Botanica Pacifica. A journal of plant science and conservation. 2024. 13(2): 3–13
DOI: 10.17581/bp.2024.13202

REVIEW PAPER

# A review of Labrador tea diversity in Northeast Asia

Diana R. Iunusova & Maria A. Polezhaeva*

Diana R. Iunusova
e-mail: dianaiunusova@mail.ru

Maria A. Polezhaeva*
e-mail: polezhaevam@mail.ru

Institute of Plant and Animal Ecology,
Ural Division RAS, Ekaterinburg, Russia

* corresponding author

Manuscript received: 18.03.2024
Review completed: 05.06.2024
Accepted for publication: 13.06.2024

## ABSTRACT

Labrador teas are a small but systematically complex group of species of the Ericaceae family. The group is represented by cold-resistant evergreen shrubs, common in the boreal and subarctic zones of the northern hemisphere, both in Eurasia and North America. Described historically as part of the distinct genus *Ledum* L., Labrador teas were later included in the genus *Rhododendron* as a subsection *Ledum* in subgenus *Rhododendron*. The high variability of morphological characters, their dependence on geographical and environmental factors, makes it difficult to clearly distinguish from 4 to 9 described taxa. Labrador teas play a key ecological role as dominants in damp communities of temperate and cold climates and are often pioneers in successional communities of disturbed habitats. This species complex is also interesting as a model group for studying the processes of hybridization and diversification, since different species tend to coexist in sympatry, especially in northeast Asia. This review summarizes the results of studying the species diversity of Labrador teas, mainly in Northeast Asia, changes in their taxonomy and hypotheses of origin.

**Keywords:** closely related species, hybridization, *Ledum*, *Rhododendron tomentosum*, sympatry, taxonomy

## РЕЗЮМЕ

**Юнусова Д.Р., Полежаева М.А. Обзор разнообразия багульников в Северо-Восточной Азии.** Багульники – небольшая, но систематически сложная группа видов семейства Ericaceae. Группа представлена холодостойкими вечнозелеными кустарниками, распространенными в бореальной и субарктической зонах северного полушария, как в Евразии, так и в Северной Америке. Описанные исторически как часть отдельного рода *Ledum* L., багульники позднее были включены в род *Rhododendron* в качестве подсекции *Ledum* в подроде *Rhododendron*. Высокая изменчивость морфологических признаков, их зависимость от географических и экологических факторов затрудняет четкое разграничение от 4 до 9 описанных таксонов. Багульники играют ключевую экологическую роль как доминанты во влажных сообществах умеренного и холодного климата и часто являются пионерами в сукцессионных сообществах нарушенных местообитаний. Этот видовой комплекс также интересен как модельная группа для изучения процессов гибридизации и диверсификации, поскольку различные виды обычно сосуществуют в симпатрии, особенно в северо-восточной Азии. В данном обзоре обобщены результаты изучения видового разнообразия багульников, главным образом, в Северо-Восточной Азии, изменения в их таксономии и гипотезы происхождения.

**Ключевые слова:** близкородственные виды, гибридизация, *Ledum*, *Rhododendron tomentosum*, симпатрия, таксономия

Recently, a special place in the focus of botanists has been occupied by cold-resistant species, common in the boreal, subarctic and arctic zones, as the most sensitive to global climate change (Rantanen et al. 2022). The distribution and diversity of these species largely depends on the dynamics of their ranges, caused by climate fluctuations of the late Pleistocene (Hewitt 2004). The vast treeless or sparse forest spaces that emerged during the last phases of cooling were populated by communities adapted to new environmental conditions (Musil 1985). Species of the Ericaceae family often dominate in such communities. Shrub and subshrub growth forms, high reproductive characteristics, including the ability for clonal reproduction, and ecological plasticity provided them with an advantage in the spaces of the Northern Hemisphere (Khokhryakov & Mazurenko 1986). In recent years, the taxonomy of genera including complexes of closely related species has been interpreted through biogeographic analysis of the formation of the ranges of individual species and the history of their postglacial migrations. This approach allows us to shed light on the processes of microevolution in populations, identify events of hybridization or, conversely, the formation of differentiation under conditions of long-term isolation, as well as the paths of adaptive evolution of new taxa (Cubino et al. 2021, Ikeda 2022).

Historically, Labrador teas were described as a distinct genus *Ledum* of the family Ericaceae by Carl Linnaeus in his 1753 work "Species Plantarum" (Linnaeus 1753). They are evergreen shrubs and subshrubs, represented by both spreading and erect forms up to 1.2 m in height. Commonly Labrador teas grow on nutrient-poor acidic soils in humid areas of the boreal zone, as well as in subarctic communities. Labrador teas occupy a wide range in the northern hemisphere from Chukotka around 72°N to the mountainous habitats of Europe, reaching their southern limit approximately in the Czech Republic in Europe and

North East China and Japan in Asia (Hultén & Fries 1986, Radoměřský et al. 2023). In North America, they advance southward to nearly 35°N, growing especially massively in northern Alaska, and in Canada (Hultén & Fries 1986, Judd & Kron 2009). In the boreal zone of North America, Labrador teas are often associated with forest phytocenoses dominated by black spruce forest stands (Calmes & Zasada 1982); in north-eastern Eurasia, usually grows in association with larch (Wang et al. 2001); in the European part – with light pine forests (Mucina et al. 2016), or on sandstone areas and peatlands with birch (Mofikoya et al. 2018, Radoměřský et al. 2023). Due to their ability to spread vegetatively by broodstock and efficient nitrogen assimilation through mycorrhiza (Malloch & Malloch 1981), Labrador teas often aggressively take over territory in open disturbed communities and in post-fire succession, slowing the regeneration of complete forest communities (Thiffault & Jobidon 2006, Hébert & Thiffault 2011).

Labrador tea shoots contain an essential oil with a high content of ledol and a number of other secondary metabolites, and are used in medicine as an antimicrobial and anti-inflammatory agent (Tanasienko 1982). From ancient, *Ledum*, which has a folk name "Bog Labrador tea", has been used in traditional medicine, by aboriginal people both in Eurasia and in North America (Blondeau & Roy 2004, Dampc & Luczkiewicz 2013, Rapinski et al. 2015). In Russia, some species of Labrador teas are included in the official list of pharmacy plants that are commercially harvested from the wild and widely used in folk medicine (Belousova et al. 1990, 1999). There is a lot of works investigating the content, composition and biological activity of metabolites of *Ledum* in different areas of its growing range (Belousova et al. 1990, Dampc & Luczkiewicz 2013, Rapinski et al. 2015).

In spite of the resource importance of Labrador teas, there is still no clear view on the taxonomic content of this group. Due to the high polymorphism of vegetative organs and the ability to hybridize, it is difficult to establish species boundaries, especially in the southern part of Northeast Asia, which makes Labrador teas an interesting model object for studying speciation. Labrador teas includes 4 to 5 or more species distributed in Eurasia and 2 to 4 species distributed in North America (Hultén 1930, 1948, Ohwi 1965, Savile 1969, Viereck & Little 1972, Khokhryakov 1991, Harmaja 1990, 1991, 1999, 2002, Judd & Kron 2009, Usenko 2010).

## BOTANICAL FEATURES

All Labrador teas species are evergreen shrubs from spreading to erect from 0.2–1.2 m tall. Shoots of all Labrador teas species are often densely pubescent at first, balding with time. Leaves are perennial, linear, entire, with developed cuticle at upper side, with rolled at edges in varying degrees; lower side with pubescence and glandular. The leaves vary in length from 0.8 to 7 cm. The pubescence of both shoots and leaves varies from species to species and may be white, reddish-brown or mixed. Numerous flowers in umbrella-shaped inflorescences are collected on shoot tips. Corolla white or slightly pinkish 10–15 mm, deeply incised of five elements, calyx five-toothed. Each flower has 5–10 stamens longer than the pistil. The pistil contains a compound seedpod and a single column retained by the fruit. The species blooms in May–August. The fruit is a dry elongated elliptic capsule opening into five segments from below. The fruit persists through the winter (Hultén 1930, 1948, Khokhryakov 1991, Harmaja 1990, 1991, 1999, 2002, Judd & Kron 2009).

