



From America to Eurasia: a multigenomes history of the genus *Abies*

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ABSTRACT

The origin of conifer genera, the main components of mountain temperate and boreal forests, was deemed to arise in the Mesozoic, although paleontological records and molecular data point to a recent diversification, presumably related to Neogene cooling. The geographical area(s) where the modern lines of conifers emerged remains uncertain, as is the sequence of events leading to their present distribution. To gain further insights into the biogeography of firs (*Abies*), we conducted phylogenetic analyses of chloroplast, mitochondrial and nuclear markers. The species tree, generated from ten single-copy nuclear genes, yielded probably the best phylogenetic hypothesis available for *Abies*. The tree obtained from five regions of chloroplast DNA largely corresponded to the nuclear species tree. Ancestral area reconstructions based on fossil calibrated chloroplast DNA and nuclear DNA trees pointed to repeated intercontinental migrations. The mitochondrial DNA haplotype tree, however, disagreed with nuclear and chloroplast DNA trees. It consisted of two clusters: one included mainly American haplotypes, while the other was composed of only Eurasian haplotypes. Presumably, this conflict is due to intercontinental migrations and introgressive hybridization, accompanied by the capture of the mitotypes from aboriginal species by the invading firs. Given that several species inhabiting Northeastern Asia carry American mitotypes and mutations typical for the American cluster, whereas no Asian mitotypes were detected within the American species, we hypothesize that *Abies* migrated from America to Eurasia, but not in the opposite direction. The direction and age of intercontinental migrations in firs are congruent with other conifers, such as spruces and pines of subsection *Strobus*, suggesting that these events had the same cause.

1. Introduction

Disjunct distributions of related taxa in Eurasia and North America are an important feature of temperate and boreal flora of the Northern Hemisphere. While the disjunct distribution of angiosperm groups is regarded as a consequence of migrations primarily from Eurasia to America, gymnosperms often spread in the opposite direction (Wang and Ran, 2014; Wen et al., 2016), possibly because boreal forests were more extensive in North America at that time than in Eurasia.

Abies (firs) is one of the largest genera of the family Pinaceae with circumboreal dispersal (Liu, 1971; Krylov et al., 1986; Farjon and Rushforth, 1989; Debreczy and Rácz, 2011; Farjon and Filer, 2013). These evergreen conifers are important elements of the boreal and temperate mountain forests as well as taiga forests, covering the plains in Siberia and North America. Recent taxonomic classifications of firs are rather controversial and, depending on the recognition of weakly divergent taxa, they vary in the number of species: Eckenwalder (2009) recognized 40 species, Farjon and Filer (2013) 47 and Debreczy and

Rácz (2011) 65. Fir fossils, both in North America and Eurasia, are known from the Cretaceous (Kremp, 1967; Xiang et al., 2007). However, the fragmented nature of paleontological records and the uncertain relationship of the fossils to extant species restricts the possibility to draw conclusions regarding the time periods and sequence of intercontinental migrations.

Previous molecular phylogenies of *Abies*, based on sequences of three chloroplast DNA (cpDNA) fragments (Aguirre-Planter et al., 2012), plastome sequences of seven *Abies* species, phytochrome genes of 11 species and *matK* gene of nearly all *Abies* species (Holman, 2014), five regions of cpDNA and three fragments of mitochondrial DNA (mtDNA) (Semerikova and Semerikov, 2014a,b), three fragments of cpDNA, two fragments of mtDNA and nuclear ribosomal DNA internal transcribed spacer (nrITS) regions (Xiang et al., 2015), revealed the main features of the evolutionary history of firs. Importantly, they showed the existence of several major groups of fir species and resolved phylogenetic relationships among them. The simultaneous distribution of some phylogenetic groups within Eurasia and North America

