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LOCAL DIVERSITY *VERSUS* GEOGRAPHICAL DISTRIBUTION OF ARTHROPODS OCCURING IN A SANDSTONE ROCK LABYRINTH

ABSTRACT: Rocks have been overlooked as subjects for ecological study. However, the system of narrow and deep vertical spaces (gorges, crevices, abysses) in sandstone rocks supports a highly diverse mosaic of habitats. The patterns of air temperatures and the assemblages of arthropods were studied along the environmental gradient in the Poseidon Sandstone Labyrinth within the Adršpašsko-Teplické Skály National Nature Reserve, NE Bohemia, Czech Republic. The labyrinth, developed in Cretaceous sandsones at an altitude of about 600 m, is approximately 740 m long and 550 m wide. It consists of a broken, interconnected network of deep vertical crevices, crevice caves, and talus caves in extensive block accumulations. The total length of the human-accessible underground spaces is estimated to be at least 27 km, the vertical range is 105 m. The annual course of air temperature was monitored on the sun-exposed upper rock margin (max. 26.5°C, min. −7.3°C, mean 6.1°C), as well as in the cold and dark crevice cave (max. 9.6°C, min. −1.9°C, mean 3.7°C). Due to the climatic inversion in the deep vertical spaces, mountain bryophytes and vascular plants occur here. A total of 2285 arthropods belonging to eight taxonomic groups were evaluated; spiders and beetles were the most numerous. We registered 304 species, which colonize the totality of habitats in the labyrinth: cold bottom parts, dark caves, shady rock walls, as well as the sun-exposed upper rock margins. The cold parts of the labyrinth harbour populations of sixteen species of mountain arthropods (beetles, spiders and a harvestman) and five species of arthropods with distributions in tundra or boreal forests, and similar disjunctive habitats in the temperate zone in central Europe (spiders and a mite). The first record of the Arctic predatory mite *Rhagidia gelida* in central Europe was in the Poseidon Labyrinth in 1986; this species proved to be a bio-indicator of the long-lasting periglacial microclimate in central Europe. Prior to discovery of the spider *Sisicus apertus* in the Poseidon Labyrinth, it had been recorded in central Europe in the Alps and in the High Tatra Mountains at altitudes of 1150 to 2300 m. At the present time, we consider the Poseidon Sandstone Labyrinth to be a paleorefugium of cold-adapted arthropods.

KEY WORDS: sandstone; microclimate; paleorefugium; arthropods

1. INTRODUCTION

Sandstones of varying age and composition cover considerable portions of the Earth's surface. Few sandstone occurrences are known from the arctic zone. The sandstones of humid tropical climates are usually affected by intensive surface and sub-surface silicification, and transformed into secondary quartzite (Venezuela). Today, the large areas of sandstone are mostly found in arid and semi-arid environments (e.g. USA, Arabia, and North Africa), but also in the temperate zone of Europe (Cílek *et al.* 2007). The majority of Central European sandstone areas are organized as 'rock cities', mazes of usually narrow vertical gorges and sandstone blocks that somewhat resemble an actual town or city (Cílek *et al.* 2007). Selective denudation processes have extensively modified them (Härtel *et al.* 2007b). The Bohemian Cretaceous Basin, which broadly extends across the northern parts of the Czech Republic and on into Poland and Germany, is an especially extensive area with numerous prominent sandstone features (Balatka and Sládek 1984, Härtel *et al.* 2007a).

Generally, rock walls have been overlooked as subjects for ecological study (Larson *et al.* 2000). However, the system of numerous narrow and deep vertical spaces (gorges, crevices, abysses) in these sandstone areas supports a highly diverse mosaic of habitats: sun-exposed rock margins and rock walls, shaded rock walls, dark bottoms of crevices, and aphotic caves. The diversity of communities on a steep microclimatic gradient has been partly documented for mosses (Zittová-Kurková 1984), vascular plants (Sádlo *et al.* 2007, Härtel *et al.* 2007c), earthworms (Pižl 2007), and spiders (Růžička 1992, 2007).

The aims of this study were to: a) document the thermal regime in a sandstone rock labyrinth; 2) describe the assemblages of arthropods in relation to the vertical thermal gradient; and 3) assess the ecological and biogeographical significance of a sandstone rock labyrinth.

