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Application of malacological analysis to reconstruction of regional and local environmental changes: the Cisowa Skała locality (the Carpathians, southern Poland)

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An isolated limestone hill (Cisowa Skała), located in the Podhale Basin in southern Poland, has yielded mollusc shells and small vertebrate bones in deposits filling small karst forms such as rock shelters, characteristic molluscan assemblages can be identified, the succession of which reflects changes in the environment and also microhabitat variations depending on local factors, such as slope exposure and type of vegetation. These local factors markedly affect regional environmental trends determined primarily by climate change and, during the last several hundred years, also by human activity. Such malacological analysis enables effective palaeogeographical reconstructions, both on the scale of geographical regions and for microhabitats.

Key words: karst sediments, molluscs, environmental changes, Holocene, Podhale Basin, Pieniny Klippen Belt.

INTRODUCTION

Small karst forms (e.g., rock shelters, niches, fissures) are commonly found in areas of carbonate rocks. They contain sedimentary deposits and organic remains such as vertebrate bones and mollusc shells, which provide valuable information on the geological history of these karst areas. These deposits are usually thin, typically represent short intervals of time and strongly reflect local environmental conditions. This local influence may hinder the analysis of regional environmental trends. However, it provides unique material that enables the reconstruction of microhabitats and their spatial distribution across a relatively small area. This aspect is fundamental to understanding variations in environmental conditions which decide the course of biological and geological processes. Observing present-day natural habitats, it is clear that they comprise a diverse mosaic of microhabitats. Any regional reconstructions which necessitate an averaging of data inevitably lead to imposing uniformity of conditions within reconstructions of large areas, hence erasing their internal diversity. Thus, in order to decipher the geological history of geographical regions, it is important to distinguish the regional environmental trends that decide their development, from the local factors that (sometimes greatly) modify these trends. The nature of habitats in the karst areas, resulting from specific patterns of relief and microclimate, determines the strong diversity in the composition and structure of the faunal and floral communities inhabiting them. This relationship has been emphasized in many studies (e.g., Ložek, 1972a; Kemencei et al., 2014; Raschmanová et al., 2018; Bátori et al., 2019). Isolated limestone tors characterized by a wide variety of habitat types, such as Cisowa Skała, are excellent objects of such study.

Areas built of carbonate rocks are usually home to diverse mollusc assemblages. Snails find favourable living conditions there, and the presence of calcium carbonate in the soils fosters the preservation of their shells in a subfossil state. At the same time, molluscs are a group highly suitable for reconstructing local habitats. This mainly stems from the shell's low resistance to chemical and mechanical destruction, which limits shell transport after the organism's death. The molluscan assemblages found in sedimentary deposits can therefore be treated as autochthonous or paraautochthonous malacocenoses that in their ecological structure are closely related to the conditions prevailing during deposition. Studies of malacocenoses in deposits of small karst forms have been undertaken in several European countries, in particular in the Czech Republic and Slovakia (e.g., Ložek, 1972a, b, 1980, 1981, 1989, 2012), Russia (e.g., Yakovlev et al., 2013; Danukalova et al., 2014, 2020), Hungary (e.g., Kemencei et al.,

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2014; Sümegi and Náfrádi, 2015) and Poland (e.g., Stworzewicz, 1973; Nadachowski et al., 1989; Alexandrowicz et al., 1992; Dagan-Gintner et al., 1992; Cyrek et al., 2000; Alexandrowicz and Stworzewicz, 2003; Alexandrowicz, 1992, 2000a, b, 2001; Alexandrowicz and Rudzka, 2006; Szymanek et al., 2016; Krajcarz et al., 2020; Wilczyński et al., 2020).

This paper is devoted to the reconstruction of spatial diversity and changes over time in microhabitats within the area of an isolated limestone tor, and is based on subfossil mollusc remains preserved within sedimentary infills of small karst forms deposited during the Late Glacial and Holocene.

STUDY AREA

The studies were conducted at Cisowa Skała, located in the eastern part of the Podhale Basin in the Carpathians (GPS: 49°26'23" N and 20°07'36" E; Fig. 1). The Podhale Basin is a tectonic depression delimited by the Tatras massif to the south and the Flysch (Outer) Carpathians to the north. It is a synclinorium, gently folded during the Early Miocene, filled with Paleogene flysch deposits. The Podhale Basin is crossed by a Mesozoic limestone zone – part of the Pieniny Klippen Belt. This limestone forms numerous rocky hills, clearly distinguished in the generally monotonous and flat landscape of the Podhale (Klimaszewski and Starkel,1972; Fig. 1). Cisowa Skała itself forms an isolated rocky hill with a relative height of ~60 m. It is built of Middle Jurassic limestones, which form small rocky walls with a height of less than 10 m (Fig. 2). Numerous minor karst forms are developed among the rocky walls, mainly niches and rock shelters, open fractures, pits and cavities. Some of these are filled with rubble and sand material containing numerous well-preserved mollusc shells, and at times also vertebrate bones. Cisowa Skała is characterised by a significant diversity of habitats. Its northern slopes are overgrown by a forest largely composed of *Pinus*. The western and eastern slopes are unforested and are covered with grasses and shrubs. The southern slope is characterised by the presence of xerophilous plants. Cisowa Skała is located in an agricultural area and is surrounded by unforested land, turned to agricultural fields and pasture (Figs. 2 and 3).

MATERIAL AND METHODS

The malacological analysis was performed in accordance with the methods described by Ložek (1964) and Alexandrowicz and Alexandrowicz (2011). During the field study, in which the profiles analyzed were localated, described and sampled, several dozen small karst forms were identified. In most of them, deposits were not found or their thickness was very small (up to 5 cm). In ten profiiles, thicker sequences (from 10 to 90 cm) were found. These profiles (Cs-I–Cs-X) were subjected to detailed malacological study. The samples weighed ~2–3 kg and represented all layers identifiable within a profile. Laboratory processing included washing on a 0.5 mm mesh sieve, followed by picking of shell material and vertebrate bones. The malacological analysis encompassed 43 samples

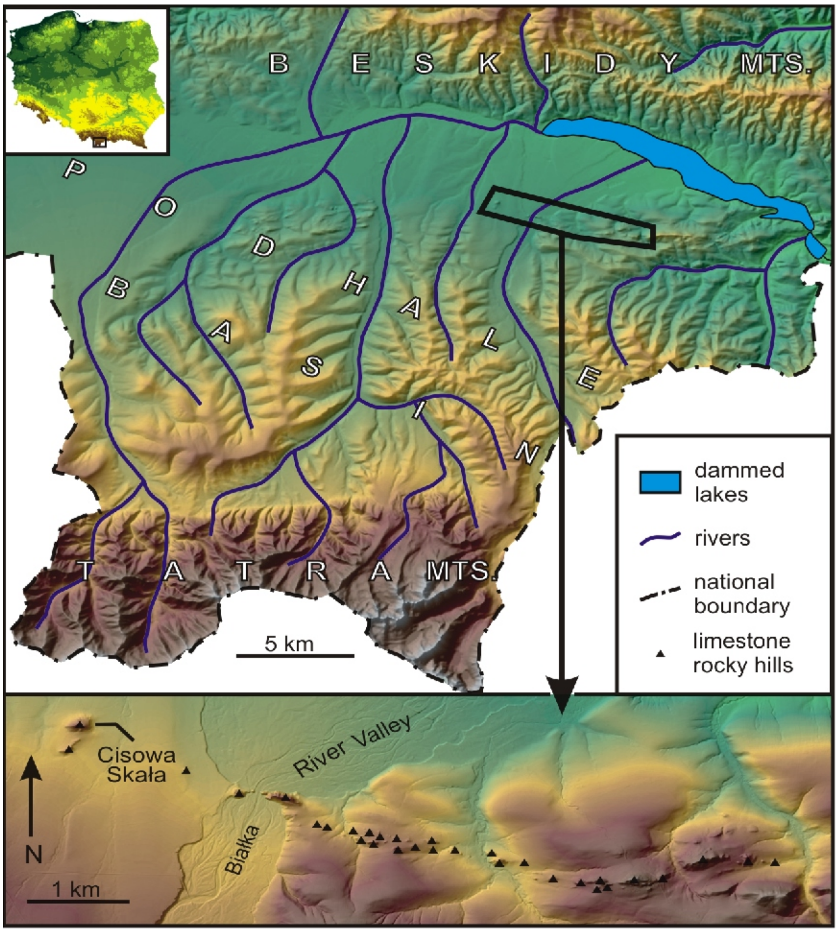

Fig. 1. Location of the Cisowa Skała hill (map base: www. polska.e-mapa.net)

