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Stable isotopes of Upper Weichselian land snails from Lakitelek (Hungary): a contribution to understanding the climatic context of the Upper Palaeolithic of the Hungarian basin

Alexander Verpoorte, Simon Troelstra, Kay Beets and Pál Sümegi

The occupation history of the Hungarian basin between 30,000 and 15,000 ^{14}C yr BP is important for understanding the refugia during the last glacial maximum and the subsequent recolonization of the mid-latitudes of Europe. The stable isotope record from land snail shells is reported here as a pilot study of its contribution to our knowledge of the ecological conditions in this period. Land snail shells from the Lakitelek section in Hungary cover the period of 11,000 to 30,000 ^{14}C yr BP. Values for $\delta^{13}C$ and $\delta^{18}O$ have been measured for Pupilla muscorum specimens from 18 separate layers. Average $\delta^{13}C$ values range from -5.9 to -10.2‰. Though there is no clear long-term trend, two distinct peaks with depleted values are present, suggesting periods of increase in C_3 vegetation. Average $\delta^{18}O$ values range from -1.8 to -5.4‰. The weak cyclic pattern in the data can be explained by a time lag between temperature and relative humidity effects. The stable isotope data do not correspond in a consistent manner with the main ecological trends based on land snail assemblage composition.

1 INTRODUCTION

The climatic downturn of the last glacial maximum (LGM) had a clear impact on the human settlement history of Europe. The initial expansion of early modern humans from about 35 ka BP onwards into northern latitudes stopped and human populations started to retreat into refugia in southwestern Europe, the Mediterranean and the southern Balkans. The impact of global climatic change on the timing and extent of the range contraction differs from region to region. The settlement history of the Hungarian basin shows a distinct pattern for this period (Otte 1998; Dobosi 2000; Verpoorte 2004; 2009; Lengyel 2009). Only a few sites are known for the period preceding the last glacial maximum. The main occupation phase is dated between 21 and 17 ka BP, when settlement of regions north of the Hungarian basin was sparse and widely dispersed. The current evidence suggests that the basin was deserted shortly after 17 ka BP. Recolonization took place around 13 ka BP with the onset of climatic amelioration in the Late Glacial.

The paleoenvironment of pleniglacial Hungary is mainly known from detailed malacological and anthracological studies (Krolopp and Sümegi 1995; Willis *et al*. 2000; Rudner and Sümegi 2001; Sümegi and Krolopp 2002). In this paper we report on a stable isotope record of land snail shells from Lakitelek brickyard to enhance our understanding of the environmental conditions in the Hungarian basin.

2 CLIMATE, STABLE ISOTOPES AND SNAIL SHELLS

Stable isotope studies of land snail shells can contribute to our understanding of the local climatic conditions (Goodfriend 1992; 1999; Bonadonna *et al*. 1999; Goodfriend and Ellis 2000; Balakrishnan and Yapp 2004; Balakrishnan *et al*. 2005b; Zanchetta *et al*. 2005; Beets *et al*. 2006; Colonese *et al*. 2007; 2010; Yanes *et al*. 2011). The snail shell aragonite is primarily derived from amino acids from the diet of the snail. Shell formation takes place only when the snail is active. The active period depends on moisture and temperature. Most land snails are active during or after rain events and at temperatures between 10 and 27 ºC, most likely late spring and summer conditions (Balakrishnan *et al*. 2005). The stable oxygen and carbon isotopes of the snail shell reflect local conditions during these active periods.

The relationship between climatic conditions and stable isotope composition is not straightforward, but mediated by snail activity. Stable carbon isotopes have been shown to depend predominantly on the plant diet derived from the local vegetation combined with atmospheric carbon dioxide and physiological effects (Goodfriend and Ellis 2000; Liu *et al*. 2007). The isotopic composition of the vegetation differs mainly according to the photosynthetic pathway utilized by the plants. Plants with C3 photosynthetic pathways, mainly trees and forbs (Ehleringer *et al*. 1997), have average $\delta^{13}C$ values of -27‰, whereas C4 plants, in particular grasses, have characteristic values of about -13‰. In addition, snails eat dead and decaying plant material which has an offset of 0-3‰ (Liu *et al*. 2007).

The interpretation of stable oxygen isotopes is more complicated. Zanchetta *et al*. (2005) found a fairly good relationship between oxygen isotopic composition of local rainfall and living land snail shells in Italy. However, the relationship does not apply under arid conditions (Zanchetta *et al*. 2005, 31). Balakrishnan *et al*. (2005) argue that the shell $\delta^{18}O$ values are controlled by a combination of local temperature, relative humidity and the isotopic composition of available water (local rainfall and ambient water vapour). Kehrwald *et al*. (2010) have used $\delta^{18}O$ values to gain insight into the source and trajectory of precipitation in modern and LGM Europe. Changes in stable oxygen isotopes seem to depend on at least two climatically relevant parameters.

