

MIDDLE PLEISTOCENE STRATIGRAPHY OF THE DEPOSITS IN ZA HÁJOVNOU CAVE (JAVOŘÍČKO KARST, NORTHERN MORAVIA, CZECH REPUBLIC)

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Abstract. Za Hájovnou Cave (Javoříčko Karst, northern Moravia, Czech Republic) is a unique Middle Pleistocene locality. Paleontological material comes from different types of sediments in superposition of fluvial deposits of the sinkhole which was active until the maximum of the Cromerian Interglacial I, MIS 19 (B/M palaeomagnetic boundary, 781 ka). Stratigraphic interpretation was based mainly on $^{230}\text{Th}/\text{U}$ dating, sedimentology, study of mammal assemblages and palynology. Sediments were divided into 5 groups of layers on the basis of lithological content and character of bone preservation. The 2nd group of layers was the most important for the stratigraphy of the Middle Pleistocene deposits.

Three warm stages were documented by the study of sediments and their palaeontological content. We presuppose two stratigraphical alternatives. Alternative A: warm stage III corresponds most probably to MIS 9a, warm stage II could correspond to MIS 9c, warm stage I corresponds to MIS 11. Alternative B: warm stage III corresponds most probably to MIS 9a, warm stage II could correspond to MIS 9c, warm stage I corresponds to MIS 9e. The alternative A (warm stage I corresponds to MIS 11) is supported by the exclusive presence of evolutionary older forms of *P. fossilis*. If the alternative A is valid than very warm MIS 9e is absent. The alternative B (warm stage I corresponds to MIS 9e and all discussed warm stages agree with MIS 9) is supported by palynological record. The presence of *Pterocarya* is considered to be typical for Holsteinian with the last occurrences in Central Europe in MIS 9a. Against the alternative B speaks exclusive occurrence of evolutionary older lions in layers of the 2B group. Although both above mentioned alternatives are possible, the exclusive presence of evolutionary older group of lions in sediments of warm stage I support strongly alternative A. The youngest warm stage III does not exceed MIS 9a. Therefore, we consider all three warm stages in Za Hájovnou Cave as belonging to Holsteinian sensu lato.

■ Javoříčko Karst, Za Hájovnou Cave, Middle Pleistocene, lithology, palaeozoology, palynology, Holsteinian s.l.

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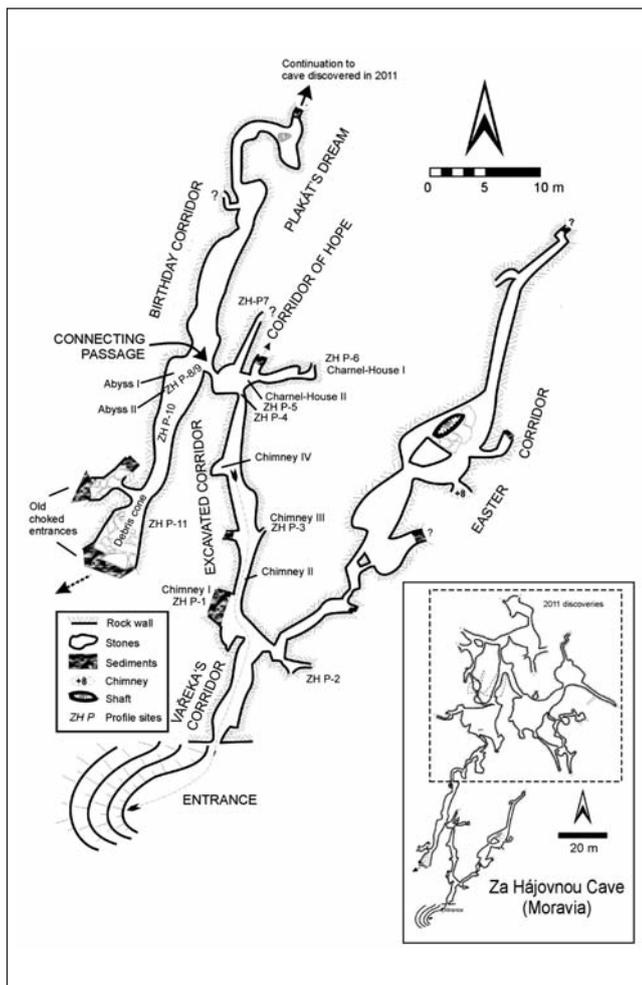
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Introduction

The Za Hájovnou Cave (49° 40' N, 16° 55' E) is situated in northern Moravia (Czech Republic) within the territory of Javoříčko Karst. The studied cave corridors, with total length of ~200 m, is a former sinkhole and has been active from the Early Pleistocene until the beginning of the Middle Pleistocene dated within the maximum of the Cromerian Interglacial I, MIS 19 (B/M palaeomagnetic boundary, 781 ka, ZH P-5, layer 4; Kadlec et al. 2005, 2014). Different types of non-fluvial silt with various content of debris are situated in superposition of fluvial deposits. They contain a large quantity of vertebrate fossils as well as abundant palynological finds. Palaeontological remains have been found only within non-fluvial cave deposits.

Two main sub-parallel and sub-horizontal corridors of slightly different sedimentological record can be distinguished in the cave – the Vykopaná chodba (= Excavated Corridor) (there was the sinkhole entrance) and the Narozeninová chodba (= Birthday Corridor) with separate entrance, but connected by the Spojovací chodba (= Connecting Passage). The Spojovací chodba was filled with sediments from the Vykopaná chodba, which continue to Narozeninová chodba. The cave sediments within studied sections correspond mostly to the Middle Pleistocene (Musil 2005a, 2014). A more detailed stratigraphy of cave deposits in Za Hájovnou Cave has never been discussed.

This contribution is a result of cooperation of many experts, R. Musil (the head of this project, cave research, description of individual sections, as well as their



Text-fig. 1. The plan of Za Hájojnou Cave, survey of Tomica, A. (Musil 2005a, supplemented).

lithostratigraphic setting), M. Sabol (lion remains), M. Ivanov (small mammals), N. Doláková (palynology). Although many papers of the different branches of the Za Hájojnou Cave research have been previously published (Přírodovědné studie Muzea Prostějovska, 8/2005, 5–184, in Czech, 14 papers), this synthetic paper is focused mainly on the stratigraphy of Za Hájojnou Cave sediments.

Material and methods

The Za Hájojnou Cave is a typical bear cave of the Middle Pleistocene which assemblage is characterized by the dominance of *Ursus cf. deningeri* (Wagner 2005, Musil 2005b). Fossil remains of other vertebrate species are represented only by some isolated finds. Other large mammals are represented by *Panthera fossilis*, *Panthera spelaea* (known from the Late Pleistocene deposits) and the very scant findings of *Canis* sp., *Bos/Bison* sp., *Equus* sp., *Sus scrofa* and *Rupicapra/Capra* sp. (Ábelová 2005).

