Radiocarbon chronology of Late Pleistocene large mammal faunas from the Pannonian basin (Hungary)

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Geochronological data from the mammal fauna of the Pannonian basin during the Late Pleistocene are compiled. Thirty-four megafaunal samples (including both fossil bone and associated materials such as charcoal), previously radiocarbon dated by accelerator mass spectrometry and conventional methods, range from 43 to 10.3 ^{14}C ka BP (47–13 ka cal BP). Thus, most samples date within Marine Isotope Stage (MIS) 3 and 2 of the Late Pleistocene, and indicate that the mammoth steppe fauna was able to colonize this region during a period of rapid environmental change. The radiocarbon evidence fits well into the known colonization pattern of the mammoth steppe and shows a continuous distribution in the Late Weichselian grassland areas of East Central Europe. • Key words: megafauna, extinction, late Quaternary, East Central Europe, climate change.

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The cold-adapted large mammals, also known as *Mammuthus-Coelodonta* Faunal Complex (Kahlke 1999), which were common in a wide area of Eurasia during the Late Pleistocene, also existed in the Pannonian basin (Fig. 1). The presence of these cold-adapted mammalian faunas is common in the fossil record of the region (Szabó 1873, Schafarzik 1884, Jánossy 1986, Vörös 1987, Schréter 1917, Kretzoi 1942, Jánossy & Vörös 1979, Konrád *et al.* 2010, Varga *et al.* 2010, Katona *et al.* in press). Despite the abundance of such fossils, few specimens have been radiometrically dated. Where site studies have been performed, they have typically been geographically restricted and have not examined population/extinction dynamics in the wider Pannonian basin. Furthermore, many such works have not been internationalized, having being published only in Hungarian language journals and theses. Jánossy (1986) and Pazonyi (2004) previously reviewed the fossil record (including radiocarbon dating) of the Late Pleistocene Pannonian basin. The book authored by Jánossy (1986) describes all animal assemblages of the Hungarian Pleistocene deposits, with complete faunistic lists and with detailed explanation of the stratigraphical arrangements. In the paper by Pazonyi (2004), examination of communities is based on ecotype analysis that employs trophic preferences and body size of species, as well as species richness of communities. This latter study is based mainly on microvertebrate findings in cave deposits. In the present paper additional radiocarbon dates (*e.g.* studies in Hungarian: Vörös 1989, Krolopp *et al.* 1995, Sümegi *et al.* 1998, Pazonyi 2006, Ringer *et al.* 2006) that update and complete (*e.g.* archeological studies: Vörös 1991, 2000; Dobosi & Hertelendi 1993; Hertelendi 1993; Adams 2002; Dobosi 2006) this information are provided. A key to understanding Late Pleistocene megafaunal extinction dynamics is knowledge of megafaunal ecological response(s) to long-term environmental perturbations. Late Pleistocene vertebrate fossil localities from Hungary allows for testing of anthropogenic versus climate change megafauna extinction hypotheses. These chronologies have been correlated with the published paleoclimatic knowledge of the Late Pleistocene in the Pannonian basin.

Abbreviations. – Marine Isotope Stage – MIS; Greenland Stadials – GS.

Materials and methods

The selected taxa are the following species: woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799), cave bear (*Ursus spelaeus* Rosenmüller, 1794), reindeer (*Rangifer tarandus* Linnaeus, 1758), elk (*Alces alces* Linnaeus, 1758) and wild horse (*Equus* sp. Linnaeus, 1758). The

