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The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene)

12. The Hipparions (Equidae, Perissodactyla, Mammalia)

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ZUSAMMENFASSUNG

Maramena hat einige wenige *Hipparion*-Reste geliefert, die zu einer ziemlich kleinen schlanken Art mit sehr hypsodonten Zähnen und einem sehr eigenartigen dritten Metatarsale (MT III) gehören: die distale articulare Breite dieses Knochens ist größer als die supra-articulare Breite. Dieses Merkmal ist einmalig unter den altweltlichen Hipparionen und ist nur von *Nannippus* aus dem Blancan von Nordamerika bekannt.

Hypsodontie, Proportionen des MT III und die geringe Häufigkeit der *Hipparion*-Fossilien verglichen mit anderen Ungulaten sind Kriterien, die man in der Zone 5 von SEN et al. (1978) erwarten kann und deuten auf ein postturoolisches Alter hin. Oberflächenfunde, die einen großen Astragalus und ein mittelgroßes distales MC III einer zweiten Art geliefert haben, sprechen für ein ruscinisches Alter.

SUMMARY

Maramena has yielded a few fossils of *Hipparion* belonging to one rather small, slender species, with very hypsodont teeth and a very peculiar third metatarsal (MT III): The distal articular breadth of the bone is larger than the supra-articular breadth. This feature is unique among Old World hipparions and is known only in the *Nannippus* of the Blancan of North America.

Hypsodonty, proportions of the MT III and scarcity of the hipparion fossils relatively to the other ungulates, are all characters one can expect in the zone 5 of SEN et al. (1978) and point to a post Turolian age. Surface findings including one very large astragalus and one middle-sized distal MC III of a second species suggest a Ruscinian age.

RÉSUMÉ

Quelques restes d'*Hipparion* trouvés *in situ* à Maraména (Grèce) appartiennent à une espèce de petite taille, gracile, à dentition très hypsodonte. Le troisième métatarsien (MT III) est très particulier: la largeur distale articulaire est plus grande que la largeur distale sus-articulaire; ce caractère, exceptionnel chez un hipparion de l'Ancien Monde, n'est connu que chez *Nannippus* du Blancan d'Amérique du Nord.

L'hypsodontie, les proportions du MT III et la rareté des restes d'*Hipparion* relativement aux restes d'autres Ongulés sont des traits qu'on peut s'attendre à rencontrer dans la zone 5 de Sen et al. (1978) et qui suggèrent un âge post-turolien. Parmi les fossiles récoltés en surface, un très grand astragale et un MC III de taille moyenne d'une autre espèce semblent indiquer un âge ruscinién.

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Material and methods

The genus *Hipparion* is represented by 5 adult associated very worn upper cheek teeth, 4 adult unworn lower cheek teeth and one lower lacteal, an entire adult third metatarsal and juvenile associated calcaneum, astragalus, navicular and big cuneiform.

The material was studied according to the recommendations of the New York *Hipparion* Conference (EISENMANN et al., 1988). Hypsodonty indices were calculated according to STAESCHE & SONDAAR (1979). Ratio diagrams of SIMPSON (1941) help to compare the metatarsals from Maramena and other sites, using as base of reference personal measurements (table 1 and 2) for *H. mediterraneum* from Pikermi.

Description

Dentition: Because of the degree of wear of the five associated upper molars (MA 901), it is not possible to describe the morphology. Protocone and fossettes are still visible only on the M3 (pl. 1, fig. 2). Length and width of the M3 are approximately 21 and 18 mm. The other upper teeth are worn down to the roots. Contrary to the uppers, the lower cheek teeth all belong to probably one very young individual (MA 902). There are two unworn m1 (pl. 1, fig. 1 and 3); their height is 62 mm; at 1 cm from the base, the length is 20,5 and the width is about 11 mm. Very probably associated are a fragmentary right m2 (MA 903) and a fragmentary left germ of p2 (MA 904, pl. 1, fig. 4).

The lower cheek teeth are middle-sized. They fall in the upper half of the variation observed at Kinik (STAESCHE & SONDAAR, 1979, fig. 8). Kinik (Turkey) is a late Turolian locality with probably 3 species of hipparions.

Adult right metatarsal (MT III) (MA 905): The metatarsal is small and slender (table 1). The facets for cuneiform and cuboid are well developed. The proximal epiphysis is large relatively to the distal epiphysis. The distal articular breadth is larger than the supra-articular (pl. 1, fig. 5)

Small metapodials of hipparion are known from the Early Vallesian (Sebastopol) to the Late Turolian (El Arquillo, EISENMANN, in press). The smallest is *H. periarquillo* from El Arquillo whose distal widths range from 17 to 19 mm. KOUFOS (1988) referred to this species a few metapodials from Dytiko (MN 13) that are notably bigger. We refer them tentatively to *H. matthewi* (fig. 1),

The general biozonation is given according to MEIN (1990).

