# Holocene history of the mammalian fauna in the Northern Bohemian sandstone region (Czech Republic)

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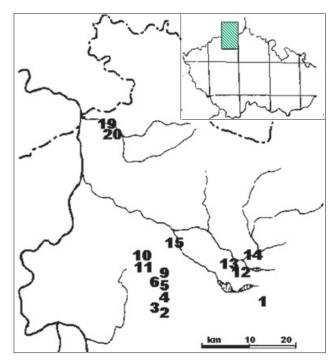
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### Introduction

The recent fauna of the Central Europe is composed of three chorologic units: (i) paleochoric elements of the interglacial communities which invaded their current ranges during the Holocene from glacial refugia, (ii) paleochoric elements of the glacial comunities which survived the Holocene environmental changes, and (iii) the apochoric elements of the Holocene which did not appear in Central Europe prior to the Holocene interglacial and/or the post-Neolithic period (Horáček and Ložek 1988). Although that statement is apparently valid for all regions of central Europe, in general, the particular regions differ quite a lot in the actual contribution of the respective chorologic units to local faunas as well as in the history by which the recent faunal structures were established. The fossil record available from various regions of Central Europe (Koenigswald and Taute 1979, Kordos 1982, Nadachowski 1989, Storch 1995, Horáček 2000) show considerable local differences in (a) the tempo and mode of reappearance of individual species of the groups (i) and (iii) as well as in (b) the patterns of postglacial survival in the (ii) elements, and in that (c) the individual species often differ in the timing of their postglacial range changes. The recent results of molecular phylogeography (Avise 2000, Bilton et al. 1998, Hewitt 1999) suggest, moreover, that individual species differ also in localisation of expected glacial refugia (Steward and Lister 2001, Horáček 2000). For these and other reasons, contemporary biogeography turns its attention to the specificities of local conditions and local biotic histories as important sources of global biodiversity (Brown and Lomolino 1998).

The most relevant way to trace these local faunal histories is to examine them by means of a direct fossil record. For that purpose, the record provided by the continuous sedimentary series covering a period from the Late Pleistocene glacial

maximum to the recent time are of greatest siginificance. During the last few decades a considerable amount of this kind of record was obtained, and thus from the Czech Republic and Slovakia about 90 continuous sequences are available (cf. e.g. Horáček and Ložek 1988). Of course, in most instances, direct information on the vertebrate faunal past, as revealed by the continuous fossil record, is limited to karst regions. This is due to the karst environment providing all of the essential preconditions for a vertebrate fossil record: (a) depositional traps exposed to continuous sedimentation, appearing at the source places of (b) continuous accumulation of bone remains and – first of all – (c) the calcareous sediments neccessary for



**Figure 1:** Geographic position of the fossiliferous sites discussed in the text. For key to numbers see Table 1.

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preserving the calcareous vertebrate remains. The cave entrances or debris deposits under cliff faces (i.e. the frequent nesting places of various avian predators) are typically the best places for such purpose and most of the series come from just such a context.

Unfortunately, not all the karstic regions in Central Europe meet all the prerequisites, and, moreover, the overall extent of karst areas is quite small. They form a minute part of Central Europe – in Czech Republic it is only 0.7 % of the total area (Bosák et al. 1989). Consequently, for most regions of Central Europe, almost no information on faunal development is available which significantly limits actual comprehension of the geographic variation in faunal history and its local specificities. At least for that reason, any data obtained from a non-karstic region is to be looked upon as information of considerable significance. This is the case for the extensive set of records that we obtained during recent decades from the Northern Bohemian sandstone area.

The recent sediments and soils appearing in sandstone regions of Bohemia are deficient in carbonates and thus, at first sight, are guite inappropriate for the preservation of bones. Nevertheless, as demonstrated elsewhere (Cílek 2000a and this volume), this was not the case during most of the middle and early Holocene, at least in some regions. The first series demonstrating this fact was investigated in the 1950s and was published under the name Zátyní near Dubá (Prošek and Ložek 1952). Amongst others, it provided clear proof of a Mesolithic occupancy and, moreover, one of few Holocene records of *Emys orbicularis* in Central Europe. Most of the data surveyed in this paper resulted from an interdisciplinary research project inspired by that record. The research began in 1992 under the leadership of V. Cílek and J. Svoboda. Since then, about 50 sites have been excavated and 29 of them have provided vertebrate remains along with numerous archaeological and sedimentological records.

