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Springtails (Collembola) in the Subpolar Landscapes of the Northern Hemisphere

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Abstract—An overview of previously published and new information on the collembolan fauna and assemblage structure in the polar desert zone is presented. So far, 71 springtail species from 37 genera and 11 families have been reliably recorded within the zone. Eleven species are added to the previously known fauna of Franz Josef Land, and the very north of Novaya Zemlya has been surveyed for the first time. Even the much better known fauna of Bolshevik Island, Severnaya Zemlya is enriched by 3 species. The known species richness of springtails of Ellef Ringnes Island, Canadian Arctic Archipelago, is also increased from 8 to 13 species. Most genera except *Folsomia* and *Hypogastrura* include only 1, more rarely 2 species in each study region of the polar desert zone. Species with circumpolar distribution patterns comprise more than 60% of the total list, but only 10 species are common to all the three provinces; this obviously indicates a certain regional specificity. Besides, the faunas of different provinces (and regions within a province) vary markedly in the proportion of species with more southern distribution patterns. Nevertheless, the collembolan assemblages in all the three provinces of the polar desert zone are rather similar at the structural level, this being a direct consequence of the general depletion of the complexes against the background of high total abundance and less pronounced habitat specificity of the common species.

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The polar desert zone occupies the marginal position on the global climate gradient. Within the limits considered herein (Fig. 1), this natural zone occupies a fairly restricted territory and is represented almost exclusively on islands of the Arctic Ocean (Sochava and Gorodkov, 1956; Aleksandrova, 1971, 1983; Chernov et al., 2011; Matveyeva et al., 2015); it approximately corresponds to subzone *A* in the *Circumpolar Arctic Vegetation Map* (CAVM Team, 2003). The only mainland area where polar desert communities occur is the north of the Taimyr Peninsula (Matveyeva and Chernov, 1976; Chernov and Matveyeva, 1979). Nearly all the studied taxa are strongly impoverished in these high-latitude landscapes. However, faunistic and floristic impoverishment is the principal but not the sole distinctive feature of polar deserts. Also unique is the structure of the polar desert communities that exist at the very limits of habitability. Such communities are generally believed to have many specific traits in their taxonomic composition, spatial structure, succession dynamics, and energy and trophic relations, and to drastically differ in these aspects from the cenoses of the tundra zone (Chernov, 1978; Chernov et al., 1979, 2011; Chernov and Matveyeva, 1979; Makarova, 2002a, 2002b; Matveyeva et al., 2015).

The presence of springtails on the Arctic Ocean islands became known as early as the beginning of the past century (Carpenter, 1900). However, even the collembolan faunas of three geobotanical provinces of the polar desert zone (Aleksandrova, 1983; Matveyeva et al., 2015) have been only sketchily studied, and their known composition is evidently far from complete. There are practically no published data on the structure of collembolan assemblages in polar deserts, except for two Russian papers that appeared in the late 1980s (Chernov et al., 1977, 1979) and one more recent work (Babenko, 2000). Within the Barents Province, the only territory where the collembolan fauna is sufficiently well studied is Nordaustlandet (Summerhayes and Elton, 1928; Fjellberg, 1997; Coulson et al., 2011), the northernmost large island of the Svalbard Archipelago. There is also somewhat outdated information on the composition of the collembolan fauna of Franz Josef Land (Carpenter, 1900; Bulavintsev and Babenko, 1983). No faunistic data are available for the north of Novaya Zemlya.

Springtails in the polar deserts of the Siberian Province are only slightly better studied. Besides the clearly outdated material obtained in the Cape Chelyuskin area on the Taimyr Peninsula (Linnaniemi,

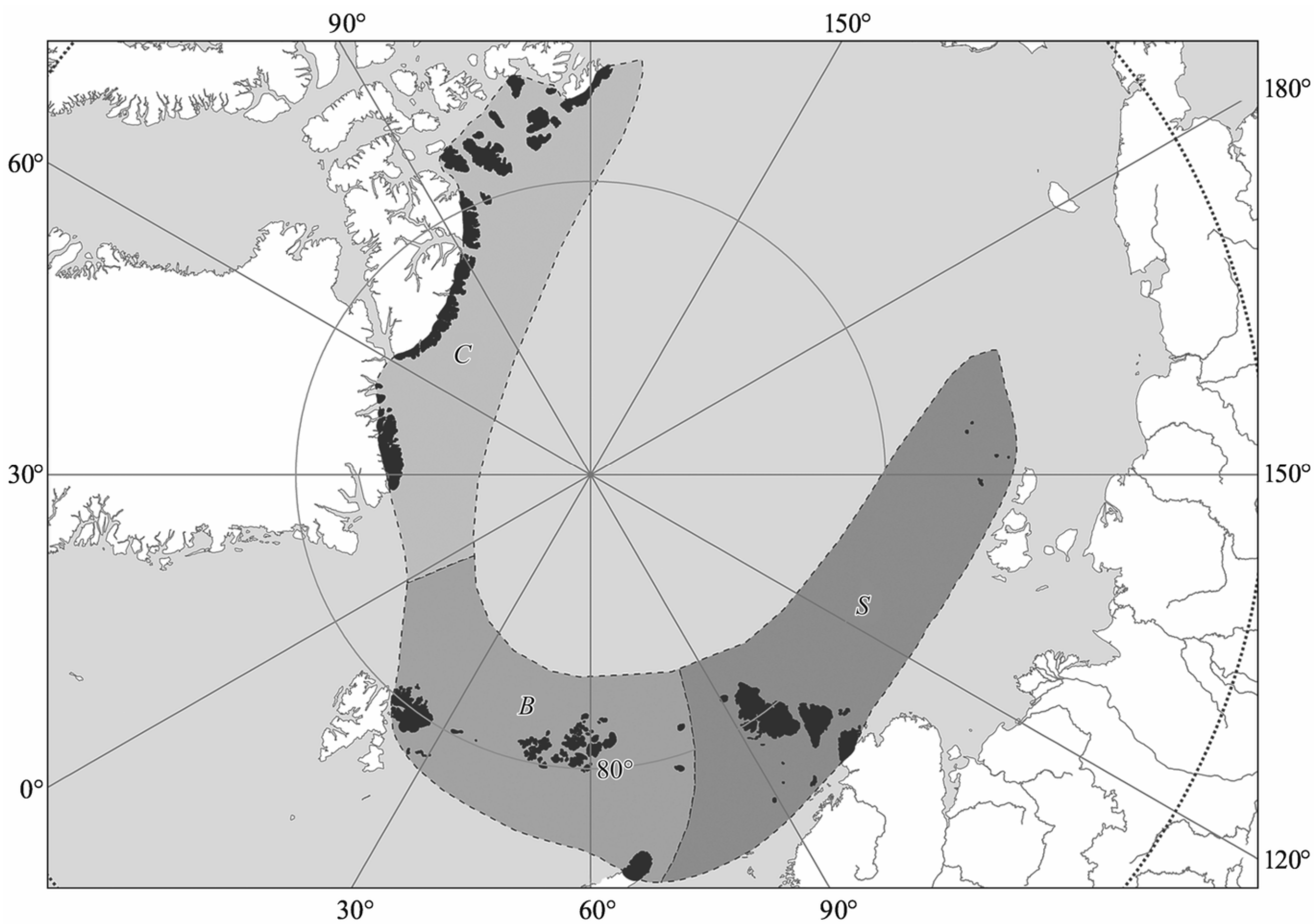

Fig. 1. Polar deserts in the Northern Hemisphere (after Matveyeva et al., 2015). Geobotanical provinces: *B*, Barents; *C*, Canadian; *S*, Siberian.

1933; Chernov et al., 1977, 1979), the results of V.I. Bulavintsev's collections on the Severnaya Zemlya Archipelago were published (Bulavintsev and Babenko, 1989). These data were later summarized in a special paper (Babenko and Bulavintsev, 1997), which also included the results of my short visit to Cape Chelyuskin in 1994. Besides, the results of O.L. Makarova's collections made in 1997 in the Solnechnaya Bay area in the south of Bolshevik Island were also partly published (Babenko, 2000).

Within the polar desert part of the Canadian Arctic Archipelago, springtails were studied only on two of the Queen Elizabeth Islands: Ellef Ringnes (McAlpine, 1964, 1965) and King Christian (Addison, 1980); these findings were covered in a special review (Fjellberg, 1986). The recently revised (Fjellberg, 2015) material from Peary Land in Greenland (Hammer, 1954) was collected quite far to the south of Frederick E. Hyde Fjord, i.e., outside the polar desert zone as defined above, and these data are not considered here.

Since the mid-1990s, I have accumulated a sufficient amount of material collected by my colleagues on various islands of the Arctic Ocean. This material allows me to considerably supplement or clarify the composition of the regional faunas of all the three provinces, which is the main goal of this paper. Besides, the new data clearly have not only faunistic but also ecological significance and can be used in comparative analysis of the collembolan population of different polar desert regions. Correspondingly, analysis of the structure of the soil assemblages of Collembola makes up an equally important part of this research.

MATERIALS AND METHODS

This work is based on the following unpublished material:

Franz Josef Land: Northbrook (Cape Flora), Alger, Heiss, Hall (Cape Tegethoff), and Prince George Land (Cape Crowther) islands, manual collection, August 2012, M. Gavrilo; Hooker (Tikhaya Bay) and Northbrook (Cape Flora) islands, soil samples and manual collection, July 2015, A. Babenko; Northbrook Island (Cape Flora), soil samples and traps, July 2016, A. Semikolennykh; Hooker and Salm islands, soil traps and manual collection, August 2016, A. Krasheninnikov.

Novaya Zemlya Archipelago: Russkaya Gavan Bay, Cape Zhelaniya, Oranskiye Islands, soil samples and manual collection, July 2015, A. Babenko; Cape Zhelaniya and Oranskiye Islands, traps and manual collection, August 2016, A. Krasheninnikov.

