POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	59	2	367–380	2011

Regular research paper

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CENTRAL EUROPEAN HABITATS INHABITED BY SPIDERS WITH DISJUNCTIVE DISTRIBUTIONS

ABSTRACT: The purpose of the study is to find which habitats within Central Europe support the persistence of isolated populations of spider species of both boreal and Alpine origins. Twenty-five species exhibited disjunctive distributions with their main sub-area in the tundra or boreal forest, and isolated sub-areas in the temperate zone of Central Europe. Six species exhibited disjunctive distributions with their main sub-area in the Alps, and isolated sub-areas in the temperate zone in Central Europe. Only (approximately) one-third of the species of boreal origin have the same habitat, as in the boreal zone. Two-thirds of the species inhabit different habitats, or have narrowed their ecological valency. Screes play an important role in the survival of these isolated populations of species of boreal origin in the temperate zone, together with mountain summits, mountain forests, and peat bogs. Extensive complexes of sandstone rocks also enables the survival of isolated populations of species of boreal origin.

KEY WORDS: spiders, glacial relicts, boreomontane species, screes, sandstone rocks

1. INTRODUCTION

Discontinuity of the areas is a characteristic of the majority of animal species, and the study of these discontinuities and their causes is the chief source of data for causal zoogeography (Udvardy 1969). Discontinuity of the distribution area can occur when a population diminishes under unfavorable conditions, in which the outlying populations are ‘relicts’ from an earlier, more widespread, and continuous distribution (Tallis 1991). Distinctive disjunctive areas with a main sub-area in the boreal zone (or in the Alps), and with isolated sub-areas in the temperate zone are typical for the glacial relicts in Europe. This distinctive type of distribution area developed as a consequence of the changes in biota during the Pleistocene climatic oscillations.

In the glacial era, the Czech Republic formed a narrow ice-free passage between the Northern European and Alpine areas of glaciation. The tundra and forest tundra of this territory which consisted of both boreal and Alpine elements represented an important corridor, connecting the ice-free regions in the East with Western Europe (Ložek 1997). During the Late Glacial, the territory was covered by forest tundra. After the Pleistocene/Holocene transition, the warmer climate, more or less, corresponded to the present one (Kuneš *et al.* 2007). Species of boreal and/or Alpine origin retreated; however, isolated populations still persist in suitable habitats.

At present, disjunctive occurrences of some spider species are a 'memory' of the movement of their ranges during Central Europe's changing climate during the Pleistocene and Early Holocene. Generally, we can designate these areas as "Eurosiberian north-south-disjunctions" and "Eurosiberian south-north-disjunctions" (Reinig 1965).

Typical "arctic-alpine species" occur in the main sub-area in arctic tundra today; their sub-areas are in the alpine belt of mountains in the temperate climatic zone. The typical "boreo-montane" species occur in the main sub-area in boreal forests today; their sub-areas are in the mountain forests in the temperate climatic zone. Holdhaus (1954) created a transitional category of "boreo-alpine species" (Muster 2001). Species of Alpine origin, which have their distributions reaching-up to the North, are designated in Central European literature as "de-alpine" species.

However, to assign a specific species into some of these categories causes problems; you can't overlook the disunity of classifications (Muster 2001). For example, the spider *Acantholycosa norvegica* is classified as boreo-montane by Prószyński and Staręga (1971), as subarctic-subalpine by Thaler (1998), and as arctic-alpine by Relys (2000). Are these above-mentioned biogeographical terms thus useful for the characterization of a species?

To contribute to this problem, the answer to the principal question: "which habitats enable the survival of the isolated populations of spider species of boreal or Alpine origin within Central Europe?" is sought.

2. MATERIALS AND METHODS

2.1. Study area

The Czech Republic occupies a key position, from a biogeographical point of view. It is in the temperate zone of Europe, with a regular weather pattern and no great extremes during either winter or summer; the 50% continentality index line (Barry and Chorley 1987) passes between Bohemia and Moravia. Despite the country's small size, its climate exhibits important local differences that are based on altitudinal diversity (115–1602 m a.s.l.). The oscillation of climate during the Quaternary period, which brought about the repeated shifting and reconstitution of its vegetation zones, is exhibited to its full extent within the territory of the Czech Republic.

