Discussion and conclusions

It is possible to use mollusc's thanatocoenoses as indicator for Late Glacial/Holocene boundary. In the lower beds down from this boundary is developed pure malacofauna consisting of species with wide ecologic valence, that are able to sustain cold climatic conditions. Holocene period is typical in appearance more exigent species demanding for more moist and warmer climate. Late Glacial/Holocene boundary is situated in the profile between layers 6 and 5 and its main feature is presence of fine debris and large blocks indicating accession of damper stage. The pollen analyse has yielded results consistent with mollusc analyse.

Studied section expresses development of the southern part of the Moravian Karst since the Last Glacial stage until the Young Holocene. When obtained results are compared with the ones detected in profiles at northern part of the Moravian Karst (Ložek and Vašátko, 1991), it is evident, that the karst landscape developed during the Late Glacial and Postglacial stages was similar in both parts of the karst area.

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Quaternary-Malacological Analyses for Modelling of the Upper Weichselian Palaeoenvironmental Changes in the Carpathian Basin

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ABSTRACT: Most species of the Quaternary mollusc fauna exist nowadays and the ecological demands of living species are known and their extrapolation for the Quaternary is worked out. The species composition of land snail assemblages is largely depended on microclimate and local habitat, especially vegetation cover. The Quaternary malacological analysis of loess area in the Carpathian Basin is promising, because species of various palaeoecological indicators appeared and migrated quickly from different palaeobiogeographical parts of Europe, firstly from the lower Danube region. We collected fine-stratigraphical samples from 20 Late Pleistocene loess sequences for sedimentological, quartermalacological analysis and radiocarbon dating. Chronology was obtained from 60 radiocarbon age determinations. According to these radiocarbon-dated palaeoecological records we reconstructed the palaeoclimatological, palaeoecological, palaeobiogeographical changes during the Late Weichselian. The Mollusc fauna changes indicate nine short-time (1000–3000 years), cyclically palaeoclimatological changes which repeatedly transformed the palaeoecological condition and vegetation in the Carpathian Basin between 32–12 ka.

KEY WORDS: mollusc analysis, loess sequences, Carpathian Basin, Late Weichselian.

Introduction

Most species of the Quaternary molluscan fauna exist nowadays, the ecological demands of living species are known and their extrapolation for the Quaternary is worked out. Quaternary malacological studies therefore provide the most detailed data for palaeoenvironmental and palaeoclimatological conditions of the Quaternary periods, especially during the intervals of loess deposition because molluscan shells are well preserved in loess accumulations, characterized by high concentrations of calcium carbonate. Species compositions of terrestrial snail assemblages largely depend on microclimate and local habitat, especially the vegetation cover. Quaternary malacological analysis of the loess area in the Carpathian Basin is promising, because species of various palaeoecological indicators appeared and migrated quickly from different palaeobiogeographical parts of Europe, particularly from the lower Danube region. The Late Pleistocene environmental history of the Carpathian Basin can be regarded as one of the missing links in our understanding of the last glacial development of Europe. In terms of its location and geology the Carpathian Basin provides an important area of low relief among main mountain ranges of Central Europe (Carpathians, Alps, Dinaric Alps).

We collected fine-stratigraphical samples from 20 Late Pleistocene loess sequences for sedimentological and Quaternary-malacological analyses and for radiocarbon dating. Chronology was obtained from 60 radiocarbon age determinations. Based on this radiocarbon-dated palaeoecological record, it was possible to reconstruct the palaeoclimatological, palaeoecological and palaeobiogeographical changes during the Upper Weichselian.

Upper Weichselian molluscan fauna changes in space and time

As suggested by Quaternary-malacological data and radiocarbon dating of 21 Late Weichselian loess profiles, the climate (temperature, rainfall, humidity) and vegetation cover oscillated cyclically (Table 1) in the Carpathian Basin (Krolopp and

Sümegi, 1995; Sümegi, 1995). The dominance of different palaeoecological indicator groups changed on a very wide scale (Table 1). The molluscan fauna indicates primarily the conditions of microenvironments (Ložek, 1964; Krolopp and Sümegi, 1995) but the basic trends of the temperature, vegetation and humidity can be drawn in the Carpathian Basin during the last loess formation phase.