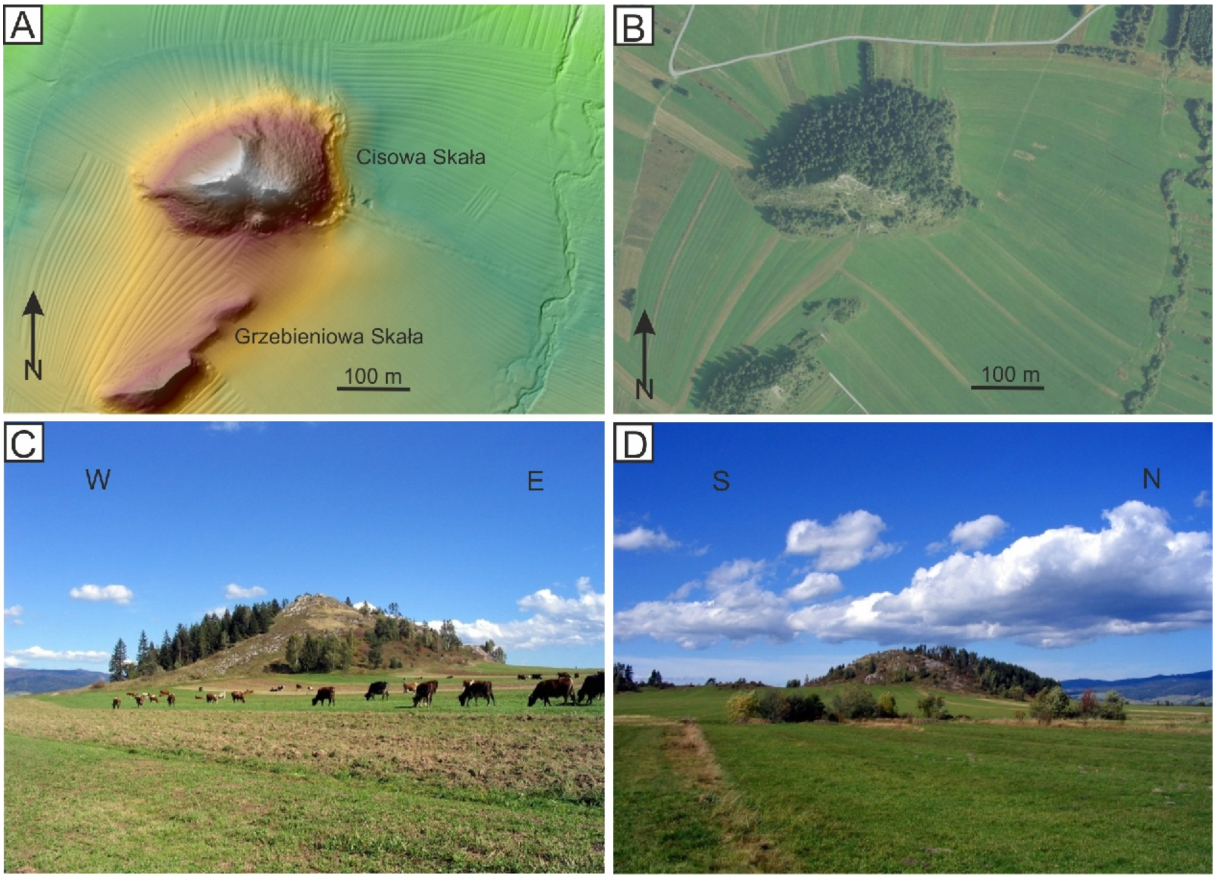

Fig. 2. Recent environment of the surroundings of Cisowa Skała

A – hypsometric map (map base: www.polska.e-mapa.net); **B** – satelite photo (photo base: www. polska.e-mapa.net); **C** – View of southern slopes; **D** – view of eastern slopes (photos by R. Wójtowicz, available from: www. fotografie.nowytarg.pl)

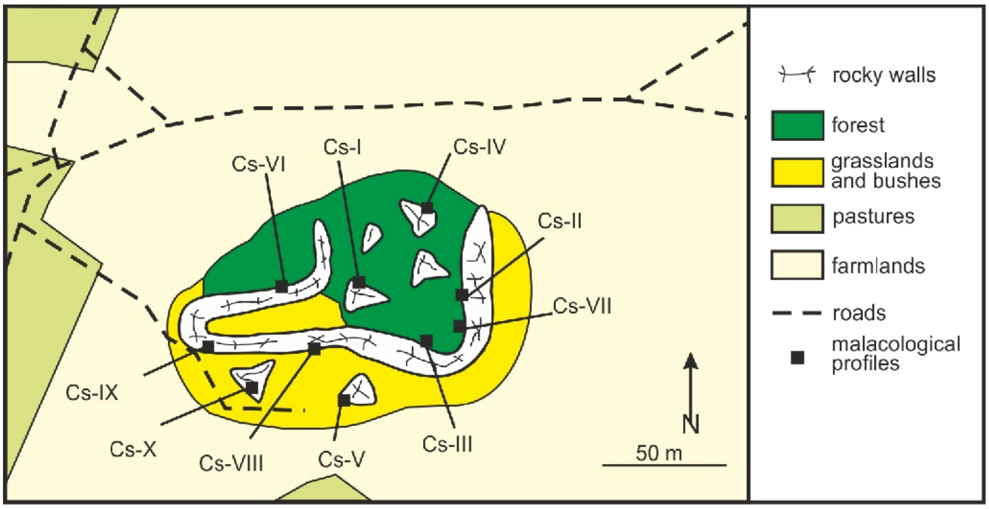

Fig. 3. Plant cover and location of profiles (Cs-I–Cs-X)

of which 35 contained identifiable subfossil molluscs. Identifications were made based on guides (Wiktor, 2004; Welter-Schultes, 2012; Horsák et al., 2013) and our own comparative collection. In the next stage, percentage compositions of individual species in the samples were calculated. Taxa were classified into ecological groups: F_F – shadow-loving, forest species, F_B – shadow-loving species living in light forests and bushy zones, F_H – shadow-loving species of humid habitats, O_X – xerophilous and petrophilous species, O_O – open-country species, M_D – mesophilous species of dry habitats, M_I – mesophilous species of moderately wet habitats, M_H – mesophilous species of wet habitats, H – hygrophilous species according to the scheme developed by Ložek (1964); Alexandrowicz and Alexandrowicz (2011) and modified by Juřičková et al. (2014b). These data were used to construct malacological spectra, which served as the basis for reconstructing the palaeoenvironment. Analysis of a similarity dendrogram (applying UPGMA method and Morisita's formula; Morisita, 1959) enabled identification of the characteristic types of fauna. Calculations were done using the *PAST* statistical software (Hammer et al., 2001). Vertebrate remains were identified by A.N. Motuzko (Faculty of Geography, Belorussian State University). The stratigraphic positions of the deposits were determined either based on the characteristics of the molluscan assemblages by comparison with those in profiles elsewhere, in particular those of adjacent areas, or based on radiocarbon dating, calibrated using the *OxCal* software (Bronk Ramsey, 2017). The radiometric analyses (seven conventional dates) were conducted in the Absolute Dating Methods Centre, Institute of Physics, Silesian University of Technology in Gliwice (laboratory reference number: Gd, five samples) and in the Radiocarbon Laboratory in Skała (laboratory reference number: MKL, two samples). Well-preserved shells of *Arianta arbustorum*, *Isognomostoma isognomostomos* and *Euomphalia strigella* were selected for dating. The shells were cleaned to remove deposits (both on the surface and inside). The presence of shells in similar settings and their direct relationship to the time of deposition indicate that the dates obtained can be used to determine the age of the deposits (Goslar and Pazdur, 1985).

