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Črvenka loess-paleosol sequence revisited: local and regional Quaternary biogeographical inferences of the southern Carpathian Basin

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Abstract: Studies of Quaternary malacological assemblages from the loess-paleosol section of Črvenka (Vojvodina region, Serbia) provided the opportunity to examine the paleobiogeographic dynamics of the southern part of the Carpathian Basin.
The results of quantitative-statistical, paleoecological and paleobiogeographical analyses performed on 9185 specimens of 38 mollusc species from six stratigraphic units showed that the study area was a transition area between the refuge areas in the Carpathian Basin during the Pleistocene.

Keywords: biogeography; refuge; molluscs; Črvenka village; Vojvodina; Carpathian Basin; Quaternary

1 Introduction

New results have been attained from paleoecological analyses of the southern part of the Carpathian Basin [1–4] especially in the field of Quaternary malacological analyses in the Vojvodnia (Vajdaság) region [5–10]. Malacological studies merit to Endre Krolopp, Quaternary malacologist (who passed away in 2010), and his follower Pál Sümegi and finally his Ph.D. students Dávid Molnár and Júlia Hupuczi. Endre Krolopp and Pál Sümegi started the re-examination of Quaternary malacological data and provided a collection of sediment profiles, both from cores and outcrops from historical Hungary (which included the whole Carpathian Basin until 1918) [4, 11–18].

The comparative malacological analysis of the late Pleistocene loessy sediments in the Carpathian Basin started in the 1980s. By that time it became clear by radiocarbon dated malacological loess profiles in the eastern part of the Carpathian Basin that the late Pleistocene environment in this basin was not uniform [17, 19–21]. On the basis of Quarternary malacological data, a mosaic-like environment was reconstructed for the end of the Pleistocene that determined the composition of mollusc assemblages [4, 17, 18, 22–26]. This approach provided the opportunity to analyse the biogeographical situation of the Carpathian Basin at the end of the last glacial. In this paper, we introduce the results of the malacological analysis from a section in the Črvenka brickyard [10, 27], located in the Vojvodina region (Serbia), in the southern part of the Carpathian Basin. Data from the Črvenka section were compared to those from other loess sections in the southern part of the Carpathian Basin [1, 3, 17–19, 28].

Comprehensive stratigraphical, chronological and sedimentological examinations were carried out at the Črvenka brickyard site under the direction of Slobodan Marković in the last few years [9, 27]. The study site at Črvenka (N 45°39.75', E 19°28.77', 108 m a.s.l.) lies in the southern part of the Carpathian Basin (Fig. 1) and is situated in a brickyard exposure on the south-western edge of the Bácska Loess Plateau.

2 Sampling and methods

One profile, comprising four sections was sampled (Fig. 2). Mollusc shells retrieved from wet-screened sediment samples were collected for further examination at the Department of Geology and Palaeontology, University of Szeged. Shells were identified using malacological keys [35–38] and classified into ecological and biogeographical groups

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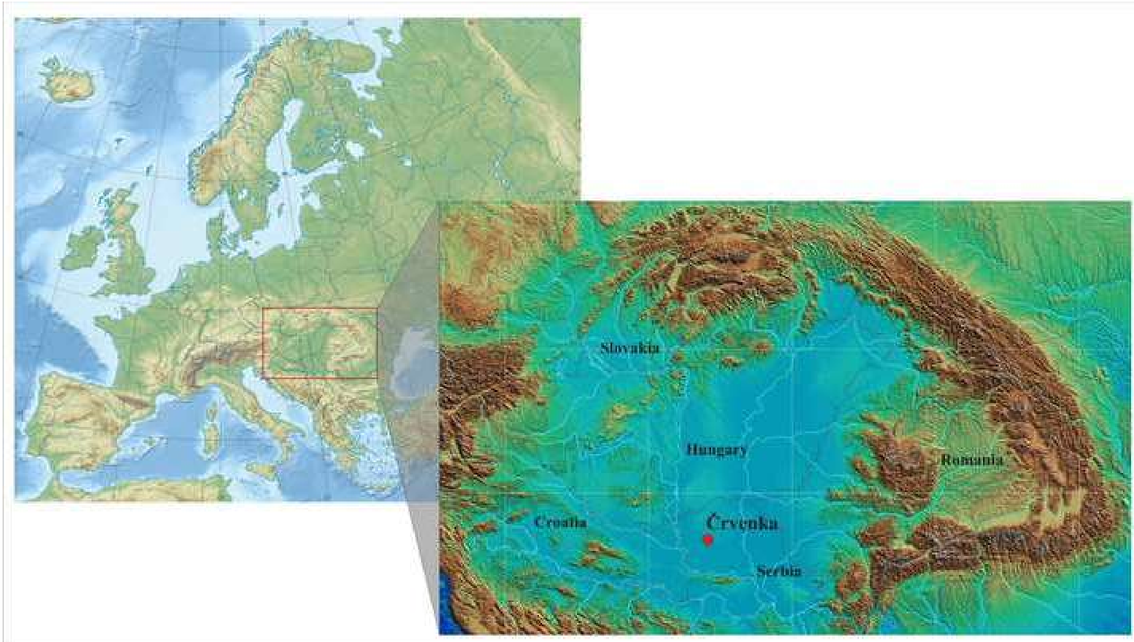


Figure 1: Location of the Črvenka brickyard in Europe and in the Carpathian Basin.

based on the system published by Krolopp-Sümegi [15, 16], Sümegi-Krolopp [17, 18], and Sümegi [4]. Relative frequencies of each taxon and the ecological groups were plotted on diagrams. Malacological zones (MZ1, MZ2, etc.) were delineated via cluster analysis. Bray-Curtis similarity calculations [39] were followed by Orlóci-Ward-type clustering [40, 41]. Numerical analyses were done with NUCOSA [42]. Clusters on the dendograms were taken to represent a single malacological zone [43, 44] Detection of local malacological zones was according to international malacological standards [45–53].

The distribution of glacial and recent species found at Črvenka were reconstructed with the help of international data [4, 18, 22, 35–38, 45–55] and the Hungarian Quaternary Malacological Data Base (which was developed in the 1990s) [22, 56]. The creation of the Hungarian Quaternary Malacological Data Base (HQMDB) was connected to the research work of Endre Krolopp and Pál Sümegi (K-46878 grant: The creation of a Quaternary Malacological Data Base in Hungary, Hungarian Scientific Research Fund) and this Data Base was extended to several areas of the Carpathian Basin by the present authors.

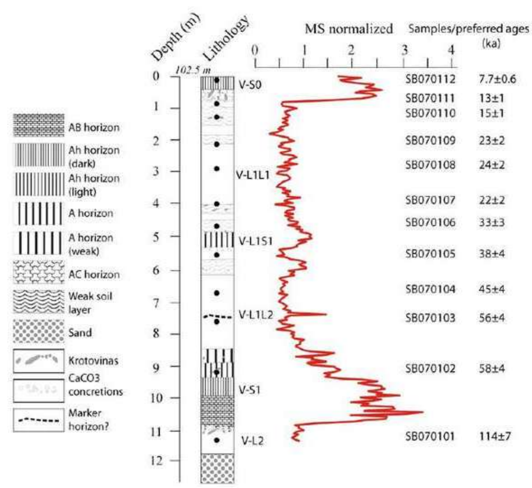


Figure 2: Lithostratigrapy, OSL ages and magnetic susceptibility results in the Črvenka section (based on Marković et al. [9] and Stevens et al. [27]; the datum 114 kyr is an unestimated age).

3 Results

Thirty eight species (3 freshwater gastropods, 34 terrestrial gastropods, 1 bivalve) were identified from 6500 whole shells and about 3500 broken shells of molluscs from 35 samples of the loess profile at Črvenka, Vojvodina. Originally 38 samples were taken for malacological analyses, but only 35 samples contained identifiable mollusc shells. On the basis of statistical analyses (Fig. 3, 4) and the consistent changes of the malacological fauna, 8 local malacological zones were defined in the Črvenka section (Fig. 5, 6, 7, and 8).

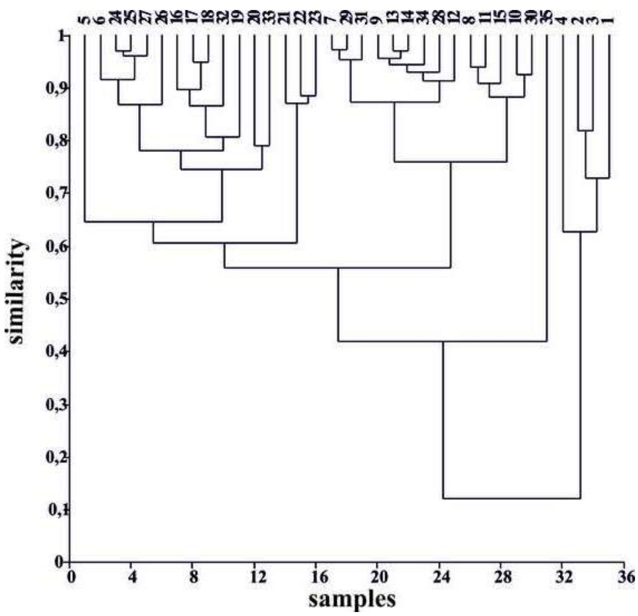


Figure 3: The results of the cluster analyses of the malacofauna from the Črvenka loess profile.

