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Article

Representatives of the sections *Aigeiros* Duby and *Tacamahaca* Spach (genus *Populus* L., Salicaceae) and their hybrids in cities of central and eastern European Russia

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Abstract

The article contains an overview of cultivated species and hybrids and also morphological and phenological comparisons of black and balsam poplars (sect. *Aigeros* and sect. *Tacamahaca*) that occur in three cities of European Russia: Moscow, Izhevsk, and Tula. The survey has revealed a very low number of pure species. Probable parentage is proposed for a number of hybrid poplars widely deployed by the urban green industry. Consequences of poplar hybridization in natural habitats and urban settings are discussed. New nothospecies, *Populus* ×*nevensis* Nasim. is described.

Keywords: cultivars, hybridization, hybrids, introgression, morphology, phenology, *Populus*, new nothospecies, Russia, Salicaceae

Introduction

Representatives of the genus *Populus* L. (Salicaceae) from the sections *Aigeiros* Duby (black poplars) and *Tacamahaca* Spach (balsam poplars) play an important role in street plantings in large cities of the central and eastern parts of European Russia, as they are resistant to atmospheric contamination and tolerant of elevated soil salinity (Bogdanov, 1965; Bakulin, 1990). These trees have been traditionally planted along busy streets and major transport arteries. Black and balsam poplars are particularly valuable in those regions where native representatives of the named sections are absent, since they are less prone to invasions there, as compared, for example, to *Acer negundo* L. (Mayorov *et al*., 2012).

There are no native species of black or balsam poplars in eastern European Russia (Sokolov *et al*., 1951), except for *P. nigra* L., whose northern limit extends to the southern and eastern parts of the region, reaching Izhevsk on the Kama River. It is believed that poplars

abundantly cultivated in this area were introduced as early as the late 17th century—first from Asia, then from North America, mostly via Europe (Yakushina, 1982).

The climatic conditions of central and eastern European Russia are completely within the requirements of the following six poplar species with extensive natural distribution areas, which may occasionally overlap (Sokolov *et al*., 1951): two North American balsam poplars, *P. balsamifera* L. and *P. trichocarpa* Torr. & Gray ex Hook., two Asiatic balsam poplars, *P. suaveolens* Fisch. ex Poiteau & A.Vilm. and *P. laurifolia* Ledeb., the Eurasian *P. nigra* of black poplars, and the North American *P. deltoides* W.Bartram ex Marshall, also belonging to black poplars.

In addition to their high intraspecific variablity, the named poplar species also considerably differ from each other (Skvortsov, 2010; Mayorov *et al*., 2012). Due to leaf polymorphism within an individual tree, it is necessary to obtain three types of shoots for confident identification: brachyblasts (short shoots), elongated shoots, and adventitious shoots (root suckers); field identification of live specimens is the preferred method (Tsaryov, 1979; Mayorov *et al*., 2012, Nasimovich and Kostina, 2015). Capsule structure characters are also critical for identification. (Skvortsov, 2006; Kostina and Schanzer, 2014; Kostina and Nasimovich, 2014).

Each of the black and balsam poplars is well delineated, differing from other species as well as intersectional hybrids by a number of characters, of which the very important are leaf petiole characters (Skvortsov and Belyanina, 2005; Skvortsov, 2010; Mayorov *et al*., 2012; Nasimovich and Kostina, 2015).

In black poplars, petioles are relatively long, about the length of the leaf blade (rarely to 1.5–2 times as long or as short); glabrous; distally flattened in plane perpendicular to the leaf blade, without a groove on the adaxial side. In balsam poplars, petioles are relatively short: the same length as the blade or up to 10 times as short; hairy or sometimes glabrous, terete or sometimes slightly flattened at right angle to the leaf blade or otherwise in the plane of blade; with a well-developed, usually wide groove along nearly the entire petiole length. In intersectional hybrids, petioles from about the same length as that of blades to about 1.5–2.5 times as short; pubescent (rarely glabrous); distally conspicuously flattened at right angle to plane of the leaf blade; with narrow, occasionally interrupted grooves on the adaxial side.

While dealing with cultivated and naturalized poplars from certain regions in European Russia, the focus has been traditionally placed on identification of species, yet there is a need for further clarification of hybrids. Another emerging challenge is finding the percentage of certain

species' genes in the composition of the gene pool employed for cultivated material within a certain region. It is possible that some species have never made it directly to European Russia and these were only certain genes of these species that arrived here with the introduction of hybrids. One cannot exclude the possibility that some hybrids have been introduced under erroneously applied species' names.

Some researchers of the flora of central and eastern European Russia (Tsvelev, 2001; Reshetnikova *et al*., 2010) as well as breeders (Bogdanov, 1965; Tsaryov, 1979, 2001; Starova, 1980; Bakulin, 1990) have documented in the region all the six species of poplars named above. Yet A.K.Skvortsov (2010) and A.N.Puzyryov (Baranova and Puzyryov, 2012) did not include *P. trichocarpa* Torr. & Gray ex Hook., and J.A.Nasimovich (Mayorov *et al*., 2012) had doubts regarding the presence of *P. balsamifera* L.

The absence of mechanisms providing reproductive isolation is typical for representatives of the sections *Tacamahaca* and *Aigeiros* (Starova, 1980; Broeck *et al*., 2005; Šiler *et al*., 2014). Due to this, intrasectional and intersectional hybrids are easily formed wherever species' natural areas overlap (Eckenwalder, 1984, 1996; Rood *et al*., 1986; Smith and Symata, 1990; Demeritt, 1990; Likhovid, 1994). When cultivated in proximity to each other, black and balsam poplars also tend to produce hybrids (Bogdanov, 1965; Starova, 1971; Broeck *et al*., 2005). Poplar hybrids and cultivars used for plantings have been selected either through breeding or using spontaneous hybrids as a source. Poplars' excellent capacity for propagation from cuttings allows for abundant planting material that can be obtained promptly and relatively inexpensively (Bogdanov, 1965; Starova, 1980).

Prior to the era of molecular genetics, parent species of hybrids were identified through comparisons of hybrid characteristics with those of species or cultivars growing nearby, except for occasions when hybridization was performed artificially on cut-off or isolated branches of cultivated plants.

