

CHARPENTIERIA (ITALA) ORNATA (ROSSMÄSSLER, 1836) (GASTROPODA: PULMONATA: CLAUSILIIDAE) ON THE NORTHERN FRINGES OF ITS RANGE – A NATIONALLY ENDANGERED SPECIES SURVIVING DUE TO HUMAN ACTIVITIES

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Abstract Charpentaria ornata is a SE-Alpine species which reaches the extreme north-east of its range in isolated populations in the Czech Republic and the extreme south-west of Poland, where it is known from this study only from eight abandoned limestone quarries in the western part of the Krowiarki range (Lower Silesia, region of Kłodzko). It is a red-listed species in the Polish fauna. These quarries harbour a total of 39 gastropod species, a mixture of open-country, tolerant and specifically forest species. *Ch. ornata* associates with open country species, and its density declines as tree cover increases. At this edge of its range, it appears unable to survive in full forest cover, although this is the natural climax vegetation of the region. Comparison with the more southerly populations in the Czech Republic shows that in warmer conditions it can survive full canopy cover, and is part of a rich, natural clausiliid fauna. It seems most likely that the species spread north from Czech sites in the mid-Holocene climatic optimum, and survived later as a result of early forest clearance exposing limestone crags to more xerothermic conditions. Later reforestation was offset in these few sites by quarrying. Thus, in contrast to most threatened species of land gastropod, effective conservation requires the maintenance of highly disturbed habitats in an early stage of succession.

Key words Charpentieria ornata, Clausiliidae, ecology, endangered species, succession, pioneer species

INTRODUCTION

Populations of species at the edge of their ranges often show a patchy distribution, and they can demonstrate the nature of the environmental factors that limit their distribution. In particular cases, such peripheral populations may represent the only ones present in a national territory, and thus attract local “red-listing” or other conservation measures (Maltz, 2003; Wiktor, 2004a).

Charpentieria ornata (Gastropoda: Pulmonata: Clausiliidae) is regarded as an eastern Alpine (Ložek, 1956; Riedel, 1988; Hlaváč, 2002; Wiktor, 2004b), or a south-eastern Alpine species (Kerney et al. 1983; Wiktor, 1960, 1964, 2004a). Its main distribution range includes the northern part of the Dinaric Mts and the south-eastern part of the Alps (Wiktor, 1960; Riedel, 1988). Outside this area it has a few outlying localities in the Czech Republic (Ložek, 1955, 1956; Wiktor, 1960; Hlaváč, 2002; Juříčková et al. 2006), and its northernmost localities are situated in the extreme south of Poland near Żelazno (Lower Silesia: region of Kłodzko), where it is found in several abandoned limestone quarries in the western part of the Krowiarki range (Wiktor, 1960, 1964, 2004a, b; Riedel, 1988) (Figure 1).

Over most of its range, *Ch. ornata* is a thermophile, living in open or partly vegetated habitats, usually including insolated, calcium-rich rocks. Sometimes, however it is found in forests on tree trunks, in leaf-litter, screes at the base of rocks or in castle ruins (Ložek, 1955; Wiktor, 1960, 1964, 2004a, b; Riedel, 1988; Juříčková and Kučera, 2005).

Literature data on its occurrence in Poland come from the end of the 19th c., the 1920s and the 1960s (Merkel, 1894; Sprick, 1921; Wiktor, 1960, 1964); later publications (Riedel, 1988; Wiktor, 2004a, b) cite the earlier information making clear that it required verification, especially as *Ch. ornata* is now regarded as critically endangered in Poland (Wiktor and Riedel, 2002; Wiktor, 2004b).

This paper presents the results of: 1) surveying the area in Poland in which *Ch. ornata* occurs, 2) an ecological analysis of malacocoenoses of which the species forms a part, 3) estimating population sizes in the best sites, 4) considering its history in the region, and 5) identifying the main ecological limitations on the species, and hence specifying the threats to it, and the measures necessary for its protection.

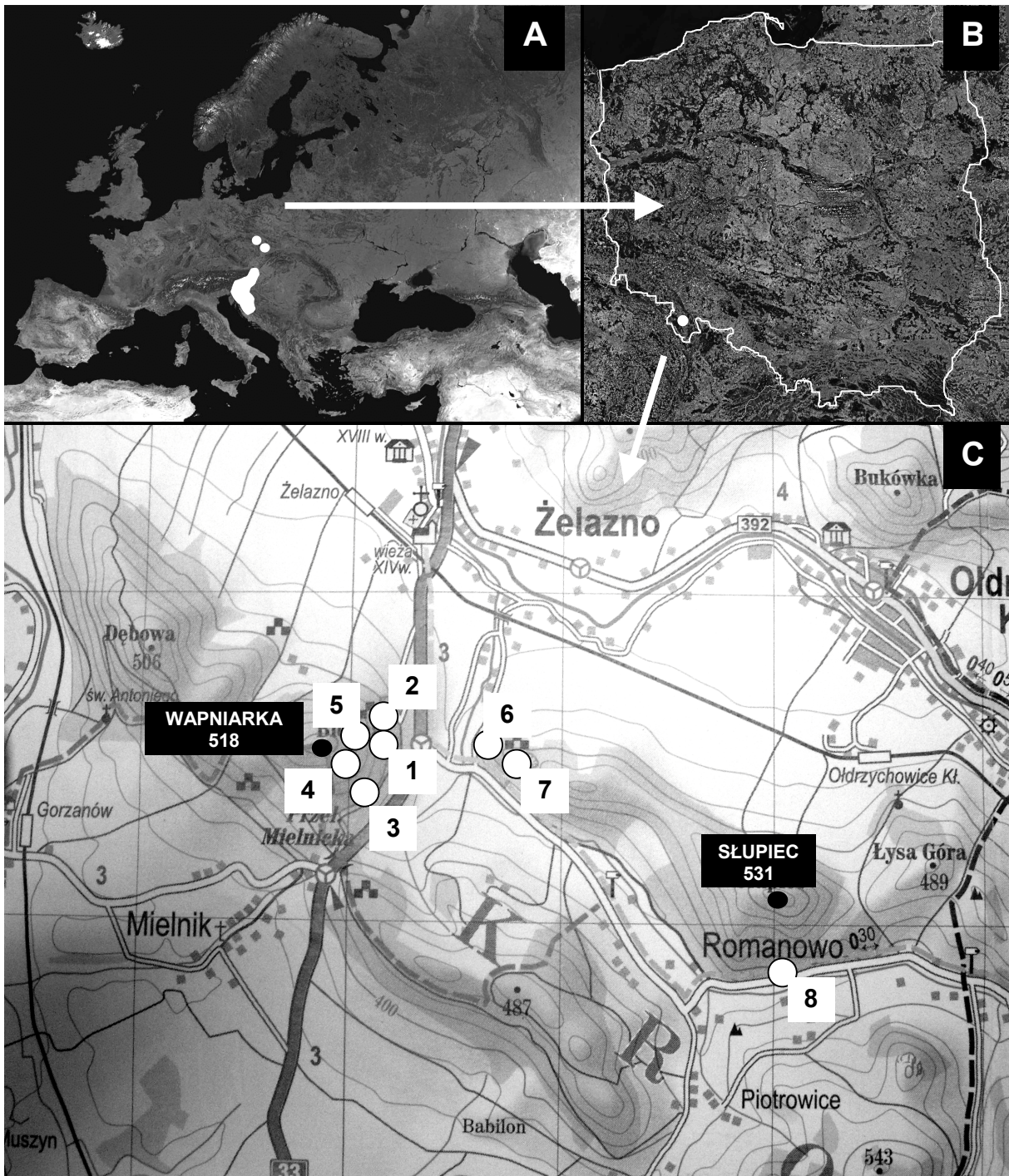


Figure 1 Distribution of *Ch. ornata* in Europe (A), Poland (B) and the region of Kłodzko (sites in the Krowiarki range) (C)

STUDY AREA

The Krowiarki range is the northern extension of the massif of Mt. Śnieżnik in the Sudetes (Figure 1). Most summits lie between 446 and 670 m a.s.l., only a few summits in its south-eastern part exceed 800 m. The range is mainly built of metamorphic rocks, with outcrops of Palaeozoic marbles; limestones and dolomites form inter-

calations among mica schists. Its western part harbours karstic hills. Their present form is the result of karstic phenomena which started during the Palaeogene and subsequent Pleistocene frost erosion and Holocene erosion and denudation; consequently the carbonate outcrops are now dome-like mogotes. On these hard limestone substrates only, soils may be brown and

red rendzinas (Walczak, 1968).

