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Malacofauna of Late Quaternary loess-like deposits in the Polish Carpathians

ABSTRACT: Quaternary loess-like loams covering the major part of the Polish Carpathians locally contain plant remains, snail shells and mammal bones. Molluscan assemblages found in loamy sediments are similar to malacofauna described from the loess series of the Carpathian Foreland. They comprise nearly 20 taxa, the most characteristic being *Succinea oblonga elongata* SANDBERGER, *Pupilla loessica* LOŽEK and *Vallonia tenuilabris* (BRAUN). The malacofauna is mainly connected with the descending phases of the Brørup interstadial and the interpleniglacial period, which were dated by C-14 method, as well as with the late glacial sediments. The variation of malacofauna, analysed with taxonomic methods, reflects the environmental conditions of deposition and the ecological conditions under which fauna and flora developed during the last glacial period.

INTRODUCTION

Loess-like deposits are the most widespread Quaternary sediments in the Carpathians. They cover the major part of the Carpathian Foothills and intramontane depressions, while in the Beskidy and Bieszczady Ranges they occur mainly in the lower parts of slopes and on the Pleistocene river terraces. The sediments are represented by several lithologic types of the loess--like loams, locally bedded and/or with intercalations of sand and gravel, sandy loams with an admixture of rock detritus, and unbedded loams containing blocks and fragments of sandstones, limestones and marls. The series of loamy sediments may attain a thickness of 10 or even 20 meters. They sometimes contain fossil soil horizons and intercalations of silts with plant detritus, peaty silts or peats. Near the outcrops of limestones, marls and sandstones with calcareous cement, the loess-like deposits have an admixture of calcium carbonate. In such sediments snail shells, as well as bones and teeth of mammals, may be preserved.

The Quaternary loess-like loams of the Carpathians were described by several authors as sediments of different origin. Comprehensive studies of the geological conditions of occurrence, the structure and lithology of loams and the corresponding slope deposits were carried out by KLIMASZEWSKI

(1948, 1971), STUPNICKA (1960), STARKEL (1960) and CEGŁA (1960, 1963). The malacofauna of these sediments is as yet little known. It was found in a few localities in Slovakia and Moravia (LOŽEK 1964, 1967). In the Polish Carpathians it was described from one profile only (Krościenko; KLIMASZEWSKI & *al.* 1950), and the occurrences of snail shells were reported by ŚRODOŃ (1968), MALICKI (1950), KULCZYCKI & HALICKI (1950). Systematic studies of the malacofauna from the Carpathian loamy sediments were undertaken by the present author in co-operation with Dr. A. WÓJCIK and Dr. W. ZUCHIEWICZ, and presented in a few preliminary reports (ALEXANDROWICZ 1985a, 1987, 1988; ALEXANDROWICZ & WÓJCIK 1986; ALEXANDROWICZ & ZUCHIEWICZ 1988a, b). In two profiles malacologic analysis was completed by C-14 dating made by Dr. M. PAZDUR, Institute of Physics, Silesian Polytechnic in Gliwice.

MALACOFAUNA LOCALITIES

Investigations were carried out in more than 80 outcrops, but malacofauna was found in 17 localities. At 12 sites abundant snail shells represented a few species, whereas in 5 localities only single specimens were found, usually belonging to one taxon. From 6 other sites, now inaccessible, malacofauna was reported by the other authors (*see* Text-fig. 1).

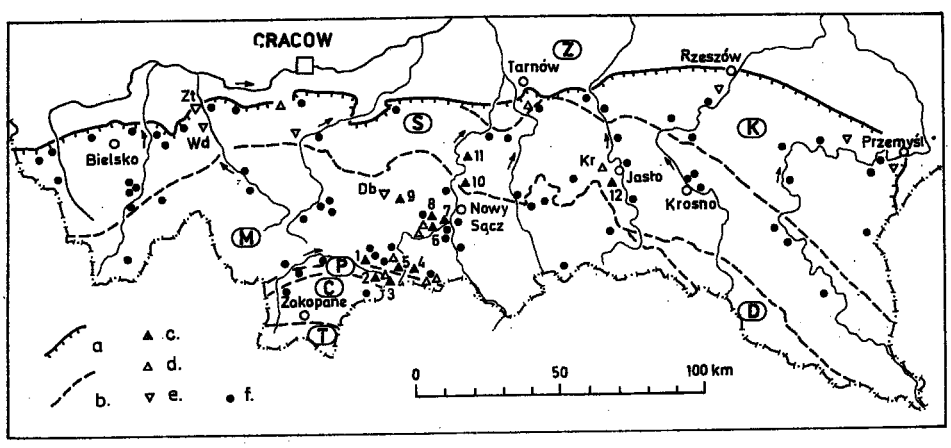

Fig. 1. Localities with mollusc-bearing loess-like deposits in the Polish Carpathians
a — northern margin of the Carpathians, **b** — boundaries of tectonic units: **T** — Tatra Mts, **C** — Podhale Flysch, **P** — Pieniny Klippen Belt, **M** — Magura nappe, **D** — Dukla nappe, **S** — Silesian nappe, **K** — Skole nappe, **Z** — Fore-Carpathian Depression
Localities with mollusc-bearing sediments: **c** — localities described in the paper, **d** — localities mentioned in the paper, **e** — localities described by other authors, **f** — localities with loess-like deposits devoid of fauna

MIZERNA

A profile of loess-like loams (*1* in Text-fig. 1) is exposed in a small brickyard near Czorsztyn, at the upper edge of the Dunajec terrace rising 20-25 m above the river level on the north slope of the valley. In outcrops situated in the vicinity of this site, in the villages of Maniowy and Brzeziny, BIRKENMAJER & ŚRODOŃ (1960) described gravels with an insert of clays and peats.

In the Mizerna brickyard the gravels are overlain by grey unbedded loess-like deposits containing scarce pebbles and sandstone fragments. Two bones of a horse, *Equus* sp. (determined by Dr. A. NADACHOWSKI), were found in this layer. The successive layer is represented by dark-grey silty loams with a 5–8% admixture of organic matter. The loams contain a malacofaunal assemblage comprising 7 taxa, with abundant *Succinea oblonga elongata* SANDBERGER and *Pupilla loessica* LOŽEK. Their age determined by C-14 method is 27.4 ka y.BP. The uppermost part of the profile consists of yellow loams and sandy loams with single fragments of intensely weathered sandstones and shales. The loamy series in the profile attains a thickness of 6m (Text-fig. 2).

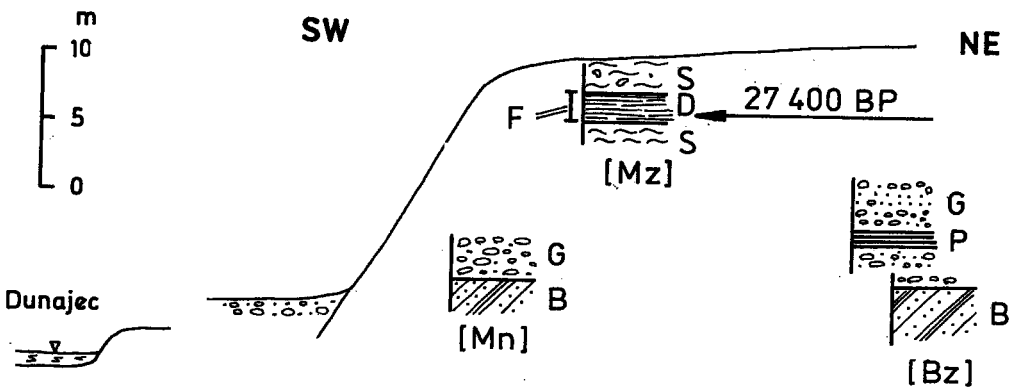

Fig. 2. Mizerna near Czorsztyn
Mz – outcrop in the brickyard at Mizerna, **Mn** – outcrop at Maniowy, **Bz** – outcrop at Brzeziny
Lithology (for Text-figs 2–5 and 7): B – basement of Quaternary sediments, W – fossil soil, G – sands and gravels, A – loamy sands, L – yellow sandy loams, S – loams with rock detritus, D – grey silty loams, P – peaty silts and peats, F – occurrence of molluscs

NIEDZICA

The Quaternary sediments exposed near the Niedzica castle (*2* in Text-fig. 1) lie on the 20-24m high erosional terrace of the river Dunajec, covering intensely folded Cretaceous limestones, marls, sandstones and shales (Text-fig. 3). The lowermost part of the profile is made up of sand and gravel containing numerous pebbles of rocks supplied from the Tatra Mts (granites and quartzites). The gravels are overlain by sandy loams with rock detritus, grading into sandy and silty loams with fauna and higher up, into sandy loams with numerous fragments of limestones, marls and sandstones. The loamy series in this profile is more than 10m thick. From the yellow silty loams comes the incomplete skeleton of a mammoth, *Mammuthus primigenius* (BLUMENBACH), described by KULCZYCKI & HALICKI (1960). The molluscan assemlage found in these loams includes 6 taxa and is characterized (ALEXANDROWICZ 1985a) by the dominant content of *Succinea oblonga elongata* SANDBERGER.

