



THE MALACOFUNA OF THE CASTLE RUINS IN MELSZTYN NEAR TARNÓW (ROŻNÓW FOOTHILLS, SOUTHERN POLAND)

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ABSTRACT: The castle ruins in Melsztyn are situated in the Dunajec River valley between Tarnów and Zakliczyn. The castle hill holds a rich malacofauna. The presence of numerous open-country, calciphile forms is a unique feature of this assemblage. Its composition and structure seem to be directly related to anthropogenic environmental changes caused by the construction and maintenance of the castle. The fauna from Melsztyn includes many species which are very rare in the Beskidy Mountains, such as *Helicella obvia*, *Cochlicopa lubricella*, *Euomphalia strigella* and, particularly, *Truncatellina cylindrica*, which is the dominant component of the assemblage. These species seem to be anthropogenic immigrants. The Melsztyn castle ruins, like other castle remnants in the Beskidy Mts, constitute a refugium for terrestrial faunas, especially calciphilous, open-country species. The environmental, scenic and historical value of the castle hill fully entitles the site to be classified as a legally protected nature-landscape complex.

KEY WORDS: molluscan assemblage, castle ruins, anthropogenic pressure, Rożnów Foothills, southern Poland

INTRODUCTION

The Beskidy Mts with their foothills are part of the region known as the Outer Carpathians. They are mainly composed of a monotonous series of conglomerates, sandstones and shales, which constitute a rock formation termed flysh. Such formations do not usually contain calcium carbonate, or it occurs merely as cement for the sandstones. Consequently, the malacofauna of the Outer Carpathians (Flysh Carpathians) is relatively poor and not very diverse, compared to the neighbouring areas which abound in carbonate rocks (Pieniny Mts, Cracow-Częstochowa Upland). Localities with a significantly increased calcium level in the substratum are thus particularly interesting and include only a few limestone zones such as Cieszyn Silesia, and the environs of Żywiec and Andrychów. Castle ruins represent a very attractive object of malacological studies, since they offer favourable habitat conditions for mollusc faunas of exceptional composition and structure (ALEXANDROWICZ 1995). Sandstone, used as building material, was nearly al-

ways acquired from the immediate neighbourhood of the castle. Blocks of sandstone were bonded with calcareous mortar. As a result, specific, highly artificial and anthropogenic habitats with a substantially elevated calcium level were formed within the castle walls. Another important factor was deforestation accompanying the construction of the buildings, and resulting in natural forest communities being replaced by open habitats. This fact is particularly important in the areas which are poor in carbonate rocks (limestones, marls, dolomites). Owing to a higher calcium content in the substratum, castle ruins provide favourable living conditions for petrophilous and calciphilous species of plants and animals, including molluscs. This makes them natural refugia for land snail assemblages (ALEXANDROWICZ 1995, JUŘIČKOVÁ & KUČERA 2005a, b). The expansion of housing estates and the associated development of transport, involving especially agricultural products, which created favourable conditions for migration of species

from other areas, have also played a significant role. Finally, the increased calcium level facilitates preservation of empty shells for relatively long periods of time. It leads to enrichment of shell thanatocoenoses developing within the ruins.

Molluscan assemblages inhabiting castle ruins have so far been described in a number of locations, mostly in Germany (e.g. ZEISSLER 1969, 1975, 1980, MÜNZIG 1977, MATZKE 1985, HALDEMANN 1990, BÖSSNECK 1996), the Czech Republic (e.g. LOŽEK 1959, 1975, JUŘIČKOVA 2005, JUŘIČKOVA & KUČERA 2005a, b), Austria (JAUERNIG 1995) and Great Britain (ROUSE & EVANS 1994). Such studies have also been carried out in Poland in the Sudetes (WIKTOR 1959, POKRYSZKO 1984), in the Cracow-Częstochowa Upland (URBAŃSKI 1973, ALEXANDROWICZ 1988) and in the Carpathians (ALEXANDROWICZ 1995). The

above-mentioned authors emphasised the specificity of the castle ruin fauna. This specificity results from anthropogenic pressure on the one hand, and from the formation of artificial habitats, which often create very favourable conditions for the development of malacocoenoses, on the other.

There are more than ten castles of various sizes within the area of the Flysh Carpathians. Most of them were built in the Middle Ages in order to protect trade routes that ran across the range of the Beskidy Mts from the south to the north. Therefore, they were located mainly along the valleys of major rivers, namely the Raba, Dunajec, Wisłok and San.

The main objective of this study is a detailed faunistic analysis of the molluscan assemblages of the castle hill in Melsztyn, with particular focus on the species that can be regarded as anthropogenic migrants.

