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ASSEMBLAGES OF MOLLUSCS FROM SULISŁAWICE (MAŁOPOLSKA UPLAND, SOUTHERN POLAND) AND THEIR SIGNIFICANCE FOR INTERPRETATION OF DEPOSITIONAL CONDITIONS OF CALCAREOUS TUFAS IN SMALL WATER BODIES

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Abstract: Small water bodies, occurring behind barriers across valleys, create very advantageous conditions for the sedimentation of calcareous tufas. These sediments usually contain rich and diversified malacocoenoses. The composition and structure of these associations are closely linked to environmental changes during the accumulation of the sediments. At the Sulisławice locality, the remnants of two barriers, composed of hard, calcareous tufa, were found. Behind them, sequences of granular, calcareous tufas were preserved, forming terraces, elevated up to 3 m above the level of the present stream bed. The age of the sediments was obtained from radiocarbon dating and is referable to the Atlantic Phase. The rich malacofauna, occurring in these tufas, permitted the recognition of four types of faunistic association, in a sequence that corresponds to phases in the development of the water bodies. Three of them are characterised by the dominance of aquatic species and permit the reconstruction of specific features of the body of water. In the fourth association, terrestrial species predominate. A detailed, malacological analysis was the basis for a model of the evolution of the water bodies, occurring behind the barriers. The model is more widely applicable to the sediments of similar origin, frequently found in upland regions of Poland and other parts of Europe.

Key words: calcareous tufas, malacofauna, environmental changes, Holocene, Małopolska Upland, southern Poland.

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INTRODUCTION

Calcareous tufas are deposits, particularly favourable for the preservation of molluscan shells. They are associated with relatively undisturbed sedimentation, as well as with high calcium carbonate content. The former minimises the risk of shell destruction during sedimentation, whereas the latter inhibits chemical dissolution and physical damage of the shells, already present in the sediment. There is only minor redeposition of shell material, which facilitates the interpretation of changes in the nature of habitats and related variation in environmental conditions at and near the site of deposition. It should be noted that the associations of molluscs, occurring in the sediments, are reflections of both regional conditions and the local characteristics of the environment. The first aspect provides a basis for identifying the trends of palaeogeographical and climatic conditions on a regional scale, while the second aspect provides a unique opportunity for the reconstruction of the conditions in both terrestrial and aquatic habitats, usually not feasible by other methods. The earliest descriptions of calcareous tufas in Poland date back to the end of the 19th century and the beginning of the 20th century. Methodical studies on the malacological associations in calcareous tufas were carried out only during the last 30 years. These studies were carried out at a number of locations in the mountain and upland belts, as well as in the Polish Lowlands, and are described in a great number of scientific articles and popular-science publications.

Calcareous tufas are formed in several types of sedimentary environment. Small water bodies (dammed lakes) arising upslope of rock, colluvium, and hard tufa barriers, and even beavers' dams across river valleys are among the most common, depositional settings of these sediments. In

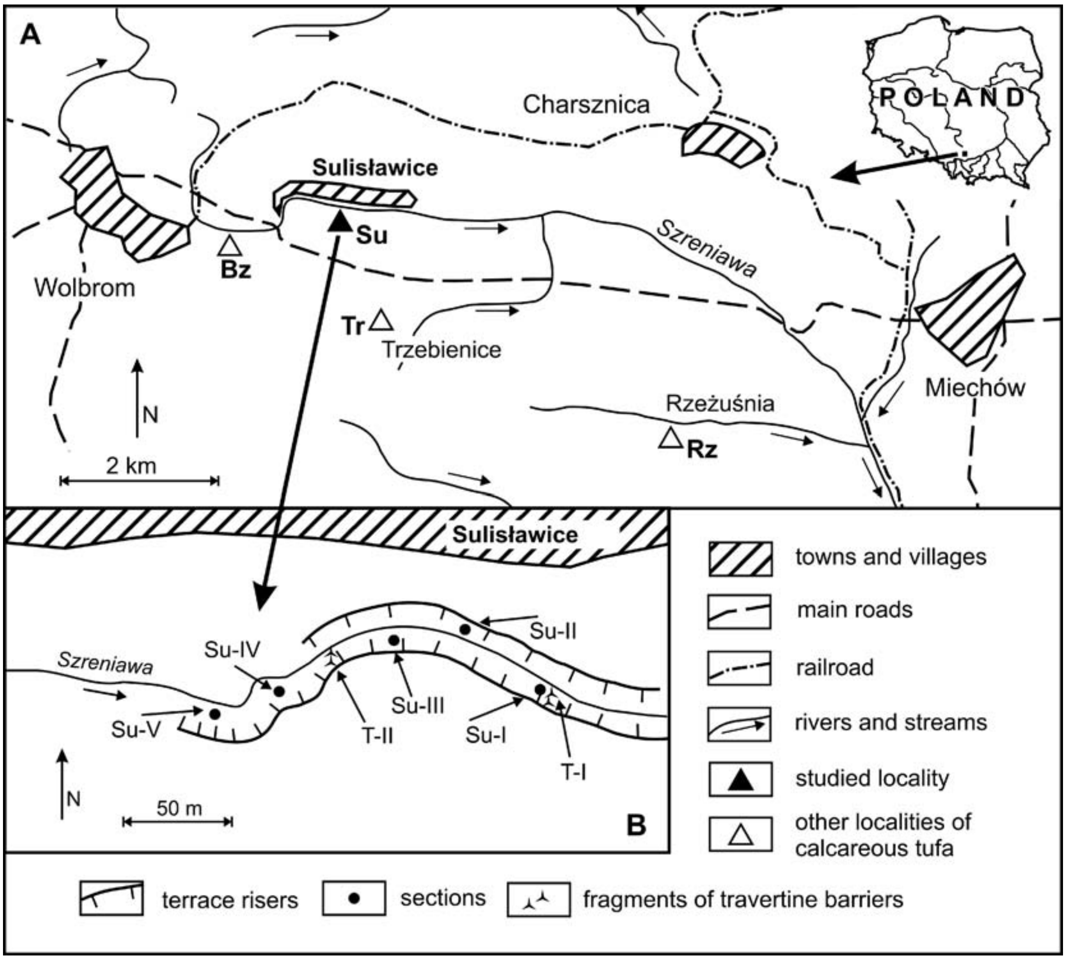

Fig. 1. Location of site, and sections of calcareous tufas at Sulisławice; A. Location of sites: Bz – Brzozówka, Tr – Trzebienice, Rz – Rzeżuśnia, Su – Sulisławice; B. Location of sections: Su-I – Su-V – outcrops of calcareous tufa, T-I, T-II – barriers composed of hard, calcareous tufa

such bodies of water, fine- and medium-grained, as well as silty, calcareous tufas accumulate, often accompanied by sands and fine gravels, as well as peat intercalations. Usually, some remnants of the barriers, in the form of interconnected colluvial tongues or beds of hard calcareous tufa, can also be found. Undisturbed sedimentation in dammed lakes, often over long periods, has favoured the presence of an abundant, diversified and well preserved malacofauna in the resulting deposits. Such sediments, containing numerous molluscan shells, were described at a number of locations in the Carpathians (S. W. Alexandrowicz, 1993, 1996, 1997a; W. P. Alexandrowicz, 1997, 2004, 2009a, 2013) and Mid-Polish Uplands (e.g., S. W. Alexandrowicz, 1983, 1989, 1991, 1997b; W. P. Alexandrowicz, 2004; W. P. Alexandrowicz and Gołas-Siarzewska, 2013). The tufas, exposed in the Szreniawa River valley at Sulisławice, also belong to this type of deposit.

GEOLOGICAL SETTING

Outcrops of calcareous tufas are situated in the Szreniawa River valley, between Wolbrom and Miechów (ca. 2 km west of Wolbrom), in the centre of Sulisławice village (Fig. 1A). The GPS coordinates of the section Su-I are 50°22'45"N and 19°50'1"E (Fig. 1B).

The locality at Sulisławice is situated at the border of two major structural units, the Cracow-Silesian Monocline, and the Miechów Basin (Bukowy, 1968). Limestones and marls, of Upper Jurassic and Lower Cretaceous age occur below the relatively compact Quaternary cover and are seen in scattered outcrops, The cover of Pleistocene sediments is almost uninterrupted and is of variable thickness. These sediments are represented mainly by Vistulian loesses, which form an uninterrupted cover, from several to a dozen or more metres thick. Fluvioglacial sands also have been reported (Bukowy, 1968). The fluvial sediments are muds, sands, and gravels, filling the river and stream valleys, and are of Holocene age. In this area, there are also vast peat-bogs, which have been developing there since the Boreal Phase. They have been the subject of detailed, palynological studies (Obidowicz, 1976; Latałowa and Nalepka, 1987). In the area around Wolbrom, Holocene calcareous tufas are also found. These are isolated occurrences in the valleys of the Szreniawa River (Brzozówka and Sulisławice) and the streams Trzebienicki (Trzebienice), and Gołcza (Rzeżuśnia) (Fig. 1A). These locations were the sites of sedimentological and lithological studies (Szulc, 1984; Domański, 1988), isotope analyses (e.g., Pazdur, 1987; Pazdur *et al.*, 1988a, b), as well as malacological analyses (Domański, 1988; S. W. Alexandrowicz and Domański, 1991; W. P. Alexandrowicz, 2000, 2004). The studies, completed in recent years at the Sulisławice location, have provided abundant, new material, which was the basis for much more detailed, palaeoecological and stratigraphic interpretations.