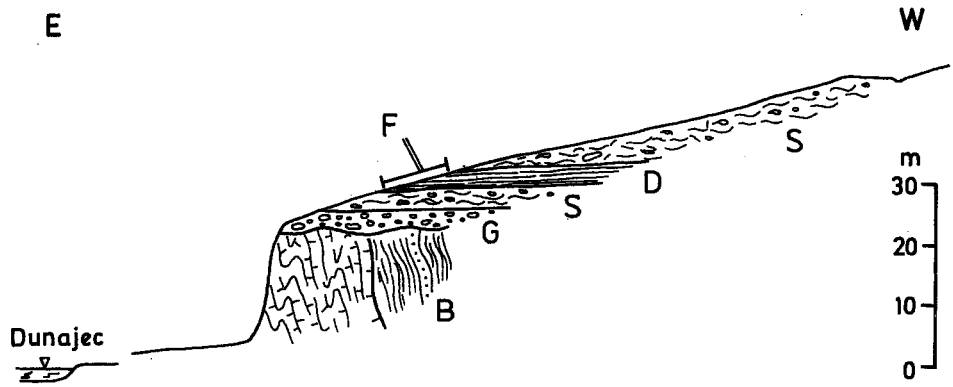

Fig. 3. Niedzica; explanation as for Text-fig. 2

SROMOWCE – SZCZAWNICA – KROŚCIENKO

Loess-like loams containing mollusc shells occur in several localities situated along the Dunajec valley. The profile exposed at Sromowce-Kąty (*3* in Text-fig. 1) comprises grey clays abounding in plant remains and the superjacent sandy loams (DYAKOWSKA 1947). The C-14 dating has revealed that the clays with flora are older than 50 ka y.BP (MAMAKOWA, MOOK & ŚRODOŃ 1975). In their top part scarce snail shells representing 3 taxa were found. Single specimens of *Succinea oblonga elongata* SANDBERGER were also found in the sandy loams with rock detritus, exposed in the Limbargowy stream at Kąty.

At Szczawnica (*4* in Text-fig. 1) numerous snail shells were found by Professor K. BIRKENMAJER in sandy loams on the right bank of the Zdrojowy stream. The molluscan assemblage consists of 7 taxa, including abundant *Succinea*, *Pupilla* and *Clausilia*. Fragments of shells of *Succinea oblonga elongata* SANDBERGER also appear in yellow sandy loams with rock detritus exposed at a few sites at Szlachtowa and Biała Woda, in the Grajcarek river valley to the east of Szczawnica.

Two sites with fauna are known at Krościenko. In the Ociemny stream valley (*5* in Text-fig. 1) loams abounding in limestone, marl and sandstone fragments contain scarce snail shells assigned to three species. Similar sediments, owing their origin to solifluction, were accessible in the profile of a well on the high terrace of the Dunajec at Krościenko. From the lower part of this profile KLIMASZEWSKI & *al.* (1950) described grey loams with plant remains (e.g. *Dryas octopetala*) and malacofauna. The letter was determined by Professor J. URBAŃSKI, who recognized 5 taxa: *Succinea oblonga elongata* – one adult and one juvenile specimen – determined as "*S. oblonga*" with the indication of features corresponding to the "*elongata*" variety; *Pupilla loessica* – a few specimens determined as "*Pupilla muscorum*" without a tooth in the aperture (a feature typical of the species *P. loessica* which was defined at a later date then URBAŃSKI's determination); *Columella columella* – numerous shells determined by the cited author as "*C. edentula columella*", the form now recognized as a separate species; *Clausilia dubia* – three shells; *Clausilia* sp. – indeterminable shell fragments, possibly of the same species.

PŁUSY

Sediments containing mollusc shells occur on the left slope of the Dunajec valley, in a small gully between Gołkowice and Podegrodzie (*6* in Text-fig. 1). The site comprises two outcrops described by ZUCHIEWICZ (1985). One is a scarp cutting the Dunajec terrace with a height of

15-20m (*Pt A* in Text-fig. 4). The lower part of the profile is made up of unbedded loams devoid of fossils. They are overlain by sandy loams intercalated by irregular layers and lenses of sands and loams with the debris of flysch sandstones, marls and shales derived from the Magura nappe. All the sandy-gravel inserts contain scarce snail shells representing 4 taxa.

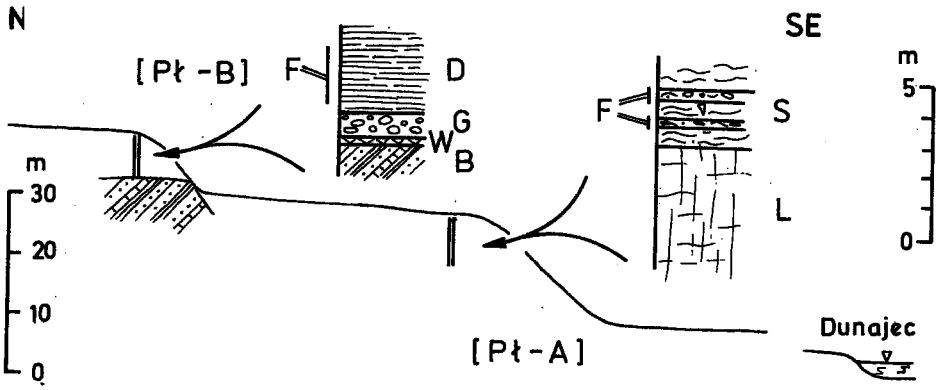

Fig. 4. Płusy: **Pł-A** – lower outcrop (Płusy *A*), **Pł-B** – upper outcrop (Płusy *B*); explanation as for Text-fig. 2

In the other outcrop gravels and loams are exposed. They cover the rock socle of the Dunajec terrace rising to 25-30m above the river level (*Pt B* in Text-fig. 4).The top surface of the flysch rocks represented by sandstones, marls and shales (Łącko Beds) shows evidence of weathering and pedogenesis. It is covered with sands and gravels containing numerous pebbles of granites and quartzites supplied from the Tatra Mts. On the gravels there rest sandy and silty loess--like loams abounding in snail shells. The malacofauna assemblage consists of 8 taxa, including numerous *Pupilla*, *Vallonia* and *Helicopsis*.

Single shells of *Succinea oblonga elongata* SANDBERGER were found in two outcrops of yellow loams situated on the left bank of the Dunajec valley to the south of the site described above, at Jazowsko and Naszacowice.

PODEGRODZIE – JURASOWA

Loess-like loams containing poor malacofauna occur in a few small outcrops between these villages (*7*, *8* in Text-fig. 1). The profile in the southern part of Podegrodzie comprises yellow loams passing upwards into loams with intercalations and lenses of gravels, and into loams with rock detritus. In the upper part of this profile snail shells assigned to three species were found, including numerous specimens of *Succinea oblonga elongata* SANDBERGER. Silty loams with inserts of fine-grained sand are exposed in another outcrop, on the left bank of a stream at Jurasowa. They contain a molluscan assemblage that consists of 8 taxa reprenented by few specimens.

LIMANOWA – SOWLINY

Slope sediments formed by solifluction are exposed in a large brickyard situated in the western part of the town of Limanowa, on the left slope of the Sowlina stream vallex (*9* in Text--fig. 1). They are represented by grey and yellowish grey sandy loams intercalated by loams containing numerous sandstone and shale fragments. The rock debris locally forms large

accumulations, appearing as lenses in the loams (Text-fig. 5). In the lower part of the profile there is a peat layer, now inaccessible (ŚRODOŃ 1987). A sample of this peat, given to the author by Professor A. ŚRODOŃ, was C-14 dated as 29.6 ka y.BP. The loams contain plant remains and abundant snail shells. The malacofaunal assemblage consists of 6 taxa, *Succinea oblonga elongata* SANDBERGER being most amply represented.