STUDY AREA

The castle in Melsztyn is a large fortress situated partly on a rocky hill rising approximately 40 m above the level of the Dunajec River. It is sited between Tarnów and Zakliczyn in the Rożnów Foothills and it used to be the northernmost stronghold defending the

route along the Dunajec River valley (Fig. 1). The castle was built in the 14th century and was later expanded several times. In the late 18th century it was severely damaged by a great fire. The present ruins include the remains of buildings, towers and defensive

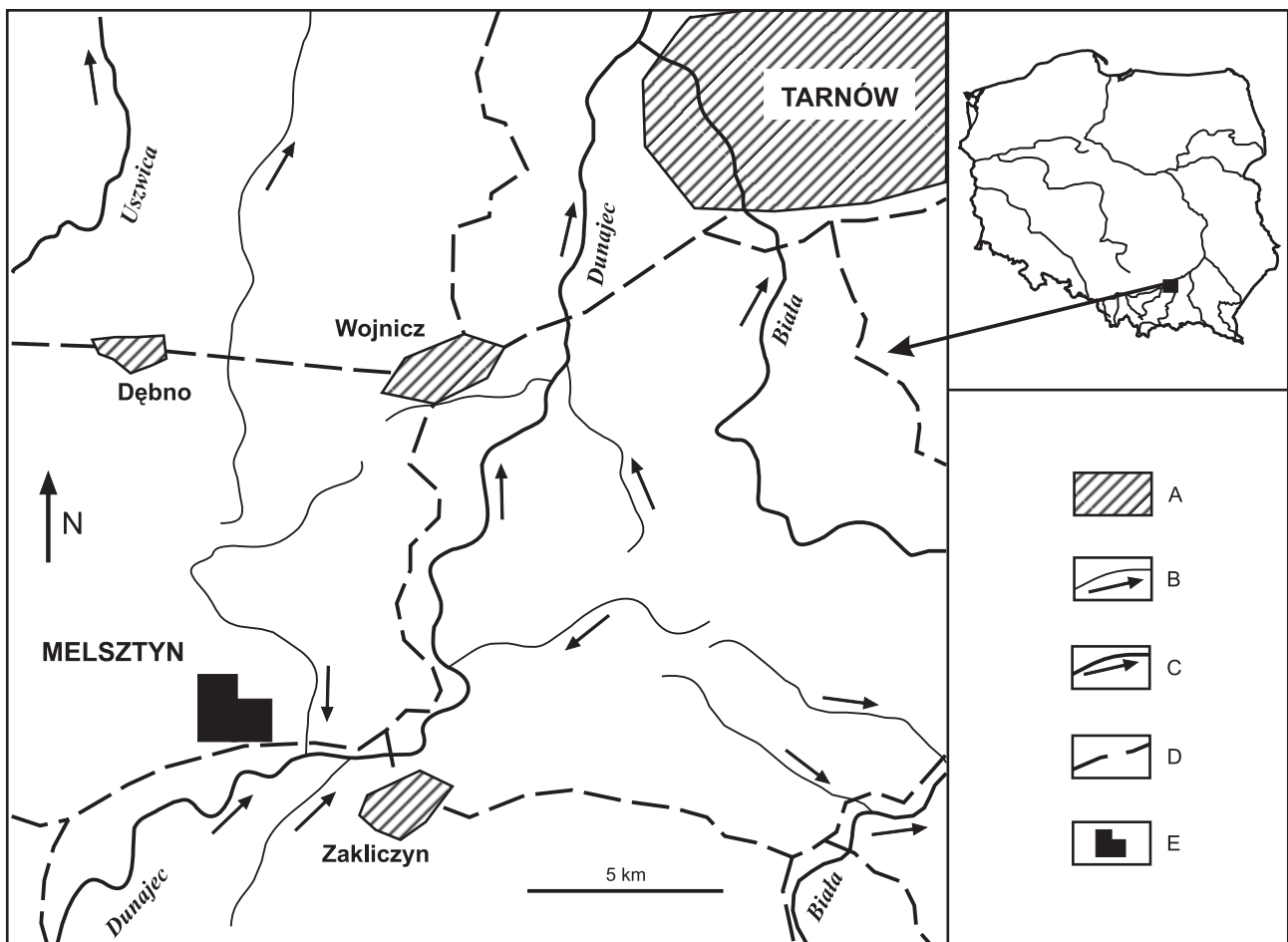


Fig. 1. Location of the castle in Melsztyn: A – towns and villages, B – streams, C – rivers, D – main roads, E – castle in Melsztyn

walls (Fig. 2). The castle hill in Melsztyn is made of coarse-grained, thick-bed sandstones and conglomerates of low calcium content (Ciężkowice Beds) (CIESZKOWSKI et al. 2010). The hill is currently overgrown by natural, sparse mixed coniferous or deciduous forests with *Pinus*, *Acer*, *Carpinus* and *Fraxinus* as dominant taxa and a shrub-dominated understorey

MATERIAL AND METHODS

The samples analysed here were taken in March 2010 in 10 sites within the ruins (Fig. 2) using the method described by DZIĘCZKOWSKI (1972), ALEXANDROWICZ (1987) and ALEXANDROWICZ & ALEXANDROWICZ (2011). Individual samples (Me-1 – Me-10; Fig. 2) were collected from the plots demarcated within the ruins. Each sample represented a 0.5 × 0.5 m square. The material was extracted to the depth of 5 cm. After drying, all identifiable specimens were selected. Due to the season when the samples were collected (early spring), the analysed material consisted mainly of empty shells (ca. 95%) and contained very few live specimens (ca. 5%). The species were identified and the specimens of each taxon were counted.

