DISTRIBUTION AND HABITAT PREFERENCES OF CLAUSILIIDS (GASTROPODA: PULMONATA: CLAUSILIIDAE) IN THE EASTERN PART OF THE POLISH CARPATHIANS

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ABSTRACT: Seventeen species of Clausiliidae are recorded from the Bieszczady Mts, the Beskid Niski Mts and the Sanocko-Turczañskie Mts. Five (Macrogastra borealis (O. Boettger), M. tumida (Rossm.), Balea stabilis (L. Pfeiffer), Vestia gulo (E. A. Bielz) and Bulgarica cana (Held)) are common in all the studied regions. Balea fallax (Rossm.), Vestia elata (Rossm.), Clausilia dubia Drap. and C. pumila C. Pfeiffer are the rarest species. Macrogastra plicatula (Drap.) and Balea biplicata (Mont.) inhabit only the western part of the Beskid Niski Mts. The distribution of species was investigated with reference to altitude above sea level, habitat and microhabitat types. Ruthenica filograna (Rossm.), Macrogastra plicatula (Drap.), Laciniaaria plicata (Drap.) and Balea biplicata (Mont.) occur below 800 m a.s.l. Claudisia cruciata Studer and Balea stabilis (L. Pfeiffer) are absent below 400 m a.s.l. The richest communities (up to 8 clausiliid species recorded sympatrically) inhabit alder forests in the valleys. Macrogastra tumida (Rossm.), Ruthenica filograna (Rossm.) and Vestia turgida (Rossm.) are characteristic for these habitats. Beech woods are inhabited by tree-climbing clausiliids (Cochlodina orthostoma (Menke), Claudisia cruciata Studer, Macrogastra borealis (O. Boettger), Bulgarica cana (Held)) and – in more humid sites – by litter dwellers (M. tumida (Rossm.), Vestia gulo (E. A. Bielz), V. turgida (Rossm.).) In the studied region Laciniaaria plicata (Drap.) prefers anthropogenic habitats (e.g. stone walls, cemeteries).

KEYWORDS: Clausiliidae, habitat preferences, vertical distribution, co-occurrence of land snails and plants, the Carpathians

INTRODUCTION

Twenty four species of Clausiliidae are known to occur in Poland (RIEDEL 1988). Their general distribution in the country is known, but some regions, among them the eastern part of the Carpathians, were only partly studied, or the 19th c. data need verification. Information on ecology of the species is scattered in the Polish literature. The objective of the study was to verify the data on the geographical and vertical distribution of Clausiliidae and to estimate their ecological preferences.

Polish clausiliids represent three subfamilies: Alopinae (genera: Cochlodina Férussac, 1821, Charpentieria Stabile, 1864), Clausiliinae (Clausilia Draparnaud, 1805, Ruthenica Lindholm, 1924, Macrogastra Hartmann, 1841) and Baleinae (Laciniaaria Hartmann, 1844, Balea Gray, 1824, Vestia P. Hesse, 1916, Bulgarica O. Boettger, 1877). According to NORDSIECK (1979) Alinda H. et A. Adams, 1955 and Pseudalinda O. Boettger, 1877 are subgenera of the genus Balea.

Most Polish clausiliids are widely distributed in Central and Central-Eastern Europe; seven species have Carpathian distributions. Only few species inhabit the entire country. The highest number of taxa was recorded from western Poland, mostly the Sudetes, where species of E. Alpine distribution, Charpentieria ornata (Rossmässler, 1836) and Cochlodina costata (C. Pfeiffer, 1828), occur. Nineteen clausiliid species were recorded from the Polish Carpathians and the submontane region [Pogórze] (RIEDEL 1988).
In the second part of the 19th c. the malacofauna of this part of Poland was investigated in the vicinity of towns in the submontane region north of the Beskid Niski and the Bieszczady: Przemyśl (KOTULA 1882), Strzyżów (BAKOWSKI 1878, KROL 1879), Błażowa (BRZEK 1933). The first and until now the most complete study of the malacofauna of higher mountains was published over 120 years ago by KOTULA (1882), who listed species inhabiting the upper part of the San River (Halicz, Tarnica, Otryt(?)) and Strwiąż River catchment areas (Oratyk, Ostrykówiec, Kamien- na Ławorta, Chwaniów in the Sanocko-Turczańskie Mts). At the same time the malacofaunas of the Carpathians and the submontane zone in Ukraine were investigated (BAKOWSKI 1881, 1882). The 19th c. malacological studies in the Carpathians were summarized by BAKOWSKI & LOMNICKI (1892) and later by URBAŃSKI (1957).

In the 1950s and 1960s terrestrial gastropods were intensively collected in the Bieszczady Mts (Ustrzyki Górne, Wetlina, Dwernik, Cisna, Komarica). Most of the collected clausiliids, stored in the Institute and Museum of Zoology, PAS, Warsaw, were identified by LIKHAREV (1962), but some were not examined at all, or the results were never published (A. RIEDEL, personal communication). Recently, the literature data on the malacofauna of the Bieszczady were summarized by STWORZEWICZ & PAWŁOWSKI (2000) and updated by SULIKOWSKA-DROZD (2002). The malacofauna of the Slovak slopes of the Bieszczady was studied by LOZĘK & GULIĆKA (1955, 1962).

Published records of the malacofauna of the Beskid Niski are limited to a paper on a single locality (Uście Gorlickie) by JACZKIEWICZ & RAFLSKI (1966). I found samples of clausiliids from further few localities in the region (vicinity of Krempna, Dukla and Szymbark) in museum collections.

Information on some clausiliid localities in the studied area can also be found in KAZUBSKI (1959), JACZKIEWICZ (1965), STĘPCZAK (1970), STWORZEWICZ (1973), MATZKE (1980), DZIECZKOWSKI (1988) and ALEXANDROWICZ (1995).

According to the literature, 13 clausiliids species occur in the Bieszczady (DZIECZKOWSKI 1988, RIEDEL 1988), and 19 species in the Beskid Niski and Pogórze (RIEDEL 1988).

Clausiliids live on tree trunks, on steep slopes, in leaf litter and debris, under stones and timber (LIKHAREV 1962). Many species spend most of their lives on tree trunks, hiding in bark crevices and in moss during unfavorable weather conditions. Rarely, they are found on coniferous trees. Other species stay on the soil surface and in ground litter and only during rainy weather climb trees to avoid drowning (LIKHAREV 1962). Many inhabit rock faces and screes. In shaded habitats, the same species often climb rocks and trees. According to LOŻEK (1962), among clausiliids inhabiting Central European forests, six species live in soil and nine on rotting timber; none of them is classified as a calciphile.

Their diet consists of rotting vegetation, fungi, lichens and algae growing on rocks and trees (LIKHAREV 1962). In laboratory the snails chose rotting herbs, preferably with soft tissues, but no preference for particular plant species was observed (FROMMING 1954). Rock- and wall-dwelling Balea perversa forages on various lichen species, but it can also grow and reproduce when kept on a diet consisting of only Xanthoria parietina (BAUR & BAUR 1997). According to FOG (1979), the diet of clausiliids living on rotting stumps consists mostly of bacteria; fungus fruiting bodies and spores could hardly be the main food of the snails. Exceptionally, Cochlodina laminata often aggregates on fruiting bodies of Trametes versicolor (FOG 1979).

STUDY AREA

TOPOGRAPHY

The study area is located in the Carpathians in S. E. Poland (Fig. 1). It can be divided into three main geographical regions: the Beskid Niski, the Western Bieszczady and the Sanocko-Turczańskie Mts (KON-DRACKI 2000).

The Beskid Niski is a 100 km long mountain range, a part of the main Carpathian watershed, situated between the Tylicka Pass (Kamienica River valley) and the Łupkowsa Pass (Osla wa and Osławica River valleys), the easternmost part of the Western Carpathians. The topography is varied; the highest summits are in the western part (Lackowa 997 m a.s.l.). There are a few low passes crossing the range, among them the Dukielska Pass, the lowest in the Carpathian range (500 m a.s.l.). The range towers 150–400 m above the uplands of Pogórze Jasielskie and Pogórze Bukowskie in the north.

The rest of the area is a part of the Eastern Carpathians. The Western Bieszczady (known also as High Bieszczady, and the Slovak part – Bukowskie Mts) extend to the east of the Beskid Niski Mts and to the west of the Użoke Pass and the sources of the San River. They are 65 km long. The highest summit reaches 1,346 m a.s.l., besides, 11 peaks in the eastern part of the range exceed 1,200 m. All the mountain ranges are parallel and directed from northwest to southeast. The Sanocko-Turczańskie Mts, called also the Low Bieszczady, are situated to the northeast of the Western Bieszczady. Their ridges are also parallel.
and ascend gradually towards southeast (Magura Łomniańska 1,024 m a.s.l.).

GEOLOGY AND SOIL

The mountain ranges are built of flysch (sandstones, siltstones and shales), with a locally significant content of calcium carbonate (up to 35% in the Bieszczady). Soils were thoroughly studied in the Bieszczady National Park (SKIBA et al. 1998). The soils here are predominantly cambisols. The most common are dystric cambisols, occurring on non-calcareous flysch formations and on deep and calcified regolith covering calcium-rich flysch rocks. In dystric cambisols pH is low in the whole profile (4.0–5.0), while in eutric cambisols it ranges from 5.5 to 6.5. Semi-hydrogenic and hydrogenic soils occupy small and scattered areas on slope bends and in valleys. Their high pH (5.5–7.0) is due to the influence of nutrient-rich water coming from underground. Semi-hydrogenic soils provide the most fertile forest habitats in the Bieszczady Mts.

CLIMATE

Climatic conditions in the region depend mostly on altitude, but the limits of climatic zones are generally higher on southern slopes and on convex ridges than on northern slopes and in concave valleys. In the Beskid Niski the average annual temperature is +8°C at 200 m a.s.l. and +4°C at 1,000 m (OBRĘBSKA-STARKLOWA 1973). Two vertical climatic zones can be distinguished: moderately warm and moderately cool.

Three climatic vertical zones are distinguished in the Bieszczady: moderately warm, moderately cool and cool (NOWOSAD 1996). In lower parts the average annual temperature exceeds +6°C and the vegetation season lasts 200–214 days. On the highest ridges the average annual temperature is lower than +3°C and the vegetation season lasts 181–192 days. Minimum temperatures occur in January (mean temperature from −3.4°C in valleys to −6.7°C on the highest ridges), and maximum in July (+18°C at the foothills of the Beskid Niski and +11.5°C on the highest ridges of the Bieszczady). Mean annual precipitation is ca. 800–900 mm in most of the Beskid Niski and in the lower parts of the Bieszczady, 800–1,000 mm in the Sanocko-Turczańskie Mts; it increases with elevation to 1,135 mm in Wetlina and probably exceeds 1,200–1,300 mm on the highest ridges. The highest monthly rainfall is in July, the lowest in January, February and October. Rainless periods last no more than 50 days in the Polish Carpathians. Snow cover is present from the second half of October on the ridges and from the second part of November in the valleys. The mean number of days with snow cover varies from 94 to 180. The timberline follows the isotherm of +2°C (ca. 1,000–1,200 m a.s.l.).

HISTORY OF HUMAN INFLUENCE

Human activity in the region started comparatively late. According to REINFUSS (1990) colonisation of the foothills of the Beskid Niski dates back to the 10th–11th c. Then, between the 14th and the 16th centuries, the upper parts of the area were inhabited by colonisers from Rus and the Vlachs of Balkan ori-
gin. They brought Orthodox religion, pastoral economy and peculiar folk culture. At the end of the 16th c. colonisation of the Beskid Niski was completed (REINFUSS 1990) and more than 90% villages were already built (GRZESIK & TRACZYK 1992); likewise, most villages in the Bieszczady were established by that time (OLSZANSKI 1992). The population density increased at the end of the 19th c. In the Beskid Niski it was estimated at 50 person km\(^{-2}\) (REINFUSS 1990) and in the Bieszczady at 80–100 people per 100 ha of agricultural lands (ZARZYCKI & GLOWACINSKI 1986). Cattle and sheep grazed on mountain meadows, whose lower boundaries were artificially lowered to 1,000 m, and in the woodland. Crop fields spread locally up to 900 m a.s.l. (ZARZYCKI & GLOWACINSKI 1986). In the Bieszczady the forested area was reduced in the 19th and 20th centuries due to massive logging (ZARZYCKI & GLOWACINSKI 1986).

The dramatic end to the local communities and traditional agriculture was brought by the resettlement of countrymen (in years 1940 and 1944–46 partly voluntarily to USSR, and under compulsion of countrymen (in years 1940 and 1944–46 (MICHAŁOWSKI 1993), fertile humid meadows were drained (e.g. in Wetlina) (REINFUSS 1990). After the deportation of the civilians (ca. 105,000–120,000 people from the Beskid Niski alone) much of their property was demolished. The changes in population density can be illustrated by examples. The village Wołosate, established in 1557 in the Bieszczady, in 1931 was inhabited by 1,084 people living in 179 cottages; in 1946 the whole population was expelled (AUGUSTYN 1999). The village Wisłok, in the Beskid Niski, was before the Second World War inhabited by 2,809 people; nowadays there are only 100 houses there (GRZESIK & TRACZYK 1992). The former owners were forbidden to come back till 1956, many never returned; more families came back to the Beskid Niski than to the Bieszczady. Some former villages are only distinguishable by the ruderal vegetation and wild fruit trees; in many places also stone foundations and walls of cemeteries are visible. The new colonisation was sparse and not always adapted to harsh local environment (POTOCKI 1992); in the 1970s, some huge but profitless state cattle farms were built (e.g. in Wetlina) (MICHAŁOWSKI 1993), fertile humid meadows were drained (e.g. in Wołosate in the 1980s) (AUGUSTYN 1999). Today it is one of the most sparsely populated parts of the country (25.67 person km\(^{-2}\) in Powiat Bieszczady) (STAN ŚRODOWISKA W WOJEWÓDZTWIE PODKARPACKIM 2000).

**VEGETATION**

In the Beskid Niski two vertical vegetation zones can be distinguished: the foothill zone, up to 530 m a.s.l., and the mountain forest zone, while in the Bieszczady there are three such zones: the foothills (known as *country of valleys*) up to 500–550 m a.s.l., the forest zone (timberline at 960–1,260 m a.s.l.) and the mountain meadows (*poloninas*).

The present vegetation in the region is shaped not only by climatic and soil conditions but also by human activity. Anthropogenic influence ceased about half of the 20th c., which resulted in secondary succession changes of great importance for the fauna (ZARZYCKI & GLOWACINSKI 1986).

