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New material of Vallesian Late Miocene hipparions (Mammalia, Perissodactyla) from the lower Axios Valley, Macedonia, Greece

With 18 Text-figures, 17 Tables and 4 Plates

GEORGE D. KOUFOS

Abstract

The hipparions from Vallesian Late Miocene localities of the Axios valley (Macedonia, Greece) are described and compared with those from Eurasia. In addition to the previously recognized species, *H. primigenium* and *H. macedonicum*, a third species has been determined mainly in the material from the locality of "Pentalophos 1", PNT. It has primitive features and it is similar to *H. depereti* but with some differences and thus it is referred as *H.* aff. *depereti*. Some implications for the age of the Axios hipparions and their phylogenetical relationships are discussed.

Key words: Equidae, *Hipparion*, taxonomy, phylogeny, Vallesian, Late Miocene, Macedonia, Greece.

Kurzfassung

[Neues Material spätmiozäner Hipparionen (Vallesium; Mammalia, Perissodactyla) aus dem unteren Axios-Tal, Mazedonien, Griechenland.] — Das neue Hipparion-Material wird beschrieben und mit eurasischen Faunen verglichen. Zusätzlich zu den bisher vorliegenden Arten, *H. primigenium* und *H. macedonicum*, konnte eine dritte Art bestimmt werden – hauptsächlich von der Lokalität „Pentalophos 1", PNT. Diese hat primitive Merkmale und ist *H. depereti* ähnlich. Sie zeigt jedoch einige Unterschiede, so daß sie als *H.* aff. *depereti* beschrieben wird. Einige Schlußfolgerungen bezüglich des geologischen Alters und der phylogenetischen Beziehungen der *Hipparion*-Formen vom Axios werden diskutiert.

Introduction

The Vallesian hipparions of the southeastern Mediterranean are poorly known, although there is some information from Turkey (SEN et al. 1978; STAESCHE & SONDAAR 1979) and from Bulgaria (FORSTÉN 1978). In Greece, Vallesian hipparions are known from the locality of Kastellios, Crete (BRUIJN et al. 1971) and from the Axios valley (KOUFOS 1984, 1986). The available material from Kastellios is scarce, while that of the Axios valley is richer. The Axios valley Vallesian hipparions come from three localities. The best known is that of "Ravin de la Pluie" RPl (text-fig. 1) which is well-known from the presence of the hominid primate *Ouranopithecus macedoniensis*. The locality has been dated as late Vallesian, MN 10 (KOUFOS 1990; BONIS & KOUFOS 1999).

Another Vallesian locality of the lower Axios valley is that of "Pentalophos 1" (PNT) which is also relatively rich in hipparions. However, the age of the material from this locality

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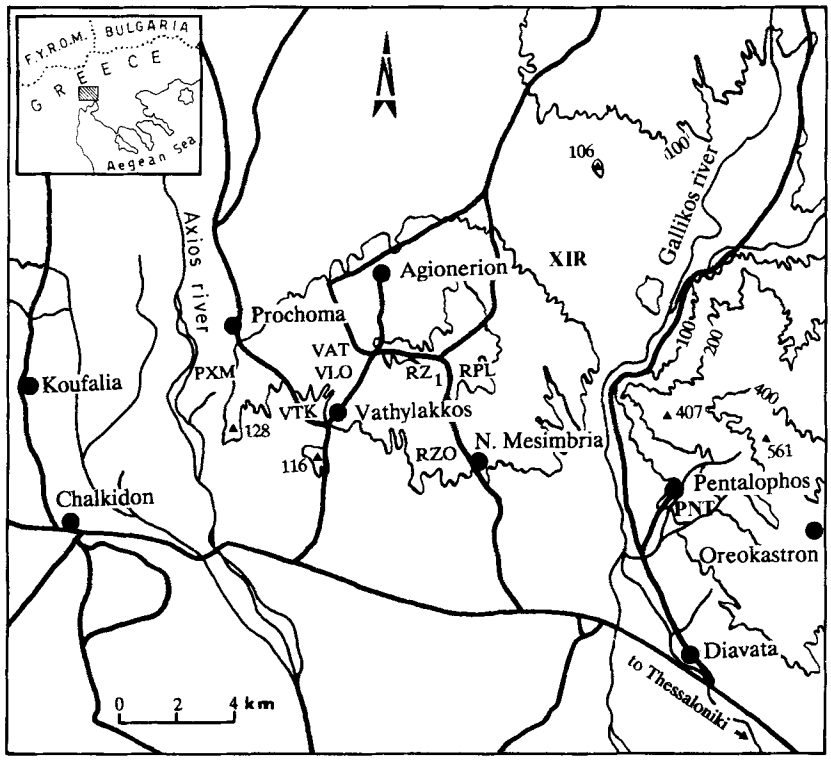
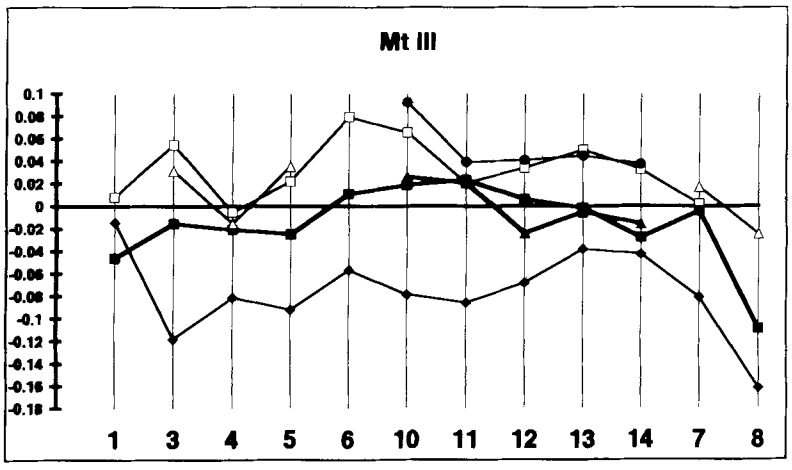


Text-fig. 1. Topographic map of the lower Axios valley indicating the Vallesian localities. – 1. "Ravin de la Pluie", RPl; 2. "Ravin de Zouaves 1", RZ_1; 3. "Pentalophos 1", PNT; 4. "Xirochori 1", XIR.



Text-fig. 2. Logarithmic ratio diagram comparing all third metatarsals of *Hipparion*, found in "Ravin de la Pluie", RPl. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 10.
Δ RPl-3; □ RPl-39; ● RPl-11; ▲ RPl-45; ■ RPl-61; ◆ RPl-38.

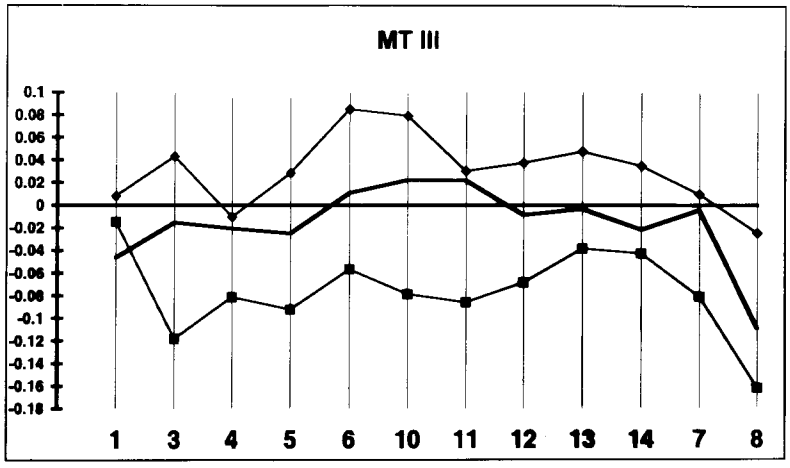
is puzzling but most of the faunal data suggest a Vallesian age (BONIS & KOUFOS 1999). The Pentalophos hipparions have never been published, and were referred to *Hipparion* sp. (large size) and *Hipparion* sp. (small size). A complete study and comparison of this material is quite interesting because it will add new information about the Vallesian hipparions in the southeastern Mediterranean. The fossiliferous site "Pentalophos 1", PNT, is located in a ravine near the village of Pentalophos, about 20 km west of Thessaloniki (text-fig. 1). The fossiliferous horizon is situated in a series of red-brown conglomerates, sands and gravels rich in clay, belonging to the Nea Messimvria Formation. The upper part of Nea Messimvria Formation is dated as late Vallesian (KOUFOS 1980, 1990; BONIS et al. 1988; BONIS & KOUFOS 1999).

A few hipparions are also known from the locality of "Ravin des Zouaves 1" (RZ_1) which is also dated as late Vallesian. It is situated north of the village of Nea Messimvria very close to RPl (text-fig. 1) and both belong to the same stratigraphic level (BONIS & KOUFOS 1999). The hipparion remains from RZ_1 are few but they will be included in this paper. There is also another Vallesian locality in the Axios valley named "Xirochori 1" (XIR) but the hipparions are represented only by some isolated and fragmentary teeth. New material of hipparions has been also unearthed from RPl, since the last revision (KOUFOS 1986), which is interesting for the study of the rest of the material from the other localities. So, a short revision of the RPl hipparions, including the new evidence, will be also given here.

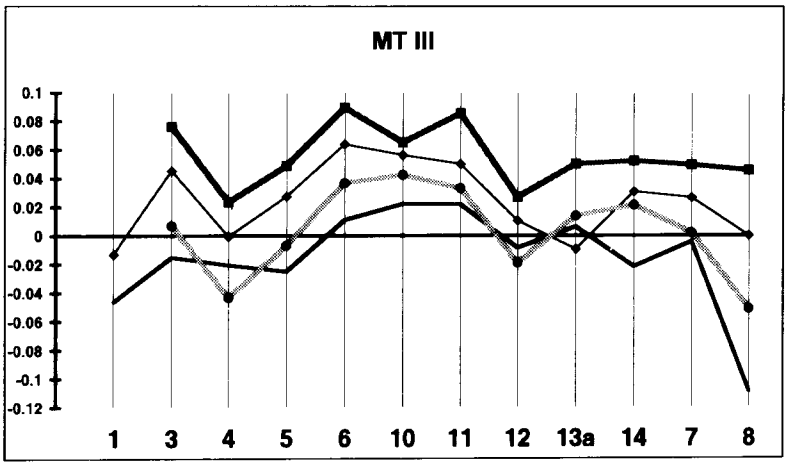
The material will be measured and studied according to the system proposed by EISENMANN et al. (1988). In the logarithmic ratio diagrams *H. mediterraneum* from Pikermi is used as the standard of comparison; for its measurements see KOUFOS (1987a). All the studied material is stored in the University of Thessaloniki, Laboratory of Geology and Palaeontology (LGPUT).

Locality "Ravin de la Pluie" RPl

The RPl hipparions have been studied previously and two species were recognized, *H. primigenium* (VON MEYER 1829) (pl. 4 fig. 3a) and *H. macedonicum* KOUFOS 1984 (pl. 4 fig. 3c KOUFOS 1984, 1986). *H. primigenium* (VON MEYER 1829) is characterized by large size, richly plicated upper cheek teeth, plicated or crenulated flexids in the lower teeth and relatively short and robust metapodials. *H. macedonicum* is a small-sized form with rich to moderate enamel plication, crenulated enamel in the flexids of the lower teeth and long slender metapodials. Besides the clear presence of these two species, there is a proximal part of a Mt_{III} (RPl-45) whose dimensions are between those of *H. primigenium* and *H. macedonicum*, indicating the possible presence of a medium-sized *Hipparion* (KOUFOS 1986: 77, text-fig. 5).



Text-fig. 3. Logarithmic ratio diagram comparing the third metatarsals of the three different *Hipparion* species from "Ravin de la Pluie", RPl. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 8.
◆ *H. primigenium*, RPl, n=1-3; — *H.* aff. *depereti*, RPl, n=1-2; ■ *H. macedonicum*, RPl, n=1.



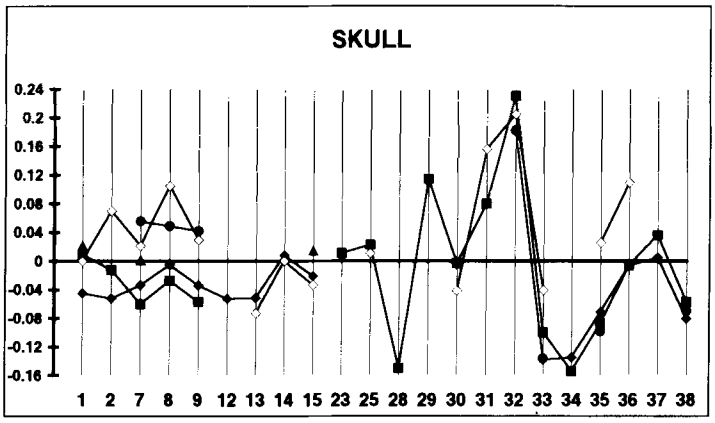
Text-fig. 4. Logarithmic ratio diagram comparing the third metatarsals of *H.* aff. *depereti* from "Ravin de la Pluie", RPl with *H. depereti* from Montredon (France). Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 10.
— *H.* aff. *depereti*, RPl, n=1-2; ◆ *H. depereti*, Montredon, mean, n=1-5 (EISENMANN 1988); ■ *H. depereti*, Montredon, min, n=1-5 (EISENMANN 1988); ● *H. depereti*, Montredon, max, n=1-5 (EISENMANN 1988).

