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MOLLUSC THANATOCENOSES OF THE VISTULA RIVER IN THE SOUTHERN PART OF THE CRACOW UPLAND

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ABSTRACT: Shell-abounding thanatocenoses were collected from recent sediments of the Vistula River near Cracow formed during a few flood episodes. They are composed of 65 species of aquatic and terrestrial molluscs. Considerable differences between particular mollusc assemblages deposited on the river banks are controlled by both the intensity of flood and the changes of the fauna inhabiting the catchment area, mainly the floodplain and the river itself. Living specimens and empty shells of *Potamopyrgus antipodarum* (Gray) were found for the first time in thanatocenoses accumulated in Tyniec in 1999 and 2000.

KEY WORDS: molluscs, thanatocenoses, fluviatile sediments, migration of species, Cracow Upland, Poland

INTRODUCTION

The Vistula River crosses the southernmost part of the Cracow Upland along a relatively narrow gate, ca. 300–400 m wide and 15 km long, called the Cracow Gate. It is bordered by several rocky hills, of a height ranging from 50 to 160 m above the valley bottom. The Holocene terrace and the floodplain with traces of abandoned river meanders are developed on the bottom of the valley. In the vicinity of Tyniec, the mentioned gate (the Tyniec Gate) is the narrowest part of the whole Vistula River Valley.

The water level fluctuates considerably during the year, being the lowest at the end of the summer and increasing in the spring (March/April), mainly due to the thaw in the Carpathians. Every few years, it rises also in June/July and rarely in September, after a prolonged rainfall or heavy downpours. Each spring the river rises by about 2 meters or more, reaching the warning or even the critical level, although most of its upper course has been regulated. Once in several years, an extreme flood event takes place, as the water level rises 5–6 m and even up to 8 m above the mean value (PUNZET 1977, 1981, SOJA & MROZEK 1990, SOJA 1994, 1996). During each spring thaw, the mean water discharge in Tyniec is exceeded 3–5 times, while during heavy and extreme floods it reaches 20–40 times mean value. About fifteen such events were noted in the 20th century (BIELAŃSKI 1997, FISZER 1999), the most recent being those of 1970, 1985 and 1997.

The catchment area of the Vistula River in its upper course (upstream of the Tyniec Gate) covers 7,524 km^2. A part of the area extending in the Beskidy Mts is considerably wooded, while the other part, comprising the Upper Silesian Basin and the Cracow Upland, is to a high degree deforested. The section of the valley between Oświęcim and Cracow (50 km) is bordered by flood embankments limiting the penetration of the river over the floodplain and the lower terrace. In consequence, the material removed by water currents and deposited on the river banks originates mainly from this limited part of the valley bottom and partly also from tributaries.

Flood sediments containing plant debris, fragments of wood and branches, anthropogenic remains, as well as mollusc shells, are formed during each rise of the water level. Big accumulations of such a material are not spread evenly along the whole river course, but present in a few places, were they are repeatedly deposited. Such places are particularly suitable for studies on the structure and differentiation of thanatocenoses.

MATERIAL AND METHODS

The most interesting locality, where mollusc thanatocenoses accumulate within the Cracow Gate, is situated on the right bank of the river, at the foot of the rocky hill crowned by the old monastery in Tyniec (Fig. 1). It occurs on the external of the channel bend, in its proximal part. A few large blocks of limestone are visible just on the bank, below the rocky wall. They fell down during the earthquake in 1786 (S. W. ALEXANDROWICZ 1956). Another locality was found on the left bank of the river, at the foot of the Wawel Hill in Cracow (S. W. ALEXANDROWICZ 1988).

