

## The role of *Hylastes cunicularius* Erichson (Coleoptera: Scolytidae) in transferring uropodine mites in a mountain spruce forest

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**ABSTRACT:** The bark beetle *Hylastes cunicularius* was studied in the Tatra Mountains, West Carpathians, to clarify its role in transferring phoretic uropodine mites during dispersal in a mountain spruce forest. Emphasis was placed on the proportion of beetles vectoring deutonymphs of uropodine mites, and on assemblage structure, frequency distribution and placement of uropodids on the bark beetle vector. A total of 3,302 adults of *H. cunicularius* were caught into flight interception traps, of which 529 (16%) vectored a total of 1,020 individuals and four species of uropodine mites: *Trichouropoda pecinai* Hirschmann & Wisniewski, *Trichouropoda obscura* (C.L.Koch), *Uroobovella vinicolora* (Vitzthum), *Uroobovella ipidis* (Vitzthum). The uropodine mite assemblage was dominated by *T. pecinai*, which represented 94.6% of the collected mite individuals. *T. pecinai* and *U. vinicolora* were documented as new associates of *H. cunicularius*. Frequency distribution of uropodids on the beetle was L-shaped. The number of vectored mites and the number of dispersing individuals of *H. cunicularius* were positively correlated.

**Keywords:** *Hylastes cunicularius*; mountain spruce forest; uropodine mites; West Carpathians

Bark beetles (Coleoptera: Scolytidae) are ecological factors triggering tree and forest decline (BERRYMAN 1986; CHRISTIANSEN, BAKKE 1988; SCHELHAAS et al. 2003). They are vectors (phoronts) of numerous mite species transmitting tree pathogens, mycangial symbionts and fungal antagonists of bark beetles (MOSER et al. 2005). Uropodine mites (Acarina, Mesostigmata: Uropodina) are typical representatives of phoretic mites on bark beetles. Their knowledge in forest ecosystems is primarily connected with the bark beetle species of economic importance such as *Dendroctonus frontalis* Zimmerman (MOSER, ROTON 1971; MOSER 1976) and *Scolytus multistriatus* Marsham (HAJEK et al. 1985) in North America, *Ips typographus* Linnaeus (MOSER, BOGENSCHÜTZ 1984; MOSER et al. 1989a,b; KACZ-

MAREK, MICHALSKI 1994), *Scolytus multistriatus* and *S. pygmaeus* (Fabricius) (MOSER et al. 2005) in Europe, *Ips typographus japonicus* Nijima in Japan (MOSER et al. 1997).

*H. cunicularius* (Coleoptera: Scolytidae) has a wide distribution in coniferous forests in Europe and Asia (Siberia and Caucasus) (PFEFFER 1989; JOHANSSON et al. 1994). It is frequent and abundant in lowland and mountain areas, everywhere where its principal host plants Norway spruce (*Picea abies* [L.] Karst.) and Scots pine (*Pinus sylvestris* [L.]) occur. In clear-cut and windthrow areas or in forest plantations, locally, it is reported to be a forest pest. Damage results from maturation feeding of adult beetles on the bark of young coniferous trees (PFEFFER et al. 1954; PFEFFER 1955, 1995; SCHWENKE

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1974; EIDMANN et al. 1991; WERMELINGER et al. 2002). *Hylastes* species act as vectors of fungal tree pathogens worldwide (WITCOSKY et al. 1986; LEWIS, ALEXANDER 1986; FERREIRA, FERREIRA 1987). The adults of *H. cunicularius* transmit ophiostomatoid fungi (MATHIESEN-KÄÄRIK 1953; KIRISITS 2007) and transfer phoretic uropodine mites (HIRSCHMAN 1971; KOFLER, SCHMÖLZER 2000).

The literature is scant concerning the transfer of uropodids by *H. cunicularius* in spruce forests. To clarify the role of *H. cunicularius* as a vector of phoretic uropodine mites during dispersal in a mountain spruce forest, the following questions have been addressed:

- (1) what is the proportion of beetles vectoring uropodine mites in the beetle population?,
- (2) what is the species composition and diversity of uropodine mite assemblage on the beetle?,
- (3) which type of frequency distribution characterizes distribution of uropodine mites on the beetle?,
- (4) how are predominant uropodid species located on the beetle?