After the depopulation of the Beskid Niski, in the foothill zone, on abandoned fields and meadows, secondary forest stands were planted, mainly of pine; more locally spontaneous succession of alder, ash and sycamore took place (MICHALIK & MICHALIK 1998). At least four different ways of succession can be distinguished, depending on the habitat fertility, exposition, vegetation in the neighbourhood and former land use (ZAJDEL 1998). Since the valleys were densely populated, older forests are very rare in the zone. Patches of old alder and ash forests *Carici remotae-Fraxinetum* and hornbeam forests *Tilio-Carpinetum* can be sporadically found. Alder woods are present along rivers and in wet habitats. The mountain forest zone is limited to the higher summits and thus distributed as insular patches. The Carpathian beechwood (*Dentario glandulosae-Fagetum*) predominates in the zone, accompanied by the acidophilous mountain beechwood (*Luzulo nemorosae-Fagetum*), sycamore forests (*Sorbo-Aceretum* and *Lunario-Aceretum*) and mesotrophic fir forests (community *Rubus hirtus – Abies alba*) (MICHALIK & MICHALIK 1998).

The Bieszczady are covered mostly by deciduous forests; the rich Carpathian beech wood (*Dentario glandulosae-Fagetum*) predominates (80% forested area; ca. 50% total area) (MICHALIK & SZARY 1997). True primaeval forests are only preserved in the most inaccessible parts of the range; most of the stands were previously exploited but the species composition is close to natural. Acidophilus mountain beechwood and sycamore forests occur locally. Alder woods (*Alnetum incanae*) grow along rivers and streams up to 900 m a.s.l. Alder swamps (*Callho-Alnetum*) occur in isolated patches on low permeable soil. Subalpine shrubs of *Alnus viridis* spread in more humid places above the timberline. About 14% of the forested area is occupied by secondary forest communities. Some spruce and mixed stands were planted, but most of unused farmland was spontaneously overgrown by grey alder, ash, goat willow and hazel. Between the First and the Second World War grey alder grew only in stream valleys but after the resettlement of people grey-alder short-living forests spread over abandoned fields and mountain slopes, occupying in the 1970s six times greater area than in the 1950s (TOKARZ 1975).

The Bieszczady National Park (since 1973, area: 29,202 ha) and the Magura National Park (1995, area: 19,962 ha) have protected the most valuable parts of the region.
ORIGIN OF THE MALACOFAUNA

The present composition of the Carpathian fauna has been shaped during climatic fluctuations since the Miocene (Górecki et al. 1995, and literature contained therein). The study area was not covered by the pleistocene glaciations, which reached the foothills up to 420 m a.s.l. (Klimaszewski 1967), but was under the influence of periglacial climate. After glaciations, major routes of immigration of the lowland malacofauna to Poland were from the west (north of the Alps) and from the southeast, along the northern slopes of the Carpathians, while montane species migrated along the mountain ridges from refuges in the Eastern Alps and in the Southern Carpathians (Wiktor 2004). The Beskid Niski Mts are regarded as the main transverse barrier in the distribution of gastropods in the Carpathians (Polinski 1927, 1930). Some E. Carpathian species, e.g. Carpathia calophana (Westerlund, 1881), Perforatella dibolithion (M. Kimakowicz, 1884), or Trichia bielzi (E.A. Bielz, 1860) reach as far west as the vicinity of the DukIELs Pass, while distribution ranges of the W. Carpathian or E. Alpine species, e.g. Perforatella umbrosa (C. Pfeiffer, 1828), Trichia unidentata (Draparnaud, 1805), or Causa holosericea (Studer, 1820), do not cover the Beszczyzdy in the east (Riedel 1988). Other W. Carpathian species, e.g. Trichia lubomirskii (Łóśarski, 1881), reach the eastern boundary of their ranges in the Beszczyzdy. In his analysis of the Beszczyzdy as the zoogeographical region, Pawlowski (2000) distinguished the presence of the eastern mountain taxa, western mountain taxa, and expansive southern taxa which penetrate into valleys through the lowest Carpathian passes in the Beskid Niski.

MATERIAL AND METHODS

SAMPLING AND IDENTIFICATION

In 1997–2000 almost 9,500 specimens of Clausiliidae were collected in the studied region. Additionally, collections from the area stored in museums and scientific institutes in Warsaw, Wroclaw, Krakow, Poznań, Lviv and Łódź were investigated (193 samples were found with more than 2,500 specimens).

The specimens were identified based on the following publications: Łóžek (1956, 1964), Urbanski (1957), Likharev (1962), Kerney et al. (1983). The nomenclature and systematic arrangement follow Nordsieck (1979, 1993). Division into ecological and biogeographical groups follows Łóžek (1964) and Riedel (1988), respectively.

Quantitative studies consisted in searching for gastropods in their possible shelters: soil, litter, moss, live trees and rotting trunks and logs, old stone walls, stream banks, under pieces of bark, timber and stones. Each collecting session lasted 30 minutes. Quantitative samples were taken with Ökland frame of 20 cm side in 11 forest patches in the Beszczyzdy National Park. The quantitative sampling was described in detail in Sulikowska-Drozd (2005).

Geographical distribution and ecological preferences were analysed for clausiliids derived from 221 sites (Fig. 2) (for the list of sites see Appendix). The altitude of the sites was read from topographic maps with minimal accuracy of 25 m. In the statistical analysis the vertical range above sea level was divided into 5 categories: <400 m, 400–599 m, 600–799 m, 800–999 m and >1,000 m. The habitats were classified based on humidity, shadiness, type of vegetation and human influence (Table 1). Habitats A, G, O, Z are situated in the county of valleys, habitat B represents the forest zone, and habitat P – mountain meadows (poloninas). Most W habitats are situated in the country of valleys, but some of them also in the forest zone. Habitats B, G, O and W represent forested area, while A, Z and P were situated outside forests. These categories were used also for museum samples whenever the information on the labels was sufficient.

Quantitative samples (400 cm²) were classified into three categories of humidity (1 – very humid, partly submerged, 2 – humid, 3 – not very humid) and three categories of herb cover (1 – without herbs, 2 – single plant species and single shoots, 3 – many species or shoots). Plant species were identified and counted in the samples.

STATISTICAL ANALYSES

In order to characterise the malacoconomicos the following indices were applied: dominance (D), the proportion of the species (per cent) in the malacoeconomicos, was denoted by D5 (> 20.0% – eudominant); D4 (10.1–20.0% – dominant); D3 (5.1–10.0% – subdominant); D2 (1.1–5.0% – recedent); and D1 (≤ 1.0% – subrecedent) (Alexandrowicz 1987); constancy (C), the percentage of localities in which the species was found, was denoted by C5 (80.1–100.0% localities – euconstant); C4 (60.1–80.0% – constant); C3 (40.1 – 60.0% – subconstant), C2 (20.1 – 40.0% – accessory); and C1 (≤ 20.0% – accidental) (Alexandrowicz 1987); frequency of occurrence at a quantitative sampling site (F); percentage of sub-samples containing a given species in relation to the total
number of sub-samples in the site (DZIECZKOWSKI 1988); Q index, which combines dominance and frequency indices in a given type of habitat (GÖRNY & GRUM 1981). The division of species into characteristic, accompanying and accessory ones follows GÖRNY & GRUM (1981).

Ökland’s method (ÖKLAND 1990) and $\chi^2$ test (ZAR 1984) enabled assessment of habitat and altitudinal preferences of the species. Calculations included only species with at least 25 records (including museum collection if the information on the labels was sufficient).

To examine co-occurrence of species, Czekanowski’s formula modified by DYDUCH-FALNIOWSKA (1991) was used, as well as Decamps’s formula (DYDUCH-FALNIOWSKA 1991, after DECAMPS 1967). The former was also used to calculate the co-occurrence of clausiliid and plant species.

Statistical analyses were performed using STATISTICA software (STANISZ 1998).

Table 1. Habitat types

<table>
<thead>
<tr>
<th>Main symbol</th>
<th>Habitat</th>
<th>Additional symbol</th>
<th>Microhabitat</th>
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<tbody>
<tr>
<td>B</td>
<td>Mountain forest zone (mostly beech woods)</td>
<td>Bz</td>
<td>Litter</td>
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<tr>
<td></td>
<td></td>
<td>Bp</td>
<td>Living trees</td>
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<tr>
<td></td>
<td></td>
<td>Bkl</td>
<td>Logs, stumps</td>
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<td></td>
<td></td>
<td>Bw</td>
<td>Close to sapping springs and brooks</td>
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<tr>
<td>G</td>
<td>Forests of submontane zone – hornbeam forests</td>
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<td></td>
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<tr>
<td>O</td>
<td>Humid forests – alder woods</td>
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<tr>
<td>W</td>
<td>Secondary forests overgrowing neglected fields and meadows (with Alnus incana, Salix caprea and Corylus avellana)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>Anthropogenic habitats</td>
<td>Az</td>
<td>Parks, gardens, cemeteries, along roads</td>
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<td></td>
<td></td>
<td>Am</td>
<td>Stonewalls</td>
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<tr>
<td></td>
<td></td>
<td>Aw</td>
<td>Bridges</td>
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<tr>
<td>Z</td>
<td>Humid scrub along rivers and brooks, without trees</td>
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<td></td>
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<tr>
<td>P</td>
<td>Herbage above the timberline, poloninas</td>
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<td></td>
</tr>
<tr>
<td>S</td>
<td>Rocks</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>Alluvial deposits</td>
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</tbody>
</table>
RESULTS

Seventeen species of Clausiliidae (71% Polish species) were recorded from the studied area. Their distribution in the three studied regions is shown in Table 2.

VERTICAL DISTRIBUTION

*Cochlodina orthostoma, Macrogastra borealis, M. tumida, Vestia gulo, V. turgida, Bulgarica cana* were found in the whole studied altitudinal range, while *Ruthenica filograna, M. plicatula, Clausilia pumila, Lacinaria plicata, Balea biplicata, V. elata* only in its lower part. *Balea stabilis* and *Clausilia cruciata* were missing from the lowest-situated sites (Fig. 3).

The upper distribution limits of *L. plicata, V. elata* and *Clausilia pumila* followed approximately the upper boundary of the moderately warm climatic zone, with average annual temperature higher than +6°C, and vegetation season longer than 200 days. *Cochlodina laminata, R. filograna, M. plicatula* and *B. biplicata* reached the moderately cool climatic zone (annual average temperature higher than +4°C). Only the first of the species reached the upper part of this zone.

The vertical distribution of *Clausilia cruciata* corresponded to the moderately cool and cool climatic zones. Two localities of the species located lower than these zones were situated in deep river valleys with cool mesoclimate. The species probably does not occur in places where average annual temperature exceeds +6°C.

Based on the frequency analysis (Table 3) three species groups could be distinguished:

a) Species occurring at the lowest-situated sites (<400 m a.s.l.) (*Cochlodina laminata, B. biplicata, L. plicata*) and at the same time rarely found in or absent from the upper part of the studied region (>800 m): *R. filograna, L. plicata, B. biplicata, M. plicatula* (differences statistically significant). Few localities of *C. laminata* were located above 1,000 m a.s.l.

b) Species avoiding the lowest-situated sites (<400 m a.s.l.), where they were significantly less frequent or entirely missing: *C. orthostoma, M. borealis, Clausilia cruciata, B. stabilis*. *Cochlodina orthostoma* occurred significantly more frequently than 800 m, while *Macrogastra borealis* had the highest constancy in medium altitudinal divisions and was not very frequent in the highest zone (>1,000 m).

c) Species occurring with similar constancy in the whole altitudinal range: *Bulgarica cana, Vestia gulo, V. turgida and M. tumida*. Some minor differences between divisions resulted from uneven distribution of preferred habitats along the vertical gradient. According to Økland’s (1990) method, *V. gulo* was significantly more common between 400 and 599 m, which corresponded with the occurrence

### Table 2. Distribution of Clausiliidae in the studied regions

<table>
<thead>
<tr>
<th>No</th>
<th>Species</th>
<th>Beskid Niski</th>
<th>Sanocko-Turczańskie Mts</th>
<th>Western Bieszczady</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Cochlodina laminata</em> (Mont.)</td>
<td>+++</td>
<td>+++</td>
<td>++</td>
</tr>
<tr>
<td>2</td>
<td><em>Cochlodina orthostoma</em> (Menke)</td>
<td>++</td>
<td>+</td>
<td>++</td>
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<tr>
<td>3</td>
<td><em>Ruthenica filograna</em> (Rossm.)</td>
<td>++</td>
<td>–</td>
<td>–</td>
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<tr>
<td>4</td>
<td><em>Macrogastra plicatula</em> (Drap.)</td>
<td>+++</td>
<td>++</td>
<td>+++</td>
</tr>
<tr>
<td>5</td>
<td><em>Macrogastra borealis</em> (O. Boet.)</td>
<td>+++</td>
<td>+++</td>
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</tr>
<tr>
<td>6</td>
<td><em>Macrogastra tumida</em> (Rossm.)</td>
<td>+++</td>
<td>+++</td>
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</tr>
<tr>
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<td>N</td>
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</tr>
<tr>
<td>8</td>
<td><em>Clausilia cruciata</em> (Stud.)</td>
<td>–</td>
<td>++</td>
<td>+++</td>
</tr>
<tr>
<td>9</td>
<td><em>Clausilia pumila</em> C. Pfr.</td>
<td>N</td>
<td>–</td>
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<td><em>Balea biplicata</em> (Mont.)</td>
<td>+++</td>
<td>–</td>
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<tr>
<td>12</td>
<td><em>Balea fallax</em> (Rossm.)</td>
<td>–</td>
<td>+</td>
<td>–</td>
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<tr>
<td>13</td>
<td><em>Balea stabilis</em> (L. Pfr.)</td>
<td>+++</td>
<td>+++</td>
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</tr>
<tr>
<td>14</td>
<td><em>Vestia elata</em> (Rossm.)</td>
<td>+</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>15</td>
<td><em>Vestia gulo</em> (E.A. Bielz)</td>
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<td>+++</td>
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<tr>
<td>16</td>
<td><em>Vestia turgida</em> (Rossm.)</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
</tr>
<tr>
<td>17</td>
<td><em>Bulgarica cana</em> (Held)</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
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</tbody>
</table>

* very rare species (found at ≤2% sites in the region), ++ rare species (found at 2.1–20% sites), +++ common species (found at more than 20.1% sites), N found only in alluvial deposits, – not found
Fig. 3. Vertical distribution of Clausiliidae

- **Cochlodina laminata**: 
  - >1,000: 1,075
  - 800–999: (–)
  - 600–799: (–)
  - 400–599: (–)
  - <400: 275