RESULTS

Fifty-seven species of terrestrial snail, represented by almost 14,000 specimens, were determined in the material analysed. The number of species in individual samples ranged from 6 to 46, while the number of specimens ranged from 101 to 1,310 (Table 1). A dozen bones and teeth of small vertebrates (mainly rodents) belonging to 7 taxa were also identified.

MALACOFAUNA

Species belonging to 9 ecological groups were present in the material analysed.

Ecological group F_F includes shadow-loving species preferring dense forests of low or moderate soil moisture content. This is the main component of the fauna (up to 70%) in profiles I–VII. It occurs more rarely in the other profiles (Figs. 4 and 5). Species with varied ecological requirements concerning both the dominant plant type and temperature are found here. On the one hand, there are taxa characteristic of coniferous forests growing in a moderately cold climate with continental influence (*Discus ruderatus*). On the other hand, there are snails of deciduous forest communities and indicating a relatively warm climate with oceanic or southern European influences (*Ruthenica filograna*, *Discus perspectivus*). There are many mountain species, particularly Carpathian and Carpathian-Alpine ones (*Vitrea diaphana*, *Eucobresia nivalis*; Table 1).

Ecological group F_B includes shadow-loving taxa that prefer more open biotypes than group F_F, in particular thin, well-lit forests and areas covered with shrubs. It is an important component of the fauna in profiles I-VII, and their share may exceed 50% (Figs. 4 and 5). Among species belonging to this group, two are of particular importance for palaeoenvironmental considerations: *Vertigo ronnebyensis* and *Semilimax kotulae*. Both these forms are typical of a cold climate. The first has been found in the Podhale Basin at several locations of Late Glacial and Early Holocene age. At present it does not occur in this area. The second form is a frequent element of subfossil mollusc assemblages, and at present is a relict species in the Podhale area (e.g., Alexandrowicz, 1997, 2013a; Wiktor, 2004; Alexandrowicz et al., 2014; Table 1).

Ecological group F_H includes shadow-loving species that require relatively humid habitats. It does not have a strong representation in the fauna analysed, and the most numerous species is *Vitrea crystallina* (Figs. 4, 5 and Table 1).

Ecological group O_X includes a relatively narrow group of taxa inhabiting open habitats. It constitutes an important component of malacocenoses identified in profile IX (Fig. 5), and its members (*Pupilla sterii*, *Chondrina clienta* and *Pyramidula pusilla*) are numerous. All these species are characteristic of very dry, open xerothermic habitats and strongly lit bare limestone tors (Table 1).

Ecological group O_O includes open-country species inhabiting grasslands of varying humidity. It is the dominant component of malacocenoses identified in profiles VIII and X (Fig. 5), where its participation can reach 80%. Its most numerous representatives are *Vallonia pulchella* and *Vallonia costata* – snails typical of open environments, usually grassy, with diverse humidity and temperature requirements. This group also includes *Columella columella*. It is a cold-living taxon that inhabits modern northern Europe and isolated high-mountain locations, where it lives above the timberline (Pokryszko, 1990). On the other hand, it is a common component of malacocenoses of the Late Glacial and Early Holocene, identified at numerous sites in Europe (e.g., Limondin-Lozouet and Rousseau, 1991; Preece and Day, 1994; Rousseau et al., 1994; Mania, 1995; Preece, 1998; Meyrick, 2001, 2002; Meyrick and Preece, 2001; Gedda, 2001, 2006; Limondin-Lozouet, 2011). Within the Podhale Basin, its latest occurrences are related to deposits dated to the Late Glacial and Early Holocene (e.g., Alexandrowicz, 1997, 2013a; Alexandrowicz et al., 2014). At present it does not occur in Poland except for the Tatra Mountains (Pokryszko, 1990; Alexandrowicz, 2001; Wiktor, 2004; Table 1).

Ecological groups M_D, M_I and M_H include taxa of high ecological tolerance, inhabiting dry (group M_D), medium humid (group M_I) and humid (group M_H) habitats. They are a supplementary component of malacocenoses, and their share does not exceed 30% (Figs. 4 and 5). One taxon represented in greater numbers is *Arianta arbustorum*, preferring shaded habitats of fairly high humidity (Table 1).

Ecological group H species typical of humid habitats is represented by only one species: *Vertigo geyeri*. It is a cold-loving, tundra form, characteristic of the Late Glacial and identified in numerous profiles around Europe from this stratigraphic position (e.g., Ložek 1964; Alexandrowicz, 1997, 2004; Limondin-Lozouet and Rousseau, 1991; Limondin-Lozouet, 1992, 2011; Krolopp and Sümegi, 1993; Preece and Day, 1994; Rousseau et al., 1994; Mania, 1995; Preece, 1998; Meyrick, 2001, 2002; Meyrick and Preece, 2001; Gedda, 2001, 2006). It is also frequently found in Late Glacial and Early Holocene deposits in the Podhale Basin (Alexandrowicz, 1997, 2004, 2013a, 2015; Alexandrowicz et al., 2014), and at present lives at isolated locations in this area (Schenková et al., 2012; Schenková and Horsák, 2013). Shells of *Vertigo geyeri* were found in profiles Cs-I – Cs-III (Fig. 4 and Table 1).

VETEBRATE FAUNA

Infrequent bones and teeth of small vertebrates were found in profiles I, III and V (Figs. 4 and 5). Profiles I and III contained the remains of the cold-loving tundra species *Dicrostonyx gulielmi*, *Lemmus lemmus*, *Microtus gregalis/agrestis*. Rich ver-

Table 1

Composition of malacofauna from deposits filling small karst forms at Cisowa Skała

E	Taxon	Profiles										Σ
		I	II	III	IV	V	VI	VII	VIII	IX	X	
	Acicula parcelineata (Cless.)			1	7	8						16
	Platyla polita (Hartm.)	12		2	43	55	39					150
	Argna bielzi (Rossm.)				18	29	35			1		83
	Vertigo pusilla Müll.	2	5	3	34	54	25	17	1			141
	Acanthinula aculeata (Müll.)	27		1	32	68	27					155
	Ena montana (Drap.)		5	5	5	15	35	20				85
	Cochlodina laminata (Mont.)	6	14	21	48	63	4	5				161
	Cochlodina orthostoma (Menke)	2	1	8	13	50	5	2	10		7	98
	Ruthenica filograna (Rossm.)			5	82	106	6	1				200
	Macrogastra plicatula (Drap.)	11	4	11	12	51	3					92
	Pseudalinda stabilis (L. Pfe.)				9	21						30
F_F	*Discus ruderatus* (Hartm.)	120	114	81	122	13	1					451
	Discus perspectivus (Mühlf.)				47	253						300
	Vitrea diaphana (Studer)	20	6	5	32	86	8	20				177
	Vitrea transsylvanica (Cless.)			2	40	79	13					134
	Vitrea subrimata (Reinh.)		2	3	44	105	76	12				242
	Meditterranea depressa (Sterki)	1	2	8	34	37	7	6	6			95
	Aegopinella pura (Ald.)	7	3	2	77	124	64	17				294
	Semilimax semilimax (Fér.)		3	1	7	14	3					28
	Eucobresia nivalis (Dum.&Mort.)	9	9	7	46	17	5					93
	Petasina unidentata (Drap.)	15	11	8	15	25						74
	Faustina faustina (Rossm.)				32	64	18	10		3		127
	Isognomostoma isognomostomos (Schr.)	3			63	86	76	26				254
	Vertigo alpestris Ald.						45	8				53
	Vertigo ronnebyensis (West.)	44	60	15	2							121
	Alinda biplicata (Mont.)	5		11	14	25	17	12			11	95
	Discus rotundatus (Müll.)				97	104	1	11				213
F_B	*Aegopinella minor* (Stab.)	1		1	54	58	17					131
	Semilimax kotulae West.	71	125	45	17	5						263
	Fruticicola fruticum (Müll.)			7	75	84	17	3			2	188
	Monachoides incarnatus (Müll)	9		5	15	82	22	9				142
	Vestia turgida (Rossm.)	1			3	2						6
F_H	*Vitrea crystallina* (Müll.)	10		20	58	76		2				166
	Monachoides vicinus (Rossm.)	4			25	73		3				105
	Pupilla sterri (Voith)					183			25	82	66	356
O_X	*Pyramidula pusilla* (Vallot)					97	14	9	36	168	79	403
	Chondrina clienta (Weste.)					103	13		35	156	53	360
	Vallonia coststa (Müll.)			10		348	3	8	146	261	367	1143
	Vallonia pulchella (Müll.)			20		459	1	5	236	416	798	1935
O_O	*Pupilla muscorum* (L.)			41	4	236		5	127	378	318	1109
	Columella columella (Mart.)	51	81	23	2							157
	Truncatellina cylindrica (Fér.)			9		231		3	55	209	203	710
M_D	*Cochlicopa lubricella* (Porro)			6		110	1	8	41	31	103	300
	Euomphalia strigella (Drap.)					35	8		19	5	67	134
	Cochlicopa lubrica (Müll.)			1	29	93	25	11	11	7		177
	Clausilia dubia Drap.	79	12	51	73	107	34	24	28	40	22	470
M_I	*Punctum pygmaeum* (Drap.)	9	11	20	41	107	34	7	18	2		249
	Euconulus fulvus (Müll.)	15	34	15	27	76	31	16	5	5		242
	Perpolita hammonis (Ström)	8	21	19	43	90	22	16	11	10		240
	Vitrina pellucida (Müll.)			2	11	43	5	14	11	1		87
	Limacidae	10	29	19	14	53	23	7	15	24	9	203
	Carychium tridentatum (Risso)	8		1	16	29	49					103
M_H	*Vertigo substriata* (Jeffr.)	49	31	18	31	8						137
	Arianta arbustorum (L.)	122	115	58	37	33						365
H	*Vertigo geyeri* Lind.	35	39	8								82
Number of species		**31**	**24**	**46**	**47**	**55**	**38**	**29**	**18**	**17**	**13**	**13936**
Number of individuals		**765**	**737**	**600**	**1563**	**4388**	**832**	**317**	**830**	**1799**	**2105**	