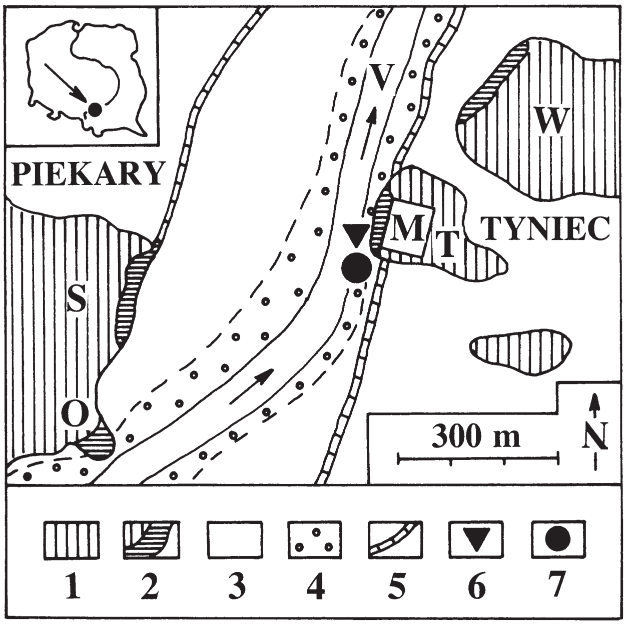

Fig. 1. Location map of the Tyniec Gate. 1 – Upper Jurassic limestones, 2 – outcrops of limestones (rocky walls and tors), 3 – Holocene terrace of the Vistula River, 4 – floodplain, 5 – flood embankments, 6 – traces of the rock-fall, 7 – thanatocenoses, T – rocky hill with the Tyniec Monastery (M), W – Winnica hill, S – Stróżnica hill, O – Okrążek rocky hill, V – Vistula River

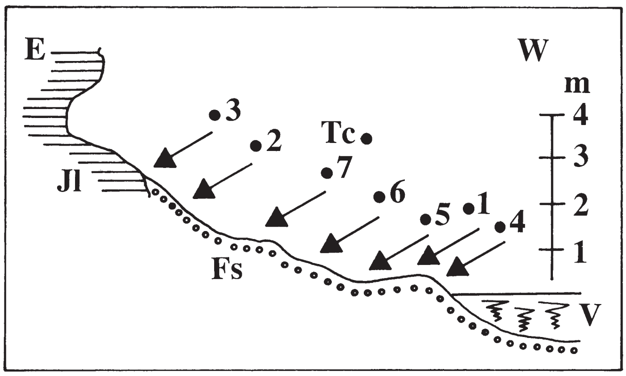

Fig. 2. Cross section through the Vistula River Valley at the foot of the Tyniec rocky hill. Jl – Upper Jurassic limestones, Fs – fluviatile sediments, Tc1-7 – thanatocenoses associated with particular flood episodes, V – Vistula River

Flood sediments were collected several times in 1982–2000, as single or twin samples (3–4 kg) and as series of samples (5 samples, 1–2 kg each). They derive from the following flood events (Fig. 2):

* Increased water level after the spring thaw in 1982 – thanatocenosis deposited about 50 cm above the water level, sandy sediment enriched with plant remains and mollusc shells (single sample, Tyniec – Tc-1).
* Flood in early summer 1985 – thanatocenosis composed of fragments of wood and branches with numerous mollusc shells, deposited about 2 m above the water level, within a clump of bushes (two samples, Wawel Hill – Tc-2).
* Extreme flood event in July 1997 – fragments of wood and branches, plant debris, anthropogenic material and mollusc shells accumulated 2.5 m above the water level, just below the rocky wall of the hill in Tyniec (two samples – Tc-3).
* Water level increased as a result of rainfall in June 1999 – plant debris rich in mollusc shells, deposited along external side of a natural levee, 30–40 cm above the water level (five samples, Tyniec – Tc-4).
* Slight increase in water level caused by a warming during late winter 2000 (end of February) – a patch of flood sediment accumulated within a small depression behind a natural levee, 20–30 cm above the water level (five samples, Tyniec – Tc-5).
* Water level increased after the spring thaw in March 2000 – accumulation of plant debris with mollusc shells, situated below the escarpment of a low terrace, about 70 cm above the water level (one sample, Tyniec – Tc-6).
* Overbank flow at the end of March 2000 – a small patch of flood sediment composed of plant debris with mollusc shells, deposited on the surface of a low terrace, 100–120 cm above the water level (one sample, Tyniec – Tc-7).

