

**REFUTING IDEAS BASED ON SMALL BATCH OF DATA:  
MALACOTHERMOMETRY AID IN THE RECONSTRUCTION OF  
MEAN JULY PALEO-TEMPERATURES IN THE CARPATHIAN BASIN  
FOR THE LAST GLACIAL OF THE PLEISTOCENE\***

**TÖBB TERMÉSZETTUDOMÁNYI ADATOT ÉS KEVESEBB MÍTOSZT –  
MALAKOHŐMÉRŐ MÓDSZERREL REKONSTRUÁLT EGYKORI JÚLIUSI  
HŐMÉRSÉKLETI ADATOK A JÉGKOR UTOLSÓ LÖSZKÉPZŐDÉSI  
PERIÓDUSÁBAN KIFEJLŐDÖTT VALÓDI SZÁRAZFÖLDI KÖRNYEZETRE  
VONATKOZÓAN A KÁRPÁT-MEDENCÉBEN**

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**Abstract**

*There are several ways in which terrestrial molluscs can be used to capture or model the former paleo-temperatures. The most frequently used approaches are based on the utilization of the dominance values of the cold-loving and thermophilous species for the separation of relatively milder and colder periods. In other approaches, the abundance of the cold-loving forms is used to capture the short-term stadials. These previously mentioned approaches rely on the presumption that the fluctuations observable in the specimen number or percentages of cold-loving or thermophilous forms is related to the fluctuations of the paleo-temperature. On the other hand, the terrestrial mollusc faunas are also well-suited for capturing climate changes for the past 100 000 years utilizing their modern distribution patterns, similarly to insects, vertebrates and paleobotanical data. In this paper we present an updated version of the paleo-climatological, paleo-ecological model prepared by Sümegei (1989), and referred to as the malaco-thermometer method. The model uses the recent distribution, composition as well as dominance values of the individual species for the reconstruction of the paleo-temperatures. The original method has been successfully applied to numerous radiocarbon-dated localities within the Carpathian Basin. In some works, hypothetical paleo-temperature curves based on the original model has been presented. However, there is one important deviation from the previously mentioned methods, namely that the activation temperatures for the terrestrial gastropods were captured not as the recorded mean July paleo-temperatures of the growth season in the center of distribution, but rather those recorded along the rims. Applications of the updated method and results gained via its utilization are presented.*

**Kivonat**

*A szárazföldi Mollusca faunát többféleképpen használhatjuk fel az egykori hőmérsékleti viszonyok modellezésére. Legelterjedtebben a hidegkedvelő és enyhébb éghajlatot igénylő fajok dominanciáját használják fel a relatíve hidegebb és enyhébb szakaszok elkülönítésére. Ismeretesek olyan módszerek is ahol a hidegkedvelő malakofauna abundanciáját használták fel rövidebb ideig tartó stadiális szakaszok rekonstrukciójára. Mindegyik módszer azzal számol, hogy az enyhébb éghajlatot kedvelő, vagy a hidegkedvelő faunaelemek egyedszámának, vagy százalékos arányának változása összefüggésben van az egykori hőmérséklet változásaival. Ugyanakkor a recens elterjedései alapján a bogármaradványokhoz, a gerinces adatokhoz és a paleobotanikai adatokhoz hasonlóan a szárazföldi csiga fajok is jól felhasználhatók az utolsó százezer év éghajlati változásainak rekonstrukciójában. Az egyes szárazföldi csiga fajok recens elterjedése, a fauna összetétele, dominanciaviszonyai alapján készített, nemzetközi szinten is újnak számító paleoklimatológiai rekonstrukciós modellt, az ún. "malakohőmérő"-t Sümegei (1989) készítette. Ezzel a módszerével korábban már több, radiokarbon adatokkal datált kárpát-medencei lelőhely őshőmérsékleti körülményeit rekonstruáltuk, sőt némely tanulmány már hipotetikus őshőmérsékleti görbéket is felrajzolt ezen módszer alapján. Ugyanakkor a különböző, az előbb felsorolt bioindikációs csoportokhoz képest jelentős eltérés, hogy a malako-hőmérő esetében az egyes Mollusca fajok*

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*hőmérsékleti aktivitási tartományát nem az elterjedés centrumában mért júliusi középhőmérséklettel jellemeztük, hanem az elterjedés periferiáin mérhető tenyészidőszak hőmérsékletekkel próbáltuk lehatárolni. A jelen tanulmány a módszer egy továbbfejlesztett változatának alkalmazását mutatja be.*

KEYWORDS: LATE QUATERNARY, LANDSNAIL, PALEOCLIMATOLOGY, MALACO-THERMOMETER, UPPER PALEOLITHIC

KULCSSZAVAK: NEGYEDIDŐSZAK VÉGE, SZÁRAZFÖLDI CSIGÁK, PALEOKLIMATOLÓGIA, MALAKOHŐMÉRŐ, FELSZŐ PALEOLITIKUM

### **Introduction**

The major aim of the present paper is to give an overview of the different paleoclimatic conditions and their alterations within the area of the Carpathian Basin during the Last Glacial (Alpean stratigraphy - Würmian Glacial: Spötl et al. 2019; Marine Isotope Stage or marine oxygen-isotope stages, or oxygen isotope stages (OIS): MIS4, MIS3, MIS2 levels: Antoine et al. 2009; Jullien et al. 2009; Johnsen et al. 2001; Rasmussen et al. 2006, 2008, 2014) primarily for the terminal part of it, via the paleo-climatological evaluation of the mollusc faunas retrieved from the loess-covered areas of NE Hungary, and their comparison with similar faunas from other Hungarian localities, primarily of Southern Hungary. I also intend to discuss the effects these factors posed on the Upper Paleolithic human communities. Furthermore, I would like to present a new stratigraphic system for the above mentioned period, which is based on the newly gained results of my work, and though congruent with the past findings, it provides a better resolution and in certain aspects carries new attributes as well. In order to accomplish the task of successfully capturing the most complex, wide-ranging view of the former paleoecology, several new methods, or at least new in the field of Quaternary mollusc studies (Krolopp 1961, 1965a, b, c, 1966, 1967, 1973, 1977, 1983, 2003; Krolopp & Sümegi 1995; Ložek 1964, 1990, 2001; Alexandrowicz 1988; Rousseau, 1990, 1991, 2001; Rousseau & Kukla 1994; Rousseau & Wu 1997; Rousseau et al. 1992, 1994, 1998, 2000; Magnin 1993; Alexandrowicz 2014; Wu et al. 2018) have been introduced into my work, ranging from biometric analysis to complex statistical evaluations. The well-known malaco-thermometric method, postulated in my university doctoral thesis in 1989 (Sümegi 1989), have been upgraded with the help of recent findings (Sümegi 1996, 2005, 2007). This upgraded version and a comparison with other paleo-climatological methods and approaches is also presented in this paper.

The model uses the recent distribution, composition as well as dominance values of the individual species for the reconstruction of the paleo-temperatures. This method has been successfully applied to numerous radiocarbon-dated localities within the Carpathian Basin (Sümegi et al. 1991; Szőör et al. 1991a, b; Hertelendi et al. 1992; Sümegi & Krolopp 2002). Krolopp (2003) went

even further to set up hypothetical paleo-temperature curves based on this model. However, the method has not been described scientifically so far, except for a PhD thesis (Sümegi 1989).

There are several ways in which the molluscs can be used to capture or model the former paleo-temperatures. The most frequently used approaches are based on the utilization of the dominance values of the cold-loving and thermophilous species for the separation of relatively milder and colder periods (Krolopp 1967, 1973, 1983; Magnin 1993). In other approaches, the abundance of the cold-loving forms is used to capture the short-term stadials (Sümegi et al. 1991; Nyilas & Sümegi 1991). These previously mentioned approaches rely on the presumption that the fluctuations observable in the specimen number or percentages of cold-loving or thermophilous forms is related to the fluctuations of the paleo-temperature (Magnin 1993). But is this truly the case?

Evans (1972), Rousseau et al. (1991a, b) and Davies (2008) noted that alterations in the dominant values are not only dependant exclusively on, thus mark temperature changes but are also a factor of several other parameters like humidity, the composition of the vegetation, changes in the number of predators preying upon molluscs or those of the parasites, plus the quality of the habitat seen in substrate composition, carbonate content, pH (Arnason & Grant 1976; Müller et al. 2005; Horsák et al. 2007; Sulikowska-Drozd & Horsák 2007; Sulikowska-Drozd et al. 2013).

These latter two can be excluded in case of the loess layers having a neutral pH and relatively large carbonate content. Conversely, several research on the recent mollusc faunas implemented by Fröming (1954), Ant (1963), Sólymos & Nagy (1997), Sólymos & Sümegi (1999) pointed out that such parameters as humidity, air temperature, and light intensity are the most influential factors in the activity potential of molluscs (Arnason & Grant 1976; Abdel - Rehim 1987; Magnin 1993; Staikou 1999). From several ecological studies it also seems apparent (Ant 1963) that the environmental components have mosaic-like scattered distribution in areas studded with woodlands, woodland margins and bushes (Arnason & Grant 1976; Martin & Sommer 2004; Horsák et al. 2007; Sulikowska-Drozd & Horsák 2007). This pattern is also observable in the mollusc faunas adapting to these

conditions. Consequently, it is very hard to accurately capture the true ecological requirements of woodlands species in contrast to open area dwellers, due to the significant differences in the micro and mesoclimatic conditions in a woodland (Arnason & Grant 1976; Sümegei 1989, 1996, 2005, 2007; Martin & Sommer 2004; Horsák et al. 2007; Sulikowska-Drozd & Horsák 2007; Sulikowska-Drozd et al. 2013).

Taking an account of all these results, initially those taxa were chosen for the purpose of paleo-temperature reconstruction which were steppe, at the most forest-steppe dwellers, because there is only a slight chance for the presence of actual differences between the light intensities or humidities of these habitats. Plus there are no significant deviations between the micro- and regional climate here (Arnason & Grant 1976; Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 2001).

From the ecological studies of the recent faunas it seems also quite apparent (Owen & Bengtson 1972; Arnason & Grant 1976; Domokos 1995), that there are considerable deviations between the temperatures required for mollusc activation (movement, feeding etc.), and perishing (Domokos 1982). Furthermore, it is also obvious that the individual molluscs are active only in a certain part of the year, the so-called growth season and hibernate during the periods with unfavorable conditions- too arid or too cold (Owen & Bengtson 1972; Arnason & Grant 1976; Domokos 1982, 1995; Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991; Müller et al. 2005; Sulikowska-Drozd et al. 2013).

Thus, the detailed investigations of molluscs can yield information regarding the environmental conditions of the growth or active season alone (Arnason & Grant 1976; Owen & Bengtson 1972; Müller et al. 2005; Sulikowska-Drozd & Horsák 2007; Sulikowska-Drozd et al. 2013). When all these parameters are noted, we are facing a less wide temperature spectrum, in which molluscs tend to live, move, feed etc. actively (Sümegei 1989). This interval can be regarded as the activation interval of terrestrial gastropods. The tolerance of the mollusc species studied so far tended to follow a normal distribution (Domokos & Fűköh 1984, 1986; Sólymos et al. 2002; Domokos & Sólymos 2013; Domokos et al. 2014). Thus, we have every reason to believe that the activation temperature curves, embedding the ranges of unfavorable conditions as well, will be characterized by similar

shapes (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991).

The activation temperatures of the individual mollusc species is determined from the recent distribution of the forms under study and the measured temperatures of the growth season recorded at mesoclimatic stations (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991). This is, however, rather problematic in several ways (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991). First of all, it is the microclimatic parameters that primarily influence the activation of terrestrial molluscs, and mainly that of the air temperatures recorded 1-2 cm above the ground (Arnason & Grant 1976; Abdel-Rehim 1987; Nyilas & Sümegei 1987; Sümegei et al. 1991; Sólymos 1996; Sólymos & Nagy 1997; Sólymos & Sümegei 1999). Thus the temperatures recorded at the mesoclimatic stations at a height of 2 m above the ground are only distantly correlated with the actual activation temperatures of the mollusc species, following only perhaps a similar trend (Arnason & Grant 1976; Sümegei 1989, 1996, 2005, 2007). This can only be changed by recording the microclimatic parameters along with numerous other factors like humidity and light intensity during investigations on the recent faunas (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991). These measurements, presently going on and likely to continue in the fitotron (or more precisely in the malacotron: Sümegei 1989, 1996, 2005, 2007) will hopefully help us to make our model more accurate and realistic (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991).

On the other hand, the terrestrial mollusc faunas are also well-suited (Sümegei 1989, 1996, 2005, 2007) for capturing climate changes for the past 100,000 years utilizing their modern distribution patterns, similarly to insects (Coope 1975, 2002; Coope et al. 1971; Ashworth 1996, 2001), vertebrates (Hokr 1951; Kretzoi 1957, 1977; Kordos 1977, 1981, 1987) and paleobotanical data (Skoflek 1990; Heusser 1973; Iversen 1944; Járainé-Komlódi 1966, 1968, 1969, 1987; Magyari 2002; Magyari et al. 2001).

### ***The theory behind the method***

There is one important deviation from the previously mentioned methods, namely that the activation temperatures for the terrestrial gastropods were captured not as the recorded mean July temperatures of the growth season in the center of distribution, but rather those recorded along the rims (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991). What does this exactly mean?