2.2. Material evaluation

I analyzed data on 830 spider species that are located in the Czech Republic. Data on those species with disjunctive distributions with the main sub-area in the boreal zone, or in the Alps, were analyzed. The database from the Catalogue of spiders of the Czech Republic (Buchar and Růžička 2002) was the main source of data on habitats that are inhabited in the Czech Republic; other literature (cited in Appendix I and II) were the sources of data on habitats that are inhabited in the main sub-areas. The nomenclature of the spiders follows Platnick (2010).

3. RESULTS

3.1. Habitats of species of boreal origin

Twenty five species exhibited a disjunctive distribution area with the main sub-area in tundra or boreal forest, and isolated sub-areas in the temperate zone of Central Europe (Appendix I). They inhabit the alpine and sub-alpine belt of mountains, spruce forests, peat bogs, scree slopes, and sandstone rock complexes. The species inhabiting the zonal habitats have a delimited altitudinal range for their occurrence. Those species inhabiting mountain spruce forests can descend into the lower altitudes in inverse valleys; the same is true for those species that survive in sandstone rock complexes. Those species inhabiting scree slopes occur throughout the entire altitudinal range (Fig. 1).

Nine species inhabit Central European habitats that are analogous to the habitats in their main sub-area (Appendix I, Fig. 2). Two species of forest tundra inhabit Central European summit tundra, two species of peat bogs inhabit Central European peat bogs, four species of boreal forests inhabit Central European mountain coniferous forests, and one species inhabits the bare surfaces of stony accumulations within the zone of boreal forests and temperate zone.

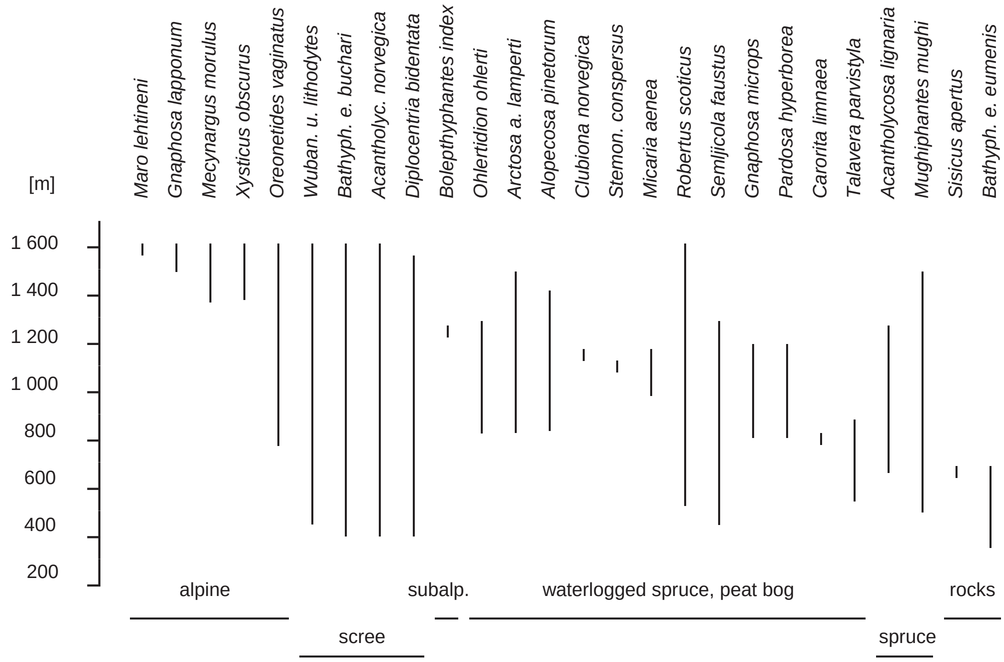

Fig. 1. Boreal spiders of the Czech Republic. Main habitats and altitudinal range.

