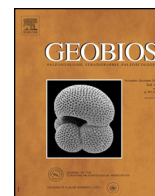




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## Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)

### Synthesis<sup>☆</sup>



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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.

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## 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
<i>Ouranopithecus macedoniensis</i>	<i>Ouranopithecus macedoniensis</i>	<i>Ouranopithecus macedoniensis</i>	<i>Ouranopithecus macedoniensis</i>
<i>Hipparion macedonicum</i>	Hyaenidae indet.	Hyaenidae indet.	Hyaenidae sp.
<i>Hipparion cf. primigenium</i>	<i>Hipparion</i> sp. (large)	<i>Hipparion primigenium</i>	<i>Hipparion</i> aff. <i>giganteum</i>
<i>Bohlinia attica</i>	<i>Hipparion macedonicum</i>	<i>Hipparion macedonicum</i>	<i>Hipparion macedonicum</i>
<i>Palaeotragus</i> sp.	Rhinocerotidae indet.	Rhinocerotidae indet.	<i>Dihoplus pikermiensis</i>
<i>Mesembriacrus</i> cf. <i>melentisi</i>	<i>Microstonyx major</i>	<i>Microstonyx major</i>	" <i>Diceros</i> " <i>neumayri</i>
<i>Prostrepsiceros</i> aff. <i>houtumschindleri</i>	<i>Helladotherium duvernoyi</i>	<i>Helladotherium duvernoyi</i>	<i>Microstonyx major</i>
<i>Tragoportax</i> cf. <i>rugosifrons</i>	<i>Bohlinia attica</i>	<i>Bohlinia attica</i>	<i>Helladotherium duvernoyi</i>
	<i>Bohlinia nikitiae</i>	<i>Bohlinia nikitiae</i>	<i>Bohlinia attica</i>
	<i>Palaeotragus</i> cf. <i>rouenii</i>	<i>Palaeotragus</i> cf. <i>rouenii</i>	<i>Bohlinia nikitiae</i>
	<i>Tragoportax gaudryi</i>	<i>Tragoportax</i> cf. <i>gaudryi</i>	<i>Palaeotragus</i> sp.
	<i>Prostrepsiceros houtumschindleri syridisi</i>	<i>Prostrepsiceros houtumschindleri syridisi</i>	<i>Prostrepsiceros syridisi</i>
	<i>Oiceros</i> aff. <i>atropatenes</i>	<i>Oiceros</i> aff. <i>atropatenes</i>	<i>Hispanodorcus</i> cf. <i>orientalis</i>
	? <i>Gazella</i> sp.	? <i>Gazella</i> sp.	<i>Miotragocerus</i> sp.
	Bovidae indet.	Bovidae indet.	Antilopinae indet.
	NIK	NIK	NIK
	Hyaenidae indet.	Hyaenidae indet.	<i>Mesopithecus</i> sp.
	<i>Choerolophodon pentelici</i>	<i>Choerolophodon pentelici</i>	<i>Adcrocuta eximia eximia</i>
	<i>Hipparion</i> sp. (small)	<i>Hipparion dietrichi</i>	<i>Amphimachairodus giganteus</i>
	<i>Helladotherium duvernoyi</i>	<i>Hipparion macedonicum</i>	<i>Choerolophodon pentelici</i>
	<i>Nisidorcus planicornis</i>	<i>Helladotherium duvernoyi</i>	<i>Hipparion phillipus</i> nov. sp.
	cf. <i>Tragoportax</i> sp.	<i>Nisidorcus planicornis</i>	<i>Hipparion macedonicum</i>
	<i>Oiceros</i> sp.	<i>Tragoportax</i> cf. <i>rugosifrons</i>	<i>Hipparion sithonis</i> nov. sp.
	<i>Ouzocerus</i> sp.	cf. <i>Ouzoceros</i>	" <i>Diceros</i> " <i>neumayri</i>
		<i>Gazella</i> aff. <i>capricornis</i>	<i>Ancylotherium pentelicum</i>
		<i>Gazella</i> aff. <i>gracile</i>	<i>Helladotherium duvernoyi</i>
			<i>Palaeotragus rouenii</i>
			<i>Palaeotraginae</i> indet.
			<i>Tragoportax amalthaea</i>
			<i>Miotragocerus</i> sp.
			<i>Gazella pilgrimi</i>
			<i>Gazella</i> cf. <i>capricornis</i>
			<i>Nisidorcus planicornis</i>
			<i>Palaeoreas lindermayeri</i>
			<i>Palaeoryx</i> cf. <i>pallasi</i>

