

Chapter 15

The Plio-Pleistocene Large Mammal Record of Greece: Implications for Early Human Dispersals into Europe

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Abstract Extensive fieldwork and detailed studies during the last three decades have enriched our understanding of the Plio-Pleistocene large mammal record of Greece. While the unearthed material is abundant, it is not evenly distributed throughout the Plio-Pleistocene; therefore, there are time intervals in this period for which the known large mammal fauna is limited and our knowledge is poor. The Greek Plio-Pleistocene large mammal record reveals a paleoenvironmental transition from open woodlands in late Pliocene, to savannah-like landscape during the early Pleistocene, and to open grasslands during the late early Pleistocene. During this environmental shift, several taxa arrived in Greece in their westward expansion, whereas others made their last European appearance. The arrival of *Homo* in Europe is discussed in relation to the Greek faunal record. The available data cannot clearly distinguish between an African or an Asian origin, but the latter is supported by more evidence.

Keywords Villafranchian • Greek mammal faunas • Biochronology • *Homo* dispersal into Europe

Introduction

In comparison with the Miocene, the Plio-Pleistocene fossil mammal record of Greece is relatively poor. Until the late 1980s, the known mammal localities were relatively few and

the fossil collections fragmentary, with questionable stratigraphic indications, insufficient to provide taxonomic and/or chronological information suitable for age determination. Moreover, the Middle and Late Pleistocene findings from deposits in-filling caves or fissures cannot provide answers concerning biochronology and/or paleoecology. The published data from this period are therefore rare and sporadic. With the exception of extensive studies of the Megalopolis, Volax, Tourkovounia, and Grevena Basin faunas (Melentis 1961, 1964; Sickenberg 1967, 1968; Symeonidis and de Vos 1976; Steensma 1988), most of the publications report isolated specimens.

During the last three decades, extensive fieldwork in several old and new Plio-Pleistocene fossiliferous sites has provided substantial new collections, which were important for the systematics of the mammal faunas in the region, and for understanding their relationships with the known Eurasian assemblages. Despite the discontinuity of the fossil record, the available faunas provided a good Plio-Pleistocene (Villafranchian) mammal biochronology (Koufos 2001 and ref. cited). These new data carry important paleobiogeographical implications and allow us to put forward paleoecological and paleoenvironmental interpretations.

Here, we summarize the fauna, biochronology, and biostratigraphy of the Plio-Pleistocene large mammal localities of Greece, their paleoenvironmental setting, and their trans-European biogeographic relationships, with special emphasis on their implications for early human dispersals into Europe. Localities with large mammals and good stratigraphic and biochronologic backgrounds are shown in Fig. 15.1. While there are several Pleistocene localities on the islands of the Aegean Sea, they will not be discussed in this article, as they constitute endemic faunas.

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Fig. 15.1 Map of Greece indicating the Plio-Pleistocene large mammal localities; the Pliocene localities marked by an asterisk and the Pleistocene ones by a dot. 1. *SLT* Silata, 2. *MAR* Maramena, 3. *KES* Kessani, 4. *MEV* Megalon Emvolon, 5. *PTL* Ptolemais, 6. *APO* Apollakia, 7. *MIL* Milia, 8. *DMT* Damatria, 9. *TRV* Tourkovounia 3–5,

10. *SES* Sesklon, 11. *DFN* Dafnero, 12. *VOL* Volax, 13. *VTR* Vatera, 14. *GER* Gerakarou 1, 15. *VSL* Vassiloudi, 16. *KRI* Krimni 1, 17. *LIB* Libakos, 18. *ALK* Alykes, 19. *RVL* Ravin of Voulgarakis, 20. *APL* Apollonia, 21. *KLT* Kalamoto

Large Mammal Faunas and Biochronology

Latest Turolian/Early Ruscinian Faunas (5.3–4.2 Ma)

Large mammal Pliocene localities are rare in Greece and, as a result, the available faunal information is limited. The earliest large mammal Pliocene elements have been recognized

in the faunas of Maramena (*MAR*), Silata (*SLT*), and Kessani (*KES*) of Northern Greece (Fig. 15.1). All localities are rich in micromammals, which suggest an age at the Turolian/Ruscinian boundary (Schmidt-Kittler 1995; Vassiliadou et al. 2003; Vasileiadou et al. 2012; Koufos 2006a; Koufos and Vasileiadou 2015; Fig. 15.2).

Fauna: *Mesopithecus* sp., *Martes lefkonensis*, *Promeles macedonicus*, *Lutra affinis*, *Promephitis* sp., *Chasmaporthetes* sp., *Paramachaerodus orientalis*, *Choerolophodon pentelici*,

