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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

Upper Miocene mammalian faunas of the Axios Valley (Macedonia, Greece) and their contribution to the study of the Neogene in the Eastern Mediterranean

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The Late Miocene vertebrate localities in the Axios Valley (Macedonia, Greece) were discovered at the beginning of the last century by the French geologist Camille Arambourg, who made a large fossil collection and carried it back to France. During the last 50 years, extensive fieldwork have been carried out by a Greek–French team, which has yielded a large number of fossils. Important data on fauna, stratigraphy, biochronology, and palaeoecology were obtained from the study of this collection. The fauna of the Axios Valley proved diverse, comprising numerous groups of mammals and number of new taxa. It is divided into five distinct faunal assemblages, which cover chronologically the entire Late Miocene period. These faunas have been systematically studied, dated, and correlated with the European MN (mammal Neogene) biozones. Their analysis has been a major contribution to the understanding of palaeoenvironmental conditions and climatic changes during the Late Miocene in Greece and the wider Eastern Mediterranean region. The faunas of the Axios Valley have a well-established geographic, stratigraphic, systematic, and chronological background. They were the first to appear in the Eastern Mediterranean and can be used as a comparative fauna for the Late Miocene. Subsequent works in Greece and Türkiye added more data, further improving our understanding of the Neogene period in the Eastern Mediterranean. This paper is an attempt to summarise the work done on the Axios Valley Late Miocene mammal fauna in the last 50 years and present the results.

Introduction

Since the beginning of the 20th century, there has been only limited evidence of vertebrate fossils in the wider area of Thessaloniki (Macedonia, Greece). The only known remains were those of some tortoises. They were found on the eastern border of the city, in an area formerly called Capudjlar, now known as Pylaea (Del Campana 1917, 1919). During World War I (1915–1916), the French and British armies arrived and set up camp in the vicinity of Thessaloniki. The French Army camped around the village of Vathylakkos, east of Thessaloniki, and dug trenches for pro-

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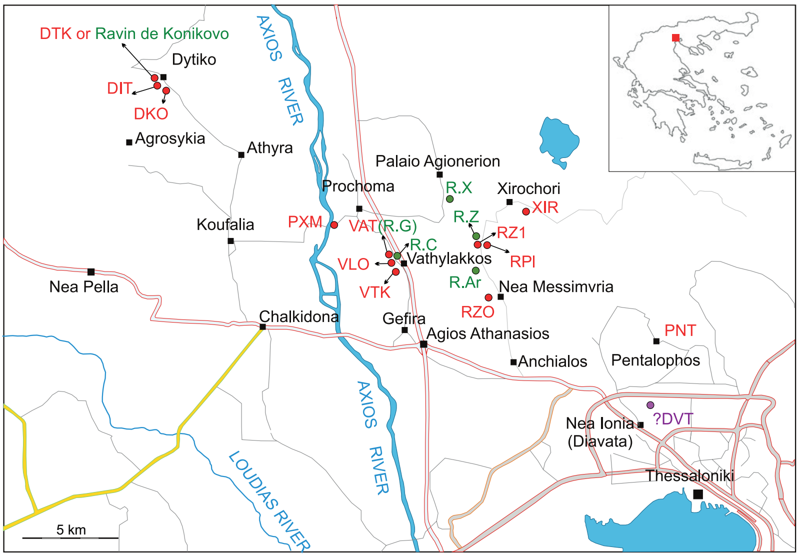

Fig. 1. Axios Valley with the positions of the Late Miocene mammal localities. New localities (abbreviations set in red): DTK = Dytiko 1, DIT = Dytiko 2, DKO = Dytiko 3, PNT = Pentalophos 1, PXM = Prochoma 1, RPl = Ravin de la Pluie, RZ1 = Ravin des Zouaves 1, RZO = Ravin des Zouaves 5, VLO = Vathylakkos 1, VTK = Vathylakkos 2, VAT = Vathylakkos 3, XIR = Xirochori 1; Arambourg's localities (abbreviations set in green): R.Ar = Ravin Ar, R.C = Ravin C, R.G = Ravin G or Ravin de Vatilük (= Vathylakkos 3, VAT), R.X = Ravin X, R.Z = Ravin des Zouaves, Ravin de Konikovo (= Dytiko 1, DTK); Andrews' locality (abbreviation set in violet): DVT, Diavata. The positions of the new localities are based on their geographic coordinates, while those of the old localities are based on the map in Arambourg and Piveteau (1929: fig. 1). The location of Diavata is uncertain as it is based only on the information in Andrews (1918) that it is near the village with the same name, hence it is marked with '?'.

tection. During the preparation of the trenches, the French geologist and army officer Camille Arambourg noticed the presence of fossils. Further exploration of the area led to the discovery of several localities (Fig. 1), and thus Arambourg began excavating and collecting fossils. The "Arambourg collection" is housed at the Muséum national d'Histoire naturelle in Paris and it is quite rich. It was thoroughly studied and described in a monograph *Les Vértébres du Pontien de Salonique* (Arambourg & Piveteau 1929). However, there are two earlier works evidencing the presence of Late Miocene mammals in the Axios Valley. The first (Andrews 1918) describes a large hyaenid and some fossil remains of hipparion bones discovered near the village of Diavata (formerly known as Dudular and now Nea Ionia; Fig. 1). The second (Bourcart 1919) mentions the presence of mammal fossils near the village of Vathylakkos, information given to the author by C. Arambourg.

No excavations were carried out in the Axios Valley until 1972 when the Laboratory of Geology and Palaeontology at Aristotle University of Thessaloniki (Prof. John K. Melentis) and the Laboratory of Vertebrate Palaeontology and Human Palaeontology of the University Paris VI and later Poitiers (Prof. Louis de Bonis) started a new fieldwork campaign, the preliminary results of which were published the following year (de Bonis *et al.* 1973). I joined the Axios Valley team in 1976, and since the retirement of Prof. J. Melentis in 1989 have continued the collaboration with Prof. L. de Bonis. Some of C. Arambourg's old localities were rediscovered and several new ones were found. Numerous fossils recovered from the various fossiliferous sites are stored at the Aristotle University of Thessaloniki.

Here, I attempt to (i) summarise the palaeontological, biochronological and palaeoecological data resulting from the study of the Axios Valley collection, (ii) show the importance of this collection, and (iii) demonstrate the contribution of the Axios mammalian fauna to the Neogene stratigraphy of Greece and the Eastern Mediterranean.

