

Oribatid Mites as Inhabitants of Lichens in the Taiga Zone of Northeastern Europe: Biotopic Association and Ecological Groups of Species

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Abstract—The ground (*Cladina arbuscula*, *C. rangiferina*, *C. stellaris*, *Cetraria islandica*) and epiphytic (*Hypogymnia physodes* and *Bryoria subcana*) lichens in taiga forests of the European Northeast were examined as habitats of oribatid mites. In total, in different species of lichens, 55 species of oribatids from 30 families were found. Five ecological groups of oribatid mites as inhabitants of lichens were identified. It was found that the specificity of the oribatid mite population in epiphytic lichens consisted of dominant arboricolous species also not numerous arboricolous species. Dominant hemiedaphic species and not numerous hemiedaphic species were characteristic of ground lichens. The arboricolous–hemiedaphic group includes species that live in both ground and epiphytic lichens. The ecologically vicariating species in relation to epiphytes were identified; these are species of the genera *Carabodes*, *Mycobates*, *Oribatula*, and *Phauloppia*.

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INTRODUCTION

Oribatid mites are permanent and numerous inhabitants of the lichen and moss cover on trees (Trave, 1963; Biazrov, 1988; Melekhina and Biazrov, 1997), soil, stones, and coastal rocks (Gjelstrup and Søchting, 1979; Coloff, 1983; Niemi and Vilkkamaa, 1988; Tarba, 1992). Complexes of species associated with lichens as habitats have been determined in various regions (Strenzke, 1952; Pschorn-Walcher and Gunhold, 1957; Andre, 1975, 1979, 1984, 1985; Seyd, 1988; Seyd and Seaward, 1984). Oribatids were considered as components of lichen consortia (Trave, 1963; Biazrov et al., 1971). The biotopic preferences of oribatid mites living in lichens of different life forms, growing on different substrates in various plant communities, have been studied (Biazrov and Melekhina, 1992, 1994; Melekhina and Biazrov, 1997; Shtanchaeva, 1997). Oribatid mites—inhabitants of epiphytic lichens—were presented as bioindicators of radioactive contamination of natural ecosystems (Melekhina and Krivolutsky, 1993).

In the taiga zone, lichens play a significant part in the composition of forest biocenoses and are distinguished by the diversity of species (Pystina, 2003). Data were obtained on the taxonomic composition and distribution characteristics of oribatid mites in lichens of various species and life forms (Melekhina, 2000, 2001).

The purpose of this work is to analyze the taxonomic diversity and biotopic preferences of oribatid mites living in lichens and to identify complexes of species associated with soil cover lichens and epiphytic lichens in the coniferous forests of the taiga zone of northeastern Europe.

MATERIALS AND METHODS

Studies were conducted in the vicinity of the village of Kazhym of Koigorodskii district of the Republic of Komi (60°19'58" N, 51°32'00" E). The climate in the study area is temperate continental, with long winters and short cool summers. The average monthly temperatures in January and July are –15 and +17°C, respectively. The frost-free period lasts ~100 days; annual precipitation reaches up to 700 mm; the average maximum snow depth in the forest is 100 cm (*Atlas...*, 1997).

The predominant plant formations are coniferous taiga phytocenoses. In the middle taiga subzone, spruce forests dominate on the plains, the tree layer that consists of the Siberian spruce *Picea obovata* Lebed., sometimes mixed with birch and fir. The most typical associations are bilberry–green-moss spruce forests; small forest shrubs, mainly bilberries and lingonberries (Yudin, 1954; *Les...*, 1999), prevail in the grass–shrub layer. Pine forests formed by the common pine *Pinus silvestris* L. are developed on sandy terraces and interfluvial plains; lichen pine forests are wide-

Table 1. Studied habitats of oribatid mites in coniferous plant communities

Lichens	Plant community			
	pine forest		spruce forest	
	lichen–green moss	bilberry	bilberry	green moss
	Ground radial-lobed bushy erect			
<i>Cladina arbuscula</i>	+	+	+	–
<i>Cladina rangiferina</i>	+	+	+	+
<i>Cladina stellaris</i>	+	+	–	+
	Ground flat-lobed bushy			
<i>Cetraria islandica</i>	+	+	+	–
	Epiphytic foliose			
<i>Hypogymnia physodes</i>	+	+	+	–
	Epiphytic bushy hanging			
<i>Bryoria subcana</i>	–	–	–	+

spread. The forest stand is most often pure pine, sometimes mixed with birch; larch and spruce are less common. The grass–shrub layer is sparse. Shrubs are represented by lingonberries, bilberries, and crowberries; lichens are prevalent in the ground cover; mosses are found in shady places (Yudin, 1954; Lesa..., 1999). The dominants of the soil cover are usually lichens of the genus *Cladina*: *C. stellaris* (Opiz.) Brodo, *C. rangiferina* (L.) Nyl., and *C. arbuscula* (Wallr.) Hale & W.L. Culb, while *Cetraria islandica* (L.) Ach. occurs frequently (L.) Ach. (Pystina, 2003).

Observations were carried out in two types of pine communities (lichen–green-moss and bilberry pine forests) and two types of spruce communities (bilberry and green-moss spruce forests). Lichen populations of different species and life forms were examined as habitats for oribatid mites: ground *Cladina arbuscula*, *C. rangiferina*, *C. stellaris*, and *Cetraria islandica*, epiphytic *Hypogymnia physodes* (L.) Nyl. and *Bryoria subcana* (Nyl. ex Stiz.) Brodo et D. Hawksw. (Table 1). The species affiliation of the collected lichens was determined by L.G. Biazrov. Lichen taxonomy is given according to Santesson's classification (Santesson, 1993), and life forms are given according to Golubkova and Biazrov's classification (Golubkova and Biazrov, 1989).

The material was collected in July–August of 1989–1992. The thalli of *H. physodes* were collected at a height of 1.5–2.0 m from pine trunks in pine forests and from the trunks and branches of spruces in bilberry spruce forests. *B. subcana* was taken from the trunks and branches of spruce. Collections of epiphytes from ten trunks constituted an average sample. Samples of ground lichens and soil, each 100 cm² in area, were taken in tenfold replication in each plant community twice during the observation period (in 1989 and 1992). The soil was taken at a depth of 10 cm separately from lichens. A total of 80 soil samples, 80

samples of ground lichens, and 32 samples of epiphytic lichens with a volume of 2 L each were analyzed.

