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Vlastimil RŮŽIČKA[1*], Miloslav ZACHARDA[2]

[1] Institute of Entomology, Biology Centre, AS CR, Branišovská 31, 370 05 České Budějovice, Czech Republic, *e-mail: vruz@entu.cas.cz (*corresponding author*)
[2] Institute of Systems Biology and Ecology, AS CR, Na Sádkách 7, 370 05 České Budějovice, Czech Republic, e-mail: Zacharda@usbe.cas.cz

VARIATION AND DIVERSITY OF SPIDER ASSEMBLAGES ALONG A THERMAL GRADIENT IN SCREE SLOPES AND ADJACENT CLIFFS

ABSTRACT: The thermal regime of a phonolite scree slope on Klíč Mt., North Bohemia, Czech Republic, was monitored by miniature data loggers. The spiders were collected throughout the entire scree field area and on the adjacent cliff. In 2005 and 2006, the mean internal temperatures at the lower margins of the scree slope were 0.1 and 0.5°C, whereas the mean external ambient temperatures were 6.8 and 7.2°C, respectively. The difference, therefore, is 6.7°C. The long-term cooling of the basal portions, along with the winter heating of the central and upper parts of the scree, are the most specific microclimatic phenomena. The boreomontane species inhabit the extremely cold vents at the lower margins of the scree slope. Species of alpine origin inhabit the middle portions of the scree slope. Six thermophilous species inhabit the sun-exposed rock margins of Klíč Mt., which is nearly at the uppermost limit of their vertical distribution in the Czech Republic.

KEY WORDS: biodiversity, microclimate, rock wall, scree slope, spiders

1. INTRODUCTION

There are two main natural habitats that comprise bare bedrock: solid cliffs and scree slopes, that consist of accumulations of rock blocks and stones. Among terrestrial habitats there are few gradients of environmental factors and accompanying biota that have been shown to be more distinct than those found on scree slopes (Růžička *et al.* 1995), as well as on cliffs (Larson *et al.* 1989, 2000).

Scree accumulations represent island habitats in the temperate zone (Růžička 1990b, Růžička and Klimeš 2005). They exhibit distinct temperature gradient between the surface and the inner space of scree, and between the upper and lower margins of scree slopes (Molenda 1989, Růžička 1990b, Růžička *et al.* 1995, Wunder and Möseler 1996). Ice can form and periglacial microclimate can persist on the lower margin of scree slopes, especially in lower altitudes (Balch 1900, Molenda 1996, Růžička 1999b, Gude and Molenda 2000, Zacharda *et al.* 2005, 2007). Extensive underground spaces represent a special type of underground environment (Molenda 1989, Růžička 1990b, 1999a). Cliffs are island-like habitats in the temperate zone and also exhibit specific microclimatic phenomena (Larson *et al.* 2000, Blick *et al.* 2002). However, these two habitats are usually studied separately. Assemblages of spiders inhabiting screes in the Czech Republic are well known (Růžička and Klimeš 2005), whereas those on the rock walls are known poorly (Růžička 2000, 2007).

The objectives of this study are (1) to provide ecological data on spider assemblages in the understudied cliff and adjacent scree slope habitat to elucidate their relationships along the thermal gradient in the scree slope; (2) to attempt to evaluate ecological demands and geographic distribution of the collected species of spiders.

2. MATERIALS AND METHODS

2.1. Study site

Klíč Mt. (759 m a.s.l.) is a solitary phonolite knob in the Lužické Hory Mts (Fig. 1) within the Sudeten, North Bohemia, near the town of Nový Bor (50°47‘N, 14°34‘E). The climate at this site is temperate with mean annual air temperature of 6.0–8.8°C, and typical January and July mean air temperature of 3.8°C and 16.8°C, respectively. Annual precipitation measured at nearby weather stations totals 600–750 mm with maximum snow depths in January of 20–35 cm.

The southwest-facing phonolite scree slope, with a gradient of approximately 35°, is composed of rockfall and weathering-derived blocks ranging from 40 to 80 cm in diameter. The frost cliff looms over the scree field at an altitude of 600 m a.s.l. (Sýkora 1972).

Most of the scree slope's surface is bare. Cold air permanently seeps from the lower margins of the scree slope at an altitude of 540 m a.s.l., which is covered with mosses and lichens. This part of the scree was investigated geophysically on June 19, 2001. The blocky layer's thickness was estimated to be approximately 10 m, and small ice lenses were inferred (Gude *et al.* 2003).