**Table 1.:** The activation temperatures as well as the mean or optimal values of these for the mollusks used in the “malacothermometer model”**1. táblázat:** A malakohőmérő modellben szereplő csigák átlagos és optimális aktivitási hőmérsékleti értékei

The mollusc species used in the malaco-thermometer model	The assumed activation temperature ranges calculated from the modern distributions	The mean or optimal value of the activation temperatures taken to signify the former mean July paleotemperatures
<i>Succinea oblonga</i>	13-19 °C	16 °C
<i>Columella edentula</i>	10-20 °C	15 °C
<i>Columella columella</i>	5-15 °C	10 °C
<i>Vertigo genesii</i>	5-15 °C	10 °C
<i>Vertigo modesta</i>	5-15 °C	10 °C
<i>Pupilla muscorum</i>	10-22 °C	16 °C
<i>Pupilla triplicata</i>	16-24 °C	20 °C
<i>Pupilla sterri</i>	5.5-16.5 °C	11 °C
<i>Vallonia costata</i>	10-24 °C	17 °C
<i>Vallonia tenuilabris</i>	4-14 °C	9 °C
<i>Granaria frumentum</i>	17-26 °C	21.5 °C
<i>Clausilia dubia</i>	12-20 °C	16 °C
<i>Punctum pygmaeum</i>	9-22 °C	15 °C
<i>Vitrea crystallina</i>	11-21 °C	16 °C
<i>Trichia hispida</i>	10-20 °C	15 °C
<i>Cepaea vindobonensis</i>	18-26 °C	22 °C

In case of a species with a relatively extensive distribution area, say from the Mediterranean up to the highest boreal latitudes (e.g.: *Pupilla muscorum*), the optimal temperature used in our model derived from not the center of this taxon's distribution, but the mean July temperature recorded in the northern boreal peripheries were considered, while in case of the Mediterranean the more humid fall and winter temperatures were used (Sümegei 1989, 1996, 2005, 2007 Sümegei et al. 1991). In case of the Mediterranean, humidity acts as a limiting factor on terrestrial gastropods, especially during the hot and dry summer days. However, during the more humid fall and winter days, the temperature becomes the main factor influencing the activation of these molluscs, with humidity losing importance as a limiting factor of activation. This way the temperature tolerance ranges of terrestrial species characterized with an extensive distribution area and considered to be eurythermic (Meijer 1985; Kuijper 1985) can be more precisely captured (Sümegei 1989).

Initially, the activation temperatures for the hottest month (July) of the growth season were determined for 8 species (Sümegei 1989, 1996, 2005, 2007). This was later on extended to 16 species to meet the requests of fellow researchers (Sümegei 1996, 2005, 2007). Among these, there are forms with highly different distributional areas, characterized by activation temperatures in different ranges as well (**Table 1.**).

In case of cold-resistant (Chlachula 1991; Chlachula et al. 2004; Rousseau & Puisségur 1999; Rousseau et al. 1992; Moine et al. 2005) *Succinea oblonga*, the 13 °C minimal activation temperature values were observable in the distribution margins of the species at Scotland (Kerney & Cameron 1979; Kerney et al. 1983), Finland (Routio & Valta 2011) and Western Siberia (Welter-Schultes 2012). Here the temperature acts as a limiting factor during the relatively intensively humid growth season. The maximum value of 19 °C comes from the scattered southern distribution margins, like the Hungarian wetlands (Bába 1989).

The activation temperature ranges of the Northern Asian (Meng 2009; Meng & Hoffmann 2009; Horsák et al. 2010, 2015), xeromontane, cold-loving (Rousseau 1986, 1989) *Vallonia tenuilabris* were set up on the basis of personal encounters gained in the Altai Mts. as part of an expedition in 1989 (Sümegei 1996, 2005, 2007; Sümegei et al. 1991). This species appears from an altitude of 2100 – 2200 m to the height of the Alpine tundra, shrub and grasslands located at 3000 - 3500 m ASL (Meng 2009; Meng & Hoffmann 2009; Horsák et al. 2010, 2015) forming a glacial refugia (Bennett et al. 1991; Willis et al. 2000; Stewart & Lister 2001; Stewart et al. 2010; Rull 2010; Keppel et al. 2012; Horsák et al. 2015). The activation range of *V. tenuilabris* is completely different from that of *Succinea oblonga* and tends to be congruent with the periodic fluctuations observable in the abundance and dominance rates of the two species in the Hungarian loess profiles (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1991).

The highest activation temperatures were recorded for *Pupilla muscorum*, which is by no means surprising, as this species inhabits a region extending from the tundra down to the Mediterranean (Kerney et al. 1983; Welter-Schultes 2012). According to the available data for fossil and modern populations, the morphological plasticity of *Pupilla muscorum* supposed to be the result of ecophenotypical adaptations to varying environmental and climatic conditions (Rousseau & Laurin, 1984; Rousseau 1997).

*Pupilla triplicata* is known to invade areas in Central and Southern Europe (Sólymos 2008; Horsák et al. 2013; Balashov & Kryvokhyzha 2015; Georgiev & Stoycheva 2010), which are characterized by mean July temperatures below 20 °C (Carpathians, foothills of the Alps, ). However, it has only a scattered distribution restricted to the southern, drier and warmer slopes with a carbonate rich bedrock in these regions (Georgiev & Stoycheva 2010). The cold-loving *Pupilla sterri* goes up as high as 2700–2800 m ASL in the mountains (Soós 1943; Klemm 1974; Bába 1980; Myšák 2009; Duda et al. 2018).

The species *Columella columella* tends to have a similar distribution, but this form goes even higher up to the kingdom of ice and snow to a height of 2900-3000 m ASL (Klemm 1974; Kerney et al. 1983; Ložek 1990; Juříčková & Ložek 2008). Thus its presence indicates colder mean July temperature values than the ones marked by *Pupilla sterri*.

The gastropod *Columella columella* is a typical Arcto-Alpine element (Kerney et al. 1980; Ložek 1990; Juříčková & Ložek 2008), appearing during the most important cooling periods of the Pleistocene (Rousseau 1990; Rousseau et al. 1990) and has an Arctic- Subarctic distribution today

(Klemm 1974; Kerney et al. 1983; Meng et al. 2011). Though the distributions of *C. columella* and *C. edentula* partially overlap, they tend to complement each other both vertically and horizontally in the montane regions (Kerney et al. 1983; Limondin - Lozouet & Antoine 2001; Hausdorf 2006; Meng et al. 2011).

Similar changes are observable in the dominance values of the two taxa in the Hungarian Pleistocene profiles, where they tend to overlap each other but their dominances are contrasting (Krolopp 1973, 1983; Krolopp & Sümegei 1995; Sümegei 1989, 1996, 2005, 2007; Sümegei & Krolopp 1995, 2002, 2006). Similar trends are observable in case of the species *Trichia hispida*, *Succinea oblonga*, *C. edentula*, *Clausilia dubia*, *Vitrea crystallina* (Wäreborn 1970; Kappes et al. 2006; Horsák et al. 2007; Davies 2008; Szybiak et al. 2009; Sólymos et al. 2009; Pilate 2009).

The Arcto-Alpine *Vertigo genesii*, *Vertigo modesta* and *Columella columella* has similar characteristics (Frest & Dickson 1986; Hausdorf & Henning 2003; Alexandrowicz & Rudzka 2006; Hájek et al. 2011; Schenková & Horsák 2013; Krolopp 1973, 1983; Krolopp & Sümegei 1993; Sümegei 1989, 1996, 2005, 2007) (**Table 1.**). The ecological requirements of these taxa, and their temperature tolerance as well as ranges of activation temperatures are more or less the same.

The Southern-South-eastern European *Cepaea vindobonensis* and *Granaria frumentum* require different temperature conditions (Currey & Cain 1968; Jones 1973; Cameron 1992; Magnin 1993; Welter-Schultes 2012; Dvořáková & Horsák 2012) marking milder climatic periods. Their indicative temperatures seem to be well-correlated with the results of recent microclimatic research (Domokos 1982; Füköh & Domokos 1984, 1986; Magni 1993; Sólymos & Sümegei 1999). Similar trends are observable in case of the widely-distributed *Vallonia costata* and *Punctum pygmaeum* (Kerney et al. 1983; Baur 1987; Magni 1993; Welter-Schultes 2012; Hettenbergerová et al. 2013).

Conversely, the reconstructed activation temperatures of the extensive *Clausilia dubia* and *Vitrea crystallina* (Wäreborn 1970; Kappes et al. 2006; Horsák et al. 2007; Davies 2008; Szybiak et al. 2009; Sólymos et al. 2009; Pilate 2009) requiring lush vegetation cover are rather sketchy and entered into the original list of species on the request of my former supervisor Endre Krolopp in 1996 (Sümegei 1996). The error comes from the presently observable high difference between the microclimatic and mesoclimatic parameters characterizing the habitats inhabited by these forms, yielding a significant uncertainty in the model of paleo-temperature reconstruction (Wäreborn 1970; Kappes et al. 2006; Horsák et al. 2007; Davies

2008; Szybiak et al. 2009; Sólymos et al. 2009; Pilate 2009).

The reliable introduction of these taxa into the model would require detailed documentation of their ecological requirements among field and lab conditions. For the calculation of the mean July paleo-temperatures the mean values of the activation temperature ranges of the individual taxa (**Table 2.**) have been utilized along with their abundance values (Sümegei 1989, 1996). A similar formula was used in paleobotanical studies for such purposes (Skoflek 1977, 1990).

**Table 2.:** Classification of July paleotemperature according to malacothermometer method (Sümegei 1989, 1996)

**2. táblázat:** Az egykori júliusi középhőmérséklet meghatározása malakohőmérő módszerével (Sümegei 1989, 1996)

$$T = \frac{\sum_{i=1}^N A_i T_i}{\sum_{i=1}^N A_i}$$

$A_i$  = The abundance of a given  $i$  species in the sample

$T_i$  = The optimum temperature of a given  $i$  species in the sample

$N$  = Number of species used for the estimation

$T$  = Estimated July paleotemperature (°C)

Modelling the relationship of the Upper Paleolithic communities and the environment of the Carpathian Basin during the Upper Würmian (terminal phase of MIS3 and MIS2)

The first radiocarbon-dated chronological unit represents a period between 35,000–25,000 cal BP years. This unit was correlated by the Denekamp interstadial (West 1984; Lisá et al. 2018) located at the boundary of the Middle and Upper Pleniglacial in Western Europe (Zagwijn 1961, 1974), and between the SPECMAP 2 and 3 isotopic stages (Shakleton 1977; Shakleton & Opdyke 1973; Shakleton et al. 1983, 1984; Imbrie et al. 1984; Rudimann et al. 1986) and the terminal phase of MIS3 and MIS2 stage (Svensson et al. 2006; Rasmussen et al. 2006, 2008, 2014). This paleosol horizon dated into this period can be correlated with the Stillfried B paleosol (Fink 1954; Valentine & Dalrymple 1976; Velichko 1990; Szöör et al. 1991; Zöller et al. 1994; Terhorst et al. 2011, 2014; Peticzka et al. 2010). According to the available malacological data, this period can be divided into two parts. The older phase between 35,000 – 30,000 cal BP years was characterized by milder and more humid conditions (Krolopp & Sümegei 1992, 1995; Sümegei 2011).

For this time period we could infer mean July paleo-temperatures ranging around 19-20 °C in the southern parts of the Carpathian Basin, 18 °C in the central parts of the Great Hungarian Plains, and 17 °C in the Northern Mid-Mountains and the southern foothills of the Northern Carpathians, respectively (Sümegei & Krolopp 1995, 2002; Sümegei et al. 2000, 2002). This NE-SW trend observable in the distribution of the temperature values is congruent with the differences observable between the individual parts of the country even today; i.e. a 2-3 °C difference between the northern and southern parts (Réthly 1937, 1948; Bacsó et al. 1953; Bacsó 1959; Péczely 1998; Szelepcsényi et al. 2014, 2016). Furthermore, we had only minimal deviations from the modern temperature values here being in the range of 2-3 °C implying the presence of very mild conditions between 35,000–30,000 cal BP years.

According to our paleobotanical data, a mixed-leaved taiga dominated by spruce must have emerged in the area of the Northern Mid-Mountains and its foothills during this time. It might be important to know in reconstruction of the surrounding environment of the Upper Paleolithic hunters, that several *Picea* charcoal remains studied by Edina Rudner (Willis et al. 2000; Rudner & Sümegei 2001) have been recovered from the Upper Paleolithic sites and loess section themselves (Bodrogkeresztúr, Henye-tető Upper Palaeolithic horizon in fossil soil layer: 26 318 ± 365 BP = 29661-31090 cal BP years (2σ range – calibration: Reimer et al. 2014); Megyaszó, Szeles-tető, loess section, fossil soil horizon: 27, 070 ± 680 BP = 29 700-32 607 (2σ range); Püspökhatvan – Diós, Öregszőlő, Upper Palaeolithic horizon in fossil soil layer: 27, 700 ± 300 BP = 31 046-32 361 (2σ range); Hont-Parassa III/Orgonás, loess section, fossil soil horizon: 27, 350 ± 610 BP = 30 276-32 902 (2σ range).

All these data from archaeological sites seem to underlie that the earliest Gravettian hunting groups appearing during an interstadial at the end of the Middle Würmian (Gáboriné-Csánk 1980; T. Dobosi 2000) or at the terminal phase of MIS3, Dansgaard-Oeschger (D-O) or Greenland (GI) interstadial 05 and 04 horizons (Bond et al. 1992, 1993, 1999) which evolved together (Sümegei et al. 2019) some places in the Carpathian Basin. The Carpathian Basin must have populated spruce open woodlands (open parkland type) containing thermophilous arboreal elements (*Carpinus* – hornbeam, *Salix* – willow, *Alnus* – alder, *Betula* – birch, *Pinus sylvestris* – Norway pine and possibly *Corylus* – hazelnut, *Tilia* – elm, *Quercus* – oak) as well (Sümegei et al. 1999, 2013a, 2016). Sporadic changes in the dominance of shade-loving mollusc species, as well as the scattered charcoal remains forming major spots refer to the presence of a

variegated mixed taiga woodland containing steppe elements (forest steppe or open parkland: Sümegi et al. 2012, 2016). The differences in exposure between the slopes might have contributed to the emergence of minor spots (local level: Sümegi et al. 2012), characterized by warmer conditions harboring thermo-mesophilous arboreal elements within the spruce open parkland (local refugia: Willis et al. 1995; micro-environmental oases: Willis et al. 2000). A modern analogy of this spruce open woodland can be found in the Altai Mts. where a mixed spruce woodland of loose stands can be found at lower elevations containing such elements as Norway pine, alder, willow and oak (*Quercus mongoliensis*) (Sümegi 1996, 2005, 2007; Sümegi et al. 1999, 2013a). According to the data of Stieber (1967) and Rudner & Sümegi (2001) this spruce open woodland (open parkland type) can be traced within the Carpathian Basin as far as the Transdanubian Mid-mountains, turning gradually into forest steppes dominated by Norway pine and birch in the southern parts of Transdanubia and the Danube-Tisza Interfluve.