2. MATERIAL AND METHODS

2.1. Study site

The Adršpašsko-Teplické Skály National Nature Reserve is a labyrinth of sandstone rocks located within the Broumovsko Protected Landscape Area, NE Bohemia (Vítek 1979). The Poseidon Sandstone Labyrinth is situated at the core of Teplické Skály rocks (50°35'N, 16°08'E). The labyrinth ranges approximately 740 m from north to south, and is approximately 550 m wide. The labyrinth consists of a broken, interconnected network of deep vertical crevices. Mounds of debris are commonly found within them, filling the entire width of some of the especially wide crevices. Wedged blocks of sandstone and other debris have created multilevel, wholly dark debris caves, often many meters deep. Small streams flow through some crevices. The whole system is divided into three parts by narrow gorges. The middle portion is situated on a structural plateau (Figs 1, 2). The total length of the human-accessible underground spaces in the Poseidon Labyrinth is estimated to be at least 27 km. The vertical range is 105 m (Mlejnek *et al.* 2009a, b). It is a multi-process terrain, exhibiting features of crevice and talus pseudokarst (Halliday 2007).

Due to the climatic inversion in the deep vertical spaces, montain bryophytes, *Pohlia drummondii* (Müll. Hal.) A.L. Andrews, *Diplophyllum taxifolium* (Wahlenb.) Dumort., and *Dicranum elongatum* Schleich. ex Schwägr., as well as vascular plants, *Homogyne alpina* (L.) Cassini, *Cicerbita alpina* (L.) Wallroth, and *Viola biflora* L., occur here at low altitudes (Sýkora and Hadač 1984). Hamet and Vancl (2005) cataloguised beetles of the Broumovsko Protected Landscape Area. The arachnofauna of the Adršpašsko-Teplické Skály National Nature Reserve has been studied by Růžička (1992) and Růžička and Kopecký (1994). The occurrence of several cold adapted species have been registered.

2.2. Field temperature measurements

Data-loggers (Model TGU-0050, Gemini Data Loggers Ltd., UK) with internal thermistors were used to measure the temperature (accuracy ± 0.2°C), with a logging interval of three hours, between June 2007 and June 2008. The external air temperature was monitored on the upper rock margin of the Dragon's Abyss (680 m a.s.l.) in a shady place where data logger I was situated approximately 1 m above the soil surface. The internal air temperature was measured at two locations in the cold and humid bottom portions of the labyrinth (600 m a.s.l.): Siberia Gorge, a 2 m wide corridor along the brook (data logger II); and in a crevice cave, about 40 cm wide (data logger III) (Figs 1, 2).