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

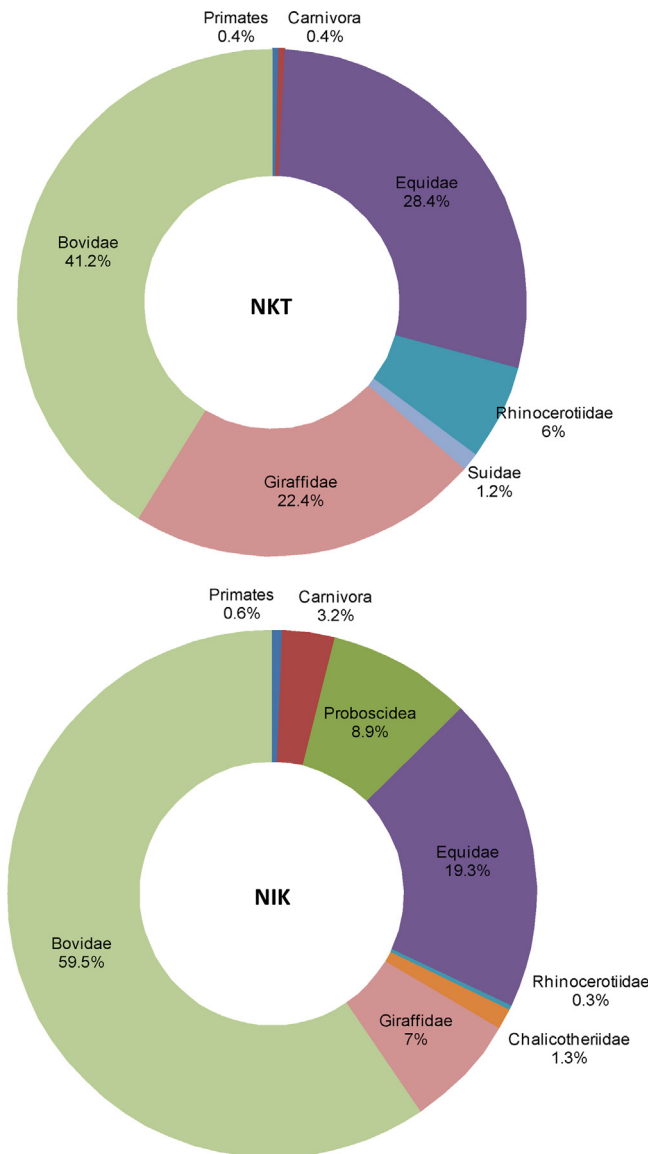
The revised faunal list of NKT includes 15 mammalian taxa (Table 1), representing four orders and seven families. Though the number of identifiable specimens (NISP) is biased towards giraffids

(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  $\alpha$ -taxonomy of four additional taxa (excepted *Hispanodorcus* 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  $\alpha$ -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



**Fig. 1.** Faunal composition of the Nikiti 1 (NKT) and 2 (NIK) mammal assemblages based on the number of the identifiable specimens (NISP) per higher rank taxon (order or family).