Systematic geological and palaeontological research of cave deposits in the Za Hájojnou Cave started in 2001. Up to the present time, altogether 13 sections were excavated (Musil 2014). Samples of sediments were gradually taken from all macroscopically distinct layers. All studied sections

and individual layers have their unique designation. Macroscopically visible osteological remains were collected out of the sediments in front of the cave entrance and labelled with the number of section and layer. At the same time we have made a detailed description of all macroscopically visible features of each sedimentary unit. Sediments of selected layers were floated in water on the sieves (sizes 2 mm, 1 mm and 0.5 mm) to obtain fossil remains of all the small fauna. Standard maceration with HCl (20%), HF, KOH and HCl (10%) and heavy liquid ZnCl₂ (density = 2 g/cm³) was used for palynological samples. Approximately 50 palynological samples have been studied.

For our stratigraphical conclusions we used published data of different authors (Lisá 2005, Čatloš and Fejdi 2005, Zeman 2005, Štelcl and Zimák 2005, Kadlec et al. 2005, Musil 2005a, b, Wagner 2005, Sabol 2005, Ivanov 2005, Doláková 2005, Lundberg et al. 2014) as well as data in this issue.

²³⁰Th/U dating of speleothems

The oldest cave deposits are represented by fluvial sediments of the previous sinkhole. Their substantial part deposited within the Early Pleistocene because B/M palaeomagnetic boundary (781 ka) have been reported from the upper part of fluvial sediments below the non-fluvial deposits (Kadlec et al. 2014). Few speleothems suitable for the ²³⁰Th/U dating have been found in the cave (Lundberg et al. 2014):

1. Vykopaná chodba, ZH P-4, only 4 cm thick cave bottom sinter situated under the cave roof, the underlying sediments were removed by former speleological excavations. It is situated ~ 4 m from the Kostnice II (= Charnel-House II), sampled at 1 cm from base, 224 ± 4 ka (MIS 7a after Cohen and Gibbard 2011, 7b after Dansgaard et al. 1993).

2. Vykopaná chodba, ZH P-5, the Kostnice II, layer 2a – upper part, isolated fragment of broken sinter was dated, 145 ± 1 ka (MIS 6 after Cohen and Gibbard 2011), 267 ± 3 ka, (MIS 8 after Cohen and Gibbard 2011). Fragment of sinter of younger age apparently came into this layer accidentally.

3a. Narozeninová chodba, ZH P-10, the middle part of this corridor. Cave bottom sinter was formed after the formation of the erosional rill. The sample was taken from the underlying of the layer 3 in the roof of debris cone (layer 4). The 10 cm thick cave bottom sinter was sampled at 0.3 cm from top, 178 ± 1ka (MIS 7a after Cohen and Gibbard 2011, MIS 6 after Dansgaard et al. 1993).

3b. Narozeninová chodba, ZH P-10, the same cave bottom sinter and section as above. Sample for dating was taken at the base of the sinter, 239 ± 4 ka (MIS 7e after Cohen and Gibbard 2011, MIS 7e after Dansgaard et al. 1993).

4. Narozeninová chodba, ZH P-11, the base of the cave bottom sinter below the layer 1 was dated, 118 ± 1 ka (MIS 5e after Cohen and Gibbard 2011).

Tab. 1. Za Hájovnou Cave. Stratigraphic classification of layers on the basis of U/Th dating and lion findings.

stratigraphy	U/Th dating paleo-magnetism	Vykopaná chodba	comments	Chodba naděje	comments	Kostnice I.	comments	comments
Holocene MIS 1		ZH P 1/1						very low boulders upper part of Komín I
Last Glacial MIS 2		ZH P 1/2,3,4,5						loessic loam
Middle Pleistocene MIS 7a-7b	224 ± 4ka	ZH P 4						cave bottom sinter under the cave roof
MIS 8	267 ± 3 ka	ZH P 5						sinter fragments
MIS 9a warm stage III		ZH P 5/ 2b,3b	younger group of lions interglacial climatic conditions	ZH P 7a/3a	younger group of lions			group 2 A ¹ , younger group of lions torrential rainfalls, the surface of hill covered with grass
MIS 9e-I warm stage I		ZH P 3/3, ZH P 3/4	older group of lions	ZH P 7b/3 (partly), ZH P 7b/4, ZH P 7b/6	older group of lions	ZH P 6/1 ZH P 6/2	older group of lions	older group of lions groups 2A ¹ , 2 A ²
Cromerian complex Interglacial I	B/M	ZH P 6/4						without palaeontological findings fluvial sediments
Early Pleistocene		ZH P 6/5–8						without palaeontological findings fluvial sediments

Lithology in relation to the preservation of the osteological material

The sequence of sediments from the Za Hájovnou Cave can be divided into the following sedimentary groups based on their different lithological content (Musil 2014).

Sediments of the 1st group

This group is represented by the loessic loam of the yellow-brown colour which forms the supporting structure of very angular to rounded limestone clasts of varying content (20–70%) and size (up to 50 mm). Calcareous nodules are present. Typical loess is more or less calcareous (up to 35%), predominantly silty deposit with weak admixtures of clay and sand particles. It probably originated as a result of sialitic-carbonate weathering under arid and cold climatic conditions in steppe environment (Růžičková et al. 2003). Within this group layers with coarse and very angular limestone gravels (about 30 mm) alternate with layers containing very coarse rounded gravels (40–50 mm). The very angular coarse gravels were formed in cold climate.

The following layers belong to this group: Vykopaná chodba, ZH P-1, layers 2, 3, 4, 5, Narozeninová chodba, ZH P-11, layer 1.

Sediments of the 2nd group

This group is represented by coarse silt usually containing medium sized (10–15 mm) to coarse (25–30 mm) angular limestone gravels and frequent quartz clasts. Manganese or calcareous nodules are present. Layers contain considerable amount of speleothems, e.g. fragments of cave bottom sinters, stalactites, straw stalactites. These sediments, generally brown in colour with various shades, are rich in bone remains

with a very similar state of preservation in different layers. Layers can be divided into two different groups.

2A¹: Layers with chaotically arranged limestone debris of various sizes, containing a greater amount of coarse gravels in each of the layers (30–80%) with strong superficial corrosion. Limestone clasts of various sizes (30–65 mm) are coated by manganese crust. They are easily disintegrated as a result of weathering. Clasts of subangular vein quartz and sub-rounded quartz (up to 10%, about 5–10 cm) and medium to coarse rounded quartz gravels (up to 10%, average 1–2 cm) are also frequent. Layers of this group of sediments contain large and small manganese nodules (oxides and hydroxides, about 2 mm in diameter) and abundant speleothems including fragments of macrocrystalline cave bottom sinters and needle-fibre calcite aggregates, fragments of calcitic stalagmites, fragmentary stalactites, straw stalactites and fragments of thin sinter plates. Loam sinters and bone beds (breccia) are also present. All the preserved bones are usually very fragmentary, transversely broken and sometimes completely disintegrated. Only teeth are well preserved. Oval pieces of bone spongiosis (2–3 cm in diameter) are abundant. Whole bones are totally missing. The surface of many bones is coated by a brown coloured sinter crust which is 1–2 mm thick. The surface of most of bones is black as a result of manganese coating and frequently full of longitudinal cracks, which are filled with loam. This indicates that bones were lying on the surface for an extended period of time.