The species' assignment to the ecological groups followed LOŻEK (1964), ALEXANDROWICZ 1987 and ALEXANDROWICZ & ALEXANDROWICZ (2011). Constancy (C) and dominance (D) were calculated according to ALEXANDROWICZ (1987) and ALEXANDROWICZ & ALEXANDROWICZ (2011). The C-D structure was established for the entire analysed material, thereby making possible distinction of the components of the assemblage. The diversity of the fauna according to its structural characteristics was described using synthetic indices: constancy index (C_i) and dominance index (D_i) (ALEXANDROWICZ & ALEXANDROWICZ 2011). Determination of the dominant and accessory species in the collection was based on the Q index (geometric mean of C and D) (ALEXANDROWICZ 1987, ALEXANDROWICZ &

with *Corylus*, *Sorbus* and *Sambucus* and with grass associations (ALEXANDROWICZ 1995). Preliminary studies of the castle ruins in Melsztyn were conducted by ALEXANDROWICZ (1995) who identified 22 snail species inhabiting the ruins. Later studies yielded more material and revealed the presence of several new taxa.

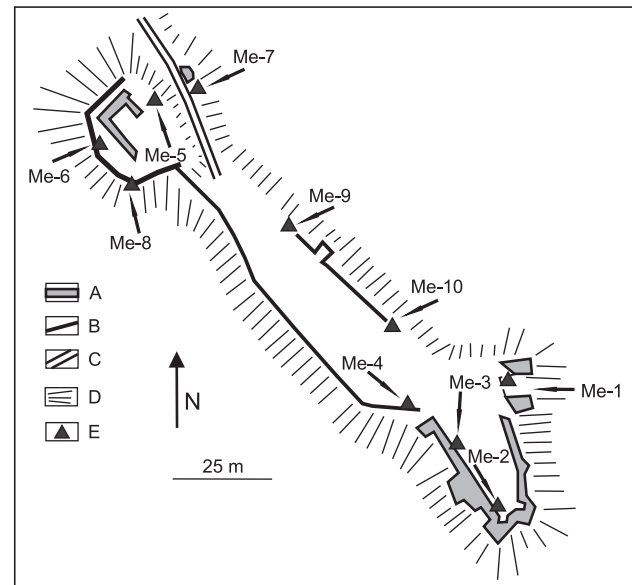


Fig. 2. Map of the castle in Melsztyn: A – well preserved ruins of buildings, B – castle wall, C – road, D – slopes, E – samples (Me-1 – Me-10)

ALEXANDROWICZ 2011). The taxonomic analysis made it possible to determine similarities between particular samples and identify clusters of samples of similar composition and structure. A dendrogram was generated using the method described by MORISITA (1959) and calculated using the PAST statistical software package (HAMMER et al. 2001).

RESULTS

The number of species per sample varied from 13 to 23, whereas the number of specimens ranged from 203 to 1,925. The entire material comprised 9,354 specimens of 36 land snail taxa, including one collective category consisting of slug vestigial shells (Limacidae and Agriolimacidae) (Table 1).

The malacofauna of the castle hill in Melsztyn included species of three ecological groups: F – shade-loving taxa, O – open country snails, M – mesophilous species (Table 1). Forms typical of humid terrestrial habitats and aquatic molluscs were not found.

The shade-loving forms constituted 13% of the assemblage. Most species were represented by single specimens. Only *Vertigo pusilla*, *Acanthinula aculeata* and *Perforatella incarnata* occurred in greater numbers. It is notable that snails preferring damp habitats and species typical of dense canopy forests constituted only a very small proportion of the assemblage (Fig. 3, Table 1). Open-country snails were dominant components of the studied fauna (nearly 55% of the assemblage). The most abundant species was *Truncatellina cylindrica* (4,403 shells – 47% of all specimens col-

