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SPATIAL DISTRIBUTION AND DIVERSIFICATION OF MOLLUSC COMMUNITIES IN FLOOD SEDIMENTS WITHIN THE RIVER VALLEY BASED ON THE EXAMPLE FROM THE BESKID MAŁY RANGE (WEST CARPATHIANS, SOUTHERN POLAND)

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Abstract: Diverse malacofauna communities have been found in flood sediments accumulated in the Ponikiewka stream valley in the Beskid Mały range (Polish West Carpathians). The analyzed material included 60 taxa of molluscs represented by over 15,000 specimens. The composition and structure of malacofauna refer to the features of the environment in which sedimentation took place. The research indicates a limited scale of shell material transport within the valley. Longitudinal transport takes place over short distances, particularly in high-energy flows leading to mechanical destruction of shells. Transportation across the valley is inhibited by vegetation growing on the flat floodplain and plays only a marginal role in valleys over 30 m wide. Research on the deposition mechanisms in thanatocenosis that are currently emerging is very important for the methodology of interpreting the environment based on fauna communities found in Quaternary fluvial sediments.

Key words: flood deposits, molluscs, thanatocenosis, river valley, Carpathians, S. Poland

1. INTRODUCTION

Flood deposits accumulate in river valleys during periods of high water levels. Depending on the size of the flood and the height of the flood wave, they appear in the valley bottom (floodplain) or on slopes of the valley. These deposits are made of plant fragments: branches, leaves and finer detritus with admixture of sand and silt. A common component of these sediments are anthropogenic waste. Flood deposits often contain animal remains: chitin covers of insects, especially beetles, fish scales, and sometimes the bones of small vertebrates. However, the most common animal component of flood sediments are mollusc remains. Such accumulations of empty shells not covered with sediments are called thanatocenosis (Wasmund, 1926; Dodd & Stanton, 1981; Alexandrowicz & Alexandrowicz, 2011). The issue of similarity in the composition and structure of thanatocenosis and the biocenosis it derives from was the subject of many studies (e.g. Janin, 1983; Briggs et al., 1990; Cummins, 1994; Niedźwiedzki, 2002). This similarity is high at first, but decreases in a relatively short time. This is the result of many processes, the most important among which is the chemical dissolution of shells as due to the effect of humic acids.

Analyses of mollusc shell thanatocenosis in flood sediments have been conducted for many years, particularly in Germany (e.g. Foeckler, 1991; Ilg et al., 2009, 2012), the Czech Republic, Slovakia (e.g. Pišút & Čejka, 2002; Čejka et al., 2008; Čiliak et al., 2015) and Poland (e.g. Alexandrowicz, 1997, 1999, 2000a, b, 2002). These were most often used as a tool in fauna research to determine the composition of the malacofauna inhabiting a given area and to find some species difficult to find using other methods (e.g. Horsák et al., 2009; Alexandrowicz, 2010, 2019a). Studies on the spatial distribution of malacofauna within river valleys and its diversity were also conducted (e.g. Jurkiewicz-Karnkowska, 2009, 2019; Myšák & Horsák, 2011; Juřičková et al., 2013; Horáčková et al., 2015).

An extremely important cognitive aspect resulting directly from research on shell thanatocenosis in flood sediments is the opportunity to use conclusions to reconstruct the conditions of sedimentation of Quaternary, especially Holocene fluvial sediments.

Subfosil fauna communities in fluvial sediments are widely used in paleoenvironmental analyzes. It should be emphasized that these communities were originally thanatocenosis, which were later covered with sediments and became taphocenosis being the basis of malacological research. Thus, understanding the mechanisms of thanatocenosis deposition is of vital importance for the methodology of reconstructing environments during the Quaternary period. On the one hand, thanatocenosis studies allow a direct assessment of the degree of projecting the nature of habitats in the composition and structure of fauna communities. On the other hand, they allow observation and evaluation of redeposition and mixing processes in malacocoenosis representing different types of habitats and natural micro-habitats. These issues will be the main topic of the presented study.

2. STUDY AREA

The research involves the Ponikiewka stream valley. It is a small left-bank tributary of the Skawa River that cuts through the Beskid Mały range near the city of Wadowice, approx. 60 km southwest of Cracow (Fig. 1A). The Beskid Mały range, a part of the Western Beskidy Mts, is made of flysch formations, primarily sandstone and shales representing the Upper Cretaceous and Palaeogene (Paul et al., 1996). The massif is overgrown by dense mixed or coniferous forest communities. Many places include natural communities of the Carpathian beech forest (*Dentario glandulosae-Fagetum*). Agricultural areas: arable fields and pastures are primarily concentrated in river valleys. Due to the significant reduction in agricultural activity during the last 20-30 years, the expansion of forests and shrub communities is leading to the disappearance of open, woodless habitats.

Ponikiewka stream valley is located in the eastern part of the range. Its source is located at an altitude of approx. 870 m a.s.l. and the estuary about 280 m a.s.l. (Fig. 1B). At first, the stream flows through a very narrow, deep, V-shaped valley with a rocky