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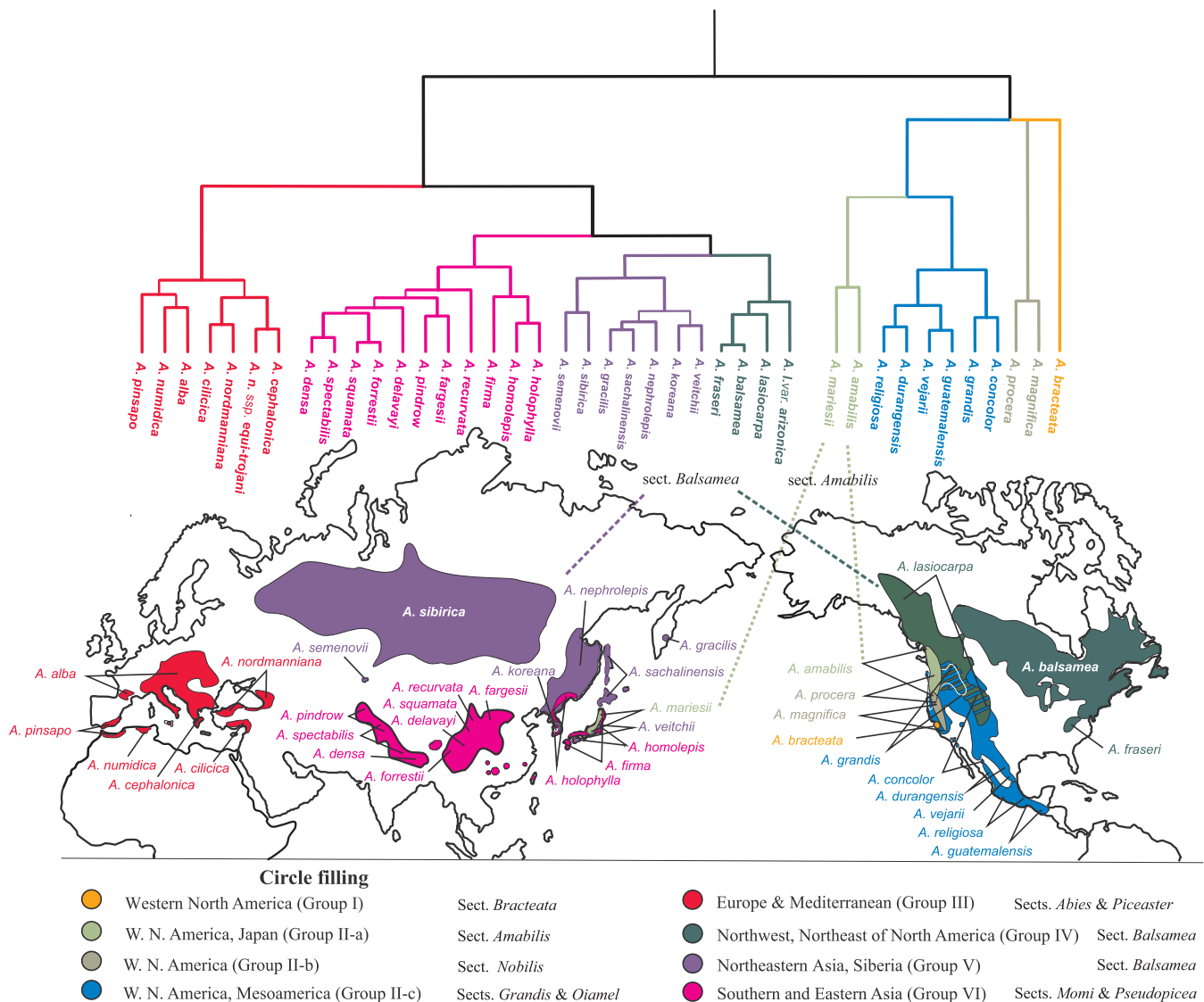


Fig. 1. Geographical distribution of the genus *Abies*. The areas of fir species included in the phylogenetic analysis are shown approximately. Subspecies/varieties are not presented. The nDNA species tree, corresponding to Fig. 5, is schematically displayed above the map. The distributions of the major taxonomic groups, their respective names and branches on the phylogenetic tree are marked with the same colors as in Fig. 5. Additional colors were used to label the subgroups II-a, II-b and II-c. The correspondence of the groups and subgroups to taxonomic sections (Farjon and Rushforth, 1989) are provided. The intercontinental disjunctions within the sections are indicated by dashed lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

suggests the multiplicity of intercontinental migrations. These data suffer, however, from gaps in species coverage and/or insufficient variability of DNA fragments, employed in the analysis. In addition, the proposed phylogenetic reconstructions were based on single-locus or a few loci data and reflected the genealogy of individual loci (cpDNA, mtDNA or nrITS), which might not correspond to each other and to the genealogy of the species. For example, the positions of some clades (e.g., sect. *Balsamea*) in the nrITS tree strongly contradict the cpDNA phylogeny (Xiang et al., 2015; Semerikova and Semerikov, 2016).

Phylogenetic methods based on multiple independent loci take into account the stochasticity of the individual locus genealogy and thus they have an advantage over methods that use cytoplasmic and single locus nuclear markers (Rokas et al., 2003; Brito and Edwards, 2009). In a study of *Abies* nuclear phylogeny (Semerikova and Semerikov, 2016), we used the AFLP (Amplified Fragment Length Polymorphisms) method, which employs multiple, unlinked dominant markers distributed throughout the genome (Vos et al., 1995). The nuclear phylogenetic tree derived from AFLP data was much more congruent with chloroplast trees (Semerikova and Semerikov, 2014a; Holman, 2014;

Xiang et al., 2015) than the one inferred from nrITS (Xiang et al., 2015). Several deep clades of the AFLP tree, however, had low support values, thus leaving a number of important questions unanswered. Moreover, the divergence time estimates for the main lineages of modern firs employing the cpDNA tree (Semerikova and Semerikov, 2014a) substantially contradicted the results, obtained by combining nrITS, cpDNA and mtDNA data (Xiang et al., 2015) and, therefore, require an independent study employing nuclear multilocus data.

In species of the family Pinaceae including firs (Vendramin and Ziegenhagen, 1997; Liepelt et al., 2002), mtDNA is maternally inherited, cpDNA is paternally inherited, and nuclear DNA (nDNA) is of biparental origin. Thus, gene flow of mtDNA, limited by seed dispersal, is substantially lower than that of pollen-transmitted cpDNA and nuclear markers, which are distributed by both seeds and pollen. In part because of these different modes of inheritance in conifers, rates of introgression are higher for mtDNA than for cpDNA and nDNA (Du et al., 2009). Consequently, unlike nuclear and chloroplast DNA, characterized by a close correspondence between the structure of genetic variability and species boundaries, mtDNA haplotypes may be

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