The locality has the status of a Nature Reserve. Thermophilous oak forest and relict plant species growing on the west-facing cliff face are subject to nature conservation (Mackovčin *et al.* 2002).

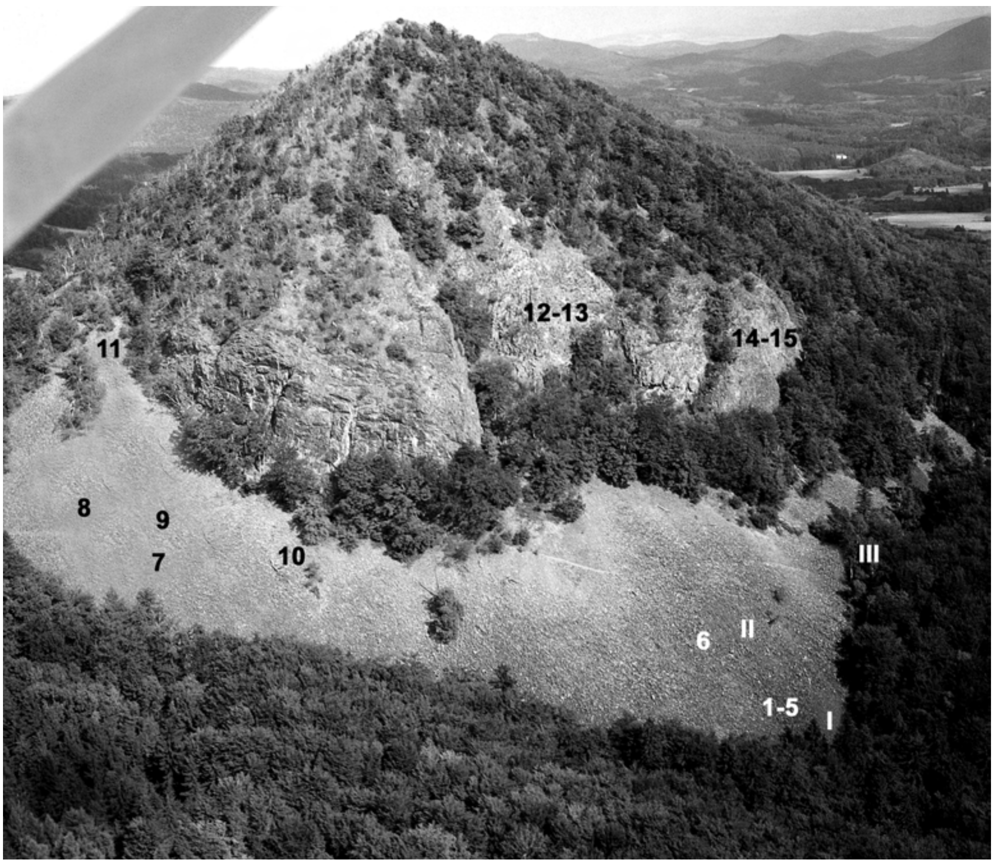

Fig. 1. Klíč Mt. with the locations of the samples (Arabic numerals) and data-loggers (Roman numerals). Photo: M. Zacharda.

2.2. Field temperature measurements

Data-loggers (Model TGU-0050, Gemini Data Loggers Ltd., UK) with internal thermistors (accuracy ± 0.2°C) were used to measure the temperature, with a logging interval of three hours. The temperature measurements were carried out independent of the collection of spiders, using three data-loggers. The temperature was measured at the cold and humid lower scree margin, with the long-term cold-air seepage (data-logger I); as well as in the hot and dry middle scree portion, with the winter warm air exhalations (data-logger II). For the internal temperature measurements, the loggers were placed into subsurface voids of the scree at depths of 50 cm. The external air temperature was monitored in a shady place, at which data-logger III was situated on a spruce tree, approximately 2.5 m above the soil surface (Fig. 1).

