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New names for Schreiner and Stout poplar hybrids, trees of major importance in forestry and landscaping

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Abstract: Among the widely cultivated poplars, some of the most significant are those developed by Ernst J. Schreiner and Arlow B. Stout. These poplars were developed through controlled hybridization in the United States in the early 20th century, and the selected clones were efficiently distributed worldwide over the following decades. Despite their apparent prevalence in cultivation, their identification remains a significant challenge. Among the most frequently grown Schreiner and Stout clones are those derived from the crosses *Populus suaveolens* × *P. trichocarpa* and *P. suaveolens* × *P.* ×*berolinensis*. However, formal names were never proposed for these hybrids; consequently, they must be assigned to individual clones, further complicating their nomenclature. In this paper, based on historical data, morphological studies, and anatomical analyses of leaf petioles, it is demonstrated that these hybrids possess distinct characteristics that facilitate easy identification. Two new nothospecies, *Populus* ×*schreineri* and *Populus* ×*stoutii* are proposed and described. Both taxa exhibit clear hybrid traits; however, *P.* ×*schreineri* is morphologically closer to *P. suaveolens* (sect. *Tacamahaca*), while *P.* ×*stoutii* shows a distinct influence from the black poplar section (sect. *Aigeiros*). The main diagnostic features enabling their identification are highlighted, with particular emphasis on the petiole anatomy.

Keywords: identification, intrasectional hybridization, anatomical traits, new nothospecies

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Introduction

The development of the paper industry in the United States at the beginning of the 20th century, combined with the growing demand for fast-growing biomass, prompted a search for new solutions. As a result, the first large-scale breeding programs in the world were initiated in the USA. The key traits sought included ease of rooting, rapid growth, resistance to diseases and pests, and high timber yield

