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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-Turczańskie 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.), *Laciniaria plicata* (Drap.) and *Balea biplicata* (Mont.) occur below 800 m a.s.l. *Clausilia 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), *Clausilia 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 *Laciniaria plicata* (Drap.) prefers anthropogenic habitats (e.g. stone walls, cemeteries).

KEY WORDS: 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: Alopiinae (genera: *Cochlodina* Férussac, 1821, *Charpentieria* Stabile, 1864), Clausiliinae (*Clausilia* Draparnaud, 1805, *Ruthenica* Lindholm, 1924, *Macrogastra* Hartmann, 1841) and Baleinae (*Laciniaria* 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 (BĄKOWSKI 1878, KRÓL 1879), Błażowa (BRZĘK 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, Ostrykowiec, Kamienna Laworta, Chwaniów in the Sanocko-Turczańskie Mts). At the same time the malacofaunas of the Carpathians and the submontane zone in Ukraine were investigated (BĄKOWSKI 1881, 1882). The 19th c. malacological studies in the Carpathians were summarized by BĄKOWSKI & ŁOMNICKI (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, Komańcza). 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 LOŽEK & GULIČKA (1955, 1962).

Published records of the malacofauna of the Beskid Niski are limited to a paper on a single locality (Uście Gorlickie) by JACKIEWICZ & RAFALSKI (1960). 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), JACKIEWICZ (1965), STĘPCZAK (1970), STWORZEWICZ (1973), MATZKE (1980), DZIĘCZKOWSKI (1988) and ALEXANDROWICZ (1995).

According to the literature, 13 clausiliids species occur in the Bieszczady (DZIĘCZKOWSKI 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 LOŽEK (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 (FRÖMMING 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 (KONDRACKI 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 Łupkowska Pass (Osława 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 Użocka 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

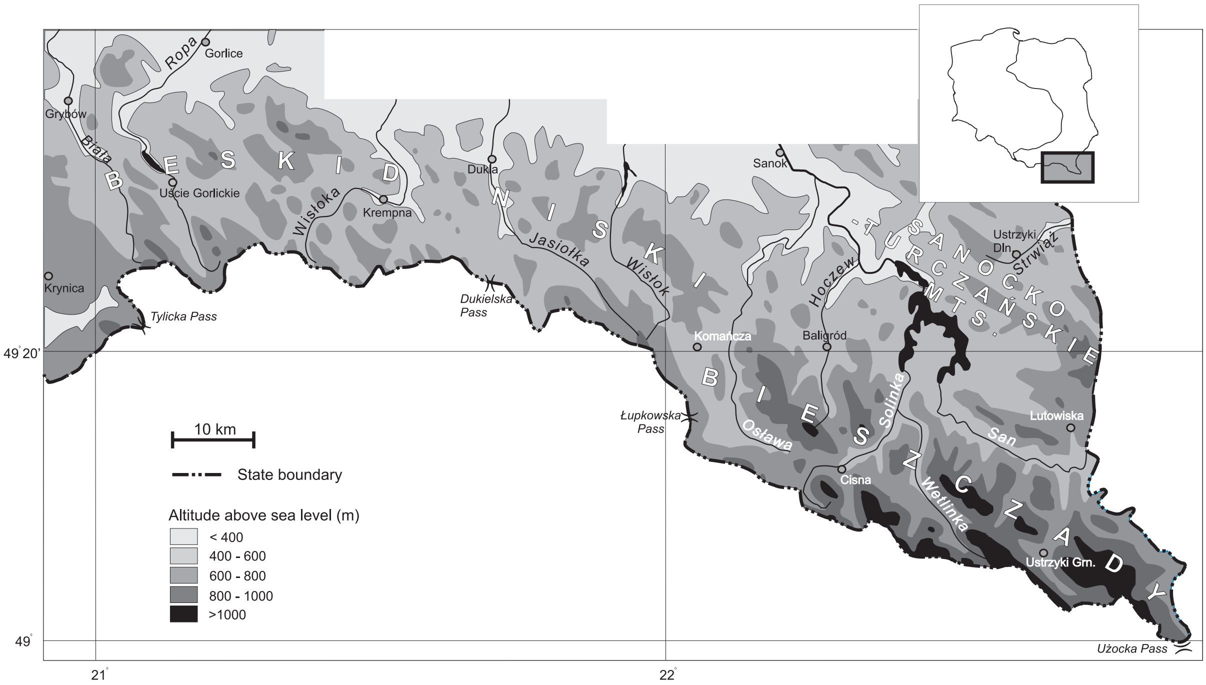

Fig. 1. Study area

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 decalcified 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 origin. 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 (OLSZAŃSKI 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 & GŁOWACIŃSKI 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 & GŁOWACIŃSKI 1986). In the Bieszczady the forested area was reduced in the 19th and 20th centuries due to massive logging (ZARZYCKI & GŁOWACIŃSKI 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 during Operation Vistula in 1947 – to western and northern Poland) (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 & GŁOWACIŃSKI 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 (*Caltho-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 (POLIŃSKI 1927, 1930). Some E. Carpathian species, e.g. *Carpathica calophana* (Westerlund, 1881), *Perforatella dibothrion* (M. Kimakowicz, 1884), or *Trichia bielzi* (E.A. Bielz, 1860) reach as far west as the vicinity of the Dukielska 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 holosericum* (Studer, 1820), do not cover the Bieszczady in the east (RIEDEL 1988). Other W. Carpathian species, e.g. *Trichia lubomirskii* (Ślósarski, 1881), reach the eastern boundary of their ranges in the Bieszczady. In his analysis of the Bieszczady as the zoogeographical region, PAWŁOWSKI (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, Wrocław, Kraków, 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: LOŽEK (1956, 1964), URBAŃSKI (1957), LIKHAREV (1962), KERNEY et al. (1983). The nomenclature and systematic arrangement follow NORDSIECK (1979, 1993). Division into ecological and biogeographical groups follows LOŽEK (1964) and RIEDEL (1988), respectively.

Qualitative 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 Økland frame of 20 cm side in 11 forest patches in the Bieszczady 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 cm^2) 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 malacocoenoses the following indices were applied: dominance (D), the proportion of the species (per cent) in the malacocoenosis, 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

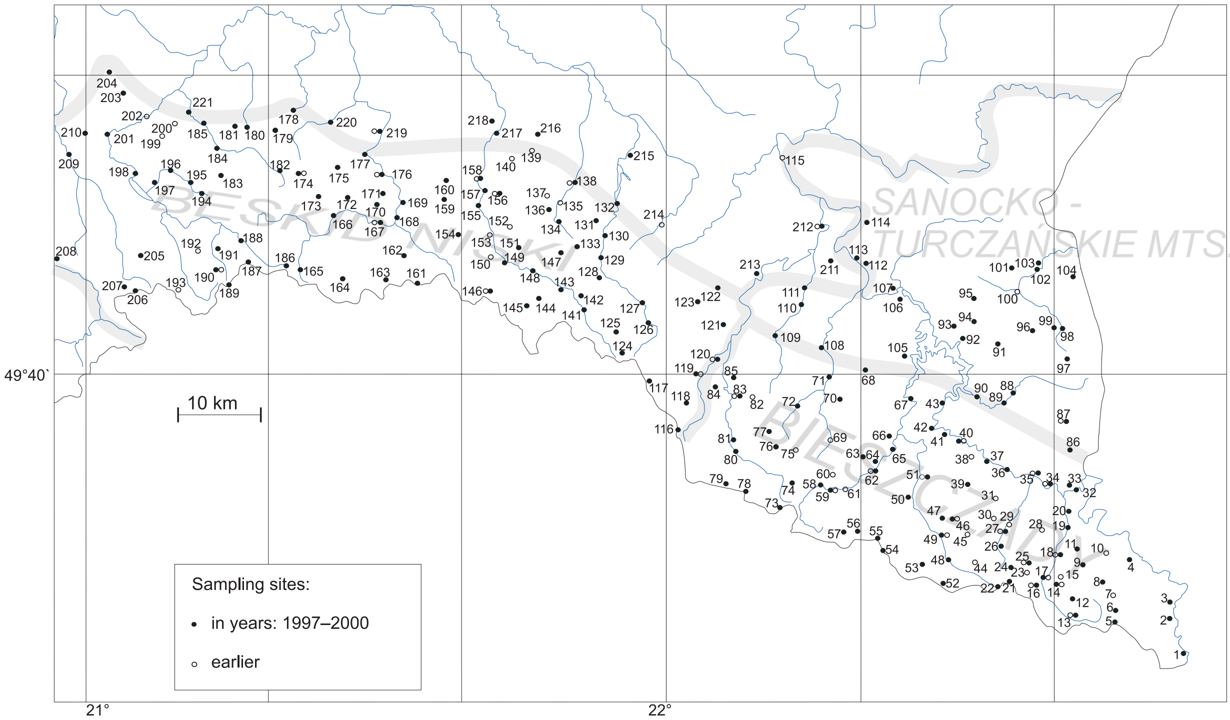

Fig. 2. Sampling sites in the study area

number of sub-samples in the site (DZIĘCZKOWSKI 1988); Q index, which combines dominance and frequency indices in a given type of habitat (GÓRNY & GRÜM 1981). The division of species into characteristic, accompanying and accessory ones follows GÓRNY & GRÜM (1981).

Økland's method (ØKLAND 1990) and χ^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

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

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, Laciniaria 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 higher 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

No	Species	Beskid Niski	Sanocko-Turczańskie Mts	Western Bieszczady
1	*Cochlodina laminata* (Mont.)	+++	+++	++
2	*Cochlodina orthostoma* (Menke)	++	++	+++
3	*Ruthenica filograna* (Rossm.)	++	+	++
4	*Macrogastra plicatula* (Drap.)	++	–	–
5	*Macrogastra borealis* (O. Boet.)	+++	+++	+++
6	*Macrogastra tumida* (Rossm.)	+++	+++	+++
7	*Clausilia dubia* Drap.	N	+	+
8	*Clausilia cruciata* (Stud.)	–	++	+++
9	*Clausilia pumila* C. Pfr.	N	–	+
10	*Laciniaria plicata* (Drap.)	+++	+++	+
11	*Balea biplicata* (Mont.)	+++	–	–
12	*Balea fallax* (Rossm.)	–	+	–
13	*Balea stabilis* (L. Pfr.)	+++	+++	+++
14	*Vestia elata* (Rossm.)	+	–	+
15	*Vestia gulo* (E.A. Bielz)	+++	+++	+++
16	*Vestia turgida* (Rossm.)	+++	++	+++
17	*Bulgarica cana* (Held)	+++	+++	+++
	Number of species	15	13	14

+ 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

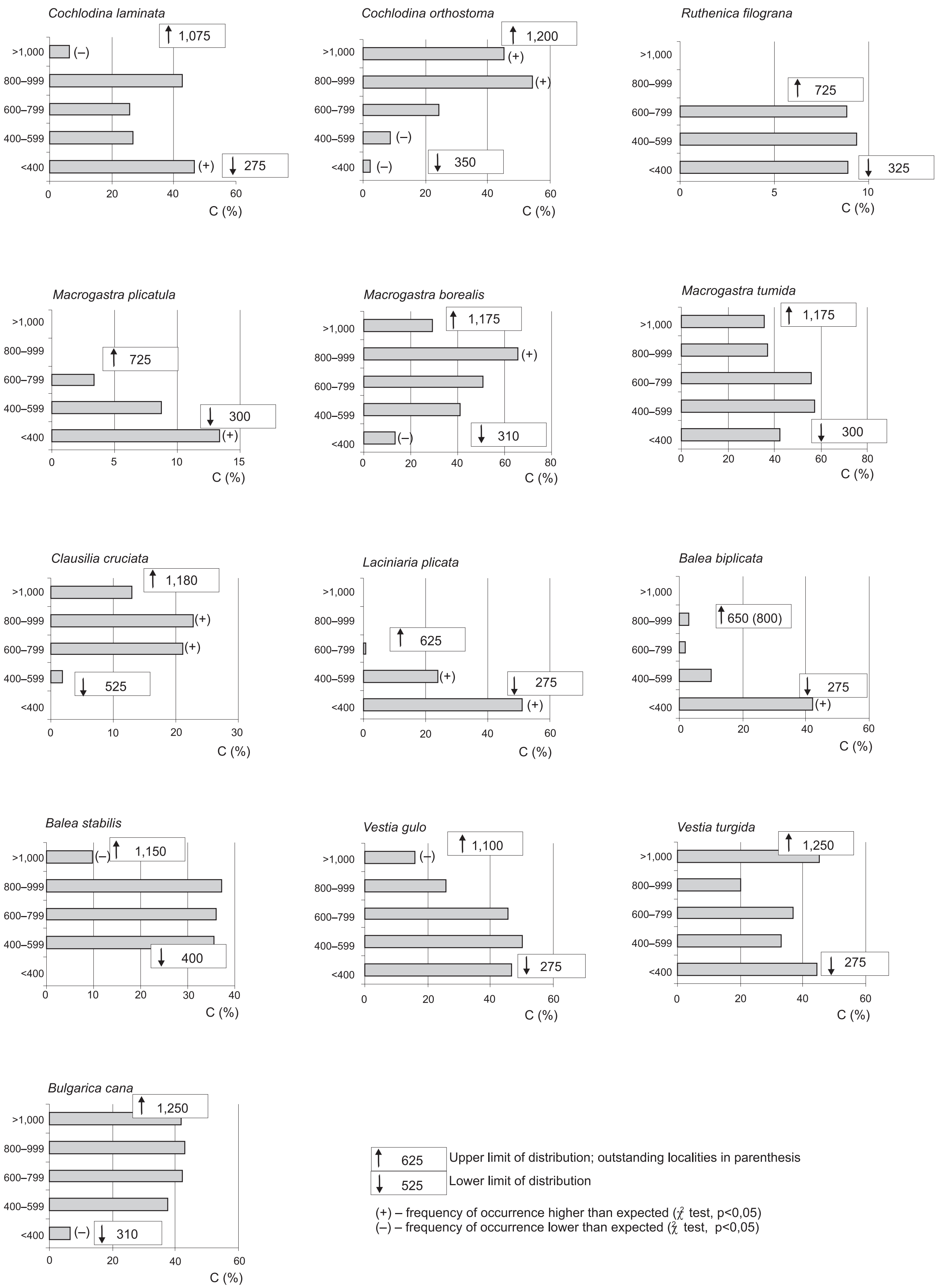

Fig. 3. Vertical distribution of Clausiliidae

Table 3. Frequency of clausiliid occurrence in different elevation zones (Økland's method)

