



Translations

Bay-leaved willow (*Salix pentandra* L.) and related species: Taxonomic and geographic overview¹

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The genus *Salix* is comprised of about 400 species and distributed on most continents of the world—from the temperate belt of the Southern Hemisphere, across the Tropics, and all the way north, nearly to the very limit of higher plant distribution in the Arctic. It is only in the Antarctic, Australia, New Zealand, Indonesia, and Oceania that willows do not occur. Willow species exhibit all kinds of geographic patterns from circumpolar or nearly pan-boreal to strictly local. Despite that, the genus *Salix* has hardly ever been employed for generalizations in botanical geography. At best one can find in the checklists some very general remarks on distribution of certain species, most of the time with many lags and without much accuracy. Data available from willow studies are seldom used for historic studies of floras, rare attempts to employ this information being largely unsuccessful.

The reason for this situation seems to be a poor understanding of the systematics within the genus, vague perceptions about species' distributions, and particularly lack of comparisons between species occurring far away from each other. After treatments published by N.J.Andersson (1867, 1868), which are now much out of date, nothing has been produced in the world that would deal in detail, on the world scale, with any natural part of the genus *Salix* (let alone the genus as a whole). C.K.Schneider (1916) closely approached this task during his late years. His experience embraced North American as well as Chinese species; however, his vast dendrological interests became an obstacle for him to immerse in the systematics of *Salix* deeply enough to describe the phylogenetic relationships and florogenetic connections of the genus with compelling clarity.

Another prominent willow scholar, B.Floderus, whose knowledge of the subject perhaps wasn't as extensive as Schneider's, though was deeper, also made an attempt in his late years

¹Reports on Morphology and Systematics of Salicaceae. XI. Transactions of the Moscow Society of Naturalists (MOIP), 1960, ser. biol., vol. 3, sect. bot., pp. 247-262

(Floderus 1939) to produce a complete overview of two willow groups: the cycles of *S. phyllicifolia* L. and *S. myrsinites* L. However, his result does not appear satisfactory: even the limits of both chosen groups were circumscribed with many lags. For example, *S. divaricata* Pall. was included in the *Myrsinites* group, even though it is completely alien there. On the other hand, *S. fumosa* Turcz., undoubtedly closely related, was not included; neither was *S. chlorocladus* Flod. = *S. arctophila* Cocker., a species described by Floderus himself.

I shall also mention an attempt undertaken by R.Scharfetter (1953) to construct a phylogenetic scheme for the willows of Central Europe, which would be at the same time florogenetic. This work will be discussed in the final part of this review.

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While attempting a new systematic treatment of the USSR willows, the author was making all efforts to employ any material pertaining to foreign species available in depositories of this country. This approach revealed quite a few cases of remarkable similarities between our native species and those from Central Asia, East Asia, and particularly from North America. For example, many similarities have surfaced between the Siberian *S. jennisensis* (F. Schm.) Flod. and *S. pyrifolia* Anderss. within the part of its range in eastern Canada (Skvortsov 1959); or, say, between the Californian *S. laevigata* Bebb and *S. acmophylla* Boiss. from Southwest Asia, particularly from southern Turkmenia and southern Tajikistan (Skvortsov 1960a). These observations appear to be rather interesting from the historical geography perspective.

Further studies of available material enabled the author to undertake a trial treatment of not just separate pairs of related species, but rather an entire small group of related species—a cycle of those close to *S. pentandra* L., which is the subject of this article.

Along with the author's own collections made during various field trips, the following herbarium holdings were used for this work: those of the Botanical Institute in Leningrad (LE), including the Arctic Vegetation Section holdings, which have not yet been incorporated in the general collection; of the Main Botanic Garden in Moscow; and the Botanical Institute in Yerevan. The author would like to express his sincere gratitude for all the attention to his work and the help of the managers of these depositories. Still more critical data were obtained through observations of the Moscow University Botanic Garden living collection [assembled by the author].

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Five species are attributed to this cycle: *S. pentandra* L., *S. pseudopentandra* Flod., *S. serissima* (Bailey) Fern., *S. paraplesia* Schneid., and *S. pentandroides* A. Skvorts. The cycle is placed within the section *Pentandrae* (Dumort.) auct. Customarily, and especially in the American literature, a few more species are placed in this section, particularly, *S. lasiandra* Benth., *S. lyielii* (Sarg.) Heller, *S. lucida* Muhl., and *S. caudata* (Nutt.) Heller. There is no doubt, however, that these species don't belong to the immediate cycle of *S. pentandra* and are related more remotely. (I am going to give this fact more consideration when discussing *S. serissima*.) Since a discussion about the proper extent of the section *Pentandrae* is not the goal of this article, the cycle of species in question is going to be simply named here the group *Pentandrae s. str.*

This group is very natural. Its most important characteristics can be summarized as follows. These are tall shrubs or small trees (rarely mid-sized trees). Young branches are completely glabrous, shiny, as if varnished, until the age of two years. Floriferous and vegetative buds look absolutely the same. The outer bud scale is glabrous and shiny; it usually dies and hardens at the start of winter with just a narrow belt of live tissue left at the very base. Leaf primordia in the bud considerably exceed the ament primordium. The outermost leaf primordium is very wide, broadly oval or reniform when spread, with parallel venation, and completely embracing the rest of the bud content, so that its margins reach each other or even overlap on the abaxial side. Stipules are mostly missing or wanting; when present, they are glandular-dotted not only along the margin, but across the upper surface. Petioles of developed leaves bear 2–3 pairs of glands or gland clusters at the blade origin. Leaves are completely glabrous, shiny, somewhat paler or even whitish on the undersurface, though never glaucous. Marginal glands of young leaves usually emit resin. Buds break the latest among all willow species; flowering is also late, serotinous; capsules ripen only in the second half of the summer, and seed dispersal continues over the winter and into the next spring. Aments with open capsules and cotton sticking out are persistent throughout the winter (Fig. 5-B). Aments are borne at tips of leafy branchlets 2–6 cm long. Capsules are glabrous, large (7–10, sometimes even 11 mm long at maturity), thick-walled, often reddish; their styles no longer than 1 mm. There are 4 to 10 stamens; anthers open almost simultaneously in all the flowers in the ament; however, anthers in a single flower do not open all at once. In each staminate flower, there are two nectaries, which are often many-lobed; in a pistillate flower there is a single entire nectary (rarely two nectaries).