Mollusc zone MZ1 can be placed at 11.0-11.5 m, into the L2 loess horizon. This zone is characterized by the presence of *Succinea oblonga,* which prefers cold climate conditions and the cryophilous species *Pupilla sterri* is dominant. Eurytopic gastropod species such as *Pupilla muscorum*, *Vallonia costata* and *Pupilla triplicata* (between 11.0 and 11.25 m), which prefers a mild climate, are also found in the MZ1 zone. MZ1 is characterized by cold-resistant Eurosiberian, cryophilous Central European mountain, mesophilous, Holarctic, and xero-thermophilous Central and South-eastern European mollusc species, dwelling in a relatively cool, forest-steppe environment with mosaic-like structure. According to OSL data [27], this loess layer and the *Succinea oblonga – Pupilla sterri* paleoassociation formed around 114,000 years ago, within the MIS 5. The faunal composition and the dominance value of the cryophilous *Pupilla sterri* suggest that the V L2 loess layer formed under glacial climate conditions. The mollusc faunal composition suggests a typical dry and cool loess steppe or forest-steppe environment developed in

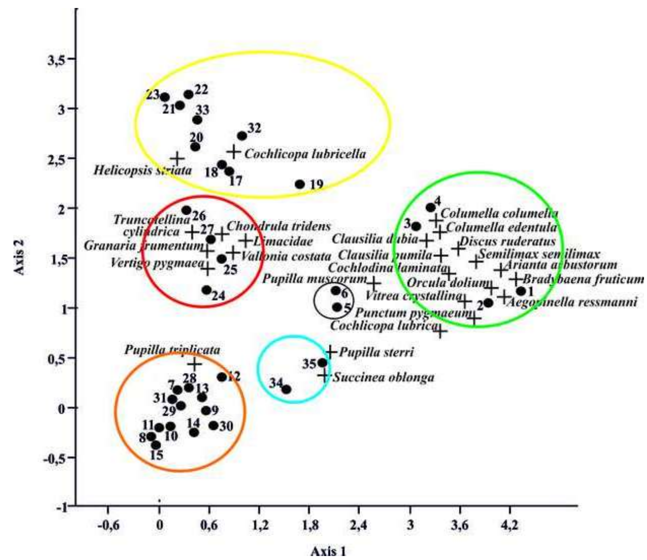
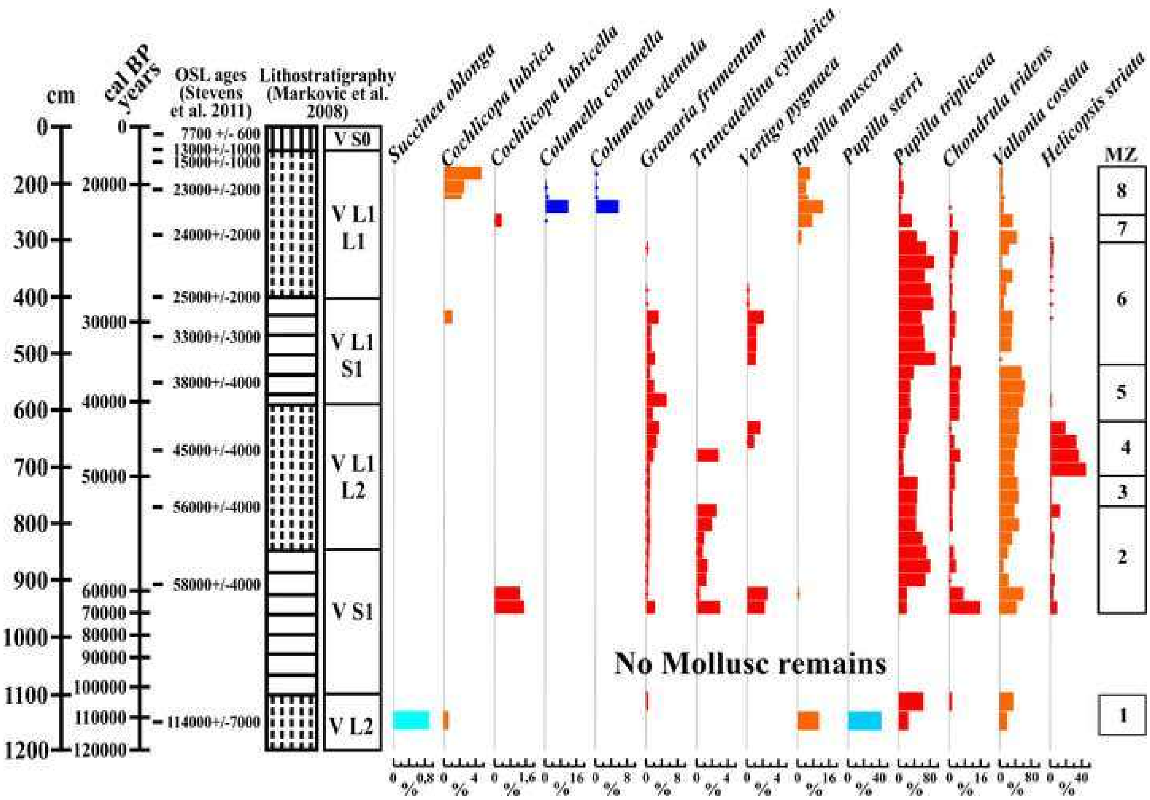


Figure 4: The results of the detrendend correspondence analyses of the malacofauna from the Črvenka loess profile.

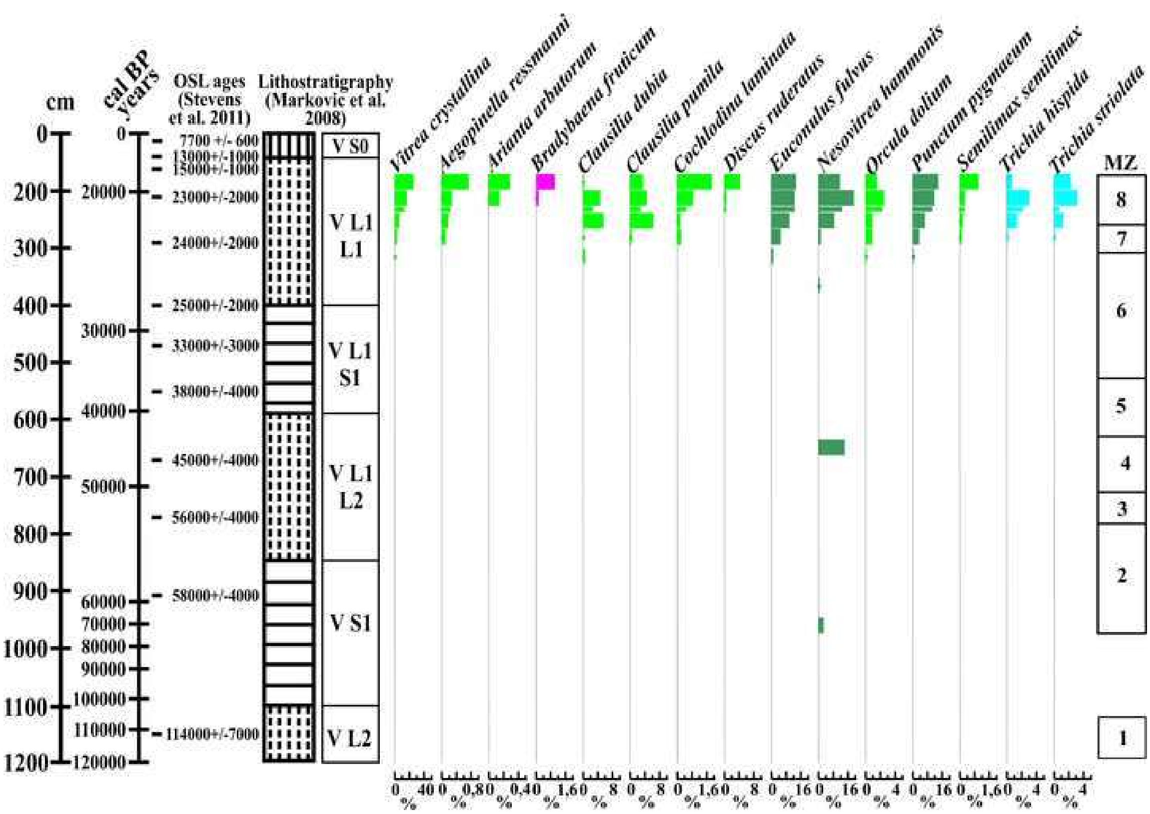
the study site where short grass covered about 80% of the surface. Based on faunal change, the transition zone of MIS6/MIS5 presumably occurred between 11.00 and 11.25 m, where cryophilous *Pupilla sterri* and cold resistant *Succinea oblonga* disappeared and mesophilous and thermophilous species dominated.

No mollusc remains have been found between 11.0 and 9.5 metres where a well-developed soil layer formed [9]. Previous taphonomic analyses [2–4, 19–22, 57] indicate that it is due to the dissolution of shells during pedogenesis. Mollusc remains at 9.5 metres depth are 70,000 years in age according to OSL data. From this depth the presence of mollusc remains was continuous to the top of the profile. These data allowed for the reconstruction of the environmental change for the end of the Pleistocene, specifically for MIS 3 and MIS 2 [58–60] (Fig. 5). This is one of the most complete terrestrial environment historical analyses in the Carpathian Basin for these chronological horizons.

The MZ2 developed between 9.5 and 7.7 m. Based on the chronological data [27, 30–32] this zone formed between 58,000 and 56,000 cal BP years. MZ2 is characterized by a higher dominance of warm-loving, mild climate preferring, xerophilous and mesophilous, species that preferred open vegetation including: *Cochlicopa lubricella*, *Truncatellina cylindrica*, *Granaria frumentum*, *Vertigo pygmaea*, *Pupilla muscorum* and *Pupilla triplicata*. Species that preferred a forest-steppe environment such as *Vallonia costata* also gained greater importance in the MZ2 zone. Shade-loving and hygrophilous species are absent from this zone. MZ2 is characterized by the paleoassociation of *Cochlicopa lubricella*, *Truncatellina cylindrica*,



(a)



(b)

Figure 5: a) The dominance changes of mollusc species from the Črvenka loess profile; b) The dominance changes of mollusc species from the Črvenka loess profile.

