

TRANSLATOR'S NOTES

Thirty years have passed since this book was published in Russian; yet it remains the only reliable source of data and manual for those who want to know the willows of Russia and adjacent countries. Books like this should be available to readers worldwide.

English-speaking readers of this book have to keep in mind the following details concerning names and notions.

Before 1917, major administrative units within the territory of Russia were called governments. During the Soviet and Post-Soviet time, governments were and are now named *oblast's* (*oblast* means *area*). Some of the larger ones are called *kray's*. *Kray* sufficiently corresponds to *province*, hence *kray's* will be called *provinces* here.

Oblast's and provinces are divided into smaller entities called *rayon's*, which may well correspond to *districts*. Each province, oblast, and district has its central city or town.

Names of provinces, oblast's, and districts are adjectives derived from names of their capitals: *Tambovskaya Oblast* is a derivative from *Tambov*, *Krasnoyarskiy Province* from *Krasnoyarsk*, *Krasnoyarskiy District* from *Krasnyy Yar*. In English, flexions are optional, so that one may say either *Moscow Oblast* or *Moskovskaya Oblast*, *Tver Oblast* or *Tverskaya Oblast*, and so on.

Since the time this book was published in Russian, the political map has changed tremendously. Entire countries have disappeared (like the USSR or East Germany), or emerged (like Ukraine or Czech Republic), or changed their names (like Belarus, formerly Byelorussia). Many cities restored their original names after the collapse of the Soviet regime: St. Petersburg, Nizhniy Novgorod, Samara, Tver, Bishkek, and others. Some of the states that became independent denied russified spellings of their cities' names: Tallinn in Estonia, Ashgabat in Turkmenia, and many others. In the translation, I used different approaches when dealing with this problem. One can find references to "old" and "new" names. Some of traditional Russian spellings (like Ashkhabad) are retained, as they are still used in Russia, others are abandoned (Beijing is used instead of Peking). One particularly curious situation is to be mentioned here in order to avoid confusion: when the authorities in Leningrad made their decision about restoration of the original name, those ruling the oblast did not oblige. Therefore, Leningradskaya Oblast still retains its name of the Soviet period, while its center is called St. Petersburg.

To facilitate a better orientation of the reader, an index of geographical names with brief explanations has been added as a supplement.

Some traditional expressions of the Russian physical geography are unfamiliar to English-speaking readers. For example, there exists a commonly used term for the temperate climate territory within the European part of Russia. In Russian, it sounds like *srednyaya polosa* (which literally means *the Middle Stripe*). Here, we will call it *the European temperate belt*. Another expression describes the territory of European Russia north of the fertile chernozem soil area: *the non-chernozem belt* (versus *chernozem belt*).

There is some confusion in understanding the name *Central Asia*. In Russia and the USSR, traditionally, Central (*Tsentralnaya*) Asia was understood as the territory of the Tibet and Mongolian Plateau, while the term *Middle* (*Srednyaya*) *Asia* was retained for the southern states, formerly republics of the USSR, now independent: Kirghizia (Kyrgyzstan), Uzbekistan,

Tadjikistan, Turkmenia (Turkmenistan), and a part of Kazakhstan. In the English-speaking countries, the situation is different. Webster's Geographical Dictionary formerly advised to use the name *Soviet Central Asia* for what was *Middle Asia* in Russian. This convenient option is obviously not available any more. In the Oxford Atlas of the World (1997), the territory of the former southern Asiatic republics of the USSR is called merely *Central Asia*, which may bring about some confusion. In this translation, we will stick to the term *Middle Asia*. It sounds somewhat outdated (the name *Middle Europe* was also abandoned for *Central Europe*), yet it helps to discriminate between two different territories, though the "real" Central Asia is mentioned in the book just some few times.

In Russia, a trivial way to name territories close to prominent objects is to derive their names from names of these landmarks with the help of prefixes *cis-* or *pre-* (*pri-*) or *trans-* (*za-*). That has some correspondence in English, but not fully. Common examples of translated names are *Transcaucasia* (*Zakavkazye*), *Transbaykalia* (*Zabaykalye*), and *Transcarpathia* (*Zakarpatye*). *Ciscaucasia* does not sound that perfect, although it is acceptable (I preferred *the Northern Caucasus* as a synonym). In Russian, there exist more names of that kind, which are unfamiliar to English readers. I tried to translate them using this uniform approach: and hope that *Prepolar Urals*, *Pre-Uralia*, *Trans-Uralia*, *Prebalkhashia*, *Trans-Onega Region*, and other *pre-* and *trans-* names will find their way when introduced to English.

Physical geographers of Asiatic Russia recognize a peculiar vertical zone of scanty alpine vegetation that develops in the severe conditions of East and Northeast Asia, *goltsy* (pl.), which may be translated as *barren heights*. Every particular mountain that is topped by vegetation of that kind is as well called *golets* (sing.). The territories below the barren heights are distinguished as yet another vertical zone, the name for which may be expressed as *subgoltsy*. However, this sounds awkward, and I used a descriptive expression *around barren heights* instead.

Wetlands is the term used to express the general meaning of the Russian *bolota*, except the cases when it was possible to distinguish bogs, fens, swamps, and other types from the context.

Some proper names (last names as well as geographical ones) have two spellings in this book: in English and Latin, such as *Görz* (*Goerz*), *Nazarov* (*Nasarov*), *Shlyakov* (*Shljakov*), *Polyakov* (*Poljakov*). Some, like *Lakschewitz*, have the latinized version only, the way they are known in the literature.

There is a number of local geographical terms that hardly have any analogs in other languages. These are retained and italicized in the text unless they constitute parts of geographical names, like "Bor" or "Kryazh". One can find their explanations on the following list.

LIST OF RETAINED LOCAL TERMS¹

Bor — Russian, a dry pine forest (e. g., Buzulukskiy Bor).

Golets (sing.), *goltsy* (pl.) — Russian, a barren height; in Siberia, a mountain that is higher than the upper forest limit, covered with the alpine tundra vegetation or without vegetation (e. g., Arshan Golets).

¹ The explanations of these terms are translated and adapted from a Russian geographical reference book (F. Milkov, 1970. A reference book on physical geography. *Mysl* Publishers, Moscow.)

- Kolok* (sing.), *kolki* (pl.) — a small grove, mixed-wood, or aspen (on the Russian Plain), or birch (in West Siberia), within the forest-steppe belt.
- Kryazh* — a chain of hills, usually, a remnant of eroded uplands (e. g., Yeniseiskiy Kryazh).
- Layda* — Finnish, a meadow on the Arctic Ocean Coast occupying a slanting shore that is flooded during high tides.
- Loshchina* — Russian, an ancient linear erosional depression with high, steep slopes that has surface runoff.
- Lozhbina* — Russian, an ancient linear erosional depression with slanting slopes that has surface runoff.
- Oblast* — Russian, territorial and administrative unit with a central city (its name constitutes an adjective derived from the name of the city); districts (*rayon*'s) are subordinate entities with smaller cities and towns as centers.
- Pad* — in Siberia and the Far East, a deep valley or shallow depression, often forested, usually having a stream on its bottom (e. g., Kedrovaya Pad Preserve).
- Plavni* (always pl.) — in southern Russia and neighboring territories, parts of flood plains of large rivers that are flooded during most of the year and develop a dense cover of *Phragmites*, *Scirpus*, *Typha*, *Carex*, and other water-loving plants.
- Sai* (pl.) — in Kazakhstan and Middle Asia, gullies, ravines, or dry beds of seasonal streams.
- Saz* (sing.), *sazy* (pl.) — in Middle Asia, a paludal, often saline meadow in the mountains. *Sazy* are very typical for the *syrt*'s in the Central Tien Shan as well as Pamirs.
- Solonchak* — a kind of saline soil in the desert or semi-desert belt, rarely in the steppes; a territory having the soil of that kind.
- Sopka* — 1. in Transbaykalia and the Far East, a round-topped hill or mountain.
2. on the Kamchatka Pen., a volcano (e. g., Klyuchevskaya Sopka).
- Stolby* (always pl.) — in Siberia and the Urals, distinct rocks of peculiar shapes formed as a result of the erosional process (e. g., Stolby near Krasnoyarsk).
- Syrt* — in Kazakhstan and Kirghizia, an elevated plain area: watershed plateau or uplands. *Syrt*'s may vary as regards their elevation from about 300 m (the watershed area between the Volga and Ural rivers) to high elevations (in the Tien Shan).
- Tugai* (pl.) — forested territories in flood plains or valleys of large rivers in Middle and Central Asia; the forests mostly composed of poplars, willows, and tamarisks.
- Yernik* — in Siberia and the Far East, a dwarf birch shrubland (sometimes together with low or creeping willows) in the tundra belt, or on bogs in the forest belt, or on barren heights.
- Zapadina* — Russian, a shallow depression of a round shape with enclosed drainage on a flat drainage divide in the steppe or forest-steppe belt.

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FOREWORD TO THE ENGLISH EDITION

I could never have foreseen the possibility of publishing my book on *Salix* in English. The idea belongs to my younger friend, Alexei G. Zinovjev. Only thanks to his energy in solving all problems connected with the translation, editing, and publication, this book is coming into existence. Unfortunately, being densely occupied by other responsibilities, I have not been able to undertake any substantial revision or updating. All new species and nomenclature combinations mentioned in this translation were proposed in the original publication of 1968. (The pagination of the original publication is shown in the margins for easy references.) Citation of the literature remains the way it was back in 1968. Only a few purely technical faults detected in the original edition have been corrected. And, to meet the new political realities, relevant changes had to be introduced into paragraphs treating the geographic distribution of species. As a kind of partial substitute for updating, I am supplying here the following enumerations: new *Salix* species described since 1966 from the geographic area treated in my book; my own publications on *Salix* since 1967; and the most important publications by other authors.

My cordial thanks are due to Alexei G. Zinovjev for his indefatigable pushing of everyone's efforts (including my own as well); to Irina N. Kadis for her interested and careful translation; to the Arnold Arboretum of Harvard University for the financial support of the preparation of the book; to the Department of Biology at the University of Joensuu for granting the use of their facilities and promotion of the publication; to Jorma Tahvanainen and Heikki Roininen for all their help and inspiration during the editing and publishing process; and, of course, to my old good friend, George W. Argus, who has taken up the tedious task of the scientific recension of the manuscript.

March 1, 1999

A. Skvortsov

*To my parents
with infinite gratitude*

FOREWORD

The genus *Salix* is one of the largest in the flora of the USSR and the largest one in the dendroflora. In the majority of the USSR regions, willows play an important role in the vegetation structure and are commonly utilized for a variety of purposes. In well-watered habitats, particularly, river valleys, banks of streams, and lake shores, willows are nearly always among dominating plants. In the forest belt, they are as well found in other habitats. In the vegetation cover of the forest-tundra and tundra, their role is especially prominent. Among our arborescent species, willows are the ones reaching the highest latitudes in the north. Only dwarf birches and some heather species can compete with them. In the subalpine and alpine zones of many mountain systems, willows are nearly as important as in the arctic regions: in the mountains, as well, very few arborescent plants can ascend as high as willows do.

In the economics, the willows are used in many different ways. They are a source of cheap wood, the main or even the only one in many regions. They are indispensable for stabilization of soil on slopes and banks and fixing of sand. As ornamental plants, weeping and white willows along with red osiers are most popular; however, the assortment of ornamental willows may be further enriched. Willows are also excellent forage plants: their foliage and young shoots are favorites of sheep, goats, cattle, and reindeer. The ability of willows to bloom very early in spring makes them particularly valuable as nectariferous plants. They are as well utilized as a source of various chemical compounds, such as tannin or salicin. They provide excellent material for wickerwork and shaft bows: baskets, furniture, yurt frames, and vine stalks are made of willows. Naturally, different species are more or less suitable for different purposes.

In spite of wide distribution and various applications, the willows are still insufficiently known as regards their systematics. Poor knowledge of the willow systematics constitutes a problem when regional vegetation is being described in detail. It is also an obstacle for appropriate utilization of willow species. Confusion in the systematics of the genus *Salix* affects general botanical research in such areas as, for example, segregating of botanical districts or study of development of cryo- and mesophilic floras.

The genus *Salix* has been long considered to be a difficult one for the systematics. "Species of this genus are extremely difficult to clarify" (Linnaeus)¹. "In temperate and cold regions, countless willows are strikingly, luxuriously inconstant in their habits, which is a matter of trouble and confusion for botanists" (Endlicher)². "The genus is notorious for the variation that occurs

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¹ "Species huius generis difficillime extricantur" (Linné 1753: 1022).

² "In temperatis et frigidiusculis hemisphaerae borealis utrinque continentis innumerae Salices mira formarum inconstantia luxuriant, botanicorum crux et scandalum" (Endlicher 1841: 178).

within species, and for poor definition of morphological boundaries between many of the commonly recognized species" (Raup 1959: 7).

The major causes of that "notoriousness" of the genus are considerable genotypical polymorphism of species and a large range of specimens' variability together with intricate differences between some species (see chapter 3, section 4). Two more circumstances complicate the whole picture. The first one is sex differentiation of plants and different time of development for flowers and leaves, which prevents the observer from seeing all relevant characters on a single plant. The second complication is comparatively high frequency of natural interspecific hybrids.

Among numerous Russian researchers who studied the willows, the most prominent were R. Trautvetter, E. Wolf, P. Lakschewitz, and M. Nazarov. Works of a number of West European and Japanese researchers were as well of great importance. M. Nazarov summarized knowledge and notions acquired by 1935–36 in his review of the genus *Salix* compiled for the "Flora of the USSR" (volume 5, 1936). Authors of nearly all of subsequent "floras" and other publications on the systematics of the willows used that work by M. Nazarov as a framework, either following his treatment completely or making only some insignificant changes (mostly describing new species). However, the review of the genus *Salix* in the "Flora of the USSR", though being very important and significant, was nothing more than a compilation which lacked critical revision of the material available by 1935–36. A critical approach would have made it possible to treat many facts in a very different way even at that time. More than thirty years passed since M. Nazarov finished his work. These were the years of intensive investigation of the flora of this country. Bulky new collections are now mostly concentrated in newly-developed botanical research institutions. New herbarium collections from Asiatic Arctic and the extreme Northeast as well as those from Yakutia, the Far East, and Middle Asia are particularly numerous. The USSR territory has become larger. The concept of the species and understanding of species criteria have developed considerably. Finally, abundant new literature sources have appeared, which need critical evaluation and comparison. Suffice it to say that new willow species that have been described since 1936 count 48.

These circumstances obviously reveal the necessity of a new critical treatment of the willows of the USSR.

The author started his research in 1949–51 with a study of the willows in the temperate belt of the European Russia during the wintertime. The study demonstrated that some morphological characteristics of the willow buds were very constant and of great taxonomical value. That made it possible to create a key for identification of those willows during the winter (Skvortsov 1955). In 1953, the author traveled around Alma Ata and along the Ili River. Attempts to identify specimens from Middle Asia revealed complete confusion in the taxonomy of the Middle Asiatic willows. That was the challenge that stimulated the author to start a thorough study of the willows. In 1955, the author got an opportunity to begin his regular work on the revision of the systematics of willows growing on the territory of the USSR.

Having been brought up as a biologist and systematist, the author considers the species limits to exist objectively. According to this notion, a space that a particular species occupies in nature constitutes its very important characteristic, indeed, not less important than any morphological or physiological characters of individuals belonging to that species. Therefore, the author was trying to equally divide his attention between geographical characteristics of species and their morphological characters and differences. The territory of the USSR is really huge, yet to be restricted by the USSR border means failure to provide complete geographical descriptions for

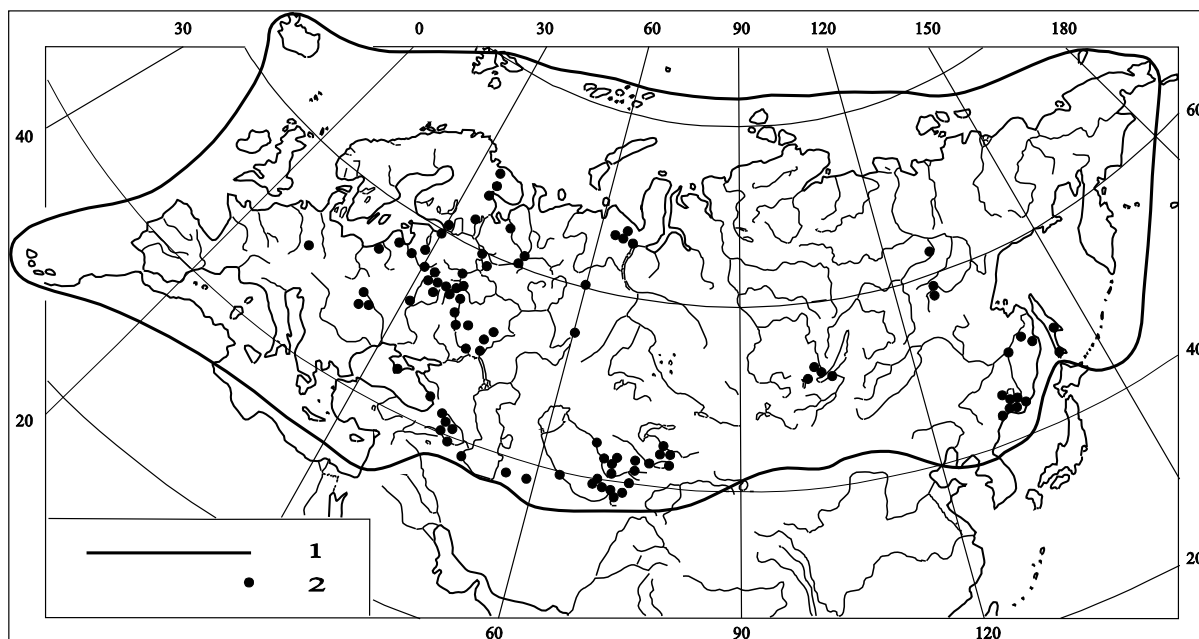


Fig. 1. Study area (1) and places of the author's own observations and collections (2)

the majority of species: their areas appear to be cut by political boundaries, and parts of areas beyond the borders remain unclarified. After a long period of hesitations, I made a decision to broaden my research in order to include a revision of the systematics of willows within floras of a number of adjacent and other closely located countries, particularly, those of Western Europe, Northern Africa, Asia Minor, and also the western part of China, Northeast China, Mongolia, and North Korea. That made it possible to present complete species ranges, at least their Old World parts. To accomplish this task, I had to include 18 European species alien to the USSR flora. See Fig. 1 for boundaries of the area under consideration.