(Bugała & Stecki, 1961). The choice fell on poplars (*Populus* L.), which are among the most economically important and fastest-growing trees in temperate climates (Korbik, 2020; Stolarski, 2025). The project for extensive poplar breeding was initiated as early as 1916 by Ralph H. McKee, Professor of Chemical Engineering at Columbia University, who wrote about the need to cross dozens of poplar varieties to breed hybrids suitable for pulpwood production (Stout et al., 1927). This idea was ultimately realized by Ernst J. Schreiner of the Oxford Paper Company and Arlow B. Stout of the New York Botanical Garden. The breeding work was conducted between 1925 and 1927, based on poplar collections located at the New York Botanical Garden in New York City, Highland Park in Rochester, and the New York State Experimental Station at Geneva, New York, USA (Stout et al., 1927; Stout & Schreiner, 1933). Crosses were made using 34 species, varieties, and various clones of poplars, resulting in approximately 13000 seedlings. Over the following years, the best-growing individuals were selected. Between 1930 and 1936, 150 of the best selections were distributed worldwide to meet demand for saplings for experimental planting. During this period, poplars were identified by working numbers (e.g. '96-4', '97-28', '97-38'). In 1936, the "OP" designation – standing for "Oxford Poplar" from the Oxford Paper Company – was adopted, combined with a clone number (e.g. 'OP 41', 'OP 46', 'OP 47'). Shortly thereafter, the designation was changed to "NE" (Northeastern Forest Experimental Station) while retaining the original numbering ('NE 41', 'NE 46', 'NE 47') (Schreiner, 1971). Schreiner and Stout described 10 of the most promising clones, which were distributed to plantations in the USA and worldwide (Schreiner, 1971). For these poplars, alphanumeric designations were later replaced by cultivar names referring to the research stations ('Andover', 'Androscoggin', 'Frye', 'Geneva', 'Maine', 'Oxford', 'Rochester', 'Roxbury', 'Rumford', and 'Strathglass') (Schreiner & Stout, 1934). In the 1970s, up to 40 of the best clones were made available to the State Forest Nurseries in the USA, where selection names were preceded by a country code, e.g. 'USA-NE-41' previously described as 'OP 41' and 'NE 41' (Schreiner, 1971). Earlier, between 1934 and 1938, Poland (Kórnik Arboretum) was among the first research centers to receive Schreiner and Stout hybrids from the Morton Arboretum. Several shipments were delivered to Poland, including 10 named clones and 17 described alphanumerically. From Poland, these poplars were subsequently distributed to neighboring countries, such as the Czech Republic, as well as to more distant regions, including China (Bugała, 1973; Schreiner, 1974; Mottl, 1989). In the following years, both the ongoing World War II and severe winters (particularly the winter of 1939/40) verified the suitability of these hybrids for cultivation in Poland's climatic conditions. After the war, three clones in the Kórnik collection drew particular attention for their growth vigor; in the experimental plots, they were marked only with the numbers 194, 275, and 277. Lacking detailed information, these clones were provisionally labelled with the prefix "Hybrida" or "H" (e.g., 'Hybrida 275' or 'H275'). Outside of Poland, these poplars also appeared under the "P" designation (referring to the Polish origin of the propagation material; e.g., 'P275'). Over the years, it turned out that these cultivars were also known outside Poland and were equally popular in many places, where they functioned under their correct designations as 'NE 42' (= 'Hybrida 275'), 'NE 44' (= 'Hybrida 277'), and 'NE 49' (= 'Hybrida 194') (Bugała, 1973). Among these, the 'NE 42' poplar became one of the most widely cultivated due to its healthy growth and male sex (which prevents the production of seed cotton); it was the only one among previously unnamed clones to receive a formal name 'Meggylevelű' (Benetka et al., 2009; Bartha, 2021; FAO, 2021). The distribution of these hybrids spanned nearly all continents, starting with North America (1933-1954), South America (1939-1954), Europe (1934-1974), Africa (1938), Australia (1946-1949), and finally Asia (1953-1974) (Schreiner, 1974). Currently, Schreiner and Stout hybrids can be found not only in timber plantations but also frequently enriching residential greenery, roadside belts, parks, and abandoned or degraded urban and industrial sites, often forming both avenues and mid-field woodlots (Niemczyk et al., 2016; Seneta & Dolatowski, 2025). Besides the Schreiner and Stout hybrids, other cultivars were also selected, including two similar to 'Meggylevelű' named 'Kórnik 6' and 'Kórnik 8', developed at the Kórnik Arboretum in Poland (Stecki, 1980). Unfortunately, work on these poplars has almost completely ceased, and the further fate of these trees is unknown (Bojarczuk, pers. comm. 2021). Poplars cross-breed exceptionally easily, especially among the sections *Aigeiros* Duby, *Leucoides* Spach, and *Tacamahaca* Spach (Proshkin, 2024). These sections are so closely related that, for years, they have been grouped by some authors under the subgenus *Eupopulus* Dode, which was accepted by Bugała (1973) and supported by recent molecular studies (Wang et al., 2022). The poplars discussed in this paper are not only developed within breeding programmes but may also arise spontaneously where parental taxa co-occur, particularly in association with *Populus suaveolens* Fisch. ex Poit. & A.Vilm. This phenomenon is documented, for example, in the case of the mentioned Kórnik hybrids designated as "Kórnik", where the pollen donor remained unknown until the clear presence of *Populus trichocarpa* Torr. & A.Gray ex Hook. traits was demonstrated, most notably the exfoliating young bark – a feature unique to this species (Stecki, 1980). Concurrently, *Populus ×berolinensis* K.Koch may act as a pollen donor and recipient due to its early flowering, a trait inherited from section *Tacamahaca*, as it originated as a hybrid between *Populus nigra* L. and *Populus laurifolia* Ledeb. The latter species forms common phylogenetic clades with, among others, *P. suaveolens*, and these taxa appear to transition continuously into one another, hybridizing readily (Klimov & Proshkin, 2024). In parts of its range, *P. laurifolia* also hybridizes easily with *P. nigra* (Shang et al., 2016), suggesting that hybrids involving all three taxa may occur naturally. We also recorded spontaneous hybrids involving *Populus ×stoutii* Andrzejczak and Korbik in cultivation, observed in Żerański Park in Warsaw (Poland), where cultivars of both *P. ×berolinensis* and *P. ×stoutii* were grown together, creating conditions favorable for spontaneous hybridization. Notably, hybrids between Asian species of section *Tacamahaca* and *P. nigra* usually clearly exhibit morphological characteristics of black poplars (Nasimovich et al., 2019). In this case, it is particularly visible in the translucent leaf margin and petiole anatomy. These traits are observable not only in *P. ×berolinensis*, but also in other hybrids with strong genetic contribution from section *Tacamahaca*, such as *P. ×stoutii*, as well as in their backcrosses and other related hybrids that may occur – for this reason, the mentioned characters are relatively stable and useful for identification. Hybrids already present in cultivation may indeed be named and classified under the International Code of Nomenclature for Cultivated Plants (ICNCP). However, this framework requires highly specialized knowledge of cultivar identification. In many cases, it is difficult to assign such hybrids to a particular cultivar because the distinguishing features may be very subtle. Moreover, placing them in cultivar groups does not fully reflect their diversity and origin, especially when similar hybrids still may arise independently in nature or in cultivation. For these reasons, we consider the treatment of these hybrids under nothospecies names in accordance with the International Code of Nomenclature for algae, fungi, and plants (Madrid Code) (Turland et al., 2025) to be justified. Despite their widespread cultivation, Schreiner and Stout hybrids continue to pose serious identification challenges. Therefore, there is a clear need for their segregation, description, and the determination of their most significant diagnostic characteristics for a correct understanding of the genus and its practical application, especially in cultivation.