The vegetation is partly submontane and partly characteristic of the lower mountain zone. The original submontane forests were composed of hornbeam, oak and maple, with an admixture of pine and spruce; the higher slopes were covered in beechwood with an admixture of rowan, sycamore, fir, maple, lime and hazel, in places also with pine, larch and birch (after Walczak, 1968).

Climatically the region of Kłodzko (including Krowiarki) is the most continental part of Lower Silesia. The vegetation season lasts 29-30 weeks (mean daily temperature above 5°C), the summer – 8-10 weeks (mean daily temperature above 15°C); the annual sum of precipitation is 600-800 mm (Walczak, 1968).

Since the advent of man in the area (first settlements near Bystrzyca Kłodzka c. 3000 BC) the environment of the Krowiarki has been undergoing considerable changes. In the 12th-13th Centuries A.D. the area became densely populated; developing agriculture (fertile soils) and building implied mass clear-felling of the submontane forests. Quarrying of marble and limestone started (first quarries with manual labour near Mielnik, Żelazno and Romanowo) in the 16th century with the development of masonry. Production of charcoal for lime kilns and metal smelting, as well as huge demand for building and fuel timber resulted in clear-felling being extended to include the lower mountain zone, resulting in nearly complete deforestation of the slopes and exposure of the rocky outcrops. At the beginning of the 19th century reforestation of the Sudetes started, with spruce plantations on mountain slopes, and in the 1860s the first large quarries were opened in the Krowiarki, using modern quarrying methods (Walczak, 1968).

Today the quarried and reforested hills are surrounded by cultivated fields, so that the whole range forms an archipelago of forest islands. The dominant component of the forest is spruce, with an admixture of beech, oak, birch and pine; only in the western part of the range, among others on the slopes of Mt. Słupiec and Mt. Wapniarka (Figure 1), is deciduous forest found, with a considerable proportion of beech and an admixture of sycamore, oak and hazel, and sometimes lime. Some of the slopes are dissected by numerous and now mostly abandoned quarries which form a characteristic part of the landscape.

METHODS

GENERAL SURVEY

Field studies (spring 2004 - autumn 2006) covered an area in the western part of the Krowiarki, between the villages of Żelazno, Mielnik, Stary and Nowy Waliszów, Trzebieszowice and Ołdrzychowice Kłodzkie (Figure 1). Special attention was paid to abandoned quarries and natural limestone outcrops. Each site at which *Ch. ornata* was found was surveyed on more than one occasion, searching by eye for all species for at least two hours in different weather conditions and seasons (spring, summer, autumn) and considering all available microhabitats. In sites where adequate quantities of litter were present, samples of 10-15 l litter were taken, sieved through a sieve of 10 x 10 mm mesh. Large gastropods retained by this mesh were removed, and the residue discarded. Material passing through the sieve was bagged, dried in the laboratory, sieved through 2 x 2 mm mesh, and both the resulting fractions were sorted. Live clausiliids, helioids and slugs were identified in the field and released, the remaining material was identified in the laboratory and deposited in the Museum of Natural History, Wrocław University. Nomenclature and systematic arrangement follow Riedel (1988).

Completeness of the faunistic lists for the examined sites was tested with the Chao index based on number of specimens found (Cameron and Pokryszko, 2005). The following indices were used to characterise the malacofauna: 1) Whittaker's indices I_W and I_{MAX} , indicating the degree of between-site heterogeneity (Pokryszko and Cameron, 2005); 2) index of faunal originality IFO (Ejsmont-Karabin, 1995); 3) Nei index of similarity (N) (Pokryszko and Cameron, 2005).

In order to compare the species composition of malacocoenoses of quarries at different stages of succession, the species were grouped in the following categories: 1) stage I species (rock faces and ledges with short herbaceous vegetation); 2) stage II species (rocks with herbaceous vegetation, shrubs and small trees: pine and birch); stage III species (rocks with shrubs and trees, mainly maple and beech); stage IV species (rocks with trees, mainly maple and lime); euryoecious species found at all succession stages. This ecological grouping uses the categories established

Table 1 List of limestone quarries in the western part of the Krowiarki range; sources: 1. Jońca (1984), 2. own observations, 3. Wiktor (1960), 4. Wiktor – personal communication; approximate area: small - several dozen m², medium – several hundred m², large – several thousand m²

No.	Site location	Approximate age ¹⁾ (2004)	Approximate area	Status
1	Mt. Wapniarka, 1.4 km S of Żelazno	~ 30 years (closed down in the 1970s) ¹	large	abandoned
2	Mt. Wapniarka, 1.4 km S of Żelazno	~ 10 years (closed down in the 1990s) ²	medium	abandoned
3	Mt. Wapniarka, 1.4 km S of Żelazno	?	small	abandoned
4	Mt. Wapniarka, 1.4 km S of Żelazno	~ 50 years (closed down in the 1950s) ³	medium	abandoned
5	Mt. Wapniarka, 1.4 km S of Żelazno	~ 30 years (closed down in the 1970s) ¹	large	abandoned
6	Mt. Słupiec group, 1.2 km S of Odrzychowice Kłodzkie, W slope	~ 10 years (closed down in the 1990s) ²	medium	re-opened in 2005
7	Mt. Słupiec group, 1.2 km S of Odrzychowice Kłodzkie, W slope	~ 20 years (closed down in the 1980s) ⁴	medium	abandoned
8	Mt. Słupiec group, Romanowo Dolne, S slope	?	medium	abandoned

Table 2 Ecological groups of gastropods (according to Riedel, 1988) for the three quarries analysed in detail (Wapniarka) and for the entire malacofauna recorded in all sites with *Ch. ornata*

Ecological group	SITE 1	SITE 2	SITE 4	ALL SITES (1-8)
woodland species (W)	11	2	13	15
shrubland species (S)	7	6	7	7
open-country species (O)	3	3	2	4
europyocious species (E)	5	4	3	6
petrophilous species (P)	1	1	1	1
xerothermophilous species (X)	3	4	1	4
synanthropic species (H)	1	1	0	1

by Ložek (1964), with subsequent minor modifications by Riedel and Wiktor (1974), Riedel (1988), Wiktor (1989) and Pokryszko (1990) in a more simple and generalised form. Thus, xerothermophilous species are characteristic for stage I, open country species are assigned to stage II, shrubland species to stage III and woodland species to stage IV, with the reservation that the distinction is not completely clear-cut because almost none of the species is exclusive to one stage. Based on the character of vegetation of quarries at different age (corresponding to succession stages I-IV) species were then assigned to groups A, B and C, representing different times of colonisation of the quarries.

POPULATION STUDIES

Three closely situated quarries at different stages of succession were surveyed from April till September 2005 in order to estimate the density and abundance of *Ch. ornata*. A rock face where the species had been earlier observed was selected in each quarry (eastern wall in the oldest, northern wall in the intermediate and southern wall in the youngest quarry). On each rock face all live specimens were collected from an area of 10 m² rock face during two hours. On each occasion the population density was estimated directly as observed population density: number of individuals collected from the sampling area divided by the number of square metres.