Geological background and localities

The Axios mammal fossiliferous sites are located to the west of Thessaloniki, near the estuaries of the Axios river (Fig. 1). Geotectonically, the area is included in the Axios Zone, more precisely in the Peonias subzone. The basement of the basin is comprised of ophiolites, ophiolitic conglomerates, marbles, schists, and granitic intrusions (Mercier 1968). The deposition in the basin started in the Eocene–Oligocene with marine sediments and continued until the beginning of the Early Miocene. Deposition continued during the Middle-Late Miocene with brackish deposits, followed by fluvio-terrestrial ones since the Late Miocene-Early Pliocene (Christodoulou 1965, Kalkreuth *et al*. 1991). The fossil-bearing sites are located within the Late Miocene–Early Pliocene fluvio-terrestrial deposits. The Late Miocene deposits of the Axios Valley are divided into three formations (Koufos 1989) described below.

Nea Messimvria Formation

The Nea Messimvria Formation (Fm.) consists of fluvio-terrestrial sands, gravels and compact to lose conglomerates mixed with reddish-brown clays and silts. It outcrops to the southeast of the villages of Agioneri, Nea Filadelphia and Nea Messimvria, and extends to the south where it is covered by recent deposits from the Axios and Gallikos rivers (Fig. 1). Geophysical prospecting of the area indicated the presence of a possible major fault across the Axios river (Mercier 1968), which probably caused an uplift on the eastern side. The subsequent erosion removed the overlain Vathylakkos Fm. deposits, revealing several fossiliferous sites. During the new field campaign, four localities were discovered: Pentalophos 1 (PNT), Xirochori 1 (XIR), Ravin de Pluie (RPl), and Ravin des Zouaves 1 (RZ1). The fossiliferous sites Ravin des Zouaves (R.Z) of Arambourg and Piveteau (1929), and Diavata (DVT) of Andrews (1918) are also situated within this formation (Fig. 1). Additionally, there is an old locality of C. Arambourg Ravin X (R.X), which could belong to either the Nea Messimvria Fm. or the Vathylakkos Fm.

Vathylakkos Formation

This formation consists of yellowish marls at the base, followed by alternating beds of grey-whitish sandy marls, sands, and gravels with intermittent crossbedding. The Vathylakkos Fm. is exposed between the western bank of the Axios river and around the villages of Vathylakkos, Prochoma and Agioneri (Fig. 1). From this area, Arambourg mentions the localities of Ravin G (R.G) or Ravin de Vatilük, Ravin Ar (R.Ar) and Ravin C (R.C) (Fig. 1) (Arambourg & Piveteau 1929). During the new fieldwork in the area, new fossiliferous sites were discovered within Vathylakkos Fm., the most important being Ravin des Zouaves 5 (RZO), Prochoma 1 (PXM), Vathykakkos 1 (VLO), Vathylakkos 2 (VTK) and Vathylakkos 3 (VAT), the latter corresponds to the old site Ravin G or Ravin de Vatilük (Fig. 1).

Dytiko Formation

This formation comprises fluvial–fluvio-terrestrial deposits consisting of alternating yellowish-whitish marls, sandy marls, sands, gravels, and freshwater limestones at the top (Koufos 1989). The Dytiko Fm. outcrops on the western bank of the Axios River around the village with the same name (Fig. 1). Only one fossiliferous locality, called Ravin de Konikovo (former name of Dytiko), was mentioned by Arambourg and Piveteau (1929). This site was rediscovered and it is mentioned as Dytiko 1 (DTK). Two other sites were found across the Platanoremma, a tributary of the Axios River, named Dytiko 2 (DIT) and Dytiko 3 (DKO) (Fig. 1). It is worth mentioning that several other localities were recognised in the Axios Valley, but the fossils were very few and incomplete.

Late Miocene mammal fauna of Axios Valley

The fauna of the Axios Valley was dominated by large mammals. The small mammals were rare and their fossils are typically discovered incidentally during excavating and preparing the large-mammal fossils. Despite extensive sediment washing, no promising specimens of micromammals were found, possibly due to the high-energy deposits and coarse sediments. However, some teeth of small mammals were discovered (Table 1). The murids are the most important, with *Progononys cathalai* providing the initial evidence for a Vallesian age of Ravin de la Pluie (de Bonis & Melentis 1975), and *Parapodemus gaudryi* confirming the Turolian age of Vathylakkos 3 (Koufos 2006a).

The carnivoran sample from the Axios Valley is quite diverse, with a significant number of species representing ~20% of the total number of genera and species (Fig. 2 and Table 1). Small carnivores are common, including representatives from the hyaenid genera *Protictitherium* and *Plioviverrops* (de Bonis & Koufos 1991, Koufos 2000). A new species, named *Protictitherium thessalonikensis*, was discovered at Ravin de la Pluie (Koufos 2012a). The large-sized hyaenid *Adcrocuta eximia* is present in most of the Axios Valley localities with two subspecies, the typical *A. e. eximia* and *A. e. leptorhyncha* (de Bonis & Koufos 1981, Koufos 2000).

Table 1. Fauna of the Late Miocene mammal localities of Axios Valley. + = presence of a taxon; – = absence of a taxon;? = estimated age. For abbreviations of the localities *see* Fig. 1.

Locality	PNT	DVT	XIR	RPI	RZ1	R.Z	R. X	RZO	R.Ar	PXM	VLO	VTK	VAT	R.C	DTK	DIT	DKO
MN biozone	9	?9	10	10	10	?10	10, 11	11	?11	12	12	12	12	?12	13	13	13
“*Metailurus*” *parvulus*	–	–	–	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–
?*Gazella*	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
?*Valerimys*	–	–	–	–	–	–	–	sp.	–	–	–	–	–	–	–	–	–
?*Hyaenictis*	–	–	–	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–
?*Procapreolus* sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	sp.	–	–
Acerorhinus	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Adcrocuta eximia	–	–	+	+	+	–	+	+	–	+	–	–	+	–	–	–	–
Amphimachairodus giganteus	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–
Amphiorycteropus gaudryi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Amphiorycteropus pottieri	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ancylotherium hellenicum	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anisodon macedonicum	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+
Bohlinia attica	–	–	–	cf.	–	+	–	–	–	–	+	+	+	–	+	+	–
Chalicotherium goldfussi	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Chasmaporthetes bonisi	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–
Chilotherium samium	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Choerolophodon anatolicus	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Choerolophodon pentelici	–	–	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+
Dinocrocuta	–	–	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dinocrocuta gigantea	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dinocrocuta salonicae	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dorcatherium puyhauberti	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	sp.	sp.
Dytikodorcas longicornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Eomellivora piveteaui	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Gazella	–	–	sp.	–	–	–	–	–	sp.	–	–	sp.	–	–	–	–	–
Gazella capricornis	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Gazella deperdita	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	–
Gazella pilgrimi	–	–	–	–	–	–	+	+	–	+	–	–	+	+	–	–	–
Gazella schlosseri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Helicotragus rotundicornis	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Helladorcas	–	–	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helladorcas geraadsi	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helladotherium duvernoyi	–	–	–	–	–	–	+	+	–	+	–	–	–	–	–	–	–
Hipparion	–	sp.	sp.	–	–	+	sp.	–	sp.	sp.	–	–	–	sp.	–	–	–
Hipparion macedonicum	+	–	–	+	+	–	–	+	–	+	–	+	+	–	cf.	–	cf.
Hipparion mediterraneum	–	–	–	–	–	–	–	cf.	–	–	–	–	–	–	–	–	–
Hipparion moldavicum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	aff.	aff.	aff.
Hipparion phillipus	–	–	–	–	–	–	–	+	–	+	+	+	+	–	–	–	–
Hipparion platygenys	–	–	–	–	–	–	–	–	–	–	–	–	–	–	aff.	aff.	aff.
Hipparion proboscideum	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Hipparion sebastopolitanum	cf.	–	–	cf.	–	–	–	–	–	–	–	–	–	–	–	–	–

