

Equidae

George D. KOUFOS

Aristotle University of Thessaloniki,
Department of Geology, Laboratory of Geology and Palaeontology,
GR-54124 Thessaloniki (Greece)
koufos@geo.auth.gr

Sevket SEN

CR2P UMR 7207 (MNHN, CNRS, UPMC, Sorbonne Universités),
Département Histoire de la Terre, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
sen@mnhn.fr

Published on 24 June 2016

urn:lsid:zoobank.org:pub:80DB85DC-7A7E-425E-9BED-57CBBDD2A872

Koufos G. D. & Sen S. 2016. — Equidae, in Sen S. (ed.), Late Miocene mammal locality of Küçükçekmece, European Turkey. *Geodiversitas* 38 (2): 225-243. <http://dx.doi.org/10.5252/g2016n2a5>

ABSTRACT

The locality Küçükçekmece includes a limited hipparion sample mainly consisting of isolated teeth and some postcranial remains. Using various methods, the teeth and postcranials are separated in two different size groups. The first group, characterized by large size, rich enamel plication, deep and thin plis, double-triple pli caballin, oval protocone with flattened lingual border, absence of lingual hypoconal groove, short and robust metapodials, is related to *H. sebastopolitanum* Borissiak, 1914 from Sebastopol, Ukraine and it is referred to as *H. aff. sebastopolitanum*. The second group with very large size, very rich enamel plication, very deep plis, double-multiple pli caballin, oval protocone with flattened lingual border, presence of lingual hypoconal groove, plicated or crenulated flexid's borders in the lower teeth, short and robust metapodials larger than those of the first form, is closer to *H. giganteum* Gromova, 1952 from Grebeniki, Ukraine and it is identified here as *H. aff. giganteum*. *Hipparion sebastopolitanum* and *H. giganteum* are known from the Ukrainian early and late Vallesian localities of Sebastopol and Grebeniki, respectively. The similarities of the first form with *H. cf. sebastopolitanum* from the Vallesian localities Pentalophos 1 and Ravin de la Pluie in Axios Valley (Macedonia, Greece), and of the second form with *H. aff. giganteum* from the terminal Vallesian locality of Nikiti 1 (Chalkidiki, Greece) support a Vallesian age for the Küçükçekmece fauna; more precisely an age from upper early Vallesian to the end of Vallesian is quite possible. The limited data of the dental and postcranial morphology of the Küçükçekmece hipparions indicate a probable forest and warm/humid environment.

KEY WORDS

Equidae,
Hipparion,
late Vallesian,
Istanbul region,
paleobiogeography.

RÉSUMÉ

Equidae.

Le site de Küçükçekmece a livré un échantillon limité appartenant à des hipparions, constitué principalement de dents isolées et de quelques restes post-crâniens. En utilisant diverses méthodes d'analyse, les dents et les os post-crâniens sont séparés en deux groupes de taille différente. Le premier groupe, caractérisé par sa grande taille, à émail très plissé, à plis profonds et minces, à double ou triple pli caballin, à protocône ovale avec bord lingual aplati, absence de sillon hypoconal lingual, à métapodes courts et robustes, ressemble à *Hipparion sebastopolitanum* Borissiak, 1914 de Sébastopol en Ukraine et il est appelé *H. aff. sebastopolitanum*. Le second groupe est de très grande taille, à émail très richement plissé, avec des plis très profonds, à double ou multiple pli caballin de pli, à protocône ovale avec bord lingual aplati, avec la présence du sillon hypoconal lingual, dents inférieures avec des bords de flexides plissés et crénelés, à métapodes courts et robustes, plus grands que ceux de la première forme, est très proche de *H. giganteum* Gromova, 1952 de Grebeniki en Ukraine, et il est attribué à *H. aff. giganteum*. *Hipparion sebastopolitanum* est connu en Ukraine au Vallésien inférieur, tandis que *H. giganteum* au Vallésien supérieur, à savoir respectivement à Sébastopol et Grebeniki. Les ressemblances de la première forme avec *H. cf. sebastopolitanum* des localités vallésiennes de Pentalophos 1 et Ravin de la Pluie dans la Vallée d'Axios (Macédoine, Grèce) et de la seconde forme avec *H. aff. giganteum* du gisement de Nikiti 1 (Chalcidique, Grèce) datant du Vallésien terminal plaident en faveur d'un âge vallésien pour la faune Küçükçekmece, plus précisément un âge entre la fin du Vallésien inférieur au Vallésien supérieur. Bien que limitées, les données extraites de la morphologie dentaire et post-crânienne des hipparions de Küçükçekmece indiquent que l'environnement du site était probablement une forêt chaude et humide.

MOTS CLÉS

Equidae,
Hipparion,
Vallésien supérieur,
région d'Istanbul,
paléobiogéographie.

INTRODUCTION

The fossiliferous deposits of Küçükçekmece are known since the 1930's when Malik & Nafiz (1933) described a mammal fauna from the east bank of Küçükçekmece lagoon. The hipparions are poorly represented including a few isolated teeth described as *H. gracile* Kaup, 1833. Quite later, Nicolas (1978) found a new fossiliferous site in the west banks of the lagoon and named it Küçükçekmece West to distinguish it from that of Malik & Nafiz (1933), which is hereafter named Küçükçekmece East. The material of the new site is part of that studied in this volume and according to Nicolas (1978) includes two hipparions, *H. cf. primigenium* and *H. eldaricum* Gabunia, 1959. Based on the mammal fauna and also on mollusks from the underlying and overlying horizons, Nicolas (1978) correlated the Küçükçekmece West fauna to late Chersonian or correlative with the mid Vallesian. Two late Miocene mammal localities are also reported from the wider area; the localities Ramiz and Osmaniye that yielded some scarce remains of mammals including a few hipparion teeth (Yalçınlar 1952). Details about the geology, stratigraphy and history of the Küçükçekmece area are given in Lom *et al.* (2016). The known hipparion material from Küçükçekmece is described and compared with other hipparion samples from the wider area of Eastern Mediterranean region and an effort for its determination is given in the present article. However, the poor and fragmentary material (mainly isolated teeth and postcranial fragments) and the bad preservation make difficult precise determinations.

MATERIAL AND METHODS

The majority of the studied Küçükçekmece material is housed at the Muséum national d'Histoire naturelle, Paris (MNHN),

while a few specimens are stored at Istanbul Technical University (ITU). The history of palaeontological investigations in the Küçükçekmece region is given by Sen (2016). The MNHN specimens (Nicolas 1978 collection) are labeled as MNHN.F.TRQ while the ITU material is without catalogue numbers and they are referred with the prefix KÇ and personal numbering in the present article. The ITU material was measured by SS and that of MNHN by GDK. All the material is measured and described according to Eisenmann *et al.* (1988). All 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) is used for the principal component analysis (PCA) and Office Excel 2010 for the Simpson's log10-ratio diagrams. The description of the material is mainly based on the MNHN.F collection.

ABBREVIATIONS

AKC	Esme-Akçaköy, Turkey;
GRE	Grebeniki, Ukraine;
GSL	Gaiselberg, Austria;
HOW	Höwenegg, Germany;
INZ	Inzersdorf, Austria;
ITU	Istanbul Technical University, Turkey;
M	measurement;
MNHN.F	Muséum national d'Histoire naturelle, Paris, Palaeontology collection;
NKT	Nikiti-1, Macedonia, Greece;
PNT	Pentalophos 1, Axios Valley, Macedonia, Greece;
RPI	Ravin de la Pluie, Axios Valley, Macedonia, Greece;
RUD	Rudabánya, Hungary;
SEB	Sebastopol, Ukraine;
SIN	Sinap, Turkey;
YLF	Yulaflı, Turkey.

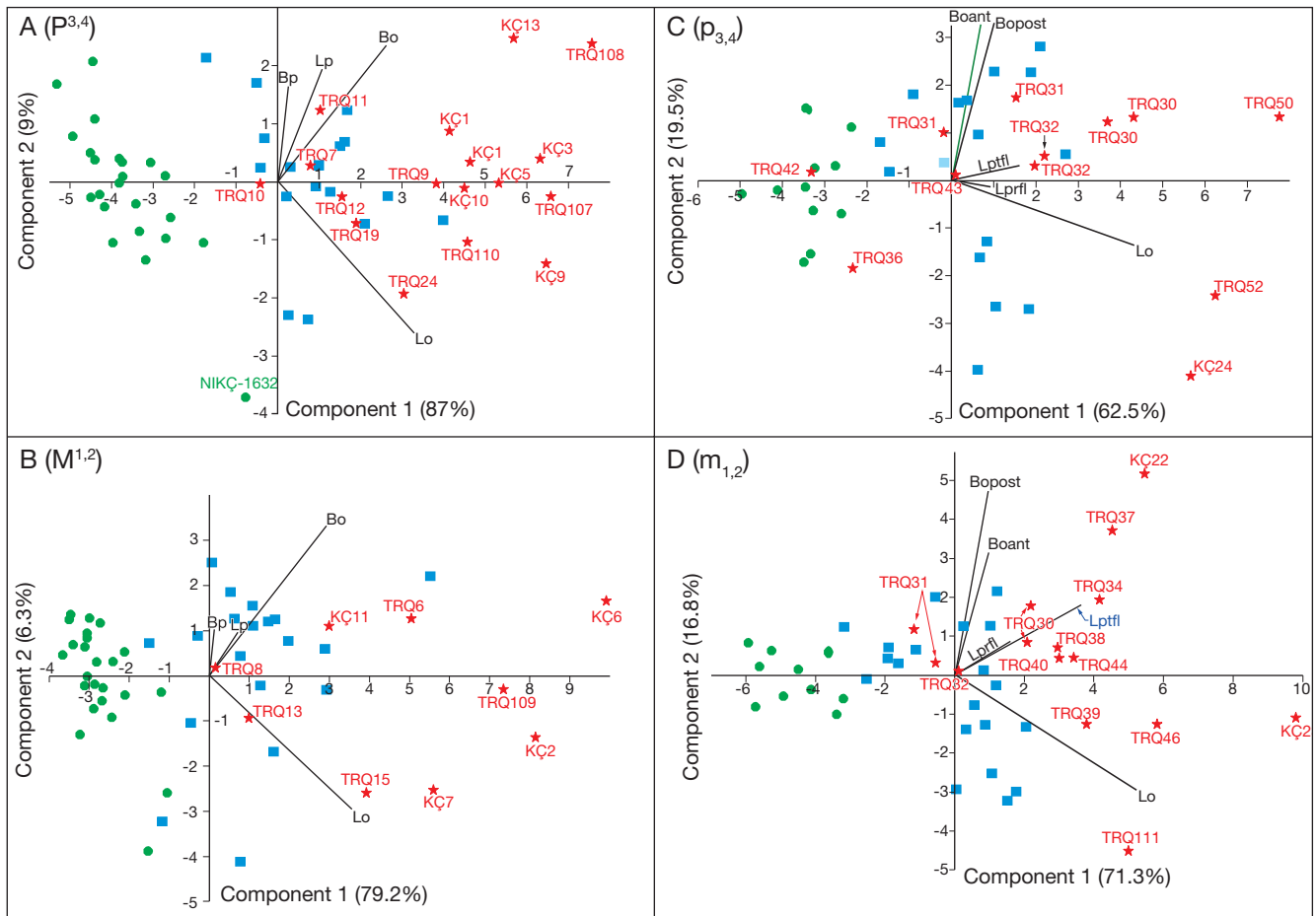


FIG. 1. — Principal component analysis separating the Küçükçekmece upper and lower cheek teeth of hipparions: **A**, upper premolars; **B**, upper molars; **C**, lower premolars; **D**, lower molars. Symbols: ●, *H. macedonicum* Koufos, 1984, Nikiti 2, NIK (Koufos & Vlachou 2016); ■, *H. philippus* Koufos & Vlachou, 2016, Nikiti 2, NIK (Koufos & Vlachou 2016); ★, Küçükçekmece material.