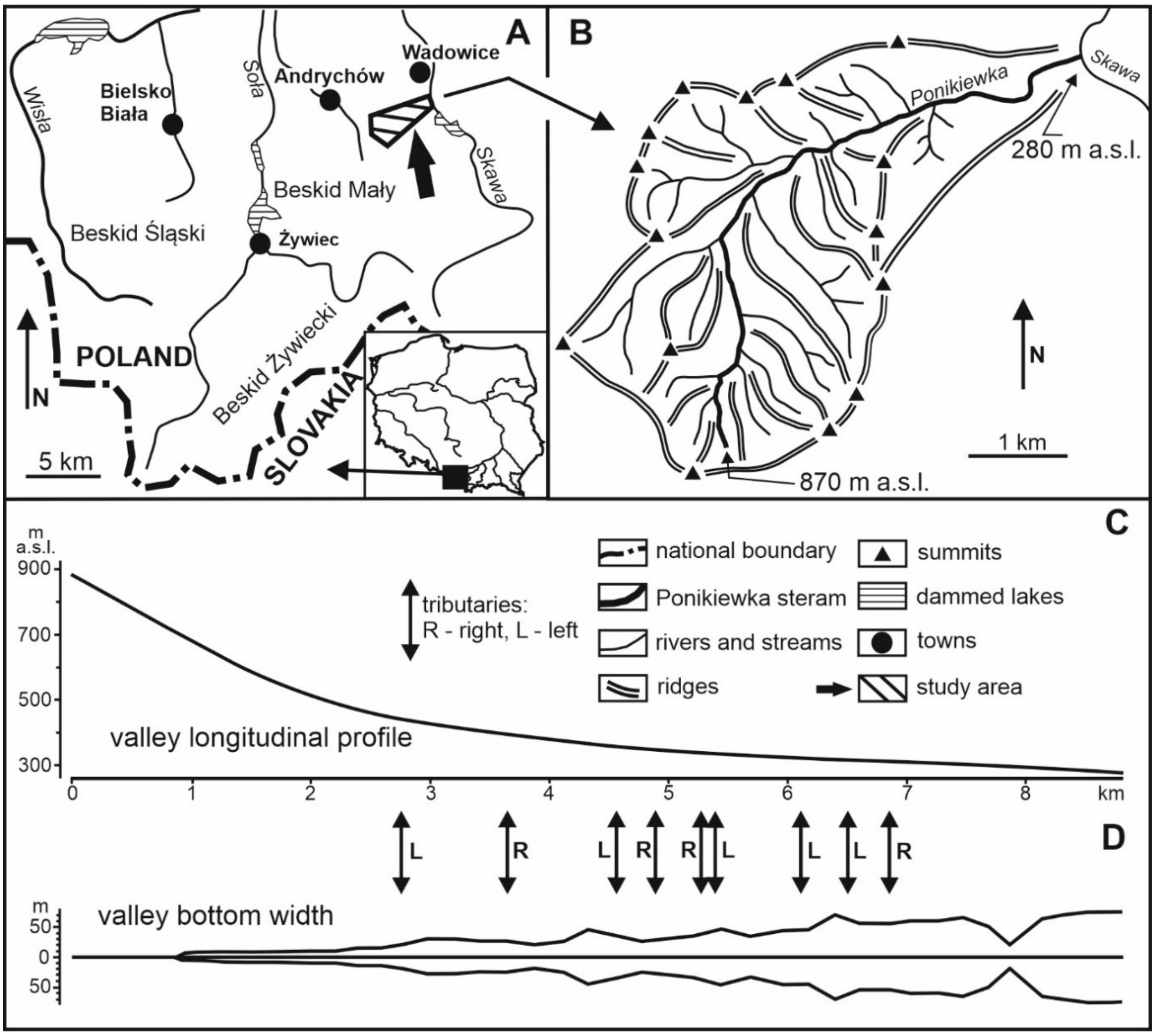

Figure 1. Localization of study area (A), morphology of Ponikiewka stream catchment (B), longitudinal profile (C) and valley bottom width (D)

bottom. It is surrounded by steep slopes covered with dense forests (Figs 1C, 2). About 1 km from the source, the valley widens and a narrow (up to 10 m) floodplain appears along the riverbed, located up to 0.7 m above the stream level. At the same time, flysch outcrops disappear from the stream's bed, their place being taken by gravel alluvia. Downstream of Ponikiewka, the floodplain is becoming wider (Fig. 1C). On the banks of the stream there are dense thickets with a large share of willow and alder, as well as hygrophilous herbaceous plants (Fig. 2). The flat bottom of the valley is limited by terrace slopes reaching 7 m in height, increasing at the mouths of the tributaries up to 10 m. These terraces are built of gravel and river sand, covered by slope sediments, and their formation can probably be linked with the last glaciation (Zuchiewicz, 1986; Alexandrowicz, 1991). There are buildings of the village of Ponikiew and arable land on the flat terrace surfaces. The largest area, however, is covered primarily by mixed forests, gradually shifting into deciduous forests down the valley (Fig. 2).

Malacofauna occurring in the Beskid Mały range includes 78 species of land shelled snails, several species of water molluscs and a dozen taxa of slugs (Alexandrowicz, 2019a, b).

3. MATERIAL AND METHODS

A section of the Ponikiewka stream valley approx. 6,500 m long was analyzed. Detailed tests were carried out at 32 sites. The distance between individual sites was around 200 m (Fig. 2). Samples were taken from individual sites at least from two swellings in different years. The width of the valley was measured at each site. The vegetation as well as the manner of economic use of the valley bottom and its slopes were also observed. Determinations of shell material were made using keys (Kerney et al., 1983; Wiktor, 2004; Welter-Schultes, 2012; Horsák et al., 2013) and a comparative collection. The numbers of each taxon were determined in the samples. Individual species of molluscs were included into ecological groups according to the scheme developed by Ložek (1964), Alexandrowicz & Alexandrowicz (2011) and Juřičková et al. (2014). The data compiled this way was used to construct the malacological spectrum of individuals (MSI). In order to characterize the main fauna components, the structure of constancy and dominance (C-D) was calculated. The Q index (geometric mean C and D) indicating the species that play the most vital role in the material (Alexandrowicz & Alexandrowicz, 2011). The use of statistical methods: analysis of the similarity dendrogram based on the Morisita algorithm (Morisita, 1959) and principal component analysis (PCA) allowed distinguishing fauna types and indicating the crucial factors determining their diversity. Statistical calculations were made using the PAST software (Hammer et al., 2001). These data served

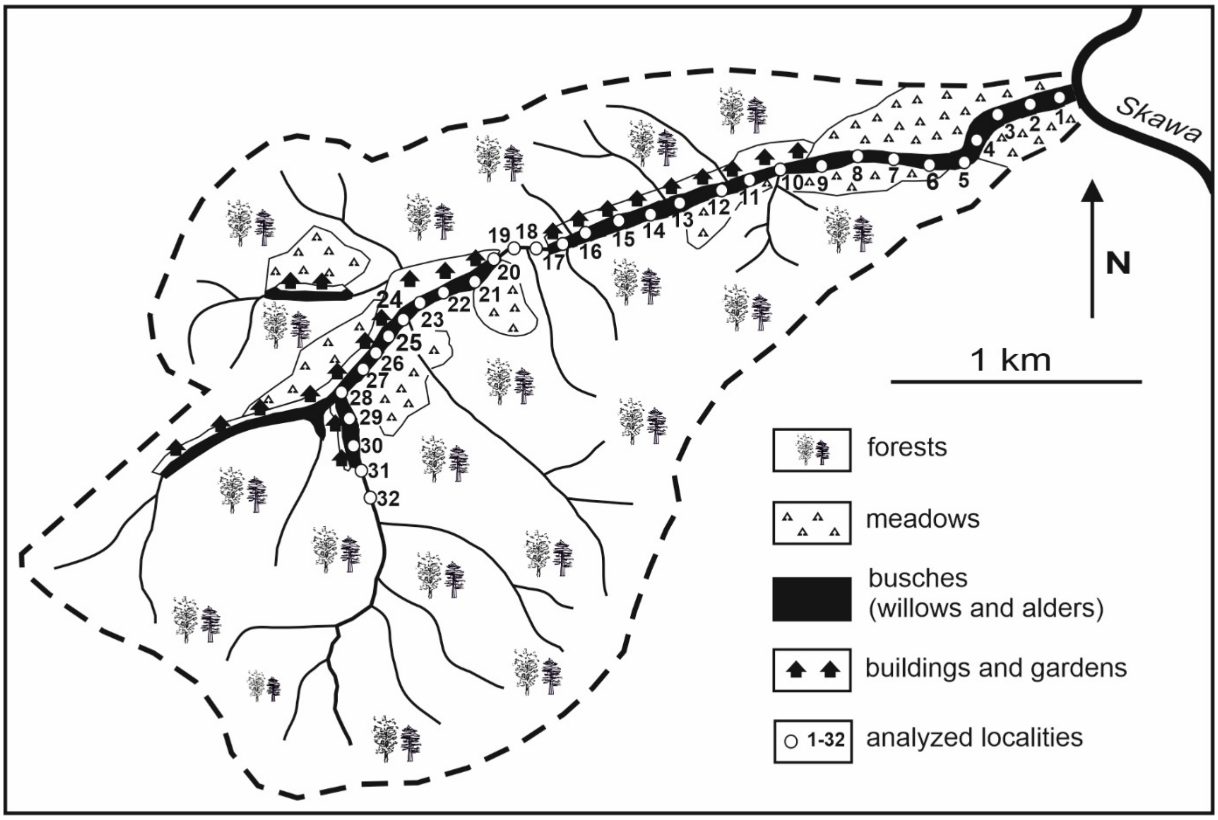

Figure 2. Land use and localization of research sites

as the basis for considerations regarding the correlation between ecological features in thanatocenosis and the environment they were deposited in, and to determine the impact of transport along and across the valley on the composition and structure of the mollusc community.