A specific feature of Labrador teas species is that stable systematic characters related, for example, to the structure of generative organs, do not play a major role in the systematics of these species. At the same time parameters of vegetative organs (leaf size, branch size, direction of growth, degree of wrapping of leaf margin, degree and color of pubescence), on the basis of which different species of Labrador teas are distinguished, vary greatly and may be related to the habitats. *Ledum* subsection species differ from representatives of other subsections of the genus *Rhododendron* by both generative and vegetative characters.

## SYSTEMATICS

One of the most widespread representatives of the Labrador teas was described as a highly polymorphic Holarctic species *Ledum palustre* L. (Linnaeus 1753). For a long time it was considered that only this species grows on the territory of the whole Eurasia. Therefore, the species characteristics of *L. palustre* were identified with those of the whole genus *Ledum*. Species *L. groenlandicum* Oeder., *L. glandulosum* Nutt. and *L. columbianum* Piper. were described later in North America (Müller 1771–1777, Nuttall 1843, Piper 1906). However, the high variability of morphological traits over time has led to the designation within *L. palustre* of a large number of separate taxonomic units of different ranks from races to subspecies and species. N.A. Busch in "Flora of Siberia and the Far East" (Busch 1915) distinguished some different forms in the status of varieties: large and broad-leaved *Ledum palustre* var. *dilatatum* Wahlb., narrow-leaved *Ledum palustre* var. *angustum* E. Busch and prostrate *Ledum palustre* var. *decumbens* Ait. Later, V.L. Komarov in his "Identifier of plants of the Far East Territory" (Komarov 1932) first divided *L. palustre* s.l. into four species: *L. palustre* s. str. L., *L. decumbens* (Ait.) Lodd., *L. hypoleucum* Kom. and *L. dilatatum* (Wahlb.) Kom. One of the largest revisions of the composition of the genus on the territory of Eurasia was carried out by A.I. Tolmachev in his work "Towards the cognition of Eurasian species of the genus *Ledum* L." (Tolmachev 1953). He proposed his interpretation of the taxonomy of wild Labrador teas on the territory of Russia, also proposing four species: *L. palustre* s. str. with two varieties – var. *dilatatum* and var. *angustum*, *L. decumbens*, *L. hypoleucum*, and also included a new species – *L. macrophyllum* Tolm. Tolmachev categorized the entire diversity of *Ledum* species from North America and Eurasia into 4 morphological series. The *Glandulosa* series represented by the North American species *L. glandulosum* Nutt., which includes large shrubs with long-petioled leaves that are whitish on the underside (young ones are green on both sides). The *Hypoleuca* series comprises medium-sized shrubs, white pubescent underneath and is represented by the North American species *L. columbianum* Piper. and the Far Eastern species *L. hypoleucum* Kom. The *Latifolia* series includes medium-sized shrubs, reddish pubescent underneath, represented by the North American *L. latifolium* Jacq. (= *L. groenlandicum*), Far Eastern *L. macrophyllum* Tolm. and Japanese species *L. nipponicum* Nakai. The *Palustria* series includes small shrubs with slender branches and linear reddish-pubescent leaves and includes the wide-range Eurasian species *L. palustre* L. and *L. decumbens* (Ait.) Lodd. Subsequently, his approach was revised by a number of botanists, so V.N. Voroshilov distinguished three species in the "Identifier of plants of the Far East of the USSR" (1982): *L. palustre* L. with subspecies *L. palustre* subsp. *angustissimum* Worosch., *L. decumbens* (Ait.) Lodd. and *L. hypoleucum* Kom. (citing *L. macrophyllum* Tolm. as a synonym) with the variation *L. hypoleucum* var. *palustriforme* (Tolm.) Worosch.

The ambiguity of interpretation of the taxon volume is related to the great variability of morphological characters of different Labrador teas species. High variability of leaf anatomical and morphological characters, as well as chemical composition, was observed for the European widespread *L. palustre* (synonym of *Rhododendron tomentosum*), which is due to the influence of geographical and ecological factors (Belousova et al. 1990, Krylova & Proksheva 1995, Jesionek et al. 2019). At the same time, polymorphism of vegetative organs and diversity of transitional forms between numerous species of *Ledum*, widespread in the Russian Far East and North America, are more often explained by the processes of interspecific hybridization (Hitchcock 1956, Mazurenko & Khokhryakov 1986). For example, the differences between the North American *L. glandulosum* Nut. and *L. columbianum* Piper. were limited only to different leaf morphology, so it was decided to combine them (Hitchcock & Cronquist 1978). The status of some species in the Russian Far East is still ambiguously interpreted by botanists, either towards enlargement or fragmentation of taxa. A significant contribution to the study of the biology of Labrador teas in the Russian Far East was made by M.T. Mazurenko and A.P. Khokhryakov (Mazurenko & Khokhryakov 1986, Khokhryakov & Mazurenko 1987). They applied an ecological approach to describe the diversity of morphological forms of Labrador teas. Studying the features of biomorphs (plant life morphs), they showed that each species has a number of biomorphs, depending on the stage of ontogenesis and growing conditions, which have overlaps in morphological variability in different species. Thus, they confirmed the invalidity of distinguishing taxonomic units on the basis of only morphology. The authors also emphasized the parallel coexistence of broad-leaved forms of *Ledum* in Eurasia – *L. hypoleucum*, *L. macrophyllum*, *L. nipponicum* and, in a similar setting, on the opposite side of the Pacific Ocean in California, Oregon, British Columbia – *L. columbianum*, *L. glandulosum*, *L. californicum* Kellogg 1863 (= *L. glandulosum*), highlighting the key speciation function of Beringia in the history of formation of the *Ledum* species complex. The northern border of the Asian and North American group of tall broad-leaved wild Labrador teas is located at approximately the same latitude (50°N), and smaller narrow-leaved forms *L. groenlandicum* and *L. decumbens* are distributed further north (Mazurenko & Khokhryakov 1986).

All the above-mentioned contradictions with the systematics of Labrador teas began back when they were considered representatives of the independent genus *Ledum*. The situation changed after the work of Kron & Judd (1990), who revised phylogenetic relationships within the tribe *Rhodorea* with the use of cladistic methods to analyze a number of phylogenetically significant morphological characters. As a result, the authors proved the inclusion of *Ledum* in the genus *Rhododendron* as part of the subgenus *Rhododendron*, section *Rhododendron*, in the status of subsection (Kron & Judd 1990). The features on the basis of which the association of *Ledum* and *Rhododendron* is monophyletic include leathery leaves, scales (glandular multicellular peltate trichomes). To the section *Rhododendron* Labrador teas are included because they have non-lacerate scales and simple trichomes in the border of the peltate scales. To (or in the status of sister group) subsection *Edgeworthia* (Hutchinson) Sleumer – on the basis of presence of long multicellular trichomes on stem and abaxial side of leaf, and unicellular (papillose) pubescence of leaf epidermis (these two synapomorphic characters leaving azaleas as outgroup), the same as absence of radiate fringed cells within peltate scales, revolutionary arrangement of leaves in the bud and also the heterogeneous medulla and bilateral vascular bundle in petiole. Many of the autopomorphic traits of *Ledum* species are the result of adaptation to a forest lifestyle. Since both, *Rhododendron* and *Ledum*, were described by Linnaeus in his Species Plantarum (1753), the authors proposed two new combinations for Labrador teas: *Rhododendron palustre* (L.) Kron & Judd and *Rhododendron groenlandicum* (Oeder) Kron & Judd.

