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REVIEW ARTICLE

B chromosomes in Conifers (Study Case of the Genus *Picea* A. Dietr.)

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ABSTRACT

Data on B chromosomes in the genus *Picea* (Spruce) species are presented. Species of this genus are good objects for studying many problems on the role and origin of supernumerary chromosomes in conifers. Classical methods for studying chromosomes with staining of preparations with acetohematoxylin and the method of fluorescent *in situ* hybridization (FISH) were used. We report the B chromosomes occurrence in five *Picea* species and confirmed the data of different authors for seven species. At present, supernumerary chromosomes are found in 23 *Picea* species including the interspecies hybrid *P.* × *fennica*. B chromosomes of *Picea* species are smaller than A chromosomes; their size (4-6 µm) is 25-30% of the size of A chromosomes. The B chromosomes of spruce species are either meta- or submetacentric, which have been designated as B_1 and B_2 types respectively. The number of B chromosomes per cell in spruce species varies from one to six. It is generally agreed that B chromosomes are derived from A chromosomes through chromosome arrangements They differ from A chromosomes in sequence composition. The results allow us to consider that B chromosomes are of importance for organisms and possibly may play a role in their adaptation.

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1. Introduction

B chromosomes (Bs), supernumerary, accessory or additional chromosomes, are extra ones to ordinary (regular) chromosome sets (A chromosomes, As). They are found in vertebrate and invertebrate animals, fishes, amphibians, fungi, ferns, gymnosperm and angiosperm plants (Müntzing, 1974; Orlov, 1974; Jones, 1975, 1995; Jones & Rees, 1982; Jones & Houben, 2003; Green, 2004; Palestis et al., 2004; Trivers et al., 2004; Jones et al., 2008; Kunakh, 2010; Houben et al., 2011, 2013, 2014; Borisov, 2014; Datta et al., 2016; Borisov & Myshliavkina, 2019; Muratova, 2021). B chromosomes are widely distributed among different organisms and are a general phenomenon in eucaryotes. This paper aims to present data on B chromosomes in *Picea* A. Dietr. (Spruce) species. This research is of interest because species of the genus *Picea* are suitable objects for studying many problems on the role and origin of B chromosomes in conifers.

2. Materials and Methods

In present review materials consist of the publications on chromosome numbers of conifers. The information has been compiled from own publications on this subject and different papers and reviews on conifer cytogenetics and karyology (Khoshoo, 1961, 1962; Mehra, 1968; Hizume, 1988; Jones,

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2017; Rastogi & Ohri, 2020; Ohri, 2021; and others). Furthermore, to obtain these data electronic databases were also used (*B-chrom*, n.d.; *Chromosome Counts Database*, n.d.; *Index to Plant Chromosome Numbers*, n.d.; *The Plant rDNA Database*, n.d.). The method is the process of reading literature sources and extracting the names of *Picea* species with B chromosomes from these papers.

3. Results and Discussion

3.1. Distribution B Chromosomes in the Genus *Picea*

The genus *Picea* (Spruce) includes from 35 to 50 species and is subdivided into three sections: *Picea* (*Eupicea*), *Casicta* and *Omorika* (Bobrov, 1978). Species from the genus *Picea* are stable diploids and include 24 A chromosomes (2n=24) like most other taxons of the family Pinaceae (Khoshoo, 1961, 1962; Mehra, 1968; Hizume, 1988; Rastogi & Ohri, 2020; Ohri, 2021). Our investigations contain more than 20 species of this genus (Medvedeva & Muratova, 1987; Muratova & Frolov, 1995; Muratova & Vladimirova, 2001a, 2021b; Muratova et al., 2002, 2004, 2008, 2019, 2020; Vladimirova et al., 2003, 2007; Sedel'nikova et al., 2004, 2011; Vladimirova & Muratova, 2005, 2006; Karpyuk & Muratova, 2005; Karpyuk et al., 2009; Kvitko et al., 2009; Pimenov et al., 2012; Goryachkina et al., 2013; Tashev et al., 2014, 2015). Some species have been studied in different parts of the range, in normal and extreme conditions: Near borders of the ranges of the species, in the swamps, in the mountains, and in the regions of anthropogenic influence. Literature data are used for karyological characteristics of the other spruce species (Kruklis, 1971; Pravdin et al., 1976; Teoh & Rees, 1977; Liu & Li, 1985; Hizume, 1988, 2017; Hizume et al., 1988, 1989; Broka, 1990; Shi & Wang 1994; Farukshina et al., 1997; Li et al., 2001; Shibata & Hizume, 2008; and others). According to the classification of morphological types of chromosomes *Picea* species contain eight pairs long of metacentric chromosomes and four pairs are short meta- or submetacentric ones.