continued

Table 1. Continued.

Locality MN Biozone	PNT 9	DVT ?9	XIR 10	RPI 10	RZ1 10	R.Z ?10	R. X 10,11	RZO 11	R.Ar ?11	PXM 12	VLO 12	VTK 12	VAT 12	R.C ?12	DTK 13	DIT 13	DKO 13
Hippopotamodon major	–	–	–	–	–	–	+	+	–	+	–	+	+	–	+	–	–
Hispanodorcas orientalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Hyaenictitherium wongii	–	–	–	–	+	–	–	+	–	–	–	+	+	–	–	–	–
Hystrix primigenia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Ictitherium viverrinum	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–
Majoreas woodwardi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Majoreas	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	sp.	–
Mesembriacerus melentisi	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
Mesopithecus	–	–	–	–	–	–	–	–	–	–	–	sp.	sp.	–	–	–	–
Mesopithecus delsoni	–	–	–	–	–	–	cf.	+	–	–	–	–	–	–	–	–	–
Mesopithecus monspessulanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–
Mesopithecus pentelicus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+
Micromys steffensi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Miodiceros neumayri	+	–	+	–	–	–	+	+	–	–	–	–	+	–	+	–	–
Miotragocerus	sp.	–	–	–	–	–	–	–	–	–	–	–	sp.	–	–	–	–
Miotragocerus macedoniensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+
Miotragocerus parvidens	–	–	–	–	–	–	–	+	–	+	–	–	–	+	–	–	–
Nisidorcas planicornis	–	–	–	–	–	–	–	+	–	+	+	+	+	–	–	–	–
Oioceros rothi	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–
Ouranopithecus macedoniensis	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Ouzocerus gracilis	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Ouzocerus pentalophosi	+	–	cf.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pachytragus	–	–	–	–	–	–	–	–	sp.	–	–	–	–	–	–	–	–
Palaeogiraffa macedoniae	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Palaeogiraffa major	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Palaeogiraffa pamiri	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Palaeoreas lindermayeri	–	–	–	–	–	+	–	+	–	–	+	–	+	–	+	–	–
Palaeoreas lindermayeri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Palaeoryx pallasi	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–
Palaeoryx sp.	–	–	–	sp.	–	–	–	–	–	–	–	–	–	–	sp.	sp.	–
Palaeotragus coelophrys	+	–	sp.	cf.	–	–	–	–	–	–	–	–	–	–	–	–	–
Palaeotragus rouenii	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	–
Palerinaceus	–	–	–	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–
Parapodemus gaudryi	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Plesiogulo crassa	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Plioviverrops cf. guerini	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Plioviverrops orbignyi	–	–	–	–	–	–	–	+	–	+	–	+	–	–	–	–	–
Pristifelis	–	–	–	–	–	–	–	–	–	–	–	–	sp.	–	–	–	–
Procobus melania	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	sp.	–
Progonomys cathalai	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Propotamochoerus aegeaus	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Prostrepsiceros	–	–	–	–	–	–	–	–	sp.	–	–	–	–	–	–	–	–
Prostrepsiceros axiosi	–	–	–	–	–	–	–	+	–	+	–	–	+	–	–	–	–
Prostrepsiceros rotundicornis	–	–	–	–	–	–	+	+	–	–	–	–	–	+	–	–	–
Prostrepsiceros vallesiensis	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Protictitherium crassum	cf.	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Protictitherium intermedium	–	–	–	aff.	–	–	–	–	–	–	–	–	–	–	–	–	–
Protictitherium thessalonikensis	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Protoryx	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Protoryx carolinae	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Protragelaphus theodori	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Protragelaphus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	sp.
Samotherium major	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–
Samotragus praecursor	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
Spermophilinus	–	–	–	sp.	–	–	–	–	–	–	–	–	–	–	–	–	–
Stryfnotherium exophthalmon	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Tragoportax	–	–	–	–	–	–	–	–	–	–	–	–	–	–	sp.	sp.	–
Tragoportax amalhhea	–	–	–	–	–	–	+	+	aff.	–	–	+	+	–	–	–	–
Zygolophodon turicensis	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–

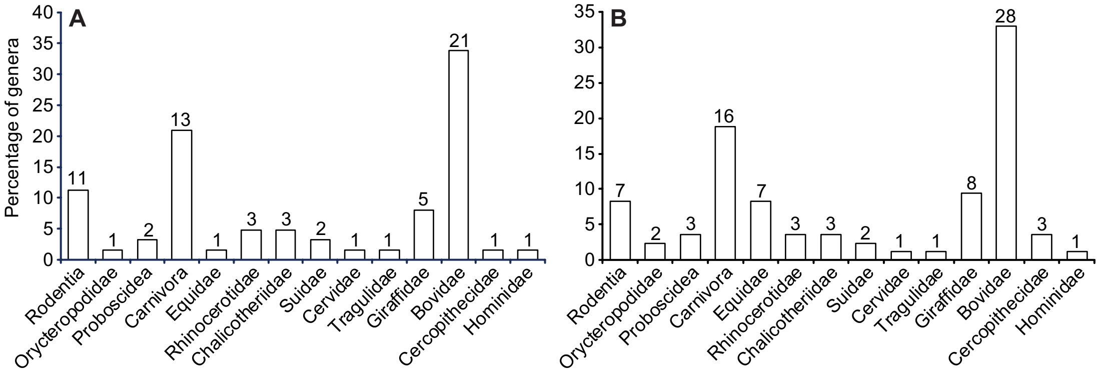

Fig. 2. Composition of the Late Miocene fauna of the Axios Valley at the (**A**) genus and (**B**) species levels. The numbers of genera and species for each family are given above the bars in **A** and **B**, respectively.