Later, the inclusion of *Ledum* in the genus *Rhododendron* was confirmed at the molecular genetic level on the basis of nuclear DNA marker – ITS1-ITS2, where *Ledum* and the lepidote group of rhododendrons formed a monophyletic group (Gao et al. 2002, Kutsev & Karakulov 2010). The analysis of variability in the nuclear RPB2-I gene (Goetsch et al. 2005), showed that *Ledum* species (*R. tomentosum* and *R. hypoleucum*) belong to the subgenus *Rhododendron* of the section *Rhododendron*. However, a study of chloroplast DNA (cpDNA) markers (Kurashige et al. 2001) combined *R. tomentosum* and *R. albrechtii* together into a low-supported sister group to the subgenera *Rhododendron* and *Hymenanthes*. Despite the noncongruence of phylogenies constructed using nuclear and chloroplast markers, the *Ledum* branch is always placed strictly within the genus *Rhododendron*.

Although the fact of including *Ledum* in the genus *Rhododendron* is accepted by the botanical community, most Russian botanists use outdated nomenclature. This is not surprising, as the transfer of *Ledum* to the genus *Rhododendron* has only increased confusion with species names.

Following the publication of the study by K. Kron and W. Judd, new combinations were proposed by Harmaya (1990, 1991, 1999, 2002). Below we present Harmaja's nomenclature together with outdated synonyms, which are widely used by botanists in Russia. We do not give descriptions of the taxa themselves, which can be found in Harmaja's publications, but we give the ecology and distribution of the selected species, according to Russian-language botanical literature for Far Eastern species (from

Mazurenko & Khokhryakov 1986, Khokhryakov & Mazurenko 1987, Khokhryakov 1991, Usenko 2010) and for North American species according to Savile (1969) and according to information in the worldwide database Global Biodiversity Information Facility (GBIF 2023) (Table 1). Distribution patterns and photos of some Labrador tea species are given in Figures 1 and 2. However, it should be kept in mind that the species in consideration have a characteristic habitus in the most favorable environmental conditions. When conditions change, plants begin to take transitional forms and become difficult to identify.

1. ***Rhododendron tomentosum*** Harmaja, 1990 (*R. palustre* (L.) Kron & Judd, 1990; *Ledum palustre* L. var. *dilatatum* Wahlenb., 1812; *L. palustre* L., 1753)

Hypoarcto-boreal Holarctic species, preferring peaty soils. Shrub with erect branches 0.3–1 m high. Young shoots with rather dense reddish pubescence. Leaves are linear, 25-45 mm long, 2.5–3.5 mm wide on a short petiole, wrapped along the edge, but with a well visible underside. The fruit capsules are about 5 mm, on straight or almost straight pedicels.

Narrow-leaved and broad-leaved forms are distinguished throughout the species' range. Narrow-leaved var. *longifolium* Freyn, 1902 was described in Amur Region, var. *angustum* E. Busch in Siberia, 1915, ssp. *angustissimum* Worosch. – in the Far East. The broad-leaved form var. *dilatatum* Wahlb. is described for Northern Europe and Altai. These forms can hardly be distinguished as independent species, as they often grow in a mixture with the common form (Khokhryakov & Mazurenko 1987).

2. ***Rhododendron subarcticum*** Harmaja, 1990. (*R. tomentosum* ssp. *decumbens* (Aiton) Elven & D.F. Murray, 2008; *R. tomentosum* Harmaja ssp. *subarcticum* (Harmaja) Wallace, 1992; *Ledum palustre* L. ssp. *decumbens* (Ait.) Hultén, 1930; *L. decumbens* (Aiton) Lodd. ex Steud, 1841)

Mainly hypoarctic Asian-American circumpolar species. Widespread in Arctic tundra, southward occurring in alpine and subalpine mountain belt. Usually prostrate with stalked branches, but sometimes an ascending shrub with height up to 30 cm. Young shoots with very dense dark reddish-brown pubescence. Leaves are smaller than in other *Ledum* species, 8–20 mm, 1.5–3 mm wide, oval-long or linear in shape with a strongly curved margin. The Fruit capsules are 3–3.5 mm long with abruptly bent stalks at the apex.

3. ***Rhododendron subulatum*** (Nakai) Harmaja, 2002. (*L. subulatum* (Nakai) A.P. Khokhr. & Mazurenko, 1991; *L. palustre* L. ssp. *angustissimum* Vorosch., 1978; *L. palustre* L. var. *angustum* E. Busch.; *L. palustre* L. var. *subulatum* Nakai, 1917)

Far Eastern species. It differs from other species by its almost needle-shaped leaves. Leaves are 10–50 mm long and 1–3 mm wide with dark hairs on the underside of the leaf. Flowers may have a pale pinkish tint.

4. ***Rhododendron tolmachevii*** Harmaja, 1990 (*L. macrophyllum* Tolm., 1953; *L. palustre* L. var. *yesoënse* Nakai, 1922; *L. maximum* (Nakai) A.P. Khokhr. & Mazurenko, 1991; *L. palustre* var. *maximum* Nakai, 1917).

Okhotsk-Amur-Japanese swamp species. Erect large shrub up to 1.2 m with thick branches. Leaves oblong-oval flat or weakly involute with reddish pubescence to 8 cm, 1.5 cm wide. Flowers are 6–8 mm long, on straight or slightly bent pedicels.

The name *L. maximum* (Nakai) A.P. Khokhr. & Mazurenko was proposed by A.P. Khokhryakov and M.T. Mazurenko to be hybridogenic: by the character of pubescence it has all transitions to the Amur–Japanese species *R. hypoleucum*, and by the size and shape of leaves – to the Eurasian species *R. tomentosum* (Probatova et al. 2007).

5. ***Rhododendron hypoleucum*** (Kom.) Harmaja, 1990 (*L. hypoleucum* Kom., 1916)

Amur–Japanese species, inhabits shady and thin places, damp mixed and dark coniferous forests. Quite a large shrub up to 1.2 m with straight thick branches. Leaves are oblong-oval flat or weakly wrapped whitish-oblong from below to 8 cm, 1.5 cm wide. Flowers 6–8 mm long, on straight or slightly bent pedicels.

6. ***Rhododendron diversipilosum*** (Nakai) Harmaja, 1999. (*L. palustre* L. ssp. *diversipilosum* (Nakai) H. Hara, 1956; *L. palustre* L. var. *diversipilosum* Nakai, 1917; *L. nipponicum* (Nakai) Tolm.)

Japanese–Sakhalin species. The species is found in bogs, in the undergrowth of subalpine forests and in the alpine shrub zone. The species is characterized by a "compressed" arrangement of leaves at the ends of twigs, their small size and ovate-lanceolate shape. The pubescence on the underside of the leaves is dense dark reddish. It differs from *R. tolmachevii* and *R. hypoleucum* by the sharper form of leaves with long mixed white-red pubescence on the underside of the leaf. The plant is 30–70 cm tall, with elliptical leaves and inflorescences with many white flowers.

7. ***Rhododendron groenlandicum*** (Oeder) Kron & Judd, 1990 (*L. palustre* L. ssp. *groenlandicum* (Oeder) Hultén, 1948; *L. latifolium* Jacq., 1789; *L. groenlandicum* Oeder, 1771)

North American arctic and subarctic shrub. Grows predominantly on sphagnum bogs throughout Canada and also in the northwestern USA, where it moves southward as far south as northwestern Oregon. A 30–120 cm tall shrub with densely pubescent young shoots that become glabrous over time. Leaves are pubescent with white hairs on the underside, which redden on ageing leaves. The edges of the leaves are strongly curved inward.

8. ***Rhododendron neoglandulosum*** Harmaja, 1990 (*L. glandulosum* Nutt., 1843)

Grows in moist coniferous forests in the Cordillera region on the border with southern British Columbia and southwestern Alberta. An erect shrub 100–200 cm tall. Leaves are pubescent with white hairs on the underside, leaves straight or with a slightly wrapped margin.

9. ***Rhododendron columbianum*** (Piper) Harmaja, 1990 (*L. columbianum* Piper, 1906; *L. glandulosum* Nutt var. *columbianum* (Piper) Hitchc.)

North American swamp species. Grows in moist habitats at altitudes from sea level to 3500 m. Grows up to 2 m in height. Leaves grow close to the stem, with white hairs on the lower leaf surface. It is considered a hybrid between *R. groenlandicum* and *R. neoglandulosum* species (Savile 1969).