### Material and methods

A detailed list of sites, excavation history and techniques, lithologic data and other information is published elsewhere (Svoboda et al. 2003). In most instances the respective sections

Locality	Reference number (Figure 1)	Year of excavation	Further data
Bezděz – západ	01	2000	Table 6
Dolský mlýn A	19	2001	Table 7
Dolský mlýn B	19	2001	Table 8
Dřevčice – Pod Černou louží	08	1998	Table 4
Dřevčice: Pod kamennou hlavou		1997	
Dřevčice: Srní převis		1997	
Heřmánky: Žlutá skála	11	1997	
Holany: U kameného mostu		1997	
Hradčany – Donbas	14	2000	
Hradčany – U obory	13	2000	
Hradčany – Uhelná rokle A	12a	2000	
Hradčany – Uhelná rokle B	12b	2000	
Labské pískovce: Studený: Sojčí převis	22	1999	
Lakota		1998	Table 10
Lhota near Dubá — Butterberg 1	06	1995	
Lhota near Dubá – Butterberg 2	06	1995	
Lhota near Dubá – Butterberg: převis u jeskyně	06	1997	
Lhota near Dubá – Šídelník A	09a	1998	Table 3
Lhota near Dubá – Šídelník B	09b	1998	Table 3
Lhota near Dubá – převis nad Máselníkem	06	1997	
Nízká Lešnice	03	1998	Table 5
Okrouhlík	20	2001	
Zahrádky – Pod Zubem (Sosnová)	15	1996	Table 10
Zahrádky-Peklo	16	1996	
Zámecký převis		1997	
Zátyní u Dubé	Ložek and Prošek 1952		

**Table 1.** List of sites yielding the vertebrate remains as excavated in particular years of the project. Bold print indicates sites with a significant amount of vertebrate fossils

**Table 2.** Assumptive stratigraphic allocation of particular layers in the most significant series. For respective archaeological context and C14 data see Svoboda (2003)

Locality	Šídelník	Pod Černou Louží	Nízká Lešnice	Bezděz	Uhelná rokle	Zahrádky, Pod zubem
Further data	Table 3	Table 4	Table 5	Table 6		
Upper Holocene				4		
Eneolithic		3		5 6		
Lifeontific		3		7		
Neolithic	3	4	1	8	5	
		4			5	
Boreal		6	2	9		
		5		x	7	7
Preboreal	6	8	3		9	
		9	4		10	
Late Wistulian			5			

Table 3. Vertebrate record (MNI) in series Lhota u Dubé – Šídelník A a B (1998). C14 dating: Šídelník A76–79 cm: 7941 cal. BP; Šídelník A 90 cm: 8596 cal.BP

		Šídelník <i>l</i>	A		Šídelník B				
layer (cm)	30–80	80-100	90–100	100	70	70-75	80	178–191	237
Anura, indet.		1			1				
Talpa europaea	1	1			1		1		
Erinaceus sp.			1						
Sciurus vulgaris						1			
Castor fiber									
Apodemus (Sylvaemus) sp.		1				1		2	
Clethrionomys glareolus	1	1			1	1		2	
Arvicola terrestris								1	
Microtus cf. arvalis				1					
Microtus subterraneus						1			
Lepus europaeus		1		1	1			1	
Sus scrofa								1	
Alces alces		1							
cf. Cervus elaphus	1	1						1	
Capreolus capreolus			1	1		1	1	3	1
Martes martes		1				1			
Total: individuals	3	8	2	3	5	5	2	11	1
Total: spp.	3	8	2	3	5	5	2	7	1

represent a series of sandy loams deposited under rocky overhangs in shallow but steep slopes of sandstone gorges, often including apparent traces of human activity (fire-places, artifacts etc.).