Severnaya Zemlya Archipelago: Bolshevik Island (southern part), soil samples and traps, July–August 1997–1998, 2000, O. Makarova.

Canadian Arctic Archipelago: Ellef Ringnes Island, Isachsen Bay, soil samples and traps, July 2005, O. Makarova.

Data were statistically processed in the PAST software (Hammer et al., 2001), using cluster analysis and non-metric MDS tools, and also standard indices of faunistic similarity (*Jaccard* and *Dice*) and rank correlation (*Rho*). The species that contributed most to differentiation between the faunas of different regions were revealed using the SIMPER option and the quantitative Bray-Curtis index BC_{ji} based on log-normalized [ln $(x + 1)$] primary data.

RESULTS

The fauna. So far, 71 species of Collembola from 37 genera and 11 families have been reliably recorded within three geobotanical provinces of the polar desert zone (Table 1); this number comprises approximately one-sixth of the known fauna of the treeless northern territories.

The material from Franz Josef Land revealed 11 species of Collembola which had not been previously recorded for this archipelago: *Anurida alpina*, *Friesea quinquespinosa*, *Hypogastrura serrata*, *Desoria neglecta*, *D. violacea*, *Folsomia coeruleogrisea*, *F. longidens*, *F. palaearctica*, *F. quadrioculata*, *Isotomodella alticola*, and *Sminthurides malmgreni*. Of these, the least expected was the finding of *H. serrata* (sensu Fjellberg, 1998, i.e., considering this species a senior synonym of *H. ripperi* Gisin, 1952), represented by not only adults but also juveniles, in the material from the seabird colony of Northbrook Island. To the best of my knowledge, this widespread compost-dwelling species was never before recorded at such high latitudes; its nearest known localities lie in Sweden, Iceland, and the Faroe Islands (Fjellberg, 1998).

The northern part of the Novaya Zemlya Archipelago was studied for the first time. This "southernmost region of the polar desert zone" (Matveyeva et al., 2015, p. 17) quite naturally revealed a number of springtail species with comparatively southern ranges, such as *Protaphorura pjasinae*, *Parisotoma notabilis*, *Pseudisotoma sensibilis*, and *Tetracanthella wahlgreni*. Some of these species were abundant.

The known fauna of the Severnaya Zemlya Archipelago was supplemented with only three new records (*Podura aquatica*, *Ballistura wrangeliensis*, and *Heterosminthurus putoranae*), all of them represented by single specimens. The presence of six more relatively rare species (*P. pjasinae*, *Willemia scandinavica*, *W. similis*, *A. alpina*, *F. coeruleogrisea*, and *I. alticola*) was noted earlier (Babenko, 2000). All these forms are typical of more southern regions, and on Severnaya Zemlya they together comprised no more than several percent of the total abundance even in the warmest habitats.

The known diversity of the collembolan fauna of Ellef Ringnes Island (Canadian Arctic Archipelago) was increased from 8 to 13 species. The species identity of representatives of 3 genera (*Anurida*, *Willemia*, and *Vertagopus*) was clarified, and 3 previously unrecorded species (*F. bisetosa*, *F. quadrioculata*, and *Megalothorax* sp.) were found on the island.

Species with circumpolar ranges, i.e., cosmopolitan and trans-Holarctic ones, comprised over 60% of the total list. However, only 10 species occurred in all the three provinces: *Oligaphorura groenlandica*, *H. concolor*, *H. sensilis*, *W. scandinavica*, *W. similis*, *A. polaris*, *Agrenia bidenticulata*, *F. quadrioculata*, *Vertagopus arcticus*, and *V. brevicaudus*. Besides, representatives of the genus *Megalothorax* whose species identity remains to be clarified were also recorded in all the studied regions except Franz Josef Land. Not all the species widely distributed in the polar deserts are common or abundant. For example, both species of the genus *Willemia* are restricted to the warmest communities within each region. *Folsomia quadrioculata* is common on Nordaustlandet Island of the Svalbard Archipelago (Fjellberg, 1997) and in the north of Novaya Zemlya but it is not the most abundant representative of the genus in other regions. Only one mature

Table 1. Species of Collembola recorded in the polar desert zone of the Northern Hemisphere

Species	Barents Province			Siberian Province		Canadian Province	
	Nordaustlandet [a]	Franz Josef Land [b]	Novaya Zemlya [c]	Severnaya Zemlya [d]	Cape Chelyuskin [e]	Ellef Ringnes Island [f]	King Christian Island [g]
Podura aquatica Linnaeus, 1758	–	–	–	+	–	–	–
Tullbergia simplex Gisin, 1958	+	–	–	–	–	–	–
Mesaphorura macrochaeta Rusek, 1974	+	+ [1]	–	–	–	–	–
Oligaphorura groenlandica (Tullberg, 1876)	+	+	+	+	+	+	+
O. ursi (Fjellberg, 1984)	+	–	+	–	–	–	–
Hymenaphorura anatolii Pomorski, 2001	–	–	–	+ [2]	–	–	–
H. sibirica (Tullberg, 1876)	–	–	+	–	–	–	–
Protaphorura pjasinae (Martynova, 1976)	–	–	+	+	+	–	–
P. subarctica (Martynova, 1976)	–	–	+	–	–	–	–
P. taimyrica (Martynova, 1976)	–	–	–	+ [3]	–	–	–
Supraphorura furcifera (Börner, 1901)	–	–	+	–	–	–	–
Megaphorura arctica (Tullberg, 1876)	+	–	–	–	–	–	–
Thalassaphorura duplopunctata (Strenzke, 1954)	+	–	+	–	–	–	–
Hypogastrura concolor (Carpenter, 1900)	+	+	+	+	–	+	–
H. humi (Folsom, 1916) [4]	–	–	–	–	–	?	–
H. fjellbergi Babenko et Bulavintsev, 1993	–	–	–	+	–	–	–
H. sensilis (Folsom, 1919)	+	+	+	+	+ [5]	+ [6]	+
H. serrata (Ågren, 1904)	–	+	–	–	–	–	–
H. tullbergi (Schäffer, 1900)	+	+	+	+	+	–	–
H. trybomi (Schött, 1893)	–	+	–	+	+	–	–
H. viatica (Tullberg, 1872)	+	–	+	–	–	–	–
Ceratophysella longispina (Tullberg, 1876)	+	+	+	+	+	–	–
C. palustris Martynova, 1978	–	–	+	–	–	–	–
Bonetogastrura nivalis (Martynova, 1973)	+	+	+	+	+	–	–
Willemia anophthalma Börner, 1901	+	–	–	–	–	–	–
W. scandinavica Stach, 1949	+	+	+	+	+	+ [7]	–
W. similis Mills, 1934	+	–	–	+	–	+	–
Xenylla humicola (Fabricius, 1780)	+	–	+	–	–	–	–
Anurida alpina Agrell, 1939	–	+	+	+	–	–	–
A. maritima (Guérin, 1836)	+	–	–	–	–	–	–

Table 1. (Contd.)

Species	Barents Province			Siberian Province		Canadian Province	
	Nordaust-landet [a]	Franz Josef Land [b]	Novaya Zemlya [c]	Severnaya Zemlya [d]	Cape Chelyuskin [e]	Ellef Ringnes Island [f]	King Christian Island [g]
A. polaris (Hammer, 1954)	+	+	+	+	+	+ [8]	–
Friesea mirabilis (Tullberg, 1871)	–	–	–	+	–	–	–
F. quinquespinosa Wahlgren, 1900	+	+	+	–	–	–	–
Micranurida pygmaea Börner, 1901	+	–	–	–	–	–	–
Xenyllodes armatus Axelson, 1903	+	–	–	–	–	–	–
Agrenia bidenticulata (Tullberg, 1876)	+	+	+	+	+	+	–
Archisotoma besselsi (Packard, 1877)	+	–	+	–	–	–	–
A. polaris Fjellberg et Poinsot, 1975	+	–	–	–	–	–	–
Ballistura wrangeliensis Martynova, 1973	–	–	–	+	+	–	–
Desoria neglecta (Schäffer, 1900)	+	+	+	–	–	–	–
D. olivacea (Tullberg, 1871)	? [9]	–	–	–	–	–	–
D. tshernovi (Martynova, 1974)	+	+	–	+	+	–	–
D. violacea (Tullberg, 1876)	–	+	+	–	–	–	–
Folsomia cf. *altamontana* Yosii, 1971	–	–	–	+ [10]	–	–	–
F. amplissima Potapov et Babenko, 2000	–	–	–	+ [11]	–	–	–
F. binoculata (Wahlgren, 1899), form a	+ [12]	+ [13]	+	+ [13]	+	–	–
F. binoculata (Wahlgren, 1899), form b	–	+	+	+	+	–	–
F. bisetosa Gisin, 1953	+	–	–	–	–	+	–
F. coeruleogrisea (Hammer, 1938) [14]	+	+	–	+	–	–	–
F. longidens Potapov et Babenko, 2000	–	+	–	–	–	–	–
F. microchaeta Agrell, 1939	–	–	+	–	–	–	–
F. palaearctica Potapov et Babenko, 2000	–	+	–	–	–	–	–
F. quadrioculata (Tullberg, 1871)	+	+	+	+	–	+	–
F. regularis Hammer, 1953	–	–	–	–	–	+	+
F. sexoculata (Tullberg, 1871)	+	–	+	–	–	–	–
F. taimyrica Martynova, 1973	+	+	+	+	+	–	–
Isotoma anglicana Lubbock, 1862	+	–	–	–	–	–	–
I. sp. aff. *variodentata* Dunger, 1982	–	–	+	+ [15]	+ [16]	–	–
Isotomodella alticola (Bagnall, 1949)	+	+	–	+	–	–	–
Isotomurus chaos Potapov et Babenko, 2011	–	–	–	+ [17]	–	–	–

Table 1. (Contd.)

