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The Relict Mite *Rhagidia gelida* (Acari, Rhagidiidae) as a Biological Cryoindicator of Periglacial Microclimate in European Highland Screes

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Abstract

The periglacial temperature regime in cool scree slopes located at subalpine altitudes of only 300–600 m a.s.l. in the Czech highlands is described and proved by the occurrence of a relict population of the predatory mite *Rhagidia gelida* Thorell (Acari, Prostigmata, Rhagidiidae). The mite has a circum-boreal pattern of distribution today, but its disjunct populations have an island-like pattern of distribution in the cool screes in the Czech highlands. *R. gelida* is univoltine, freezing intolerant, and considered a biological cryoindicator of the periglacial microclimate. As coolness is needed for *R. gelida* to survive in the cool screes, it is concluded that the scree slope patchy permafrost-like habitats have lasted continuously, perhaps persisting in modified form as paleorefugia, since the Pleistocene.

Introduction

Talus or scree formations develop through mechanical weathering of bedrock and are abundant both in arid zones and on hill and mountain slopes in zones that have experienced periglacial activity. In central Europe, talus formation occurred during the Pleistocene glaciation at low latitudes along vast periglacial zones that faced northern continental and southern alpine glaciers. At present, this weathering activity dominates on high mountains and at high latitudes. However, in some scree formations in subalpine landscapes in central Europe, perennial periglacial-like microclimates still prevail in shallow field depressions, or "ice-hollows," that are cold all year round. Temperatures fluctuate around 0°C during the vegetative season so that solid ice is often present until late summer or early autumn. Ice hollows have been mentioned in the scientific literature for more than 200 years (e.g., Schaller, 1785; later, Pleischl, 1838; Balch, 1900; and recently, Mareš, 1959; Kubát, 1971; Möseler and Molenda, 1999; Zacharda, 2000b; Gude et al., 2003; among others). However, little scientific research has been carried out on cool screes, as they appear lifeless and are difficult to sample. Consequently, the published information on these sites has not changed for many decades. Until recently, most studies were confined to simple observations of cool and warm air outflows in summer and winter, respectively (Balch, 1900; Mareš, 1959). No precise continuous time series of microclimatic measurements (Hinkel et al., 2001) has been collected in these localities to describe basic seasonal heat transport processes.

Recent European microclimatological studies have identified small discontinuous permafrost-like patches in cold screes with periglacial microclimates. These sites have been found at 300–500 m a.s.l., i.e., about 1500–2000 m below the present limit for permafrost in European mountains (Gude et al., 2003). Biological surveys of these sites have found periglacial relict species of beetles (Molenda, 1996), non-vascular plants (Němcová, 2001), and chelicerates (Zacharda, 1993; Růžička and Zacharda, 1994).

These discoveries have stimulated interest in the ecology of these geo-ecosystems. One of the extant periglacial relicts is the predatory rhagidiid mite, *Rhagidia gelida* Thorell, 1872. Until the 1980s the mite was known only from the Arctic (Zacharda, 1980), where it was "widely distributed on the northern coast, having been collected in tundra from Cape Beaufort to Tuktoyaktuk" (Strandtmann, 1971). It was later found in central Europe; for example, in deep sandstone gorges and screes with a permanently cool microclimate in Adršpach-Teplice