Some *Picea* species include one or more B chromosomes. Our data are the first study case of B chromosomes occurrence in five *Picea* species: *P. abies* (L.) H. Karst., *P. breweriana* S. Watson, *P. pungens* Engelm., *P. purpurea* Mast. [*P. likiangensis* var. *purpurea* (Mast.) Dallim. et A. B. Jacs.], *P. schrenkiana* Fisch. et C. A. Mey. (Muratova et al., 2002; Vladimirova et al., 2007; Muratova et al., 2008; Karpyuk et al., 2009; Sedel'nikova et al., 2011; Pimenov et al., 2012; Goryachkina al., 2013; Tashev et al., 2014, 2015).

Furthermore, we found B chromosomes in *P. ajanensis* (Lindl. et Gord.) Fisch. ex Carrière, *P.* × *fennica* (Regel.) Kom., *P. glauca* (Moench) Voss, *P. glehnii* Mast., *P. koyamae* Shirasawa, *P. meyeri* Rehder et E. H. Wilson, *P. obovata* Ledeb., *P. sitchensis* (Bong.) Carrière (Medvedeva & Muratova, 1987; Muratova & Frolov, 1995; Muratova & Vladimirova, 2001a; Muratova et al., 2002, 2008; Vladimirova et al., 2003, 2007; Sedel'nikova et al., 2004, 2011; Karpyuk & Muratova, 2005; Goryachkina al., 2013). Materials on these species confirmed the data of other authors on B chromosomes in *Picea* (Kruklis, 1971; Moir & Fox, 1972; Pravdin et al., 1976; Rees et al., 1977; Teoh & Rees, 1977; Liu & Li, 1985; Broka, 1990; Gamaeva, 1992; Farukshina et al., 1997; Butorina & Bogdanova, 2001; Hizume, 1988, 2017; Hizume et al., 1988; Shibata & Hizume, 2008; Goryachkina al., 2013).

In addition, other authors found B chromosomes in *P. complanata* Mast. [*P. albertiana* S. Brown **(***P. glauca* var. *albertiana* Sarg.), *P. brachytyla* var. *complanata* (Mast.) W. C. Cheng et Rehd.], *P. crassifolia* Kom., *P. engelmannii* Engelm., *P. jezoensis* (Siebold et Zucc.) Carrière, *P. hondoensis* Mayr [*P. jezoensis* var. *hondoensis* (Mayr) P. A. Schmidt, *P. likiangensis* (Franch.) E. Pritz., P. *linzhiensis* (W.C. Cheng & L.K. Fu) Rushforth (*P. likiangensis* var. *linzhiensis* W.C. Cheng & L.K. Fu), *P. microsperma* Carrière [*P. jezoensis* var. *microsperma* (Lindl.) W.C. Cheng et L. K. Fu], *P. wilsonii* Mast. (Teoh & Rees, 1977; Liu & Li, 1985; Hizume, 1988, 2017; Hizume et al., 1988, 1989, 1991; Shi & Wang, 1994; Hizume & Kuzakawa, 1995; Li et al., 2001; Shibata & Hizume, 2008).

Currently, B chromosomes are found in 23 *Pice*a species including interspecies hybrid *P. ×fennica*. B chromosomes found in taxons of all three sections of the genus *Picea*: *Picea*, *Casicta* and *Omorika.* One B chromosome (2n=24+1B) occurs in *P. breweriana, P. complanata,* × *P. fennica*, *P. jezoensis*, *P. likiangensis*, *P. linzhiensis*, *P. microsperma*, *P. pungens*, *P. purpurea*, and *P. schrenkiana*. Five species: *P. koyamae*, *P. crassifolia* Kom., *P. hondoensis* Mayr, *P. engelmannii* and *P. wilsonii*, have one to two B chromosomes (2n=24+1-2B). The number of Bs varies from one to three (2n=24+1-3B) in *P. ajanensis* and *P. meyeri*; *P. obovata* and *P. abies* have one to four B chromosomes (2n=24+1-4B). Karyotypes of *P. glehnii* and *P. sitchensis* contain from one to five B chromosomes (2n=24+1-5B). The highest number of B chromosomes per cell (six) was registered in *P. glauca* and *P. albertiana*. Karyotypes of *Picea* species with varying numbers of B chromosomes are given in Figure 1.