Among the new material from RPl, there is a complete metatarsal (RPl-61) whose size fits quite well with that of RPl-45 (text-fig. 2). The distinction of the small-sized RPl-38 belonging to *H. macedonicum* is clear, RPl-61 and RPl-45 match together, while the rest belongs to the large-sized *H. primigenium*. The RPl medium-sized hipparion is shorter and more robust than *H. macedonicum*, while it is shorter and more slender than *H. primigenium* (text-fig. 3). Thus, the presence of a third, medium-sized hipparion in RPl is clear.

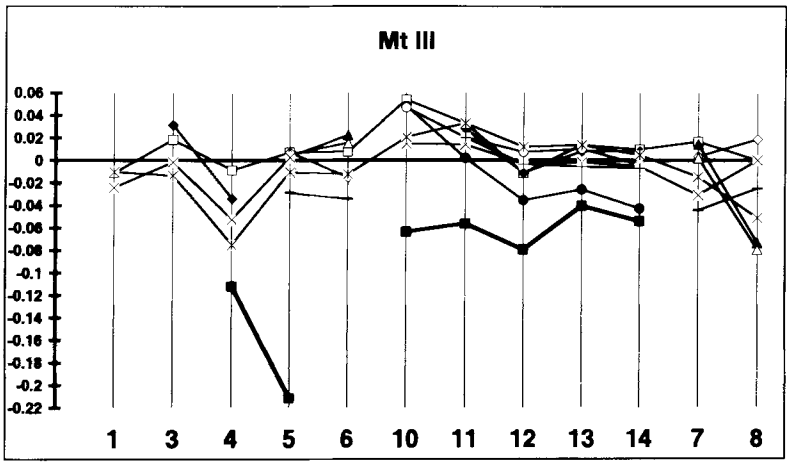
Medium-sized hipparions are known from the Vallesian of western Europe. A new species, *H. depereti* has been described from the localities of Montredon and Soblay by SONDAAR (1974). Later, two species have been recognized in Montredon material, *H. depereti* and a small-sized form with strong similarities to *H. macedonicum* (EISENMANN 1988). A comparison of the RPl medium-sized form with *H. depereti* from Montredon suggests that it has similar proportions with the latter species (text-fig. 4). However, it is slightly more slender than the minimum values of *H. depereti* (text-fig. 4). The slenderness index (11/1) for the RPl medium-sized Mt_{III} is 15.3 versus 15.1 (14.6-16.4) for the Mt_{III} of *H. depereti* from Montredon (measurements from EISENMANN 1988). The most significant difference between RPl medium-sized Mt_{III} and that of Montredon is the shorter depth of the distal medial condyle (meas. 14 in text-fig. 4). Considering that there is only one complete Mt_{III} from RPl and the Montredon sample is poor, the comparison is not reliable because we don't know the exact ranges of variation for both samples. The RPl medium-sized hipparion could belong to *H. depereti* but the limited known material and the slightly more slender metatarsal than that of *H. depereti* precludes a firm comparison and it is better to refer to this as *H.* aff. *depereti* SONDAAR 1974 (pl. 4 fig. 3b), for the moment.

Locality "Pentalophos 1" PNT

The hipparions from "Pentalophos 1" have not been previously studied and they were referred to *Hipparion* sp. (large-sized) and *Hipparion* sp. (small-sized). The presence of two hipparions in PNT is clear from both the cranial remains and the metapodials (text-figs 5, 6). The skulls PNT-118 and PNT-136 match together, while PNT-116 and PNT-123 with larger dimensions are distinguished from the first two (text-fig. 5). The skull PNT-137 belongs to a young-adult individual preserving the very worn milk teeth, while $M_{1,2}$ have been arisen, and M_3 is still unworn. The individual has reached its final size and thus some measurements are close to the small-sized group. However, most of its dimensions are similar to those of the large-sized skulls from PNT (text-fig. 5). Moreover, the nasal cavity of PNT-137 is longer than that of the small-sized group (meas. 31 in text-fig. 5), while the preorbi-



Text-fig. 5. Logarithmic ratio diagram comparing the skulls found in "Pentalophos 1", PNT. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 1.
■ PNT-118; ◆ PNT-136; ◇ PNT-137; ▲ PNT-116; ● PNT-123.



Text-fig. 6. Logarithmic ratio diagram comparing the third metatarsals found in „Pentalophos 1", PNT. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measure-ments see tab. 10.
○ PNT-4; ■ PNT-87; ▲ PNT-17; ◇ PNT-112; * PNT-19; — PNT-113; + PNT-22; Δ PNT-120; ◆ PNT-38; □ PNT-121; ● PNT-39; × PNT-150.

tal fossa is longer, wider and closer to the tooth row (meas. 31, 33, 35, 36, 38 in text-fig. 5). The palate is also longer (meas. 2 in text-fig. 5). Taking into account all these features, PNT-137 must belong to the large-sized group. Similar results are evident from the comparison of the metatarsals. All of them except PNT-87 match together (text-fig. 6) indicating the presence of two hipparions. The comparison of the available upper cheek teeth also indicates the presence of two forms in the PNT sample (text-fig. 7).

Hipparion aff. *depereti* SONDAAR 1974

Pls 1, 2; Pl. 3 fig. 2; Pl. 4 fig. 1

Locality: "Pentalophos 1", PNT, Macedonia, Greece.

Age: Late Vallesian, Late Miocene.

Material: Frontal part of the skull, PNT-137; left frontal part of the skull with P^2-M^3 sin, PNT-123; muzzle with I^1-P^4 sin and I^1-C dex, PNT-116; maxilla with P^2-M^3 dex and sin, PNT-2; left upper tooth row with dp^1-M^3, PNT-138; $P^{3,4}$ dex, PNT-44; $M^{1,2}$ sin, PNT-101; mandible with P_2-M_3 dex and sin, PNT-151; mandible with the snout and the left mandibular ramus, PNT-117; mandible with P_2-M_2, PNT-54; right mandibular ramus with P_4-M_3, PNT-40; left mandibular ramus with M_1-M_2, PNT-79; $P_{3,4}$ dex, PNT-148; $2M_{1,2}$, PNT-59, 111; $3M_3$, PNT-51, 81, 149; carpals+Mc_{III}+Mc_{II}+Mc_{IV}+Ph_I+Ph_{II}+Ph_{III} +lateral phalanges, PNT-57; distal part of Mc_{III}+Ph_I+Ph_{II}+Ph_{III}, PNT-114; distal part of Mc_{III}, PNT-29; distal part of femur+distal part of tibia+cuboid+big cuneiform+scaphoid+calcaneum+astragalus, PNT-150; calcaneum+astragalus, PNT-147; calcaneum, PNT-35; Mt_{III}+Ph_I, PNT-38; 3 Mt_{III}, PNT-19, 121, 150; 3 proximal parts of Mt_{III}, PNT-4,2,39; 4 distal parts of Mt_{III}, PNT-17, 60, 120, 122; 3 first phalanges, PNT-140, 141, 145.

Description

The available skull material includes only frontal parts and some maxillary remains. The skull PNT-137 belongs to a young-adult individual, the molars have been arisen but the milk teeth are still preserved. The partial skull PNT-123 preserves the left facial part of the skull with the fossa and the orbit, as well as the left tooth row. PNT-116 preserves the muzzle and the left premolar row of an aged individual, while PNT-2 is a maxilla of a very old individual.

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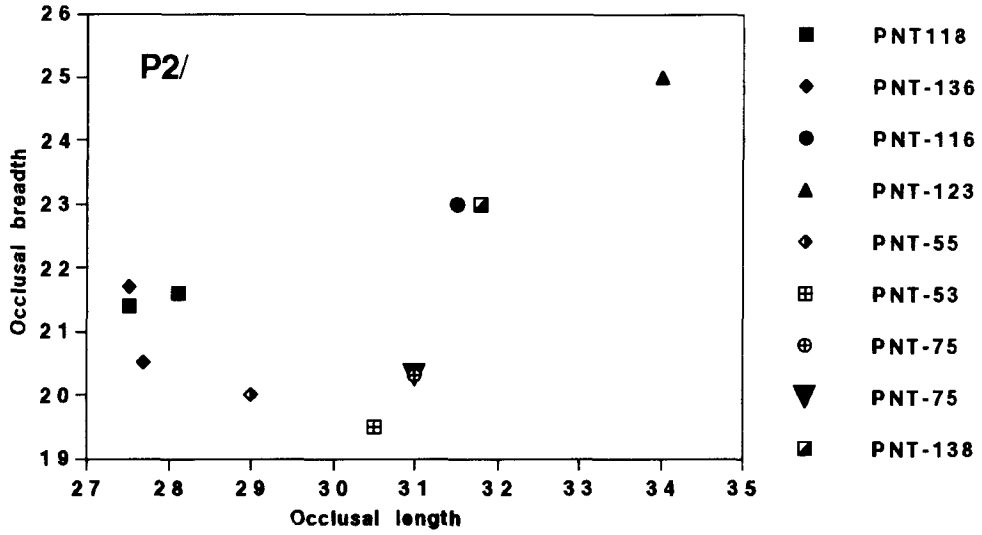
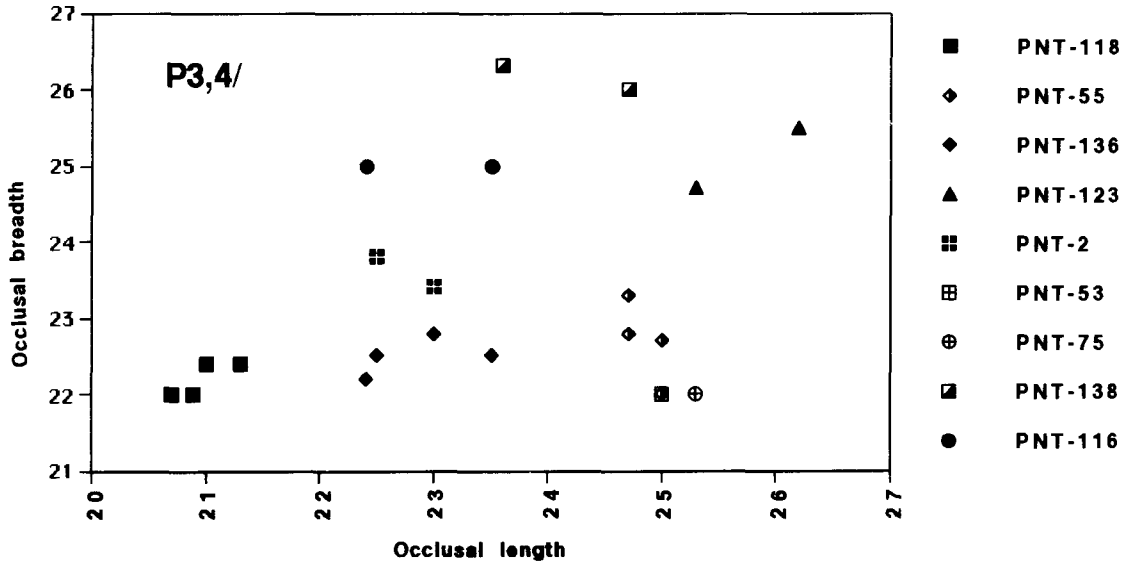
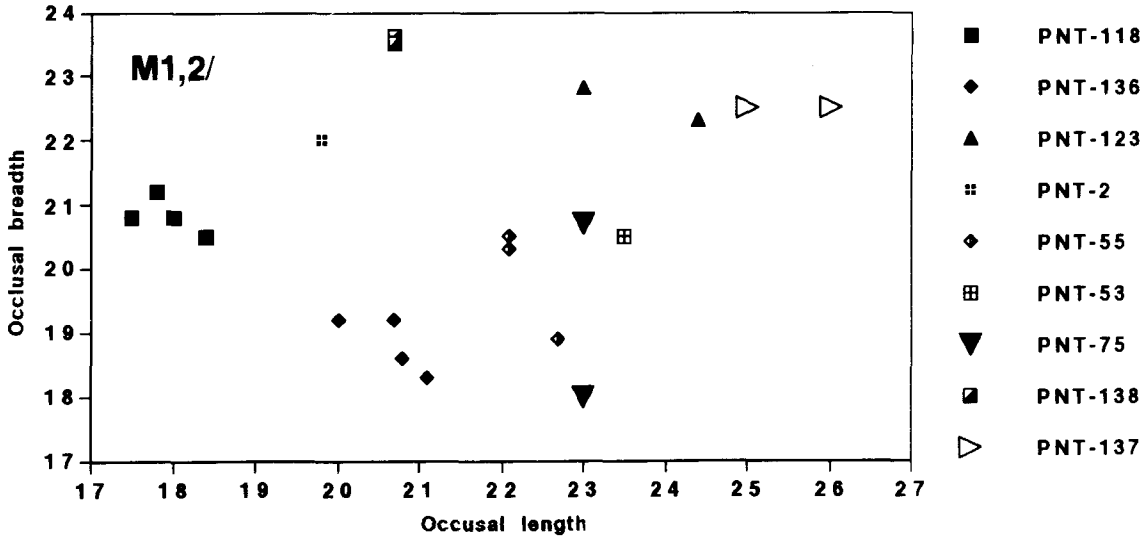
Text-fig. 7. Scatter diagram (L_o/B_o) comparing the upper cheek teeth found in "Pentalophos 1", PNT.


