

# Terrestrial molluscan records of Weichselian Lower to Middle Pleniglacial climatic changes from the Nussloch loess series (Rhine Valley, Germany): the impact of local factors

OLIVIER MOINE, DENIS-DIDIER ROUSSEAU AND PIERRE ANTOINE

BOREAS



Moine, O., Rousseau, D.-D. & Antoine, P. 2005 (August): 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*, Vol. 34, pp. 363–380. Oslo. ISSN 0300-9483.

Two malacological sequences sampled in loess sections P1 and P3 of Nussloch (Rhine Valley, Germany) provide the most complete and precise molluscan record of western Europe for the Weichselian Lower and Middle Pleniglacial from about 70 to 34 cal. kyr BP. Qualitative and statistical analyses were performed on 134 mollusc samples. In the most complete Lower Pleniglacial record (P1), malacofauna changes reflect three short phases of vegetation development and climatic improvement related to soils and probably interstadials. A steppe to herb/shrub tundra shift characterizes the Lower-Middle Pleniglacial transition and is followed in both malacological records by the same general environmental trend (decline in vegetation and humidity increase) ending with a new increase in temperature and vegetation cover at the top of P3. In the Middle Pleniglacial, the impact of each shorter climatic change on the malacofauna is less recognizable due to a higher sediment compaction and also to being differently recorded in both sequences as the local topography affects soil water resources, soil and vegetation development and malacofauna adaptation. A comparison shows that the western European biostratigraphical framework can thus be improved by coupling molluscan records from loess sections to pollen sequences.

Olivier Moine (e-mail: omoine@isem.univ-montp2.fr), Institut des Sciences de l'Evolution (UMR CNRS 5554), Paléoenvironnements, Université Montpellier II, cc 61, Place E. Bataillon, 34095 Montpellier Cedex 5, France; Denis-Didier Rousseau, Institut des Sciences de l'Evolution (UMR CNRS 5554), Paléoenvironnements, Université Montpellier II, cc 61, Place E. Bataillon, 34095 Montpellier Cedex 5, France and Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY 10964, USA; Pierre Antoine, UMR CNRS 8591 – Laboratoire de Géographie Physique, 1, Place Aristide Briand, 92 195 Meudon cedex, France; received 31st August 2004, accepted 9th February 2005.

Fossil terrestrial mollusc communities are extremely useful when reconstructing environmental changes in Quaternary loess sequences from different continents (Limondin-Lozouet & Antoine 2001; Rousseau 2001; Lauriol *et al.* 2002; Sümegei *et al.* 2002; Wu *et al.* 2002; Rossignol *et al.* 2004). Terrestrial molluscs are mainly sensitive to temperature and moisture (Ložek 1964; Puisségur 1976; Solem 1984). At the European scale at least, temperature partially constrains species geographical distribution (Moine *et al.* 2002). The vegetation type, which depends partially on both temperature and moisture, also affects the molluscan assemblage composition, protects molluscs from large weather variations and provides them with food (Kerney *et al.* 1983). Moreover, a recent high resolution study has shown that malacofauna composition and dynamics changes, related to millennial timescale climatic variations during the Weichselian Upper Pleniglacial at Nussloch (Rhine Valley, Germany), were not related to taxa life traits (Moine 2003). This reinforces the usefulness of molluscs in palaeoenvironmental and palaeoclimatic reconstructions, especially in loess sequences where they are the only biological remains

present in large amounts. However, a better understanding of the combined impact of local environment and regional climate on molluscan communities, as well as a more detailed knowledge of the ecological tolerance of mollusc species, is still required to improve palaeoenvironmental interpretations. For several years, malacological studies are thus (re)investigated at high resolution for different areas and time intervals.

The 17-m-thick loess sections of Buzzard's Roost and Eustis (Nebraska, Great Plains) have recorded the last North American deglaciation during the 21 to 12 kyr BP interval. They are about 50 km apart, show nearly identical lithological records and their malacozone boundaries, based on the main malacofauna changes, are nearly synchronous (Rossignol *et al.* 2004). These malacozones correspond to those defined by Leonard (1952) for the whole Great Plains and their composition is similar in both sequences. However, whereas both similar presence/absence intervals and long-term trends in species populations generally may respond to regional or global climatic changes, shorter variations in species proportions and abundances, or

different magnitude of long-term trends, more probably highlight local perturbation effects.

In central England, two tufas, located 10 km apart and deposited under similar environmental conditions, recorded the base of the Holocene (Meyrick & Preece 2001). Their similar molluscan successions led to defining synchronous malacozones as correlated with those of the regional molluscan succession defined at Holywell Coombe, southeast England (Preece 1998). Radiocarbon-dating of malacozone boundaries suggests a broad synchronicity of the environmental changes resulting from the strong climatic oscillations of the Lateglacial. However, the influence of both local conditions and relative distance from the refugia of some species probably explains the small differences in faunal composition and species proportions, as well as the timing of first appearances and last occurrences of species, observed in both records (Preece 1998).

At Conty (northern France), five molluscan successions encompassing the Lateglacial have been sampled in fluvial deposits of neighbouring channels of the Selle river (Limondin & Antoine 2001). Their similar molluscan species first appearances, last occurrences and proportions allowed the definition of a common malacological zonation in agreement with the regional one related to the Lateglacial climatic oscillations. Here, also, species proportions differences mainly highlight the influence of the local environment.

Consequently, the goal of this study is to investigate two very close (about 320 m apart) malacological records from Nussloch (Rhine Valley, Germany) encompassing the Weichselian Lower and Middle Pleniglacial for which high-resolution continuous terrestrial records of palaeoenvironmental changes lack, except few pollen sequences. The aims are thus: (1) to analyse the palaeoenvironmental changes at Nussloch during the Early Weichselian to Weichselian Middle Pleniglacial, (2) to characterize the local environmental influence on the malacofauna by comparing adjacent records, and (3) to distinguish the impact of local environment from that of regional or global climatic changes.

## Material and methods

### *Site location and chronology*

The two loess sequences studied here, P1 and P3, are located in the Nussloch quarry on the eastern side of the Rhine Valley (Germany), on top of the Odenwald Plateau, about 10 km south of Heidelberg (Fig. 1; Antoine *et al.* 2001). The local topography of the area is formed by loess 'gredas', which are dune-like structures oriented NNW–SSE parallel with the local dominant winds and built up during the loess deposition

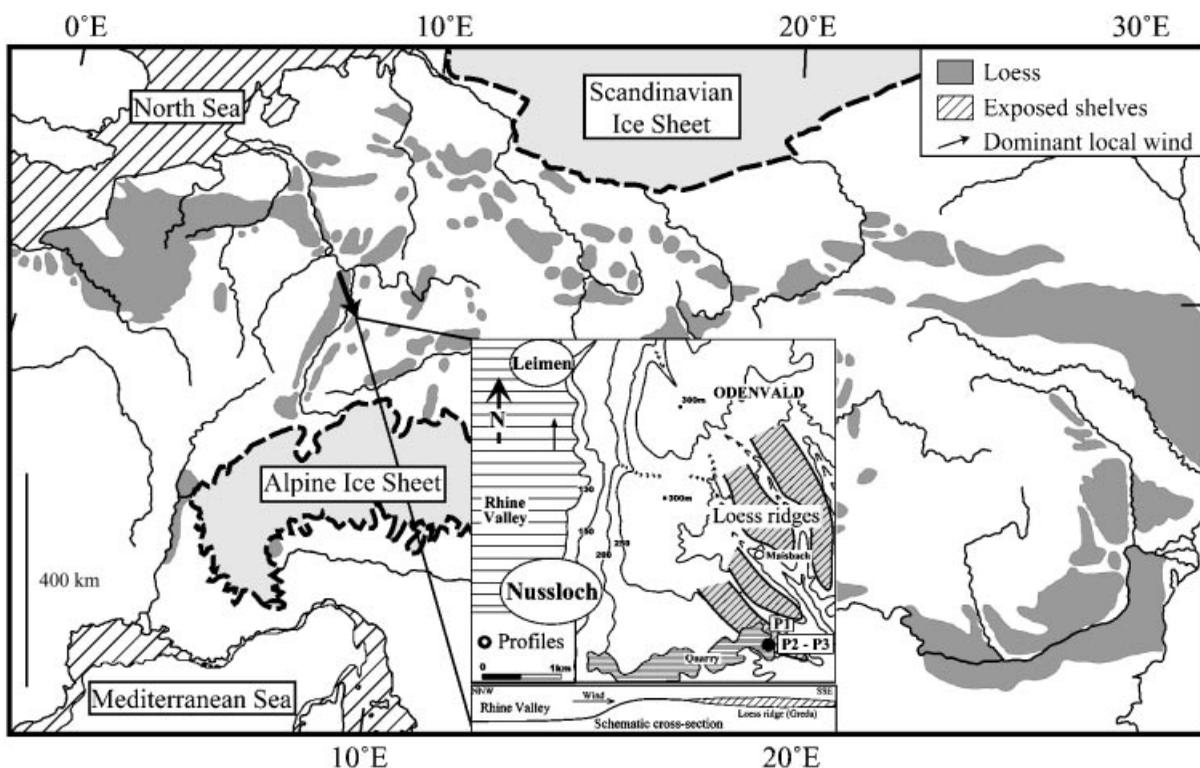


Fig. 1. Location of the Nussloch sections and simplified local geomorphology.

(Léger 1990). P1 was located on the side of one of these gredas, and P3 in the middle. Both sections have now disappeared, as the quarry is still active. The two studied sequences were about 320 m apart. The chronological framework of both sequences is based on  $^{14}\text{C}$  dating of loess organic matter (Hatté *et al.* 2001), thermoluminescence (TL) (Zöller *et al.* 1988), and optically stimulated luminescence (OSL) dates (Lang *et al.* 2003), which have provided ages between 160 and 34 kyr BP, encompassing the Saalian, Eemian, Early Weichselian and the Weichselian Lower and Middle Pleniglacial (Fig. 2). The chronostratigraphical interpretation of both sequences is based on multi-disciplinary analyses of Fe,  $\text{CaCO}_3$ , loess grain-size (Antoine *et al.* 2001) and of organic matter (Hatté *et al.* 2001), combined with lithological correlations from other NW European loess sequences that also recorded the last climatic cycle (Antoine *et al.* 2001). Since detailed descriptions of the stratigraphy, lithology and pedology of the Nussloch loess sequences have already been published (Antoine *et al.* 2001), we will only summarize their main lithological and pedo-stratigraphical characteristics (Fig. 2).

#### Lithological descriptions

The base of P1 is a calcareous loess (unit 1) attributed to the Saalian on the basis of thermoluminescence and amino acid analyses (Antoine *et al.* 2001; Gnieser 1997). According to the bracketing dates, the thick overlying brown soil (units 2a and 2b) characterizes the Eemian interglacial. Its top is truncated and overlain by a complex of two soils bracketing clayey colluvium, all attributed to the Early Weichselian, i.e. Eemian interglacial–Weichselian Pleniglacial transition (units 3, 4, 5). The Lower Pleniglacial deposits include loess alternating with thin and soliflucted tundra gleys (units 6b to 12) and end with a thick sandy loess unit (unit 13). The Middle Pleniglacial deposits start with a cambisol (unit 14 – Gräselberger Boden) developed at the top of the sandy loess layer. Then, due to thermokarst processes, a depression was developed in the cambisol and the sandy loess (Fig. 3) and was subsequently filled with organic-rich and sandy loams, including peat layers, some bone, charcoal and wood remains (unit 15). This infilling is overlain by alternating loess and gley units (units 16 to 19). The  $5^\circ$  tilt of units 13 to 19 is due to the local topography created during the deposition of the sandy loess layer (unit 13) and probably enhanced by the thermokarst incision.

P3 begins with a sandy loess layer and a thin interglacial brown soil, both overlain with thick, probably hillwashed and redeposited, loessic colluvium (units 6a, Cpx A, Cpx B). The following thick sandy loess layer (unit 13) is easily correlated with that of P1 thanks to its lithological characteristics and aspect. In the absence of dates, units 6a, Cpx A, Cpx B and 13 have been attributed to the Lower Pleniglacial using

lithological considerations. The subsequent loess and gley alternation (units 16 to 19) and a second cambisol (unit 20 – Lohner Boden) characterize the Middle Pleniglacial. Both Middle Pleniglacial lithological records are similar except that the top of P1 is probably incomplete. Unlike P1, the Middle Pleniglacial units of P3 have been horizontally deposited. Moreover, the available dates and the absence of thermokarst above the Gräselberger Boden (unit 14) in P1 suggest a hiatus at the top of this unit in both sequences.

