



MOLLUSCAN COMMUNITIES FROM CAVE AND SLOPE DEPOSITS OF THE LIMESTONE ROCKY HILLS IN THE EASTERN PART OF PODHALE BASIN (SOUTHERN POLAND)

WITOLD PAWEŁ ALEXANDROWICZ, DOMINIKA RUDZKA

Chair of Environmental Analysis and Cartography, AGH University of Science and Technology,
Al. A. Mickiewicza 30, 30-059 Kraków, Poland (e-mail: teska4@op.pl, drsusel@wp.pl)

ABSTRACT: Small karst forms are commonly observed within isolated limestone rocky-hills in the eastern part of Podhale Basin. They are usually filled by deposits developed as loams with limestone scree or initial rendsina-type soil. Mollusc shells occur frequently in both types of sediments. Molluscan assemblages comprise mainly land snails including woodland, open-country and mesophile species. Mollusc-bearing slope and cave deposits were collected from twenty six outcrops in six localities. The succession of molluscan assemblages provides a basis for palaeogeographical, palaeoecological and stratigraphical studies, as well as for reconstruction of environmental changes during the Late Glacial and Holocene.

KEY WORDS: mollusc assemblages, slope sediments, cave sediments, environmental changes, Holocene, Podhale Basin

INTRODUCTION

Podhale Basin extends between the Tatra Mountains and the Beskid Mountains. It consists of the Zakopane Trough, the Gubałówka Foothills, Orawa-Nowy Targ Basin and a part of the Pieniny Klipen Belt. The geological structure of this area is much differentiated. The southern part of the described region (the Zakopane Trough and the Gubałówka Foothills) is composed of Podhale Flysch, developed as dark or gray shales intercalated by fine- and middle-bedded sandstones with carbonate matrix. The northern part of Podhale Basin (Orawa-Nowy Targ Basin) is formed of flysch belonging to Magura Nappe. This basement is partly overlain by terrigenous sediments of Neogene age that fill a large intermontane depression. Northern and southern flysch areas are separated by the Pieniny Klipen Belt. This zone is composed of strongly folded Jurassic and Cretaceous rocks, mainly limestones, marls and radiolarites. In the eastern part of the Podhale Basin limestones mentioned above build isolated clippes and rocky hills. The geological bedrock

formation of this region favours development of karst processes.

Snail communities from slope deposits filling small karst forms have been reported by several authors. Numerous logs of such deposits from Cracow-Częstochowa Upland (STWORZEWICZ 1973, 1988, S. W. ALEXANDROWICZ 1992, 2000, W. P. ALEXANDROWICZ 2000), Sudety Mts (PAKIET 1999), Pieniny Mts (S. W. ALEXANDROWICZ et al. 1985) and Tatra Mts (W. P. ALEXANDROWICZ 2001) have been published. Rich and differentiated molluscan fauna has been described from many localities of slope and cave sediments from karst areas in Slovakia and the Czech Republic (LOŹEK 1980, 1981, 1982, 2000 and numerous others). These assemblages provide a basis for palaeogeographical, palaeoecological and stratigraphical studies as well as for reconstruction of environmental changes and human impact.

Sediments filling small karst forms such as caves, rock shelters, rocky niches, open fissures, as well as deposits forming debris fans and covering flat rocky

slopes have been recognised in numerous localities in the eastern part of Podhale Basin. Sequences of mollusc-bearing deposits come from hill-rocks Cisowa Skała, Obłazowa Skała, Kramnica, Korowa Skała, Krzysztofkowe Skały and Falsztyn (Fig. 1). Some of these profiles have already been investigated for malacological purposes (W. P. ALEXANDROWICZ 1997), but earlier results are now supplemented with abundant new materials not analysed to date.

Structural and textural features are strongly dependent on the lithological type of rocks forming the hills. Two main types of sediments can be distinguished. One is composed of more or less distinctly bedded, yellow, yellowish-brown, yellowish-gray or even red loams, usually abounding in limestone scree. Fragments of limestone are angular and 3–12 cm in diameter. Particular layers contain unsorted material of different size. Limestone debris containing coarse material occurs in the lowermost intervals of the profiles. It usually becomes finer upwards but is often in-

tercalated with somewhat coarser debris. The thickness of these deposits varies between 0.1 and 0.7 m, usually 0.2–0.3 m. Loams and fragments of rocks were found in profiles of debris fans accumulated at the foot of the slopes as well as in open fissures, rock shelters and niches. The second type of sediments comprises the rendsina-type soils developed on the surface of the rock-hills, mainly in rocky ledges and flat parts of slopes. The soil profiles are composed of a limestone scree with dark or black mull-humus matrix. In the top part of several logs stone-free horizons were found. The mentioned type of soil represents the initial rendsina characterised by a very small thickness, usually not exceeding 0.2 m. Mollusc shells occur in both types of sediments. In several logs they are accompanied by bones and teeth of mammals, mainly rodents.

This study is a contribution to scientific project N° 10.10.140.489 sponsored by AGH University of Science and Technology in Cracow.

MATERIAL AND METHODS

Twenty six profiles of slope deposits derived from six localities were studied in detail (Figs 1–3). Samples for malacological analyses were collected from selected intervals, depending on the thickness of successions and lithology of sediments. The average sample weight was about 3 kg. In total, the analysis included 60 samples containing subfossil shells of molluscs. The samples were washed, so as to extract all the mollusc shells and their fragments that could be determined. The whole analysed material comprised 63 species of land snails and 1 species of water mollusc, as well as shells of slugs identified as *Limacidae*, all these being represented by 14,692 speci-

mens. Eighteen taxa of mammals, mainly rodents, were found, too.

Malacological analysis was carried out using the standard methods described and defined by LOŹEK (1964) and S.W. ALEXANDROWICZ (1987, 1999). For determination of the structure of molluscan fauna, malacological individual spectra (MSI) were applied. All the species were divided into ecological groups representing five comprehensive categories: F – shade-loving species living in forests and/or in shrubland (woodland), O – open-country snails inhabiting places of varied humidity (meadows, bare rocks, xerothermic habitats), M – species of wide eco-