Species	Barents Province			Siberian Province		Canadian Province	
	Nordaust-landet [a]	Franz Josef Land [b]	Novaya Zemlya [c]	Severnaya Zemlya [d]	Cape Chelyuskin [e]	Ellef Ringnes Island [f]	King Christian Island [g]
Parisotoma notabilis (Schäffer, 1876)	–	+ [18]	+	–	–	–	–
Pseudisotoma sensibilis (Tullberg, 1876)	–	–	+	–	–	–	–
Scutisotoma subarctica (Gisin, 1950)	–	–	+	–	–	–	–
Tetracanthella wahlgreni Axelson, 1907	–	–	+	–	–	–	–
Vertagopus arcticus Martynova, 1969	+	–	–	+ [19]	+	+ [20]	–
V. brevicaudus (Carpenter, 1900)	–	+	–	+	+	+	+
Corynothrix borealis Tullberg, 1876	–	–	–	+	+	–	–
Lepidocyrtus lignorum (Fabricius, 1793)	+	–	–	–	–	–	–
Megalothorax sp. gr. *minimus* Willem, 1901 [21]	+	–	+	+	+	+	+
Sminthurides armatus Bretfeld, 2000 [22]		–	–	+	–	–	–
S. malmgreni (Tullberg, 1876)	+	+	+	–	–	–	–
Sminthurinus concolor (Meinert, 1896)	+	–	–	–	–	–	–
Heterosminthurus putoranae Bretfeld, 2000	–	–	–	+	–	–	–
Total number of species (forms)	39	27	36	36	20	13	5

[a] Summerhayer and Elton, 1928; Fjellberg, 1997; Coulson et al., 2011.

[b] Hooker, Graham Bell, Alexandra Land, Rudolf, Northbrook, Alger, Heiss, Hall, Salm, and Prince George Land islands: Carpenter, 1900; Bulavintsev and Babenko, 1983; Babenko and Bulavintsev, 1997; M. Gavrilo (collections of 2012), A. Babenko (collections of 2015); A. Semikolennykh (collections of 2016); A. Krasheninnikov (collections of 2016).

[c] Russkaya Gavan Bay, Cape Zhelaniya; Oranskiye Islands: A. Babenko (collections of 2015); A. Krasheninnikov (collections of 2016).

[d] Bolshevik, October Revolution, and Komsomolets islands: Bulavintsev and Babenko, 1989; Babenko and Bulavintsev, 1997; Babenko, 2000; O. Makarova (collections of 1997–1998, 2000).

[e] Linnaniemi, 1933; Chernov et al., 1977, 1979; Babenko and Bulavintsev, 1997.

[f] McAlpine, 1964, 1965; Fjellberg, 1986; O. Makarova (collections of 2005).

[g] Addison, 1980; Fjellberg, 1986.

[1] The species was recorded on Franz Josef Land (Bulavintsev and Babenko, 1983, as *M. krausbaueri* Börner, 1901) based on a single specimen from Graham Bell Island. This specimen still exists; it is in fact a juvenile of *M. macrochaeta*.

[2] Recorded on Bolshevik Island (Severnaya Zemlya) as *H. sibirica* (Babenko and Bulavintsev, 1997).

[3] Earlier recorded as *P.* cf. *cancellata* (Gisin, 1956) (Babenko and Bulavintsev, 1997).

[4] The record of this species on the Canadian Arctic Archipelago (McAlpine, 1964, 1965) is doubtful. According to O. Makarova's material, the most common similar species present on Ellef Ringnes Island is *H. concolor*.

[5] This species was apparently recorded on Cape Chelyuskin (Linnaniemi, 1933) as *H. viatica*.

[6] This species was probably recorded on Ellef Ringnes Island (McAlpine, 1964, 1965) as *H.* sp. nr. *trybomi* (see Fjellberg, 1986).

[7] Both species of this genus found on Ellef Ringnes Island may have been recorded (McAlpine, 1964, 1965) as *W.* sp. nr. *anophthalma*.

[8] Recorded (McAlpine, 1964, 1965) as *A*. sp. prob. *granaria*.

[9] There is only one old record of the species from this region (Summerhayer and Elton, 1928), which evidently needs to be confirmed, considering the radical changes in the group's taxonomy.

[10] Recorded on the archipelago (Babenko and Bulavintsev, 1997) as *F*. sp. gr. *sexoculata*.

[11] Originally recorded (Babenko and Bulavintsev, 1997) as *F*. sp. gr. *taimyrica*.

[12] Originally recorded (Fjellberg, 1997) as *F. regularis*.

[13] Both color forms of this species were recorded as *F. regularis* (Babenko and Bulavintsev, 1997); their status remains obscure.

[14] In my opinion, the status of this species still needs to be clarified. It was recorded on the High Arctic islands as *F. gracilis* (Stach, 1962) (Fjellberg, 1984), *F. alpha* Grow et Christiansen, 1976 (Fjellberg, 1986, 1997; Babenko and Bulavintsev, 1997; Babenko, 2000), and *F. janstachi* Potapov et Babenko, 2000. Later (Fjellberg, 2007) these three forms were synonymized, though the problem will probably be solved only by the modern molecular methods.

[15] Recorded as *Isotoma* sp. (Babenko and Bulavintsev, 1997).

[16] This species was most probably identified by Linnaniemi (1933) as *I. viridis* var. *riparia* based on a single damaged specimen from Cape Chelyuskin.

[17] Recorded as *I. plumosus* Bagnall, 1940 (Babenko and Bulavintsev, 1997).

[18] This record (Bulavintsev and Babenko, 1983: as *Isotoma notabilis*; Bulavintsev and Babenko, 1989: as *I.* (*Parisotoma*) sp.) was based on a single specimen from Graham Bell Island. Its identification cannot be confirmed; the slide appears to be missing.

[19] Earlier recorded (Babenko and Bulavintsev, 1997) as *V. pallidus* Martynova, 1974.

[20] The record of *Isotoma violacea* Tullberg (McAlpine, 1964, 1965) from Ellef Ringnes Island most probably refers to any of the two *Vertagopus* species. No representatives of the genus *Desoria* were found in the recent material from the same locality.

[21] It was earlier assumed that only one cosmopolitan species of this genus, namely *M. minimus*, occurred in the northern regions. However, the recent revision (Schneider and D'Haese, 2013) showed this assumption to be false. The most common but probably not the only representative of the genus occurring in most of the polar desert regions (north of Novaya Zemlya, Bolshevik Island in the Severnaya Zemlya Archipelago, and Ellef Ringnes Island in the Canadian Arctic Archipelago) is an undescribed species characterized by the absence of seta *X* on *Ant*.4 and the presence of two sublobal hairs on the outer lobe of the maxilla (= *Megalothorax* sp. 1 sensu Babenko et al., 2017).

[22] Examination of the preserved slide showed that this species was earlier mistakenly recorded from Severnaya Zemlya as *Jeannenotia stachi* (Jeannenot, 1955) (Bulavintsev and Babenko, 1989; Babenko and Bulavintsev, 1997; Babenko, 2000). In the latter publication the species was listed twice, as *J. stachi* and as *Stenacidia* sp. Its record for Franz Josef Land (Bulavintsev and Babenko, 1989, table 1) was a printing error.

Table 2. Relative abundance (%) of different species of Collembola and integral parameters of their assemblages in the principal plant associations of Bolshevik Island, Severnaya Zemlya (collections of 1997–1998, 2000, O. Makarova)

Species	Nival and hydromorphic associations			Zonal associations				Relatively dry and warm intrazonal associations			Zoogenic assemblages	
				Deschampsio–Aulacomnietum turgidi		*Stellario edwardsii–Hylocomietum alaskani*						
	snow field near spring	spring side	bog, *Scapanio–Dupontietum fisheri*	regular cyclical (polygonal) type	sporadically spotted (clumpy) type	*typicum* with *Carex ensifolia* subsp. *arctisibirica*	*saxifragetosum cespitosae*	*Dryas punctata–Hylocomium splendens* var. *alaskanum*	*Gymnomitrio corallioidis–Racomitrietum lanuginosi*	poppy "meadow," *Saxifraga platisepala–Poa abbreviata*	lemming colonies	owl feeding place
F. binoculata form b	**64.1**	**6.3**	**68.8**	**59.1**	**64.0**	**73.5**	3.2	**24.6**	**46.2**	**42.9**	**46.9**	**15.6**
V. arcticus	**5.8**	1.1	**23.1**	**8.0**	**7.0**	**12.5**	**11.6**	**13.5**	**28.4**	**13.2**	**6.8**	**4.5**
H. tullbergi	0.02	0.1	1.7	3.2	**5.6**	1.1	**63.5**	**46.0**	**9.8**	**13.9**	3.6	0.2
F. taimyrica	**20.2**	0.3		**16.0**	**9.8**	2.9	1.6	1.4	3.0	**21.2**	**17.1**	1.8
A. bidenticulata	1.6	**88.6**	0.4	0.6	0.9	0.1	0.1	–	0.03	0.7	0.6	0.004
O. groenlandica	1.9	0.1	3.1	2.9	**5.8**	3.0	**7.3**	–	2.7	0.7	**16.8**	0.7
V. brevicaudus	1.3	0.3	0.2	3.7	3.6	0.4	0.2	–	0.7	**5.1**	0.2	–
A. polaris	0.5	–	0.1	1.1	0.4	–	0.5	–	2.7	0.5	1.9	0.03
H. trybomi	0.9	0.8	0.5	0.6	1.1	0.2	0.5	–	–	0.6	0.1	–
C. longispina	1.9	1.2	0.8	2.4	0.5	0.03	–	–	–	0.9	0.3	–
F. binoculata form a	0.6	0.1	–	1.8	0.5	2.0	–	–	0.5	–	0.9	–
B. nivalis	0.2	0.1	–	–	0.1	–	–	0.3	2.7	–	0.7	1.3
H. sensilis	1.0	1.0	0.4	0.7	0.8	–	–	–	–	–	–	–
M. sp. gr. *minimus*	–	–	–	–	–	**3.9**	**11.4**	1.2	1.8	–	0.2	–
C. borealis	–	–	–	–	–	–	–	**4.0**	0.03	0.01	0.01	0.02
A. alpina	–	–	–	–	–	0.5	–	0.3	0.1	0.1	–	0.004
W. similis	–	–	–	–	–	–	–	1.3	0.1	–	0.1	–
H. concolor	–	–	–	–	–	–	–	–	–	–	3.7	**75.6**

Table 2. (Contd.)