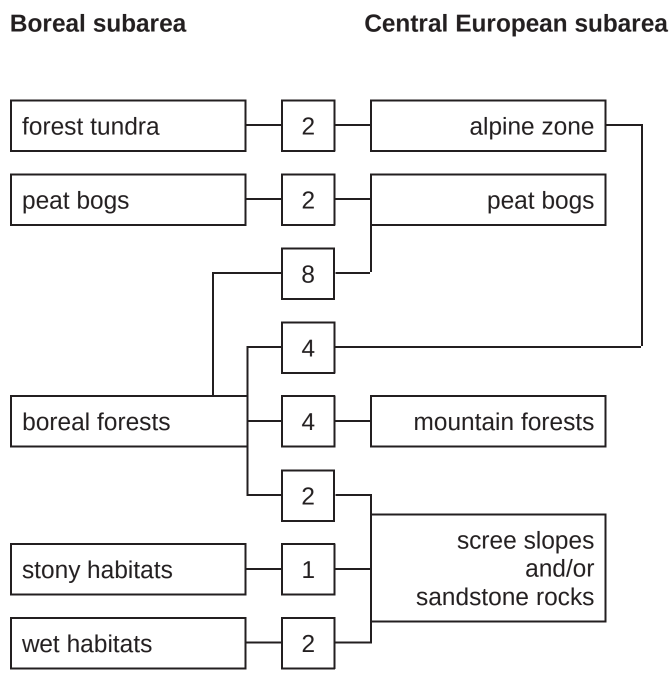

Fig. 2. Boreal spiders of the Czech Republic. Number of species inhabiting the Central European habitat of the analogous type (horizontal direction), and of a different type (other directions); compared to the habitat in the boreal zone.

Sixteen species inhabit different habitats, or have narrowed their ecological valency (Appendix I, Fig. 2). Four species of the boreal forests inhabit the Central European mountain tundra. One of these (*Bolepthyphantes index*), inhabiting the boreal forest's shrubs and lower canopy, was exclusively recorded above timberline in leeward spaces of anemo-orographic systems (Jeník 1997) within the Czech Republic; *viz* in glacial corries in both the Krkonoše and Hrubý Jeseník Mts. Eight species of boreal forests exclusively inhabit peat bogs. One species of boreal forests (*Sisicus apertus*) was found among the moss in inverse gorges in a sandstone rock complex. Another species of the boreal forests (*Diplocentria bidentata*) inhabits the lower margins of scree slopes with ice formations and sandstone rock complexes.

Bathyphantes eumenis (sensu Wozny and Czajka 1985; recently confirmed by Tanasevitch and Marusik *in litt.*) inhabits the boreal zone's various humid habitats. The nominate, pigmented subspecies (*B. e. eumenis*) in Central Europe occurs exclusively in the sandstone rock complexes in NE Bohemia and Poland. The troglomorphic subspecies (*B. e. buchari*) exclusively inhabits the inner crevices in scree slopes throughout Central Europe, just north of the Alps.

Wubanoides uralensis inhabits the boreal zone's various humid habitats. The Central European subspecies (*W. u. lithodytes*) exclusively inhabits the inner crevices of scree slopes. The main subarea of *Robertus scoticus*, *Maro lehtineni*, *Mecynargus morulus*, *Semljicola faustus*, *Pardosa hyperborea*, *Gnaphosa lapponum*, and *Talavera parvistyla* lies in Fennoscandia and/or European part of Russia. The main subarea of other species includes Siberia and often extends in North America.

In the main subarea, *Maro lehtineni*, and *Talavera parvistyla* have been recorded in a few specimens only; other species can be abundant in suitable habitats. In the Czech Republic, several species are very rare, recorded in very few specimens: *Maro lehtineni* – 1 specimen, *Carorita limnaea* – 2 specimens, *Sisicus apertus* – 3 specimens, *Bolepthyphantes index* – 4 specimens, *Xysticus obscurus* – 5 specimens, *Micaria aenea*, *Clubiona norvegica*, and *Talavera parvistyla* (6–10 specimens); other species are abundant in suitable habitats.

The southern borders of the Central European sub-areas of boreal species do not accumulate, and form no distinctive geographic border. *Wubanoides uralensis* and *Pardosa hyperborea* reach the southernmost point of their distribution in Bohemia. The distribution of *Bathyphantes eumenis buchari* reaches the Schwarzwald Mts., the territory of *Gnaphosa microps* and *Carorita limnaea* reaches to southern Germany, at the foothills of the Alps. The other species, by their distribution, reach the Alps.

3.2. Habitats of species of Alpine origin

Six species exhibit a disjunctive distribution area, with their main sub-area in the Alps, and isolated sub-areas in the temperate zone of Central Europe (Appendix II).