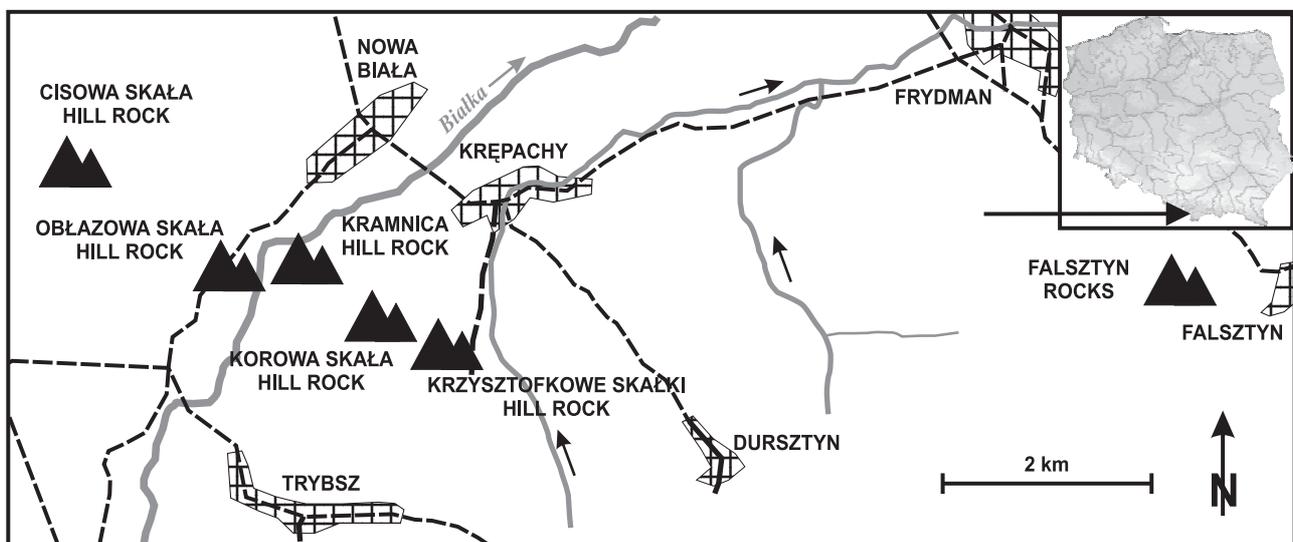


Fig. 1. Location of the sections of deposits filling small karst forms in the eastern part of Podhale Basin



logical tolerance (mesophile, catholic), H – hygrophile snails, W – water molluscs. The structure of constancy (C) and dominance (D) was presented according to the method described by DOBROWOLSKI (1963). Four groups of molluscs could be distinguished in each zone: CD – common species represented by numerous specimens ($C > 50\%$, $D > 5\%$), Cd – common species represented by a limited number of specimens ($C > 50\%$, $D < 5\%$), cD – rare species represented by numerous specimens ($C < 50\%$, $D > 5\%$) and cd – rare species represented by a limited num-

ber of specimens ($C < 50\%$, $D < 5\%$). The succession of mollusc assemblages was illustrated with a triangular diagram. Indices of differentiation of fauna (TDA), normalised constancy and dominance indices (C_i , D_i) and Q index – geometric mean of constancy and dominance (S. W. ALEXANDROWICZ 1987, 1999) – were calculated for the whole fauna. Zoogeographical composition of the fauna was analysed based on the traditional scheme (LOŻEK 1964, S. W. ALEXANDROWICZ 1987).

RESULTS

MOLLUSCS-BEARING DEPOSITS

Small karst forms filled by sediments containing organic remains are developed within the zone of occurrence of Jurassic and Lower Cretaceous limestones belonging to the Pieniny Klipen Belt. They are accessible in isolated clippes and rock-hills. Twenty six logs of these deposits were studied in detail (Figs 1–3).

Cisowa Skała

Fifteen samples of mollusc-bearing deposits (Ps-1 – Ps-15) were collected from six sections (Ps-I – Ps-VI) (Figs 1, 2). Initial rendzina-type soils appeared in logs Ps-I, Ps-II and Ps-V. They were situated on two flat rocky ledges in the lower (Ps-I and Ps-II) and middle (Ps-V) part of the southern slope of the hill. Five samples comprised a relatively poor molluscan assemblage dominated by open-country species, mainly

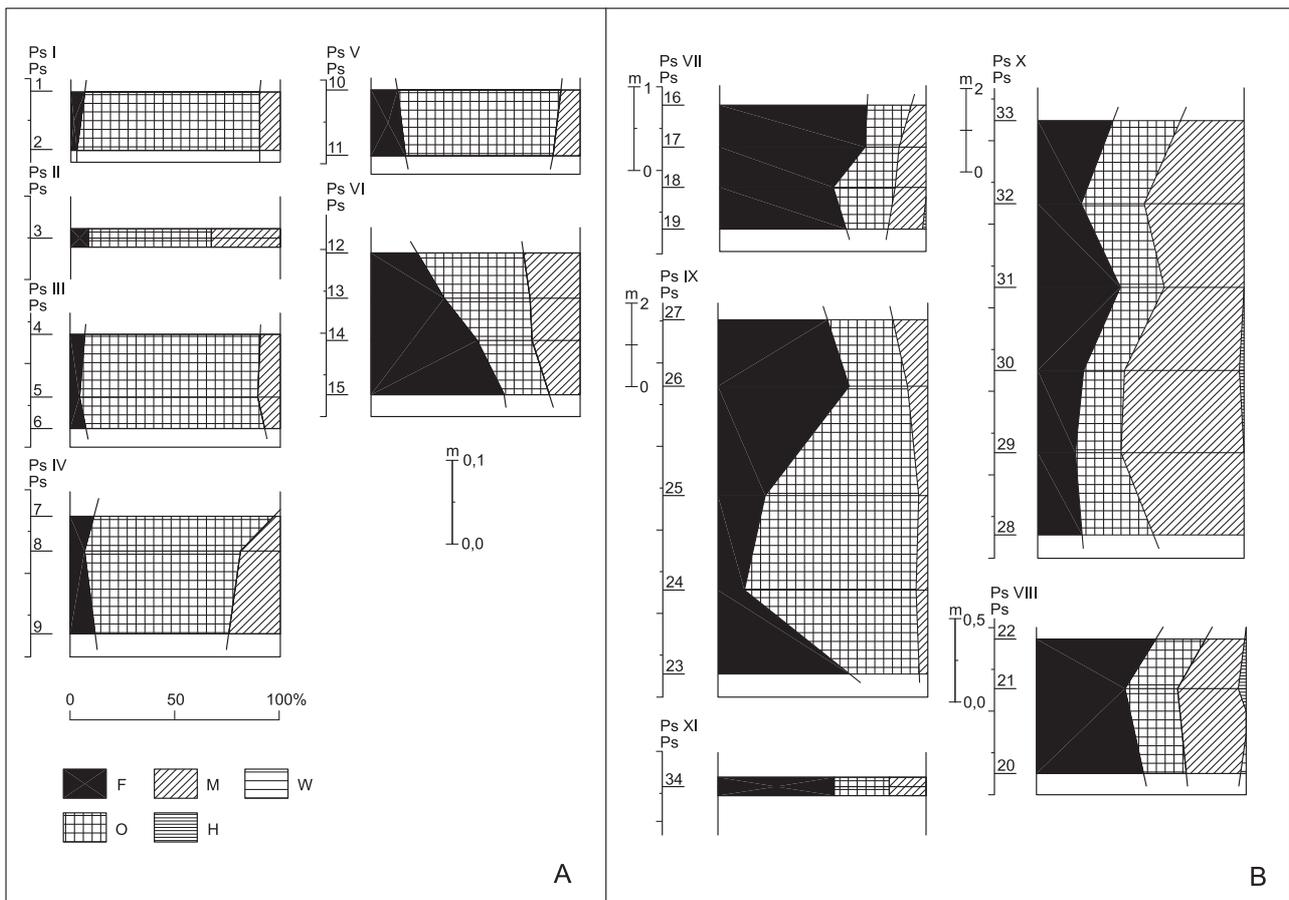


Fig. 2. Malacological composition of profiles in Cisowa Skała Hill Rock (A) and Obłazowa Skała Hill Rock (B): F – shade-loving species, O – open-country species, M – mesophile species, H – hygrophile species, W – water species, P – profiles of cave sediments

Pupilla muscorum (L.), *Vallonia pulchella* (Müll.) and *V. costata* (Müll.), with admixture of snails living on rock faces (*Pyramidula pusilla* (Vall.)) and xerophile taxa (*Truncatellina cylindrica* (Fér.), *Cochlicopa lubricella* (Rossm.)). Similar mollusc assemblages were found in yellowish loams abounding in limestone scree, covered by initial rendsina sampled in two rock niches developed on the south-western slope of Cisowa Skała (profiles Ps-III and Ps-IV, samples Ps-4 – Ps-9). Quite a different fauna occurred in loams filling large rock shelter developed in the upper part of the northern slope of the hill (profile Ps-VI, samples Ps-12 – Ps-15). Woodland species accompanied by catholic taxa were the most important components of this assemblage (*Ruthenica filigrana* (Rossm.), *Vitrea subrimata* (Reinh.), *Aegopinella pura* (Ald.) and others). Open-country snails occurred more frequently only in the uppermost interval of the sequence (Fig. 2). The occurrence of single bones and teeth of rodents was also noted.