SEPARATION OF THE MATERIAL

The separation of the material is based on the size and the distinguished groups represent size-groups. Principal component analysis and Simpson's log-ratio diagrams are mainly used for the separation. Scatter diagrams, using different couples of measurements, are also used to confirm the results of the other methods, as well as to separate some small bones, but they are not included in the article because they have not something more to add. The separation of the isolated cheek teeth is possible using PCA (Fig. 1). The medium-sized *H. philippus* Koufos & Vlachou, 2016 and the small-sized *H. macedonicum* Koufos, 1984 from Nikiti 1 (Koufos & Vlachou 2016) are used as comparative samples; their dental metrical data are all from complete tooth rows of skulls, mandibles or their fragments. The cheek teeth of the comparative species are well separated by PC1; likely the Küçükçekmece sample is separated in two size groups (Fig. 1). Two $p_{3,4}$, MNHN.F.TRQ36 and TRQ42, are situated far from the small-sized group (Fig. 1C) but this is probably due to their advanced wear (4th wearing stage) and the related decrease of their length. The metapodials

can also help taxonomically to segregate the material but the poor and fragmentary Küçükçekmece sample prevents PCA, while Simpson's log-ratio diagrams give a clear separation (Fig. 2A, B). In fact the metapodials are separated in two size-groups, which can be correlated to those taken from the dental comparison. The second group is represented by single Mc_{III} and Mt_{III} specimens (MNHN.F.TRQ165 and TRQ84 respectively), which are clearly larger than those of the first group. Other bones that can provide reliable data for taxonomic discrimination are the astragalus, and the first and second phalanges of the third digit (Fig. 2C-E). The PCA of these bones suggests a clear separation in two size groups by PC1. The comparison of the other bones, though their number is limited, also suggests two different hipparions. In the following the first small-sized group will be referred as form-A and the larger second group as form-B.

SYSTEMATIC PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821

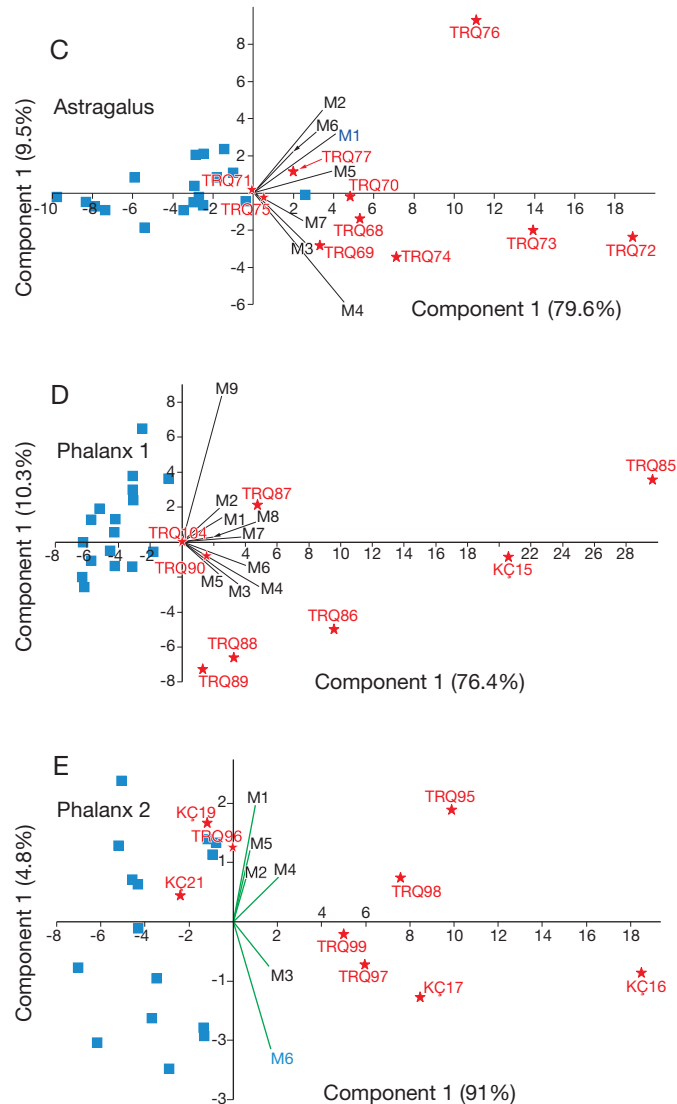
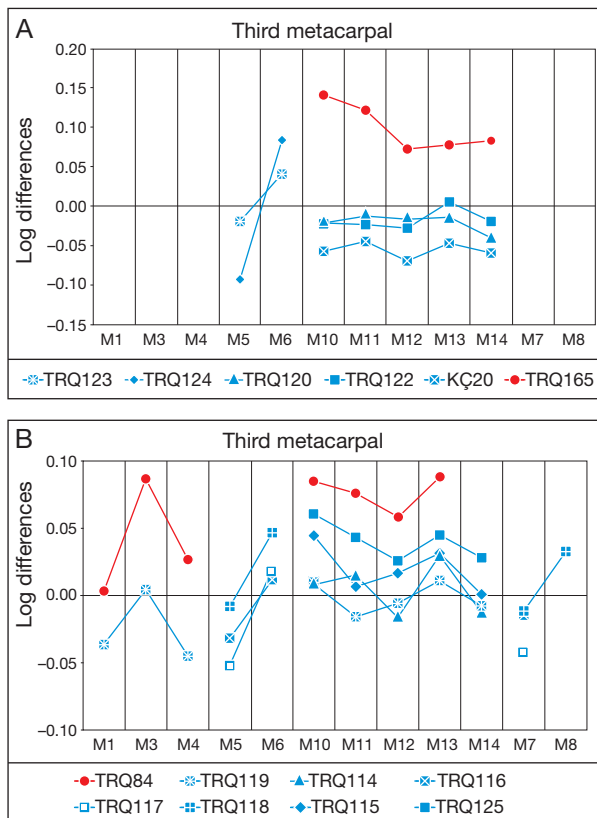


FIG. 2. — Separation of the Küçükçekmece postcranial remains of hipparions. **A, B**, Simpson's log-ratio diagrams comparing the third metacarpals (**A**) and third metatarsals (**B**); reference: *H. mediterraneum* Roth & Wagner, 1854, Pikermi (Koufos 1987); **C-E**, principal component analysis separating the astragalus (**C**), first phalanx (**D**) and second phalanx (**E**). Abbreviations: see Figure 1.

Genus *Hipparion* de Christol, 1832

Hipparion aff. *sebastopolitanum*

LOCALITY. — Küçükçekmece, Turkey.

AGE. — Late Vallesian, MN 10; Late Miocene.

MATERIAL. — See Table 1.

MEASUREMENTS. — See Table 1.

DESCRIPTION

Mandible

Three mandibular fragments (MNHN.F.TRQ30, TRQ31, TRQ32) are the most complete remains in the Küçükçekmece hipparion sample; TRQ30 preserves the complete cheek tooth row, TRQ31 the p3-m3 row and TRQ31 the p3- m1 row (Fig. 3). The mandibular ramus of TRQ30 is deep and thick,

the symphyseal part is broken but the beginning of symphysis is well distinguished, indicating a possible short muzzle. The tooth row is elongated (p2-m3 = 148.5 mm) suggesting a large hipparion. The teeth are worn, especially in MNHN.F.TRQ31, TRQ32 (VIth wearing stage).

Upper cheek teeth

The upper cheek teeth have richly plicated enamel in the fossette's borders with thin and deep plis (Fig. 4). The plication number (sum of plis in the fossette's borders + pli caballin) ranges from 14-27 (mean 19.8) plis in the P3,4 and it is 16 in the M1,2. The pli caballin is double-triple and the main one is large. The protocone is free, oval, lingually flattened in some teeth and bears a reduced spur; the latter is strong in the unworn-little worn teeth (MNHN.F.TRQ12, TRQ15). In the much worn teeth the protocone becomes more rounded and is connected with the protoloph (TRQ19). The distal hypoco-