At Sulisławice, calcareous tufas form a terrace, with a maximum height of up to 3 m above the present stream bed. Within the terrace, two outcrops of hard, highly porous, white tufas are found. Earlier they probably formed barriers, dividing the valley; behind them were small and shallow water bodies, filled with loose varieties of tufa, containing numerous molluscan shells (Fig. 1B).

The section Sulisławice I (Su-I) is situated directly at the lower barrier (T-I, Fig. 1B). On muds with many limestone clasts, rest two layers of silty, yellowish calcareous tufas, each 0.2 m thick. They are intercalated with hard, white, porous, slightly laminated tufas (0.6 m). The uppermost part of the section is composed of recent soil. The total thickness of the section is 1.2 m (Figs 1B, 2). The Sulisławice II (Su-II) section is situated some 50 m above Su-I. The grey, laminated calcareous muds are overlain by sandy, fine- and medium-grained and silty calcareous tufas. There are also two intercalated beds, containing blocks of hard tufas, with diameters of up to 10 cm. The thickness of the section is 2.6 m (Figs 1B, 2). In the Sulisławice III (Su-III) outcrop, situated 30 m above Su-II, there are medium- and fine-grained, sandy tufas, underlain by silty calcareous tufas and muds, containing numerous angular limestone blocks. The thickness of the section is 2.25 m (Figs 1B, 2). The next two outcrops are situated above the higher barrier (T-II, Fig. 1B). At the lowest part of the first outcrop (Sulisławice IV – Su-IV), grey, slightly laminated calcareous muds (0.85 m) can be found, covered by peat, containing a few clasts of tufa (0.05 m). Above them rests a 2.1-m-thick series of, fine- and medium-grained, sandy tufas. In its middle part, there are blocks of hard tufa, with diameters of up to 10 cm (usually 5–8 cm), forming a clearly distinguishable layer. The thickness of the entire section is: 3.0 m. The samples for radiocarbon dating were collected from the bottom and top parts of the series (Figs 1B, 3). The last of the sections, Sulisławice V (Su-V), is situated about 60 m above the upper barrier. There, grey muds with numerous limestone clasts are overlain by white, strongly calcareous muds and by silty and fine-grained, sandy tufas. The thickness of the section is about 1.3 m (Figs 1B, 3).

MATERIALS AND METHODS

Malacological analysis was undertaken on 37 samples, covering intervals of 10, 15 or 20 cm, depending on the lithological characteristics of the sediments, and weighed about 2 kg each. The samples represented all of the layers, distinguished in the section, except for the hard tufas (Figs 2, 3). The samples were flushed on a 0.5 mm sieve, and dried, after which all mollusc shells, both of juvenile and adult individuals, were collected, together with fragments of shells that could be identified easily. The latter were extrapolated into whole specimens, in accordance with the formula, proposed by S. W. Alexandrowicz (1987a). The number of species in the samples varied from 7 to 36 and the number of specimens from 22 to 1734, respectively. The entire material studied comprised 18,366 specimens of 50 taxa (33 taxa of terrestrial snails, 13 species of aquatic snails, and three species of bivalves, as well as the calcareous plates of slugs – Limacidae) (Tables 1, 2).

The malacological analysis was carried out on the basis of the standard methods, described by Ložek (1964), S. W. Alexandrowicz (1987a) and S. W. Alexandrowicz and W. P. Alexandrowicz (2011). The ecological requirements of particular species of snails and bivalves were determined, on the basis of a number of studies (e.g., Ložek, 1964, 2000; Piechocki, 1979; Piechocki and Dyduch-Falniowska, 1993; Wiktor, 2004). Individual species were classified into the following ecological groups: F – shade-loving species, O – species of open habitats (meadow species), M – mesophilous species, and H – hygrophilous species. Among the aquatic taxa, three groups were distinguished (S. W. Alexandrowicz, 1987a; S. W. Alexandrowicz and W. P. Alexandrowicz, 2011): T – taxa typical of episodic bodies of water, S – species of permanent bodies of water, and R – river and stream (reophilous) species. The percentages of particular species and ecological groups formed the basis for the construction of malacological diagrams. These in turn provided a basis for palaeoenvironmental interpretations and descriptions of the environmental changes during deposition. Additionally, in order to delineate changes in the environment, two- and three-component diagrams were drawn. The two-component diagrams were developed on the basis of the percentages of two selected, ecological groups. The choice of diagram components is intended to demonstrate changes in proportions of these groups, in connection with (1) the stratigraphic succession of sediments and (2) the evolution and transformation of the environment. Combining three ecological groups (three-component diagram) permits the recognition of particular types of mollusc association and their sequence in the vertical profile. Therefore, interpreting such a diagram provides a good basis for reconstruction of the environment. The antilogarithm of taxonomic diversity (TDA) index (S. W. Alexandrowicz, 1987a; S. W. Alexandrowicz and W. P. Alexandrowicz, 2011) was also calculated for each sample. The TDA index is a modification of the Shannon-Wiener diversity index, widely used in faunistic research. Unlike the latter, it is of a normalised type (the results of calculations are in the range 0–1). Accordingly, the TDA index facilitates the comparison of diversity for different samples and its graphical presentation is also simpler. The taxonomic analysis allowed the determination of the similarities between particular samples analysed and the recognition of mollusc associations with similar composition and structure. Development of a dendrogram was based on the method, described by Morisita (1959) and the statistical calculations were completed, using the PAST statistical software package (Hammer *et al.*, 2001).

The stratigraphic range of the calcareous tufas was determined from both the composition and structure of the malacofaunal associations and radiocarbon dating. The ra-