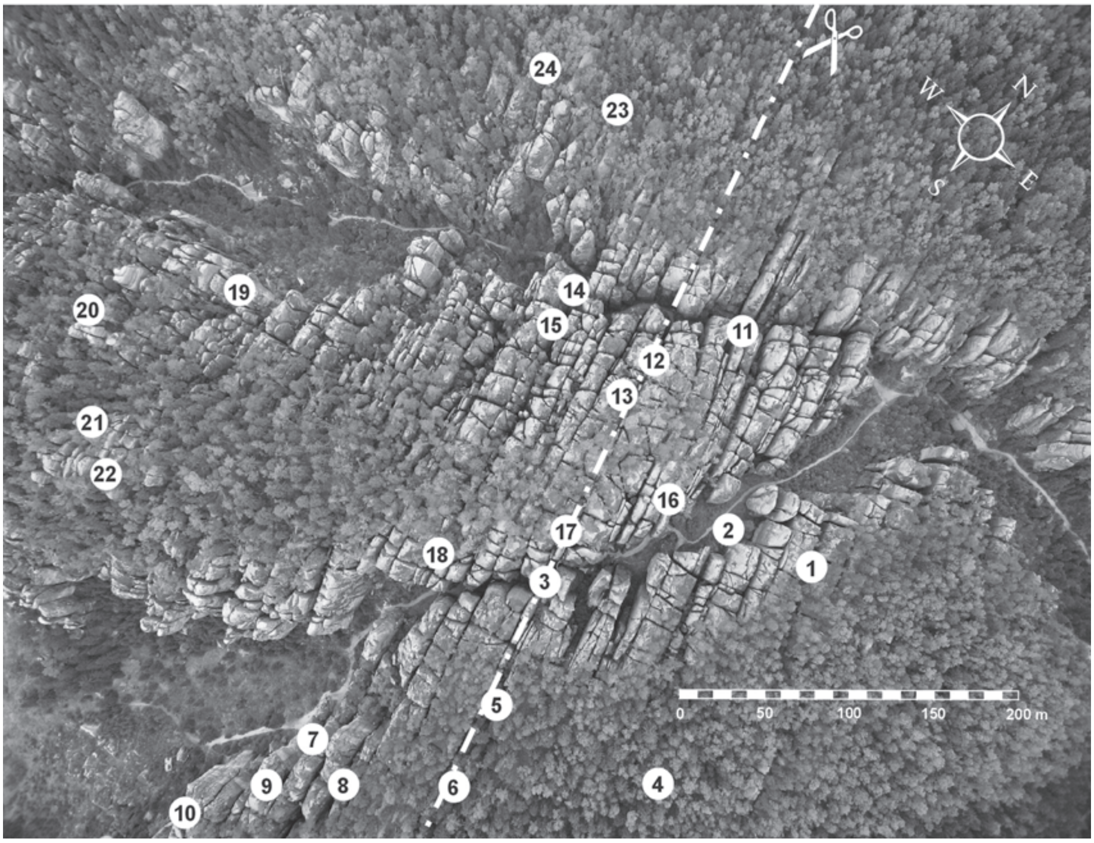

Fig. 1. The Poseidon Labyrinth, Adršpašsko-Teplické Skály National Nature Reserve, NE Bohemia, a bird's eye view. The locations of the samples (arabic numerals) are marked. Dot-and-dash line marks the cross-section in Fig. 2. Photo: L. Jenka.

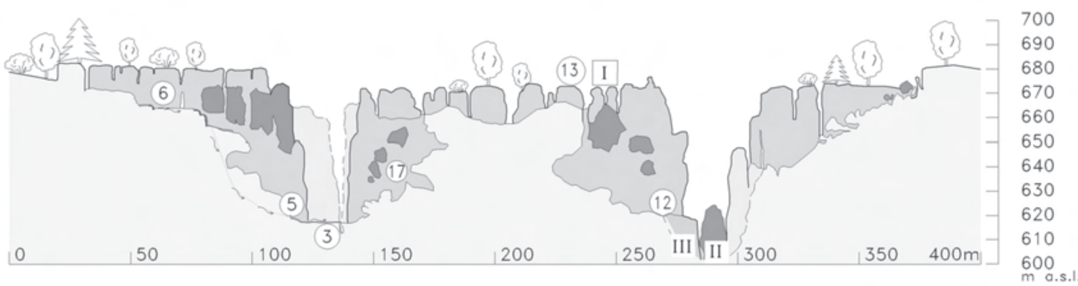

Fig. 2. The Poseidon Labyrinth, in cross-section. The locations of the samples (arabic numerals) and data-loggers I and II (Roman numerals) are marked. A projection of the location of data-logger III is marked; in fact, it was installed in the neighbouring, parallel crevice. Drawn by V. Ouhrabka.

2.3. Sampling

Field research was conducted discontinuously from 1986 to 2008 in the frame of research programme of the Academy of Sciences and the Cave Administration of the Czech Republic. The arthropods were trapped in various types of pitfall traps, which were exposed for one year. The traps were placed on the soil surface, in mosses, under fallen wood, and among stones. Arthropods were also collected by means of sieving of the moss and detritus, as well as by hand sorting. Climbing equipment was used to collect the arthropods on the bare cliff walls, and hanging board traps were used to collect arthropods on cliff walls overgrown by lichens and heather (Růžička 2000). To obtain more representative samples, we combined catches obtained by all sampling methods at the same place. This resulted in 24 final samples from the whole spectrum of habitats situated at different parts of the rocky labyrinth (Fig. 1): the most cold narrow bottom parts (Nos. 11, 12, 14, 16); other bottom parts (Nos. 2, 3, 7, 15, 17); shady and dark inner spaces along the whole altitudinal range, and cold mossy crevices in the upper parts of the labyrinth (Nos. 1, 4, 5, 6, 8, 10, 19, 20, 21, 24); and from the sun-exposed top rocks, both partly bare and overgrown by heather (Nos. 9, 13, 18, 22, 23).

2.4. Data analysis

Variation in the frequency of individual species was summarized using the classical unimodal ordination method – detrended correspondence analysis (DCA), using Canoco for Windows program, version 4.5 (ter Braak and Šmilauer 2002). Species counts were log-transformed, and the downweighting option for rare species applied. Ordination diagrams display the taxa with their weight in analysis at least 20% of the taxon with maximum weight, as well as those aiding interpretation of the diagrams, due to their specific distributional/ecological attributes.

