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Molluscan succession from Holocene tufas in the Czech Karst (Czech Republic)

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Abstract: A detailed molluscan succession from Holocene calcareous tufa deposits at the Kotýz Ridge and in the Císařská Gorge in the Czech Karst provides the most complete record from central Bohemia. The succession has been reconstructed from three profiles and chronology provided by AMS radiocarbon dating of charcoal and dating of carbonate by the U-series method. The early Holocene malacofaunas represented by occurrences of index species *Discus ruderatus*, accompanied by other boreo-montane elements (*Vertigo substriata*, *Vertigo alpestris*, *Perpolita petronella*), dominate in the earliest phases of tufa formation that is dated by the U-series method to 9460 ± 1200 years BP and 5920 ± 1520 years BP in the Císařská Gorge, or before the interval 5070–4800 years BC at the Kotýz Ridge. The change in composition of molluscan assemblages follows in the form of total replacement to Holocene Climatic Optimum (Atlantic, Epiatlantic) malacofaunas, consisting of several indicative elements (e.g. *Bulgarica cana*, *Truncatellina claustralis*), which are extinct or relatively rare in that region today, and even in the Czech Republic as well. The youngest phases of molluscan successions are represented by the accession of modern immigrants *Xerolenta obvia* and *Oxychilus cellarius*, never documented before from the Subboreal period in this region.

Key words: Holocene, Czech Republic, radiocarbon age, calcareous tufas, malacofauna.

Introduction

The faunal response to climatic and vegetational change during the Postglacial is known in far less detail, although the information is good for certain groups in certain regions. Land snails are unusual amongst invertebrates having a reasonably good fossil record, which could potentially be used to address several of the basic biogeographical and paleoenvironmental questions. The most valuable sequences are obviously those, which are continuous, cover long periods of time and furnish fossil assemblages that faithfully reflect the living communities from which they were derived. Relatively few deposits containing land snails fulfil all these conditions but calcareous tufa deposits meet these requirements in large measure (Preece 1991). The term tufa, sometimes subsumed under travertine, has been used for a range of secondary calcium carbonate deposits, but is here restricted to precipitates formed primarily by the degassing of bicarbonate-rich groundwaters around small springs. Many such deposits began to form during the early Holocene and are often several meters thick covering areas several hectares in extent. Tufas often yield shells of land snails and freshwater molluscs in abundance, so that by sampling the deposit at suitably fine resolution, it is possible to reconstruct the faunal history of the site in some details.

Over large parts of Europe from the British Isles to the Mediterranean and from Spain to the Czech Republic, Slovakia and Poland, the rates of calcareous tufa deposition were high in the early and middle Holocene, but declined markedly thereafter (Weisrock 1986). Over much of Europe, it has been postulated that in the late Holocene (since ~2500 years BP) there was a sharp decline in the deposition of tufa (Goudie et al. 1993). There has been a considerable debate about the causes of this phenomenon, with some authors stressing the importance of natural climatic changes, and others asserting that miscellaneous human activities (e.g. deforestation connected with agricultural activities) were crucial.

The Czech Karst, formed by Paleozoic limestones and located in the central part of Bohemia between Praha and Zdice, is an area with numerous deposits of calcareous tufa. In this karst area about 70 localities where calcareous tufa precipitates or was deposited in the past are known (Kovanda 1971; Ložek 1992; Kadlecová & Žák 1998). Several tens of springs in the Czech Karst deposited calcareous tufa from their waters during the early and middle Holocene. Tufa deposition continues at a number of localities in the Czech Karst at present, as well (Kadlecová & Žák 1998). In general, the three morphogenetic types of tufa accumulations can be distinguished (using terminology of Pedley 1990): 1 — *valley-side*, with perched spring accumulations on slopes, small in extent but locally large in thickness (a very frequent type, but carbonate precipitation is usually limited for this type under present-day conditions), 2 — *fluvial* accumulations in surface streams, usually braided but rarely small barrage types (with less or more intensive active deposition under present-day conditions), and 3 — *lacustrine and paludal* accumulations (inactive under present-day conditions, deposited in flat valleys, typically during the Holocene Climatic Optimum). Most of the calcareous tufa bodies of the Czech Karst show very similar lithological and biostratigraphic patterns, reflecting Holocene climatic, hydrological and biotic conditions (Ložek 1992). The largest calcareous tufa body in the Czech Karst is that at Svatý Jan pod Skalou (literally St. John under Rock), a 17 m thick valley-side-accumulation, representing a significant site for the Holocene stratigraphy and a unique archive of local climate and nature development (Ložek 1967; Kovanda 1971; Žák et al. 2001).

Geographical, geological and hydrogeological settings

The Czech Karst extends between Praha and Zdice over an area of ca. 200 km^2. With its NE margin, this karst area reaches to the territory of Prague. It is a warm and dry area lying at 210–500 m a.s.l. with total annual precipitation of 500 mm and average annual temperature of 8–9 °C (Quitt 1971).

The Czech Karst is located in the central part of the Prague Synform. This basin contains a continuous succession of Ordovician to Middle Devonian deposits accompanied by volcanic activity (Chlupáč et al. 1998). The Czech Karst itself, located south-west of Prague, is composed of upper Silurian shales, limestones and basalt lava flows (diabases) plus volcaniclastic rocks (tuffs) and Lower to Middle Devonian limestones and shales. During the Late Paleozoic Variscan Orogeny, sediments of the Prague Synform were folded into complicated anticlinal and synclinal structures and faulted (Chlupáč et al. 1998).

Groundwaters of the Paleozoic basin fill emerge in many places in the Czech Karst: along exposed boundaries between limestones and non-carbonate rocks near the bottoms of karstic valleys, and at fault intersections. Most of the karst springs are characterized by relatively stable discharge (between 0.1 and $20\,l\cdot s^{-1}$) and temperature, somewhat exceeding the average annual temperature of the area in some cases, which resulted from deeper karst-water circulation (Kadlecová & Žák 1998; Žák et al. 2001).

Detailed molluscan successions are reported here from the tufa sequence at Kotýz Ridge (49°55′12″ N, 14°02′55″ E), a tufa cascade deposited from karst water resurging in a spring named "Kotýz Good Water" lying about 5 km south of Beroun, and from two tufa cascades in Císařská Gorge (49°55′39″ N, 14°07′47″ E), about 6 km south-east of Beroun (Fig. 1). "Kotýz Good Water" spring is located on a transversal fault in Silurian shales and lens-like bodies of basalt flows. The water probably follows the fault and cracks from the near Devonian Koněprusy Limestone. The spring is the site of continuing precipitation of calcareous tufa while an inactive tufa cascade is preserved in the slope about 15 m above the spring. The Císařská Gorge is a valley 700 m long and over 100 m deep (Kadlecová & Žák 1998). Tufa is intensively precipitated from waters of a spring in the upper part of the valley. Tufa forms three cascades, marked by numbers I, II and III in the upstream direction (Fig. 1). Only Cascades I and II were subjects of this study.