At Dobra, about 12 km west of Limanowa (*Db* in Text-fig. 1), similar sediments contain in their lower part abundant plant remains, the age of which was determined at 32.55 ka y.BP by C-14 dating (ŚRODOŃ 1968, KLIMASZEWSKI 1971).

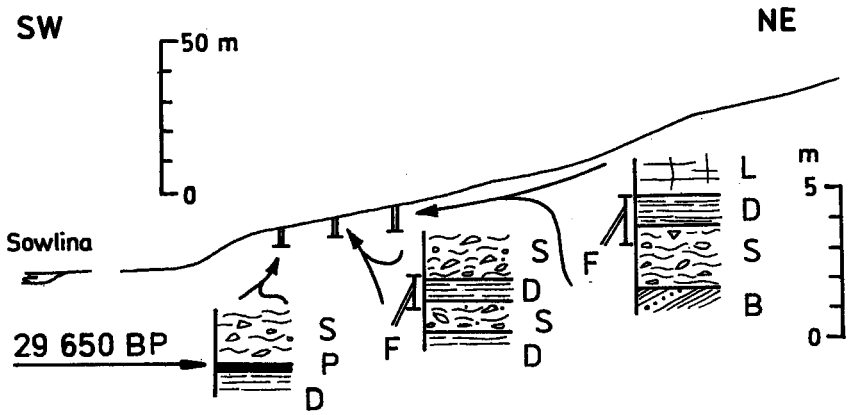

Fig. 5. Sowliny near Limanowa; explanation as for Text-fig. 2

SIENNA

Yellow sandy loams and grey loams with numerous fragments of sandstones and shales are exposed in a small brickyard near the church at Sienna (*10* in Text-fig. 1). A peat layer was reported from their bottom (ALEXANDROWICZ & ZUCHIEWICZ 1988a). The sediments abound in snail shells representing 9 taxa, primarily *Succinea oblonga elongata* SANDBERGER and *Pupilla loessica* LOŽEK.

ROZTOKA

At 14-18m high terrace on the right of the Dunajec river near Rożnów (*11* in Text-fig. 1) gravels are overlain by yellow loess-like loams (locally 8m thick) which were dated with thermoluminiscence method by Dr. J. BUTRYM (Institute of Earth Sciences, Lublin University). Three TL datings range between 27 and 17 ka y.BP (ALEXANDROWICZ & ZUCHIEWICZ 1988b). The loams contain malacofauna representing 9 taxa. In the lower part of the profile the assemblage is the richest, including species typical of steppes (*Helicopsis striata* MÜLLER, *Pupilla sterri* VOITH), while in the upper part species with moderate ecological requirements are dominant (Text-fig. 6).

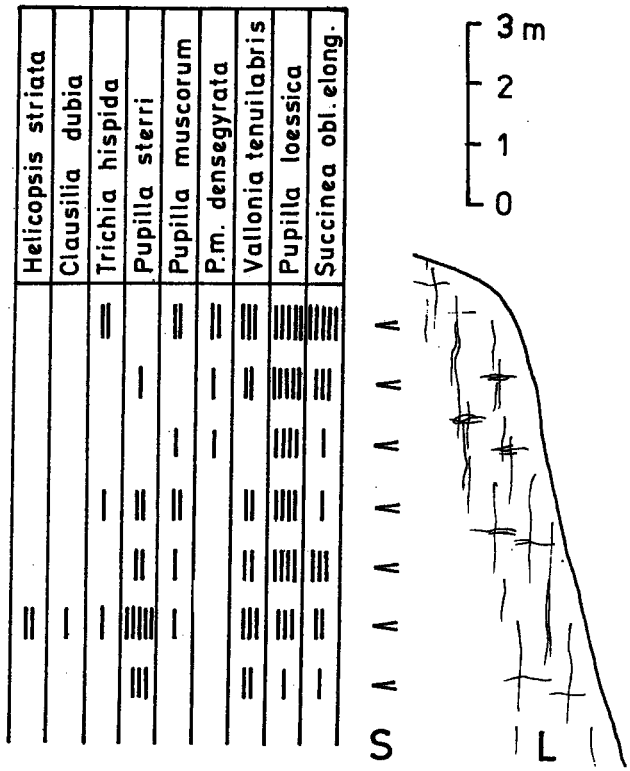

Fig. 6. Malacological profile of the outcrop at Roztoka
L – loess-like loams, S – sampling sites

OSOBNICA – PUSTKI

Vistulian sandy and loamy sediments are exposed in a large outcrop near the confluence of the rivers Bednarka and Ropa, about 5 km west of Jasło (*12* in Text-fig. 1). The outcrop cuts a wide flattening rising to 20-25m above the level of the river Ropa. The lower part of the profile is made up of sands and grey sandy loams with intercalations of fine-grained gravels. Its top part is covered with fossil soil with limonite concretions and a trace of illuvial horizon. The higher part of the profile is represented by yellow and grey loess-like loams with sandy silt inserts with a total thickness of more than 5m (ALEXANDROWICZ & WÓJCIK 1986). The loams resting directly on the soil abound in snail shells (Text-fig. 7). The assemblage comprises 8 taxa of which *Pupilla muscorum* (LINNAEUS) and *Vallonia tenuilabris* (BRAUN) are most abundant.

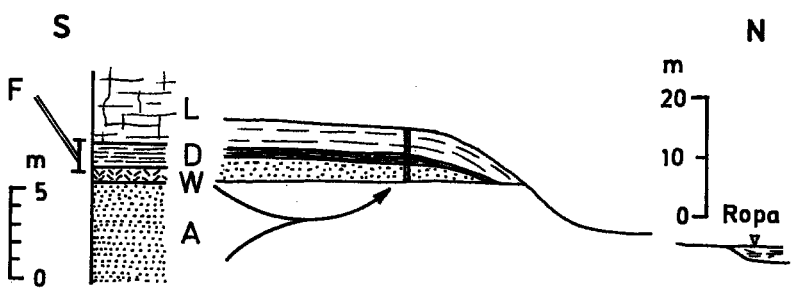

Fig. 7. Osobnica near Jasło; explanation as for Text-fig. 2

OTHER LOCALITIES

Loess-like deposits containing snail shells were found in several localities in the Carpathian Foothills. SOBOLEWSKA, ŚRODOŃ & STARKEL (1964) described a profile of slope sediments comprising loams with silt and sand intercalations from a brickyard at Wadowice (*Wd* in Text-fig. 1). In the bottom part of the profile a peat insert occurs, its age being older than 40 ka y.BP. In the loams above the peat, a few fragments of *Succinea* shells were found. Sandy loams and grey silts with plant detritus, more than 40 000 years old, were also described from Zator (*Zt* in Text-fig. 1). Bones of vertebrates but no molluscs were found in these sediments (KOPEROWA & ŚRODOŃ 1965).

In a brickyard at Myślenice snail shells were reported from silty loams intercalated by loams with rock detritus (CEGŁA & STARKEL 1967, ŚRODOŃ 1968). The outcrop is non-existent now, but single specimens of *Succinea oblonga elongata* SANDBERGER could be found there ten years ago.

Loess-like loams with inserts of fine-grained sand are exposed at Rzozów near Skawina. They contain shells of *Succinea oblonga elongata* SANDBERGER and *Pupilla loessica* LOŽEK. Similar sediments with single fragments of snail shells are known from the area of Gdów and Tarnowiec. Loams defined as bedded loesses containing numerous shells of *Succinea* and *Pupilla* occur in three localities between Rzeszów and Przemyśl (MALICKI 1950).

A site with Vistulian fauna was found near Jasło by Dr. A. WÓJCIK, and called Jasło-Bryły. On the left side of the Wisłoka valley at Krajowice, about 5 km north of Jasło, ashen-grey and brown silts rest on the terrace rock socle made up of the Krosno Beds. They contain shells of aquatic molluscs: *Valvata cristata* MÜLLER, *Armiger crista* (LINNAEUS), *Hippeutis complanatus* (LINNAEUS), *Gyraulus laevis* (ALDER), *Lymnaea peregra* (MÜLLER), *Pisidium nitidum* (JENYNS), *P. milium* HELD, *P. subtruncatum* MALM, as well as shells of land snails: *Pupilla loessica* LOŽEK and *Succinea oblonga elongata* SANDBERGER. These sediments grade upwards into peat silts and peats with abundant plant remains. The C-14 dating indicates that the bottom part of peat silts is older than 45 ka y.BP, whereas an age of 35.5 and 34.3 ka y.BP was determined from the top part. The silts with fauna and flora attain a thickness of about 1m and are overlain by a thick loamy series with sand intercalations (*see* ALEXANDROWICZ, MAMAKOWA & WÓJCIK 1985).