The following layers belong to this group: Vykopaná chodba, ZH P-3, layer 4, ZH P-5, layer 2a, 2b, ZH P-7b, layer 3 (?), 4 (?); Spojovací chodba, ZH P-8a, layers 2a, 2b; Narozeninová chodba, ZH P-8b, layers 2a, 2b, ZH P-9, layer 3, ZH P-10, layer 3.

2A²: A small amount of limestone subangular coarse gravels (10–20%), with a large proportion of calcareous

Tab. 2. Za Hájovnou Cave. Sedimentary groups and their stratigraphic classification.

stratigraphy	U/Th dating	Spojovací chodba	Narozeninová chodba	comments	comments (sedimentology)
Last Glacial MIS 2			ZHP 11/1a		loessic loam
Last Interglacial (Eem) MIS 5e	118 ± 1 ka		ZHP 11		cave bottom sinter
Middle/Late Pleistocene			ZHP P-8b/1,1c,1d, ZH P-9/1,2, ZH P-10/1,2	<i>Ursus spelaeus</i>	gravitational redepositon
Middle Pleistocene MIS 7a	178 ± 1 ka		ZHP P-10/cave bottom sinter		end of formation of cave bottom sinter
MIS 7e	239 ± 4 ka		ZHP P-10/cave bottom sinter		beginning of formation of cave bottom sinter
			ZHP P-10		origin of erosion rill after the development of layer 3 and before the origin of cave bottom sinter
MIS 9a warm stage III		ZHP 8a/2a, ZHP 8a/2b	ZHP 8b/2a, 2b, ZHP 9/3, ZHP 10/3	interglacial climatic conditionns	group 2 A ¹
MIS 9c warm stage II			ZHP 8b/4, ZHP 9/4, ZHP 10/4, ZHP 11/4	warm climatic oscillation	debris cone
MIS 9e/11 warm stage I			ZHP 9/5, ZHP 9/6	older group of lions climax phase of interglacial, continuous deciduous forest	group 2 B

nodules (the largest 30 x 15 mm). Fragments of subangular vein quartz (up to 3%). A smaller quantity of bone beds (breccia) have been found. Bone surfaces are mostly coated by sinter. The sinter crust on the bones shows that they were laying on the surface of sediments without immediate burial. The sienna loessic loam situated between gravels deposited during the Middle Pleistocene which is documented by superposed layers with the presence of *Ursus cf. deningeri*.

The following layers belong to this group: Vykopaná chodba, ZHP P-3, layer 5, ZHP P-6, layer 2.

2B: Layers of loose coarse silt of dark-brown colour containing larger manganese nodules (unlike calcareous nodules which are sporadic) and manganese crusts up to 0.5 cm thick. Limestone debris is widely absent. Coarse-grained material is represented by fine limestone gravels (2%, up to 4 mm) or very coarse limestone gravels (< 1%, up to 50–60 mm). Layers contain also rounded to well rounded quartz gravels (~ 1–2%, up to 10 mm) and abundant subangular vein quartz (5–7 cm), further sporadic clasts of culm schists (up to 20 mm). Layers contain fragments of thin sinter plates (1 cm), fragments of stalagmites, many loam sinters, fragments of macrocrystalline cave bottom sinter about 10 cm thick, as well as clayey or loessic raddles of rusty colour. Unlike the group A, bones are always complete and unbroken. They are not regularly scattered, they rather lie in clusters, sometimes even in anatomical position. They are very well preserved without traces of extensive weathering. Their surface is smooth and yellowish brown in colour.

The following layers belong to this group: Narozeninová chodba, ZHP P-9, layer 5, 6.

Comments. The two groups (A and B) differ substantially in the amount and size of limestone debris. The character of bones preservation is another great difference between groups A and B. In the group A, the bones are invariably fragmentary, while in the group B they are nearly

always complete, and often in the anatomical position. They are never weathered.

Sediments of the 3rd group

This group represents sediments of the debris cone. The bottom of debris cone is formed almost exclusively by limestone boulders up to 1 m in diameter. The space between limestone clasts is only sporadically filled with coarse silt of brownish colour. The thickness is ~2 m or more.

The following layers belong to this group: Narozeninová chodba, ZHP P-8b, layer 4, ZHP P-9, layer 4, ZHP P-10, layer 4, ZHP P-11, layer 4.

Sediments of the 4th group

This group represents clayey to fine sandy fluvial sediment of rusty-brown to brown colour with very sporadic (< 5%) limestone debris. If present, weathered limestone clasts (up to 4 cm), coated by manganese crust, show tendency to disintegration. There are also present disintegrated pebbles (up to 3 cm) of culm greywackes and shales (above 5%) and fragments of vein quartz (up to 2 cm). Palaeontological remains are absent.

The following layers belong to this group: Vykopaná chodba, ZHP P-5, layer 4 (B/M boundary), layers 5–8, ZHP P-7a, layer 4.

Čatloš and Fejdi (2005) found that all minerals found in fluvial sediments (garnet, chlorite, idiomorphic quartz, magnetite, pyrite, limonitised pyrite, mica, and zircon) originate from the upper reaches of the Špraněk River catchment. This river does not flow towards the Za Hájovnou Cave in present time. Javoříčka Stream, a tributary of the Špraněk River, flows in the valley below the cave today. The drainage pattern transformed during

the Early Pleistocene, as previously assumed by Panoš (1964).

The above mentioned minerals were found not only in fluvial sediments, but also in many other cave layers. It means that their transport to the slopes above the cave took place before the sinkhole formation, or the valley must have been filled with Badenian marine sediments (Musil 2005a). The Badenian deposits could be found in the near surroundings.

Sediments of the 5th group

Infiltration cave sediments which occur only in the uppermost layers mainly within karstic chimneys. They represent thinly laminated clayey silt always without limestone clasts. This silt is sometimes bicolour, i.e. darker brown and brick red. Infiltration cave sediments indicate slow and repetitive cyclic accumulation and apparently originated at different times.

The following layers belong to this group: Vykopaná chodba, ZH P-3, layer 1, ZH P-5, layers 1a, 1b, Chodba naděje (= Corridor of Hope), ZH P-6, layer 2, Spojovací chodba, ZH P-8a, layer 1.

Some layers have undergone gravitational redeposition. In part, these sediments come from the Late Pleistocene (*Ursus spelaeus* findings). They are found only in the Narozeninová chodba: ZH P-8b, layer 1, 1d, ZH P-9, layers 1 and 2, ZH P-10, layer 1 and 2.

Middle Pleistocene palaeobiological record from studied sections

Findings of lions

The findings of the lions do not show an uniformity in metric and morphological characters and all the finds can be divided into two groups. 1) The lion remains attributed to *Panthera fossilis* (REICHENAU, 1906) on the basis of morphological and metric data, demonstrate relatively big individuals of lion-like felids close to these from other European Middle Pleistocene sites. They were found in layers dated to MIS 9 and/or older (MIS 11–13). Typical individuals of the species are known from the MIS 11–13 period.

