Systematics and phylogeny of *Larix* Mill. based on morphological and anatomical analysis

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**Abstract**
Complex comparative morphological investigation of different representatives of *Larix* was carried out to assess the taxonomic value of some characters of vegetative and reproductive organs. In this study, the needle anatomy of 12 *Larix* species were investigated. The results showed that the shape of the needle in cross-section, the presence of secretory structures, and the number of hypodermis layers on the lateral margin of needles are of taxonomic and diagnostic value at the species level. We also have been checked the taxonomic status and geographical distribution of some critical taxa. *Larix archangelica* × *L. dahurica* was found in the Yamal-Nenets autonomous district. Hybridogeneous nature of larch, growing in Kamchatka and the need to describe it as a separate species are confirmed. It is found that a typical section *Larix* by the morphology of vegetative and reproductive organs are clearly divided into 4 groups.

**Background**
In different taxonomic treatments, the genus *Larix* Mill. includes between 11 [1] up to 20 species. Nine of them are found in the wild in the territory of Russia [2]. Despite numerous studies, devoted to the systematics of the Russian species of the genus *Larix* [2-14], there are still many unresolved questions. The greatest number of taxa have been reported for the Far East region namely: *L. kamtschatica* (Rupr.) Carrière, *L. ochotensis* Kolesn., *L. maritima* Sukacz., *L. lubarskii* Sukacz., *L. komarovii* B. Kolesn., *L. middendorfii* Kolesn., whereas *L. czekanowskii* Szafer and another two larch taxa are wild growing in the territory of Eastern Europe (*L. archangelica* Laws. and *L. polonica* Racib. ex Wóycicki).

The taxonomic treatment of these taxa by different authors [2, 3, 15, 16] vary considerably [17].
In the work of Bobrov [2, 3] provides data on 10 wild-growing species (including 3 nature hybrids). Koropachinsky [6] in treatment of Pinaceae for "Vascular plants of the Soviet Far East" allocated only three enough stable species: *L. olgensis*, *L.

In the treatment of genus Larix for the "Conspectus Florae Europae Orientalis" [18], two wild species [Arkhangel Larch (L. archangelica) and the Polish Larch (L. decidua Mill. subsp. polonica (Racib. ex Wóycicki) Domin] and 10 cultivated species (including two hybrids) were recognized. It is worth mentioning that other treatments of Larix are incomplete, containing only limited information on the taxa growing in the territory of Russia and the countries of the former USSR [1, 19].

According to Farjon [1], only 3 species grow in Russian Far East: Larix gmelinii (Rupr.) Kuzen.- L. gmelinii var. gmelinii, L. gmelinii var. japonica (Maxim. ex Regel) Pilg. and L. gmelinii var. olgensis (A.Henry) Ostenfeld & Syrach-Larsen. At the same time, Farjon considers Larix kamtschatica as synonyms for the type variety - L. gmelinii (Rupr.) Kuzen.var. gmelinii with L. cajanderii Mayr, as well as some other Far Eastern larch (L. komarovii Kolesn., L. middendorfii Kolesn., L. ochotensis Kolesn.).

Thus, a single monographic summary of the Russian wild and cultivated larch species is not currently available, and treatments of the genus in "Flora of the USSR" and in a number of other floras may be considered as outdated. Related species with uncertain taxonomic position have been discussed in the literature and the questions of their taxonomic identity, status and geographical distribution are still open or unresolved. One of reasons of this, could be is the absence of a sufficiently stable set of morphological characters with diagnostic value. Therefore, one of the goals of this work was to search for those characters of vegetative and reproductive organs that can be successfully used for the preparation of identification keys of Larix taxa.

Materials and Methods

We have studied specimens of Pinaceae kept in Russian (LE, LECB, KFTA, MW, MHA, NS, NSK, TK, KW, VLA) and foreign herbaria (C, E, HBG, KRAM, K, KOR, PE, PR, PRC, BP, W, Z etc), including type [20, 21] as well as digital images of type specimens in various foreign herbaria available on the Internet.

The morphology and distribution of L. decidua subsp. polonica in Poland and adjacent countries) were studied for 70 herbarium specimens and samples for molecular research were collected from natural habitats in Beskids, Lubań and Zelonka, Poznan.