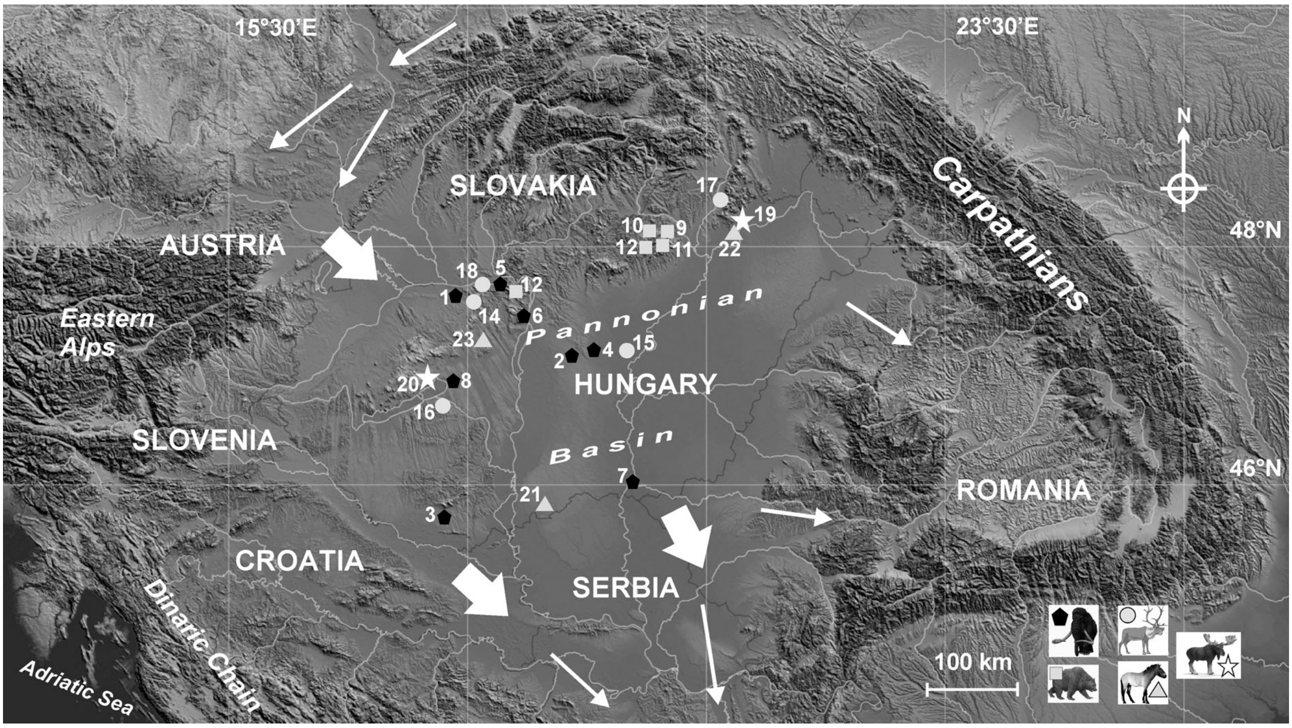

Figure 1. Location of paleontological and archaeological sites cited in the table and Fig. 2. The white arrows indicate generally accepted migrations of large mammals in the Late Pleistocene (Kahlke 1999, Svoboda *et al.* 2005).

large-bodied mammal record presented here was compiled by the author from published papers and reports, and includes over 20 fossil deposits (Fig. 1) that contain dental and postcranial elements. A total of 34 radiocarbon dates was documented; majority of the dated materials are teeth and bones as well as charcoal (Table 1). Of the dates, three were previously published by the author (but one is only a corroborated date which is not included in the table), and 32 by other researchers. Some dates are presented for the first time here in an English language international journal. Most of the specimens (22) were dated using conventional radiocarbon dating and 12 using accelerator mass spectrometry (AMS). Radiocarbon ages are quoted both uncalibrated and in calendar years (calibrated using CalPal-2007 software; Danzeglocke *et al.* 2011). The results are in summarized in Table 1. Since the specimens were dated in different laboratories over a period of time, the methods used for pre-treatment and dating vary. This adds an element of uncertainty in comparing dates. On the other hand, compiling results from different dating laboratories maximizes the information content in the study. It is also known that the reliability of radiocarbon dates decreases beyond 30 ka, so such dates should be treated with caution. The problem should be less critical for dates performed more recently, especially by AMS; but there are always exceptions. A recent study by Price *et al.* (2011) found major problems with AMS dating beyond 30 ka. Information on the vegetation and environmental conditions relating to mammoth steppe habitats in the study region has been obtained from earlier published biostratigraphical (Vörös 1987), paleoecological (Pazonyi 2004, 2006), pleolimnological (Hetényi *et al.* 2010), and paleobotanical (Rudner & Sümegi 2001) records.