Oblazowa Skała

Several rock shelters, niches and ledges occur on the southern and western slopes of Oblazowa Skała. Nineteen samples (Ps-16 – Ps-34) were taken from five profiles (Ps-VII – Ps-XI; Figs 1, 2).

Two small rock shelters filled by loams with angular fragments of limestones were found in the middle part of the western slope (profiles Ps-VII and Ps-VIII, samples Ps-16 – Ps-22). These deposits contained a rich mollusc fauna. The occurrence of cold-tolerant species typical for Late Glacial, such as *Vertigo genesii* (Gredl.), *Columella columella* (G. Mart.) and *Semilimax kotulae* (West.) is an interesting feature of the assemblage otherwise characterised by numerous shells of *Arianta arbustorum* (L.) and *Discus ruderratus* (Fér.). In samples Ps-16 – Ps-19 mollusc shells were accompanied by remains of cold-loving rodents: *Lemmus lemmus* (L.), *Dicrostonyx gulielmi* (Stand.) and others. Open-country snails and species inhabiting open rock faces complete this community. A large rock niche is developed within the lower part of the southern slope of Oblazowa Skała (Ps-IX, Ps-23 – Ps-27). A loam partly rich in rock debris was excavated at the bottom of this karst form. Its mollusc assemblage was dominated by two ecological groups of snails. The first one included shade-loving taxa with both forest (*Mediterranea depressa* (Sterki), *Cochlodina orthostoma* (Menke)) and shrubland (*Fruticicola fruticum* (Müll.)) snails. Taxa inhabiting open rock faces, *Pyramidula pusilla* (Vall.) and *Chondrina clienta* (West.), belong to the second group. Loams rich in limestone scree form a debris fan situated at the bottom of the western slope of Oblazowa Skała (Ps-X, Ps-28 – Ps-33). Its relatively poor molluscan fauna was dominated by mesophile species (*Nesovitreia hammonis* (Ström), *Euconulus fulvus* (Müll.), *Clausilia dubia* Drap.). Open-country and woodland snails were accessory

components of the assemblage. The remaining ecological groups were practically absent. A small fissure occurs in the middle part of the western rock face of the hill (Ps-XI, Ps-34). Its loamy sediments contained a rich community dominated by woodland species (Fig. 2).

Rich and differentiated molluscan assemblages of Vistulian and Holocene age have been described in detail from the Oblazowa Cave (W. P. ALEXANDROWICZ & STWORZEWICZ 2003). The above mentioned deposits contain also numerous bones of vertebrates, mainly rodents, as well as a very rich and unusual archaeological material (VALDE-NOWAK et al. 2003).

Kramnica

A few small rock shelters and ledges occur on the southern rock face of Kramnica (Ps-XII – Ps-XVII; Ps-35 – Ps-41) (Figs 1, 3). Mollusc-bearing deposits were represented both by loams with angular fragments of limestone and by initial rendsina-type soil. Rich molluscan assemblages were obtained from these profiles. Open-country species: meadow-dwellers *Vallonia pulchella* (Müll.) and *V. costata* (Müll.), xerophile *Truncatellina cylindrica* (Fér.) and *Cochlicopa lubricella* (Rossm.), and petrophile *Pyramidula pusilla* (Vall.) and *Chondrina clienta* (West.) were dominant components of this fauna. Woodland and mesophile snails were also numerous, while taxa of the remaining ecological groups were completely absent (Fig. 3).

Korowa Skała

Four sections of mollusc-bearing slope deposits derive from Korowa Skała (Ps-XVIII – Ps-XXI, Ps-42 – Ps-52) (Figs 1, 3). Two rock niches (Ps-XVIII, Ps-XIX; Ps-42 – Ps-48) are situated at the bottom of the northern slope of the hill. They are partly filled with loam abounding in limestone scree up to twenty centimetres thick. The mollusc assemblage was composed of species representing four ecological groups. Woodland and open-country taxa occurred frequently (*Mediterranea depressa* (Sterki), *Fruticicola fruticum* (Müll.), *Arianta arbustorum* (L.)). Catholic and hygrophile snails were less numerous. In the lower part of Ps-XIX section the occurrence of cold-tolerant species such as *Vertigo genesii* (Gredl.), *V. geyeri* Lindh., *V. modesta* (Say), *Columella columella* (G. Mart.) and *Semilimax kotulae* (West.) is noteworthy. The remaining two logs (Ps-XX and Ps-XXI; Ps-49, Ps-50) were situated in the upper part of the southern slope. Rendsina-type soils up to ten centimeter thick contained a mollusc assemblages characterised by a high proportion of meadow-dwelling, xerophile and petrophile species: *Pupilla muscorum* (L.), *Truncatellina cylindrica* (Fér.) and *Pyramidula pusilla* (Vall.), accompanied by shade-loving snails: *Mediterranea depressa* (Sterki), *Cochlodina orthostoma* (Menke) and *Vitrea transsylvanica* (Cless.) (Fig. 3)