We never know beforehand, which characters in any particular case will prove to be most important for species discrimination. Therefore, the most critical issue for the systematics of species is a possibility to study the largest possible number of characters in the largest possible number of specimens. Today, these are mostly traditional macromorphological characters that can be studied in accordance with that requirement. That is why consideration of these characters still remains the basis for the species systematics. The most effective methods are observations in nature, studies of herbarium collections, and, to a lesser extent, observations of cultivated plants. According to the literature data, the study of chromosomes is so far practically useless for the systematics of the willows; preliminary results of the research done by my colleague, M. Golysheva, appear to be similar. Therefore, I did not use the caryological method. The investigation of leaf anatomy proved to be much more fruitful.

Results of the research revealed that the real species composition of the USSR willows is very different from the one described in the literature. For example, of 203 species named in the literature for the USSR flora, 96 have proved to be synonyms and are to be eliminated from the list of distinct species. And this is not the matter of merely lumping "small" species into "large" ones. The author is by no means an advocate of "large" species-conglomerates. The matter is that the species have not been studied well enough. It is common knowledge that to "close" a species,

that is, prove its identity to another one described earlier, one has to study it much more thoroughly than to "open" it (all one has to do in order to "open" a species is to write and publish its description in Latin).

As the author proceeded with the work, some results were presented in separate publications (Skvortsov 1955–1968; Skvortsov, Golysheva 1966; Skvortsov, Derviz-Sokolova 1966). Contents of those publications is not duplicated here. Nearly all of comments and arguments regarding special problems of the taxonomy and nomenclature are omitted in this book as well as data on the leaf anatomy. However, one can find references to previously published material in appropriate places. Unfortunately, it was impossible to provide precise references to my review of the *Salicaceae* in the "Arctic Flora of the USSR", since by the time I finished working on the manuscript of this book, the review had not yet been published.

Due to restrictions regarding the volume of the book, I had to omit detailed morphological descriptions of species. Anyway, the presence of such descriptions does not appear to be critical in a publication addressed primarily to professionals. The possibility of applying the contents of the book for practical needs is provided through identification keys as well as diagnoses of sections and subsections.

On the other hand, I considered it important to include a few general chapters preceding the systematic overview. They constitute an introduction to the systematic part and, at the same time, contain essential conclusions and generalizations that may follow the systematic overview. A brief historical essay (chapter 1) may be of general interest even for taxonomists working on other groups as a certain piece of the history of the systematics.

The author hopes that this work will help to make our knowledge of the willows of the USSR and adjacent countries more consistent with modern achievements of systematics and floristics in these countries. By no means does the author feel that this work contains clues to all problems that exist in the area. Of course, a number of unsolved questions remain (see, for instance, notes to *S. saxatilis*, *S. rhamnifolia*, *S. phylicifolia*, or *S. rosmarinifolia*). New material and observations are needed to clarify them; there is no doubt that new problems will emerge with the future advance of the research.

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Finally, I would like to name a person who is very special for me. This is my first mentor in the field of systematics, P. A. Smirnov.

Part One: General Overview

Chapter 1

WILLOW SYSTEMATICS IN RUSSIA AND ADJACENT COUNTRIES: A BRIEF HISTORICAL ESSAY

1. EPOCH OF LINNAEUS

C. Linnaeus established 29 species of willows in 1753, and only one of these, *S. babylonica*, was of non-European origin. Later C. Linnaeus described three more species: *S. depressa* (Fl. Suecica, ed. 2, 1755), *S. aegyptiaca* (Centuria plantarum 1, 1755), and *S. retusa* (Species pl., ed. 2, 1763). However, *S. depressa* was treated as a synonym of *S. lanata* by the author himself (1763). Thus, there remained 31 species in all publications during C. Linnaeus' lifetime.

C. Linnaeus was keenly aware of special problems within the systematics of the genus *Salix* and was very careful with it. In his "Species plantarum", an important note follows the description of the genus: "Species huius generis difficillime extricantur. Solum palustre, arenosum, alpestre, calidum mutavit mira metamorphosi species, ut de iisdem hesitarint saepius Botanici... Incipienda itaque harum historia e novo..." (Linnaeus 1753: 1022). He was extremely cautious in recognizing species absent from Scandinavia. There were eight: *S. triandra*, *S. babylonica*, *S. helix*, *S. rosmarinifolia*, *S. aegyptiaca*, *S. retusa*, *S. vitellina*, and *S. purpurea*. However, he had an opportunity to observe the latter two in cultivation in Sweden. In fact, Linnaeus used numerous Russian specimens of willows while writing his "Species plantarum". He also constantly referred to Russian "floras", mainly, "Flora Sibirica" by J. Gmelin. C. Linnaeus established intensive correspondence with J. Gmelin and claimed that he received specimens of each of J. Gmelin's species (compare Stern 1957: 106). Still, he recognized only 7 out of 15 species described by J. Gmelin, just those previously found in Europe. That is to say, C. Linnaeus approved none of J. Gmelin's Siberian species. Even the most distinct of them, *S. berberifolia*, was not included in "Species plantarum", although it had been depicted by J. Gmelin. C. Linnaeus cultivated some of the willows in order to study them more thoroughly, for instance, *S. depressa*, which had been brought by him from Lapland.

Of 31 species described by C. Linnaeus, 7 are now treated as synonyms, leaving a total of 24 species. He recognized all but two of the Scandinavian species he had at his disposal. These two were *S. starkeana* and *S. myrsinifolia*. Therefore, one can consider C. Linnaeus' efforts to gain understanding of willows and build "harum historia e nova" as being generally successful.

C. Linnaeus' authority and principles dominated European botany for some time after his death. The last third of the 18th century was a time of intensive development in botanical research and publication of numerous new "floras". Nevertheless, the number of willow species in these "floras" remained rather modest. They were mostly Linnaean species. In Western Europe, J. Scopoli (1772), M. Villars (1776–1789), and G. Hoffmann (1785–1791) made the most important contributions to the willow studies of that period. "Historia Salicum" by G. Hoffmann was the first monograph on the genus *Salix* planned on a grand scale (up to three color plates for each species). However, less than half of that work was completed, and only 15 species were described.

The most important floristic work of the Linnaean period in Russia was "Flora Rossica" by P. Pallas (1788). There were 35 willow species presented, 26 of which were described by C. Linnaeus. (At present, there are at least 65–70 willow species known for the same territory, and 21 of them are Linnaean ones.) In his travels, P. Pallas paid little attention to willows. He himself collected only a small portion of the species he described. The majority of willows, including almost all the Siberian species, were collected for him by V. Zuyev, N. Sokolov, and others. P. Pallas also used collections of J. Gmelin. Confusion and inconsistency mark P. Pallas' descriptions and designations of species. His identification of those specimens, which have survived to the present, appears also insufficient. For instance, there are at least three different species under the name of "*Salix fusca*": *S. saxatilis*, *S. rectijulis*, and *S. sphenophylla*. *S. viminalis* and *S. alba* are both under the name of "*S. serotina*". There are also two different *S. arbuscula* with two different descriptions in "Flora Rossica" (p. p. 80 and 83). Due to the carelessness of P. Pallas, almost all of his new species remained obscure and dubious for a long time. "Omnes fere Salices Pallasii sunt dubiae", as C. Willdenow mentioned (1806: 683). Therefore, one would not say that P. Pallas opened a new page in the study of the Russian willows, although he was much more successful with other genera, such as *Astragalus*.

2. LATE 18th—FIRST THIRD OF 19th CENTURY IN WESTERN EUROPE: NUMEROUS DESCRIPTIONS OF NEW SPECIES.

One can notice a drift away from Linnaean concepts and weakening of C. Linnaeus' authority over the European botany starting from the end of the 18th century. This tendency could be clearly traced as early as G. Hoffmann's works. By the beginning of the 19th century, C. Willdenow became the most authoritative figure for the majority of European botanists, as if he himself had written "Species plantarum". One more characteristic feature of that period was determination of botanists to describe the diversity of willows to the greatest possible extent. This effort resulted in numerous descriptions of new species, as at that time any morphological differences were considered to be taxonomical ones.

J. Scopoli used to disagree with the ideas of C. Linnaeus. In the first edition of his "Flora Carniolica" (1760), he accepted neither the system nor nomenclature created by C. Linnaeus. In the foreword to the second edition of the "Flora" (1772), J. Scopoli wrote: "I retained the species' names by Linnaeus, although the majority of them are arbitrary, many are obscure, and only some are didactic." Nevertheless, J. Scopoli's work couldn't avoid C. Linnaeus' influence and obviously reflected the epoch. Thus, J. Scopoli claimed his approach to species in the sense stated by C. Linnaeus: "Laboravi equidem ut limites invenirem et numerosas varietates ad suas species reducerem" (1772, vol. 2: 252). — "Indeed, I worked to find the limits and reduce numerous varieties to appropriate species." Later, the adage "work to search for limits" and "reduce

12 varieties to species" became unpopular. Descriptions of new species began to multiply at an incredible rate. While in "Flora Anglica" by W. Hudson (ed. 3, 1798) there were only 16 Linnaean species, there were already 45 species in "Flora Britannica" published by J. Smith just six years later (1804). Of these 45 species, 19 were proposed by J. Smith himself. Later, he continued describing new willow species in the illustrated "English Botany", which he edited. In 1806, C. Willdenow could already mention 116 species (including non-European ones), of which 30 were those described by him. By 1828, according to W. Koch (1828), there were 182 willow species described, 165 of which originated from Europe. In 1835, there were 71 species of willows mentioned just for the territory of the British Isles (Hooker 1835). At present, only 19 species are recognized for the British Isles.

Along with the dramatic increase of species numbers in the "floras", there was total a decrease in the number of varieties. No varieties were mentioned by C. Willdenow within the 116 species and almost none were recognized by J. Smith.

J. Schleicher appeared to be the most extravagant splitter of species. He published a large set of exsiccatae on the willows of Switzerland with 120 new species named. Indeed, he did not formally describe any of these species, they were just *nomina nuda* in his catalogues (Schleicher 1807, 1821). Fortunately, we can pay them no attention now. However, that was not possible some 150 years ago, when the rule to ignore *nomina nuda* did not yet exist. The majority of J. Schleicher's "species" were actually forms of *S. myrsinifolia*. Later on, people tried to explain that outburst of "species-creation". There were suspicions that J. Schleicher had done this purposefully, in order to profit from selling more of his exsiccatae, but this is probably not true. J. Schleicher's approach was an extreme one, but it was not accidental. His treatment of species had much in common with that of J. Smith. It lasted and emerged later in works by A. Jordan and especially those by M. Gandoger in the later half of the century (see section 3).

Of course, there were also attempts to divide the genus. C. Rafinesque (1817, 1831) and P. Opiz (1852) both introduced whole new series of genera instead of taking *Salix* in the broad sense. A. Kerner (1860) had less pretension, as he only segregated *S. reticulata* in the genus *Chamitea*.

As a result of intensive studies on willows, a number of new monographs were published during the period under consideration including those by W. Wade (1811), which was a bulky, yet weak compilation, by N. Seringe (1815), N. Host (1828), W. Koch (1828), J. Forbes (1829), J. Sadler (1831), and E. Fries (1832). N. Seringe's monograph was rather modest in terms of species-splitting. As it came together with the author's 88 exsiccatae (1805–1814), it still retains its value. The book by N. Host was ambitious, yet unfinished work with 108 color plates in folio. The author intended to do something similar to G. Hoffmann, but on an even larger scale. Yet even at the time the book was published, its scientific value was definitely not that great in comparison with more unassuming works by N. Seringe and W. Koch. As for J. Forbes' monograph, which included color plates and diagnoses for each of 140 clones of willows cultivated in Woburn, it was valuable for purposes of a rare book collector rather than taxonomist.

Works by Scandinavian authors of that period, primarily those of G. Wahlenberg (1812, 1816) and E. Fries (1825, 1828, 1832, 1840) were also overloaded with new species. Nevertheless, those monographs were of importance, as they fixed the particular understanding of the Linnaean species.

3. STABILIZATION OF SPECIES NUMBER IN WESTERN EUROPE: FROM KOCH TO WIMMER AND BUSER

Numerous new species with slight variations were described despite Linnaeus' warnings not to treat each difference as one between species. Inevitably, opponents to that approach soon appeared. It was W. Koch, one of the most attentive and precise early 19th century European researchers, who first opposed splitting of willow species (Koch 1820). Reasoning from his own observations of willows in nature, W. Koch emphasized that willows had a wide ranges of variability. In the same work, he was also determined to abolish J. Schleicher's "species". In his review of the European willows (1828), he proceeded even further and, in spite of the authority of J. Smith and C. Willdenow, resolutely reduced the number of the European species to 48. (Currently, we would eliminate 13 more species from these 48, treating them either as synonyms or hybrids.)

I. Tausch (1832) was another opponent of splitting species. He studied the willows thoroughly in C. Willdenow's Herbarium, compared them with what was written about them by C. Willdenow, and highlighted many contradictions, noncompletions, and superfluous species. Both W. Koch and I. Tausch broke the tendency of species-splitting, although they were unable to stop it completely. Indeed, I. Tausch himself published a few superfluous species' diagnoses and included even more of them in his exsiccatae "Plantae selectae Bohemicae" and "Dendrotheca Bohemica". In 1837, when Koch's principal and authoritative work, the "Synopsis" was published (Koch 1837), his approach became ultimately dominant in Central Europe.

A. Kerner (1860) made the next progressive step towards the understanding of the European willows, yet it was F. Wimmer who finally reviewed and clarified the European species. Both A. Kerner and F. Wimmer published sets of excellent exsiccatae along with their monographs (Wimmer, Krause, "Herbarium Salicum", fasc. 1–11, 1849–1857; A. Kerner, J. Kerner, "Herbarium österreichischer Weiden", decades 1–9, 1863–1869). The last one of F. Wimmer's publications, "Salices Europaeae" (1866), summarized all of his previous contributions to the willow research. The breadth, accuracy, and detail of that monograph surpassed all previous works published on willows. It was a final landmark in a hundred years' research on the willows since the time of C. Linnaeus. Naturally, it became the standard in the willow systematics for many years. F. Wimmer reduced the number of the European species still more, to 34. (Presently, 58 species are recognized in Europe, but one must keep in mind that F. Wimmer had almost none of southern and northeastern European specimens at his disposal.)

F. Wimmer gave very detailed descriptions of all plant parts, habitats, and geographical distribution. He paid special attention to infraspecific variability depicting it by means of description as well as recognizing varieties. F. Wimmer's main achievement was that he managed to reveal hybrid nature of many "species" proposed earlier by others. Of course, even before F. Wimmer there had been some assumptions and even confident statements about the existence of willow hybrids. The earliest one was made by J. Scopoli (1760: 111), who noted a possibility of pollination by alien willow species: "fecundae ex alieno mare feminae a me plures observatae". A. P. De Candolle (1832) also mentioned the ability of willows to form hybrids, although his remark was rather obscure. A. Kerner, too, treated some of forms as hybrids. Yet it was F. Wimmer, who succeeded in cleaning the heavy ballast of hybrids from the list of the European willow species. There are descriptions of 57 hybrids in "Salices Europaeae". Making decisions about hybrid nature of specimens, F. Wimmer not only relied upon his own keen eye of

14 a morphologist and taxonomist, but also enlisted assistance of M. Wichura, who was working on artificial crossings of willows under F. Wimmer's leadership in Breslau (Wichura 1854, 1865). Of course, only a part of proposed hybrid combinations could be verified in experiments. Some willows were mistakenly treated by F. Wimmer as hybrids. For example, he considered *S. laggerii* to be the hybrid *S. glauca* × *S. appendiculata*, although he himself had described *S. laggerii* as a species. We now know that it is a perfectly distinct species. In any event, those occasional errors by no means diminish F. Wimmer's achievements.