RESULTS

GENERAL SURVEY

The study area holds 16 quarries. In 2004 14 of them were abandoned (one reopened in the spring of 2005). *Ch. ornata* was found in eight of them. Geographically, these eight sites form one cluster of five sites on the eastern slope of Mt. Wapniarka, and two sites on the western slope of Mt. Słupiec, but one on the south-eastern slope of Mt. Słupiec is more isolated (Figure 1 and Table 1). No live snails or shells were found on the rock outcrops located along the ridge of Mt. Słupiec and on the nearby hills in the region of Piotrowice and Romanowo (a locality of *Ch. ornata* reported by Wiktor, 1960).

A total of 39 gastropod species were found in the eight localities with *Ch. ornata*. The species

composition of the malacofauna of these sites, and of Czech sites also containing *Ch. ornata* (see discussion) is given in the Appendix. The value of the Chao index (based on individuals) for each site was 0, the index for the whole area was 2 (likely presence of two uncollected species). Thus the samples represent nearly all the fauna actually present at each site.

SPECIES COMPOSITION AND RICHNESS

The number of species per site ranged from 17 to 32 (mean: 24.75 ± SE 2.05) (for species composition see Appendix). The frequency of occurrence in the eight quarries is presented in Figure 4. Out of 38 species accompanying *Ch. ornata*, nine (32%) occurred in all sites and 27 (71%) occurred in more than half the sites; only four species were restricted to single sites. The sites were moderately heterogeneous ($I_W = 1.57$) but much of this is due to differences in richness; the I_{MAX} value (1.22) was smaller, indicating that the richest site (1) held most of the aggregate fauna. The IFO which also reflects heterogeneity ranged from 0.152 to 0.259 (mean: 0.197 ± SE 0.012). Its value was the highest for the oldest quarry (site 4, 0.259), and for larger quarries (2 sites) overall the range was from 0.187 to 0.259 (mean 0.211 ± SE 0.01). For small quarries (2 sites) the range and mean are lower (range 0.152 to 0.156; mean 0.154 ± SE 0.002). The mean IFO value (0.197) reflects the low proportion of rare and the high proportion of common species in the samples.

SIMILARITY AND SUCCESSION

As suggested by the results above, the faunas of sites occupied by *Ch. ornata* are rather similar. Figure 3 shows the dendrogram of similarities using the Nei index. The minimum similarity among the quarries is c. 70%. The most similar malacocoenoses were those of the two largest and richest quarries (1 and 5), located in a line from the base to the summit of Mt. Wapniarka and closed down in the 1970s. Likewise communities from sites 6 and 7, situated close together on the western slope of Mt. Słupiec, were very similar, as well as those from the two smallest quarries (3 and 8), where the limestone had been quarried using manual labour. Similarity reflects size and age since closure, and not geographical position. There were positive correlations between the estimated age of the quarry and

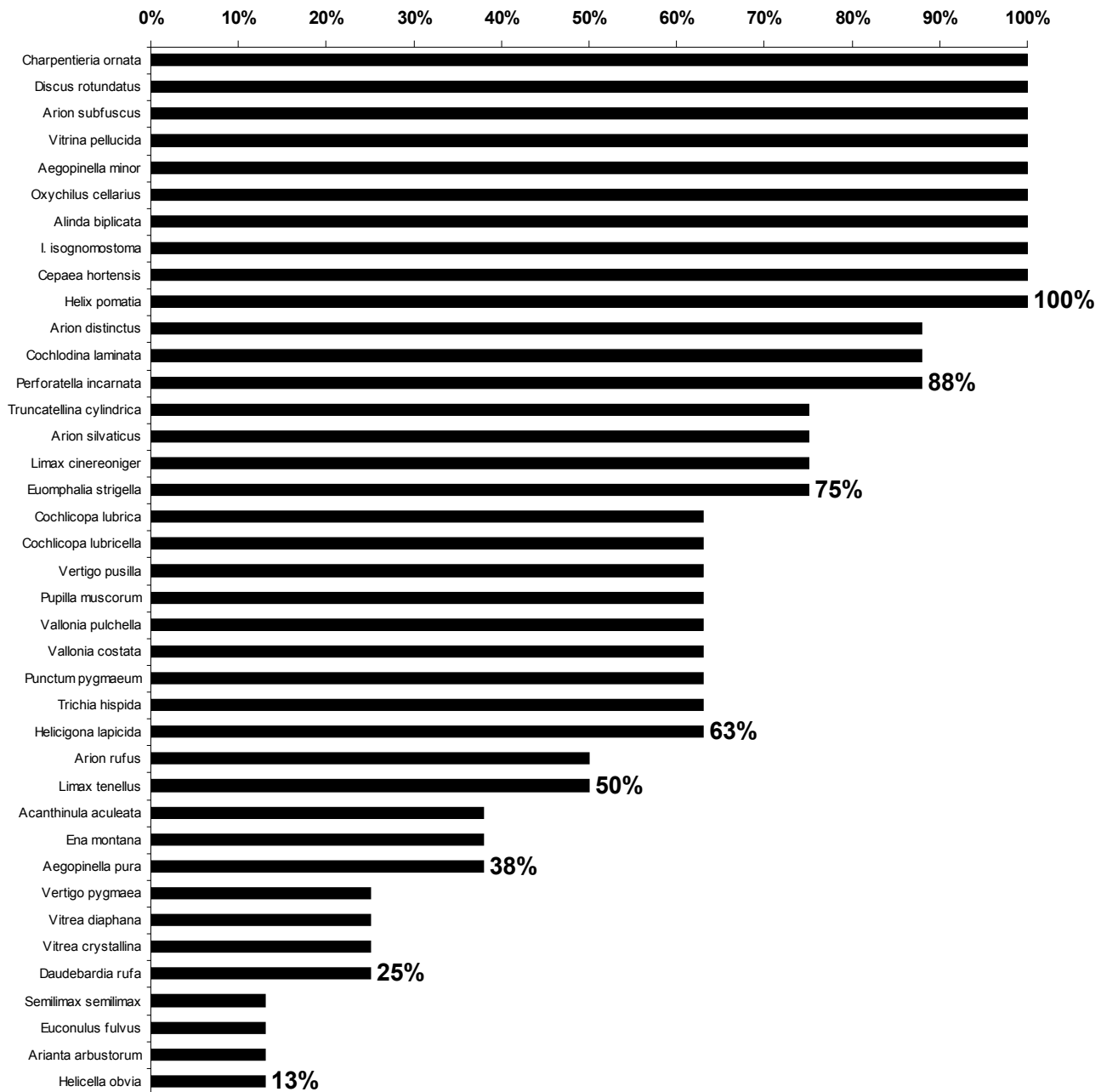


Figure 2 Constancy of occurrence of species accompanying *Ch. ornata* in the eight sites in the Krowiarki range

the number of species ($r = 0.64$, $0.1 > P > 0.05$), and between the quarry size and the number of species ($r = 0.88$, $P < 0.05$).