4. RESULTS

A total of 55 land snail taxa were found in the flood deposit samples. The presence of calcareous plates from slugs has also been revealed. Due to the inability to mark them, they were included in the common category - *Limacidae*. The fauna was supplemented by five species of water molluscs (4 snails and 1 bivalve). In total, the analyzed material comprised nearly 15,000 specimens, over 2,000 identifiable fractions, and a significant number of small, unidentifiable shell fragments. The number of taxa in individual sites ranged from 13 to 40, and for specimens from 100 to 977 (Fig. 3). The full list of marked fauna is shown in Table 1.

4.1. Malacofauna

Typical forest species (ecological groups F_F and F_B) are an important component of the group in the upper part of the valley. At this section they can even

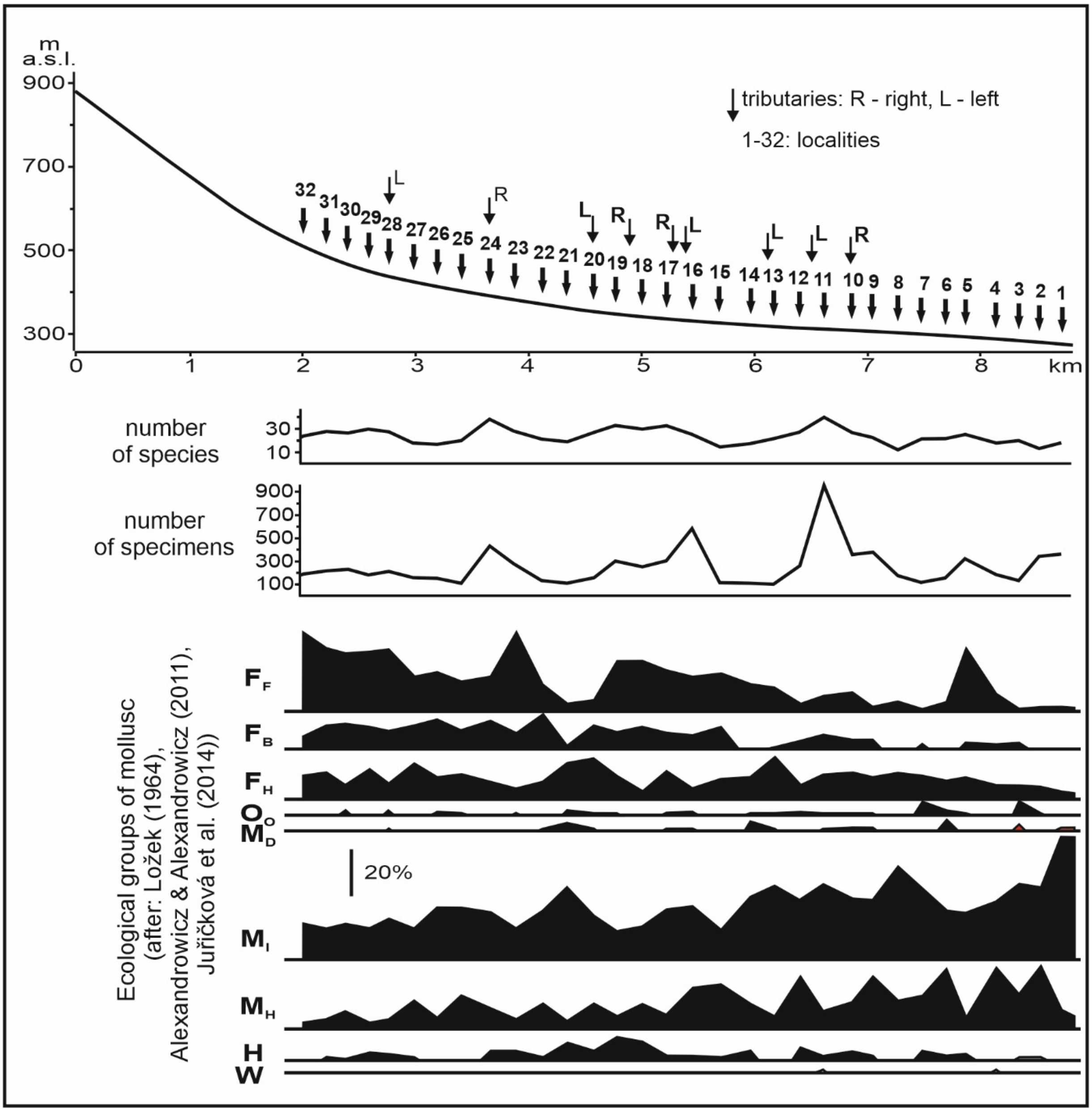

Figure 3. Ecological structure of malacofauna from flood deposits from Ponikiewka stream valley.
F_F - shadow-loving species, F_B - shadow-loving species of light forests and bushes, F_H - shadow-loving species of humid habitats, O_O - open-country species, M_D - mesophilous species of dry habitats, M_I - mesophilous species of moderately wet habitats, M_H - mesophilous species of wet habitats, H - hygrophilous species, W - water species

Table 1. Malacofauna from flood deposits from Ponikiewka stream valley.

	D (D<5%)	Q	E		D (D>5%)	Q	E
C (C>50%)	*Vitrina pellucida* (Müll.)	20.60	M_I		*Columella aspera* Wald.	34.50	M_I
	Perpolita hammonis (Ström.)	18.80	M_I		*Columella edentula* (Drap.)	32.00	F_H
	Carychium tridentatum (Risso)	17.20	M_H		*Aegopinella pura* (Ald.)	29.50	F_F
	Discus rotundatus (Müll.)	17.10	F_B		*Cochlicopa lubrica* (Müll.)	29.20	M_I
	Vertigo pusilla Müll.	14.30	F_F		*Trochulus villosus* (Rossm.)	25.60	M_H
	Trochulus lubomirskii (Ślós.)	14.30	M_I				
	Perpolita petronella (L.Pfe.)	13.30	M_H				
	Carychium minimum Müll.	10.80	H				
	Aegopinella minor (Stab.)	10.70	F_B				
	Euconulus fulvus (Müll.)	9.86	M_I				
	Monachoides incarnatus (Müll.)	9.76	F_F				
	Punctum pygmaeum (Drap.)	8.26	M_I				
	Succinea putris (L.)	7.86	H				
	Mediterranea depressa (Sterki)	7,83	F_F				
	Oxychilus deubeli (Wagner)	7.42	M_I				
	Cochlicopa lubricella (Rossm.)	6.74	M_D				
	Vallonia pulchella (Müll.)	6.13	O_O				
c (C<50%)	*Perforatella bidentata* (Gmel.)	7.73	M_H				
	Vestia turgida (Rossm.)	6.84	F_H				
	Succinella oblonga (Drap.)	6.68	M_H				
	Platylla polita (Hartm.)	5.67	F_F				
	Fruticicola fruticum (Müll.)	4.91	F_B				
	Daudebardia rufa (Drap.)	4.66	F_F				
	Lucilla syngleyana (Pils.)	4.57	M_I				
	Arianta arbustorum (L.)	4.52	M_H				
	Vitrea crystallina (Müll.)	4.43	F_H				
	Monachoides vicinus (Rossm.)	4.09	F_H				
	Zonitoides nitidus (Müll.)	4.09	H				
	Acanthinula aculeata (Müll.)	3.94	F_F				
	Morlina glabra (West.)	3.92	F_B				
	Vitrea contracta (West.)	3.39	M_I				
	Vestia gulo (Bielz.)	3.39	F_H				
	Vertigo pygmaea (Drap.)	3.35	O_O				
	Ancylus fluviatilis Müll.	3.30	W				
	Vertigo alpestris Ald.	2.73	F_B				
	Cepaea nemoralis (L.)	2.73	F_B				
	Isognomostoma isognomostomos (Schröt.)	2.44	F_F				
	Macrogastra tumida (Rossm.)	2.02	F_H				
	Eucobresia nivalis (Dum et Mort.)	2.02	F_F				
	Daudebardia brevipes (Drap.)	1.81	F_F				
	Pisidium personatum Malm.	1.71	W				
	Discus ruderatus (Hartm.)	1.67	F_F				
	Vallonia costata (Müll.)	1.65	O_O				
	Vitrea transsylvanica (Cless.)	1.64	F_F				
	Laciniaria plicata (Drap.)	1.64	F_B				
	Alinda bilpicata (Mont.)	1.59	F_B				
	Vitrea diaphana (Stud.)	1.30	F_F				
	Helix pomatia (L.)	0.76	F_B				
	Limacidae	0.76					
	Semilimax semilimax (Fér.)	0.54	F_F				
	Vitrea subrimata (Reinh.)	0.40	F_F				
	Petasina unidentata (Drap.)	0.40	F_F				
	Radix peregra (Müll.)	0.39	W				
	Galba truncatula (Müll.)	0.39	W				
	Vertigo substriata (Jeffr.)	0.39	M_H				