Species	Nival and hydromorphic associations			Zonal associations				Relatively dry and warm intrazonal associations			Zoogenic assemblages	
				Deschampsio–Aulacomnietum turgidi		*Stellario edwardsii–Hylocomietum alaskani*						
	snow field near spring	spring side	bog, *Scapanio–Dupontietum fisheri*	regular cyclical (polygonal) type	sporadically spotted (clumpy) type	*typicum with Carex ensifolia* subsp. *arctisibirica*	*saxifragetosum cespitosae*	*Dryas punctata–Hylocomium splendens* var. *alaskanum*	*Gymnomitrio corallioidis–Racomitrietum lanuginosi*	poppy "meadow," *Saxifraga platisepala–Poa abbreviata*	lemming colonies	owl feeding place
F. cf. *altamontana*	–	–	–	–	–	–	–	**6.5**	–	0.1	–	–
I. alticola	–	–	–	–	–	–	–	–	1.2	–	0.1	–
F. coeruleogrisea	–	–	–	–	–	–	–	–	–	–	0.2	0.4
D. tshernovi	–	–	0.9	–	–	–	–	–	–	–	–	–
P. taimyrica	–	–	–	–	–	–	–	0.7	–	–	–	–
I. cf. *variodentata*	–	–	–	–	–	–	–	0.2	–	–	–	–
S. armatus	–	–	–	–	–	0.1	–	–	–	–	–	–
P. pjasinae	–	–	–	–	–	–	–	–	–	–	0.04	–
W. scandinavica	–	–	–	–	–	–	–	–	–	–	0.01	–
Total number of ind.	4312	9626	3091	6716	9135	3123	1658	1260	3457	7222	6929	25868
Number of samples	11	7	9	15	15	5	10	10	10	10	10	6
Total number of species	13	12	11	12	13	13	10	12	15	13	20	12
Mean number of species per sample ($M \pm SD$)	7.5 ± 1.9	8.7 ± 1.1	6.6 ± 1.1	9.7 ± 1.0	10.6 ± 1.5	8.2 ± 1.5	6.1 ± 1.7	6.4 ± 2.2	7.0 ± 1.6	9.2 ± 1.5	8.6 ± 2.2	6.3 ± 2.4
Median	8	9	7	10	10	8	6.5	6	7.5	9.5	8.5	6
Mean density, ind./dm^2 ($M \pm SD$)	1568.0 ± 1270.6	5500.6 ± 8808.8	1373.3 ± 1518.7	1913.4 ± 1866.5	2794.8 ± 1936.6	2498.4 ± 2880.2	663.2 ± 381.9	560.0 ± 409.3	1382.8 ± 787.7	2888.8 ± 1764.8	2721.2 ± 1995.4	11059.0 ± 9741. 9
Median	1440	668	712	982	2580	1180	626	436	1464	2578	2394	9241

Here and in Tables 4–7, the relative abundance values exceeding the arbitrary subdominance threshold (3.9%) are shown in bold.

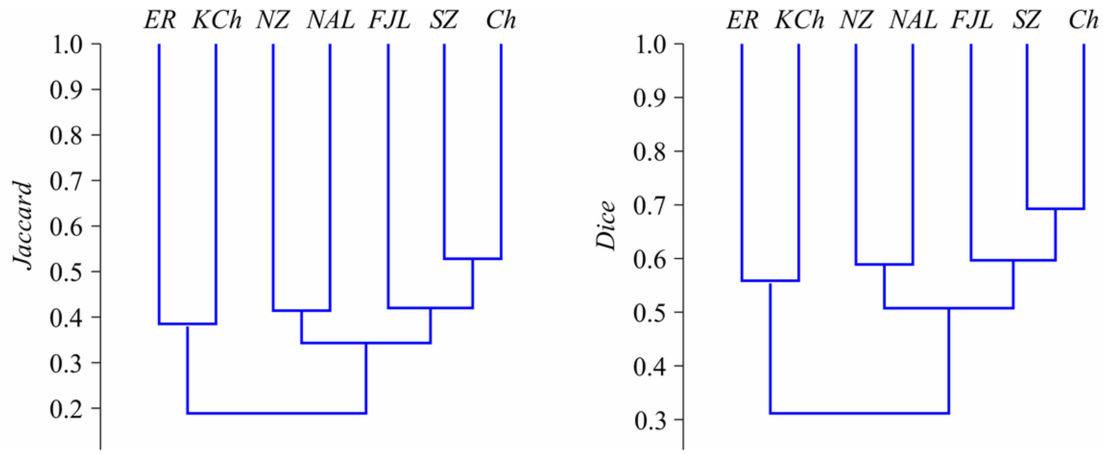

Fig. 2. Cluster analysis of similarity of the collembolan faunas of different regions within the polar desert zone (PAST software, *Jaccard* and *Dice* indices): *NAL*, Nordaustlandet; *FJL*, Franz Josef Land; *NZ*, Novaya Zemlya; *SZ*, Severnaya Zemlya; *Ch*, Cape Chelyuskin; *ER*, Ellef Ringnes Island; *KCh*, King Christian Island.

specimen was found in the available material from Franz Josef Land. This species was also absent in quantitative samples from the south of Bolshevik Island, though single specimens occurred in V.I. Bulavintsev's collections from all the three large islands of this archipelago. Within the Canadian Province, the species was recorded on Ellef Ringnes Island only in grass-forb habitats on south-facing slopes. The rest of the above species are quite common in the polar desert regions but rarely reach the dominant status in the principal habitats.

The fauna of the Barents Province is noticeably more diverse, with no less than 58 species. Besides, it comprises the greatest number (33) of forms which have not yet been recorded in other provinces. Strangely enough, among them there are almost no species with European (or amphi-Atlantic) ranges, except *Megaphorura arctica*, *Isotoma anglicana*, and possibly *Sminthurinus concolor* (see Babenko, 2017). Most of the species recorded only in the Barents Province are either widespread forms largely inhabiting the tundra zone or even more southern territories, or forms with mostly Siberian and Sibero-American ranges whose western boundaries lie in northeastern Europe. The latter group includes, in particular, such species as *Hymenaphorura sibirica*, *P. subarctica*, *C. palustris*, *D. violacea*, *F. longidens*, and *F. palaearctica*, none of which has yet been found in the polar deserts of the Siberian Province.

The known fauna of the Siberian Province is almost half as diverse, with only 36 species. It should be noted that only the south of Severnaya Zemlya has been more or less adequately studied. The available material from the east of the province, i.e., islands of the De Long group (Zhokhov Island, V.I. Bulavintsev's collections), is too fragmentary to produce a realistic picture of the soil complexes of Collembola. For the time being, it may be noted that, apart from the dominant forms typical of polar deserts, the collembolan fauna of the zonal habitats of Zhokhov Island also includes abundant species with more southern ranges, such as *F. quadrioculata*. Only 12 species are restricted to this province; most of them, namely *P. aquatica*, *H. anatolii*, *P. taimyrica*, *H. fjellbergi*, *F. mirabilis*, *B. wrangeliensis*, *F. amplissima*, *Isotomurus chaos*, *Sminthurides armatus*, and *H. putoranae*, occur only in specific assemblages and are represented there by single specimens. According to the available material, only *F.* cf. *altamontana* and *Corynothrix borealis* may reach the subdominance level (> 3.9%) in the relatively dry and warm intrazonal associations of Bolshevik Island (see Table 2).

The known collembolan fauna of the Canadian Province is the least diverse: it comprises only 13 species, not counting *H. humi* (see note 4 to Table 1). Such low diversity does not seem to result from some specific features of this province but merely reflects a very insufficient knowledge of the regional fauna. One species, *F. regularis*, is absent in the other provinces of the polar desert zone, being replaced there by a very close Palaearctic form *F. binoculata*.

On the whole, the faunas of the three provinces were found to be similar but not at all identical. Of the total list, 31 species (over 40%) were recorded only

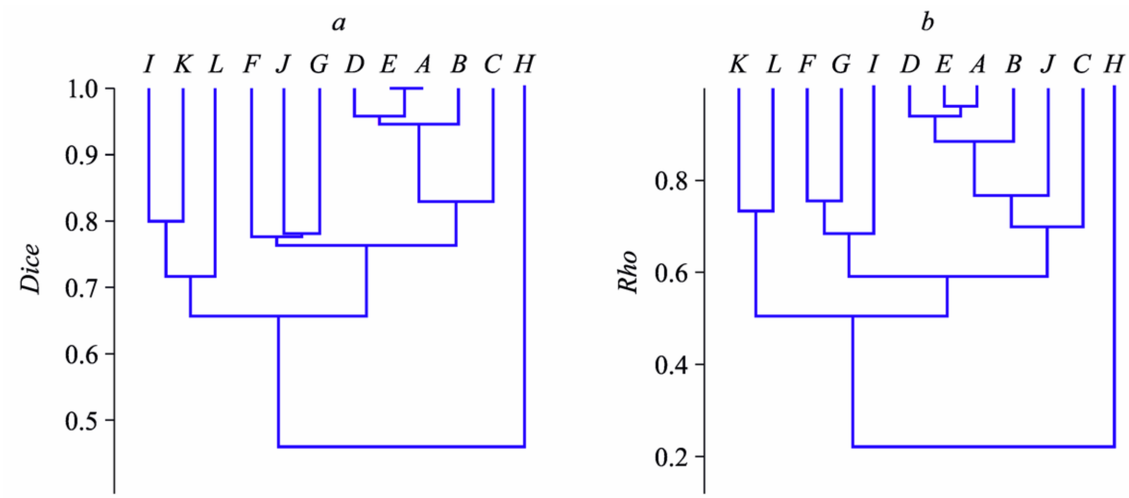

Fig. 3. Cluster analysis of similarity of the cenotic faunas (*a*) and population (*b*) of Collembola in the examined plant communities of Severnaya Zemlya (PAST software, *Dice* and *Rho* indices): *A*, snow field near a spring; *B*, spring side; *C*, bog; *D*, zonal association *Deschampsio–Aulacomnietum turgidi*, polygonal type; *E*, the same, clumpy type; *F*, zonal association *Stellario edwardsii–Hylocomietum alaskani typicum*; *G*, the same association but var. *saxifragetosum cespitosae*; *H*, *Dryas punctata–Hylocomium splendens*; *I*, association *Gymnomitrio corallioidis–Racomitrietum lanuginosi*; *J*, poppy "meadow," *Saxifraga platisepala–Poa abbreviata*; *K*, lemming colonies; *L*, an owl feeding place.