Species no.	Species	Total for all sites (n=418)		<400 m a.s.l. (n_1=45) 10.80%				400 m–599 m a.s.l. (n_2=160) 38.30%				600 m–799 m a.s.l. (n_3=147) 35.20%				800 m–999 m a.s.l. (n_4=35) 8.40%				>1000 m a.s.l. (n_5=31) 7.40%			
		N	$\frac{100N}{418}$	N_1	$\frac{100N_1}{N}$	F_1	$1.96S_1$	N_2	$\frac{100N_2}{N}$	F_2	$1.96S_2$	N_3	$\frac{100N_3}{N}$	F_3	$1.96S_3$	N_4	$\frac{100N_4}{N}$	F_4	$1.96S_4$	N_5	$\frac{100N_5}{N}$	F_5	$1.96S_5$
1	*M. tumida*	217	51.9	19	8.8	–18.5	26	92	42.4	10.7	32	82	37.8	7.4	11	13	6.0	–28.6	20*	11	5.1	–31.1	31*
2	*V. gulo*	182	43.5	21	11.5	6.5	31	80	44.0	14.9	11*	67	36.8	4.5	13	9	5.0	–40.5	32*	5	2.7	–63.5	–29
3	*M. borealis*	179	42.8	6	3.4	–68.5	23*	66	36.9	–3.7	12	75	41.9	19.0	13*	23	12.8	52.4	35*	9	5.0	–32.0	36
4	*B. cana*	153	36.6	3	2.0	–81.5	–20	60	39.2	2.3	14	62	40.5	15.1	15	15	9.8	16.7	43	13	8.5	14.9	45
5	*V. turgida*	148	35.4	20	13.5	25.0	59	53	35.8	–6.5	15	54	36.5	4.0	16	7	4.7	–44.0	36*	14	9.5	28.4	47
6	*B. stabilis*	126	30.1	0	0	–100.0	0	57	45.2	18.0	42	53	42.1	19.6	17*	13	10.3	22.6	50	3	2.4	–67.6	–35
7	*C. laminata*	119	28.5	21	17.6	62.9	47*	43	36.1	–5.7	20	38	31.9	–9.4	21	15	12.6	50.0	274	2	1.7	–77.0	–270
8	*C. orthostoma*	84	20.1	1	1.2	–88.8	–19	14	16.6	–56.7	19*	36	42.8	7.6	20	19	22.6	169.0	75*	14	16.7	125.7	80*
9	*L. plicata*	62	14.8	23	37.1	243.5	78*	38	61.3	60.1	–	1	1.6	–95.5	–9	0	0	–100.0	0	0	0	–100.0	0
10	*C. cruciata*	46	11.0	0	0	–100.0	0	3	6.5	–83.0	–19	31	67.4	91.5	–	8	17.4	107.0	113	4	8.7	17.6	–102
11	*B. biplicata*	39	9.3	19	49.7	350.9	101*	16	41.0	7.0	29	3	7.7	–78.1	–23	1	2.6	–69.0	–60	0	0	–100.0	0
12	*R. filograna*	32	7.7	4	12.5	15.7	–101	15	46.9	22.5	34	13	40.6	15.3	22	0	0	–100.0	0	0	0	–100.0	0
13	*M. plicatula*	25	5.9	6	24.0	122.2	139	14	56.0	46.2	22*	5	20.0	–43.2	–41	0	0	–100.0	0	0	0	–100.0	0

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

Table 4. Frequency of clausiliid occurrence in different habitats (Økland's method)

Species no.	Species	Total for all sites (n=469)		Beechwoods B (n_1=171) 36.50%				Humid scrub Z (n_2=102) 21.70%				Anthropogenic habitats A (n_3=86) 18.30%				Secondary forests W (n_4=44) 9.40%			
		N	100N/469	N_1	$100N_1/N$	F_1	$1.96S_1$	N_2	$100N_2/N$	F_2	$1.96S_2$	N_3	$100N_2/N$	F_2	$1.96S_2$	N_4	$100N_4/N$	F_4	$1.96S_4$
1	*M. tumida*	236	50.3	76	32.2	–11.8	11*	62	26.3	21.2	16*	35	14.8	–19.1	19*	24	10.2	8.5	28
2	*V. gulo*	209	44.6	71	33.9	–7.1	11	70	33.5	54.4	17*	18	8.6	–53.0	18*	18	8.6	–8.5	31
3	*M. borealis*	203	43.3	101	49.7	36.2	18*	27	13.3	–38.7	18*	30	14.8	–19.1	21	24	11.8	25.5	32
4	*B. cana*	163	34.7	81	49.7	36.2	12*	15	9.2	–57.6	18*	22	13.5	–26.2	24*	20	12.3	30.9	39
5	*V. turgida*	162	34.5	34	20.9	–42.7	14*	49	30.2	39.2	22*	30	18.5	1.1	25	13	8.0	–14.9	37
6	*B. stabilis*	142	30.3	68	47.9	31.2	14*	25	17.6	–18.9	25	15	10.6	–42.1	25*	16	11.3	20.2	44
7	*C. laminata*	127	27.1	59	46.5	27.3	16*	19	15.0	–30.9	25	17	13.4	–26.8	29	15	11.8	25.5	49
8	*C. orthostoma*	94	20.0	58	61.7	69.0	9*	6	6.4	–70.5	22	9	9.6	–47.5	31*	13	13.8	46.8	62
9	*L. plicata*	65	13.8	6	9.2	–74.8	20*	16	24.6	13.4	42	22	33.8	84.7	49*	3	4.6	–51.1	–52
10	*C. cruciata*	48	10.2	24	50.0	37.0	22*	5	10.4	–52.1	–39	3	6.3	–65.6	–39	10	20.8	121.3	170
11	*B. biplicata*	42	8.9	5	11.9	–67.4	26*	17	40.5	86.6	54*	12	28.6	56.3	65	3	7.1	–24.5	80
12	*R. filograna*	37	7.9	9	24.3	–33.4	34	11	29.7	36.9	59	5	13.5	–26.2	57	5	13.5	43.6	–107
13	*M. plicatula*	32	6.8	11	34.4	–5.7	38	7	21.8	0.5	60	8	25.0	36.6	72	3	9.4	0	–102

Species no.	Species	Total for all sites (n=469)		Alderwoods O (n_5=29) 6.20%				Hornbeam forests G (n_6=21) 4.50%				Herbage above the timberline P (n_7=12) 2.60%				Rocks S (n_8=4) 0.90%			
		N	100N/469	N_5	$100N_5/N$	F_5	$1.96S_5$	N_6	$100N_6/N$	F_6	$1.96S_6$	N_7	$100N_7/N$	F_7	$1.96S_7$	N_8	$100N_8/N$	F_8	$1.96S_8$
1	*M. tumida*	236	50.3	25	10.6	71.0	–27	8	3.4	–24.4	28	6	2.5	–3.8	–56	0	0	–100.0	0
2	*V. gulo*	209	44.6	23	11.0	77.4	33*	6	2.9	–35.5	–42	3	1.4	–46.2	–54	0	0	–100.0	0
3	*M. borealis*	203	43.3	12	5.9	–4.8	40	9	4.4	–2.2	48	0	0	–100.0	0	0	0	–100.0	0
4	*B. cana*	163	34.7	14	8.6	38.7	50	11	6.7	48.9	59	0	0	–100.0	0	0	0	–100.0	0
5	*V. turgida*	162	34.5	22	13.6	119.4	45*	4	2.5	–44.4	–47	10	6.2	138.5	–63	0	0	–100.0	0
6	*B. stabilis*	142	30.3	11	7.7	24.2	57	5	3.5	–22.2	–60	1	0.7	–73.1	–51	1	0.7	–22.2	–141
7	*C. laminata*	127	27.1	7	5.5	–11.3	56	10	7.9	76.0	77	0	0	–100.0	0	0	0	–100.0	0
8	*C. orthostoma*	94	20.0	4	4.3	–30.6	–62	2	2.1	–53.0	–64	1	1.1	–57.7	–76	1	1.1	22.2	–221
9	*L. plicata*	65	13.8	7	10.8	74.2	105	8	12.3	173.3	140*	0	0	–100.0	0	3	4.6	444.4	–310
10	*C. cruciata*	48	10.2	4	8.3	33.9	–120	0	0	–100.0	0	2	4.2	61.5	–207	0	0	–100.0	0
11	*B. biplicata*	42	8.9	3	7.1	14.5	117	1	2.4	–46.6	102	0	0	–100.0	0	1	2.4	166.6	–467
12	*R. filograna*	37	7.9	6	16.2	161.3	–169	1	2.7	–40.0	115	0	0	–100.0	0	0	0	–100.0	0
13	*M. plicatula*	32	6.8	2	6.3	1.6	–127	1	3.1	–31.1	–131	0	0	–100.0	0	0	0	–100.0	0

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. turgida* 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. χ^2 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 antropogenic 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. turgida* 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 turgida* 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. turgida* 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. turgida* 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 turgida* 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

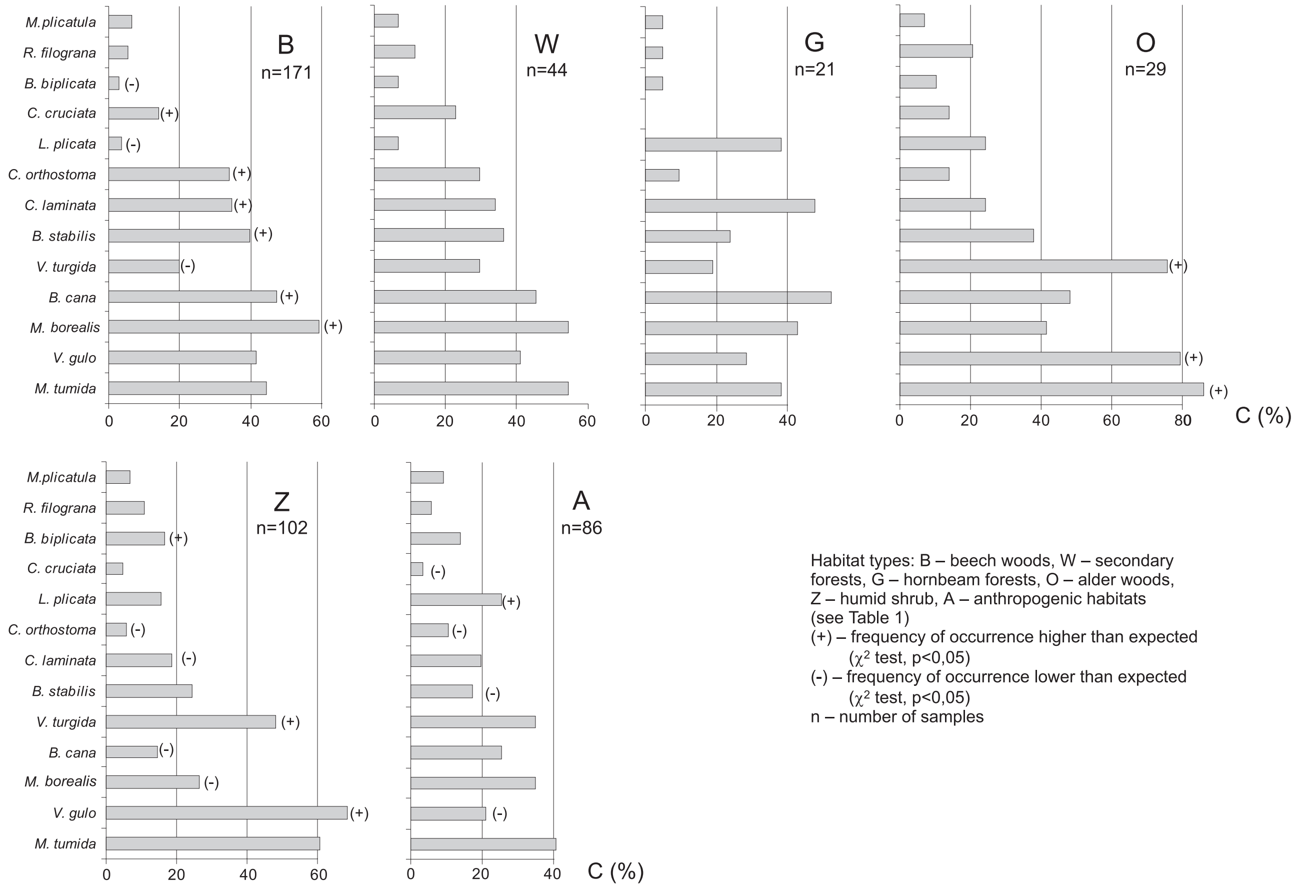

Fig. 4. Distribution of Clausiliidae in habitat types

Table 5. Distribution of species in selected habitat types

Habitat type*	Characteristic species (fastidiouds)	Accompanying species (indifferent)	Accompanying species (frequenting)	Accidental species
B	*Cochlodina laminata* *C. orthostoma* *Macrogastra borealis*	*Balea stabilis* *Bulgarica cana*	*Macrogastra tumida* *Vestia gulo* *V. turgida* *Clausilia cruciata*	*Ruthenica filograna* *Macrogastra plicatula* *Laciniaria plicata* *Balea biplicata*
G	*Laciniaria plicata* *Cochlodina laminata*	*Bulgarica cana* *Macrogastra borealis*		
O	*Macrogastra tumida* *Vestia turgida* *Ruthenica filograna*	*Vestia gulo*	*Cochlodina laminata* *Macrogastra borealis* *Laciniaria plicata* *Balea stabilis* *Bulgarica cana*	*Cochlodina orthostoma* *Clausilia cruciata* *Macrogastra plicatula* *Balea biplicata*
W	*Clausilia cruciata*	*Bulgarica cana* *Balea stabilis*		
Z	*Balea biplicata* *Macrogastra plicatula*	*Vestia gulo*	*Macrogastra tumida* *Vestia turgida*	
A	*Laciniaria plicata*		*Cochlodina laminata* *Macrogastra borealis* *M. tumida* *Vestia gulo* *V. turgida* *Bulgarica cana*	*Cochlodina orthostoma* *Ruthenica filograna* *Macrogastra plicatula* *Clausilia cruciata* *Balea biplicata* *B. stabilis*

*for explanation see Table 1

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. *Laciniaria 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*