C,c - constancy, D,d - domination Q - geometric mean C and D, Ecological groups of molluscs (after: Ložek (1964), Alexandrowicz & Alexandrowicz, (2011), Juřičková et al. (2014)): F_F - shadow-loving species, F_B - shadow-loving species of light forests and bushes, F_H - shadow-loving species of humid habitats, 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, W - water species constitute up to 70% of the community (Fig. 3). Noteworthy is the numerous occurrences of taxa with relatively high ecological requirements (*Aegopinella pura*, *Vertigo pusilla*, *Discus rotundatus*). In the lower course of the stream, the share of forest forms significantly decreases, except for the sections where the narrowing of the valley is observed (Fig. 3). Shade-loving species typical of high-humidity habitats (ecological group F_H) play a very important role in this fauna. These forms are a typical component of the communities found on the bottom of river and stream valleys. The most numerous representative is *Columella edentula*, common in both the upper and lower course of the stream (Fig. 3). Forest fauna consists primarily of widely distributed mountain and upland species inhabiting significant areas in Central Europe. Noteworthy is the presence of Carpathian endemics and subendemics: *Vestia gulo*, *Vestia turgida* and *Macrogastra tumida* (Alexandrowicz, 2019a, b). Open-country snails (ecological group O) and dry-loving mesophilous forms (ecological group M_D) are only represented by a few specimens and play a marginal role in the community (Fig. 3).

The second main component of the molluscan assemblage, apart from shade-loving species, are wet-loving, mesophilous taxa (ecological groups M_I and M_H). Their share in the complex can even reach up to 90% and increases downstream (Fig. 3). Species belonging to said ecological groups are characterized by high tolerance both in terms of the degree of shading in their habitats as well as humidity conditions. They are the primary component of communities inhabiting the bottoms of river and stream valleys (*Columella aspera*, *Trochulus villosus*). Most of the species included in this group are common forms with extensive geographical spread. Undoubtedly, the greatest fauna curio is the presence of *Lucilla syngleyana*. It is a North American taxon that was dragged into Europe. It leads an underground lifestyle, and therefore is very difficult to find, and its spread in Central Europe is poorly understood (Horsák et al., 2009; Alexandrowicz, 2010). Analyzes of flood deposits carried out in the Beskid Mały range area confirmed the presence of this taxon (Alexandrowicz, 2002, 2010, 2019a, b). Hygrophilous snails complement the community.

Water molluscs are a small admixture. Rheophilous species (*Ancylus fluviatilis*) tend to predominate here (Fig. 3).

4.2. Constancy and domination

Analysis of the structure of constancy and dominance of malacofauna identified in flood deposits in the Ponikiewka valley allows indicating the group of species playing the most vital role in the community. The highest classes of constancy and dominance (C-V; D-IV) are achieved by two taxa: *Columella edentula* and *Columella aspera*. The next three species (*Aegopinella pura*, *Cochlicopa lubrica* and *Trochulus villosus*) reach classes C-V and D-III (Fig. 4). These snails are the most important components of this malacofauna. *Columella edentula*, *Columella aspera* and *Trochulus villosus* are taxa preferring shady or semi-open habitats with significant humidity; *Aegopinella pura* is a common forest species, and *Cochlicopa lubrica* is a snail with very high ecological tolerance, often found in many types of biotopes. The use of the Q index (geometric mean of C and D) allows arranging the community in terms of taxa that play the major role in it. All five species mentioned above belong to the common and numerous categories (C>50%, D>5%). The values of the Q index range between 34.50 and 25.60. The next group includes forms that are commonplace but few in numbers (C>50%, D<5%). This includes 17 taxa, mainly forest and mesophilous ones, with Q values between 20.60 and 6.13. The largest group (59 taxa) are rare species (C<50%, D<5%), with Q values from 7.73 to 0.39 (Table 1).

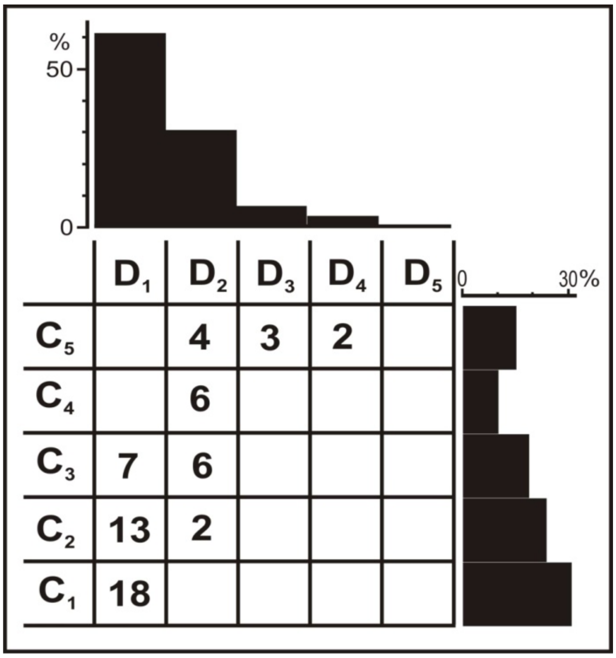

Figure 4. Constancy and domination structure of malacofauna from flood deposits from Ponikiewka stream valley. C_{1-5} - constancy classes, D_{1-5} - dominance classes

5. DISCUSSION

The results of the study of shell thanatocenosis in the Ponikiewka stream valley can be considered from various points of view. Firstly, the data collected allow characterizing the fauna of molluscs inhabiting the catchment basin. 55 species of shelled terrestrial snails were found here, which constitutes 70% of taxa inhabiting the Beskid Mały range. The occurrence of several rare species should be considered interesting: *Vestia turgida*, *Vestia gulo*, *Macrogastra tumida*, *Oxychilus daubeli* and *Helicodiscus syngleyanus* (Alexandrowicz, 2019a, b). Secondly, the data obtained provide an opportunity to compare and assess the similarities in the composition and structure of mollusc communities inhabiting particular sections of the valley with the features of thanatocenosis deposited there. This allows drawing conclusions about the transport and sedimantation mechanisms of shell material within the valley. Detailed consideration of these processes and regularities is fundamental to conducting malacological analyzes and reconstructing paleoenvironments based on subfossil fauna communities present in Quaternary fluvial deposits.