2.3. Sampling and data analysis

The spiders were primarily trapped in pitfall traps made of rigid plastic. The traps are comprised of a board (20 × 25 cm) which forms an artificial horizontal surface and a can (13 cm high, 10.5 cm in diameter) that is inserted in the center of the board. The traps contained a mixture of 7% formaldehyde and 10% glycerol with a few drops of a surfactant (Růžička 1982). The traps were placed among the stones inside the scree, at a depth of approx. 20–110 cm. Climbing equipment was used to collect the spiders on the steep cliff wall. The traps were hung on the cliff wall by means of wires and hooked nails, which were hammered into crevices of the wall. A band of emery tape was stuck on the back edge of the trap and shaped in order to bridge the gap between the pitfall and the rock surface (Růžička 2000). Spiders were also collected by means of sieving moss and detritus, as well as by hand sorting.

In total, 15 samples were collected at different parts of the mountain slope (Fig. 1):

1. Lower margin of the scree slope, pitfall trap (PT), depth of 20 cm, Oct 1999-Jun 2000
2. Lower margin of the scree slope, pitfall trap (PT), depth of 25 cm, Oct 1999-Jun 2000
3. Lower margin of the scree slope, pitfall trap (PT), depth of 30 cm, Oct 1999-Jun 2000
4. Lover margin of the scree slope, sieving of detritus, Oct 1999
5. Lover margin of the scree slope, sieving of mosses, Oct 1999
6. Middle part of the scree slope, hand picking among bare stones, Jun 2001
7. Middle part of the scree slope, PT, depth of 100 cm, Nov 1989-May 1991
8. Middle part of the scree slope, PT, depth of 110 cm, Nov 1989-May 1991
9. Middle part of the scree slope, PT, depth of 40 cm, Nov 1989-May 1991
10. Upper margin of the scree slope, pitfall trap, depth of 30 cm, Nov 1989-May 1991
11. Shady, rock wall, hanging PT, Apr-Sep 2000
12. Sun exposed, steep upper rock margin, hanging PT, Apr-Sep 2000
13. Sun exposed, steep upper rock margin, hanging PT, Apr-Sep 2000
14. Sun exposed, vertical upper rock margin, hanging PT, Apr 2000-May 2001
15. Sun exposed, vertical upper rock margin, hanging PT, Apr-Sep 2000

Because the installation of a large number of pitfall traps and/or picking more samples would have conflicted with nature conservation policy, we could not obtain larger amounts of material.

The characteristics given by Buchar and Růžička (2002) were used to provide the basic ecological information on the spider species.

The range of semi-quantitative *humidity* data that characterizes habitats as: very dry, dry, semi-humid, humid, or very humid were used as well as *phytogeographic district* that characterizes the species occurrence. The Czech Republic can be divided into three districts: *thermophyticum* (a region of thermophilous flora and vegetation, where non-forest phytocoenoses with species of the sub-meridional vegetation zone prevail), *mesophyticum* (a region of deciduous forests with the flora of the temperate zone) and *oreophyticum* (a region of mountain flora where spruce prevails in the natural forests).

The nomenclature of the taxa follows that of Platnick (2008) in the world spider catalogue. Voucher specimens were deposited in the collection of V. Růžička.

Species abundances were log-transformed, and the community variation summarized by the detrended correspondence analysis (DCA) method, using Canoco for Windows 4.5 software (Ter Braak and Šmilauer 2002).

3. RESULTS

3.1. Thermal regime

In the colder basal parts of the scree, the year-round pattern of the internal temperature is influenced by the melt of the near-surface interstitial ice. There, the cool downslope airflows of approx. 0°C stream out of the ground vents which cool the basal parts of the scree (Fig. 2).

In the vents of the central parts of the scree, the course of the temperature fluctuations follows that of the external atmospheric temperature. However, particularly at the onset of the winter season, warm ascending exhalations are expelled from the middle inner portions of the scree, mainly during frosty spells, which increase the temperature of the scree slope (Fig. 3).