Table 1. Malacofauna of the ruins of Melsztyn castle. Ecological groups (E) of molluscs (after: LOŹEK 1964, ALEXANDROWICZ 1987 and ALEXANDROWICZ & ALEXANDROWICZ 2011): F – shade-loving taxa, O – open-country taxa, M – mesophilous taxa

| E | Taxon | Samples Me- | | | | | | | | | |
|---|--|-------------|-------|-------|-------|-----|-----|-------|-----|-----|-----|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| F | <i>Vertigo pusilla</i> O. F. Müller, 1774 | | 23 | 35 | 73 | 12 | 12 | | 11 | 6 | 4 |
| F | <i>Acanthinula aculeata</i> (O. F. Müller, 1774) | 20 | 12 | 7 | 9 | 25 | 44 | | 43 | 1 | 6 |
| F | <i>Vitrea crystallina</i> (O. F. Müller, 1774) | | 5 | | | | | | | | |
| F | <i>Vitrea subrimata</i> (Reinhardt, 1871) | | | | | 1 | | | | | |
| F | <i>Aegopinella minor</i> (Stabile, 1864) | 8 | 92 | 47 | 29 | 27 | 86 | 38 | 53 | 8 | 27 |
| F | <i>Oxychilus depressus</i> (Sterki, 1880) | 2 | | | | 2 | 2 | 3 | | 1 | |
| F | <i>Oxychilus glaber</i> (Rossmässler, 1835) | | | 4 | 3 | | | 6 | | | |
| F | <i>Macrogastera plicatula</i> (Draparnaud, 1801) | | | 4 | | | | | | | |
| F | <i>Clausilia cruciata</i> (Studer, 1820) | | | | 18 | | 17 | | | | |
| F | <i>Alinda biplicata</i> (Montagu, 1803) | 9 | 11 | 133 | 48 | | 40 | | | | |
| F | <i>Bradybaena fruticum</i> (O. F. Müller, 1774) | | | | | | | | | 2 | |
| F | <i>Perforatella incarnata</i> (O. F. Müller, 1774) | 2 | 22 | 15 | 5 | 27 | 26 | 17 | 16 | 1 | 5 |
| F | <i>Cepaea hortensis</i> (O. F. Müller, 1774) | | | | 2 | | | | | | |
| O | <i>Truncatellina cylindrica</i> (Férussac, 1807) | 597 | 578 | 752 | 417 | 46 | 263 | 1,475 | 151 | 54 | 70 |
| O | <i>Vertigo pygmaea</i> (Draparnaud, 1801) | | 4 | 1 | 1 | | | | | | |
| O | <i>Pupilla muscorum</i> (Linnaeus, 1758) | 21 | 11 | 5 | 9 | 4 | | | 3 | | |
| O | <i>Vallonia costata</i> (O. F. Müller, 1774) | 29 | 62 | 18 | 25 | | | 2 | 8 | | |
| O | <i>Vallonia pulchella</i> (O. F. Müller, 1774) | 24 | 98 | 61 | 107 | 10 | 19 | 34 | 73 | 11 | 4 |
| O | <i>Ceciloides acicula</i> (O. F. Müller, 1774) | | | | | | | 1 | | | |
| O | <i>Euomphalia strigella</i> (Draparnaud, 1801) | | | | | | | 18 | | | |
| O | <i>Helicella obvia</i> (Menke, 1828) | 36 | 6 | | | 4 | 7 | | | | |
| M | <i>Carychium tridentatum</i> (Risso, 1826) | | | | | 9 | | | | | |
| M | <i>Cochlicopa lubrica</i> (O. F. Müller, 1774) | 12 | 54 | 1 | | | | 27 | 48 | 2 | 4 |
| M | <i>Cochlicopa lubricella</i> (Porro, 1838) | 2 | 8 | | | | | | 4 | | |
| M | <i>Vertigo alpestris</i> Alder, 1838 | | | | 2 | | | | | | |
| M | <i>Columella edentula</i> (Draparnaud, 1805) | | 10 | | 1 | 2 | 3 | | | | |
| M | <i>Punctum pygmaeum</i> (Draparnaud, 1801) | 13 | 169 | 133 | 205 | 96 | 132 | 61 | 82 | 23 | 39 |
| M | <i>Vitrina pellucida</i> (O. F. Müller, 1774) | 168 | 204 | 105 | 122 | 34 | 112 | 230 | 100 | 53 | 21 |
| M | <i>Vitrea contracta</i> (Westerlund, 1871) | | | 3 | | 2 | 7 | | 2 | | |
| M | <i>Nesovitrea hammonis</i> (Ström, 1765) | | 19 | 4 | | 2 | 2 | | 2 | | |
| M | Limacidae, Agriolimacidae | | 1 | 1 | | | | | | | |
| M | <i>Euconulus fulvus</i> (O. F. Müller, 1774) | 1 | 14 | 7 | 17 | 3 | 3 | 2 | 2 | 2 | 10 |
| M | <i>Laciniaria plicata</i> (Draparnaud, 1801) | | | 47 | 187 | 17 | 91 | 11 | 10 | 43 | 6 |
| M | <i>Clausillia dubia</i> Draparnaud, 1805 | | | 53 | 47 | 3 | 31 | | | | |
| M | <i>Trichia villosula</i> (Rossmässler, 1838) | | 8 | 11 | 14 | 13 | 8 | | 8 | | 3 |
| M | <i>Trichia lubomirskii</i> (Ślósarski, 1881) | | 9 | 3 | | | | | 4 | | 2 |
| | Total species | 15 | 22 | 23 | 21 | 20 | 19 | 14 | 18 | 13 | 13 |
| | Total specimens | 944 | 1,420 | 1,450 | 1,341 | 339 | 905 | 1,925 | 620 | 207 | 203 |

