Geobios 49 (2016) 85–118

Available online at
ScienceDirect
www.sciencedirect.com

Elsevier Masson France
EM|consulte
www.em-consulte.com

Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)

Equidae☆

George D. Koufos *, Theodora D. Vlachou

Aristotle University of Thessaloniki, Department of Geology, Laboratory of Geology and Palaeontology, GR-54124 Thessaloniki, Greece

ARTICLE INFO

Article history:
Received 6 March 2015
Accepted 19 January 2016
Available online 27 January 2016

Keywords:
Equidae
New species
Late Miocene
Greece
Taxonomy
Biostratigraphy
Palaeobiogeography

ABSTRACT

Hipparionines represent the greatest part of the Nikiti 2 (NIK) fossil mammal collection. The determination of the material suggests the presence of four distinct species, two small, a medium and a large sized form. The small-sized forms attributed to *Hipparion macedonicum*, well known in northern Greece, and to *H. sithonis* nov. species. The weak canine fossa and the retraction of the narial opening above P2-P3 separate the latter species from *H. macedonicum*. Furthermore *H. sithonis* is slightly larger with more robust metapodials. The medium-sized NIK hipparion differs from other known medium-sized forms, representing the new species *Hipparion philippus*. Finally the large-sized form, represented in the studied material only by few specimens, has been assigned to *H.* cf. *proboscideum*. The morphological characters of the studied material and their stratigraphic range suggest an early Turolian to lower middle Turolian (MN 11–lower MN 12) age for the NIK fauna. Last, based on the hipparions found in NIK and the Eastern Mediterranean province in general, some hypotheses about the palaeobiogeography of the Aegean area and the phylogenetic relations among the hipparion species are discussed.

1. Introduction

The late Miocene mammal localities of Greece provided a great number of hipparion remains and several articles have been published describing and comparing this material. A systematic study of the Greek hipparions started at the beginning of the 1980s and it is still continued (Koufos, 1980, 1982, 1984, 1986, 1987a,b,c, 1988a,b, 2000a,b, 2006; Vlachou and Koufos, 2002, 2004, 2006, 2009; Vlachou, 2013). The material studied in this article originates from the locality of Nikiti 2 (NIK), situated in the Chalkidiki Peninsula (Macedonia, Greece); for more information about the history, the stratigraphy and the age of this locality see Koufos (2016) and Koufos et al. (2016).

The NIK hipparion sample was collected in two fieldwork periods: 1993–1998 and 2004–2009. In this article, the first collection period is referred to as "old collection" and the second one as "new collection". The hipparionine horses predominate in the entire NIK collection, representing more than 50% of the collected specimens. Even though the "old collection" is rich in hipparions, it includes a few, fragmentary and badly preserved cranial remains; their study allowed the recognition of three different hipparionine taxa (Vlachou and Koufos, 2002a,b): *H. dietrichi* (Wehrli, 1941), *H. macedonicum* Koufos, 1984, and *Hipparion* sp. (large-sized). The "new collection" increases remarkably the number of sampled specimens, including more than 15 skulls (most of them well-preserved), several mandibles and numerous postcranial bones, which allow a better distinction and determination of the NIK hipparions leading to the recognition of four distinct species. The present article, using both collections, revises the morphology and taxonomy of the NIK hipparions. The material is compared to the already known Greek hipparion samples from the Axios Valley, Samos, Perivolaki and Pikermi, but with several Eurasian samples as well.

2. Material and methods

The studied material is housed in the Laboratory of Geology and Palaeontology of the Aristotle University of Thessaloniki (LGPUT). The distinction of the NIK hipparion species is based on morphological and metrical data, handled in different ways. Scatter diagrams, Box and Whiskers plots, Simpson's Log-ratio diagrams, cluster analysis, and principal component analysis (PCA) on the cranial and postcranial material (all using the PAST software; Hammer et al., 2001), help to the description of the studied material, the identification of some crucial characters, and the comparison of the NIK hipparion species with those from other Eurasian localities. The Pikermi *H. mediterraneum* Roth and Wagner, 1854, is used as reference for the Log-ratio diagrams

☆ Corresponding editor: Dimitris S. Kostopoulos.