The proportion of various ecological groups in the malacocoenoses depended on the habitat conditions in the quarries. Detailed observations included three quarries in the Mt. Wapniarka group (Figure 4), of different age and advancement of succession. In site 2 (the youngest quarry) the proportion of xerothermophilous, open-country and shrubland species was high and that of forest-dwellers was much lower. In site 1, older than 2, the percentage of forest-dwell-

ers was very high, while xerothermophilous and open-country species constituted a smaller proportion. In the oldest quarry (site 4) forest-dwellers dominated, shrubland species formed a considerable proportion, whereas open-country and xerothermophilous species constituted only a few percent (Table 2, Figure 5). Assigning species to consecutive stages of succession (Figure 6), showed that in the youngest quarry species of stage I were relatively numerous (30%), and in the remaining quarries their proportion decreased (16% and 3%, respectively); species of stage IV dominated in the oldest quarry (52%);

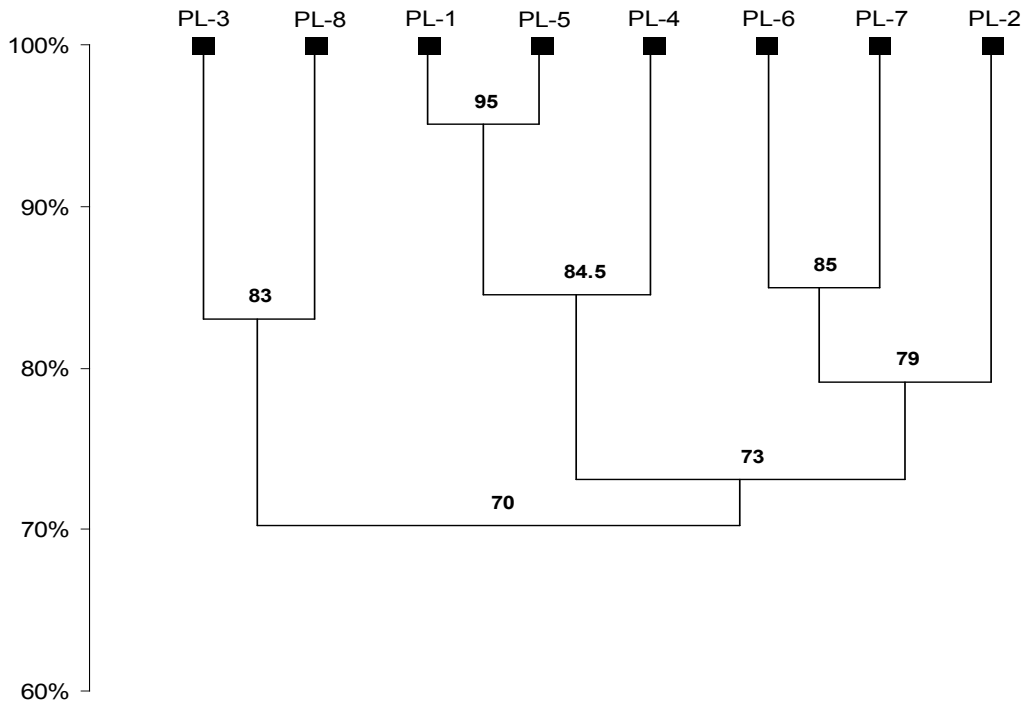


Figure 3 Similarity diagram of malacocoenoses from the eight Polish sites of *Ch. ornata* (Nei, %)

their percentage in the intermediate quarry was smaller (39%), and in the youngest quarry it was only 15% (Figure 7).

POPULATION STUDIES

The three quarries on Mt. Wapniarka were also surveyed for population density of *Ch. ornata* (Table 3). The density, estimated by direct counts was the highest in site 1 (10.4–15.4 indiv./m²; mean: $14 \pm \text{SE } 9.61$), followed by site 2 (9–11.6 indiv./m²; mean: $10.18 \pm \text{SE } 4.49$). The distribution of snails on each rock face was far from even or random: most specimens were found in places with small ledges covered in herbaceous vegetation, or crevices, while only single or no snails were found in places with smooth surface, with no plants or crevices. It is likely that these direct counts underestimate population density in Site 2 to a greater extent than in the others; ongoing mark-recapture studies (Maltz, unpublished) show a lower rate of recapture than in Site 1, although numbers found by direct search are very similar. The density was least (1.3–2.1 indiv./m²; mean: $1.7 \pm \text{SE } 2.31$) in the oldest, most forested quarry (site 4). The exposed rock faces with the sampling plots in the two younger quarries were from c. 200 to c. 400 m² in area, which, assuming the mean density of c. 12 indiv./m², results

in c. 36,000 individuals per rock face, and thus the abundance of *Ch. ornata*, depending on the quarry, can be roughly estimated as several thousand to a few hundred thousand individuals.

DISCUSSION

LOCAL DISTRIBUTION AND ECOLOGICAL SUCCESSION
The striking feature of the distribution of *Ch. ornata* in these isolated northern populations is the absence of the species from natural limestone crags under forest cover, and its preference for open and only recently abandoned quarries. Thus, the closest modern equivalent of the natural climax vegetation type is uninhabited, while recently abandoned anthropogenic habitats in the early stages of succession are favoured.

This preference is clear not only from the physical character and history of the quarries in which the species was found, and in its varying abundance among them, but also by the tendency to associate with other species often regarded as pioneers, or as characteristic of open and even xerothermic habitats.

The definition of "pioneer" in this context is necessarily imprecise. Published information on colonisation of habitats undergoing primary

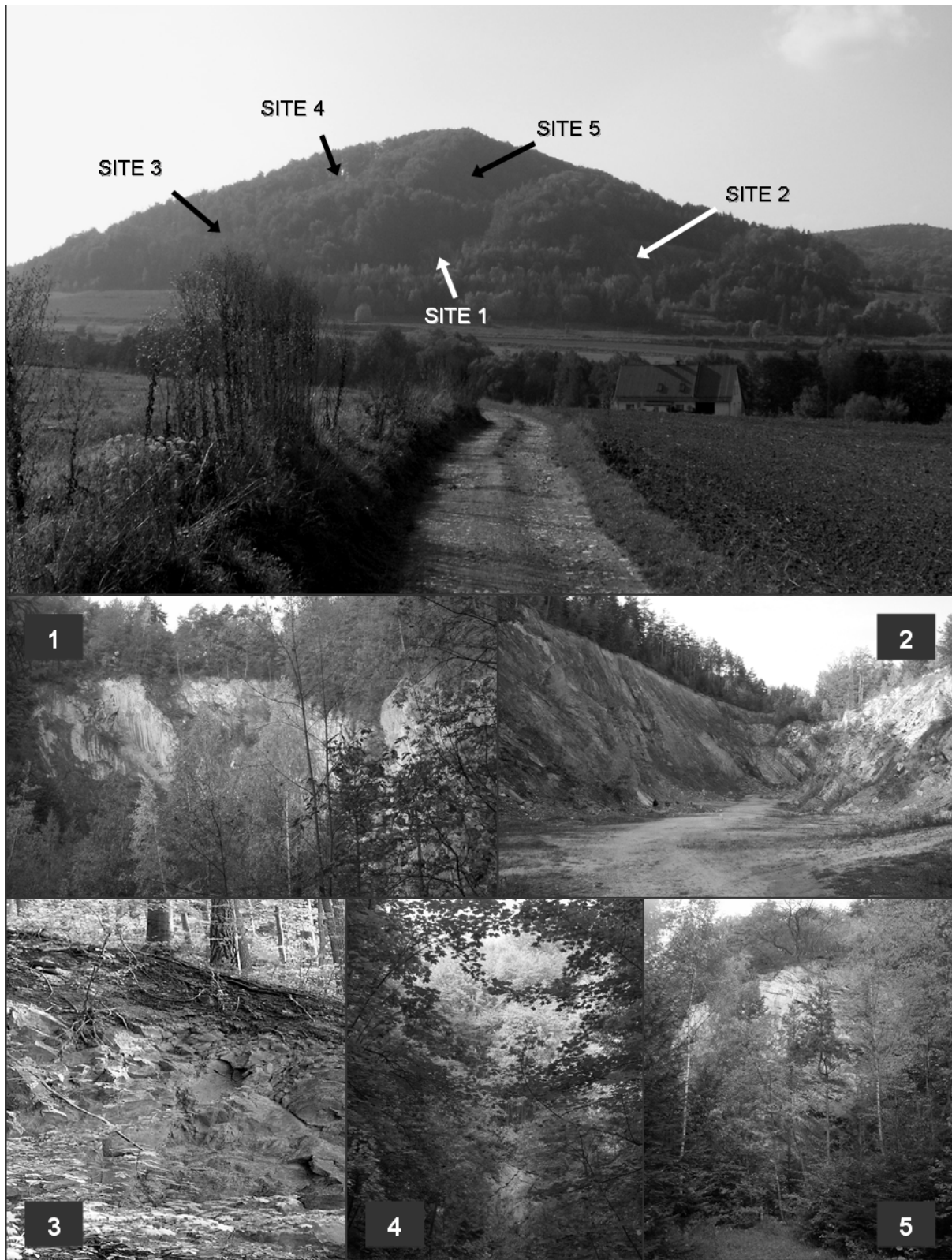


Figure 4 Location of five abandoned quarries on the north-eastern slope of Mt. Wapniarka

or secondary succession by terrestrial snails is scarce. In each of the studied cases the authors attempted to distinguish a group of pioneering species. For the islands of Swedish lakes Mälaren

and Vänern, within the first 100 years after their appearance, or for the islands off the northern coast of the Baltic, the group includes *Zonitoides nitidus*, *Nesovitrea hammonis*, *Succinea putris*,