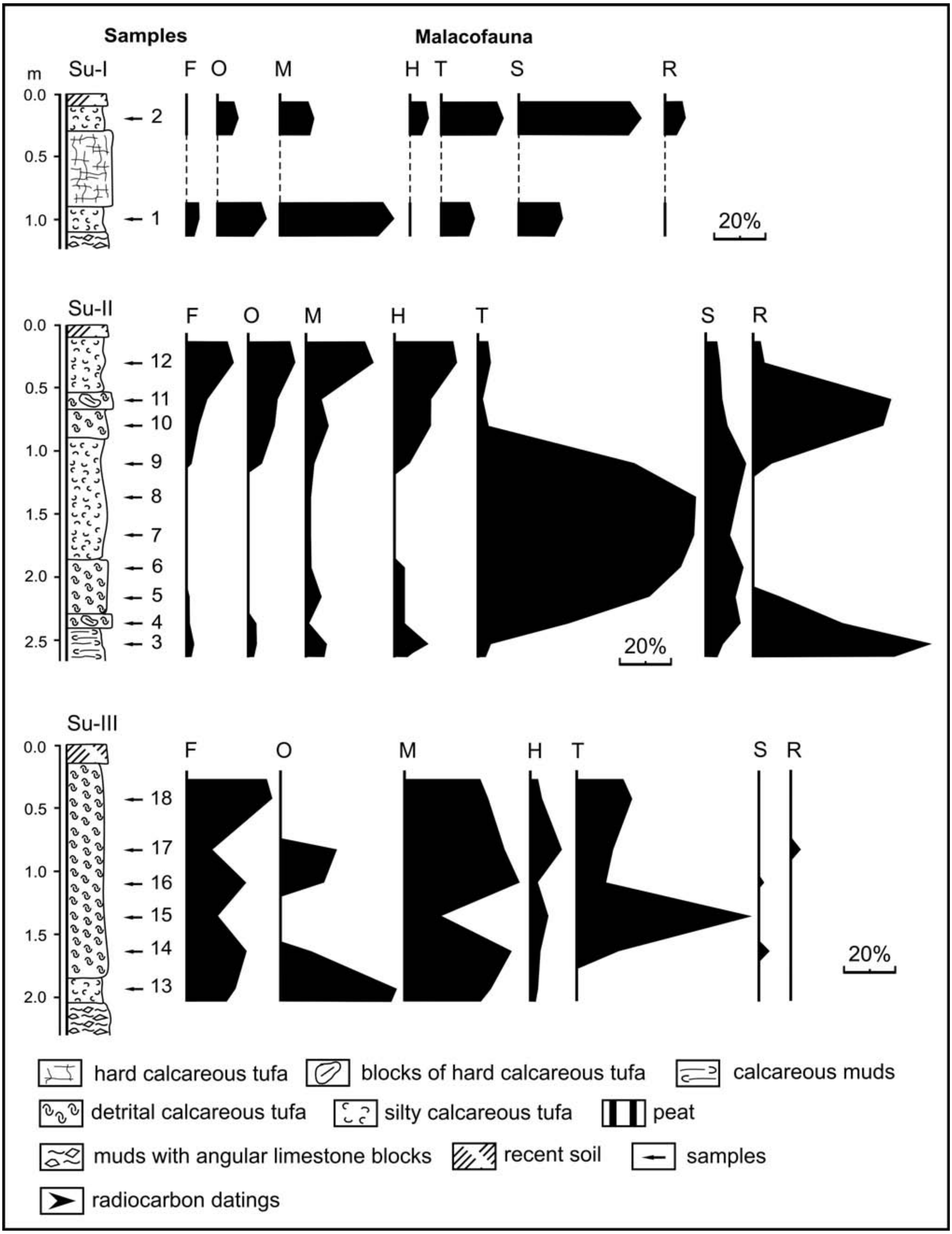

Fig. 2. Lithology and malacofauna of sections Su-I, Su-II, Su-III; Ecological groups of molluscs (according to Ložek, 1964; S. W. Alexandrowicz, 1987a; S. W. Alexandrowicz and W. P. Alexandrowicz, 2011): F – shade-loving species, O – species of open habitats, M – mesophilous species, H – hygrophilous species, T – species of episodic bodies of water, S – species of permanent bodies of water, R – river and stream (reophilous) species

Table 1

Composition of malacofauna in sections Su-I, Su-II, Su-III

E	Section	Su-I		Su-II										Su-III					
	Taxon Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
F	*Acicula polita* (Hartm.)				1	1				2	1	2	2	1		1	1	1	1
	Vaertigo pusilla Müll.				1	1	1			1	3	2	3	1	1				
	Discus rotundatus (Müll.)					1				1	1	3	1		2				
	Discus ruderatus (Fér.)			2	1	1	1			1	1	2	1					2	1
	Vitrea crystallina (Müll.)	1		1	1	1							3	1	2		3	3	1
	Oxychilus depressus (Sterki)	1	1										1						
	Cochlodina laminata (Mont.)					1				1		1	1						
	Bradybaena fruticum (Müll.)			3	2	2	1	1	1	3	3	3	3	1			2	1	1
O	*Truncatellina cylindrica* (Fér.)												1						
	Vertigo pygmaea (Drap.)												2				1		
	Vallonia costata (Müll.)	2	2	3	3	1				3	3	4	4	2	2		2	4	
	Vallonia pulchella (Müll.)	2	2	3	2	1	1			3	3	4	3	2	2		2	3	
M	*Carychium tridentatum* (Risso)		1	3	3	3	3	3	3	3	4	3	3	2	2		3	3	1
	Cochlicopa lubrica (Müll.)	2	1	1	1					1	1	1	3		1		2	2	
	Cochlicopa lubricella (Porro)												3				1		
	Vertigo substriata (Jeffr.)			1														1	
	Vertigo angustior Jeffr.			2			1	2	1	1	1								
	Punctum pygmaeum (Drap.)		1	3	1	3	1	1			1	2	2	1	2	1	2	4	2
	Vitrina pellucida (Müll.)		1					1			1		1						
	Vitrea contracta (West.)	4	1									1							
	Nesovitrea hammonis (Ström)		2	2	2	2		1		2	2	2	2		2		2	2	
	Nesovitrea petronella (L.Pfe.)				1					1	1				1		1	1	
	Limacidae		1		1			1		1	1	1	1						
	Euconulus fulvus (Müll.)		1	3	1		1	1		1	1	2	3		2	1	1	1	1
	Trichia hispida (L.)												2		1				
H	*Carychium minimum* Müll.			3	4	3	3	3	2	4	4	4	4	1	1	1	1	3	1
	Succinea putris (L.)		1	3	3	1	1						3					1	
	Cochlicopa nitens (Gall.)												1					1	
	Vertigo antivertigo (Drap.)			2					1	2	1								
	Zonitoides nitidus (Müll.)				2	1				3	1	2	3		1				
	Perforatella rubiginosa (A. Sch.)				3	3	1			3	3	3	3						
T	*Valvata cristata* Müll.		3	3	4	5	5	6	5	5	3	3	1					1	1
	Aplexa hypnorum (L.)									3	1								
	Galba truncatula (Müll.)		1		3	1	3	3	3	4	1	2	2			1		1	
	Anisus leucostomus (Mill.)	3	3	3	5	6	6	6	6	5	3	1	3		3	2	3	3	2
	Pisidium obtusale (Lam.)					1	3	2	1	1									
S	*Physa fontina lis* (L.)	3	4			2	3	3	4	4	1	2	1		1		1	1	
	Radix balthica (L.)		1	3	3	3	4	4	4	4	3	4	3					1	
	Gyraulus albus (Müll.)			2	3	1	1	2	1	2									
	Armiger crista (L.)			1	2	3	3	3	2	1					1				
	Acroloxus lacustris (L.)	1	3							1									
	Pisidium subtruncatum Malm			3	3	2	3	1	2		3	1							
	Pisidium casertanum (Poli)			3	3	3	3	3	1	2	3								
R	*Bithynella austriaca* (Fraue.)		2															2	
	Ancylus fluviatilis Müll.			5	4	3	2			1	5	5	2						
	Pisidium personatum Malm		2	5	5	4	1			3	5	5	3						

E – ecological groups of molluscs (according to Ložek, 1964; S. W. Alexandrowicz, 1987a; S. W. Alexandrowicz and W. P. Alexandrowicz, 2011): F – shade-loving species, O – species of open habitats, M – mesophilous species, H – hygrophilous species, T – species of episodic bodies of water, S – species of permanent bodies of water, R – river and stream (reophilous) species. Number of specimens – *1* – 1–3, *2* – 4–10, *3* – 11–31, *4* – 32–100, *5* – 100–316, *6* – 317–1000 (according to S. W. Alexandrowicz, 1987a; S. W. Alexandrowicz and W. P. Alexandrowicz, 2011)

Table 2

Composition of malacofauna in sections Su-IV and Su-V

E	Section	Su-IV															Su-V			
	Taxon Sample	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
F	*Acicula polita* (Hartm.)		1	2					1								1	1	1	1
	Vaertigo pusilla Müll.	1	1						2						1			2	3	1
	Discus rotundatus (Müll.)		1				1	1	1								1	1	2	
	Discus ruderatus (Fér.)	1									1					1		1	2	
	Vitrea crystallina (Müll.)	2	2	1	1												1	1	2	
	Oxychilus depressus (Sterki)																		1	
	Cochlodina laminata (Mont.)	1																1	1	
	Bradybaena fruticum (Müll.)	2	2		1			1	1							1	3	3	3	1
O	*Truncatellina cylindrica* (Fér.)																		1	2
	Vertigo pygmaea (Drap.)																1		1	3
	Vallonia costata (Müll.)	2	3	1	1				1							3	3	3	4	4
	Vallonia pulchella (Müll.)	2	3	1						1		1				2	3	3	4	4
	Euomphalia strigella (Drap.)	2	1	1															1	1
M	*Carychium tridentatum* (Risso)	3	4	3	2		1	1	2		1		2		1	3	3	3	3	2
	Cochlicopa lubrica (Müll.)	4	4	1	3	3	1									1	1	2	2	1
	Cochlicopa lubricella (Porro)		2																	
	Columella edentula (Drap.)	1	1													1				
	Vertigo substriata (Jeffr.)								2		1							1		
	Vertigo angustior Jeffr.														3			1	3	
	Punctum pygmaeum (Drap.)	3	4	1	2		1		1		1		2		1	1	1	2	2	1
	Vitrina pellucida (Müll.)	1	1															1	1	2
	Vitrea contracta (West.)																1	1	1	1
	Nesovitrea hammonis (Ström)	3	2	2	1	1			1							1	1	3	3	2
	Nesovitrea petronella (L.Pfe.)																	1	1	1
	Limacidae	1		1				1								1	1	1	1	2
	Euconulus fulvus (Müll.)	3	4	2	1				1		1		1		1	1	1	2	2	3
	Trichia hispida (L.)																	1	1	1
H	*Carychium minimum* Müll.	3	4	2	2	1			3		1		3		2	3	4	4	4	3
	Succinea putris (L.)	3	1	2	1	1		2	2	1	2	2		2	2	2	3	2	2	2
	Cochlicopa nitens (Gall.)	1	1														1	1		1
	Vertigo antivertigo (Drap.)		1						1				1		1	1		1	1	
	Vertigo geyeri Lindh.										1		1							
	Zonitoides nitidus (Müll.)	3	4	2	1			1	2		1	1	2	1		2	3	2	2	1
	Perforatella rubiginosa (A. Sch.)		1														3	2	3	2
T	*Valvata cristata* Müll.	6	5	5	3	4	3	4	5	3	5	2	3	3	5	5	4	1	1	
	Aplexa hypnorum (L.)			1													1			
	Galba truncatula (Müll.)	3	3	1	1	1				1			2	3	4	3	3	2	1	2
	Anisus leucostomus (Mill.)	6	6	4	4	4	3	4	6	3	6	3	5	4	6	5	4	3	2	1
	Pisidium obtusale (Lam.)							3												
S	*Physa fontina lis* (L.)	1				2	1	1	3		3	3	4	3	4	3	3	2	1	
	Radix balthica (L.)				1			1	2	2	3	4	4	3	5	3	3	3	2	1
	Stagnicola palustris (Müll.)			1	1												1			
	Armiger crista (L.)																1			
	Acroloxus lacustris (L.)	1		1				4		2						3	1			
	Pisidium subtruncatum Malm										2	2								
	Pisidium casertanum (Poli)							3		4	3	2								
R	*Ancylus fluviatilis* Müll.							2		3	2	5	4	4	5	4	3	4	2	1
	Pisidium personatum Malm	1						4	2	4	3	5	4	5	5	5	3	4	3	1