on one archipelago, 46 species (64.8%), only in one province, and 14 species (19.7%), in two provinces. The highest similarity between the faunas of different island groups assessed by *Jaccard* index was only slightly greater than 0.5. The corresponding values of *Dice* index, placing emphasis on the co-occurrence of species, varied within the range of 0.5–0.7. In both cases, separate clusters united the two Canadian islands, two southernmost (and/or warmer) regions of the Barents Province (Nordaustlandet and Novaya Zemlya), and also Franz Josef Land and two localities of the Siberian Province (Fig. 2).

The population. Of the available quantitative material, the most adequate collections were made by O.L. Makarova in 1997–1998 and 2000 in the south of Bolshevik Island, the Severnaya Zemlya Archipelago. Altogether, her study covered over a dozen plant associations which were quite representative of the coastal plain vegetation of this island. The descriptions of individual collection sites are to be found in the paper devoted to the composition and structure of the regional acarocenoses (Makarova, 2002), and also in a special study of the vegetation of Bolshevik Island (Matveyeva, 2006). The collembolan assemblages of the region (Table 2) usually comprise from 10 to 13 species (mean 13.0 ± 2.5, median 12.5, maximum 20). Their population density is usually high but extremely variable depending on the vegetation mosaic. The highest density, sometimes exceeding 10 000 ind./dm^2, is typical of zoogenic habitats; the mean values lie within a range of 1000–2000 ind./dm^2, and the minimal ones rarely drop below 600 ind./dm^2. The most characteristic feature of the collembolan population is very high faunistic similarity (up to a totally identical species composition) between the complexes inhabiting the soils of sharply contrasting habitats, for instance, zonal associations and nival assemblages in spring valleys (Fig. 3*a*). The only collembolan population really different from the general pool was found in such a specific intrazonal community as *Dryas punctata–Hylocomium splendens* var. *alaskanum*, which was quite rare in the study region (Matveyeva, 2006). This assemblage also stood out during analysis of the population structure; the clustering pattern based on rank distribution of species did not strongly differ from the faunistic one, though the former appeared somewhat more realistic (Fig. 3*b*). A separate cluster united zoogenic assemblages, namely lemming colonies and owl feeding places. One of the relatively warm and dry intrazonal associations, *Gymnomitrio corallioidis–Racomitrietum lanuginosi*, was clustered together with the one zonal assemblage *Stellario edwardsii–Hylocomietum alaskani* showing certain similarity to *Salici polaris–Hylocomietum alaskani*, the principal type of zonal vegetation of the Arctic tundra subzone on Taimyr (Matveyeva, 1998). It is also quite natural that these two clusters were set apart from the rest of the studied assemblages which were very similar in composition and structure.

Table 3. Agreement between the actual position of soil samples and the predicted classification of the collembolan populations of different plant communities of Bolshevik Island (linear discriminant analysis)

Observed classification		Agreement percentage	Predicted classification										
			Deschampsio–Aulacomnietum turgidi		*Stellario edwardsii–Hylocomietum alaskani*		*Dryas punctata–Hylocomium splendens alaskanum*	*Gymnomitrio corallioidis–Racomitrietum lanuginosi*	snow field near spring	spring side	bogs	lemming colonies	owl feeding place
			type 1	type 2	*saxifragitosum cespitosae*	*typicum* with *Carex ensifolia*							
Deschampsio–Aulacomnietum turgidi	type 1	93.3	**14**	1	–	–	–	–	–	–	–	–	–
	type 2	86.7	–	**13**	–	–	–	–	–	–	–	2	–
Stellario edwardsii–Hylocomietum alaskani	*saxifragitosum cespitosae*	100.0	–	–	**10**	–	–	–	–	–	–	–	–
	typicum with *Carex ensifolia*	60.0	1	–	–	**3**	–	–	1	–	–	–	–
Dryas punctata–Hylocomium splendens alaskanum		100.0	–	–	–	–	**9**	–	–	–	–	–	–
Gymnomitrio corallioidis–Racomitrietum lanuginosi		100.0	–	–	–	–	–	**10**	–	–	–	–	–
Snow field near spring		100.0	–	–	–	–	–	–	**11**	–	–	–	–
Spring side		71.4	–	–	–	–	–	–	2	**5**	–	–	–
Bogs		88.9	–	–	–	–	–	1	–	–	**8**	–	–
Lemming colonies		92.9	–	–	–	–	–	1	–	–	–	**13**	–
Owl feeding place		100.0	–	–	–	–	–	–	–	–	–	–	**6**
Total		91.9	15	14	10	3	9	12	14	5	8	15	6

Table 4. Relative abundance (%) of different species of Collembola and integral parameters of their assemblages on the coastal terrace of Cape Flora (Northbrook Island, Franz Josef Land)

Species	Lower slope		Middle slope	Upper slope
	moss cushions near spring, with *Saxifraga rivularis*, *Cerastium alpinum*, and *Cochlearia groenlandica*	association with dense cover of *Alopecurus alpinus*		seabird colony
A. bidenticulata	3.3	0.01	0.01	0.04
A. polaris	0.7	1.9	1.6	0.04
C. longispina	**4.1**	2.4	1.6	1.5
F. binoculata form a	**19.4**	**15.3**	**15.5**	2.2
F. binoculata form b	**20.0**	**33.6**	**19.2**	0.01
F. taimyrica	**47.3**	**36.1**	**56.3**	**17.1**
H. concolor	0.2	2.5	1.9	**78.8**
O. groenlandica	**4.4**	**4.5**	2.1	0.3
A. alpina	0.2	0.04	0.2	–
B. nivalis	0.2	0.04	0.4	–
F. quinquespinosa	0.02	2.1	0.2	–
H. tullbergi	0.005	0.9	1.0	–
D. neglecta	–	–	0.01	–
D. tshernovi	–	0.5	–	–
D. violacea	0.01	–	–	–
H. serrata	–	–	–	0.1
W. scandinavica	–	0.02	–	–
Total number of ind.	21410	11436	30195	22088
Number of samples	6	15	12	5
Total number of species	13	14	13	9
Mean number of species per sample ($M \pm SD$)	9.8 ± 1.2	8.6 ± 1.5	9.2 ± 1.2	7.6 ± 0.9
Median	10	9	9	8
Mean density, ind./dm^2 ($M \pm SD$)	14273.3 ± 9458.0	3049.6 ± 1503.8	10065.0 ± 3784.4	17670.4 ± 19027.0
Median	10872	3416	9778	13760

The studied assemblages of the polar deserts of Bolshevik Island had a fairly limited set of dominants. The smaller and more intensely colored form of *F. binoculata* (form b) was very abundant almost everywhere and often reached the eudominance level (39.4%). Another as polytopic though less abundant form was *V. arcticus*. High relative abundance in many biotopes was also typical of *F. taimyrica* and *H. tullbergi*, the latter clearly preferring warmer and better drained habitats despite its local ubiquitous presence. *Oligaphorura groenlandica* was dominant in only one biotope and quite abundant in two more biotopes. *Megalothorax* sp. gr. *minimus* had a high density in one of the zonal associations but did not reach the dominance level. Five more species, *A. bidenticulata*, *V. brevicaudus*, *C. borealis*, *H. concolor*, and *F.* cf. *altamontana*, were dominants or subdominants in one of the assemblages studied.

Despite the polytopic occurrence of most of the abundant species and high similarity between the cenotic collembolan complexes in the polar deserts of Bolshevik Island, these complexes were by no means identical but, on the contrary, characterized by quite distinct sets of species. This was clearly indicated by the results of discriminant analysis which showed most of samples to be identifiable (Table 3). However, these differences were difficult to formalize.