- **Cochlodina orthostoma**: 
  - >1,000: 1,200
  - 800–999: (+)
  - 600–799: (–)
  - 400–599: (–)
  - <400: 350

- **Ruthenia filograna**: 
  - >1,000: 725
  - 800–999: (–)
  - 600–799: (–)
  - 400–599: 325
  - <400: (–)

- **Macrogaster plicatula**: 
  - >1,000: 725
  - 800–999: (–)
  - 600–799: 300
  - 400–599: (–)
  - <400: (–)

- **Macrogaster borealis**: 
  - >1,000: 1,175
  - 800–999: (+)
  - 600–799: 310
  - 400–599: (–)
  - <400: (–)

- **Macrogaster tumida**: 
  - >1,000: 1,175
  - 800–999: (+)
  - 600–799: 300
  - 400–599: (–)
  - <400: (–)

- **Clausilia cruciata**: 
  - >1,000: 1,180
  - 800–999: (+)
  - 600–799: 525
  - 400–599: (–)
  - <400: 275

- **Laciniaria plicata**: 
  - >1,000: 625
  - 800–999: (+)
  - 600–799: 275
  - 400–599: (–)
  - <400: (–)

- **Balea biplicata**: 
  - >1,000: 650 (800)
  - 800–999: (–)
  - 600–799: 275
  - 400–599: (–)
  - <400: (–)

- **Balea stabilis**: 
  - >1,000: 1,150
  - 800–999: (–)
  - 600–799: 400
  - 400–599: (–)
  - <400: (–)

- **Vestia guio**: 
  - >1,000: 1,100
  - 800–999: (–)
  - 600–799: 275
  - 400–599: (–)
  - <400: 275

- **Vestia turgida**: 
  - >1,000: 1,250
  - 800–999: (–)
  - 600–799: 275
  - 400–599: (–)
  - <400: 275

- **Bulgarica cana**: 
  - >1,000: 1,290
  - 800–999: (–)
  - 600–799: 310
  - 400–599: (–)
  - <400: 310

---

**Legend**

- ↑ 625 Upper limit of distribution; outstanding localities in parenthesis
- ↓ 525 Lower limit of distribution

- (+) – frequency of occurrence higher than expected (χ² test, p<0.05)
- (–) – frequency of occurrence lower than expected (χ² test, p<0.05)
Table 3. Frequency of clausiliid occurrence in different elevation zones (Økland’s method)

<table>
<thead>
<tr>
<th>Species no.</th>
<th>Species</th>
<th>Total for all sites (n=418)</th>
<th>&lt;400 m a.s.l. (n1=45)</th>
<th>400 m–599 m a.s.l. (n2=160)</th>
<th>600 m–799 m a.s.l. (n3=147)</th>
<th>800 m–999 m a.s.l. (n4=35)</th>
<th>&gt;1000 m a.s.l. (n5=31)</th>
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</thead>
<tbody>
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<td></td>
<td>N</td>
<td>100N</td>
<td>100N1</td>
<td>N</td>
<td>F1</td>
<td>1.96S1</td>
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</table>

ni – number of localities in category i
N – total number of localities with the species
Ni – number of localities with the species in i category
Fi – frequency deviation
Si – standard deviation for Fi
* – deviation significantly different from zero at a 0.05 probability level
### Table 4. Frequency of clausiliid occurrence in different habitats (Okland’s method)

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<tr>
<th>Species no.</th>
<th>Species</th>
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<th>100N</th>
<th>N_i</th>
<th>100N_i</th>
<th>F_i</th>
<th>1.96S_i</th>
<th>N</th>
<th>100N</th>
<th>N_i</th>
<th>100N_i</th>
<th>F_i</th>
<th>1.96S_i</th>
<th>N</th>
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<th>N_i</th>
<th>100N_i</th>
<th>F_i</th>
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</tbody>
</table>

n = total number of investigated localities

n_i = number of localities in category i

N = total number of localities with the species.

N_i = number of localities with the species in i category.

F_i = frequency deviation.

S_i = standard deviation for F_i.

* = deviation significantly different from zero at a 0.05 probability level
of the species’ preferred habitat — alder wood. V. gulo and V. turigida were less often found between 800 and 999 m, and M. tumida occurred significantly less frequently in the two highest zones, but it was also recorded in the Bieszczady at 1,175 m a.s.l. χ² test shows that V. gulo avoids the highest altitude division (>1,000 m a.s.l.), and B. cana avoids sites situated below 400 m (in this altitudinal division many deforested habitats were searched for clausiliids).

The rarest species were collected in the lower part of the area: Clausilia pumila – 300–575 m, Balea fallax – 525 m, V. elata – 300–650 m. C. dubia had localities in the upper part of the mountain forest zone (the highest site 1,120 m) and at the northern boundary of the studied area (350 m).

HABITAT DISTRIBUTION

Most clausiliids were found at least sporadically in all the examined types of habitats, but the differences in the constancy of occurrence illustrate their habitat preferences (Table 4, Fig. 4). Based on statistical analyses, two groups of species could be distinguished: I – preferring forests of the lower mountain forest zone and II – preferring humid habitats.

I. Species of the mountain forest zone (B): Cochlodina laminata, C. orthostoma, Bulgarica cana, Macrogastra borealis, Clausilia cruciata and Balea stabilis. These species less often occurred in humid scrub (Cochlodina laminata, C. orthostoma, M. borealis, Bulgarica cana) and in anthropogenic habitats (C. orthostoma, Balea stabilis, Bulgarica cana).

II. Species of humid habitats which significantly more often occurred in humid scrub (Z) and/or in alder woods (O): Balea biplicata, M. tumida, V. turigida and V. gulo. With the exception of V. gulo they occurred less frequently in beech woods (statistically significant differences).

Laciniaria plicata was outside these two groups; it seemed to avoid beech woods, and was significantly more frequent in hornbeam forests of the foothill zone and in anthropogenic habitats. Ruthenica filograna and M. plicatula were quite rare and it was probably the reason why the analyses did not reveal any significant differences.

Almost all species were recorded in all studied habitats, only Clausilia cruciata was never found in hornbeam forest, which grows below the vertical range of the species.

In most studied habitats Macrogastra tumida and Vestia turigida dominated among clausiliids, and Balea stabilis was subdominant. V. gulo reached high abundance in all habitats except anthropogenic ones. M. borealis dominated in beech woods. Compared to other habitats, Cochlodina laminata, C. orthostoma and Bulgarica cana reached a higher dominance class in beech woods and Ruthenica filograna in alder woods. Clausilia cruciata was among dominants in secondary forests. This species and also Balea stabilis and Bulgarica cana reached their highest dominance class there. M. plicatula, Balea biplicata and V. gulo reached the highest dominance classes in humid scrub.

On the basis C and Q indices typical species for different habitat types were distinguished (Table 5). No habitat had an exclusive species.

In the mountain forest zone (B) snails living on trunks and logs prevailed among “fastidious” species. M. tumida, V. turigida and V. gulo (leaf-litter dwellers) had a high Q index, they did not find optimal conditions in beech woods and reached higher frequency classes in alder woods. M. tumida, V. turigida and V. gulo occurred with medium frequency in leaf-litter, but were sporadically found on logs and at the base of trunks. M. tumida and V. gulo, more frequently than other species, inhabited humid microhabitats close to flushes and on the banks of small brooks.

Nearly all clausiliids had a low frequency in forests of the foothill zone (G); three species were moderately frequent (C>40%) there. Laciniaria plicata was found in hornbeam forests more frequently than in other types of habitat (statistically significant difference). Cochlodina laminata may also be classified as a characteristic species, since it had a higher dominance class there compared to other habitats. Bulgarica cana and Macrogastra borealis occurred there frequently, but they found optimal conditions in the mountain forest zone (the highest Q).

Humid forests, alder woods (O), were inhabited by the highest number of species. In leaf-litter eight species of Clausiliidae were found to occur sympatrically.

The clausiliid fauna of secondary forests was very similar to that of beech woods. In the Bieszczady Clausilia cruciata was the characteristic species for this habitat, while in the Beskid Niski there were no characteristic species. Bulgarica cana and Balea stabilis had very similar C and Q values in beech woods and secondary forests with no distinct preference.

Balea biplicata and Macrogastra plicatula may be classified as characteristic for humid scrub, but they occurred only in the Beskid Niski. Vestia gulo had similar C and Q values for humid forests and scrub. The species had a weaker affinity for habitats of low light intensity than other hygrophilous clausiliids. Macrogastra tumida and Vestia turigida occurred with high but not maximal frequency in humid scrub. Humid scrub is not an extremely preferable habitat for clausiliids (C values for all species were lower). The constancy of tree-climbing species (Macrogastra borealis and Bulgarica cana) decreased the most.

Laciniaria plicata was the only species more frequently collected in anthropogenic habitats; it was constant on stonewalls (C>60%), but not so frequently found in other types of man-made habitats. Similarly, Cochlodina laminata and Balea biplicata were more frequently found on stonewalls than in other
Fig. 4. Distribution of Clausiliidae in habitat types

Table 5. Distribution of species in selected habitat types

<table>
<thead>
<tr>
<th>Habitat type*</th>
<th>Characteristic species (fastidiouds)</th>
<th>Accompanying species (indifferent)</th>
<th>Accompanying species (frequenting)</th>
<th>Accidental species</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>Cochlodina laminata</td>
<td>Balea stabilis</td>
<td>Macrogastra tumida</td>
<td>Ruthenica filograna</td>
</tr>
<tr>
<td></td>
<td>C. orthostoma</td>
<td>Bulgarica cana</td>
<td>Vestia gulo</td>
<td>Macrogastora pictata</td>
</tr>
<tr>
<td></td>
<td>Macrogastora borealis</td>
<td></td>
<td>V. turgida</td>
<td>Lacinia cana</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Clausilia cruciata</td>
<td>Balea bicipicata</td>
</tr>
<tr>
<td>G</td>
<td>Lacinia cana</td>
<td>Bulgarica cana</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Can. laminata</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O</td>
<td>Macrogastra tumida</td>
<td>Vestia gulo</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>V. turgida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ruthenica filograna</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>Clausilia cruciata</td>
<td>Bulgarica cana</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>B. bicipicata</td>
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</tr>
<tr>
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<td>Macrogastora borealis</td>
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</tr>
<tr>
<td>Z</td>
<td>Balea bicipicata</td>
<td>Vestia gulo</td>
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</tr>
<tr>
<td></td>
<td>Macrogastora pictata</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>Lacinia cana</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*for explanation see Table 1

Habitat types: B – beech woods, W – secondary forests, G – hornbeam forests, O – alder woods, Z – humid shrub, A – anthropogenic habitats (see Table 1)
(+): frequency of occurrence higher than expected ($\chi^2$ test, p<0.05)
(-): frequency of occurrence lower than expected ($\chi^2$ test, p>0.05)
n = number of samples
anthropogenic habitats. The lowest constancy of all species assessed in anthropogenic sites could be a result of a significant diversity of these sites in terms of humidity and light intensity.

Clausiliids were very seldom found on bare rocks in the studied area. Lacinaria plicata was the most common species here.

Habitats above the timberline (P) were inhabited by six species of clausiliids. The most frequent were Vestia turgida (C>80%) and Macrogastra tumida (C>40%). Clausilia cruciata was abundant only on the Bukowe Berdo Mt.

It is remarkable that the occurrence of species in alluvial deposits (N) depended on their habitat and microhabitat preferences rather than on their overall abundance. Macrogastra tumida, Vestia gulo, V. turgida were found most frequently and abundantly; they live in leaf litter in humid alluvial forest or scrub and may be easily washed out by flood. C. laminata (very frequent) and L. plicata (very abundant) inhabited stonewalls and bridges in the river valleys. C. orthostoma and Clausilia cruciata were missing in alluvial deposits, Bulgarica cana and M. borealis were rare and not abundant, since tree-climbing species are less vulnerable to flooding.

**MICROHABITATS**

Microhabitat preferences of clausiliids of the lower mountain forest zone are shown in Fig. 5. Cochlodina laminata, C. orthostoma, Clausilia cruciata, Macrogastra tumida, M. borealis, Vestia gulo, V. turgida and Bulgarica

![Distribution of Clausiliidae among different microhabitats in mountain forest](image-url)
canae differed significantly in their frequency in leaf-litter and on timber. *M. tumida*, *V. turgida* and *V. gulo* occurred mostly in litter, but sporadically were found on logs and on the base of tree trunks. *M. tumida* and *V. gulo* were most often found in very wet places near flushes and close to brooks. Other species were not usually found in leaf-litter. *Cochlodina orthostoma* showed a clear affinity to live trees, and other species climbed both trunks and logs without significant preferences ($\chi^2$ test, p>0.05). *Balea stabilis* could not be associated with any microhabitat.

The frequency of *M. tumida*, *V. turgida*, *V. gulo*, *B. stabilis* and *R. filograna* in the 400 cm$^2$ samples was analysed with reference to humidity and the presence of vegetation in the microhabitat (Figs 6 & 7). It appears that the occurrence of the species was determined by the humidity of microhabitat, in both sampling seasons. *V. turgida* occurred in moderately humid microhabitats, while *M. tumida* in moderately and very humid ones. Clausiliids were less frequently found in places devoid of herbs, but only for *V. turgida* (autumn samples) the differences were significant ($\chi^2$ test, p<0.05). *B. stabilis*, *V. gulo* and *R. filograna* were too rare in the samples to be included in the statistical analyses.

CO-OCCURRENCE OF SNAILS AND HERBS

Co-occurrence indices for clausiliids and plant species in samples were low and did not indicate any strong relationship (Table 6).

**CO-OCCURRENCE OF SNAILS AND HERBS**

Co-occurrence indices for clausiliids and plant species in samples were low and did not indicate any strong relationship (Table 6).

**Fig. 6. Distribution of Clausiliidae in microhabitats of different moisture**

*Macrogastra tumida* occurred in 59% samples with *Asarum europaeum* and *Cirsium oleraceum*, 57% with *Cardamine amara*, 30–50% samples with *Stellaria nemorum*, *Lysimachia nemorum* and *Filipendula ulmaria*. The highest co-occurrence index values were recorded for *Macrogastra tumida* and *Stellaria nemorum* and *Lysimachia nemorum*. In spring the species was also found in microhabitats with *Cardamine amara* and *Asarum europaeum*, and in autumn with *Glechoma hirsuta* and *Caltha palustris*.