2) The individuals of *P. fossilis* from layers dated to MIS 9 and/or younger exhibit characteristics similar to so called “intermediate forms” (towards *Panthera spelaea*) from the Saalian Complex (MIS 6–8). These forms are preliminarily named by some authors (e.g. Argant 2010 or Marciszak et al. 2014) as “*P. intermedia*” (nomen nudum).

According to one of co-authors (Sabol 2014), *P. spelaea* has not to be a descendant of European palaeopopulations of *P. fossilis*. It is not excluded that *P. fossilis* evolved autochthonously in Europe and it gained some characteristics convergent with those of the Late Pleistocene *P. spelaea* at the end of the Middle Pleistocene (so called “intermediate forms” from MIS 6–8). *P. spelaea* probably evolved in Asia and penetrated Europe during the Late Pleistocene (or during the Middle/Late Pleistocene transmission resp.), when replaced autochthonous palaeopopulations of *P. fossilis*.

From the biostratigraphic point of view, all records of lion-like felids from the European Middle Pleistocene are so far attributed to *P. fossilis* with stratigraphical range from MIS 17 to MIS 8 (6), representing probably two “subspecies” (*P. fossilis fossilis* from MIS 17 to MIS 9 and *P. fossilis “intermedia”* from MIS (9) 8 to MIS 6) or two “chronospecies” (*P. fossilis* from MIS 17 to MIS 9 and *P. aff. fossilis* (= *P. “intermedia”*) from MIS (9)8 to MIS 6) with interfragmentary boundary at MIS 9. Based on that, the Za Hájojnou Cave could play an important role in our knowledge of the *P. fossilis* evolution and the MIS 9 horizon could be a crucial. Unfortunately, limited quantity of suitable fossils as well as suitable characteristics do not enable to specify our conclusions and the abovementioned scenario is so far only hypothetical.

From the relationship viewpoint of cave lion (*P. spelaea*) to modern lion (*P. leo*), some authors (predominantly of the western provenience) regard cave lion as only an extinct subspecies of modern lion, falling back on results of ancient mitochondrial DNA analysis. On the other hand, some Russian scientists (such as Baryshnikov and Boeskorov 2001 or Sotnikova and Nikolskyi 2005), however, regard cave lion as a separate species on the basis of cranial and dental morphometrics. In addition, the results of phylogenetic analysis (Burger et al. 2004, Barnett et al. 2009) rather shows that cave lion forms a distinct clade that is close related to extant lions from Africa and Asia.

Voles and lemmings

Fauna of small mammals, especially voles (arvicolid), is of particular importance for stratigraphic classification of the layers within studied sections. Remains of voles and lemmings were described only from two sections including ZH P-2 and ZH P-8b (Ivanov and Vöröš 2014):

Velikonoční jeskyně (= Easter Corridor), ZH P-2, layers 6a, 6ab, 6b (*Microtus gregalis*, *M. arvalis/agrestis*, *M. oeconomus*, *Clethrionomys glareolus*, *Lemmus lemmus*, *Dicrostonyx* cf. *torquatus*, *Arvicola cantiana*). Layer 7a–f (*Microtus gregalis*, *M. arvalis/agrestis*, *M. oeconomus*, *Clethrionomys glareolus*, *Dicrostonyx* cf. *torquatus*).

Spojovací chodba, ZH P-8b, layer 1c. This layer is affected by gravitational redeposition of sediments of various ages. (*Microtus gregalis*, *M. arvalis/agrestis*, *M. aff. “coronensis”*), layers 2a, 2b (*Microtus gregalis*, *M. arvalis/agrestis*, *M. oeconomus*, *Clethrionomys glareolus*, *Arvicola terrestris*).

As regards ZH P-2 section remains of voles and lemmings indicate that the assemblage is most probably of Saalian age. Layer 7(a–f) probably deposited during the MIS 8 and MIS 7, whereas layer 6 is also of the Saalian age but it originated later, probably within MIS 6 (Ivanov and Vöröš 2014). Fossil remains of other groups are very scarce in ZH P-2 and there is no radiometric dating from this section. Therefore, the stratigraphic classification is not widely discussed.

The Middle Pleistocene vole assemblage from ZH P-8b, namely that of the layers 2a and 2b which are both situated in the Vykopaná chodba, as well as in the Narozeninová chodba, appears to be older than assemblages from ZH P-2 (Ivanov and Vöröš 2014).

Palynospectra

Number of palynomorphs was very different in individual layers of studied sections. Some layers were rich in pollen and spores; other contained only sparse grains without substantial relevance. Other studied samples were sterile (Doláková 2014). Short description of studied sections is as follows:

Velikonoční jeskyně, ZH P-2: Layers 6 (sterile) and 7 were studied. Overestimation of small Asteroideae, pollen of other herbs (*Chrysosplenium/R. trichophylus*, Poaceae, *Galium*, Ranunculaceae) was observed in the layer 7. No pollen of trees has been observed. This oryctocoenosis gives evidence for mechanical selection during transport with sediment flow. However, according to the study of cave sediments (Balcarka, Doláková 2004; Pod Hradem, Doláková, personal data) such palynospectra are typically found in sediments from the steppe environment of colder climatic stages.

Vykopaná chodba, ZH P-5: layer 1b – only several grains (*Pinus*, *Betula*, Asteraceae). Layers 2a and 2b were rich in palynological content (similar, but impoverished as ZH P-8b – see below). Layer 3 only single findings (*Picea*, *Fagus*, *Buxus*). Layers 5, 6 and 7 sterile

Narozeninová chodba, ZH P-8b: Layer 1 only several pollen grains (*Pinus*, Asteraceae). Layers 2a and 2b rich in palynomorphs. Frequent tree elements elements (*Pinus* up to 40%, general - *Carpinus*, *Tilia*, *Quercus*, sporadic – *Acer*, *Hedera*). Single pollen of *Pterocarya*, *Ilex*, *Buxus*, or *Celtis/Juglans* were found. Layer 4 lower part (debris cone) has different palynological content (*Corylus* and herbs prevail, *Carpinus* and *Tilia* occur) if compared to layer 4 upper part from ZH P-10 and 11.

Narozeninová chodba, ZH P-9: Layer 5 in underlayer of a debris cone. Different pollen spectra, including variability in total content of pollen grains, were observed in individual depths of this macroscopically uniform layer. In the 9.5 m – trees prevailed over herbs (67:33%), representing vegetation of deciduous woodland with only a small admixture of conifers (5%). *Corylus* was most abundant (over 40%), *Carpinus*, *Tilia*, *Quercus*, *Juglans* and *Alnus* (reached about 15%). In the overlying samples there was an increased proportion of *Pinus*, Asteroideae and other herbs and a decrease in *Corylus*, *Alnus* and *Tilia* until they became absent at the 7.5–6.5 m level. From the 3 m upwards the pollenspectra were approaching to the ones from debris cone (layer 4 lower part) and layers 2a, 2b (from ZH P-5 and ZH P-8b) without pre-Quaternary elements.