Radiocarbon data of the megafauna

Mammuthus primigenius

Fossil remains of woolly mammoth are common in Hungary; *ca* 400 specimens have been recovered, including are six complete skeletons (Vörös 1981, Konrád *et al.* 2010). However, radiocarbon dates are available for only seven specimens (Figs 1, 2). The oldest occurrence woolly mammoth in the Pannonian basin is uncertain, but seems to correspond with the end of the Middle Pleistocene or the first episodes of the Late Pleistocene (Vörös 1981, Jánossy 1986). The first dated appearance of *M. primigenius* is *ca* 50–36 ka in Hungary (Vörös 1981). The Csajág mammoths represent the youngest known and most complete records of woolly mammoth in Hungary (Katona *et al.* 2010, in press). The Csajág date (15.8–16.7 ka cal BP) is important in that it provides the youngest firmly dated record of mammoths in Hungary. The recently published date on an adult tooth is the youngest mammoth date from Hungary; the others are slightly older date at 19,099 ± 248 cal a BP

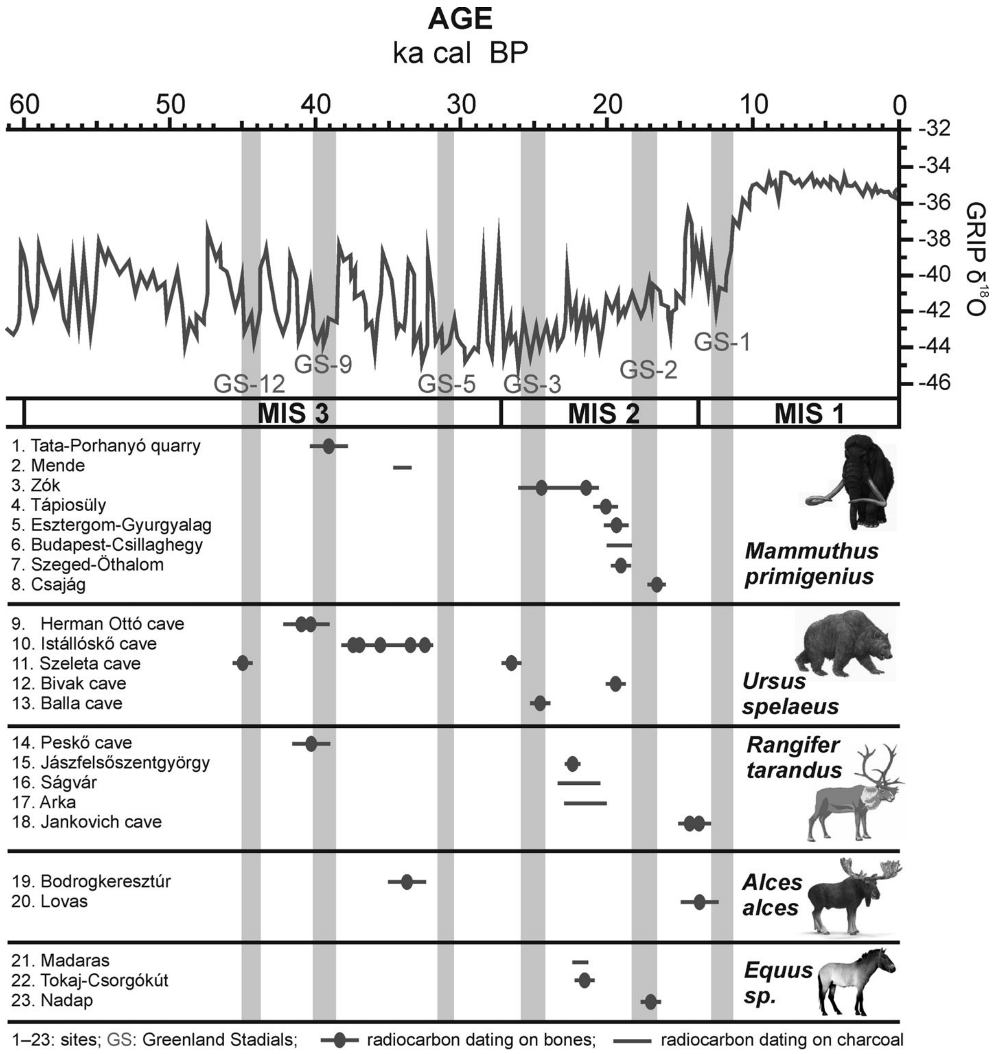

Figure 2. Chronological distribution of the Late Pleistocene cold-adapted large mammal finds in Hungary compared to the GRIP paleoclimatic oxygen curve and the marine isotope stages (MIS). The vertical blue bands indicate the main cold episodes: Greenland Stadials (GS).

from Szeged-Öthalom (Krolopp *et al.* 1995), and 19,354 ± 354 cal a BP from Esztergom-Gyurgyalag (Vörös 1991). However, these finds are only bone fragments from Late Upper Gravettian (Epigravettian) culture layers. In contrast, the Csajág remains (together with Zók remains, 21,250 ± 450 cal a BP; Konrád *et al.* 2010) associated skeletons in stratified context, provide clear evidence that the mammoth was native to Hungary at this time. Based on the known dates, the woolly mammoth disappeared entirely from the Pannonian basin *ca* 16,000 yrs ago.

Ursus spelaeus