A contemporary of F. Wimmer, N. Andersson, who lived in Sweden, also devoted a large part of his life to the study of willows. N. Andersson's early work on the Lapland willows (1845) was not very important in comparison to the studies by G. Wahlenberg and E. Fries. It is of no interest now. His later works on the willows of India (1851, 1860) and North America (1858) are much more valuable. N. Andersson's treatment became the groundwork for the presentation of the genus *Salix* in J. Hooker's "Flora of British India" (Hooker 1890). All later authors referred to J. Hooker when speaking about the Himalayan willows. Therefore, the concept of the Himalayan willows has not changed much since the time of N. Andersson. N. Andersson also presented the genus *Salix* in "Prodromus" by A. P. De Candolle (1868). There were 160 willow species included in the world flora. Along with this brief review, N. Andersson planned to publish a detailed monograph, but he completed only half (1867). Although N. Andersson was able to embrace the vast diversity of the genus, his treatment was not that precise, keen, or fundamental in comparison with F. Wimmer's work. F. Wimmer's influence was obvious in N. Andersson's monographs of 1867 and 1868.

R. Buser in Switzerland was as thorough an expert on willows as F. Wimmer. Perhaps, R. Buser was even more acute. In 1883, he prepared an excellent, broad review of the willows of Switzerland, but it was left unpublished for unknown reasons. It only became available to readers many years after R. Buser's death (Buser 1940). Inevitably, it was already partially out of date. During his life, R. Buser succeeded in publishing only a few very short articles (1881, 1887, 1894, 1897, 1909). However, he had an excellent understanding of willows. As for limits of the Central European willow species, one would hardly object to his treatment today. R. Buser used geographical distribution along with other data to make decisions about species distinctness. Some of the species abolished by F. Wimmer were admitted by R. Buser.

R. Buser's observations on hybrids were also of importance. Following F. Wimmer's treatment, willow hybrids became fashionable. They were found everywhere, including many cases that had nothing to do with hybrids. R. Buser was the first to vigorously protest against hybridomania (Buser 1887, 1909). He was also the first to conclude that hybrids between closely related species of willows occur much more rarely than those between remote species. Thus, one most often finds hybrids between representatives of different sections (Buser 1940). Unfortunately, during R. Buser's lifetime all of his publications had restricted distribution. Dealing only with some special issues, they did not have significant impact upon the development of willow systematics.

At the end of the 19th century, there appeared a curious product of botanical literature: the "Flora of Europe" by M. Gandoger. It consisted of 28 volumes; volume 21 was dedicated to the genus *Salix*. There were 1,600 species of European willows, 1,576 of which were proposed by M. Gandoger (1890) himself. He divided *S. purpurea* into 62 species, *S. reticulata* into 67, and *S. caprea* into 76 species! M. Gandoger considered his concept of species to be theoretically justified by A. Jordan.

Obviously, there is no need to discuss our attitude towards these "species" by M. Gandoger. Still, the question remains: how should one treat M. Gandoger's published binary names from the formal, purely nomenclatural point of view? H. Fuchs (1960) stated that from the formal point of view M. Gandoger's specific names were as good as names published by any other author. W. Rothmaler (1962) sharply objected to H. Fuchs' opinion saying that taxonomists were already suffering from an enormous load of synonyms. Hence, it was absolutely impossible to take a few more thousands plant names into consideration merely because of the existence of a bizarre book that no one treated seriously. Actually, this problem can be resolved rather easily, and without any emotional outbursts. M. Gandoger himself created a reason for us to reject his species names. The point is that his small "species" (micro species) were included in species of normal size. Thus, binary names were superior to other binary names. However, the modern rules of nomenclature do not allow for existence of any taxon inside another taxon of the same rank. Neither binary names for infraspecific taxa are allowed by the rules. Therefore, none of the 1576 species names by M. Gandoger mentioned in his "Flora of Europe" have any validity at any rank.

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4. LATE 19th—THE END OF THE 30's OF 20th CENTURY IN WESTERN EUROPE: IN SEARCH OF HYBRIDS. UNDERSTANDING SPECIES IN THE SENSE OF ASCHERSON

In his fundamental and influential work, F. Wimmer claimed the number of European species to be finally fixed and rather modest. At the same time, he emphasized the polymorphism of willow species as well as considerable opportunities for them to form hybrid combinations. Following this observation by F. Wimmer, researchers rushed to recognize and describe new varieties, forms, and hybrids in the genus *Salix*. That approach became common practice during the period of the late 19th—early 20th century, after the publication of the "Synopsis" by P. Ascherson and P. Graebner. A multilevel infraspecific taxa hierarchy was elaborated in this book to an extreme extent. In fact, that period also saw the establishment of the so-called "morpho-geographical" direction of the research in both the West European and Russian systematics. The new approach meant treating a species not only as a structural unit, but also ecological and geographical entity consisting of many individuals and occupying its own niche in nature. As to P. Ascherson's school, it still retained its purely typological approach to taxonomical units describing them from the formal point of view. Researchers of that school stayed far away from considering geographical and ecological features of species. They also never realized that morphological differences of specimens did not always indicate taxonomical differentiation of species.

P. Ascherson's approach prevailed in studies of the genus *Salix* during the period under consideration. The most prominent work on the European willows after the publication of Wimmer's book was a large review of the genus in P. Ascherson's and P. Graebner's "Synopsis" written by O. Seemen (1908–1910). There, according to the concept of the entire "Synopsis," the infraspecific subdivisions were elaborated for each species on a regular basis. The number of hybrids described was enormous: there were 213 simple hybrids and 59 triparental and tetraparental ones. (F. Wimmer had none of triplets or quadruplets). It is a curious fact that O. Seemen had two absolutely different approaches to European and exotic species. His understanding of European species was broad, and he would describe many varieties, forms, and hybrids between species. At the same time, while treating exotic Asian and African willows, he would describe every couple of specimens as a new species, mentioning neither varieties nor hybrids, as if he was converted to another faith. One should mention also that the first monograph on the willows of Japan was written by O. Seemen (1903).

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The next prominent figure in the European willow studies after O. Seemen was a Swedish botanist S. Enander. His two major works were exsiccatae of the Scandinavian willows (Enander 1905–1910), thoroughly collected and accurately commented, and also an investigation on the willows in C. Linnaeus' Herbarium (Enander 1907). Later, S. Enander did not publish anything of significance, and only annotations on herbarium labels indicate his activities. S. Enander was a dedicated, accurate, and authoritative researcher, so that even R. Görz and B. Floderus considered themselves to be his pupils; yet one should frankly say that he did not understand willows properly. The main issue, consideration of species limits, was desperately lost in his work amidst endless numbers of varieties, subvarieties, forms, subforms, and even subsubforms along with all kinds of double, triple, and quadruple hybrids that one could imagine. S. Enander's treatment of the Siberian willows was most characteristic for his approach. Although he undertook a trip to Siberia in 1913 with the only purpose to gain better knowledge of willows, he did not succeed in understanding any of the Siberian species treating them as hybrid combinations of European species familiar to him. For instance, S. Enander considered the most distinct species from Kamchatka collected by V. Komarov, *S. sphenophylla*, to be "*S. arctica* × *lanata* × *reptans*". Other species were treated by him in a similar manner.

Following the historical sequence, we have to discuss an input made by A. Toepffer next. Essentially, it was an enormous set of exsiccatae ("Salicetum Exsiccatum", fasc. 1–15) published in 1906–1929. The number of exsiccatae was as large as 772. From the very beginning, these were mostly casual forms growing in the Freising Nursery near München. However, later on, A. Toepffer started to publish material specially collected in the Balkans, Alps, and even in Africa and Asia. As for Asiatic specimens, these were often presented on large-sized photographs. In his comments to these exsiccatae, A. Toepffer appeared to be an Ascherson's follower, although he was much more moderate in describing new forms and species. Also, the biological approach was not alien to him. He was the author of a detailed monograph on the willows of Bavaria (Toepffer 1914, 1915) as well as an excellent essay on the genus *Salix* for the famous "Lebensgeschichte der Blütenpflanzen Mitteleuropas" by O. Kirchner, E. Loew, and C. Schröter (Toepffer 1925).

R. Görz started by describing innumerable subforms and triple hybrids. He followed S. Enander, however, not losing his "sense of species" that much (Görz 1922; see also his exsiccatae "Salices Brandenburgenses Selectae"). Later, when his attention was drawn to Caucasian and Asiatic willows, he switched to another extreme describing superfluous species in exactly the same way as O. Seemen had done before him. Strange though it may seem, at the same time, he considered a number of new, perfectly distinct Caucasian and Chinese species at his disposal to be hybrids. Indeed, the majority of "hybrids" in his Brandenburg Exsiccatae did not actually exhibit any signs of hybridity. Another series of exsiccatae by Görz, "Salicaceae Asiaticae" (1931–1934), which consisted of 75 entries, appears to be much more valuable.

The latest outstanding personality among P. Ascherson's followers and hybrid-describers was that of B. Floderus. He published monographs on the willows of the Novaya Zemlya (1912), Greenland (1923), and Scandinavia (1931) along with a large series of articles on the European, Siberian, and even some East Asiatic willows. He started as a follower of S. Enander describing endless numbers of hybrids. Distinct species were literally lost among them. B. Floderus resolutely claimed that "pure" species were rare and hybrids absolutely dominated the willows on the territories of the Novaya Zemlya, Greenland, Kamchatka, and to some extent even northern Scandinavia. Yet in his latest works, he changed his attitude towards hybrids and moved

somewhat away from the hybridomania. In these works, we see him as an experienced and often keen researcher.

A few more works of the period under consideration are worth mentioning as they stood apart from the major, *Aschersonian* trend of the research. These were two monographs on the willows of the British Islands by F. White (1890) and E. Linton (1913). Along with his monograph, E. Linton published a hundred of exsiccatae of British willows. A. Camus and E.-G. Camus (Camus, Camus 1904, 1905) also wrote a bulky monograph on the European willows (two volumes and an atlas); yet it was just a cursory compilation that does not appear ingenious.

5. IN RUSSIA AND THE USSR: FROM TRAUTVETTER TO NAZAROV

During the post-Linnaean period, the study of the willows in Russia had some peculiarities as compared to the West European research process. Therefore, we would consider it separately. An article by F. Bray (1818) is hardly worth mentioning here, since it only contained some "new" species descriptions weakly written in J. Smith's style. Two monographs by E. Trautvetter, "De Salicibus Livonicis" and "De Salicibus Frigidis", both published in 1832, became the first really important works on the subject since the time of P. Pallas. E. Trautvetter was a very accurate researcher and attentive to detail. He luckily escaped the species-splitting fashion of that period and treated species close to W. Koch's sense. Immediately, he became the best willow expert in the country. For nearly 60 years, most of treatments on willows published in Russia belonged to him. His next work after those of 1832 was an overview of the genus *Salix* in C. Ledebour's "Flora Altaica" (1833). One must admit that there E. Trautvetter generally followed C. Ledebour's outline and approach. Then came his "Salicetum", which was an unfinished review of the willows of the world, as well as a series of treatments in numerous Siberian "florulas" published by the Academy of Sciences and St. Petersburg Botanical Garden (Trautvetter 1847, 1877, 1878, etc.; Trautvetter, Meyer 1856).

Besides these works by E. Trautvetter, the most important treatments of willows with new species descriptions were made by C. Ledebour (for the whole Russian territory, 1834, 1850), N. Turczaninow (for East Siberia and Transbaykalia, 1854), Fr. Schmidt (for the Yenisei and Sakhalin, 1869, 1872), and E. Regel (for Middle Asia, 1880, 1882). All of these works shared a common spirit, close to that of E. Trautvetter's. They depicted a general concept and approach to species typical for the Russian taxonomy and floristics, which became fully developed by the 19th century. New species were described very accurately and with caution. Sometimes, there was even too much caution, so that some distinct species from Siberia and the Far East were left undistinguished. The number of new species named in the 19th century was not even larger than that named in the 20th century (of course, if synonyms were not taken into account).

Along with Russian authors, a large contribution to the study of willows in this country was made by N. Andersson, whose name has been already mentioned. He treated the collections accumulated by 1850–1855 at the St. Petersburg Botanical Garden and described a number of new species.

The hybridomania had not yet spread among Russian salicologists of the 19th century. They were still concentrating on distinguishing species. A drift towards the new approach became evident in 1875, when J. Schmalhausen published his study of natural hybrids in St. Petersburg Government. However, the hybridological trend developed in full only when E. Wolf gained the

18 major authority in the willow research after E. Trautvetter's death. E. Wolf, a professor of the St. Petersburg Forest Institute, was a good dendrologist and horticulturist; nevertheless, as a taxonomist, he was rather poor. His bulky work on the willows of the European Russia (1900) was quite within Ascherson's concept. All his effort was concentrated on naming new varieties and hybrids. At the same time, he left many species misunderstood or obscure. Indeed, there was hardly anything valuable in his treatments that added to the knowledge of the European willows. Yet he did a much better job treating the genus *Salix* for the "Flora of the Southeast" (1930). After 1900, E. Wolf's attention was driven to the willows of Asiatic Russia, mostly those of Middle Asia. His approach to the Middle Asiatic willows was quite opposite to that towards European taxa. Much alike O. Seemen before him, he was inclined to distinguish numerous varieties and forms when considering the willows of European Russia. At the same time, treating plants from Middle Asia, he was ready to see a new species nearly in every new specimen he received. He segregated 18 new species (Wolf 1903a, 1903b, 1905, 1906, 1907, 1908, 1909, 1911, 1912, 1929), of which only 5 are left; the others turned out to be either synonyms or hybrids.

P. Lakschewitz was E. Wolf's contemporary. However, his approach towards describing new varieties and forms in Europe as well as new species in Asia was much more moderate. There is no doubt, he was a keener eye, and his decisions were more correct in comparison with those made by E. Wolf. Unfortunately, P. Lakschewitz did not write much. His notes to the exsiccatae for the "Herbarium of the Russian Flora" (1911, 1914) were his only work published. He also treated willows for "Flora Caucasica critica" by N. Kuznetsov, N. Bush, and A. Fomin, but that treatment was never published, because the "Flora" itself was discontinued. (Actually, it is unknown if the part on willows was ever ready to be published.) According to numerous annotations left by P. Lakschewitz in the St. Petersburg Herbarium, he also worked on an overview of the Siberian willows, but neither this work was ever brought to an end. P. Lakschewitz made many collections, particularly, in the Baltic States, but these collections of his are presumably lost (Rasinš 1959: 84).

There is nearly nothing left written by F. Teploukhov. As a dendrologist and forest scientist, he had a particularly keen interest in the willows and maintained a vast herbarium collection, mainly of willows from Pre-Uralia, and also some from Central Europe. That collection has survived, at least in part, in St. Petersburg. F. Teploukhov's treatments and opinions were important for many of his contemporaries (for example, see Petunnikov 1901), although he did not consider himself to be a taxonomist and avoided any written statements on taxonomical topics.

Among those Russian botanists of the pre-revolutionary period who made a considerable input to the study of willows, one should also name P. Siuzev. Although he did not leave any major works, he was a prominent willow collector, who worked mostly in the Urals, Central Russia, and the Far East. It is also important to mention the names of K. Kupffer, who studied the willows in the Baltic States and published a number of samples in the "Herbarium of the Russian Flora", and D. Syreishchikov, who depicted and described the willows of Moscow Government with great accuracy (Syreishchikov 1907). V. Dobrovlyanskiy (1891) undertook a detailed comparative study of the willow (and poplar) leaf anatomy. Unfortunately, his work was not illustrated, hence it actually could never be used for the systematic purposes.

In the 20's and early 30's, a large portion of Russian willow collections was sent to Germany, for R. Görz's treatment, and also to Sweden, to B. Floderus. B. Floderus also had at his disposal much of material collected by Swedish expeditions in the Yenisei and Lena basins, Kamchatka,

and other regions. Both authors published a number of works, either entirely or to a large extent devoted to the Russian willows (Floderus 1926a, 1930, 1933a, 1936, 1939, 1941; Görz 1928, 1930, 1933, 1934a, 1934b, 1934c, 1936, 1937). Yet these works by R. Görz and B. Floderus made little progress in understanding of the Russian willows. Part of the problem was that neither B. Floderus nor R. Görz had a chance to observe Russian willows in nature. Another drawback was their purely typological approach to species. 19

Rather than seeking help from abroad, some Russian researchers of the 20's and 30's preferred to treat their willow collections themselves. For example, V. Komarov in his "Flora of Kamchatka" and "Key to Species of the Far East" relied mainly upon his own identification of species. The same is true for the "Flora of West Siberia" by P. Krylov. Also, B. Gorodkov and A. Tolmachev examined arctic willow collections of their own with great care.