One species that inhabits the sub-alpine and alpine zones in the Alps occurs in the Czech Republic among moss in the transition

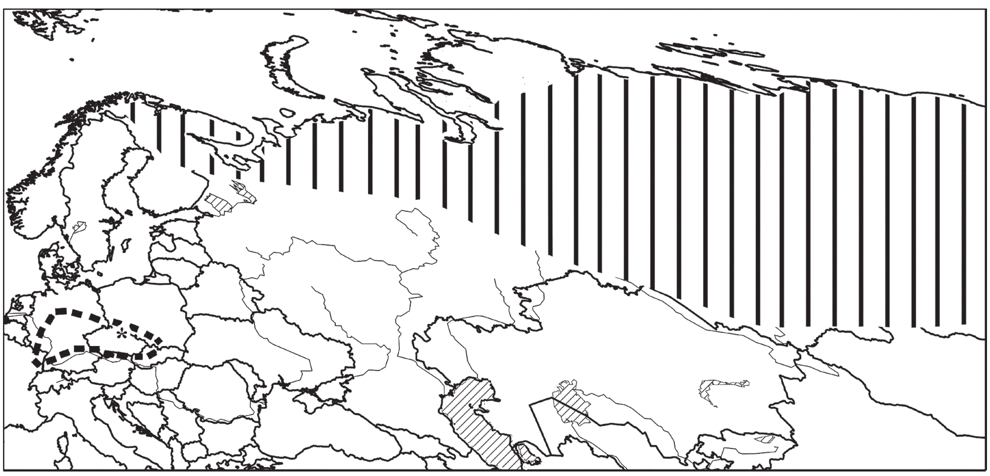

Fig. 3. Distribution of *Bathyphantes eumenis* in Europe and Asia. The main boreal sub-area of *B. e. eumenis* is marked with vertical line pattern, and its Central European sub-area is marked with an asterisk. The Central European sub-area of *B. e. buchari* is bounded by the dashed line. After Marusik *et al.* (2000), Buchar and Růžička (2002), Růžička (1989), Blick (1991), and Sacher (1999). Mollweide projection.

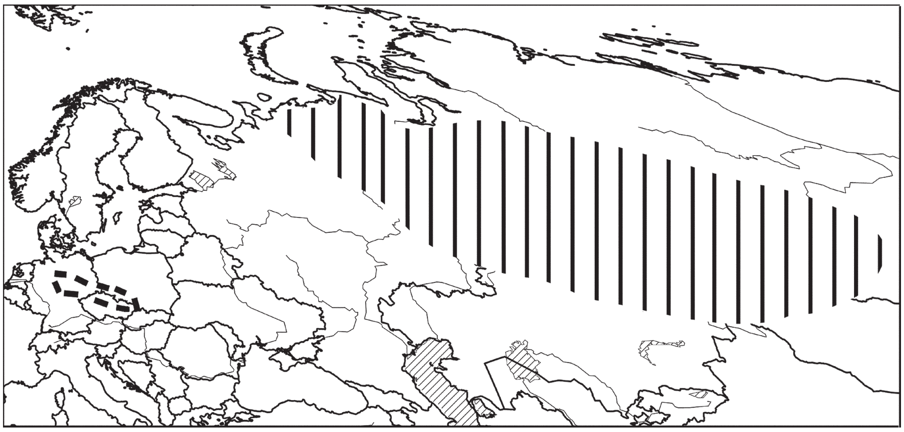

Fig. 4. Distribution of *Wubanoides uralensis*. The main boreal sub-area of *W. u. uralensis* is marked with vertical line pattern. The Central European sub-area of *W. u. lithodytes* is bounded by the dashed line. After Marusik *et al.* (2000), Buchar and Růžička (2002), and Schikora (2004). Mollweide projection.

zone between the forest and peat bog. Three species inhabit the scree slopes in the Alps and Central Europe, and one species inhabits scree forests. One species inhabiting beech forests in the Alps was recorded in the forest scree in the Czech Republic.

In the main subarea, all species can be abundant in suitable habitats. In the Czech Republic, we have recorded only one specimen of *Comaroma simoni*; other species are abundant in suitable habitats.