In addition, a very large hyaenid was discovered at the Diavata locality in the Axios Valley (Andrews 1918). It had originally been described as *Hyaena salonicae*, but later Qiu *et al*. (1988) transferred it to *Dinocrocuta*. During the new campaigns in the Axios Valley, a very large hyaenid, *D. gigantea*, was discovered in Pentalophos 1 and Xirochori 1 (Koufos 1995, 2000). The hunting hyaena *Chasmaporthetes* was first identified in the Late Miocene of Europe and described as a new species, named *C. bonisi*. The species was first identified from Dytiko 1 and later found from Ravin des Zouaves 5 (Koufos 1987a, de Bonis & Koufos 1994). The mustelids *Plesiogulo crassa* and *Eomellivora piveteaui* were identified for the first time in Europe and Greece, respectively (Koufos 1982, 2012b).

The Primates include the families Cercopithecidae and Hominidae, which represent 4% of the genera and 5% of the species identified in the Axios Valley fauna (Fig. 2). The family Cercopithecidae includes only the genus *Mesopithecus* with three species (Table 1). *Mesopithecus delsoni* is a new species discovered in the locality Ravin des Zouaves 5, distinct from the typical *M. pentelici* from Pikermi. Furthermore, an intermediate form between *M. delsoni* and *M. pentelicus* was recognized at the Vathylakkos localities (de Bonis *et al*. 1990, Koufos 2009a, 2009b). Whether the presence of *M. monspessulanus* was possible in the Dytiko fauna had not been clear. Recently, however, it was confirmed in the localities Dytiko 1 and 2 (de Bonis *et al*. 1990, Koufos 2009a, 2019a). A new hominoid, *Ouranopithecus macedoniensis* was discovered in the localities Ravin de la Pluie and Xirochori 1, which has some relationships with the hominines (de Bonis *et al*. 1974, 1990, Koufos 2015, 2022 and references therein).

Equids are abundant in the Axios Valley localities and in most of them they represent more than 50% of the collected material. However, they represent 8% of the species identified in the Axios Valley (Fig. 2), indicating less diversification than that of the bovids. Seven species, including a new one, were identified in the Axios Valley (Tables 1 and 2). The new species *H. macedonicum* was originally recognised in Ravin de la Pluie and later found at all the Axios Valley fossiliferous sites (Koufos 1984, 2016, Vlachou 2013). A medium-to-large form similar to *Hipparion sebastopolitanum*, previously unknown from the southern Balkans, was identified in the Axios fauna (Vlachou 2013). Two new hipparion species originally described from the Late Miocene locality of Nikiti 2 (Macedonia, Greece) were also discovered in the Axios Valley (Koufos & Vlachou 2019). The presence of *H. proboscideum*, which was previously known from the island of Samos (Wherli 1941), was also identified for the first time in continental Greece (Koufos 1987b, Koufos & Vlachou 2019).

The rhinocerotids are not so common in the Axios Valley fauna. They represent only 4% of the determined species but include three genera and species (Fig. 2). The common Late Miocene species *Miodiceros neumayri* is present in all localities of Axios Valley (Table 1). *Chiloth-*

erium samium, a rhinocerotid known from the island of Samos, occurred for the first time in continental Greece at the locality Pentalophos 1. Furthermore, some remains of *Acerorhinus* sp. were also recognised in Pentalophos 1 (Giaourtsakis 2022 and references therein). The chalicotheres are known from a few specimens belonging to three genera and species (Fig. 2 and Table 1). Two of them, *Ancylotherium hellenicum* and *Anisodon macedonicum*, are new species discovered in Pentalophos 1 and Dytiko 3, respectively (de Bonis *et al*. 1995, Koufos 2012c).

Giraffids are well represented in the fauna of the Axios Valley, accounting for 8% of the genera and 9% of the species identified (Fig. 2). They are present in all the localities of the Axios Valley and represent five genera and eight species (Fig. 2 and Table 1). The new genus *Palaeogiraffa* includes three clearly distinct species (Table 1), that can be used as biochronological markers (de Bonis & Bouvrain 2003). The small-sized giraffids *Palaeotragus gaudryi* and *P. rouenii* are present alongside the large-sized *Bohlinia attica*, *Helladotherium duvernoyi* and *Samotherium major*, the last one was first described in

Table 2. The new species found in the Axios Valley mammal localities and their age. The new genera are marked with an asterisk.

Taxa	MN biozone				
	MN 9	MN 10	MN 11	MN 12	MN 13
Cercopithecidae					
Mesopithecus delsoni			x		
Hominidae					
Ouranopithecus macedoniensis		x			
Percrocutidae					
Dinocrocuta salonicae	x				
Hyanidae					
Protictitherium thessalonikensis		x			
Chasmaporthetes bonisi			x		x
Equidae					
Hipparion macedonicum	x	x	x	x	x
Chalicotheriidae					
Ancylotherium hellenicum	x				
Anisodon macedonicus				x	x
Suidae					
Propotamochoerus aegeaus			x		
Tragulidae					
Dorcatherium puyhauberti				x	
Giraffidae					
Palaeogiraffa macedoniae*	x				
Palaeogiraffa major		x			
Bovidae					
Dytikodorcas longicornis*					x
Helladorcas geraadsi*	x				
Hispanodorcas orientalis					x
Majoreas woodwardi*					x
Mesembriacerus melentisi*		x			
Miotragocerus macedoniensis					x
Ouzocerus gracilis*		x			
Ouzocerus pentalophosi	x				
Prostrepsiceros axiosi			x		
Prostrepsiceros vallesiensis		x			
Protragelaphus theodori					x
Strifnotherium exofthalmon*			x		

continental Greece (Geraads 1979, Laskos & Kostopoulos 2024).

The family Bovidae is the most abundant in the Axios Valley fauna, comprising 34% of the genera and 33% of the species, with 21 genera and 28 species identified (Fig. 2). Among them there are six new genera and twelve new species (Tables 1 and 2) (Bouvrain 1975, 1978, 1979, 1980, 1982, 1996, 1997, 2001, Bouvrain & de Bonis 1978, 1984, 1985, 1986, 2007, Kostopoulos 2004, 2020, 2022, 2024, Kostopoulos & Soubise 2018). The abundance of bovids, high degree of diversification and several new taxa provide important biochronological data that help to date the fauna.

Suids, tragulids, cervids and orycteropodids are poorly represented among the identified taxa, accounting for only 1%–2% of the total, and there are only 1–2 species per genus or family (Fig. 2 and Table 2). It is worth noting that a new suid, *Propotamochoerus aegaeus*, was discovered at Ravin des Zouaves 5 (Table 1) (Lazaridis *et al*. 2022).