P2/
Occlusal breadth
Occlusal length
PNT118
PNT-136
PNT-116
PNT-123
PNT-55
PNT-53
PNT-75
PNT-75
PNT-138


P3,4/
Occlusal breadth
Occlusal length
PNT-118
PNT-55
PNT-136
PNT-123
PNT-2
PNT-53
PNT-75
PNT-138
PNT-116


M1,2/
Occlusal breadth
Occusal length
PNT-118
PNT-136
PNT-123
PNT-2
PNT-55
PNT-53
PNT-75
PNT-138
PNT-137

The muzzle is short and narrow, while it is relatively wider at the incisors' borders. The palate is elongate and relatively narrow. The anterior border of the choanae is situated at the posterior half of M^2. The nasal cavity is short and its posterior border is situated above the middle of the diastema C-P^2. The preorbital fossa is single, egg-shaped, deeply pokketed posteriorly with well defined borders. It is situated enough far from the orbit; the preorbital bar varies between 39.5-41.5 mm. The lacrymal is large and slightly invades the posterior border of the preorbital fossa. The orbit is partially preserved in both available skulls and seems to be rounded or oval. The anterior border of the orbit is situated slightly behind the posterior end of M^3. The facial crest is strong and its anterior end is situated above M^1.

The upper tooth row is relatively long and slightly curved or straight. The cheek teeth are long and wide. The hypsodonty cannot be calculated because there are no unworn teeth. However, from the available tooth rows the teeth seem to be more brachydont than hypsodont. The enamel plication is high in the moderately worn teeth (PNT-123, 138) but in the very worn dentition it is less (PNT-2,116). The plis are narrow and deep, being smaller in the worn teeth. The pli caballin is usually double or triple and the plis are relatively small. In the very worn teeth (PNT-2,116) the pli caballin disappeared or is represented by a crenulation of the enamel at its position. The protocone is oval with a reduced spur which is more clearly visible in the less worn teeth (PNT-123), but in the worn and very worn teeth it is very often connected to the protoloph. The fossettes are always free and closed except the P^2 of PNT-138 and 123 whose fossettes are connected. The hypocone is anteroposteriorly aligned with the protocone, it is elliptical, posteriorly angular in the less worn teeth and rounded in the very worn teeth. There is a well developed lingual hypoconal sinus which is clear even in the heavily worn teeth, and it is more pronounced in P^2 and M^3. The distal hypoconal sinus is deep and V-shaped in the less worn teeth, while in the very worn teeth it is narrow. In the less worn M^3 of PNT-123 and 138 one or two hypoconal islets are distinguished. The dp^1 is present in three of the available maxillae.

The mandible has a short and narrow snout. The index 2/7 is 220.7 indicating a relatively short snout. The same index is 227 for *H. primigenium* of RPl and 253.7 for *H. brachypus* HENSEL 1862 from Pikermi suggesting short and elongate snouts respectively. The symphysis is relatively long, its posterior border is situated slightly in front of P_2. The tooth row is elongated. The incisors are curved and they are situated in a rounded row; I_3 is elongate and not constricted labiolingually. The paraconid of P_2 is relatively long. The premolars are relatively short and wide having a robust appearance. The metaconid is rounded, while the metastylid is triangular. The flexids have plicated or crenulated enamel, a primitive feature observed in the Vallesian hipparions of Europe. The parastylid is moderately developed and a protostylid is clearly developed in all teeth. The latter is strong and columnar and is developed along half of the tooth's height. The entoconid is rounded in the premolars and elliptical in the molars. The linguaflexid is open, U-shaped and deep, touching the ectoflexid in all teeth. The ectoflexid is narrow and deep separating metaconid and metastylid. A single rudimentary pli caballinid is present in all teeth and it disappears with wear. The ectostylid is absent in all teeth. The hypoconulid is well developed, especially in the molars, while it is relatively very long in M_3. Among the material there is an unworn $M_{1,2}$. The hypsodonty index of EISENMANN et al. (1988) is 45.4, while that of SONDAAR (1961) is 226.6. A single measurement cannot allow general conclusions about the hypsodonty, but it is an indication of moderate hypsodonty.

The available material of metapodials is scarce; there is a complete Mc_{III}, three complete Mt_{III}, and some proximal and distal fragments of Mt_{III}. Most of the metatarsals belong to a medium sized form (text-fig. 6) which can be correlated with the skulls described above. The metacarpal is short and robust. The index 11/1 is 17 indicating short and robust metapodials. This index is 17.9 for *H. brachypus* from Pikermi, a species with short and robust metapodials. This index is also similar to that (17.5) of *H. primigenium* from Eppelsheim or to that (17.4) of *H. primigenium* from Höwenegg (data from SONDAAR 1974 and BERNOR et al 1997). The same index for *H. depereti* from Montredon is 17.7 (data from EISENMANN 1988).

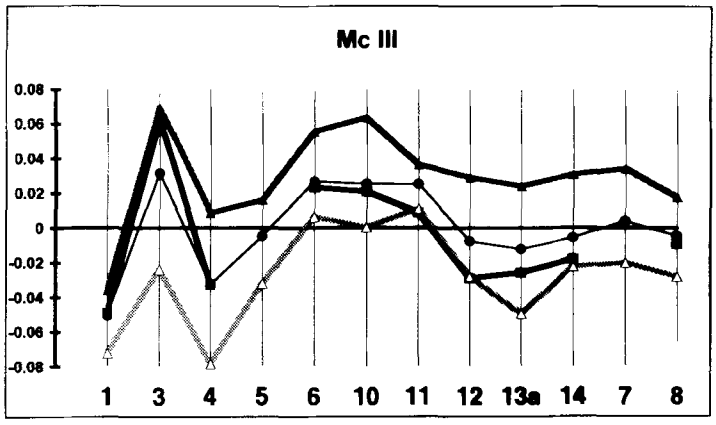
The metatarsals are also short and robust. The index 11/1 is 14.3 versus 16 for *H. brachypus* from Pikermi, 16.0 for *H. primigenium* from Eppelsheim, 15.1 for *H. depereti* from Montredon and 15.5 for *H. primigenium* from Höwenegg. However, the PNT hipparion seems to have a slightly smaller mean index indicating somewhat more slender metatarsals. The facet for cuneiform II is present in 7 of 8 available specimens, 87.5%. The short and robust metapodials of the PNT hipparion suggest relationships with the primitive Vallesian forms.

The keel is weak and not projecting; the calculated keel index (12/13) is 120 for Mc_{III} and 124.2 for Mt_{III}. The small keel index is also evidence for a Vallesian hipparion.

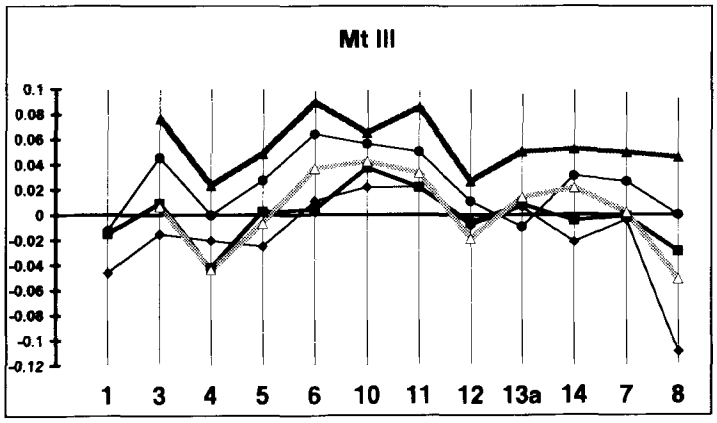
Discussion

The Pentalophos medium-sized hipparion has some similarities with that of "Ravin de la Pluie" (RPl) referred to above, as well as with *H. depereti.* The latter is a medium-sized Vallesian hipparion known from the localities of Montredon and Soblay (France). Cranial material from these localities is unknown and thus a straight comparison with the PNT skulls is impossible. However, the metapodials and especially the metatarsals can provide some comparative data. The RPl and PNT medium-sized metatarsals are very similar and both are close to those of *H. depereti* (text-fig. 8). However, they are more slender than those of *H. depereti* with relatively thinner distal articulation. Their lines are very near or sometimes below the line for the minimum values of *H. depereti.* Considering the PNT metacarpal (a sole complete specimen) it is also slender and closer to the minimum values of *H. depereti* (text-fig. 9).

Such differences are also seen for the metapodials of *H. primigenium* from RPl. They are more slender than those of the typical *H. primigenium* from Eppelsheim (KOUFOS 1986). This difference can be explained by the different palaeoecological conditions between northwestern and southeastern Europe. The former region is characterized by the presence of forests, while the latter constitutes a savannah-like province (BONIS et al. 1992). The short and robust metapodials characterize the forestrial hipparions, while the long and slender ones indicate hipparions living in an open environment.



Text-fig. 8. Logarithmic ratio diagram comparing the third metacarpal of *H.* aff. *depereti* from "Pentalophos 1", PNT with *H. depereti* from Montredon (France). Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 7.
■ *H.* aff. *depereti*, PNT, n=1-3; • *H. depereti*, Montredon, mean, n=5-9 (EISENMANN 1988); Δ *H. depereti*, Montredon, min, n=5-9 (EISENMANN 1988); ▲ *H. depereti*, Montredon, max, n=5-9 (EISENMANN 1988).

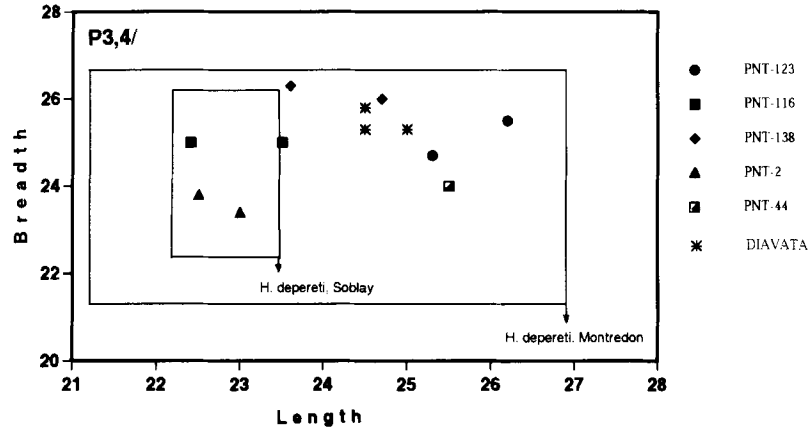


Text-fig. 9. Logarithmic ratio diagram comparing the third metatarsals of *H.* aff. *depereti* from "Pentalophos 1", PNT with *H.* aff. *depereti* from "Ravin de la Pluie", RPl and *H. depereti* from Montredon (France). Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 10.
■ *H.* aff. *depereti*, PNT, n=3-7; ◇ *H.* aff. *depereti*, RPl, n=1-2; • *H. depereti*, Montredon, mean, n=1-5 (EISENMANN 1988); Δ *H. depereti*, Montredon, min, n=1-5 (EISENMANN 1988); ▲ *H. depereti*, Montredon, max, n=1-5 (EISENMANN 1988).

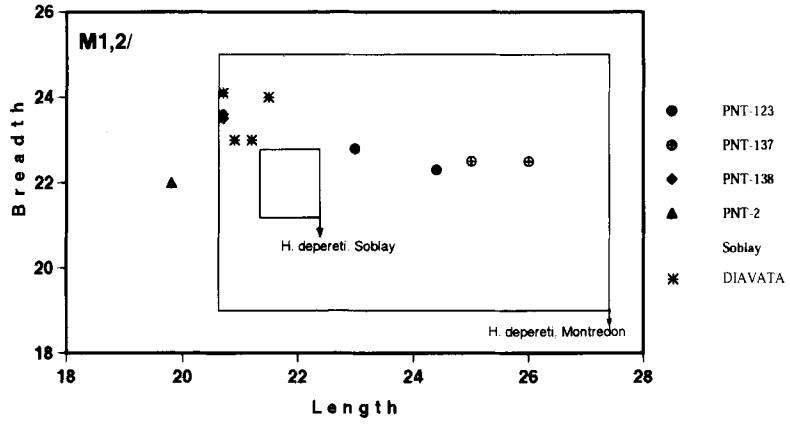
The hipparions from Montredon and Soblay have been described by SONDAAR (1974) and EISENMANN (1988). The species *H. depereti* has been erected by SONDAAR (1974) with the following characters: medium-sized with very massive limbs, moderate enamel plication in the upper cheek teeth and with short and massive metapodials. Some years later EISENMANN (1988) revised the Montredon material and she distinguished two hipparions, the medium-sized *H. depereti* and a small-sized form named *Hipparion* sp. which is very similar to *H. macedonicum* from RPl. According to EISENMANN (1988) *H. depereti* is smaller than the typical Vallesian hipparions but with similar morphological features (rich enamel plication in the upper cheek teeth, absence of confluent or open fossettes in the upper premolars, moderate hypsodonty and massive metapodials), while the index of the keel development for Mc_{III} and the frequency of the presence of the facet for cuneiforme II is closer to the Turolian forms. Considering the medium-sized metapodials of PNT, they are close to but more slender than those of *H. depereti* (text-figs 8, 9) reflecting the different palaeoecological conditions. The robustness and keel indices for these metapodials are also very close to those of *H. depereti* from Montredon (tab. 1).

