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Hipparion macedonicum revisited: New data on evolution of hipparionine horses from the Late Miocene of Greece

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The new expeditions to the Axios Valley (Macedonia, Greece) provided a new set of fossils from the various localities. Among the material collected from the Late Miocene hominoid bearing mammal locality Ravin de la Pluie (RPl) were some remains of *Hipparion macedonicum*, which was originally described from this locality. The most important is the skull and associated mandible, the first from the type locality. The new material is compared with the previously collected material of the taxon from the Vallesian and Turolian levels of Greece, as well as with corresponding material from Eurasia. The RPl skull is compared with the type skull of *H. matthwei*, a taxon, which several times has been referred as synonym to *H. macedonicum*. The comparison indicated several differences which distinguish the two species. *Hipparion macedonicum* has a continuous stratigraphic range from the Vallesian to middle Turolian and it is possibly present in the late Turolian. The comparison of the chronologically different samples of *H. macedonicum* indicates that the Vallesian form of *H. macedonicum* has larger size, shorter narial opening, longer tooth rows, rich enamel plication, more elongated and narrow plis, more robust metapodials and less running legs than the Turolian form. Some of the morphological changes are related to the habitat, which was more closed, warmer and wetter in the Vallesian than Turolian.

Key words: Mammalia, Equidae, systematic, evolution, palaeoecology, Miocene, Greece.

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Introduction

The Late Miocene mammal locality Ravin de la Pluie (RPl, Axios Valley, Macedonia, Greece) is well-known because of the presence of the hominoid primate *Ouranopithecus macedoniensis*. The RPl fauna is quite rich including mainly mammals (Koufos 2006b, 2012a, b, and references cited therein) and suggesting correlation to the late Vallesian (MN 10) with a magnetostratigraphically estimated age of ~9.3 Ma (Koufos 2013 and references cited therein). The hipparions, in comparison to the Turolian localities, are rare in the RPl sample and classified to two species: *H.* cf. *H. sebastopolitanum* Borissiak, 1914 and *H. macedonicum* Koufos, 1984. The first taxon was described earlier as a form of *H. primigenium* by Koufos (1986, 2000) but recently Vlachou (2013) transferred it to *H.* cf. *H. sebastopolitamum*; the other taxon, *H. macedonicum,* was originally described from RPl (Koufos 1984, 1986). During the last expeditions in Axios Valley new material of *H. macedonicum* has been unearthed from RPl, including mainly mandibular remains but also the first skull, providing new information about the cranial morphology of *H. macedonicum* from the type locality. The new material of *H. macedonicum* from RPl is described and compared with the known material of the taxon from other localities in this article, providing information for its morphology, relationships, evolution, as well as its stratigraphic and geographic distribution.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York; LGPUT, Laboratory of Geology and Palaeontology, University of Thessaloniki, Greece.

Locality abbreviations.—AKK, Akkaşdağı, Turkey; DYTI, localities of Dytiko 1, 2, 3, Axios Valley, Greece; DKO, Dytiko 3, Axios Valley, Greece; KTA-B, Kemiklitepe-A, B, Turkey; KRY, Kryopigi, Greece; MTLA, Mytilinii-1A, Samos, Greece; MYT, Mytilinii-3, Samos, Greece; NIK, Nikiti-2, Greece; NKT, Nikiti-1, Greece; PER, Perivolaki, Greece; PIK, Pikermi, Greece; PXM, Prochoma 1, Axios Valley, Greece; Q1, Quarry 1, Samos, Greece; Q5, Quarry 5, Samos, Greece; RPl, Ravin de la Pluie, Axios Valley, Greece; RZ1, Ravin des Zouaves 1 , Axios Valley, Greece; RZO, Ravin des Zouaves 5, Axios Valley, Greece; SIN, Sinap, Turkey; TAR, Taraklia, Ukraine; PAV, Pavlodar, Kazakhstan; PNT, Pentalophos 1, Greece; VATH, localities of Vathylakkos, Greece.

Other abbreviations.—DAP, antero-posterior diameter; HS, habitat score; KI, Keel Index; Mc_{III} , third metacarpal; Mt_{III}, third metatarsal; PCA, principal component analysis; POF, preorbital fossa; POB, preorbital bar (length preorbital fossa–anterior orbit); SI, Slenderness Index.

Material and methods

The studied material, except the new collection, includes also the old one described earlier (Koufos, 1984, 1986); all studied material is housed in the Laboratory of Geology and Palaeontology, University of Thessaloniki (LGPUT). The biometric study of the material follows the recommendations of Eisenmann et al. (1988); all the measurements are given in mm with an accuracy of 0.1 mm. Upper and lower case letters denote upper and lower teeth, respectively. The software PAST (Hammer et al. 2001) used for the principal component analysis (PCA) and box-plot diagrams and Office Excell 2010 for Simpson's log-ratio diagrams. All metrical data for the Greek material, as well as for those from Kemiklitepe A–B and Akkaşdaği are from author's database; those for *Hipparion elegans* and *H. moldavicum* are taken from www.vera-eisenmann.com. *Hipparion mediterraneum* from Pikermi was used as reference species in the Simpson's log-ratio diagrams and the measurements were taken from Koufos (1987).

Systematic palaeontology

Family Equidae Gray, 1821

Genus *Hipparion* de Christol, 1832

Hipparion macedonicum Koufos, 1984

Figs. 1–3.

1980 *Hipparion* sp.; Koufos 1980: 292.
1984 *H. macedonicum*; Koufos 1984: 386, figs. 2, 3.
1986 *H. macedonicum* Koufos, 1984; Koufos 1986: 71, pls. 1–3.
2013 *H. macedonicum* Koufos, 1984; Vlachou 2013: 318.

Type material: Holotype: mandible with i1–m3 dex and i1–m2 sin, LGPUT RPl-21 (Fig. 3A). Paratype: skull and associated mandible, LGPUT RPl-125 (Figs. 1, 3C).

Type locality: Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece.

Type horizon: Late Vallesian, MN 10; Late Miocene; GPTS = ~9.3 Ma (Koufos 2013 and references cited therein).

Material.—The given list includes only the new undescribed previously specimens. Skull and associated mandible, LGPUT RPl-125; right frontal part of the skull with the muzzle and the tooth row, LGPUT RPl-142; left maxillary fragment with P3–M2, LGPUT RPl-287; partial mandible with i1–m2 dex and sin, LGPUT RPl-286; partial mandible with p2–m2 dex and p2–m3 sin, LGPUT RPl-290; left mandibular fragment with p2–m3, LGPUT RPl-281; right mandibular fragment with p2–m3, LGPUT RPl-282; left mandibular fragment with p2–p4, LGPUT RPl-291; proximal part of Mc_{III}, LGPUT RPl-285; proximal part of tibia, LGPUT RPl-284; distal epiphysis of tibia, LGPUT RPl-288; distal part of Mt_{III}, LGPUT RPl-292.

Emended diagnosis.—Small size; relatively elongated and narrow muzzle; shallow narial opening, the nasal notch is retracted above the middle of the C-P2 diastema; elliptical, shallow, antero-posteriorly oriented, not pocketed posteriorly with moderately developed margin, and open anteriorly POF; moderate POB; infraorbital foramen encroaches upon the antero-ventral border of the POF; moderate enamel plication in the upper cheek teeth with narrow and deep plis; simple-double pli caballin; elliptical-oval and isolated protocone; often connection of the fossettes; very rare presence of a weak lingual hypoconal groove; often presence of functional dP1; elongated and slender metapodials.

Hipparion matthewi differs from *H. macedonicum* having smaller size, shorter muzzle, deeper narial opening (nasal notch is retracted above the mesial half of P2), ovoid with well-defined borders, deeper, dorso-ventrally oriented POF and infraorbital foramen situated in front but outside of POF. *Hipparion nikosi* differs from *H. macedonicum* having smaller size (similar to *H. matthewi*) and remarkably deeper narial opening (nasal notch is retracted above the P3–P4) distinguishing it well from all known small hipparions of the Eastern Mediterranean region. *Hipparion moldavicum* with larger size, longer muzzle, wider incisive row, deeper narial opening (nasal notch is retracted above or in front of P2), larger, deeper and posteriorly pocketed POF, infraorbital foramen situated below the antero-ventral rim of POF and larger metapodials differs from *H. macedonicum*. *Hipparion sithonis* Koufos and Vlachou, 2016 is different in the slightly larger size, the deeper narial opening (nasal notch is retracted above the mesostyle of P2), the presence of canine fossa, the antero-ventrally oriented and with well-defined borders POF, and the relatively shorter and robust metapodials. *Hipparion uzunagizli* differs from *H. macedonicum* in the longer and wider muzzle, the deeper narial opening (nasal notch is retracted above the mesial margin of P2), the longer POB, the larger, subtriangular, antero-ventrally oriented and posteriorly pocketed POF. *Hipparion kecigibi* with larger size, short and wider muzzle, subtriangular, deeply pocketed posteriorly and larger POF is separated from *H. macedonicum*. *Hipparion elegans* differs in the larger size, the subtriangular with well-defined borders POF, the longer and wider snout, the longer tooth rows, and the large and slenderer metapodials.

Measurements.—The measurements of the new material are given in Supplementary Online Material (SOM: tables 1, 2) available at http://app.pan.pl/SOM/app61-Koufos_SOM.pdf.

Fig. 1. Equid *Hipparion macedonicum* Koufos, 1984 (LGPUT RPl-125) → from Ravin de la Pluie, Axios Valley (Macedonia, Greece), late Vallesian, MN 10 (Late Miocene). **A**–**D**. Skull in right (**A**) and left (**B**) lateral, lateral-dorsal (**C**), and ventral (**D**) views. **E**. Left tooth row in occlusal view.


