

THE GREEK LATE NEOGENE-QUATERNARY URSIDS IN RELATION TO PALAEOGEOGRAPHY AND PALAEOENVIRONMENT

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Abstract: The family Ursidae appears to be a sensitive mammal group, promptly reflecting large but also small scale changes in global environmental conditions. Although the Greek ursid record is extremely incomplete, especially regarding the late Miocene-early Pliocene period, it is evident that the main evolutionary and ecological trends of the family are roughly depicted. The presence of Ursidae in Greece, and the southern Balkans in general, is highly controlled by palaeoecological factors concerning primarily climatic and vegetational changes.

Key words: Ursidae, Greece, palaeoenvironment, distribution, Cenozoic.

INTRODUCTION

The Greek Neogene/Quaternary continental record exhibits an important archive of fossil mammal assemblages spanning in time from the middle Miocene up to the late Pleistocene. Although most large mammal families occur regularly, the presence of Ursidae shows strong fluctuations in time and space. Of the three recognized European Neogene Ursidae subfamilies (GINSBURG, 1999), Phoberocyoninae (MN1-MN6) and Hemicyoniinae (MN1-MN7/8) have never been recorded in Greece, whereas Ursinae (MN3-recent) are exceptionally rare in late Miocene and middle-late Pliocene assemblages, but quite common in middle-late Pleistocene ones. In this short communication, the presence of ursids in Greece is discussed with respect to the general palaeozoogeographic dynamics of the family during Neogene and Quaternary.

Starting with *Phoberogale bonali*, the oldest European occurrence of the family Ursidae, discovered in French late Paleogene deposits (GINSBURG, 1999), the chronological and geographical distribution of ursids in Europe appears to be highly heterogeneous, reflecting major environmental changes. Therefore, the Greek ursids are also regarded in relation to their palaeoenvironment, as it is extracted from the palaeoecological spectra of the accompanied large mammal faunas.

THE GREEK URSIDAE RECORD

Apart from their presence in middle-late Pleistocene cave deposits, ursids are usually rare in the Greek fossil record both in number of specimens and species. Currently, three genera with eight species are known from 19 large mammal faunas spanning in time from the middle Turolian (~7.5 Ma) to the latest Pleistocene (~10,000 years) (tab. 1, fig. 1). *Bosdagius felinus* SICKENBERG, 1968 from Volakas is considered to be synonymous with the widespread *Ursus etruscus*, whereas *Ursavus ehrenbergi* THENIUS, 1947 from Halmyropotamos is regarded as a valid species, although its relations with other representatives of the genus are still uncertain.

Ursids appear in Greece during middle Turolian and from middle-late Villafranchian onwards (fig. 1). Two main factors are responsible for the significant gap in the Greek ursid record during latest Miocene-middle Pliocene (tab. 1, fig. 1). The absence of Ursids from the well-known and rich large mammal faunas of Dytiko (MN13, late Miocene; Axios valley), Maramena (MN13/14, latest Miocene-earliest Pliocene; Serres basin) and Megalo Emvolon (MN15, early Pliocene; Thermaikos basin) is possibly related to the environmental changes at the beginning of Pliocene, as will be discussed below. On the other hand, their absence during the early Villafranchian

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Table 1
Chronological distribution of Greek ursids.

Epochs	Ages	Localities	Species	
Pleistocene	Late	Vraona	<i>Ursus arctos</i>	
		Agrapha Cave	<i>Ursus spelaeus</i> -group	
		Ioannina Cave	<i>Ursus spelaeus</i> -group	
	Middle	Villafranchian	Loutra Arideas Cave A	<i>Ursus ingressus</i> **
			Drama	<i>Ursus spelaeus</i> -group
			Petalona Cave	<i>Ursus cf. deningeri</i> ; <i>Ursus spelaeus</i> -group
			Makinia	<i>Ursus cf. etruscus</i>
Early	Kastritsi (Achaia)		<i>Ursus cf. etruscus</i>	
Pliocene	Villafranchian		Apollonia	<i>Ursus etruscus</i>
			Libakos	<i>Ursus</i> sp.
		Late	Vassiloudi	<i>Ursus etruscus</i>
		Middle	Volakas	[<i>Bosdagius felinus</i>]*
			Dafnero	<i>Ursus etruscus</i>
Sesklo	<i>Ursus etruscus</i>			
Late Miocene	Ruscinian	Early		
		Late		
	Turolian	Pikermi	<i>Ursavus</i> sp., <i>Indarctos atticus</i>	
		Samos	<i>Ursavus cf. depereti</i> , <i>Indarctos atticus</i>	
		Halmyropotamos	<i>Ursavus ehrenbergi</i>	
Early	Perivolaki	<i>Ursavus depereti</i>		

*=nomen nudum; **=*Ursus arctos* is also mentioned but outside cave A. Data from: DE BONIS & KOUFOS, 1999; KOUFOS & KOSTOPOULOS, 1997; RABEDER & TSOUKALA, 1990, TSOUKALA, 1992, TSOUKALA & RABEDER, 2006.

