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Systematics and distribution of spruce species in the North-West of Russia

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Abstract: Norway spruce (*Picea abies*) and Siberian spruce (*P. obovata*) are among the most important forest-forming coniferous species in the boreal part of Eurasia. Despite numerous publications on the taxonomy of Norway spruce and closely related taxa (*P. obovata* Ledeb. and *P. fennica* (Regel) Kom.), the problem of their identification, as well as clarification of their taxonomic status, has not been solved so far. Species delimitation is particularly challenging when *P. abies*, *P. obovata* and *P. fennica* occur in sympatry.

Our study aims to assess taxonomic value of proposed earlier and search for stable diagnostic characters of cones and their scales to distinguish *Picea abies* and its sympatric in the North-West of Russia *P. fennica* and *P. obovata*. In addition, we analyzed and updated information on geographical distribution and phytocenotic characteristics of the above-mentioned species in the North-West of the European part of Russia.

We examined herbarium specimens and cones sampled from 88 trees from 22 *Picea* stands located throughout the study region. Each tree was represented on average by 5 cones, in total 415 cones were analyzed. Morphometric analyses included 16 morphological characters of cones and their scales selected based on our own observations and published data.

Multivariate comparison had shown a large overlap between *P. obovata* and *P. fennica*, while individuals of *P. abies* formed a separate and less overlapping cluster. Among the six qualitative (discrete) characters, shape of seed scale and shape of its upper margin have non-overlapping frequency distributions and can separate *P. abies* and *P. obovata*.

Several new diagnostic characters are proposed: morphology and size of bract scales and ratio of the size of seed scales and bract scales. Phytocenotic analysis showed that different spruce taxa occupy specific habitats, which in their turn connected with the latitudinal gradient: in normally drained habitats, *Picea obovata* is found mainly in poor shrubby-green-mossy forests, which are typical of the northern and middle parts of the Northern taiga; *Picea abies* – in richer green-mossy habitats (Vaccinioso-hylocomiosum, Oxalidoso-hylocomiosum, Hylocomiosum), which begin to occur already from the middle part of the Northern taiga. *Picea fennica* occupies both habitats.

Keywords: *Picea*, diagnostic characters, morphology, plant variation, geographic distribution

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Introduction

Genus *Picea* A. Dietr. has circumpolar distribution throughout the northern hemisphere and comprises 34–38 species (Farjon, 2001, 2017). The largest number of species is found in Central and Western China, as well as in North America (Farjon & Filer, 2013). *Picea abies* (L.) H. Karst. is common in Europe and *P. obovata* Ledeb. found from Fennoscandia and Ural to the Far East, covering Siberia (Tsuda et al., 2016). Exact limits of the distribution ranges and taxonomic status of *P. abies* and *P. obovata* have been much debated since many diagnostic morphological traits of the two species are blurred by introgressive hybridization in their contact zones (cf., Tollefsrud et al., 2015; Tsuda et al., 2016). Intermediate morphological states are described either as clinal or geographic variation without taxonomic recognition (Schmidt-Vogt, 1977; Popov, 1996a; Volkova et al., 2014) or treated at intraspecific taxonomic level (Teplouchoff, 1868; Sukachev, 1928, 1938; Lindquist, 1948; Jalas & Suominen, 1973; Schmidt-Vogt, 1974, 1977; Hämet-Ahti et al., 1992; Tutin et al., 1993; Jonsell, 2000; Latałowa & Knaap, 2006 etc.), or as hybrids *P. fennica* (Regel) Kom. (Ramenskaya, 1983; Tzvelev, 2000; Schmidt, 2005; Notov, 2005; Averyanov et al., 2006) or as a separate species of a hybrid, origin, Finnish spruce (*P. fennica* (Regel) Kom.) (Komarov, 1934; Bobrov, 1971, 1974, 1978, 1983; Lantratova, 1985; Mamaev, 2000; Bakin et al., 2000; Kravchenko, 2007; Doronina, 2007). Monographers of conifers (Beissner, 1909; Komarov, 1934; Bobrov, 1971, 1974, 1978, 1983; Farjon, 1990, 2001, 2017) and most of the current Russian literature (Lantratova, 1985; Mamaev, 2000; Bakin et al., 2000; Kravchenko, 2007) consider all three taxa (*P. abies*, *P. obovata* and *P. fennica*) as separate species.

Bobrov (1944) suggested introgressive hybridization as a possible explanation of the origin of *P. fennica*. According to this theory, intermediate forms between *Picea abies* and *P. obovata*, inhabiting the NE Europe, are "the result of a long-time hybridogenic interaction of European and Siberian species" (Bobrov, 1944). Recurrent hybridization between the Norwegian (*P. abies*) and Siberian spruce (*P. obovata*) in their contact zones is widely accepted (Bobrov, 1944, 1978, 1983; Shcherbakova, 1973; Popov, 1996a, 2000, 2003, 2010; Il'inov et al., 2011).

The territory of the North-West of Russia includes Leningrad, Pskov, Novgorod, Murmansk regions and Karelia. Most common spruce species in the territory are *P. abies* and *P. x fennica* (Tzvelev, 2000; Averyanov et al., 2006; Doronina, 2007). *P. obovata* is recorded in Svirsky (environs of village Voznesenie) and Vepsovsky districts of the Leningrad region (Tzvelev, 2000). In the Leningrad region *Picea abies* prevails, whereas *P. fennica* usually occurs as an admixture in coniferous forests throughout eastern and north-eastern parts of the region. For the Novgorod Region (Yurova et al., 2009), only 2 species are given – *P. abies* and *P. x fennica*. Only *P. abies* occurs in the Pskov region (Efimov & Konechnaya, 2018).

North-West Russia was a contact zone between *P. abies* and *P. obovata* during the Early and Middle Pleistocene (Bobrov, 1983; Popov, 2003, 2010, 2014) or from the middle Holocene (Sukachev, 1928, 1938; Danilov, 1943; Schmidt-Vogt, 1974, 1977). At the end of the Mikulin (Eemian) Interglacial more thermophilic *P. abies* began its range expansion to the east and replaced *P. obovata* creating a secondary contact zone of introgression with *P. obovata*. In the second half of the Holocene hybridogenic forms of these species migrated north across Prionezhie, Karelia, Finland, mostly the Kola Peninsula and further south along Sweden and Norway, except for the extreme north of the Scandinavian countries and the Kola Peninsula, where the Siberian *P. obovata* also remained during the last glaciation (Bobrov, 1983; Parducci et al., 2012, but not confirmed by recent study by Alsos et al., 2020).

Molecular genetic studies supported that *P. abies* and *P. obovata* are separate taxa (Tollefsrud et al., 2008, 2015; Lockwood et al., 2013; Aarrestad et al., 2014; Tsuda et al., 2016). Tollefsrud et al. (2008) has shown that the genetic border between *P. abies* and *P. obovata* is situated east of the Ural Moutains, in the Ob River. These results also agree with morphological data on cone scale shapes (Popov, 2003). According to Tollefsrud et al. (2015) cpDNA analyses points at a split between the two species (*P. abies* and *P. obovata*), and the creation of a hybrid zone, predating the LGM. Based on microsatellite analyses, individuals of *P. fennica* did not constitute a separate genetic cluster (Potokina et al., 2013), but their hybrid origin was supported by the genetic admixture from both parental groups *P. abies* and *P. obovata*.

Alternative taxonomic treatment considers *P. abies* and *P. obovata* as infraspecific taxa of a single species (Schmidt-Vogt, 1977; Popov, 1996a; Volkova et al., 2014) based on a lack of morphological and genetic specificity of intermediate forms united under "*P. fennica*", as well as referring to continuous and adaptive nature of the clinal morphological variation in direction from West to East.

Most commonly used diagnostic character to delimit two species *Picea abies* and *P. obovata* is a shape of seed scales (cf., Farjon, 1990, 2017), but there is no agreement in application of other characters. Morphology of seed scales was used as an evidence supporting introgressive hybridization between *P. abies* and *P. obovata* (Tatarinov, 1989; Popov, 1996a, 1996b, 2000, 2003, 2010, 2014). These studies, however, did not take into account characters of bract scales and vegetative organs (needles, young shoots).

Our earlier studies (Orlova & Egorov, 2011; Orlova, 2012; Orlova et al., 2017) identified 14 new characters of vegetative organs: the location and number of stomatal lines on the sides of the needles, the presence of white wax coating on them; length, the shape of cross-section, pubescence of the pulvini of annual shoots, the angle of their deviation from the axis of the shoot; the shape of the apical buds and their scales, the deviation of the bud scales from the bud; the ratio of the length of the profiles (basal scales at the base of the apical buds) and apical buds. These studies also suggested that general morphology of mature cones, i. e. their shape and size, shape of the base of cones, seed scale deviation from the axis of the cone, the number of parastiches; shape and size of seed scales, shape and the integrity of its upper margin; size and shape of bract scales – are valuable diagnostic characters of *P. abies* and closely related taxa. However, earlier studies did not include any statistical analysis of these new characters of cones and their scales.

The main aim of our study was to apply morphometric methods to estimate taxonomic value of proposed earlier and search for stable diagnostic characters of cones and scales to distinguish *Picea abies* and its sympatric in the North-West of Russia *P. fennica* and *P. obovata*. Additonally, we analyzed and updated information on geographical distribution and phytocenotic characteristics of the above-mentioned species in the North-West of the European part of Russia.

Materials and methods

Plant material

Field work was conducted during the field season of 2009–2010 in the Murmansk Region, the Republic of Karelia and the Leningrad region (the eastern and south-eastern parts). We aimed to clarify the geographic distribution (Fig. 1, 2, Appendix 1) and phytocenotic characters of *P. abies*, *P. obovata,* and *P. fennica* the North-West European part of Russia (Table 1). We set up 22 plots where 4 (min–max) trees of similar age and height were selected. For each individual tree, we took 5(4–6) cones and pressed one shoot with needles. Here we present results based on cone morphology only. All herbarium material, collected during these expeditions has been deposited in Herbarium of Komarov Botanical Institute RAS (LE).

In Table 1 the geobotanical (phytocenotic) zonation of the taiga by Alexandrova and Yurkowskaya (Aleksandrova & Jurkovskaya, 1989) was adopted with the further division of the Northern taiga into the following regions: the northern part (Kola-Tuloma district and the northern part of the Kandalaksha district), the middle part (the southern part of the Kandalaksha district and Pjaozersky-Toposersky district) and the southern part (Kujtinsko-Vigoserskiy district) (Orlova & Egorov, 2011). This subdivision is based on climatic observations (Egorov et al., 2015). In particular, the southern part of the northern taiga is distinguished clearly by warmth supply (the sum of active temperatures above 0 °C), in the temperature range 1652–1816 °C, and is characterized by minimal overlapping of the ecological characteristics' values of the adjacent forest regions (Egorov et al., 2015).

Table 1 provides the information on the frequency of occurance of spruce taxa in forest regions, which was calculated based on the ratio of number of trees of a particular taxon to the total number of trees .The species were identified based on the tree cones collected under particular tree. The names of the communities are given in a broad sense and were compiled during desk processing based on dominant and indicator species.

During the 2011–2017 a survey of floristic diversity of the islands in the Gulf of Finland and the Vyborg Bay (Leningrad Region), on the coast of the Gulf of Finland (Kurgalsky Peninsula and the vicinities of

Table 1. Characteristics and geographic location of 32 selected plots of spruce taxa in the taiga regions of the North-West of Russia (Orlova & Egorov, 2011, with modifications).

