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Diversity of Predatory Rhagidiid Mites (Acari: Rhagidiidae) Inhabiting Montane Stony Debris in the Ötztal Alps, North Tyrol, Austria

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Abstract

Critical revision is presented of taxa comprising 27 verified species of Rhagidiidae from the Alps. Assemblages of endemic, Palearctic, and Holarctic Rhagidiidae inhabiting montane stony debris in the Ötztal Alps, North Tyrol, Austria, consist of 2 to 9 species, and *Poecilophysis pseudoreflexa* is the most abundant and widely distributed species. The highest species richness and endemism are in the mid-alpine zone (2400–2600 m a.s.l.) and the high alpine zone (2600–2800 m a.s.l.). A particular assemblage of rhagidiids of low diversity occurred in voids of a bare scree slope. Cluster and numerical multivariate analyses revealed that (1) the different altitudinal niches of a majority of common species overlap, but some species become rare with increasing altitude; (2) additional species of rhagidiid mites might be expected to be found in special, previously uncollected microhabitats; (3) rhagidiid mites having some affinities to specific environmental factors can be distinguished; (4) the altitudinal gradient proved to be the significant complex environmental factor influencing the occurrence of mites; (5) moisture proved to influence abundance of mites but has no direct relation to species identity; and (6) in contrast, dryness proved to be bound with the occurrence of particular species of rhagidiid mites.

Introduction

Spiders and mites are the dominant arachnid groups, both for their diversity and abundance, in the Austrian Alps (Thaler, 1994, 2003). Among the mites, representatives of the predatory family Rhagidiidae frequently occur at high altitudes above timberline in the uppermost parts of alpine, subnival, and low nival zones with a prevailing severe climate. Here, they mostly live under stones and in wet stony debris in periodically occurring snow beds located in shaded ground depressions that are frequently covered with snow until mid- or late summer. These psychrophilic species are cool-adapted, and they can frequently be observed actively running here and there and feeding mostly on springtails (Collembola) under stones covered with snow in the alpine nival zone. They are univoltine, with their active developmental stages (larvae, proto-, deuto-, tritonymphs, and adults) appearing successively during the growing season.

Rhagidiid mites have frequently been collected in various habitats in the Alps, including caves (Willmann, 1932, 1934). To date, 41 species of rhagidiid mites have been reported from the Alps (Franz, 1943, 1954; Irk, 1941; Janetschek, 1959, 1993; Mihelčič, 1957; Schmölzer, 1962; Schweizer and Bader, 1963; Thor and Willmann, 1941; Willmann, 1951, 1953a, 1953b; Zacharda, 1980, 1994, 2000a, 2000b, 2000c, 2000d), but only 27 species are taxonomically well recognized and confirmed (Table 1). The reason for this was that until 1980, owing to a previous lack of knowledge and confused taxonomic placement, their reliable identification was impossible and most of the Rhagidiidae collected in the Alps were misidentified as *Rhagidia terricola* (C. L. Koch), *R. intermedia* Willmann, *R. reflexa* (C. L. Koch), *R. gigas* (Canestrini), and *R. dalmatina* Willmann.

Janetschek (1993) provided data on the localities of rhagidiids that he had collected in the Zillertal Alps (Janetschek, 1959). These taxa were originally determined by Willmann (1951, 1953a, 1953b), remained deposited in his collection, and subsequently were re-examined by Zacharda (1980), who identified and verified 8 species collected in the Alps, i.e., *Poecilophysis pratensis* (C. L. Koch, 1835); *P. wankeli* (Zacharda, 1978); *Foveacheles osloensis* (Sig Thor, 1934); *F. willmanni* Zacharda, 1980; *F. alpina* Zacharda, 1980; *Evadorhagidia janetscheki* (Willmann, 1953); *Shibaia longisensilla* (Shiba, 1969) and *Thoria uniseta* (Sig Thor, 1909). Later, *F. unguiculata* Zacharda, 1994 was described, and 9 species of rhagidiids were confirmed to occur in the Alps (Zacharda, 1994). In 1992–1993, Zacharda collected numerous rhagidiid mites in stony debris habitats in various alpine zones (Reisigl and Keller, 1987) in the vicinity of Obergurgl, the Ötztal Alps (Central Alps, Northern Tyrol, Austria).

Because the gradient of diversity of the rhagidiid mites in the different alpine habitats and altitudinal zones above timberline has not been studied until now, the purpose of this investigation was to describe assemblages of rhagidiid mites, determine their heterogeneity in the investigated habitats and altitudinal zones, and assess the biogeographic significance of the collected taxa and their interrelations to some environmental factors. Descriptions of newly discovered taxa have been published (Zacharda, 2000a, 2000b, 2000c, 2000d), but subsequent questions remain to be answered that would extend the objectives of this study: (1) Is there a specific assemblage of rhagidiid mites inhabiting deep underground voids of montane scree slopes just at the upper limit of timberline, or is this habitat occupied by the same species occurring in the high altitude screes of alpine non-forested zones? (2) Is there any interrelation between environmental factors such as (a) altitude of alpine zones, (b) substratum humidity, (c) vegetation cover, and (d) habitat solar exposition, and species abundance and composition of assemblages of rhagidiid mites?

Material and Methods

LOCALITIES

Mites were collected in 1992 and 1993 in the vicinity of Obergurgl (11°02′E, 46°52′N), the silicate bedrock area of the Ötztal Alps (Fig. 1), at various altitudes above timberline ranging from ~2000 m a.s.l. in the low alpine zone up to ~3000 m a.s.l. in the low nival zone (Reisigl and Pitschmann, 1958; Reisigl and Keller, 1987; Meyer and Thaler, 1995).

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TABLE 1

Faunal list of well recognized and verified species of Rhagidiidae that have been collected in the Alps. Patterns of distribution: (E)—endemic, (P)—Palearctic, (H)—Holarctic.