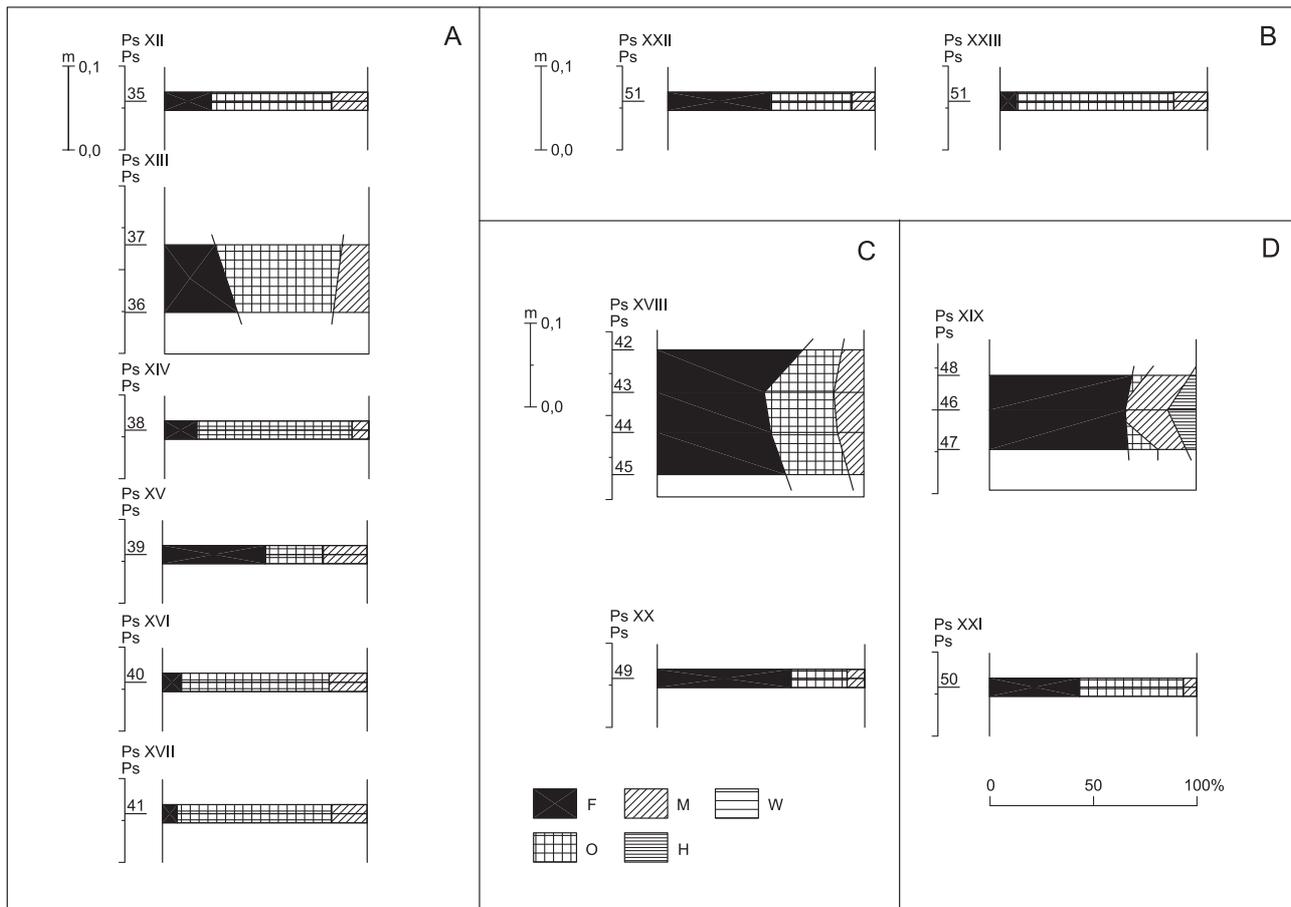


Fig. 3. Malacological composition of profiles in Kramnica Hill Rock (A), Krzysztokowe Skały Hill Rock (B), Korowa Skała Hill Rock (C) and Falsztyn Rocks (D); for lettering see Fig. 2

Krzysztokowe Skały

Two logs of mollusc-bearing sediments were found within Krzysztokowe Skały (Ps-XXII, Ps-XXIII; Ps-51, Ps-52) (Figs 1, 3). Loams with angular limestone scree fill a small rock shelter located at the bottom of the eastern slope of the hill. The mollusc fauna was dominated by species inhabiting rock faces, as well as by shade-loving snails typical for woodland areas (*Pyramidula pusilla* (Vall.), *Discus ruderatus* (Fér.), *Isognomostoma isognomostomos* (Schröt.)). Initial rendsina up to 10 centimetres thick appears on a rock ledge at the top of the southern slope of Krzysztokowe Skały. The fauna was less differentiated, containing mainly meadow snails (*Vallonia pulchella* (Müll.)) (Fig. 3)

Falsztyn Rocks

Eight samples of mollusc-bearing deposits (Ps-53 – Ps-60) were collected from three sections (Ps-XXIV – Ps-XXVI) (Figs 1, 3). A relatively poor fauna derives from the loam with limestone scree filling the open fissure in the western clippe of Falsztyn Rocks (Ps-XXIV, Ps-53 – Ps-56). Woodland snails, accompanied by meadow-dwellers, were its most important components. The remaining two sections are situated

within the western clippe. The first (Ps-XXV, Ps-57), representing initial rendsina, appears on a small, flat ledge in the middle part of the southern slope. The mollusc fauna was rich and dominated by species typical for open rock faces (*Pyramidula pusilla* (Vall.), *Chondrina clienta* (West.)) and grassland snails: *Vallonia pulchella* (Müll.) and *V. costata* (Müll.). Shade-loving and catholic taxa were accessory components of the assemblage. Profile Ps-XXVI was situated next to the preceding one. Its loam, abounding in angular rock debris, contained a poor molluscan assemblage, dominated by open-country species, mainly living on open rock faces (*Pyramidula pusilla* (Vall.), *Chondrina clienta* (West.)) (Fig. 3). Remains of rodents, such as *Microtus agrestis* (L.) and *Clethrionomys glareolus* (Scher.), occurred in all the samples.

MOLLUSC ASSEMBLAGES

The molluscan assemblages found in the cave and slope deposits described above include 63 snail species as well as shells of slugs (Limacidae). The number of species per sample varies between 6 and 40, while the number of specimens ranges from 17 to 3,774. The constancy (C) and dominance (D) structure is

characterised by low values of dominance. Four species are the main components of the fauna and reach the highest values of C-D: *Vallonia pulchella* (Müll.) (5-4), *Pyramidula pusilla* (Vall.) (4-4), *Fruticicola fruticum* (Müll.) (4-3) and *Chondrina clienta* (West.) (4-3). On the other hand, 28 species can be regarded as accessory components characterised by very low C-D indices (class 1-1) (Fig. 4A). The low values of normalised constancy and dominance indices ($C_i=25.78$ and $D_i=10.55$), as well as high values of differentiation index $TDA=0.813$ correspond with quantitative diversity of particular assemblages (Fig. 4A). Similar relations have been noted for the fauna of cave and slope deposits described from small karst forms of Cracow-Częstochowa Upland (S. W. ALEXANDROWICZ 2000, W. P. ALEXANDROWICZ 2000).

The species belong to three C-D categories and are ordered according to Q index values (geometrical

A

	D-1	D-2	D-3	D-4	D-5
C-5				1	
C-4		5	2	1	
C-3	3	7	1		
C-2	13	3			
C-1	28				

$\Sigma_{tax} = 64$ $C_i = 25.78$ $TDA = 0.813$
 $\Sigma_{spec} = 14,692$ $D_i = 10.55$

- Vallonia pulchella* (D-4; C-5)
- Pyramidula pusilla* (D-4; C-4)
- Fruticicola fruticum* (D-3; C-4)
- Chondrina clienta* (D-3; C-4)

B

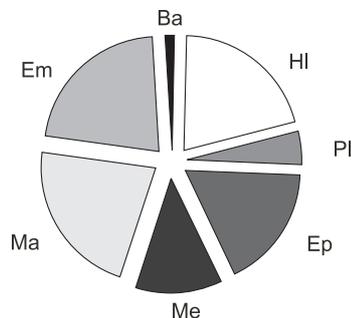


Fig. 4. Structure of mollusc assemblages: A – constancy (C) and dominance (D) structure; Σ_{tax} – number of species, Σ_{spec} – number of specimens, C_i , D_i , TDA – indices (see text); B – zoogeographical structure: HI – Holarctic species, PI – Palearctic species, Ep – European species, Me – Central-European species, Ma – Carpathian-Alpine species, Em – South-European species, Ba – Boreal species

mean of C and D) (Table 1). The first group (CD) comprises five species: *Pyramidula pusilla* (Vall.), *Chondrina clienta* (West.), *Fruticicola fruticum* (Müll.), *Vallonia pulchella* (Müll.) and *V. costata* (Müll.) characterised by the highest Q values. They can be regarded as dominant taxa in the described fauna. Accessory components (10 species and slug shells (Limacidae)) belong to the second class (Cd), while the remaining 47 species occur rarely (class cd) (Table 1).