#### Mollusc assemblage analysis

Samples of 10 litres (about 15 kg) were taken continuously every 10 cm (Fig. 3), sieved and washed to extract the mollusc shells, which were counted and identified. The P3 and P1 sections provided 208967 and 157915 individuals, respectively. Four successive samples, 15-, 20-, 10- and 10-cm-thick, respectively were also taken within the thermokarst filling (Antoine *et al.* 2001), apart from the main P1 sampling column (Fig. 3) because of its reduced lateral extent, and then included in the P1 record. Originally taken to check the molluscan richness in the thermokarst filling, the volume of these samples is only about 5 litres. To be comparable with those of other samples, their species abundances should thus have been multiplied by 2. However, if this volume had been greater, additional species might have been identified. Hence, to avoid any disjunction between richness and abundances in the statistical analyses, we keep the original counts.

Following the classification established by Ložek (1964) and Puisségur (1976), the 26 terrestrial species recognized are mesophilous (10) or they characterize open habitats (5), semi-open (5), steppe (1), damp (1) and swampy habitat (2) (Table 1), or were only identified at the genus level (2). The five aquatic species characterize low-energy water rich in vegetation, periodic swamps, or habitats poor in aquatic vegetation. Some of them presently occur in several of these environments. The slug group, gathering several slug species with different ecological requirements, has not been used in environmental reconstructions. All mollusc counts have been summed up as species abundances and proportions (Figs 4, 5, 6, 7), and both Juveniles/Adults ratios (J/A) and Juveniles/Total ratios (J/T) have also been performed for *Pupilla muscorum* (Figs 4, 6):

$$\frac{J}{A} = \frac{Ax - Ap}{E + Ap} \quad \text{and} \quad \frac{J}{T} = \frac{Ax - Ap}{E + F}$$

The calculation of such indices is restricted to a few species for which the precise counting of apices ( $Ax$ ) and apertures ( $Ap$ ) is easy and not precluded by the fragile nature of these elements (e.g. *Pupilla muscorum*, *Clausilia dubia* and *Clausilia parvula*).  $E$  and  $F$  are entire and broken individuals, respectively,

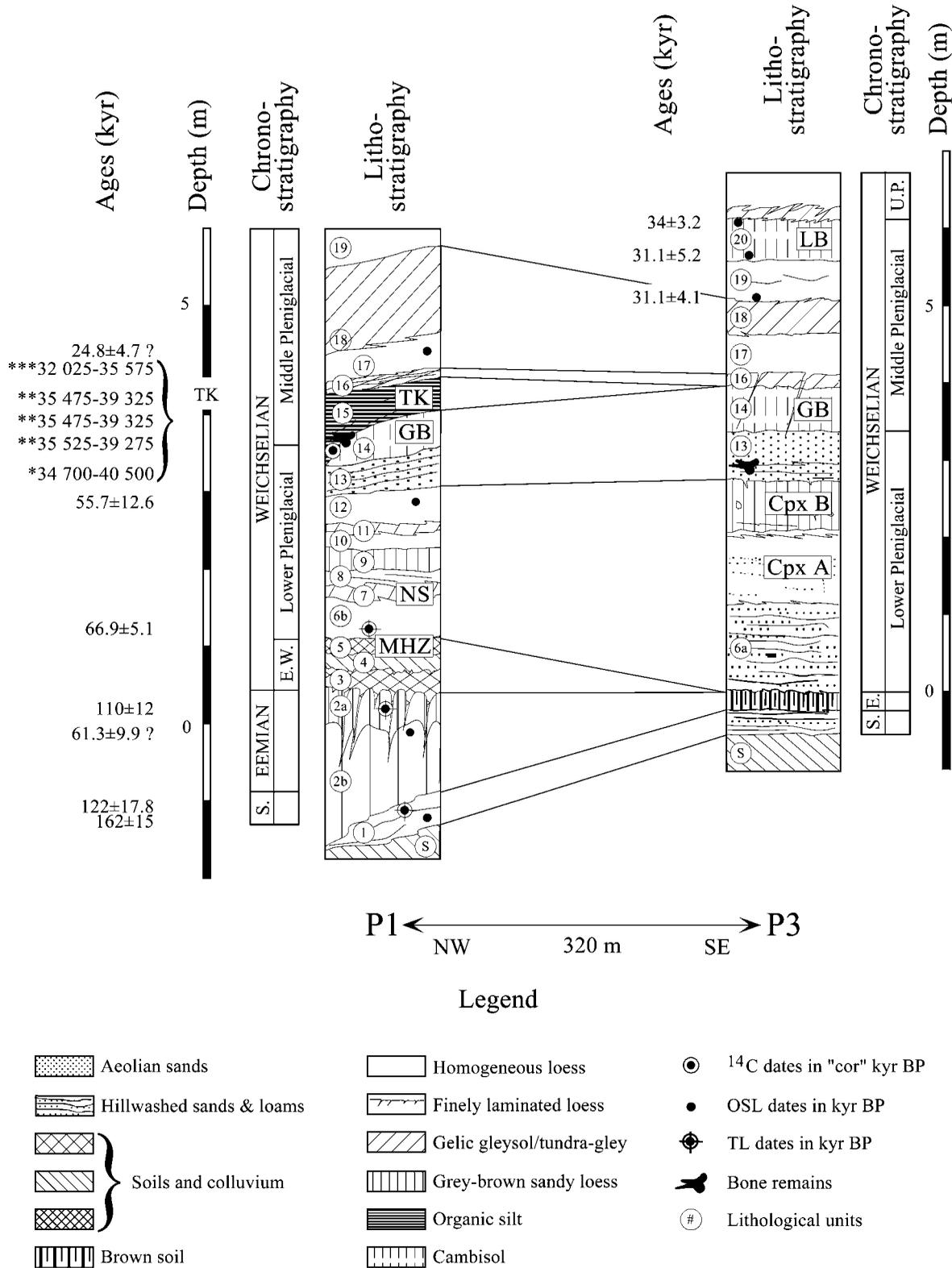


Fig. 2. Stratigraphy of P1 and P3 sections and correlations based on the lithology (modified after Antoine *et al.* 2001). Abbreviations: Lohner Boden (LB), thermokarst (TK), Gräselberger Boden (GB), Nussloch Soil (NS), Mosbacher Humus-Zone (MHZ), Saalian (S.), Early Weichselian (E.W.) and Upper Pleniglacial (U.P.). Location of  $^{14}\text{C}$  samples in the thermokarst: basal contact\* (horse bone), lower\*\* and upper\*\*\* half (wood). Dashed lines indicate uncertain correlations. See Fig. 3 for thermokarst and Gräselberger Boden position in the original section.  $^{14}\text{C}$ , OSL and TL ages are from Hatté *et al.* (2001), Lang *et al.* (2003) and Zöller *et al.* (1988), respectively.

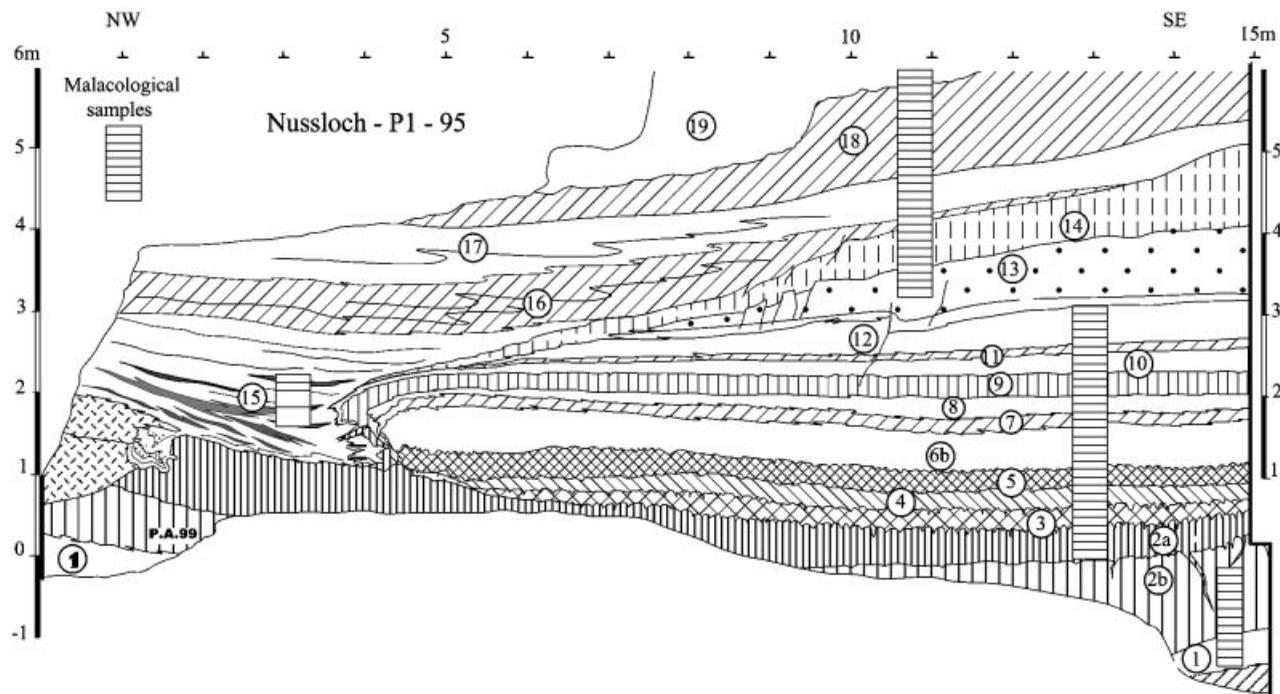


Fig. 3. Sketch of P1 section (modified after Antoine *et al.* 2001). Legend as in Fig. 2.

and  $F$  is the largest of  $A_x$  and  $A_p$ . Only results obtained for *P. muscorum* are discussed, as this species is the only one present throughout both sequences. The  $J/A$  and  $J/T$  variations are assumed to reflect changes in the reproduction rate and juvenile survival, which principally depends on temperature parameters during the reproduction season (Moine 2003). However, negative values for both ratios indicate a lack of apices compared to the number of apertures, and thus a taphonomic bias, such as wind action and/or carbonate dissolution. For example, couples of extreme values such as ( $J/A=0$ ;  $J/T=0$ ) or ( $J/A=0$ ;  $J/T=1$ ) indicate the absence of juveniles or adults, respectively. Given the mean time-span of about several hundred years, represented by a sample in the Lower and Middle Pleniglacial deposits, an absence of juveniles or adults must certainly reflect a taphonomic bias in the few poor assemblages encountered. However, these extreme values cannot be related to a particular preservation bias of terrestrial mollusc shells. With the exception of wind action and/or carbonate dissolution, all other biases, listed and checked by Carter (1990), in well-developed calcareous soils can neither have occurred nor be checked in the Nussloch loess deposits. Thus, the environmental interpretation of a few assemblages, characterized by couples of extreme  $J/A$  and  $J/T$  values, is considered less reliable than for the other assemblages.

A correspondence analysis (CA) has been performed on mollusc counts to determine the dominant ecological factors that influence molluscan assemblage composition, and to compare their variations throughout both

sequences (Figs 8, 9). With this method, observations (assemblages) and variables (species) can be plotted on the same diagram, i.e. species are plotted near assemblages in which they dominate. The abundance counts have been coded in classes, defined on a logarithmic scale of base 2, in order to reduce the influence of their high variability in the analysis (Rousseau 1987). Because of their few sporadic occurrences, *Vertigo genesii*, *Pupilla cf. alpicola*, *Pupilla sterri*, *Discus* sp. and *Vertigo* sp. appeared extremely scattered on the original species CA diagram, and all other species were grouped in a very compact cluster. Therefore, these few taxa have been introduced in the correspondence analysis as supplementary variables. In addition, a hierarchical ascendant classification has been performed on both species and assemblage coordinates of the first five axes of the correspondence analysis (Fig. 10). Hence, the species ecological requirements (Table 1) are used to determine the ecological significance of the species CA diagram axes (Fig. 8). The environmental changes are then deduced for all the assemblages, and consequently for every lithological unit (Fig. 11). Calculations were performed with Statistica 6.0 (StatSoft Inc., Tulsa, OK).