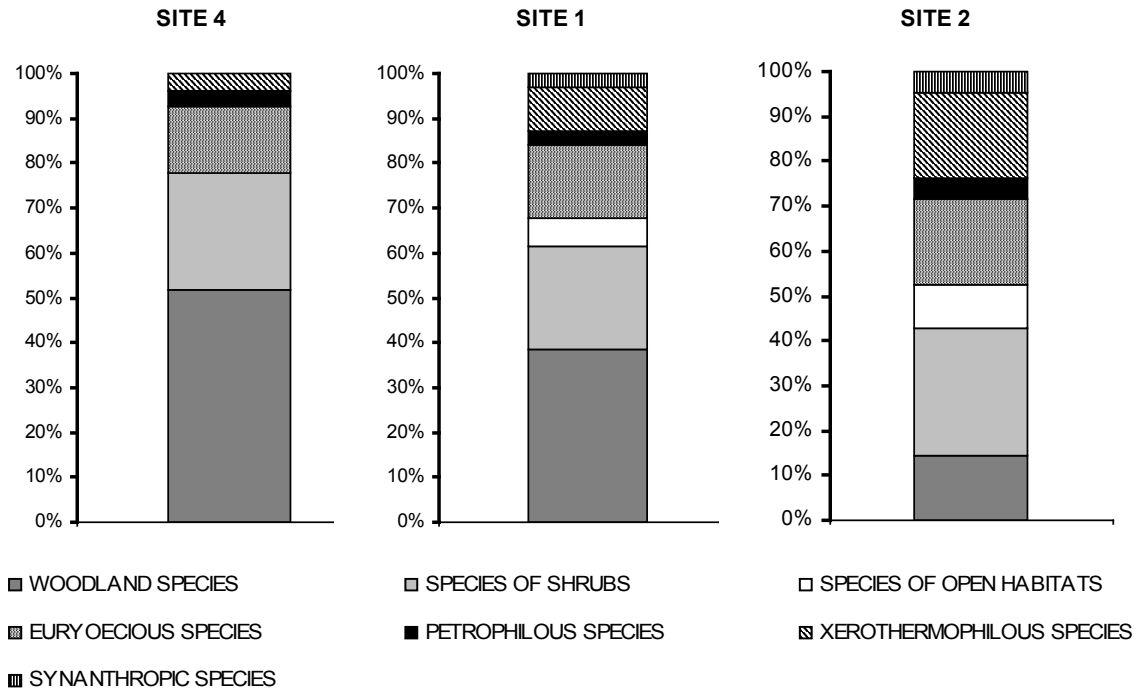


Figure 5 Ecological composition of malacocoenoses in the three quarries of different age on Mt. Wapniarka

Cochlicopa lubrica, *Euconulus fulvus*, *Vallonia pulchella* and *Vitrina pellucida* (Valovirta, 1979; Baur and Bengtsson, 1987; Waldén, 1992); in mining waste-heaps near Kielce, aged c. 30–60 years, pioneer species include *Cochlicopa lubrica*, *C. lubricella*, *Columella edentula*, *Truncatellina cylindrica*, *Vallonia costata*, *V. pulchella*, *Punctum pygmaeum*, *Arion subfuscus*, *Vitrina pellucida*, *Nesovitrea hammonis*, *Euconulus fulvus*, *Perforatella incarnata* and *Trichia hispida* (Barga-Więcławska, 1997). In field copses in Lower Silesia, formed within the last 50–80 years, the best colonisers are *Vitrina pellucida*, *Nesovitrea hammonis*, *Cochlicopa lubrica*, *Punctum pygmaeum*, *Arion subfuscus*, *Trichia hispida*, *Perforatella incarnata*, *Aegopinella pura*, *Vallonia pulchella*, *V. costata* and *Helix pomatia* (Baucz-Malij, 2001). Although there are species in common in these accounts, and also in the quarries studied here, different initial conditions, different sources, and simple accident all play a part in determining the order and identity of colonists.

The quarries where *Ch. ornata* occurs are typical examples of anthropogenic habitats undergoing a secondary succession. Their colonisation is effected mainly through immigration from adjacent habitats which in that area include forested summits with limestone outcrops, meadows

and cultivated fields. Even forest faunas show a heterogeneous species composition because the forests in the Krowiarki are much fragmented and subject to varying management practices; many are completely secondary. Colonisation of quarries, like that of field copses or industrial waste-heaps, has a random element, and depends directly on the habitats in their nearest proximity (Barga-Więcławska, 1997; Baucz-Malij, 2001), though conditions in all newly abandoned quarries are very similar, and would exclude arrivals for which the habitat was unsuitable. Hence, not all potentially pioneer species are found in all quarries. There is a distinction to be made between pioneers which have very broad environmental tolerances, such as *Cochlicopa lubrica*, *Arion subfuscus*, *Vitrina pellucida* and *Trichia hispida*, and which persist in older quarries, and may indeed have arrived from nearby forests, and species such as *Helicella obvia*, *Pupilla muscorum*, *Truncatellina cylindrica*, *Cochlicopa lubricella*, *Vertigo pygmaea*, *Vallonia pulchella* and *V. costata*, which are typical of open or xerothermic habitats (Riedel, 1988). Thus, among the occupied quarries, these species are abundant in younger quarries (e.g. site 2), with mainly open rocks, while in older ones, more vegetated (e.g. sites 1, 4), only single live specimens and/or single shells are

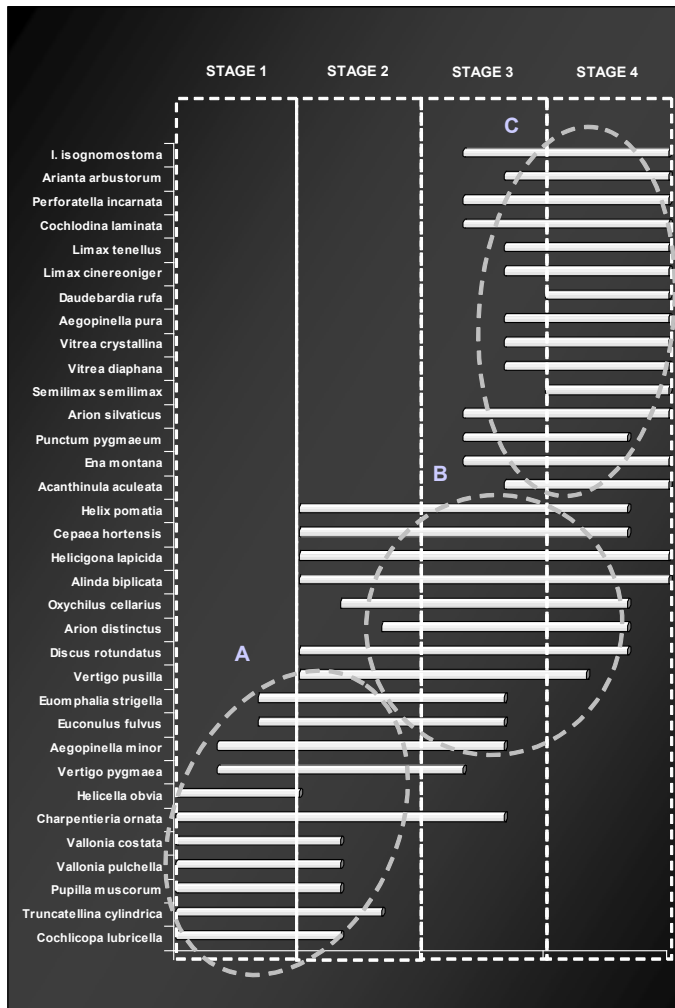


Figure 6 Assigning species to groups corresponding to succession stages 1-4, with the groups of colonisers indicated: A – pioneer species, B – later colonisers, C – last colonisers (euryoecious species omitted)

found. This would indicate that with advancing succession their populations are becoming or have just become extinct. An extreme example is *Helicella obvia*: live individuals today can only be found in site 2 (quarry closed down c. 10 years ago), while in site 1 (abandoned for c. 30 years) only single, eroded shells were found; in site 4 (c. 50 years) there were not even old shells, though at the end of the 1950s live specimens were collected there (Wiktor, 1960). A similar trend was observed for *Pupilla muscorum* and *Cochlicopa lubricella*.