M. Nazarov started his observations of willows as early as the pre-revolutionary years. His excellent collections of the willows from Vladimir Government are now kept in Moscow and St. Petersburg. In the 20's and 30's, Nazarov studied the willows of Prebaykalia. He came along with his first publication on willows only in 1933. When there appeared a need for a treatment of the willows for the "Flora of the USSR," it happened that M. Nazarov was the only person able to handle the project. He only had two or three years to complete the entire task, a time too short to review the material available in Leningrad alone. As one can see from many of M. Nazarov's annotations in herbaria, he was a very conscientious worker and managed to go through all material available in Moscow and the Botanical Institute in Leningrad. He succeeded in identifying those particular plants which had been implied by his predecessors when they had described species. These data were correctly presented in the "Flora of the USSR". Yet M. Nazarov was hardly able to revise the species and decide which of them were worthy of recognition. The only way out of that situation was to accept primarily all the species previously described. Hence, it was a compilation of data in the literature verified against herbarium material, which was prepared for the "Flora of the USSR". It contained only insignificant fragments of critical analysis. Nevertheless, M. Nazarov's review, in the way he managed to prepare it, fitted well enough with the general approach to species in the "Flora", since in its early volumes there was a trend towards distinguishing "small" species as well as towards prompt, not necessarily critical treatments. M. Nazarov also made reviews of the genus for the "Flora of Transbaykalia", "Flora of the Ukrainian SSR", "Flora of the Byelorussian SSR" (the latter two were published after the World War II). He pursued the studies of willows of the entire USSR territory with special emphasis on the Caucasus and East Siberia. However, he never published any corrections or additions to the "Flora of the USSR".

6. JAPANESE SCHOOL

Since the late 19th century, taxonomists native of Japan joined the studies of the East Asiatic flora and soon started to play a prominent role. Japanese authors who made the largest input into willow studies were, first of all, T. Makino, G. Koidzumi, T. Nakai, and A. Kimura. T. Makino's major credit was the establishment of a very large herbarium, where willows were excellently represented (the main collection is preserved in Tokyo, although some duplicates can be found in other herbaria, for instance, in St. Petersburg). T. Makino's approach to species was rather conservative. However, due to this approach, all the willow species in his "Flora of Japan" (1956) were consistently revised from the same critical point of view, whereas in the "Flora" by J. Ohwi

(1965) there was more of compilation. As for G. Koidzumi, T. Nakai, and A. Kimura, none of them ever published a full list of Japanese willows which would be in accordance with their own concepts. After T. Makino with his conservative approach, both G. Koidzumi and A. Kimura appeared to be "species-splitters" in Japan, much alike O. Seemen and E. Wolf in Europe and Russia. Of course, on their lists of newly described species there were some real ones, which was quite natural when dealing with rich and poorly explored floras of Japan, Sakhalin, and the Kurils. Yet the majority of "new" species by G. Koidzumi and A. Kimura were merely synonyms. Abundance of newly-described species along with restricted availability of original material make it extremely difficult to understand these species and compare them with the continental willows. Types and sometimes entire herbarium material on the majority of species by A. Kimura are preserved in his private collection. Exsiccatae of Japanese willows are only represented by a few numbers published by R. Görz (1931) and also the "Japanese Flora" series by the Museum of Natural History in Tokyo. One must admit, however, that diagnoses by A. Kimura are very detailed, precise, and often accompanied by excellent photos (though one would not say the same about species descriptions by G. Koidzumi).

T. Nakai had a more realistic attitude to species: he would not hesitate to assign to synonyms even species he himself had described before. His major achievement was a publication of a voluminous "Flora sylvatica Koreana". The part treating willows was very well written there (Nakai 1930). One can gain good understanding of species even without referring to the herbarium thanks to excellent quality of descriptions and illustrations.

A cytotaxonomical research of the genus *Salix* has been carried by Y. Suda, a pupil of A. Kimura (Suda 1958–1960, 1963).

7. AFTER WORLD WAR II: THE USSR AND WESTERN EUROPE

The main feature of the taxonomy during the post-war decades was a slow, gradual shift from the purely typological to biological concept or, to be more precise, the populational concept of species. This caused a drift away from the purely formal, *Aschersonian* infraspecific systematics. Any interest in morphological descriptions of interspecific hybrids was disengaged. Descriptions of hybrids were removed from texts to footnotes or merely disappeared from the majority of "floras" and monographs.

Some perfect, distinct European species had been long hiding under names of hybrids. Understanding of this fact was attributed to a more realistic approach to species and rejection of *Aschersonian* intricate hierarchy of infraspecific taxa. This led to rehabilitation of a number of West European species, which had been misunderstood and mistakenly considered to be either hybrids or varieties. Besides, ranges and limits of many of the West European species were clarified. A number of significant publications on the systematics and geography of the West European willows appeared during these years (Almeida 1944; Chmelař 1963a, 1963b; Fijałkowski 1958a, 1958b; Franco 1949; Neumann 1955; Pawłowski 1946; Rechinger 1938, 1947; Vicioso 1951). Some treatments published as parts of "floras" deserve special attention (Stoyanov, Stefanov 1948; Beldie 1952; Chassagne 1956; Dostál, 1950; Lawalrée 1952; Pawłowski 1956; Rechinger 1957, 1964).

Unfortunately, the most recent of K. Rechinger's treatments in "Flora Europaea" (1964) is not wholly satisfactory. Following B. Floderus, the author considered a number of forms with obscure morphological characteristics and indefinite geographical ranges to be species.

Moreover, he added a few unclear species of his own. There are also some significant faults regarding species distribution.

J. Wilkinson (1944) published detailed data on willow chromosomes. The results of that investigation made it clear that the willow systematics cannot benefit very much from the chromosome research.

During the post-war decades, many new works on willows were published in the USSR, 21 mostly within regional "floras". A number of new botanical research centers, which had been organized before the World War II, became active after the War, generating new regional "floras". These "floras" were created neither in Moscow, nor in Leningrad, as it had been before, but right in the areas of investigation. A. Grossheim (1945) conducted a new survey of the Caucasian willows, which constituted a considerable improvement in comparison with the previous research by R. Görz. R. Shlyakov (1957) wrote a very detailed and accurate review of the willows from the Kola Peninsula. Unfortunately, he trusted B. Floderus too much and consequently accepted a number of superfluous species. Due to that and also because he admitted the idea of hybridization on a mass scale, species limits appear to be rather vague in the "Flora of Murmansk Oblast". Both V. Drobov (1941a, 1941b, 1953) and P. Polyakov (1960) devoted their research to the willows of Middle Asia and Kazakhstan. V. Drobov would not clarify the species described earlier; instead he added still more superfluous ones to the list of the Middle Asiatic willows, which had already been overloaded. P. Polyakov's treatment was much more realistic and definitely made a progress, although it was not free from confusion in understanding of some willows and the number of species was still too large there. M. Popov (1959) primarily followed N. Turczaninow and M. Nazarov in his treatment of the genus *Salix* for the "Flora of Central Siberia". Although M. Popov made numerous observations on his own, he never managed to bring them into a system. Besides, he would exaggerate the role of hybridization in nature, in accordance with his theoretical notions. L. Malyshev's approach was much more neat (Malyshev 1965).

One should also mention here reviews of the Ukrainian willows (Nazarov, Kotov, Gerzhedovich 1952), the willows of Leningrad Oblast (Korchagin 1957), Estonia (Krall, Viljasoo 1965), and Latvia (Rasinš 1959).

However, in spite of these numerous treatments, no considerable general progress was achieved during the period after the war in comparison with the "Flora of the USSR", except some special occasions and particular regions. Indeed, the least progress was made in understanding of the systematics and geography of willows in the largest and richest areas of their distribution in this country: Siberia, the Far East, and Middle Asia. The Caucasian willows also remained insufficiently clarified. There were still many discrepancies even in the knowledge of the European Russian willows. Hence, when the volume of the review "Trees and Shrubs of the USSR" (Pravdin 1951) containing the survey of willows was to be published some 15 years later than the appropriate volume of the "Flora of the USSR", the taxonomical part still had to be borrowed from M. Nazarov's treatment in the "Flora". As for data on species geographical ranges, these were taken from a rather cursory compilation by Th. Schmucker (1942).

All attempts to build a natural system of the genus *Salix* have been concentrating so far on revealing of groups of close filiation, that is, sections. This research is still going on and is far from being completed, especially in regard of the entire genus. Since the major units of relation remain obscure, it is certainly impossible to interpret the relation itself. Therefore, evolutionary concepts have been hardly approached in the literature on *Salix*. So far there has been not enough data to rely upon, it has been too early to start.

Chapter 2

MATERIAL AND METHODS

1. NOTION OF SPECIES THAT THE AUTHOR COMPLIES WITH

The main subject of this book is presentation of the willow systematics at the species level. Since the essence of the species has been often subject to argument and is not always uniformly understood, the author feels necessary to make a brief statement concerning his own understanding of the species. This notion of the species, in the author's opinion, is best matched with our current knowledge about the nature of the species and supported by results of the study of the willows.

Species do exist objectively. That is to say, not only do there exist specimens that comprise species, and not only do these specimens really differ from each other, but also borders between species do exist naturally, and one can and should detect the location of these borders. I absolutely reject the understanding of the species as a certain conventional domain, nothing but a convenient way to classify live objects. This view has long been known and especially promoted by J. Gilmour and S. Walters (Gilmour 1940; Gilmour, Walters 1964).

A species is neither a totality of properties and features, nor a version of structure and function, but a certain integral natural entity consisting of numerous individuals biologically connected with one another. This is a part of the life stream on the Earth distinct from other similar parts, that is, from other multitudes of individuals. A border between two species or two multitudes of living beings inevitably arises as soon as each of these multitudes enters its own specific way of historical development.

The panmixis, the normal sexual reproduction process, provides natural grounds for the integrity of species. The panmixis is characteristic for the overwhelming majority of plants and animals. It was the existence of sexual reproduction, which led to division of live organisms into species. If the panmixis is disturbed, then the normal species structure is inevitably ruined and various abnormalities arise, which may make it impossible to define species limits. Most typical examples of these abnormalities in the plant world are apomictic groups, which always constitute problems for the systematics. The panmixis, at the same time, is a mechanism that provides considerable genotypic diversity within a species. All groups of plants that have normal sexual reproduction are characterized by infraspecific genotypic variability, the individual one as well as populational; any specimen as well as population is genotypically different from any other one.

The major issue of the systematics on the species level is detecting species limits that objectively exist in nature. For this purpose, it is important to keep away from any attempts to apply a purely deductive method, that is, never to rely upon any notions about taxonomical significance of characters a priori. A taxonomical value of a particular character may be assessed only by an inductive procedure, treating each individual instance separately. Using this approach, one will necessarily have to deal with very "polymorphic" species along with "uniform" ones;

some too "large", and some too "small". In certain cases, differences between species may appear to be "significant", while in others, "insignificant". We don't have to worry about these results. Indeed, we cannot demand that nature should arrange all the species to our convenience, so that they would be easy to distinguish and besides appear neither too big nor small to us.

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Of course, the interspecific divide that we are concerned with does not have to be always distinct and clear. On some occasions, it may be difficult to decide whether we deal with one or two species not because of our insufficient knowledge of plants, but due to the natural situation itself, since species may be not sufficiently isolated. Neither these results should trouble us, as long as we are able to adequately depict the existing circumstances in the most realistic manner. Occasionally, in situations like these, it is the category of subspecies, which works well for description; in other cases, one has to provide detailed verbal comments.

Distinction of species and detection of their objective limits are based on the study of the following three groups of biological facts, i. e., three types of characters.

1. Morphological and biological characters that can be observed in individual specimens. All kinds of them are principally equal for the systematics: macromorphological, anatomical, cytological, physiological, biochemical, etc. As for the real taxonomical value of any particular character in a particular case, it is to be evaluated only ad hoc and is determinate by the degree of constancy of that character and extent of hiatus between species. From time to time, there appear opinions that some particular characters are generally more important than other. That point of view is unacceptable. For instance, A. Löve (1964) believed cytological characters to be of an exceptional value, treated them as superior to traditional macromorphological ones. However, the very reason macromorphological characters have become traditional is that they are much more convenient to apply in comparison with, say, cytological ones. In systematics, where one never knows beforehand, which character will turn out to be important, the most critical is a researcher's ability to look through as many characters as possible in the largest possible number of specimens. Even the most intricate and sophisticated methods, if applied only to some solitary specimens, would never provide any reliable information about species limits, which can only be obtained when treating material en masse. Hence, speaking about fundamental equivalency of all groups of characters, one has to admit at the same time that practically it is the traditional morphological examination, which still remains the most reliable method of systematics in spite of all advances of chemistry, cytology, etc.

2. A group of characters that describe relations of plants and environment, i. e., ecological and geographical ones. An eco-geographical description of a species is not less important than its morpho-physiological properties. It is an eco-geographical description, which makes it possible to understand a species as a natural object with its own unique niche. Matching results of a morphological investigation with eco-geographical data is one of the major criteria of accuracy when tracing species limits. If there is a contradiction between results of morphological research and ecological or geographical information, then species limits remain doubtful.

3. Genetic characters provide the direct biological connection between specimens. The panmixis, i. e., normal sexual reproduction, is the mechanism that promotes biological coherence and stability of species. Barriers that restrict the panmixis break this coherence. If these barriers last long, then the stream of life, which is initially whole, becomes eventually separated into individual streamlets, each of them with its own history. That is to say, one species gets divided into several ones.

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The possibility of obtaining hybrids between groups as well as the vitality and fertility of these hybrids have been often used as major taxonomical criteria in distinguishing groups. However, the degree of genetic compatibility (or incompatibility), which determinates a possibility of hybridization, is just one of many physiological features. Hence, its taxonomical value may be very variable in different instances. One must bear in mind that a species is not an aggregation of characteristics, but a certain natural formation. Therefore, it is not the degree of potential genetic compatibility (or incompatibility) that matters when searching for species limits, but duration and completeness of the actual genetic isolation. As a result of such isolation, the stream of life, once integral, becomes divided, and both structural and functional differences emerge. It makes no difference, whether it was the genetic incompatibility, ecological differentiation, or geographical disjunction, which was responsible for the genetic isolation. If populations, though potentially quite compatible, are actually separated; if each of them has had its own history, has developed its own set of characters, and occupies its specific niche in nature, then, without doubt, we should assign these populations to different species. If, on the contrary, an experiment shows incomplete or even poor genetic compatibility of populations, that is not supported by morphological, ecological, or geographical differences, then the populations belong to the same species.

The three groups of characters that were mentioned above correspond to three historical stages of our understanding of the species. First of all, the species was recognized as a morpho-physiological phenomenon, certain morpho-physiological entity; later on, the species appeared to be an eco-geographical phenomenon; and finally, genetic one.

A subspecies, as well as species, is a multitude of living beings rather than an assortment of characters. A subspecies is a species that is not well enough isolated. Since it is not sufficiently isolated, its limits cannot be as distinct and clear as those of species. (A practical conclusion which is derived from this statement is that it is not always possible to identify a specimen as a subspecies; assignment of each and every specimen to a subspecies cannot be mandatory.) Of course, some subspecies are more distinct than others. When we deal with the most clearly isolated ones, we have to decide if it is more realistic to treat them as species. As to the least separated ones, the question is if it makes sense to distinguish them at all.

The major criterion for separating a subspecies, as well as species, is the extent of its isolation. If specimens of one population are fairly different from those of another population, this fact alone is not sufficient to segregate the populations in subspecies. We would be able to distinguish subspecies only if we can draw a border between them, at least a vague one. If we cannot trace a border, then we cannot distinguish subspecies. In that case, one has to describe the infraspecific variability in terms that do not belong to the hierarchy of taxonomical units, such as the cline, ecotype, geographical pattern of individual characters and genes, and so on.

25 Here is a typical problem a researcher has practically to deal with. Suppose, there are two or more disjunct areas, and all the plants from each area have some specific characters that make them different from plants growing in other areas. However, these distinctive characters are very "insignificant". Should we treat these disjunct populations as subspecies or separate species? To my mind, in the majority of cases, the latter decision appears to be more reasonable: we should count them as species. Not only the majority of Russian botanists, who prefer "small" species, do comply with this view, but also such prominent researchers of the "western" school as K. Rechinger and H. Merxmüller came to similar conclusions. Their opinions on this problem (Merxmüller 1960: 156, 158; Rechinger 1960: 173) completely agree with what was expressed

by V. Komarov in the introduction to his "Flora of Kamchatka" (1927). Within the genus *Salix* (for instance, in the section *Pentandrae* or subsection *Arbusculae*), one can find impressive examples that prove the accuracy of this concept.

If a species does not include any subspecies, we call it monotypic (i. e., containing a single nomenclatural type). A species that is divided into subspecies is polytypic (containing two or more nomenclatural types). In Russia, there prevails a tendency, started by V. Komarov and supported by the "Flora of the USSR" to present species as monotypic ones. What might be considered as a subspecies by an advocate of the polytypic concept, is treated as a separate species in the "Flora of the USSR". In the West, the opposite tendency is more likely to be found. However, there is no irreconcilable contradiction between these points of view. Not infrequently, a particular situation may be described in terms of the "polytypic" as well as "monotypic" concept. For example, the Siberian spruce, according to V. Komarov, is a distinct species. However, one may also treat the European and Siberian spruces as subspecies of one species. Each of approaches has its own advantages as well as drawbacks. I am more disposed towards admitting the two species, as it helps to express my opinion about the existence of a secondary transitional zone of contact between *Picea abies* and *P. obovata* as well as my personal interest to the historical development of the European flora. However, if one's goal is pure recording of the factual status quo, it may be even more reasonable to accept the existence of a single species with two subspecies. The pair of species *Salix starkeana* and *S. bebbiana* constitutes a very similar case.