A
B
C
D
E
50 mm
(A–D)
20 mm

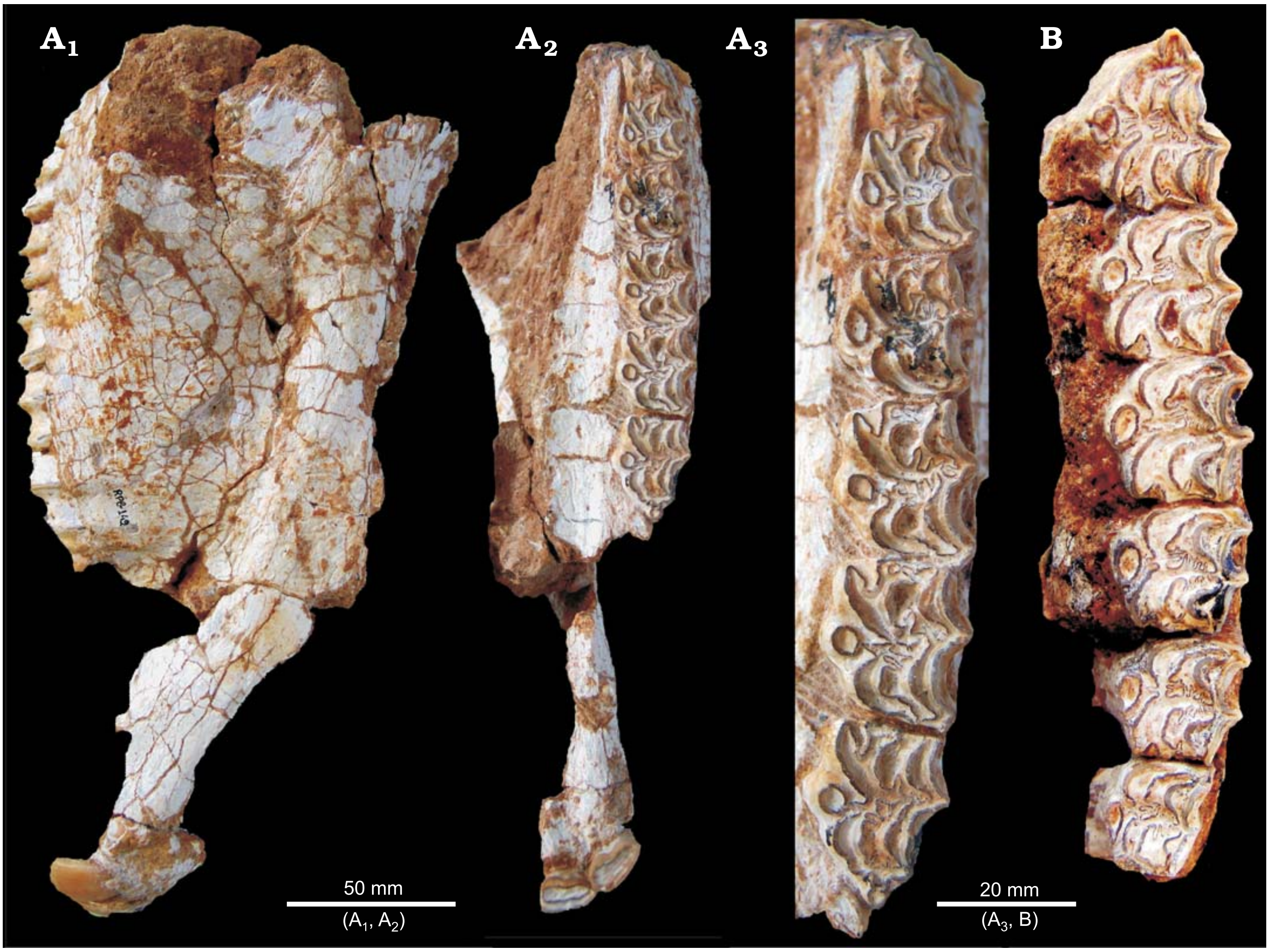

Fig. 2. Equid *Hipparion macedonicum* Koufos, 1984 from Ravin de la Pluie, Axios Valley (Macedonia, Greece), late Vallesian, MN 10 (Late Miocene). **A**. LGPUT RPl-142, right frontal part of skull in lateral (A_1) and occlusal (A_2) views, right tooth row in occlusal view (A_3). **B**. LGPUT RPl-37, left tooth row in occlusal view.

Description.—LGPUT RPl-125 is a partially preserved skull lacking the occipital part (Fig. 1A–D); its left side is better preserved (the ventral and distal part of the orbit and the zygomatic arch are preserved) than the right one which is more damaged. The skull is laterally compressed and the dimensions are slightly influenced being smaller. The muzzle is relatively elongated and narrow; the narial opening is shallow; the nasal notch is retracted above approximately ½ of the distance between the canine and P2. The incisive row is rounded and all incisors are well developed. The buccinator fossa is very deep and pocketed posteriorly. The POF is better preserved in LGPUT RPl-142 (Fig. 2A_1) and in the right side of LGPUT RPl-125 (Fig. 1A). It is elliptical, shallow, antero-posteriorly oriented, not pocketed posteriorly with moderately developed margin, and open anteriorly. The infraorbital foramen encroaches upon the antero-ventral border of the POF. The partially preserved right orbit of LGPUT RPl-125 indicates that the POB is probably moderate and the mesial orbital margin is situated above the middle of M3. The palate is laterally compressed and gives the impression that it is very narrow. The choanae are narrow and their anterior margin is at the middle of M1.

The upper cheek tooth row is well preserved, short and moderately worn in all studied specimens; in LGPUT RPl-142 it is unworn-little worn (II^d stage; the M3 is erupted) (Figs. 1E, 2A_3, B). The tooth rows of LGPUT RPl-125 and LGPUT RPl-142 preserve a functional dP1. The P2 has a short and rounded anterostyle, well separated from the protoloph and connected fossettes in all specimens, except LGPUT RPl-37 (Fig. 2B). The enamel in the fossette's borders is plicated and the plis are elongated and moderately deep; this morphology is clear in the moderately worn teeth of LGPUT RPl-37. The mean plication number ranges between 7–17 (mean 14.1) in the premolars and 10–17 (mean 13.6) in the molars. The pli caballin is single in all teeth, except LGPUT RPl-37 where it is double in the premolars. The protocone is isolated in all teeth, rounded-oval in the premolars and oval-lenticular in the molars; a weak spur occurs in the little worn teeth of LGPUT RPl-142 (Fig. 2A_3, B). The hypocone is elliptical-angular but it is rounded in M3 of all specimens. The distal hypoconal groove is deep in the less worn teeth and shallower in the more worn ones. In all M3 there is a deep lingual hypoconal groove separating well the hypocone while a very weak lingual hypoconal groove occurs in some teeth.

Although the mandible and the lower teeth of *H. macedonicum* from RPl have been described earlier on the basis of the holotype LGPUT RPl-21 and LGPUT RPl-17, the five new mandibles (LGPUT RPl-125, 281, 282, 286, 290) add more data (Fig. 3). The mandible relative to its size has high mandibular corpus; its height is remarkably reduced and became small in front of p2. The snout is relatively elongated and narrow. The incisive row is rounded and narrow between the distal margins of the i3s; in LGPUT RPl-125 seems to be wide but this is due to a strong dorso-ventral compression and deformation which flattened the incisive area. The symphysis is relatively short, like in the holotype LGPUT RPl-21.

The lower teeth are well preserved in most of the available mandibles (Fig. 3). The paraconid of the p2 is elongated and projects mesially. The parastylid is open mesially in the less worn teeth but it is closed and joined with the protostylid in the much worn ones (LGPUT RPl-17). The protostylid is moderately high occurred in the half-worn teeth; it is well distinguished in LGPUT RPl-17, 125, 290, while in the holotype LGPUT RPl-21 just appeared and it is clearly separated from the parastylid. The metaconid is elliptical-rounded in the premolars, and rounded in the molars. The linguaflexid is open, V-shaped and deep touching the ectoflexid in the worn and much worn teeth. The ectoflexid is narrow and very deep, especially in the molars. The metastylid is elliptical in the premolars and more rounded in the molars. There are plications or crenulations in the preflexid and postflexid enamel which gradually disappear by the attrition.

The postcranial remains of *H. macedonicum* from RPl are a few; except those desribed earlier (Koufos 1984, 1986), the new material includes some bone fragments, the size of which correlates them to the RPl small-sized hiparion.

Remarks.—*Hipparion macedonicum* was originally described on a small suite of mandibles, maxillary fragments and post cranial remains from RPl (Koufos 1984, 1986) but soon it was recognized in several localities of Axios Valley (PNT, RZ1, RZO, PXM, VATH) and later in Nikiti (NKT, NIK), as well as in Perivolaki (PER) (Koufos 1987b, c, 1988, 2000; Vlachou and Koufos 2002, 2006; Koufos and Vlachou 2016). The cranial characters of the taxon are mainly known from an almost complete skull from the Turolian locality PXM and some partial skulls from the other Turolian localities of northern Greece (Koufos 1987c, 1988; Vlachou and Koufos 2006; Koufos and Vlachou 2016). LGPUT RPl-125, as it originates from the type locality, allows to study the cranial morphology of *H. macedonicum* in its typical site, as well as to see its evolutionary relationships with the younger forms of the species, and other small-sized hipparions.

The mean values of the RPl cranial and mandibular remains are compared with the corresponding ones of *H. macedonicum* from other localities, as well as with other *Hipparion* taxa known from Eurasia. The PCA for the skull

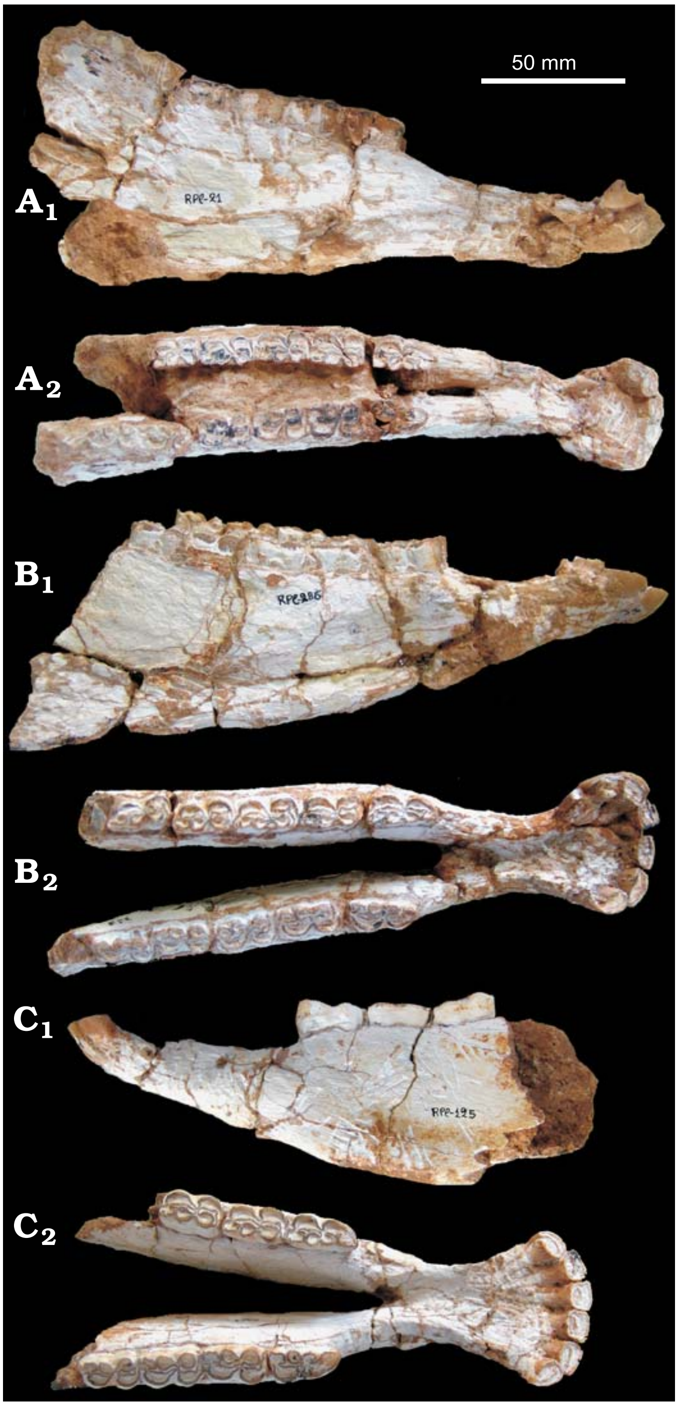

Fig. 3. Equid *Hipparion macedonicum* Koufos, 1984 from Ravin de la Pluie, Axios Valley (Macedonia, Greece), late Vallesian, MN 10 (Late Miocene). **A**. Holotype LGPUT RPl-21, mandible in right lateral (A_1) and occlusal (A_2) views. **B**. LGPUT RPl-286, mandible in right lateral (B_1) and occlusal (B_2) views. **C**. LGPUT RPl-125, mandible in left lateral (C_1) and occlusal (C_2) views.