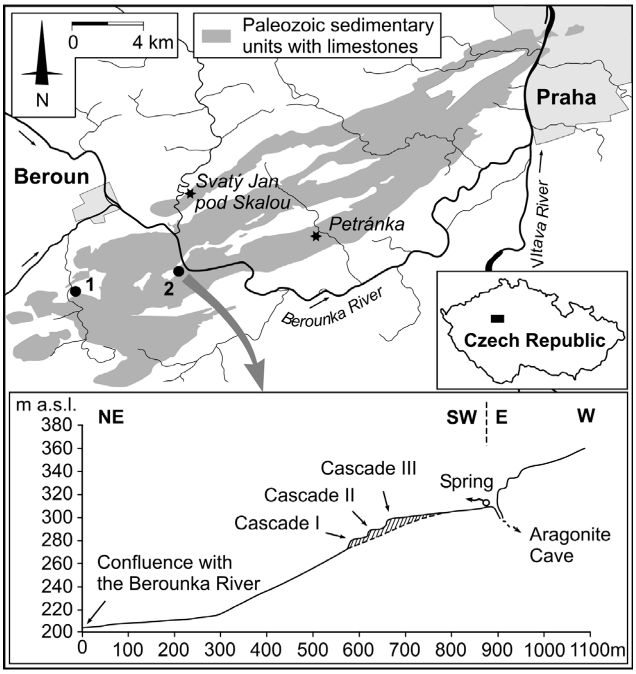

Fig. 1. Schematic map of the geographical position of calcareous tufas at Kotýz Ridge (No. 1) and in the Císařská Gorge (No. 2). Stars-like symbols mark tufa accumulations Svatý Jan pod Skalou and Petránka.

Material and methods

Malacozoological analyses

Acquisition of samples for paleomalacological and biostratigraphic analyses followed the unified methodology of Ložek (1964). If permitted by the character of the sediment, samples of the matrix approximately 4 l in volume were taken from all macroscopically distinguishable beds within the studied tufa sections. Molluscs were extracted from the sediments by a combination of washing and sieving. After careful drying, each sample was disaggregated in water. Floating snails, which included most of the shells in any sample, were repeatedly decanted into a 0.5-mm sieve and then dried in laboratory conditions. After, the sediment was divided into several arbitrary size fractions by sieving, to facilitate the picking of shells. These were systematically removed from the sediment fraction, which was sprinkled onto a black sorting tray and examined under a binocular microscope at variable magnification (×6 to ×50). The molluscs were picked using an entomological pair of delicate forceps. Individual shells (shell apices and undamaged shells) were counted, but non-apical fragments of species were also scored to whole individuals following the standard methodology (Ložek 1964).

The results are given in the form of tables of ecological and biostratigraphical categories (Tables 1, 2), including the number of taxa and the number of individuals. The percentage frequency mollusc diagram expresses relative proportions of the total number of species (MSS malacospectra) and total number of individuals (MSI malacospectra) within the principal ecological groups in that sample (Fig. 3). Attribution of molluscan species to the ecological categories in the tables and diagram follows Ložek (1964) and Alexandrowicz (1987). These ecological attributions must be regarded as rather general, for several species do not fit neatly into any one specific habitat. Taxonomic nomenclature follows Juřičková et al. (2001). All the specimens resulting from this study have been deposited in the Institute of Geology AS CR in Prague.

Radiocarbon dating analyses

Dating analyses were performed in the Poznań Radiocarbon Laboratory, Poland. Small pieces of charcoal (after treatment with hot solutions of acid, alkali, and acid to remove all carbonate carbon and easily soluble organics) were measured by the AMS (Accelerator Mass Spectrometry) method. The ^{14}C data on organic matter have been calibrated for variable initial ^{14}C concentration using the OxCal v3.5 calibration program (Bronk 2001).

Kotýz Ridge

The tufa cascade at Kotýz Ridge (No. 1 in Fig. 1) is preserved in the slope 15 m above the present karst spring. The tufa sequence was exposed by a test hole (Fig. 2). The section can be subdivided into 16 beds, including the layers underlaining and overlaining the tufa body. Molluscan shells are present in all layers, excepting Beds Nos. 15, 14, and 10 (Table 1). Although the basal complex (Beds Nos. 16 to 10) is of very low species diversity due to poor fossilization ability, it occasionally yielded species like *Vertigo substriata*, *Perpolita petronella* and *Vitrea crystallina*, characteristic of the early Holocene. This complex completely lacks typical glacial species, however, the accompanying species *Vallonia costata* and *V. pulchella* indicate the presence of open habitats of dry to mesic character. The malacofauna from the overlying Beds Nos. 9 to 1 markedly differs from that of the basal complex (Beds Nos. 16 to 10) in the fossil malacofauna they contain. The bed of solid structural tufa (Bed No. 9) already shows a gradual increase in forest species, but the open ground species still maintain a markedly higher abundance. It was only in this bed that the early Holocene species *Discus ruderatus* was rarely encountered. From Bed No. 8 upwards, a rapid boom of forest species occurs at the expense of open-country elements. Molluscan species in this bed document closed woodland conditions, also persisting in the overlying complex (Beds Nos. 7 to 4). Fossil molluscs from Bed No. 8 and from the interval of Beds Nos. 7 to 4 indicate environmental conditions of the Holocene Climatic Optimum, namely a massive expansion of woodland molluscan species such as *Bulgarica cana*, *Vitrea diaphana*, *Platyla polita*, *Vertigo pusilla* etc., and high abundance of the hygrophilous element *Carychium tridentatum*, whereas the open-country elements and the majority of catholic elements disappeared or became very

