	–	–	–	–	65.1	67.6	44.5	35.2	40.7
s	–	–	–	–	–	–	1.54	1.96	2.01	2.65	1.55
v	–	–	–	–	–	–	2.47	3.01	4.84	8.36	4.04
						Hipparion moldavicum					
n	–	–	–	–	–	–	7	6	7	7	6
mean	–	–	–	–	–	–	57.90	61.32	38.70	27.73	35.02
min	–	–	–	–	–	–	57.3	60.0	37.8	24.4	34.3
max	–	–	–	–	–	–	58.8	62.2	39.7	30.0	36.6
s	–	–	–	–	–	–	0.61	0.73	0.66	1.73	0.86
v	–	–	–	–	–	–	1.06	1.19	1.71	6.24	2.45

TABLE 11. — Akkaşdağı hipparions, measurements of the radius (in mm); **1**, maximal length; **2**, internal length; **3**, minimal breadth of diaphysis; **4**, DAP of the diaphysis at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, proximal maximal breadth; **8**, distal articular breadth; **9**, distal articular DAP; **10**, distal maximal breadth; **11**, diameter of the articular facet for navicular; **12**, idem for triquetrum.

	1	2	3	4	5	6	7	8	9	10	11	12
							Hipparion brachypus					
n	2	2	2	2	2	2	2	3	4	4	4	3
mean	290.00	274.50	41.30	26.65	68.95	35.90	74.25	58.70	35.83	69.10	22.48	12.90
min	280.0	264.0	38.8	26.1	68.7	35.3	74.2	57.1	33.1	67.1	19.9	12.3
max	300.0	285.0	43.8	27.2	69.2	36.5	74.3	60.8	39.9	72.2	24.2	13.3
s	–	–		–	–	–	–	1.90	3.09	2.18	1.89	0.53
v	–	–		–	–	–	–	3.24	8.62	3.15	8.40	4.10
							Hipparion* cf. *longipes					
n	2	2	2	2	6	4	6	2	2	2	2	2
mean	307.5	290	37.7	26.1	65	34.60	69.62	54.10	34.25	62.80	22.30	11.85
min	305.0	288.0	37.0	25.9	63.0	34.2	67.0	53.6	33.2	59.7	22.3	10.7
max	310.0	292.0	38.4	26.3	66.2	35.0	71.7	54.6	35.3	65.9	22.3	13.0
s	–	–	–	–	1.09	0.37	1.51	–	–	–	–	–
v	–	–	–	–	1.68	1.06	2.17	–	–	–	–	–

	1	2	3	4	5	6	7	8	9	10	11	12
					Hipparion dietrichi							
n	2	2	2	2	5	6	5	6	7	6	7	6
mean	309	297.5	35.95	26.4	63.72	34.02	66.48	53.02	33.19	62.23	22.06	12.18
min	303.0	295.0	35.2	25.8	63.1	33.4	64.8	49.8	32.3	59.2	20.5	10.4
max	315.0	300.0	36.7	27.0	64.2	35.8	68.8	56.0	34.5	65.6	23.9	13.5
s	–	–	–	–	0.51	0.91	1.59	2.09	0.95	2.33	1.12	1.11
v	–	–	–	–	0.80	2.68	2.40	3.94	2.86	3.75	5.07	9.13
					Hipparion moldavicum							
n	1	1	1	1	4	4	4	2	2	2	2	2
mean	257.50	252.00	32.20	22.00	54.03	29.63	57.43	44.30	29.35	51.30	17.65	11.00
min	–	–	–	–	52.9	28.4	56.6	43.2	29.1	51.2	16.5	10.6
max	–	–	–	–	56.2	30.3	58.9	45.4	29.6	51.4	18.8	11.4
s	–	–	–	–	1.56	0.87	1.06	–	–	–	–	–
v	–	–	–	–	2.88	2.95	1.85	–	–	–	–	–

TABLE 12. — Akkaşdağı hipparions, measurements of the third metacarpal (in mm); **1**, maximal length; **2**, internal length; **3**, breadth of the diaphysis (in the middle); **4**, DAP idem at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, maximal diameter of the articular facet for os magnum; **8**, diameter of the anterior facet for hamatum; **9**, idem for the cuneiform II; **10**, distal maximal supra-articular breadth; **11**, distal maximal articular breadth; **12**, distal maximal DAP of the keel; **13**, distal minimal DAP of the lateral condyle; **13a**, distal minimal DAP of the medial condyle; **14**, distal maximal DAP of the medial condyle.