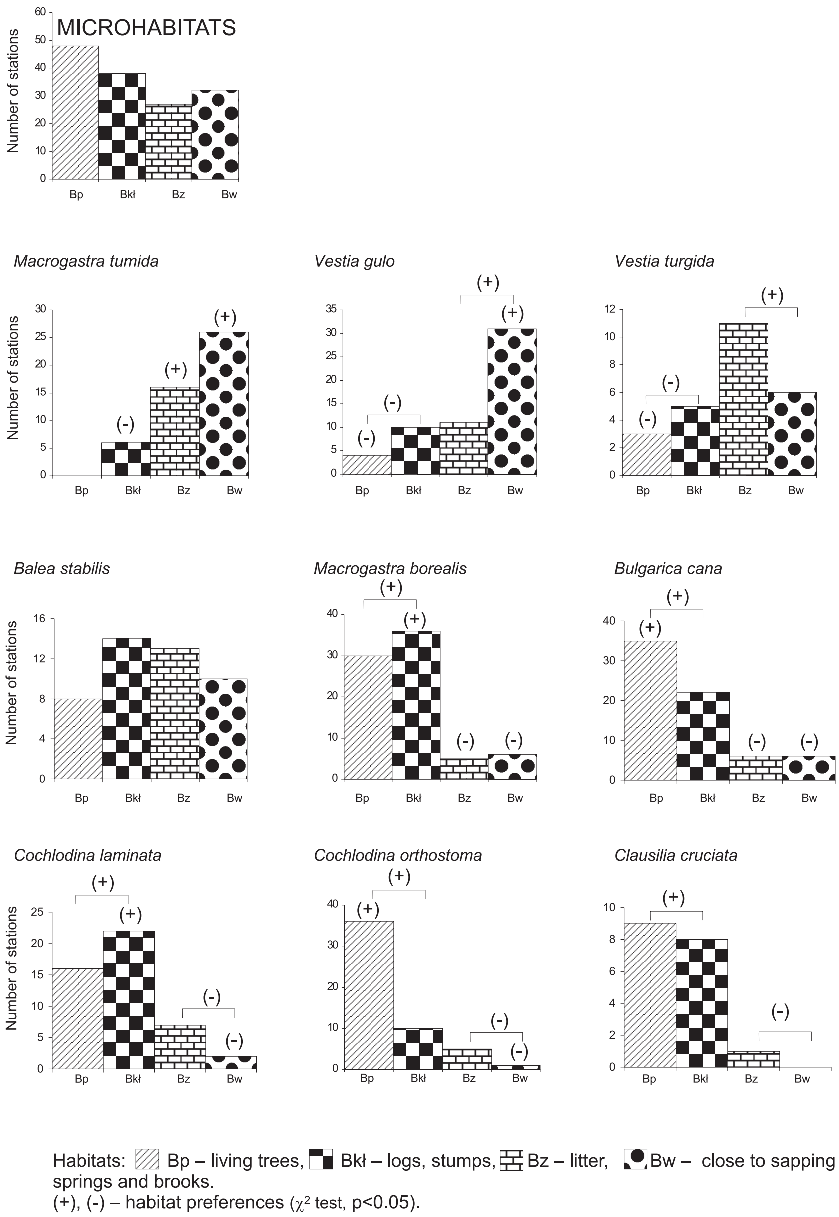

Fig. 5. Distribution of Clausiliidae among different microhabitats in mountain forest

cana 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 (χ^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 (χ^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).

Macrogastra tumida occurred in 59% samples with *Asarum europaeum* and *Cirsium oleraceum*, 57% with *Cardamine amara*, 30–50% samples with *Caltha palustris*, *Filipendula ulmaria*, *Chrysosplenium alternifolium* and with Umbelliferae. 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 europeum, 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 *Caltha 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.

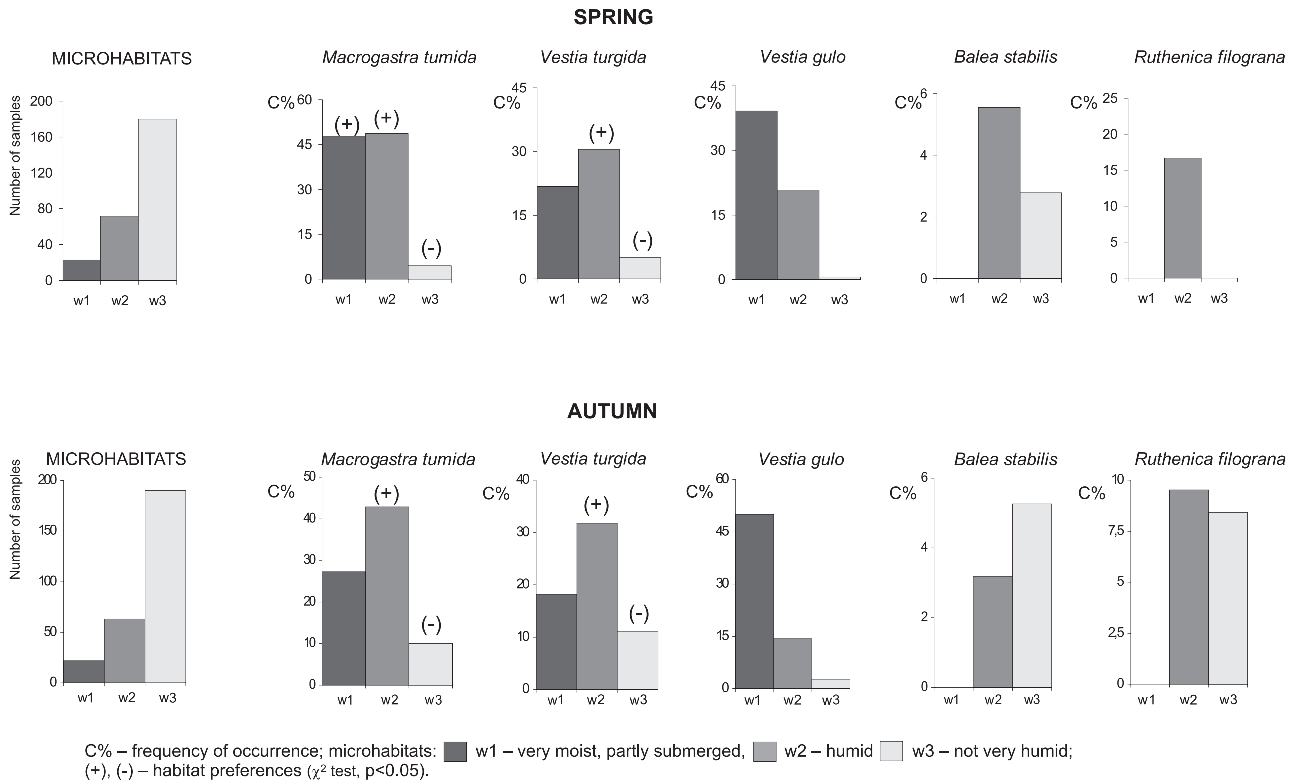

Fig. 6. Distribution of Clausiliidae in microhabitats of different moisture

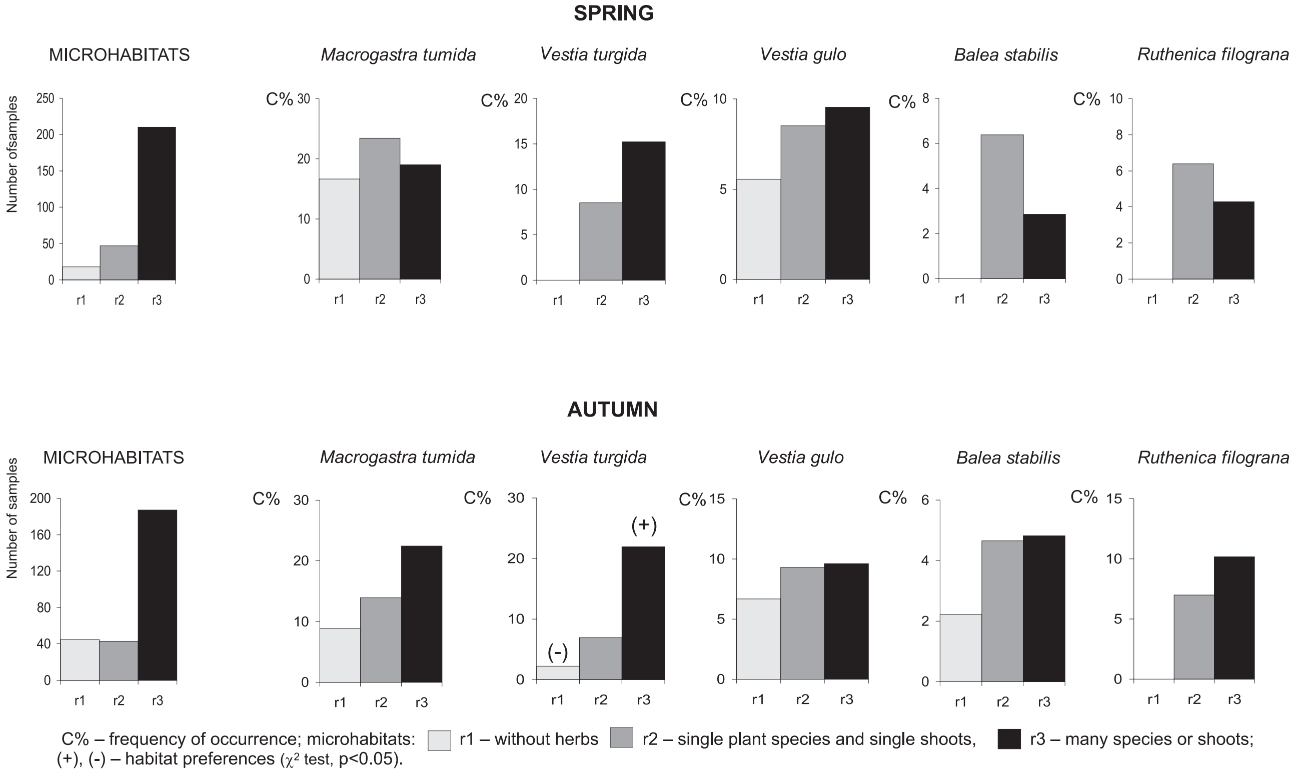

Fig. 7. Distribution of Clausiliidae in microhabitats of different herb cover

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 (Bereżki, 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, *Vestia gulo* and *Macrogastra tumida* co-occurred in humid places, in alder woods

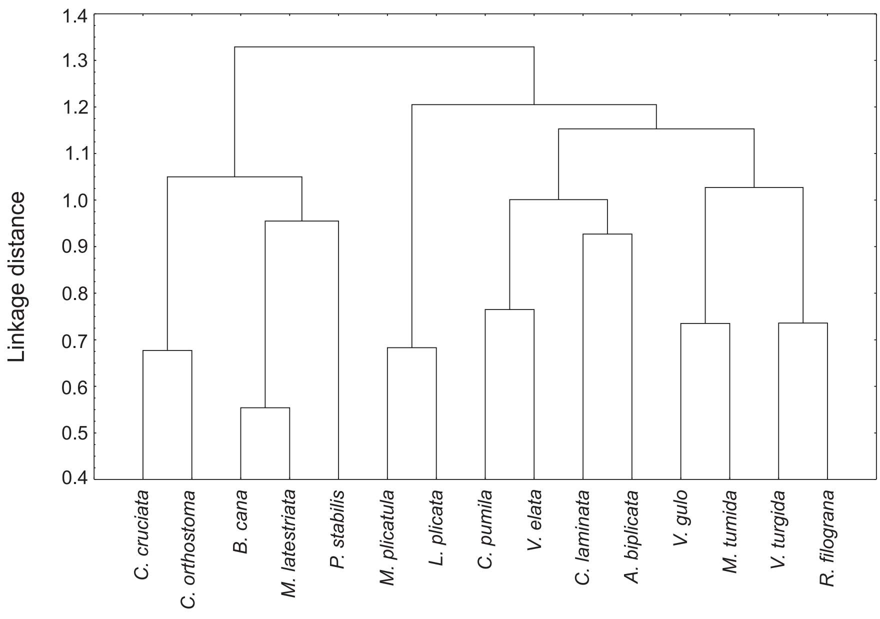

Fig. 8. Co-occurrence of Clausiliidae in the studied area

Table 6. Co-occurrence indices for clausiliids and plant species (in 400 cm^2 samples)

Plant species	All samples n=550						Spring samples n=275						Autumn samples n=275					
	Clausiliidae						Clausiliidae						Clausiliidae					
		M. tumida	*V. turgida*	*V. gulo*	*R. filogr.*	*B. stabilis*		*M. tumida*	*V. turgida*	*V. gulo*	*R. filogr.*	*B. stabilis*		M. *tumida*	*V. turgida*	*V. gulo*	*R. filogr.*	*B. stabilis*
	a	106	81	50	34	21	a	54	36	25	12	9	a	52	45	25	22	12
	b	Czekanowski's index					b	Czekanowski's index					b	Czekanowski's index				
Stellaria nemorum	116	<u>0.28</u>	<u>0.23</u>	0.11	0.12	0.01	60	<u>0.28</u>	0.15	0.09	0.17	0.03	56	<u>0.28</u>	<u>0.32</u>	0.12	0.08	
Oxalis acetosella	96	0.08	0.12	0.01	0.02	0.05	48	0.10	0.17	0.00	0.03		48	0.06	0.09	0.03		0.10
Galium odoratum	79	0.06	0.18	0.03		0.08	44	0.02	0.10	0.03		0.11	35	0.11	<u>0.25</u>	0.03		0.04
Glechoma hirsuta	59	0.18	<u>0.21</u>	0.07	<u>0.30</u>	0.13	19	0.08	0.15	0.05	<u>0.26</u>		40	<u>0.26</u>	<u>0.26</u>	0.09	<u>0.32</u>	0.19
Lysimachia nemorum	44	<u>0.24</u>	<u>0.37</u>	0.06	0.05	0.06	19	<u>0.22</u>	<u>0.25</u>	0.09	0.06		25	<u>0.26</u>	<u>0.46</u>	0.04	0.04	0.11
Symphytum cordatum	38	0.06	0.08	0.02		0.03	36	0.09	0.14	0.03		0.04	2					
Dentaria glandulosa	36	0.04	0.02		0.03	0.07	35	0.07	0.03		0.04	0.09	1					
Petasites sp.	34	0.11	0.19	0.10	0.18		21	0.05	0.18	0.09	0.06		13	0.18	<u>0.21</u>	0.11	<u>0.29</u>	
Allium ursinii	32	0.10	0.09	0.07	0.15	0.11	32	0.16	0.15	0.11	<u>0.23</u>	0.15	0					
Caltha palustris	25	0.18	0.09	<u>0.37</u>			14	0.15	0.04	<u>0.36</u>			11	<u>0.22</u>	0.14	<u>0.39</u>		
Calamagrostis arundinacea	23	0.02	0.06				9	0.03	0.09				14		0.03			
Umbeliferae	23	0.17	0.13	<u>0.27</u>			11	0.18	0.04	<u>0.39</u>			12	0.16	<u>0.21</u>	0.16		
Cardamine amara	21	0.19	0.08	<u>0.48</u>			9	<u>0.22</u>	0.09	<u>0.41</u>			12	0.16	0.07	<u>0.54</u>		
Mercurialis perennis	20	0.03	0.12				12	0.06	0.08				8		0.15			
Chrysosplenium alternifolium	20	0.11	0.14	0.17		0.05	7	0.10	0.09	0.13			13	0.12	0.17	<u>0.21</u>		0.08
Filicinae	18	0.03	0.02			0.05	8	0.03	0.05				10	0.03				0.09
Rubus hirtus	18	0.03	0.02				10	0.03	0.04				8	0.03				
Festuca drymeja	18						10						8					
Rumex alpinus	17	0.07	0.10	0.06			8	0.06	0.09	0.06			9	0.07	0.11	0.06		