(MN16, middle Pliocene) is evidently due to the scarcity of contemporaneous faunas in SE Europe of this age.

DISCUSSION

During the early Miocene (MN1-MN3), ursids were restricted in the laurophyllus evergreen forests of central-western Europe (France, Spain, Germany, Austria), represented mostly by carnivorous species with running ability (fig. 2). Their limited spatial distribution suggests strong dependence on environmental factors (e.g. climate, vegetation), whereas the Eastern Paratethys and the active Fore-Carpathian basins (POPOV *et al.*, 2006) must have prevented a southward migration.

From the end of early Miocene to the end of middle Miocene (MN4-MN7+8), ursids show their widest geographic expansion from Turkey to Spain, and their greatest species diversification (especially during MN5) (fig. 2). The abundance of omnivorous ursids in relation to carnivorous ones shows a general trend to increase throughout this period (fig. 3), contrasting the pattern of general decrease in number of ursid species after MN5

(fig. 2). Although the extended land between the Eastern Paratethys and the Mediterranean was connected with the European mainland both from the east and west (POPOV *et al.*, 2006), ursids did not invade this area, being restricted northwards of the Alpine Chain.

During the Vallesian, the middle Miocene warm subtropical conditions in Europe came to an end and tropical forests were replaced by deciduous and sclerophyllus ones, while grassy/bushy landscapes gradually extended from the east to the west (KOUFOS, 2006a and literature therein). As a result, the European ursids declined drastically (fig. 2); phoberocyonines and hemicyonines permanently disappeared, whereas forest-dependent primitive omnivorous ursines remained in several refuge areas of Western Europe, causing a high signal during MN9 (fig. 3). Nevertheless, at the end of the Vallesian (MN10), the carnivorous ursine genus *Indarctos*, already known from MN7+8 assemblages, predominated (fig. 3) and for the first time *Indarctos arctoides*, a medium-sized (160 kg) meat eater, invaded the eastern Balkan area (Moldova

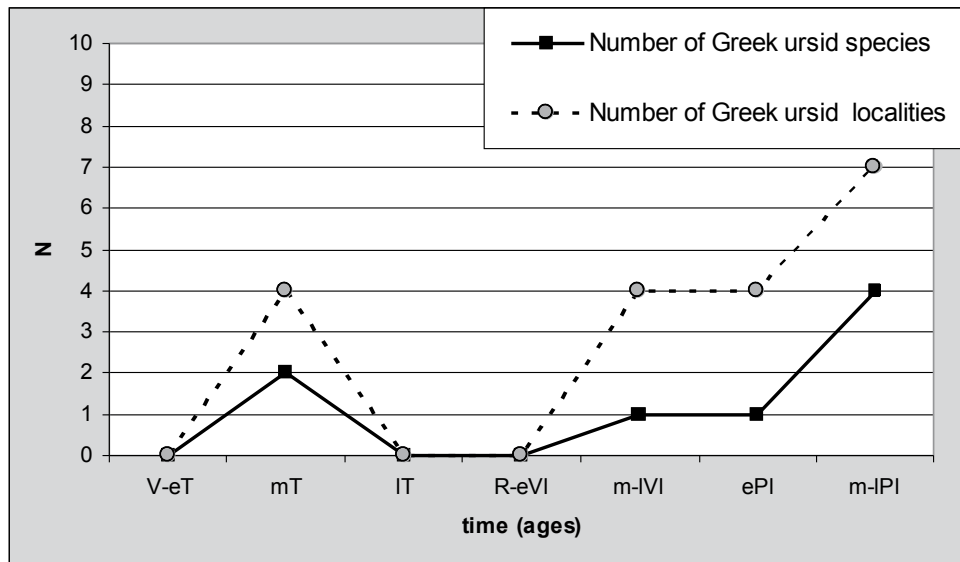


Figure 1. Time distribution of Greek ursids. Data from KOUFOS & KOSTOPOULOS, 1997 and pers. obs. Abbreviations: V: Vallesian; T: Turolian; R: Ruscinian; VI: Villafranchian; PI: Pleistocene; e: early; m: middle; l: late.

