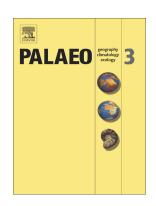
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Cave deposits as a sedimentary trap for the Marine Isotope Stage 3 environmental record: the case study of Pod Hradem, Czech Republic

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Abstract

Pod Hradem Cave, located in the Moravian Karst, Czech Republic, offers an excellent opportunity for environmental reconstructions of Marine Isotope Stage 3 (MIS 3) in Central Europe due to its detailed sedimentary record dated 50,000 to 28,000 cal BP. Identifying the natural environments of the Middle to Upper Palaeolithic (MUP) transition is necessary to understand the settlement strategies and related behaviour of both Neanderthals and Anatomically Modern Humans, both of whom may have occupied the region at the same time. A multidisciplinary excavation was carried out between 2011 and 2016. Detailed analyses of the sediments, vertebrate microfauna, pollen and charcoal revealed minor but observable fluctuations in climate, with little change in the surrounding vegetation. The Pod Hradem palaeoenvironmental dataset is complex, but generally reflects a predominantly glacial climate with a range of vegetation types and habitats during the Late Pleistocene, followed by the warmer and more humid Holocene. The MUP transition as recorded in Pod Hradem Cave was a glacial environment interrupted by two relatively warmer periods. Central Europe experienced extreme climate fluctuations during MIS3, as recorded from different sedimentary archives, but it seems that the Pod Hradem Cave environment may have acted as a buffer zone, ameliorating those extremes, and providing a suitable refuge for both bears seeking winter hibernation dens and occasionally visiting humans.

1. Introduction

The extreme variability of Late Pleistocene climatic change in Europe is now widely acknowledged, and an increasing number of high-resolution climatic records demonstrate frequent high-amplitude climatic changes (Blockley et al., 2012; Moseley et al., 2014). During that time hominin populations in many different geoclimatic regions repeatedly experienced environmental shifts that sometimes occurred on decadal time scales (Allen et al., 1999; Bradtmöller et al., 2012; Clement and Peterson, 2008; van Andel and Davies, 2003). Rapid climate change during Marine Isotope Stage (MIS) 3 influenced the behaviour of Palaeolithic populations as evidenced by cultural changes and probably population breakdowns (Bradtmöller et al., 2012). Several studies examine the complexity of the Early Upper Palaeolithic (EUP) and Anatomically Modern Human (AMH) interaction in the Middle Danube region (Nerudová et al., 2016; Rougier et al., 2007; Svoboda et al., 2002; Trinkaus et al., 2003, 2013). The Danube Corridor and the Population Vacuum models for the early migration of modern humans into the Upper Danube Basin around 40 ka BP are linked to major climatic fluctuations around the time of Heinrich Event 4 cooling and so provide a framework for the geographic expansion of AMH into Europe (Conard and Bolus, 2003, 2008). When Europe was being colonized by AMH, the impact of subsequent extreme climate changes caused other environmental conditions to switch repeatedly. A number of researchers discuss the adverse reaction of Neanderthal populations to climatic stress (e.g. El Zaatari et al., 2016; Jiménez-Espejo et al., 2007; Tzedakis et al., 2007; Stringer et al., 2003). Successful adaptation to abrupt environmental changes has been cited as a hallmark of AMH and was achieved through innovation in both technology and social organisation, to create what Gamble (1999) described as 'a dispersal specialist with a global distribution'. The variability selection model proposes that as hominid evolution during the late Pleistocene era

was increasingly dominated by great environmental instability, it resulted in hominids being exceptionally proficient in behavioural novelty, diversity and highly sophisticated use of environmental data (Potts, 1998). In general terms, the Neanderthals were also able to successfully adapt to many climatic changes during their long occupation of Europe and parts of Asia, however interpreting the evidence using the variability selection model, it appears that this characteristic may not have been as developed in Neanderthals as in AMH.

Identifying the palaeoenvironment at the time of the MUP (Middle to Upper Palaeolithic) transition is necessary to understand the settlement strategies and the behaviour of Neanderthals and AMH. Given the likelihood of early arrival of AMH in Moravia (Hoffecker, 2009; Richter et al., 2008) and the newly calculated ages for late Mousterian (e.g. Higham et al., 2014), it is plausible that both hominids may have occupied Moravia at the same time (also see Hublin, 2015). As Pod Hradem Cave provides a well stratified sedimentary archive for the period from 50,000 to 28,000 years ago, recording occasional human visits, the main questions of this of this study are as follows: (i) Can we reconstruct the palaeoenvironments in the cave surroundings from the sedimentary archive data and other proxy data?; (ii) Is it possible to reconstruct the climatic trends for the period of the MUP transition?; and (iii) Did humans visit the cave during specific climatic periods?

2. Climate and regional settings

2.1. Climate and environment of Middle Europe in MIS 3The rapid episodic changes that took place during the MIS 3 period are well described on the global scale, but the regional patterns were complex and are less well understood. Terrestrial and marine proxies show that western European and offshore environments were affected strongly by Dansgaard–Oeschger (D–O) (Dansgaard et al., 1993) and Heinrich (H) events (Heinrich, 1988) that correlate

roughly with the Greenland record. Greenland stadials were generally contemporaneous with semi-desert or steppe vegetation and Greenland interstadials with forests (see e.g., Sánchez Gońi et al., 2008). Until recently, the effects of the D–O and H events on Central European biomes were virtually unknown; however, a recent study at the Hölloch cave has demonstrated that the climate of the high-elevation northern Alps was as responsive to D–O forcing mechanisms as Greenland (Moseley et al., 2014).

Vegetation communities changed frequently in response to those climate shifts, and are probably a detailed reflection of the regional scale of climatic changes, as for example in the case of Western, Central and Eastern Europe (Sirocko et al., 2016; Pirson et al., 2012; Allen et al., 1999; Feurdean et al., 2014). Although pollen analyses are available for short sections of sedimentary profiles in Moravia and adjacent regions (see Doláková 2002; Jankovská 2006; Jankovská and Pokorný, 2008; Rybníčková and Rybníček, 2014; Seitl et al. 1986; Svobodová, 1988), the lack of accurate dating prevents their integration into an overall scheme for local Late Pleistocene vegetation patterns. Therefore, the detailed Late Pleistocene climatic and environmental history of the central European region is not well known, especially the archaeologically significant period of the Middle to Upper Palaeolithic (MUP) transition, ca. 50–35 kyr (see e.g., Gamble, 1999; Svoboda et al., 2009; van Andel and Davies, 2003).

Broad climate trends for Europe during the period just before and during the MUP transition can be summarized as follows: a cold period occurred between 66 and 60 kyr near the end of MIS 4 when the Fennoscandinavian ice sheet spread south from northern Europe (van Andel and Davies, 2003). At the beginning of MIS 3, at about 57 ka (Lisiecki and Raymo, 2005) (compare with the suggestion of 59 ka in Pettitt and White, 2012), the ice

withdrew rapidly and the climate remained moderately warm until it again began to deteriorate from about 44 ka (Barron et al., 2003). This deterioration continued to the end of MIS 3 (28 ka). With the onset of MIS 3, cold stadial events occurred more frequently until about 37 ka, after which the temperatures were as cold as, or even colder than the Last Glacial Maximum (LGM) (approximately 27 to 16 kyr) (see Davies and Gollop, 2003). The relatively short-term, millennial-scale D–O oscillations are difficult to correlate with archaeological events in practice because archaeological events are generally dated at a lower resolution than climatic events (van Andel and Davies, 2003), so the climatic oscillations during MIS 3 make any direct links between human behaviour and climatic conditions possible only at a general level (Barron et al., 2003).

Generalised climatic models are not applicable to individual sites or even regions. Europe is highly complex geographically and geomorphologically, so various microclimatic variables such as local topography and solar exposure need to be taken into account in any reconstruction (Blades, 1999). It is likely that Europe comprised a mosaic of different environments during this period. The relevance and validity of former local stratigraphic schemes also needs to be taken into account (Lisa et al., 2018; Vandenberghe and van der Plicht, 2016).

2.2. Caves as a possible environmental archive for MUP transition climate changes

Several different terrestrial sedimentary archives are available for palaeoenvironmental reconstructions of MIS 3 in Central Europe. The most widespread and much studied are loess deposits (Haesaerts et al., 2003; Sima et al., 2013), especially those associated with archaeological materials (Antoine et al., 2013; Fusch et al., 2013; Lisá et al.,

2014; Svoboda, 2009). The advantages of using the loess record derive from the near-continuous sedimentation across long distances allowing comparisons between sites, but the open conditions of loess formation means the loess record can provide only limited details.

Sedimentary deposits in caves provide another archive within which human as well as climatic impacts can be studied. Although cave sediments generally cannot provide palaeoenvironmental records with as much precision as marine or lacustrine deposits, partly because of hiatuses in deposition and inherent lack of dating precision, many such sites nevertheless act as sediment traps, and significant conclusions can be drawn from their sedimentary records (Karkanas and Goldberg, 2013; Woodward and Goldberg, 2001). The investigation of cave sites needs to be accompanied by detailed geomorphological, sedimentological, paleoecological and geochronological studies of the off-site Quaternary record (Woodward and Bailey, 2000).

Most of the environmental information for MIS 3 recorded in cave deposits has come from southern and western Europe (Courty and Vallverdu, 2001; Ellwood et al., 2001; Finlayson et al., 2006; Jennings et al., 2009; Karkanas and Kyparissi-Apostolika, 1999; Madella et al., 2002; Pirson et al. 2012; Walker et al., 2013; Zilhão et al., 2016). Collectively those deposits have provided information about the climate, which has varied from warm and humid through cooler and drier environments with different phases of hiatus or post-depositional change. On the other hand, only a handful of Central European caves have produced a detailed MIS 3 sedimentary record.

Important cave sites with long stratigraphic histories are found in the Ach (Brillenhöhle, Sirgenstein, Geissenklösterle, and Hohle Fels) and Lone Valleys

(Bocksteinhöhle, Bockstein-Törle, Hohlenstein-Stadel, Hohlenstein-Bärenhöhle and Vogelherd) (Bolus, 2003) and in Bavaria (Hunas) (Rosendahl et al., 2011). The problem is that few of them have produced substantial data for detailed environmental interpretation. The most promising is probably Hohle Fels Cave in the Swabian Jura, where the younger phase of MIS 3 was micromorphologically recorded and described (Barbieri et al., 2017; Goldberg et al., 2003). Much of the sedimentary record of Hohle Fels Cave was derived from the interior of the cave where the finer matrix was partially phosphatized—the phosphorus likely derived from hibernating bears—and where the sediment had been subjected to cryoturbation and ice lensing under cold, damp conditions. These cold-related features became increasingly well developed in the Gravettian and Magdalenian layers, reflecting more marked cooling during these periods. Barbieri et al. (2017) document the presence of reworked manganese nodules, reworked soil aggregates and fragmented, laminated clay coatings which were redeposited in the Bockstein area (Lone Valley near Hohle Fels) during the period approximately $32 - 28^{-14}$ C BP. These deposits represent relic soils that developed around the site in steppe and forest environments.

Geographically closer to our study area, Kůlna Cave (see Valoch, 1988) is situated just 4 km to the north of Pod Hradem Cave (see Fig. 1). Several other caves further afield have segments of the MIS 3 period documented, but a common problem is lack of adequate dating and analysis. These include Repolust Cave in Austria (Brandl et al., 2001), Dzeravá Skala Cave in Slovakia (Kaminská et al., 2004), and several caves in southern Poland including Bisnik (Krajcarz et al., 2014), Ciemna Cave (Valde-Nowak et al., 2014), and Nietoperzowa Cave (Chmielewski, 1962). The most substantial MIS 3 records were recorded in Dzeravá Skala Cave and Nietoperzowa Cave.

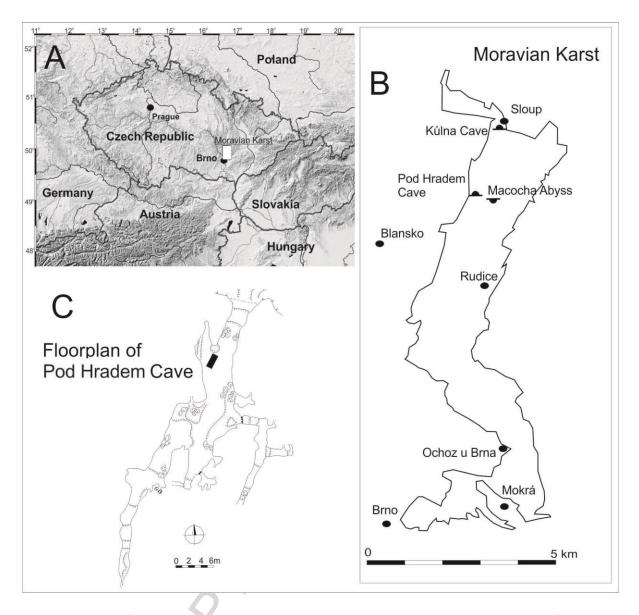


Fig. 1. Location of Pod Hradem Cave. White rectangle on map A represents the map of Moravian Karst (B). The floorplan of Pod Hradem Cave (C) is based on Audy (1997). Black rectangle represents the location of the 2011 – 2016 excavation.

The middle section of the Dzeravá Skala Cave sedimentary record represents MIS 3 sedimentation. This occurs as a complex of redeposited limestone debris of various clast sizes, with clay-rich fillings of varying coloration and remnant particles of earlier paleosols. This material was probably transported into the cave through the cave chimney, resulting in a low degree of sorting, subsequently affected by post-depositional processes such as

cryoturbation and mechanical disturbance. Some of these sediments are rich in phosphates (reflected in greenish-to-greyish coloration), while others show rusty coloration due to presence of Fe³⁺ as well as the presence of Mn, all of which suggests a moist environment, not only during the original formation of the sediments, but also episodically during the redepositional events (Kaminská et al., 2004, 2005). Nietoperzowa Cave (Chmielewski, 1962) has produced a sedimentary record for the last climatic cycle (see e.g. Guiot 1990) with a generally good resolution. The last glacial period is represented by several warmer (Aurignacian interstadial, or Paudorf oscillation) and cooler periods. According to the authors, there is an apparent mismatch between the dating results and proxy data; the ¹⁴C dates fall into a warmer period, whereas the sediment and bone proxy data suggest a cold environment.

2.3. Pod Hradem Cave

Pod Hradem Cave is in the northwestern part of the Moravian Karst (N49.371748, E16.72265) in southern Moravia, a region in the eastern Czech Republic (see Fig. 1). The cave entrance faces north–northeast and opens onto a very steep slope, approximately 60 m above the floor of the Pustý Žleb, a canyon-like valley. The canyon extends for 7.5 km and forms part of the drainage network of a deeply dissected karst landscape. The site is 409 m above sea level and less than 300 m from a surface opening of the mainly subterranean Punkva River. The area is geologically complex, with Devonian clastic sediments alternating with Vilémovice and Josefov limestones. Outlier outcrops of the Brno granodiorite massif occur to the west of the cave.