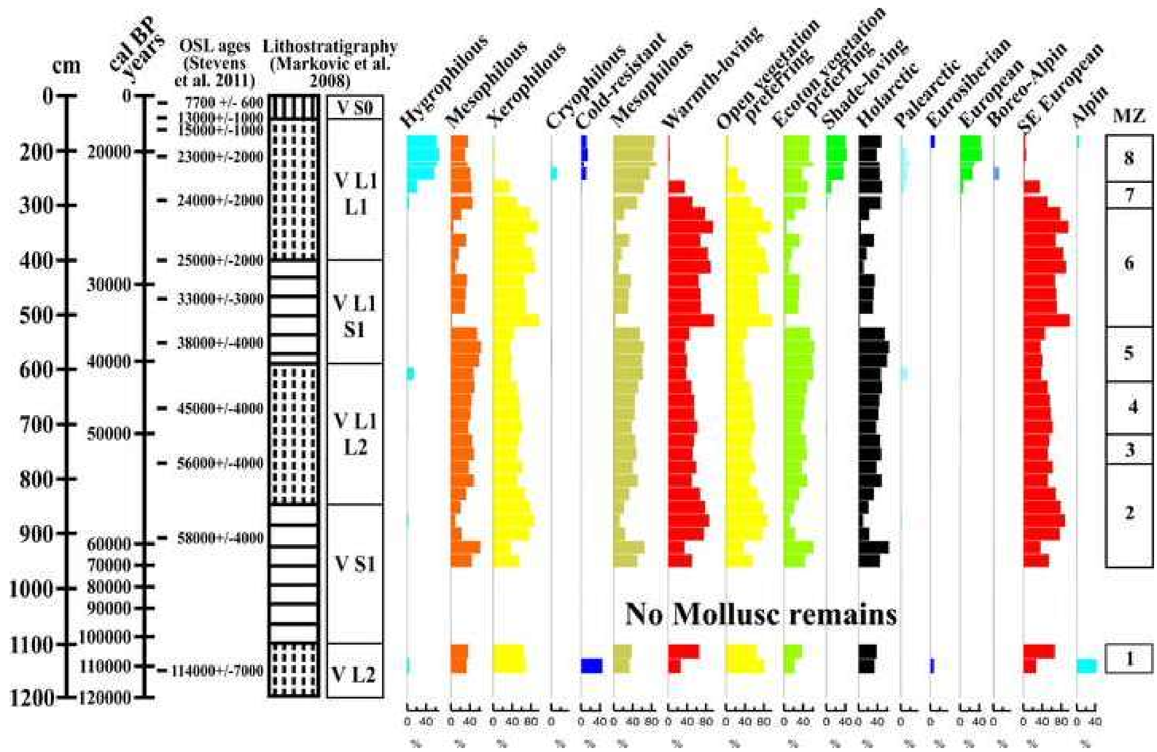


Figure 6: The dominance changes of the mollusc-based paleoecological fauna from the Črvenka loess profile.

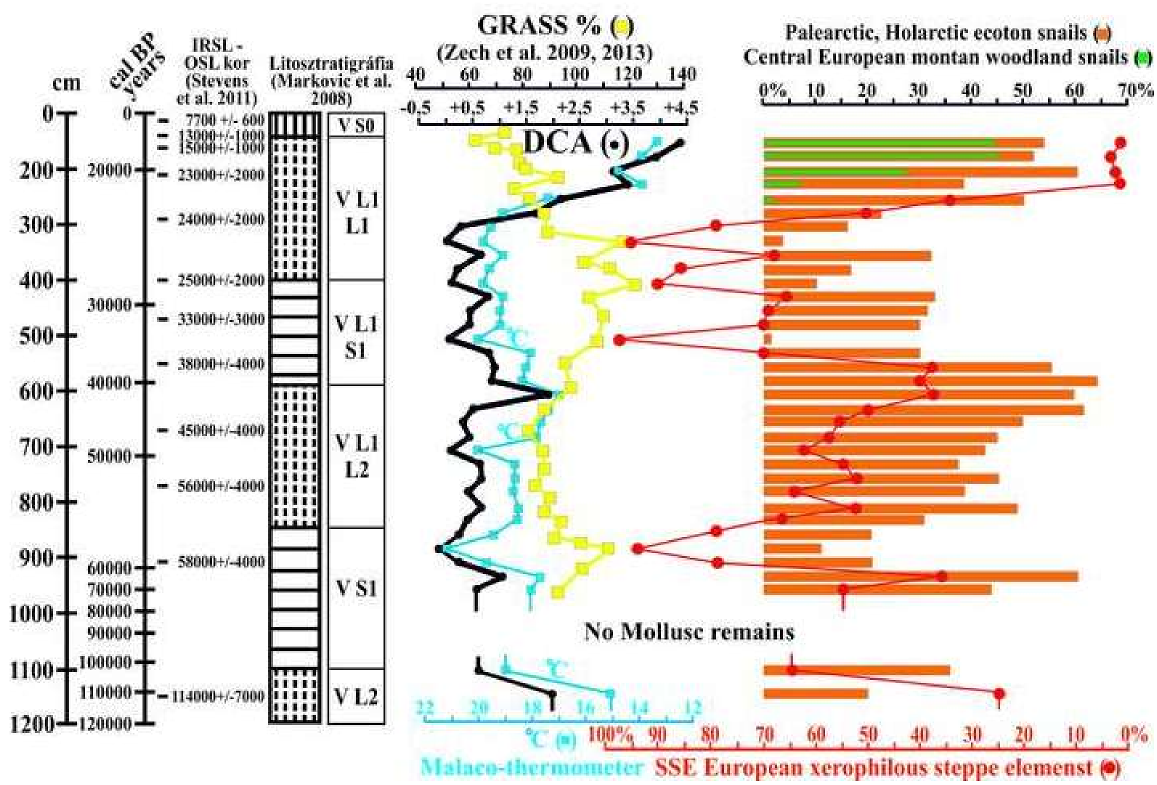


Figure 7: The changes of the different palaeoecological indicator groups from Črvenka loess profile.

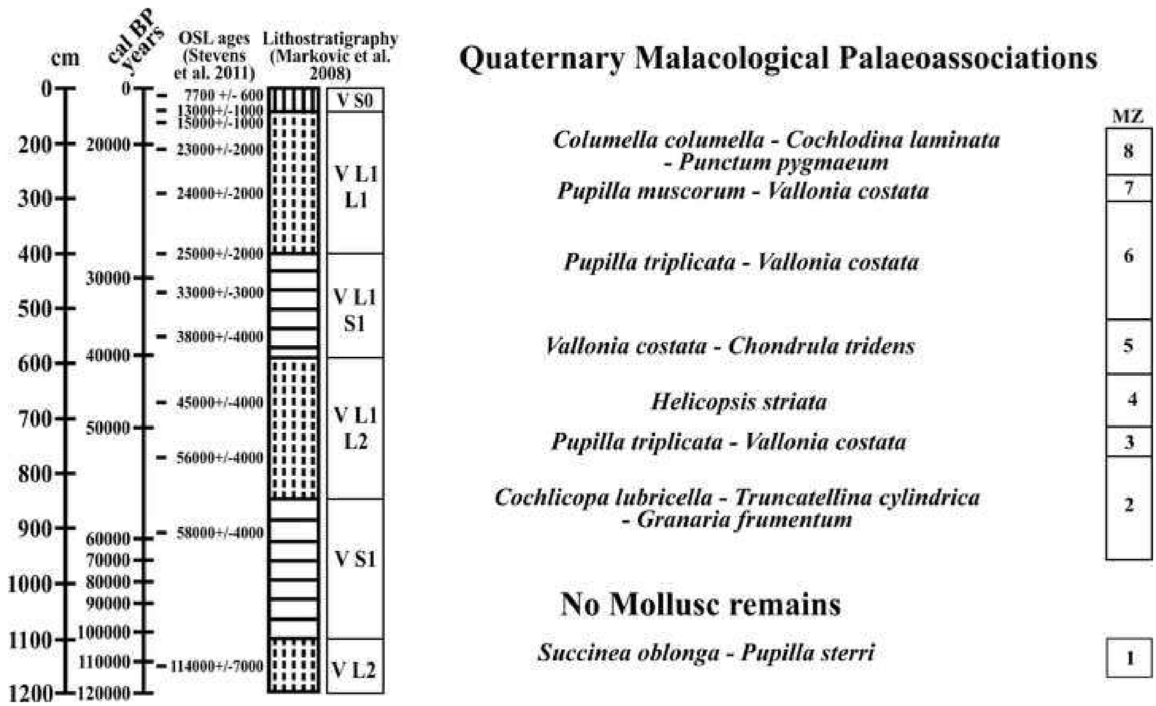


Figure 8: The Quaternary malacological paleoassociations from the Črvenka loess profile.

and *Granaria frumentum* (Fig. 5). This species composition appeared only in this level of the profile (Fig. 5, 6, 7, 8). *C. lubricella, T. cylindrical, G. frumentum* and other species such as *Vertigo pygmaea, Pupilla triplicata, Chondrula tridens, Helicopsis striata* and *Pupilla muscorum* are typical in temperate steppe-forest and steppe environments. The malacofauna characterized the Early Holocene in the central part of the Great Hungarian Plain . Therefore, the malacofauna from the top part of the S1 soil and early L1 loess layers in the črvenka profile is similar to the Early Holocene mild temperate steppe, forest-steppe malacofauna of the Great Hungarian Plain [4, 25, 61]. According to the Quaternary malacological data from the loess profiles of the Carpathian Basin this paleoassociation formed in a forest-steppe environment during a mild climatic phase [18, 52, 61]. This malaco-association is characteristic in the early MIS 3 (Fig. 8), during the Greenland Interstadial 17 level [60] which is completely different from the composition of the mollusc fauna of the Carpathians, Dinaric Alps and Alps. In the Carpathians, Dinaric Alps and Alps and in their foothills *Clausilia pumila*, *Clausilia dubia*, *Magrocastra ventricosa, Punctum pygmaeum* and *Vitrea crystallina* species dominate during the early MIS 3 [2–4, 6, 36, 56, 57]. These species prefer shade and forested habitats, which indicate a forested environments and dwell in forested areas recently, as well [66–76]. These findings suggest that there is a huge difference between the malacofauna of the črvenka loess profile and the Carpathians, Dinaric Alps and Alps during the early MIS 3. During this period, a forest environment developed in the mountain and foothill area, while steppe/forest steppe environments formed in the Great Hungarian Plain.

The MZ3 developed between 7.7 and 7.2 metres. On the basis of the chronological data this zone corresponds to 56,000-50,000 cal BP years. The fauna suffered a remarkable change compared to the earlier zones. This is indicated by the disappearance of *Truncatellina cylindrica* and *Vertigo pygmaea*, and the decreasing abundance of *Granaria frumentum* and *Chondrula tridens*. *Vallonia costata* (Holarctic spreading, forest steppe preferring) and *Pupilla triplicata* (preferring carbonated underlay and steppe environment) dominated in this zone. This association can be found on the southern exposure natural steppe and forest-steppe areas in the middle mountain range zone of the Carpathian Basin [34, 66, 67, 77–81].