Unfortunately, the language is not always used in its precise meaning. Sometimes, the expression "monotypic species" is understood not in a nomenclatural but rather morphological sense, meaning "morphologically homogeneous". However, any "homogeneous species" is a pure chimera unless it is apomictic. Indeed, no species can be completely uniform, that is, morphologically "monotypic", so far as the mutational process, natural selection, and sexual reproduction within species are concerned. One cannot approve a very imperfect intention of V. Komarov found in the introduction to the "Flora of the USSR" to "treat as distinct species all individual plants, even those very similar to others, if they exhibit a certain inherited common feature making them different" (Komarov 1934: 7). This insufficient statement makes it possible to treat any local population as a separate species each time a particular single gene, rare or suppressed in other populations of the species, is manifested. That point of view greatly reminds one of A. Jordan and M. Gandoger and actually opens the way to uncontrolled species-splitting arbitrariness. The eco-geographical concept of the species, which was constantly emphasized by V. Komarov elsewhere in his works, was unfortunately missing from that statement.

Also, I have strong objections against some deviations in treating the notion of the polytypic species. Not infrequently, a complicated group, which an author has either ignored or failed to understand, is presented as "a polytypic species". In so doing, the author piles up everything to subspecies, whether these are real subspecies, cultivars, valid species, morphological variants without any particular geographical destination, vague taxa described a long time ago and not understood by anybody at present, or even pure synonyms. Formally, it all looks excellent: the system appears to be elaborated "in detail", there are even some new combinations proposed; however, the actual result is a mess. Particularly, the West European literature is sinful of "polytypic species" of that kind.

In plants that demonstrate normal sexual reproduction, it makes no sense to distinguish further taxonomical groups within subspecies: these groups would be too obscure. The general notion of population is sufficient to describe all parts of species smaller than subspecies. Any conspicuous, constant, or in a way interesting peculiarities, which are not necessarily restricted

to a particular population, are to be treated as a variety. At present, this notion is accepted rather in a morphological sense, as its taxonomical content is fairly indefinite (when speaking of wild plants; in cultivated plants this term has a certain special meaning). The "form" is equally vague, although, following common practice, they have listed it along with variety in the "International Rules of Nomenclature" together with other taxonomical units.

2. OBSERVATIONS IN NATURE

A conclusion which has to be necessarily derived from the outlined notion of the species is that observations in nature are most significant and critical when working on the species systematics. If these are not possible, then at least herbarium material has to be analyzed en masse. The author was trying his best to follow these obligations and managed to observe 85 species of willows in their natural setting, most of them repeatedly in different regions.

Most reliable and complete results are obtained when using a method that I would call the method of taxonomical transects (profiles). First, a landscape rich in willows is chosen, then all specimens are identified, one after another without any exceptions. This approach provides material for ecological analysis of species and at the same time highlights ranges of their variability along with differences from each other. Simultaneously, herbarium samples are collected in order to depict all variations in each species most completely.

Another method of studying willows in nature, which is usually recommended in the literature, involves collecting two or three times during one season from a single marked specimen. This method works very well as an introduction to the willow study. However, this is hardly possible to apply when dealing with willows on exotic territories that are only accessible by expeditions. Then, instead of marking specimens in nature, we have to take cuttings and cultivate samples for observations in a botanical garden (see section 4). Besides, the method of marked specimens is generally less valuable, since a researcher is necessarily concentrating on morphological details of some few specimens, whereas a transect shows him a whole range of variability of the entire population presented by a multitude of specimens. To be precise, it is only the method of transect, which can be named truly taxonomical. The methods of marking and cultivation may just provide morphological data that need further taxonomical interpretation.

27 The author observed and studied willows in nature at the following destinations (cf. Fig. 1). The letter P in parentheses means that taxonomical profiles were set in large populations at those particular locations.

1. The Kola Pen. around Kola, Aug. 1946. —2. The Khibins, Belaya R. Valley, and the vicinity of Imandra Railw. St., Aug. 1946, Jul. 1956 (P). —3. The southern coast of the Kandalaksha Bay around Poyakonda Railw. St., Aug. 1966. —4. Southern Karelia: Kivach Preserve and Konchozero, Jul. 1956 (P). —5. Suburbs of St. Petersburg (Leningrad): Pavlovsk and Pushkin, Apr. 1954, Mar. 1961 (P); Zelenogorsk, Mar. 1961; Kavgolovo, Mar. 1962. —6. The vicinity of Izborsk (Pskov Obl.), Jul. 1959. —7. The Abava R. Valley between Kandava and Sabile (Western Latvia), Jul. 1959. —8. The Zapadnaya Dvina R. Valley between Plyavin and Koknese and surrounding watershed areas, Jul. 1959 (P). —9. Kurshskaya Kosa around Nida, Jul. 1961 (P). —10. The vicinity of Velizh (Smolensk Obl.), Jul. 1960 (P). —11. Slobodskoy and Demidovskiy distr. (Smolensk Obl.), Jul. 1962. —12. The Dnieper R. Valley near Yartsevo (east of Smolensk), Jul. 1958 (P). —13. The southern Smolensk Obl. between Roslavl and Shumyachi, Jul. 1957 (P). —14. Znamenskiy Distr. (eastern Smolensk Obl.), Jul. 1958 (P). —15. The vicinity of Tarusa (Kaluga Obl.), May 1957, (P). —16. North of Moscow: near Podsolnechnaya Railw. St. and Ozeretskoye, 1949–1953 (P). —17. West of Moscow: Zvenigorod, Golitsyno, Alabino Railw. St., 1949, 1960–65 (P). —18. East of Moscow: Losinyy Ostrov, Balashikha, and Khripan railw. st., 1949–1953 (P). —19. South of Moscow: along the Pakhra R. from Kolychevo to Borovskoy Kurgan, 1948–1953 (P). —20. Serpukhov and Kashira distr. near the Oka R. (Moscow Obl.), 1945–1953 (P). —21. Mikhailov Distr. (Ryazan Obl.), Jul. 1948. —22. The Upper Don R. Valley near

Galichya Gora, May, Jul. 1949, Aug. 1965. —23. Khoperskiy Preserve (Voronezh Obl.), Jul. 1963. —24. Around Voronezh in the Voronezh R. Valley and Voronezhskiy Preserve, Jul. 1965. —25. Petrovsk Distr. (Saratov Obl.), Jun. 1949. —26. Krasnoyarskiy and Rudnyanskiy distr. (Volograd Obl.): the Tersa and Medveditsa valleys and the drainage divide area between the Medveditsa and Ilovlya, May 1959, Jun. 1961 (P). —27. Dubovka Distr. (Volograd Obl.), May 1962. —28. The Volga R. islands near Volgograd, May 1962 (P). —29. Archeda Sands between Frolovo and the R. Don (Volograd Obl.), May 1962, Jun. 1963 (P). —30. The Dnieper R. Valley near Kiev, Oct. 1957. —31. Around Ivano-Frankovsk, near Lvov, Sep. 1957. —32. The Carpathians along the line Vorokhta—Yasinya—Rakhov, Sep. 1957 (P). —33. The vicinity of Khust in Transcarpathia, Sep. 1957. —34. The southern coast of the Crimea Pen. around Alushta, Jul. 1966. —35. Around Vologda, Sep. 1960. —36. Around Kirillov (Vologda Obl.), Sep. 1960. —37. Solvychevodsk and Velikiy Ustyug vicinities (Arkhangelsk Obl.), Sep. 1960 (P). —38. Around Zvoz on the Northern Dvina R. (upstream of the Yemtsa R. Mouth), Sep. 1960 (P). —39. Ilimskiy Preserve in the Southern Urals, Jun. 1950. —40. Around Denezhkin Kamen Mt. in the Northern Urals, Jun.-Oct. 1951 (P). —41. The Upper Sob R. in the Polar Urals, Jul.-Aug. 1964 (P). —42. The Upper Khadata R. (left tributary of the Shchuchya) in the Polar Urals, Jul. 1964 (P). —43. The Lower Ob R. Valley near Labytnangi, Aug. 1964 (P). —44. The vicinity of Seyda Railw. St. (south of Vorkuta), Jul. 1964. —45. The Gorge of the Lower Bzyb R. (Abkhazia), Apr. 1953. —46. The Aragva R. Valley near Mtskheta, Apr. 1953. —47. The vicinity of Kirovakan (northern Armenia), Sep. 1962 (P). —48. Around Idzhevan and between Idzhevan and Krasnoselsk (northern Armenia), Apr. 1953 (P), Sep. 1962. —49. Razdan Distr. on the Upper Marmarik R. (Armenia), Sep. 1962 (P). —50. The Kasakh R. Canyon upstream of Ashtarak (Armenia), Apr. 1953 (P). —51. The Tsav R. Valley south of Kafan (southern Armenia) and the Okhcha R. Valley near Pirchevan Railw. St. (southwestern Azerbaijan), Oct. 1962 (P). —52. Talysh: between Lenkoran and Lerik (southern Azerbaijan), Oct. 1962. —53. Near Kasmalyan in Zuvandskaya (Diabarskaya) Depression, Talysh (southern Azerbaijan), Oct. 1962. —54. The vicinity of Kara-Kala in the western Kopet-Dag, Oct. 1956. —55. The Firyuzinskoye Gorge in the Kopet-Dag, near Ashkhabad, Oct. 1956 (P). —56. The Amu Darya R. Valley near Farab Railw. St., Oct. 1956. —57. The Zeravshan R. upstream of Samarkand, Apr. 1958 (P). —58. The Zeravshanskiy Rg. south of Samarkand (Aman-Kutanskoye Forestland), Oct. 1956, Apr. 1958. —59. The Upper Kashka Darya R. upstream of Kitab, Apr. 1958. —60. The Varzob R. Gorge north of Dushanbe, Oct. 1954, May-Jun. 1965 (P). —61. The Lower Gunt R. near Mordzh and Chartym (the Western Pamirs), Sept. 1954 (P). —62. The vicinity of Khorog; along the Shakh dara and Pyandzh, Sep. 1954 (P). —63. Dzhamantal Stow near Murgab (the Eastern Pamirs), Sep. 1954. —64. Chigirchik Pass southeast of Osh, Sep. 1954. —65. Ak-Terek Forestland near the foot of the Baubash-ata Rg. (north of Dzhahal-Abad), Oct. 1954. —66. Parkentskiy Preserve (the western Chatkalskiy Rg. in the Western Tien Shan), Oct. 1962 (P). —67. The Angren R. Valley in the Western Tien Shan, Oct. 1956, May 1958 (P). —68. The vicinity of Gazalkent and the Chimgan Massif in the Western Tien Shan, Oct. 1956, May 1958 (P). —69. The lower reaches and canyon of the Dzhebogly R. (the northwestern edge of the Talasskiy Rg.), May 1958 (P). —70. The Arys R. near Tamerlanovka and Darmina State Farm, May 1958 (P). —71. The Syr Darya R. Valley near Yany-Kurgan and Tartugay, Oct. 1956. —72. Around Burno-Oktyabrskoye in the depression between the Karatau and Talasskiy ranges, May 1958. —73. The Talas R. Valley upstream of Budenny, May 1958 (P). —74. The R. Chu in Buamskoye Gorge near Rybachye, Sep. 1956, Jun. 1958 (P). —75. Northern slopes of the Terskey Rg. near Przhevalsk and Dzhety-oguz Resort, Sep. 1956, Jun. 1958 (P). —76. The Zailiyskiy Rg. near Alma Ata, Sep. 1953, May 1958, Sep. 1963 (P), May 1965 (P). —77. The Ili R. Valley near Iliysk, Sep. 1953, May 1958, Sep. 1963 (P). —78. Sarytogoy Stow on the Lower Charyn R., Sep. 1963 (P). —79. Kurtogoy Stow on the Middle Charyn R., May 1965. —80. The vicinity of Irkutsk and the Lower Kitoy R., Aug. 1955 (P). —81. Around Listvennichnoye on Lake Baykal, Aug. 1955. —82. The Lower Selenga R. Valley downstream of Ulan Ude, Aug. 1955 (P). —83. Tunkinskaya Valley near Arshan and the Arshan Golets, Aug. 1955 (P). —84. The vicinity of Vysokogornaya (Muli) Railw. St. in the northern Sikhotealin, Sep. 1955 (P). —85. The vicinity of Sovetskaya Gavan, Sep. 1955. —86. The vicinity of Vladivostok, Sep.-Oct. 1955 (P). —87. The Suyfun Valley near Razdolnoye Railw. St. north of Vladivostok, Sep. 1955. —88. The vicinity of Kangauz Railw. St. (between Vladivostok and Suchan), Sep. 1955. —89. Suputinskiy Preserve (near Ussuriysk), Oct. 1955. —90. Kedrovaya Pad Preserve and Cape Gamov in the southernmost Maritime Prov., Oct. 1955 (P). —91. The vicinity of Ilyinka on the western shore of Lake Khanka, Oct. 1955 (P). —92. The Upper Suchan R., Sep. 1967. —93. The Ussuri R. Valley near Khabarovsk, Oct. 1955. —94. The vicinity of Yakutsk, Aug. 1967. —95. The vicinity of Aldan, Sep. 1967. —96. Around Bolshoy Nimnyr,

the Aldanskoye High Plateau, Sep. 1967. —97. The vicinity of Yuzhno-Sakhalinsk, Oct. 1967. —98. The vicinity of Poronaysk on Sakhalin, Oct. 1967. —99. The Harz Mountains, Oct. 1964.

3. HERBARIUM MATERIAL

In addition to own collections, the following herbarium material was examined and taken into consideration by the author (the year in parentheses indicates the time when each particular part was inspected).

A. Major Domestic Depositories

Herbarium in the Botanical Institute of the USSR Academy of Sciences in Leningrad (St. Petersburg): Main (1964), European Russia (1963), Siberia and the Far East (1964), the Caucasus (1963), Middle Asia (1960), East Asia (1965);

Moscow University: the entire collection (1963);

Tomsk University: Transbaykalia and Krasnoyarsk Province (1955), Mongolia (1960), major part of West Siberian collection (1955);

Tashkent University: the entire collection (1959);

Botanical Institute of the Georgian Academy of Sciences in Tbilisi: the Caucasian collection (1962);

Botanical Institute of the Armenian Academy of Sciences in Yerevan: the Caucasian collection (1962);

Botanical Institute of the Azerbaijanian Academy of Sciences in Baku: the entire collection (1962);

Botanical Institute of the Kazakh Academy of Sciences in Alma Ata: the entire collection (1965);

Botanical Institute of the Tadjik Academy of Sciences in Dushanbe: the entire collection (1962);

Botanical Institute of the Ukrainian Academy of Sciences in Kiev: the Ukrainian collection of the Soviet period (1957);

Institute of Biology of the USSR Academy of Sciences, the Urals Branch in Sverdlovsk (Yekaterinburg) (1953 and a part of later collections).

B. Domestic Depositories of Smaller Magnitude¹

Main Botanical Garden in Moscow (1966);

All-Union Institute of Medicinal Plants (1966);

Geographical Department of the Moscow University (1963);

Lvov University: a part of the collection (1957);

Lvov Museum of Nature (1957);

Perm University: a part of the collection (1953);

Polar-Alpine Botanical Garden in the Khibins: a part of the collection (1956);

Chernovtsy University (1962);

¹ Although these depositories are considerably smaller than those listed above, they proved to have critical material for treatment of some very important regions, such as Adzharia, the Carpathians, Kopet-Dag, and Kuril Islands.

Dagestan University in Makhachkala (1962);
 Batumi Botanical Garden (1962);
 Botanical Institute of the Uzbek Academy of Sciences in Tashkent: a part of the collection (1956–1959);
 Leninabad (Khodzhent) Pedagogical Institute (1962);
 Leningrad (St. Petersburg) Academy of Forest Technology (1961);
 Far East Branch of the USSR Academy of Sciences in Vladivostok (1967);
 Sakhalin Science Institute (1967);
 Yakutian Branch of the USSR Academy of Sciences (1967);
 Novosibirsk Botanical Garden of the USSR Academy of Sciences (1964);
 Caucasian National Preserve (1962);
 Ashkhabad Botanical Garden of the Turkmenian Academy of Sciences (1959).

C. Material from Foreign Herbaria

The following institutions have granted the author material for examination, either directly or through the courteous assistance of the St. Petersburg Botanical Institute.

Florence University: the majority of its European funds, ca. 3,000 samples (1964);
 People's Museum in Prague: the All-European Collection, ca. 2,000 samples (1966);
 Museum of Natural History in Wien: the Near East Collection and some European groups, ca. 400 samples (1964);
 British Museum: a part of the holdings on the Near East and Himalayas (1966);
 Royal Botanical Garden in Edinburgh: collections from Asia Minor and the Himalayas, ca. 300 samples (1966);
 National Herbarium in Munich: some European groups, ca. 300 samples (1963);
 Royal Botanical Garden in Kew: a number of authentic specimens and English species;
 Trinity College in Dublin: some Irish species;
 Museum of Natural History in Paris: a number of authentic specimens and material from Northern Africa and France;
 National Museum in Stockholm: a number of authentic specimens and some Scandinavian samples;
 Botanical Museum in København: material on the Near East;
 Bergen University: collections from the Himalayas;
 Graz University: a number of alpine species;
 Jena University (Haussknecht's Herbarium): a large part of the Near East funds;
 Sofia University: a number of Bulgarian species;
 Tokyo University: a number of authentic specimens;
 United States National Herbarium in Washington, D. C.: material from Asia;
 Arnold Arboretum of Harvard University in Boston, MA: a number of authentic specimens and some Asiatic species;
 Indian Botanical Service in Calcutta: Himalayan species.