As mentioned above, no cranial or mandibular remains of *H. depereti* are known, and a comparison will be based on the dental remains. The size of the studied upper cheek teeth is within the range of variation for *H. depereti* from Montredon (text-figs 10 a, b). There is only one M^{1-2} (PNT-2) which is out of this range of variation but this tooth is extremely worn and its dimensions are smaller in comparison with the others. Similar results are also seen for the lower cheek teeth (text-figs 11 a, b). The enamel plication for *H. depereti* is moderate. The plication number for the upper teeth of the PNT material is similar to that for *H. depereti* from Montredon (tab. I). The slightly smaller mean plication number of the PNT sample can be also explained by the different palaeoecological conditions between the western and eastern Mediterranean. Usually the forest hipparions have rich enamel plication with deep plis, allowing them to cut the fresh green grass, while those living in open environments have less plicated enamel with shallow plis which leave more open areas in the occlusal surface of the teeth for chewing hard grass (FORSTÉN 1968).

Among the studied material there are six first phalanges which have moderate size and belong to one species. Three of them have been found in natural association with metapodials, two (PNT-57, 114) belong to the anterior and one (PNT-38) to the posterior leg. The distinction of the anterior and posterior phalanges of *Hipparion* is not easy. Usually the posterior phalanges are shorter and more robust than the anterior ones; such differences can be observed between PNT-38 and PNT-57, 114. The first phalanges of *H. depereti* from Montredon are referred together without distinction (EISENMANN 1988), and for comparative reasons I mixed the PNT



10 a



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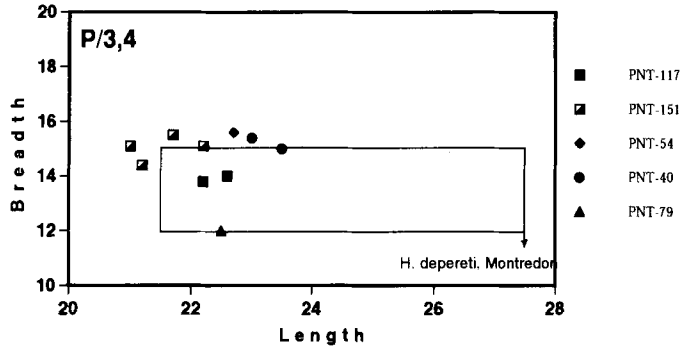
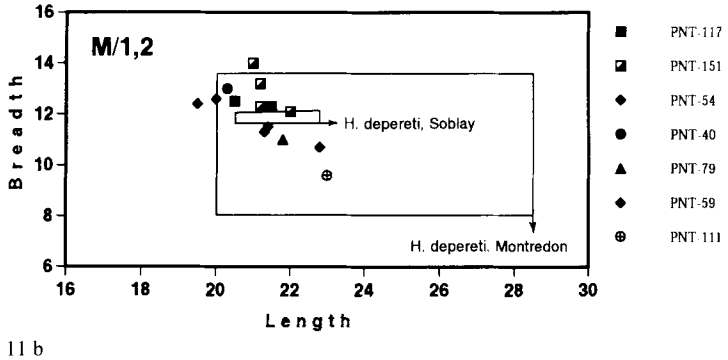


11 a



11 b

Text-figs 10 a, b. Scatter diagrams (L_0/B_0) comparing the upper cheek teeth of *H.* aff. *depereti* from "Pentalophos 1", PNT and Diavata, DVT with those of *H. depereti* from Montredon and Soblay (France).

sample. The PNT first phalanges have more or less similar height but they are more slender than those of *H. depereti* (text-fig. 12).

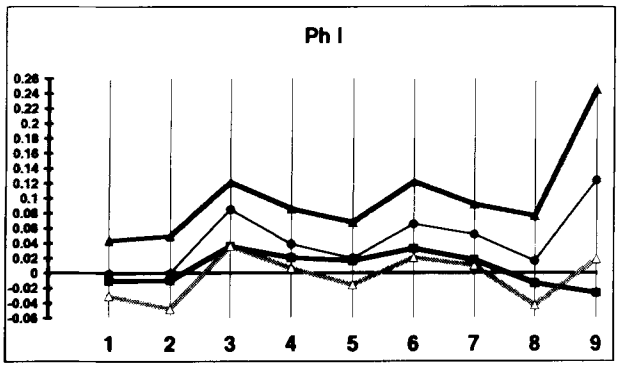
Two astragali of similar size are available from PNT, belonging to the middle-sized form. Their comparison with *H. depereti* from Montredon indicates that they are smaller than the mean value of this species, while the distal articulation surface is significantly smaller (text-fig. 13). This feature fits quite well with the slender metatarsals of the PNT hipparion rather than those of Montredon. Similar results are also seen from the comparison of the calcaneum (text-fig. 14), which is near the minimum values for *H. depereti* of Montredon but smaller and more slender.

Taking into account all the above mentioned characters, the PNT medium-sized hipparion is close to *H. depereti,* however, it has less enamel plication in the upper cheek teeth and more slender limb bones.

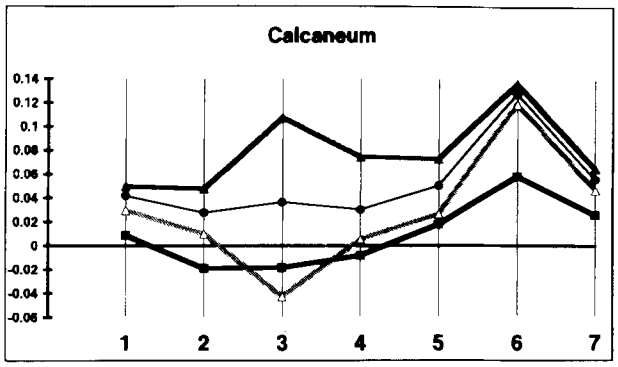
Several Vallesian hipparions are known from Europe, the most common of which is *H. primigenium* known from several localities (see BERNOR et al. 1996). Two other Vallesian species are known from Spain, *H. catalaunicum* PIRLOT 1956 from Can Llobateres and *H. koenigswaldi* SONDAAR 1961 from Nombrevilla. Another Vallesian species from Turkey is referred to the name *H. ankyranum* OZANSOY 1965 (STAESCHE & SONDAAR 1979).

A comparison of the studied skulls of the PNT medium-sized hipparion with the skull of *H. primigenium* from the Vienna Basin (BERNOR et al. 1988) is useful for the distinction of the PNT material from this species. *H. primigenium* is characterized by a moderately long and wide muzzle and short nasal opening, its posterior end is situated anteriorly to P^2. The PNT skull has a short and narrow muzzle which differentiates it from *H. primigeni-*

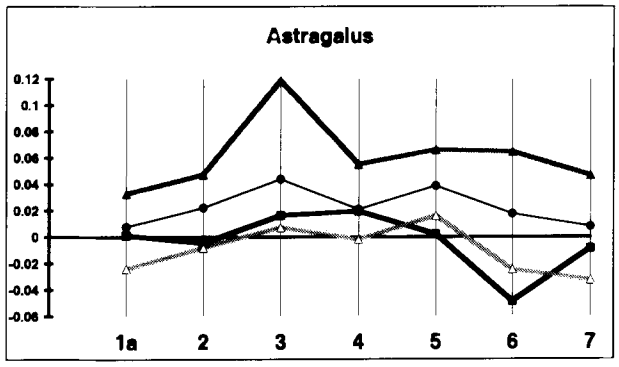
Text-figs 11 a, b. Scatter diagrams (L_0/B_0) comparing the lower cheek teeth of *H.* aff. *depereti* from "Pentalophos 1", PNT with those of *H. depereti* from Montredon and Soblay (France).



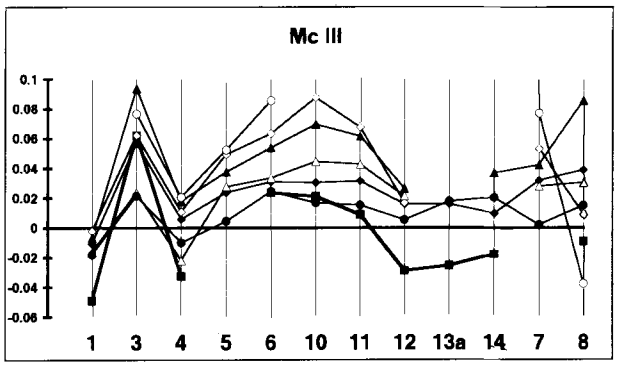
Text-fig. 12. Logarithmic ratio diagram comparing the first phalanges of *H.* aff. *depereti* from "Pentalophos 1", PNT with *H. depereti* from Montredon (France). Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 11.
■ *H.* aff. *depereti*, PNT, n=4-5; ● *H. depereti*, Montredon, mean, n=12-24 (EISENMANN 1988); Δ *H. depereti*, Montredon, min, n=12-24 (EISENMANN 1988); ▲ *H. depereti*, Montredon, max, n=12-24 (EISENMANN 1988).



Text-fig. 14. Logarithmic ratio diagram comparing the calcaneum of *H.* aff. *depereti* from "Pentalophos 1", PNT with *H. depereti* from Montredon (France). Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 8.
■ *H.* aff. *depereti*, PNT, n=1-3; ● *H. depereti*, Montredon, mean, n=2-4 (EISENMANN 1988); Δ *H. depereti*, Montredon, min, n=2-4 (EISENMANN 1988); ▲ *H. depereti*, Montredon, max, n=2-4 (EISENMANN 1988).



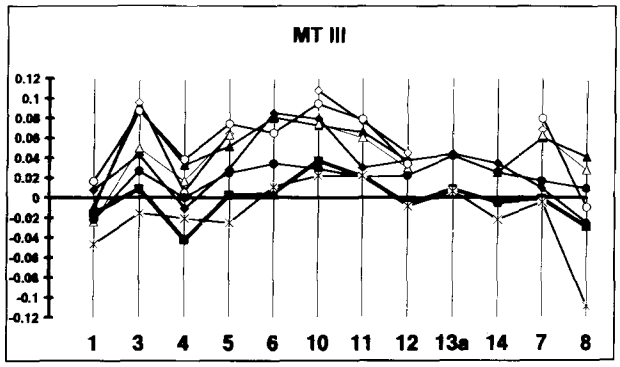
Text-fig. 13. Logarithmic ratio diagram comparing the astragalus of *H.* aff. *depereti* from "Pentalophos 1", PNT with *H. depereti* from Montredon (France). Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 9.
■ *H.* aff. *depereti*, PNT, n=1-2; ● *H. depereti*, Montredon, mean, n=11-20 (EISENMANN 1988); Δ *H. depereti* Montredon, min, n=11-20 (EISENMANN 1988); ▲ *H. depereti*, Montredon, max, n=11-20 (EISENMANN 1988).



Text-fig. 15. Logarithmic ratio diagram comparing the third metacarpal of *H.* aff. *depereti* from "Pentalophos 1", PNT with the Vallesian species of Eurasia. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 7.
■ *H.* aff. *depereti*, PNT, n=1-3; ◆ *H. primigenium*, RPl, n=1-3; ◇ *H. primigenium*, Eppelsheim, n=1 (SONDAAR 1974); ▲ *H. primigenium*, Höwenegg, n=10-16 (BERNOR et al. 1997); Δ *H. catalaunicum*, Can Llobateres, n=6 (SONDAAR 1974); ● *H. ankyranum*, Yassioren, n= 4-5 (original measurements); ○ *H. koenigswaldi*, Nombrevilla, n=1 (SONDAAR 1961).

um, while the nasal opening is also short but smaller in absolute dimensions than that of *H. primigenium*. The morphology of the preorbital fossa closely resembles that of *H. primigenium* (egg-shaped, deeply pocketed posteriorly, short preorbital bar) and in this feature the PNT skull is similar to the primitive hipparions. The tooth row dimensions of the PNT skull are similar to those of *H. primigenium*. The dental morphology of both samples is quite similar (brachydonty, double or complex plicaballin, closed fossettes, clear lingual hypoconal sinus, well developed protostylids, plicated or crenulated enamel margins in the flexids), however, the protocone shape is different. In the PNT skull it is rounded or oval, while in *H. primigenium* it is lingually flattened. Compared to *H. primigenium* the PNT teeth are smaller and they have less plicated enamel in the fossettes. All the above features suggest that the skull of the PNT medium-sized *Hipparion* is similar to the Vallesian primitive hipparions, but it also has some differences which distinguish it from the typical *H. primigenium*.