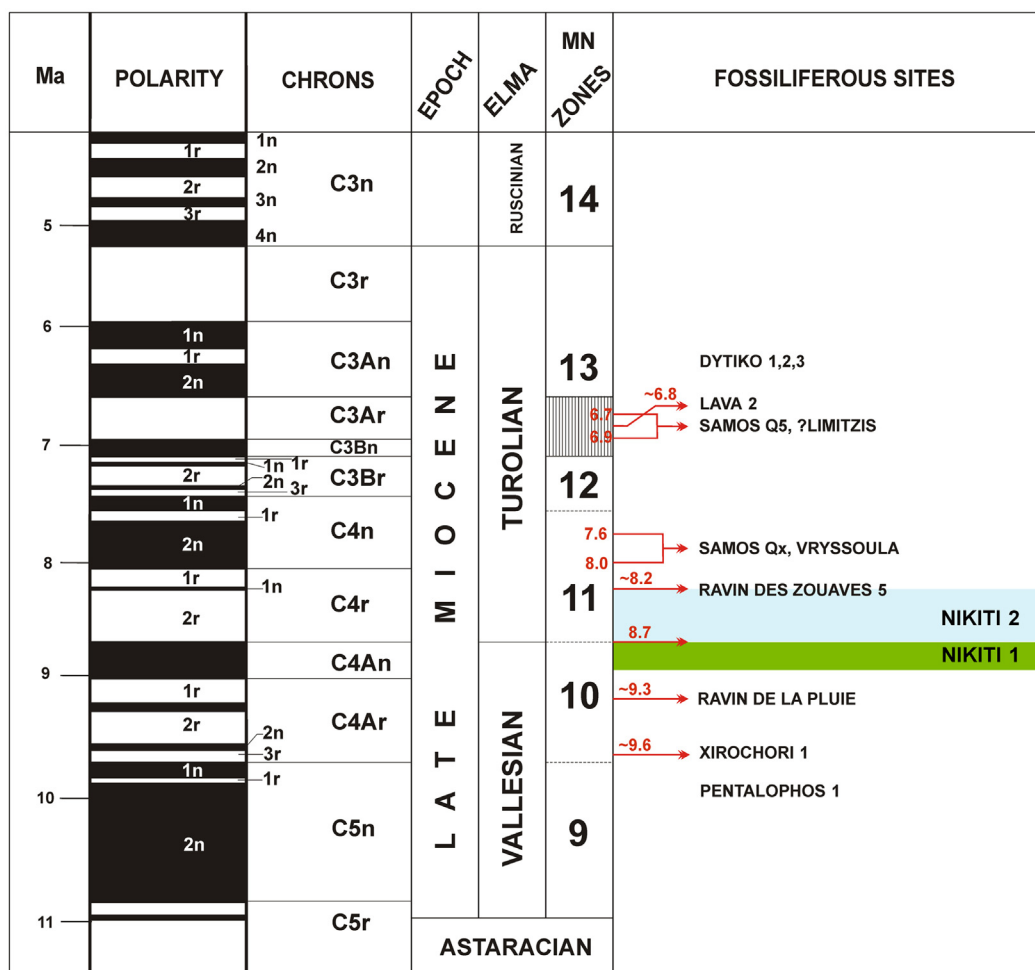
magnetostratigraphic study. Hence, age estimates are strictly based on biochronological data and correlations, primarily with the well-known and neighboring late Miocene fossil record of the Axios Valley, as well as with other faunal assemblages from Greece and adjacent regions (Fig. 2). Based on mammal identifications provided earlier, the NKT mammal assemblage was originally dated to late Vallesian–early Turolian (MN 10–MN 11) and later as latest Vallesian (uppermost MN 10), with an estimated age between 9.3 and 8.7 Ma (Koufos, 2013). We may reframe this age boundary based on the current state of knowledge.

Two hipparions have been recognized in the NKT fauna, the small-sized *Hipparion macedonicum* and the large-sized *H. aff. giganteum* (Table 1). The first taxon occurs from the upper part of early Vallesian (MN 9; locality Pentalophos 1 [PNT], Axios Valley) to the lower part of middle Turolian (MN 12; localities of Vathylakkos [VATH], Axios Valley, and Perivolaki [PER], central Greece). The narrow muzzle, the weak preorbital fossa, and the elongated and gracile metapodials of the NKT *H. macedonicum* are features recognized in the Vallesian morph of this species. On the other hand, the NKT large-sized hipparion is more advanced than