MALACOFAUNAL ASSEMBLAGES

The malacofauna of loess-like deposits is represented by 18 species of snails, and by the shells of slugs determined conventionally as the Limacidae (Table 1). The structure of molluscan assemblages, taking into account the indices of constancy and dominance of taxa (*C* and *D* in Table 1), shows that the principal components are two species: *Succinea oblonga elongata* SANDBERGER and *Pupilla loessica* LOŽEK. Four species, viz. *Vallonia tenuilabris* (BRAUN), *Pupilla muscorum* (LINNAEUS), *Clausilia dubia* DRAPARAUD, and *Columella columella* (MARTENS), are characterized by medium values of the two indices, while the remaining taxa are represented by few specimens or appear in a few localities only. Seven species, having minimum values of *C* and *D* indices, may be regarded as accessory components of the malacofauna in question (Text-fig. 8).

The recognized molluscan assemblages found in particular localities differ from one another in the number of taxa and in presence or dominance of some characteristic species (Table 1). The similarities and differences between these assemblage were determined on the basis of taxonomic analysis carried out by quantitative method, using STEINHAUS' formula (MARCZEWSKI & STEI-

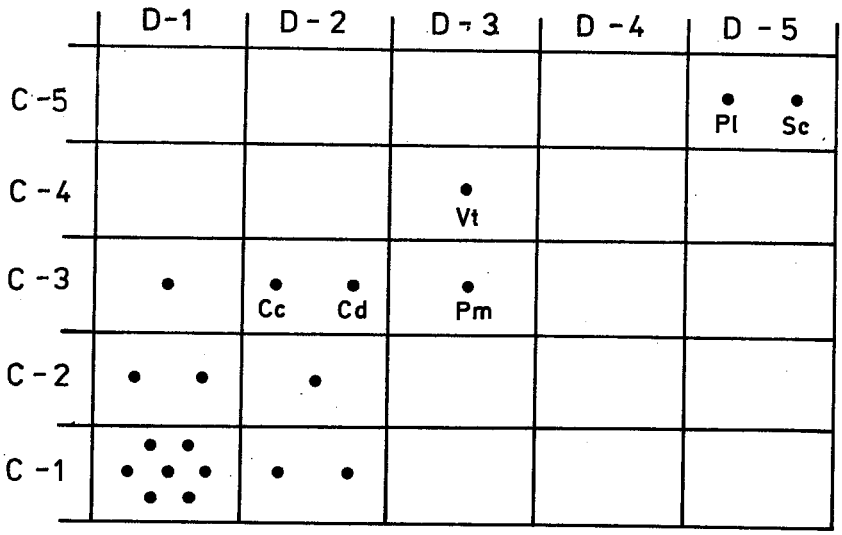

Fig. 8. Indices of constancy and dominance of species in molluscan assemblages from the Carpathian loess-like deposits
C-1, ... C-5 – classes of constancy index, D-1, ... D-5 – classes of dominance index
Sc – *Succinea oblonga elongata*, **Pl** – *Pupilla loessica*, **Vt** – *Vallonia tenuilabris*, **Pm** – *Pupilla muscorum*, **Cd** – *Clausilia dubia*, **Cc** – *Columella columella*

Table 1

Malacofauna of Late Quaternary loess-like deposits in the Polish Carpathians
C – constancy index, **D** – dominance index
Number of mollusc shells (in logarithmic scale): **I** – 1-3 specimens, **II** – 4-9, **III** – 10-31, **IV** – 32-99, **V** – 100-316, **VI** – 317-999

Taxon	Localities 1	2	3	4	5A	5B	6A	6B	7	8	9	10	11	12	C	D
Semilimax kotulai	III				I					I		I		I	2	1
Arianta arbustorum		I													1	1
Pupilla sterri								II					IV		1	2
Chondrula tridens								I							1	1
Helicopsis striata								IV					III		1	2
Vertigo parcedentata	III														1	1
Pupilla muscorum		II		III	I			V		II		I	II	V	3	3
Pupilla musc.densegyrata												I	II	IV	2	2
Pupilla musc.bidentata								I							1	1
Pupilla loessica	IV	III	II	III	I	II	II	V	I	II	III	IV	VI	II	5	5
Vallonia costata								I							1	1
Vallonia tenuilabris		II	I	II			I	IV		I		III	IV	IV	4	3
Columella columella	I			I		III	II				II	II			3	2
Euconulus fulvus										I					1	1
Clausilia dubia		II		III		I		III		I	I	I	I		3	2
Trichia hispida				II				I				I	II		2	1
Limacidae	I							I	I	I	I			I	3	1
Succinea oblonga elongata	V	VI	III	IV	III	II	IV	V	III	II	V	V	V	II	5	5
Lymnaea truncatula	I						I				I				1	1
Gyraulus laevis														I	1	1

NHAUS 1959, ALEXANDROWICZ 1977). The results are presented on a dendrogram which divides the material into two sets corresponding to two association varieties (*Dn* in Text-fig. 9).

One set, designated as *A*, contain assemblages characterized by a considerable number of species (7-11 taxa, 5 taxa in one case) and a large number of specimens. It divides into two subsets: A_1 and A_2. The subset A_1 includes the sites at Niedzica, Szczawnica, Płusy *B*, Sienna, and Roztoka; A_2 – the sites at Jurasowa and Osobnica. In all these localities abundant are such species as *Succinea oblonga elongata* SANDBERGER, *Pupilla loessica* LOŽEK, *P. muscorum* (LINNAEUS), and *Vallonia teniulabris* (BRAUN), which are commonly accompanied by *Clausilia*

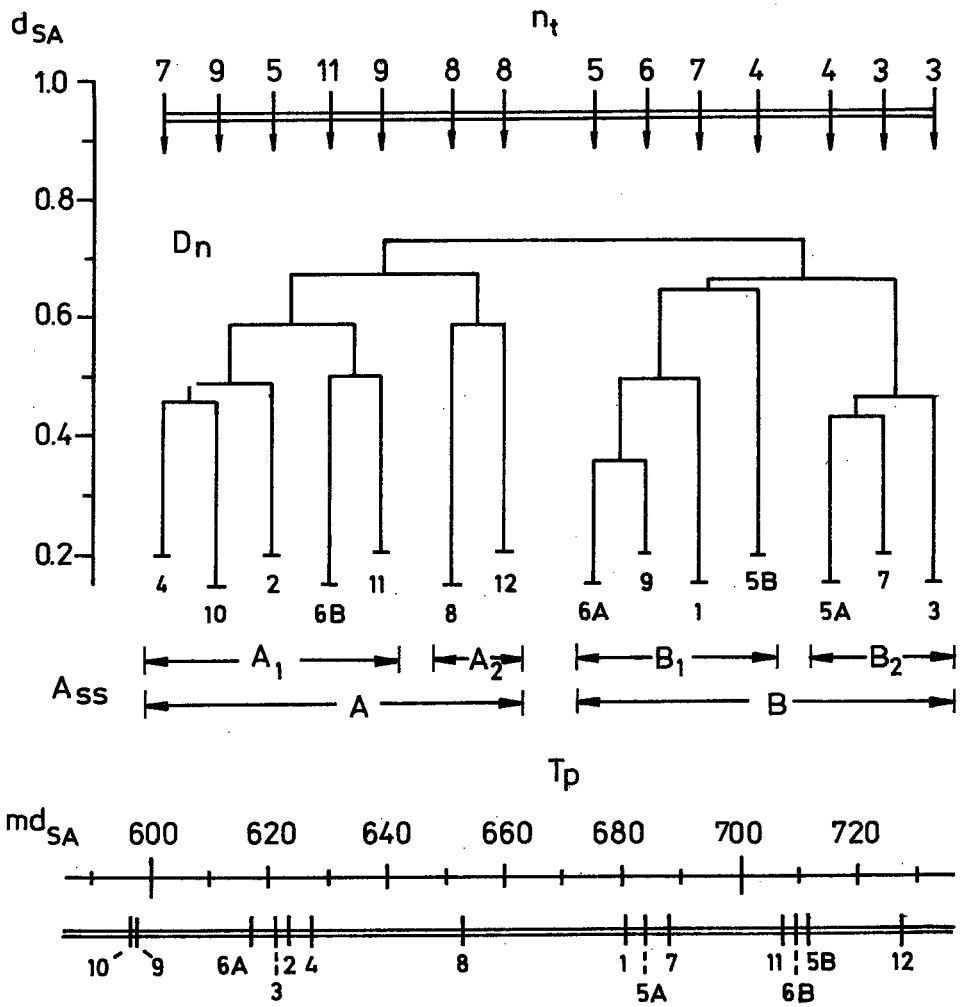

Fig. 9. Taxonomic dendrogram of molluscan assemblages from the Carpathian loess-like deposits
d_{SA} – taxonomic distance, md_{SA} – mean taxonomic distance, n_t – number of species,
Dn – dendrogram, A_{SS} – sets (*A*, *B*) and subsets (A_1, A_2, B_1, B_2) described in the paper,
Tp – typological sequence of assemblages
1–12 – localities described in the paper