*Vestia turgida* occurred most often (30–50% samples) in microhabitats with *Asarum europaeum*, *Lysimachia nemorum*, *Cardamine pratensis*, *Chrysosplenium alternifolium*, *Petasites sp.*, *Mercurialis perennis* and *Ajuga reptans*. The highest co-occurrence index was found for *V. turgida* and *Lysimachia nemorum* (spring and autumn), *Stellaria nemorum* and *Glechoma hirsuta* (autumn).

43% samples with *Balea stabilis* derived from microhabitats close to trunks and logs. Every fourth sample and 45% specimens were collected under *Acer*. The species showed no preference for herb vegetation.

*Vestia gulo* was found in 81% samples with *Cardamine amara* and 56% with *Cardiha palustris*. The species occurred also frequently (30–50% samples) close to other plant species typical for humid forests: *Chrysosplenium alternifolium*, *Cirsium oleraceum*, *Filipendula ulmaria*. High values of co-occurrence index were recorded for *V. gulo* and *Cardamine amara*, *Caltha palustris* and *Umbeliferae*.
Ruthenica filograna was collected under Alnus incana (30% samples). The highest co-occurrence index was recorded for R. filograna and Glechoma hirsuta.

CO-OCCURRENCE OF CLAUSILIIDS

Several clausiliid species may co-occur in the same site (Fig. 8). The maximum number of species co-occurring in one site was nine, inhabiting trunks, logs and leaf-litter (Berežki, secondary forest). Bulgarica cana, Macrogastra borealis, Clausilia cruciata, Cochlodina orthostoma and, to a lesser extent, Balea stabilis constituted the group of species inhabiting the mountain forest zone and climbing trees. Clausilia cruciata and Cochlodina orthostoma formed a subgroup, because they occurred only in the highest part of the Bieszczady.

Among other species, Vestiia gulo and Macrogastra tumida co-occurred in humid places, in alder woods and leaf-litter. (Berežki, secondary forest). Bulgarica cana, Macrogastra borealis, Clausilia cruciata, Cochlodina orthostoma and, to a lesser extent, Balea stabilis constituted the group of species inhabiting the mountain forest zone and climbing trees. Clausilia cruciata and Cochlodina orthostoma formed a subgroup, because they occurred only in the highest part of the Bieszczady.

Fig. 7. Distribution of Clausiliidae in microhabitats of different herb cover

Fig. 8. Co-occurrence of Clausiliidae in the studied area
Table 6. Co-occurrence indices for clausiliids and plant species (in 400 cm$^2$ samples)

<table>
<thead>
<tr>
<th>Plant species</th>
<th>All samples n=550</th>
<th>Spring samples n=275</th>
<th>Autumn samples n=275</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clausiliidae</td>
<td>Clausiliidae</td>
<td>Clausiliidae</td>
</tr>
<tr>
<td></td>
<td>M. tumida</td>
<td>V. turgida</td>
<td>V. gulo</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. tumida</td>
<td>a 106</td>
<td>81</td>
<td>50</td>
</tr>
<tr>
<td>V. turgida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. gulo</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R. filogr.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. stabilis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Czekanowski’s index</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stellaria nemorum</td>
<td>116 0.28 0.23 0.11 0.12 0.01</td>
<td>60 0.28 0.15 0.09 0.17 0.03</td>
<td>56 0.28 0.32 0.12 0.08</td>
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<td>Oxalis acetosella</td>
<td>96 0.08 0.12 0.01 0.02 0.05</td>
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<td>48 0.06 0.09 0.03 0.10</td>
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<td>Galium odoratum</td>
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<td>Glechoma hirsuta</td>
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<td>0.30 0.13</td>
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<td>Lysimachia nemorum</td>
<td>44 0.24 0.37 0.06 0.05 0.06</td>
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<td>Cardia palustris</td>
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<td>Chrysopogon alternifolius</td>
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<td>Filicinae</td>
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<td>10 0.03 0.09</td>
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<td>Festuca drymeja</td>
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<tr>
<td>Rumex alpinus</td>
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<td>8 0.06 0.09 0.06</td>
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</table>
Table 6 continued

<table>
<thead>
<tr>
<th>Plant species</th>
<th>All samples n=550</th>
<th>Spring samples n=275</th>
<th>Autumn samples n=275</th>
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<td>Clausiliidae</td>
<td>Clausiliidae</td>
<td>Clausiliidae</td>
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<tr>
<td></td>
<td>M. tumida V. turgida V. gulo R. filogr. B. stabilis</td>
<td>M. tumida V. turgida V. gulo R. filogr. B. stabilis</td>
<td>M. tumida V. turgida V. gulo R. filogr. B. stabilis</td>
</tr>
<tr>
<td></td>
<td>a 106 81 50 34 21</td>
<td>a 54 36 25 12 9</td>
<td>a 52 45 25 22 12</td>
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<td>b Czekanowski’s index</td>
<td>b Czekanowski’s index</td>
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<tr>
<td>Asarum europaeum</td>
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<td>Cirsium oleraceum</td>
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<tr>
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<td>Anemone nemorosa</td>
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<td>Milium effusum</td>
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<td>Filipendula ulmaria</td>
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<td>5 0.08</td>
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<td>9</td>
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<td>Rubus idaeus</td>
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<td>6 0.07</td>
<td>7 0.04 0.11</td>
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<td>Lunaria meliviva</td>
<td>10 0.03</td>
<td>7 0.03</td>
<td>3 0.04</td>
</tr>
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</table>

n – number of samples, a – number of samples with snail species, b – number of samples with plant species; values of Czekanowski’s index > 0.20 are underlined
and on stony river banks, while *Vestia turgida* and *Ruthenica filograna* were found together also in humid alder woods, but avoided less permeable places.

*Cochlodina laminata*, *Clausilia pumila*, *Balea biplicata* and *Vestia elata* constituted a closely-knit group. They occurred in the lower part of the studied area in humid alluvial forests. A separate pair of species (*Macrogastra plicatula* and *Laciniaria plicata*) was typical for humid habitats, as well as for anthropogenic ones.

In microhabitats (20 cm × 20 cm), no more than three species were recorded together. *M. tumida*, *V. turgida* and *R. filograna* most frequently co-occurred. In alder swamps *M. tumida* and *V. gulo* had the highest co-occurrence index. *B. stabilis* occurred in the same microhabitats as *V. turgida*. *M. tumida* was found usually with *V. turgida*, but in alder swamps with *V. gulo*. Members of the genus *Vestia* replaced each other in microhabitats (low co-occurrence values in all investigated sites). *V. gulo* was found in very humid places, even submerged and *V. turgida* in moderately humid, not swampy patches.

**SPECIES REVIEW**

1. **Cochlodina laminata** (Montagu, 1803)

   No. of specimens: 455


   **Zoogeography:** The species is distributed almost throughout Europe, except its northern and southern fringes (LIKHAREV 1962). It is the most common clausiliid in Poland, widespread in the whole country (RIEDEL 1988). *C. laminata* was collected on the Pogórze and in the Sanocko-Turczańskie Mts by KOTUŁA (1882). It was first recorded from the Bieszczady (without exact localities) by RIEDEL (1988) and from the Beskid Niski by JACKIEWICZ & RAFALSKI (1960).

   *C. laminata* is common in the Beskid Niski, in the Sanocko-Turczańskie Mts and in the western part of the Bieszczady (the Os³awa River catchment area) (Fig. 9). In contrast, it is rare and not abundant in the highest part of the Bieszczady, where a few localities in the Polonina Wielka range were found. In the Slovak part of the Eastern Carpathians *C. laminata* is less common than in the Western Carpathians (LOZEK & GULIĆKA 1962), and it was not recorded from the nature reserve "Stužica" (LOZEK & GULIĆKA 1955). According to BAKOWSKI (1882), the species is also rare in the highest range of the Eastern Beskid (Czarnohora, Ukraine)

![Fig. 9. Distribution of Cochlodina laminata in the studied area](image)
**Vertical distribution:** *C. laminata* reaches 1,900 m a.s.l. in the Swiss Alps (Kerney et al. 1983) and 2,330 m in the eastern part of the Austrian Alps (Frank 1992). In the Carpathians (Tatra Mts) some specimens were collected at 1,700 m (Dyduch-Falniowska 1991), but only in the lower mountain forest zone *C. laminata* was found frequently (Kotula 1884, Dyduch-Falniowska 1991). Similarly, in the Eastern Carpathians in Ukraine the clausiliid reaches the upper range of the lower mountain forest zone (1,200–1,300 m a.s.l.), and only on southern slopes enters the lower parts of the upper mountain forest zone (Baidashnikov 1989).

In the studied region *C. laminata* was significantly more frequent in the localities below 400 m a.s.l. and only sporadically found higher than 800 m (the highest site at 1,075 m). The vertical range of the species in the Bieszczady is lower in comparison with its records from the Western Carpathians.

**Habitat:** *C. laminata* inhabits deciduous and mixed forests, in the mountains also coniferous woods, it is less often found in scrub, parks and gardens. It prefers moderately humid and shaded habitats. In wet weather it climbs rocks and tree trunks (Riedel 1988). The snails hide under ground litter, stones and logs (Urbański 1939). According to Ložek (1962) *C. laminata* tolerates low calcium content in the soil, but Falkner et al. (2001) claim that the species is associated with calcareous sites.

The species was found in most studied habitats (Bz, Bp, Bk, Bw, G, O, Z, W, Az, Am, Amw) it was collected from trunks of *Fagus, Acer pseudoplatanus, Carpinus, Fraxinus, Salix caprea, Alnus incana* and *Ulmus*, and from logs of *Fagus, Acer pseudoplatanus* and less often of *Abies*. *C. laminata* prefers beech woods and avoids humid scrub. In beech woods it climbs logs, stumps (47% samples from beech wood) and trunks (34%). Additionally, it was one of the species found frequently in hornbeam forests.

2. **Cochlodina orthostoma** (Menke, 1828)

No. of specimens: 450

**Sites:** 5, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21, 22, 24, 25, 27, 34, 39, 46, 47, 48, 49, 52, 53, 54, 55, 56, 59, 61, 62, 63, 68, 72, 73, 76, 77, 79, 80, 82, 83, 84, 85, 87, 93, 95, 111, 114, 117, 118, 119, 128, 131, 133, 141, 148, 156, 158, 161, 172, 174, 173, 187, 189, 190, 192, 213

**Zoogeography:** The distribution range of *C. orthostoma* consists of two isolated parts: the lowland range (south-eastern coast of the Baltic Sea and Middle Russian Upland) and the mountain part (the Carpathians and west to upper Bavaria, isolated localities in Switzerland) (Likharev 1962). In Poland the species inhabits the northern part of the country, as well as mountains and uplands (Riedel 1988). The species was recorded from the Bieszczady by Kotula.
C. orthostoma is rare in the Beskid Niski and inhabits only higher mountain ridges (Fig. 10). In the Western Bieszczady it is widely distributed, and in the vicinity of Ustrzyki Górne the species is even common. In the Sanocko-Turczańskie Mts C. orthostoma is rare.

**Vertical distribution:** In the Southern Carpathians the species reaches 2,000 m a.s.l. (SOÖS 1959). In the Eastern Carpathians in Ukraine it is distributed from uplands to the lower mountain forest zone, and on southern slopes also to the upper mountain forest zone (to 1,500–1,600 m a.s.l.) (BAIDASHNIKOV 1989). According to KOTULA (1884) and STOBIECKI (1880), C. orthostoma reached the upper limit of its distribution at 1,600 m in the Western Carpathians. At present, the species is only sporadically found above 1,400 m (DYDUC-FALNIOWSKA 1991). In comparison with the 19th c. records, it has become less frequent in the whole Tatra Mts and only single specimens are usually found (DYDUC-FALNIOWSKA 1991). In the Slovak part of the Bieszczady C. orthostoma is distributed in the mountain forest and subalpine zones, and less frequent in submontane localities (LOŻEK & GULIČKA 1962). In the studied region C. orthostoma was collected from 350 m (site 114) up to 1,200 m (site 8), being significantly more frequent above 800 m a.s.l., and only sporadically found below 600 m a.s.l.

**Habitat:** Cochlodina orthostoma inhabits moderately humid places, deciduous and mixed forests, mountain meadows. It climbs tree trunks and rocks (ALEXANDROWICZ 1987, RIEDEL 1988). According to LOŻEK (1962) the species tolerates low calcium content in the soil, but is a calciphile according to FALKNER et al. (2001).

The species was collected in all the studied habitats. C. orthostoma was most abundant in the mountain forest zone, above all on trunks (69% samples in beech woods). It was collected from Acer pseudoplatanus, Fagus, Salix caprea, Alnus incana, Carpinus, Ulmus and Fraxinus, also from logs of Fagus and Acer. According to URBANSKI (1939), it lives mainly on the ground under leaf litter, logs, stones and it is not closely associated with tree trunks which it climbs only during wet weather. It avoids localities with direct human influence and humid scrub. However, it was also found on the mount Krzemień above the timberline, in the patch of Rumex alpinus. In sycamore forests the density of C. orthostoma ranged from 1 to 13 specimens m⁻², and the snails aggregated close to sycamore trunks.

3. Ruthenica filograna (Rossmässler, 1836)

**No. of specimens:** 477

**Sites:** 10, 15, 16, 17, 18, 19, 26, 27, 29, 32 (N), 35, 45, 49, 59, 61, 85, 106, 119, 127, 129, 130, 140, 141, 143, 156, 168, 176, 198, 203, 215

**Zoogeography:** R. filograna is an Eastern European species, distributed over almost whole of Poland, Lithuania, Latvia, Estonia, the whole Carpathians and to southeastern Alps (LIKHAREV 1962). Isolated localities are known from the French Alps at the Mediterranean Sea and from E. and S. Germany and Switzerland (KERN et al. 1983). In Poland it is very rare in many regions and locally its populations seem to have become extinct (RIEDEL 1988).

In the studied region a few localities were previously known from the Sanocko-Turczańskie Mts (KOTULA 1882, BAKOWSKI & ŁOMNICKI 1892), the Bieszczady (RIEDEL 1988), vicinity of Dukla and Uście Gorlickie in the Beskid Niski (JACKIEWICZ & RAFLAŚK 1960, RIEDEL 1988). In this study, scattered populations of R. filograna (often very dense) were found in the Beskid Niski and in the Western Bieszczady (Fig. 11). In contrast, in the Sanocko-Turczańskie Mts the species was recorded from one locality only (106).