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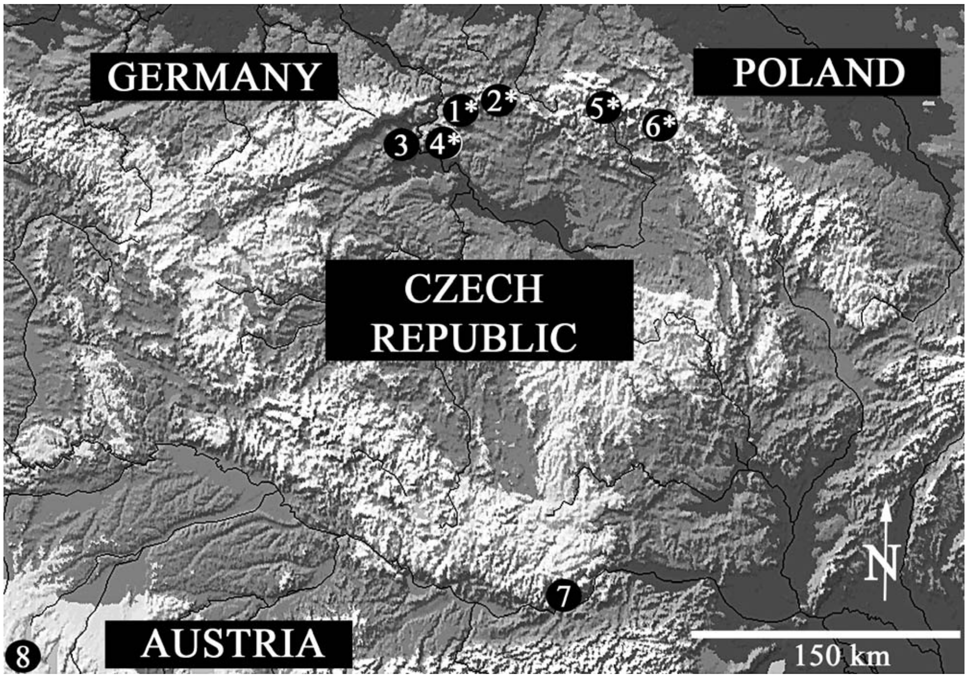

FIGURE 1. Location map of the study sites in central Europe. Sites supporting *R. gelida* are marked with asterisks. 1*—Kamenná Hůra, 2*—Klíč hill, 3—Boreč hill, 4*—Plešivec hill, 5*—Krkonoše Mountains, 6*—Adršpach-Teplice Rocks, 7—Dyje River valley, 8—Obergurgl, Ötztal Alps. Sites 1–7 are in the Czech Republic, and Site 8 is in Austria.

Rocks, NE Bohemia (50°36′N, 16°8′E), and in montane screes in the Krkonoše (Giant) Mountains (50°45′N, 15°40′E), north Bohemia, the Czech Republic, at an altitude of about 1400 m a.s.l. (Zacharda, 1993). Recently, *Rhagidia gelida* has also been found in two areas of about 100 m^2 each, at the base of scree slopes with periglacial-like microclimates at 300–500 m a.s.l. in the České Středohoří–highland and Lužické Hory Mountains, north Bohemia. These two new sites are recognized as the southernmost known habitats of disjunct relict populations of this mite.

The main objective of this study was to describe the cool scree habitat and the life cycle of the relict predatory mite *Rhagidia gelida* as a biological cryoindicator which documents the relict cool, periglacial-like microclimate that prevails in these two screes during the vegetative season. In addition, continuous temperature measurements and geophysical surveys of the internal structure of the screes were undertaken.

Site Description

Twenty different scree slopes in the České Středohoří–highland and the Lužické Hory Mountains were examined during the vegetative season for cool, periglacial-like microclimates (Zacharda, 2000b). Only four sites with such a microclimate were found at the base of the following scree slopes: Boreč hill near Lovosice (50°31′N, 14°2′E), Plešivec hill near Litoměřice (50°33′N, 14°7′E), Kamenná Hůra near Merboltice village (50°42′N, 14°21′E), all in the České Středohoří–highland, and Klíč hill near the Svor village (50°49′N, 14°04′E), in the Lužické Hory Mountains (Fig. 1). All these sites are in north Bohemia, Czech Republic. Subsequent research was focused on the latter two ice-retaining screes as they support populations of *Rhagidia gelida* mites and seem to be the most typical sites.

The Kamenná Hůra olivine basalt scree slope is located in the Kamenná Hůra Nature Reserve, which covers an area of 56.7 ha. The bare, open screes on the slopes of the Kamenec massif (519 m a.s.l.) are among the largest screes in the České Středohoří–highland (Fig. 1). They originated through mechanical weathering of a tertiary basalt plateau overlying chalky clay. The climate is mild, with an average annual temperature of about 8°C, and January and July average air temperatures of –2 to –3°C and 16°C, respectively. Several natural ice hollows are found at 300 m altitude at the base of the large northern scree field (Fig. 2). Accumulations of bedrock boulders about 40–80 cm diameter are densely covered with pads of many species of nonvascular plants. Among these plants are subarctic or subalpine liverworts (*Gymnomitrion corallioides* and *Diplophyllum taxifolium*) and moss (*Polytrichum alpinum*), and mountain liverworts (*Lophozia hatcheri*, *L. sudetica*, and *Tritomaria quinquedentata*) and moss (*Bryum alpinum*) (Němcová, 2001). Norway spruce (*Picea excelsa*), birch (*Betula* sp.), and rowan tree (*Sorbus aucuparia*) grow on the periphery of the ice hollow.