	1	2	3	4	5	6	7	8	9	10	11	12	13	13a	14
							Hipparion brachypus								
n	6	6	6	5	8	8	6	6	5	6	6	6	6	6	6
mean	227.37	219.72	32.02	25.04	45.29	31.93	37.88	13.87	6.80	44.77	42.42	32.22	26.60	27.15	29.50
min	223.3	214.0	30.5	24.0	43.2	30.6	36.7	12.1	6.4	41.4	38.7	31.6	25.8	26.3	27.9
max	230.9	224.3	34.6	25.7	46.5	34.4	39.2	16.1	7.6	46.9	44.5	33.4	27.9	28.1	30.7
s	2.99	3.65	1.33	0.59	1.08	1.12	0.78	1.20	0.42	2.17	1.82	0.56	0.68	0.60	1.08
v	49.89	60.83	22.14	11.84	13.47	14.00	12.96	20.04	8.49	36.24	30.36	9.35	11.26	10.08	17.92
							Hipparion* cf. *longipes								
n	11	11	11	11	12	13	11	13	9	11	8	9	9	10	10
mean	249.04	243.08	27.25	24.95	40.45	28.52	35.92	9.88	6.66	39.11	37.06	30.36	24.71	25.43	27.67
min	246.4	240.2	25.4	23.3	36.6	26.5	33.4	8.4	4.7	36.0	35.8	28.7	22.6	24.1	26.6
max	253.1	247.3	29.0	26.4	42.4	30.2	37.2	11.1	8.4	42.2	39.6	31.7	26.0	26.7	29.4
s	2.49	2.59	1.12	0.99	1.71	1.24	1.35	0.79	1.08	1.72	1.32	1.05	1.06	0.83	0.90
v	1.00	1.07	4.12	3.97	4.22	4.36	3.75	8.00	16.20	4.39	3.56	3.48	4.29	3.26	3.25
							Hipparion dietrichi								
n	8	8	10	9	11	12	11	11	10	10	9	9	9	10	10
mean	233.44	228.74	29.11	23.91	41.49	29.34	35.19	11.45	5.75	38.52	37.29	30.78	25.57	26.27	27.54
min	214.4	220.3	26.8	22.3	39.1	26.5	33.0	10.4	3.2	36.0	34.2	29.0	23.8	24.5	25.5
max	241.7	233.7	30.7	25.0	43.3	36.8	37.1	12.2	7.9	41.0	40.2	32.5	27.3	27.9	29.2
s	8.65	4.30	1.18	0.90	1.30	2.61	1.29	0.59	1.60	1.82	1.95	1.42	1.13	1.10	1.22
v	3.70	1.88	4.07	3.74	3.13	8.89	3.66	5.16	27.83	4.73	5.24	4.62	4.42	4.17	4.42
							Hipparion moldavicum								
n	6	7	7	6	7	8	7	8	5	9	9	6	9	9	9
mean	218.91	213.15	24.04	21.29	35.11	25.26	29.42	10.01	4.65	33.02	31.54	26.13	21.10	21.70	23.64
min	210.8	203.8	22.1	19.2	31.7	21.2	27.2	8.7	2.7	29.7	27.6	23.6	19.3	20.1	21.2
max	228.2	223.3	27.0	23.8	38.0	27.3	32.8	11.7	6.0	37.2	35.2	28.5	23.0	23.6	25.5
s	6.06	6.37	1.52	1.07	1.83	1.65	1.54	0.84	1.14	1.96	1.62	1.24	1.06	0.96	1.17
v	2.77	2.99	6.32	5.03	5.21	6.55	5.25	8.37	24.48	5.92	5.13	4.76	5.01	4.45	4.96