Materials and methods

Nomenclature analysis

The poplar hybrids bred by Schreiner and Stout have been characterized from the beginning by an unclear taxonomic status, which has led to various naming practices, multiple names referring to the same clone, and difficulties in clear identification. Since the original authors did not assign taxonomic units to the resulting hybrids, the Schreiner and Stout hybrids have been treated and named quite specifically and precisely as cultivars from the beginning. The *Populus* Schreiner-Stout Group, proposed by Dolatowski and Zieliński (2021), encompasses all cultivars selected by Schreiner and Stout known in cultivation, grouping them together regardless of their origin – that is, regardless of whether they resulted from intersectional crosses and showing characteristics of black and balsam poplars (= *Populus* nothosect. *Tacageiros* Dolat. & Ziel.) or are intersectional hybrids exhibiting traits exclusively of balsam poplars (= *Populus* sect. *Tacamahaca*). Such a broad approach, encompassing poplars derived from crossing trees of dozens of species and varieties, unfortunately, has little value and is scarcely more precise than treating these trees within *Populus* s.l. This leads to clear difficulties in definitive identification, which further connects to their proper use in plantations, where high production value is essential, or in landscape plantings, where individuals with high resistance to urban conditions, including healthy and fast-growing ones, are desired. Although Schreiner and Stout hybrids are well-known and frequently encountered in Europe, they are very often misidentified as "Balsam Poplar" or *Populus maximowiczii* Henry (Seneta, 1994), not to mention the difficulty of assigning a specific cultivar name to a particular specimen. Assigning a nothospecific name to each parental combination provides a practical taxonomic framework that bridges the gap between broad group designations and precise cultivar identification. This approach ensures higher taxonomic resolution while remaining more practically accessible for identification than the distinction of individual cultivars. A similar approach was taken by Tikhomirov (2023), who proposed the name *Populus ×cinovskisii* Val.N. Tikhom. for the cultivar 'Lettland' (a putative hybrid of *P. trichocarpa* and most likely *P. ×berolinensis*, widely cultivated in Belarus, Estonia, Latvia and Lithuania). However, unlike that hybrid, the Schreiner and Stout hybrids are represented by numerous cultivars of documented genetic origin (Schreiner & Stout, 1934; Radetzky, 1990; Fehrenz & Havel, 2010; Liesebach, 2010); thus, distinguishing them as nothospecies is even more taxonomically justified. At the same time, their spontaneous occurrence additionally supports their treatment as nothospecies. Given that these are relatively common and represented by numerous cultivars, recognizing and describing them under independent names helps to clarify their taxonomic status. These trees are sufficiently distinctive and important that treating them solely as cultivars or cultivar groups causes them to become obscured among numerous other cultivar names and limits the practical possibilities for their identification. The Schreiner and Stout hybrids most commonly found in cultivation can be divided into two combinations, including hybrids between *P. suaveolens* × *P. trichocarpa* and *P. suaveolens* × *P.* ×*berolinensis*. Although Schreiner and Stout originally used *P. maximowiczii* for their breeding work, it is now considered that this species, along with *Populus koreana* Rehder, belongs to *P. suaveolens* s.l. (Greenaway et al., 1992; Borkhert et al., 2023; POWO, 2025). Unlike *P. suaveolens*, the taxonomic status of *P. trichocarpa* has been unclear in recent years, as this name is sometimes treated as a synonym of *Populus tristis* Fisch. (Skvortsov, 2008, 2010; POWO, 2025). Nevertheless, the works of Skvortsov (2008, 2010) do not present definitive arguments, and the morphological characteristics of the only clone known in cultivation as 'Tristis' (= *P. tristis*) clearly match *Populus balsamifera* L.; consequently, this poplar is also treated as its cultivar, i.e., *P. balsamifera* 'Tristis' (Väre et al., 2021). The treatment of 'Tristis' as a cultivar of *P. balsamifera* is further supported by molecular data available in the Thünen Institute database. Similarly, Tikhomirov (2023) maintains *P. trichocarpa* as the correct name, rejecting its synonymization with *P. tristis* – a view we share in this paper. We adopt 'Meggylevelű' (syn. 'NE 42', 'H275') as the representative clone for hybrids between *P. suaveolens* × *P. trichocarpa*. In research on poplar genotypes, Fehrenz and Havel (2010) used 'Meggylevelű' clone (labeled as "H275") and 'Androscoggin' (labeled as "A"), confirming that both represent *P. suaveolens* × *P. trichocarpa* hybrids. Regarding the second combination, *P. suaveolens* × *P.* ×*berolinensis*, the 'Geneva' clone serves as the primary representative; its parental origin has been confirmed by molecular studies (Liesebach et al., 2010).

Morphological investigation

Living plants, as well as herbarium specimens of individuals representing selected clones of the described hybrids, i.e., 'Androscoggin' ♂, 'Meggylevelű' (syn. 'NE 42') ♂, 'Geneva' ♀, 'Oxford' ♀, 'NE 44' ♀, and 'NE 49' ♂, as well as clones representing the parental species of the crosses, i.e., *P.* ×*berolinensis* 'Berlin' (used as a male parent clone in the breeding program), *P. suaveolens* 'Tardissima' (formerly *P. maximowiczii*; used as a female parent clone in the breeding program), and *P. trichocarpa* 'Senior' (used as a male parent clone in the breeding program), were examined for morphological traits under dissecting microscope to provide detailed description of both nothospecies. The morphological features of the selected trees were further compared with the characteristic traits of their corresponding sections. Terminology consistent with Beentje (2016) and Wang et al. (2022) was applied.