## PLOIDY

For Eurasian Labrador tea species, polyploidy is shown in most cases in contrast to North American ones. At the same time, for other few species of rhododendrons widely distributed in the boreal and mountain zones of Eurasia, mainly in Russia, such as *R. aureum* Georgi, *R. dauricum* L. s.l., *R. parvifolium* Adams, *R. adamsii* Rehder. polyploidy is absent or extremely rare (Aleksandrova 1975). Regarding the chromosome numbers of Labrador tea species there is rather scarce and contradictory information in the literature. Both the diploid $2n = 26$ chromosome number, basic to all rhododendron species, and the tetraploid $2n = 52$ are found in Labrador tea species. We summarized the available data on chromosome number measurements of different species of Labrador teas species (Table 2). Only diploid chromosome number is known for the American

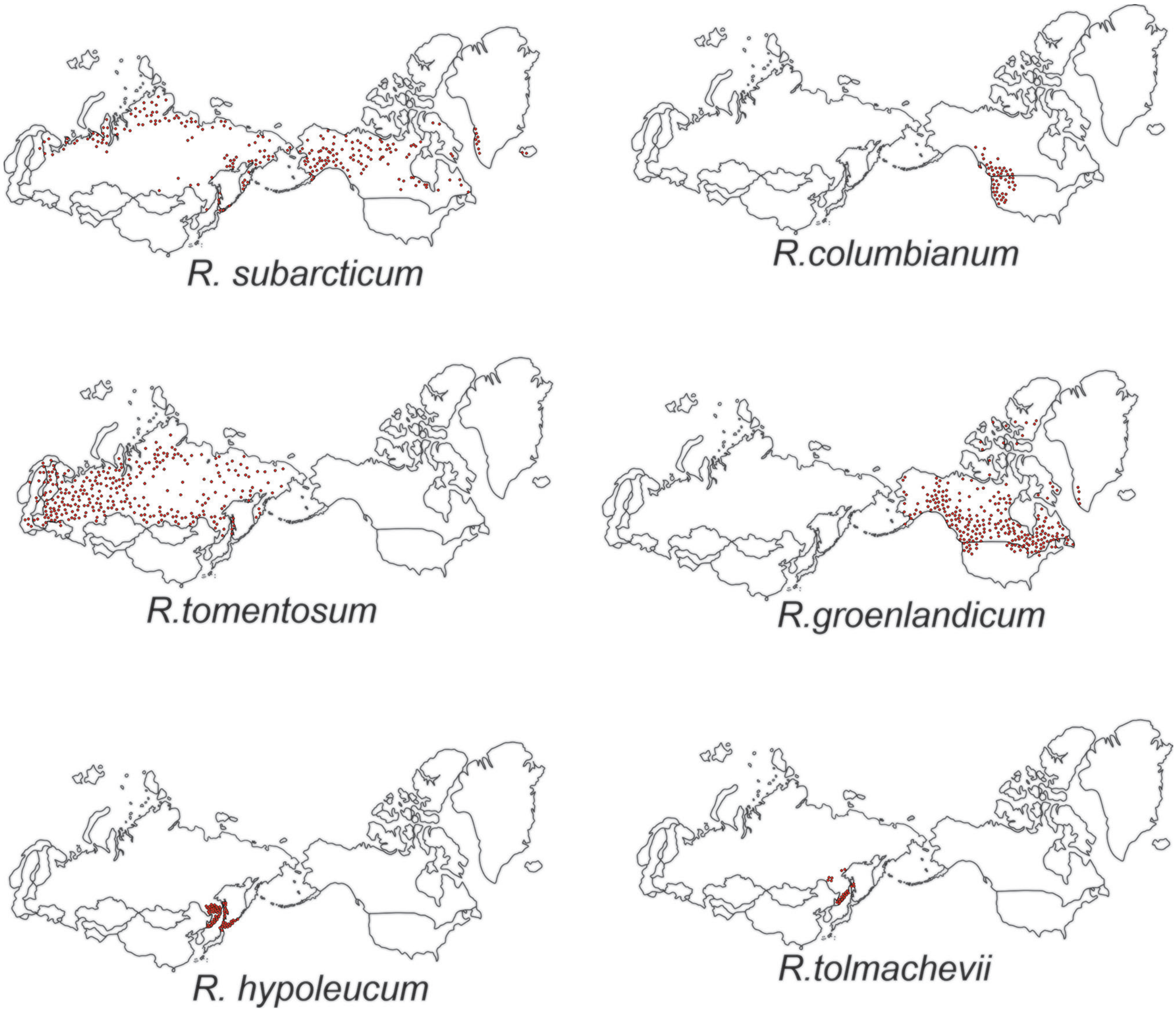

**Figure 1** Distribution pattern of some Labrador tea species compiled from GBIF (2024), Dudov & Seregin (2024) and iNaturalist (2024)

**Table 1.** Comparing of distribution for different species from the genus *Rhododendron* subsection *Ledum*.

| Species | Range extent | Distribution |
|---|---|---|
| *Rhododendron tomentosum* | From Chukotka to the Czech Republic | Eurasian species |
| *Rhododendron subarcticum* | West Greenland, North America (from Baffin Land to Alaska), Northeast Asia (Hokkaido, Russian Far East, Northern Siberia east of the Yenisei River). | Arctic or subarctic circumpolar species |
| *Rhododendron subulatum* | Eastern Asia (except in the north) mainly in Russia but also extending to NE China, North Korea and Japan | Amur-Japanese species |
| *Rhododendron tolmachovii* | Sakhalin Island, in the Amur River area, in the Sikhote-Alin Mountains, along the coast of the Sea of Okhotsk, in the basins of the Aldan and Anadyr rivers, in North Korea, on Hokkaido Island. | Okhotsk-Amur-Japanese swamp species |
| *Rhododendron hypoleucum* | North of Sakhalin Island, northern Sikhote-Alin to Sovetskaya Gavan settlement (Khabarovsk Territory), lower reaches of the Amur River | Amur-Japanese species |
| *Rhododendron diversipilosum* | Japan, Sakhalin Island, Kuril Islands | Japan, Sakhalin Island, Kuril Islands |
| *Rhododendron groenlandicum* | Canada, from northwestern USA to Oregon on the East Coast | North American Arctic and subarctic species |
| *Rhododendron neoglandulosum* | In the western USA to southern British Columbia, east of the Cascade Mountains to southeastern British Columbia and southwestern Alberta in the Rocky Mountains. | North American swamp species |
| *Rhododendron columbianum* | the western United States and in western Canada | North American swamp species |