All the species belonging to the group look very much alike. Differences are

pronounced with respect to shoot diameter and, to some extent, coloration; bud shape and location; type of trichomes on the leaf primordia in the bud and, accordingly, on the cataphylls (proximal, underdeveloped leaves on the shoot); leaf color; stomata distribution on the leaves; characteristics of bract apical parts; and also the average anther size.

All the species are very ornamental due to spectacular shiny foliage and regular, rather dense crowns. They undoubtedly deserve to be widely cultivated and used in the green industry.

1. *Salix pentandra* L.

Linnaeus 1753, Sp. pl., 1 ed.: 1016; Wimmer 1866, Salic. Eur.: 22; Camus A. et E. 1904, Monogr. saul. France: 96; Seemen 1908, in Aschers. et Graebn. Synopsis 4: 61; Toepffer 1925, in Kirchner, Loew u. Schroeter, Lebensgeschichte, 2, 1: 390; Krylov 1930, Flora Zapadnoy Sibiri [Flora of West Siberia] 4: 727, p.p.; Nasarov 1936, in Flora SSSR [Flora of the USSR] 5: 205, p.p.; Hultén 1950, Atlas N 578; Shlyakov 1956, Fl. Murm. 3: 55; Rechinger f. 1957, in Hegi, Ill. Fl. Mitteleur., 2 ed., 3, 1: 65. There is a number of old synonyms that have not been in use for about a hundred years; those are listed in Seemen and Camus.

Described from Sweden. Type specimen in Linnaeus' Herbarium in London.

Diameter of ordinary shoots (measured in winter or fall between the 3rd and 4th bud, counting from the apex of the shoot) is 1.7–2.2 mm; buds deviating from shoots at an acute angle [during winter] (though usually appressed to shoots before the leaves drop), lanceoloid or lanceoloid-oblong, acute or slightly pointed, but without beaks, almost round on the cross-section, sized 5–9 x 2.2–3.5 x 2.0–2.8 mm (Fig. 1). Upper leaf surface without stomata, rarely with a few, mostly along veins. Bracts mostly with 1–2 glands at apex. Stamen filaments 3.5–5 (6) mm long; anthers 0.5–0.6 (rarely 0.7) mm in dry specimens collected soon after pollen dispersal.

These characters are remarkably consistent all across the species distribution area (though the author did not examine specimens from England, France, and Spain).

At the northern limit, *S. pentandra* occurs only in the lowland and is restricted to the forest belt. The most typical natural habitats of *S. pentandra* across most of its area are sedge/bluejoint forested wetlands and transitional zones around sphagnum bogs.

Together with *Betula pubescens* Ehrh. and sometimes also depressed Scotch pine and Norway spruce, *S. pentandra* plays an important role in the formation of sparse canopy of these plant communities. Upon a forest clearcut, *S. pentandra* usually settles at moist forest edges and non-cultivated post-forest meadows, especially in depressions. At the southern limit, it is

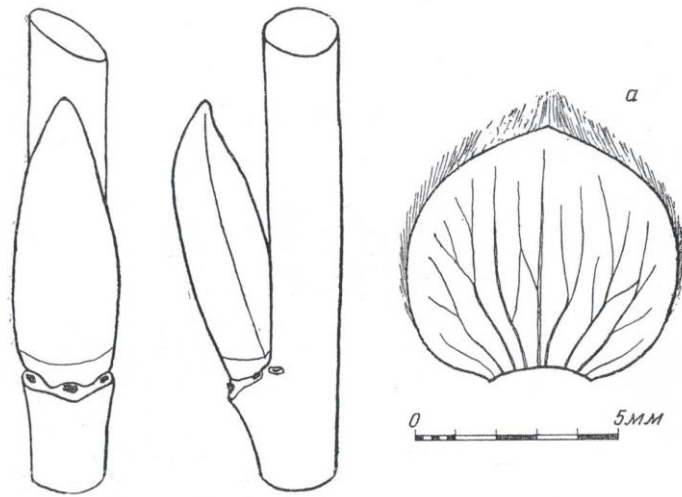


Fig. 1. Bud of *Salix pentandra* L.:
a – outermost leaf primordium, spread, view of outer surface

nearly entirely restricted to wetlands and mountains, ascending to 900–1000 m in the Sudetes and Carpathians; to 1400 m in the French Massif Central; and to 1900–2000 m in the Alps. In the forest-steppes of West Siberia, it occurs in small birch groves (*kolki*) at round shallow depressions on drainage divides (*zapadiny*). According to V.N.Andrejev (1957) and V.V.Ivanov (1949), at its southern limit, it grows in the floodplains of the Dnestr and Ural. Most often a small tree, in optimal situations bay-leaved willow can become nearly as large as brittle willow. The author observed trees to 15 m tall and 0.5 m DBH in the Oka River valley not far from the Town of Kashira. Toepffer (1925) mentioned the same maximal size.

Some sources assign *S. pentandra* to an area larger than its actual range. For example, the Czech *Forests and Hunting Atlas (Lesnický a myslivecký atlas 1955)* includes southern England, Normandy, French Mediterranean Coast, the entire Danube basin, steppes of the Northern Caucasus, and the Lower Volga. This apparently makes the geographic portrait of the species quite distorted.

2. *Salix pseudopentandra* Flod.