## Results

### Definition of the P3 malacozones

*MZ1-P3*. – The malacozone MZ1-P3 comprises unit 6a and the first two assemblages of Cpx A (Fig. 4). Among

Table 1. Ecological requirements of the identified species in P1 and P3 sections, after Adam (1960), Germain (1930), Kerney *et al.* (1983), Likharev & Rammelmeier (1962), Ložek (1964) and Zilch & Jaeckel (1962). Habitats: semi-open (2), steppe (4), open (5), mesophilous (7), damp (8) and swampy (9). Affinities: m or M: mesophilous, f: forest, r: rocks, h: moisture. Slugs (7') have been omitted, as their species have different ecological requirements. Ecological requirements of freshwater species (10) are not shown.

<i>Abida secale</i> (7fr)	Dry, sunny and hot stations with a short vegetation; only in calcareous and not granitic regions. Rarely in woody places	<i>Punctum pygmaeum</i> (7)	Fairly wet habitats with a developed vegetation cover (wood litter). Also in open stations if humidity and protection against dehydration are adequate
<i>Arianta arbustorum</i> (2f(h))	Very wet and vegetated stations. Cold-resistant. Also in open stations (humid meadows, alpine grasslands)	<i>Pupilla alpicola</i> (9)	Very wet mountain stations (swamps, peat bogs, wet grasslands) and preferring calcareous areas
<i>Clausilia dubia</i> (7fr)	Sparse forest and among rocks in fairly humid and calcareous mountain areas	<i>Pupilla muscorum</i> (5)	Open, dry or damp and sunny stations
<i>Clausilia parvula</i> (7fr)	Mostly in dry open stations with calcitic rocks and short vegetation. Rare in woods	<i>Pupilla sterri</i> (4)	Very dry and sunny stations among calcareous rocks and fallen stones, and a sparse vegetation
<i>Cochlicopa lubrica</i> (7h)	Wet stations (woods, humid meadows, swamps)	<i>Succinea oblonga elongata</i> (8)	Wet stations with a sparse vegetation (humid meadows, swamps and near brooks)
<i>Columella columella</i> (5)	Cold regions and wet stations with vegetation (herbaceous swamps, subarctic woods and grasslands)	<i>Trichia hispida</i> (7)	Everywhere except driest stations
<i>Discus rotundatus</i> (2f(m))	Very varied, humid to dry, stations with a developed vegetation cover. Sometimes among rocks and fallen stones. Also present in open stations	<i>Trichia striolata</i> (2f(m))	Wet and shaded stations with vegetation
<i>Eucobresia nivalis</i> (2f(h))	Wet, stony and open stations at high altitudes, even near the snow cover	<i>Vallonia costata</i> (5)	Varied open, dry and humid, stations with stones. Rarely in woods or swamps
<i>Euconulus fulvus</i> (7)	Mostly in very humid and humid stations with vegetation (woods, meadows, swamps). Sometimes in dry stations when vegetation is sufficient	<i>Vallonia pulchella</i> (5)	Humid and open habitats (wet and swampy meadows, near river banks and swamps). Mostly rare in dry meadows, and very rare in woods
<i>Neostyriaca corynodes</i> (7M)	Stony meadows and near mossy calcareous rocks. Sometimes in woody valleys near brooks	<i>Vertigo genesii</i> (9)	Swampy stations (swamps, flooded meadows)
<i>Nesovitrea hammonis</i> (7h)	Varied habitats (meadows, woods, swamps) but prefers humid open stations even cold ones at altitude	<i>Vertigo pygmaea</i> (5)	Varied habitats, but prefers humid stations (wet and swampy meadows, near river banks) rather than dry and open stations
<i>Orcula dolium</i> (7fr)	Calcareous and fairly dry to wet stations (wood litter among rocks, slopes with fallen stones)	<i>Vitrea crystallina</i> (2f(m))	Cool and humid stations (woods, wet meadows, near swamps and brooks)

dominant species, proportions in *Pupilla muscorum* and *Trichia hispida* are higher than those in *Succinea oblonga*, *Vallonia costata* and *Vitrea crystallina* (Fig. 5). *Arianta arbustorum*, *Cochlicopa lubrica*, *Punctum pygmaeum*, *Vallonia pulchella* and *Vertigo pygmaea* persist in smaller proportions. The specific abundances are low and show synchronous slight variations (Fig. 4). Strong decreases in all species abundances and the disappearance of *V. crystallina*, *V. pulchella*, *P. pygmaeum*, *C. lubrica*, *V. pygmaea*, *Orcula dolium* and *Eucobresia nivalis* characterize the end of MZ1-P3.

**MZ2-P3.** – The malacozone MZ2-P3 almost completely comprises units Cpx A and Cpx B (Fig. 4). The dominant species are *Pupilla muscorum*, *Succinea oblonga* and *Trichia hispida* (Fig. 5). *Arianta arbustorum*, *Vallonia costata* and *Clausilia parvula* persist in weaker proportions than the dominant species. A few

other species already identified in MZ1-P3 occur sporadically, such as *Punctum pygmaeum*, *Orcula dolium*, *Abida secale* and *Discus* sp. (Fig. 5). Species abundance and richness values are the lowest of the sequence. A slight abundance increase occurs in the upper half of MZ2-P3. At the same time, *Trichia striolata* appears, *Vitrea crystallina* reappears, and the proportions of *P. muscorum* increase, whereas those of *A. arbustorum*, *T. hispida* and *S. oblonga* decrease (Fig. 5).

**MZ3-P3.** – The malacozone MZ3-P3 comprises units 13 to 20 (Fig. 4). The dominant species are still *Pupilla muscorum*, *Succinea oblonga*, *Trichia hispida* and *Vallonia costata* (Fig. 4). At the base of MZ3-P3, *Columella columella*, *Neostyriaca corynodes*, *Vallonia pulchella*, *Punctum pygmaeum*, *Cochlicopa lubrica*, *Orcula dolium*, *Abida secale*, *Nesovitrea hammonis*, *Vertigo pygmaea*, *Pupilla sterri* and *Euconulus fulvus* appear or reappear (Fig. 4). *C. columella* and

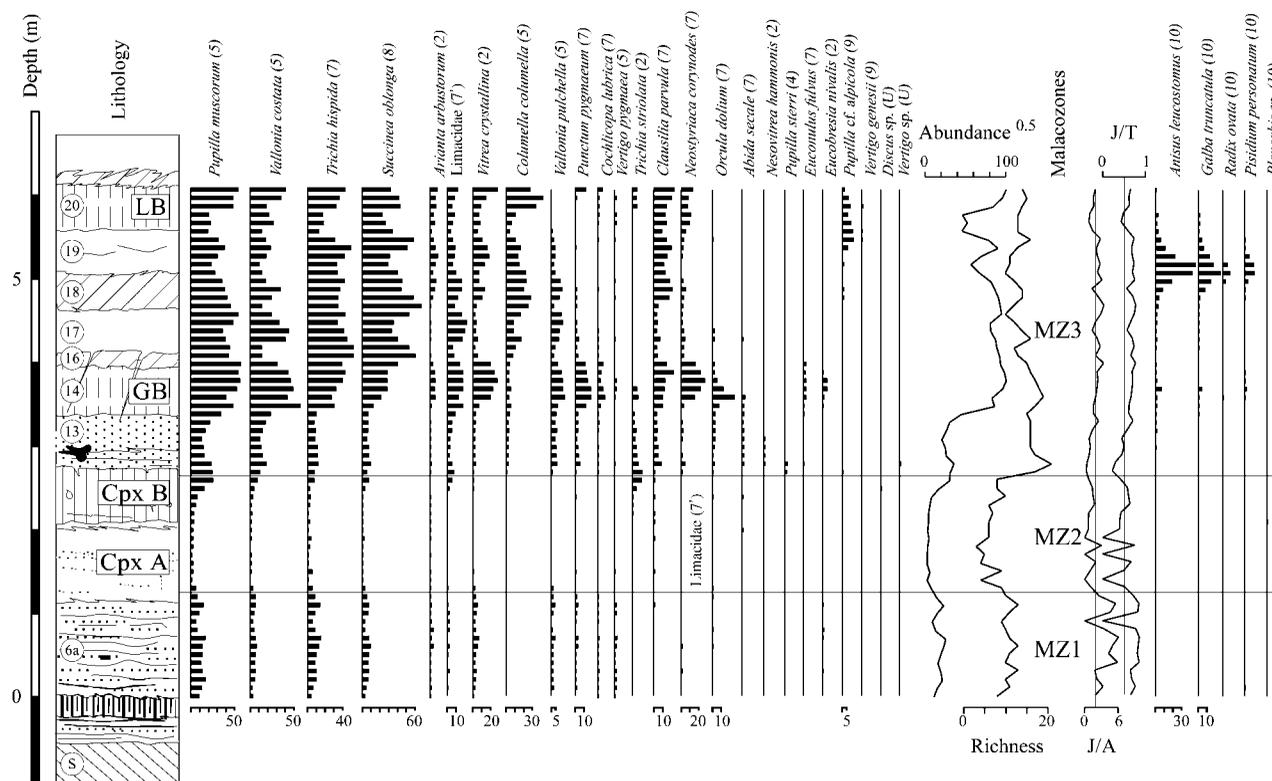


Fig. 4. Species abundance diagram of P3 section. The abundance square root was used to highlight the smallest variations. Curves of both total abundance and species richness in terrestrial species do not include freshwater species. The two curves of the Juveniles/Adults (J/A) and Juveniles/Total (J/T) ratios (black) are based on the counts of *Pupilla muscorum* shell fragments. Ecological groups: semi-open (2), steppe (4), open (5), mesophilous (7), damp (8), swampy (9), freshwater (10) and slugs (7') apart.

*N. corynodes* are continuously present toward the top of P3, contrary to other species. Richness and species abundances are thus higher in MZ3-P3 and show fluctuations that rarely coincide with lithological changes (Figs 4, 5). Only proportion of *S. oblonga* increases regularly near the top of gley units. Abundance variations of every species are not always synchronous (Fig. 4). Freshwater molluscs are present almost throughout MZ3-P3. Their population increases weakly in the middle of unit 14 and strongly at the top of the gley unit 18, where it is synchronous with a decrease in dominant terrestrial species abundances (Figs 4, 5).

#### Definition of the P1 malacozones

**MZ1-P1.** – The malacozone MZ1-P1 comprises unit 1 (Fig. 6). The dominant species are *Trichia hispida*, *Succinea oblonga* and *Pupilla muscorum*. *Arianta arbustorum* is persistent in low proportion, as is *Columella columella* restricted to the very base (Fig. 7). Species abundances are low, decreasing, and species progressively disappear (Fig. 6). The relative frequencies of *T. hispida* decrease, whereas those of *S. oblonga* increase, but are still higher than those of *P. muscorum*. Only the three dominant species constitute the last

assemblage. As the Eemian BT horizon samples are devoid of shells, they have not been assigned to any malacozone.

**MZ2-P1.** – The malacozone MZ2-P1 comprises units 3 to 13 (Fig. 6). The dominant species are *Pupilla muscorum*, *Succinea oblonga*, *Trichia hispida* and also *Vallonia costata* occurring discontinuously. *Arianta arbustorum* and *Vitrea crystallina* are persistent in low abundance. Poorly represented species include *Punctum pygmaeum*, *Vertigo pygmaea*, *Vallonia pulchella*, *Cochlicopa lubrica*, *Euconulus fulvus*, *Neostriaria corynodes*, *Orcula dolium*, *Euobresia nivalis*, *Columella columella* and *Nesovitrea hammonis*, which all occur sporadically. All species show the same abundance patterns with two maxima within units 7–8 and 10–11, and a weaker increase in unit 13. Another slight environmental change occurs within soil unit 9 and involves a small increase in *Vallonia costata*, *Vertigo pygmaea* and *Vitrea crystallina*, and the presence of *Vallonia pulchella*, *Cochlicopa lubrica*, *Euconulus fulvus* and *Nesovitrea hammonis*. The presence of several secondary species is restrained to these abundance peaks. Concerning proportions, each unit seems characterized by a particular combination of dominant species that rather suggests a succession pattern.