Table 1 lists sites which provided a relevant vertebrate sample from four sandstone regions in Northern Bohemia near Dubá, Česká Lípa, Bezděz and Hřensko (Figure 1). Their altitude varies from 188 m a.s.l. (Dolský mlýn near Hřensko) to 370 m a.s.l. (Bezděz). The stratigraphical span of the series covers mostly the period from the early Holocene to the post-Neolithic. The lowermost (supposedly Late Vistulian) and uppermost horizons (from the late Bronze Age onwards) are non-calcareous and do not yield vertebrate fossil remains as a rule (for further details see Cílek 2000a). A stratigraphic synopsis of the most significant

series and a list of C14 data (after Svoboda et al. 2003) are in Table 2.

The osteological material was obtained by means of either (i) continuous sampling during the excavation (the fragments were picked up directly from the section or from a coarse sample separated by sieving with a 3–5 mm mesh), and (ii) stratigraphical sampling from a completed section (20–100 kg per layer) and washing sediments with a 0.5 mm mesh and mechanical extraction of fossils. Most of the macrofossils were obtained by technique (i), while nearly all material of small vertebrates (which was the major source of the following paleoenvironmental and paleobiogeographic inferences) are of the source (ii). The faunal lists (including the respective

layer (cm) 45-60 100–120 | 125–150 | 150–165 | 165–190 | 210–225 60-75 75-95 Anura Bufo bufo Rana cf. temporaria Aves, Passeriformes Barbastella barbastellus Plecotus auritus Talpa europaea Sorex araneus Muscardinus avellanarius Eliomys quercinus *Sicista* sp. Apodemus (Sylvaemus) sp. Clethrionomys glareolus Arvicola terrestris Lepus europaeaus Sus scrofa Capreolus capreolus Total: individuals (85) Total: spp. (16) 

**Table 4.** Vertebrate record (MNI) in a series Dřevčice – Pod Černou louží. C14 dating: 120–125 cm: 8405 cal.BP.

sample/layer	1	2	3	4	5	6	7
layer	1	2	2	3	3	4	5
depth (cm)	0–20	20–40	40-50	60–80	90	90–110	110-140
Anura			1	1	1	1	
Aves	2		2	3	2	1	1
Talpa europaea	1		1	1	1		
Sorex araneus						1	
Sorex minutus						1	
cf. Myotis bechsteini				1			
Eptesicus serotinus				1			
Plecotus cf. auritus			1				
Barbastella barbastellus			2		2		
Pipistrellus pipistrellus			1			1	
Sciurus vulgaris			1		1		
Sicista sp.				1			
Castor fiber			1				1
Apodemus (Sylvaemus) sp.		1	2	3	3	1	
Clethrionomys glareolus				1	1	1	
Arvicola terrestris			1	1	2	1	1
Microtus cf. arvalis		1	2	1			
Microtus agrestis						2	
Microtus subterraneus				1			
Lepus europaeus	1	1		1			
Sus scrofa	1						
Capreolus capreolus		1	1				
cf. Vulpes vulpes				1			
Total: individuals	5	4	15	17	13	10	3
Total: spp.	4	4	12	13	8	9	3

**Table 5.** Vertebrate record (MNI) in a series Nízká Lešnice. C14 dating: 120 cm: 11901 cal. BP

Bezděz	layer	4	5	6	6	7	7	7	8	8	8	9	9
	depth	40–50	50–60	60–70	70–80	80–90	90	100	110	110–120 center	<b>110–115</b> left	120–125	130
Aves: Aq	uila cf. pomarina							1					
Aves inde	et.			1				2					
Aves: Pas	seriformes				1				1				
Talpa eui	ropaea				1							1	
Pipistrellu	us pipistrellus									1			
Sciurus vi	ulgaris		1	1	2		2	1	1	1		1	
Castor file	ber								1				
	<i>us (Sylvaemus)</i> sp.	1	1			1		1		1		1	
Clethrion	omys glareolus	2								1			
Arvicola 1	terrestris									1		2	
Microtus	sp.	1											
Lepus eu	ropaeaus		1	1		1	2	1					
Sus scrofe	a				1	1	1						
Alces alce	es						1	1				?	
cf. Cervus	s elaphus	1											
Capreolu	s capreolus		1		2			2	1		?		?
Martes m	nartes		1	2	1	1	1	2			1		
Canis lup	ous			1									
Vulpes vu	ulpes									1			
Total: ir	ndividuals (65)	5	5	6	8	4	7	11	4	6	2	6	1
Total: s	spp. (20)	4	5	5	6	4	5	9	4	6	2	5	1

Table 6. Vertebrate record (MNI) in a series Bezděz – západ. C14 dating: 140 cm: 7719 cal. BP

tables) and all subsequent analyses discussed in this paper operated with minimum number of individuals (MNI).