In order to distinguish between maxillary and mandibular teeth the upper ones are represented by capital letters and the lower ones by small letters. The material is preserved in the collection of the Histor. Geology-Paleontology Department, Subfaculty of Earth Sciences, University of Athens under the registration number MA ... Casts of the figured specimens are housed in the scientific collections of the Institut für Geowissenschaften, University of Mainz.

because they have about the same dimensions as the MT III from Samos (FAM 22893) whose measurements were published by BERNOR & TOBIEN (1989). All these MT III are smaller than the MT III from Maramena (table 1). The MT III of the small hipparion from Kinik, Turkey, referred to *H. matthewi* (STAESCHE & SONDAAR, 1979) are also smaller (table 1). Slender MT III of about the same maximal length as at Maramena were described by KOUFOS (1986, 1988) from Ravin de la Pluie (MN 10) and Vathy-lakkos (MN 11) and referred to *H. macedonicum*. They are very slender (fig. 1) not only at mid-diaphysis, but at the epiphysis also. In MN 13 zone, there are metatarsals of about the same length, but with wider diaphyses and epiphyses (fig. 1). Some are from Dytiko and were referred by Koufos to *H. matthewi*, others are from Venta del Moro and were referred by ALBERDI (1974) to *H. gromovae* or *H. fissurae*. We refer them to *H. cf. dietrichi*. The Maramena MT III is closer to *H. dietrichi* than to *H. macedonicum*. Figure 2 shows that its distal end is small relatively to the proximal, and that the distal supra-articular width is notably smaller than the distal articular width. This feature is unique in Old World hipparions.

Associated right juvenile tarsals (MA 906): The epiphysis of the calcaneum is missing and the bone is badly preserved but judging from the relative sizes of the big cuneiform and the proximal surface of the adult MT III, the juvenile tarsals are probably not much smaller than those of a full grown animal. Measurements of the astragalus (pl. 1, fig 8) are given in table 3.

PLATE 1

Fig. 1-8 *Hipparion* fossils found at Maramena in situ (1-5 and 8) and on the surface (6-7).

Fig. 1 *Hipparion* sp.: section of a left lower m1 (MA 902) at the upper third of the crown; × 2.2.

Fig. 2 *Hipparion* sp.: left upper M3 (MA 901); × 2.2.

Fig. 3 *Hipparion* sp.: right lower m1, unworn (MA 903); × 1.1.

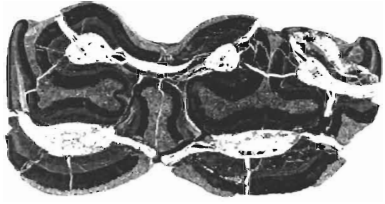
Fig. 4 *Hipparion* sp.: section of a left lower p2 (MA 904) at the upper third of the crown; × 2.2.

Fig. 5 *Hipparion* sp., small size: right third metatarsal (MA 905); × 1.1.

Fig. 6 *Hipparion* sp., middle size: fragment of left third metacarpal (MA 907); a) dorsal view; b) volar view; × 1.1.

Fig. 7 *Hipparion* sp., large size: right astragalus (MA 908), dorsal view; × 1.1.

Fig. 8 *Hipparion* sp., small size: right astragalus (MA 906), dorsal view; × 1.1.



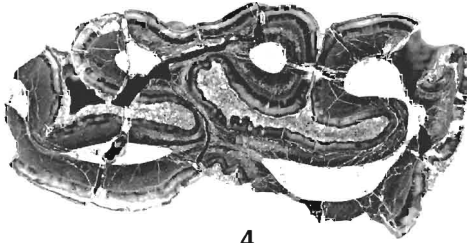
1



2



3



4



6a



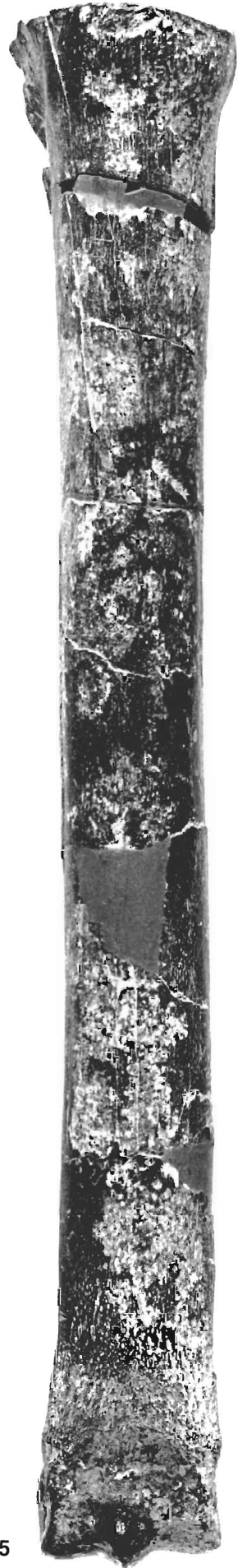
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7