D. Other Material

Various institutions and individual domestic and foreign collectors have granted the author their material, either in exchange or as presents or lent it for studying and identification. The most important contributions were made by V. N. Vekhov (the Indigirka and northern Karelia), V. P. Vinogradov and S. V. Golitsyn (Lipetsk Obl.), V. P. Vipper and

L. F. Pravdin (Transbaykalia), I. D. Guseinov (Azerbaijan), L. Demidova (northern Yakutia), T. G. Derviz-Sokolova (Chukotka and the Anadyr), S. S. Ikonnikov (the Pamirs), I. V. Kamenetskaya (Groznyy Obl. and Krasnoyarskiy Prov.); N. D. Kozhevnikova (Kirghizia), V. N. Korkina (southern Maritime Prov.), L. Makhayeva (the Lower Yenisei), L. I. Malyshev (the Eastern Sayans), N. A. Minyaev with colleagues (Pskov Obl.), G. V. Popov (the Southern Urals), L. I. Popova (Kirghizia), V. S. Preobrazhenskiy and Ye. Popovichev (the Vitim High Plateau), S. I. Sagitov (Kara-Kalpakia), N. Smirnova (the vicinity of Irkutsk), L. N. Sobolev (Kirghizia), V. V. Tuganayev (Udmurtia), V. Feldman (Novgorod Obl.), H. Em (Macedonia), J. Chmelař (Czechia and Slovakia), E. L. Swann (southeastern England), K. Larsen (Scandinavia, the Alps, Iceland), A. R. Pinto da Silva (Portugal), O. de Bolós (Catalonia), J. Chaze (France), A. Neumann (the Alps), H. Hartmann (the northwestern Himalayas), H. Halgrimsson (Iceland), S. Steindósson (Iceland).

The material enlisted above made it possible to critically review all the species presented in this book. No species was admitted relying solely on literature data. Neither any characters were used in the keys or descriptions without testing them on real plants.

4. OBSERVATIONS OF CULTIVATED PLANTS

I started a nursery of willows in the Botanical Garden of the Moscow University in 1952. I collected the majority of the samples myself in 1954–1958 during my expeditions to various regions of the USSR. By the end of 1962, when most of observations of the collected material were completed, there were 265 clones of willows from the territory of the USSR, belonging to 74 species and subspecies. If one subtracts the species that naturally grow around Moscow and can be easily studied without moving them to the botanical garden, then 67 species and subspecies in 251 clones could be counted in the collection. The list of the species grown in the nursery was published in one of the author's articles (Skvortsov 1961b).

In certain respects, observations in the nursery were of great significance. First of all, they were important for completing morphological descriptions of those species that were hard to observe at some phenological stages in nature, such as species from the Far East or Carpathians during the flowering phase.

Important data were obtained as regards *S. dasyclados* while studying the seedlings grown from several seed samples. This species sometimes, even in authoritative studies (Rechinger 1957, 1964), is still considered to be a feral hybrid. However, the seeds of *S. dasyclados* proved to be normal, regularly germinating; there is no hybrid segregation in the progeny. Of course, observations in nature and geographical data may as well prove that this is a species rather than hybrid. Yet a direct experiment is also of significance.

Finally, observations of changes, if any, when plants were shifted from their natural habitats to the nursery, enabled the author to make essential conclusions about the nature of variability in the willows (see chapter 3, section 4).

Although the observations in the nursery were very valuable and important for some parts of the study, generally, they could only play a subordinate part. 250 clones sounds a lot for a living collection, yet this is very little in comparison with some 90–100 thousand herbarium samples and 20–30 thousand clones observed in natural settings. It is absolutely impossible to represent each species in the nursery as completely as it is represented in herbarium: by series of samples from all parts of its area. Besides, the maintenance of 250 clones in the nursery is hardly easier or cheaper than that of 10 thousand herbarium samples. Finally, plants in the

nursery are grown in a completely foreign, exotic environment, being deprived of their usual natural habitats. Hence, excluding some special situations, the method of observations of cultivated clones is, of course, generally inferior to herbarium study and still more inferior to observations in nature.

5. COMPILATION OF SPECIES DISTRIBUTION MAPS

All distributional maps presented in this book are original. They are based primarily on information from labels on herbarium specimens that had been examined and identified by the author. While drawing species distribution maps within the territory of the former USSR, literature data were used only to a very minor extent. There was practically no need for literature data, as the overwhelming majority of original herbarium sources, which had been treated in the literature, were considered directly by the author. Besides, one can hardly rely on these literature data, except some, concerning particular species and regions. Maps involving territories of the adjacent Asiatic countries, from Turkey to Mongolia, are based exclusively on herbarium specimens' analysis. Along with herbarium material, some literature data were used with appropriate critical corrections for the territories of Northeast China, Korea, and Japan. Available information concerning Western Europe and Northern Africa was used extensively; however, all major features of species' distributional areas were as well controlled with the aid of herbarium material. The herbarium study resulted in rejection of some of evidence provided in the literature, such as the distribution of *S. purpurea* in Greece, Macedonia, and Asia Minor, *S. caprea* in Iran, *S. myrsinifolia* in Italy, *S. phyllicifolia* in the Pyrenees, *S. cinerea* on the Corsica and Sardinia, and so on. Of all the territory of Western Europe, strangely enough, that of Great Britain proved to be the most difficult when drawing maps of species' areas. Despite the availability of numerous "floras" and an excellent "Atlas of the British Flora" (1962), it remains unclear if such species as *S. alba*, *S. pentandra*, *S. purpurea*, and *S. viminalis* are indigenous to the British Isles and, if so, where their natural geographical limits are.

6. NOMENCLATURE, AUTHENTIC SPECIMENS, SYNONYMY

The species' names by C. Linnaeus are accepted here without revision, in the sense that was established as long ago as the early last century, based primarily on interpretations of J. Smith, G. Wahlenberg, and E. Fries. It is worth mentioning that there are still some concerns regarding at least three of the species epithets by C. Linnaeus: *arbuscula*, *arenaria*, and *rosmarinifolia*. Linnaean Herbarium was mostly preserved in England, so that some prominent subsequent researchers did not have access to it when writing on the willows of Scandinavia and Central Europe. They had to judge the Linnaean species relying upon diagnoses by C. Linnaeus, which were extremely short, and notes by J. Smith, who had the Linnaean Herbarium at his disposal. Anyway, the "method of types" did not yet exist in the last century, and authentic herbarium samples did not have the significance they have nowadays. The "legible contents" of diagnoses was usually considered to be of more importance. F. Wimmer (1866: LVI) articulated that concept as follows: "Herbarii Linnaeani ... auctoritas est nulla, ubi verba Linnaei contradicunt." ("The authority of Linnaean Herbarium equals zero if it contradicts Linnaeus' words"). C. Linnaeus himself did not assign any critical significance to the herbarium. His herbarium is far from being completely consistent with the text of "Species plantarum", and the labeling is insufficient, according to

modern criteria (Jackson 1912; Savage 1945; Stearn 1957). In 1907, S. Enander published a detailed investigation of the willow samples in the Linnaean Herbarium (Enander 1907). Unfortunately, S. Enander rarely recognized distinct species in any of the herbarium samples. Therefore, that publication did not lead to final clarification of the Linnaean species' types. Elimination of remaining confusion with regards understanding of the Linnaean names will be a challenge for future investigators of the Linnaean Herbarium. So far, we do not have any choice other than to apply the existing names in the traditional sense, the way they have been established in the European literature since the 30–50's of the last century.

Also, some old species names by other authors (J. Scopoli, C. Willdenow, F. Brotero, and others) were accepted here without referring to types, relying upon the well-established approach to these species in Europe or other sufficient evidence.

The nomenclature of the rest (the majority) of the treated species was revised. The author took every effort to examine type specimens with respect to all species names ever published regarding the flora of this country. Type specimens were available in the majority of cases, whether these were valid species names or synonyms. The Herbarium of the St. Petersburg Botanical Institute is the richest one in type specimens. In addition to the types of species described by C. Ledebour, N. Turczaninow, E. Trautvetter, N. Andersson, and subsequent authors, there is also a number of authentic specimens by P. Pallas, some of which (*S. gmelinii* Pall., *S. arbutifolia* Pall.) were newly discovered by the author, as they had been overlooked before. There, I also managed to locate the type of *S. excelsa* by S. Gmelin (Gmelin, Jr.), as well as isotypes of *S. starkeana* Willd., *S. coesia* Vill., and *S. daphnoides* Vill. Types of a number of species by E. Wolf, which were missing from the Botanical Institute, proved to be preserved in the Herbarium of the St. Petersburg Academy of Forest Technology (formerly, the Forest Institute), where I had a possibility to examine them. A comparatively small number of holo- and isotypes are kept in Moscow, Tashkent, and Alma Ata herbaria. Types of 28 species were received from abroad.

In the majority of cases, it was possible to sufficiently treat those species, types of which were not available for the study, relying on other data. For species described in North America and well-known by American authors, such as *S. vestita*, *S. alaxensis*, and *S. bebbiana*, merely a series of good American samples proved to be sufficient. A fair number of the Far East species can be reliably identified using available high-quality images of authentic samples. These are *S. miyabeana*, *S. kangensis*, *S. tontomussirensis*, *S. kimurana*, *S. metaformosa*, *S. sericeo-cinerea*, *S. sugawarana*, *S. koidzumii*, *S. taraikensis*, and *S. orotchorum*. There are some names left, mostly of plants from the Kuril Islands and Sakhalin, introduced by A. Kimura, for which there are no sufficient images available. Several attempts to reach A. Kimura's collections, which are preserved at his private herbarium, proved to be unsuccessful. Fortunately, substantial material from the Kurils and Sakhalin has been accumulated in herbaria of our country, so that there is hardly a chance to overlook any species from these islands. Hence, the only thing left to do is to attribute the existing names to real collected samples. Thanks to A. Kimura's conscientious attention to detail in descriptions of species, one can do it quite well.

33 Of all the species ever described from the territory of the former USSR, there are just two that still remain completely dubious: *S. macilenta* Anderss. and *S. behringica* Seemen. Their types were preserved in Berlin and are probably lost. Of the West European species, *S. hibernica* Rech. f. and *S. cantabrica* Rech. f. are still unclear. They have been recently described from very scanty material. Of the names accepted here, two remain somewhat doubtful. These are *S. vulpina* Anderss. and *S. kurilensis* Koidz. Since their types were

unavailable, I accepted A. Kimura's treatment for these species. Some few synonyms that are not yet sufficiently clarified are assigned question marks in the text.

The old-fashioned way to refer to samples when describing a new species did not provide that one of the samples had to be marked as the holotype. At present, we can retroactively distinguish holotypes for species described a long time ago. However, I refrained from doing that, except some occasions that appeared to be really critical, for instance, when that was necessary for clarification of species' magnitude. In cases when there was no necessity for retroactive naming of holotypes, under the heading 'Type', I used to mention all samples that had been cited in each original species description.

The synonymy in the genus *Salix* is extremely bulky, so that it is impossible (and unnecessary) to cite all of it here. Synonyms that were clarified long ago are not listed, as they have lost any significance.

Also, the nomenclature of the subgenera, sections, and subsections has been revised in this study and brought to agreement with the requirements of the International Code. When choosing names for the sections, the author mostly used those based on Eurasiatic material. The nomenclature of the sections (as well as systematics of the willows on the whole) in North America has been long developing separately, in its own special way. To make it consistent with the Eurasiatic nomenclature, may become possible only after a joint study of all the American and Eurasian willows. Any attempts to solve this problem relying on literature data would lead to nothing but blunders.

Types are named here for all the subgenera, sections, and subsections (so far, the majority of sections were not typified). The author specially addressed the nomenclature and typification of the subdivisions within the genus in a separate publication (Skvortsov 1968).

Chapter 3

ECOLOGY AND MORPHOLOGY

1. DELIMITING AND GENERAL MORPHOLOGICAL DESCRIPTION OF THE GENUS *SALIX*

The *Salicaceae* family is known to be quite natural and shows marked distinctions. Therefore, the majority of contemporary taxonomists treat it as a separate order *Salicales*. Division of the family into two major groups, the willows and poplars, is also beyond question.¹ As for the number of genera, there is yet no consensus among researchers. Many still accept the classical division into two genera, *Populus* and *Salix*. However, it is also possible to justify the acceptance of six genera: three within the poplar group (adding *Tremula* and *Turanga*) and three within the willow group (adding *Chosenia* and *Toisusu*).² To my own opinion, it is most reasonable to accept three genera: *Populus*, *Chosenia*, and *Salix*. There is no need to justify the recognition of *Populus* and *Salix*. However, I would say a few words about treating *Chosenia* as a separate genus.

The *Chosenias* are anemophilous trees, as well as the poplars. Also like the poplars (as opposed to the willows), they start to bloom only with age, on attaining a rather large size, their flowers all in the upper part of the crown. The bark on old *Chosenia* stems is very special: it exfoliates in patches, somewhat alike the bark in the willows of the section *Amygdalinae*, yet not exactly alike. According to M. Gzyryan (1955), the feature of *Chosenia* as well as *Populus* wood anatomy is homogeneous rays, a more advanced character as compared to heterogeneous rays in *Salix*. The catkins in *Chosenia* are fully drooping; nectaries completely reduced; stamens connate to bracts, their filaments not elongating during the flowering period, so that the anthers never emerge from under bracts, as it would happen in the willows.

I believe that these differences are good reasons to treat *Chosenia* as a separate genus. However, the similarity of both genera is also quite clear. The general flower structure including its developmental stages and features of anatomy is the same in *Chosenia* and *Salix* (Hjelmquist 1948). Some flowers in *Chosenia* were found to have rudimentary nectaries (Kimura 1938b). The structure of *Chosenia* buds is much alike that of *Salix cardiophylla* buds. The leaf anatomy of *Chosenia* reminds one of primitive American willows from the

¹ Yet, it does not appear reasonable to assign the rank of families to these groups, as it was proposed by L. Kupriyanova (1965): this would hide the obvious close relation between the willows and poplars.

² A. Yarmolenko's (1949) proposal to segregate the genus *Tsavo* was nothing but pure misunderstanding. There is no doubt that *Tsavo* belongs to the *Turanga* poplars.

section *Longifoliae*. Therefore, it would also be acceptable to treat *Chosenia* as a subgenus. On the other hand, it does not seem appropriate to segregate the chosenias in a separate tribe, apart from the willows, as it was proposed by T. Nakai (1930) and A. Kimura (1938b). One can say with confidence that the chosenias filiated from some primitive willows after the willows and poplars had become distinct. The anemophily in the chosenias has been definitely acquired secondarily. The anatomic differences from the willows have also developed secondarily, in parallel to those in the poplars.

Hence, it appears acceptable to treat *Chosenia* separately; however, one can hardly go along with any further divisions of the genus *Salix*. I cannot consider *Toisusu* as a distinct genus (Kimura 1928, 1934b: 396, 1938b: 392). What makes *Toisusu* different from *Salix* is nothing but drooping catkins and caducous styles. A. Kimura used these features along with the possibility for *Toisusu* and *Chosenia* to hybridize naturally to prove their close relation and placed both in the tribe *Chosenieae*, as opposed to the tribe *Salicineae*. However, many willows (*S. songarica*, *S. radinostachya* Schneid., *S. denticulata* Anderss.) also do have rather drooping catkins; and caducous styles occur, for example, in the section *Humboldtianae*. Still, one should admit that A. Kimura had a keen eye to notice that *S. cardiophylla* is set quite off other willows and point to interesting similarity of this species and *Chosenia* in a number of characters.

Other attempts to divide the genus *Salix* are of merely historical interest today. An establishment of a whole series of genera by C. Rafinesque (1817, 1838) and P. Opiz (1852) was not supported by any serious research and merely depicted the general taxa-splitting tendency of the early last century. The segregation of *S. reticulata* in the genus *Chamitea* by A. Kerner (1860) can be of course attributed to his insufficient familiarity with non-European species. Now, it is quite obvious that *S. reticulata* is not as much different from other willows as it seemed to A. Kerner.

The major features of the genus *Salix* (as opposed to *Chosenia* and *Populus*) are as follows.

The willows are woody plants of various habits and sizes ranging from huge upright trees (*S. cardiophylla* can be as tall as 35 m; *S. alba* and *S. excelsa*, to 30 m, their stem diameter up to 1 m and even more) to tiny dwarf shrubs just a few centimeters long, their stems submerged in substrate. The majority of species are shrubs. Rooting branches are quite common in the willows, but there is no root offspring, which is so typical of the poplars (an American willow *S. interior* is the only exception). One- and two-year-old seedlings still retain their terminal buds in many willow species (it appears that persistent terminal buds occur regardless of species systematic position). However, the terminal bud dies off during subsequent years, and the shoot starts to grow sympodially.¹ The willows do not have real spurs (brachyblasts), although spurs are very pronounced, for example, in the balsam poplars.