The mean, maximum, and minimum annual external air temperature were 6.8,

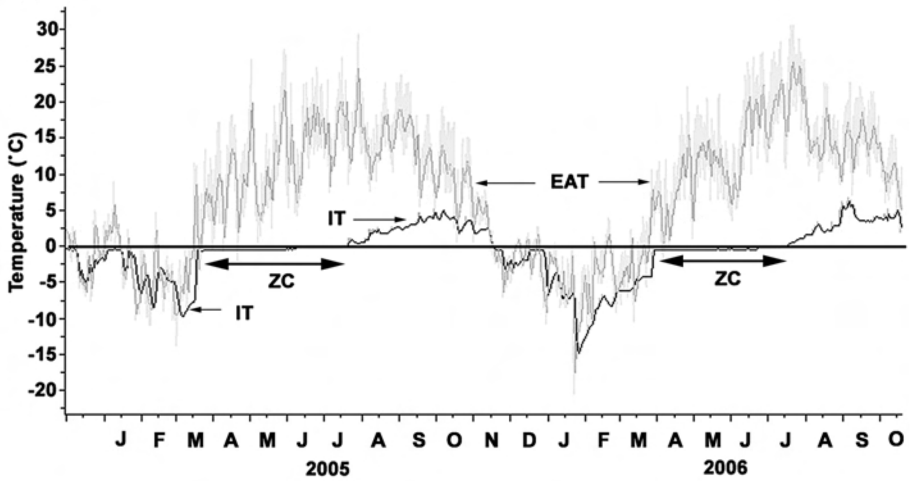

Fig. 2. Temperature variations (°C) at the Klíč study site, in the years 2005 and 2006: EAT, external ambient air temperature; IT, internal temperature at the base of the scree slope; ZC, period of the 'zero curtain' thermal regime, when the temperature remains at approx. 0°C, as near-surface interstitial ice melts.

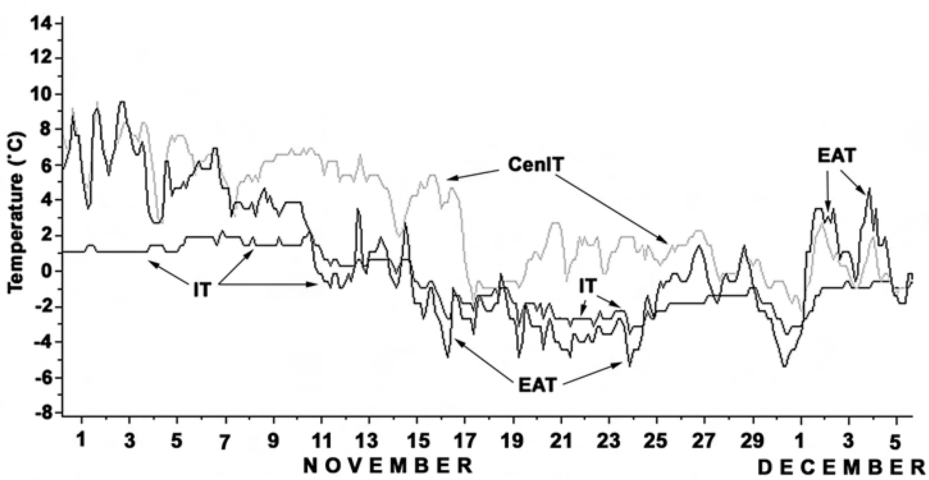

Fig. 3. Temperature variations (°C) at the Klíč study site at the onset of the winter season in 1999: EAT, external ambient air temperature; IT, internal temperature at the base of the scree slope; CenIT, temperature of the ascending warm air emissions, expelled in the central area of the scree slope.

Table 1. List of species with the number of individuals in three sample groups and their ecological characteristics. A: lower margin of the scree slope. B: middle part of the scree slope and shady rocks. C: sun-exposed rocks. Humidity: vh, very humid; h, humid; s-h, semi-humid; d, dry; vd, very dry. Phytogeographic district: T, Thermophyticum; M, Mesophyticum; O, Oreophyticum. The basic values are printed in medium font, the markedly preferred values are printed in bold, and some marginal values are shown in parentheses.