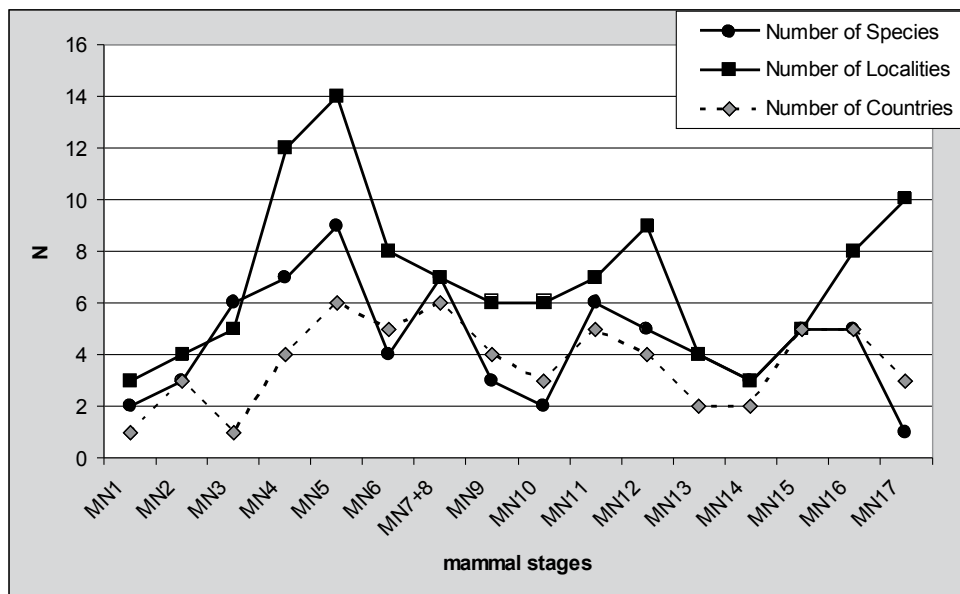


Figure 2. Time distribution of European ursids. Data from NOW 2003 and pers. obs.

and Thrace) probably through a forest corridor along the east-Aegean shore (GERAADS *et al.*, 2005) (fig. 4).

From the beginning of Turolian (MN11) until MN12, the SE of Europe enters into a more arid phase, during which sclerophyllous and xerophytic plants became more abundant and parkland environments prevailed (AGUSTI & ANTÓN, 2002). Omnivorous and carnivorous ursines recovered significantly (figs. 2, 3), but for the first time their signal became stronger in east than in west Europe

(fig. 4). During this period, ursines occupied the Balkans (Hungary, Greece, Bulgaria) and penetrated Italy.

Following the general tendency of the subfamily Ursinae to move southwards, the large omnivorous *Ursus depereti* (~100 kg), already known from the late Vallesian-early Turolian of central-western Europe (Solbay, Melchingen, Dork Dürkheim) (Now, 2003), appears in the fauna of Perivolaki (central Greece), dated at the beginning of MN12 (middle Turolian) or before 7.5 Ma

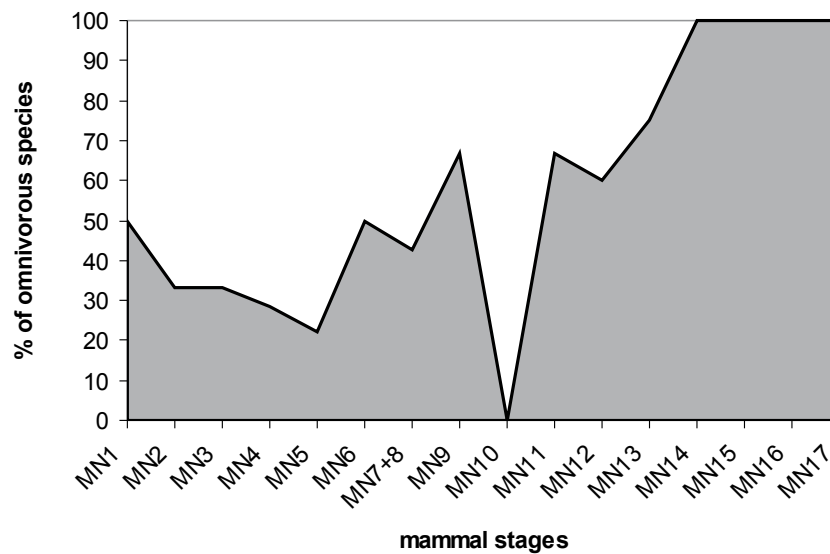


Figure 3. Time distribution of European omnivorous Ursidae. Data from NOW 2003 and pers. obs.