3 Materials and methods

3.1 Location

The Lakitelek brickyard (46°50’N, 20°E) is located near the Tisza river in the Tisza-Danube interfluvial zone in the southern part of the Hungarian basin. The samples were taken from section No 1 in 1985 by P. Sümégi. Lakitelek I is the type section for two biozones of molluscan assemblages: the mild and humid Vallonia costata zonule and the cold Pupilla sterri zonule. Average annual rainfall in the area is about 560 mm with the peak in precipitation in June. Average monthly temperatures vary from a minimum of -1.4 °C in January to a maximum of 21.2 °C in July (fig. 1).

3.2 Lithology

The section has a depth of 6 metres below the surface. The sequence consists of floodplain sediments of the Tisza at the base. The fluvial sediment is covered with wind-blown sands (3.80-5.80 m) in which two paleosols have developed. Loesses were deposited on top of the wind-blown sands. The basal part (3.20-3.80 m) of the loess sequence contains more clay than the upper part. The basal and upper parts of the loess are separated by a calcareous, clayey horizon (3.00-3.20 m) with *Pinus sylvestris* charcoals and *Microtus arvalis* teeth. The upper 0.60 m of the section consists of wind-blown sand in which a Holocene soil has developed.

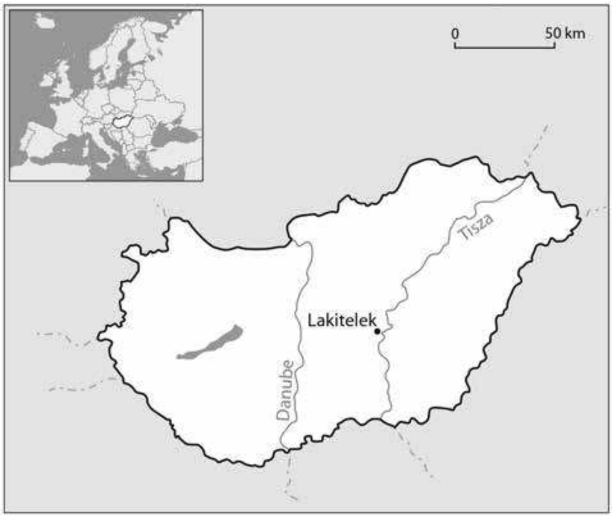

Figure 1 Location of the Lakitelek section in the Tisza Danube interfluvial zone.

3.3 Chronology

The sequence is dated by a series of five ^{14}C dates and dated between 30 and 11 ka ^{14}C yr BP (table 1). Age resolution for layers of 20 cm is estimated at about 1000 years.

3.4 Samples

The sequence was sampled for molluscs in layers of 20 cm from 0.60 m to 4.20 m depth below surface (fig. 2: see Krolopp and Sümegi 1995 and Sümegi 2005 for a description of the methodology and interpretation of molluscan faunas). For the measurements of stable isotopes of oxygen and carbon, we selected specimens from the species *Pupilla muscorum* Linnaeus 1758 that occurred throughout the section.

Pupilla muscorum is a holarctic, highly tolerant species. Its temperature resistance range is between 10 and 22 °C, with the optimum at 16 °C. The species prefers dry meadows and open, exposed, chalky locations. It lives of plant material and dead organic matter. The snail has a short lifespan of one or two summers. We assume that the fossil snails have similar feeding habits as living snails. We also assume that the isotope signal of *Pupilla muscorum* represents most of the variety of local conditions and provides an average of the wider ‘neighbourhood’ and that the species bias to local conditions is limited.

For a pilot project, one well-preserved specimen per layer was measured, giving eighteen data-points between 0.60 m and 4.20 m below surface. After this pilot, we measured four to five individual shells per level in a series of 18 layers from 0.60 to 4.20 m below surface, with a total of 88 samples (table 2). Only complete shells were selected for the analysis, when available from the layer. One local, modern specimen was measured as a reference.

3.5 Measurements

The selected shells were individually crushed first and then cleaned by repeated ultrasonification in distilled water and ethanol before stable isotope analysis. The entire shell was grounded to average changes in diet and physiology during its lifetime. Oxygen and carbon isotopes were measured on a Finnigan GasBench II. All values are expressed as per mille PDB.

4 Results

The $\delta^{13}C$ and $\delta^{18}O$ results for all samples and all layers are presented in appendix 1.

There is no correlation between carbon and oxygen isotopes of individual samples (fig. 3). The average values per layer are only weakly correlated (fig. 4). The values for layer 1, 12, 13 and 18 clearly differ from the main cluster of values.