Anatomical investigation

The anatomy of leaf petioles of preformed leaves was studied, as it represents one of the most reliable methods for identifying poplars of hybrid origin (Proshkin & Klimov, 2019). Because the upper part of the petiole is the most suitable for anatomical assessment (Klimov & Proshkin, 2019), cuts were made at 1/4 to 1/3 of the petiole length from the base of the leaf blade, just below the junction, where the vascular bundles begin to transition into leaf veins. The petiole fragments were then prepared and stained with a 1:1 mixture of safranin and toluidine blue for 1-2 minutes. Later, they were mounted on microscope slides in Canada balsam. Observations were performed using epifluorescence microscopy (Delta Optical Evolution 100 microscope equipped with a Delta Optical DLT-Cam 1080 camera and DLT Cam Viewer software; blue bandpass filter, excitation 450-480 nm, emission 500-550 nm). Because the origin of the examined clones is known, our primary goal was to identify characteristics that support identification in the field – in this case, features of the petiole cross-section that can be observed with a magnifying glass may aid in distinguishing the taxa. Poplars from the *Tacamahaca* section are characterized by a high-arched type of vascular bundle arrangement, with one large bundle and a pair of horizontally arranged bundles above; poplars of the *Aigeiros* section are characterized by a linear type, with 3-4 bundles placed vertically in one line, not in pairs. The hybrids often exhibit intermediate characteristics between both types of arrangements. Another useful anatomical feature is the thickness of the spongy parenchyma, which in section *Tacamahaca* is thicker than in section *Aigeiros* and somehow intermediate in hybrids between the two sections. This feature can be observed as a whitish-colored abaxial surface of the leaf blade, which is the result of the light refracting differently in the thicker tissue (Al Afas et al., 2007) – the thicker the tissue, the whiter the surface appears. In this study, in addition to the hybrids and parental species, we also present the leaf and petiole cross-section of *P. nigra* 'Italica', one of the parents of *P. ×berolinensis*, as representative example of the characteristics of section *Aigeiros*. However, we omitted other parent – *P. laurifolia*, as in this case it is of lesser importance from the perspective of hybrid identification.

Taxonomic treatment

Populus ×schreineri Korbik & Andrzejczak, nothosp. nov.

the hybrid between *P. suaveolens* Fisch. ex Poit. & A.Vilm. and *P. trichocarpa* Torr. & A.Gray ex Hook.

LSID: urn:lsid:ipni.org:names: 77370553-1

Holotypus. Poland. Mazovia Province, Warsaw, the Warsaw University of Life Sciences Campus; 52°09'36.7"N 21°03'02.9"E; 23.06.2024; coll. Mateusz Korbik & Dawid Andrzejczak; WA0000169587, (Fig. 1) – 'Meggylevelű' (syn. 'NE 42' & 'H275').

Populus ×stoutii Andrzejczak & Korbik, nothosp. nov.

the hybrid between *P. suaveolens* Fisch. ex Poit. & A.Vilm. and *P. ×berolinensis* K.Koch.

LSID: urn:lsid:ipni.org:names: 77370554-1

Holotypus. Poland. Mazovia Province, Warsaw, the Warsaw University of Life Sciences Campus; 52°09'47.7"N 21°02'51.3"E; 23.06.2024; coll. Mateusz Korbik & Dawid Andrzejczak; WA0000169588, (Fig. 2) – 'Geneva' (syn. 'NE 46')

Diagnosis

Populus ×schreineri – Habit as in *P. suaveolens*, differing from *P. trichocarpa* in branches that are almost regularly subwhorled. Young bark exfoliates similarly to *P. trichocarpa*, whereas it is smooth in *P. suaveolens*; epicormic shoots may be present as in *P. trichocarpa*, but are absent in *P. suaveolens*. Fast-growing shoots differ in color and cross-section. Their color resembles *P. trichocarpa*, whereas their cross-section is intermediate between the parental species: bluntly angled in the hybrid, terete in *P. suaveolens* and ± strongly angled in *P. trichocarpa*. Leaf margin ciliate, similar to *P. suaveolens*, but eciliate in *P. trichocarpa*. Neoformed leaves intermediate between the parental species in shape and size, broader than *P. trichocarpa* but more elongate than *P. suaveolens*. Preformed leaves broadly elliptic, with a rounded to broadly cuneate base, somewhat similar to *P. suaveolens*, but differing from the triangular-ovate to cordate leaves of *P. trichocarpa*; leaf blade adaxially resembling *P. trichocarpa* in being ± smooth and shiny, whereas ± wrinkled in *P. suaveolens*. Vascular bundle arrangement typical of section *Tacamahaca*, but closer to *P. suaveolens*, with the main bundle slightly notched, whereas it is entire in *P. trichocarpa*. Stamens up to 50(–60), as in *P. trichocarpa*, whereas 30–40 in *P. suaveolens*.