Number of ind.			Species	Species habitat preference	
A	B	C		Humidity	Phyto
80	-	-	*Diplocentria bidentata* (Emerton, 1882)	h	M, O
62	-	-	*Anguliphantes tripartitus* (Miller and Svatoň, 1978)	h	(M), **O**
1	-	-	*Centromerus arcanus* (O. P.-Cambridge, 1873)	h, **vh**	M, **O**
1	-	-	*Tenuiphantes alacris* (Blackwall, 1853)	s-h, h	M, **O**
1	-	-	*Diplocephalus latifrons* (O. P.-Cambridge, 1863)	s-h, h	M, O
1	-	-	*Tallusia experta* (O. P.-Cambridge, 1871)	**h**, vh	**M**, (O)
1	-	-	*Araeoncus humilis* (Blackwall, 1841)	(d), s-h, h	(T), **M**
1	-	-	*Centromerus sylvaticus* (Blackwall, 1841)	vd, d, s-h, h	T, M, O
3	19	-	*Bathyphantes eumenis buchari* Růžička, 1988	s-h, h	(M), **O**
1	1	-	*Diplocephalus cristatus* (Blackwall, 1833)	s-h	**M**, (O);
-	6	-	*Rugathodes bellicosus* (Simon, 1873)	s-h	M, O
-	4	-	*Lepthyphantes notabilis* Kulczyński, 1887	vd	(T), M, O
-	4	-	*Theonoe minutissima* (O. P.-Cambridge, 1879)	h, vh	**M**
-	3	-	*Tegenaria silvestris* L. Koch, 1872	s-h, h	**M**, (O)
-	3	-	*Euryopis flavomaculata* (C. L. Koch, 1836)	d, s-h, h	T, **M**
-	2	-	*Porrhomma myops* Simon, 1884	h	M, O
-	2	-	*Trogloneta granulum* Simon, 1922	h	M
-	2	-	*Pholcomma gibbum* (Westring, 1851)	s-h	**M**
-	2	-	*Walckenaeria capito* (Westring, 1861)	vd, h	M
-	1	-	*Harpactea lepida* (C. L. Koch, 1838)	s-h	**M**, (O)
-	1	-	*Zora nemoralis* (Blackwall, 1861)	d, s-h	(T), **M**
-	4	-	*Microneta viaria* (Blackwall, 1841)	s-h	T, **M**, O
-	1	1	*Dismodicus bifrons* (Blackwall, 1841)	h	**M**, (O)
-	1	2	*Trochosa terricola* Thorell, 1856	vd, d, **s-h**, h	T, M, (O)
-	1	4	*Hahnia pusilla* C. L. Koch, 1841	vd, d, **s-h**, h	M
-	1	23	*Drassodes lapidosus* (Walckenaer, 1802)	**vd**, d	T, M
-	-	9	*Xerolycosa nemoralis* (Westring, 1861)	vd, d, s-h	T, M, O
-	-	7	*Gnaphosa bicolor* (Hahn, 1833)	vd, **d**, s-h	T, M
-	-	7	*Theridion betteni* Wiehle, 1960	vd	**M**
-	-	5	*Aelurillus v-insignitus* (Clerck, 1757)	**vd**, d	T, **M**
-	-	5	*Zelotes puritanus* Chamberlin, 1922	**vd**	**T**, (M)
-	-	4	*Talavera petrensis* (C. L. Koch, 1837)	vd, d	T, M
-	-	2	*Heliophanus aeneus* (Hahn, 1832)	vd	(T), M
-	-	1	*Evarcha laetabunda* (C. L. Koch, 1846)	d, (h)	**T**, (M)
-	-	1	*Echemus angustifrons* (Westring, 1861)	vd	T, M
-	-	1	*Harpactea hombergi* (Scopoli, 1763)	d, s-h	T, M
-	-	1	*Porrhomma microphthalmum* (O. P.-Cbr., 1871)	vd, d, s-h	T, M
-	-	1	*Oedothorax apicatus* (Blackwall, 1850)	vd, d, s-h	T, M
-	-	1	*Amaurobius jugorum* L. Koch, 1868	vd, d	T, M
-	-	1	*Apostenus fuscus* Westring, 1851	(vd), d, s-h	T, M
-	-	1	*Walckenaeria furcillata* (Menge, 1869)	d, s-h	T, **M**
-	-	1	*Pachygnatha clercki* Sundevall, 1823	s-h, **h**	T, **M**
-	-	1	*Evarcha falcata* (Clerck, 1757)	vd, d, s-h, (h)	(T), **M**
-	-	1	*Centromerus incilium* (L. Koch, 1881)	vd, d, s-h	(T), M
-	-	1	*Pachygnatha degeeri* Sundevall, 1830	vd, d, **s-h**, h	T, **M**, (O)
-	-	1	*Walckenaeria antica* (Wider, 1834)	vd—vh (T),	**M**, (O)
-	-	1	*Robertus lividus* (Blackwall, 1836)	s-h	T, M, O
-	-	1	*Pardosa pullata* (Clerck, 1757)	s-h, h	T, M, O
-	-	1	*Ceratinella brevis* (Wider, 1834)	d, s-h	M, (O)
-	-	1	*Macrargus rufus* (Wider, 1834)	d, **s-h**	**M**, O
-	-	1	*Callobius claustrarius* (Hahn, 1833)	d, **s-h**, **h**	M, O
-	-	1	*Centromerus pabulator* (O. P.-Cambridge, 1875)	h, vh	**O**