The collected material was dried, sifted and washed in order to pick out all mollusc shells and their identifiable fragments. The following standard methods of analysis described earlier (S. W. ALEXANDROWICZ 1987, 1999) were used:

– logarithmic scale to present the number of specimens representing each taxon;
– malacospectra of species and specimens (MSS, MSI) based on five ecological groups according to the scheme defined by S. W. ALEXANDROWICZ (1992);
– indices of constancy and dominance (C–D) characterizing the structure of communities in series of samples, supplemented by normalized indices C_i and D_i;
– TDA diversity index of assemblages;
– sequence diagram illustrating the proportion of selected species in thanatocenoses connected with consecutive floods;
– two indices calculated according to the general differential formula WDI = (A–B)/(A+B) land snails – water molluscs (L–W) and higrophile snails – other land snails (H–C).

Two main components of thanatocenoses – water molluscs and land snails – should be regarded and interpreted separately because they are related to different parts of the environment. The former originate mostly from the river and partly from water bodies distributed within the floodplain, while the latter are shells washed from the valley bottom limited by flood embankments or surrounding slopes (W. P. ALEXANDROWICZ 1999). Such a method of interpretation was used also in malacological analysis of quaternary deposits (S. W. ALEXANDROWICZ 1993).

RESULTS

The described mollusc assemblages comprise about 3,500 specimens representing 65 taxa: 44 species of land snails, 17 species of water molluscs, 3 species of bivalves and slug shells (Table 1). Shells of three species are particularly abundant, reaching more than 10% of all specimens. These are: *Physa acuta* (15%), *Succinea putris* (13%) and *Zonitoides nitidus* (11%). Two species of *Carychium*, *Cochlicopa lubrica* and *Vallonia pulchella* are other land snails represented by a considerable number of shells; the same is true of water snails: *Bithynia tentaculata* and *Lymnaea peregra* (4–7% of specimens).

The thanatocenoses accumulated by particular flood episodes differ from each other to various degree. They contain 23–44 species and 277–1,095 specimens each, and are characterized by different values of the TDA index, ranging between 0.451 and 0.884 (Fig. 3). The correlation between the number of species (Nt), the number of specimens (Ns) and the TDI index is statistically insignificant. The quantitative relations: land snails – water molluscs (L–W) and higrophile species – other land snails (H–C) are very much variable (Table 2).

Four types of fauna (A–D) can be distinguished according to the malacological spectra MSS–MSI and indices L–W – C–H (Fig. 4, Table 2).

Type A – thanatocenosis Tc-1 is characterized by the dominance of water molluscs expressed by the L–W index = -0.67. They constitute 50% of species and more then 80% of specimens. *Physa acuta*, *Ancylus fluviatilis* and *Lymnaea peregra* are the main components of this assemblage, reaching 50%, 12% and 11% of shells, respectively. The index H–C = 0.62 reflects the relatively high percentage of higrophile snails (*Succinea putris*, *Carychium minimum*). The number of taxa is relatively low, like the value of TDA index.

Type B – thanatocenosis Tc-2 is more diversified, but shells of the water snail *Physa acuta* prevail again. The percentage of land and water molluscs is approximately equalized (L–W = -0.08) and the number of higrophile snails decreases in relation to specimens representing ecological groups M, F and O (H–C = -0.29). Shells of *Zonitoides nitidus*, *Cochlicopa lubrica* and *Alinda biplicata* are fairly numerous.

Type C – thanatocenoses Tc-3 and Tc-4 contain a considerable proportion of mesophile snails (more then 35% specimens), such as *Carychium tridentatum*, *Cochlicopa lubrica*, *Nesovitrea hammonis* and *Trichia villosula*. Shade-loving snails are an important component of the assemblage, reaching more then 25% of species. The high value of the L–W index and the low value of the H–C index are typical features of this type of thanatocenosis.

Type D – thanatocenoses Tc-5, Tc-6 and Tc-7 include numerous shells of higrophile snails (*Succinea putris*, *Zonitoides nitidus*, *Carychium minimum*) which constitute about half of all specimens (45–50%), while the proportion of mesophile snails and water molluscs is relatively low. Accordingly, values of the L–W index and of the H–C index are 0.62 – 0.64 and 0.15 – 0.24, respectively.