**Vertical distribution:** In the Alps R. filograna reaches 1,700 m a.s.l. Its vertical distribution in the Eastern Carpathians is limited to the submontane and lower part of the lower mountain zone (BAIDASHNIKOV 1989), but according to BAKOWSKI (1882) the species was found even at 1,200 m a.s.l. From the Tatra Mts it was recorded by KOTULA (1884) (even from 1,600 m), and URBANSKI (1947), however recent studies have not confirmed the occurrence of R. filograna in the region (DZIECZKOWSKI 1972, DYDUC-FALNIOWSKA 1991). In the Fatra Mts (Slovakia) the species is found up to 1,350 m (ŁSICKÝ & ŁOŻEK 1969). In eastern Slovakia it was recorded only from submontane forests (up to 600–700 m) (ŁOŻEK & GULIČKA 1962). This is compatible with the present results from the Bieszczady and the Beskid Niski Mts, where most R. filograna were found at 325–725 m a.s.l. There was only one sample of the clausiliid from an exceptionally high situated locality – Polonina Wielnińska (±1,000 m, 1953, leg. B. BURAWSKI). In my opinion the sample was probably mislabelled, but it might also suggest a wider vertical range of the species.

**Habitat:** R. filograna inhabits moderately humid, shaded mixed and deciduous forests. It lives in ground litter and under stones. It is often classified as a petrophilic and calciphile (KERN et al. 1983, ALEXANDROWICZ 1987, RIEDEL 1988). According to LOŻEK (1962), R. filograna tolerates low calcium content. FALKNER et al. (2001) reported that the species may be found in humid but well drained areas. Its extinction in some areas is likely to be associated with gradual deforestation (PIECHOCKI 1981).

In the studied region R. filograna was collected in humid leaf litter of different habitats (Bz, Bkl, Bw, G, O, Z, W, Az, Am). The preference for humid beech woods with Acer pseudoplatanus and Lunaria rediviva and also for alder woods and humid scrub is remarkable. A high density of R. filograna (26–61 specimen m⁻²) and very high constancy (>60%) were recorded in alder woods (Alnetum incanae carpathicum).
Macrogastra ventricosa (Draparnaud, 1801)

The occurrence of M. ventricosa in the studied region was not confirmed.

Zoogeography: This is a Central European species inhabiting the Alps, the Dinaric Alps, northern part of the Carpathians, lowlands of Central Europe and the Baltic States (LIKHAREV 1962, RIEDEL 1988). According to many authors (BAKOWSKI & ŁOMICKI 1892, GROSSU 1981, BAIDASHNIKOV 1989), the species does not occur in the Eastern Carpathians. The only locality in the Carpathian Region was reported by BAIDASHNIKOV (1992, 1996) who repeated the information given by ADAMOWICZ (1939). In Slovakia the species is very rare in the eastern part of the country. The easternmost localities are in the Slanské Vrchy (ŁOŻEK 1970) and on the river Topla in Bardejov region (ROTARIDES & WEIS 1950, after LISICKÝ 1991).

In Poland M. ventricosa inhabits most of the country, but is absent from some eastern and central regions (RIEDEL 1988). It is found sporadically in the Tatra Mts (KOTULA 1884, DZIECKOWSKI 1972, DUDUCH-FALNIOWSKA 1988, 1991). It was also reported from Muszyńska in the Beskid Sądecki by DOMOKOS & KOVACS (1992), but it was not mentioned from the same locality by ALEXANDROWICZ (1984).

In the 19th c., M. ventricosa was reported from Strzyżów in the Beskid Wschodni region (KRÓL 1879). Unpublished information from I. M. LIKHAREV and M. CHOJECKI on the occurrence of M. ventricosa in the Bieszczady is mentioned in the Catalogue of the Fauna of Poland (RIEDEL 1988). However, I did not find any specimens of M. ventricosa from the Bieszczady in the collection of the Museum and Institute of Zoology PAS, Warsaw, where LIKHAREV’s and CHOJECKI’s samples were kept. Moreover, there were some samples from the Bieszczady, misidentified by LIKHAREV and CHOJECKI as M. ventricosa, but they actually contained only M. tumida: Otryt (2 specimens), Cisna Roźki (8), Cisna (7), Dverniki Średni Wierch (8), Dverniki (2), Dvernicyzek (1), Chimiel (2), Hnatowe Berdo (2), Wetlina (1), Ustrzyki Górne (2). My identification was confirmed by H. NORDSIECK (personal communication). I did not find M. ventricosa from the studied region neither in any other collection, nor during field studies, thus the occurrence of the species in the Bieszczady, the Sanocko-Turczański Mts and the Beskid Niski can be excluded. Whether the species inhabits the northern part of the Beskid Wschodni region (sensu RIEDEL 1988) needs confirmation.

4. Macrogastra plicatula (Draparnaud, 1801)

No. of specimens: 162

Sites: 128, 131, 133, 134, 135, 137, 138, 139, 143, 145, 146, 147, 148, 149, 151, 152, 153, 156, 158, 159, 185, 204, 215, 216, 217, 218

Zoogeography: A Central European species, reaching north to the southern part of the Scandinavian Peninsula, Finland and central Russia. It has also isolated populations in the Southern Carpathians and

Fig. 11. Distribution of Ruthenica filograna in the studied area
the Crimean Peninsula (RIEDEL 1988). It is widespread in the western, northern and southwestern part of Poland, but very rare in central and eastern regions (URBAŃSKI 1957, RIEDEL 1988). Similarly, it is very rare in eastern Slovakia, the only locality in the Carpathians was found in the vicinity of the sources of the river Wisłok (LISICKÝ 1991). In the Tatra Mts, *M. plicatula* is one of the most common doorsnails (KOTULA 1884, DYDUCH-FALNIOWSKA 1991) and often forms dense populations (HUDEC & BRABENEC 1961). The species is widespread in the Pieniny Mts, but less numerous than in the Babia Góra range and in the Tatra Mts (URBAŃSKI 1939). Formerly, it was not recorded from the Bieszczady and the Beskid Niski (RIEDEL 1988). There exist two upland records: Strzyżów (BAKOWSKI 1878, 1884, KROL 1879, BAKOWSKI & ŁOMNICKI 1892) and Błażowa (BRZEK 1933). This information was repeated by SZYBIAK (1997). However, not all the 19th c. records seem reliable. In the collection of PAS, Kraków I found a sample labelled “*Clausilia plicatula*, Strzyżów, zbieral [collected by] Ź. Krol”, which contained only *M. borealis*. I have not managed to find other samples of the former collectors.

In the studied area some localities of *M. plicatula* were found in the eastern part of the Beskid Niski (catchment area of the rivers Jasiołka and Wisłok) and two specimens were collected in the northwestern part of the region in the neighbourhood of Gorlice (sites 185 and 204) (Fig. 12).

**Vertical distribution:** *M. plicatula* reaches above 2,000 m a.s.l. in the Alps, and over the upper limit of *Pinus mugo* (ca. 1,600 m) in the Western Carpathians (RIEDEL 1988). The highest situated locality in the Beskid Niski is at 725 m (site 133). The snail was most often collected between 400 and 600 m a.s.l.

**Habitat:** *M. plicatula* inhabits shady places, mostly in forests. It is a petrophile, climbing also tree trunks, indifferent to chemical composition of the soil (ALEXANDROWICZ 1987). It is also found in leaf litter and under logs (RIEDEL 1988). URBAŃSKI (1939) reported that he collected *M. plicatula* often on trunks in the Tatra Mts and the Babia Góra range, but he found the species in the Pieniny Mts in other microhabitats. In the Sudetes the species inhabits also old spruce stands and meadows adjoining forests (WIKTOR 1964).

In the studied region *M. plicatula* was found in various habitats (Bz, Bp, Bkl, Bw, G, O, Z, W, Az, Am, Aw). It was collected in forests in leaf litter, on trunks (*Alnus incana, Salix caprea, Fagus, Quercus*), as well as on logs (*Alnus and Abies*). In the neighbourhood of Jasłiska (Beskid Niski) it was very abundant in humid scrub and secondary forests.

5. *Macrogastria borealis* (O. Boettger, 1878)

No. of specimens: 1,556

**Sites:** 5, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 25, 27, 28, 29, 34, 35, 36, 37, 40, 41, 42, 43, 46, 47, 48, 49, 52, 54, 57, 58, 59, 61, 62, 63, 64, 65, 66,

![Fig. 12. Distribution of *Macrogastria plicatula* in the studied area](image-url)
Zoogeography: The distribution range of the species consists of two parts: northern – lowlands of northern Poland, Belarus, the Baltic countries and to the neighbourhood of St. Petersburg; and southern – the Carpathians, Transylvania and the Banat Region (LIKHAREV 1962, STEPCZAK 1970). STEPCZAK’s (1970) biometrical analysis showed that snails inhabiting these two areas did not differ significantly and there were no grounds to distinguish subspecies. In Poland *M. borealis* is widespread in the north and in the south (STEPCZAK 1970, RIEDEL 1988). In the Tatra Mts it is far less common than *M. plicatula* (DYDUCH-FALNIAWSKA 1991). There are many records of the species from the Bieszczady and the Beskid Niski (STEPCZAK 1970, RIEDEL 1988). At present, it is one of the most common clausiliids in the studied region (Fig. 13).

Vertical distribution: *M. borealis* does not exceed the limit of 1,200 m a.s.l. (DYDUCH-FALNIAWSKA 1991). Similarly, in the Ukrainian Eastern Carpathians the species does not occur above the lower mountain forest zone (BAIDASHNIKOV 1989). In the studied region the highest locality was located at 1,175 m (site 21), close to the upper limit of vertical distribution of the species. *M. borealis* is significantly less frequent in the samples collected below 400 m a.s.l., and the most frequent between 600 and 1,000 m.

Habitat: According to STEPCZAK (1970), the species is characteristic for the Carpathian lower forest zone and the upland forests. It inhabits mostly beech woods or other deciduous forests and quite often alder woods in river valleys. No preference for any particular tree species was observed. In coniferous forests it is rare, but can be found at the boundary between the lower and higher mountain forest zones. *M. borealis* reaches its highest constancy on logs and rotting stumps, under them and under bark. It is also found in humid habitats: on valley bottoms, forest marshes if logs are present, but not on flooded ground. It is less abundant in leaf litter (ca. 5% specimens) and on tree trunks (STEPCZAK 1970). According to URBAŃSKI (1939) it climbs tree trunks only in wet weather.

In the studied area it was found in various habitats: Bz, Bp, Bkl, Bw, G, O, Z, W, Az, Am, Aw, but only the preference for forests of the lower mountain zone was significant. *M. borealis* dominates there and avoids humid scrub. It reaches a high constancy in beech woods and secondary forests. In the forests, it was frequently collected on logs (48%) and tree trunks (39%). It was most often found on trunks of *Fagus, Acer pseudoplatanus* and *Salix caprea*, less often on *Ulmus, Carpinus, Fraxinus, Alnus, Populus, Abies* and *Malus*. Although the species was recorded from most quantitatively sampled sites, no specimen was found in leaf litter. In my

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Fig. 13. Distribution of *Macrogastrea borealis* in the studied area
opinion the species climbs living trees more frequently than it was formerly reported by URBANSKI (1939) and STĘPCZAK (1970). It shows no clear preference for humid habitats. It may well live in mountain forests of different humidity if only there are some logs and old trunks with bark hanging loosely.

6. *Macrogastra tumida* (Rossmässler, 1836)

No. of specimens: 2,572

**Sites**: 1, 2, 3, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 23, 25, 27, 31, 32, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 46, 47, 48, 49, 50, 51, 55, 59, 60, 61, 62, 63, 64, 65, 66, 67, 70, 71, 72, 73, 80, 82, 83, 85, 86, 87, 88, 89, 90, 91, 92, 95, 98 (N), 99, 102, 103, 104, 105, 106, 107, 109, 113, 116, 119, 120, 123, 125, 127, 128, 129, 130, 132, 134, 138, 139, 140, 141, 143, 146, 147, 148, 149, 155, 156, 157, 159, 166, 167, 168, 172, 173, 174, 175, 176, 178, 180, 183, 184, 192, 193, 195, 196, 197, 198, 203, 205, 206, 207, 208, 209, 210, 211, 215 (N), 217, 221

**Zoogeography**: A Carpathian species, it has also isolated localities in the Sudetes, the Czech Massif and the Šumava Mts; in Poland it inhabits the whole Carpathians and is also found in the southeastern part of Roztocze and in the Sudetes (RIEDEL 1988). It is rare in some parts of its geographical range. According to KOTULA (1884), the species is rare in the Tatra Mts and occurs only sporadically in the upper forest zone. In recent studies (DYDUCH-FALNIOWSKA 1991), it was classified as not abundant but occurring regularly. Similarly, it is widespread but usually not abundant in the Pieniny Mts (URBANSKI 1939). It was recorded from the Bieszczady and the Beskid Wschodni region (RIEDEL 1988). Presently, it is very common in the whole studied area, and often abundant (Fig. 14).

**Vertical distribution**: According to URBANSKI (1939), the upper distribution limit of *M. tumida* follows the timberline, but in the Tatra Mts it reaches as high as 2,100 m a.s.l. (DYDUCH-FALNIOWSKA 1991). In the Ukrainian Carpathians *M. tumida* occurs in all vegetation zones up to subalpine scrub of *Alnus viridis*, *Pinus mugo* and *Larix* (ca. 1,800 m a.s.l.), but is less frequent here (BAIDASHNIKOV 1989). In the studied area *M. tumida* was found between 300 and 1,175 m, also above the timberline, with a significantly lower frequency above 800 m a.s.l.

**Habitat**: The species inhabits mountain forests, where it lives in leaf litter, under stones and rotting timber (RIEDEL 1988). It prefers mixed forests, less often it is found in deciduous or coniferous forests and in scrub. It inhabits shady and humid places, and tolerates low calcium content in the soil (LOŻEK 1962). In the Bieszczady and Beskid Niski it was found in almost all studied habitats (Bz, Bp, Bkl, Bw, G, O, Z, W, Az, Am, Aw, P), but most often in humid scrub. Less frequently it inhabits beech woods and anthropogenic habitats, but sometimes it is also quite abundant there. In the forests of the lower zone it may be found in very humid places on the banks of small brooks and

![Fig. 14. Distribution of *Macrogastra tumida* in the studied area](image-url)
spring bogs (48% samples). It is seldom observed on tree trunks (*Acer pseudoplatanus, Fagus, Alnus incana, Salix caprea, Fraxinus*) and then only on their lower parts. Sporadically, it was found on rotting logs. A high density of *M. tumida* was recorded in litter of *Alnetum incanae carpathicum* (34–49 specimens m⁻²) and of *Caltho-Alnetum* (36–40 specimens m⁻²). *M. tumida* was constant and subdominant in *Alnetum incanae carpathicum*.