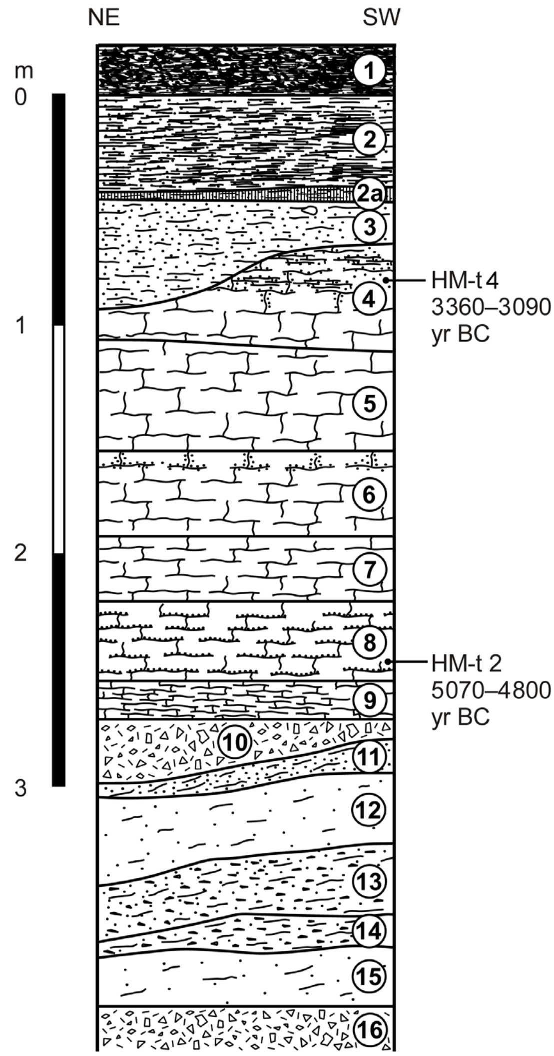

Fig. 2. The studied section of the tufa deposit at Kotýz Ridge, frontal view. Lithology: **1** — dark brown humic Rendzic Leptosol with sporadic limestone and diabase clasts (4 cm in diameter); **2** — dark yellowish brown slightly humic soil sediment with rare limestone clasts (0.5 cm); **2a** — very dark greyish brown slightly humic soil sediment; **3** — dark brown slightly humic soil sediment with abundant tufa encrustations; **4** — pale brown fine-grained tufa with coarse encrustations in the upper portion of the bed and dark stains coloured with Fe and Mn oxides; **5** — light yellowish brown tufa; **6** — yellowish brown tufa with coarse encrustations in the upper portion of the bed; **7** — very dark greyish brown tufa with rare, very dark brown Silurian shale clasts; **8** — very dark brown mouldered slightly loamy tufa with rare shale clasts; **9** — dark greyish brown solid tufa with shale clasts; **10** — very dark brown shales (clasts 1 cm in diameter), dark greyish brown loamy matrix; **11** — very dark brown shales (clasts 2 cm in diameter) with tufa encrustations (30 %), dark brown loamy matrix; **12** — very dark brown shales (clasts 2 cm in diameter) with sporadic tufa encrustations, very dark grey matrix; **13** — very dark brown shales (clasts 2 cm in diameter) with sporadic tufa encrustations, very dark greyish brown matrix; **14** — very dark brown shales (clasts 3 cm in diameter) with tufa encrustations (20 %), dark stains coloured with Fe and Mn oxides, dark yellowish brown matrix; **15** — very dark brown shales (clasts 4 cm in diameter) with sporadic tufa encrustations, very dark greyish brown loamy matrix; **16** — very dark brown shales (clasts 5 cm in diameter), very dark greyish brown loamy matrix.

Ecology and biostratigraphy				List of species	Layer													
					16	13	12	11	9	8	7	6	5	4	3	2a	2	1
A	1		!	*Acanthinula aculeata* (Müller)	–	–	–	–	3	18	77	63	24	75	7	5	1	95
			!	*Aegopinella pura* (Alder)	–	–	–	–	3	18	132	86	21	104	14	13	2	56
			!	*Bulgarica cana* (Held)	–	–	–	–	–	3	4	1	1	–	–	–	–	–
			!	*Cochlodina laminata* (Montagu)	–	–	–	–	1	5	19	6	–	15	10	5	1	3
			(G)	*Discus ruderatus* (Férussac)	–	–	–	–	3	–	–	–	–	–	–	–	–	–
			!	*Ena montana* (Draparnaud)	–	–	–	–	–	–	1	2	–	3	2	2	–	–
			!	*Helicodonta obvoluta* (Müller)	–	–	–	–	–	–	–	–	–	–	3	1	–	–
			!	*Isognomostoma isognomostomos* (Schr.)	–	–	–	–	–	–	–	–	–	1	2	4	2	1
			!	*Macrogastra plicatula* (Draparnaud)	–	–	–	–	–	2	4	–	1?	1	–	–	1	–
			!	*Merdigera obscura* (Müller)	–	–	–	–	–	–	7	1	–	–	2	1	–	–
			!	*Monachoides incarnatus* (Müller)	–	–	–	–	1	3	7	8	5	7	2	3	2	6
			!	*Petasina unidentata bohemica* (Ložek)	–	–	–	–	–	–	23	8	–	1	–	–	–	–
			!	*Platyla polita* (Hartmann)	–	–	–	–	–	3	48	19	16	28	3	2	–	1
			!	*Ruthenica filograna* (Rossmässler)	–	–	–	–	–	–	–	–	–	–	–	1	–	–
				Semilimax semilimax (Férussac)	–	–	–	–	–	–	1?	1	–	1	–	–	–	–
			!	*Sphyradium doliolum* (Bruguiére)	–	–	–	–	–	24	95	38	18	51	27	14	2	3
			(!)	*Vertigo pusilla* Müller	–	–	–	–	–	7	18	11	10	30	–	3	–	–
			!	*Vitrea diaphana* (Studer)	–	–	–	–	–	2	20	34	6	19	2	4	–	–
	2	W(M)	!	*Alinda biplicata* (Montagu)	–	–	–	–	–	–	1	10	2	8	7	2	1	2
			(+)	*Arianta arbustorum* (Linnaeus)	–	–	–	–	–	–	–	–	–	1?	–	–	–	–
			!	*Cepaea hortensis* (Müller)	–	–	–	–	–	–	1	–	–	1	–	–	1	1
			!	*Discus rotundatus* (Müller)	–	–	–	–	2	31	64	32	16	50	44	32	3	5
		W(S)	!	*Aegopinella minor* (Stabile)	–	–	–	–	6	46	181	109	25	174	35	26	5	75
			(!)	*Fruticicola fruticum* (Müller)	–	–	–	–	8	14	11	4	2	1	2	3	1	1
			!	*Helix pomatia* Linnaeus	–	–	–	–	2	6	7	1	–	–	1	2	1	2
		W(H)	(+)	*Vitrea crystallina* (Müller)	1	1	–	–	–	–	–	–	–	–	–	–	–	–
	3	W(h)	(G)	*Clausilia pumila* C. Pfeiffer	–	–	–	–	–	–	4	–	–	–	–	–	–	–
			!	*Macrogastra ventricosa* (Draparnaud)	–	–	–	–	–	8	10	2	3	5	–	2	–	–
			!	*Urticicola umbrosus* (C. Pfeiffer)	–	–	–	–	–	1	1	2	–	2	1	1	1	2
B	4	S	M	*Cecilioides acicula* (Müller)	–	–	–	–	–	–	–	(2)	–	7	37	26	83	26
			(+)	*Granaria frumentum* (Draparnaud)	–	–	–	–	–	1	–	–	–	–	–	–	–	–
				Xerolenta obvia (Menke)	–	–	–	–	–	–	–	–	–	–	–	–	1	–
		S(W)	!!	*Cepaea vindobonensis* (Férussac)	–	–	–	–	–	–	–	–	1?	2	–	2	1	–
	5		+	*Pupilla muscorum* (Linnaeus)	–	–	–	–	–	–	–	–	–	–	33	129	4	2
			(!)	*Truncatellina cylindrica* (Férussac)	–	–	–	–	1	7	4	–	–	–	75	102	86	39
			(+)	*Vallonia costata* (Müller)	1	4	–	4	85	32	10	–	1	1	91	89	112	1
				Vallonia excentrica Sterki	–	–	–	–	–	1	1	–	–	–	16	2	15	1
			G	*Vallonia pulchella* (Müller)	–	–	–	1	41	72	64	3	–	1	217	34	321	8
			(G)	*Vertigo pygmaea* (Draparnaud)	–	–	–	–	2	2	1	–	2	2	63	38	61	2
C	6		!	*Bulgarica nitidosa* (Uličný)	–	–	–	–	–	2	1	–	–	–	1	2	–	–
			(!)	*Cochlicopa lubricella* (Porro)	–	–	–	–	5	6	5	–	–	–	5	12	45	1
			(!)	*Euomphalia strigella* (Draparnaud)	–	–	–	–	–	3	2	–	–	1	1	3	2	3
	7	Me	(+)	*Cochlicopa lubrica* (Müller)	–	–	–	–	–	2	1	–	–	–	–	1	–	2
			(+)	*Euconulus fulvus* (Müller)	–	–	–	–	–	–	–	1	–	1	–	–	–	3
			(+)	*Limacidae* sp. div.	–	–	–	–	–	1	–	–	–	–	4	–	2	1
			M	*Oxychilus cellarius* (Müller)	–	–	–	–	–	–	–	–	–	–	–	1?	–	3
			(+)	*Perpolita hammonis* (Ström)	–	–	–	–	–	8	6	–	–	–	1	–	3	–
			(+)	*Punctum pygmaeum* (Draparnaud)	–	–	1	–	5	14	42	60	44	129	23	10	15	56
			+	*Trichia hispida* (Linnaeus)	–	–	–	–	–	–	–	–	–	–	2	–	1	13
			(+)	*Trichia sericea* (Draparnaud)	–	–	–	–	1	–	–	–	–	–	–	–	–	–
			(G)	*Vitrina pellucida* (Müller)	–	–	–	–	1	–	–	–	–	–	–	–	–	11
		Wf	!	*Helicigona lapicida* (Linnaeus)	–	–	–	–	–	–	–	–	–	–	1	1	1	–
			!	*Laciniaria plicata* (Draparnaud)	–	–	–	–	–	–	2	–	–	–	–	–	–	–
	8		!	*Carychium tridentatum* (Risso)	–	1	3	1	35	271	640	248	223	562	54	70	8	197
			(!)	*Columella edentula* (Draparnaud)	–	–	–	–	–	2	–	3	4	1	–	–	–	–
				Perpolita petronella (L. Pfeiffer)	–	–	–	2	6	1	–	–	–	–	–	–	–	–
				Vertigo substriata (Jeffreys)	–	–	–	1	–	–	–	–	–	–	–	–	–	–
D	9		G	*Carychium minimum* Müller	–	–	–	–	–	–	2	–	–	7	–	–	–	–
			(G)	*Vertigo angustior* Jeffreys	–	–	–	–	6	2	1	–	–	–	3	2	–	–
	10	*SQPp*	(+)	*Galba truncatula* (Müller)	–	–	–	–	–	–	–	–	–	1	2	1	–	1
		FPpQ		*Pisidium personatum* Malm	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Number of species					2	3	2	5	20	33	38	26	21	33	35	38	31	32
Number of individuals					2	6	4	9	217	618	1518	755	426	1293	793	651	785	623