Floderus 1926, Arkiv. bot. 20A (6): 57 (pro subspecie); id. 1933, Arkiv bot. 25A (10): 12 (pro specie). – *S. pentandra* ssp. *pseudopentandra* Hultén 1928, Flora Kamtch. 2: 17; Nasarov 1936, Flora SSSR [Flora of the USSR] 5: 206. – *S. pentandra* auct. mult. (non L.); praesertim Komarov 1929, Fl. Kamch. 2: 7, map; Grubov 1955, Konsp. fl. Mong.: 101; Liou Tchen ngo 1955, [Ill. Fl. Lign. Plants NE China]: map; Popov 1959, Fl. Sredn. Sib. [Flora of Central Siberia] 2: 792.

Type: Kamchatka, Opala Volcano, July 19, 1921. E. Hultén N 2225, preserved in Stockholm (S) (isotype: LE!)

So far there has not been enough clarity regarding the taxonomic status, diagnostic characters, and geographic range of *S. pseudopentandra*. Initially it was described by Floderus in the subspecies rank. In his overview of the Anadyr willows (1933), he already treated it as a species, even though he listed *S. pentandra* L. s. str. for the same region. In the Flora of the USSR (1936), Nasarov made only a brief remark about ssp. *pseudopentandra*; yet in the Moscow University Herbarium, one can find Nasarov's annotations of 1935 on specimens from the Sayan Mts., which he identified as *S. pseudopentandra*. M.G.Popov (1959) stayed completely away from the epithet *pseudopentandra*.

While studying vast herbarium material, it has become obvious to the author that *S. pseudopentandra* Flod. constitutes a good species, quite distinct from *S. pentandra*. There exists a rather large area where the ranges of the two species overlap (Fig. 6); however, all samples collected within that area can be confidently assigned to either one or the other species. This refers, for example, to rather abundant collections from the former Minusinsk, Achinsk, and Kansk uyezds preserved in Leningrad. One curious sample (Kuznetskiy Alatau, August 24, 1935, V.V.Tarchevskiy) preserved in Yerevan is particularly remarkable in this respect. It consists of two branches mounted on a single sheet, one belonging to *S. pentandra*, the other to *S. pseudopentandra*. Both are immediately recognizable.

Morphological differences between the two species are in fact rather subtle; Floderus was able to note only a few of them. One of the most conspicuous and constant is the difference in the bud shape. In *S. pseudopentandra* buds are narrow-lanceoloid or narrow-pyramidal, with pointed apices often attenuating into somewhat flattened beaks (Fig. 2). Just as in *S. pentandra*, buds form an acute angle with the branchlet during the late fall and winter. Another very constant difference is the type of pubescence on the 2–3 outer primordia in the bud, that is, the first 2–3 leaves (cataphylls) on the young shoots in spring—a character noted by Floderus. In *S. pentandra*, cataphylls are fringed with silky cilia about 1 mm long at the very margin and are either glabrous or short sericeous on the outer (lower) surface (Fig. 1a). Upon the expansion of the shoot, one or two cataphylls fall off promptly, and the rest lose their silky trichomes. In *S. pseudopentandra*, the outer 2–3 primordia are not only fringed, but also crowned with a dense cluster of long (2.0–2.5 mm) trichomes on the lower (outer) side, near the summit (Fig. 2c); in those 1–2 cataphylls that persist on the young shoot, these trichomes are not caducous, but on the contrary, quite persistent. *S. pseudopentandra* is also quite different in its foliage

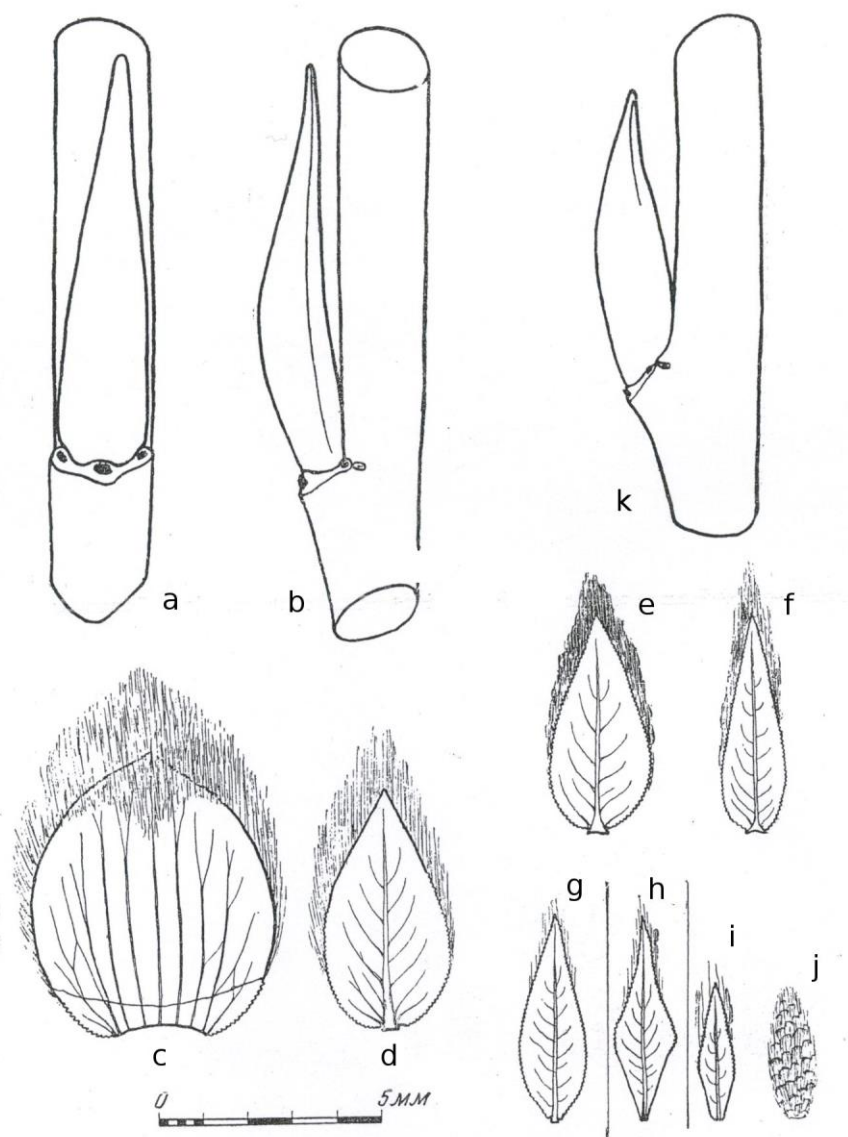


Fig. 2. Buds of *Salix pseudopentandra* Flod.:

a–b – most typical bud shape, sample from Upper Lena; c–j – content of the same bud; c – outermost leaf primordium (view of outer surface); d–i – the rest of leaf primordia (view of inner side); j – ament primordium; k – bud from Kamchatkan plant

color: it is rather pale or yellowish, while in *S. pentandra* the foliage is darker, more intensely green. Foliage tint is generally an important character in willows; however, we don't have enough means for its adequate depiction.

Upon considering large material, one can additionally identify the following important characters of *S. pseudopentandra*. Its leaves on average are narrower than in *S. pentandra*, cuneate at base, with less pronounced difference in color between the upper and underside. Dentation of the leaf margin is somewhat different: denticles are more rounded (a character noticed by Floderus). Resin production is more intensive. 1–2-year shoots are somewhat

flexuous; 2–3-year shoots are usually pale, whitish. Stomata are distributed on the leaf blade the same way as in *S. pentandra*. Aments can often be more loose than in *S. pentandra* or else of the same density. Stamen filaments are 2.5–4.0 mm long, anthers 0.4–0.5 mm long. Bracts are glandular at apex.

S. pseudopentandra has East Siberian distribution with an extension into the Manchurian Floristic Area. The northernmost point is Ozhogino on the Indigirka; the eastern limit is at the Belaya River (a tributary of the Anadyr).

As to its ecology, *S. pseudopentandra* is generally similar to *S. pentandra*. In the southern part of the range, it occurs in wetlands, while in the north it inhabits moist depressions and larch forests in river valleys. In the Sayan and Altai Mountains, it reaches to the upper forest limit (while *S. pentandra* in the Altai generally occurs at lower elevations).

It is worth mentioning that there are samples with some characters of *S. pentandra* originating from the area around Balagansk, the Lower Zeya, and from the southern Maritime Province. They have rather dark, broad leaves, which are rounded (rather than cuneate) at the base; their anthers are less than 0.6 mm long. Of course this could be just individual variability; however, a quite certain geographic range of these deviations makes another explanation plausible. It is possible that within pre-Baikalia and in the Amur basin, there used to exist isolated relict loci of *S. pentandra*, later harbored by the spreading *S. pseudopentandra*. Their traces are now preserved only in the form of separate characters showing up here and there within populations of *S. pseudopentandra*.

3. *Salix pentandroides* A.Skvortsov

Skvortsov 1960b. Dokl. AN Arm. SSR 31 (5): 299. – *S. pentandra* auct. fl. Caucas., non L.; Boiss. 1879, Fl. Or. IV: 1184; Görz 1933, Feddes Rep. sp. nov. 32: 389 et 1934, 36: 225; Nasarov 1934, Sov. Bot. 4: 128; Grossheim 1945, Fl. Kavk. ed. 2, III: 27 and map 12.

Type: staminate sample—Kubanskaya Obl., mixed birch-pine forest in the Dzhalan-kol River Gorge, May 22, 1908, N.A. and E.A. Busch, in Yerevan Institute of Botany; duplicates in Leningrad (LE); pistillate samples—Northern Caucasus, Balkaria, bank of the Bashil-Sugusu River, September 1, 1939, R.A. Elenevsky; preserved in the Moscow University Herbarium.

This species is quite different from the two previous ones as far as the shape and position of the buds: appressed to shoots during the winter, broad, ovoid, obtusish, flat on the adaxial side (Fig. 3); also having on average stouter branchlets (2–2.5 mm); multiple stomata on the upper leaf blade surface; and glandless bract apex. As opposed to *S. pentandra*, which

not infrequently exhibits vine-red colors in young branchlets and buds, all of the studied *S. pentandroides* produced shoots and buds of just olivaceous- or reddish-tawny tints. When comparing large sets, one can also observe a difference in petiole length: 6–12 (15) mm in *S. pentandra* and 3–8 (10) mm in *S. pentandroides*. Anther length in *S. pentandroides* is 0.5–0.8 mm.

S. pentandroides inhabits forest and subalpine zones, mostly within 800–2200 m range. A collection from the highest known locality is from Kelsk Volcanic Plateau, ca. 2700 m (made by V.Kreczetowicz, preserved in LE), mostly along brook banks and high-elevation wetlands. There is no data confirming its occurrences at lowland wetlands; it appears to be, in particular, absent from Colchida Depression.