Narozeninová chodba, ZH P-10: Layers 2 and 3 sterile. Layer 4 upper part (debris cone) high amount of pollen and spores – Pinaceae highly prevailing, without *Corylus*, *Carpinus* and *Tilia*.

Narozeninová chodba, ZH P-11: Layer 1 only several single grains (*Pinus*, Asteraceae, Poaceae). Layers 3b and 4 (debris cone) were rich in palynomorphs. Palynological pictures of 3b were similar to 2b of ZH P-8b. Layer 4 was analogical to layer 4 of ZH P-10.

Stratigraphic evaluation on the basis of different methods

For stratigraphic classification of individual layers and for their environmental interpretation only some methods and information obtained from earlier studies are appropriate, the most important are the following ones: $^{230}\text{Th}/\text{U}$ dating, lithology and the preservation of the osteological material, faunal biostratigraphy and palynology.

Stratigraphic evaluation on the basis of different sediment lithology and bone preservation

This chapter is based on the interpretation of sediments and their osteological content. Only fluvial sediments in the Vykopaná chodba and debris cone in the Narozeninová chodba came into the cave from the entrance. All other deposits were transported into the corridors by waters flowing through the karst chimney from the surface.

The oldest layer is made of fluvial sediments without bones and palynospectra found only in the Vykopaná chodba (ZH P-5, layers 4, 5–8 and the ZH P-7a, layer 4). In its upper part (layer 4) the B/M palaeomagnetic boundary has been detected (Kadlec et al. 2005, 2014).

A long hiatus followed after this period. From the subsequent time, two groups of stratigraphically important sediments located in superposition: the 2nd group A and B and the 3rd group (debris cone) have been found.

The 2nd group A

Well-preserved sediments at Vykopaná and Narozeninová chodba belong to the layers 2a and 2b (ZH P-5) from the Middle Pleistocene (layer 2a: $^{230}\text{Th}/\text{U}$ 267 ± 3 ka BP, Lundberg et al. 2014). Layers 3a and 3b of the same section are older. In another place (Vykopaná chodba, ZH P-6, layer 2, ZH P-3, layer 5), however, we found a loessic loam (2A²) which was situated in the underlying of layers with *Ursus cf. deningeri*. The layer 2A² is different from layers of the group 2A¹. This kind of deposit has been accumulated during completely different environmental conditions, apparently during a cold stage of the Middle Pleistocene. It can't be neither ruled out, nor proved that they could theoretically be located between the debris cone and the layers 2a and 2b in the Narozeninová chodba. Layers 2a and 2b of ZH P-5 continue through the Spojovací chodba to the Narozeninová chodba. They could still be found in the ZH P-8, ZH P-8b as layers 2a and 2b and ZH P-9, layer 3.

These layers were created during recurrent torrential rainfalls. The surface of the hill was without trees and mostly without shrubs, covered only with grass. This also corresponds to the characteristics of the microfauna (Ivanov and Vörös 2014) and plant association (Doláková 2014).

The 2nd group B

This group is known only from the Narozeninová chodba, ZH P-9, layer 5 and 6. The layers are situated immediately below the debris cone deposits.

Both groups (2A and 2B) reveal a different lithology and mode of bone preservation. Sediments of both groups are

then divided in time by the formation of the debris cone. This proves that they originated in two distinct time periods.

The 3rd group

Debris cone, layer 4 is located in the underlying bed of the 2nd group A in the Narozeninová chodba only.

Comments. Three stratigraphically distinct sedimentary units could be defined as follows: 1 – the group 2A with two sedimentary different layers (clayey silt 2A¹ and loessic loam 2A²), 2 – the group 3 (debris cone); 3 – the group 2B. All layer groups are deposited in superposition. According to palynologic findings of all groups (except group 2A, loessic loam) all groups come from different warm stages.

Stratigraphic evaluation on the basis of vertebrate assemblages

The best stratigraphical evidences of individual layers come from mammal remains. In our case lions are especially suitable for stratigraphic evaluation of many layers of studied sections. In all layers with lion remains, the remains of bear species *Ursus cf. deningeri* have been found as well.

Evolutionary trends in lions

The findings of the lions where two groups have been distinguished on the basis of *Panthera fossilis* (MIS 9 and/or older and MIS 9 and/or younger; see above, Sabol 2014) are very important for stratigraphic evaluation of most of studied sections.

The lion fossil remains of the first group were found in deposits of Vykopaná chodba (Profile ZH P-3: layers 3 and 4), the Chodba naděje (Profile ZH P-7b: layers 4 and 6, partly also layer 3), the Kostnice I (= Charnel-House I, ZH P-6: layer 1 and 2) and the Narozeninová chodba (Profile ZH P-9: layer 5). These fossils show metric and morphological characteristics (e.g. in lower carnassials or tarsal bones) that are rather typical for *P. fossilis* from the time older than MIS 9, found at sites such as Château (MIS 13; Argant et al. 2007) or Petralona (finds from \geq MIS 11; Baryshnikov and Tsoukala 2010).

The second group is represented by fossils showing more derived characters, which are known in lion-like felids from the Saalian Complex (so called “intermediate forms” found in France or in Poland) or in the Late Pleistocene *P. spelaea*. They have been excavated from fossiliferous deposits of the Chodba naděje (ZH P-7b: layer 3 partly), as well as of the profile ZH P-5 (Kostnice II, layers 2b and 3b), dated to the period \leq MIS 9. The last data are the most important, because the same layers (2a and 2b) are located in the Narozeninová chodba. They lie above the debris cone deposits.

In comparison with the fossil record of the first group, the lion fossils of the second one are slightly smaller (except for metapodial bones), showing also certain different morphological and proportional characters, observed mainly in p4s, Lm1/Lp4 x 100 index, and also in some calcaneal bones from layer 3 of the Chodba naděje (ZH P-7b). Generally, finds of the second group correspond well from metric point of view mainly with finds for example in late Saalian sediments (MIS 6) of Azé I (Argant 1991), in late

Middle Pleistocene deposits (MIS 8–6) of Wierzchowska Górna (Barycka 2008, Marciszak et al. 2014), or at Middle Pleistocene Hungarian sites (Hankó 2007). The palynological findings from the cave, however, found in the sediments with lion fossils, however, show warm interglacial period, the cold MIS 6 or MIS 8 cannot be taken therefore in account.

Moreover, found proportional differences in some calcanei from layer 3 (ZH P-7b) of the Chodba naděje (~ MIS 9) over the record from ZH P-7b, layer 5 of the Narozeninová chodba ($>$ MIS 9) probably reflect certain evolutionary trends in the ankle part of Middle Pleistocene lion-like felids, indicating possible changes in the locomotion or in the function of hindlimbs during the time.

Based on the abovementioned information in connection with additional obtained preliminary data, it seems that MIS 9 could be a crucial time interval in the intraspecific evolution of autochthonous Middle Pleistocene European lion-like palaeopopulations with a development of more advanced characters in post-Holsteinian representatives towards or parallel with these of Late Pleistocene cave lions.