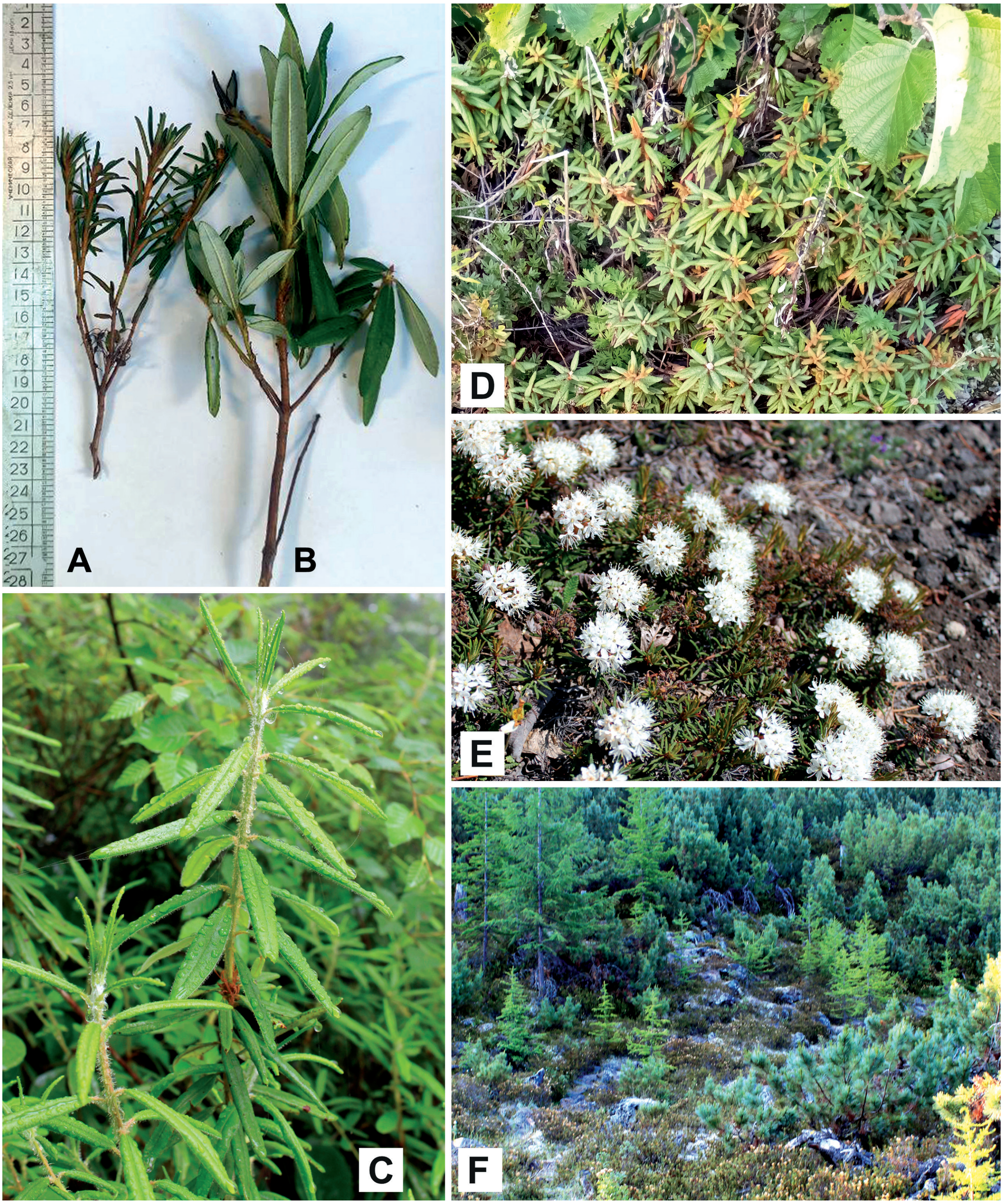

**Figure 2** Some species of Labrador teas from Northeast Asia. A – *Rhododendron tomentosum*, Khabarovsk Territory, surroundings of Komsomolsk-na-Amure, from understory; B – *R. hypoleucum*, Khabarovsk Territory, surroundings of Sovetskaya Gavan', from understory; C – *R. tolmachevii*, Primorye Territory, surroundings of Terney, understory; D – *R. diversipilosum*, Kuril Islands, Shikotan Isl., forest margin; E – *R. subarcticum*, Kamchatka Peninsula, surroundings of Esso, on the top of ridge; F – the taller form of *R. subarcticum* forms the patches at the beginning of the ascent to the ridge. It grows together with Siberian dwarf pine and larch. Kamchatka Peninsula, surroundings of Esso

hypoarctic species *R. groenlandicum*. The boreal Asian species *R. tometosum*, *R. tolmachovii* and *R. diversipilosum* are tetraploids. For the hypoarctic circumpolar species *R. subarcticum*, both diploid and tetraploid chromosome number are defined, while no data are available for the other species. These data are mostly old, and their scarcity is probably due to the very small size of chromosomes in *Rhododendron* representatives, which makes it difficult to use the Folgen staining technique, especially in polyploids. However, the modern method of flow cytometry will probably change the situation in the near

**Table 2.** The chromosome numbers for different species of Labrador teas.

| New name | Old name | $N_{ch}$ | Location | Reference |
|---|---|---|---|---|
| *R. subarcticum* | *L. decumbens* (Aiton) Small | 26 | Southern Chukotka, Rarytkin Ridge | Zhukova P. G. 1980. |
| | *L.decumbens* (Aiton) Small | 52 | Western Chukotka, Rauchua polar station, Wrangel Island | Zhukova P. G., PetrovskyV.V. 1976. |
| | *L.palustre* subsp. *decumbens* (Aiton) Hultén | 52 | Canada, Churchill, Manitoba | Love A., Love D.. 1982. |
| | *L. palustre* subsp. *decumbens* (Aiton) Hultén | 52 | West Greenland | Jorgensen C. A. 1958. |
| | *L. palustre* subsp. *decumbens* (Aiton) Hultén | 26 | Ogotoruk Creek, northwestern Alaska | Johnson A. W., Packer J. G. 1968. |
| | *L. palustre* L. ssp. *decumbens* (Ait.) Hultkn | 26 | Sondre Stromfjord, West Greenland | Lantai K., Kihlman B. 1995. |
| | *L. palustre* L. ssp. *decumbens* (Ait.) Hultkn | 26 | Tardoki-Yani Mountain, Sikhote-Alin, Russia | |
| *R. tomentosum* | L. palustre L. s. str. | 52 | Lumen, Uppsala, Sweden | Lantai K., Kihlman B. 1995. |
| | *L. palustre* L. | 52 | Czech Republic | Měsíček J. 1992. |
| *R. groenlandicum* | *L. groenlandicum* Oeder | 26 | North America | Love A., Love D. 1982. |
| *R. tolmachovii* | *L. macrophyllum* Tolm. | 52 | Sakhalin Island, Aniva District, Novo-Alexandrovsk settlement | Gurzenkov N. N. 1973. |
| *R. diversipilosum* | | 52 | Japan, Hokkaido | Wakui A. 2021. |

future, as it is now being used extensively on heath species (Wakui & Kudo 2021, Redpath et al. 2022). It is known that the presence of diploid and polyploid races is common for cold-loving heath species. For example, *Vaccinium uliginosum* L. and *V. vitis-idaea*, have high-altitude arctic diploid races and low-elevation boreal polyploid races. At the same time, polyploid races, as a rule, are distinguished morphologically by larger sizes, greater ability to hybridization and clonal reproduction (Jacquemart 1996, Wakui & Kudo 2021). In natural conditions of northeast Asia (according to personal observations of the authors in Kamchatka and Sakhalin), *Ledum* also shows a gradual decrease of individuals when climbing from low-elevation to high-elevation and during the transition from swampy to afforested areas. In Hokkaido this phenomenon was thoroughly studied on the example of *R. divesipilosum* (= *L. palustre* ssp. *diversipilosum*), which is widespread there in subalpine to alpine regions, in coniferous forests and coastal grasslands, and plants from alpine locality are smaller than from forest habitat types (Wakui 2021). Based on flow cytometry results, the authors found that all populations studied appeared to be tetraploid. No genetic differences between populations of differnt habitat types were also detected based on nuclear microsatellite marker variability (SSR) data.

Thus, it can be concluded that for the Labrador teas species complex, mixed ploidy is not a characteristic of altitudinal races, but rather reflects the division into boreal and high-mountain arctic species that are in succession relationships on a larger geographic scale. This is most pronounced in the mountainous regions surrounding the North Pacific – North America with the Cordilleras extending meridionally from south to north and Asia with a chain of mountains along the east coast. In this area, the distribution of Labrador teas species reflects the migration of floras between the two continents.

The presence of polyploid closely related species or races is characteristic of evolutionarily young taxa, as polyploids are thought to have a number of advantages in territory occupation under unstable conditions. If we accept the secondary nature of polyploid boreal species of Labrador teas from Asia (*R. tomentosum*, *R. tolmachovii*, *R. hypoleucum*, *R. diversipilosum*) relative to the diploid hypoarctic North American *R. groenlandicum*, we can assume that modern Labrador teas spread to Eurasia from North America. Khokhryakov & Mazurenko (1986) suggest that as early as in the Late Oligocene – Middle Miocene, Labrador teas spread from North America to Asia through Beringia as part of coniferous-broadleaved forests. Then, during the glacial periods of the Pleistocene, when coniferous-broadleaved forests in Beringia were destroyed, broadleaved Labrador teas disappeared as well (the modern northern limit of its distribution is at rather low latitudes – not higher than 50°N). Later, the species returned to North America over the same bridge, but already in the form of *R. subarcticum*, a circumpolar hypoarctic species adapted to the harsh conditions of the Arctic. The mixed ploidy of *R. subarcticum* in northeastern Asia and North America may indicate the existence of both diploid (Johnson & Packer 1968, Zhukova 1980, Lantai & Kihlman 1998) and tetraploid (Jorgensen 1958, Zhukova 1976, Love & Love 1982) populations in these regions, indicating the existence of gene flow through Beringia until recently. The older origin of *R. subarcticum*, which also has diploid populations in Asia, is questioned by Mazurenko & Khokhryakov (1987), who suggested a possible secondary diploidization of this species.