the large-sized *H. cf. sebastopolitanum* from the late Vallesian locality Ravin de la Pluie (RPI, Axios Valley; Vlachou, 2013; Koufos and Vlachou, 2016), magnetostratigraphically dated at ~9.3 Ma (Sen et al., 2000). The NKT large-sized hipparion exhibits strong similarities with *H. giganteum* from Grebeniki (Ukraine), correlated to the late Vallesian (MN 10; Vangengeim and Tesakov, 2013). The presence of the hominoid primate *Ouranopithecus macedoniensis* in NKT also suggests a late Vallesian age as the species is originally known from the localities XIR and RPI (Axios Valley; Koufos, 2006), which are magnetostratigraphically dated at ~9.6 and ~9.3 Ma, respectively (Sen et al., 2000). The assumed occurrence of this species in the middle Turolian of Bulgaria (Spassov et al., 2012) is still pending confirmation; the only current evidence comes from an isolated P4 collected by an amateur several years ago. *Ouranopithecus turkae* from the early Turolian (Ünay et al., 2006) site Çorakyerler (Turkey) differs from the Greek hominoid (Güleç et al., 2007), while Begun (2009) considers that the Çorakyerler hominoid represents a different genus. The NKT *Miotragocerus* sp. is roughly at the same evolutionary stage than *M. pannoniae* from the early Vallesian (MN 9) locality Höwenegg (Germany), and certainly more primitive than the boselaphines recorded in NIK and other Turolian mammal assemblages from the Axios Valley. Among rhinocerotids found in NKT (Koufos et al., 2016b) “*Diceros*” *neumayri* covers the whole late Miocene, whereas *Dihoplus pikermiensis* is mainly known from the Turolian. Although *D. pikermiensis* is referred from the Vallesian locality Eldari I (Georgia) in the NOW database (Fortelius, 2014), Vangengeim and Tesakov (2013) does not include this species in their list, and therefore its Vallesian presence is doubtful and needs confirmation. The presence of *Microstonyx major* in NKT is again an evidence of a younger age as this species vastly occurs in Turolian assemblages of the Eastern Mediterranean region. Finally, apart from NKT, *Prostrepsiceros syridisi* is recorded in the Turkish Turolian locality Sivas (Bibi and Güleç, 2008), which according to Made et al. (2013) cannot be younger than 8.1 Ma, possibly even older than 8.3 Ma.

Judging from the above evidences, it is clear that the NKT mammal assemblage should be widely framed between 9.3 and 8.2 Ma, i.e., between Ravin de la Pluie (RPI) and Ravin des Zouaves 5 (RZO), being distinct in faunal structure from both assemblages of the Axios Valley. The NKT fauna is also sharply distinct from the stratigraphically succeeding NIK fauna, and as in the case of RPI/RZO, the NKT and NIK assemblages closely box the *Ouranopithecus*/*Mesopithecus* turnover in Greece. Among surrounding local fossil mammal assemblages, NKT shows possibly the best match with Grebeniki (Ukraine), Poksheshti, and Raspopeny (Moldova) as they share the occurrence of *Hipparion giganteum*, *Microstonyx major*, *Miotragocerus*, and possibly *Prostrepsiceros* (Vangengeim and Tesakov, 2008a, 2008b). Stratigraphic calibrations consistently correlate those sites with the Sarmatian/Meotian boundary, for which, however, there is no age consensus (Sen, 1997; Vangengeim and Tesakov, 2008a, 2008b, 2013). In spite of recent arguments by Vangengeim and Tesakov (2013), we favor here an earlier view by Pevzner and Vangengeim (1993) and Sen (1997), further supported by recent radiometric datings and magnetostratigraphy (Vasiliev et al., 2011). According to these authors, the Sarmatian/Meotian boundary is dated at ~8.6 Ma, which is close to the Vallesian/Turolian boundary (~8.7 Ma; Agustí et al., 2001); this implies a terminal Vallesian age for the Nikiti 1 (NKT) fauna (Fig. 2). Interestingly, the presence of *Mesopithecus* in Grebeniki (Andrews et al., 1996) indicates that we are again near the hominoid/cercopithecoid turnover and that either colobine monkeys had already penetrated the terminal Vallesian mammal fauna of the area at its northern edges (north Black Sea), or that Grebeniki is slightly younger than NKT.

Based mostly on the presence of *Nisidorcas planicornis* as well as on the *H. “dietrichi”* (= *H. philippus* nov. sp.; Koufos and Vlachou,

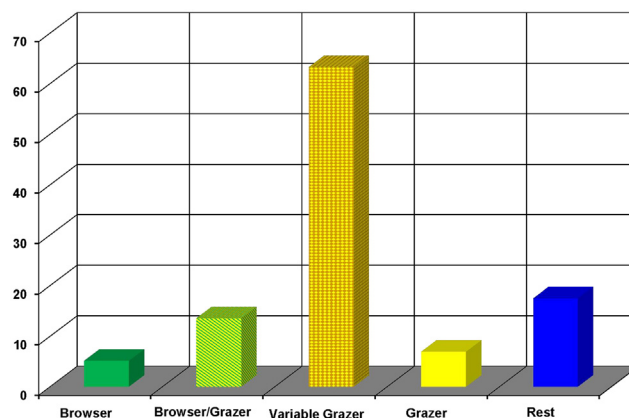


**Fig. 2.** Biochronology and biostratigraphic position of the two Nikiti mammal localities. The estimated ages of the localities are taken from Sen et al. (2000), Kostopoulos et al. (2003), Koufos et al. (2006b), and Hordijk and de Bruijn (2009). ELMA: European Land Mammal Age.