The questions are of considerable biological interest for understanding the role of *H. cunicularius* in transferring phoretic uropodids by the beetle vector.

## MATERIAL AND METHODS

### Study area and sample plots

The study was carried out in the Tatra Mountains, West Carpathians, Central Europe, in three separate sample plots established in the valleys Tomanova dolina (1,280–1,360 m a.s.l.), Velická dolina (1,460 to 1,520 m a.s.l.) and Bielowodská dolina (1,360 to 1,560 m a.s.l.) in 2004. The plots represent the forest area of approximately 170 km<sup>2</sup>. They are Norway spruce-dominated (share of spruce 95%) forest reserves with frequent occurrence of dying and dead trees, the latter in the form of decaying trunks and logs on the ground or snags. Dwarf pine (*Pinus mugo* Turra), European larch (*Larix decidua* Miller), Arolla pine (*Pinus cembra* [L.]), rowan (*Sorbus aucuparia* [L.]) and different willow species (*Salix* spp.) occur locally, sharing the rest 5%. The ground layer is typically formed by raspberry (*Rubus idaeus* [L.]), bilberry (*Vaccinium myrtillus* [L.]) and other mountain plants. Forest structure (canopy 50–80%) is modified by the wind, avalanches and bark beetles, of which *Ips typographus* (L.) is the most important with regard to spruce forest decline. Only a slight alteration of forest structure by man (tree felling, timber removal) can be noticed locally.

### Sampling bark beetles and deutonymphs of uropodine mites

Window flight trapping was used as the sampling method. A total of 6 flight interception traps were set for bark beetles and other invertebrates in each sample plot. Traps were fixed to spruce trees which were 0.4–0.5 m thick at dbh, characterized by complete needle loss in the crown and presence of fresh wounds on lower parts of trunks, at heights of 1.3–1.6 m, measured from the ground to the lower margin of trap panes. In each sample plot they were positioned at a distance of 100–150 m, on two vertical transects which were approximately 200 m distant from each other. Traps consisted of two transparent acrylic panes (0.4 × 0.6 m each) crossed at right angles, a circular dark green funnel (diameter 0.4 m) placed below the panes, and a collector containing water, coarse salt (NaCl) and a few drops of detergent. Salt preserved invertebrates, detergent reduced the surface tension of the solution in trap collectors. Traps were emptied at the end of each month, over the period 15<sup>th</sup> May–30<sup>th</sup> September 2004.

In the laboratory, the individuals of *H. cunicularius* were separated from other organic material sampled in traps and placed in vials containing 70% ethanol. Then, they were examined for deutonymphs of uropodine mites. The deutonymphs were extracted from the beetles manually, using pincers. They were mounted into microscopic slides, each specimen separately using Liquido de Swan, and kept prepared for determination and further study.

Individuals of *H. cunicularius* were identified according to PFEFFER (1989, 1995), deutonymphs of uropodine mites according to MAŠÁN (2001).

### Data analysis

#### Proportion of *H. cunicularius* adults vectoring uropodine mites

Two groups were distinguished in the population of *H. cunicularius* with regard to the transfer of uropodine mites: (1) individuals vectoring mites and (2) individuals not vectoring mites. Testing for differences in the number of individuals between group 1 and group 2 was performed using the Wilcoxon test for two groups arranged as paired observations. It was resorted to the nonparametric test as the data did not meet the assumptions of parametric methods of data analysis after transformation. Next, the proportion of mite vectors in the population of *H. cunicularius* was calculated as a percentage of the beetles sampled. Spearman's coefficient of rank

Table 1. Adults of *Hylastes cunicularius* vectoring deutonymphs of four uropodine mite species in three separate sample plots in a mountain spruce forest in Tatra Mountains, West Carpathians. N – number of individuals, D(%) - dominance of abundance of mite species