dubia DRAPARNAUD and *Trichia hispida* (LINNAEUS). Two localities in the subset A_1 (Płusy *B* and Roztoka) are distinguished on the dendrogram from the others by the presence of *Pupilla sterri* (VOITH) and *Helicopsis striata* (MÜLLER).

The other set, designated as *B*, is also divided into two subsets: B_1 and B_2. A characteristic feature of the associations is the smaller number of taxa and specimens. Besides the species common in all the material studied (*Succinea oblonga elongata* SANDBERGER and *Pupilla loessica* LOŽEK), the assemblages contain *Columella columella* (MARTENS) and *Lymnaea truncatula* (MÜLLER).

The molluscan assemblages assigned to the above sets and subsets were found in different sediments and in different topographic position. There is no relationship between the obtained ordering of assemblages and their occurrence on terraces or slopes of different inclination, in sediments of different age, or at sites with different exposition and altitude. The similarities between the assemblages are chiefly controlled by the local conditions and the environmental variation, as well as by the oscillations of climate.

The fauna studied comprises taxa representing six ecological groups according to LOŽEK's definition (1964). The malacospectrum of species (*MSS*) shows a fairly even content of respective groups, in contrast to the malacospectrum of individuals (*MSI*), in which two groups are definitely dominant (*C* in Text-fig. 10). One group includes snails inhabiting open environments (*Pupilla*, *Vallonia*), the other — euryecological snails, having a preference for moist environments (*Succinea*). Species placed in the four remaining groups are practically of no significance.

The sets *A* and *B* distinguished on the dendrogram (*Dn* in Text-fig. 9) differ in the content of ecological groups presented on *MSI* spectra (*A* and *B* in Text-fig. 10). The set *A* is characterized by the sligth prevalence of snails representing group 5 (*Pupilla*) over snails of group 8 (*Succinea*), while in the set *B* the ecological group 8 clearly dominates over all the others. This means that the set *A* comprises localities corresponding to dry and insolated habitats, whereas the set *B* — moist environments. The assemblages assigned to the set *A* have more species than those belogning in the set *B*, the average values being 8.2 and 4.4, respectively. It appears, therefore, that associations with *Pupilla* and *Succinea* occupied environments in which the conditions were more favorable for the development of malacofauna than in the localities which yielded assemblages with *Succinea*. Still less favorable conditions prevailed in localities in which scarce shells of snails, belonging almost entirely to the genus *Succinea*, were found (*e.g.* Wadowice, Myślenice).

The matrix of taxonomic distances d_{SA} used to construct the dendrogram, may also be used to distinguish the most typical and representative assemblages. This involves a determination of the mean taxonomic distances for all the analyzed associations. Those which have the lowest mean d_{SA} values are the most similar to all the others (ALEXANDROWICZ 1977). The arrangement of the molluscan assemblages according to the increasing mean d_{SA} values gives the following ordering (*Tp* in Text-fig. 9):

(*i*) the assemblages from Sienna and Roztoka are the most typical of the Vistulian loess-like loams in the Carpathians, having mean d_{SA} values of 0.59–0.60;

(*ii*) the assemblages from Niedzica, Kąty, Szczawnica and Płusy can also be regerded as typical and representative because their mean d_{SA} values range between 0.61 and 0.63;

(*iii*) of the other assemblages only that from Jurasowa is distinguished by $d_{SA} = 0.65$, whereas all the others have mean d_{SA} values of 0.68 and 0.69 or greater than 0.71. These associations are more differentiated and less typical of the analyzed set.

The occurrence of snail species in the described localities and the faunal assemblages were analyzed with the qualitative taxonomic method, using STEINHAUS' formula (MARCZEWSKI & STEINHAUS 1959, ALEXANDROWICZ 1977). The matrix of taxonomic distances d_{St} was used to construct a dendrogram showing relations between the respective taxa (*Dn* in Text-fig. 11). The dendrogram divides the whole malacofauna into two sets (*A* and *B*), revealing interrelations between some species. Four of them form a dual subset characterized by taxonomic distances less than 0.60. They are: *Succinea oblonga elongata* — *Pupilla loessica* and *Vallonia tenuilabris* — *Pupilla muscorum*. Two other species, *Clausilia dubia* — *Trichia hispida*, joined at the same level, show a relationship with the species mentioned above. Worth noting is also the close similarity in the occurrence of *Helicopsis striata* and *Pupilla sterri*, representing species preferring steppe environments.

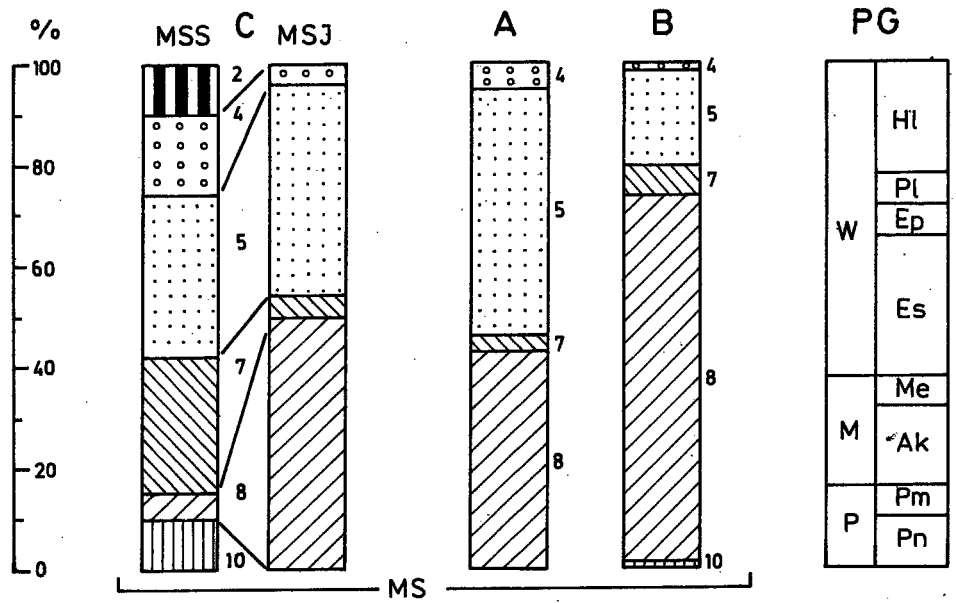

Fig. 10. Malacospectra: **MS** — ecological spectra (*after* LOŽEK 1964), **C** — summary spectra, **MSS** — malacospetrum of species, **MSI** — malacospectrum of individuals; **A** — spectrum (*MSI*) of set A; **B** — spectrum (*MSI*) of set B

Symbols of ecological groups of molluscs: 2 — snails of shaded and moderately shaded habitats, 4 — xerophilous species, 5 — species of open enviromnents, 7 — mesophile snails of moderately moist habitats, 8 — mesophile snails of moist environments, 10 — aquatic molluscs

PG — zoogeographical spectrum: W — widespread species, Hl — Holarctic species, Pl — Palearctic species, Ep — European species, Es — Eurosiberian species, M, Me — Middle-European species, Ak — Alpine-Carpathian species, P — South-European species, Pm — Ponto mediterranean species, Pn — Mediterranean species

On the basis of mean taxonomic distances d_{Si} all the species were arranged according to the increasing values of this index. Species having a low value can be considered as the most typical components of the malacofauna studied. Four groups of taxa were distinguished (*Tt* in Text-fig. 11):

(*i*) characteristic species: *Succinea oblonga elongata* SANDBERGER, *Pupilla loessica* LOŽEK, *P. muscorum* (LINNAEUS), *Vallonia tenuilabris* (BRAUN);
(*ii*) distinctive species: *Clausilia dubia* DRAPARNAUD, *Trichia hispida* (LINNAEUS), *Helicopsis striata* (LINNAEUS), *Pupilla sterri* (VOITH), and the Limacidae;
(*iii*) accompanying species: *Semilimax kotulai* (WESTERLUND), *Columella columella* (MARTENS), *Pupilla muscorum densegyrata* LOŽEK, *Chondrula tridens* (MÜLLER), *Vallonia costata* (MÜLLER);
(*iv*) accessory species: *Lymnaea truncatula* (MÜLLER), *Gyraulus laevis* (ALDER), *Vertigo parcedentata* (BRAUN), *Euconulus fulvus* (MÜLLER), *Arianta arbustorum* (LINNAEUS).