While the area of the Hajdúság in the Tiszántúl harbored thermo-mesophilous steppe elements at the same time (Sümegi 1989; Szőőr et al. 1991a, b; Hertelendi et al. 1992). Finally, the areas of the Hortobágy, Nagykunság, and Körös – Maros Interfluve were characterized by floodplain areas studded by alkaline steppes (Sümegi et al. 2013b). These open vegetation areas were studded by gallery forests running along the watercourses, and were characterized by hydromorphic, black earth and alkaline soils, parallel with the podzolic soils of the Northern Mid-Mountains (Sümegi, 1996, 2005). The area of the Danube-Tisza Interfluve was characterized by wind-blown sand deposition and movement as well as the development of soils under a highly special forest steppe vegetation composed of dominantly Norway pines and birches. The southern parts of Transdanubia were covered by evenly distributed woodlands, and clear signs referring for the closure of the arboreal vegetation could have been found in the former fauna and flora there. To my mind (Sümegi 1995, 1996, 2005, 2007), a major environmental boundary must have emerged in the center of the Carpathian Basin dividing it into two parts characterized by different evolutionary histories of the vegetation. These regional differences follow the same trends as observable today, only the composition of the vegetation was different from the modern one. These differences between this former vegetation characterized by a dominance of pines at 35,000 – 30000 BP years, and the modern vegetation characterized by a dominance of deciduous trees must be attributed to the shorter growth periods and the cooler winter temperatures during the interstadial. Nevertheless, it's rather surprising that the Gravettian sites of this period are restricted to

the spruce open parklands of the Northern Mid-Mountains (Sümegi, 2014; Sümegi et al. 2016).

Several researchers, primarily geographers (Tarnocai & Schweitzer 1998; Fábrián et al. 1998, 2000; Kovács et al. 2007; Obrecht et al. 2019) have questioned the reliability of our July paleo-temperature reconstructions considering them too high. They have also debated our data referring to the presence of thermo-mesophilous arboreal elements in the vegetation, especially that of *Carpinus* (hornbeam) along with the presence of two biogeographical units, despite the fact that several archeologists have noted the presence of two climatic-economic units within this relatively closed system of the Carpathian Basin during the Upper Paleolithic, based on archeological results (Gáboriné Csánk 1980 p. 217).

In order to put an end on these debates, we have attempted to compare our vegetation, malacological, vertebrata and paleo-environmental data (Jánossy 1979, 1986; Járainé-Komlódi 2000; Willis et al. 2000; Sümegi 2005) with those of the neighboring areas to disprove the hypothesis according to which the Carpathian Basin was nothing else but an alternation of cold and warm desert conditions during the stadials and interstadials of the Würmian (Tarnocai & Schweitzer 1998; Fábrián et al. 1998, 2000; Kovács et al. 2007; Obrecht et al. 2019).

According to malacological data from thickest loess profiles in the Carpathian Basin, a cold phase developed in the Carpathian Basin between 30,000 and 29,000 cal BP years. This stadial phase had relatively low July mean temperatures around  $15 \pm 1$  °C (Sümegi et al. 2019). Based on the distribution data of molluscs (Sümegi et al. 2019) low growing season and low winter temperatures (between -6°C and -17 °C) as well as low annual temperatures prevailed (between +5 °C to +7 °C) in this phase.

After this rapid cold stage a new temperate (interstadial) phase formed between 29,000 and 25,000 / 24,500 cal BP years. It was characterized by 17-18 °C July paleo-temperatures and drier conditions (Sümegi 1989, 1996, 2005, 2007, 2014). This period is characterized by the reappearance of the SSE European xero-thermophilous temperate grassland dweller *Granaria frumentum* along with other steppe dwelling elements. The composition of land snail faunas and indicator elements refers to the emergence of dry summer seasons with high continentality in the Carpathian Basin.

The next paleo-climatological - malacological horizon started from 25,000/24,500 cal BP years. *Granaria frumentum* disappeared, the dominance of the thermophilous species declined and some cold-resistant and cryophilous species, such as tundra-like environment favorable Boreo-Alpine

*Columella columella* and N-Asian xeromontan *Vallonia tenuilabris* occurred in this horizon. The dominance of the mesophilous species increased. A cold climatic phase developed and typical loess fauna formed in the analyzed region.

But the fauna composition of this zone was not homogenous. On the other hand, according to the findings of the sedimentological (Pécsi 1975, 1977, 1993), malacological (Sümegei 1989, 1996, 2005; Sümegei & Krolopp 1995, 2002), anthracological (Rudner & Sümegei 2001), and palynological investigations of the Upper Würmian (MIS2) profiles in the Carpathian Basin (Sümegei et al. 1999, 2013; Magyari 2002; Magyari et al. 1999) the loess formation was not continuous in this area during the Upper Würmian or the Upper Pleniglacial as in Western Europe (West 1984). But this strong cooling phase was interrupted by several alternating short warming and cooling, lasting for some hundred or some thousand years (micro-interstadial) which slowed down loess accumulation in the area.

The first micro-interstadial was recorded at 23,000 cal BP years, and was characterized by an increase in mesophilous land snails. The southern areas of the Carpathian Basin witnessed an expansion of the thermophilous elements of the mollusk fauna during this time (*Granaria frumentum*), while the waterbank areas were populated by euryptic, hygrophilous, shade-loving forms requiring larger vegetation cover and inhabiting the modern boreal woodlands as well (*Clausilia dubia*, *Perofratella bidenetata*, *Arianta arbustorum*, *Discus rudneratus*). Conversely, the shade-loving elements have undergone an increase in the south-western parts of the basin (*Orcula dolium*, *Vitrea crystallina*).

These paleo-environmental data imply the survival of the formerly existing mosaic-patterning in the environment (and the flora) during this time, leading to the emergence of mixed, extinct floral and faunal associations. However, a characteristic increase in the dominance of the mesophilous, forest steppe dweller *Vallonia costata* is clearly observable in the majority of the profiles for this time (*Vallonia costata* zonula: Sümegei 1989). These short dominance changes of the different ecological tolerant species suggest that some dynamic climatic changes developed in the analyzed area during the beginning phase of the MIS2. The malacothermometer data showed the July paleo-temperature changed around 17°C in this horizon.

After 23,000 cal BP all the thermophilous species disappeared, but the dominance of the cold-resistant and cryophilous species increased until 18,000 / 17,000 cal BP years. According to the malacothermometer data, July paleo-temperatures ranged between 11–14 °C in this cold phase representing the Last Glacial Maximum. A large number of

woodland-dwellers, such as *Orcula dolium*, *Discus rudneratus* turn up in the malacofauna around 21,000 cal BP years. According to the dominance values and distributions of *Punctum pygmaeum* along with other woodland dwellers and elements preferring larger vegetation cover (*Orcula dolium*, *Discus rudneratus*, *Mastus venerabilis*, *Semilimax semilimax*, *S. kotulai*, *Vitrina pellucida*, *Vestia turgida*, *Arianta arbustorum*), extensive closed woodlands and gallery forests as well as forest-steppes must have developed in the southern parts of Transdanubia and the Great Hungarian Plains, along the major water courses and in certain parts of the mid-mountains in the Carpathian Basin during this (Dunazug Mts., Tokaj Mts.).

This paleo-ecological state resembles mostly to the mosaic-like vegetation of the taiga - forest steppe border zone in Southern Siberia (Sümegei 1989, 1996, 2005, 2007; Sümegei et al. 1999, 2012, 2013a, b). According to the general distribution of the elements preferring larger vegetation cover this time, the northward expansion of woodlands must have started off from the woodland refugia of the Northern Balkans, as well as the southern parts of the Great Hungarian Plains. On the other hand, the presence of forest covered regions inferred for the areas of the mid-mountains during this paleo-ecological horizon refer to the existence of woodland refugia within the Carpathian Basin as well during the end of the Pleistocene, (one of such refugia could have been identified in the Kereszt Hill of the Tokaj Mts. region: Sümegei 2005) or Bükk Mountain (Sümegei & Náfrádi 2015), from where the woodland elements could have started their expansion to other areas during times with favorable ecological conditions.

According to the appearance of *Orcula dolium*, *Discus rudneratus* and the dominance maximum of *Punctum pygmaeum*, *Clausilia dubia*, *Vitrina pellucida*, and *Vitrea crystallina* in the fauna a relatively milder climate must have emerged in this horizon, characterized by mean July paleo-temperatures ranging about 15±1 °C.

After 21,000 cal BP years the fauna composition changed very dynamically. The dominance of the mesophilous species decline, cold-resistant and cryophilous species such as *Trichia hispida*, *Columella columella*, *Vallonia tenuilabris*, and *Pupilla sterri* dominated again in this horizon. The July paleo-temperature decreased and stabilized between 11-14 °C. Cold – humid growing seasons developed in this climatic phase and a mosaic-like vegetation harboring tundra, scrub and boreal elements emerged in the Carpathian Basin.

The molluscs tend to react rather sensitively to environmental changes appearing at a micro or local scale. Thus via observing the transformations in the mollusc fauna, we can get a better view of the



former environmental changes at a higher resolution compared to the one we get by studying the more mobile vertebrate elements of the fauna, enabling the detection of even small-scale changes (Kretzoi 1977). According to our findings, the classical so-called Dokuchaev zonation of the soils and the vegetation was not present in the area of the Carpathian Basin not even during the time of loess formation, hampering the utilization of the Northern European boreal taiga areas as modern analogies of this region. However, via the analysis of the mollusc fauna, we could have justified the presence of a climatic interface in the center of the Carpathian basin assumed by Kretzoi (1977) as well on the basis of the distribution patterns observable in the former vertebrate fauna.

Between 18,000–16,000 cal BP years, the thermophilous species re-occurred and the dominance of the cryophilous species declined. Cold-resistant and mesophilous steppe dwelling elements prevailed in this interstadial horizon. A relatively milder climate must have emerged between 18,000 and 16,000 cal BP years, characterized by mean July paleo-temperatures around  $15 \pm 1$  °C

This previously mentioned persistence was characteristic to the interface of the major climatic zones, observable in the north-south and east-west trending of the continuous transformations of the flora and the fauna equally present during both the stadials and interstadials. Since it was only the absolute values of the temperature and the humidity that underwent a change, the general trends at a macro-scale were preserved in all cases. Via the observable changes in the paleo-temperature, colder and milder climatic phases corresponding to cycles of 1500/1000-5000 years could have been identified.

These climatic fluctuations had considerable effects on the Upper Paleolithic communities (Gábori & Gábori 1957; T. Dobosi & Vörös 1986, 1987). These smaller scale changes of some ten kys fundamentally determined the composition and migration of the animal herds upon which these humans preyed. Nevertheless, it might be also interesting to know how the mosaic-pattern influenced these Upper Paleolithic groups. In order to address this problem, the distribution of the individual environmental components was compared with that of the Upper Paleolithic sites.

The necessary data for this work derived from various archeological papers on the one hand (T. Dobosi 1967, 1975, 1989, 1992, 1994, 1996, 2000; T. Dobosi & Simán 1996; T. Dobosi & Vörös 1986, 1987; T. Dobosi et al. 1983, 1988; Gábori & Gáboriné Csánk 1957; Gábori 1954, 1955, 1968, 1969, 1980, 1981, 1984; Gáboriné Csánk 1978, 1980, 1984; Banner 1936; Vértes 1964/1965, 1965, 1966) as well as our personal paleo-environmental database created via the study of the loess profiles. A comparison of these results was plausible either with the help of radiocarbon dates, or via making direct paleo-environmental observations at the excavation sites themselves.

