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Last Glacial paleoenvironments of the West Carpathians in the light of fossil malacofauna

Prostředí posledního glaciálu v Západních Karpatech ve světle fosilní malakofauny

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Abstract: Talus accumulations at Farkašovo (Central Slovakia) and Brzotín (Slovak Karst) represent a facies equivalent of loess at higher altitudes. Their malacofauna consists of a peculiar mixture of cold- and warm-climate elements, including such thermophiles as *Helicodonta obvoluta, Isognomostoma isognomostomos, Petasina unidentata* etc., generally considered as characteristic interglacial fossils. Both sites are situated in protected areas at the foot of steep limestone slopes. However, the above mentioned thermophilous species attain in the adjacent Carpathian ranges the mountain to subalpine forest zones where they live under near-glacial conditions. Their fossil occurrence together with glacial index elements such as *Vallonia tenuilabris* or *Pupilla loessica* indicates that at the southern foot of Carpathian mountains a woodland zone existed even during the Last Glacial. It resembled the local mountain to subalpine forest belts and obviously included refugia of a number of climatically demanding species. Its upper limit occurred probably at the altitude ± 600 m. Since the regional altitudinal difference between the snow and upper forest lines is ± 1000 m, the glacial nival zone might be situated above 1600 m, which is in agreement with the altitudinal position of the West Carpathian glaciation. The glacial forest zone in the Carpathian foothills was thus situated between the loess steppe and alpine grassland belts, providing suitable conditions for the survival of a number of thermophiles. This reconstruction should be confirmed by further records and must not be applied more westerly, particularly in the Bohemian Highlands.

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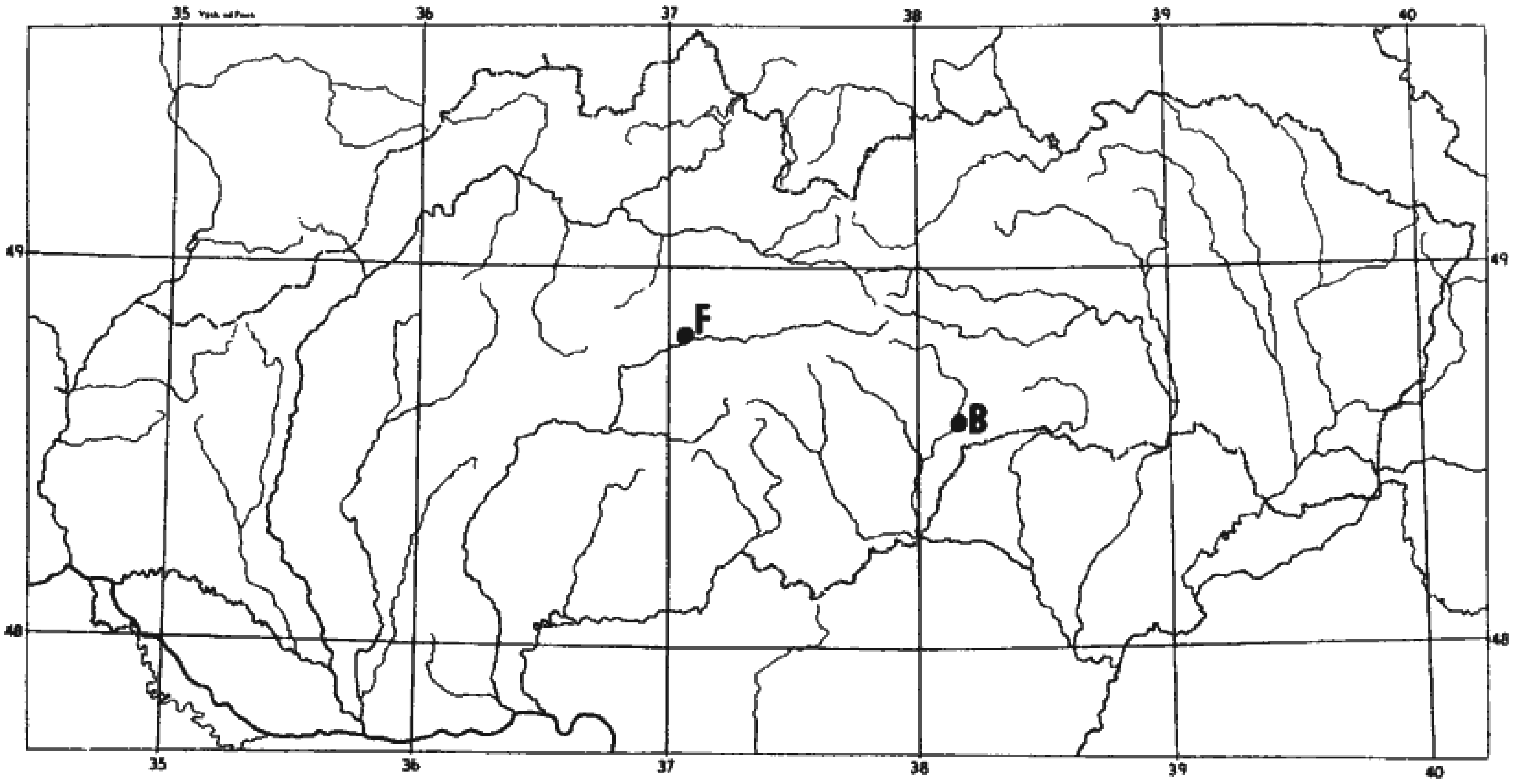
It has recently become clear that there is a conflict between current interpretations of glacial environments based on periglacial phenomena and some paleobotanical observations and the evidence given by a number of fossil faunal records from Central and southeastern Europe (Musil 2002, Ložek – Horáček 2004). It has been commonly assumed that the pleniglacial landscape of Central Europe had a subpolar character. Tundra-like grasslands on continuous permafrost were reconstructed even south of the 50° of northern latitude, which is particularly true of western Europe (e.g. Frenzel 1967).

However, this paleoenvironmental scenario, although plausible, appears to be weekly supported in the light of a number of paleontological records and paleoecological reconstructions, as stressed, for instance, by Musil (2002), who relied mainly upon the nutritional requirements of pleniglacial mammalian communities. His supposition is supported by findings of glacial vertebrates from high Alps as well as by certain pollen analyses from the West Carpathians which document the existence of woodland even at higher elevations (Jankovská 2004, Jankovská, Chromý – Nižnianská 2002). In this connection older pollen analyses from loess (Frenzel 1964) or the study of Ambrož (1947) focused on paleoenvironmental conditions during the loess formation should also be mentioned. The latter is supported by the paleoclimatic reconstruction of Szöör et al. (1991). As to the interpretation of periglacial phenomena, the sceptical approach of Penck (1938) also deserves more attention than it has received. In this connection it is also worth mentioning that the species richness of glacial malacocoenoses increase from western Europe towards the east (Rousseau 2001), which can be also traced in loess assemblages from inner Bohemia, through Moravia to the Danube lowland in south Slovakia (Ložek 1964). The aim of this paper is to describe some new malacological records which may throw more light on the above problems.

Zoning of glacial malacocoenoses

Before analyzing the new malacological records it is necessary to recapitulate briefly what is known of the zonal differentiation of glacial malacofaunas that may be considered in the interpretation of the findings presented in this paper.

The great majority of glacial malacofaunas come from



1. Location of investigated sites in Slovakia: 1 – Farkašovo, 2 – Brzotín (bank of the Slaná River).

loess. Despite the fact that the loesses formed in different glacials and regions, the loess assemblages are rather homogeneous and consist of a peculiar mixture of steppe, subpolar and catholic elements (LOŽEK 1991). In particular regions they are associated with various local species, for instance with *Neostyriaca corynodes* and *Orcula dolium* at the foot of the Alps, *O. dolium* and *Vestia turgida* in Carpathian region or *Clausilia parvula* in western parts of Central Europe. In the marginal zone at the foot of mountain ranges the admixture of euryoecic species increases, for instance of *Punctum pygmaeum, Euconulus fulvus, Vitrea crystallina, Clausilia dubia* and *Perpolita hammonis* in the Carpathian Váh Valley. The above mentioned increase in species richness towards the east results, for instance, from a comparison of loess malacocoenoses of Central Bohemia with those of the Carpathian Basin.