Table 6 continued

Plant species	All samples n=550						Spring samples n=275						Autumn samples n=275					
	Clausiliidae						Clausiliidae						Clausiliidae					
		M. tumida	*V. turgida*	*V. gulo*	*R. filogr.*	*B. stabilis*		*M. tumida*	*V. turgida*	*V. gulo*	*R. filogr.*	*B. stabilis*		*M. tumida*	*V. turgida*	*V. gulo*	*R. filogr.*	*B. stabilis*
	a	106	81	50	34	21	a	54	36	25	12	9	a	52	45	25	22	12
	b	Czekanowski's index					b	Czekanowski's index					b	Czekanowski's index				
Asarum europaeum	17	0.18	0.16	0.09	0.16		12	0.21	0.25	0.16	0.25		5	0.14	0.08		0.07	
Cirsium oleraceum	17	0.16	0.08	0.18	0.16	0.05	6	0.17	0.05	0.26	0.11	0.13	11	0.16	0.11	0.11	0.18	
Senecio fuschii	17	0.02	0.02			0.05	8	0.03					9		0.04			0.10
Ajuga reptans	16	0.08	0.10	0.03	0.12		12	0.09	0.08		0.08		4	0.07	0.12	0.07	0.15	
Anemone nemorosa	16	0.07	0.04				16	0.11	0.08				0					
Milium effusum	16	0.03	0.04	0.03			9	0.03					7	0.03	0.08	0.06		
Filipendula ulmaria	15	0.13	0.06	0.18			10	0.19	0.09	0.29			5	0.07	0.04	0.07		
Myosotis palustris	15	0.07	0.06	0.12			11	0.12	0.13	0.22			4					
Viola biflora	14		0.04				14		0.08				0					
Luzula sylvatica	13	0.05	0.06				9	0.10	0.04				4		0.08			
Alchemilla sp.	13	0.03	0.06				8	0.06	0.05				5		0.08			
Galeobdolon luteum	13		0.04				4		0.10				9					
Rubus ideaus	13	0.03	0.02			0.06	6	0.07					7		0.04			0.11
Carex pilosa	13						8						5					
Cardamine pratensis	11	0.03	0.11				3	0.04	0.10				8	0.03	0.11			
Carex brizoides	11	0.03	0.02			0.13	1						10	0.06	0.04		0.13	0.18
Urtica dioica	10	0.05	0.04				6	0.03	0.05				4	0.07	0.04			
Thalictrum aquilegifolium	10		0.02				2		0.05				8					
Lunaria rediviva	10	0.03					7	0.03					3	0.04				

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

Sites: 10, 11, 13, 32, 34 (N), 37, 39, 42, 46, 47, 53, 57, 68, 72, 74, 76, 77, 78, 79, 80, 81, 84, 85, 87, 93, 94, 95, 101, 102, 103, 104, 106, 111, 112, 117, 118, 119, 124, 128, 129, 130, 132, 133, 134, 138, 139, 140, 142, 143, 145, 146, 148, 149, 151, 152, 155, 156, 157, 158, 161, 164, 166, 167, 168, 171, 173, 174, 175, 176, 177, 178, 179, 182, 183, 185, 186, 187, 190, 192, 198, 205, 208, 209, 213, 215, 217, 218, 219, 220, 221

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 KOTULA (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 Osława 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 Połonina Wetlińska range were found. In the Slovak part of the Eastern Carpathians *C. laminata* is less common than in the Western Carpathians (LOŽEK & GULIČKA 1962), and it was not recorded from the nature reserve "Stužica" (LOŽEK & GULIČKA 1955). According to BĄKOWSKI (1882), the species is also rare in the highest range of the Eastern Beskidy (Czarnohora, Ukraine)

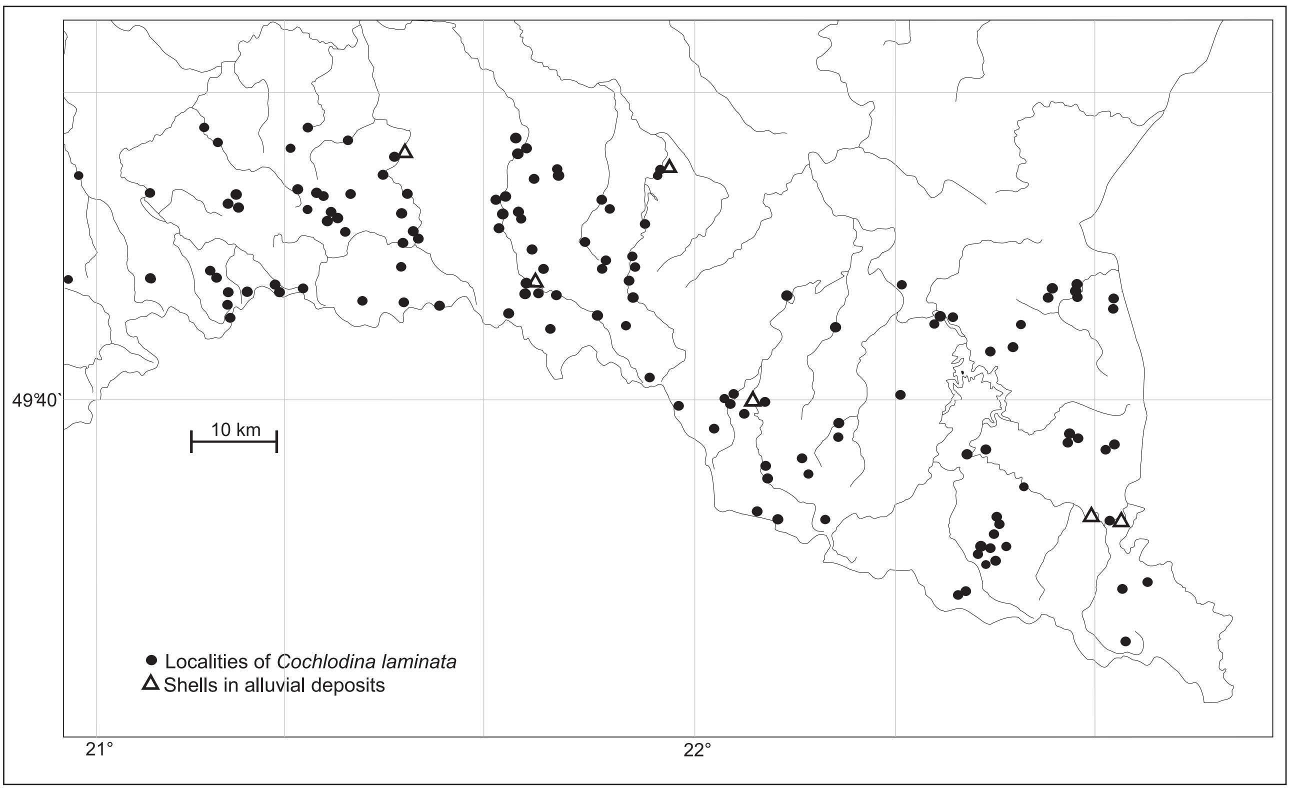

Fig. 9. Distribution of *Cochlodina laminata* in the studied area

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, Bkł, 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 See 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

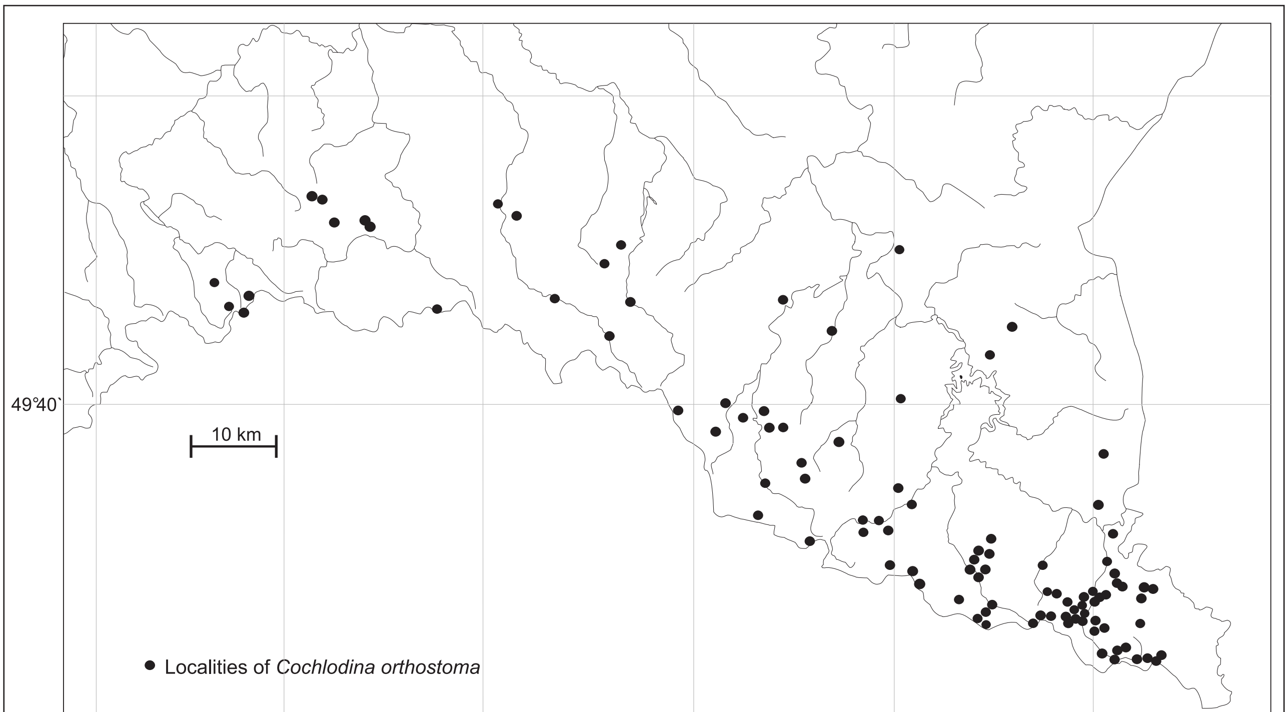

Fig. 10. Distribution of *Cochlodina orthostoma* in the studied area

(1882), and from the Beskid Niski by JACKIEWICZ & RAFALSKI (1960).

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. (SOÓS 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 (DYDUCH-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 (DYDUCH-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 (LOŽEK & 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 LOŽEK (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 URBAŃSKI (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 (KERNEY 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, BĄKOWSKI & ŁOMNICKI 1892), the Bieszczady (RIEDEL 1988), vicinity of Dukla and Uście Gorlickie in the Beskid Niski (JACKIEWICZ & RAFALSKI 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 BĄKOWSKI (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 URBAŃSKI (1947), however recent studies have not confirmed the occurrence of *R. filograna* in the region (DZIĘCZKOWSKI 1972, DYDUCH-FALNIOWSKA 1991). In the Fatra Mts (Slovakia) the species is found up to 1,350 m (LISICKÝ & LOŽEK 1969). In eastern Slovakia it was recorded only from submontane forests (up to 600–700 m) (LOŽEK & 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 – Połonina Wetlińska (±1,000 m, 1953, leg. B. BURAKOWSKI). 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 petrophile and calciphile (KERNEY et al. 1983, ALEXANDROWICZ 1987, RIEDEL 1988). According to LOŽEK (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, Bkł, 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*).

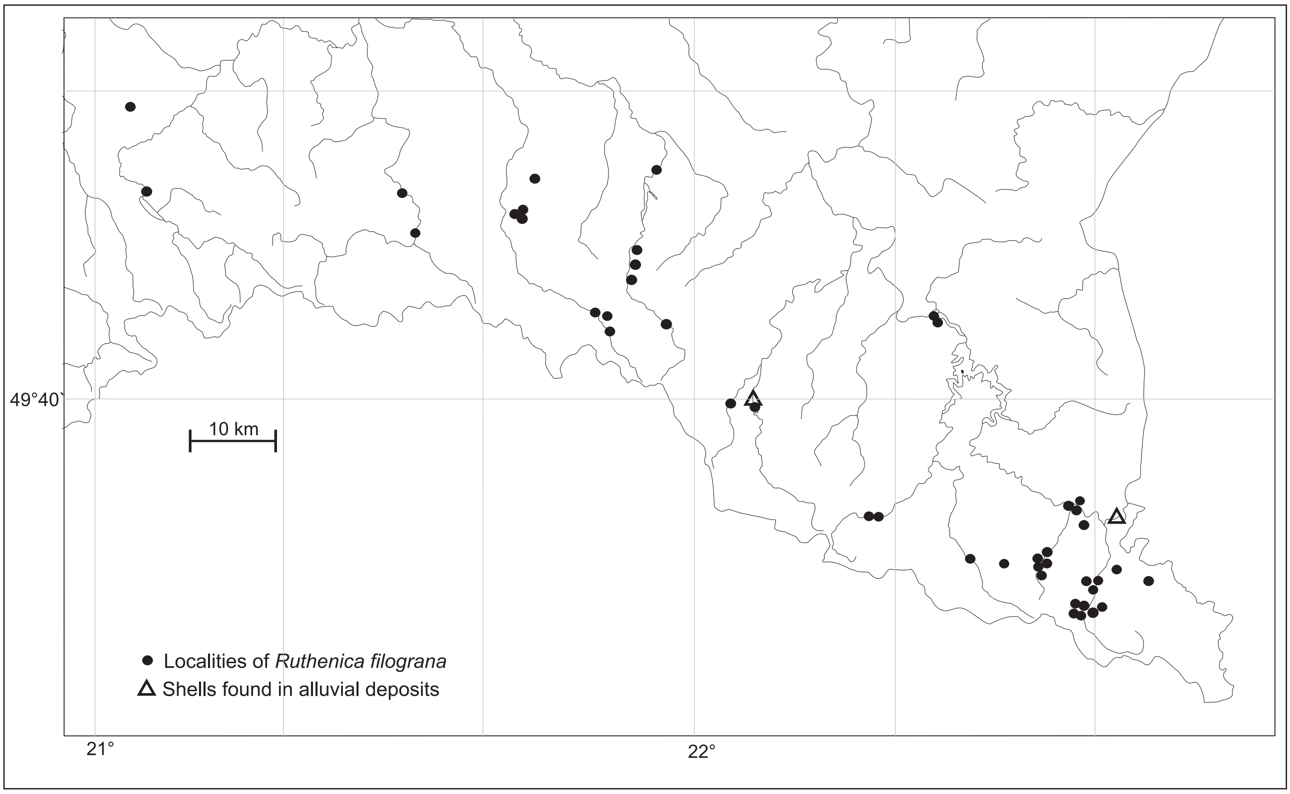

Fig. 11. Distribution of *Ruthenica filograna* in the studied area

?. *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 (BĄKOWSKI & ŁOMNICKI 1892, GROSSU 1981, BAIDASHNIKOV 1989), the species does not occur in the Eastern Carpathians. The only locality in the Ciscarpathian 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 (LOŽEK 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, DZIĘCZKOWSKI 1972, DYDUCH-FALNIOWSKA 1988, 1991). It was also reported from Muszyna 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 Rożki (8), Cisna (7), Dwernik Średni Wierch (8), Dwernik (2), Dwerniczek (1), Chmiel (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-Turczańskie 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 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 (BĄKOWSKI 1878, 1884, KRÓL 1879, BĄKOWSKI & ŁOMNICKI 1892) and Błażowa (BRZĘK 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, zebrał [collected by] Ż. Król", 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, Bkł, 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 Jaśliska (Beskid Niski) it was very abundant in humid scrub and secondary forests.