The relevant (i.e., determinable) material was obtained from 60 layer-samples in 16 sections (Table 1). In total, the material covers at least 420 individuals (MNI) belonging to 40 species of vertebrates, mostly tetrapods: 14 spp. of small ground mammals, 5 bats, 3 birds, 3 reptiles and 2 amphibians. Although in most instances the record was rather fragmentary and heterogeneous, in three sites, namely Nízká Lešnice, Dřevčice – Pod Černou louží, Lhota near Dubá – Šídelník it was sufficiently rich and regular. There, the highest concentration of fossils was about 40 individuals (MNI) per 100 kg of sediment.

### Results

At no site was the record particularly rich, of course. However, a comparison of the faunal development in the individual series (compare Tables 2–9 for details) allows some general remarks. First, it suggests that all the faunal series have several characteristics in common:

(1) A remarkable characteristic of the record is a high contribution of woodland elements or those demanding a dense forest understorey, viz. *Clethrionomys*, *Sylvaemus*, *Sciurus*, in

- almost all samples. In few sites the core of the woodland elements is supplemented also with *Microtus subterraneus* (Nízká Lešnice 3), a form demanding structurally varied relief with forest vegetation and a thick soil layer. Also the record of large mammals fits quite a well into that picture: the woodland species such as *Capreolus capreolus*, *Cervus elaphus*, *Martes martes*, *Alces alces*, *Sus scrofa*, *Vulpes vulpes*, *Meles meles* appear in almost every site.
- (2) In contrast, the open- ground elements, such as *Microtus arvalis*, are apparently not dominant at any site. They are frequent in the uppermost horizons only. In the lowermost layers, they do not form the essential component of the community as is common in most of other series both in Bohemia and Moravia until the Atlantic period. The glacial index fossils such as *Microtus gregalis* or *Dicrostonyx gulielmi* were not found at all.
- (3) The species demanding marshy or semi-aquatic habitats are regular in most community samples. In particular, Arvicola terrestris and Microtus agrestis, at three localities (Stará skála, Nízká Lešnice, Pod zubem) and Microtus oeconomus. Beaver, Castor fiber, occured in 7 community samples in 5 localities, typically in the close vicinity of streams (3 individuals at Pod zubem).

Sicista betulina was recorded at two sites. This species has been locally extinct in most regions since the middle Holocene. It is a lighte demanding species of semi-open biotopes, typically with a birch cover and a rich, dense and varied herb vegetation. It is a very characteristic element of the early Boreal when its distribution was almost continous throughout Central Europe. Today it is a rare relic surviving in a few mountain localities. Muscardinus avellanarius was also recorded. This species prefers shrubby and low forests with mesic conditions and habitats rich in elements of the forest ecotone, such as Corylus, Rubus etc. Both Sicista and Muscardinus appeared in the basal layers of particular series, i.e. at the earlier stages of the Mesolithic occupancy of the sites. In contrast to Sicista, Muscardinus has inhabited these habitats in the sandstone regions until recently (cf. Anděra 1986).

Worth mentioning is that no records of *Glis glis* are available. Apparently, the habitat conditions available in the studied region did not fit the requirement of that species, i.e. for a warm subxerothermic broad-leaved woodland. Despite the apparent dense wood-land cover thoughout most of the Holocene, the xerothermic broadleaved forest (supposedly in contrast to xerothermic pine vegetation) did not appear in the region under study.