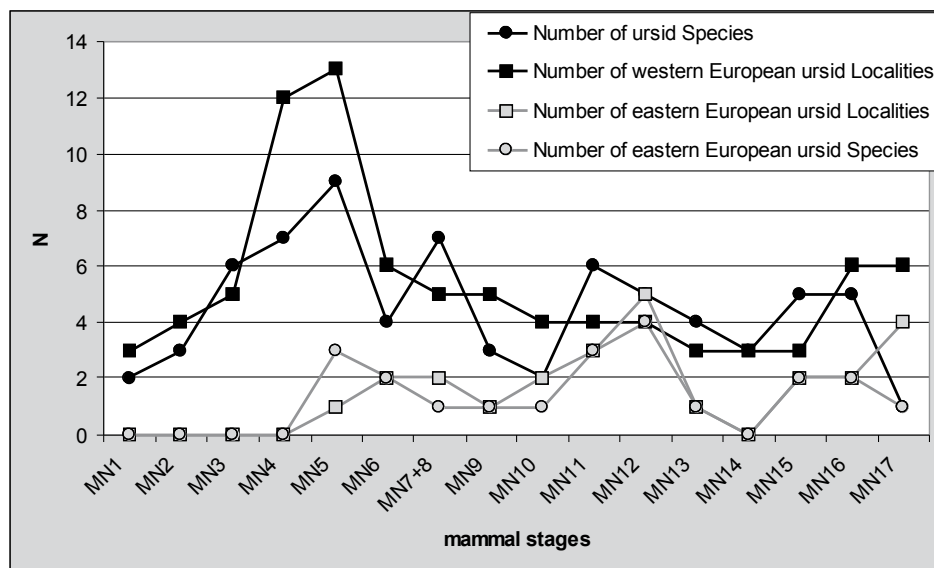


Figure 4. Comparison between the time distribution of ursids in western and eastern Europe. Data from Now (2003) and pers. obs.

(KOUFOS, 2006b). The palaeoecological reconstruction of Perivolaki and the contemporaneous fauna of Hadjidimovo in Bulgaria (KOUFOS *et al.*, 2006, MERCERON *et al.*, 2006) support an open bushy/woody landscape with grassy undergrowth, in which meal-by-meal mixed feeding bovids and grazing-mixed feeding hipparions predominate in a fauna that can still support browsers.

Perivolaki and Hadjidimovo represent the last phase of the early Turolian east European large mammal association, toward the classical "pikermian biome" of MN12,

characterized by a more advanced stage of the opening of tree cover. Such a seasonal environment with grassy vegetation and bushy/wooded patches (BONIS *et al.*, 1992, KOUFOS *et al.*, 2006, MERCERON *et al.*, 2006), with a diverse fauna of mostly open dwellers, such as *Helladotherium*, *Microstonyx*, *Gazella*, *Prostrepsiceros*, *Tragoportax*, *Palaeoryx*, *Pachytragus/Protoryx* and slender *Hipparion* morphotypes, can support more varied omnivore assemblages. As a result, a new ailuropodine ursid, *Indarctos atticus* arrived in the Balkan area (Kalimanci, Bulgaria)