4.1 Stable carbon isotopes (figs 5 and 6)

$\delta^{13}C$ values of individual shells range from a maximum of -5.9‰ to a minimum of -10.2‰. This is about three-fold the

Depth (m)	Lab no.	14C Age (yr BP)	δ^{13}C ‰	Cal BP(95.4% prob)
0.60-0.80	DEB-1092	11,770 ± 250	-6.05	14470-13100
1.40-1.60	DEB-1075	14,840 ± 300	-8.41	18650-17250
2.20-2.40	DEB-1562	16,720 ± 200	-7.45	20300-19450
3.00-3.20	DEB-1536	21,940 ± 400	-7.99	27690-25220
5.80-6.00	DEB-1095	30,000 ± 550	-8.49	36240-33300

Table 1 Radiocarbon dates on shells for Lakitelek (Krolopp and Sümegi 1995; δ^{13}C-data from Hertelendi *et al*. 1992). Calibration using OxCal4.1 with IntCal09 (Bronk Ramsey 2009).

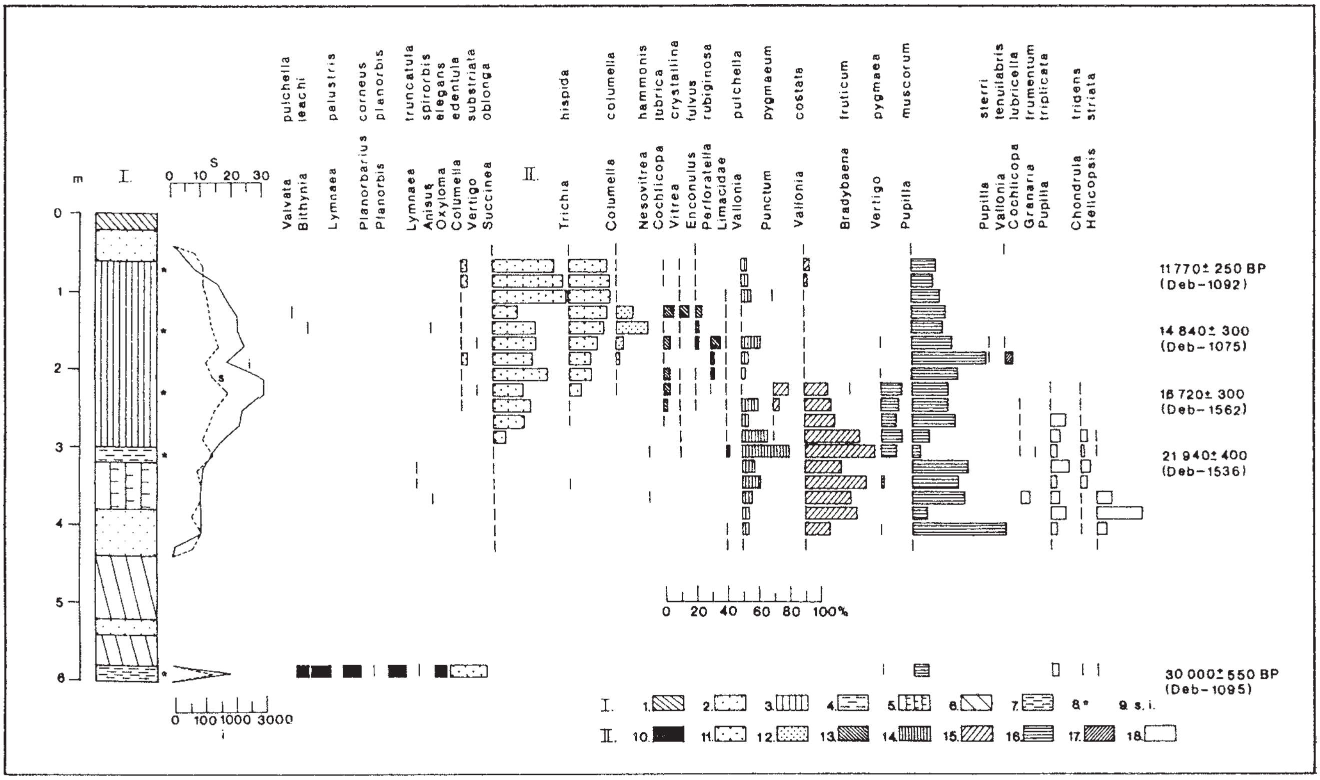

Figure 2 Molluscan faunal composition of Lakitelek (after Krolopp and Sümegi 1995)

I Lithology: 1 Holocene soil, 2 wind-blown sand, 3 loess, 4 humic horizon, 5 clayey loess, 6 soil horizon, 7 floodplain sediments, 8 radiocarbon samples, 9 s = number of species; i = number of individuals.