A large, free, open phonolite scree is found on the SW slope of Klíč Mountain (759.5 m a.s.l.) Nature Reserve in the Lužické Hory Mountains (Fig. 1). The climate is wet and mild to cool, with an average annual temperature of 6–7°C, and January and July average air temperatures of –4 to –3°C and 16°C, respectively. The scree slope originates from mechanical weathering and rockfall activity and consists of bedrock blocks 40–80 cm in diameter. There is a distinct field depression, where outflows of cool air are perceivable to a man, particularly in hot summers, at the SSW base (524 m a.s.l.) of the scree. The entire ice-hollow area is covered with lichen and moss pads consisting of species such as the reindeer lichen *Cladonia rangiferina* and *C. uncinalis*; the liverworts *Calypogeia integristipula*, *Diplophyllum taxifolium*, *Lophozia hatcheri*, and *L. sudetica*; and the mosses *Grimmia donniana*, *G. incurva*, *Polytrichum alpinum*, *P. formosum*, *Racomitrium sudeticum*, and *R. heterostichum* (Sýkora, 1972; Němcová, 2001). Small, dwarfish Norway spruce trees (*Picea excelsa*) and rowan trees (*Sorbus aucuparia*) grow on the periphery. This habitat resembles tundra (Billings, 1973; Danks, 1979). Botanists consider both *Polytrichum alpinum* and *Grimmia incurva* as subarctic-subalpine species of mosses that often indicate cool sites such as ice hollows when found in low-altitude screes (Němcová, 2001). On the NW and SE outskirts of the ice hollow, the vegetation pattern changes to a Vaccinio-Abietion plant community, with Norway spruce and rowan trees, and the Calamagrosti arundinaceae-Fagetum plant community, respectively (Sýkora, 1972).

Continuous temperature measurements, geophysical estimates of scree ice content within the screes, and long-term collections of invertebrates were performed at both sites.

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FIGURE 2. The ice hollow at the base of the Kamenná Hůra scree slope, 300 m a.s.l., 21 March 2003, ambient air temperature +7°C, cool air outflow temperature –1°C.

Methods and Material

TEMPERATURE MEASUREMENTS

Scree thermal properties were first investigated at both sites with a hand-held temperature probe (recalibrated with a precise mercury thermometer) for a coarse characterization of the thermal regime. The coolest places were identified for more intensive study by comparing the temperature of the substratum and the surrounding air. Once these relatively cool areas were identified, their thermal regime was studied by placing miniature temperature Tiny Talk data loggers (Gemini Data Loggers Ltd., U.K.; sensor accuracy ±0.2°C) in subsurface air voids at about 50–70 cm depth. Similarly, temperature data loggers were placed just below, and 3 m above, the surface of the scree. Logging intervals of 2 or 3 h were set up. The temperature data loggers were left in place for one year (Fig. 3).

At the Kamenná Hůra ice hollow, in the area of around 100 m^2 populated by the mite *R. gelida*, the substratum surface temperature was taken along 20-m-long transects, along and perpendicular to a contour line and intersecting the ice hollow at its coolest part (Fig. 4). Measurements were taken at 65-cm intervals along the transects using the handheld temperature probe, the top of which was laid on the substratum surface.

GEOPHYSICAL SURVEY OF THE INTERNAL STRUCTURE OF THE SCREE

In the early summer of 2001, refraction seismic and direct-current (DC) resistivity tomography techniques were used to investigate the scree interior. Both are standard methods for non-invasive investigations of the near subsurface and have been extensively used for ground ice detection (e.g., Vonder Mühll et al., 2002). The aim of the geophysical surveys was to determine the depth and ice content of the scree.

A multi-electrode system (Syscal Instruments R 1) with 48 electrodes and 2.5- and 5-m spacing was used to measure DC resistivity, i.e., the electric potential between electrodes to 30 m depth.

As an alternative indicator of the composition of scree, the refraction seismic surveys were performed using a 12-channel seismograph (Geometrics Smartseis), a sledgehammer, and 2.5-m geophone spacing. The investigation depth was limited to a 10–20 m depth because of the small number of receivers (geophones) and the low energy generated by the sledgehammer source.