The cave bears (*Ursus spelaeus* group) are extinct ursids of wide European and Asian distribution (Pacher & Stuart 2009). Karst depressions and caves were the source for most of the important early discoveries of extinct Pleistocene animals such as cave bears (Kempe & Döppes 2009). Middle Pleistocene fossil remains of *U. spelaeus* have been found in the Suba-Lyuk cave in Hungary (Jánossy 1986). This species inhabited the northern mountainous area (the cave sites presented here; Fig. 1) of Hungary throughout the greater part of the Late Pleistocene. The radiocarbon dates of cave bears are between 46 and 19.5 ka cal BP (Table 1). A molar and a bone fragment of a cave bear were selected for radiocarbon dating from the Herman Ottó cave. Both specimens are *ca* 41 ka cal BP: the oldest AMS ^{14}C dated cave bear finds. Another specimen was dated 46,580 ± 1466 cal a BP from Szeleta cave using conventional measurement. Pacher & Stuart (2009) suggested that the cave bear had disappeared about 27.8 ka cal BP. Therefore, it is possible that the specimen dated 19,169 ± 318 cal a BP in the Bivak cave is too young, and hence not a cave bear. It remains possible that it was misidentified, perhaps confused with brown bear (*U. arctos*). The period from GS 9 (in MIS 3) until GS 5 was characterized by the absolute predominance of the cave bear in the Pannonian basin (Fig. 2). The youngest, dated *U. spelaeus* (with accompanying fauna like *Crocuta crocuta spelaea*) is from the Balla cave which age is ~24 ka cal BP (Vogel & Waterbolk 1972). The fossil bearing layer is overlain by yellow clay containing Magdalenian tools and human remains (Vörös 1987, age: 18,150 ± 200 ka BP, Geyh *et al.* 1969). Climatic cooling, coupled with decreased vegetational productivity were probably responsible for its disappearance from this region (Stuart & Lister 2007, Pacher & Stuart 2009). There is little or no convincing evidence of human involvement in cave bear extinction (Pacher & Stuart 2009).