Populus ×stoutii – Habit as in *P. suaveolens*, differing from *P. ×berolinensis* in branches that are almost regularly subwhorled. Bark as in both parents when young; in older trees, fissured as in *P. suaveolens*, whereas ± deeply furrowed in *P. ×berolinensis*; epicormic shoots may be present as in *P. ×berolinensis*. Fast-growing shoots terete differing from the ±angled shoots of *P. ×berolinensis*. Leaves showing a strong influence of *Tacamahaca* section with partly translucent margin as in *P. ×berolinensis*, whereas non-translucent in *P. suaveolens*. Neoformed leaves strongly sinuate, as in *P. ×berolinensis*, but in size and shape as in *P. suaveolens*. Preformed leaves similar to *P. suaveolens*, but, in addition to ±translucent margin, the serration resembles that of *P. ×berolinensis* (and section *Aigeiros*), with the basal half of the blade slightly more coarsely serrate than the distal half. Leaf petiole ±terete and slightly grooved as in *P. suaveolens*, but the bundle arrangement showing features of both *Aigeiros* and *Tacamahaca* sections – vascular bundles are arranged linearly in one large bundle and two horizontal pairs of smaller bundles. Flowers and fruits as in *P. suaveolens* but sometimes with two stigmas and two-valved capsule, corresponding to *P. ×berolinensis*. Fruits ripen very late (mid-summer to early autumn), whereas in *P. ×berolinensis* they ripen in late spring to early summer.

Comparison of parent species and described nothospecies in Table 1.

Descriptions

Populus ×schreineri (Fig. 3) – **Habit:** Fast-growing tree reaching up to 35 m in height; crown oval to spreading. Branches arranged at wide angles, distant and almost regularly subwhorled (in false whorls); they form angles of 60–90° with the stem. Stem straight, usually single, and extending to the tree apex. **Bark:** Exfoliating when young in small flakes; later greyish-green and smooth; old bark dull grey and fissured, mostly in the lower parts of the stem. Epicormic shoots sometimes present. **Shoots:** Reddish-brown to brownish-grey; sparsely pubescent to glabrescent; fast-growing shoots bluntly angled. **Leaves:** Heterophylly moderately expressed; margin ciliate, not translucent; abaxial surface whitish and often strongly stained with resin. Leaf blade markedly leathery, with reticulate venation that is ± conspicuous; upper surface ± smooth or weakly impressed and slightly shiny. Petiole surface glabrous. **Neoformed leaves:** Broadly ovate, large, up to 25 cm long; apex acute and short, rarely twisted; base

Fig. 1. Holotype of *Populus ×schreineri* Korbik & Andrzejczak, WA0000169587

Fig. 2. Holotype of *Populus ×stoutii* Andrzejczak & Korbik, WA0000169588

rounded to broadly truncate; margin rarely sinuate; petiole 3–5 cm long. **Preformed leaves:** Ovate to broadly elliptic, large, ca. 20 cm long; apex acute and usually short; base rounded to broadly cuneate; serration even along the margin; petiole about 5–7 cm long. **Petiole cross-section:** Terete, usually grooved; vascular bundles of the high-arched type, with one large bundle and a pair of horizontally arranged bundles above; the large bundle sometimes notched at the base. **Inflorescence and infructescence:** Rachis glabrous; male flowers with about 40–50(–60) stamens; female flowers unknown.

Populus* ×*stoutii (Fig. 3) – **Habit:** Fast-growing tree reaching up to 30 m in height; crown oval, narrow, and dense. Branches ascending, almost regularly subwhorled (in false whorls); they usually form angles of 45°–50° with the stem (rarely wider). Stem straight, usually single, and extending to the tree apex. **Bark:** Greyish-green and smooth when young; old bark dull grey and fissured, mostly in the lower parts of the stem. Epicormic shoots sometimes present. **Shoots:** Brownish-grey to greenish-grey; usually ± densely pubescent; fast-growing shoots terete. **Leaves:** Heterophylly moderately expressed; margin ciliate, partly translucent; abaxial surface greyish-green to ± whitish, usually slightly stained with resin. Leaf blade ± leathery, sometimes relatively thinner; reticulate venation conspicuous and ± distinctly impressed on the upper surface. Petiole densely pubescent. **Neoformed leaves:** Broadly elliptic to ovate, large, up to 25 cm long; apex acuminate, slightly twisted; base rounded to subcordate; margin strongly sinuate; petiole 4–5 cm long. **Preformed leaves:** Ovate to elliptic, ca. 15 cm long; apex shortly acuminate to acute; base cuneate to rounded, sometimes subcordate; basal half of the blade slightly more coarsely serrate than the distal half; petiole about 4–6 cm long. **Petiole cross-section:** Terete, slightly grooved; vascular bundles intermediate between the high-arched type and the linear type of section *Aigeiros*, with one large bundle and two pairs of horizontally arranged bundles above;