In the literature referring to central and eastern European Russia, one can often find such hybrid names as *Populus* ×*canadensis* Moench, *P.* ×*berolinensis* K.Koch, *P.* ×*moscoviensis* R.E. Schroed. ex Wolkenst., *P.* ×*rasumovskoe* R.E.Schroed. ex Wolkenst., *P.* ×*petrovskoe* R.E. Schroed. ex Wolkenst., *P.* ×*nevensis* Bogdanov. (Tsaryov, 1979: Tsvelev, 2001; Reshetnikova *et al*., 2010; Baranova and Puzyryov, 2012).

The latter name, *P.* ×*nevensis* was invalidly published by P.L.Bogdanov (1965) as the taxon was described only in Russian and without type citation. As to putative parent species involved with the named hybrids, a range of opinions have been expressed regarding each hybrid

(Regel, 1889; Dippel, 1892; R.E.Schroeder, 1899; Tsvelev, 2001), except for *P.* ×*canadensis*, the only one whose parentage has been verified so far.

In revisions of flora in certain regions, researchers often designate the most distinctive and copious hybrids using existing names. The choice of a certain name is dictated primarily by comparisons of the hybrid's characters and those of native species currently or formerly present within the area, according to the researcher's assumptions (Tsvelev, 2001; Skvortsov, 2010; Mayorov *et al*., 2012).

Green industry workers in Moscow distinguish only two hybrids: *P.* ×*canadensis* and *P.* ×*berolinensis* along with ornamental forms of *P. simonii* Carrière: *P. simonii* var. *fastigiata* C.K.Schneid., and *P. simonii* f. *pendula* C.K.Schneid. Brief descriptions and phenological notes exist for these taxa, while the rest of the poplars have been erroneously placed under a single name *P. balsamifera,* even though they obviously differ from each other in many respects, including morphology, phenology, disease and insect tolerance, and other characteristics crucial for successful cultivation (Mayorov *et al*., 2012).

The goal of this study was a comparison of the most commonly cultivated poplars in Moscow, Izhevsk, and Tula from morphological and phenological standpoints in order to provide material for subsequent molecular genetics analyses aiming at delimitation of existing homogeneous entities. The choice of cities was determined by significant previously conducted research studies. In Moscow, as a result of extensive work by scientists, including A.K.Skvortsov, a comprehensive herbarium collection has been accumulated, representing wild poplars (including North American species) as well as cultivated. J.A.Nasimovich (Mayorov *et al*., 2012) has identified and described major cultivars and hybrids grown in Moscow. A.N.Puzyryov has been studying poplars in Izhevsk for many years and accumulated vast herbarium material from this city (Baranova and Puzyryov, 2012). Samples representing poplars cultivated in Tula are the courtesy of L.V.Khorun.

Materials and methods

The authors studied the herbarium material accumulated at MHA and conducted a survey of streets, yards, gardens, parks, and waste grounds in Moscow, Izhevsk, and Tula and also the living collections of Moscow botanic gardens (Main Botanic Garden of the Russian Academy of Sciences and Moscow State University Botanic Garden). Collected herbarium specimens were identified employing the keys and descriptions published by Tsaryov (1979), Tsvelev (2001), and J.A.Nasimovich (Mayorov *et al*., 2012) and following the taxonomic treatment proposed in

the latter work. While describing hybrids and cultivars, the emphasis was on the structure of leaf blades collected from brachyblasts within the crown, the presence of ridges on adventitious and elongated shoots, as well as on the sex representation, morphology of capsules, general habit, phenology, and tolerance to diseases and pests.

Decisions regarding parental species for each hybrid were based on morphological characters. Descriptions of hybrids are enhanced by illustrations depicting leaves (all at the same scale, approximately half actual size) collected from brachyblasts. Table 1 provides data on the distribution of the most common hybrids, their parent species, sex ratios in populations, and structure of capsules.

We understand the limits of *P. suaveolens* (= *P. maximowiczii* Henry, *P. koreana* Rehder, *P. ussuriensis* Kom., *P. komarovii* J.J.Vassil. ex Vorosch.), *P. laurifolia* (= *P. pilosa* Rehder, *P. amurensis* Kom.), *P. nigra* (= *P. italica* Du Roi, *P. pyramidalis* Rozier), and *P. simonii* following A.K.Skvortsov (2010). In our broad approach to *P. deltoides*, we follow Eckenwalder (1977, 2010), who treats *P. monilifera* Aiton and *P. wislizenii* Sarg. as subspecies of *P. deltoides*: *P. deltoides* subsp. *monilifera* (Aiton) Eckenw. and *P. deltoides* subsp. *wislizenii* (Sarg.) Eckenw. The North American balsam poplars, *P. balsamifera* and *P. trichocarpa*, have been understood in the sense of A.Rehder (1949).

Results

Intersectional hybrids with misapplied species names

The North American *Populus balsamifera* has not been found anywhere within the three surveyed cities. Intra- or intersectional hybrids of black and balsam poplars have been frequently taken for *P. balsamifera* (Mayorov *et al*., 2012). These hybrids differ from *P. balsamifera* in leaf shape and color as well as in presence of an often interrupted groove running along the petiole. Some individuals with leaves superficially similar to those of *P. balsamifera*, at the same time, possess three-lobed capsules on very short pedicels, which are quite different from those in *P. balsamifera*. Sometimes male individuals with leaves similar to *P. balsamifera* may be encountered; however, they cannot be decisively identified as *P. balsamifera* due to lack of capsules. Putative hybrids bearing two-valved capsules differ from *P. balsamifera* in leaf shape and color and the presence of a discontinuous groove on the petiole.

Another North American species with a vast distributional area, *P. trichocarpa*, has not been recognized in our study, either. In the living collections of the Main Botanic Garden of the Russian Academy of Sciences (MHA) and Moscow University Botanic Garden, there are trees

labeled *P. trichocarpa.* They have three-valved pubescent capsules and leaves shaped similarly to those of *P. trichocarpa*; however, the interrupted petiole groove exposes their intersectional hybrid nature. Amidst trees planted in Moscow and its vicinity, one can occasionally find some approximating *P. trichocarpa*.

The Asian *Populus laurifolia*, has not been detected in this study, either; however, this species must have been involved as one of the parent species with a number of hybrids. This is manifested in the presence of ridges on the adventitious shoots in these hybrids.