Taiga regions (forests), Number of plots	Plant communities	Range of plots' location, N latitude	*Picea obovata* (%)	*Picea fennica* (%)			*Picea abies* (%)
				Form close to *Picea obovata*	Intermidiate form	Form close to *Picea abies*	
North taiga, N part of the subzone	*Fruticuloso-hylocomiosum*	68°10'39"–67°34'51"	70–90(95)	(5)10–30	0	0	0
Northern taiga, the middle part of the subzone	*Fruticuloso-hylocomiosum*, more rarely *Vaccinioso-hylocomiosum*	67°09'50"–65°14'40"	50(40–60)	30–35	(0)15–20	0	0
Northern taiga, S part of the subzone	*Vaccinioso-hylocomiosum, Sphagnosum*	64°24'39"–63°05'59"	5–40	10–20	0–60	(0)15–30	0–40
Middle taiga	*Vaccinioso-hylocomiosum, Sphagnosum*	62°51'20"–60°48'17"	0–20	10	30–75	0–50	10–55
Southern taiga	*Oxalidoso-hylocomiosum* *Vaccinioso-hylocomiosum, Sphagnosum*	59°26'54"–59°15'15"	0	0–10	0–5	0–35	60–90

Lomonosov) special attention was given to the native species of conifers. Extensive herbarium materials (cones and vegetative shoots) 100 herbarium specimens were collected to get knowledge about the distribution of *Picea* taxa on the islands of the eastern Gulf of Finland (Fig. 1, 2, Appendix 1).

Morphometric analysis

For the morphometric analyses we included material collected from 22 *Picea* stands (sampling plots) from Leningrad and Murmansk regions, and S. and N. Karelia. Detailed description of collections is

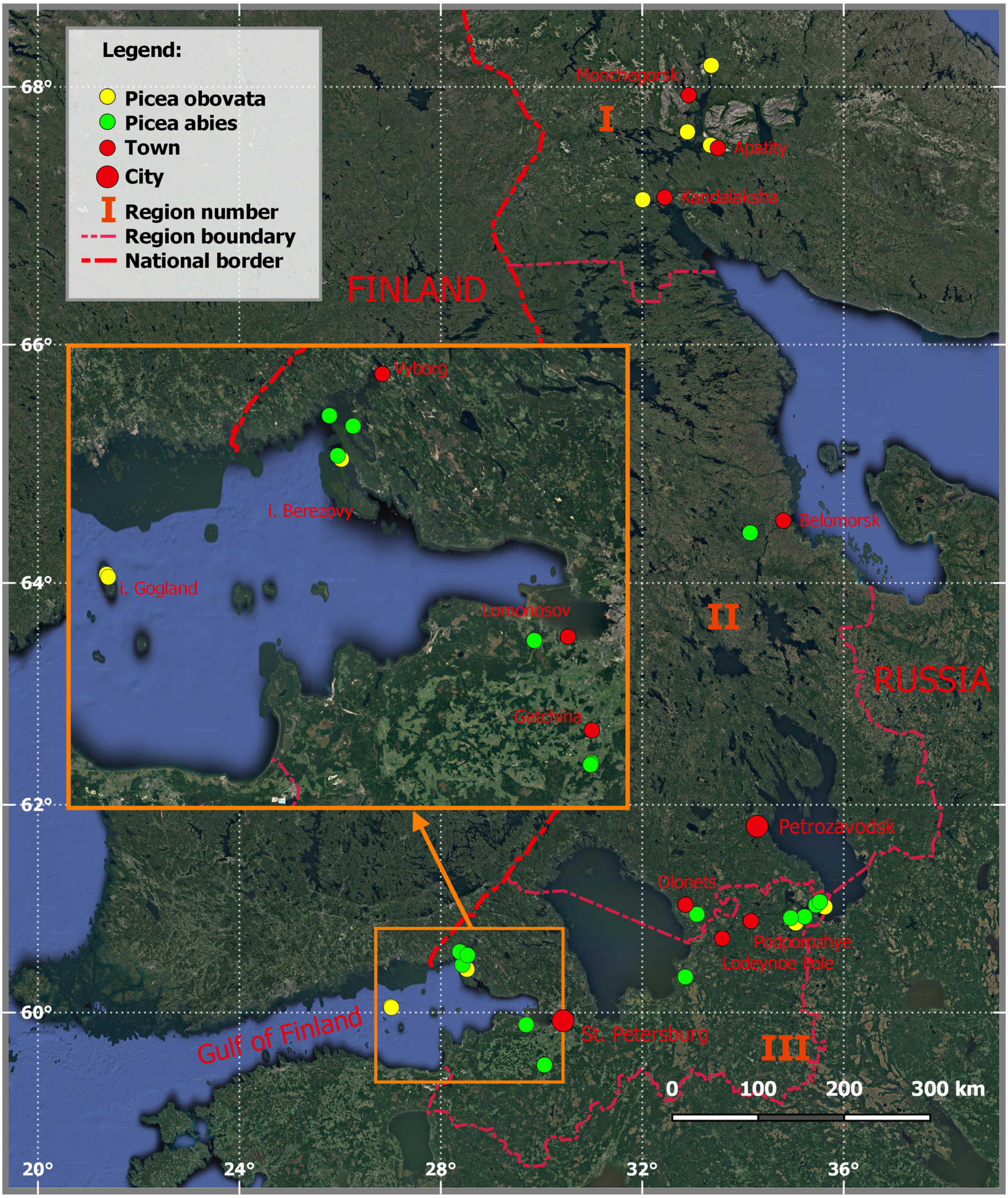

Fig. 1. Sampled populations of *Picea abies* and *P. obovata* in the North-West of Russia. Region number: I – Murmansk, II – Karelia, III – Leningrad

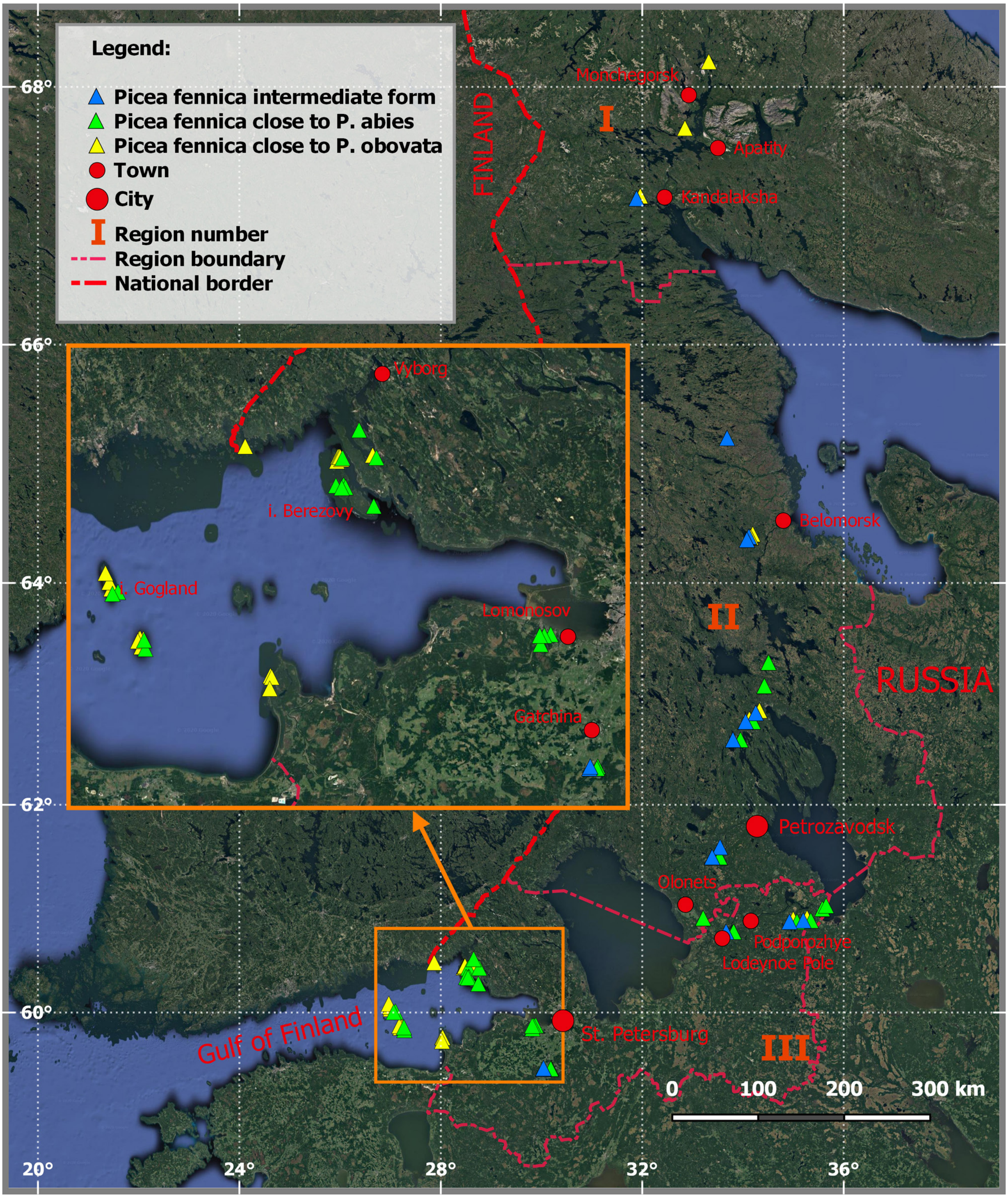

Fig. 2. Sampled populations of three forms of *Picea fennica* in the North-West of Russia. Map symbols as in Fig. 1

provided in Appendix 1. In total 88 trees were surveyed. From each tree we included 5 (4–6) cones to account for individual variability. Total number of trees analyzed were 10 for *P. abies* (45 cones); 13 for *P. obovata* (60 cones) and 21 for *P. fennica* (115 cones). Some individuals were identified as "*fennica abies*" or "*fennica obovata*" to document intermediate forms resembling *"abies" or "obovata"* more closely. We studied 23 trees of *P. fennica* close to *P. abies* (=*P. fennica* x *P. abies*) (99 cones) and 21 trees identified as *P. fennica* close to *P. obovata* (=*P. fennica* x *P. obovata*) (96 cones). In total 415 cones were analyzed. Based on our preliminary morphological observations of both reproductive characters and vegetative characters of

Table 2. Qualitative and quantitative characteristics used in morphometric analyses of three species of *Picea*

N	Morphological character	Abbreviation	Character states codes
		Qualitative characters:	
1.	Shape of cones	ShCo	ovoid-cylindrical – *OvCyl*; ovoid – *Ov*; narrowly-ovoid – *NarOv*
2.	Shape of cone basis	ShBasCo	rounded – *Rou*; cuneate – *Cun*; plane – *Pl*
3.	Shape of seed scale	ShSSc	rhombic – Rh; widely rhombic – *WiRh*; obovate – *Ob*
4.	Shape of upper margin of seed scale	ShUpM	cuneate-triangular – *CunTri*; cuneate- narrowed – *CunNar*; triangular – *Tri*; widely-triangular – *WiTri*; triangular-truncated, bent inwardly – *TriTruBeInw*; rounded-triangular – *RouTri*; rounded-triangular, bent inwardly – *RouTriBeInw*; rounded-triangular – *RouTri*; rounded-triangular, bent inwardly – *RouTriBeInw*; widely-rounded-triangular – *WiRouTri*; rounded – *Rou*; widely-rounded – *WiRou*; rounded with cusp – *RouCusp*; widely-rounded with cusp – *WiRouCusp*
5.	Integrity of upper margin of seed scale	EntUpM	entire – *Ent*; dentate – *Dent*; undulate – *Undul*
6.	Shape of bract scale	ShBract	narrowly-obovate – *NarOb*; obovate – *Ob*; rhombic – *Rh*; narrowly-rhombic – *NarRh*; lanceolate – *Lanc*; widely-lanceolate - *WiLanc*
		Quantitative characters:	
7.	Cone length	Lc	
8.	Cone width	D	
9.	Ratio of cone length to cone width	LcD	
10	The number of parastiches	NuPa	
11.	Seed scale deviation from the axis of the cone	DevAx	
12.	Seed scale length	H	
13.	Seed scale width	W	
14.	Ratio of seed scale length to seed scale width	HW	
15.	Height of visible part of seed scale	I_A	
16.	Tongue height	L	
17.	Bract scale length	k	
18.	Bract scale width	c	
19.	Ratio of bract scale length to seed scale width	kH	

shoots and needles (Orlova & Egorov, 2011; Orlova, 2012) we chose most stable characters delimiting *P. abies* and closely related taxa. For each cone we analysed 16 morphological characters (including 6 qualitative), both new and traditionally used to distinguish *P. abies*, *P. obovata* and *P. fennica*. (Table 2, Fig. 3). In addition, 3 ratios were studied to describe shape of seed scales and cones and to compare seed to bract scales lengths. Morphological characters and their coding are provided in Table 2. Details of measurements are given on Fig. 3.