The presented clustering of species indicates that there is close similarity between the malacofauna of the Late Pleistocene Carpathian loess-like loams and the malacofauna of loess series both from Poland and from other European countries.

In the loesses of Czechoslovakia, LOŽEK (1964, 1965, 1970) distinguished characteristic species, distinctive species, local taxa and species thriving in water or swamp environments; he regarded *Pupilla loessica* LOŽEK, *P. muscorum densegyrata* LOŽEK and *Vallonia tenuilabris* (BRAUN) as representing the characteristic species; *Succinea oblonga elongata* SANDBERGER, *Pupilla muscorum* (LINNAEUS), *P. sterri* (VOITH) and *Helicopsis striata* (LINNAEUS) as the distinctive species; *Vallonia costata* (MÜLLER), *Chondrula tridens* (MÜLLER), *Clausilia dubia* DRAPARNAUD and *Semilimax kotulai* (WESTERLUND) as local species. The complete list of taxa cited by LOŽEK (1965, 1976) includes more than 50 species. It appears that this fauna is more diversified than the assemblages found in the Carpathian loess-like deposits, but generally not more than 10 taxa are reported from the individual profiles and stratigraphic members of loesses. Similar molluscan assemblages, with abundant *Pupilla muscorum* (LINNAEUS), *Trichia hispida* (LINNAEUS), *Succinea oblonga* DRAPARNAUD and *Vallonia costata* (MÜLLER), as well as scarce *Pupilla loessica* LOŽEK, occur in the loesses of West Germany and France (REMY 1969, PUISSEGUR 1978).

In Poland ten types of molluscan assemblages were distinguished in loesses of the Małopolska Upland (ALEXANDROWICZ 1985b). The most common are associations with *Succinea oblonga elongata* SANDBERGER and with *Pupilla loessica* LOŽEK and their varieties, characterized by the abundance or presence of such species as *Clausilia dubia* DRAPARNAUD, *Semilimax kotulai* (WESTERLUND), *Columella columella* (MARTENS), and *Vallonia tenuilabris* (BRAUN). This malacofauna is similar to that found in the Carpathian loams.

The investigated fauna from the Polish Carpathians comprises several zoogeographical elements (*PG* in Text-fig. 10). Over 60% of species belong to widespread taxa, mainly Holarctic and Eurosiberian. In this group were also placed taxa typical of loesses, not known from the present-day fauna (*Pupilla loessica* LOŽEK, *P. muscorum densegyrata* LOŽEK, *Succinea oblonga elongata* SANDBERGER). The Middle European element is represented by species of wide ecological valency. These are mainly snails living in the Alps and the

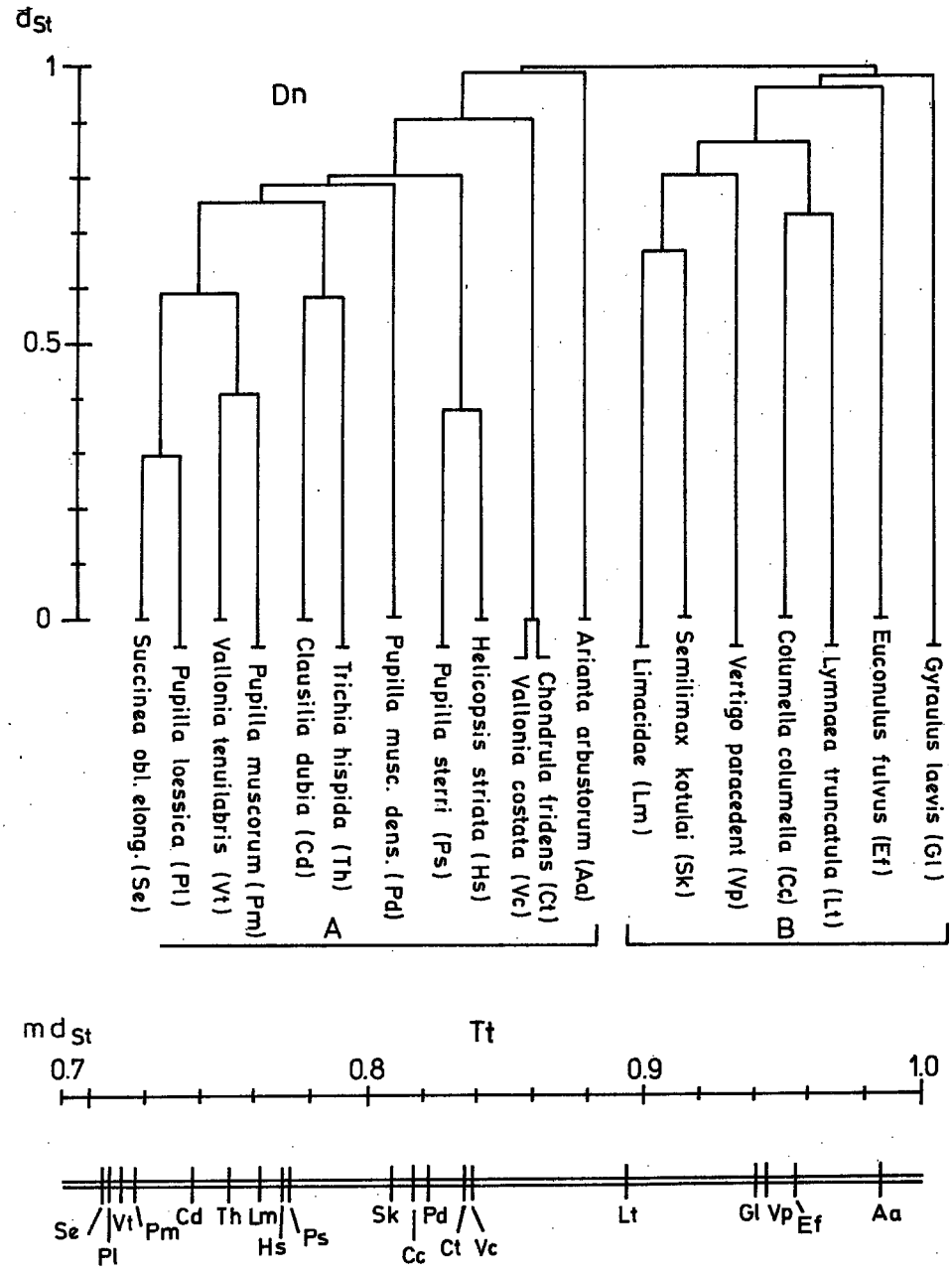

Fig. 11. Taxonomic dendrogram of mollusc species
d_{St} – taxonomic distance, md_{St} – mean taxonomic distance, Dn – dendrogram, A, B – sets of species described in the paper, Tt – typological sequence of species

Carpathians, as well as snails which have a discontinous Boreal-Alpine range, e.g. *Columella columella* (MARTENS). Three taxa, i.a. *Helicopsis striata* (LINNAEUS), were assigned to the South-European element. They are snails typical of open environments, dry and insolated habitats, mainly of steppes, showing the ability to adapt themselves to the conditions of cold climate. The presented zoogeographical spectrum (*PG* in Text-fig. 10) characterizes both the composition and provenance of malacofauna which inhabited the woodless area of the Carpathians being under the influence of periglacial climate.