Although not as extreme in its preference as some of these species, *Ch. ornata* clearly falls in this group. Although I do not have faunal lists for sites without *Ch. ornata* in the immediate vicinity, it is possible to compare these faunas with forest faunas on limestone elsewhere in the

Sudetes: these have a much larger proportion of strictly forest-dwelling species, and none of the open/xerothermic pioneers (see below, and Table 2). The variation in density among the three quarries in which detailed studies were carried out also supports its pioneer status. In the oldest quarry, c. 50 years old (site 4), much forested today, only a few live specimens are found (density 1-2 indiv./m²), which would indicate a decline of the population as in the 1950s the snail was still abundant there and open rock faces were numerous (Wiktor, 1960), repeating the pattern seen in *H. obvia*. Similarly, it seems probable that density is higher in Site 2 than in Site 1, though this requires further analysis.

Among other species, all of which are regularly found in forests, many are common to all the quarries. The most restricted, however, are species such as *Acanthinula aculeata*, *Semilimax semilimax*, *Vitrea diaphana*, *V. crystallina* and *Daudebardia rufa*, found only in the older, much vegetated quarries, where *Ch. ornata* is hard to find. Overall, it seems that *Ch. ornata* is limited at this northern extremity of its range to a narrow range of short lived and very anthropogenic habitats. This raises questions about the origins and age of these populations, as well as issues of conservation management.

WIDER DISTRIBUTION AND ORIGINS

The Polish localities of *Ch. ornata* with the nearby, similarly isolated, Czech localities form the north-eastern, and very disjunct part of its range. Some of the Czech localities: Javoříčský Karst in central Moravia (Hlaváč, 2002) and the Peliny Nature Reserve near Choceň in East Bohemia (Juříčková, Horská & Hrabáková, 2006) have been well-studied faunistically. The habitats in both areas are natural rock outcrops, to varying extent covered in natural deciduous or mixed forests, contrary to the anthropogenic Polish sites. Most sites in Javoříčský Karst and in Choceň hold rich malacocoenoses (up to 44 species recorded) (see Appendix and Table 2). In Javoříčský Karst, besides rare calciphile xerothermophilous species such as *Pyramidula pusilla*, *Orcula dolium*, *Granaria frumentum*, *Chondrina clienta* and *Pupilla sterri*, living on open, insolated rocks, the following species are found in more shaded and damper places: *Aegopis verticillus*, *Oxychilus depressus*, *O. glaber*, *Daudebardia rufa*, *Trichia lubomirskii*, *Helicodonta obvoluta* and *Chilostoma faustinum*

Table 3 Population density of *Ch. ornata* in the three quarries analysed in detail (Wapniarka)

Site no.	Site characteristics	Number of individuals per 10 m ²		Number of samples	Mean recapture rate (%)	Mean number of individuals/m ²
		range	mean			
1	the biggest and most diverse quarry, closed down in the 1970s (insolated rocks, shrubs, trees)	104 -154	140	5	43.2	14
2	the youngest quarry, closed down in the 1990s (insolated rocks, shrubs)	90 - 116	101.8	5	13.5	10 (10.18)
4	the oldest quarry, closed down in the 1950s (forest, humid rocks)	13 - 21	17	3	0	2 (1.7)

Table 4 Comparison of the Polish and selected Czech sites of *Ch. ornata* with respect to the number of species and ecological indices; 1) data based on Hlaváč (2002), Juříčková, Horsák & Hrabáková (2006)

Country	Poland	Czech Republic ¹⁾
total species	39	68
mean species/site	24.75 (± SE: 2.12)	31.33 (± SE: 5.77)
range	16-32	14-44
Whittaker's I	1.576	2.17
I _{MAX}	1.219	1.545
mean IFO	0.197 (± SE: 0.012)	0.334 (± SE: 0.044)
Woodland species (%)	38	47

(Hlaváč, 2002), while the malacofauna in Choceň includes such rarities as *Pupilla sterri*, *Tandonia rustica*, *Cochlodina costata* and *Helicodonta obvoluta* (Juříčková *et al.*, 2006), which indicates both a considerable heterogeneity among these habitats and their primaeval character. In the Czech sites 10 clausiliid species form a part of the accompanying malacofauna, a typical indicator of stable forest cover (Pokryszko and Cameron, 2005); in the Polish sites only two clausiliids co-occur with *Ch. ornata*, both with rather euryoecious habits. In terms of faunal similarity (Figure 8), the group of Polish localities forms a separate cluster ($N \geq 0.7$), while four of the Czech localities form a cluster which is more similar to the Polish sites ($N = 0.53$), than to the remaining two rather species-poor malacocoenoses in Javoříčský Karst ($N = 0.49$). The similarity of the Polish localities to the fauna of Choceň and of Javoříčský Karst con-

sidered separately is much greater in the former case ($N = 0.61$) than in the latter ($N = 0.49$). The similarity with the Choceň malacocoenosis is even greater when the Polish sites are treated as a single malacocoenosis (out of 39 species from the quarries and 44 in Choceň, 30 are shared, thus $N = 0.72$). This may be the area (Choceň, Orlické Mts.) from which *Ch. ornata* colonised the Polish localities.

The localities of *Ch. ornata* in the Czech Republic hold not only richer and more natural malacocoenoses; the proportion of forest-dwellers there is higher (Table 2). They are situated more to the south and some of them are more forested, compared to the Polish sites. Moreover, the Czech sites do not form a distinct cluster in the similarity diagram (Fig. 8) and appear much more heterogeneous. This is especially important in view of the fact that the Polish localities are on