3. RESULTS AND DISCUSSION

3.1. Thermal regime

The course of the air temperature fluctuations on the upper rock margin follows that of the external atmospheric temperatures in the region (max. 26.5°C, min. –7.3°C, mean 6.1°C). The course of the air temperature at the bottommost portions of the labyrinth exhibit limited daily and annual fluctuations, and this documents a markedly cold microclimate (Fig. 3). The air temperature in the gorge exhibits limited daily fluctuations; the summer temperature usually does not exceed 12°C (max. 13.6°C, min. –6.6°C, mean 3.7°C). The air temperature in the crevice cave does not exhibit daily fluctuations; the summer air temperature usually does not exceed 8.5°C. On the other hand, the crevice cave almost never freezes, so the average annual air temperature is the same as in the gorge (max. 9.6°C, min. –1.9°C, mean 3.7°C).

The temperature characteristics in the bottom parts of the Poseidon Sandstone Labyrinth, and those from similar habitats in the Czech Republic are compared in Table 1. For all subsurface habitats, the amplitude of the temperature variations is much less than that of the surface habitats (Culver and Pipan 2009). In typical karst caves, the mean annual air temperature is similar to the mean annual air temperature in the region. In some types of subterranean spaces, the cold air falls into it; consequently, the mean annual air temperature is less than that of the surrounding region.

Scree slopes with a dynamic regime of air flow exhibit specific temperature conditions (Růžička 1999b, Zacharda *et al.* 2007). When the external air temperature falls below 0°C during the winter season, cold air falls into the subterranean spaces through interspaces in the entire area of the scree field. The stones are cooled, and ice is formed. Downslope cool airflow causes the mean annual temperature to be approx. 0°C on the lower margins of the scree slope during both spring and summer.

The rocky labyrinth is formed by a rock mass with deep, narrow crevices, crevice caves, and talus caves. Here, in the winter the cold surrounding air only enters the subterranean spaces into the labyrinth through narrow crevices when the external air temperature falls below 0°C. In contrast to the scree slopes, the cold air does not flow through the labyrinth which is gradually cooled, and the rock mass preserves the cold during the subsequent spring and summer. All habitats which are compared in Table 1 have their own thermal specifics, and the rocky labyrinth lies somewhere between that of the caves and freezing scree slopes.

3.2. Arthropods

3.2.1. Main trends in compositional variation

A total of 2285 specimens belonging to eight taxonomic groups were evaluated. The most numerous groups were Coleoptera (165 spp., 733 ind.) and Araneae (111 spp., 1262 ind.). They were followed by Hymenoptera: Formicidae (7 spp., 206 ind.), Opiliones (7 spp., 15 ind.), Pseudoscorpiones (4 spp., 37 ind.), Acari: Rhagidiidae (4 spp., 28 ind.), Diplopoda (4 spp., 26 ind.), and Chilopoda (2 spp., 2 ind.).

The diversity of ecological demands of arthropods reflects the microclimatic diversity in the labyrinth. The DCA analysis (based on complete data) arranged the sampling locations along compositional gradients, with the two most important ones presented in ordination diagram in Fig. 4. The main gradient of the species compositional changes runs along the first (horizontal) ordination axis. The sampling locations in the coolest parts of the labyrinth are near the left side of the diagram, while the samples from the upper rock margins are at the right side. The other locations are shown between these two extremes, without any prominent clustering. Based on the a priori knowledge of the ecological requirements of species and their location in the ordination space (see Figs 5–6), the first axis can be interpreted as a gradient of temperature (increasing from left to right), while the second axis as a gradient of light availability (increasing from top to bottom).

The most numerous spider species were *Bathyphantes eumenis* (L. Koch, 1879), *Centromerus arcanus* (O. P.-Cambridge, 1873), and *Diplocephalus helleri* (L. Koch, 1869), occurring in the bottommost labyrinth portions; and *Alopecosa taeniata* (C. L. Koch, 1835), *Callobius claustrarius* (Hahn, 1833), *Harpactea lepida* (C.L. Koch, 1838), *Coelotes terrestris* (Wider, 1834), and *Xerolycosa nemoralis* (Westring, 1861), occurring in the other parts of the labyrinth. The most numerous beetle species were *Apocatops nigrita* (Erichson, 1837), *Proteinus brachypterus* (Fabricius, 1792), *Omalium caesum* Gravenhorst, 1806, *Trechus pulchellus* Putzeys, 1846, *Lesteva longoelytrata* (Goeze, 1777), and *Catops picipes* (Fabricius, 1787), occurring in the bottom labyrinth parts; *Plintus tischeri* Germar, 1824 occurring among the moss in mid-labyrinth portions; and *Hylobius abietis* (Linné, 1758),

Table 1. Air temperatures (°C) in the Czech Republic, *average* – average annual air temperature; *min* – annual air temperature minimum; max – annual air temperature maximum; range – average annual range of air temperatures, 1961–2000 (Tolasz *et al.* 2007), and at model localities in the Czech Republic. Cave interior: Kateřinská cave (350 m a.s.l.), 2008–2009 (unpubl.); Rocky labyrinth: Poseidon Labyrinth (600 m a.s.l.), 2007–2008 (this study, data logger No. III); Scree slope with ice formation: Klíč Mt.(540 m a.s.l.), 2003–2004 (Zacharda *et al.* 2007); Ice cave: Naděje cave (620 m a.s.l.), 2003–2004 (Zacharda *et al.* 2007).