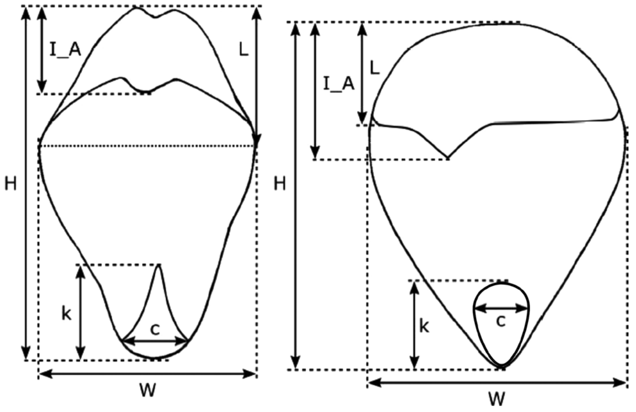

Fig. 3. Reproductive morphological characters of *Picea abies* (left) and *P. obovata* (on right): I_A - Height of visible part of seed scale; L – Tongue height; H – Seed scale length; W – Seed scale width; k – Bract scale length; c – Bract scale width

Statistical analyses

All statistical analyses were run using in SPSS v 24 (IBM Corp. Resealed 2016, IBM SPSS Statistics for Windows Vers. 24, Armonk, NY: IBM Corp.)

We applied summary statistics to describe both intra- and inter-group variation of quantitative (continuous) morphological characters (Table 3), as well as frequency distributions of the various states of the coded categorical characters. For the continuous morphological characters, we run univariate analyses of variance to test if the mean values defined by taxonomic groupings are significantly different. F-test of between subject effects were run using morphological characters as a dependent variable and taxonomic group as a factor variable with 5 categories (“*obovata*”, “*fennica*”, “*fennica_ob*”, “*fennica_ab*” and “*abies_ab*”). Multiple comparisons between taxonomic groups were run using Tukey HSD-test to identify which of the means differ (Appendix 2). To test the null hypothesis that the error variance of the dependent variable is equal across groups, we used Levene’s test prior to the analyses of variance. All characters

Table 3. Descriptive statistics (group averages – Mean, Minimum (Min), Maximum (Max) values and Standard error of mean (SE.) of 13 morphological characters selected for morphometric analyses of *P. abies* – "abies", *P. obovata* – "obovata", P. *fennica* – "fennica", as well as *P. fennica* close to *P. abies* ("fen_ab") and *P. fennica* close to *P. obovata* ("fen_ob"). Abbreviations of character names correspond to those given in Table 2

Taxon		Lc	D	LcD	NuPa	DevAx	H	W	HW	l_A	L	k	c	kH
"abies"	N=10													
	Mean	12.08	4.17	2.91	12.22	41.3	22.24	14.32	1.56	7.12	4.26	6.74	2.10	0.30
	Min	10.78	3.76	2.55	9.80	30.00	19.72	12.60	1.43	5.64	2.48	5.70	1.52	0.25
	Max	13.74	4.50	3.66	13.50	58.00	26.00	16.00	1.78	8.00	6.62	7.83	3.12	0.35
	SE	0.33	0.07	0.12	0.31	2.75	0.51	0.40	0.03	0.25	0.42	0.24	0.14	0.01
"fen_ab"	N=23													
	Mean	7.85	3.73	2.11	9.54	46.44	19.668	12.92	1.54	5.81	2.70	5.96	2.06	0.30
	Min	6.20	3.04	1.68	6.80	32.20	16.66	10.50	1.35	4.00	1.46	4.46	1.44	0.24
	Max	9.76	4.32	2.53	12.00	65.60	23.00	15.00	1.93	7.62	5.64	7.50	2.76	0.37
	Std. E.	0.19	0.06	0.05	0.28	1.79	0.35	0.26	0.02	0.20	0.18	0.16	0.05	0.01
"fen_ob"	N=21													
	Mean	5.70	2.85	2.01	6.72	59.45	15.70	11.0	1.41	4.19	1.63	5.04	2.02	0.32
	Min	3.76	2.20	1.60	5.40	27.00	11.94	8.73	1.07	2.88	0.62	4.00	1.30	0.26
	Max	7.94	3.74	2.30	9.20	81.40	21.00	15.74	1.60	6.06	4.10	6.00	2.62	0.40
	SE	0.24	0.09	0.04	0.22	2.82	0.59	0.38	0.03	0.23	0.20	0.12	0.05	0.01
"fennica"	N=21													
	Mean	6.67	3.35	1.99	7.6762	52.48	17.37	11.65	1.49	4.66	2.04	5.59	2.11	0.32
	Min	4.60	2.54	1.63	5.60	28.20	13.58	9.02	1.27	3.22	0.94	3.94	1.72	0.23
	Max	8.78	4.28	2.71	11.40	74.40	21.46	15.26	1.79	7.48	3.94	7.40	2.48	0.49
	SE	0.28	0.11	0.05	0.36	2.38	0.55	0.37	0.02	0.21	0.17	0.19	0.04	0.01
"obovata"	N=13													
	Mean	5.41	2.92	1.86	6.40	76.57	13.74	10.31	1.34	4.00	1.24	4.74	2.15	0.34
	Min	4.06	2.24	1.61	5.50	57.50	10.06	8.62	1.17	3.00	0.52	4.08	1.88	0.27
	Max	7.34	3.78	2.14	8.00	91.00	16.34	12.26	1.62	5.13	1.88	5.46	2.60	0.42
	SE	0.26	0.11	0.05	0.22	2.32	0.45	0.32	0.03	0.19	0.12	0.11	0.05	0.01

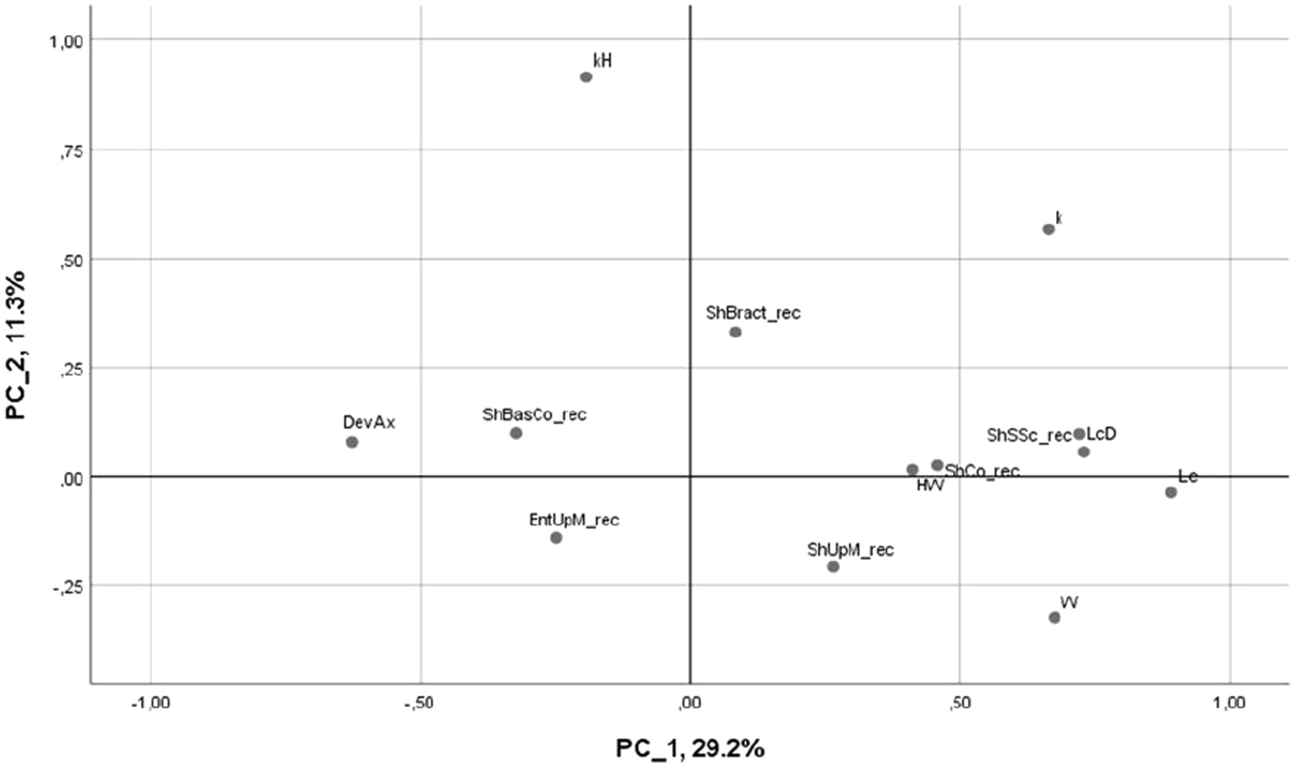

Fig. 4. Factor loadings of 13 measurements analyzed for 415 individuals of typical and intermediate individuals in the space of two main factors of their variability: PC_1 (29.2%) and PC2 (11.3%)

were subjected to multivariate analyses (Principal Component Analysis) implemented in SPSS. Qualitative characters were recoded as numeric in order to be included in the multivariate analysis. Our initial analysis included all 415 cones. We run Principal Component Analysis (PCA) to find out if selected morphological traits of cones produce ordination of the individuals corresponding to our identification of the specimens based on a wider range of morphological characters. Subsequently, we averaged our data matrix by individual tree and repeated the PCA analysis. Since both runs gave similar results we included only those based on average values, i.e. for 88 trees (Fig. 4, 5). Finally, we run Linear Discriminant analyses (LDA) on a selected subset of six non-correlated characters to produce a classificatory function delimiting *P. abies, P. obovata, P. fennica (*Table 4). Morphological variants identified as "*fennica abies*" and "*fennica obovata*" were included in the analysis as separate groups (Fig. 6). Homogeneity of covariances was