During field trips to Kamtschatka (Ust- Ust-Kamchatsk and Milkovo districts), Yakutia (Lenskie Stolby Natural Park), North Pribaikalye (Irkutskaya region, Olkhonskiy district), Krasnojarsk (Stolby Reserve) and Yamal-Nenets autonomous district (YNAD), the natural populations of Larix taxa were, herbarium specimens of larches and specimens for molecular and anatomical investigations were collected and the vegetation and soils at sample plots was recorded (Figure 1). Samples of L. olgensis
A. Henry and L. komarovii B. Kolesn. were collected from eight sample plots at Primorsky Krai, on the route from Vladivostok to Terney.

Complex research of larch plantations in the Leningrad region included: the Okhtinsky educational and experimental forestry (Vsevolozhsk district), the larch plantations in Vyborg village Chulkovo, the natural monument "Petrovskhinskaya larch grove" (Kirovsk region) and the reserve "Lindulovskaya grove" (Roshinsky district).

During 2005-2012, the taxonomic composition and condition of larches in the parks of cities north of the European part of Russia were investigated: Kirovsk and Apatity (Murmansk region), Petrozavodsk (also supplemented by material from previous studies), St. Petersburg, Novgorod and Velikie Luki (Pskov region).

The surface of shoots and needles of different taxa of Larix were photographed and studied using a stereoscopic fluorescence microscope SteREO Lumar.V12; this revealed a number of morphological features of initial taxonomic significance, such as the waxy coating, the thickness of the cuticle, the shape of epidermal cells and stomata. The surface of the needles of 15 different taxa was therefore studied using the scanning electron microscope. The needle and bark anatomy of 12 larch species collected in Kamchatka, in European part of Russia and Poland were investigated.

Results and Discussion
Differences between taxa and distribution

Complex comparative morphological investigation of different representatives of Larix allowed to reveal some new characters of vegetative organs with diagnostic value for systematics size and shape of the mature cones, the number of rows of seed scales (parastiches), the degree of deviation of seed scales from the axis of cones, the shape of the upper edge and the degree of pubescence in seed scale; size, shape and color of the bract scales, the ratio of the length of the seed and bract scales, as well as some signs of vegetative organs - color and degree of pubescence of young shoots (auxiblasts); sizes and shape of needles, arrangement and abundance of stomata, shape of epidermal cells and structure of cuticule.

Differences between taxa and distribution

In the course of this research the taxonomic status and geographical distribution of some critical taxa such as L. polonica Racib. ex Woycicky, L. archangelica Laws., L. dahurica Laws., L. cajanderi Mayr, L. cajanderi from Kamchatka, L. kamtschatica (Rupr.) Carr., L. olgensis A. Henry, L. komarovii B. Kolesn. taxonomic status has been checked.

It was found that a typical section Larix in morphology of vegetative and reproductive organs are clearly divided into 4 groups:

I (ser. Eurasiatiae and Europaeae): Young shoots are light brown. Needles 30-50 mm long, with obtuse tip, widest in the middle, amphystomatic, on the upper side with 1-2 stomatal lines on both sides from midrib, on the downside with 2-4 stomatal lines on both sides from keel. Cones 2-3 cm long, with 22-38 scales in 5-7 series, ovate or oblong, with rounded scales;

II (ser. Americaneae, Olgensiformes, Larix kamtschatica): Young shoots are pinkish-brown. Needles (15) 20-30 mm long, with rounded apex, hipostomatic, with a
distinct keel on the downside. Cones 1-2.5 cm long, with 12-25 (30) scales in 3-6 rows, with rounded or slightly notched seed scales.

III - ser. Paucisquamatae (Larix dahurica, L. cajanderi): Young shoots are light brown. Needles 15-30 mm long, widest in the middle, with rounded tip, amphistomatic, with a distinct keel on the downside. Cones 1.8-2.0 (-2.5) cm long, with 10-16 scales in 3-4 rows, the upper edge of seed scales is truncated, often emarginate.

IV (Larix kaempferi): Young shoots are pinkish-brown. Needles 15-30 (-60) mm long, amphistomatic, on the upper side and on the downside with a well-developed keel. Cones 2-3.5 cm long, with 45-50 (-70) scales in 5-9 rows, the edge of thin seed scales is wavy and bent outwards.

Species of Group III (ser. Paucisquamatae) occupies an intermediate position between the previous two.

The young shoots of species from section Multiseriales are pinkish-brown. Needles markedly extended upward, with a rounded top, its downside with well-developed keel. This section allocated into 2 groups of species: I - the needles are amphistomatic and with a well-developed keel (L. mastersiana, L. occidentalis and L. potaninii); II - the needles are hipostomatic and with weakly developed keel (L. speciosa, L. griffithii and L. himalaica). We believe that the allocation of the groups we deserve consideration in the rank of the individual sections of the genus.

