POLSKA AKADEMIA NAUK
ZAKŁAD OCHRONY PRZYRODY I ZASOBÓW NATURALNYCH

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ANNA DYDUCH–FALNIOWSKA

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ŚLIMAKI TATR POLSKICH

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Redaktor: Kazimierz Klimek

Sekretarz Redakcji: Małgorzata Makomaska-Juchiewicz

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P O L S K A   A K A D E M I A   N A U K
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S T U D I A   N A T U R A E

SERIA A - WYDAWNICTWA NAUKOWE

Nr 38

Praca wykonana w ramach zadania badawczego nr 06.02.03. CPBP 04.09. "Gatunkowa i biocenotyczna ochrona zwierząt w Polsce" realizowanego w latach 1986 - 1990, koordynowanego przez Instytut Ekologii PAN

Zeszyt recenzował: Andrzej Piechocki

A b s t r a c t : 81 snail species have been recorded from the Polish Tatras. 5 species have shares greater than 5% in the malacofauna. These are *Piramidula rupestris, Clausilia dubia, Vitrea diaphana, Columella edentula* and *C. columella*. Among them only *C. edentula*, holarctic species, has a large, continuous range. For remaining species the Tatras are an important refuge. *Chilostoma rossmaessleri, Macrogastra ventricosa, Bulgarica cana, Acicula parcelineata, Oxychilus depressus, Lehmannia macroflagellata, L. nyctelia* and *Causa holosericum* are threatened with extinction in the Polish Tatras.

The species diversity of Tatra malacocenoses varies from 0.54 to 4.23. Of the 46 snail communities analysed from the point of view of species number (S), species diversity (H') and equitability (J'), 31 are structurally similar. They are included in one group by the Single Linkage (or Nearest Neighbour) Method. Other malacocenoses form small groups consisting of one - three elements.

The species composition, species diversity, ecological and zoogeographical character of the malacofauna are modified by altitude. The potential malacofauna of the Tatras corresponds with that characteristic of interglacjal and postglacjal periods. The *Dentario glandulosae - Fagetum* association in a few valleys is the refuge of the malacofauna typical of primeval Tatra forests in low situations. The malacofauna of alpine zone preserved its natural values to a high degree.

The most serious threats to gastropods of the Tatras are: the degradation of forest litter, acidification and urbanization of Zakopane Basin.

T r e ś ć : W Tatrach Polskich występuje 81 gatunków ślimaków lądowych. Pięć najliczniej i najczęściej występujących (ich udziały są większe niż 5% w całym materiale) to *Piramidula rupestris, Clausilia dubia, Vitrea diaphana, Columella edentula* i *C. columella*. Tylko jeden z tych gatunków, *C. edentula*, ma duży zwarty zasięg, dla pozostałych Tatry stanowią znaczące refugium. Zagrożone wymarciem na obszarze Tatr są: *Chilostoma rossmaessleri, Macrogastra ventricosa, Bulgarica cana, Acicula parcelineata, Oxychilus depressus, Lehmannia macroflagellata, L. nyctelia* i *Causa holosericum.*

Różnorodność gatunkowa malakocenoz tatrzańskich osiąga wartości od 0.54 do 4.23. Grupowanie uwzględniające liczbę gatunków (S), różnorodność gatunkową (H') i równomierność (J') wykazuje, że większość z nich (60%) jest strukturalnie podobna. Pozostałe malakocenozy tworzą małe 2 - 3 elementowe grupy.

Skład gatunkowy, różnorodność, ekologiczny i zoogeograficzny charakter malakofauny zmieniają się wraz ze wzrostem wysokości nad poziom morza. Potencjalna malakofauna Tatr zbliżona jest do tejże z interglacjałów i postglacjału. *Dentario glandulosae - Fagetum* w kilku dolinach jest refugium pierwotnej, bogatej malakofauny, charakterystycznej dla niższych partii Tatr. Zachowana została w dużym stopniu swoistość i wartość przyrodnicza zespołów mięczaków strefy alpejskiej Tatr.

Najpoważniejsze zagrożenie dla ślimaków omawianego terenu stanowią: degradacja ściółki w lasach, wzrost zakwaszenia wód i urbanizacja Kotliny Zakopiańskiej.

I. Introduction

The molluscs of the Tatra Mountains (Tatras) have been an object of naturalists' interest for over 100 years. The first notes on the snails and bivalves of these mountains, very difficult of access in those days, were made by Nowicki (1867, 1868, 1869), Jachno (1870) and Król (1878). The publications of Bąkowski (1883) and Kotula (1884) are the oldest monographic elaborations dealing with the malacofauna of the Polish Tatras. Bąkowski's was only a systematical list of species he collected. Kotula, on the other hand, produced a faunal and ecological study that was very innovative at the time and which has kept its scientific value until now. Kotula (1884) accentuated the vertical distribution of snails and he considered altitude as a basic influence on the malacofauna of the investigated area. But he did not neglect the significance of vegetation and soil conditions.

Among the few later papers on the malacofauna of the Tatras, only that by Hudec and Brabenec (1961) concerning the Slovakian part of these mountains bears comparison with the study by the Polish naturalist.

A great contribution to the knowledge of the Tatra molluscs was made by the Hungarian malacologist J. Hazay (1885). He described *Spelaeodiscus* (*Aspasita*) *tatricus* (= *Helix triaria* var. *tatrica*) - a species endemic to the Bielskie (Belanské) Tatras. Two relatively recent popular-scientific publications by Urbański (1962) and Ložek (1974) joined the list of papers concerning Tatra malacofauna. They review earlier publications and data included in monographs about particular systematic groups of snails.

In recent years interest in Tatra molluscs has revived. Certain aspects of the malacofauna of the Polish Tatras were studied by Dzięczkowski (1972), Wiktor (1973) and Umiński (1975, 1980, 1983). Some data can be also found in a few publications quoted in further chapters of this paper. Kroupova (1986) made a comprehensive study on the malacocenoses of Liptov. Taking into account the results of contemporary malacological investigations, Kroupova verified the data on the occurrence of species, the classification of which had been revised. Malacocenoses described by Kroupova (1986) were taken as an ecological characteristic of the landscape.

Faunal and ecological research on molluscs has been carried out in the Polish Tatras recently also. The present monograph, the first publication of this kind since Kotula's time, is the product of this research, some results of which have already been published (Dyduch-Falniowska, Fyda 1986; Dyduch-Falniowska 1988; Dyduch-Falniowska, Tobis 1989). This monograph describes the distribution of particular species and analyses their mutual relations and biotope relations. In addition, it points to the pressure of human and natural influences and proposes ways to prevent the degradation of the malacofauna.

Contents

Spis treści

II. Study area

The Polish Tatras have been studied in every respect (Tatrzański Park Narodowy 1962, Klimek in press). From the point of view of the malacofauna, the most important characteristics of this area are its altitude (900 - 2499 m a.s.l.) and the vertical differentiation of abiotic and biotic conditions, as well as the differentiation of the substratum into calcareous and non-calcareous types.

As almost the whole area of the Polish Tatras are included in the Tatra National Park these both terms are used interchangeably in the paper. The author investigated the whole area of the Tatra National Park (TNP) and the Zakopane Basin. Snails were recorded from localities shown on the map (fig. 1). The majority of localities were in the Western Tatras. The list of localities is in Appendix I.

III. Material and methods

Material was collected from 1982 to 1990, in the same phenological period (i. e., at the turn of July and in August) to maintain the comparability of data. In 1985, 1989, and 1990 snails were gathered in June also. The present paper is based on material collected by a semi-quantitative method, with the proportions among species maintained. Snails and slugs were collected for an equal time-span each time, on each locality (sweeping with entomological net, sieving and sorting litter, collecting under stones, pieces of wood and bark). They were preserved in ethyl alcohol (finally 75%). Altogether 25,000 specimens were collected.

For determining the occurrence and share of particular species in the malacocenoses of every station of TNP the author used the categories of Alexandrowicz (1987). Constancy, the percentage of localities in which a species was found, was denoted by C5 if the species was reported in 80.1 - 100% of the localities (euconstant); C4, 60.1 - 80% (constant); C3, 40.1 - 60% (subconstant); C2, 20.1 - 40% (accessoric); and C1, < 20% (accidental). Domination, the share of species (in per cent) in a malacocenose, was denoted by D5 if this share was > 20% (eudominant); D4 if it was 10.1 - 20% (dominant); D3, 5.1 - 10% (subdominant); D2, 1.1 - 5% (recedent); and D1, < 1% (subrecedent). The categories of domination reached by a given species in different malacocenoses and the category of constancy are given in parentheses after the description of the present distribution of species.

General domination is the share of a species in the malacofauna, i.e. the ratio of the number of individuals of a given species to that of all species.

To examine relations within particular malacocenoses as well as between them, the co-occurrence of species (1) and then the similarity of malacocenoses of particular localities (2) was analysed.

(1) Co-occurrence, understood as the frequency of the conterminous presence of two species, was evaluated with the help of binary and non-binary indices. To calculate these indices, the author used the formulae given below in the paragraph concerning the similarity of communities (modifying the meaning of particular

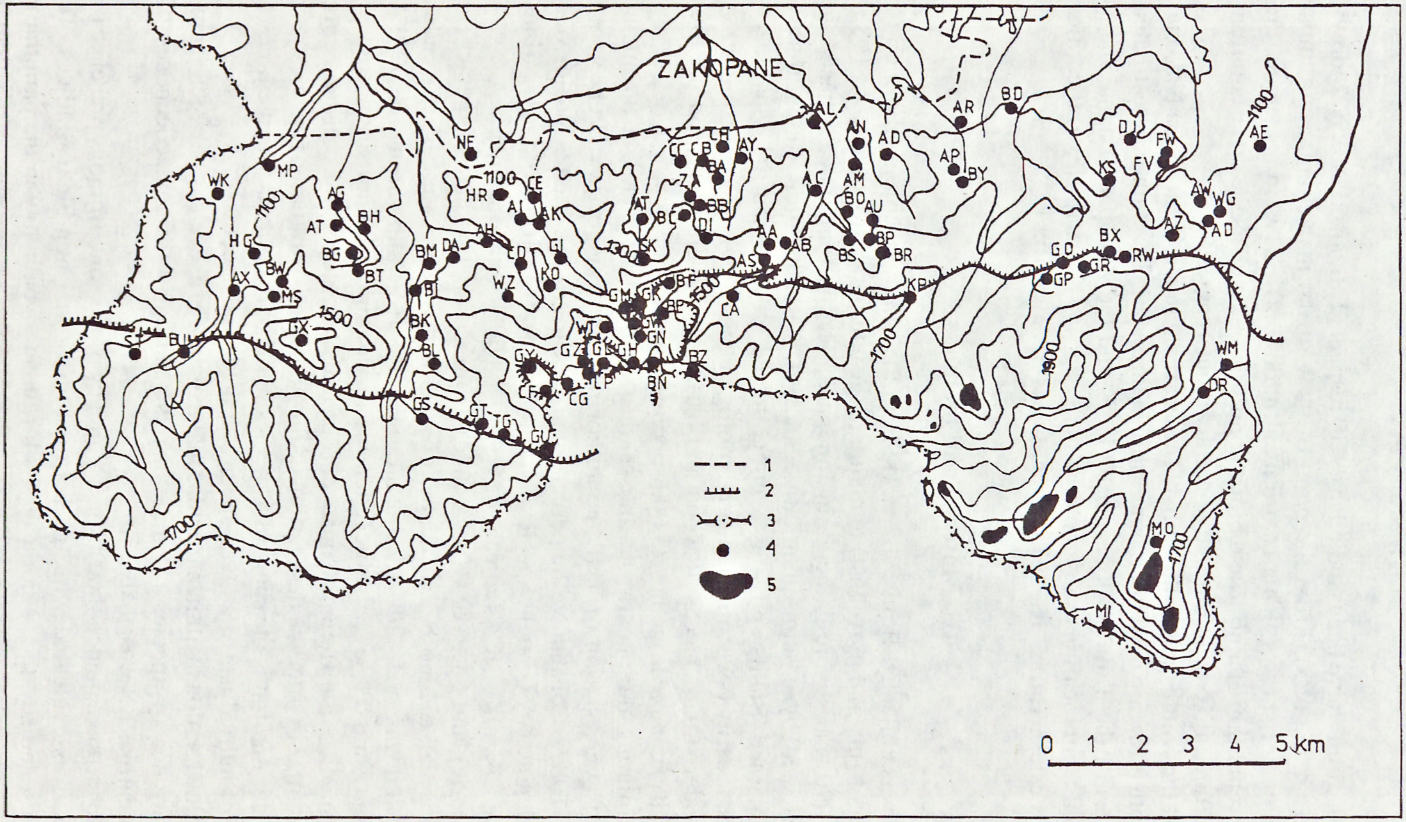


Fig. 1. Distribution of studied localities in the Tatra National Park (TNP). 1 - Park boundary, 2 - southern boundary of calciferous roks, 3 - State boundary, 4 - localities, 5 - lakes

Ryc. 1. Rozmieszczenie badanych stanowisk w TPN. 1 - granica Parku, 2 - południowa granica skał wapiennych, 3 - granica państwa, 4 - stanowiska, 5 - jeziora symbols: a - number of localities of species 1, b - number of localities of species 2, c - number of localities common to species 1 and 2). When those formulae were used to examine the similarity of faunas, usually the localities (samples) were tested for similarity and the species were treated as characteristics. In this paper it is the similarity of species which is analysed and the localities of species are taken as characteristics. In addition, the following equation (after Decamps 1967, as corrected by Yates) was used:

$$Oc = \frac{(C - P)N - N/2}{\sqrt{A(N - A)B(N - B)}}$$

where: Oc - co-occurrence index
A - number of localities where *i* species occurred,
B - number of localities where *j* species occurred,
C - number of localities common to *i* and *j*,
N - total number of localities,
P - probability of the co-occurrence of species *i* and *j* at N localities, P = AB/N.

(2) The similarity of animal communities can be discussed in respect to quality (species composition) as well as quality and quantity (relative abundance of particular species in cenoses). Similarity is an effect of interspecific relations in communities (Connor, Simberloff 1978, Hamill, Wright 1988) as well as habitat conditions. This connection of animal communities with habitat conditions induced zoogeographers to ground the methods of regional geography on similarity indices that had been used mainly in biocenology (Udwardy 1978).

In the relevant literature one can find many formulae used to compare animal communities. There are two general groups of indices: binary and non-binary. The shortcomings and advantages of similarity indices have been discussed frequently. The interpretation of results of calculation must take into account the limitations of particular indices. One should use at least a few indices, to increase the validity of the statistical calculations. For analysing the similarity of Tatra snail communities (malacocenoses), the author made use of the following formulae (Wolda 1981):

1. Baroni-Urbani and Buser's

$$S = \frac{\sqrt{cd} + c}{\sqrt{cd} + a + b - c}$$

2. Czekanowski's known as Sorensen's

$$QS = \frac{2c}{a + b}$$

3. Bray and Curtis's

$$1 - BC = 1 - \frac{\sum |n_{1i} - n_{2i}|}{\sum (n_{1i} + n_{2i})}$$

4. Bray and Curtis's after logarithmic transformation of the data $[\ln(n_{ij} + 1)]$

5. Canberra metric

$$1 - CM = 1 - \frac{1}{k} \sum \frac{|n_{1i} - n_{2i}|}{(n_{1i} + n_{2i})}$$

6. Canberra metric after logarithmic transformation of the data $[\ln(n + 1)]$.

7. Squared Euclidian distance (Clifford and Stephenson's)

$$1 - D^2 = 1 - \sum (p_{1i} - p_{2i})^2$$

8. Squared Euclidian distance after logarithmic transformation of the data $[\ln(n_{ji} + 1)]$

9. Percentage similarity (Renkonen's)

$$PS = \sum \min(p_{1i}, p_{2i})$$

10. Percentage similarity after logarithmic transformation of the data $[\ln(n_{ji} + 1)]$

11. Morisita index

$$C = \frac{2 \sum n_{1i} \; n_{2i}}{\left(\frac{\sum n_{1i}^2}{N_1^2} + \frac{\sum n_{2i}}{N_2^2} \right) N_1 N_2}$$

Additionally, Mountford's and Dice's association indices were calculated but little used in this work.

where:
- a - the number of species in sample 1
- b - the number of species in sample 2
- c - the number of species in common between 1 and 2
- d - the number of species absent in both 1 and 2
- k - the number of species in 1 and 2 combined a+b-c
- n - the number of individuals of species *i* in sample *j*
- N - the number of individuals in sample *j*
- p - the proportion of species *i* in sample $j = n_{ji} / N_j$

To group the species and malacocenoses from above calculations of co-occurrence and similarity the method of dendrites was used. The accepted procedure allowed clusters to be distinguished on the basis of a direct inner criterion (Marek, Noworol 1983).

To describe communities we often use specific indices of diversity and equitability (eveness), the former computed according to Shannon-Weaver formula (Lloyd, Zar, Karr 1968) and the latter according to Pielou (1975). They were also used at the processing of data in the present studies.

IV. List of the terrestrial snails of the Polish Tatras

The systematic arrangement and nomenclature of species are after the key by Kerney, Cameron, and Jungbluth (1983). The zoogeographic character of species (given after the name) was based on the judgement of Ložek (1956); Kerney, Cameron, and Jungbluth (1983); Riedel (1988); and Wiktor (1989). In square brackets are the domination and constancy of particular species in the malacocoenoses of the Polish Tatras, according to the scheme used by Alexandrowicz (1987) for the malacology of Quaternary deposits.

Aciculidae

1. *Acicula parcelineata* (Clessin, 1911), Carpathian (fig.2)

In the years 1983-1990 the species was collected in the litter of the beech forests on Mt Wierch Spaleniec and in the Dolina Białego, D. Olczyska, and D. Spadowca valleys. It was also found in Kuźnice, in an area overgrown by *Petasites albus.* Altogether 15 specimens were collected. All its localities were in the lower mountain forest zone, in forest litter [D1, D2, C1].

Jackiewicz (1974) observed the close connection of the species with *Mnium sp.* It seems that during the last two decades the habitat preferences of *A. parcelineata* in the Polish Tatras have changed slightly.

So far, the distribution of *A. parcelineata* in the Polish Tatras has been unknown. Urbański (1957) only mentioned the occurrence of *A. parcelineata* in this area, giving no precise data. Jackiewicz (1974) reported 3 specimens from two localities not published earlier, the Lityński valley, near waterfall - Tatra Mts. leg. Jankowski 1916 and Kuźnice, on the road to Mt Nosal - leg. Jankowski 1932. The first locality has not been identified by the present author; there is no Lityński valley in the Tatras. The second was confirmed in 1990.

Undoubtedly, the species under discussion is rare in the Polish Tatras and it is connected with the litter of *Dentario glandulosae - Fagetum.* The greater number of its present localities may result from a more thorough examination of the malacofauna of forest litter in these studies.

The occurrence of *A. parcelineata* in the High Tatras (Ložek 1956) was not confirmed. The biotopes preferred by this species in the Western Tatras do not occur there. Kroupova (1986) reports the species from the Chocské vrhy and Nizke Tatry mountains.

2. *Acicula polita* (Hartman, 1840), Central European (fig.2)

Specimens were collected in the litter of beech forests in the Mała Łąka valley, on Mt Wierch Spaleniec, in the Dolina Białego, D. Lejowa and D. Ku Dziurze valleys, and in epilithic grasslands on the Przysłop Miętusi saddle, in the Wąwóz Kraków gorge, on a rocky wall below the Polana Kondratowa glade (Na Czoło - about 1300 m a. s. l.), on Mt Sarnia Skała, in the Dolina Jaworzynka valley, in the Niżnia Polana Kominiarska glade and Łysa Skałka. The species is much rarer in spruce forests, where it occurs only at lower altitudes - eg. on Mt Filipczański Wierch.

There were 48 specimens collected. The species was collected regularly, though in small numbers (usually 1 or 2 in each locality) in the lower mountain forest *(Dentario glandulosae-Fagetum* and *Abieti-Piceetum)*, and rarely in the upper mountain forest. [D1, D2, C2].

From the Polish Tatras it was reported by Bąkowski (1883) (single specimens from the Dolina Strążyska and D. Za Bramką valleys) and by Kotula (1884) (four localities, up to the timber line). *A. polita* localities in the Polish Tatras are slightly different from those in the Liptovské Tatry mountains (Kroupova 1986), most likely due to different microclimates. The Polish slopes of the Tatras are cooler and *A. polita* shows a strong preference for warm habitats.

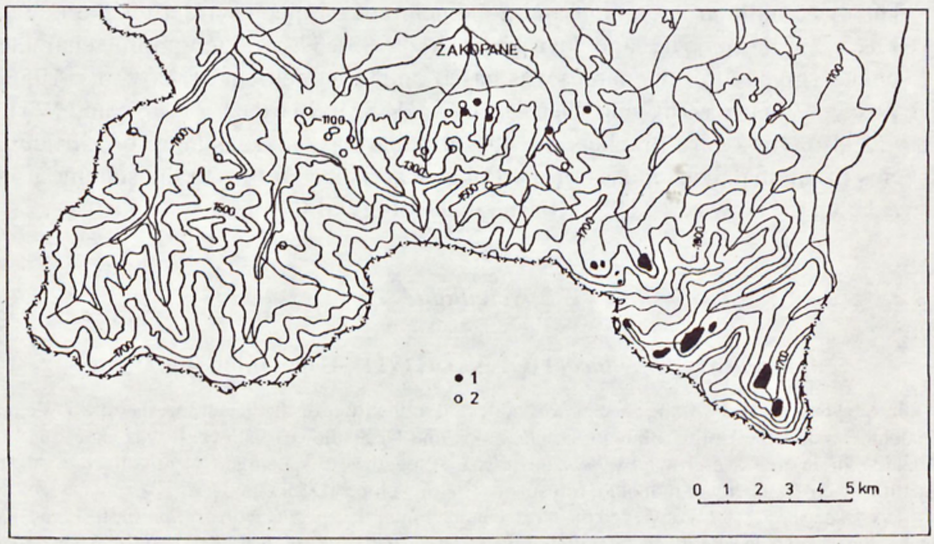


Fig. 2. *Acicula parcelineata* (1) and *A. polita* (2) in TNP

Ryc. 2. *Acicula parcelineata* (1) i *A. polita* (2) w TPN

Ellobiidae

3. *Carychium minimum* (O.F. Müller, 1774), Euro-Siberian (fig. 3)

The species was found in forest litter on Mt Wierch Spaleniec, in the Dolina Olczyska and D. Spadowca valleys, and in the Kamienny Żleb gully above the Polana Huciska glade. All these localities are humid. They abound in decaying organic matter. 29 specimens were found, 1-9 in each locality [D1, D2, C1].

These localities are at higher altitudes than those identified by Kotula (1884) but similar to those reported from the Liptovské Tatry mountains by Hudec and Brabenec (1961) and Kroupova (1986). It is possible that the upper limit of the species in the Polish Tatras has shifted upward due to changes in the flora of the Zakopane Basin.

4. *Carychium tridentatum* (Risso, 1826), European (fig. 3)

The species occurs in habitats similar to *C. minimum*'s: the Dolina Ku Dziurze, D. Białego, D. Olczyska, D. Spadowca, and D. Strążyska valleys. But *C. tridentatum* is much more numerous. Over 500 specimens were collected [D1, D2, C1].

Neither Bąkowski (1883) nor Kotula (1884) reported the species from the Tatras. Perhaps they could not tell this taxon from the preceding one. Hudec and Brabenec's observations (1961) show a congenial distribution of these two species in the Liptovské Tatry mountains and according to Kroupova (1986) their share in the malacocenoses is equal.

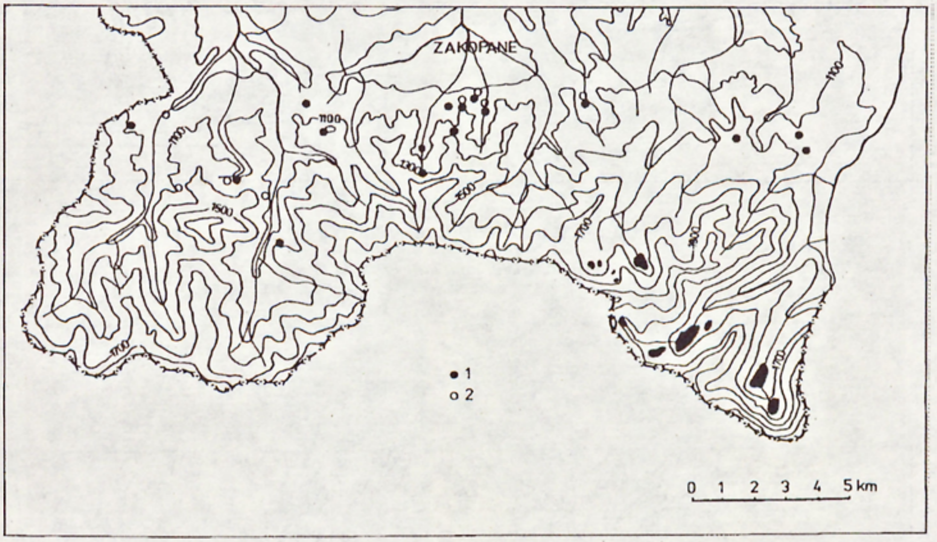


Fig. 3. *Carychium tridentatum* (1) and *C. minimum* (2) in TNP

Ryc. 3. *Carychium tridentatum* (1) i *C. minimum* (2) w TPN

Cochlicopidae

5. *Cochlicopa lubrica* (O.F. Müller, 1774), Holarctic (fig. 4)

In the Polish Tatras it is a very common snail, recorded from more than 30 localities (almost 50% of all the investigated ones), and found above 2000 m a.s.l. as well (Czerwone Wierchy). It is particularly frequent on in-forest glades, which points to the increasing synanthropization of the flora (Dyduch-Falniowska, Fyda 1986; Dyduch-Falniowska 1988).

Most of the nearly 400 specimens were collected in glades. The share of *C. lubrica* in the malacocenoses of these habitats is much higher than in other Tatra biotopes [D1-D5, C3].

Bąkowski (1883) mentioned the species only from Zakopane. According to Kotula (1884) it was common up to the dwarf mountain pine zone. In the Liptov malacocenoses *C. lubrica* is a constant and often dominant species (Kroupova 1986), and not uncommon in other parts of the Slovakian Tatras (Hudec, Brabenec 1961).

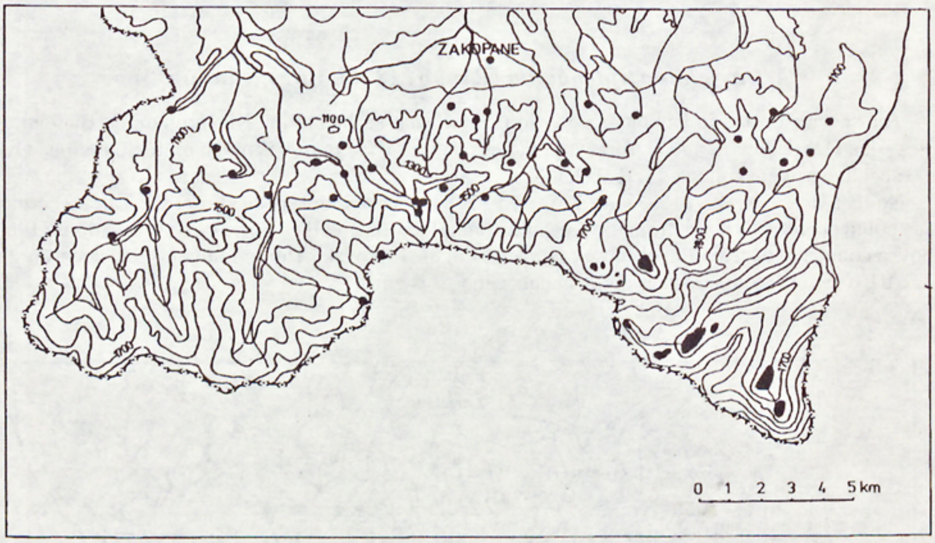


Fig. 4. *Cochlicopa lubrica* in TNP

Ryc. 4. *Cochlicopa lubrica* w TPN

Fig. 5. *Pyramidula rupestris* in TNP

Ryc. 5. *Pyramidula rupestris* w TPN

6. *Pyramidula rupestris* (Draparnaud, 1801), Submediterranean (fig. 5)

It is the commonest snail species in the Tatras. Petrofilous, it lives on rocks in the lower mountain forest zone as well as in the top parts of the range. In the material collected the species was represented by nearly 1900 specimens [D1-D5, C4].

These observations confirm Kotula (1884) and other authors on the malacocenoses of the Slovakian Tatras (Hudec, Brabenec 1961; Kroupova 1986).

Vertiginidae

7. *Columella edentula* (Draparnaud, 1805), Euro-Siberian (fig. 6)

One of the commonest *Vertiginidae* species in the lower Tatras, it is numerous on herbaceous plants and in the litter of all valleys. At higher altitudes it is rarer, but reaches the dwarf mountain pine zone. More than 1100 specimens of *C. edentula* were collected in the Tatras [D1 - D5, C4].

This species is most likely identical with *Pupa incarnata* Mich. (Kotula 1884), but its distribution in the Tatras as described by Kotula does not correspond with present observations. The occurrence of *C. edentula* in the Slovakian Tatras (Hudec, Brabenec 1961; Kroupova 1986) is similar to Polish Tatra data.

8. *Columella columella* (G. V. Martens, 1830), Boreal-mountain (fig. 6)

The species is limited to the tops of the Western Tatras, where it dominates the malacocenoses. It lives in epilithic grasslands with *Saxifraga aizoon, S. aizoides*, or *Dryas octopetala, Salix herbacea* and *S. reticulata*, occurring above 1500 m.a.s.l. (Pokryszko 1987, 1990).

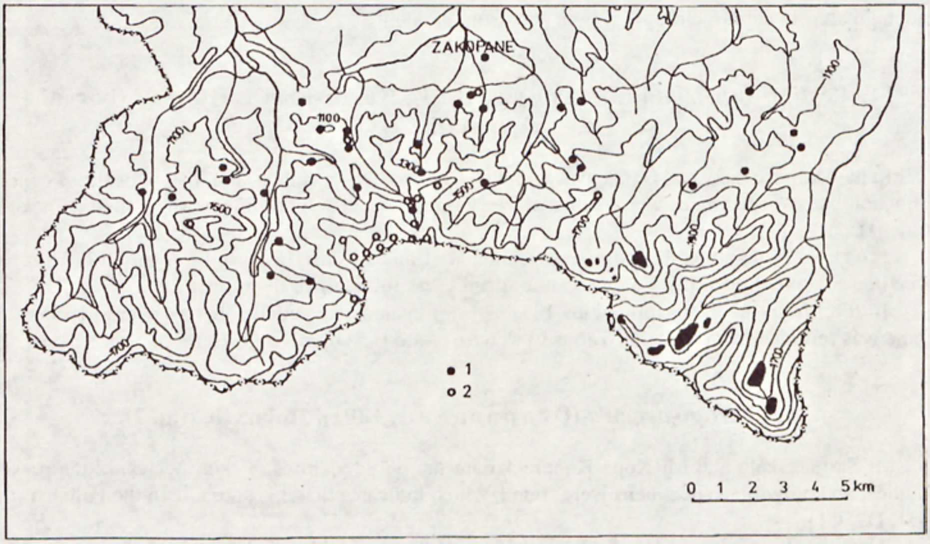


Fig. 6. *Columella edentula* (1) and *C. columella* (2) in TNP

Ryc. 6. *Columella edentula* (1) i *C. columella* (2) w TPN

In spite of its smaller range compared with the preceding taxon, a similar number of specimens was collected [D1 - D5, C2].

Kotula's (1884) conchological remarks indicate that it is identical with *Pupa edentula* Drap. var. *Gredleri* Clessin, and again the author doubts that these two species were correctly identified.

9. *Truncatellina cylindrica* (Ferrusac, 1807), West Palearctic (fig. 7)

The species occurs rarely in the Tatra National Park. It seems to live in large but isolated populations. Besides live specimens, some localities abounded in empty shells. During the five-year studies some two hundred specimens of *T. cylindrica* were collected in Przysłop Miętusi, just below the Polana Kondratowa glade, in Wielkie Koryciska, and in the Dolina Białego and D. Ku Dziurze valleys. Connected with xerothermic grasslands on limestones, it seems to occur up to the timber line [D1-D3, D5, C1].

Under the name *Pupa minutissima* Hartm. this species was reported by Kotula (1884) only from the Dolina Smytnia valley. The greater numbers of *T. cylindrica* recorded at present seem connected with the method of sampling. In the present studies the material from sieving was more thoroughly examined.

In the Slovakian Tatras *T. cylindrica* is somewhat more frequent (Hudec, Brabenec 1961). However, the species does not regularly occur in the malacocenoses described by Kroupova (1986).

10. *Vertigo pusilla* (O.F. Müller, 1774), European (fig. 7)

This one was found several times in the litter of *Dentario glandulosae-Fagetum* in the Dolina Olczyska valley. A single specimen was collected in the Dolina Lejowa valley. Altogether 41 specimens were gathered [D1, D2, C1].

Kotula (1884) reported this species from only one locality (Dolina Za Bramką valley). He considered it very rare. He pointed to the close connection of *V. pusilla* with mosses.

Kroupova's observations show that the share of this species in the Liptov malacocenoses is much greater. In certain biotopes it is an accessory element.

11. *Vertigo substriata* (Jeffreys, 1833), North-East European (boreal - alpine) (fig. 7)

In the Dolina Strążyska, D. Olczyska, and D. Chochołowska valleys and in two localities near D. Chochołowska 6 specimens were collected. Very rare, it occurs chiefly in the lower mountain forest zone [D1, D2, C1].

Kotula probably collected more specimens of this species, because he reported it from five localities and mentioned that on mosses the species was found up to the timber line.

In the Liptovské Tatry mountains *V. substriata* occurs accidentally (Kroupova 1986). The same was reported from the High Tatras by Hudec and Brabenec (1961).

12. *Vertigo pygmea* (Draparnaud, 1801), Holarctic (fig. 7)

Mt Sarnia Skała and Mt Kopa Kondracka are the only localities of this species, in the present studies, and only three specimens were found, which indicates that it is sporadic in the Polish Tatras [D1, D2, C1].

This distribution is completely different from Kotula's (1884). He said it was numerous but chiefly in "regio culta", in Zakopane.

The present situation of *V. pygmea* in the Slovakian Tatras seems the same as in the Polish Tatras. The species was reported only by Kroupova (1986), who found it in Liptov sporadically.

Fig. 7. *Truncatellina cylindrica* (1), *Vertigo pusilla* (2), *V. antivertigo* (3), *V. substriata* (4) and *V. pygmea* (5) in TNP

Ryc. 7. *Truncatellina cylindrica* (1), *Vertigo pusilla* (2), *V. antivertigo* (3), *V. substriata* (4) i *V. pygmea* (5) w TPN

13. *Vertigo arctica* (Wallenberg 1858), Holarctic, circumpolar (fig. 8)

More than 130 specimens of this species were collected in the tops of the Tatras, which points to its regular occurrence in epilithic grasslands above the dwarf mountain pine. *V. arctica* is most frequent in patches of *Saxifraga aizoides* and *Dryas octopetala* [D1-D5, C1].

Kotula (1884) reported the species from two localities in the Polish Tatras and he maintained that it was very rare.

The pattern of *V. arctica* distribution in the Belanské Tatry mountains (Hudec, Brabenec 1961) seems like that observed now in TNP. But Kroupova (1986) cites only the localities recorded by Dr V. Ložek from the West Tatras.

14. *Vertigo alpestris* (Alder, 1838), Boreal-alpine (fig. 8)

The species is common in all Tatra biotopes. More than 600 specimens were collected during the present study. In the two mountain forest zones it occurs in litter, and at higher altitudes in epilithic grasslands, exactly as Pokryszko (1990) described [D1-D5, C2].

Kotula (1884) considered *V. alpestris* a very rare species connected with mosses. In the Slovakian Tatras, in the malacocenoses described by Kroupova (1986), it occurred sporadically and in small numbers; it was more numerous in the material collected by Hudec and Brabenec (1961).

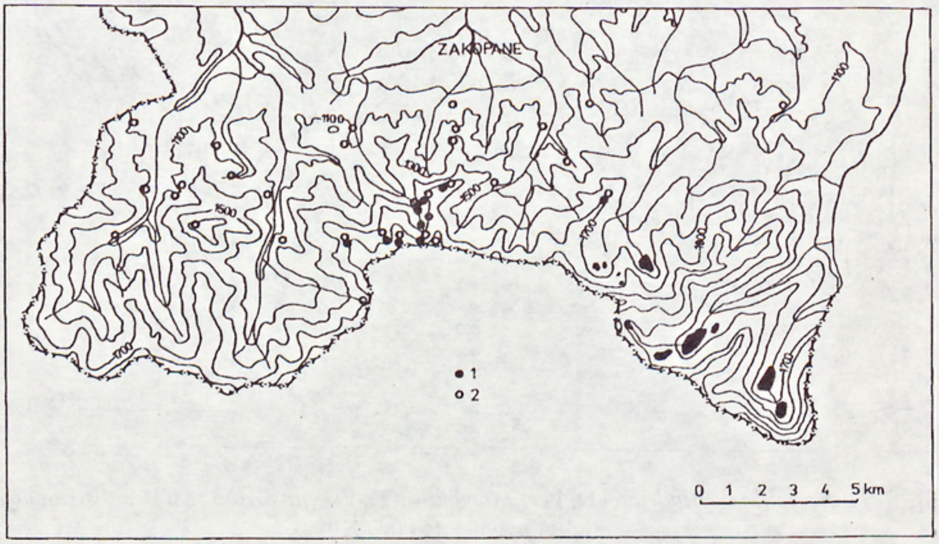


Fig. 8. *Vertigo arctica* (1) and *V. alpestris* (2) in TNP

Ryc. 8. *Vertigo arctica* (1) i *V. alpestris* (2) w TPN

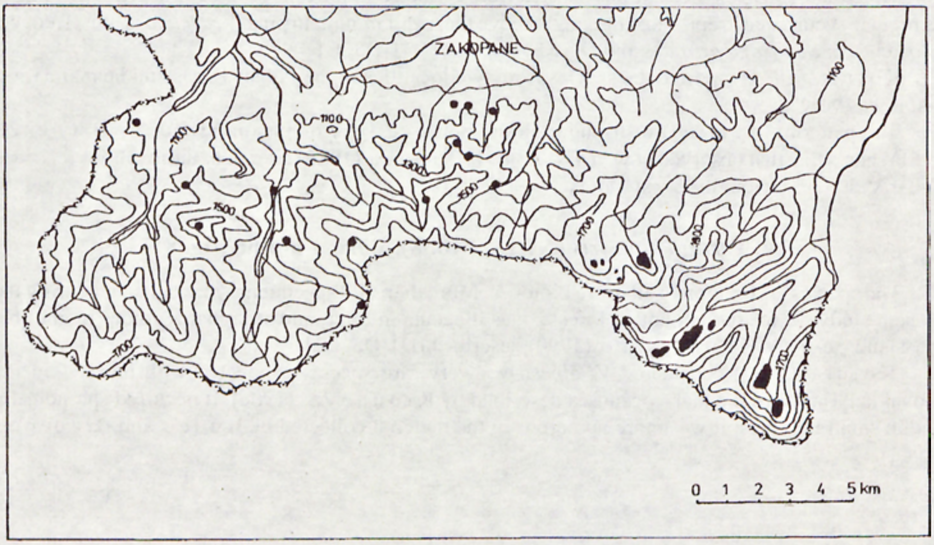


Fig. 9. *Orcula dolium* in TNP

Ryc. 9. *Orcula dolium* w TPN

Orculidae

15. *Orcula dolium* (Draparnaud, 1801), Alpine and Carpathian (fig. 9)

The species has a patchy distribution in the Polish part of the West Tatras. Strong populations occur in grasslands on calcareous rocks in the two mountain forest zones. Mostly single specimens are found further up. Nearly 300 specimens were found. The connection of this species with calcareous substrata seems to be stronger than that of many other Tatra species. Its conchological variability within one locality as well as among all localities is great. That will be a subject of separate studies. [D1-D5, C1].