The described fauna is composed of species of various geographical ranges (Fig. 4B). Three distributional groups can be distinguished. Widespread taxa, including Holarctic, Palearctic and European components, form the greatest proportion (44%) of the fauna. The remaining two groups – Central-European and species of limited distribution reach up to 33% each. The high proportion of mountain snails inhabiting the Alps and the Carpathians, as well as South-European and Mediterranean species, is the characteristic feature of this fauna. The zoogeographic structure of molluscan assemblages found in the described small karst forms is similar to that noted from slope sediments, calcareous tufa and fluvial sediments form Podhale Basin and the Tatra Mts (W. P. ALEXANDROWICZ 1997, 2001, 2004). Molluscan fauna of cave and slope deposits from Cracow-Częstochowa Upland and the Sudety Mts is characterised by a clearly different zoogeographic composition (S. W. ALEXANDROWICZ 1992, 2000, PAKIET 1999, W. P. ALEXANDROWICZ 2000).

The triangular malacological diagram in Fig. 5 illustrates the diversity of molluscan assemblages. Four main types of fauna can be distinguished.

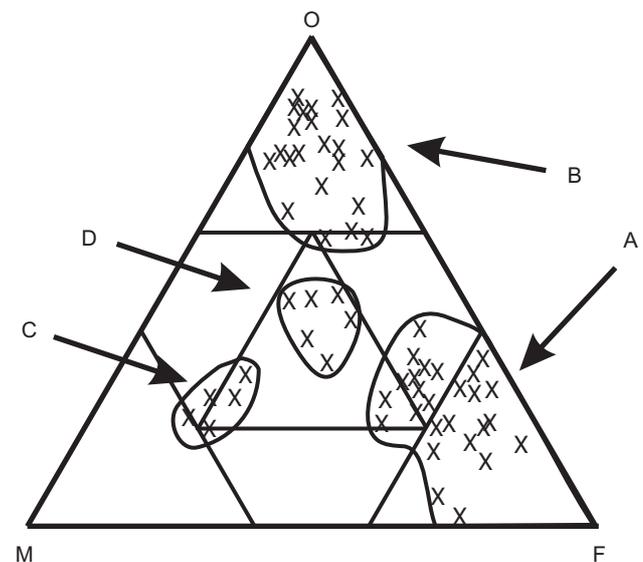


Fig. 5. Ecological types of mollusc assemblages: F – shade-loving species, O – open-country species, M – mesophile species, A, B, C, D – types of assemblages (see text)



Assemblage with high proportion of woodland snails (Fig. 5 assemblage A)

This fauna is characterised by the presence of numerous shade-loving taxa, usually accompanied by

mesophile species. Open-country snails form only an accessory component of the assemblage. Two sub-assemblages can be recognised. One corresponds with forested areas. It is a very rich and diverse fauna composed of shade-loving snails of dense coniferous,

Table 1. Structure of mollusc assemblages according to constancy and dominance categories: C – constancy >50%, D – dominance >5%, c – constancy <50%, d – dominance <5%, Q – geometric mean of constancy and dominance

	D	Q	d	Q	
C	<i>Pyramidula pusilla</i>	34.88	<i>Pupilla muscorum</i>	17.46	
	<i>Chondrina clienta</i>	32.62	<i>Mediterranea depressa</i>	15.56	
	<i>Fruticicola fruticum</i>	24.57	<i>Truncatellina cylindrica</i>	15.55	
	<i>Vallonia pulchella</i>	24.11	<i>Cochlicopa lubricella</i>	12.70	
	<i>Vallonia costata</i>	17.76	<i>Clausilia dubia</i>	10.30	
			<i>Limacidae</i>	10.02	
			<i>Isognomostoma isognomostoma</i>	9.12	
			<i>Discus ruderratus</i>	8.78	
			<i>Vitrea subrimata</i>	7.36	
			<i>Faustina faustina</i>	7.02	
			<i>Cochlodina orthostoma</i>	6.84	
	c			<i>Pupilla sterri</i>	11.31
				<i>Vitrea pellucida</i>	8.15
			<i>Nesovitrea hammonis</i>	6.78	
			<i>Monachoides vicinus</i>	6.36	
			<i>Ena montana</i>	6.32	
			<i>Vitrea diaphana</i>	6.11	
			<i>Carychium tridentatum</i>	5.99	
			<i>Euconulus fulvus</i>	4.54	
			<i>Balea biplicata</i>	4.47	
			<i>Argna bielzi</i>	3.69	
			<i>Platyla polita</i>	3.68	
			<i>Vitrea crystallina</i>	3.36	
			<i>Cochlicopa lubrica</i>	2.97	
			<i>Vertigo alpestris</i>	2.86	
			<i>Arianta arbustorum</i>	2.64	
			<i>Semilimax kotulae</i>	2.59	
			<i>Punctum pygmaeum</i>	2.40	
			<i>Aegopinella pura</i>	2.15	
			<i>Macrogastrea plicatula</i>	1.99	
			<i>Aegopinella minor</i>	1.88	
			<i>Aegopinella nitens</i>	1.75	
			<i>Euomphalia strigella</i>	1.63	
			<i>Petasina unidentata</i>	1.62	
			<i>Ruthenica filograna</i>	1.60	
			<i>Vitrea transsylvanica</i>	1.56	
		<i>Vertigo pygmaea</i>	1.43		
		<i>Vertigo pusilla</i>	1.17		
		+ 20 species	<1.00		

deciduous or mixed forests: *Discus ruderatus* (Fér.), *Ena montana* (Drap.), *Vitrea subrimata* (Reinh.), *Mediterranea depressa* (Sterki) and others. Species inhabiting shrubland and sparse forests (*Fruticicola fruticum* (Müll.)), as well as mesophile taxa (*Vitrina pellucida* (Müll.), *Clausilia dubia* Drap.), are accessory components. Meadow-dwelling and petrophile taxa form an admixture. Single shells of cold-tolerant snails, such as *Semilimax kotulae* West. and *Vertigo modesta* (Say), are also present. Another subassemblage is typical for partly shaded habitats. Shade-loving snails preferring sparse forests, such as *Fruticicola fruticum* (Müll.), *Arianta arbustorum* (L.) and *Aegopinella minor* (Stab.), are the most important components of this fauna. They are accompanied by species of dense forests (*Ena montana* (Drap.), *Vitrea subrimata* (Reinh.), *Mediterranea depressa* (Sterki)) and catholic taxa (*Vitrina pellucida* (Müll.), *Nesovitrea hammonis* (Ström)). Open-country molluscs (*Vallonia pulchella* (Müll.), *V. costata* (Müll.), *Pyramidula pusilla* (Vall.), *Chondrina clienta* (West.)) are also common.

The community dominated by woodland species is typical for forested parts of the tors and rock hills. It is more often found in small karst forms developed at the foot of the northern, eastern or western slopes covered by differentiated forest formations (dense or sparse) or shrubs. The described fauna was recognised in twenty seven samples.