Sample plot	Western		Central		Eastern	
	N	D (%)	N	D (%)	N	D (%)
<i>Hylastes cunicularius</i>	390		40		99	
<i>Trichouropoda pecinai</i>	664	94.3	94	92.2	207	96.7
<i>Trichouropoda obscura</i>	35	5.0	8	7.8	5	2.3
<i>Uroobovella ipidis</i>					1	0.5
<i>Uroobovella vinicolora</i>	5	0.7			1	0.5

correlation ( $R$ ) was used to test for the significance of the association between the number of vectored mites and the number of dispersing individuals of *H. cunicularius*. The nonparametric test was employed for this relationship as the data did not conform to a bivariate normal distribution (SOKAL, ROHLF 2000). Statistical analyses were performed in the STATISTICA 7.0 program (StatSoft 2005).

#### Species composition and diversity of uropodine mite assemblage

The assemblage structure of uropodine mites on *H. cunicularius* was characterized by abundance and dominance of abundance of mite species recorded in particular sample plots over the period 15<sup>th</sup> May–30<sup>th</sup> August 2004 (no beetles were caught in September). Diversity of uropodine mite assemblages on the beetle vector was characterized by Simpson's diversity index (SIMPSON 1949) (Table 1). Rarefaction analysis was done to clarify the relationship between the number of mite species and the number of mite individuals collected in the study area (Fig. 1). Computation of diversity index and rarefaction were performed in the PAST program (HAMMER et al. 2009).

#### Frequency distribution of uropodine mites

To characterize the frequency distribution of uropodine mites on *H. cunicularius* a bar diagram was constructed. In the diagram, numbers of uropodine mites on individuals of the beetle were arranged as distinct classes (observations) on the abscissa ( $x$ -axis), corresponding frequencies (cases) were shown on the ordinate ( $y$ -axis) (Fig. 2).

#### Location of attachment of the uropodid *Trichouropoda pecinai*

The predominant uropodid, *T. pecinai*, was selected to study its placement on the body of *H. cunicularius*. For this purpose, a total of 100 individuals of

*H. cunicularius* were drawn at random from the beetle population vectoring *T. pecinai* over the period 15<sup>th</sup> May–30<sup>th</sup> June 2004 (main flight period of the beetle in the study area). Frequency of occurrence and dominance of abundance of *T. pecinai* were calculated separately for legs, abdomen, elytra, thorax, head and pronotum of the beetle; frequency as the number of attachments (observed cases) over all attachments (cases) possible ( $N = 100$ ), dominance as the number of mite individuals on a particular body part over the total number of mites found attached to the beetle ( $N = 220$  mites, Fig. 3).

## RESULTS

During dispersal, the individuals of *H. cunicularius* vectoring deutonymphs of uropodine mites (vectors, phoronts) were always (in each trap) significantly less numerous than those not vectoring them ( $N_1 = N_2 = 18$ ,  $T = 9.0$ ,  $Z = 3.332$ ,  $P < 0.001$ , Wilcoxon test). The proportion of mite vectors in the beetle population varied markedly in the study area. It was

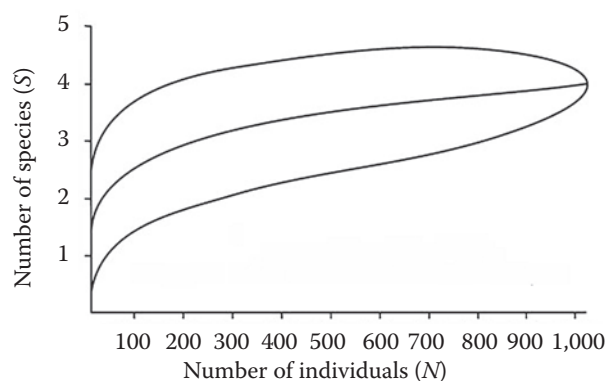


Fig. 1. The rarefaction curve of pooled numbers of deutonymphs of uropodine mites vectored by the adults of *Hylastes cunicularius* in a mountain spruce forest. 95% confidence interval indicated. Tatra Mountains, West Carpathians