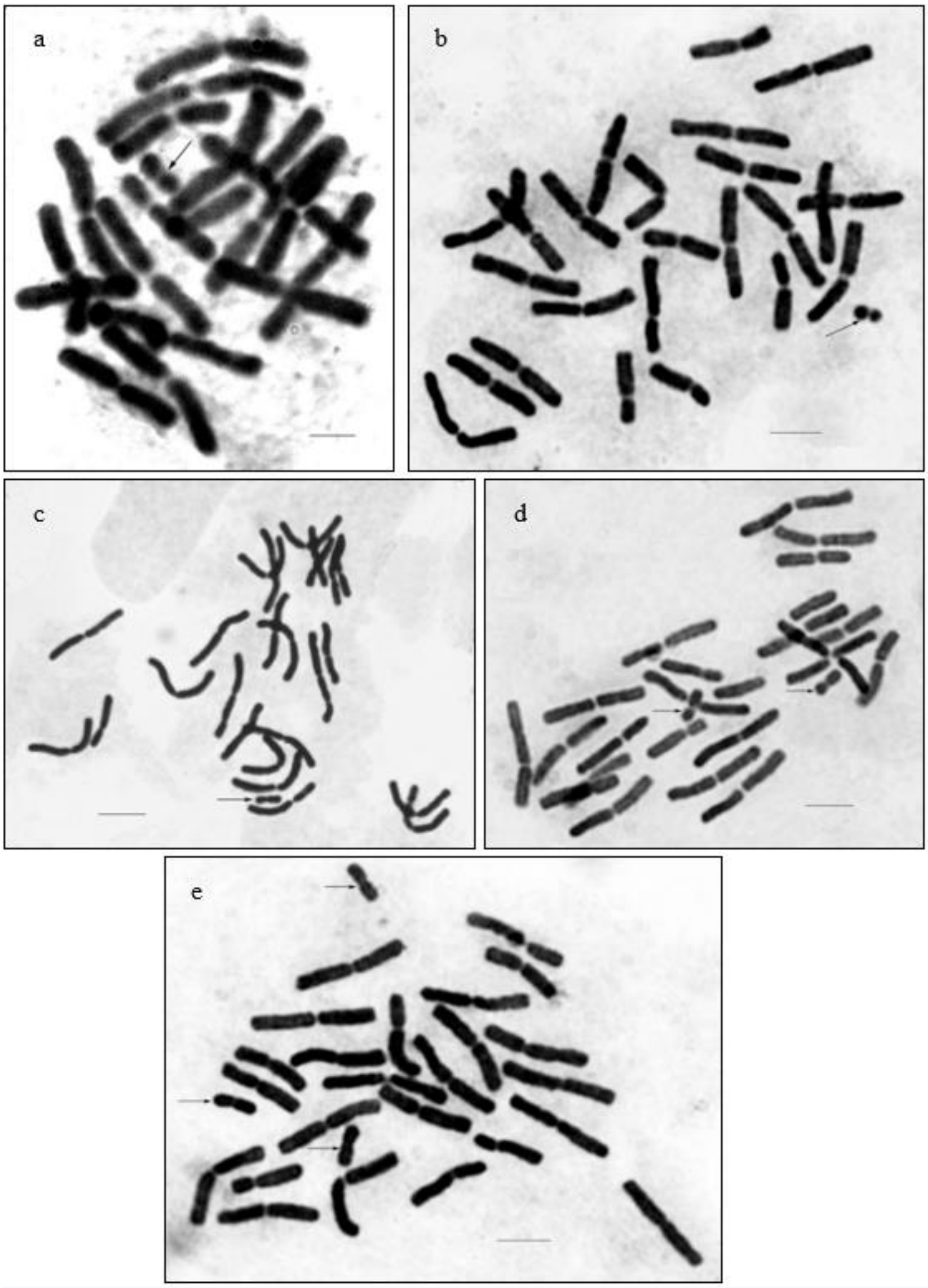

Figure 1. Karyotypes of spruce species with B chromosomes: (a) *P. abies* with one B chromosome (2n=24+1B), bar indicates 5 μm, photo by A. V. Pimenov; (b) *P. koyamae* with one B chromosome (2n=24+1B), bar indicates 10 μm, photo by O. V. Goryachkina; (c) *P. sitchensis* with one B chromosome (2n=24+1B), bar indicates 10 μm, photo by O. V. Goryachkina; (d) *P. meyeri* with two B chromosomes (2n=24+2B), bar indicates 10 μm, photo by O. V. Goryachkina; (e) *P. glauca* with three B chromosomes (2n=24+3B), bar indicates 10 μm, photo by O. V. Goryachkina. Chromosomes were stained with acetohematoxylin. Arrows point B chromosomes.