5.1. Thanatocenosis diversity

Studies of mollusc communities inhabiting river valleys, particularly flood plains, have been conducted for a long time. Many studies have been devoted to the results of these observations. However, these focused mainly on large river valleys (e.g. Foeckler, 1991; Alexandrowicz, 1997, 1999, 2000a, b, 2002, 2019a; Pišút & Čejka, 2002; Čejka et al., 2008; Ilg et al., 2009, 2012; Horsák et al., 2009; Jurkiewicz-Karnkowska, 2009, 2019; Myšák & Horsák, 2011; Juřičková et al., 2013; Horáčková et al., 2015; Čiliak et al., 2015), while the interest in smaller streams was relatively low.

An analysis of the similarity dendrogram (Fig. 5) allowed distinguishing three groups of sites. Group A consists of 15 sites, mainly representing the lower course of the Ponikiewka stream. At this section, the bottom of the valley is flat and relatively wide (usually over 100 m). It rises a maximum of 0.5 above the stream bed, so it is regularly flooded during the swellings. The bottom itself is overgrown by dense bushes of alder and willow. The valley slopes are largely transformed as a result of human activity, occupied by grassy and built-up areas (Table 2). The second group of sites (group B; 8 sites) are the flood deposits representing the central part of the valley. In this zone, the valley narrows to a width of 50-90 m. Compact alder and willow bushes and hygrophilous herbaceous plants grow on the flat bottom. The stream cuts into a depth of up to 70 cm. Dense mixed forests grow on the valley slopes, especially on the right one, and on the left bank there is a flat terrace rising up to 5 m above the riverbed level, largely built-up (Table 2). The remaining 9 sites represent group C. Most of them are located in the upper reaches of the valley, with the exception of site 5, located in the lower section and sites 18 and 19 in the central section. A common feature of all elements of group C is the presence of a narrow valley, not more than 40 m wide. Along the riverbed indented to a depth of 1 - 1.3 m there is a narrow, disappearing belt of dense alder-willow bushes. The valley slopes are steep and usually forested. A terrace up to 8-10m high stretches along the left bank (Table 2). In the highest part, the valley assumes the character of a V-shaped shear with a rocky bottom. No flood sediments were found within this section.

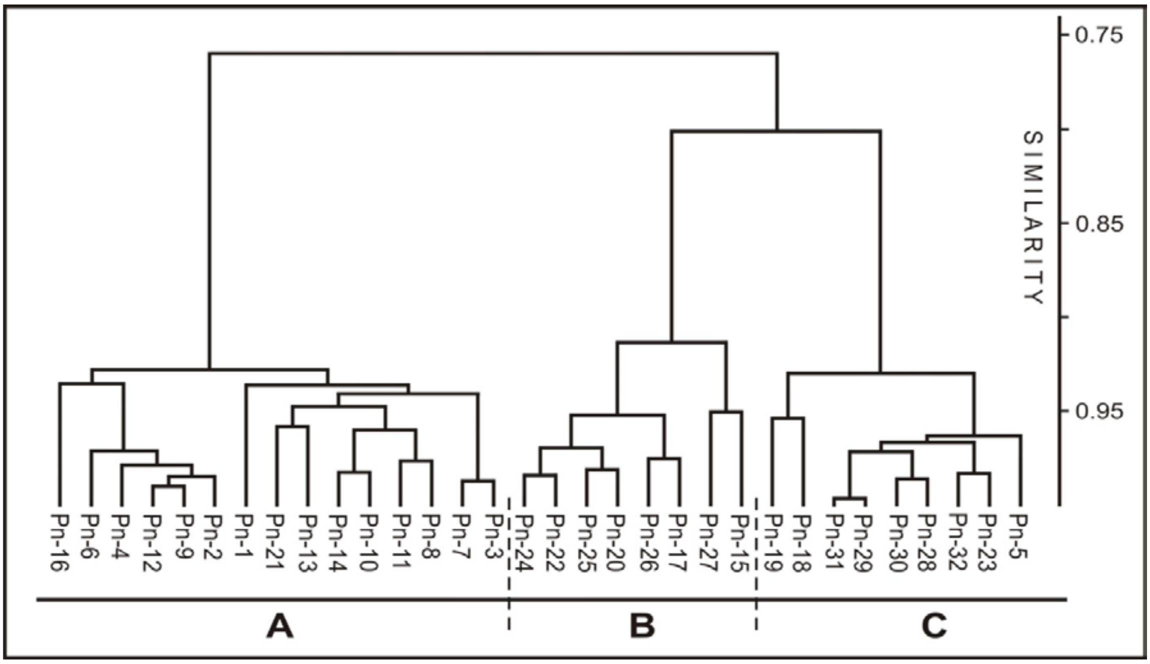

Figure 5. Cluster analysis of malacofaona flood deposits from Ponikiewka stream valley.
1-32 - research sites, A, B, C - types of molluscan fauna described in text

Table 2. Characteristic of Ponikiewka stream valley

RS	WVB [m]	PF-VB	PF-VS-R	PF-VS-L	TAX	SPC	EG [%]				
							F	O	M	H	W
1	150	bushes (*Alnus*, *Salix*)	meadows	meadows	18	371	8	0	92	0	0
2	150	bushes (*Alnus*, *Salix*)	meadows	meadows	14	370	11	1	86	2	0
3	140	bushes (*Alnus*, *Salix*)	meadows	meadows	20	136	14	10	74	2	0
4	130	bushes (*Alnus*, *Salix*)	meadows	meadows	18	196	23	0	76	0	1
5	40	forest (*Fraxinus*, *Acer*)	forest	meadows	25	325	58	1	37	4	0
6	100	bushes (*Alnus*, *Salix*)	meadows	meadows	21	152	18	3	76	3	0
7	130	bushes (*Alnus*, *Salix*)	meadows	meadows	21	104	19	9	66	6	0
8	120	bushes (*Alnus*, *Salix*)	meadows	bulidings	12	179	23	0	77	0	0
9	120	bushes (*Alnus*, *Salix*)	meadows	bulidings	23	396	23	1	73	3	0
10	110	bushes (*Alnus*, *Salix*)	meadows	bulidings	28	363	35	1	58	6	0
11	110	bushes (*Alnus*, *Salix*)	meadows	bulidings	40	977	35	1	60	3	1
12	140	bushes (*Alnus*, *Salix*)	meadows	bulidings	27	270	19	2	71	8	0
13	90	bushes (*Alnus*, *Salix*)	forest	bulidings	21	100	43	1	56	0	0
14	90	bushes (*Alnus*, *Salix*)	forest	bulidings	18	107	31	1	62	6	0
15	70	bushes (*Alnus*, *Salix*)	forest	bulidings	15	105	51	0	47	2	0
16	90	bushes (*Alnus*, *Salix*)	forest	bulidings	24	584	34	2	61	3	0
17	17	bushes (*Alnus*, *Salix*)	forest	bulidings	34	301	54	1	42	3	0
18	60	forest (*Picea*, *Abies*)	forest	forest	30	252	51	0	37	12	0
19	50	forest (*Picea*, *Abies*)	forest	forest	34	300	58	1	26	15	0
20	70	bushes (*Alnus*, *Salix*)	meadows	bulidings	27	142	48	1	45	6	0
21	90	bushes (*Alnus*, *Salix*)	meadows	bulidings	19	103	30	3	56	11	0
22	50	bushes (*Alnus*, *Salix*)	forest	bulidings	21	125	50	0	48	2	0
23	40	bushes (*Alnus*, *Salix*)	forest	bulidings	29	277	67	1	26	6	0
24	50	bushes (*Alnus*, *Salix*)	forest	bulidings	39	436	51	0	43	6	0
25	50	bushes (*Alnus*, *Salix*)	forest	bulidings	20	104	45	1	54	0	0
26	60	bushes (*Alnus*, *Salix*)	forest	bulidings	18	144	58	2	40	0	0
27	60	bushes (*Alnus*, *Salix*)	forest	bulidings	19	148	60	0	38	2	0
28	40	bushes (*Alnus*, *Salix*)	forest	bulidings	26	206	60	3	33	4	0
29	30	bushes (*Alnus*, *Salix*)	forest	bulidings	30	176	71	0	24	5	0
30	30	bushes (*Alnus*, *Salix*)	forest	bulidings	26	224	62	3	34	1	0
31	20	forest (*Picea*, *Abies*)	forest	forest	28	212	72	0	26	2	2
32	20	forest (*Picea*, *Abies*)	forest	forest	23	180	73	0	27	0	0