Kotula (1884) also pointed to the great conchological variability of *O. dolium*, specimens of which were numerous in his material also. His observations seem to indicate that the Tatra National Park hosts *O. dolium* Mich. *var. uniplicata* Pot. et Mich.

The species is a constant element in the malacocenoses of the Slovakian Tatras (Hudec, Brabenec 1961; Kroupova 1986). In this part of its range it also shows great conchological variability (Ložek 1956).

Chondrinidae

16. *Chondrina clienta* (Westerlund, 1884), East Alpine and South-East European (fig. 10)

Mt Nosal, Dolina Kościeliska, and D. Białego valleys are the only localities of this species in the present studies, and only in the first of these localities was its population numerous [D1, D5, C1].

For Kotula *Ch. clienta* was not common either, in the area included now in the Tatra National Park. Apart from the above localities, he also mentioned Siodło and Dolina Mała Łąka valley with the Polana Miętusia glade, all three were on the basis of the data of other malacologists.

Nor is this species frequent in the malacocenoses investigated by Hudec and Brabenec (1961) and by Kroupova (1986) in the Slovakian Tatras.

Chondrina tatrica Ložek, 1948 was not found during the present studies. Kroupova (1986) reported this West Carpathian endemite. There is a need for comparative studies on *Ch. clienta* and *Ch. tatrica*, with special regard to the range of their variability.

Pupillidae

17. *Pupilla sterri* (Voith, 1840), South-East European and Central European (fig. 10)

The species is clearly restricted to the tops of the Tatras. Some populations seem fairly numerous. On Mt Giewont and on Gęsia Szyja a dozen or so specimens were collected. 33 specimens were gathered altogether [D1, D2, D4, C1].

Kotula (1884) also found that *P. sterri* was not frequent in the area of the present Tatra National Park. In the Slovakian Tatras, it was recorded from the Liptovské Tatry range (Hudec and Brabenec 1961), and Kroupova (1986) reported it, after Ložek and Soos, from Chocské vrchy, the Nizke Tatry mountains and from some other ranges.

18. *Argna bielzi* (Rossmaessler, 1859), Carpathian (fig. 10)

This is a Carpathian endemite forming fairly numerous populations at lower altitudes (in the Dolina Kościeliska, D. Ku Dziurze, and D. Spadowca valleys); it reaches the dwarf mountain pine zone

(Siodło). It occurs chiefly in litter or under stones. In the material collected in TNP *A. bielzi* was represented by 150 specimens [D1-D5, C1].

In K o t u l a ' s publication (1884) this species was referred to as *Pupa biplicata* M i c h . *var. bielzi* R o s s m . and it seems to have been much more frequent in that time.

In Liptovské Tatry *A. bielzi* occurs more regularly but is not a constant element in malacocenoses of this area either (H u d e c, B r a b e n e c 1961; K r o u p o v a 1986).

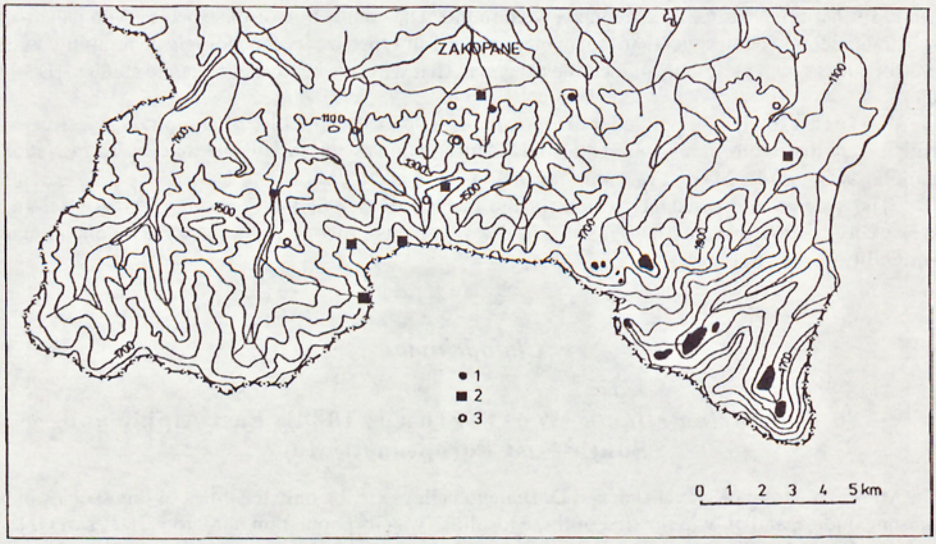


Fig. 10. *Chondrina clienta* (1), *Pupilla sterri* (2) and *Argna bielzi* (3) in TNP

Ryc. 10. *Chondrina clienta* (1), *Pupilla sterri* (2) i *Argna bielzi* (3) w TPN

Valloniidae

19. *Vallonia costata* (O.F. M ü l l e r, 1774), Holarctic (fig. 11)

The only records of this species common in lowlands, come from the Dolina Jaworzynka valley (4 specimens) [D1, D2, C1].

It was much more numerous in K o t u l a ' s (1884) material. In the Belanské and Liptovské Tatry mountains it was reported from several localities (H u d e c, B r a b e n e c 1961; K r o u p o v a 1986).

20. *Vallonia pulchella* (O.F. M ü l l e r, 1774), Holarctic (fig.11).

Common in lowlands, like *V. costata,* in TNP the species has been recorded only from the Dolina Chochołowska glade and Kopy Sołtysie [D1, C1].

These localities are higher than those mentioned by K o t u l a (1884) who collected *V. pulchella* up to the lower mountain forest zone.

K r o u p o v a (1986) reported this species from several Tatra ranges: the Chocské vrchy, Liptovské Tatry, and Nizke Tatry mountains, among others.

21. *Acanthinula aculeata* (O.F.Müller, 1774), West Palearctic (fig. 11)

Careful examination of sieved samples turned up only one specimen (in the Dolina Filipka valley) [D1, C1].

Kotula (1884) also mentioned only one locality for this species, but after other authors. In other parts of the Tatras, in forest litter in the Chocské vrchy and Nizke Tatry mountains, the occurrence of *A. aculeata* is also ephemeral (Kroupova 1986).

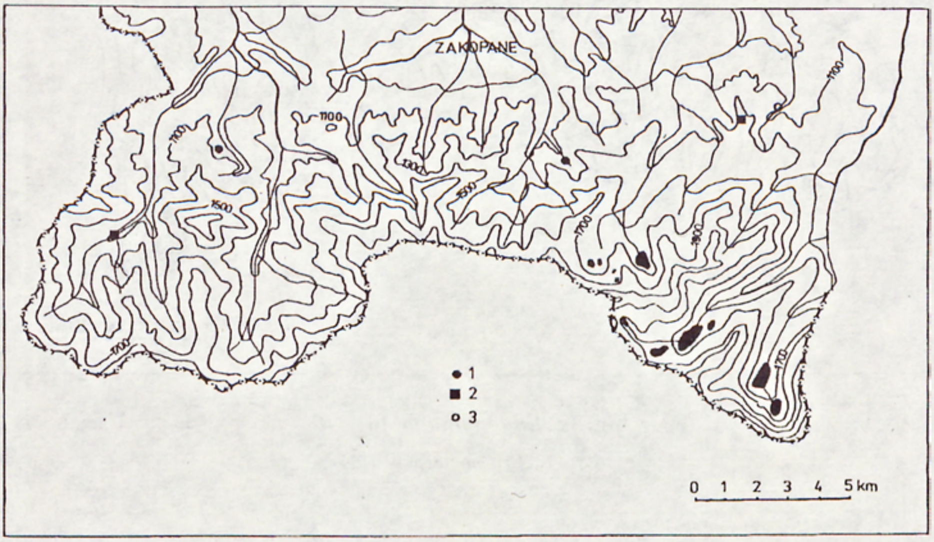


Fig. 11. *Vallonia costata* (1), *V. pulchella* (2) and *Acanthinula aculeata* (3) in TNP

Ryc. 11. *Vallonia costata* (1), *V. pulchella* (2) i *Acanthinula aculeata* (3) w TPN

Enidae

22. *Ena montana* (Draparnaud, 1801), Central European, Alpine-Carpathian (fig. 12)

This mountain forest species occurs in many localities, chiefly in lower and upper mountain forest zones. In each sample it was represented by several specimens. *E. montana* populations are rather small. Altogether 104 specimens were collected [D1-D3, C1].

The list of localities given by Kotula (1884) shows that a century ago *E. montana* was much more frequent and numerous.

At present, this snail seems to be most frequent in the Liptovské Tatry mountains, though it is accessory or subrecedent in those malacocenoses (Hudec, Brabenec 1961; Kroupova 1986).

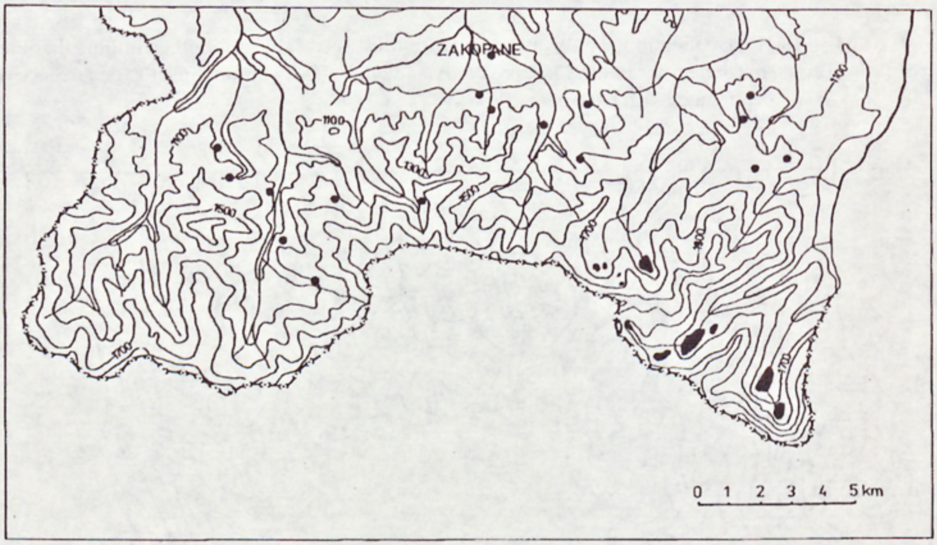


Fig. 12. *Ena montana* in TNP

Ryc. 12. *Ena montana* w TPN

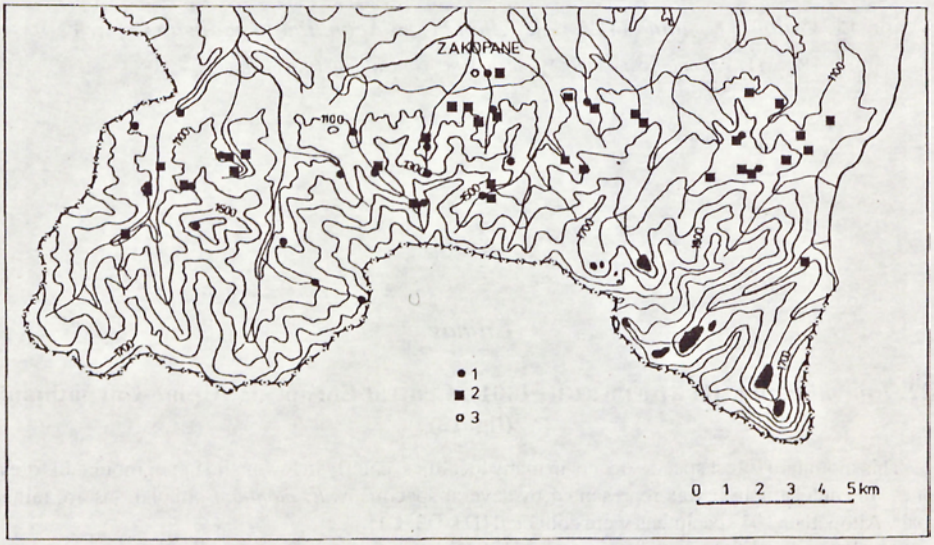


Fig. 13. *Punctum pygmaeum* (1), *Discus ruderatus* (2) and *D. rotundatus* (3) in TNP

Ryc. 13. *Punctum pygmaeum* (1), *Discus ruderatus* (2) i *D. rotundatus* (3) w TPN

Endodontidae

23. *Punctum pygmaeum* (Draparnaud, 1801), Holarctic (fig. 13)

This species occurs in the malacocenoses of all Tatra biotopes. It is connected chiefly with forest litter, and at higher altitudes with epilithic grasslands. 112 specimens were collected [D1-D3, C2].

Kotula (1884) mentioned only one locality for this species (Dolina Za Bramką).

P. pygmaeum has been recorded from the Belanské and Liptovské Tatry mountains, where it is not common either (Hudec, Brabenec 1961). In the malacocenoses described by Kroupova (1986) this species is accidental and subrecedent.

24. *Discus ruderatus* (Ferrusac, 1821), Holarctic (Palearctic) (fig. 13)

It is one of the more common species, confined rather to open habitats (treefalls) than to those overgrown with dense forest. The largest populations occur on in-forest glades (Wielka Polana, Niżnia Polana Kominiarska). It lives under tree bark or under stones. Most of the 400 specimens collected were from biotopes under strong human pressure [D1-D5, C3].

In Kotula's times (1884) the species was common too. It was observed most often under tree bark.

Hudec and Brabenec found it rather common in the Slovakian Tatras. According to Kroupova (1986) it occurs only in communities of xerothermic or subxerothermic meadows as an accidental or accessory and subrecedent element.

Arionidae

25. *Arion subfuscus* (Draparnaud, 1805), European (fig. 14)

This is the most common slug in the area under study. The collected material (over 200 specimens) included specimens representing all Tatra biotopes from the Zakopane Basin to the highest peaks (Mt Mięguszowiecki - 2438 m a.s.l.) [D1-D4, C3].

One hundred years ago the distribution of the species was similar (Kotula 1884; Wiktor 1973).

In the Slovakian Tatras it is also very common (Hudec, Brabenec 1961) though in the malacocenoses described by Kroupova (1986) it occurs only as accidental and subrecedent.

26. *Arion silvaticus* (Lohmander, 1937), European (fig. 15)

The species has been recorded from the Zakopane Basin and from lower altitudes in TNP. 42 specimens were collected. The remarks on the systematics of *Arionidae* and on the number and distribution of particular species apply to *A. silvaticus* also [D1, D2, C1].

Data on *A. hortensis* from Kotula (1884) enable a partial reconstruction of the Tatra distribution of *A. silvaticus* in those times. If its habitat preferences have not changed radically we may suppose that a century ago it was only slightly less common at lower altitudes than *A. subfuscus*.

From the Slovakian Tatras the species was reported only by Kroupova (1986), but as in the previous case more detailed information was lacking. Probably at least part of the records of *A. circumscriptus* in Hudec and Brabenec (1961) concern *A. silvaticus*.

27. *Arion fasciatus* (Nilsson, 1822), North-West European (European) (fig. 15)

Half of the collected material of this species (altogether over 40 specimens) come from the Zakopane Basin. In TNP *A. fasciatus* occurs rather singly, and it is found up to the tops of the Tatras [D1-D3, C1].

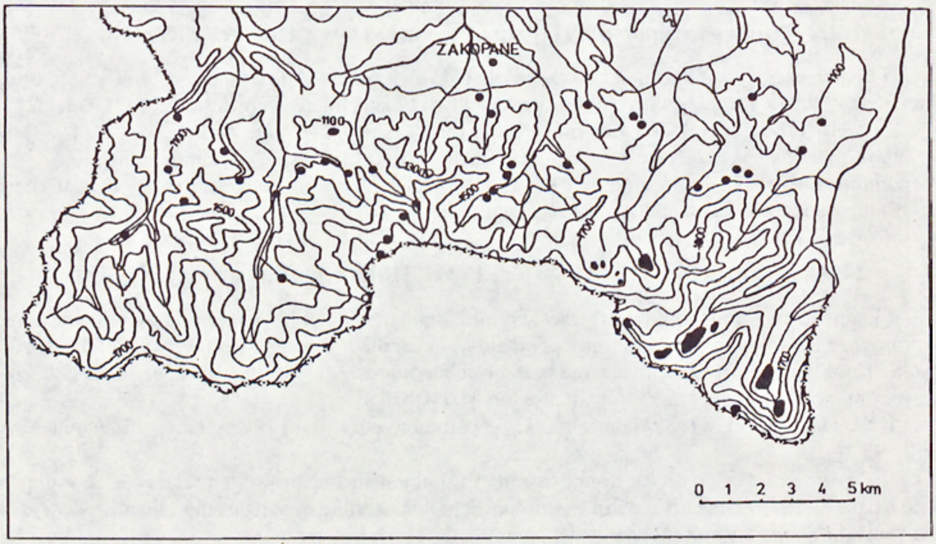


Fig. 14. *Arion subfuscus* in TNP

Ryc. 14. *Arion subfuscus* w TPN

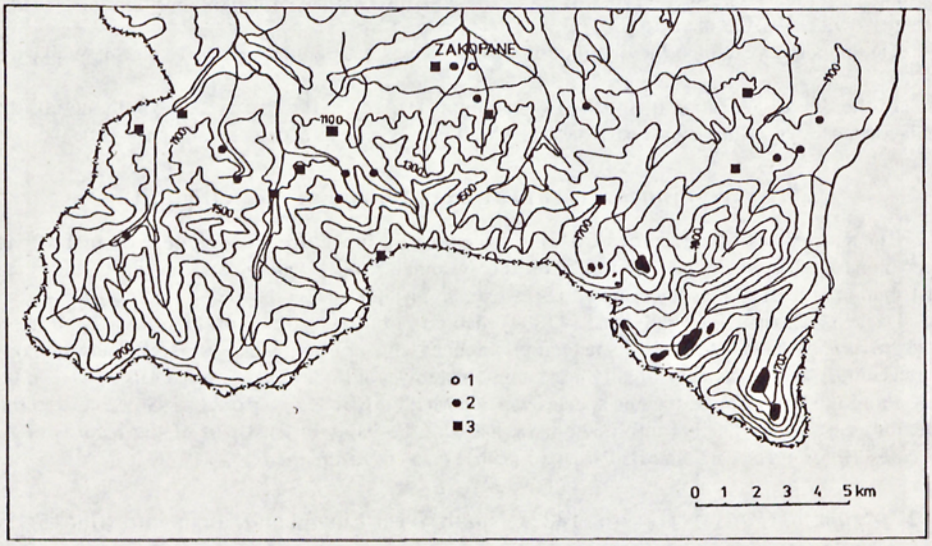


Fig. 15. *Arion hortensis* (1), *A. silvaticus* (2) and *A. fasciatus* (3) in TNP

Ryc. 15. *Arion hortensis* (1), *A. silvaticus* (2) i *A. fasciatus* (3) w TPN

As with *A. silvaticus* it seems that a century ago the number of *A. fasciatus* was slightly lower than that of *A. subfuscus*.

From the Slovakian Tatras the species was mentioned only by Kroupova (1986), and as before it was probably identified by Hudec and Brabenec (1961) as *A. circumscriptus*.

Vitrinidae

28. *Vitrina pellucida* (O.F. Müller, 1774), Holarctic (fig. 16)

This is one of the commonest species in all types of habitats, but most numerous on in-forest glades and in stream valleys (Wielka Polana, Polana Waksmundzka, Dolina Spadowca and Dolina Kościeliska). *V. pellucida* reaches the high densities (Umiński 1983, Dyduch-Falniowska, Tobis 1989) [D1-D4, C3].

A similar distribution for *V. pellucida* was observed by Kotula (1884). Data from Hudec and Brabenec (1961) and Kroupova (1986) point to the important role of this species in the present malacocenoses. In Liptov it is a constant and dominating element in some communities.

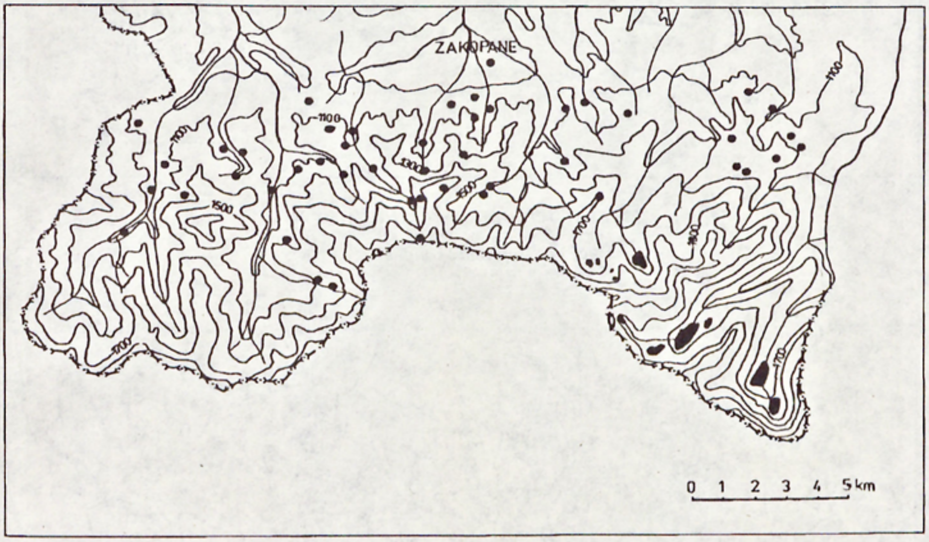


Fig. 16. *Vitrina pellucida* in TNP

Ryc. 16. *Vitrina pellucida* w TPN

29. *Semilimax kotulae* (Westerlund, 1883), Alpine-Carpathian (fig. 17)

The species is common at all altitudes in the Tatras. Nearly 300 specimens were found. Most of them occurred in samples singly. Only in the Polana Waksmundzka glade, Dolina Tomanowa valley, and the Przełęcz Małołącka pass were the *S. kotulae* populations numerous (from ten to twenty to some tens of specimens). The species shows a preference for habitats on crystalline substratum, rinsed by water flowing down calcareous slopes. Some aspects of population dynamics of *S. kotulae* were studied by Umiński (1983) [D1-D5, C3].

These observations concur with Kotula (1884), except that he found these snails more often and at higher altitudes.

In the Liptov malacocenoses *S. kotulae* occurs chiefly as accidental or recedent species (K r o u p o v a 1986). In other parts of the Slovakian Tatras it is not very numerous but occurs regularly (H u d e c and B r a b e n e c, 1961).

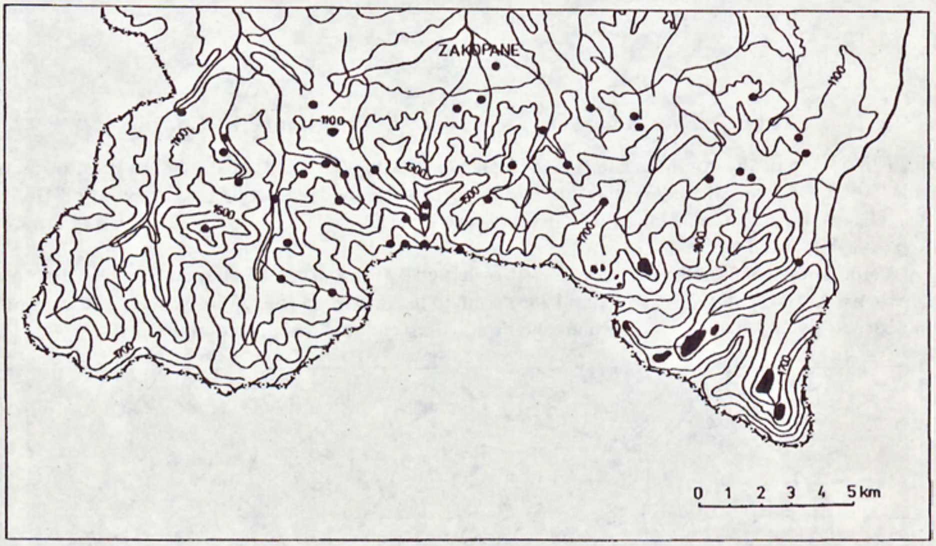


Fig. 17. *Semilimax kotulae* in TNP

Ryc. 17. *Semilimax kotulae* w TPN

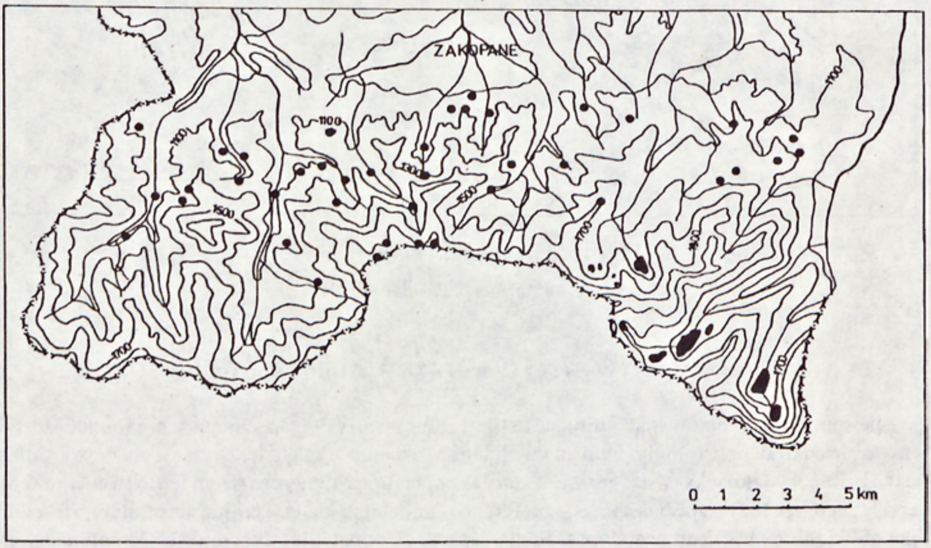


Fig. 18. *Eucobresia nivalis* in TNP

Ryc. 18. *Eucobresia nivalis* w TPN

30. *Eucobresia nivalis* (Dumont et Mortillet, 1852), Alpine-Carpathian (fig. 18)

This snail is uniformly distributed all over the Tatras from their lowest to highest parts. The species never forms large populations, and it is recorded chiefly as single specimens. The author found 155 specimens, half as many as *S. kotulae* specimens, but the number of records (localities) was similar to *S. kotulae*. Umiński (1983) presented some interesting aspects of *E. nivalis* population in the Tatras [D1-D5, C3].

Kotula (1884) found *E. nivalis* common up to the timber line. Its distribution in the region of Liptov (Kroupova 1986) is similar to that in TNP. In the malacocenoses described by Kroupova (1986) it is accidental and (sub) recedent. In other parts of the Slovakian Tatras it occurs frequently and in great numbers.

Zonitidae

31. *Vitrea diaphana* (Studer, 1820), Carpathian-Alpine (fig. 19)

This is one of the five most numerous species in TNP. It occurs from the Zakopane Basin up to the alpine meadow zone; in the lower mountain forest zone it is connected with forest litter, and at higher altitudes chiefly with epilithic grasslands. In humid litter the species forms large aggregations, while in epilithic grasslands it lives singly. That is why most of the over 1100 specimens collected come from localities in the lower mountain forest zone [D1-D5, C4].

Kotula (1884) pointed to the common occurrence of this species up to the dwarf mountain pine zone. He did not mention it from higher altitudes. In the region of Liptov also *V. diaphana* shows a clear preference for lower mountain forest (Kroupova 1986). In fertile forest habitats it is a constant and recedent species. In other habitats it occurs only sporadically or not at all. Hudec and Brabenec's observations (1961) indicate that in other parts of the Slovakian Tatras *V. diaphana* has a very similar distribution.

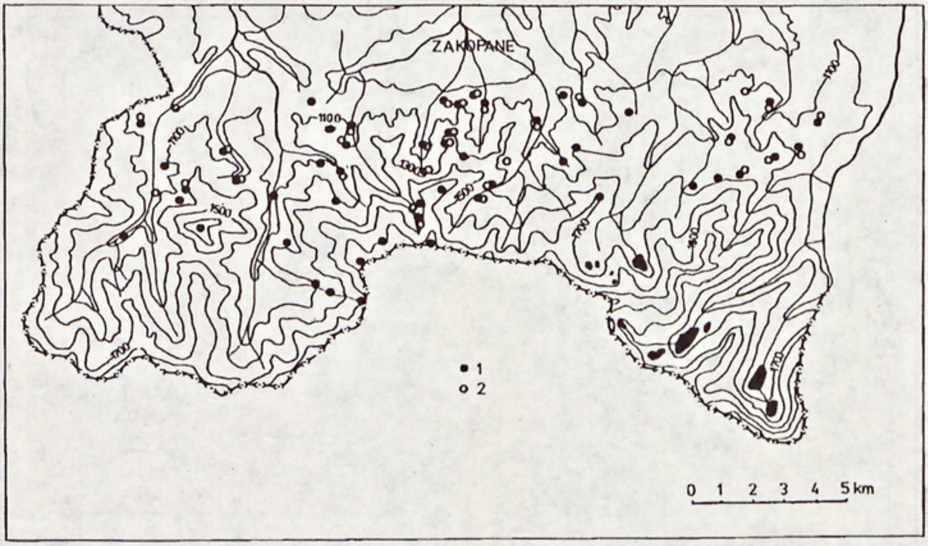


Fig. 19. *Vitrea diaphana* (1) and *V. transsylvanica* (2) in TNP

Ryc. 19. *Vitrea diaphana* (1) i *V. transsylvanica* (2) w TPN

32. *Vitrea transsylvanica* (Clessin, 1877), Carpathian (fig. 19)

This Carpathian endemite is not common in TNP. It reaches ca. 1800 m a.s.l. and usually accompanies *V. diaphana* but is much less numerous. The number of *V. transsylvanica* (about 300 specimens) was one third that of *V. diaphana* [D1-D4, C2].

One hundred years ago the situation of the species in the Polish Tatras was similar to now (Kotula 1884). In the Slovakian Tatras *V. transsylvanica* is less numerous than *V. diaphana*, also. In the malacocenoses described by Kroupova (1986) it is accessory or accidental and recedent or subrecedent. In other parts of the Slovakian Tatras it has a similar distribution (Hudec, Brabenec 1961).

33. *Vitrea subrimata* (Reinhardt, 1871), Alpine and South European (fig. 20)

The author recorded the species from a few localities, from the lower mountain forest zone to alpine meadows (Krzesanica, 2122 m a.s.l.). In seven localities, 18 specimens were collected [D1, D2, C1].

Kotula (1884) pointed to *V. subrimata*'s preference for mosses. He considered this species frequent and numerous. Kroupova's observations connect *V. subrimata* with forest malacocenoses in which it is accessory or accidental and (sub)recedent. Hudec and Brabenec (1961) indicate that *V. subrimata* occurs irregularly in the Slovakian Tatras. In the Belanské Tatry and in the west part of the Liptovské Tatry mountains populations are numerous and large. In the High Tatras and in the southern part of Liptov the species occurs rarely and in small numbers.

34. *Vitrea crystallina* (O.F. Müller, 1774), European (fig. 20)

80 specimens of *V. crystallina* have been recorded from 15 localities which indicates that in TNP it is not numerous or frequent. Its localities are chiefly in the lower mountain forest; at higher altitudes it occurs only sporadically. The Przełęcz Tomanowa pass is its highest locality (1686 m a.s.l.) [D1-D4, C1].

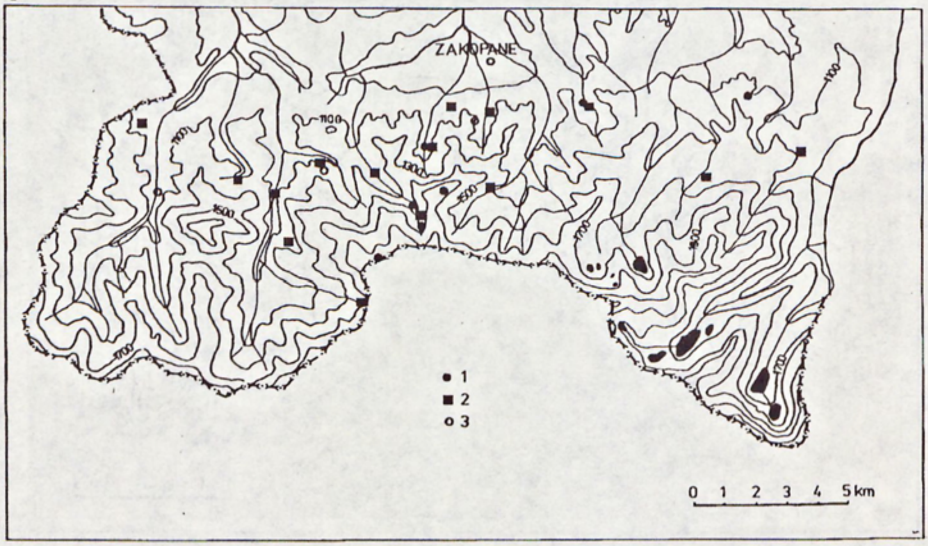


Fig. 20. *Vitrea subrimata* (1), *V. crystallina* (2) and *V. contracta* (3) in TNP

Ryc. 20. *Vitrea subrimata* (1), *V. crystallina* (2) i *V. contracta* (3) w TPN

Like other representatives of the genus *Vitrea* it was formerly much more frequent. Kotula (1884) pointed to its connection with mosses.

In the Liptov malacocenoses *V. crystallina* seems to play a more important role as an accessory or accidental element (in one type of community even constant). Regarding dominance it is subdominant, recedent or subrecedent. In other parts of the Slovakian Tatras *V. crystallina* is not very frequent. It forms large populations only occasionally (Hudec, Brabenec 1961).

35. *Vitrea contracta* (Westerlund, 1871), West Carpathian (fig. 20)

Altogether only 15 specimens in four localities were found (Dolina Spadowca and D. Chochołowska, between Zahradziska and Przysłop Miętusi, Zakopane Basin). In TNP, as in the other parts of its range, the species is not frequent. These are the first records of *V. contracta* from the Polish Tatras [D1, D2, C1].

From the Slovakian Tatras it was reported only by Kroupova (1986). In five malacocenoses she described, the species is accessory or accidental and recedent or subrecedent.

36. *Aegopinella pura* (Alder, 1830), European (fig. 21)

The species has been found in all Tatra biotopes. Most of the over 40 localities recorded are stream valleys. The highest locality is Kocioł Litworowy (1800-1900 m a.s.l.). Altogether over 500 specimens were collected [D1-D5, C3].

Kotula (1884) also considered *Ae. pura* a very common species and pointed to its connection with mosses. Its role in the Liptov malacocenoses is different. At lower altitudes in fertile forests, it is constant, in other biotopes - mostly accessory or accidental. It is subdominant (in secondary spruce forests) or recedent or subrecedent. This species occurred in nine types of malacocenoses in the area investigated by Kroupova (1986). According to Hudec and Brabenec (1961) in other parts of the Slovakian Tatras *Ae. pura* is frequent and numerous.

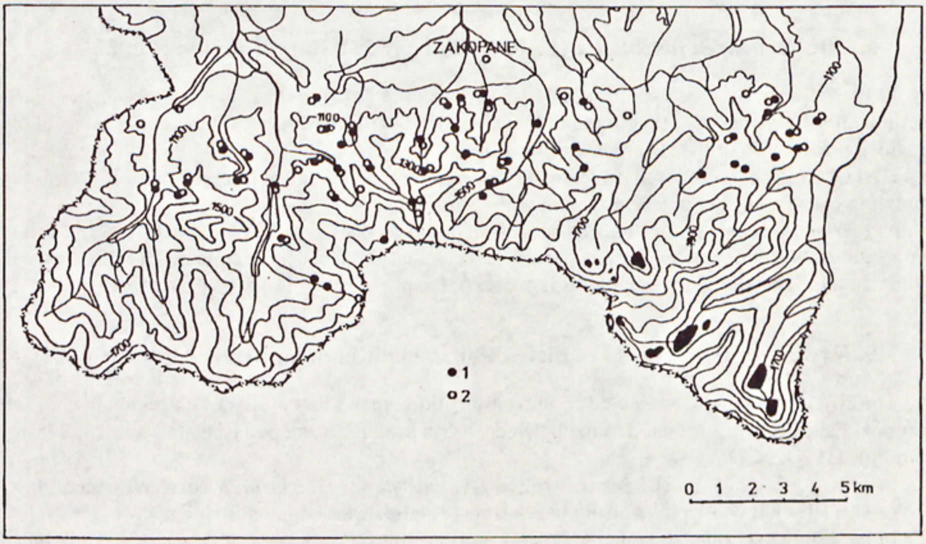


Fig. 21. *Aegopinella pura* (1) and *Ae. nitens* (2) in TNP

Ryc. 21. *Aegopinella pura* (1) i *Ae. nitens* (2) w TPN

37. *Aegopinella nitens* (Michaud, 1831), Alpine and Central European (fig. 21)

Its distribution in TNP is similar to that of *Ae. pura*. The species has been recorded from about 40 localities. More than 500 specimens were collected. It prefers stream valleys and reaches the upper limit of the dwarf mountain pine zone. The highest locality is the Przełęcz Małołącka pass (1924 m a.s.l.) [D1-D5, C3].