We have studied the anatomy of the needles and bark of young (one, two and three-year) shoots of 12 species (about 25 samples) of the genus Larix, collected in Kamchatka, in the European part of Russia, as well as in Poland. Among them are representatives of almost all series typical section Larix:

- ser. Europaeae Bobr.: Larix decidua subsp. decidua and Larix decidua subsp. polonica;
- ser. Eurasiaticae Sukacz.: Larix sibirica and Larix archangelica;
- ser. Paucisquamatae Sukacz: Larix cajanderi;
- ser. Kaempferianae Sukacz.: Larix kaempferi, Larix kamtschatica;
- ser. Olgensiformes Kolesn.: Larix lubarskii;
- ser. Americanae Kolesn.: L. laricina;

Hybridogeneous species Larix x czechanowski (L. sibirica x L. dahurica);
Hybrids: L. x marschlinii (L. decidua x L. kaempferi), Larix kaempferi x L. kamtschatica.

**Needles.** Our investigations of a cross section of the needles have shown that it is important for the diagnostics and classification of larch are the next signs:
- the shape of the contour of the cross section of the needles,
- the presence of secretory structures and the number of layers of hypoderma on the lateral edges of the needles.

Cross-section of the needles (in the central part), presence of secretory structures and number of hypodermis layers on the lateral margins of needles, number of stomatal lines on abaxial side of the needle are taxonomic value. Needles shape are varies on a cross section from triangular (L. czechanowski, L. kamtschatica (LO 12-11), L. lubarskii, L. laricina (LO 25-11), L. decidua subsp. polonica), to rhomboid (L. decidua, L. kaempferi, L. kamtschatica (LO 19-11, LO 21-11), L. kaempferi x L. kamtschatica (LO 20-11), L. laricina, L. olgensis, L. sibirica. Between two of these stages there are transitional forms: L. x marschlinii, L. cajanderii have more or less
triangular shape on a cross-section of the needle, but adaxial side of the needle is slightly convex. The shape of needles of *L. archangelica* from different habitats are different on a cross-section: *L. archangelica* (LO 22-11, LO 24-11) from Lindulovskaya grove needles have an oval shape, whereas the same species from Solovki island (LO 11-11) has shape between oval and triangular, but closer to the triangular.


Species of the two series occupy large areas of Europe and the Asian part of Russia. As mentioned above, according to the results of our studies, this group of species is clearly distinguished primarily for its large cones (2-3 cm long), with 22-38 seed scales in 5-7 parastiches, ovoid or oblong, rounded by the upper edge of the seed scales. Needles 30-50 mm long, obtuse at apex, widest in the middle, amphistomatic, with obscure keel on the downside and stable, light-brown color of young shoots.

However, species of ser. Europaea Bobr. (1) is clearly different from ser. Eurasiaticae Sukacz. (2) by some features of the morphology of the bract and seed scales. Seed scales of young cones (1) on the upper edge slightly wavy; bract scales of ripe cones in length (including tip) equal to not less than two thirds of seed may also be slightly in excess of their length (only at the base of the cones). In (2) seed scales of young cones on the upper edge rounded, whole. Bract scales are very small (up to ¼ the height of seed) and only visible at the base of the cones.

According to our research, the Polish larch (*L. decidua* subsp. *polonica*) differs from *L. decidua* subsp. *decidua* by having shorter needles (15-20 mm long), a more pronounced white coating of the needles on the lower surface, the number and location of stomatal lines on the lower surface (2-3 stomatal lines closer to the margins), blunt tip of needles, different size and shape of cones and slightly pubescent seed scales. The comparative study also clarified the geographic distribution of these taxa in Poland and neighboring countries.

The Arkhangelsk larch (*L. archangelica*) differs from *L. sibirica* by having fewer stomatal lines (2-3 on each side of the keel versus 3-5 in *L. sibirica*), large cones (2.3-3.7 cm long, 2.5-3.5 cm wide) with more (25-50) seed scales (persistent on the plants), the wider size (12-20 mm) and purple-brown color of the old cones and the clearly spoon-shaped seed scales at the base of the cones.

The earliest name of this taxon in the rank of species - *Larix archangelica* Lawson, but its validity was disputed for a long time, because it was considered nomen nudum [2]. Tsvelev [14] has convincingly proved its priority due to the presence in the protologue brief morphological description.

It should be noted that sometimes the seed scales of *Larix archangelica* even in the Arkhangel and Vologda region are slightly (very slightly) notched at the top and the surface of the seed as it scales with a small dent in the longitudinal (in the typical *L. sibirica* is not selected). This feature of scale structure is particularly pronounced near the north-eastern edge of the range *L. archangelica*.