MZ4 is in the interval 7.2-6.2 metres, where some small changes occurred in the composition of the malacofauna. This zone is characterized by a dominance of warm-loving, xerophilous and open habitat preferring *Helicopsis striata* (20-46 %). In this zone, besides the dominance of *Helicopsis striata*, *Vallonia costata* and *Chondrula tridens* reached considerable importance. There is a drop in the abundance of *Pupilla triplicata*, therefore this zone is characterized by the paleoassociaition of *Helicopsis striata, Vallonia* *costata*, and *Chodrula tridens*. Nowadays similar mollusc associations characterize the carbonate-rich loess steppes of the southern part of the Great Hungarian Plain [82, 83]. Based on the calculated dominance values of the individual paleoecological groups, this zone was characterized by mesophilous, xerophilous, mild climate preferring Holarctic, Central and Southeastern European mollusc species, dwelling in a mild steppe environment. This loess layer formed in a typical dry and mild loess steppe environment, where short grassland covered a minimum of 50% of the surface. The *Helicopsis striata*-dominated malacofauna from a short grassland environment with a lithosol soil clearly differed from the fauna of the temperate forest steppe with a deep, organic rich, black earth soil type.

MZ5 developed between 6.2 and 5.0 metres. It is characterized by a peak of the Holarctic mesophilous forest-steppe preferring species *Vallonia costata* (47-64%). The ratio of warm-loving, xerophilous and open habitat preferring *Chondrula tridens* (5-6%) is also significant. According to OSL data, this malacofauna lived between 40,000 and 34,000 cal BP years. During MZ5, species that preferred cold and humid micro environments, especially *Succinea oblonga*, spread on the ranges and hills of the Carpathian Basin [64–67]. On the basis of data from Črvenka, it seems that a different paleoassociation evolved on the southern part of the Great Hungarian Plain in an arid environment in the later part of the MIS 3. This *Vallonia costata-Chondrula tridens* paleoassociation settled in a typical mesophilous forest steppe environment in the study site. The composition of the malacofauna and the dominance of mollusc taxa suggest that humidity and vegetation cover were higher than in the previous malacological zone (MZ4). The remarkable change of the malacofauna likely reflects a cooler climate with local relative humidity increasing. Thus, the vegetation density increased in a cooler and more humid micro-environment and probably reforestation started in the area. The malacological data suggest that this loessy layer formed in a typical mild loess forest-steppe environment.

The MZ6 is located between 5.0 and 3.0 metres. The chronological data suggest that this zone formed between 35,000 and about 25,000 cal BP years. The most important change in this zone is a drastic decrease in the proportions of *Vallonia costata* accompanied by a considerable increase of the dry open vegetation habitat preferring *Pupilla triplicata* (58-93%). Today this species lives in carbonate-rich open vegetation environments in the mountain and hilly regions in Central Europe [34, 66, 67, 84]. The general composition of the fauna and the presence of species such as *Granaria frumentum, Vertigo pygmaea* and *Helicopsis striata* indicate lower grassland cover for larger parts of the surface compared to the previous zone. This loessy layer formed in a typical dry and temperate steppe environment [25, 82, 83], where short grassland covered more than 60% of the surface based on the composition of mollusc fauna.

The fauna changed significantly between 3.0 and 2.5 metres, in the MZ7, dated between 24,000 and 23,000 cal BP years. The ratio of thermophilous species [34, 66, 67, 82–84] decreased intensively (Fig. 5, 6, 7, and 8), however a few specimens of *Cochlicopa lubricella*, *Granaria frumentum, Pupilla triplicata, Chondrula tridens* and *Helicopsis striata* were present in this zone of the profile. This faunal change indicates a transition from a mild-dry to a cold-wet environment.

Rather important changes have been observed in the MZ8 (2.5-1.65 metres), where cold-loving and cold-resistant species (*Columella columella*, *C. edentula*) have relatively large dominances (Fig. 5). Moreover, a significant dominance increase of forest and ecotone (forest-steppe transition) species (e.g., *Clausilia pumila, C. dubia, Cochlodina laminata, Vitrea crystallina, Aegopinella ressmanni, Arianta arbustorum, Orcula dolium, Discus ruderatus, Semilimax semilimax* and *Punctum pygmaeum*) occurred. The dominance of the shade-loving and intense vegetation cover preferring mollusc was between 50 and 70% in this zone. Although several mollusc species had significant dominance in this stage, the paleoassociation of *Columella columella, Cochlodina laminata* and *Punctum pygmaeum* mostly characterized this zone. The chronological data suggest that MZ8 formed between 23,300 and 18,000 cal BP years. The most important change in this zone is the decline of warm-loving, steppe preferring species, such as *Granaria frumentum, Pupilla triplicata, Chondrula tridens, Helicopsis striata* and the mesophilous species *Vallonia costata*. In addition, the considerable increase in the hygrophilous, cold-resistant, open vegetation preferring European *Trichia hispida* and *T. striolata* is significant. This faunistic change points to the emergence of a colder climatic period in the study area. This is most likely coeval with the Late Pleniglacial (recorded in the southern part of the Great Hungarian Plain) where the peak in abundance of the Boreo-Alpin *Columella columella* has been observed [1, 4, 18]. Based on the malacothermometer method [4, 21] the mean July paleotemperature was between 13-14°C in this phase, 7-9°C lower than today.

The peak in abundance of shade loving molluscs suggests that the lower summer temperature interlocked higher humidity and vegetation density. The composition of the mollusc fauna indicates a mosaic-like environment during the Late Pleniglacial dust accumulation phase, when tundra-like Boreo-Alpine species and Holarctic mesophilous steppe, forest steppe environment preferring taxa lived together with shade loving Central-European, European, and Alpine mountain species in the study site. This mosaic-like vegetation cover supported the expansion of both woodland and open vegetation habitat preferring molluscs. The composition of the fauna refers to mosaic-like forest steppe, open parkland vegetation within tundra-like spots and a cool, but humid climate development during the dust accumulation period. The most diverse mollusc fauna has been found in this zone (Fig. 5).

4 Discussion

Paleoecological results of the Črvenka profile

The Črvenka profile (just over 11 m) has been interpreted by Marković et al. [9] to cover the Holocene soil (V-S0), the entire sequence of last glacial units (collectively V-L1), the Last Interglacial soil (V-S1) and the very upper part of the penultimate glacial loess (V-L2). Stratigraphic studies of loess and paleosols at various exposures in the Vojvodina region have used lithologic and pedogenetic criteria, magnetic susceptibility variations, aminostratigraphy and luminescence dating as the primary basis for correlation between sites. Marković et al. [9] designated the Vojvodinian loess-paleosol chronostratigraphic units by names that follow the Chinese loess stratigraphic system (e.g., [29]), beginning with the prefix "V" referring to the Vojvodina region (Fig. 2).

According to thechronostratigraphic model in Marković et al. [9], loess unit V-L2 accumulated during the penultimate glacial marine isotope stage (MIS) 6 and the paleosol unit V-S1 correlates with the Last Interglacial MIS 5; however, chronological data and previous loess stratigraphic analysis [33, 34] indicate that the uppermost part of V-S1 is likely younger than MIS 5 and partly developed during MIS 4 [33, 34]. Yet, it must be noted that the radiometric ages older than 50-60 kyr are underestimated for the črvenka profile described in Stevens et al. [27]. Underestimation is supported by the malacofauna shift in upper MZ1, suggesting placement of the MIS5/MIS6 transition at 11-11.25 m (middle V L2). V-S1 is overlain by composite loess unit V-L1, which is correlated with MIS 4-2. The structure of the last glacial loess, V-L1, varies in different loess localities across the Vojvodina region. The lower subhorizon of V-L1, termed V-L1L2, accumulated above the paleosol V-S1. The middle last glacial is apparently represented in the area by a poorly developed soil complex, V-L1S1. Thus the youngest loess layer, V-L1L1, would have accumulated during the upper last glacial period and V-S0 formed during the Holocene. The lithostratigraphical and chronological analysis of the črvenka profile [9] were published in other studies [27, 30–32].

The oldest assemblages were found in the L2 loess stage. This stage formed in a cold climate period with a 15°C average July temperature in a loess steppe environment. During the following stage, a fossil soil level developed and mollusc remains did not turn up. The malacofauna could be traced again from 70,000 cal BP years (Fig. 5, 6, 7, 8).

Considering the results of the detrended correspondence analyses made on the molluscs fauna, and the results of plant alkene examinations [85, 86], the dominance changes of paleoecological groups and the changes of the average July temperature by the malacothermometer, we were able to reconstruct the environmental changes during the MIS 3 and MIS 2 periods. Since the sampling range was 25 cm [27, 30, 32, 85, 86], the faunal changes have been examined at a scale of approximately 1250 years (Fig. 5, 6, 7 and 8). The faunal statistical analyses confirmed that the Črvenka malacofauna followed the climate trend that was demonstrated in the North Greenland Ice Core Project, particularly for the Greenland Interstadials between GI17 and GI12 [113]. A higher resolution sampling technique would have allowed for a more precise reconstruction for all GI stages on a malacological base.

It is very important that the vegetation reconstructed from plant alkenes [85] correlated (Fig. 7) with the malacofauna as was previously thought [25]. On the basis of the malacological results, the open vegetation covered area (steppe) extended during mild climatic periods, but during cold climate periods the closed vegetation cover (forests) extended throughout the study area. This change was most significant during the Last Glacial Maximum (LGM) when cold loving fauna, indicating tundra-subarctic environments, spread in northern and western Europe. In Črvenka, in the southern Carpathian Basin, the mollusc fauna was characterized by forest-loving and cold-loving Arcto-Alpine and Central European mountain species.

On the basis of the paleoecological trends in the southern part of the Great Hungarian Plain, and as a result of higher temperature, an arid local environment developed with short-grassed steppe during the interstadials of the last glacial. During cold periods, vegetation density increased and forest steppe and long-grassed steppe were dominant. At the same time, mosaic-like vegetation cover developed where several species with different ecological demands dwelt during the mild and cold climate periods.

As a result of the mosaic-like environment, a species rich malacofauna evolved; however the increase in temperature caused the number of species to decline and over-all biodiversity decreased. More humid periods during the cold climate phases were favourable to the mollusc fauna. This can be seen in the Črvenka loess profile where species rich malacofauna developed during cold climate periods.

The last glacial environment history and paleobiogeographical changes in the southern part of the Great Hungarian Plain

The observed changes in the Črvenka loess profile are not unique in the Carpathian Basin. Actually, it is well known that the malacofauna of the southern Great Hungarian Plain is different than that observed in northern, western and eastern Europe [13, 14, 17, 18]. Furthermore, the Črvenka malacofauna is different from the malacofauna recorded at other sites in the Carpathian Basin [17, 22, 23, 26, 87].

The most important difference in species composition is the constant presence of warm loving, aridity resistant (xerothermophilous) steppe elements, especially *Cochlicopa lubricella, Granaria frumentum, Pupilla triplicata, Chondrula tridens* and *Helicopsis striata*, which showed considerable dominance during interstadials [18].