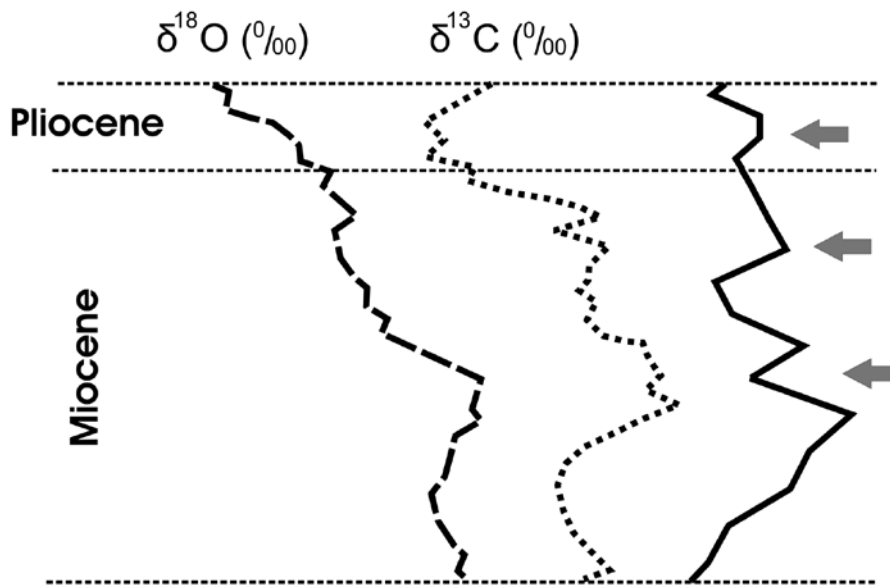


Figure 5. Comparison between the global deep-sea oxygen (dash-line) and carbon isotope (dot-line) records with the ursid diversity during Neogene (black line). (Curves adapted from ZACHOS *et al.*, 2001).

and accompanied *Ursavus* in the late middle Turolian Greek faunas (Pikermi, Samos). This terrestrial species was much larger in size than the Vallesian representatives of the genus, reaching 350 kg in weight and had flexible feeding habits, adapted to switch between a plant dominated and meat dominated diet (VIRANTA, 2004).

From the end of the Miocene (MN13) to the beginning of the Pliocene (MN14), a new phase of warm-humid climate with low amplitude changes allowed ursids to undergo a second decline (fig. 2), during which carnivorous species were permanently replaced by omnivorous ones (fig. 3). The effects of this environmental inversion seem to be stronger in east Europe (fig. 4). At the same time, the rare MN11-MN12 ailuropodine *Agriotherium* spread rapidly. Although *Agriotherium* was considered to be a carnivorous genus, it was later shown that its diet mostly consisted of plants, together with animal material obtained by scavenging (SORKIN, 2006 and literature therein). As a response to the climatic shift toward more humid conditions and following the general trend of the family, both *Ursavus* and *Indarctos* disappeared from the latest Miocene-early Pliocene Greek record (localities Dytiko, Maramena). Indeed, during this period, Greece, and the Balkans in general, entered into a wet phase, which is directly reflected in the extended lignitogenesis of the beginning of Pliocene. Wooded/bushy landscapes alternate with some grassy ones (MERCERON *et al.*, 2005 and literature therein) and forest-dependent species such

as tragulids, cervids and chalicotheres re-appeared in the area. In Western Europe, small and primitive representatives of the genus *Ursus* made their first appearance in the established evergreen/mixed forests dominated by Taxodiaceae (AGUSTI & ANTÓN, 2002). *Ursus minimus*, the first member of the *U. arctos/U. thibetanus* lineage, was a temperate-forest dweller originated probably from an Asian ursavi ancestor (AGUSTI & ANTÓN, 2002). *Agriotherium* and primitive *Ursus* widely overlap in time but they rarely co-exist, suggesting quite different ecological profiles and habitats.

Since the early Pliocene, the Greek mammal record (MN14-MN16) is rather poor (KOUFOS & KOSTOPOULOS, 1997), it is not clear if the absence of ursids from Greece is due to taphonomic biases or environmental factors. The presence of omnivorous ursines in Western Europe significantly increased during MN15, but from MN16 to the end of Pliocene, the number of species decreased drastically (figs. 2, 4). This was certainly the effect of the first glaciation process in the Northern Hemisphere, which allowed an important European faunal turnover, highly controlled by the new climatic conditions and the establishment of a double seasonality model.

Most European ursine species failed to survive until the end of Pliocene (MN17). From 2.5 Ma onwards (MN16 -MN17), the southern Balkans and neighboring areas entered into a new arid phase, related to the glacial-interglacial dynamic established in the North-