Trees fitting the description of yet another Asian species, *Populus suaveolens*, have been occasionally found in Moscow and Izhevsk. At the Main Botanic Garden in Moscow, there are a few living specimens of this species grown from cuttings of wild origin.

Populus deltoides occurs neither in Izhevsk nor in Tula. In Moscow one can find trees resembling this species, as far as the shape and color of their leaves. They are mostly trees with staminate flowers; yet in the Main Botanic Garden living collection there are plants with pistillate flowers whose leaves are characteristic of *P. deltoides,* though capsules are two- or three-valved. The true *P. deltoides* has three- or four-valved capsules (Eckenwalder, 2010). Plants cultivated in Moscow may represent intrasectional hybrids between *P. deltoides* and *P. nigra*, which are morphologically similar to *P. deltoides*.

Populus nigra occurs infrequently in the surveyed cities. The green industry primarily uses plants with staminate flowers and pyramidal crowns, the Italian poplar (*P. italica* Du Roi). In Moscow and especially in Izhevsk, many spontaneous trees on waste grounds and along railroads resemble *P. nigra*; however, upon a closer examination, they prove to be intersectional hybrids.

We have detected an active hybridization process taking place in a natural population on the Kama River floodplain, about 30 kilometers from Izhevsk. This process involves *Populus nigra* on the one hand and various poplars cultivated in surrounding towns and villages on the other. Individuals of pure *Populus nigra* must have glabrous petioles without grooves. (Komarov, 1936; Skvortsov, 2006, 2010; Bakulin, 2007). Pubescent petioles and the presence of an inconspicuous petiole groove are characters providing evidence of hybridization. At least some leaves on growth shoots in hybrid individuals have slightly flattened and very lightly grooved petioles that are often pubescent. Besides, leaves of these individuals are characterized by a more rounded base of the blade, never cuneate like in *P. nigra*.

Species with dubious taxonomic status

Populus tristis Fisch. may occasionally be found in Moscow and Izhevsk. Its natural area and origin remain unknown.

Twigs stout, dark gray, terete. Terminal buds very long (to 3 cm). Petioles of some leaves exhibit narrow groove commonly interrupted not far from origin. Leaf blades in mature trees 8–12 × 6–8 cm (length-to-width ratio averaging 1.5); adaxial leaf surface dark green, abaxial very light-colored (Fig. 1).

Trees are mostly with staminate flowers; J.A.Nasimovich also found plants with carpellate catkins in Moscow. These usually had three- and sometimes two-valved capsules. *Populus tristis* has been widespread in Izhevsk. Green industry workers currently make efforts to eliminate this poplar from the city due to its intensive root suckering, poor ornamental qualities, and insufficient longevity. We could not locate any young plantings of *P. tristis* in Moscow, either. No *P. tristis* have been found in Tula.

Populus simonii is missing from Izhevsk and Tula. In Moscow ornamental forms of this poplar, *P. simonii* f. *pendula* and *P. simonii* f. *fastigiata*, described by C.K.Schneider (1916) have been commonly used. These forms differ significantly from one another not only by habit, but also by leaf shape. Among these trees only those with staminate flowers have been found.

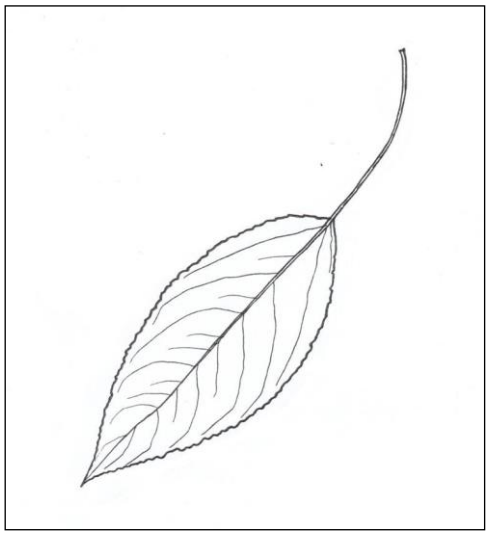

Figure 1. A typical leaf of *Populus tristis* Fisch.

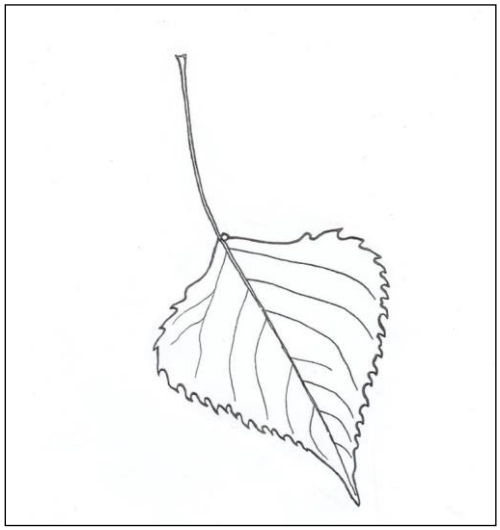

Figure 2. A typical leaf of *Populus canadensis* Moench

Intrasectional hybrids

In Moscow one can find highly ornamental forms of *Populus* ×*canadensis*, which are, as previously mentioned, morphologically similar to *P. deltoides*. Leaves dark green, often coriaceous, cordate to truncate at the base, usually with two or more basilaminar glands. Most of the trees scattered across the city have staminate flowers. Of these, the most common are trees

with comparatively small, light-colored leaves spatulate at base (that is, narrow cuneate proximally, then broad cuneate more distally), with either one or two basilaminar glands or without glands (Fig. 2). This variation of *P.* ×*canadensis* is represented by plants with staminate flowers and carpellate catkins. Capsules are on well-pronounced stipes, opening with 2–3, rarely 4 valves. Remarkably, all plants of *P.* ×*canadensis* in Moscow are 50–60 years old. No plantings younger than that have been found. *P.* ×*canadensis* has not been located in Izhevsk; however, poplars of similar habits sometimes occur along railroads and at rundown urban lots. In Tula *P.* ×*canadensis* has been found in insignificant quantities. It may have been 'swallowed' through hybridization or had always been scarce.