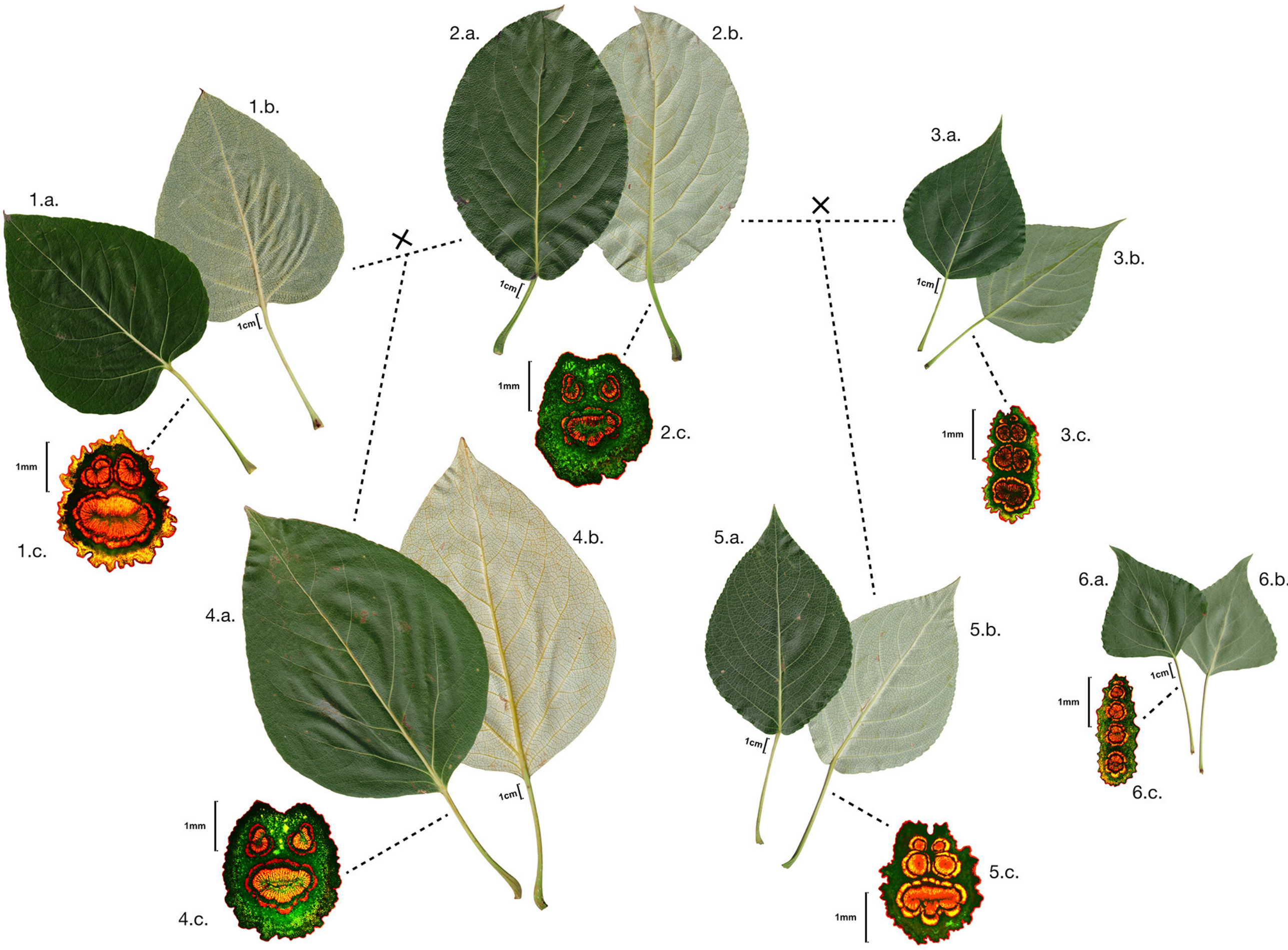

Fig. 3. Preformed leaves and their petiole cross-section: 1. *P. trichocaropa* – 1.a. adaxial surface, 1.b. abaxial surface, 1.c. petiole cross-section; 2. *P. suaveolens* – 2.a. adaxial surface, 2.b. abaxial surface, 2.c. petiole cross-section; 3. *P.* ×*berolinensis* – 3.a. adaxial surface, 3.b. abaxial surface, 3.c. petiole cross-section; 4. *P.* ×*schreineri* – 4.a. adaxial surface, 4.b. abaxial surface, 4.c. petiole cross-section; 5. *P.* ×*stoutii* – 5.a. adaxial surface, 5.b. abaxial surface, 5.c. petiole cross-section; additional *P. nigra* 'Italica' as an example of *Aigeiros* section traits – 6.a. adaxial surface, 6.b. abaxial surface, 6.c. petiole cross-section

Table 1. Comparison of morphological and anatomical traits of *P.* ×*schreineri*, *P.* ×*stoutii*, and their parental species