3.2. Size, Morphology and Structure of *Picea* B Chromosomes

B chromosomes of *Picea* species are smaller than the A chromosomes of the same species. Sizes of A chromosomes of these species are from 9 to 15 μm. Usually length of *Picea* B chromosomes (4-6 μm) is 25-30% that of A chromosomes (Kruklis, 1971; Moir & Fox, 1972; Pravdin et al., 1976; Hizume et al., 1988, 1989; Muratova & Vladimirova, 2001b; Muratova et al., 2002, 2004, 2008, 2019, 2020; Vladimirova, 2002; Sedel’nikova et al., 2004; Shibata & Hizume, 2008; Karpyuk et al., 2009; Tashev et al., 2014, 2015; Hizume, 2017). The B chromosomes of spruce species are either meta- or submetacentric, which have been designated as B_1 and B_2 types respectively (Kruklis, 1971; Teoh & Rees 1977; Liu & Li, 1985; Hizume et al., 1988, 1989; Muratova et al., 2008, 2019, 2020).

In *P. breweriana, P. crassifolia, P. koyamae, P. schrenkiana, P. jezoensis, P. microsperma* the first type of B chromosomes were found only (B_1); in *P. likiangensis, P. pungens* and *P. hondoensis* the second type occurs (B_2). But in the majority of *Picea* species investigated (*P. abies, P. ajanensis, P. albertiana, P. complanata* (*P. brachytyla* var. *complanata*), *P. engelmannii, P. jezoensis, P. glauca, P. meyeri, P. obovata, P. sitchensis*) both types of B chromosomes are found. It has been proposed that submetacentric B chromosomes have originated as a result of pericentric inversions of the metacentric ones (Teoh & Rees, 1977; Kean et al., 1982; Fox, 1987). Other variants of B chromosomes exist in *P. glehnii*. This species has a large metacentric B chromosome, two short meta- and submetacentric Bs, one small metacentric and very small submetacentric ones. It is possible these types of B chromosomes originated later (Muratova & Vladimirova, 2001a).

B chromosomes in conifers can be eu- or heterochromatic. B chromosomes of some spruce species which were visible as chromocenters at interphase after stained with different stain solution, including Giemsa (*P. glauca, P. glehnii, P. sitchensis*, and *P. obovata*) are heterochromatic (Moir & Fox, 1972; Teoh & Rees, 1977; Kean et al., 1982; Fox, 1987; Hizume et al., 1988; Muratova et al., 2002). B chromosomes of *P. complanata* are euchromatic (Hizume et al., 1991). The metaphase B chromosomes of *P. obovata* and *P. glauca* were more condensed in contrast to their A chromosomes (Teoh & Rees, 1977; Vladimirova, 2002).

B chromosomes are part of the evolution system of the eucaryotic genome. It is generally agreed that B chromosomes are derived from A chromosomes through chromosome arrangements: Fragmentation, duplications, amplifications, and gene silencing (Jones & Rees, 1982; Jones & Houben, 2003; Jones et al., 2008; Kunakh, 2010; Houben et al., 2014; Borisov & Myshliavkina, 2019). After the divergence of B chromosomes from A chromosomes their evolution was independent. B chromosomes differ from A chromosomes in the organization of genetic material. B chromosomes of some plants and animals include many highly repeated DNA sequences and often do not encode genes. They may contain ribosomal, mitochondrial, and virus-type sequencies and possess A chromosome derived pseudogenes. Studies on some species have provided information about the occurrence of different repetitive DNA families, such as AT-rich sequences, C-CMA_3 - DAPI bands, Ty3/gypsy retroelements, Gypsy LTR-RTs, and others (Jones et al., 2008; Kunakh, 2010; Houben et al., 2014; Borisov & Myshliavkina, 2019).