Voles and lemmings (Arvicolinae) assemblages

Most of representatives of rodent fauna are reported from the ZH P-8b (Narozeninová chodba), layer 2a and 2b. *Microtus (Microtus) arvalis/agrestis*, *Microtus (Microtus) gregalis*, *Microtus (Pallasinus) oeconomus* and probably *Clethrionomys glareolus* are known in Central Europe as early as in Cromerian complex (Maul and Markova 2007, Kučera et al. 2009) they represent taxa inhabiting Central European region till present times. *Arvicola terrestris* indicates a Late Pleistocene (or Holocene) contamination because *in situ* remains of the Middle Pleistocene *Ursus cf. deningeri* have been reported from layers 2a and 2b (Musil 2014). The earliest occurrence of *Clethrionomys glareolus* postdates the earliest occurrence of *Clethrionomys acrorhiza* and cannot be older than Cromerian Interglacial III (Maul and Markova 2007). Because the first distinct *Clethrionomys glareolus* are known in Central Europe as early as MIS 10 the common occurrence with possible *U. deningeri* supports correlation with Holsteinian s.l. (sensu Dowling and Coxon 2001, Scourse 2006) or early Saalian stage. The total absence of typically glacial species (lemmings) indicates temperate climatic conditions during the deposition of layers 2a and 2b that could belong to MIS 9. However, this assumption should be supported by independent data (see the discussion below).

The age of the overlying layers 1c (ZH P-8b) is indistinct because of gravitational redeposition during the Holocene (Musil 2014). However, biometrical studies of m1 occlusal surface of *Microtus (Stenocranius) gregalis* and *Microtus (Microtus) arvalis/agrestis* are in accordance with studies reported from the early Middle Pleistocene Stránská Skála-cave (= Bear cave, probably MIS 16 or MIS 12; Kučera et al. 2009). Although there is reason to presuppose that layers were originally deposited during a warm period between the Middle and Late Pleistocene, we cannot distinguish a more precise their age. Unusual occurrence of ancient *Microtus* aff. “*coronensis*” known from the lower part of the Cromerian Complex, is most probably a result of gravitational redeposition as it was also documented by the character of deposits (Musil 2014).

Stratigraphic evaluation on the basis of palynology

Palynospectra of layers 2a and 2b (Vykopaná chodba, ZH P-5 Narozeninová chodba) have essential position from the stratigraphic point of view.

The palynospectra from samples of Vykopaná chodba, ZH P-5, (layers 2a, 2b), Narozeninová chodba, ZH P-8b (layers 2a, 2b), ZH P-9 (layer 3), ZH P-10 (layer 3) and ZH P-11 (layer 4, debris cone) similarly confirmed the mild climate character with frequent tree elements during the sediment deposition (*Carpinus*, *Tilia*, *Juglans*, *Quercus*, sporadic *Acer*, *Hedera*). The single pollen of *Pterocarya*, *Ilex*, *Buxus*, or *Celtis/Juglans* as the surviving members of pre-Quaternary floras were found. These plants are typical for the climatic optimum of the Holsteinian s.l. (Dyjakowska 1952, Vodičková-Knebllová 1961, Břizová 1989, Lang 1994, Biňka et al. 1997, Reille et al. 2000, Urban and Sierralta 2012).

The last appearance of *Pterocarya* in Central Europe is known from the uppermost MIS 9a substage of Holsteinian s.l. (sensu Dowling and Coxon 2001, Scourse 2006) It is unknown in a warmer stage of MIS 7 (Lang 1994, Litt et al. 2008, Roucoux, 2008).

Due to absence of any other typically pre-Quaternary pollen and spores (especially Sapotaceae, *Engelhardia*, evergreen Fagaceae and others) not existing in the Early and Middle Pleistocene interglacials and known as redepositions in the Quaternary sediments of the Moravian Karst (e.g. Ochoz Cave; Doláková and Nehyba 1999) we can highly consider the pollen as *in situ* in the studied sediments.

The samples from layer 5: 9.5–10 m of the section ZH P-9 (Narozeninová chodba) show a good accordance with *Corylus* expansion described by Urban and Sierralta (2012) from Schöningen lignite mine profile 12B Lpaz R 3b; MIS 9 (Urban et al. 2011, Bittmann 2012, Urban and Sierralta 2012).

Frequent *Carpinus* and single findings of *Pterocarya*, *Fagus*, *Abies* and *Taxus* also point to similarity with Schöningen pollen spectra. Only small amount of *Carpinus* pollen in section at Praclaux was found (Reille et al. 2000). More frequent occurrence of *Ilex*, *Hedera* and *Buxus* from localities of Western Europe indicates a rather oceanic climate (Reille et al. 2000, Dowling and Coxon 2001).

These elements were sporadically found in layers 2a, 2b and 3b Vykopaná chodba, ZH P-5) as well as in debris cone (Narozeninová chodba). In the underlying sediments – despite of warm character of palynospectra – they have not been found.

Different pollen pictures were observed in the upper part of debris cone (Narozeninová chodba, layer 4) in comparison with lower part and with the uppermost sample from abyss (ZH P-9, Narozeninová chodba, layer 5: 0.2 m). The highest share of *Pinus* (over 60%), together with minority of other trees (*Carpinus*, *Tilia*, *Quercus*, absence of *Corylus*), has been found in the upper part of debris cone. On the other hand, only 10% of *Pinus*, over 25% of *Corylus*, common *Carpinus* and *Tilia* without riparian elements and more herbs have been found in lower part of debris cone. These differences could indicate climatic variations (deteriorations) during the debris cone deposition. Changes during transport or changes in chemical conditions, even gradual redeposition of original external sediments cannot be excluded.

The palynospectra recorded from section ZH P-9 layer 5 (Narozeninová chodba) show several changes in very uniform sediments. Samples were picked from the following depths: 0.2 m, 1.2 m, 1.4 m, 2 m, 3 m, 5.5 m, 6.5 m, 8–9 m, 9.5 m and 10 m. The lowermost samples, 9.5 m and 10 m, were the most different from the overlying ones.

In the bottom sequence, trees prevailed over herbs (67:33%) with greatest share of *Corylus* (over 50%) together with riparian *Alnus* and mesophytic *Carpinus*, *Tilia*. Several grains of *Juglans* and *Viscum* were also found. There was the lowest portion of *Pinus* and Asteroideae from all samples. Only Poaceae represented more plentiful herbs. This palynospectrum probably represented the vegetation of deciduous forest with only small admixture of conifers. In the overlying samples portion of *Pinus*, Asteroideae and other herbs increased and *Corylus*, *Alnus* and *Tilia* decreased as far as to be missing. The samples from depths of 6.5–7.5 m were sterile. It is difficult to decide this phenomenon to be the result only of climate deterioration or also of taphonomic reasons. The overlying samples (depth 3–1.2 m) again contain thermophilous trees, such as *Carpinus*, *Tilia* and *Quercus*.