5. *Macrogastra 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,

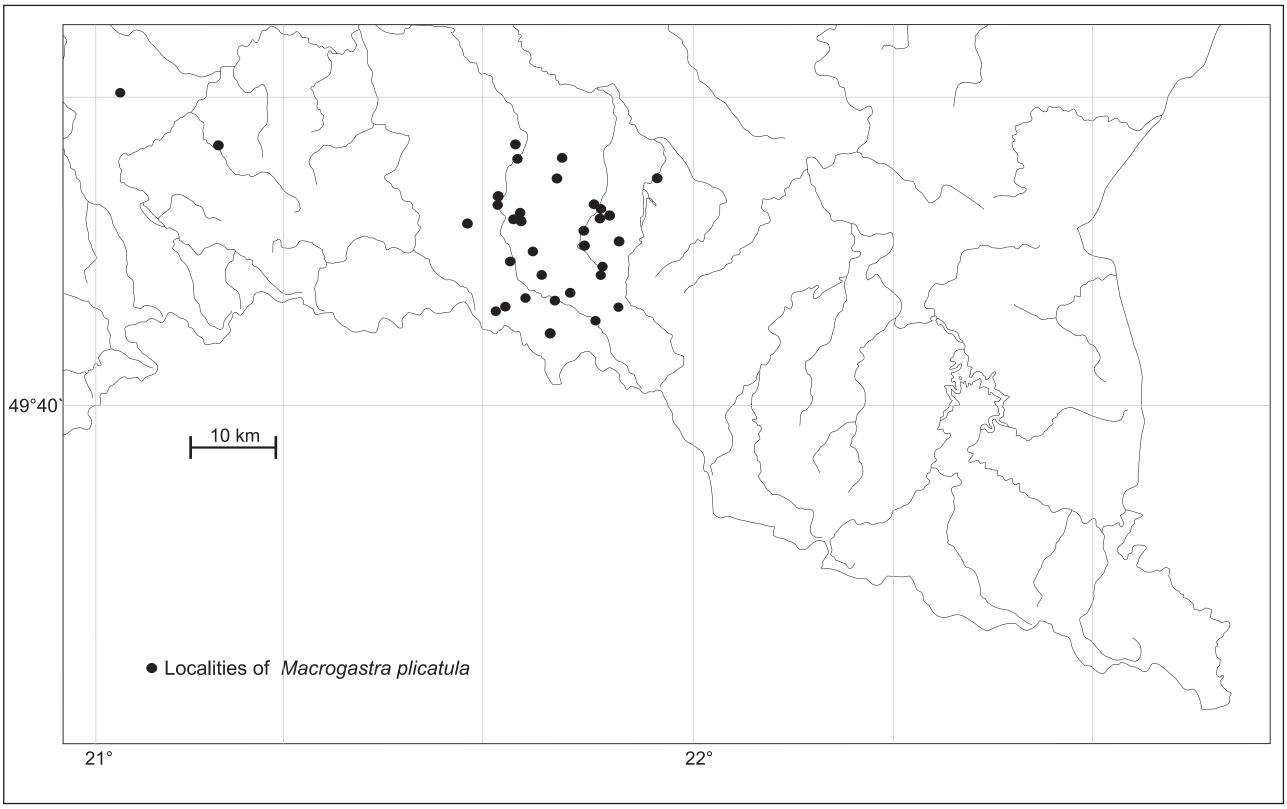

Fig. 12. Distribution of *Macrogastra plicatula* in the studied area

68, 70, 71, 72, 75, 76, 77, 78, 79, 80, 81, 84, 85, 87, 88, 89, 90, 91, 93, 96, 97, 100, 101, 102, 103, 104, 105, 106, 109, 110, 111, 114, 117, 119, 120, 122, 123, 127, 128, 129, 130, 133, 138, 139, 143, 151, 152, 156, 160, 161, 167, 168, 170, 171, 172, 173, 174, 176, 177, 179, 181, 182, 183, 185, 186, 187, 182, 190, 191, 192, 193, 206, 213, 214, 215 (N)

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, STĘPCZAK 1970). STĘPCZAK'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 (STĘPCZAK 1970, RIEDEL 1988). In the Tatra Mts it is far less common than *M. plicatula* (DYDUCH-FALNIOWSKA 1991). There are many records of the species from the Bieszczady and the Beskid Niski (STĘPCZAK 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-FALNIOWSKA 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 STĘPCZAK (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 (STĘPCZAK 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, Bkł, 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

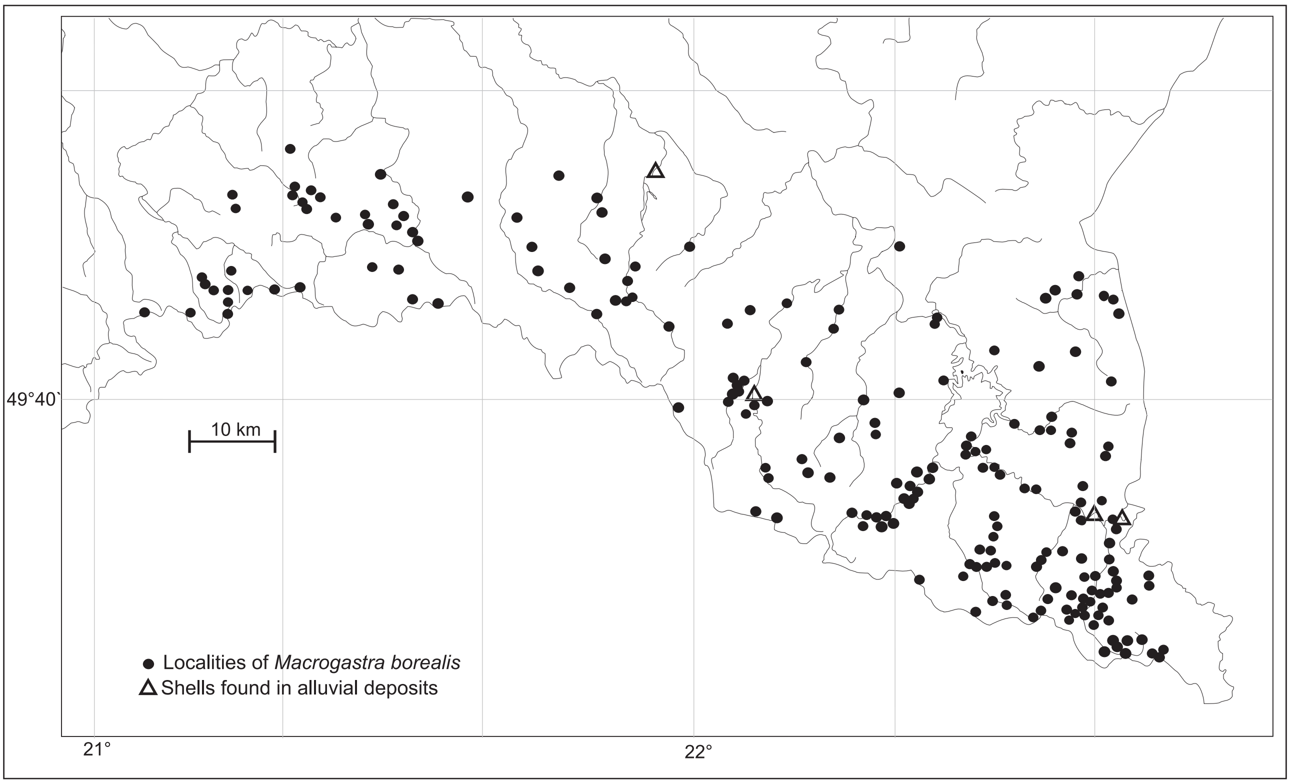

Fig. 13. Distribution of *Macrogastra borealis* in the studied area

opinion the species climbs living trees more frequently than it was formerly reported by URBAŃSKI (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 (URBAŃSKI 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 URBAŃSKI (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 (LOŽEK 1962). In the Bieszczady and Beskid Niski it was found in almost all studied habitats (Bz, Bp, Bkł, 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

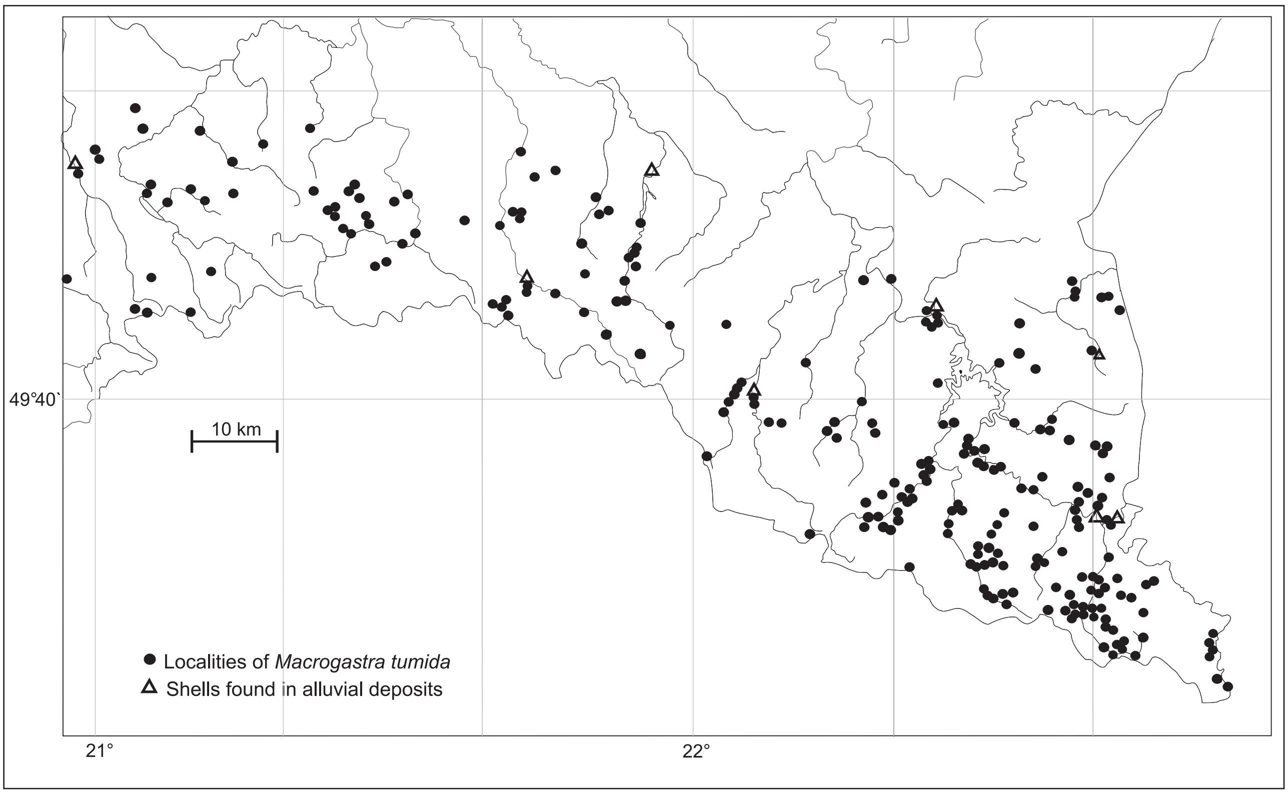

Fig. 14. Distribution of *Macrogastra tumida* in the studied area

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 (Pasmo Graniczne) in the nature reserve "Stužica" (LOŽEK & GULIČKA 1955, 1962). Records from the Beskid Wschodni (RIEDEL 1988) pertain only to the Pogórze region (Odrzykoń castle near Krosno – BĄKOWSKI 1878; vicinity of Przemyśl – KOTULA 1882) and the Sanocko-Turczańskie Mts: Kamienna Laworta (KOTULA 1882), or are very general (BĄKOWSKI & 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 Pasmo 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. (LOŽEK &