29.4, and −13.9°C (2005), and 7.2, 30.6, and −20.7°C (2006). The mean, maximum, and minimum annual interior temperature of the basal part of the scree slope were 0.1, 5.1, and −9.9°C (2005), and 0.5, 6.7, and −14.8°C (2006). The mean annual negative temperature anomaly at the lower margin of the scree slope was 6.7°C.

3.2. Diversity of spiders

A total of 298 spiders were captured. Fifty-two species and thirteen families were identified (Table 1). The catch in a pitfall trap amounts from 4 to 19 specimens in scree, and from 10 to 31 specimens on sun-exposed rock margin.

The DCA analysis represented by an ordination diagram showed the different positions of the collected samples of spiders (Fig. 4). The main gradient of the species compositional changes runs along the first (horizontal) ordination axis, and represents the two distinct groups: group A with samples 1–5, and group C with samples 12–15. These two groups are interconnected by samples with an intermediate species composition: group B, samples 6–11. Each group is characterised by the presence of stenotopic species.

Group A corresponds to the lower margins of the scree slope, where the cold exhalations and ice formations were observed. It was there that 10 species of the family Linyphiidae were captured. This assemblage is characterized by the presence of species with an affinity for humid habitats and Oreophyticum. *Diplocentria bidentata*, *Anguliphantes tripartitus,* and *Bathyphantes eumenis buchari* were the most abundant species. *Diplocentria bidentata* and *Bathyphantes eumenis* have the boreomontane distribution area (Table 1).

Group B corresponds to the middle and upper parts of the scree slope, with a moderate microclimate and a shady rock wall. In total, 18 species from nine families were captured. This assemblage is characterized by the presence of species with a preference for semi-humid habitats and Mesophyticum. *Lepthyphantes notabilis*, *Rugathodes bellicosus*, and *Trogloneta granulum* are of alpine origin (Table 1).

Group C corresponds to the sun exposed rocks. In total, 30 species from ten families were captured there. This assemblage is characterized by the presence of species that prefer dry to very dry habitats, *i.e.*, the Thermophyticum and Mesophyticum. Here, the typical species are *Drassodes lapidosus*, *Xerolycosa nemoralis*, *Gnaphosa bicolor*, *Theridion betteni*, *Aelurillus v-insignitus*, and *Zelotes puritanus*. Six species here occur near their uppermost limit of vertical distribution in the Czech Republic (*Gnaphosa bicolor*, *Zelotes puritanus*, *Evarcha laetabunda*, *Echemus angustifrons*, *Amaurobius jugorum*, *Centromerus incilium*) (Table 1).

4. DISCUSSION AND CONCLUSIONS

Scree habitats are extremely energy-poor environments, similar to caves (Culver and Pipan 2009). Based on the material from

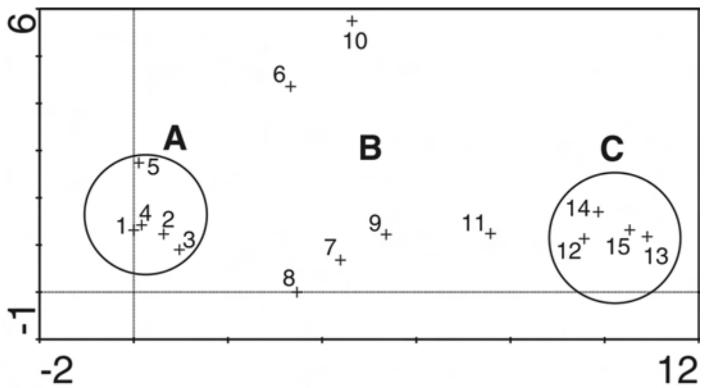

Fig. 4. DCA ordination diagram with sample points, displaying the first two ordination axes of DCA (explaining, respectively, 15.5% and 8.4% of the total variation – inertia). Compact groups of samples: A (lower margin of scree slope) and C (sunexposed rocks), and interconnecting samples B (middle and upper parts of scree slope) were distinguished (see Table 1).