Table 5. Relative abundance (%) of different species of Collembola and integral parameters of their assemblages in some communities of Tikhaya Bay (Hooker Island, Franz Josef Land, collections of 2015)

Species	Coastal terrace		Slope above terrace		Rubini Rock
	polygonal association with *Salix polaris* in troughs	moss cushions near spring, with cover of *Alopecurus alpinus* and *Ranunculus sulphureus*	gently sloping area with *S. polaris*, *Papaver* sp., and dense cover of *A. alpinus*	lichen cover on talus	ornithogenic substrates
C. longispina	0.4	**5.9**	0.8	0.9	1.9
F. binoculata form a	**6.5**	**15.8**	**5.7**	3.5	**4.2**
F. binoculata form b	**38.3**	**21.6**	**15.9**	**50.2**	0.01
F. taimyrica	**12.2**	**32.2**	**6.4**	**12.7**	**16.7**
A. polaris	0.1	0.7	–	0.6	0.1
D. neglecta	0.9	1.5	**5.3**	–	0.02
D. violacea	**15.9**	–	**8.3**	**10.5**	0.004
F. quinquespinosa	–	**3.9**	1.4	0.1	0.01
H. concolor	1.5	**7.7**	**11.2**	–	**76.4**
H. tullbergi	**14.2**	–	3.2	**15.0**	0.01
O. groenlandica	1.1	2.5	0.8	–	0.1
W. scandinavica	**6.6**	–	**4.3**	**5.8**	0.4
A. alpina	1.0	0.5	–	0.4	–
D. tshernovi	0.7	0.1	**4.1**	–	–
F. longidens	0.5	**7.6**	0.3	–	–
A. bidenticulata	–	–	–	0.1	0.03
F. coeruleogrisea	–	–	–	–	0.1
F. palaearctica	–	–	**32.4**	–	–
I. alticola	–	–	0.04	–	–
S. malmgreni	0.02	–	–	–	–
V. brevicaudus	0.2	–	–	–	–
F. quadrioculata		0.01	–	–	–
Total number of ind.	5259	10288	4494	685	23244
Number of samples	6	4	6	2	8
Total number of species	16	13	15	11	14
Mean number of species per sample ($M \pm SD$)	12 ± 1.4	11.8 ± 1.3	10.3 ± 1.9	9.5 ± 0.7	5.5 ± 2.4
Median	12	12	11	9.5	5.5
Mean density, ind./dm^2 ($M \pm SD$)	3506.0 ± 2496.9	10288.0 ± 4502.7	2996.0 ± 1423.3	1370.0 ± 121.6	11622.0 ± 23379.4
Median	2958	9246	3144	1370	2284

The quantitative material for Franz Josef Land is available from only two localities: Cape Flora (Northbrook Island) (Table 4) and Tikhaya Bay (Hooker Island) (Table 5). The former locality lies approximately half a degree of latitude to the south, but its collembolan complexes were found to be homogeneous and less diverse: they included 17 species as compared with 22 found in Tikhaya Bay. The obvious reasons for this were the homogeneous vegetation (an almost continuous cover of Alpine foxtail) and

Table 6. Relative abundance (%) of different species of Collembola and integral parameters of their assemblages in the northern part of Novaya Zemlya (collections of 2015)

Species	Russkaya Gavan	Cape Zhelaniya				Oranskiye Islands
	polygonal assemblage on gentle slope, mosses in troughs with *Salix polaris*	moss cushions with *Saxifraga oppositifolia* and *Papaver polare*	ornithogenic substrates	lake shore with isolated plants of *Phippsia algida*	cushions of *Racomitrium lanuginosum* in rocky talus	ornithogenic substrates
A. polaris	2.1	0.7	**6.1**	0.1	0.3	0.5
C. longispina	1.2	0.4	0.1	**14.1**	1.2	0.1
F. taimyrica	**17.2**	**21.8**	**81.8**	**19.6**	**7.5**	**47.8**
H. tullbergi	**7.0**	2.9	2.0	**4.3**	**28.7**	**5.6**
P. pjasinae	1.8	**8.5**	0.8	0.02	0.3	**6.5**
A. bidenticulata	0.3	0.02	–	0.1	0.3	0.4
F. binoculata form b	–	**54.9**	1.5	**36.4**	**12.8**	**6.4**
F. microchaeta	2.4	**6.2**	3.5	–	**42.6**	3.4
D. violacea	**4.6**	3.1	0.4	–	3.2	–
H. viatica	1.3	0.01	0.2	–	–	0.005
O. groenlandica	–	0.4	–	**21.0**	1.4	0.1
F. quadrioculata	**41.0**	0.01	–	–	–	**27.6**
H. sensilis	0.1	0.04	–	4.4	–	–
O. ursi	1.0	0.4	2.0	–	–	–
A. alpina	1.6	0.2	–	–	–	–
F. sexoculata	–	0.04	–	–	–	1.5
F. quinquespinosa	0.1	0.3	–	–	–	–
P. notabilis	–	0.02	–	–	1.7	–
P. sensibilis	3.6	0.01	–	–	–	–
T. wahlgreni	0.7	0.01	–	–	–	–

Table 6. (Contd.)

Species	Russkaya Gavan	Cape Zhelaniya				Oranskiye Islands
	polygonal assemblage on gentle slope, mosses in troughs with *Salix polaris*	moss cushions with *Saxifraga oppositifolia* and *Papaver polare*	ornithogenic substrates	lake shore with isolated plants of *Phippsia algida*	cushions of *Racomitrium lanuginosum* in rocky talus	ornithogenic substrates
C. palustris	0.1	–	–	–	–	–
M. sp. gr. *minimus*	3.6	–	–	–	–	–
P. subarctica	2.7	–	–	–	–	–
S. subarctica	**6.7**	–	–	–	–	–
S. malmgreni	0.1	–	–	–	–	–
S. furcifera	0.3	–	–	–	–	–
X. humicola	0.1	–	–	–	–	–
T. duplopunctata	–	0.01	–	–	–	0.2
D. neglecta	–	0.01	–	–	–	–
H. sibirica	–	0.01	–	–	–	–
B. nivalis	–	–	1.7	–	–	–
Total number of ind.	670	11288	3129	5345	345	22197
Number of samples	4	12	2	4	2	6
Total number of species	23	23	11	9	11	13
Mean number of species per sample ($M \pm SD$)	13.8 ± 1.0	9.8 ± 1.6	10.0 ± 0.0	7.0 ± 0.8	9.0 ± 0.1	8.3 ± 2.0
Median	13.5	9.5	10	7	9	8
Mean density, ind./dm^2 ($M \pm SD$)	670.0 ± 444.7	3762.7 ± 2246.1	8130.0 ± 3385.6	5345.0 ± 3459.2	690.0 ± 291.3	3699.5 ± 2546.2
Median	560	3172	8130	5122	690	3957.5

Table 7. Relative abundance (%) of different species of Collembola and integral parameters of their assemblages in Isachsen Bay, Ellef Ringnes Island (collections of O. Makarova, 2005)

Species	Nival assemblages	Bog	Zonal community	Cushions of *Racomitrium lanuginosum*	Cushions of *Saxifraga oppositifolia*	Meadow patches on south facing slopes	Bird feeding place	Lemming burrows
F. regularis	**24.2**	**31.5**	**77.3**	**42.2**	**30.7**	**11.1**	**3.9**	**17.5**
V. brevicaudus	**18.3**	**23.6**	0.1	**48.2**	**15.1**	1.0	0.8	0.1
H. concolor	–	3.3	**5.9**	**7.3**	**48.7**	**51.5**	**93.0**	**60.8**
M. sp. gr. *minimus*	1.2	–	**8.3**	0.3	**3.9**	2.8	0.1	0.1
O. groenlandica	0.9	**16.6**	**4.3**	–	1.6	2.1	0.4	1.4
A. polaris	–	1.1	3.1	2.0	–	0.5		0.04
V. arcticus	–	0.1	0.8	–	–	0.1	–	0.1
H. sensilis	**55.1**	**21.5**	–	–	–	2.4	–	–
A. bidenticulata	0.2	2.2	–	–	–	–	–	–
F. bisetosa	–	–	–	–	–	**12.7**	2.0	**18.3**
W. similis	–	–	–	–	–	**6.7**	1.0	1.6
W. scandinavica	–	–	0.1	–	–	1.0	0.5	–
F. quadrioculata	–	–	–	–	–	**8.2**	–	–
Total number of ind.	2403	1727	4278	396	1182	2744	8585	7913
Number of samples	7	7	15	5	5	10	2	6
Total number of species	6	8	8	5	5	12	8	9
Mean number of species per sample (*M* ± *SD*)	4.3 ± 0.5	6.4 ± 1.0	5.0 ± 0.8	3.6 ± 1.1	5 ± 0	7.7 ± 2.2	5.5 ± 2.1	4.9 ± 1.6
Median	4	6	5	4	5	8	5.5	5
Mean density, ind./dm^2 (*M* ± *SD*)	1373.1 ± 801.6	986.9 ± 702.9	1140.8 ± 679.7	316.8 ± 244.3	945.6 ± 334.0	1097.6 ± 725.6	17180.0 ± 17805.0	4521.7 ± 5194.2
Median	1276	680	1000	288	1020	1134	17170	2812

strong influence of the uphill seabird colonies. The total species richness of individual cenoses was similar on the two islands. The mean number of species per biotope was 12.3 ± 2.2 (median 13) for Cape Flora and 13.8 ± 1.9 (median 14) for Tikhaya Bay, i.e., almost the same as in the south of Severnaya Zemlya. The principal dominants found at Cape Flora included only three "species" of the genus *Folsomia* (*taimyrica* and both color forms of *binoculata*), whereas *H. concolor* formed the bulk of the collembolan population in the seabird colonies. The range of dominants and subdominants was considerably wider in Tikhaya Bay. Apart from the same species of the genus *Folsomia* and *H. concolor*, in some biotopes the set of abundant forms may include nearly ten more species, in particular *Ceratophysella longispina*, *H. tullbergi*, *W. scandinavica*, *F. quinquespinosa*, *F. longidens*, *F. palaearctica*, *D. neglecta*, *D. violacea*, and *D. tshernovi*. The studied collembolan assemblages of the archipelago had high population densities varying from 1400 to 18000 ind./dm^2 (median > 3400), probably due to the general influence of seabird colonies.