Chronology

The study of the material from each of the new sites in the Axios Valley has yielded a rich fauna and significant biochronological data. Additional age data were obtained from a magnetostratigraphic study of the Axios Valley deposits (Sen *et al*. 2000). These results allowed accurate age determination and correlation with the European MN (mammal Neogene) biozones (Fig. 3) (Koufos 2013, 2024 and references therein). The classical disadvantages of most old collections are the lack of locality information on the fossils, unclear information on the geographic and stratigraphic position of the localities, as well as mixing of the material and the small number of fossils. Regarding the old "Arambourg collection" from the Axios Valley, there is quite good information about the geographical position of the localities, given in a topographic map of the area (Arambourg & Piveteau 1929: fig. 1). There is also enough information about the sedimentary characteristics of the deposits to understand which formation they belong to in the Axios Valley. In the case of some specimens, the locality is given on the specimen, but in most this information is lacking. For the majority of the Arambourg's localities, the faunal record is poor and with limited identifications (Table 1) (Arambourg & Piveteau 1929). In a recent paper (Koufos 2023), I attempted to correlate the old fossiliferous sites with the new ones, using all the data given in Arambourg and Piveteau (1929) and my personal observations (Fig. 3). This correlation showed that Ravin de Vatilük or R.G and Ravin de Konikovo correspond to new localities Vathylakkos 3 and Dytiko 1, respectively. The mammal faunas of the Axios Valley span the entire Late Miocene period, from the early Vallesian (MN 9) to the end of Turolian (MN 13). Five Late Miocene faunal assemblages are distinguished in Axios Valley material, corresponding with MN 9 to MN 13 biozones, which are referred to as e.g. MN 9 fauna (Koufos 2024).

Comparison of the Late Miocene faunal units of the Axios Valley

The faunas were analysed using multivariate methods that consider the presence or absence of certain genera or species to assess the similarity between them. The matrix included all genera and species, also those marked as cf. or aff.; for example, *Hipparion* cf. or aff. *macedonicum* was included in the fauna if *H. macedonicum* was absent. In the species analysis, undetermined species (e.g., *Hipparion* sp. or ?*Hipparion*) were excluded. Two multivariate methods, cluster analysis (CA; implemented in PAST; Hammer *et al*. 2001) and non-metric multidimensional scaling analysis (NMDS; implemented in PAST; Hammer *et al*. 2001) were used. In both analyses, the Bray-Curtis similarity index was used.

The cluster analysis at the genus and species levels revealed the presence of two distinct clusters (*a* and *b*), with similarities of about 35% and 20% at the genus and species levels, respectively (Fig. 4). Cluster *a* comprises the Turolian faunas and is further divided into two sub-clusters, a_1 and a_2 (Fig. 4). Sub-cluster a_1 includes the MN 11 and MN 12 faunas, with high similarities of about 65% at the genus level and 60% at the species level. The MN 13 fauna showed lower similarities of about 45% and 25% at the genus

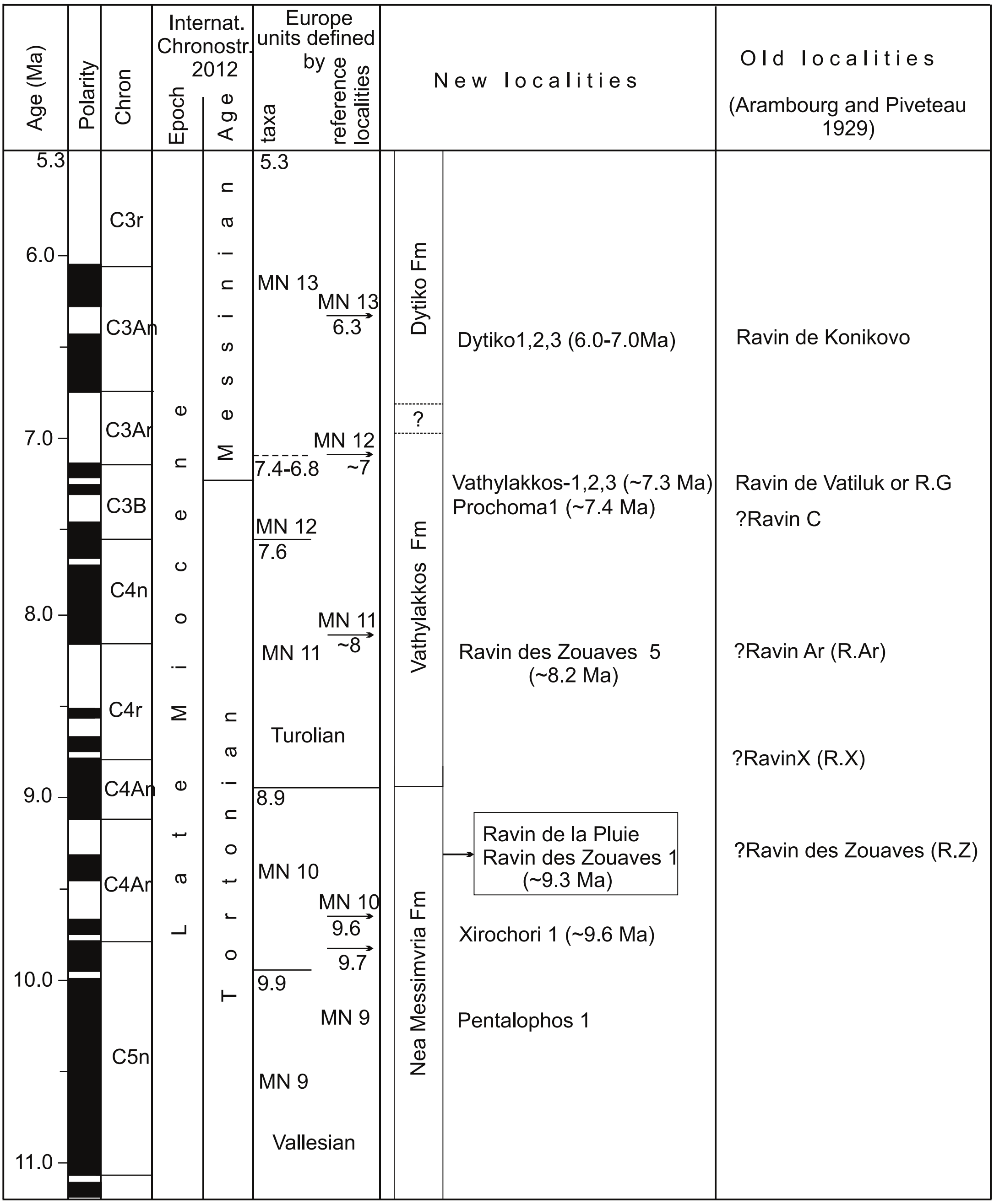

Fig. 3. Biostratigraphy of the Late Miocene mammal localities in the Axios Valley, Macedonia, Greece (European MN biozones in the first column). Chronological units and their boundaries are from Hilgen *et al.* (2012), stratigraphic position and age of the Arambourg's localities are based on Koufos (2022). The question mark in front of the locality abbreviations indicates that its age is estimated based on the information in Arambourg and Piveteau (1929) and the revised faunal list.