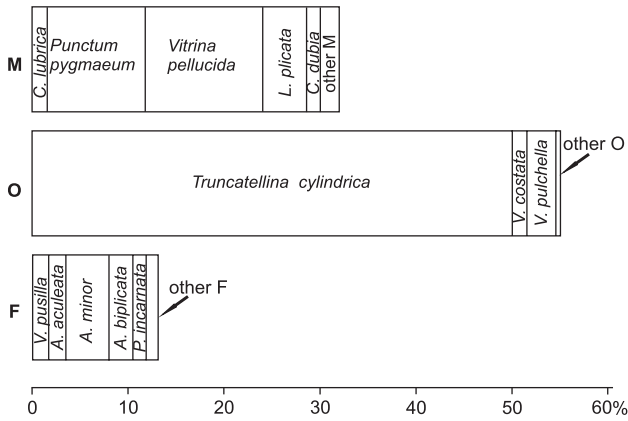


Fig. 3. Ecological and taxonomical composition of malacofauna inhabiting the ruins of Melsztyn castle. Ecological groups of molluscs (after: LOZEK 1964, ALEXANDROWICZ 1987 and ALEXANDROWICZ & ALEXANDROWICZ 2011): F – shade-loving taxa, O – open-country taxa, M – mesophilous taxa

lected). *Vallonia pulchella* and *V. costata* were common as well. Among mesophilous taxa, which represented slightly over 32% of the assemblage, *Vitrina pellucida*, *Punctum pygmaeum* and *Laciniaria plicata* are noteworthy (Fig. 3, Table 1).

Figure 4 presents the constancy and dominance structure of the studied fauna. As many as eight out of 36 taxa (22%) reached the highest constancy class (C-5) and occurred in all the analysed samples. The most abundant species was *T. cylindrica*, with the highest constancy (class C-5) and the highest dominance (class D-5). The species was present in all the samples and was always represented by a large number of specimens. Two other species: *V. pellucida* and *P. pygmaeum*, occurred in all the samples, but were less numerous

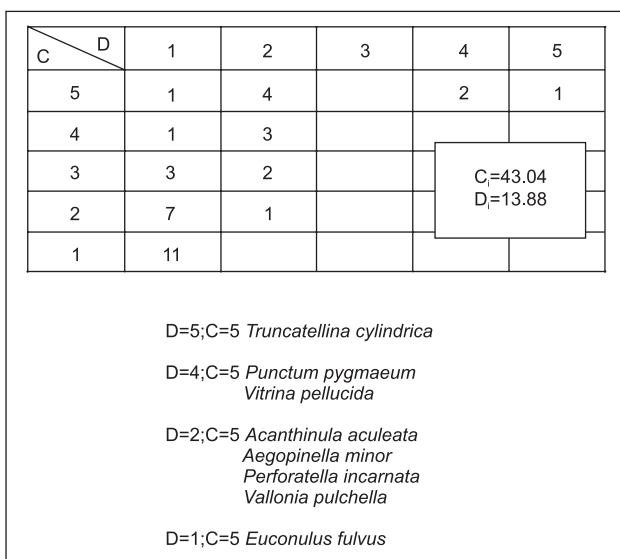


Fig. 4. Constancy and dominance structure of molluscan fauna from the ruins of Melsztyn castle: C – constancy, D – dominance, C_i – synthetic constancy index, D_i – synthetic dominance index (after: ALEXANDROWICZ & ALEXANDROWICZ 2011)

(constancy C-5, dominance D-4). Furthermore, the following 5 taxa reached the highest constancy class: *A. aculeata*, *Aegopinella minor*, *Perforatella incarnata*, *V. pulchella* and *Euconulus fulvus*. However, their numbers were considerably smaller (dominance D-2 or D-1). The remaining taxa appeared in very small numbers. Even though some of them had a high constancy (even C-4), their dominance was always low (D-1 or D-2) (Fig. 4). The value of the standardised constancy index (C_i=43.04) was very high and implied a similar species composition across the samples. On the other hand, the relatively low value of the standardised dominance index (D_i=13.88) reflects the abundant occurrence of just a few taxa, whereas other species represent less significant admixtures in the fauna. In Table 2 the Q index indicates the significance of individual species in the studied assemblage. High Q values are characteristic of common and abundant forms; very rarely found species show low Q values. Taxa of high constancy and dominance have the highest Q values. Dominant species, which constitute the most significant component of the analysed fauna, are marked by the Q value exceeding 8.00. This group comprises 13 taxa. Species with Q values ranging from 8 to 2 represent supplementary elements, which are significant for ecological interpretations of molluscan assemblages (12 species). The remaining 11 taxa with Q values below 2 are accessory components of small significance (Table 2).

