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

Artiodactyla☆

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ABSTRACT

The artiodactyl assemblage of the upper Miocene fossil locality Nikiti 2, Northern Greece, is rediscussed in the light of new data provided by a second, five-year long round of fieldwork. The significantly enriched artiodactyl material allows revising and updating previous systematic interpretations. Along with the previously recorded *Helladotherium duvernoyi, Gazella* cf. *capricornis*, and *Nisidorcas planicornis*, two more giraffids *(Palaeotagus rouenii*, and Palaeotraginae indet.) and two additional bovid taxa (*Gazella pilgrimi*, and *Palaeoryx* cf. *pallasi)* are recognized. Bovid material previously referred to *Tragoportax* aff. *rugosifrons* is reinterpreted here as partly belonging to *T. amalthea*, and partly to a second boselaphine taxon close to *Miotragocerus.* Furthermore, the medium-sized spiral horned antelope originally referred to as cf. *Ouzocerus* is now attributed to a primitive morphotype of *Palaeoreas lindermayeri*. As a whole, the updated artiodactyl assemblage from Nikiti 2 includes three giraffid and seven bovid taxa. According to local biochronological evidence and the primitiveness of both *Palaeoreas* and *Nisidorcas*, an early Turolian age is suggested for the Nikiti 2 fauna.

1. Introduction

The fossiliferous site of Nikiti (Koufos et al., 1991) is located at the northernmost corner of the Sithonian branch of the Chalkidiki peninsula, N. Greece. The site is placed into the upper part of the homonymous lithostratigraphic formation of sands, sandstones and red-beds outcropping ENE of the Nikiti village (Koufos, 2016). The site includes four fossil localities with Nikiti 1 (NKT) and Nikiti 2 (NIK) being the most productive in terms of density and completeness of fossil mammal remains. Stratigraphically, NIK stands ca. 20 m above NKT and within the same alternations of reddish silty sands with gravel intercalations (Kostopoulos and Koufos, 1999: fig. 1; Koufos, 2016). An age between 9.3 and 8.7 Ma has been proposed for NKT (Koufos, 2006), whereas Kostopoulos (2009a) correlated NIK to the lower part of the early Turolian, with an estimated age between 8.7 and 8.0 Ma. Previous systematic works on the mammal remains from NKT and NIK focused on the sharp taxonomic differences between these two faunal assemblages that tightly frame the Vallesian/Turolian boundary in N. Greece (e.g., Koufos, 2006) and the hominoid/cercopithecine turnover (Andrews et al., 1996).

Two rounds of systematic excavations took place in Nikiti. The first one lasted six years starting with the discovery of the NKT locality in 1990 (Koufos et al., 1991). Giraffid and bovid material discovered at that time from NIK were described by Kostopoulos et al. (1996) and Kostopoulos and Koufos (1999), respectively. According to these authors, the artiodactyl assemblage of NIK includes: *Helladotherium duvernoyi, Tragoportax* aff. *rugosifrons*, *Gazella* aff. *capricornis*, *Nisidorcas planicornis*, and cf. *Ouzocerus* sp.

A second round of five years of excavations (2005–2009) focused on the NIK locality and greatly improved its fossil record. Numerous new specimens of giraffids and especially bovids, including fairly complete skulls and postcranials in natural articulation were unearthed at this time. These new findings are discussed here; they allow an overall reappraisal of the artiodactyls of the NIK locality.

2. Material and methods

The fossil artiodactyl material from NIK is stored in the Laboratory of Geology and Paleontology of the Aristotle University of Thessaloniki (LGPUT). The present study focuses on dental and postcranial material of giraffids and cranial and dental material of bovids from NIK; bovid postcranials, though very abundant, are not included here and will be part of a separate forthcoming study. The basic morphology of most identified species has been already given in previous works (Kostopoulos et al., 1996; Kostopoulos and Koufos, 1999). Additional descriptions are included wherever necessary. The main goal of this paper is to update and revise previous determinations of the artiodactyl assemblage of the NIK locality, according to the additional evidences provided by the second fieldwork season.

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Lower teeth are in lower case, and upper teeth in upper case letters; the premolar to molar row length ratio is indicated as P/M for the upper and p/m for the lower tooth row. Measurements are given in millimeters; all row data are given as Supplementary Tables S1–S17. Dental terminology generally follows Heintz (1970) but lower premolars of giraffids are described according to Geraads et al. (2013). Statistical analyses were achieved using the PAST software (Hammer et al., 2001).

Institutional abbreviations: **AMNH**, American Museum of Natural History, NY; **AMPG**, Athens Museum of Geology and Paleontology, National and Kapodistrian University of Athens; **LGPUT**, Laboratory of Geology and Paleontology, Artistotle University of Thessaloniki; **MNHN.F**, Museum National d'Histoire Naturelle, Paris; **MMTT**, Maragheh collection in the Laboratory of Evolutionary Biology, Howard University, Washington; **MTA**, Natural History Museum, General Directorate of Mineral Research and Exploration, Ankara; **NHMA**, Aegean Museum of National History, Samos Island, Greece; **NHML**, Natural History Museum, London; **PIM**, Palaeontological Institute Münster.