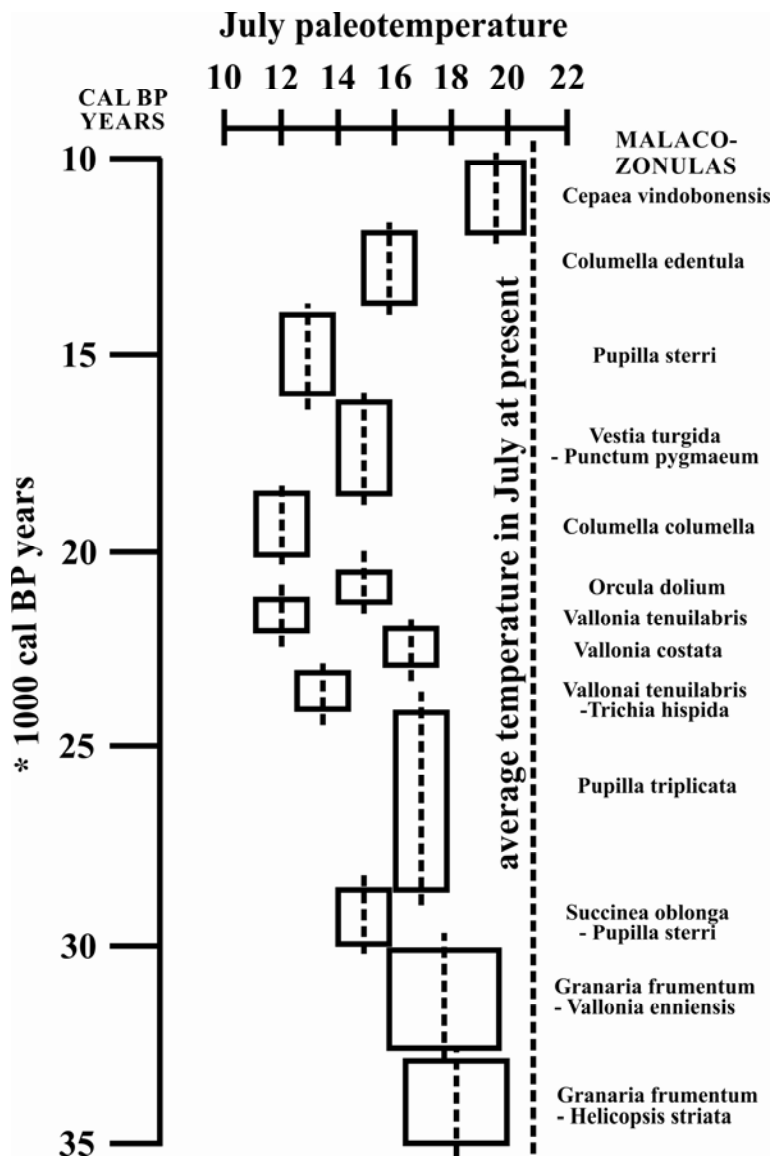
After this afforestation stage, another cold maximum must have developed in the basin corresponding to the last significant appearance of the cold-loving elements (*Columella columella*, *Pupilla sterri*, *Vallonia tenuilabris*). This stadial horizon dated to the end of the Upper Würmian and the beginning of the Late Glacial can be observed in almost every Hungarian loess profiles (Sümegei 1988). According to the results of detailed chronological and paleontological studies (Sümegei 1988) this zone termed as the *Pupilla sterri* zonula (16,000–14,000 cal BP years) must correspond to the oldest Dryas stage of the palynological studies.

After this cold peak, the cold-loving elements underwent a gradual retreat then finally completely disappeared from the Hungarian loess deposits, and there was a dominance peak of the cold-resistant, hygrophilous elements (*Succinea oblonga*, *Columella edentula*, *Vertigo parcedentata*, *Trichia hispida*) around 14,000-12,000 cal BP years (Sümegei 1989). These latter taxa appeared in mass volumes in the profiles, sometimes representing even 90% of the total fauna as well. Based on the malacofauna composition a transition climatic and environmental phase developed during the last loess forming period.

## Summary

### MIS3 stage

According to the findings of complex radiocarbon dated malacological studies implemented on 27 loess/paleosol profiles in Hungary, the period dated between 35,000 and 10,000 cal BP years were characterized by cyclic climatic oscillations (Fig. 1).



**Fig. 1.:**

Malacothermometer reconstructed July paleotemperature changes from 35,000 cal BP to 10,000 cal BP years in the Carpathian basin

dashed line: average July paleotemperature value,

boxes: maximum and minimum values of July paleo-temperature

**1. ábra:**

A malakohőmérő módszerével rekonstruált júliusi középhőmérséklet változásai 10 000 és 35 000 cal BP évek között a Kárpát-medencében

szaggatott vonal: átlagos júliusi középhőmérséklet,

négyzetek oldalai: minimum és maximum értékek

The interstadials correlate well with the Dansgaard – Oeschger (DO) interstadials 8, 7, 6, 5, 4, 3, 2 (Bond et al. 1992, 1993, 1999) seen in the Greenland ice core oxygen isotope records. The start of the intervening cold phases on the other hand correlate with Heinrich events 1, 2, 3, 4 and the LGM (Bond et al. 1999; Cacho et al. 1999; Voelker et al. 1998; Voelker 2002; Antoine et al. 2001; Rousseau et al. 2002; Daniau et al. 2007; Wohlfarth et al. 2008; Veres et al. 2010). These data overall confirm that millennial scale climate variability during second half of the MIS3 and MIS2 stages (Svensson et al. 2006; Rasmussen et al. 2006, 2008, 2014) had profound effect on the terrestrial ecosystems in the continental interior of SE Europe leading to the expansion of mixed boreal forest steppes in the interstadials. Conversely, the ecotone of cold steppe, taiga and tundra mosaics

underwent an expansion during the stadial phases (Sümegei 2005, 2011; Sümegei et al. 2012).

The first radiocarbon-dated chronological and paleo-climatological unit determined from the inferred paleoclimatic changes dates between 35,000 – 29,000 cal BP years. This phase was characterized by milder and more humid conditions (Krolopp & Sümegei, 1992, 1995; Sümegei 2011). For this time interval according to malaco-thermometer method (Sümegei, 1989, 1996, 2005, 2007) we could infer mean July paleo-temperatures ranging around 19-20 °C in the southern parts of the Carpathian Basin, 18 °C in the central parts of the Great Hungarian Plains, and 17 °C in the Northern Mid-Mountains and the southern foothills of the Northern Carpathians, respectively (Sümegei & Krolopp 1995, 2002; Sümegei et al. 2000, 2002). Based on the occurrence of indicator snail species,

a mixed taiga-steppe vegetation developed with mean January temperatures ranging between  $-3\text{ }^{\circ}\text{C}$  and  $-10\text{ }^{\circ}\text{C}$  and annual temperatures between  $+6\text{ }^{\circ}\text{C}$  and  $+9\text{ }^{\circ}\text{C}$ . The earliest Gravettian hunters appeared during this interstadial phase in the Carpathian Basin.

According to malacological data from thickest loess profiles in the Carpathian Basin, a short but intense cold phase formed 30,000 and 29,000 cal BP years in the Carpathian Basin. During this stadial, the otherwise relatively low July mean temperatures further decreased. Mean July paleo-temperatures were around  $15 \pm 1\text{ }^{\circ}\text{C}$  in this phase (Sümegei et al. 2019). Based on mollusc distribution data (Sümegei et al. 2019) low growing season and low winter temperatures (between  $-7\text{ }^{\circ}\text{C}$  and  $-17\text{ }^{\circ}\text{C}$ ) prevailed. In addition, annual temperatures were likewise very low (between  $+5\text{ }^{\circ}\text{C}$  to  $+7\text{ }^{\circ}\text{C}$ ).

The next interstadial phase representing the period between 29,000 - 25,000/24,500 calBP years was characterized by higher July paleo-temperatures ( $16-17\text{ }^{\circ}\text{C}$ ) and drier conditions (Sümegei 1989, 1996, 2005, 2007, 2014) in the Carpathian Basin. This paleo-ecological horizon was classified as the *Pupilla triplicata* zonula which is rich in burnt charcoal fragments (Sümegei 2014). This burnt horizon is overlain by loess again. However, the loess and the underlying paleosol tend to be interfingering marking the significance of cyclically fluctuating bioactivities during the initiation of dust accumulation.

### MIS2 stage

The next paleo-climatological - malacological horizon started from 25,000/24,500 cal BP years. The dominance of the thermophilous species declined and some cold-resistant and cryophilous species like the Boreo-Alpin *Columella columella* and N-Asian xeromontane *Vallonia tenuilabris* occurred. The dominance of mesophilous species increased. A cold climatic phase developed and typical loess fauna formed in the analyzed region.

Yet the fauna of MIS2 was far from being homogenous. Therefore this strong cooling phase was interrupted by several alternating short warming and cooling, lasting for some hundred or some thousand years (microinterstadial) which slowed down dust accumulation in the area. The first microinterstadial was recorded at 23,000 cal BP years, and was characterized by an increase in mesophilous land snails. The southern areas of the Carpathian Basin witnessed an expansion of the thermophilous elements of the mollusc fauna during this time. Conversely, the shade-loving elements have undergone an increase in the south-western parts of the basin (*Orcula dolium*, *Vitrea crystallina*). These paleo-environmental data imply the survival of the formerly existing mosaic-patterning in the environment, leading to the

emergence of mixed, extinct floral and faunal associations. However, a characteristic increase in the dominance of the mesophilous, forest steppe dweller *Vallonia costata* is clearly observable in the majority of the profiles for this time (*Vallonia costata* zonula: Sümegei 1989). Mean July paleo-temperatures changed to  $17\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$  in this short interstadial.

After 23,000 cal BP years the fauna composition changed very dynamically. The dominance of the mesophilous species decline, cold-resistant and cryophilous species such as *Trichia hispida*, *Columella columella*, *Vallonia tenuilabris*, and *Pupilla sterri* dominate this horizon and Boreo-Alpine elements such as *Vertigo genesii*, *Vertigo parcedentata* (Pokryszko 1993; Van Helsdingen 1996; Hausdorf 2006; White et al. 2008; Meng 2008) occur. The July paleo-temperature decreased and stabilized between  $11-14\text{ }^{\circ}\text{C}$  in the Carpathian Basin. Cold – humid growth seasons developed and a mosaic of tundra, tundra-like vegetation spots, cold steppes, shrublands with scattered stands of arboreal vegetation emerged.

The second relative temperate phase formed around 21,000 cal BP years. According to the appearance of *Orcula dolium*, *Discus ruderatus* and the dominance maximum of *Punctum pygmaeum*, *Clausilia dubia*, *Vitrina pellucida*, and *Vitrea crystallina* in the fauna a relatively milder climate must have emerged in this horizon, characterized by mean July paleo-temperatures ranging about  $15 \pm 1\text{ }^{\circ}\text{C}$ .

After 21,000 cal BP years, the fauna composition changed very dynamically again. There is a decline in mesophilous species with dominance of cold-resistant and cryophilous species (*Trichia hispida*, *Columella columella*, *Vallonia tenuilabris*, *Pupilla sterri*) until 18,000 cal BP years. Boreo-Alpine elements (*Vertigo genesii*, *Vertigo parcedentata*) (Pokryszko 1993; Van Helsdingen 1996; Hausdorf 2006; White et al. 2008; Meng 2008) also reappear in the fauna. July paleo-temperatures decreased and stabilized between  $11-14\text{ }^{\circ}\text{C}$ . Cold – humid growth seasons developed in this climatic phase.

Between 18,000 – 16,000 cal BP years there is a decline in cryophilous species accompanied by the reoccurrence of thermophilous species. The dominant forms in this interstadial horizon are cold-resistant and mesophilous steppe like environment dwelling elements. These include the Central European montane shade-loving species like *Vestia turgida*, *Cochlodina cerata*, *Semilimax semilimax*, *Semilimax kotulai*, *Cochlodina laminata*. The composition of the mollusc fauna indicates the emergence of a relatively milder climate with mean July paleo-temperatures ranging around  $15 \pm 1\text{ }^{\circ}\text{C}$ .

After this afforestation stage another cold maximum must have developed in the basin

corresponding to the last significant appearance of the cold-loving elements (*Columella columella*, *Pupilla sterri*, *Vallonia tenuilabris* and *Vertigo pseudosubstata*). This stadial horizon dated to the end of the Upper Würmian and the beginning of the Late Glacial (around 16,000-13,500 cal BP years) can be observed in almost every Hungarian loess profiles (Sümegi et al. 1991). Based on detailed chronological and paleontological studies (Sümegi et al. 1991; Szöör et al. 1991), this zone was termed as the *Pupilla sterri* zonula. There was a decrease in July paleo-temperatures to stable values between 12-14 °C.

After this cold peak, the cold-loving elements underwent a gradual retreat then finally completely disappeared from the Hungarian loess deposits. There is a dominance peak of the cold-resistant, hygrophilous elements (*Succinea oblonga*, *Columella edentula*, *Trichia hispida*) around 13500-12000 BP (Sümegi 1989). These latter taxa appeared in mass volumes in the profiles, sometimes representing even 90% of the total fauna as well. This period is characterized by somewhat milder and more humid conditions. It also marks the last appearance of the loess fauna (*Columella edentula* zonula). The composition of the mollusc fauna indicates the emergence of relatively milder climate with mean July paleo-temperatures around  $15 \pm 1$  °C.

After 12,000 BP, cold-loving elements (*Columella columella*, *Vallonia tenuilabris*) completely disappear from the central part of the Carpathian Basin. Afterwards there is a decrease in the proportions of cold-resistant forms as well (between 11,000-9,000 BP years), retreating back into the colder refugia of the basin (e.g. Bátorliget). On the other hand, the steppe-forest steppe dwellers start to expand (*Cepaea vindobonensis* zonula) gradually becoming dominant elements of the fauna (Sümegi 1989). According to this transformation in the mollusc fauna, colder loess steppes and mixed taiga woodlands, characterized by mean July paleo-temperatures between 12-16 °C were gradually overtaken by milder temperate forest steppes containing steppe and deciduous woodland elements (mean July paleo-temperatures 16-22 °C). All this led to the cessation of loess formation in the basin between 12,000-10,000 cal BP years. Cessation of loess formation in the Carpathian Basin was coeval with the disappearance of the periglacial environmental conditions (Willis et al. 1995).

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### References

ABDEL - REHIM, A.H. (1987): Microclimatic adaptation and differences in food consumption and assimilation efficiency of different shell colour morphs of the land snail *Arianta arbustorum*. *Journal of Zoology* **211** 717–725.

ALEXANDROWICZ, S.W. (1988): Malacofauna of Late Quaternary loess-like deposits in the Polish Carpathians. *Acta Geologica Polonica* **38** 85–106.

ALEXANDROWICZ, W.P. (2013): Malacological sequence from profile of calcareous tufa in Groń (Podhale Basin, southern Poland) as an indicator of the Late Glacial / Holocene boundary. *Quaternary International* **293** 196–206.

ALEXANDROWICZ, W.P. (2014): Malacological sequence of Weichselian (MIS 5-2) loess series from a profile in Grodzisko Dolne (southern Poland) and its palaeogeographic significance. *Quaternary International* **319** 109–118.