In Kotula's times (1884) *Ae. nitens* was one of the commonest snails and the distribution of its localities was generally the same; in the lower Tatras it was more frequent, grew rarer with increasing altitude.

In Liptov it was found in six malacocenoses. In two of them it was constant and in the others it was accessory or accidental. *Ae. nitens* was dominant, recedent or subrecedent (Kroupova 1986). Most of the localities reported by Hudec and Brabenec (1961) from other parts of the Slovakian Tatras are stream valleys, and their populations were characterized as "strong."

38. *Nesovitrea hammonis* (Strom, 1765), Palearctic (fig. 22)

A not very frequent species, it was collected in 20 localities from the Zakopane Basin up to the tops of the Zakopane Tatras (Małołączniak, 2096 m a.s.l.). This snail clearly prefers in-forest glades which constitute one third of its localities and yield more than 63% of the specimens collected [D1-D4, C2].

According to Kotula (1884) *N. hammonis* was very common in wet areas and reached only the lower limit of the dwarf mountain pine zone.

In Liptov it is a constant element in malacocenoses inhabiting wet meadows, and in valleys overgrown with deciduous, coniferous or mixed forests on non-limestone substratum. As an accessory or accidental element it occurs in a dozen or so malacocenoses. It may be dominant, subdominant, recedent or subrecedent (Kroupova 1986). According to Hudec and Brabenec (1961) *N. hammonis* (=*Perpolita radiatula*) is relatively most abundant in the west part of the Liptovské Tatry mountains, but it is not among the most common species. In the Belanské Tatry mountains it was recorded only from one locality.

39. *Nesovitrea petronella* (L. Pfeiffer, 1853), Boreal-alpine (fig. 22)

124 specimens were collected from 11 localities in the Polish Tatras. In some places the species accompanies *N. hammonis*. It is rarer then *N. hammonis,* but like that species it prefers in-forest glades, in which nearly 80% of the specimens were collected [D1-D4, C1].

Kotula (1884) considered it a form of *N. hammonis* and pointed to its connection with the upper mountain forest zone and dwarf mountain pine zone.

N. petronella seems more frequent in the Polish Tatras than in the Slovakian Tatras. In Liptov it occurs only in the two types of malacocenoses as accidental and recedent or subrecedent (Kroupova 1986). In the Belanské Tatry mountains it occurs only sporadically (Hudec, Brabenec 1961).

40. *Oxychilus depressus* (Sterki, 1880), Carpathian and East Alpine (fig. 23)

The fifteen specimens collected in eleven localities make this a sporadic species in the Tatra National Park. Its localities were found between 900 m a.s.l. (Ścieżka pod Reglami) and 1650 m a.s.l. (Siodło) [D1, D2, C1].

In previous studies the species was called *Hyalina glabra f. striaria* Westerlund. According to Kotula (1884), it was frequent from beech forests to the dwarf-mountain pine zone.

In the Liptovské Tatry mountains *O. depressus* is considered accessory or accidental and mostly subrecedent in eleven snail communities connected with various types of habitats (Kroupova 1986). In the Vysoké and Belanské Tatry mountains its populations are frequent and large (Hudec, Brabenec 1961).

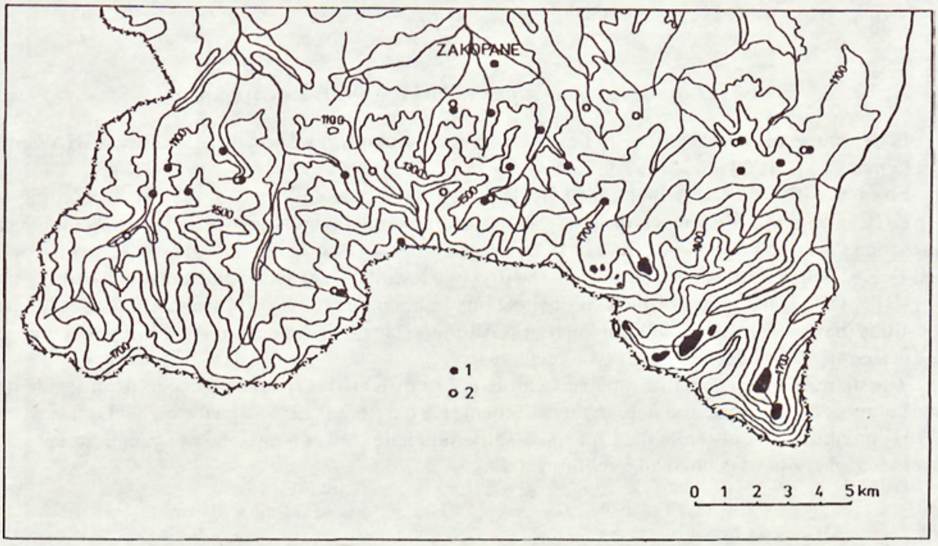


Fig. 22. *Nesovitrea hammonis* (1) and *N. petronella* (2) in TNP

Ryc. 22. *Nesovitrea hammonis* (1) i *N. petronella* (2) w TPN

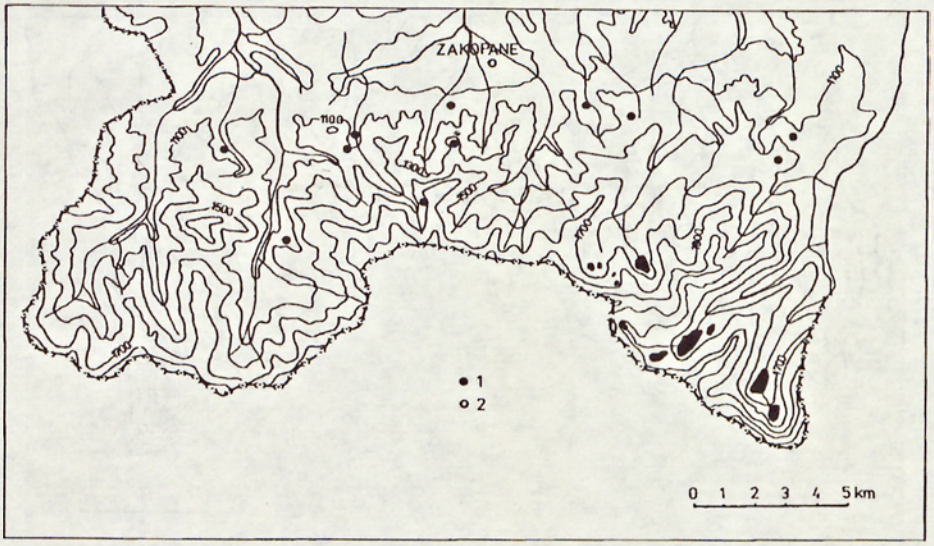


Fig. 23. *Oxychilus depressus* (1) and *O. glaber* (2) in TNP

Ryc. 23. *Oxychilus depressus* (1) i *O. glaber* (2) w TPN

Limacidae

41. *Limax cinereo-niger* (Wolf, 1803), European

In the course of several years' studies the species was found only once, on Mt Filipczański Wierch (1225 m a.s.l.) [D1, C1].

From the Tatras it was mentioned by Kotula (1884) and Wiktor (1973). According to Kotula *L. cinereo-niger* was common from the lower mountain forest zone up to the dwarf mountain pine zone. Wiktor mentioned it only from lower altitudes - Ścieżka pod Reglami, Dolina Roztoki and D. Kościeliska valleys. Material from the first two localities had been collected much earlier, and Wiktor (1973) made use of museum collections in his monograph on slugs. Only the last of the localities may be considered as contemporary. All this seems to indicate that the Tatra population of *L. cinereo-niger* has declined rapidly in recent years.

The share of this species in the malacocenoses of Liptov is also very small; it occurs as an accidental and subrecedent element, and only in three of them (Kroupova 1986). Hudec and Brabenec (1961) mentioned it only from the Liptovské Tatry mountains but as a rare and not numerous species. *L. cinereo-niger* has declined all over the Tatras.

42. *Lehmannia nyctelia* (Bourguignat 1861), North African and South-East European (fig. 24)

The snail was found in three localities (Morskie Oko, Dolina Roztoki, Nędzówka- at Ścieżka pod Reglami) [D1, D4, C1].

Wiktor (1973) recorded it from the Tatra National Park (and also from Poland) for the first time. The localities given by this author (some of them based on museum collections) and those mentioned before are on non-limestone (crystalline) substratum, except Nędzówka and Dolina Kościeliska. Previous records indicate that the species was never common in the Tatras.

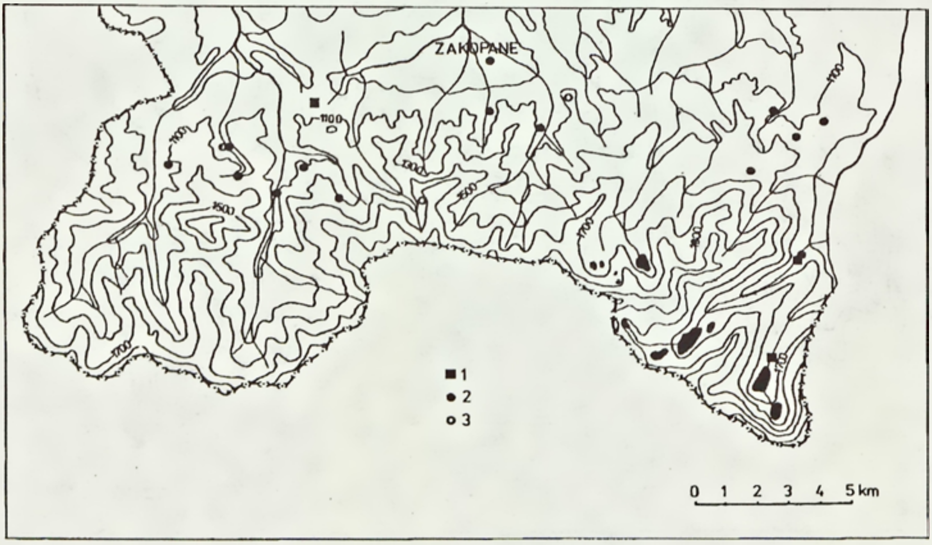


Fig. 24. *Lehmannia nyctelia* (1), *L. marginata* (2) and *L. macroflagellata* (3) in TNP

Ryc. 24. *Lehmannia nyctelia* (1), *L. marginata* (2) i *L. macroflagellata* (3) w TPN

43. *Lehmannia marginata* (O.F. Müller, 1774), European (fig.24)

This snail occurs in the Zakopane Basin and in the lower mountain forest zone, and at higher altitudes only sporadically: it reaches 1400 m a.s.l. It usually was represented by few specimens in a sample. *L. marginata* does not form concentrations [D1-D4, C1].

Some other morphologically similar species happened to be reckoned among *L. marginata*, so it is difficult to verify Kotula's information (1884) on the occurrence of *Limax arborum* Bouch. (*Lehmania marginata* Mül.). As suggested by Riedel (1988) Kotula most likely numbered *L. marginata* and *L. macroflagellata* (probably also *L. nyctelia*) in this taxon. Wiktor (1973) mentioned some verified localities of *L. marginata*, among them - Wrota Chałubińskiego (2022 m a..l.) and Mt Wołowiec (2064 m a.s.l.). This species seems to occur on non-limestone substratum more willingly than other species do.

According to Hudec and Brabenec (1961) *L. marginata* is relatively most frequent and numerous in the Liptovské Tatry mountains but according to Kroupova (1986) it occurs there in only four types of malacocenoses, in one type as a constant element, and in the remaining three as accidental and recedent or subrecedent. The malacocenoses are chiefly connected with forests, with lower altitudes.

44. *Lehmannia macroflagellata* (Grossu et Lupu, 1962), Carpathian (fig. 24)

Five specimens (two on the Gubałówka hill) were collected in four localities. This points to the almost sporadic occurrence of this snail in TNP [D1, D4, C1].

As it mentioned earlier, until lately *L. macroflagellata* was identified as *L. marginata*. Verified localities of this species were given by Wiktor (1973), most of them from the High Tatras, others from the crystalline parts south of Dolina Chochołowska. The species shows a clear preference for non-limestone substrata.

The species was mentioned from the Slovakian Tatras by Kroupova (1986) as accidental and subrecedent or subdominant in three types of forest malacocenoses.

45. *Bielzia coerulans* (M. Bielz, 1851), Carpathian (fig. 25)

The species is uniformly distributed over the whole area of TNP and Zakopane Basin, but it is not numerous. It occurs in all types of habitats up to the dwarf mountain pine zone (the highest locality is Morskie Oko lake - 1450 m a.s.l) [D1-D5, C2].

The present distribution of this species is similar to that of 100 years ago, but probably *B. coerulans* was much more numerous (Kotula 1884), like many other species. Some localities of *B. coerulans* were given by Wiktor (1973).

Its distribution in the other Tatra ranges is similar (Hudec, Brabenec 1961). It occurs in six types of malacocenoses in the Liptovské Tatry mountains as accidental or accessory and as subdominant, recedent, or subrecedent (Kroupova 1986).

46. *Deroceras agreste* (Linnaeus, 1758), West Palearctic (fig. 26)

The species occurs in the Zakopane Basin, in the lower mountain forest zone, and on in-forest glades (up to 1400 m a.s.l.). It frequently forms aggregations of up to thirty specimens each. About 30% of the samples had 10-47 specimens each. In forests this species usually occurs singly, and in human-caused habitats or in their immediate vicinity, it occurs in concentrations [D1-D5, C2].

In previous publications *D. agreste* was reckoned among *Limax agrestis* Linnaeus, 1758 (together with some other species), so it is difficult to compare Kotula's data with current observations.One may assume that a half of his records of *L. agrestis* concern *D. agreste*. The species was mentioned from the Polish Tatras by Dzięczkowski (1972) and Wiktor (1973), from localities situated in the lower mountain zone.

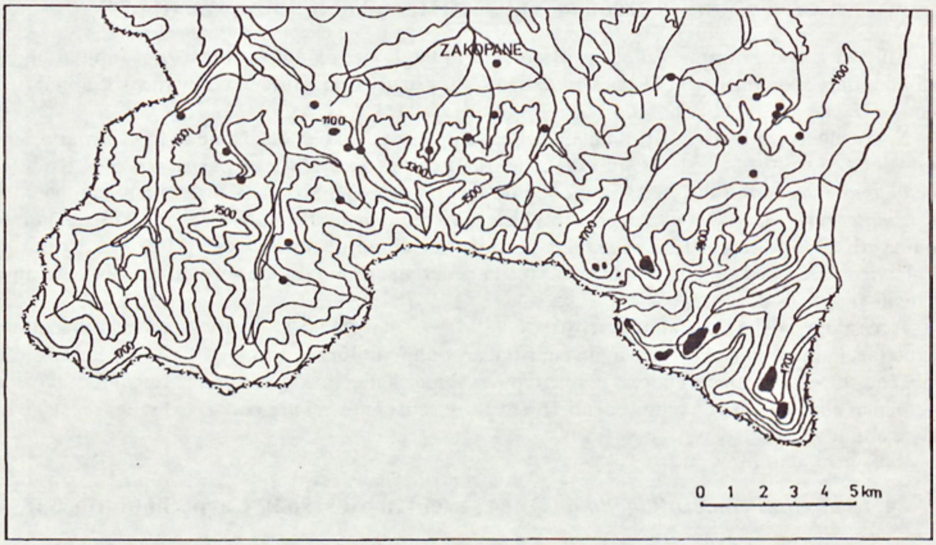


Fig. 25. *Bielzia coerulans* in TNP

Ryc. 25. *Bielzia coerulans* w TPN

According to Hudec and Brabenec (1961) *D. agreste* is not frequent and numerous in the valleys of the Slovakian Tatras. One may suppose that this information concerns *D. agreste* or *D. reticulatum*. In Kroupova (1986) these two species are treated separately, and *D. agreste* is given from only one type of malacocenoses as accidental and subrecedent.

47. *Deroceras reticulatum* (O.F. Müller, 1774), European (fig.26)

In TNP it is rarer than *D. agreste,* more abundant only in the material from the Gubałówka hill and Zakopane Basin (73% of the specimens). It is connected with human-caused habitats more closely than *D. agreste* is [D1, D2, D4, D5, C1].

Remarks on the systematic position of *D. agreste* also apply to *D. reticulatum.* One may only suppose that some observations of *L. hortensis* may refer to *D. reticulatum.* Wiktor (1973) mentioned only two localities of *D. reticulatum* from the investigated area - Zakopane and the Dolina Kościeliska valley.

Only Kroupova (1986) includes data on the occurrence of *D. reticulatum* in the Slovakian Tatras, and more precisely in the Liptovské Tatry mountains. The species is an accessoryc or accidental and subrecedent element in five types of malacocenoses. Three of them are forest communities.

48. *Boettgerilla pallens* (Simroth, 1912), Caucasian (fig. 27)

The author collected 91 specimens in the investigated area. The majority of them were found in the lower mountain forest zone, in enclaves of original vegetation characteristic of these parts of the Tatras, e. g. in the Dolina Spadowca, D. Białego, and D. Strążyska valleys. In the Zakopane Basin *B. pallens* was observed under stones and on walls in parks, and in clusters of old trees [D1, C1].

Studies on the spatial structure of malacocenoses in forest litter in the Dolina Spadowca valley (Dyduch-Falniowska, Tobis, 1989) provided information on the distribution of *B. pallens.*

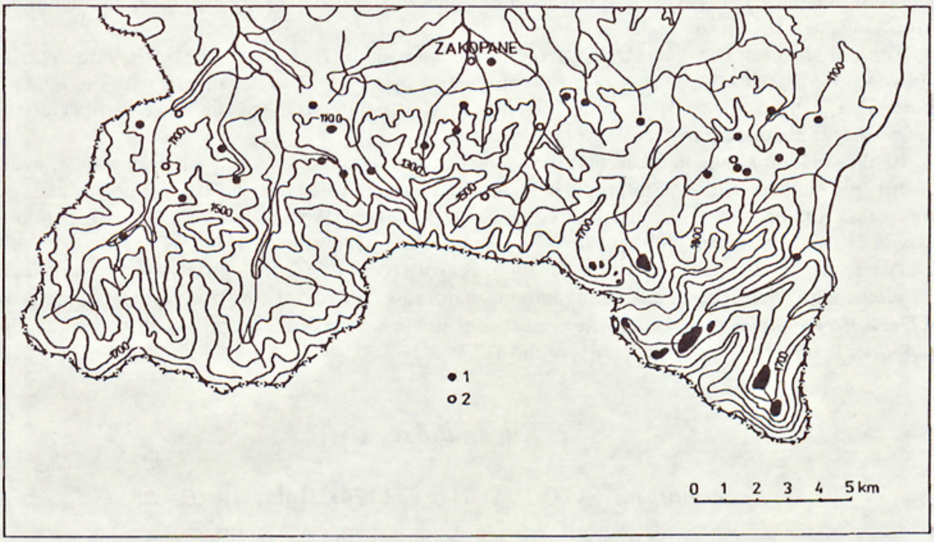


Fig. 26. *Deroceras agreste* (1) and *D. reticulatum* (2) in TNP

Ryc. 26. *Deroceras agreste* (1) i *D. reticulatum* (2) w TPN

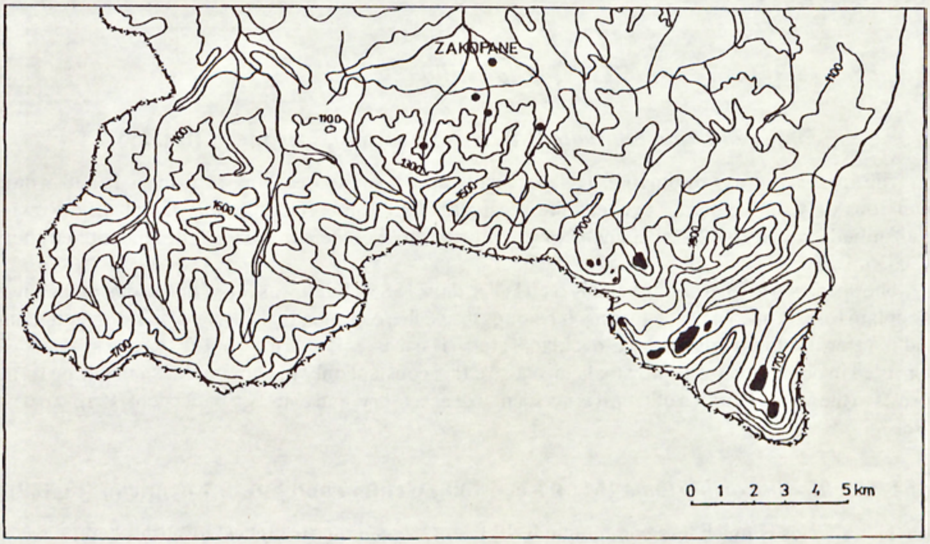


Fig. 27. *Boettgerilla pallens* in TNP

Ryc. 27. *Boettgerilla pallens* w TPN

Relations between this species and other components of the malacocenose, and the biotope, are a subject of separate studies.

The abundance of *B. pallens* is positively correlated with dry forest litter (r = 0.40), with *Petasites albus* (r = 0.52), with the density of snail community (r = 0.41), and negatively with the index of equitability (J'), (r = -0.45). In the other localities in TNP and in the Zakopane Basin the species also prefers places abounding in decaying organic matter.

Its distribution seems to mean that the species is an original element of the Tatra fauna, which recently has expanded into synanthropic habitats. But this conclusion is inconsistent with observations from other authors. From the first record in Central Europe (Wiktor 1959) the distribution of *B. pallens* has been thoroughly investigated (Colville, Lloyd-Evans, Norris 1973; De Wilde, van Goethem, Marquet 1983; Kroupova 1986). In light of these observations, *B. pallens* is an alien species infiltrating into malacocenoses approximating the original communities of *Dentario glandulosae-Fagetum*, the richest ones in the area in terms of both quality and quantity. *B. pallens* is unknown from other parts of the Tatras.

Euconulidae

49. *Euconulus fulvus* (O.F. Müller, 1774), Holarctic (fig. 28)

The snail has been recorded from all types of Tatra biotopes. In general it occurs individually. Only a few of the 80 samples contained more than 10 specimens. Those localities more abundant in *E. fulvus* are valleys: Dolina Olczyska, D. Białego, D. Strążyska and D. Spadowca. The snail was regularly sampled in the top parts of Czerwone Wierchy [D1-D4, C3].

In Kotula's times (1884) the distribution of the species under discussion was similar, except that it occurred only up to the upper limit of the dwarf mountain pine zone.

In the Slovakian Tatras the species is also frequently found, though in small numbers. In the Liptov malacocenoses it is a constant (euconstant), accessory or accidental element of fourteen malacocenoses. It is mostly recedent and sometimes subdominant or subrecedent (Hudec, Brabenec 1961; Kroupova 1986).

Clausiliidae

50. *Cochlodina laminata* (Montagu, 1803), European (fig. 29)

The species is fairly common in TNP. It usually occurs singly, reaching 1700 m a.s.l., and is more numerous only on the border between the West and High Tatras (Gęsia Szyja, Jarząbczak, Rówień Waksmundzka). Nearly 200 specimens were collected, 40% of them in the localities mentioned above [D1-D5, C2].

The species was also common in Kotula's day (1884), but it was more numerous in the lower mountain forest zone, in beech forests. It belongs to species common in the Belanské Tatry mountains, and is rarer in other parts of the Slovakian Tatras (Hudec, Brabenec 1961). The species was observed in eight types of Liptov malacocenoses. It is constant only in communities inhabiting fertile forests in the Velka Fatra. In others, it is accidental or accessory, and chiefly subrecedent (Kroupova 1986).

51. *Cochlodina orthostoma* (Menke, 1830), Central and South European (fig. 29)

This species is much less common in TNP than *C. laminata*. Its highest localities barely exceed 1400 m a.s.l. Samples of single specimens were usual. Samples over 10 were sporadic. This species seems connected more strongly with the valleys of the West Tatras than *C. laminata* is. 119 specimens in 22 localities were collected [D1-D3, C2].

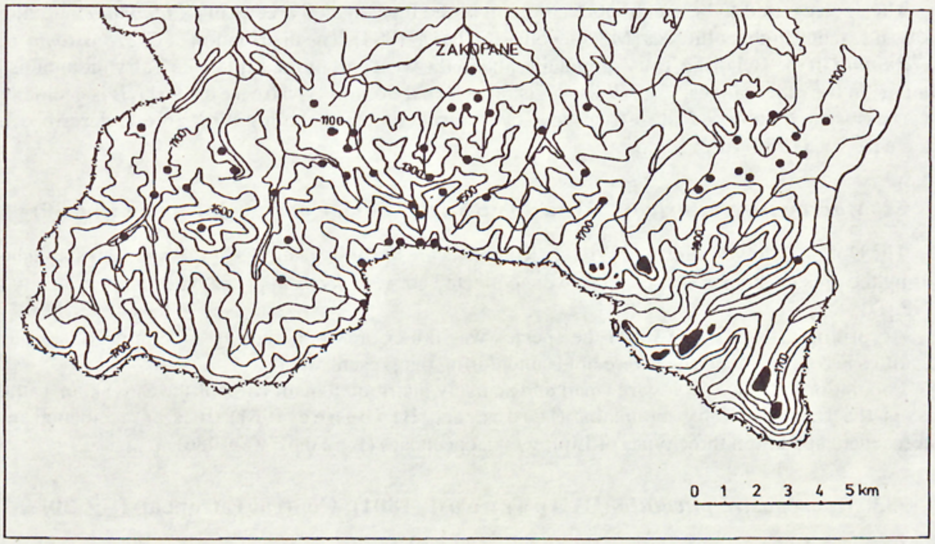


Fig. 28. *Euconulus fulvus* in TNP

Ryc. 28. *Euconulus fulvus* w TPN

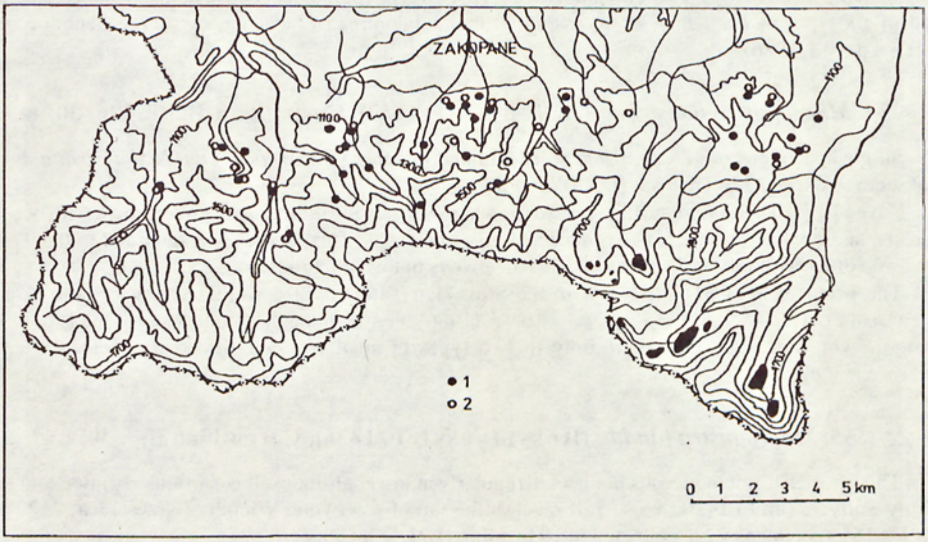


Fig. 29. *Cochlodina laminata* (1) and *C. orthostoma* (2) in TNP

Ryc. 29. *Cochlodina laminata* (1) i *C. orthostoma* (2) w TPN

The species used to be much more common in the investigated area than *C. laminata*, and most likely it reached higher altitudes (Mt Giewont - Kotula 1884). The distribution of *C. orthostoma* and *C. laminata* in the Belanské Tatry mountains and in the west part of the Liptovské Tatry mountains is similar. In the other ranges, *C. orthostoma* is rarer (Hudec and Brabenec 1961). It is accidental or accessory and subrecedent in five types of malacocenoses (including three forest) described by Kroupova (1986) from Liptov.

52. *Macrogastra ventricosa* (Draparnaud, 1801), Central European (fig. 30)

The Dolina Lejowa valley and Wielkie Koryciska are the only localities of this species established during the present studies. 4 specimens were collected. *M. ventricosa* appears to occur sporadically in TNP [D1, D2, C1].

According to Kotula (1884) the species was rather rare a century ago. Certain Polish Tatra localities Kotula mentioned were not found during the present studies.

Populations of this species are small and sparsely distributed in all parts of the Slovakian Tatras, except the Belanské Tatry mountains (Hudec and Brabenec 1961). It is an accidental and subrecedent species in three types of Liptov malacocenoses (Kroupova 1986).

53. *Macrogastra plicatula* (Draparnaud, 1801), Central European (fig. 30)

It is one of the two commonest clausiilids in TNP. Frequent in valleys, and at higher altitudes less numerous, its range extends above the upper limit of the dwarf mountain pine zone (Przełęcz Tomanowa - 1686 m a.s.l.). Nearly 1000 specimens were collected in 34 localities, a few to twenty specimens in one sample [D1-D5, C3].

A similar *M. plicatula* distribution was given by Kotula (1884). He described the conchological variability of this species in detail identifying the material collected as *Cl. plicatula* Drap. *var. in uncta* Parr. and *Cl. plicatula* Drap. *var. cruda* Zgl. In his opinion this conchological variability was connected with altitude.

In the Slovakian Tatras *M. plicatula* often forms strong populations (Hudec, Brabenec 1961). In the Liptovské Tatry mountains it occurs in two types of malacocenoses as a constant element, and in six types as accidental or accessory. It is a subdominant, recedent, or subrecedent species (Kroupova 1986).

54. *Macrogastra latestriata* (A. Schmidt, 1857), Carpathian-Baltic (fig. 30)

Single specimens of *M. latestriata* were sampled together with *M. plicatula*. *M. latestriata* does not seem to exceed 1200 m a.s.l. [D1, D2, C1].

Kotula (1884) mentioned this species from ten to twenty localities, mostly overgrown with beech forests, and he determined its occurrence as fairly numerous. This species was recorded in the TNP by some other naturalists (Stępczak 1970), always in low situations.

The occurrence of *M. latestriata* in the Slovakian Tatras is of a similar character (Hudec, Brabenec 1961). According to Kroupova (1986) its role in the malacocenoses of the Liptov is insignificant, since it occurs there only in two types of snail communities as an accidental and subrecedent element.

55. *Macrogastra tumida* (Rossmaessler, 1836), Carpathian (fig. 30)

This species is not numerous but occurs regularly at lower altitudes; it is particularly abundant on Kopy Sołtysie (up to 1420 m a.s.l.). It reaches the top of Czerwone Wierchy (Krzesanica, 2122 m a.s.l.). 151 specimens were collected in 19 localities [D1-D3, C2].

In Kotula's opinion it was a rare species, occurring only sporadically in the upper mountain forest zone. In other parts of the Tatras (Slovakia) it more often forms strong populations (Hudec, Brabenec 1961), but its distribution in the Liptovské Tatry mountains seems like that in TNP. In the malacocenoses described by K r o u p o v a (1986) it is accidental or accessory and recedent or subrecedent.

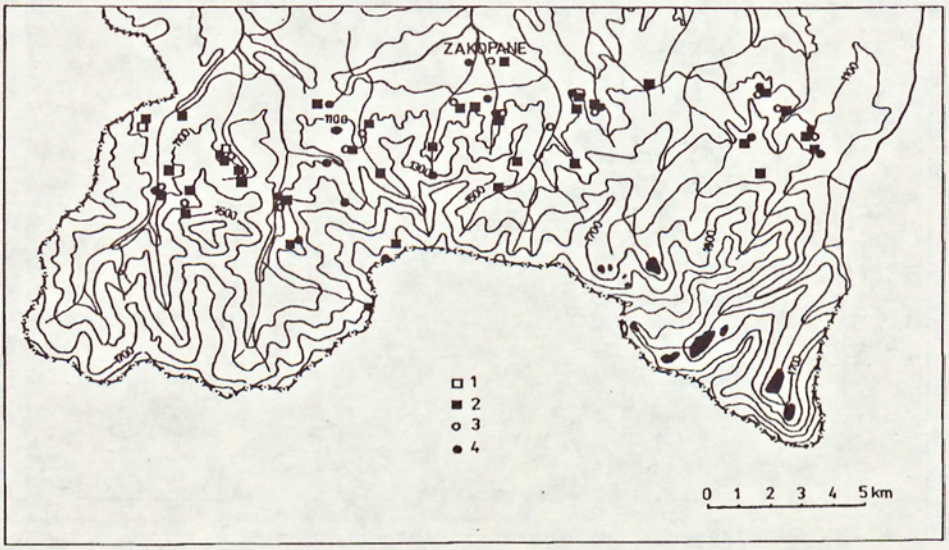


Fig. 30. *Macrogastra ventricosa* (1), *M. plicatula* (2), *M. latestriata* (3) and *M. tumida* (4) in TNP

Ryc. 30. *Macrogastra ventricosa* (1), *M. plicatula* (2), *M. latestriata* (3) i *M. tumida* (4) w TPN

56. *Clausilia dubia* (D r a p a r n a u d, 1805), Central European (fig. 31)

C. dubia is the most common species in all types of Tatra biotopes, from the lowest to highest parts of the West Tatras. It was sampled in more than half of the examined localities, often in large numbers. Nearly 1500 specimens were collected. Like many other species in the Tatras *C. dubia* shows great conchological variability. The index of conchological variability is greater in localities at higher altitudes. [D1-D5, C3].

K o t u l a (1884) considered *C. dubia* a common species, but in K o t u l a ' s material the difference between the numbers of this species and those of the other *Clausiliidae* was not so great as nowadays. This author also pointed to the correlation between conchological variability and altitude. A typical form was observed up to the lower limit of dwarf mountain pine, and that of *C. dubia* D r a p . *var. obsoleta* A. S c h m i d t was found above that point. *C. dubia* D r a p . *var. curta* W e s t e r l . and *C. dubia* D r a p . *var. Grimmeri* P a r r . were also found.

C. dubia is common in all parts of the Slovakian Tatras (H u d e c , B r a b e n e c 1961) and it occurs in nine types of malacocenoses described by K r o u p o v a (1986). K r o u p o v a found it in four types as a constant element (const. - 3, euconst. - 1), and in the others as accessory or accidental. It may be subdominant, recedent or subrecedent.

57. *Clausilia cruciata* (S t u d e r, 1820), Alpine and North European (fig. 32)

The species occurs regularly though in small numbers at lower altitudes up to 1300 m a.s.l. 139 specimens were collected, ten times fewer than *C. dubia* [D1-D5, C2].

In K o t u l a ' s material the numbers of these two species were similar, both described as common. In the Slovakian Tatras *C. cruciata* is connected with lower altitudes (H u d e c , B r a b e n e c 1961).

In K r o u p o v a (1986) the role of this species in Liptov malacocenoses is small; it occurs in only two types as an accidental and subrecedent element.

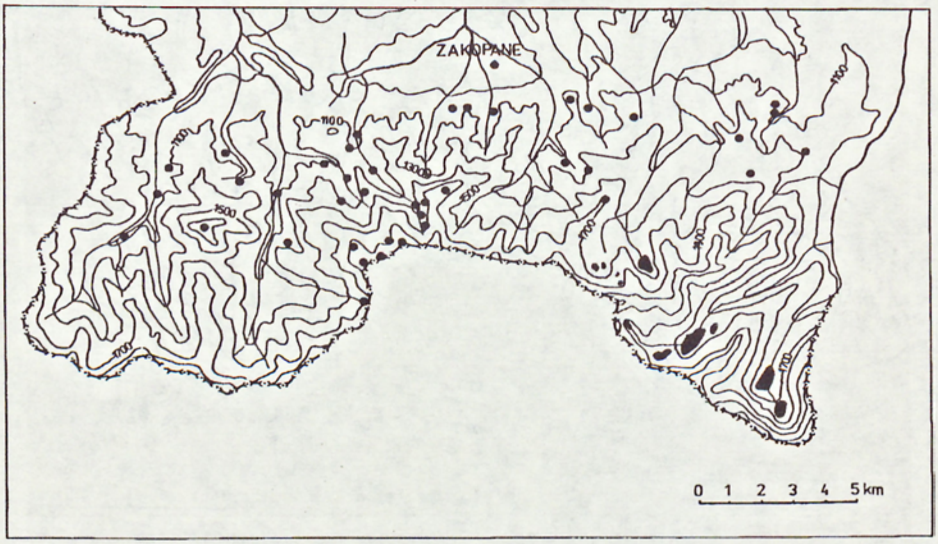


Fig. 31. *Clausilia dubia* in TNP

Ryc. 31. *Clausilia dubia* w TPN

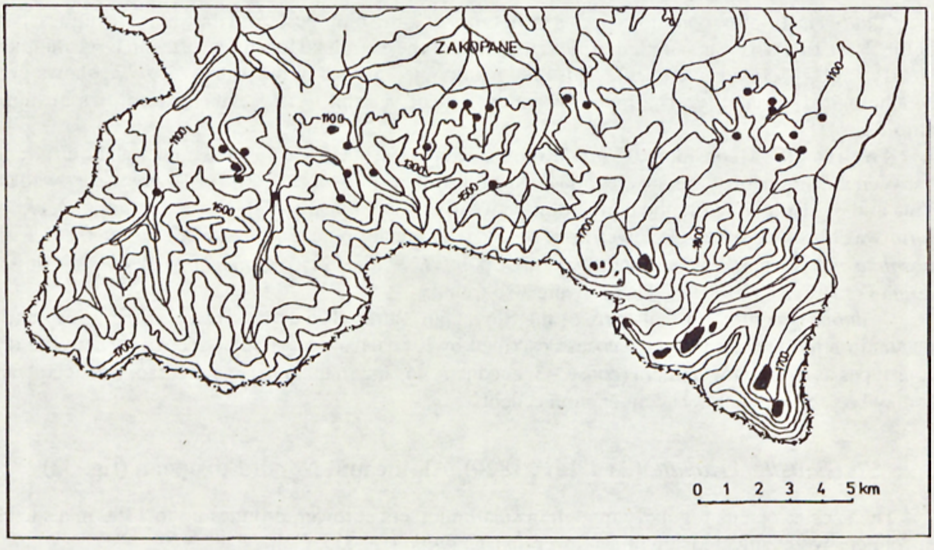


Fig. 32. *Clausilia cruciata* in TNP

Ryc. 32. *Clausilia cruciata* w TPN

58. *Vestia turgida* (R o s s m a e s s l e r , 1836), Carpathian (fig. 33)

This species occurs regularly throughout TNP, in all types of biotopes: at lower altitudes in the litter of *Dentario glandulosae-Fagetum* and higher up in epilithic grasslands. It reaches the top of Czerwone Wierchy. More than 650 specimens were collected in 50 localities. Its very high conchological variability merits separate, detailed studies [D1-D5, C4].