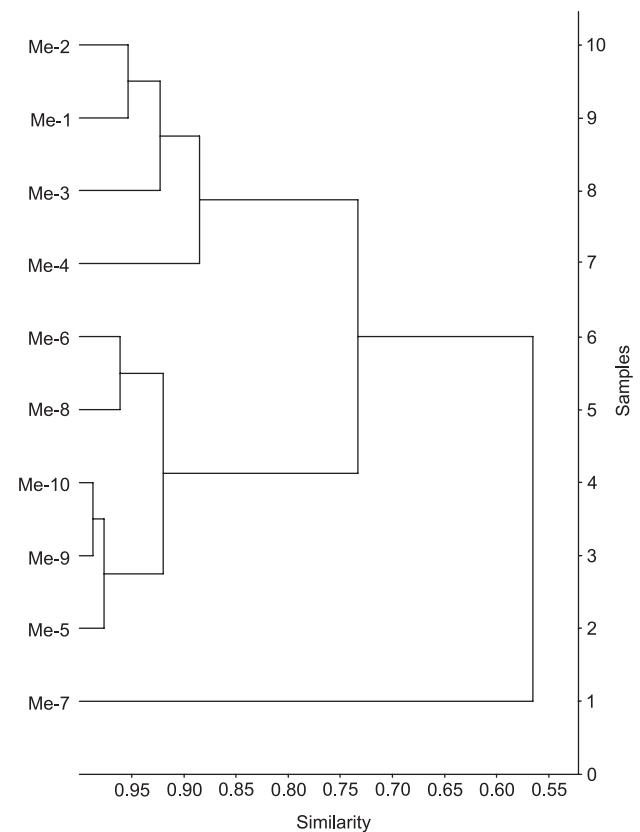


Fig. 5. Taxonomic dendrogram of samples from the snail assemblage from the ruins of Melsztyn castle

Table 2. Structure of molluscs assemblages from the ruins of Melsztyn castle according to categories of constancy, dominance and Q index: C – constancy, D – dominance, Q – geometric mean of C and D (after: ALEXANDROWICZ 1987, ALEXANDROWICZ & ALEXANDROWICZ 2011)

| | D (D>5%) | Q | D<5% | Q |
|-----------|---------------------------------|-----------------------------|-------------------------------|-------|
| C (C>50%) | <i>Truncatellina cylindrica</i> | 68.63 | <i>Vallonia pulchella</i> | 21.70 |
| | <i>Vitrina pellucida</i> | 35.07 | <i>Aegopinella minor</i> | 21.04 |
| | <i>Punctum pygmaeum</i> | 31.93 | <i>Laciniaria plicata</i> | 18.76 |
| | | | <i>Acanthinula aculeata</i> | 12.73 |
| | | | <i>Vertigo pusilla</i> | 12.26 |
| | | | <i>Perforatella incarnata</i> | 12.04 |
| | | | <i>Alinda biplicata</i> | 11.33 |
| | | | <i>Cochlicopa lubrica</i> | 10.52 |
| | | | <i>Vallonia costata</i> | 9.61 |
| | | | <i>Euconulus fulvus</i> | 8.06 |
| | | | <i>Trichia villosula</i> | 6.95 |
| | | | <i>Pupilla muscorum</i> | 5.85 |
| | | | <i>Nesovitrea hammonis</i> | 3.94 |
| | | | <i>Oxychilus depressus</i> | 2.43 |
| C (C<50%) | | | <i>Clausilia dubia</i> | 7.82 |
| | | | <i>Euomphalia strigella</i> | 4.77 |
| | | | <i>Oxychilus glaber</i> | 3.42 |
| | | | <i>Trichia lubomirskii</i> | 2.76 |
| | | | <i>Clausillia cruciata</i> | 2.72 |
| | | | <i>Columella edentula</i> | 2.61 |
| | | | <i>Vitrea contracta</i> | 2.45 |
| | | | <i>Cochlicopa lubricella</i> | 2.12 |
| | | | <i>Helicella obvia</i> | 1.38 |
| | | | <i>Vertigo pygmaea</i> | 1.34 |
| | | | <i>Carychium tridentatum</i> | 0.94 |
| | | | <i>Vitrea crystallina</i> | 0.71 |
| | | | Limacidae, Agriolimacidae | 0.63 |
| | | | <i>Macrogastra plicatula</i> | 0.63 |
| | | | <i>Bradybaena fruticum</i> | 0.44 |
| | | | <i>Cepaea hortensis</i> | 0.44 |
| | | | <i>Vertigo alpestris</i> | 0.44 |
| | | <i>Vitrea subrimata</i> | 0.32 | |
| | | <i>Ceciliooides acicula</i> | 0.32 | |