1. *Coccorhagidia pittardi* Strandtmann, 1971 (H)
2. *Foveacheles brevichelae* Zacharda, 1980 (H)
3. *Foveacheles cegetensis* Zacharda, 1983 (P)
4. *Foveacheles halltalensis* Zacharda, 2000 (P)
5. *Foveacheles osloensis* (Sig Thor, 1934) (P)
6. *Foveacheles proxima* Zacharda, 2000 (E)
7. *Foveacheles willmanni* Zacharda, 1980 (E)
8. *Foveacheles alpina* Zacharda, 1980 (E)
9. *Foveacheles unguiculata* Zacharda, 1994 (E)
10. *Evadorhagidia bezdezensis* Zacharda, 1980 (P)
11. *Evadorhagidia corcontica* Zacharda, 1993 (P)
12. *Evadorhagidia janetscheki* (Willmann, 1953) (E)
13. *Evadorhagidia oblikensis* Zacharda, 1980 (P)
14. *Poecilophysis pratensis* (C. L. Koch, 1835) (H)
15. *Poecilophysis wankeli* (Zacharda, 1978) (H)
16. *Poecilophysis pseudoreflexa* Zacharda, 1980 (H)
17. *Poecilophysis spelaea* (Wankel, 1861) (P)
18. *Poecilophysis saxonica* (Willmann, 1934) (H)
19. *Rhagidia gigas* (Canestrini, 1886) (H)
20. *Rhagidia parvilobata* Zacharda, 1995 (H)
21. *Rhagidia distisolenidiata* Zacharda, 1995 (H)
22. *Rhagidia diversicolor* (C. L. Koch, 1835) (H)
23. *Rhagidia longiseta* Zacharda, 2000 (E)
24. *Shibaia longisensilla* (Shiba, 1969) (H)
25. *Thoria uniseta* (Sig Thor, 1909) (P)
26. *Troglocheles archetypica* Zacharda, 2000 (E)
27. *Troglocheles aggerata* Zacharda, 2000 (E)

The environmental conditions prevailing in this region have been described in detail by Reisigl and Pitschmann (1958), and more recently by Janetschek et al. (1987). Low temperatures, a short growing season, reduction of habitat structure, little plant cover, and the effect of wind and snow cover distribution are the most important ecological factors influencing montane biota in this area (Meyer and Thaler, 1995). Because, for the most part, only adult specimens of the rhagidiid mites can be reliably identified to species and because these occur in cool montane habitats at the end of the growing season, hand collections were timed from the end of August to the beginning of September when the alpine landscape was not yet covered with snow.

Samples of mites (S1–S10) were collected in 10 various localities in six different alpine habitats and altitudinal zones (ALP1–ALP6) (Table 2).

COLLECTION

The distribution of rhagidiid mites in nature is not random. Their preferences for particular microhabitats where they are aggregated are clearly visible to a collector. A really random and unbiased sampling of these mites is therefore difficult. Epigeic and hypolithic mites, i.e., mites living in voids under stones, were collected by way of hand sorting using a small aspirator containing ethanol as a preservative. To standardize a sampling effort, the greatest possible number of individuals was always collected in the investigated localities (Magurran, 2003). Only limited kinds of sampling techniques are available and appropriate for rhagidiid mites inhabiting deep underground voids in scree slopes. Large pitfall traps made of rigid plastic, about 13 cm high and 10.5 cm in diameter (Růžička, 1988) were positioned ~50–100 cm under the surface of the scree slopes. The traps contained an aqueous mixture of 7% formalin and 20% glycerol, plus a few drops of detergent. They were left in place for 1 year, from 4 June 1991 to 26 June 1992, after which they were removed and the catch was processed in the laboratory. Mites, initially preserved in ethanol, were transferred to lactic acid in temporary slide preparations (Krantz, 1978), examined under a standard light microscope under a bright field and identified to species (Zacharda 1980, 1995a, 1995b, 1996, 2000a, 2000b, 2000c, 2000d).

SPECIES DIVERSITY MEASURES

Species abundance data were plotted as a rank/relative abundance graph (the Whittaker plot) to estimate and illustrate an expected impact

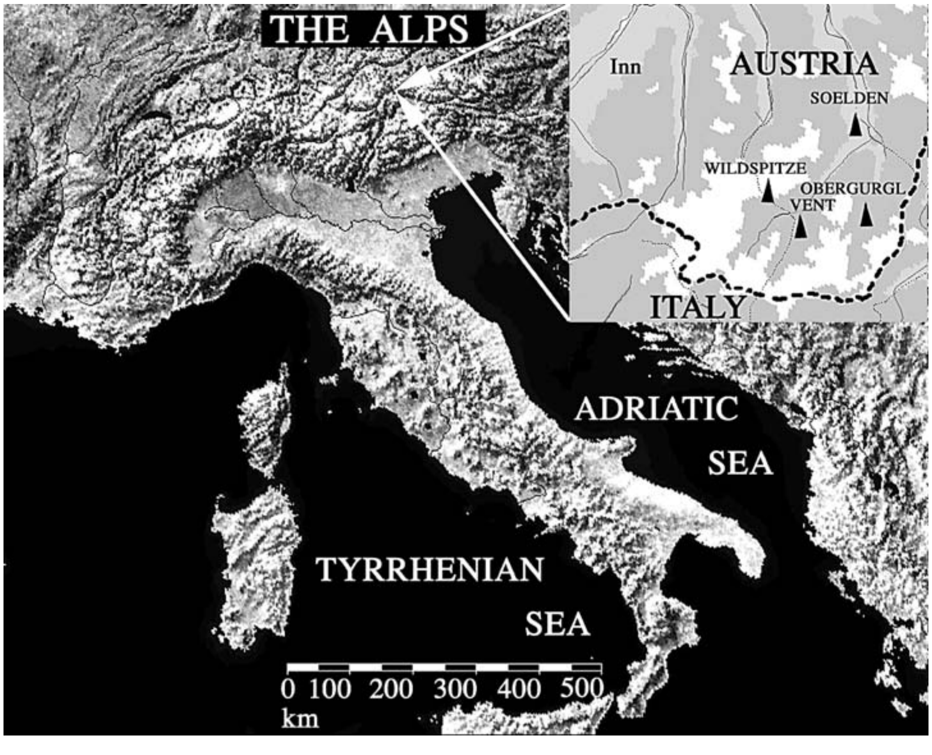

FIGURE 1. Map of location of Obergurgl (46°52′N, 11°02′E), the Ötztal Alps, North Tyrol, Austria, showing the place of collection.

of different alpine zones (ALP1–ALP6) on the assemblages of rhagidiid mites with respect to their species heterogeneity (species richness and evenness) in the alpine environment, (Magurran, 2003). Numerical species richness was estimated by a Chao1 nonparametric estimator (Magurran, 2003, p. 87), diversity by Simpson's index (D), and species evenness by Simpson's E1/D index (Magurran, 2003, p. 114–116). The Simpson's index was computed by the BioDiversity Professional v.2 software package (http://www.nhm.ac.uk/zoology/bdpro).