Territory/Habitat	Average	Min	Max	Range
Czechia	7–8	–25–(–13)	22–35	46
Cave interior	7.5	7.0	8.2	1.2
Rocky labyrinth	3.7	–1.9	9.6	11.5
Freezing scree slope	–0.1	–11.2	8.0	19.2
Ice cave	1.0	–7.3	2.1	9.4

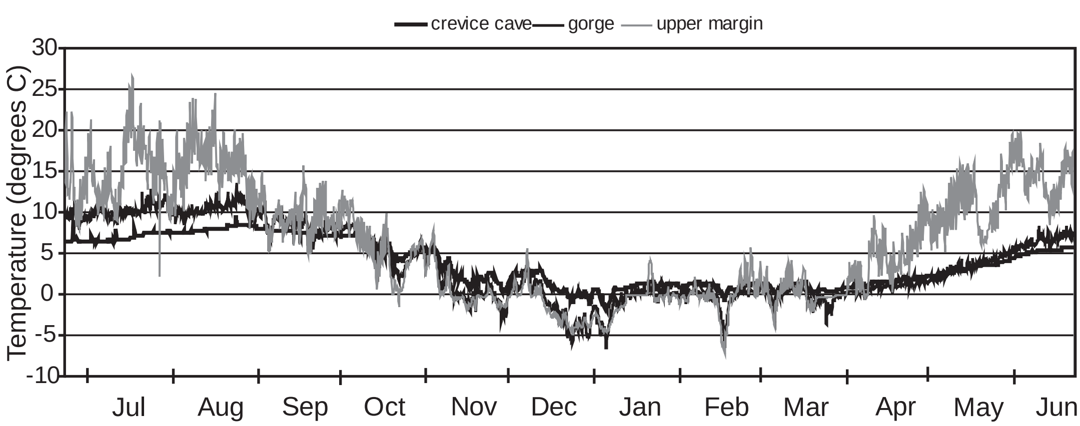

Fig. 3. Temperature variations (°C) in the Poseidon Labyrinth in the years 2007 and 2008: I – external air temperature on the upper rock margin, II – internal air temperature in the gorge, III – internal air temperature in the crevice cave.

occurring on the upper labyrinth margin. The species collected on the upper rock margin were usually those, which are typical for forests, or forest margins. Some of the species collected in the deeper parts of the labyrinth have more specific ecological demands: they can be tied to rock surface, to underground spaces, and/or to the cold microclimate.

Spiders, according to their climbing abilities, can inhabit bare rock surfaces through the whole temperature gradient studied. Buchar and Růžička (2002) designated species, which are able to colonize vertical surfaces, i.e. oblique, vertical, and overhanging surfaces of rocks, rock blocks, walls of buildings, etc. These species colonize the labyrinth throughout the entire altitudinal range from the coldest parts – *Bathyphantes eumenis*, through dark spaces in deep crevices and caves – *Meta menardi* (Latreille, 1804), *Metellina merianae* (Scopoli, 1763), *Nesticus cellulanus* (Clerck, 1757), up to the sun-exposed top rocks – *e.g. Theridion betteni* Wiehle, 1960 (Fig. 5).

The environmental conditions in the labyrinth exhibit some similarity to conditions in cave habitats and in scree slopes with ice formation. The leiodid beetle *Catops longulus* Kellner, 1846 inhabits cave entrances and scree slopes. *Porrhomma egeria* Simon, 1884, *Porrhomma convexum* (Westring, 1851), *Porrhomma pallidum* Jackson, 1913, *Nesticus cellulanus*, *Meta menardi*, and *Metellina merianae* are typical species in all subterranean habitats in central Europe; not only in caves, but also in scree slopes (Růžička 1999a). The occurrence of cold-adapted boreal and mountain species is characteristic for scree slopes with ice formation (Table 2). All of these, and some other specialised species of arthropods, were documented in the Poseidon Sandstone Labyrinth.