Maximum abundance of some warm loving species increased in different periods of time, and the proportion of these species significantly changed according to the local environmental conditions (in several areas of the Southern part of the Great Hungarian Plain). But it can be observed that the dominance changes and the decrease of the proportions of thermophilous species occurred in a consistent way in several areas [1, 3, 26].

A significant change occurred in the development of the mollusc faunas at the end of the glacial. Holarctic species preferring long-grass steppe appeared in cold periods. The paleoassociation of *Pupilla muscorum* and *Vallonia costata* became significant. During warm periods, species preferring short-grass steppe with Pontic distribution, such as *Cochlicopa lubricella, Granaria frumetum, Helicopsis striata*, dominated, but Holartic forest steppe elements were also present. During the temperate-cold periods the elements of the Pannonian forest-steppe became dominant, especially *Pupilla muscorum* and *Vallonia costata*, though the warm loving, xerophilous, Pontic species still occurred. These data suggest that during the last glacial, between 60,000 and 24,000 cal BP years, Pannonian forest steppe mosaics existed in the southern part of the Carpathian Basin with different conditions. As a result, macro-climatic changes periodically influenced the mosaics in such a way that the extension of patches followed climate changes.

The mollusc association of temperate Pannonian forest steppe environment changed during the LGM. Tundra and taiga species, such as *Columella columella, Cochlodina laminata, Puctum pygmaeum* appeared, and a mosaic-like Boreal forest steppe, consisting of tundra, cold steppe, and taiga patches evolved in the southern part of the basin. This type of vegetation occurs in southern Siberia and the Altai Mountains today [4, 17, 18, 23, 24, 26, 54, 55, 88]. In parallel to that, the ratio of thermophilous species, such as *Granaria frumentum* and *Helicopsis striata*, decreased in this level of the profile and euryok thermophilous species (*Chondrula tridens*) subsited, probably in south oriented slopes.

This type of boreal forest-steppe and the connected paleoassociation of *Columella columella, Cochlodina laminata, Punctum pygmaeum* existed until about 16,000-15,000 cal BP years. Then cold loving elements gradually retreated and mesophilous and thermophilous elements appeared in this area [17, 18, 89]. Thus at the Pleistocene-Holocene transition, a mosaic-structured Pannonian forest steppe, with recent submediterranean and continental elements developed in the southern part of the Carpathian Basin [1, 17, 18, 25, 62, 90].

5 Conclusions

Comparison of other mollusc assemblages with assemblages occurring in the črvenka succession indicates that the Late Pleistocene environments in this area were different from those observed in the western, eastern and northern European loess records [33, 47, 68, 69, 91–101]. The Late Pleistocene environment in Central and Western Europe varied from glacial tundra (indicated by *Columella collumela* fauna: [33]) to interglacial humid deciduous forest habitats (represented by *Helicigona banatica* fauna types: [33]). Temperate grassland and forest steppe habitats (indicated by *Truncatellina cylindrica*, *Granaria frumentum*, *Pupilla triplicata*, *Helicopsis striata* and *Chondrula tridens*) dominated in the southern part of the Carpathian Basin. The main reason for these environmental differences is the increase of the sub-Mediterranean (Pontic) and continental climatic influences as a result of the increasing distance from the Atlantic Ocean.

Nevertheless, the most important factor regarding these regional climatic differences is the “basin effect” in the inner and southern parts of the Carpathian Basin due to the uplift of the Alps, Dinaric Alps and Carpathians mountain ranges during the Cenozoic. As a result of the emergence of the mountain range a negative precipitation effect developed in the inner and southern part of the basin. This condition shows similarity with the continental climate and was amplified by the sub-Mediterranean climate effect that can be observed nowadays as well, especially by the considerable sunshine duration [25, 102, 103].

A sub-Mediterranean climate, with higher sunshine duration and temperature, and decreased precipitation characterised the study area during the end of the Pleistocene. Therefore, this area evolved differently compared to other parts of Europe during the Pleistocene and also during the Holocene. Aridity was so extreme that during warm periods the lower timberline [104] persisted through this area during the Pleistocene, and was likely located here even during cold periods with increased humidity [105]. In these ecological conditions, arboreal species were present but their growth was insignificant.

On the basis of the local environment sensitive mollusc species, the lower tree line and timberline were not defined, but rather followed local changes. As a result, a wide transition zone evolved with forest steppe between the lower timberline and tree line. During warm periods, temperate grassland vegetation patches dominated with sporadic forest steppe like patches in the study area. This allowed temperate open parkland type vegetation to develop. During colder periods, as a result of the increasing humidity, the area of forest steppe increased and Holarctic forest steppe mollusc species became more dominant in addition to Pontic fauna elements. Using the malacological results, the most extensive arboreal vegetation cover developed during the LGM in the profile (forest cover reached 50-60%) besides the boreal forest steppe.

The best indicator species of a temperate grassland environment is the xerothermophilous *Granaria frumentum* whose most significant expansion occurred in the Carpathian Basin at 60,000 cal BP years (Fig. 9) [1, 3–8, 17, 18, 62]. After the last interglacial, at about 60,000 cal BP years, *G. frumentum* spread into other parts of Central Europe, in the Czech Basin, the Vienna Basin, and into the Carpathians and Alps to a height of approximately 1000 metres a.s.l. [33, 64, 65, 68, 69, 88, 106]. The spread of this species indicates that the temperate forest steppe expanded to the foothills and lower mountain regions. After 60,000 cal BP years, the significance of *G. frumentum* decreased. Between 40,000 and 30,000 cal BP years, *G. frumentum* increased in the southern part of the Carpathian Basin and decreased towards the north (Fig. 9). Between 30,000 and 24,000 cal BP years the species declined and occurred only in the southern areas. After 24,000 cal BP years *G. frumentum* turned up only sporadically and only in the southern Carpathian Basin. During the LGM (between 24,000-18,000 cal BP years) only a few specimens were found in the loess profiles of Mecsek Mountain, but *G. frumentum* was absent from the other parts of the GHP and Vojvodina region (Fig. 9) [89, 107]. Therefore,the theories about a refuge area for thermophilous species in the Vojvodina region, namely the refuge of Pannonian steppe elements [8], cannot be proven because their continuous appearance cannot be demonstrated during the LGM. *Granaria frumentum* likely subsisted on south oriented slopes with the highest sunshine duration in the isolated mountains of the southern Carpathian Basin (Mecsek, Villány Mountains and Fruska Gora) during the LGM.

These data support the Quaternary paleobiogeographical models [17, 18, 22, 23, 89, 107], that these isolated mountains in the southern part of the Carpathian Basin were the refuge areas of the Moesian and Illyrian fauna elements (and probably flora), including temperate grassland taxa [17, 22, 23, 89, 107]. In these diverse mountains, on the south oriented slopes, the local and extralocal sunshine and higher temperatures compensated for the decreasing regional temperatures during the LGM.

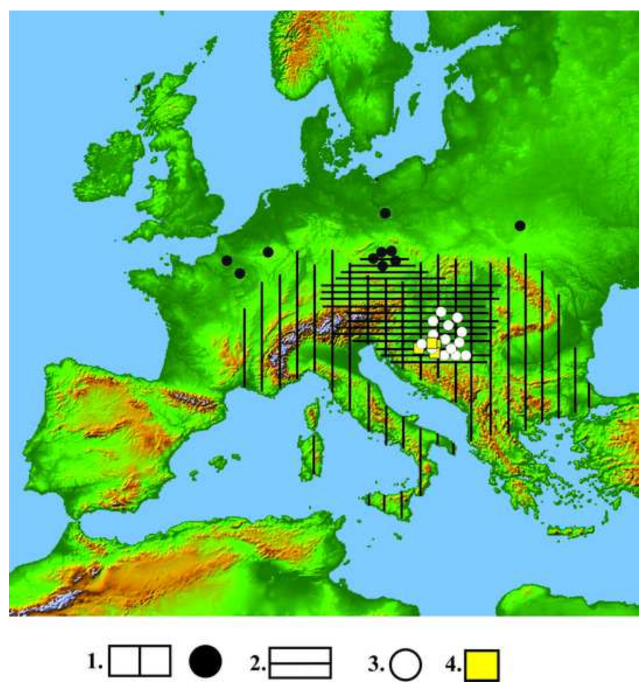


Figure 9: Recent and Pleistocene distribution of *Granaria frumentum* based on the Hungarian Quaternary Malacological Data Base (1. Recent distribution of *Granaria frumentum*, 2. Distribution of *Granaria frumentum* at about 60,000 cal BP years, 3. Distribution of *Granaria frumentum* between 25,000 – 35,000 cal BP years, 4. Distribution of *Granaria frumentum* during the Last Glacial Maximum (LGM)).

6 Summary

At the end of the Pleistocene the southern part of the Carpathian Basin, including the Vojvodina region, served as a transition zone [108] rather than a refuge area. Species spread from the refuges during favourable climatic and environmental phases to this fluctuation area and receded to the refuges during unfavourable conditions.

This dynamic relationship [107, 108] between the fluctuation area and the refuges characterized the development of the Boreal forest steppe vegetation during the LGM. In the southern part of the Carpathian Basin, and in the Črvenka loess profile, the shade-loving *Cochlodina laminata* appeared. Today this species is widespread in the Central European forested mountain zone. Similarly, forest habitat preferring Central European mountainous *Clausilia pumila*, *Semilimax semilimax* and *Aegopinella ressmanni* species spread during the LGM. These species turned up only from the profiles of the southern Carpathian Basin and probably their refuge area was Mecsek Mountain (Fig. 10).