The composition of loess malacofauna has no present-day analogue in Europe, but characterizes the loess steppe as a peculiar giant biome of glacial periods. Of particular importance is the striking difference of loess assemblages from those of the high north.

By contrast, malacological records from areas out of the loess zone are rather sparse, which is particularly true of the Czechlands. In Slovakia, the situation is more favourable thanks to a number of fossil records from karstlands situated in a wide range of altitudes (200–1600 m). The composition of molluscan assemblages differs from the loess fauna in the presence of a number of species, including several more demanding woodland elements, as documented by the records from the caves Velká Jasovská jaskyňa (LOŽEK et al. 1957), Velká Ružínska jaskyňa (LOŽEK 1999) or Mažarná in the Velká Fatra Mts. (LOŽEK 1980) as well as from the alluvial fan at Pivková dolinka in the Low Tatra Mts. (LOŽEK 1986). Besides the rupestral snail *Chondrina clienta* it is also a case of some woodland elements such as *Faustina faustina* and *Cochlodina cerata* – that is even from elevations (800–1000 m) corresponding to the present-day montane zone, hence 500–700 m above the upper limit (± 300 m) of the loess belt. These data thus suggest that in the West Carpathians further zones occurred which were situated above the loess steppe belt and inhabited by a number of woodland elements.

Moluscan faunas from Farkašovo and Brzotín

Location. – Both sites are situated in the Slovak part of the West Carpathians, Farkašovo in Central Slovakia, Brzotín in southeastern Slovakia (Fig. 1). Selected records from these sites were briefly commented in the study on paleoecology of Quaternary mollusca (LOŽEK 2000).

Methods. – Serial sampling from closely subdivided sections and quantitative analyses have allowed detailed faunal successions to be reconstructed for both sites. Molluscs were extracted from the sediments by a combination of washing and sieving. After drying, each sample was disaggregated in water. The residual sediment was then wet-sieved, air-dried and the molluscs were picked using delicate pincers. The number of shells and fragments extracted was counted over using the standard method (LOŽEK 1964) that gives the approximate number of individuals present for each species. The results are presented in tables 1 and 2 where molluscs have been assigned to ecologic and biostratigraphic groups, which provides a general indication of former environmental changes.

FARKAŠOVO

Site description

The site in question is situated in the valley of the Hron River at the southern foot of the Nízké Tatry (Low Tatra) Mts. west of the Nemecká village. The talus accumulation is exposed in a small pit at the foot of the Farkašovo Hill (581 m) that is built up by Triassic limestone. The deposit overlies a terrace level ca. 8 m above the Hron River that corresponds to the level covered farther downstream by accumulations of eolian loams (dust loams) that represent the lime-deficient facies of loess at higher moister altitudes. Fig. 2 shows the exact location of the section, basic geographical data are presented in the following table:

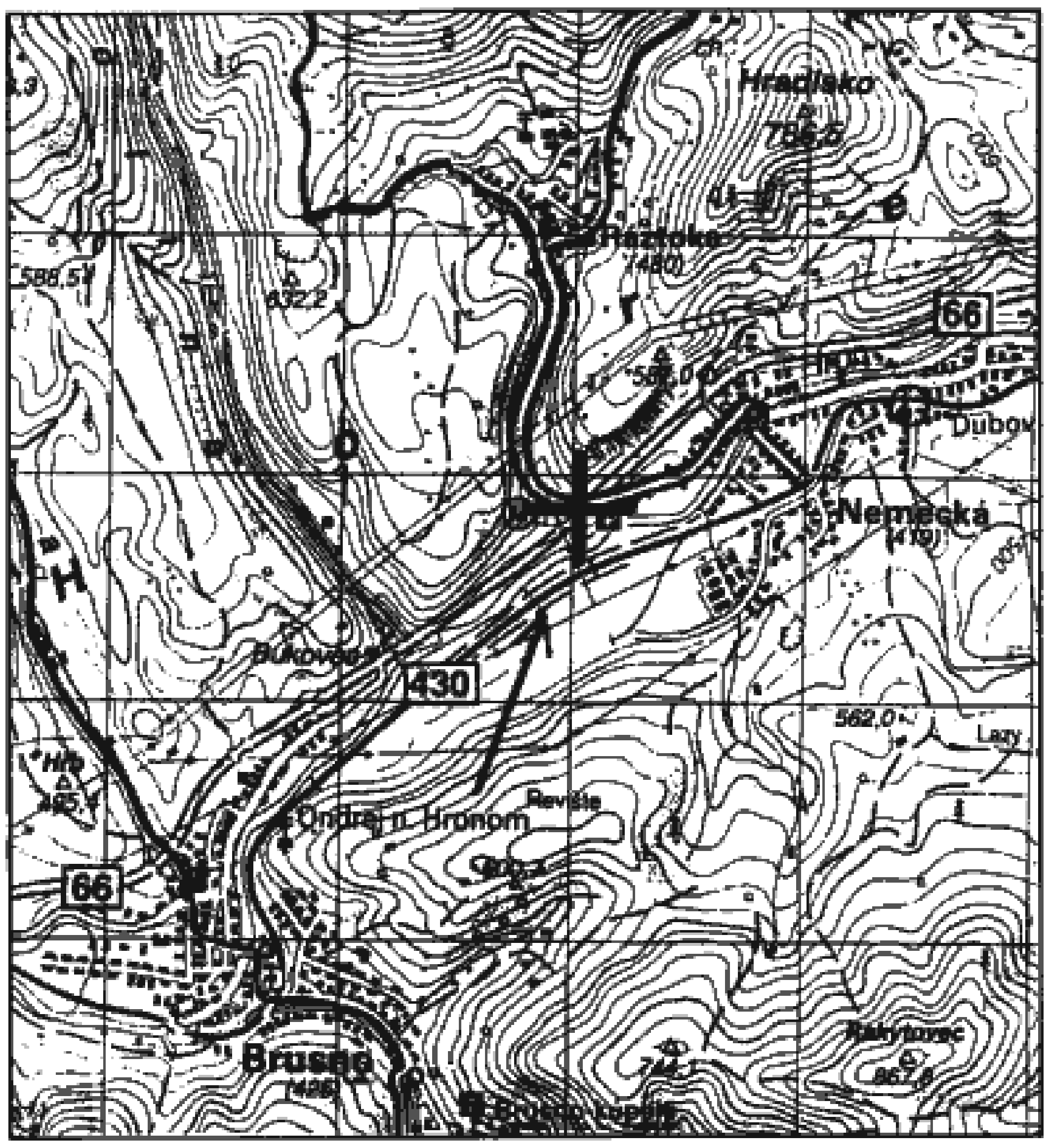
Latitude: 48° 38′ 50″
Longitude: 19° 24′ 60″
Altitude: 420 m
Mean annual rainfall: 816 mm
Mean annual temperature: 7.5 °C
Mean temperature of July: 18.1 °C
Mean temperature of January: –4.2 °C
Mean temperature of vegetation period: 14.3 °C

Stratigraphy

The talus accumulation is composed of a mixture of larger mostly angular blocks and finer rubble of local bedrock mixed in a loamy matrix. The column of the excavation (Fig. 3) appears rather monotonous except for layers 4 and particularly 5 whose matrix is apparently loess-like. The uppermost layers 1–3 represent a soil with decalcified fine earth, with more or less corrosionally rounded scree, which is particularly true of the layer 3 that corresponds to a B_t-horizon of a luvisol or even of an initial stage of terra fusca.