Table 1: Assemblages of Mollusca in individual layers of calcareous tufa at Kotýz Ridge. Layer number relate to Fig. 2. Ecological characteristics: General ecological groups: **A** — woodland (in general); **B** — open country; **C** — woodland/open country; **D** — water, wetlands. Ecological groups: **1** — woodland (*sensu stricto*); **2** — woodland, partly semi-open to open habitats [W(M) — mesic, W(S) — xeric, W(H) — damp]; **3** — damp woodland; **4** — xeric open habitats [S — in general, S(W) — partly shaded habitats]; **5** — open habitats in general (moist meadows to steppes). Woodland/open country: **6** — predominantly dry; **7** — mesic or various (Me — mesic in general, catholic, Wf — mesic rocks, scree woodland); **8** — predominantly damp; **9** — wetlands, banks; **10** — aquatic habitats (*S* — swamps, *Q* — springs, *F* — running waters, *Pp* — periodic). Biostratigraphic characteristics: **+** — loess species, **(+)**— local or occasional loess species, **!** — species characteristic of warm phases, **(!)** — eurythermic species of warm phases, **!!** — index species of warm phases, **G** — species surviving the Glacial out of the loess zone, **(G)** — ditto as relics, **M** — modern immigrants (late Holocene index species). Presence in layers: **1** — number of individuals, **1?** — only approximate determination, **(1)** — contamination, **–** — absent.

Table 2: Assemblages of Mollusca in selected layers of calcareous tufa in the Císařská Gorge. Mollusc finds relate to Figs. 4 and 5. Cascade I: **sample 1** — the layer of massive porous brown yellowish calcareous tufa; **sample 2** — the layer of limestone scree cemented by brown porous carbonate. Cascades II — sample from the layer of limestone scree cemented by brown porous carbonate. Ecological and biostratigraphical characteristics see Table 1.