Over 30000 specimens of sexually mature oribatid mites have been identified. Groupings of oribatid mites were compared by the species composition and population structure using methods of analysis of faunal material (Pesenko, 1982). The share of each species in the population structure ($P_{ij}, \%$), the degree of participation of the habitat in the distribution of the species ($q_{ij}, \%$), and the degree of relative biotopic association of species (F) were determined. Based on these indicators, the species affiliation to an ecological group was determined. When describing the dominance structure, Engelman's classification was used (Potapov and Kuznetsova, 2011): eudominant, 39.4–100; dominant, 12.4–39.3; subdominant, 3.9–12.3; scanty/numerically insignificant (recedent) 1.3–3.8; and rare (subrecedent), <1.3%. The taxonomy of oribatid mites is given according to the classification of Subías (Subías, 2019).

The distribution of species in lichen population of different regions was analyzed (Strenzke, 1952; Trave, 1963; Andre, 1975, 1979, 1984, 1985; Gjelstrup and Söchting, 1979; Solhøy and Koponen, 1981; Seyd and Seaward, 1984; Niemi and Vilkkamaa, 1988; Stary, 1988; Biazrov and Melekhina, 1992, 1994; Tarba, 1992; Shtanchaeva, 1997; Melekhina and Biazrov, 1997; and others).

RESULTS AND DISCUSSION

Species composition, dominance structure. In the habitats studied, a total of 90 species of oribatid mites were found, representatives of 33 families; 55 species from 30 families were found in lichens of four plant communities. The most species-rich were the families Oribatulidae (five species), Suctobelbidae (seven),

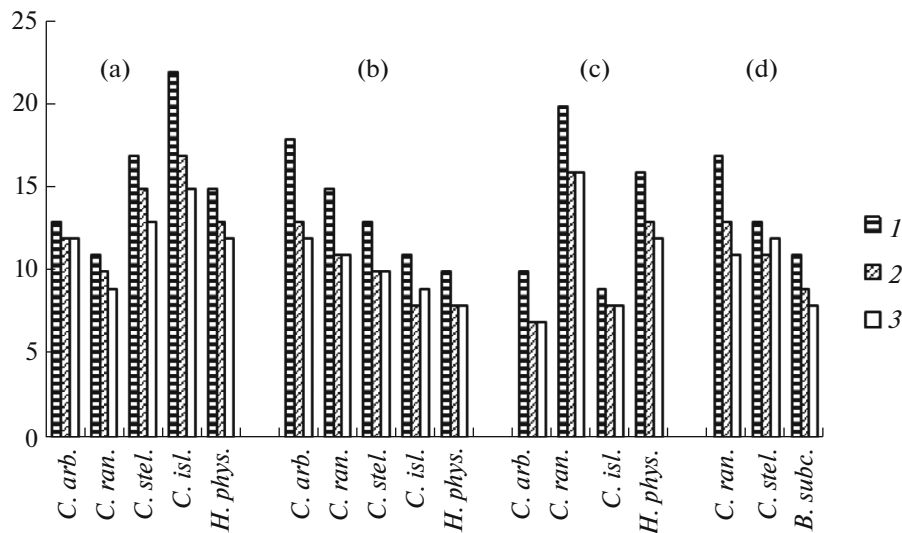


Fig. 1. The number of taxa of oribatid mites in ground and epiphytic lichens of pine and spruce plant communities (*C. arb.*, *Cladina arbuscula*; *C. ran.*, *Cladina rangiferina*; *C. stel.*, *Cladina stellaris*; *C. isl.*, *Cetraria islandica*; *H. phys.*, *Hypogymnia physodes*; and *B. subc.*, *Bryoria subcana*). (a) Lichen-green-moss-pine forest, (b) bilberry-pine forest, (c) bilberry-spruce forest, (d) green-moss-spruce forest; (1–3) number of species, genera, and families, respectively.

Crotoniidae (three), Phthiracaridae (three), and Carabodidae (three). Most families were represented by 1–2 species each. The largest number of taxa was noted, as a rule, in ground lichens (Fig. 1). In Tables 2–5, the species that showed a positive or negative biotopic association to a particular habitat are given.

In the ground lichens of the lichen-green-moss pine forest, dominant were the oribatids *Carabodes subarcticus* Trägårdh, 1902, *Scheloribates laevigatus* (Koch, 1835), and *Trhypochthonius cladonicolus* (Willmann, 1919); the latter was among the dominants only in lichens of the genus *Cladina*, acting as a eudominant in *C. rangiferina* (Table 2). The group of subdominants included *C. marginatus* (Michael, 1884) and *Tectocephus velatus* (Michael, 1880). In the ground *Cetraria islandica*, the largest share was represented by *Ceratoppia quadridentata* (Haller, 1882), *Camisia biurus* (Koch, 1839), and *Adoristes ovatus poppei* (Oudemans, 1906). The population of oribatid mites of the epiphytic lichen *H. physodes* was specific. It was dominated by the abundance of *Oribatula* (*Z.*) *propinqua* (Oudemans, 1902) (eudominant) and *Carabodes labyrinthicus* (Michael, 1879); the subdominants were *Diapterobates humeralis* (Hermann, 1804) and *Phauloppia nemoralis* (Berlese, 1916). Most species were characterized by a positive biotopic association with the epiphyte; 7 out of 15 species were found only in this lichen, including dominants and one subdominant (*D. humeralis*), as well as rare and small species *Furcoppia dentata* (Willmann, 1950), *Gratoppia foveolata* (Paoli, 1908), *Suctobelbella acutidens* s. str. (Forsslund, 1941), and *Liebstadia pannonica* (Willmann, 1951). The thallus of *H. physodes* was habitat to the largest proportion of individuals of species such as *P. nemoralis*, *Chamobates pusillus* (Berlese, 1895), and

Trichoribates berleseii (Jacot, 1929). Individuals of *Diapterobates oblongus* (L. Koch, 1879) were evenly distributed between the epiphyte and ground lichen *C. islandica*.

The oribatid groupings in the ground lichens of the genus *Cladina* in the bilberry pine forest were characterized by a multi dominant population structure. The species *C. subarcticus* and *C. marginatus* dominated steadily; a large proportion of individuals always belonged to *C. subarcticus* (Table 2). The species *T. cladonicolus* in the lichen *C. stellaris* was a dominant, but in *C. arbuscula* and *C. rangiferina*, a subdominant. The group of dominants in *C. arbuscula* also included *T. velatus*. The subdominants were *S. laevigatus* and *Oribatula tibialis* (Nicolet, 1855) in *C. arbuscula* and *A. ovatus poppei* and *C. labyrinthicus* in *C. rangiferina*. In *Cetraria islandica*, in contrast to *Cladina* lichens, only *C. subarcticus* and *T. velatus* were the dominant group, the first of which acted as a eudominant. The subdominant was *A. ovatus poppei*. The species *T. cladonicolus* was not found here. Only in the thalli of *C. islandica* were four species found, including *C. quadridentata*. The most specific was the population of the epiphytic lichen *H. physodes*. The basis of its population structure was *C. labyrinthicus* (eudominant), *P. nemoralis* (dominant), and *O. (Z.) propinqua* (subdominant), the latter two were not noted in ground lichens. Only in the thalli of *H. physodes* was the species *F. dentata*, a subprecedent, present. In the epiphyte, single specimens of *Suctobelbella acutidens duplex* (Strenzke, 1950) with a negative index *F* were found.