Mollusca

The main body of molluscan fauna (Table 1) is largely composed of elements that occur in loess or loess-like sediments in the foothill area of the West Carpathians such as *Vitrea crystallina, Pupilla sterri, P. triplicata, Vallonia costata, Clausilia dubia, Orcula dolium.* Of particular importance are *Pupilla loessica* and *Vallonia tenuilabris* which are index species of pleniglacial loesses and were recorded only in layers 4 and 5 characterized by the loess-like matrix. This is also true of *Pupilla muscorum* and partly also of the culminating *Succinella oblonga.* Of particular concern is also the presence of *Faustina cingulella* in layers 4–6 since it is a case of a subalpine element which descended to the foothill zone during the glacial phases (Ložek 1990). These snail communities reflect a parkland to semi-open woodland similar to scots pine – larch stands in dolomite areas of the mountain to upper mountain belts of the West Carpathians. During the formation of layers 5 and 4 a narrow zone of loess steppe patches along the Hron River became established.



2. Farkašovo, showing the sampling location.

However, the whole sequence of snail assemblages includes several species such as *Faustina faustina, Oxychilus depressus, Aegopinella minor, Cochlodina cerata*, and even *Helicodonta obvoluta* which are less tolerant to severe climatic conditions and never occur in loess. Of prime importance in this context are the high amounts of *F. faustina* even in the loess-like horizons 4 and 5. It is thus reasonable suppose that, even during the Weichselian pleniglacial, in the protected valleys of central West Carpathians favorite refugia of a number of demanding woodland snails persisted.

Brzotín – left bank of the Slaná River

Site description

Downstream of Brzotín (S of Rožňava, Slovak Karst) the Slaná River exposed by side cutting thick talus accumulations at the foot of precipitous valley walls with magnificently exposed limestone cliffs called Brzotínske skaly (678.8 m). The exposure was cleaned and the sedimentary sequence closely subdivided and sampled. It should be stressed that the site as well as the whole region of the Slovak Karst lie out of the loess zone, but not far from the Great Hungarian Plain, being protected from the north and northwest by higher mountain ranges of the West Carpathians. The exact location

Farkašovo

3. Farkašovo Hill, profile through the depositional sequence.
1 – dark brownish grey, humic loam, crumb structure, corroded clasts, 2 – greyish brown clayey loam, polyhedral peds, rounded limestone clasts, 3 – brown clayey loam, polyhedral jointing, sparse rounded clasts.
Layers 1–3 are lime-deficient, malacologically sterile, representing a soil of terra fusca-like luvisol type. The underlying sedimentary sequence consists of calcareous loams with variable amount of limestone scree; therefore, only the color of matrix and character of scree are given in the following description: 4 – yellowish brown, medium-sized scree, partly rounded, clayey infiltrations; 5 – greyish ochreous, loess-like, rather rich in 2–5 cm (10 cm) clasts; 6 – pale greyish brown, angular rubble (3–5 cm), with coarser stones (10–25 cm); 7 – angular rubble (3–6 cm, 10 cm) poor in greyish brown matrix; 8 – greyish brown, 2–5 cm rubble, horizon with coarser stones (10–15 cm), coarse boulder at the surface; 9 – brownish grey, 5–10 cm clasts (to 20 cm); 10 – rusty brown, lower in clasts (to 25 cm); 11 – pale brownish grey with diffuse brown streaks, angular 5 cm scree, scattered clasts to 15 cm.

of the site is shown on the map (Fig. 4), basic geographic data are given in the following table:
Latitude: 48° 36′ 45″
Longitude: 20° 29′ 31″
Altitude: 250 m
Mean annual rainfall: 663 mm
Mean annual temperature: 8.0 °C
Mean temperature of July: 18.5 °C
Mean temperature of January: – 3.8 °C
Mean temperature of vegetation period: 14.8 °C

Stratigraphy

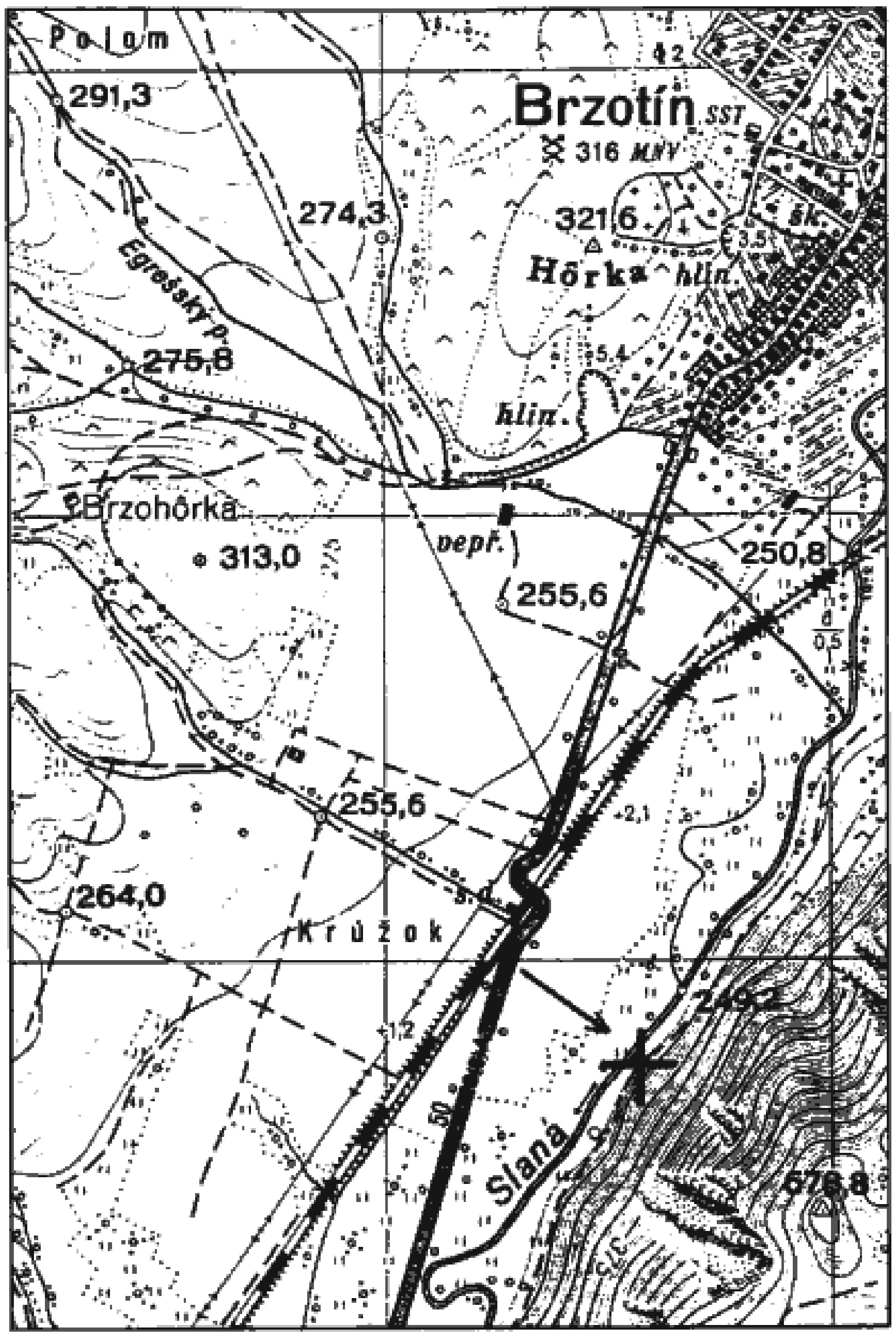
The whole depositional sequence consists of small- to medium-sized angular to subangular limestone fragments and coarser blocks in several horizons. The matrix is a brown calcareous loam with characteristic reddish tint (Fig. 5). As a whole the talus accumulation appears rather monotonous except for blocky horizons and layers 7 and 12 that are a little loess-like. The sequence is capped by a rendzina soil (1, 2).