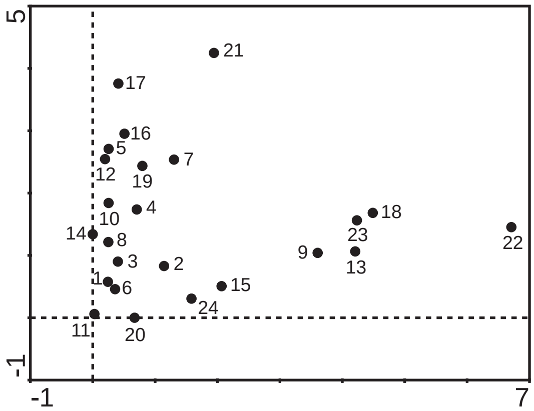

Fig. 4. DCA ordination diagram with sample points (see Fig. 1) displaying the first two ordination axes of DCA, explaining 19% of the total variation.

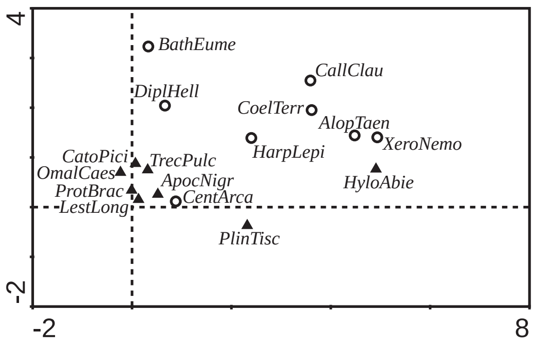

Fig. 5. DCA ordination diagram with the most abundant species of spiders (O): *BathEume* = *Bathyphantes eumenis*, *CentArca* = *Centromerus arcanus*, *DiplHell* = *Diplocephalus helleri*, *AlopTaen* = *Alopecosa taeniata*, *CallClau* = *Callobius claustrarius*, *HarpLepi* = *Harpactea lepida*, *CoelTerr* = *Coeloes terrestris*, *XeroNemo* = *Xerolycosa nemoralis*; and beetles (▲): *ApocNigr* = *Apocatops nigrita*, *ProtBrac* = *Proteinus brachypterus*, *OmalCaes* = *Omalium caesum*, *TrecPulc* = *Trechus pulchellus*, *LestLong* = *Lesteva longoelytrata*, *CatoPici* = *Catops picipes*, *PlinTisc* = *Plintus tischeri*, *HyloAbie* = *Hylobius abietis*.

3.2.2. Mountain species

European species, usually occurring in higher altitudes, represent the characteristic species group in the Poseidon Sandstone Labyrinth. In the Czech Republic, these species are usually recorded in the border mountains: Šumava Mts., Krkonoše Mts., Orlické Hory Mts., and Jeseníky Mts. Rarely, they descent into lower altitudes, into the inversion sites. We found seven mountain spiders, *Anguliphantes tripartitus* (Miller & Svatoň, 1978), *Centromerus arcanus*, *Diplocephalus helleri*, *Mansuphantes arciger* (Kulczyński, l882), *Mughiphantes pulcher* (Kulczyński, 1881), *Micrargus georgescuae* Millidge, 1976, *Nusoncus nasutus* (Schenkel, 1925), and a harvestman *Platybunus pallidus* Šilhavý, 1938. Beetles represent the most numerous group of mountain species: *Sericus subaeneus*

Table 2. The occurrence (marked by ●) of characteristic spiders and rhagidiid mites in underground habitats in the Czech Republic (Buchar and Růžička 2002, Zacharda *et al.* 2005).

Species	Karst caves	Pseudokarst caves	Scree slopes	Poseidon Lab.
Nesticus cellulanus	●	●	●	●
Meta manardi	●	●	●	●
Metellina merianae	●	●	●	●
Porrhomma convexum	●		●	●
Porrhomma egeria	●	●	●	●
Porrhomma pallidum		●	●	●
Bathyphantes eumenis		●	●	●
Diplocentria bidentata			●	●
Anguliphantes tripartitus			●	●
Rhagidia gelida			●	●
Oreonetides vaginatus				●
Sisicus apertus				●