The groups of dominants and subdominants in the ground lichens of the bilberry spruce forest included *C. subarcticus*, *C. marginatus*, and *T. velatus*, while in

Table 2. Distribution of oribatid mites by habitats in pine forests

Species/habitat/biotope association indices	<i>Cladina arbuscula</i>			<i>Cladina rangiferina</i>			<i>Cladina stellaris</i>			<i>Cetraria islandica</i>			<i>Hypogimnia physodes</i>		
	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>
<i>Phthiracarus laevigatus</i>	—	—	—	—	—	—	1.0	60.0	0.52	0.5	20.0	-0.04	—	—	—
<i>P. longulus</i>	—	—	—	0.9	70.0	0.80	—	—	—	0.4	30.0	0.23	—	—	—
<i>Trhypochthonius cladonicolus</i>	—	—	—	44.4	57.4	0.68	20.4	42.1	0.21	0.4	0.5	-0.98	—	—	—
<i>Camisia biurus</i>	—	—	—	—	—	—	0.3	25.0	-0.17	1.2	75.0	0.83	—	—	—
<i>Furcoppia dentata</i>	—	—	—	—	—	—	—	—	—	—	—	—	1.2	100	1.0
<i>Ceratoppia quadridentata</i>	—	—	—	—	—	—	—	—	—	1.0	88.9	0.93	0.4	11.1	0.27
<i>Adoristes ovatus poppei</i>	0.3	3.0	-0.77	1.8	19.7	-0.01	1.6	28.8	-0.08	4.1	48.5	0.55	—	—	—
<i>Eneremaeus oblongus sivestris</i>	0.3	8.0	-0.47	—	—	—	1.9	92.0	0.92	—	—	—	—	—	—
<i>Graptoppia foveolata</i>	—	—	—	—	—	—	—	—	—	—	—	—	0.9	100	1.0
<i>Suctobelbella acutidens duplex</i>	—	—	—	—	—	—	1.5	90.0	0.90	0.3	10.0	-0.41	—	—	—
<i>Carabodes labyrinthicus</i>	—	—	—	—	—	—	—	—	—	—	—	—	32.1	100	1.0
<i>C. marginatus</i>	7.7	30.5	0.29	6.5	26.7	0.18	4.7	30.5	-0.04	2.7	11.7	-1.0	0.4	0.6	-0.85
<i>C. subarcticus</i>	50.4	24.0	0.13	27.8	13.6	-0.23	49.5	38.7	0.14	46.1	23.7	0.07	—	—	—
<i>Tectocephus velatus</i>	0.7	5.9	-0.59	5.0	43.5	0.51	1.6	28.8	-0.08	2.6	23.5	0.07	—	—	—
<i>Trichoribates berleseii</i>	0.3	13.3	-0.22	0.7	33.3	0.33	—	—	—	—	—	—	3.3	53.4	0.88
<i>Chamobates pusillus</i>	0.1	33.3	0.35	—	—	—	—	—	—	—	—	—	0.8	66.7	0.93
<i>Diaperobates humeralis</i>	—	—	—	—	—	—	—	—	—	—	—	—	6.1	100	1.0
<i>D. oblongus</i>	—	—	—	—	—	—	—	—	—	0.5	50.0	0.57	1.6	50.0	0.86
<i>Oribatula (Z.) propinqua</i>	—	—	—	—	—	—	—	—	—	—	—	—	45.5	100	1.0
<i>Phauloppia nemoralis</i>	—	—	—	—	—	—	0.1	9.1	-0.65	—	—	—	4.1	90.9	0.98

Table 2. (Contd.)

Species/habitat/biotopic association indices	<i>Cladina arbuscula</i>			<i>Cladina rangiferina</i>			<i>Cladina stellaris</i>			<i>Cetraria islandica</i>			<i>Hypogimnia physodes</i>		
	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>
<i>Scheleoribates laevigatus</i>	38.0	35.3	0.38	11.8	11.3	-0.33	13.8	21.1	-0.28	31.6	31.8	0.27	1.6	0.5	-0.86
<i>Pergalumna nervosa</i>	0.6	50.0	0.61	—	—	—	0.1	12.5	-0.54	0.3	25.0	0.11	0.4	12.5	0.33
Bilberry—pine forest															
<i>P. longulus</i>	—	—	—	2.2	65.0	0.69	1.2	35.0	0.24	—	—	—	—	—	—
<i>T. cladonicolus</i>	10.3	34.3	0.03	10.1	25.7	0.02	15.7	40.0	0.33	—	—	—	—	—	—
<i>C. biurus</i>	0.3	33.0	0.01	—	—	—	0.7	67.0	0.71	—	—	—	—	—	—
<i>Heminothrus longisetosus</i>	0.6	28.0	-0.12	2.2	72.0	0.77	—	—	—	—	—	—	—	—	—
<i>F. dentata</i>	—	—	—	—	—	—	—	—	—	—	—	—	0.4	100	1
<i>A. ovatus poppei</i>	1.5	18.5	-0.36	6.0	55.4	0.57	—	—	—	9.7	26.1	0.63	—	—	—
<i>E. oblongus silvestris</i>	1.4	91.7	0.91	0.2	8.3	-0.57	—	—	—	—	—	—	—	—	—
<i>S. acutidens duplex</i>	—	—	—	2.5	65.3	0.69	1.2	30.4	0.14	—	—	—	—	—	—
<i>C. labyrinthicus</i>	1.9	5.8	-0.78	11.9	27.4	0.06	6.4	14.7	-0.32	2.9	1.9	-0.60	55.1	50.2	0.80
<i>C. marginatus</i>	15.0	38.6	0.13	16.3	32.0	0.17	14.1	27.7	0.07	2.9	1.7	-0.65	—	—	—
<i>C. subarcticus</i>	31.9	30.0	-0.06	35.2	25.3	0.01	43.8	31.4	0.16	63.2	13.3	0.32	—	—	—
<i>T. velatus</i>	12.7	62.3	0.54	2.0	7.5	-0.61	—	—	—	13.2	14.5	0.36	0.4	0.6	-0.89
<i>T. berleseii</i>	1.4	100	1.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Oribatula tibialis</i>	8.4	59.6	0.50	2.2	12.0	-0.42	—	—	—	—	—	—	—	—	—
<i>O. (Zygoribatula) exilis</i>	0.6	83.3	0.82	—	—	—	—	—	—	—	—	—	0.4	16.7	0.29
<i>O. (Z.) propinqua</i>	—	—	—	—	—	—	—	—	—	—	—	—	8.5	100	1
<i>P. nemoralis</i>	—	—	—	—	—	—	—	—	—	—	—	—	33.1	100	1
<i>S. laevigatus</i>	9.0	62.0	0.54	2.3	12.3	-0.40	—	—	—	1.7	2.7	-0.49	0.4	0.9	-0.85

P is the proportion of the species in the population structure (%); *q* is the degree of habitat participation in the distribution of the species (%); *F* is the index of the relative biotopic association of the species; “—” indicates that the species was not registered; for Tables 2—4.