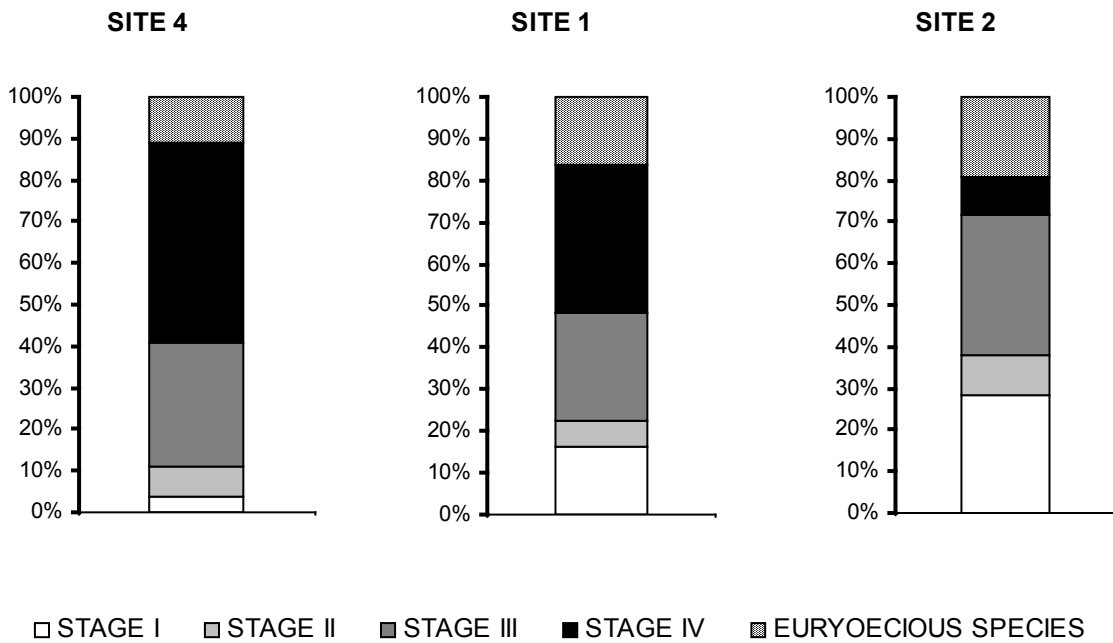
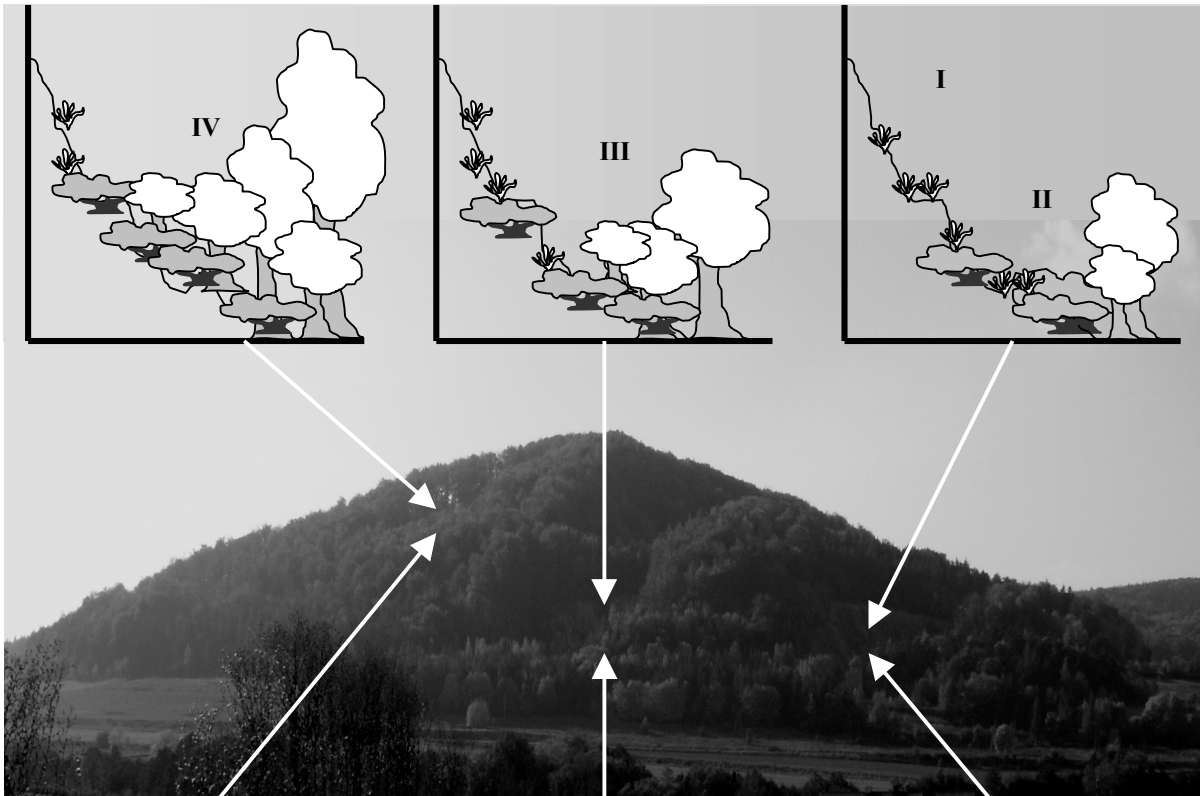


Figure 7 Proportion of species associated with succession stages: 1-4 in the malacocoenoses in the three quarries of different age on Mt. Wapniarka

the border of distribution range of the species. Many data indicate that species whose habitat spectrum is rather wide within the main distribu-

tion area become more fastidious on the fringes of their range (Pokryszko, 1990, 2003). Two natural, forest Polish sites on limestone, situated close to

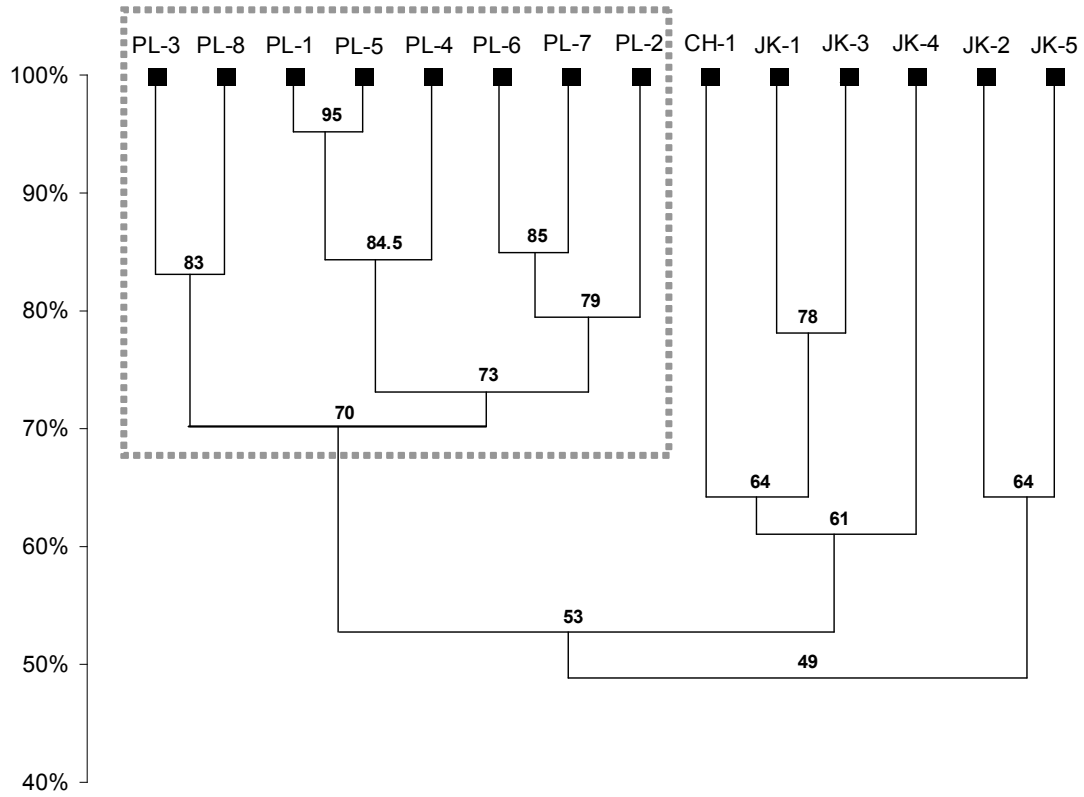


Figure 8 Similarity diagram (Nei, %) for the Polish sites of *Ch. ornata* and selected sites in the Czech Republic (based on data from Hlaváč, 2002; Juříčková, Horský & Hrabáková, 2006)