separates well the various *Hipparion* taxa according to their size (Fig. 4A). The small-sized hipparions match in the lower and the medium-sized ones in the upper half of the PC2, while the very small and large forms are displayed in the two extremes of the PC1. The RPl skull matches *H. macedonicum* suggesting that metrically is very close to

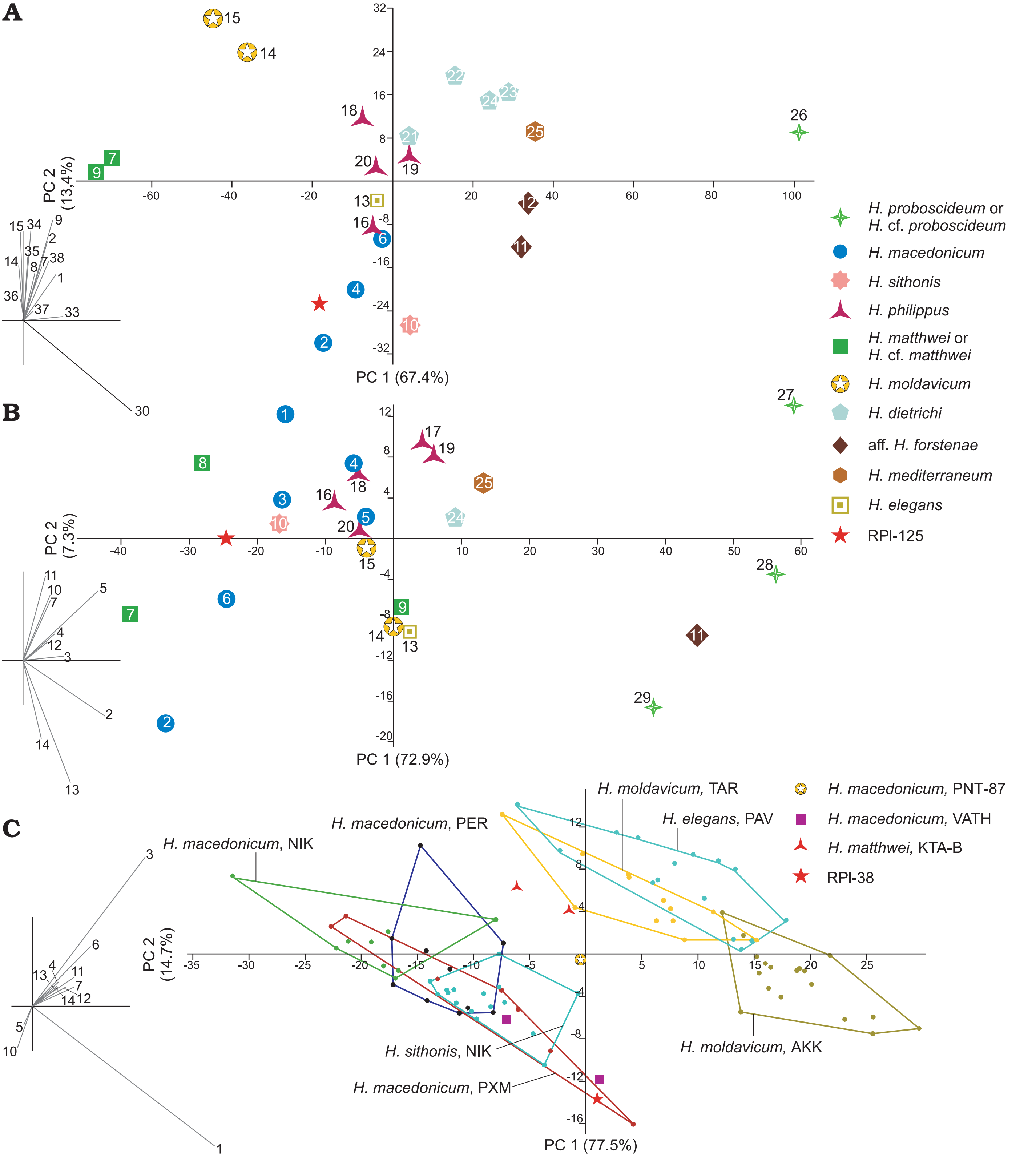

Fig. 4. Principal component analysis of the skull (**A**), mandible (**B**), and third metatarsal (**C**) of the RPl small-sized hipparion in comparison with other small-sized forms of Eurasia, indicating its strong size-similarities with *Hipparion macedonicum*. As the available specimens are fragmentary, lacking measurements the mean cranial dimensions for each locality are used. The used variables (various measurements of the skull, mandible and Mt_{III}) and their influence to the distinction of the specimens is given in the left part of the diagrams. The convex hulls indicate the allocation of the measurements in the space for its sample. *Hipparion dietrichi*, *Hipparion mediterraneum*, and *Hipparion proboscideum* or *Hipparion* cf. *proboscideum* are used as comparative samples. *Hipparion macedonicum*: 1, NKT; 2, NIK; 3, RZO; 4, PXM; 5, VATH; 6, PER. *Hipparion matthewi*: 7, Samos (unknown locality), holotype; 8, KTA-B. *Hipparion* cf. *matthwei*: 9, MTLA. *Hipparion sithonis*: 10, NIK. aff. *Hipparion forstenae*: 11, MTLA; 12, Samos Q1. *Hipparion* →

this taxon. The type of *H. matthewi* Abel, 1926 and the skulls described as *H.* cf *matthewi* are well separated from the RPl skull being quite smaller. Three other small-sized species have skulls comparable in size to the RPl one (Fig. 4A). *Hipparion elegans* Gromova, 1952 differs from the RPl in several morphological features (see below). The other two are *H. sithonis* Koufos and Vlachou, 2016 and aff. *H. forstenae* Zhegallo, 1971 and both are separated from *H. macedonicum* and RPl skull having canine fossa. The PCA for the mandible, although the distinction of the various taxa is not sufficient, the RPl mandible is closer to *H. macedonicum* and *H. sithonis* than to *H. matthewi* which has smaller mandible (Fig. 4B).

The Mt_{III} sample of the various species is rich and can allow a good comparison. The PCA separates well the Mt_{III} of the various taxa according to their mid-shaft length and width (Fig. 4C). The RPl Mt_{III} is into the area of *H. macedonicum* and can be referred to it; however, it is clear that there is a great overlapping between the various taxa e.g. the Mt_{III} of *H. macedonicum* and *H. sithonis* cannot be distinguished, as they overlap each other (Fig. 4C). The distinction of hipparions having similar size and the attribution of the postcranials to the one or the other taxon (except having complete skeletons) is, in most cases, arbitrary. The correlation is mainly based on size or some morphological features, if there are, e.g., *H. macedonicum* and *H. sithonis* are well-separated by their skull morphology (presence or absence of canine fossa) but the distinction of the postcranial remains is difficult or even impossible. The presence of two hipparions in RPl, a large- and a small-sized one makes the distinction of the postcranials easier, but we cannot exclude the possibility of a second large or small hipparion in the sample.

Comparisons

***Hipparion macedonicum*.**—As it is mentioned above *H. macedonicum* is reported from several Vallesian and Turolian localities of Greece. The RPl skull has similar proportions to an almost complete skull from the middle Turolian locality PXM (Fig. 5A). The differences are limited and restricted to the slightly longer and wider muzzle, the shorter tooth rows, the wider incisive row, and the slightly deeper narial opening (Fig. 5A: measurements 1, 7–9, 14, 15, 30). A set of cranial remains of *H. macedonicum*, described from the early Turolian locality NIK (Koufos and Vlachou 2016) differs from the RPl skull in the shorter and wider muzzle and the shorter tooth rows (Fig. 5A: measurements 1, 7–9, 15). The skull of *H. macedonicum* from the Middle Turolian locality PER differs from the RPl one in the longer muzzle and palate (this difference is artificial; as it was referred in the description the deformation of the skull LGPUT RPl-125 affects the palate breadth), as well as the shorter tooth rows (Fig. 5A: measurements 1, 2, 7–9). A partial skull from the late Turolian locality DKO, reported as *H.* cf. *macedonicum* by Vlachou (2013), has similarities with the RPl skull but it differs from it in the wider muzzle and shorter tooth rows (Fig. 5A: measurements 2, 7–9, 15). Taking in mind the Vallesian age of the RPl, there is a trend in *H. macedonicum* for reduction of the tooth rows, increase of the narial opening depth, and increase of the muzzle width from Vallesian to Turolian. The mandible LGPUT RPl-125 has similar morphological characters to the holotype of *H. macedonicum* (LGPUT RPl-21). In mean values the RPl mandible has similar proportions to *H. macedonicum* from the various localities (Fig. 6A). However, the NIK mandible seems to have less high mandibular corpus than those from the other localities; this is artificial and possibly due to the fact that these measurements (Fig. 6A: measurements 10–12) come from a single and badly preserved mandible from NIK. The RPl Mt_{III} has similar proportions to *H. macedonicum* from the other localities but it is slightly longer with smaller articular facet for the cuboid (IV tarsal), (Fig. 7A: measurements 1, 8). The DYTI Mt_{III}, though its proportional similarity to *H. macedonicum,* it is remarkably smaller than the RPl one (Fig. 7A).

***Hipparion matthewi*.**—It is a small-sized hipparion originally described on a skull and associated mandible from an unknown locality of Samos. A direct comparison of LGPUT RPl-125 with a cast of the holotype (LGPUT OK/557), indicated that LGPUT RPl-125 differs from *H. matthewi* having: larger size (Figs. 4A, 5B, 6B); longer muzzle (Fig. 5B: measurement 1); less deep narial opening, the nasal notch is retracted above the middle of the C-P2 diastema, while in OK/557 is above the mesial half of the P2; shorter palate (Fig. 5B: measurement 2); both skulls are laterally compressed and may be this difference is not so indicative; morphologically different POF, in LGPUT OK/557 it is ovoid with well-defined borders, deeper, dorso-ventrally oriented and the infraorbital foramen is situated in front of the POF (but outside of it); longer snout (Fig. 6B: measurement 2).

Hipparion matthewi is reported from the middle Turolian localities Kemiklitepe A–B (KTA–B) of Asia Minor by some mandibular and postcranial remains (Koufos and Kostopoulos 1994; Vlachou 2013). The KTA-B mandible has similar proportions to the type of *H. matthewi*. It differs from the RPl one in the shorter and narrower snout and the slightly shorter premolar row (Fig. 6B: measurements 2, 4). The KTA-B metatarsal is slightly shorter, wider in the mid-shaft with smaller distal epiphysis than the RPl one (Fig. 7B: measurements 1, 3, 11–14).