Mollusca

In comparison with molluscan records from Farkašovo, the malacofauna from Brzotín is much richer in species (Table 2) that belong to various ecological groups incl. the main group A which comprises woodland elements. By contrast, characteristic loess species such as *Pupilla* ssp., *Succinella oblonga* and *Vallonia tenuilabris* occur only in small amounts, being absent from several layers. Despite this, in accordance with Farkašovo, they can be traced throughout the section. However, *Clausilia dubia, Orcula dolium* and *Vitrea crytallina* that occur in peri-Carpathian loesses, particularly in the Váh river valley, are well represented throughout the whole succession, which is true also of *Faustina faustina.* Further open-ground (group 5) and catholic elements (group 7 Me) are scattered in small quantitiess throughout the deposit.

However, the most unexpected feature of this fauna is the presence of a number of climatically demanding species, which are generally believed to be characteristic fossils of warm periods (Interglacials, Holocene). This is particularly true of *Helicodonta obvoluta, Isognomostoma isognomostomos*, and *Laciniaria plicata* that occur almost in all layers, the latter sometimes in rather high amounts. Scattered records of *Daudebardia rufa, Monachoides incarnatus, Petasina unidentata, Ruthenica filograna, Vitrea diaphana, Discus rotundatus, Fruticicola fruticum* and *Carychium tridentatum* provide a similar evidence.

The malacological evidence presented here suggests that the talus deposits in question were deposited during a period of peculiar climatic conditions which allowed



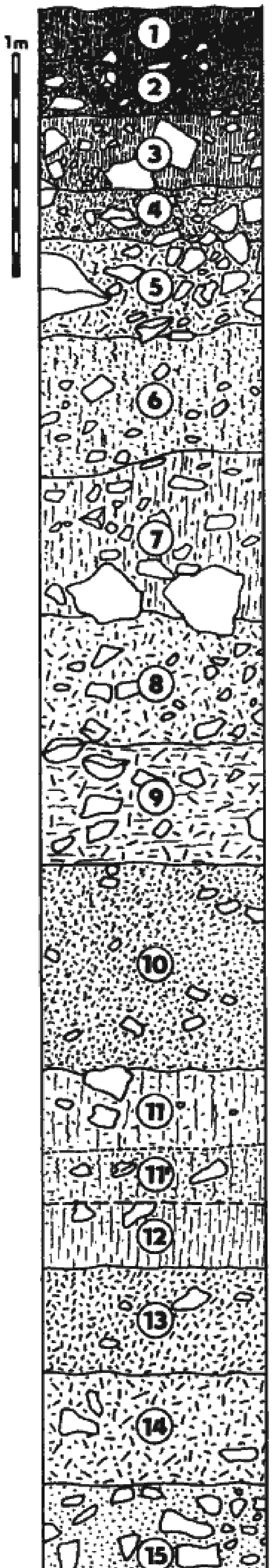
4. Brzotín, bank of the Slaná River, showing the sampling location (+).

the coexistence of tolerant elements adapted to severe glacial condition with much more demanding woodland species such as *H. obvoluta* or *I. isognomostomos*. These snails prefer mesic scree forests in hilly to mountainous areas of middle and southeastern Central Europe, but their range progressively declines towards the east and northeast. *H. obvoluta* is mostly confined to warm regions, whereas it is lacking in northern mountain ranges of the West Carpathians. Suitable habitats occur also at present in lower parts of the slopes of Brzotínske skaly. However, the question arises, whether such habitats could exist here even during the Last Glacial and where the associated open-ground elements were living.

Discussion

The composition of fossil molluscan communities in both sites reflects climatic conditions that were much more severe than the present ones. This is documented by the occurrence of such elements as *Vallonia tenuilabris, Discus ruderatus* or *Vertigo alpestris* as well as by the absence of a number of woodland species which are widespread in the area in question at present,

Brzotín



5. Brzotín – profile through the depositional sequence. The whole succession consists of limestone scree with loamy calcareous matrix so that only the colour of matrix and character of scree are described: 1 – dark brownish grey, humic, crumb structure, very poor in rubble; 2 – dark greyish brown, humic, crumbly, coarser clasts; 3 – greyish brown, coarser stones, rich in fine rubble; 4 – greyish brown with reddish tint, coarser stones, very rich in fine rubble; 5 – pale greyish brown, high in clasts of various size, boulder; 6 – pale reddish brown, rich in pseudomycelia and $CaCO_3$ coatings, diffuse reddish spots, fine rubble (5 cm), sparse coarser stones; 7 – pale brown, partly reddish, compacted, numerous diffuse pseudomycelia and $CaCO_3$ coatings, partly loess-like, 5–10 cm rubble, boulders at the base; 8 – pale reddish brown, rubble 5–10 cm, finer fragments sparser, $CaCO_3$ efflorescences less marked; 9 – reddish brown, without $CaCO_3$ efflorescences, coarser clasts; 10 – reddish brown, rather non-coherent, very rich in fine rubble, sparse coarser clasts; 11 – pale brown, loess-like, rich in coarser stones; 11' – as 11, rich in fine rubble; 12 – greyish ochreous, low in rubble, coarse subangular stones; 13 – reddish brown, very high in fine rubble, scattered coarse stones; 14 – markedly reddish brown, medium-sized rubble (4–5 cm), scattered coarser stones; 15 – greyish brown with reddish tint, very high in finest rubble (1 cm) coarser stones (10–20 cm); 16 – markedly reddish brown, rich in medium-sized fragments (5–10 cm), subangular, fine rubble (1–2 cm), surface of some stones corrosionally sculptured.