ENVIRONMENTAL DATA SOURCES

Ecological interrelations of mites to their environment were observed and data collected for further numerical multivariate analysis. The following data were recorded for each locality: (1) quantitative: (i) altitude (range 2000–3050 m a.s.l.), (ii) insolation was represented by insolation index (cos [aspect – 202.5°] × tg [slope]; Geiger, 1966); (2) semiquantitative: (iii) moisture (ordinal scale 0–4: 0—dry, 1—slightly moist, 2—moist, 3—moist to wet, 4—wet), (iv) vegetation cover (ordinal scale 0–3: 0—bare ground, 1—sporadic small patches covering less than 40% of ground surface, 2—patches covering 40–60% of ground surface, 3—patches covering 70–100% of ground surface); (3) categorial (indicator, so-called "dummy" variables): alpine zones (ALP1–ALP6) (see above in the description of localities).

NUMERICAL ANALYSIS

The species abundance data were log-transformed for all analyses. Samples of species assemblages were clustered considering their co-occurrences in the same sample by Bray-Curtis single linkage similarity using group-average clustering. The cluster analysis was computed by the BioDiversity Professional v.2 software package (http://www.nhm.ac.uk/zoology/bdpro).

To describe supposed interrelations between individual species and their assemblages to different environmental factors such as altitude, vegetation, stand cover, and insolation in their montane habitats, the multivariate analysis was used (Jongman et al., 1987, Legendre and Legendre, 1998). Both unconstrained and constrained ordinations were additionally computed in Canoco for Windows v. 4.5 (ter Braak and Šmilauer, 2002). The interspecific correlations were computed by Principal Component Analysis (PCA). Subsequently, the positions of alpine zones were passively projected as indicator "dummy" variables (Lepš and Šmilauer, 2003, pp. 8, 155–156). The relationships between the species and the environmental variables were studied by direct gradient analysis (constrained ordination; see Lepš and Šmilauer, 2003), and the statistical significance of the species-environment relation was tested with a Monte Carlo permutation test (MCPT) in Canonical Correspondence Analysis (CCA). Although the most striking environmental gradient was the altitudinal one (we expected the linear response of species to environment), we selected a method with unimodal species response to environment due to the analysis results of ecological gradient length in Detrended Correspondence Analysis (the beta diversity in community composition, measured as the length of the largest gradient, was 4.458; for an explanation see Lepš & Šmilauer, 2003, p. 51). For further analyses in CCA, the centering by species and biplot scaling were selected, and the standardization by species was selected due to the species differences in quantity. The explanatory effects of particular environmental variables were evaluated in MCPT by the stepwise procedure that selects variables with the best fit of species data. The MCPT procedure tests the significance of regression (F-statistics and probability of Type I error) under the null hypothesis of independence of species data on the environmental variables. Number of permutations was arbitrarily assigned to 999. The significantly important environmental variables were visualized by the ordination biplots in Cano Draw v. 4.12 (ter Braak and Šmilauer, 2002). Eigenvalues (λ) mean explanatory power of axes, and they express their relative importance (Lepš and Šmilauer, 2003).

TABLE 2

Alpine altitudinal zones (ALP1–ALP6) and surface sample localities (S1–S10) in the vicinity of Obergurgl, the Ötztal Alps, Austria.

Altitudinal zone	Sample no. (locality, Lc)	Elevation (m a.s.l.)	Comments
ALP1	S1	2000	Obergurgl settlement, the west slope of the Spitzkögele hill, 2000 m a.s.l., just above the field station of the University of Innsbruck, in moist to wet interstitial voids at a depth of ~70 cm under the surface of the bare scree slope, collected in pitfall traps left in place from June 1991 to June 1992.
ALP2	S2	2300	Rotmoostal, the lower part of low alpine zone (2000–2400 m a.s.l.) above timberline, collected by hand sorting under stones of gravel of the frontal glacier moraine between pads of *Silene acaulis*, 31 August 1993.
ALP3	S3	2350	Gaissbergtal, the upper part of the low alpine zone (2350 m as.l.) above timberline, collected by hand under stones in alpine *Curvuletum* grassland, 9 September 1993.
ALP4	S4	2400	Rotmoostal valley, the mid-alpine zone (2400–2600 m a.s.l.), on the west slope of the Kirchenkogel mountain. collected by hand under stones and in the wet rhizosphere of *Saxifraga aizoides*, 31 August 2003.
ALP4	S5	2500	Rotmoostal valley, the mid-alpine zone (2400–2600 m a.s.l.), on the right-hand slope of the Rotmoosferner glacier moraine, collected by hand in moist to wet substrates under stones and pads of *Saxifraga aizoides*, 1 September 1993.
ALP4	S6	2400	Langtal valley, the mid-alpine zone (2400–2600 m a.s.l.), Neue Karlsruher Hütte tourist base, collected by hand under larger stones partly buried with fine gravel and soil in a wet snow bed with dominant *Polytrichum* sp. and *Salix herbacea*, 8 September 2003.
ALP5	S7	2800	Rotmoostal valley, the high alpine zone (2600–2800 m a.s.l.), on the south slope of the Kirchenkogel mountain, collected by hand under stones between pads of *Cerastium cerastoides*, 1 September 1993.
ALP5	S8	2700	Ramol mountain range, Gurgler Schartl, the high alpine zone (2600–2800 m a.s.l.), collected by hand under stones partly buried with soil, at a low edge of a scree slope in a wet snow bed with dominant *Salix herbacea* and *Polytrichum* sp., 9 September 1993.
ALP6	S9	3050	Ramolkogel mountain, the low nival zone (3000–3400 m a.s.l.), collected by hand under stones and sporadic pads of *Cerastium cerastoides* along a trail above the Ramolhaus tourist base, 2 September 1993.
ALP6	S10	3000	Festkogel mountain, summit plateau, the low nival zone (3000–3400 m a.s.l.), with sporadic specimens of *Ranunculus glacialis* and pads of *Silene acaulis* or *Cerastium cerastoides*, collected by hand under stones.