AGE AND PALEOGEOGRAPHICAL ENVIRONMENT

Loamy sediments accumulated through solifuction, slope wash and wind action are associated with cold climatic periods. They formed during successive glaciations, while in the interglacial periods they were largely transformed by soil processes and were subjected to erosion and denudation. Silty and sandy loams and loams with rock detritus, widespread throughout the Polish Carpathians, can be regarded as sediments of different age, but the bulk of them originate from the last glaciation (KLIMASZEWSKI 1948, 1967; STARKEL 1968, 1984; DZIEWAŃSKI & STARKEL 1962, 1967). Their age was determined in several localities, chiefly by radiocarbon dating. Additional clues were provided by the presence of organic sediments, silt with plant remains, peats, and fossil soils (Table 2).

Table 2
Carbon-14 dating of loess-like deposits in the Polish Carpathians

Locality	Symbol in Fig.1.	Age BP	Symbol of laboratory and test N°
Mizerna (Czorsztyn)	1	27 400 ± 600	Gd - 1917
Sowliny (Limanowa)	9	29 650 ± 650	Gd - 1880
Dobra (Limanowa)	Db	32 550 ± 450	GrN - 5111
Krajowice (Jasło)	Kr	34 300 ± 1000	Gd - 1588
Krajowice (Jasło)	Kr	35 500 ± 1500	Gd - 1628
Krajowice (Jasło)	Kr	>42 000	Gd - 2109
Krajowice (Jasło)	Kr	>45 000	Gd - 1641
Wadowice	Wd	>40 000	K - 716
Zator	Zt	>40 000	K - 719
Sromowce-Kąty	3	>48 200	GrN - 6803
Sromowce-Kąty	3	>51 200	GrN - 6251

The C-14 datings indicate that the majority of loams with flora and fauna can be assigned in all probability to one of the two interstadials of the last glaciation, and also to the late glacial period. The first interstadial comprises sediments older than 40 or 50 ka y.BP, that is, passing the determination limits of the C-14 method. The second is represented by sediments ranging from 27 to 36 ka y.BP (Table 2). According to the stratigraphic scheme used by STARKEL (1980, 1984) for the Vistulian in Carpathians, the older phase of climatic warming can be compared with the Brørup interstadial, and the yonger phase with the Hengelo and Denekamp interstadials, *i.e.* with the interpleniglacial period. The latter phase was distinguished in the Polish Carpathians as the Paudorf interstadial (ŚRODOŃ 1968; KLIMASZEWSKI 1967, 1971). The fossil soil found at Płusy and Osobnica, as well as those reported by CEGŁA (1963) from Jasło, Nowy Sącz and Żywiec, may be related to this phase. They are soils of the initial type, similar to the Komorniki-type tundra soil from the Małopolska Upland, described and interpretated by JERSAK (1973) as a characteristic indicator of the interpleniglacial period.

OLDER INTERSTADIAL

This phase is represented by the Zator, Wadowice and Sromowce-Kąty sites. The upper age limit of the sediments in these profiles is determined at 40–50 ka y.BP (Text-fig. 12).

Paleobotanical studies indicate that the greater part of the Carpathians and their Foothills were covered with forests with numerous *Pinus*, *Picea*, and *Betula*, as well as *Alnus* in wet areas. Locally *Abies* and *Populus*, and even *Carpinus* were present (DYAKOWSKA 1947; SOBOLEWSKA, ŚRODOŃ & STARKEL 1964; MAMAKOWA, MOOK & ŚRODOŃ 1975). In the climatic optimum of the interstadial, the timber line could have reached up to 1000m a.s.l. (STARKEL 1968, 1984). The climate and widespread forests created favorable life conditions for several snail species.

The closing phase of the Brørup interstadial is characterized by the increasing content of *Pinus* and the expansion of habitats occupied by herbaceous plants, what corresponds to the lowering of the timber line. The Carpathians, and the Carpathian Foothills became progressively encompassed within the zone of park tundra and tundra with depressions occupied by swamps and water bodies. This period is represented by the sediments from Zator, which contain a flora pointing to the progressive deterioration of climatic conditions, typical of the descending phase of the interstadial and the following pleniglacial period (KOPEROWA & ŚRODOŃ 1965).

The intense development of slope wash and solifluction is reflected in all the profiles studied. Organogenic sediments with flora were covered with silty and sandy loams and loams with rock detritus, containing locally shells of *Succinea*, *Pupilla* and *Vallonia* (localities Sromowce-Kąty, Wadowice). An

assemblage of aquatic molluscs with *Valvata*, the Planorbidae, *Lymnaea* and *Pisidium* was reported by ALEXANDROWICZ, MAMAKOWA & WÓJCIK (1985) from the vicinity of Jasło (locality Krajowice). In several localities there were also found bones and teeth of large mammals, indicative of the descending phase of the older interstadial passing into the pleniglacial period of the Middle Vistulian (*see* Text-fig. 12).

YOUNGER INTERSTADIAL

Interpleniglacial sediments containing flora and fauna were reported from many localities. On the basis of five available C-14 datings, their age was determined as ranging between 36 and 27 ka y.BP (Table 2). It must be assumed, however, that the warming characteristic of this period began about ten thousand years earlier (*see* Text-fig. 12). From the paleobotanical studies carried out by ŚRODOŃ (1968) and others it may be inferred that the timber line at that time did not rise above 500m, sometimes reaching up to a height of 600–700m a.s.l. (STARKEL 1968, 1984). The greater part of the Carpathians lay within the zone of park tundra and tundra with stretches of forests in which *Pinus* and *Betula* with an admixture of *Picea* and *Larix* were the dominant tree genera. The optimum phase of the interstadial was reported from Białka Tatrzańska in the Podhale Foothill (*see* Text-fig. 1), where it is marked by the appearance of a few plant species having higher climatic requirements (SOBOLEWSKA & ŚRODOŃ 1961). In the Carpathian Foothills and in the Carpathian valleys forests were more widespread and varied.

Silts with plant remains, peaty silts and peats deposited during the interpleniglacial period usually contain flora represented chiefly by species typical of open environments (localities Orawka, Dobra, Myślenice; *see* ŚRODOŃ 1968). During the interstadial, and particularly in its descending phase, the slope wash and solifluction, as well as deflation, were very active. They resulted in the accumulation of sandy and silty loams and loams with rock detritus, which locally attained a thickness of 10m. In some profiles the loams contain snail shells and bones of large mammals.

In two localities C-14 datings were made for the sediments with malacofauna. At Sowliny, the sediments were found to be younger than 29.6 ka y.BP,and at Mizerna the age of silts with snail shells was determined at 27.4 ka y.BP. In three other profiles (Sienna, Płusy, Osobnica) loess-like loams with fauna rest on peat or fossil soil, so they represent the descending phase of the interpleniglacial period. Basing on the similarity of fauna, the sites of Niedzica, Szczawnica, Jurasowa, and Roztoka can also be regarded as belonging in this group. The malacofauna found in these nine localities represents both sets distinguished on the basis of taxonomic analysis (Text-fig. 9). Its variation is primarily determined by the local conditions, but it may also reflect the age of sediments and the changing climatic conditions. The latter possibility is implied by the succession of assemblages in the Roztoka profile. In the lower

part of this profile malacofauna is represented by 6–8 snail species including *Helicopsis striata* (MÜLLER), *Pupilla sterri* (VOITH), and *Clausilia dubia* DRAPARNAUD, while in the upper part it comprises only three species with abundant *Pupilla loessica* LOŽEK and *Succinea oblonga elongata* SANDBERGER (*see* Text-fig. 6). This impoverishment of malacofauna may be related to the successive deterioration of climatic conditions in the closing phase of the interstadial.

LATE GLACIAL

The Dryas sediments with snails occur at Krościenko (*5* in Text-fig. 1). They contain characteristic flora with *Dryas octopetala*, *Salix reticulata*, and *Saxiphraga aizoon* (see KLIMASZEWSKI & *al.* 1950), but they were not dated. The molluscan assemblage is poor and it consists of four species represented by a few specimens. Compared with all the other assemblages, it has the higher value of mean taxonomic distance, so it is the least typical of the malacofauna described (*Tp* in Text-fig. 9). It corresponds to fauna living under the Subarctic conditions above the timber line. Similar assemblages, characterized by a small number of taxa, were found in some other outcrops at Krościenko-Ociemny, Płusy and Podegrodzie. It is feasible that these assemblages also represent fauna of the late glacial period.