TABLE 13. — Akkaşdağı hipparions, measurements of the tibia (in mm); **1**, maximal length; **2**, medial length; **3**, minimal breadth of the diaphysis; **4**, DAP of the diaphysis at the level of 3; **5**, proximal maximal breadth; **6**, proximal maximal depth; **7**, maximal distal breadth; **8**, maximal distal DAP.

	1	2	3	4	5	6	7	8
				Hipparion brachypus				
n	–	–	–	–	–	–	7	8
mean	–	–	–	–	–	–	72.41	48.44
min	–	–	–	–	–	–	68.4	45.5
max	–	–	–	–	–	–	77.9	52.0
s	–	–	–	–	–	–	3.34	1.85
v	–	–	–	–	–	–	4.61	3.81
				Hipparion* cf. *longipes				
n	–	–	–	–	–	–	14	14
mean	–	–	–	–	–	–	66.28	45.30
min	–	–	–	–	–	–	62.8	43.2
max	–	–	–	–	–	–	70.5	48.8
s	–	–	–	–	–	–	1.80	1.61
v	–	–	–	–	–	–	2.71	3.56
				Hipparion dietrichi				
n	–	–	–	–	–	–	14	14
mean	–	–	–	–	–	–	66.28	45.30
min	–	–	–	–	–	–	62.8	43.2
max	–	–	–	–	–	–	70.5	48.8
s	–	–	–	–	–	–	1.80	1.61
v	–	–	–	–	–	–	2.71	3.56
				Hipparion moldavicum				
n	5	5	5	5	7	6	30	30
mean	321.80	310.00	37.16	27.08	80.31	70.42	57.62	39.04
min	315.0	300.0	35.0	26.7	78.7	67.0	51.8	36.7
max	330.0	318.0	39.6	27.5	82.4	74.1	61.2	41.3
s	6.72	7.21	2.00	0.29	1.52	2.34	2.22	1.13
v	2.09	2.33	5.37	1.09	1.89	3.32	3.86	2.89

TABLE 14. — Akkaşdağı hipparions, measurements of the astragalus (in mm); **1**, maximal length (height): articulation surface for navicular-top of the internal condyle; **2**, maximal diameter of the internal condyle; **3**, trochlear breadth: middle of the internal-middle of the external condyles; **4**, maximal breadth (in projection); **5**, distal articular breadth; **6**, distal articular DAP; **7**, maximal DAP of the internal condyle.

	1	2	3	4	5	6	7
				Hipparion brachypus			
n	10	11	11	11	11	10	9
mean	60.63	61.04	28.84	58.09	47.27	34.41	51.49
min	10.0	11.0	11.0	11.0	11.0	10.0	9.0
max	62.5	63.3	30.8	65.1	52.5	36.2	53.8
s	1.08	1.27	1.46	2.87	2.15	1.17	1.31
v	1.78	2.09	5.07	4.95	4.56	3.41	2.55

	1	2	3	4	5	6	7
			Hipparion* cf. *longipes				
n	29	26	27	26	25	28	22
mean	57.50	57.55	26.35	54.01	44.53	32.87	47.52
min	55.1	53.5	24.0	51.1	41.6	29.1	44.0
max	60.2	60.0	29.3	56.6	47.8	34.8	50.9
s	1.44	1.92	1.39	1.49	1.53	1.16	1.74
v	2.51	3.33	5.26	2.76	3.43	3.54	3.66
			Hipparion dietrichi				
n	24	21	24	27	24	24	19
mean	51.82	52.55	24.13	50.19	40.80	29.00	43.11
min	49.0	50.1	22.0	45.6	37.3	26.4	40.0
max	60.5	59.3	27.5	59.5	49.5	32.5	46.6
s	2.41	2.30	1.64	2.72	3.31	1.58	2.07
v	4.64	4.38	6.78	5.43	8.10	5.44	4.81
			Hipparion moldavicum				
n	9	10	12	8	7	9	7
mean	47.95	48.66	22.59	47.54	37.85	27.67	40.73
min	47.4	46.9	20.9	45.3	36.6	26.2	40.5
max	50.0	51.3	24.8	50.4	40.0	29.7	41.2
s	0.90	1.44	1.09	1.58	1.10	1.04	0.28
v	1.87	2.97	4.84	3.32	2.90	3.76	0.68