The C–D structure of the assemblages has been studied in two thanatocenoses collected as series of samples. In one (Tc-4) *Carychium tridentatum,* as the most important component, belongs to class C–D = 5–4 and six species – to class C–D = 5–3, while seven species are accessory components (C–D = 1–1). The other thanatocenosis (Tc-5) includes two species belonging to classes C–D = 5–5 and 5–4 (*Succinea putris* and *Zonitoides nitidus*), four species of class C–D = 5–3 and fourteen are accessory elements (C–D = 1–1). Normalized values of constancy and dominance (C_i and D_i) are nearly the same in both the mentioned assemblages (Table 3).

The number and proportions of shells representing particular species of land and water snails, de-

Table 1. Mollusc assemblages in the thanatocenoses of the Vistula River. E – ecological groups of molluscs: F – shade-loving snails, O – open-country species, M – mesophile snails, H – higrophile snails, W – water molluscs; 1–7 – numbers of samples, c-d-n – indices of constancy – dominance (1–5) and number of specimens (I–V). Number of specimens: I – 1–3, II – 4–9, III – 10–31, IV – 32–99, V – 100–316 (S. W. ALEXANDROWICZ 1987)

E	T A X O N	Sample										
		1	2	3	4 c	4 d	4 n	5 c	5 d	5 n	6	7
F	*Vertigo pusilla* O. F. Müller				2	1		1	1	I		
F	*Ena montana* (Draparnaud)				1	1	I					
F	*Discus rotundatus* (O. F. Müller)			I	1	1	I	1	1	I	I	I
F	*Vitrea diaphana* (Studer)				2	1	I					
F	*Vitrea crystallina* (O. F. Müller)		II	I	4	2	III	3	1	II		
F	*Oxychilus glaber* (Rossmässler)			I								
F	*Macrogastra ventricosa* (Draparnaud)				1	1	I	4	1	II		
F	*Macrogastra plicatula* (Draparnaud)							1	1	I		
F	*Alinda biplicata* (Montagu)		III	I	3	1	II	1	1	I		
F	*Bradybaena fruticum* (O. F. Müller)	I	II	III	2	1	I	4	1	II	II	II
F	*Perforatella bidentata* (Gmelin)	I	II	II	4	2	II	1	1	I	I	I
F	*Perforatella incarnata* (O. F. Müller)		II	II								
F	*Perforatella vicina* (Rossmässler)				2	1	I					
F	*Perforatella umbrosa* (Pfeiffer)				1	1	I					
F	*Arianta arbustorum* (Linnaeus)		II	I	2	1	II					
F	*Cepaea nemoralis* (Linnaeus)		I									
F	*Helix pomatia* Linnaeus		II	II	3	1	I	1	1	I		
O	*Cochlicopa lubricella* (Porro)		I									
O	*Truncatellina cylindrica* (Férussac)			I	2	1	I	1	1	I		
O	*Vertigo pygmaea* (Draparnaud)			II	2	1	I	4	2	III		I
O	*Pupilla muscorum* (Linnaeus)		II	I								
O	*Vallonia pulchella* (O. F. Müller)	II	III	IV	5	3	IV	5	2	III	III	III
O	*Vallonia costata* (O. F. Müller)		II	II							I	I
O	*Cecilioides acicula* (O. F. Müller)			II	3	1	II	1	1	I		
O	*Helicella obvia* (Menke)		I									
M	*Carychium tridentatum* (Risso)	I	II	II	5	4	IV	5	2	IV	III	III
M	*Succinea oblonga* Draparnaud	I	I	I	3	2	II	4	2	III	II	II
M	*Cochlicopa lubrica* (O. F. Müller)	II	IVI	IV	5	3	IV	5	3	IV	III	III
M	*Columella edentula* (Draparnaud)			II	2	2	II	4	2	III	II	III
M	*Punctum pygmaeum* (Draparnaud)				2	2	II	3	1	III	I	
M	*Vitrina pellucida* (O. F. Müller)			II	2	1	I					
M	*Vitrea contracta* (Westerlund)		II	I	5	3	IV	5	2	III	II	III
M	*Nesovitrea hammonis* (Ström)		I	II	5	2	III	3	2	III		III
M	*Oxychilus draparnaudi* (Beck)		II									
M	*Limacidae*		I									
M	*Euconulus fulvus* (O. F. Müller)				3	2	III	5	2	IV	II	II
M	*Clausilia dubia* Draparnaud				5	1	II	5	1	I	I	I
M	*Laciniaria plicata* (Draparnaud)			I	4	2	III	3	1	I	I	
M	*Trichia hispida* (Linnaeus)	I						1	1	I		I
M	*Trichia villosula* (Rossmässler)	I	III	III	5	2	III	5	2	III	II	II
H	*Carychium minimum* O. F. Müller	III		II	4	1	II	5	3	IV	II	IV
H	*Succinea putris* (Linnaeus)	III	III	III	5	3	IV	5	5	V	IV	IV