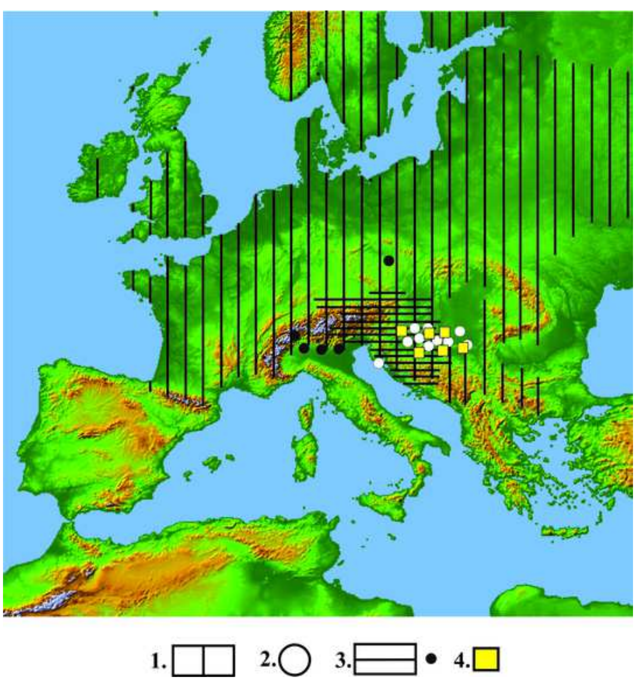


Figure 10: Recent and Last Glacial Maximum (LGM) distribution of the forest habitat preferring molluscs based on the Hungarian Quaternary Malacological Data Base (1. Recent distribution of *Cochlodina laminata*, 2. Distribution of *Cochlodina laminata* during the Last Glacial Maximum, 3. Recent distribution of *Aegopinella ressmanni*, 4. Distribution of *Aegopinella ressmanni* during the Last Glacial Maximum).

On the basis of atmospheric physical models [109], trees and shrubs, including conifers and deciduous trees, and fauna elements subsisted on the southern sides of isolated mountains between 500-600 meters during the coldest and driest stages of the LGM. At this elevation atmospheric moisture precipitated and compensated for the Pleistocene regional aridity. On the south oriented slopes, a favourable microclimate developed for temperature sensitive forest ecosystems. These conditions allowed for the development of local forest refuge areas in the mid mountain zones of the Alps, Carpathians and Dinaric Alps. Mecsek Mountains was probably a refuge area for both temperate grassland environment preferring and temperate shade-loving species as a result of its microclimatic diversity (Fig. 9 and 10). Taking into account the cold valleys in the northern part of the mountain, it had a kind of dual role. Namely, refuge areas existed in different parts of Mecsek Mountains: during colder periods, it harboured elements preferring a milder climate, while during warmer periods, species favouring a colder climate subsisted. Villány Mountain may have had a similar role, however due to its lower height and less diverse surface it was a refuge area for temperate grassland favouring species.

Analysis of the mollusc species from Fruska Gora was started by Endre Krolopp and Pál Sümegi in 2000 [1-3,5-8,111]. Unfortunately, we have only a few malacologically analyzed profiles from the eastern part of the mountain that cover 1200-1500 years long intervals. Thus the refuge role of this area is not clear yet, only hypothetical [108,109].

On the basis of the Quartermalacological analyses and the Hungarian Quartermalacological Data Base, the southern part of the Great Hungarian Plane including the Vojvodina region is a fluctuation area between refuges of the southern Carpathians, the rim of the Dinaric Alps and the isolated mountains in its northern foreground. In this fluctuation zone, temperate (Pannonian type) grassland and forest steppe developed during warm and dry periods, while during colder climate phases boreal type (that is observed in south Siberia today) steppe taiga and taiga steppe [111, 112] evolved. This environmental development differs from the observed evolution in the northern part of the Carpathian Basin and from the western, eastern and northern European ones. The reason for the difference is the higher temperature and rare drought on a local-regional level. So the most important factor in the development of the drier microclimate in the southern Great Hungarian Plain and Carpathian Basin is the basin effect as a result of the uplift of mountains and the distance from the ocean.

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References

[1] Hupuczi, J., Sümegi, P., The Late Pleistocene paleoenvironment and paleoclimate of the Madaras section (South Hungary), based on preliminary records from mollusks, Central European Journal of Geosciences, 2010, 2, 64-70

[2] Hupuczi, J., Molnár, D., Galovic, L., Sümegi, P., Preliminary malacological investigation on the loess profile at Šarengrad, Croatia, Central European Journal of Geosciences, 2010, 2, 57-63

[3] Molnár, D., Hupuczi, J., Galovic, L., Sümegi, P., Preliminary malacological investigation on the loess profile at Zmajevac, Croatia, Central European Journal of Geosciences, 2010, 2, 52-56

[4] Sümegi, P. Loess and Upper Paleolithic environment in Hungary, Aurea Kiadó, Nagykovácsi, 2005

[5] Marković, C.B., Kukla, G., Sümegi, P., Milkovits, L., Jovanovits, M., Gaudenyi, T. The Last Glacial Cycle Paleoclimatic Record of Ruma Loess Section (Vojvodina, Yugoslavia), Zbornik Radova, 2000, 30, 5-13

[6] Marković, S.B., Oches, E.A., Gaudenyi,T., Jovanovic, M., Hambach, U., Zöller, L., Sümegi, P., Paleoclimate record in the Late Pleistocene loess-paleosol sequence at Miseluk (Vojvodina, Serbia), Quaternaire, 2004, 15, 361 – 368

[7] Marković, C.B., Oches, E., Sümegi, P., Jovanovits, M., Gaudenyi, T., An introduction to the Middle and Upper Pleistocene loess–paleosol sequence at Ruma brickyard, Vojvodina, Serbia, Quaternary International, 2006, 149, 80-86

[8] Marković, S.B., Oches, E.A., McCoy, W.D., Gaudenyi, T., Frechen, M., Malacological and sedimentological evidence for "warm" climate from the Irig loess sequence (Vojvodina, Serbia), Geophysics, Geochemistry and Geosystems, 2007, 8, Q09008, DOI: 10.1029/2006GC001565.

[9] Marković, S.B., Bokhorst, M., Vandenberghe, J., Oches, E.A., Zöller, L., McCoy, W.D., Gaudenyi, T., Jovanović, M., Hambach, U., Machalett, B., Late Pleistocene loess–palaeosol sequences in the Vojvodina region, North Serbia, Journal of Quaternary Science, 2008, 23, 73–84.

[10] Marković, S.B., McCoy, W.D., Oches, E.A., Savić, S., Gaudenyi, T., Jovanović, M., Stevens, T., Walther, R., Ivanišević, P., Galić, Z., Paleoclimate record in the Late Pleistocene loess-palaeosol sequence at Petrovaradin Brickyard (Vojvodina, Serbia).GeologicaCarpathica, 2005, 56, 483-491.

[11] Krolopp, E., Alföldi mélyfúrások Zsigmondy - Halaváts-féle Mollusca anyagának reviziója. II. A hódmezővásárhelyi, szegedi, szarvasi és kecskeméti artézi kútfúrás, Földtani Intézet Évi Jelentése l974-ről, l976, 133-156 (in Hungarian)

[12] Krolopp, E., Alföldi mélyfúrások Zsigmondy - Halaváts-féle Mollusca anyagának reviziója. III. A zombori (Sombor), szabadkai (Subotica), nagybecskereki (Zrenjanin) artézikút-fúrások, Földtani Intézet Évi Jelentése l975-ről, 1977, 145-161 (in Hungarian)

[13] Krolopp, E., Sümegi, P., Vorkommen von *Vestia turgida* (Rossmässler, 1836) in den Pleistozänen Sedimenten Ungarns, Soosiana, 1990, 18, 5-10 (in German)

[14] Krolopp, E., Sümegi, P., Dominance level of the species *Punctum pygmaeum* (Draparnaud, 1801) a biostratigraphical and palaeoecological key level for the Hungarian loess sediments of the Upper Würm, Soosiana, 1991, 19, 17-23

[15] Krolopp, E., Sümegi, P., A magyarországi pleisztocén *Vertigo* fajok elterjedése, Folia Historico naturalia Musei Matraensis, 1992, 17, 27-36 (in Hungarian)

[16] Krolopp, E., Sümegi, P., *Vertigo modesta* (Say, 1824), *Vertigo geyeri* (Lindholm, 1925) and *Vertigo genesii* (Gredler, 1856) species in Pleistocene formations of Hungary, Malakológiai Tájékoztató, 1993, 12, 9-14

[17] Sümegi, P., Krolopp, E., Late Quaternary Palaeoecology and Historical Geography of Hungary based on quartermalacological and radiocarbon analyses, Proceedings of 12th International Malacological Congress, Vigo, Spain, 1995, 330-331

[18] Sümegi, P., Krolopp, E., 2002. Quartermalacological analyses for modeling of the Upper Weichselian palaeoenvironmental changes in the Carpathian Basin, Quaternary International, 2002, 91, 53-63

[19] Sümegi P., Upper Pleistocene geohistory of Hajdúság region, MSc Thesis, 1986, Kossuth University, Debrecen (Hungary), 96

[20] Sümegi P., The quartermalacological investigations of the brickyard profile at Lakitelek (Hungary) Malakológiai Tájékoztató, 1988, 8, 5-7

[21] Sümegi P., Upper Pleistocene evaluation of Hajdúság region based on fine-stratigraphical (sedimentological, paleontological, geochemical) analyses, University Doctor's Thesis, 1989, Kossuth University, Debrecen (Hungary), 96

[22] Sümegi P., Quartermalacological analysis of Late-Pleistocene loess sediment of the Great Hungarian Plain, Malacological Newsletter, 1995, Supplement, 1, 79-111

[23] Sümegi P., Comparative paleoecological and startigraphical valuation of the NE Hungarian loess areas, PhD (CSc) Thesis, 1996, Debrecen – Budapest, 120

[24] Sümegi P., Magyari E., Daniel P., Hertelendi E., Rudner E., Reconstruction of the Quaternary geohistory of the White lake at Kardoskut (Hungary), Földtani Közlöny, 1999, 129, 479-519

[25] Sümegi, P., Persaits, G., Gulyás, S., Woodland-Grassland Ecotonal Shifts in Environmental Mosaics: Lessons Learnt from the Environmental History of the Carpathian Basin (Central Europe) During the Holocene and the Last Ice Age Based on Investigation of Paleobotanical and Mollusk Remains. In: Myster, R.W. ed. Ecotones Between Forest and Grassland. Springer Press, New York, 2012,

[26] Sümegi, P., Magyari, E., Dániel, P., Molnár, M., Törőcsik, T. 28,000-year record of environmental change in SE Hungary: terrestrial response to Dansgaard-Oeshger cycles and Heinrich-events. Quaternary International, 2013, 278, 34-50

[27] Stevens, T., Marković, S.B., Zech, M., Hambach, U., Sümegi, P., Dust deposition and climate in the Carpathian basin over an independently dated last glaciale/interglacial cycle, Quaternary Science Rewiews, 2011, 30, 662-681

[28] Krolopp, E., Sümegi P., Hertelendi, E., Kuti L., Kordos, L., Szeged környéki löszképződmények keletkezésének paleoökológiai rekonstrukciója, Földtani Közlöny, 1995, 125, 309-361