TABLE 15. — Akkaşdağı hipparions, measurements of the calcaneum (in mm); **1**, maximal length; **2**, length of the proximal part; **3**, minimal breadth; **4**, proximal maximal breadth; **5**, proximal maximal depth; **6**, distal maximal breadth; **7**, maximal medial depth.

	1	2	3	4	5	6	7
			Hipparion brachypus				
n	1	1	2	2	2	1	1
mean	113.80	73.30	24.40	37.30	53.50	57.90	56.40
min	–	–	24.2	37.0	52.8	–	–
max	–	–	24.6	37.6	54.2	–	–
s	–	–	–	–	–	–	–
v	–	–	–	–	–	–	–
			Hipparion* cf. *longipes				
n	7	6	6	5	6	7	7
mean	114.74	77.20	21.35	34.22	51.98	50.29	51.26
min	109.1	69.6	19.3	31.4	48.7	46.4	46.2
max	123.6	84.7	23.2	36.5	55.2	54.9	55.1
s	5.05	5.39	1.75	1.85	2.17	2.88	2.99
v	4.40	6.98	8.19	5.39	4.18	5.73	5.83
			Hipparion dietrichi				
n	9	8	16	8	10	19	19
mean	104.02	67.64	20.21	31.70	47.35	47.11	47.81
min	96.7	63.9	17.8	30.1	43.5	41.4	42.1
max	13.7	71.4	22.0	35.3	52.1	52.0	51.9
s	5.73	2.17	1.33	1.57	2.64	2.72	2.75
v	5.51	3.21	6.58	4.97	5.57	5.77	5.74

	1	2	3	4	5	6	7
				Hipparion moldavicum			
n	10	10	13	9	9	14	12
mean	95.33	63.47	18.75	28.30	41.87	41.74	43.37
min	90.5	56.7	17.9	19.7	39.1	38.2	40.3
max	98.2	66.7	21.3	30.8	45.9	47.2	46.5
s	2.81	3.20	0.96	3.57	2.20	2.70	2.06
v	2.95	5.05	5.15	12.62	5.25	6.48	4.75

TABLE 16. — Akkaşdağı hipparions, measurements of the third metatarsal (in mm); **1**, maximal length; **2**, internal length; **3**, breadth of the diaphysis (in the middle); **4**, DAP idem at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, maximal diameter of the articular facet for the cuneiform; **8**, diameter of the articular facet for cuboid; **9**, idem for cuneiform II; **10**, distal maximal supra-articular breadth; **11**, distal maximal articular breadth; **12**, distal maximal DAP of the keel; **13**, distal minimal DAP of the lateral condyle; **13a**, distal minimal DAP of the medial condyle; **14**, distal maximal DAP of the medial condyle.