Trait	*P. trichocarpa*	*P.* ×*schreineri*	*P. suaveolens*	*P.* ×*stoutii*	*P.* ×*berolinensis*
Tree					
Height [m]	up to 35–40(–60*)	up to 35	up to 30	up to 30	up to 30
Crown shape	oval to vase-shaped, with ascending and spreading branches; the stem may divide into several leaders	oval to spreading; branches at wide angles, distant and almost regularly subwhorled – they form with a stem an angle of 60° to 90°; the stem is straight, usually single, and reaching the tree apex	broadly oval to spreading and open; branches at wide angles, distant and almost regularly subwhorled; the stem is straight, usually single, and reaching the tree apex	oval, narrow, and dense; branches ascending – almost regularly subwhorled; they usually form with a stem an angle of 45° to 50° (rarely more); the stem is straight, usually single, and reaching the tree apex	broadly conical and narrow, very dense; branches ±ascending; the stem may divide into several leaders
Trunk					
Bark	exfoliating when young in small flakes; later greyish green and ±smooth; old bark dark grey and deeply furrowed; epicormic shoots may be present on the lower parts of the stem	exfoliating when young in small flakes; later greyish green and smooth; old bark dull grey and fissured – mostly in the lower parts of the stem; sometimes epicormic shoots present	greyish green and smooth when young; older stays smooth for a long time, later dull grey and ±fissured; epicormic shoots absent	greyish green and smooth when young; old bark dull grey and fissured – mostly in the lower parts of the stem; sometimes epicormic shoots present	greyish green when young; older dark grey and ±deeply furrowed; sometimes with burls and epicormic shoots growing in the lower parts of the stem
Shoots					
Color	reddish-brown to brownish-grey	reddish-brown to brownish-grey	brownish-grey to greenish-grey	brownish-grey to greenish-grey	yellowish-grey to grey
Shape	fast growing shoots angled	fast growing shoots bluntly angled	fast growing shoots terete	fast growing shoots terete	fast growing shoots angled
Pubescence	usually ±densely pubescent	sparsely pubescent to glabrescent	densely pubescent to glabrous	usually ±densely pubescent	usually sparsely pubescent
Neoformed leaves (on long shoots)					
Shape	oblong-lanceolate	broadly ovate	broadly elliptic; orbicular towards the apex	broadly elliptic to ovate	broadly ovate
Blade width × length [cm]	8–11 × 20–25	(12–)13–15 × 20–25	10–16 × (15–)19–22	13–16(–20) × 20–25	8–9 × 13–15(–20)
Petiole length [cm]	3–5	3–5	1,5–3	4–5	4–5
Apex	acute and long; flat	acute and short; rarely twisted	acuminate and very short – sometimes almost completely reduced; usually twisted	acuminate; slightly twisted	acuminate; rarely twisted
Base	rounded; sometimes subcordate to ±truncate	rounded to broadly truncate	rounded to ±cuneate	rounded to subcordate	rounded to subcordate
Margin	usually flat	rarely sinuate	rarely sinuate	strongly sinuate	strongly sinuate
Preformed leaves (on brachyblasts)					
Shape	triangular–ovate to cordate	ovate to broadly elliptic	ovate to broadly elliptic; sometimes lancolate	ovate to elliptic	ovate-rhombic
Blade width × length [cm]	7–10 × 10–15	10–14 × (15–)17–22	(6–)9–12 × 15–17(–20)	(5–)8–11 × (12–)14–16(–18)	4–7 × 7–10

Petiole length [cm]	3–5	5–7	4–7	4–6	3–4
Apex	acute; sometimes long; flat	acute; usually short	shortly acuminate to acute; usually ±twisted	shortly acuminate to acute;	acuminate; usually long
Base	usually cordate to rounded; rarely truncate to cuneate	rounded to broadly cuneate;	rounded to cuneate; sometimes subcordate	cuneate to rounded; sometimes subcordate	cuneate to rounded;
Margin	serration even along the margin	serration even along the margin	serration even along the margin	the basal half of the blade is slightly more coarsely serrate than the distal one	the basal half of the blade is distinctly more coarsely serrate than the distal one;
Petiole cross-section (on preformed leaves)					
Shape	terete; usually grooved;	terete; usually grooved;	terete; usually grooved;	terete; slightly grooved	oval to slightly flattened;
Bundles arrangement	high-arched type with one large bundle and a pair of horizontally arranged bundles above;	high-arched type with one large bundle and a pair of horizontally arranged bundles above; the large bundle is sometimes notched at the bottom;	high-arched type with one large bundle and a pair of horizontally arranged bundles above; large bundle sometimes ±divided into group of three horizontally arranged smaller bundles;	intermediate between the high-arched type and the linear type of section *Aigeiros*; one large bundle and two pairs, each horizontally arranged bundles above; the large bundle is usually notched at the bottom;	intermediate, but closer to the linear type of section *Aigeiros*; one large bundle and three pairs, each horizontally arranged bundles above; the large bundle is slightly notched at the bottom;
Other leaf features					
Translucent margin	no;	no;	no;	partly;	partly;
Ciliate margin	no;	yes;	yes;	yes;	usually no;
Abaxiall surface	greyish-green to whitish; often strongly stained with resin;	whitish; often strongly stained with resin;	whitish; slightly to strongly stained with resin;	greyish-green to ±whitish; usually slightly stained with resin;	greyish-green; slightly stained with resin;
Leafblade	markedly leathery	markedly leathery	markedly leathery	±leathery; sometimes relatively thinner	weakly leathery
Venation	reticulate venation weakly conspicuous; upper leaf surface ±smooth and slightly shiny;	reticulate venation ±conspicuous; upper leaf surface ±smooth or just a weakly impressed and slightly shiny;	reticulate venation conspicuous and distinctly impressed above – surface wrinkled	reticulate venation conspicuous and ±distinctly impressed above	reticulate venation weakly conspicuous; upper leaf surface ±smooth;
Petiole surface	glabrous to sparsely pubescent;	glabrous;	densely pubescent;	densely pubescent;	sparsely pubescent;
Inflorescence and infructescence					
Rachis	pubescent;	glabrous;	glabrous to pubescent;	glabrous to ±pubescent;	glabrous to sparsely pubescent;
Stigmas	3	n/a**	3–4	(2–)3–4	2–3
Stamens	40–50(–60)	(30–)40–50(–60)	30–40	30–40	30–40
Capsules	3 valved; globose and densely hairy	n/a**	3–4 valved; ovoid-globose and glabrous	(2–)3–4 valved; ovoid-globose and glabrous	2–3 valved; ovoid and glabrous
Fruit rippening	late spring to early summer	n/a**	mid-summer to early fall	mid-summer to early fall	late spring to early summer