For explanation see Table 1

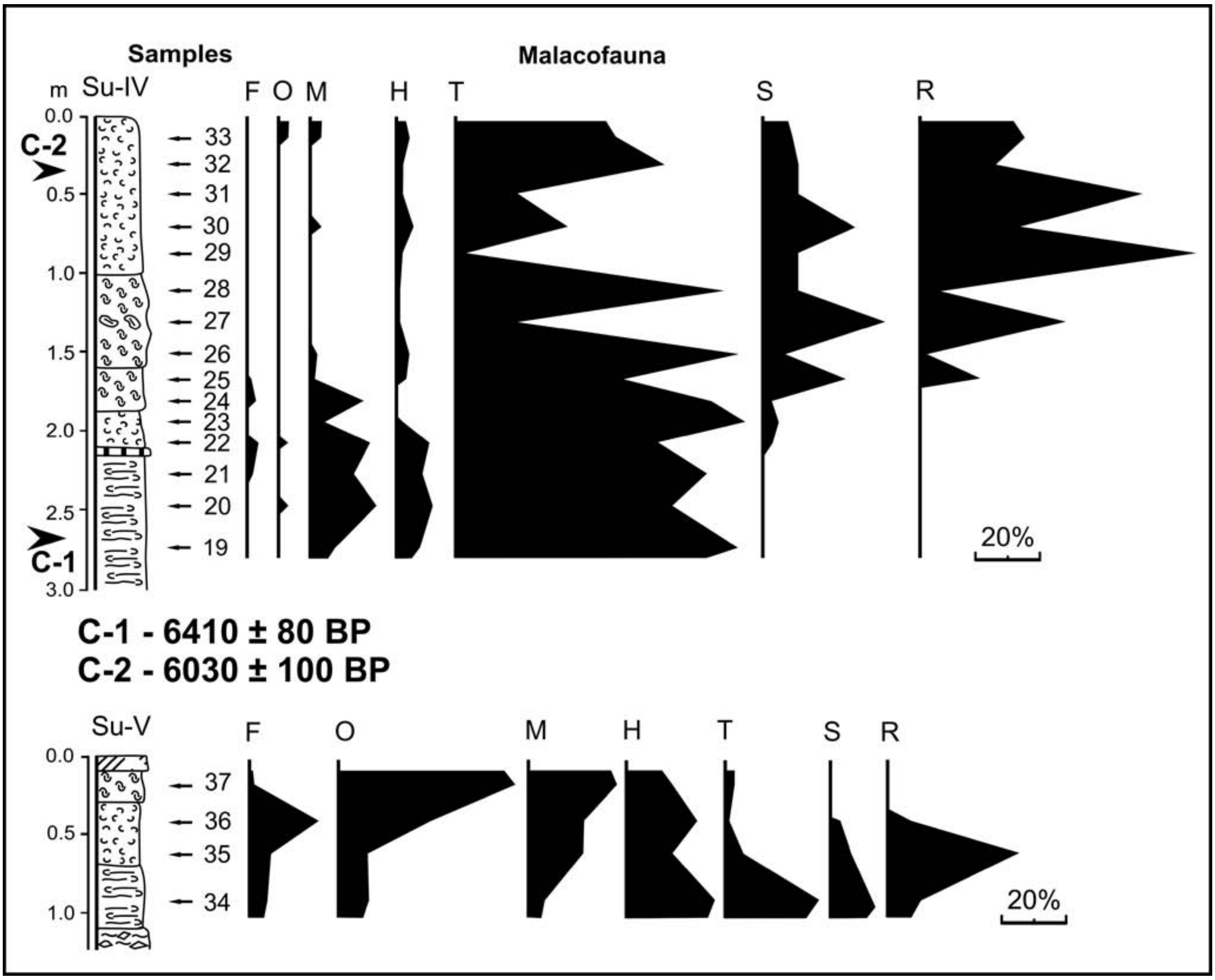

Fig. 3. Lithology and malacofauna of sections Su-IV and Su-V; C-1, C-2 – radiocarbon datings; for other explanations, see Fig. 2

diocarbon analyses of two samples were conducted, using molluscan shells. Those most commonly used for dating were well preserved shells of the large snails (*Bradybaena fruticum*, *Euomphalia strigella*, *Cochlicopa lubrica* and *Zonitoides nitidus* – sample C–1 and *Radix balthica*, *Anisus leucostomus* and *Ancylus fluviatilis* – sample C–2). The masses of particular samples were 40–50 g. All analyses were undertaken in the Radiocarbon Laboratory in Skała, near Kraków, by Prof. M. Krąpiec. The results of these measurements were then calibrated, on the basis of a calibration curve (Stuiver *et al.*, 1998), using the OxCal V 3.9 software package (Bronk Ramsey, 2003).

RESULTS

The locality at Sulisławice represents the infilling of water bodies, resulting from the damming of the Szreniawa River valley by two barriers, composed of hard calcareous tufa. At present, they are poorly exposed. Behind the barriers are loose calcareous tufas, containing a very rich malacofauna. These sediments reflect the gradual filling of the water bodies. The malacofauna provides a basis for the reconstruction of environmental changes during the deposition of the sediments.

Section Su-I (Fig. 2), situated directly at the lower barrier, is characterised by a poor fauna. In the lower part (sample Su-1) of it, terrestrial, meadow and mesophilous species (*Vallonia pulchella*, *Vallonia costata*, and *Vitrea contracta*) predominate. The aquatic taxa, *Physa fontinalis* and *Anisus leucostomus*, also are an essential component of this association (Fig. 2).

Sample Su-2 contains a richer and more diverse malacofauna. The noteworthy features of this fauna include a remarkably higher proportion of aquatic species, typical of episodic bodies of water (*Anisus leucostomus*) and taxa of broad, ecological tolerance, namely *Acroloxus lacustris* and *Valvata cristata* (Fig. 2). The samples, collected from section Su-I, are characterised by relatively low numbers of taxa and specimens and by low values of the TDA index, indicating their relatively homogenous composition (Fig. 4).

Section Su-II represents the central part of the dammed lake. From this sequence of calcareous tufas, 10 samples (Su-3 – Su-12) were collected (Fig. 2). In this section, three