The cave has developed from solution widening along a vertical joint in a relatively narrow band of NE-SW oriented Lažánky limestone, sandwiched between the Brno massif

and Josefov limestone to the west and Vilémovice limestone to the east. There are two major fault lines near Pod Hradem Cave; the cave has formed along one of these fault lines, oriented NNE–SSW, intersecting the entire northern length of the karst system (Dvořák, 1965). The cave has a single small entrance that is currently 3 m wide and 1.5 m high, but distinct unaltered chemical weathering marks indicate that until only several decades ago (probably up until the major excavation campaign in the 1950s—see below) the sediment at the cave entrance was about 80 cm deeper (so the cave entrance was about half its present height until then). The main corridor is almost 20 m long and widens on the right (west) side (locations of squares A, B, and C), then opens into a large hall (14 m long, 10 m wide and 5-7 m high). Three corridors of varied lengths continue further inside (see Fig. 1).

The first archaeological excavations at Pod Hradem Cave were undertaken at the end of the nineteenth century. Jan Knies conducted limited excavations in 1890, 1896, 1897, and 1898 (Knies, 1901) and Richard Trampler continued the excavation in 1897 (Trampler, 1898). Both of these excavators subsequently published plans and descriptions of their excavations, both reported finding animal bones and Trampler (1898) also reported a 'cultural layer' at a depth of 1.3 to 1.5 m, although no artefacts were discovered. Knies concluded that most of the material (sediment and animal bones) was deposited in the cave through its chimneys. A major excavation in 1956–58 by Rudolf Musil and Karel Valoch uncovered an area of 90 m². Their findings suggested use of the site as a cave bear (*Ursus spelaeus*) hibernation den, with occasional human visits between 44,800 and 25,050 cal yr BP. Several radiocarbon samples were obtained from a 'black humic layer' (Valoch, 1965), leading to the definition of the 'Pod Hradem Interstadial' on the basis of two radiocarbon dates of 33,300 ± 1100 (GrN-848) and 33,100 ± 530 (GrN-1724) ¹⁴C BP (Valoch, 1965; Vogel and Zagwijn, 1967), i.e. 40,091–36,474 and 38,542–36,690 cal yr BP. Several more

radiocarbon determinations were obtained in 2008 and 2010 on cave bear bones (see Neruda and Nerudová, 2011; Nerudová et al., 2012) suggesting the deposit accumulated between 48,590 and 32,630 cal yr BP.

Gargett (1996) found abundant support for the hypothesis that Pod Hradem was a cave bear hibernation den, including the small, fragile bones of several neonates near the back of the main chamber. The most recent research in this cave in 2011-2016 (Nejman et al., 2013; Nejman et al., 2017) uncovered one complex sedimentary section, situated approximately 10 m from the cave entrance (compare with Valoch, 1965), which can be divided chronostratigraphically into 12 strata. That excavation recovered small numbers of artefacts of different ages (Nejman et al., 2017), suggesting low-level use of this cave by humans throughout the EUP period. A chronology was built using 17 radiocarbon dates on 15 samples of ultrafiltered collagen from unmodified bone, and 1 radiocarbon date on a fragment of charcoal pretreated with ABOx-SC, calibrated against IntCal13 (Reimer et al. 2013) and modelled in OxCal (Ramsey 2009) (see Nejman et al., 2017 for full details). The date ranges quoted here are given at 95.4% probability and based on the Boundary ages in the Bayesian model which provide an age estimate for the start and end of the sedimentation in each unit. Notable artefacts were recovered from Layer 6 (between 40790-38790 and 40410-36820 cal BP), yielding a unique Early Aurignacian bone bead, an imported porcelanite flake, and a tooth flake (Wright et al., 2014). The most substantial archaeological deposit was recovered from Layer 10 (48240-45450 and 47490-44590 cal BP) which yielded burnt bones, a large amount of charcoal, manuports, and several stone artefacts (Nejman et al., 2017).

The caves of the Moravian Karst have until now provided only scant environmental information for the MIS 3 period (Doláková, 2000, 2002, 2007, 2010; Doláková and Nehyba,

1999; Lisá et al., 2013; Nejman et al., 2017; Seitl et al., 1986; Sroubek et al., 2001; Svobodová, 1988), in spite of the fact that the area was probably visited repeatedly during the MUP transition (Musil and Valoch, 1966; Neruda and Nerudová, 2013; Nerudová et al., 2012; Valoch, 1996). Pod Hradem Cave, with its extensive MIS 3 sedimentary record is changing this state of knowledge.

3. Methodology

3.1 Sedimentology and micromorphology

A basic sedimentological description following standard field criteria is one of the key procedures in starting geoarchaeological research (Woodward and Goldberg 2001). It is based on parameters such as colour, texture, and internal organization (Table 1) and also includes micromorphology. The colour of sediments was identified in both wet and dry state using a Munsell soil colour chart. Seven micromorphological samples were collected using plaster and foam from the eastern wall of Square A following macroscopic divisions (Fig. 2). Large thin sections (approximately 140 x 70 mm) were prepared in the laboratory by Julie Boreham, Reach, GB (www.earthslides.com) and examined under plain and cross-polarised light at different magnifications (40-800x). The descriptions and interpretations followed mainly the formats used by Stoops (2003), Bullock and Murphy (1983), Goldberg and Macphail (2006), and Stoops et al. (2010).

Table 1. Basic description of layer properties, colour estimated in wet and dry state, grain size, pH and the percentage weight of skeleton.

Layer	Depth	Sampling	Munse	ell Colour	Field Observations
	(cm)	Depths	wet	dry	
		(cm)	wet	ury	
	0 5		40)/D	40)/D	
1	0 - 5	0 - 5	10YR	10YR	Dark brown sandy granular silt, sharp transition into layer 2
			2/2	5/1	
2	5 - 8		10YR	10YR	Non continuous layer of micritic and sparitic carbonates
			4/2	8/3	composed of dark greyish brown dense silty sand, abrupt
					transition into layer 3
3	8 - 38	10 - 20	7,5YR	10YR	Stony brown sandy clay in upper part to light brown sandy
			5/3	7/3	clayey silt in lower part; large amount of fine grained
		20 - 30	7,5YR	10YR	corroded limestone detritus, abrupt wavy transition into
			5/4	6/3	layer 4; limestone clasts 3 – 5 cm in diameter very common
		30 - 38	10YR	10YR	
			3/3	5/3	
4	38 - 59	38 -50	10YR	10YR	Stony brown granular sandy silt in upper part to clay silt in
			2/3	6/3	lower part, gradual transition into layer 5; limestone clasts 3
		50 - 59	10YR	10YR	– 5 cm in diameter common
		C	2/3	6/3	
5	60 - 80	60 - 74	10YR	10YR	Brown sandy granular to angular blocky clay in upper part to
		~	3/3	6/1	very dark grayish brown silt in lower part, abrupt transition
		74 - 80	10YR	10YR	into layer 6; limestone clasts 3 – 5 cm in diameter common
			3/2	6/1	
6	80 - 98	80 - 90	10YR	10YR	Light brown angular blocky clay silt in upper part to light
			4/3	7/4	brown sandy silt in lower part; large amount of fine grained
		90 - 98	7,5YR	10YR	corroded limestone detritus, abrupt transition into layer 7

			4/6	7/4	
7	98 - 115	98 - 115	7,5YR	10YR	Extremely stony light brown sandy silt with edge shape of
			4/6	7/4	non-continuous thickness, sharp wavy transition into layer 8,
					limestone detritus show preferred sub-horizontal
					orientation
8	115 - 135	115 - 125	10YR	10YR	Dark brown angular blocky to granular sandy silt, abrupt
			3/3	6/3	transition into layer 9; limestone clasts 3 – 5 cm in diameter
		125 - 135	10YR	10YR	present
			3/3	6/4	-2-
9	135 - 150	135 - 145	10YR	10YR	Brown angular blocky sandy clayey silt, abrupt to gradual
			3/3	7/4	irregular transition into layer 10; limestone clasts 3 – 5 cm in
					diameter present
10	150 - 170	145 - 155	7,5YR	10YR	Dark brown dense clayey silt, abrupt irregular transition into
			2.5/2	6/2	layer 10; limestone clasts 3 – 5 cm in diameter present
		155 - 165	7,5YR	10YR	
			2.5/2	5/2	
11	170 - 180	165 - 175	7,5YR	10YR	Dark brown dense sandy clayey silt; limestone clasts 3 – 5
			3/3	5/2	cm in diameter common
12	180 - 200	175 - 185	7,5YR	10YR	Dark brown dense silty clay, abrupt irregular transition into
			2.5/2	5/2	layer 11; limestone clasts 3 – 5 cm in diameter as well as
		()			occasional quartz pebbles present

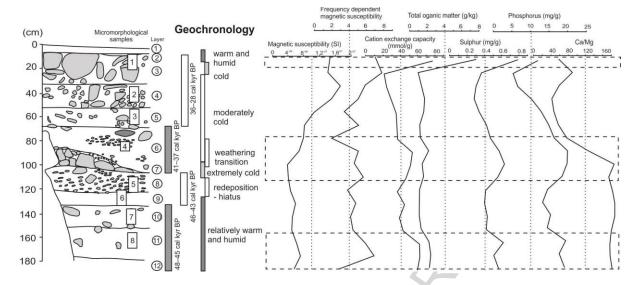


Fig. 2. Stratigraphic profile of Pod Hradem Cave (Sq. A, northern wall) with lithological units, and the main proxies documenting the influence of depositional and post-depositional changes. The positions of the micromorphological samples are marked with numbers on the stratigraphic profile.

3.2 Geochemistry, grain size distribution, and magnetic proxies

Nineteen bulk sediment samples from the 11 stratigraphic units were collected at approximately 10 cm vertical intervals (Table 1). Bulk samples were collected to acquire comparable proxies related to the climatic and pedogeochemical signal (Goldberg et al., 2013, Holliday and Garther, 2007). Total carbon (TC) concentrations (as weight percentage) were obtained on subsamples of dry sediment of known weight (~0.5 g) using a PRISMACS analyser, involving sample combustion in an electric arc furnace in the presence of oxygen to quantify the carbon dioxide produced and provide TC and total sulphur values. A further subsample of sediment was fired at 500 °C for 24 hours to remove organic carbon, and the carbon content was then determined using a Leco analyzer, obtaining total inorganic carbon (TIC) concentrations (in weight percent). The total organic carbon (TOC) content (weight percent) was determined from the difference between the TC and TIC concentrations. Geochemical composition of cave sediments and reference samples outside the cave were

measured by ICP EOS from a solution (approximately 1 g of material was leached in 40 ml of HCl and then 0.5 ml of the solution diluted with 4.5 ml of distilled water). Due to the poor sorting of the sediments, grain size was estimated in two ways. At first, the weight percentage of detrital fragments greater than 2 mm was estimated by dry sieving. The bulk samples were also measured using the pipette method based on Flint and Flint (2002). The coarse/fine (C/F) ratio was estimated from thin sections.

Magnetic susceptibility was measured using an Agico MFK1-FA Kappabridge at two different operating frequencies, f1 = 976 Hz and f3 = 15 616 Hz, amplitude of AC field was 200 A/m (peak value). Readings of the unconsolidated samples were taken in plastic bags; the measured susceptibility values were normalized by the mass of each sample and expressed as mass susceptibility [m³/kg]. Frequency dependent magnetic susceptibility, kFD, is characterized by the following commonly accepted parameter (Dearing et al., 1996): kFD = $100 \times (kf1 - kf3) / kf1$ [%], where kf1 and kf3 are susceptibilities at frequency f1 (976 Hz) and frequency f3 (15 616 Hz), respectively, and these were calculated for each sample.

3.3. Palaeobotany

Eleven palynological samples were collected from Square A, northern wall, from Layers 1, 3–12 (Fig. 3). The preparation of samples followed standard protocol (HCl, HF, KOH and HCl (10%) and heavy liquid ZnCl₂ (density = 2g/cm³) (e.g. Doláková, 2002). Identification and counting of more than 200 grains from each sample was done using a Nikon Alphapot 2 microscope following mainly Reille (1995) and Beug (2004). Pollen diagrams were created using the POLPAL programme (Walanus and Nalepka, 1999).

Asteraceae grains were presented separately on the pollen diagram as they are well known for their differential preservation (due to resistance to mechanical and chemical degradation) so some of the grains are likely to be reworked. Most of the charcoal was separated by flotation using a 0.25 mm sieve and 601 determinations from 43 samples were made. Some of the bigger charcoal pieces were collected separately during the excavation. Charcoal analysis was restricted to fragments of the largest fraction (>1 mm) and anatomical sections of the fragments were observed using a reflected light microscope with 200–500× magnification. These were identified to taxon according to the reference collection and standard identification keys (Heiss, 2000; Schweingruber, 1990).

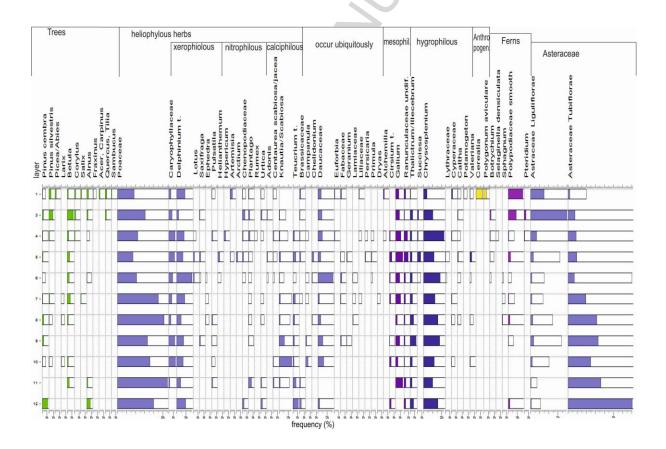


Fig. 3. Pollen diagram (see text for layer chronology).

3.4. *Fauna*

Microfauna bones and teeth were collected from square B during the 2012 field season. Sediment samples (30 to 40 kg of fine-grained fraction per layer) were wet-sieved using a 0.7 mm mesh, and fossils were mechanically extracted from the dried concentrate. Approximately 300 identifiable items were obtained and identified using a stereoscopic microscope. They represent at least 126 individuals (MNI) belonging to 20 species (see Table 2). Thousands of mostly highly fragmented bones of large fauna (mainly cave bear) were also recovered however, their potential as a palaeoenvironmental proxy was very limited so this information will be presented elsewhere.