Table 4. Pairwise comparisons of LDA classification accuracy for *Picea* taxa based on 6 morphometric measurements of cones and their scales: *P. abies* - "abies", *P. obovata* – "obovata", *P. fennica* – "fennica", as well as *P. fennica* close to *P. abies* ("fen_ab") and *P. fennica* close to *P. obovata* ("fen_ob"). Columns represent predicted taxonomic group. Values in bold indicate the count or percentage (%) of individual cones correctly classified for each taxonomic group

		Predicted Group Membership					Total
		abies	fennica_ab	fennica_ob	fennica	obovata	
Count	abies	**37**	8	0	0	0	45
	fennica_ab	1	**71**	2	22	2	98
	fennica_ob	0	6	**30**	34	26	96
	fennica	1	36	33	**38**	7	115
	obovata	0	0	15	3	**42**	60
%	abies	**82.2**	17.8	0.0	0.0	0.0	100
	fennica_ab	1.0	**72.4**	2.0	22.4	2.0	100
	fennica_ob	0.0	6.3	**31.3**	35.4	27.1	100
	fennica	0.9	31.3	28.7	**33.0**	6.1	100
	obovata	0.0	0.0	25.0	5.0	**70.0**	100

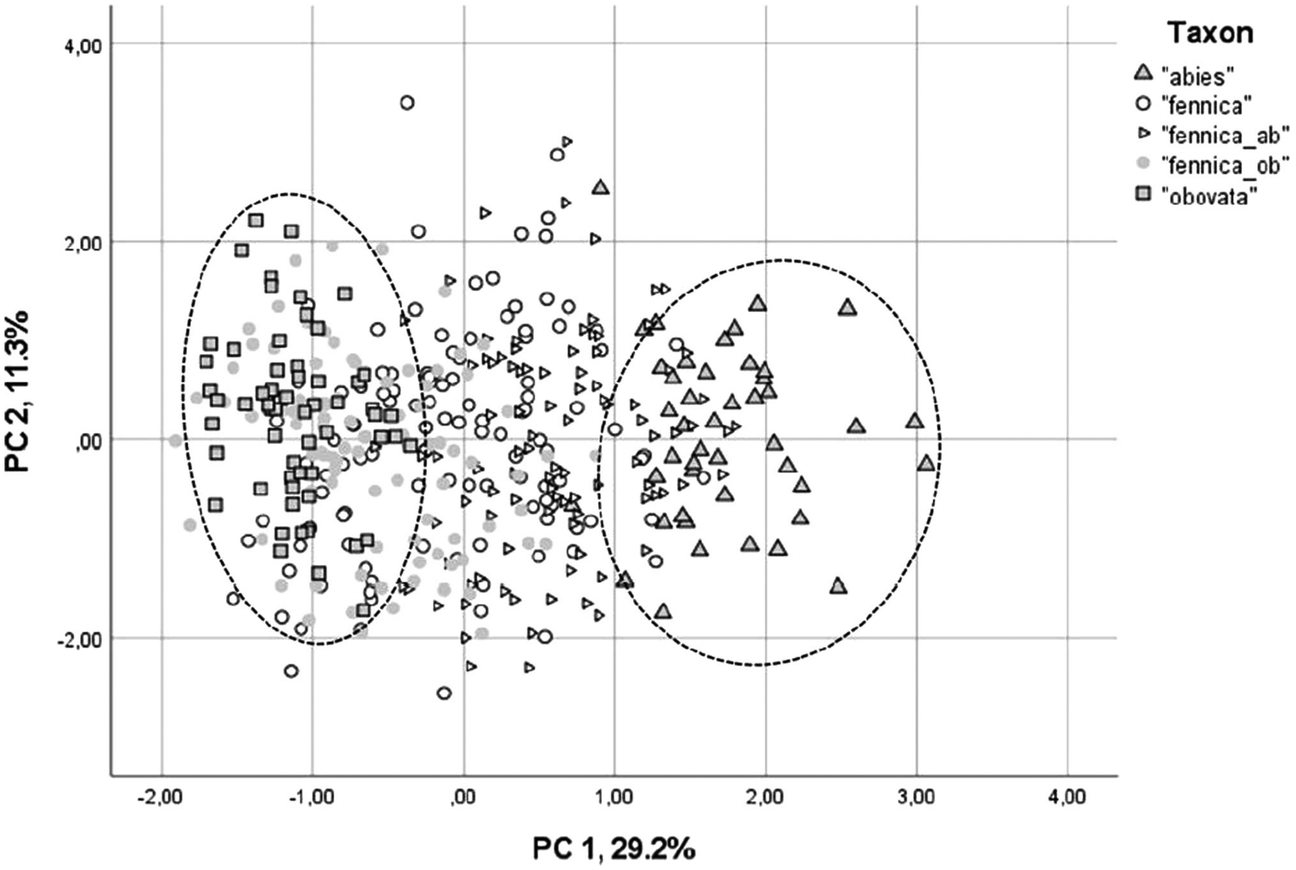

Fig. 5. Ordination of 415 individual cones of *P. abies, P. obovata, P. fennica* complex in space of two main factors of their variability PC_1 and PC_2

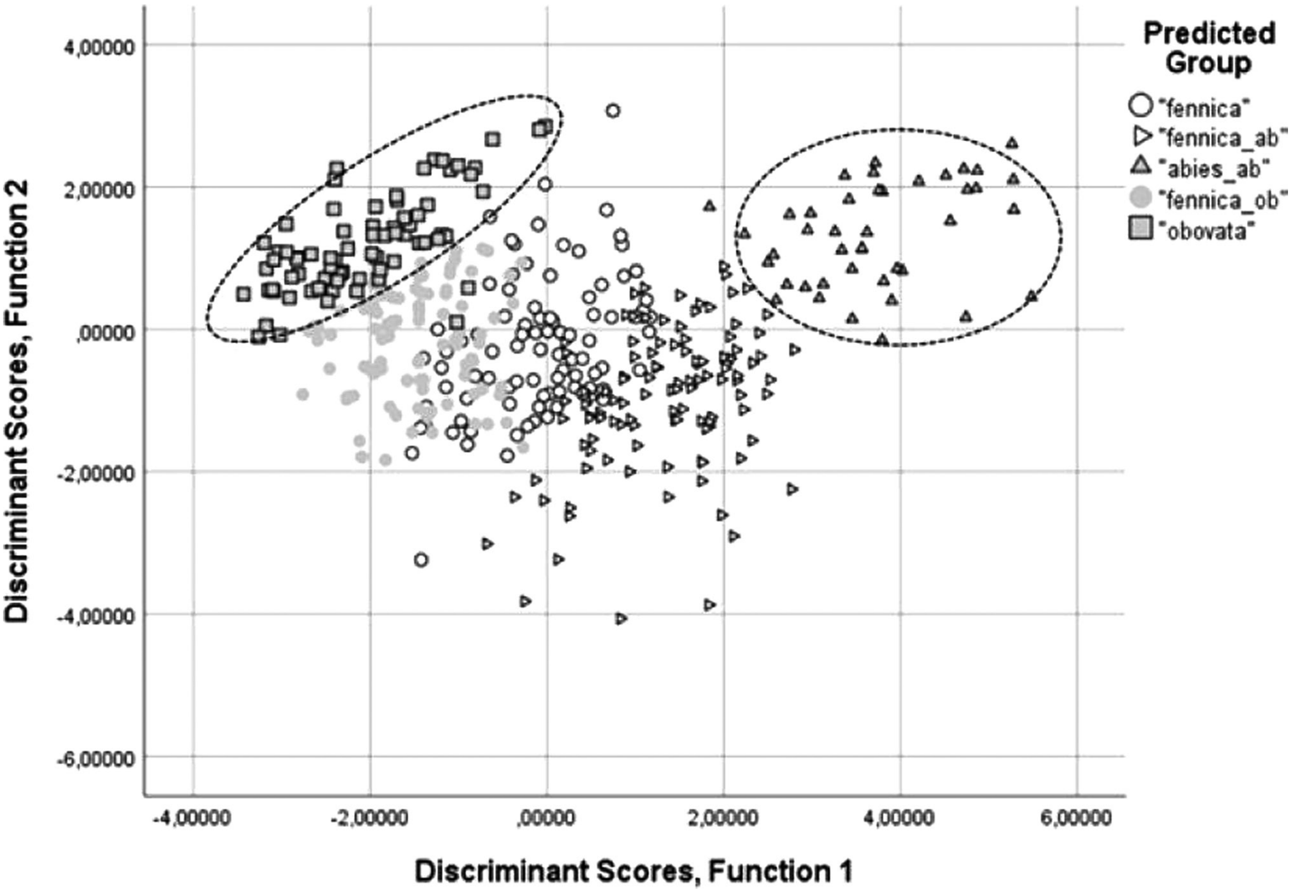

Fig. 6. Classificatory discriminant analysis built on 13 selected characters of cones and their scales to delineate *Picea* taxa of the NW Russia

tested with Box's M test in SPSS. Predictor variables were entered together and within-group covariance matrix was used to separate the groups. To estimate accuracy of the LDA predictive model we used cross validation. This was done only for the cases included in the analysis; each case was classified by the functions derived from all cases other than that case.

Results

Morphometric analyses

Relative proportions of encoded states of the six qualitative (discrete) characters were visualized using pie-charts to study their intra-populational variation. Two of them ShSSc (shape of seed scale), ShUpM (shape of upper margin) have revealed non-overlapping distributions of character states between *P. abies* and *P. obovata* (Fig. 7), while the rest demonstrated high intra-populational morphological diversity. The shape of bract scale (ShBract) had shown that obovate shape of the bract scale is typical of *P. obovata* and *P. fennica* complex, but is not found in *P. abies*. On the other side, narrowly-rhombic shape of bract scale distinguishes *P. abies* from the rest of the taxa. The remaining characters have overlapping values between *P. abies* and *P. obovata,* but can still be used as a supplementary.

Analyses of variance produced statistically significant differences in means of all analyzed continuous morphological characters (F= 4.6–78.3, df=4, p<<0.0001), apart from the bract scale width (c). Pairwise comparisons of the mean values (Appendix 2) had shown that there is only one character – seed scale length (H) having its mean values significantly different in all five taxonomic groups. Most of the other characters would differentiate four groups instead of five, e.g., Lc, D, I_A, k – *"obovata"+"fennica_ob"* vs. *"fennica"*, *"fennica_ab"*, *"abies_ab"*; or DevAx – *"abies_ab"+ "fennica_ab"* vs. *"fennica"*, *"fennica_ob"*, *"obovata"*.