The only palynological results from profile ZH P-9, layers 5 and 6 cannot provide sufficient data to decide whether the sediments relate to MIS 11 or MIS 9 (the position of Holsteinian Interglacial is broadly discussed, e.g. Geyh and Müller 2005, Scourse 2006, Nitychoruk et al. 2006, Roe et al. 2009, Bittmann 2012, Urban and Sierralta 2012). The findings of *Pterocarya* in upper part of ZH P-9 and probable deterioration of climate in depths of 6.5–9 m of layer 5 in ZH P-9 is in a good accordance with these interpretations.

Discussion

The Za Hájojnou Cave represents a former sinkhole, which has been active until the beginning of the Cromerian Interglacial I, MIS 19 (B/M palaeomagnetic boundary, 781 ka; Kadlec et al. 2005, 2014). From the standpoint of sediments we can distinguish two entirely different groups of layers divided by debris cone in the Narozeninová chodba. The fossiliferous cave sediments allowed study of a relatively abundant Middle Pleistocene vertebrate assemblage with the greatest number of findings belonging to *Ursus cf. deningeri* (Wagner 2005, Musil 2005b). Other vertebrates including lions and small vertebrates (voles and lemmings, amphibians, reptiles) are much less frequent. Palaeobotanical remains, represented by palynomorphs, are well documented from most of layers within studied sections. Stratigraphic interpretations are based on several methods including ²³⁰Th/U dating, sediments lithology, preservation of bones, evolutionary trends in lions and bears, vole assemblages, as well as palynology.

Most of the sediments (the 2nd group of sediments) from studied sections can be dated back to the Middle Pleistocene (groups 2A¹, 2A² and 2B) as it was documented above all by palaeontological research and ²³⁰Th/U dating. Below we focus on the sediments which we consider as belonging to Holsteinian s.l. (MIS 9 and MIS 11 sensu Dowling and Coxon 2001, Scourse 2006). Although many recent papers correlate warm period of the Holsteinian Interglacial with

MIS 11 (e.g. Nitychoruk et al. 2005, 2006), there are other papers which correlate Holsteinian Interglacial with MIS 9 (Geyh and Müller 2005, Litt et al. 2008). We agree with opinion of Nitychoruk et al. (2005, 2006) who correlate Holsteinian Interglacial (i.e. Holsteinian s.s.) with MIS 11. *Pterocarya*, which is considered as typical Holsteinian marker, is unknown in the fossil record since the beginning of the Saalian stage with exception of redeposited Neogene palynomorphs. The last abundant occurrence of *Pterocarya* was reported from the MIS 9a substage (Urban et al. 2011, Urban and Sierralta 2012). Therefore, we tend to support opinions of Dowling and Coxon (2001) and Scourse (2006) who consider Holsteinian *sensu lato* as complex containing warm stages MIS 9 and MIS 11.

Middle Pleistocene stratigraphy of studied sections in Za Háčovou Cave

The sequence of layers in the Vykopaná chodba along with the adjacent Chodba naděje is different from the layers in the Narozeninová chodba. Layers 2a and 2b of the ZH P-5 (Vykopaná chodba) are most important for stratigraphic correlation of cave sediments among different sections because they continue through the Spojovací chodba to the Narozeninová chodba without any interruption. Layer of loessic loam located in sections ZH P-3 layer 5 and ZH P-6 layer 2 (group 2A²) have been found only in the Vykopaná chodba. These layers contained calcareous nodules (up to 3–4%). Presence of loessic loam in sections indicate colder environment.

Two different groups of sediments (2A¹, 2A² and 2B) of the 2nd group could be distinguished in the cave on the basis of sedimentology and character of bone preservation. They certainly document mutually different environment during their deposition. According to the palynological point of view both groups (except of 2A²) originated in warm climate. In the Narozeninová chodba, both groups (2A¹ and 2B) are separated by large debris cone (layer 4) that stretches the entire length of this corridor.

Two evolutionary different groups of lions were reported from the layers 2A¹ and 2A². Evolutionary advanced (younger) group of *Panthera fossilis* consists of findings which show similarities to an intermediate form between *Panthera fossilis* and *Panthera spelaea*. It corresponds to MIS 9 or can be even younger. The evolutionary older group, also reported from the sedimentation group 2A, indicates most probably MIS 9 or older age (Sabol 2014). Layers of the group 2B consist of only evolutionary older forms of *Panthera fossilis*.

The above mentioned stratigraphic interpretation of the studied material based on lion remains is in accordance with the studies of vole assemblage (Ivanov and Vöröš 2014) from ZH P-8b (Narozeninová chodba), layers 2a and 2b (group 2A). The presence of distinct *Clethrionomys glareolus* indicates that layers 2a and 2b has most probably not been deposited before MIS 10. Along with bank vole also *Ursus cf. deningeri* was reported from the same layer. Moreover, the vole assemblage indicates relatively warm and humid climatic conditions with open woodland environment above the cave. The same environment confirms the study of

sediments. ²³⁰Th/U dating (267 ± 3 ka) of the sinter from ZH P-5, developed in the upper part of the layer 2a in Kostnice II, corresponds to MIS 8. However, both composition of vole assemblage and pollen spectra (with frequent tree elements including abundant *Carpinus*, *Tilia*, *Juglans* and *Quercus* and rare occurrence of *Pterocarya*) indicating mild climate in layers 2a, 2b (documented both in ZH P-5 and ZH P-8b) excludes cold climatic conditions typical for MIS 8. As regards *Pterocarya*, it disappeared from the palynological record before the Saalian stage and it is unknown in Central European pollen records starting from the MIS 7 warm stage. Therefore, we consider the age of layers 2a and 2b corresponding to MIS 9a substage of the Holsteinian s.l. as the most probable (we call it warm stage III).

Palynological findings in debris cone sediments (ZH P-8b, layer 4 – lower part) document that it also originated in a mild climate, similarly to layers 2a and 2b in both corridors. However, there is a substantial difference in composition of the palynospectra where *Corylus* and herbs prevail instead of *Carpinus* and *Tilia*. This pollen assemblage indicates warm period (warm stage II) which is less distinct than above mentioned warm stage III (MIS 9a). Because of the fact that MIS 9e substage is the warmest period within the whole MIS 9 (Urban et al. 2011) we presuppose that warm stage II could probably correspond to MIS 9c substage. ²³⁰Th/U dating of the cave bottom sinter in the roof of layer 3 in ZH P-10 (base 239 ± 4 ka) corresponds to MIS 7e (Lundberg et al. 2014). However, it is to be noted that this cave bottom sinter is created after origin of erosion rill (Musil 2014) and we don't know the time span between the origin of erosion rill and origin of cave bottom sinter. The cave bottom sinter show on long time period (61 ka) of its formation (surface 178 ± 1 ka, Lundberg et al. 2014).