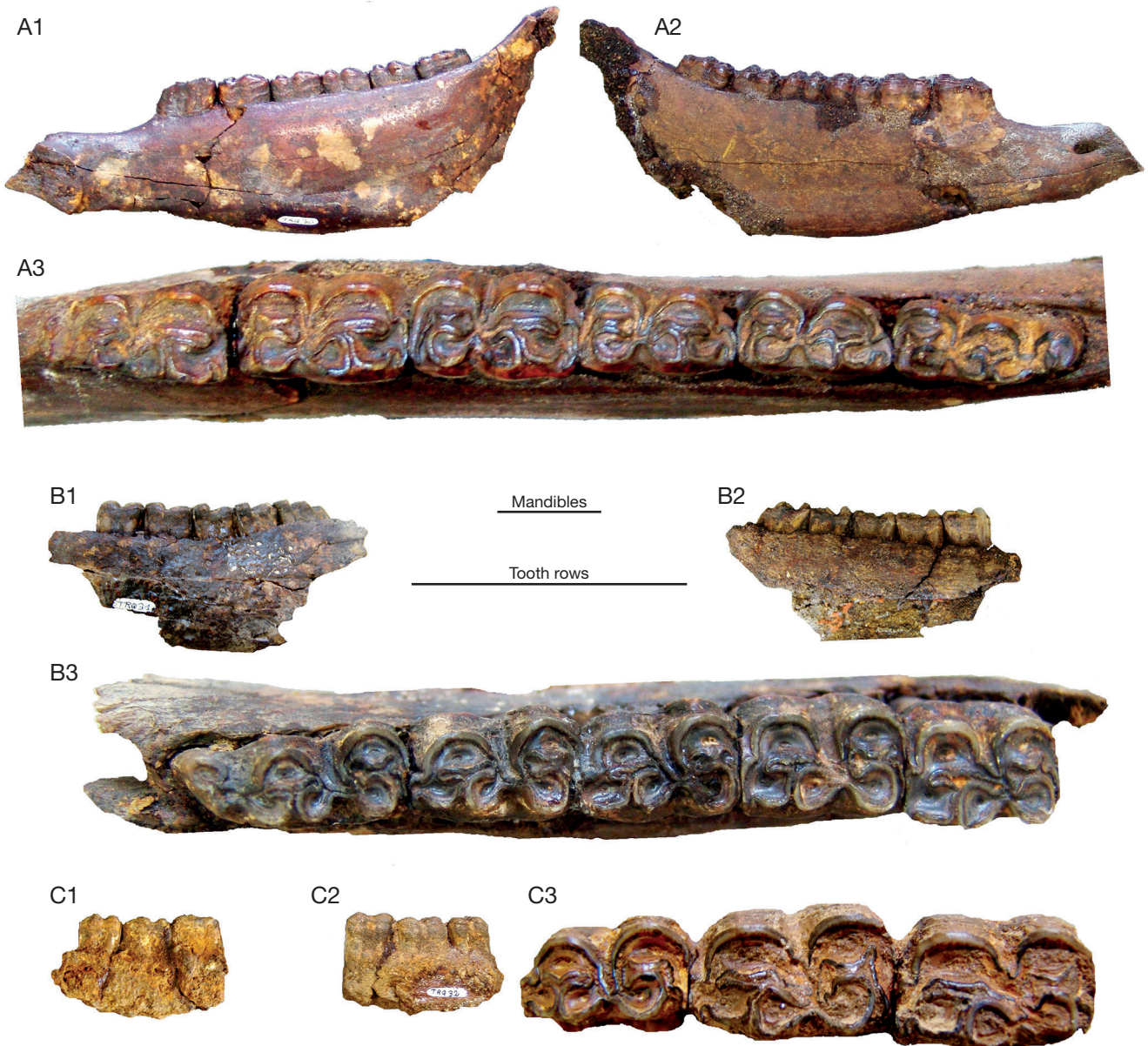


FIG. 3. — *Hipparion* aff. *sebastopolitanum*, Küçükçekmece, Turkey, Vallesian: **A**, right mandibular fragment with p2-m3 (MNHN.F.TRQ30) in lingual (**A1**), labial (**A2**) and occlusal (**A3**) views; **B**, right mandibular fragment with p3-m3 (TRQ31) in lingual (**B1**), labial (**B2**) and occlusal (**B3**) views; **C**, left mandibular fragment with p3-m1 (TRQ32) in lingual (**C1**), labial (**C2**) and occlusal (**C3**) views. Scale bars: 5 cm.

nal groove is deep, V-shaped but the wear gradually reduces its depth and breadth (TRQ19). A clear lingual hypoconal groove can be distinguished in the little worn TRQ24 and a faint one in the worn TRQ7. The height of the unworn M1,2 TRQ15 is 54 mm and its hypsodonty index (tooth length at 1 cm above the roots \times 100/height) is 38.3.

Lower cheek teeth

The p2 bears an elongated paraconid (anterostylid) pointed in MNHN.F.TRQ33 and more rounded in TRQ30 (Figs 3A; 4). The premolars are short and wide in comparison to the molars. The parastylid is well developed in all teeth and it is continuous across the mesial border of the teeth. The metaconid is elliptical-rounded. The metastylid is triangular and the entoconid almost

squarish with a small spur in the mesio-buccal corner. There is no ectostylid. The $m_{1,2}$ have a small protostylid restricted to the lower part of the tooth; despite its advanced attrition, it remains isolated and unconnected with the parastylid in the $m_{1,2}$ of TRQ30, TRQ31 but in the less worn teeth of TRQ32 it is not observable. The ectoflexid of the molars is deep and reaches the posterior border of the prefixid (TRQ30) or it is in touch with the linguaflexid. The pli caballinid is very weak in the molars. The pre- and post-flexid borders are plicated or crenulated. Two isolated m3, TRQ41 (Fig. 5) and KÇ25, might belong to this hipparion. The eruption way of the m3 in equids affects the value of its length and makes difficult a precise comparison. The size of TRQ41 and KÇ25 is similar to that of TRQ30, TRQ31 and both can be included to this hipparion.



FIG. 4. — *Hipparion* aff. *sebastopolitanum*, Küçükçekmece, Turkey, Vallesian, upper and lower cheek teeth. The position of the teeth is given in Table 1. Scale bar: 4 cm.



FIG. 5. — *Hipparion* aff. *giganteum*, Küçükçekmece, Turkey, Vallesian, upper and lower cheek teeth; the specimens MNHN.F. TRQ14, TRQ17, TRQ41, and TRQ106 cannot be certainly attributed to one of the Küçükçekmece hipparions. The position of the teeth is given in Table 1. Scale bar: 4 cm.

Metapodials

The metapodials of form-A dominate in the Küçükçekmece sample but are all incomplete (Fig. 6); the distal fragment of the Mc_{III} MNHN.F.TRQ21 is not included in the sample as it is strongly eroded and its measurements are not reliable. The sample of proximal and distal fragments of the Mc_{III} are close in size to *H. mediterraneum* Roth & Wagner, 1854 from Pikermi (Fig. 2) but their length is unknown. The keel index ($M12 \times 100/M13$) is on average 117 vs 117 for *H. primigenium* from Höwenegg, 115 from Akçaköy and 116 from Eppelsheim; for the strong keel bearing metacarpals of *H. mediterraneum* from Pikermi and *H. philippus* from Nikiti 2 the keel index is 119 and 123 respectively. The Mt_{III} is short and relatively robust; the slenderness index ($M11 \times 100/M1$) is on average 15.3 vs 16.2 for *H. primigenium* from Höwenegg, 14.3 from Akçaköy and 15.2 from Vienna Basin. The same index for the slender metatarsals of *H. mediterraneum* from Pikermi and *H. philippus* from Nikiti 2 is 13.7. The keel index for Mt_{III} is on average 121 vs 121 for *H. primigenium* from Höwenegg and Akçaköy, and 122 from Vienna Basin; the keel index of *H. mediterraneum* from Pikermi and *H. philippus* from Nikiti 2 with strong keel is 127 on average [data taken from Koufos (1987), Bernor *et al.* (1997, 2003) and Koufos & Vlachou (2016)]. Thus, the metapodials of the Küçükçekmece form-A are short and relatively robust with weakly developed keel.

Hipparion aff. *giganteum* Gromova, 1952

LOCALITY. — Küçükçekmece, Turkey.

AGE. — Late Vallesian, MN 10; Late Miocene.

MATERIAL. — See Table 1.

MEASUREMENTS. — See Table 1.

DESCRIPTION

Upper cheek teeth

The upper cheek teeth are large with very rich enamel plication in the fossette's borders and with thin and very deep plis (Fig. 5); the plication number ranges between 14–31 in the premolars and between 23–24 in the molars. The protocone is large, elliptical-oval with flattened lingual wall in the less worn teeth; in MNHN.F.TRQ110 it bears a small mesial spur. The pli caballin is simple to triple. The distal hypoconal groove is well developed and deep while a large lingual hypoconal groove is present in the premolars and a small one in the molars. The P2 TRQ106 has a small and pointed anterostyle, closed fossettes, very rich enamel plication in the fossette's borders (mean plication number = 21), isolated and oval protocone with a small mesial spur, triple pli caballin, deep and narrow distal hypoconal groove, and a shallow and clear lingual hypoconal groove (Fig. 5). The presence of the lingual hypoconal groove, the very rich enamel plication, the multiple pli caballin, and the size of the P2 TRQ106 fit well with the Küçükçekmece form-B morphology.

Lower cheek teeth

The lower premolars are unworn or less worn preventing the description of their occlusal morphology (Fig. 5). However, the lower molars (MNHN.F.TRQ46, TRQ111) are more worn and their morphology is clear. The parastylid is well developed and high in TRQ46. The ectoflexid is narrow and deep in the molars with a weak pli caballinid, and the linguaflexid is deep and V-shaped. The pli caballinid is weak and it is reduced by the wear. The metaconid and metastylid are rounded (in the less worn teeth they are elliptical) and the entoconid squarish. The preflexid and postflexid borders are plicated and (or) crenulated. There is not any trace of the ectostylid.

Metapodials

There is only a fragment of the Mc_{III} and an almost complete Mt_{III} (Fig. 6). The slenderness index is 17 for the Mt_{III} and the keel index is 117 for the Mc_{III} and 118 for the Mt_{III} , indicating short and robust metapodials with weak keel.

RESULTS

The main morphological characters of the Küçükçekmece hipparions, like the rich-very rich enamel in the fossette's borders of the upper cheek teeth, the thin and deep plis, the multiple pli caballin, the large protocone with straight lingual wall and spur, the presence of the lingual hypoconal groove, the relatively short and wide $p_{3,4}$, the plicated and/or crenulated enamel in the flexid's borders of the lower teeth, the relatively short and robust metapodials with weak keel, are characters indicating Vallesian hipparions. Several hipparions are known from the Vallesian of Eastern Mediterranean. In the Vallesian of northern Greece, in addition to *H. macedonicum* which is a small-sized hipparion, two other species *H. cf. sebastopolitanum* and *H. aff. giganteum* are known from the localities Pentalophos 1 (PNT), Ravin de la Pluie (RPL) and Nikiti 1 (NKT), (Vlachou 2013; Koufos *et al.* 2016). Forstén (1978) reported *H. primigenium* (von Meyer, 1829) from Bulgaria but the collection is old and needs revision. Several Vallesian hipparions are known from Turkey. *Hipparion ankyranum* Ozansoy, 1965 from Sinap, Turkey was described by Ozansoy (1965) but Bernor *et al.* (2003) considered that this name must be restricted only to the type specimen. The same authors described from Sinap five more taxa, *H. sinapensis* Bernor, Scott, Fortelius, Kappelman & Sen, 2003, *H. uzunagizli* Bernor, Scott, Fortelius, Kappelman & Sen, 2003, *H. kecigibi* Bernor, Scott, Fortelius, Kappelman & Sen, 2003, *Hipparion* sp. 1 and *Hipparion* sp. 2, based mainly on cranial remains. The large-sized *H. primigenium* is reported from the early Vallesian locality of Esme-Akçaköy (AKC), (Bernor *et al.* 2003) while a similar in size hipparion, named *H. cf. primigenium*, is known from the late Vallesian locality of Yulaflı (YLF), Turkey (Geraads *et al.* 2005).