Table 1. Farkašovo, molluscan succession

Ecologic and biostratigraphic characteristics				List of species	Layer							
					11	10	9	8	7	6	5	4
A	1	W	!!	*Aegopis* cf. *verticillus* (LAMARCK)	–	–	–	–	–	1	–	–
			!	*Causa holosericea* (STUDER)	1?	1?	–	–	–	–	–	–
			!	*Daudebardia rufa* (DRAPARNAUD)	–	–	–	–	–	–	(1)	–
			(G)	*Discus ruderatus* (FÉRUSSAC)	–	1	–	–	–	–	–	–
			!	*Ena* cf. *obscura* (MÜLLER)	–	–	–	–	–	–	–	1
			(!)	*Faustina faustina* (ROSSMÄSSLER)	–	–	–	–	–	1	–	–
			!	*Faustina faustina/rossmässleri*	10	13	12	8	–	7	6	3
			(!)	*Faustina* agg.	–	–	–	–	–	13	10	11
			!	*Helicodonta obvoluta* (MÜLLER)	–	–	–	–	–	2	–	–
			!	*Isognomostoma isognomostomos* (SCHRÖTER)	–	–	–	–	–	–	–	1
			!	*Monachoides incarnatus* (MÜLLER)	–	–	–	–	–	1	–	1
			(G)	*Oxychilus depressus* (STERKI)	4	2	1	1?	–	3	–	–
			!	*Vitrea diaphana* (STUDER)	–	–	–	–	–	–	–	1
	2	W(M)	(+)	*Arianta arbustorum* (LINNÉ)	–	–	–	1	–	1	–	–
			!	*Discus rotundatus* (MÜLLER)	–	–	–	–	–	–	–	1
		W(S)	!	*Aegopinella minor/nitens*	1	–	–	–	–	–	–	–
			(!)	*Fruticicola fruticum* (MÜLLER)	–	–	–	–	–	–	–	1
			(G)	*Cochlodina cerata* (ROSSMÄSSLER)	1	–	–	–	–	–	–	–
			(!)	*Cochlodina cerata/laminata*	–	1	–	–	–	–	–	1
			!	*Helix pomatia* LINNÉ	–	–	–	–	–	1?	–	–
		W(H)	(+)	*Vitrea crystallina* (MÜLLER)	26	20	22	7	4	12	9	14
	3		(+)	*Vestia turgida* (ROSSMÄSSLER)	–	–	–	–	–	–	1?	–
B	4	S	(+)	*Chondrula tridens* (MÜLLER)	–	–	1	–	–	–	–	–
			M	*Cecilioides acicula* (MÜLLER)	–	–	–	–	–	–	–	1
			+	*Pupilla sterrii* (VOITH)	2	5	50	49	7	16	39	104
			(+)	*Pupilla triplicata* (STUDER)	–	5	33	48	–	16	6	32
	5	O	++	*Pupilla* cf. *loessica* LOŽEK	–	–	–	–	–	–	–	8
			+	*Pupilla muscorum* (LINNÉ)	–	–	–	–	–	–	–	15
			(+)	*Vallonia costata* (MÜLLER)	13	11	28	32	3	16	13	39
			++	*Vallonia tenuilabris* (A. BRAUN)	–	–	–	–	–	–	17	59
		OR	G	*Faustina cingulella* (ROSSMÄSSLER)	–	–	–	–	–	10	4	4
C	6		(!)	*Euomphalia strigella* (DRAPARNAUD)	–	–	–	–	–	–	–	1
	7	Me	(+)	*Cochlicopa lubrica* (MÜLLER)	–	–	–	–	–	–	–	2
			(+)	*Euconulus fulvus* (MÜLLER)	–	–	2	–	–	–	–	–
			(+)	*Perpolita* cf. *hammonis* (STRÖM)	–	–	–	–	–	–	–	1
			(+)	*Punctum pygmaeum* (DRAPARNAUD)	–	–	2	–	–	–	–	–
			+	*Trichia* cf. *hispida* (LINNÉ)	–	–	–	–	–	–	1?	3
			!	*Vitrea contracta* (WESTERLUND)	–	–	–	–	–	–	–	1
		R(W)	(+)	*Clausilia dubia* DRAPARNAUD	40	21	104	88	10	76	74	217
			(+)	*Orcula dolium* (DRAPARNAUD)	205	151	166	30	–	56	114	124
			G	*Vertigo alpestris* ALDER	–	1	4	47	–	4	2	–
	8		+	*Succinella oblonga* (DRAPARNAUD)	1	–	9	10	–	7	81	264
D	10	Q		*Bythinella austriaca* agg.	–	–	–	–	–	–	–	1
Number of species					11	12	13	11	4	18	15	27

for instance *Platyla polita, Sphyradium doliolum, Acanthinula aculeata, Ena montana, E. obscura, Discus perspectivus, Oxychilus orientalis, O. glaber, Cochlodina laminata, C. orthostoma, Macrogastra* ssp, *Alinda biplicata, Bulgarica cana, Cepaea vindobonensis* etc. Predictions about how terrestrial molluscs will respond to glacial cooling, may only be based on modern ecological studies.

For this reason, we must seek environments which may be suitable for the coexistence of cold-climate species with the above thermophilous elements at present. Such conditions occur in extreme boundary habitats of the above-mentioned thermophilous species in the wider surroundings of the sites in question, for instance in the top part of the karst plateau Muránska planina where a number of these species live at the altitudes of 1200–1300 m, which corresponds to the montane and supramontane zones (Ložek 1949). Similar conditions occur also at the southern slope of the Nízke Tatry Mts., for instance in the surroundings of Moštenica. Altitudinal belts with the highest modern occurrences of demanding woodland species recorded in glacial talus deposits near Brzotín (at elevation 250 m) are summarized bellow:

Mountain belt (ca 800–1200/1300 m), mixed beech-spruce-fir-sycamore-elm forest: *Helicodonta obvoluta* (1200 m), *Monachoides incarnatus* (1200 m), *Laciniaria plicata* (exceptionally to 1300 m); *Vitrea contracta, Aegopinella minor* and *Daudebardia rufa* (1000 m).

Upper mountain belt (ca 1200–1400/1550 m), predominantly spruce, larch in rocky habitats: *Discus rotundatus* (relict occurrence on the Klenovský Vepor Mt.).

Subalpine belt (1400/1550–1800 m), alpine meadows with *Pinus mugo* and *Salix silesiaca* stands: *Faustina faustina* (1800 m), *Isognomostoma isognomostomos* (1600 m), *Petasina unidentata* (1800 m), *Ruthenica filograna* (1600 m), *Cochlodina cerata* (1600 m), *Vitrea diaphana* (ca 1600 m), *Fruticicola fruticum* (1400 m), *Monachoides vicinus* (1800 m), *Carychium tridentatum* (1400 m).

Alpine belt (alpine grasslands, more than 1800 m): *Aegopinella pura* (1900–2000 m).

The above evidence demonstrates that the surveyed species are able to survive even at the altitudes 1000–1500 m (some of them to 1800 m), where the mean annual temperature attains only 4–2 °C and the rainfall 900–1250 mm. However, these data are very approximate, being in rocky limestone mountains largely modified by local meso- and microclimatic conditions. Nevertheless, the resulting information provides a useful baseline for recognizing what is "normal" for rates of climate change and accompanying faunal dynamics.

Temperature conditions of the highest occurrences of the surveyed thermophilous snails indicate that the mean temperatures at both sites could be at the glacial times 4.5–5.0 °C lower than at present. It is likely that they were somewhat lower, perhaps at about 6–7 °C, with respect to the longer and colder continental winter characterizing the glacial. This might correspond to an average close above 0 °C, whereas the temperature of vegetation period would remain sufficiently high to enable the survival of more demanding elements.

In view of local relief conditions we may assume that the upper forest line at both sites was situated at ca 600 m, so that the steep sides of the Slaná Valley as well of the Farkašovo Hill were covered by mountain to subalpine woodland with open rocky patches. Thus, the glacial fall in tree limit came to 900 m.

In this context it is worth mentioning that this assumption is consistent with the altitudinal position of the West-Carpathian mountain glaciation. In the Alps the altitudinal difference between the snow line and upper forest limit ranges from 700 m to 1000 m. The latter value may be true also of the more continental Carpathian area so that in the light of our reconstruction the glacial snow line in the West Carpathians occurred approximately in 1600 m, which is in good agreement with the fact that only mountain ranges exceeding this altitude, particularly the High and Low Tatras bear traces of an important glaciation.

The analyses of snail assemblages from Farkašovo and Brzotín and several further lines of evidence indicate that between the zone of alpine grasslands at 600–1600 m and the loess steppe belt at the foot of Carpathian foothills a zone of mountain to subalpine woodland persisted during the Last Glacial which probably included patches of warmer protected habitats at places with suitable relief and substratum conditions. In general, it seems that it corresponds to the forest steppe/tundra belt at the periphery of the Pannonian Basin reconstructed for the last pleniglacial by Frenzel (1967, p. 213). This zone provided refugia for a number of molluscan species that are generally considered inter-

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Explanation to Tables 1 and 2

Ecological characteristics

Main ecologic groups: A – woodland in general, B – open country in general, C – woodland/open country, D – wetlands and aquatic habitats.

Ecologic groups: 1 – closed forest, 2 – predominantly woodland, locally semi-open to open habitats: W(M) – mesic, W(S) – xeric, W(H) – damp: 3 – moist woodland, alder carrs, riverine forests; 4 – warm-dry grassland or rocks: S – in general, XL – limestone rocks, S(W) – partly shaded habitats; 5 – open country in general (moist grassland to steppe); woodland/open country: 6 – predominantly dry, 7 – mesic or various: Me – in general, MR – mesic rocks, R(W) – scree woodland; 8 – predominantly damp, 9 – wetlands, banks, 10 – aquatic habitats.