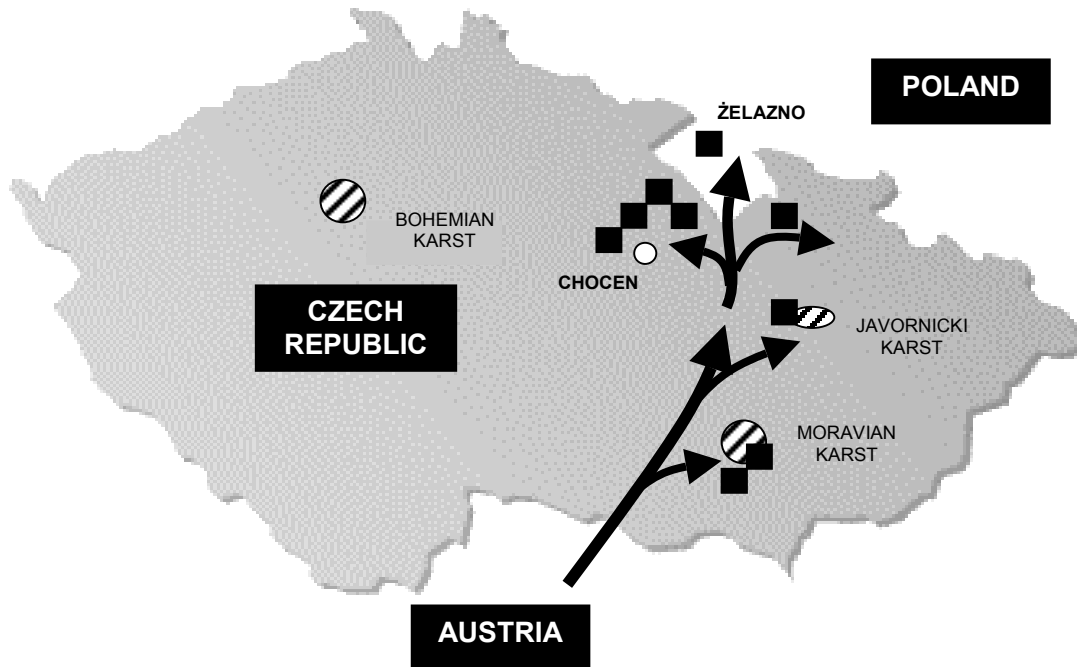


Figure 9 Probable northward migration route of *Ch. ornata* during the Atlantic period (black arrows) and the present insular localities in the Czech Republic (Hlaváč, 2002) and Poland (solid squares)

the localities in the Krowiarki (Rogowa Kopa in Stołowe Mts and Mt. Miłek in Kaczawskie Mts), hold no *Ch. ornata* but otherwise rich malaco-coenoses (Table 2), with the percentage of forest-dwellers similar to that found in the Czech sites: 57% and 47%, respectively (Pokryszko, Cameron & Maltz, 2004, and unpublished).

The presence of *Ch. ornata* only in anthropogenic habitats in Poland might suggest human transport in recent times. While impossible to disprove (there are no suitable Holocene deposits known), the evidence suggests that the most likely period for *Ch. ornata* to have extended its range to include the present-day Czech Republic and the Kłodzko region was the Atlantic climatic optimum when thermophilous deciduous trees started their northward expansion, forming multispecies forests in the formerly glaciated areas (Stworzewicz, 1989). At that time many species from the south and south-west of Europe spread to the north and north-east. These included Alpine species, among others *Ch. ornata* (S. Alpine), *Cochlodina costata* (E. Alpine-Dinaric) and *Macrogastra badia* (E. Alpine) (Riedel, 1988). Except the thermophilous *Ch. ornata*, they are associated with humid forests (*C. costata* is additionally a calciphile and a petrophile), which were favoured by the warm and humid climate of the Atlantic period. Climatic conditions and the optimum species composition of forests are probably primary factors which affected their expansion in that period. They could compensate for deficiencies in other habitat factors (e.g. non-limestone rocks, calcium availability from organic instead of mineral compounds etc.) which are now regarded as necessary for their survival. Suggestions of some authors regarding the colonisation of Lower Silesia by such snails, mainly by *Ch. ornata*, in the interglacial Masovien I (Holstein) and dubbing them "interglacial relicts" (Urbański, 1948; Wiktor, 1956, 1960, 1964) seem unfounded, since none of these species, because of their habitat requirements, would have survived subsequent glaciations. The argument advocated here implies that in the warmer conditions of the climatic optimum, *Ch. ornata* could tolerate full forest cover in Poland, as it now does in more central parts of its range. By chance, enough populations survived the cooling climate to exploit the more xerothermic habitats created by human activity, perhaps initially on crags exposed by forest clearance, and later in

quarries.

Judging by the present relic distribution, the route of northward movement after glacial retreat can be envisaged as running from the Austrian Alps along the south-eastern part of the Czech-Moravian Upland and across the Dražanská Upland towards the Orlické Mts., and then through the Międzyzylesie Pass to the region of Kłodzko (Figure 9). This is supported by the distribution of Czech localities, which are arranged linearly from south to north, with a high concentration in the valleys of the Orlice and in the region of the Orlicke Mts, and by the absence of localities in the Bohemian Karst (Ložek, 1956; Hlaváč, 2002). The species has not been found in the Czech Quaternary deposits (Ložek, 1955).

Today the localities of *Ch. ornata* in the Czech Republic and Poland are limited to limestone: mainly natural outcrops in the former and artificial quarry walls in the latter case (Ložek, 1955, 1956; Wiktor, 1960, 1964, 2004a, b; Riedel, 1988; Hlaváč, 2002; Juříčková and Kučera, 2005, Juříčková *et al.*, 2006). Because of their physico-chemical properties (e.g. heat capacity, hysgroscopic character, high pH, ability to buffer soil solutions, susceptibility to erosion) limestone rocks create a specific microclimate, and provide convenient shelters. Their presence, first of all as open rock faces, is now the main decisive factor for the occurrence of the species in its northernmost localities, as it probably compensates for the climatic changes since the climatic optimum. In contrast to the Polish populations, *Ch. ornata* in the Czech localities, situated on the southern side of the Sudetic-Carpathian range, have survived till present in natural habitats in a milder climate.

CONSERVATION IMPLICATIONS

In the Krowiarki range human activities have fortuitously ensured the survival of *Ch. ornata*. Clear-felling, starting in prehistoric times, and peaking in the 12th c. contributed to creation of huge open areas, including mountain tops and uncovering natural limestone outcrops on which local populations could survive. The first recorded attempts at limestone quarrying in the area were made in the 16th c. (small quarries as artificial rock outcrops); large quarries of the 19th and 20th c. became new areas available

for colonisation and at the same time refuges when reafforestation of the Krowiarki started. At that time succession on natural outcrops and the planting of conifers were probably the main reasons for the extinction of the species outside the quarries. Usually anthropopressure is thought to have negative effects, especially when it involves destruction of natural forest habitats. Out of 88 gastropod species of Poland for which threat categories have been specified (Pawłowska & Pokryszko, 1998), as many as 49 (56%) are endangered because of forest destruction, transformation and fragmentation; many others are threatened by destruction of natural wetland. For two Alpine clausiliids: *C. costata* and *M. badia*, which probably immigrated to Lower Silesia at the same time as *Ch. ornata*, and which are primarily forest-dwellers, such human activity proved to be disastrous. The first species has its only recent locality on Mt. Miłek near Wojcieszów (Pokryszko *et al.*, 2004), the second occurs in single sites in the Bystrzyckie and Stołowe Mts (Wiktor, 1964); only one of the sites has been recently confirmed, Zieleniec near Duszniki Zdrój (Pokryszko, Wiktor and Maltz – unpublished). The populations of the two species in these sites show a low density. Similarly, the less threatened *Helicodonta obvoluta* is dependent on continuous forest cover, and a supply of rotting timber (Maltz, 2003). The populations of *Ch. ornata*, especially those inhabiting the younger and larger quarries, are in a fairly good condition as shown by their abundance. The only danger to this clausiliid is forest succession in the quarries. Because all the sites are close together, they may be threatened by some random events resulting in extinction of all the individuals. In order for the species to survive, the quarries should be actively protected, mainly through regular clear-cutting in places where the rock faces become excessively shaded.

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