128 pitfall traps processed by Růžička and Klimeš (2005), the mean annual catch in a pitfall trap exposed on the surface of a scree amounts 18 spiders, in a trap installed at a depth of 50 cm 10 spiders, and at a depth of 100 cm 7 spiders. For comparison, the mean annual catch in one trap installed in the meadow habitat amounts 430 spiders (Růžička 1987).

Though screes and rocks are different habitats, they are similar in some aspects. They are formed mainly by bare bedrock and they can exhibit similar microclimatic phenomena. This may result in constitution of similar assemblages of invertebrates. In contrast, some species of invertebrates are strictly specific either to the rock cliffs or screes. For example, *Lepthyphantes notabilis*, *Rugathodes bellicosus*, *Trogloneta granulum*, and *Porrhomma myops* are exclusively scree inhabitants. *Theridion betteni* is an exclusive cliff inhabitant.

Cold air seepage at the lower margins of the scree slope is the most important environmental factor influencing the existence of the particular assemblage of spiders with a limited number of species (Růžička and Klimeš 2005). On Klíč Mt., spiders of boreal origin, *Bathyphantes eumeis buchari* and *Diplocentria bidetata*, inhabit the extremely cold spaces at the lower margins of the scree slope. *Bathyphantes eumenis buchari* also lives in the middle part of the scree slope, but only at a depth below one meter. This assemblage of spiders is complemented by the predatory mite *Rhagidia gelida* Thorell, 1872 (Acari: Prostigmata). This Arctic mite proved to be a bio-indicator of the long-lasting periglacial microclimate in central Europe (Zacharda *et al.* 2005).

Species of alpine origin such as *Rugathodes bellicosus*, *Lepthyphantes notabilis*, and *Trogloneta granulum* avoid extremely cold scree voids and live in the middle parts of the scree slope (Růžička 1990a).

Thermophilous species *Gnaphosa bicolor*, *Zelotes puritanus*, *Evarcha laetabunda*, *Echemus angustifrons*, *Amaurobius jugorum*, and *Centromerus incilium* were collected on the SW-exposed cliff face of Klíč Mt. at the altitude of approx. 650 m a.s.l., though these species usually occur at an altitude of 300 to 500 m a.s.l., at most (Buchar and Růžička 2002). Similarly, Blick *et al.* (2002) recorded the occurrence of species with mediterran and submediterran origin on south-exposed rocks in temperate zone. Some thermophilous species narrow their ecological niche exclusively to southern exposed rocky habitats towards the north (Růžička 2000). Jonsson (1995) recorded the occurrence of several thermophilous species in the rocky habitats at high latitudes in Sweden.

Spiders associated with stony biotopes were studied in the taiga and tundra zones of Beringia by Marusik (2004). Stony habitats of this region are very diverse and in some regions cover more than 90% of the surface. The stony deserts occupy flat and semi-flat surfaces, and exhibit an extremely severe microclimate. Unlike in Europe, the stony habitats of north-east Siberia are not discontinuous insular refugia. Therefore, species can easily spread (also in an historical aspect) from one area to another. The northeastern Siberian stony habitats are rich in species of spiders. In the Beringian fauna over forty percent of the exclusive scree inhabitants of spiders are endemics. Consequently, the Beringian and European stony habitats are occupied by only a few common species of spiders.

In temperate zone, scree slopes with dynamic air regime are predisposed to form an undercooled core inside. The seepage of cold air from the permanently frozen (or undercooled) core causes the formation of a very narrow strip or spots of a relict arctic microclimate at the lower margin of the scree slope. Such scree slopes can host geographically isolated populations of northern species of invertebrates. On the other hand, sun-exposed rocks represent one of the warmest habitats of a landscape and can harbor isolated populations of thermophilous species in higher altitudes and latitudes.

Despite both rock walls and scree slopes are explicitly cited as important habitats in the Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive No. 92/43/EEC), they still remain among the insufficiently explored habitats. However, we must emphasize that these habitats, and especially the complexes of scree slope with adjacent rock wall, are exceedingly important for nature and global biodiversity conservation and deserve more of scientific attention.

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