Table 3. Distribution of oribatid mites by habitats in a bilberry spruce forest

Species/habitat/biotopic association indices	<i>Cladina arbuscula</i>			<i>Cladina rangiferina</i>			<i>Cetraria islandica</i>			<i>Hypogimnia physodes</i>		
	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>
<i>Phthiracarus laevigatus</i>	—	—	—	0.3	14.3	-0.50	3.7	85.7	0.95	—	—	—
<i>Camisia biurus</i>	—	—	—	2.0	100	1	—	—	—	—	—	—
<i>Ceratoppia quadridentata</i>	—	—	—	0.3	11.1	-0.60	—	—	—	3.0	88.9	0.92
<i>Adoristes ovatus poppei</i>	—	—	—	0.3	2.0	-0.92	30.5	98.0	0.99	—	—	—
<i>Suctobelbella acutidens duplex</i>	3.5	84.6	0.87	—	—	—	—	—	—	0.7	15.4	-0.27
<i>Carabodes labyrinthicus</i>	0.9	37.5	0.20	—	—	—	—	—	—	2.0	62.5	0.68
<i>C. marginatus</i>	10.7	30.3	0.05	15.6	51.8	0.37	12.4	17.9	0.13	—	—	—
<i>C. subarcticus</i>	56.6	52.2	0.47	35.0	37.7	0.10	21.8	10.1	-0.20	—	—	—
<i>Tectocephus velatus</i>	15.1	38.4	0.22	10.5	31.2	-0.04	23.6	30.4	0.44	—	—	—
<i>Cymbaeremaeus cymba</i>	—	—	—	—	—	—	—	—	—	0.7	100	1
<i>Trichoribates berlesei</i>	—	—	—	0.5	50.0	0.34	0.6	25.0	0.33	0.4	25.0	0.03
<i>Chamobates pusillus</i>	3.8	32.4	0.09	4.3	43.3	0.21	—	—	—	3.4	24.3	0.08
<i>Diapterobates oblongus</i>	—	—	—	—	—	—	—	—	—	0.4	100	1
<i>Oribatula tibialis</i>	4.1	48.2	0.40	3.8	51.9	0.37	—	—	—	—	—	—
<i>O. (Zygoribatula) exilis</i>	—	—	—	—	—	—	—	—	—	3.0	100	1
<i>O. (Z.) propinqua</i>	—	—	—	—	—	—	—	—	—	1.1	100	1
<i>Phauloppia nemoralis</i>	—	—	—	0.3	0.4	-0.98	—	—	—	81.0	99.6	0.99
<i>Scheloribates laevigatus</i>	1.9	7.8	-0.65	16.4	79.2	0.77	6.2	13.0	-0.06	—	—	—

Table 4. Distribution of oribatid mites by habitats in the green-moss–spruce forest

Species/habitat/biotopic association indices	<i>Cladina rangiferina</i>			<i>Cladina stellaris</i>			<i>Bryoria subcana</i>		
	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>	<i>P</i>	<i>q</i>	<i>F</i>
<i>Trhypochthonius cladonicolus</i>	7.1	58.5	0.73	3.6	41.5	0.35	–	–	–
<i>Ceratoppia quadridentata</i>	–	–	–	0.4	50.0	0.49	0.2	50.0	–0.12
<i>Adoristes ovatus poppei</i>	4.1	73.7	0.85	1.1	26.3	0.02	–	–	–
<i>Eueremaes oblongus silvestris</i>	4.4	31.2	0.34	7.0	68.8	0.73	–	–	–
<i>Graptoppia foveolata</i>	–	–	–	–	–	–	0.1	100	1
<i>Suctobelbella acutidens duplex</i>	2.9	100	1	–	–	–	–	–	–
<i>Carabodes labyrinthicus</i>	2.7	90.0	0.95	–	–	–	0.1	10.0	–0.84
<i>C. marginatus</i>	0.6	4.4	–0.66	9.3	95.6	0.97	–	–	–
<i>C. subarcticus</i>	53.1	48.5	0.61	40.2	51.2	0.51	0.1	0.3	–0.99
<i>Tectocephus velatus</i>	9.4	69.6	0.82	2.9	30.4	0.12	–	–	–
<i>Trichoribates berlesei</i>	0.9	20.0	0.05	–	–	–	1.1	80.0	0.51
<i>Diapterobates humeralis</i>	–	–	–	–	–	–	12.5	100	1
<i>D. oblongus</i>	–	–	–	–	–	–	–	–	–
<i>Mycobates tridactylus</i>	–	–	–	–	–	–	0.2	100	1
<i>Oribatula tibialis</i>	5.0	100	1	–	–	–	–	–	–
<i>O. (Zygoribatula) exilis</i>	–	–	–	–	–	–	0.8	100	1
<i>O. (Z.) propinqua</i>	–	–	–	–	–	–	1.1	100	1
<i>Phauloppia nemoralis</i>	0.6	0.2	–0.98	–	–	–	83.5	99.8	0.99
<i>Scheloribates laevigatus</i>	1.2	2.9	–0.77	27.9	94.9	0.96	0.3	2.2	–0.97

the lichens of the genus *Cladina*, *C. subarcticus* was the most abundant (in *C. arbuscula*, it was a eudominant). In the lichen *C. islandica*, the first dominant was *A. ovatus poppei*, which was rare in *C. rangiferina* and absent in *C. arbuscula*. The species *S. laevigatus* dominated in *C. rangiferina* and was subdominant in *C. islandica*. Sixteen species were found in the thalli of *H. physodes*, and one species absolutely dominated: *P. nemoralis* (>80% of all individuals; $F = 0.99$). This lichen contained the largest proportion of individuals of *C. quadridentata* ($F = 0.92$) and *C. labyrinthicus* ($F = 0.68$). For almost all species, except one, *S. acutidens duplex*, a positive association with the epiphyte was determined. Nine species were found in *H. physodes* alone, including *Cymbaeremaes cymba* (Nicolet, 1855), *Oribatula (Z.) exilis* (Nicolet, 1855), *O. (Z.) propinqua*, and *D. oblongus*, which were rare or few in number.