Ecology and biostratigraphy				List of species	Cascade I		Cascade II
					2	1	
A	1		!	*Acanthinula aculeata* (Müller)	–	40	4
A	1		!	*Aegopinella pura* (Alder)	–	51	3
A	1		!	*Cochlodina laminata* (Montagu)	–	3	–
A	1		!	*Cochlodina orthostoma* (Menke)		1	1
A	1		(G)	*Discus ruderatus* (Férussac)	10	1	21
A	1		!	*Ena montana* (Draparnaud)	–	2	3
A	1		!	*Isognomostoma isognomostomos* (Schr.)	–	2	3
A	1		!	*Macrogastra plicatula* (Draparnaud)	–	5	2
A	1		!	*Merdigera obscura* (Müller)	–	2	–
A	1		!	*Monachoides incarnatus* (Müller)	1	1	1
A	1		(G)	*Oxychilus depressus* (Sterki)	–	3	1
A	1		!	*Petasina unidentata bohemica* (Ložek)	–	7	2
A	1		!	*Platyla polita* (Hartmann)	2	23	1
A	1		!	*Ruthenica filograna* (Rossmässler)	–	5	1
A	1			*Semilimax semilimax* (Férussac)	–	4	1
A	1		!	*Sphyradium doliolum* (Bruguiére)	–	107	2
A	1		(!)	*Vertigo pusilla* Müller	–	60	7
A	1		!	*Vitrea diaphana* (Studer)	–	10	–
A	2	W(M)	!	*Alinda biplicata* (Montagu)	–	8	–
A	2	W(M)	!	*Cepaea hortensis* (Müller)	–	2	–
A	2	W(M)	!	*Discus rotundatus* (Müller)	–	124	4
A	2	W(S)	!	*Aegopinella minor* (Stabile)	–	43	1
A	2	W(S)	(!)	*Fruticicola fruticum* (Müller)	3	2	1
A	2	W(H)	(+)	*Vitrea crystallina* (Müller)	14	27	4
A	3	W(h)	(G)	*Clausilia pumila* C. Pfeiffer	–	1	–
A	3	W(h)	!	*Macrogastra ventricosa* (Draparnaud)	–	16	–
A	3	W(h)	!	*Urticicola umbrosus* (C. Pfeiffer)	–	10	–
B	4	S(W)	!!	*Truncatellina claustralis* (Gredler)	–	3	–
B	5		(!)	*Truncatellina cylindrica* (Férussac)	–	9	–
B	5		(+)	*Vallonia costata* (Müller)	19	305	11
B	5		G	*Vallonia pulchella* (Müller)	–	–	2
B	5		(G)	*Vertigo pygmaea* (Draparnaud)	–	1	–
C	6		!	*Bulgarica nitidosa* (Uličný)	–	7	–
C	6		(!)	*Cochlicopa lubricella* (Porro)	–	10	–
C	7	Me	(+)	*Cochlicopa lubrica* (Müller)	1	12	1
C	7	Me	(+)	*Euconulus fulvus* (Müller)	3	7	2
C	7	Me	(+)	*Limacidae* sp. div.	–	2	1
C	7	Me	(+)	*Punctum pygmaeum* (Draparnaud)	17	124	1
C	7	Me	+	*Trichia hispida* (Linnaeus)	–	1	–
C	7	Me	(G)	*Vitrina pellucida* (Müller)	–	1	–
C	7	Wf	!	*Laciniaria plicata* (Draparnaud)	–	1	–
C	7	Wf	G	*Vertigo alpestris* Alder			2
C	8		!	*Carychium tridentatum* (Risso)	–	595	32
C	8		(!)	*Columella edentula* (Draparnaud)	–	18	–
C	8			*Perpolita petronella* (L. Pfeiffer)	–	–	3
Number of species					9	42	28
Number of individuals					70	1656	118

rare (e.g. *Vallonia excentrica* and *Truncatellina cylindrica* are completely absent from Beds Nos. 6 to 4).

The abundance of open-country species increases and that of moist woodland species decreases within Beds Nos. 2 and 3. After the decline of tufa deposition the cascade was covered by dark brown humic soil sediment with an increasing number of rock fragments redeposited from the upper part of the slope. The appearance of modern immigrants (e.g. *Oxychilus cellarius*) is characteristic of this uppermost bed.

Radiocarbon dates and chronology of tufa deposition

Charcoal from Beds Nos. 8 and 4 was subjected to ^{14}C dating (Table 3, Fig. 2). Based on the obtained data and the occurrence of fossil molluscan assemblages, horizons of different age can be distinguished in the tufa accumulation. Tufa deposition started in the Boreal period. Solid tufa with rare shale fragments (Bed No. 9) contains molluscan fauna indicating a moist, light forest environment with decreasing abundance of species *Discus ruderatus*, *Trichia sericea* and *Perpolita petronella*. The underlying Beds Nos. 16 to 10 can thus generally be dated to the Late Glacial to Preboreal because of the sporadic occurrence of tolerant molluscan species and the prevalence of early Holocene elements. The interval between Beds Nos. 8 and 4 is characterized by extensive development of woodland communities; the abundance of hygrophilous elements dominated by *Carychium tridentatum* indicates a humid climate. This interval can be attributed to the Holocene Climatic Optimum — Atlantic and Epiatlantic, as was also confirmed by ^{14}C dating to the period of 5070–3090 years BC (Fig. 2). In Bed No. 3, the accumulation of tufa declines, and the recovered molluscan assemblages from this bed point to a prominent drying and a massive retreat of forests, reflected by a prominent spread of open-country elements such as *Truncatellina cylindrica*,

Table 3: AMS radiocarbon age determinations from charcoal recovered from the calcareous tufa at Kotýz Ridge.

Sample name	Material	Conv. Age ± Err. yr BP ^{14}C	Calib. Age y. BC ^{14}C (95.4 % probability)	Laboratory code
HM-t 2	charcoal	6054 ± 42	5070–4800	Poz-1303
HM-t 4	charcoal	4508 ± 33	3360–3090	Poz-1304