	1	2	3	4	5	6	7	8	9	10	11	12	13	13a	14
							Hipparion brachypus								
n	8	8	8	8	7	7	6	8	7	14	12	11	12	10	12
mean	257.75	251.84	31.11	30.30	44.64	36.34	40.73	11.78	7.19	44.94	41.74	35.71	27.72	28.64	30.14
min	245.2	239.0	26.4	26.9	42.1	34.5	37.7	10.4	4.5	41.4	36.2	32.7	24.7	27.7	25.3
max	266.0	260.0	32.4	33.2	47.2	37.5	43.7	14.3	10.1	48.2	43.8	37.5	31.7	29.7	31.8
s	7.53	7.68	2.01	1.87	2.00	1.00	1.96	1.42	2.10	1.92	2.25	1.60	1.69	0.73	1.83
v	2.92	3.05	6.47	6.17	4.48	2.75	4.81	12.06	29.27	4.28	5.39	4.49	6.09	2.54	6.06
							Hipparion* cf. *longipes								
n	15	7	14	12	17	18	18	18	17	20	18	20	19	20	18
mean	284.40	269.31	29.11	30.23	43.29	34.29	40.17	10.68	6.95	39.84	38.51	33.19	26.15	28.11	28.36
min	275.5	266.1	26.6	28.1	40.7	32.3	37.5	9.5	4.5	37.2	37.4	31.1	25.0	25.9	25.5
max	302.0	272.8	31.7	31.7	45.1	39.0	42.4	13.0	9.0	41.5	41.9	35.2	27.8	30.4	30.3
s	7.82	2.01	1.56	1.17	1.28	1.65	1.34	1.14	1.39	1.09	1.14	1.10	0.89	1.53	1.46
v	2.75	0.74	5.37	3.87	2.96	4.81	3.34	10.65	20.00	2.75	2.95	3.31	3.40	5.45	5.14
							Hipparion dietrichi								
n	12	12	11	10	18	16	16	14	15	15	13	16	15	14	15
mean	262.31	256.57	27.61	28.86	40.73	32.64	37.79	10.71	6.32	37.74	37.50	31.56	24.57	25.48	27.21
min	253.1	246.2	25.8	27.1	32.0	28.4	31.9	8.0	4.1	35.6	35.9	28.2	21.5	22.7	24.0
max	270.5	264.1	29.6	31.0	45.0	35.9	41.1	14.0	8.5	39.7	39.9	33.4	26.6	27.9	30.9
s	5.98	5.89	1.31	1.24	3.01	1.97	2.34	1.90	1.25	1.21	1.19	1.33	1.24	1.45	1.75
v	2.28	2.29	4.73	4.29	7.39	6.05	6.19	17.76	19.83	3.21	3.17	4.21	5.07	5.68	6.44
							Hipparion moldavicum								
n	19	24	23	21	29	30	26	24	29	31	30	33	33	32	32
mean	246.27	241.76	24.23	25.19	35.75	28.72	33.01	8.53	2.31	34.50	32.97	28.19	22.43	23.38	24.60
min	236.6	230.6	20.3	21.6	29.4	24.5	29.5	5.4	0.0	29.3	28.4	25.1	20.0	20.3	21.2
max	256.5	256.5	26.3	28.4	43.4	31.3	38.9	11.0	7.3	39.3	38.3	32.1	26.1	28.5	28.6
s	5.38	6.05	1.44	1.32	2.31	1.44	1.67	1.15	2.43	2.23	2.25	1.71	1.36	2.16	1.63
v	2.18	2.50	5.96	5.22	6.46	5.02	5.05	13.53	105.01	6.47	6.82	6.06	6.05	9.25	6.64

TABLE 17. — Akkaşdağı hipparions, measurements of the first phalanx (in mm); **1**, maximal length; **2**, anterior length: middle of the proximal articular facet- middle of the distal facet; **3**, minimal breadth of the diaphysis; **4**, proximal breadth; **5**, proximal DAP; **6**, distal breadth at the tuberosities; **7**, distal articular breadth; 8, distal articular DAP.

