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 Sümegi (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 rekonstruálására. 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 rekonstruálásában. Az egyes szárazföldi csiga fajok recens elterjedése, a fauna összetétele, dominanciaviszonyai alapján készített, nemzetközi szinten is újnak számító paleoklimatológiai rekonstrukciós modellt, az ún. "malako-hőmérő"-t Sümegi (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 bio-indikációs 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 perifériáin 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, FELSŐ 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; Rassmussen 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; Rousseu 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; Szöőr 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 & Grant1976; 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; Sümegi 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; Sümegi 1989, 1996, 2005, 2007; Sümegi 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 (Domokos1982). 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; Sümegi 1989, 1996, 2005, 2007; Sümegi 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 (Sümegi 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 (Sümegi 1989, 1996, 2005, 2007; Sümegi 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 (Sümegi 1989, 1996, 2005, 2007; Sümegi et al. 1991). This is, however, rather problematic in several ways (Sümegi 1989, 1996, 2005, 2007; Sümegi 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 & Sümegi 1987; Sümegi et al. 1991; Sólymos1996; Sólymos & Nagy 1997; Sólymos & Sümegi 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; Sümegi 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 (Sümegi 1989, 1996, 2005, 2007; Sümegi et al. 1991). These measurements, presently going on and likely to continue in the fitotron (or more precisely in the malacotron: Sümegi 1989, 1996, 2005, 2007) will hopefully help us to make our model more accurate and realistic (Sümegi 1989, 1996, 2005, 2007; Sümegi et al. 1991).

On the other hand, the terrestrial mollusc faunas are also well-suited (Sümegi 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 (Sümegi 1989, 1996, 2005, 2007; Sümegi 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
Succinea oblonga	13-19 °C	16 °C
Columella edentula	10-20 °C	15 °C
Columella columella	5-15 °C	10 °C
Vertigo genesii	5-15 °C	10 °C
Vertigo modesta	5-15 °C	10 °C
Pupilla muscorum	10-22 °C	16 °C
Pupilla triplicata	16-24 °C	20 °C
Pupilla sterri	5.5-16.5 °C	11 °C
Vallonia costata	10-24 °C	17 °C
Vallonia tenuilabris	4-14 °C	9 °C
Granaria frumentum	17-26 °C	21.5 °C
Clausilia dubia	12-20 °C	16 °C
Punctum pygmaeum	9-22 °C	15 °C
Vitrea crystallina	11-21 °C	16 °C
Trichia hispida	10-20 °C	15 °C
Cepaea vindobonensis	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 (Sümegi 1989, 1996, 2005, 2007 Sümegi 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 (Sümegi 1989).

Initially, the activation temperatures for the hottest month (July) of the growth season were determined for 8 species (Sümegi 1989, 1996, 2005, 2007). This was later on extended to 16 species to meet the requests of fellow researchers (Sümegi 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 ºC 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 ºC 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; Horsak 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 (Sümegi 1996, 2005, 2007; Sümegi 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; Horsak 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. tenulabris* 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 (Sümegi 1989, 1996, 2005, 2007; Sümegi 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*is 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 ºC (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; Juřičková & 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; Juřičková & 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 & Sümegi 1995; Sümegi 1989, 1996, 2005, 2007; Sümegi & 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 & Sümegi 1993; Sümegi 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 ore 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; Fűköh & Domokos 1984, 1986; Magni 1993; Sólymos & Sümegi 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 (Sümegi 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 (Sümegi 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 (Sümegi 1989, 1996)

2. táblázat: Az egykori júliusi középhőmérséklet meghatározása malakohőmérő módszerével (Sümegi 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 estamination

T = Estaminated 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; Rassmussen 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; Szöőr 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 & Sümegi 1992, 1995; Sümegi 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 (Sümegi & Krolopp 1995, 2002; Sümegi 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; Szelepcsény 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 & Sümegi 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-Oschger (D-O) or Greenland (GI) interstadial 05 and 04 horizons (Bond et al. 1992, 1993, 1999) which evolved together (Sümegi et al. 2019) some places in the Carpathian Basin. The Carpathian Basin must have populated spruce open woodlands (open parkland type) containing thermos-mesophilous arboreal elements (*Carpinus* – hornbeam, *Salix* – willow, *Alnus* – alder, *Betula* – birch, *Pinus sylvestris* – Norway pine and possibly *Corylus* – hazelnut, *Tilia* – elm, *Quercus* – oak) as well (Sümegi 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; Szöőr 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; Fábián et al. 1998, 2000; Kovács et al. 2007; Obreht 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; Fábián et al. 1998, 2000; Kovács et al. 2007; Obreht 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 $15\pm1\ ^{o}C$ (Sümegi et al. 2019). Based on the distribution data of molluscs (Sümegi et al. 2019) low growing season and low winter temperatures (between $-6^{o}C$ and $-17\ ^{o}C$) 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-termophilous 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 (Sümegi 1989, 1996, 2005; Sümegi & Krolopp 1995, 2002), anthracological (Rudner & Sümegi 2001), and palynological investigations of the Upper Würmian (MIS2) profiles in the Carpathian Basin (Sümegi 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 eurytpic, hygrophilous, shade-loving forms requiring larger vegetation cover and inhabiting the modern boreal woodlands as well (*Clausilia dubia, Perofratella bidenetata, Arianta arbustorum, Discus ruderatus*). 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: Sümegi 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 malaco-thermometer 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 malaco-thermometer 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 ruderatus* 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 ruderatus, Mastus venerabilis, Semilimax semilimax, S. kotulai, Vitrina pellucida, Vestia turgida, Arianta arbostrum*), 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 (Sümegi 1989, 1996, 2005, 2007; Sümegi 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: Sümegi 2005) or Bükk Mountain (Sümegi & 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 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±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 ± 1 ^{o}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 (Sümegi 1988). According to the results of detailed chronological and paleontological studies (Sümegi 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 (Sümegi 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.**).