* on natural stands; ** no female trees known in cultivation.

the large bundle usually notched at the base. **Inflorescence and infructescence:** Rachis glabrous to ± pubescent; male flowers with about 30–40 stamens; female flowers with (2–)3–4 stigmas. Capsules ovoid-globose, glabrous, (2–)3–4-valved, ripening from mid-summer to early autumn.

Eponymy

Both epithets, "schreineri" and "stoutii", refer to Ernst J. Schreiner and Arlow B. Stout, who carried out the breeding program that resulted in the numerous hybrids, of which we describe the most popular in this paper.

Specimens Examined

Poland, Mazovia Province, Pęchcin

Szmit Nursery: 52°52'07.1"N, 20°34'12.4"E (*P.* ×*schreineri* 'Androscoggin' & 'Meggylevelű'; *P.* ×*stoutii* 'Geneva', 'Oxford', 'NE 44' & 'NE 49'; *P.* ×*berolinensis* 'Berlin' & 'Petrowskiana'; *P. trichocarpa*; *P. suaveolens*);

Poland, Mazovia Province, Warsaw

Botanical Garden in Powsin: 52°06'22.6"N, 21°05'36.4"E (*P.* ×*stoutii* 'Geneva') & 52°06'21.7"N, 21°05'35.4"E (*P.* ×*schreineri* 'Meggylevelű'); Alojzy Pawełek Square: 52°13'26.8"N, 20°58'05.9"E (Group of *P.* ×*stoutii* 'Oxford' & 'NE 44'); Warsaw University of Life Sciences Campus: 52°09'36.7"N, 21°03'02.9"E (*P.* ×*schreineri* 'Meggylevelű'); 52°09'47.7"N, 21°02'51.3"E (*P.* ×*stoutii* 'Geneva') & 52°09'50.4"N, 21°02'48.8"E (*P.* ×*stoutii* 'NE 49'); 52°09'49.4"N, 21°02'55.5"E & 52°09'37.0"N, 21°02'57.4"E (*P.* ×*berolinensis* 'Petrowskiana'); 13 Związku Walki Młodych Street – 52°09'31.6"N, 21°02'16.1"E (*P. suaveolens* 'Hellas'); 58 Zygmunta Modzelewskiego Street: 52°10'54.2"N, 21°00'53.2"E (*P. suaveolens* 'Hellas'); Chinese Embassy in Poland: 52°15'00.8"N, 21°00'01.4"E (*P. suaveolens* 'Tardissima'); Łazienki Królewskie: 52°12'50.5"N, 21°01'54.3"E (*P. suaveolens* 'Hellas'), 52°12'56.0"N, 21°02'00.7"E & 52°12'54.2"N, 21°01'38.7"E (*P.* ×*berolinensis* 'Petrowskiana'); Primary School No. 221: 52°14'09.4"N, 20°59'23.3"E (*P. trichocarpa* 'Senior'); Warsaw, Special Primary School No. 394: 52°11'36.2"N, 21°00'31.5"E (*P. suaveolens* 'Hellas'); 52/54 Słowackiego Street: 52°16'17.3"N, 20°58'30.9"E (Group of *P.* ×*berolinensis* 'Berlin'); Jana Pawła Street: 52°14'36.9"N, 20°59'31.9"E (Group of *P.* ×*berolinensis* 'Berlin' & 'Petrowskiana'); Praski Park: 52°15'11.2"N, 21°01'37.7"E (*P.* ×*berolinensis* 'Berlin').

Poland. Łodź Province, Łódź

Łódź Botanical Garden: 51°45'20.3"N, 19°24'04.9"E (*P.* ×*schreineri* 'Androscoggin'); 3/5 Wojciecha Kilara Street – 51°47'30.7"N, 19°25'51.0"E (*P.* ×*stoutii* 'Oxford');

Poland. Łodź Province, Rogów

Rogów Forestry Experimental Station: 51°49'41.0"N, 19°54'27.9"E (*P.* ×*schreineri* 'Meggylevelű') & 51°49'41.0"N, 19°54'27.9"E (*P. suaveolens* 'Tardissima');

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