E – ecological groups of molluscs (after Ložek, 1964; Alexandrowicz and Alexandrowicz, 2011; Juřičková et al., 2014b): F_F – shadow-loving, forest species, F_B – shadow-loving species living in light forests and bushy zones, F_H – shadow-loving species of humid habitats, O_X – xserophilous and petrophilous species, O_O – open-country species, M_D – mesophilous species of dry habitats, M_I – mesophilous species of moderately wet habitats, M_H – mesophilous species of wet habitats, H – hygrophilous species

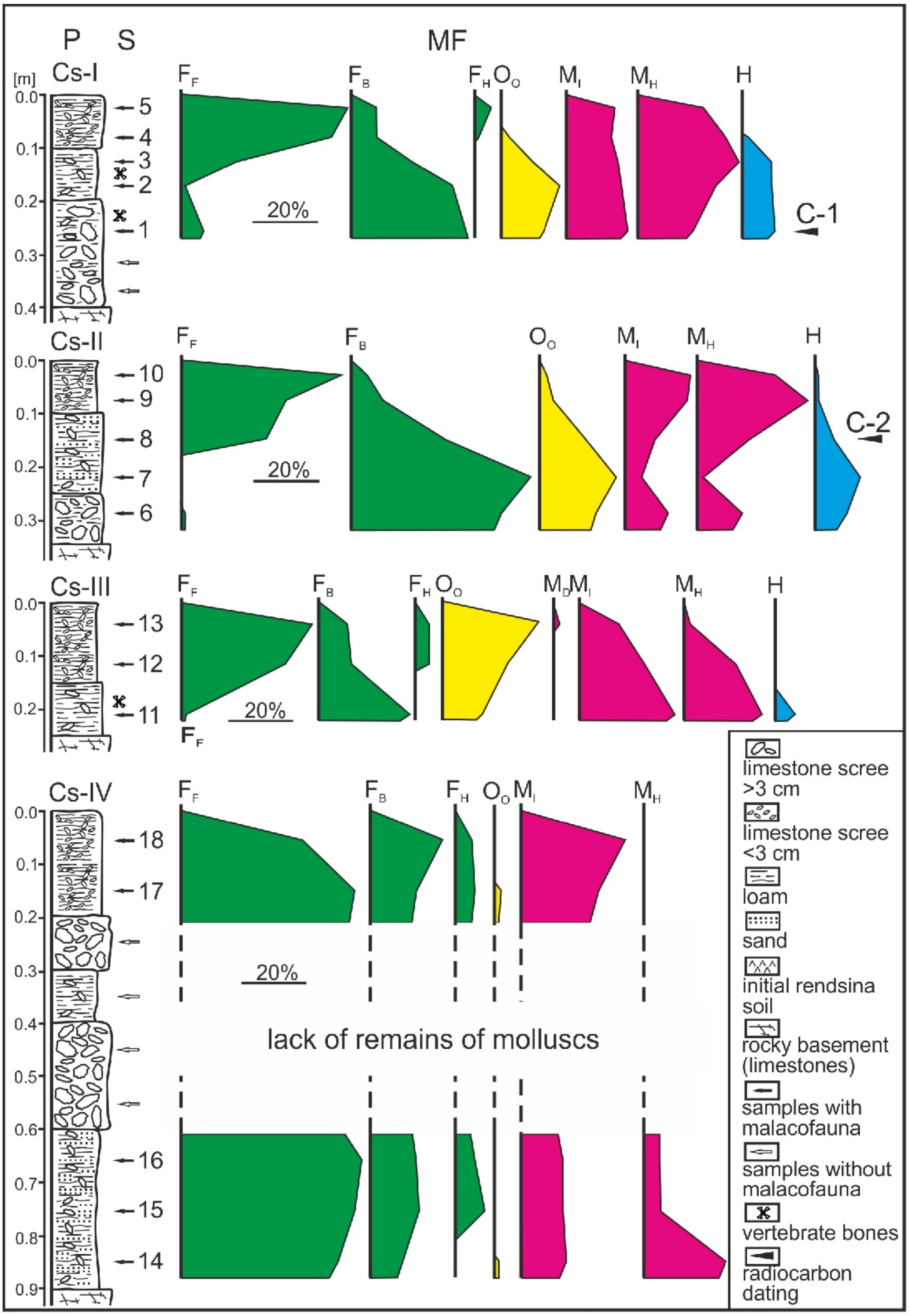

Fig. 4. Malacological percentage diagram (profiles Cs-I–Cs-IV)