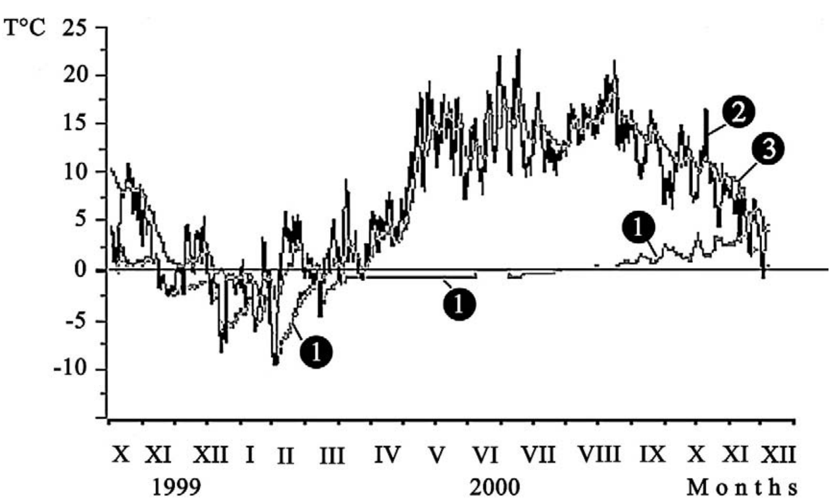

FIGURE 3. The seasonal temperature fluctuations in the Kamenná Hůra scree slope. 1—sensor depth 0.6 m at the base of the scree slope, the annual mean temperature –0.42°C (year 2000). 2—sensor depth 0.6 m in the mid-area of the scree slope. 3—atmospheric air temperature, sensor 2.5 m above the surface of the base of the scree.

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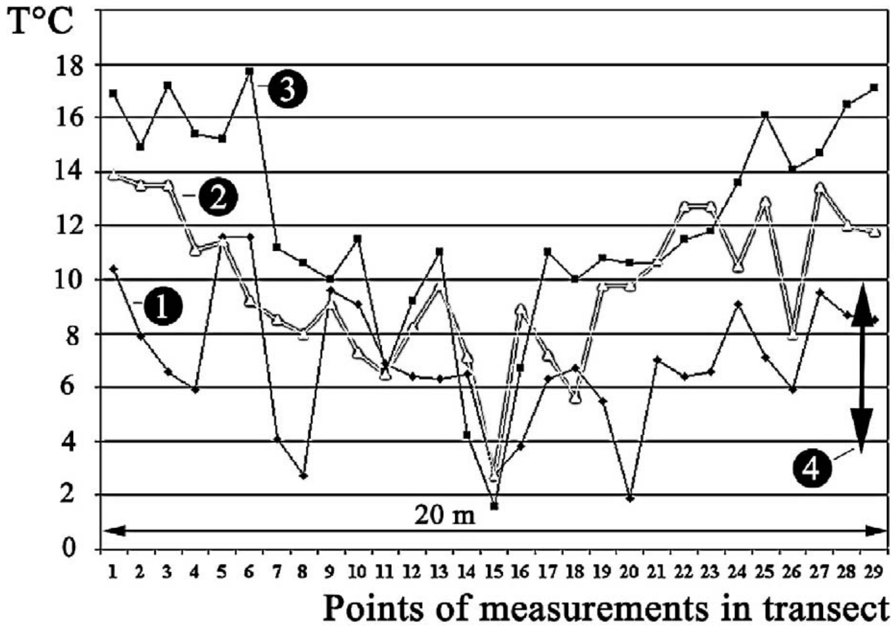

FIGURE 4. The surface temperature as measured in transects in the Kamenná Hůra ice hollow. 1—N-S transect perpendicular to a contour line. 2—SE-NW transect 45° oblique to a contour line. 3—E-W transect along a contour line. 4—temperature range of occurrence of Rhagidia gelida. Measurements taken on 22 August 2001, 13:00–15:00 p.m.

By using a combination of seismic and direct-current resistivity data, researchers can distinguish between ice, water, air, and rock occurrences in the subsurface (Hauck and Vonder Mühll, 2003).