The quantitative material from the north of Novaya Zemlya is very scanty (Table 6), so that at present the nature and specificity of the regional collembolan population can be only preliminarily assessed. The composition and structure of the collembolan complexes of Cape Zhelaniya, the extreme northern point of the archipelago, showed considerable differences from the other polar desert regions of the Palaearctic. Despite intense anthropogenic disturbance of the territory, examination of the small preserved fragments of

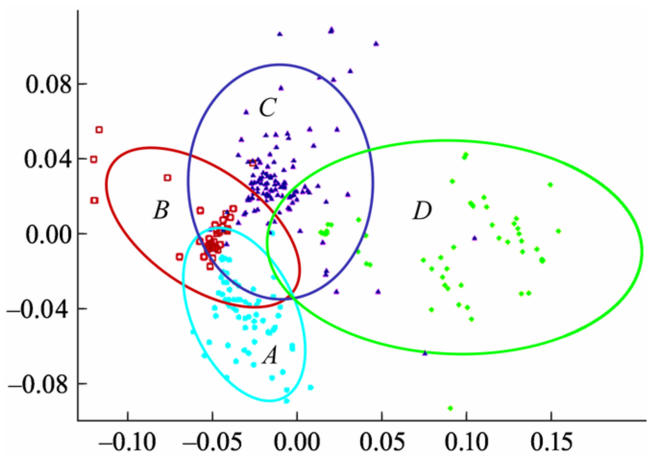

Fig. 4. Ordination of the collembolan populations of different polar desert regions (PAST software, non-metric MDS, *Rho* index): *A*, Franz Josef Land; *B*, Novaya Zemlya (north); *C*, Severnaya Zemlya; *D*, Ellef Ringnes Island.

vegetation revealed 24 species of springtails. It is significant that they included not only the typical inhabitants of polar deserts but also species which had not been previously recorded in this zone, for instance *P. pjasinae*, *H. sibirica*, *F. microchaeta*, *P. sensibilis*, and *T. wahlgreni*. Judging by the very limited material from Russkaya Gavan Bay (four soil samples from a single habitat), the local collembolan assemblages seemed to have a still more southern appearance; in particular, their dominant set already included such a polyzonal species as *F. quadrioculata*. At the same time, the main structural parameters of the collembolan assemblages in the north of Novaya Zemlya, namely the number of species per sample and the increased background density, were quite similar to those of other polar desert regions.

Ellef Ringnes Island of the Canadian Arctic Archipelago occupies the most isolated position of all the studied polar desert regions. On the one hand, the principal collembolan assemblages of this region were clearly impoverished as compared with the Palaearctic ones (Table 7). On the other hand, their mass species included not only such High Arctic forms as *F. regularis*, *V. brevicaudus*, *H. concolor*, *O. groenlandica*, and *H. sensilis* but also the hypoarctic species *F. bisetosa* and the polyzonal *F. quadrioculata*, though the two latter forms were associated with the richest and warmest communities. The high originality of the collembolan population of this island was also confirmed by the results of multidimensional scaling based on quantitative data (Fig. 4). Still, the general appearance of these assemblages (a small core of abundant polytopic forms and a relatively diverse set of rarer forms, especially numerous in specific intrazonal habitats) was quite comparable to the typical variant of the polar desert zone. On the whole, the regional differences seem to be mainly determined by the abundance ratios of the mass forms, although the qualitative differences, i.e., the presence or absence of certain species, are also significant, especially for the Canadian Province (Table 8).

DISCUSSION

Despite the High Arctic regions being remote and difficult to access, the Collembola of the polar deserts seem to have been studied almost as well as those of most other natural zones. This is certainly the result of the relatively simple structure and low diversity of the biota, because of which the diversity and specific features of the soil inhabitants can be assessed more or less correctly even with comparatively little available material. The collembolan fauna of the polar deserts is extremely impoverished, most genera being represented by only 1, less frequently 2 species; this situation is also observed in nearly all the other taxa (Korotkevich, 1972; Chernov and Matveyeva, 1979; Belikov and Randla, 1987; Korte et al., 1995; Makarova, 2002a; Alekseev et al., 2003; Makarova et al., 2007, 2012; Chernov et al., 2011). For example, of 22 genera of Collembola recorded on Bolshevik Island, 16 genera (or 73%) are represented by only 1 species each, 4 genera are represented by 2 species each, and only the genera *Folsomia* and *Hypogastrura* still comprise many species. Correspondingly, the collembolan faunas of the polar desert regions are characterized by the lowest species-to-genus ratios: 1.3 for Cape Chelyuskin, 1.6 for Nordaustlandet, the north of Novaya Zemlya, the fauna of Severnaya Zemlya, and Ellef Ringnes Island, and 1.8 for Franz Josef Land. The ratio for the collembolan fauna of the whole of Taimyr Peninsula is 3.0, and that for its southern tundras is 2.7.

There appears to be a certain contradiction between the wide ranges of most springtails occurring in polar deserts, where cosmopolitan and trans-Holarctic species comprise over 60%, and the observed faunistic specificity of different regions within the zone. For instance, only 10 species have been recorded in all the three polar desert provinces. However, in my opinion, this contradiction is a seeming one. In the extremely severe environment of polar deserts, even very subtle differences in the conditions of different provinces or

Table 8. Species which contributed most to the difference between the collembolan populations of different provinces of the polar desert zone (PAST software, SIMPER, Bray-Curtis index)

Species	Normalized mean abundance: ln (N + 1)			Species contribution to BC_{ji} index	
	Barents Province	Siberian Province	Canadian Province	BC_{ji}	Cumulative (%)
F. binoculata form b	4.0	3.9	–	7.7	9.9
F. taimyrica	5.1	2.5	–	7.7	19.7
H. concolor	1.9	0.4	3.0	5.9	27.2
F. regularis	–	–	4.2	5.5	34.3
V. arcticus	–	2.9	0.4	5.1	40.8
H. tullbergi	1.8	2.3	–	4.8	47.0
F. binoculata form a	2.9	0.8	–	4.6	52.9
O. groenlandica	2.1	1.7	1.8	4.2	58.3
V. brevicaudus	0.03	1.4	1.9	3.7	63.1
C. longispina	2.0	0.9	–	3.5	67.6
A. polaris	1.6	0.8	0.6	3.0	71.5
H. sensilis	0.2	0.4	1.3	2.3	74.5
A. bidenticulata	0.5	1.0	0.2	2.3	77.4
M. sp. gr. *minimus*	0.1	0.4	1.3	2.2	80.3
H. trybomi	–	0.9	–	1.5	82.3
P. pjasinae	0.7	0.03	–	1.2	83.8
D. violacea	0.8	–	–	1.2	85.3
B. nivalis	0.3	0.4	–	1.0	86.6
W. scandinavica	0.5	0.03	0.2	1.0	87.9
F. quadrioculata	0.4	–	0.3	1.0	89.2
Other 38 species	6.7	1.3	1.7	13.8	17.7
Sum				83.3	100.0

regions may prevent or facilitate the expansion of many species into the marginal part of the latitudinal gradient, even though the same species may have a circumpolar distribution in more southern areas. Besides, the varying level of knowledge of different regions should be taken into account.

The published estimates of the collembolan faunistic diversity in different polar desert regions usually did not exceed the level of 10–15 species (McAlpine, 1964, 1965; Addison, 1980; Chernov et al., 1977, 1979; Bulavintsev and Babenko, 1983; 1989; Fjellberg, 1986; Babenko and Bulavintsev, 1997). The only noticeable exception was Nordaustlandet, from which 34 species were known already at the end of the past century (Fjellberg, 1997), and at least 39 species are known at present (Coulson et al., 2011). This work has somewhat leveled the difference by noticeably increasing the species richness of the known polar desert faunas of other provinces. In particular, the collembolan diversity on Bolshevik Island has become almost equal to that on Nordaustlandet: 36 and 39 species, respectively. Since the total number of vascular plant species known from this island of the Svalbard Archipelago noticeably yields to the floristic richness of Bolshevik Island (52 and 68 species, respectively; see Matveyeva et al., 2015),[1] it may be assumed that the number of collembolan species currently known for Severnaya Zemlya is still far below the actual diversity. It is interesting that within the Siberian Province, this island fauna turned out to be considerably richer than that of the more southern mainland polar deserts of Cape Chelyuskin. First of all, it is reasonable to presume that the fauna of Bolshevik Island has been more thoroughly studied, since the available material from Cape Chelyuskin is much scantier.

[1] At the same time, the known diversity of mosses is higher on Nordaustlandet: 150 vs. 122 species (see Afonina, 2015).

However, this does not seem to be the only reason for the lower diversity of the Cape Chelyuskin fauna. Under such severe climatic conditions, even minor differences in heat availability may be crucial. According to the local weather station data, the long-term mean temperatures of July at Cape Chelyuskin and Solnechnaya Bay (Bolshevik Island) are not at all equal: 1.5°C and 2.2°C, respectively. This fact probably accounts for the noticeable differences in the occurrence and density of even some High Arctic species. An example of this kind is the distribution of *O. groenlandica*, *H. sensilis*, and *A. polaris* which are noticeably less common in the assemblages of Cape Chelyuskin and clearly prefer the warmest biotopes there. The significantly greater species richness of cenotic faunas of Solnechnaya Bay as compared with Cape Chelyuskin (13.0 ± 2.5 and 9.7 ± 1.6 species, respectively) is also evidently related to the greater heat availability in the former region. Also important are the different levels of landscape differentiation of these polar desert regions. Approximately half the species recorded at Solnechnaya Bay occur only in local biotopes that have no analogs on Cape Chelyuskin, where intrazonal plant communities are practically absent (Chernov et al., 1979; Matveyeva, 1979).