ALEXANDROWICZ, W.P. & RUDZKA, D. (2006): Molluscan communities from cave and slope deposits of the limestone rocky hills in the eastern part of Podhale Basin (Southern Poland). *Folia Malacologica* **14** 191–201.

ARNASON, E. & GRANT, P.R. (1976): Climatic selection in *Cepaea hortensis* at the northern limit of its range in Iceland. *Evolution* **40** 499–508.

ANT, H. (1963): Faunistische, ökologische und tiergeographische Untersuchungen zur Verbreitung der Landschnecken in Nordwestdeutschland. *Abhandlungen des Landesmuseums für Naturkunde Münster* **25** 1–125.

ANTOINE, P., ROUSSEAU, D.D., MOINE, O., KUNESCH, S., HATTÉ, C., LANG, A., TISSOUX, H., ZÖLLER, L. (2009): Rapid and cyclic aeolian deposition during the Last Glacial in European loess: a high-resolution record from Nussloch, Germany. *Quaternary Science Reviews* **28** 2955–2973.

ASHWORTH, A.C. (1996): The response of arctic Carabidae (Coleoptera) to climate change based on the fossil record of the Quaternary Period. *Annales Zoologici Fennici* **33** 125–131.

ASHWORTH, A.C. (2001): Perspectives on Quaternary Beetles and Climate Change. In:

- GERHARD, L.C., HARRISON, W.E., HANSON, B.M. eds., *Geological Perspectives of Global Climate Change*. American Association of Petroleum Geologists. Tulsa, Oklahoma, *Studies in Geology* **47** 153–168.
- BACSÓ, N., KAKAS, J. TAKÁCS, L. (1953): *Magyarország éghajlata*. Országos Meteorológiai Szolgálat, Budapest, 1–226.
- BACSÓ, N. (1959): *Magyarország éghajlata*. Akadémiai Kiadó, Budapest, 1–302.
- BALASHOV, I.A., & KRYVOKHYZHA, M.V. (2015): Distribution patterns of terrestrial mollusks in the chalk steppe and neighboring phytocenoses of the Oskol River Valley in the Dvorichanskyi National Nature Park, Ukraine. *Russian Journal of Ecology* **46** 370–376.
- BANNER, J. (1936): Az első alföldi paleolit telep. *Dolgozatok* **12** 1–7.
- BÁBA, K. (1989): A history and present day situation of the investigation of the recent land snails in the Great Hungarian Plain. *Tiscia* **15** 93–102.
- CAMERON, R.A.D. (1992): Change and stability in *Cepaea* populations over 25 years: a case of climatic selection. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **248** 181–187.
- CACHO, I., GRIMALT, J.O., PELEJERO, C., CANALS, M., SIERRA, F.J., FLORES, J.A., SHACKLETON, N. (1999): Dansgaard-Oeschger and Heinrich event imprints in Alboran Sea paleotemperatures. *Paleoceanography* **14** 698–705.
- CHLACHULA, J. (2001): Pleistocene climate change, natural environments and palaeolithic occupation of the upper Yenisei area, south-central Siberia. *Quaternary International* **80** 101–130.
- CHLACHULA, J., KEMP, R.A., JESSEN, C.A., PALMER, A.P., TOMS, P.S. (2004): Landscape development in response to climatic change during Oxygen Isotope Stage 5 in the southern Siberian loess region. *Boreas* **33** 164–180.
- COOPE G.R. (1975): Climatic fluctuation in northwest Europe since the last interglacial, indicated by fossil assemblages of coleoptera. In: WRIGHT, A.E. & MOSELEY, F. eds., *Ice ages. Ancient and modern*. Seel House Press, Liverpool, 153–168.
- COOPE, G.R. (2002): Changes in the thermal climate in northwestern Europe during marine oxygen isotope stage 3, estimated from fossil insect assemblages. *Quaternary Research* **57** 401–408.
- COOPE, R.G., MORGAN, A. AND OSBORNE, P.J. (1971): Fossil Coleoptera as indicators climatic fluctuations during the Last Interglacial in Britain. *Palaeogeography, Palaeoclimatology, Palaeoecology* **10** 87–101.
- CURREY, J.D. & CAIN, A.J. (1968): Studies on *cepea*, IV. Climate and selection of banding morphs in *cepea* from the climatic optimum to the present day. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **253** 483–498.
- DAVIES, P. (2008): *Snails: archaeology and landscape change*. Oxbow Books, Oxford, 1–199.
- T. DOBOSI, V. (1967): Új felső-paleolit telep az Alföldön. *Archaeológiai Értesítő* **94** 184–193.
- T. DOBOSI, V. (1975): Magyarország ős- és középső kőkori lelőhely katasztere. Register of Palaeolithic and Mesolithic Sites in Hungary. *Archaeológiai Értesítő* **102** 64–76.
- T. DOBOSI V. (1981): Pilismarót-Diós: Új őskőkori telep. *Communicationes Archaeologicae Hungariae* (1981) 9–21.
- T. DOBOSI, V. (1989): Madaras-Téglavető felsőpaleolit telep. Régészeti feldolgozás. *Cumania* **1145–58**.
- T. DOBOSI V. (1993): Jászfelsőszentgyörgy-Szúnyogos, felső-paleolit telep. *Tisicum* **8** 54–60.
- T. DOBOSI V. (1994): Contribution to the Upper Palaeolithic topography. *Acta Archeologica Academiae Scientiarum Hungaricae* **46** 3–20.
- T. DOBOSI V. (1996): Upper Palaeolithic in the Danube bend. In: SVOBODA, J., ŠKORDLA, P., OCHES, O.W. eds., *Palaeolithic in the Middle Danube Bend. Spisy Archeologického ústavu*, **5**, Brno, 25–37.
- T. DOBOSI V. (2000): Archaeological investigations at Bodrogkeresztúr-Henye. In: T. DOBOSI V. ed., *Bodrogkeresztúr-Henye (NE-Hungary) Upper Palaeolithic site*. Magyar Nemzeti Múzeum Kiadványa, Budapest, 5–111.

- T. DOBOSI, V. & KÖVECSES-VARGA, E. (1991): Upper Palaeolithic site at Esztergom-Gyurgyalag. *Acta Archeologica Academiae Scientiarum Hungaricae* **43** 233–255.
- T. DOBOSI, V. & SIMÁN, K. (1996): New Upper Palaeolithic site at Megyaszó-Szelestedő. *Communicationes Archaeologicae Hungariae* (1996) 5–22.
- T. DOBOSI, V. & VÖRÖS, I. (1986): Chronological revision of the Pilisszántó rock-shelter II. *Folia Archeologica* **37** 25–43.
- T. DOBOSI, V. & VÖRÖS, I. (1987): Chronological revision of the Pilisszántó rock-shelter I. *Folia Archeologica* **38** 7–64.
- T. DOBOSI, V., VÖRÖS, I., KROLOPP, E., SZABÓ, J., RINGER, Á., SCHWEITZER, F. (1983): Upper Palaeolithic Settlement in Pilismarót-Pálrét. *Acta Archeologica Academiae Scientiarum Hungaricae* **35** 288–311.
- T. DOBOSI, V., JUNGBERTH, B., RINGER, Á., VÖRÖS, I. (1988): Palaeolithic settlement at Nadap. *Folia Archaeologica* **39** 13–39.
- DOMOKOS, T. (1982): Morphometrical study of the chronocline of *Granaria frumentum* (Draparnaud, 1801) (Gastropoda: Chondrinidae). *Miscellanea Zoologica Hungarica* **1** 45–51.
- DOMOKOS, T. (1995): A Gastropodák létállapotáról, a létállapotok osztályozása a fenomenológia szintjén. *Malakológiai Tájékoztató* **14** 79–82.
- DOMOKOS, T. & FÜKÖH, L. (1984): A *Granaria frumentum* (Draparnaud, 1801) héjmorfológiája klímavizsgálatok tükrében (Gastropoda: Chondrinidae). *Folia Musei Historico-naturalis Musei Matraensis* **9** 91–107.
- DOMOKOS, T. & FÜKÖH, L. (1986): Relationship between microlimate and the shell morphology of *Granaria frumentum* (Draparnaud, 1801) (Gastropoda, Chondrinidae). *Proceedings of the 8th International Malacological Congress*, Budapest, 69–74.
- DOMOKOS, T. & SÓLYMOS, P. (2013): Néhány délkelet-alföldi adat a *Granaria frumentum* (Draparnaud, 1801) héjmorfológiájának klímafüggéséhez (Gastropoda: Chondrinidae). *Folia Historico Naturalia Musei Matraensis* **370** 5–13.
- DOMOKOS, T., SÓLYMOS, P., KOVÁCS, CSNÉ (2014): Balaton környéki biotópokból (Tihany, Külső-Somogy) származó *Granaria frumentum* (DRAPARNAUD, 1801) héjmorfológiájának klímafüggése (Gastropoda: Chondrinidae). *Kaposvári Rippl-Rónai Múzeum Közleményei* **3** 87–96.
- DANIAU A.L., SÁNCHEZ-GOÑI, M.F., BEAUFORT, L., LAGGOUN-DÉFARGE, F., LOUTRE, M.F., DUPRAT, J. (2007): Dansgaard-Oeschger climatic variability revealed by fire emissions in southwestern Iberia. *Quaternary Science Reviews* **26** 1369–1383.
- DUDA, M., HARING, E., BULATOVIĆ, A., HILLE, A., KRUCKENHAUSER, L., MACEK, O., MARKOVIĆ, J., PINSKER, D., REIER, S., SEFC, K., SLAPNIK, R., SITTENTHALER, M., SONNLEITNER, M., VALENTINČIĆ, J., SATTMANN, H. (2018): The snail summiteers gastropod faunas of some exposed alpine locations in the Gesäuse National Park. *Arianta* **6** 41–46.
- DVOŘÁKOVÁ, J., & HORSÁK, M. (2012): Variation of snail assemblages in hay meadows: disentangling the predictive power of abiotic environment and vegetation. *Malacologia* **551** 51–163.
- EVANS, J.G. (1969): Land and freshwater Mollusca in archaeology: chronological aspects. *World Archaeology* **1** 170–183.
- EVANS, J.G. (1972): *Land Snails in Archeology*. Seminar Press, London, 1–436.
- FÁBIÁN, S., KOVÁCS, J., VARGA, G. (1998): Új szempontok a Kárpát-medence felső-würmi ösföldrajzi viszonyaihoz a homokékek alapján. *Közlemények a JPTE TTK Természetföldrajz Tanszékéről* **8** 3–14.
- FÁBIÁN, S., KOVÁCS, J., VARGA, G. (2000): Újabb szempontok hazánk periglaciális klímájához. *Földrajzi Értesítő* **49** 189–204.
- FINK, J. (1954): Die fossilen Böden im österreichischen Löß. *Quartär* **6** 85–107.
- FREST, T. J., & DICKSON, J. R. (1986): Land snails (Pleistocene-recent) of the Loess Hills: A preliminary survey. *Proceedings of the Iowa Academy of Science* **93** 130–157.
- FRÖMMING, E. (1954): *Biologie der Mitteleuropäischen Landgastropoden*. Deucher et Humboldt, Berlin, 1–541.

- GÁBORI, M. (1954): A piliszántói kőfülke magdaléniai kultúrája és eredete. *Archaeológiai Értesítő* **81** 3–9.
- GÁBORI, M. (1956): Rénszarvas vadászok nyomán a Duna mentén. *Élet és Tudomány* **10/14** 747–750.
- GÁBORI, M. (1968): Archaeology and prehistory of the Hungarian loess-Palaeolithic. In: PÉCSI, M. ed., *Löss – periglacial - Palaeolith Symposium*. MTA Földrajzkutató Intézet Kiadványa, Budapest, 19–27.
- GÁBORI, M. (1969): Palaeolitische Schnecken depots von Szob. *Acta Archeologica Academiae Scientiarum Hungaricae* **29** 3–11.
- GÁBORI, M. (1980): *Paleolit i mezolit*. In: TITOV, V. S. & ERDÉLYI, I. eds., *Archeologiya Vengrii*. Moskva, Nauka 29–72.
- GÁBORI, M. (1981): Az ősember korának kutatása Magyarországon. *A Magyar Tudományos Akadémia Filozófiai és Történettudományi Osztályának Közleményei (II)* **30/1** 91–109.
- GÁBORI, M. (1984): A régibb kőkor Magyarországon. In: BARTHA, A.-SZÉKELY, Gy. eds., *Magyarország története I*. Akadémiai Kiadó, Budapest, 69–115.
- GÁBORI, M. & GÁBORI V. (1957): Études archéologiques et stratigraphiques dans les stations de loess paléolithiques de Hongrie. *Acta Archeologica Academiae Scientiarum Hungaricae* **8** 3–117
- GABORI-CSANK, V. (1978): Une oscillation climatique a la fin du Würm en Hongrie. *Acta Archeologica Academiae Scientiarum Hungaricae* **30** 3–11.
- GABORINE CSANK, V. (1980): *Az ősember Magyarországon*. Gondolat Kiadó, Budapest, 1–264.
- GABORINE CSANK, V. (1984): *A felső paleolitikum nyoma Budapesten. Budapest Régiségei* **25** 7–14.
- GEORGIEV, D., & STOYCHEVA, S. (2010): Notes on the ecology and species diversity of the inland molluscs of Samothraki Island (North-Eastern Greece). *North-Western Journal of Zoology* **6** 71–78.
- HAUSDORF, B. (2006): Latitudinal and altitudinal diversity patterns and Rapoport effects in north-west European land snails and their causes. *Biological Journal of the Linnean Society* **87** 309–323.
- HAUSDORF, B. & HENNIG, C. (2003): Nestedness of north-west European land snail ranges as a consequence of differential immigration from Pleistocene glacial refuges. *Oecologia* **135** 102–109.
- HÁJEK, M., HORSÁK, M., TICHÝ, L., HÁJKOVÁ, P., DÍTĚ, D., JAMRICOVÁ, E. (2011): Testing a relict distributional pattern of fen plant and terrestrial snail species at the Holocene scale: a null model approach. *Journal of Biogeography* **38** 742–755.
- VAN HELSDINGEN, P.J., WILLEMSE, L., SPEIGHT, M.C. (1996). Background Information on Invertebrates on the Habitats Directive and the Bern Convention: Mollusca and Echinodermata (Vol. 3). *Nature and environment* **81** Council of Europe Publishing, Strasbourg, 1–533.
- HERTELENDI, E., SÜMEGI, P., SZŐÖR GY. (1992): Geochronologic and paleoclimatic characterization of Quaternary sediments in the Great Hungarian Plain. *Radiocarbon* **34** 833–839.
- HETTENBERGEROVÁ, E., HORSÁK, M., CHANDRAN, R., HÁJEK, M., ZELENÝ, D., DVOŘÁKOVÁ, J. (2013): Patterns of land snail assemblages along a fine-scale moisture gradient. *Malacologia* **56** 31–43.
- HEUSSER, C.J. (1972): *Climatic records of the Last Ice Age for Pacific Mid-latitudes in the Americas*. Abstracts of 9th INQUA Congress, New Zealand, Christchurch, 150–151.
- HOFFMANN, M.H., MENG, S., KOSACHEV, P.A., TERECHINA, T.A., SILANTEVA, M.M. (2011): Land snail faunas along an environmental gradient in the Altai Mountains (Russia). *Journal of Molluscan Studies* **77** 76–86.
- HOKR A. (1951): A method of the quantitative determination of the climate in the Quaternary Period by means of mammal associations. *Sbornik Ceskoslovenke Republiky Statniho Geologickeho* **18** 209–219.
- HORSÁK, M., HÁJEK, M., DÍTĚ, D., TICHÝ, L. (2007): Modern distribution patterns of snails and plants in the Western Carpathian spring fens: is it a