Table 2. List of small vertebrates

(MNI) and their habitats.												open	rocky		
Pod Hradem, MNI	11	10	9	8	7	6	5b	5	4	3	MNI	ground	habitats	marsh	woodland
Pisces indet	1						1		2	3	7			***	
Sorex cf. araneus					1			1		5	2	*		*	**
Sorex cf. minutissimus								70		1	1	*		*	**
Plecotus auritus							M			1	1				**
Barbastella barbastellus								1			1		*		*
Chiroptera sp.				0			1				1				
Allactaga sp.		_(-/							1	1	***			
Cricetulus migratorius	1	(C)						1			2	***			
Cethrionomys cf. glareolus	1									1	2				***
Arvicola terrestris										1	1			**	
Microtus gregalis				1	2		4	4	5	11	27	***			*
Microtus arvalis/agrestis				1				2	2	5	10	***		20	

Microtus oeconomus									1		1		*	***	
Microtus nivalis							2	5	4	15	26	***			
Microtus indet.		1			2	3		3			9				
Dicrostonyx gulielmi			1		1		1	1	1	4	9 ***				
Lemmus cf. lemmus					1		2	3	1	1	8 ***			*	
Ochotona sp.								1		5	1 **	**			
Lepus sp.								1	1	1	2				
Canis sp.						•	N		1	1	2				
Ursus spelaeus neon.	1	1	1	1		1	1	1	1	1	9				
Ursus spelaeus ad.	1			1		1					3				
			~												
Total MNI (small mammals)	2	1	1	2	7	3	10	22	15	42	105	22	6	10	12
Total spp. (small mammals)	2	1	1	2	5	1	5	10	7	11	17	9	3	5	7
Total (MNI)	7	2	2	4	7	5	12	23	19	47	126				

Total (spp.) 4 2 2 3 5 2 7 11 10 14 20

open ground * * * * ** *** * *** ***

rocky habitats ** *** ** ***

marsh * * * * *

woodland *

Legend: * - rare, ** - present, *** - common

Table 3. Ecological categories of pollen taxa.

Ecological groups						freq	uency	in laye	ers			
	typical taxa / layer	1	3	4	5	6	7	8	9	10	11	12
Trees (AP)				(C								
Conifers and unambitious trees	Pinus silvestris, Pinus cembra, Betula, Salix	xxx	xxx	xxx	xx	xxx	xx	xx	xx	х	х	Х
	Larix	C	O,				х	х		х		
Moderate climate trees	Alnus, Picea, Abies	XX	х	х		х					х	х
	Corylus	xx	х	х								
Temperate climate trees	Carpinus, Acer, Fraxinus, Tilia, Quercus,	XXX	х									
sum of AP		35	23	12	8	18	19	10	3	6	3	5
Open treeless landscape (NAP)												
heliophilous herbs:		I.										
grasses	Poaceae	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	xxx
daises (Asteraceae)	Cichorioideae/Asteroideae	X	X/xxx	xxx/X	xx/X	xx/X	xx/X	xx/X	xx/X	xx/X	Х	Х
other heliophilous	Artemisia, catchflyes Caryophyllaceae (Silenaceae), larkspur											
	(Delphinium), Saxifraga	X	xx	Х	х	Х	х	xxx	xxx	х	xx	xxx
xerophilous	Ephedra					х	х	х				
	thistles (Centaurea), pasqueflower (Pulsatila), Helianthemum	xx		xxx	xx			х	х	х	х	

nitrophilous	Arctium, Artemisia, Chenopodiaceae, plantains (Plantago), Rumex,											
	Urtica	xxx	xx	xxx	xx	x	х	x	х		x	x
calciphilous	Adonis, Centaurea scabiosa, Dryas, Lotus, Scabiosa, Teucrium	х	xx	xxx	xxx	xxx	xxx	xxx	xxx	Х	х	
ubiquitous occurence	f. e. Anemone, Brassicaceae, bellflower (Campanula), Chelidonium,											
	carrot family (Daucaceae) , Euphorbia, Fabaceae, Geranium,											
	Lamiaceae, Liliaceae, Persicaria, Primula, Ranunculaceae, Rumex	X	хх	Х	xxx	х	xx	xxx	xxx	х	х	х
mesophilous herbs:	Alchemilla, Cirsium, Galium, Hypericum, Ranunculus	xxx	хх	Х	Х	Х	Х	xx	xxx	xxx	xx	Х
hygrophilous herbs:	Caltha, Cyperaceae, Lythraceae, Succissa, Thalictrum, Valeriana	XX	хх	xxx	xxx	xxx	xx	xxx	xx	xx		
	Chrysosplenium/Batrachium trichophylus	XX										
anthropogenic												
indicators:	Cerealia,+-Polygonum aviculare	xxx										
sum of NAP		226	217	339	233	576	335	355	258	337	135	172
Ferns and mosses	Polypodiaceae, Botrychium, Sphagnum	Х	xxx	xx	xx	xx	х	xx	х			х
sum of ferns	NO	41	17	7	7	4	3	7	1			1
Aquatic green Algae	Botryococcus, Pediastrum	х	Х	xx	XX						х	

Legend: x - sporadic appearance (1-2 grains), xx - present in small amount (3-10 grains), xxx - common appearance (10 – 25 grains), X - abundant > 25.

4. Results

We recognized 12 sedimentary layers in the excavated section (Fig. 2; Table 1). To improve the interpretation of climatic and local variations, the plant taxa were grouped into fifteen major ecological categories (see Table. 3). This section summarizes information pertaining to the individual layers grouped into phases of deposition based on common features. All age estimates are based on AMS results in cal yr BP (Nejman et al. 2017).

4.1. Phases of deposition

4.1.1 Layers 10–12

Layers 10, 11, and 12 are dated to approximately 48-45 cal kyr BP. These layers consist mainly of organic silts, and micromorphological observations indicate they have a spongy microstructure. This is usually associated with a highly phosphatic matrix. Other micromorphologically observable features include partly decomposed organic matter, a high concentration of microcharcoal, bone fragments, and a large number of phosphorus nodules as well as impregnations (generating the phosphatic matrix). The decomposed organic matter and high concentration of phosphates could be caused by accumulation of animal excrement (Braillard et al., 2004). The higher concentration of bear bones in Layer 11 could indicate that the organic matter represents the remains of bear denning (Brown, 1993; Pearson, 1975). In Layer 11 higher levels of nitrophilous plant pollens are observed (Table 3, Fig. 3). It is however difficult to distinguish fine-grained burnt or buried organic matter and therefore the possibility that the microcharcoal is connected to anthropogenic activities cannot be excluded. Stone artefacts, burnt bones, and macrocharcoal were recovered in Layer 10 so it is likely that the microcharcoal is also of anthropogenic origin. Geochemically, Layers 10 and 11 are characterised by elevated concentrations of P, S, Na, Ca, Fe and TOC. These signals are more likely to be the result of animal denning and excrement accumulations (Braillard et

al., 2004), however climatic input cannot be excluded (Holliday and Garther, 2006) especially when the enhancement of the magnetic signal is taken into consideration (Jordanova, 2016). A similar result was obtained at Hunas cave (Rosendahl et al., 2011), where layer J consisting of yellowish grey silty material containing medium fine scree also had increased values of magnetic signal and was also dated to GIS (Greenland Interstadial) 12-14.

The vertebrate assemblage indicates open ground habitats, but elements indicative of a woodland environment are also present (*Clethrionomys glareolus* and *Plecotus auritus*). Results of anthracological analyses indicate the presence of *Larix/Picea*, *Betula*, *Pinus cembra*, *Popules/Salix* and *Juniperus*, which could indicate the presence of taiga conifers in the cave vicinity. A large mineralized fragment of *Pinus cembra* may suggest human consumption of pine nuts (see Nejman et al., 2017).

Arboreal pollen from Layer 10 is congruent with the anthracological findings, which indicate the presence of conifers. Contemporary landscapes with steppe grassland species and open canopy coniferous forest in southern Siberia (e.g. Chytrý et al., 2010) are similar to the Pod Hradem MIS 3 assemblages.

The presence of *Knautia*, *Scabiosa*, *Campanula*, and *Centaurea scabiosa* palynomorphs, which are large and morphologically suitable for catching in animal hair, could be associated with the presence of cave bears in this layer.

4.1.2 Layers 8 and 9

Layers 8 and 9 were dated to approximately 46–43 cal kyr BP. They consist of sandy silt with a micromorphologically detected granular microstructure. Although granular microstructure is also present in the upper part of the profile (Layers 3–5), the sediment matrix (fine-grained material enclosing larger grains of limestone) differs. The chemical signature does not show elevated concentrations of P and TOC that are usually indicators of increased humidity or biological activity (Egli et al., 2008; Braillard, et al., 2004). Significant indicators of a human and/or animal (bear) presence, such as microcharcoal, decomposed organic matter, and bone fragments, are present, but overall the granular microstructure suggests redeposition (van Vliet-Lanoë, 2010). Granular microstructure can form either by colluviation (and associated rolling of grains), or freezing/thawing processes, or both. Freeze—thaw action makes the individual particles fragile, which in turn makes them more susceptible to redeposition by colluviation, so these two processes often co-occur, giving rise to granular microstructure.

Layer 9 contains the smallest proportion of tree pollen (only fragments of *Pinus cembra*) of all layers and also of hygrophyta and ferns. In Layer 8 these elements increase moderately. Layer 9 has a higher concentration of wood charcoal (*Larix/Picea* and *Pinus cembra*), so in this regard it is similar to Layers 10 and 11. Many ethnoanthracological studies (e.g. Biran et al., 2004; Henry and Théry-Parisot, 2014; Türker and Kaygusuz, 1995) reveal that firewood gathering is a frequent and repeated activity, and firewood gathering would normally take place near to archaeological sites. Open sites from this time in the southern Moravian landscape have yielded both Bohunician and Szeletian lithic assemblages (Oliva, 2005; Valoch, 1996).

4.1.3 Layers 6 and 7

The formation of layers 6 and 7 is strongly connected. Layer 6 was dated to approximately 41-37 cal kyr BP, chronologically corresponding with GIS 8. The development of the soil sediments is consistent with Denekamp Interstadial (Vandenberghe and van der Plicht, 2016) and soils marked as PK1 (Kukla, 1969). The Interstadial "Pod hradem" was also placed in this timespan, however this regional and outdated term should now be abandoned (Lisa et al., 2018). The sediment consists of silty sand to sandy silt with spongy and subangular blocky microstructure. The subangular blocky microstructure is interpreted as a post-depositional feature associated with processes that occurred during formation of Layer 4, i.e. a cold environment when Layer 6 was already part of the substrate. The climatic signal is difficult to interpret. The chemical signal of soils at the climatically cooler sites such as mineral transformations and weathering reactions are to a larger extent determined by organic acids (Egli et al., 2008). Therefore increased values of P, Na, S, and Ca can be interpreted as a signal of a more humid environment (Egli et al., 2008). The greater concentrations of limestone detritus can also be interpreted as a result of a more humid environment (Woodward and Goldberg, 2001). The greater concentrations of microcharcoal can be interpreted as the result of more intensive fires, or human presence (Woodward and Goldberg, 2001) These patterns have also been observed in the lower part of Layer 5. Archaeological material recovered from Layer 6 was classified as Early Aurignacian on the basis of a diagnostic bone bead, a tooth flake, and one porcelanite artefact (Wright et al., 2014). This discovery is unique not only in the context of the Moravian Karst but also in Central Europe (Wright et al., 2014). Valoch (1965) reported 11 porcelanite artefacts that he classified as Aurignacian (also see Nerudová et al., 2012). Although the recorded depths of these 11 artefacts have a wide spread (between 20 and 100 cm), some correspond to our

Layer 6. Layer 7 was dated to approximately 42 cal kyr BP which corresponds to Heinrich Event 4 (H4) (see van Andel and Davies, 2003).

A high percentage of carrot family pollen is unusual (over 15% Daucaceae); this frequently occurred in pollen clumps in Layer 6. The presence of *Alnus* is consistent with a warmer climate, whereas *Pinus cembra* charcoal indicates a cooler climate. Marked changes in pollen spectra between Layers 6 and 7—predominance of Asteroideae and decreased diversity of pollen in Layers 7 through 11—is probably related to changes in chemical processes affecting the sediments (see above paragraph). All microfauna species are indicative of a glacial landscape, except for one woodland specimen (*Sorex araneus*). The combination of warmer and cooler climate indicators could be a sign of a generally cool climate with some short warm interstadials. Alternatively they could indicate non-analogue taxonomic combinations—a common feature of MIS 3 taxonomic assemblages (Stewart et al., 2003).

This period overlaps with the age of the AMH skeletons found at Mladeč (Teschler-Nicola, 2006) approximately 40 km northeast of Pod Hradem Cave.

4.1.4 Layers 3 to 5

Layers 3, 4, and the upper part of Layer 5 were AMS dated to approximately 36–28 cal kyr BP. The upper part of Layer 3 contained many cave bear bones and has been dated with a single cave bear phalanx to between 29,235 and 28,110 cal yr BP (SANU-30907). Asteraceae/Liguliflorae (Cichorioideae) dominate in the pollen spectrum only in this layer. The higher proportion of nitrophilous herbs such as Chenopodiaceae and the accumulation of Asteraceae-Liguliflorae (predominantly *Taraxacum* pollen type) could be indicating human or animal agency, for example, nitrophilous pollen grains being brought into the cave

attached to cave bear fur, or in their food. A similar overrepresentation of the *Taraxacum* genus was documented by Villa et al. (2010) in the Upper Pleistocene hyena den Bois Roche Cave.

The deposition of Layers 3 and 4 overlaps with two relatively short interstadials Greenland Interstadial 3 (GI 3) and GI 4 (see van Andel and Davies 2003); however, it is possible that this sediment was also contaminated by Holocene material, because a) the chemical and magnetic signatures, b) the presence of *Taxus baccata* and *Populus/Salix* charcoal, and c) *Quercus* and *Tilia* pollen grains, all strongly suggest an entrenched, relatively warm, humid climate (i.e., interglacial rather than interstadial). Bioturbation documented in micromorphological sample 1 (see Table 4) provides a mechanism for such contamination. AMS sample SANU-30907 (~28-29 ka) also dates the latest occurence of cave bears in our stratigraphic section. This age is consistent with the majority of other youngest dates for cave bears in Europe (Pacher and Stuart 2009). Barbieri et al. (2017) report an erosional event for the timespan of 32 – 28 BP in the Lone Valley. The sedimentary record of Pod Hradem Cave for the timespan between 28 cal kyr BP and the beginning of the Holocene is represented as a hiatus in our section.