The small-sized hipparions of Eastern Mediterranean region were reported as *H. matthewi* or *H.* cf. *matthewi* for a long time. Most of them have significant differences from the type of *H. matthewi* (e.g., some skulls from Q5 of Samos interpreted as *H. matthwei* by Sondaar (1971) are different

elegans: 13, PAV. *Hipparion moldavicum*: 14, TAR; 15. AKK. *Hipparion philippus*: 16, NIK; 17, RZO; 18, PXM; 19, VATH; 20, PER. *Hipparion dietrichi*: 21, MTLA; 22, MTLB; 23, Samos Q4; 24, Samos Q1. *Hipparion mediterraneum*: 25, PIK. *H. proboscideum*: 26, Samos Qx; 27, MTLA; 28, Samos Q1. *Hipparion* cf. *proboscideum*: 29, PER.

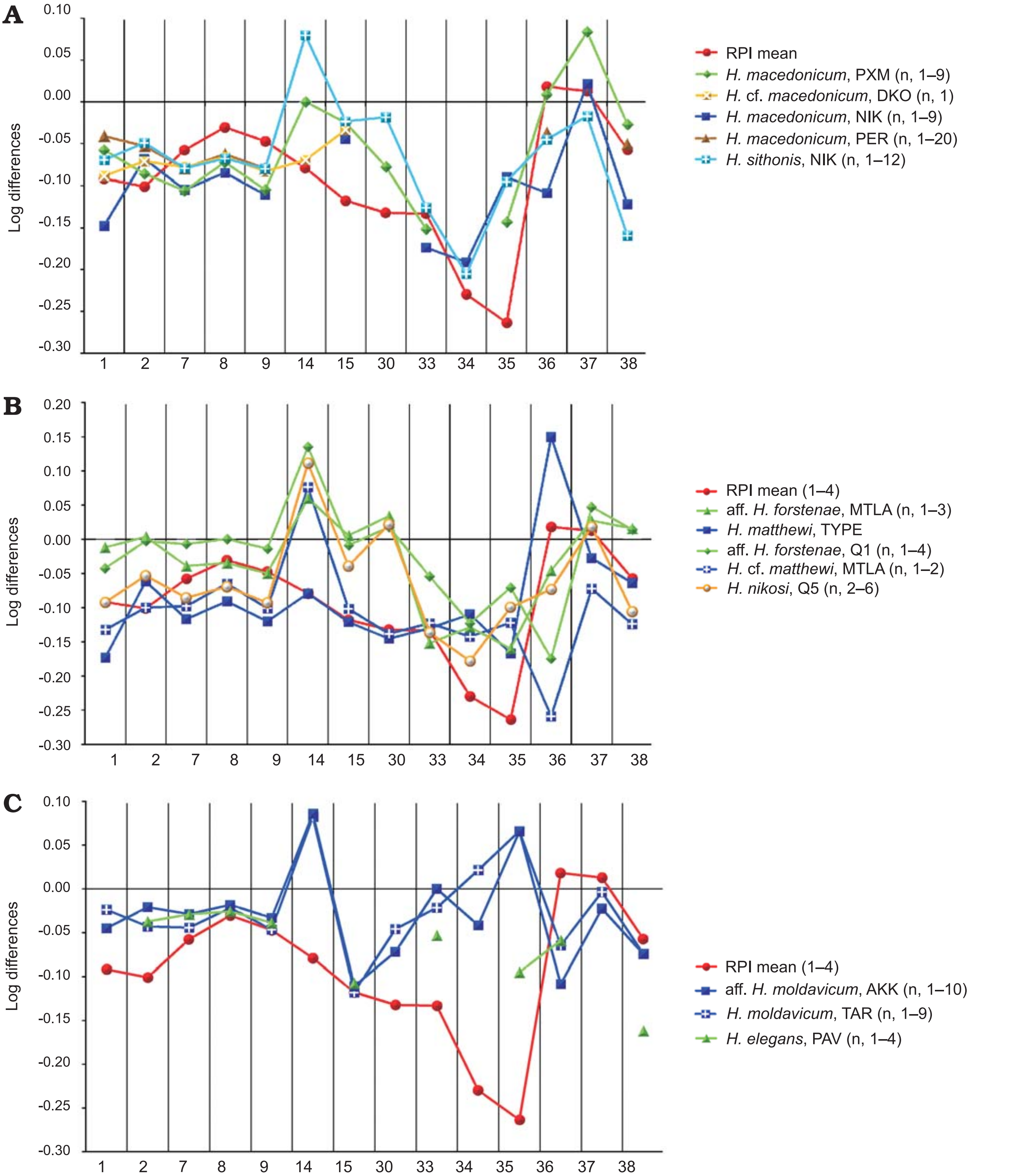

Fig. 5. Logarithmic ratio diagram comparing the RPl skull with *Hipparion macedonicum* and other small-sized hipparions from various localities. *Hipparion mediterraneum* from Pikermi (Koufos 1987a) is used as standard of comparison. The metrical data for the hipparions from Greek localities and AKK are from author's archive; those for *Hipparion moldavicum* from TAR and *H. elegans* from PAV are taken from http://www.vera-eisenmann.com.

and remarkably larger than the type skull). In my opinion, except the type skull and mandible of *H. matthewi*, all the rest material, attributed to this taxon or described as *H.* cf. *matthewi* could belong or not to *H. matthewi* but either the material needs revision or it is limited for certain determination. The revision of the Sondaar's (1971) cranial material described as *H. matthewi* indicated that it belongs to *H. nikosi* (very deep narial opening) and to *H.* cf. *dietrichi*,

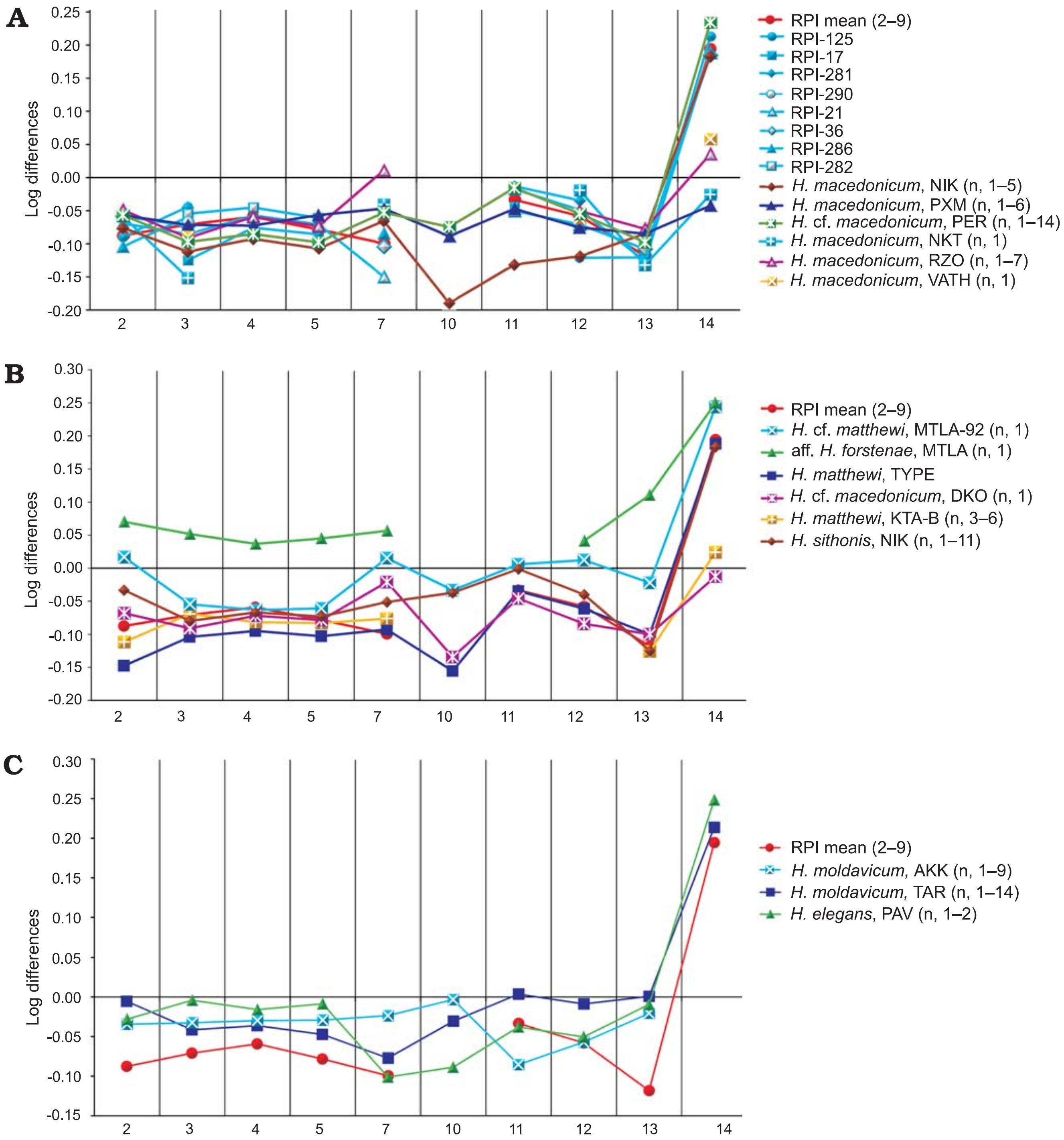

Fig. 6. Logarithmic ratio diagram comparing the RPl mandible with *Hipparion macedonicum* and other small-sized hipparions from various localities. *Hipparion mediterraneum* from Pikermi (Koufos 1987a) is used as standard of comparison. The metrical data for the hipparions from Greek localities and AKK are from my own archive; those for *Hipparion moldavicum* from TAR and *Hipparion elegans* from PAV are taken from http://www.vera-eisenmann.com.

while the fragmentary specimens and the postcranial remains potentially can belong to any small- to medium-sized hipparion (Vlachou and Koufos 2006, 2009; Vlachou 2013). Thus, it is necessary to define first the taxonomic status of *H. matthewi* (the only certain specimen is the holotype) by finding new material in the Samos localities. Unfortunately, we could not find such a small-sized hipparion during our recent excavations in Samos (Vlachou and Koufos 2009).