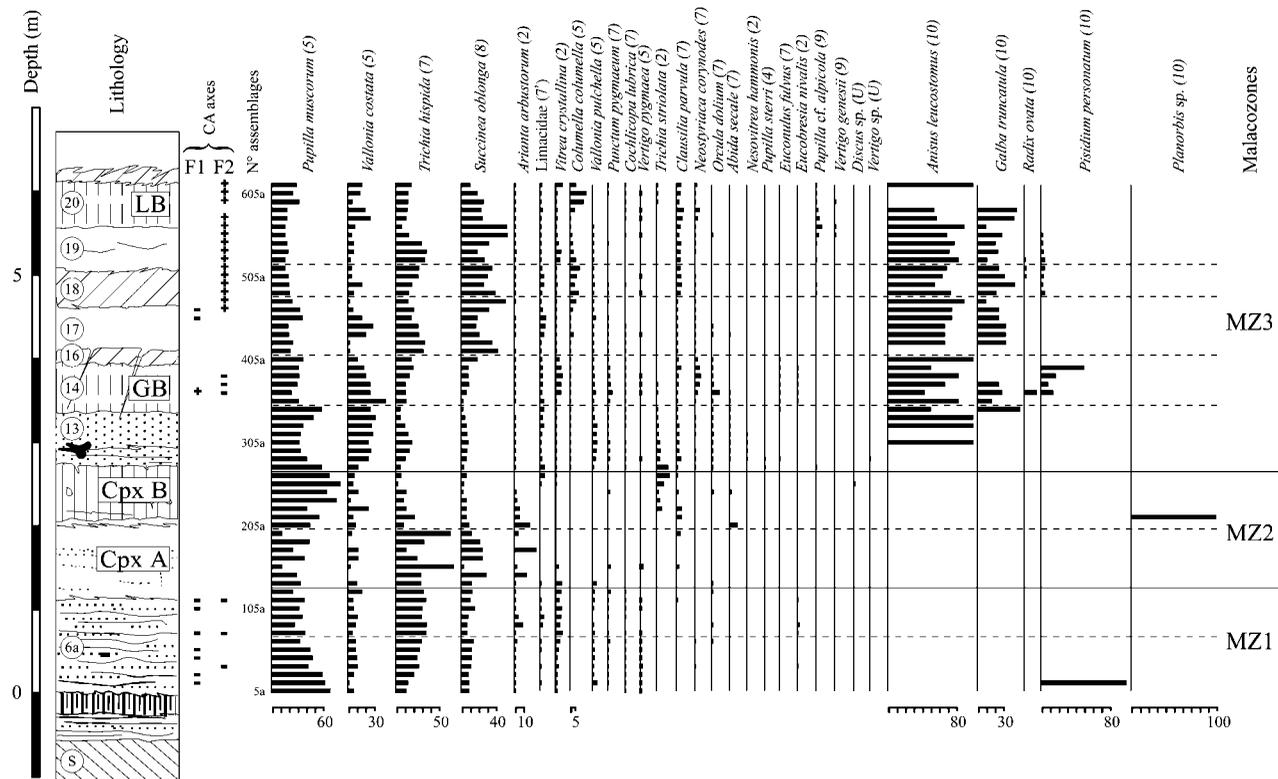


Fig. 5. Species proportions diagram for the P3 section. Dashed lines separate the different malaco-subzones. (+) and (-) signs indicate the positive and negative contributions of each assemblage to the two axes of the correspondence analyses. Ecological groups: semi-open (2), steppe (4), open (5), mesophilous (7), damp (8), swampy (9), freshwater (10) and slugs (7) apart.

**MZ3-P1.** – The malacozone MZ3-P1 comprises units 14 to 19 (Fig. 6). The dominant species are *Pupilla muscorum*, *Succinea oblonga*, *Trichia hispida*, *Trichia striolata* and *Vallonia costata*. It is characterized by the highest richness of the studied sequence, an important decrease in the proportions of *P. muscorum*, and the appearance of *T. striolata* and its large proportion increase. New secondary species also appear, such as *Clausilia dubia*, *Clausilia parvula* and *Columella columella*, and mostly persist throughout this malacozone (Fig. 7). The secondary species already present in MZ2-P1 show larger proportions in MZ3-P1. Fluctuations in species abundances are mostly synchronous and independent of lithological changes. The proportions of dominant species show weaker fluctuations than in MZ2-P1, except in the last four assemblages where *T. striolata* strongly increases whereas *P. muscorum*, *V. costata* and *C. parvula* clearly decrease (Fig. 7). Contrary to MZ3-P3, freshwater mollusc species only occur sporadically in MZ3-P1.

**Concluding remarks.** – About half of the identified species have both large modern ecological range (Table 1) and wide geographical distribution in Eurasia (Kerney et al. 1983; Likharev & Rammelmeier 1962), and the others can survive in poorly vegetated places.

*Pupilla muscorum* (open habitat), *Trichia hispida* (mesophilous), *Succinea oblonga* (damp habitat), *Vallonia costata* (open habitat), and also *Trichia striolata* (semi-open habitat) in the upper half of P1, dominate most of the assemblages (about 70–90%) (Figs 5, 7), which reflects the persistence of the same steppe to tundra-like vegetation. Only the general malacofauna diversification at the Lower-Middle Pleniglacial boundary can be correlated between both sequences. Smaller variations in species proportions and abundances, or total abundance and richness, do not allow the definition of a common mollusc succession framework, even for the similar Middle Pleniglacial lithological records (Figs 2, 5, 7).

#### Correspondence analysis (CA) and hierarchical ascendant classification (HAC)

The first five axes of the correspondence analysis explain 72.12% of the total variability (F1=30.24%, F2=16.49%, F3=12.10%, F4=7.94% and F5=5.33%). Since a quadratic relationship between axes 1 and 3 is highlighted by a Guttman effect (Benzecri & Benzecri 1980), the signification of the third axis cannot be clearly distinguished from that of the

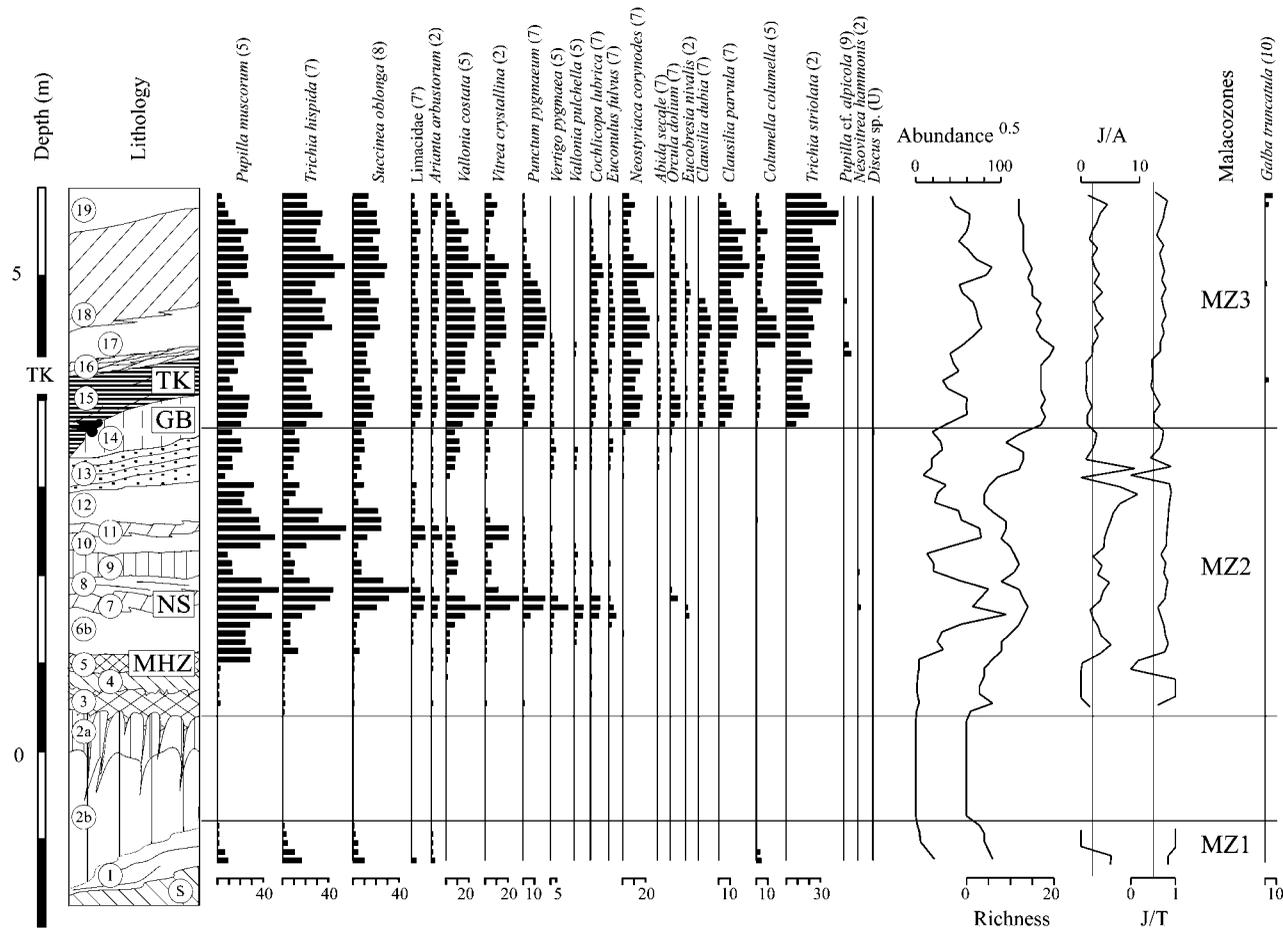


Fig. 6. Species abundance diagram of the P1 section. Explanations as in Fig. 4.

first one. Moreover, the less the explanation percentage of an axis, the less clear its significance. Hence, only the first two axes, F1 and F2, defining the first factorial plane have been considered (Figs 8, 9).

*Species HAC.* – The hierarchical ascendant classification, performed on the species coordinates of the first five axes of the species correspondence analysis, allowed eight clusters (S1 to S8) to be determined using the associated aggregation curve (not shown) (Figs 8, 10). S1 includes two mesophilous species from calcareous areas with a small arboreal cover and rocks. However, *A. secale* also prefers dry and sunny stations, as opposed to *C. dubia* inhabiting fairly moist locations (Table 1). This may explain their separation just below the defined threshold (Fig. 10) and their distant plot in the species CA diagram (Fig. 8). The differentiation between S2 and S3 is subtler. Indeed, S2 groups mesophilous species preferring moisture, arboreal vegetation and rocks, and species of semi-open moist stations (*C. lubrica*, *P. pygmaeum*, *O. dolium*, *E. nivalis* and *E. fulvus*). In S3, the species characterize mesophilous

environments with or without arboreal vegetation and rocks, and semi-open and open habitats (*C. parvula*, *N. corynodes*, *C. columella* and *T. striolata*). Hence, species of S3 indicate a sparser vegetation cover and *C. columella* a moister environment (Table 1). The species of S4 are common in loess assemblages throughout the European loess belt (Ložek 1968). Even though they belong to different ecological groups (semi-open, open, mesophilous and damp habitats), they all tolerate climatic variations, especially cold. *P. muscorum*, *S. oblonga* and *T. hispida* are the most tolerant species and they dominate every malacological assemblage at Nussloch. *A. arbustorum* is closer to *V. crystallina*, as both species are the most vegetation-dependent of this cluster. *V. costata* has intermediate requirements between the first two groups. A too moist environment may have limited its population at Nussloch. S5 groups *V. pulchella* and *V. pygmaea*, characteristic of open and moist habitats. The large populations of *V. pulchella* throughout P1 explain its proximity to the dominant species cluster S4. In the lower part of the species CA diagram, *V. pygmaea* is plotted close to *N. hammonis* as *V. pulchella* requires less vegetation. S6 groups the