The northern borders of the Central European sub-areas of the Alpine species do not accumulate, and they form no distinctive geographic border. *Gnaphosa badia* reaches the northernmost point of its distribution in the Bohemian Forest; *Clubiona alpicola* in the Krkonoše Mts.; *Lepthyphantes notabilis* and *Trogloneta granulum* in central Germany; *Comaroma simoni* in northern Germany; and the distribution area of *Rugathodes bellicosus* extends up to Scandinavia.

4. DISCUSSION

Land surfaces at higher latitudes in the northern hemisphere presently support a range of forest, scrub, tundra, and peatland communities that may collectively be called the 'coldland complex'. Physiognomically and floristically similar communities also occur at higher altitudes, on mountains further south (Tallis 1991). Twenty spider species with a disjunctive distribution area of boreal origin inhabit Central European habitats of this type. However, their habitat conservatism is limited; they often inhabit habitats of a different type than that found in the main subarea. Those species inhabiting scree slopes occur throughout the entire altitudinal range. Therefore, the simple terms 'arctic-alpine' and 'boreo-montane' only represent the model, and cannot express the diversity of the species' habitat demands.

Five species of boreal origin inhabit lesser known habitats, *viz* scree slopes, and sandstone rock complexes. Four species of Alpine origin also inhabit open scree slopes, and two species inhabit scree forests.

4.1. Screes

These accumulations of stone result from the weathering of primarily compact rocks. Stony habitats are very common and widespread throughout both taiga and tundra zones (Marusik 2004), and also as island habitats in Central Europe. Typically, there is an abrupt difference between both temperature and moisture conditions on the surface of the scree and those in the inner zone, as well as on the upper and lower parts of the scree slope. The surface of the sun-exposed upper margin of a scree slope can heat-up to 50°C on sunny days, while the lower parts of a scree slope, with dynamic air streaming, can often be characterized by ice formation. The ice can persist until late summer or throughout the

Fig. 5. Basalt Kamenec hill, Nature Reserve, North Bohemia (50.706°N, 14.354°E). Lower margin of the scree slope (330 m a.s.l.) is inhabited by spiders and a mite of boreal origin (*Bathyphantes eumenis*, *Diplocentria bidentata*, and *Rhagidia gelida*). The middle part is inhabited by spiders of boreal origin (*Acantholycosa norvegica*, *Wubanoides uralensis*), and of Alpine origin (*Lepthyphantes notabilis*, *Rugathodes bellicosus*). Photography by L. Jenka.

Fig. 6. Poseidon Sandstone Labyrinth, Adršpašsko-Teplické Skály National Nature Reserve, NE Bohemia (50.583° N, 16.133° E), a bird's eye view. The lower portions (600 m a.s.l.) are inhabited by invertebrates of boreal origin: spiders *Bathyphantes eumenis*, *Diplocentria bidentata*, *Sisicus apertus*, *Oreonetides vaginatus*; and a mite *Rhagidia gelida*. Photography by L. Jenka.

entire year (Růžička *et al.* 1995) in the coarse of which, permanent cold air seepage forms a space with an average temperature below zero, unlike the temperatures elsewhere in the region (Zacharda *et al.* 2005, Zacharda *et al.* 2007).

Central European screes are richly colonized by mosses (Lüth 1999, Němcová 2000) and invertebrates: beetles (Molenda 1996), spiders (Růžička 1990b, Růžička and Klimeš 2005), and mites (Zacharda 1993). The occurrences of four boreal spiders are very closely tied to scree habitats in the Czech Republic.

Acantholycosa norvegica exclusively inhabits the surface of stony accumulations throughout the entire area of its distribution, both in the main sub-area from Scandinavia to the Far East, and in isolated sub-areas in Central Europe (Marusik *et al.* 2003). The Central European populations are treated as a separate subspecies (*A. norvegica sudetica* (L. Koch, 1875)) and represent the focus of some current research (Kropf 1999).