COLLECTION OF MITES

Rhagidia gelida inhabits voids between scree fragments. *R. gelida* were collected with eight large, winged pitfall traps. The traps were made of rigid plastic, about 13 cm high and 10.5 cm in diameter (Růžička, 1988) and were set out in 2000–2001 in two separate ice hollows about 10–50 cm under the surface of the scree. They contained a mixture of 7% formalin and 20% glycerol, plus a few drops of detergent. They were left in place for periods of about one month, after which they were removed and the catch was processed in the laboratory.

Results

PERIGLACIAL CONDITIONS

Continuous temperature monitoring documented periglacial-like microclimates in small areas of about 100 m^2 at the bases of the investigated scree slopes (Fig. 2). In the years 2000 and 2001 in Kamenná Hůra and Klíč, an average annual air temperature in these areas, at about 0.6 m depth, was –0.42 and –0.75°C, and +0.145 and +0.329°C, respectively. In frosty winter months the screes were cooled through contact with cold atmospheric air and solid ice developed there gradually from melting snow and rainfall. During spring and summer the cooled blocks and ice within the screes kept the air in voids between them cold and cold air also flowed out of the scree at its base. For example, at the Kamenná Hůra site on 17 May 2000, the air temperature at the base of the scree ranged from –0.4 to +6°C. Solid ice was repeatedly found between bedrock blocks just under the scree surface during spring and summer months. Surface ice was also observed at Kamenná Hůra on 1 September 2003 after the hottest summer in Bohemia in 228 years.

Geophysical surveys along and across the coolest places at the bases of the screes showed that the blocky layer was 10–15 m deep and 15–20 m deep at Kamenná Hůra and Klíč, respectively. The survey also provided strong evidence of small ground ice accumulations within the Klíč-scree voids (Gude et al., 2003). These probable ice occurrences have diameters of less than 2 m across and are 2–5 m below the surface. At Kamenná Hůra the evidence for ground ice occurrence was unclear, although one similar anomaly was found in the resistivity and seismic results. Its location right at the margin of the blocky layer indicated that it represented bedrock rather than ice (Gude et al., 2003).

SEASONAL OCCURRENCE AND ACTIVITY OF RHAGIDIA GELIDA

R. gelida (Fig. 5) was restricted to cool areas of about 100 m^2 around ice hollows at the base of the scree slopes. These areas at the boundary of organic and mineral substrata formed a mosaic of cold and warm microclimates (Fig. 4) with temperatures ranging from about +2 to +19°C on hot summer days. These temperature differences were caused by local outflows of cool air from fissures between blocks of bedrock close to microsites heated by direct sunlight that penetrated the foliage of neighboring trees.

The microhabitat of *R. gelida* was determined through repeated direct observations of mite movement on bare and moist block walls or in fissures between blocks and adjacent moss pads in August. In these places along the transect, the temperature ranged from +3.8 to +10.0°C as indicated in Figure 4.

The first nymphs of *R. gelida* appeared in May while adults were absent (Fig. 6). The first adults appeared in June and were most numerous in July and August. Females usually had 1–4 brownish, bean-shaped eggs in their opisthosomal cavities. In June, the mean male-biased sex ratio was 1:1.5 ($n = 53$), while from July to August the mean female-biased sex ratio was 1:3.7 ($n = 1431$). However, later in September the number of adults sharply decreased, and in October only 1 specimen was collected. These data suggest that *R. gelida* is a univoltine species.

Discussion

Recent European microclimatological studies have identified small discontinuous permafrost-like patches in cold screes with periglacial microclimates. Though permafrost-like conditions in the sense of modern usage in Canada and U.S.A., i.e., "ground (soil and/or rock) that remains at or below 0°C for at least two years" (French, 1996), have been verified by numerous underground temperature measurements in several scree slope systems, by observations of ground ice in mid- and