Table 4. Detailed micromorphological description of the section.

unit	Micro-	voids	Grain size	Coarse fraction	matrix	Organic matter	Inorganic	Pedofeatures
	structure		distributio				components	
			n					
1A =	massive	vughs and cracks	C/F _(100µm) =	micritic and sparitic	grey	partly decomposed and decomposed (50	bone	passage features, excremental features
layer 2		- rare	20:80; silty	calcium carbonate and	crystalline	– 100μm – 60 – 70%), charcoal and	fragments –	
			sand	limestone clasts		microcharcoal - present	small, very	
						,c ^C	rare	
1B =	granular	complex packing	C/F _(500µm) =	subangular to angular Q	crystalline,	black decomposed dots of buried organic	bone	passage features; Mn nodules – small star-
layer 3		voids,	3:97;	and Ptg, occasionally	grey brown	matter – present, microcharcoal –	fragments –	like shaped, rare but present, excremental
		occasionally	C/F _(50µm) =	mica, common fragments		present, partly decomposed, brown in	present,	features, fine grained dirty clay or silty
		cracks or vughs	40:60	of limestone and		complex packing voids, not mixed within	occasional	coating on grain or granulae surfaces. CaCO ₃
				speleothema		the single granulae – common, charcoal –	spherulites	coating with Fe hypocoating forming rims of
			sandy			fine grained black		limestone clasts
			clayey silt	101				
2 =	granular	complex packing	C/F (500µm)=	subangular to angular Q	crystalline,	decomposed small black dots	abundant	dirty silty coating present
lavor 4		voids, cracks or	3:97;	and Ptg and limestone	brown,		bone	
layer 4		planes	C/F _(50μm) =	clasts, occasionally mica,	slightly		fragments	
		occasionally	40:60	bigger limestone clasts	phosphatic			
		occur inside	sandy silt					
		subangular single						
		blocks						

3 =	complex	complex packing	C/F (100µm)=	limestone subangular	brown,	decomposed small dots, occasionally	Bone	presence of small Fe/Mn nodules, big clasts
Javar F	(spongy,	voids, irregular	20:80 silty	clasts, Q and Ptg,	crystalline,	bigger (up to tens of microns),	fragments	have fine grained silty coating and
layer 5	planar,	voids, planes	sand	occasionally mica	slightly	microcharcoal – rare but present	present	occasionally dirty clay coating
	granular)				phosphatic			
4 =	spongy	Complex packing	C/F _(100µm) =	limestone subangular	brown to	common decomposed black small dots,	Bone	Small Fe/Mn nodules - rare
Lavor 6		voids, irregular	20:80	clasts, Q and Ptg,	orange,	occasionally bigger (up to tens of	fragments	
Layer 6		voids, cracks	clayley	occasionally mica	crystalline,	microns), microcharcoal – present	present	
			sandy silt		slightly	. 15		
					phosphatic			
5 =	granular,	complex packing	C/F _(500µm) =	differs according to the	highly	rich or organic matter, decomposed black	Bone	silty coating, rims on surfaces of bigger clasts
layer 8	some	voids, cracks or	30:70;	aggregate composition,	phosphatic	dots common, charred thin lumps of	fragments	
layer o	aggregates	planes	C/F _(50µm) =	but generally prevailing	light brown	black matter very common, partly	present	
	show	occasionally	40:60	limestone clasts, Q, Ptg	to orange	decomposed fragments of organic matter		
	internal	occur inside	sandy silt	and mica	brown	– present		
	bands	subangular single						
		blocks						
6 =	complex	complex packing	C/F (100µm)=	limestone subangular	brown to	common decomposed black small dots,	Bone	silty coating or rims along clasts are present
Layer 9	(spongy to	voids, irregular	20:80	clasts, Q and Ptg,	orange,	occasionally bigger (up to tens of	fragments	just occasionally, small Fe/Mn nodules –
Layer 9	subangular	voids, cracks	clayey silt	occasionally mica	crystalline,	microns), microcharcoal – present, brown	present	rare, but present
	blocky)				slightly	decomposed to partly decomposed		

					phosphatic	organic matter – present		
7 =	complex	Irregular voids,	C/F (500µm)=	Angular Q, Ptg,	highly	common decomposed black dots of	Bone	FeOH hypocoating of limestone clasts, CaCo3
layer 10	(spongy to	channels, cracks	3:97;	subangular limestone	phosphatic	different sizes, sometimes difficult to	fragments,	coating of pores, Fe OH nodules, rare, but
	subangular	and compound	C/F (50µm)=	clasts	dark	distinguish from charred organic matter,	bones	present
	blocky)	packing voids	40:60		orange,	sometimes as small lumps of charred	charred and	
			clayey silt		crystalline	organic matter	uncharred	
8 =	spongy	Irregular voids,	C/F	Angular Q, Ptg,	highly	common decomposed black dots of	Bone	FeOH hypocoating of limestone clasts, Fe OH
Layer 11		compound	(500µm)=	subangular limestone	phosphatic	different sizes, sometimes difficult to	fragments,	nodules, rare, but present, CaCO3
Layer 11		packing voids,	3:97; C/F	clasts	dark	recognize from charred organic matter,	bones	concentrations
		small cracks	(50μm)=		orange,	sometimes as small lumps of charred	charred and	
			40:60		crystalline	organic matter	uncharred	
			sandy					
			clayey silt					

In the remainder of Layer 3 and in Layer 4, granular microstructure suggests a very cold climate (van Vliet-Lanoë, 2011), but the origin of this microstructructure is not necessarily synsedimentary, i.e. the pollen record and geochemical signal more likely document the phase before the cold event (H2). The internal structure of some of the larger clasts in the upper part of Layer 5 displays a platy microstructure that also occurs, but less frequently, within individual clasts in Layer 4. The upper part of Layer 5 has moderate P and TOC values which is consistent with decreased biological activity generally considered to be associated with colder periods. In these layers the only arboreal pollen present is Pinus cembra and Betula. The presence of less weathered alumosilicates is reflected in the elevated concentrations Al, K and Mg in Layer 4. This pattern can be interpreted as an increase in aeolian deposition outside the cave (increased wind activity and consequent aeolian deposition of loess is also associated with colder periods during the last glacial) (Antoine et al., 2014). The elevated concentration of alumosilicates is more pronounced than in other colder periods (e.g. Layers 7 or 9 – see below). This could be because Layer 4 corresponds chronologically to H3 which lasted longer than H4 (therefore the climate signature is stronger).

The lower part of Layer 5 transitions into spongy microstructure, which indicates a moderately warmer climate. P and TOC values increase concomitantly in the lower part of Layer 5. Layer 5 also contains the greatest diversity of herbs and increased occurrence of ferns and hygrophytes. Rare colonies of *Pediastrum integrum* were present only during the formation of Layer 5. This species commonly occurs in late glacial lakes (Komárek and Jankovská, 2001).

Layers 3 and 4 did not yield any archaeological material in our trench; Layer 5 yielded one chert blade. This does not necessarily indicate an absence of people from the cave—our excavation area in 2011–2012 and 2016 was only 3 m². Valoch (1965) excavated a total area of 90 m² on the eastern side of the cave, and classified five artefacts as Gravettian—found at various depths between 20 and 70 cm (Nerudová et al., 2012). The chronostratigrahic positions of these artefacts correspond to Layers 3–5 as identified in our section. The timespan of 28–35 cal kyr BP has sometimes been designated as part of the Pavlovian phase of the Gravettian period (Svoboda et al., 2002).

Several artefacts previously recovered from Pod Hradem Cave have been attributed to this period (Nerudová et al., 2012; Valoch, 1965). At other sites in the Moravian Karst, Gravettian occupation has been documented unequivocally only in Kůlna Cave (Layers 7a, 6b) (Valoch, 1988), typologically in Křížova cave (Valoch, 1960) while the well-known open Moravian sites (e.g. Dolní Věstonice, Pavlov, Předmostí) furnish ample evidence for the presence of sophisticated hunter–gatherers in southern Moravia (Svoboda 2002).

4.1.5 Layers 1 and 2

Layer 1 contained ceramic and metal artefacts (Doležel, pers. comm. 2012) some of which are associated with the early Medieval occupation of Blansek castle, situated on a clifftop above the cave. Pelíšek described this layer in the adjacent test pit (Profile 2—see Pelíšek in Valoch, 1965:113–115) as "dark-grey, clay humus loam, recent rendzina", which is consistent with our findings (Table 1). A small amount of *Fagus sylvatica* was retrieved from this layer. Pollen analyses revealed spectra typical for the younger part of the Holocene (rich spectra of warm climate trees) as well as clear indicators of human impact (Cerealia); see Fig. 3. Layer 2 is a thin and discontinous band of fine-grained carbonate (moonmilk). The massive microstructure together with elevated values of P, Na, S, and Ca indicate this formed in a

relatively humid, warm environment (see e.g., Stoops et al., 2010). Frequent occurence of microcharcoal and limestone detritus corroborates this interpretation. Both magnetic susceptibility and frequency dependent magnetic susceptibility have elevated values; this enhancement is also consistent with a warmer environment (Dearing et al., 1996, Evans and Heller, 2002). Chronostratigraphically, this layer corresponds to the Atlantic climatic optimum, which can be subdivided into three distinct phases encompassing the intervals from 9000 to 7500 cal yr BP, the Mesolithic, around 7500–6300 cal yr BP, the Early and Middle Neolithic, and the Younger Neolithic after 6300 cal yr BP (Kalis et al., 2003).

4.2 General trends of the environmental record

While the pollen record does not appear to change markedly throughout the studied period, and all the pollen associations testify to prevailing cold and dry steppe vegetation (except Layer 3) with only small patches of shrubs, trees and bodies of water (Fig. 3 and 5, Table 3), the macroscopic evaluation of the studied section shows significant differences between lower and upper parts of the section. The lower part of the section (Layers 8–12) shows markedly darker hues and a relatively higher frequency of bone fragments, microcharcoal, and charred organic matter (Table 1). The most common herbaceous plants are grasses (Poaceae) and daisies (Asteraceae) (Fig. 3). These layers also show high proportions of clay followed by a sharp decrease between Layers 8 and 7 (Fig. 2). Generally, the darker layers are typical, with higher values of P, S, and organic content connected with the well-developed spongy microstructure (Fig. 4, Table 4). Single specimens indicating woodland/forest species vegetation were detected in Layers 7 and 11 (Fig. 5).

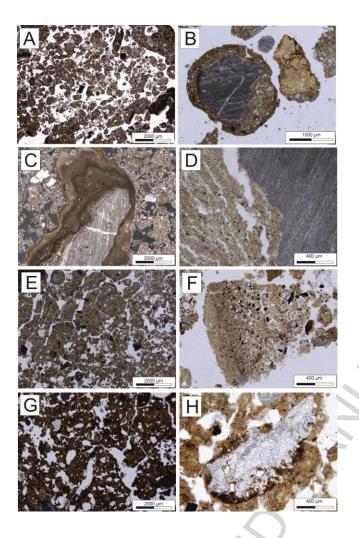


Fig. 4. A selection of the main micromorphological features observed in the samples: A—granular microstructure typical for frost action, sample 1 from Layer 3 (PPL); B—detail of the dense rims on surfaces of rounded granulae, sample 2 from Layer 4 (PPL); C—newly formed calcite neoformations on the surface of limestone clasts, sample 1 from Layer 3 (PPL); D—platy microstructure, sample 2 from Layer 4 (PPL); E—spongy to planar microstructure, sample 3 from Layer 5 (PPL); F—subrounded clasts of redeposited lithified matrix similar to material in Layers 10 and 11, sample 5 from Layer 8 (PPL); G—spongy microstructure of a highly phosphatic matrix, sample 7 from Layer 10 (PPL); H—corroded surface of a limestone clast, sample 7 from Layer 10 (PPL).

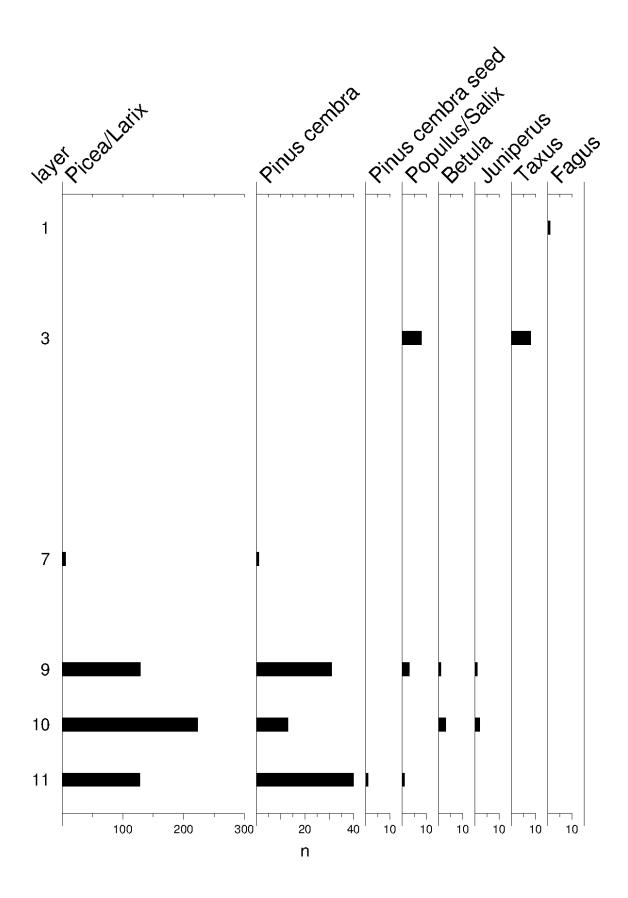


Fig. 5. Results of charcoal analyses (n = number of charcoal records).

In Layer 7 there is a sharp transition, reflected not only in the colour change, but also in the higher proportion of larger stone clasts of limestone and smaller limestone detritus. This is the only layer that thins out across the section and it can be seen in Fig. 2 as it forms a 'cap' over the lower layers. The limestone clasts in this layer as well as in the layer above show distinct weathering crusts with CaCO₃ neoformations or overgrowths. The deposition of Layer 7 was a turning point in the sedimentation regime in several ways: the Ca/Mg ratio decreases dramatically in this layer as do the values of phosphorus and sulphur (Fig. 2). A reverse trend (i.e. reduction) in magnetic susceptibility values was also detected in this layer (Fig. 2). The sedimentary record above the transition shows less detectable changes. Layers 6 and 5 show lighter hues than those above and below (Table 1), but they still possess a spongy microstructure (Table 4, Fig. 4). Values of magnetic susceptibility are enhanced, while the values of other proxies presented decreasing trends (Fig. 2).