result of historical development? *Journal of Molluscan studies* **73** 53–60.

HORSÁK, M., CHYTRÝ, M., HÁJKOVÁ, P., HÁJEK, M., DANIHELKA, J., HORSÁKOVÁ, V., ERMAKOV, N., GERMAN, D.A., GERMAN, D.A., KOČÍ, M., LUSTICK, P., NEKOLA, J.C., PREISLEROVÁ, Z., VALAHOVICH, M. (2015): European glacial relict snails and plants: environmental context of their modern refugial occurrence in southern Siberia. *Boreas* **44** 638–657.

HORSÁK, M., CHYTRÝ, M., POKRYSZKO, B. M., DANIHELKA, J., ERMAKOV, N., HÁJEK, M., HÁJKOVÁ, P., KINTROVÁ, K., KOČÍ, M., KOBESOVÁ, S., LUSTYK, P., OTÝPKOVÁ, Z., PELÁNKOVÁ, B., VALAHOVICH, M. (2010): Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full - glacial Europe. *Journal of Biogeography* **37** 1450–1462.

HORSÁK, M., JUŘIČKOVÁ, L., PICKA, J. (2013): *Měkkýši České a Slovenské republiky. Molluscs of the Czech and Slovak Republics.* Kabourek, Zlín, 1–264.

IMBRIE, J., HAYS, J.D., MARTINSON, D.G., MCLNTYRE, A., MIX, A.C., MORLEY, J.J., PISIAS, N.G., PRELL, W.L., SHACKLETON, N.J. (1984): The orbital theory of Pleistocene climate: support from a revised chronology of the marine delta 1~O record. In: BERGER, A.L. IMBRIE, J., HAYS, J., KUKLA, G., SALTZMAN, B. eds., *Milankovitch and Climate*, Part 1. Reidel Publishing, Boston, 169–305.

IVERSEN, J. (1944): *Viscum, Hedera* and *Ilex* as climate indicators: A contribution to the study of the post-glacial temperature climate. *Geologiska Föreningen i Stockholm Förhandlingar* **66** 463–483.

JÁNOSSY, D. (1979): *A magyarországi pleisztocén tagolása gerinces faunák alapján.* Akadémiai Kiadó, Budapest, 1–206.

JÁNOSSY, D. (1986). *Pleistocene vertebrate faunas of Hungary.* Elsevier, Amsterdam, 1–206.

JÁRAINÉ-KOMLÓDI, M. (1966): Adatok az Alföld klíma- és vegetációtörténetéhez I. *Botanikai Közlemények* **53** 191–201.

JÁRAINÉ-KOMLÓDI, M. (1968): The late Glacial and Holocene flora of the Great Hungarian Plain. *Annales Universitatis Scientiarum Budapestiensis - Sectio Biologica* **9-10** 199–225.

JÁRAINÉ-KOMLÓDI, M. (1969): Adatok az Alföld klíma- és vegetációtörténetéhez II. *Botanikai Közlemények* **56** 43–55.

JÁRAINÉ-KOMLÓDI, M. (1987): Postglacial Climate and Vegetation History in Hungary. Pécsi, M.-Kordos, L. eds. *Holocene environment in Hungary.* Geographical Research Institute Hungarian Academy of Sciences, Budapest, 37–47.

JÁRAINÉ-KOMLÓDI, M. (2000): A Kárpát-medence növényzetének kialakulása. *Tilia* **9** 5–59.

JOHNSEN, S. J., DAHL - JENSEN, D., GUNDESTRUP, N., STEFFENSEN, J. P., CLAUSEN, H. B., MILLER, H., MASSON-DALMOTTE, V., SVEINBJÖRNSDÓTTIR, A.E., WHITE, J. (2001): Oxygen isotope and palaeotemperature records from six Greenland ice - core stations: Camp Century, Dye - 3, GRIP, GISP2, Renland and NorthGRIP. *Journal of Quaternary Science* **16** 299–307.

JONES, J.S. (1973): Ecological Genetics and Natural Selection in Molluscs: Climatic selection has an important effect on some patterns of gene distribution in snail populations. *Science* **182** 546–552.

JULLIEN, E., GROUSSET, F.E., HEMMING, S.R., PECK, V.L., HALL, I.R., JEANTET, C., BILLY, I. (2006): Contrasting conditions preceding MIS3 and MIS2 Heinrich events. *Global and Planetary Change* **54** 225–238.

JUŘIČKOVÁ, L. & LOŽEK, V. (2008): Molluscs of the Krkonoše Mts. (Czech Republic). *Malacologica Bohemoslovaca* **7** 55–69.

KAPPES, H., TOPP, W., ZACH, P., KULFAN, J. (2006): Coarse woody debris, soil properties and snails (Mollusca: Gastropoda) in European primeval forests of different environmental conditions. *European Journal of Soil Biology* **42** 139–146.

KLEMM, W. (1974): Die Verarbeitung der rezenten Land-Gehäuse-Schnecken in Österreich. *Denkschriften der Österreichischen Akademie der Wissenschaften/Mathematisch-Naturwissenschaftliche Classe* **117** 1–513.

KEPPEL, G., VAN NIEL, K.P., WARDELL - JOHNSON, G.W., YATES, C.J., BYRNE, M., MUCINA, L., ANTONIUS, G.T., SCHUT, S., HOPPER. S.D., FRANKLIN, S.E. (2012): Refugia: identifying and understanding safe



havens for biodiversity under climate change. *Global Ecology and Biogeography* **21** 393–404.

KERNEY, M.P. & CAMERON, R.A.D. (1979): *A Field Guide to the Land Snails of Britain and Northwest Europe*. Collins, London, 1–288.

KERNEY, M. P., PREECE, R. C., TURNER, C. (1980): Molluscan and plant biostratigraphy of some Late Devensian and Flandrian deposits in Kent. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* **291** (1044) 1–43.

KORDOS, L. (1977): Changes in the Holocene climate of Hungary reflected by the “vole-thermometer” method. *Földrajzi Közlemények* **25** 144–160.

KORDOS L. (1981): Éghajlatváltozás és környezetfejlődés. *MTA X. Osztályának Közleményei* **14** 209–221.

KORDOS L. (1987): Climastratigraphy of Upper Pleistocene Vertebrates and the condition of loess formation in Hungary. *GeoJournal* **15** 163–166.

KOVÁCS, J., FÁBIÁN, S. Á., SCHWEITZER, F., VARGA, G. (2007): A relict sand - wedge polygon site in north - central Hungary. *Permafrost and Periglacial Processes* **18** 379–384.

KRETZOI, M. (1957): Wierbeltierfaunistische Angaben zur Quartärchronologie der Jankovich Höhle. *Folia Archeologica* **9** 16–21.

KRETZOI, M. (1977): Ecological conditions of the "loess period" in Hungary as revealed by vertebrate fauna. *Földrajzi Közlemények* **25** 75–89.

KROLOPP, E. (1961): A tihanyi felsőpleisztocén Mollusca fauna. The Mollusc fauna of the Upper Pleistocene of Tihany. *Földtani Intézet Évi Jelentése 1957-1958-ról* 505–509.

Krolopp, E. (1965a): A Dorog-Esztergomi-medence pleisztocén képződményeinek biosztratigráfiai vizsgálata. *Földtani Intézet Évi Jelentése 1963-ról* 133–145.

KROLOPP, E. (1965b): A kulcsi pleisztocén képződmények biosztratigráfiai vizsgálata. In: Rónai, A. et al. : A kulcsi löszfeltárás szelvénye. *Földtani Intézet Évi Jelentése 1963-ról* 167–187.

KROLOPP, E. (1965c): Mollusc fauna of the sedimentary formations of the Quaternary period, Hungary. *Acta Geologica Hungarica* **9** 153–160.

KROLOPP, E. (1966): A Mecsek hegység környéki löszképződmények biosztratigráfiai vizsgálata. *Földtani Intézet Évi Jelentése 1964-ról* 137–187.

KROLOPP, E. (1967): A pleisztocén Mollusca fauna paleoökológiai vizsgálata. *Őslénytani Viták* **8** 1–4.

KROLOPP, E. (1973): Quaternary malacology in Hungary. *Földrajzi Közlemények* **21** 161–171.

KROLOPP, E. (1977): Middle Pleistocene Mollusc Fauna from the Vértesszőlős Campsite of Prehistoric Man. *Földrajzi Közlemények* **101** 188–204

KROLOPP, E. (1983): Biostratigraphic division of Hungarian Pleistocene Formations according to their Mollusc fauna. *Acta Geologica Hungarica* **26** 62–89.

KROLOPP, E. (1990): Molluscan fauna from Vértesszőlős. In: KRETZOI, M. & T. DOBOSI, V. eds., *Vértesszőlős: site, man and culture*. Akadémiai Kiadó, Budapest, 163–182.

KROLOPP, E. (2003): *Pleisztocén Mollusca-faunánk taxonómiai, faunisztikai, rétegtani és paleoökológiai értékelése*. Akadémiai doktori értekezés (Academic Doctoral thesis), Budapest, 1–75.

KROLOPP, E. & SÜMEGI, P. (1992): A magyarországi löszök képződésének paleoökológiai rekonstrukciója Mollusca-fauna alapján. In: SZŐÖR, GY. (szerk.) *Fáciesanalitikai, paleobiogeokémiai és paleoökológiai kutatások*. MTA Debreceni Bizottsága, Debrecen, 247–263.

KROLOPP, E. & SÜMEGI, P. (1993): Pleistocene Vertigo species from Hungary. *Scripta Geologica Special Issue* **2** 263–268.

KROLOPP, E. & SÜMEGI, P. (1995): Palaeoecological reconstruction of the Late Pleistocene, based on Loess Malacofauna in Hungary. *GeoJournal* **36** 213–222.

KUIJPER, W.J. (1985): Malacological research of Weichselian deposits at the Maastricht-Belvédère pit. *Analecta Praehistorica Leidensia* **18** 106–107.

LIMONDIN - LOZOUET, N. & ANTOINE, P. (2001): Palaeoenvironmental changes inferred from malacofaunas in the Lateglacial and early Holocene fluvial sequence at Conty, northern France. *Boreas* **30** 148–164.