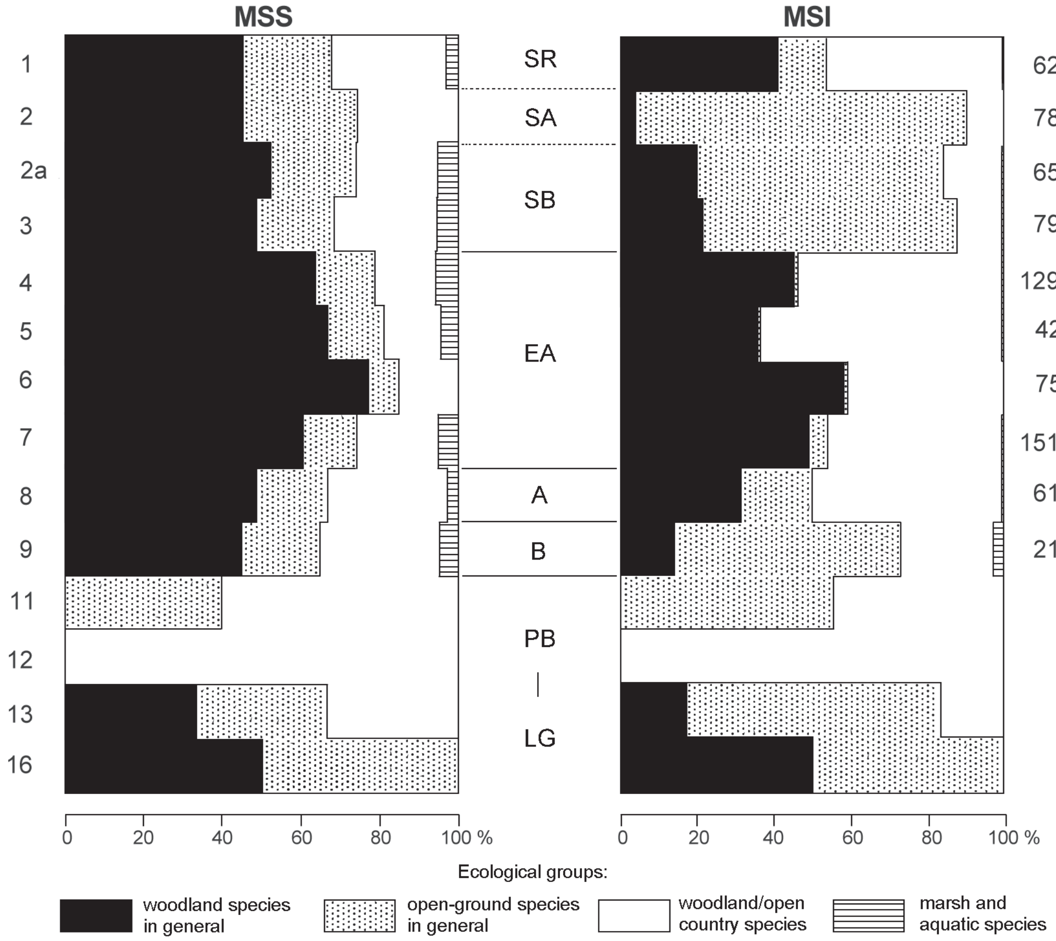

Fig. 3. Malacospectra MSS and MSI of Kotýz Ridge. Left-side column — layer, middle — chronology (LG — Late Glacial, PR — Preboreal, B — Boreal, A — Atlantic, EA — Epiatlantic, SB — Subboreal, SA — Subatlantic, SR — Subrecent), right-side column — total number of individuals.

Pupilla muscorum, *Vertigo pygmaea* and common representatives of the genus *Vallonia.* This trend continues in the overlying strata. Beds Nos. 3 to 1 must be therefore placed to the late Holocene (Subboreal, Subatlantic and Subrecent), which is also indicated by the appearance of modern immigrants such as the steppe mollusc *Xerolenta obvia* in Bed No. 2 and the ecologically indifferent *Oxychilus cellarius* in Bed No. 1.

Císařská Gorge

Tufa is intensively precipitated from waters of a spring in the upper part of the valley. It forms three cascades, marked by numbers I, II and III in the upstream direction. Only Cascades I and II were subjects of this study (No. 2 in Fig. 1).

Limestone scree cemented by carbonate is deposited on the base of the thickest cascade — Cascade I. Above the scree, a bed of solid structural tufa was deposited, laterally interfingering with slope sediments. A young tufa accumulation is presently growing in the erosive channel cutting the cascade (Fig. 4). Cascade II, lying ca. 130 m upstream, has an analogous lithological character (Fig. 5).

In both cascades, samples corresponding to their radiometrically dated bed level (Hlaváč et al. 2003) were selected for malacozoological and malacostratigraphic analysis (sampling points in Figs. 4 and 5, Table 2). Fossil molluscs from the bed of massive porous brown yellowish calcareous tufa from Cascade I (Fig. 4) are markedly dominated by woodland species. The gastropods *Sphyradium doliolum*, *Platyla polita*, *Vertigo pusilla*, *Aegopinella pura*, *Discus rotundatus*, *Macrogastra ventricosa*, *Alinda biplicata*, *Clausilia pumila* and other species were found in high amounts. These are accompanied by woodland species of medium size (*Monachoides incarnatus*, *Urticicola umbrosus*, *Cepaea hortensis*), again highly abundant. Catholic species of ecologic group C reach higher abundance than open-country and forest-free elements, which are considerably less frequent and restricted only to the species *Vallonia costata* and the rare *Truncatellina cylindrica*, probably transported from the ambient steep slopes. Fossil malacocoenosis clearly indicates a moist, closed forest covering the valley area, which was getting lighter towards higher elevations.

A poor molluscan assemblage dominated by *Vallonia costata*, *Punctum pygmaeum* and *Vitrea crystallina* was

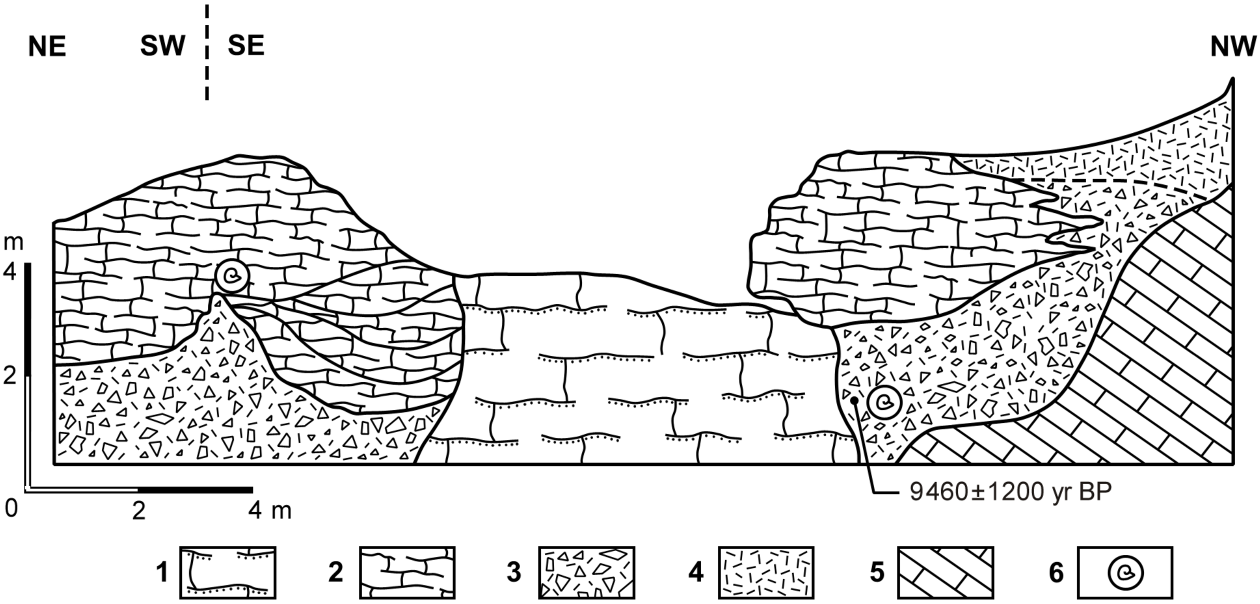

Fig. 4. Tufa Cascade I in the Císařská Gorge, frontal view. Lithology: **1** — the youngest calcareous tufa; **2** — massive porous brown yellowish calcareous tufa; **3** — limestone scree cemented by brown porous carbonate, angular clasts with average size of 4 cm; clast size up to 10 cm in the upper part; **4** — grey loose limestone scree; **5** — limestone bedrock; **6** — sampling point on fossil molluscs.