Assemblage with high proportion of open-country snails (Fig. 5 assemblage B)

This relatively rich assemblage comprises mainly meadow species and snails inhabiting open rock faces. The remaining ecological groups are only its accessory components. Two subassemblages can be distinguished. A high proportion of grassland snails: *Vallonia pulchella* (Müll.), *V. costata* (Müll.) and *Pupilla muscorum* (L.), accompanied by xerophile *Cochlicopa lubricella* (Porro), is characteristic of the first subassemblage. Species living on rock faces: *Pyramidula pusilla* (Vall.) and *Chondrina clienta* (West.), are subordinate components of the mentioned fauna. Woodland and mesophile taxa occur sporadically. The dominance of petrophile snails living on open rock faces: *Pyramidula pusilla* (Vall.), *Chondrina clienta* (West.), *Pupilla sterii* (Voiht) and *Truncatellina cylindrica* (Fér.), accompanied by grassland forms: *Vallonia pulchella* (Müll.), *V. costata* (Müll.) and xerophile *Cochlicopa lubricella* (Porro), is typical for the second subassemblage.

The fauna dominated by open-country snails is characteristic of the deposits filling rock shelters and flat rock niches developed on the southern slopes of the hills. It is also commonly found in the profiles of rendsina-type soils. This fauna occurs in twenty two samples.

Assemblage with high proportion of mesophile snails (Fig. 5 assemblage C)

The assemblage is quite poor and characterised by the dominance of species of wide ecological tolerance: *Clausilia dubia* Drap., *Vitrina pellucida* (Müll.), *Nesovitrea hammonis* (Ström), accompanied by woodland and open-country taxa. Cold-tolerant species: *Semilimax kotulae* West., *Vertigo modesta* (Say), *V. genesii* (Gred.), *V. geyeri* Lindh. and *Columella columella* (G. Mart.) are present in few samples.

The assemblage occurs in small rock niches and in debris fans developed at the foot of the slopes. It was recognised in five samples.

Mixed assemblage with representatives of three ecological groups (Fig. 5 assemblage D)

The assemblage represented in the remaining six samples is characterised by roughly equal proportions of different ecological groups, though in individual samples different species of these groups dominate.

The mentioned molluscan assemblages correspond with the fauna of subfossil molluscs reported from cave and slope deposits of Podhale Basin (W. P. ALEXANDROWICZ 1997, W. P. ALEXANDROWICZ & STWORZEWICZ 2003), the Pieniny Mts. (S. W. ALEXANDROWICZ et al. 1985) and Cracow-Częstochowa Upland (S. W. ALEXANDROWICZ 1992, 2000, W. P. ALEXANDROWICZ 2000). Similar assemblages have been described in detail from numerous localities in Slovakia and the Czech Republic (LOŹEK 1980, 1981, 1982, 2000 and others).

AGE OF SEDIMENTS

The molluscan assemblages found in the described sediments correspond with the Holocene or even with the Late Glacial. The oldest fauna was found in profiles in Obłazowa Skala (Ps-VII) and Korowa Skala (Ps-XIX). The occurrence of species typical for cold, arctic climate: *Semilimax kotulae* West., *Vertigo modesta* (Say), *V. genesii* (Gred.), *V. geyeri* Lindh. and *Columella columella* (G. Mart.), is a characteristic feature of this community. Numerous remains of rodents typical for arctic tundra: *Lemmus lemnus* (L.), *Microtus agrestis* (L.) and *Clethrionomys glareolus* (Scher.) and some others were also found. The described sediments accumulated during the Younger Dryas – the last cold phase of the Late Glacial. Sediments of the Younger Dryas age containing a similar mollusc and rodent fauna have been described from Obłazowa Cave (VALDE-NOWAK et al. 2003) and from several localities in the Czech Republic and Slovakia (LOŹEK 1980, 1981, 1982). The rich fauna with a high proportion of forest snails found in log Ps-VIII comprises numerous shells of *Discus ruderatus* (Fér.) accompanied by forest species of high thermal toler-

ance: *Ena montana* (Drap.) and *Arianta arbustorum* (L.). Cold-loving taxa, especially *Semilimax kotulae* West. are also present. The described assemblage is similar to the “Ruderatus-fauna” regarded as typical for the Early Holocene (DEHM 1967, S. W. ALEXANDROWICZ 1987, LOŻEK 2000, W. P. ALEXANDROWICZ 2004). The molluscan fauna found in the loamy de-

posits filling small karst forms and in rendsina-type soils (all analysed profiles except those described above: Ps-VII, Ps-VIII and Ps-XIX) corresponds with the Late Holocene. Its taxonomic composition and structure are very similar to the recent fauna of the described rocky hills (Fig. 6A).

CONCLUSIONS

The deposits filling small caves, rock shelters, rock niches or fissures, developed within flat surfaces of the rock hills, as well as those forming debris fans at the foot of rock faces are relatively thin. They represent two main lithological types: loam with limestone scree and dark rendsina-type soils. Snail shells occur commonly in both types of deposit. The development of molluscan assemblages indicates environmental changes. The sequence begins with a fauna typical of cold climate and rather open, moderately humid environment. Snail shells are accompanied by remains of rodents characteristic for tundra or steppe-tundra. The described interval is associated with the cold, terminal phase of Late Glacial – Younger Dryas. At the beginning of Holocene a rapid warming of the climate was followed by forest expansion. Rocky hills were wooded by dense coniferous forests. Mollusc as-

semblages of Early Holocene age are characterised by the dominance of woodland species accompanied by mesophiles (Fig. 6A, B). The main phase of development of mixed and deciduous forest in Podhale Basin corresponds with the Middle Holocene. This stage is well documented in malacological sequences described from logs of calcareous tufa and fluvial deposits (W. P. ALEXANDROWICZ 1997, 2004) and in palynological profiles (KOPEROWA 1962, OBIDOWICZ 1990). Unfortunately, cave mollusc-bearing sediments associated with the Middle Holocene were not recognised in the studied profiles. The majority of the profiles described above corresponds with the Late Holocene (Fig. 6A, B). Similar stratigraphic sequences of molluscan assemblages have been described from localities of deposits filling small karst forms in Cracow–Częstochowa Upland (S. W. ALEXANDROWICZ