The mandibular fragments MNHN.F.TRQ30 and TRQ31, though their limited measurements, are compared with some Vallesian hipparion taxa of the wider area (Fig. 7A). Both specimens are close to *H. primigenium* from Höwenegg,

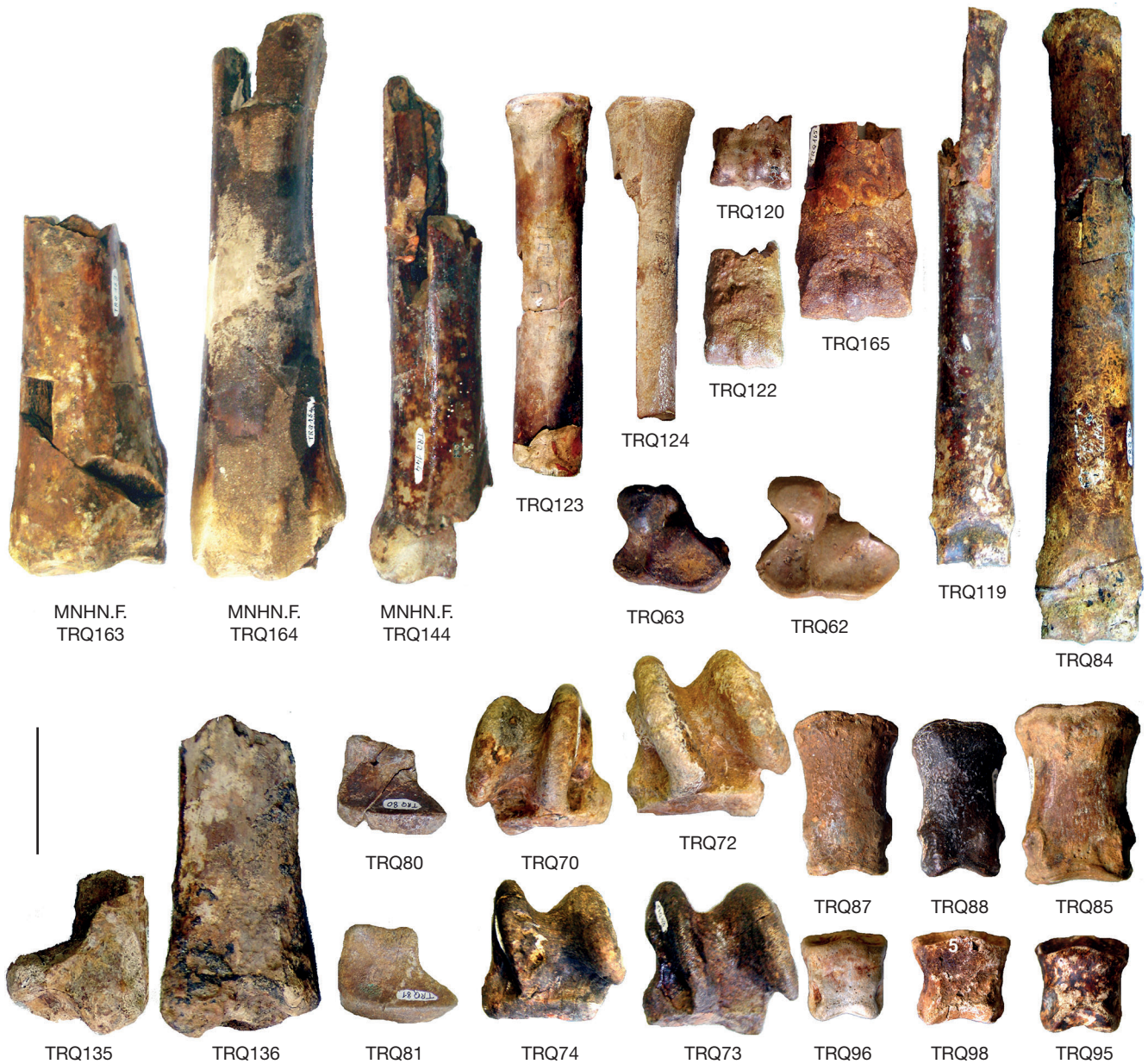


FIG. 6. — *Hipparion* aff. *sebastopolitanum* and *H.* aff. *giganteum*, Küçükçekmece, Turkey, Vallesian, postcranial remains. The determination of the bones is given in Table 1. Scale bar: 5 cm.

Germany, but their tooth rows are shorter. They also have similarities with *H.* cf. *sebastopolitanum* from the Greek localities Pentalophos 1 and Ravin de la Pluie, as well as with *H.* aff. *giganteum* from Nikiti 1, Greece; the latter taxon differs from the Küçükçekmece mandibles in having higher mandibular corpus (M11, M12 in Fig. 7A). The dental morphology and size of the Küçükçekmece mandibles are closer to *H.* cf. *sebastopolitanum* from Pentalophos 1. The specific determination of the isolated teeth of hipparions is almost impossible because of the more or less similar morphology, the wear influence to the dental dimensions, and the great number of similar size taxa.

Third metapodials provide quite reliable results for specific determination of equids, but the limited and fragmentary

Küçükçekmece material is not suitable. The Mc_{III} of the Küçükçekmece form-A is compared with *H.* *primigenium*, *H.* cf. *sebastopolitanum* and the Sinap Vallesian hipparions (Fig. 8A). It differs from the Mc_{III} of aff. *H.* *uzunagizli* having more robust distal part, larger DAP of the proximal articular facet and larger DT in the mid-shaft (M3, M6, M11-M14 in Fig. 8A). The Mc_{III} of *H.* *sinapensis* and aff. *H.* *kecigibi* differs also from the Küçükçekmece form-A being larger. The Mc_{III} of *H.* *primigenium* from various localities is significantly larger than that of the Küçükçekmece form-A (Fig. 8B). The Yulafli Mc_{III} , described as *H.* cf. *primigenium*, seems to be closer to the Küçükçekmece form-A and might belong to the same taxon. The Küçükçekmece Mc_{III} is proportionally similar to *H.* cf. *sebastopolitanum* from the Greek sites Pentalophos 1

and Ravin de la Pluie, especially to the previous one (Fig. 8A); the observed minor differences are probably due to their limited samples. This similarity indicates that the hipparions of these localities could belong to the same taxon. The Mt_{III} of the Küçükçekmece form-A is more slender than that of aff. *H. kecigibi* from Sinap; it is smaller and more robust than *H. sinapensis*, aff. *H. uzunagizli* and *H. primigenium* from the various Sinap localities (Fig. 8D). On the other hand, although shorter it has similar size and proportions to the *H. cf. sebastopolitanum* from Pentalophos 1 (Fig. 8C), confirming its close relationships with this hipparion form. The astragalus of the Küçükçekmece form-A is smaller than *H. primigenium* and *H. aff. giganteum* but it has similar size and proportions with *H. cf. sebastopolitanum* from Pentalophos 1 (Fig. 7B). The first phalanx is also proportionally similar with Pentalophos 1 and Ravin de la Pluie *H. cf. sebastopolitanum* and remarkably smaller than *H. primigenium* and *H. giganteum* (Fig. 7C).

The sample of the Küçükçekmece form-B lacks cranial or mandibular remains, while the available isolated teeth cannot provide reliable results for its identification. The single known Mc_{III} fragment of the Küçükçekmece form-B, although larger than *H. giganteum* from Grebeniki (Ukraine) and *H. aff. giganteum* from Nikiti 1, might be attributed to this species (Fig. 8B). The other skeletal elements are similar in size to *H. giganteum* and *H. primigenium* from various localities (Fig. 8C, D). The similarity of the Küçükçekmece form-B astragalus with *H. aff. giganteum* from Nikiti 1 is quite clear but it is also close to *H. primigenium* (Fig. 7B). Concerning the first phalanx it is larger in size than the typical *H. giganteum* from Grebeniki and *H. aff. giganteum* from Nikiti 1 (Fig. 7C). Vlachou (2013) and Koufos & Vlachou (2016) noted the similarity of *H. aff. giganteum* from Nikiti 1 with *H. intrans* from the early Vallesian locality of Rudabánya, Hungary. Actually the single known Mt_{III} of *H. intrans* is metrically similar to the Küçükçekmece form-B as well as to *H. giganteum* from Grebeniki and *H. aff. giganteum* from Nikiti 1 (Fig. 8C). Despite its similarity with the Mt_{III} of these hipparions, it is longer than all, but this difference could be artificial since it is the only known specimen of *H. intrans*. Taking in mind the above similarities, the Küçükçekmece form-B can be considered as closer to *H. giganteum* but the limited and fragmentary material cannot allow a precise determination and for this reason it is identified as *H. aff. giganteum*.

DISCUSSION

The general morphological characters of the Küçükçekmece hipparions, like the large size, the rich-very rich enamel plication, the elliptical protocone with flattened lingual border, the double-multiple pli caballin, the presence of lingual hypoconal groove and the relatively short and robust metapodials indicate that they belong to *H. primigenium*-Group of Bernor *et al.* (1996) or to “*primigenium*-morphotype” of Vlachou (2013). The similarities with *H. sebastopolitanum* and *H. giganteum* support this assignment, as both taxa belong to the same morphotype.

H. primigenium was originally described from the Vallesian locality of Eppelsheim, Germany based on a fragmentary dental material (von Meyer 1829). A nice and rich sample of *H. primigenium*, including several complete skeletons, is known from Höwenegg, Germany (Bernor *et al.* 1997). The dental size and morphology of the Küçükçekmece hipparions have some general similarities to that of the Höwenegg *H. primigenium* but they differ from this taxon. The Küçükçekmece form-B has less enamel plication in the upper cheek teeth and larger size. Its postcranials, except astragalus, are larger than *H. primigenium* and closer to *H. giganteum*; even astragalus is very similar to *H. aff. giganteum* from Nikiti 1 (Figs 7, 8). The Küçükçekmece form-B differs from *H. primigenium* having smaller size, less enamel plication in the upper cheek teeth, frequently absent lingual hypoconal groove and more robust metapodials.

H. giganteum is known from Grebeniki (GRE), Ukraine and is characterized by its large size (P2-M3=152-156 mm), rich enamel plication, multiple pli caballin and presence of the lingual hypoconal groove, characters that are present in the Küçükçekmece form-B. The metapodials of *H. giganteum* are relatively short and robust with weak keel; the slenderness and keel index are 17 and 121 on average for the Mc_{III}, as well as 16 and 130 for the Mt_{III}, respectively; these indices are very close to those for the Küçükçekmece form-B (117 for Mc_{III} and 16 and 118 for Mt_{III} respectively). The morphological characters and the dimensions of the Küçükçekmece form-B suggest close relationships with *H. giganteum* but the fragmentary and poor material prevents a certain attribution. Instead to describe the Küçükçekmece form-B as *Hipparion* sp., which has no meaning, it is better to refer it to as *H. aff. giganteum* indicating their relationships.

H. sebastopolitanum is also known from Ukraine, found at the locality Sebastopol, and characterized by rich enamel plication, double pli caballin, oval protocone, presence of the lingual hypoconal groove, and relatively short and robust metapodials (Borissiak 1914: pl. 8, figs 6-8; Watabe 2004). The morphology of the Küçükçekmece form-A resembles that of *H. sebastopolitanum*, while its postcranials fit well those from the Greek localities Pentalophos 1 and Ravin de la Pluie described as *H. cf. sebastopolitanum* (Figs 7, 8). These similarities of the Küçükçekmece form-A with *H. sebastopolitanum* allow us to refer this to as *H. aff. sebastopolitanum*.