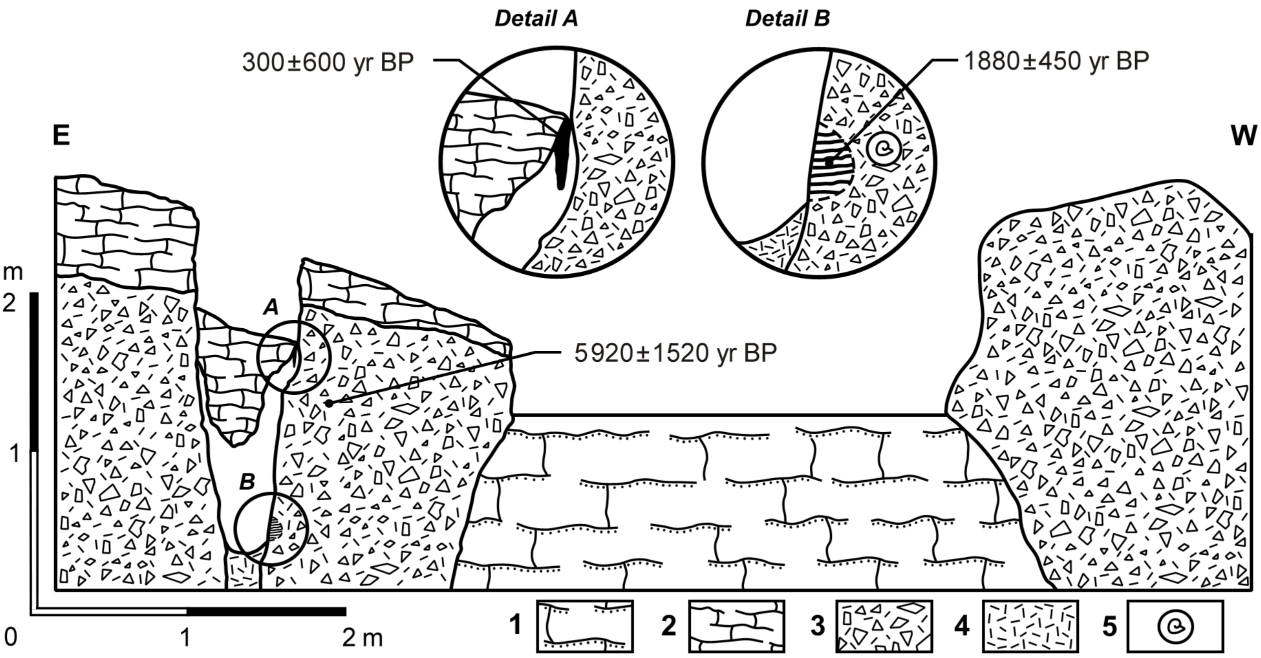

Fig. 5. Tufa Cascade II in the Císařská Gorge, frontal view. Lithology: **1** — the youngest calcareous tufa; **2** — massive porous yellowish brown calcareous tufa; **3** — limestone scree cemented by brown porous carbonate, angular clasts with average size of 4 cm, clast size up to 10 cm in the upper part; **4** — grey loose limestone scree; **5** — sampling point on fossil molluscs. Detail "A" shows a bed of dated carbonate precipitated on plant roots. Detail "B" shows the position of carbonate laminae precipitated in a small cavity developed in limestone scree.

recorded in the underlying bed of limestone scree cemented by brown porous carbonate from Cascade I (Fig. 4). These tolerant species were occasionally accompanied by the early Holocene element of *Discus ruderatus* and ecologically indifferent *Cochlicopa lubrica* together with *Euconulus fulvus*. The rate of woodland species in this bed was very low being represented only by the species *Monachoides incarnatus* and *Platyla polita*. A similar snail assemblage was also observed in the sample collected from the bed of limestone scree cemented by brown porous carbonate from Cascade II (Fig. 5). The common *Discus ruderatus* and *Perpolita petronella* are associated with

Vertigo alpestris, *Discus rotundatus*, *Aegopinella minor*, *Trichia hispida* and *Ena montana*, accompanied by the indifferent species *Punctum pygmaeum*, *Cochlicopa lubrica* and *Euconulus fulvus*. Both of these beds are completely lacking any of the prominent elements of continuous forest characteristic of the Holocene Climatic Optimum or the youngest Holocene.

Radiometric dates and chronology of tufa deposition

As indicated by molluscan remains in the beds of limestone scree cemented by brown porous carbonate from Cascades I and II, their fill can be dated to the early Holocene. This is suggested not only by the common occurrence of early Holocene species *Discus ruderatus*, *Perpolita petronella*, *Vitrea crystallina* and even *Vertigo alpestris*, but also by the notable absence of elements indicative of a continuous forest of the Climatic Optimum. The early Holocene age of the scree is also confirmed by the radiometric age of its carbonate matrix — 9460 ± 1200 years BP (Hlaváč et al. 2003). The encountered assemblages indicate rather the Boreal period (sample from Cascade I), or possibly a transition between the Boreal and early phases of the Atlantic (sample from Cascade II) with carbonate matrix dated at 5920 ± 1520 years BP (Hlaváč et al. 2003). The landscape of this period had the character of open areas alternating with patches of shady deciduous forests having, however, a different composition than the present ones. Moisture conditions were already more favourable but still did not permit the development of more continuous woodland complexes, as documented by the notable absence of demanding woodland molluscan species or only a low proportion of hydrophilous elements.

In contrast with the underlying beds, malacostratigraphic analysis of a sample from the bed of massive porous brown yellowish calcareous tufa from Cascade I (Fig. 4) yielded malacofauna indicating the Holocene Climatic Optimum — Atlantic and Epiatlantic (*sensu* Jäger 1969). The evidence for this is the almost complete absence of open-country elements as well as by the lack of early Holocene elements or elements from the youngest phases of the Holocene. In a time succession, the Císařská Gorge was first filled with talus with angular scree fragments in the early Holocene (Preboreal, Boreal to early phases of the Atlantic). The scree was later overlain by accumulations of structural tufa precipitated during the Holocene Climatic Optimum (Atlantic, Epiatlantic).

Discussion and conclusions

Holocene development of tufa cascades of the Czech Karst shares many common features conditioned by climatic and hydrologic influence. The formation of cascade, on the bottoms of karstic valleys, must have postdated the end of intensive fluvial erosion characteristic of the Glacial/Holocene boundary (see Vandenberghe 1993; Vandenberghe et al. 1994, a.o.). The tufa is usually underlain by limestone talus derived from the ambient slopes. Thicknesses of preserved talus depend largely on the character of the source Paleozoic rocks forming valley slopes (e.g. stratification and tectonic deformation) and on the erosive potential of the stream at the site the cascade started to develop. Molluscan assemblages found in talus beneath the tufa are evidence of the Boreal age of these colluvia.