EPOCH		AGE (Ma)	CHRONS	MAMMAL LOCALITIES	FIRST LOCAL APPEARANCES	LAST LOCAL APPEARANCES
MIDDLE	Gallerian		C1n			
EARLY PLEISTOCENE	VILLAFRANCHIAN	1.0	C1r	APL, RVL, ?PLN ?KLT	<i>Canis apolloniensis</i> , <i>Lycaon</i> , <i>Equus apolloniensis</i> , <i>Stephanorhinus hundsheimensis</i> , <i>Soergelia</i> , <i>Præovibos</i> , <i>Arvernoceros</i> (large-sized), <i>Præmegaceros</i>	<i>Palaeotragus</i> , <i>Gazellospira</i> , <i>Leptobos</i> , <i>Eucladoceros</i>
		1.5		LIB, ALK KRI, ?TSR GER, VSL	<i>Hippopotamus antiquus</i> , <i>Pontoceros</i> , <i>Pr. aff. savini</i> <i>Bison</i> <i>Canis</i> , <i>Panthera</i> , <i>Pachycrocuta</i> , <i>Antilope</i>	<i>Nyctereutes</i> , <i>Pliocrocuta</i> , <i>Croizetoceros</i> , <i>Gazella</i> , <i>Procamploceras</i>
		2.0	C2n	VOL, SES, DFN, VTR	<i>Vulpes</i> , <i>Meles</i> , <i>Megantereon</i> , <i>CEC</i> , <i>GGG</i> , <i>Paradolichopithecus</i> , <i>Mammuthus</i>	
		2.5	C2r	?TRV	<i>Lynx</i>	
		3.0		?DMT	<i>Equus</i> , <i>Sus strozzi</i> , ? <i>Leptobos</i>	
		3.5	C2An	MIL	<i>Homotherium</i> , <i>Ursus etruscus</i> , <i>Tapirus</i> , <i>Dicerorhinus jeanvireti</i> , <i>Sus arvernensis</i> , <i>Croizetoceros ramosus</i> , <i>Alephis</i>	<i>Hipparion</i>
PLIOCENE	RUSCINIAN	4.0	APO	MEV ?PTL	<i>Pliocrocuta</i> <i>Dolichopithecus</i> , <i>Nyctereutes</i> , <i>Parabos</i>	
		4.5	C3n			
		5.0				
MIOCENE	TUROLIAN		C3r	KES MAR, SLT	<i>Sus minor</i>	

Fig. 15.2 Biostratigraphic table of the Plio-Pleistocene large mammal localities of Greece with the first and last local appearance of the various taxa

Hipparion cf. mediterraneum, *Hipparion* sp. (large), *Hipparion* sp. (small), “*Korynochoerus*” *palaeochoerus*, *Microstonyx major*, *Pliocervus graecus*, *Norbertia hellenica*, *Gazella* sp. (Schmidt-Kittler 1995; Koufos 2006a; Vasileiadou et al. 2012).

Some ruminants (?*Helladotherium* sp., *Samotherium cf. boissieri*, *Tragoptax gaudryi*, *Tragoptax cf. amalthea*, *Ouzoceros aff. gracilis*) described as part of the Maramena fauna (Schmidt-Kittler 1995) are poorly documented and their identification is questionable. The fossiliferous site KES in Thrace (Fig. 15.1) provided a rich micromammalian fauna that indicates a Turolian/Ruscinian age; however, large mammals are very few and fragmentary. Among the collected isolated teeth, Vasileiadou et al. (2012) identified the suid *Sus minor* and the equid *Hipparion* sp. together with some indeterminable cervids and bovinds.

Late Ruscinian (4.2–3.5 Ma)

Our knowledge of the large mammal fossil record from the Late Ruscinian in Greece is also limited, as localities with

large mammals from this time period are scarce. The best known such site is Megalon Emvolon (MEV) near Thessaloniki (Fig. 15.1), which has yielded a diverse faunal assemblage (Koufos 2006b). Some large mammal bones are also known from Allatini (AL) near Thessaloniki, and a few isolated specimens have been collected from the lignitic deposits of the Ptolemais Basin (PTL) in Western Macedonia, Greece (Fig. 15.1), as well as from Apolakkia (APO) on the island of Rhodes (Fig. 15.1).

Fauna: *Dolichopithecus rusciniensis* (Spasov and Geraads (2007) refer this taxon to *D. balcanicus*), *Nyctereutes tingi*, *Eucyon odessanus*, *Pliocrocuta perrieri*, *Anancus arvernensis*, *Hipparion longipes*, *Hipparion crassum*, *Rhinocerotidae* indet., *Sus minor*, *Metacervoceros cf. rhenanus*, *Cervidae* indet., *Parabos macedoniae*, *Gazella borbonica*, *Koufotragus bailloudi* (Meulen and Kolfoschoten 1986; Theodorou et al. 2000; Doukas and de Bruijn 2002; Koufos 2006b).

The fauna of MEV (Koufos 2006b), with both small and large mammals, is one of the richest Pliocene assemblages in the Eastern Mediterranean dating to the Late Ruscinian (MN15). The locality of the PTL is very poor in large mammals; however, it has yielded *Dolichopithecus rusciniensis*

and *Hipparion crassum* specimens. The exact position of the level from which these fossils originate is unknown. The lignitic-pits of PTL are active, and the fossils possibly originate from the younger levels of the Pliocene deposits, corresponding to Late Ruscinian (Koufos 2001; Doukas and de Bruijn 2002). The locality of APO on the island of Rhodes includes some hipparion remains and is situated below the chronostratigraphically younger locality of Damatria (DMT), which has yielded *Equus* specimens. Therefore, it is possible to associate APO with a Late Ruscinian age (Meulen and Kolfoschoten 1986; Fig. 15.2).

Early Villafranchian (3.5–2.6 Ma)

This time-span covers the Late Pliocene and corresponds to the European Large Mammal zone (MN 16). The end of the Early Villafranchian has been recently defined as the Plio/Pleistocene boundary, dated at 2.58 Ma (Gibbard et al. 2010). Early Villafranchian localities in Greece are scarce and the known fauna is quite poor. Only one locality, Milia (MIL) in the Grevena Basin, is ascertained as Early Villafranchian, while Damatria (DMT) in the island of Rhodes (Fig. 15.1) might also be of this age.