and species levels, respectively, with sub-cluster a_1 (Fig. 4); thus, it was separated in sub-cluster a_2 (Fig. 4). Cluster *b* includes the Vallesian MN 9 and MN 10 faunas, with similarity of approximately 47% and about 30% at the genus and species levels, respectively. The similarity

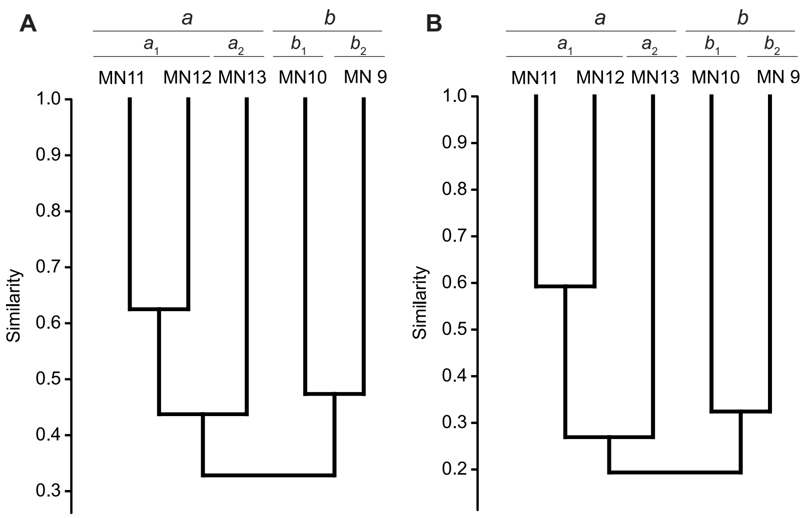

Fig. 4. Cluster analysis (CA) using the Bray-Curtis' similarity index for the Axios Valley Late Miocene faunas at the (**A**) genus and (**B**) species levels.

between the two faunas at the species level was low, leading to the subdivision of cluster *b* into two sub-clusters, b_1 and b_2, corresponding to the MN 9 and MN 10 faunas, respectively (Fig. 4).

The NMDS analysis separated well the Vallesian (Fig. 5, left-hand sides of the plots) from the Turolian (Fig. 5, right-hand sides of the plots) faunas at both the genus and species levels. In both plots (Fig. 5), the faunas of MN 9 and MN 10 occupy different quartiles, which indicates low similarity. The faunas of MN 11 and MN 12 are in the lower right quartile. Their proximity, both at the genus and species levels, indicates a high degree of similarity (Fig. 5). The MN 13 fauna is in the upper right quartile, far from the other Turolian faunas, indicating dissimilarity (Fig. 5). In conclusion, two main faunal changes can be recognised in the Late Miocene of the Axios Valley: one at the Vallesian/Turolian boundary and another at the end of the Turolian. The latter led to the Pliocene and modern fauna.

Palaeoecology

The systematic study of the Axios Valley mammal faunas provided important preliminary palaeoecological information on the Late Miocene environment (de Bonis *et al*. 1979, Koufos 1980). More detailed palaeoecological studies began in the early 1990s when a reasonable number of specimens were collected. Faunal composition was examined, multivariate analysis of faunas from different localities and comparisons with modern and/or fossil faunas from known environments were carried out, and mesowear and/or microwear analyses of the teeth were performed.

In the early 1990s, the first palaeoecological analysis of the Axios Valley mammal fauna utilising multivariate methods was carried out. The results suggest that: (i) the Vallesian palaeoenvironment was open and dry, (ii) the early and middle Turolian faunas also shared an open and drier environment than that of the Vallesian, and (iii) during the late Turolian (Dytiko localities, MN 13 fauna in this article), conditions became more humid, gradually leading to the wet Pliocene environment (de Bonis *et al*. 1992).

The Vallesian open and dry palaeoenvironmental conditions in Axios Valley were confirmed in other studies. The dental microwear analysis of the hominoid *Ouranopithecus macedoniensis* suggested that it was feeding on hard and abrasive items such as roots, tubers, and grass (Merceron *et al*. 2005a). Similar analysis of the bovids from the Vallesian localities Pentalophos 1, Xirochori 1, and Ravin de la Pluie showed that they inhabited an environment with a rich herbaceous layer, mainly consisting of graminoids, and low trees and bushes (Merceron *et al*. 2007). Furthermore, the carbon stable isotope ratios of the bovid enamel suggest the

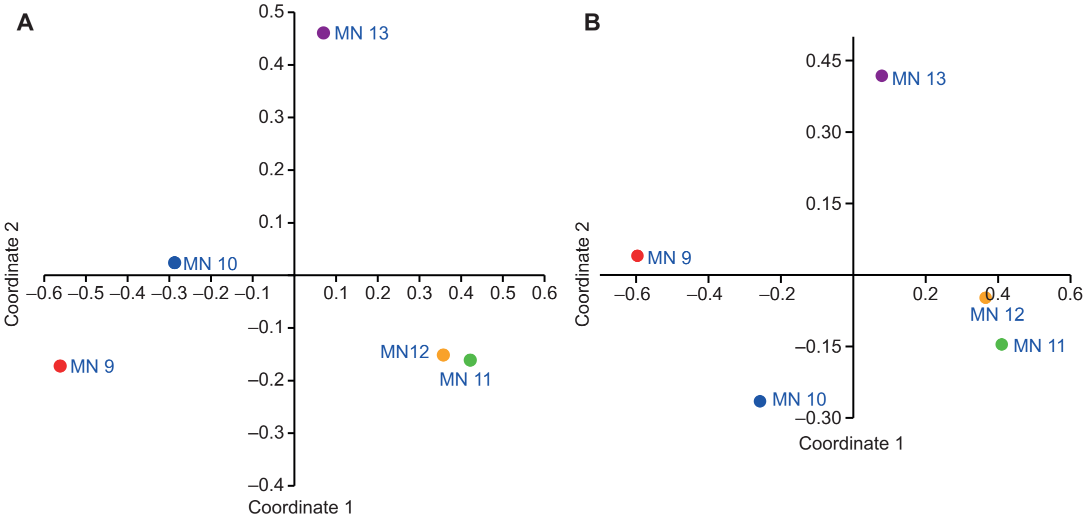

Fig. 5. Non-metric multidimensional scaling analysis (NMDS) using the Bray-Curtis similarity index for the Axios Valley Late Miocene faunas at the (**A**) genus and (**B**) species levels.

absence of dense forested landscapes (Merceron *et al*. 2013). The carnivorans' guild structure of the Axios Valley and the multivariate analysis of them in comparison with modern faunas indicated that they were living in open environments (Koufos & Konidaris 2011). These data support the hypothesis of an open and relatively dry environment for the Vallesian. The high abundance of bovids and giraffids (Fig. 2), the medium-high enamel plication of the cheek teeth, and the slender metapodials of hipparions (Koufos 1986, Vlachou 2013) support the above results for the Vallesian environment. Furthermore, the dental microwear in the Vallesian form of *H. macedonicum* suggests less dry conditions than suggested by the dental microwear in the Turolian form of the same species (Orlandi-Oliveras *et al*. 2022: 15, fig. 4). All the data available from studies of the Vallesian faunas suggest an open and dry environment with a thick herbaceous floor, covered with low trees and bushes.