Explanations as in Table 1

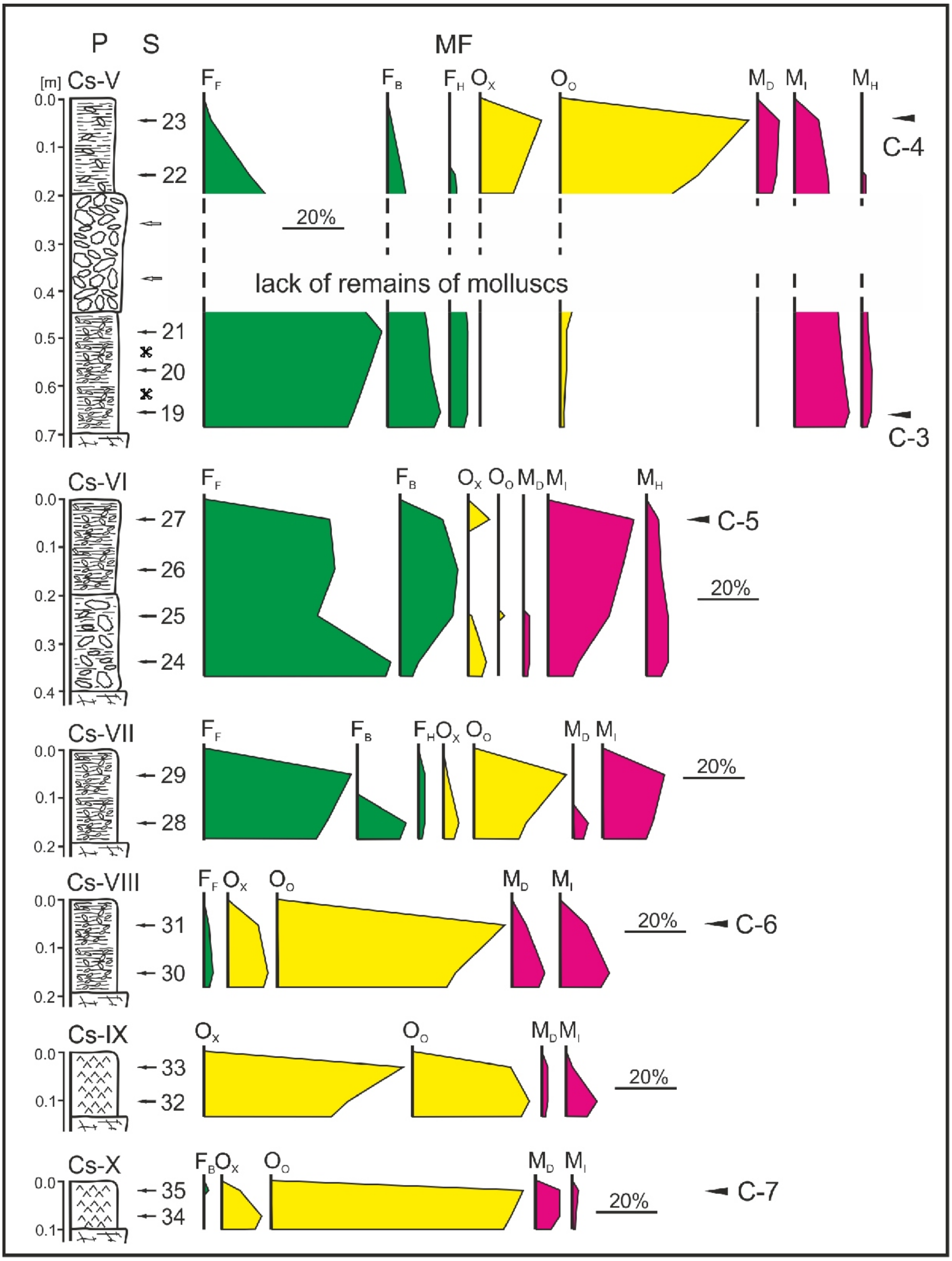

Fig. 5. Malacological percentage diagram (profiles Cs-V–Cs-X)

For explanations see Figure 4 and Table 1 tebrate communities of a similar composition, most likely representing the Late Glacial, were found in a small rock shelter at the base of the north slope of Cisowa Skała (Nadachowski et al., 2015). Other than the bone remains of cold-loving vertebrates, *Dicrostonyx gulielmi* and *Microtus gregalis* as well as bird bones (*Lagopus* sp.) were also found there. Bone remains of cold-loving species, inhabiting tundra or steppe-tundra environments, have also been found in several other rock shelters in the Podhale region (Alexandrowicz, 1997; Alexandrowicz and Rudzka, 2006), as well as in cave deposits at Obłazowa Skała (Valde-Nowak et al., 2003). A slightly different vertebrate assemblage was identified in profile V. A lack of tundra species is notable; instead there are taxa with slightly higher thermal requirements such as *Mustella nivalis* and *Sorex sp.*

MOLLUSCAN ASSEMBLAGES

The fauna was grouped according to the presence of assemblages characterizing specific environmental parameters using a dendrogram of similarities. On this basis, five types of molluscan assemblage were distinguished, differing in species composition and ecological preference (Fig. 6).

Assemblage A is characterized by a relatively poor species composition. Its most important characteristic is the presence of species typical of a cold climate, as well as taxa with high thermal tolerance. At the same time, forms with greater ecological requirements were not found. The most important components of this fauna are taxa typical of slightly shady environments (*Semilimax kotulae*, *Vertigo ronnebyensis*, *Arianta arbustorum*), as well as species characteristic of more open biotopes, sometimes of increased moisture (*Columella columella*, *Vertigo geyeri*). This fauna indicates a cold climate and the presence of shady habitats, possibly shrubs and/or sparse open forest. Assemblages of similar composition have been frequently described from Central and Western Europe (e.g., Limondin-Lozouet and Rousseau, 1991; Limondin-Lozouet, 1992, 2011; Krolopp and Sümegi, 1993; Preece and Day, 1994; Rousseau et al., 1994; Mania, 1995; Preece, 1998; Meyrick, 2001, 2002; Meyrick and Preece, 2001; Gedda, 2001, 2006; Juřičková et al., 2014a; Horáčková et al., 2015). They are also known from sites studied within the Podhale Basin (Alexandrowicz, 1997, 2004, 2013a; Alexandrowicz et al., 2014). As regards its age, the described fauna relate to the Late Glacial, and in particular, to its cold final stage (Younger Dryas), it also appears in the Early Holocene. Dating of *Arianta arbustorum* shells (10350 ±140 BP; 12679–11704 and 11663–11652 cal BP; C-1) from sample Cs-1 (profile Cs-I) is consistent with this stratigraphic interpretation (Fig. 4 and Table 2).

Assemblage B is characterized by a different species composition and ecological structure. Its characteristic feature is an abundant presence of shade-loving taxa, representing up to 70% of all species present. *Discus ruderatus* plays a special role here. This taxon is an indicator of a cold climate with continental features and the presence of compact forest stands with a significant share of conifers. It is accompanied by other species living in shady environments, mainly forms that are relatively ecologically undemanding (*Cochlodina laminata*, *Petasina unidentata*, *Vertigo substriata*). Shells of cold-loving snails (*Semilimax kotulae*, *Vertigo ronnebyensis*) are also found, but their share in the assemblage is significantly lower than in assemblage A. This fauna indicates a cold climate and compact coniferous forests. Its composition refers to the so-called *Ruderatus*-fauna – an assemblage characteristic of the Early

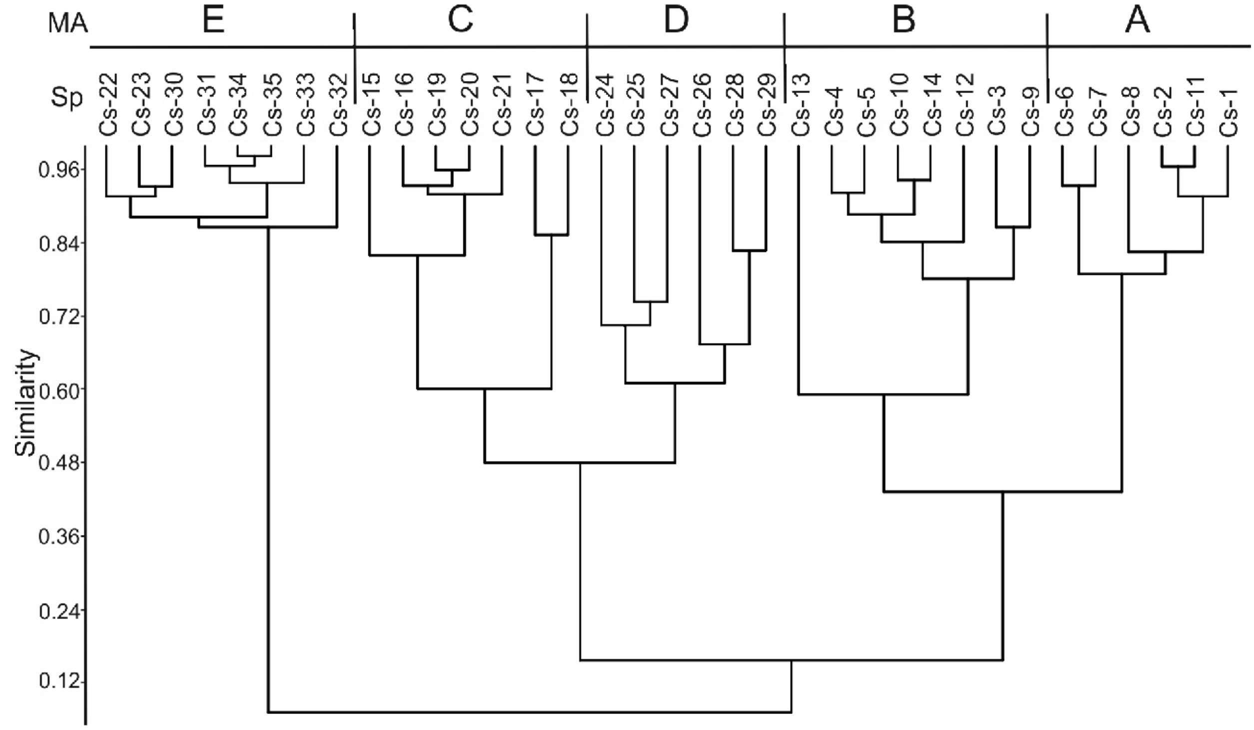

Fig. 6. Cluster analysis of malacofauna from deposits filling small karst forms at Cisowa Skała