[29] Kukla G. J., Loess stratigraphy in central *China*, Quaternans Science Reviews, 1987, 6, 191–219

[30] Marković, S.B., Hambach, U, Jovanović, M., Stevens, T., O'Hara-Dhand, K., Basarin, B., Smalley.I.J., Buggle, B., Zech, M., Svirčev, Z., Milojković, N., Zöller, L. Loess in Vojvodina re-

gion (Northern Serbia): the missing link between European and Asian Pleistocene environments. Netherlands Journal of Geosciences 2012, 91, 173-188
[31] Marković, S.B., Timar-Gabor, A., Stevens, T., Hambach, U., Popov, D., Tomić, N., Obreht, I., Jovanović, M., Lehmkuhl, F., Kels, H., Marković, R., Gavrilov, M.B. 2014. Environmental dynamics and luminescence chronology from the Orlovat loess-palaeosol sequence (Vojvodina, Northern Serbia). Journal of Quaternary Science, 2014, 29, 189-199
[32] Marković, S.B., Stevens, T., Kukla, G.J., Hambach, U., Fitzsimmons, K.E., Gibbard, P., Buggle, B., Zech, M., Guo, Z.T., Hao, Q.Z., Wu, H., O'Hara-Dhand, K., Smalley, I.J., Ujvari, G., Sümegi, P., Timar-Gabor, A., Veres, D., Sirocko, F., Vasiljević, Dj.A., Jari, Z., Svensson, A., Jović, V., Kovács, J., Svirčev, Z. The Danube loess stratigraphy - new steps towards the development of a pan-European loess stratigraphic model. Earth Science Reviews, in press
[33] Bronger A. Correlation of loess-paleosol sequences in East and Central Asia with SE Central Europe - Towards a continental Quaternary pedostratigraphy and paleoclimatic history. Quaternary International, 2003, 106-107, 11-31
[34] Singhvi AK, Bronger A, Sauer W, Pant RK. 1989. Thermoluminescence dating of loess-paleosol sequences in the Carpatian Basin. Chemical Geology, 1989, 73, 307-317
[35] Welter-Schultes, F., European non-marine molluscs, a guide for species identification, Planet Poster Editions, Göttingen, 2012
[36] Kerney, M.P., Cameron, R.A.D., Jungbluth, J.H., Die Landschnecken Nord- und Mitteleuropas, P. Parey, Hamburg-Berlin, 1983,
[37] Ložek, V., Quartärmollusken der Tschechoslowakei, Rozpravy Ústredniho ústavu geologického, 1964, 31, 1-374
[38] Soós, L., The Mollusc fauna of the Carpathian Basin, Akadémiai Kiadó, Budapest, 1943,
[39] Southwood, T.R.E., Ecological methods with particular reference to the study of insect populations, Chapmann and Hall, London, 1978,
[40] Podani, J., Some classification and ordination methods for statistical analyses of malacological and coenological data, I. Állattani Közlemények, 1978, 65, 103-113
[41] Podani, J., Some classification and ordination methods for statistical analyses of malacological and coenological data, II. Állattani Közlemények, 1979, 66, 85-97
[42] Tóthmérész, B., 1993. NuCoSA 1.0: Number Cruncher for Community Studies and other Ecological Applications, Abstracta Botanica 7, 283-287
[43] Molnár A., Sümegi P., Classification and ordination methods in the division of the Pleistocene malacological zones of Debrecen I. profile, Soosiana, 1990, 18, 11-16
[44] Molnár. A., Sümegi P., Klasszifikációs és ordinációs módszerek pleisztocén malakológiai zónák lehatárolásához, 37-42, In: Szöőr, Gy., ed. Fáciesanalitikai, paleobiogeokémiai és paleoökológiai kutatások. MTA Debreceni Bizottsága, Debrecen, 1992 (in Hungarian)
[45] Alexandrowicz, S.W., Malacofauna of the Late Quaternary loess-like deposits in the Polish Carpathians. Acta Geologica Polonica, 1988, 38, 85–106
[46] Alexandrowicz W.P., Dmytruk R., Molluscs in Eemian-Vistulian deposits of the Kolodiiv section, Ukraine (East Carpathian Foreland) and their palaeoecological interpretation, Geological Quarterly, 2007. 51, 173–178
[47] Alexandrowicz, W.P. Malacological sequence of Weichselian (MIS 5-2) loess series from a profile in Grodzisko Dolne (southern Poland) and its palaeogeographic significance. Quaternary International, 2014, 319, 109–118
[48] Alexandrowicz, W.P., Boguckyj, A., Dmytruk, R., Łanczont, M., Molluscs of loess deposits in the Halyc Prydniestrov'ja region Studia Geologica Polonica, 2002, 119, 253–290. [In Polish with English summary].
[49] Alexandrowicz, W.P., Ciszek, D., Gołas-Siarzewska, M., Malacological characteristic of the Weichselian Upper Pleniglacial loess profile in Tłumaczów (SW Poland). Geological Quarterly, 2013, 57, 433–442
[50] Alexandrowicz, W.P., Dmytruk, R., Molluscs in Eemian-Vistulian deposits of the Kolodiiv section, Ukraine (East Carpathian Foreland) and their palaeoecological interpretation. Geological Quarterly, 2007, 51, 173–178
[51] Willis, K.J.-Sümegi, P.-Braun, M.-Tóth A. The Late Quaternary environmental history of Bátorliget, N.E. Hungary. Palaeogeography, Palaeoclimatology, Palaeoecology, 1995, 118, 25-47
[52] Sümegi, P, Deli, T. Results of the quartermalacological analysis of the profiles from the central and marginal areas of Bátorliget marshland. In: Sümegi, P.-Gulyás, S. eds. The geohistory of Bátorliget Marshland. Archaeolingua Press, 183-207., Budapest, 2004
[53] Sümegi, P., New chronological and malacological data from the Quaternary of the Sárrét area, Transdanubia, Hungary. Acta Geologica Hungarica, 2003, 46, 371-390
[54] Horsák, M., Chytrý, M., Pokryszko, B.M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kintrová, K., Kocí, M., Kune sová, S., Lustyk, P., Otýpková, Z., Pelánková, B., Valachovic, M., Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe, Journal of Biogeography, 2010, 37, 1450-1462
[55] Hoffmann, M.H.-Meng, S.-Kosarchev, P.A.-Terechina, T.A.-Silanteve, M.M. Land snail faunas along an environmental gradient in the Altai Mountains (Russia), J. Molluscan Studies, 2010, 77, 76-86
[56] Krolopp, E., Biostratigraphic division of Pleistocene formations in Hungary according to their mollusc fauna, Malacological Newsletter, Supplement 1, 1995, 17-78
[57] Krolopp, E., Quaternary malacology in Hungary. Földrajzi Közlemények, 1973, 21, 161-171
[58] Shackleton, N.J., Fairbanks, H.R.G., Chiu, T.-C., Parrenin, F., Absolute calibration of the Greenland time scale: implications for Antarctic time scales and for D14C, Quaternary Science Reviews, 2004, 23, 1513–1522
[59] Johnsen, S.J., Dahl-Jensen, D., Gundestrup, N., Steffensen, J.P., Clausen, H.B., Miller, H., Masson-Delmotte, V., Sveinbjörnsdottir, A.E., White, J., Oxygen isotope and palaeotemperature records from six Greenland ice-core stations: Camp Century, Dye-3, GRIP, GISP2, Renland and NorthGRIP, Journal of Quaternary Science, 2001, 16, 299–307
[60] Andersen, K.K., Svensson, A., Johnsen, S.J., Rasmussen, S.O., Bigler, M., Röthlisberger, R., Ruth, U., Siggaard-Andersen, M.-L., Steffensen, J.P., Dahl-Jensen, D., Vinther, B.M., Claussen, H.B., The Greenland ice core chronology 2005, 15-42 kyr. Part 1: constructing the time scale, Quaternary Science Reviews, 2006, 25, 3246–3257
[61] Szilágyi, G., Sümegi, P., Molnár, D., Sávai, Sz., Mollusc-based paleoecological investigations of the Late Copper - Early Bronze