MALACOFAUNA AS INDICATOR OF PALEOGEOGRAPHICAL CONDITIONS

The changes of climate and the evolution of paleogeographical environment occurring during the Vistulian were the major factors controlling the development and diversification of malacofauna found in loamy sediments. During the interstadials, the conditions prevailing throughout the Carpathians, especially in the Carpathian Foothills and intramontane depressions, were favorable for the development of a large number of mollusc species, both land and aquatic. However, assemblages characteristic of the optimum phases of interstadials are not as yet known because no sediments corresponding to these phases have been found in which calcareous shells have been preserved. Subfossil malacofauna occur in loamy deposits accumulated chiefly by slope wash and solifluction in the pleniglacial period and in the transitional phases between warm and cold periods. In consequence, the faunal succession includes only associations corresponding to the periods of cooling and representing environments occupying areas near and above the timber line.

Over the last hundred thousand years in the Carpathians there have been at least three periods with the conditions promoting the formation of sediments abounding in molluscs shells. They are reflected by three phases of development of fauna, representing similar stages of successive, cyclic changes of climate and environment (Text-fig. 12).

The oldest fauna, assigned to the closing phase of the Brørup interstadial, is very little known. It is represented by only three species of land snails, common in all the material studied, and eight species of aquatic molluscs. Malacofauna representing the descending phase of the interpleniglacial period (Hengelo-Denekamp interstadial, Paudorf interstadial) is the most abundant and diversified. Some assemblages contain taxa with higher ecological requirements or species typical of dry, steppe environments, while others are only characterized by the presence of species of wide ecological valency, adapted to the life under Subarctic conditions. In the late glacial sediments malacofauna is known from a few outcrops, but only one profile comprises sediments whose age was determined by palynological analysis. The fauna in these sediments is poor, corresponding to one of the cold phases of the Dryas.

The findings of bones and teeth of large mammals are also connected with two interstadials and mainly with their descending phases (Text-fig. 12). Such species as *Mammuthus primigenius* (BLUMENBACH), *Rangifer tarangus*

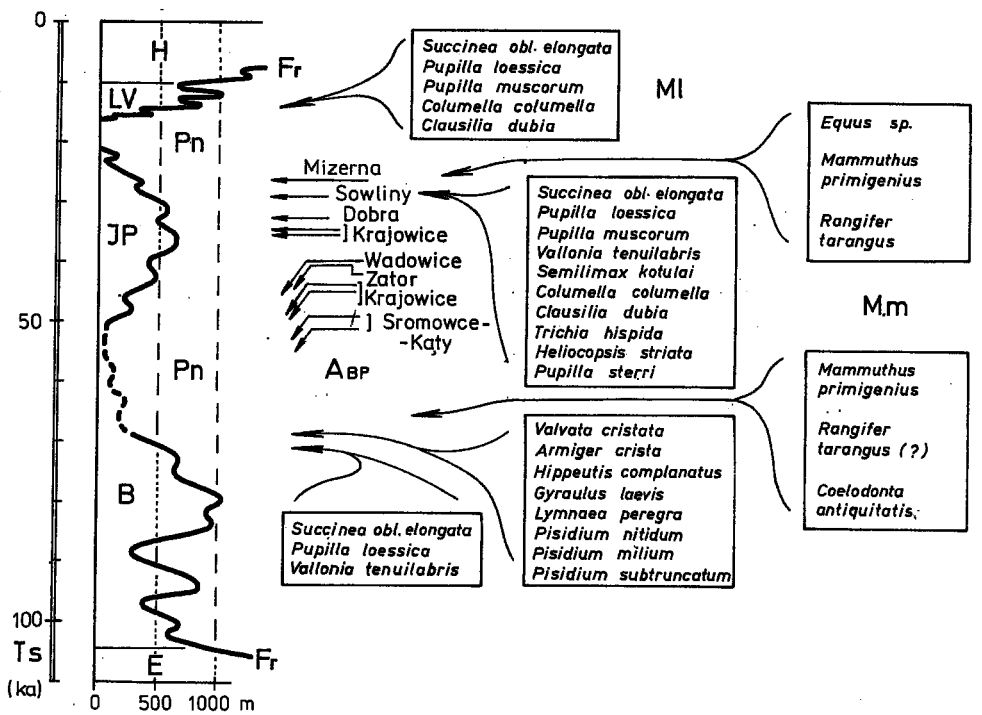

Fig. 12. Fauna of Vistulian loess-like deposits in the Polish Carpathians
Ts – time scale in thousands years (*ka*); Fr – reconstruction of changes in the position of timber line (*after* STARKEL 1978); E – Eemian interglacial period, B – Brørup interstadial, Pn – pleniglacial periods, IP – interpleniglacial period, LV – late glacial period, H – Holocene A_{BP} – localities with sediments dated with C-14 method, Ml – malacofaunal assemblages, Mm – species of mammals

(LINNAEUS), *Equus* sp. and *Coelodonta antiquitatis* (BLUMENBACH), are typical of the Subarctic environment and areas extending above the timber line.

Snail shells appear the most commonly in silty loams and loams with a small admixture of fine-grained sand. Such loams contain the richest molluscan assemblages consisting both of a large number of specimens and a considerable number of taxa (localities Niedzica, Szczawnica, Płusy, Sienna, Roztoka). Malacofauna is less common in loams with rock detritus, and the assemblages found in such sediments are poor and show little variety (localities Krościenko-Ociemny, Podegrodzie). The former lithologic type of loams represents sediments accumulated mainly by slope wash, the latter – sediments owing their origin to solifluction. According to STARKEL's (1968) scheme of the evolution of Vistulian deposits in the Carpathians, it can by assumed that in the phases of climatic pessima (pleniglacial periods) the intense action of solifluction took place, in the optimum phases (interstadials) weathering and pedogenesis processes prevailed, whereas in the transitional phases (descending and ascending phases of interstadials) slope wash was the dominant process (STARKEL 1968; DZIEWAŃSKI & STARKEL 1962, 1967). The occurrence of malacofauna in different types of loamy sediments confirm the above scheme because in most localities the mollusc-bearing sediments show a relationship to the transitional phases.

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MALAKOFAUNA PÓŹNOCZWARTORZĘDOWYCH GLIN LESSOPODOBNYCH W KARPATACH*

(Streszczenie)

Przedmiotem pracy jest analiza malakofauny występującej w glinach czwartorzędowych, pokrywających znaczną część polskich Karpat, zwłaszcza pogórza i kotliny śródgórskie. Osady te są wykształcone jako gliny lessopodobne, pylaste i piaszczyste oraz jako gliny z fragmentami piaskowców i łupków, przechodzące w rumosze stokowe. W glinach występują lokalnie szczątki flory i fauny, głównie skorupki ślimaków oraz zęby i kości ssaków. Zespoły mięczaków znalezione w 23-ch stanowiskach (fig. 1–7) obejmują 20 taksonów, z których najliczniej reprezentowane są: *Succinea oblonga elongata* SANDBERGER, *Pupilla loessica* LOŽEK, *P. muscorum* (LINNAEUS) oraz *Vallonia tenuilabris* (BRAUN), uznane za gatunki charakterystyczne (tab. 1 oraz fig. 11). Analiza taksonomiczna pozwoliła na wyróżnienie dwóch typów zespołów, związanych z siedliskami o bardziej i mniej korzystnych warunkach ekologicznych. Najbardziej typowe asocjacje występują w Siennej i Roztoce nad Dunajcem (fig. 8–9). Opisywana malakofauna jest bardzo podobna do fauny z lessów Wyżyny Małopolskiej, co wyraża się w składzie zespołów (fig. 10). W Karpatach skorupki mięczaków grupują się w osadach związanych z trzema fazami ocieplenia w obrębie ostatniego glacjału (fig. 12). Pierwsza z nich, starsza niż 50000 lat BP, może być odniesiona do interstadiału Brørup, a druga – o wieku 35–27000 lat BP – do okresu interpleniglacjalnego z interstadiałami Hengelo i Denekamp (tab. 2). Trzecia faza może odpowiadać późnemu glacjałowi. Okresy pojawiania się fauny wiążą się z wahaniami górnej granicy lasu (*por.* STARKEL 1978), z rozwojem roślinności tundrowej i stepowej, a także z nasilaniem się procesów stokowych.