¹ R. Scharfetter (1953: 86) mistakenly considered terminal buds to be persistent in mature specimens of some tropical willows. He also considered the sympodial growth in the willows to be induced: caused by migration of the willows to regions with the temperate climate. This assumption does not have any proof. The sympodium is quite common in tropical species as well as non-tropical. Species of temperate climates normally finish their annual growth, the point of their terminal growth dying off, much earlier than the fall comes; it is only in epicormic shoots, that the cessation of growth sometimes happens to be induced. The poplars may be regarded as one more illustration of the evolutionary importance of a swing to sympodium, although we cannot yet point to the real cause of that change. The group of boreal poplars (aspens) has preserved the monopodial manner of branching, whereas the southern group of *Turanga* poplars, which is also represented in African tropical regions, switched to the sympodium similarly to the willows. Some of the arctic willows have underground stolons, which grow monopodially.

The axillary buds in the willows are covered each with one scale. The scale is rather coriaceous and actually consists of two connate prophylls. These can have their margins either distinct, overlapping on the adaxial side of a bud, or connate, and then the scale looks cap-like. In mesophilic species of the forest belt, the stipules usually are fully developed and then they are green and assimilating; however, often they are reduced, completely or almost completely. The petioles are either channeled or round on the transection, but never as compressed on both sides as in many poplars. Leaf blade margins are usually more or less glandular-dentate, rarely completely entire. Lobed or deltoid leaf blades, which are typical for some poplars, never occur in willows.

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The inflorescence is a unisexual catkin, mostly erect, occasionally more or less drooping, either sessile (on a previous-year shoot) or terminating a foliated shoot of a moderate size. Flowers are sessile, located in bract axils¹, their perianths lacking. They are replaced by one or two (or a few) nectariferous glands, which occasionally are connate into a lobed glandular disk. These glands are obviously homologous to the cup-shaped disk in the poplars (which is sometimes called perianth). Probably, they are modified bracteoles and also maybe other phyllomes of a reduced flower axis. The stamens count from two to twelve; if two or three, then they are transversely arranged, their anthers extrorse; if many, then they are positioned randomly. The pollen is sticky; pollination is performed by insects. Anemophily in some species (e. g., *S. polaris*) has been mentioned in the literature, yet this is very doubtful. The pollen grains of the willows morphologically resemble those of the chosenias, but are very different from those of the poplars (Kupriyanova 1965). The ovaries are usually stipitate (borne on gynophores), each consisting of two transversal carpels, paracarpous. The ovules are anatropic, counting four to twelve per ovary, each with a single integument. The seeds are very small, as small as in the poplars and chosenias, each with a basal bundle of trichomes (of placental origin). There is no endosperm, and the embryo contains chlorophyll. The germination is extremely prompt.

The willow chromosomes are small and uniform. The basic number is 19 in the willows as well as the rest of the family. Occasionally, 22 chromosomes were reported, which was probably a result of chromosome fragmentation. Two or three different chromosome numbers are found in many willow species. The maximal one, $2n = 190$, is known in *S. myrsinites* and *S. glauca* ssp. *callicarpaea*, which appear to be decaploids (Wilkinson 1944; Löve, Löve 1961).

The genus *Salix* consists of some 330–350 species distributed across major parts of world's continents. The willows are missing from Australia, New Zealand, Oceania, Antarctic, as well as eastern Indonesia, tropical Western Africa, and eastern Brazil. The rest of the tropical area is inhabited by some few species. The willows are most widespread in northern Eurasia, northern North America, and in the mountains of China.

¹ There is no doubt that bracts are modified leaves of the rachis. In some species (*S. fragilis*, *S. capusii*, and others), one can often observe gradual transition from normally developed leaves to bracts along the rachis. In the section *Vetrix*, one can find ear-shaped outgrowths at the base of the lowermost bracts: apparently, these correspond to stipules in normal leaves. In case a catkin proliferates, bracts develop back into leaves. Therefore, any attempts to treat bracts as a part of the flower axis (Fisher 1928) seem very unnatural and cannot be accepted. This was actually demonstrated by Hjelmquist as early as 1948 (Hjelmquist 1948). In poplars, too, bracts constitute a part of the rachis, rather than flower axis. Hence, so far we cannot confirm any hypotheses assuming the original complex, ramified structure of the inflorescence in *Salicaceae*.

2. ECOLOGY

The whole *Salicaceae* family is known to be very demanding for water and light. *Salicaceae* are also famous for the ability to colonize freshly emerging substrates. A considerable part of the species are pioneer plants on river alluvia. In dry climate conditions, aside from river banks and shores of ponds and pools, *Salicaceae* can survive only in habitats with elevated moisture, such as depressions, gullies, gulches, or kettle holes. On the contrary, in favorable, humid climates they colonize all kinds of habitats. These major ecological features of the family are pronounced most in the seed structure. The seeds are minute, dispersed by wind in large quantities, and, in the majority of species, germinate extremely promptly on exposed surfaces of moist substrates. It is the green, completely formed embryo as well as soft permeable skin that add to the ability of the seeds to germinate as early as the first day on their dispersal. (This applies to temperate and warm climates and suitable environments. In Arctic, it takes seeds two or three days or even more time to germinate). At the same time, this prompt germination together with essential lack of feeding reserves inside the seeds become harmful in the shade as well as in conditions of insufficient moisture.

R. Scharfetter (1953: 95) considered this lack of reserves and prompt seed germination to be a proof of tropical filiation of the family ("an atavism of the tropical past"); yet these features are not at all atavistic. They rather constitute a major contemporary mechanism used by *Salicaceae* to conquer a variety of habitats. Besides, skipping the dormant period is by no means an absolute rule for the seeds of *Salicaceae*. In the section *Pentandrae*, seeds ripen in the fall, but germinate usually in the spring. In nature, seeds of some arctic willows may retain their germinating ability throughout the wintertime and germinate during the following spring. According to my own observations, these are *S. lanata*, *S. myrsinites*, *S. reticulata*, and probably some other species. Apparently, this is a useful adaptation to the ecological conditions. *S. pentandra* inhabits primarily transitional graminoid wetlands dominated by *Carex* and *Calamagrostis* and paludal open woodlands. Dense and tall ground cover usually develops there by June. If the seeds of *S. pentandra* got ripen by that time, the same way as it happens to many other willow species, its seedlings would inevitably die. As the seeds germinate in early spring, the seedlings manage to complete their first annual increment as early as June-July. Neither it is favorable for arctic willow seeds to germinate at the start of the winter, even when they ripen by the first frosts in the fall. It is much better for them to start growing in the beginning of the following summer. S. Sagitov (1964) found out that in the Amu Darya Delta, the time for willow seeds to ripen is consistent with that of flood decrease when substrates suitable for willow colonization become exposed. Similar correlations may be found for still more localities and substrates. 37

The willows and poplars have much in common in terms of ecology. Yet the willows appear to be much more adaptable in comparison with the poplars. They have succeeded to develop a considerably wider range of habits and adapt to much more variable environments. Accordingly, the number of willow species is about 10 times as large as the number of poplars. One can compare the willow and poplar habits and habitats with the help of Table 1.

Table 1. Comparison of the genera *Populus* and *Salix*

<i>Populus</i>	<i>Salix</i>
All species are trees.	Perfect trees constitute a minority of species. The vast majority of the willows are either shrubs and dwarf shrubs or transitional forms between shrubs and short-stemmed trees.
The poplars mostly reproduce by abundant root suckers.	The willows rarely develop root suckers.
Warm temperate regions are the richest ones in poplar species.	Cold temperate regions are the richest ones in willow species.
The poplars are missing from the tundra and alpine zones as well as from paludal and oligotrophic substrates.	The willows are especially abundant in tundra and alpine zones. Many willows inhabit paludal and oligotrophic substrates.

Now, let us take a more close look particularly at willow ecology. First of all, there exist two major ecological groups: the alluvial and non-alluvial species. Members of the first group are very demanding to aeration and need a rapid water flow. Hence, they usually inhabit deposits (alluvia or drifts) that accumulate along river beds and runoff hollows. These are mostly trees or vigorous, tall shrubs, often harvested for their flexible, virgate shoots, typically narrow-leafed. Some species need special kinds of alluvial deposits. For example, *S. songarica*, *S. alba*, and *S. wilhelmsiana* prefer fine sandy or sandy-muddy deposits; *S. viminalis*, *S. schwerinii*, *S. turanica*—either sand or fine pebbles; *S. niedzwieckii* and *S. elaeagnos*—rough, coarse pebbles.

Non-alluvial species may colonize various substrates including clayey, peaty, moss-covered and, of course, sandy ones. These have less demands for substrate aeration and often cope with stagnant water, paludification, or even stay content with a rather moderate moisture of regular forest or meadow soils. Here belong forest, rock, wetland, tundra, and alpine species. Though their habits may vary considerably, broad leaves are generally typical for members of this group as well as a reduced ability to produce slender rods.

Alluvial species on the whole have wider latitudinal and altitudinal ranges in comparison with non-alluvial ones. For instance, via river valleys, species that are generally restricted to the forest belt may reach either the steppes and semi-deserts (like *S. triandra*, *S. viminalis*, *S. elbursensis*) or the tundra (*S. viminalis*, *S. dasyclados*, *S. udensis*). Alluvial willows *S. pycnostachya*, *S. capusii*, *S. wilhelmsiana* have absolute altitudinal ranges of about 3,000 m in Middle Asia; *S. alaxensis* and *S. boganidensis*, about 1,000 m in the Kolyma Basin. Non-alluvial species tend to be more restricted both to appropriate latitudes and altitudes.

Distinguishing between the two described ecological groups is very important; however, it should not be considered as an absolute rule. Both at high elevations and high arctic latitudes, where true, large alluvial shrubs cannot survive, alluvial habitats are often occupied by some non-alluvial species instead. To take an example, in the Pamir-Alay, non-alluvial *S. coesia* and *S. rosmarinifolia* ssp. *schugnanica* invade alluvia starting from an elevation of about 3,000 m. Non-alluvial *S. reptans* and *S. nummularia* often invade alluvial sand at the Lower Yenisei and Lower Lena. Besides, in the mountains there are many habitats of an intermediate status, like runoff hollows, which have neither any distinct river beds nor any large sediment deposits. Along these hollows, alluvial willows occur together with non-

alluvial ones. Even within the forest and forest-steppe belts, where the differences between alluvial and non-alluvial species are most pronounced, there are still some intermediate habitats. These are, for example, oxbow lakes on flood plains, banks of bayous, or muddy banks of slow rivers. There, as well, non-alluvial species meet alluvial ones. For instance, *S. triandra*, a typical alluvial species, may be often found in the like habitats together with *S. cinerea*, which is non-alluvial. This is especially true for southern locations. Also, on high river levees, behind the band of alluvial species, there occurs a non-alluvial *S. myrsinifolia*, sometimes together with *S. caprea*. *S. acutifolia* may grow on either alluvial or inland sand (in the latter case, far away from any rivers).

Willow species also vary in their demands to moisture. Some willows would not tolerate constant water saturation up to the surface of the soil. These are *S. jensiseensis*, *S. recurvigemmis*, *S. caprea*, as well as the species belonging to the section *Daphnella*. On the contrary, *S. myrtilloides*, *S. lapponum*, *S. fuscescens*, *S. rosmarinifolia*, *S. pyrolifolia*, *S. cinerea* are especially common in saturated habitats. However, lesser and shorter periods of saturation are also sufficient for these species. Indeed, they would benefit from a better drainage. In intact nature, *S. pentandra* occurs on forested graminoid wetlands and in transitional zones around *Sphagnum* bogs. There, it has a habit of a small, often somewhat overtopped tree. However, if the territory is drained, *S. pentandra* would grow into a really large tree, as tall as *S. alba* or *S. fragilis*. Obviously, many willows occupy overwatered and paludal sites not because they need these conditions, but rather to escape competition with other trees. This is also confirmed by experience of willow cultivating. Such paludal species as *S. lapponum*, *S. myrtilloides*, and others would do very well in conditions of a drainage divide area, in a climate with the positive water balance, once the competition with other trees and herbs is eliminated.

Some species are very sensitive to the substrate acidity and extent of its mineralization. Alpine and arctic species usually are restricted either to basic or acidic bedrock. The species that are confined mostly to basic bedrock (erupted as well as sedimental one) are: *S. reticulata*, *S. vestita*, *S. polaris*, *S. alpina*, *S. rotundifolia*, *S. saxatilis*, *S. berberifolia*, *S. waldsteiniana*, *S. glabra*, *S. crataegifolia*, *S. tarraconensis*, *S. recurvigemmis*, *S. jensiseensis*, *S. kuznetzowii*, *S. caucasica*, and *S. elaeagnos*. Among lowland species, those associated with eutrophic mineralized substrate are: *S. triandra*, *S. songarica*, *S. cinerea*, *S. kochiana*, *S. vinogradovii*, and *S. ledebourana*. It is quite natural for these species to exhibit some salt-resistant properties, although none of the willows can survive on true *solonchak*'s. In contrast, species confined to siliceous bedrock, granite, and oligotrophic substrate are: *S. herbacea*, *S. nummularia*, *S. breviserrata*, *S. phlebophylla*, *S. aurita*, *S. atrocinerea*, *S. glauca*, and *S. helvetica*. However, in some peculiar situations, basiphilic species may occur on acidic bedrock, like *S. polaris* in the Sayans (Malyshev 1965), as well as acidophilic ones on limestone, like *S. phlebophylla* on Mount Tardoki-Yani in the northern Sikhote-Alin (observed by V. Shaga) or in the vicinity of Uelen and Nayakhan on the Chukchi Peninsula (observed by T. Derviz-Sokolova). Apparently, many other species do not exhibit any particular preferences to the substrate acidity, although there are still not enough data on the majority of willows.

A high light demand has been already mentioned here as a common property of the whole Salicaceae family. Indeed, none of the willows would prefer the shade instead of open sun. Still, some of them can tolerate the shade to a considerable extent and hence grow in the woods, most of all, *S. caprea*. It would survive even amidst a dense canopy, unless its crown

is totally shaded by larger trees. *S. hastata* occurs in the understory of subarctic birch stands in the Khibins and Urals. *S. silesiaca* is quite frequently found in the Carpathian and Sudetian spruce forests, as long as these are not too dense. Also, *S. starkeana*, *S. bebbiana*, *S. abscondita*, and *S. taraiensis* tolerate some shade and frequently occur under transparent canopies of pine and larch forests. Quite opposite to that, some of the Middle Asiatic willows are light-demanding to the extent that makes them suffer even in the partial shade. *S. wilhelmsiana* would grow only in absolutely open, isolated clusters and perish amidst closed thickets formed by other willow species.

Willows are very different as regards their requirements for air humidity and temperature. Whereas the soil moisture and mineral composition may be similar, say, on the Kola Peninsula and in Middle Asia, atmospheric conditions in these regions are absolutely different. These differences have impact on organ structures in willows. Species from arid regions typically have transparent crowns and small, narrow leaves with plenty of stomata not only underneath, but also on the upper leaf surface. Their reticulation is dense; however, veins are prominent on neither side being submerged into the parenchyma. On the leaf transection, one can notice an enlarged number of cell layers, firm and uniform (with little variation in the layer height); cells approximate the palisade type; the structure of leaves is close to isolateral.

Willows of temperate forest, forest-tundra, and subalpine regions generally have rather broad and soft leaves with none of stomata on the upper side, both the micro- and macrostructure of the leaves being distinctly bilateral. The majority of alpine and high-latitude arctic species (*S. polaris*, *S. herbacea*, *S. nummularia*, *S. berberifolia*, *S. alpina*, *S. retusa*, *S. phlebophylla*, *S. rotundifolia*, and others) exhibit the so-called *cryoxeromorphic* leaf structure: their leaves are small, coriaceous, the structure approaching the isolateral type, resembling the one in arid willows on the micro- as well as macro-scale (a leaf looks the same on both sides; stomata are also found on both sides).

40 Due to their ability to invade newly emerged substrates, willows are very common in a vast variety of secondary habitats, which came into being as a result of human activities. Willows normally inhabit diversified habitats, like ruts, quarries, mounds, neglected fields and vegetable gardens, etc., unless the soil is too dry. In the coniferous and mixed-forest belt, willows occupy extensive areas on abandoned meadows. On the other hand, forest plots, when degrading due to unplanned cuttings, may also gradually turn into willow thickets via the stages of either birch or aspen woods. Most common species in secondary habitats of European Russia and West Siberia are *S. aurita*, *S. cinerea*, *S. starkeana*, *S. phylicifolia*, and *S. myrsinifolia* (the latter one is replaced by *S. silesiaca* in the Carpathians). In European Atlantic regions, these are *S. repens* and *S. atrocinnerea*; in East Siberia and the Far East, *S. bebbiana*, *S. taraiensis*, *S. rosmarinifolia*, and *S. brachypoda*. Some of these species (particularly, *S. myrsinifolia*, *S. starkeana*, and *S. taraiensis*) have become so common and characteristic of secondary habitats that now it is even difficult to tell what was their original, natural niche.