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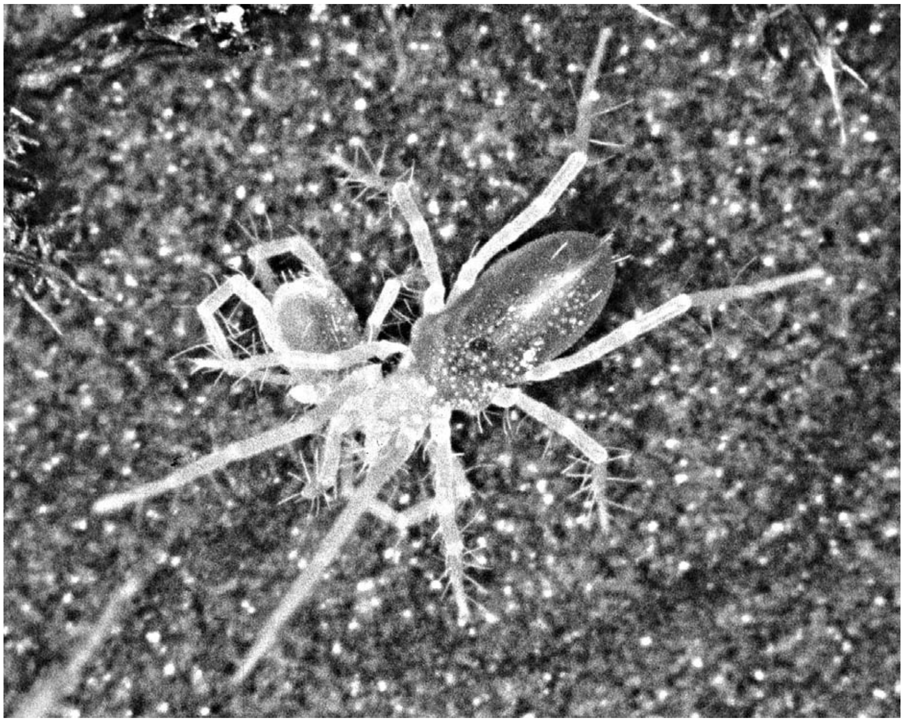

FIGURE 5. The cool tolerant predatory mite *Rhagidia gelida*, with hoarfrost on its dorsum, cannibalizing a member of its own species.

late summer, and by geophysical surveys, it has not been definitely resolved whether these sites do fit within the conventional definitions of permafrost or not (Gude et al., 2003). Complementary long-term series of temperature measurements and studies on latent heat processes in the ice-retaining screes are still needed.

During the European Pleistocene glaciation there was a vast periglacial zone between the Alps and the northern continental ice sheet. This zone was subject to severe nival climate and permafrost with associated upper active layer cryogenic processes such as intensive frost weathering, solifluction, and growth of ice wedges. Similar conditions still prevail in the Arctic (Ives, 1974; Schrott, 1999). The predatory mite *R. gelida* frequently occurs in the Arctic and was also collected in Barrow, Alaska (Strandtmann, 1971), in high arctic tundra meadow on the Arctic Coastal Plain where surface temperatures reach +8–13°C during the summer (MacLean and Pitelka, 1971; Hinkel et al., 2001). The temperature regimes of the surface organic layer in the Klíč and Kamenná Hůra scree ice hollows are strikingly similar to those near Barrow, Alaska. In the Arctic the mite has only been collected in localities with permafrost (Fig. 7) and periglacial microclimate. Direct observations in the Kamenná Hůra and Klíč ice hollows show that this species is strictly limited to areas where the substratum surface temperature is +3.8 to +10.0°C. It is difficult to believe that this strictly cold, stenotherm mite (Danks, 1979) could have migrated into the ice hollows during the Holocene either from some mountain refugia, e.g., screes of the Krkonoše Mountains, or across vast temperate areas from the Arctic. The only plausible explanation is that *R. gelida* is

