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

Synthesis☆

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ABSTRACT

The study of the new and old collections of the Nikiti vertebrate localities included in this volume provides several new evidences for the taxonomy, composition, chronology and palaeoecology of these late Miocene mammal faunas. The faunal list of both primate bearing localities is enriched and improved by addition of new taxa and revision of older identifications; two new species are recognized in the Nikiti 2 (NIK) fauna (two hipparionine horses) and one subspecies from Nikiti 1 (NKT) is upgraded to the species level. The NKT and NIK faunas include 15 and 19 mammalian taxa, respectively. The mammalian faunas from both sites consist of almost the same families; the absence of some of them in NKT or NIK is most probably artificial. The chronology of the Nikiti mammal assemblages is based on biochronological data only, which allow the correlation of NKT to the terminal Vallesian (between 9.3 and 8.7 Ma) and that of NIK to the earliest Turolian (between 8.7 and 8.3 Ma). Concerning their age in relation with other neighboring mammal assemblages, NKT is younger than Ravin de la Pluie (Axios Valley, Greece) and isochronous or slightly older than Grebeniki (Ukraine). The NIK assemblage is older than Ravin des Zouaves 5 (Axios Valley) and Sivas (Turkey), dated at ~8.2 Ma and ~8.3 Ma, respectively. The available morphoecological, dental microwear-mesowear, and enamel isotopic analyses of the herbivores, as well as study of the phytolites suggest an open-light cover landscape for both localities. As documented previously in the Axios Valley, the Nikiti mammal fauna exhibits a significant reorganization through the Vallesian/Turolian boundary, including the *Ouranopithecus/Mesopithecus* replacement. However, this faunistic event is not consistent with the results of independent studies (isotope, dental wear, etc.) that fail to confirm significant climatic or vegetational changes across the same time interval.

1. Introduction

Known since the beginning of the 1990s and partly explored over the past years in a series of papers (Koufos, 2006 and references therein), the upper Miocene vertebrate fossiliferous sites of Nikiti (Chalkidiki, Greece) bring together taxonomic, ecological and biochronological evidences which are extensively discussed in this *Geobios* volume (Koufos and Kostopoulos [eds.], 2016). Updated and revised data coming from previous excavations (1990–1999) join new and unpublished ones provided by a second fieldwork session (2004–2009) in order to unveil a picture of the late Miocene faunal and habitat spectrum of the Balkans within southeastern Europe. As the fossil succession of Nikiti is also related to the European primate record, a paleoanthropological insight is also provided. Here, an attempt to synthesize the data exposed in this volume and elsewhere aims to further discuss the position of the Nikiti fauna in time and space.

2. Fossil sites and taphonomical setting

Several fossil spots were discovered around the Nikiti village, at the northern part of the Sithonia branch of the Chalkidiki Peninsula and within the coarse fluvial deposits of the homonymous lithostratigraphic formation as well as in the overlying Nikolaos Fm. (Koufos, 2016a). Among them, two sites attracted our main interest due to their fossil richness, quality and primate record: Nikiti 1 (NKT) and Nikiti 2 (NIK), the former being stratigraphically located ~20 m below the latter. The exhaustively exploited NKT locality, partly destroyed by road works, provided only 271 identifiable fossil skeletal remains, exclusively of mammals. The fossils

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Table 1
Mammal faunal lists of the two fossiliferous sites of Nikiti based on previous and present works.