- LIMONDIN, N. & ROUSSEAU, D.D. (1991): Holocene climate as reflected by a malacological sequence at Verrières, France. *Boreas* **20** 207–229.
- LISÁ, L., NERUDA, P., NERUDOVA, Z., NEJMAN, L. (2018): Podhradem Interstadial; A critical review of the middle and late MIS 3 (Denekamp, Hengelo) in Moravia, Czech Republic. *Quaternary Science Reviews* **182** 191–201.
- LOŽEK, V. (1964): Quartärmollusken der Tschechoslowakei. *Rozpravy Ústředního ústavu geologického* **31** 1–374
- LOŽEK, V. (1990): Molluscs in loess, their paleoecological significance and role in geochronology - Principles and methods. *Quaternary International* **7** 71–79.
- LOŽEK, V. (2001): Molluscan fauna from the loess series of Bohemia and Moravia. *Quaternary International* **76** 141–156.
- MAGNIN, F. (1993): Quaternary non-marine Mollusca and palaeoclimates in Mediterranean France. *Scripta Geologica. Special Issues* **2** 275–289.
- MAGYARI E. (2002): *Climatic versus human modification of the Late Quaternary vegetation in Eastern Hungary*. PhD Thesis, Debrecen, 1–150.
- MAGYARI, E., JAKAB, G., RUDNER, E., SÜMEGI, P. (1999): Palynological and plant macrofossil data on Late Pleistocene short term climatic oscillations in North-east Hungary. *Acta Palaeobotanica Supplement* **2** 491 – 502.
- MAGYARI, E., DAVIS, B., SÜMEGI, P., SZŐÖR, GY. (2001): Past Climate variability in the Carpathian Basin based on pollen and Mollusc-derived Palaeoclimate reconstructions: 0–25,000 cal yr. BP. PAGES - PEP3: Past Climate Variability Through Europe and Africa, *Abstracts of the Past Global Climate Conference*, Aix-en-Provence, France. <http://at.yorku.ca/c/a/g/c/01.htm>
- MARTIN, K. & SOMMER, M. (2004): Relationships between land snail assemblage patterns and soil properties in temperate - humid forest ecosystems. *Journal of Biogeography* **31** 531–545.
- MEIJER, T. (1985): The Pre-Weichselian Nonmarine Molluscan Fauna from Maastricht-Belvédère (Southern Limburg, the Netherlands) in Maastricht-Belvédère: Stratigraphy, Palaeo-environment and Archaeology of the Middle and Late Pleistocene Deposits. *Analecta Praehistorica Leidensia* **18** 75–103.
- MENG S. (2008): Neue Daten zur Verbreitung der Vertiginidae (Gastropoda: Pulmonata) in Zentralasien. [New distribution data for Vertiginidae (Gastropoda: Pulmonata) in Central Asia]. *Mollusca* **26** 207–219.
- MENG, S. (2009): Rezente zentralasiatische und pleistozäne mitteleuropäische Faunen mit Vallonia tenuilabris (A. Braun, 1843). *Mollusca* **27** 61–82.
- MENG, S., & HOFFMANN, M. H. (2009): Pupilla loessica Ložek 1954 (Gastropoda: Pulmonata: Pupillidae) - “A Living Fossil” in Central Asia?. *Quaternary Science Journal* **58** 55–69.
- MOINE, O., ROUSSEAU, D.D., ANTOINE, P. (2005): 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** 363–380.
- MÜLLER, J., STRÄTZ, C., HOTHORN, T. (2005): Habitat factors for land snails in European beech forests with a special focus on coarse woody debris. *European Journal of Forest Research* **124** 233–242.
- NYILAS I. & SÜMEGI P. (1987): Adatok az imókői (É-Magyarország: Bükk-hg.) növény-társulások Mollusca faunájához. *Malakológiai Tájékoztató* **7** 43–47.
- NYILAS I. & SÜMEGI P. (1991): The Mollusc fauna of Hortobágy at the end of the Pleistocene (Würm3) and in the Holocene. In: MEIER-BROOK, C. ed., *Proceeding of 10th International Malacological Congress*, Tübingen, 481–486.
- MYŠÁK, J. (2009). Malakofauna PR Hemže-Mýtkov. *Malacologica Bohemoslovaca* **8** 56–62.
- OBREHT, I., ZEEDEN, C., HAMBACH, U., VERES, D., MARKOVIĆ, S. B., LEHMKUHL, F. (2019): A critical reevaluation of palaeoclimate proxy records from loess in the Carpathian Basin. *Earth-Science Reviews* **190** 498–520
- OWEN, D.F., & BENGTON, S.A. (1972): Polymorphism in the land snail *Cepaea hortensis* in Iceland. *Oikos* **23** 218–225.
- PELBÁRT, J. (2000): Data to the mollusc fauna of the Carpathian Biosphere Reserve, Ukraine

(Mollusca). *Miscellanea Zoologica Hungarica* **13** 85–90.

PETICZKA, R., HOLAWA, F., RIEGLER, D. (2010): Structural analyses on the modified paleosol-sequence of “Stillfried B” with high resolution measurements of selected laboratory parameters. *Quaternary International* **222** 168–177.

PÉCSI, M. (1975): Lithostratigraphical subdivision of the loess sequences in Hungary. *Földrajzi Közlemények* **23** 228–239.

PÉCSI, M. (1977): A hazai és az európai löszképződmények paleogeográfiai kutatása és összehasonlítása. *Geonómia és Bányászat, MTA X. Osztályának Tudományos Közleményei* **10** 183–221.

PÉCSI M. (1993): *Negyedkor és löszkutatás*. Akadémiai Kiadó, Budapest. pp?

PÉCZELY, GY. (1998): *Éghajlatlan*. Nemzeti Tankönyvkiadó, Budapest, 1–336.

PILATE, D. (2009): Structure of terrestrial snail communities of Euro-Siberian alder swamps (*Cl. Alnetea glutinosae*) in Latvia. *Acta Zoologica Lituanica* **19** 297–305.

POKRYSZKO, B.M. (1993): Fen malacocenoses in Dovrefjell (S. Norway). *Fauna Norvegica Series A* **14** 27–38.

POKRYSZKO, B.M., & CAMERON, R.A.D. (2005): Geographical variation in the composition and richness of forest snail faunas in northern Europe. *Records of the Western Australian Museum, Supplement* **68** 115–132.

RASMUSSEN, S. O., ANDERSEN, K. K., SVENSSON, A. M., STEFFENSEN, J. P., VINTHER, B. M., CLAUSEN, H. B., SIGGAARD-ANDERSEN, S.J., LARSEN, L.B., DAHL-JENSEN, D., BIGLER, M., RHÖTHLISBERGER, R., FISCHER, HANSSON, M.E., RUTH, U. (2006): A new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research: Atmospheres* **111** D06102, doi: 10.1029/2005JD006079

RASMUSSEN, S. O., SEIERSTAD, I. K., ANDERSEN, K. K., BIGLER, M., DAHL-JENSEN, D., JOHNSEN, S. J. (2008): Synchronization of the NGRIP, GRIP, and GISP2 ice cores across MIS 2 and palaeoclimatic implications. *Quaternary Science Reviews* **27** 18–28.

RASMUSSEN, S. O., BIGLER, M., BLOCKLEY, S. P., BLUNIER, T., BUCHARDT, S. L., CLAUSEN, H. B., GKINIS, V. (2014): A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quaternary Science Reviews* **106** 14–28.

REIMER, P.J., BARD, E., BAYLISS, A., BECK, J.W., BLACKWELL, P.G., BRONK-RAMSEY, C., BUCK, C.E., CHENG, H., EDWARDS, R.L., FRIEDRICH, M., GROOTES, P.M., GUILDERSON, T.P., HAFLIDASON, H., HAJDAS, I., HATT E.C., HEATON, T.J., HOGG, A.G., HUGHEN, K.A., KAISER, K.F., KROMER, B., MANNING, S.W., NIU, M., REIMER, R.W., RICHARDS, D.A., SCOTT, E.M., SOUTHON, J.R., TURNEY, C.S.M., VAN DER PLICHT, J. (2014): IntCal13 and MARINE13 radiocarbon age calibration curves 0–50000 years cal BP. *Radiocarbon* **55** 1869–1887.

RÉTHLY, A. (1937): *Magyarország éghajlata*. Magyar Királyi Országos Meteorológiai és Földmágnasségi Intézet kiadványa, Budapest, 1–37.

RÉTHLY, A. (1948): Magyarország éghajlata. In: RÉTHLY, A. & AUJENSZKY, L. eds., *Agrometeorológia*. Quick Kiadó, Budapest, 95–109.

ROUSSEAU, D.D. (1986): Intérêt paléobiogéographique de *Pupilla loessica* Ložek et de *Vallonia tenuilabris* (A. Braun) pour le Pléistocène Ouest-européen. *Comptes rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre* **303** 257–262.

ROUSSEAU, D.D. (1989): Réponses des malacofaunes terrestres quaternaires aux contraintes climatiques en Europe septentrionale. *Palaeogeography, Palaeoclimatology, Palaeoecology* **69** 113–124.

ROUSSEAU, D.D. (1991a): Statistical analyses of loess molluscs for paleoecological reconstructions. *Quaternary International* **7** 81–89.

ROUSSEAU, D.D. (1991b): Climatic transfer function from Quaternary molluscs in European loess deposits. *Quaternary Research* **36** 195–209.

ROUSSEAU, D.D. (1997): The weight of internal and external constraints on *Pupilla muscorum* L. (Gastropoda: Stylommatophora) during the Quaternary in Europe. In: HUNTLEY, B.,

- CRAMER, W., MORGAN, A.V., PRENTICE, H.V., ALLEN, J.R.M. eds., *Past and Future Rapid Environmental Changes*. Springer, Berlin, Heidelberg, 303–318.
- ROUSSEAU, D.D. (2001): Loess biostratigraphy: new advances and approaches in mollusk studies. *Earth-Science Reviews* **54** 157–171.
- ROUSSEAU, D.D. & LAURIN, B. (1984): Variations de *Pupilla muscorum* L. (Gastropoda) dans le Quaternaire d'Achenheim (Alsace): une analyse de l'interaction entre espèce et milieu. *Géobios* **17** 349–355.
- ROUSSEAU D.D. & KUKLA G. (1994): Late Pleistocene climate record in the Eustis loess section, Nebraska, USA, based on land snail assemblages and magnetic susceptibility. *Quaternary Research* **42** 176–187.
- ROUSSEAU, D.D. & WU, N. (1997): A new molluscan record of the monsoon variability over the past 130 000 yr in the Luochuan loess sequence, China. *Geology* **25** 275–278.
- ROUSSEAU, D.D. & PUISSÉGUR, J.J. (1999): Climatic interpretation of terrestrial malacofaunas of the last interglacial in southeastern France. *Palaeogeography, Palaeoclimatology, Palaeoecology* **151** 321–336.
- ROUSSEAU D.D., PUISSEGUR, J.J., LAUTRIDOU J.P. (1990): Biogeography of the Pleniglacial malacofaunas in Europe. Stratigraphic and climatic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **80** 7–23
- ROUSSEAU, D.D., PUISSEGUR J.J., LECOLLE, F. (1992): West-European molluscs assemblages of isotopic stage 11 (Middle Pleistocene): climatic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **92** 15–29.
- ROUSSEAU, D.D., SOUTARMIN, N., GAUME, L., ANTOINE, P., LANG, M., LAUTRIDOU, J.P., SOMME, J., ZÖLLER, L., LEMEUR, I., MEYNADIER, L., FONTUGNE M., WINTLE, A. (1994): Histoire du dernier cycle climatique enregistrée dans la séquence loessique d'Achenheim (Alsace, France), à partir de la susceptibilité magnétique. *Comptes rendus de l'Académie des Sciences Paris II* **319** 551–558.
- ROUSSEAU, D.D., KUKLA, G., ZÖLLER, L., HRADILOVA, J. (1998): Early Weichselian dust storm layer at Achenheim in Alsace, France. *Boreas* **27** 200–207.
- ROUSSEAU, D.D., WU, N.Q., GUO, Z.T. (2000): The terrestrial mollusks as new indices of the Asian paleomonsoons in the Chinese loess plateau. *Global and Planetary Change* **26** 199–206.
- ROUSSEAU, D. D., ANTOINE, P., HATTÉ, C., LANG, A., ZÖLLER, L., FONTUGNE, M., OTTMAN, B.D., LUCK, J.M., MOINE, O., LABONNE, M., BENTALEB, I., JOLLY, D. (2002): Abrupt millennial climatic changes from Nussloch (Germany) Upper Weichselian eolian records during the Last Glaciation. *Quaternary Science Reviews* **21** 1577–1582.
- RUDNER, E. & SÜMEGI, P. (2001): Recurring taiga forest steppe habitats in the Carpathian Basin in the Upper Weichselian. *Quaternary International* **76/77** 177–189.
- RUDDIMAN, W.F., RAYMO, M., MCINTYRE, A. (1986): Matuyama 41,000-year cycles: North Atlantic Ocean and northern hemisphere ice sheets. *Earth and Planetary Science Letters* **80** 117–129.
- RULL, V. (2010): On microrefugia and cryptic refugia. *Journal of Biogeography* **37** 1623–1625.
- SHACKLETON, N.J. (1977): The oxygen isotope stratigraphic record of the Late Pleistocene. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* **280** 169–182.
- SHACKLETON, N.J. & OPDYKE, N.D. (1973): Oxygen isotope and palaeomagnetic stratigraphy of Equatorial Pacific core V28-238: Oxygen isotope temperatures and ice volumes on a 10 5 year and 10 6 year scale. *Quaternary Research* **3** 39–55.
- SHACKLETON, N.J., HALL, M.A., LINE, J., SHUXI, C. (1983): Carbon isotope data in core V19-30 confirm reduced carbon dioxide concentration in the ice age atmosphere. *Nature* **306** 319–322.
- SHACKLETON, N.J., BACKMAN, J., ZIMMERMAN, H.T., KENT, D.V., HALL, M.A., ROBERTS, D.G., SCHNITKER, J.G., BALDAUF, A., DESPRAIRIES, R., HOMRIGHAUSEN, P., HUDDLESTON, J.B., KEENE, A.J., KALTENBACK, K.A.O., KRUMSIEK, M.A.C., MURRAY, J.W., WESTBERG-SMITH, J. (1984): Oxygen isotope calibration of the onset of ice-rafting and history of glaciation in the North Atlantic region. *Nature* **307** 620.
- SCHENKOVÁ, V. & HORSÁK, M. (2013): Refugial populations of *Vertigo lilljeborgi* and *V. genesii* (Vertiginidae): new isolated occurrences in

central Europe, ecology and distribution. *American Malacological Bulletin* **31** 323–330.

STAIKOU, A.E. (1999): Shell temperature, activity and resistance to desiccation in the polymorphic land snail *Cepaea vindobonensis*. *Journal of Molluscan Studies* **65** 171–184.

SKOFLEK, I. (1977): *Plant remains from the Vértesszőlős travertine*. Manuscript, Tata, 1–46.

SKOFLEK, I. (1990): Plant remains from the Vértesszőlős travertine. In: KRETZOI, M. & T. DOBOSI, V. eds., *Vértesszőlős: site, man and culture*. Akadémiai Kiadó, Budapest, 77–123.