Fauna: *Anancus arvernensis*, *Mammuth borsoni*, *Homotherium crenatidens*, *Ursus etruscus*, *Agriotherium* sp., *Hipparion crassum*, *Equus* sp., *Dicerorhinus jeanvireti*, *Tapirus arvernensis arvernensis*, *Sus arvernensis arvernensis*, *Sus strozzii*, *Croizetoceros ramosus*, *Procapreolus cusanus*, Cervidae indet. (medium-sized), *Alephis* sp., *Gazella borbonica*, *Gazella* sp., cf. *Procamptoceras*, Boselaphini indet. (large-sized), Bovini indet., (Meulen and Kolfoschoten 1986; Loghem et al. 2010; Guerin and Tsoukala 2013; Cregut-Bonnoure and Tsoukala 2014; Lazaridis and Tsoukala 2014; Tsoukala et al. 2014).

The age of the MIL locality is considered as Early Villafranchian, dating to ca. 3.0–2.5 Ma (Loghem et al. 2010; Guerin and Tsoukala 2013). The locality DMT, which has yielded *Equus*, *Sus strozzii* and probably *Leptobos*, is stratigraphically situated above the *Hipparion*-bearing site APO (Meulen and Kolfoschoten 1986), and may correspond to the first occurrence of modern horses in Greece. The genus *Equus* arrived in Western Europe at ca. 2.6 Ma—as recorded in Montopoli fauna (Azzaroli et al. 1988; Rook and Martínez-Navarro 2010)—signaling the beginning of the Middle Villafranchian. Thus, the maximum age of the DMT fauna must be at the Early-Middle Villafranchian boundary (Koufos 2001; Fig. 15.2). This age is consistent with the arrival of *Equus* in Romania (Radulescu and Samson 2001), as well as with the last evidence of *Mammuth borsoni*, which is present in Europe until the end of the Early Villafranchian (Spassov 2003).

Middle Villafranchian (2.6–1.8 Ma)

Although the known Greek Middle Villafranchian localities are numerous (Koufos 2001), most of them are old discoveries, identified based on isolated remains that lack stratigraphic information. Several new sites discovered over the last two decades, however, have substantially enriched our understanding of this period in Greece. The collections from Dafnero-1 (DFN), Sesklon (SES) and Vatera (VTR), as well as those from Volax (VOL) and Tourkovounia-3, 5 (TRV) (Fig. 15.1) have yielded a rich and well-studied fauna.

Fauna: *Paradolichopithecus arvernensis*, *Anancus arvernensis*, *Mammuthus meridionalis*, *Chasmaporthetes lunensis*, *Pliohyaena perrieri*, *Baranogale* cf. *helbingi*, *Meles thoralis*, *Nyctereutes megamastoides*, *Vulpes alopecoides*, *Vulpes praecorsac*, *Homotherium crenatidens*, *Lynx issiodorensis*, *Megantereon cultridens*, *Ursus* cf. *etruscus*, *Equus stenonis* cf. *vireti*, *Stephanorhinus* cf. *etruscus*, *Palaeotragus inexpectatus*, *Metacervoceros* ex gr. *rhenanus*, *Croizetoceros ramosus*, *Eucladoceros tegulensis*, *Euthyceros thessalicus*, *Galogoral meneghinii*, *Gazella bouvrainae*, *Gazella aegea*, *Gazella borbonica*, *Gazellospira torticornis*, ?*Procamptoceras* sp., ?*Caprini* indet. (Koufos 2001, 2006b; de Vos et al. 2002; Athanassiou 2014).

The set of localities VOL, SES, DFN, and VTR all include a similar fauna, dated to the Late-Middle Villafranchian at ca. 2.5–2.0 Ma (Koufos and Kostopoulos 1997; Koufos 2001; de Vos et al. 2002; Fig. 15.2), which is referred to as the Middle Villafranchian large mammal assemblage (hereafter MVLMA) of Greece.

Late Villafranchian (1.8–1.2 Ma)

While several Late Villafranchian localities with large mammals are known from Greece, rich assemblages with sufficient stratigraphic information are far fewer. The localities of Gerakarou-1 (GER), Krimni (KRI), Vassiloudi (VSL), Tsiotra Vrissi (TSR) and Platanochori (PLN) situated in the Mygdonia Basin; Alykes (ALK) in Thessaly; and Libakos (LIB) in the Grevena Basin (Fig. 15.1), studied in recent years, have recently provided us with abundant information on a very rich fauna.

Fauna: *Mammuthus meridionalis*, *Canis arnensis*, *Canis etruscus*, ?*Homotherium* sp., *Panthera onca toscana*, *Pachycrocuta brevirostris*, *Pliohyaena perrieri*, *Pannonictis* sp., *Meles dimitrius*, *Ursus etruscus*, *Equus stenonis mygdoniensis*, *Stephanorhinus etruscus*, *Sus strozzii*, *Hippopotamus antiquus*, *Palaeotragus martini*, *Croizetoceros ramosus*, *Eucladoceros tegulensis*, *Metacervoceros* aff. *rhenanus*, *Praedama* aff. *savini*, *Pseudodama* cf. *nestii*, *Antelope koufosi*, *Gazella bouvrainae*, *Gazellospira torticornis*,

Leptobos cf. *etruscus*, *Pontoceros ambiguus*, *Bison*, sp., *Procampoceras* sp. (Koufos 2001, 2006b; Van der Made and Tong 2008; Konidaris et al. 2015).