Molluscs/Age	32–25 ka BP	25–23 ka BP	23–20 ka BP	20–18 ka BP	18–16 ka BP	16–14 ka BP
Cryophilous	0–10%	40–80%	10–30%	30–50%	5–20%	10–50%
Cold-resistant	5–30%	20–60%	20–50%	30–40%	10–40%	20–40%
Mesophilous	5–70%	10–40%	30–50%	10–30%	30–60%	10–40%
Thermophilous	20–95%	0–2%	5–10%	0–1%	2–10%	1–5%
Hygrophilous	0–30%	0–10%	10–30%	10–30%	10–50%	10–30%
Mesophilous	5–50%	20–60%	20–50%	10–30%	40–50%	10–30%
Xerophilous	20–95%	40–80%	10–50%	40–80%	10–50%	40–80%
Woodland	1–30%	0–1%	5–30%	0–1%	5–60%	1–5%
Ecoton	4–60%	2–40%	10–60%	5–50%	20–60%	10–50%
Open land	30–95%	60–98%	10–85%	50–94%	10–75%	50–80%

Tab. 1. Dominance of different palaeoecological molluscan groups in the Late Pleistocene time intervals from 21 radiocarbon-dated Hungarian loess profiles.

The interval of 32–25 ka BP yielded abundant specimens of *Granaria frumentum, Pupilla triplicata, Vallonia enninsis, Chondrula tridens* with *Clausilia dubia, Vitrea crystallina.* This fauna indicates a climate similar to the present one. Based on malaco-thermometer method (Sümegi, 1996; Hertelendi et al., 1992) the July paleo-temperature reached 17–20 °C in this phase.

The Quaternary-malacological data suggest that higher temperatures dominated the southern part of the Carpathian Basin where some real thermophilous, recent South-Southeastern European but ancient Balcan molluscan elements (e.g. *Granaria frumentum, Vallonia enniensis*) occurred. The dominance of palaeoecological groups indicates that a light-rich, more open and drier vegetation type developed in the southern part of the Carpathian Basin. These data suggest that a palaeoenvironmental change-line developed in the central part of the Carpathian Basin. South of this line, similar Submediterranean climate and faunal effect as today can be seen. North of this line, especially in piedmont areas, the dominance of woodland and hygrophilous species was higher. These data suggest that the closer vegetation might have developed in the northern part and the piedmont areas of the Carpathian Basin during this interval. Such climate resulted in soils formation: this way, a typical paleosol layer, the Mende Upper Soil Complex (Pécsi, 1993), was formed. This soil is malacologically placed to the Granaria frumentum-Vallonia enniensis and Pupilla triplicata zonules (Krolopp and Sümegi, 1995).

A layer containing abundant cryophilous species (especially the North Asian, xeromontane *Vallonia tenuilabris*) covers the above described horizon. The accompanying fauna does not contain any species living in a milder climate, but only mesophilous forms tolerating cold climate *(Columella edentula, Succinea oblonga, Pupilla muscorum*). The dominance of *Vallonia tenuilabris* gradually decreased from the northeastern part of the Carpathian Basin to its southern part. This change, reflecting the effect of the extreme continental climate, was stronger in the northeastern part of the Carpathian Basin. This points to a significant cooling and to a dominant role of cold continental steppe in the Carpathian Basin at 25–23 ka BP. The loess layer was thus deposited during one of the cold peaks of the Würm glacial. Although the July paleo-temperature decreased to 12–15 °C, some forested spots survived in this cold and dry phase in protected, milder and wet microclimatic piedmont areas (Sümegi and Hertelendi, 1998).

Layers of the Hungarian loess profiles, deposited at 23–20 ka BP, indicate a climatic variation when compared to the previously described cryophilous species retreated and mesophilous, highly tolerant, more or less hygrophilous elements (*Vallonia costata, Pupilla muscorum*) became dominant and some thermophilous molluscan species occurred and spread again. The climate might have been relatively mild and humid if compared to the previous one. The July mean paleo-temperature increased to 15–19 °C and the shade-loving, woodland elements began to spread in the Carpathian Basin. These data suggest that a mild and wet phase developed during the microinterstadial and interrupted the loess formation process. This ecostratigraphical interval is well correlable with the lower humic level in the Dunaújváros-Tápósüly Loess Complex (Pécsi, 1993; Pécsi et al., 1979), indicating climatic conditions during this short-lasting soil event. This reforested palaeoecological interval is placed to the Vallonia costata zonule (Krolopp and Sümegi, 1995).

This milder period was followed by renewed significant cooling at 20–18 ka BP, when cryophilous species became dominant again, and climate-preferring forms disappeared. The *Collumella columella*, typically found in tundra or tundra-like environments (Rousseau, 1991) was one of the dominant molluscan elements in this phase. This indicates significant cooling, a new cold peak in the Late Würm and development of cold loess steppe environment in the Carpathian Basin at 18–16 ka BP. The July paleo-temperatue decreased to 12–15 °C. The composition of malacofauna in this interval indicates a stadial level, named Columella columella zonule (Krolopp and Sümegi, 1995).