MA (A–E) – molluscan assemblages described in text, Sp – samples

Table 2

Results of radiocarbon dating

Date	Age BP	Age cal BP	Lab. code	Material	Profile	Sample
C-1	10350 ±140 BP	12679–11704 cal BP (95.2%) 11663–11652 cal BP (0.2%)	Gd-12178	Molluscs shells	Cs-I	Cs-1
C-2	9150 ±80 BP	10554–10542 cal BP (0.8%) 10512–10190 cal BP (94.6%)	Gd-5623	Molluscs shells	Cs-II	Cs-9
C-3	7050 ±70 BP	8009–7722 cal BP (95.4%)	MKL-1393	Molluscs shells	Cs-V	Cs-19
C-4	2450 ±60 BP	2710–2357cal BP (95.4%)	MKL-8344	Molluscs shells	Cs-V	Cs-23
C-5	470 ±30 BP	543–491 cal BP (95.4%)	Gd-11531	Molluscs shells	Cs-VI	Cs-27
C-6	1950 ±50 BP	1992–1741 cal BP (95.4%)	Gd-10456	Molluscs shells	Cs-VIII	Cs-31
C-7	320 ±30 BP	466–306 cal BP (95.4%)	Gd-10454	Molluscs shells	C-X	Cs-35

Holocene (Dehm, 1967). Similar faunas are found in deposits of that period in Europe (e.g., Preece and Day, 1994; Preece, 1998; Preece and Bridgland, 1999; Gedda, 2001, 2006; Žak et al., 2002; Meyrick, 2002; Limondin-Lozouet and Preece, 2004; Limondin-Lozouet, 2011; Juřičkova et al., 2014a; Horáčková et al., 2015). At a similar stratigraphic level, they have also been described from sites in the Podhale Basin (Alexandrowicz, 1997, 2013a, 2015; Alexandrowicz, et al., 2014). The Early Holocene age of the described assemblage is shown by results of dating of *Arianta arbustorum* shells from sample Cs-9 (profile Cs-II): 9150 ±80 BP (10554–10542 and 10512–10190 cal BP; C-2; Fig. 4 and Table 2).

Assemblage C is characterized by a great variability of species. Shade-loving, mainly forest species are a dominant group here. Numerous occurrences of forest taxa preferring a warm climate with pronounced oceanic features (*Discus perspectivus*, *Discus rotundatus*, *Ruthenica filograna*) are noted here. At the same time, cold-loving snails have disappeared (apart from *Semilimax kotulae*). The occurrence of taxa characteristic of assemblage B, typical of coniferous forests (*Discus ruderatus*), also decreases significantly. This malacocenosis characterizes compact forest areas with a large proportion of deciduous trees. Its composition and structure refer to the *Perspectivus*-fauna (Dehm, 1987), described forom many sites in Middle and Western Europe and characteristic of the Middle Holocene (e.g., Ložek, 1972b; Alexandrowicz, 1997, 2004, 2015; Meyrick, 2002; Žak et al., 2002; Alexandrowicz and Rybska, 2013; Alexandrowicz et al., 2014, 2016; Limondin-Lozouet and Preece, 2014; Juřičková et al., 2014a, 2020; Horáčková et al., 2015). This interpretation of its age is consistent with the result of carbon dating of *Arianta arbustorum* shells (7450 ±70 BP; 8009–7722 cal BP; C-3) from sample Cs-19 (profile Cs-V; Fig. 4 and Table 2).

Assemblage D is ecologically diverse. Two groups of species can be distinguished here. The first consists of shade-loving taxa. A decrease in species diversity and a limited share of forms typical of compact mixed forests (dominating in assemblage C) is noted here. Taxa living on shady rock debris (*Vitrea subrimata*, *Meditterranea depressa*, *Isognomostoma isognomistomos*) gain in importance. The second group includes mesophilous taxa with significant ecological tolerance (*Euconulus fulvus*, *Punctum pygmaeum*). Species living on shady rock walls (*Vertigo alpestris*, *Clausila dubia*) and mountain forms with relatively low ecological requirements (*Ena montana*) are numerous in this fauna. The result of dating of *Isognomostoma isognomistomos* shells (sample Cs-27; profile Cs-VI) was 470 ±30 BP (543–491 cal BP; C-5; Fig. 5 and Table 2) and indicates a Late Holocene age. Similar malacocenoses of that age were found at sites described from the Carpathians (e.g., Alexandrowicz, 2004; Alexandrowicz et al., 2014, 2016; Juřičková et al., 2020; Dabkowski, 2020; Frodlová and Horsák, 2021).

Assemblage E is characterized by a low-diversity species composition, with a predominant role of snails from open environments, representing up to 85% of the assemblage. Species typical of grasslands (*Vallonia pulchella*, *Vallonia costata*), petrophilous taxa living on uncovered rock walls (*Pyramidula pusilla*, *Chondrina clienta*) and xerophilous forms (*Pupilla sterii*, *Euomphalia strigella*) occur here. A very low share of mesophilous species and an almost complete lack of shade-loving forms was noted. This assemblage characterizes dry, completely open sites exposed to strong sunlight and uncovered limestone rock walls. This fauna represents the Late Holocene, as indicated by age dating (*Euomphalia strigella* shells): C-4: 2450 ±60 BP (2710–2357 cal BP) (sample Cs-23, profile Cs-V), C-6: 1950 ±50 BP (1992–1741 cal BP) (sample Cs-31, profile Cs-VIII) and C-7: 320 ±30 BP (466–306 cal BP) (sample Cs-35, profile Cs-X; Fig. 5 and Table 2). Assemblages of a similar composition and age were found on limestone rocks in the Cisowa Skała vicinity (Alexandrowicz, 1997; Alexandrowicz and Stworzewicz, 2003; Alexandrowicz and Rudzka, 2006). Similar Late Holocene faunas are also known from other limestone regions of the Carpathians (e.g., Ložek, 2000; Alexandrowicz, 2001; Gołas-Siarzewska, 2012).

DISCUSSION

Changes in the natural environment of Podhale occurring in the Late Glacial and the Holocene are well known, mainly due to description of numerous malacological and palynological profiles found in this region (e.g., Obidowicz, 1990; Alexandrowicz, 1997, 2019; Rybníček and Rybníčková, 2002; Alexandrowicz and Rybska, 2013; Alexandrowicz et al., 2014). The results of these studies indicate a regional trend of environmental change and enable designation of phases associated with specific assemblages of fauna and flora. These regional environmental trends have been, and still are modified, to a variable extent by local factors, frequently influencing only small areas. In consequence, this leads to formation of micro-sites characterized by specific and particular environmental conditions, reflected both in the organic world, and in the course of geological processes.