Biostratigraphic characteristics

+ – characteristic loess species, ++ – index loess species, (+) – local or accidental loess species, G – species surviving the glacial out of the loess zone, (G) – dtto, as relics, ! – warm-climate species, !! – interglacial index species, (!) – eurythermal warm-climate species, M – modern (= Postglacial) immigrants.

1? – determination approximate only, (2) – allochthonous (reworked) shells.

Table 2. Brzotín, bank of the Slaná River – molluscan succession

Ecologic and biostratigraphic characteristics				List of species	Layer							
					16	15	14	13	12	11b	11a	10
			!	*Aegopinella pura* (ALDER)	–	–	–	–	–	–	–	–
			(!)	*Cochlodina cerata/laminata*	–	–	–	–	–	–	–	–
			!	*Daudebardia rufa* (DRAPARNAUD)	–	–	–	–	–	–	–	–
			(G)	*Discus ruderatus* (FÉRUSSAC)	1	–	–	–	–	1	–	–
			!!	*Drobacia banatica* (ROSSMÄSSLER)	–	–	–	–	–	–	–	–
			(!)	*Faustina faustina* (ROSSMÄSSLER)	116	216	14	1	2	24	19	12
	1		!	*Helicodonta obvoluta* (MÜLLER)	3	1	1	–	–	2	1	1?
			!	*Isognomostoma isognomostomos* (SCHRÖTER)	7	6	1	–	–	5	4	2
			!	*Monachoides incarnatus* (MÜLLER)	–	–	1	–	1	1	–	1
			(G)	*Oxychilus depressus* (STERKI)	–	–	–	–	–	1?	–	–
			!	*Petasina unidentata* (DRAPARNAUD)	1	–	–	–	–	–	–	–
			!	cf. *Pseudalinda stabilis* (L. PFEIFFER)	–	–	–	–	–	–	–	1
A			!	*Ruthenica filograna* (ROSSMÄSSLER)	–	–	–	–	–	–	–	–
			!	*Vitrea diaphana* (STUDER)	–	–	–	–	–	3	–	–
			(+)	*Arianta arbustorum* (LINNÉ)	1	–	–	–	–	–	–	–
		W(M)	!	*Discus rotundatus* (MÜLLER)	–	2	–	–	–	–	1	1
			!	*Limax* sp.	–	–	–	–	–	1	–	–
			G	*Semilimax kotulae* (WESTERLUND)	–	1	–	–	–	1	–	–
	2		!	*Aegopinella minor* (STABILE)	–	–	–	–	–	–	–	–
		W(S)	(G)	*Cochlodina cerata* (ROSSMÄSSLER)	1	9	–	–	–	3	1?	–
			(!)	*Fruticicola fruticum* (MÜLLER)	1	1	–	–	–	–	1	1
			!	*Helix pomatia* LINNÉ	–	–	–	–	–	–	–	1?
		W(H)	(+)	*Vitrea crystallina* (MÜLLER)	16	23	2	1	1	3	7	3
	3		G	*Monachoides vicinus* (ROSSMÄSSLER)	1	1	–	–	–	–	–	–
			(+)	cf. *Vestia turgida* ((ROSSMÄSSLER)	1	–	–	–	–	–	–	–
			(+)	*Chondrula tridens* (MÜLLER)	1	–	–	–	–	–	–	–
	4		+	*Pupilla sterri* (VOITH)	2	1?	–	–	–	3?	–	–
			(+)	*Pupilla* cf. *triplicata* (STUDER)	–	4?	–	–	–	–	–	–
			(G)	*Chondrina clienta* (WESTERLUND)	–	–	–	–	–	2	–	–
B			+	*Pupilla* cf. *muscorum* (LINNÉ)	–	1	–	–	–	–	–	–
			++	*Pupilla* cf. *densegyrata* LOŽEK	–	–	–	–	–	–	–	–
	5	O	(!)	*Truncatellina cylindrica* (FÉRRUSSAC)	–	–	–	–	–	–	1	–
			(+)	*Vallonia costata* (MÜLLER)	–	6	–	–	–	3?	–	–
			++	*Vallonia tenuilabris* (A. BRAUN)	2	2	–	–	–	–	–	2
	6		!	*Milax* sp.	1	–	–	–	–	–	–	–
			(+)	*Euconulus fulvus* (MÜLLER)	1	2	1	–	–	–	–	–
		Me	(+)	*Punctum pygmaeum* (DRAPARNAUD)	–	1	–	–	–	–	–	–
			+	*Trichia* cf. *hispida* (LINNÉ)	–	1	1	–	–	–	–	–
	7		!	*Vitrea contracta* (WESTERLUND)	8	–	–	–	–	–	–	–
			(+)	*Clausilia dubia* DRAPARNAUD	43	54	6	1	–	17	6	2
C		R(W)	!	*Laciniaria plicata* (DRAPARNAUD)	9	9	2	–	1	14	7	6
			(+)	*Orcula dolium* (DRAPARNAUD)	27	54	5	1	1	7	3	3
			G	*Vertigo alpestris* ALDER	1	2	2	–	–	3	2	2
			!	*Carychium tridentatum* (RISSO)	–	–	–	–	–	–	1	1
	8		(!)	*Columella* cf. *edentula* (DRAPARNAUD)	1	–	–	–	–	–	–	–
			+	*Succinella oblonga* (DRAPARNAUD)	–	–	–	–	–	–	1	–
			(G)	*Vertigo substriata* (JEFFREYS)	1	–	–	–	–	–	–	–
D	9		(+)	*Succinea* cf. *putris* (LINNÉ)	2	–	–	–	–	1	–	–
Number of species					24	21	11	4	5	20	14	15

Layer							
9	8	7	6	5	4	3	2
–	–	–	–	–	–	2	–
–	–	–	–	–	1	1	1
–	–	1	–	–	–	4	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	1	–
13	12	12	13	12	12	10	3
1?	1	2	1	1	2	1	–
1	2	2	1	1	3	1	2
–	–	–	–	–	1	–	–
–	–	–	1?	–	1?	–	–
–	–	–	–	–	–	–	1
–	1	–	–	–	–	–	–
–	–	–	–	1	1	2	–
–	–	–	–	–	1	3	–
–	6	1	2	1?	1	1?	1?
–	–	–	–	–	1?	–	–
–	–	–	–	–	–	–	–
–	–	1	–	–	–	–	–
–	–	–	–	–	–	1	–
1?	–	–	1	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	2	1	1	3	8	2	–
–	–	–	–	–	–	–	1
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	1	–	–	2	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	1?	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
1	–	4?	–	3	2	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	1	–	–	–	–
–	–	–	1	–	1	4	–
4	24	5	2	9	19	8	3
2	2	1	2?	3	2	2	1?
2	3	4	–	2	4	–	1
5	1	5	1	1	3	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	1	–	–
–	–	–	–	–	2	1	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
9	10	13	12	12	20	16	9

glacial or Holocene. Our paleoenvironmental scenario thus supports the old hypothesis of the Ancient Matra Refugium in the northeastern part of the Pannonian Basin (Krippel 1971). However, this paleoenvironmental reconstruction, although plausible, appears to be inadequately supported so far and must be confirmed by further fossil records.

Conclusions

The molluscan assemblages from talus accumulations at Farkašovo and Brzotín (bank of the Slaná River) provide important information on glacial paleoenvironments in the West Carpathians that may be summarized as follows:

- In areas corresponding to the present-day hill-country belt mixed pleniglacial malacofaunas were recorded which consisted both of glacial open-country elements and of some woodland species that are considered characteristic of warm periods (interglacials, Holocene).
- Their survival in glacial contexts is explained with respect to their occurrences under severe conditions of the mountain to subalpine belts, at elevations 800–1600 m, in the adjacent West Carpathian mountain ranges (Muránska planina, Low Tatra).
- Molluscan assemblages from Farkašovo and Brzotín, inclusive of several records from other sites, indicate that during the Last Glacial corresponding conditions occurred much lower in the hill-country belt at altitudes 250–600 m, which corresponds to an 800–1000 m fall in vegetation altitudinal belts.
- On the assumption that the altitudinal difference between the snow line and upper forest limit in the area in question may be 1000 m, the supposed reconstruction of altitudinal vegetation belts is in good agreement with the Last Glaciation of the West Carpathians which developed only in mountain ranges exceeding 1600 m (particularly the High and Low Tatras). However, this hypothesis cannot be applied to regions situated more westerly, for instance to the Bohemian Highlands.
- In view of the above, it is very likely that in the southern foothills of the West Carpathians glacial refuges of a number of climatically demanding woodland species existed.