In K o t u l a (1884) this species was probably assigned to three taxa: *C. turgida* Z g l ., *C. elata* Z g l ., and *C. fallax* R o s s m . From the distribution K o t u l a gave the species was rather common in the present area of TNP. In the Slovakian Tatras *V. turgida* is distributed ununiformly - common in the Belanské Tatry and in the west part of the Liptovské Tatry mountains, rarer in the High Tatras and in the southern part of the Liptovské Tatry mountains (H u d e c , B r a b e n e c 1961). At present it is accessory or accidental and recedent or subrecedent in six Liptov malacocenoses (K r o u p o v a 1986).

59. *Bulgarica cana* (H e l d , 1836), East and South-East European (fig. 33)

The seven specimens collected from three localities indicate its very rare occurrence in TNP [D1, D2, C1].

K o t u l a (1884) consider ed *B. cana* a rather common taxon, confined to beech and fir and reaching the upper limit of their range. It was also observed in the Belanské Tatry mountains and in the western part of the Liptovské Tatry mountains (H u d e c , B r a b e n e c 1961).

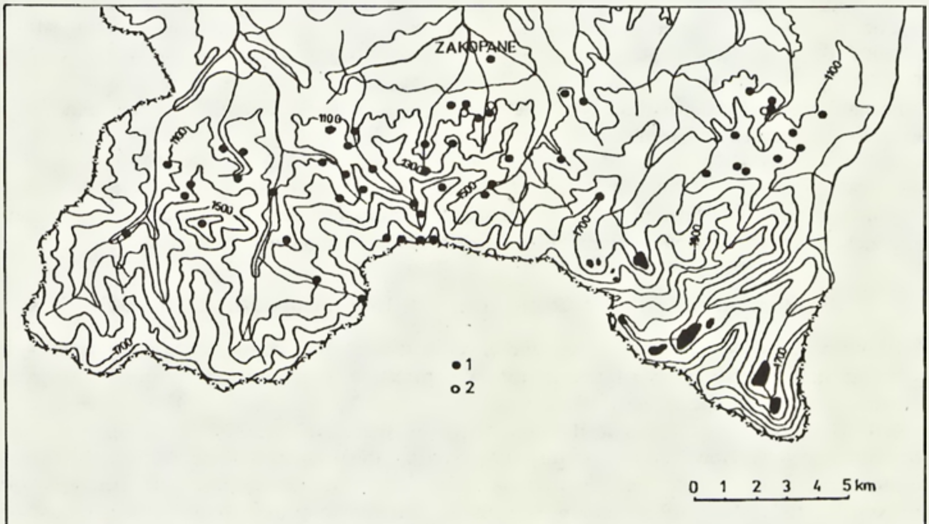


Fig. 33. *Vestia turgida* (1) and *Bulgarica cana* (2) in TNP

Ryc. 33. *Vestia turgida* (1) i *Bulgarica cana* (2) w TPN

Bradybaenidae

60. *Bradybaena fruticum* (O.F. Müller, 1774), Central and East European, Asiatic

Single specimens found in Wielkie Koryciska point to a sporadic occurrence of *B. fruticum* in the present area of TNP [D1, C1].

Kotula (1884) found one locality of this species at the upper limit of beech (Suchy Potok). Other records of *B. fruticum* from the Polish Tatras (Jachno 1870, Bąkowski 1883) are probably from the Zakopane Basin.

B. fruticum is not very frequent in the Belanské Tatry mountains, nor in the western part of the Liptovské Tatry mountains (Hudec, Brabenec 1961). It occurs in eight molluscan communities of the Liptov region. In one of them it is constant; in the others it is accidental or accessory and recedent or subrecedent (Kroupova 1986).

Helicidae

61. *Perforatella incarnata* (O.F. Müller, 1774), Central and South European

A single locality of *P. incarnata* has been found just above Kuźnice. Like *B. fruticum,* it occurs in TNP only sporadically [D1, C1].

P. incarnata was observed in lower situations previously as well. Bąkowski (1883) mentioned it from Dolina Strążyska, and Dzięczkowski (1972) found it in Dolina Białego.

Hudec and Brabenec (1961) recorded this species from only one locality in the High Tatras, and from a few places in the western of the Liptovské Tatry mountains. *P. incarnata* is a constant element in three malacocenoses investigated by Kroupova (1986) and in eight other ones it is accidental or accessory. It is a recedent or subrecedent species.

62. *Perforatella vicina* (Rossmaessler, 1836), Carpathian (fig. 34)

It occurs regularly, though generally in small numbers, at lower altitudes. The highest locality is at about 1400 m a.s.l. There were 148 specimens from over twenty localities, chiefly in forest litter [D1-D4, C2].

Formerly *P. vicina* was also considered as a common but not very numerous species in the Polish Tatras. Its confinement to beech was stressed (Martens 1869, Bąkowski 1883, Kotula 1884, Dzięczkowski 1972). In the Slovakian Tatras the species also does not form large aggregations either, and it occurs rather at lower altitudes (Hudec, Brabenec 1961). It is a constant element of the malacocenoses of fertile forests in the Nizke Tatry mountains and an accidental or accessory component of seven other snail communities. It is a recedent or subrecedent species.

63. *Trichia villosula* (Rossmaessler, 1836), Carpathian (fig. 35)

Humid valleys are biotopes favoring the development of large populations of this species. Its occurrence in the Polish Tatras is limited to the lower mountain forest. A few localities of *T. villosula* yielded more than 300 specimens [D1-D4, C1].

Kotula (1884) noted widespread occurrence of this species in the Polish Tatras, up to the dwarf mountain pine zone. However, the localities he gave from the present TNP are at lower altitudes. In the Slovakian Tatras *T. villosula*'s distribution varies depending on the range. The species is commonest in the Belanské Tatry mountains, rarer in the western part of the Liptovské Tatry mountains, and rarest in the High Tatras as well as in the southern Liptovské Tatry mountains (Hudec, Brabenec 1961). It plays an important role in the malacocenoses described by Kroupova (1986). In four of them it is a constant (euconstant and constant), dominant or subdominant species, and in the other ten it is accidental or accessory and recedent or subrecedent.

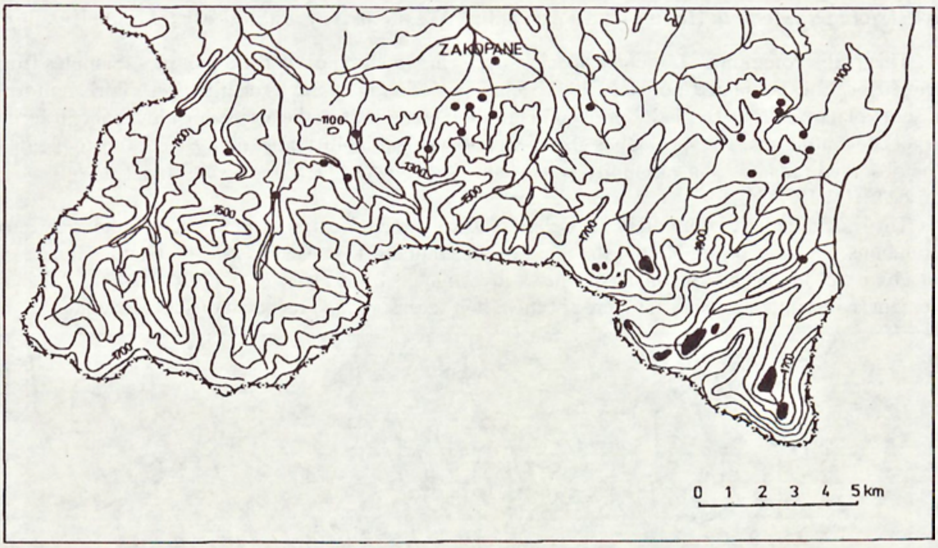


Fig. 34. *Perforatella vicina* in TNP

Ryc. 34. *Perforatella vicina* w TPN

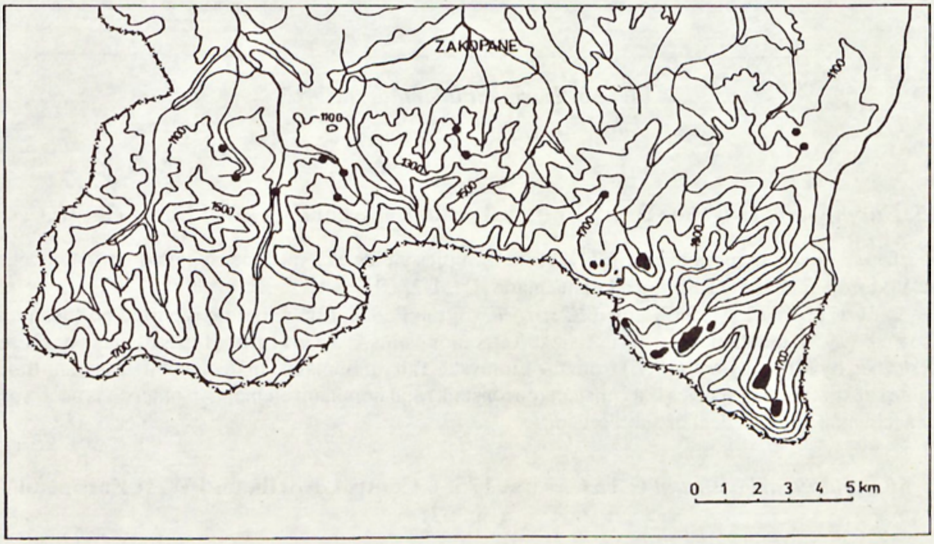


Fig. 35. *Trichia villosula* in TNP

Ryc. 35. *Trichia villosula* w TPN

64. *Trichia unidentata* (Draparnaud, 1805), West Carpathian and East Alpine (fig. 36)

This is the commonest *Helicidae* species, occurring in all types of Tatra biotopes. Samples from over 50 localities contained more than 700 specimens of *T. unidentata*. Its distribution is fairly uniform. In some places, in forests, glades or even in epilithic grasslands in the alpine meadow zone, it forms larger concentrations. The species has great conchological variability, apparently according to biotope. The observed range of this variability is between *T. unidentata* Draparnaud and *T. u. bohemica* Ložek [D1-D5, C4].

The species is very common in the Belanské Tatry mountains and in the western Liptovské Tatry mountains but rarer in the High Tatras and in the southern Liptovské Tatry mountains (Hudec, Brabenec 1961). In four malacocenoses investigated by Kroupova (1986) it is a constant element (constant, euconstant), in three of them it is accessory, and recedent or subrecedent.

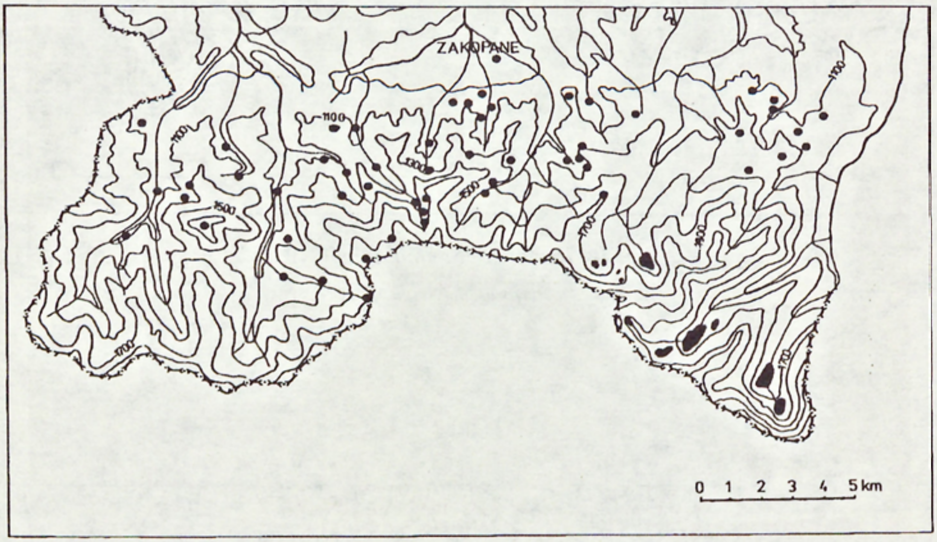


Fig. 36. *Trichia unidentata* in TNP

Ryc. 36. *Trichia unidentata* w TPN

65. *Euomphalia strigella* (Draparnaud, 1801), East and Central European (fig. 37)

The snail occurs sporadically in TNP: four localities yielded 15 specimens, including 10 collected at Wiktorówki near the Rusinowa Polana glade [D1, D2, C1].

Only Urbański (1947) noted *E. strigella* in the Polish Tatras, but he reported no localities. Ložek (1974) mentioned it from the Nizké Tatry mountains. It occurs in nine types of malacocenoses described by Kroupova (1986) from the Liptovské Tatry mountains. In open habitats on non-limestone substratum, the species is a constant (euconstant) and dominant element, in others it is accessory or accidental and recedent or subrecedent.

66. *Arianta arbustorum* (Linnaeus, 1758), Central, North, and West European (fig. 37)

This is a common species recorded from 40 localities, but only now and then is it more numerous. It prefers open habitats such as Polana Kondratowa glade, Niżna Polana Tomanowa glade, and Mt Krzesanica [D1-D5, C3].

Kotula (1884) also pointed to the connection of *A. arbustorum* with grassy habitats, from the foothills up to the top of Czerwone Wierchy. It is rather common in the Slovakian part of the Tatras (Hudec, Brabenec 1961). In two types of Liptovské Tatry malacocenoses Kroupova (1986) found *A. arbustorum* to be constant and subdominant or recedent. It is accidental or accessory and recedent or subrecedent element in five malacocenoses of open habitats and in one forest community.

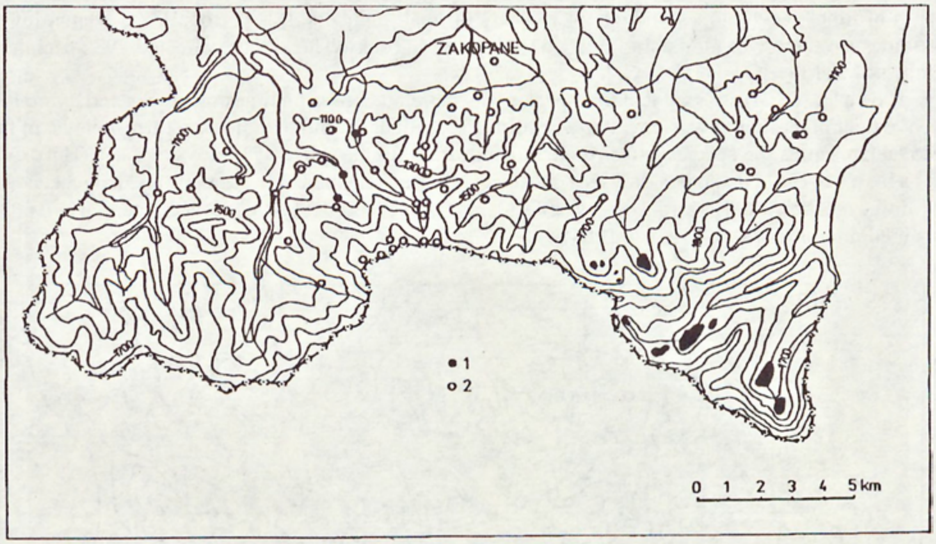


Fig. 37. *Euomphalia strigella* (1) and *Arianta arbustorum* (2) in TNP

Ryc. 37. *Euomphalia strigella* (1) i *Arianta arbustorum* (2) w TPN

67. *Chilostoma faustinum* (Rossmaessler, 1835), Carpathian (fig. 38)

It occurs in small numbers but regularly in all types of Tatra biotopes. 280 specimens were collected in over 45 localities [D1-D5, C3].

The species has been mentioned from the Tatras by many authors from Nowicki (1867) to Dzięczkowski (1972). Kotula (1884) pointed to its great conchological variability and he distinguished three forms. In other parts of the Tatras the species is more frequent at lower altitudes. Its populations are large and numerous only in the Belanské Tatry mountains (Hudec, Brabenec 1961). It was found in eleven malacocenoses of the Liptov region. In three of them it was a constant (euconstant) element, and in the remaining ones accidental or accessory. It is a recedent or subrecedent species (Kroupova 1986).

68. *Chilostoma rossmaessleri* (L. Pfeiffer, 1842), West Carpathian

Two specimens found in the Dolina Olczyska valley and in the Wołowy Żleb gully match the conchological description of this species. But the great conchological variability of *Ch. faustinum* warrants studying these two species together in detail [D1, C1].

Kotula (1884) pointed to different habitat preferences in *Ch. rossmaessleri* and *Ch. faustinum*. He stressed *Ch. rossmaessleri* connection with spruce. In Kotula's times the species was widely distributed but not numerous. According to Hudec and Brabenec (1961) the two species occur sympatrically in the Slovakian Tatras, though *Ch. rossmaessleri* seems much rarer and less numerous.

This is confirmed by K r o u p o v a (1986). *Ch. rossmaessleri* occurs in only four types of snail communities as an accidental and subrecedent species.

69. *Chilostoma cingulellum* (R o s s m a e s s l e r, 1837), West Carpathian (fig. 38)

Ch. cingulellum is one of the commoner species of the family *Helicidae* in TNP. It occurs in all types of limestone biotopes, though everywhere in small numbers. It is petrophilous: even at lower altitudes (in the lower mountain forest zone) it lives on rocks. The author collected 198 specimens from 14 localities [D1-D3, D5, C1].

K o t u l a (1884) stressed that this species was more numerous on limestone rocks and dolomites above the timber line. It was rare at lower altitudes, particularly at the outlets of Tatra valleys. In the Slovakian Tatras the species is distributed ununiformly. In the range of Liptovské Tatry (H u d e c, B r a b e n e c 1961) it appears only as a constant and recedent element in the epilithic malacocenoses of alpine meadows and as an accessory or accidental and subrecedent or recedent element in two other snail communities (K r o u p o v a 1986).

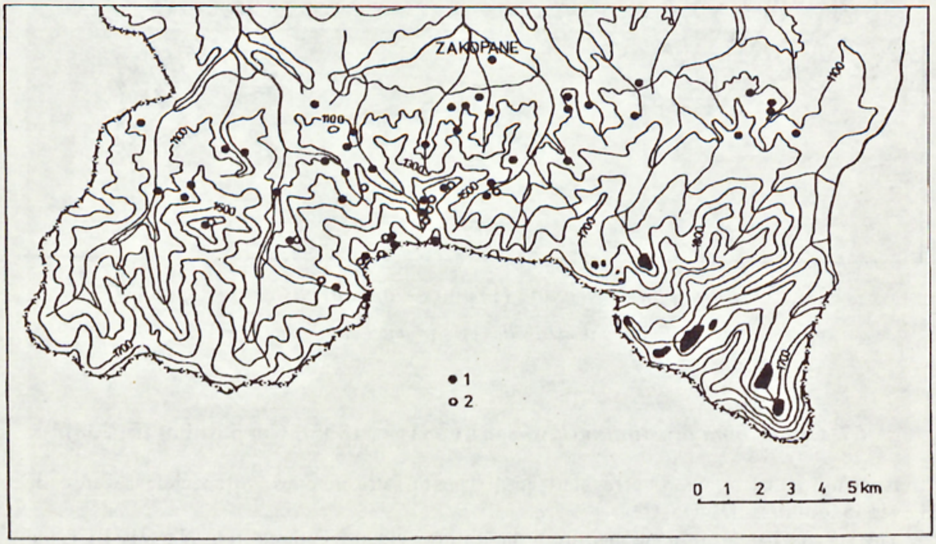


Fig. 38. *Chilostoma faustinum* (1) and *Ch. cingulellum* (2) in TNP

Ryc. 38. *Chilostoma faustinum* (1) i *Ch. cingulellum* (2) w TPN

70. *Isognomostoma isognomostoma* (S c h r o t e r, 1874), Alpine-Carpathian (fig. 39)

The snail regularly occurs in various biotopes up to about 1400 m a.s.l. It is connected above all with forest litter and tree bark. Nearly 250 specimens were collected in 26 localities [D1-D4, C2].

A century ago this species was also common, reaching the lower limit of the dwarf mountain pine zone (N o w i c k i 1869, J a c h n o 1870, K o t u l a 1884). It is also common in the Slovakian Tatras but more frequent at lower altitudes. Now and then it forms strong populations (H u d e c, B r a b e n e c 1961). It occurs in nine malacocenoses in the Liptov region (K r o u p o v a 1986). In two of them it is a constant element, and in the remaining ones accessory or accidental. It is recedent or subrecedent species.

71. *Causa holosericum* (Studer, 1820), Alpine-Carpathian (fig. 39)

C. holosericum is similar to *I. isognomostoma* in its habitat preferences but it is much rarer. The ten to twenty specimens collected in six localities (the highest - Kopa Magury, 1704 m a.s.l.) indicate the almost sporadic occurrence of this species in TNP [D1, D2, C1].

Older data show a similar occurrence (particularly in respect to numbers) for *C. holosericum* and *I. isognomostoma* (Kotula 1884). *C. holosericum's* distribution in the Slovakian Tatras seems like that in the Polish part (Hudec, Brabenec 1961), as indicated by the share of the species in five malacocenoses of the Liptovské Tatry range (Kroupova 1986). There it is an accessory or accidental and recedent or subrecedent element.

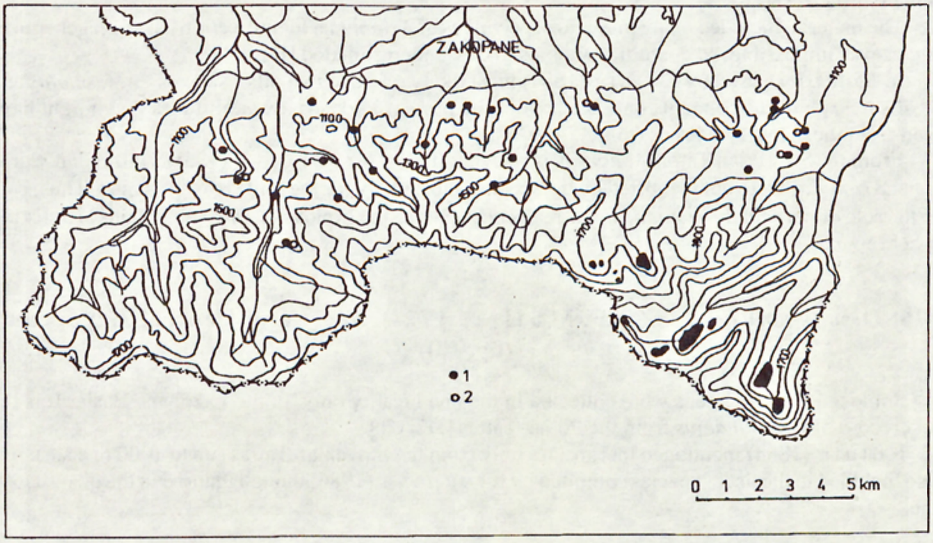


Fig. 39. *Isognomostoma isognomostoma* (1) and *Causa holosericum* (2) in TNP

Ryc. 39. *Isognomostoma isognomostoma* (1) i *Causa holosericum* (2) w TPN

Species recorded only in the Zakopane Basin

72. *Succinea oblonga* (Draparnaud, 1801), West European

Single specimens were found in meadows between Zakopane and the village of Nędzówka. Its occurrence in the Zakopane Basin is similar to that in other parts of the Tatras (Hudec, Brabenec 1961, Kroupova 1986) as well as to that observed in Kotula's times (Kotula 1884) [D1, C1].

73. *Succinea putris* (Linnaeus, 1758), Euro-Siberian

S. putris is slightly more frequent than *S. oblonga*, in meadows mainly to the west of Zakopane. Its distribution there is similar to that in the other parts of the Tatras (Hudec, Brabenec 1961), [D1, C1].

74. *Vertigo antivertigo* (Draparnaud, 1801), Palearctic (fig. 7)

This is a rare species. Single specimens were found in old stands in the area of Zakopane. In Slovakia *V. antivertigo* is also connected with lower altitudes (Hudec, Brabenec 1961; Kroupova 1986) [D1, C1].

75. *Arion hortensis* (Ferrusac, 1819), South and West European (fig. 15)

This species was found only in the Zakopane Basin (13 specimens), all in localities shaped by human influence (D1, C1).

The material included many immature specimens of *Arionidae*. Identification based on generative organs was impossible, so quantities are most likely underestimated [D1, C1].

A. hortensis as used by Kotula (1884) most likely refers to two other species - *A. fasciatus* and *A. silvaticus*, but this concerns only the area of the present Park. At lower altitudes they might have been from those two species or from *A. hortensis*.

From the Slovakian Tatras *A. hortensis* was reported by Kroupova (1986) as intravilan. Some of her *Arionidae* were not identified by the species, most likely for the same reason as ours. Thus, data on the role of particular *Arionidae* in the malacocenoses of the Liptovské Tatry mountains are lacking in her report.

76. *Discus rotundatus* (O.F. Müller, 1774), West and Central European (fig. 13)

Some tens of specimens were collected in the one locality only, in the Zakopane Basin. It is the first record of *D. rotundatus* from the Polish Tatras [D2, C1].

Kotula (1884) mentioned this species only from the Slovakian Tatras (up to 1000 m a.s.l.). It is also included in the list of species compiled by Kroupova (1986) though ignored in the quantitative data.

77. *Oxychilus glaber* (Rossmaessler, 1835), South and Central European (fig. 23)

The author recorded this species only from the Zakopane Basin. This indicates that the species has survived there despite human-caused changes in its habitat. In Kotula's times it was probably known as *Hyalina glabra f. typica*, and was found up to 900 m a.s.l. [D1, C1].

In the malacocenoses investigated by Kroupova (1986) in the range of Liptovské Tatry its share is greater. It occurs in eight of these malacocenoses as an accessory, accidental or subrecedent species. It was also recorded from the Tatra Basin in the Belanské Tatry mountains (Hudec, Brabenec 1961).

78. *Limax maximus* (Linnaeus, 1758), South and West European

In the Zakopane Basin it occurs regularly all over the town of Zakopane; as in the other regions of Poland, it is connected with human-caused habitats [D1, C1].

Until quite recently this species was mistaken for *L. cinereo-niger*. That is why it is difficult to establish whether it was brought to this place lately or whether it has lived here a long time reckoned as *L. cinereo-niger*. In light of the present distribution of these two species and views about their ranges (Wiktor 1973, Riedel 1988), the author accepts it as a new component of Zakopane Basin malacofauna.

There are no records of *L. maximus* from the other Tatra ranges as yet (Hudec, Brabenec 1961; Kroupova 1986).

79. *Lacinaria plicata* (Draparnaud, 1801), Central and South European

Single specimens of *L. plicata* were found in the area of the Zakopane Basin [D1, C1].

So far the species has been recorded neither from the Polish nor from the Slovakian Tatras. Information from Martens (1869) is considered as a mistake (Riedel 1988).

80. *Perforatella rubiginosa* (A. Schmidt, 1853), Euro-Siberian

This is a lowland species. The single specimen found in the Zakopane Basin points to its sporadic occurrence there [D1, C1].

One may suppose that the records of *Helix sericea* Drap. *var. coroneola* Cless. concern this species (Kotula 1884). In those times the species appeared in the foothills of the Polish Tatras only sporadically. *P. rubiginosa* was mentioned from the Slovakian Tatras only by Kroupova (1986) as an accessory or accidental and recedent or subrecedent element in eight snail communities.

81. *Trichia hispida* (Linnaeus, 1758), European

Like *P. rubiginosa* this species is limited to the Zakopane Basin, but there it is common; usually found on old walls and herbaceous plants [D4, C1].

Earlier it was mentioned from the Polish Tatras only by Martens (1869) and Jachno (1870), not by Kotula (1884). The observations of Martens and Jachno very likely concerned localities in the Zakopane Basin. *T. hispida* does not seem to occur at higher altitudes. It is not recorded from the Slovakian Tatras (Hudec, Brabenec 1961; Kroupova 1986).

Remarks: *Vitrea inopinata* (Ulicny, 1887), *Semilimax semilimax* (Ferrussac, 1802), *Eucobresia diaphana* (Draparnaud, 1805) and *Limax tenellus* (O. F. Müller, 1774) were misrecorded from the Polish Tatra (Dyduch-Falniowska, Fyda 1986, Dyduch-Falniowska 1988, and Dyduch-Falniowska, Tobis 1989). The occurrence of *Deroceras rodnae* (Grossu et Lupu 1962) required further studies.

V. Ecological and zoogeographical characteristics of the malacofauna of the Polish Tatras

1. Species composition, relative abundance, structure of domination, and rare species

During the several years of investigation, 81 snail species were recorded from the Tatra National Park. Their occurrence varies greatly. Most of them occur infrequently, irregularly and in small numbers. Almost all species are sometimes subrecedent (D1); 62, recedent (D2); 43, subdominant (D3); 44, dominant (D4); and 29, eudominant (D5). If only the highest categories to which particular species attain are considered, 16 occur only as subrecedent (D1), 18 are recedent (D2) at the most, 4 are subdominant (D3), 14 are dominant (D4), and 29 are eudominant at least once (D5) (fig. 40).

Frequencies of general domination and constancy decline (more rapidly in the case of domination) exponentially (figs 41, 42). The general distribution pattern of domination approximates that known for other competitive communities (Trojan 1975).

The present studies show that in all malacocenoses only five species have general domination greater than 5%. Those are *P. rupestris, C. dubia, V. diaphana, C. edentula* and *C. columella.* Among them only *C. edentula*, a holarctic species, has

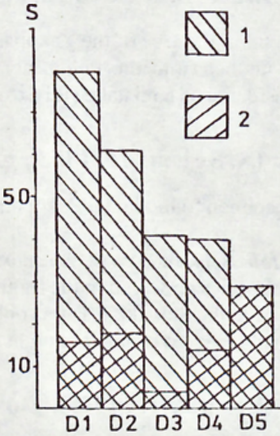


Fig. 40. Species domination in malacofauna of the Polish Tatras (according to division by A l e x a n d r o w i c z 1987), 1 - total species number in particular classes of domination, 2 - species number in particular classes of domination; only the highest values reached by species were included

Ryc. 40. Dominacja gatunków w malakofaunie Tatr Polskich (według podziału A l e x a n d r o w i c z a 1987), 1 - liczba gatunków w poszczególnych kategoriach dominacji, 2 - liczba gatunków w kategoriach dominacji z uwzględnieniem tylko najwyższych wartości osiąganych przez gatunki

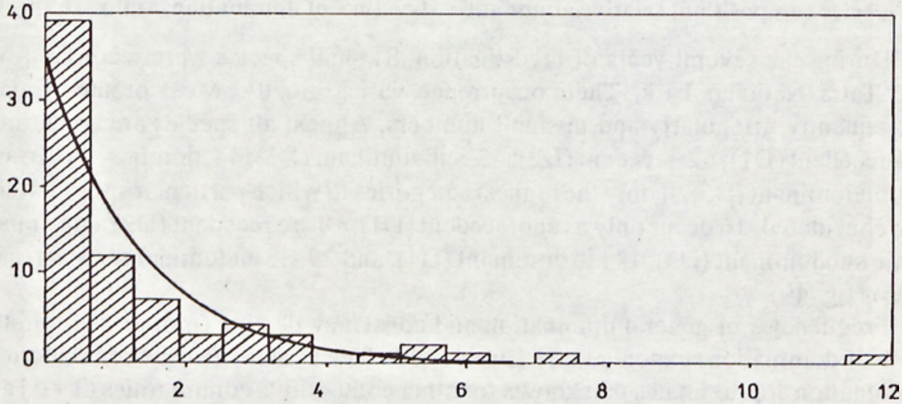


Fig. 41. Distribution of species domination in malacofauna of the Polish Tatras, abscissa - classes of domination, ordinate - frequency (number of species)

Ryc. 41. Rozkład dominacji gatunków w malakofaunie Tatr Polskich, rzędna - klasy dominacji, odcięta - frekwencja (liczba gatunków)

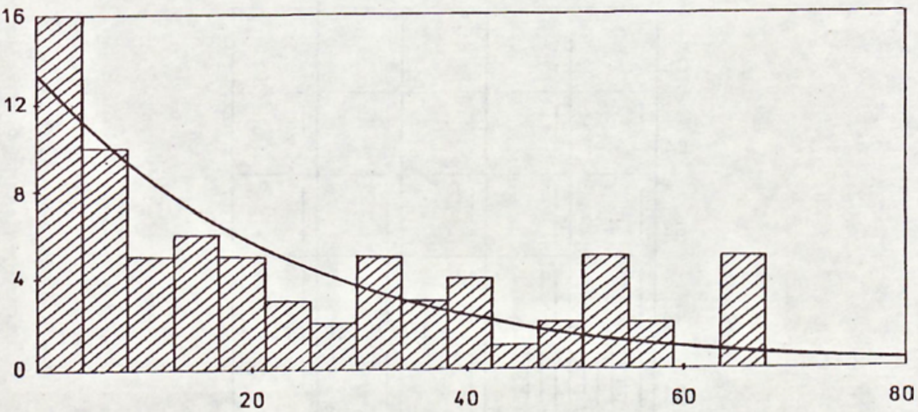


Fig. 42. Distribution of constancy in malacofauna of the Polish Tatras, abscissa - classes of constancy, ordinate - frequency (number of species)

Ryc. 42. Rozkład stałości gatunków w malakofaunie Tatr Polskich, rzędna - klasy stałości, odcięta - frekwencja (liczba gatunków)

a large, continuous range. The remaining species have either much smaller, continuous ranges (*V. diaphana*: Carpathian, Alpine, north Balkan) or large but disrupted ones. TNP is an important refuge for these species, and their presence contributes to the natural uniqueness of this area. Two of the species mentioned, *P. rupestris* and *C. columella*, are stenotopic; others have wider ecological spectra.

The group of over 30 species that are recedent (D1 - D2) at the most and occur only accidentally (C1) is of special interest. In view of their distribution the author examined causes of low domination and constancy in the malacofauna of the Polish Tatras (fig. 43). The review of these species begins with the rarest ones (the points lying lowest and farthest to the left in fig. 43).

The lowland species *V. antivertigo, A. aculeata, O. glaber, L. cinereo-niger,* and *B. fruticum* seemed to be rarest. Among them, only *L. cinereoniger* was once common in the Tatras. It occurred up to the lower limit of the dwarf mountain pine zone. *V. antivertigo* had been previously numerous in the Zakopane Basin (Kotula 1884). Next to them in the group under discussion are *V. pygmaea, V. pulchella, L. maximus* and *H. rossmaessleri.* The first three are not characteristic of the Tatra fauna. The last one, which most likely had been commoner (Kotula 1884), is a West-Carpathian species known from Czecho-Slovakia and Poland (Kerney, Cameron, Jungbluth 1983). The systematics and distribution of this species are still unclear and need more detailed studies. The taxon is regarded as an endemite (Hudec, Brabenec 1961; Riedel 1988), but no recent data on its population are available.

M. ventricosa and *B. cana* are two other species in the group under discussion. *M. ventricosa* has been recorded in two localities only, which is alarming because it was once rather common in the Tatras (Kotula 1884). The causes of this drastic

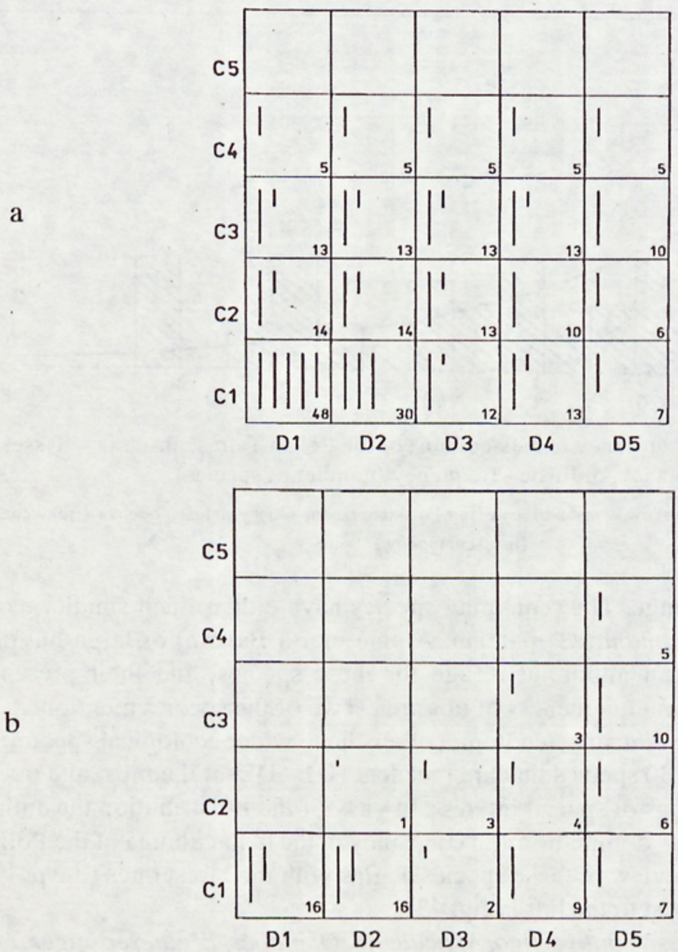


Fig. 43. Structure of the Tatra malacofauna, characterized by the distribution of constancy (C) and domination (D) of species (after Alexandrowicz 1987); a - based on shares in all malacocenoses, b - based on the highest shares

Ryc. 43. Struktura malakofauny tatrzańskiej wyrażona rozkładem stałości (C) i dominacji (D) gatunków (według Alexandrowicza 1987), a - z uwzględnieniem wszystkich udziałów gatunków w malakocenozach; b - z uwzględnieniem jedynie najwyższych kategorii dominacji osiąganych przez gatunki

decline should be examined, and active protection should be undertaken. *B. cana,* like *M. ventricosa*, was previously frequent. Kotula (1884) stressed that it was confined to the fir and beech, so the opinion that the reduction of its population is a direct consequence of vegetation changes seems right. *P. incarnata* is (and was) a very rare snail in the Polish Tatras. These mountains are likely beyond its ecological range.