In the green-moss–spruce forest in the thalli of *C. rangiferina*, *C. subarcticus* was the eudominant. The subdominant group consisted of five species: *Eueremaes oblongus silvestris* (Forsslund, 1956), *A. ovatus poppei*, *T. cladonicolus*, *T. velatus*, and *O. tibialis*. In the thalli of *C. stellaris*, two species, *C. subarcticus* and *S. laevigatus*, were the eudominant and dominant, respectively, and two species, *C. marginatus* and *E. oblongus silvestris*, were subdominant. In the epiphytic lichen *B. subcana*, two species prevailed in abundance: *P. nemoralis* and *D. humeralis*, the first of

which is a eudominant. All other species were rare. Only in the epiphyte were *O. (Z.) propinqua*, *O. (Z.) exilis*, *D. humeralis*, *G. foveolata*, *Mycobates tridactylus* Willmann, 1929, and *Micreremus brevipes* (Michael, 1888) found. For the species *C. quadridentata*, *C. labyrinthicus*, *C. subarcticus*, and *S. laevigatus*, a negative index F was determined.

In the ground lichens of pine and spruce forests, apart from the species listed in Tables 2–4, *Euphthiracarus cribrarius* (Berlese, 1904), *Trhypochthonius tectorum* s. str. (Berlese, 1896), *Galumna lanceata* (Oudemans, 1900), and *Parachipteria punctata* (Nicolet, 1855) were registered.

In the soils of the lichen–green-moss–pine, bilberry–pine, bilberry–spruce, and green-moss–spruce forests, 30, 28, 30, and 26 species were found, respectively. The dominants were two or three species of the following species: *T. velatus*, *Oppiella nova* (Oudemans, 1902), *C. pusillus*, *S. laevigatus*, and *C. subarcticus*; groups of subdominant species consisting of 1–6 species were distinguished (Table 5). The species *S. laevigatus* belonged to dominants or subdominants. The species *C. subarcticus*, the first dominant in ground lichens, was one of the dominants in the soil of the lichen–green-moss–pine forest. Groups of subdominants were identified in all communities, which were composed of the species *C. pusillus*, *Dissorhina ornata globosa* (Paoli, 1908), *Suctobelbella*

Table 5. Species composition and relative abundance (%) of oribatid mites in the soil of various plant communities

Species/plant community	Pine forest		Spruce forest	
	lichen—green moss	bilberry	bilberry	green moss
<i>Trhypochthonius cladonicolus</i>	0.3	—	—	—
<i>Damaeus bituberculatus</i>	0.3	1.9	1.3	3.3
<i>Adoristes ovatus poppei</i>	0.8	1.8	3.6	3.9
<i>Dissorhina ornata</i> s. str.	—	—	4.4	—
<i>D. ornata globosa</i>	2.5	—	—	7.8
<i>Oppiella (Moritzoppiella) neerlandica</i>	0.9	1.4	1.7	—
<i>Oppiella nova</i>	2.1	22.3	21.4	11.4
<i>Quadroppia quadricarinata</i>	—	3.5	2.4	3.0
<i>Suctobelbella acutidens</i> s. str.	4.6	—	6.7	—
<i>S. longicuspis</i> s. str.	1.7	4.7	—	—
<i>S. singularis</i>	0.9	1.3	—	3.7
<i>S. baloghi</i>	—	6.2	—	—
<i>Carabodes marginatus</i>	3.6	1.5	0.6	0.9
<i>C. subarcticus</i>	20.9	3.1	3.6	3.9
<i>Tectocephus velatus</i>	28.0	36.6	5.5	27.8
<i>Ceratozetella sellnicki</i>	—	—	5.1	—
<i>Chamobates pusillus</i>	3.0	1.7	17.4	9.8
<i>Oribatula tibialis</i>	0.2	1.1	1.3	—
<i>Scheloribates laevigatus</i>	17.4	2.1	7.1	5.8

baloghi (Forsslund, 1958), *S. acutidens* s. str. (Forsslund, 1941), *Ceratozetella sellnicki* (Rajski, 1958), and *S. laevigatus*.

The most common in the soil were the species of the family Oppiidae: *Dissorhina ornata* s. str. (Oudemans, 1900), *D. ornata globosa*, *Oppiella (Moritzoppiella) neerlandica* (Oudemans, 1900), *Rhinoppia subpectinata* (Oudemans, 1900), *Microppia minus* (Paoli, 1908), and *O. nova*, as well as species of the family Suctobelbidae: *Suctobelbella acutidens* s. str., *S. acutidens sarekensis* (Forsslund, 1941), *S. baloghi*, *S. longicuspis* Jacot, 1937, *S. perforata* (Strenzke, 1950), and *S. subtrigona* (Oudemans, 1900). The species of the family Quadroppiidae *Quadroppia quadricarinata* (Michael, 1885) was also common in the soil. Representatives of these families are common in soils of zonal and intrazonal communities in northern Europe (Melekhina, 2011).

Species that were not found in lichens were found in the soil: *Phthiracarus globosus* (Koch, 1841), *Acrotritia ardua* s. str. (Koch, 1841), *Mesotritia flagelliformis* (Ewing, 1909), *Oribotritia fennica* Forsslund et Märkel, 1963, *Heminothrus (P.) peltifer* (Koch, 1839), *Cepheus cepheiformis* (Nicolet, 1855), *Ceratozetes gracilis* (Michael, 1884), *Diapterobates notatus* (Thorell, 1871), *Fuscozetes fuscipes* (Koch, 1844), *Edwardzetes edwardsi* (Nicolet, 1855), *Eupelops occultus* (Koch, 1835), *E. plicatus* (Koch, 1835), *Neoribates*

roubali (Berlese, 1910), *Achipteria coleoptrata* s. str. (Linnaeus, 1758), and *A. italica* (Oudemans, 1914).

Therefore, different groups of habitats differed in the composition of the dominant species: *C. subarcticus*, *C. marginatus*, *T. velatus*, *T. cladonicolus*, *S. laevigatus*, and *A. ovatus poppei* dominated in ground lichens; *P. nemoralis*, *O. (Z.) propinqua*, *C. labyrinthicus*, and *D. humeralis* were prevalent in epiphytic lichens; *O. nova*, *C. pusillus*, *C. sellnicki*, and *T. velatus* dominated in the soil. In pine forests epiphytes, the first in abundance were *O. (Z.) propinqua* and *C. labyrinthicus*, and in spruce forests (both bushy and leafy epiphytes), *P. nemoralis* was the absolute dominant.