Translated by the author
Recommended for print by J. Hlaváč

←
In 11b two fragments resembling *Soosia diodonta*

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Prostředí posledního glaciálu v Západních Karpatech ve světle fosilní malakofauny

(Resumé anglického textu)

VOJEN LOŽEK

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V posledních letech se stále více projevuje rozpor mezi výpovědí fosilních faun obratlovců i měkkýšů včetně řady dalších poznatků a dosud převládajícími představami o glaciálním prostředí vycházejícími především z interpretace stop různých periglaciálních jevů. Představy o subpolárním rázu naší krajiny lze sotva sladit s nároky řady druhů, které se běžně vyskytují i v sedimentech z pleniglaciální fáze a jejichž přežití ukazuje na životní podmínky podstatně odlišné od stavu na vysokém severu nebo v oblastech hlubokého permafrostu. Tyto rozpory rozebral u nás nejnověji MUSIL (2002), řada kritických úvah se však objevuje porůznu i v dřívějších publikacích vycházejících i z abiotických dokladů, jako je třeba studie o spraších, kterou již před půl stoletím uveřejnil AMBROŽ (1947). Nicméně bližší pohled na tuto problematiku mohou poskytnout jen další paleontologické doklady.

Co se týče glaciální malakofauny, naprostá většina nálezů pochází ze spraší, a je proto složkou velmi svébytné bioty sprašové stepi, která neposkytovala vhodné podmínky pro přežití převážně mezofilních druhů teplých období. Sprašová step ovšem představovala jen jeden z vegetačních stupňů, jehož horní hranice v průměru probíhala ve 300 m. Vyšší stupně měly nepochybně vlhčí ráz a podle různých náznaků měly v předhoří Alp a Karpat spíše charakter parkové krajiny, označené ve FRENZELOVĚ (1967) rekonstrukční mapě pleniglaciální vegetace Evropy jako lesostep nebo lesotundra. Zatímco v českých zemích nejsou vhodné podmínky pro fosilizaci měkkýšů v tomto stupni, podařilo se ve slovenských Karpatech najít místa, kde se ulity mohly zachovat. Mezi nimi poskytly nejbohatší nálezy úpatní akumulace svahovin pod vrchem Farkašovo v údolí Hronu u Nemecké a na levém břehu Slané pod Brzotínem na úpatí strmých srázů Brzotínských skal.

Oba profily byly podrobně zpracovány a výsledky kvantitativních rozborů shrnují tabulky 1 a 2, zahrnující i ekologická a biostratigrafická data. V obou případech jde o nezvyklou směs druhů, které průkazně přežily glaciál na našem území nebo glaciál přímo charakterizují (*Vallonia tenuilabris*), a některých klimaticky poměrně náročných lesních prvků, dosud běžně považovaných za význačné fosilie teplých období (*Helicodonta obvoluta, Isognomostoma isognomostomos, Petasina unidentata* atd.). Ty se uplatňují zejména v Brzotíně, což odpovídá poloze lokality v teplé chráněné oblasti Slovenského krasu při jihovýchodním úpatí Západních Karpat, tedy v oblasti tzv. Pramatry, považované řadou botaniků i zoologů za glaciální refugium klimaticky náročnějších druhů střední Evropy.

Jedním z dokladů možných přežití těchto druhů během glaciálu v této oblasti je jejich dnešní výskyt v montánních až subalpínských polohách v blízkých vyšších pohořích, především na Muráňské planině a na jižních rozsochách Nízkých Tater, tedy v pásmu s průměrnými ročními teplotami mezi 4–2 ° C a srážkami 800–1250 mm. Teplotní rozdíl oproti údolí Slané obnáší tedy 6 ° C, výškový až 1000 m. Rozdíl teploty byl zřejmě větší vzhledem k větší kontinentalitě pleniglaciálu. Nicméně s ohledem na utváření reliéfu lze předpokládat, že horní hranice lesních porostů uvedeného typu ležela ve Slovenském krasu kolem 600 m. Vyjdeme-li z toho, že nivální stupeň ve Východních Alpách leží zhruba 1000 m nad horní hranicí lesa, dostaneme se v našem případě k hodnotě 1600 m, což se překvapivě shoduje s výškovou polohou zalednění Západních Karpat, které významně postihlo jen pohoří přesahující tuto výšku, tedy především oboje Tatry, se značným omezením na jižních svazích Nízkých Tater.

Malakofauny z Farkašova a především z Brzotína nasvědčují, že ve východní polovině Západních Karpat se i během pleniglaciálu udrželo na jižních chráněných úpatích pásmo lesů srovnatelných s dnešními porosty montánního až subalpínského stupně v této oblasti. Zde pak mohla přežít řada druhů s poměrně vysokými nároky na teplotu a vlhkost. Uvedený lesní stupeň zde odděloval pásmo sprašové stepi v panonských pahorkatinách a nížinách od holí ve vyšších polohách Karpat a pro mnoho druhů (nejen měkkýšů!) představoval jedno z refugií, umožňující přežití pleniglaciálu v blízkosti jejich současného areálu.

Do jaké míry lze tento závěr vztahovat i na území dále k západu, tedy především na české země, mohou objasnit jen další fosilní doklady. V každém případě je však zřejmé, že periglaciální pásmo směrem k jihovýchodu velmi rychle vyznívalo a že se i ve střední Evropě nacházely okrsky, kde mohly přežít pleniglaciál i klimaticky značně náročné druhy.

Vysvětlivky k obrázkům

1. Poloha zkoumaných lokalit v rámci Slovenska (1 – Farkašovo, 2 – Brzotín, břeh Slané).

2. Farkašovo, poloha lokality (+).

3. Farkašovo, profil vrstevního sledu.
1 – hnědavě tmavošedá humózní, hrubě drobtovitá hlína, korodované úlomky; 2 – šedavě hnědá jílovitá hlína polyedrické odlučnosti, zaoblená vápencová suť; 3 – hnědá jílovitá hlína polyedrické odlučnosti, nízký podíl zaoblených úlomků.
Vrstvy 1–3 jsou odvápněné, malakologicky sterilní; odpovídají půdě na rozhraní luvizemě a terry fusky. Podložní souvrství tvoří vápnité hlíny s proměnlivým podílem vápencové suti (v popisu proto uvádíme jen barvu výplně a charakter suti): 4 – žlutohnědá, jílovité záteky, střední suť, některé úlomky zaoblené; 5 – šedavě hnědožlutá sprašovitá, dosti četné úlomky 2–5 cm, méně do 10 cm; 6 – šedavě žlutohnědá, převládá ostrohranná převážně drobná suť (3–5 cm) s příměsí větších kusů (10–25 cm); 7 – ostrohranná převážně drobná drť (3–6 cm, 10 cm) nedokonale vyplněná šedohnědou hlínou; 8 – šedavě hnědá, úlomky 2–5 cm, poloha 10–15 cm, na povrchu balvan; 9 – hnědavě šedá, suť 5–10 cm, jednotlivě až 20 cm; 10 – narezlá, méně úlomků až 25 cm; 11 – světle hnědošedá, difuzní hnědavé šmouhy, ostrohranná suť 5 cm, roztroušeně až 15 cm.