2016)-*H. macedonicum* association, the NIK faunal assemblage was originally considered as early Turolian in age (MN 11; Koufos, 2013). A reappraisal is, however, necessary in the light of its significantly enriched faunal list. The Turolian age of the NIK assemblage is strongly supported by the presence of the hyaenid *Adcrocuta eximia eximia*, the felid *Amphimachairodus giganteus*, the advanced morph of the gomphothere *Choerolophodon pentelici*, and the chalicotherid *Ancylotherium pentelicum* (Koufos, 2012, 2016b; Konidaris and Koufos, 2016; Koufos and Kostopoulos, 2016a,b).

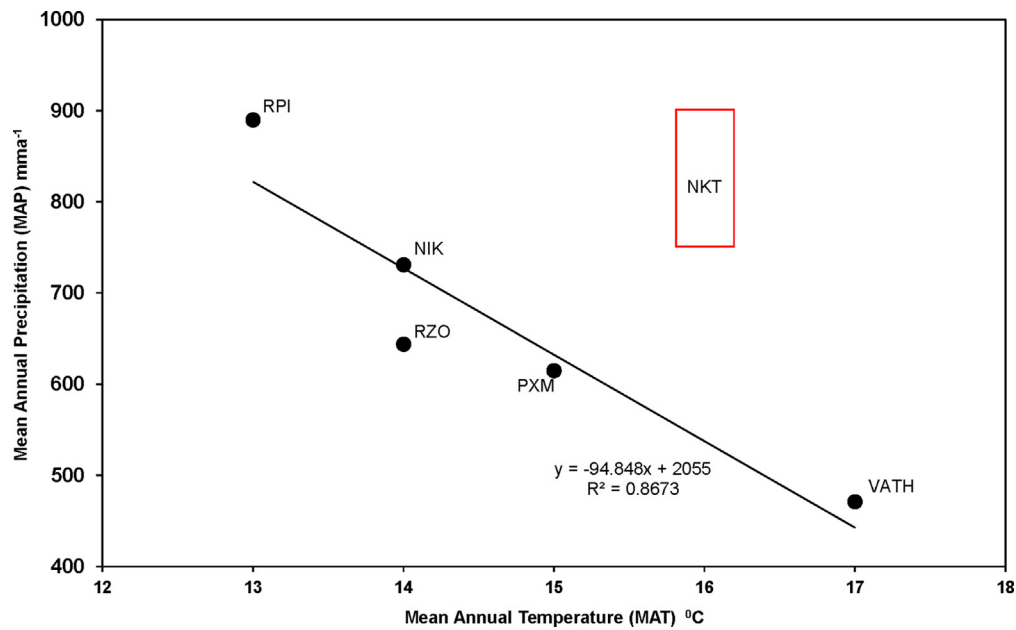
The presence of the cercopithecoid *Mesopithecus* is again a clear evidence for a Turolian age (Andrews et al., 1996; Koufos, 2003, 2009, 2016c). Despite the poor material, the NIK *Mesopithecus* has larger dimensions than the typical *M. pentelicus* from Pikermi, being closer to the large-sized forms *M. delsoni* and *Mesopithecus* sp. A (Koufos, 2016c), characterizing the early-middle Turolian of Greece (Koufos, 2009). The NIK hipparions belong to four different taxa (Table 1). The relatively wider muzzle of *H. macedonicum* from NIK (Koufos and Vlachou, 2016) is a character occurring in the early-early middle Turolian forms of the species (Vlachou, 2013). The new species *H. philippus* is also present in the localities RZO, Prochoma 1 (PXM) and VATH of the Axios Valley, and PER (Koufos and Vlachou, 2016), all of them dated to the early-early middle Turolian (Koufos, 2013). Furthermore, the proportional resemblance between *H. philippus* metapodials from NIK and RZO (Koufos and Vlachou, 2016) points to an early Turolian age. The NIK artiodactyl association fits very well with those from RZO, PXM, VATH and PER. Additionally, *Palaeoreas lindermayeri* and *Nisidorcas*