Principal Component Analyses (PCA) were applied to two data matrices: one included all 415 individual cones and other included averaged values of measured characters per tree. Both data sets produced very similar results and here we present only those which are based on individual measurements. Application of PCA analyses revealed a large group of correlated characters. Seven highly correlated characters were considered redundant and were excluded from the final PCA analysis. Two main axes PC_1

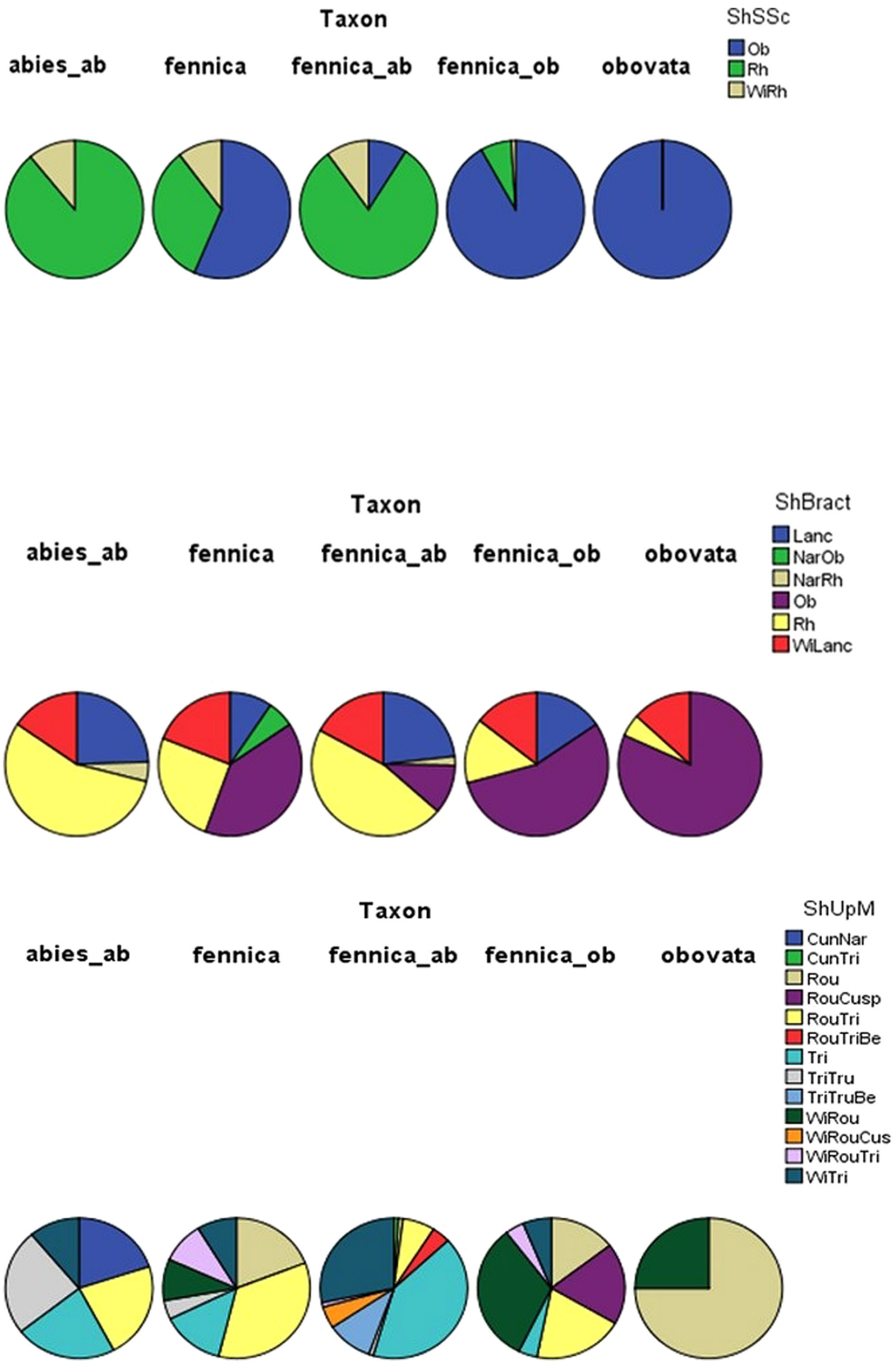

Fig. 7. Pie-charts visualizing differences in numerical proportions of the character states of the most informative discrete morphological characters delineating *Picea abies*, *P. obovata* and intermediate forms of *P. fennica* complex. Abbreviations of character names correspond to those given in Table 2

& PC_2 explained 40.5 % of total variation of the character matrix, comprising 13 selected characters of cones and their scales (Fig. 4). Characteristics of cone length (Lc), elongation of cones (LcD), length of bract scales (k) and shape of seed scale (ShSSc_rec) had the highest positive correlations with PC_1 (Fig. 4, Table 2). Ratio of the bract scale length to seed scale length (kH) had the highest factor loadings on the PC_2 (Fig. 4), variation in this character described rather within species, but not between species differences. Comparison of the *Picea* taxa in the PC space had shown a large overlap between *P. obovata* and *P. fennica* complex, while individuals of *P. abies* formed more separate and less overlapping cluster on its own. This result has been reproduced and even reinforced by the Discriminant analysis (Fig. 6). Six variables were retained to produce Canonical Discriminant functions based on absolute size of correlation within function: Cone length (Lc), Seed scale deviation from the axis of the cone (DevAx), Seed scale width (W), Ratio of seed scale length to seed scale width (HW), Height of visible part of seed scale (I_A) and Bract scale length (k). As the result of analysis, four discriminant functions were built explaining in total 98.3% of total variance. Cross-validation of classification resulted in correct identification of 82.2% for *P. abies* and 70.0% for *P. obovata*. Identification of *P. fennica* groups gave the highest percent for "*fennica abies*" – 72.4%, and low success for "*pure fennica*" – 33.3% and "*fennica obovata*" – 31.3% (Table 4).

Distribution and phytocenotic characters of *Picea* taxa in North-West Russia

In the northern part of the Northern taiga in the Murmansk Region indigenous spruce forests are formed mainly by *P. obovata* (up to 95 %) (Table 1). The form of *P. fennica*, close to *P. obovata* (5–30%) occurs almost throughout the Murmansk Region up to the suburbs of Olenegorsk (68°10'39.4" N, 33°19'12.6" E, 146 m a. s. l.), where its proportion is about 10%. However, in the southern part of the Kandalaksha district, in the far south-west and the south of the Murmansk Region (67°03'50.1" N, 31°57'35.9" E, 7 m a. s. l.), which belong according to our division to the middle part of the Northern taiga, the proportion of *P. obovata* is decreasing, meanwhile the share of the form of *P. fennica* close to *P. obovata* is increasing (Fig. 1, 2, Table 1). Moreover, the intermediate form of *P. fennica* also occurs in a small amount (15–20%). A similar pattern is observed also in the Kem and Louhi regions of the North Karelia, which belong to the middle part of the Northern taiga.

Spruce forests in the northern and middle parts of the Northern taiga region are represented by *Fruticuloso-hylocomiosum* communities. The ground cover of such communities is formed by mosses, among which green mosses (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Bruch et al., *Dicranum polysetum* Sw.) dominate, and common undershrubs (*Vaccinium myrtillus* L., *V. vitis-idaea* L., *V. uliginosum* L., *Empetrum hermaphroditum* Hagerup, *Ledum palustre* L.), usually codominating. In some communities *Chamaepericlymenum suecicum* (L.) Asch. et Graebn. and sometimes common boreal short herbs are abundant.

In the middle part of the Northern taiga region bilberry-green moss spruce forests (*Vaccinioso-hylocomiosum*) are spread. They differ from dwarfshrub-green moss communities (*Fruticuloso-hylocomiosum*) by the absence of bog dwarf shrubs and precence of boreal short herbs (*Luzula pilosa* Baumg., *Maianthemum bifolium* (L.) F. W. Schmidt, *Trientalis europaea* L., *Melampyrum pratense* Tausch ex W. D. J. Koch). In northern variants of *Vaccinioso-hylocomiosum* communities the group of boreal short herbs may be poorly represented. Bilberry-green moss spruce forests are richer variant of green moss forests (*Hylocomiosum* group), than *Fruticuloso-hylocomiosum* communities.

The northernmost locality of *Picea abies* var. *abies* was recorded in the southern part of the Northern taiga in the Belomorskiy district of the North Karelia (64°24'38,7" N, 34°11'36.9" E, 123 m a. s. l.), where the proportion of this taxon is about 5% (Fig. 1, Table 1). The proportion of *P. obovata* and the form of *P. fennica* close to *P. obovata* slightly decreases here (about 40 and 20% respectively), but the role of the form of *P. fennica* close to *P. abies* and intermediate form of *P. fennica* significantly increases (15 and 20% respectively). In this part of the Northern taiga the proportion of *P. abies* var. *abies* could be up to 40% (Table 1), but in general *P. fennica* and its forms predominate in the area; their proportion in the forests is 50–90%. In the southern part of the Northern taiga the maximum proportion of *P. fennica* (60%) was recorded in *Fruticuloso-hylocomiosum-Sphagnosum* plant communites in Segezha district (63°18'34.0" N, 34°26'19.1 E, 113 m a.s.l.) (Belyaev et al., 2010).

In the southern part of the Northern taiga, *Picea abies* var. *abies* was observed in high-productive for this area bilberry-greenmoss communities (*Vaccinioso-hylocomiosum*), just in which here probably may exist this taxon as the most demanding to soil fertility. The sphagnous spruce forests, characterized by a sufficient proportion of *Sphagnum girgensohnii* Russow and green mosses are fairly rare in the area. Common species of oligotrophic habitats (e.g., *Carex globularis* Roth, *Rubus chamaemorus* L.) are typical in this northern variant of spruce forest.

Maximum proportion of *Picea fennica* in spruce forests in the study area was recorded in the middle taiga region, where it varies from 30 % up to 75%, the average value is 45%. The relative occurance of 75% was reported for *P. fennica* in *Vaccinioso-hylocomiosum* plant community in Medvezhegorskiy district (62°51'19.8"N, 34°19'40.1"E, 127 m a. s. l.), and seems to be maximum in this region. In the southern part of the Middle taiga the proportion of *P. fennica* decreases to 30% in Lodejnopolsky district of the Leningrad Region. The percentage of the form, close to *P. obovata* is 10%, and the occurrence of the form of *P. fennica*, close to *P. abies* is 0–50% (Table 1, Fig. 2).

In the middle taiga in Karelia a tendency to gradual increasing of *Picea abies* in the composition of spruce forests takes place from 10% in the northern part of the region (Medvezhegorsky district) up to 45% in the southern part (Olonetskiy district), and reaches maximum (55%) in Lodeynoye Pole district in the Leningrad Region (60°48'16.7" N, 33°44'23.4" E., 33 m a.s.l.). Spruce forests in this region are represented by billberry-greenmoss and sphagnous plant communities.

In the southern Karelia there are stands, formed by *Picea obovata* and the form of *P. fennica* close to *P. obovata*, as well as *Pinus friesiana* Wich. One of these sites was discovered in 2009 near the city of Petrozavodsk (near the stone quarry in the southern part of the city). But in general the proportion of *P. obovata* in the forests of this region is very small (0–5%) (Belyaev et al., 2010).

To the south-west of Petrozavodsk – in Pryazha district (61°36’51.1” N, 33°37’09.0” E 163 m a.s.l.; 61°31’08.6” N, 33°27’43.4” E, 172 m a.s.l.), and also in the village of Pyazhieva Selga in Prionezhskiy district (c. 50 km to SW of Petrozavodsk), the proportion of *P. abies* var. *abies* is about 20–30%, but the role of *P. fennica*, close to *P. abies* and *P. obovata* increases (50% and 15–20% correspondingly).

In the southern taiga region within the Leningrad Region the proportion of *P. abies* var. *abies* in spruce forests is 60–90 %. The rate of *P. fennica*, according to our data, is small, just 0–10 %. Geobotanical investigations revealed that these taxa occur here in different plant communities from *Sphagnosa*-type to *Hylocomiosa* (*Vacciniosum* and *Oxalidosum*) forests on well-drained soils. *Oxalidoso-Hylocomiosum* spruce forests are high-productive in these conditions and are characterized by the presence of some hemiboreal species (e.g., *Stellaria nemorum* L., *Anemone nemorosa* L., *Galeobdolon luteum* Huds.) in the herb-undershrub layer. In these communities *P. abies* var. *abies* predominates, meanwhile the forms of *P. fennica* can occur as an admixture, without any preferences in growing conditions.