As the metapodials provide good material for comparison and they are preserved in all the above mentioned Vallesian samples of *H. primigenium* they will be compared with the PNT ones. The studied metapodials from PNT are smaller than all the others and significantly more slender (text-figs 15, 16). Their difference from the typical *H. primigenium*, as well as *H. catalaunicum* and *H. koenigswaldi* is quite clear. Their distinction from the RPl *H. primigenium* is also evident (text-figs 15, 16). The latter is closer to the large-sized hipparions of Europe. The medium-sized form from RPl fits quite



Text-fig. 16. Logarithmic ratio diagram comparing the third metatarsal of *H.* aff. *depereti* from "Pentalophos 1", PNT with the Vallesian species of Eurasia. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 10.
■ *H.* aff. *depereti*, PNT, n=3-7; * *H.* aff. *depereti*, RPl, n=1-2; ◆ *H. primigenium*, RPl, n=1-3; ◇ *H. primigenium*, Eppelsheim, n=1 (SONDAAR 1974); ▲ *H. primigenium*, Höwenegg, n=10-16 (BERNOR et al. 1997); Δ *H. catalaunicum*, Can Llobateres, n=6 (SONDAAR 1974); ● *H. ankyranum*, Yassioren, n= 4-5 (original measurements); ○ *H. koenigswaldi*, Nombrevilla, n=1 (SONDAAR 1961).

Tab. I. Enamel plication and metapodial indices of *H.* aff. *depereti* from "Pentalophos 1", PNT "Ravin de la Pluie", RPl and *H. depereti* from Montredon

	H. aff. *depereti* PNT	*H.* aff. *depereti* RPl	*H. depereti* MONTREDON (EISENMANN, 1988)
Plication number			15
P^2	18	-	18
$P^{3,4}$	17	-	22
$M^{1,2}$	19	-	18
M^3	17	-	
Mc_{III}			
Robusticity Index (11/1)	17.0	-	17.7
Keel Index (12/13)	120.0	-	120.2
Mt_{III}			
Robusticity Index (11/1)	14.3	15.4	15.1
Keel Index (12/13)	124.2	125	121.9

well in size with that from PNT (text-fig. 16) indicating that the two forms are similar.

Taking into account all the above mentioned data the PNT and RPl medium-sized hipparion has strong similarities with *H. depereti*. However, it has more slender limb bones and less enamel plication than the latter species. These differences are probably due to the different palaeocological conditions under which the animal lived and the two samples may represent two ecologic or geographic variations. The PNT and RPl medium-sized hipparion could belong to *H. depereti* but cranial material is absent in the Montredon sample, while the metapodials which provide good comparative data are very few in the PNT and RPl material. Thus, it is better at present to refer the RPl and PNT medium-sized form as *Hipparion* aff. *depereti*. The erection of a new species is questionable for the reasons mentioned above, and the differences between the Montredon and Axios samples are not strong enough to support such an idea.

Hipparion macedonicum KOUFOS 1984

Pl. 3 fig. 1; Pl. 4 fig. 2

Locality. "Pentalophos 1", PNT, Macedonia, Greece.

Age: Late Vallesian, Late Miocene.

Material: 2 frontal parts of the skull, PNT-118, 136; maxilla with P^2-M^3 sin and P^3-M^3 dex, PNT-55; left maxillary fragment with dp^1-P^{2-3}-dp^4-M^{1-2}, PNT-53; right maxillary fragment with P^2-M^3, PNT-75; $5P^2$, PNT-43, 96, 98, 99, 110; $P^{3,4}$ dex, PNT-97; $5M^{1,2}$ PNT-21, 102, 100, 104, 109; right mandibular fragment with dp_4-M_1, PNT-125; left mandibular fragment with P_3-M_1, PNT-78; $M_{1,2}$ sin, PNT-119; $2M_3$, PNT-80, 107; proximal part of radius, PNT-88; Mt_{III}, PNT-87.

Description

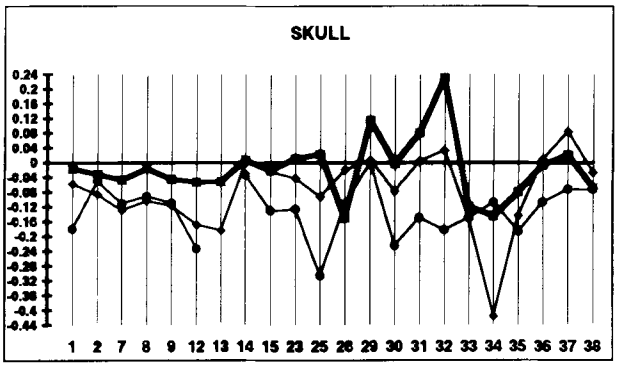
Two partial skulls were found; both preserve the frontal part of the skull with the muzzle and both tooth rows. The muzzle is relatively narrow and long. The nasal opening is short and its posterior border is quite anterior of P^2. The preorbital fossa is deep, egg-shaped and anteroposteriorly oriented, not deeply pocketed posteriorly but with a posterior rim. It is situated far from the orbit, the preorbital bar is 44 mm. The orbit is rounded and its anterior border is well behind M^3. The facial crest is strong and its anterior end is situated above the mesostyle of M^1. The infraorbital foramen encroaches the anteroventral border of the preorbital fossa. The dp^1 is present in PNT-118, PNT-55 and PNT-53. The palate is relatively long and narrow with narrow choanae; their anterior border is at the level of the middle of M^2.

The upper tooth row is relatively short and mainly straight. There is one unworn P^2 and one $M^{1,2}$ whose hypsodonty index calculated according to SONDAAR (1961) is 144 and 289.5, while according to EISENMANN et al. (1988) it is 69,4 and 34.5, respectively. In both cases the tooth seems to be quite hypsodont. The enamel plication is moderately rich. In the little worn teeth (PNT-75, 53, 55, 136) the enamel plication is high with relatively deep plis, while in the very worn dentition (PNT-118) the plis are less and shallower. The pli caballin is usually double, long and only in the very worn teeth is it very small or absent (PNT-118). The protocone is oval-subtriangular with a reduced spur. In the very worn teeth it is connected with the protoloph (PNT-118). The fossettes are free and closed. There is an exception in P^2 where the fossettes are connected in the small and very worn teeth (PNT-75, 118). The hypocone has an elongate elliptical shape with deep distal hypoconal sinus. The lingual hypoconal sinus is clearly seen in all available teeth.

The available lower teeth are either small or very worn and their morphology is not visible. The postcranials are very few but the available third metatarsal is long and slender and its keel index 115.7 is very close to the Vallesian forms (SEN et al. 1978; KOUFOS 1986).

Discussion

The species was originally described from the Vallesian locality of "Ravin de la Pluie" (KOUFOS 1984, 1986), while later it was found in the Turolian localities of "Ravin des



Text-fig. 17. Logarithmic ratio diagram comparing the skull of *H. macedonicum* from "Pentalophos 1", PNT with *H. macedonicum* from "Prochoma 1", PXM and *H. matthewi*, type from Samos. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 1.
■ *H. macedonicum*, PNT, n=1-2; ◆ *H. macedonicum*, PXM, n=1 (KOUFOS 1987b); ● *H. matthewi*, TYPE, Samos (original measurements).

Zouaves 5", "Prochoma 1" and "Vathylakkos-3" (KOUFOS 1987b, 1987c, 1988) in the lower Axios valley. The studied skulls from PNT are very close to that of *H. macedonicum* from PXM (text-fig. 17). Their lines are parallel but the PNT skull has slightly larger proportions. However, the material from each site includes only one specimen and thus the range of variation are unknown. The differences from the type skull of *H. matthewi* (ABEL 1926) are clear (text-fig. 17). The shorter and narrower muzzle, the shorter nasal cavity, and the shorter preorbital bar distinguish the PNT skull from *H. matthewi*. The high enamel plication of the PNT teeth and their size compare closely with those of *H. macedonicum*.

The available postcranials are very few. Nevertheless, the sole third metatarsal has similar proportions to those of *H. macedonicum* from the various fossiliferous sites of Axios valley (text-fig. 18). Its keel index (SEN et al. 1978) fits quite well with that of the Vallesian hipparions. Taking into account all these similarities the small-sized hipparion from PNT can be attributed to *H. macedonicum*.

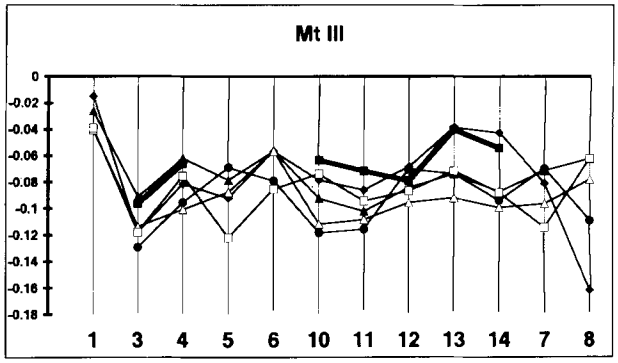
Locality "Ravin des Zouaves 1", RZ_1

The fossiliferous site RZ_1 is situated near the locality of RPl about 200 m apart. Both belong to the same stratigraphic horizon and they have been dated as late Vallesian, MN 10 (BONIS & KOUFOS 1999). The hipparion remains collected from RZ_1 are few including the partial skull and the mandible of a young individual with milk dentition, as well as a few postcranials. Among the latter there is a complete third metatarsal which has similar size and proportions to those of *H. macedonicum* (text-fig. 18). A distal part of a tibia and an isolated second phalanx belong to a larger form of hipparion, however, it is impossible to compare them with the sample from RPl as such material is absent at this locality. The second phalanx is near the maximum values of *H. depereti* from Montredon (EISENMANN 1988), as well as near the mean values for PNT. In any case both second phalanx and distal tibia are shorter than the minimum values for *H. primigenium* of Höwenegg (BERNOR et al. 1996). Taking into account all these features the distal tibia and the second phalanx from RZ_1 are closer to the middle-sized form from RPl and PNT, and must be referred as *H.* aff. *depereti*. The dimensions of the RZ_1 postcranials are given in tab. 15.

Locality "Diavata" DVT

Some hipparion remains from the village of Diavata (text-fig. 1) have been known since the beginning of the century (ANDREWS 1918). The exact site where they were found is unknown The problem of the location of the fossiliferous site, the description, comparison and age of these hipparion remains have been discussed before (KOUFOS 1985, 1995) The fossiliferous site is near the village of Diavata, about 10 km west of Thessaloniki and it is in the Nea Messimvria Formation (KOUFOS 1985). About 2 km away is the locality of "Pentalophos 1" which is in the same formation.

The morphological characters and the dimensions of the Diavata hipparion suggest similarities to the primitive hipparions. Their characters are: medium size, moderate enamel plication, oval protocone with a reduced spur, well-developed lingual hypoconal sinus and double or triple pli caballin. All these features are similar to those of *H. depereti*. Moreover, the dental dimensions of the Diavata hipparion are within the ranges of variation for *H. depereti* from PNT, Montredon and Soblay (text-fig. 10). This similarity with *H. depereti* has been noted by KOUFOS (1985). The limited material and the poor knowledge of the Vallesian hipparions of the Axios valley at that time did not allow a certain determination and the material was referred as *Hipparion* sp. Following the discovery of the new locality of PNT and the study of its hipparions we can say that the Diavata material is similar to the PNT *H.* aff. *depereti* and can be referred to the same name. The age of the Diavata locality together with the age of *Dinocrocuta salonicae* was a problem and was discussed previously



Text-fig. 18. Logarithmic ratio diagram comparing the third metatarsals of *H. macedonicum* from "Pentalophos 1", PNT with *H. macedonicum* from the various localities of Axios valley. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987a). For the numbers of measurements see tab. 10.
■ *H. macedonicum*, PNT, n=1. – KOUFOS 1986, 1987b,c, 1988: ◆ *H. macedonicum*, RPl, n=1; □ *H. macedonicum*, RZ_1, n=1 ● *H. macedonicum*, RZO, n=1-4; Δ *H. macedonicum*, PXM, n=5-8; ▲ *H. macedonicum*, Vathylakkos, n=2-4.

(KOUFOS 1995). The proposed age for the Diavata locality was Vallesian (KOUFOS 1985, 1990, 1995). The similarity of the Diavata hipparion with the PNT *H.* aff. *depereti* now confirms this age.

Conclusions

As described in the introduction, the Vallesian hipparions of Greece are few and their morphology and phylogeny are poorly known. However, in the Axios valley there are three Vallesian localities with quite rich material which has provided interesting data about the Vallesian hipparions of southeastern Europe.

The early Vallesian macromammalian faunas are unknown in the Axios valley or elsewhere in Greece. However, the presence of forms similar to the primitive *H. primigenium* are reported to from the wider area (FORSTÉN 1978; STAESCHE & SONDAAR 1979). During the Vallesian these primitive hipparions were widely distributed in central and western Europe and are reported under various names. However, all of them belong to large-sized forms, with richly plicated upper teeth and short robust metapodials.