Populus ×*moscoviensis* constitutes an intrasectional hybrid of balsam poplars: *P. laurifolia* × *P. suaveolens*. We have reported elsewhere (Mayorov *et al*., 2012; Kostina and Nasimovich, 2013) that *P.* ×*moscoviensis* occurs rather frequently in Moscow and appears quite variable. However, according to our latest conclusions, nearly all of those Moscow samples previously identified as *P.* ×*moscoviensis* appear to represent various intersectional hybrids, while *P.* ×*moscoviensis*, which at the start of the 20th century was a common tree on Moscow boulevards (Syreisczikov, 1907), is now nearly entirely absent. Both in Moscow and Izhevsk it is currently represented by just a few old trees. Morphological characters testifying to hybridization in these poplars are interrupted or poorly defined petiole grooves as well as the presence of basilaminar glands. Similarly to the Moscow poplars, those from Izhevsk and Tula that have been traditionally placed with *P.* ×*moscoviensis* also exhibit characters of intersectional hybrids.

Intersectional hybrids

While some intersectional hybrids are morphologically intermediate between black and balsam poplars, others may approximate either section.

Populus ×*petrovskoe* R.E.Schroed. ex Wolkenst. [? *P. deltoides* var. *monilifera* Henry × *P.* ×*moscoviensis* (*P. laurifolia* × *P. suaveolens*)] is a highly ornamental large-leaf hybrid. By the leaf shape and habit, this poplar resembles *P. deltoides* yet differs from it by more rounded leaves. In addition to that, it sometimes has an ill-defined petiole groove. Annual twigs are nearly terete to angled, sometimes ridged, with terminal and axillary buds to 2 cm long. Leaf blades to 12–14 × 10 cm (length-to-width ratio on average 1.5); ovate to broadly ovate, their maximal width very close to leaf base (within one-fourth to one-third of blade length from blade base), broad cuneate to rounded at base, more rarely cordate to cordate-truncate, base margin very gradually turning into convex lateral margin. Blade apex acute, attenuate, forming a narrow point 1–2 cm long. A pair of basilaminar glands is usually present, although this is not true for

every leaf (Fig. 3). The hybrid is represented by plants with staminate flowers only. Green industry workers have started to use *P.* ×*petrovskoe* for plantings in Izhevsk on a large scale. There are young plantings of this hybrid in Moscow as well. *P.* ×*petrovskoe* has not been found in Tula.

A highly ornamental cultivar occupying an intermediate position between black and balsam poplars is easily recognizable by its characteristically rounded leaves. According to a recent hypothesis by Nasimovich and Puzyryov (unpublished), this is a hybrid of *Populus nigra* and *P. suaveolens*. It has been given a tentative name '*Populus nothosp*. A.' Represented by plants with staminate flowers only, this poplar is characterized by a spreading crown with somewhat weeping branches. It typically exhibits rounded leaves (either ovate or broad ovate or else elliptic) with apex abruptly contracted into subulate point 1–2.5 cm long. Short shoots slightly puberulent. Petioles from puberulent to pubescent, from 1 to 4–5(7) cm long, flattened in blade plane, terete, or somewhat flattened at right angle to blade plane, either without groove or with a narrow, interrupted groove on adaxial side. Leaf blades 8–9(11) × 5–6(8) cm, length-to-width ratio on average less than 1.5 (sometimes up to 2 due to additional length of pointed apex); maximal width near mid-blade or somewhat shifted toward blade base (when length of subulate apex subtracted, maximal width nearly exactly at middle); leaf base broad cuneate or rounded; basilaminar glands absent (Fig. 4).

We failed to find any published name for this hybrid cultivar. It has recently been mentioned as a hybrid *Populus nigra* × *P. suaveolens* (Mayorov *et al*., 2012); however, since balsamic poplars' characters in this case clearly dominate over those of black poplars, we cannot exclude a back-cross with *P. suaveolens*. This tree has been planted in Moscow and lately also in Izhevsk.

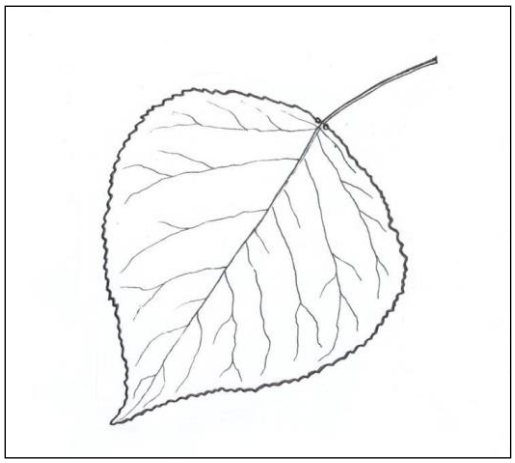

Figure 3. A typical leaf of *Populus* ×*petrovskoye* R.E.Schroed. ex Wolkenst.

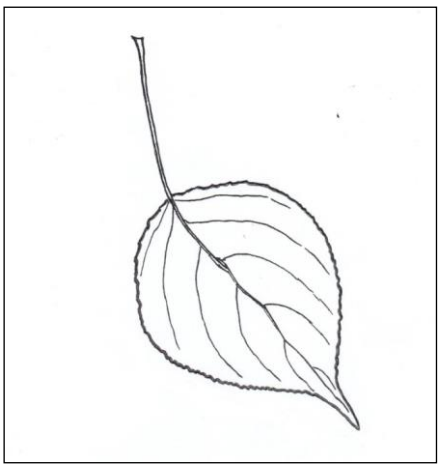

Figure 4. A typical leaf of *Populus nothosp*. A

Green industry workers in Izhevsk have started to use yet another highly ornamental intersectional cultivar under a provisional name ‘*Populus nothosp*. B.' This may be an artificial hybrid of *P. deltoides* and *P. longifolia*. Young twigs terete or slightly angled. Leaf blades fairly large, up to 10–14 × 8–12 cm (their length typically only slightly exceeding width, though length-to-width ratio may reach 1.5), broad ovate, sometimes (in smaller leaves) ovate, ovate-elliptic, or round, their maximal width slightly to dramatically shifted from mid-blade toward base (within one-third to one-fifth of blade length from base); base slightly cordate, rarely (in small leaves) rounded; apex acute, more or less attenuate into a point 3–7 mm long. Adaxial blade surface dark green; abaxial one grayish-white with a greenish tint, much lighter than adaxial. Midrib light yellow, 0.7–1.0 mm wide, prominent against background color of blade. Most (not only the largest) leaves feature a pair of conspicuous basilaminar glands; rarely glands few. Leaves of elongated shoots, when compared to brachiblasts, are somewhat narrower, ovate, with cordate or cordate-truncate base, often lacking attenuate point at apex. In shoots of this type, basilaminar glands are present in about one-half of leaves. (Fig. 5). The trees are of medium size, with very wide crowns. The cultivar is represented only by plants with staminate flowers.