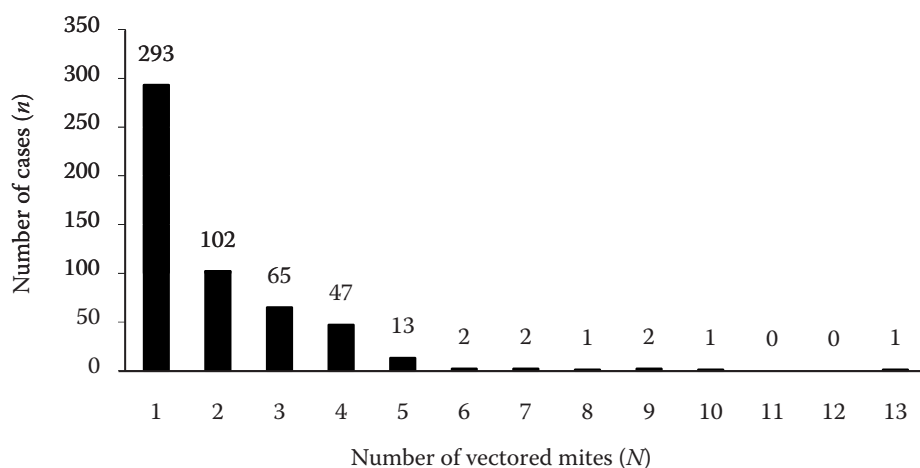


Fig. 2. Frequency distribution of 1,020 individuals of uropodine mites (deutonymphs of four species, a single species strongly predominating) phoretic on 529 adults of *Hylastes cunicularius*. Tatra Mountains, West Carpathians

5.8% in the valley Velická dolina ( $N = 695$ ), 17.6% ( $N = 2,204$ ) in Tomanova dolina and 24.6% ( $N = 403$ ) in Bielovodská dolina.

Of the 3,302 individuals of *H. cunicularius* sampled in the study area, 529 (16%) were vectoring a total of 1,020 individuals and four species of uropodine mites (Table 1; Fig. 2). In each sample plot, the mite assemblage was strongly dominated by a single species, *T. pecinai* (dominance of the mite over 90%, Table 1). The mite species composition in the study area was as follows: *T. pecinai* (965 individuals and 94.6%), *T. obscura* (48 individuals and 4.7%), *U. vinicolora* (6 individuals and 0.6%) and *U. ipidis* (one individual and 0.1%,  $N = 1,020$ ). Diversity of mite assemblage was low in each sample plot. Simpson's index of diversity of mite assemblage ranged from 0.064 in the valley Bielovodská dolina to 0.108 in Tomanova dolina and 0.145 in Velická dolina, giving the value of 0.103 for the study area as a whole. The rarefaction curve of the pooled numbers of uropodine mites on *H. cunicularius* constructed for the study area showed only a slight increase in spe-

cies richness with the increasing number of sampled uropodids (Fig. 1).

Typically, the frequency distribution of uropodine mites on *H. cunicularius* was L-shaped (Fig. 2). Most uropodids in the study area (28.7%) were transferred as a single individual. The beetles vectoring one, two, three and four mite individuals contributed together to the entire mite transfer by 86.3%; cases where five mites and more were found attached to the phoront were rare and their contribution to the entire mite transfer was much lower – the rest 13.7% ( $N = 1,020$ ). A single specimen of the beetle was found to transfer a maximum of 13 uropodids. The total number of vectored uropodids in the study area was almost doubled compared to the number of beetle vectors (Fig. 2). Based on the sample evidence, the number of vectored mites and the number of individuals of the beetle in traps were positively correlated ( $N_1 = N_2 = 18$ ,  $t(16) = 5.644$ , Spearman  $R = 0.816$ ,  $P < 0.001$ , Spearman's rank correlation).