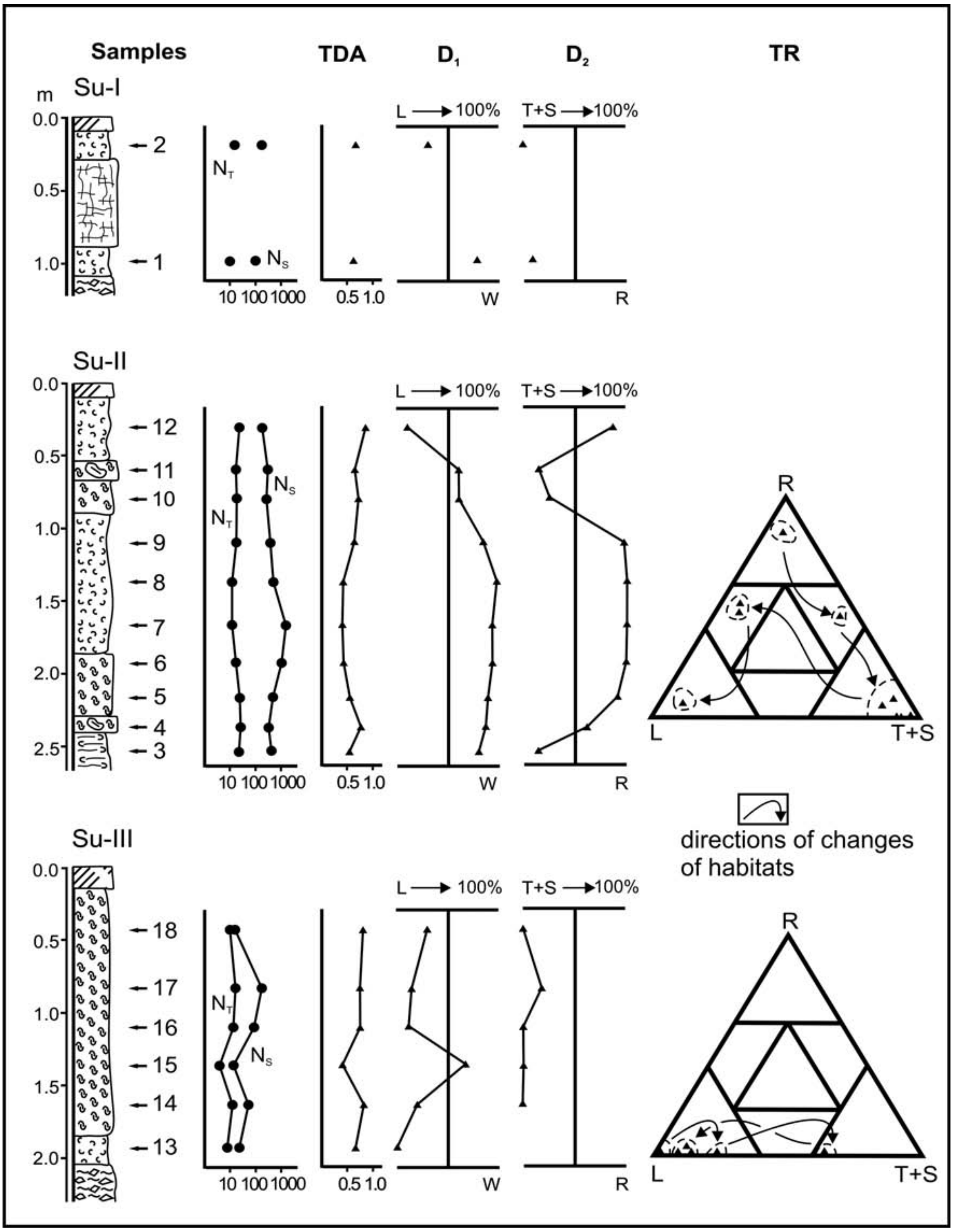

Fig. 4. Development of molluscan fauna in sections Su-I, Su-II, Su-III; N_t – number of taxa, N_s number of specimens, TDA – antilogarithm of taxonomical diversity index (according to S. W. Alexandrowicz, 1987a; S. W. Alexandrowicz and W. P. Alexandrowicz, 2011), D_1, D_2 – two-component diagrams, TR – three-component diagram. Ecological groups of molluscs (according to Ložek, 1964; S. W. Alexandrowicz, 1987a; S. W. Alexandrowicz and W. P. Alexandrowicz, 2011): L – land snails, W – water molluscs, T – species of episodic bodies of water, S – species of permanent bodies of water, R – river and stream (reophilous); for other explanations see Fig. 2

intervals can be distinguished, markedly different in terms of structure and the composition of faunistic associations. The lower part of the sequence (samples Su-3 and Su-4) is characterised by a very large proportion of species, typical of fast-flowing streams with a stony bottom, namely *Ancylus fluviatilis* and *Pisidium personatum*. They are accompanied by forms with broad, ecological tolerance (*Pisidium subtruncatum*, *Pisidium casertanum*, *Radix balthica*), as well as snails, typical of episodic bodies of water, namely *Anisus leucostomus*. Terrestrial species constitute only a small proportion. The association is typical of streams and minor rivers (Fig. 2). The samples, collected from the middle part of the section Su-II (Su-5 – Su-9), have an entirely different composition. The predominant, ecological group there consists of species, typical of bodies of water that have been overgrown by vegetation and are subject to seasonal drying, namely *Anisus leucostomus*, *Galba truncatula*, as well as forms with broad, ecological tolerance, such as *Valvata cristata*. Other aquatic species are of secondary importance, whereas terrestrial snails are practically absent. This fauna suggests an environment, comprising a small, periodically drying-up body of water, with abundant vegetation (Fig. 2). In the upper part of the section Su-II (samples Su-10 – Su-12), there is an abrupt increase in the proportion of species, typical of streams, *Ancylus fluviatilis* and *Pisidium personatum*, accompanied by the disappearance of forms, living in permanent or episodic bodies of water. At the same time, there is an increa- sed occurrence of terrestrial snails, mainly hygrophilous (*Carychium minimum*, *Perforatella rubiginosa*) and mesophilous (*Carychium tridentatum*, *Cochlicopa lubrica*) forms. Also present are species, living in open, meadow habitats, *Vallonia pulchella*, *Vallonia costata*, and even the typical forest taxa, *Discus rotundatus* and *Vertigo pusilla*. In the upper part of the section, terrestrial snails become the predominant group (Fig. 2). The malacofauna in samples, collected from section Su-II, is rich and diverse. This is supported by both high numbers of taxa and specimens in particular samples, as well as by high values of the TDA index (Fig. 4). The changes in the composition and structure of malacocoenoses in section Su-II are seen on the two-component diagrams. Except for the uppermost sample, the prevalence of aquatic species over terrestrial ones continues throughout the entire sequence. This is an indicator of drying-up biotopes and the disappearance of the body of water (Fig. 4). Also observed are essential changes in the structure of the aquatic component itself. The reophilous molluscs predominate in the lower and upper parts of the section, whereas in the middle interval, the principal role is assumed by taxa, typical of stagnant water (Fig. 4). The three-component diagram shows the transformations in the character of the predominant habitats, starting from the stream envi- ronment, through the phase of functioning as a small body of water to the period of dominance by terrestrial habitats (Fig. 4).

Section Su-III represents the distal part of the dammed lake. In six samples (Su-13 – Su-18), the terrestrial taxa, mainly mesophilous forms (*Carychium tridentatum*, *Punctum pygmaeum*) and meadow species (*Vallonia pulchella*, *Vallonia costata*) occur in large numbers. They are accompanied by very rare, shade-loving and hygrophilous snails. The aquatic element is of lesser importance, represented principally by *Anisus leucostomus* (Fig. 2). The fauna of molluscs, occurring in the samples, collected from the Su-III section, is generally poor and poorly diversified. This characteristic is confirmed by the low numbers of taxa and specimens and by the relatively low values of the TDA index (Fig. 4). The two-component diagrams indicate the lasting prevalence of terrestrial species. A minor increase in the proportion of aquatic forms is found only in the middle part of the sequence described above (sample Su-15) (Fig. 4).

Section Su-IV represents the central part of the upper, dammed lake. Fifteen samples, containing numerous molluscan shells, were collected. The malacological analysis indicated two distinct intervals, characterised by the presence of markedly different, faunal associations. The lower interval (samples Su-19 – Su-26) is characterised by a very large proportion of aquatic species, living in shallow, periodically drying-up bodies of water, namely *Anisus leucostomus* and *Galba truncatula*, as well as forms, with broad, ecological tolerance, such as *Valvata cristata*. The association is supplemented by land snails, mainly mesophilous and hygrophilous, primarily *Carychium tridentatum*, *Euconulus fulvus*, *Cochlicopa lubrica*, *Carychium minimum*, and *Zonitoides nitidus*. The taxa, associated with open habitats, and shade-loving taxa are of secondary significance. In the upper interval of the section (samples Su-27 – Su-33), there is a marked increase in the proportion of species, typical of permanent bodies of water, such as *Physa fontinalis*, *Acroloxus lacustris*, *Radix balthica*, and the reophilous forms, *Ancylus fluviatilis*, and *Pisidium personatum*. In a parallel development, there is a decrease in the significance of aquatic taxa, resistant to drying, and land snails disappear almost completely (Fig. 3). The numbers of species and specimens in the samples, collected from section Su-IV, change within broad limits. In some samples, more than 1000 specimens were identified, whereas in other samples there were merely dozens of specimens. The values of the TDA index also show major fluctuations. In the majority of samples, these reach high values, indicating high diversity. There are, however, also some samples, in which the TDA index has a low value and this emphasizes the low diversity of the fauna (Fig. 5). Both the two- and three-component diagrams indicate (1) the prevalence of aquatic environments throughout deposition, and (2) the predominance of species, occupying episodic bodies of water, in the lower part of the section, and the development of small, permanent pools of water, as well as the increased significance of flowing water in the upper part (Fig. 5). Samples for radiocarbon dating were obtained from section Su-IV. The first was taken from the bottom part of the sequence, between samples Su-19 and Su-20 (6410 ± 80 years BP, 5470–5320 cal. years BC; MKL-1097), whereas the second represented the top interval, between samples Su-31 and Su-32 (6030 ± 100 years BP, 5060–4790 cal. years BC; MKL 1080) (Fig. 3). These results indicate that deposition of the sediments, forming section Su-IV, occurred in the Atlantic Phase of the Holocene.