The localities of GER and VSL are from the same stratigraphic horizons of the Mygdonia Basin and mark the earliest occurrence of the genus *Canis* in Greece. The first appearance of *Canis* s.s. in Western Europe is dated at the end of Middle Villafranchian, recognized in the localities of Senèze (France), C. St Giakomo (Italy) and Slivnitsa (Bulgaria), which are all dated to ca. 1.95 Ma (Sotnikova and Rook 2010; Kahlke et al. 2011). The GER and VSL faunal assemblages, which have yielded abundant canid remains are slightly younger, and can be correlated to the middle/late Villafranchian transition at ca. 1.8 Ma (Koufos 2001).

The large-sized *Pachycrocuta* is a common and widespread taxon, covering all of Eurasia from Spain to China; for this reason the “*Pachycrocuta*-event” was proposed to have replaced the “wolf-event” (Rook and Martínez-Navarro 2010). The coexistence of *Pliocrocuta perrieri* and *Pachycrocuta brevirostris* in GER is indicative of this fauna’s transitional character from the Middle to the Late Villafranchian. The faunas from LIB and ALK are similar to the GER fauna, but also include new faunal elements, like *Hippopotamus* and *Pontoceros*, indicating a younger age than GER (Fig. 15.2). The combined fauna from these sites is referred to as the Late Villafranchian large mammal assemblage (hereafter LVLMA) of Greece.

Epi-Villafranchian (1.2–0.8 Ma)

The Epi-Villafranchian localities of Greece are scarce. Only three sites, Apollonia 1 (APL), Platanochori (PLN) Ravin of Voulgarakis (RVL), and probably Kalamoto (KAL) (Fig. 15.1), are well known localities associated with this time period (Fig. 15.2). These collections are new, and all come from localities situated in the Mygdonia Basin (Macedonia, Greece). APL has yielded a rich fauna of large mammals; the RVL fauna includes mainly small mammals of Early Biharian age (Koliadimou and Koufos 1998). The fauna of Kalamoto has not yet been thoroughly studied, but the available preliminary determinations (Tsoukala and Chatzopoulou 2005) suggest more Epi-Villafranchian than Late Villafranchian age. The combined fauna of these localities will be referred to as Epi-Villafranchian large mammal assemblage (hereafter EVLMA).

Fauna: *Mammuthus meridionalis*, *Canis etruscus*, *Canis arnensis*, *Canis apolloniensis*, *Lycaon* (= *Xenocyon*) sp., *Vulpes alopecoides*, *Ursus etruscus*, *Meles dimitrius*, *Mustela* sp., *Pachycrocuta brevirostris*, *Megantereon cultridens* (small variety), *Lynx issiodorensis*, *Equus apolloniensis*, *Stephanorhinus hundsheimensis*, *Hippopotamus antiquus*, *Praemegaceros pliotarantoides*, *Arvernoceros* cf.

veretschagini Cervus sp., *Dama* sp., *Pontoceros ambiguus mediterraneus*, *Soergelia brigittae*, *Praeovibos mediterraneus*, *Bison* (*Eobison*) sp., *Ovis* sp., *Hemitragus/Capra* sp., cf. *Leptobos etruscus* (Athanassiou and Kostopoulos 2001; Koufos 2001; Tsoukala and Chatzopoulou 2005; Konidaris et al. 2015).

Local Large Mammal Events and Environmental Context

The known Plio-Pleistocene large mammal localities of Greece represent discontinuous evidence, and significant gaps remain between geographic areas, especially for the Pliocene (Fig. 15.3). The oldest known localities are MAR, SLT and KES, with small mammal assemblages that suggest the Miocene/Pliocene boundary, even though the large mammal association retains a more “Miocene character” (Koufos and Vasileiadou, 2015 and references therein). The large mammal faunas of these sites mark the last local occurrence of several taxa such as *Mesopithecus*, *Choerolophodon*, *Promeles*, *Paramachaerodus*, large giraffids, and boselaphine-like bovids. Additionally, the replacement of the large Miocene suid *Microstonyx*—well distributed across Eurasia during the Late Miocene—by a small suine *Sus minor* with possible Asian origin is initially recorded in the KES.

Despite limited data for the Ruscian of Greece, this rather dramatic faunal turnover represents the terminal phase of a progressive environmental restructuring following the desiccation of the Mediterranean Sea during the Messinian Crisis, between 7.0 and 5.0 Ma (Koufos 2006c; Kostopoulos 2009; Eronen et al. 2009). The faunal renewal concluded with the early Pliocene climatic optimum, which allowed for a warmer and more humid climate (Agustí and Antón 2002). This is well documented by the extensive lignite deposits of this time interval in Northern Greece and surrounding regions. “Wet” conditions seem to continue into the second half of the Ruscian, which is marked in Greece and southwestern Europe by the arrival of several new taxa, such as the canid *Eucyon odessanus*, the hyaenid *Pliocrocuta perrieri*, the bovine-like bovid *Parabos* and the primate *Dolichopithecus*, the latter of possible African origin (Sotnikova and Rook 2010; Eronen and Rook 2004). The proboscidean taxa *Anancus* and *Mammuth* known from the Miocene continue into the Pliocene.