Thus, the greater faunistic richness observed on Bolshevik Island is not merely the result of more thorough material collection. First, it is related to the less severe conditions and terrain of the island; second, it reflects the specific features of differentiation of the collembolan fauna and population in the polar desert zone. This zone typically has almost identical species complexes in the principal plant associations and an increased number of locally occurring species that play no considerable cenotic role. The collembolan population of Cape Chelyuskin also reveals this characteristic feature. The first study of Collembola in this region (Chernov et al., 1977, 1979) showed very high similarity between the cenotic and local faunas, i.e., similarity of the species composition of individual plant communities and "the complete species list of a relatively small territory including all the most characteristic landscapes of the given zone" (Chernov, 1975, p. 160). The soil collembolan assemblages of the examined vegetation units differed only in the relative abundance of species, i.e., in variants of rearrangement within practically the same species set. The highly polytopic distribution of species was regarded as the most typical feature of the soil population of the polar desert zone On the whole, this conclusion was totally correct. On the other hand, the almost complete identity of the cenotic faunas noted in the cited research was partly due to the fact that the study was focused on the most typical communities. During the surveys carried out in the same area in 1994, the principal communities also had a very similar composition of the soil complexes, especially with regard to changes in the taxonomic status of some species. However, a single sample collected in a drained patch with *Salix polaris* on a coastal steep, only 2 m^2 in area, yielded four species previously unrecorded in the main habitats and increased the known local fauna by as many as 20%.

It may be assumed that some uncharacteristic collembolan species with low density and local distribution occur in any northern region. The set of such species seems to be variable, being determined by the outcome of colonization and survival at the limits of the adaptive zone. The participation of these sporadic species is particularly noticeable in the polar desert faunas, not only because of the low total diversity but also due to the greater number of forms that can barely survive under such severe conditions but cannot maintain a considerable level of abundance.

In all likelihood, this phenomenon is not specific to Collembola but quite common in both plants and animals of the polar deserts. For instance, of 74 species of true mosses[2] known from Cape Chelyuskin (Blagodatskikh et al., 1979), 19 species were recorded only based on the previously published lists (i.e., they were not found during the cited research) while 30 species were characterized as "rare" and "very rare." Of the four species of beetles recorded on Severnaya Zemlya, only *Micralymma brevilingue* Schiødte (Staphylinidae) has relatively high occurrence and density, and the remaining species are known from very few specimens found in local habitats with the most favorable microclimatic conditions (Makarova et al., 2007).

The maximum recorded densities of collembolans in the polar desert regions usually much exceed the values known for more southern communities, including tundra ones. This is confirmed not only by the material reported herein but also by all the earlier publications. For example, the maximum densities recorded in moss cushions on Cape Chelyuskin

[2] By now, this number has increased to 90 (Afonina, 2015).

exceeded 3500 ind./dm^2, and the mean value was 1000 ind./dm^2 (Chernov et al., 1979). An equally high abundance of collembolans was recorded on Franz Josef Land, where their density often exceeded 3000 ind./dm^2 in biotopes with a well-developed moss-lichen layer, whereas in old ivory gull nests along river valleys and even on coastal terraces with depleted vegetation it sometimes reached 15 000 ind./dm^2 (Babenko and Bulavintsev, 1997). The known tendency for the collembolan population density to increase from south to north (Chernov, 1975; Petersen and Luxton, 1982; Ananjeva et al., 1987, etc.) is particularly evident in the polar desert regions and may be quite reasonably associated with drastic faunistic impoverishment of the soil population. This phenomenon is known as Thienemann's rule or the principle of cenotic compensation (Chernov, 2005). Naturally, the high density and biomass of collembolans in polar desert communities are not indicative of high productivity of their assemblages. They most probably reflect the extended life span, i.e., simultaneous existence of many consecutive generations of collembolans in the Far North. Another considerable factor may be the relatively low density of predators in the polar desert soils (Chernov et al., 1979; Makarova, 2002a; Makarova et al., 2007), although collembolans seem to be the principal prey of many small predators in these habitats (e.g., see Makarova et al., 2007). Also important is the general weakening of cenotic interactions, including competition, within the saprotrophic complex, which is believed to be a common feature of assemblages formed under severe climatic conditions.

Apart from highly polytopic occurrence of the mass species, the distribution of Collembola in the polar desert landscapes is characterized by expansion of species from hydromorphic tundra communities into zonal habitats (Chernov et al., 1979). It is the hygrophilous species that have the dominant status in most habitats within this zone, including those with the greatest heat availability. The composition of collembolan assemblages in the warmest habitats of the polar desert zone would seem very strange to a researcher familiar with the spatial distribution of this taxon in the tundra zone. Co-occurrence of typical hygrophiles, meadow inhabitants, and species which in the tundra zone are associated with drained rubbly slopes is an excellent example of Liebig's law of the minimum; it shows that, despite the small amount of precipitation and the physiological dryness determined by low availability of water at low temperatures (e.g., Sømme and Block, 1991), it is not humidity that limits the distribution of organisms in polar deserts. Again, it should be emphasized that this phenomenon is by no means specific to Collembola. For example, co-occurrence of plant species "whose ecological optima lie at the opposite ends of the gradient in the tundra zone" (Matveyeva, 2006, p. 25) was repeatedly noted for various intrazonal associations of Severnaya Zemlya.

The core of the polar desert fauna of Collembola is formed by the families Hypogastruridae, Isotomidae, and Onychiuridae, generally typical of the Far North. However, the ratio of these taxa in the polar desert assemblages considerably differs from that in the tundras. As compared with even the northernmost part of the tundra zone, the family Hypogastruridae is better represented in the local faunas and cenotic assemblages of polar deserts. The family Isotomidae also retains high abundance and diversity. However, species of the genus *Desoria*, probably the most diverse genus in the tundra zone, are noticeably suppressed in polar deserts. Only one species of this genus, *D. tshernovi*, is relatively common but usually scarce in the Palaearctic polar deserts, and two more species, *D. neglecta* and *D. violacea*, are sporadically recorded. The ecological vicariants of the genus *Desoria* in polar deserts are other large representatives of the family Isotomidae: *V. brevicaudus*, *V. arcticus*, and *A. bidenticulata*. Species of the genus *Folsomia* act as dominants of the collembolan assemblages in all the types of communities. The family Onychiuridae clearly declines in terms of both fauna and population; species of the genus *Protaphorura* almost completely disappear and play no significant cenotic role, and only *O. groenlandica* remains relatively common.

Nearly all the abundant species of Collembola inhabiting polar deserts have zonal Arctic ranges, and many of them are true euarctic forms showing the highest abundance in the northernmost regions. There is even one endemic species, *V. brevicaudus*, whose range barely extends beyond the polar desert zone; this is quite unusual for such a primitive and ancient taxon as Collembola. However, in the Canadian Arctic Archipelago this species occurs not only in the polar desert but also on the more southern Cornwallis Island (Fjellberg, 1986), therefore it would be more correctly described as a zonal subendemic. Exceptions to this general rule are *F. quadrioculata* (dominant in some communities in the north of Novaya Zemlya and subdominant in the warmest assemblages of Ellef Ringnes Island), and also *W. scandinavica*, *F. palaearctica*, and *D. neglecta* that are mass species in some assemblages on Hooker Island. Most of the species that are rare and locally distributed in polar deserts are typical inhabitants of the tundra zone. This group also includes a few widespread polyzonal species whose distribution optima lie still further south. All these "southern" forms usually comprise no more than 10% of the total population density even in the communities with the most favorable microclimate, but sometimes they make up a considerable part of cenotic faunas.

The drastically depleted fauna of polar deserts and the small thickness of the inhabited layer still do not exclude the possibility of vertical stratification of soil assemblages, at least in terms of occurrence of representatives of different life forms. The soil assemblages of most communities include epibionts (*A. bidenticulata*, *V. brevicaudus*), upper hemiedaphobionts (*H. trybomi*, *H. tullbergi*, *C. longispina*), lower hemiedaphobionts (*B. nivalis*, *F. binoculata*), and euedaphobionts (*F. taimyrica*, *O. groenlandica*). However, true atmobionts are absent there since representatives of this life form are suppressed already in the southern part of arctic tundras (Ananjeva et al., 1987).

The collembolan populations of all the three polar desert provinces show striking similarity at the structural level, first of all in the general impoverishment of the complexes combined with weakened biotopic associations of individual species. In other words, the assertion that "under the most severe climatic conditions, formation of invertebrate assemblages largely amounts to shuffling of the same set of species which inhabit, with varying densities, a very wide range of biotopes and microbiotopes" (Chernov et al., 1979, p. 43), is totally correct. The faunas of different provinces (and regions within one province) primarily differ in the proportion of uncharacteristic species with more southern distribution optima. Species with more northern ranges usually occur in several regions. Naturally, there are significant exceptions to this rule, especially in the Canadian Province which lacks a number of Palaearctic species, such as *H. tullbergi*, *H. trybomi*, *C. longispina*, *F. taimyrica*, *F. binoculata*, and several others. The aspect of soil complexes changes abruptly to the south of the polar desert zone. Only 1° of latitude separates Cape Chelyuskin from the northernmost studied region of arctic tundras, namely the Rybnaya River on Pronchishchev Coast in the northeast of Taimyr (76.63°N, 111.00°E). Nearly all the species recorded on Cape Chelyuskin also occur in this northern tundra belt and even act as dominants there, the only significant exception being the absence of *V. brevicaudus*. However, the collembolan populations of these two fairly close regions reveal quite essential differences. For instance, the fauna of the arctic tundra region includes a number of *Desoria* species, in particular *D. pjasini* (Martynova), *D. atkasukiensis* (Fjellberg), *D. tshernovi*, *D. violacea*, and *D. neglecta*. Of these, only *D. tshernovi* was recorded in the polar deserts within this Arctic sector (in the Cape Chelyuskin area and on Severnaya Zemlya), where it was much less abundant and polytopic. Also noticeable is the shift of biotopic preferences in the most typical High Arctic forms: the species characteristic of the polar desert assemblages lose their dominant status and move from zonal habitats to hydromorphic intrazonal biotopes: nival stations (*A. polaris*, *A. alpina*, *B. nivalis*), waterlogged lowlands (*F. binoculata*, *C. longispina*), and waterside areas (*A. bidenticulata*). On the whole, it may be concluded that the fauna and structure of the cenotic collembolan assemblages of polar deserts are sufficiently specific and certainly not identical to those of the tundra zone, even though they are formed under the influence of the same global trend.

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