The last of the sections analysed (Su-V) represents the distal part of the higher, dammed lake. In four samples (Su-34 – Su-37), a malacofauna of considerable species diversity was found. In the section, there are two distinctly different associations of molluscs. The lower interval, including samples Su-34 and Su-35, is characterised by a high proportion of aquatic species. Viewed from the bottom upwards (Su-34), these are principally forms, typical of stagnant waters, usually species of broad, ecological tolerance and those, capable of surviving through the drying up of a water body, namely *Anisus leucostomus*, *Galba truncatula*, and *Valvata cristata*. Higher up (sample Su-35), there is an increase in the proportion of species, typical of flowing wa-

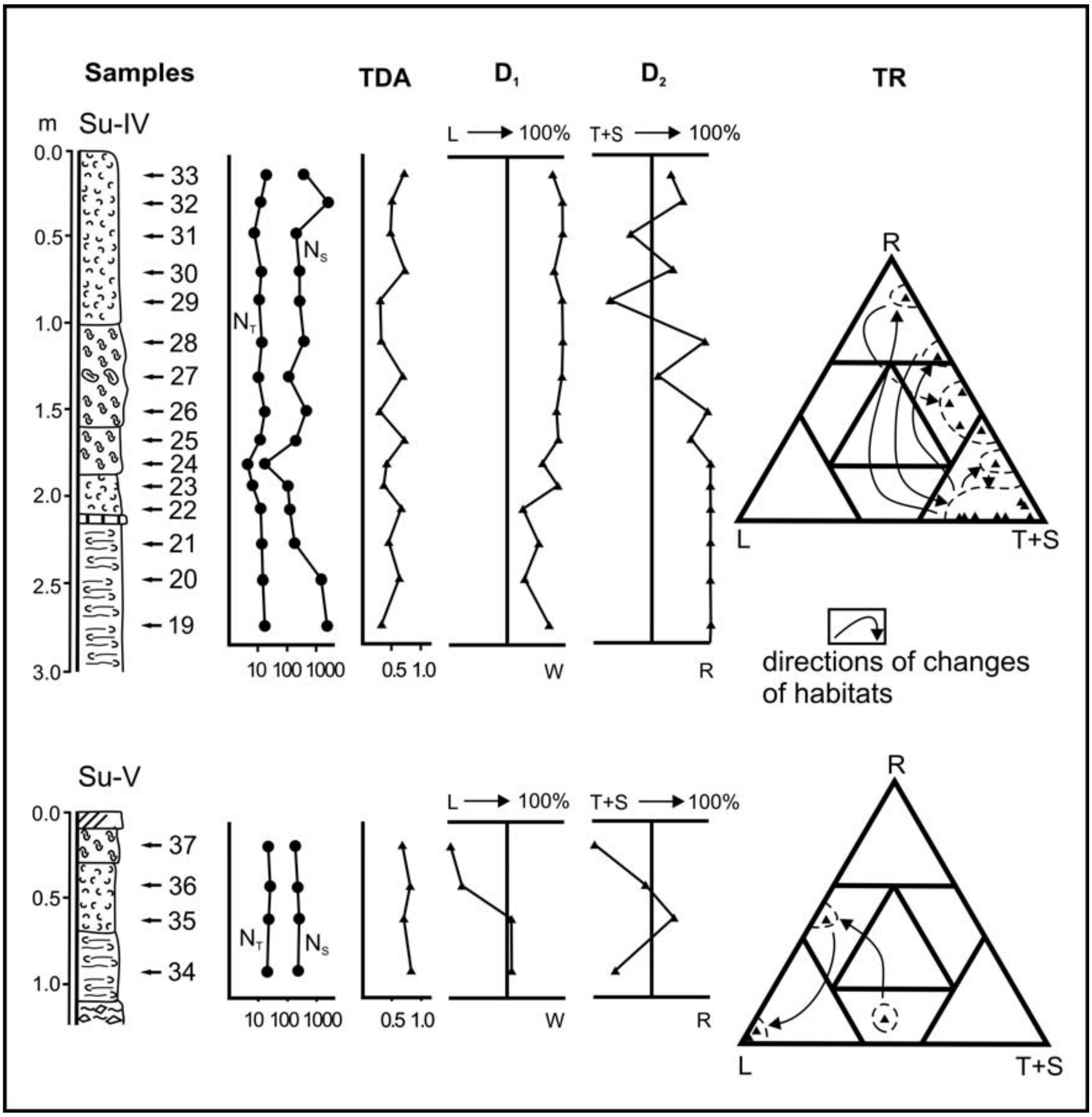

Fig. 5. Development of molluscan fauna in sections Su-IV and Su-V; for explanations see Figs 2 and 4

ter, *Ancylus fluviatilis* and *Pisidium personatum,* which become a predominant component of the association. The upper interval is characterised by the clear prevalence of land snails. There are numerous species, typical of open environments, such as *Vallonia pulchella* and *Vallonia costata*, which are accompanied by the mesophilous forms: *Carychium tridentatum* and *Nesovitrea hammonis* and, to a lesser extent, by the moisture-loving taxa (*Carychium minimum* and *Perforatella rubiginosa*) and the shade-loving taxa, *Vertigo pusilla* and *Bradybaena fruticum* (Fig. 3). The numbers of taxa and specimens in particular samples of section Su-V comparable. Similarly minor fluctuations are shown by the TDA index and its high values reflect major diversity in the association (Fig. 5). The two- and three-component diagrams suggest a sustained and significant proportion of land snails, especially in the top portion of the sequence and, except for a short episode (sample Su-35), a rather minor role of flowing water (Fig. 5).

DISCUSSION

The malacofauna, found at Sulisławice, shows, diversification in vertical sections. The corresponding faunal associations can be distinguished in the sediments, which were laid down, so as to fill bodies of water. This indicates similar sedimentation conditions for the tufas and also, indirectly, the similar stratigraphic positions of the sections.

It is essential to consider a sedimentation model for the calcareous tufas at Sulisławice. These sediments could have formed through the infilling of small, shallow bodies of water, impounded behind barriers, composed of hard tufa, as well as the result of deposition in pools (paludal model), developing on the floor of the Szreniawa River valley (e.g., Pedley, 1990, 2009; Pentecost, 1995). It is difficult to solve this problem unambiguously, because of the insufficient degree of exposure of the sediments. However, the first possibility is supported by more lines of evidence. The distribution of hard, calcareous tufa exposures is the first among them. Their outcrops are visible on both banks of the Szreniawa River valley, which attests to the fact that they once formed continuous barriers across the valley. The second indication comes from the sequence of fauna, observed in the sections. In the top and bottom parts of the sections, species that preferred water courses with rapid currents are present, whereas in the middle part of the intervals, there is a predominance of species, typical for stagnant waters, including also forms, typical of shallow, permanent bodies of water. For these reasons, in a further part of the study, a 'lake model' will be considered, which assumes the existence of two bodies of water, developing behind barriers. The differences, although minor, observed in the features of the fauna in the sections, representing the bodies of water, may confirm that these developed at least to some extent independently.

The taxonomical analysis permitted the recognition of four types of malacofaunal association. They correspond to different conditions, obtained during the course of sedimentation (Fig. 6). Three of these types are characterised by the prevalence of aquatic molluscs, whereas in the last association there is a considerable proportion of terrestrial forms.

The association with species, typical of flowing water, was found in seven samples, representing the lower and upper part of section Su-II (samples Su-3, 10 and 11), the higher interval of section Su-IV (samples Su-27, 29 and 31), and middle part of section Su-V (sample Su-35) (Fig. 6). The characteristic feature of this association is the very abundant occurrence of species, living in rivers and streams, such as *Ancylus fluviatilis* and *Pisidium personatum*. The former prefers a stony substrate and a relatively rapid current, whereas the latter shows remarkable, ecological tolerance and may appear both in water courses with stony, as well as with muddy bottoms, and is often found in spring zones. *Pisidium personatum* is typical of Late Glacial and Holocene Carpathian tufas (W. P. Alexandrowicz, 2004, 2009b, 2010). The occurrence there of *Bithynella austriaca* is a curiosity. This form is characteristic of spring zones and streams with rapid currents (Piechocki, 1979). The species is frequently a dominant component of the Late Holocene calcareous tufas, described from the Carpathians (W. P. Alexandrowicz, 2004, 2009b, 2010), whereas in the Mid-Polish Uplands, it occurs only sporadically (S. W. Alexandrowicz, 1983; W. P. Alexandrowicz, 2004). It is also only very rarely found in sediments, older that the Subatlantic Phase. The presence of the association described above signifies the dominant role of fluvial processes. In the sections at Sulisławice, a fauna of this type appears usually in either the lower or upper part of the sequence, corresponding to the phases, immediately preceding the formation of barriers and to periods of their being breached, with subsequent draining of the dammed lakes.