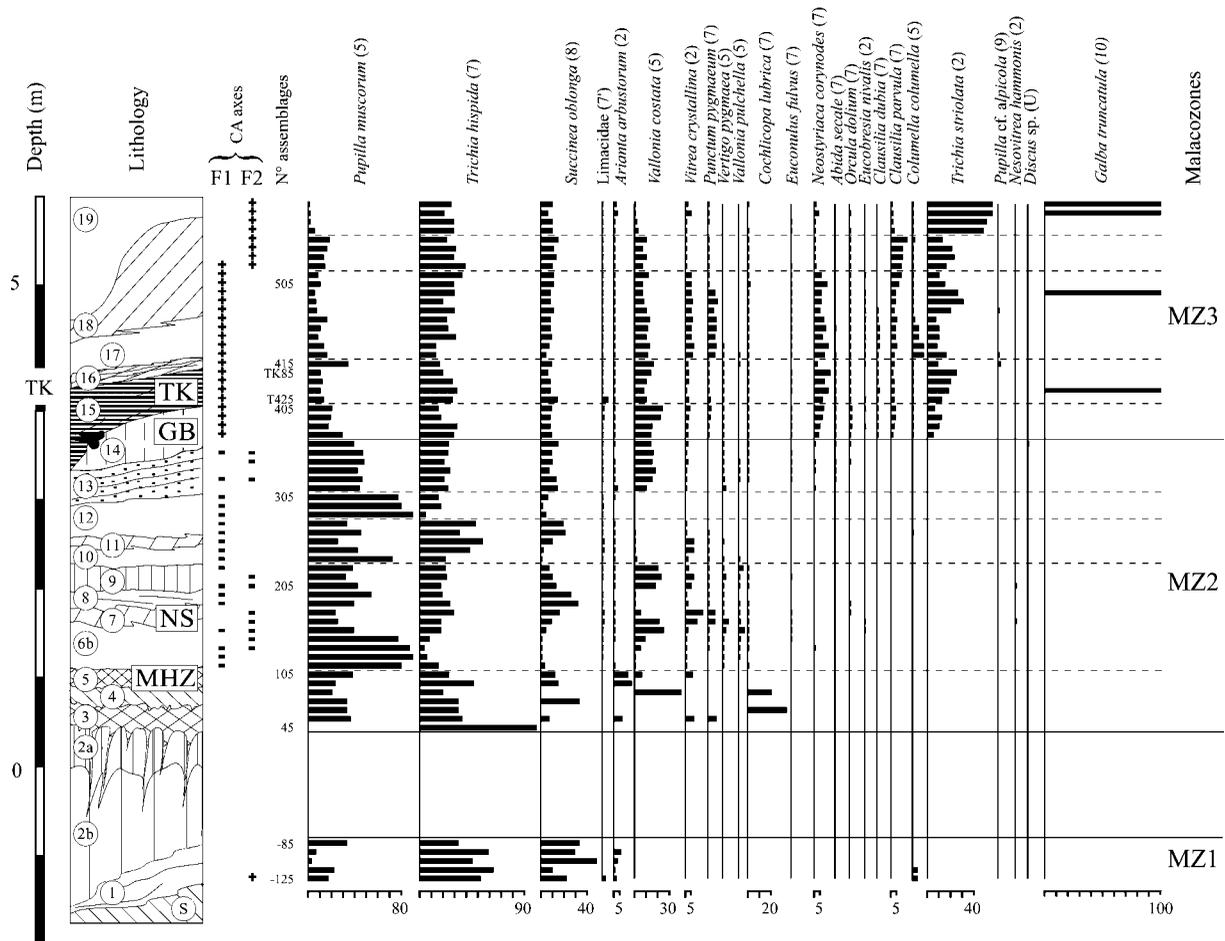


Fig. 7. Species proportions diagram for the P1 sequence. Explanations as in Fig. 5.

moisture-demanding species *V. genesii* and *P. cf. alpicola*. The uncertain *Pupilla* specimens are closer to *V. genesii* than to *P. muscorum*, which has suggested their allocation to *P. cf. alpicola*, which has similar ecological requirements to *V. genesii*. A confident identification cannot actually be based on such a statistical analysis. As S7 groups a few poorly represented species (*N. hammonis*, *Vertigo* sp. and *P. sterri*), no precise environmental characterization is possible for this cluster (Table 1). S8 includes only *Discus* sp., indicating a habitat with a developed vegetation cover. However, its rare and weak appearances are useless, and may rather explain its relationship with S7. Consequently, the analysis of the hierarchical ascendant classification indicates that the species distribution in the CA diagram is realistic and mostly determined by vegetation and moisture.

**Species CA.** – Species contribute significantly to the general variability of each axis when their inertia is greater than that of the theoretical mean contribution, i.e. 1/21 or 4.76% (Fig. 8). Along F1, *T. striolata*, *C.*

*dubia*, *N. corynodes* and *O. dolium* contribute positively, and *P. muscorum*, *T. hispida*, *V. pulchella*, whereas *S. oblonga* contribute negatively (Fig. 8). The positive side of F1 is characterized by vegetation-requiring species, and the negative side mainly by typical loess species with a wide ecological tolerance (Table 1). F1 thus expresses a gradient between two open environments: tundra, toward its positive side, and steppe, slightly less vegetated, toward the negative one. Along F2, *C. columella* and *C. parvula* contribute positively, whereas *V. pygmaea*, *E. fulvus*, *P. pygmaeum*, *C. lubrica* and *E. nivalis* contribute negatively. All are vegetation-requiring species. Nevertheless, *C. columella*, preferring higher moisture, mainly characterizes the positive side of F2, whereas the negative one is characterized by species preferring less moist conditions (Table 1). Moreover, the position of *V. genesii* and *P. cf. alpicola* beyond that of *C. columella* toward the positive extremity of F2 supports this interpretation. F2 thus expresses a moisture gradient. Consequently, environmental trends can also be determined from the disposition of the assemblages in the CA diagram.

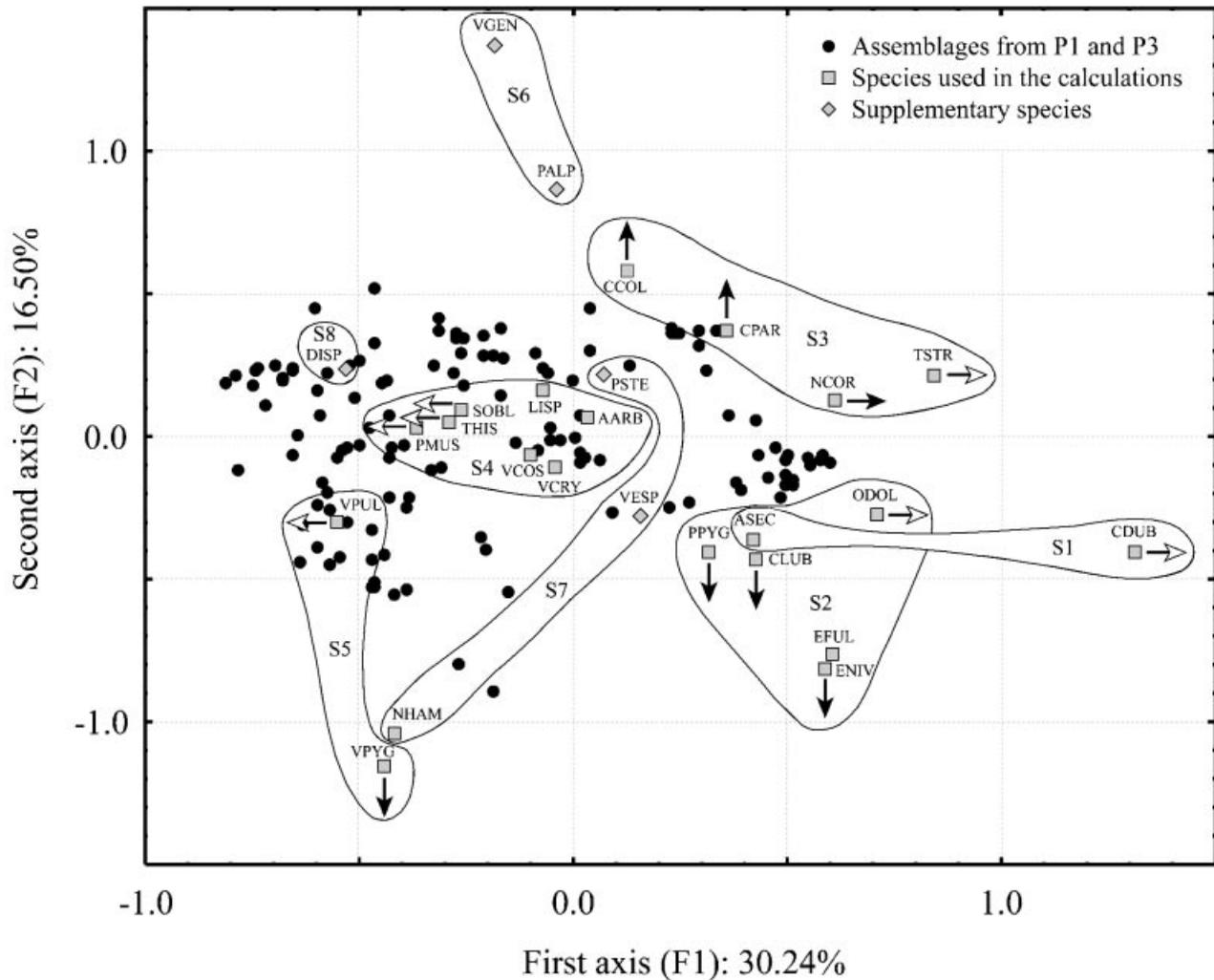


Fig. 8. Correspondence analysis performed on assemblages and species of P1 and P3 sections. Arrows indicate the significantly contributing species for each axis. Species clusters determined by the hierarchical ascendant analysis are contoured by a solid line. Abbreviations: AARB=*Arianta arbustorum*, ASEC=*Abida secale*, CCOL=*Columella columella*, CDUB=*Clausilia dubia*, CLUB=*Cochlicopa lubrica*, CPAR=*Clausilia parvula*, DISP=*Discus* sp., EFUL=*Euconulus fulvus*, ENIV=*Eucobresia nivalis*, LISP=Slugs, NCOR=*Neostyriaca corynoides*, NHAM=*Nesovitrea hammonis*, ODOL=*Orcula dolium*, PALP=*Pupilla* cf. *alpicola*, PMUS=*Pupilla muscorum*, PPYG=*Punctum pygmaeum*, PSTE=*Pupilla sterri*, SOBL=*Succinea oblonga*, THIS=*Trichia hispida*, TSTR=*Trichia striolata*, VCOS=*Vallonia costata*, VCRY=*Vitrea crystallina*, VESP=*Vertigo* sp., VGEN=*Vertigo genesii*, VPUL=*Vallonia pulchella* and VPYG=*Vertigo pygmaea*.

**CA assemblages.** – Assemblages contribute significantly to the general variability of each axis when their inertia is greater than that of the theoretical mean contribution, i.e. 1/127 or 0.7874% (Fig. 9). The depth (in cm) of their central point names assemblages. A suffix 'a' has been added to assemblages from P3 (Figs 5, 7) and a prefix 'T' or 'TK' to those of the thermokarst.

For F1, the positively contributing assemblages are located in Middle Pleniglacial units (14–18 (lower half)-P1) and in unit 14-P3 (Figs 5, 7). Their high proportion of secondary species characterize well-developed shrub tundra vegetation. The negatively

contributing assemblages are mostly located in Lower Pleniglacial units (6b, 8, 12)-P1, and also in units (9, 10, 13)-P1 and 6a-P3 (Figs 5, 7). The assemblages are dominated by *P. muscorum*, *S. oblonga* and *T. hispida*, and include secondary species such as *A. arbustorum*, *C. lubrica*, *V. costata*, *V. crystallina*, *V. pygmaea*, *P. pygmaeum*, *V. pulchella* and *E. fulvus* (Figs 4, 6). Such a composition characterizes a rather moist and vegetated steppe environment. It is generally the same for P1 and P3 assemblages, except for a few differences caused by sporadically occurring species.