RS - research sites, WVB - valley bottom width, PF-VB - plant formations on valley bottom, PF-SL - plant formations on valley slopes right (R), left (L), TAX - number of species, SPC - number of specimens, E - ecological groups: F - shadow-loving O - open-country, M - mesophilous, H - hygrophilous, W - water

The main components analysis allows distinguishing the most important ecological components of thanatocenosis in different parts of the valley. The primary, differentiating groups should be considered forest species (group F_F), shade-loving species in rare forests and shrub zones (group F_B) and mesophilous taxa of medium-moist (group M_I) and humid environments (group M_H) (Fig. 6). The first two of these are the main component of mollusc communities present in sediments deposited in narrow sections of the valley, especially in its upper part. Mesophilous species preferring in humid zones, in turn, are the dominant component of thanatocenosis accumulated in wider parts of the valley (Fig. 6).

5.2. Shell material transport

The material obtained from the Ponikiewka stream valley gives the opportunity to characterize the mutual relations between living malacocoenosis, morphology and the manner of economic use of the valley, the transport processes, and the composition and structure of thanatocenosis in flood sediments. In the analyzes carried out, the dense distribution of test sites (approx. every 200 m) is particularly relevant, allowing for tracking changes in thanatocenosis over short distances and directly correlating them with the local natural environment of the valley.

Transport and deposition of shell material during the flood was described by several authors (e.g. Pip, 1988; Briggs et al., 1990; Cummins, 1994; Moulthon, 1999; Foeckler et al., 1991, 2006; Ilg et al., 2009, 2012; Jurkiewicz-Karnkowska, 2009; Poiriera et al., 2010; Alexandrowicz & Alexandrowicz, 2011; Horáčková et al., 2014, 2015; Čiliak et al., 2015). The most of such analyses were focused on valleys of

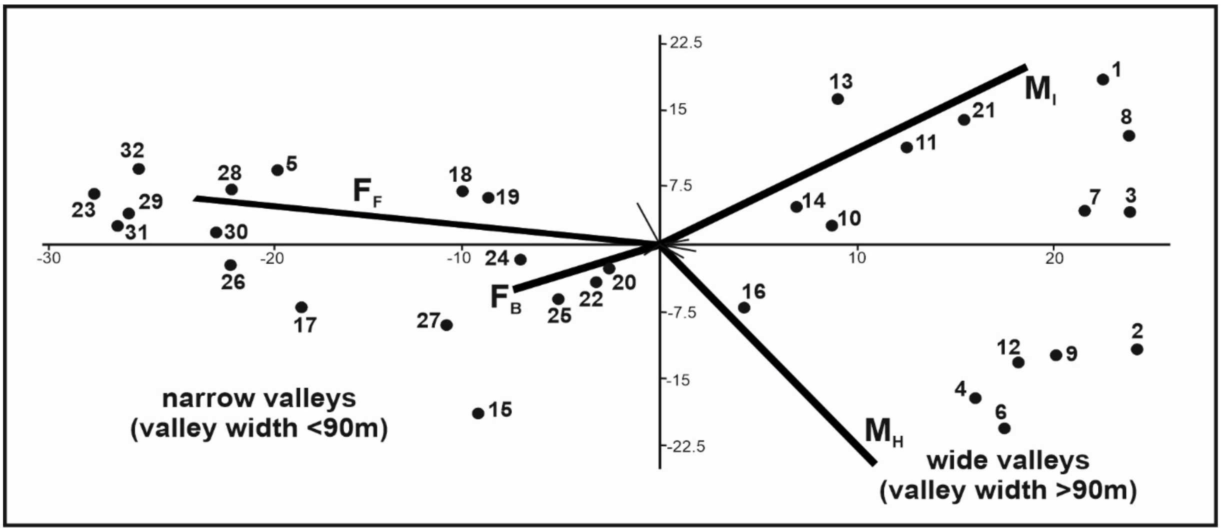

Figure 6. Principal component analysis (PCA) of malacofauna flood deposits from Ponikiewka stream valley. F_F, F_B, M_I, M_H - ecological groups of molluscs - for explanations see Table 1 and Fig. 3, 1-32 - research sites

large rivers, while the significantly smaller attention attaching to smaller streams. Differences of the morphology of valleys of large rivers and small streams are considerable and significantly effects the spatial differentiation of thanatocenosis. The course of the flood-swelling is the second important factor that impacts composition and ecological structure of death assemblages of molluscs. In large river valleys the flood wave rises relatively slowly. Simultaneously usually streamline flows dominate and mainly fine-grained material is transported. In valleys of smaller streams, particularly in mountainous areas flood-swellings are usually rapid. They are accompanied by high-energy, turbulent inflows transporting coarse-grained material. The abovementioned elements cause that the mechanisms of transport and deposition of the molluscan thanatocenosis in the valleys of large rivers run differently than in valleys of smaller streams.

Several elements can be distinguished in the cross-section of a typical river valley. The floodplain is of great relevance to the considerations of shell thanatocenosis. It is a flat area slightly raised above the level of the riverbed and flooded during the swellings. Flood sediments and mollusc shells are deposited in the floodplain. In large river valleys, the width of the floodplain can significantly exceed several hundred meters. In smaller stream valleys, especially in mountainous areas, the width of this zone usually does not exceed 200 meters, decreasing to only a few meters, particularly in the source sections. The floodplain in the Ponikiewka stream valley stretches along the riverbed over almost the entire analyzed section. Its width varies from a few to over 100 m. The bottom of the valley is usually covered with bushes with alder and willow as well as hygrophilous herbaceous plants. The features of the floodplain at individual sites are presented in Tab. 2. The floodplain is limited by clear slopes with a 5-10 m height, stretching along the entire valley. This is the edge of the terrace, probably formed during the Weichselian Glaciation. Similar terraces of this age were found in numerous Carpathian valleys (Zuchiewicz, 1986; Alexandrowicz, 1991). The terrace area is largely covered with mixed forests, anthropogenically transformed in some places and occupied by buildings or arable fields and pastures (Fig. 7).

Due to the large diversity of habitats in the valley cross-section, there are also diverse malacocoenosis. The possibility of comparing the composition and structure of thanatocenosis with the modern fauna of snails inhabiting individual sections of the valley gives an opportunity to assess the scale of shell material transport across the valley. The sites in the upper part of the valley showed a significant similarity in the structure of the ecological living fauna and shell thanatocenosis. In both cases, forest and mesophilous taxa played a dominant role (Figs. 5, 8). The greatest similarity was observed in the narrowest parts of the valley (group A; Figs. 5, 8). As the width of the floodplain increases, there is a progressive decrease in the share of fauna living on the valley slopes (mainly forest species), compensated by the increase in the relevance of mesophilous and hygrophilous taxa inhabiting the floodplain (group B, Figs 5, 8). When the valley bottom reaches a width of about 100 m, the differences between malacocenoses living on the slopes of the valley and thanatocenosis in flood sediments are already very significant (group C, Figs 5, 8). They manifest themselves both in the species composition and in the ecological structure of fauna.