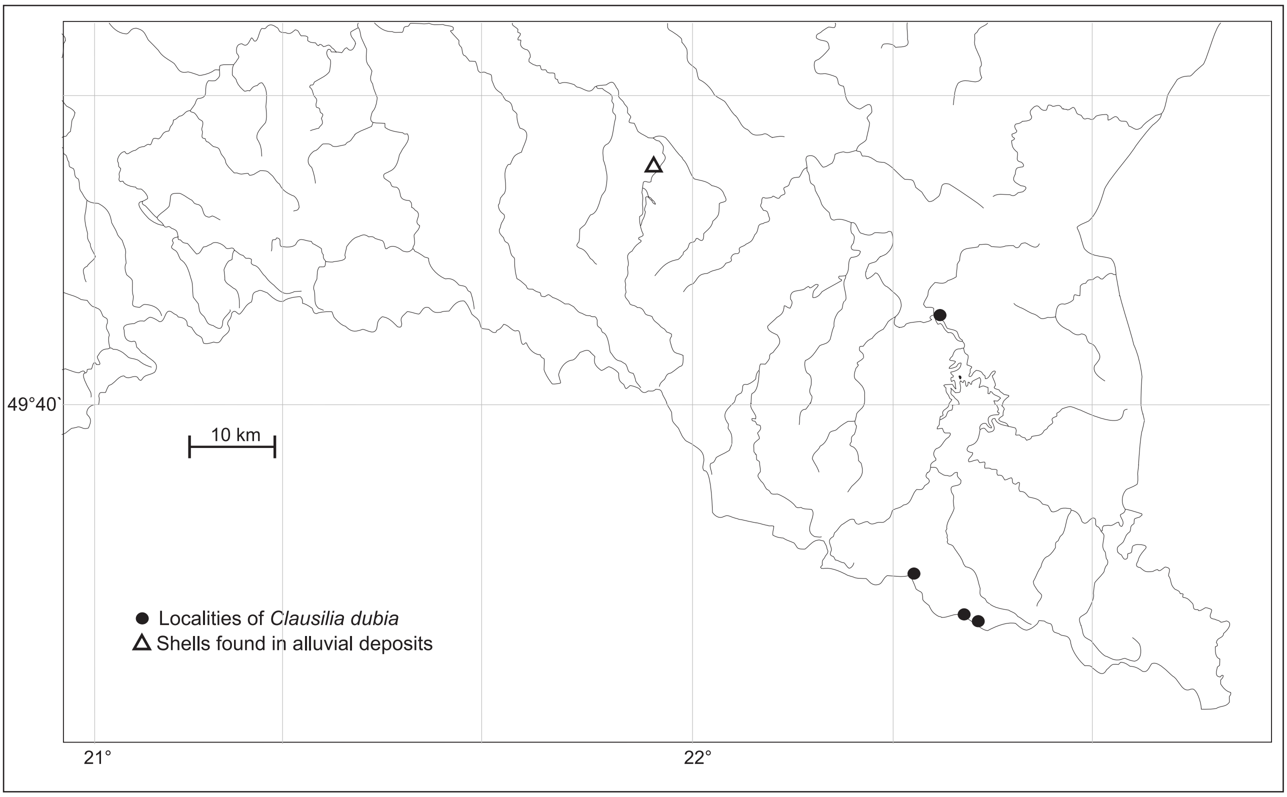

Fig. 15. Distribution of *Clausilia dubia* in the studied area

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-Turczańskie Mts (KOTULA 1882, 1884, BĄKOWSKI & ŁOMNICKI 1892) and from the vicinity of Przemyśl (BĄKOWSKI 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 & WEIS 1950, after LISICKÝ 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 Sądecki (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-Turczańskie 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 at 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 (WIKTOR 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-

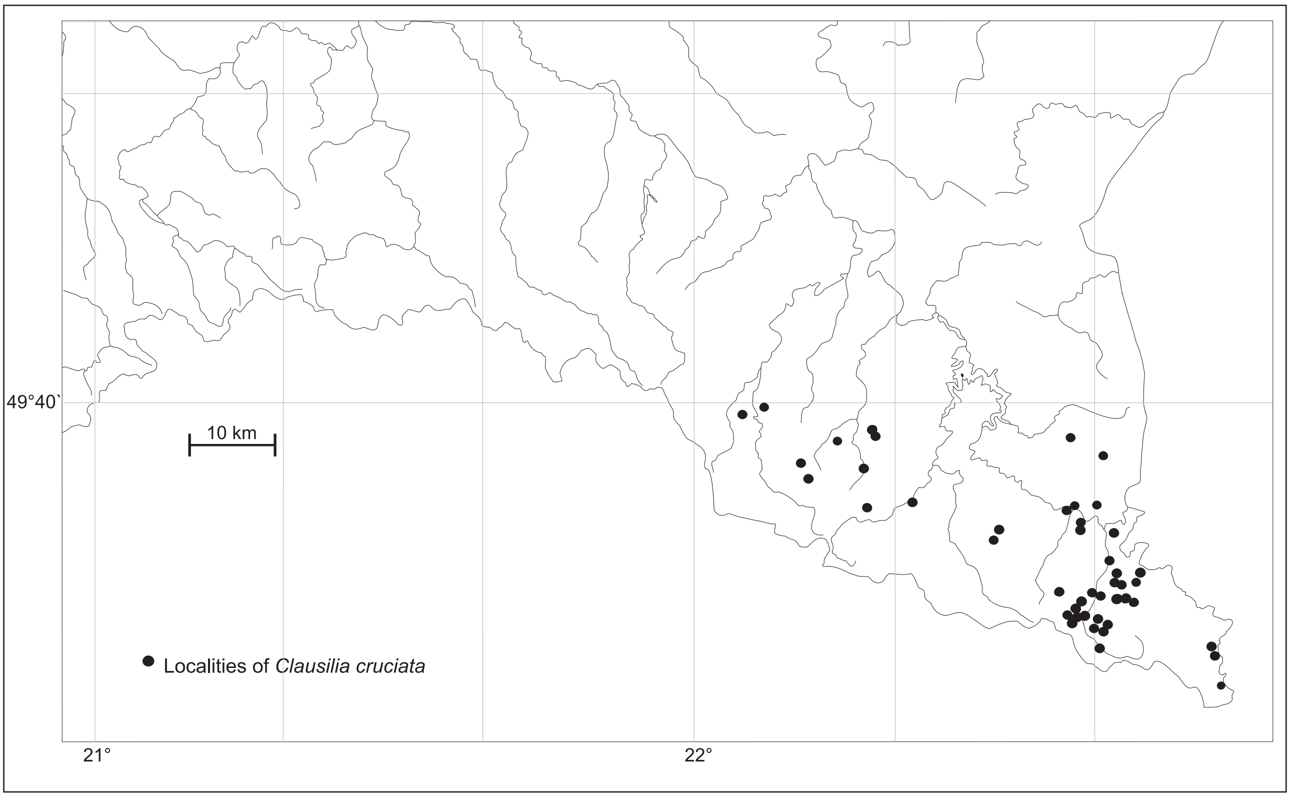

Fig. 16. Distribution of *Clausilia cruciata* in the studied area

clusively on trunks and logs. It was not found in quantitative samples of leaf litter. It was collected on trunks of *Fagus, Acer pseudoplatanus, Ulmus, Alnus* 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 dying. 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 valley (LISICKÝ 1991). In Poland it is widespread, apart from the Carpathians, where it is rare. It was not recorded from the uplands of Southern Poland, the occurrence 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 (DZIĘCZKOWSKI 1972, DYDUCH-FALNIOWSKA 1991). It was recorded from the vicinity of Przemyśl (KOTULA 1882, BĄKOWSKI 1884) and from Dwernik and Ustrzyki Górne in the Bieszczady (RIEDEL 1988, based on LIKHAREV's personal communication). 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 Bieszczady (the upper valley of the San River, e.g. Dwernik) (Fig. 17).

Vertical distribution: According to LIKHAREV (1962) *C. pumila* reaches 1,400 m. FRANK (1992) collected 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 meadows. In the studied area *C. pumila* was recorded from several types of habitats: Bz, G, O, W, Az, Aw. It was usually 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).

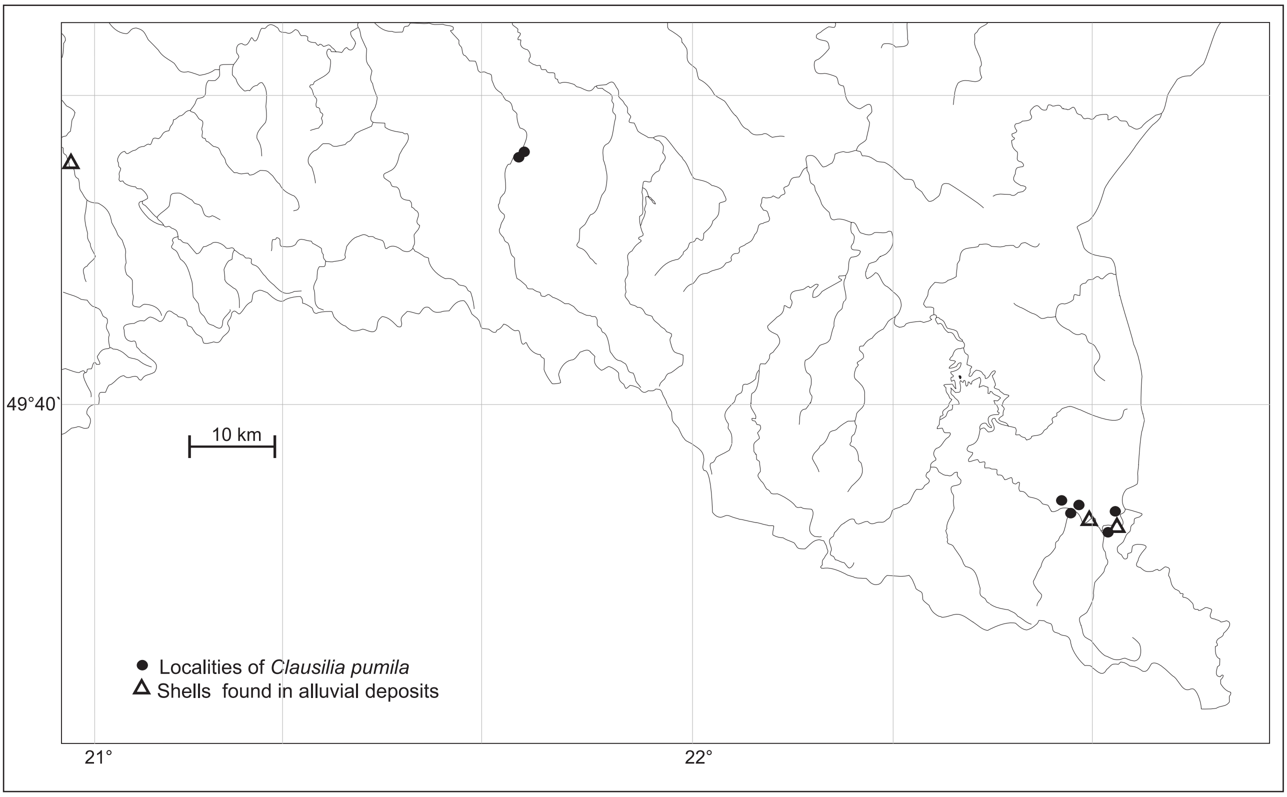

Fig. 17. Distribution of *Clausilia pumila* in the studied area

10. *Laciniaria plicata* (Draparnaud, 1801)

No. of specimens: 667

Sites: 40, 43, 66, 71, 85 (N), 88, 91, 95, 100, 102, 106, 107, 108, 109, 110, 111, 112, 114, 115, 119, 120, 121, 122, 126, 127, 128, 129, 130, 134, 135, 136, 138, 147, 148, 149, 157, 158, 159, 160, 161, 167, 176, 177, 185, 191, 197, 198, 212, 213, 215, 216, 217, 219, 221

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 (DZIĘCZKOWSKI 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 Ondavska Vrchovina Mts (LOŽEK & GULIČKA 1962). There are numerous records of *L. plicata* from the Beskid Wschodni (BĄKOWSKI 1878, 1884, KRÓL 1879, KOTULA 1882, 1884, BĄKOWSKI & ŁOMNICKI 1892, BRZĘK 1933), and from the Sanocko-Turczańskie Mts (Wojtkowa) (KOTULA 1882, BĄKOWSKI & ŁOMNICKI 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 (LOŽEK 1962). In the Pieniny Mts it was collected in dry woods under rocks, on trunks and stonewalls (URBAŃSKI 1939). I collected *L. plicata* from various habitats: Bkł, Bw, G, O, Z, W, Az, Am, Aw, S. It was frequently found in anthropogenic habitats, and in hornbeam forests, very rarely in beech woods. It dominated on stonewalls and concrete bridges. It was also collected on sandstones in the vicinity of Ustrzyki Dolne and on steep slopes of flysch.

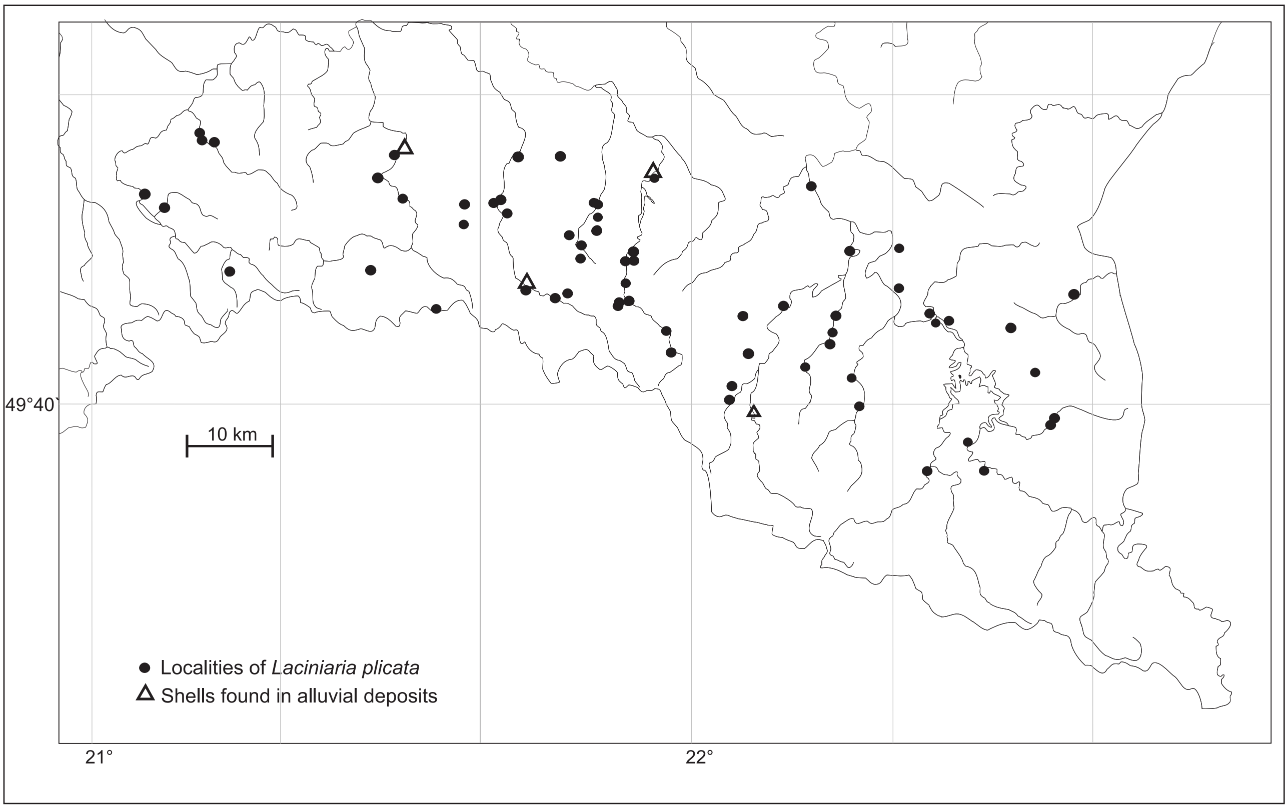

Fig. 18. Distribution of *Laciniaria plicata* in the studied area

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, BĄKOWSKI 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 POLIŃSKI's information). It is very rare in eastern Slovakia, the easternmost localities are situated west of the Dukielska 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 "Przełom Jasiołki", 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: Bł, 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.