B. eumenis has a circumpolar distribution area, including North America and Greenland (Růžička 1988). In Europe, it was recorded in northern Finland (Palmgren 1975, Koponen 1976). It is widely distributed in Russia (Eskov 1994, Mikhailov 1997) and the Far East (Marusik *et al.* 2000). It is one of the most eurybiotic linyphiid species. It lives in forest and mountain tundra belts in various biotopes (except for dry and warm): in detritus, and under stones (Marusik *in lit.*). It inhabits inundated meadows; alder, birch and willow patches along rivers; gravel slopes in the goltsy desert (Eskov 1988); and, it also inhabits stone belts and cliffs (Koponen 1976). The troglomorphic subspecies (*B. e. buchari*) was first recorded in Europe in 1962 (Buchar 1967b), and was described by Růžička (1988). Its distribution is known from the Vosges Mts. to the Low Tatras Mts. (Růžička 1994b); it was not recorded in the Alps (Růžička and Thaler 2002) (Fig. 3). *B. e. buchari* colonizes exclusively the inner crevices of scree slopes. In the Krkonoše Mts., it does not live very deep under the surface at the highest altitudes (1200–1550 m). It inhabits crevices down to a depth of one meter at altitudes of 600–1200 m. At altitudes of 300–600 m, it either inhabits deep scree crevices; or spaces near the surface on the lower margins of scree slopes, with ice formations and with permanent all-year cold air seepage. It lives on bare stone surfaces.

Wubanoides uralensis occurs in the taiga zone from areas along of the Yenisey River up the Barents Sea (Eskov and Marusik 1992, Marusik *et al.* 2000). Its different habitats include *Larix*-forest, moraine (Eskov and Marusik 1992), stacked trees from fire-logging, rocky banks, *Alnus fruticosa* leaf litter, and mountain tundra (Eskov 1986). The occurrence of this species was discovered in Europe in 1987 (Růžička *et al.* 1989). During extensive research of spiders in scree slopes within the Czech Republic (Růžička and Klimeš 2005), this species was only recorded around the northern border mountains. It was also recorded in the Harz Mts. in Germany (Schikora 2004, Fig. 4). A new troglomorphic subspecies (*Wubanoides uralensis lithodytes*) was described by Schikora (2004) for Central European populations. *W. u. lithodytes* exclusively colonizes the inner crevices of scree slopes, there living on bare stone surfaces. It was often found together with *B. s. buchari*; however, it was never found in places with ice formation.

Diplocentria bidentata is an exclusive moss inhabitant (Růžička and Klimeš 2005). In the Czech Republic, the majority of specimens were found at mid altitudes (300–550 m a.s.l.); exclusively in moss on the lower margins of scree slopes with permafrost-like microclimatic conditions.

Because of the permafrost, deeper free subterranean spaces cannot exist in most parts of Siberia; consequently, there are no cavernicolous fauna in eastern Siberia (Marusik 2004). Subterranean spaces in the temperate zone are available for colonization by invertebrates. Extensive inner crevices in scree slopes represent important subterranean spaces, in which the earliest steps of underground evolution take place (Růžička 1999). The development of troglomorphisms, body de-pigmentation, and leg elongation are characteristic for *Wubanoides uralensis lithodytes* (see Schikora 2004), and *Bathyphantes eumenis buchari* (see Růžička 1988). The same situation is observed in those species of Alpine origin: *Rugathodes bellicosus*, in scree slopes at lower altitudes, creates a small depigmented form (Růžička 1990a, 1998); *Comaroma simoni* exhibits a tendency for microphthalmy at lower altitudes (Kropf 1998).

The spiders of boreal origin inhabit a wide spectrum of scree microhabitats, according to the temperature: in extremely cold spaces on the lower margins of frozen scree slopes at lower altitudes (*B. eumenis*, *D. bidentata*); sometimes at intermediate areas (*W. uralensis*); and in sun-exposed spaces (*A. norvegica*). Species of Alpine origin avoid extremely cold spaces, and inhabit shaded spaces in scree forests (*Trogloneta granulum*, and *Comaroma simoni*) or sun-exposed places (*C. alpicola*, *L. notabilis*, and *R. bellicosus*) (Fig. 5).

Scree slopes exhibit the same biogeographical characteristics as peat bogs. They are an important element of landscapes in the temperate zone, in which they contain boreal invertebrates. In this zone, they are usually fragmented into habitat islands; they are azonal or extrazonal habitats, relative to the surroundings. Some species which are highly stenotopic (tyrphobionts, resp. lithobionts) in the temperate zone occur in many habitats in the boreal zone (*i.e.* are eurytopic). Geographical races or subspecies are known among invertebrates with a disjunctive distribution that inhabit peat bogs (Mikkola and Spitzer 1983, Spitzer and Danks 2006) and scree slopes in the temperate zone.