TABLE 3

A list of species of rhagidiid mites collected in 10 different localities (Lc1 to Lc10) in the vicinity of Obergurgl, the Ötztal Alps, Austria.

Names of species	Locality									
	Lc1	Lc2	Lc3	Lc4	Lc5	Lc6	Lc7	Lc8	Lc9	Lc10
Rhagidia gigas	0	1	0	0	0	1	0	0	0	0
Rhagidia parvilobata	0	4	1	4	7	1	0	0	0	0
Rhagidia distisolenidiata	0	3	0	0	0	0	0	0	0	0
Rhagidia longiseta	0	0	0	0	0	0	0	2	0	0
Rhagidia diversicolor	0	0	0	0	0	0	0	12	0	0
Poecilophysis pratensis	0	1	0	0	0	0	0	0	0	0
Poecilophysis wankeli	0	0	0	0	0	1	0	1	0	0
Poecilophysis spelaea	0	0	0	0	0	1	0	0	0	0
Poecilophysis pseudoreflexa	0	0	0	5	35	35	10	45	8	0
Poecilophysis saxonica	0	5	0	0	0	0	0	0	0	0
Foveacheles brevichelae	0	0	0	0	0	0	3	0	0	0
Foveacheles cegetensis	0	0	0	0	0	0	0	0	1	0
Foveacheles unguiculata	0	0	0	0	5	0	2	0	1	6
Foveacheles halltalensis	0	0	0	0	0	9	2	1	0	2
Foveacheles proxima	0	0	0	0	0	0	0	3	0	0
Coccorhagidia pittardi	0	0	0	0	0	0	0	0	1	0
Evadorhagidia bezdezensis	0	0	0	0	0	0	0	0	2	0
Evadorhagidia corcontica	0	0	0	0	0	1	0	0	0	0
Evadorhagidia oblikensis	2	0	0	0	0	0	0	0	0	0
Troglocheles archetypica	0	0	0	0	0	0	2	2	1	0
Troglocheles aggerata	9	0	0	0	0	0	0	0	0	0

Results

FAUNISTICS

A total of 238 specimens of collected rhagidiid mites belonging to 6 genera were examined, and 21 species were identified. Among them, endemic (E), Palearctic (P), and Holarctic (H) species can be recognized (Table 1).

DIVERSITY

Poecilophysis pseudoreflexa, *Rhagidia parvilobata*, *Foveacheles unguiculata*, and *F. halltalensis* were the most abundant species, and they occurred in 6, 5, 4, and 4 localities, respectively. *Troglocheles archetypica* occurred in 3 localities in the high alpine and subnival zones. Other species occurred sporadically, with only a few individuals, hence their abundance was low. *Rhagidia diversicolor* occurred plentifully in only one locality (Lc. 8) in the high alpine zone (Table 3).

The lowermost abundance of rhagidiid mites was indicated in the alpine meadow with the *Curvuletum* plant cover (ALP3) where only one specimen of rhagidiid mite was collected (Fig. 2). *Troglocheles aggerata* has its narrow niche strictly confined to cool, moist underground scree voids. *Poecilophysis pseudoreflexa*, *Rhagidia parvilobata*, *Foveacheles unguiculata*, *F. halltalensis*, and partly also *Troglocheles archetypica* are species with broad, overlapping niches. The assemblages of rhagidiid mites collected in different alpine zones ALP1, ALP2, ALP4, ALP5, and ALP6 (see Table 2), consisted of 2 to 9 species. The respective values of Simpson's index (D) for diversity, evenness measure E1/D, and Chao 1 species richness estimate are presented in Table 4.

CLUSTER ANALYSIS

Considering the co-occurrences of different species in the same sample (Table 3), the cluster analysis of samples 1 to 10 collected in 10 different localities (Table 2) confirms that there is a group of samples (4–10) collected from the mid-alpine zone (ALP4) to the high alpine (ALP5) and the low nival (ALP6) zones that is clearly separated from the other samples (Fig. 3). The underground scree voids, sample 1, are a unique habitat with endemic *Troglocheles aggerata* as the dominant species. Similarly, the lower part of the low alpine zone (ALP2), with *Rhagidia distisolenidiata*, *R. gigas*, *Poecilophysis pratensis*, and *P. saxonica* that occurred only there (cf. Table 3), differs strikingly from the other samples. Also, the dense *Curvuletum*–plant cover, sample no. 3, where only 1 specimen of rhagidiid mite was collected, differs from the other samples strikingly. Because many species were common in samples 7 to 10, the high alpine zone and the low nival zone with the respective altitudes varying only from 2700 to 3050 m a.s.l. could be amalgamated with a common assemblage of species of rhagidiid mites. But some of these species, such as *Poecilophysis pseudoreflexa*, *Foveacheles halltalensis*, or *Troglocheles archetypica*, become rare with altitude, similarly as *Rhagidia parvilobata*, which occurs from the low alpine zone (ALP2) to the mid-alpine zone (ALP4).