II Molluscan ecological groups: 10 aquatic species, 11 cold tolerant, hygrophilous species preferring open habitats, 12 frigophilous, hygrophilous species preferring open habitats, 13 highly tolerant, subhygrophilous species preferring transitional zones between open and closed vegetation, 14 subhygrophilous species preferring milder climate and transitional zones between open and closed vegetation, 15 highly tolerant, mesophilous species living in transitional zones between open and closed vegetation, 16 highly tolerant, mesophilous species preferring open areas, 17 frigophilous, aridity tolerant species preferring open habitats, 18 xerophilous species preferring milder climate living in open steppic environments.

average range of 1.3‰ within the layers. The range within layers varies between 0.6‰ and 3.7‰. Ranges of over 2‰ are found for layers with one or two outliers (layers 8, 13 and 16). Average values per layer range from -6.7‰ to -9.8‰. Standard errors for the layers average 0.5‰.

There is no clear trend in the data. Only two layers stand out with exceptionally depleted values: layer 12 has a value of -9.1±0.65‰ and layer 18 has a value of -9.8±0.5‰. Two layers have slightly enriched average values: layer 7 (-6.8±0.25‰) and layer 16 (-6.8±0.4‰, dismissing the outlier value of sample 16-05).

4.2 *Stable oxygen isotopes* (figs 7 and 8)

The values for δ^{18}O range between –1.8‰ and –5.4‰. The range of values within layers varies between 0.7‰ and 2.9‰, with an average of 1.8‰. The range of values within

Layer	Depth (m)	N	Comments
1	0.6-0.8	2+3 fragments	layer with fragmented shells, only two complete P.m. shells
2	0.8-1.0	4	
3	1.0-1.2	5	
4	1.2-1.4	5	
5	1.4-1.6	5	
6	1.6-1.8	5	
7	1.8-2.0	5	
8	2.0-2.2	5	
9	2.2-2.4	5	
10	2.4-2.6	4	
11	2.6-2.8	5	
12	2.8-3.0	5	
13	3.0-3.2	3+2 fragments	13.4 blue/grey colour, layer with fragmented shells
14	3.2-3.4	5	
15	3.4-3.6	5	
16	3.6-3.8	5	16.2 reddish/brown stains, 16.5 small shell
17	3.8-4.0	5	17.3 greenish stains
18	4.0-4.2	5	

Table 2 Sample information and number of samples per layer.

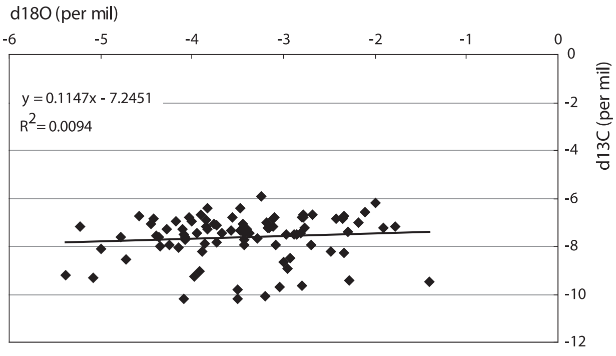

Figure 3 All individual datapoints for carbon and oxygen stable isotopes.

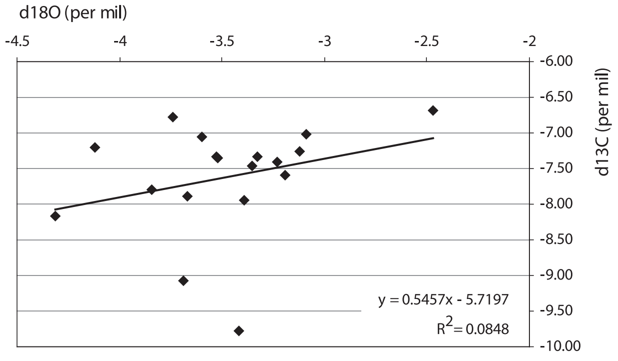

Figure 4 Average values for carbon and oxygen isotopes for each layer.

layers is half of the range in all $\delta^{18}O$ data. Average values per layer range from -2.5‰ to -4.3‰. The average standard deviation is 0.70. Layers 13 and 15 have relatively depleted average values, whereas layer 1 is relatively enriched in ^{18}O. There are no clear long-term trends in the data. However, the average values for layers 12 to 2 display a weak cyclic pattern. The values vary between more depleted values of c. -3.7‰ in layer 2, 7 and 11 and enriched values of c. -3.1‰ in layers 5 and 9. The layers 12 to 2 consist of eolian loess deposits.