For F2, the positively contributing assemblages are located on top of both sequences in units (18–20)-P3,

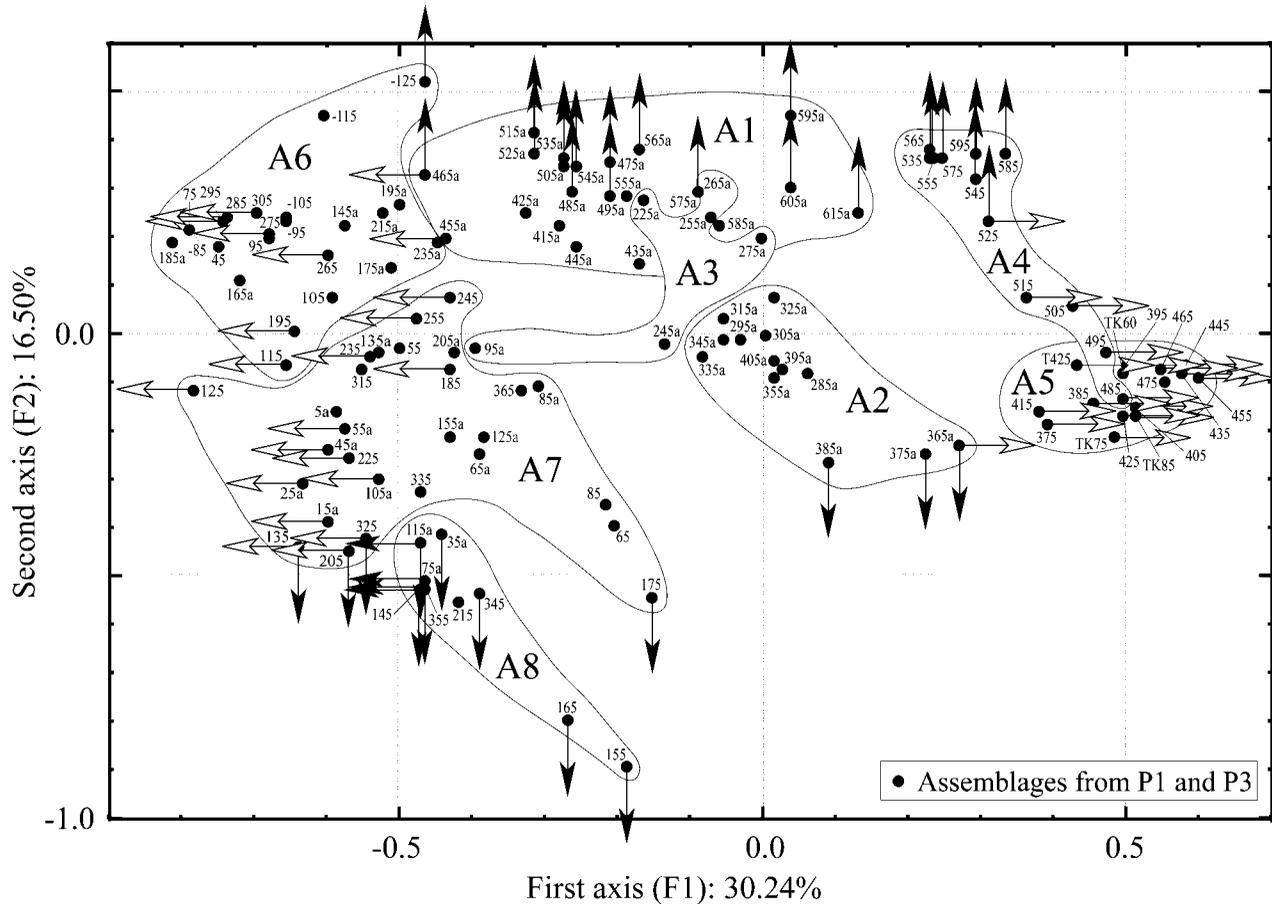


Fig. 9. Correspondence analysis carried out on assemblages and species of P1 and P3 sections. Assemblage clusters determined by the hierarchical ascendant analysis are contoured by a solid line. Explanations as in Fig. 8.

and in units (18 (upper half), 19)-P1 (Figs 5, 7). The negatively contributing assemblages are located in units (6b (upper half), 7, 9, 13)-P1, and in unit 6a-P3 (Figs 5, 7). However, the differences between positively and negatively contributing assemblages for F2 are less obvious than for F1, and have to be described independently for each section P1 and P3. In P1, assemblages that contribute positively are characterized by lower proportions of *P. muscorum*, *V. costata*, *E. fulvus* and *E. nivalis*, and higher proportions of *T. hispida*, *N. corynodes* and *O. dolium* (Fig. 4). They also include *C. parvula*, *C. columella* and *T. striolata*, whereas negatively contributing assemblages include *V. pygmaea* and *V. pulchella*. In P3, assemblages that contribute positively are characterized by lower proportions of *P. muscorum*, *P. pygmaeum*, *V. pygmaea* and *E. fulvus*, and higher proportions of *S. oblonga*, *C. columella* and *N. corynodes* (Fig. 6). They also include *P. cf. alpicola* and *V. genesii*, whereas negatively contributing assemblages include *E. nivalis*. Hence, given the ecological requirements of all these species (Table 1), the positively contributing assem-

blages of both sequences suggest a slightly moister environment than the negatively contributing assemblages.

Therefore, the assemblage CA diagram supports both vegetation and moisture gradients, defined along F1 and F2, respectively, on the basis of the species CA diagram. This reinforces their environmental significance and will ease the characterization of assemblage groups resulting from the hierarchical ascendant analysis.

*HAC assemblages.* – The hierarchical ascendant classification, simultaneously performed for all the assemblages of P1 and P3, has identified 8 clusters, arbitrarily named A1 to A8 (Figs 10, 11). Assemblages of every lithological unit can be included in the same cluster or spread in several clusters.

The three clusters A6 to A8, on the left of the CA diagram (Fig. 11), group most of the Lower Pleniglacial assemblages located below the Gräselberger Boden (unit 14) in both sequences (Fig. 2). The assemblage scattering shows an absence of links between Lower

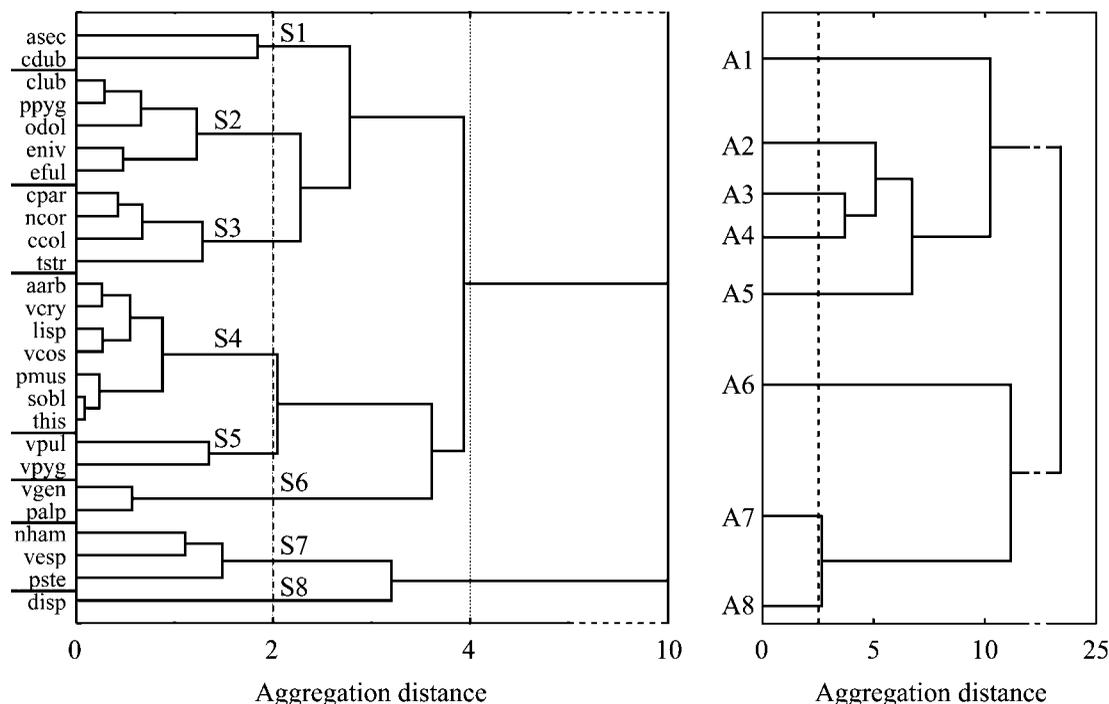


Fig. 10. Dendrograms of the hierarchical classification analyses carried out on assemblages and on species. Individualized clusters have been named arbitrarily. Thresholds in dashed lines have been defined using the aggregation curves (not shown). The dichotomies below the significance threshold have been deleted to simplify the assemblage dendrogram. Clusters A1 to A5 mostly include Middle Pleniglacial assemblages. Saalian, Eemian, Early Weichselian and Lower Pleniglacial assemblages are mostly grouped in clusters A6 to A8.

Pleniglacial molluscan records of P1 and P3, and a similar variable steppe to tundra scarce vegetation.

The five clusters A1 to A5 include most of the Middle Pleniglacial assemblages of P3 (A1, A2, A3) and P1 (A3, A4) (Fig. 11). As assemblages of the Lower Pleniglacial unit 13-P3 show a diversified malacofauna characteristic of the Middle Pleniglacial, they are also included in A2. A3 groups several assemblages of Cpx B-P3. In the CA diagram (Fig. 11), the scattered occurrence of Cpx B-P3 assemblages may highlight the transition between poor and rich molluscan phases of P3. In the broad cluster formed by A1, A2 and A3, the assemblage scattering shows that, from the lower right corner to the upper left one, the lithological units succeed one another according to the following order: 14, 13, 16, 17, 16, 18 and 19. With regard to the CA axis signification, this alignment underlines the occurrence of an environmental trend from a dry herb tundra (lower right corner) to a moist tundra (upper left corner) throughout the Middle Pleniglacial of P3. In the second broad cluster formed by A4 and A5, a roughly similar distribution highlights a parallel environmental trend from a dry shrub tundra (lower right corner) to a moist herb tundra (upper left corner) throughout the Middle Pleniglacial of P1. The main transition occurs progressively in unit 18 in P1, whereas it seems to occur earlier in unit 17 in P3.

## Discussion

### *Comparison between both environmental successions of P1 and P3*

*Saalian, Eemian and Early Weichselian.* – Saalian (unit 1) and Early Weichselian (units 3–5) mollusc assemblages are included in MZ1-P1 and at the basis of MZ2-P1, respectively. Their malacofauna is poor and characterized by extreme values of J/A and J/T ratios (Fig. 6). As in the Eemian brown soil, the low CaCO<sub>3</sub> content of the sediment (EOLE, unpublished) suggests a bias due to carbonate dissolution. In the three upper Saalian assemblages, the preservation of only a few individuals of the dominant species, *P. muscorum*, *T. hispida* and *S. oblonga*, is thus probably due to the downward development of the overlying Eemian soil (units 2a and 2b). In the two basal Saalian assemblages, these three dominant species are associated with *C. columella* and *A. arbustorum*. Such an association of tolerant and cold-adapted species indicates a harsh environment and moister glacial conditions than during the Lower Pleniglacial (Fig. 11). Compared to those of MZ1-P1, Early Weichselian assemblages, located at the base of MZ2-P1, show a low richness increase that might characterize a slightly moister and more vegetated environment. However, this interpretation is not very