B chromosomes of *Picea* do not bear the secondary constrictions. Silver-staining has revealed bright bands on B chromosomes in Siberian spruce (*P. obovata*) indicating the possibility of its nucleolar-organizing ability (Vladimirova, 2002). However, application of fluorescent *in situ* hybridization (FISH) with probes of 5S and 45S ribosomal RNA genes in *P. obovata* and *P. pungens* has revealed absence of these genes on B chromosomes (Figure 2). These data are in agreement with results of Japanese investigators: B chromosomes of *P. hondoensis* (*P. jezoensis* var. *hondoensis*), *P. engelmannii*, *P. koyamae* also did not have loci of 5S rDNA or 18S rDNA. Fluorescent banding for B chromosomes of *P. glauca* and *P. sitchensis* displayed CMA bands. The B chromosomes of *P. glehnii, P. koyamae, P. likiangensis, P. obovata* revealed DAPI-bands. In B chromosomes of *P. brachytyla, P. jezoensis, P. hondoensis* no CMA and DAPI bands were observed (Hizume & Kuzakawa, 1995; Shibata & Hizume, 2008; Hizume et al., 1988, 1989; Hizume, 2017). DAPI is fluorescent stain for AT-rich regions in DNA, CMA (chromomycin A_3) is a stain for GC-rich regions.

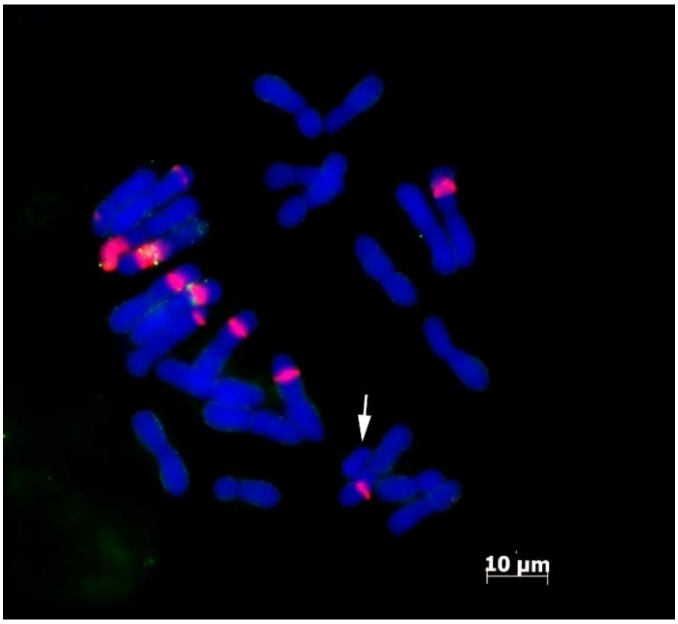

Figure 2. Fluorescent *in situ* hybridization (FISH) of *P. koyamae* with probes of 5S and 45S ribosomal RNA genes. B chromosome (arrow point) has no FISH signals. Photo by O. V. Goryachkina.

3.3. B Chromosomes in Mitosis, Meiosis, Inheritance, Effects on the Organism

In the mitosis of *P. obovata* with B chromosomes irregularities as lagging chromosomes, three poles and disorderly distribution of the chromosomes in anaphase I, single and double bridges, fragments and some other anomalies were revealed. Regular division of B chromosomes was noted; in many cases they moved to the poles first, ahead of other chromosomes. The percentage of mitosis anomalies in trees with B chromosomes was higher and their spectrum was wider (Muratova et al., 2001; Vladimirova, 2002).

At meiosis they affect the distribution and frequency of chiasmata and don't recombine with A chromosomes. In Siberian spruce (*P. obovata*) and Sitka spruce (*P. sitchensis*) in metaphase I in pollen mother cells B chromosomes formed bivalents and did not pair with A chromosomes. Their behavior at metaphase I suggested that they are distributed at random at the first meiotic division (Kean et al., 1982; Kruklis, 1982). Studies on the B chromosomes transmission in *P. obovata* and *P. sitchensis* revealed that they are transmitted through both female and male tracks. However, in *P. obovata* B chromosomes mainly inherited from mother plants (Kruklis, 1982; Muratova & Vladimirova, 2001b).

Usually, the presence of B chromosomes does not affect the phenotype. In many cases a large number of supernumerary chromosomes have negative influence on fertility and viability (Teoh & Rees, 1977; Jones & Rees, 1982). Siberian spruce trees with 3-4 B chromosomes were characterized by reduced pollen fertility, a smaller number of seeds, and a slight reduction in growth, 1 or 2 supernumerary chromosomes did not affect these features (Kruklis, 1971, 1982). In *P. glauca*, the seeds of trees with B chromosomes in the karyotype germinated on average one day earlier (Teoh & Rees, 1977). Studies of *P. sitchensis* did not reveal the influence of B- chromosomes on the growth rate (Moir & Fox, 1976).