As mentioned above, the Early Villafranchian is poorly represented in Greece. This gap in the large mammal record does not allow us to closely follow any faunal reorganizations that might have ensued after the first glaciation in the Northern Hemisphere and the subsequent increase in thermal seasonality (Agustí and Antón 2002; Kahlke et al. 2011 and ref. cited). Nevertheless, the effect of these major environmental events

Composition of the Greek Villafranchian Faunas

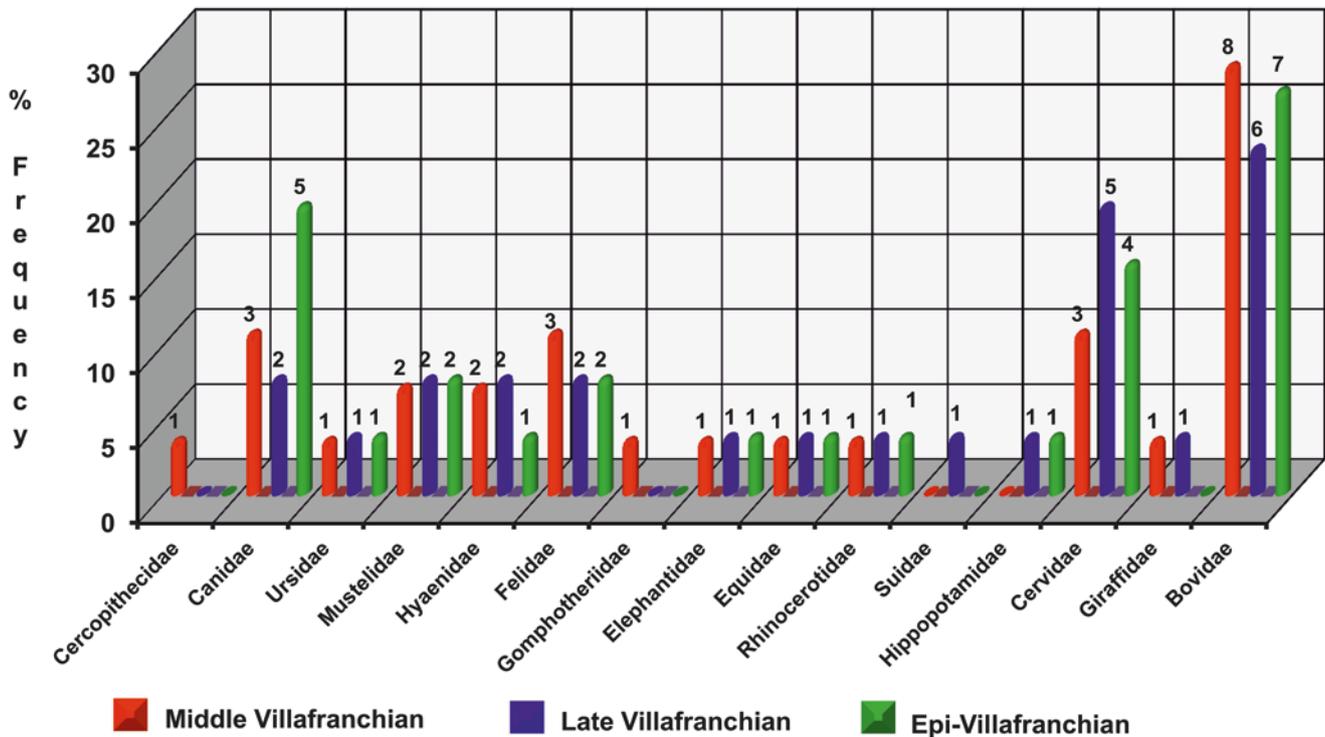


Fig. 15.3 Composition of the Villafranchian faunas of Greece; the number in each bar indicates the number of species found

is evident in the Greek record as a series of extinctions and replacements. Several typical elements of the Late Rucsinian large mammal fauna of Greece (*Dolichopithecus*, *Parabos*, *Alephis*, *Eucyon*) made their last appearance or disappeared. The modern horses (*Equus*) replaced hipparionines, while *Sus minor* was replaced by more advanced suines. *Homotherium*, *Ursus etruscus*, *Croizetoceros*, and the Asian *Leptobos* arrived at the same time, enriching the Early Villafranchian mammal community.

The Middle Villafranchian (2.6–1.8 Ma) is characterized by a gradual decrease in global temperature and a progressive aridification of Southern Europe (Kahlke et al. 2011). The effect of these environmental changes has not been fully traced in the Balkan record yet. However, they might be related with the appearance of archaic forms of *Mammuthus* in Romania, Bulgaria, and Greece (Lister and van Essen 2003; Kostopoulos and Koulidou 2015).

The mammal diversity increased significantly in Greece during this period. The MVLMA includes eight bovid taxa (representing 28.6% of the fauna), three cervids (10.7% of the fauna), and various carnivores (11 taxa, ~40% of the fauna; Fig. 15.3). The giraffids, rhinos, equids, elephantids, and gomphotheriids were also present, represented by a single taxon respectively (Fig. 15.3). *Equus* remains predominate in the collected material. The MVLMA is characterized by the first local appearance of the bovid association *Gazella bou-*

vraiae-Gazellospira-Gallogoral (GGG) and the cervid association *Croizetoceros-Eucladoceros-Metacervoceros* (MEC) together with *Vulpes*, *Meles*, *Megantereon*, *Palaeotragus inexpectatus*, and the large cercopithecine monkey *Paradolichopithecus* with terrestrial lifestyle, which appears for the first time in VTR (Fig. 15.2).

The paleoecological conditions in Greece during the Villafranchian were first studied by Kostopoulos and Koufos (1998, 2000 and ref. therein). The authors analyzed the Villafranchian large mammal faunas and compared them with modern faunas from known environments. The rich mammal fauna of the DFN, VOL, and SES is characterized by the predominance of mixed-feeders and grazers, the presence of a large-sized stenoroid horse, and an equilibrium in the cervid/bovid composition. Dental micro- and meso-wear analyses of the SES herbivores (Rivals and Athanassiou 2008) indicate that the bulk of the taxa are classified among extant mixed feeders, confirming previous results suggesting an open environment similar to the modern woodland savannah (Kostopoulos and Koufos 2000).