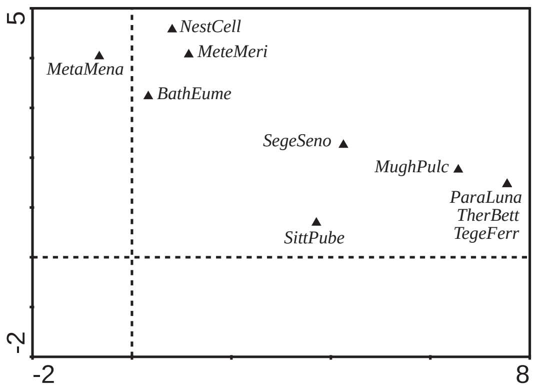

Fig. 6. DCA ordination diagram with spider species inhabiting bare rock surfaces: *BathEume* = *Bathyphantes eumenis*, *MetaMena* = *Meta menardi*, *NestCell* = *Nesticus cellulanus*, *MeteMeri* = *Metellina merianae*, *SegeSeno* = *Segestria senoculata* (Linné, 1758), *SittPube* = *Sitticus pubescens* (Fabricius, 1775), *MughPulc* = *Mughiphantes pulcher*, *ParaLuna* = *Parasteatoda lunata* (Clerck, 1757), *TherBett* = *Theridion betteni*, *TegeFerr* = *Tegenaria ferruginea* (Panzer, 1804).

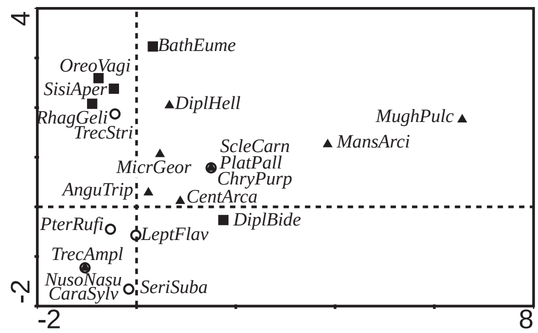

Fig. 7. DCA ordination diagram with boreal species of spiders and a mite (■): *BathEume* = *Bathyphantes eumenis*, *OreoVagi* = *Oreonetides vaginatus*, *SisiAper* = *Sisicus apertus*, *DiplBide* = *Diplocentria bidentata*, *RhagGeli* = *Rhagidia gelida*; mountain species of spiders and a harvestman (▲): *NusoNasu* = *Nusoncus nasutus*, *AnguTrip* = *Anguliphantes tripartitus*, *MicrGeor* = *Micrargus georgescuae*, *DiplHell* = *Diplocephalus helleri*, *CentArca* = *Centromerus arcanus*, *MansArci* = *Mansuphantes arciger*, *MughPulc* = *Mughiphantes pulcher*, *PlatPall* = *Platybunus pallidus*; and mountain species of beetles (●): *TrecAmpl* = *Trechus amplicollis*, *CaraSylv* = *Carabus sylvestris*, *PterRufi* = *Pterostichus rufitarsis*, *TrecStri* = *Trechus striatulus*, *SeriSuba* = *Sericus subaeneus*, *LeptFlav* = *Leptusa flavicornis*, *ScleCarn* = *Sclerophaedon carniolicus*, *ChryPurp* = *Chrysolina purpurascens purpurascens*.

(W. Redtenbacher, 1842), *Sclerophaedon carniolicus* (Germar, 1824), *Chrysolina purpurascens purpurascens* (Germar, 1822), *Carabus sylvestris sylvestris* Panzer, 1793, *Pterostichus rufitarsis cordatus* Latzner, 1842, *Trechus amplicollis* Fairmaire, 1859, *Trechus striatulus* Putzeys, 1847, and *Leptusa flavicornis* Brancsik, 1874 (Fig. 7). These species usually inhabit the subalpine belt, mountain forests, peat bogs, spring areas, gravel banks, scree slopes, and rocks. In comparison with mountain spiders, mountain beetles represent a more compact group; they occur on the left side of the ordination diagram. This can be caused by a closer dependence of the beetle larvae on the cold soil environment. Spiders are not so closely tied to the soil environment, they also inhabit detritus (*Mansuphantes arciger*), or bare rock surfaces (*Mughiphantes pulcher*) on the upper rock margins.

3.2.3. Boreal species

Four species of spiders, *Bathyphantes eumenis*, *Diplocentria bidentata* (Emerton, 1882), *Oreonetides vaginatus* (Thorell, 1872), *Sisicus apertus* (Holm, 1939), and one species of the rhagidiid mite, *Rhagidia gelida* Thorell, 1872, were found in the cold spaces of the Poseidon Sandstone Labyrinth. Here, and in some other isolated subareas in the temperate zone in central Europe, these species have a disjunctive pattern of distribution; whereas vast areas of tundra and boreal forests are the main habitats where they usually occur. The last three species are situated near the left margin of the ordination diagram in Figure 7.