The next group, in respect of frequency, includes *A. parcelineata, S. oblonga, V. costata, A. hortensis, O. depressus, E. strigella* and *C. holosericum*. Only some of them have ecological ranges comprising the Tatra biotopes. *S. oblonga* and *V. costata* are lowland, xerophilous species with a wide distribution. The Tatra mountains are at the limit of their ecological ranges. *A. parcelineata, O. depressus*, and *C. holosericum* have much smaller ranges (especially *A. parcelineata*) and they seem to prefer mountain habitats. But their biology is poorly known, so the chances of their active protection are only meagre.

V. subrimata is the last species whose share in the material was less than 0.1%. Its occurrence in the Tatras is similar to that in the other parts of its range.

Summing up, the majority of taxa very subrecedent or accidental (domination < 0.1% and constancy, in general, < 10%) in the Tatra malacocenoses is non-specific to this area, both in respect of zoogeography and ecology. They are rather insignificant for the quality of studied malacofauna. It is alarming that *Ch. rossmaessleri, O. glaber, M. ventricosa, B. cana, A. parcelineata, O. depressus, and C. holosericum* have similar occurrences because these species have mostly small ranges, in many cases restricted to the Carpathians and adjacent areas. Moreover, they are specialized taxa, preferring habitats particularly sensitive to man's activity.

The category of species with these dominance and constancy intervals (D1 - D2, C1) does not include species preferring untypical biotopes (e.g., on crystalline substratum), which have rather high domination (D4) but, like the previous species, are rare. These are, among others, *L. macroflagellata* and *L. nyctelia*. They also contribute to the faunal uniqueness of the Tatras. Their biology is also poorly known, so it is very difficult or even impossible to protect all them actively.

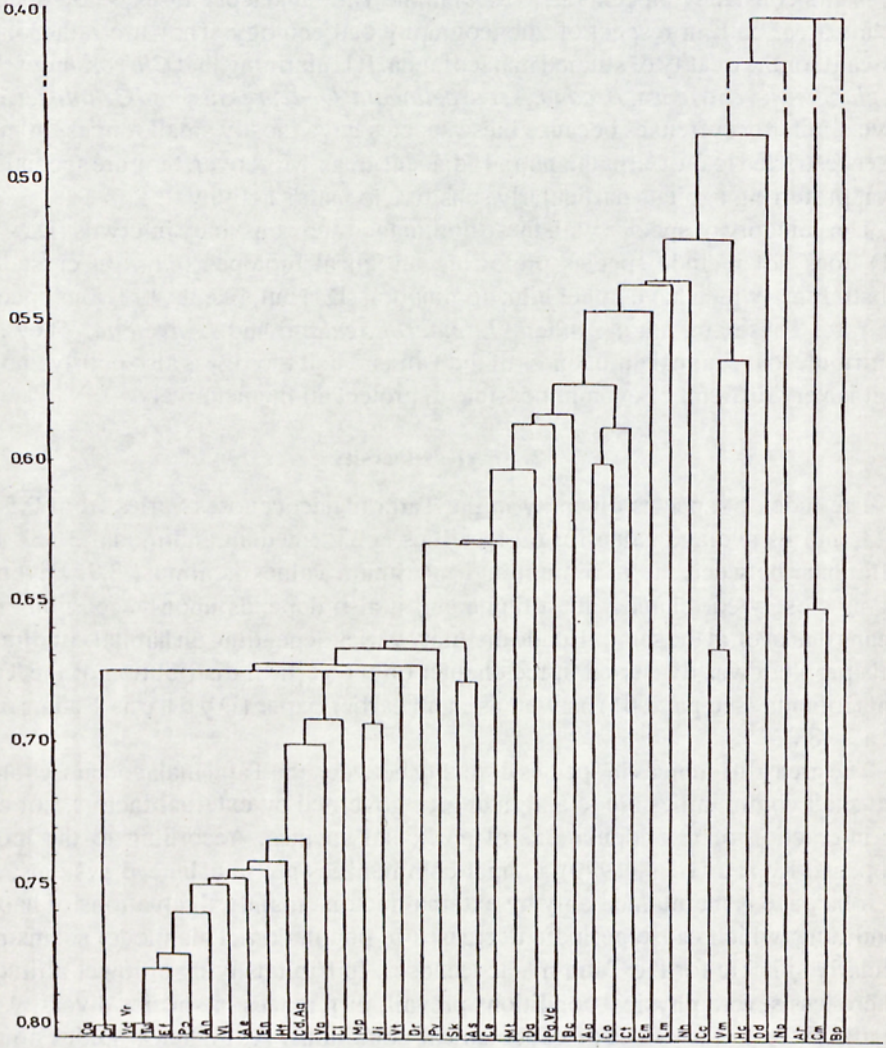
2. Species diversity

The index of species diversity in the Tatra malacocenoses varies from 0.54 to 4.23, and its average value for 69 localities is 3.2 (median and modal 3.35). The difference between the minimum and maximum values is almost 3.7. Diversity seems closely correlated with altitude and it also depends upon vegetation. This means that even at the same altitude diversity varies depending on habitat conditions. This problem was discussed in the chapter on the vertical distribution of the Tatra malacofauna (see page 61) as well as in an earlier paper (Dyduch-Falniowska 1988).

The great differences in species diversity between the Tatra malacocenoses show that snail communities are to a high degree governed by external factors, not only by interaction of the populations of particular species. According to the model proposed by Huston (1979), animal communities are unbalanced systems, and their balance is maintained only by external factors, mainly fluctuations of habitat conditions which cause periodic decreases in population. This model seems particularly suitable for the Tatra malacocenoses. In habitats lying at lower altitudes, where less severe physical conditions prevail, differences in species diversity can be attributed to the effect of geobotanical conditions. At higher altitudes abiotic factors, particularly climatic ones, play a more important role. In general they reduce diversity, eliminating certain species and decreasing the reproduction of others.

3. Co-occurence of snails

Co-occurrence was analysed only for snails that occur in the Tatra malacocenoses fairly regularly (40-50 species). Recedent and accidental species (e.g., *A. aculeata, L. cinereo-niger, B. fruticum, V. pulchella, Ch. rossmaessleri*) was not included. An analysis of co-occurrence has revealed no relationship between these species and any others recorded from the Tatras.



A binary analysis of 43 species based on Czekanowski's (known as Sorensen's) formula has shown that 23 (*C. laminata, C. cruciata, V. diaphana, V. turgida, T. unidentata, E. fulvus, P. rupestris, Ae. nitens, V. pellucida, Ae. pura, E. nivalis, Ch. faustinum, C. dubia, A. arbustorum, V. alpestris, C. lubrica, M. plicatula, I. isognomostoma, V. transsylvanica, D. ruderatus, P. vicina, S. kotulae, A. subfuscus* - fig.44) tend to co-occur. The remaining species seem to be connected more weakly with that group as well as with each other. The interpretation of the index values obtained is difficult because no comparative data are available. A dendrogram (fig.44) suggests that species with similar distribution (Czekanowski's index 0.65) includes taxa connected with forest litter and forests (deciduous). Other species seem to be poorly associated. They are snails with a narrow ecological range such as *Aciculidae, O. dolium,* and *B. pallens.*

Decamp's index of co-occurrence shows that some species have a tendency to form pairs: *C. cruciata* with *C. laminata, V. arctica* with *C. columella, C. minimum* with *A. parcelineata,* and *I. isognomostoma* with *M. plicatula.* We can also distinguish a group of nine species *(C. cruciata, C. laminata, I. isognomostoma, M. plicatula, P. vicina, Ae. nitens, Ch. faustinum, D. agreste, Ae. pura)* whose simultaneous occurrence is more probable than that of others (fig. 45).

Fig. 44. Co-occurrence of snails in the Polish Tatras, based on Czekanowski's (Sorensen's) index: *Aa - A. arbustorum, Ab - A. bielzi, Ae - Ae. pura, Af - A. fasciatus, An - Ae. nitens, Ap - A. polita, Ar - A. parcelineata, As - A. subfuscus, Av - A. silvaticus, Bc - B. coelurans, Bp - B. pallens, Ca - C. laminata, Cc - C. columella, Ce - C. edentula, Cd - C. dubia, Ch - C. holosericum, Ci - Ch. clienta, Cl - C. lubrica, Cm - C. minimum, Co - C. orthostoma, Ct - C. tridentatum, Da - D. agreste, Dt - D. reticulatum, Ef - E. fulvus, Em - E. montana, En - E. nivalis, Es - E. strigella, Hc - Ch. cingulellum, Hf - Ch. faustinum, Ii - I. personatum, Lm - L. marginata, Ml - M. latestriata, Mp - M. plicatula, Mt - M. tumida, Nh - N. hammonis, Np - N. petronella, Od - O. dolium, Pg - P. pygmaeum, Pp - P. rupestris, Pr - P. rubiginosa, Ps - P. sterri, Sk - S. kotulae, Tc - T. cylindrica, Th - T. hispida, Tu - T. unidentata, Tv - T. villosula, Va - V. alpestris, Vc - V. crystallina, Vd - V. diaphana, Vl - V. pellucida, Vm - V. arctica, Vp - V. pusilla, Vr - V. turgida, Vt - V. transsylvanica*

Ryc. 44. Współwystępowanie ślimaków w Tatrach Polskich na podstawie wskaźnika Czekanowskiego (Sorensena): *Aa - A. arbustorum, Ab - A. bielzi, Ae - Ae. pura, Af - A. fasciatus, An - Ae. nitens, Ap - A. polita, Ar - A. parcelineata, As - A. subfuscus, Av - A. silvaticus, Bc - B. coelurans, Bp - B. pallens, Ca - C. laminata, Cc - C. columella, Ce - C. edentula, Cd - C. dubia, Ch - C. holosericum, Ci - Ch. clienta, Cl - C. lubrica, Cm - C. minimum, Co - C. orthostoma, Ct - C. tridentatum, Da - D. agreste, Dt - D. reticulatum, Ef - E. fulvus, Em - E. montana, En - E. nivalis, Es - E. strigella, Hc - Ch. cingulellum, Hf - Ch. faustinum, Ii - I. personatum, Lm - L. marginata, Ml - M. latestriata, Mp - M. plicatula, Mt - M. tumida, Nh - N. hammonis, Np - N. petronella, Od - O. dolium, Pg - P. pygmaeum, Pp - P. rupestris, Pr - P. rubiginosa, Ps - P. sterri, Sk - S. kotulae, Tc - T. cylindrica, Th - T. hispida, Tu - T. unidentata, Tv - T. villosula, Va - V. alpestris, Vc - V. crystallina, Vd - V. diaphana, Vl - V. pellucida, Vm - V. arctica, Vp - V. pusilla, Vr - V. turgida, Vt - V. transsylvanica*

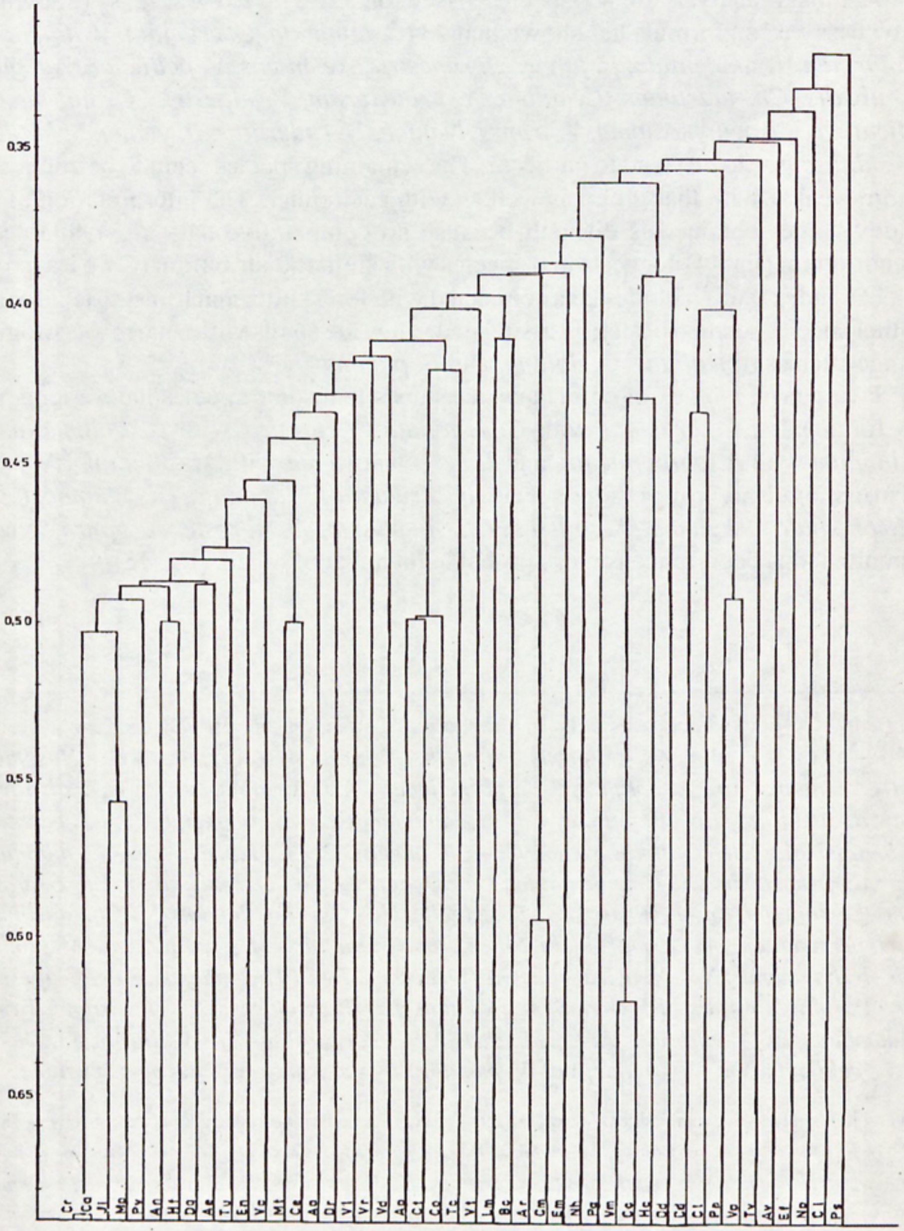


Fig. 45. Co-occurrence of snail species in the Polish Tatras, based on D e c a m p s index; literal denotations as in fig. 44

Ryc. 45. Współwystępowanie ślimaków w Tatrach Polskich na podstawie wskaźnika D e c a m p s a ; oznaczenia literowe jak na ryc. 44

I suppose that binary analysis shows pairs or groups of species which occur together on account of the quality of the locality. The species interactions are rather indirect and of no importance for the formation of malacocenoses.

An analysis of the co-occurrence of species based on their relative abundance (Morisita index) produces a different picture. Two groups of species can be distinguished. One of them concentrates around *V. diaphana, Ae. pura, A. silvaticus,* and *V. transsylvanica*. It includes also *C. tridentatum, B. pallens, E. nivalis, E. fulvus, E. montana, Ae. nitens, A. subfuscus,* and *D. agreste.* The other group is connected with the pair *A. fasciatus* and *M. plicatula* and includes *C. dubia, P. rupestris* and *V. alpestris.* Apart from those we observe a tendency to the formation of pairs, and rarely triples, *T. unidentata* and *Ch. faustinum*; *B. coerulans* and *C. cruciata*; *V. crystallina* and *C. holosericum*; and *N. hammonis, N. petronella* and *D. ruderatus* (fig. 46).

The analysis based on the relative abundance of species yields very low indices of co-occurrence for snails which were grouped together by the results of the binary analysis (and also by intuition). *C. columella, V. arctica,* and *Ch. cingulellum* are a few of them. The first two are linked by their ecological niches, more by their character (quality) than by factors influencing relative abundance, such as food, and the carrying capacity of their habitats. Searching for influences governing the density of both taxa, the author proposes an analysis of physical conditions (climatic and others). *Ch. cingulellum* is a stenotopic, petrophilous taxon, and most probably the size of its population is determined by the kind of substratum.

According to the Decamp's index the most closely co-occurring species are *C. cruciata* and *C. laminata*. The Czekanowski (Sorensen) index yields the same pair and also the triple *V. diaphana, V. turgida,* and *T. unidentata*. The Morisita index yields *V. diaphana* and *Ae. pura.* The first two indices, which give consistent results, show that the co-ccurrence of *C. cruciata* and *C. laminata* is permanent, though their relative numbers change. The Morisita index, incorporating information on the relative abundance of this pair, is lower than the indices shown on the dendrogram (fig. 46), but in spite of this *C. cruciata* is most closely connected with *C. laminata* (Morisita index - 0.4671). Searching for influences governing the occurrence of groups from non-binary analysis I propose studies on food, biotic characters of sites and species preference.

Many previous studies aimed to find the "major factors" governing the relations between snail species. Boycott (1934), Burch (1955), Karlin (1961), Grime and Blythe (1969), and Cameron (1978) pointed different factors determining malacological variety. Dillon's results (1980) show no direct dependence of species composition upon a single habitat condition. The occurrence of each species seems influenced by different factors. Summing up, I can say that the qualititative and quantitative richness of species is a resultant of certain unknown features and dependences (latent regularities - Dillon's term), unknown in part because they are not measurable. Their cumulative effect is in the proportions between the number of species and their abundance in communities, which is called "interspecific

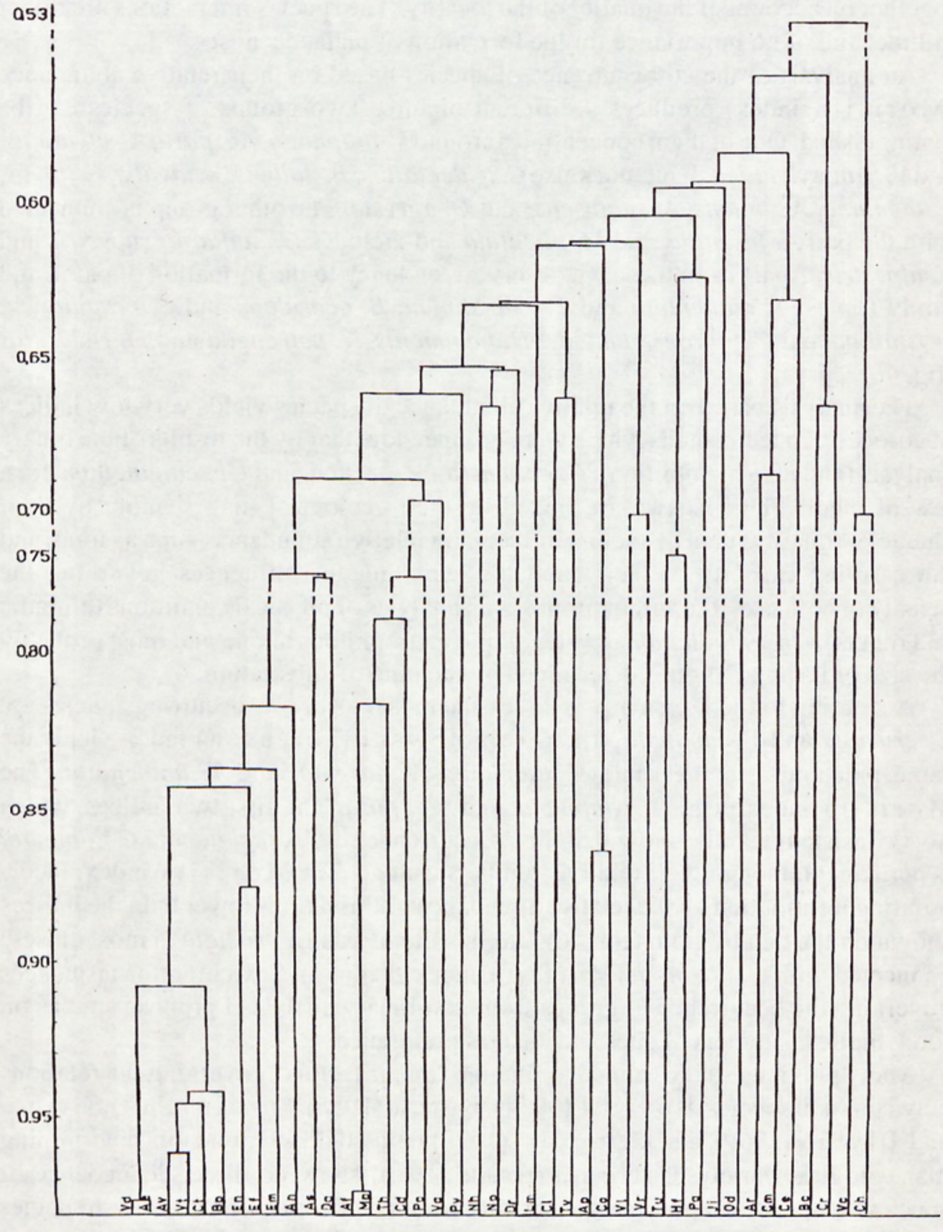


Fig. 46. Co-occurrence of snail species in the Polish Tatras, based on M o r i s i t a index; literal denotations as in fig. 44

Ryc. 46. Współwystępowanie ślimaków w Tatrach Polskich na podstawie wskaźnika M o r i s i t y ; oznaczenia literowe jak na ryc. 44

tension" by S t u g r e n (1976). In the present studies, indices of co-occurrence (see "Material and methods") are accepted as a measure of this tension.

In view of these results the question of the relations between taxa in malacocenoses should be considered in both their qualitative and their quantitative aspects. The likelihood of occurrence of species in a given area is determined by factors different from those influencing their abundance. This is an important conclusion, indicating that each species should be dealt with individually when the functioning of malacocenoses is described, as well as when one examines the causes of the qualitative and quantitative degradation of the Tatra malacofauna.

H a s t i n g s (1987) disscused the role of co-occurrence in the formation of natural communities. He believes that an analysis of co-occurrence is not likely to show even strong competition, despite opposing experimental data (S t r o n g et al. 1984). The earlier mentioned difference in the results of clustering from binary and non-binary indices suggest that it is useful to test both techniques. We may offer the hypothesis that a non-binary analysis yields other kinds of species interactions than a binary analysis does. For example, the dendrogram based on the M o r i s i t a index (fig. 46) points to the close co-occurrence of some *Zonitidae* which have very similar niches, most likely even partly overlapping. To test the above hypothesis, we should examine the biology of species from pairs or from larger groups of species obtained on the basis of clustering.

4. The vertical distribution of the malacofauna

The number of species in biotopes at the same altitude a.s.l. varies greatly; in some lower situations the number is smaller than or similar to that in the alpine zone.

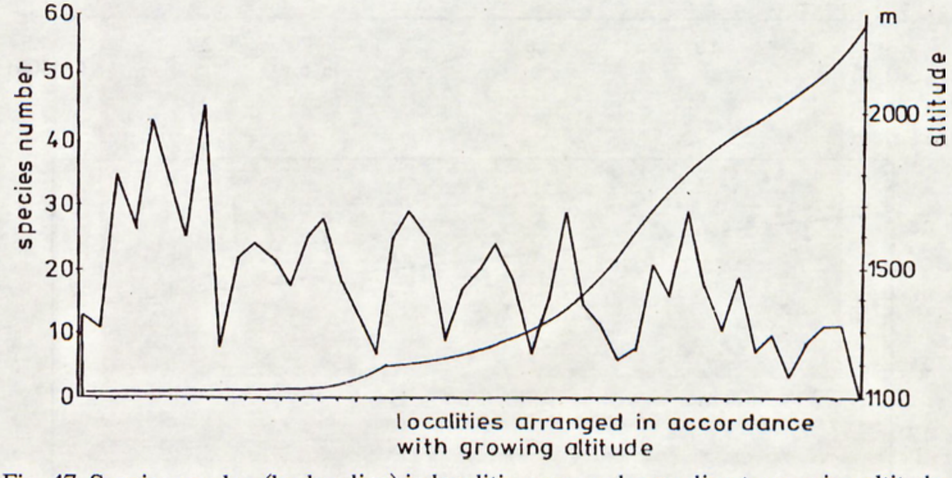
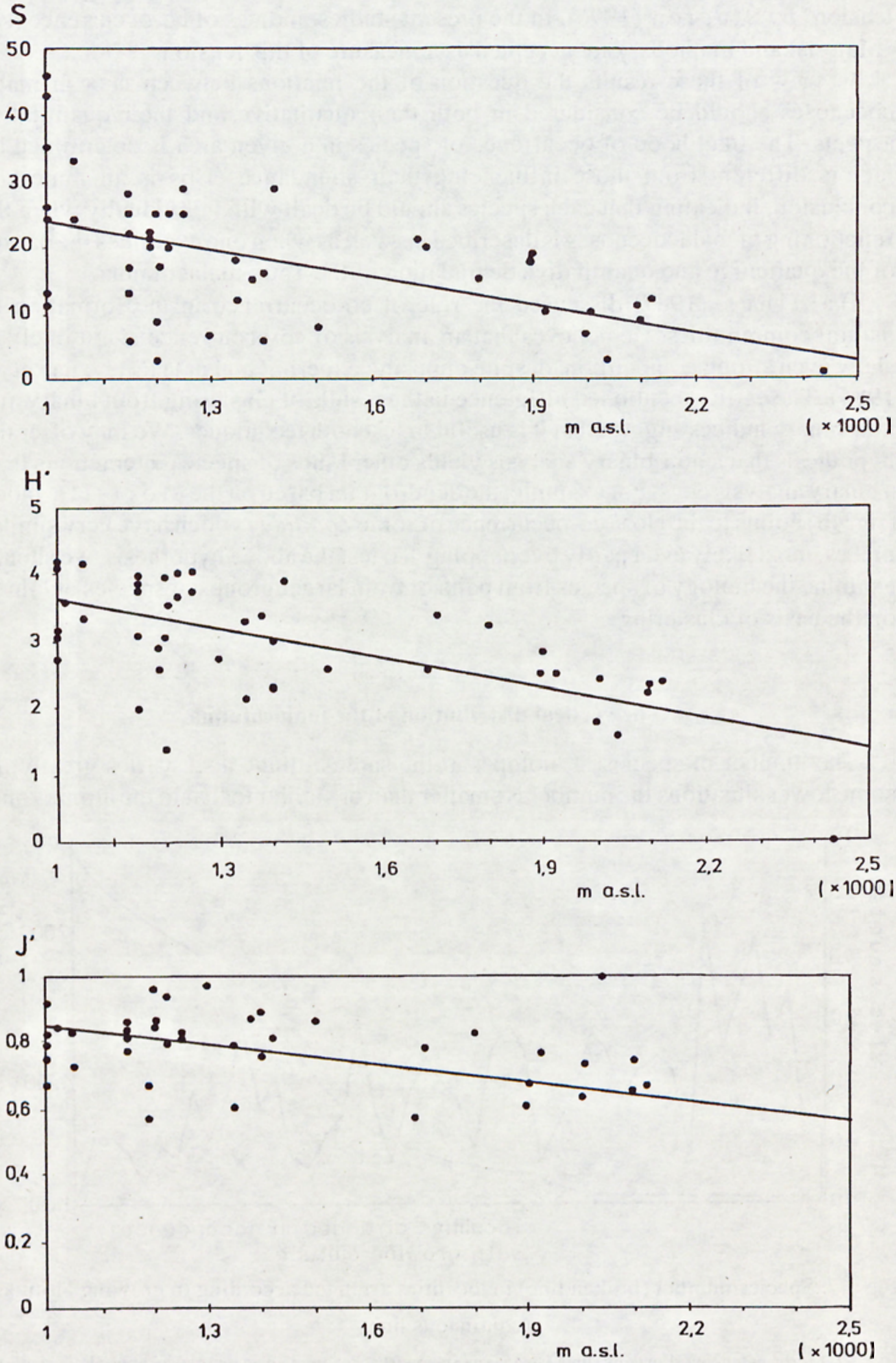


Fig. 47. Species number (broken line) in localities arranged according to growing altitude (continuous line)

Ryc. 47. Liczba gatunków ślimaków (linia łamana) na stanowiskach w gradiencie wysokości npm. (linia ciągła)


S
50
40
30
20
10
0
1
1,3
1,6
1,9
2,2
2,5
m a.s.l.
(× 1000)
H'
5
4
3
2
1
0
1
1,3
1,6
1,9
2,2
2,5
m a.s.l.
(× 1000)
J'
1
0,8
0,6
0,4
0,2
0
1
1,3
1,6
1,9
2,2
2,5
m a.s.l.
(× 1000)

However, a general decrease in the nmber of taxa as altitude increases is evident (figs 47, 48). The values of the species diversity (H') and equitability (J') indices change in the same way (figs. 48). The correlation coefficients of these values with altitude a.s.l. vary from -0.5 to -0.6. Apparently the differentiation of biotopes lowers correlation coefficients, e.g., in the diagram, an altitude of 1150 m a.s.l. corresponds with few values (from 6 to 28) in the number of species.

A cluster analysis (Single Linkage or Nearest Neighbor Method) for species diversity H', equitability J' and number of species S has revealed that most malacocenoses occurring up to 1500 m a.s.l. are structurally similar and they belong to group I, which includes 31 (67%) localities out of the 46 that were analysed. The malacocenoses of beech forests in the Dolina Olczyska and Dolina Białego valleys form group II, which has the greatest number of species and the highest index of species diversity. The remaining malacocenoses form pairs or they are separate categories (fig. 49). So, the structure of malacocenoses (species number, relation of species diversity to species number, number of rare species) is rather similar in most of TNP habitats and it changes only slightly with altitude.

Many species reach the upper limit of their ranges in the Tatras, which considerably influences the differentiation of snail communities in a hipsometric gradient. Above 2000 m a. s. l. we observe 21 species: *C. lubrica, P. rupestris, C. columella, V. pygmea, V. arctica, V. alpestris, P. sterri, A. subfuscus, S. kotulae, E. nivalis, V. diaphana, V. subrimata, N. hammonis, E. fulvus, M. tumida, C. dubia, V. turgida, T. unidentata, A. arbustorum, Ch. faustinum* and *Ch. cingulellum.* Four taxa *A. fasciatus, V. pellucida, N. petronella,* and *C. holosericum* reach the upper limit of their ranges between 1700 and 2000 m a. s. l. Many more taxa (19) have their upper range limit between 1400 and 1700 m a. s. l. To these belong *A. bielzi, E. montana, P. pygmaeum, D. ruderatus, A. silvaticus, V. crystallina, Ae. pura, Ae. nitens, O. depressus, L. macroflagellata, B. coerulans, D. agreste, D. reticulatum, C. laminata, C. orthostoma, M. plicatula, C. cruciata, P. vicina,* and *I. isognomostoma. C. columella* and *V. arctica* have these same altitudes as their lower range.

Slightly fewer species reach the upper limit of their occurrence between 1100 and 1400 m. a. s. l.: *A. polita, C. tridentatum, S. oblonga, C. edentula, T. cylindrica, O. dolium, Ch. clienta, V. costata, V. pulchella, V. transsylvanica, V. contracta, L. cinereo-niger, L. nyctelia, L. marginata, M. latestriata, T. villosula,* and *E. strigella,* altogether 17 species.

1100 m a. s. l. is the upper limit of *A. parcelineata, C. minimum, S. putris, V. pusilla, V. substriata, B. pallens, M. ventricosa, B. cana*, and *B. fruticum.*

Fig. 48. Regression of species number S, species diversity H', and equitability J' according to altitude

Ryc. 48. Regresja liczby gatunków S, różnorodności gatunkowej H' i równomierności J' w zależności od wysokości npm

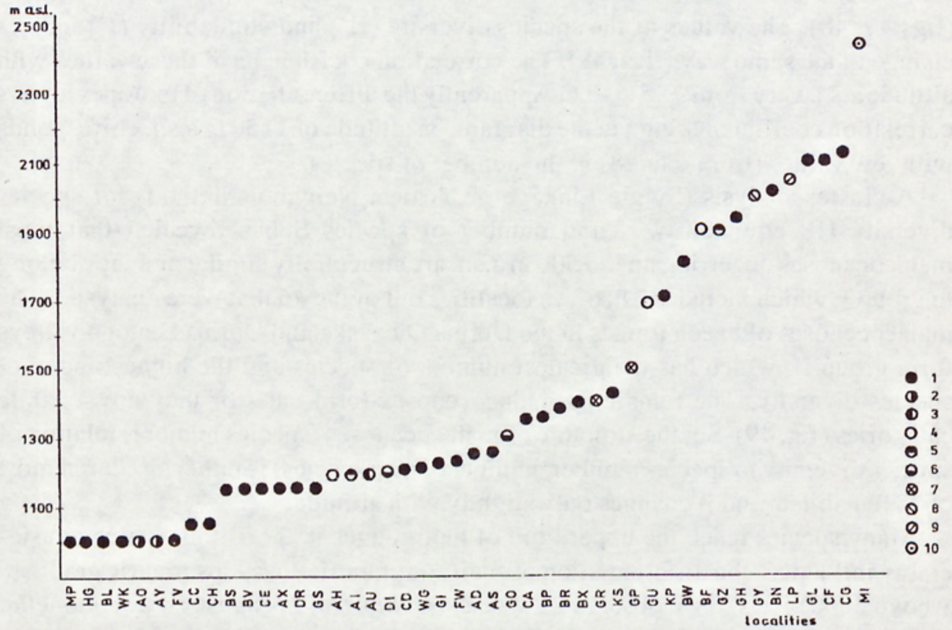


Fig. 49. Clustering of malacocenoses with regard to species number S, species diversity H' and equitability J', arranged according to altitude (1-10 - distinguished groups; denotations of localities as in Appendix 1)

Ryc. 49. Grupowanie malakocenoz ze względu na liczbę gatunków S, różnorodność H' i równomierność J' w gradiencie wysokości npm. (1-10 - wyróżnione grupy; oznaczenia stanowisk jak w Appendix 1)

There is a group of 10 species restricted to the Zakopane Basin: *S. oblonga, S. putris, V. antivertigo, D. rotundatus, A. hortensis, O. glaber, L. maximus, L. plicata, P. rubiginosa,* and *T. hispida.*

The differentiation of the ranges of species results in the qualitative differentiation of malacocenoses. Accepting altitude intervals of up to 1100 m, 1100 - 1400 m, 1400 - 1700 m, 1700 - 2000 m, and above 2000 m a.s.l., the author examined the similarity of malacofauna according to Czekanowski's formula. The diagram based on this index shows that qualitative changes are parallel to the gradient of altitudes. The malacofauna changes gradually, and above 2000 m it has the greatest autonomy, i. e. its similarity to all others is least (Table I, fig. 50).

Not all aspects of zonation of malacofauna in the Tatras are examined here. Some aspects of qualitative and quantitative change with growing altitude are discussed in the chapter dealing with human pressures. Since altitude a.s.l. is the main factor on the living conditions of snails, it touches practically all questions concerning the malacofauna of this area.

TABLE I

Similarity of the malacofauna of different altitudinal zones in the Polish Tatras, I—above 2000 m a. s. l., II—1700-2000 m a. s. l., III—1700-1400 m a. s. l., IV—1400-1100 m a. s. l., V—lower than 1100 m a. s. l., VI—Zakopane Basin

Podobieństwo malakofauny stref wysokościowych w Tatrach Polskich, I—powyżej 2000 m npm, II—1700-2000 m npm, III—1700-1400 m npm., IV—1400-1100 m npm., V—do 1100 m npm., VI—Kotlina Zakopiańska

	II	III	IV	V	VI
I	50.7	38.2	24.9	26.5	19.0
II		52.0	34.2	41.5	26.4
III			42.3	51.1	36.3
IV				52.2	44.6
V					46.2

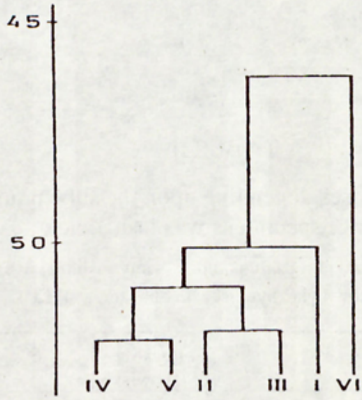


Fig. 50. Qualitative similarity of malacofauna of marked zones in TNP; denotations of zones as in Table I

Ryc. 50. Podobieństwo jakościowe malakofauny wybranych stref wysokościowych w TPN; oznaczenia stref I - VI jak w Tab. I

5. Malacocenoses and the substratum

It is difficult to determine the substratum's influence on the Tatra malacofauna on the basis of faunal and ecological studies. For substratum preferences in particular species we can make use of Ložek's classification (1955). This author distinguished indifferent, petrocalciphilous (occurring on calcareous rocks), calciphilous, and acidophilous species. No acidophilous species were recorded from the Tatras, but four calciphilous were found: *C. columella, V. arctica, V. alpestris, O. dolium.* There were three petrocalciphilous: *P. rupestris, Ch. clienta,* and *Ch. cingulellum.*

All other species are indifferent according to Ložek (1955). But it is difficult to agree entirely with him because a simple comparison of the distribution of the malacofauna with the geological map of the Tatras shows that only localities on calcareous substrata, or at least rinsed with surface waters flowing down limestone slopes, are inhabited by snails. On non-calcareous substrata they occur only rarely, and then only eurytopic species such as *A. subfuscus.*

The numbers for species and for species diversity in snail communities occurring on the same substratum is often different. Most localities were on dolomitic limestones. There, the number of species varied from 2 to 29, and species diversity reached 4.18. Spruce forests on this substratum is a community harboring very rich and highly diverse malacocenoses (the valley of Filipczański Potok) as well as extremely poor ones (Kuźnice - Boczań). With other plant cover (e.g., epilithic grasslands) and the same substratum the differences between snail communities are less (Table II). The parameters examined are also slightly less varied (S, 6 - 25; H,' 1.84 - 3.93) for localities on a loamy gravel moraine (Table II).