4.2. Sandstone rocks

Sandstone favors the development of a dense system of narrow, deep gorges, which support the highly diverse mosaic of specific habitats (Härtel *et al.* 2007). Castellated sandstone rocks (so-called 'rock cities') in the border region between Northeastern Bohemia and Poland (Vítek 1979) exhibit the coldest microclimate among European sandstones. The bottoms of the gorges are characterized by low potential irradiation, the long duration of snow cover, high air humidity, along with both low air and soil temperatures (Herben 1992).

Bathyphantes eumenis occurs in both Siberia and North Europe in various cold and humid habitats (see above). The pigmented subspecies (*B. e. 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). This spider colonizes in the shady, cold, lower portions of deep gorges in the castellated sandstone rocks. It spins its webs on the bare surfaces of rock walls within narrow gorges and in shallow subterranean crevices.

The Poseidon rock system in the centre of the Adršpašsko-Teplické Skály Rocks National Nature Reserve (Fig. 6) represents the core of this area, an extremely complicated pseudo-karst system (Mlejnek *et al.* 2009). Together with *Bathyphantes eumenis*, also *Diplocentria bidentata*, *Sisicus apertus*, and *Oreonetides vaginatus* were recorded here (Růžička *et al.* 2010). The Poseidon system was also the first place for the recording of the northern predatory mite *Rhagidia gelida* Thorell, 1872 in Central Europe; later, it was found in mountain scree slopes (Růžička and Zacharda 1994). In scree slopes with ice formation, at altitudes of 300–600 m a.s.l., it is considered to be an indicator of permanently frozen core (Zacharda *et al.* 2005).

4.3. Paleorefugia

Nekola (1999) presented the concept of paleorefugia, in which habitats support now-fragmented relicts of the formerly widespread matrix community (whereas neorefugia have formed more recently than the matrix). He evaluated "algific talus slopes" in the temperate zone in northeastern Iowa as being paleorefugia. These habitats are characterized by ice formation in the inner cavities, and a year-round cold air seepage in the lower margins (where soil temperatures rarely exceed 15°C in the summer). Algific talus slopes harbor vascular plants and land snail taxa that are disjunctive in Iowa from the area of their continuous distribution in boreal forests.

The temperatures on the lower margins of our model scree slopes do not exceed 8.0°C in summer (Zacharda *et al.* 2007, Růžička and Zacharda 2010). In the Poseidon sandstone rock system, the temperatures usually do not exceed 8.5°C in summer (Růžička *et al.* 2010). Due to the microclimatic buffering, which mimics the periglacial regional climate, cold-adapted organisms were able to persist here, up to modern times. Therefore, scree slopes with ice formation and sandstone rock complexes in Central Europe can serve as paleorefugia.

ACKNOWLEDGMENTS: This study was supported by the Institute of Entomology (Project No. Z50070508). I hereby want to thank J. Buchar, L. Klimeš, and K. Spitzer for their useful advice.

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Received after revision June 2011

APPENDIX I
Spiders with a north-south disjunction of the distribution area. Habitats in the Czech Republic and in the main sub-area.