From the viewpoint of faunal development, the record of *Eliomys quercinus* (Pod Černou louží) is particularly important. The recent distribution of this species in the Czech Republic is now limited to a few localities in sandstone regions (Anděra 1986). In Central Europe, *Eliomys quercinus* is apparently an apochoric element of the Holocene interglacial (no records are available in the Middle and Early Pleistocene). Together with a few other records, this one provides clear support for a spread of this species prior to Neolithic deforestration. Exactly the same

holds true for another species that was recorded at two sites of the present series, Pipistrellus pipistrellus (cf. Nízká Lešnice, Bezděz). This is a lithophilous element of a warm open country which is common in the Holocene fossil record (particularly the post-Neolithic) but in Central Europe it is absent from any record prior to the Holocene. It contrasts with the other bat species of the same habitat requirements, Eptesicus serotinus, which appeared at two sites (Nízká Lešnice, Okrouhlík). Out of the bats, Barbastella barbastellus is the most common in the sample. This species is typical of cooler woodland habitats with exposed rocks which it often uses for roosting and hibernation. The dendrophilous species, Plecotus auritus and Myotis bechsteini are represented by one record each. Worth mentioning is the appearance of a mole (Talpa europaea) at one site (Pod Černou louží) which indicates a deep soil layer and structurally stabilised valley bottom.

The osteological material collected during archaeological excavations provided extensive information on the large mammals supposedly hunted by Mesolithic people. In that respect (cf. Table 8) we have demonstrated preferential hunting for medium-sized game (hare and roe deer) supplemented with occasional large ungulates (red deer, elk and wild boar). Specialised hunting for fur (marder, wild cat and squirrel) is apparent at least at two sites (Pod Zubem, Bezděz) as well as specialised fishing in another site (Dolský mlýn).

## Discussion and conclusions

These records provide good information on the local faunal history during the early Holocene, roughly speaking from the

Dolský mlýn A	layer	4a	4	4-5	5	6	
	depth	40–50	70–80	80–90	90–105	105–110	130
Pisces		1	3	4			
Aves indet.				1			
Aves: Passeriform	es			1			
Talpa europaea					1		
Erinaceus sp.							
Eptesicus serotinu	IS				1		
Sciurus vulgaris				1			
Apodemus (Sylvae	emus) sp.		2				
Clethrionomys gla	areolus		1				
Arvicola terrestris					1		1
Lepus europaeus			1			1	
cf. Cervus elaphus	ī			1			
Capreolus capreo	lus		1	1			
Canis lupus			1	1	1		
Total: individua	ls	1	9	10	4	1	1
Total: spp.		1	6	8	4	1	1

**Table 7.** Vertebrate record (MNI) in a series Dolský mlýn A.

**Table 8.** Vertebrate record (MNI) in a series Dolský mlýn B

Dolský mlýn B	layer	4	5	6	6	9	9
	depth (cm)	55	85-90	110	110–120	130–135	"objekt 9"
Pisces	•					2	2
Anura, indet.						1	
Ophidia indet.						1	
Aves indet.				1			
Barbastella barba	astellus						1
Castor fiber				1			
Apodemus (Sylva	emus) sp.	1			1	1	1
Clethrionomys gla	areolus				1		
Arvicola terrestris	5				1		
Lepus europaeus			1		1	1	
Alces alces				?			
cf. Cervus elaphu.	5					1	
Capreolus capreo	olus						
cf. Meles meles						1	
Martes martes						1	
Vulpes vulpes					1		
Total: individua	ıls	1	2	2	5	9	4

**Table 9.** List of taxa supposedly hunted by Mesolithic people in the total samples obtained from the Northern Bohemian sandstone region

	Number of sites	Community samples	MNI
Sciurus vulgaris	6	12	18
Castor fiber	5	7	9
Lepus europaeus	13	24	35
Capreolus capreolus et cf.	10	17	20
cf. Cervus elaphus	5	8	9
Alces alces	7	10	10
Sus scrofa	5	6	8
Bosl Bison	2	2	2
Meles meles	3	3	3
Martes martes	5	14	26
Felis sylvestris	1	1	4
cf. Vulpes vulpes	3	3	3
Canis lupus	2	2	3
Aves, Passeriformes	5	15	23
Aves, non Passeriformes	5	6	8
Pisces 15 cm	2	4	6
Pisces 25 cm	2	2	2
Pisces 50 cm	1	1	1
Pisces 100 cm	1	1	1