Study of the RPl hipparions indicated the presence of *H. primigenium* and of another small-sized hipparion named *H. macedonicum* (KOUFOS 1984, 1986). Although the possible presence of a second hipparion in the late Vallesian locality of Masia del Barbo (Spain) was noted, *H. macedonicum* was the first certain evidence. Later on, two different species were distinguished in the Montredon material, the medium-sized *H. depereti* and a small-sized form similar to *H. macedonicum* (EISENMANN 1988). *H. primigenium* from "Ravin de la Pluie" (RPl) has some differences from the type material from Eppelsheim (Germany). It is slightly smaller with less enamel plication and more slender metapodials (KOUFOS 1986). These differences can be explained by the different palaeoecological conditions in the two areas, savannah-like in southeastern Europe versus forest in nothwestern Europe (BONIS et al. 1992).

The second hipparion from RPl has small size richly to moderately plicated enamel in the upper teeth and elongated slender metapodials, characters which fit well with life in an open environment. *H. macedonicum* is clearly present in all late Vallesian localities of the Axios valley and Chalkidiki (KOUFOS 1990; KOUFOS et al. 1991), but it is also present in the early Turolian (KOUFOS 1990). Until 1984 the small-sized hipparions were reported from the Turolian only, and *H. macedonicum* from Axios was the first evidence for their presence at least in the late Vallesian. Small-sized hipparions are also noted from the late Miocene of neighbouring areas (Bulgaria, Skopia) (FORSTÉN 1978, 1989) but as the collections are old and mixed there are no clear data about their ages. The species *H. macedonicum* has been included in *H. matthewi* by FORSTÉN (1989), while she considered that the RPl fauna is possibly younger than Vallesian. However, the age of RPl was well documented by clear faunal data (KOUFOS 1980, 1986, BONIS et al. 1988). The late Vallesian age of the RPl locality was later confirmed by more faunal evidence and recently by magnetostratigraphy (KOUFOS 1990; BONIS et al 1992; BONIS & KOUFOS in press; SEN et al., in press).

On the other hand, the specific identity of *H. macedonicum* is clearly demonstrated in the articles of KOUFOS (1986, 1987b, 1987c, 1990, 1998) and BERNOR et al. (1996). Based on Axios valley material from stratigraphically certain horizons and from the type material of *H. macedonium* and *H matthewi* the differences between the two species are summarised in tab. II.

The possible presence of a third medium-sized hipparion in the late Vallesian was noted in the material from "Ravin de la Pluie" (KOUFOS 1986). The sole known specimen (piece of metatarsal) was a weak argument for the presence of a medium-sized hipparion in the late Vallesian (KOUFOS 1990). However, newly unearthed material from RPl, as well as the material from PNT, has confirmed the presence of a third hipparion in the Vallesian faunas of the Axios valley.

KOUFOS (1990) has supported the idea that, according to their size, three distinct evolutionary branches of hipparions have appeared in the Vallesian. All originated from the primitive stock of the early Vallesian large-sized forms. According to WOODBURNE et al. (1996) the lowest stratigraphic datum of *Hipparion* can be estimated as being between 10.5-11.0 Ma. The beginning of the late Vallesian (MN10) has been dated to 9.5 Ma (STEININGER et al. 1996) or 9.7 Ma (SEN 1997). Taking into account these recent datings we can postulate that the hipparions had a rapid evolution after their arrival and dispersion in Eurasia. This evolution begun at the end of the early Vallesian and continued in the late Vallesian and into the Turolian with several species represented. The locality of "Pentalophos 1" seems to confirm this idea. The fauna of "Pentalophos 1" is quite exceptional and different from the others known from the Vallesian of the Axios valley, however, some faunal and stratigraphical data allow an age determination. The locality is situated in the Nea Messimvria Formation whose upper parts are considered as late Vallesian in age (BONIS et al. 1988; BONIS & KOUFOS 1999). Recent magnetostratigraphic studies suggest for the faunas found in the upper layers of Nea Messimvria Formation (localities "Xiro-

Tab. II. Differences of *H. macedonicum* and *H. matthewi*.

	H. macedonicum Type	*H. matthewi* Type
Muzzle	Relatively long - wide	Short-narrow
Nasal cavity	Elongated	Short
Enamel plicaiton	Rich-Moderate-Deep plis	Simple-Shallow plis
Pli caballin	Simple-double	Simple
Lingual hypoconal sinus	Present	Absent
Parastylid	Strong	Moderate
Enamel in the fliexid's borders	Slightly plicated or crenulated	Simple
Pli caballinid	Small present in the premolars	Absent
Metapodials	Long-Slender	Long-Slender

chori 1", "Ravin de la Pluie" and "Ravin des Zouaves 1") an age between 9.6-9.3 Ma (SEN et al., in press). These dates support the late Vallesian age of the upper part of the Nea Messimvria Formation.

The presence in PNT of a giraffid which has similarities with *Decennatherium* but is different from *D. pachecoi* (GERAADS 1989) can also be considered as an indication of a Vallesian age. It is smaller and more primitive than *Decennatherium* sp. from RPl and could suggest for PNT an age older than that of RPl. The aardwark found in PNT is similar to *Orycteropus pottieri* found in the Vallesian levels of Middle Sinap Tepe in Turkey (BONIS et al. 1994). The presence of *Dinocrocuta gigantea* reinforces the Vallesian age, as these large percrocutas are known from Vallesian sites as Bou Hanifia and Yassioren (KOUFOS 1995). The bovids from Pentalophos are different from those of the other known Vallesian localities of the Axios valley. However, the presence of a primitive *Protoryx* and of *Ouzecerus* together with the absence of *Tragoportax* are strong indications for a Vallesian age (BOUVRAIN 1997). The presence of *H. macedonicum* and *H.* aff. *depereti* does not contradict the Vallesian age of PNT, as both have been found in late Vallesian (MN 10) localities and their presence in PNT reinforces its Vallesian age. Considering all the above mentioned biochronological data the PNT fauna can be dated as Vallesian, while the giraffids and bovids suggest an age older than that of RPl. As the RPl fauna is dated to 9.6-9.3 Ma (SEN et al., in press) then PNT must be slightly older. If we accept the MN 9 / MN 10 boundary as being 9.7±0.1 Ma (SEN 1997) or 9.5 Ma (STEININGER et al. 1996) then the PNT fauna can be considered as belonging to the upper MN 9 or to the lower MN 10. Such an age fits quite well with the evolutionary pattern of hipparions proposed above.

During the middle Vallesian (~10 Ma) the primitive stock of *H. primigenium* which had arrived and dispersed in the Mediterranean evolved rapidly and the three main branches of hipparions appeared. These branches remained during the late Vallesian and then they diversified in the Turolian. Each branch has been adapted to the local palaeoecological conditions and thus different forms appeared in the various geographic areas. The lower Axios valley material from the Vallesian localities RPl, RZ_1 and PNT demonstrates clearly this stage of hipparion's evolution. Unfortunately, the other known Vallesian locality of the Axios "Xirochori 1" (XIR) has not yet yielded hipparions except for a few teeth which cannot provide certain data for comparison. As the excavations will be continued more material will be unearthed providing new data about the Vallesian hipparions and their relationships.

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SKULL	*Hipparion* aff. *depereti*					*Hipparion macedonicum*				
	n	mean	min	max	s	n	mean	min	max	s
1	2	119.50	116.5	122.5	4.24	2	112.00	105.0	119.0	9.90
2	1	124.50	124.5	124.5		2	98.50	94.0	103.0	6.36
7	3	83.07	78.4	88.8	5.28	2	70.15	68.0	72.3	3.04
8	2	75.15	70.3	80.0	6.86	2	60.60	59.1	62.1	2.12
9	2	156.25	154.0	158.5	3.18	2	129.65	126.2	133.1	4.88
12	-	-	-	-	-	1	32.60	-	-	-
13	1	49.00	49.0	49.0	-	1	51.50	-	-	-
14	1	27.00	27.0	27.0	-	1	27.50	-	-	-
15	2	54.00	51.0	57.0	4.24	1	52.50	-	-	-
23	-	-	-	-	-	1	333.50	-	-	-
25	1	91.50	91.5	91.5		1	94.00	-	-	-
28	-	-	-	-	-	1	40.80	-	-	-
29	-	-	-	-	-	1	59.00	-	-	-
30	1	125.00	125.0	125.0	-	1	136.50	-	-	-
31	1	180.00	180.0	180.0	-	1	151.00	-	-	-
32	2	40.45	39.4	41.5	1.48	1	44.00	-	-	-
33	2	64.00	57.0	71.0	9.90	2	59.40	56.8	62.0	3.68
34	-	-	-	-	-	2	52.35	51.2	53.5	1.63
35	1	53.00	53.0	53.0	-	2	37.10	36.4	37.8	0.99
36	1	28.00	28.0	28.0	-	2	29.00	-	-	-
37	-	-	-	-	-	2	45.85	44.2	47.5	2.33
38	1	76.85	68.0	85.7	12.52	2	68.15	66.3	70.0	2.62

Tab. 1. *Hipparion* aff. *depereti* and *H. macedonicum*, "Pentalophos 1", PNT, Macedonia, Greece, skull.

1. Muzzle length: Prosthion – middle of the line connecting the anterior borders of P^2; 2. Palatal length middle of the line connecting the anterior borders of P^2 to anterior border to choanae; 8. Molar length (alveolar); 9. Toothseries length (alveolar); 12. Maximal breadth of choanae; 13. Palatal breadth between $P^4$and M^1; 14. Minimal muzzle breadth; 15. Muzzle breadth: breadth between the posterior border of I^3; 23. Anterior ocular line: prosthion – most external point of the posterior border of the orbit; 25. Facial height: height of the skull in front of P^2; 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 berween the back of the preorbital fossa and the foramen infra-orbitale; 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 foramen infra-orbitale above the alveolar border; 38. Height of the back of the preorbital fossa above the alveolar border.

Tab. 2. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, mandible.
1. Maximal length: posterior point of the articular condyle – anterior point situated between the two I_1 (in projection); 2. Muzzle length: middle of the line connecting the anterior borders of P_2 to a point situated between the two I_1; 3. Premolar length (alveolar); 4. Molar length (alveolar); 5. Toothseries length (alveolar); 6. Distance from posterior end of M_3 – posterior border of the vertical ramus; 7. Muzzle breadth: breadth at the posterior borders of I_3; 8. Height articular conduyle – base of the horizontal ramus; 9. Height incisura mandiblae – base of the horizontal ramus; 10. Height of the jaw behing M_3; 11. Idem between P_4 and M_1; 12. Idem in front of P_2; 13. Symphysial length; 14. Minimal breadth of the symphysis.

MANDIBLE	n	mean	min	max	s
1	-	-	-	-	-
2	1	117.00	-	-	-
3	3	71.17	68.0	73.0	2.75
4	2	70.95	70.7	71.2	-
5	2	142.00	140.0	144.0	-
6	-	-	-	-	-
7	1	53.00	-	-	-
8	-	-	-	-	-
9	-	-	-	-	-
10	2	88.50	87.0	90.0	-
11	2	66.50	62.0	71.0	-
12	3	49.67	48.0	51.0	1.53
13	1	78.00			
14	2	21.25	20.5	22.0	-
15	-	-	-	-	-
16	1	92.00	-	-	-

Tab. 3. *Hipparion* aff. *depereti,* "Pentalophos 1",, PNT, Macedonia, Greece, upper cheek teeth.
L_o=occlusal length, B_o=occlusal breadth, L_p=protocone length, B_p=protocone breadth, EF=enamel formula, H=height.

		n	mean	min	max	s			n	mean	min	max	s
p2	L_o	3	33.33	31.5	36.7	2.92	M1	L_o	3	21.07	19.5	23.0	1.78
	B_o	3	23.67	23.0	25.0	1.15		B_o	4	22.60	21.7	23.6	0.80
	L_p	3	7.93	7.1	8.7	0.80		L_p	5	7.56	7.0	8.2	0.52
	B_p	3	5.50	5.0	6.0	0.50		B_p	3	5.07	4.7	5.5	0.40
	EF	3	3.6, 7, 5, 1 / 2					EF	2	1.5, 7.5, 6.5, 1 / 2			
	H	1	17.00	-	-	-		H		-	-	-	-
p3	L_o	5	23.98	22.5	26.2	1.49	M2	L_o	5	23.18	19.8	26.0	2.75
	B_o	5	24.74	23.4	26.0	1.11		B_o	6	22.53	22.0	23.5	0.51
	L_p	5	7.64	7.2	8.0	0.38		L_p	6	7.97	7.5	8.5	0.35
	B_p	3	5.80	4.9	6.3	0.78		B_p	4	4.33	3.7	5.3	0.69
	EF	5	1.2, 5.4, 4.2, 1 / 1.4					EF	4	4.6, 6, 4.6, 1.3 / 2			
	H	-	-	-	-	-		H		-	-	-	-
p4	L_o	4	23.38	22.2	25.3	1.42	M3	L_o	5	23.52	21.6	26.0	1.88
	B_o	3	25.33	24.7	26.3	0.85		B_o	5	19.94	17.7	21.5	1.39
	L_p	5	7.98	7.5	8.2	0.29		L_p	4	7.63	7.1	8.2	0.56
	B_p	3	5.97	4.7	6.7	1.10		B_p	2	4.70	3.7	5.7	-
	EF	3	1.3, 6, 6, 1 / 2.3					EF	2	2, 8.5, 5.5, 2 / 2.5			
	H	-	-	-	-	-		H		-	-	-	-
p3,4	L_o	1	25.5	-	-	-	M1,2	L_o	1	-	-	-	-
	B_o	1	24	-	-	-		B_o	1	22.5	-	-	-
	L_p	1	7.1	-	-	-		L_p	1	7.8	-	-	-
	B_p	1	4.8	-	-	-		B_p	1	4.5	-	-	-
	EF	1	6, 8, 7, 2 / 2					EF	1	0, 8, 4, 1 ,/ 2			
	H	1	23	-	-	-		H	-	-	-	-	-

Tab. 4. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, lower cheek teeth.
L_o=occlusal length, B_o ant=anterior occlusal breadth, B_o post=posterior occlusal breadth, L_{prfl}=preflexid length, L_{ptfl}=postflexid length, EF=enamel formula, H=height.