5 INTERPRETATION AND DISCUSSION

5.1 Sampling and taphonomic effects

The samples derive from 20 cm levels and clearly are time-averaged samples to some degree. Two layers contain additional indications for a mixed assemblage of shells. Layers 1 and 13 consist mainly of fragmented shells; there were not sufficient complete shells available for 5 samples. This may explain the outlying average values for $\delta^{13}C$ and $\delta^{18}O$ for these two layers. Layer 1 is located immediately below the coversand with the Holocene soil. It probably

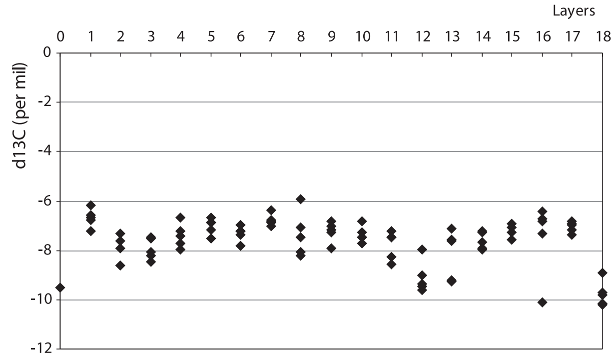

Figure 5 Carbon isotope values for all layers (0 denotes 'modern' value for comparison).

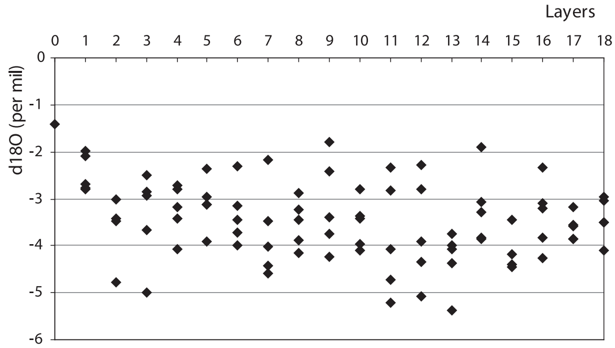

Figure 7 Oxygen isotope values for all layers (0 denotes 'modern' value for comparison).

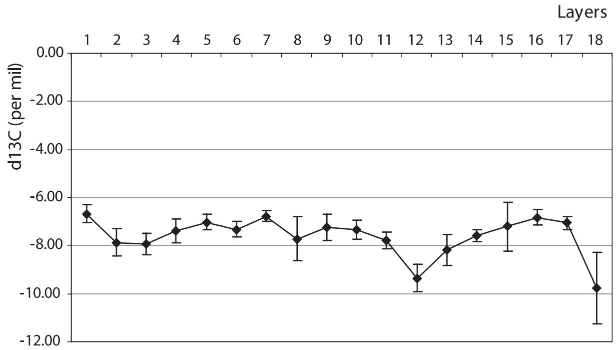

Figure 6 Average carbon isotope values with one standard deviation for all layers.

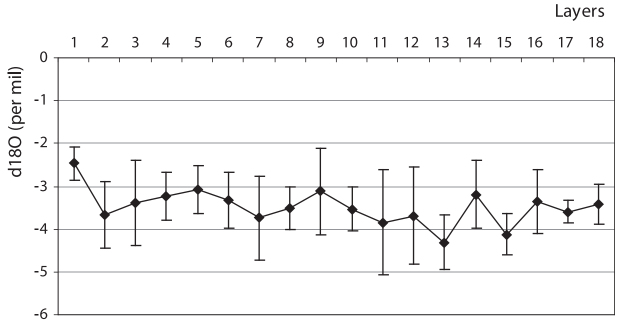

Figure 8 Average oxygen isotope values with one standard deviation for all layers.

consists of mixed material from the late glacial to Holocene transition, with a wide range of potential values for both carbon and oxygen.

Layer 13 is a humic horizon formed in the top of clayey loess dated to 21940±400 BP (DEB-1536). The five measured shells clearly fall into two groups. The two lower values of about -9.2‰ correspond with the values for layer 12 on top, whereas the three higher values of about -7.5‰ correspond with the values for the underlying layer 14. These results also affect the reliability of the radiocarbon date. It is not clear whether it dates the overlying eolian loess or the formation of a weak soil or the underlying clayey loess.

One other $\delta^{13}C$ outlier could be due to taphonomic processes. The value of sample 16-05 is -10.1‰, deviating more than 3‰ from the average for the remaining four samples (-6.8±0.4‰). Sample 16-05 was measured on a relative small shell, that could be intrusive, perhaps from the lowest layer 18.

There is no correlation between stable isotope values and the proportion of *Pupilla muscorum* in the molluscan fauna. There is also no significant difference in values between the three lithological units loess, clayey loess and coversand.