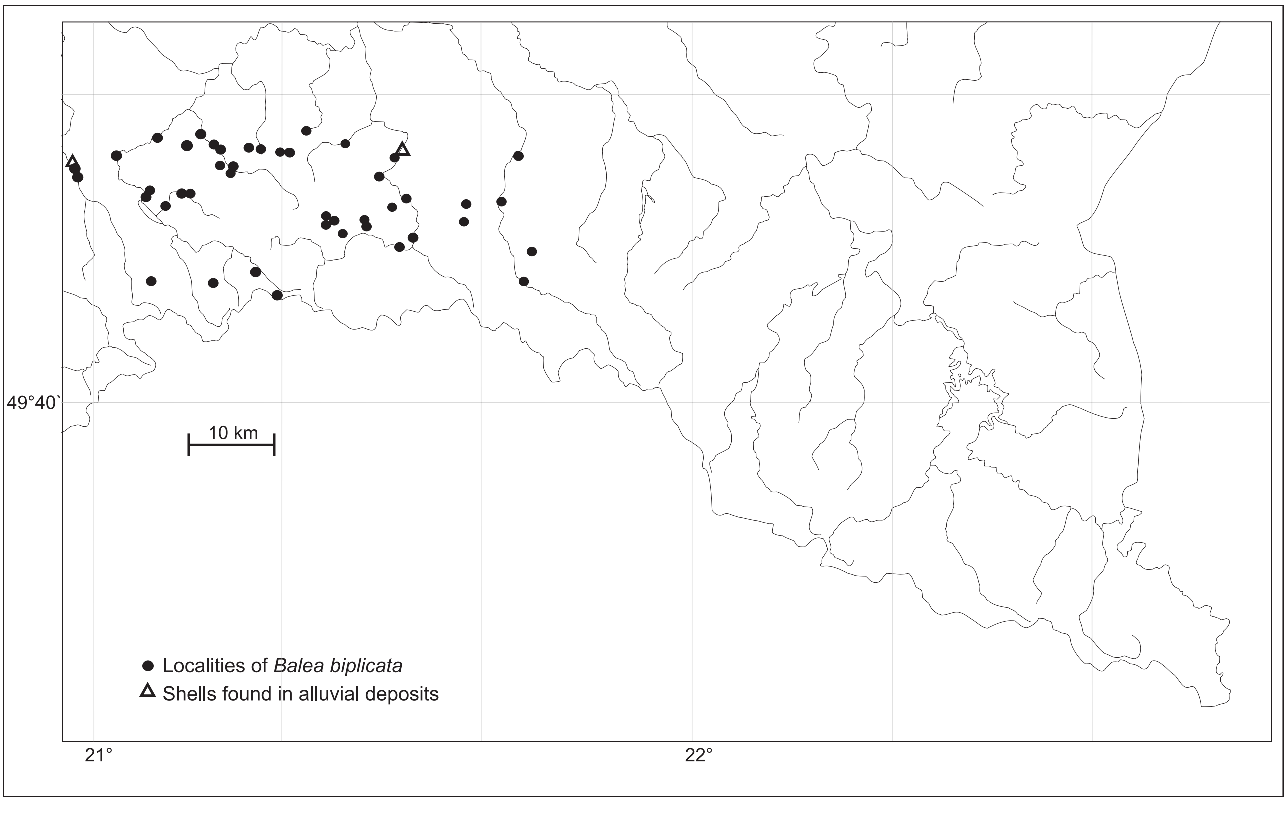

Fig. 19. Distribution of *Balea biplicata* in the studied area

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 BĄKOWSKI. 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. POLIŃSKI'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,

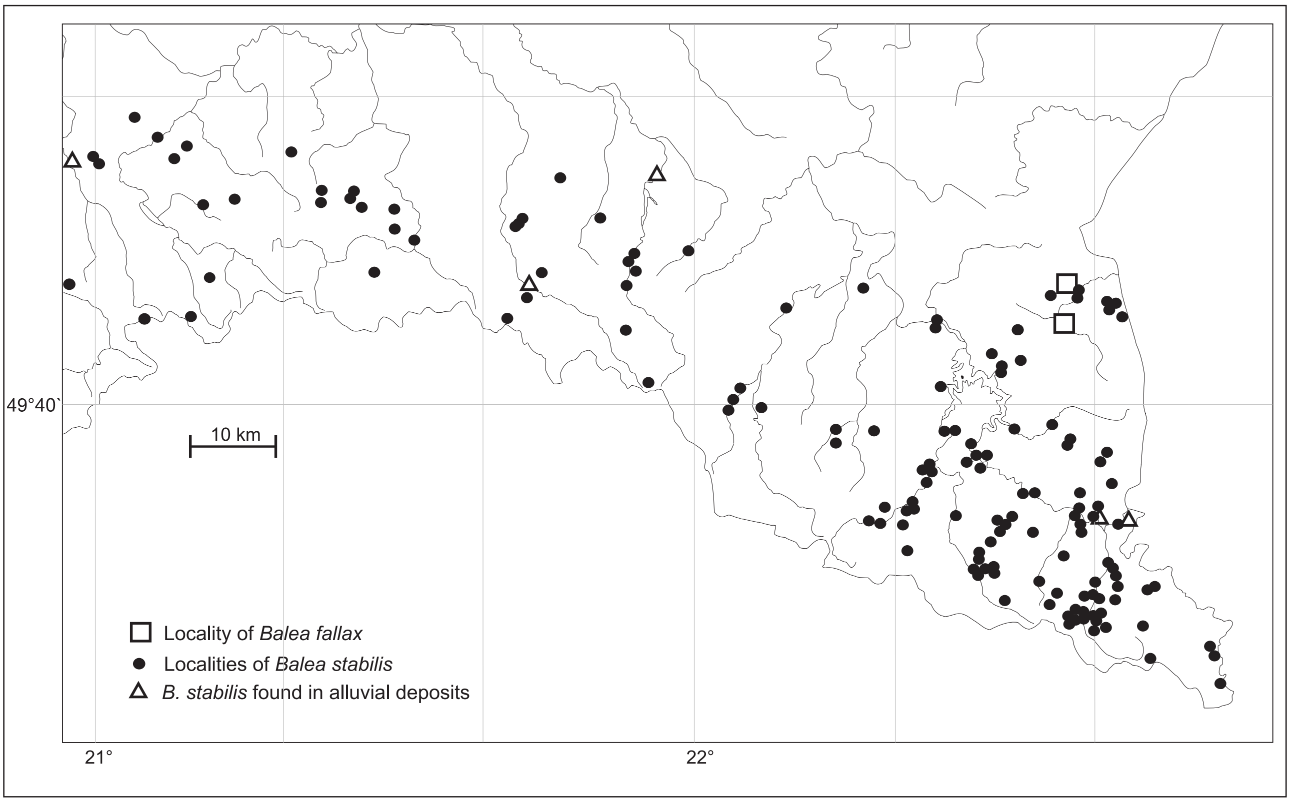

Fig. 20. Distribution of *Balea fallax* and *Balea stabilis* in the the studied area

48, 49, 51, 59, 61, 62, 65, 66, 67, 70, 72, 85, 86, 87, 88, 90, 92, 93, 95, 100, 101, 102, 103, 104, 105, 106, 119, 120, 124, 129, 130, 138, 139, 142, 146, 149, 151, 156, 167, 168, 170, 174, 175, 176, 179, 183, 192, 193, 195, 199, 200, 202, 203, 206, 208, 209 (N), 210, 211, 213, 214, 215 (N)

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 (URBAŃSKI 1939). It was numerously recorded in the Tatra Mts, last time by DZIĘCZKOWSKI (1972), but it was not found by DYDUCH-FALNIOWSKA (1991). According to URBAŃSKI (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 (URBAŃSKI 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 (LOŽEK & GULIČKA 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 URBAŃSKI (1939), it never climbs tree trunks. However, LOŽEK (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 URBAŃSKI (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* (Rossmässler, 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 (LOŽEK 1956, HUDEC 1963) and partly Transylvania and the Southern Carpathians (RIEDEL 1988). In Poland it was formerly known only from the Bieszczady, Pogórze Środkowobeskidzkie (vicinity of

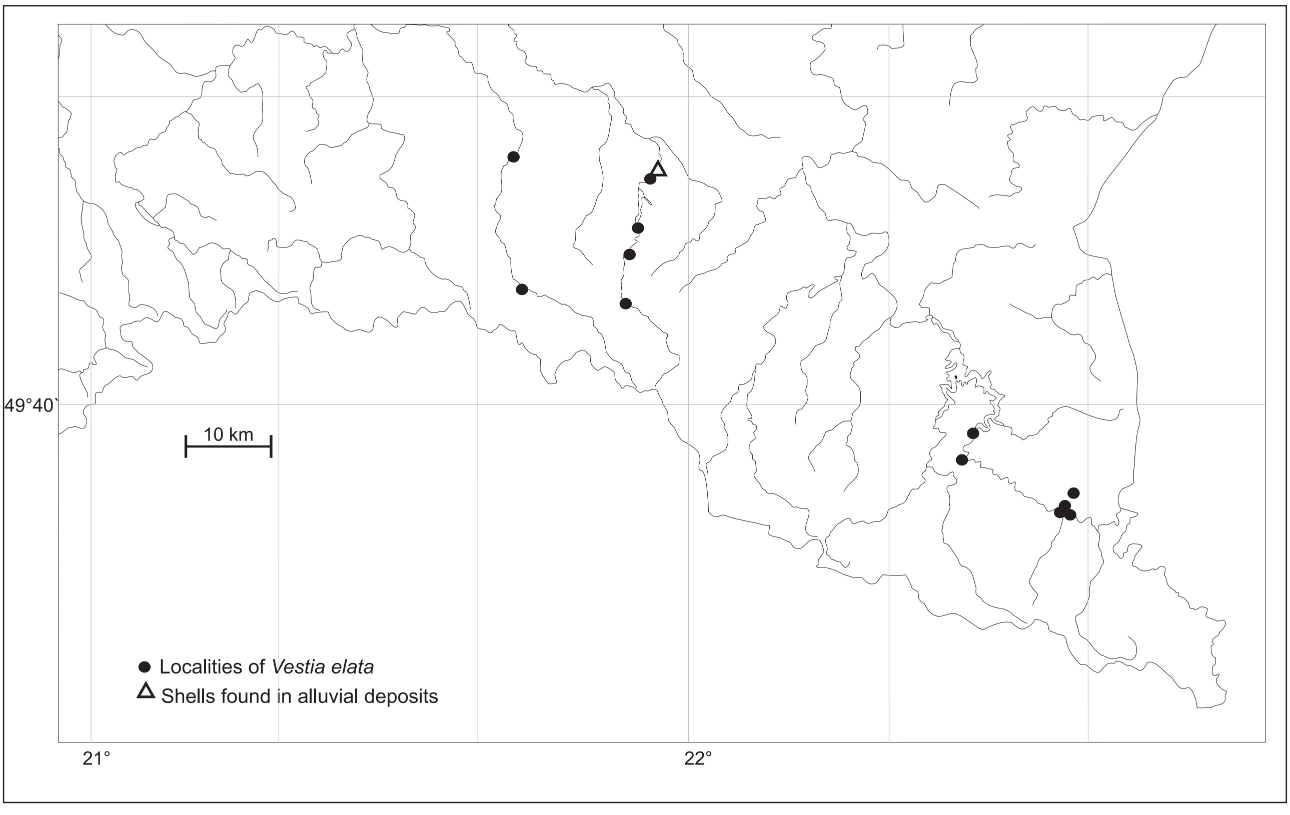

Fig. 21. Distribution of *Vestia elata* in the studied area

Strzyżów) (STWORZEWICZ 1973, RIEDEL 1988) and some isolated, relict localities in the Świętokrzyskie Mts (URBAŃSKI 1937, PIECHOCKI 1981).

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 (BĄKOWSKI'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 Worochta (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,

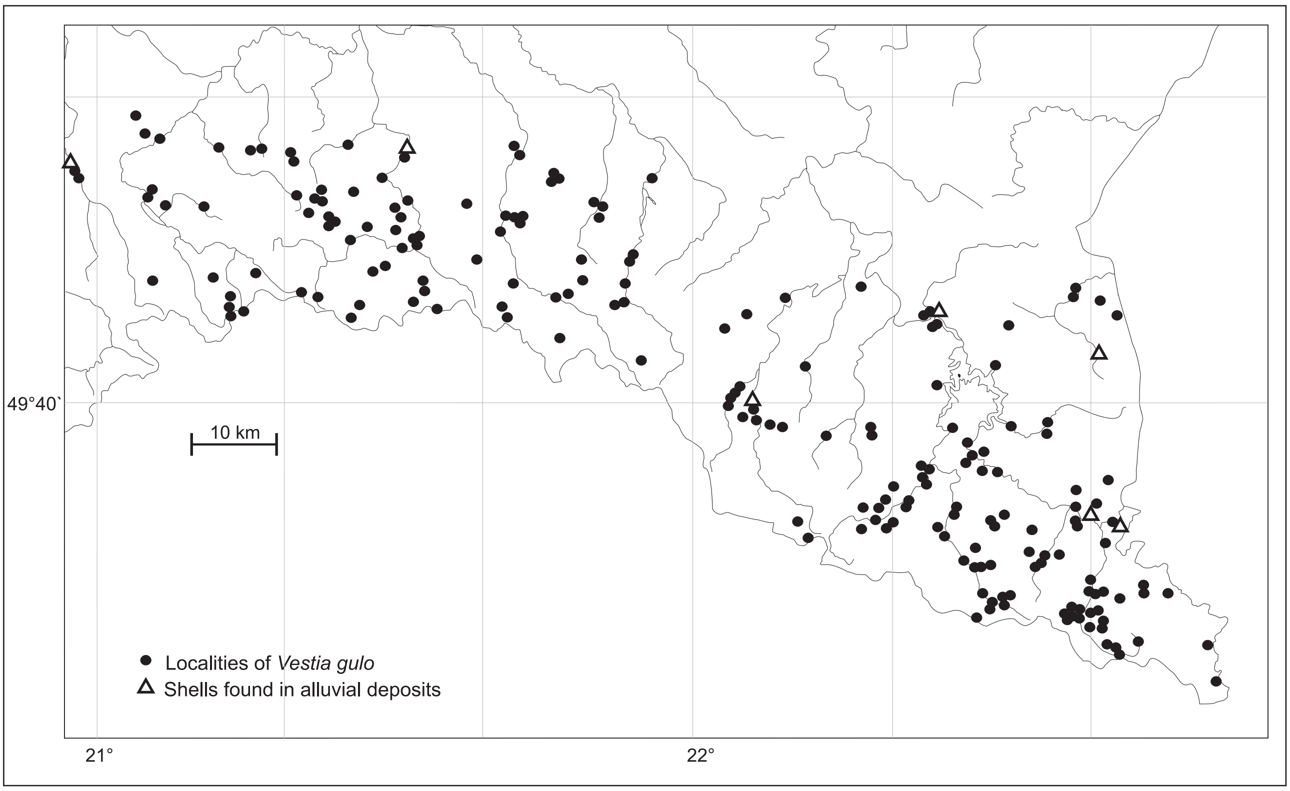

Fig. 22. Distribution of *Vestia gulo* in the studied area

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 – URBAŃSKI 1932; the Pieniny Mts – URBAŃSKI 1939) it is quite common, but missing in the Tatra Mts (URBAŃSKI 1947, 1957, DYDUCH-FALNIOWSKA 1991). It was recorded from the Bieszczady (KOTULA 1882, URBAŃSKI 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* (URBAŃSKI 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 URBAŃSKI (1939, 1957) the lower mountain forest zone is the upper limit of its vertical distribution. Exceptionally, URBAŃSKI (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. LOŽEK & GULIČKA (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 URBAŃSKI (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 lymnaeids on wet soil, on moss-covered stumps and on stones constantly drained with water (URBAŃSKI 1939). It is indifferent to low calcium content in the soil (LOŽEK 1962). In the studied area it was collected in various habitats: Bz, Bp, Bkł, 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,