Along with the taxa listed here, other poplars occupying intermediate positions between black and balsam poplars have been commonly used in all three cities. They may be represented either by plants bearing carpellate catkins only or by plants with both staminate flowers and carpellate catkins.

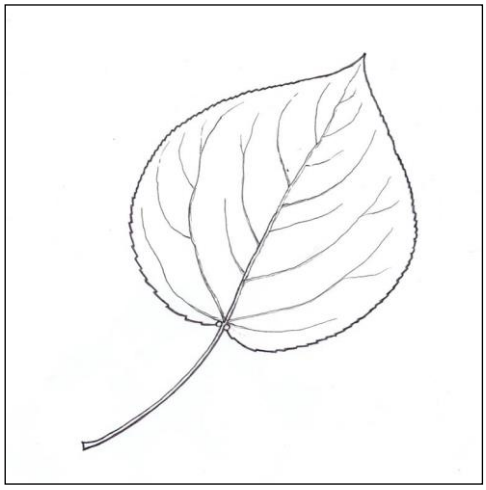

Figure 5. A typical leaf of *Populus nothosp*. B

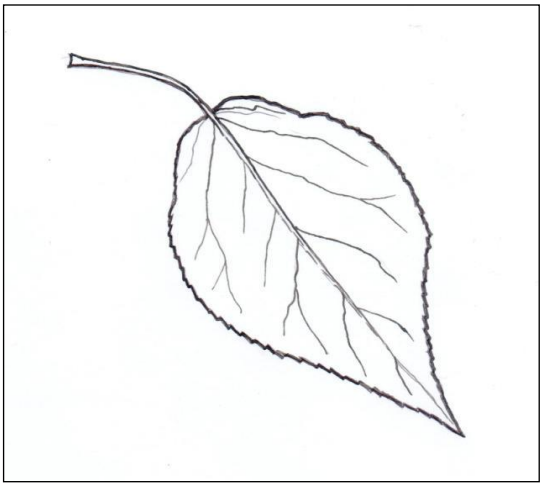

Figure 6. A typical leaf of *Populus sibirica* G.V.Krylov & G.V.Grig. ex A.K.Skvortsov

Populus ×*sibirica* G.V.Krylov & G.V.Grig. ex A.K.Skvortsov. According to Skvortsov (2007), this poplar is a product of hybridization of *P. balsamifera* and *P. nigra*. J.A.Nasimovich (Mayorov *et al*., 2012) suggested that instead of *P. balsamifera*, two Asiatic species, *P. laurifolia* and *P. suaveolens* participated in the formation of *P.* ×*sibirica.* This is a tree of medium size with a sparse crown. Young growing twigs in crowns of adult trees terete or somewhat angled and may be ridged in saplings and vigorous adventitious shoots. Leaf petioles on short shoots 1.5–4 cm long, 2–3 times shorter than leaf blades. Leaf blades 8–10 × 5–7 cm (length-to-width ratio on average 1.5, sometimes 2), ovate, ovate-elliptic or ovate-rhombic to round-rhombic, their maximal width slightly shifted from mid-blade toward base (within one-fourth to one-third of blade length from base); base cuneate, broad cuneate, or pyriform (rounded or slightly cordate close to petiole, distally becoming broad cuneate); apex acute, gradually attenuate in relatively broad point 1–2 cm long. Basilaminar glands usually absent or present in only the largest leaves and then small and somewhat distanced from the blade base. Leaves fall off in early autumn. Capsules glabrous, elongate (on average 9×5 mm), with gradually attenuate beak, 2-valved (rarely 3-valved), stipitate; stipe 1–3 mm long (Fig. 6). Predominantly plants with carpellate catkins. This is one of the most common poplars in Moscow, Izhevsk, and Tula.

Populus* ×*nevensis Nasim., **nothosp. nov.**

(urn:lsid:ipni.org:names: 77160039-1).

Type: Central European Russia: Moscow, Kursk Railway Line, near the station Tekstilshchiki, along railroad. Tree 15 m high. 9.VI.1987, *V.D.Bochkin* (holotype: MHA!).

Paratypes: Central European Russia: Moscow, SAO. Park Dubki. Near eastern entrance. 24.V.2011, *Y.A.Nasimovich & I.M.Averchenkov* (MHA!); Moscow, 14 Panfyorov Street, a fallen tree. 29.VII.2011, *Y.A.Nasimovich* (MHA!).

– *Populus* ×*nevensis* Bogdanov, Topolya Kult.: 75. 1965, **nom. inval.**

This poplar has been known in literature as a clonal cultivar described by P.L.Bogdanov (1965) as a hybrid of *P.* ×*canadensis* and *P. balsamifera.* J.A.Nasimovich (Mayorov *et al*., 2012) interprets *P.* ×*nevensis* as a complex hybrid of four species: *P. laurifolia*, *P. suaveolens*, *P. deltoides*, and *P. nigra* due to the fact that 'balsam poplar' during Bogdanov's times was actually *P.* ×*moscoviensis* (*P. laurifolia* × *P. suaveolens*).

This is a tall magnificent tree with a dense crown. Foliage color is lighter than in *P.* × *sibirica*, leaves on average are larger and, most importantly, broader (to 9–12 × 7–8 cm) than in *P.* ×*sibirica*, their length only slightly (to 1.5 times) larger than width, broad ovate, with

maximal width within one-fourth to two-fifths of blade length from base. About half of all leaves feature basilaminar glands (Fig. 7).

There are plants with carpellate catkins and staminate flowers. Capsules are similar to those of *Populus* ×*sibirica*. This poplar is very common in Moscow and Izhevsk but not as frequent in Tula.

Populus ×*sibirica* and *P.* ×*nevensis* differ from each other not only by habit or by their leaf shapes and colors, but also phenologically: by the timing of leaf expansion and shedding, fruit ripening, as well as by their tolerance to pests and diseases.