The woodland species lost their dominance but survived through this unfavourable environmental change because, as a result of mosaic environment, some mild and humid microclimatic locations developed in the piedmont zone where the microenvironment was favourable for shade-loving elements (Sümegi and Hertelendi, 1998).

The above mentioned loess layer is covered by another one, with extremely characteristic fauna. The mesophilous, Holarctic species *Punctum pygmaeum*, which prefers dense, especially ecoton vegetation, marks a peak in dominance (5–70%, Krolopp and Sümegi, 1991). While the accompanying woodland fauna forms appear in significant proportion, as *Vestia turgida*, which has today a Carpathian area (Krolopp and Sümegi, 1990), and the Boreo-alpine *Discus ruderatus* and Central European *Clausilia dubia, Semilimax kotulai, Vitrea crystallina* in the northern part and on the river size zone of the Carpathian Basin. At the same time, shade-loving Central European *Cochlodina laminata, Discus perspectivus*, Holarctic *Vitrina pellucida*, Western European *Semilimax semilimax* spread in the southern part of the Carpathian Basin (Sümegi et al., 1998). This change in faunal composition indicates a relatively mild climate with a significant amount of precipitation in the Carpathian Basin. According to the malacothermometer, the July mean paleo-temperature increased to 15–17 °C. This change resulted in the spread of forests and formation of soils. A number of Gravetti-type archaeological sites are associated with this level (Dobosi et al., 1983). This ecostratigraphic interval may be identified with the upper humic horizon of the Dunaújváros–Tápiósüly Loess Complex in Hungary (Pécsi, 1993), which is

placed to the Punctum pygmaeum - Vestia turgida zonule on the basis of malacological data.

The Quaternary-malacological data suggest that higher temperature developed in the southern part of the Carpathian Basin where some Central European molluscan elements (e.g. *Cochlodina laminata, Discus perspectivus* - Hum, 1997) occurred (Fig. 3). While real Carpathian endemic elements (e.g. *Vestia turgida*) with boreal molluscs (e.g. *Discus ruderatus, Semilimax kotulai*) spread in the northern and eastern part of the Carpathian Basin. The difference in the composition of malacofauna indicates that two forest types developed in the Carpathian Basin. These data confirm that a palaeoenvironmental changeline developed in the central part of the Carpathian Basin. South of this line, Submediterranean climate and fauna effect can be seen; relict spots of Central European forest elements developed and existed here. North of this line, especially in piedmont areas and the river size zone, Subcarpathian. climate and relict spots of Carpathian woodland molluscan species developed and existed in the Carpathian basin (Sümegi et al., 1998). These Quaternary-malacological data suggest that a mosaic environment developed with important forest refugia and relict areas in the Carpathian Basin during the Late Würm period (Sümegi and Hertelendi, 1998; Sümegi et al. 1998; Willis et al., 1999).

Above, a humic loess level was formed during the mentioned forested interval, and another loess layer was deposited with cryoxerophilous fauna characteristic for a cold and dry climatic phase. This loess layer contains the last fauna with significant dominance of cryoxerophilous species (*Pupilla sterri, Vallonia tenuilabris*). This faunal level indicates the last stadial phase of the Weichselian, which developed at 14–16 ka BP.

Conclusion

The molluscan fauna changes indicate nine short-term (1000–3000 years), cyclical palaeoclimatological changes which repeatedly transformed the palaeoecological conditions and vegetation in the Carpathian Basin between 32 and 12 ka BP. On the other hand, the Quaternary molluscs suggest that the Upper Weichselian environment was mosaic-like and inhomogeneous in the analysed region and some palaeoecological barriers developed parallel at the micro-, meso-, and macro-level. The various ecologically tolerant molluscan species could spread from these different ecological spots or parts of the Carpathian Basin during the climatic changes.

The distribution and dominance of different shade-loving species indicates that wet and cool (*Carpathian* type) forest spots with *Precarpathian* fluctuation area developed in the northern and northeastern parts of the Carpathian Basin while wet and mild (*Illyrian* type) forest refugial areas with *Preillyrian* fluctuation areas formed in the southern part. Probably, the Late Pleistocene distribution of xerophilous *Granaria frumentum* reflects the ancient Submediterranean climatic effect while the spatial dominance of cryoxerophilous *Vallonia tenuilbaris* indicates the past continental climate influence.

The malacofaunas suggest that the Carpathian Basin was a large zone of fauna migration during the Upper Weichselian, where animals or plants favouring different ecological habitats could occur and spread from these relict areas or quickly back to the relict areas during intervals of climatic and environmental change.

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