4. Brzotín, poloha lokality (+).

5. Brzotín, profil vrstevního sledu.
Celé souvrství pozůstává z vápencových sutí s hlinitou vápnitou výplní – proto uvádíme jen barvu výplně a charakter suti: 1 – tmavě hnědošedá humózní, drobtovitá, téměř bez skeletu; 2 – tmavě šedohnědá, drobtovitá, hrubší úlomky, málo drobných; 3 – světleji šedohnědá, větší kameny, četné drobné úlomky; 4 – narudle šedavě hnědá, větší kameny, velmi četné drobné úlomky; 5 – našedle světle hnědá, hojná suť různé velikosti, balvan; 6 – narudle světle hnědá, provápněná, četná pseumycelia a $CaCO_3$ povlaky, místy červenější a sypčejší, drobný skelet (5 cm), jednotlivé větší kusy; 7 – světle hnědá, místy narudlá, ulehlá, četná difúzní pseudomycelia a $CaCO_3$ povlaky, sprašovité partie, skelet 5–10 cm, naspodu balvany; 8 – světle hnědá slabě narudlá, skelet 5–10 cm, méně drobné úlomky, vápnité výkvěty nevýrazné; 9 – narudle hnědá, bez $CaCO_3$ výkvětů, hrubší skelet; 10 – narudle hnědá, poměrně sypká, velmi četné drobné úlomky, řídce větší kusy; 11 – světle hnědá sprašovitá, četné větší kameny; 11' – dtto, hojné drobné úlomky; 12 – šedookrová, málo drobných úlomků, velké tupohranné kameny; 13 – rudohnědá, velmi hojný drobný skelet, ojedinělé hrubší kusy; 14 – výrazně rudohnědá, střední skelet (4–5 cm), roztroušeně větší kameny; 15 – šedavě hnědá s narudlým odstínem, přeplněná drobnou sutí (± 1 cm), větší kameny (10–20 cm); 16 – výrazně rudohnědá, četné středně velké kusy (5–10 cm), hrany otupené, hojná drť (1–2 cm), povrch některých kamenů jemně skulpturovaný.

Vysvětlivky k tabulkám

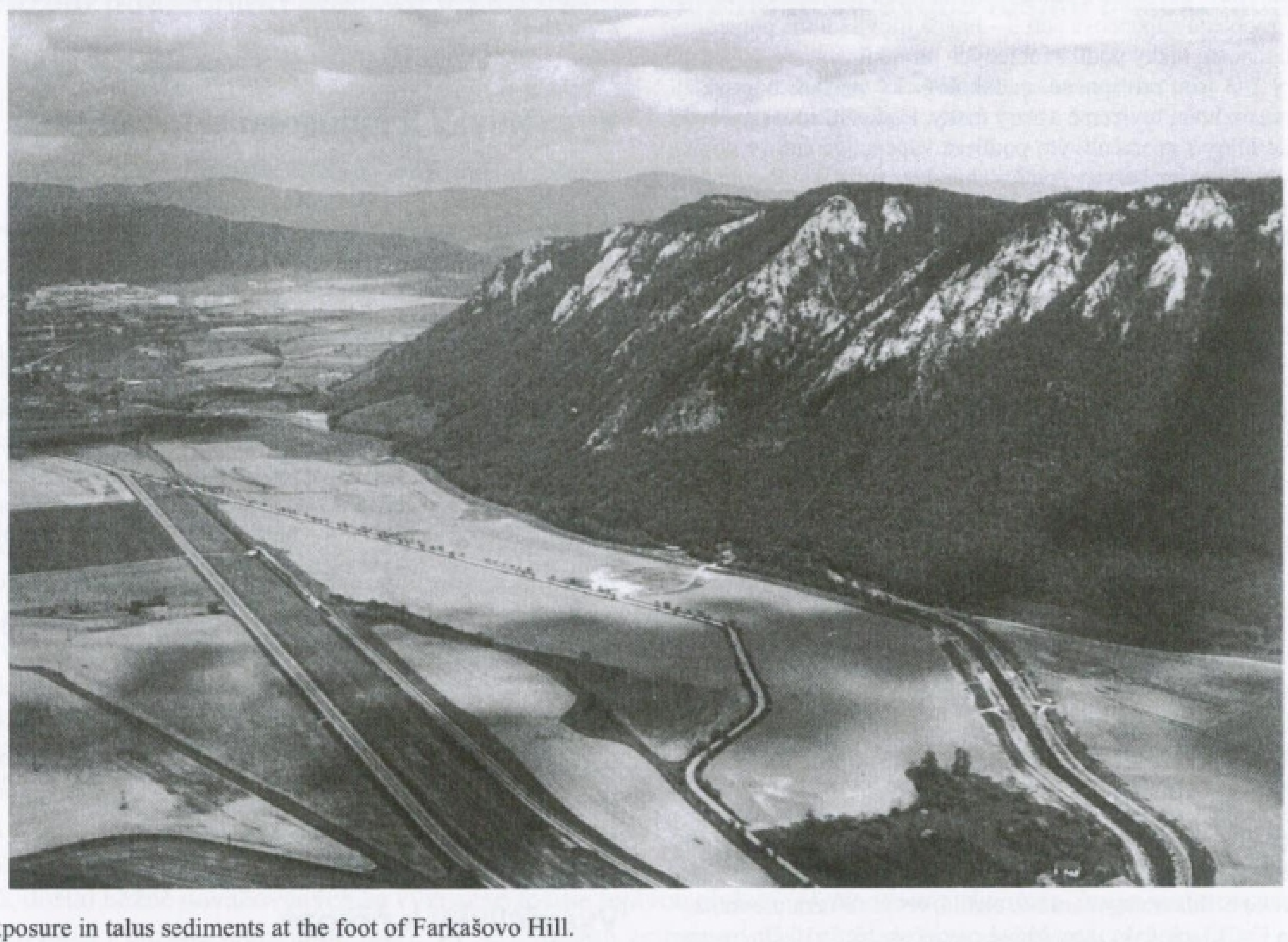
Tabulka 1. Farkašovo – měkkýší fauna.

Tabulka 2. Brzotín (břeh Slané) – měkkýší fauna.

Obecné vysvětlivky k tabulkám 1 a 2
Ekologické charakteristiky
Hlavní ekologické skupiny: A – les všeobecně, B – bezlesí, C – les i bezlesí, D – mokřady, vodní stanoviště.
Ekologické skupiny: 1 – zapojený les; 2 – převážně les, místy i polootevřená až bezlesá stanoviště: W(M) – svěží, W(S) – suchá, W(H) – vlhká; 3 – zamokřené lesy, luhy a olšiny; 4 – xerotermní bezlesí a skály: S – všeobecně, XL – vápencové skály, S(W) – částečné zastínění; 5 – bezlesí všeobecně, vlhké louky až stepi; les i bezlesí: 6 – převážně suché, 7 – svěží nebo různé: Me – všeobecně, MR – svěží skalní stanoviště, R(W) – skály i lesní sutě; 8 – převážně vlhké, 9 – mokřady, břehy vod, 10 – vody.
Biostratigrafické charakteristiky
+ – význačné sprašové druhy, ++ – vůdčí sprašové druhy, (+) – místní a náhodné sprašové druhy, G – druhy přežívající glaciál mimo pásmo spraší, (G) – dtto, jako relikty, ! – druhy teplých období, !! – vůdčí druhy interglaciálů, (!) – eurytermní druhy teplých období, M – moderní (postglaciální) imigranti.
3? – přibližné určení, (2) – přemístěné ulity.

Vysvětlivky k příloze

1. Odkryv na úpatí vrchu Farkašovo (foto V. Ložek). 2. Údolí Slané pod Brzotínem; šipka označuje polohu profilu (foto V. Ložek).



1. Exposure in talus sediments at the foot of Farkašovo Hill.
2. The Slaná River Valley downstream of Brzotín: the arrow shows the investigated site at the foot of Brzotínske skaly.

Photos by V. Ložek