Biotope association. Species that have shown biotope association to a series of habitats or to a specific habitat have been identified. Thus, *C. subarcticus*, which was dominant in ground lichens, showed an association with lichens of the genus *Cladina*. In relation to *C. islandica*, the *F* index was positive in the bilberry—pine forest and negative in the bilberry—spruce forest. In epiphytes, *C. subarcticus*, as a rule, did not occur; it was noted singly in *B. subcana*, with a negative *F* index. In a pine grove in the vicinity of Kevo (Finland), *C. subarcticus* was confined to the ground *Stereocaulon paschale* and *Cladina stellaris*, but was not found in the epiphyte (Biazrov and Melekhina, 1994). It was found in the ground cover lichens of Northern Norway (Biazrov and Melekhina, 1992), in lichen wastelands of Northern Finland (Solhøy and

Koponen, 1981), and in the epiphytes of Moscow oblast (Melekhina and Biazrov, 1997).

The species *Carabodes labyrinthicus* was associated with epiphytes in pine forests and the bilberry–spruce forest ($F = 0.68–1.0$). This species was found exclusively in the epiphyte in the lichen–green-moss–pine forest; in the bilberry–pine forest, it was also found in four ground lichens. The F index for three of them (*C. stellaris*, *C. arbuscula*, and *C. islandica*) was negative. In spruce forests, *C. labyrinthicus* was found in ground lichens of the genus *Cladina*, with a low abundance. *C. labyrinthicus* was one of the dominants in the thalli of *H. physodes* in the forests of Moscow oblast (Melekhina and Biazrov, 1997) and was present in the epiphyte and in the ground lichens in the pine grove of Kevo, Finland (Biazrov and Melekhina, 1994) and in the ground *Cetraria nivalis* in a dry lichen–moss wasteland in Norway (Biazrov and Melekhina, 1992). Willmann (1933) called *C. labyrinthicus* a xerophilous species typical of lichens and tree bark; Seyd and Seaward (1984) placed it in the group of invertebrates that prefer lichens as habitats and a food source. *C. labyrinthicus* was one of the most numerous species in the epiphytes in southern Belgium (Andre, 1975, 1979, 1984, 1985); it was noted as a characteristic inhabitant of lichen cover on trees in Northern Germany (Strenzke, 1952) and Poland (Niedbala, 1970), Denmark (Gjelstrup and Söchting, 1979) and in the forests of the Middle Alps (Pschorn-Walcher and Gunhold, 1957).

For the species *Carabodes marginatus* in pine forests, a positive association was found with the species of the genus *Cladina* and a negative one, for *Cetraria islandica*. Single specimens of *C. marginatus* were found in the epiphyte *H. physodes* of the lichen–green-moss–pine forest, with a negative index F . In the soil, *C. marginatus* was characterized by a low abundance. This species was previously noted as an inhabitant of lichen and moss–lichen groups (Trave, 1963; Solhøy and Koponen, 1981; Seyd and Seaward, 1984; Biazrov and Melekhina, 1992; Melekhina and Biazrov, 1997).

The species *Trhypochthonius cladonicolus* was associated with lichens of the genus *Cladina* in pine forests; the highest F index was determined for *C. rangiferina*. For *C. islandica*, F was negative. In epiphytes, it was not found. The species *T. cladonicolus* Seyd and Seaward (1984) was included in the group of species that prefer lichens as a habitat and food source, and also live on other plants.

The species *Phauloppia nemoralis* was associated with epiphytes both in pine forests ($F = 0.98–1.0$) and in spruce forests ($F = 0.99$). In spruce forests this species was an absolute dominant (>80% of all individuals). We found *P. nemoralis* individuals in the epiphytes of the middle taiga forests in different seasons of the year. It was previously noted that this species is a characteristic lichen inhabitant (Seyd and Seaward, 1984).

The species *Oribatula (Z.) propinqua*, found exclusively in epiphytes, was a eudominant and subdominant in *H. physodes* in pine forests and rare in spruce forests. The species *O. (Z.) propinqua* was one of the dominants in the thalli of *H. physodes* in the pine forest of Bryansk oblast (Shtanchaeva, 1997), it was found on the bark of pine trees in Poland (Niedbala, 1970).

The species *Scheloriabates laevigatus* showed a positive association with the lichens of the genus *Cladina*; sometimes it was noted in epiphytes as a scarce or rare species, with a negative F index. It was common in the soil, and sometimes it acted as a dominant. *S. laevigatus* is known to be a eurytopic species; it had previously been found in epiphytic lichens (Stary, 1988; Tarba, 1992; Melekhina, 1999; Melekhina and Biazrov, 2007).

The species *Oribatula tibialis* showed an affiliation to *C. arbuscula* in the bilberry–pine forest and to *C. rangiferina* in the green-moss–spruce forest. It was found in the soil, where it was a recedent or subrecedent. The species *O. tibialis* is known as eurytopic; it was often found in rock and epiphytic lichens of Abkhazia (Tarba, 1992).

The species *Tectocephus velatus* was associated with ground lichens; in epiphytes it was extremely rare, with a negative value of the F index. In soil, it was a dominant or subdominant. The species *T. velatus* was found in epiphytic lichens in Moscow oblast (Melekhina and Biazrov, 1997) and in the southern Czech Republic (Stary, 1988), as well as in the moss cover on trees and stone walls in Germany (Pschorn-Walcher and Gunhold, 1957).

The species *Adoristes ovatus poppei* was associated with the lichen *C. islandica*; it was not found in epiphytes. In the soil of the green moss spruce forest, it was a subdominant; in other plant communities, it was rare and few in number. In Poland, *A. poppei* was found mainly in the forest litter, sometimes on tree trunks (Niedbala, 1970).

The species *Diapterobates humeralis* was associated with epiphytic lichens in both pine and spruce forests, as both a dominant and subdominant. The species *Trichoribates berlesei* was found in both ground and epiphytic lichens; it showed an affiliation to epiphytes in the lichen–green-moss–pine forest and green-moss–spruce forests ($F = 0.88$ and 0.51 , respectively). We found this species (called *Trichoribates trimaculatus*) in the thalli of *H. physodes* on pine trunks in the vicinity of Kiev (Melekhina and Krivolutsky, 1993). In Belgium, it belonged to the group of dominants in epiphytic lichens, both leafy and bushy ones (Andre, 1976, 1979, 1984, 1985). In Poland it was noted on oak trunks (Niedbala, 1970). In Germany it was often found in the moss–lichen tree cover and was assigned to the group of leading forms with a clear xerophilic character (Pschorn-Walcher and Gunhold, 1957).

The species *Ceratoppia quadridentata* was noted in both ground and epiphytic lichens. It was associated

with the epiphyte *H. physodes*. In *B. subcana*, it was found with a low abundance. In the epiphytes of coniferous forests of the middle taiga, we found *C. quadridentata* in winter (Melekhina, 2001). This species was found on tree trunks in Abkhazia (Tarba, 1992).

