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

Equidae☆

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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

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Lazaridou and Tsoukala (2014). *H. phlegrae* is closely related to *H. campbelli*, *H. dietrichi* and *H. philippus* nov. sp. (*H. dietrichi* in this article), all these species sharing common characters with *H. prostylum*. Based on the cranial and postcranial material, *H. philippus* nov. sp. appears closer to *H. macedonicum* than to *H. prostylum*, *H. campbelli* or to any other Vallesian or early Turolian hipparion. It is probably a local species (probably endemic of the southern Balkans) most likely derived from *H. macedonicum* during early MN 11, taking advantage of the grassland expansion across all Eurasia during the Turolian. The first appearance datum of *H. philippus* nov. sp. is recorded in the NIK fauna dated to the early Turolian, MN 11 (8.7–8.2 Ma; Koufos et al., 2016) and the last one in PER or STM fauna, both dated to upper early MN 12 (Koufos et al., 2006a,b; Geraads et al., 2011).

H. sithonis nov. sp. was erected to describe a new hipparion morphology (small size, presence of the canine fossa, short POB) unknown in the southern Balkans but known only from Asia. This morphology was originally recognized in the early Turolian localities of China where it is was described under the species name *H. forstenae* (Bernor et al., 1990), and in the late Turolian localities Q1 and MTLA of Samos, referred to either as *H.* cf. *forstenae* by Vlachou and Koufos (2009) or as *H.* aff. *forstenae* by Vlachou (2013). According to Deng (2006), the late Miocene Greek and Chinese mammal faunas have a few similarities at the specific level. Furthermore, the faunal exchange or dispersal between the two regions was gradually increased from the early Vallesian to the middle Turolian. However, the common species, apart from the suid *Microstonyx major*, were mainly carnivores. Based on these results and keeping in mind the presence of *H. sithonis* nov. sp. in the early Turolian fauna of NIK, we presume that *H. sithonis* nov. sp. migrated eastwards during the time interval from7.3 to 7.1 Ma and then evolved to *H.* aff. *forstenae* by increasing its size (Fig. 27(c)), the distance of the POF from the orbit and the massivity of the postcranials (Fig. 28(b)), adapting to the drier conditions of EAD. The disadvantage of this approach is that there are no records of *H. sithonis* nov. sp. in the lower middle Turolian (early MN 12) of Greece. However, we consider this absence to be more artificial than real, because *H. sithonis* nov. sp. is comparable in size with *H. macedonicum* and the small-sized hipparions are poorly represented in the Greek faunas younger than NIK. *H. sithonis* nov. sp. shares several morphological characters with *H. macedonicum* from which it is probably derived.

6. Conclusions

The study of the NIK hipparions indicates the presence of four different taxa:

- the small-sized *H. macedonicum* known from the Vallesian and Turolian of Greece;
- the poorly represented large-sized *H.* cf. *proboscideum* that shares *H. proboscideum*. The presence of *H. proboscideum* is reported from several localities of the continental Greece but only in the early Turolian locality RZO it has been recognized by cranial remains. In all other localities (PXM, PER, NIK) some postcranials have been found which are refered to as *H.* cf. *proboscideum* because of their size similarities with this species (Koufos, 1987b; Vlachou and Koufos, 2002, 2006);
- the new small-sized *H. sithonis* nov. sp. that bears canine fossa and deep narial opening that clearly distinguish it from *H. macedonicum* having weak canine fossa and relatively shallower narial opening. It is characterized by short and relatively wide muzzle, moderately deep narial opening (nasal notch retracts well behind the mesostyle of the P2), shallow, oval-subtriangular, not posteriorly pocketed and antero-ventrally oriented POF placed close to the orbit, small and elliptical-oval protocone, very small and simple pli caballin, low-moderate enamel plication in the upper cheek teeth, no plicated or crenulated lower cheek teeth, rudimentary or absent pli caballinid, and elongated and slender metapodials. *H. sithonis* nov. sp. probably derived from *H. macedonicum* with which it shares several morphological features;
- the new medium-sized form, named *H. philippus* nov. sp., characterized by short and wide muzzle, short narial opening (nasal notch retracts above the middle of the diastema P2–C), weak, shallow, elliptical-subtriangular, antero-ventrally oriented, not posteriorly pocketed POF situated far from the orbit, wide and oval choanae with their anterior margin at the contact between M1 and M2, short and wide snout, high and thick mandibular corpus, short symphysis, moderate enamel plication in the upper cheek teeth, protocone elliptical-oval and isolated, except in the worn teeth, simple and large pli caballin and pli caballinid, low plicated flexid borders in the lower cheek teeth, and elongated and slender metapodials. The cranial and postcranial characters of *H. philippus* nov. sp. are more closely related to *H. macedonicum* than to the typical *H. dietrichi* or to *H. prostylum* and *H. campbelli*; it probably represents a local form derived from the former species during early Turolian.

The relatively wide muzzle of *H. macedonicum* indicates a Turolian age (Vlachou, 2013). The presence of *H. philippus* nov. sp. is traced in other Greek localities (RZO, PXM, VATH and PER) all dated to the early-middle Turolian. Therefore, the NIK hipparions suggest an early-middle Turolian age for this locality. The metapodial morphology, the enamel plication, the dental microwear (Merceron et al., 2016) of the NIK hipparions suggest an open savannah-like environment agreeing with older palaeoecological studies for the late Miocene of the wider area. The different hipparion assemblages among the eastern and western domain of the Aegean Sea (WAD and EAD respectively) indicates that the two regions were isolated during the early Turolian to early-middle Turolian. A drop of the sea level during the latest Tortonian (Jiménez-Moreno et al., 2013) probably restored the communication between the two domains for a short time interval (7.3–7.1 Ma), allowing the invasion of *H. sithonis* to the EAD and the invasion of *H. brachypus* and *H. nikosi* to the WAD. The different hipparion assemblages suggest soon after the time of 7.1 Ma the communication among the two domains interrupted again.

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Appendix A. Supplementary information

Supplementary information (Tables S1–S15) data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.geobios.2016.01.001.

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