The association with species of permanent bodies of water occurred in four samples, representing sections Su-II (sample Su-4), and Su-IV (samples Su-25, 30, and 33) (Fig. 6). The characteristic feature of this fauna is the significant proportion of species, preferring permanent bodies of stagnant water, such as *Physa fontinalis* and forms with broad, ecological tolerance, *Valvata cristata* and *Radix balthica*. These species are usually the molluscs, which can inhabit both permanent and periodically drying bodies of water, namely *Anisus leucostomus* and *Galba truncatula*. The composition of this association indicates both shallowness of the water and abundant vegetation growth. The associations of similar characteristics were described at many locations of lacustrine chalk in the north of Poland (W. P. Alexandrowicz, 1999, 2007), as well as in the Carpathians (S. W. Alexandrowicz, 1987b) and were interpreted as indicators of the gradual disappearance of large, open lakes and their transformation into small, shallow and intensively overgrown bodies of water.

An association with species of episodic bodies of water was identified in 16 samples, representing sections Su-II, Su-III, Su-IV, and Su-V (Fig. 6). It is the most common association and the most characteristic of the calcareous tufas at Sulisławice. The typical characteristics of this fauna include the prevalence of aquatic species and the dominant role of molluscs, which could survive periods of drought. The indicator species should include *Anisus leucostomus* (the most numerous species – 5,695 specimens – more than 30% of all the shells identified), *Galba truncatula*, and *Pisidium obtusale*. These taxa are almost always accompanied by numerous shells of *Valvata cristata* and often also by bivalves with broad, ecological tolerance, such as *Pisidium casertanum* and *Pisidium subtruncatum*. Sometimes there is a significant admixture of terrestrial snails, particularly hygrophilous *Carychium minimum* and *Perforatella rubiginosa* and a mesophilous species, associated with a humid habitat *Carychium tridentatum*. The association presented is one of the most characteristic of the Late Glacial and Holocene malacological series and has been described at very many locations of calcareous tufas (S. W. Alexandrowicz, 1983, 1997b; W. P. Alexandrowicz, 1997, 2004), as well as in sections of lacustrine chalk (S. W. Alexandrowicz, 1987b; W. P. Alexandrowicz, 1999, 2007).

The last two associations, mentioned above, represent periods, where small, shallow and episodic lakes appeared behind barriers. They also mark the sedimentation phases of the loose, calcareous tufas that gradually filled the water bodies. These associations are particularly typical of the sections, associated with the central, deepest parts of both of the dammed lakes (sections Su-II and Su-IV).

The mixed association occurs in 10 samples from sections Su-I, Su-II, Su-III, and Su-V (Fig. 6). The characteristic feature of this fauna is a considerable proportion of terrestrial species. They are for the most part forms typical of humid and waterlogged habitats (e.g., *Perforatella rubiginosa*, *Carychium minimum*) and mesophilous taxa (e.g., *Carychium tridentatum*, *Nesovitrea hammonis*, and *Punctum pygmaeum*). Less common are snails, typical of relatively dry, open biotopes, such as *Vallonia pulchella*, and *Vallonia costata*, the shade-loving snails, *Bradybaena fruticum*, and *Vitrea crystallina*, and taxa, characteristic of forests, *Discus ruderatus*, and *Vertigo pusilla*. The mixed faunas are particularly characteristic of sections, representing the distal parts of dammed lakes (sections Su-III and Su-V).

The associations, described above, occur in sections, representing dammed lakes, which indicates similarity in the conditions of sedimentation. This is an essential premise

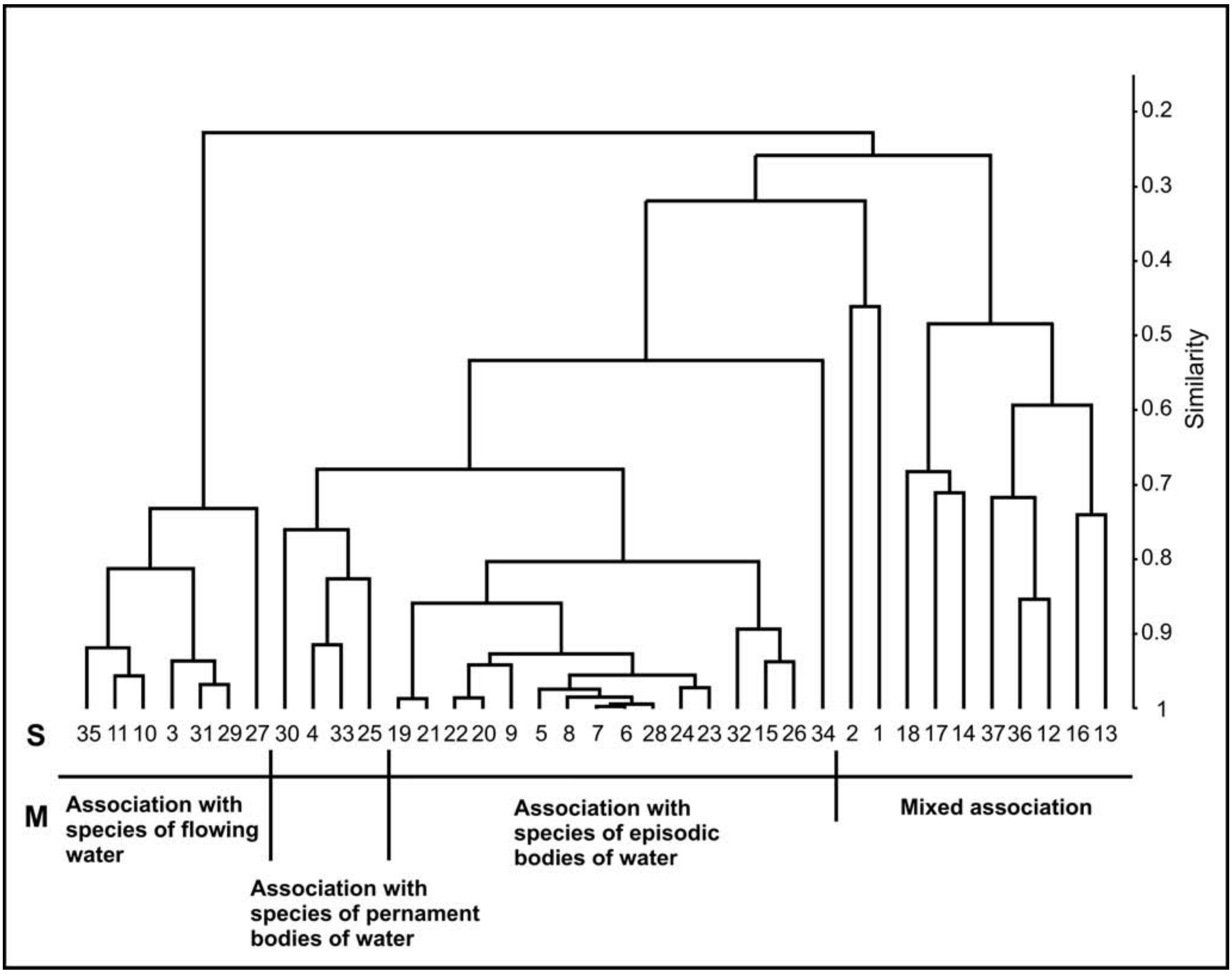

Fig. 6. Types of molluscan fauna from sections of calcareous tufa at Sulisławice; S – samples, M – molluscan assemblages described in text

for considerations of the stratigraphy and suggests that the sediments, filling both lakes, are of equal age. The radiocarbon dates for two samples collected at the bottom and the top of the section Su-IV, permit determination of the time frame for the water bodies and establishment of the stratigraphic range of the sediments.

The age, determined from the analyses of snail shells, is often loaded with error. The reservoir effect is suspected of being responsible for the old age, obtained in radiocarbon dating. This effect is observed at many locations of calcareous tufas, associated with the Late Glacial and Holocene (e.g., Pazdur *et al.*, 1988a, 1988b; Gradziński *et al.*, 2001). Thus, it is very likely that the radiocarbon ages, obtained for samples from the sediments at Sulisławice, are somewhat older than the true dates. On the other hand, in the close proximity to the profile studied, there are several other outcrops of sediments, containing similar molluscan assemblages, and age determinations made there yielded very similar results (Pazdur *et al.*, 1988a, 1988b; W. P. Alexandrowicz, 2004). Moreover, palynological studies at peat localities near Wolbrom have permitted the description of the stages in environmental change (Obidowicz, 1976; Latałowa and Nalepka, 1987). The results of these analyses correlate well with the conclusions, derived from malacological analyses. These facts indicate that even though the ages, obtained at Sulisławice, are perhaps too old, the errors in dating are not excessively large. These errors do not influence the interpretations, or the conclusions derived from them, in any significant way.

The age of the bottom part was determined to be 6410 ± 80 years BP (5470–5320 cal. years BC; MKL-1097), whereas the age of the top part was estimated at 6030±100 years BP (5060–4790 cal. years BC; MKL 1080) (Fig. 4). Thus the phases of emergence, existence and disappearance of the dammed lakes coincide with the Atlantic Phase or the beginning of the Boreal Phase, most probably, with the moist periods, distinguished by Starkel (1977).