	1	2	3	4	5	6	7	8
				Hipparion brachypus				
n	3	3	2	3	3	2	3	3
mean	64.60	59.17	28.95	41.73	32.50	35.05	34.40	20.43
min	63.3	59.0	27.0	40.8	32.4	33.1	32.7	19.3
max	65.5	59.5	30.9	43.6	32.7	37.0	36.2	22.1
s	1.15	0.29	2.76	1.62	0.17	2.76	1.75	1.47
v	1.79	0.49	9.53	3.87	0.53	7.87	5.09	7.21
				Hipparion* cf. *longipes				
n	3	3	3	3	2	3	3	3
mean	68.70	62.67	28.70	42.07	33.80	34.13	34.27	20.90
min	68.5	61.5	27.6	41.0	32.5	32.9	33.4	20.6
max	69.1	63.6	29.3	42.7	35.1	35.0	35.5	21.1
s	0.35	1.07	0.95	0.93	1.84	1.10	1.10	0.26
v	0.50	1.71	3.32	2.21	5.44	3.21	3.20	1.27
				Hipparion dietrichi				
n	9	9	7	9	8	7	10	9
mean	63.38	57.77	25.10	36.67	29.56	30.16	30.51	18.43
min	61.8	56.0	23.0	34.0	26.3	27.9	28.3	16.8
max	64.7	59.8	26.5	38.4	32.8	32.9	32.7	20.1
s	1.02	1.15	1.21	1.47	2.11	1.90	1.63	1.13
v	1.61	2.00	4.83	4.02	7.13	6.30	5.34	6.15
				Hipparion moldavicum				
n	1	3	3	3	3	2	2	2
mean	59.20	56.50	23.10	32.90	28.10	28.50	28.20	17.80
min	–	54.4	23.0	31.9	26.5	28.2	27.9	17.7
max	–	57.7	23.2	34.1	29.3	28.8	28.5	17.9
s	–	1.82	0.10	1.11	1.44	–	–	–
v	–	3.23	0.43	3.38	5.13			

TABLE 18. — Akkaşdağı hipparions, measurements of the second phalanx (in mm); **1**, maximal length; **2**, anterior length (as in the first phalanx); **3**, minimal breadth of the diaphysis; **4**, maximal proximal breadth; **5**, proximal DAP; **6**, distal articular maximal breadth; **7**, distal articular DAP.

	1	2	3	4	5	6	7
				Hipparion brachypus			
n	4	4	4	4	4	4	3
mean	41.10	31.08	30.60	37.73	27.20	33.98	20.77
min	40.7	30.4	27.6	36.0	26.7	32.7	19.2
max	41.4	32.0	32.8	40.9	27.7	36.8	22.6
s	0.36	0.68	2.17	2.22	0.48	1.91	1.72
v	0.87	2.19	7.10	5.89	1.75	5.61	8.26

	1	2	3	4	5	6	7
				Hipparion* cf. *longipes			
n	6	5	6	5	5	6	6
mean	42.90	32.70	32.87	40.14	28.80	35.62	22.00
min	42.4	30.7	31.0	38.0	27.8	33.0	20.8
max	43.6	34.3	35.6	43.0	29.8	40.0	23.5
s	0.39	1.29	1.63	2.18	0.95	2.45	0.98
v	0.92	3.94	4.97	5.43	3.28	6.88	4.47
				Hipparion dietrichi			
n	7	8	8	6	7	8	6
mean	39.60	29.94	27.65	35.35	25.49	31.41	19.33
min	39.2	28.9	26.2	34.3	25.4	30.6	18.7
max	40.3	31.1	28.9	36.7	25.9	32.3	19.8
s	0.35	0.72	0.97	0.90	0.19	0.57	0.40
v	0.87	2.41	3.50	2.56	0.73	1.83	2.09
				Hipparion moldavicum			
n	4	4	4	4	4	4	4
mean	20.18	15.78	14.89	18.62	13.05	16.33	10.25
min	0.3	0.7	1.0	0.9	0.2	0.6	0.4
max	40.3	31.1	28.9	36.7	25.9	32.3	19.8
s	22.60	16.45	14.69	19.53	14.55	17.49	10.43
v	112.00	104.24	98.67	104.92	111.43	107.10	101.76

TABLE 19. — Akkaşdağı hipparions, measurements of the third phalanx (in mm); **1**, length from the posterior edge of the articular surface to the tip of the phalanx; **2**, anterior length; **3**, maximal breadth; **4**, maximal articular breadth; **5**, articular depth; **6**, maximal height.