The Küçükçekmece hipparions have similarities with the hipparions of the Black Sea from Grebeniki and Sebastopol. Various opinions have been expressed about the age of both localities. The most recent revision of all bio- and geo-chronological data suggests an early Vallesian (MN 9) age for Sebastopol and a late Vallesian (MN 10) age for Grebeniki (Vangengeim & Tesakov 2013). The strong similarity of the Küçükçekmece form-A with the early Vallesian *H. cf. sebastopolitanum* from Pentalophos 1, dated to the early Vallesian, MN 9 (Koufos 2013; Konidaris *et al.* 2016) supports its Vallesian age. More exactly Pentalophos 1 is considered slightly older than the locality Xirochori 1 of Axios Valley (Macedonia, Greece) which is dated at c. 9.6 Ma (Sen *et al.* 2000). Therefore an age at the upper part of early Vallesian,

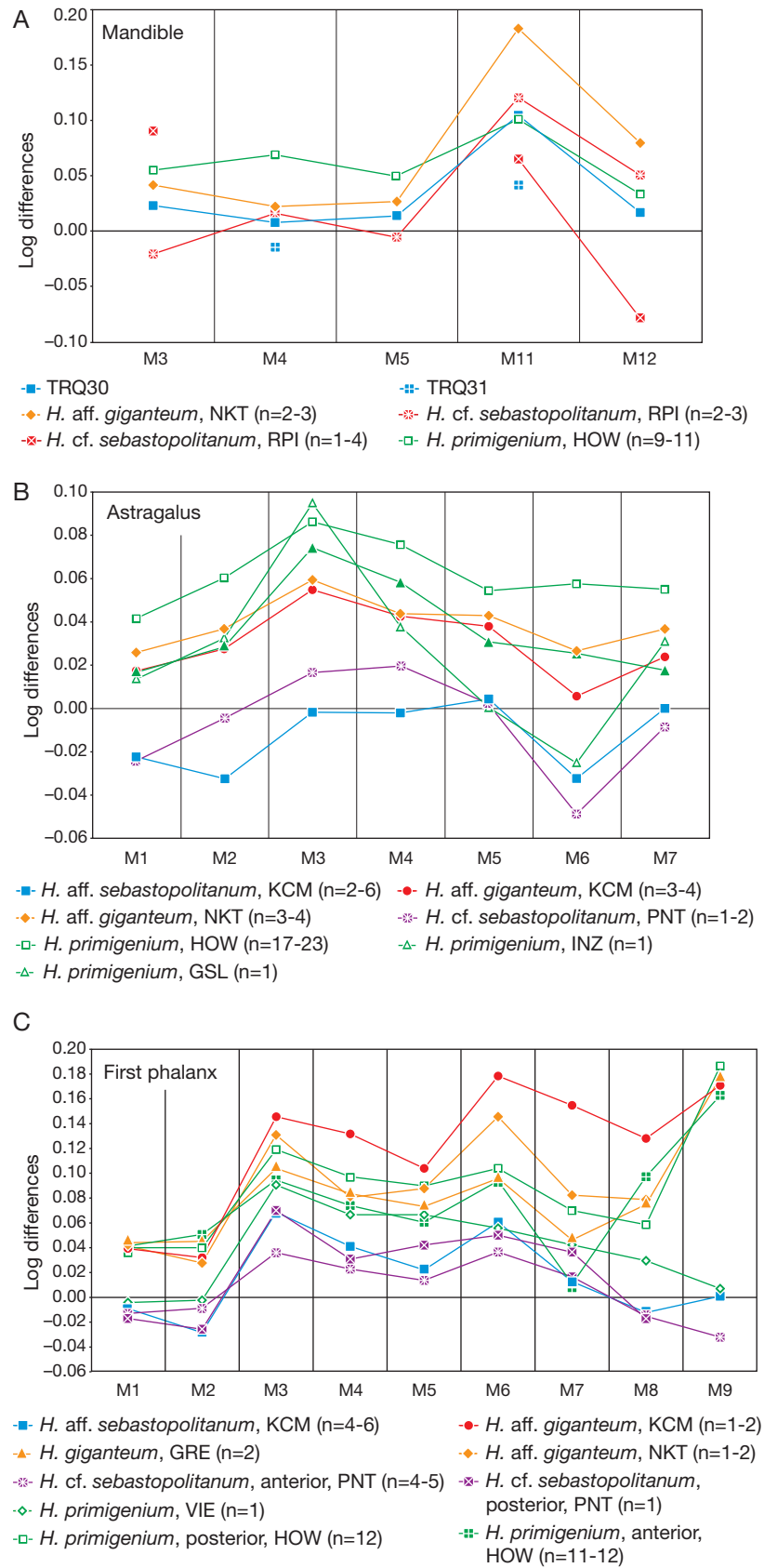


FIG. 7. — Simpson's log-ratio diagrams comparing the mandible (A), astragalus (B) and first phalanx (C) of the Küçükçekmece hipparions with various species. Reference: *H. mediterraneum*, Pikermi (Koufos 1987); data taken from Bernor *et al.* (1988, 1997), Koufos (2000a, b) and <http://www.vera-eisenmann.com>.

MN 9 is possible for Pentalophos 1. Likely, the similarity of the Küçükçekmece form-B with *H. aff. giganteum* from Nikiti 1 confirms its Vallesian age as Nikiti 1 is dated to the terminal Vallesian (Koufos *et al.* 2016). The similarity of the Küçükçekmece form-A Mc_{III} to that from Yulafli (Fig. 7B), dated to the late Vallesian (Geraads *et al.* 2005) supports the Vallesian age of the Küçükçekmece fauna. Considering the hipparion biochronological data an age from the upper early Vallesian to the end of Vallesian is quite possible for Küçükçekmece.

The limited fossil material does not allow for a comprehensive analysis of Küçükçekmece palaeoenvironmental setting. However, the dental morphology of hipparions can provide some indications. The rich enamel plication with deep and thin plis is related with the feeding preferences of hipparions and consequently to the environment. Gromova (1952) and Forstén (1968) related this dental morphology with non-abrasive vegetation suggesting a closed habitat as it allows the broken up of soft food (herbs, leaf) but not those of hard particles because the intervening space between the enamel lamellae is very narrow. The habitat score of Scott (2004) has been calculated for the two available Küçükçekmece metatarsals and its values -0.86 and -1.15 indicate an environment close to the forest one. Geraads *et al.* (2005) suggest a forest/humid environment for the neighboring late Vallesian Yulafli fauna, confirming the above indications for the Küçükçekmece environment. Therefore, the limited data of the hipparion morphology indicate a possible closed and warm/humid environment for Küçükçekmece.

CONCLUSIONS

In conclusion the Küçükçekmece hipparion remains, though their fragmentary character and small sample size, can be separated into two size forms. The Küçükçekmece form-A is characterized by its large size, richly plicated upper teeth (less enamel plication than in form-B) with deep and thin plis in the upper cheek teeth, single to double pli caballin, oval protocone with flattened lingual border, rare presence of a weak lingual hypoconal groove, rare plicated or crenulated enamel in the flexid's borders of the lower cheek teeth and relatively short and robust metapodials (smaller than the Küçükçekmece form-B). All the morphological and metrical data of the Küçükçekmece form-A are comparable to those of *H. sebastopolitanum* and it is referred to as *H. aff. sebastopolitanum*.

The form B is characterized by its very large size, very rich enamel plication in the upper cheek teeth with very deep and thin plis, double-multiple pli caballin, oval protocone with flattened lingual border, presence of lingual hypoconal groove, plicated or crenulated enamel in the flexid's borders of the lower cheek teeth and short and robust metapodials. Its morphology and size suggest similarities to *H. giganteum* and thus it is referred to as *H. aff. giganteum*.

The morphology of both Küçükçekmece hipparions, their similarity to *H. giganteum* and *H. sebastopolitanum*, as well as

their strong similarities with the corresponding forms from the Vallesian Greek localities Pentalophos 1, Ravin de la Pluie and Nikiti 1 suggest for Küçükçekmece an age from the upper part of early Vallesian to the end of Vallesian. It is noteworthy that the Küçükçekmece mammal collection is poor and an extensive field work is necessary for more precise and reliable taxonomic and biochronologic results. The limited data from the study of the Küçükçekmece hipparions indicate a possible forest/warm/humid environment for Küçükçekmece.

Acknowledgements

We would like to thank Mehmet Sakıncı (ITU), Christine Argot and Vincent Pernègre (MNHN) for access to the Küçükçekmece collections under their care, and for facilities in their study. G.D.K. thanks S. Sen for inviting him to participate in the study of the Küçükçekmece fauna. We are grateful to Philippe Loubry (CNRS-MNHN) and Ozan Erdal (ITU) for the photos of Küçükçekmece hipparions. Many thanks also to the referees Raymond-Louis Bernor and Serdar Mayda for their useful comments which greatly improved this article.

REFERENCES

- BERNOR R.-L., KOUFOS G.D., WOODBURN M. & FORTELIUS M. 1996. — The evolutionary history and biochronology of European and southeastern Asian late Miocene and Pliocene hipparionine horses, in BERNOR R. L., FAHLBUSCH V. & MITTMANN H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 7-46.
- BERNOR R.-L., TOBIEN H., HAYEK L.-A. C. & MITTMANN H.-W. 1997. — *Hippotherium primigenium* (Equidae, Mammalia) from the late Miocene of Höwenegg (Heugau, Germany). *Andrias* 10: 307-338.
- BERNOR R.-L., KOVAR-EDER J., LIPSCOMB D., RÖGL F., SEN S. & TOBIEN H. 1988. — Systematic, stratigraphic, and paleoenvironmental contexts of first-appearing hipparion in the Vienna Basin, Austria. *Journal of Vertebrate Paleontology* 8: 427-452.
- BERNOR R.-L., SCOTT R. S., FORTELIUS M., KAPPELMANN J. & SEN S. 2003. — Systematics and evolution of the late Miocene hipparions from Sinap, Turkey, in FORTELIUS M., KAPPELMANN J., SEN S. & BERNOR R.-L. (eds), *The Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York: 220-281.
- BORISSIAK A. A. 1914. — Sevastopolskaya fauna melkopitayushikh. *Trudy geologicheskogo komiteta* n.s. 87: 1-154 (in Russian with French summary).
- EISENMANN V., ALBERDI M.-T., GIULI C. DE & STAESCHE U. 1988. — Methodology, in WOODBURN M. & SONDAAR P. Y. (eds), *Studying Fossil Horses*. E.J.Brill press, Leiden and New York: 1-71.
- FORSTÉN A. M. 1968. — Revision of the palearctic *Hipparion*. *Acta Zoologica Fennica* 119: 1-134.
- FORSTÉN A. M. 1978. — A review of the Bulgarian *Hipparion*. *Geobios* 11 (1): 31-41.
- GERAADS D., KAYA T. & MAYDA S. 2005. — Late Miocene large mammals from Yulafli, Thrace region, Turkey, and their biogeographic implications. *Acta Palaeontologica Polonica* 50 (3): 523-544.
- GROMOVA V. 1952. — Le genre *Hipparion*. *Bureau de Recherches géologiques et Minières CEDP* 12: 1-288.
- HAMMER C., HARPER D. A. T. & RYAN P. D. 2001. — PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4 (1): 1-9.