The extent to which mollusc shells are transported along the valley is much more difficult to estimate than transverse transport. Empty shells usually have good buoyancy because they are filled with air or gases resulting from the decomposition of the mollusc's dead body. Shell transferability depends on two primary parameters. First of all, it is the morphology of the shell itself (e.g. shape, size, wall thickness). These elements determine the mechanical resistance and are largely responsible for the selective destruction of shells during transport (e.g. Hagan et al., 1998; Chaves-Campos et al., 2012; Lowe & Walker, 2014; Rumm et al., 2018). The second important element is the nature of the valley. The valleys of lowland rivers are characterized by a slight slope and a large width. As a result, even during periods of high water, fine-grained material is transported and the water flow is calm. Due to this, mechanical destruction of the shells takes place on a small scale and they can be moved over considerable distances. At the same time, the rise and fall of flood waters occurs relatively slowly, which allows the segregation of shell material within the flood plain (Pišút & Čejka, 2002; Čejka et al., 2008; Ilg et al., 2009, 2012; Horsák et al., 2009; Jurkiewicz-Karnkowska, 2009, 2019; Myšák & Horsák, 2011; Juřičková et al., 2013; Horáčková et al., 2015; Čiliak et al., 2015). These processes are completely different in mountain streams. Narrow valleys with prominent drops during flood periods generate high-energy turbulent flows, often transporting coarse material. As a result, due to the numerous collisions, the shell material is quickly destroyed, which significantly hinders its transport over greater distances. Usually, the rapid subsidence of the flood wave counteracts the sorting of shell material within the floodplain. The valley analyzed is an example of a mountain stream. Comparing the composition and structure of

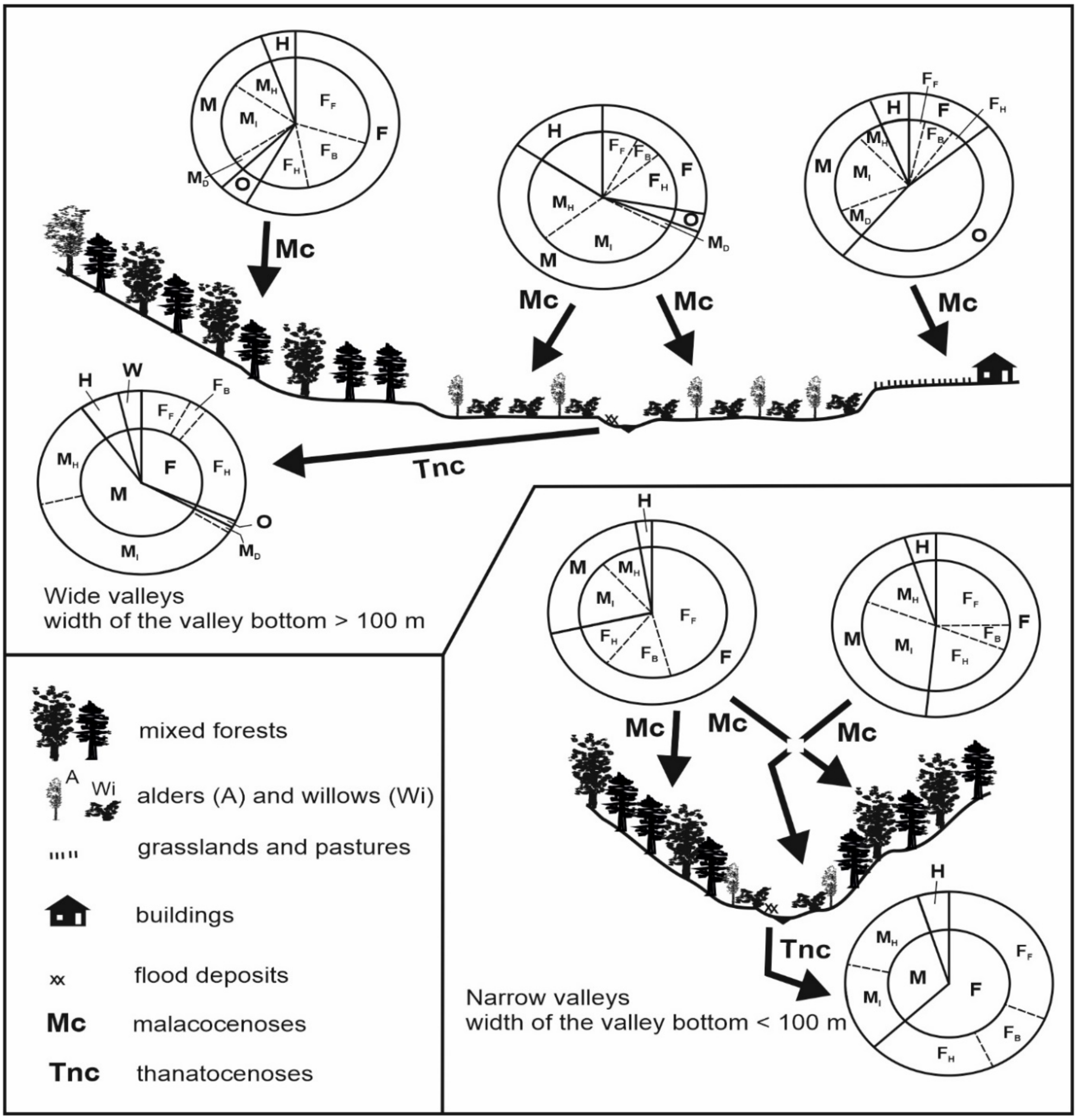

Figure 7. Spatial diversity of malacocenoises and thanatocenosis across river valley