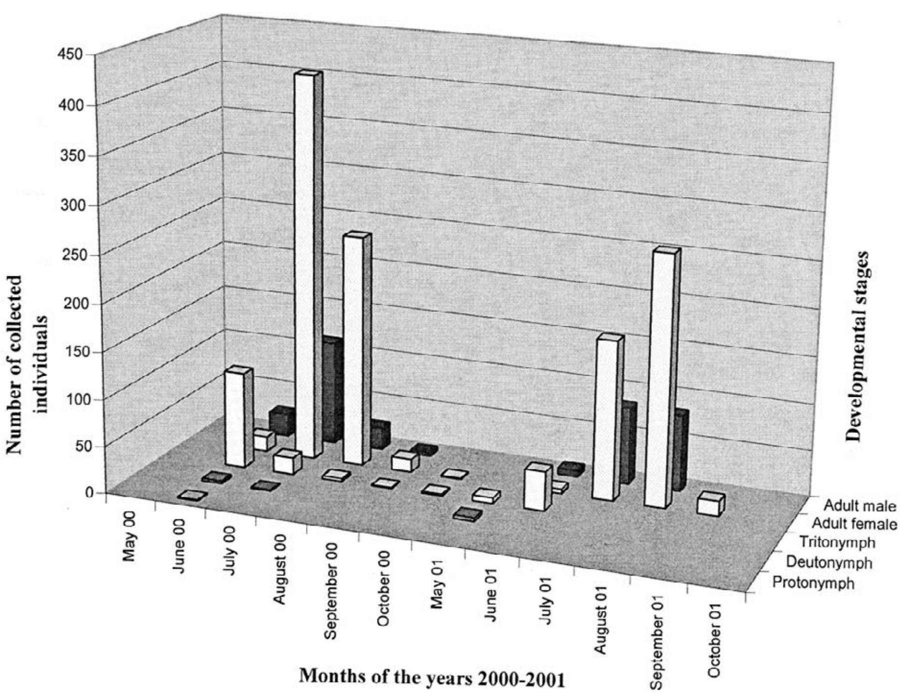

FIGURE 6. The seasonal occurrence of developmental stages of *Rhagidia gelida* in pitfall traps used in the locality Kamenná Hůra.

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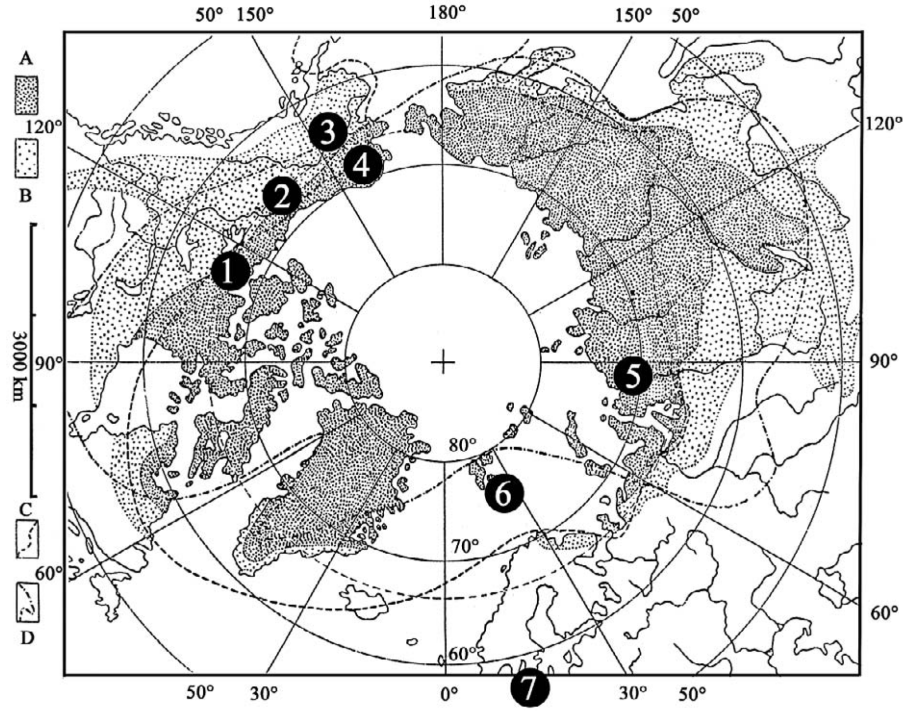

FIGURE 7. The contemporaneously known geographic distribution of Rhagidia gelida in the arctic region and central Europe. 1—Atkinson Point, N.W.T., Canada. 2—Tuktoyaktuk, Alaska. 3—Fairbanks, Alaska. 4—Barrow, Alaska. 5—the mouth of the Jenisey River. 6—Svalbard, Spitzbergen, Beeren Eiland. 7—cool screes in the Czech Republic. See also a location map in Figure 1. Densely dotted pattern—continuous permafrost. Sparsely dotted pattern—discontinuous permafrost. Dashed line—July isotherm, +10°C. Dashed-and-dotted line—January isotherm, –20°C. The map showing geographic distribution of the permafrost was taken from Ložek (1973) and is slightly adapted.

a glacial or, strictly speaking, periglacial (sensu Molenda, 1996) relict that has survived in the periglacial-like microclimate of the ice hollows, at least from the height of the last Pleistocene glaciation, when most of Europe was tundra (Matthews, 1979).