The predominant uropodid, *T. pecinai*, was found attached to the legs, abdomen, elytra, thorax, head

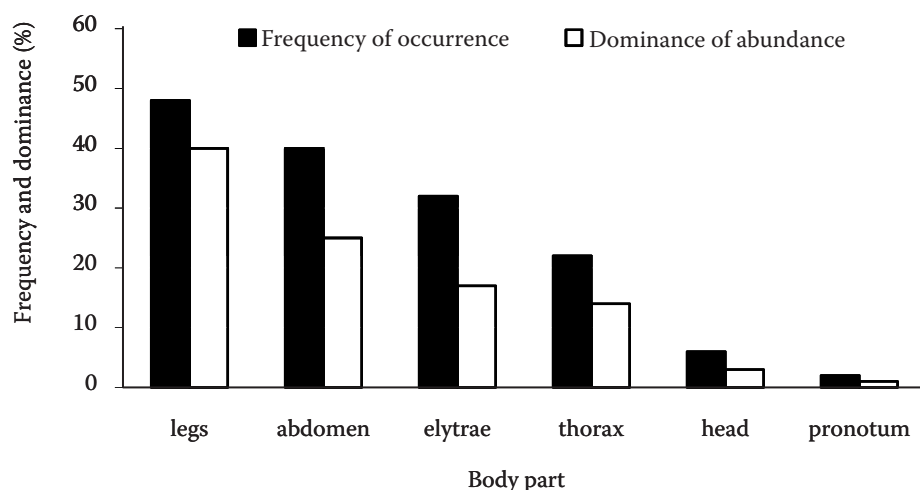


Fig. 3. Location of the attachment of 220 individuals of *Trichouropoda pecinai* on 100 individuals of *Hylastes cunicularius* drawn at random from the beetle population vectoring mites. Frequency of occurrence and dominance of abundance of the mite. Tatra Mountains, West Carpathians

and pronotum of *H. cunicularius*. It was most frequent and most abundant on the legs of the beetle ( $F = 48\%$ ,  $D = 40\%$ ) (Fig. 3).

## DISCUSSION

The results give information on the adults of *H. cunicularius* dispersing outside their breeding sites (roots, moist logs of spruce touching the ground, etc.). It is known that fresh cuts on host material enhance the attraction of *H. cunicularius* (EIDMANN et al. 1991). The beetles were noticed to be attracted to wounds (caused by avalanches, tree and rock fall) on lower parts of trunks of spruce trees holding traps, however, we did not record their development in those trees. In the study area, dispersing individuals of the beetle occur in high numbers in both forest interiors and open habitats such as windthrow areas, etc. Most beetles (97%,  $N = 529$ ), and also most mites (98%,  $N = 1,020$ ), were sampled over the period 15<sup>th</sup> May–30<sup>th</sup> June.

The phoretic uropodine mite species in the study can be found in insect galleries under the bark or in wood of dying or dead trees (MAŠÁN 2001). As deutonymphs are attached tightly to the body of bark beetles with the anal pedicel, they take the advantage of phoresy to disperse. KIELCZEWSKI et al. (1983) listed a total of 181 mite species, and 21 species of uropodine mites among them, as the associates of 45 different bark beetle species in Poland. PFEFFER (1955), HIRSCHMANN (1971), KOFLER and SCHMÖLZER (2000) recorded four uropodine mite species as the associates of *H. cunicularius* or *Hylastes* spp. in Europe: *T. obscura*, *T. dialveolata* Hirschmann & Zirngiebl-Nicol, *U. ipidis* and *U. dryocoetis* Vitzthum. Thus, two species of uropodids in the study, *T. pecinai* and *U. vinicolora*, are documented as new associates of *H. cunicularius*.

The predominant mite species in the study, *T. pecinai*, benefited from the phoresy on the beetle more than did the other three mite species (Table 1). *T. pecinai*, described in 1986, occurs at altitudes between 1,100 and 1,400 m a.s.l., and may also be found as low as 700 m or up to 2,000 m a.s.l. (MAŠÁN 2001). Despite its occurrence in litter and soil, MAŠÁN (2001) considered it as corticolous rather than inhabiting the soil detritus. As *H. cunicularius* develops in moist substrates having contact with soil (see above), the association of *T. pecinai* with it is not surprising. At the present moment, we know nothing about trophic requirements of *T. pecinai*, however, laboratory experiments revealed the feeding of *T. obscura* on tiny nematoda (KRŠIAK 2009).