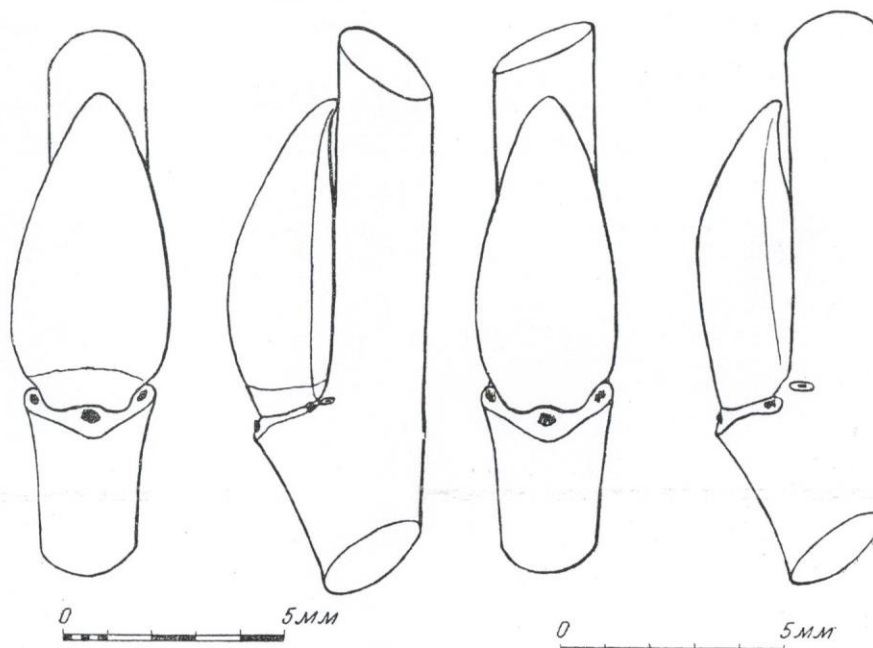


Fig. 3. Bud of *Salix pentandroides* A.Skv.

Fig. 4. Bud of *Salix serissima* (Bailey) Fern.

4. *Salix serissima* (Bailey) Fernald

Fernald 1904, *Rhodora* 6: 6; Schneider 1919, *J. Arnold Arbor.* 1: 1; Ball 1921, *Bot. Gaz.* 72 (4): 220; id. 1926, *Canad. Field-Natur.* 40: 145; id. 1949, *Madroño* 10: 84, cum mappa; Raup 1943, *Sargentia* 4: 92, cum mappa; Fernald 1950, *Gray's Manual* Ed. 8: 505; Gleason 1952, *Britton and Brown Ill. Flora NE US*, Ed. 3, 2: 8; Scoggan 1957, *Flora Manitoba*: 230; V.Bailey 1958, *Amer. Midl. Nat.* 59: 438. – *S. lucida* var. *serissima* Bailey 1887, *Bull. Geol. Nat. Hist. Surv. Minnesota* 3: 19. – *S. lucida* auct. malt. prausertim hortul. europ., non Muhl.

Type: Minnesota, Mud River, Lake Vermilion, July 28, 1886, Arthur, Bailey, and Holway B357, in *Columbian Field Museum*, US (Fernald 1904).

The author had access to 15 herbarium samples (13 in LE), which provided him enough insight into the morphology of the species.

S. serissima is much like *S. pentandroides*: its buds are rather broad, lanceoloid or ovoid, more or less flat on the adaxial side; appressed to shoots during the winter (Fig. 4, observed in a cultivated clone). Bracts were eglandular in all studied samples; anthers rather large (0.6–0.8 mm). However, leaves are without stomata on the upper surface or having very few along the midvein. Petioles are comparatively long. Bright red tones are prominent in the coloration of shoots and young buds. On the whole, *S. serissima* morphologically appears to be somewhat intermediate between *S. pentandra* and *S. pentandroides* (Fig. 5A).

S. serissima is distributed in eastern temperate North America (Fig. 7). Even though around the Hudson Bay its area extends into sub-Arctic, it matches the distribution of the rich hardwood forest with Tertiary elements around the Great Lakes and along the Atlantic Coast. The range of the willow concurs with ranges of such plants as *Asimina triloba* (L.) Don., *Cercis canadensis* L., *Magnolia acuminata* L., *Liriodendron tulipifera* L., *Platanus occidentalis* L.,

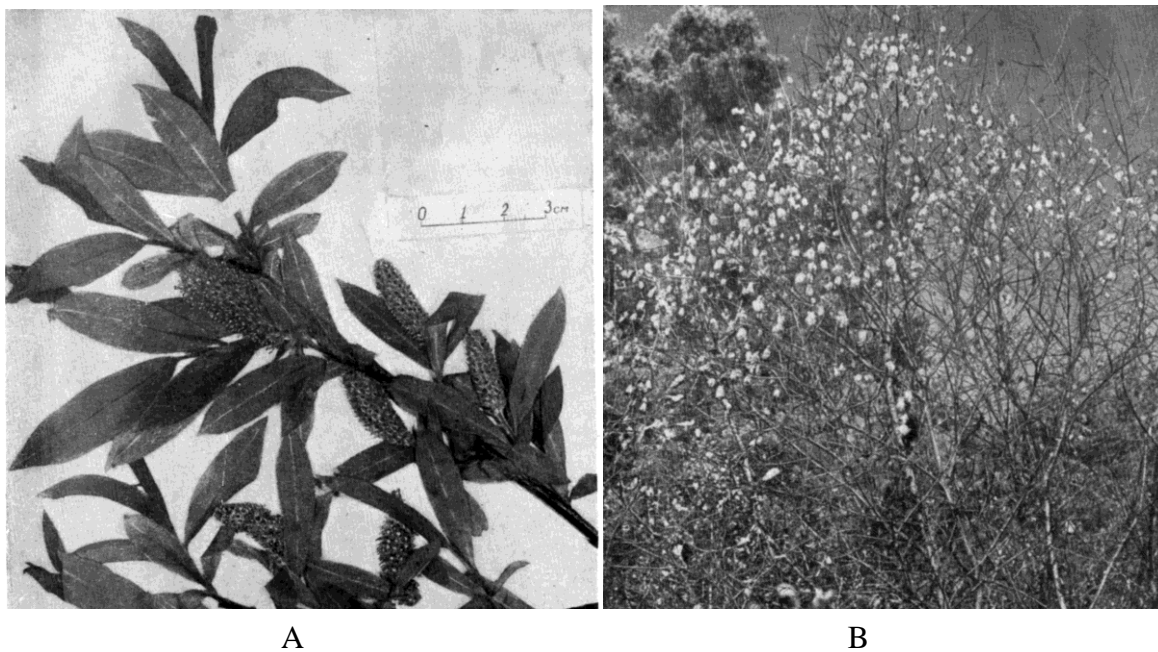


Fig. 5. A. *Salix serissima* (Bailey) Fern. sample from Alberta, Canada. Wetland in an interdunal depression near Fort Saskatchewan. June 10, 1939. G.H. Turner (1265).