Rangifer tarandus

Fossil remains of *Rangifer tarandus* from the last glacial of Eurasia are extremely common (Kahlke 1999). Close to the Csajág mammoth site (*ca* 30 km to the south) a Gravettian reindeer hunters' campsite was discovered at Ságvár and was dated to 21–20 ka cal BP (Vörös 1982). The reindeer is the most common cold-adapted large mammal species found in Hungarian Pleistocene sites, with most remains occurring within archaeological contexts (Vörös 1982, 1987). The abundance of reindeer bones discovered in Hungarian sites of the Gravettian culture has led prehistorians to consider that these hunter-gatherer groups were highly dependent on this animal resource (Vörös 1982, Dobosi 2005). The oldest, dated *R. tarandus* is from the Peskő cave which age is ~40 ka cal BP (Vogel & Waterbolk 1972). The reindeer generally occurs in large numbers in every site. The majority of dated specimens are from MIS 2.

Alces alces

Elk (*Alces alces*) were among the first large mammals to recolonize Central Europe after the last glaciation (Kahlke 1999, Schmölcke & Zachos 2005). Already during the Allerød they established themselves in most parts of the area. In the early Holocene their distribution range extended from the Pyrenees to Denmark and from Austria to Great Britain and also covered East Central Europe where they still occur today (Schmölcke & Zachos 2005). Elk finds are also common is the Pannonian basin, although only two specimens have been radiocarbon dated (Fig. 2). An almost complete skeleton of *Alces brevirostris* that was discovered in Ördöglyuk cave in the vicinity of Budapest is of special importance. It was dated to MIS 12 (Vörös 1985). Kahlke (1999) suggested that *Alces brevirostris* is possible ancestor of modern elk. The oldest directly dated find is from an open-air site in the surroundings of Bodrogkeresztúr (*ca* 33 ka cal BP). Last appearance (absolute dated) of elk in the Pannonian basin is from the end of MIS 2 (13.5 ka cal BP).

Equus sp.

Within the early Middle Pleistocene, the caballoid horses (*Equus* spp.) rapidly became the dominant group in the Pannonian basin as well. In the brickyard of Madaras (Fig. 1) many fossil specimens were unearthed (Vörös 1989). Although maxillary bones with teeth and postcranial bones including the pelvis were recovered, only associated charcoal has been dated (*ca* 21.6 ka cal BP). Some bones of *Equus germanicus* were found in loess deposit near Tokaj. The age of the recovered specimens is 20 ka cal BP (Sümegi & Hertelendi 1998). A fossil faunal assemblage discovered near Nadap is dominated by horse (Dobosi & Hertelendi 1993.) Radiocarbon dates have been obtained on horse phalange from this site, of which age is 16 ka cal BP (Dobosi & Hertelendi 1993).

Paleoenvironment, paleogeography and megafaunal extinction

The occurrence of the mammoth steppe fauna between 46 and 13 ka cal BP in Hungary was not a singular biogeographic event. During this time span the animals repeatedly occupied steppe-like landscapes of the Carpathian (Pannonian) basin, when sufficient resources were present to allow their subsistence.

Although no mammoth steppe fauna has been radiocarbon dated between GS 5 and GS 3 (33–25 ka), it is possible that this is simply an artefact of sampling. According to Rudner & Sümegi (2001), in this time interval, the climatic conditions during the summer period in the Pannonian basin were similar to those prevailing today. Based on the malacothermometer method, the mean July temperature was calculated and values are 18–19 °C for the southern parts of the Pannonian basin and 16–17 °C for the northern part of Hungary (Sümegi & Krolopp 2002). Between 27 and 25 ka cal BP a significant change in environmental conditions for the Pannonian basin can be traced, initiating the process of loess formation (Újvári *et al.* 2010). This change refers to a significant cooling and development of a cold continental steppe–forest steppe environment with tundra-like spots in Hungary (Sümegi & Krolopp 2002). Two cool treeless-steppe periods existed between 25 and 12 ka cal BP (25–23 ka BP and 20–18 ka BP). In this period 'microinterstadials' were described by Rudner & Sümegi (2001), dated to 23–20 ka cal BP and 18–16 ka cal BP. The occurrence of the microinterstadial is further supported with biogeochemical proxies, including plant-derived biomarkers and stable C and N isotopes (by Schatz *et al.* 2011). This short phase of a warmer, wetter climate was characterized by an increase in the abundance of intermediate and woodland-dwelling mollusks, suggesting the development of a

Table 1. AMS ^{14}C and conventional radiocarbon dates of large mammal remains from the Pannonian basin.