Locality abbreviations: **NKT**, Nikiti 1, Greece; **NIK**, Nikiti 2, Greece; **RZO**, Ravin des Zouaves 5, Greece; **PXM**, Prochoma, Greece; **VTK**, **VLO** and **VAT**, Vathylakkos 1, 2 and 3, respectively, Greece; **PER**, Perivolaki, Greece; **PIK**, Pikermi, Greece; **HD**, Hadjidimovo, Bulgaria; **MAR**, Maragheh, Iran; **AK**, Akkaşdağı, Turkey.

Nomenclatural and measurement abbreviations: **L**: length; **W**: width, **H**: height; **LPM/Lpm**: length of the upper/lower premolar-molar series; **MNI**: minimum number of individuals; **NISP**: number of identified specimens; **n**: number of specimens. Additional abbreviations are given in Supplementary material.

3. Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Family Giraffidae Gray, 1821
Genus ***Helladotherium*** Gaudry, 1860

Type-species: *Helladotherium duvernoyi* (Gaudry and Lartet, 1856); Pikermi, Greece; late Miocene.

Helladotherium duvernoyi (Gaudry and Lartet, 1856)
Figs. 1, 2

Studied material: Part of left mandibular ramus with p2-m3, NIK-1; part of right mandibular ramus with p2-m3, NIK-1804; left mandibular ramus, NIK-1057; scapula, NIK-766; radio-ulna, NIK-1151; tibia, NIK-1805; talus, NIK-70, NIK-1017; posterior first phalanx, NIK-1096.

Measurements: See Tables S1–S3.

Description: LGPUT NIK-1804 seems to belong to the same individual as LGPUT NIK-1, although discovered ten years later. All studied tooth rows represent senile to very old individuals. The foramen mental of the mandible LGPUT NIK-1057 is large, oval-shaped and opens 100 mm in front of the p2 (Fig. 1). The caudal edge of the symphysis is placed at the level of the mental foramen. The ventral profile of the horizontal ramus between the mental foramen and the p2 is well concave (Fig. 1). The molar part of the horizontal ramus deepens significantly from p2 to m3. The ascending ramus of the mandible is wide ventrally and tapers gently to the top. Behind the m3, the anterior margin of the ascending ramus forms a 70° angle with the alveolar level, whereas the caudal margin is weakly concave in the upper part. The angle of the mandible is wide, and projects posteroventrally; it is marked by a thick, crest-like lateral lip. The vascular notch is weakly marked ventrally. The coronoid process is wide and slightly curves backwards with its tip remaining in front of the posterior level of the mandibular condyle. The condyle is subhorizontal and strongly projects lingually. The pterygoid fossa is wide and shallow, whereas the masseteric fossa is not marked.

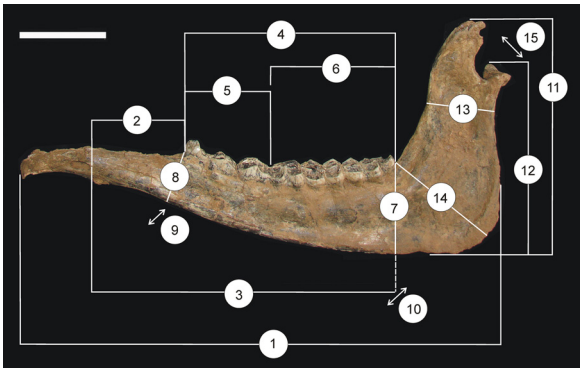

Fig. 1. *Helladotherium duvernoyi* from Nikiti 2, Greece. Mandibular ramus NIK-1057 in labial view and system of measurements (Table S1). Measures 9 and 10 represent ventral width of the mandibular corpus in front of p2 and behind m3, respectively; measure 15 corresponds to the transverse (mediolateral) diameter of the mandibular condyle. Scale bar: 10 cm.

Dental features of NIK-1804 (Fig. 2(A)) are identical to those of LGPUT NIK-1 (Fig. 2(B)), which basic tooth morphology has been already given by Kostopoulos et al. (1996). The p2 is primitively simple and long (representing more than 80% of the p3 length), with a barely traced anterolingual stylid, which is, however, much more developed and distinct in LGPUT NIK-1057 (where the length of the p2 reaches 90% of the p3 length). The parasinusid of p3 closes early in wear, so the anteriorly directed paraconid fuses with the parastylid. The anterior valley (mesosinusid) of p3 should be originally open, but closes 10–13 mm above the base of the crown, not because of the junction of metaconid with the paraconid but due to thin cingular wings. At the same tooth, the postmetacristid is long in LGPUT NIK-1 and NIK-1804, reaching the lingual point of the hypoconulid. The entoconid of LGPUT NIK-1 and NIK-1804 is short, so the metasinusid and telosinusid communicate until an advanced stage of wear. In LGPUT NIK-1057 the metaconid seems

Fig. 2. *Helladotherium duvernoyi* from Nikiti 2, Greece. **A**. Right toothrow p2-m3, NIK-1804 in occlusal (A1) and labial (A2) views. **B**. Left toothrow p2-m3, NIK-1 in lingual view. Scale bar: 5 cm.