5.2 *Variation in the Pleistocene $\delta^{13}C$ and $\delta^{18}O$ values*

Stable carbon and oxygen isotope values were measured for 88 samples from Lakitelek. The $\delta^{13}C$ values range between -5.9 and -10.2‰. In a previous study on the quaternary paleoclimate in Hungary, Hertelendi *et al.* (1992) reported $\delta^{13}C$ values measured on shell samples for radiocarbon dating (fig. 9). The Pleistocene values range between -10.8‰ and -6.1‰. No other shell data for Central Europe are available at present. From a more southern location, Colonese *et al.* (2007) reports $\delta^{13}C$ values from late glacial levels (12.5-11 ka BP) in the Grotta del Romito in southern Italy. The values are measured on two different species. The specimens of *Discus rotundatus* have values between -12.1‰ and -7.5‰. The few values for *Helix* cf. *ligata* vary from -9.6‰ to -8.7‰. Late glacial data on *Vallonia* sp. shells from Folsom (New Mexico, USA) range from -13.7 to -8.2‰ (Balakrishnan *et al.* 2005a). The current data from Lakitelek are in good accordance with the previous data from Hungary. Relative to the data from late glacial southern Italy and New Mexico, the Lakitelek values are slightly higher.

The $\delta^{18}O$ values for Lakitelek range between –1.8‰ and –5.4‰. Shell data for the LGM of Hungary range from

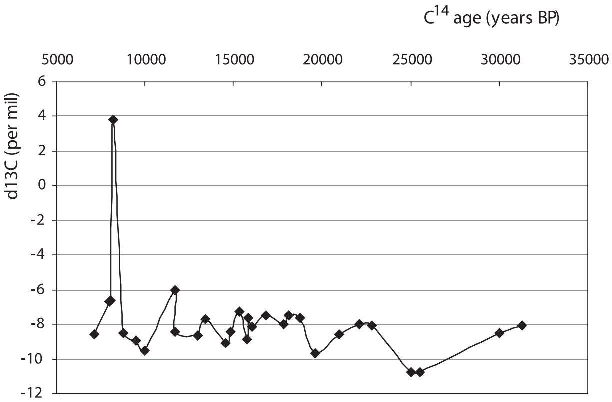

Figure 9 Published carbon isotope values against radiocarbon years as reported in Hertelendi *et al*. (1992) (note the low values at 25 ka BP, similar to layer 18 in Lakitelek).

-1.50‰ to -7.17‰ (Kehrwald *et al*. 2010). The values for Lakitelek are generally consistent with these data.

5.3 *Interpretation of stable carbon isotopes*

The range of $\delta^{13}C$ values between -5.9 and -10.2‰ corresponds to dietary values of approximately -18‰ to -22‰ (based on a constant offset of 12‰). The values indicate a dominantly C3 vegetation. Two clear peaks in layers 12 and 18 of depleted values of -9‰ could indicate two phases of increased dominance of C3 vegetation in the snail diet during its active period averaged over about one millennium. The layers 7 and 16 with enriched values of -6.8‰ could indicate an admixture of local C4 vegetation.

However, these interpretations are not consistently supported by the other evidence.

Layer 12 is dated to about 21 ka BP (circa 26000 cal BP). It is located just above the humic horizon of layer 13 correlated with the h2-initial soil of the Hungarian loess stratigraphy. The humic horizon is associated with a molluscan assemblage typical of the Vallonia costata zonule that signals a mild and relatively humid environment. It corresponds with a peak in molluscan species with a preference for the transitional ecozone between open and closed vegetation.

This correspondence is not the case for layer 18. Layer 18 must be older than 22 ka BP and younger than 30 ka BP. The sediment consists of coversand. There is no indication of soil formation associated with the layer and there is no distinct increase in species associated with more closed environments.

Layer 7, dated between 14.8 and 16.7 ka BP, is associated with the Pupilla sterri zonule. The faunal assemblage contains species that prefer open habitats and are adapted to cold and dry conditions. It is correlated with the Older Dryas. However, layer 16, with an age between 22 ka and 30 ka BP, is associated with a snail assemblage containing species of both open and more closed vegetation.

Several other proxies indicate a general shift in the environment from more closed to more open habitats around 16-17 ka BP. In Lakitelek, snail species of the transitional zone between open and closed vegetation such as *Vallonia costata* are well represented in the lower layers 18 to 9. Species that prefer open habitats such as *Succinea oblonga* and *Trichia hispida* are dominant in the layers 8 to 1. Charcoal data from the entire Hungarian basin (Willis *et al*. 2000; Sümegí and Rudner 2001) suggest a similar change. They indicate the presence of coniferous trees such as *Pinus* and *Picea* sp. in the Hungarian basin under glacial conditions. Dates range from 32 ka to 16.5 ka BP, but the charcoal evidence is absent for the period after 16.5 ka BP until the Late Glacial. This general change in vegetation is, however, not reflected in $\delta^{13}C$ values. The average value for layers 18 to 9 is -7.9 ± 1.1‰, whereas the average for layers 8 to 1 is -7.3 ± 0.6‰. The peak values in layers 7, 12, 16 and 18 are not correlated with vegetation changes (as reflected in snail species) in a consistent manner either. It suggests that the $\delta^{13}C$ record from Lakitelek reflects variation in diet of *Pupilla muscorum* in the local environment near the meandering and/or braiding Tisza river, rather than regional vegetational changes in the Hungarian plain.