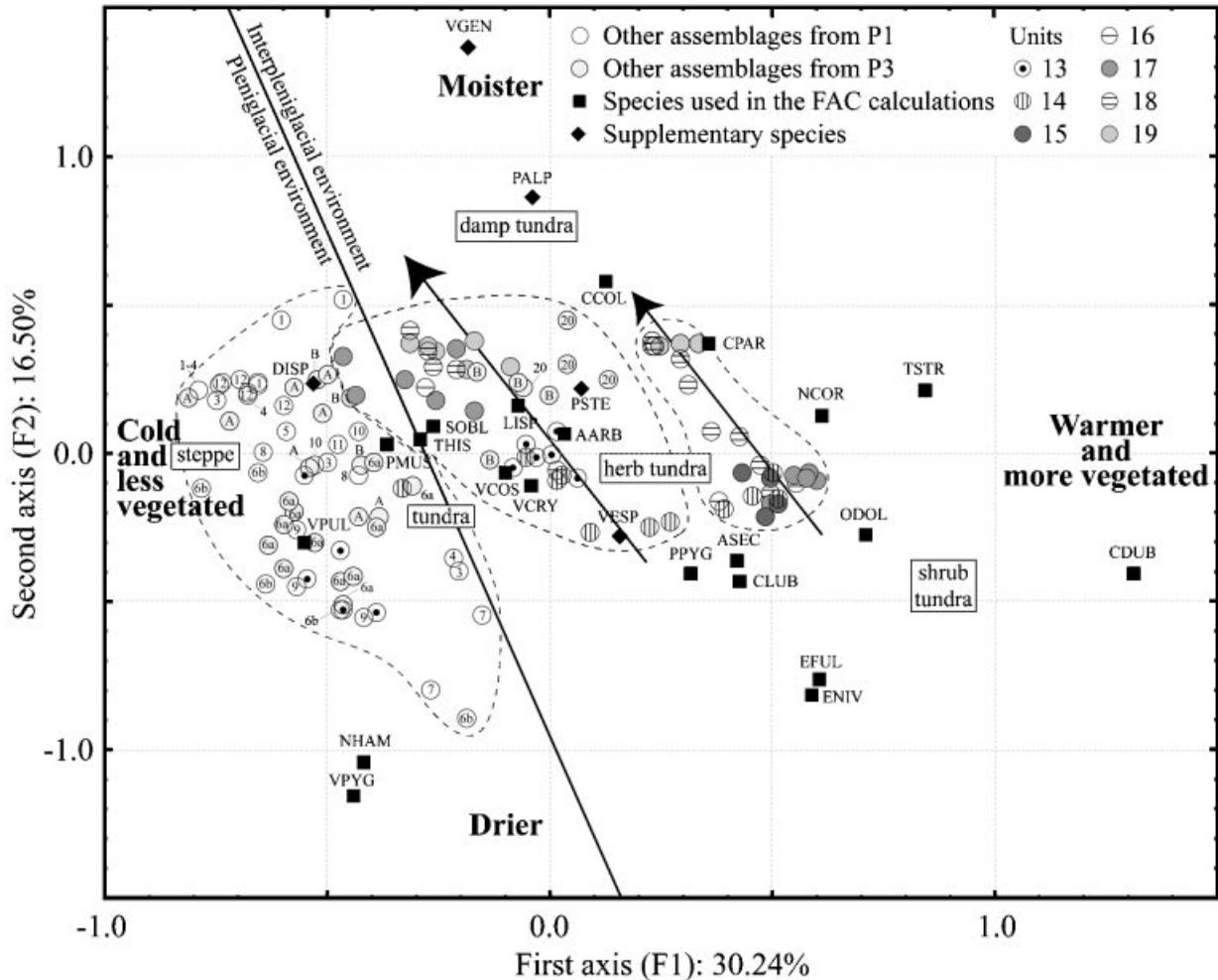


Fig. 11. Synthetic diagram of the correspondence analysis results. Arrows indicate the common general environmental trends recorded by P1 and P3 mollusc assemblages during the Middle Pleniglacial. Explanations as in Fig. 8.

reliable, as extreme values of J/A and J/T ratios for these assemblages suggest probable bias (Fig. 6), and both correspondence analysis and hierarchical ascendant classification cannot clearly distinguish them from unbiased Lower Pleniglacial assemblages.

**Lower Pleniglacial.** – Lower Pleniglacial assemblages, included in units 6 to 13 in P1 and P3, correspond to MZ2-P1, MZ2-P3 and the base of MZ3-P3 (Figs 5, 7). According to its lithological features, unit 6a in P3 has no exact equivalent in P1 (Antoine *et al.* 2001). Mollusc assemblage composition characterizes a slightly moist and shaded steppe to tundra environment that establishes in the lower half and remains stable in the upper one. Unit 6b assemblages have a lower richness than unit 6a assemblages and are plotted just on the left in the CA diagram (Fig. 11), which indicates a slightly more open environment. The regular and similar variations of species abundances and proportions in unit 6a do not suggest that shells were

reworked as sediment particles. Nevertheless, without absolute ages, statistical analysis of molluscan data only does not clarify the relation between both units.

The correlation between units Cpx A and Cpx B in P3 with units 7 to 12 in P1 is also problematic. In MZ2-P1, low abundance and richness, high proportions of *P. muscorum* and low proportions of *T. hispida*, *S. oblonga* and *V. costata*, indicate a cold, dry and poorly vegetated environment in loess units (6b, 8, 10, 12). In contrast, in tundra gleys (units 7, 11), arctic soil (unit 9) and sandy loess (unit 13), species abundance increase and the reappearance of several moisture-loving species, such as *V. pygmaea* and *E. nivalis*, and most of the vegetation requiring species, such as *P. pygmaeum*, *V. pulchella*, *C. lubrica*, *E. fulvus*, *A. secale* and *O. dolium* (Fig. 6), characterize climatic improvements greater than those of the Upper Pleniglacial loess-gley alternation of P3 involving fewer species and no appearances (Moine 2003). In MZ2-P3, low abundance and richness characterize a very cold and poorly

vegetated environment drier in Cpx B dominated by *P. muscorum* than in Cpx A dominated by *T. hispida* and *S. oblonga*. However, extreme values of *J/A* and *J/T* ratios and very low abundances throughout Cpx A and the lower half of Cpx B preclude reliable interpretations, except for the upper half of Cpx B, where *P. muscorum* abundance increases, followed by *T. hispida*, *S. oblonga*, *V. costata* and *T. striolata* (Fig. 4). However, *P. muscorum* proportions (about 60%) still strongly dominate, and the appearance and small abundance increase in *T. striolata* and *V. crystallina* reflect only a slight vegetation increase. Consequently, palaeoenvironmental interpretations of both Lower Pleniglacial molluscan records are different.

In CA diagrams (Figs 9, 11), the random scattering of Lower Pleniglacial mollusc assemblages of both sections among clusters A6, A7, A8, except those of Cpx-P3 grouped in cluster A3, precludes highlighting a relationship between both malacological records from the statistical analysis. Besides, given the sensitivity of species abundance to climatic warming (Moine 2003), the differences between both Lower Pleniglacial abundance records may imply that both sequences do not have the same deposition timing, or do not represent the same time interval, and cannot be correlated in this way. Consequently, on the basis of the geochronological framework and the lithological/pedological interpretations (Antoine *et al.* 2001), the Lower Pleniglacial malacological record of P1 is considered as certainly more complete and more representative of the environmental and climatic changes during this period than the probably reworked P3 colluvium (Fig. 2).

The investigation of the Lower Pleniglacial lithological record of sequences P2 and P4, located 20 m NW and 50 m SW of P3, respectively, highlights the limited lateral extension of units 6a, Cpx A, Cpx B-P3 present in P2 and P3, and units 6b to 11-P1 present only in P1 (Antoine *et al.* 2002). Moreover, horizontal internal structure and deposition of units 6a, Cpx A and Cpx B and regular trends of their species abundances and richness suggest that they do not result from three distinct collapse events that would have mixed reworked shells. They may rather result from phases of intense draining favoured by humidity increases associated with soil and gley development (Léger 1990), but no dating method allows this hypothesis to be checked. The last deposit of the Lower Pleniglacial is a coarse sandy loess layer (units 13, 14) laterally connected with a 5 to 6-m-high sand dune located between P1 and P3 (Antoine *et al.* 2001). The subsequent development of the Gräselberger Boden distinguishes unit 14. The sand deposition implies stronger local winds and a short transportation distance (Pye 1995), probably from the Rhine Valley, as suggested by rare earth element analyses (Rousseau *et al.* 2002). The MZ2-MZ3 boundary occurs at the top of unit 13 in P1, and at its base in P3. Moreover, the malacological transition at the base of unit 13 is more progressive in P3 than in P1, as

highlighted by the plot of uppermost Cpx B assemblages among P3 Middle Pleniglacial assemblages and by minima of the *J/A* and *J/T* ratios in P3 instead of couples of extreme values in P1 probably due to a taphonomic bias of wind action. A reworking of the early sandy deposits in P1, in association or subsequent to the erosion of the top of unit 12, is more likely than a delayed sandy loess deposition to explain the less progressive and earlier poor-to-rich malacofauna transition in P1. Terrestrial molluscs usually dig into the soil for protection against extreme temperature and moisture variations, and the preferential occurrence of death when they are buried may cause a discrepancy between the age of loess deposits and age of their related mollusc populations. However, this hypothesis and its consequences have not been considered as there are no available means of checking them.

The formation of the slope in P1 began with the erosion of unit 12 and was then enhanced by the sand layer deposition (Fig. 3). Topography may also have influenced both vegetation and malacofauna development since the early beginning of the sandy loess deposition. In the sandy loess layer, *P. muscorum* and *V. costata* dominate molluscan assemblages. The presence of *P. sterri* at the base of unit 13-P3 and of *A. secale* in units (13, 14) of P1 and P3 indicates a drier and milder environment than in other units. The appearance of numerous vegetation-requiring species, such as *V. pulchella*, *N. corynodes*, *N. hammonis*, *O. dolium*, *P. pygmaeum*, *C. lubrica*, *V. pygmaea*, *E. fulvus*, *C. parvula*, *C. dubia* and *T. striolata*, implies an important vegetation development, while the occurrence of *C. columella* and *E. nivalis* indicates the persistence of cold and humid places. Given high species abundances, these assemblages without real modern analogues are probably less due to taphonomic bias than to unusual climatic conditions, like a period of highly contrasted seasonality able to favour all these species with somewhat opposite ecological requirements. In addition, trapping and accumulation of the sandy loess may also have been favoured by a more developed vegetation. However, different malacofauna composition (Fig. 11) and total abundance and richness variations toward their synchronous maximums in the middle of unit 14 (Figs 4, 6), probably due to a climatic optimum, reflects different vegetation developments and malacofauna dynamics throughout P1 and P3. The slower colonization of P1 by less ecologically tolerant species may be directly due to the northwest exposure of the 5° slope, probably facing the local dominant winds, or indirectly to a reduced vegetation development.

*Middle Pleniglacial.* – With the exception of the thermokarst filling, the two Middle Pleniglacial records include the same lithological units. Both total richness and abundance are higher than in the Lower Pleniglacial, but abundance remains high and variable, whereas

richness slightly decreases. Proportions of *S. oblonga* and *T. hispida* increase, in contrast to those of *P. muscorum* and *V. costata*. Secondary species, such as *N. hammonis*, *A. secale*, *P. pygmaeum*, *C. lubrica*, *N. corynodes*, *O. dolium*, *E. fulvus* and *E. nivalis*, decrease or disappear, whereas *C. columella* and *P. cf. alpicola* appear and increase especially in P3. Secondary species proportions are higher in P1 than in P3, but follow the same trend, which indicates a more vegetated environment in P1 and similar increase in moisture and decreases in temperature and vegetation throughout the Middle Pleniglacial (Fig. 11). A new phase of warmer and more vegetated environment is also indicated by assemblages of the Lohner Boden (unit 20-P3) at the top of the P3 sequence. The persistence of both rich malacofauna and shrub/herb tundra during the Middle Pleniglacial is probably due to a milder climate and lower seasonal moisture increases resulting from soil ice or snow melt than during both Lower and Upper Pleniglacial. However, several differences follow from the slope context in P1.

First, the presence of an underlying water table under the regressive thermokarst (Fig. 3) suggests that its incision, several metres in width, is due to surface drainage and soil water inflow enhanced by the slope context and probably resulting from soil ice water release or precipitation during a warmer period. Its mollusc assemblages contain *C. dubia*, which is the most vegetation-requiring species of both sequences and presently lives in sparse forest and rocky environments (Table 1). However, this species is present from units 14 to 17 of P1. Therefore, despite its presence and that of wood fragments, no major malacological changes distinguish thermokarst mollusc assemblages from the others or suggest local woodland during its filling.

Second, the tundra gley formation is generally associated with moister conditions and is highlighted by proportional increases in the damp habitat species *S. oblonga* (Figs 5, 7) in P1 Lower Pleniglacial, and P3 Middle and Upper Pleniglacial (Moine 2003), but not in the tilted Middle Pleniglacial deposits of P1. The gley thickness may depend on the duration and/or intensity of these moist phases. Where molluscs have been sampled in P1, gley unit 16 is as thin as in P3 but laterally thickens from the top to the base of the slope (Fig. 3). Solifluction features and small erosion channels, filled with sands and shells, indicate the down slope drainage of water and particles (Antoine *et al.* 2001; Van Vliet-Lanoë 1985) that may explain the thickening of gley unit 16 above the thermokarst. The gley unit 18 is half as thick in P3 as in P1 and the presence of freshwater snails and ostracods at its top in P3 indicates a waterlogged environment with temporary puddles (Figs 4, 5). The slope context in P1 may have favoured the soil water inflow leading to the formation of low ice content permafrost able to thaw more quickly and deeply than in the P3 horizontal context, precluding the formation of both ponds and a

thick gley as in P3. Nevertheless, particle drainage may also explain the thickness of gley unit 18-P1.