TABLE II

Differentation of the malacocenoses depending upon the substratum and vegetation in the Polish Tatras ("*" - number of specimens was insufficient to calculate H' and J')

Zróżnicowanie malakocenoz w zależności od rodzaju podłoża i szaty roślinnej w Tatrach Polskich ("*" - liczba osobników była zbyt niska do obliczenia H' i J')

Substratum Podłoże	Vegetation Roślinność	Locality Stanowisko	S	H'	J'
alaskites alaskity	epilithic grasslands murawy naskalne	BN	10	2.43	0.73
		GL	11	2.23	0.64
		GY	7	1.77	0.63
alluvial cones stożki napływowe	*Piceetum tatricum* *Glad. - Agrost. alp.*	RW	23	3.86	0.85
	Glad. - Agrost. alp.	BX	16	3.01	0.75
		BU	17	3.45	0.84
		HG	11	2.72	0.79
dark limestones, dolomites ciemne wapienie, dolomity	*Pinus mugo* epilithic grasslands murawy naskalne	GX	16	3.10	0.77
	epilithic grasslands murawy naskalne	MS	20	3.21	0.74
		KP	20	3.39	0.78
		CF	9	2.35	0.74
		CG	12	2.41	0.67

Table II cont.

dolomitic limestomes wapienie dolomiczne	*Abieti - Piceetum*	AH	22	2.56	0.57
		FV	24	4.18	0.91
	Piceetum - tatricum	BP	12	2.14	0.60
		SK	17	3.51	0.86
	dense spruce forest zwarty las świerkowy	AK	2	*	*
		AR	3	*	*
	Abieti - Piceetum *Dent. gland. - Fagetum*	CE	25	3.77	0.81
	Dent. gland. - Fagetum	AT	29	4.08	0.84
	Glad. - Agrost. alp.	BS	22	3.85	0.86
	Pinus mugo epilithic grasslands murawy naskalne	DA	8	*	*
		FW	20	4.04	0.93
	epilithic grasslands murawy naskalne	AP	16	2.93	0.73
		BR	15	3.39	0.87
		GN	9	1.26	0.40
		GM	16	3.38	0.84
		BC	14	2.49	0.65
		BW	19	3.19	0.75
dolomitic sandstones piaskowce dolomitowe	*Abieti - Piceetum*	NE	20	2.60	0.60
		HR	20	3.08	0.71
sandy-gravelous fluvial and lacustrine sediments; piaszczysto-żwirowe osady rzeczne i żwirowe	*Abieti - Piceetum*	AX	28	3.99	0.83
granitoids granitoidy	*Piceetum tatricum*	WM	3	*	*
	epilithic grasslands murawy naskalne	MI	1	*	*
gravel-loamy moraine sediments gruzowo-gliniaste osady morenowe	spruce forest las świerkowy	GS	6	1.84	0.71
		AC	16	3.61	0.90
	Glad. - Agrost. alp.	GT	12	3.01	0.84
		TG	6	2.42	0.93
		GO	7	2.72	0.97
		GI	25	3.67	0.79
		CD	25	3.95	0.85

Table II cont.

grey, pinkish and dark limestones szare, różowe i ciemne wapienie	epilithic grasslands murawy naskalne *Abieti - Piceetum*	WK	26	3.16	0.67
	epilithic grasslands murawy naskalne	KO	6	2.33	0.90
		WT	2	*	*
		BL	35	4.22	0.82
		BF	18	2.52	0.60
		GH	10	2.51	0.76
	raspberry field maliniak *Abieti - Piceetum*	BH	9	3.02	0.95
red quartzitic sandstones and shales czerwone piaskowce kwarcytyczne oraz łupki	*Piceetum tatricum*	GR	6	2.41	0.94
	spruce forest las świerkowy	ST	8	2.59	0.86
	epilithic grasslands murawy naskalne	GU	21	2.52	0.57
red sandstones, shales, dolomites, limestones; czerwone piaskowce, łupki, dolomity, wapienie	*Abieti - Piceetum* *Glad. - Agrost. alp.*	DI	9	*	*
	Car. - Fest. tatrae *Glad. - Agrost. alp.*	BT	37	4.00	0.77
	Dent. gland. - Fagetum	CC	33	4.17	0.83
sandy-gravelous fluvio-glacial sediments; żwirowato-piaszczyste osady fluwioglacjalne	*Piceetum tatricum* *Glad. - Agrost. alp.*	WG	17	3.54	0.87
	Dent. gland. - Fagetum *Abieti - Piceetum*	BI	37	3.53	0.68
		AO	43	4.05	0.75
shales, greenish sandstones, organodetritial limestones; łupki i zielonawe piaskowce, wapienie organodetrytyczne	*Abieti - Piceetum*	AW	27	3.76	0.79
	Dent. gland. - Fagetum	CH	24	3.35	0.73
slope debris gruz zboczowy	epilithic grasslands murawy naskalne	GW	15	3.22	0.82
		GZ	19	2.83	0.67
	Glad. - Agrost. alp.	AB	16	3.43	0.86
		CA	18	3.30	0.79
	Piceetum tatricum	DR	13	3.09	0.83

The highest number of species (43) appears for malacocenoses on sandy gravelous fluvioglacial sediments. The highest diversity (4.2) is on dolomitic limestones and red sandstones, shales, dolomites and limestones. A comparison of the highest values of S, H', and J' shows which substratum (at the optimum vegetation, as seen from the malacological point of view) is most favourable for snails. Other factors such as altitude a. s. l. were here excluded. The granitoids are especially unsuitable for snail communities (Table III).

TABLE III

Differentation of malacocenoses according to the substratum ("*" as in Table II)

Zróżnicowanie malakocenoz w zależności od rodzaju podłoża ("*" podobnie jak w tabeli II)

Substratum Podłoże	S	H'	J'
alaskites alaskity	11	2.43	0.63-0.73
alluvial cones stożki napływowe	23	3.86	0.75-0.85
dark limestones, dolomites ciemne wapienie, dolomity	20	3.39	0.67-0.78
dolomitic limestones wapienie dolomityczne	29	4.18	0.40-0.91
dolomitic sandstones piaskowce dolomitowe	20	3.08	0.60-0.71
fluvial and lacustrine sands and gravel piaszczysto-żwirowe osady rzeczne i jeziorne	28	3.99	0.83
granitoids granitoidy	3	*	*
gravel loamy moraine gruzowo-gliniaste osady morenowe	25	3.95	0.71-0.97
grey, pinkish and dark limestones szare, różowawe i ciemne wapienie	35	4.22	0.95
red quartzic sandstones and shales czerwone piaskowce kwarcytyczne i łupki	21	2.59	0.57-0.94
red sandstones, shales, dolomites, limestones czerwone piaskowce, łupki, dolomity, wapienie	37	4.17	0.77-0.83
sandy-gravelous fluvioglacial sediments żwirowo-piaszczyste osady fluwioglacjalne	43	4.05	0.68-0.87
shales, greenishsandstones, organodetrital limestones łupki, zielonawe piaskowce, wapienie organodetrytyczne	27	3.76	0.73-0.79
slope debris gruz zboczowy	18	3.43	0.79-0.86

6. The phytosociological background of malacological differentiation

The main types of biotopes inhabited by molluscs in the Polish Tatras are epilithic grasslands (situated mainly in the alpine zone but often at lower altitudes), *Gladiolo-Agrostidetum alpinetosum* on in-forest glades, *Piceetum tatricum, Abieti - Piceetum, Dentario glandulosae-Fagetum* and mixed habitats, particularly in the forest zones. Certain snail species are confined to a strictly determined habitat; others occur in different biotopes. *T. cylindrica, C. columella, V. arctica,* and *V. alpestris* are connected with epilithic grasslands. *P. rupestris* and *Ch. clienta* can be found only on rocks, while *B. pallens* prefers *Dentario glandulosae-Fagetum.* It is difficult to estimate to what degree these connections are conditioned by preferences for vegetation, and how much they depend on other habitat factors, but no doubt these dependences determine the composition of malacocenoses living in habitats of different vegetation. We may call these dependences paratrophic (after Trojan 1975 and Chajłov 1971).

The malacocenoses of epilithic grasslands are greatly varied; the species number is between a few and 35 (most often ten to twenty), species diversity reaches 4.2 (most often between 2 and 3). In *Gladiolo-Agrostidetum alpinetosum* the range of these values is smaller: the number of species varies from 6 to 25, and diversity is about 3 (Table IV). *Abieti - Piceetum* and *Piceetum tatricum*, as mentioned above, are sometimes very rich but more frequently are very poor from the malacological point of view. All mixed habitats are also inhabited by greatly different malacocenoses (Table IV).

TABLE IV

Differentation of malacocenoses according to vegetation ("*" as in Table II)

Zróżnicowanie malakocenoz w zależności od roślinności ("*" podobnie jak w tabeli II)

Vegetation Roślinność	Stanowisko Locality	S	H'	J'
epilithic grasslands murawy naskalne	BN	10	2.43	0.73
	GL	11	2.23	0.64
	GY	7	1.77	0.63
	MS	20	3.21	0.74
	KP	20	3.39	0.78
	CF	9	2.35	0.74
	CG	12	2.41	0.67
	AP	16	2.93	0.73
	BR	15	3.39	0.87
	GN	9	1.26	0.40
	GM	16	3.38	0.84
	BC	14	2.49	0.65
	BW	19	3.19	0.75
	MI	1	*	*
	KO	6	2.33	0.90
	WT	2	*	*
	BL	35	4.22	0.82
	BF	18	2.52	0.60
	GH	10	2.51	0.76
	GU	21	2.52	0.57
	GW	15	3.22	0.82
	GZ	19	2.83	0.67

Table IV cont.

Gladiolo - Agrostidetum alpinetosum	BX	16	3.01	0.75
	BU	17	3.45	0.84
	HG	11	2.72	0.79
	BS	22	3.85	0.86
	GT	12	3.01	0.84
	TG	6	2.42	0.93
	GO	7	2.72	0.97
	GI	25	3.67	0.79
	CD	25	3.95	0.85
	AB	16	3.43	0.86
	CA	18	3.30	0.79
Abieti - Piceetum	AH	22	2.56	0.57
	FV	24	4.18	0.91
	NE	20	2.60	0.60
	AX	28	3.99	0.83
	AW	27	3.76	0.79
Piceetum tatricum	BP	12	2.14	0.60
	SK	17	3.51	0.86
	HR	20	3.08	0.71
	GR	6	2.41	0.94
	RW	23	3.86	0.85
	DR	13	3.09	0.83
	WM	3	*	*
spruce forest las świerkowy	AK	2	*	*
	AR	3	*	*
	GS	6	1.84	0.71
	AC	16	3.61	0.90
	ST	8	2.59	0.86
Dentario glandulosae - Fagetum	AT	29	4.08	0.84
	CC	33	4.17	0.83
	CH	24	3.35	0.73
raspberry patch, maliniak *Abieti - Piceetum*	BH	9	3.02	0.95
Abieti - Piceetum *Gladiolo - Agrostidetum alpinetosum*	WG	17	3.54	0.87
Abieti - Piceetum *Dentario glandulosae - Fagetum*	CE	25	3.77	0.81
	BI	37	3.53	0.68
	AO	43	4.05	0.75

Table IV cont.

Pinus mugo *epilithic grasslands* *murawy naskalne*	GX DA FW	16 8 20	3.10 * 4.04	0.77 * 0.93
epilithic grasslands, murawy naskalne *Abieti - Piceetum*	WK	26	3.16	0.67
Carici - Festucetum tatrae *Gladiolo - Agrostidetum alpinetosum*	BT	37	4.00	0.77

7. The importance of exposure for molluscs

Most valleys in the Polish Tatras lie along meridions and they incise deeply into the north-facing slopes. Their malacocenoses are typical of northern slopes, and they are generally poorer than those of the Slovakian (southern) part of the Tatras. From available information the Slovakian malacofauna may be estimated at about 100 species of terrestrial snails (Hudec, Brabenec 1961, Ložek 1974, Kroupova 1986). This number is about 20 more than in the northern part of the Tatras (i. e., in TNP).

It is more difficult to estimate the effect of exposure on snails for a single mountain in the Polish Tatras. At lower situations all localities are exposed northwards. At slightly higher altitudes, e.g., Mt Sarnia Skała and Mt Wielki Kopieniec, there were no significant differences in species composition, species diversity or even numbers, among snail communities inhabiting similar biotopes such as epilithic grasslands. In the alpine zone, in the Czerwone Wierchy range differences in species richness observed between the northern and southern slopes (in favor of the northern) seem to be connected with the difference in substrata. Southern slopes are crystalline, and northern slopes are calcareous. As with many other questions about the distribution of snails in the Tatras, this also needs further study.

8. Effect of the moisture in the substratum on molluscs

Moisture in the substratum influences the distribution of snails indirectly, through vegetation. The impoverishment of malacofauna as altitude increases may be an effect of decreasing moisture. As altitude increases plant communities retain less and less water, and the amplitude of changes in substratum moisture increases, too. The other problem is the influence of atmospheric humidity on molluscs, particularly important for slugs. This factor certainly contributes to the impoverishment of malacofauna with increasing altitude. This is indicated by the sparseness of slugs.

The differentiation of the number of snail species as well as of their density and diversity (H') depending on humidity can be observed within the same phytosociological unit. The highest values of these indices were noted in the most humid patch of *Dentario glandulosae-Fagetum* (patch I in Table V), lower in the remaining ones, which had correspondingly smaller humidities (patches II and III in Table V).

The difference of altitude a. s. l. was in this case only some tens of meters (Dyduch-Falniowska, Tobis 1989).

TABLE V

Average values of some parameters of malacocenoses in the patches of *Dentario glandulosae-Fagetum* of a different humidity: I-very wet patch, II-moderately wet patch, III-dry patch

Średnie wartości niektórych parametrów malakocenoz w płatach *Dentario glandulosae-Fagetum* o różnej wilgotności: I-płat bardzo wilgotny, II-średnio wilgotny, III-suchy

Parameters / Parametry — Patch / Płat	S	N [ind/sqm]	H'
I	25.0	554	3.5
II	14.3	150	2.9
III	16.3	140	3.1

9. Groups or communities of snails

The above title suggests an attempt at a stance towards the problem of the connections between species, which has been touched in the chapter on co-occurrence. An analysis of co-occurrence has shown, among other things, that the presence of particular species is correlated to different degrees, which means that there are different probabilities of the simultaneous occurrence of these species.

The composition of malacofauna at a given moment is a resultant of the annual cycle (which can be ignored when material from the same phenological periods is analysed), atmospheric conditions in a given season, and also possible changes over many years' cycles. The values listed in Table VI allow comparison of the results of observations from six localities. Two of them were examined four times, two localities three times, and two localities twice. The number of species noted in this period varied from 13 to 42. The per cent of taxa that were observed only once was high (from 37.5 to 68.75). In the investigations repeated four times, only one taxon was observed in the material each time. That does not necessarily mean that the other species were absent, but that they were too rare to detect. Since a searched area often is very small, on Giewont Mt. for example, one may ask whether the species living in one locality form a more or less accidental group or a community of taxa connected by mutual dependences such as paratrophic (Trojan 1975). The distribution of species frequencies in various years is similar (fig. 51). This constant pattern, in spite of taxonomical differences, makes us to look for the causes of this constancy. Since the present studies were in principle faunal and relatively short, the author can not answer the above question definitively. However, the direction for further studies is clear. The existence of a constant pattern of species frequency

TABLE VI

Dynamics of malacocenose composition (designations of localities as in Appendix I)

Dynamika składu malakocenoz (oznaczenia stanowisk jak w Appendix I)

Locality Stanowisko	Season number Liczba sezonów	Total species number Ogólna liczba gatunków	Species recorded Gatunki stwierdzone							
			quadruply czterokrotnie		trebly trzykrotnie		twice dwukrotnie		once raz	
			number liczba	%	number liczba	%	number liczba	%	number liczba	%
BF	4	16	1	6.25	3	18.75	3	18.75	9	56.25
BX	4	16	1	6.25	3	18.75	6	37.5	6	37.5
AB	3	16			2	12.5	3	18.75	11	68.75
AF	3	42			7	16.7	14	33.3	21	50
MS	2	19					11	57.9	8	42.1
DR	2	13					5	38.5	8	61.5

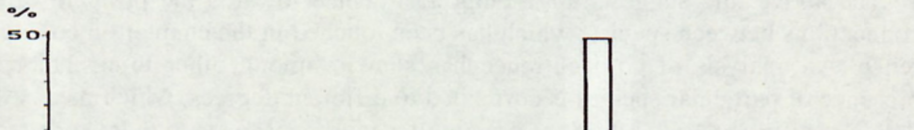


Fig. 51. Distribution of species frequency in various years on the same locality (Giewont-BF)

Ryc. 51. Rozkład frekwencji gatunków w różnych latach na tym samym stanowisku (Giewont - BF) reflects a relatively constant structure of malacofauna, i.e., its structural parameters are approximately even from year to year despite changes in species composition. I use the term "community" for this "relatively constant structure" which in my opinion is the effect of the interspecific relations. These relations should be addressed by autecological and population studies.

10. The similarity of snail communities of some localities

The diagrams of similarity drawn from Baroni-Urbani and Buser's as well as Czekanowski's indices are identical (fig. 52-1). Similar effects are also obtained by grouping according to Canberra metric, squared Euclidian distance, and percentage similarity indices after logarithmic transformation (fig. 52 - 5, 7, and 9). The same indices without logarithmic transformation give quite a different picture. Without it, dendrograms based on the squared Euclidian distance and percentage similarity (fig. 52 - 4, 6, 8) are convergent. The diagram from the Morisita index approximates the diagram from the percentage similarity (fig. 52 - 8, 10). Very different arrangements are obtained from the Mountford and association indices. These extreme differences and the lack of a clear tendency to form groups, made the author ignore arrangements based on these two indices, especially in light of earlier negative opinions (Wolda 1981).

Four communities from localities at high altitudes strongly tend to form a separate group. These are the malacocenoses from Mt Giewont (BF), Przełęcz Tomanowa (GU), Mt Kopa Magury (KP), and Mt Kominiarski Wierch (GX). In seven cases the arrangement within this group is identical (fig. 52 - 1, 4, 5, 7, 9 Baroni-Urbani and Buser's index, Mountford's index). The most similar pair are the communities of Przełęcz Tomanowa (GU) and Mt Kominiarski Wierch (GX). In four arrangements the most similar are the malacocenoses of Mt Giewont (BF) and Przełęcz Tomanowa (GU) (fig. 52 - 2, 3, 8, 10). This result justifies the conclusion that the malacofauna species composition of alpine meadows is distinct from that of other TNP zones.

In seven dendrograms the malacocenoses of Dolina Lejowa (AF), Niżnia Polana Kominiarska (BT) and Dolina Olczyska (AO) are most similar. Around them other snail communities of the forest zone are arranged in a different pattern.

This seems to suggest that apart from the above-mentioned alpine zone group, a second one including malacocenoses from lower localities can be distinguished. Within this group, in some dendrograms there are two sub-groups (fig. 52 - 6, 8, 10). In all of these, there is a greater sub-group formed mainly by the malacocenoses of the Tatra valleys, and another smaller one of malacocenoses from various localities. In those dendrograms where the non-alpine group is not divided into sub-groups, there is a strong similarity among valley communities. The remaining ones join them successively with lower and lower similarities to the valley groups. This points to a strong qualitative polarization of malacocenoses in a hypsometric gradient: once more, factors connected with altitude directly determine the conditions of development for malacofauna in TNP. Attempts at analysing similarity from geobotanical data confirm the separateness of the "alpine" group but do not explain the arrangement of communities by similarity indices better than an altitude criterion.

Fig.52.1

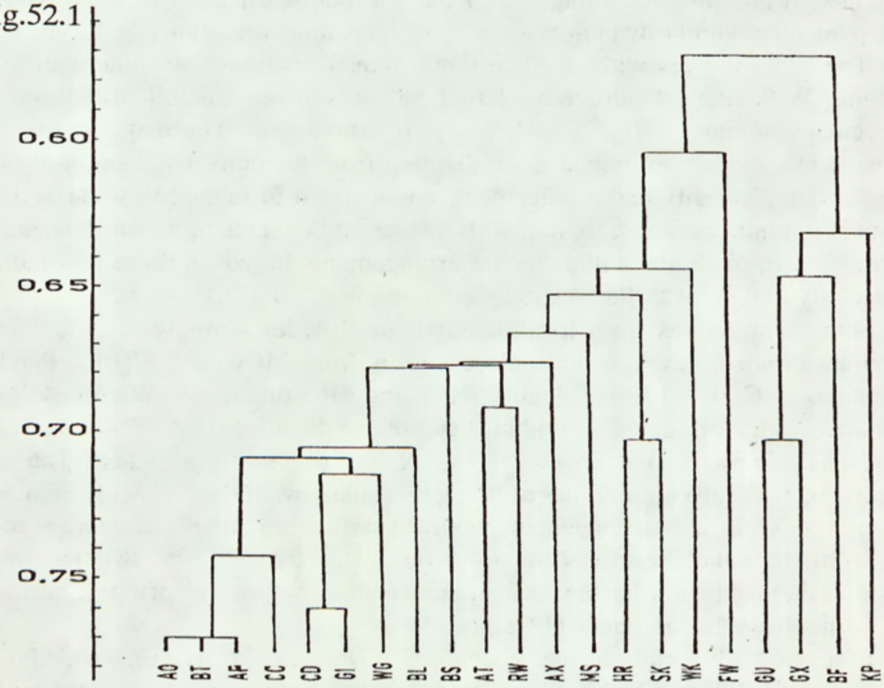


Fig. 52.1-10. Dendrograms of qualitative similarity of selected Tatra malacocenoses based on indices by: 1 - Czekanowski, 2 - Bray and Curtis, 3 - Bray and Curtis after logarithmic transformation, 4 - Canberra metric, 5 - Canberra metric after logarithmic transformation, 6 - Squared Euclidian distance, 7 - Squared Euclidian distance after logarithmic transformation, 8 - Renkonen, 9 - Renkonen after logarithmic transformation, 10 - Morisita

Ryc. 52.1-10. Dendrogramy podobieństwa jakościowego wybranych malakocenoz tatrzańskich według wskaźników: 1 - Czekanowskiego, 2 - Bray'a i Curtisa, 3 - Bray'a i Curtisa zlogarytmowany, 4 - Canberry, 5 - Canberry zlogarytmowany, 6 - kwadrat odległości Euklidesowej, 7 - kwadrat odległości Euklidesowej po zlogarytmowaniu, 8 - Renkonena, 9 - Renkonena po zlogarytmowaniu, 10 - Morisity

Fig.52.2

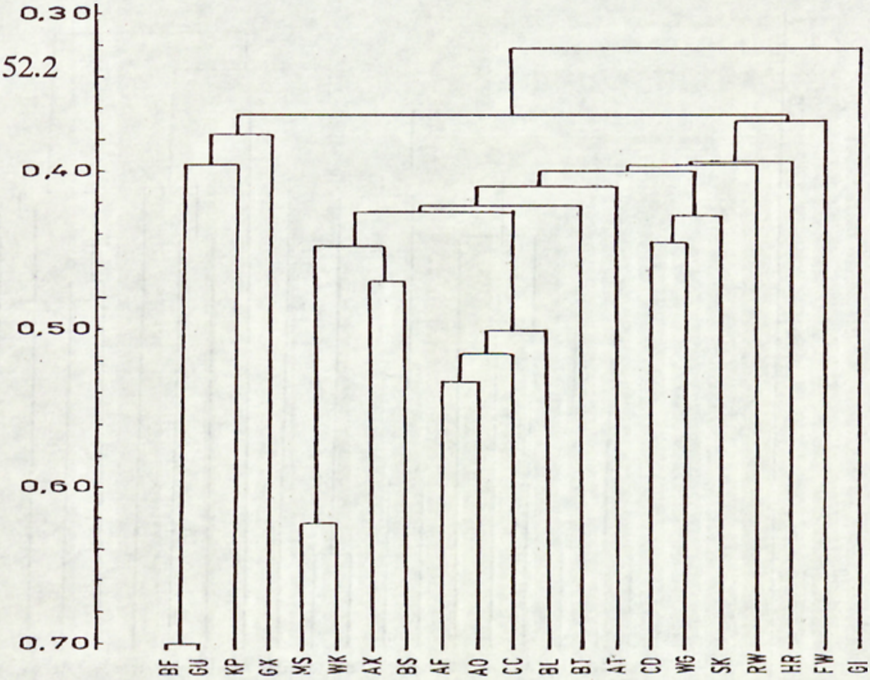


Fig.52.3

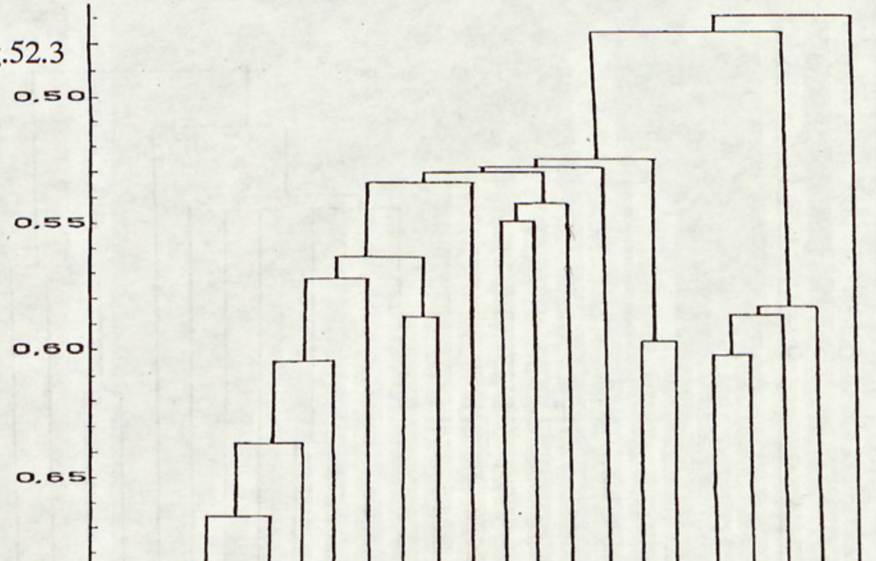


Fig.52.4

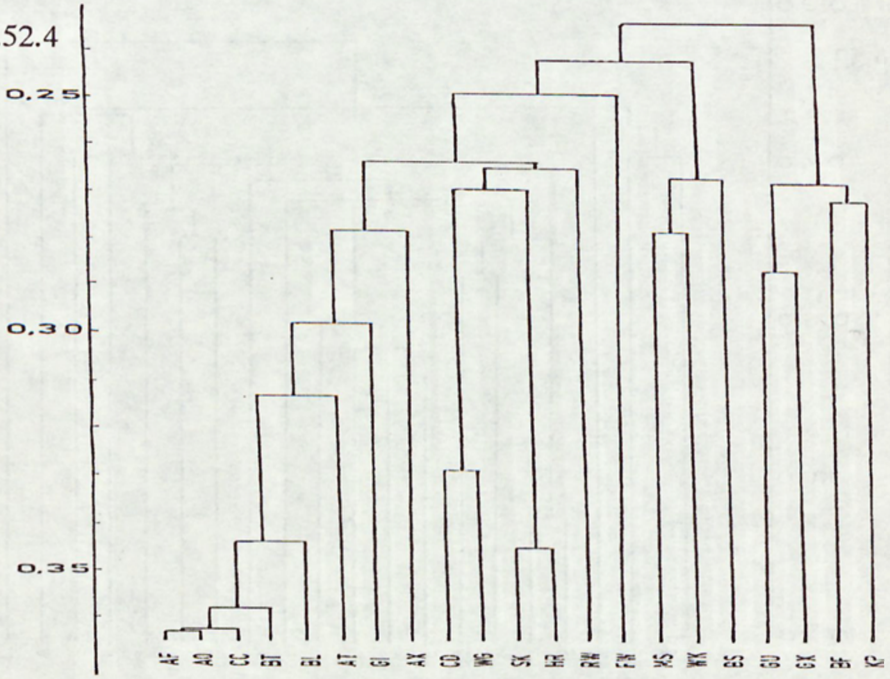


Fig.52.5

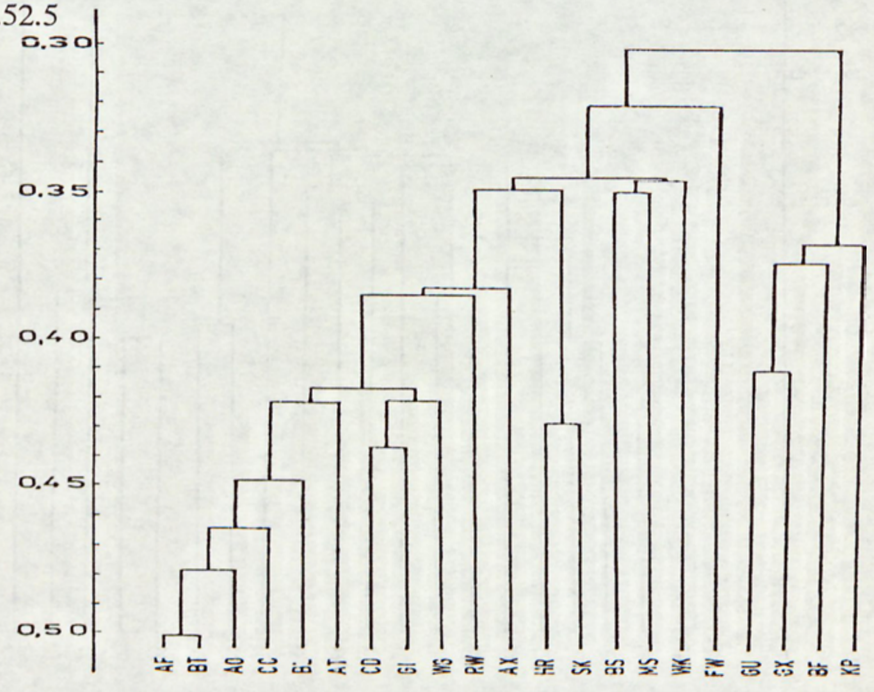


Fig.52.6

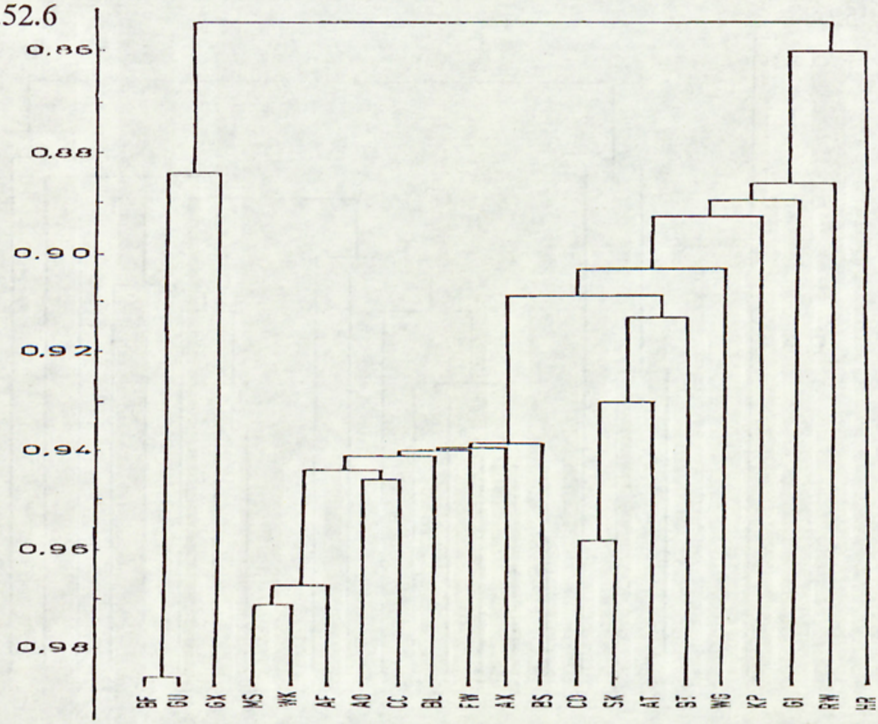


Fig.52.7

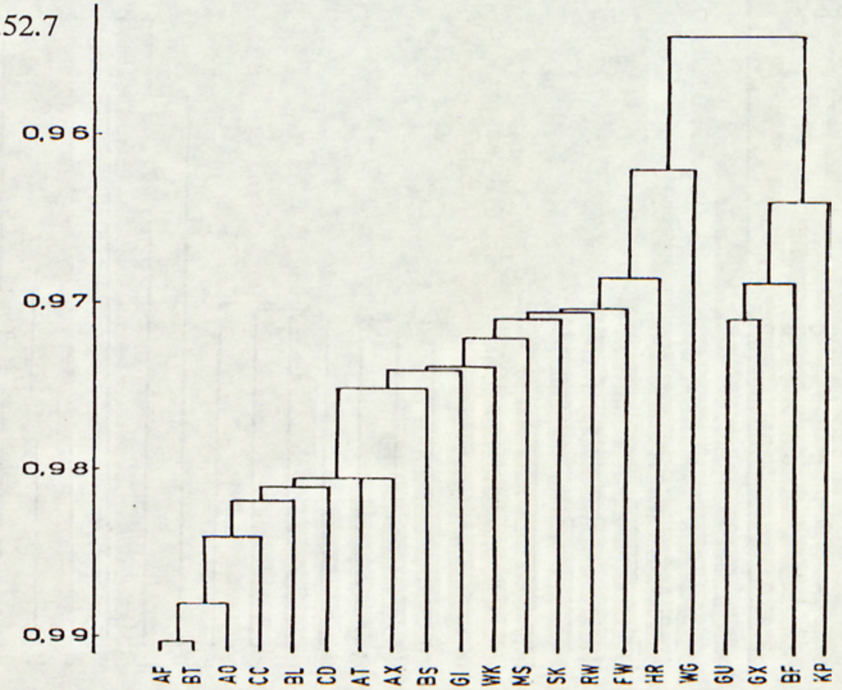


Fig.52.8

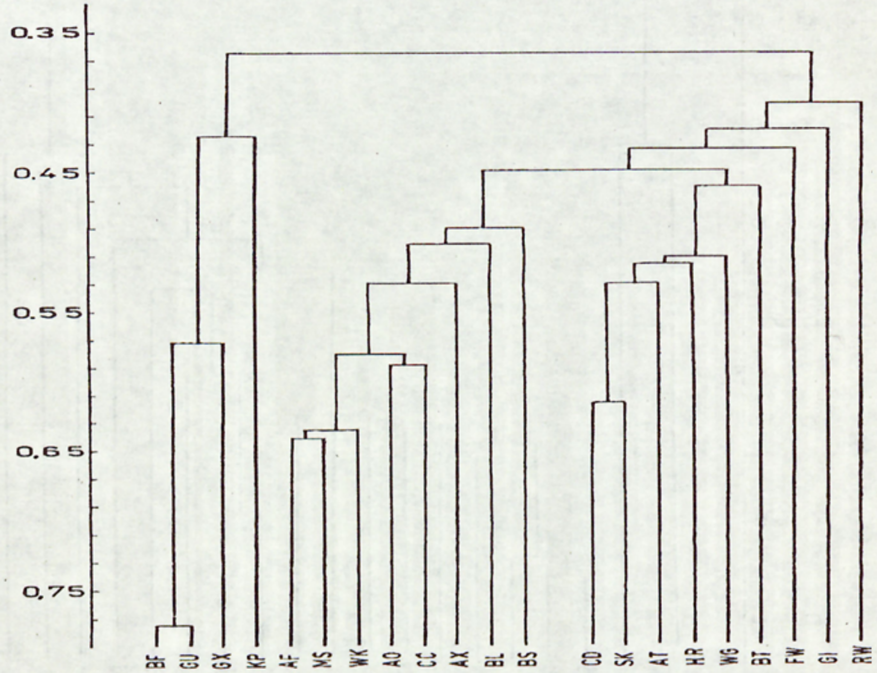


Fig.52.9

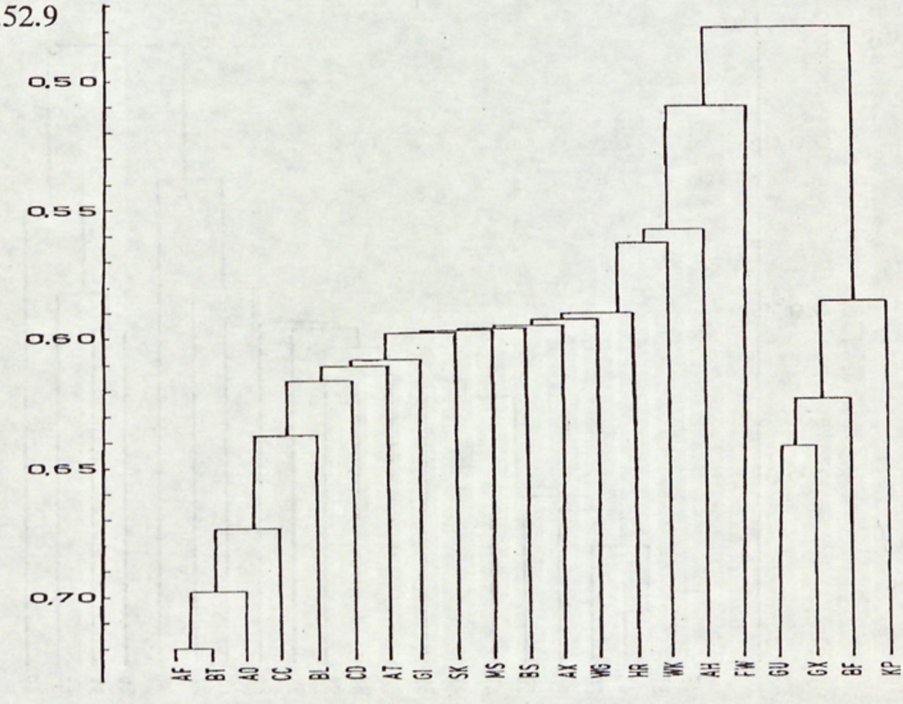
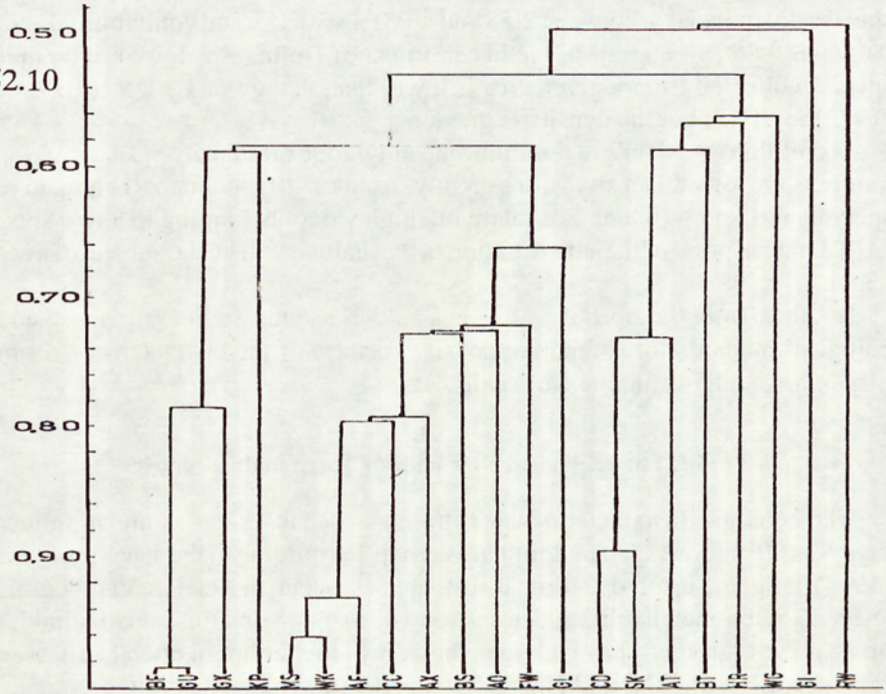


Fig.52.10



11. The density of molluscs in some types of Tatra biotopes

In spite of the growing number of malacological publications, a synthesis of different observations is still lacking, and methodological differences, often only slight, make direct comparisons impossible. In qualitative studies the phenology of molluscs is neglected generally, and this is also true of malacocenological investigations (e.g., D y d u c h 1980, D z i ę c z k o w s k i 1988). But phenology should be taken into account: populations develop at different rates in different species; relative abundance as well as modes of life change. As mentioned earlier (see Material and methods), this paper compares observations from the same phenological period.