*planicornis* from NIK show less advanced characters than *P. lindermayeri* from Pikermi (Greece) and Hadjidimovo (Bulgaria), and *N. planicornis* from RZO and VATH of Axios Valley, respectively (Kostopoulos, 2016), altogether indicating an early Turolian age, probably older than RZO (magnetostratigraphically dated at ~8.2 Ma; Sen et al., 2000). Hence, an age between 8.7 and 8.2 Ma is suggested for the Nikiti 2 mammal assemblage (Fig. 2). Similarities between *Struthio* cf. *karatheodoris* from NIK and



**Fig. 3.** Dietary composition of the Nikiti 2 (NIK) herbivore assemblage based on the number of identifiable specimens per feeding category (Merceron et al., 2016).





**Fig. 4.** Scatter diagram showing the mean annual temperature (MAT) and the mean annual precipitation (MAP) estimated for the mammal assemblages from Nikiti and Axios Valley (Macedonia, Greece) (Rey et al., 2013).

*S. brachydactylus* from Grebeniki (Koufos et al., 2016a) might indicate that the NIK assemblage is closer to the lower limit of the estimated time interval.

## 5. Paleocology and Paleobiogeography

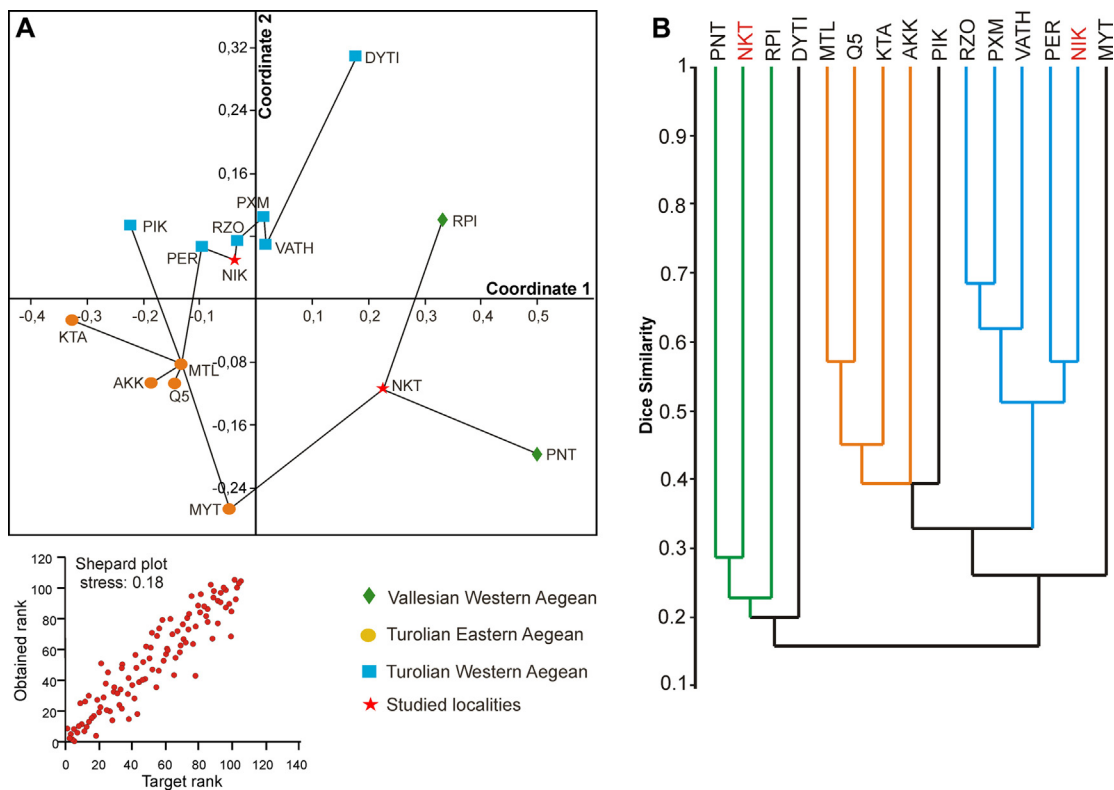
Morphoecological and dental wear analyses reveal the palaeoecological profile of NKT and NIK mammalian assemblages (Rey et al., 2013; Konidaris et al., 2016; Koufos and Vlachou, 2016; Merceron et al., 2016). Additionally, Merceron et al. (2016) discuss these faunas in relation to the general palaeoenvironmental frame depicted from previous studies on the upper Miocene of Northern Greece and Southern Balkans. The NIK fauna is dominated by variable grazers (Fig. 3) whereas NKT might be switched more towards a mixed feeding (*Hipparion macedonicum*, *Hipparion* aff. *giganteum*, *Palaeotragus*, *Prostrepsiceros syridisi*) to browsing (*Bohlinia*, *Helladotherium*, *Miotragocerus*) spectrum (Koufos et al., 2006a). Rey et al. (2013) also provide an estimated mean annual temperature (MAT) of 16 °C for NKT; for NIK the estimated MAT is 14 °C associated with a mean annual precipitation (MAP) of 731 mm.a<sup>-1</sup>.