ENVIRONMENTAL ANALYSIS

A few groups of species having some affinities to different alpine zones can be distinguished (Fig. 4). *Troglocheles aggerata* and *Evadorhagidia oblikensis* are strictly confined in moist to wet interstitial voids of the bare scree slope (ALP1). On the opposite side of the altitudinal gradient, in the low nival zone (ALP6), a group of species consisting of *Foveacheles cegetensis*, *Evadorhagidia bezdezensis*, and *Coccorhagidia pittardi* is well distinguished. The high alpine zone (ALP5) has the highest species richness and, probably,

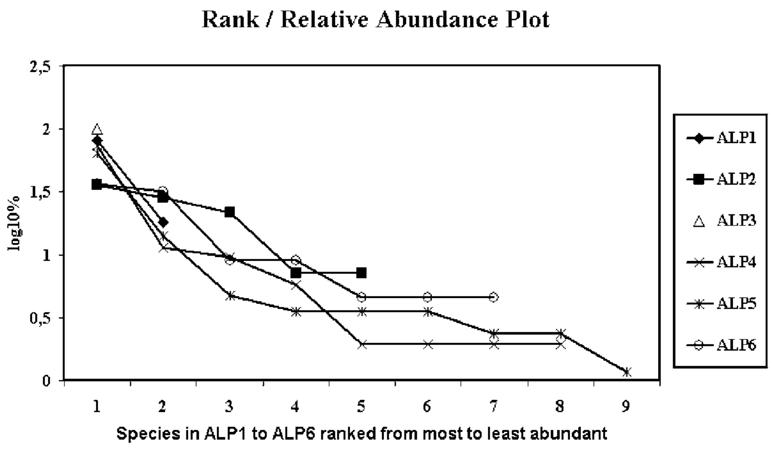

FIGURE 2. A rank/relative abundance plot for ALP1 to ALP6. X-axis = species in ALP1 to ALP6 ranked from the most to least abundant. Y-axis = log10 of relative abundance (% of the total) of mites.

TABLE 4

Values of Simpson's (D) and E1/D indexes of diversity, evenness, and species richness, respectively, for assemblages of mites collected in alpine zones ALP1 to ALP6. Note: as (D) increases, diversity decreases.

Index	ALP1	ALP2	ALP4	ALP5	ALP6
Simpson's of diversity (D)	0.673	0.209	0.532	0.380	0.221
Reciprocal (1/D)	1.486	4.789	1.879	2.634	4.529
E1/D Simpson's of evenness	0.743	0.957	0.234	0.292	0.647
S = number of species	2	5	8	9	7
Chao 1 species richness estimation	2	5	8	9.5	11.5

endemism as the majority of newly described taxa of rhagidiid mites, i.e., *Troglocheles archetypica*, *Foveacheles proxima*, and *Rhagidia longipes* were collected only there. *Poecilophysis pratensis*, *Rhagidia distisolenidiata*, and partly also *Rhagidia gigas* are psychrophilic, forest as well as meadow-inhabiting species, and here occur in the low alpine zone (ALP2). The mid-alpine zone (ALP4) is inhabited by *Poecilophysis pseudoreflexa*, *Poecilophysis spelaea*, *Evadorhagidia corcontica*, and *Foveacheles unguiculata*.

EFFECTS OF ENVIRONMENTAL FACTORS

Of all of the evaluated environmental variables, (i.e., alpine zones, altitude, moisture, vegetation cover, heat index), only three were significant (Table 5). As shown in Figure 5, species having some affinities to specific environmental factors can be distinguished. They are separated into four quadrats of the diagram. ALP1 presents the uniqueness of the deep scree underground, and the species assemblage is fully covered by the species-environment correlation (Table 6, the 1st canonical axis $\lambda = 1$). The altitudinal gradient (ALTIT) (Fig. 5) proved to be important as the significant complex factor and represents variability relevant to axes 2 and 3. Moisture (MOIST) proved to have a different effect because it is an important environmental factor influencing abundance of mites (number of specimens = 10.714 MOIST − 8.243; $R^2 = 0.368$) but has no direct relation to species identity. Both moisture and altitude correlate negatively with the second ordination axis (Table 7). The position of *Poecilophysis pratensis*, *P. saxonica*, and *Rhagidia distisolenidiata* in the biplot diagram is opposite the moisture factor (Fig. 5).

Discussion

Reisigl and Keller (1987) briefly outlined a paleoclimatic and phytogeographic scenario of history of the present flora of the Alps in which they distinguished Tertiary immigrants from the Arctic, Mediterranean, and Asia, i.e., south Siberia and the high Asian mountains. Some of these floral elements survived the subsequent Quaternary glaciation of the Central Alps in refugia (or paleorefugia *sensu* Nekola, 1999) located mostly along the southern rim of the Alps. During the postglacial era they, together with some other floral elements inhabiting the surrounding periglacial tundra, emigrated to newly open alpine habitats. A similar scenario was presented by Meyer and Thaler (1995) for the alpine fauna. In his faunistic synopsis of the spiders of North Tyrol, Thaler (1998) recognized three main chorological groups of spiders presently occurring in this region: (1) species endemic in the alpine zone of the Alps, (2) arctic-alpine species, and (3) Holarctic mountain species occurring discontinuously from Europe to the New world. This classification also fits the Rhagidiidae collected in the alpine region of Obergurgl in North Tyrol. Because that region was extensively glaciated during the Pleistocene (Janetschek, 1956), it is presumed that all species of rhagidiid mites presently occurring in the Ötztal Alps are immigrants, but it is still uncertain which regions they have emigrated from during the Holocene. As with the spiders, some rhagidiid species may represent old faunistic elements (Thaler, 1998) that emigrated from unglaciated montane nunataks or refugia located predominantly along the southern and eastern ice-free peripheral rim of the Alps, while others could have migrated through the unglaciated European periglacial corridor from the Arctic, and from the steppes and mountains of Asia.