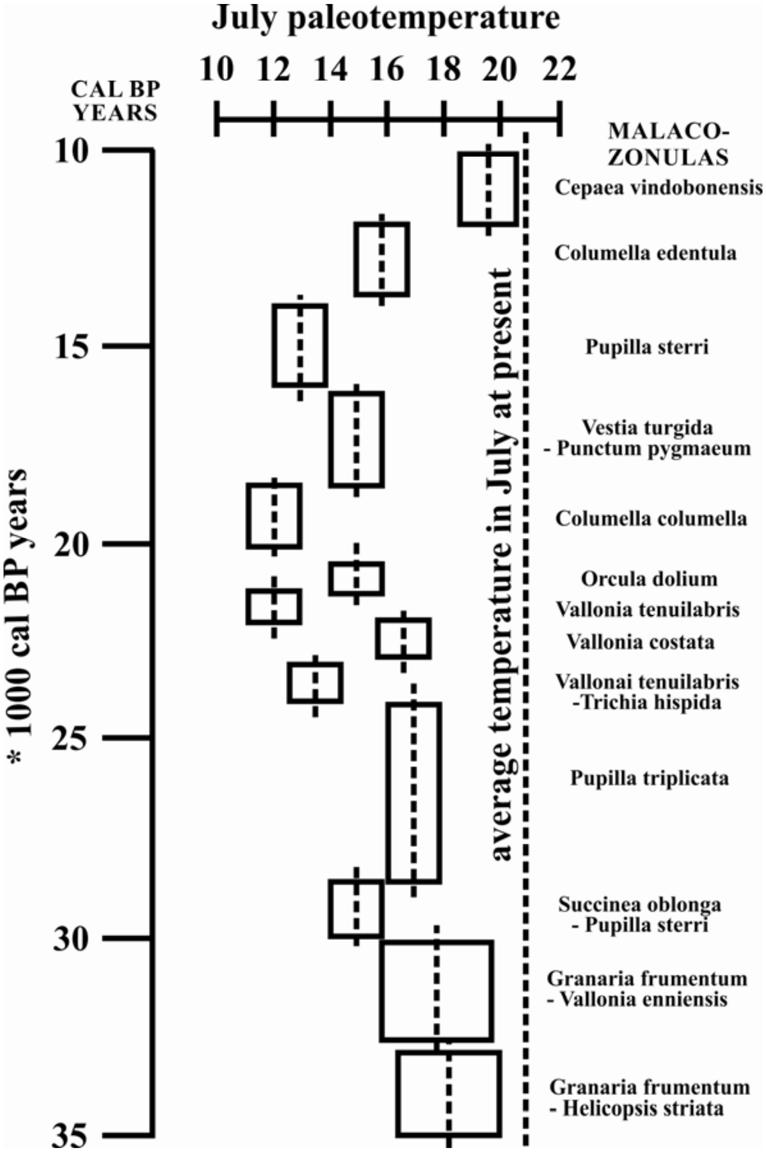

Fig. 1.:

Malacothermometer reconstructed July paletemperature 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 középhőméséklet 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; Rassmussen 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 (Sümegi 2005, 2011; Sümegi 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 & Sümegi, 1992, 1995; Sümegi 2011).For this time interval according to malaco-thermometer method (Sümegi, 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 (Sümegi & Krolopp 1995, 2002; Sümegi 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 °C and -10 °C and annual temperatures between +6 °C and +9 °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 ± 1 °C in this phase (Sümegi et al. 2019). Based on mollusc distribution data (Sümegi et al. 2019) low growing season and low winter temperatures (between -7 °C and -17 °C) prevailed. In addition, annual temperatures were likewise very low (between +5 °C to +7 °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 °C) and drier conditions (Sümegi 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 (Sümegi 2014). This burnt horizon is overlain by loess again. However, the loess and the underlying paleosol tend to be interfingered 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: Sümegi 1989). Mean July paleo-temperatures changed to 17 °C ± 1 °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 °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±1 °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 °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±1 °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 pseudosubstiata*). 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; Szöőr 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 ^{o}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 ± 1 ^{o}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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