No. Figs 1 and 2	Location	Species	Dated material	Lab code	^{14}C a BP ± 1σ	cal a BP ± 1σ	Reference
1	Tata-Porhanyó quarry	*Mamm. p.*	charred bone	GrN-3023	33,330 ± 900	38,369 ± 1707	Vogel & Waterbolk (1967)
2	Mende	*Mamm. p.*	charcoal	Mo-422	29,800 ± 600	33,968 ± 531	Vinogradov *et al.* (1968)
3	Zók	*Mamm. p.*	tusk*	AA-80678	17,760 ± 200	21,250 ± 450	Konrád *et al.* (2010)
4	Tápiósüly	*Mamm. p.*	tooth	Hv-1615	16,750 ± 400	20,060 ± 528	Geyh *et al.* (1969)
5	Esztergom-Gyurgyalag	*Mamm. p.*	bone	Deb-1160	16,160 ± 200	19,354 ± 354	Vörös (1991)
6	Budapest-Csillaghegy	*Mamm. p.*	charcoal	Deb-3160	15,935 ± 150	19,109 ± 241	Sümegi *et al.* (1998)
7	Szeged-Öthalom	*Mamm. p.*	bone	Deb-3344	15,916 ± 168	19,099 ± 248	Krolopp *et al.* (1995)
8	Csajág	*Mamm. p.*	tooth*	GdA-2011	13,315 ± 35	16,249 ± 413	Katona *et al.* (in press)
9	Herman Ottó cave	*Ursus spe.*	tooth*	Beta-178806	35,410 ± 660	40,253 ± 1008	Ringer *et al.* (2006)
	Herman Ottó cave	*Ursus spe.*	bone*	Beta-178807	35,630 ± 630	40,426 ± 1017	Ringer *et al.* (2006)
10	Istállóskő cave	*Ursus spe.*	bone*	ISGS-A-0188	31,608 ± 295	35,536 ± 493	Adams (2002)
	Istállóskő cave	*Ursus spe.*	bone*	ISGS-A-0187	32,701 ± 316	37,219 ± 717	Adams (2002)
	Istállóskő cave	*Ursus spe.*	bone*	ISGS-A-0184	33,101 ± 512	37,600 ± 884	Adams (2002)
	Istállóskő cave	*Ursus spe.*	bone*	ISGS-A-0186	27,932 ± 224	32,447 ± 320	Adams (2002)
	Istállóskő cave	*Ursus spe.*	bone*	ISGS-A-0185	29,035 ± 237	33,520 ± 359	Adams (2002)
11	Szeleta cave	*Ursus spe.*	bone*	ISGS-A-0131	22,107 ± 130	26,574 ± 409	Adams (2002)
	Szeleta cave	*Ursus spe.*	bone	ISGS-4464	42,960 ± 860	46,580 ± 1466	Adams (2002)
12	Bivak cave	*Ursus spe.?*	bone	Gd-15614	15,970 ± 270?	19,169 ± 318	Pazonyi (2006)
13	Balla cave	*Ursus spe.*	bone	GrN-4661	20,000 ± 190	23,929 ± 363	Vogel & Waterbolk (1972)
14	Peskő cave	*Rangif. tar.*	bone	GrN-4950	35,200 ± 670	40,112 ± 983	Vogel & Waterbolk (1972)
15	Jászfelsőszentgyörgy	*Rangif. tar.*	bone	Deb-1674	18,500 ± 400	22,145 ± 534	Hertelendi (1993)
16	Ságvár	*Rangif. tar.*	charcoal	GrN-1783	18,900 ± 100	22,783 ± 286	Vogel & Waterbolk (1964)
	Ságvár	*Rangif. tar.*	charcoal	GrN-1959	17,760 ± 350	21,302 ± 587	Vogel & Waterbolk (1964)
	Ságvár	*Rangif. tar.*	charcoal	GrN-1957	17,400 ± 100	20,849 ± 306	Vörös (1982)
	Ságvár	*Rangif. tar.*	charcoal	GrN-1958	18,600 ± 150	22,212 ± 353	Vörös (1982)
17	Arka	*Rangif. tar.*	charcoal	A-518	18,700 ± 190	22,360 ± 400	Haynes *et al.* (1966)
	Arka	*Rangif. tar.*	charcoal	GrN-4038	17,050 ± 350	20,410 ± 544	Vogel & Waterbolk (1964)
18	Jankovich cave	*Rangif. tar.*	bone	Gd-15626	12,440 ± 230	14,685 ± 480	Pazonyi (2006)
	Jankovich cave	*Rangif. tar.*	bone	Gd-15629	11,720 ± 190	13,632 ± 241	Pazonyi (2006)
19	Bodrogkeresztúr	*Alces alces*	bone/charcoal?	GX-195	28,700 ± 300	33,170 ± 467	Vörös (2000)
20	Lovas	*Alces alces*	bone*	ETH15199	11,740 ± 100	13,623 ± 157	Dobosi (2006)
21	Madaras	*Equus* sp.	charcoal	Hv-1619	18,080 ± 405	21,676 ± 589	Vörös (1989)
22	Tokaj-Csorgókút	*Equus* sp.	bone	Deb-2722	16,940 ± 250	20,254 ± 446	Sümegi & Hertelendi (1998)
23	Nadap	*Equus* sp.	phalange*	GrA-16563	13,050 ± 70	15,939 ± 398	Dobosi & Hertelendi (1993)