Only at one place we know underlying beds of the debris cone, namely in the section ZH P-9, layers 5 and 6 (Narozeninová chodba). Layers 5 and 6 contain sediments of the 2nd group (group 2B) with totally different sedimentology and bone preservation compared to the group A. Bones are not fragmentary here without traces of weathering that is typical for bones of group 2A lying stratigraphically above the debris cone. The stratigraphic position of layers 5 and 6 within ZH P-9 section is not fully resolved. The evolutionary older forms of lions indicate that layer 5 corresponds with MIS 9 or it is older. On the basis of above mentioned results we can presuppose that this layer corresponds either to MIS 9e substage or MIS 11 (i.e. Holsteinian Interglacial, according to Nitychoruk et al. 2005, 2006). The findings of the lowermost part of this layer at a depth of 10–9.5 m show a total prevalence of thermophilic tree species with trees/herbs ratio 2/1. Occurrences of *Corylus* (over 40%), riparian *Alnus*, mesophytic *Carpinus*, *Tilia*, *Juglans*, *Quercus* and *Viscum* together with significantly low representation of *Pinus* and *Asteroidae* indicate continuous deciduous forest with small admixture of conifers. The overlying samples show subsequent increase in representation of *Pinus* and herbs and decrease in broadleaf deciduous trees. Although samples from the depths of 7.5–6.5 m were completely sterile, thermophilous trees again occur in overlying samples from depth 3–1.2 m. The absence of pollen grains cannot be safely explained. It can be result of deterioration of climatic conditions but taphonomic reasons are also possible. In any

case, we consider plant assemblage of the whole layer 5 as belonging to warm stage I. This assemblage differs strongly from associations of warm stages II and III and apparently indicates fully interglacial conditions. We consider warm stage I as interglacial corresponding either to MIS 9e substage or MIS 11.

As results from the above mentioned biostratigraphical evidence, we presuppose three separate warm stages (warm stage I, II and III) being in superposition only in Narozeninová chodba in this cave. Three warm stages have been also reported from Schöningen locality, Germany (Mania and Thieme 2007). That indicates also the stratigraphically similar Schöningen locality, where three interglacials have been discovered by Mania and Thieme (2007): I – Holsteinian Interglacial (the oldest), II – Reinsdorf Interglacial and III – Dömnitz (Schöningen) Interglacial. These interglacials are located between deposits of Elsterian glacial and Saalian subglacial moraine (Serangeli et al. 2012). Reinsdorf interglacial, recently dated by $^{230}\text{Th}/\text{U}$ method to 343–280 ka (MIS 9), indicates climatic optimum, full and late interglacial phases and beginning of the subsequent climatic deterioration (Urban et al. 1991). Sediments of Dömnitz Interglacial (MIS 7) are incomparably overlain by glacial deposits of the Saalian (Drenthe) ice advance (Urban 2007). Although much of the work in Schöningen locality was dedicated to the biostratigraphy and the palynology, stratigraphic correlation of the interglacials, and even their absolute age is still controversial. The greatest attention is paid to the Reinsdorf Interglacial. Palynological data and $^{230}\text{Th}/\text{U}$ dating suggest that the Reinsdorf Interglacial may be regarded as part of the Holsteinian *sensu stricto* (Serangeli et al. 2012, Lang and Winsemann 2012, Sierralta et al. 2012). Reinsdorf Interglacial could represent locally developed type of the Holsteinian corresponding to MIS 9 (Bittman 2012). Faunal assemblage is younger in comparison with the Hoxnian Interglacial (MIS 11) and therefore, correlation with MIS 9 is very probably (Schreve 2012). Therefore, sediments of the Dömnitz Interglacial below the Saalian subglacial moraine should belong to MIS 7, $^{230}\text{Th}/\text{U}$ 180–227 ka (Serangeli et al. 2012).

Three major interglacials were usually recognised in continental sediments during the late Middle Pleistocene between Elsterian and Saalian as it was documented in numerous localities e.g. in Great Britain and France (Kolfschoten 2012). The Za Hájoynou Cave offers another possible perspective on the stratigraphy of warm (or even interglacial) stages in MIS 9 and MIS 11.

Conclusions

From the above mentioned interpretations from the Za Hájoynou Cave we can distinguish three warm stages in superposition (warm stage III, II and I). While warm stage III corresponds most probably to MIS 9a substage, warm stage II could correspond to MIS 9c substage. Based on palynological record, only warm stage I we can consider as belonging to climatic optimum of interglacial period.

Two alternatives of the stratigraphical position of the studied successions of cave deposits can be presupposed.

Alternative A:

Warm stage I – corresponds to the MIS 11. The palynospectra indicate interglacial climatic optimum with continuous deciduous forest. Only evolutionary older forms of lions are present with metric and morphological characteristics rather typical for *Panthera fossilis* from the time older than MIS 9.

Warm stage II – corresponds to the MIS 9c substage. Palynological spectra with absence of *Pterocarya* and lower share of broadleaf deciduous forest elements indicate less distinct warm climatic oscillation when compared to warm stages I and III. Only evolutionary older forms of lions are present similarly to warm stage I.

Warm stage III – corresponds to MIS 9a substage. Palynological spectra with *Pterocarya* indicate interglacial climatic conditions which are not as optimal as within warm stage I (higher share of *Pinus* and herbs). Vole assemblage indicates open environment. Both evolutionary older and evolutionary younger forms of lions are present in 2A¹ with exclusive presence of evolutionary younger group in layer 2a, 2b.

Alternative B:

Warm stage I – corresponds to the MIS 9e substage. The palynospectra indicate interglacial climatic optimum with continuous deciduous forest. Only evolutionary older forms of lions are present with metric and morphological characteristics rather typical for *Panthera fossilis* from the time older than MIS 9.

Warm stage II – corresponds to the MIS 9c substage. Palynological spectra with absence of *Pterocarya* and lower share of broadleaf deciduous forest elements indicate less distinct warm climatic oscillation when compared to warm stages I and III. Only evolutionary older forms of lions are present similarly to warm stage I.

Warm stage III – corresponds to MIS 9a substage. Palynological spectra with *Pterocarya* indicate interglacial climatic conditions which are not as optimal as within warm stage I (higher share of *Pinus* and herbs). Vole assemblage indicates open environment. Both evolutionary older and evolutionary younger forms of lions are present in 2A¹ with exclusive presence of evolutionary younger group in layer 2a, 2b.

The only distinction between the two above mentioned alternatives is different stratigraphical correlation of the warm stage I which in every case indicates development of plant assemblage including interglacial climatic optimum. The alternative A (warm stage I corresponds to MIS 11) is supported by the exclusive presence of evolutionary older forms of *P. fossilis* (probably older than MIS 9) in layers of the 2B group below the debris cone. If the alternative A is valid than very warm MIS 9e substage is absent.

The alternative B (warm stage I corresponds to MIS 9e and all discussed warm stages agree with MIS 9) is also supported by palynological record. The presence of *Pterocarya* is considered to be typical for Holsteinian with the last occurrences in Central Europe in MIS 9a. Against the alternative B speaks exclusive occurrence of evolutionary older lions in layers of the 2B group.

The studies of lions in Za Hájovnou Cave indicate that MIS 9 was most probably crucial for their evolution. Although both above mentioned alternatives are possible, the exclusive presence of evolutionary older group of lions in sediments of warm stage I support strongly alternative A. We consider alternative A as more probable. The youngest warm stage III does not exceed MIS 9a substage. Therefore, we consider all three warm stages in Za Hájovnou Cave as belonging to Holsteinian sensu lato.

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