Stable isotope compositions inferred from tooth enamel of equid and bovid taxa from two couples of sites crossing the Vallesian/Turolian boundary (RPI/RZO and NKT/NIK) in Northern Greece, reveal average temperatures and precipitations compatible with those of recent Mediterranean-like climates (*sensu* Köppen's classification), possibly with a high seasonal amplitude signal and a dominance of a C<sub>3</sub> vegetation (Merceron et al., 2013; Rey et al., 2013). Rey et al. (2013) record a weak increase of MAT associated with a rather stronger decrease in MAP from RPI to VATH (Fig. 4), which is consistent with the general precipitation decrease in Central-Eastern Europe (Böhme et al., 2011) and may mirror a slight opening and aridification from the late Vallesian to the early middle Turolian. At the same time, several dental wear studies show that most of the mesoherbivore taxa recorded in this region during early to early middle Turolian are classified around variable grazers (Koufos et al., 2006a; Merceron et al., 2007, 2016; Fig. 3). Mixed feeding and grazing habits also revealed for the bulk of the Vallesian ungulate association of the area (Merceron et al.,

2005, 2007). Consistently, bovids, equids, and primates from both sides of the Vallesian/Turolian boundary show locomotor adaptations suitable for open-to-light cover habitats (Bouvrain and Bonis, 1984; Kostopoulos, 2000; Youlatos and Koufos, 2010; Youlatos et al., 2012; Vlachou, 2013; Koufos and Vlachou, 2016), supporting the Mediterranean savanna parkland model proposed by Merceron et al. (2016).

*Contra* large-scale proxies that exhibit a rather stable type of vegetation cover under a gentle trend of aridification mostly controlled by precipitation rather than temperature (Rey et al., 2013), the meso-herbivore mammal association (up to 500 kg), which made up to 60% of those faunas (either by means of MNI, NISP or number of taxa), shows remarkable changes (Table 1). Only half of the meso-herbivore species occurring in the XIR (Xirochori 1, Axios Valley)-RPI time interval continue up to NKT: *H. cf. sebastopolitanum* is replaced by *H. aff. giganteum*, and *Mesembriacerus melentisi*-*Samotragus praecursor*-*Prostrepsiceros vallesiensis* (RPI) by *Prostrepsiceros syridisi*-*Miotragocerus sp.*-*Hispanodorcus cf. orientalis* (NKT). Possibly at the same time, *Microstonyx major* enters the fauna (Table 1). The hominoid *Ouranopithecus* indicates some flexibility in these meso-herbivore structural faunal changes, being present in both fossil associations. It exits between the NKT and NIK time levels, during which changes are more radical, including both replacements and several new entries (e.g., *Mesopithecus*, *Nisidorcus*, *G. pilgrimi*, *Palaeoreas*, *Tragoportax*, and at least two new hipparionine species; Table 1) that allow doubling of the mesoherbivore diversity. This renewed mammal association will remain stable until the middle Turolian (Kostopoulos, 2009).