	1	2	3	4	5	6
			Hipparion brachypus			
n	4	3	3	3	3	3
mean	61.05	58.93	65.13	42.37	26.63	41.03
min	58.0	55.2	61.5	41.2	26.0	39.9
max	63.0	62.5	69.2	43.2	27.2	41.6
s	2.35	3.65	3.87	1.04	0.60	0.98
v	3.85	6.20	5.94	2.46	2.26	2.39
			Hipparion* cf. *longipes			
n	4	4	4	2	5	3
mean	55.68	54.63	58.45	39.15	24.52	35.03
min	53.9	50.5	56.4	37.8	22.8	34.1
max	60.8	58.3	60.7	40.5	26.0	36.7
s	3.42	3.86	1.80	–	1.53	1.45
v	6.14	7.06	3.07	–	6.23	4.13
			Hipparion dietrichi			
n	3	3	3	4	3	3
mean	52.90	51.60	49.33	36.78	23.50	31.33
min	50.7	47.3	47.3	34.3	21.1	28.7
max	56.6	55.0	50.7	38.5	25.0	33.1
s	3.22	3.93	1.80	1.87	2.10	2.32
v	6.09	7.61	3.64	5.09	8.94	7.42
			Hipparion moldavicum			
n	3	3	1	2	4	2
mean	46.90	45.73	37.60	35.15	21.40	29.40
min	45.5	44.3	–	34.6	18.9	29.2
max	48.2	47.4	–	35.7	23.7	29.6
s	1.35	1.56	–	–	1.72	–
v	2.88	3.42	–	–	8.04	–

TABLE 20. — Similarities and differences of the skull and dental morphology of *Hipparion dietrichi* (type skull, Samos and Axios Valley), *H. molayanensis* (Molayan), *H. prostylum* (Maragha) and *H. dietrichi* (Akkaşdağı).

Features	***H. dietrichi* (type)**	***H. dietrichi***	***H. prostylum***	***H. dietrichi* (Akkaşdağı)**	***H. molayanensis***
Preorbital fossa (POF)	Slightly developed with well defined peripheral rim	Slightly developed with only the posterior rim well defined, no posteriorly pocketing	Slightly developed with only the posterior rim well defined, posteriorly pocketing	Slightly developed with only the posterior rim well defined, posteriorly pocketing	Slightly developed and occasionally well defined posteriorly
POF placement	Far from the facial crest	Far from the facial crest	Close to the facial crest	Far from the facial crest	(?) Far from the facial crest
Preorbital bar (POB)	(42 mm)	39-49 mm	34.2-43 mm	40-45 mm	48.5 mm
Muzzle length	Short (93 mm)	Short (85-108 mm)	Short (94-104 mm)	Short(?) (106-117 mm)	Short(?) (105-110 mm)
Muzzle width	Broad(?) (56 mm)	Broad (56-70 mm)	"Robust"	Broad (64-68 mm)	Broad (45.5-49 mm)
Nasal opening (location of the nasal notch)	Short (above the P2 anterostyle)	Short (above the anterior part of P2)	Short (above the P2 anterostyle or anterior to it)	Short (above the P2 anterostyle or anterior to it)	Short (above the anterior part of P2)
Distance from posterior edge to the nasal notch to anterior rim of the orbit (NN-ORBIT)	137 mm	147-164 mm	100-113.5 mm	(146.4)-151.6 mm	(150 mm)
Distance from prosthion to the posterior of the nasal notch (PROST-NSL)	120 mm	101-128 mm	114.7-120.6 mm	(100)-120.5 mm	(115)-(121 mm)
L (P2-M3)	137 mm	134.3-149 mm	120.4-151.2 mm	154.6-158.7 mm	143 mm
Plication number on M1	"Simple to moderate"	"Simple to moderate"	9-19	7-19	15-24
Pli caballin	"Often single"	"Often single"	Single to multiple (1-4)	Single to multiple (1-3)	Single to multiple (1-3)