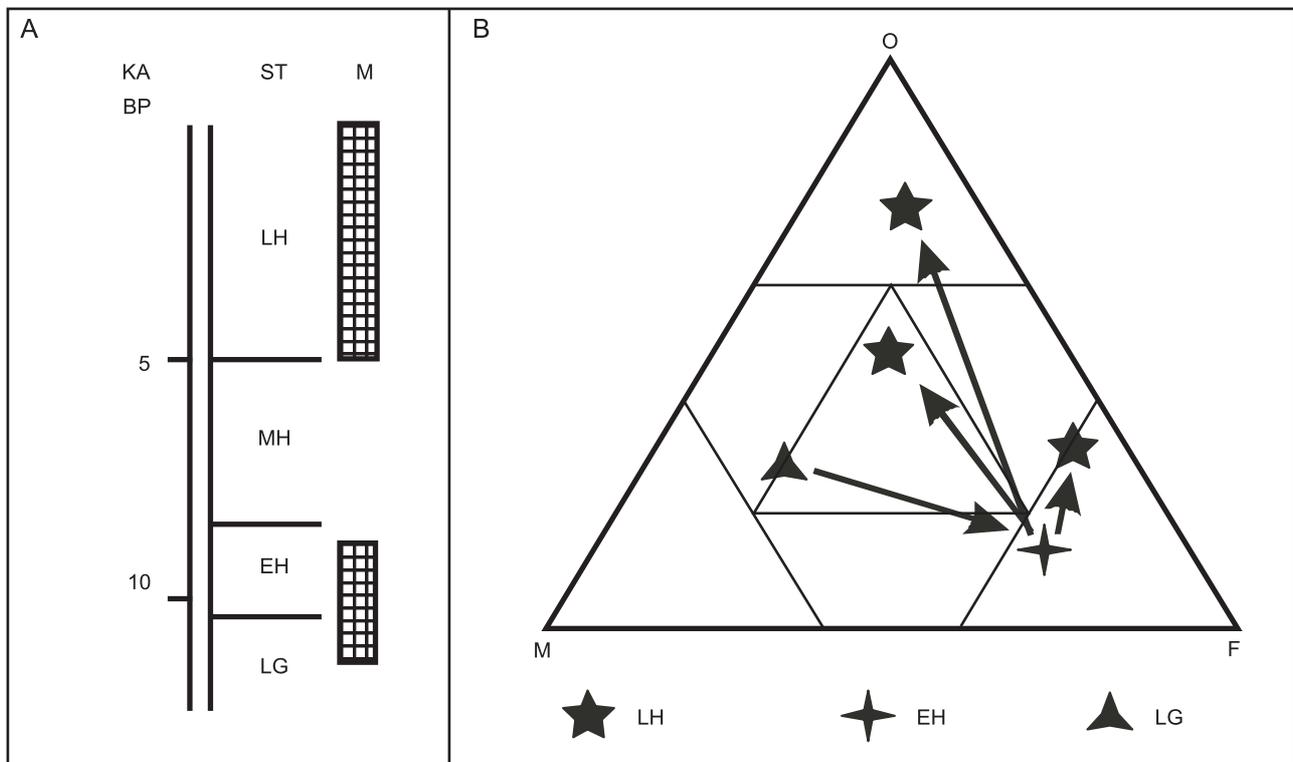


Fig. 6. Stratigraphic range of mollusc assemblages (A) and succession of communities (B); A: Ka BP – age in thousand years, ST – stratigraphic subdivision: LG – Late Glacial, EH – Early Holocene, MH – Middle Holocene, LH – Late Holocene, M – mollusc fauna; B: F – shade-loving species, O – open-country species, M – mesophile species, LG – Late Glacial, EH – Early Holocene, LH – Late Holocene

1992, 2000, W. P. ALEXANDROWICZ 2000), Podhale Basin (W. P. ALEXANDROWICZ 1997), the Tatra Mts (W. P. ALEXANDROWICZ 2001), Sudety Mts (PAKIET 1999), Pieniny Mts (S. W. ALEXANDROWICZ et al. 1985) as well as from numerous localities in Slovakia and the Czech Republic (LOZEK 1980, 1981, 1982, 2000 and others). Cave sediments reported from large caves usually represent a large time span, including not only the Holocene or Late Glacial, but also the Vistulian, Last Interglacial or even older phases of Pleistocene (STWORZEWICZ 1973, 1988, S. W. ALEXANDROWICZ et al. 1992, MADEYSKA 1988, W. P. ALEXANDROWICZ & STWORZEWICZ 2003 and others).

The mollusc assemblages from cave deposits described above are strongly differentiated. Their taxonomic composition and structure depends of several factors. The most important are: lithology of lime-

stones, kind and size of karst form, slope relief, forest cover and vegetation type. Especially, sediments filling small karst forms contain different molluscan assemblages. The dominance of woodland snails, especially the forest-dwellers, is typical for relatively deep rock shelters and fissures developed on northern slopes of hills. Species inhabiting shaded or partly shaded rock faces as well as mesophile taxa complete this fauna (Fig. 7 assemblage A). Sediments filling flat rock niches, and accumulated on rock ledges contain molluscan assemblages composed mainly of meadow and xerophile snails inhabiting dry grasslands with an admixture of petrophile taxa (Fig. 7 assemblage B). Loam with limestone scree and initial rendsina-type soils deposited in fissures and ledges developed on steep rocky slopes comprises relatively poor molluscan assemblages dominated by snails of open rock