In the Turolian period, the open environment of the Vallesian remained and a new fauna appeared, which was quite different from that of the Vallesian (Figs. 4, 5 and Table 1). Stable isotope analyses of the hipparionins' teeth suggest a slight increase in mean annual temperature and a decrease in mean annual precipitation from early Vallesian to late Turolian (Rey *et al*. 2013). Although the temperature increase was small, the environment became drier and more open, with many grasslands. This is evident from the analysis of the faunal composition and comparison with modern faunas from known environments (de Bonis *et al*. 1992). However, de Bonis *et al*. (1992) found indications of an increase in humidity during the late Turolian. This was supported by the appearance of cervids and tragulids (Table 1), the presence of the more arboreal cercopithecid *M. monspessulanus* (Koufos 2019a, 2019b), the presence of several new taxa of bovids, and the presence of hipparions different from those of the early and middle Turolian (Vlachou 2013). The dental microwear pattern of the Dytiko bovids suggests that they were either grazers or mixed feeders, also lent support to this hypothesis (Merceron *et al*. 2005b).

The effects of an increase in humidity are more pronounced in some faunas found in the neighbouring area of the Axios Valley and dated to the Turolian/Ruscinian boundary (MN 13/14). The faunas from the localities of Maramena and Metochi 1, 2 (Serres Basin), Silata (Chalkidiki Peninsula) and Kessani (Xanthi Basin, Thrace) bear evidence of this humidity increase. The fauna of those localities consisted of small and large mammals (Koufos 2024), including taxa living in open, dry environments and taxa living in closed and humid conditions. The dense and wet environment of Maramena is evidenced by the presence of abundant lacustrine snails, terrestrial snails, presence of castorids, flying squirrels, a lot of cervids, and the presence of *Lutra*. On the other hand, there are hipparions, several bovids, giraffids and rhinos suggesting open conditions (Schmidt-Kittler 1995). The other localities also provided a micromammalian fauna similar to that of Maramena (Syrides *et al*. 1997, Vasileiadou *et al*. 2003, Koufos & Vasileiadou 2015). These findings indicate a patchy environment during the late Turolian, with open grassy areas and wooded or bushy vegetation near water sources (Schmidt-Kittler 1995, Vasileiadou *et al*. 2003, Merceron *et al*. 2005b, Koufos 2006b, 2013).

What does Axios Valley research mean for Greece and Eastern Mediterranean Neogene?

Prior to the 1970s, our knowledge of Late Miocene faunas in Greece was limited to old collections and corresponding publications from Pikermi, Samos and "Salonique" (Roth & Wagner 1854, Gaudry 1862–1867, Forsyth Major 1888, 1894, Schlosser 1904, Andree 1926, Arambourg & Piveteau 1929, Werhli 1941, Gentry 1970, Sondaar 1971). Some short articles also discussed isolated specimens or small faunules found in various Greek sites (e.g. Paraskevaidis 1940, Mitzopoulos 1942–1947, 1961, von Freyberg 1951, Psarianos 1958). However, as mentioned earlier, the old collections are not without problems, and therefore cannot provide clear stratigraphic information and age estimates. New excavations of the Late Miocene of Greece were started by Greek and foreign palaeontologists in the 1970s, resulting in new collections of small and large mammals. The study of these collections has provided important data for the Neogene of Greece. It was at this time that field campaigns began in the Axios Valley.

During the last 50 years, the Axios Valley research yielded a vast collection of mammal fossils from various well-known localities. The Axios Valley faunal assemblage has a clear geographic and stratigraphic background, a well-known and recently updated systematic classification, accurate dating, well-known correlation with European MN biozones, and a good understanding of its palaeoenvironmental and palaeoclimatic conditions. The Axios Valley faunal complex is the first to occur in the Eastern Mediterranean region with these characters and can be used as a comparative basis for the Late Miocene of Greece and the Eastern Mediterranean region. Subsequent studies were conducted on the Maramena, Pikermi, Samos, Perivolaki, Nikiti, and Kerassia faunas of Greece, as well as on the Kemiklitepe, Sinap, and Akkashdagi faunas of Türkiye, and published as collections of papers in monograph volumes (Sen 1994, 2005, 2016, Schmidt-Kittler 1995, Fortelius *et al*. 2003, Koufos 2006, Koufos & Nagel 2009, Koufos & Kostopoulos 2016) and in journals (Theodorou *et al*. 2010, 2013, Filis *et al*. 2019, Kampouridis *et al*. 2019 and references therein). Similar projects and studies from Bulgaria provided new data on the Late Miocene faunas of the area (Spassov 2002, Spassov *et al*. 2006, 2012, 2018, Geraads & Spassov 2009, Geraads *et al*. 2011). All those studies provided additional data and contributed remarkably to the knowledge of the Neogene stratigraphy of the Eastern Mediterranean.

In case of Greece, all above-mentioned studies allow to correlate all known mammal fossiliferous sites of Greece, and to present a biostratigraphic table for the Late Miocene with all available data (Koufos 2013, 2024 and references therein). The Vallesian of Greece was unknown until 1970 when the Kastelios locality was discovered on the island of Crete. Its fauna includes a limited sample of large mammals and correlates with MN 9 (de Bruijn *et al*. 1971, Koufos 2024 and references therein). Magnetostratigraphic data suggest that the chronological limits of the Kastelios section are between 11.47–10.30 Ma (Sen *et al*. 1986). The discovery of the Axios Valley Vallesian localities has provided significant palaeontological and biochronological data for the Late Miocene of Greece and the wider Eastern Mediterranean region. Our knowledge of the southeastern Mediterranean Vallesian was increased by the study of the old and new collections from the Sinap localities (Türkiye) and their dating (Fortelius *et al*. 2003).