Talus in the Císařská Gorge is secondarily cemented by carbonate precipitated from karst waters. Radiometric age of the cement was determined at 9460 ± 1200 years BP and 5920 ± 1520 years BP (Hlaváč et al. 2003). The tufa cascade at Svatý Jan pod Skalou also started to accumulate in the Boreal (Žák et al. 2001, 2002). Massive structural tufas with minimum clastic component were deposited on all cascades under the climatically favourable condition of the Atlantic. Accumulations of these structural tufas reach up to 2–5 m in thickness (Kovanda 1971; Ložek 1992). Deposition of tufa continued in the late period of the Holocene Climatic Optimum (Epiatlantic). Short-term climatic oscillations, however, occurred in the Epiatlantic, being characterized by alternation of periods of relative aridity and humidity. These short-term climatic oscillations are indicated by horizons of initial carbonate soils and by talus intercalations in the tufa successions. Climatic oscillations culminated in a markedly dry and warm period in the Subboreal (e.g. Jäger 1969). As a result, the sedimentary record in younger portions of the tufa cascades is lithologically more variable, with alternating beds of friable and compact tufa, colluvio-fluvial sediments and soil horizons (Žák et al. 2001). Principal accumulation stages of tufa cascades in the Czech Karst are terminated in the late Subboreal at 2500 BP (Žák et al. 2002).

The decline of cascade development was due to the coming dry period, probably manifested in a discharge reduction of the karst springs. Reduced water discharges could have resulted from subrosion, which created new paths in the basal portions of the tufa bodies. Karst waters ceased to flow on top of the cascade surfaces. The onset of this dry period dates to the Late Bronze Age (LBA); it resulted in dramatic changes in vegetation and in molluscan communities, but also in a decrease in the activity of river systems. These phenomena have been documented from many regions of the Czech Republic. A major environmental change dating to the LBA has been documented from central and northern Bohemia on the basis of multidisciplinary study of sediments deposited under sandstone rock-shelters. Changes in molluscan communities indicate deforestation associated with more intensive agricultural use of land (Svoboda et al. 1996; Cílek et al. 1996).

It can be assumed that erosion and destruction of tufa cascades in the Czech Karst occurred during several flash precipitation events in the Little Ice Age (LIA) and due to increased precipitation and severe floods in the 20th century. Larger volumes of water flowing through the Císařská Gorge during the LIA are also indicated by the radiometric age of the carbonate precipitated on plant roots in Cascade II (Hlaváč et al. 2003). The carbonate was precipitated on the root at 300 ± 600 years BP, namely at the time of the undoubted existence of the fracture destroying the cascade (see above). At that time, however, water must have been still flowing across the upper part of the cascade.

The molluscan assemblages detected in the tufa bodies show many common features. Malacospectral analyses of tufa at Kotýz Ridge (Fig. 2) revealed the proportions of molluscs of the main ecological groups. As the underlying complex of the tufa bodies at Kotýz (Beds Nos. 16–11) contain very poor malacozoological material, the ratio between the woodland malacofauna component and open-habitat component or indifferent species is biased to a considerable degree. In contrast, the overlying beds contain high numbers of molluscan species already and are fully eligible for statistical evaluation. As shown by the malacospectra, the overlying beds of the Atlantic-Epiatlantic Climatic Optimum marked by intensive tufa accumulation are dominated by woodland species in the malacocoenoses, while open-country species are scarcely represented (Svatý Jan pod Skalou, Kotýz) or present in very low proportions at Petránka (Hlaváč et al. 2003). This indicates closed woodland formations with prevalence of moisture demanding molluscan species. After the Epiatlantic phase, climatic oscillations culminate with the Subboreal period characterized by a reduced woodland component and the onset of open-country elements. This is particularly obvious from the malacospectra of tufas from Svatý Jan pod Skalou and Kotýz (Hlaváč et al. 2003). In the Petránka tufa in the Karlické Valley, the Subboreal period is characterized by the abundant occurrence of gastropod *Vallonia costata*, a typical open-country species, however, the woodland component still maintains a clear dominance. Molluscan assemblages from the youngest Holocene phases often share the features of modern communities as shown by molluscan occurrences in the neighbourhood of the tufa bodies (Ložek 1974; Hlaváč 2002).

The Kotýz Ridge and Císařská Gorge assemblages contain a number of species that are absent in the Czech Karst at present. Indeed, they include the boreo-montane species *Discus ruderatus*, *Vertigo substriata*, *Vertigo alpestris*, and *Perpolita petronella*, that are confined to montane and submontane zones in the Czech Republic at present, while during early Holocene they formed the leading index *Discus ruderatus*-fauna (Ložek 1964). Other species, for instance *Bulgarica cana*, although occurring during the Holocene Climatic Optimum at Kotýz Ridge, or in the Císařská Gorge, and at Svatý Jan pod Skalou (Žák et al. 2001, 2002) is now extinct in the Czech Karst and even extremely rare in the Czech Republic. These early Holocene land snail assemblages have no exact modern analogues in the Czech Republic, whereas the malacofaunas of the Climatic Optimum have survived in a few relic forest habitats, for instance in the near by Křivoklát Area.

There are relatively few continental sites that have been investigated in such details as these Kotýz Ridge and Císařská Gorge sequences and those often lack secure radiocarbon dates. Much work has been undertaken in Central Europe, particularly in the Czech Republic and Slovakia (e.g. Ložek 1964, 1982), Hungary (Füköh et al. 1995) and Poland (e.g. Alexandrowicz 1983). Only the tufa deposits at Svatý Jan pod Skalou and Švarcava (Czech Republic) as well as Slovenská dolina Valley (Slovak Republic) provide radiocarbon dates (Šilar & Ložek 1988; Žák et al. 2001). In addition, a considerable number of ^{14}C-dated Holocene snail successions are available from archaeological excavations in North-Bohemian sandstone rock-shelters (Svoboda 2003) and from calcareous tufa deposits in southern Poland (Alexandrowicz 2004). Faunal development shows strong parallels with the succession described from the Czech Karst. Early Holocene assemblages are rather different than present-day molluscan faunas at these sites. Also middle Holocene ones are again far richer than the faunas living in those regions today. The species composition described from Western Germany and Luxembourg are, however, quite different. The species *Spermodea lamellata* and *Leiostyla anglica* characterize middle Holocene assemblages there (Meyrick 2001, 2003), whereas they are unknow in Central Europe. Some work has recently been undertaken on sequences in Britain and close to Britain (Preece & Day 1994; Limondin-Lozouet 1998; Meyrick & Preece 2001), but these regions are too distant for meaningful comparisons. Further discussion should be deferred until more mid-European sites have been investigated. Only then it will be possible to consider the Czech data in its full European and British context.

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