The potential species matrix (bark beetle species x uropodine mite species) in spruce forests in Central Europe is quite robust. In the West Carpathians, *H. cunicularius* is within the guild of approximately 30 native bark beetle species developing in Norway spruce (PFEFFER 1989, 1995), and there are at least seven species of phoretic uropodine mites known to be vectored by them, namely: *T. pecinai*, *T. obscura*, *T. polytricha* (Vitzthum), *T. sibirica* Wisniewski and Michalski, *T. tuberosa* Hirschmann and Zirngiebl-Nicol, *U. ipidis* and *U. vinicolora* (KRŠIAK 2009).

The uropodine mite assemblage on *H. cunicularius* was not rich in species (Table 1). Its low diversity may be explained by a highly excessive number of *T. pecinai* compared to that of other mite species in the study (Table 1). Considering the slight steepness of the species accumulation curve in the study area (Fig. 1), no great increase in species richness ( $S$ ) with an increasing number of mite individuals ( $N$ ) can be expected. On the other hand, a few new uropodine mite associates of *H. cunicularius* may still be documented in the study area.

Based on the results, undoubtedly, frequent transfers of a few mites (one up to four mite individuals) by their beetle vectors contribute to the entire mite transfer and passive dispersal much more than a few transfers of larger quantities of mites (five mites and more in the study) (Fig. 2). This clarifies the role (function) of *H. cunicularius* in the transfer of phoretic uropodids in a mountain spruce forest.

Affinity to the legs of *H. cunicularius* is typical of *T. pecinai* (KRŠIAK 2007). We found the mite on tibiae but never on tarsi and femora which seem to be too exposed to attach. Also, the mite was scarce on the head and prothorax of the beetle (Fig. 3) where mechanical removal is highly likely. The particular body parts of *H. cunicularius* do not provide phoretic uropodids an equal chance to attach tightly and hold successfully (body parts differ in size, shape and texture; some body parts are more exposed than the other ones, etc.). The asymmetry in Fig. 2 indicates that selection against uropodids on *H. cunicularius* may exist, however, a special ecological and behavioural study is required to reveal this in detail. The placement of mite species on bark beetle species reflects strategy of their attachment and dispersal in nature. The preferred location of attachment is known to differ with mite species (MOSER et al. 2005).

Dispersing individuals of *H. cunicularius* were relatively loosely associated with uropodine mites and their transfer potential for uropodids was not fully exploited. On the other hand, the proportion

of uropodine mite vectors in the beetle population was as high as 25% locally, and the total number of uropodids transferred in the study area was almost doubled compared to the number of vectors (Table 1; Fig. 2). Considering this, together with abundant occurrence of *H. cunicularius* in the study area and ability of the beetle to disperse over large distances (NILSSEN 1984; JOHANSSON et al. 1994), the important role of *H. cunicularius* in transferring uropodine mites cannot be overlooked. As the number of vectored mites positively correlates with that of dispersing individuals of *H. cunicularius*, more transferred mites are expected at sites where the beetle population is high than at sites where the beetle is infrequent and not abundant.

*H. cunicularius* belongs to the group of bark beetles intimately associated with blue-stain fungi, meaning that a large percentage of individuals (up to 100%) carries ophiostomatoid fungi (KIRISITS 2007). This increases the chance that ophiostomatoid fungi will also be transmitted by phoretic uropodine mite associates of *H. cunicularius*. A special study on this phenomenon is recommended.