In the Tatras it is possible to estimate density, expressed as the number of specimens per 1 sq.m., only in some biotopes. Fairly detailed density estimates were made in *Dentario glandulosae-Fagetum* (D z i ę c z k o w s k i 1972, D y d u c h - F a l n i o w s k a , T o b i s 1989) and in epilithic grasslands in the alpine meadow zone (D y d u c h - F a l n i o w s k a , P o k r y s z k o , in manuscript). The investigations of D y d u c h - F a l n i o w s k a and T o b i s (1989) were concentrated on forest litter using a square technique, so species living on tree trunks or on rocks were ignored. It was found that 1 sq.m. of the Tatra beech forest harbors from 11 to 28 species (SX=5.9), and density varies from 67 to 594 specimens/sq.m. (SX=218.4);

species diversity H' is between 2.58 and 4.08 (SX=0.41), and equitability J' between 0.65 and 0.86 (SX=0.09). In the beech forest of Dolina Spadowca, the number of species collected from a given area is lower than that given by Dzięczkowski (1972) for TNP, but the density is greater.

In epilithic grasslands of the alpine meadow zone the density of snails and species numbers are lower. Density varies greatly, from ca. 20 specimens/1 sq.m. to ca. 400 specimens/1 sq.m. (which is a relatively high value) belonging to a few species (2 - 10). Other aspects of their distribution in that habitat will be the subject of a separate paper.

In other Tatra biotopes it was impossible to use the commonly accepted malacological methods for estimating density because of the character of distribution, dispersion, and low numbers of snails.

12. The ecological character of Tatra malacocenoses

The ecological character of the Tatra malacocenoses varies much. In localities below 1100 m forest species dominate - group 1 according to the scheme of Ložek (1964). Higher, up to 1200 m, forest species occur in smaller numbers. Steppe species, other open habitat species (group 4, 5), and sometimes also humid, shady area species (group 8) have a larger share. Still higher up, in open habitats such as the tops of Nosal (AN) and Niżnia Świstówka (GM) the situation is similar, while in forest habitats *(Piceetum tatricum)* forest species dominate again, up to 1500 m a. s. l.

Malacocenoses occurring above 1600 m a. s. l. are dominated by steppe (group 4) and euryecological species (group 7). Representatives of these two groups prevail up to the alpine zone, to over 2000 m a. s. l. (fig. 53).

The ecological character of snail communities inhabiting Tatra forest glades underlines their strong connection with forests. Forest species (1) are the dominant group here, and next to it are the euryecological species (7). These observations reveal the non-specific character of glade malacocenoses.

13. Zoogeographic elements in the Tatra malacofauna

According to the authors cited in chapter I, the malacofauna of the Polish Tatras includes 32 zoogeographic elements. It is very heterogenous. All these elements were reckoned in 9 categories of ranges; mountain species were treated separately (Table VII). Most species, in general as well as below 1400 m a. s. l. and above 1600 m a. s. l., belong to the European range. Mountain species make up more than half of the taxa above 1600 m a. s. l., and a little more than 45% below 1400 m a. s. l. Carpathian taxa constitute the bulk of the mountain species. It is very significant that localities above 1600 m a. s. l. are rich in typical mountain species (70% of which are Carpathian and Carpathian-Alpine species). These localities are their refuge.

TABLE VII

Zoogeographical elements in malacofauna of TNP

Elementy zoogeograficzne w malakofaunie TPN

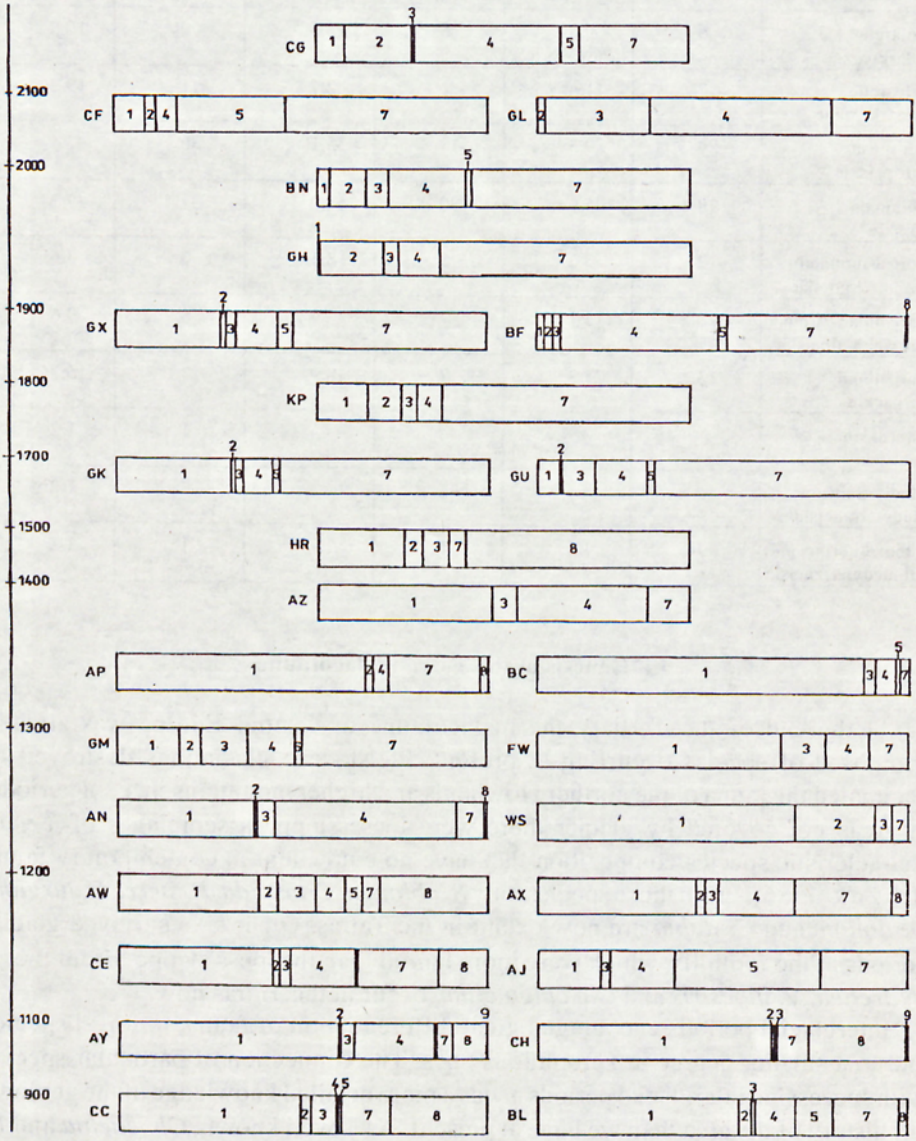
Species Gatunki	below 1400 m do 1400 m		above 1600 m powyżej 1600 m		total ogólnie	
	S	%	S	%	S	%
Holarctic holarktyczne	6	9.8	5	13.5	9	10.8
Palearctic palearktyczne	7	11.4	1	2.7	11	13.2
European europejskie	24	39.3	13	35.1	36	43.4
Mountain górskie	28	45.9	20	54.0	31	37.3
Boreal-mountain borealno-górskie	2	3.2	3	8.1	3	3.6
Carpathian-Alpine karpacko-alpejskie	8	13.1	7	18.9	8	9.6
Carpathian karpackie	13	21.3	7	18.9	13	15.7
Caucasian kaukaski	—	—	—	—	1	1.2
Mediterranean medyterranejskie	—	—	—	—	1	1.2
Submediterranean submedyterranejski	1	1.6	1	2.7	1	1.2

14. Genesis of the Tatra malacofauna

At the end of the Tertiary the malacofauna of Central Europe was already composed of species occurring at present. Pleistocene glaciations destroyed or decimated the fauna of the northern lowlands and higher mountains. In cool periods, in areas not covered by glacier there were loess steppe assemblages of a very characteristic species composition that have no equivalent in contemporary fauna (Ložek 1986). From those species only *S. oblonga, T. hispida, P. sterri, V. turgida, O. dolium* and *C. dubia* are now extant in the Tatras. Other taxa survived glacial periods at the foothills, which were more humid than the loess steppe. From those, *V. arctica, V. alpestris* and *Ch. cingulellum* occur in the Tatras now.

Interglacial periods encouraged great differentiation of fauna, in forest species and to a smaller degree in xerophilous ones. The connection of particular species with successive interglacial periods needs a more detailed knowledge of the geological history of the area than we have at present. As is well known, *Ch. clienta* and *P.*

A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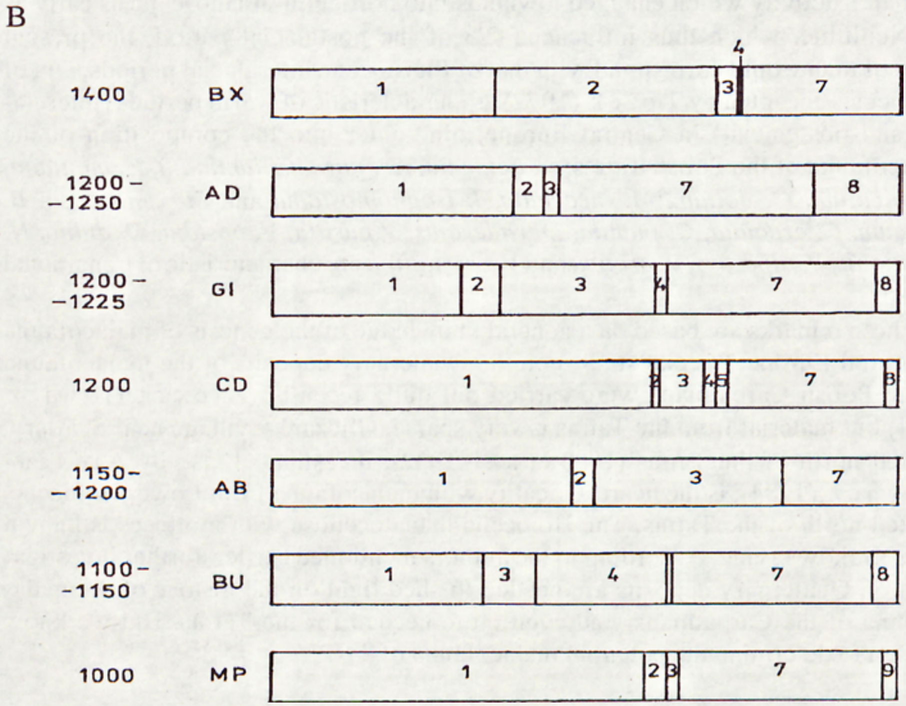

Fig. 53. Ecological character of the Tatra malacocenoses: A - all main types of habitats, B - in-forest glades. Ecological groups after L o ż e k (1964): 1 - forest species, very rare in other biotopes; 2 - forest species which are common in gardens and parks as well; 3 - forest and shade-loving species typical of very wet habitats; 4 - steppe species; 5 - open habitat snails; 6 - xerotermophilous snails; 7 - euryecological snails; 8 - species of wet (but not very wet) habitats; 9 - snails of swamps and very wet habitats; denotations of localities as in Appendix I

Ryc. 53. Charakter ekologiczny malakocenoz tatrzańskich: A - wszystkich podstawowych typów siedlisk, B - polan śródreglowych. Grupy ekologiczne wg L o ż k a (1964): 1 - gatunki leśne, bardzo rzadko przechodzące do innych biotopów; 2 - gatunki występujące głównie w lasach ale pospolite również w parkach, ogrodach itp.; 3 - gatunki leśne i cieniolubne, typowe dla siedlisk bardzo wilgotnych; 4 - gatunki stepowe; 5 - ślimaki środowiska otwartego, związane z siedliskami o różnej wilgotności; 6 - gatunki typowe dla suchych, ciepłych biotopów kserotermicznych; 7 - ślimaki euryekologiczne; 8 - gatunki charakteryzujące stanowiska wilgotne, ale nie podmokłe, o różnym stopniu zacienienia; 9 - ślimaki siedlisk bardzo wilgotnych, bagiennych, podmokłych, oznaczenia literowe stanowisk jak w Appendix I

rupestris are thermophilous species that survived cool periods in periglacial areas. Their refuges were most likely very small and up to now they have not been discovered. Nor is there any evidence concerning forest species, except *D. ruderatus, M. vicina* and *Ch. faustinum*. In the opinion of L o ż e k (1986), were it not for man's activity which changed lowlands into horticultural landscape as early as the Neolithic, which thus influenced 2/3 of the postglacial period, the present malacofauna would correspond with that of Pleistocene interglacial periods. Out of ten species accepted by Ložek (1972) as characteristic of warm periods (interglacial and postglacial) in Central Europe, nine enter into the composition of the malacofauna of the Polish Tatras: *A. aculeata, Ae. pura, C. laminata, E. montana, M. plicatula, O. dolium, M. incarnata, I. isognomostoma* and *M. ventricosa*. *B. fruticum, C. cruciata, C. pumila, D. ruderatus, V.pusilla, V. costata, C. dubia, N. hammonis, V. alpestris, V. arctica* and *V. crystallina* are characteristic of transitional periods.

These remarks are based on a general knowledge of the genesis of malacofauna in Central Europe. Special studies on the Quaternary deposits of the malacofauna of the Polish Carpathians were carried out quite recently (Alexandrowicz 1984) but material from the Tatras is very sparse. Gliczarów village near Szaflary, located north of the Tatras (Urbański 1932), investigated also by Alexandrowicz (1984), is the nearest locality with malacofauna from Lower Holocene, located north of the Tatras. The Holocene thanatocenose with molluscs is known from Kraków ravine. According to the authors mentioned earlier, further investigations on Quaternary deposits are needed to shed light on the history of the malacofauna of the Carpathians, and even more needed for the Tatras. But we know enough to determine the potential malacofauna of TNP.

VI. The potential and present malacofauna of the Polish Tatras

Knowing the geological history of the area and its neighborhood, and in light of geobotany, one can maintain that the malacofauna of TNP corresponds with that of the interglacial and postglacial periods. The presence of the taxa we listed confirms this: they include 90% of the species characteristic of warm periods and over 70% from transitional periods. The vertical differentiation of climatic and geobotanical conditions results in a natural differentiation of the malacofauna into communities connected with open habitats above the timber line (epilithic grasslands and bare rocks) and forest communities. Above 1600 m a.s.l., the malacofauna of these biotopes has preserved its autonomy: mountain elements dominate (Carpathian, or more precisely Carpathian-Alpine - see Table VII). Forest communities include those characteristic of *Dentario glandulosae-Fagetum, Abieti-Piceetum* and *Piceetum tatricum.* It is not possible to reconstruct the original composition of the malacocenoses inhabiting *Abieti-Piceetum* and *Piceetum tatricum*. Beech forests in the Dolina Spadowca, D. Białego, and some other valleys are refuges for the original malacofauna of the Tatra lower mountain forest zone (Dzięczkowski 1972; Dyduch-Falniowska 1988; Dyduch-Falniowska, Tobis 1989).

The Tatra habitats are much more diverse now than previously - physically, chemically and geobotanically - mainly as a consequence of man's activity. Below the timber line we found such diverse biotopes as in-forest glades. The forests themselves also have undergone changes. On in-forest glades, utilized in different ways and to varying degrees, communities new to the Tatras have developed (Dyduch-Falniowska, Fyda 1986; Dyduch-Falniowska 1988). The transformation of forest communities went in a direction very disadvantageous to snails. The replacement of beech forests in the lower mountain forest zone by spruce monocultures caused a considerable contraction of habitats available for snails. The degradation of forest litter under the canopy of dense spruce stands (Fabijanowski 1962) resulted in the elimination of the majority of snail species (too low humidity due to increased flow of water, and acidification of habitat) (Dyduch 1980; Dyduch-Falniowska, Tobis 1989). One may suppose that these dense spruce stands sometimes constitute ecological barriers as well. To be sure, the malacocenoses of particular valleys are more similar to each other than to other kinds of habitats, but even neighboring valleys often differ in some measure; one only needs to look at the position of snail communities inhabiting the Dolina Strążyska (AT) and D. Ku Dziurze (CC) valleys (fig. 52).

VII. Natural and human pressure in the formation of the present malacofauna of the Polish Tatras

Protected mountain areas face two kinds of pressure: (1) natural habitat effects resulting from the gradual change in physical and chemical conditions as altitude increases, and (2) man's activity. Vegetative changes, both natural and human caused, are important for animal communities. To recognize the effect of human pressure, it helps to know the effects of changes in natural conditions. For this purpose the author made a description of changes in malacocenoses in a hipsometric gradient, and investigated the decrease in the number of species and species diversity in malacocenoses. Attention was given to changes in their ecological character, and to qualitative and qualitative-quantitative similarity.

For all examined malacocenoses, the regression of the number of species and species diversity of malacocenoses in a hipsometric gradient is expressed by the following equations: $y = 39.45 - 0.014\,x$, ($r = -0.49$) for number of species, and $y = 4.59 - 1.06543\,E - 3x$, ($r = -0.43$) for species diversity (fig. 54). The regression and correlation coefficients representing this reduction will be determined as factual. The same equations for optimum, or more precisely potential (original), habitats for particular altitudinal zones (such as *Dentario gladulosae-Fagetum* for the lower mountain forest zone) are as follows: $y=51.68-0.02x$, ($r=-0.75$) for the number of species and $y=5.48-1.53095E-3x$, ($r=-0.80$) for species diversity (fig. 55). Their correlation and regression coefficients will be labeled expected or optimum.

The author suggests that the difference between expected and actual indices are a measure of the effects of man's activity. It can be expressed by a proportion of the values of the correlation and regression coefficients.

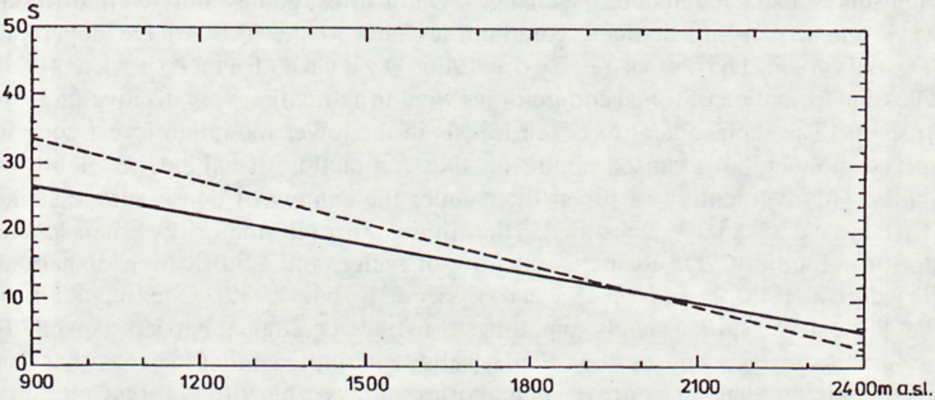

Fig. 54. Regression of the species number (S) of all malacocenoses of TNP in relation to altitude

Ryc. 54. Regresja liczby gatunków S wszystkich malakocenoz TPN w zależności od wysokości npm

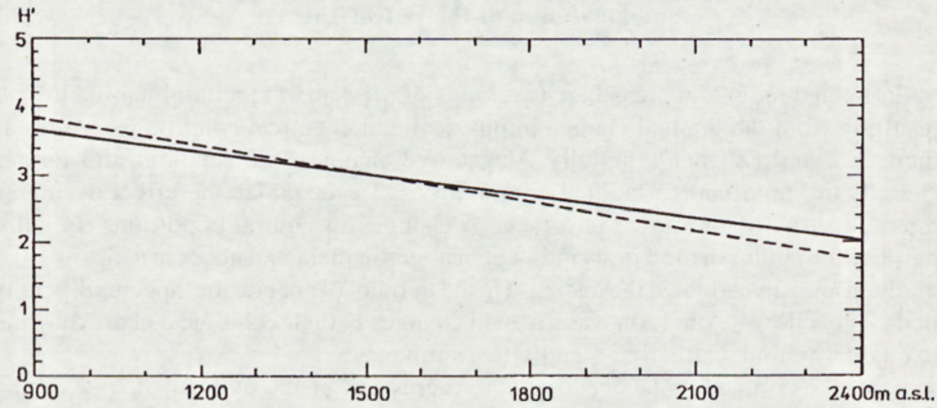

Fig. 55. Regression of species diversity (H') of malacocenoses in optimum biotopes of TNP in relation to altitude

Ryc. 55. Regresja różnorodności H' malakocenoz w siedliskach optymalnych w zależności od wysokości npm

The equation $y_f = a_f + b_f x$ describes the factual regression at the correlation coefficient r_f, while the equation $y_o = a_o + b_o x$ shows the regression in optimum conditions at correlation coefficient r_o. The measure of transformation (D) is the ratio of correlation and regression coefficients:

$$D_b = \frac{b_f}{b_o} \qquad D_r = \frac{r_f}{r_o}$$

These coefficients may be calculated for different parameters of malacocenoses, e.g., number of species, species diversity, density, etc. In the present paper calculations were limited to the two first parameters. The indices of transformation based on species number are $D_{bS} = 0.7$, $D_{rS} = 0.65$, and those based on species diversity: $D_{bH} = 0.7$, $D_{rH} = 0.54$. It results from this that the deformation of the composition of Tatra malacocenoses and of their structure, more precisely of the relative abundance of different species, is similar. The Tatra malacofauna should be examined more closely, e.g., in different transects. This might enable the best preserved and the most endangered parts to be identified. Perhaps this method could be used for the planning of the restoration of snail habitats.

As altitude changes the ecological character of the malacofauna changes as well (fig. 56). In localities at lower altitudes 40 - 50% of the taxa are according to L o ż e k ' s classification (1964) forest species which only rarely occur in other biotopes. Their share in malacocenoses inhabiting the tops of the Tatras is between one and a few percent. The percentage of steppe species varies greatly: in some

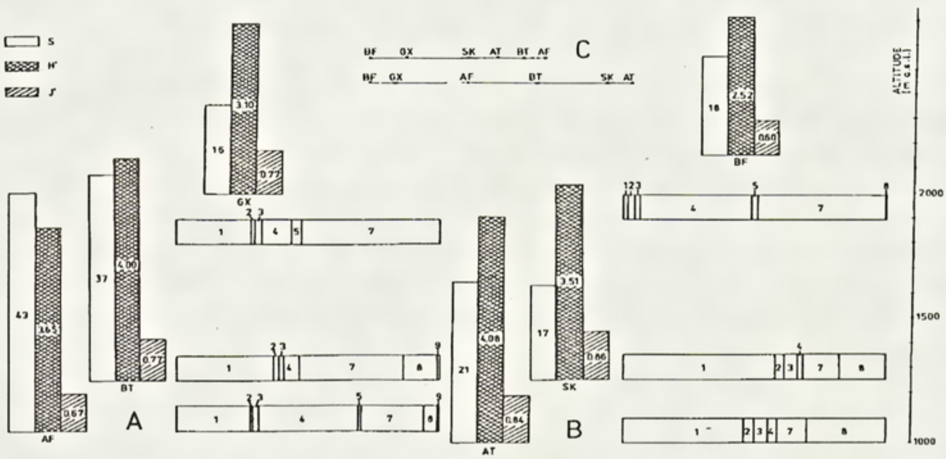

Fig. 56. Some effects of pressure of natural factors in chosen localities of TNP, illustrated by two series: A - Dolina Lejowa valley (AF), Niżnia Polana Kominiarska glade (BT), Mt Kominiarski Wierch (GX) and B - Dolina Strążyska valley (AT), Siklawica (SK), Mt Giewont (BF), and C - taxonomic distances of communities according to: B a r o n i (above) and M o r i s i t a (lower) indices. S - number of species, H' - species diversity, J' - eveness, 1 - 9 ecological groups by L o ż e k 1964

Ryc. 56. Niektóre skutki presji warunków naturalnych w wybranych siedliskach TPN na przykładzie dwóch serii: A - Dolina Lejowa (AF), Niżnia Polana Kominiarska (BT), Kominiarski Wierch (GX) i B - Dolina Strążyska (AT), Siklawica (SK), Giewont (BF) oraz C - odległości taksonomicznej zespołów wg indeksu B a r o n i e g o (powyżej) i M o r i s i t y (poniżej). S - liczba gatunków w zespole, H' - różnorodność gatunkowa, J' - równomierność, 1-9 - grupy ekologiczne wg L o ż k a (1964) series it decreases with increasing altitude; in others it increases. The problem of semi-natural open habitats (glades) arises once more. The proportion of euryecological species grows markedly with altitude, sometimes up to 50%. Examples (fig. 56) illustrate this process in three stages. The Niżna Polana Kominiarska glade, though it is a semi-natural habitat, was placed in the scheme purposely. The snail community which has developed there has characteristics similar to those of natural habitats in the Tatras (Dyduch-Falniowska, Fyda 1986; Dyduch-Falniowska 1988).

Ecological changes are in part connected with the varying composition of species, i. e., qualitative zonation of the malacofauna. Qualitative similarity between localities in the alpine zone is greater than the similarity between each of them and the malacocenoses of lower altitudes. Analysis of qualitative and quantitative indices confirms this conclusion; only the arrangement of the most similar pairs of malacocenoses is slightly different (fig. 56). In the extreme conditions of the alpine zone, the pressure of physical and chemical factors apparently has a greater effect on the development of malacocenoses than on the malacofauna of neighboring localities at lower altitudes.

VIII. Changes in the Tatra malacofauna over the last hundred years

Until now, Kotula (1884) has been a basic source of information on Tatra molluscs. Despite the lapse of over 100 years, the results of his studies remain valuable thanks to his precise presentation.

Of the two species of *Aciculidae* recorded from the Polish Tatras during the present study, only *A. polita* was mentioned by Kotula (1884) as very rare. In contemporary material this species is found rarely but regularly. *A. parcelineata* is much rarer. Probably the difference stems from the fact that in the present studies the malacofauna of forest litter was examined much more thoroughly than in the research by Kotula (1884).

The family *Ellobiidae* is now represented by two species, of which only *C. minimum* was mentioned by Kotula (1884). The description of habitats he gave suggests that he collected *C. minimum* outside the Park, at lower altitudes. It is difficult to judge whether these were specimens of *C. tridentatum*, as Berger (1963) and Riedel (1988) seem to suggest. This last species is now really much more frequent than *C. minimum*, which appears only rarely in the lowest sections of Tatra valleys.

Succineidae, occasionally found in recent years, are a new and most likely ephemeral component of the Tatra malacofauna. This addition to the list of Tatra species points to the undesirable trend of changes.

Of the family *Vertiginidae*, Kotula (1884) mentioned *P. inornata* and *P. edentula var. Gredleri.* To judge by his description of the appearance of these species the first is *C. edentula* and the second *C. columella.* But the distribution of the species given by this author raises doubts. At present *C. columella* [*C. edentula var.*

Gredleri according to K o t u l a (1884)] occurs in the Czerwone Wierchy range and on other summits of the highest Tatras above 1800 m a. s. l., while *C. edentula (P. inornata*) occurs at lower altitudes. K o t u l a ' s observations do not show so distinct separation of the ranges of these species. Moreover, they indicate that *P. edentula var. Gredleri (C. columella)* reaches the upper limit of the dwarf mountain pine zone, and *P. inornata (C. edentula)* up to "the land of crags," which is inconsistent with their present distribution. *V. arctica* occurs together with *C. columella* in the top parts of the Tatras. K o t u l a (1884) mentioned this species mainly from the Slovakian Tatras. It is difficult to recognize the location of *O. dolium, Ch. clienta, P. sterii,* and *A. bielzi* in the Polish Tatras. Certainly these species have only a few localities there. According to K o t u l a (1884) they were rare, too.

As in the last century, *Valloniidae* occur now mainly at lower altitudes, and in the area of the TNP only occassionally. Nor has the occurrence of *Enidae* and *Endodontidae* changed radically. It is striking that K o t u l a (1884) mentioned *P. pygmaeum* from but one locality (in the Dolina za Bramką valley, most likely). In the author's material this species was found in small numbers but regularly (23 localities). It is possible that in K o t u l a ' s investigations forest litter was examined only superficially, so that he underestimated the frequency of *P. pygmaeum* as well as that of other species connected with litter.

From *Arionidae* only the occurrence of *A. subfuscus (A. olivaceus)* is beyond doubt. It is still one of the commonest snails found in all Tatra biotopes. Behind the name *A. hortensis* in K o t u l a ' s paper (1884) are most likely *A. silvaticus* and *A. fasciatus.* The range of *A. hortensis* is limited to the Zakopane Basin.

As to *Zonitidae*, differences concern mainly taxonomy. The records of *V. contracta* in recent years need confirmation. It is striking that K o t u l a regarded *Ae. nitens* as the commonest species of the Tatras up to the dwarf mountain pine zone. Now it is found regularly but only in small numbers or rarely. No doubt the abundance of this species has considerably decreased.

The family *Limacidae* in K o t u l a ' s material was represented by four species. In the author material there are six, or nine if the Zakopane Basin is included. A more important difference is the presence of *L. maximus,* although only in the Zakopane Basin, and the occasional occurrence of *L. cinereo-niger*, whose distribution in K o t u l a ' s times was comparable with that of *A. subfuscus.* Three species of *Lehmannia* that now occur in the Tatras were most likely identified by K o t u l a (1884) as *L. marginata.* The locality of *L. tenellus* given by the author lies outside TNP. Now as then, this species is noted neither from the area of the Park nor from the Zakopane Basin. It was recorded only from Gubałówka, on Walowa Góra Mt. (its record in the paper by D y d u c h - F a l n i o w s k a and F y d a (1986) was incorrect). The ridge of Gubałówka may be the limit of the range of the species in this region.

D. agreste and *D. reticulatum* are species which at the end of the last century were treated as one taxon. Their distribution has not changed considerably since those times.

B. pallens recently has been of special interest to European malacologists because of its expansion, observed all over Europe during the last forty years. There is much to be said about the synanthropic character of this expansion. Its occurrence in the Tatras does not fully confirm it. In the Zakopane Basin, as in many other regions of Europe, the species is found in rubbish heaps and in town parks. In TNP it was collected in the Dolina Strążyska, D. Spadowca and D. Białego valleys, where it lives in patches of *Dentario glandulosae-Fagetum*, which are enclaves of original Tatra vegetation.

As to *Clausiliidae* the absence of *C. filograna* in contemporary material requires comment. In the Polish Tatras K o t u l a (1884) found only one specimen of this species in the Dolina Strążyska valley, its remaining localities were in the Slovakian Tatras. Snails of the genus *Cochlodina*, reported to be common in the last century, still occur abundantly. *C. orthostoma* was previously much commoner than *C. laminata*. Now the reverse holds. The author's material includes *C. cruciata* and *L. plicata* not mentioned by K o t u l a (1884) from the Polish Tatras. *L. plicata* was found only in the Zakopane Basin. The *C. fallax* and *C. elata* recorded by K o t u l a (1884) were probably *V. turgida*.

The differences between K o t u l a 's results and the author's seem connected with the fact that the author included litter malacofauna more completely. This concerns mainly *Aciculidae, Carychium,* and *P. pygmaeum.* But most differences are due to environmental changes. It is difficult to supply documentary evidence for biotic and abiotic changes, because the old descriptions do not provide data amenable to quantitative analysis.

A comparison of K o t u l a s ' s descriptions of snail localities (1884) with their present distribution leads to vegetative changes as a cause of the differences in species composition between contemporary and former malacofauna. The replacement of *Dentario glandulosae-Fagetum* by spruce monocultures over large areas had catastrophic consequences for the malacofauna. Forest species occur now only in the litter of small patches of *Dentario glandulosae-Fagetum,* on the edges of in-forest glades, on isolated rocky walls in spruce forests, in gullies, near streams, in areas cleared by wind, etc. The large, dense complexes of spruce forests are almost deprived of litter which could be a refuge for molluscs. Moreover, the increased flow of rain water makes the retention of adequate humidity on slopes impossible. The increased acidity of soils eliminates many snail species, as was brought out in observations from the Dolina Spadowca valley (D y d u c h - F a l n i o w s k a, T o b i s 1989). Only the most resistant species such as *A. subfuscus, D. agreste,* and *D. reticulatum* can live there. The increased acidity of soils can be explained not only by changes in the plant cover. For a few years a decrease in the pH of rain-water and soils as well as a very high lead content in soils and in the forest herb layer (particulary in mosses) has been recorded. Lead levels may be compared with the concentrations near intersections in the center of Cracow (M i r e k 1990).

The effects of very low pH and high concentrations of lead are obvious even though we do not have enough information, especially about lead. We need only compare the present species composition and distribution of species with those of 100 years ago. Mosses previously considered habitats abounding in snails are now almost depleted of them, and these plants are particularly able to accumulate heavy metals.

K o t u l a (1884) includes no quantitative data. However, he gives the impression that in those days snails were much more numerous in the Polish Tatras, that it was much easier to collect them, so the detailed sorting of litter seemed unnecessary. K o t u l a mentioned that he identified more than 10 thousand specimens of *Clausiliidae* (not only from the Tatras). Obviously, he was accustomed to working on abundant material. This impression of the abundance of malacofauna was confirmed in the notes of some naturalists from 30 - 50 years ago. Nowadays the collection of sufficient material is very time-consuming. Of course, these kinds of information are not unequivocal and precise, but they must be considered because the Tatra malacofauna may lose its natural value if observed tendency continue.

IX. The malacofauna of the Polish Tatras in terms of Tatra malacofauna as a whole

In TNP, i.e., in the West Tatras and in part of the High Tatras as well as in the park buffer zone, 81 snail species were found, including 10 recorded only from the Zakopane Basin. According to H u d e c and B r a b e n e c (1961) the High Tatras harbor 58 taxa, the Belanské and Liptovské Tatry mountains, 74 and 79 respectively. Among the species given for TNP, 11 were not reported from the Slovakian Tatras by H u d e c and B r a b e n e c (1961) and 13 were not reported by K r o u p o v a (1986) from Liptov. K r o u p o v a noted nearly 20 species of terrestrial snails not found in TNP, and H u d e c and B r a b e n e c about 10. The High Tatras are certainly poorest in snails, particularly the Polish part; other parts are similar in their richness of species. Species occur with different frequencies in different ranges. The differences and similarities between the malacocenoses of all Tatra ranges needs synchronous comparative studies. Now, we know only that marked differences exist.

X. Causes of qualitative and quantitative changes in the Tatra malacofauna; threats and perspectives for protection

TNP includes areas of not very rich but interesting malacofauna. The number of species persuades about the role of this Park in the preservation of molluscs. The number of species reported by K o t u l a (1884) from areas now included in TNP was smaller then nowadays. However, this addition to the list of species is only formal. This results from many causes, mostly from the qualitative degradation of habitats and of the malacofauna.

The distribution and abundance of snails, especially of rare species, has changed drastically. The decrease in density can not be directly estimated, but a comparison between previous and present localities in the lower mountain zone indicates that average densities have fallen many times. This is accompanied by decreases in populations of species previously abundant, such as *Ch. clienta* or *M. ventricosa*. Snails are disappearing from mosses or other patches of epilithic vegetation, which in older literature were considered abundant microhabitats.

Changes in habitat conditions important for snails have different causes. Some of them are external: rainwater, and in turn the soil, have become strongly acidified in TNP. This problem is still unsolved. The acidification results in the impoverishment of snail communities living on open rocky walls, even limestone, as well as on epilithic grasslands. In forests (mainly in spruce forests) the acidification is even stronger due to the spruce monoculture in certain areas, with completely degraded litter. It is particularly acid in wet depressions, because the flow of rainwater from slopes in spruce forests is much quicker than in beech forests with similar topography. Windfalls, occurring after the destruction of spruce forests by Tatra foehn, often favour the development of malacocenoses (e.g. in Dolina Roztoki). So apart from acid rain a danger results from forest plantations, which also increase the acidity of habitat and thus threaten to eliminate snails.