Third, *S. oblonga* proportions increase at the top of gley units 16 and 18 and at the base of unit 18 in P3, whereas they remain constant in P1 and seem replaced by increases in proportions of *T. striolata*. Moreover, the damp habitat ecological group is represented only by *S. oblonga* and the semi-open habitat principally by *T. striolata*. The water draining in a slope context may thus prevent water accumulation and favours both vegetation diversification and increases in vegetation-requiring species. Consequently, composition differences of P1 and P3 malacofaunas highlight the drier and more vegetated slope context of P1 during the Middle Pleniglacial and the different response to the same warmer climatic phases impacting the environment.

Excepting *S. oblonga* proportions, no other malacological parameter previously related to millennial timescale climatic changes for the Upper Pleniglacial record of P3 (Moine 2003) has been identified and related to the loess-gley alternation of both Middle Pleniglacial records. Both higher compaction of Middle Pleniglacial sediments and low population density, combined with the sampling method limits, and the different topographical context make more difficult the distinction and correlation of short fluctuations of the malacofauna composition and ecological parameters between both sequences and with lithological and millennial timescale climatic changes, i.e. stadial-interstadial transitions.

#### *Comparisons with other palaeoclimatic records*

In western Europe, only the loess sequence of Achenheim (Alsace, France) presents a continuous malacological record including the Lower and Middle Pleniglacial (Rousseau 1987). However, its lower sampling resolution and the lack of absolute ages preclude identification of rapid environmental changes and precise correlations with Nussloch sections. As new absolute ages are not yet available in Nussloch, correlations proposed by Antoine *et al.* (2001) with interstadial oscillations or complexes of the NW European biostratigraphical framework (Behre 1989; Caspers & Freund 2001) have not been modified, i.e. the Gräselberger Boden (unit 14) with Moershoofd/Hengelo intervals, the thermokarst (unit 15) with Huneborg I/II oscillations and the Lohner Boden (unit 20) with the Denekamp complex. A comparison with this biostratigraphical framework and with that defined for the northern Alpine Foreland by Preusser (2004) shows that the Lower Pleniglacial malacological record of P1 is more complex. It includes at least four diversification phases of the malacofauna, probably related to interstadials, whereas the same period is only characterized by the Schalkholz stadial in palynological frameworks that are generally less expanded than loess sequences during the coldest Pleniglacial periods.

On the contrary, the Middle Pleniglacial interstadials identified in pollen sequences cannot be clearly correlated with diversification phases of the malacofauna in both P1 and P3 records owing to their higher compaction. Nevertheless, given their similar lithological record, a higher mollusc sampling resolution should improve the identification and characterization of the interstadial environmental changes during the Middle Pleniglacial. Consequently, in parallel with the definition of a European stratigraphical framework for loess-paleosol sequences, which is still in progress, the appropriate sampling of malacological records will help to identify and characterize millennial timescale environmental changes, fill temporal lacks of pollen sequences and alleviate their absence in continental Europe.

## Conclusion

The two sections, P1 and P3, sampled in close proximity in the Nussloch quarry provide two lithological and malacological records encompassing the Weichselian Lower and Middle Pleniglacial. The P1 loess section yields the most complete and precise malacological record of the Lower Pleniglacial available in western Europe, with at least three phases of vegetation development and climatic improvement probably linked with interstadial warmings, whereas the deposition timing of the P3 colluvium remains unclear. The Lower-Middle Pleniglacial transition is marked by a diversification of the malacofauna, an increase in all species abundances and in proportions of vegetation-requiring taxa that characterizes a milder climate and a steppe-to-herb/shrub-tundra vegetation shift. Throughout the Middle Pleniglacial, the two molluscan records highlight similar trends to increasing moisture and declining vegetation cover, except at the top of P3 in the Gräselberger Boden cambisol where they characterize a warmer and more vegetated environment. Nevertheless, on the basis of the malacofauna composition, shorter environmental changes cannot easily be identified and correlated between the two sequences. This is because of the higher compaction of Middle Pleniglacial loess and the slope context in P1 draining local moisture, generating a locally drier environment than in the horizontal context of P3, and different malacological records for the same climatic changes, that have to be taken into account in any comparison between malacological records and other palaeoenvironmental records. Succinct comparisons with the western European biostratigraphical framework, mainly based on pollen records, show the potential of molluscan records from loess sequences in improving this framework for glacial times, especially Weichselian Lower and Upper Pleniglacial intervals.

*Acknowledgements.* – The study was supported by the EOLE project (Enregistrement des Événements Eoliens dans les séquences Lössiques du dernier cycle climatique en Europe, CNRS ECLIPSE

Program) and by a grant from the French Research Ministry. We thank Dr. Eike Neubert for his help in identifying *Neostyriaca corynodes* and Dr. Alex Chepstow-Lusty and Dr. William McCoy for assistance with the English. We also thank the Heidelberger Zement Company for allowing us access to the Nussloch quarries. The original manuscript was considerably improved thanks to valuable comments of the two reviewers, Dr. Richard Preece and Prof. Bernard Lauriol, and to the editorial help of Professor Jan A. Piotrowski. This is an ISE-M contribution 2005–007 and LDEO contribution 6768.

## References

- Adam, W. 1960: *Mollusques. I. Mollusques terrestres et dulcicoles*. 402 pp. Institut royal des Sciences naturelles de Belgique, Bruxelles.
- Antoine, P., Rousseau, D.-D., Hatté, C., Zöller, L., Lang, A., Fontugne, M. & Moine, O. 2002: Événements éoliens rapides en contexte loessique: l'exemple de la séquence du pléniglaciaire supérieur weichsélien de Nussloch (vallée du Rhin, Allemagne). *Quaternaire* 13, 199–208.
- Antoine, P., Rousseau, D.-D., Zöller, L., Lang, A., Munaut, A.-V., Hatté, C. & Fontugne, M. 2001: High-resolution record of the last Interglacial–glacial cycle in the Nussloch loess-paleosol sequences, Upper Rhine Area, Germany. *Quaternary International* 76/77, 211–229.
- Behre, K.-E. 1989: Biostratigraphy of the last glacial period in Europe. *Quaternary Science Reviews* 8, 25–44.
- Benzecri, J. P. & Benzecri, F. 1980: *Pratique de l'analyse de données*. 424 pp. Dunod, Paris.
- Carter, S. P. 1990: The stratification and taphonomy of shells in calcareous soils: implications for land snail analysis in archaeology. *Journal of Archaeological Science* 17, 495–507.
- Caspers, G. & Freund, H. 2001: Vegetation and climate in the Early- and Pleni-Weichselian in northern central Europe. *Journal of Quaternary Science* 16, 31–48.
- Germain, L. 1930: *Mollusques terrestres et fluviatiles*. Librairie de la Faculté des Sciences. 477 pp. Paris.
- Gniesser, D. 1997: *Aminostratigraphy of Loess-Paleosol Sequences in Southern Germany*. M.Sc. thesis, University of Massachusetts, 131 pp.
- Hatté, C., Pessenda, L.-C., Lang, A. & Paterne, M. 2001: Development of accurate and reliable <sup>14</sup>C chronologies for loess deposits: application to the loess sequence of Nussloch (Rhine valley, Germany). *Radiocarbon* 43, 611–618.
- Kerney, M. P., Cameron, R. A. D. & Jungbluth, J. H. 1983 *Die Landschnecken Nord- und Mitteleuropas*. 384 pp. Paul Parey, Hamburg.
- Lang, A., Hatté, C., Rousseau, D.-D., Antoine, P., Fontugne, M., Zöller, L. & Hambach, U. 2003: High resolution chronologies for loess: comparing AMS-<sup>14</sup>C and optical dating results. *Quaternary Science Reviews* 22, 953–959.
- Lauriol, B., Cabana, Y., Cinq-Mars, J., Geurts, M.-A. & Grimm, F. W. 2002: Cliff-top eolian deposits and associated molluscan assemblages as indicators of Late Pleistocene and Holocene environments in Beringia. *Quaternary International* 87, 59–79.
- Léger, M. 1990: Loess landforms. *Quaternary International* 7/8, 53–61.
- Leonard, A. B. 1952: Illinoian and Wisconsinian molluscan faunas in Kansas. *University of Kansas Paleontological Contributions. Mollusca*, 1–38.
- Likharev, I. M. & Rammelmeier, E. S. 1962: *Terrestrial Mollusks of the Fauna of the U.S.S.R.* 574 pp. Oldbourne Press, Jerusalem.
- 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.

- Ložek, V. 1964: Quartärmollusken der Tschechoslowakei. *Rozpravy Ustředního ústavu geologického* 31, 1–374.
- Ložek, V. 1968: The loess environment in Central Europe. In Schultz, C. & Frye, J. C. (eds.): *Loess and Related Eolian Deposits of the World, Proceedings 7th INQUA Congress, Boulder, 1965*, 67–80. University of Nebraska Press, Lincoln.
- Meyrick, R. A. & Preece, R. C. 2001: Molluscan successions from two Holocene tufas near Northampton, English Midlands. *Journal of Biogeography* 28, 77–93.
- Moine, O. 2003: *Analyse des changements rapides de l'environnement à l'aide des faunes de mollusques terrestres durant la dernière période glaciaire en domaine continental européen*. Doctoral dissertation, University of Montpellier II, 260 pp.
- Moine, O., Rousseau, D.-D., Jolly, D. & Vianey-Liaud, M. 2002: Paleoclimatic reconstruction using Mutual Climatic Range on terrestrial mollusks. *Quaternary Research* 57, 162–172.
- Preece, R. C. 1998: Mollusca. In Bridgland, D. R. & Preece, R. C. (eds.): *Late Quaternary Environmental Change in North-west Europe. Excavations at Holywell Coombe, South-east England*, 158–212. Chapman & Hall, London.
- Preusser, F. 2004: Towards a chronology of the Late Pleistocene in the northern Alpine Foreland. *Boreas* 33, 195–210.
- Puisségur, J.-J. 1976: Mollusques continentaux quaternaires de Bourgogne. Significations stratigraphiques et climatiques. Rapports avec d'autres faunes boréales de France. *Mémoires géologiques de l'Université de Dijon* 3, 1–241.
- Pye, K. 1995: The nature, origin and accumulation of loess. *Quaternary Science Reviews* 14, 653–667.
- Rossignol, J., Moine, O. & Rousseau, D.-D. 2004: New data from the Last Glacial loess deposits in mid-continent North America. Comparison between Buzzard's Roost and Eustis mollusk sequences, Nebraska, USA. *Boreas* 33, 145–154.
- Rousseau, D.-D. 1987: Paleoclimatology of the Achenheim series (Middle and Upper Pleistocene, Alsace, France). A malacological analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59, 293–314.
- Rousseau, D.-D. 2001: Loess biostratigraphy: new advances and approaches in mollusc studies. *Earth Science Reviews* 54, 157–171.
- Rousseau, D.-D., Antoine, P., Hatté, C., Lang, A., Zöller, L., Fontugne, M., Ben Othman, 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.
- Solem, A. 1984: A world model of land snail diversity and abundance. In Solem, A. & Van Bruggen, A. C. (eds.): *World-Wide Snails. Biogeographical Studies on Non-Marine Mollusca*, 6–23. E. J. Brill & W. Backhuys, Leiden.
- Sümege, P., Kertész, R. & Hertelendi, E. 2002: Environmental change and human adaptation in the Carpathian Basin at the late glacial/postglacial transition. In Jerem, E. & Biro, K. T. (eds.): *Archaeometry 98. Proceedings of the 31st Symposium*, Budapest, 26 April to 3 May 1998. Volume I, 170–177. Archaeopress, Oxford.
- Van Vliet-Lanoë, B. 1985: Frost effects in soils. In Boardman, J. (eds.): *Soils and Quaternary Landscape Evolution*, 117–158. John Wiley, Chichester.
- Wu, N. Q., Liu, T. S., Liu, X. P. & Gu, Z. Y. 2002: Mollusk record of millennial climate variability in the Loess Plateau during the Last Glacial Maximum. *Boreas* 31, 20–27.
- Zilch, A. & Jaeckel, S. G. A. 1962: *Mollusken*. 293 pp. Quelle Meyer, Leipzig.
- Zöller, L., Stremme, H. & Wagner, G. A. :1988: Thermolumineszenz-datierung an Löss-Paläoboden-Sequenzen von Nieder-, Mittel- und Oberrhein/Bundesrepublik Deutschland. *Chemical Geology* 73, 39–62.