* Corresponding author.
E-mail address: koufos@geo.auth.gr (G.D. Koufos).

http://dx.doi.org/10.1016/j.geobios.2016.01.001
0016-6995/

(data taken from Koufos, 1987c). The samples of *H.* cf. *dietrichi* (=*H. philippus* nov. sp. in this article) and *H. macedonicum* from the Axios Valley and PER (Vlachou, 2013), as well as *H.* cf. *proboscideum* from PER (Vlachou and Koufos, 2006; Vlachou, 2013) are used as comparative material. Body mass is estimated using various methods proposed by Alberdi et al. (1995), Damuth and MacFadden (1990), Eisenmann and Sondaar (1998), and Scott (1990). Efforts are also made to approach the ecological preferences of the NIK hipparions using Scott's (2004) method. The biometric study follows the recommendations of Eisenmann et al. (1988). All measurements were taken using a digital caliper; they are given in mm with an accuracy of 0.1 mm.

Abbreviations:

Localities: **AKK**: Akkaşdağı, Turkey; **BAS**: Basiboz, FYROM; **BEL**: Beluska, FYROM; **GRE**: Grebeniki, Ukraine; **HD**: Hadjidimovo, Bulgaria; **KTA-B**: Kemiklitepe A, B, Turkey; **KRY**: Kryopigi, Greece; **MAR**: Maragheh, Iran; **MLN**: Mytilinii 4, Samos, Greece; **MTLA**: Mytiliniii 1A, Samos, Greece; **MTLB**: Mytilinii 1B, 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 Valey, Greece; **Q1**: Quarry 1, Samos, Greece; **Q2**: Quarry 2, 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; **STR**: Strumyani 1, Bulgaria; **STM**: Strumyani 2, Bulgaria; **TAR**: Taraklia, Ukraine; **PAV**: Pavlodar, Kazakhstan; **PNT**: Pentalophos 1, Axios Valley, Greece; **VATH**: localities of Vathylakkos, Axios Valley, Greece; **VOZ**: Vozarci, FYROM.

Other: AMNH: American Museum of Natural History; **FYROM**: Former Yugoslavian Republic of Macedonia; **HS**: habitat score; **LGPUT**: Laboratory of Geology and Palaeontology, University of Thessaloniki; **POF**: preorbital fossa; **POB**: preorbital bar (length preorbital fossa-anterior orbit); **meas.:** measurement; **SI**: Slenderness Index.

3. Material separation

The separation of the NIK cranial remains is based on 14 morphological characters (Table S1, Appendix A). The cluster analysis of these characters, using the Bray-Curtis index, suggests the presence of three clearly distinguished skull morphologies (Fig. 1). The first one is well correlated to the *dietrichi*-morphotype and the other two are better correlated to the *macedonicum*-morphotype of Vlachou (2013). The *dietrichi*-morphotype differs from the other two skull morphologies in the larger size, the short and wide muzzle, the weak POF peripheral rim, the longer POB, the lacrimal development and the morphology of the pli caballin. The skulls correlated to the *macedonicum*-morphotype are divided in two morphological groups based on the presence/absence of the canine fossa, the depth of the narial opening and the development of the POF peripheral rim.

The Log-ratio diagram comparing the NIK skulls confirms the above separation (Fig. 2(a)). There is a large-sized hipparion form (it will be referred to as form-C) (meas. 6–9) clearly distinguished from the other two forms by the larger POB (meas. 32), the wider muzzle (meas. 15) and the larger distance between the POF ventral rim and the facial crest (meas. 36). The two small-sized forms differ slightly in size (meas. 7–9), the POB (meas. 32), the muzzle morphology and the narial opening depth (meas. 30). In more details, the larger small-sized form (meas. 7–9) (it will be referred to as form-B) has a more elongated and narrow muzzle (meas. 1, 15; Fig. 2(a)); the nasal notch is retracted above P2 or P2/P3 and retains a weak canine fossa. The smaller one (it will be referred to as form-A) has no canine fossa and the nasal notch restricted in front of P2, making the distinction of the two small-sized forms