*Larix archangelica* x *L. dahurica* was found in the Yamal-Nenets autonomous district. Analysis of herbarium material held in LE showed that this hybrid originated in the Arkhangel region (Kanin Peninsula), in the Nenets autonomous district in Tobolsk and Tyumen region.

Hybrids of Dahurian larch with Archangelsk larch, *L. archangelica* x *L. dahurica*, clearly have the following characteristics: from *L. archangelica* - much smaller (2-2.5
cm long) cones with fewer stomatal lines (3-5) and slightly emarginated at the edge of the bare seed scales and from *L. dahurica* - notably spoon-shaped seed scales with inward curved edge, and shorter (20-25 mm long) needles. It is considered that the question about the distribution and taxonomic status of the hybrid is very important and further careful study in Arkhangel Region, and Komi, and Yamal, in the northern region of Western Siberia is necessary.

**The study of larch of ser. Olgensiformes Kolesn.**

Special attention in this investigation was paid to the comparative study of morphology and geographical distribution of Olga larch, *L. olgensis*, as well as some of the critical taxa such as *L. komarovii*, *L. ochotensis*, *L. lubarskii* and *L. maritima*.

The range of *L. olgensis* covers the Russian Far East, the eastern slopes of the Sikhote-Alin Mountains (Southern Primorye), Olga, Kavalerovsky, Dal’negorsk, Lazo and partly areas along the coast from boo Valentine to the Gulf of Vladimir in the north [22]. Outside of Russia, it was found in the northern part of the Korean peninsula adjacent to the Sea of Japan, and in the Jilin Province of Northeast China [23]. In the nature, *L. olgensis* is a rare species. *L. komarovii* is confined to the eastern Sikhote, Shkotovsky and Terneisky region [24]. According to Gukov [23], these species shows a wide band merging with the area of *L. olgensis* and reaching to the lower areas of the Amur. In the southern half of the Sikhote-Alin region, in the area of *L. olgensis*, there is a wide contact between these species.

Larch, growing in Kamchatka, is different from the typical *L. cajanderi* due to its pinkish young shoots (typically light yellow), slightly pubescent indumentum (typically hairless), slightly curved saber needles (typically more or less straight), different placement of stomatal lines and larger cones. A comparative study of herbarium and living material from larch in Kamchatka confirmed its hybridogeneous origin and the need to describe it as a separate species.

Our studies confirmed the presence of the Olga larch, *L. olgensis*, in the Southern Primorye and its close relationship with *L. komarovii*. We found a broad contact of the two taxa and hybrid individuals *L. olgensis* x *L. komarovii*. Such hybrids were also observed at the Red River, spring Mramornyi in Kavalerovskiy and Dalnegorsk districts (Figure 3).

Mature cones of *Larix olgensis* are ovate or ovate-globose, seed scales with short pubescence, and with rounded upper edge, tight to the cone axis or diverging at a very slight angle. Bract scales are at a length of about half the length of the seed, dark brown. Needles 20-25 mm long, 1.3-1.8 mm width, strongly flattened, widest in the upper third, with rounded tip, um straight, with the upper side of the green, without stomatal lines in upper side and with a fairly bright white stomatal bands in the deep furrows of 4-5 stomatal lines each on both sides of the heavily favored keel. Young shoots of a pinkish light brown, dense pubescence light brown or reddish hairs, older - pinkish-brown or gray (Figure 4).

*Larix komarovii* is characterized by broadly spherical or a flattened-spherical, fairly loose cones. Its seed scales adjacent to the cone axis at an angle 45-60°; glabrous or very slightly pubescent, with wavy upper edge. Young shoots are very weakly pubescent, almost naked; needles in *Larix komarovii* different in morphology and dimensions: long (25-30 mm long, 0.7-0.8 mm width), with obtuse apex, and shorter
(15-25 mm long, 0.7-1.2 mm width) - on the top side with a single stomatal line on each side of the midrib, on the downside - with 2 stomatal lines on both sides of the keel (Figure 2).

According to this study, the largest areas are occupied by L. komarovii and its hybrids with Olga larch, while typical L. olgensis is confined mainly in the coastal and adjacent areas, possibly indicating an ongoing process of gradual replacement of Olga larch by the more northern L. komarovii. However, the range of L. olgensis extends much further north than previously thought [23]; in the present study it was found near Terney village (45°06′18″ N, 136°31′36″ E). Further research in the wild is needed to clarify this issue.