E	T A X O N	Sample										
		1	2	3	4 c	4 d	4 n	5 c	5 d	5 n	6	7
H	*Vertigo antivertigo* (Draparnaud)				1	1	I	1	1	I	I	I
H	*Zonitoides nitidus* (O. F. Müller)	II	IV	III	5	3	IV	5	4	V	IV	IV
H	*Perforatella rubiginosa* (Schmidt)	I	III	II	5	2	II	5	2	III	III	III
W	*Viviparus viviparus* (Linnaeus)		I									
W	*Valvata cristata* O. F. Müller	I			2	1	I				I	I
W	*Potamopyrgus antipodarum* (Gray)				5	2	III	5	2	III	I	II
W	*Bithynia tentaculata* (Linnaeus)	II	II	II	5	3	IV	5	3	IV	III	III
W	*Physa fontinalis* (Linnaeus)	I										
W	*Physa acuta* Draparnaud	V	V	IV	5	2	III	5	3	IV	III	III
W	*Lymnaea peregra* (O. F. Müller)	IV	III	III	4	2	II	4	2	III	II	III
W	*Lymnaea truncatula* (O. F. Müller)	I	II		2	2	II	4	2	III	II	III
W	*Planorbis planorbis* (Linnaeus)		I	I	1	1	I	2	1	I		
W	*Anisus leucostomus* (Millet)		I		2	2	II	5	2	III	I	I
W	*Anisus vorticulus* (Troschel)		II					4	1	II		I
W	*Anisus contortus* (Linnaeus)										I	
W	*Gyraulus albus* (O. F. Müller)		I					1	1	I	I	I
W	*Segmentina nitida* (O. F. Müller)							1	1	I		
W	*Planorbarius corneus* (Linnaeus)	I	III	I				1	1	I		
W	*Ancylus fluviatilis* O. F. Müller	IV	III	I								
W	*Acroloxus lacustris* (Linnaeus)	III										
W	*Sphaerium corneum* (Linnaeus)	II	II	II	2	1	I					
W	*Pisidium subtruncatum* Malm	I			1	1	I	1	1	I		
W	*Pisidium casertanum* (Poli)							2	1	I		

posited on the river banks of the Tyniec Gate by overbank flows during the last nineteen years, change markedly (Fig. 5). One of the most important components of the water fauna – *Physa acuta* – dominates in assemblages accumulated in 1982 and 1985 (67 and 70% of water molluscs), then its percentage decreases (54% in 1997) reaching a relatively stabilized value in the last two years (23–30%). On the contrary, specimens of *Bithynia tentaculata* considerably increase in number during the mentioned period, like those of *Lymnaea truncatula*. A stable proportion characterizes another species of *Lymnaea* (*L. peregra*), whereas

Table 2. Selected indices characterizing thanatocenoses of the Vitula River in the Cracow Gate. Nt – number of species, Ns – number of specimens, TDA – index of diversity, L–W – relation between land- and water molluscs, H–D – relation between higrophile species and other land snails

	Tc-1	Tc-2	Tc-3	Tc-4	Tc-5	Tc-6	Tc-7
Nt	23	36	35	44	43	29	30
Ns	488	476	337	535	1095	277	378
TDA	0.451	0.695	0.832	0.884	0.801	0.798	0.840
L-W	-0.67	-0.08	0.60	0.55	0.62	0.64	0.62
H-D	0.62	-0.29	-0.79	-0.55	0.17	0.15	0.24