In the Alps at that time, there was the glacial advance, known as the Frosnitz phase (e.g., Patzelt, 1977; Bortenschlager, 1982). Later studies showed, however, that this cooling period was not strongly marked (Haas *et al.*, 1998) and in some regions, almost impossible to define (Mayewski *et al.*, 2004; Joerin *et al.*, 2006; Ivy-Ochs *et al.*, 2009). In this period, there were also considerable fluctuations in the humidity of the climate. These events have been reconstructed, both on the basis of changing water levels in the lakes, and changes in fluvial activity. The Atlantic Phase was a period of increased water levels in lakes, both in the Alpine zone (e.g., Magny, 1993, 2004; Debret *et al.*, 2010) and in the European Lowlands (Ralska-Jasiewiczowa and Starkel, 1988; Starkel *et al.*, 1996; Wojciechowski, 1999), as well as intensified fluvial activity (Starkel, 1990, 1995; Kalicki, 1991). The humid and relatively warm climate, prevailing in this period, was favourable for the sedimentation of calcareous tufas. In many sections, including those at Sulisławice, there was clear acceleration in the deposition of these sediments, as well as the aggradational lift of valley bottoms and emergence of barriers (e.g., Jäger and Ložek, 1968, 1983; S. W. Alexandrowicz, 1983, 1997b; Hennig *et al.*, 1983; Pazdur *et al.*, 1988b; Gradziński *et al.*, 2001; Meyrick, 2001, 2002; Gedda, 2001, 2006; Žak *et al.*, 2002; W. P. Alexandrowicz, 2004; W. P. Alexandrowicz and Gołas-Siarzewska, 2013). The rapid shifts in proportions between forms, typical of stagnant waters, and reophilous forms (Fig. 5), observed in the upper part of section Su-IV, could have been the result of intensified flooding. In the periods with elevated water levels, there was increased transportation of shell material. This increase pertains primarily to shells of molluscs living in the stream bed, above the maximum limits of the lakes. All this activity resulted in the augmentation of malacocoenoses by reophilous species. The increased frequency and intensity of flooding in the period around 5000 BC could have been caused by changes in the climate (e.g., Starkel *et al.*, 1996, 2006; Starkel, 2001, 2005), or by human activities, involving primarily the deforestation of slopes (e.g., Kalicki, 2006; Dobrowolski *et al.*, 2010). The data, obtained from palynological analyses undertaken on peat bogs in the area around the Wolbrom, indicate that anthropogenic effects were at a minimum during sedimentation of the calcareous tufas at Sulisławice. Traces, confirming the presence of humans, are known from the vicinity of Wolbrom from as early as the beginning of the Atlantic Phase, but the pollens of cultivated plants were found only later in palynological sections, in the Iron Age (Obidowicz, 1976; Latałowa and Nalepka, 1987). In the areas, not modified by human impact, shade-loving and mesophilous snails usually prevail, whereas in areas under strong anthropogenic pressure, the fauna is comprised almost exclusively of forms, typical of dry, open environments, often accompanied by species, directly associated with human activities, such as *Cecilioides acicula* (Müll.) and *Oxychilus inopinatus* (Uli.) (S. W. Alexandrowicz *et al.*, 1997; S. W. Alexandrowicz, 1997b; W. P. Alexandrowicz, 2004; W. P. Alexandrowicz and S. W. Alexandrowicz, 2010).

In southern Poland, the calcareous tufas, deposited in dammed lakes, are known at many localities throughout both the Carpathians and the Mid-Polish Uplands. In the sediments of lakes in both areas, the malacofauna is rich and diverse, although the composition and structure of faunal associations differ significantly. The localities in the Carpathians are characterised by markedly higher proportions of terrestrial species and particularly shade-loving forms, whereas the frequency of occurrence of aquatic molluscs, especially those typical of more open and permanent bodies of water, is markedly lower. These differences are caused by the dissimilar morphologies of river valleys. The Carpathian valleys, for instance, are usually narrower and have steep slopes. Owing to this shape, the amounts of material, coming from the slopes, is large, and the malacocoenoses are enriched by species living on slopes that are often forested. On the other hand, the valleys within the upland area are flat-bottomed and relatively wide, thus making it very difficult or sometimes virtually impossible for fauna associations, living near the river bed to mix with the associations, living on the deforested slopes. Studies of recently deposited flood sediments indicate that a flat valley bottom, the width of which exceeds ten metres, constitutes an insurmountable barrier to shell material, washed down from the slopes (e.g., W. P. Alexandrowicz, 2002; Ilg *et al.*, 2009).

The second essential difference is associated with the nature of the processes, leading to the appearance of barriers across valleys. Almost all locations with calcareous tufas, filling dammed lakes, identified in the Carpathians (S. W. Alexandrowicz, 1993, 1996, 1997a; S. W. Alexandrowicz and Z. Alexandrowicz, 1999; W. P. Alexandrowicz, 2009a, 2013), are associated with landslide zones. The landslide tongues that blocked the valleys had the effect of preventing outflow and as a result, led to the development of dammed lakes. Colluvial barriers, however, lack the possibility of vertical increase and therefore the dimensions, shape and depth of the bodies of water so created were determined by the height of the barrier and by the morphology of the valley. As a consequence, these bodies of water could exist only for short periods of time, before being filled by sediments, or the dam was breached and normal flow was restored in the valley. This situation results in a relatively small thickness of sediment, usually not exceeding 1–1.5 m (S. W. Alexandrowicz, 1993, 1996; W. P. Alexandrowicz, 2009a, 2013), and only in exceptional cases do they reach 5 m (S. W. Alexandrowicz, 1996, 1997a). In the valleys of upland streams, the flow restriction is almost always caused by expanding barriers, composed of hard, calcareous tufa. The process of their development may be initiated by the accumulation of plant material, such as trunks and branches, or perhaps even leaves, on the stream bed. Such an accumulation may also be connected with the activities of beavers. Later in the process, a gradual heightening of the barriers took place, as a result of the deposition of calcareous tufas, occurring both on the barriers themselves and in the lakes, developing behind them (e.g., S. W. Alexandrowicz, 1983, 1989, 1991, 1997b; Szulc, 1984, 1986; W. P. Alexandrowicz, 2004). As a result of this process, a thick series of calcareous tufas developed, in some instances up to 8–9 m thick. As a result of their being breached, so-called tufa terraces developed, examples of which are found in valleys, dissecting the southern edge of the Ojców plateau, west of Kraków (locations e.g., in the valleys of the Racławka, Szklarka, Będkówka, and Sąspówka streams) (S. W. Alexandrowicz, 1983, 1989, 1991, 1997b; Szulc 1984, 1986; W. P. Alexandrowicz, 2004), and also in the Wolbrom area (sections in Rzeżuśnia and Trzebienice, and the Sulisławice location, considered in the present study) (Szulc, 1984; Domański, 1988; S. W. Alexandrowicz and Domański, 1991; W. P. Alexandrowicz, 2000, 2004).

CONCLUSIONS

The sections, described above, represent an example of carbonate sedimentation in lakes, where streams were dammed by barriers, composed of hard calcareous tufa. The rich and diversified fauna of molluscs, identified there, provides a good foundation for the definition of a model for the development of bodies of water behind such barriers. It is possible to distinguish three principal phases. The first is linked to the period, immediately preceding the development of a barrier. Usually, there is a characteristic association of molluscs, with dominance of reophilous species, often also containing a significant admixture of terrestrial snails, particularly those typical of moist and/or shaded habitats. The next phase corresponds to the period of the deposition of calcareous tufas in a dammed lake, developed as a result of its formation and gradual accumulation over a developing barrier. This episode is associated with the occurrence of malacoenoses, with a considerable proportion of species, typical of stagnant waters. These may include both episodic forms and those, typical of permanent bodies of water. The proportion of terrestrial fauna is usually low. The prevalent species include hygrophilous, mesophilous and shade-loving snails, typical of moist habitats. The temporary occurrence of reophilous forms may be linked with phases of intensified flooding, whereas the increases in the proportion of terrestrial taxa indicate phases, when habitats were drying up. The phase, described above, usually covers a relatively long period of time, several hundred, and in exceptional cases even as much as several thousand years. In the last stage, dissection of the barriers occurs, followed by the incision of the sediments, filling the dammed lakes, resulting in the formation of 'tufa terraces'. These processes entail significant changes in the composition and structure of the associations of molluscs. Aquatic species disappear, replaced by poor faunas, with terrestrial species. The results of malacological studies, undertaken at a number of localities in the upland regions of Poland and Europe, confirm the universal character of this model for the development, filling and draining of dammed lakes, developing behind barriers, composed of hard, calcareous tufa. Most often, the diversity of the composition and structure of malacocoenoses, observed at various locations, is the effect of the local conditions, principally the morphology of a particular valley, the characteristics of a predominant type of vegetation, and the impact of humans. In terms of stratigraphic considerations, the essential modifying factors include climatic conditions and changes to them during the course of sediment deposition.

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