In-forest glades, as habitats of a human origin, give rise to much controversy. With the molluscs that live there the situation is also unclear. In some glades (Polana Kalatówki, Polana Chochołowska) there is a qualitative and quantitative degradation of their malacofauna, but in others (Polana Rusinowa, Niżnia Polana Kominiarska), in spite of their utilization for pasture, there are snail communities similar to communities living in natural habitats. In the first case, the snail species composition of the glade is not similar to that of adjacent areas, and at the same time there is a high synanthropization of the malacofauna. The removal of sheep from glades could be expected to favor the regeneration of communities. This applies to Polana Kondratowa, for example. A halt to grazing would begin the succession: the gradual overgrowth of glades. In the short term this may benefit the snails. The best solution would be for the glades to be mown or grazed by sheep every few years for 1-3 seasons, to maintain the glades and reduce the negative effects of pasturage. Too intense grazing is dangerous for malacofauna, but moderate grazing stimulates the creation of new (for the area) malacocenoses. Certain glades together with semi-open habitats such as gullies, rocky walls, etc. may constitute refuges for molluscs that had to leave the dense stands of spruce. This is true of the environs of Niżnia Polana Kominiarska.

One controversial problem is the effect of tourist traffic on the nature of the Park. It can influence the malacofauna indirectly, through changes in vegetation. A gradual increase in the number and abundance of synanthropic plants causes the expansion of euryecologic, cosmopolitan species such as *C. lubrica, V. pellucida,* and *A. subfuscus* (Dyduch-Falniowska, Fyda 1986). Sometimes lowland species such as *T. hispida* penetrate the Tatras. Often it is difficult to discriminate between the effects of grazing, tourist traffic and other consequences of man's activity.

XI. Conclusions

Malacological research in the Polish Tatras was the first faunal and ecological study there since K o t u l a ' s research completed 100 years ago (1884). It provides a means to evaluate changes in the malacofauna of the national park as well as to indicate threats and suggests methods of counteracting them.

Species

The malacofauna of the investigated area includes 81 species, of which 10 occur only in the Zakopane Basin. The distribution of the majority of species is shown on maps (figs 2 - 39).

There are five species whose shares in the malacofauna exceed 5%. These are: *P. rupestris, C. dubia, V. diaphana, C. edentula,* and *C. columella.* Among them only *C. edentula*, a holarctic species, has a large continuous range. The remaining species have much smaller ranges, continuous or disrupted. TNP is an important refuge for these species and their presence contributes to the area's high natural value.

Most of the taxa occurring as extremely subrecedent and accidental components of the Tatra malacocenoses (dominance < 0.1%, constancy - mostly < 10%) are non-specific to this area in terms of zoogeography and ecology. Unfortunately, the occurrence of *Ch. rossmaessleri, M. ventricosa, B. cana, A. parcelineta, O.depressus,* and *C. holosericum* is of a similar character. These are species whose ranges are generally small and often limited to the Carpathians and adjacent areas. Moreover, they are specialized taxa preferring habitats especially susceptible to human-caused changes. *L. macroflagellata* and *L. nyctelia* like previously mentioned species are very rare and they add to the natural value of the Tatras. The biology of these species is poorly known and it is difficult if at all possible to protect them actively. Nevertheless, attempts must be made soon.

Population and communities

The occurrence of particular snail species is correlated to various degrees, and a binary analysis gives results different from a non-binary one. Binary analysis points up groups of species whose co-occurrence is connected with quality of habitats (there are no direct connections between their populations); non binary analysis points to qualitative-quantitative dependencies. Numbers of specimens are correlated. The first kind of inter-specific relations may be illustrated by the examples of *C. cruciata* and *C. laminata* or *V. diaphana, V. turgida* and *T. unidentata.* An example of qualitative-qualitative dependence is *V. diaphana* and *Ae. pura.*

The co-occurrence of species is connected with the problem of species diversity in molluscan communities. Species diversity ranges from 0.54 to 4.23 in the Tatra malacocenoses (according to the Shannon-Weavera formula). The number of species also varies greatly in these communities, which results from the differentiation of habitats.

Zonation

As altitude increases the number of taxa as well as the indices of diversity and equitability decrease markedly (figs. 47, 48). But they do not decrease in direct proportion because of the local variation of habitat conditions at given altitudes. For example, 1150 m a.s.l. corresponds with several values for species number, from 6 to 28. In spite of this, the Single Linkage (or Nearest Neighbor) Method for species diversity H', species equitability J' and species number S shows that most of the malacocenoses up to 1500 m a.s.l. are structurally similar and belong to group including 31 (67%) of 46 localities analysed. The malacocenoses of beech forests in the Dolina Olczyska and Dolina Białego valleys form separate group, with the greatest number of species and the highest index of species diversity. Other localities form pairs or constitute separate categories according to the above grouping (fig. 49).

In spite of this structural similarity of communities their species composition varies greatly, due in part to the fact that species in the Tatras reach the upper limit of their ranges at different altitudes. Above 2000 m a.sl. 21 taxa were found; 4 species reach their upper limit between 1700 and 2000 m a.s.l., 19 between 1400 and 1700 m, and 17 between 1100 and 1400 m.

The differentiation of ranges results in the vertical differentiation of species composition in malacocenoses. The author examined the qualitative similarity of malacocenoses in terms of these altitude intervals. Qualitative changes occur parallelly to altitude changes: the malacofauna changes gradually, and above 2000 m a.s.l. it has the greatest autonomy, i.e., it is least similar to those occurring below (Table I, fig. 50).

The ecological character of malacocenoses also changes with altitude. Forest species dominate up to 1500 m a.s.l. Above 1600 m a.s.l., steppe and euryecological ones prevail (fig. 53).

We can also use zonation to discuss the zoogeographical character of snails in TNP. Most of the 32 zoogeographical elements have European ranges. Above 1600 m a.s.l. mountain taxa constitute more than 50%, and below 1400 m a.s.l. slightly more than 45%. Among mountain taxa, Carpathian species prevail. It is important that Tatra localities above 1600 m a.s.l. harbor typical mountain fauna, including mainly Carpathian and Carpathian-Alpine species (70%). These localities are refuge for them.

Potential and present malacofauna

The potential malacofauna of TNP is characteristic of interglacial and postglacial periods. Within this fauna forest communities and, above the timber line, communities of open habitats (assemblages of epilithic grasslands and bare rocks) naturally developed. Zoogeographical analysis of species above 1600 m a.s.l. shows that the malacofauna of these habitats has preserved its autonomy. It is dominated by mountain, Carpathian (more precisely Carpathian-Alpine) taxa (Table VII). Forest associations include beech (*Dentario glandulosae-Fagetum*) and spruce forests (*Abieti-Piceetum, Piceetum tatricum*). Nowadays it is impossible to reconstruct the original composition of malacocenoses typical of *Abieti-Piceetum* and *Piceetum tatricum.* But the beech forests in Dolina Białego and D. Strążyska, and in some other valleys are now refuges for malacofauna typical of the Tatra lower mountain forest zone.

At present the Tatra habitats are much more differentiated than previously, due mainly to man's activity. Below the timber line there are habitats such as in-forest glades, with much different physical, chemical and geobotanical conditions, and the forests themselves have changed greatly. Glades, used by man in different ways and to different degrees, have been inhabited by molluscs that form new assemblages there.

Changes that have occurred in forest associations are very unfavourable for snails. The replacement of beechwood in the lower mountain zone by spruce monoculture caused a considerable shrinkage of the habitat available for snails. The degradation of forest litter connected with the presence of dense spruce stands (Fabijanowski 1962) is tantamount to the elimination of the majority of molluscan species, because of too low humidity (increased flow of water) and too high acidity (Dyduch 1980; Dyduch-Falniowska, Tobis 1989). These spruce monocultures may constitute barriers to isolated snail communities inhabiting rocky walls, on Mt Sarnia Skała and Mt Nosal, for example.

Natural and human pressure

Beside the pressure of natural habitat conditions, there exists human-caused pressure. It is not always possible to separate the effects of natural pressure from pressure of human origin. Their combined effects are observed at different levels of the organization of Tatra malacocenoses.

At the species level the reduction of population size, habitat area, and number of localities for very rare species (e. g. *A. parcelineata, M. ventricosa*) are seen. At the community level there is lower species diversity in anthropogenic and semi-natural habitats, i.e., in dense spruce forest and in-forest glades. The regression of the number of species and species diversity for all Tatra malacocenoses is much weaker than for malacocenoses representing only original habitats. The same finding applies to the value of correlation coefficients between those indices and altitude (fig. 55).

The comparison of older data (K o t u l a 1884) and present results is clear: the number of snails in the Polish Tatras has dropped considerably. This is a general phenomenon, so it must be attributed to external factors affecting all Tatra biotopes, some of them particularly strongly. Mosses growing on rocks, which once were preferred by many snail species, are now depleted of them. This may be the effect of the strong acidity of rainwater and the accumulation of heavy metals in the mosses of the Tatras. Heavy metals were mentioned, among other influences, by M i r e k (1990) and W r ó b e l ed. (1989).

Possibilities for counteracting the threats

To stop the further degradation of Tatra malacofauna we might suggest these steps:

- reorient forest management methods toward the reconstruction of the original plant communities, and particularly of *Dentario glandulosae-Fagetum* in the lower mountain zone;
- establish a flexible program for the protection of non-forest communities, including a resolution of the problem of grazing so that the glades could be preserved without causing an inordinate increase in the population of euryecological species at the expense of those characteristic of the Tatras;
- reduce the pressure of urbanization and tourist traffic, particularly in the neighborhood of glades; they are much more harmful to the malacofauna than grazing is;
- reduce emissions of atmospheric pollutants from the Zakopane Basin and other sources;
- begin active protection of the most threatened species (field experiments conducted by malacologists) together with the restoration of biotopes.

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Nature Protection Research Centre
Polish Academy of Sciences
ul. Lubicz 46, 31-512 Cracow, Poland

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Streszczenie

Celem badań malakologicznych w Tatrach Polskich było studium faunistyczno-ekologiczne, które m. in. pozwoli ocenić skuteczność ochrony malakofauny na terenie parku narodowego, wskazać ewentuane zagrożenia i możliwość przeciwdziałania degradacji malakocenoz.

Na badanym terenie, pozostającym w granicach Tatrzańskiego Parku Narodowego (TPN) stwierdzono występowanie 81 gatunków ślimaków lądowych, z których 10 pojawia się tylko w Kotlinie Zakopiańskiej (ryc. 2 - 39). Ich udziały w malakocenozach zostały określone za pomocą kategorii dominacji i stałości [D, C] wg. wartości zaproponowanych przez A l e x a n d r o w i c z a (1987).

Dominacja ogólna pięciu gatunków przekracza 5%. Są to kolejno: *P.rupestris, C. dubia, V. diaphana, C. edentula i C. columella*. Spośród nich tylko *C. edentula* jest gatunkiem holarktycznym. Pozostałe mają zasięgi znacznie mniejsze, zwarte lub porozrywane. TPN stanowi znaczące refugium tych gatunków, a ich obecność jest jednym z elementów decydujących o wartości przyrodniczej tego terenu.

Gatunki

Większość taksonów występujących w malakocenozach tatrzańskich ekstremalnie subrecedentnie i akcydentalnie (dominacja < 0.1%, stałość przeważnie < 10%), to gatunki niespecyficzne pod względem zoogeograficznym i ekologicznym dla tego terenu. Niestety podobny charakter rozmieszczenia mają: *Ch. rossmaessleri, M. ventricosa, B. cana, A. parcelineata, O. depressus, C. holosericum,* ślimaki, których zasięgi są przeważnie niewielkie i często ograniczone do Karpat i terenów sąsiadujących. Są to taksony wyspecjalizowane, preferujące siedliska szczególnie wrażliwe na działania antropogeniczne. Poza kategorią gatunków wyznaczonych przez wspomniane przedziały dominacji i stałości (D1 - D2 i C1) znalazły się także takie, które preferując nietypowe biotopy np. o podłożu krystalicznym, są w wysokiej klasie dominacji np. D4, a tak jak poprzednie są taksonami bardzo rzadkimi. Do takich zaliczają się *Lehmannia macroflagellata* i *L. nyctelia*. One także należą elementów, których obecność decyduje o wartości przyrodniczej Tatr. Biologia tych i poprzednio wymienionych ślimaków jest bardzo słabo poznana i zadaniem trudnym, czy wręcz niemożliwym wydaje się podjęcie teraz prób aktywnej ochrony a jest to w najbliższym czasie konieczne.

Populacje i zespoły

Występowanie poszczególnych gatunków ślimaków jest w różnym stopniu skorelowane. Odmienne są wyniki analizy binarnej i niebinarnej współwystępowania. Pierwsza pokazuje te grupy gatunków, których współwystępowamie wynika z jakości siedlisk, populacje są niezależne od siebie; analiza niebinarna wskazuje te przypadki, gdy zależność ma charakter ilościowy. Skorelowane są wielkości populacji. Jako przykład pierwszego rodzaju związku wymienić można *C. cruciata* i *C. laminata* oraz *V. diaphana, V. turgida* i *T. unidentata*, przykładem zależności ilościowej jest *V. diaphana* i *Ae. pura*.

Ze współwystępowaniem gatunków łączy się problem różnorodności gatunkowej zespołów. W malakocenozach tatrzańskich jest ona bardzo różna, wg. formuły S h a n n o n a - W e a v e r a , od 0.54 do 4.23. Równocześnie różnią się one bardzo liczbą gatunków a wiąże się to ze skalą zróżnicowania siedlisk.

Zonacja

W Tatrach, jak na każdym terenie górzystym, gradient warunków siedliskowych związanych z wysokością bezwzględną jest podstawowym czynnikiem naturalnym determinującym rozwoj fauny, tu malakofauny. Ewidentny jest spadek liczby taksonów, wskaźników różnorodności i równomierności (ryc. 47, 48) wraz ze wzrostem wysokości. Zróżnicowanie siedliskowe na tej samej wysokości powoduje, że zależność ta nie jest tak prosta, np. wysokości 1150 m npm. odpowiada na wykresie kilka wartości na osi liczby gatunków od 6 do 28. Mimo powyższego analiza skupień (Single Linkage or Nearest Neighbor Method) ze względu na różnorodność gatunkową H', równomierność J' i liczbę gatunków S pokazuje, że większość malakocenoz do 1500 m npm. jest zbliżona strukturalnie, należą do grupy obejmującej 31 (67%) z 46 analizowanych stanowisk. Malakocenozy buczyn w Dolinach Olczyskiej i Białego stanowią odrębną grupę, o największej liczbie gatunków i najwyższym wskaźniku różnorodności gatunkowej. Podobnie inne stanowiska łączą się w pary, lub też stanowią, zgodnie z wynikami powyższego grupowania, odrębne kategorie (ryc. 49).

Mimo tego podobieństwa strukturalnego zespołów, mamy do czynienia z dużymi różnicami składu gatunkowego. Jest on m. in. konsekwencją osiągania przez poszczególne gatunki górnej granicy zasięgu w Tatrach. Powyżej 2000 m npm. notowano 21 taksonów, między 1700 - 2000 górną granicę zasięgu osiągają 4, między 1400 a 1700 - 19, a między 1100 a 1400 - 17, około 1100 - 8.

Konsekwencją zróżnicowania zasięgów poszczególnych gatunków jest pionowe jakościowe zróżnicowanie malakocenoz. Przyjmując powyższe przedziały prześledzono podobieństwo jakościowe ich malakofauny. Zmiany jakościowe są równoległe do gradientu wysokości, malakofauna zmienia się stopniowo, a powyżej 2000 m npm. zachowuje największą autonomię, tzn. jej podobieństwo do wszystkich pozostałych jest najmniejsze (tab. I, ryc. 50).

Wraz z wysokością nad poziom morza zmienia się także charakter ekologiczny. Do około 1500 m npm. dominują gatunki leśne, powyżej 1600 m npm. gatunki stepowe i euryekologiczne (ryc. 53).

W kontekście zonacji rozpatrywać można także charakter zoogeograficzny ślimaków tatrzańskich. Wśród 32 elementów zoogeograficznych najwięcej jest gatunków o zasięgu europejskim. Górskie stanowią ponad połowę taksonów powyżej 1600 m npm., a nieco ponad 45% poniżej 1400. Taksony karpackie stanowią z kolei dominująca część wśród górskich. W przytoczonych obserwacjach szczególnie istotne jest, że stanowiska powyżej 1600 m npm. są bogate w faunę typowo górską i stanowią jej refugium, przy czym w 70% są to gatunki karpackie i karpacko-alpejskie.

Malakofauna potencjalna i aktualna

Potencjalna malakofauna Tatr odpowiada tejże z interglacjałów i postglacjału. W sposób naturalny zróżnicowała się na zespoły siedlisk otwartych powyżej górnej granicy lasu z podziałem na murawy naskalne i gołe turnie, oraz zespoły leśne. Wyniki analizy elementów zoogeograficznych powyżej 1600 m wskazują, że malakofauna tych siedlisk "zachowała autonomię", dominują elementy górskie, karpackie, dokładniej karpacko-alpejskie (tab. IV). Zespoły leśne to buczyny *Dentario-glandulosae-Fagetum* i bór świerkowy *Abieti-Piceetum* oraz *Piceetum tatricum*. Aktualnie nie ma możliwości rekonstrukcji składu pierwotnych malakocenoz *Abieti-Piceetum* i *Piceetum tatricum* , natomiast buczyny w Dolinie

Białego, Spadowca i kilku innych stanowią refugium malakofauny pierwotnej dla regla dolnego Tatr (Dyduch-Falniowska 1988, Dyduch-Falniowska, Tobis 1989). Aktualnie siedliska tatrzańskie są o wiele bardziej zróżnicowane, co wynika przede wszystkim z działalności ludzkiej. Poniżej górnej granicy lasu mamy bardzo zróżnicowane pod względem warunków fizyko-chemicznych i geobotanicznych siedliska jakimi są polany śródreglowe, a same lasy uległy daleko posuniętym modyfikacjom. Polany, w różnym stopniu i różnie użytkowane zostały zasiedlone przez mięczaki tworzące nowe zespoły (Dyduch-Falniowska, Fyda 1986, Dyduch-Falniowska 1988). Przemiany zespołów leśnych poszły w bardzo niekorzystnym dla malakofauny kierunku. Zastąpienie w reglu dolnym buczyn świerczynami przyniosło znaczne zmniejszenie powierzchni siedlisk dostępnych dla ślimaków. Degradacja ściółki leśnej związana z obecnością zwartych drzewostanów świerkowych (Fabijanowski 1962) oznacza eliminację większości gatunków mięczaków ze względu na zbyt małą wilgotność siedlisk (przyśpieszony spływ wód) i ich zakwaszenie (Dyduch 1980, Dyduch-Falniowska, Tobis 1989). Niekiedy mogą one stanowić bariery dla zespołów wyspowo rozmieszczonych na izolowanych ścianach skalnych, np. Sarniej Skale czy Nosalu.

Presja naturalna i antropogeniczna

Obok presji naturalnych czynników siedliskowych obserwujemy presję antropogeniczną, która pojawia się na marginesie prawie każdego z powyżej omawianych zagadnień. Rozgraniczenie skutków obu rodzajów presji nie zawsze jest możliwe. Określenie skutków działalności ludzkiej wymaga bardzo dokładnego obrazu presji, która wynika z gradientu naturalnych czynników siedliskowych.

Oba rodzaje presji powodują: (1) ograniczenie liczebności, areału i liczby stanowisk ślimaków występujących subrecedentnie i akcydentalnie, wymienionych powyżej, (2) w zespołach widoczne jest obniżenie różnorodności gatunkowej w siedliskach antropogenicznych i seminaturalnych, tj. w zwartych drzewostanach świerkowych i na polanach śródreglowych. Regresja liczby gatunków i różnorodności gatunkowej uwzględniająca wszystkie malakocenozy tatrzańskie jest o wiele słabsza niż wtedy, gdy bierze się pod uwagę tylko siedliska pierwotne. To samo dotyczy wielkości współczynnika korelacji wspomnianych wskaźników z wysokością bezwzględną. (ryc. 55).

Korzystając z tych spostrzeżeń zaproponowano niezgodność pomiędzy nimi uznać za miarę efektu działań antropogenicznych. Wyrażałby ją procentowy stosunek wartości odpowiednich współczynników korelacji i regresji.

Równanie $y_f = a_f + b_f x$ - opisuje regresję faktyczną przy współczynniku korelacji r_f, równanie $y_o = a_o + b_o x$ opisuje regresję w warunkach optymalnych przy współczynniku korelacji r_o. Miarą przekształcenia (D) będzie stosunek współczynników korelacji i regresji:

$$D_b = \frac{b_f}{b_o}$$

$$D_r = \frac{r_f}{r_o}$$

Powyższe wskaźniki można liczyć w stosunku do różnych parametrów malakocenoz, np. liczby gatunków, różnorodności gatunkowej, zagęszczenia itp. W przedstawianej pracy ograniczono się do dwóch pierwszych z wymienionych parametrów. Wskaźniki przekształcenia malakocenoz oparte na liczbie gatunków wynoszą: D_{bS}=0.70; D_{rS}=0.65, a na różnorodności gatunkowej: D_{bH}=0.70; D_{rH}=0.54. Wynika z powyższego, że odkształcenie składu malakocenoz tatrzańskich i ich struktury, dokładniej stosunków ilościowych pomiędzy różnymi gatunkami, jest podobne.

Równolegle do gradientu hypsometrycznego następuje zmiana charakteru ekologicznego malakofauny (ryc. 56). W niżej położonych siediskach, 40 - 50% to gatunki określane przez Ložka (1964) jako leśne, bardzo rzadko przechodzące do innych biotopów, ich udział w szczytowych malakocenozach wynosi od jednego do kilku procent. Gatunków stepowych w niektórych seriach wraz z wysokością jest mniej, w innych więcej. Znaczący jest wzrost, wraz z wysokością, udziału ilościowego gatunków euryekologicznych, niekiedy do około 50%. Przykłady przedstawione na załączonej rycinie pokazują ten proces w trzech etapach, podkreślić należy, iż celowo umieszczono w schemacie Niżną Polanę Kominiarską choć jest siedliskiem seminaturalnym, ale na znacznej jej powierzchni wykształcił się zespół ślimaków o cechach odpowiadających malakocenozom siedlisk naturalnych.

Z analizy starszych danych (Kotula 1884) i zagęszczenia ślimaków aktualnie obserwowanego w różnych siedliskach widoczne jest generalne obniżenie liczebności ślimaków w Tatrach Polskich. Jest ono do tego stopnia ogólne, że przypisać je trzeba przyczynom zewnętrznym, dotykającym wszystkie biotopy; niektóre z nich w szczególnie silnym stopniu. Brak teraz ślimaków w mchach naskalnych, które dawniej były siedliskiem preferowanym przez liczne gatunki. Stosunkowo niewiele jest ślimaków na skałach. Przypuszcza się, że jest to wynik silnego zakwaszenia wód opadowych w Tatrach i kumulacji metali ciężkich w mchach (m. in. Wróbel - red. 1989, Mirek 1990).

Możliwości przeciwdziałania zagrożeniom

Powstrzymanie dalszej degradacji malakofauny wymaga:

- całkowitej zmiany metod gospodarki leśnej, sterowanie w kierunku odtworzenia pierwotnych zbiorowisk roślinnych. Chodzi przede wszystkim o stworzenie warunków rozwoju *Dentario glandulosae-Fagetum* w reglu dolnym;
- elastycznego programu ochrony siedlisk nieleśnych uwzględniającego racjonalne rozwiązanie problemu wypasu, tak by polany zachowując swą specyfikę nie powodowały nadmiernego wzrostu populacji gatunków euryekologicznych, kosztem specyficznych dla Tatr;
- zmniejszenie nacisku urbanizacyjnego i ruchu turystycznego; ich efekty, szczególnie w okolicy polan, są bardziej szkodliwe niż wypas;
- ograniczenie emisji zanieczyszczeń atmosferycznych z Kotliny Zakopiańskiej i innych źródeł;
- podjęcie - równolegle do restytucji siedlisk - aktywnej ochrony najbardziej zagrożonych gatunków w warunkach eksperymentu terenowego prowadzonego przez malakologów.

Appendix 1

List of localities

Lista stanowisk

Denotation Oznaczenia	Locality Stanowisko	Altitude Wysokość npm.	Vegetation Roślinność	Substratum Podłoże
AA	Kalacka Turnia	1200	*Piceetum tatricum*	light grey limestones and dark marls with cherts
AB	Polana Kalatówki	1150-1200	*Glad.-Agrost. alp.*	slope debris, gravel-loamy moraine
AC	Kuźnice - Kalatówki	1150	spruce forest	gravel-loamy moraine
AD	Polana Rusinowa	1200-1250	*Glad.-Agrost. alp.* *Hieracio-Nardetum*	light-grey limestones, dark marls, gravel-loamy moraine
AE	Wierch Poroniec - Goły Wierch	1100-1250	*Piceetum tatricum*	sands and gravels, dark limestones
AF	Dolina Lejowa	1000	*Dent. gland.-Fagetum, Abieti-Piceetum*	conglomerates, light grey limestomes, dark marls
AG	Polana Lejowa	1000-1050	*Glad.-Agrost. alp.* *Abieti-Piceetum*	dark-grey platy dolomites, grey pinkish and dark limestones
AH	Site between Zahradziska and Przysłop Miętusi	980-1188	*Abieti-Piceetum*	dolomitic limestones and limestones
AI	Przysłop Miętusi	1188	epilithic grasslands	yellow dolomites, black limestones, shales, and breccias
AK	Przysłop Miętusi-Dolina Mała Łąka	1000-1188	spruce forest	dolomitic limestones and dolomites
AL	Dolina Bystrej	990	spruce forest, *Glad.-Agrost. alp.*	sandy-gravelous fluvioglacial sediments
AM	Kuźnice - Nosal	1000-1150	spruce forest	sandy-gravelous fluvioglacial sediments
AN	Nosal	1205	epilithic grasslands	organodetrital limestones
AO	Dolina Olczyska	900-1000	*Dent. gland.-Fagetum, Abieti-Piceetum*	sandy-gravelous fluvioglacial sediments
AP	Wielki Kopieniec	1328	epilithic grasslands	dolomitic limestones, limestones and dolomites
AR	Kopieniec - Toporowa Cyrhla	1050-1250	spruce forest	dolomitic limestones, gravel-loamy morainal sediments
AS	Site between Polana Kalatówki and Polana Kondratowa	1200-1300	*Piceetum tatricum*	yellow dolomites, black limestones, shales, and breccias
AT	Dolina Strążyska	1000-1100	*Dent. gland.-Fagetum*	dolomitic limestones and dolomites
AU	Wysokie	1287	*Piceetum tatricum*	dolomitic limestones and dolomites

Appendix 1 cont.

AW	Wiktorówki	1100	*Abieti-Piceetum*	shales, greenish sandstones, organodetrital limestones
AX	Dolina Chochołowska	1150	*Abieti-Piceetum*	fluvial sands and gravel, limestones, dolomites
AY	Dolina Białego	950-1000	*Dent.gland.-Fagetum*, epilithic grasslands	dolomitic limestones, limestones, shales, yellow dolomites
AZ	Gęsia Szyja	1489	*Carici-Festucetum tatrae*	dolomitic limestones, limestones, dolomites
BA	Igła - slope	1100	*Dent. gland.-Fagetum, Abieti -Piceetum*	dolomitic limestones, limestones, dolomites
BB	Igła - top	1207	*Piceetum tatricum*, epilithic grasslands	shales, greenish sandstones, dark organodetrital limestones
BC	Sarnia Skała	1377	epilithic grasslands	dolomitic limestones, yellow dolomites, black limestones
BD	Niżni Staw Toporowy	1100	spruce forest	sandy-gravelous fluvioglacial sediments
BE	Below Przełęcz Kondracka	1650	*Pinus mugo*	dark limestones, dolomites, black limestones, shales
BF	Giewont	1895	epilithic grasslands	grey, pinkish and dark limestones
BG	Diabliniec	1241	*Piceetum tatricum*	dark organodetrital limestones, interbeds of black shales
BH	Scieżka Nad Reglami-near Niżnia Polana Kominiarska	1100	raspberry patch, *Abieti -Piceetum*	grey and pinkish limestones, marls
BI	Dolina Kościeliska	1000-1050	*Dent. gland.-Fagetum, Abieti-Piceetum*	sandy-gravel fluvial sediments, dolomites, limestones
BK	Polana Pisana	1050	*Glad.-Agrost. alp.*	fluvial and lacustrine sands and gravels, alluvial cones
BL	Wawoz Kraków	1000	epilithic grasslands	grey, pinkish and dark limestones
BM	Near Jaskinia Mroźna	1000	*Abieti-Piceetum*	grey, pinkish and dark limestones, dolomites
BN	Kopa Kondracka	2005	epilithic grasslands	alaskites
BO	Boczań	1209	spruce forest	dolomitic limestones, limestones, dolomites
BP	Skupniów Upłaz - forest	1300-1350	*Piceetum tatricum*	dolomitic limestones, limestones, dolomites
BR	Skupniów Upłaz	1350-1378	epilithic grasslands	dolomitic limestones, limestones, dolomites

Appendix 1 cont.

BS	Dolina Jaworzynka	1100-1150	*Glad.-Agrost. alp.*	dolomitic limestones, dolomites, black limestones, shales
BT	Niżnia Polana Kominiarska	1140	*Carici-Fest.ucetum tatrae, Glad.-Agrost. alp.*	red sandstones, conglomerates, shales, dolomites, marls
BU	Polana Chochołowska	1100-1150	*Glad.-Agrost. alp.*	alluvial cone, slope debris, gravel-loamy moraine
BW	Kamienny Żleb above Polana Hucisko	1100	epilithic grasslands, *Piceetum tatricum*	dolomitic limestones, limestones, dolomites
BX	Polana Waksmundzka	1400	*Glad.-Agrost. alp.*	alluvial cone
BY	Polana Kopieniec	1180-1200	*Glad.-Agrost. alp.*	partly gravel-loamy moraine, partly dolomitic limestones
BZ	Suchy Wierch Kondracki	1890	*Vaccinium myrtillus Pinus mugo*	metamorphic rocks
CA	Polana Kondratowa	1320-1350	*Glad.-Agrost. alp.*	slope debris, gravel-loamy moraine
CB	Wierch Spaleniec	1050-1100	*Dent. gland.-Fagetum*	sandstones, conglomerates, shales, dolomites, limestones
CC	Dolina Ku Dziurze	900-1050	*Dent. gland.-Fagetum*	red sandstones, shales, limestones, dolomites
CD	Polana Miętusia	1200	*Glad. -Agrost. alp.*	gravel-loamy moraine, shales, yellow dolomites
CE	Dolina Mała Łąka	1150	*Abieti-Piceetum, Dent. gland.-Fagetum*	dolomitic limestomes, dolomites, gravel-loamy moraine
CF	Ciemniak	2096	epilithic grasslands	dark limestones, dolomites
CG	Krzesanica	2122	epilithic grasslands	dark limestones, dolomites
CH	Dolina Spadowiec	900-1050	*Dent. gland.-Fagetum*	shales, greenish sandstones, organodetrital limestones
DA	Adamica	1203	*Pinus mugo*, ephilithic grasslands	dolomitic limestones, limestones and dolomites
DI	Białe (above Dolina Białego)	1200	*Abieti-Piceetum, Glad.-Agrost. alp.*	red sandstones, conglomerates and shales and dolomites
DJ	Jarząbczak	1000-1100	*Piceetum tatricum*	organic and organodetrital limestones
DR	Dolina Roztoki	1150-1200	*Piceetum tatricum*	slope debris (screes, scree cones)
FV	Dolina Filipka	950-1000	*Piceetum tatricum*	dolomitic limestones, limestones and dolomites
FW	Filipczański Wierch	1225	*Pinus mugo*, epilithic grasslands	dolomitic limestones, limestones and dolomites

Appendix 1 cont.

GG	Gubałówka	1070-1120	*Piceetum tatricum, Glad.-Agrost. alp.*	sandstones and shales
GH	Przełęcz Małołącka	1924	epilithic grasslands	grey, pinkish and dark limestones
GI	Wielka Polana	1200-1225	*Glad.-Agrost. alp.*	gravel-loamy moraine sediments, slope debris
GK	Siodło	1650	epilithic grasslands, *Pinus mugo*	yellow dolomites, black limestones, shales, breccias
GL	Małołączniak	2096	epilithic grasslands	alaskites
GM	Niżnia Świstówka	1250	epilithic grasslands, *Alchemilla sp.*	limestones, dolomitic limestones
GN	Przełęcz Małołącka	1700-1900	epilithic grasslands	limestones, dolomitic limestones
GO	Polana Pańszczyca	1300	*Glad.-Agrost.. alp.*	gravel-loamy moraine sediments, ramparts, alluvial cone
GP	Site between Dolina Pańszczycy and Polana Pańszczyca	1400-1500	*Piceetum tatricum*	limestones
GR	Site between Polana Waksmundzka and Polana Pańszczyca	1400	*Piceetum tatricum*	red quartzitic sandstones and shales
GS	Dolina Tomanowa	1100-1200	spruce forest	gravel-loamy morainal sediments with moraine ramparts
GT	Niżnia Polana Tomanowa	1300-1400	*Glad.-Agrost. alp.*	gravel-loamy morainal sediments with moraine ramparts
GU	Przełęcz Tomanowa	1686	epilithic grasslands	red quartzitic sandstones and shales
GW	Wyżnia Świstówka	1700-1800	epilithic grasslands	slope debris
GX	Kominiarski Wierch	1829	*Pinus mugo*, epilithic grasslands	dark limestones and dolomites
GY	Twardy Upłaz	1900-2000	epilithic grasslands	alaskites
GZ	Kocioł Litworowy	1800-1900	epilithic grasslands	slope debris
HG	Polana Hucisko	1000	*Glad.-Agrost. alp.*	alluvial cones
HR	Hruby Regiel	1339	*Piceetum tatricum*	dolomitic sandstones
KO	Kobylarz	1400	ephilitic grasslands	grey and pinkish limestones, marls with sandstone interbeds
KP	Kopa Magury	1704	epilithic grasslands	dark limestones and dolomites, grey pinkish, dark limestones
KS	Kopy Sołtysie	1334-1420	*Glad.-Agrost. alp.*	black limestones, spotty limestones, spongiolites
KZ	Kotlina Zakopiańska	0850-0900	synanthropic vegetation	dolomitic sandstones,sandy gravelous fluvioglacial sediments

Appendix 1 cont.

LP	Przełęcz Litworowa	2037	epilithic grasslands	dark limestones and dolomites
MI	Mięguszowiecki Szczyt	2438	epilithic grasslands	granitoids
MO	Morskie Oko	1450	*Piceetum tatricum*	gravel-loamy moraine, slope debris, morainal ramparts
MP	Polana Merkusia	1000	*Glad.-Agrost. alp.*	dark-grey platy dolomites
MS	Wąwóz Między Ściany	1100	epilithic grasslands	dark limestones and dolomites
NE	Nędzówka	900	*Abieti-Piceetum*	dolomitic sandstones
RW	Site near Rówień Waksmundzka	1300	*Piceetum tatricum*	alluvial cones
SK	Siklawica in Dolina Strążyska	1250	*Piceetum tatricum,*	
ST	Stawiance	1250	*Piceetum tatricum*	red quartzitic sandstones and shales
TG	Wyżnia Polana Tomanowa	1300-1400	*Glad.-Agrost. alp.*	gravel-loamy morainal sediments, moraine ramparts
WG	Goły Wierch	1206	*Piceetum tatricum, Glad.-Agrost. alp.*	sandy gravel moraine sediments, limestones
WK	Wielkie Koryciska	1000	epilithic grasslands, *Abieti-Piceetum*	grey dolomites, nodular limestones
WM	Wodogrzmoty Mickiewicza	950	*Abieti-Piceetum*	granitoids
WT	Wielka Turnia	1847	epilithic grasslands	grey pinkish and dark limestones
WZ	Wołowy Żleb	1250-1400	*Piceetum tatricum,* epilithic grasslands	limestones
ZA	Zawieszka	1220	*Abieti-Piceetum,* grasslands	dolomitic limestones, dolomites and limestones

WYDAWNICTWA ZAKŁADU OCHRONY PRZYRODY POLSKIEJ AKADEMII NAUK

Nr 36. **Rola parków narodowych w ochronie szaty roślinnej i krajobrazu Polski** (Importance of national parks for conservation of vegetation and landscape in Poland). Zespół autorów (red. Z. Denisiuk), 1990. . . . . cena 15000zł

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Nr 37. **Population of White Stork *Ciconia ciconia* (L.) in Poland. Part II** (Populacja bociana białego *Ciconia ciconia* (L.) w Polsce. Część II). Zespól autorów (red. Z. Jakubiec), 1991 . . . . cena 25000zł

ser. B

Nr 29. **Park Narodowy na Babiej Górze - Człowiek i przyroda.** Zespól autorów (red. K. Zabierowski), 1985. . . . . cena 10000zł

Nr 32. **System ochrony przyrody i krajobrazu województwa krośnieńskiego.** Zespół autorów (red. S. Michalik), 1987. . . . . cena 5000zł

Czerwona lista zwierząt ginących i zagrożonych w Polsce (Red list of threatened animals in Poland). Zespół autorów (red. Z. Głowaciński), 1991 . . . cena 30000zł

"CHROŃMY PRZYRODĘ OJCZYSTĄ"

R. **14** (1958)(zesz. 4 i 5) R. 31 (1975)(zesz. 2, 3/3, 5 i 6)
R. **32** (1976)(zesz. 3, 4, 5 i 6)
R. **33** (1977)(zesz. 5/6)
R. **34** (1978)(zesz. 1, 2, 3, 4 i 6)
R. **35** (1979)(zesz. 1-6)
R. **36** (1980)(zesz. 1-6)
R. **37** (1981)(zesz. 1-6)
R. **38** (1982)(zesz. 1-6)
R. **39** (1983)(zesz. 1-6)
R. **40** (1984)(zesz. 1-6)
R. **41** (1985)(zesz. 1, 2 i 5)
R. **43** (1987)(zesz. 4 i 5/6)
R. **44** (1988)(zesz. 1-6)
R. **45** (1989)(zesz. 1-6)
Cena pojedynczego zeszytu - 500zł, podwójnego - 1000zł

R. **47** (1991)(zesz. 1-2 cena 13000zł, zesz. 3-6 cena 9000zł)

Powyższe wydawnictwa są do nabycia w naszym Zakładzie (adres: 31-505 Kraków, ul. Ariańska 1, I p.). Możemy je również przesłać za zaliczeniem pocztowym.

REDAKCJE

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