Hipparion sithonis.—It is a new small-sized hipparion described from the early Turolian locality NIK (Koufos and Vlachou 2016). The presence of the canine fossa in *H. sithonis* differentiates it from the RPl skull. Its size is similar to the RPl form but it differs from it in the longer palate, shorter tooth rows, deeper narial opening (the nasal notch is retracted well behind the mesostyle of the P2), wider and antero-ventrally oriented POF (Fig. 5A: measurements 2, 7–9,

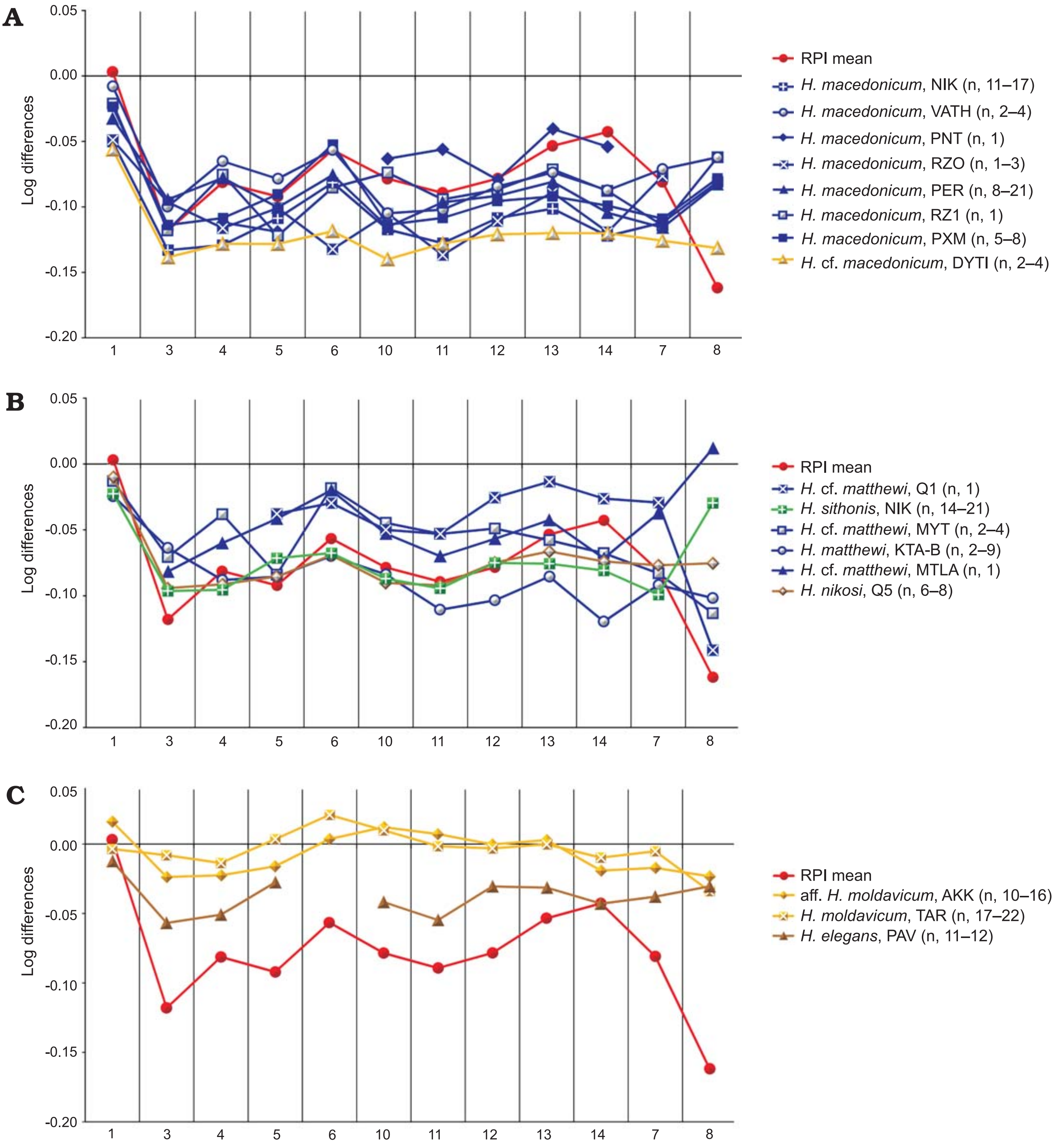

Fig. 7. Logarithmic ratio diagram comparing the RPl third metatarsal with *Hipparion macedonicum* and other small-sized hipparions from various localities. *Hipparion mediterraneum* from Pikermi (Koufos 1987a) is used as standard of comparison. The metrical data for the hipparions from Greek localities and AKK are from my own archive; those for *Hipparion moldavicum* from TAR and *Hipparion elegans* from PAV are taken from http://www.vera-eisenmann.com.

30) and longer snout. The metatarsal of *H. sithonis*, though its proportions are similar to the RPl one, it is shorter with larger articular facet for the fourth tarsal (cuboid) than the RPl one (Fig. 7B: measurements 1, 8).

Hipparion nikosi.—*H. nikosi* Bernor and Tobien, 1989 is a small-sized hipparion from Samos (unknown locality) characterized by a very deep narial opening, the nasal notch is retracted above the P4 (Bernor and Tobien 1989). Recently

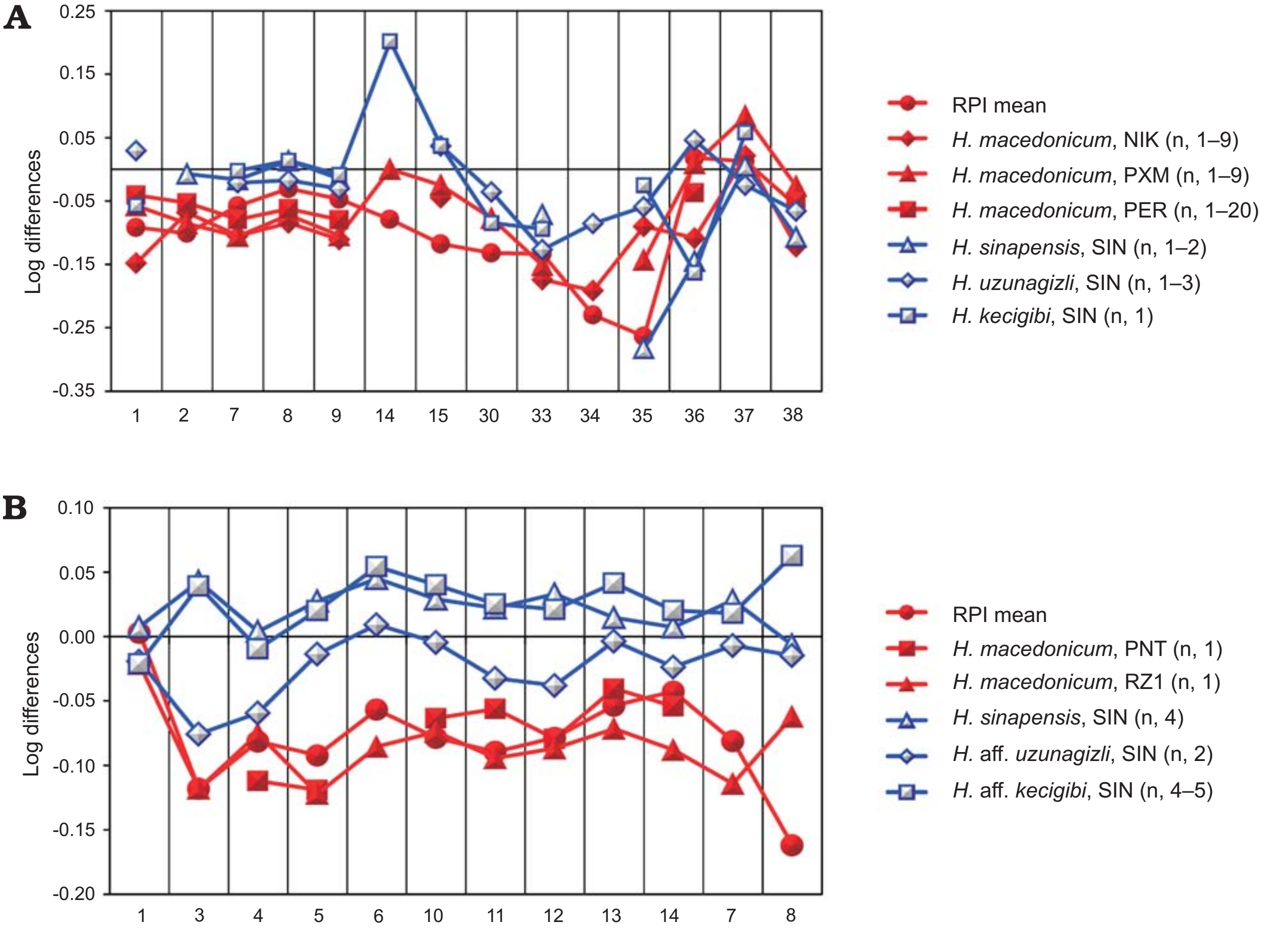

Fig. 8. Logarithmic ratio diagram comparing the RPl skull (**A**) and third metatarsal (**B**) with the Vallesian hipparions from Sinap, Turkey. *Hipparion mediterraneum* from Pikermi (Koufos 1987a) is used as standard of comparison. The metrical data for the Sinap material were provided to me by Raymond L. Bernor (unpublished material, personal communication, 2007).

Vlachou (2013) reported some skulls (AMNH 22888, 22907, 22936, 22908) from Q5 of Samos, to this species. The size of *H. nikosi* skull is close to that of the RPl form but it differs from it in the slightly longer palate, shorter tooth rows and deeper narial opening (Fig. 5B: measurements 2, 7–9, 30). The metapodials from Q5, attributed to *H. nikosi* by Vlachou (2013) are proportionally very close to the RPl form as well as to those of *H. macedonicum* from the other localities (Fig. 7A, B).

Hipparion elegans.—The small-sized *H. elegans* Gromova, 1952 is originally described from Pavlodar, Kazakhstan (Gromova 1952) and it is reported as synonym of *H. matthewi* or closer to *H. moldavicum* Gromova, 1952 (Forstén 1968, 1997; Pesquero et al. 2011). The skull of *H. elegans* differs remarkably from the RPl one in the longer palate, as well as the size and position of the POF (Fig. 5C: measurements 2, 33, 35, 36, 38). Based on the figures of Gromova (1952) its POF is sub-triangular with well-defined borders. The mandible has longer and wider snout, longer tooth rows, and remarkably longer symphysis (Fig. 6C: measurements 2, 3–5, 13). The metatarsal of *H. elegans* is slenderer with larger proximal articular surfaces than the RPl one and *H. macedonicum* from the other localities (Fig. 7C).

Hipparion moldavicum.—It is a small- to medium-sized hipparion known from Taraklia (Ukraine) but later it was recognized in the wider Black Sea region, Turkey and Iran (Bernor 1985; Watabe and Nakaya 1991; Watabe 2004; Koufos and Vlachou 2005). *Hipparion moldavicum* Gromova, 1952 is larger than the RPl form (Figs. 5C, 6C) having deeper narial opening (in the AKK skulls the nasal notch is retracted above the P2), weak posterior pocketing of the POF, infraorbital foramen below the antero-ventral border of the POF, longer snout, wider incisive row, and longer symphysis (Figs. 5C, 6C).The Mt_{III} of *H. moldavicum* is quite larger than those of the RPl ones (Fig. 7C).