Koufos et al. (1991)	Bonis and Koufos (1999)	Koufos (2006)	Present article
NKT	NKT	NKT	NKT
Ouranopithecus macedoniensis	*Ouranopithecus macedoniensis*	*Ouranopithecus macedoniensis*	*Ouranopithecus macedoniensis*
Hipparion macedonicum	Hyaenidae indet.	Hyaenidae indet.	Hyaenidae sp.
Hipparion cf. *primigenium*	*Hipparion* sp. (large)	*Hipparion primigenium*	*Hipparion* aff. *giganteum*
Bohlinia attica	*Hipparion macedonicum*	*Hipparion macedonicum*	*Hipparion macedonicum*
Palaeotragus sp.	Rhinocerotidae indet.	Rhinocerotidae indet.	*Dihoplus pikermiensis*
Mesembriacerus cf. *melentisi*	*Microstonyx major*	*Microstonyx major*	*"Diceros" neumayri*
Prostrepsiceros aff. *houtumschindleri*	*Helladotherium duvernoyi*	*Helladotherium duvernoyi*	*Microstonyx major*
Tragoportax cf. *rugosifrons*	*Bohlinia attica*	*Bohlinia attica*	*Helladotherium duvernoyi*
	Bohlinia nikitiae	*Bohlinia nikitiae*	*Bohlinia attica*
	Palaeotragus cf. *rouenii*	*Palaeotragus* cf. *rouenii*	*Bohlinia nikitiae*
	Tragoportax gaudryi	*Tragoportax* cf. *gaudryi*	*Palaeotragus* sp.
	Prostrepsiceros houtumschindleri syridisi	*Prostrepsiceros houtumschindleri syridisi*	*Prostrepsiceros syridisi*
	Oiceros aff. *atropatenes*	*Oiceros* aff. *atropatenes*	*Hispanodorcas* cf. *orientalis*
	?Gazella sp.	*?Gazella* sp.	*Miotragocerus* sp.
	Bovidae indet.	Bovidae indet.	Antilopinae indet.
	NIK	NIK	NIK
	Hyaenidae indet.	Hyaenidae indet.	*Mesopithecus* sp.
	Choerolophodon pentelici	*Choerolophodon pentelici*	*Adcrocuta eximia eximia*
	Hipparion sp. (small)	*Hipparion dietrichi*	*Amphimachairodus giganteus*
	Helladotherium duvernoyi	*Hipparion macedonicum*	*Choerolophodon pentelici*
	Nisidorcas planicornis	*Helladotherium duvernoyi*	*Hipparion phillipus* nov. sp.
	cf. *Tragoportax* sp.	*Nisidorcas planicornis*	*Hipparion macedonicum*
	Oioceros sp.	*Tragoportax* cf. *rugosifrons*	*Hipparion sithonis* nov. sp.
	Ouzocerus sp.	cf. *Ouzoceros*	*"Diceros" neumayri*
		Gazella aff. *capricornis*	*Ancylotherium pentelicum*
		Gazella aff. *gracile*	*Helladotherium duvernoyi*
			Palaeotragus rouenii
			Palaotraginae indet.
			Tragoportax amalthaea
			Miotragocerus sp.
			Gazella pilgrimi
			Gazella cf. *capricornis*
			Nisidorcas planicornis
			Palaeoreas lindermayeri
			Palaeoryx cf. *pallasi*

NKT: Nikiti 1; NIK: Nikiti 2.

were densely accumulated in a pocket of about 5 × 3 m and severely affected by syn- and post-fossilization factors. Mammal remains included all anatomical parts (from complete skulls to ribs and tarsal bones) but very few if any in anatomical connection and a lot of them crashed. There was, also, prevalence for big bones to be preserved. Rolling was absent but in several cases fossils were eroded by recent plant and soil activity.

The much richer NIK site, extensively exploited during the second fieldwork season, provided as much as 2000 fossil specimens, again almost entirely mammals, but isolated specimens of land turtles and paleognath birds as well. The fossil layer covers several dozens of square meters where fossils appear in successive small and dense concentrations with less tightly-spaced findings between them. Most are black due to manganese oxides but otherwise complete and perfectly preserved. All anatomical parts are equally present and anatomical connections, frequently of complete legs or crania, are common. Both the sedimentary context (Koufos, 2016a) and the features of the fossiliferous accumulations indicate that NKT represents a deposit of higher energy than NIK. The oryctocenosis provided by the NIK flooding event is certainly closer to the thanatocenosis than in NKT and therefore taphonomic bias appears more severe in the latter locality.

3. Faunal structure

The revised faunal list of NKT includes 15 mammalian taxa (Table 1), representing four orders and seven families. Though the number of identifiable specimens (NISP) is biased towards giraffids (22.4% of NISP; Fig. 1), the number of species does not markedly differ from the average of other contemporaneous faunal assemblages from SE Europe (counting usually between 10 and 20 species). The almost complete absence of carnivores (only one worn DP3 described so far; Koufos, 2016b) is, however, a taphonomic deception. Compared to previous studies, the current revision allows recovering two rhinocerotid taxa at the species level, taxonomic upgrading of *Prostrepsiceros* and improving the α-taxonomy of four additional taxa (excepted *Hispanodorcas* cf. *orientalis* which was part of a previous revision by Kostopoulos, 2014; Table 1). The final faunal list of NIK includes seven orders and 11 families, together representing 19 mammalian species, plus one ostrich and a small tortoise. Two new hipparionine species are recognized and α-taxonomy is significantly improved (Table 1).

As in most late Miocene mammal assemblages from SE Europe, the bulk of both faunal associations consist of bovids and hipparionine horses, together representing more than 70% of either Minimum Number of Individuals (MNI) or NISP (Fig. 1). The reduction of giraffids from 22.4% in NKT to only 7% in NIK may reflect a general turnover, as giraffids also have a stronger signal in the Vallesian faunas of the Axios Valley (Macedonia, Greece) when compared to the Turolian ones, but the magnitude of this event is certainly blurred by taphonomical artifacts in NKT. The absence of suids in NIK and proboscideans in NKT is most probably also artificial.

4. Biochronology

The loose and coarse texture of sediments bearing both Nikiti 1 (NKT) and Nikiti 2 (NIK) sites (Koufos, 2016a) prohibits any