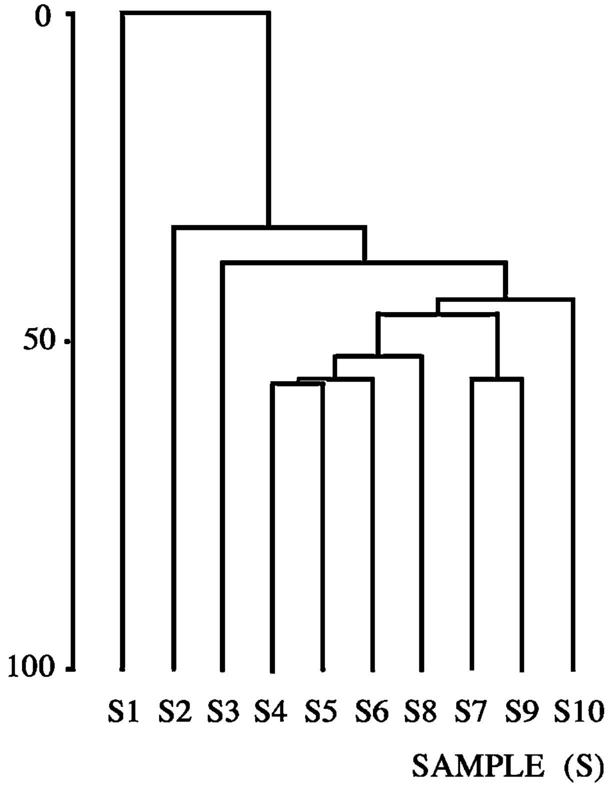

FIGURE 3. Cluster analysis (Bray-Curtis, single linkage) of 10 samples of rhagidiid mites collected in 10 different localities (see Table 2).

Based on our present knowledge of the biogeographic distribution of Rhagidiidae, Palearctic, Holarctic, and endemic species of rhagidiid mites inhabiting various alpine habitats in the Ötztal Alps can be recognized.

PALEARCTIC SPECIES

Evadorhagidia oblikensis, *E. corcontica*, *E. bezdezensis*, *Foveacheles cegetensis*, and *Poecilophysis spelaea* have a Palearctic pattern of distribution. *P. spelaea* is a troglodytic species that occurs frequently in European caves from Scandinavia (Hippa et al., 1989) to the Balkans (Thor and Willmann, 1941). It also occurs in cool and moist interstitial habitats of stony debris in central Europe (Růžička and Zacharda, 1994). *F. halltalensis*, which occurs in the Ötztal Alps from mid- to high alpine and subnival habitats, was also collected in subterranean cool scree voids at ~300 m altitude in northern Bohemia (Zacharda, unpublished data).

HOLARCTIC SPECIES

Rhagidia gigas, *R. parvilobata*, *R. distisolenidiata*, *R. diversicolor*, *Poecilophysis pseudoreflexa*, *P. pratensis*, *P. saxonica*, *P. wankeli*, and *Foveacheles brevichelae* are species with a Holarctic pattern of distribution. *P. pseudoreflexa* is the dominant, most abundant species in the mid- to high alpine and subnival zones of the Ötztal Alps.

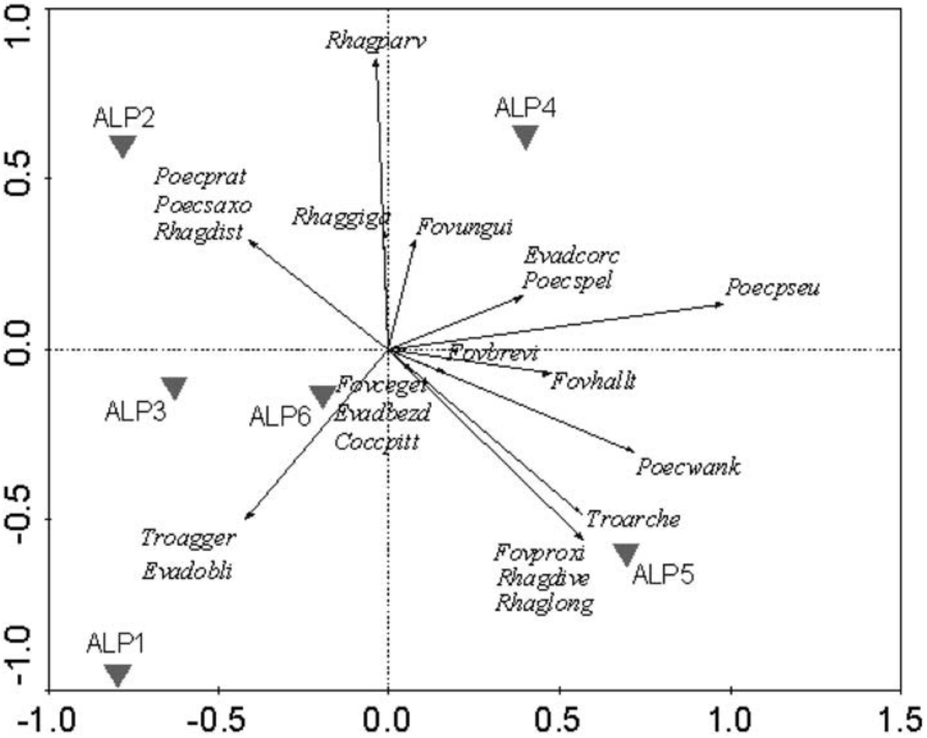

FIGURE 4. Interspecific correlations as visualized by Principal Component Analysis (PCA). They are separated in four quadrats of the diagram. X-axis represents the 1st axis (λx = 0.438), Y-axis represents the 2nd axis (λy = 0.157); arrows are positions of species, and triangles are passively projected environmental centroids of alpine zones. They illustrate habitat preferences of the main species. They are: *Coccorhagidia pittardi* (*Coccpitt*), *Evadorhagidia bezdezensis* (*Evadbezd*), *Evadorhagidia corcontica* (*Evadcorc*), *Evadorhagidia oblikensis* (*Evadobli*), *Foveacheles brevichelae* (*Fovbrevi*), *Foveacheles cegetensis* (*Fovceget*), *Foveacheles halltalensis* (*Fovhallt*), *Foveacheles proxima* (*Fovproxi*), *Foveacheles unguiculata* (*Fovungui*), *Poecilophysis pratensis* (*Poecprat*), *Poecilophysis pseudoreflexa* (*Poecpseu*), *Poecilophysis saxonica* (*Poecsaxo*), *Poecilophysis spelaea* (*Poecspel*), *Poecilophysis wankeli* (*Poecwank*), *Rhagidia distisolenidiata* (*Rhagdist*), *Rhagidia diversicolor* (*Rhagdive*), *Rhagidia gigas* (*Rhaggiga*), *Rhagidia longiseta* (*Rhaglong*), *Rhagidia parvilobata* (*Rhagparv*), *Troglocheles aggerata* (*Troagger*), and *Troglocheles archetypica* (*Troarche*). Note the most extreme position of ALP1 (deeper underground scree voids) and species-empty position of ALP3 (dry Curvuletum–pasture without specific mites).