8



5

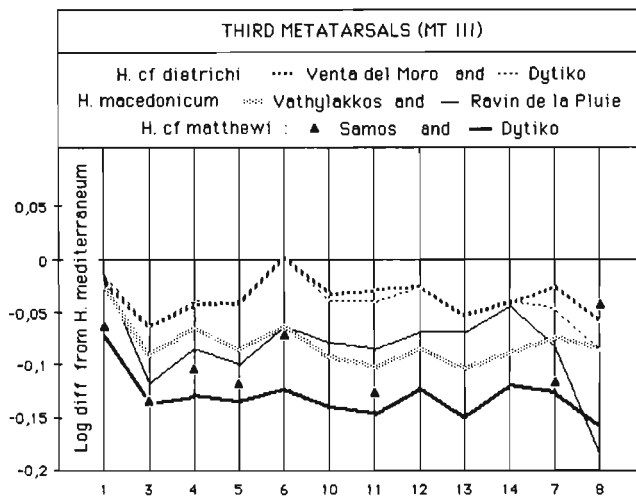


Fig. 1: Ratio diagrams of *Hipparion* third metatarsals done according to the data in table 1. The definitions of the measurements are given in table 1.

Conclusions

Judging from the hypsodonty and the character of the third metatarsal, the hipparion of Maramena is very "evolved". The hypsodonty index of the m1 (100 height/length at 1 cm) is at least 300, which is at the top of the variation observed at Kinik (STAESCHE & SONDAAR 1979, fig. 9).

The teeth of Kinik reach the highest values observed by SEN et al. (1978). Unfortunately, there are no data on the hypsodonty indices at Dytiko, nor at Venta del Moro (both MN 13).

The distal end proportions are not typical for an hippa-

Tab. 1. Third metatarsals of *Hipparion*: measurements in millimeters done and /or published by V. EISENMANN (VE), G. KOUFOS (GK), R. BERNOR (RB & HT), P. SONDAAR (PS); n = number of specimens. Prox. = proximal, artic. and art. = articular, diam = diameter. The measurements given for *H. mediterraneum* of Pikermi are used as base of reference in the ratio diagrams.

| Third metatarsals | VE n = 1 Maramena <i>H. sp. small</i> | VE n = 2-14 Venta del M. <i>H. cf. dietrichi</i> | GK 1988 n = 3-13 Dytiko <i>H. cf. dietrichi</i> | GK 1986 n = 1 Ravin Pluie <i>H. macedonic.</i> | GK 1988 n = 2-4 Vathylakkos <i>H. macedonic.</i> |
|-------------------------------------|--|---|--|---|---|
| 1: Maximal length | 232,0 | 235,0 | 238,3 | 239,0 | 233,0 |
| 3: Minimal breadth | 22,0 | 22,1 | 22,1 | 19,5 | 20,7 |
| 4: Depth at level of 3 | 23,0 | 24,2 | 24,4 | 22,0 | 23,0 |
| 5: Prox. artic. breadth | 33,0 | 34,4 | 34,1 | 30,0 | 30,9 |
| 6: Prox. artic. depth | 28,0 | 29,0 | 28,9 | 25,0 | 25,0 |
| 10: Dist. max. supra-art. breadth | 27,0 | 31,2 | 30,7 | 28,0 | 27,1 |
| 11: Dist. max. articular breadth | 28,0 | 30,3 | 29,5 | 26,6 | 25,6 |
| 12: Dist. max. depth of the keel | 26,0 | 26,6 | 26,6 | 24,1 | 23,2 |
| 13: Dist. min. depth lat. condyle | 21,0 | 21,1 | 21,2 | 20,4 | 18,8 |
| 14: Dist. max. depth med. condyle | 22,7 | 23,4 | 23,5 | 23,3 | 21,0 |
| 7: Max. diam. art. facet 3rd tarsal | 33,0 | 23,5 | 30,9 | 28,5 | 29,1 |
| 8: Diameter artic. facet 4th tarsal | 9,0 | 8,3 | 7,8 | 6,2 | 7,8 |