Distribution of *Picea taxa* on the islands of the Gulf of Finland

Earlier Finnish spruce has been known only from the Berezovye Islands Archipelago (Severny Berezovy and Maly Berezovy) (Glazkova & Tzvelev, 2007). Monitoring studies on the islands of Vyborg Bay and the Gulf of Finland in 2011–2017 showed, that Finnish spruce occurs on most of the islands as an admixture in coniferous forests (mostly spruce and small-leaved-spruce stands). Noteworthy is the fact that on the islands of the Gulf of Finland all three forms of *P. fennica* have been recorded (Appendix 1, Fig. 2). Thus, on the islands Gogland, Moschny, Bolshoy Tyuters, Severny Berezovy, Maly Berezovy, Dolgy Greben’, Zaovrazhensky and some others both *P. fennica* close to *P. abies* and *P. fennica* close to *P. obovata* occur. The form of *P. fennica* close to *P. obovata* seemingly predominates on the islands. It also was recorded on Kurgalsky Peninsula and the neighbouring islands, as well as on the islands near the northern coast of the Gulf of Finland close to the Russian-Finnish border (Dolgy Greben’, Krasny, Kozliny etc.) and on Zaovrazhensky Island in the Vyborg Bay. However, on the Berezovye Islands Archipelago *P. fennica* close to *P. abies* occurs more often. Intermediate form of *P. fennica* has been recorded only on the outer islands of the Gulf of Finland (Bolshoy Tyuters, Gogland, Moschny, Seskar). Noteworthy is also the fact that on some islands of the eastern Gulf of Finland occur also intermediate forms of some other taxa (e. g., species of *Solidago, Phleum, Potentilla, Juniperus, Pinus*), probably formed also as a result of introgressive hybridization of parental species (Orlova & Glazkova, 2018).

Among the most recent discoveries is occurrence of Siberian spruce on the islands Gogland (Suursaari) and Severny Berezovy (Piisaari). *P. obovata* was found in different parts of the island Gogland (Coll. Glazkova, Appendix 1, Fig. 1). We have also recorded some isolated occurances *Picea obovata and P. fennica* close to *P. obovata* in the southern Karelia, in the vicinity of Petrozavodsk (Coll. Orlova, 2009).

Analysis of the forest floor and undergrowth data, reveals that the form of *P. fennica* close *to P. obovata* usually occurs in herb-rich deciduous-spruce forest with nemoral species in herbaceous layer, sometimes in more poor birch-spruce and birch-pine forests, whereas the form of *P. fennica* close to *P. abies*, on the contrary, often grows in fairly poor-of-species blueberry and bilberry-green moss spruce and small-leaved-coniferous forests.

Discussion

Our results based on the six qualitative (discrete) characters have revealed that the two characters: ShSSc (shape of seed scale) and ShUpM (shape of upper margin) have non-overlapping distributions and can separate *P. abies* and *P. obovata*, while the rest of the studied characters have demonstrated high intra-populational morphological diversity. Diagnostic value of these characters in delimiatation of these species have been already demonstrated in earlier studies (Danilov, 1943; Lindquist, 1948; Bakshaeva, 1963, 1966, 1971; Parfenov, 1971; Pravdin, 1975; Bobrov, 1971, 1974, 1978; Farjon, 1990).

In addition, our study had demonstrated diagnostic value of the bract scales of mature cones (length, width and shape). Bract scale length (k) values were correlated with the complex of diagnostic characters of seed scales and can be used in indentification keys. Obovate shape of the bract scale (ShBract) is typical of *P. obovata* and *P. fennica* complex, but is not found in *P. abies*. While narrowly-rhombic shape of bract scale distinguishes *P. abies* from the rest of the taxa. Bract scale width is correlated with ShBract. Being a quantitative character it can be provided along with ShBract in the indentification keys. However, these characters are rarely (Farjon, 1990) used in the taxonomy of the *Picea* species.

Comparison of the *Picea* taxa in the PC space had shown a large overlap between *P. obovata* and *P. fennica* complex, while individuals of *P. abies* formed more separate and less overlapping cluster on its own. Multivariate ordination with PCA and cross-validation of Discriminant function model are consistent with the findings of Potokina et al. (2013) who applied microsatellite markers to study genetic diversity in populations of spruce in the North-West of European Russia. Molecular genetic studies have strongly indicated existing gene flow between populations of *P. fennica* and *P. obovata,* as well as also between *P. obovata* and *P. abies* (Potokina et al., 2013; Volkova et al., 2014). Processes of introgressive hybridization, having continued so far in the area of contact of parental species, evidently lead to smoothing of characteristics of the Finnish spruce, that finally prevents the final formation of *P. fennica* as a separate stable species and can be interpreted as a complex result of both historical and ongoing hybridization.

As a result of our geobotanical studies, the distribution of Picea taxa in the North-West of the European part of Russia has been specified. Our study in 2011 in the north-eastern part of the Leningrad Region revealed, that *P. obovata* occurs in small amount only in the spruce forests, located near the town Podporozhye and village of Voznesenye, which agree with the literature (Tzvelev, 2000). However, the information about the occurrence of *P. obovata* in the east and the north-east of the Leningrad Region needs to be confirmed, because only two mature cone of P. obovata was collected form these place.

The key for the determination of *Picea abies* and closely related taxa in North-West of Russia

1\. Needles gradually pointed, located on shoots pectinately. Annual shoots are slightly pubescent, often winding; pulvini of annual shoots often clustered by 3–4. Profills of apical buds glabrous, exceed the length of buds greater than 1,5 times. Cones 9,5–15,3 cm long, narrowly obovate or obovate-cylindrical, more or less direct, with cuneate-shaped base. Seed scales rhombic or widely rhombic, by the the upper margin triangular or widely triangular or oval, unequal dentate. Bract scales 4,5–8,7 mm long, 1,2–3,9 mm wide, rhombic, wrong rhombic or lanceolate, acute or obtuse 1. *P. abies* var. *abies*

\+ Needles shortly pointed or varied in shape of apex (short pointed or gradually pointed). Annual shoots are more or less densely pubescent. Profills of apical buds shorter. Cones shorter 2.

2\. Upper margin of seed scales widely rounded, entire. Needles shortly pointed, annual shoots more or less direct, often short and densely pubescented by simple and glandular hairs. Profills of apical buds markedly pubescent, approximately equal to bud or 2/3 of its length 2. *P. obovata*

\+ Upper margin of seed scales unequally dentate, wavy or rounded, suddenly narrowed. Shape of needle apex: short and gradually pointed. Annual shoots are more or less densely pubescent. Profills of apical buds glabrous or pubescent approximately equal to bud or 2/3 of its length 3.

3\. Upper margin of seed scales triangle, sharpened. Annual shoots are covered with simple hairs. Profills of apical buds and pulvini naked. Profills approximately equal to the bud, pulvini of annual shoots rectangular and often clustered by 3–4 3. *P. fennica* close to *P. abies (=P. fennica* × *P. abies)*

\+ Seed scales with rounded, irregularly toothed, wavy or noticeably elongated upper margin. Annual shoots are covered with simple and glandular hair. Profills of apical buds and pulvini pubescent. Profills approximately equal 2/3 of buds length, pulvini square or glass-shaped and arranged evenly 4.

4\. Seed scales with rounded, irregularly toothed upper margin. Annual shoots, pulvini and profills densely pubescent. Needles mainly short pointed 4. *P. fennica* close to *P. obovata (=P. fennica* × *P. obovata)*

\+ Seed scales with noticeably elongated upper margin. Annual shoots, pulvini and profills slightly pubescent. Needles short pointed and gradually point .5. *P. fennica* (Regel) Kom. var. *fennica*

P. abies var. *abies*

Needles 10–16 mm long, 1–1,5 mm wide, quadrangular, gradually pointed, with 2–4 stomatal lines on each face; needles positioned on shoots pectinately. Annual shoots are slightly pubescent, with both long and short simple hairs; biennial shoots are glabrous or pubescent similarly. Pulvini of annual shoots are 0,5–1 mm long, rectangular or more expanded upward, often clustered by 3–4. Apical buds glabrous or slightly pubescent; profills are glabrous, exceed the length of buds greater than 1.5 times. Cones 9,5–15,3(Lc=12,2±1.5) cm long, 3,4–4,9(D=4,2±0,4) cm wide, and its length to width ratio 2,4–3,8 (LcD=3,0±0,4), narrowly obovate or obovate-cylindrical, more or less direct, with cuneate-shaped base. Seed scales 15,0–28,0(H=22,1±2.8) mm long, 9,0–20,0(W=14,2±2.0) mm wide, deviated from the axis by 30–60°, rhombic or widely rhombic, by the upper margin triangular, widely triangular or oval, unequal dentate. Height of visible part of the seed scale 4,0–10,0(I_A=7,1±1.3) mm. Tongue height 2,0–7,5(L=4,4±1.6) mm. Bract scales 4,5–8,7(k=6,7±1,1) mm long, 1,2–3,9(c=2,1±0,6) mm wide, rhombic, wrong rhombic or lanceolate, with acute or obtuse apex. Bract scale length to seed scale length ratio 0,20–0,45 (kH=0,30±0,05).

Picea obovata

Needles 8–15(20) mm long, 1–1,8 mm wide, quadrangular, suddenly sharpened, more or less straight, with 2–5 stomatal lines on each face. Annual shoots 2–2,5 mm width, more or less direct, often short and densely pubescent by hairs of 3–5 types. Pulvini of annual shoots 0,3–0,7(–1,2) mm long, glass-likely-square to rectangular, pubescent, disposed evenly. Apical buds 4–5 mm long, 3–4 mm wide, ovoid-conical, densely pubescent; profills of apical buds markedly pubescent, approximately equal to the bud or 2/3 of its length. Cones 3,7–8,5(Lc=5,5±1,2) cm long, 1,7–4,0(D=3,0±0,6) cm wide, and also its ratio 1,4–2,8 (LcD=1,9±0,3), cylindrical or ovoid-cylindrical, with rounded or plate base. Seed scales 9,3–19,0(H=13,8±2,3) long and 7,4–14,0(W=10,4±1,8) wide, obovate, by upper margin widely rounded, entire. Height of visible part of seed scale 2,0–7,0(I_A=4,1±1.0). Tongue height 0,3–2,5(L=1,3±0.6). Bract scales 3,2–6,3(k=4,6±0,8) mm long, 1,5–3,2(c=2,2±0,3) mm wide, obovoid, rounded, sometimes triangle or widely rhombic with obtuse apex. Ratio of bract scale length to seed scale length 0,23–0,50 (kH=0,35±0,06).