## ORIGIN

The question about the origin of Labrador tea species remains open and requires the study of ploidy of large-leaved boreal North American species, as well as comparison of the genetic structure of Asian and North American species. The occurrence of a common ancestor of species and their diversification on the North American continent (as suggested by Mazurenko & Khokhryakov 1986, 1987) is not typical for the genus *Rhododendron* and much less for the section *Rhododendron*. The genus *Rhododendron* is thought to have originated in the early Paleocene about 50–68 million years ago (Irving & Hebda 1998, Shrestha et al. 2018, Xia et al. 2022). The evolutionary outburst and divergence of the four sections *Tsutsusi*, *Schistanthe*, *Rhododendron* (to which *Ledum* belongs) and *Ponticum* is dated to the Miocene. Regarding the place of origin of the genus, many authors agree that it was the northern latitudes occupied by boreal forests in eastern Asia (Milne 2006). From here, there was a migration to Europe, North America, and also to the south, where large-scale processes of mountain formation and strengthening of monsoon climate became powerful factors of speciation (Khan et al. 2021, Xia et al. 2022). Interestingly, in a recent study of the phylogeny of the genus *Rhododendron* (Xia et al. 2022), it was shown that in the subgenus *Rhododendron*, Labrador tea species (*R. hypoleucum* and *R. tomentosum*) separated first (about 27 million years ago, in the late Oligocene), forming an external sister clade to species of section *Schistanthe*, distributed mainly in the Malay Archipelago, and section *Rhododendron*, including Asian species as well as *R. ferrugineum* and *R. hirsutum* from Europe. Thus, Labrador tea species are the only representatives of their subgenus *Rhododendron* distributed in North America. In addition, Labrador tea, always considered one of the youngest groups of the genus *Rhododendron* in evolutionary terms, due to their adaptation to cold conditions and wide range, according to recent data, may have an older origin. Apparently, the dispersal of *Ledum* ancestor to North America occurred before the beginning of active diversification within the subgenus *Rhododendron* (in the second half of Miocene), and their evolution initially occurred either only in North America or in parallel from both sides of the North Pacific Ocean. At the same time, when the most active processes of speciation of other *Rhododendrons* occurred when moving southward from the boreal zone to the regions of the Himalaya–Hengduan Mountains and the Malay Archipelago – the centers of modern diversity of the entire genus *Rhododendron*, the evolution of the *Ledum* group developed in the northern direction, towards to the harsh regions of the Arctic and Subarctic.

The first attempt to clarify phylogenetic relationships directly within the *Ledum* subsection using molecular genetic markers was made by Hart et al. (2017) using chloroplast and nuclear DNA variability data on 8 herbarium specimens representing different species from Asia and North America. In this work, the authors identified incongruence between phylogenetic trees based on markers from different genomes. Phylogeny based on nuclear markers (ITS1 and GBSS-1/waxy) indicated a monophyletic origin of the subsection, combining the sequences of all specimens into a single clade with high support, distinguishing them from rhododendrons of other sections, but with low resolution between different *Ledum* species. Data on variability of cpDNA markers (*pl*32-*trn*L, *trn*S-*trn*G, *trn*V-*ndh*C) showed that all *Ledum* species are divided into Asian and North American clades, in each of which *Ledum* species are more related to other rhododendron species than to each other. Thus, it surprisingly appeared that the North American species of *Ledum* species *R. columbianum*, *R. neoglandulosum*, and *R. groenlandicum* form a common clade with *R. hippophaeoides*, *R. orbiculatum*, sister to *R. albiflorum*, the only American representative of the subgenus *Hymenanthes*. The authors interpret these results as consequences of the hybrid origin of modern Labrador teas, which captured chloroplasts from rhododendrons from other sections. It should be noted that it is currently known about the possibility of intersectional crossing of Labrador tea species both in cultural (Theqvist 2013) and in natural conditions (Dalgaard & Fredskild 1992), which indicates a decrease in reproductive barriers between representatives of different sections of rhododendrons.

We recently attempted to analyze the genetic structure of Labrador tea species on Sakhalin Island based on cpDNA (Iunusova et al. 2023). We analyzed four sympatric Labrador tea species (*R. tomentosum*, *R. subarcticum*, *R. tolmachevii* and *R. hypoleucum*) from 18 populations, 94 individuals for five markers (*trn*H-*psb*A, *pet*B-*pet*D, 3'*trn*V(UAC)-*ndh*C, K2R-K707, *atp*B-*rbc*L). The results showed high variability and high differentiation between populations. However, genetic variability corresponded not to the species distinguished, but to the geographic structure, which fell into northern Sakhalin and southern Sakhalin groups. The separation between groups roughly corresponds to the phytogeographic boundary of the island, south of which the North Japanese type flora predominates and the presence of northern boreal species decreases. The unresolved star pattern in the haplotype network suggests that rapid diversification of Labrador teas with ongoing genetic exchange has occurred on Sakhalin, so the current taxonomic treatment does not reflect clearly defined taxonomic units. This unexpected result indicates that when analyzing such a polymorphic group with a complex history, it is important to use genetic markers with different types of inheritance and dense samples of each species across the distribution area.

## CONCLUSION

Since species of the section *Ledum* have in their distribution an intercontinental disjunction between Eurasia and North America, as well as a specific pattern of distribution both in the southern part of North Asia with high biodiversity and tend to be more older and younger circumboreal distribution, this group is of interest for understanding speciation processes in the Northern Hemisphere. To capture the whole complexity of the *Ledum*'s genetic landscape we need to analyze its genetic structure properly for revealing patterns, explaining (1) evolution of subsection *Ledum* species from boreal to subarctic, (2) hybrid processes between them and (3) the migration history of these species in the Pacific region as a whole.

## ACKNOWLEDGMENTS

This research was financially supported by a grant of the Russian Science Foundation, No 23-24-00173, https://rscf.ru/project/23-24-00173/.

## LITERATURE CITED

Aleksandrova, M.S. 1975. *Rhododendrons of the natural flora of the USSR*. Nauka, Moscow, 112 pp. (in Russian). [Александрова М.С. 1975. Рододендроны природной флоры СССР. Москва: Наука. 112с.]

Belousova, N.I., V.A. Han & A.V. Tkachyov 1999. Chemical composition of *Ledum* essential oil. *Khimiya rastitel'nogo syr'ya* 3:5–38 (in Russian). [Белоусова Н.И., Хан В.А., Ткачёв А.В. 1999. Химический состав эфирного масла багульников // Химия растительного сырья. № 3. С. 5–38].

Belousova, N.I., V.A. Khan & T.P. Berezovskaya 1990. Intraspecies chemical variability of the essential oil of *Ledum palustre*. *Chemistry of Natural Compounds* 26:398–405.

Blondeau, M. & C. Roy 2004. Atlas of plants of the Nunavik villages. Sainte-Foy, QC: Editions Multimondes, 610 pp.

Busch, E.A. 1915. Ericaceae, genus *Rhododendron*. In: *Flora Sibiriae et Orientis Extremi*. *Petrograd* 2:13–41 (in Russian). [Буш Е.А. 1915. Вересковые. Род Рододендрон // Флора Сибири и Дальнего Востока. Петроград. Вып. 2. С. 13–41].