The presence of charred organic matter and microcharcoal is not ubiquitous, but bone fragments were detected in all layers (Table 4). Layers 6 and 5 revealed pollen of plants that grow near water courses (hygrophilous—e.g., *Caltha*, Cyperaceae, *Valeriana*), or plants typical of moderately moist substrates (Fig. 3, Table 3). The geochemical signal does not change significantly in the upper part of the section, but the microstructure of deposits becomes subangular and granular. Generally the upper part of the section was subjected to less intensive weathering (Fig. 4, Table 4).

Another transition in the macroscopic, micromorphological and geochemical signals appears in the upper part of Layer 3, where all the measured proxies start to display increasing values (Fig. 2, Tables 1 and 4). Single specimens indicating woodland/forest species vegetation were detected in Layers 3 and 4, reflecting the presence of interstadial

conditions (Table 2), but the granular microstructure in these layers (Fig. 4, Table 4) indicates the presence of cold conditions. It is important to remember that the climate the sediment formed in is reflected in the sediment microstructures however, a subsequent change in the climatic regime can result in further changes to the microstructure.

The microfaunal vertebrate record provides robust paleoenvironmental information particularly for Layers 3, 4, and 5, which were relatively rich in fossils. In the lower layers microfaunal remains occur less frequently, but do not significantly differ from the upper layers. In all layers the remains are dominated by index elements of glacial open ground habitats (Microtus gregalis, M.arvalis/agrestis, Dicrostonyx gulielmi, Lemmus lemmus). Several satellite elements were also identified. These are typical for MIS 3 communities of Central Europe, but rather rare in Early MIS 3 and LGM communities (see Horáček and Ložek, 1988; Horáček and Sánchez-Marco, 1984; van Kolfschoten, 2014; Nadachowski, 1982; Nadachowski et al., 2009). These include Cricetulus migratorius, Ochotona pusilla, and particularly *Allactaga* cf. *major*. The latter is rare in Central Europe. An unusual feature is the dominant presence of Microtus (Chionomys) nivalis, an important species for interpretation of the local environmental context. Extensive stone debris-fields rich in herb vegetation are the typical habitat for this species (it is now restricted to the alpine zone and/or corresponding habitats in the Balkans). Appearance of semi-aquatic species such as Arvicola terrestris (Layer 3), Microtus oeconomus (Layer 4), and fish indicate the presence of marshy habitats along an active stream in the valley below the cave. Clethrionomys glareolus and Plecotus auritus, (in Layers 3 and 11), and Sorex araneus (in Layers 4 and 7), indicate arboreal vegetation—patches of woodland habitats either on the slopes or the valley bottom.

5. Discussion

5.1 Provenance of cave deposits

Tracing the provenance of cave deposits is one of the most important questions for palaeoclimatic reconstructions (Goldberg et al., 2003) and for understanding the context of formation of cultural deposits (Goldberg and Sherwood, 2006). The multiproxy data presented here show that the sediments of Pod Hradem Cave are derived from both roof fall and mixed fine and coarse material entering as colluvium through the cave entrance. The presence of coarse sands in Layer 12 could be indicative of some relicts of Tertiary deposits. These were also found in chimneys in the form of sedimentary relicts impregnated by carbonates (Bajer et al., 2013), but some of the coarser sands could have derived over long periods from colluvium entering the cave, or weathering of the cave floor.

The chemical analyses (Fig. 2) and mineralogical composition (Table 4) in combination with grain size analyses (Fig. 2) suggest that the sources of at least some of the fine sediment fraction in Pod Hradem Cave are loess deposits of Quaternary age. Aeolian deposition in Pod Hradem Cave is less pronounced than in Kůlna Cave (Sroubek et al., 2001) due to its topographic position, and this is probably why pollen of anemophilous (wind pollinated – *Pinus*, *Betula*) trees are fewer in number. Direct wind deposition of loess into the cave as suggested for example by Sroubek et al. (2001) for the nearby Kůlna Cave is unlikely at Pod Hradem due to its geomorphological setting. Instead it is likely that much of the fine sediment was transported into the cave as slopewash or colluvial creep of non-lithified deposits from the sedimentary cones at its entrance.

The only identified exception is the sediment making up Layer 8, where micromorphological observations suggest a reworked cave deposit. It consists of aggregates possessing an internal structure and composition similar to the underlying Layers 9, 10, and 11. Its deposition therefore probably occurred as a high-energy colluvial event moving lithified material deeper into the cave interior. Valoch (1965) suggested that the source of fine-grained material in deeper parts of the cave may also be small chimneys that breach the cave roof. These small entry points are unlikely to have contributed extensive quantities of excavated sediment. We have not been able to test this hypothesis as our section is located only 10 m from the entrance. Colluvial material can be observed spreading into the cave mouth from talus cones on both sides of the entrance.

The main source of the coarse sedimentary fraction is the local limestone. It is present in all the Pleistocene sediments investigated. Roof-fall occurring as blocks or granules, probably broken down by mechanical action in the deposit, was the main contributor to the sediment mass. The presence of calcium carbonate (CaCO₃) crystals and other carbonates throughout the deposit indicates that limestone blocks were the major contributor to the fine sediment, and the bulk of the deposit consists of limestone fragments ranging in size from boulders to clasts of 1 mm in size recovered in sieve residues. Coarse to medium sand grains recovered during sieving are both quartz and limestone.

The amount, size, and type of weathering of limestone clasts vary throughout the deposit. The high proportion of limestone debris in all size classes was initially considered to be the result of very cold conditions followed by frost weathering similar to that described by Goudie and Viles (2008). A major block-fall accumulation is certainly responsible for forming Layer 7, limestone blocks also make up a significant part of Layer 6 and are also

common in Layers 3 and 4. While roof-fall episodes may in some instances be associated with very cold periods, and triggered by freezing water expanding in joints and along bedding lines, it is difficult to envisage repeated freeze-thaw episodes having triggered frost shattering of the rock in Pod Hradem Cave, especially as there is no water seepage, no point of entry for seepage of water along bedding planes or joints within the cave, and no evidence for this having occurred in the past. Under this scenario, no particular climatic event needs be invoked to explain roof-fall occurrences. The evidence gathered from pollen, macroflora, and microfauna suggest generally uniform conditions over time making frost shattering unlikely as the cause of particular roof-fall events. Joint cracking and granular disintegration attributable to general weathering processes can best explain the block falls.

Another source of sedimentary material is use of the cave by animals and people. Examples include organic sediments from the breakdown of denning material for bear hibernation and the accumulation of animal faeces. This is especially the case for the lower part of the section which is clearly rich in phosphates. Goldberg et al. (2003) suggested bear denning and guano as the main sources of organic matter and phosphate in cave sediments that they investigated, but remains of denning activities by other carnivores and omnivores are also possible sources. Although guano is frequently the source of the organic component in cave sediments, this is unlikely in Pod Hradem because most of the sediments were deposited during the Last Glacial period with unfavourable conditions for bat hibernation. The presence of phosphate-rich deposits in Pod Hradem Cave are more likely linked to hibernating bears (see Andrews et al., 1999; Goldberg and Macphail, 2006; Schiegl et al., 2003). The question of bear denning in caves has not been discussed widely. Brown (1993) reported that a bear den generally consists of grasses, moss, leaves, conifer needles, and tree branches, seven to nine inches deep. Pearson (1975) noted that only three of the ten dens he

investigated were lined with twigs and grass, and this could not be correlated with any particular sex or age class. Rogers (1981) observed modern black bears preparing nests of vegetation in burrows and caves in order to make a dry, comfortable space to rest for up to six months. In one example, a female and her two cubs worked for some time, first dragging all the detritus out of the space, then moving in the new vegetation, then dragging it all out again before producing a "satisfactory" bed (Rogers, 1981:68). According to Navarro et al. (2001), zoophilous pollen grains with morphological adaptations to facilitate their entrapment in animal hair could introduce such grains into the pollen spectra of cave samples.

5.2. Site formation processes

Understanding site formation processes is one of the main prerequisites for geochronological reconstructions. Goldberg and Macphail (2006) propose that the variations in sedimentation and associated syn-depositional processes have occasionally been associated with Pleistocene climatic fluctuations and the detailed study of cave deposits by micromorphology and other micro-techniques has revealed new insights into the geological and archaeological records. The varied sedimentary features observed micromorphologically in Pod Hradem Cave can be linked to impregnation by phosphate rather than to intensive frost action. The accumulation of phosphate and the lack of characteristic frost features such as distinctive vertical and horizontal micro-fractures in the sediment fabric reflects relatively stable and warmer conditions. The presence of organic matter and microcharcoal could well be associated with human visits to the cave. Phosphates are common in cave sediments and apparent as brown, yellow, orange-yellow or grey tints in the groundmass. The typical microstructure of these organic-rich layers is spongy (Karkanas and Goldberg, 2010; Wilson and Righi, 2010). Spongy microsctructure commonly occurs in Layers 11 and 10, and to a lesser extent in Layers 9, 6, and 5.

The Pod Hradem Pleistocene sediments investigated during this project were all deposited during MIS 3 (Nejman et al., 2017), so frost features were expected. For example micromorphological analysis of sediments at Hohle Fels Cave showed a marked increase in cryoturbation during the Late Pleistocene in deposits that spanned the Gravettian and Magdalenian periods (Goldberg et al., 2003). Also Lisá et al. (2014) reported lenticular microstructure typical for freeze-thaw cycles (van Vliet-Lanoë, 2010) in nearby Kůlna Cave for the end of MIS 3 and MIS 2. In Pod Hradem Cave, well-developed granular microstructure was observed in two stratigraphic units. Granular microstructure is common in frost-affected soils with a fine silt to clayey texture (Crampton, 1977; van Vliet-Lanoë, 2010). Such microstructure usually occurs in the upper part of a soil most susceptible to multidirectional frost and to frequent freeze-thaw cycles, so it is possible that this microstructure in Pod Hradem Cave could indicate some synchronous freeze-thaw action as the sediments were deposited. When interpreting this record it is important to keep in mind that these processes can act on deposits that did not necessarily aggrade in the same type of environment, i.e. sediment that originally formed in a much warmer environment (as indicated by pollen, bones, chemical signals). No comparable excavation findings have been noted, but we know that Pelíšek (in Valoch, 1965) documented a very similar set of layers in an adjacent stratigraphic profile (No. 2). In this profile Pelíšek (Valoch, 1965:113–115) reported almost identical layers to those we designated as Layers 1-5, except that in his profile they are somewhat thicker. This could indicate that the cave floor sloped down towards the east side of the cave (field observations confirm this) so the accumulated sediments were thicker than on the western side where our 2011–2016 trench was located.

Two units where the formation processes are particularly complex are Layers 8 and 6-7. The formation of Layer 8 has already been described—its origin is due to the redeposition of previously lithified cave entrance deposits with two types of aggregates mixed. Some of the aggregates have a matrix similar to that of Layer 9 and some have a bedded matrix similar to that observed in Layers 10 and 11. These aggregates are partly rounded with compact surfaces, suggesting colluviation, but are also consistent with frost action. Because Layer 7 corresponds geochronologically to the H4 event, it is assumed the formation of Layer 8 occurred under high-energy processes during climate fluctuations preceeding H4. The formation of Layer 6 is connected to the underlying Layer 7 which consists almost entirely of limestone detrital material that fell as blocks, perhaps associated with frost shattering. This formed a hard crust. The bones that accumulated there were barely incorporated into the crust and most remained on top of the undulating rocky surface. During the subsequent deposition of Layer 6 the climate became warmer, organic detritus was deposited and gradually these materials formed the bone-rich sedimentary layer. As sedimentation proceeded and sediments filled the interstices between the bones, stratigraphic mixing of bones and sediments of different ages occurred, forming a sedimentary palimpsest. There was no mechanical disruption involved so the resulting sediments display no micromorphological evidence for disturbance while the radiocarbon dates for bones produce varied ages (Nejman et al., 2017; Wright et al., 2014). A second possible explanation for the bone accumulation in Layer 6 presents the possibility that the older bones exposed on the surface were redeposited together with the colluviated material. In our opinion, this hypothesis is unlikely because the colluviation process requires relatively higher energy than was observed macroscopically and micromorphologically.

5.3. General picture of the MIS 3 environment in karstic area

There is a dearth of information about the natural environment in the Moravian Karst during MIS 3. Most of the available information comes from the excavation of Pod Hradem Cave (Nejman et al., 2013; Wright et al., 2014; Valoch, 1965), and Kůlna Cave (Lisá et al., 2014; Lisá et al., in preparation; Sroubek et al., 2001; Valoch, 1988). Based on our results, the environmental record of Pod Hradem Cave suggests a relatively mild glacial landscape throughout the MIS 3 period. Microstructures suggesting cold events are present only in layers which apparently formed during Heinrich events. It appears likely that the cave environment ameliorated the extreme temperatures of the external landscape and provided a comfortable hibernation location for bears during winter, and an occasional shelter for humans passing through the Pustý Žleb valley. Previous scholars have proposed that Pod Hradem Cave was a hibernation den for cave bears (Gargett, 1996; Valoch, 1965) and our results have confirmed this conclusion (see Nejman et al., 2017).

The low proportion of arboreal species and corresponding high frequency of grass and herb palynomorphs throughout the sequence suggests that the cave surroundings may have been dominated by grasslands/herb fields with occasional occurrence of trees and partly hygrophilous vegetation near the watercourse on the valley floor below the cave. Following Sirocko et al (2016) we suggest this pollen assemblage reflects a tundra - steppe environment with enclaves of boreal forest. It needs to be taken into account that the specifics of the morphology of the local karstic landscape, microclimate and taphonomic processes have influenced the character of this pollen assemblage.

Palynomorphs are transported into caves with sedimentary particles or through the activity of animals. This fact causes several complications for interpretations—selection, degradation, and secondary accumulation due to variable resistance and the possibility of

consequent mixing of older palynomorphs with more recent ones. This complicates reconstructions of vegetation communities (Carrión et al., 1999; Doláková, 2002; Navarro et al., 2001; Villa et al., 2010). The comparison of pollen spectra from different layers shows that fewer selectively represented pollen spectra in the upper part of the section (Layers 3–6) correspond with the vegetation cover outside the cave than the spectra in the lower part of the section. The composition of the pollen spectra in the lower layers was more affected by the chemical transformation that corresponds with the changing Ca/Mg weathering index, as well as by the other proxies discussed above. Despite these complications, such data are still useful for interpretations of palaeovegetation communities (Carrión et al., 1999).

Herbs grew in the vicinity of the cave throughout MIS 3, and are thus not indicative of specific climatic episodes. Members of the *Helianthemum* genus were observed in the midsection of the profile (Layers 5 and 6). These plants, as well as other heliophytes such as *Thalictrum* are characteristic genera in this area for the MIS 3 period (Doláková, 2000, 2002). There was a marked decrease of Asteraceae compared with the underlying layers.