Sinap hipparions.—Bernor et al. (2003) described a number of new hipparions from the Vallesian deposits of Sinap, Turkey on the basis of their cranial remains. All are larger than *H. macedonicum* (Fig. 8A). *Hipparion sinapensis* Bernor, Scott, Fortelius, Kappelman, and Sen, 2003 from the early Vallesian, MN 9 (10.55–9.97 Ma) of Sinap is separated from *H. macedonicum* by the longer muzzle, longer palate, longer tooth rows, longer POB (~41 mm), as well as the subtriangular, antero-ventrally oriented, deeply pocketed posteriorly, and situated closer to the facial crest POF (Fig. 8A: measurements 1, 7–9, 36). The Mt_{III} of *H. mace-*

donicum has similar length but it is more slender than that of *H. sinapensis* (Fig. 8B). *Hipparion uzunagizli* Bernor, Scott, Fortelius, Kappelman, and Sen, 2003, known from the early Vallesian, MN 9 (9.967–9.918 Ma) of Sinap differs from *H. macedonicum* in the longer and wider muzzle, the deeper narial opening (nasal notch retracted above the mesial margin of the P2), the more far situated orbit, the remarkably longer POB, the subtriangular, antero-ventrally oriented, and posteriorly pocketed POF, as well as the more robust metatarsal (Fig. 8B: measurements 1, 2, 15, 30). On the other hand, the two species have some similarities as the tooth rows length (slightly larger in *H. uzunagizli*; Fig. 8A), the shape of the POF and the presence of a functional dP1. Bernor et al. (2003) mentioned that the POF of *H. uzunagizli* is going to be egg-shaped with antero-posterior orientation and reduced size being closer to that of *H. macedonicum* in which it is elliptical, reduced and antero-posterioly oriented. The third hipparion from the early Vallesian, MN 9 (9.683 Ma) of Sinap is *H. kecigibi* Bernor, Scott, Fortelius, Kappelman, and Sen, 2003, separated from *H. macedonicum* in the short and relatively very wide muzzle, the longer tooth rows, the deep posterior pocketing of POF and the remarkably more robust metatarsals (Fig. 8). The two taxa have similar depth of the narial opening (Fig. 8A: measurement 30), as well as elliptical-subtriangular shaped, antero-posteriorly oriented, and moderately deep POF. Both *H. uzunagizli* and *H. kecigibi* shared some morphological characters with *H. macedonicum* indicating close relationships.

Discussion

Hipparion macedonicum is common in the Late Miocene of Greece with a continuous occurrence in the deposits of Axios Valley (Macedonia, Greece). The oldest known occurrence of *H. macedonicum* is traced in PNT and correlated to the early Vallesian, MN 9 (Fig. 9). The peculiar character of the PNT fauna, in comparison to the other ones of Axios Valley, was early recognized and an early Vallesian (MN 9) age speculated (Koufos 2013 and references cited therein). The early Vallesian age of PNT was confirmed by the presence of *Choerolophodon anatolicus* (Ozansoy, 1965) characterizing early Vallesian (Konidaris et al. 2016). The last occurence of *H. macedonicum* is reported from PER (Fig. 9), dated to the upper part of the middle Turolian (upper MN 12), at about 7.3–7.1 Ma (Koufos et al. 2006b). The taxon is possibly present in the late Turolian, MN 13 localities DYTI of Axios Valley (Fig. 9). It is described as *H.* cf. *macedonicum* by Vlachou (2013) and it is smaller than the typical *H. macedonicum* with some differences mentioned above but the limited and badly preserved material cannot allow confirming its confident presence. A small-sized hipparion from the Bulgarian localities Kocherinovo 2 and Kalimantsi 1 was described as *H.* cf. *macedonicum* and *H.* gr. *macedonicum* respectively; both localities are correlated to early Turolian, MN 11 (Spassov et al. 2006; Hristova et al. 2013; Fig. 9). Earlier Eisenmann (1988) recognized a small-sized hipparion in the late Vallesian locality of Montredon, France and described it as *H.* cf. *macedonicum*. Based on the data, from the Greek localities *H. macedonicum* has a continuous presence in the Late Miocene faunas of Europe (Fig. 9). Vlachou (2013) considered that *H. macedonicum* could be synonym to (i) "*H. minus*" Pavlow, 1890 from Sebastopol, Moldavia dated to early Vallesian, MN 9 (Vangengeim and Tesakov 2013); (ii) *Hipparion* sp. from Sumeg, Hungary dated to late Vallesian, MN 10 (Bernor et al. 1999); and (iii) *H.* cf. *macedonicum* from Montredon, France dated to late Vallesian, MN 10 (Eisenmann 1988). If this hypothesis is true and taking in mind its possible presence in Bulgaria, the taxon appeared or arrived in southeastern Europe in the early Vallesian (MN 9) and migrated to Central and Western Europe, where it was found in the late Vallesian (MN 10).

The above comparisons of *H. macedonicum* from the various fossiliferous sites, from a first point of view, indicate some intraspecific changes related to the time. We shall try to check these changes and how they are related. Looking to the diagrams of Figs. 5–7 it is clear that there are some changes in *H. macedonicum* from Vallesian to Turolian.

Body mass.—The body mass is a good size indicator for the equids and it is related to the size of the metapodials. The main variables used for its estimation are the distal maximal suprarticular breadth and the distal minimal depth of the lateral condyle (Scott 1990; Eisenmann and Sondaar 1998). On the other hand, Alberdi et al. (1995) estimated the body mass of the equids using the proximal DAP of the first phalanx. As the phalanges are absent in RPl and the other Vallesian localities, the body mass estimation is based on metapodials using the following formulas of Eisenmann and Sondaar (1998) which show the highest R-values:

W1. $\ln(\text{body mass}) = -5{,}768+3.011 \times (\ln Mc10)$ $R = 0.94$
W2. $\ln(\text{body mass}) = -3.152+2.665 \times (\ln Mc13)$ $R = 0.92$
W3. $\ln(\text{body mass}) = -4.525+1.434 \times (\ln(Mc10 \times Mc13))$ $R = 0.94$
W4. $\ln(\text{body mass}) = -4.362+2.634 \times (\ln Mt10)$ $R = 0.93$
W5. $\ln(\text{body mass}) = -4.552+3.100 \times (\ln Mt13)$ $R = 0.94$
W6. $\ln(\text{body mass}) = -4.585+1.443 \times (\ln(Mt10 \times Mt13))$ $R = 0.94$

The body mass is calculated for each metapodial with all formulas and then the mean value for each used variable and sample is given in Fig. 10. Vlachou and Koufos (2002) mentioned that the body mass of *H. macedonicum* decreases in relation to the time. In fact, the mean body mass of *H. macedonicum* decreases from Vallesian to the end of Turolian with the youngest *H.* cf. *macedonicum* from DYTI having the smaller body mass than all other forms (Fig. 10) confirming the above hypothesis. The body mass for the NKT *H. macedonicum* is similar to the Turolian forms and this is probably due to its younger age (terminal Vallesian; Koufos et al. 2016). The mean body mass for the Vallesian *H. macedonicum* ranges between 72.3–121 kg, between 49.5–94.7 kg for the early–middle Turolian form, and between 56.9–67.5 for the late Turolian form). Exceptionally the W2 mean value

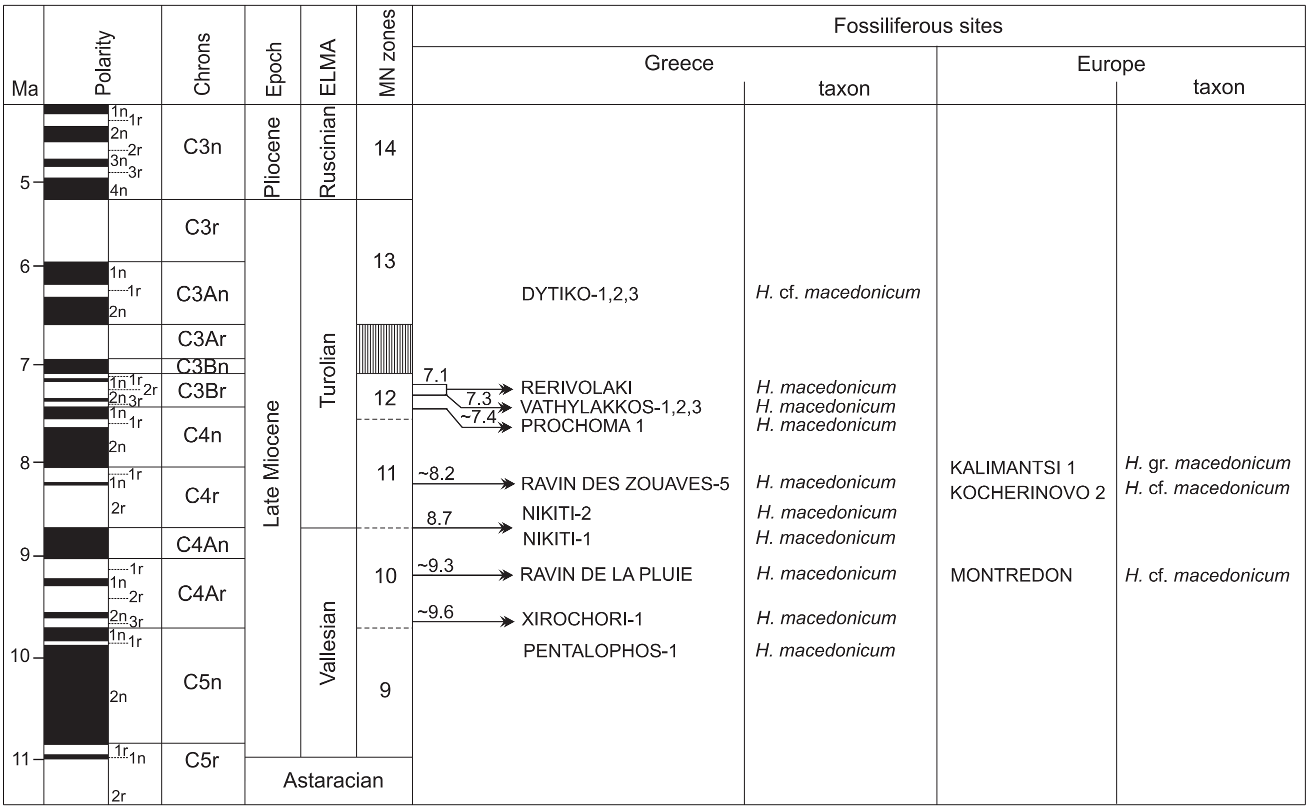

Fig. 9. Stratigraphic table indicating the distribution of *Hipparion macedonicum* in Europe. The geomagnetic time scale is from Cande and Kent (1995). The shaded area in the MN zones express the different opinions for the MN 12/13 boundary; according to Sen (1997) it is at ~7.0 Ma while according to Steininger et al. (1999) it is at ~6.6 Ma.

of VATH *H. macedonicum* is high (107.2 kg) but such high W2 values are also observed in the NIK and PER sample.

Tooth row length.—The length of the tooth rows is a variable also related to the size of the equids and it is used for comparisons between them. The length for the upper and lower tooth rows of *H. macedonicum* from the various localities is given in the Box-plot diagrams of Fig. 11. Although the data from the Vallesian localities are limited, restricted only in the RPl sample, it is clear that the mean length of the tooth rows is higher in the Vallesian than Turolian forms of *H. macedonicum*, indicating a related to the time size reduction (Fig. 11).

Enamel plication.—The enamel plication of the upper cheek teeth of hipparions is a variable related to their feeding preferences and consequently to the environment. Gromova (1952) related the low enamel plication with hard food and relatively open habitat while the rich enamel plication suggests soft food and closed habitat. Forstén (1968) considered that the forest hipparions are characterized by deep, narrow and almost parallel plications in the fossette borders which allow the broken up of soft food (herbs, leafs) but not those of hard particles because the intervening space between the enamel lamellae is very narrow. In contrast the enamel plis of the hipparions, living in open habitats, are fewer, irregular, short and the single plis wide allowing a large intervening space between them; this pattern supports the grinding of tough grass rich in silica. The enamel plication of the teeth is given by the plication number which is the sum of plis in the fossette borders and pli caballin. The plication number for the upper cheek teeth of *H. macedonicum* from the various sites decreases from the Vallesian to Turolian (Fig. 12), suggesting a habitat change to more open and dry conditions.