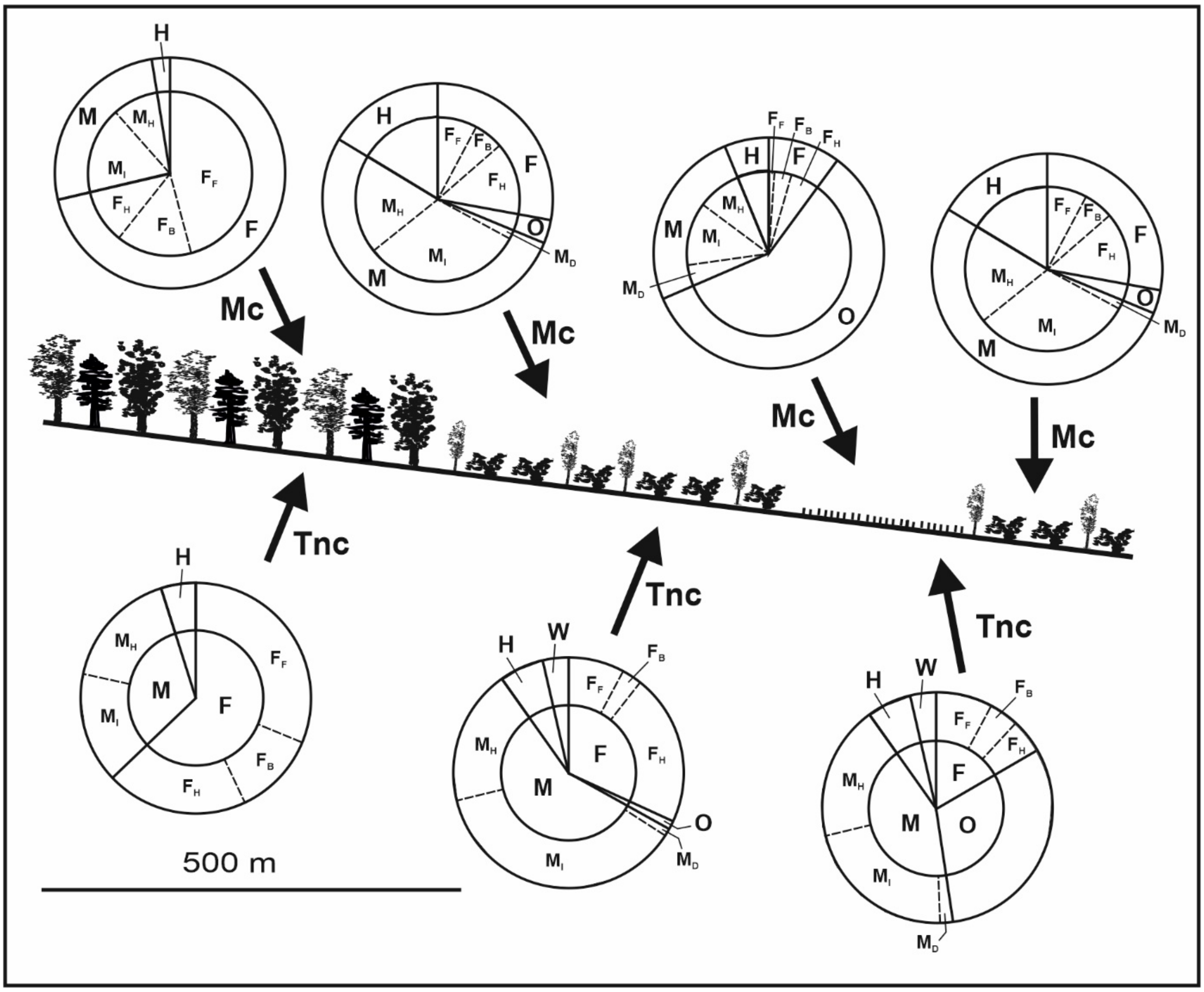

Figure 8. Spatial diversity of malacocenoises and thanatocenosis along river valley

malacocoenosis with the features of thanatocenosis deposited below, one can draw conclusions regarding the distance at which shells are transported during floods. Such observations were carried out on sections where the nature of the habitats and, consequently, the mollusc communities inhabiting them change rapidly. When comparing the features of the initial malacocenosis with the nature of the thanatocenosis deposited below, one can observe a progressive change in the species composition and structure of the community. It manifests itself mainly in the disappearance of individual taxa and in changes in the proportion between ecological groups. As they move away from the sediment supply area, thanatocenosis increasingly differ from their initial malacocoenosis. Observations carried out in selected sections of the Ponikiewka valley indicate that in the case of mountain streams, transport takes place over short distances (500 - 700 m) (Fig. 8). These observations are confirmed by the conclusions of the analysis of flood sediments carried out in other mountain stream valleys (Alexandrowicz, 1997, 1999, 2000a, b, 2002, 2019a).

6. CONCLUSIONS

Shell thanatocenosis contained in the flood deposits in rivers and streams are an extremely interesting research subject. First of all, they are used in fauna analyzes to give an image of the species diversity of molluscs within the valley and its surroundings (e.g. Foeckler, 1991; Alexandrowicz, 1997, 1999, 2000a, b, 2002, 2019a; Pišút & Čejka, 2002; Čejka et al., 2008; Ilg et al., 2009, 2012; Horsák et al., 2009; Jurkiewicz-Karnkowska, 2009, 2019; Myšák & Horsák, 2011; Juřičková et al., 2013; Horáčková et al., 2015; Čiliak et al., 2015). Such analyzes often allow finding species that are very difficult to recover during traditionally conducted searches (e.g. Pišút & Čejka, 2002; Horsák et al., 2009; Alexandrowicz, 2010). Studies of shell offsets also provide important information about the variability, diversity and characteristics of malacocoenosis inhabiting floodplains and their relationship with short-term environmental changes, often resulting from human activity (Alexandrowicz, 2002; Horáčková et al., 2014, 2015). An important aspect of the analysis of thanatocenosis is the ability to assess the degree of similarity of their composition and ecological structure to living malacocoenosis inhabiting a given area. With this, it is possible to determine the extent to which the features of the mollusc communities present in the flood sediments correspond to the features of the environment in which these sediments are deposited. The opportunity to capture these similarities and differences is of great importance for the course of paleoecological and paleoenvironmental analyzes based on malacofauna found in fluvial Quaternary sediments, and especially from the Holocene (e.g. Keen, 1990; Limondin-Lozouet & Antonie, 2001; Antonie In references list is Antoine et al., 2007, 2010; Schreve et al., 2007; Alexandrowicz & Skoczylas, 2017; White et al., 2013, 2017; Alexandrowicz, 2019c, d, 2020).

The composition and structure of the mollusc community is highly dependent on the morphological features of the valley, especially the width of the flood plain. In the case of large rivers with flat and wide flood plains, the dominant component of thanatocenosis are the species inhabiting the valley bottom itself; usually there is also a significant admixture of water taxa associated either with the river or with water reservoirs (permanent or seasonal) present on the floodplain (Čejka et al., 2008; Jurkiewicz-Karnkowska, 2008, 2009, 2019; Myšák & Horsák, 2011; Rumm et al., 2018). The share of taxa living on the slopes of the valley is usually minimal, and only increases in the places in estuaries and tributaries. In the case of narrow valleys, the share of taxa coming from their slopes is usually significant, the larger the narrower the valley is. Research in the Ponikiewka valley indicates that flood plains over 100 m wide block the delivery of shell material from slopes to the riverbed.

The transport of shell material along the river is affected by many factors. The conducted analyzes indicate that the displacement of shells in rivers with a smaller slope occurs over much longer distances. On the one hand, this is due to a calmer flow, and on the other, to the fact that mainly fine-fraction material is transported. This model of shell transport is typical for lowland rivers (Čejka et al., 2008; Myšák & Horsák, 2011). Rapid, turbulent flows dominate in mountain rivers and coarse-grained material is transported. In such conditions, the possibility of mechanical destruction of shells is very high. Therefore, they can be moved over short distances. Research carried out in the Ponikiewka valley and several other river valleys in the Carpathians (Alexandrowicz, 1997, 1999, 2000a, b, 2002, 2019a) indicates that the transport of shell material is possible up to a distance of about 1 km.

Thanatocenosis in mountain streams usually contain only a small admixture of aquatic species, in contrast to communities present in the valleys of lowland rivers, where the share of aquatic taxa can be very high.

These observations are of great importance for the interpretation of subfossil fauna communities present in fluvial Quaternary deposits. It is obvious that every taphocenosis (a set of organisms that did not undergo the process of fossilization but are covered with sediment) has undergone the stage of thanatocenosis during its development. At the same time, geological processes (e.g. transport and deposition) are and were governed by the same laws, now and in the past. Thanks to this, it can be stated that the formation of thanatocenosis took place identically during last year's flood as well as during the floods 1,000 and 10,000 years ago. Thus, studies of modern flood sediments and mollusc communities contained therein form the basis for studies of fluvial Quaternary sediments. The research presented in this study in the valley of a small mountain stream is a good example of the use of such analyzes.

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