The LVLMA has the same taxonomic structure as the MVMLA. Carnivores (nine taxa) constituted ~35% of the assemblage, followed by bovids with six taxa (23.1%) and cervids with five taxa (19.2%). The rest of the families were represented by a single taxon each (Fig. 15.3). The mammal fauna of the GER and VSL date to the lower part of the Late

Villafranchian. They were characterized by an equilibrium of browsers and grazers, a dominance of the intermediate feeders, and more than 50% of open to open/mixed dwellers, suggesting a savannah-like woodland environment (Kostopoulos and Koufos 2000). During this time interval, however, *Canis* replaced *Nyctereutes*, while *Panthera* and *Pachycrocuta* made their first appearance, the latter coexisting with *Pliohyaena* for a short period. This faunal re-organization, correlated to the strong glacial pulses that begun at *ca.* 1.8 Ma (Agustí and Antón 2002 and ref. therein), continued for some time (as evidenced by the KRI, LIB ALK). It was marked by the last occurrences of *Palaeotragus inexpectatus*, *Gazella*, *Gazellospira* and *Leptobos*, and the appearance of new taxa such as the African *Hippopotamus*, as well as the Asian *Bison* and *Pontoceros* (Fig. 15.2). From approximately 2.0 to 1.0 Ma, gradual deforestation and an environmental shift toward more open and grassy landscapes were recorded across Southern Europe, affecting the woodland taxa, which were drastically eliminated (Agustí and Antón 2002; Kahlke et al. 2011).

The last phase of this faunal renewal took place during the Epi-Villafranchian (1.2–0.8 Ma), when the Mid-Late Villafranchian large mammal association collapsed for good and a new faunal association emerged. During the Epi-Villafranchian, the last newcomers (bisons, hippos, etc.) were already firmly established in Greece. Several new immigrants—including the small *Megantereon*, members of the *Praemegaceros* and *Megaloceros* lineages, *Soergelia*, and *Praeovibos*—arrived at this time.

The EVLMA is dominated by the carnivores (11 taxa; 32.2%), among which the canids prevail (five taxa; 19.2%). The canids were enriched by the arrivals of *Lycaon* (also known as *Xenocyon*), and *C. apolloniensis*, a form intermediate between *C. etruscus* and *C. mosbachensis* (Fig. 15.2; Koufos and Kostopoulos 1997). At the same time, there was a remarkable increase in the relative body size of herbivores, especially perissodactyls and artiodactyls. The equids were represented by a large-sized species in some respects similar to *E. ex gr. süssenbornensis* (Koufos et al. 1997). The cervids were known by giant forms (*Praemegaceros*, *Arvernoceros*) and the bovids by heavy ovibovines and bovines, like *Bison (Eobison)* (Fig. 15.2). Furthermore, the browsers declined significantly and the grazers and intermediate feeders became predominant (Kostopoulos and Koufos 2000). All of these observations indicate open-grassy landscapes subject to mild climatic conditions.

Early Humans and the Greek Mammal Record

According to the most parsimonious biogeographic models, Greece has a crucial position along the most likely route for human dispersals between Africa and Eurasia (i.e., the

Levantine Corridor) (O'Regan et al. 2006; Muttoni and Scardia 2010; Tourloukis and Karkanas 2012; Harvati 2016; Spassov 2016; Strait et al. 2016; and ref. cited in all). Several studies emphasized, directly or indirectly, the high paleoanthropological potential of the Greek Early Pleistocene fossil record (Harvati et al. 2009; Dennell 2010; Muttoni et al. 2010; Tourloukis and Karkanas 2012; Tourloukis 2016, and ref. cited in all). However, despite some isolated lithic artifacts of doubtful stratigraphic provenience, Early Paleolithic human remains are currently scarce in Greece (Harvati et al. 2009; Tourloukis and Karkanas 2012). This absence contrasts with both the rich Early-early Middle Pleistocene Greek fossil mammal record, which has yielded several thousands of specimens ascribed to a large number of fossil mammal taxa (Koufos 2001), and the significant and rather continuous Late Miocene to Pliocene and late Middle Pleistocene to Holocene primate fossil record of Greece (Koufos 2006b; Galanidou 2004; Harvati et al. 2009). In our opinion, the apparent Early Pleistocene gap in the human fossil record of Mainland Greece can be ascribed to the interplay of taphonomic factors (see Tourloukis 2016) and inadequate fieldwork, especially given the evidence from the Kozarnika cave in Bulgaria (Guadelli et al. 2012), and the new early Paleolithic sites at Rodafnidia on Lesbos (Galanidou et al. 2013; 2016) and Marathousa 1, Megalopolis on the Peloponnese (Panagopoulou et al. 2015).

At the boundary between the biogeographic zones of Western Asia, Africa/Middle East, and Europe, the large mammal record of Greece and the Southern Balkans remains crucial for the understanding of early human dispersal patterns toward Western Europe, despite the current absence of recorded human activity or fossil remains. Additionally, as it borders land in all directions, it is the most important entrance area for mammals dispersing into Europe from east to west and south to north.