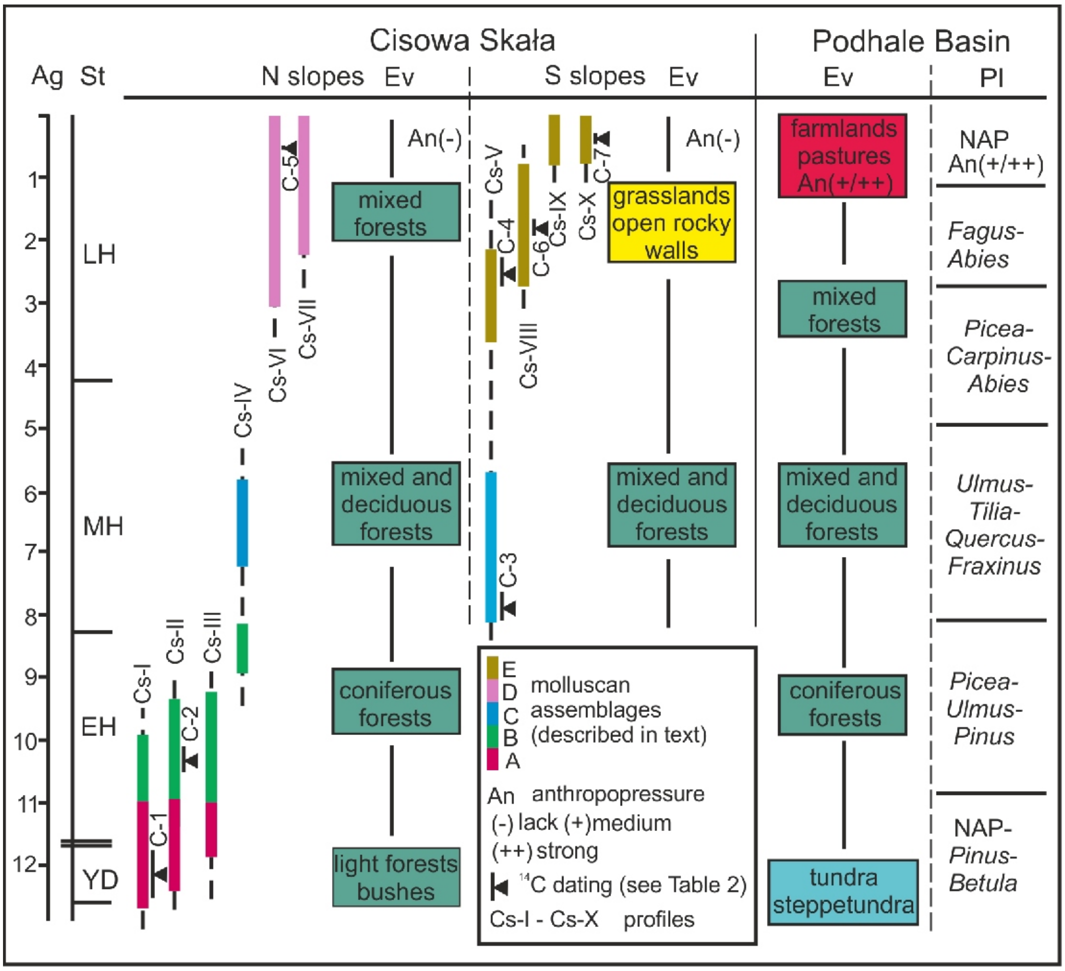

Fig. 7. Environmental changes of Cisowa Skała during the Late Glacial and Holocene

Ag – age (cal BP), St – stratigraphy (after Walker et al., 2019), Ev – environment, Pl – local pollen zones (after Obidowicz, 1990)

The presence of malacocenoses with a relatively low share of taxa typical of shady environments and containing numerous shells of cold-resistant species is characteristic of the Late Glacial (especially of the Alleröd Phase and the colder Younger Dryas Phase following it), as well as of the beginning of the Holocene. The malacofauna indicates a domination by open sites constituting a tundra mosaic (in wetter areas) and steppe-tundra (in dryer areas). Locally, shrubs or sparse open forests were found in small areas (Fig. 7). A relationship between faunas of such composition with the above was shown in numerous profiles described in Europe (e.g., Ložek, 1964; Preece, 1998; Alexandrowicz, 2004; Limondin-Lozouet and Rousseau, 1991; Limondin-Lozouet, 1992; Krolopp and Sümegi, 1993; Preece and Day, 1994; Mania, 1995; Meyrick, 2001, 2002; Meyrick and Preece, 2001; Gedda, 2001, 2006). Malacocenoses of similar composition and structure was also found in many profiles described from the Podhale region (e.g., Alexandrowicz, 1997, 2013a, 2015, 2019; Alexandrowicz et al., 2014). Numerous radiocarbon dates of this age support the stratigraphic arrangement resulting from malacological analyses. In the palynological profiles, the interval discussed is associated with a phase of domination by herbaceous plants with a low share of tree pollen, mainly of *Betula* and *Pinus* (NAP-*Betula*-*Pinus* phase; Obidowicz, 1990; Rybníček and Rybníčková, 2002; Fig. 7). The vertebrate faunas, characterized by many tundra species (*Dicrostonyx gulielmi*, *Lemmus lemmus*, *Microtus gregalis/agrestis*) lead to similar conclusions (Alexandrowicz, 1997; Valde-Nowak et al., 2003; Alexandrowicz and Rudzka, 2008; Nadachowski et al., 2015). At that time, shady environments predominated on Cisowa Skała. Their presence is indicated by the oldest of the molluscan assemblages described above (assemblage A), the stratigraphic position of which is indicated by radiocarbon dating (10350 ±140 BP; 12679–11704 and 11663–11652 cal BP; C-1; Table 2 and Fig. 7). The presence of forest assemblages on limestone hills at the end of the Late Glacial and the beginning of the Holocene is a phenomenon frequently observed in central Europe (Juřičková et al., 2014a, 2018, 2019; Mitka et al., 2014; Horsák et al., 2019). Those isolated forest regions surrounded treeless tundra or steppe-tundra formations and survived here in periods of unfavourable climate. This was possibly associated with slightly better thermal and moisture conditions. An important factor which supports the maintenance of forest communities is also soil cover. Limestone bedrock supports more fertile soils (of rendzina type) than in the surrounding areas built of flysch. Such locations are of great significance, as they represent refugia of forest assemblages (both flora and fauna). When environmental, especially climate, conditions improved, forest expansion took place rapidly from these areas, together with assemblages of shadow-loving fauna. Probably, the presence of such refugia enabled very fast spreading of forests at the beginning of the Holocene (Juřičková et al., 2014a, 2018, 2019; Mitka et al., 2014; Horsák et al., 2019). At the same time, the presence of the compact plant cover on limestone rocks facilitated chemical dissolution of carbonates and increased the intensity of the karst processes. Thus, relatively numerous, small karst forms filled with Late Glacial deposits, containing mollusc shells and bones of small vertebrates, are found on Cisowa Skała. Similar observations have been made on other limestone hills in the Podhale (Alexandrowicz and Rudzka, 2006) and in other areas of Central Europe (e.g., Pazdur et al., 1995; Ridush, 2012; Fig. 7).

The expansion of forests, mainly of continental coniferous type, to the Podhale region is correlated with the gradual warming of the climate, starting at the beginning of the Holocene. Then, the assemblage with *Discus ruderatus* appeared, which is characteristic of that period (Dehm, 1967). That fauna has been noted at this stratigraphic position at numerous sites at the Podhale region (Alexandrowicz, 1997, 2013a, 2015, 2019; Alexandrowicz and Rybska, 2013; Alexandrowicz et al., 2014) and many other sites in Europe (e.g., Ložek, 1964, 2000; Alexandrowicz, 2004; Preece and Day, 1994; Preece, 1998; Preece and Bridgland, 1999; Gedda, 2001; Žak et.al., 2002; Meyrick, 2002; Limondin-Lozouet and Preece, 2004; Limondin-Lozouet, 2011). Its stratigraphic position is well-documented by many radiocarbon dates. In the palynological profiles, a rapid increase in the share of tree pollen is observed, initially of coniferous trees (*Pinus* and *Picea*), and with the warming of the climate, also of deciduous trees (*Corylus*, *Ulmus*, *Betula*; phase *Picea-Ulmus-Pinus*; Obidowicz, 1990; Fig. 7). In the interval discussed, sites of a similar type dominated on Cisowa Skała. Probably the entire hill was covered by forest with a large share of coniferous trees. Deposits of that age contain the characteristic fauna with *Discus ruderatus* (assemblage B). Its Early Holocene age is documented by radiocarbon dates of 9150 ±80 BP; 10554–10542 and 10512–10190 cal BP; C-2 (Fig. 7 and Table 2).