Picea fennica, close to *P. abies* (=*P. fennica* × *P. abies*)

Differs from *P. abies* by strong variability in the structure of the apex of needles (often it can be both gradually or suddenly sharpened), annual shoots are smaller (7,5–11 cm long), more densely pubescent by short simple hairs, cones often curved, with triangle, sharpened by upper margin seed scales. Needles 10–16 mm long, 1–1,5 mm wide, quadrangular, apex gradually or suddenly sharpened. Annual shoots are covered with simple hairs. Profills of apical buds and pulvini glabrous. Profills approximately equal to the bud, pulvini of annual shoots rectangular and often clustered by 3–4. Cones 5,7–10,5(Lc=7,9±1.2) cm long, 2,5–5,3(D=3,7±0.5) cm wide, and also length to width ratio 1,6–2,7 (LcD=2,1±0,3), obovate-cylindrical or obovate, often curved, with cuneate, rarely rounded base. Seed scales 12,5–27,0(H=19,8±3,2) mm long, 8,5–19,0(W=13,1±2,1) mm wide, rhomboid-obovate, by upper margin by the upper margin triangular, acute. Height of visible part of seed scale 3,2–10,0(I_A=5,9±1,6) mm long. Tongue height 0,7–6,8(L=2,7±1,1) mm long. Bract scales 3,2–9,0(k=6,1±1,1) mm long and 1,0–3,5(c=2,1±0,5) mm wide, rhombic, lanceolate or widely lanceolate, rarely obovate, with obtuse, sometimes rounded, apex, very variable. Ratio of bract scale length to seed scale length 0,19–0,53 (kH=0,31±0,06).

P. fennica, close to *P. obovata* (=*P. fennica* × *P. obovata*)

Differs from *P. obovata* by strong variability in the structure of the apex of needles (often it can be both gradually or shortly sharpened), and from *P. fennica,* close to *P. abies*, by the location of needles (located on shoots in more than two rows, often corimbosely), markedly densely pubescent annual and biennial shoots (3–4 hair types: long, surrounding, short simple and glandular hairs. Needles 12–15 mm long, 1–1,8 mm wide, quadrangular, mainly short pointed. Annual shoots, pulvini and profills densely pubescent. Cones 3,0–10,3(Lc=5,7±1,4) cm long, 1,3–5,1(2,8±0,6) cm width, and also its ratio 1,4–2,8 (LcD=1,9±0,3), narrowly-ovoid or ovoid-cylindrical, often curved, with rounded, rarely cuneate base. Seed scales 9,0–22,6(H=15,8±2,5) mm long, 7,0–18,0(11,00±1,8) mm wide, ovoid or widely-rhombic. Height of visible part of seed scale 2,3–14,0(I_A=4,1±1,5) mm long. Tongue height 0,2–5,0(L=1,7±1,2) mm long. Bract scales 3,0–7,0(k=5,0±0,9) mm long, 1,0–3,0(c=2,1±0,4) mm wide, obovate, rarely lanceolate or widely-lanceolate, sometimes rhombic, very variable. Ratio of bract scale length to seed scale length 0,20–0,49 (kH=0,33±0,06).

P. fennica (Regel) Kom. var. *fennica*

Differs from other close taxa by noticeably elongated and rounded upper margin of seed scales, and also by middle pubescented apical buds, pulvini and profills.

Needles 12–15 mm long, 1–1,8 mm wide, quadrangular, short pointed and gradually pointed. Annual shoots, pulvini and profills middle pubescent by simple and glandular hairs. Cones 3,5–10,5(Lc=6,8±1,5) cm long, 1,8–5,5(3,4±0,7) cm wide, and also its ratio 1,3–2,9 (LcD=2,0±0,3), obovate-cylindrical, narrowly obovate or obovate, with varying shape of cone base – from rounded to wedge. Seed scales 11,0–23,0(H=17,5±2,9) mm long and 1,4–16,7(11,7±2,2) mm wide, rhomboid-obovate, obovate or widely obovate; at the upper margin noticeably elongated, deviating at 30–45° from the cone axis. Height of visible part of seed scale 2,5–9,4(I_A=4,7±1,4) mm long. Tongue height 0,5–8,0(L=2,1±1,2) mm long. Bract scales 2,7–9,0 (k=5,6±1,1) mm long, 1,0–3,7(c=2,1±0,5) mm wide, triangular, rhombic or widely lanceolate, obtuse. Ratio of bract scale length to seed scale length 0,23–0,50 (kH=0,35±0,06).

Conclusion

Based on our results, the most valuable characteristics for delimitation of *Picea abies* and closely related taxa (*P. obovata* Ledeb. and *P. fennica* (Regel) Kom.) are morphological characteristics of mature cones and their scales. Some of these characteristics (morphology and size of bract scales and ratio of the size of seed scales and bract scales *etc.*), proposed here and show to be conservative and valuable for the systematics and diagnostics of these taxa. It was shown that obovate shape of the bract scale (ShBract) is typical of *P. obovata* and *P. fennica* complex, and it is not found in *P. abies*. While narrowly-rhombic shape of bract scale distinguishes *P. abies* from the rest of the taxa. Seed scales of *Picea fennica* by upper margin triangle to noticeably elongated, unequally dentate, wavy or rounded, suddenly narrowed. Cones (3–)6–11 cm long, from cylindrical to oblong-ovate, often curved. Also this taxon differs from parental species by noticeably pubescent young shoots and strong variability in the structure of the apex of needles (often it can be both gradually or shortly sharpened even within one shoot).

We provided identification key for these species which includes among others 14 new characteristics of vegetative organs, e.g. young shoots, its pulvini, apical buds and their scales and profills (basal thickened scales at the base of buds).

The distribution of spruce taxa in the North-West Russia is determined by the latitudinal gradient. Phytocenotic analysis showed that different spruce taxa occupy certain habitats, which in their turn connected with the latitudinal gradient. *P. obovata* usually forms dwarfshrub-green moss spruce forests in the Northern taiga, *P. fennica* forms bilberry-green moss and sphagnous spruce forests in the southern part of the Northern taiga and in the middle taiga, and *P. abies* predominates in sphagnous, oxalis-green moss and bilberry-green moss spruce forests in in the middle and southern taiga regions. Phytocenotic range of *P. abies* and *P. fennica* overlap in the middle taiga region. As a result of long-term monitoring investigations on the numerous islands in the Gulf of Finland and the Vyborg Gulf, new interesting and important information on the distribution of taxa close *P. abies* in this area was collected. Analysis of the distribution of *P. fennica* on the islands of the Gulf of Finland showed that besides the widespread *P. abies*, Finnish spruce is rather common on the islands, and represented by both as typical "*fennica*" as well as the putative backcrosses to "*obovata*" and "*abies*". Processes of introgressive hybridization, having continued so far in the area of contact of parental species, evidently lead to smoothing of characteristics of the Finnish spruce, that finally prevents the final formation of *P. fennica* as a separate stable species. Noteworthy is also the fact that on some islands of the eastern Gulf of Finland occur also intermediate forms of some other taxa (e. g., species of *Solidago, Phleum, Potentilla, Juniperus, Pinus*), probably formed also as a result of introgressive hybridization of parental species.

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References

Aarrestad PA, Myking T, Stabbetorp OE & Tollefsrud MM (2014) Foreign Norway spruce (*Picea abies*) provenances in Norway and effects on biodiversity. NINA Report 1075.

Aleksandrova VD & Jurkovskaya TK (1989) Geobotaničeskoe rajonirovanie Nečernozem'â evropejskoj časti RSFSR. Nauka, Leningrad, Russia.

Alsos IG, Sjögren P, Brown AG, Gielly L, Merkel MKF, Paus A, Lammers Y, Edwards ME, Alm T, Leng M, Goslar T, Langdon CT, Bakke J & van der Bilt WGM (2020) Last Glacial Maximum environmental conditions at Andøya, northern Norway; evidence for a northern ice-edge ecological "hotspot". Quaternary Science Reviews 239: 106364. doi:org/10.1016/j.quascirev.2020.106364.

Averyanov AV, Budantsev AL, Geltman DV, Konechnaya GYu, Krupkina LI & Sennikov AN (2006) Illûstrirovannyj opredelitel' rastenij Leningradskoj oblasti. KMK Scientific Press Ltd., Moscow, Russia.

Bakin V, Rogova TV & Sitnikov AP (2000) Sosudistye rasteniâ Tatarstana. Publishing House of Kazan University, Kazan, Russia.

Bakshaeva VI (1963) Meždvidovye gibridy eli sibirskoj i eli evropejskoj: Naučnaâ konferenciâ, posvâŝennaâ itogam rabot instituta Lesa Karel'skogo filiala N SSSR za 1962 g. OV Kuusinen Petrozavodsk State University, Petrozavodsk, Russia, pp. 50–51.

Bakshaeva VI (1966) Izmenčivost' i formovoe raznoobrazie eli v Karelii: Avtoreferat dissertacii... kandidata biologičeskih nauk. OV Kuusinen Petrozavodsk State University, Petrozavodsk, Russia.

Bakshaeva VI (1971) Âvlenie dissimetrii morfologičeskih priznakov vegetativnyh organov sosny i eli v Karelii. Lesovedenie 6: 55–61.

Beissner L (1909) Handbuch der Nadelholzkunde; Systematik, Beschreibung, Verwendung und Kultur der Ginkgoaceen, Freiland-Coniferen und Gnetaceen, für Gärtner. Forstleute und Botaniker. P. Parey, Berlin, Germany.

Belyaev DY, Potokin AF, Orlova LV, Byalt VV, Ivanov SA & Egorov AA (2010) Širotnaâ differenciaciâ el'nikov s učetom geografičeskogo rasprostraneniâ *Picea abies*, *P. obovata* i *P. fennica* nac Severo-Zapade Evropejskoj časti Rossii: Sovremennye problemy i perspektivy racional'nogo lesopol'zovaniâ v usloviâh rynka: Sbornik materialov Meždunarodnoj naučno-praktičeskoj konferencii molodyh učenyh i specialistov (10–11 noâbrâ 2010 v Sankt-Peterburgskoj Gosudarstvennoj Lesotehničeskoj akademii) (ed. by VA Sokolova et. al.), MSP, St. Petersburg, Russia, pp. 64–69.

Bobrov EG (1944) Ob osobennostâh flory èrratičeskoj oblasti (odin iz putej formirovaniâ). Sovetskaâ Botanika 2: 3–20.

Bobrov EG (1971) Istoriâ i sistematika roda *Picea* A. Dietr. Novosti Sistematiki Vysših Rastenij 7: 5–40.

Bobrov EG (1974) Pinophyta (Gymnospermae) – Hvojnye: Flora evropejskoj časti SSSR. Vol. 1 (ed. by AA Fedorov) Nauka, Leningrad, Russia, pp. 100–116.

Bobrov EG (1978) Lesoobrazuûŝie hvojnye SSSR. Nauka, Leningrad, Russia.

Bobrov EG (1983) Introgressivnaâ gibridizaciâ i geoistoričeskie smeny formacij taežnoj zony SSSR. Botaničeskij Žurnal 68: 3–9.

Danilov VN (1943) Izmenčivost' semennyh češuj *Picea excelsa*. Botaničeskij Žurnal 2: 191–202.

Doronina AYu (2007) Vascular plants of the Karelian Isthmus (Leningrad Region). KMK Scientific Press Ltd., Moscow, Russia.

Efimov PG & Konechnaya GYu (2018) Konspekt flory Pskovskoj oblasti (sosudistye rasteniâ). KMK Scientific Press Ltd., St-Petersburg-Moscow, Russia.

Egorov AA, Afonin AN & Orlova LV (2015) On the borders the taiga vegetation and distribution of natural taxa *Picea* in northwest Russia: Book of abstracts, 24th International Workshop of the European Vegetation Survey. Typology and process as two complementary facets of vegetation survey and mapping. Vegetation in coastal and inland dunes and cliffs (ed. by V Briand & S Rapinel) 4–8 May 2015. University of Rennes, Rennes, France.