5.4 *Stable oxygen isotopes*

The $\delta^{18}O$ values for Lakitelek range between –1.8‰ and –5.4‰. There are no clear long-term trends or distinct peaks in the data. The range of values is large throughout the section. It can indicate seasonal fluctuations in temperature and/or precipitation. Following Balakrishnan *et al*. (2005), snail shell $\delta^{18}O$ values are dependent on a combination of temperature, isotopic composition of rainfall and relative humidity. The composition of the land snail assemblage provides independent information of trends in temperature and humidity in the Lakitelek sequence. Species like *Vallonia costata* prefer moister conditions, whereas other species like *Pupilla triplicata* are highly aridity tolerant. The composition of the fauna in Lakitelek shifts around layer 11 from a dominance of mesophyl and arid tolerant species in the lower layers to a dominance of hygrophyl and subhygrophyl species in the upper part. There is no evidence in the $\delta^{18}O$ values that reflects this shift in local humidity.

The temperature tolerance of the species suggests that the shift in humidity is accompanied by a shift from milder to colder climatic conditions. The increase of *Columella columella* and *Pupilla sterri* indicates very cold conditions in layers 7 to 5. $\delta^{18}O$ values for layers 5 and 6 are relatively high (-3.1‰ and -3.3‰), but layer 7 has a low value of -3.7‰. *Vertigo pygmaea* and *Vallonia pulchella* indicate relatively mild conditions in layers 13 to 9. The corresponding $\delta^{18}O$ values for layers 13 to 10 are relatively low (-4.3‰ to -3.5‰), but the average for layer 9 is relatively high (-3.1‰).

One explanation for the lack of change in average $\delta^{18}O$ values, despite changes in temperature and humidity reflected in the molluscan fauna, is that the effects of a decrease in temperature and an increase in relative humidity and/or rainfall on the $\delta^{18}O$ values are counterbalanced (Balakrishnan *et al*. 2005).

Kehrwald *et al*. (2010) demonstrate a gradient with $\delta^{18}O$ declining towards the ENE in LGM land-snail shell data. They interpret the gradient to indicate a mid-latitude Atlantic source for the rainwater in Europe. Their data from Hungary and Serbia show another gradient. Here, $\delta^{18}O$ decreases in a northward direction, implying a Mediterranean source of precipitation. This is consistent with a southward displacement of the North Atlantic Drift during the last glacial maximum. Our Lakitelek data fit well within this pattern.

6 CONCLUSION

The record of $\delta^{13}C$ and $\delta^{18}O$ values of *Pupilla muscorum* shells from the Lakitelek section covers the period from 11,000 up to 30,000 ^{14}C yr BP. This period is poorly represented in environmental datasets from Central Europe such as pollen records or speleothems (e.g. Constantin *et al*. 2007). However, the climatic signal of the stable isotope values is complicated. A comparison with environmental trends, as reflected in the composition of the land snails, shows that the main shifts in local and regional vegetation, temperature and moisture regime are not reflected in the $\delta^{13}C$ and $\delta^{18}O$ values. The peaks in the average values for both stable isotopes are also not consistently associated with specific molluscan indicators of open/closed vegetation, temperature or moisture. The variation in $\delta^{13}C$ values is interpreted as local variation within the vegetation zone exploited by *Pupilla muscorum* rather than regional patterns of vegetation change. The $\delta^{18}O$ values hardly change over time in the Hungarian basin, but the values are consistent with a Mediterranean source for precipitation and a southward displacement of the North Atlantic Drift determining the climatic and environmental conditions in the Hungarian basin.

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Appendix

Supplementary material
Individual data for the samples from Lakitelek, Hungary

Identifier	^{13}C			^{18}O		
		Average	**s.d.**		**Average**	**s.d.**
ek/01-01	-6.18			-1.99		
ek/01-02	-6.55			-2.10		
ek/01-03	-6.79			-2.79		
ek/01-04	-7.21			-2.77		
ek/01-05	-6.68			-2.68		
layer 1		**-6.68**	**0.37**		**-2.47**	**0.39**
EK-2.2	-8.64			-3.00		
ek/02-03	-7.61			-4.78		
ek/02-04	-7.32			-3.47		
ek/02-05	-7.94			-3.42		
layer 2		**-7.88**	**0.57**		**-3.67**	**0.77**
ek/03-01	-7.52			-2.86		
ek/03-02	-7.48			-3.67		
EK-3.3	-8.09			-4.99		
ek/03-04	-8.19			-2.49		
ek/03-05	-8.48			-2.93		
layer 3		**-7.95**	**0.44**		**-3.39**	**0.99**
ek/04-01	-7.70			-4.07		
EK-4.2	-7.23			-3.18		
EK-4.3	-7.43			-3.43		
ek/04-04	-6.66			-2.78		
ek/04-05	-7.97			-2.70		
layer 4		**-7.40**	**0.50**		**-3.23**	**0.55**
ek/05-01	-7.51			-2.97		
ek/05-02	-6.86			-3.12		
EK-5.3	-7.17			-3.11		
ek/05-04	-6.69			-3.91		
ek/05-05	-6.86			-2.35		
layer 5		**-7.02**	**0.33**		**-3.09**	**0.56**
ek/06-01	-7.83			-3.73		
ek/06-02	-7.23			-3.45		
ek/06-03	-6.96			-4.00		
ek/06-04	-7.24			-3.16		
ek/06-05	-7.38			-2.30		
layer 6		**-7.33**	**0.32**		**-3.33**	**0.65**
ek/07-01	-6.39			-3.47		
ek/07-02	-6.87			-4.42		