Coccorhagidia pittardi is an arctic-alpine species that was discovered in Alaska (Strandtmann, 1971), but later was also collected in the High Tatras, Slovakia, at an altitude of 2200–2367 m a.s.l. (Zacharda, 1980) and in the Himalaya at 3900 m a.s.l. (Zacharda and Daniel, 1987). Recently, the species was also discovered in the Ardovska cave, in the Slovak Paradise National Park, Slovakia, where it can be considered a periglacial relict (Zacharda, unpublished data). *C. berlesei* Sig Thor (Thor and Willmann, 1941) and *C. divergens* Mihelčič, 1957, were also reported from high altitudes in the Alps (Franz, 1954; Mihelčič, 1957). However, these taxa were described only very briefly, and are still of uncertain taxonomic placement. One of them may be conspecific with *Coccorhagidia pittardi*.

ENDEMIC SPECIES

Representatives of the genus *Troglocheles* can be considered endemic in the Alps and adjacent mountain systems such as the Pyrenees (*T. vandeli* Zacharda, 1987), the Swabian Alb in Germany (*T. gineti* sensu Rack, 1974), the Karst Alps in Slovenia [*T. strasseri* (Willmann, 1932)], and the Venetian Alps in Italy [*T. conciana* (Lombardini, 1951)]. They occur mostly in caves, and *T. strasseri*, *T. strasseri tiroliensis*, *T. gineti*, *T. vornatscheri*, and also in part *T. vandeli* are troglomorphic, i.e., morphologically adapted to caves (Zacharda, 1979). In the Pleistocene-glaciated regions of the Alps, these species invaded cave systems during the post-Pleistocene, but not in regions that were not glaciated. There, the mites could occupy the cave habitats well before the period of Pleistocene glaciation.

T. aggerata lives in open voids under the surface of alpine bare scree slopes and it is morphologically adapted to this environment (Zacharda, 2000b). Our results of cluster analysis corroborate ecological divergence of this scree underground habitat (ALP1) and confirm its significance and importance for conservation and adaptive evolution of chelicerates (Růžička, 1999).

Only *T. archetypica* is epigeic in the high alpine to subnival zones. *T. archetypica* either evolved from a paleoendemic ancestor in alpine unglaciated nunataks or marginal unglaciated zones of the Alps and subsequently dispersed to unglaciated alpine biotopes during the postglacial Holocene, or it evolved quite recently during the Holocene (Zacharda, 2000b).

Rhagidia longiseta, *Foveacheles unguiculata*, and *F. proxima* are currently known only from the Alps and can also be considered to be endemic.

A specific assemblage of rhagidiid mites with a low diversity was found in the deep underground voids of a bare scree slope just at

TABLE 5

Permutation test of selected significant environmental variables (restricted model, variance explained by all variables = 3.15, no. of permutations = 999).

Factor	fit	*p*-value	*F*-ratio
ALP1	1.00	0.001	2.94
ALTIT	0.59	0.015	2.00
MOIST	0.51	0.034	1.97

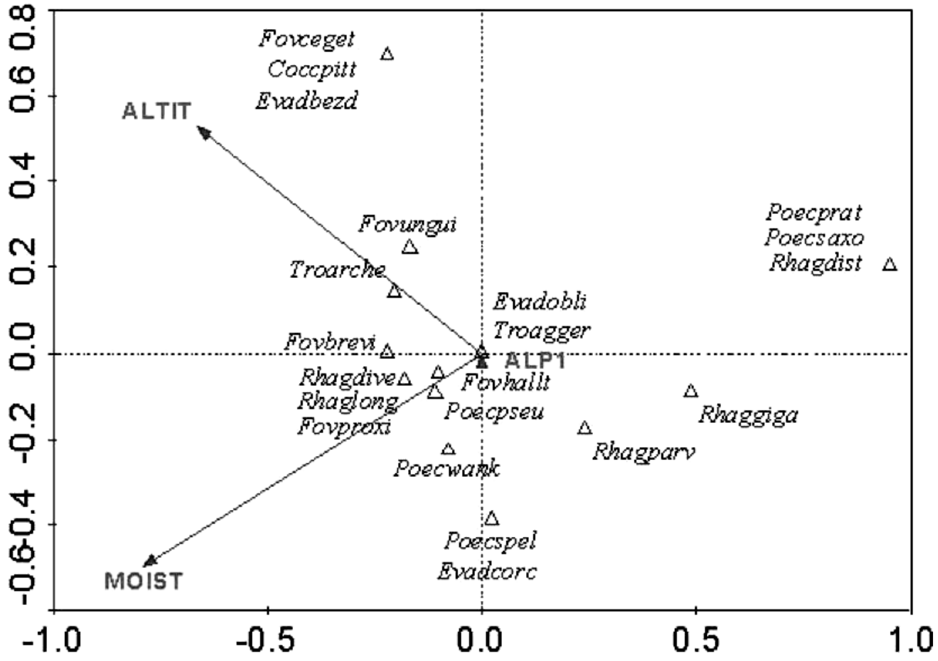

FIGURE 5. Species-environment CCA biplot diagram of the second (λx = 0.75) and third (λy = 0.35) ordinal axes of the restricted model. Explanations: arrows are significant environmental factors, ALTIT (altitude), MOIST (moisture), ALP1 (deep scree voids) together with *Evadorhagidia oblikensis* (Evadobli) and *Troglocheles aggerata* (Troagger) are in the centroid, because they are fully represented by the first ordinal axis (not visualized, λ = 1.0); triangles are species positions in ordinal space, *Coccorhagidia pittardi* (*Coccpitt*), *Evadorhagidia bezdezensis* (*Evadbezd*), *Evadorhagidia corcontica* (*Evadcorc*), *Evadorhagidia oblikensis* (*Evadobli*), *Foveacheles brevichelae* (*Fovbrevi*), *Foveacheles cegetensis* (*Fovceget*), *Foveacheles halltalensis* (*Fovhallt*), *Foveacheles proxima* (*Fovproxi*), *Foveacheles unguiculata* (*Fovungui*), *Poecilophysis pratensis* (*Poecprat*), *Poecilophysis pseudoreflexa* (*Poecpseu*), *Poecilophysis saxonica* (*Poecsaxo*), *Poecilophysis spelaea* (*Poecspel*), *Poecilophysis wankeli* (*Poecwank*), *Rhagidia distisolenidiata* (*Rhagdist*), *Rhagidia diversicolor* (*Rhagdive*), *Rhagidia gigas* (*Rhaggiga*), *Rhagidia longiseta* (*Rhaglong*), *Rhagidia parvilobata* (*Rhagparv*), *Troglocheles aggerata* (*Troagger*), and *Troglocheles archetypica* (*Troarche*).