L. TEETH		n	mean	min	max	s			n	mean	min	max	s
P_2	L_o	4	26.75	26.0	28.5	1.19	M_1	L_o	7	20.61	19.5	21.8	0.78
	B_o ant	3	11.27	10.8	12.0	0.64		B_o ant	7	12.67	11.0	14.0	0.92
	B_o post	4	12.15	5.8	15.0	4.28		B_o post	6	11.80	10.5	16.0	2.09
	L_{prfl}	3	5.70	5.5	6.0	0.26		L_{prfl}	7	5.67	5.2	6.6	0.50
	L_{ptfl}	3	7.07	6.2	8.3	1.10		L_{ptfl}	7	6.90	5.5	8.5	1.13
	EF	1	0, 0, 0 / 0					EF	5	0.4, 0.2, 0 / 0.2			
	H	-	-	-	-	-		H	-	-	-	-	-
P_3	L_o	4	22.38	21.7	23.0	0.56	M_2	L_o	6	21.57	21.2	22.0	0.35
	B_o ant	4	14.63	14.0	15.4	0.58		B_o ant	5	11.90	11.3	12.3	0.47
	B_o post	4	14.90	14.0	15.5	0.64		B_o post	5	11.56	9.8	15.0	1.99
	L_{prfl}	3	6.60	5.0	8.0	1.51		L_{prfl}	6	5.87	5.0	6.7	0.59
	L_{ptfl}	3	6.80	4.0	8.8	2.50		L_{ptfl}	6	5.80	4.5	8.0	1.24
	EF	2	1, 0, 0 / 0.5					EF	4	0.5, 0.2, 0 / 0.2			
	H	-	-	-	-	-		H	-	-	-	-	-
P_4	L_o	7	22.23	21.0	23.5	0.87	M_3	L_o	7	26.70	23.0	28.3	1.78
	B_o ant	6	14.30	12.0	15.6	1.28		B_o ant	7	10.34	9.0	11.0	0.76
	B_o post	6	13.02	10.5	14.0	1.30		B_o post	7	9.03	8.0	9.6	0.57
	L_{prfl}	5	6.52	5.6	7.7	0.83		L_{prfl}	7	6.34	5.4	7.6	0.82
	L_{ptfl}	5	7.84	5.0	11.3	2.73		L_{ptfl}	7	7.49	6.1	8.7	0.90
	EF	3	1, 0.3, 0 / 0.3					EF	5	0.4, 0.6, 0.2 / 0.4			
	H	-	-	-	-	-		H	-	-	-	-	-
$P_{3,4}$	L_o	1	24.00	-	-	-	$M_{1,2}$	L_o	2	23.15	22.8	23.5	-
	B_o ant	1	13.00	-	-	-		B_o ant	2	10.35	10.0	10.7	-
	B_o post	1		-	-	-		B_o post	2	9.40	9.3	9.5	-
	L_{prfl}	1	11.50	-	-	-		L_{prfl}	1	7.80	-	-	-
	L_{ptfl}	1	6.50	-	-	-		L_{ptfl}	1	9.50	-	-	-
	EF	1	1, 1, 0 / 1					EF	1	0,1,0 / 0			
	H	-	-	-	-	-		H	1	46.00	-	-	-

Tab. 5. *Hipparion macedonicum,* "Pentalophos 1", PNT, Macedonia, Greece, upper cheek teeth. Abbreviations as in tab. 3.

U. TEETH		n	mean	min	max	s			n	mean	min	max	s
P^2	L_o	12	28.73	26.0	31.0	1.66	M^1	L_o	8	20.84	17.5	23.5	2.27
	B_o	12	20.53	17.4	23.0	1.49		B_o	8	20.30	19.2	21.2	0.73
	L_p	11	7.04	6.0	8.5	0.74		L_p	8	6.81	6.2	7.3	0.34
	B_p	11	4.84	4.0	6.8	0.93		B_p	8	4.20	3.5	5.5	0.77
	EF	11	3.4, 4.2, 2.2, 1.1 / 1.3					EF	6	2.4, 5.4, 4.1, 0.9 / 1.4			
	H	1	35.00	-	-	-		H	-	-	-	-	-
P^3	L_o	8	23.53	20.7	25.3	1.74	M^2	L_o	6	20.67	18.0	23.0	2.10
	B_o	8	22.50	22.0	23.3	0.48		B_o	7	19.23	18.0	20.8	1.08
	L_p	8	7.14	6.5	7.5	0.32		L_p	7	6.59	6.0	6.8	0.28
	B_p	8	4.45	3.7	5.7	0.81		B_p	7	4.47	3.5	5.7	0.93
	EF	8	2.7, 3.7, 4.6, 1 / 1					EF	7	2.4, 4.3, 2.7, 1 / 1			
	H	-	-	-	-	-		H	-	-	-	-	-
P^4	L_o	6	22.72	20.9	25.0	1.72	M^3	L_o	3	20.63	18.2	22.0	2.11
	B_o	5	22.42	22.0	22.7	0.31		B_o	3	16.57	13.3	18.2	2.83
	L_p	4	7.15	6.8	7.5	0.40		L_p	3	6.53	6.5	6.6	0.06
	B_p	4	4.60	3.5	5.9	1.28		B_p	3	4.00	2.5	5.0	1.32
	EF		1.8, 5, 2, 1.1 / 1					EF	2	0, 6, 4.5, 2.5/0			
	H	-	-	-	-	-		H	-	-	-	-	-
$P^{3,4}$	L_o	1	23.50	23.5	23.5	-	$M^{1,2}$	L_o	5	20.92	18.5	22.5	1.54
	B_o	1	22.20	22.2	22.2	-		B_o	5	20.26	16.0	23.0	3.09
	L_p	1	7.60	7.6	7.6	-		L_p	4	6.65	6.3	7.3	0.45
	B_p	1	4.00	4.0	4.0	-		B_p	4	4.70	4.1	5.3	0.55
	EF	1	4, 8, 3, 2 / 2			-		EF	4	2.2, 6, 6, 1.5 / 2			
	H	-	-	-	-	-		H	1	51.00	-	-	-

Tab. 6. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, radius.
1. Maximal 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.

Radius	*Hipparion* aff. *depereti*					*H. macedonicum*	
	n	mean	min	max	s	n	
1	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-
3	-	-	-	-	-	1	28.0
4	-	-	-	-	-	1	20.3
5	1	64.00	-	-	-	1	53.5
6	1	34.00	-	-	-	1	27.3
7	2	64.50	62.0	67.0	-	1	57.2
8	2	47.50	45.0	50.0	-	-	-
9	2	27.30	26.0	28.6	-	-	-
10	2	54.50	52.0	57.0	-	-	-
11	2	19.20	18.1	20.3	-	-	-
12	2	11.05	10.5	11.6	-	-	-

Tab. 7. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, third metacarpal.
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 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; 16. Diameter for the articular facet for Mc_{II}.

Mc_{III}	*Hipparion* aff. *depereti*				
	n	mean	min	max	s
1	1	193.00	-	-	-
2	1	189.00	-	-	-
3	1	29.50	-	-	-
4	-	-	-	-	-
5	-	-	-	-	-
6	1	26.00	-	-	-
7	-	-	-	-	-
8	1	9.50	-	-	-
9	-	-	-	-	-
10	3	36.50	36.0	37.0	0.71
11	3	33.50	33.0	34.0	0.71
12	3	25.25	25.0	25.5	0.35
13	3	20.65	19.5	21.8	1.63
13a	3	21.35	21.0	21.7	0.49
14	3	23.35	22.7	24.0	0.92
15	-	-	-	-	-
16	-	-	-	-	-

Tab. 8. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, calcaneum.
1. Maximal length; 2. Maximal diameter of the medial condyle; 3. Breadth of the trochlea (at the apex of the condyle); 4. Maximal breadth; 5. Distal articular breadth; 6. Distal articular breadth; 7. Maximal medial depth.

CALCANEUM	*Hipparion* aff. *depereti*				
	n	mean	min	max	s
1	1	101.0	-	-	-
2	2	61.75	57.0	66.5	-
3	3	17.97	16.7	20.0	1.78
4	2	28.10	26.0	30.2	-
5	2	44.10	42.7	45.5	-
6	2	43.50	41.0	46.0	
7	3	44.83	44.0	46.0	1.04

Tab. 9. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, astragalus.
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.

ASTRAGALUS	*Hipparion* aff. *depereti*				
	n	mean	min	max	s
1	2	50.00	50.0	50.0	-
2	2	50.40	50.3	50.5	-
3	2	24.50	24.0	25.0	-
4	1	52.50	-	-	-
5	1	39.70	-	-	-
6	2	26.95	26.7	27.2	-
7	2	42.25	42.0	42.5	-

Tab. 10. *Hipparion* aff. *depereti* and *H. macedonicum,* "Pentalophos 1", PNT, Macedonia, Greece, third metatarsal.
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.

Mt_{III}	*Hipparion* aff. *depereti*					*H. macedonicum*	
	n	mean	min	max	s	n	mean
1	3	238.83	234.0	241.5	4.19	-	-
2	3	233.17	227.5	236.0	4.91	1	225
3	4	26.13	24.8	27.5	1.21		-
4	4	24.08	22.3	26.0	1.57	1	20.5
5	7	36.94	34.7	37.7	1.12	1	22.8
6	6	28.33	26.3	30.0	1.40	-	-
7	7	33.79	31.0	35.7	1.78	-	-
8	7	8.43	7.5	9.4	0.75	-	-
9	4	4.00	2.8	4.8	0.86	-	-
10	5	36.56	34.7	38.0	1.50	1	29
11	7	34.10	32.6	35.0	0.87	1	27.5
12	7	27.79	26.0	29.0	0.98	1	23.5
13	7	22.39	21.0	23.0	0.72	1	20.3
13a	7	22.71	21.4	25.2	1.23		
14	7	25.43	23.3	26.3	1.02	1	22.7
15	4	112°	107°	115°	3.40	1	97°

Tab. 11. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, first phalanx.
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; 9. Minimal length of the trigonum phalangis; 10. Medial supratuberosital length; 11. Lateral supratuberosital length; 12. Medial infratuberosital length; 13. Lateral infratuberosital length.

Ph I	*Hipparion* aff. *depereti*						
	n	mean	min	max	s	n	
1	5	56.40	54.0	58.5	1.60	1	56.2
2	5	52.46	51.6	54.0	1.02	1	50.5
3	5	25.46	24.3	26.5	0.84	1	27.5
4	5	36.30	35.0	38.0	1.12	1	37.0
5	5	27.84	25.3	30.1	1.90	1	29.7
6	4	29.55	27.7	31.2	1.81	1	30.5
7	4	29.43	28.2	30.5	1.03	1	31.0
8	5	17.58	16.0	19.5	1.36	1	17.5
9	5	16.90	15.0	20.0	1.92	1	
10	5	41.74	40.0	44.3	1.72	1	40.0
11	5	43.10	41.5	45.0	1.39	1	43.0
12	5	14.66	12.6	16.3	1.58	1	16.2
13	5	13.30	11.5	14.8	1.32	1	13.2
	Manus					Pedis	

Tab. 12. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, second phalanx.
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.

Ph II	*Hipparion* aff. *depereti*			
	n	mean	min	max
1	2	35.75	34.5	37
2	2	28.15	27.3	29
3	2	28.5	28	29
4	2	37.1	36.2	38
5	2	25.15	24.8	25.5
6	2	32	32	32
7	2	20.5	20	21
	Manus			

Tab. 13. *Hipparion* aff. *depereti,* "Pentalophos 1", PNT, Macedonia, Greece, third phalanx.
1. Length from the posterior edge of the articular surface to the tip of the phalanx; 2. Anterior length; 3. Maximal breadth; 4. Articular breadth; 5. Articular depth; 6. Maximal height; 7. Angle between the sole and the dorsal line; 8. Circuference of the sole.

Ph III	*H. aff.depereti*
1	46
2	50
3	-
4	48.5
5	19.4
6	35
7	32.5
8	-
	Manus

Tab. 14. *Hipparion primigenium, Hipparion* aff. *depereti* and *Hipparion macedonicum,* "Ravin de la Pluie", RPl, Macedonia, Greece.