ern Hemisphere. During the middle-late Villafranchian (MN17), the mammal faunas from Greece already show a more open and arid character than the contemporaneous faunas of west Europe (KOSTOPOULOS & KOUFOS, 2000): *Gazella* persisted here associated with the new Asian immigrant *Gallogoral*, the widespread *Gazellospira* and the giraffid *Mitilanotherium*, all indicative of open/bushy landscapes. These conditions were expanded southwestwards until the end of Pliocene (KOSTOPOULOS *et al.*, 2002; AGUSTI & ANTÓN, 2002). At the same time, ursines re-appeared in the southern Balkans: a species intermediate between *Ursus minimus* and *U. etruscus* is recorded in the Bulgarian locality of Varshets (early MN17) (SPASSOV, 2002). From MN17 to the end of early Pleistocene, *U. etruscus*, a medium-sized (~90 kg) close relative of the living black and brown bear, became the single representative of the family (figs. 2, 4), occupying the entire territory south to the Alpine Chain, from Spain to Greece and also probably to China. The post-Olduvai expansion of steppes and cooler temperate conditions in southern Eurasia seem to have favored the widespread of the species, which is more rapidly spreading in the east (fig. 4). Although the *U. etruscus* record remains scarce in the Balkans, the species is present in the Greek land until the end of the early Pleistocene, contributing to the open landscape mammal faunas of this period, which were dominated by primitive bisons, large ovibovines, large stenoroid horses, praemegacerids, hippos etc (KOUFOS & KOSTOPOULOS, 1997).

Early middle Pleistocene faunas seem to be missing from Greece. In central-western Europe this period is characterized by a new warm phase of alternations of mild glacial intervals with warm interglacial ones, allowing European forests to recover and temperate elements to (re-)enter (AGUSTI & ANTÓN, 2002). From middle Pleistocene onwards, the establishment of the bipolar climate in the North Alpine areas forced the south European environment to alternate between Mediterranean arid and mild-temperate, allowing the modernization of the mammal fauna, which now includes true wolves and foxes, large bovines, goats, asine horses, elephants, rhinos, fallow, red deer etc. Under these conditions, *U. etruscus* gave rise to two branches: an Asian one leading to the late Pleistocene *U. arctos-U. maritimus* and a European one leading to the early-middle Pleistocene *U. dolinensis-U. savini* and their middle Pleistocene descendant *U. deningeri* (KURTEN, 1976; GARCIA & ARSUAGA, 2001; AGUSTI & ANTÓN, 2002). Although both *U. deningeri* and *U. arctos* were highly omnivorous and not very distinct from a dietary point of view (STINER *et al.*, 1998), the

robust and mainly vegetarian *U. deningeri* already exhibited excavating and scavenging habits that were later fully expressed in its offspring, the cave bear. In Greece, *Ursus deningeri* is only known from the lower levels of the Petralona cave (~600,000 years) (TSOUKALA, 1989; RABEDER & TSOUKALA, 1990).

During the last late Pleistocene interglacial-glacial cycles, the European environmental conditions rapidly interchanged between cold-temperate and the steppe/tundra biome predominated. In Europe and the Balkans, the mammal fauna is characterized by specialized grazing bovids and equids and mixed deciduous-pine forest cervids, all together indicating a strong altitudinal control. In this context *U. deningeri* gave rise to the low altitude cave bear *U. ingressus* and the high altitude cave bear *U. spelaeus* ssp. (RABEDER & HOFREITER, 2004). The cave bear was a primarily herbivorous and specialized cave dweller (BOCHERENS *et al.*, 1994; PINTO & ANDREWS, 2004), about 30% larger than the more carnivorous brown bear, with which it coexisted in the mountain areas until the end of the last ice age.

The diversity curve of ursid species throughout Neogene fit pretty well with those of the global deep-sea oxygen and carbon isotope records (fig. 5), suggesting a high dependence on climatic conditions. Ursids positively correspond to the mid-Miocene climatic optimum, the Turolian dry warming and the early Pliocene increase of temperature and humidity, whereas they seem to react negatively to the Serravalian and Pleistocene cooling.

CONCLUSIONS

The present day record of Greek Ursidae lacks homogeneity in time distribution. However, the gaps in the data-continuum are only partly due to taphonomic biases (i.e., during early Villafranchian or early middle Pleistocene), whereas in most cases they roughly reflect general palaeoecological and palaeozoogeographical trends, related to the response of the family to global environmental changes. Ursid diversity was always low in Greece, with a maximum of two co-existing species during MN12 and late Pleistocene. The analysis shows that the presence of Ursidae in Greece together with the southern Balkans, is highly controlled by palaeoecological factors, concerning primarily large-scaled climatic and vegetational changes in Europe. Both the middle Turolian and middle Villafranchian - early Pleistocene species that appeared in Greece represent medium to large-sized highly omnivorous or flexible carnivorous offshoots of central-western European ursines, adapted to open bushy landscapes. From middle Pleistocene onwards the presence of ursids

in continental Greece is constant and comparable with other south European countries, regulated by the succession of Pleistocene stadials and interstadials.

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