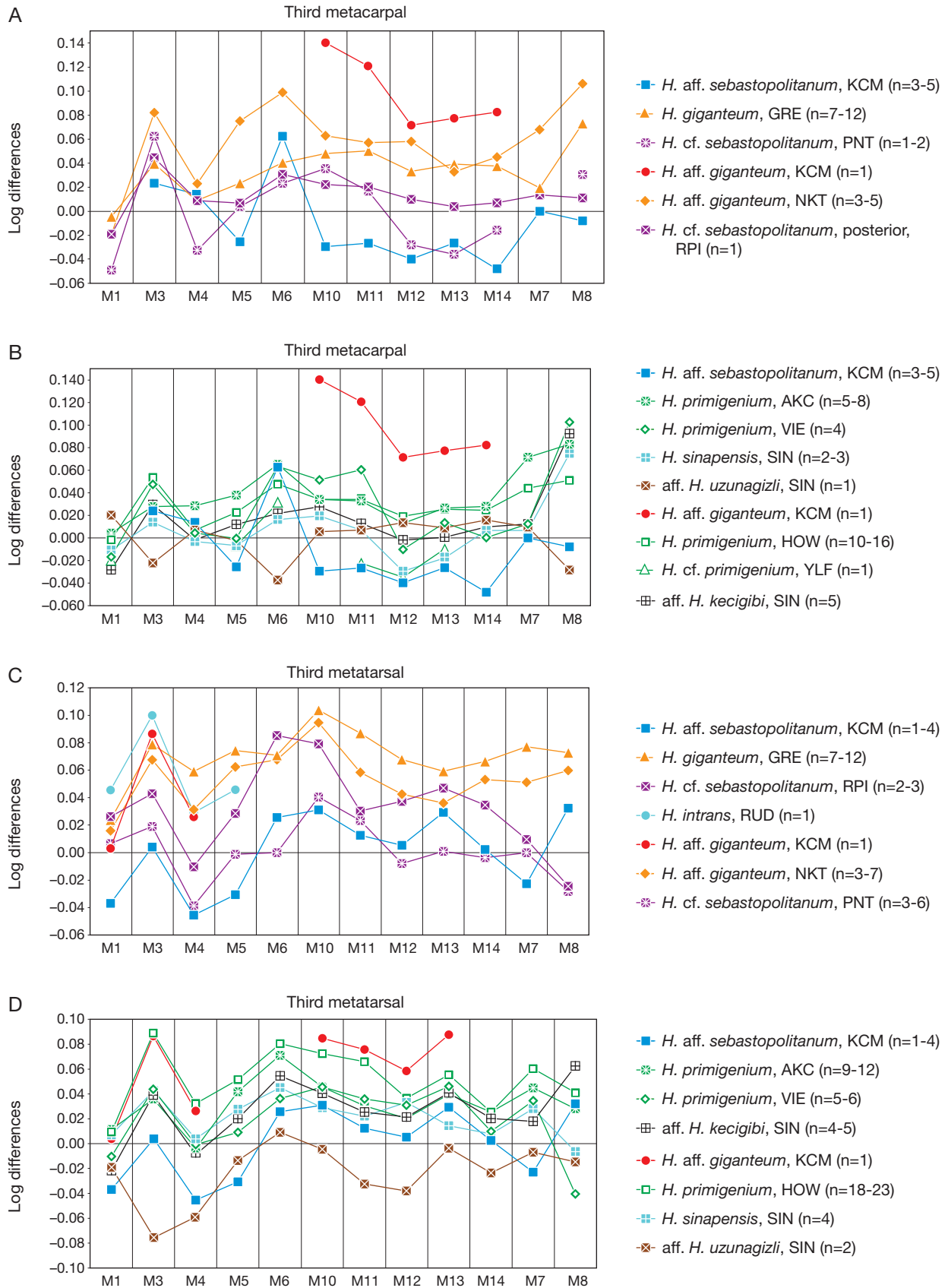


FIG. 8. — Simpson's log-ratio diagrams comparing the third metapodials of the Küçükçekmece hipparions with various species. Reference: *H. mediterraneum*, Pikermi (Koufos 1987); data taken from Bernor *et al.* (1988, 1997, 2003), Koufos (1986, 2000a, b), Geraads *et al.* (2005), and <http://www.vera-eisenmann.com>.

- KONIDARIS G. E., KOUFOS G. D., KOSTOPOULOS D. S. & MERCERON G. 2016. — Taxonomy, biostratigraphy and palaeoecology of *Choerolophodon* (Proboscidea, Mammalia) in the Miocene of SE Europe-SW Asia: implications for phylogeny and biogeography. *Journal of Systematic Palaeontology* 14 (1): 1-27. <http://dx.doi.org/10.1080/14772019.2014.985339>
- KOUFOS G. D. 1986. — Study of the Vallesian hipparions of the lower Axios Valley (Macedonia, Greece). *Geobios* 19: 61-79.
- KOUFOS G. D. 1987. — Study of the Pikermi hipparions. Part I: Generalities and taxonomy. *Bulletin du Muséum national d'Histoire naturelle Paris*, 4^e sér., 9, sect. C, 2:197-252. Part II: Comparisons and odontograms. *Bulletin du Muséum national d'Histoire naturelle Paris* 4^e sér., 9, sect. C, 3: 327-363.
- KOUFOS G. D. 2000a. — New material of Vallesian hipparions (Mammalia, Perissodactyla) from the lower Axios Valley, Macedonia, Greece. *Senckenbergiana lethaea* 80: 231-255.
- KOUFOS G. D. 2000b. — The hipparions of the late Miocene locality "Nikiti 1", Chalkidiki, Macedonia, Greece. *Revue de Paléobiologie* 19 (1): 47-77.
- KOUFOS G. D. 2013. — Neogene mammal biostratigraphy and chronology of Greece, in WANG X., FLYNN L. J. & FORTELIUS M. (eds), *Fossil Mammals of Asia – Neogene Biostratigraphy and Chronology*. Columbia University Press, New York: 595-621.
- KOUFOS G. D. & VLACHOU T. D. 2016. — Equidae, in Koufos G. D. & Kostopoulos D. S. (eds), Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). *Geobios* 49 (1-2): 85-118. <http://dx.doi.org/10.1016/j.geobios.2016.01.001>
- KOUFOS G. D., KOSTOPOULOS D. S. & VLACHOU T. D. 2016. — Revision of the Nikiti 1 (NKT) fauna with description of new material, in KOUFOS G. D. & KOSTOPOULOS D. S. (eds), Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). *Geobios* 49 (1-2): 11-22. <http://dx.doi.org/10.1016/j.geobios.2016.01.006>
- LOM N., ÜLGEN S. C., SAKINÇ M. & ŞENGÖR A. M. C. 2016. — Geology and stratigraphy of Istanbul region, in SEN S. (ed.), Late Miocene mammal locality of Küçükçekmece, European Turkey. *Geodiversitas* 38 (2): 175-195 (this volume). <http://dx.doi.org/10.5252/g2016n2a3>
- MALIK A. & NAFIZ H. 1933. — Vertébrés fossiles de Küçükçekmece. *Bulletin de la Faculté des Sciences d'Istanbul* 8: 1-119.
- NICOLAS P. J. 1978. — Un nouveau gisement de Vertébrés dans le Chersonien : Kutchuk-Tchekmedjè Quest (Thrace turque). *Comptes rendus de l'Académie des Sciences de Paris* 287: 455-458.
- OZANSOY F. 1965. — Étude des gisements continentaux et des mammifères du Cénozoïque de Turquie. *Mémoires de la Société géologique de France* 102: 1-92.
- SCOTT R. 2004. — *The Comparative Paleocology of Late Miocene Eurasian Hominoids*. PhD thesis, University of Texas, 458 p.
- SEN S., KOUFOS G. D., KONDOPOULOU D. & BONIS L. DE. 2000. — Magnetostratigraphy of the late Miocene continental deposits of the lower Axios valley, Macedonia, Greece, in KOUFOS G. D. & IOAKIM C. (eds), Mediterranean Neogene cyclostratigraphy in marine-continental deposits. *Bulletin of the Geological Society of Greece*, sp. publ. 9: 197-206.
- SEN S. 2016. — Historical background, in SEN S. (ed.), Late Miocene mammal locality of Küçükçekmece, European Turkey. *Geodiversitas* 38 (2): 153-173 (this volume). <http://dx.doi.org/10.5252/g2016n2a2>
- VANGENGEM E. & TESAKOV A. 2013. — Late Miocene mammal localities of Eastern Europe and Western Asia, in WANG X., FLYNN L. J. & FORTELIUS M. (eds), *Fossil Mammals of Asia – Neogene Biostratigraphy and Chronology*. Columbia University Press, New York: 521-545.
- VLACHOU T. D. 2013. — *Palaeontological, Biostratigraphical and Palaeoecological Study of the Greek Hipparions*. PhD Thesis, Aristotle University of Thessaloniki, 592 p. (in Greek with English summary).
- VON MEYER H. 1829. — Taschenbuch für die gesamte Mineralogie. *Zeitschrift für Mineralogie, Neue Folge* 23: 150-152.
- WATABE M. 2004. — *Phylogeny of Old World Hipparionine Horses (Equidae, Perissodactyla, Mammalia). Its Pattern and Process*. PhD Thesis, Osaka University, 551 p.
- YALÇINLAR I. 1952. — Les Vertébrés fossiles néogènes de la Turquie occidentale. *Bulletin du Muséum national d'Histoire naturelle*, 2^{ème} sér., 24 (4): 423-429.

Submitted on 9 July 2015;
accepted on 2nd March 2016;
published on 24 June 2016.

ABBREVIATIONS USED IN TABLE 1

Mandible

M3	Premolar length (alveolar);
M4	Molar length (alveolar);
M5	Tooth row length (alveolar);
M11	Depth of the jaw between p4 and m1;
M12	Idem in front of p2.

Upper Teeth

M1	L _o = occlusal length;
M2	B _o = occlusal breadth;
M3	L _p = protocone length;
M4	B _p = protocone breadth;
M5	L _b = length at 1 cm from the base of the crown;
M6	B _b = breadth at 1 cm from the base of the crown;
EF	enamel formula.

Lower Teeth

M1	L _o = occlusal length;
M2	B _o ant = anterior occlusal breadth;
M3	B _o post = posterior occlusal breadth;
M4	L _{prfl} = preflexid length;
M5	L _{ptfl} = postflexid length;
M6	L _b = length at 1 cm from the base of the crown;
M7	B _b = breadth at 1 cm from the base of the crown;
EF	enamel formula.

Radius

M8	Distal articular breadth;
M9	Internal length;
M10	Distal maximal breadth;
M11	Diameter of the articular facet for navicular;
M12	Idem for triquetrum.

Os magnum

M1	DAP;
M2	Anterior breadth;
M3	Anterior height;
M4	Distal posterior breadth;
M5	Posterior height;
M6	Diameter of the articular facet for Mc _{II} ;
M7	Idem for Mc _{III} (Gromova 1952).

Os lunatum

M1	DAP;
M2	Maximal length;
M3	Maximal height;
M4	Diameter of the articular facet for hamatum;
M5	Idem for magnum (Gromova 1952).