Slenderness and keel development.—The equid metapodials are also indicative for their habitat. Eisenmann (1995) following Gromova (1952) linked the gracility of the metapodials, expressed by the Slenderness Index (SI), to open and/or dry conditions. On the other hand, Gromova (1952) and Scott (2004) linked the metapodial diaphysis to the hipparion habitat. The SI is equal to the result of the distal maximal articular breadth divided by the maximal height of the metapodials (Gromova 1952; Eisenmann 1995). Besides the limited sample of the Vallesian metapodials there is a trend for a gradual reduction of SI from Vallesian to Turolian forms of *H. macedonicum* (Fig. 13A, B). This is in accord to the corresponding gradual reduction of the body mass (Fig. 10) as the heavier (large-sized) forms need more robust metapodials to carry their weight. The size of the sagittal keel in the distal articular surface of the metapodials is related to their lateral mobility, the larger sagittal keel the less mobility of the metapodials and the more expressed running character of hipparion (Eisenmann 1995). The development of the sagittal crest is expressed by the Keel Index (KI) which is the quotient of the distal maximal DAP of the keel by the distal minimal depth of the lateral condyle. The KI of *H. macedonicum*

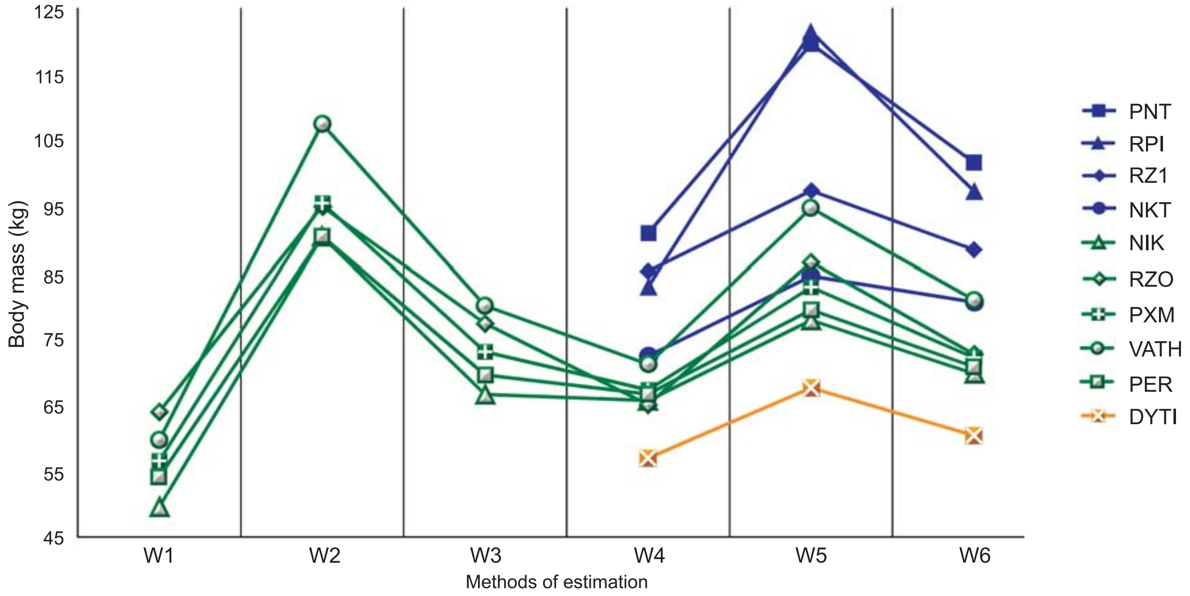

Fig. 10. Body mass of *Hipparion macedonicum* from the various Greek localities calculated by various methods and its change in relation to the time. The body mass is estimated using the metapodials (Eisenmann and Sondaar 1998); W1. ln(body mass) = -5,768+3.011 x (lnMc10); W2. ln(body mass) = -3.151+2.665 x (lnMc13); W3. ln(body mass) = -4.525+1.434 x (ln(Mc10 x Mc13)); W4. ln(body mass) = -4.362+2.634 x (lnMt10); W5. ln(body mass) = -4.552+3.100 x (lnMt13); W6. ln(body mass) = -4.585+1.443 x (ln(Mt10 x Mt13)).

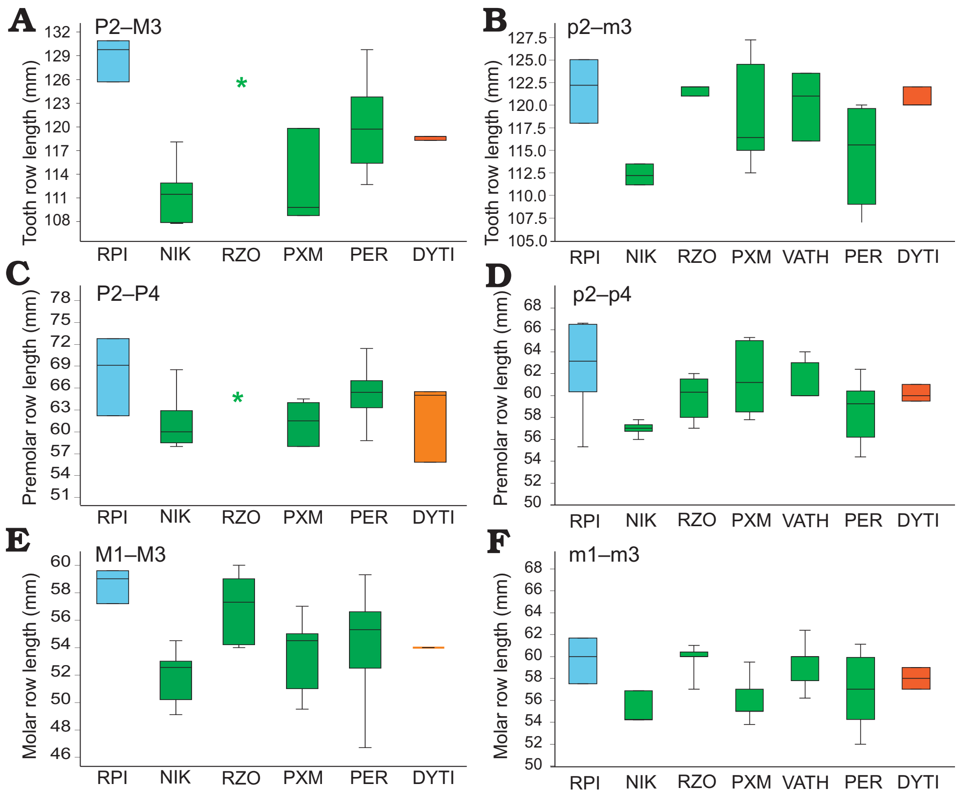

Fig. 11. Box-plot diagrams comparing the length of the upper and lower tooth row (**A**, **B**), premolar row (**C**, **D**), and molar row (**E**, **F**) of *Hipparion macedonicum* from the various Greek localities.

from the various fossiliferous sites increases from Vallesian to Turolian (Fig. 13C, D) suggesting less lateral mobility and more running character for the Turolian forms of the taxon indicating more open conditions than in the Vallesian. Scott (2004), based on the older idea of Gromova (1952) that the equid metapodials reflect the habitat, suggested the habitat score (HS) as a palaeocological indicator depending upon the metapodial variables. Negative HS corresponds to closed habitats while positive values indicate open ones; values between them indicate habitats with heavy or light cover. The calculated HS for the various forms of *H. macedonicum* suggest heavy-light cover habitat for it (Fig. 14).

The analysis of the palaeoecological characters of *H. macedonicum* from the various Late Miocene sites of Greece indicated that they significantly changed from Vallesian to Turolian suggesting in fact different habitats. The Late

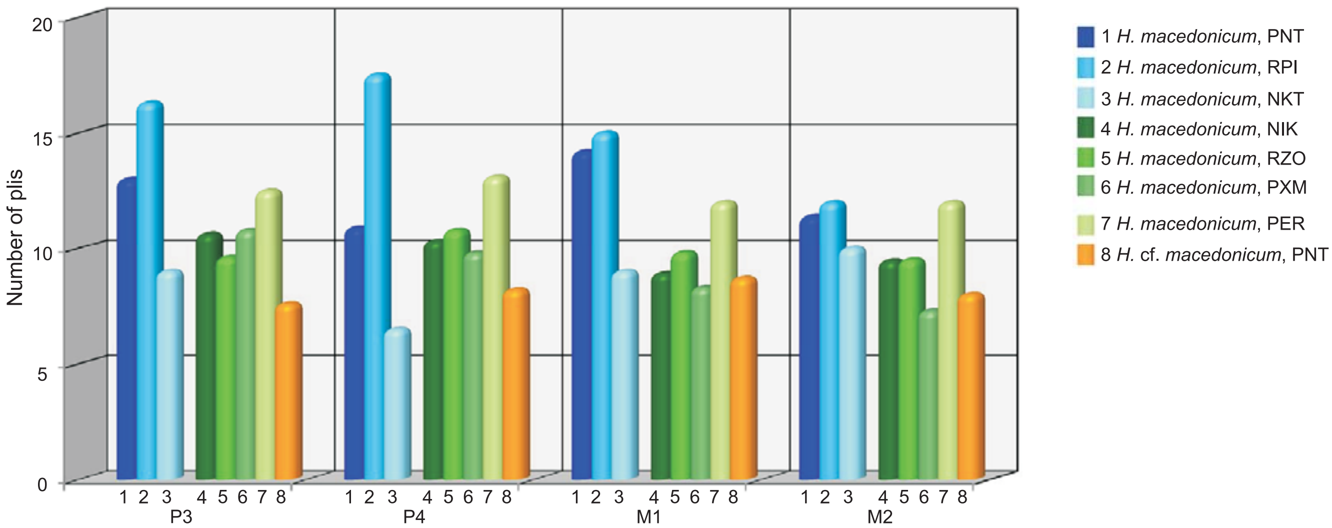

Fig.12. Plication number of the upper cheek teeth of *Hipparion macedonicum* from the various Greek localities.