Several new mammalian taxa (Table 2), as well as taxa previously unknown from Greece and Europe, have been discovered in the Axios

Valley fossil collections. The most important find was the hominoid *Ouranopithecus macedoniensis* (de Bonis *et al*. 1974, 1990), discovered at the beginning of the Axios Valley campaign. There has been a long and ongoing debate about the systematic and phylogenetic position of the Axios hominoid. Some authors classified it as Pongidae, while others as Hominidae (Ioannidou 2021, Koufos 2015 and references therein). Recent views place it within Hominidae and suggest that it can be considered a stem member of the hominin clade, together with *Graecopithecus* and/or the African *Nakalipithecus* (Pugh 2022, Urciuoli & Alba 2023).

The cercopithecid *Mesopithecus* was found in most of the localities of the Axios Valley (Table 1). Four forms have been identified by comparison of the old and new material with the typical *M. pentelicus* from Pikermi: (1) the large-sized new species *M. delsoni* from the early Turolian, (2) a form intermediate between *M. delsoni* and *M. pentelicus* from the middle Turolian, (3) *M. pentelicus* (smaller than the typical), and (4) the small-sized *M. monspessulanus* from the late Turolian (de Bonis *et al*. 1990, Koufos 2009a, 2009b, 2019a, 2019b). Based on the above, it is evident that there was a reduction in size of *Mesopithecus* during the Turolian. This finding can be used as a biostratigraphic indicator. *Mesopithecus monspessulanus* is considered a Pliocene taxon, and its presence in the late Turolian is debatable. There are some indications for its presence in the late Turolian of Italy, but the available evidence is questionable (Rook 1999, Koufos 2019b). However, the discovery of this species in the late Turolian of Axios Valley (Dytiko localities, MN 13 fauna in this article) confirms its presence in the Late Miocene. It is worth noting that the Dytiko fauna is dated as pre-Messinian (7.0–6.0 Ma; Koufos & Vasileidou 2015), which suggests that *M. monspessulanus* existed at the beginning of the late Turolian (Koufos 2019b).

It is worth mentioning that the new bovids dominated the Axios Valley fauna (Fig. 2), indicating that the palaeoenvironmental conditions were favourable for them. This is particularly evident in the Vallesian locality Ravin de la Pluie, where the number of discovered bovid specimens exceeded that of the hipparions. The new genus *Palaeogiraffa* was found in the Vallesian localities, and its dental morphology allowed for the distinction of three taxa which characterized the biozone MN 9, the beginning of the MN 10 and the upper part of the MN 10 (de Bonis & Bouvrain 2003). Additionally, a new chalicothere species, *Ancylotherium hellenicum*, was discovered in MN 9. This primitive, small-sized form is distinct from the Turolian *A. pentelicum* (Koufos 2012c). Finally, it is worth noting the discovery of a new small-sized suid, named *Propotamochoerus aegeaus*, from the early Turolian (Lazaridis *et al*. 2021).

The open and relatively dry palaeoecological conditions during Vallesian in the Axios Valley contrast with the closed and humid ones in central and western Europe. Based on this, it is interesting to consider whether this would apply to the entire Eastern Mediterranean. It is widely recognised that a significant faunal change occurred in western Europe during the middle Vallesian, referred to as the "mid-Vallesian Crisis" and later as the "Vallesian Crisis". This event led to a notable reduction in evergreen sub-tropical forests, which were replaced by deciduous forests (Agusti & Moya Sola 1990, Agusti *et al*. 1999, 2003). However, the Vallesian faunal change seems to have occurred earlier in the Eastern Mediterranean. This is supported by the analysis of the Vallesian and Turolian faunas of the Axios Valley (de Bonis *et al*. 1992). To confirm this result, the faunal composition of the Vallesian (MN 9 and MN 10) faunas from different European regions (western, central, southeastern, Black Sea) were compared with modern faunas from known environments using multivariate methods (Koufos 2006c). The results of this analysis showed that the palaeoenvironment of southeastern Europe was arid and open from the beginning of the Vallesian. In the northeastern Europe (Black Sea), the early Vallesian (MN 9) fauna suggests closed and humid conditions, while the MN 10 fauna was clearly of open and dry environments, matching the southeastern faunas (Koufos 2006c: 137–138, figs. 9–10). This indicates that: (i) the dryness extended gradually to the west and to the north, and (ii) the faunal change began earlier, in the SE Mediterranean towards the end of the Middle Miocene. It is important to note that the Middle/

Late Miocene boundary is dated at 11.2 Ma, while the early/late Vallesian boundary is dated at 9.9 Ma (Hilgen *et al*. 2012). Therefore, the "Vallesian crisis" began at least 1.3 million years earlier in the Eastern Mediterranean than in the Western Mediterranean. The "Vallesian Crisis" is thus a diachronic event that started in the Eastern Mediterranean in the uppermost Middle Miocene and ended in the western Europe in the middle Vallesian (Koufos 2006c, Ataabadi 2010). Therefore, since the Greek word "crisis" means a short-term event, it is better to call it "Vallesian faunal change".

Conclusions

Years of research in the Axios Valley near Thessaloniki have yielded a large number of mammal fossils. The collections are the result of dozens of hours of field and laboratory work by Greek, French and other researchers. In addition, researchers spent countless hours studying the collection. The question that arises is: Has it been worth all this considerable effort? The answer is "yes", as this research has yielded remarkable results for the knowledge of the Neogene of Greece and the wider Eastern Mediterranean region:

- Systematic studies of the fauna uncovered a great number of taxa also including many new genera and species (Table 2).
- Comparisons of the Axios Valley faunal assemblage allowed the identification of five distinct faunas.
- Significant biochronological data for dating and correlation with European MN biozones were obtained from the fauna and its characteristics (Fig. 3).
- Additional dating data and estimated absolute ages for the various faunas were also obtained from palaeomagnetic studies.
- Important palaeoecological data has been obtained from the analysis of distinct faunas using various methods.
- It was clearly demonstrated that the Vallesian of the Eastern Mediterranean was an open and arid environment, and that the "Vallesian Crisis" was a diachronic event in the Mediterranean region that started in the uppermost Middle Miocene.
- Axios Valley fauna, with its solid geographical and stratigraphic setting, recent and accurate systematics, and reliable dating, may provide valuable comparative material for correlative studies in Greece and the Eastern Mediterranean.
- The discovery of the new hominoid, *Ouranopithecus macedoniensis* provided evidence for the origin of the hominin clade and has caused long debate.

It is worth mentioning that the study of the collection is still in progress producing new results. I believe that the continuing study of the Axios Valley collection has much more to offer in the palaeontology of mammals and in the stratigraphy and palaeoecology of the Neogene in the Eastern Mediterranean.

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