Herbarium of the Main Botanic Garden, Moscow

B. *Salix pentandra* L. in late October. Vicinity of L'vov [Ukraine]. Photo taken by the author

Nyssa sylvatica Marsh., *Sassafras albidum* Nees, and others. Its isolated locations are known in Colorado (Rocky Mts. National Park) and along the western border of South Dakota. As to its ecology, *S. serissima* most probably has much in common with *S. pentandra* and *S. pseudopentandra*, occurring mostly in wetlands and wet meadows. In Colorado it ascends as high as 2500–2600 m.

S. serissima has been sometimes included in the horticultural collections of this country, though under the name "*S. lucida*,"—probably because it was introduced at the time when the Americans themselves could not separate these two willows. Meanwhile, as it has been already said, *S. lucida* is definitely a representative of a different cycle.

S. lucida is characterized by narrow, lance-shaped cataphylls, bud scales remaining alive through the winter, pubescent young shoots and leaves, and well-developed, persistent stipules that are lacking glands on the upper side. The leaf apex is always long-attenuate forming a very thin point; capsules are small (6–7 mm long), thin-walled, their stipes 1.0–1.5 mm long. None of these characters are found in the species group *Pentandrae s. str.*

Likewise, the western North American species *S. lasiandra* Benth. should not be included in the group *Pentandrae s. str.* (some authors recognize its northern race as a separate species, *S. lyallii* (Sargent) Heller). In *S. lasiandra* leaves are glaucous on the underside; stipules are mostly well developed, often gnawed; capsules not large (4.5–7.0 mm), their stipes 1.5–2 mm long. *S. lyallii* is additionally characterized by pubescent young leaves and shoots. Regarding smallish capsules on large stipes and particularly leaf characteristics, *S. lasiandra* and *S. lyallii* somewhat resemble *S. fragilis*. On the whole, these species as well as *S. caudata* (Nutt.) Heller are the closest to *S. lucida*.

5. *Salix paraplesia* C.Schneider

Schneider 1916, Sagent, Pl. Wilson. 3, 1: 40; Görz ex Rehder and Kobuski 1932, J. Arnold Arbor. 13, 4: 387; Hao 1936, Feddes Repert. sp. nov. Beih. 93: 48; Walker 1941, Contrib. US Nat. Herb. 28, 4: 606.

Type: Western Szechuan, Tachien-Lu, June 1904, E. Wilson (4518) in Herbarium of the Arnold Arboretum, Harvard University, USA.

I located 5 samples of *S. paraplesia* in Leningrad Botanical Institute—collections of Berezovsky from Szechuan, Przhivalsky and Potanin from Gansu: staminate specimens in flower and pistillate in fruit. The Arnold Arboretum Director Prof. Richard Howard and Dr. George Argus were so kind as to provide information on Schneider's type specimens. Dr.

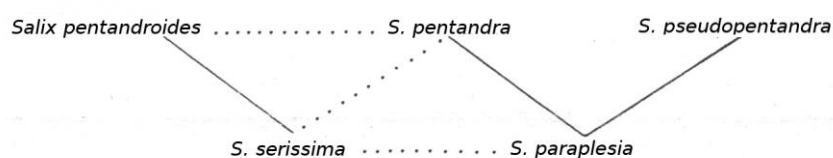
L.B.Smith from the US National Herbarium kindly sent a photo and fragments of samples cited by E.H.Walker (1941).

In all the examined samples, *S. paraplesia* had comparatively slender and somewhat flexuous shoots. Buds were rather small (to 5 mm long), narrow triangular-lanceoloid, acute, closely appressed (when observed on leafy branchlets). Cataphyll trichomes short, caducous. Leaves markedly bicolored (however, the glaucous bloom, whose presence could be implied from Schneider's descriptions, was missing); without stomata on the upper side. Bracts were glandular-serrate in some samples, entire in others; anthers small (0.4–0.5 mm).

S. paraplesia is a shrub or small tree to 6 m tall. It is distributed from southwestern Szechuan to Upper Huang He (Yellow River) and Lake Kokonor in Gansu Province, where it dwells at 2600–3600 m. According to Hao (1936), it is also known from Shensi (Shaanxi), Shansi (Shanxi), Hupeh, Hunan, and even from Zhejiang (the latter, however, appears somewhat doubtful).

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The facts listed here above can be interpreted as follows. From the purely morphological viewpoint, the relationship between these species can be depicted in the following sketch:



S. pseudopentandra here occupies the most isolated position due to characteristic bud shape, cataphyll pubescence, and leaf color. These characters make it very different from *S. pentandra*, *S. serissima*, and *S. pentandroides*, which appear to be rather similar to each other. *S. paraplesia* morphologically partially resembles *S. pseudopentandra* (slender shoots, narrow, acute buds, small anthers); in other respects it is similar to *S. pentandra* (bicolored leaves, cataphyll pubescence). The similarity between *S. paraplesia* and *S. serissima* is not that obvious (in *S. serissima* bracts are without glands, anthers and buds are larger), and even less so between *S. paraplesia* and *S. pentandroides* with its large buds, short leaf petioles, and abundant stomata on the upper leaf side.

Considering the overall morphological data, *S. paraplesia* is to be regarded the closest to the group ancestor. Of course statements like this are always largely hypothetical, and

especially as regards a group where morphological differences between species are comparatively subtle and a possibility of independent convergent development of characters cannot be excluded. However, the following observation makes it more probable: among the most primitive groups of *Salix*, this is sect. *Glandulosae* Kimura that appears to be the closest to *Pentandrae*. The most widely distributed and perhaps the only one species of this section, *S. glandulosa* Seemen, also exhibits slender shoots, small, acute buds, and small anthers.