Species	Habitat in the Czech Rep.	Habitat in the main sub-area
Gnaphosa lapponum (L. Koch, 1866)	mountain tundra (Růžička and Vaněk 1997)	low alpine heath (Koponen 1976)
Mecynargus morulus (O. P.-Cambridge, 1873)	mountain tundra (Růžička and Vaněk 1997)	low alpine heath (Koponen 1976)
Clubiona norvegica Strand, 1900	peat bogs (Růžička 1997)	peat bogs (Almquist 2006)
Talavera parvistyla Logunov & Kronestedt, 2003	peat bogs (Buchar and Růžička 2002)	peat bogs (Logunov and Kronestedt 2003)
Alopecosa pinetorum (Thorel, 1856)	waterlogged spruce forestes (Buchar and Růžička 2002)	boreal forests (Koponen 1995)
Robertus scoticus Jackson, 1914	forest wetlands (Buchar and Růžička 2002)	boreal forests (Palmgren 1972; Eskov 1987)
Mughiphantes mughi (Fickert, 1875)	spruce forests (Buchar and Růžička 2002)	boreal forests (Palmgren 1975)
Acantholycosa lignaria (Clerck, 1757)	spruce forests (Buchar and Růžička 2002)	boreal forests (Marusik *et al.* 2003)
Acantholycosa norvegica (Thorell, 1872)	screes (Kropf 1999)	stony habitats (Marusik 2004)
Maro lehtineni Saaristo, 1971	mountain tundra (Růžička and Vaněk 1997)	spruce forests (Saaristo 1971; Palmgren 1975)
Xysticus obscurus Collett, 1877	mountain tundra (Růžička and Vaněk 1997)	boreal forests (Koponen 1976; Marusik *et al.* 2002)
Oreonetides vaginatus (Thorell, 1872)	mountain tundra (Růžička and Vaněk 1997)	boreal forests (Palmgren 1975; Koponen 1987, 1995)
Bolepthyphantes index (Thorell, 1856)	mountain corries (Růžička 2000; Chvátalová 2004)	boreal forests (Helsdingen *et al.* 2001)
Ohlertidion ohlerti (Thorell, 1870)	peat bogs (Růžička 1997)	boreal forests (Marusik *et al.* 1993)
Arctosa alpigena (Doleschall, 1852)	*A. a. lamperti* Dahl, 1908: peat bogs (Kůrka 1995)	boreal forests (Buchar and Thaler 1995)
Stemonyphantes conspersus (L. Koch, 1879)	peat bogs (Buchar 1967a)	boreal forests (Marusik *et al.* 2002)
Micaria aenea Thorell, 1871	peat bogs (Růžička 1997)	boreal forests (Marusik *et al.* 2002)
Semljicola faustus (O. P.-Cambridge, 1900)	peat bogs (Kůrka 1995)	boreal forests, peat bogs (Saaristo and Eskov 1996)
Gnaphosa microps Holm, 1939	peat bogs (Kůrka 1995)	boreal forests (Grim 1985)
Pardosa hyperborea (Thorell, 1872)	peat bogs (Kůrka 1995)	boreal forests (Koponen 1976)
Carorita limnaea (Crosby and Bishop, 1927)	peat bogs (Kůrka 1990)	peat bogs, boreal forests (Palmgren 1976)
Sisicus apertus (Holm, 1939)	sandstone rocks (Růžička and Kopecký 1994)	forest wetlands (Palmgren 1975)
Diplocentria bidentata (Emerton, 1882)	screes (sandstone rocks) (Růžička and Hajer 1996)	boreal forests (Koponen 1995)
Bathyphantes eumenis (L. Koch, 1879)	*B. e. buchari* Růžička, 1988: screes (Růžička 1988)	humid habitats (Marusik *in litt.*; Koponen 1976)
Bathyphantes eumenis (L. Koch, 1879)	*B. e. eumenis*: sandstone rocks (Růžička 1992)	humid habitats (Marusik *in litt.*; Koponen 1976)
Wubanoides uralensis (Pakhorukov, 1981)	*W. u. lithodytes* Schikora, 2004: screes (Schikora 2004)	humid habitats (Eskov 1986)

APPENDIX II
Spiders with a south-north disjunction of the distribution area. Habitats in the Czech Republic and in the main sub-area.

Species	Habitat in the Czech Rep.	Habitat in the main sub-area
Gnaphosa badia (L. Koch, 1866)	between forest and peat bogs (Kůrka 1995; Růžička 1997)	ecotone along a tree line (Grimm 1985)
Clubiona alpicola Kulczyński, 1882	alpine grasslands, screes (Buchar and Růžička 2002)	alpine grasslands, stony habitats (Thaler 1981)
Lepthyphantes notabilis Kulczyński, 1887	screes (Růžička 1990a)	stony habitats (Růžička 1990a)
Rugathodes bellicosus (Simon, 1873)	screes (Růžička 1990a)	stony habitats (Růžička 1990a)
Comaroma simoni Bertkau, 1889	scree forest (Růžička and Antuš 1998)	mountain forests (Kropf 2004)
Trogloneta granulum Simon, 1922	scree forests (Růžička 1994a)	scree forests (Thaler 1975)