| | VE n = 29-36 Pikermi <i>H. mediterr.</i> | GK 1988 n = 2-4 Dytiko <i>H. cf. matthewi</i> | RB & HT 1988 n = 1 Samos <i>H. cf. matthewi</i> | PS n = 2-3 Kinik <i>H. cf. matthewi</i> |
|-------------------------------------|---|--|--|--|
| 1: Maximal length | 246,7 | 208,5 | 213,7 | |
| 3: Minimal breadth | 25,6 | 18,6 | 18,7 | |
| 4: Depth at level of 3 | 26,8 | 19,8 | 21,0 | |
| 5: Prox. artic. breadth | 37,7 | 27,6 | 28,7 | 28,9 |
| 6: Prox. artic. depth | 28,9 | 21,7 | 24,5 | 24,4 |
| 10: Dist. max. supra-art. breadth | 33,3 | 24,3 | | 27,6 |
| 11: Dist. max. articular breadth | 32,1 | 23,1 | 24,2 | 26,5 |
| 12: Dist. max. depth of the keel | 27,8 | 21,3 | | 24,4 |
| 13: Dist. min. lat. condyle | 23,6 | 16,9 | | 19,0 |
| 14: Dist. max. depth med. condyle | 25,5 | 19,5 | | 22,4 |
| 7: Max. diam. art. facet 3rd tarsal | 34,3 | 25,7 | 26,3 | 27,1 |
| 8: Diameter artic. facet 4th tarsal | 9,5 | 6,6 | 8,6 | |

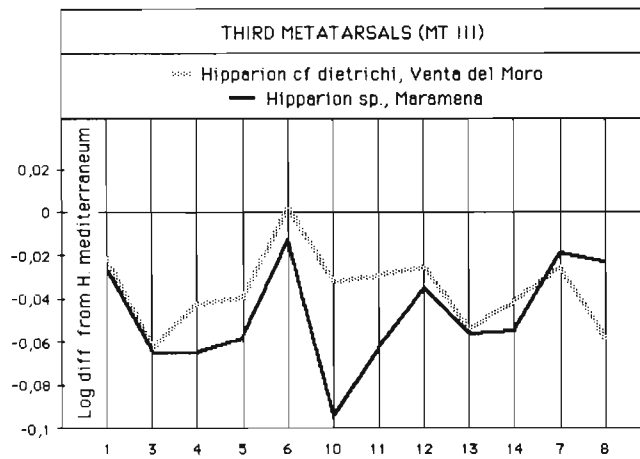


Fig. 2: Ratio diagrams of *Hipparion* third metatarsals done according to the data in table 1: *Hipparion* sp. of Maramena refers to the small species found in situ

rion: the distal articular breadth is larger than the supra-articular breadth. In hipparion-like equids, this feature is known only in the Blancan *Nannippus* from Mt Blanco and Chihuahua. These forms were probably functionally monodactyl (SONDAAR, 1968). As there is no indication at all of pathology or damage on the Maramena MT III, we believe that this feature is significant, although we have

only one specimen.

SEN et al. (1978) have given a *Hipparion* biozonation. On the basis of hypsodonty, the hipparion of Maramena could be placed in zone 4, but such metatarsal morphology as observed at Maramena is not found in this zone. The scarcity of *Hipparion* material relatively to the other ungulates at Maramena is another argument to place

Tab. 2: Third metacarpals of *Hipparion*: measurements in millimeters done and/or published by V. EISENMANN (VE), G. KOUFOS (GK); n = number of specimens. Prox. = proximal, artic. and art. = articular, Dist. = distal, max. = maximal, min. = minimal, lat = lateral, med. = medial, diam. = diameter, ant. = anterior. The measurements given for *H. mediterraneum* of Pikermi are used as base of reference in the ratio diagrams.

| Third metacarpals | VE n = 22-25 Pikermi <i>H. mediterr.</i> | VE n = 1 Maramena <i>H. sp. middle</i> | GK 1982 n = 1 Ptolamais 3 <i>H. crassum</i> | GK 1988 n = 7-19 Dytiko <i>H. mediterr.</i> |
|-----------------------------------|---|---|--|--|
| 1: Maximal length | 216,4 | | 195 | 208,7 |
| 3: Minimal breadth | 25,1 | | 30,2 | 25,5 |
| 4: Depth at level of 3 | 21,4 | | | 21,1 |
| 5: Prox. artic. breadth | 36,4 | | 42,2 | 34,7 |
| 6: Prox. artic. depth | 24,8 | | 27,7 | 23,8 |
| 10: Dist. max. supra-art. breadth | 32,8 | 35,7 | 41,8 | 33,6 |
| 11: Dist. max articular breadth | 31,7 | 33 | 37,7 | 31,6 |
| 12: Dist. max. depth of the keel | 26,4 | 29 | 32 | 26,1 |
| 13: Dist. min. depth lat. condyle | 23,1 | 24,1 | | 21,8 |
| 14: Dist. max. depth med. condyle | 24,2 | 26 | | 23,6 |
| 7: Max. diam. art. 3rd carpal | 31,3 | | | 29,8 |
| 8: Diameter ant. facet 4th carpal | 9,7 | | | 8,9 |