Transitional forms exist between *Populus* ×*sibirica* and *P.* ×*nevensis.* These are commonly used as street plantings in Moscow. Judging from label annotations to his collections, A.K.Skvortsov understood *P.* ×*sibirica* as a hybridogeneous complex of both *P.* ×*sibirica* and *P.* ×*nevensis*. Skvortsov (2007) noted that *P.* ×*sibirica* was distributed across the country, not only in cultivation, but also as a naturalized plant; therefore, some researchers had been taking it for a native species. One distinguishable form within this complex, which was sporadically recorded during our study, occurs across Moscow and features a high percentage of three-valved capsules (up to 80%).

Populus ×*rasumovskoe* R.E.Schroed. ex Wolkenst. [? *P.* ×*canadensis* (*P. deltoides* × *P. nigra*) × *P.* ×*berolinensis* (*P. laurifolia* × *P. italica*)] is similar to *P.* ×*berolinensis*, which can be occasionally encountered in Moscow. These two poplars may have been mixed, as both are semi-pyramidal. *P.* ×*rasumovskoe* differs in its broader and lighter-colored leaves (in fact the lightest-colored leaves among all poplars) deltoid to broad ovoid in outline (though small leaves are much like those in *P.* ×*berolinensis*: ovoid or rhombic). Generally, highly polymorphic leaves within a single crown are typical for this poplar. Blades sized 9(12) × 8(10) cm, their length typically slightly exceeding width (seldom to 1.5 times as long or, on the contrary, somewhat shorter); maximal blade width dramatically shifted away from mid-blade toward base (within one-fourth to one-third of blade length from base); base rounded-cuneate or composite: cuneate close to petiole, then rounded, with small sinus separating cuneate part of base from rounded; otherwise, broad cuneate at petiole, then rounded, the two parts also separated with a sinus (Fig. 8). Rather commonly, leaves of elongated shoots feature glands at the junction of petiole and leaf blade. Produces abundant root suckers that are strongly ribbed. Populations consist of mostly plants with carpellate catkins. Capsules rounded, two-valved, very rarely three-valved. This tree is often planted along busy streets in Moscow, so it has become the most common poplar in many neighborhoods. In Izhevsk one can occasionally

find plants resembling *P.* ×*rasumovskoe* from Moscow yet having darker-colored foliage and only staminate flowers. *P.* ×*rasumovskoe* is likely to be found in Tula yet remains undiscovered there.

By its habit, phenology, leaf and capsule structure, presence of copious root suckers, and other characters, *Populus* ×*rasumovskoe* differs significantly from those belonging to the '*nevensis-sibirica'* hybridogeneous complex. However, there also exist intermediate forms between the two.

We shall say a few words about those intersectional hybrids that approach balsam poplars in their leaf shape and bark characters. These appear highly variable in many respects: their branchlets colored from yellowish-gray to brownish, shoots angled to a different extent, foliage may be of variable color, and leaf petioles may vary in length. These are usually plants with carpellate catkins and three-valved, nearly sessile capsules densely distributed along the catkin axis. Capsules may vary in size and be either pubescent or glabrous.

These poplars are not planted in Moscow anymore, apparently, due to problems with their high cotton productivity. They have been encountered in Izhevsk more often than in Moscow. One of these poplars, to which the authors have assigned a temporary name *Populus nothosp*. C, is quite frequently planted along the streets of Izhevsk. Young twigs ridged or angled. Leaf blades to 10–12 × 6–8 cm, on average twice as long as broad (to 2.5 times in small leaves), oval-elliptic, more rarely ovate-elliptic, their maximal width more or less shifted away from mid-blade toward base (within one-third to two-fifths of blade length from base); base broad cuneate or more rarely narrow cuneate or nearly rounded; lateral margin practically not translucent (a feature characteristic of balsamic poplars); apex acute, attenuate in a narrow point nearly 1 cm long. Adaxial blade surface dark green, abaxial of contrasting greenish-white color. Midrib on adaxial side light yellow, 0.6–1.0 mm wide, conspicuous against background dark color of blade. Basilaminar glands usually present, though small, sometimes distorted (as if eroded). Elongated shoots may have broader leaves (length-to-width ratio not more than 1.5), with maximal width considerably closer to leaf base. Adventitious shoots strongly ridged. It is represented by plants with carpellate catkins and three-valved pubescent capsules only. *Populus nothosp*. C may turn out to be a hybrid of *Populus* ×*petrovskoe* (*P. deltoides* × *P.* ×*moscoviensis*) and *P. tristis*. A similar hybrid with less contrasted leaf coloration, *P. laurifolia* × *P. tristis*, has been occasionally used in Moscow.

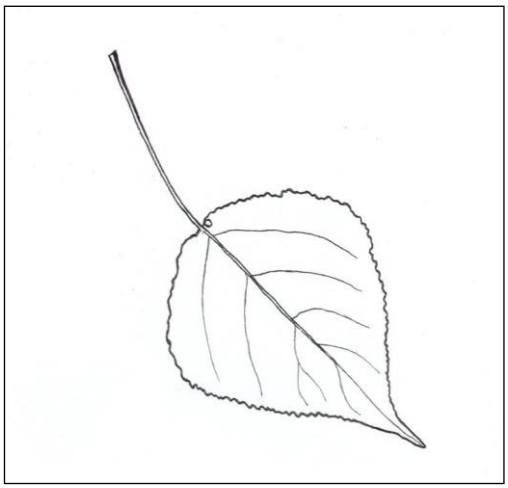

Figure 7. A typical leaf of *Populus* ×*nevensis* Nasim.

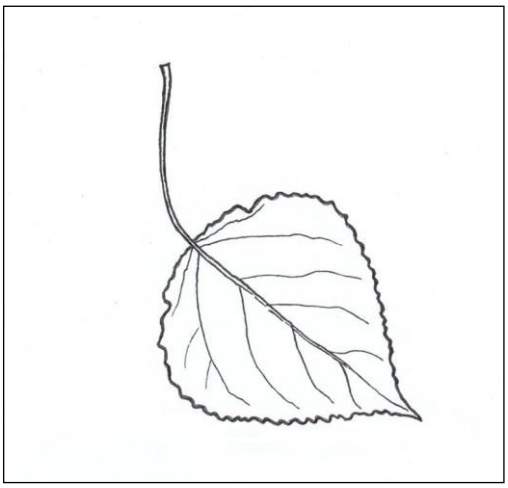

Figure 8. A typical leaf of *Populus* ×*rasumovskoe* R.E.Schroed. ex Wolkenst.