Farjon A (1990) Pinaceae, Drawings and Descriptions of the Genera *Abies*, *Cedrus*, *Pseudolarix*, *Keteleeria*, *Nothotsuga*, *Tsuga*, *Cathaya*, *Pseudotsuga*, *Larix* and *Picea*. Regnum Vegetabile, Vol. 121. Koeltz Scientific Books, Köningstein, Germany.

Farjon A (2001) World checklist and bibliography of conifers. 2rd ed. Royal Botanical Gardens, Kew, UK.

Farjon A (2017) Handbook of the world's conifers: Revised and updated edition. Brill, Leiden-Boston, Netherlands. Vol. 1.

Farjon A & Filer D (2013) An atlas of the world's conifers: An analysis of their distribution, biogeography, diversity and conservation status. Brill, Leiden–Boston, Netherlands.

Glazkova EA & Tzvelev NN (2007) Vascular plants: Natural environment and biodiversity of the archipelago Birch Island (Gulf of Finland) (ed. by EA Volkova, EA Glazkova, GA Isachenko & VN Hramtsova, a) ''Boston-Spektr'', St. Petersburg, Russia, pp. 140–190.

Hämet-Ahti L, Palmén A, Alanko P & Tigerstedt PMA (1992) Suomen puu-ja pensaskasvio. Helsinki, Finland.

Il'inov AA, Raevskii BV, Rudkovskaya OA & Topchieva LV (2011) Sravnitel'naâ ocenka fenotipičeskogo i genetičeskogo raznoobraziâ severotažnyh malonarušennyh populâcij eli finskoj (Picea x fennica). Trudy Karel'skogo Naučnogo Centra RN 1: 37–47.

Jalas J & Suominen J (1973) Gymnospermae (Pinaceae to Ephedraceae): Atlas florae Europaeae. Vol. 2. The Committee for Mapping in the Flora of Europe & Societas Biologica Fennica Vanamo, Helsinki, Finland.

Jonsell B (2000) Flora Nordica. Vol. 1. The Bergius Foundation, Stockholm.

Komarov VL (1934) Coniferales – Coniferous: Flora of the USSR. Vol. 1 (ed. by VL Komarov & MM Il'in) Publishing House of the Academy of Sciences of the USSR, Moscow, Leningrad, Russia, pp. 130–195.

Kravchenko AV (2007) A compendium of Karelian flora. Karelian Research Center of the Russian Academy of Sciences, Petrozavodsk, Russia.

Lantratova AS (1985) Analiz dendroflory Karelii. Guide. "Karelia", Petrozavodsk, Russia.

Latałowa M & van der Knaap WO (2006) Late quaternary expansion of Norway spruce *Picea abies* (L.) Karst. in Europe according to pollen data. Quaternary Science Reviews 25: 2780–2805.

Lindquist B (1948) The main varieties of *Picea abies* (L.) Karst. in Europe. Acta Horti Bergiani 14: 249–342.

Lockwood JD, Aleksić JM, Zou J, Wang J, Liu J & Renner SS (2013) A new phylogeny for the genus *Picea* from plastid, mitochondrial, and nuclear sequences. Molecular Phylogenetics and Evolution 69: 717–727.

Mamaev SA (2000) Opredelitel' derev'ev i kustarnikov Urala. Mestnye i introducirovannye vidy. Ural Branch of the Russian Academy of Sciences. Ural branch of Russian Academy of Sciences, Ekaterinburg, Russia.

Notov A (2005) Materialy k flore Tverskoj oblasti. Čast' 1. Vysšie rasteniâ. Publishing House of the Tver State University, Tver, Russia.

Orlova LV (2012) Otdel 4. Pinophyta – Golosemennye: Konspekt flory Vostočnoj Evropy. Vol. 1 (ed. by NN Tzvelev & DV Geltman) KMK Scientific Press Ltd., Moscow; St-Petersbourg, Russia, pp. 49–90.

Orlova LV & Egorov AA (2011) To the systematics and geographical distribution of Finnish Spruce (*Picea fennica* (Regel) Kom., Pinaceae). Novosti Sistematiki Vysših Rastenij 42: 5–23.

Orlova LV & Glazkova EA (2018) Review of indigenous conifers of the Russian islands of the Gulf of Finland (Baltic sea). Turczaninowia 21(2): 228–256.

Orlova LV, Potokin AF, Koptseva EM, Vasiliev EM, Kirillov PS & Egorov AA (2017) Taksonomičeskoe raznoobrazie i ih raspredelenie na territorii nacional'nogo parka "Taganaj" (Ûžnyj Ural). Izvestiâ Sankt-Peterburgskoj Lesotehničeskoj akademii 218: 43–60.

Parducci L, Tollefsrud MM, Jørgensen T, Elverland E, Alm T, Fontana SL, Bennett KD, Haile J, Matetovici I, Suyama Y, Edwards ME, Andersen K, Rasmussen M, Boessenkool S, Coissac E, Brochmann C, Taberlet P, Houmark-Nielsen M, Larsen NK, Orlando L, Gilbert MTP, Kjær KH, alsos IG & Willerslev E (2012) Glacial survival of boreal trees in Northern Scandinavia. Science 335: 1083–1086.

Parfenov VI (1971) O vnutrividovoj sistematike *Picea abies* (L.) Karst. Novosti sistematiki vysših rastenij 8: 4–11.

Popov PP (1996a) Gibridnaâ el' na severo-vostoke Evropy. Lesovedenie 2: 62–72.

Popov PP (1996b) Intergradaciâ populâcionnyh sistem eli sibirskoj v zapadnoj časti areala: Bioraznoobrazie Zapadnoj Sibiri - rezul'taty issledovanij (ed. by BP Cibul'skij) Izdatel'stvo Instituta problem osvoeniâ Severa SO RAN, Tyumen', Russia, pp. 51–64.

Popov PP (2000) Ocenka vliâniâ introgressivnoj gibridizacii elej evropejskoj i sibirskoj na strukturu populâcii: Problemy vzaimodejstviâ čeloveka i prirodnoj sredy. Vypusk 1. Materialy itogovoj naučnoj sessii Učenogo soveta instituta problem osvoeniâ Severa SO RAN, 1999 (ed. by by BP Cibul'skij & AV Matveev) Izdatel'stvo Instituta problem osvoeniâ Severa SO RAN, Tyumen', Russia, pp. 102–105.

Popov PP (2003) Structure and differentiation of spruce populations in eastern Europe and western Siberia. Russian Journal of Ecology 34: 27–33.

Popov PP (2010) Form structure and geographic differentiation of spruce populations in Northwestern Russia. Russian Journal of Ecology 41: 378–385.

Popov PP (2014) Zakonomernosti regional'noj differenciacii elej evropejskoj i sibirskoj. Nauka, Novosibirsk, Russia.

Potokina EK, Orlova LV, Vishnevskaya MS, Alekseeva EA, Potokin AF & Egorov AA (2013) Genetic differentiation of spruce populations in northwest Russia revealed with microsatellite markers. Russian Journal of Genetics: Applied Research 3: 352–360. https://doi.org/10.1134/S2079059713050080

Pravdin LF (1975) El' evropejskaâ i sibirskaâ v SSSR. Nauka, Moscow, Russia.

Ramenskaya ML (1983) Analiz flory Murmanskoj oblasti i Karelii. Nauka, Leningrad, Russia.

Schmidt VM (2005) Flora Arhangel'skoj oblasti. St. Petersburg University Publishing House, St. Petersburg, Russia.

Schmidt-Vogt H (1974) Die systematische Stellung der gemeinen Fichte (*Picea abies* [L.] Karst.) und der sibirischen Fichte (*Picea obovata* Ledeb.) in der Gattung *Picea*. Ein Beitrag zur Einführung von Erkenntnissen auf dem Gebiet forstlischer Genökologie in die Systematik der Baumarten. Allgemeine Forst und Jagdzeitung 145: 46–60.

Schmidt-Vogt H (1977) Die Fichte. Taxonomie. Verbreitung. Morphologie. Okologie. Waldgesellschaft. Bd. 1. Vellag Paul Parey, Hamburg und Berlin, Germany.

Shcherbakova MA (1973) Genèkologiâ eli obyknovennoj v raznyh lesorastitel'nyh rajonah. Institut lesa i drevesiny imeni V.N. Sukačeva SO AN SSSR, Krasnoyarsk, Russia.

Sukachev VN (1928) Lesnye porody: sistematika, geografiâ i fitosociologiâ ih. Čast' 1. Hvojnye. „Novaya derevnya", Moscow, Russia.

Sukachev VN (1938) Istoriâ rastitel'nosti SSSR vo vremâ plejstocena: Rastitel'nost' SSSR. Vol. 1 (ed. by YuD Zinserling) Publishing House of Academy of Sciences of USSR, Moscow–Leningrad, Russia, pp. 183–234.

Tatarinov VV (1989) Struktura populâcij eli v lesah Srednego Urala: Populâcionnye issledovaniâ rastenij v zapovednikah. Nauka, Moscow, Russia, pp. 130–142.

Teplouchoff Th (1868) Ein Beitrag zur Kenntniss der sibirischen Fichte – *Picea obovata* Ledeb. Bulletin de la Société Impériale des Naturalistes de Moscou 41: 1–9.

Tollefsrud MM, Kissling R, Gugerli F, Johnsen Ø, Skrøppa T, Cheddadi R, van der Knaap WO, Latałowa M, Terhurne-Berson R, Litt T, Geburek T, Brochmann C & Sperisen C (2008) Genetic consequences of glacial survival and postglacial colonization in Norway spruce: combined analysis of mitochondrial DNA and fossil pollen. Molecular Ecology 17: 4134–4150.

Tollefsrud MM, Latałowa M, van der Knaap WO, Brochmann C & Sperisen C (2015) Late quaternary history of North Eurasian Norway spruce (*Picea abies*) and Siberian spruce (*Picea obovata*) inferred from macrofossils, pollen and cytoplasmic DNA variation. Journal of Biogeography 42: 1431–1442.

Tsuda Y, Chen J, Stocks M, Källman Th, Sønstebø JH, Parducci L, Semerikov V, Sperisen Ch, Politov D, Ronkainen T, Väliranta M, Vendramin GG, Tollefsrud MM & Lascoux M (2016) The extent and meaning of hybridization and introgression between Siberian spruce (*Picea obovata*) and Norway spruce (*Picea abies*): cryptic refugia as stepping stones to the west? Molecular Ecology 25: 2773–2789.

Tutin TG, Burges NA, Chater AO, Edmonds JR, Heywood DH, Moore DM, Valentine DH, Walters SM & Webb DA (1993) Flora Europaea, 2nd ed. Cambridge University Press, Cambridge, UK.

Tzvelev NN (2000) Opredelitel‘ sosudistyh rastenij Severo-Zapadnoj Rossii (Leningradskaâ, Pskovskaâ i Novgorodskaâ oblasti). Publishing House of the St. Petersburg State Chemical-Pharmaceutical Academy, St. Petersburg, Russia.

Volkova P, Shipunov A, Borisova P, Moseng R & Ivens I (2014) In search of hybridity: the case of Karelian spruces. Silva Fennica 48: e1072. doi:org/10.14214/sf.1072.

Yurova EA, Krupkina LI & Konechnaya GJ (2009) Kadastr flory Novgorodskoj oblasti. 2nd ed. Revised and supplemented. OOO “Publishing House “LEMA””, Velikiy Novgorod, Russia.