Identifier	**^{13}C**			**^{18}O**		
		Average	**s.d.**		**Average**	**s.d.**
ek/07-03	-6.81			-4.03		
ek/07-04	-7.03			-2.18		
ek/07-05	-6.76			-4.58		
layer 7		**-6.77**	**0.24**		**-3.74**	**0.97**
ek/08-01	-7.49			-2.89		
ek/08-02	-7.05			-3.44		
ek/08-03	-5.92			-3.24		
ek/08-04	-8.08			-4.15		
ek/08-05	-8.24			-3.89		
layer 8		**-7.36**	**0.93**		**-3.52**	**0.50**
without 08-03		**-7.72**	**0.55**			
ek/09-01	-7.15			-1.78		
ek/09-02	-7.94			-4.24		
ek/09-03	-6.83			-2.42		
EK-9.4	-7.27			-3.40		
ek/09-05	-7.05			-3.76		
layer 9		**-7.25**	**0.42**		**-3.12**	**1.00**
EK-10.1	-7.26			-4.10		
ek/10-02	-7.45			-3.95		
EK-10.3	-7.70			-3.43		
EK-10.4	-7.46			-3.37		
ek/10-05	-6.81			-2.80		
layer 10		**-7.34**	**0.33**		**-3.53**	**0.52**
ek/11-01	-7.49			-4.08		
EK-11.2	-8.27			-2.34		
ek/11-03	-8.54			-4.72		
ek/11-04	-7.45			-2.81		
EK-11.5	-7.20			-5.23		
layer 11		**-7.79**	**0.58**		**-3.84**	**1.23**
ek/12-01	-7.99			-4.35		
ek/12-02	-9.02			-3.91		
ek/12-03	-9.45			-2.29		
EK-12.4	-9.62			-2.80		
ek/12-05	-9.34			-5.08		
layer 12		**-9.08**	**0.65**		**-3.69**	**1.14**
without 12-01		**-9.36**	**0.25**			
ek/13-01	-7.59			-4.08		
ek/13-02	-7.63			-4.36		
ek/13-03	-9.23			-5.38		
ek/13-04	-7.14			-3.73		
ek/13-05	-9.26			-3.98		
layer 13		**-8.17**	**1.00**		**-4.31**	**0.64**

Identifier	**^{13}C**			**^{18}O**		
		Average	**s.d.**		**Average**	**s.d.**
ek/14-01	-7.89			-3.86		
ek/14-02	-7.26			-3.83		
ek/14-03	-7.23			-1.91		
ek/14-04	-7.95			-3.08		
ek/14-05	-7.68			-3.29		
layer 14		**-7.60**	**0.34**		**-3.19**	**0.79**
ek/15-01	-6.94			-4.17		
EK-15.2	-7.25			-3.44		
ek/15-04	-7.57			-4.40		
EK-15.5	-7.07			-4.45		
layer 15		**-7.21**	**0.27**		**-4.12**	**0.47**
EK-16.1	-7.30			-4.27		
EK-16.2	-6.43			-3.84		
ek/16-03	-6.81			-3.10		
ek/16-04	-6.72			-2.34		
ek/16-05	-10.10			-3.20		
layer 16		**-7.47**	**1.50**		**-3.35**	**0.74**
without 16-05		**-6.82**	**0.36**			
ek/17-01	-6.81			-3.56		
EK-17.2	-6.99			-3.19		
ek/17-03	-7.37			-3.57		
ek/17-04	-7.17			-3.84		
ek/17-05	-6.90			-3.84		
layer 17		**-7.05**	**0.22**		**-3.60**	**0.27**
ek/18-01	-9.70			-3.04		
ek/18-02	-10.17			-4.10		
EK-18.3	-8.92			-2.96		
ek/18-04	-9.83			-3.50		
ek/18-05	-10.22			-3.50		
layer 18		**-9.77**	**0.52**		**3.42**	**0.46**