Up to now, hypotheses relating the above faunal structural changes to major climatic events and related vegetational switches failed to be proved (Merceron et al., 2013; Rey et al., 2013). The MAT in NKT, departing from the general trend (Fig. 4), and the arrival at that time of *Hipparion* aff. *giganteum* from the north Black Sea region need to be further explored. On the other hand, the early Turolian local turnovers started from the NIK level represent periods of high origination and immigration rates (Kostopoulos, 2009: fig. 4), possibly related to palaeogeographic remodeling. Reconstructions of the Black Sea region show a period of nearly complete desiccation at ~8.6 Ma (the Sarmatian/Meotian boundary) referred to as the Khersonian crisis of the Black Sea



**Fig. 5.** Non-metric multidimensional scaling (A) and UPGMA cluster analysis (B), using the Dice taxonomic similarity index, of the late Miocene faunas from Continental Greece and Asia Minor. Faunas with less than ten taxa were excluded. Solid lines in A represent Kruskal's minimum spanning tree connections; below the NMDS plot is its related Shepard plot, illustrating the overall quality of the NMDS structure (obtained rank) with respect to the observed similarity matrix (target rank). Data for the Greek localities taken from Koufos (2006, 2009), with new entries and corrections; data for the Turkish localities taken from Bonis et al. (1994) and Sen (2005). AKK: Akkaşda; DYTI: Dytiko 1, 2, 3; KTA-B: Kemiklitepe A-B; MTL: Mytilinii 1; MYT: Mytilinii 3; NIK: Nikiti 2; NKT: Nikiti 1; PER: Perivolaki; PIK: Pikermi; PNT: Pentalophos 1; PXM: Prochoma 1; Q5: Samos Quarry-5; RPI: Ravin de la Pluie; RZO: Ravin des Zouaves 5; VATH: Vathyakkos 1, 2, 3.

(Kojumdgieva, 1983; Vasiliev et al., 2015). This event may have facilitated or even forced expansion of northeastern mammal communities towards the Balkans.

Recent studies (Kostopoulos, 2009; Kostopoulos and Karaküçük, 2015: figs. 15, 16) already showed the position of the early Turolian mammal assemblages from Northern Greece with respect to those from Anatolia (Turkey). It is claimed that differences in taxonomic composition, physical characteristics (e.g., average weight) and feeding strategies of the herbivore associations altogether imply a degree of geographic isolation of the Turolian mammal assemblages of northern Greece (including NIK) from the Anatolian ones. Indeed, a non-metric multidimensional scaling (NMDS) ordination and a cluster analysis (using the PAST software; Hammer et al., 2001), both based on the same presence-absence matrix at the species level and on Dice similarity (Fig. 5), suggest a late Vallesian (PNT, RPI) to late Turolian (DYTI) gradient (Fig. 5 (A)) with the bulk of the early-middle Turolian assemblages from Continental Greece, including NIK, being grouped separately from those of Asia Minor and Anatolia (Fig. 5 (B)). The Vallesian assemblages of northern Greece, including NKT, cluster rather closely (Fig. 5 (B)), whereas the position of the late Turolian Dytiko fauna (DYTI) in both analyses is hardly explained but may be related to a flashback on more “Vallesian-like” environmental conditions.

## 6. Conclusions

Albeit extensively explored for half a century, the northern Greek late Miocene vertebrate assemblages still provide important and sometimes surprising data, allowing significant improvement

(or reset) of our understanding on the multiple and complex relationships among faunal structure, climate, and environment of the past. The quite rich Nikiti fossil site presented in this volume certainly offers such an opportunity. From a strictly taxonomic point of view, the study of the Nikiti 2 vertebrate fossils reveal the presence of two new species of hipparionine horses and strengthens the poor record of ostriches from this area. At the same time, the revision of the mammal remains from both Nikiti 1 and Nikiti 2 localities significantly enriches the available faunal lists, adding more taxa and resolving previous misconceptions. Impressive enough, the updated data show a much stronger northern (Black Sea) influence than previously thought for the late Miocene of Southern Balkans. The most significant addition appears, however, to be the presence of *Mesopithecus* in Nikiti 2. Next to the Axios Valley, this new taxonomic entry marks the Nikiti 1/Nikiti 2 couple of sites as the second record of the *Ouranopithecus/Mesopithecus* replacement in Northern Greece and SE Europe, correlated to the Vallesian/Turolian boundary. The reasons for this replacement have long been the subject of various studies which, however, did not show any dramatic climatic shift. On the other hand, the Nikiti data confirm and further support those from Axios Valley in detecting, at the same time-interval, an important structural reorganization of the mammal fauna, mostly expressed through the doubling of the meso-herbivore diversity and the increase of intermediate feeders. As the gentle aridification trend documented across the Vallesian/Turolian boundary does not seem adequate to explain this important remodelling of the mammal fauna as well as the possibly associated primate replacement, the question of what triggered those changes remains open to discussion.

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