7. *Clausilia dubia* Draparnaud, 1805

No. of specimens: 91

**Sites:** 52, 55, 100, 106, 215 (N)

**Zoogeography:** This Central European species inhabits large areas but its populations are usually isolated (LIKHAREV 1962, KERNEY et al. 1983, RIEDEL 1988). In Poland it is found mostly in the mountains. It is one of the most common doorsnails in the Pieniny Mts (URBAŃSKI 1939), but was not formerly recorded from the Polish part of the Bieszczady (RIEDEL 1988). However, it was collected on the southern, Slovak slopes of the Bieszczady (Pasma Graniczne) in the nature reserve “Sużica” (ŁOZEK & GULICKA 1955, 1962). Records from the Beskid Wschodni (RIEDEL 1988) pertain only to the Pogórze region (Odrzykoń castle near Krosno – BAKOWSKI 1878; vicinity of Przemyśl – KOTULA 1882) and the Sanocko-Turczańskie Mts: Kamienna Laworta (KOTULA 1882), or are very general (BAKOWSKI & ŁOMNICKI 1892). I also found a big sample of *C. dubia* from Ustrzyki Dolne (site 100) in the collection of the Institute of Zoology, PAS, Kraków, collected by KOTULA. In recent studies, the species was not found in Ustrzyki Dolne, but in its neighbourhood in Sanocko-Turczańskie Mts (site 106) (Fig. 15). *C. dubia* was also collected on the Polish slopes of Pasma Graniczne (sites 52, 55). These populations are spatially separated. Two empty shells of *C. dubia* were found in alluvial deposits of the Wisłok river, close to the northern border of the Beskid Niski (site 215).

**Vertical range:** *C. dubia* reaches 2,500 m a.s.l. in the Alps (RIEDEL 1988). The species is also found up to the highest parts of the Western Tatra Mts (ca. 2,100 m), and is common in all habitats (DYDUCH-FALNIOWSKA 1991). In the Ukrainian Carpathians it was recorded in the forest zones, and in the Transcarpathia in the submontane zone (BAIDASHNIKOV 1989). The altitude of the new localities in the Bieszczady and the Beskid Niski is 350 m and 1,100 m a.s.l.

**Habitat:** *C. dubia* is a eurytopic species, it is quite often found in dry places, which are avoided by other clausiliids (URBAŃSKI 1939). Mountain and lowland populations live in different habitats. In lowlands *C. dubia* inhabits humid deciduous and mixed forests, where it lives in leaf litter and under bark. In the mountains it prefers shaded rocks in open places (RIEDEL 1988). It is regarded as a petrophile, but rather indifferent to the chemical composition of the substratum (ALEXANDROWICZ 1987). In the Slovak Bieszczady it was observed on trunks of *Acer pseudoplatanus* and *Ulmus*, at 1,000–1,100 m a.s.l. (ŁOZEK &...
Gulička 1962). In the Polish Bieszczady I found *C. dubia* in the lower forest zone (trunks of *Acer pseudoplatanus* and *Fagus*, leaf litter) and in the submontane zone (a shaded stone wall).

8. *Clausilia cruciata* (Studer, 1820)

**No. of specimens:** 328

**Sites:** 1, 2, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21, 25, 34, 35, 39, 61, 62, 69, 70, 72, 76, 77, 84, 85, 87

**Zoogeography:** This is a boreo-alpine species, occurring as isolated populations in large areas of northern Europe (to 65°N) and in the mountains (Kerney et al. 1983; Riedel 1988). It inhabits the whole Carpathians and the Alps (Riedel 1988). In Poland it is quite common in the mountains, and single localities are known in other regions (Riedel 1988). The species was recorded from the Sanocko-Turczęskie Mts (Kotula 1882, 1884, Bakowski & Łomnicki 1892) and from the vicinity of Przemyśl (Bakowski 1884). It was also known from the Bieszczady (Riedel 1988). On the southern slopes of the Carpathians in Slovakia, *C. cruciata* has its easternmost locality in the vicinity of Bardejov (Rotarides & Weiss 1950, after Lisicky 1991), and it was not found in the Slovak Eastern Carpathians (Ložek & Gulička 1962). It is quite rare in the Pieniny Mts (Urbański 1939), and was found in the Beskid Sadecki (Alexandrowicz 1984). In the studied area, *C. cruciata* was found only in the Western Bieszczady and in the Ostre Range, which is a part of Sanocko-Turczęńskie Mts (Fig. 16). Most of the new localities were found in the highest part of the Polish Bieszczady – in the Wołosaty river basin. The species was not recorded from the Beskid Niski, where its range is likely to have a disjunction, as is the case with some other montane species.

**Vertical distribution:** In the Alps *C. cruciata* reaches 2,400 m and the timberline (Kerney et al. 1983). According to Kotula (1884), the upper distribution limit is around 1,450–1,600 m and according to Dyduch-Falniowska (1991) even lower – 1,300 m a.s.l. In the Kłodzko Region *C. cruciata* was found only above 650 m (Wiktör 1964), in Germany above 400 m a.s.l. (Ant 1963). In the Ukrainian Eastern Carpathians it was recorded in the forest zone and in subalpine scrub (less frequently), it was never collected in the submontane zone (below 550 m) (Baidashnikov 1989). The new localities in the Bieszczady are between 525 and 1,180 m a.s.l. Like in Ukraine, *C. cruciata* does not descend to the submontane zone, and abundant populations were recorded above the timberline.

**Habitat:** The species inhabits humid and cool forests, mostly coniferous and mixed. It lives on trunks, stumps, in tree hollows, under bark and stones (Urbański 1939, Riedel 1988). It has no clear preferences for chemical composition of the substratum (Alexandrowicz 1987). In the Bieszczady *C. cruciata* inhabits mostly beech woods, where it lives almost ex-
clusively on trunks and logs. It was not found in quanti-
tative samples of leaf litter. It was collected on trunks of Fagus, Acer pseudoplatanus, Ulmus, Atrites and most
often on living or fallen Salix caprea. It was also found
on logs of Abies. Its abundance is exceptionally high in
secondary forests, where many trees are presently dy-
ing. Dense populations were also recorded in humid
places in subalpine meadows (poloninas).

9. *Clausilia pumila* C. Pfeiffer, 1828

No. of specimens: 96

**Sites:** 32, 33, 34 (N), 35, 209 (N), 217

**Zoogeography:** The species inhabits Central and
Eastern Europe, and along the Carpathians it reaches Banat (LIKHAREV 1962, RIEDEL 1988). In Slovakia *C.
pumila* has its easternmost localities in the Poprad val-
ley (LISICKÝ 1991). In Poland it is widespread, apart
from the Carpathians, where it is rare. It was not re-
corded from the uplands of Southern Poland, the oc-
currence in the Pieniny Mts needs revision (RIEDEL
1988). It was found in the Beskid Sądecki by ALEXANDROWICZ (1984), and in the Slovak part of the
Tatra Mts by KOTULA (1884), but not recorded from the
Polish part (DZIECKOWSKI 1972, DYDUCH-
FALNIOWSKA 1991). It was recorded from the vicinity of
Przemyśl (KOTULA 1882, BAKOWSKI 1884) and
from Dwernik and Ustrzyki Górne in the Bieszczady
(RIEDEL 1988, based on LIKHAREV’s personal commu-
nication). However, considering the vertical range of
the species, the occurrence of *C. pumila* in Ustrzyki
Górne is rather unlikely.

In the present study it was for the first time found
in the Beskid Niski (alluvial deposits of the river Biała, site 209), on the border between the Beskid Niski and
Pogórze Jasielskie (site 217) and in the Western Bie-
szczady (the upper valley of the San River, e.g. Dwern
ik) (Fig. 17).

**Vertical distribution:** According to LIKHAREV
(1962) *C. pumila* reaches 1,400 m. FRANK (1992) col-
lected the species in the Alps at 1,800 m, KOTULA
(1884) at 1,000 m, and WIKTOR (1964) at 1,100 m,
though RIEDEL (1988) claims that the species avoids
higher mountains. This is compatible with records
from the Ukrainian Carpathians, where the species
enters only the submontane zone (450–550 m)
(BAIDASHNIKOV 1989). Similarly, in the studied area
*C. pumila* was found only in the submontane zone
(300–575 m).

**Habitat:** *C. pumila* lives in humid, mostly deciduous
lowland forests and in the valleys of mountain rivers. It
inhabits leaf litter and rotting logs (RIEDEL 1988).
ALEXANDROWICZ (1987) added, that the species could
also be found in humid meadows and mountain mead-
ows. In the studied area *C. pumila* was recorded from
several types of habitats: Bz, G, O, Az, Aw. It was usu-
ally found in leaf litter of humid forests. One dense
population was found in a quite dry place – in a
churchyard under an old linden (site 33).

![Fig. 17. Distribution of *Clausilia pumila* in the studied area](image-url)
10. *Laciniaria plicata* (Draparnaud, 1801)

No. of specimens: 667


**Zoogeography:** *L. plicata* inhabits Central and Eastern Europe, the Carpathians, eastern Balkans, eastern France (Jura, Vosges, Ardennes), Switzerland, parts of Germany, and has scattered localities around the coast of the southern Baltic (LIKHAREV 1962, KERNEY et al. 1983). It is one of the most common clausiliids in lowlands and uplands of Poland, but it avoids higher mountains. It is absent from the Tatra Mts (DZIÊCZKOWSKI 1988, DYDUCH-FALNIOWSKA 1991), and not abundant in the Pieniny Mts (URBAŃSKI 1939). In eastern Slovakia, the species was recorded from the Vihorlat Mts (LISICKÝ 1991) and at the foothills of the Ondavská Vrchnovina Mts (ŁOŻEK & GULIČKA 1962). There are numerous records of *L. plicata* from the Beskid Wschodni (BŁOWSKI 1878, 1884, KRÓŁ 1879, KOTULA 1882, 1884, BAKOWSKI & ŁOMNICZKI 1892, BRZEK 1933), and from the Sanocko-Turczańskie Mts (Wojtkowa) (KOTULA 1882, BŁOWSKI & ŁOMNICZKI 1892). According to RIEDEL (1988), it is absent from the Bieszczady.

At present, the species is quite common in the Beskid Niski and in the Sanocko-Turczańskie Mts (Fig. 18). It was not found in the highest parts of the Western Bieszczady, but there are a few records from the northern fringe of this region. It is absent from the Bieszczady National Park.

**Vertical range** of *L. plicata* varies between regions. In the Alps the species reaches 2,330 m (FRANK 1992). According to KOTULA (1884), it reaches only 650 m a.s.l., but in the Belské Tatra Mts it was recorded from 1,500 m (HUDEC & BRABENEC 1961). The highest situated locality in the Pieniny Mts is at about 750 m (URBAŃSKI 1939). In the Ukrainian Carpathians it enters only the submontane zone (450–550 m a.s.l.) (BAIDASHNIKOV 1989). I collected *L. plicata* in the studied region between 275 and 625 m, most frequently below 400 m.

**Habitat:** It is a eurytopic species, inhabiting leaf litter of deciduous and mixed forests, parks, ruins and rocks (ALEXANDROWICZ 1987, RIEDEL 1988). It may live in more open habitats than other clausiliids (ANT 1963), and is indifferent to low calcium level in the soil (ŁOŻEK 1962). In the Pieniny Mts it was collected in dry woods under rocks, on trunks and stenowalls (URBAŃSKI 1939). I collected *L. plicata* from various habitats: Bk³, Bw, G, O, Z, Az, Am, Aw, S. It was frequently found in anthropogenic habitats, and in hornbeam forests, very rarely in beech woods. It dominated on stenowalls and concrete bridges. It was also collected on sandstones in the vicinity of Ustrzyki Dolne and on steep slopes of flysch.

Fig. 18. Distribution of *Laciniaria plicata* in the studied area
11. *Balea biplicata* (Montagu, 1803)

No. of specimens: 286

**Sites:** 149, 152, 158, 159, 160, 166, 167, 168, 172, 173, 176, 177, 178, 179, 180, 181, 184, 185, 187, 188, 192, 196, 197, 198, 200, 201, 202, 205, 209, 217, 219, 220, 221

**Zoogeography:** *B. biplicata* inhabits Central Europe, and some scattered localities in England and in southern Scandinavia. It is absent from most of the Alps and the Eastern Carpathians, except one isolated locality in Transcarpathia (LIKHAREV 1962). The eastern limit of its distribution range crosses Poland. In the Beskidy the easternmost localities were known in Błażowa, Krosno (Odrzykoń castle), Gorlice (Uście Gorlickie), Krynica (RIEDEL 1988). The species is quite common in the Western Beskidy (STOBIECKI 1883, BAKOWSKI 1884, KOTULA 1884, URBAŃSKI 1932, ALEXANDROWICZ 2003) and in the Pieniny Mts (URBAŃSKI 1939). It was not found in the Polish Tatra Mts (KOTULA 1884, DYDUCH-FALNIOWSKA 1991), but recorded from Kotlina Nowotarska (RIEDEL 1988, based on POLINSKI’s information). It is very rare in eastern Slovakia, the easternmost localities are situated west of the Dukelska Pass in the Topla river valley (LISICKÝ 1991).

I have not recorded *B. biplicata* from the Bieszczady or the Sanocko-Turczańskie Mts (Fig. 19). The easternmost localities in the Beskid Niski are situated in Dukla, nature reserve “Przelom Jasiółki”, Krempna, Konieczna. These are slightly further to the east than the previously known distribution border.

**Vertical distribution:** According to RIEDEL (1988), *B. biplicata* usually avoids higher mountains. However, it was recorded at 2,300 m in the Austrian Alps (FRANK 1992), at 2,000 m in the Slovenian Alps (SOÓS 1959), and at 1,600 m on the Chocz Mts (Slovakia) (URBAŃSKI 1939). In my opinion, the species has a narrower vertical range close to its eastern distribution border – it lives mostly in valleys and avoids higher localities. In the Beskid Niski it was collected at low altitudes, between 275 and 650 m, and significantly more frequently below 400 m a.s.l. Only one locality is at 800 m (leg. PIECHOCKI & ABRASZEWSKA) (site 192).

**Habitat:** *B. biplicata* lives in forests, scrub, parks, and sometimes in dry places among calcareous rocks. It is found under stones, on tree trunks and rocks (URBAŃSKI 1939, RIEDEL 1988). It is indifferent to chemical composition and humidity of substratum (ALEXANDROWICZ 1987). In the Beskid Niski it was collected in various habitats: Bl, Bw, G, O, Z, W, Az, Am, S. It was significantly more frequent in humid scrub and less so in beech woods. It is among dominant clausiliid species on stonewalls.