Several groups of assemblages of different taxonomic structure can be distinguished in the dendrogram in Fig. 5. They are associated with different parts of the ruins. Samples Me-1-Me-4, constituting the first cluster, were collected in the south-west part of the building. It is the area where the largest fragments of the original castle have been preserved (Figs 2, 5). The samples collected from the defensive walls, both well preserved and those in a bad condition, in the central and north-western part of the ruins, form the second group. Within this group, it is

possible to separate smaller clusters including: samples Me-6 and Me-8 (surroundings of the fortified tower), samples Me-5, Me-9 and Me-10 (north-eastern part of the castle), and sample Me-7 (a small and very poorly preserved section of the walls near the entrance to the castle) (Figs 2, 5). Such differences result from several factors. The most important are: differences in the vegetation cover, exposure of the samples and the condition in which the original castle structures have been preserved.



DISCUSSION

The malacofauna of the Melsztyn castle ruins differs considerably from the recent malacofauna of the Beskidy Mts (e.g. DZIĘCZKOWSKI 1972, 1988, ALEXANDROWICZ 1984, 2003, 2011), from the shell thanatocoenoses of flood debris (ALEXANDROWICZ 1991, 2002), and from the assemblages from Late Holocene sediments of various origin (ALEXANDROWICZ 1985, 1997, 2004, 2009, 2010). The most important difference is the specific ecological structure: the malacofauna of Melsztyn is dominated by open-country species (e.g. *T. cylindrica*, *V. pulchella*, *V. costata*, *E. strigella*). The situation is associated with human activity. The hilltop was deforested during the castle construction (numerous old drawings showing the castle perched on top of a completely deforested hill), and since its devastation 200 years ago no dense-canopy has managed to regrow on the hill. This created unfavourable conditions for shade-loving species, which explains their small (mere 13%) proportion in the assemblage. In other, more natural localities in the Beskidy Mts, species typical of shaded habitats are nearly always the dominant group, usually considerably exceeding 50% of the assemblages (DZIĘCZKOWSKI 1972, 1988, ALEXANDROWICZ 1984, 2003, 2011). However, the most exceptional feature of the Melsztyn malacofauna is the occurrence of species that are very rarely found in natural sites in the Beskidy Mts. *T. cylindrica* is the most noteworthy species in this group. It inhabits short swards and definitely prefers places with high calcium content; it can also be found in anthropogenic habitats such as road or railway embankments (KERNEY et al. 1983, RIEDEL 1988, POKRYSZKO 1990, WIKTOR 2004). In the Polish part of the Carpathians the species is widespread only in regions where rocks with high calcium content are common – chiefly limestone rocks and also, to a lesser extent, dolomites and marls. *T. cylindrica* has been recorded from the limestone part of the Tatra Mts (DYDUCH-FALNIOWSKA 1991), as well as from the Pieniny Klippen Belt (both the Pieniny Mts and the belt of limestone rocks cutting through the Podhale Basin between Niedzica and Białka Tatrzańska) (URBAŃSKI 1939, ALEXANDROWICZ 1997, ALEXANDROWICZ & RUDZKA 2006). The species is known both in the extant fauna and in fossil sediments from the entire Holocene period (ALEXANDROWICZ 1997, 2004, ALEXANDROWICZ & RUDZKA 2006). The Beskidy mountain range and its foothills are predominantly built of flysch sediments containing at most only small amounts of carbonates. This fact and the prevalence of shaded forest habitats make the conditions unfavourable for the development of *T. cylindrica* populations. Therefore, only isolated localities are known where the species is present, and they correspond to areas composed primar-