Let's now consider the geographical distribution of these species. As far as the area of *S. pentandra* is concerned (Fig. 6), it is principally similar to areas of such species as *Tilia cordata* Mill. (including *T. sibirica* Fisch.), *Orobus vernus* L., or *Viola mirabilis* L. (see maps, e.g., Lipmaa 1938). In other words, its area matches that of central and north European and West Siberian mesophilous forest flora. Within Europe, this area closely fits that of European spruce; within West Siberia, the range of spruce/birch forests.

Stretching from Mongolia to the Kolyma and Anadyr Rivers, the area of *S. pseudopentandra* (Fig. 6) represents a completely different distribution type. Its connection with the East Siberian domain of larch forests is obvious. I believe that even a comparison of its range with that of *Caragana jubata* (Pall.) Poir. would be legitimate. Of course any ecological differences should not be considered an obstacle for such a comparison. (At times one can notice a tendency in literature to take for granted—either deliberately or unconsciously—that all species representing a certain element of a flora should also be similar ecologically. Yet is it reasonable to assume that the territory where the flora development takes place would be uniform in terms of relief, moisture, energy balance, or rock composition?)

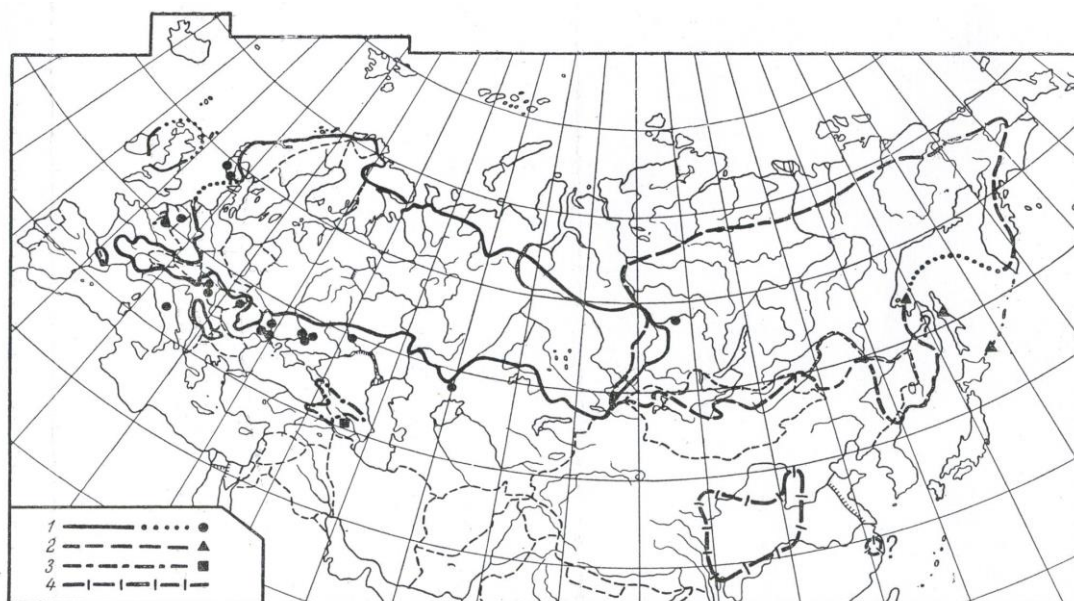


Fig. 6. Ranges of Eurasian species belonging to group *Pentandrae s. str.*
 1. *S. pentandra* L. 2. *S. pseudopentandra* Flod. 3. *S. pentandroides* A.Skv. 4. *S. paraplesia*
 C.Schneider



Fig. 7. Range of *Salix serissima* (Bailey) Fern. Compilation based on data in American literature. Dots correspond to northernmost localities that determine the northern species limit and to isolated localities in South Dakota, Colorado, Newfoundland, and Anticosti Island.

One can conclude that the *S. pentandra*/*S. pseudopentandra* pair is profoundly different from such examples as *Hepatica nobilis* Mill. and *H. asiatica* Nakai, *Anemone nemorosa* L. and *A. amurensis* (Korsh.) Kom., *Corydalis halleri* Willd. and *C. remota* Fisch., *Convallaria majalis* L. and *C. manshurica* Kom., *Carex pilosa* Scop. and *C. campylorhina* Krecz., *Salix triandra* L. and *S. nipponica* Fr. et Sav., or *S. caprea* L. and *S. hultenii* Flod. While we can assume that species separation in these pairs must have occurred during early Quaternary or late Tertiary time, formation of *S. pentandra* and *S. pseudopentandra*, now belonging to completely disparate genetic elements of the flora, must be ascribed to a much earlier time.

A close analogy to their relationships could be traced in another species pair: *Ramischia secunda* (L.) Garcke and *R. obtusata* (Turcz.) Freyn. These two species used to be confused with one another for a long time or else delimited on unconvincing grounds; meanwhile, each of the two represents an authentic genetic element (Skvortsov 1960c). *R. secunda* exhibits a

range similar to that of *Millium effusum* L., *Convallaria majalis* s.l., and even *Salix pentandra*. The major difference from *S. pentandra* is the presence of a significant Far East portion in *Ramischia secunda* range. (*S. pentandra* either never had or has lost that part, the latter scenario being not improbable.) As to the range of *Ramischia obtusata*, it is quite similar to that of *Salix pseudopentandra*, even more closely following the range of *Caragana jubata*—especially if we take into account that within the Tien Shan, Pamir-Alay, and Kashmir, where *Caragana jubata* range is reaching, there is a species of *Ramischia* very closely related to *R. obtusata*: *R. kareliniana* A.Skv. However, this parallel between *Ramischia* and *Salix* species is restricted to the Old World, as in North America, where both *Ramischia* species are rather widely distributed, the willow species *S. pentandra* and *S. pseudopentandra* are missing.

Curious morphological similarity between *S. pentandroides* and *S. serissima* may spark even more interest if one pays attention to the overlap of *S. serissima* range in its southeastern part with the ranges of such plants as *Castanea dentata* Borkh., *Carpinus caroliniana* Walt., *Celtis occidentalis* L., *Ostrya virginiana* (Mill.) K.Koch, *Smilax hispida* Muhl., or *S. rotundifolia* L. In the rest of its range, *Salix serissima* reaches colder northern and northwestern regions.