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**Fig. 19. Distribution of *Balea biplicata* in the studied area**
12. *Balea fallax* (Rossmässler, 1836)

No. of specimens: 2

**Sites:** 100, 103

**Zoogeography:** A Carpathian-Balkan species (URBAŃSKI 1958, RIEDEL 1988). In Ukraine, it inhabits northeastern slopes of the Carpathians and has few localities in Podole (BAIDASHNIKOV 1989, 1996). It is not known from Slovakia (LISICKÝ 1991) and very rare in Poland. According to RIEDEL (1988), it lives only in the Bieszczady, the Beskid Wschodni Region, Roztocze and the Świętokrzyskie Mts (where it is probably extinct now, PIECHOCKI 1981).

According to URBAŃSKI (1958), the species was formerly often confused with *B. stabilis*. This was the case with the collection of the National Natural History Museum in Lviv, gathered probably by BAKOWSKI. Many samples were misidentified. “Good” *B. fallax* in Lviv collection derived from Wojtkowa (district Dobromil, the Sanocko-Turczańskie Mts, north of Ustrzyki Dolne) (2 specimens), and from Ukraine: the Prut river valley (1), Rybno near Ivanofrankovsk (2) and Majdan Górny near Nadwórna (1). Samples from Krynica, Strzyżów, Przemyśl, Tatra Mts, and partly from Wojtkowa (9 specimens) included shells of *B. stabilis*.

Similarly, snails kept in the Institute of Zoology PAS in Kraków, derived from Przemyśl and Sękowa Wola near Sanok and identified by KOTULA as *Clausilia fallax f. minor* are in fact *B. stabilis*. In that collection, I found only one sample of *B. fallax* from the studied region (“Ustrzyki Dolne 1924 ozn. [det.] W. Poliński”) containing 1 specimen. I have not managed to find other samples of *B. fallax* in museum collections.

It is likely, that in KOTULA’s paper (1882) on the molluscs of the San and Strwiąż river basins, two species – *B. stabilis* and *B. fallax* – were mentioned together under the name *B. fallax*. “Good” *B. fallax* was probably found only on the slope of Mt. Osoń in the Sanocko-Turczańskie Mts, 5 km east of Ustrzyki Dolne. KOTULA (1882) stressed, that the specimens from that locality were big (19–20 mm high) and darker. This locality of *B. fallax* was confirmed during the present investigation (Fig. 20). *B. fallax* was found at 525 m a.s.l. in an old beech wood on a piece of rotting timber. POLINSKI’s sample, stored in Kraków, could also derive from the same forest.

**Vertical distribution & habitat:** In Transylvania the species reaches 1,800 m a.s.l. (SOÓS 1943, after URBAŃSKI 1958). In Ukraine *B. fallax* lives in the submontane and lower forest zones (BAIDASHNIKOV 1989). It inhabits leaf litter and rotting timber in humid mountain forests (RIEDEL 1988). According to PIECHOCKI (1990) in Roztocze *B. fallax* is locally very abundant in beech woods and hornbeam forests, especially on loess.

13. *Balea stabilis* (L. Pfeifer, 1847)

No. of specimens: 885

**Sites:** 1, 2, 5, 8, 9, 10, 11, 12, 14, 15, 16, 17, 18, 19, 21, 25, 26, 31, 32, 34, 35, 36, 37, 39, 41, 42, 43, 46, 47,

![Fig. 20. Distribution of Balea fallax and Balea stabilis in the the studied area](image-url)
Zoogeography: It is a Carpathian endemic, inhabiting mostly the Eastern Carpathians, Transylvania and the eastern part of the Western Carpathians (RIEDEL 1988). It is common in the Bieszczady. To the west it reaches the Tatra Mts and Podhale, to the north the vicinity of Przemyśl and probably Strzyżów (RIEDEL 1988). It is quite rare in the Pieniny Mts (URBANSKI 1939). It was numerously recorded in the Tatra Mts, last time by DZIECKOWSKI (1972), but it was not found by DYDUCH-FALNIOWSKA (1991). According to URBANSKI (1957), it was formerly misidentified in museum collections as fallax "smaller form". At present, it is common and quite abundant in the whole studied region (Fig. 20).

Vertical distribution: In Poland it reaches only the upper forest zone (URBANSKI 1957), but in the Ukrainian Eastern Carpathians it inhabits all vegetation zones (BAIDASHNIKOV 1989). On Slovak slopes of the Bieszczady it lives in the submontane and forest zones (LOZEK & GULICA 1962).

I collected B. stabilis between 400 and 1,150 m a.s.l., also above the timberline. It was most frequent between 600 and 800 m.

Habitat: It lives in humid forests under stones, rotting logs and in leaf-litter (RIEDEL 1988). According to URBANSKI (1939), it never climbs tree trunks. However, LOZEK (1956, 1962) found it close to rotting timber, under bark on tree stumps and close to tree trunks. In the studied region the species was most frequently found in beech woods, and rarely in anthropogenic habitats, but it sometimes reached a high abundance there. In many habitats (B, Z, O, Az, W, G, P) it was a subdominant species. Its microhabitat preferences are slightly different from those reported by URBANSKI (1939). In fact, B. stabilis inhabits humid but not wet places, it may be found close to tree trunks and on logs of Alnus, Salix caprea, Fagus, Fraxinus, Abies and Carpinus. Rarely, it was also found on trunks of Fagus, Fraxinus, Acer pseudoplatanus, Salix caprea, Alnus and Ulmus. Its occurrence is not associated with rich, diverse herb layer in the forest.

14. Vestia elata (Rossmannsler, 1836)

No. of specimens: 83

Sites: 35, 42, 43, 128, 130, 132, 149, 215, 217

Zoogeography: The species inhabits the Eastern Carpathians (BAIDASHNIKOV 1989), Podole (BAIDASHNIKOV 1996), the Western Carpathians in central Slovakia (LOZEK 1956, HUDEC 1963) and partly Transylvania and the Southern Carpathians (RIEDEL 1988). In Poland it was formerly known only from the Bieszczady, Pogórze Środłowobeskidzkie (vicinity of

Nineteenth century data on the occurrence of the species in the Polish Carpathians are in many cases misleading (URBAŃSKI 1957). In the collection of the National Natural History Museum in Lviv (BŁKOWSKI’s collection) most samples labelled *V. elata* included specimens of *V. turgida*, sporadically *V. gulo* or other clausiliids. Correctly identified *V. elata* derived from Strzyżów (14 specimens) and from Ukraine: Niżniów (2) and Horodnica (25) in Podole and Worocza (1). There was no *V. elata* in samples from Krynica, Babia Góra, the Tatra Mts, Wojtkowa in the Sanocko-Turczańskie Mts, and in most samples from the Ukrainian Eastern Carpathians. KOTULA (1882) reported *V. elata* from Halicz and Otryt in the Bieszczady. These samples were not found and the former record seems doubtful. The latter locality was confirmed by STWORZEWICZ (1973).

During field work I found new localities *V. elata* in the Bieszczady and first localities in the Beskid Niski (the Wisłok and Jasiołka river banks) (Fig. 22). The occurrence of the species in Dwernik on the San River was confirmed. I have not found the species in the vicinity of Strzyżów.

**Vertical distribution:** In Ukraine the vertical range of the species is limited to the lower and upper forest zones (BAIDASHNIKOV 1989). In Poland it was known to occur in the lower mountain forest zone (URBAŃSKI 1957, PIECHOCKI 1981). I collected *V. elata* between 325 and 650 m a.s.l.

**Habitat:** *V. elata* inhabits humid mountain forests, it lives under rotting logs deep in leaf litter, under bark and in screes (RIEDEL 1988). The species is not associated with any type of the substratum (ALEXANDROWICZ 1987). In the Świętokrzyskie Mts it was collected in forests with *Abies* and *Fagus*, mostly in places with rich shrub and herb layers and deep leaf-litter (PIECHOCKI 1981). In some places it forms very dense populations – ca. 200 specimens m⁻² (PIECHOCKI & BORCZYK 1990). In the Polish Carpathians it was found in humid and rich alder woods on riverbanks, in beech woods, in secondary forests with *Alnus* and *Corylus avellana* and on an old cemetery. In some places the snails were abundant, but the populations were never as dense as those in the Świętokrzyskie Mts.

15. *Vestia gulo* (E.A. Bielz, 1859)

**No. of specimens:** 1,470

**Sites:** 1, 2, 4, 9, 10, 12, 13, 14, 15, 16, 17, 18, 19, 21, 23, 25, 27, 29, 30, 31, 32, 34, 35, 38, 39, 41, 43, 44, 46, 47, 48, 49, 50, 51, 52, 57, 59, 61, 62, 63, 65, 66, 67, 70, 72, 73, 82, 83, 84, 85, 86, 88, 89, 90, 92, 95, 98 (N), 102, 103, 104, 105, 106, 107, 109, 119, 120, 122, 123, 125, 128, 129, 130, 134, 138, 139, 143, 144, 146, 147, 148, 149, 150, 154, 155, 156, 157, 160, 161, 162, 164, 165, 166, 167, 168, 170, 171, 172, 173, 174, 175, 176,

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Fig. 22. Distribution of *Vestia gulo* in the studied area
177, 179, 180, 181, 182, 185, 186, 187, 188, 189, 190, 192, 194, 195, 197, 198, 202, 203, 205, 209, 211, 213, 215, 217, 218, 219, 220

**Zoogeography:** This Carpathian endemic inhabits also Transylvania (RIEDEL 1988). In the Polish Carpathians (e.g. Babia Góra Range – URBANSKI 1932; the Pieniny Mts – URBANSKI 1939) it is quite common, but missing in the Tatra Mts (URBANSKI 1947, 1957, DZIUCH-FALNIOWSKA 1991). It was recorded from the Bieszczady (KOTULA 1882, URBANSKI 1939, KAZUBSKI 1959, RIEDEL 1988) and from the Beskid Niski (JACKIEWICZ & RAFALSKI 1960). Nineteenth century records could be partly misleading, because it was usually reported as *V. turgida* (URBANSKI 1957, RIEDEL 1988). It is common and abundant in the studied area (Fig. 22).

**Vertical distribution:** It occurs in all vegetation zones in the Eastern Carpathians (BAIDASHNIKOV 1989), though according to URBANSKI (1939, 1957) the lower mountain forest zone is the upper limit of its vertical distribution. Exceptionally, URBANSKI (1932) found *V. gulo* at 1,300 m in the Babia Góra Range. I collected the species between 275 and 1,100 m a.s.l., also above the timberline. It was significantly more frequent between 400 and 600 m, less so between 800 and 1,000 m a.s.l. LOZEK & GULICKA (1962) reported *V. gulo* from the subalpine zone on the Slovak slopes of the Bieszczady.

**Habitat:** The species occurs in mountain forests, in very humid places, on the banks of brooks, under stones, among rotting sticks and leaves (RIEDEL 1988). According to URBANSKI (1939) *V. gulo* avoids banks of big streams and rivers; it inhabits surroundings of springs and marshes, often among *Petasites albus*. It was collected together with limnæids on wet soil, on moss-covered stumps and on stones constantly drained with water (URBANSKI 1939). It is indifferent to low calcium content in the soil (LOZEK 1962). In the studied area it was collected in various habitats: Bz, Bp, Bkl, G, O, Z, W, Az, Aw, P. In the lower mountain forest zone it was most often found in very wet places (55% samples). Very rarely it climbs the lower part of trunks of *Acer pseudoplatanus*, *Fraxinus*, *Alnus* and *Salix caprea*. Sometimes it was collected on logs of *Fagus*, *Abies* and *Salix*. It was significantly more frequent in alder woods and humid scrub, rare in anthropogenic habitats. In its preferred habitats it formed dense populations (39–59 specimens m⁻²).

16. *Vestia turgida* (Rossmässler, 1836)

No. of specimens: 1,954

**Sites:** 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19, 21, 23, 25, 26, 27, 29, 31, 32, 34, 35, 37, 39, 41, 42, 46, 48, 49, 50, 51, 52, 55, 57, 59, 58, 61, 62, 64, 65, 67, 71, 72, 80, 85, 86, 87, 88, 89, 90, 119, 120, 127, 128, 130, 129, 132, 134, 135, 138, 141, 143, 144, 146, 148, 149, 155, 156, 161, 162, 166, 167, 168, 169, 173, 174,

Fig. 23. Distribution of *Vestia turgida* in the studied area
Habitat: The species inhabits mountains and submontane areas, humid forests and scrub, forest marshes, but it may also occur in drier habitats (RIEDEL 1988). ŁOŻEK & GULIČKA (1962) claim that on Slovak slopes of the Bieszczady it lives in leaf litter along brooks, in forest marshes and in rich herbage in subalpine zone. However, URBAŃSKI (1939) noticed that V. turgida in the Pieniny Mts avoided wet places (LOŻEK & GULIĆKA 1962). In the studied area it was found in various habitats, but most frequently in alder woods and humid scrub, quite rarely in beech woods, where it mostly stays in leaf-litter (46% samples). Sporadically it may be found on trunks of Fagus, Acer pseudoplatanus, Fraxinus, Ulmus and Salix caprea and on logs of Fagus, Acer pseudoplatanus and Tilia. It inhabits also humid places in open areas, including poloninas. In most habitats it dominates among clausiliids. The highest densities were recorded in Abietum incanae and Aceri-Fagetum (24–49 specimens m⁻²).

Vertical distribution: In the Tatra Mts the species occurs regularly in every type of habitat up to 2,100 m a.s.l. (DYDUCH-FALNIOWSKA 1991), and in the Babia Góra Range up to 1,600 m (URBAŃSKI 1932). Similarly, in the Ukrainian Carpathians it inhabits all vegetation zones (BAIDASHNIKOV 1989). In the Bieszczady the highest localities are located above the timberline, at 1,250 m (sites 6, 8, 21). It is less frequent between 800 and 1,000 m, where the samples were taken mostly on tree trunks.