SÓLYMOS, P. (1996): Ecological and biogeographical investigation of the recent mollusc fauna of Szársomlyó (S Hungary), southern side. *Malakológiai Tájékoztató* **15** 61–67.

SÓLYMOS, P., & NAGY, A. (1997): The recent mollusc fauna of the Szársomlyó (S Hungary): spatial pattern and microclimate. *Malakológiai Tájékoztató* **16** 35–42.

SÓLYMOS, P. & SÜMEGI P. (1999): The shell morpho-thermometer method and its application in palaeoclimatic reconstruction. *Annales Universitatis Scientiarum Budapestiensis, Sectio Geologica* **32** 137–148.

SÓLYMOS, P., SÜMEGI, P., DOMOKOS, T. (2002): A héj morfo-hőmérő módszer és alkalmazásai a paleoökológiában / The shell morpho-thermometer method and its uses in palaeoecology. *Földtani Közlemény* **132** 257–263.

SÓLYMOS, P. FARKAS, R., KEMENCEI, Z., PÁLL-GERGELY, B., VILISICS, F., NAGY, A., HORNUNG, E. (2009): Micro-habitat scale survey of land snails in dolines of the Alsó-hegy, Aggtelek National Park, Hungary. *Mollusca* **27** 167–171.

SULIKOWSKA-DROZD, A. & HORSÁK, M. (2007): Woodland mollusc communities along environmental gradients in the East Carpathians. *Biologia* **62** 201–209.

SULIKOWSKA-DROZD, A., MALTZ, T. K., KAPPES, H. (2013). Brooding in a temperate zone land snail: seasonal and regional patterns. *Contributions to Zoology* **82** 85–S1.

SÜMEGI, P. (1988): A lakiteleki téglagyári szelvény quartermalakológiai vizsgálata. *Malakológiai Tájékoztató* **8** 5–7.

SÜMEGI, P. (1989): *Hajdúság felső-pleisztocén fejlődéstörténete finomrétegtani (üledéktani, öslénytani, geokémiai) vizsgálatok alapján*. [Upper Pleistocene evaluation of Hajdúság region based on fine-stratigraphical (sedimentological, paleontological, geochemical) analyses]. Egyetemi doktori értekezés, University of Debrecen, Debrecen (Hungary), 1–96. (in Hungarian)

SÜMEGI P. (1990): Első adatok a nyírségi lápok pleisztocén végi kialakulásáról. *Calandrella* **4** 13–15.

SÜMEGI, P. (1996): *Az ÉK-magyarországi löszterületek összehasonlító ökoszisztémái és sztratifikai értékelése*. [Comparative paleoecological and stratigraphical valuation of the NE Hungarian loess areas] Kandidátusi (PhD) értekezés, Budapest – Debrecen, 1–120. (in Hungarian with English abstract)

SÜMEGI, P. (2005): *Loess and Upper Paleolithic environment in Hungary*. Aurea Kiadó, Nagykövácsi, 1–312.

SÜMEGI, P. (2007): *Magyarország negyedidőszak végi környezettörténete*. [Late Quaternary environmental history of Hungary] MTA Doktori Értekezés, Budapest – Szeged, 1–428. (in Hungarian with English abstract)

SÜMEGI, P. (2014): Modeling the relationship of the Upper Paleolithic communities and the environment of the Carpathian Basin during the Upper Würmian. pp. 319–340. In: T. BÍRÓ, K., MARKÓ, A., BAJNOK, P. eds., *Aeolian scripts new ideas on the lithic world studies in honour of Viola T. Dobosi*. Magyar Nemzeti Múzeum kiadványa, Budapest,

SÜMEGI, P. & KROLOPP, E. (1995): A magyarországi würm korú löszök képződésének paleoökológiai rekonstrukciója. *Földtani Közlemény* **124** 125–148.

SÜMEGI, P. & KROLOPP, E. (2002): Quaternary malacological analyses for modeling of the Upper Weichselian palaeoenvironmental changes in the Carpathian Basin. *Quaternary International* **91** 53–63.

SÜMEGI, P. & NÁFRÁDI, K. (2015): A radiocarbon, dated cave sequence and the Pleistocene/Holocene transition in Hungary. *Open Geosciences* **7** 783–798.

SÜMEGI P., MAGYARI E., DÁNIEL P., HERTELENDI E., RUDNER E. (1999): *A*

*kardoskúti Fehér-tó negyedidőszaki fejlődéstörténetének rekonstrukciója. Földtani Közlöny* **129** 479–519.

SÜMEGI, P., RUDNER, E., BESZEDA, I. (2000): Stratigraphical and palaeoecological investigation of the fossil soil comprising Upper Palaeolithic tools at Bodrogkeresztúr – Henye. In: T. DOBOSI, V. ed., *Bodrogkeresztúr – Henye (NE Hungary) Upper Palaeolithic site*. Magyar Nemzeti Múzeum, Budapest, 217–220.

SÜMEGI, P., SZŐÖR, GY., HERTELENDI, E. (1991): Palaeoenvironmental reconstruction of the last period of the Upper Würm in Hungary, based on malacological and radiocarbon data. *Soosiana* **19** 5–12.

SÜMEGI, P., KROLOPP, E., RUDNER, E. (2002): Negyedidőszak végi ökoszisztémái változások térben és időben a Kárpát-medencében. *Földtani Közlöny* **132** 5–22

SÜMEGI, P., PERSAITS, G., GULYÁS, S. (2012): 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, 17–57.

SÜMEGI, P., MAGYARI, E., DÁNIEL, P., MOLNÁR, M., TÖRŐCSIK, T. (2013a): 28,000-year record of environmental change in SE Hungary: terresrestrial response to Dansgaard-Oeshger cycles and Heinrich-events. *Quaternary International* **278** 34–50.

SÜMEGI, P., SZILÁGYI, G., GULYÁS, S., JAKAB, G., MOLNÁR, A. (2013b): The Late Quaternary Paleocology and Environmental History of the Hortobágy, an unique Mosaic Alkaline Steppe from the Heart of the Carpathian Basin, Central Europe. In: PRIETO, M.B.M & DIAZ, T.B. eds., *Steppe Ecosystems Biological Diversity, Management and Restoration*. Nova Publishers, New York, 165–194.

SÜMEGI, P., TÖRŐCSIK, T., NÁFRÁDI, K., SÜMEGI, B.P., MAJKUT, P., MOLNÁR, D., TAPODY, R.O. (2016): Radiocarbon dated complex paleoecological and geoarchaeological analyses at Bodrogkeresztúr – Henye Gravettian site (NE Hungary). *Archeometriai Műhely* **XIII/2** 35–45.

STEWART, J.R., LISTER, A.M., BARNES, I., DALÉN, L. (2010): Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society* **277** 661–671.

STEWART, J.R., & LISTER, A.M. (2001): Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution* **16** 608–613.

SVENSSON, A., ANDERSEN, K. K., BIGLER, M., CLAUSEN, H. B., DAHL-JENSEN, D., DAVIES, S. M., SIGFUS, J.J., MUSCHELER, R., RASUSSEN, S.O., RHÖTHLISBERGER, R., STEFFENSEN, J. P. & VINTHER, B.M. (2006): The Greenland ice core chronology 2005, 15–42ka. Part 2: comparison to other records. *Quaternary Science Reviews* **25** 3258–3267.

SZELEPCSÉNYI, Z., BREUER, H., SÜMEGI, P. (2014): The climate of Carpathian Region in the 20th century based on the original and modified Holdridge life zone system. *Central European Journal of Geosciences* **6** 293–307.

SZELEPCSÉNYI, Z., BREUER, H., KIS, A., PONGRÁCZ, R., SÜMEGI, P. (2016): Assessment of projected climate change in the Carpathian Reigon using the Holdridge life zone system. *Theoretical and Applied Climatology* **2016** 1–18.

SZŐÖR, GY., SÜMEGI, P., HERTELENDI, E. (1991a): Malacological and isotope geochemical methods for tracing Upper Quaternary climatic changes. In: PÉCSI, M. & SCHWEITZER, F. eds., *Quaternary environment in Hungary*. Akadémiai Kiadó, Budapest, 61–73.

SZŐÖR, G., SÜMEGI, P., BALÁZS, É. (1991b). Sedimentological and geochemical analysis of upper pleistocene paleosols of the Hajdúság region, NE Hungary. In: PÉCSI, M. & SCHWEITZER, F. eds., *Quaternary environment in Hungary*. Akadémiai Kiadó; Budapest, 47–59.

SZYBIAK, K., BŁOSZYK, J., KORALEWSKA-BATURA, E., GOLDYN, B. (2009): Small-scale distribution of wintering terrestrial snails in forest site: relation to habitat conditions. *Polish Journal of Ecology* **57** 525–535.

TARNOCAI, C. & SCHWEITZER, F. (1998): Cryogenic features in Canada and Hungary and their significance for past climate. *Geografia Fisica e Dinamica Quaternaria* **21** 87–92.

TERHORST, B., THIEL, C., PETICZKA, R., SPRAFKE, T., FRECHEN, M., FLADERER, F. A.,

- ROETZEL, R. NEUGEBAUER-MARESCH, C. (2011): Casting new light on the chronology of the loess/paleosol sequences in Lower Austria. *Eiszeitler & Gegenwart (Quaternary Science Journal)* **60** 270–277.
- TERHORST, B., KÜHN, P., DAMM, B., HAMBACH, U., MEYER-HEINTZE, S., SEDOV, S. (2014): Paleoenviromental fluctuations as recorded in the loess-paleosol sequence of the Upper Paleolithic site Krems-Wachtberg. *Quaternary International* **351** 67–82.
- VALENTINE, K.W.G. & DALRYMPLE, J. B. (1976): Quaternary buried paleosols: a critical review. *Quaternary Research* **6** 209–222.
- VELICHKO, A.A. (1990): Loess-paleosol formation on the Russian Plain. *Quaternary International* **7** 103–114.
- VERES, D., DAVIES, S. M., WOHLFARTH, B., PREUSSER, F., WASTEGÅRD, S., AMPEL, L., HORMES, A., POSSNERT, G., RAYNAL, J.-P. AND VERNET, G. (2008): Age, origin and significance of a new middle MIS 3 tephra horizon identified within a long-core sequence from Les Echets, France. *Boreas* **37** 434–443.
- VÉRTES, L. (1964/65): Das Jungpaläolithikum von Arka in Nord-Ungarn. *Quartär* **15/16** 79–132.
- VÉRTES, L. (1965): *Az őskőkor és az átmeneti kőkor emlékei Magyarországon*. Akadémiai Kiadó, Budapest, 1–385.
- VÉRTES, L. (1966): The Upper Palaeolithic site on Mt. Henye at Bodrogkeresztúr. *Acta Archeologica Academiae Scientiarum Hungaricae* **18** 3–14.
- VOELKER, A. H. (2002): Global distribution of centennial-scale records for Marine Isotope Stage (MIS) 3: a database. *Quaternary Science Reviews* **21** 1185–1212.
- VOELKER, A.H.L., SARNTHEIN, M., GROOTES, P.M., ERLINKREUSER, H., LAJ, C., MAZAUD, M., NADEAU, M.J., SLEICHER, M. (1998): Correlation of marine 14C ages from the Nordic seas with the GISP2 isotope record: implications for 14C calibration beyond 25 ka BP. *Radiocarbon* **40** 517–534.
- WÄREBORN, I. (1970): Environmental factors influencing the distribution of land molluscs of an oligotrophic area in southern Sweden. *Oikos* **20** 285–291.
- WELTER-SCHULTES, F.W. (2012): *European Non-Marine Molluscs, a Guide for Species Identification: Bestimmungsbuch für europäische Land-und Süßwassermollusken*. Planet Poster Editions, Göttingen, 1–674.
- WEST, R.G. (1984): Interglacial, interstadial and oxygen isotope stages. *Dissertationes Botanicae* **72** 345–357.
- WHITE, D., PREECE, R.C., SHCHETNIKOV, A.A., PARFITT, S.A., DLUSSKY, K.G. (2008): A Holocene molluscan succession from floodplain sediments of the upper Lena River (Lake Baikal region), Siberia. *Quaternary Science Reviews* **27** 962–987.
- WILLIS, K.J., SÜMEGI, P., BRAUN, M., TÓTH A. (1995): The Late Quaternary environmental history of Bátorliget, N.E. Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **118** 25–47.
- WILLIS, K.J., RUDNER, E., SÜMEGI, P. (2000): The full-glacial forests of central and southeastern Europe: Evidence from Hungarian palaeoecological records. *Quaternary Research* **53** 203–213.
- WOHLFARTH, B., VERES, D., AMPEL, L., LACOURSE, T., BLAAUW, M., PREUSSER, F., ANDRIEU-PONEL, V., KÉRAVIS, D., LALLIER-VERGÈS, E., BJÖRCK, S., DAVIES, S., DE BEAULIEU, J.L., RISBERG, J., HORMES, A., KASPER, H.U., POSSNERT, G., REILLE, M., THOUVENY, N., ZANDER, A. (2008): Rapid ecosystem response to abrupt climate changes during the last glacial period in western Europe, 40–16 ka. *Geology* **36** 407–410.
- WU, N., LI, F., ROUSSEAU, D. D. (2018): Terrestrial mollusk records from Chinese loess sequences and changes in the East Asian monsoonal environment. *Journal of Asian Earth Sciences* **155** 35–48.
- ZAGWIJN, W.H. (1961): Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. Part I: Eemian and Early Weichselian. *Mededelingen Geologische Stichting* **14** 15–45.
- ZAGWIJN, W.H. (1974): Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. Part II: Middle Weichselian. *Mededelingen Rijks Geologische Dienst* **25** 101–111.
- ZÖLLER, L., OCHES, E. A., MCCOY, W.D. (1994): Towards a revised chronostratigraphy of

loess in Austria with respect to key sections in the Czech Republic and in Hungary. *Quaternary Science Reviews* **13** 465–472.