Very similarly to this, the range of *S. pentandroides* partially overlaps with those of *Castanea sativa* Mill., *Carpinus caucasica* Grossh., *Celtis caucasica* Willd., *Ostrya carpinifolia* Scop., *Smilax excelsa* L., while the rest of *S. pentandroides* area covers colder alpine areas. Apparently, one should conclude that both *S. serissima* and *S. pentandroides* represent the cool-temperate Tertiary deciduous flora.

A disjunction between *S. paraplesia* and *S. serissima* ranges is also worthy of attention. No doubt this is another remarkable example of an East Asia/eastern North America disjunction, a phenomenon well known from the time of Asa Gray. As it was noted by Li (1952), the basin of the middle and upper reaches of the Yangtze is the area containing the most elements related to those in eastern North America. *S. paraplesia* was described precisely from that area. Many of disjunct species areas used by Li as examples are very closely following the areas of our two willows, for example, species of *Stylophorum* or *Gymnocladus* (Li 1952: maps 18, 25). Similarly to the ranges of *S. serissima* and *S. pentandroides*, the range of *S. paraplesia*, while partially overlapping the area of hardwood Tertiary flora, significantly extends to colder mountainous regions. Therefore, *S. paraplesia* should also be treated as a representative of the cool-temperate component of the Tertiary flora.

Li believes that the connection of East Asian and eastern North American plants is most

pronounced in warm-temperate and subtropical species, while cool-temperate and Arctic Asiatic species are mostly connected with western North America. Apparently our material testifies in favor of some corrections to this statement.

Let us now cast a glance at the distribution of all the five willow species of the sect. *Pentandrae*. The development of contemporary temperate floras in the Northern Hemisphere may be rather effectively illustrated with this example.

As it could be derived from the morphological analysis, the central, key position in the group shall be assigned to *S. paraplesia*. The distribution of this species adds an argument in favor of such a hypothesis. The range of *S. paraplesia* to a large extent lies exactly within the area that more than any other area can be considered the cradle of today's temperate flora. (For justification of this concept, see Fedorov (1957) and Takhtajan (1957).) More than that, *Glandulosae*, a section closely related to *Pentandrae*, though more primitive (and generally one of the most primitive in *Salix*) consisting of subtropical (and perhaps even tropical, like *S. warburgii* Seemen on Taiwan) species is restricted exclusively to Japanese-Chinese flora. This fact leaves us even less doubt regarding the East Asian origin of the group *Pentandrae*.

This makes it obvious that data on willow systematics and geography are no less suitable for historical geography studies than material on any other angiosperm group. However, it is plausible to start with narrowly delimited groups—sections or even section parts. Each group has to be natural and studied taxonomically in enough detail.

R.Scharfetter (1953: 411) believed that historical research could be successful only when a genus was considered in its entirety. His attempt to apply this approach to willows has proved that his starting thesis was completely erroneous. It was precisely the starting message that caused his failure to project his phylogenetic scheme (questionable, the way it was) onto the timeline. Upon arbitrarily choosing 27 Central European species from the world's willows, artificially separating them from their relatives distributed elsewhere in the world, and arbitrarily including 17 of these in one superficial group 'Mononectariae' (thus uniting representatives of 9 different sections!), Scharfetter found it possible to state that all the differentiation within this group took place during the postglacial time!

Had Scharfetter exercised a wider approach familiarizing himself at least partially with American and Asiatic species, he would have inevitably concluded that the group, which he considered to be a compact phylogenetic cluster with a single stem existing even as late as the late Glacial, was in fact composed of only the tops pruned off of a number of very different genealogical lines, whose stems date as far back as early Tertiary. All the sections represented

in Central Europe (except for the ancient, but probably monotypic section *Incanae*) have their representatives on other continents. Most of these sections are as compound as section *Pentandrae*, each comprising a few subsections or cycles, in turn, consisting each of a few rows. Within the rows, ancient disjunctions are not uncommon.

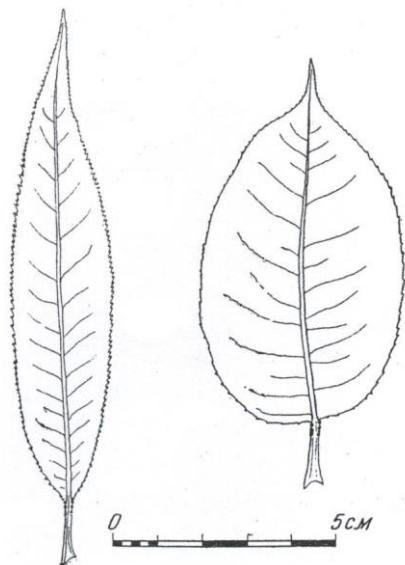


Fig. 8. Range of individual (genotypic) variability in leaf shape of *Salix pentandra* L. Contours of two leaves, which are normally developed, taken from normal, non-hybrid individuals. Both collected in the same locality: near Volgoverkhovye [at the Volga River origin], Ostashkov District, Kalinin [Tver] Oblast on August 17, 1936 by T.Trofimov. Moscow University Herbarium. Such differences do not have any taxonomic value.

It can be concluded that, with respect to slowness of evolutionary changes and consistency in preservation of some very particular morphological characters throughout historic epochs as well as across continents, willows perhaps are even ahead of many other angiosperm groups.

Of course this does not prevent willows from varying enormously (to some extent, geographically and ecologically, but mostly individually) with respect to other characters, which are not of taxonomic importance. In sect. *Pentandrae*, examples of these non-essential variable characters would be absolute dimensions of leaves and length-to-width ratio, ament length, stamen number, shape of nectaries, bract shape and pubescence, and others. Fig. 8 can serve as an illustration of leaf variability in *S. pentandra*.

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