In addition to planted material, we also located self-sown poplar trees at vacant lots, rundown streets, and along railroad tracks in both Moscow and Izhevsk. These trees may resemble *Populus* ×*sibirica, P.* ×*nevensis,* or their hybrids, and occasionally *P.* ×*rasumovskoe*. Remarkably, when these spontaneous plants grow in proximity to ornamental cultivars, one can find intermediate forms nearby, apparently originating from seed. Some of these hybrids are quite ornamental, so it may be possible to recommend them as source trees for the green industry.

In Moscow and Izhevsk one may sometimes encounter entire arrays of interesting poplar forms that are to be attributed to intersectional hybrids. While some of them are planted, others are spontaneous from seed. Some have leaves resembling those of *Populus balsamifera* or *P. trichocarpa*.

We have not found any pure species of poplars in the living collections of the Main Botanic Garden and Moscow University Botanic Garden, except for a few wild collected specimens of *Populus suaveolens* s.l. in the Main Botanic Garden. The collections in both gardens primarily consist of intersectional hybrids, the most interesting of which appear to be *P.* 'Oxford' (*P. berolinensis* × *P. maximowiczii*) and *P.* ×*generosa* A.Henry (*P. deltoides* s.l. × *P. trichocarpa*) (Plotnikova *et al*., 2005).

Ornamental characteristics of poplars

The hybrids deployed by the green industry differ from each other in their phenology. *Populus* ×*sibirica* produces leaves the earliest: a week earlier than *P.* ×*nevensis* and many other hybrids. *P.* ×*canadensis* and *P.* ×*rasumovskoe* are the latest to expand leaves. Most

Table 1. Species and hybrids from Sect. *Aigeiros* Duby and *Tacamahaca* Spach (genus *Populus*) most commonly encountered in Moscow, Izhevsk, and Tula

Name	Putative parent species	Cities where taxa were encountered	Catkins (sex representation)	Number of valves in capsules
Populus longifolia Fisch.		Moscow, Izhevsk	mostly staminate	2–3
Populus simonii Carrière		Moscow	staminate	
Populus ×*canadensis* Moench	[! *P. deltoides* s.l. (? *P. monilifera* Aiton) × *P. nigra*]	Moscow, Tula (seldom)	staminate carpellate	2–3, sometimes 4
Populus × *moscoviensis* R.E. Schroed. ex Wolkenst.	*P. laurifolia* × *P. suaveolens*	Moscow (very seldom), Izhevsk (very seldom) Tula (very seldom)	carpellate	3
Populus ×*berolinensis* K.Koch	*P. laurifolia* × *P. italica*	Moscow (rare)	staminate	
P.opulus×*petrovskoe* R.E. Schroed. ex Wolkenst.	? *P. deltoides* var. *monilifera* Henry × *P.* × *moscoviensis*	Moscow, Izhevsk	staminate	
Populus nothosp. A	[? *P. nigra* × *P. suaveolens* s.l.; ? (*P. nigra* × *P. suaveolens* s.l.) × *P. suaveolens* s.l.]	Moscow, Izhevsk	staminate	
Populus nothosp. B	*P. deltoides* × *P. longifolia*	Izhevsk	staminate	
Populus nothosp. C	[? (*P. deltoides* × *P. laurifolia*) × *P. longifolia*]	Izhevsk	carpellate	3
P. ×*sibirica* G. Kryl. et Grig. ex A.K.Skvortsov.	? *P. moscoviensis* × *P. nigra*	Moscow (common), Izhevsk (common), Tula (common)	mostly carpellate	2, sometimes 3
P. ×*nevensis* Nasim.	? *P.*× *moscoviensis* × P.× *canadensis*	Москва (common), Izhevsk (common), Tula	carpellate, staminate	2, sometimes 3
Populus ×*rasumovskoe* R.E.Schroed. ex Wolkenst.	? *P.* × *canadensis* × *P.* × *berolinensis*	Moscow (common), Izhevsk?	mostly carpellate	2, sometimes 3

poplars shed leaves in late September/early October. *P*. ×*rasumovskoe*, drops its leaves the latest; *P*. *simonii* and *P*. ×*canadensis* retain green leaves until winter.

Poplars differ by the capsule ripening time. *Populus*. ×*sibirica* and *P*. ×*canadensis* are the first ones to produce cotton; they are followed by *P*. ×*nevensis*, and a week later also by *P*. ×*rasumovskoe*. Those morphologically approximating balsam poplar are the latest to ripen.

Poplars also differ by their habit: height, crown shape, and density. For example, *Populus* ×*rasumovskoe* has a nearly fastigiate crown with lower branches promptly dying off. Pruning facilitates rejuvenation of this cultivar and restoration of its ornamental quality. *P*. ×*sibirica* and its hybrids with *P*. ×*nevensis* also benefit from pruning, particularly since the latter have brittle wood. At the same time, neither *P*. ×*canadensis* nor *P*. ×*nevensis* require any pruning, as they form strong, long-leaved branches.

Ornamental forms of *P*. *simonii* do not require any pruning, either.

In poplars, leaves vary not only by their expansion/abscission times, but also by their shape, size, and coloration. Differences in color become most conspicuous during spring and fall. Leaves of *Populus* ×*nevensis* and those of *Populus nothosp*. B attain a beautiful yellow color in the fall.

The least resistant of these poplars to cladosporiosis is *Populus* ×*sibirica* and its hybrids with *P*. ×*nevensis*. During humid years, these cultivars sustain significant cladosporiosis damage and then may shed leaves as early as mid-August. Black poplars and their hybrids are more susceptible to rust.