As perennial coolness is a prerequisite for the relict mite *R. gelida*, it is plausible that the periglacial-like microclimate that causes permafrost-like patches appeared with scree formation during the Pleistocene. In other words, the relict mite can be considered as an indicator that a perennial cool microclimate has persisted in these ice-retaining screes throughout the Holocene.

Geographically and climatically isolated ice hollows are thought to be island-like refugia for relict species of landscape biota (Hellwig, 1999). Nekola (1999) designated North American cool algific talus slopes located in the driftless area (Paleozoic plateau) in the Upper Midwest, U.S.A., as paleorefugia. They show a similar microclimatic scree slope phenomenon to that described above and support extant colonies of the periglacial relict candidate land stenotherm snails (Frest, 1991). The occurrence of these snails indicates the periglacial-like microclimate in the ice-retaining talus slopes. These paleorefugia represent habitats that are older than the surrounding biological matrix and support communities or populations unable to survive elsewhere in the landscape.

Some of the cool, ice-retaining scree slopes in the Czech Republic, which support populations of the mite *R. gelida*, also support spiders such as *Bathyphantes simillimus*, *Leptyphantes tripartitus*, *Diplocentria bidentata*, *Latithorax faustus*, or *Wubanoides uralensis* (Růžička and Zacharda, 1994; Růžička, 1999) and non-vascular plants with a boreo-alpine pattern of distribution (Němcová, 2001). These sites seem to fit Nekola's concept of paleorefugia, and the above-mentioned taxa can be also considered relicts, although in the case of the spiders or non-vascular plants, presence can also be explained by airborne travel.

The question then arises: Do these local, disjunct, scree-inhabiting populations differ from each other and the present boreal or Arctic populations? This question could be answered using molecular biology.

It should also be mentioned that in the Czech Republic the mite *R. gelida* occurs only in the northern part of north to NE Bohemia (Fig. 1). This corresponds to approximate borders of the maximum Pleistocene continental glaciation. In contrast, up until now this mite has never been collected in any cool screes in central and south Bohemia or south Moravia. For example, *R. gelida* does not occur in a cool phonolite scree on Boreč hill near Lovosice (50°31′N, 14°2′E), i.e., only about 15 km in a direct line from the southernmost occurrence of this mite in scree located at the foot of Plešivec hill near Litoměřice, although the periglacial microclimate here resembles that in the Klíč and Kamenná Hůra study sites. Similarly, *R. gelida* is absent from the cool screes of ice caves in the Dyje River valley, south Moravia (Růžička, 1996). This mite has never been collected from the subnival alpine zone of the Austrian Ötztal Alps in the vicinity of Obergurgl, Tirol, with a severe alpine climate and permafrost (Haeberli and Patzelt, 1982), where assemblages of rhagidiid mites were studied at an altitude of 2000–3000 m a.s.l. in 1993–1994 by Zacharda (2000a). Thus, the ice hollows at the foot of the Plešivec hill near the town of Litoměřice (50°33′N, 14°7′E) are currently the southernmost known locality of this species in central Europe.

The disjunct populations of *R. gelida* in the ice hollows still exhibit seasonal biological adaptations correlated with an adverse winter period. Univoltine mites are cold stenotherms which are only active and multiply during the summer. Currently it is not known why the mite prefers a cool habitat. It could be a lack of competition because no other species of rhagidiid mites have been collected in this habitat, or the species may be more than cool tolerant and may have the ability to move, feed, multiply, etc. at low temperatures. Probably it is freezing intolerant, i.e., cannot survive ice formation within its body, but can survive ice formation around it in its habitat. However, neither dormancy nor cold-hardiness (Danks, 1979) has been studied in this mite.

Conclusions

Periglacial microclimates occur at bases of scree slopes located at the subalpine altitude of only 300–600 m a.s.l. in the Czech Republic, central Europe. Particular geo-ecosystems supporting disjunct populations of the cool tolerant relict species of nonvascular plants and invertebrates have evolved in these cool places. Among these, the

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predatory prostigmatic mite *R. gelida* is the periglacial relict and can be considered a biological cryoindicator of the periglacial microclimate. The mite *R. gelida* is univoltine. This is an adaptation to adverse climatic conditions typical of extant species of invertebrates that live in the Arctic. As perennial coolness is needed for *R. gelida* to survive in these habitats, it is concluded that the scree slope patchy permafrost-like habitat in the study sites is long-lasting, and perhaps has persisted in modified form since the Pleistocene.

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