The species *Cymbaeremaeus cymba* was found exclusively in the epiphyte *H. physodes* in the bilberry–spruce forest. Previously, it was noted in epiphytic lichens (*H. physodes*, *Parmelia sulcata*) in winter as well (Melekhina, 2001). The species *C. cymba* was found in epiphytes in the vicinity of Kiev (Melekhina and Krivolutsky, 1993), in Moscow oblast (Biazrov et al., 1971), in Poland (Niedbala, 1970), and in Belgium (Andre, 1984). It was called a typical wood-dwelling species in Abkhazia (Tarba, 1992). Willmann (1931) called the species *C. cymba* arboricolous xerophilous.

The species *Scapheremaeus palustris* (Sellnick, 1924), which is not numerous, was associated with the epiphytic *H. physodes* bilberry spruce forest. This species was noted in the epiphytic cover in winter as well (Melekhina, 2001). In some cases, *S. palustris* was found in soil lichens, singly; it was not found in the soil.

The species *Oribatula (Z.) exilis* was associated with epiphytes. This species has been noted repeatedly in epiphytic lichens (Biazrov et al., 1971; Melekhina and Krivolutsky, 1992; Shtanchaeva, 1997). In Moscow oblast, it was most abundant in the leafy epiphytes *Parmelia sulcata* and *H. physodes* (Melekhina and Biazrov, 1997); in the vicinity of Poznan (Poland), it was present on the bark of oak and spruce (Niedbala, 1970). In Abkhazia, *O. (Z.) exilis* is classified as an arboricolous species (Tarba, 1992); Pshorn-Walcher and Gunhold (Pshorn-Walcher and Gunhold, 1957) included it in the group of leading species with a clear xerophilic character.

The species *Eueremaeus oblongus silvestris* showed an affiliation to the lichens of the genus *Cladina*; it was found in different species with different abundance. The species *E. oblongus* was called a typical wood-dwelling species in Abkhazia (Tarba, 1992), was numerous in leafy and bushy epiphytes in Belgium (Andre, 1979, 1984), and was often found in epiphytes in Germany (Pshorn-Walcher and Gunhold, 1957). Strenzke (Strenzke, 1952) placed it in the group of xerophilous species.

The species *Diapterobates oblongus* was associated with epiphytes in the lichen–green-moss–pine forest ($F = 0.86$) and bilberry–spruce forest ($F = 1.0$), to the ground *C. islandica* in the lichen–green-moss–pine forest ($F = 0.57$). For a number of species with a small abundance, the biotopic confinement to ground or epiphytic lichens was revealed. Thus, the species *Phthiracarus longulus* (Koch, 1841) and *Heminothrus longisetosus* (Willmann, 1925) showed affiliation to *C. rangiferina* and *C. stellaris* in pine forests, and *Phthiracarus laevigatus* (Koch, 1844) and *Neoribates aurantiacus* (Oudemans, 1914), to *C. islandica* in spruce and pine forests, respectively.

Ecological groups. Relative to the investigated series of habitats typical of spruce and pine forests of north-eastern Europe, ecological groups of oribatid mites were identified. When determining whether a species belongs to a particular ecological group, the values of the indices F , q , and P were taken into account. The names of the ecological groups reflect the association of species with a certain group of habitats and their numerical characteristics. Five groups of species are associated with lichens; two groups are associated with soil.

The group of dominant arboricolous species included *C. labyrinthicus*, *O. (Z.) propinqua*, *P. nemoralis*, and *D. humeralis*, which were dominant and subdominant in epiphytes and showed a positive biotopic association with them ($F = 0.99–1.0$). The not numerous arboricolous species were found only in epiphytes with a small abundance: *F. dentata*, *M. tridactylus*, *C. cymba*, and *M. brevipes*.

The arboricolous–hemiedaphic group was composed of species that lived in both epiphytic and ground lichens and were few in numbers everywhere; these are the species *C. quadridentata*, *O. (Z.) exilis*, *T. berlesei*, *D. oblongus*, *S. palustris*, and *Pergalumna nervosa* (Berlese, 1914).

The group of hemiedaphic dominant species included *C. subarcticus*, *C. marginatus*, *T. velatus*, *T. cladonicolus*, *S. laevigatus*, *A. ovatus poppei*, and *O. tibialis*, which were dominants and subdominants in ground lichens and showed biotopic affiliation to them; they were very rare in epiphytes. A not numerous hemiedaphic species were found in ground lichens ($F > 0$). They were also found in the soil with a small abundance. Some of them were observed singly in epiphytes ($F < 0$). These are the species *P. longulus*, *P. laevigatus*, *E. cribrarius*, *C. biurus*, *H. longisetosus*, *T. tectorum* s. str., *N. dorsalis*, *E. oblongus silvestris*, *S. acutidens duplex*, *G. lanceata*, *P. punctata*, and *N. aurantiacus*.

The species that were found only in the soil were subdivided into two ecological groups: epiedaphic and euedaphic species. The epiedaphic group includes species that, according to the system of life forms of Krivolutsky (Krivolutsky et al., 1995), belong mainly to the inhabitants of the soil surface and upper horizons of the litter, and partially to the inhabitants of the thickness of the litter. These are the species *P. globosus*, *A. ardua* s. str., *M. flagelliformis*, *O. fennica*, *H. (P.) peltifer*, *C. cepheiformis*, *C. gracilis*, *C. sellnicki*, *D. notatus*, *F. fuscipes*, *E. edwardsi*, *E. occultus*, *E. plicatus*, *N. roubali*, *A. coleoptrata* s. str., and *A. italica*. The euedaphic group includes species that belong to the life form of the inhabitants of shallow soil wells. These are *D. ornata* s. str., *D. ornata globosa*, *O. (O.) nova*, *O. (M.) neerlandica*, *R. subpectinata*, *M. minus*, *Q. quadricarinata*, *S. acutidens* s. str., *S. acutidens sarekensis*, *S. baloghi*, *S. longicuspis*, *S. perforata*, and *S. subtrigona*.

Various authors identified complexes of species of oribatid mites associated with lichens. Strenzke (Strenzke, 1952) named two oribatid synusias characteristic of mosses and lichens growing on stones: hygrophilic and xerophilic. The leading species of these two synusias was *Oribatula* (*Z.*) *exilis*. In Germany, Pschorn-Walcher and Gunhold (1957) identified two synusias of oribatid mites that are characteristic of the epiphytic cover of trees: xerophilic hemiedaphne of open landscapes and xerophilic hemiedaphne of closed landscapes. Each synusia consisted of representatives of several ecological groups. The authors identified four ecological groups: leading species with a clear xerophilic nature, xerophilic forms of open landscapes, xerophilic forms of closed landscapes, and euryecological species, or satellite species. Coloff (1983) described two groups of species of oribatid mites associated with lichens on coastal cliffs in England: growing in the supralittoral zone and directly on the coast. For oribatids inhabiting in the epiphytic lichens of Belgium, Andre (Andre, 1984, 1985) identified groups of species that he called zoosociological classes. The species composition of the classes is determined, according to the author, by the morphological type of the epiphyte. Consequently, in different regions, specific complexes of species of oribatid mites are distinguished for lichens as habitats.