Discussion

According to the results of the survey, the following species have contributed to the current diversity of poplars in Moscow: *Populus suaveolens*, *P*. *laurifolia*, *P*. *nigra*, and *P*. *deltoides*. One cannot completely exclude the possibility of other species' participation in addition to these. In Izhevsk, poplar diversity has been formed primarily on the basis of *P*. *suaveolens*, *P*. *laurifolia*, and *P*. *nigra*, but also with participation of *P*. *longifolia*. As compared to the situation in Moscow, *P*. *deltoides* has been less productive in Izhevsk. However, due to recent intensive use of *P*. ×*petrovskoe* and *P*. *nothosp*. B in this city, the share of *P*. *deltoides* in the formation of the poplar genetic pool must grow. Major primary species in Tula have been *P*. *suaveolens*, *P*. *laurifolia*, and *P*. *nigra*. *P*. *suaveolens* and *P*. *laurifolia* may have reached this city in hybrid form, as *P*. ×*moscoviensis*.

The practically complete absence of pure poplar species within the surveyed territory can be attributed to their high hybridization potential. Adventive poplars could have been represented by pure species in case they were selected from wild populations and then propogated asexually. With reproduction by seed, the probability of hybridization significantly increases.

Among the poplars in Moscow and Izhevsk, one may segregate a group of highly ornamental plants apparently represented by male clones of *Populus ×petrovskoe, Populus nothosp*. A, *Populus nothosp*. B, and also *P. simonii*. These are products of artificial selection. They constitute not more than 5% of the total amount of poplars in these cities.

As already mentioned, the most abundant trees are hybridogeneous complexes of *Populus ×sibirica* and *P. ×nevensis* as well as *P. ×rasumovskoe*, represented by both plants with staminate flowers and those with carpellate catkins. They have also been propagated vegetatively and planted in the cities. Representatives of this group may also reproduce by seed. Trees of this group originating from seed dominate the less developed territories of Moscow, Izhevsk, and Tula—those areas where street beautification has been insufficient. Hybrids that resulted from hybridization between *P. ×sibirica*, *P. ×nevensis,* or *P. ×rasumovskoe* look very similar to each other. Yet when these hybrids cross with the highly ornamental cultivars, the resulting forms appear to be more variable and include individuals that are drastically close in habit to these highly ornamental poplars.

Summarizing these observations in the three cities, one can distinguish two processes developing in different directions. On the one hand, breeders' efforts have resulted in the production of highly ornamental cultivars, which have been propagated by cuttings and planted out. Recently the trend has been to produce cultivars consisting of either staminate or sterile plants in order to avoid poplar cotton in the cities.

On the other hand, in nurseries and on rundown land parcels, a constant process of spontaneous hybridization among poplars has been taking place en masse. This process, as mentioned by J.A.Nasimovich (Mayorov *et al*., 2012), leads to the formation of 'an average city poplar,' whose habit is inherited from an assortment of species, hybrids, and cultivars initially introduced to a certain region, depending upon the extent of their participation in the hybrid formation. In cities of eastern and central European Russia, it varies slightly, approaching the habit of *P. ×sibirica, P. ×nevensis,* or *P. ×rasumovskoe*. Spontaneous hybridization is a process unwanted by the green industry, as it degrades the diversity of poplar forms in cities and elevates the percentage of plants with carpellate catkins, which leads to spreading of poplar

cotton. A low share of highly ornamental hybrids among poplars of Moscow, Izhevsk, and Tula tells us that the ornamental potential of *Populus* remains largely underused.

Spontaneous hybridization in poplars takes place in natural habitats as well as in cultivation; however, the consequences in these two situations are very different. Researchers (Eckenwalder, 1984) have recorded cases of spontaneous hybridization among the North American poplar species *Populus deltoides, P. balsamifera, P. trichocarpa.* Hybridization areas are usually not wide (10–15 km) and contain not only first- and second-generation hybrids, but also specimens representing subsequent generations that appear as a result of crossings among the formed hybrids and back-crossings (Broeck *et al*., 2005; Braatne, Wilson, 1999).

In Asia, wherever *Populus nigra* and *P. laurifolia* grow together, spontaneous hybridization also takes place. Solitary hybrid forms with various combinations of morphological characters typical for participating species are occasionally found in mixed populations. Some hybrids occupy an intermediate position between parent species with regard to leaf shape, presence of shoot ridges, size and shape of capsules. As to other characters, hybrids tend to approximate one or the other parent species; in fact the absolute majority of trees in a mixed stand have a habit of either *P. laurifolia* or *P. nigra*. Yet in the overlap zone of *P. nigra* and *P. laurifolia*, no plants actually represent pure species. Seed collected from trees that were morphologically close to either *P. laurifolia* or *P. nigra* produced progeny of rather variable sizes and exhibiting significant morphological diversity (Likhovid, 1994). There is no data on hybridization of *P. suaveolens* and *P. laurifolia* in the area of their overlap (Bakulin, 2004).

One can conclude that in zones of species' distribution overlap, natural selection eliminates all those hybrids that are habitually significantly different from parental species, encouraging those that deviate the least from one of the parents, which typically occupy different ecological niches.

Whenever cultivars cross with native species within their distribution areas in the urban environment, in drastically altered natural ecosystems, introgressive hybridization takes place. This may lead to a complete elimination of a native species, which literally sinks amidst cultivars. A process of this kind is now going on in Europe, where *Populus nigra* hybridizes with multiple cultivars of *P.* ×*canadensis* grown in plantations as well as with the ornamental *P. italica*.

Another worrisome likely consequence of this process is formation of hybrids with a high invasive potential, which can completely ruin natural ecosystems. (Brus *et al*., 2010;

Cagelli *et al*., 1995; Broeck *et al*., 2005). In intact ecosystems, hybrid seeds have very low chances of germination and survival due to discourse of their reproduction cycles with the natural environment (Braatne and Wilson, 1999).

Conclusions

In the three cities, the levelling effect of spontaneous hybridization has been mitigated by artificial hybridization, asexual propagation, and planting of highly ornamental, vigorous poplar cultivars.

Due to their tendency to easily form hybrids and their ability to reproduce asexually, poplars constitute a great potential source of cultivars capable of occupying various ecological niches in cities. In Moscow and Izhevsk, at least four species have been participating in the hybridization, whereas in Tula there have been no less than three contributing species.

In the regions where native poplar species are present, their hybridization with cultivated varieties in disturbed habitats constitutes a real threat to the existence of these native species.

In natural habitats, in situations when the areas of native poplar species overlap, there are constant hybridization processes, yet the natural selection is directed toward elimination of those hybrids that significantly deviate from pure species.

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