Calmes, M.A. & J.C. Zasada 1982. Some reproductive traits of four shrub species in the black spruce forest type of Alaska. *The Canadian Field-Naturalist* 96:35–40.

Cubino, J.P., Z. Lososová, G. Bonari, E. Agrillo, F. Attorre, E. Bergmeier, I. Biurrun, J.A. Campos, A. Čarni, M. Ćuk, ... & M. Chytrý 2021. Phylogenetic structure of European forest vegetation. *Journal of Biogeography* 48:903–916.

Dalgaard, V. & B. Fredskild 1992. × *Ledodendron vanhoeffeni* (syn.: *Rhododendron vanhoeffeni*) refound in Greenland. *Nordic Journal of Botany* 13(3):253–255.

Dampc, A. & M. Luczkiewicz 2013. *Rhododendron tomentosum* (*Ledum palustre*). A review of traditional use based on current research. *Fitoterapia* 85:130–143.

Dudov S. V. & A. P. Seregin 2024. *Atlas of the Russian Flora: Electronic resource*. Available at: https://plant.depo.msu.ru/. Last accessed 06.06.2024.

Gao, L.M., D.Z. Li, C.Q. Zhang & J.B. Yang 2002. Infrageneric and sectional relationships in the genus *Rhododendron* (Ericaceae) inferred from ITS sequence data. *Acta Botanica Sinica* 44(11):1351–1356.

Goetsch, L., J. Andrew, J.A. Eckert & B.D. Hall 2005. The molecular systematics of *Rhododendron* (Ericaceae): A phylogeny based upon RPB2 gene sequences. *Systematic Botany* 30(3):616–626.

GBIF 2023. *Global Biodiversity Information Facility (GBIF) occurrence downloads, 12 November 2023*. URL: https://www.gbif.org/ru/species/2882984; https://www.gbif.org/ru/species/4165978; https://www.gbif.org/ru/species/4169545

Gurzenkov, N.N. 1973. Studies of chromosome numbers of plants from the south of the Soviet Far East. *V.L. Komarov Lectures* 20:47–61 (in Russian). [Гурзенков Н.Н. 1973. Исследования хромосомных чисел растений юга Дальнего Востока // Комаровские чтения. Вып. 20. С. 47–61].

Harmaja, H. 1990. New names and nomenclatural combinations in *Rhododendron* (Ericaceae). *Annales Botanici Fennici* 27(2):203–204.

Harmaja, H. 1991. Taxonomic notes on *Rhododendron* subsection *Ledum* (*Ledum*, Ericaceae), with a key to its species. *Annales Botanici Fennici* 28(2):171–173.

Harmaja, H. 1999. *Rhododendron diversipilosum*, comb. nov. (Ericaceae). *Annales Botanici Fennici* 35:263–264.

Harmaja, H. 2002. *Rhododendron subulatum*, comb. nova (Ericaceae). *Annales Botanici Fennici* 39(3):183–184.

Hewitt, G. 2000. The genetic legacy of the quaternary ice ages. *Nature* 405:907–913.

Hébert, F. & N. Thiffault 2011. The biology of Canadian weeds. 146. *Rhododendron groenlandicum* (Oeder) Kron and Judd. *Canadian Journal of Plant Science* 91(4):725–738.

Hitchcock, C.L. 1956. The *Ledum glandulosum* complex. *Leaflets of Western Botany* 8:1–8.

iNaturalist. Available at: https://www.inaturalist.org/. Last accessed 06.06.2024.

Khokhryakov, A.P. & M.T. Mazurenko 1986. The role of Beringia in the evolution and dispersal of North Pacific Ericaceae. In: *Biogeography of the Beringian sector of the sub-Arctic. Proceedings of the tenth All-Union Symposium "Biological Problems of the North"* (F.B. Chernyavsky, I.A. Chereshnev, eds), pp. 35–51, FESC AS USSR, Vladivostok (in Russian). [Хохряков А.П., Мазуренко М.Т. 1986. Роль Берингии в эволюции и расселении северопацифических вересковых // Биогеография Берингийского сектора субарктики. Тезисы десятого всесоюзного симпозиума «Биологические проблемы севера» / под ред. Чернявского Ф.Б., Черешнева И.А. Владивосток: ДВНЦ РАН. С. 35–52].

Khokhryakov, A.P. & M.T. Mazurenko 1991. Ericaceae. In: *Vascular Plants of the Soviet Far East, vol 5* (S.S. Kharkevich, ed.), pp. 119–166, Nauka, St. Petersburg (in Russian). [Хохряков А.П., Мазуренко М.Т. 1991. Вересковые – Ericaceae Juss. // Сосудистые растения Советского Дальнего Востока / отв. ред. С.С. Харкевич. Санкт-Петербург: Наука. Т. 5. С. 119–166].

Hultén, E. 1930. *Flora of Kamtchatka and the adjacent islands, part 4*. Almqvist and Wiksells, Stockholm.

Hultén, E. 1968. *Flora of Alaska and neighboring territories: A manual of the vascular plants*. Standford University Press, Stanford.

Hultén, E. & M. Fries 1986. *Atlas of North European vascular plants: north of the Tropic of Cancer. Vol. 1–3*. Koeltz Scientific Books edition, 1172 pp.

Ikeda, H. 2022. Decades-long phylogeographic issues: complex historical processes and ecological factors on genetic structure of alpine plants in the Japanese Archipelago. *Journal of Plant Research* 135:191–201.

Jacquemart, A.L. 1996. *Vaccinium uliginosum* L. *Journal of Ecology* 84(5):771–785.

Jesionek, A., A. Kokotkiewicz, A. Mikosik-Roczynska, K. Ciesielska-Figlon, P. Luczkiewicz, A. Bucinski, A. Daca, J.M. Witkowski, E. Bryl, B. Zabiegala & M. Luczkiewicz 2019. Chemical variability of *Rhododendron tomentosum* (*Ledum palustre*) essential oils and their pro-apoptotic effect on lymphocytes and rheumatoid arthritis synoviocytes. *Fitoterapia* 139:104402.

Johnson, A.W. & J.G. Packer 1968. Chromosome numbers in the flora of Ogotoruk Creek, N.W. Alaska. *Botanical Naturalist* 121:403–456.

Jorgensen, C.A. 1958. The flowering plants of Greenland. A taxonomical and cytological survey. *Kongelige Danske Videnskabernes Selskabs Skrifter* 9:1–172.

Judd, W.S. & K.A. Kron 2009. *Rhododendron*. In: *Flora of North America north of Mexico, vol. 8* (Flora of North America Editorial Committee, eds), pp. 453–543, Oxford University Press, New York.

Komarov, V.L. 1932. *Identifier of plants of the Far East Territory*. Izdatel'stvo AN SSSR, Moscow, 622 pp. (in Russian). [Комаров В.Л. 1932. Определитель растений Дальневосточного Края. Москва: Изд-во АН СССР. 622 с.].

Kurashige, Y., J.-I. Etoh, T. Handa, K. Takayanagi & T. Yukawa 2001. Sectional relationships in the genus *Rhododendron* (Ericaceae): evidence from *mat*K and *trn*K intron sequences. *Plant Systematics and Evolution* 228:1–14.

Kutsev, M.G. & A.V. Karakulov 2010. Reconstruction of phylogeny of the genus *Rhododendron* L. (Ericaceae) from Russia based on ITS1-ITS2 sequence. *Turczaninowia* 13:59–62 (in Russian). [Куцев М.Г., Каракулов А.В. 2010. Реконструкция филогении рода *Rhododendron* L. (Ericaceae) флоры России на основе последовательностей спейсеров ITS1–ITS2 // Turczaninowia. № 13. С. 59–62].

Lantai, K. & B. Kihlman 1995. The chromosome numbers of *Ledum palustre* ssp. *decumbens* and of some related taxa. *Hereditas (Lund)* 122:181–184.

Li, S., A. Brault, M. Sanchez Villavicencio, P.S. Haddad 2016. *Rhododendron groenlandicum* (Labrador tea), an antidiabetic plant from the traditional pharmacopoeia of the Canadian Eastern James Bay Cree, improves renal integrity in the diet-induced obese mouse model. *Pharmaceutical Biology* 54(10):1998–2006.