Tab. 3: Astragali of *Hipparion*: measurements in millimeters done and published by P. SONDAAR (PS); n = number of specimens, \bar{x} = mean, min. = minimum, max. = maximum, diam. = diameter, med. = medial.

| Astragalus | PS 1961 Eppelsheim, n = 6 <i>H. primigenium</i> | | | PS Maramena <i>H. sp. small</i> | PS Maramena <i>H. sp. big</i> |
|-------------------------------|---|-----------|------|---------------------------------------|-------------------------------------|
| | min | \bar{x} | max | n = 1 | n = 1 |
| 1: Maximal length | 52,5 | 57,2 | 61,5 | 47,5 | 61,2 |
| 2: Maximal diam. med. condyle | | | | 44,8 | 60,2 |
| 3: Breadth of the trochlea | | | | 17,8 | 31,0 |
| 4: Maximal breadth | 53,5 | 56,4 | 58,2 | 43,2 | 58,5 |
| 5: Distal articular breadth | 42,3 | 44,0 | 46,2 | 36,2 | 47,1 |
| 6: Distal articular depth | 31,1 | 31,8 | 33,7 | 26,9 | 35,0 |
| 7: Maximal medial depth | | | | 38,0 | 54,0 |

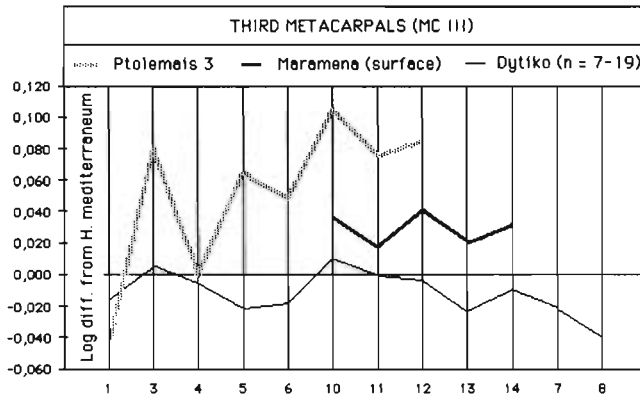


Fig. 3: Ratio diagrams of *Hipparion* third metacarpals done according to the data in table 2. The definition of the measurements are given in table 2. Maramena (surface) refers to the middle sized species found on the surface (see post scriptum).

Maramena in a younger zone. In this case, the Maramena *hipparion* might be of Ruscinian age and could belong to the zones MN 14 or 15.

Post scriptum: After the manuscript was finished, new material was brought to us. It was collected on the surface, prior to the excavations and includes a middle-sized distal end of MC III (MA 907, pl. 1, fig. 6a, 6b and table 2) and a very large astragalus (MA 908, pl. 1, fig. 7; table 3). None of these specimens can belong to the small species found in situ. Moreover, the astragalus seems too big to belong to the same species as the MC III.

On the MC III, the distal keel is very developed. Such a feature is unusual in Turolian *hipparions*, but occurs in the MC III described by KOUFOS (1982) from Ptolemais 3. Figure 3 compares the MC III of the Upper Turolian (MN 13 zone) *hipparion* from Dytiko KOUFOS, 1988),

the Maramena fragment and the Ptolemais 3 metacarpal (KOUFOS, 1982) The relatively large value for the depth of the keel (measurement 12) is striking. According to van der WEELD, 1979, quoted by KOUFOS, Ptolemais belongs in the MN 14 zone but it is placed in the MN 15 zone by MEIN (1990).

The astragalus is larger than in *H. primigenium* of Eppelsheim (table 3) and a little bit smaller than in Çalta (Turkey). The astragali of Çalta are the largest we have ever seen in European *hipparions*. Çalta is the type locality for *Hipparion* zone 5 of SEN et al. (1978) and was placed then in the MN 14 zone; it is now placed by MEIN (1990) in the zone MN 15.

Thus, the fossils of probably two species found on the surface, as well as the small *Hipparion* in situ, point to a Ruscinian age for Maramena.

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