Preboreal to the early post-Neolithic period (10 to 5 ky BP). Unfortunately, we did not succeed in obtaining any direct evidence on the structure of the glacial fauna of this region and thus are also unable to discuss the topical question of whether, and to what degree, the varied landscape of the Northern Bohemian sandstone region may have served as a glacial refugium (cf. Steward and Lister 2001, Horáček 2000). In any case, the beginning of the Holocene, as evidenced by the bottom members of the investigated series, is characterized

here by greatly diversified communities with considerably diverse habitat preferences with major roles for both the woodland elements and those demanding mesic semi-covered habitats. Worth mentioning is that such a community pattern is retained almost contuinuously until beginning of the late Holocene (i.e., including the early post-Neolithic period). The same holds for the other constitutional specificities of the respective communities: appearance of wetland elements (including rare relic species such as *Microtus oeconomus*,

*M. agrestis* or *Castor fiber*) and those inhabiting rocky habitats (particularly the lithophilous bats).

In comparison with the data from karstic regions, the studied series in the sandstone regions are remarkable also for the absence of a xerothermic stage with reexpansion of the open ground elements. Most of the open ground elements that soon reappeared with the Neolithic deforestration in other regions do not apear here at all, e.g. *Cricetus cricetus, Spermophilus citellus, Crocidura* spp. The early appearance of the garden dormouse (*Eliomys quercinus*), accompanied by the locally extinct *Sicista betulina*, suggests that the Northern Bohemian sandstone region has served as a refugium for this species

since the beginning of its Holocene immigration and a centre for its mid-European appearance. For this and other reasons, this region is quite specific and worthy of further study.

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Table 10. List of vertebrate records in the sites not presented in Tables 3-8. 1) high concentration of small bone fragments in all layers

Locality	Depth	Records (numbers indicate numbers of items)	C14 dating
Pod Zubem		1 Bufo bufo, 7 Rana temporaria, 6 Aves Passeriformes indet., 7 Aves, non Passeriformes, 2 Talpa europaea, 2 Spermophilus cf. citellus, 1 Sciurus vulgaris, 7 Arvicola terrestris, 1 Microtus avalis, 1 Microtus agrestis, 1 Microtus oeconomus, 1 Microtus indet., 2 Clethrionomys glareolus, 10 Apodemus sylvaticus, 3 Castor fiber, 4 Felis sylvestris, 10 Martes martes, 2 Putorius putorius, 5 Vulpes vulpes, 2 Canis lupus, 6 Lepus europaeus, 2 Cervus elaphus, 2 Capreolus capreolus, 1 cf. Alces alces, 1 Bos sp., 3 Sus scrofa, 2 cf. Capra.	7461–9124 cal. BP.
Zahrádky, Peklo		1 Clethrionomys glareolus	
Zámecký Rockshelter		1 Lepus europaeus, 1 cf. Capreolus capreolus	
Holany: U kamenného mostku		indet. fragments	
Pustý kámen, Velký převis		1 cf. Capra	
Dřevčice: Pod kamennou hlavou		indet. fragments cf. <i>Lepus</i> (juv.)	
Heřmánky: Žlutá skála			
Dřevčice: Srní převis			
Převis Pod Máselníkem		Felis cf. lybica dom., cf. Capreolus	
Butterberg, převis u jeskyně		Bufo bufo, indet. fragments	
Labské pískovce, Sojčí převis		Rana temporaria	
Uhelná rokle 2A	35–50	Lepus europaeus, cf. Cervidae, gr. Alces alces – md. and long bone fragments	
	45–50	Alces alces	
	55–60	Capreolus capreolus juv. ex.	
	100–115	cf. Capreolus capreolus	
	base	1 Anguis fragilis, 1 Microtus cf. arvalis, 3 Vallonia sp.	
Uhelná rokle, U obory	loess horizon	1 fragment – tibia Arvicolidae	
Okrouhlík <sup>1)</sup>	40-50	Aves gr. <i>Pica</i> , cf. <i>Cervus</i> fragments	
	50–60	Capreolus capreolus juv. a ad. ex.	
Lakota	40–70:	Alces alces tip of an antler	
	80–100	Lepus europeaus, Castor fiber, Castor fiber 1M1, Clethrionomys glareolus, Apodemus (Sylvaemus) sp., epus europaeus, LArvicola terrestris, Sus scrofa, Meles meles	
	120-130	Sciurus vulgaris, cf. Lepus europaeus	
	130-140	Aves indet.	