**Urban and forest larch plantations**

Studies of the taxonomic composition and condition of larch trees in urban and forest plantations of northwest Russia showed that 10 species (including the natural hybrid) species are to be found—or a total of 24 taxa and cultivars (Table 1). The most frequently found and more abundant in urban parks were L. decidua, L. archangelica and L. sibirica.

In urban parks of St. Petersburg and Apatity, there are double and even triple hybrids of four parental taxa (L. decidua, L. archangelica, L. sibirica, L. dahurica). The introduction of plant species into St. Petersburg has continued for more than 300 years [25]. These studies confirmed that in St. Petersburg there is a high diversity of native species of larch and hybrid taxa. Studies undertaken by us in 2005, confirmed that, indeed (L. polonica, L. kaempferi, L. x marschlinsii, L. occidentalis, L. principis-ruptprechtii). Analysis of the occurrence of hybrid taxa revealed that their share in the larch trees in St. Petersburg might reach 20%. The cultigen hybrid larch trees (see Table 1) also occurred in the parks of neighboring countries such as Finland [26] and Estonia [27, 28].

Analysis of the taxonomic diversity of forest plantations of larch in the Leningrad region showed that along with the usual species, L. decidua, L. archangelica, L. sibirica, L. dahurica, there are taxa such as L. czekanowskii, L. x marschlinsii, L. kamtschatica, L. kaempferi x L. kamtschatica. The earliest plantings of larches in the north-west of Russia were made with L. archangelica (1738) at the Lindulovskaya larch grove on the Karelian Isthmus. At 278 years it is oldest plantation of larch in the world. The average height of the larches was 41 m and the maximum was 52 m with a diameter of 1 m [29, 30].

According to this research [29] in the Lindulovskaya grove there are currently 4 species of larch, L. sibirica, L. archangelica, L. decidua, L. kamtschatica, and one hybrid, L. kaempferi x L. kamtschatica.

Petrovschinskaya larch grove is located on the slope of the Baltic-Ladoga ledge on the Putilovis limestone plateau. It is a rather old plantation (200-250 years) of L. sibirica and L. archangelica. it had self-seedlings.

The age of larch plantation in Okhta forestry is 80-120 years and the species composition of larches include L. decidua, L. archangelica and L. czekanowskii. The youngest of the surveyed cultures of larches are in the Vyborg district, near Vyborg, on the Ploskiy Cape, in the recreation Andersin. Practically all of the stands (age 25-30 years) were generated by self-seeding. Seeds are spread from alley planting of L. sibirica, L. archangelica, L. decidua and L. x marschlinsii.
Conclusions
Complex comparative morphological investigation of different representatives of *Larix* allowed to check some characters for their taxonomic value such as: the size and shape of mature cones; the number of parastyches; the degree of deviation of seed scales from the axis of the cones; the form of the upper edge and the degree of pubescence of seed scales; the size, shape and color of bract scales; the ratio of the length of the scale and of bract scales, as well as some of the characters of vegetative organs such as the color and the degree of pubescence in young shoots; the size, shape and color of the needles, their form, the presence and the number of stomatal lines on both sides of needles. The shape of the needle in cross-section, the presence of secretory structures and the number of hypodermis layers on the lateral margin of needles are of taxonomic and diagnostic value on the species level.

The composition of larches in urban green areas northwest of the European part of Russia varies widely (up to 19 taxa in St. Petersburg region). The most frequent and abundant in green areas of cities are *L. decidua*, *L. archangelica* and *L. sibirica*. In the green areas and forest plantations are found double and triple hybrid larches, whose share in St. Petersburg is about 20%.

Summarizing it should be noted that some of the problems of systematics in larches are not yet sufficiently understood. It is planned to use data of molecular genetic studies to address these issues.

Acknowledgement
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References


**Table 1.** The taxonomic composition of the genus *Larix* in urban parks and forest plantations of northwestern European Russia

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* GS – green standing of urban parks
** According to current field studies and data from previous studies
Figure 1. Location of our collecting of Larix samples in Russia
Figure 2. Mature cones of *Larix komarovii* B.Kolesn. in the vicinity of village Vysokogorsk (Primorskiy kray, Kavalerovskiy district).
Figure 3. The larch mountain rhododendron forb-lichen in the vicinity of town Dalnegorsk, spring Mramorniy.
Figure 4. Mature cones of *Larix olgensis* A. Henry in the vicinity of village Moryak-Rybolov (Primorskiy kray, Olginskiy district).