Bathyphatnes eumenis was first recorded in Central Europe in Poland in 1984 by Woźny and Czajka (1985); and its occurrence in an adjacent part of Bohemia was confirmed two years later by Růžička (1992). The common occurrence of *Bathyphantes eumenis* and *Diplocentria bidentata* are known from high mountains and also in the scree slopes with ice formation (Růžička 1988; Růžička and Klimeš 2005).

Up to this time, the occurrence of *O. vaginatus* was only known from the Krkonoše and Šumava Mts. (1200–1500 m) (Buchar and Růžička 2002). The Arctic mite *Rhagidia gelida* proved to be a bio-indicator of the long-lasting periglacial microclimate in central Europe (Zacharda *et al.* 2005).

Fig. 8. Distribution of *Sisicus apertus* within Europe. Continuous distribution in North Europe, and sporadic distribution in Central Europe. After various authors (see Table 3).

Sisicus apertus has a Holarctic distribution (Marusik and Koponen 2005). It occurs in moss in the boreal forests in North America (Buckle *et al.* 2001), Russia, Estonia (Mikhailov 1997), and Scandinavia (Palmgren 1975, Åkra and Hauge 2008). It was also recorded in the SW part of Greenland (Marusik *et al.* 2006). The southernmost and westernmost portions of the Euro-Siberian taiga zone reaches to NE Poland; *Sisicus apertus* was recorded there in the Knyszyn Forest Landscape Park (Staręga 2003). In central Europe, this species has only been recorded in the Alps, in the High Tatras, and in the Poseidon Sandstone Labyrinth (Table 3, Fig. 8).

3.3. Ecosystem

Based on the analysis of organic fragments in what are probably early Late Glacial sediments (15000–10000 years ago) from the Adršpašsko-Teplické Skály rock complex, the climatic conditions of that time are characterised as similar to the contemporary situation at the polar limit of the northern Siberian forest tundra. Based on pollen analysis of Early Holocene sediments (10000–7500 years ago), the sandstone landscape is characterised as sparse, mostly birch-rich taiga, with an admixture of pine. After the Pleistocene/Holocene transition, the warm climate (more or less corresponding to the present one) supported continuously developing ecosystems of the landscape matrix. The geomorphology and dimensions of the sandstone rock complex, without doubt, allowed for the existence of different and contrasting stands over a very small spatial scale; so that thermophilous communities of sandstone plateaus could exist alongside psychrophilous communities at the bottoms of deep crevices. This diversity has existed since the end of the Late Glacial (Kuneš *et al.* 2007).

Nekola (1999) presented the concept of paleorefugia; habitats that support now-fragmented relicts of a formerly widespread matrix community (whereas neorefugia have formed more recently than the matrix). He

Table 3. The survey of records of the spider *Sisicus apertus* in Central Europe.

Locality, reference	Habitat	Altitude
Liechtenstein, Arnold (2001)	scree	?
Unterengadin: Ramosch (CH) Thaler (1995)	A. scree slope with cold air exhalations B. lower margin of the scree slope	1 145 m 1 200 m
Graubünden: Bergün-Preda (CH) Vogelsanger (1948)	moss among rock blocks	1 910 m
Sextener Dolomiten: Schluderbach (I) Thaler (1993)	scree slope overgrown by spruces	1 350 m
Stubaier Alpen: Gschnitz (A) Thaler (1969)	lower margin of the scree slope	2 300 m
High Tatras, Malá Studená Dolina (SK) Miller (1974)	moss on brook bank in spruce forest	> 1 500 m
Poseidon Labyrinth (CZ) Růžička & Kopecký (1994)	a system of deep crevices in rocks	600 m

evaluated algific talus slopes in temperate zone in North-eastern Iowa as paleorefugia. These habitats are characterised by ice formation in the inner cavities and all-year-round cold air seepage onto the lower margin, where soil temperatures rarely exceed 15°C in the summer. The temperature in the bottommost parts of the Poseidon Labyrinth does not exceed 9.6°C in the summer, thanks to its spatial structure and enormous dimensions.

4. CONCLUSIONS

Our temperature measurements and biological investigations document the high diversity of the microclimate and assemblages of arthropods in the Poseidon Sandstone Labyrinth. Due to the microclimatic buffering, which mimics the periglacial regional climate, cold adapted organisms were able to persist in this rock complex to the current time. The Poseidon Sandstone Labyrinth thus represents a paleorefugium whose biota partly predates the surrounding deciduous forest matrix.

Finally, with this Poseidon Sandstone Labyrinth case study, we would like to encourage similar ecological research of other rock labyrinths worldwide.

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