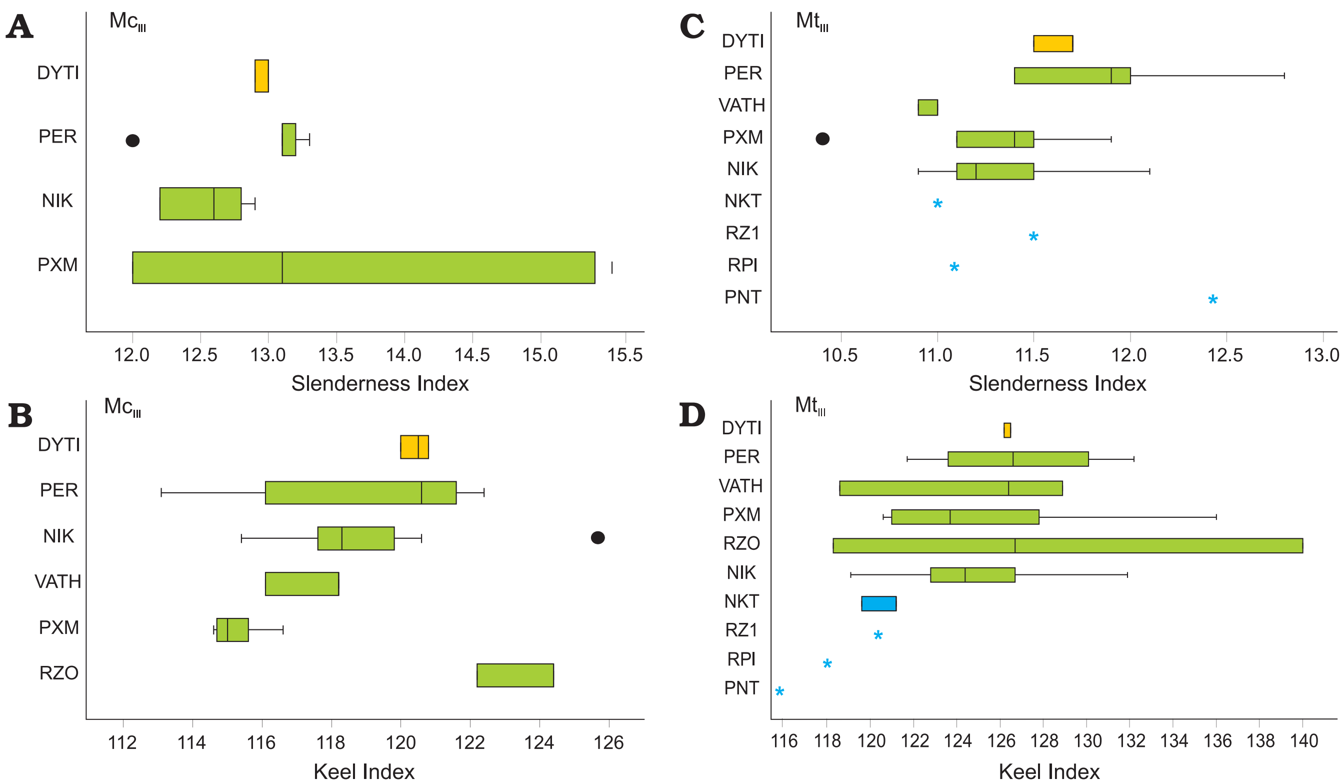

Fig. 13. Slenderness and Keel indexes for the third metacarpal (**A**, **B**) and metatarsal (**C**, **D**) of *Hipparion macedonicum* from the various Greek localities. Dots indicate outliers.

Miocene palaeoenvironment of northern Greece was determined using various parameters, such the comparison of the fossil mammal faunas with modern ones, dental microwear, and isotope analysis of the enamel. All data suggested: (i) open, dry and warm habitat similar to the modern savannah like ones (savannah bushland, grassland, gallery forests or mixed) and (ii) less dry and warm conditions in the Vallesian than the Turolian (Bonis et al. 1992; Koufos 2006a; Koufos et al. 2006a, 2009a, 2016; Kostopoulos 2009; Merceron et al. 2005, 2007; Konidaris et al. 2016). The open character of the Late Miocene habitat is also confirmed from the habitat scores of *H. macedonicum* metapodials which suggest a heavy-light cover habitat (Fig. 14). The $\delta^{18}O_p$ values of apatite phosphate in the teeth of hipparions from northern Greece suggest a mean air temperature increasing from 13±3°C to 17±2°C during late Vallesian–middle Turolian. The mean annual precipitation, during the same time interval, reduced from $890(^{+109}{}_{-100})$ mm a^{-1} to $471(^{+58}{}_{-54})$ mm a^{-1} (Rey et al. 2013). In addition, extensive studies in the wider Eastern Mediterranean region confirm the open, warm and dry character of the palaeoenvironment during Late Miocene (Bonis et al. 1992; Koufos 2006a; Strömberg et al. 2007; Merceron

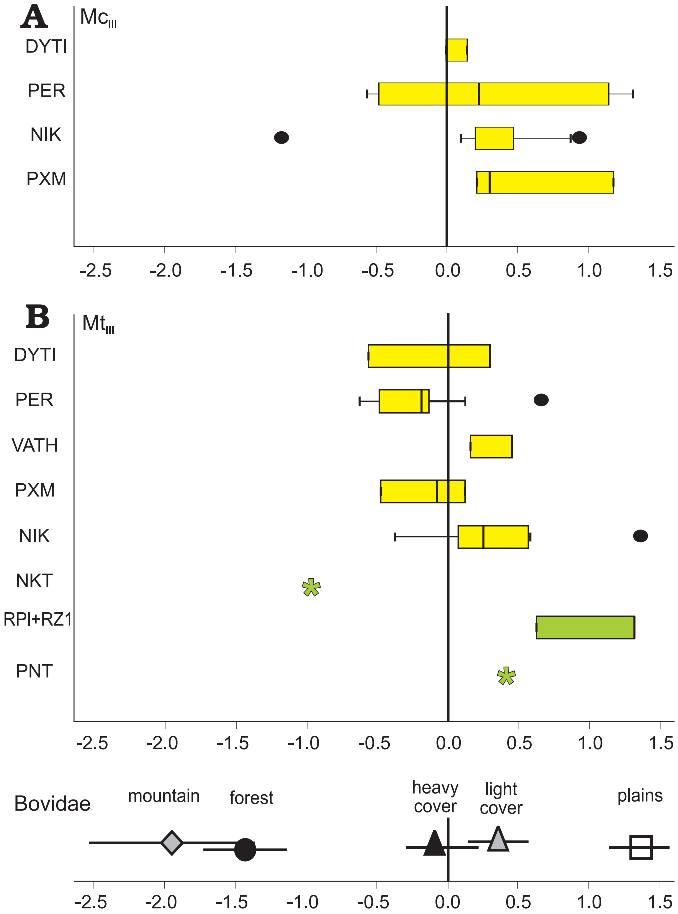

Fig. 14. Habitat scores for the third metacarpals (**A**) and metatarsals (**B**) of *Hipparion macedonicum* from the various Greek localities; the habitat scores are calculated following Scott (2004). Dots indicate outliers and asterisks single specimens.

et al. 2004, 2006, 2016; Eronen et al. 2009; Kostopoulos 2009; Koufos and Konidaris 2011).

The various skeletal and dental characters of *H. macedonicum* confirm the habitat change from Vallesian to Turolian. The Vallesian form of *H. macedonicum* is larger with rich enamel plication and more robust metapodials having more lateral mobility or in other words less expressed running character in the legs (Figs. 12, 13) than the Turolian one, characters indicating relatively less open and dry habitat. In such an environment the soft food (fresh grasses, leafs) is more abundant and thus the plication number in the Vallesian form of *H. macedonicum* is higher than that of the Turolian one (Fig. 12). In contrast, the Turolian form of *H. macedonicum* is smaller with less enamel plication, and more slender metapodials with less lateral mobility than the Vallesian one, suggesting a lightweight form running in the open landscape and feeding on the grass floor.

Hipparion macedonicum is reported as a member of the "*Cremohipparion*"-group which includes a number of taxa (Bernor et al. 1996). According to these authors *H. macedonicum* is considered as sister-taxon of *H. moldavicum* which originates from the primitive *H. primigenium* group. Vlachou (2013) placed *H. macedonicum* in the *H. macedonicum*-morphotype reporting its close relationships to *H. moldavicum*. In fact the relatively elongated and narrow muzzle, the shallow narial opening, the antero-posteriorly oriented with reduced posterior pocketing of the POF, the moderate-high enamel plication of *H. macedonicum* are primitive characters observed in *H. moldavicum* and confirm their relationship. The morphology of LGPUT RPl-125 is in accord to these observations and confirms them. Vlachou (2013) also noted the reduction of the POB and the metapodial gracility, characters appeared in the early Vallesian (MN 9) *H. uzunagizli* from Sinap Tepe, Turkey and increased in *H. macedonicum* which seems to be more derived with smaller size, shallower POF, absence of posterior pocketing in POF and slenderer metapodials. The possible relationships of *H. macedonicum* and *H. uzunagizli* are also mentioned in the comparisons. Taking in mind the size reduction and increase of the metapodial slenderness of *H. macedonicum* with the time, the PNT form of *H. macedonicum* could be similar to *H. uzunagizli*. This is in contrast to the fact that the metapodials of the PNT *H. macedonicum* are similar to the RPl and RZ1 ones, while those of *H. uzunagizli* are closer in size to those of *H. moldavicum* (Figs. 7C, 8B) but this is probably due to the PNT and Sinap limited material. The morphology of *H. macedonicum* is closely related to *H. moldavicum* and it is quite possible to derive from this taxon as it is proposed earlier (Bernor et al. 1996; Koufos and Vlachou 2005; Vlachou 2013).

Conclusions

The new material of *H. macedonicum* from the type locality, especially the skull and associated mandible, provided interesting data for this species. *Hipparion macedonicum* is usually synonymized with *H. matthwei* because of their size similarity (Forstén and Garevski 1989; Zhouhri and Bensalmia 2005). The main problem for this confusion, in my opinion, is the unknown taxonomic status and locality of *H. matthwei*. This taxon is only based on the holotype (skull and associated mandible from Samos); as it was mentioned above some skulls from Q5 of Samos referred to *H. matthewi* belong to *H. nikosi* or *H.* cf. *dietrichi* (Vlachou 2013). On the other hand, there are several fossiliferous sites in Samos which belong to different stratigraphic levels with different age (Koufos et al. 2009b) and it is impossible to correlate the holotype of *H. matthewi* to them. Besides these problems the comparison of the RPl skull of *H. macedonicum* with the holotype of *H. matthwei* indicated several morphological differences distinguishing the two taxa. The distinction of the two species was also clear from the study of some skull remains of *H. macedonicum* from the early Turolian locality NIK described recently (Koufos and Vlachou 2016). Bernor et al. (1996) and Vlachou (2013) considered that *H. matthewi* originates from *H. macedonicum*; moreover the last author suggested that *H. matthewi* of Samos and Asia Minor originated from a late Vallesian form of *H. macedonicum* which migrated in this area and adapted to the local conditions. This approach is possible but the limited material from Samos cannot complete the scheme. Considering the name *H. matthwei*, I propose to keep it only for the holotype until to find more material in Samos or in Asia Minor for certain comparisons and taxonomic results.

The study of the entire material of *H. macedonicum* suggests that the Vallesian form of the taxon differs from the Turolian one. The comparison of the two forms indicates that the first is characterized by large size, short narial opening (the nasal notch is retracted above the middle of the C-P2 diastema), long tooth rows, rich enamel plication, elongated and narrow plis, relatively robust metapodials and less running legs. The Turolian form is small with relatively elongated narial opening (the nasal notch retracted above the P2), short tooth rows, low enamel plication with short and wide plis, slender metapodials and running legs. This morphology reflects the habitat of both forms which was more open, dry and warm during the Turolian, an approach agreeing well to the known palaeoecological results based on various methods and indicators.

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