*AMS dating; ? – taxon questionable, most likely *U. arctos*

forest-steppe environment with significantly more trees than in the preceding periods (Sümegi & Krolopp 2002, Schatz *et al.* 2011).

Those data suggest that during the cold continental steppe–forest steppe environment (25 and 12 ka cal BP), the Pannonian basin had an extremely continental arid climate with a small amount of solid precipitation, possessed firm soil, and was dominated by open plant communities (herb, grass and low shrubs) and some trees. But there were also intervals (*e.g.* 18–16 ka BP) in which trees and shrubs expanded, so called tree-steppe or 'open parkland' environment (Schatz *et al.* 2011).

The cause or causes of late Quaternary megafaunal extinction continue to be debated (Koch & Barnosky 2006). Large herbivorous vertebrates have strong interactions with vegetation, which may consequently affect the structure, composition and dynamics of plant communities in many ways (Johnson 2009). Herbivory converted stands of tall forest into open parkland or grassland by suppressing woody regeneration; these open areas would be invaded by thickets of thorny scrub resistant to browsing, which, in turn, provided patchy refuges where seedlings of palatable trees could re-establish; emergent trees then shaded out under storey scrubs and grew into forest stands destined to repeat the cycle (Johnson 2009). The limited data available so far indicate the probable extinction of the cave bear before *ca* 24 ka cal BP, and woolly mammoth *ca* 16 ka cal BP in the Pannonian basin. The patterns of last occurrence of such taxa strongly indicate a close relationship between vegetational changes (in response to climatic changes) and distributional shifts prior to extinction (Stuart & Lister 2007). Data from Hungarian excavations do not support the blitzkrieg or attritional overkill hypotheses, which suggest that the losses should have occurred over short timescales of only 500–1500 years (Barnosky *et al.* 2004). The possible role of humans in limiting the natural expansion of these species requires further investigation.

The lowlands of Lower Austria – Moravia – South Poland form an important natural corridor in Central Europe, allowing migrations of both animals and humans between the Danube valley and the North European Plain (Svoboda *et al.* 2005). The Morava River valley runs in a roughly south-to-north direction, connecting, via the Danube and Tisa River valleys, the Hungarian Pannonian Plain through Serbia (via the Vardar River valley in Macedonia) to northern Greece in the south (Fig. 1). The large mammals probably used this route for dispersal in the Late Pleistocene. The Pannonian basin was an interesting and important "transition-region" with refugial character as well as distribution of typical Pleistocene faunal elements.

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