During the Middle Holocene, the Podhale region was covered by compact deciduous and mixed forests, with a large share of species with high thermal requirements (*Tilia*, *Fraxinus*, *Quercus*, *Ulmus*) (*Ulmus-Tilia-Quercus-Fraxinus* phase; Obidowicz, 1990; Rybníček and Rybníčková, 2002; Fig. 7). This forest assemblage is associated with the presence of very rich and diverse molluscan assemblages, with numerous shadow-loving species of high ecological requirements. Those malacocenoses correspond to the so-called *Perspectivus*-fauna (Dehm, 1987), considered characteristic of the Middle Holocene (e.g., Ložek, 1964; Alexandrowicz, 1997, 2004, 2015, 2019; Mania, 1995; Meyrick, 2002; Žak et al., 2002; Alexandrowicz and Rybska, 2013; Limondin-Lozouet and Preece, 2014; Juřičková et al., 2014a, 2020; Alexandrowicz et al., 2014, 2016; Horáčková et al., 2015; Fig. 7). At that time Cisowa Skała was covered by compact forests with a significant share of deciduous trees. Malacocenoses of that period are characterized by a large share of forest species, including also forms of high thermal requirements, with a simultaneous disappearance of cold-tolerant species (assemblage C). Its relation with the Middle Holocene is documented by the radiocarbon date of 7050 ±70 BP; 8009–7722 cal BP; C-3 (Fig. 7 and Table 2). This malacocenosis is found on both the north and south slopes of the hill, and this indicates a low diversity of sites. No significant differences between the Cisowa Skała environment and its nearer and farther surroundings were observed during the Early and the Middle Holocene (Fig. 7).

The climate changes noticeable at the end of the Middle and the beginning of the Late Holocene, and in the older part of the Late Holocene, led to a decrease in the species diversity of forests and a significant reduction in the occurrence of thermophilous species (e.g., Alexandrowicz, 2004; Alexandrowicz et al., 2014, 2016; Juřičková et al., 2020; Dabkowski, 2020; Frodlová and Horsák, 2021). In consequence, a noticeable depletion of molluscan assemblages occurred, with a simultaneous change in the ecological structure of the assemblages. The Podhale region was covered by mixed forests (*Picea-Carpinus-Abies* and *Fagus-Abies* phases; Obidowicz, 1990; Rybníček and Rybníčková, 2002; Fig. 7). Climate changes significantly influenced the differentiation of microsites on Cisowa Skała. The regression of forests observed on the Podhale region and a general deterioration of conditions for their development were probably the main cause underlying the progressive deforestation of Cisowa Skała. The geological structure of the substrate and the exposure of its slopes clearly played an important role in this process. A significant exposure to sunlight and a reduction in moisture associated with a gradual disappearance of the forest led to the development of dry, grass, xerothermic and treeless sites, which spread over the southern slopes of the hill (Fig. 7). Forest sites were preserved on its northern slopes, with much lower exposure to sunlight (Fig. 7). This situation was preserved and can be seen until today. These changes also resulted in a significant differentiation of the fauna. On the exposed southern slopes live malacocenoses that are relatively poor in species and characterized by a dominance of species typical of grasslands and that inhabit exposed limestone walls (assemblage E). The radiocarbon dating results indicate that this fauna appeared here already in the older part of the Late Holocene (C-4: 2450 ±60 BP (2710–2357 cal BP), C-6: 1950 ±50 BP (1992–1741 cal BP) and remained here until historical times, C-7: 320 ±30 BP (466–306 cal BP) (Fig. 7 and Table 2). The malacofauna that inhabits the southern slopes of Cisowa Skała today also has a similar species composition. A distinctively different assemblage of snails was found on the northern slopes of the hill. It is dominated by shade-loving and mesophilous species, indicating the presence of shady sites (assemblage D). This fauna remained in that zone throughout the entire Late Holocene (radiocarbon date: 470 ±30 BP (543–491 cal BP; C-5) and lives there also today (Fig. 7 and Table 2).

Since the 13th century, human activities have played an increasingly important role in shaping the Podhale environment. These are manifested as extensive deforestation, visible mainly in the area of the flat northern part of Podhale, and in the wide valleys of larger rivers (Alexandrowicz, 2013c, 2020). In palynological profiles, a significant increase in the share of pollen of herbaceous plants, including crop plants, is observed in that period, accompanied by a significant decrease in the occurrence of tree pollen (NAP phase; Obidowicz, 1990; Rybníček and Rybníčková, 2002). In the molluscan assemblages, the species of open environments start to play increasingly an important role (assemblage E; Fig. 7). At that time, the surroundings of Cisowa Skała were deforested and transformed into crop fields and pastures. Cisowa Skała itself, as a place unfavourable for agricultural activities, was not subjected to intense human activity. For this reason, it has maintained its natural character to this day (Figs. 2 and 7).

The differentiation of microsites described is reflected not only in differences between the faunal and floral assemblages, but also noticeable in the pattern of geological processes. The limestones forming Cisowa Skała undergo karst processes. Observations conducted during the search for malacological sites found evidence of different development of karst forms on the southern and the northern slopes. The relief of the northern slopes is more diverse. Numerous niches, cracks and shelters can be found there. Frequently, they are filled with clay and rubble deposits, usually of small thickness. On the southern slopes, the manifestations of karst relief are less clear. They take the form of small niches and narrow cracks; however, they are usually sediment-free. In some of them, and on some small rock shelves, black initial rendzina soils of small thickness can be found. These differences are definitely associated with local environment conditions. The northern slopes are covered by the forest and characterized by lower temperatures and higher moisture. These conditions support the development and maintenance both the karst forms themselves, and of the sediments filling them. On the southern slope, a large exposure to sunlight and a sparse plant cover favour high temperatures and low moisture. In these conditions, the karst relief is much less well developed, and the main type of sediment is black rendzina soils representing a period of the last several hundred years (Alexandrowcz and Rudzka, 2006; Kemencei et al., 2014; Raschmanova et al., 2018; Bátori et al., 2019).

CONCLUSION

Isolated geological outcrops lithologically divergent from the properties of their direct vicinity are a highly interesting object of study. This regards firstly the specific nature of the geological processes occurring there, which are a result of multiple abiotic and biotic factors, changes in climate and finally in human activity. Secondly, the specific geological structure has a great impact on the nature and characteristics of the faunal and floral assemblages present in such areas. Cisowa Skała is an excellent example of such a site. A malacological study and lithological observations have led to several conclusions.

1. Cisowa Skała has a specific geological structure of limestone bedrock that result here in specific natural habitats, and in consequence, also floral and faunal assemblages (both currently and in the past). Study of such places allows interpretations of environmental change, and also for reconstructions of their internal diversity.
2. Environmental changes of the Podhale Basin during the Late Glacial and the Holocene are clearly identified thanks to the many palynological and malacological profiles described herein. The malacological studies conducted at Cisowa Skała indicate a significant influence of local factors modifying the regional trend of environmental changes. Particularly significant differences are visible during Late Glacial and Late Holocene.
3. During the Late Glacial, the area of the Podhale Basin was covered by treeless vegetation (tundra and/or steppe-tundra). Suitable temperature, humidity and soil conditions supported the maintenance of forest patches on Cisowa Skała, and also of shade-loving mollusc species typical of these.
4. In the Late Holocene, a strong diversity of microhabitats related to the morphology and geological structure of Cisowa Skała can be observed. On the dry southern slopes exposed to strong sunlight, grass biotopes inhabited by open-country, petrophilous and xerothermic species. On the northern slopes, forest assemblages were maintained, and the malacofauna is dominated by shade-loving taxa.
5. Because of unfavourable terrain conditions for human activity, Cisowa Skała has never been under strong anthropopressure and maintained its natural character, as opposed to the surrounding area.
6. The results of these studies point to an important environmental role of isolated objects with specific features. These can serve as refuges and enable the survival of specific faunal and/or floral assemblages, which in turn enables their quick expansion into surrounding areas if the conditions change.
7. The reconstruction produced shows that malacological analysis belongs to a small group of methods which allow for identification of the space diversity of microhabitats and their characteristics.

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