Habitat: The species inhabits mountains and submontane areas, humid forests and scrub, forest marshes, but it may also occur in drier habitats (RIEDEL 1988). ŁOŻEK & GULIČKA (1962) claim that on Slovak slopes of the Bieszczady it lives in leaf litter along brooks, in forest marshes and in rich herbage in subalpine zone. However, URBAŃSKI (1939) noticed that V. turgida in the Pieniny Mts avoided wet places (e.g. banks of streams), where it was replaced by V. gulo. V. turgida stays on the soil under leaves, in humid places, often under logs and loose-hanging bark of old stumps, it seldom climbs tree trunks (URBAŃSKI 1939). It tolerates low calcium content in soil (ŁOŻEK 1962). It can live on moist meadows and subalpine meadows (ALEXANDROWICZ 1987). In the studied area it was found in various habitats, but most frequently in alder woods and humid scrub, quite rarely in beech woods, where it mostly stays in leaf-litter (46% samples). Sporadically it may be found on trunks of Fagus, Acer pseudoplatanus, Fraxinus, Ulmus and Salix caprea and on logs of Fagus, Acer pseudoplatanus and Tilia. It inhabits also humid places in open areas, including poloninas. In most habitats it dominates among clausiliids. The highest densities were recorded in Abietum incanae and Aceri-Fagetum (24–49 specimens m⁻²).
DISCUSSION

GENERAL DISTRIBUTION AND CONSERVATION STATUS

In the Western Bieszczady 14 clausiliid species were found. *Laciniaria plicata*, inhabiting the northern fringes of the studied region is new for the Bieszczady (see DZIECKOWSKI 1988, RIEDEL 1988). Fifteen species were recorded from the Beskid Niski, four less than the number recorded for the whole Beskid Wschodni region sensu RIEDEL (1988). The Sanocko-Turczañskie Mts, which were studied in less detail, are inhabited by at least 13 clausiliid species. According to RIEDEL (1988), the majority of species are common for the three regions, but *Macrogastra plicatula*, *Clausilia dubia*, *Laciniaria plicata*, *Balea biplicata* and *Balea perversa* were supposed to occur only in the Beskid Wschodni. During the present investigation I found *C. dubia* and *L. plicata* also in the Bieszczady. The only locality of *B. perversa* in southeastern Poland is situated in the Pogórze Dynowskie – outside the geographical scope of the project. Central European species *B. biplicata* and *M. plicatula* live within the geographical boundaries of the Beskid Niski, where they have their eastern distribution limits, and thus do not penetrate into the Bieszczady.

Eight species of Clausiliidae occurring in the Bieszczady and the Beskid Niski are included in the Polish Red List (WIKTOR & RIEDEL 2002) and two more (*Ruthenica filograna* and *Bulgarica cana*) are regarded as endangered by PAWLÓWSKA & POKRYSZKO (1998). The species are exposed to indirect threats such as habitat destruction by logging alluvial forests or changing water regime. Among endangered species *Vestia elata* and *Balea fallax* should have the highest conservation status due to their rarity. Some of the species, mainly Carpathian endemics, endangered globally in Poland, are in fact very common and abundant in the studied area (*M. tumida*, *B. stabilis*, *V. gulo* and *V. turgida*).

HABITAT PREFERENCES

The clausiliid fauna of the submontane hornbeam forests (habitat G) is extremely poor. This is probably a result of massive deforestation in this zone. Small remnants of hornbeam forests are scattered at low altitudes (<500 m a.s.l.), close to their upper distribution limit (ZARZYCKI 1971), where they occupy steep sunny slopes with shallow and dry soil (MICHALIK & SZARY 1997). In the Bieszczady hornbeam forests have

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Fig. 24. Distribution of *Bulgarica cana* in the studied area
survived in small patches along rivers, mostly outside the National Park (MICHALIK & SZARY 1997). In the Beskid Niski most hornbeam forests have been devastated or considerably transformed (MICHALIK & MICHALIK 1998).

According to PISARSKI (1971) the fauna of the Bieszczady hornbeam forests consisted of woodland, skiphilous species. Contrary to what could be expected, woodland clausiliids (ŁOZEK’s (1964) ecological groups 1 and 3) were only sporadically or rarely found there, and the most frequent species L. plicata is an eurytopic snail.

Records from the neighbouring regions support my observations on the poverty of clausiliid communities in the submontane zone. According to KORNUSHEIN (1988), xerophilous snails occur in hornbeam forests in Ukraine, and many woodland snails are missing, especially clausiliids. Only in the most humid places C. laminata, L. plicata and R. filograna can be found. BAIDASHNIKOV (1989) claims, that the malacocoenoses of the submontane zone in the Eastern Carpathians differ from those of higher zones in the presence of C. pumila and L. plicata, and in the Transcarpathia also of Vestia turgida procera. Additionally C. cruciata is absent from the zone. Similarly, KOTULA (1882) regards C. pumila and L. plicata as typical for foothill fauna, compared to higher zones (450–1,340 m). In eastern Slovakia L. plicata, C. laminata, C. orthostoma, R. filograna, M. tumida, M. borealis and B. stabilis occur in submontane malacocoenoses, but on south-facing slopes only L. plicata, C. laminata can be found (ŁOZEK 1961–62, ŁOZEK & GULICKA 1962).

The situation is different in the lowland part of Poland, where malacocoenoses of hornbeam forests are rich, but still Clausiliidae are not their most important components (exception the constant C. laminata) (see DZIECKOWSKI 1988). In the Białowieża Primeval Forest eight species were recorded in hornbeam forests (DYDUCH 1980, DZIECKOWSKI 1988) and L. plicata and M. plicatula dominated (DYDUCH 1980).

The majority of samples were taken in the lower mountain forest zone. The climatic conditions (higher annual rainfall) and abundance of forests favour clausiliid species associated with bark and rotting timber, tree- and log-dwellers, such as C. laminata, C. orthostoma, M. borealis, C. cruciata and B. cana. They inhabit Dentario glandulosae-Fagetum in all the Carpathian ranges in Poland. Their abundance cannot be adequately estimated with quadrat sampling method (see DZIECKOWSKI 1972, 1988). Based on the equal-time sampling I found that M. borealis dominated among clausiliids in the mountain forest zone and C. orthostoma and B. cana belonged to the subdominant group. These species are especially abundant in patches of old, almost natural forests, where rotting timber is not removed.

Litter-dwelling clausiliids (M. tumida, B. stabilis, V. gulo and V. turgida) constitute another group characteristic for mountain forest zone in the Bieszczady and the Beskid Niski. Compared to the entire malacocoenosis in Dentario glandulosae-Fagetum, they are not abundant. These species (except B. stabilis) reach higher dominance classes in sycamore and alder forests. Litter-dwellers are characteristic for the mountain forest zone and missing in submontane forests (DZIECKOWSKI 1971, 1972, 1988), but their occurrence is limited to more humid and fertile patches. Similarly, DYDUCH-FALNIOWSKA & TOBIS (1989) noticed that clausiliids were abundant in beech woods only on the stream banks in the Tatra Mts.

In the Slovak part of the Bieszczady ŁOZEK & GULICKA (1955) recorded the same clausiliid species from the mountain forest zone. They found that C. laminata was missing and M. tumida, V. gulo and V. turgida occurred only along stream banks. According to KOTULA (1882), C. laminata, C. orthostoma, V. turgida, M. tumida, B. cana and B. stabilis were widespread in the zone between 450 and 1,340 m. KOTULA (1882) regarded C. laminata as a characteristic species, presumably because his altitudinal zone “upper foothills” comprised the upper part of the hornbeam forest zone as well as the mountain forest zone. Secondly, he conducted his studies mostly in the Przemyskie Upland and the Sanocko-Turczañskie Mts and not in the Western Bieszczady, where the species is quite rare, at least at present. M. plicatula and C. dubia, which are most widespread and common in the lower mountain forest zone in the Tatra Mts (DYDUCH-FALNIOWSKA 1991), are rare in the studied area and thus recendent in the malacocoenosis structure.

Some clausiliids are found above the timberline in the Bieszczady. V. turgida and M. tumida are most common there. They live close to springs and in patches of tall herbs (Rumex alpinus). Patches of Rumex alpinus are remnants of former intensive sheep and cattle grazing in this zone (ZARYCZYKI 1971). They indicate ammonium-rich places of former cattle pens. In KOTULA’s (1882) time sheepherding was flourishing in the Bieszczady Mts. Unfortunately, he did not sample snails in this zone.

The abiotic factors operating in these localities cannot be directly compared with those of subalpine zone of the Czarnohora or the Tatra Mts. The subalpine zone in the Bieszczady is situated ca. 500 m lower and was at least partly man-made. These factors resulted in many similarities between these localities in the Bieszczady and clearings in the Tatra mountain forest zone, from which DYDUCH-FALNIOWSKA (1990) reported six clausiliid species, with V. turgida as the most common and often abundant. In the Tatra Mts the same clausiliid species occur in clearings and above the timberline (V. turgida, M. tumida, C. dubia and less often M. plicatula) (DYDUCH-FALNIOWSKA 1991). In the Czarnohora V. turgida is also the most
widespread clausiliids in the subalpine zone, besides *M. tumida*, *C. cruciata*, *B. stablis* and *V. gulo* occur there (BAIDASHNIKOV 1989). *V. turgida* and *C. dubia* were recorded in subalpine zone of the Babia Góra Range (URBAÑSKI 1932). ŁOŻEK & GULICKA (1955) found *C. orthostoma*, *B. cana*, *V. turgida* and more rarely *M. borealis* in dwarf beech and sycamore forest, which reaches the highest summits of Slovak slopes of the Bieszczady. The malacocoenoses of the zone above the timberline are still poorly known in the Bieszczady.

Alluvial forests of the studied area (habitat O) have the richest clausiliid fauna, and many species are constant here (C>60%). These habitats are particularly endangered by human influence (KLIMEK 1990). On uplands they have been destroyed as a result of colonisation and agriculture. In the Beskidy they have preserved the diversity of microclimate and vegetation, and are every year restored by flooding. According to BAIDASHNIKOV (1985) mountain species in river valleys are favoured by thermal inversion and cold microclimate; on the other hand hygrophilous species from lower localities could reach higher altitudes through these corridors.

BAIDASHNIKOV (1985) recorded *M. tumida* and *V. gulo* from forests of *Alnus incana* and patches of *Tussilago farfara* in the valleys, and found *V. turgida* in humid places along streams in the mountain forest zone of the Ukrainian Carpathians. *V. gulo*, *B. biplicata*, *R. filigrana*, *L. plicata* and *M. ventricosa* were sub-dominants in the valley of Pieniński Potok (SZYMIAK 2000). Patches of *Petasites* on stream banks adjoining forests were inhabited by *C. sumida* and *B. biplicata* in the Sudetes (POKRYSZKO 1984, MALTZ 1999). Clausiliid fauna of humid scrub in the studied area was similar to those of alder woods, but with lower abundance of tree climbing species. In the Sudetes open humid habitats harbour more clausiliid species than humid forested areas (MALTZ 1999).

The distinction between humid scrub and anthropogenic habitats was based on traces of human influence, but in respect of shadow and vegetation they were often alike. Anthropogenic habitats were investigated in the villages (inhabited and deserted) and along roads and bridges. They were stonewalls, ruins, cemeteries and dumping grounds. Anthropogenic influence is at present strong only in the valleys and in the northern part of the studied area. The region is among the most sparsely populated in the country, and bigger towns are situated outside the geographical borders of the Beskid Niski and the Bieszczady.

Higher calcium and nitrogen content in the soil of anthropogenic habitats could favour the snail occurrence. It is generally known that gastropods are numerous in old ruins (ŁOŻEK 1962). In the studied region all clausiliids were found at least sporadically in man-made habitats. *L. plicata*, which inhabits old stonewalls, shows a higher frequency of occurrence in anthropogenic habitats. The species is light-tolerant (ANT 1963). *L. plecata* and *B. biplicata* are the most common clausiliids in ruins of Carpathian castles (ALEXANDROWICZ 1995). *L. plecata* is also the most widespread clausiliid in Lviv, inhabiting different types of human-influenced habitats (SVERLOVA 1998). According to KOSINSKA (1979), it is indifferent to man-made habitats. On stonewalls I found also *C. laminata*, which, according to KOSINSKA (1979), avoids anthropogenic habitats. Other authors claim that the species is moderately associated with man-made habitats (SVERLOVA 1998, FALKNER et al. 2001). SVERLOVA (2000) found *M. borealis* and *B. cana* in parks in Lviv. In the studied area *B. cana* avoids anthropogenic habitats.

The species composition of clausiliid communities and the frequency of individual species in secondary forests (habitat W) are similar to those in the lower mountain forest zone. It contradicts PISARSKI’s (1971) opinion, that the fauna of this habitat is extremely poor. *Alnus incana* has a positive effect on the chemical composition and structure of the soil. It enriches the soil with nitrogen and increases porosity of clay soils (RYGIEL 1980). *Alnus* leaf-litter is quickly decomposed and becomes a source of easily assimilated food (ZIMKA & STACHURSKI 1976). Feeding experiments with slugs show that leaf-litter of *Alnus glutinosa* and *Salix caprea* is more palatable to them than partly decomposed leaves of *Fagus silvatica* (JENNINGS & BARKHAM 1975). *Alnus incana* lives only 40–50 years, thus secondary forests abound now with logs and rotting trees. In my opinion the number of sites favourable for tree climbing and litter dwelling clausiliids has increased, as alder forest spread after 1947. In the last 50 years snails have migrated from the neighbouring mountain forests and humid scrub to abandoned fields. According to PAUL (1978), *Cochlodina laminata* spreads at a rate of 1 m per year. Thus, it is likely that in the secondary forests only the parts adjoining the sources of colonisers are inhabited by clausiliids.

Although herb cover and plant species richness are the best determinants of clausiliid abundance in forest patches (SULIKOWSKA-DROZD 2005), with respect to microhabitats I found no close association between the snails and herbs. Co-occurrence indices between snail and plant species in 400 cm² samples were low and varied between seasons. Among most common herbs (collected in more than 25 samples), *Lysimachia nemorum*, *Glechoma hirsuta* and to some extent *Petasites* sp. and *Stellaria nemorum* seem to favour the occurrence of clausiliids. In contrast, co-occurrence indices for clausiliids and *Oxalis acetosella*, *Galium odoratum*, *Dentaria glandulosa* and *Symphytum cordatum* were low. DYDUCH-FALNIOWSKA & TOBIS (1989) found similar differences in the occurrence of gastropods between microhabitats with *Oxalis acetosella* and *Petasites albus* in the Tatra Mts. Hygrophilous species (*Caltha palustris*, *Cardamine amara*, *Cirsium oleraceum*, *Filipendula ulmaria*)
were good indicators (constancy >30%) of V. gulo and M. tumida. I suspect that the snails occur in particular humidity, shadow and fertility situations, rather than being directly associated with any herb species. According to GRIME & BLYTHE (1969), CAMERON (1973), and Dyduch-Falniowska & Tobis (1989) co-occurrence between snails and plants is not a result of gastropod food requirements, but depends on abiotic conditions, which are also preferable for plants. Even if herbs are not food source, microhabitats with vegetation may have some advantages for snails. They preserve a higher relative air humidity above the soil and provide shelters to hide from predators. Generally, clausiliids were more frequently found in samples with rich vegetation, but this was statistically confirmed only for V. turgida (autumn sampling).

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