Mt III	*H.H. primigenium*			*H. aff. depereti*		*H. macedonicum*
	RPI-3	RPI-39	RPI-11	RPI-61	RPI-45	RPI-38
1	-	252	-	222.3	-	239
2	-	246	-	218	-	235
3	27.5	29	-	24.7	-	19.5
4	25.6	26.2	-	25.3	-	22
5	40.2	39	-	35	-	30
6	35.1	34.2	-	29.2		25
7	35.7	34.5	-	34	-	28.5
8	8.5	-	-	7	-	6.2
9	5	-	-	4.1	-	4.5
10	-	39	41.5	35	35.6	28
11	-	34	35.5	34.2	34	26.6
12	-	30.5	31	28.6	26.7	24.1
13	-	25	24.7	22.2	22	20.4
13a	-	24.8	24.5	22.7	22.5	20.5
14	-	27.7	28	24.1	24.8	23.3

Tab. 15. *Hipparion macedonicum* (third metatarsal) and *Hipparion* aff. *depereti* (tibia and second phalanx) "Ravin de Zouaves 1", RZ_1, Macedonia, Greece.

RZ1	1	2	3	4	5	6	7	8	9	10	11	12	13	13a	14	15
Mt_{III}	226	220	19.5	22.3	28	23.4	26.4	7.8	3.2	28.3	26.1	23.1	18.9	19.0	21.0	126
Tibia	-	-	-	-	-	-	63.5	40	-	-	-	-	-	-	-	-
Ph_{II}	39.5	30	29.7	38.3	26	30.7	20	-	-	-	-	-	-	-	-	-

Plate 1

Figs 1-3. *Hipparion* aff. *depereti* SONDAAR 1974
"Pentalophos 1", PNT, Macedonia, Greece.

1. Frontal part of the skull, PNT-137; lateral view. 1/2 nat. size.
2. Right frontal part of the skull, PNT-123; lateral view. 2/3 nat. size.
3. Muzzle and part of the left maxilla, PNT-116; occlusal view. 3/4 nat. size.

1

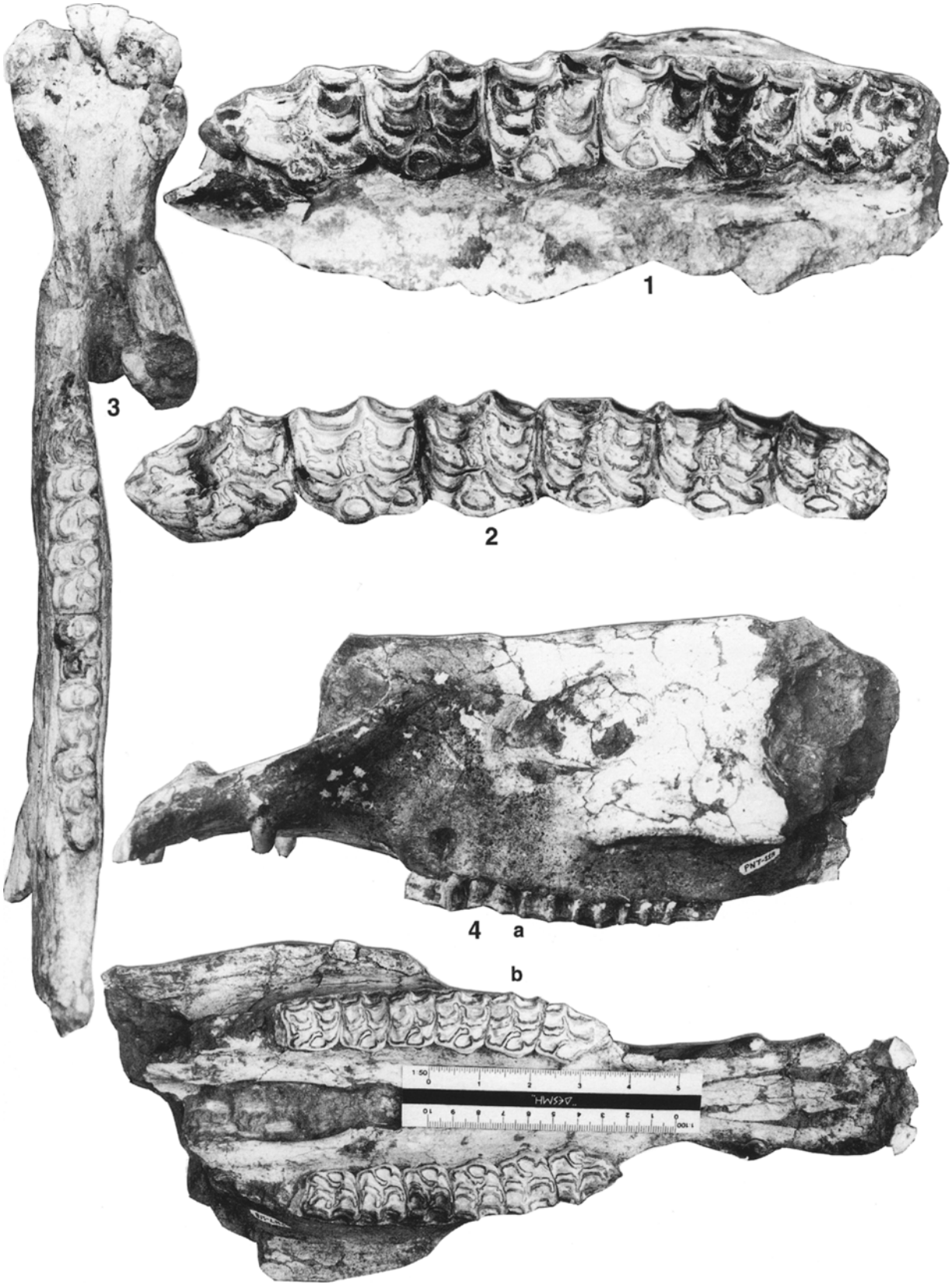
2

3

Plate 2

Figs 1-4. *Hipparion* aff. *depereti* SONDAAR 1974
"Pentalophos 1", PNT, Macedonia, Greece.

1. Maxillary fragment with dp^1 – M^3 sin, PNT-138; occlusal view. Nat. size.
2. Left tooth row of the skull, PNT-123; occlusal view. Nat. size.
3. Mandible with P2- m3 sin, PNT-117; occlusal view. 2/3 nat. size
4. Frontal part of the skull, PNT-118. – a) lateral and b) occlusal view. 1/2 nat. size.



G. D. KOUFOS: New material of Vallesian Late Miocene hipparions (Mammalia, Perissodactyla) from the lower Axios Valley, Macedonia, Greece

Plate 3

Figs 1. *Hipparion macedonicum* KOUFOS 1984
"Pentalophos 1", PNT, Macedonia, Greece.
1. Frontal part of the skull, PNT-118. – a) lateral and b) occlusal view. 1/2 nat. size.

Fig. 2. *Hipparion* aff. *depereti* SONDAAR 1974
"Pentalophos 1", PNT, Macedonia, Greece.
2. Left anterior leg, PNT-57; anterior view. 1/2 nat. size.

1

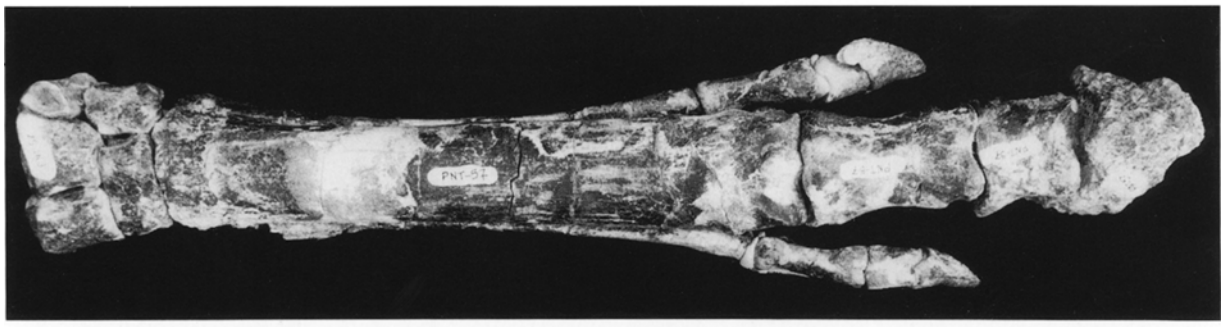


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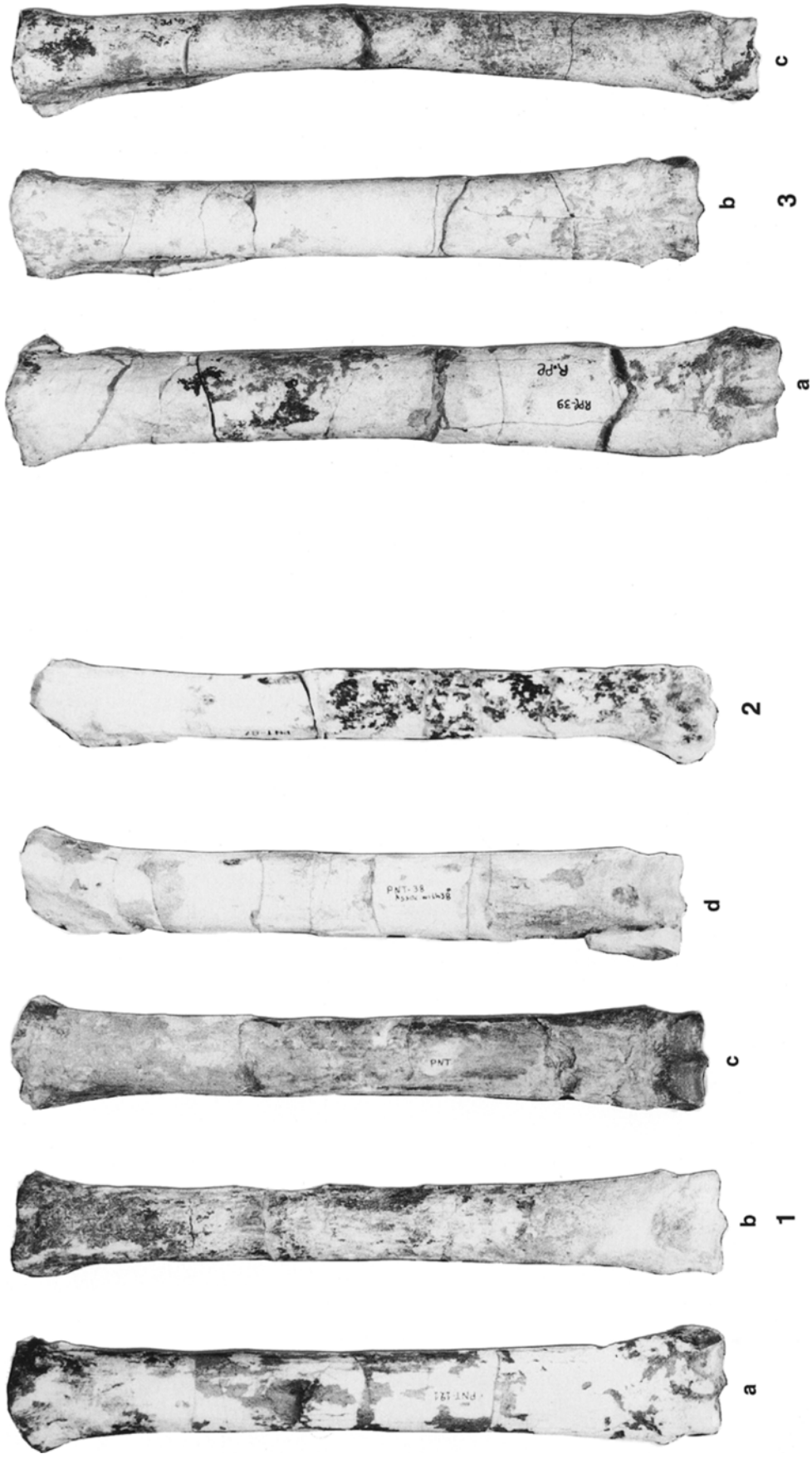
Plate 4

Figs 1. *Hipparion* aff. *depereti* SONDAAR 1974
"Pentalophos 1", PNT, Macedonia, Greece.
1. Third metatarsals. – a. PNY-121, b. PNT-19, c. PNT-150 and d. PNT-38; anterior view. 1/2 nat. size.

Fig. 2. *Hipparion macedonicum* KOUFOS 1984
"Pentalophos 1", PNT, Macedonia, Greece.
2. Third metatarsal, PNT-87, anterior view. 1/2 nat. size.

Figs 3. Third metatarsals; "Ravin de la Pluie", RPl, Macedonia, Greece.
3a. *Hipparion primigenium* (VON MEYER 1829)
RPl-39, anterior view. 1/2 nat. size.
3b. *Hipparion* aff. *depereti* SONDAAR 1974
RPl-61, anterior view. 1/2 nat. size.
3c. *Hipparion macedonicum* KOUFOS 1984
RPl-38, anterior view. 1/2 nat. size.



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