Linnaeus, C. 1753. *Species Plantarum, T. 1*, p. 391, Stockholm.

Love, A. & D. Love 1982. In: A Löve (ed.), IOPB chromosome number reports LXXV. *Taxon* 31(2): 344–360.

Malloch, D. & B. Malloch 1981. The mycorrhizal status of boreal plants species from northeastern Ontario. *Canadian Journal of Botany* 59:2167–2172.

Mazurenko, M.T. & A.P. Khokhryakov 1987. Biomorphological evolution of Far Eastern *Ledum* species. *Zhurnal obshchei biologii* 48(2):190–201. [Мазуренко М.Т., Хохряков А.П. 1987.Биоморфологическая эволюция дальневосточных багульников // Журнал общей биологии. Т. 48, № 2. С. 190–201].

Měsíček, J. 1992. *List of Chromosome Numbers of the Czech Vascular Plants*. Academia, Praha, 144 pp.

Mofikoya, A.O., K. Miura, R.P. Ghimire, P. Rajendra, J.D. Blande, M. Kivimäenpää, T. Holopainen & J.K. Holopainen 2018. Understorey *Rhododendron tomentosum* and leaf trichome density affect mountain birch VOC *Emissions in the Subarctic. Scientific Reports* 8:13261.

Mucina, L., H. Bültmann, K. Dierßen, J-P. Theurillat, T. Raus, A. Čarni, K. Šumberová, ... & L. Tichý 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19:3–264.

Musil, R. 1985. Paleobiogeography of terrestrial communities in Europe during the Last Glacial. *Acta Musei Nationalis Pragae* 41B:1–83.

Müller, O.F. 1771–1777. *Flora danica vierter band*. Gedruckt bey Martin Hallager. Kopenhagen.

Nuttall, T. 1843. Description and Notices of new or rare plants in the natural orders Lobeliaceae, Campanulaceae, Vaccinieae, Ericaceae, collected in a journey over the continent of North America, and during a visit to the Sandwich Islands, and Upper California. *Transactions of the American Philosophical Society* 8:1–270.

Ohwi, J. 1965. *Flora of Japan (in English)*. Smithsonian Institution, Washington, DC, 1067 pp.

Piper, C. 1906. Flora of the state of Washington. *Contributions from the United States National Herbarium* 11:441.

Probatova, N.S., V.Yu. Barkalov & E. Rudyka 2007. *Caryology of the flora of Sakhalin and Kuril Islands*. Dalnauka, Vladivostok, 390 pp. (in Rusian). [Пробатова Н.С., Баркалов В.Ю., Рудыка Э.Г. 2007. Кариология флоры Сахалина и Курильских островов. Владивосток: Дальнаука. 390 с.]

Radoměřský, T., P. Bobek, M. Man, H. Svitavská Svobodová, & P. Kuneš 2023. Modelling the location of interglacial microrefugia for cold-adapted species: insights from the terrain-mediated distribution of *Rhododendron tomentosum* in a temperate region in central Europe. *Preslia* 95:267–296.

Rantanen, M., A.Y. Karpechko, A. Lipponen, K. Nordling, O. Hyvärinen, K. Ruosteenoja, T. Vihma & A. Laaksonen 2022. The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment* 3:168.

Rapinski, M., L. Musallam, J.T. Arnason, P. Haddad, A. Cuerrier 2015. Adipogenic activity of wild populations of *Rhododendron groenlandicum*, a medicinal shrub from the James Bay Cree traditional pharmacopeia. *Evidence-Based Complementary and Alternative Medicine* 2015:492458.

Redpath, L.E., R. Aryal, N. Lynch, J.A. Spencer, A.M. Hulse-Kemp, J.R. Ballington, J. Green, ... & H. Ashrafi 2022. Nuclear DNA contents and ploidy levels of North American *Vaccinium* species and interspecific hybrids. *Scientia Horticulturae* 297:110955.

Savile, D.B. O. 1969. Interrelationships of *Ledum* species and their rust parasites in western Canada and Alaska. *Canadian Journal of Botany* 47(7):1085–1100.

Shotyk, W., M.B. Javed & T. Noernberg 2020. Trace elements in Labrador Tea (*Rhododendron groenlandicum*): How predominant sources to the plants impact the chemical composition of hot water extracts. *Environmental Resources* 183: 109272.

Tanasienko, F.S. 1985. *Essential oils. Content and composition in plants*. Kiev, 286 pp. (in Russian). [Танасиенко Ф.С. Эфирные масла. Содержание и состав в растениях. Киев. 286 с.].

Theqvist, K. 2013. *Hybridity of lepidotes in Rhododendron subsection Ledum based on some hybridization results*. https://www.rhodogarden.com/cross/hybridity.html Last accessed 06.04.2023.

Thiffault, N. & R. Jobidon, 2006. How to shift unproductive *Kalmia angustifolia–Rhododendron groenlandicum* heath to productive conifer plantation. *Canadian Journal of Forest Research* 36:2364–2376.

Tolmachev, A.I. 1953. Toward the cognition of Euroasian species of the genus *Ledum* L. In: *Botanicheskie materialy gerbariya Botanicheskogo instituta AN SSSR* 15:1–306 (in Russia). [Толмачев А.И. 1953. К познанию евроазиатских видов рода *Ledum* L. // Ботанические материалы гербария Ботанического института АН СССР. Т. 15. С. 1–306].

Usenko, N.V. 2010. *Trees, shrubs, and vines of the Far East: a reference book*. Priamurskie Vedomosti, Khabarovsk, 304 pp. (in Russian). [Усенко Н.В. Деревья, кустарники и лианы Дальнего Востока: справочная книга. Хабаровск: Приморские Ведомости. 304 с.].

Viereck, L.A., E.L. Little, Jr. 1972. *Alaska trees and shrubs. Agricultural Handbook, Number 410*. U.S. Department of Agriculture, Washington, 265 pp.

Voroshilov, V.N. 1982. *Identifier of plants of the Far East of the USSR*. Nauka, Moscow, 674 pp. (in Russian). [Ворошилов В.Н. 1982. Определитель растений советского Дальнего Востока. Москва: Наука. 674 с.].

Xia, X.M., M.Q. Yang, C.L. Li, S.X. Huang, W.-T. Jin, T.-T. Shen, F. Wang, ... & X.-Q. Wang. 2022. Spatiotemporal evolution of the global species diversity of *Rhododendron*. *Molecular Biology and Evolution* 39(1):msab314.

Wakui, A. & G. Kudo, 2021. Ecotypic differentiation of a circumpolar Arctic-alpine species at mid-latitudes: variations in the ploidy level and reproductive system of *Vaccinium vitis-idaea*. *AoB Plants* 13(3):plab015.

Wakui, A. 2021. *Ecotypic differentiation of northern plant species in mid-latitudes: the mechanisms of population maintenance in two ericaceous alpine species in northern Japan*. A Dissertation for the Degree of Doctor. Graduate School of Environmental Science, Hokkaido University. 102 pp.

Wang, C., S.T. Gower, Y. Wang, H. Zhao, P. Yan, B.P. Bond-Lamberty 2001. The influence of fire on carbon distribution and net primary production of boreal *Larix gmelinii* forests in north-eastern China. *Global Change Biology* 7:719–730.

Zhukova, P.G. 1980. Chromosome numbers of some Southern Chukotka plant species. *Botanicheskii Zhurnal* 65(1):51–59 (in Russian). [Жукова П.Г. 1980. Хромосомные числа некоторых видов растений Южной Чукотки // Ботанический журнал. Том 65, № 1. С. 51–59].

Zhukova, P.G. & V.V. Petrovsky 1976. Chromosome numbers of some Western Chukotka II plant species. *Botanicheskii Zhurnal* 61(7):963–969 (in Russian). [Жукова П.Г., Петровский В.В. 1976. Хромосомные числа некоторых видов растений Западной Чукотки // Ботанический журнал. Т. 61, № 7. С. 963–969].