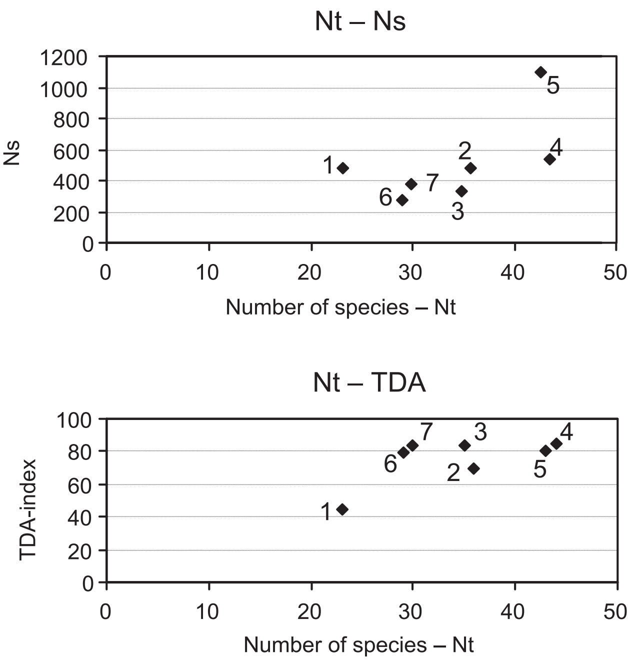

Fig. 3. Relations between the number of species (Nt), number of specimens (Ns) and diversity index (TDA) in the thanatocenoses (1–7)

Table 3. Constancy – dominance (C–D) structure of two selected thanatocenoses; C_i and D_i – normalized indices of constancy and dominance

Tc-4	D1	D2	D3	D4	D5
C5	1	5	6	1	
C4	1	4			
C3	3	2			
C2	10	4			
C1	7				

C_i = 0.52 D_i = 0.17

Tc-5	D1	D2	D3	D4	D5
C5	2	8	4	1	1
C4	2	5			
C3	3	1			
C2	2				
C1	14				

C_i = 0.55 D_i = 0.17

Ancylus fluviatilis occurs in assemblages associated with floods of 1982 and 1985. Empty shells and a few living specimens of *Potamopyrgus antipodarum* (= *P. jenkinsi*) were found in thanatocenoses deposited by the summer flood in June 1999 and by spring thaws in the late winter and early spring of 2000. A few of them have a spiral keel on the younger whorls, below the suture (forma *carinata* Marshall, forma *aculeata* Overton). The mean size of shells is 5.05 ± 0,07 mm × 2.76 ± 0.06 mm. It corresponds to those described from other populations (Fretter & Graham 1978, Falniowski 1987).

Shells of the higrophile snail *Succinea putris* are particularly numerous in thanatocenoses formed in 1982 (23% land snails) and in 2000 (27–29% land snails). The distribution of the other higrophile snail – *Zonitoides nitidus* is similar, while specimens of *Cochlicopa lubrica* and *Vallonia pulchella* are relatively