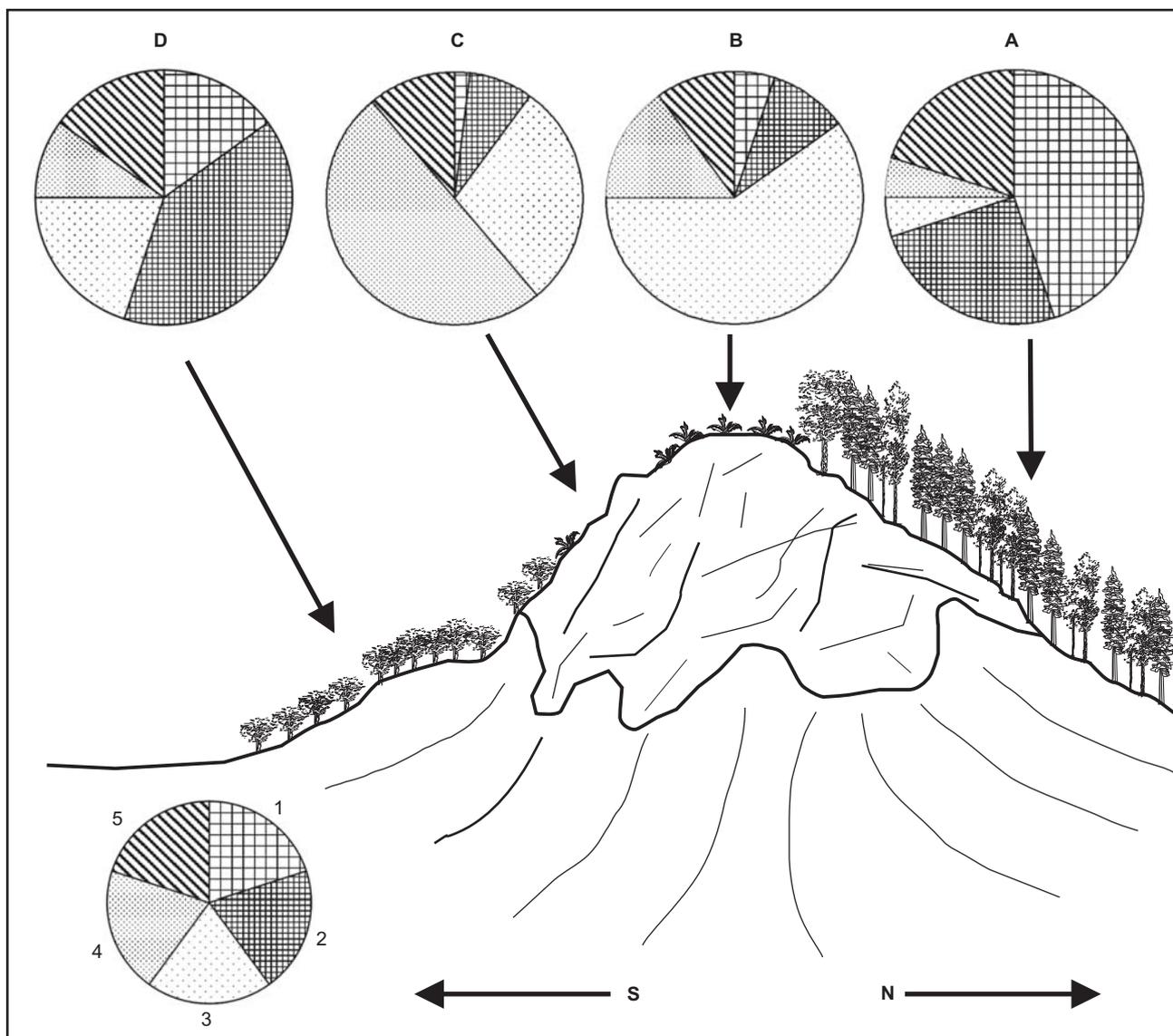


Fig. 7. Mollusc assemblages in deposits filling small karst forms: A, B, C, D – types of assemblages (see text), 1 – forest species, 2 – shrubland and sparse forest species, 3 – grassland species, 4 – petrophile species, 5 – mesophile species, S – southern slopes, N – northern slopes



faces accompanied by open-country and xerophile species (Fig. 7 assemblage C). Debris fans and rock niches developed at the foot of southern, eastern and western slopes of the hills usually comprises rich molluscan assemblages with a high proportion of woodland species, represented mainly by shrubland taxa (Fig. 7 assemblage D). Limestone clippings in the eastern part of Podhale Basin are surrounded by cultivated areas. The main phase of agriculture develop-

ment in this region is associated with the last 500 years (KOPEROWA 1962, OBIDOWICZ 1990, W. P. ALEXANDROWICZ 1997). However, natural processes controlling deposition of sediments filling small karst forms, as well as molluscan communities inhabiting rocky hills are only insignificantly changed by human activity.

REFERENCES

- ALEXANDROWICZ S. W. 1987. Analiza malakologiczna w badaniach osadów czwartorzędowych. *Zesz. Nauk AGH, Kwart. Geologia* 12: 3–240.
- ALEXANDROWICZ S. W. 1992. Malacofauna from a rock-shelter in Ruskie Skąły Tors (Będkowska Valley, Cracow Upland). *Folia Quatern.* 63: 27–34.
- ALEXANDROWICZ S. W. 1999. Tanatocenozy muszlowe w rzeczonym środowisku sedimentacyjnym – metody badań i interpretacji. *Zesz. Nauk AGH, Kwart. Geologia* 25: 211–295.
- ALEXANDROWICZ S. W. 2000. Malacofauna of Holocene cave sediments of the Cracow Upland (Poland). *Folia Quatern.* 71: 85–112.
- ALEXANDROWICZ S. W., DROBNIOWICZ B., GINTER B., KOZŁOWSKI J. K., MADEYSKA T., NADACHOWSKI A., PAWLKOWSKI M., SOBCZYK K., SZYNDLAER Z., WOLAN N. 1992. Excavation in the Zawalona Cave at Mników (Cracow Upland, Southern Poland). *Folia Quatern.* 63: 43–76.
- ALEXANDROWICZ S. W., NADACHOWSKI A., RYDLEWSKI J., VALDE-NOWAK P., WOŁOSZYN B. 1985. Subfossil fauna from cave in the Sobczański Gully (Pieniny Mts., Poland). *Folia Quatern.* 56: 57–78.
- ALEXANDROWICZ W. P. 1997. Malakofauna osadów czwartorzędowych i zmiany środowiska naturalnego Podhala w młodszym wistulianie i holocenie. *Folia Quatern.* 68: 7–132.
- ALEXANDROWICZ W. P. 2000. Molluscan assemblages from cave and slope sediments of the Częstochowa Upland (Poland). *Folia Quatern.* 71: 113–137.
- ALEXANDROWICZ W. P. 2001. Molluscan assemblages filling small karst forms in the Tatra Mountains (Southern Poland). *Acta Carstologica* 30: 125–142.
- ALEXANDROWICZ W. P. 2004. Molluscan assemblages of Late Glacial and Holocene calcareous tufa in Southern Poland. *Folia Quatern.* 75: 3–309.
- ALEXANDROWICZ W. P., STWORZEWICZ E. 2003. Snails (Gastropoda). In: *Obłazowa Cave human activity, stratigraphy, and palaeoenvironment* (VALDE-NOWAK P., NADACHOWSKI A., MADEYSKA T., eds), pp. 91–94, Institute of Archeology and Ethnology, Pol. Acad. Sci., Kraków.
- DEHM R. 1967. Die landschnecke *Discus rudneratus* im Postglacial Süddeutschlands. *Mitt. Bayer. Staats. Pal. Hist. Geol.* 7: 135–155.
- DOBROWOLSKI K. 1963. Próba analizy pojęcia “rzadki gatunek”. *Ekol. Pol.* B3: 207–212.
- KOPEROWA W. 1962. Późnoglacialna i holocenińska historia roślinności Kotliny Nowotarskiej. *Acta Paleobot.* 2: 3–57.
- LOŹEK V. 1964. Quatärmollusken der Tschechoslowakei. *Rozpr. Ustř. Ust. Geol.* 31: 1–374.
- LOŹEK V. 1980. Quaternary molluscs and stratigraphy of the Mažarna Cave. *Čs. Kras.* 30: 67–80.
- LOŹEK V. 1981. Příroda Statni Přírodní Rezervace Rozsutec v najbládsi geologické minulosti. *Rozsutec Stat. Přír. Rez.*: 31–52.
- LOŹEK V. 1982. Mekki ŠPR Čierny Kamen ve Velke Fatře. *Ochrana Přírody* 3: 113–133.
- LOŹEK V. 2000. Palaeoecology of Quaternary Mollusca. *Antropozoikum* 24: 35–59.
- MADEYSKA T. 1988. Osady jaskiń i schronisk Doliny Sąpowskiej. In: *Jaskinie Doliny Sąpowskiej* (CHMIELEWSKI W., ed.), pp. 39–45, Prac Inst. Archeol. UW.
- OBIDOWICZ A. 1990. Eine pollenanalytische und moorkundliche studie zur vegetationsgeschichte des Podhale-Gebietes (West-Karpaten). *Acta Paleobot.* 30: 147–219.
- PAKIET M. 1999. Nowe dane o holocenińskiej malakofaunie Sudetów. *Kwart. AGH Geologia* 25: 339–362.
- STWORZEWICZ E. 1973. Kopalna fauna ślimaków (Gastropoda) ze schroniska nad Jaskinią Niedostępną w okolicach Ojcowa. *Acta Zool. Cracov.* 18: 301–309.
- STWORZEWICZ E. 1988. Fauna mięczaków jaskiń i schronisk Doliny Sąpowskiej. In: *Jaskinie Doliny Sąpowskiej* (CHMIELEWSKI W., ed.), pp. 35–49, Prac Inst. Archeol. UW.
- VALDE-NOWAK P., NADACHOWSKI A., MADEYSKA T. (eds.) 2003. *Obłazowa Cave human activity, stratigraphy, and palaeoenvironment*. 176 pp., Institute of Archeology and Ethnology, Pol. Acad. Sci., Kraków.

Received: August 5th, 2006

Accepted: November 30th, 2006