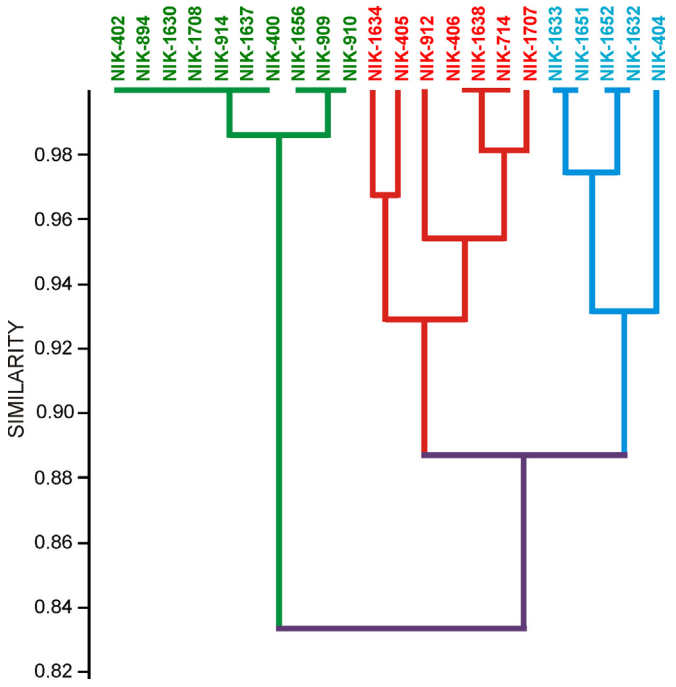

Fig. 1. UPGMA cluster analysis, using the Bray-Curtis similarity index, of the NIK cranial remains based on the 14 morphological characters listed in Table S1, Appendix A.

quite easy. The mandibles are also separated in three groups mainly distinguished by the premolar length (meas. 3), the muzzle length (meas. 1) and the height of the horizontal ramus (meas. 10–12) (Fig. 2(b)).

The morphometric analysis of the postcranial remains suggests the presence of four hipparion forms in the NIK sample. The Log-ratio diagrams allowed the distinction of three well represented slender-built hipparions (forms-A, B, C) and a large, relatively robust-built hipparion represented only by two Mc_{III} and one astragalus (Fig. 3(a, b)) which will be referred to as form-D. The SI (=[meas. 11] × 100 / [meas. 1]), following the size differences, indicates that the larger form has the most robust metapodials, and *vice versa*. The slenderness of the robust metapodials is better correlated to the *proboscideum*-morphotype, whereas the slenderness of the two smaller forms is comparable to that of the *macedonicum*-morphotype (Fig. 4). The medium-sized form is almost as slender as *H.* cf. *dietrichi* from Axios Valley and PER belonged to the *dietrichi*-morphotype, illustrating correlation among them.

The PCA of the metapodials confirms the above observations, revealing the distinction of four groups (Fig. 5). In order to get a better idea about the size and morphology of the NIK metapodials, the known species *H. mediterraneum* from Pikermi, *H. macedonicum* and *H.* cf. *dietrichi* (=*H. philippus* nov. sp. in this article) from the Axios Valley and PER, as well as *H.* cf. *proboscideum* from PER are compared using a PCA. The characters with highest loadings are the total length (meas. 1), the proximal articular width (meas. 5), the proximal articular diameter (meas. 7), the maximal distal supra-articular width (meas. 10) and the distal articular width (meas. 11). The first component (PC1) clearly separates the Mc_{III} sample in three groups on the basis of size (meas. 1, 5, 10, 11) (Fig. 5(a)). The second component (PC2) separates the large-sized specimens in two groups based mainly on the dimensions of the proximal and distal articular surfaces (meas. 5, 7, 10, 11), as well as the mid-shaft width (meas. 3) (Fig. 5(a)). Two small-sized groups are distinguished: the first group, including the smallest metapodials, is close to *H. macedonicum*, and the second one partly overlaps the *H. macedonicum* distribution. It is probably larger than *H. macedonicum* and well separated from the