Recent paleoanthropological discoveries place the first, but so far geographically isolated, occurrence of *Homo* in Eurasia at 1.77 Ma at Dmanisi, Georgia (Gabunia et al. 2000; Agustí and Lordkipanidze 2011 and references therein). New data, discussed by Moncel (2010) and Bar-Yosef and Belfer-Cohen (2013) seem to indicate wider early hominin dispersal into Asia at *ca.* 1.8–1.7 Ma ago. Dmanisi would presumably represent the best evidence of it so far. A second important dispersal of humans is evidenced in southern Europe at *ca.* 1.4 Ma. This dispersal is supported by the lithic artifacts of Fuente Nueva 3 and Baranco León 5, Spain, between 1.2 and 0.8 Ma, recorded by solid fossil human evidence in Baranco León 5, Sima del Elefante and Gran Dolina, Spain, Denizli, Turkey, and by lithic artifacts in several other sites around the Northern and Eastern Mediterranean (Martínez-Navarro et al. 1997; Muttoni and Scardia 2010; Muttoni et al. 2011; Dennell 2010; Carbonell et al. 2008; Van der Made 2011; Moncel 2010; Rodríguez et al. 2011; Arzarello et al. 2012; Bar-Yosef and Belfer-Cohen 2013;

Torro Moyano et al. 2013; Lebatard et al. 2014). The Dmanisi “momentum” in the East and the Atapuerca record in the West suggest a delay of about 0.5 Ma in the dispersal of early humans into Europe. This raises questions regarding the cause(s) of this lag, and the evolutionary and geographic path followed by the first “Europeans”.

In various scenarios proposed to explain the delayed arrival of *Homo* in Europe, some researchers have focused on the possible dependencies of early humans on other animals, especially mammals (Martínez-Navarro 2010; Finlayson et al. 2010; O’Regan et al. 2011; Van der Made 2011; Van der Made and Mateos 2011; Agustí and Lordkipanidze 2011 and references therein). Early humans are regarded either as a part of a defined paleocommunity, whose chrono-spatial expansion depended upon the climatically controlled adaptation of specific habitats; or, alternatively, as followers of the dispersal paths of other mammals, particularly of (certain or assumed) African origin, as a result of an increasingly carnivorous trophic behavior. Within these conceptual frameworks, a comparison of Dmanisi, Atapuerca, and similar southern European hominin-bearing faunas with the Greek fossil record provides important insights.

The carnivore assemblage of Dmanisi shows a mixture of archaic and modern elements. Among them *Meles*, *Homo-therium crenatidens*, *Lynx issiodorensis*, *Ursus etruscus*, *Vulpes alopecoides*, and *Pliohyaena perrieri* are all present in the MVLMA of Greece, dated before the Olduvai sub-chron. Their coexistence with *Canis ex gr. etruscus* (see comment in Sotnikova and Rook 2010), *Panthera onca* and *Pachycrocuta*, is very similar to the early Late Villafranchian carnivore assemblage of Greece, represented mainly by the fauna of Gerakarou. It confirms the biochronologic and geochronologic data, dating both sites to about 1.8 Ma. Therefore, the carnivore assemblage of Dmanisi is comparable to the contemporary southeastern and southwestern European assemblages, demonstrating maximum biozoogeographic similarity. The only exception is the presence at Dmanisi of a small saber-toothed cat of the genus *Megantereon*, which was variously interpreted as representing the African species *M. whitei*, a chronocline of the previous Eurasian *Megantereon cultridens*, or even a new taxon (Hemmer 2000; Palmqvist et al. 2007; Lewis and Werdelin 2010; Martínez-Navarro 2010). This species is absent from the LVLMA of Greece, as well as from the rest of contemporary mammal faunas of Europe, where typical *M. cultridens* may occur.

A similarly advanced small *Megantereon* appears for the first time in the Greek EVLMA of Apollonia-1, as well as in Bugiulesti, Romania, in Urkút, Hungary, in Pirro Nord (Pirro 10) and Monte Argentario, Italy, in Untermassfeld, Germany and in Venta Micena, Spain (Palmqvist et al. 2007; Lewis and Werdelin 2010). This pan-European dispersal is chronologically framed within the 1.4–1.0 Ma time interval. Regardless of the geographic origin of this species, it shows

the same delay in its westward expansion that we can observe in early humans compared to Dmanisi. However, the westward dispersion of the small *Megantereon* is closely followed by multiple Asian lineages of advanced canids—such as the hypercarnivorous *Lycaon (=Xenocyon)*—or members of the *C. mosbachensis* group (Sotnikova and Rook 2010) that penetrated Europe approximately at the same time, suggesting a clear renewal of the carnivore assemblage at 1.4–1.0 Ma.

Like the carnivores, the herbivore assemblage of Dmanisi incorporates both archaic and modern elements. The presence of *Mammuthus meridionalis*, *Equus stenonis*, *Stephanorhinus etruscus*, *Eucladoceros tegulensis*, *Gallogoral meneghinii*, *Gazellospira torticornis*, and paleotragine giraffids strongly resembles the Greek Middle and Late Villafranchian assemblages and reveals overall biozoogeographic relationships with Europe. *Gallogoral meneghinii* from Dmanisi closely resembles that of Volax (MVLMA) in Greece (Bukshianidze 2005), whereas the last occurrence of the paleotragine *Palaeotragus inexpectatus* in Greece is at the fauna of Libakos (LVLMA).