3.4. B Chromosomes in Different Parts of the Ranges and Provenances in *Picea*

Extensive karyological studies of Siberian spruce (*P. obovata*) from in the European part of Russia, the Urals, North Eastern Kazakhstan, Siberia has been carried out by cytologists of Russia and former USSR (Kruklis, 1971; Pravdin et al., 1976; Medvedeva & Muratova, 1987; Broka, 1990; Muratova & Vladimirova, 2001b; Muratova et al., 2002, 2008; Vladimirova, 2002; Vladimirova et al., 2003, 2007; Sedel’nikova et al., 2004, 2011; Vladimirova & Muratova, 2005, 2006; Kvitko et al., 2009; Borisov & Muratova, 2010). More than 50 natural populations of this species were studied and B chromosomes were found in half of them.

In western populations of Siberian spruce B chromosomes are rare. Populations from the Southern Urals and East Kazakhstan are the most western where B chromosomes have been found. In related species *P. abies* growing in southwestern Europe (Bulgaria) 1-4 B chromosomes were found. *P.* × *fennica*, a hybrid between *P. obovata* and *P. abies*, has one B chromosome. Accessory chromosomes often occur in trees from eastern parts of the range, in Central and Eastern Siberia especially, in extreme conditions.

B chromosomes have a widespread distribution in North American species of spruce: *P. sitchensis* and *P. glauca*. In *P. sitchensis* 29 out of 40 populations contained them. The highest frequency of B chromosomes is noted in the south of Vancouver Island, where the flora was adapted to high summer temperatures and low rainfall. *P. glauca* B chromosomes were found in 48 out of 51 studied populations. The highest frequency of B chromosomes was observed in the northeastern part of Vancouver Island and nearby areas of the continental America, characterized by low rainfall and high summer insolation (Moir & Fox 1977; Teoh & Rees 1977; Fox, 1987).

In *P. obovata* and *P. glauca* a higher frequency of B chromosomes was found among decorative forms, in introduced plants and urban stands, in contrast with natural populations (Butorina & Bogdanova, 2001; Muratova et al., 2002; Vladimirova, 2002; Borisov & Muratova, 2010). Examination of Siberian spruce (*P. obovata*) in different regions of Krasnoyarsk showed the presence of B chromosomes in all studied areas. Possibly, the appearance of B chromosomes in large industrial centers is a result of A chromosome mutations caused by industry emissions. Many authors assumed that the presence of B chromosomes in conifers could be connected with unfavorable ecological conditions of the areas where they grow (Teoh & Rees, 1977; Fox, 1987; Sedel’nikova et al., 2011; and others).

The results obtained by many authors allow us to consider that and B chromosomes are of importance for organisms and possibly may play a role in their adaptations. Plants with B chromosomes are more polymorphic and adaptive to changing environment (Jones & Rees, 1982; Kunakh, 2010; Borisov, 2014; Borisov & Myshliavkina, 2019; and others). Origin and fixing of B chromosomes give the possibility to raise the adaptive possibilities of organisms. But this hypothesis needs to be confirmed on new investigations.

3.5. Possible Origin of B Chromosomes of the Genus *Picea*

The similarity of B chromosomes of different *Picea* species in morphology, their occurrence in Siberian, Far Eastern and North American species suggest common ancient origin of the B chromosome. Broka (1990) proposed that the B chromosome arose in East Asia in the center of conifer origin. After that, B chromosomes spread to North America via the Beringian land bridge and to the Asian part of the eastern hemisphere. Fossil evidences showed that spruce entered North America in the middle of the Tertiary period (Wright, 1955). Analysis of new data obtained by sequencing nuclear, mitochondrial and chloroplast genomes confirmed the monophyletic origin of the genus *Picea* (Lockwood et al., 2013). These studies indicated that the genus split from a common ancestor of Pinaceae about 180 million years ago.

It clearly distinguishes three clades: I-Asian and European species; II-North American species; III-Asian and North American species *P. breweriana*. The version of Wright (1955) about two independent migrations of spruce from Asia to North America, which probably occurred 25 and 20 million years ago, is also confirmed.

4. Conclusion

Supernumerary chromosomes are reported for 23 *Picea* species including interspecies hybrid *P.* × *fennica*. The number of *Picea* species with B chromosomes to grow. Studies on the role of B chromosomes in evolution, and their influence on organisms require further investigations, including their molecular organization of genomes and reproductive biology.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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