Post-depositional alterations to primary sediments have been identified in the thin sections, but in spite of this we are able to divide the section into three relatively warm and humid events—Layer 1, Layers 5 and 6, Layers 10 and 11. Layers 3 and 4 and Layers 8 and 9 display micromorphological evidence of repeated freezing, or very cold events. The presence of bare, fractured limestone blocks making up Layer 7 are also consistent with a cold event. The upper part of Layer 3, as well as Layers 5 and 6, and Layers 10 and 11 display evidence of a warmer and more humid climate. Layers 5 and 6 show increased P values, spongy microstructure, and greater concentrations of TOC, N, and Fe. These values are consistent with increased biological activity which may indicate a warmer climate in a glacial landscape (see e.g. Braillard et al., 2004). This is also the case for Layers 10 and 11.

The percentage of tree palynomorphs in Layer 10 is very small (as in all other samples), but a large amount of charcoal was recovered from this layer. This can be explained by humans bringing wood into the cave and using it as fuel for fire. Although the prevailing biome outside the cave was a steppe, the range of palynomorphs indicates that the landscape was likely to have been a shifting mosaic of different vegetation communities. Woodlands and/or pockets of trees were relatively common in geomorphologically favourable locations.

This hypothetical landscape can be compared to a (contemporary) potentially analogous landscape in southern Siberia (see e.g. Chytrý et al., 2008; Chytrý et al., 2010; Horsák et al., 2010a, b), where areas of low precipitation have patches of larch and pine forests on the wetter northern slopes. It is possible that the microclimatic conditions of the northern flanks of the Pustý Žleb canyon supported small patches of larch taiga woodland and this may have been utilized by hominids who made a fire in Pod Hradem Cave 48,000 to 45,000 years ago. The jagged landscape of the Moravian Karst may have reduced aeolian transport of anemophilous plant (*Pinus*, *Betula*) so the proportions of these species could be under-represented.

The bone remains of small mammals all exhibit characteristics of taphocenoses probably originating from pellets of the Snowy Owl (*Nyctea scandiaca*), a species known to nest on the ground of cave entrances (Andrews, 1990). In the samples that we collected, small mammals are under-represented in the lower layers, but we obtained sufficient samples in Layers 3, 4, and 5 to make statements about the general palaeoenvironmental context of the site. The presence of *Microtus (Chionomys) nivalis* and other species that typically live in steppe vegetation (i.e., *Ochotona pusilla, Allactaga cf. major, Cricetulus migratorius*)

suggest that the immediate environment of the cave was dominated by debris fields rich in diversified herb vegetation. An active stream and marshy or riparian habitat was also present in the catchment area as indicated by the presence of Clethrionomys glareolus and Plecotus auritus (this is also the case for Layer 11). In comparison to LGM or early MIS 3 communities, the Pod Hradem assemblages exhibit a considerable species richness with the presence of taxa such as Allactaga sp. which are known to have colonized Central Europe only during a short period around 40–30 ka BP (Nadachowski et al., 2009). The appearance of species such as Clethrionomys and Cricetulus migratiorius (or Phodopus sp.) in Layer 11 could indicate milder conditions (cf. van Kolfschoten, 2014), and contrasts with the absence of any remains of Microtus and Dicrostonyx, the taxa forming the bulk of the glacial communities. The presence of Sorex araneus and Clethrionomys glareolus suggests continuous local survival of these species during MIS 3 in the Moravian Karst. It also supports the idea that the Moravian Karst, with its varied relief and permanent water supply, acted as a local glacial refugium similar, for example, to the valleys in the Lesser Carpathians—e.g. Dzeravá Skala cave (Horáček, 2005)—approximately 100 km southeast of Pod Hradem Cave.

A large amount of charcoal of *Larix/Picea* and *Pinus cembra* was recovered from Layer 10. These taxonomic groups suggest that woodland vegetation was present around the cave. Palynomorphs of these species were not detected in this layer, so we suggest they originate from wood that was transported into the cave by hominins. Wood transported for fuel is usually collected within the site catchment area (no more than 2 hours walking distance) (Hansen 2001). In addition to the large amount of charcoal, other evidence for human contribution includes the presence of burnt bones, manuports, and two artefacts, including a spongolite chert leaf-shaped point (see Nejman et al., 2017). A large, cracked-

open, mineralized nutshell of *P. cembra* was also found in Layer 10. It is very likely that it was cracked open by humans, although the actions of the Spotted Nutcracker (*Nucifraga caryocatactes*) cannot be excluded. Pine kernel remains have been used to argue for the consumption of roasted pine nuts by Neanderthals at Gorham's and Vanguard caves in Gibraltar, and Amud Cave in Israel (Barton, 2000; Madella et al., 2002). A similar argument has also been presented by Jennings et al. (2009) for Higueral de Valleja Cave in southern Spain. We propose that this is also a likely explanation for the Pod Hradem Cave remains although as we have no skeletal hominid remains, we do not know with certainty exactly which type of hominid frequented Pod Hradem during the deposition of Layer 10, 48,000 to 45,000 years ago.

Although the archaeological signatures are not strong in the sediments we recovered in this part of Pod Hradem Cave, the picture so far reveals that climatic periods may not have played a strong role in human movements through this area, as has already been argued for other parts of Central Europe (e.g. Moreau et al., 2015; Nigst et al., 2014).

6. Conclusions

In response to our research questions, the stratigraphic section can be divided into three main phases, based on the presence/absence of microstructures, indicating freeze-thaw action. Layers 11 and 10 represent a relatively humid and warmer phase that may have been deposited during GIS 12. Following this phase, Layers 7, 8, and (partly) 9, all possessing a granular microstructure, were deposited during a cold and arid climatic environment chronologically corresponding to H4. The presence of a spongy microstructure in Layers 6 and 5 again reflects a relatively more humid, warmer event (probably GIS 8). Another cold

event (probably H2) is documented in Layers 3 and 4. The multidisciplinary palaeoenvironmental analyses consisting of pollen, microfauna, and charcoal suggests that the environment in Layers 6 to 11 was dominated by a steppe-like landscape with the presence of a water body/swamp nearby, and pockets of trees. The microfauna and pollen data suggest a range of habitat types near the cave with a rich mosaic of vegetation communities ranging from limestone rocky steppe with a diverse herbaceous component and open scree slopes to patches of forest with swamp vegetation in the canyons and valleys. Based on our results, the Moravian Karst may have acted as a refugium during the MIS 3 period, where specialized glacial landscape species were able to survive. The archaeological evidence from Pod Hradem Cave is consistent with the Kulturpumpe and Danube Corridor models (Nejman et al., 2017). The fact that this site was occasionally visited by humans throughout the late Middle and Upper Palaeolithic periods has the potential to contribute to the debates surrounding Neanderthal/AMH coexistence.

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References

Allen, J.R.M., Brandt, U., Brauer, A., Hubberten, H.-W., Huntley, B., Keller, J., Kraml, M., Mackensen, A., Mingram, J., Negendank, J.F.W., Nowaczyk, N.R., Oberhänsli, H., Watts, W.A., Wulf, S., Zolitschka, B., 1999. Rapid environmental changes in Southern Europe during the last glacial period. Nature 400, 740–743.

Andrews P., 1990. Owls, cave and fossils: Predation, preservation and accumulation of small mammal bones in cave, with an analysis of the Pleistocene faunas from Westbury-sub-Mendip, Somerset, UK. The University of Chicago Press, London.

Andrews, P., Cook, J., Currant, A., Stringer, C., 1999. Westbury Cave. The Natural History Museum Excavations 1976–1984. Published for Cherub, the Centre for Human Evolutionary Research, University of Bristol, by the Western Academic & Specialist Press, Bristol.

Antoine, P., Rousseau, D.D., Degeai, J.P., Moine, O., Lagroix, F., Kreutzer, S., Fuchs, M., Hatté, C., Gauthier, C., Svoboda, J., Lisá, L., 2013. High-resolution record of the environmental response to climatic variations during the Last Interglacial–Glacial cycle in Central Europe: The loess-palaeosol sequence of Dolní Věstonice (Czech Republic). Quat. Sci. Rev. 67, 17–38.

Audy, I., 1997. Atlas jeskyní Moravského krasu díl I., Muzeum Blansko, Blansko.

Bajer, A., Otava, J., Vít, J., Lisá, L., 2013. Nález reliktu miocenních sedimentů v jeskyni Pod hradem, Moravský kras. Zprávy Vlastivědného muzea v Olomouci 305, 120–126.

Barbieri, A., Leven, C., Toffolo, M.B., Hodgins, G.W.L., Kind, C.J., Conard, N.J., Miller C.E., 2017. Bridging prehistoric caves with buried landscapes in the Swabian Jura (southwestern Germany). Quaternary International

http://dx.doi.org/10.1016/j.quaint.2017.08.002

Barron, J.A., Heusser, L., Herbert, T., Lyle, M., 2003. High-resolution climatic evolution of coastal Northern California during the past 16,000 Years. Paleoceanography 18, 1020, doi: 10.1029/2002 PA000768, 1.

Barton, R.N.E., 2000. Mousterian hearths and shellfish: late Neanderthal activities in Gibraltar. In: Stringer, C.B., Barton, R.N.E., Finlayson, J.C. (Eds.), Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar. Oxbow Books, Oxford, pp. 211–220.

Beug, H.J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, München.

Biran, A., Abbot, J., Mace, R., 2004. Families and firewood: a comparative analysis of the costs and benefits of children in firewood collection and use in two rural communities in Sub-Saharan Africa. Hum. Ecol. 32, 1–25.

Blades, B.S., 1999. Aurignacian lithic economy and Early Modern Human mobility: New perspectives from classic sites in the Vézère Valley of France. J. Hum. Evol. 37, 91–120.

Blockley, S.P.E., Lane, C.S., Hardiman, M., Rasmussen, S.O., Seierstad, I.K., Steffensen, N.J.P., Svensson, A., Lotter, A.F., Turney, C.S.M., Bronk Ramsey, C., 2012. Synchronisation of palaeoenvironmental records over the last 60,000 years, and an extended INTIMATE event stratigraphy to 48,000 b2k. Quat. Sci. Rev. 36, 2–10.

Bolus, M., 2003. The cultural context of the Aurignacian of the Swabian Jura. In: Zilhão, J., D'Errico, F. (Eds.), The chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, stratigraphies, cultural implications: Proceedings of Symposium 6.1 of the XIVth Congress of the UISPP, (University of Liège, Belgium, September 2–8, 2001). Trabalhos de arqueologia 33, 153–164.

Bradtmöller, M., Pastoors, A., Weninger, B., Weniger, G.-C., 2012. The repeated replacement model—rapid climate change and population dynamics in Upper Pleistocene Europe. Quat. Int. 247, 38–49.

Braillard, L., Guélat, M., Rentzel, P., 2004. Effects of Bear on Rockshelter Sediments at Tanay Sur-les-Creux, Southwestern Switzerland. Geoarchaeology: An International Journal 19, 343 – 367.

Brandl, M., Hauzenberger, C., Postl, W., Modl, D., Kurta, C., Trnka, G., 2011. Repolust Cave (Austria) revisited: Provenance studies of the chert finds. Quartar, 58, 51–65.

Brown, G., 1993. The great bear almanac. Lyons & Burford, New York.

Bullock, P., Murphy, C.P. (Eds.), 1983. Soil micromorphology. A.B. Academic Publishers, Berkhamsted.

Carrión, J.S., Munuera, M., Navarro, C., Burjachs, F., Dupré, M., Walker, M.J., 1999. The palaeoecological potential of pollen records in caves: the case of Mediterranean Spain. Quat. Sci. Rev. 18, 1061–1073.

Chmielewski W. 1962. Archaeological investigations in the Nietoperzowa Cave in the period 1956–1959. Archaeologia Polona IV, 54–63.

Chytrý M., Danihelka, J., Horsák, M., Kočí, M., Kubešová, S., Lososová, Z., Otýpková, Z., Tichý, L., Martynenko, V.B., Baisheva, E.Z., 2010. Modern analogues from the Southern Urals provide insights into biodiversity change in the early Holocene forests of Central Europe. J. Biogeogr. 37, 767–780.

Chytrý, M., Danihelka, J., Kubešová, S., Lustyk, P., Ermakov, N., Hájek, M., Hájková, P., Kočí, M., Otýpková, Z., Roleček, J., Řezníčková, M., Šmarda, P., Valachovič, M., Popov, D.,

Pišút I., 2008. Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia. Plant Ecol. 196, 61–83.

Clement, A.C., Peterson, L.C., 2008. Mechanisms of abrupt climate change of the last glacial period. Rev. Geophys. 46, 1–39.

Conard, N.J., Bolus, M., 2003. Radiocarbon dating the appearance of modern humans and timing of cultural innovations in Europe: new results and new challenges. Journal of Human Evolution 44, 331-371.

Conard, N.J., Bolus, M., 2008. Radiocarbon dating the late Middle Paleolithic and the Aurignacian of the Swabian Jura. Journal of Human Evolution 55, 886-897.

Courty, M.A., Vallverdu, J., 2001. The microstratigraphic record of abrupt climate changes in cave sediments of the Western Mediterranean. Geoarchaeology 16, 467–500.

Crampton, C.B. 1977. A study of the dynamics of hummocky microrelief in the Canadian north. Canadian Journal of Earth Sciences. 14(4): 639-649, 10.1139/e77-064.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjornsdottir, A.E., Jouzel, J., 1993. Evidence for general instability of past climate from a 250-ka ice-core record. Nature 364, 218–220.

Davies, W., Gollop, P., 2003. The human presence in Europe during the Last Glacial Period II: Climate tolerance and climate preferences of Mid- and Late Glacial hominids. In: van Andel, T.H., Davies, W. (Eds.), Neanderthals and modern humans in the European landscape during the last glaciation: archaeological results of the Stage 3 Project. McDonald Institute for Archaeological Research monographs, Cambridge, pp. 131–146.

Dearing, J.A., Dann, R.J.L., Hay, K., Lees, J.A., Loveland, P.J., Maher, B.A, O'Grady, K.,

1996. Frequency-dependent susceptibility measurements of environmental materials. Geophys. J. Int. 124, 228–240.

Doláková, N., 2000. Palynologické zhodnocení sedimentů z Ochozské jeskyně. Část 2.-Profil u Zkamenělé řeky. Geol.výzk. Mor. Slez. v. r. 1999, 5–9.

Doláková, N., 2002. Palynologické studium sedimentů Šošůvské části Sloupsko – Šošůvských jeskyní a spodní části opěrného profilu v jeskyni Kůlna. Acta Mus. Moraviae, Sci. Geol., 87, 275–288.

Doláková, N., 2007. Palynological studies in the cave sediments from the Moravian, Javoříčko and Hranice Karsts—Czech Republic. Scripta Fac. Sci. Natur. Universitatis Masarykianae Brun. Geol. 35, 47–53.