Age earth mounds (kurgans) on the Great Hungarian Plain, Central European Journal of Geosciences, 2013, 5, 465-479
[62] Krolopp, E.-Sümegi, P. Palaeoecological reconstruction of the Late Pleistocene, Based on Loess Malacofauna in Hungary, GeoJournal, 1995, 26, 213-222
[63] Svensson, A., Andersen, K. K., Bigler, M., Clausen, H. B., Dahl-Jensen, D., Davies, S. M.,Johnsen, S. J., Muscheler, R., Parrenin, F., Rasmussen, S. O., Röthlisberger, R., Seierstad, I., Steffensen, J. P., Vinther, B. M. A 60 000 year Greenland stratigraphic ice core chronology, Climate of Past, 2008, 4, 47-57
[64] Krolopp, E., Quaternary malacology in Hungary, Földrajzi Közlemények, 1973, 21, 161–171
[65] Krolopp, E., Biostratigraphic division of Hungarian Pleistocene formations according to their mollusc fauna, Acta Geologica Hungarica, 1983, 26, 69-82
[66] Sólymos, P., Magyarország szárazföldi Mollusca-faunájának ritkaságon alapuló értékelése és alkalmazási lehetőségei, Természetvédelmi Közlemények, 2004, 11, 511–520 (in Hungarian)
[67] Sólymos, P., Are current protections of land snails in Hungary relevant to conservation? Biodiversity and Conservation, 2007, 16, 347–356
[68] Ložek, V., Das Problem der Lößbildung und die Lößmollusken. Eiszeitalter und Gegenwart, 1965, 16, 61-75
[69] Ložek, V., Molluscan fauna from the loess series of Bohemia and Moravia, Quaternary International, 2001, 76/77, 141–156
[70] Rousseau, D.D. Biogeography of the Pleistocene pleniglacial malacofaunas in Europe. Stratigraphic and climatic implications. Palaeogeography, Palaeoclimatology, Palaeoecology, 1990, 80, 7-23
[71] Rousseau, D.D. – Puissegur, J.J. – Lautridou, J.P. Biogeography of the Pleniglacial malacofaunas in Europe. Stratigraphic and climatic implications. In: Rousseau, D.D. ed. Methods and concepts in European stratigraphy. Palaeogeography, Palaeoclimatology, Palaeoecology, 1990. 80, 1-24
[72] Moine, O., Rousseau, D.D., Antoine, P., Terrestrial molluscan records of Weichselian Lower to Middle Pleniglacial climatic changes from the Nussloch loess series (Rhine Valley, Germany): the impact of local factors. Boreas, 34, 2008, 363-380
[73] Limondin-Lozouet, N., Preece, R., Molluscan successions from the Holocene tufa of St Germain-le-Vasson, Normandy (France) and their biogeographical significance. Journal of Quaternary Science, 19, 2004, 55-71.
[74] Ložek, V., The loess environment in Central Europe. In: Schultz, C., Frye, J. C. eds. Loess and Related Eolian Deposits of the World, Proceedings 7th INQUA Congress, Boulder, 1965, 67–80. University of Nebraska Press, Lincoln.
[75] Preece, R. C. Mollusca. In: Bridgland, D.R., Preece, R. C. eds. Late Quaternary Environmental Change in North-west Europe. Excavations at Holywell Coombe, South-east England, 1998, 158–212. Chapman & Hall, London.
[76] Frank, C. Plio-pleistozäne und holozäne Mollusken. Teil 1 and 2. Mitteilungen der Prahistorischen Kommission der Osterreichischen Akademie der Wissenschaften 62: 1–395; 397–860
[77] Hum, L., A Mohácstól délre fekvő fiatal lösz-szelvények paleoökológiai vizsgálatai, Malakológiai Tájékoztató, 1999, 17, 37-52 (in Hungarian)
[78] Hum, L., A Szekszárd, volt Buda úti téglagyári lösz-paleotalaj sorozat palaeoökológiai vizsgálatai, Malakológiai Tájékoztató, 2000, 18, 29 – 50 (in Hungarian)
[79] Újvári, G., Három löszfeltárás malakológiai vizsgálata a Nyárád – Harkányi-sík keleti peremén, Malakológiai Tájékoztató, 2000, 118, 69-80 (in Hungarian)
[80] Tóth Á., Negyedidőszaki éghajlati ciklusok a Mecsek környéki löszök puhatestű faunájának változása alapján, Malakológiai Tájékoztató, 2000, 18, 59-67 (in Hungarian)
[81] Hum, L., Sümegi, P., Cyclic Climatic Records in Loess-Palaeosol Sequences in Southeastern Transdanubia (Hungary) on the Basis of Sedimentological, Geochemical and Malacological Examination, Geolines, 2000, 11, 99-101
[82] Bába, K., Adatok Csongrád megye (Dél-Alföld) gyepjeinek állatföldrajzi viszonyaihoz a csigák alapján, Malakológiai Tájékoztató, 1994, 13, 81-90 (in Hungarian)
[83] Bába, K., Szezonális malakológiai vizsgálatok dél-alföldi gyepeken, Malakológiai Tájékoztató, 1995, 14, 47-59 (in Hungarian)
[84] Klemm, W., Die Verbeitung der rezenten Land-Gehause-Schnecken in Österreich, Denkschriften der Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse Abteilung II, Mathematische, physikalische und technische Wissenschaften 117, 1974, 1-513
[85] Zech, M., Buggle, B., Leiber, K., Marković, S., Glaser, B., Hambach, U., Huwe, B., Stevens, T., Sümegi, P., Wiesenberg, G., Zöller, L., Reconstructing Quaternary vegetation history in the Carpathian Basin, SE Europe, using n-alkane biomarkers as molecular fossils: problems and possible solutions, potential and limitations, Eiszeitalter und Gegenwart - Quaternary Science Journal, 2010, 85, 150-157
[86] Zech, R., Zech, M., Markovic, M., Hambach, U., Huang, Y., Humid glacials, arid interglacials? Critical thoughts on pedogenesis and paleoclimate based on multi-proxy analyses of the loess–paleosol sequence Crvenka, Northern Serbia, Palaeogeography, Palaeoclimatology, Palaeoecology, 2013, 387, 165-175
[87] Sümegi, P., The results of paleoenvironmental reconstruction and comparative geoarcheological analysis for the examined area, In: Sümegi, P., Gulyás, S. eds., The geohistory of Bátorliget Marshland, 301-348, Archaeolingua Press, Budapest, 2004
[88] Chytrý, M., Danihelka, J., Kubešová, S., Lustyk, P., Ermakov, N., Hájek, M., Hájková, P., Kočí, M., Otýpková, Z., Roleček, J., Řezníčková, M., Šmarda, P., Valachovič, M., Popov, D., Pišút, I., Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia. Plant Ecology, 2008, 196, 61-83
[89] Sümegi, P., Krolopp, E., Palaeoecological reconstruction of the Ságvár-Lascaux interstadial. In: Mester, Zs., Ringer, Á. eds, A la recherche de l'Homme Préhistorique, 2000, 103-112, ERAUL 95, Ličge.
[90] Sümegi, P.-Krolopp, E. Quaternary Malacological Analyses for Modeling of the Upper Weichselian Palaeoenvironmental Changes in the Carpathian Basin. Geolines, 2000, 11, 139-142
[91] Molnár, B., Krolopp, E. Latest Pleistocene geohistory of the Bácska Loess Area. Acta Minerologica et Petrographica, 1978, 23, 245-264
[92] Ložek, V., The relationship between the development of soils and faunas in the warm Quaternary phases, Anthropozoikum, 1965, 3, 7-33
[93] Rousseau, D.D., Loess biostratigraphy e new advances and approaches in mollusk studies, Earth Science Reviews, 2001, 54, 151-171

[94] Rousseau, D.D., Gerasimenko, N., Matviischina Z., Kukla G., Late Pleistocene environments of the central Ukraine, Quaternary Research, 2001, 56, 349-356
[95] Rousseau, D.D., Antoine, P., Hatté, C., Langa, A., Zöller, L., Fontugne, M., Ben Othman, D., Luck, J.M. Moine, O., Labonne, M., Bentaleb, I., Jolly, D., Abrupt millennial climatic changes from Nussloch (Germany) Upper Weichselian eolian records during the Last Glaciation, Quaternary Science Review, 2002, 21, 1577-1582
[96] Moine, O., West-European malacofauna from loess deposits of the Weichselian Upper Pleniglacial: compilation and preliminary analysis of the database, Quaternarie, 2008, 19, 11-29
[97] Moine, O., Rousseau, D.D., Antoine, P., Terrestrial molluscan records of Weichselian Lower to Middle Pleniglacial climatic changes from the Nussloch loess series (Rhine Valley, Germany): the impact of local factors, Boreas, 2005, 34, 363-380.
[98] Antoine, P., Rousseau, D.-D., Fuchs, M., Hatté, C., Gauthier, C., Marković, S.B., Jovanović, M., Gaudenyi, T., Moine, O., Rossignol, J., High-resolution record of the last climatic cycle in the southern Carpathian Basin (Surduk,Vojvodina, Serbia), Quaternary International, 2009, 198, 19-36
[99] Antoine, P., Rousseau, D.D., Zöller, L., Lang, A., Munaut, A.V., Hatté, C., Fontugne, M., High-resolution record of the last interglacial glacial cycle in the Nussloch loess palaeosol sequences, Upper Rhine Area,Germany. Quaternary International, 2001, 76–77, 211–229
[100] Bokhorst, M.P., Beets, C.J., Marković, S.B., Gerasimenko, N.P., Matviishina, Z.N., Frechen, M., 2009.Pedo-chemical climate proxies in Late Pleistocene Serbian-Ukranian loess sequences. Quaternary International, 2009, 198, 113-123
[101] Horsák M., Chytrý M., Pokryszko B.M., Danihelka J., Ermakov N., Hájek M., Hájková P., Kintrová K., Kočí, M., Kunešová S., Lustyk P., Otýpková Z., Pelánková B., Valachovič, M., Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. Journal of Biogeography, 2010, 37, 1450-1462
[102] Szelepcsényi, Z., Breuer, H., Ács, F., Kozma, I., Biofizikai klímaklasszifikációk (2. rész: magyarországi alkalmazások). Légkör, 2009, 54, 18–23 (in Hungarian)
[103] Szelepcsényi, Z.-Breuer, H.-Sümegi, P. The climate of Carpathian Region in the 20th century based on the original and modified Holdridge life zone system. Central European Journal of Geosciences, 2014, 6, 293-307.
[104] Stevens, G.C., Fox, J.F., The causes of treeline. Annual Review of Ecology and Systematics, 1991, 22, 177-191
[105] Arno, S.F., Hammerly, R.P., Timberline. Mountain and Arctic Forest Frontiers, The Mountaineers, Seattle, 1984
[106] Krolopp, E., Distribution of some Pleistocene mollusc species in Hungary, In: Pécsi, M.-Starkel, L. eds. Paleogeography of Carpathian Regions, Geographical Research Institute Hungarian Academy of Sciences, Theory-Methodology-Practice, 1988, 47, 59–63,
[107] Sümegi P., Krolopp E., Hertelendi E., The reconstrruction of the palaeoenvironment of the Ságvár-Lascaux interstadial, Acta Geographica, Geologica et Meteorologica Debrecina, 1998, 34, 165-180
[108] Deli, T., Sümegi, P., Late Pleistocene forest refugia in the Carpathian Basin and glacial relict elements in the gastropod fauna of the analyzed region. In: Sümegi, P.-Gulyás, S. eds. The geohistory of Bátorliget Marshland. Archaeolingua Press, 207-212, Budapest, 2004
[109] Birks, H.H., The Late-Quaternary history of arctic and alpine plants, Plant Ecology and Diversity, 2008, 1, 135-146
[110] Gaudényi, T., Jovanovic, M., Sümegi, P., Markovic, S.B., Late Pleistocene palaeo-environmental history of the Irig loess section (Vojvodina, Yugoslavia). Paleograssland Research, 2002: A conference on the reconstruction and modeling of grass-dominated biomes, St-Cloud, Minnesota, 12, USA, 2002
[111] Kharuk, V.I., Dvinskaya, M.L., Im, S.T., Ranson, K.J., Tree Vegetation of the Forest-Tundra Ecotone in the Western Sayan Mountains and Climatic Trends. Russian Journal of Ecology, 2008, 39, 8-13
[112] Kuneš, P., Pelánková, B., Chytrý, M., Jankovská, V., Pokorný, P., Petr, L., Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. Journal of Biogeography, 2008, 35, 2223-2236
[113] Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gunderstrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjörnsdóttir, A.E., Jouzel, J., Bond, G., Evidence for general instability of past climate from a 250-kyr ice-core record. Nature, 1993, 364, 218-220