an upper limit of timberline (ALP1) where only two species were collected despite the pitfall traps being placed there for one year. Our results document that this habitat is occupied by different species than occur in the high altitude screes of alpine non-forested zones. In contrast, the mid-alpine zone (ALP4) and the high alpine zone (ALP5) were the most rich in species. The numerical nonparametric estimator of species richness Chao1 provided the same values of species richness in the scree underground voids (ALP1) to the mid-alpine zone (ALP4) and slightly to moderately increased values in the high alpine zone (ALP5: 9.5) and the low nival zone (ALP6: 11.5). This means that in the high alpine zone and the low nival zone further species of rhagidiid mites rarely occurring in the local assemblages might be expected to be found and that the faunal list of species from the Ötztal Alps (Table 3) should not be considered definitive. This assumption is supported by findings of subadult specimens of the genera *Evadorhagidia* and *Foveacheles* that are of uncertain taxonomic status.

As indicated by similarly steep slopes of chart curves for low, mid-, high alpine, and low nival zones (ALP2, ALP4, ALP5, ALP6) (Fig. 2) and values of evenness measure E1/D (Table 4), the more the assemblages of mites are rich in species, the more even they are as well.

The numerical environmental analysis has also corroborated that there are the positive (+) as well as the negative (–) interrelations between occurrence and abundance of assemblages of the rhagidiid mites in the different montane habitats and quantitative, semiquantitative,

TABLE 6

Axes summary statistics for restricted model (sum of all eigenvalues = 3.384, sum of all canonical eigenvalues = 2.101).

Axes	1	2	3	4	Total inertia
Eigenvalues	1.000	0.747	0.354	0.460	3.384
Species-environment correlations	1.000	0.996	0.963	0.000	
Cumulative percentage variance					
of species data	29.5	51.6	62.1	75.7	
of species-environment relation	47.6	83.1	100.0	0.0	

TABLE 7

The values of correlations between the environmental variables and the ordination axes. Environmental variables: ALTIT = altitude, MOIST = moisture, ALP1 = underground interstitial scree voids. Ordination axes: SPEC = ordinal species axes, ENVI = environmental axes.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ALTIT	MOIST
SPEC AX2	0.000	1.000							
SPEC AX3	0.000	0.012	1.000						
SPEC AX4	0.000	−0.031	−0.110	1.000					
ENVI AX1	1.000	0.000	0.000	0.000	1.000				
ENVI AX2	0.000	0.996	0.000	0.000	0.000	1.000			
ENVI AX3	0.000	0.000	0.963	0.000	0.000	0.000	1.000		
ALTIT	−0.528	−0.662	0.508	0.000	−0.528	−0.665	0.528	1.000	
MOIST	−0.351	−0.790	−0.479	0.000	−0.351	−0.793	−0.498	0.449	1.000
ALP1	1.000	0.000	0.000	0.000	1.000	0.000	0.000	−0.528	−0.351

and categorial environmental gradients such as the altitude, substratum humidity (moisture), and alpine altitudinal zones (Table 7). It is obvious that even though the altitudinal and moisture gradients are of different ecological significance, they both have influence on the species pattern positioned in the opposite direction to the environmental factor arrows in the ordination diagram (Fig. 5, the 2nd axis). Although dryness may be considered to be an opposite to moisture, it proved to be bound with the occurrence of *Poecilophysis pratensis*, *P. saxonica*, and *Rhagidia distisolenidiata*. However, these species are not strictly confined to dry habitats because they occur in various niches of terrestrial microhabitats in middle altitudes of highlands (Zacharda, 1980).

No other relevant information on the ecological interrelations between rhagidiid mites, their habitat affinities, and the respective environmental factors can be discussed because they are not known.

Conclusions

To date, 41 species of rhagidiid mites have been reported from the Alps, but only 27 species of them are taxonomically well recognized and confirmed. They are endemic, Palearctic, and Holarctic. In the Ötztal Alps they inhabit various alpine habitats, and their assemblages consist of 2 to 9 species. Among them the Holarctic *Poecilophysis pseudoreflexa* is the most abundant and widely distributed species.

A specific assemblage and low diversity of rhagidiid mites was found in the moist underground voids of a bare scree slope that was occupied by different species than occur in the high altitude screes of alpine non-forested zones. In the locality with dense *Curvuletum*–plant cover almost no rhagidiids were collected. The highest species richness and endemism were in the mid-alpine zone (2400–2600 m a.s.l.) and the high alpine zone (2600–2800 m a.s.l.). The different altitudinal niches of the majority of common species overlap, but some species become rare with altitude. Additional species of rhagidiid mites might be expected to be found in special, until-now uncollected microhabitats such as the dense turf rhizosphere or moss pads. Rhagidiid mites having some affinities to specific environmental factors can be distinguished. The endemic *Troglocheles aggerata* is strictly confined to deep moist scree underground voids as a unique habitat. The altitudinal gradient proved to be important as the significant complex environmental factor influencing the occurrence of mites. Moisture proved to be an important environmental factor influencing abundance of mites but having no direct relation to species identity. Although dryness proved to be bound with the occurrence of *Poecilophysis pratensis*, *P. saxonica*, and *Rhagidia distisolenidiata*, these species are not strictly confined to dry habitats.

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