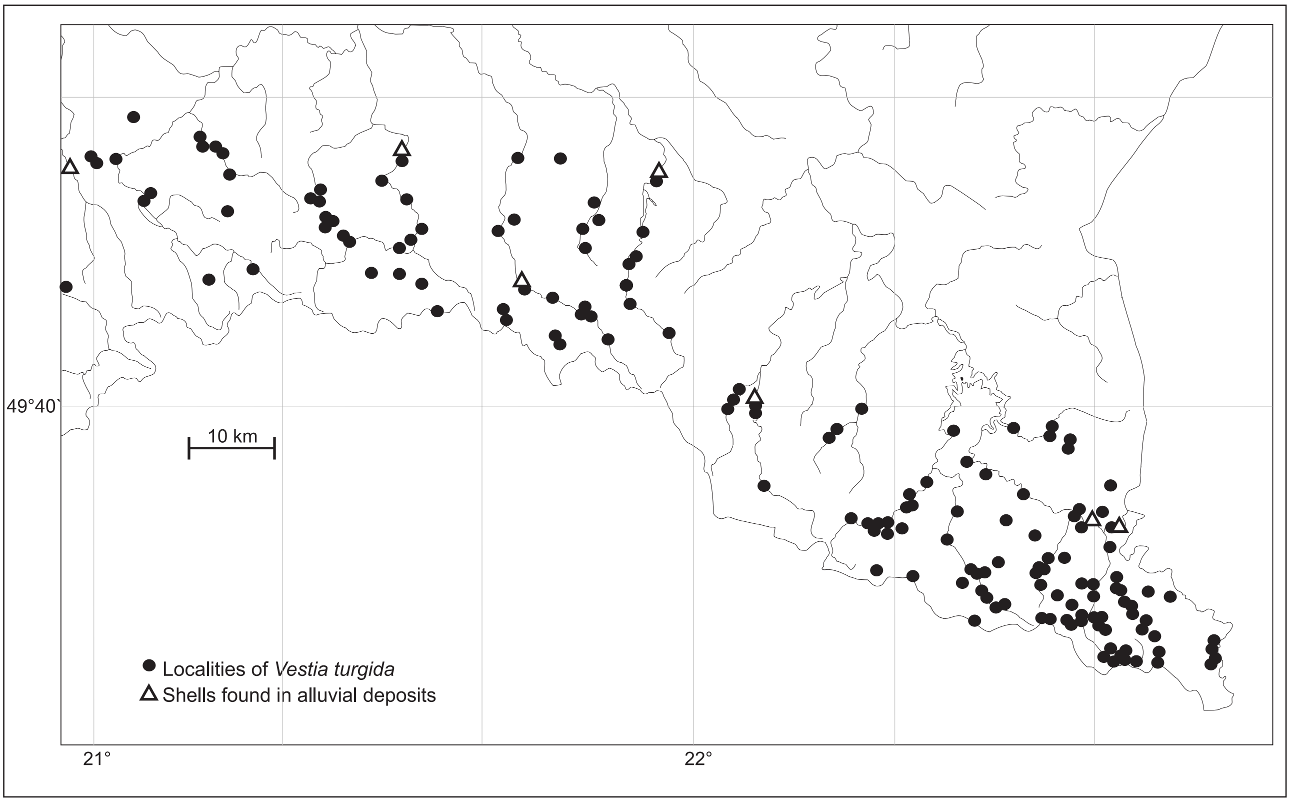

Fig. 23. Distribution of *Vestia turgida* in the studied area

176, 177, 183, 184, 185, 188, 192, 198, 201, 203, 210, 208, 209 (N), 215, 216, 217, 219, 221

Zoogeography: It is a Carpathian species, common especially in the northern part of the Carpathians, it occurs also in the Eastern Sudetes and in the Šumava Mts (RIEDEL 1988). In Poland it inhabits the whole Carpathians, but is not equally abundant everywhere; for example it is rare in the Pieniny Mts (URBAŃSKI 1939). In the old collections it was often labelled as *V. elata* (URBAŃSKI 1957, RIEDEL 1988). In my opinion, BĄKOWSKI's information on the occurrence of *V. elata* close to the timberline and on *poloniny* concerned *V. turgida*. In the Ukrainian Transcarpathian region *V. turgida* is represented by two forms: *procera* E. Bielz and *elongata* Rossmässler, occurring in the submontane zone (BAIDASHNIKOV 1989); they do not differ anatomically from the nominate species (BAIDASHNIKOV – personal communication). *V. turgida* is common and abundant in the Bieszczady and the Beskid Niski, but quite rare in the Sanocko-Turczańskie Mts (Fig. 23).

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). LOŽEK & 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 (LOŽEK 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 S*alix 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 *Alnetum incanae* and *Aceri-Fagetum* (24–49 specimens m^{-2}).

17. *Bulgarica cana* (Held, 1836)

No. of specimens: 610

Sites: 2, 5, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 26, 29, 32, 34, 35, 36, 37, 39, 40, 41, 42, 43, 46, 47, 48, 49, 50, 52, 53, 54, 55, 58, 60, 61, 62, 63, 65, 66, 67, 70, 76, 77, 78, 80, 81, 84, 85, 87, 88, 89, 90, 91, 92, 93, 95, 101, 102, 103, 104, 105, 106, 108, 111, 114, 117, 118, 119, 123, 127, 128, 129, 130, 133, 142, 147, 156, 161, 167, 168, 174, 175, 183, 186, 187, 190, 182, 191, 192, 193, 206, 211, 213, 215 (N), 220, 221

Zoogeography: *B. cana is* distributed in Central and Eastern Europe, from western parts of Germany to central Russia; in Poland it is found almost in whole country (RIEDEL 1988). There are many records of *B. cana* from the Beskid Wschodni region, mostly on Pogórze (RIEDEL 1988), and also in the Beskid Niski, in the vicinity of Gorlice (JACKIEWICZ & RAFALSKI 1960). KOTULA (1882) reports many localities from the Sanocko-Turczańskie Mts (vicinity of Ustrzyki Dolne and Krościenko). It was collected in the Stužica nature reserve on the southern slopes of Pasmo Graniczne (LOŽEK & GULIČKA 1955). For the first time it was reported from beech woods of the Polish Bieszczady by DZIĘCZKOWSKI (1988). *B. cana* is widespread but not abundant in the studied regions; usually only one or few specimens were found (Fig. 24).

Vertical distribution: In the Ukrainian Carpathians it is found only in the submontane and lower forest zones (up to 1,300 m) (BĄKOWSKI 1882, BAIDASHNIKOV 1989). It is at present very rare in the Tatra Mts and occurs only in the lower parts (DZIĘCZKOWSKI 1972, DYDUCH-FALNIOWSKA 1991). Formerly it was known as a species associated with beech woods and reaching to their upper limit (KOTULA 1884, URBAŃSKI 1932). In the Bieszczady it was collected in beech woods up to 1,250 m a.s.l. (site 21). In the Slovak part more numerous populations were found in the forest and subalpine zones than in submontane zone (LOŽEK & GULIČKA 1962).

Habitat: *B. cana* lives on tree trunks (URBAŃSKI 1939), in moderately humid deciduous and mixed forests (ALEXANDROWICZ 1987); less often it was found in leaf litter (RIEDEL 1988) and under bark of rotting stumps (URBAŃSKI 1939). According to URBAŃSKI (1939), even in dry weather it does not leave tree trunks but hides in bark crevices and under lichens. It tolerates low calcium level in soil (LOŽEK 1962). In the studied area it was found in most habitats (Bz, Bp, Bkł, Bw, G, O, Z, W, Az, Am, Aw), but preferred beech woods and avoided anthropogenic habitats and humid scrub. In the forest zone it most often climbs tree trunks (51% of samples) and logs (32 %). It was collected on trunks and logs of *Fagus, Acer pseudoplatanus, Fraxinus, Ulmus, Carpinus, Salix caprea, Abies, Populus* and *Malus*.

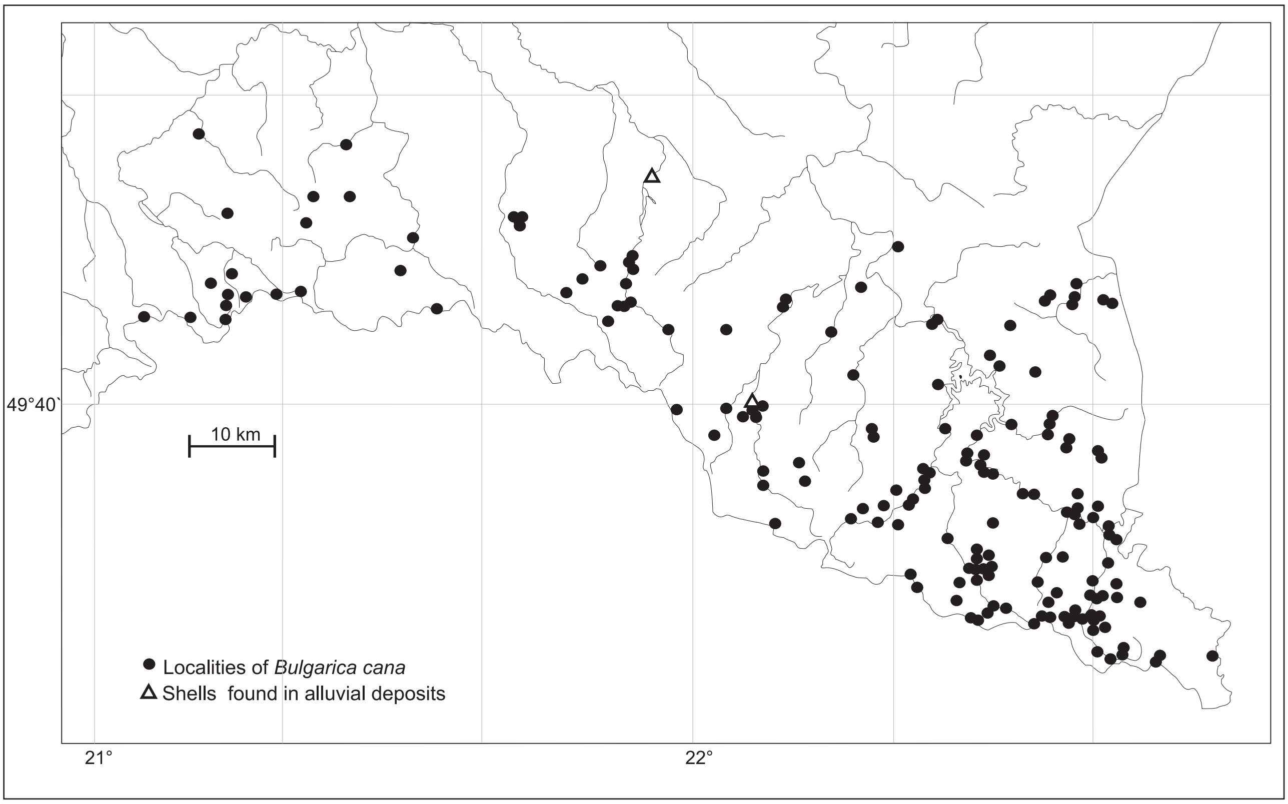

Fig. 24. Distribution of *Bulgarica cana* in the studied area

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 DZIĘCZKOWSKI 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-Turczańskie 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 south-eastern 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 PAWŁOWSKA & 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 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, skiophilous species. Contrary to what could be expected, woodland clausiliids (LOŽEK's (1964) ecological groups 1 and 3) were only sporadically or rarely found there, and the most frequent species *L. plicata* is a eurytopic snail.

Records from the neighbouring regions support my observations on the poverty of clausiliid communities in the submontane zone. According to KORNIUSHIN (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 (LOŽEK 1961–62, LOŽEK & GULIČKA 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 DZIĘCZKOWSKI 1988). In the Białowieża Primaeval Forest eight species were recorded in hornbeam forests (DYDUCH 1980, DZIĘCZKOWSKI 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 DZIĘCZKOWSKI 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 (DZIĘCZKOWSKI 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 LOŽEK & GULIČKA (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-Turczańskie 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 recedent 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 (*Rumicetum alpini*). Patches of *Rumex alpinus* are remnants of former intensive sheep and cattle grazing in this zone (ZARZYCKI 1971). They indicate ammonium-rich places of former cattle pens. In KOTULA's (1882) time shepherding 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 clausiliid in the subalpine zone, besides *M. tumida*, *C. cruciata*, *B. stabilis* and *V. gulo* occur there (BAIDASHNIKOV 1989). *V. turgida* and *C. dubia* were recorded in subalpine zone of the Babia Góra Range (URBAŃSKI 1932). LOŽEK & GULIČKA (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. filograna, L. plicata* and *M. ventricosa* were subdominants in the valley of Pieniński Potok (SZYBIAK 2000). Patches of *Petasites* on stream banks adjoining forests were inhabited by *C. pumila* 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 (LOŽEK 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. plicata* and *B. biplicata* are the most common clausiliids in ruins of Carpathian castles (ALEXANDROWICZ 1995). *L. plicata* is also the most widespread clausiliid in Lviv, inhabiting different types of human-influenced habitats (SVERLOVA 1998). According to KOSIŃSKA (1979), it is indifferent to man-made habitats. On stonewalls I found also *C. laminata*, which, according to KOSIŃSKA (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 cm^2 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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