Third metacarpal

M1	Maximal length;
M2	Internal length;
M3	Breadth of the diaphysis (in the middle);
M4	DAP idem at the level of 3;
M5	Proximal articular breadth;
M6	Proximal articular DAP;
M7	Maximal diameter of the articular facet for os magnum;
M8	Diameter of the anterior facet for hamatum;
M10	Distal maximal supra-articular breadth;
M11	Distal maximal articular breadth;
M12	Distal maximal DAP of the keel;
M13	Distal minimal DAP of the lateral condyle;
M13a	Distal minimal DAP of the medial condyle;
M14	Distal maximal DAP of the medial condyle;
M16	Diameter for the articular facet for Mc _{II} .

Tibia

M7	Distal breadth;
M8	Distal DAP.

Calcaneum

M1	Maximal length;
M2	Length of the proximal part;
M3	Minimal breadth;
M4	Proximal maximal breadth;
M5	Proximal maximal depth;
M6	Distal maximal breadth;
M7	Maximal medial depth.

Astragalus

M1	Maximal length (height): articulation surface for navicular-top of the internal condyle;
M2	Maximal diameter of the internal condyle;
M3	Trochlear breadth: middle of the internal-middle of the external condyles;
M4	Maximal breadth (in projection);
M5	Distal articular breadth;
M6	Distal articular DAP;
M7	Maximal DAP of the internal condyle.

Navicular (tarsal)

M1	Maximal DAP;
M2	Breadth (Gromova 1952).

Cuboid (tarsal)

M1	DAP (in projection across the axis of the proximal articulation facet);
M2	Anterior breadth (in projection);
M3	Posterior breadth (in projection);
M4	Diameter of the articular facet for astragalus;
M5	Idem for calcaneum;
M6	Idem for navicular;
M7	Length of the articular facet for navicular (Gromova 1952).

Third metatarsal

M1	Maximal length;
M2	Internal length;
M3	Breadth of the diaphysis (in the middle);
M4	DAP idem at the level of 3;
M5	Proximal articular breadth; 6. Proximal articular DAP;
M7	Maximal diameter of the articular facet for the cuneiform;
M8	Diameter of the articular facet for cuboid;
M9	Idem for cuneiform II;
M10	Distal maximal supra-articular breadth;
M11	Distal maximal articular breadth;
M12	Distal maximal DAP of the keel;
M13	Distal minimal DAP of the lateral condyle;
M13a	Distal minimal DAP of the medial condyle;
M14	Distal maximal DAP of the medial condyle.

First phalanx

M1	Maximal length;
M2	Anterior length: middle of the proximal articular facet-middle of the distal facet;
M3	Minimal breadth of the diaphysis;
M4	Proximal breadth;
M5	Proximal DAP;
M6	Distal breadth at the tuberosities;
M7	Distal articular breadth;
M8	Distal articular DAP;
M9	Minimal length of the trigonum phalangis;

Second phalanx

M1	Maximal length;
M2	Anterior length (as in the first phalanx);
M3	Minimal breadth of the diaphysis;
M4	Maximal proximal breadth;
M5	Proximal DAP;
M6	Distal articular maximal breadth.

Third Phalanx

M1	Length from the posterior edge of the articular surface to the tip of the phalanx;
M2	Anterior length;
M3	Maximal breadth.

TABLE 1. — List of the Küçükçekmece hipparion sample with their measurements and determination. Abbreviations: **hgig**, *H. aff. giganteum*; **hseb**, *H. aff. sebastopolitanum*. Other abbreviations used in the Table 1 are listed below.

Number	Specimen	Species	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	EF
MNHN.F.TRQ30	mnd	hseb	—	—	77.7	69.8	148.5	—	—	—	—	—	63.5	46.7	—	—	—	—	—
MNHN.F.TRQ31	mnd	hseb	—	—	—	66.2	—	—	—	—	—	—	55.0	—	—	—	—	—	—
MNHN.F.TRQ7	P3,4	hseb	21.4	21.8	6.8	5.1	20.3	22.5	22.1	—	—	—	—	—	—	—	—	—	1,7,7,4/1
MNHN.F.TRQ10	P3,4	hseb	20.5	21.4	6.2	4.2	—	—	19.3	—	—	—	—	—	—	—	—	—	1,7,7,2/1
MNHN.F.TRQ11	P3,4	hseb	20.8	22.7	7.6	4.5	19.6	22.9	27	—	—	—	—	—	—	—	—	—	1,7,10,4/2
MNHN.F.TRQ12	P3,4	hseb	22.2	22.4	6.3	4.8	20.5	22.1	30.8	—	—	—	—	—	—	—	—	—	5,9,9,2/2
MNHN.F.TRQ19	P3,4	hseb	23.1	broken	7.4	5.4	—	—	7	—	—	—	—	—	—	—	—	—	1,6,5,1/1
MNHN.F.TRQ24	P3,4	hseb	24.6	21.5	7.5	4.1	broken	—	50.0	—	—	—	—	—	—	—	—	—	2,5,5,2/2
MNHN.F.TRQ106	P2	?hgig	30.9	23.3	7.7	4.9	29.7	23.6	29.8	—	—	—	—	—	—	—	—	—	5,5,5,4/2
KÇ1	P3	hgig	24.1	24.6	7.5	4.8	—	—	—	—	—	—	—	—	—	—	—	—	—
KÇ1	P4	hgig	23.4	24.6	7.6	5	—	—	—	—	—	—	—	—	—	—	—	—	—
KÇ3	P3,4	hgig	25.4	25.4	8.9	4.2	—	—	—	—	—	—	—	—	—	—	—	—	—
KÇ5	P3,4	hgig	24.9	24.4	8.6	4.2	—	—	—	—	—	—	—	—	—	—	—	—	—
KÇ9	P3,4	hgig	26.5	24.9	6.8	4.5	—	—	—	—	—	—	—	—	—	—	—	—	—
KÇ10	P3,4	hgig	24.1	24.5	7.2	4.2	—	—	—	—	—	—	—	—	—	—	—	—	—
KÇ13	P3,4	hgig	23.8	25.8	9.5	5.9	—	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ9	P3,4	hgig	24.1	23.2	7.5	5.8	—	—	10	—	—	—	—	—	—	—	—	—	/2
MNHN.F.TRQ107	P3,4	hgig	26.3	24.7	8.5	5.5	23.4	25.1	47.1	—	—	—	—	—	—	—	—	—	7,10,6,5/3
MNHN.F.TRQ108	P3,4	hgig	25.3	26.8	10.1	5.7	23.9	28.8	30.7	—	—	—	—	—	—	—	—	—	6,8,8,2/3
MNHN.F.TRQ110	P3,4	hgig	25	23.5	7.5	4.2	23.5	23.4	24.3	—	—	—	—	—	—	—	—	—	1,5,9,3/3
KÇ7	M1,2	hseb	24.8	20.9	6.1	4.2	—	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ8	M1,2	hseb	18.9	19.5	5.8	4.1	18.2	18.7	25.0	—	—	—	—	—	—	—	—	—	1,7,6,1/1
MNHN.F.TRQ13	M1,2	hseb	20.2	broken	6.2	4.1	18.7	—	—	—	—	—	—	—	—	—	—	—	1,5,7,1/2
MNHN.F.TRQ15	M1,2	hseb	23.6	19.3	7.3	—	20.7	23.4	54.0	—	—	—	—	—	—	—	—	—	Little worn
KÇ2	M1,2	hgig	26.1	23.1	7.5	4.3	—	—	53.9	—	—	—	—	—	—	—	—	—	—
KÇ6	M1,2	hgig	25.5	26.4	8.5	4.9	—	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ6	M1,2	hgig	22.0	23.1	7.5	4.6	20.9	23.0	26.0	—	—	—	—	—	—	—	—	—	4,10,8,1/1
MNHN.F.TRQ109	M1,2	hgig	24.7	23.6	7.0	4.2	23.8	22.5	32.9	—	—	—	—	—	—	—	—	—	3,10,5,3/2
MNHN.F.TRQ14	M3	?	21.8	16.6	unworn	—	—	—	52.0	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ17	M3	?	25.4	20.7	7.3	4.9	20.5	21.2	51.0	—	—	—	—	—	—	—	—	—	3,4,5,-/2
p2	p2	hseb	28.2	11.1	13.2	7.4	9.2	—	—	—	—	—	—	—	—	—	—	—	0,0,2/1
p3	p3	hseb	24.0	12.8	13.8	7.0	12.1	—	—	—	—	—	—	—	—	—	—	—	0,1,2/1
p4	p4	hseb	24.5	13.6	13.3	7.1	12.5	—	—	—	—	—	—	—	—	—	—	—	2,1,3
m1	m1	hseb	21.7	12.2	11.3	5.9	9.2	—	—	—	—	—	—	—	—	—	—	—	2,1,3/1
m2	m2	hseb	21.9	11.5	10.6	6.1	9.0	—	—	—	—	—	—	—	—	—	—	—	1,1,0/0
m3	m3	hseb	25.0	11.0	8.8	6.0	7.0	—	—	—	—	—	—	—	—	—	—	—	1,1,1/0
p3	p3	hseb	22.2	13.6	13.2	7.4	10.2	—	—	—	—	—	—	—	—	—	—	—	2,1,2/1
p4	p4	hseb	21.1	12.8	12.6	7.2	8.8	—	—	—	—	—	—	—	—	—	—	—	1,1,3/1
m1	m1	hseb	19.5	12.0	10.2	5.5	6.7	—	—	—	—	—	—	—	—	—	—	—	1,1,0/1
m2	m2	hseb	20.0	11.3	9.5	5.7	7.3	—	—	—	—	—	—	—	—	—	—	—	0,0,0/1
m3	m3	hseb	24.1	10.5	8.8	5.9	6.6	—	—	—	—	—	—	—	—	—	—	—	1,1,0/1
p3	p3	hseb	22.8	12.4	12.4	7.0	11.1	—	—	—	—	—	—	—	—	—	—	—	1,2,1/1
p4	p4	hseb	23.0	13.1	12.2	6.9	11.0	—	—	—	—	—	—	—	—	—	—	—	1,1,1/1
m1	m1	hseb	21.0	10.9	10.1	5.9	7.0	—	—	—	—	—	—	—	—	—	—	—	1,0,0/0
p3,4	p3,4	hseb	20.8	11.2	10.2	6.3	5.4	—	—	14.0	—	—	—	—	—	—	—	—	0,0,0/0
p3,4	p3,4	hseb	19.8	13.0	10.9	5.2	4.8	—	—	9.1	—	—	—	—	—	—	—	—	0,0,0/0
p3,4	p3,4	hseb	21.0	12.4	11.5	7.0	10.7	20.3	12.9	19.5	—	—	—	—	—	—	—	—	1,0,0/1
p2	p2	?hseb	27.5	10.0	11.9	8.3	13.1	25.9	14.4	30.8	—	—	—	—	—	—	—	—	1,1,2/1
p3,4	p3,4	hgig	29.1	14.5	14.6	—	—	23.3	14.1	49.8	—	—	—	—	—	—	—	—	unworn

TABLE 1. — Continuation.