ily of limestone, such as the Cieszyn Foothills (RIEDEL 1988), the environs of Andrychów (ALEXANDROWICZ 1994) and the Przemyśl region (RIEDEL 1988). In some of these sites *T. cylindrica* used to be found on spoil heaps of limestone quarries. After the quarries ceased operating just after World War II, the spoil heaps gradually became overgrown with forest, which eventually resulted in extinction of the population of the species (ALEXANDROWICZ 1994). In the Melsztyn castle ruins, *T. cylindrica* is the most abundant snail species and constitutes almost half of the entire shell material collected. Besides the empty shells, live individuals (about 5% of collected material) were found, which proves that the species currently inhabits the castle hill. Considering the geological structure of the hill (Ciężkowice Beds with low calcium content) on the one hand and the predominance of natural forest communities surrounding the castle on the other, it is virtually impossible that *T. cylindrica* existed there before the castle construction started. Live individuals of *T. cylindrica* are likely to have been brought into the environs of the castle by humans. Deforestation of the hilltop for the purposes of castle construction, and the significant increase in calcium content as a result of using lime mortar to build the walls, have created favourable conditions for the development of its population. *T. cylindrica* may have migrated from the Cracow-Częstochowa Upland in the north-west, where it is common and abundant, or from the Pieniny Mts in the south. The Melsztyn castle is situated in the Dunajec River valley – an important and busy trade route across the Carpathians since ancient times (ŻAKI 1955, KOŁODZIEJSKI et al. 1982). Other species, very rarely found in the Beskidy Mts, such as *Helicella obvia*, *Ceciloides acicula*, *Cochlicopa lubricella* and *E. strigella*, presumably got to the castle hill via the same route and at about the same time (RIEDEL 1988, ALEXANDROWICZ et al. 1997, ALEXANDROWICZ & ALEXANDROWICZ 2010). *H. obvia* is a xerophilous and thermophilous, Pontic-Balkan species of open habitats. It has not yet been discovered in fossil deposits from Poland. Its expansion began together with intensified anthropogenic deforestation and development of trade with southern Europe. It appeared in Poland in the 16th or 17th century and found favourable conditions, especially in the limestone areas of the Cracow-Częstochowa Upland (ALEXANDROWICZ & ALEXANDROWICZ 2010). It has also colonised castle hills, affected by anthropogenic pressure, mainly along the Dunajec River valley (ALEXANDROWICZ 1995, ALEXANDROWICZ et al. 1997, ALEXANDROWICZ & ALEXANDROWICZ 2010).

Castles are mostly situated in major river valleys. These zones have both formerly and presently served as important transport routes, facilitating passive dis-

persal of snails from open areas. In the Beskidy Mts the process involves mainly forms preferring open habitats, as well as species tending to colonise cultivated lands (e.g. *C. acicula*). Viewed from this perspective, castle ruins represent important refugia for such species (MATZKE 1985, ALEXANDROWICZ 1995, JUŘIČKOVA & KUČERA 2005a, b).

The castle hill in Melsztyn is inhabited by fauna whose composition and structure differ greatly from those of Flysh Carpathian malacocoenoses (e.g. DZIĘCZKOWSKI 1972, 1988, ALEXANDROWICZ 1984, 2003, 2011). Similar conclusions have been drawn from the detailed analyses of malacocoenoses derived from other castle ruins in southern Poland (WIKTOR 1959, URBAŃSKI 1973, POKRYSZKO 1984, ALEXANDROWICZ 1988, 1995), the Czech Republic (LOŹEK 1959, 1975, JUŘIČKOVA 2005, JUŘIČKOVA & KUČERA 2005a, b), Austria (JAUERNIG 1995), Germany (ZEISSLER 1969, 1975, 1980, MÜNZIG 1977, MATZKE 1985, HALDEMANN 1990, BÖSSNECK 1996) and Great Britain (ROUSE & EVANS 1994).

Based on the data from the Melsztyn castle and from other castle hills (e.g. ALEXANDROWICZ 1995, JAUERNIG 1995, BÖSSNECK 1996, JUŘIČKOVA 2005, JUŘIČKOVA & KUČERA 2005a, b), it is possible to distinguish the main phases of diversification of the malacofauna according to habitat changes. The first stage is the period preceding the castle's construction. Malacocoenoses typical of this phase are natural communities, whose species composition and structure are compatible with the features of the fauna surrounding the hill. In the Carpathians, such molluscan assemblages are characterised by the dominance of shade-loving snails. The second stage is the construction of the castle. It involves anthropogenic deforestation and disappearance of shaded habitats, which are replaced by open ones. The fauna becomes greatly impoverished, with a considerable decrease in the

species diversity and a rapid decrease in the significance of shade-loving species. The third stage covers the period when the castle is inhabited. During this phase, an increased migration becomes evident, mainly as a consequence of human activity. Some of the species brought into the castle find favourable conditions there and can therefore develop numerous and stable populations. It involves mostly open country snails, which often prefer calcium-rich substrata. The last stage of malacocoenoses development follows the destruction of the castle. Natural plant succession takes place at this stage, concerning mainly shrub communities, and later – also forest communities. At the same time, the number of shade-loving snail species increases. Yet within the ruins more open habitats can still remain, which is usually the case, and they enable the populations of anthropogenic migrants to stay and develop. Thus, mixed and often very rich associations containing both natural (species inhabiting castle hill surroundings) and artificially (anthropogenically) introduced elements (species not occurring in the surroundings of the castle hill, and often even absent from the geographical region) appear.

The castle hill in Melsztyn, together with the castle ruins, should be placed under legal protection as a nature-landscape complex. Spectacular outcrops of the Cieżkowice sandstones which form the castle hill, as well as the malacofauna of the ruins, with its composition and structure being exceptional in the Beskidy Mountains and their foothills, represent additional, valuable natural elements in this location.

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