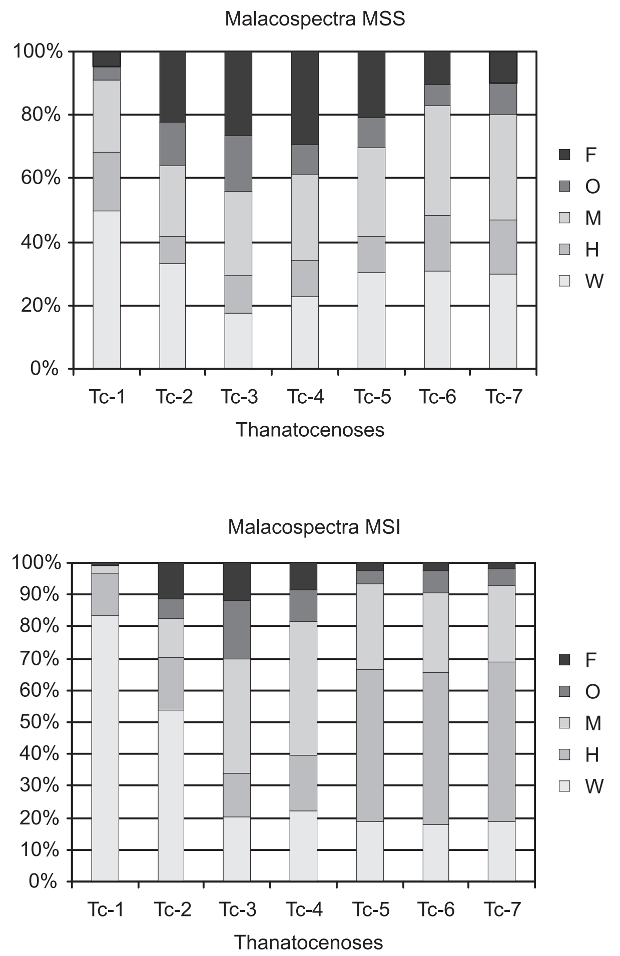

Fig. 4. Malacological spectra of species (MSS) and of specimens (MSI) of thanatocenoses Tc-1 – Tc-7. Ecological groups of molluscs: F – woodland snails, O – open-country snails, M – mesophile species, H – higrophile snails, W – water molluscs

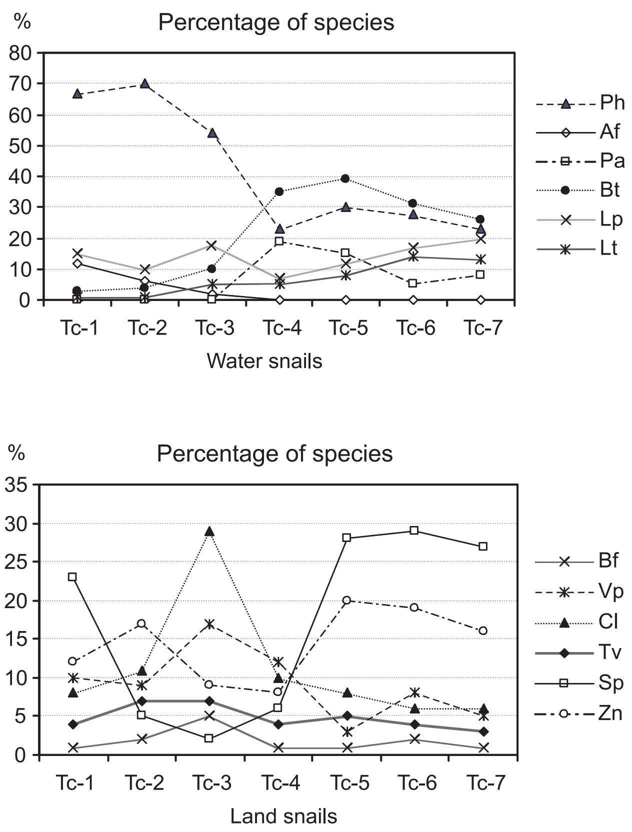

Fig. 5. Proportion of selected species in relation to the number of land snails and of water molluscs. Tc-1 – Tc-7 – thanatocenoses, Ph – *Physa acuta*, Af – *Ancylus fluviatilis*, Pa – *Potamopyrgus antipodarum*, Bt – *Bithynia tentaculata*, Lp – *Lymnaea peregra*, Lt – *Lymnaea truncatula*, Bf – *Bradybaena fruticum*, Vp – *Vallonia pulchella*, Cl – *Cochlicopa lubrica*, Tv – *Trichia villosula*, Sp – *Succinea putris*, Zn – *Zonitoides nitidus*

numerous in thanatocenoses deposited in 1997 and 1999, reaching 10–29% and 12–17%, respectively (Fig. 5). The remaining species are subordinate components of the assemblages but some of them may locally exceed 5% (*Carychium tridentatum*, *C. minimum*, *Vitrea contracta*, *Alinda biplicata*, *Bradybaena fruticum*, *Trichia villosula*, *Perforatella bidentata*).