Vicariating species. Ecologically vicariating species have been identified, i.e., representatives of one genus that are inhabitants of epiphytic lichens in different geographical regions. Representatives of the genera *Phauloppia*, *Mycobates*, *Carabodes*, and *Oribatula* (*Zygoribatula*) are considered as vicariating. Thus, the species *P. nemoralis*, which dominated in the epiphytes in our collections, was included by Seyd and Seaward (1984) in the group of invertebrates that prefer lichens as habitats and as a food source. Another species of this genus, *P. lucorum* (Koch, 1841), was characteristic of epiphytes in Belgium (Andre, 1984); it was registered on the bark of oak and pine trunks in Poland (Niedbala, 1970). According to Z. Tarba (1992), in Abkhazia, *P. lucorum* (referred to as *P. longiporosa*) was one of the dominant species in epiphytic lichens on beech trunks and was considered a typical wood-dwelling species. The same species, named *P. conformis*, was numerous in the epiphytic lichens of Germany (Pschorn-Walcher and Gunhold, 1957), most often found in the thalli of *Cladonia* spp. In southern Bohemia, *P. lucorum* and *P. nemoralis* (named *P. coin-eaui*) were dominant in the epiphytic cover of trees (Stary, 1988). *Phauloppia* sp. was the first in abundance in the lichen *H. physodes* collected from tree trunks in Moscow oblast (Melekhina and Biazrov, 1997). It can be concluded that representatives of the genus *Phauloppia* are typical of epiphytes in different regions; the species *P. nemoralis* and *P. lucorum* are ecologically vicariating.

Vicariating species include species of the genus *Mycobates*: *M. parmeliae* (Michael, 1884) and *M. tri-dactylus* Willmann, 1929. In our collections, *M. tri-dactylus* was characteristic of epiphytes. In sources, *M. parmeliae* is most often mentioned as an inhabitant of lichens. Sellnick (1949) indicated that this species prefers lichens as a habitat. *M. parmeliae* individuals were found in the lichen cover of park trees in Germany (Pschorn-Walcher and Gunhold, 1957) and in lichens of five species growing on the coastal cliffs of the Scottish Islands (Coloff, 1983).

The species of the family Carabodidae were numerous in the bushy epiphytes of southern Belgium (Andre, 1979). In different regions, various species of the genus *Carabodes* were associated with lichens as habitats. They numerically dominated in epiphytes (*Hypogymnia physodes*, *Cladonia coniocraea*) on different tree species in spruce–deciduous forests of Moscow oblast (Biazrov et al., 1971; Biazrov, 1988; Melekhina and Biazrov, 1997). In our collections, *C. labyrinthicus* was a characteristic inhabitant of epiphytes. This species was characterized by a high abundance in epiphytic lichens in Southern Belgium (Andre, 1975, 1979, 1984, 1985) and other regions. In the zone of coniferous–deciduous forests, *C. marginatus* and *C. subarcticus* were characteristic of epiphytes along with *C. labyrinthicus* (Melekhina and Biazrov, 1997). The dominant groups in the epiphytic lichens of Abkhazia included the species *C. rugosior* Berlese, 1916 (referred to as *C. femoralis*) (Tarba, 1992). Thus, the row of species *C. labyrinthicus*–*C. marginatus*–*C. rugosior*–*C. subarcticus* is an example of an ecological vicariate.

Ecological vicariates include species of the genus *Oribatula* (*Zygoribatula*): *O. (Z.) propinqua* and *O. (Z.) exilis*. The species *O. (Z.) propinqua* belonged to the number of dominants in epiphytes in our collections; it was found in this type of habitat by other authors (Niedbala, 1970; Shtanchaeva, 1997). In epiphytes, another species of this genus was repeatedly noted, *O. (Z.) exilis* (Pschorn-Walcher and Gunhold, 1957; Biazrov et al., 1971; Tarba, 1992; Melekhina and Krivolutsky, 1992; Melekhina and Biazrov, 1997).

CONCLUSIONS

The complexes of the species of oribatid mites associated with ground and epiphytic lichens in the taiga forests of northeastern Europe are determined. Relative to the series of habitats investigated, five ecological groups of oribatid mites, characteristic of lichens and two groups of soil inhabitants proper were identified. Two groups—dominant arboricolous and not numerous arboricolous—reflect the specificity of the species composition of oribatids in epiphytic lichens. These include species observed exclusively or mainly in epiphytes; in ground lichens, as a rule, they are not found. The groups of hemiedaphic dominants and hemiedaphic not numerous species that were charac-

teristic of ground lichens. One group of arboreal–hemidaphnic species was composed of species inhabiting in both ground and epiphytic lichens. Species that were found only in soil and were not noted in lichens are divided into the groups of epiedaphic and euedaphic.

It has been established that the taxonomic composition of the complexes of oribatids associated with lichens (ecological groups, zoosociological classes, and synusias distinguished by different authors) differs in different nature-climatic conditions. At the same time, species characteristic of lichens, were identified, that determine the similarity of the species composition of oribatid mites in this type of habitat in different regions of the Northern Palaearctic. Thus, the specific features of the oribatid population in epiphytes are species such as *Carabodes labyrinthicus*, *Cymbaeremaeus cymba*, *Oribatula (Z.) propinqua*, and *Micreremus brevipes* and species of the genus *Mycobates*, among others. Common species of soil lichens in different regions are *Carabodes marginatus*, *C. subarcticus*, and *Trhypochthonius cladonicolus*. In both ground and epiphytic lichens, *Oribatula (Z.) exilis*, *Euere-maeus oblongus silvestris*, *Trichoribates berlesei*, *Schel-ribates laevigatus*, and others are found. Families such as Carabodidae, Oribatulidae, Puncatoribatidae, Cymbaeremaeidae, and Ceratozetidae are quite common in groupings of oribatid mites in lichens.

A comparison of the results obtained with the published data made it possible to identify examples of the ecological vicariate of the oribatid species in epiphytic lichens as habitats. Representatives of the genera *Phauloppia (P. nemoralis, P. lucorum)*, *Mycobates (M. parmeliae, M. tridactylus)*, *Carabodes (C. labyrinthicus, C. marginatus, C. rugosior, C. subarcticus)*, and *Oribatula (Zygoribatula) (O. (Z.) propinqua, O. (Z.) exilis)* can be considered vicariating. Consequently, lichens as habitats are characterized by a certain complex of species of oribatid mites. The most specific is the population of epiphytic lichens.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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