## CONCLUSION

The importance of the passive transfer of uropodine mites assisted by *H. cunicularius* cannot be overlooked in mountain spruce forests in the Tatra Mountains and, possibly in other mountain areas in Europe too. In the study area, the bark beetle acts as a vector of at least four species of uropodine mites, of which *T. pecinai* is the most frequent and abundant. The results of the study can be used by forest entomologists and forest pathologists studying the transmission of ophiostomatoid fungi by uropodine mite associates of *H. cunicularius* in spruce forests which is highly likely. It is recommended to focus on sites and areas where a large population of *H. cunicularius* is documented and where high numbers of vectored mites are expected. Attention should mainly be paid to beetles vectoring a few mites as these are most frequent and contribute most to the entire mite transfer. The results from the forest reserves in the Tatra Mountains set standards to which results from other sites and areas can be compared.

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## References

- BERRYMAN A.A. (1986): Forest insects. Principles and practice of population management. New York and London, Plenum Press: 279.
- EIDMANN H.H., KULA E., LINDELÖW A. (1991): Host recognition and aggregation behaviour of *Hylastes cunicularius* (Coleoptera: Scolytidae) in the laboratory. *Journal of Applied Entomology*, **112**: 11–18.
- FERREIRA M.C., FERREIRA G.W.S. (1987): Insect attacks associated with forestry practices (Scarabaeidae, Melolonthinae and Curculionidae). O género *Hylastes* Erichson. *Boletim Agricola*, **43**: 5–6. (in Portuguese)
- HAJEK A.E., DONALD L., DAHLSTEIN L. (1985): Insect and mite associates of *Scolytus multistriatus* (Coleoptera: Scolytidae) in California. *Canadian Entomologist*, **117**: 409–421.
- HAMMER Ř., HARPER D.A.T., RYAN P.D. (2009): PAST – Palaeontological Statistics, ver. 1.89. User's manual.
- HIRSCHMANN H. (1971): Gangsystematik der Parasitiformes. *Acarologie*, **15**: 29–42.
- CHRISTIANSEN W., BAKKE A. (1988): The spruce bark beetle of Eurasia. In: BERRYMAN A.A. (ed.): Dynamics of Forest Insects Populations. Patterns, Causes, Implications. New York and London, Plenum Press: 479–503.
- JOHANSSON L., ANDERSEN J., NILSSEN C. (1994): Distribution of bark insects in "island" plantations of spruce (*Picea abies* (L.) Karst.) in subarctic Norway. *Polar Biology*, **14**: 107–116.
- KACZMAREK S., MICHALSKI J. (1994): Mites (Acari, Mesostigmata) in the bark beetle galleries (*Ips typographus* L.) in Poland. *Prace Komisji Nauk Rolniczych i Komisji Nauk Lesnych*, **78**: 75–82. (in Polish)
- KIELCZEWSKI B., MOSER J.C., WIŚNIEWSKI J. (1983): Surveying the acarofauna associated with Polish Scolytidae. *Bulletin de la société des amis des sciences et des lettres de Poznań*, **22**: 151–159.
- KIRISITS T. (2007): Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. In: Lieutier F., DAY K.R., BATTISTI A. (eds): Bark and wood boring insects in living trees in Europe: a synthesis. Springer Verlag: 181–237.
- KOFLER A., SCHMÖLZER K. (2000): Zur Kenntnis phoretischer Milben und ihrer Tragwirte in Österreich (Acarina: Gamasina, Uropodina). *Berichte des Naturwissenschaftlich Medicinischen Vereins in Innsbruck*, **87**: 133–157.
- KRŠIAK B. (2009): Bark beetles (Coleoptera: Scolytidae) and phoretic uropodine mites (Acarina, Mesostigmata: Uropodina) in a mountain spruce forest. [Ph.D. Thesis.] Zvolen, Ústav Ekológie lesa, Slovenská akadémia vied: 82. (in Slovak)