Despite these similarities, however, the Dmanisi fauna is enriched by a significant number of “fresh” taxa, mostly ungulates of Asian origin that seem to belong to two distinct dispersal events toward the west. The first of these ungulate events included exclusively members of Caprini (*sensu* Hassanin and Douzery 1999), like *Ovis*, *Hemitragus/Capra*, and *Praeovibos*. Their first European appearance at Slivnitsa (Bulgaria), Casa Frata (Italy), Fonelas P1 (Spain), and possibly Senèze (France) (Spassov 2000; Cregut-Bonnoure 2007; Arribas-Herrera 2008) seems sporadic and coincides with the timing of the arrival of *Canis etruscus*–*Canis arnensis* at about 1.9–1.7 Ma. The second ungulate event between 1.4 and 1.0 Ma included *Equus altidens*, megacerine cervids, early *Bison*, *Soergelia*, and possibly *Pontoceros*, most of which occurred for the first time in Greece in the faunas of Libakos (LVLMA), Kalamoto, Platanochori, and Apollonia (EVLMA).

Early bisons emerged before 2.0 Ma in the Indo-Pakistani region and were already present at Dmanisi at ca. 1.8 Ma (Kahn et al. 2010; Bukshianidze 2005). Their pan-European expansion took place between 1.6 and 1.0 Ma. Early bisons are recognized in Apollonia and Kalamoto (Greece), Pirro Nord (Italy), Vallonet (France), Venta Micena and Atapuerca (Spain), and Untermassfeld (Germany). The timing and pattern of this dispersal replicates that of *Megantereon* and in most cases coincided with the record of the first Western European human settlements (Van der Made 2011, 2013).

The earliest occurrences of *Equus altidens* in Western Europe are recorded in Venta Micena, Fuente Nueva 3, Baranco León 5 and Huescar 1 (Spain), and Pirro Nord in Italy (Alberdi and Palombo 2013). Equids may have followed the bison’s westward expansion from Asia; although, alternative options are equally possible (Van der Made 2013).

The geographic provenance and origin of *Soergelia* are poorly understood. The oldest, and somewhat problematic, record of the genus comes from the possibly Middle Villafranchian site Villany 3 in Hungary. Its next appearance is in Dmanisi, Georgia (Cregut-Bonnoure 2007; Bukshianidze 2005). In any case, *Soergelia* shows a marked south-southwestward expansion between 1.4 and 1.0 Ma, recorded in Apollonia (Greece), Kozarnika (Bulgaria), Trlica (Montenegro), Monte Agrentario (Italy), Vallonet (France), and Venta Micena (Spain) (Cregut-Bonnoure 2007; Martínez-Navarro et al. 2013).

The Caucasus may have been the native area of the spiral-horned “antelope” *Pontoceros* as its earliest known occurrence is at Dmanisi (Bukshianidze 2005). The genus later occupied the North Black Sea shores and dispersed into the Balkans, recorded at Libakos, Platanochori, and Apollonia in Greece. A similar dispersal pattern may have been followed by *Arvernoceros* and other members of the Asian *Megaloceros* and *Praemegaceros* lineages (Vislobokova 2012). During the same time span (1.4–1.0 Ma), *Praedama* aff. *savini* appeared in Europe at Libakos (Van der Made and Tong 2008; Vislobokova 2012), whereas the primitive *Praemegaceros* was originally recorded in Greece (APL, KLT) and further west (Croitor and Kostopoulos 2004; Vislobokova 2012).

Conclusions

The Early Pleistocene mammal record of Greece does not support the direct Afro-European scenario of early human dispersal. As already pointed out the model is oversimplified (Hemmer 2000; Agustí and Lordkipanidze 2011; O’Regan et al. 2006; Lewis and Werdelin 2010), and weakly supported by current evidence, based mainly on a single taxon of unambiguously African origin, the *Hippopotamus*. Instead, both at Dmanisi and in the Western European record the first evidence of humans can be associated with a particular large mammal assemblage, whose elements are either purely Asian in origin—such as bisons, caprines-ovibovines, megacerines, wolf-like canids (Sotnikova and Rook 2010; Van der Made and Mateos 2011; Vislobokova 2012)—or, those for which an Asian period of evolution cannot be excluded, like the small *Megantereon*, *Panthera* and *Pachycrocuta* (Hemmer et al. 2010; Lewis and Werdelin 2010).

The bulk of the European Early Pleistocene carnivore renewal predates the human record of the sub-continent and coincides with the “Dmanisi momentum” and the arrival of several new herbivore taxa, mainly of Asian origin, at the gates of Europe. Notable among them were caprines, which dispersed throughout Southern Europe as far west as Iberian Peninsula. The rather simultaneous appearance in south-western Europe of humans and heavy herbivores—mostly

open dwellers living in vast herds that move along plains and plateaus (like bisons, ovibovines, and megacerine deer)—is intriguing, especially when taking into account that this particular human-herbivore pattern was already present in Dmanisi.

As this herbivore fauna is directly related to open habitats, we may assume that the Dmanisi record represents the western edge of the initial or preliminary expansion of this type of environment and related mammal faunas in Eurasia, controlled by major climatic trends. As suggested by Van der Made (2011), the invasion of this fauna into Western Europe might have been prevented by the retention of more closed habitats in the western part of the continent. Given the current stage of research, it is difficult to ascertain whether humans took part in this westward expansion as members of a defined community, or if they appeared at Dmanisi accidentally/opportunistically. Two arguments may speak in favor of the first hypothesis: (1) recent discoveries put the appearance of *Homo* in Asia at the same time as Dmanisi, if not slightly earlier (Bar-Yosef and Belfer-Cohen 2013), and (2) early “expatriate” humans repeatedly show preferential association with a particular Asian herbivore assemblage of a specific habitat (i.e., semi-open savannah type ecotonal and mosaic landscapes; Finlayson et al. 2011). Extended research and continued fieldwork in several of these localities will yield a more complete picture that will help us to better answer these questions.

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