Number	Specimen	Species	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	EF
MNHN.F.TRQ52	p3,4	hgig	28.6	12.7	10.7	unworm	—	—	—	44.0	—	—	—	—	—	—	—	—	—
KC24	p3,4	hgig	27.3	9.3	10.9	8.5	11.4	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ34	m1,2	hseb	23.1	11.7	12.1	7.6	10.0	21.6	13.9	51.2	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ37	m1,2	hseb	22.8	13.4	13.1	6.8	10.8	22.1	12.8	17.1	—	—	—	—	—	—	—	—	0.0,0/1
MNHN.F.TRQ38	m1,2	hseb	23.3	11.6	11.2	6.3	8.5	22.6	13.0	28.7	—	—	—	—	—	—	—	—	2.1,0/0
MNHN.F.TRQ40	m1,2	hseb	23.8	12.4	11.0	6.7	7.5	19.4	12.1	33.9	—	—	—	—	—	—	—	—	0.0,0/0
MNHN.F.TRQ44	m1,2	hseb	23.7	11.8	11.0	6.5	8.5	23.5	13.0	24.5	—	—	—	—	—	—	—	—	2.1,0/1
KC22	m1,2	hseb	21.8	11.7	14.2	10.2	12.8	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ41	m3	?	23.1	8.8	8.0	6.6	8.4	24.9	9.4	28.6	—	—	—	—	—	—	—	—	0.1,0/0
KC25	m3	?	26.1	5.6	11.2	5.5	10.0	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ46	m1,2	hgig	25.9	10.9	9.9	7.5	10.0	—	—	51.9	—	—	—	—	—	—	—	—	2.1,0/1
MNHN.F.TRQ111	m1,2	hgig	27.6	10.1	8.2	unworm	—	—	—	56.0	—	—	—	—	—	—	—	—	—
KC23	m1,2	hgig	29.8	14.5	—	—	11.5	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ143	rad	hgig	—	—	—	—	—	—	—	49.5	28.9	60.1	17.8	11.4	—	—	—	—	—
MNHN.F.TRQ163	rad	hgig	—	—	—	—	—	—	—	50.4	33.6	57.8	19.1	12.6	—	—	—	—	—
MNHN.F.TRQ164	rad	hgig	—	—	—	—	—	—	—	—	31.0	58.8	19.5	—	—	—	—	—	—
MNHN.F.TRQ61	rad	hseb	—	—	—	—	—	—	—	—	25.6	—	16.2	—	—	—	—	—	—
MNHN.F.TRQ141	rad	hseb	—	—	—	—	—	—	—	46.8	28.6	55.1	18.0	9.9	—	—	—	—	—
MNHN.F.TRQ142	rad	hseb	—	—	—	—	—	—	—	—	28.8	—	17.5	—	—	—	—	—	—
MNHN.F.TRQ144	rad	?hseb	—	—	—	—	—	—	—	—	—	—	18.8	—	—	—	—	—	—
MNHN.F.TRQ145	rad	?	—	—	—	—	55.2	30.7	62.3	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ63	magnum	?hseb	27.53	32.3	14.78	13.15	19.4	4.26	30.26	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ62	magnum	?hgig	31.73	38.28	17.12	16.15	21.9	5.3	35.65	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ172	lunatum	?	28.65	23.48	22.2	22.93	19.3	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ120	mcili	hseb	—	—	—	—	—	—	—	—	—	32.1	31.2	25.2	21.7	22.1	Not accounted	—	—
MNHN.F.TRQ121	mcili	hseb	—	—	—	—	—	—	—	—	—	32.2	30.3	—	20.0	20.4	—	—	—
MNHN.F.TRQ122	mcili	hseb	—	—	—	—	—	—	—	—	—	32.0	30.5	25.0	22.6	23.1	—	—	—
MNHN.F.TRQ123	mcili	hseb	—	—	27.0	20.5	35.0	27.0	31.8	9.0	3.8	—	—	—	—	—	—	4.2	—
MNHN.F.TRQ124	mcili	hseb	—	—	—	24.1	34.0	29.8	31.0	9.9	—	—	—	—	—	—	—	5.4	—
KC20	mcili	hseb	—	—	—	—	—	—	—	—	—	29.5	29.0	22.7	20.1	21.1	—	—	—
MNHN.F.TRQ165	mcili	hgig	—	—	—	—	—	—	—	—	—	46.51	42.49	31.43	26.78	29.27	—	—	—
MNHN.F.TRQ135	tib	hseb	—	—	—	—	—	—	53.6	35.9	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ137	tib	hseb	—	—	—	—	—	—	56.3	36.4	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ134	tib	hgig	—	—	—	—	—	—	—	44.7	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ136	tib	hgig	—	—	—	—	—	—	59.3	38.1	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ140	tib	hgig	—	—	—	—	—	—	61.4	38.3	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ139	tib	?hseb	—	—	—	—	—	—	—	37.1	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ68	astr	hseb	50.8	—	23.8	49.8	40.3	28.0	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ69	astr	hseb	50.0	45.7	24.2	49.3	38.6	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ70	astr	hseb	51.5	48.9	22.2	49.2	39.1	26.7	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ71	astr	hseb	—	—	21.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ74	astr	hseb	49.7	—	26.6	51.5	41.6	28.4	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ75	astr	hseb	48.2	—	23.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ77	astr	hseb	50.8	—	23.0	—	—	28.9	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ78	astr	—	n.m.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ72	astr	hgig	54.0	54.4	26.4	56.7	44.7	31.2	47.8	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ73	astr	hgig	54.4	52.4	27.1	54.1	41.1	28.9	43.3	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ76	astr	hgig	56.6	56.0	—	—	43.7	31.6	—	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ64	calc	hseb	99.2	66.7	17.6	29.2	41.0	42.6	40.7	—	—	—	—	—	—	—	—	—	—
MNHN.F.TRQ65	calc	hseb	96.8	63.0	18.4	27.9	41.7	44.0	42.0	—	—	—	—	—	—	—	—	—	—

TABLE 1. — Continuation.

Number	Specimen	Species	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	EF
MNHN.F.TRQ66	calc	hseb	94.3	60.9	17.2	29.9	40.7	38.3	40.2	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ67	calc	hseb	-	58.2	19.5	27.1	39.6	-	40.8	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ128	calc	hseb	-	-	17.3	-	41.7	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ129	calc	hseb	-	-	-	-	-	-	39.7	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ126	calc	hgig	-	-	21.4	-	-	[50]	[48]	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ127	calc	hgig	-	-	-	-	-	[52]	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ82	navicular	?hseb	32.38	37.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ83	navicular	?hseb	31.31	36.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ80	navicular	?hgig	33.4	42.73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ81	navicular	?hgig	33.57	43.51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ690	cuboid	?	31.42	17.3	19.12	9	15.08	26.8	9.98	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ114	mtill	hseb	-	-	-	-	-	-	-	-	-	34.2	33.6	27.2	23.9	25.0	-	-	-
MNHN.F.TRQ116	mtill	hseb	-	-	-	-	34.5	29.3	33.2	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ117	mtill	hseb	-	-	-	-	32.9	29.7	28.0	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ119	mtill	hseb	218.0	-	25.8	23.9	-	-	-	-	-	34.3	31.3	27.8	22.9	25.3	-	-	-
MNHN.F.TRQ118	mtill	hseb	-	-	-	-	36.4	31.7	33.4	10.3	6.3	-	-	-	-	-	-	-	-
MNHN.F.TRQ115	mtill	hseb	-	-	-	-	-	-	-	-	-	37.2	32.9	29.3	23.9	25.8	-	-	-
MNHN.F.TRQ125	mtill	hseb	-	-	-	-	-	-	-	-	-	38.6	35.8	29.9	24.7	27.4	-	-	-
MNHN.F.TRQ84	mtill	hgig	239.0	-	31.2	28.2	-	-	-	-	-	40.8	38.6	32.3	27.3	-	-	-	-
MNHN.F.TRQ86	1ph3	hseb	60.4	54.0	28.6	42.2	31.7	33.6	-	18.7	17.7	-	-	-	-	-	-	-	-
MNHN.F.TRQ87	1ph3	hseb	55.3	49.2	28.0	37.2	27.2	31.1	29.8	18.6	24.8	-	-	-	-	-	-	-	-
MNHN.F.TRQ88	1ph3	hseb	55.0	47.5	28.1	37.6	29.8	32.5	29.5	18.5	16.0	-	-	-	-	-	-	-	-
MNHN.F.TRQ89	1ph3	hseb	55.7	47.1	28.5	36.8	28.8	29.9	29.7	17.7	14.5	-	-	-	-	-	-	-	-
MNHN.F.TRQ90	1ph3	hseb	-	-	-	38.3	26.9	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ104	1ph3	hseb	-	-	-	-	-	-	28.7	16.6	-	-	-	-	-	-	-	-	-
KÇ18	1ph3	hseb	57.2	53.0	24.4	34.9	26.0	29.1	28.0	16.4	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ85	1ph3	hgig	65.5	55.4	34.6	48.3	34.2	41.0	40.5	24.5	31.1	-	-	-	-	-	-	-	-
KÇ15	1ph3	hgig	61.7	59.8	31.0	45.0	31.4	36.9	36.7	20.8	23.0	-	-	-	-	-	-	-	-
MNHN.F.TRQ92	1ph3	?	Young individual	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ93	1ph3	?	Young individual	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ94	1ph3	?	Young individual	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ96	2ph3	hseb	35.8	25.5	27.2	33.7	24.0	28.5	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ100	2ph3	hseb	35.3	26.2	25.5	-	-	20.6	-	-	-	-	-	-	-	-	-	-	-
KÇ19	2ph3	hseb	35.5	28.0	26.5	32.5	23.4	27.9	-	-	-	-	-	-	-	-	-	-	-
KÇ21	2ph3	hseb	34.2	25.2	25.6	32.5	23.6	28.1	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ95	2ph3	hgig	39.1	28.0	30.9	39.9	26.4	33.6	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ97	2ph3	hgig	37.1	27.1	30.9	35.8	24.4	33.0	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ98	2ph3	hgig	37.3	26.8	29.5	38.4	26.6	33.4	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ99	2ph3	hgig	36.9	27.0	30.5	35.7	23.9	31.8	-	-	-	-	-	-	-	-	-	-	-
KÇ16	2ph3	hgig	38.9	30.6	36.2	44.7	27.1	38.9	-	-	-	-	-	-	-	-	-	-	-
KÇ17	2ph3	hgig	36.7	27.9	31.8	37.7	25.2	34.6	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ101	3ph3	?	49.3	47.6	53.4	42.3	20.9	29.3	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ102	1ph3 lat	?hseb	31.1	10.44	16.8	9.84	7.97	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ130	1ph3 lat	?hgig	35.21	11.97	18.36	11.8	9.7	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ131	1ph3 lat	?hgig	35.58	11.27	17.08	11.27	8.9	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ102	1ph3 lat	?hgig	-	-	-	-	11.27	8.38	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ103	2ph3 lat	?	23.79	14.01	17.26	11.96	-	-	-	-	-	-	-	-	-	-	-	-	-
MNHN.F.TRQ133	3ph3 lat	?	21.8	12.24	21.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-