- LEWIS K.J., ALEXANDER S.A. (1986): Insects associated with the transmission of *Verticicladiella procera*. Canadian Journal of Forest Research, **16**: 1330–1333.
- MAŠÁN P. (2001): Mites of the cohort Uropodina (Acarina, Mesostigmata) in Slovakia. Annotationes Zoologicae et Botanicae, **223**: 1–320. (in Slovak)
- MATHIESEN-KÄÄRIK A. (1953): Eine Übersicht über die gewöhnlichsten mit Borkenkäfern assoziierten Bläuepilze in Schweden und einige für Schweden neue Bläuepilze. Meddelanden från Statens Skogsforskningsinstitut, **43**: 1–74.
- MOSER J.C. (1976): Phoretic carrying capacity of flying southern pine beetles (Coleoptera: Scolytidae). Canadian Entomologist, **108**: 807–808.
- MOSER J.C., ROTON L.M. (1971): Mites associated with southern pine bark beetles in Allen Parish, Louisiana. Canadian Entomologist, **103**: 1775–1798.
- MOSER J.C., BOGENSCHÜTZ H. (1984): A key to the mites associated with flying *Ips typographus* in South Germany. Zeitschrift für Angewandte Entomologie, **121**: 437–450.
- MOSER J.C., EIDMANN H.H., REGNANDER J.R. (1989a): The mites associated with *Ips typographus* in Sweden. Annales Entomologici Fennici, **55**: 23–27.
- MOSER J.C., PERRY T.J., SOLHEIM H. (1989b): Ascospores hyperphoretic on mites associated with *Ips typographus*. Mycological Research, **93**: 513–517.
- MOSER J.C., PERRY T.J., FURUTA K. (1997): Phoretic mites and their hyperphoretic fungi associated with flying *Ips typographus japonicus* Nijima (Col., Scolytidae) in Japan. Journal of Applied Entomology, **121**: 425–428.
- MOSER J.C., KONRAD H., KIRISITS T., CARTA L.K. (2005): Phoretic mites and nematode associates of *Scolytus multistriatus* and *Scolytus pygmaeus* (Coleoptera: Scolytidae) in Austria. Agricultural and Forest Entomology, **7**: 169–177.
- NILSSEN A.C. (1984): Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. Annales Entomologici Fennici, **50**: 37–42.
- PFEFFER A. (1955): The fauna of Czechoslovak Republic 6. Bark beetles – Scolytoidea. Praha, Nakladatelství Československé akademie věd: 324. (in Czech)
- PFEFFER A. (1989): Scolytidae and Platypodidae. Praha, Academia: 137. (in Czech)
- PFEFFER A. (1995): Zentral – und westpaläarktische Borken – und Kernkäfer (Coleoptera: Scolytidae, Platypodidae). Basel, Pro Entomologia: 310.
- PFEFFER A., ČEPELÁK J., GREGOR F., KOMÁREK J., KRAMÁŘ J., KUDELA M., NOVÁKOVÁ E., OBR S., WEISER J. (1954): Forestry Zoology II. Praha, SZN: 622. (in Czech)
- SCHELHAAS M.J., NABUURS G.J., SCHUCK A. (2003): Natural disturbances in the European forests in the 19<sup>th</sup> and 20<sup>th</sup> centuries. Global Change Biology, **9**: 1620–1633.
- SCHWENKE W. (1974): Die Forstschädlinge Europas. 2. Band. Käfer (Coleoptera). Hamburg und Berlin, Paul Parey Verlag: 500.
- SIMPSON E.H. (1949): Measurement of species diversity. Nature, **163**: 688.
- SOKAL R.R., ROHLF F.J. (2000): Biometry: the principles and practice of statistics in biological research. Sixth printing. New York, W. H. Freeman: 887.
- StatSoft Inc. (2005): STATISTICA (data analysis software system), ver. 7.1. Tulsa, OK, Statsoft: 238.
- WERMELINGER B., DUELLI P., OBRIST M.K. (2002): Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. Forest Snow and Landscape Research, **77**: 133–148.
- WITKOSKY J.J., SCHOWALTER T.D., HANSEN E.M. (1986): *Hylastes nigrinus* (Coleoptera: Scolytidae), *Pissodes fasciatus* and *Steremnius carinatus* (Coleoptera: Curculionidae) as vectors of black-stain root disease of Douglas-fir. Environmental Entomology, **15**: 1090–1095.

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