Doláková, N., 2010. Palynologické výsledky studia sedimentů jeskyně Balcarka. In: Nerudová Z. (ed) Jeskyně Balcarka v Moravském krasu. Moravské zemské muzeum Brno, Anthropos, 31(3), 51-54.

Doláková, N., Nehyba, S., 1999. Sedimentologické a palynologické zhodnocení sedimentů z Ochozské jeskyně. Geol. výzk. Mor. Slez. v. r. 1998, 7–10.

Dvořák, J., 1965. Die Geologie der Umgebung der Höhle Pod hradem. In: Die Erforschung der Höhle Pod hradem 1956–1958, Anthropos 18 (N.S. 10), Moravske zemské muzeum, Brno, pp. 133–137.

Egli, M., Merkli C., Sartori, G., Mirabella, A., Plötze, M., 2008. Weathering, mineralogical evolution and soil organic matter along a Holocene soil toposequence developer on carbonate-rich materials. Geomorphology 97, 675 – 696.

El Zaatari, S., Grine, F.E., Ungar, P.S., Hublin, J.-J., 2016. Neandertal versus modern human

dietary responses to climatic fluctuations. PloS One 11, e0153277.

Ellwood, B.B., Harrold, F.B., Benoist, S.L., Straus, L.G., Morales, M.G., Petruso, K., Bicho, N.F., Zilhão, J., Soler, N., 2001. Paleoclimate and intersite correlations from Late Pleistocene/Holocene cave sites: results from Southern Europe. Geoarchaeology 16, 433–463.

Evans, M.E., Heller, F., 2002. Environmental magnetism: Principles and applications of enviromagnetics. Academic Press, Amsterdam.

Feurdean, A., Perşoiu, A., Tanţău, I., Stevens, T., Magyari, E. K., Onac, B. P., Marković, S., Andrič, M., Connor, S., Fărcaş, S., Gałka, M., Gaudeny, T., Hoek, W., Kolaczek, P., Kuneš, P., Lamentowicz, M., Marinova, E., Michczyńska, D.J., Perşoiu, I., Płóciennik, M., Słowiński, M., Stancikaite, M., Sumegi, P., Svensson, A., Tămaş, T., Timar, A., Tonkov, S., Toth, M., Veski, S., Willis K.J., Zernitskaya, V., 2014. Climate variability and associated vegetation response throughout Central and Eastern Europe (CEE) between 60 and 8 ka. Quat. Sci. Rev. 106, 206–224.

Finlayson, J.C., Giles Pacheco, F., Rodríguez-Vidal, J., Fa, D., Gutierrez Lopez, J.-M., Santiago Perez, A., Finlayson, G., Allue, E., Baena Preysler, J., Caceres, I., Carrion, J., Fernandez Jalvo, Y., Gleed-Owen, C., Jimenez Espejo, F., Lopez, P., Lopez Saez, J.-A., Riquelme Cantal, J.-A., Sanchez Marco, A., Giles Guzman, F., Brown, K., Fuentes, N., Valarino, C., Villalpando, A., Stringer, C.B., Martinez Ruiz, F., Sakamoto, T., 2006. Late survival of Neanderthals at the southernmost extreme of Europe. Nature 443, 850–853.

Flint, A., Flint, L.E., 2002. Particle density. In: Dane, J.H., Topp, G.C (Eds.), Methods of soil analysis, Part 4 Physical methods. Soil Science Society of America, Madison, Wisconsin, pp. 229–240.

Fuchs, M., Kreutzer, S., Rousseau, D.D., Antoine, P., Hatté, C., Lagroix, F., Moine, O., Gauthier, C., Svoboda, J., Lisá, L., 2013. The loess sequence of Dolní Věstonice, Czech Republic: A new OSL-based chronology of the Last Climatic Cycle. Boreas. Roč. 42, 3, s. 664–677.

Gamble, C., 1999. The Palaeolithic societies of Europe. Cambridge University Press, Cambridge.

Gargett, R.H., 1996. Cave bears and modern human origins: The spatial taphonomy of Pod Hradem Cave, Czech Republic. University Press of America, Lanham, Maryland.

Goldberg, P., Holliday, V.T., Ferring, C.R., 2013. Earth sciences in archaeology. Springer, New York.

Goldberg, P., Macphail, R., 2006. Practical and theoretical georchaeology. Blackwell, London.

Goldberg, P., Schiegl, S., Melinge, K., Dayton C., Conard, N., 2003. Micromorphology and site formation at Hohle Fels Cave, Swabian Jura, Germany. Eiszeitalter und Gegenwart 53, 1–25.

Goldberg, P., Sherwood, S.C. 2006. Deciphering human prehistory through the geoarchaeological study of cave sediments. Evolutionary Anthropology, 15, 20 – 36. DOI: 10.1002/evan.20094

Goudie, A.S., Viles H., 2008. Weathering Processes and Forms. In: Burt T.P., Chorley R.J., Brunsden D., Cox N.J., Goudie A.S. (Eds.), Quaternary and recent processes and forms (History of the Study of Landforms or the Development of Gemorphology Vol. 4.). Geological Society, London, pp. 129–164.

Guiot, J., 1990. Methodology of the last climatic cycle reconstruction in France from pollen data. Palaeogeography, Palaeoclimatology, Palaeoecology 80, 49-69.

Haesaerts, P., Borziak, I., Chirica, V., Damblon, F., Koulakovska, L., van der Plicht, J., 2003. The East Carpathian loess record: a reference for the Middle and late Pleniglacial stratigraphy in Central Europe. Quaternaire 14, 163–188.

Heinrich, H., 1988. Origin and consequences of cyclic ice rafting in the Northeast Atlantic Ocean during the past 130,000 years. Quat. Res. 29, 142–152.

Heiss, A.G., 2000. Anatomy of European and North American Woods—An Interactive Identification Key. DOI: 10.13140/RG.2.1.3000.7764

Henry, A., Théry-Parisot, I., 2014. From Evenk campfires to prehistoric hearths: Charcoal analysis as a tool for identifying the use of rotten wood as fuel. J. Archaeol. Sci. 52, 321–336.

Hoffecker, J.F., 2009. The spread of modern humans in Europe. Proceedings of the National Academy of Sciences 106, 16040–16045.

Holliday, T.V., Garther, W.G., 2007. Methods of soil P analysis in archaeology. Journal of Archaeological Science 34, 301 – 333.

Horáček, I., 2005. Small vertebrates in the Weichselian series in Dzeravá skala cave: list of the samples and a brief summary. In: Kaminska L., Kozlowski J.K., Svoboda J.A. (Eds.), Pleistocene environments and archaeology of the Dzeravá skala Cave, Lesser Carpathians, Slovakia. PAN, Krakow, pp. 157–167.

Horáček I., Ložek V., 1988. Palaeozoology and the Mid-European Quaternary past: scope of the approach and selected results. Rozpravy ČSAV, ř. MPV, 98(4), 1–106.

Horáček, I., Sánchez-Marco, A., 1984. Comments on the Weichselian small mammal

assemblages in Czechoslovakia and their stratigraphical interpretation. N. Jb. Geol. Paläont. Mh. 1984, 560–576.

Horsák, M., Chytrý, M., Danihelka, J., Kočí, M., Kubešová, S., Lososová, Z., Otýpková, Z., Tichý L., 2010a. Snail faunas in the Southern Ural forests and their relations to vegetation: an analogue of the Early Holocene assemblages of Central Europe? Journal of Molluscan Studies, 76, 1–10.

Horsák, M., Chytrý, M., Pokryszko, B.M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kintrová, K., Kočí, M., Kubešová, S., Lustyk, P., Otýpková, Z., Pelánková, B. Valachovič, M., 2010b. Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. Journal of Biogeography, 37, 1450–1462.

Hublin, J.-J., 2015. The modern human colonization of western Eurasia: when and where? Quaternary Science Reviews 118, 194-210.

Jankovská, V., 2006. Vegetation and landscape of W Carpathians (Slovakia, E Moravia) in the second half of Last Glacial period. Scr. Fac. Sci. Natur. Univ. Masarykianae Brun. Geol. 33–34, 41–43.

Jankovská, V., Pokorný, P., 2008. Forest vegetation on the last full-glacial period in the Western Carpathians (Slovakia and Czech Republic). Preslia 80, 307–324.

Jennings, R.P., Giles Pacheco, F., Barton, R.N.E., Collcutt, S.N., Gale, R., Gleed-Owen, C.P., Gutierrez Lopez, J.M., Higham, T.G.G., Parker, A., Price, C., Rhodes, E., Santiago Pérez, A., Schwenninger, J.L., Turneret, E., 2009. New dates and palaeoenvironmental evidence for the Middle to Upper Palaeolithic occupation of Higueral de Valleja Cave, southern Spain. Quat. Sci. Rev. 28, 830–839.

Jiménez-Espejo, F.J., Martínez-Ruiz, F., Finlayson, C., Paytan, A., Sakamoto, T., Ortega-Huertas, M., Finlayson, G., Iijima, K., Gallego-Torres, D., Fa, D., 2007. Climate forcing and Neanderthal extinction in Southern Iberia: insights from a multiproxy marine record. Quat. Sci. Rev. 26, 836-852.

Jordanova N., 2016. Soil Magnetism: Applications in Pedology, Environmental Science and Agriculture. Academic Press.

Kalis, A.J, Merkt, J., Wunderlich, J., 2003. Environmental changes during the Holocene climatic optimum in central Europe—Human impact and natural causes. Quat. Sci. Rev. 22, 33–79.

Kaminská, L., Kozlowski, J.K., Svoboda J., 2004. The 2002–2003 Excavations in the Dzeravá Skala Cave, West Slovakia. Anthropologie 42/3, 311–322.

Kaminská, L., Kozlowski, J.K., Svoboda, J., 2005. Pleistocene environments and archaeology of the Dzeravá skala Cave, Lesser Carpathians, Slovakia. Polish Academy of Arts and Sciences, Kraków, p. 226.

Karkanas, P., Goldberg, P., 2010. Phosphatic features. In: Stoops, G., Marcelino, V., Mees, F. (Eds.), Interpretation of micromorphological features of soils and regoliths. Elsevier, Amsterdam, pp. 521–541.

Karkanas, P., Goldberg, P., 2013. Micromorphology of cave sediments. In: Shroder, J. F., Frumkin, A. (Eds.), Treatise on geomorphology, Vol. 6, Karst geomorphology. Academic Press, San Diego, 286–297.

Karkanas, P., Kyparissi-Apostolika, N., 1999. Mineral assemblages in Theopetra, Greece: A framework for understanding diagenesis in a prehistoric cave. J. Archaeol. Sci. 26, 1171–1180.

Knies, J., 1901. Čtvrtohorní zvířena jeskyně pod hradem u Suchdola na Moravě. Časopis vlastivědného musejního spolku v Olomouci, 18, 5–12, 50–56.

Komárek, J., Jankovská, V., 2001. Review of the green algal genus *Pediastrum*. Implication for pollen analytical research. Gebrüder Borntraeger, Berlin.

Krajcarz, M.T., Bosák, P., Slechta, S., Pruner, P., Komar, M., Dresler, J., Madeyska, T., 2014. Sediments of Bisnik Cave (Poland). Lithology and stratigraphy of the Middle Palaeolithic site. Quat. Int. 326–327, 6–19.

Kukla, J., 1969. Beschreibung der wichtigsten Aufschlüsse. In: Demek, J., Kukla, J.

(Eds.), Periglazialzone, Löss und Paläolithikum der Tschechoslowakei. Geografický ústav ČSAV, Brno, pp. 97-108. Abb. 133-141.

Lisá, L., Hosek, J., Bajer, A., Matys Grygar, T., Vandenberghe, D., 2014. Geoarchaeology of Upper Palaeolithic loess sites located within a transect through Moravian valleys, Czech Republic. Quat. Int. 351, 25–37.

Lisá L., Neruda P., Nerudová Z., Nejman L., 2018. Podhradem Interstadial: A critical review of the middle and late MIS 3 (Denekamp, Hengelo) in Moravia, Czech Republic. Quaternary Science Reviews 182, 191 – 201.

Lisá, L., Škrdla, P., Havlín Nováková, D., Bajer, A., Čejchan, P., Nývltová Fišáková, M., Lisý, P., 2013. The role of abiotic factors in ecological strategies of Gravettian huntergatherers within Moravia, Czech Republic. Quat. Int. 294, 71–81.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. Paleoceanography 20(1), PA1003, doi: 10.1029/2004PA001071

Madella, M., Jones, M.K., Goldberg, P., Goren, Y., Hovers, E., 2002. The exploitation of plant resources by Neanderthals in Amud Cave (Israel): the evidence from phytolith studies.

J. Archaeol. Sci. 29, 703–719.

Moreau, L., Odar, B., Higham, T., Horvat, A., Pirkmajer, D., Turk, P., 2015. Reassessing the Aurignacian of Slovenia: Techno-economic behaviour and direct dating of osseous projectile points. J. Hum. Evol. 78, 158–180.

Moseley, G.E., Spötl, C., Svensson, A., Cheng, H., Brandstätter, S., Edwards, R.L., 2014. Multi-speleothem record reveals tightly coupled climate between central Europe and Greenland during Marine Isotope Stage 3. Geology, doi:10.1130/G36063.1

Musil, R., Valoch, K., 1966. Beitrag zur Gliederung des Würms im Mitteleuropa. Eiszeitalter und Gegenwart 17, 131–38.

Nadachowski, A., 1982. Late Quaternary Rodents of Poland with Special Reference to Morphotype Dentition Analysis of Voles. Państwowe Wydawnictwo Naukowe, Warszawa-Kraków.

Nadachowski, A. Zarski, M., Urbanowski, M., Wojtal, P., Miekina, B., Lipecki, G., Ochman, K., Krawczyk, M., Jakubowski, G., Tomek, T., 2009. Late Pleistocene environment of the Czestochowa Upland (Poland) reconstructed on the basis of faunistic evidence from archaeological cave sites. Polish Academy of Sciences, Institute of Systematic and Experimental Zoology, Krakow.

Navarro, C., Carrión, J.S., Munuera, M., Prieto A.R., 2001. Cave surface and the palynological potential of karstic cave sediments in palaecology. Rev. Paleobot. Palynol. 117, 245–265.

Nejman, L., Wood, R., Wright, D., Lisá, L., Nerudová, Z., Neruda, P., Přichystal, A., Svoboda, J., 2017. Hominid visitation of the Moravian Karst during the Middle-Upper

Palaeolithic transition: New results from Pod Hradem Cave (Czech Republic). J. Hum. Evol. 108, 131-146.