CONCLUSIONS

Thanatocenoses deposited in fluviatile sedimentary environment are related to the habitats occurring within the catchment area, to the fauna living in the river itself and in the water bodies located on the floodplain, as well as to the flood season, to the raised water level and the flow dynamics. Shell accumulations deposited on river banks after the spring thaw and the summer rainfall or downpour clearly differ from each other (KLEMM 1973). Floods penetrating the valley bottom in both the mentioned seasons of the year reach other habitats distributed on the valley bottom. Empty shells and living specimens of molluscs are therefore washed from different parts of the floodplain and river terraces (S. W. ALEXANDROWICZ 1999, W. P. ALEXANDROWICZ 1999). At such times, thanatocenoses may be enriched with particular snail species which then become their dominant components (KOTULA 1882). There are also substantial differences between thanatocenoses accumulated by big lowland rivers, by short mountain/upland streams and on lake shores (CLESSIN 1908, GEYER 1908, VOHLAND 1910, WASMUND 1926, ZEISSLER 1963, S. W. ALEXANDROWICZ 1999, S. W. ALEXANDROWICZ & FLOREK 1999).

Changes in environmental conditions of the Vistula River Valley, controlled both by the intensity of pollution and heating of water by power plants and factories, may contribute to these differences. *Physa acuta,* recorded from Tyniec for the first time by ZIĘBA & ZAĆWILICHOWSKA (1966), became very abundant in the eighties, then its number gradually decreased during the next few years (S. W. ALEXANDROWICZ 1986, 1988) and stabilized in the late nineties. This reflects the impoverishment of its population living in the Vistula River upstream of Tyniec. The changes in the distribution of *Ancylus fluviatilis* are similar; its shells occur in thanatocenoses up to the summer 1997. On the other hand, the population of *Bithynia tentaculata* becomes gradually richer, as the number of its specimens in the thanatocenoses has increased about ten times since 1982.

The occurrence of *Potamopyrgus antipodarum,* noted in Tyniec for the first time in the summer 1999, is associated with the local spreading of its populations. In Poland, the invasion of this species has been progressing since the beginning of this century, starting from the Gulf of Szczecin (1908) and the Gulf of Gdańsk (ca. 1920). About ten years later, the snail was recorded from Pomerania, spreading gradually eastward and southward, to reach the Wielkopolska Lowland in the late seventies, and the Mazury Lakeland in the nineties (URBAŃSKI 1935, 1938, EHRMANN 1956, JACKIEWICZ 1973, PIECHOCKI 1979, DROZDOWSKI 1979, BRZEZIŃSKI 1999). The rapid expansion of *Potamopyrgus* in Upper Silesia began in 1986 (STRZELEC 1993). During seven years (1989–1993), more than twenty water bodies and streams have been invaded by this snail, including the localities within the Vistula basin near Pszczyna and Dąbrowa Górnicza (STRZELEC & KRODKIEWSKA 1994, STRZELEC & JEŻ 1998). Rising of water level and floods favoured its migration along the Vistula Valley up to the Cracow Gate.

Differences between thanatocenoses accumulated by spring-floods and summer-floods are expressed mainly in quantitative relations between particular ecological groups of land snails. The assemblages deposited in early spring are characterized by positive values of the H–D index and by the dominance of two higrophile species: *Succinea putris* and *Zonitoides nitidus.* Other assemblages have negative values of this index while open-country, mesophile and even woodland snails are their important components. A few species occur in considerable numbers there: *Vallonia pulchella*, *Cochlicopa lubrica*, *Carychium minimum*, *C. tridentatum*, *Succinea putris*, *S. oblonga* and *Zonitoides nitidus.* The similarity between thanatocenoses deposited by the same summer flood (1997) in the Vistula River Valley and in the Przemsza River Valley (W. P. ALEXANDROWICZ 1999) is all the more noteworthy, since the two rivers have very different discharge.

The transport of the shell material by a river or a stream during the flood is usually short-distance and was estimated as not exceeding 30 km, and mostly limited to a few kilometers (WASMUND 1926, S. W. ALEXANDROWICZ 1997, 1998, W. P. ALEXANDROWICZ 1999). In dry valleys, washed once in a while during heavy rainfalls, as well as in small stream valleys, the transported shells are deposited quickly, compared to large rivers, where they are moved over a relatively long distance (KLEMM 1973, S. W. ALEXANDROWICZ 1999). On the other hand, the mode of displacement depends also on the the discharge of the stream/river during the spring or the summer flow.

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