Nejman, L., Wright, D., Lisá, L., Doláková, N., Horáček, I., Novák, J., Wood, R., Pacher, M., Sázelová, S., Holub, M., Přichystal, A., Nývltová Fišáková, M., Bajer, A., 2013. Hominids and palaeoenvironments in the Moravian Karst during Marine Isotope Stage 3: new excavations in Pod Hradem Cave, Czech Republic. Antiquity 087, 337, http://antiquity.ac.uk/projgall/nejman337/.

Neruda, P., Nerudová, Z., 2011. The Middle–Upper Palaeolithic transition in Moravia in the context of the Middle Danube region. Quat. Int. 294, 3–19.

Neruda, P., Nerudová, Z., 2013. The Middle-Upper Palaeolithic transition in Moravia in the context of the Middle Danube region. Quatern. Intl. 294, 3–19.

Nerudová, Z., Doláková, N., Novák, J. 2016. New information augmenting the picture of local environment at the LGM/LGT in the context of the Middle Danube region. The Holocene, 26: 1345 – 1354.

Nerudová, Z., Přichystal, A., Neruda, P., 2012b. Revize nálezů z jeskyně Pod hradem v Moravském krasu. Archeologické Rozhledy 64, 136–152.

Nigst, P.R., Haesaerts, P., Damblon, F., Frank-Fellner, C., Mallol C., Viola, B., Götzinger, M., Niven, L., Trnka, G., Hublin, J.J., 2014. Early modern human settlement of Europe north of the Alps occurred 43,500 years ago in a cold steppe-type environment. Proc. Nat. Acad. Sci. U.S. 111, 14394–14399.

Oliva, M., 2005. Palaeolithic and Mesolithic Moravia. Moravské zemské muzeu, Brno.

Pacher, M., Stuart, A. J., 2009. Extinction chronology and paleoecology of the cave bear

Ursus spelaeus. Boreas 38(2), 189-206.

Pearson A.M., 1975. The northern interior grizzly bear, *Ursus arctos* L. Canadian Wildlife Service Report Series, 34, Ottawa, pp. 1–84.

Pettitt, P., White, M., 2012. The British Palaeolithic: Human societies at the edge of the Pleistocene world. Routledge, Abingdon.

Pirson, S., Flas, D., Abrams, G., Bonjean, D., Court-Picon, M., Di Modica, K., Draily, Ch., Damlon, F., Haesaerts, P., Miller, R., Rougier, H., Toussaint, M., Semal, P., 2012. Chronostratigraphic context of the Middle to Upper Palaeolithic transition: Recent data from Belgium. Quaternary International 259, 78 – 94.

Potts, R., 1998. Variability selection in hominid evolution. Evolutionary Anthropology: Issues, News and Reviews 7, 81-96.

Reille, M., 1995. Pollen et spores d'Europe et d'Afrique du nord. Laboratoire de Botanique Historique de Palynologie, Marseille.

Richter, D., Tostevin, G., Škrdla, P., 2008. Thermoluminescence dating of the type

locality of the Bohunician (Brno-Bohunice, Czech Republic). Journal of Human

Evolution 55, 871-885.

Rogers, L., 1981. A bear in its lair. Natural History 90(10), 64-70.

Rosendahl, W., Ambros, D., Hilpert, B., Hambach, U., Alt, K.W., Knipping, M., Reisch, L., Kaulich, B. 2011: Neanderthals and monkeys in the Würmian of Central Europe – The Middle Palaeolithic site of Hunas, Southern Germany.- In: Conard, N.J. and Richter, J. (eds.), Neanderthal Lifeways, Subsistence and Technology – One Hundred Fifty Years of Neanderthal Study.- Vertebrate Paleobiology and Paleoanthropology, Volume 19, Part 4, 15 –

23, DOI: 10.1007/978-94-007-0415-2-3.

Rougier, H., Milota, S., Rodrigo, R., Gherase, M., Sarcină, L., Moldovan, O., Zilhão, J., Constantin, S., Franciscus, R.G., Zollikofer, C.P.E., Ponce de León, M., Trinkaus, E., 2007. Peștera cu Oase 2 and the cranial morphology of early modern Europeans. Proc. Nat. Acad. Sci. U.S. 104, 1165–1170.

Rybníčková, E., Rybníček, K., 2014. Palaeovegetation in the Pavlovské vrchy hills region (South Moravia, Czech Republic) around 25,000 BP: the Bulhary core. Veget. Hist. Archeobot. 23, 719–728.

Sánchez-Gońi, M.F., Cacho, I., Turon, J.-L., Guiot, J., Sierro, F.J., Peypouquet, J.-P., Grimalt, J.O., Shackleton, N.J., 2002. Synchroneity between marine and terrestrial responses to millennial scale climatic variability during the last glacial period in the Mediterranean region. Clim. Dynam. 19, 95–105.

Schiegl, S., Goldberg, P., Conard, N.J., 2003. Palaeolithic burnt bone horizons from the Swabian Jura—Distinguishing between in-situ fireplaces and dumping areas.-Geoarchaeology 18, 541–565.

Schweingruber, F.H., 1990. Anatomie europäscher Hölzer. Paul Haupt, Bern.

Seitl, L., Svoboda, J., Ložek, V., Přichystal, A., Svobodová, H., 1986. Das Spätglazial in der Barová-Höhleim Mährischen Karst. Archäologisches Korrespondenzblatt 16, 393–398.

Sima, A., Kageyama, M., Rousseau, D.D, Ramstein, G., Balkanski, Y., Antoine, P., Hatté, C., 2013. Modeling dust emission response to North Atlantic millennial-scale climate variations from the perspective of East European MIS 3 loess deposits. Clim. Past. 9, 1385–1402.

Sirocko, F., Knapp, H., Dreher, F., Förster, M.W., Albert, J., Brunck, H., Veres, D., Dietrich, S., Zech, M., Hambach, U., Röhner, M., Rudert, S., Schwibus, K., Adams, C., Sigr, P. (2016): The ELSA-Vegetation-Stack: Reconstruction of Landscape Evolution Zones (LEZ) from laminated Eifel maar sediments of the last 60,000 years.- Global and Planetary Change 142, 108 – 135.

Sroubek, P., Diehl, J.F., Kadlec, J., Valoch, K., 2001. A Late Pleistocene palaeoclimate record based on mineral magnetic properties of the entrance facies sediments of Kulna Cave, Czech Republic. Geophys. J. Int. 147, 247–262.

Stewart, J.R., van Kolfschoten, T., Markova, A., Musil, R., 2003. The mammalian faunas of Europe during Oxygen Isotope Stage Three. In: van Andel, T.H., Davies, W. (Eds.), Neanderthals and modern humans in the European landscape during the last glaciation: archaeological results of the Stage 3 Project. McDonald Institute Monographs. University of Cambridge, Cambridge, pp. 103–130.

Stoops, G., Marcelino, V., Mees, F., 2010. Interpretation of micromorphological features of soils and regoliths. Elsevier, Amsterdam.

Stoops G., 2003. Guidelines for analyses and descriptions of soil and regolith thin sections. Science Society of America, Madison.

Stringer, C., Pälike, H., van Andel, T.H., Huntley, B., Valdes, P., Allen, J.R.M., 2003. Climatic stress and the extinction of the Neanderthals. In: van Andel, T.H., Davies, W.D. (Eds.), Neanderthals and modern Humans in the European landscape of the last glaciation: Archaeological results of the Stage 3 Project. The McDonald Institute for Archaeological Research, Cambridge.

Svoboda, J.A., 2009. Čas lovců: Aktualizované dějiny paleolitu. Akademické nakladatelství CERM, Brno.

Svoboda, J.A., Havlíček, P., Ložek, V., Macoun, J., Musil, R., Přichystal, A., Svobodová, H., Vlček, E., 2002. Paleolit Moravy a Slezska. Archeologický ústav AVČR, Brno.

Svoboda, J., Králík, M., Čulíková, V., Hladilová, Š., Novák, M., Nývltová Fišáková, M., Nývlt, D., Zelinková, M., 2009. Pavlov VI: An Upper Paleolithic living unit. Antiquity, 83, 282–295.

Svobodová, H. 1988. Pollenanalytische Untersuchung des Schichtkomplexes 6-1 vor der Kůlna-Höhle. In: Valoch K.: Die erforschung der Kůlna Höhle 1961–1976. Anthropos, 24, N.S. 16, S., Brno, pp. 205–210.

Teschler-Nicola, M. (Ed.), 2006. Early modern humans at the Moravian gate. The Mladeč caves and their remains. Springer Verlag, New York.

Trampler, R., 1898. Die Burghöhle im Punkwathale in Mähren. Deutsche Rundschau für Geographie und Statistik 20, 529–538.

Trinkaus, E., Constantin, S., Zilhão, J., 2013. Life and death at the Peştera cu Oase. A setting for modern human emergence in Europe. Oxford University Press, Oxford.

Trinkaus, E., Moldovan, O., Milota, S., Bîlgăr, A., Sarcina, L., Athreya, S., Bailey, S.E., Rodrigo, R., Mircea, G., Higham, T., Bronk Ramsey, C., van der Plicht, J., 2003. An early modern human from the Peştera cu Oase, Romania. Proc. Nat. Acad. Sci. U.S. 100, 11231–11236.

Türker, M.F., Kaygusuz, K., 1995. Socio-economic analysis of fuelwood use in a rural area of Turkey. Biores Technol. 54, 285–290.

Tzedakis, P.C., Hughen, K.A., Cacho, I., Harvati, K., 2007. Placing late Neanderthals in a climatic context. Nature 449, 206-208.

Valde-Nowak, P., Alex, B., Ginter, B., Krajcarz, M.T., Madeyska, T., Miekina, B., Sobczyk, K., Stefanski, D., Wojtal, P., Zajac, M., Zarzecka-Szubinska, K., 2014. Middle Paleolithic sequences of the Ciemna Cave (Prądnik valley, Poland): The problem of synchronization. Quat. Int. 326–327, 125–145.

Valoch K., 1960. K otázce předmagdalénského osídlení jeskyní Adlerovy a Křížovy na Říčkách u Brna. Acta Musei Moraviae, Scientiae sociales, 45, 5–20.

Valoch, K., 1965. Die altsteinzeitlichen Begehungen der Höhle Pod hradem. In: Die Erforschung der Höhle Pod hradem 1956–1958, Anthropos 18 (N.S. 10), Brno, 93-106.

Valoch, K., 1988. Die erforschung der Kůlna-Höhle 1961–1976. Anthropos, 24, N.S. 16, Brno

Valoch, K., 1996. Le Paléolithique en Tchéquie et en Slovaquie. Jérôme Millon, Grenoble.

van Andel, T.H., Davies, W., 2003. Neanderthals and modern humans in the European landscape during the last glaciation: Archaeological results of the Stage 3 Project. McDonald Institute Monographs. University of Cambridge, Cambridge.

van Kolfschoten, T., 2014. The smaller mammals from the Late Pleistocene sequence of the Sesselfelsgrotte (Neuessig, Lower Bavaria). In: Freund, G., Rensch L. (Eds.), Sesselfelssgrotte VI, Naturwissenschafliche Untersuchungen, Wirbeltierfauna I. Franz Steiner Verlag Gmbh, Wiesbaden, pp. 27–117.

van Vliet-Lanoë, B., 2010. Frost action. In: Stoops, G., Marcelino, V., Mees, F. (Eds.), Interpretation of micromorphological features of soils and regoliths. Elsevier, Amsterdam, pp.

81-108.

Vandenberghe, J., van der Plicht, J., 2016. The age of the Hengelo interstadial revisited. Quat. Geochronol. 32, 21–28.

Villa, P., Sánchez Goni, M.F., Bescós, G.C., Grün, R., Ajas, A., García Pimienta, J.C., Lees, W., 2010. The archaeology and palaeoenvironment of an Upper Pleistocene hyena den: Anintegratedapproach. J. Archaeol. Sci. 37, 919–935.

Vogel, J.C., Zagwijn, W.H., 1967. Groningen radiocarbon dates VI. Radiocarbon 9, 63–106.

Walanus, A., Nalepka, D. 1999. POLPAL—Program for counting pollen grains, diagrams plotting and numerical analysis. Acta Paleobotanica 2, 659–661.

Walker, M.J., López-Martínez, M., Carrión-García, J.S., Rodríguez-Estrella, T., San-Nicolás del-Toro, M., Schwenninger, J.L., López-Jiménez, A., Ortega-Rodrigáñez, J., Haber-Uriarte, M., Polo-Camacho, J.L., García-Torres, J., Campillo-Boj, M., Avilés-Fernández, A., Zack, W., 2013. Cueva Negra del Estrecho del Río Quípar (Murcia, Spain): A late Early Pleistocene hominin site with an "Acheulo-Levalloiso-Mousteroid" Palaeolithic assemblage. Quat. Int. 294, 135–159.

Wilson, M.A., Righi, D., 2010. Spodic materials. In: Stoops, G., Marcelino, V., Mees, F. (Eds.), Interpretation of micromorphological features of soils and regoliths. Elsevier, Amsterdam, pp. 251–273.

Woodward, J.C., Bailey, G.N., 2000. Sediment Sources and Terminal Pleistocene Geomorphological Processes Recorded in Rockshelter Sequences in North-west Greece. In. I.D.L. Foster. Traces in Geomorphology. 521 – 551, John Wiley & Sons Ltd.

Woodward, J.C., Goldberg, P. 2001. The Sedimentary Records in Mediterranean Rockshelters

and Caves: Archives of Environmental Change. Geoarchaeology: An International Journal 16, 327 – 354.

Woodward, J.C., Macklin, M.G., Lewin, J., 2000. Sediment sources and terminal Pleistocene geomorphological processes recorded in rockshelter sequences in Northwest Greece. In I.D.L. Foster (Ed.), Traces in geomorphology (521 – 551). Chichester, Willey.

Wright, D., Nejman, L., d'Errico, F., Králík, M., Wood, R., Ivanov, M., Hladilová, S., 2014. An Early Upper Palaeolithic decorated bone tubular rod from Pod Hradem Cave, Czech Republic. Antiquity 88, 30–46.

Zilhão, J., Ajas, A., Badal, E., Burow, C., Kehl, M., Lòpez-Sáez, J.A., Pimenta, C., Preece, R.C., Sanchis, A., Sanz, M., Weniger, G.-C., White, D., Wood, R., Angelucci, D.E., Villaverde, V., Zapata, J., 2016. Cueva Antón: A multi-proxy MIS 3 to MIS 5a palaeoenvironmental record for SE Iberia. Quat. Sci. Rev.146, 251–273.

Highlights

- Sediment microstructures reveal cold and warm periods between 28,000 50,000 cal yr BP
- Cave sediments accumulated mainly by colluviation from cave entrance and roof fall
- Humans visited the cave during both warm and cold periods
- Steppe-like landscape with a mosaic of vegetation communities throughout MIS3