3. MORPHOLOGICAL CHARACTERS WITH RESPECT TO INDIVIDUAL ORGANS: AN OVERVIEW

Reviews of willow morphological characters were published by F. Wimmer (1866); A. Camus, E.-G. Camus (1904); A. Toepffer (1925); R. Buser (1940); and K. Rechinger (1957). The author succeeded in identifying a number of new morphological characters and

peculiarities essential for purposes of the systematics. Therefore, it appears worthwhile to present one more overview of morphological characters here. At the same time, it will serve as an illustration of the approach to examining a plant proposed by the author. This is by no means an exhaustive description of the willow morphology, for such a description is not the goal of this work. I am going to give a brief review exclusively of those characters that appear to be critical for the systematics. Besides, I will treat these characters only as far as needs of the systematics are concerned.

Few of the willows in this country are upright tall trees. Much more frequent is a habit of a vigorously branching little tree with a short stem and wide crown as well as all kinds of transitional forms from this one to a shrub. Usually, the lowermost branches of shrubs are obliquely ascending or semi-prostrate. They are often rooting, and that leads to expansion of a shrub. This is particularly typical of some wetland and tundra species. In extreme cases, the habit becomes creeping. However, in some alpine and arctic species, branches are just procumbent, but not rooting (or rooting very slowly).

In the willows, there are no true brachyblasts, such as in the birches or balsam poplars. However, in some arctic and alpine species (particularly those without a pronounced rooting habit), one can distinguish two kinds of shoots. Shoots of one kind, either orthotropic or ascending, develop only 2 to 4 leaves per season, as they are characterized by restricted, promptly terminating seasonal growth. Shoots of another kind, virgate, plagiothropic, develop up to 10–15 leaves, as they have a longer growing period. The shoot dimorphism is found, for example, in *S. nummularia*, *S. ovalifolia*, and *S. retusa*.

In many of extremely reduced arctic dwarf shrubs, stems are entirely buried in the substrate, and only leaves and catkins appear on the surface. These species usually develop true stolons: elongated shoots with rudimentary scales instead of leaves, that are slowly growing and becoming woody in the substrate. As opposed to the epiterranean shoots, the stolons grow monopodially. Since the stolons are obviously a structure that developed lately during the evolution, we may consider them as an example of a secondary change-over from the sympodium to monopodium.

At high latitudes and elevations, willows manage to develop only a single generation of shoots per summer season. However, in favorable conditions, they may develop a second generation from buds of the current season. This phenomenon is pronounced in warmer, southern parts of the coniferous forest belt, starting approximately from the latitudes of Moscow, Tomsk, and Irkutsk. In Transcaucasia and Middle Asia, two or three shoot generations would develop on the average, and even four, in especially favorable conditions. Shoots of the second and subsequent generations may be easily recognized by their lowermost internodes, which are either not or insignificantly shortened.

In many willow species, especially in the largest and oldest specimens, one can observe detachment and abscission of the weakest and most overtopped shoots from inner parts of crowns (which is, by the way, typical of many other tree species in this country). In *S. wilhelmsiana* and *S. songarica*, slender upper parts of shoots die off in the fall, and the weaker the shoot, the longer is the dying part. These dead upper parts, however, do not shed, so that shrubs of *S. wilhelmsiana* and *S. songarica* are often spangled with dry branch tops. But the most striking adaptation is observed in a Himalayan alpine species *S. lindleyana*. This dwarf willow is characterized by just some few centimeters of the annual accretion. And these are only lower parts of shoots, where reserve substances are depositing and normal buds developing by the fall. Upper shoot parts, having been utilized during the summer for assimilation needs and receiving no reserve supply for the wintertime, detach and shed in the fall.

Bark of old stems forms coarse longitudinal fissures in the majority of willows. However, in the section *Amygdalinae*, it exfoliates in patches of irregular shape. On detachment of the upper layer, whether it falls or is being torn off, the rest of the bark remains smooth (similarly to *Eucalyptus* and *Chosenia*). If you cut through the bark to the wood and turn the bark away, then its inside (which is actually the phloem) becomes visible. It is mostly white or close to white, although in some willows it is bright canary-yellow. However, that bright color is not consistent in every specimen within a species, though intensive yellow tone tends to be more constant on the inside of the root bark. The color of the bark outer surface is greatly variable in young (one- to three-year-old) shoots of all species. However, in each species, especially when a particular geographical area is considered, there is a limited range of colors that is never violated. For instance, *S. triandra* in Europe and West Siberia always has its bark somewhat yellowish and never reddish; however, in some Caucasian regions, a reddish tone is also typical for *S. triandra*. In *S. starkeana*, there is a very narrow range of bark colors from olive-rufescent to red; in *S. viminalis*, the range is from light grayish-yellow to tawny (fulvous), and so on.

Shoot bark loses its brightness and gradually turns dull with age. In some species (particularly, in the Middle Asian representatives of the section *Helix*), young shoots even go through two stages of coloration before they attain an indifferent gray tone: first reddish or reddish-brown (either solid or variegated), then, usually on the second year, light grayish-yellow, which is still rather bright. Only afterwards, shoots start to turn dull gray.

In any species, the bark of young (one- to three-year-old) shoots often has more color in arctic or mountainous regions than in temperate climates. At the same time, in extremal conditions of northern regions and alpine elevations, bark of old stems tends to be much lighter than usual: it has a yellowish or whitish tone rather than gray. For example, in the Pamirs, starting from an elevation of 3,000 m, old stems of *S. pycnostachya* have light gray, almost white bark, and old stems of *S. turanica* are ivory colored. In the Polar Urals, old stems of *S. dasyclados* and *S. viminalis* are bright yellowish, as opposed to gray and blackish in the vicinity of Moscow.

One must keep in mind that shoots, especially those collected in the early or midsummer, often turn much darker on drying because of high tannin concentrations in their bark.

In some species, the bark of one-, two-, or three-year-old branches (and occasionally of older ones as well) is uniformly covered with pruinose bloom, which can be easily rubbed off, but is coming back on drying.

Shoots may be absolutely glabrous as well as more or less pubescent. One should distinguish the following types of pubescence: silky (sericeous), when whitish accumbent trichomes are pointing all in the same direction; short tomentose, when white or, more frequently, gray, very short trichomes are rumped irregularly; velvety (velutinous), when longer, more or less upright trichomes ascend off the shoot; floccose (or arachnoidal), when long and thin trichomes are completely entangled and often felted in tufts of irregular shape. Pubescence of an aging shoot gradually loses its peculiar characters approaching the tomentose type and then disappearing at all.

The thickness of a shoot naturally depends to a large extent upon the degree of its development. However, it is possible to find limits for thickness variability range in annotinous shoots of each species, if one considers only moderately developed, average-sized shoots and measures them after they finish their seasonal growth, always at the same conventional place (as a convenient one, I accept the internode between the third and fourth buds, counting from the top).

Wood surface under shoot bark is smooth in the majority of species. However, some willows (particularly those from the section *Vetrix*) have prominent longitudinal striae (excrescences) on the wood surface, their length ranging from 2–3 to 20–30 mm. Occasionally (in *S. cinerea* and *S. aurita*), these striae are very dense, but mostly they are scattered and short. The striation appears as early as the first year of shoot growth; however, the striae become fully developed in three or four years. The extent of their development varies in specimens of the same species. Longitudinal introrse marks (furrows, not excrescences!) correspond to raised wood striae on the outside of the shoot bark, so that the bark is thinner above the wood striae. It is important to distinguish the described striae that are always randomly scattered over the wood from those tiny twin scars that are found in all willows and located on either side of each offshoot or latent bud.

Comprehensive studies of the bud morphology are of great significance for the willow systematics. The bud shape diversity was noticed a long time ago and used for identification of willows in the wintertime by H. Shirasawa (1895), H. Nilsson (1908), and T. Resvoll (1909). However, these authors dealt with a comparatively small number of species and did not go much into detail of bud morphology. Other authors concerned with the willow buds (Schneider 1903; Wolf 1908) had still more cursory approaches. Therefore, the bud morphology so far has not received an appropriate treatment.

Both position of buds on the shoot (either accumbent or deviating off the shoot) and especially bud shape are usually very constant characters. One should consider the overall outline of a bud, looking onto its back (abaxial) side; the apex shape, looking from the back (acute, or obtuse, or rounded) and from the side (straight, or bent to the shoot, or recurved off the shoot; either tapering into a beak or not); the extent of the adaxial surface flattening and distinctiveness of the lateral carinas (which correspond to carinas of two prophylls forming the bud scale). Buds should be measured in three dimensions: the length, breadth, and thickness.

Appearance of bud scales is also of importance: their margins on the adaxial side may be either connate or distinct. Scales with distinct margins occur only in some of the most primitive sections. The anatomy of a young bud scale is similar to that of a leaf. The only difference is that the epidermis of the scale, especially its outer epidermis, is much more cuticularized. Loose, green mesophyll is in-between the two epidermal layers; vessels are inside the mesophyll. By the fall, scales become more firm, and by the winter (or during early winter), in many species they die off, either entirely or partially (about $1/2$ to $4/5$). Dead scales become thinner, as their mesophylls dry up, and change color to more fulvous or even blackish, their veins usually turning dark. Scales die off mostly in floriferous buds. In the spring, dead scales fall off entirely and promptly. In some species, scales stay alive throughout the wintertime, quite the same as they were in the fall, except becoming more pigmented and cuticularized. Scales of this kind do not shed when their buds open and stay persistent for a long time at bases of new shoots, sometimes looking like little rings. Either persistent or caducous bud scales is quite a stable characteristic, which proved to be very helpful for distinguishing species in the leafless stage. However, this character is subject to geographical variability: the farther north in the Arctic and up in the mountains, the less is dying away of bud scales pronounced. Therefore, while this character proved to be diagnostic for species identification within any particular locality, it would not always work for the entire species distributional area.

Size (and frequently also shape) of buds is subject to change along the shoot. There are three major types of bud size (and shape) gradation along the shoot.

Type 1 (*alba*-type, Fig. 2). The shape of buds on the shoot is not changing or changing very gradually. One cannot distinguish floriferous buds from vegetative ones by their appearance; to find out which is which, one has to consider bud contents. Buds starting from the third one to seventh (counting from the top of the shoot) are the largest on the shoot. The uppermost bud (or the two uppermost ones) are somewhat smaller. Starting from number four (to six), bud sizes are gradually diminishing towards the base of the shoot. The majority of buds open in the spring. Lower and smaller buds give birth to weaker shoots; the lowermost and smallest buds do not open at all and stay latent. However, it is impossible to predict for sure, which bud would open and which would remain latent. Buds of the type 1 are characteristic of tall willows that flower late in the spring, their catkins borne on foliated shoots.

44 Type 2 (*arctica*-type, Fig. 3). The uppermost two or three (occasionally up to five-six) buds on the shoot are of almost identical size and shape: all are large (the very uppermost occasionally somewhat smaller). Further down the shoot there occurs a sudden pronounced change of bud size, and also sometimes shape, so that the rest of buds are much smaller, nearly equal to each other. Only the upper, larger buds get to open in the spring. Some of them give birth to floriferous shoots, others—to vegetative ones. As for the small buds, they remain latent unless exposed to a special treatment. This type of buds is primarily characteristic of arctic species with their catkins terminating normally foliated shoots.

Type 3 (*caprea*-type, Fig. 4). Floriferous buds are very different from vegetative ones in their size and often also shape. Although floriferous buds are generally located closer to the shoot top, the uppermost one or two are usually vegetative. Vegetative buds also occupy the lower part of the shoot and occur, one or two at a time, in-between groups of floriferous buds. Within the lower group of vegetative buds, their sizes gradually diminish towards the base of the shoot. It is impossible to predict, which of them would open in the following spring and which would stay latent. The bud arrangement of this type is a feature of many forest species that start to bloom early in the spring.

Although there are, of course, some intermediate cases, the type of bud size and shape gradation is very distinct in most species. It is a very important diagnostic character, typical of entire groups of related species (and even some sections).

45 When considering the contents of a bud (which does not change much throughout the wintertime), one should, first of all, compare the size of the catkin primordium and leaf primordia. Frequently, the shape of leaf primordia is also of importance, as well as manner of their venation (it may be parallelinervous!) and pubescence. Certainly, the largest buds are the most suitable to see these peculiar details. There is an opinion (see, for example, Toepffer 1925; Reching 1957) that margins of leaf primordia in the willow buds are revolute (*vernatio revoluta*), which is not true: the primordia margins are not revolute inside the bud. It is only in the springtime, when young leaves, which have already grown out of buds, but not yet fully expanded, often have their margins rolled. This rolling is particularly typical for the representatives of the section *Vimen*; it also occurs in *Vetrix*, *Arbuscella*, and occasionally in some other sections, although the character ceases to be constant there.

Bud sizes are also species-specific in certain limits. Usually, floriferous buds are larger in male specimens than in female ones, at least in species with bud gradation of the type 3 (and in *S. caprea*, they are even of a different color).

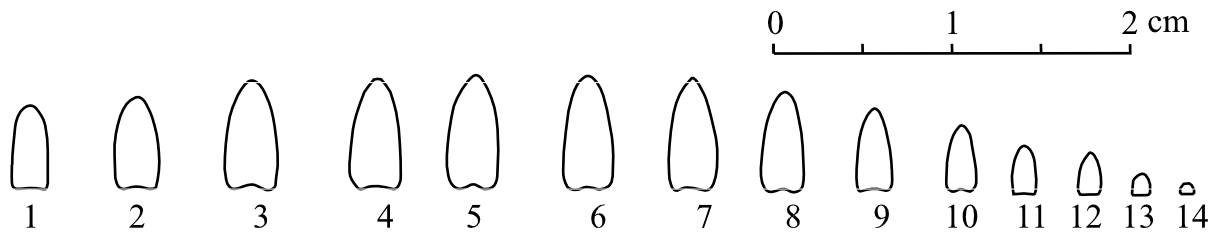


Fig. 2. Bud size gradation along a shoot of *Salix alba* (from the Altai)

Buds counted from the top of the shoot. Buds 1, 2, 10–14 vegetative; buds 3–9 floriferous. The linear scale refers to bud size. Distance between buds proportional to that on the shoot.

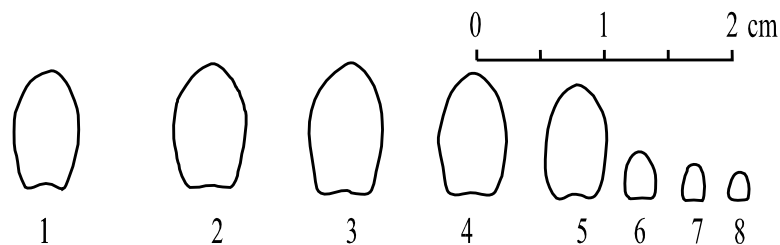


Fig. 3. Bud size gradation along a shoot of *Salix arctica* ssp. *crassijulis* (from the Commander Islands)

Buds counted from the top of the shoot. Buds 2, 3, and 5 proved to be floriferous on dissection; buds 1 and 4 proved to be vegetative; buds 6–8 dormant (not going to open during the subsequent spring). The linear scale refers to bud size. Distance between buds proportional to that on the shoot.

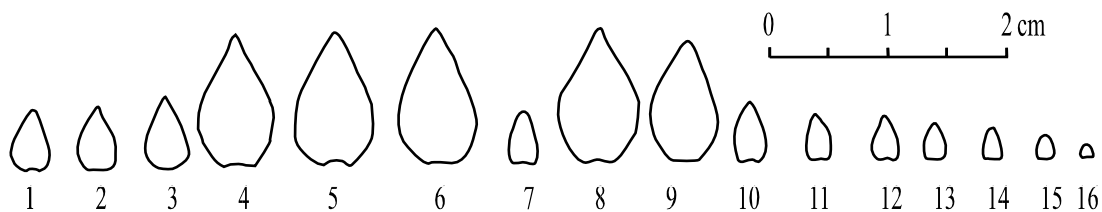


Fig. 4. Bud size gradation along a shoot of *Salix caprea* (collected near Vladivostok)

Buds counted from the top of the shoot. Buds 1–3, 7, 10–16 vegetative; buds 4–6, 8, 9 floriferous. The linear scale refers to bud size. Distance between buds proportional to that on the shoot.

In species having the bud size gradation of the type 2, the leaf number on a shoot is usually limited. In *S. polaris*, *S. herbacea*, and some other species, there are only 2–5 leaves per shoot; in larger shrubs, like *S. reinii*, *S. alata*, or *S. jenisseensis*, up to 15–25. The limitation of the number of leaves in these species is attributed to the fact that their leaf primordia are fully preformed in buds during the fall, and in the spring leaves merely expand. This is, of course, one of the adaptations to a shorter growing season. However, the number of leaves on a shoot is not always absolutely determinate. Virgate shoots in *S. nummularia* and *S. ovalifolia* with a longer growing period have already been mentioned here. Also, a stimulus from outside may induce prolonged shoot growth and formation of new leaves

even in those species that normally would have a limited number of leaves per shoot (like those mentioned above, particularly, *S. reinii* and *S. alata*).

A typical leaf arrangement in the willows is spiral (the angle of divergence is about $2/5$). Occasionally (for example, in *S. nummularia*), the leaf arrangement approaches the distichous type or, more frequently, the false opposite type when leaves are arranged in pairs, yet the divergence angle of $2/5$ is retained. An arrangement of this kind is known in a number of species from the sections *Helix* (subsection *Purpureae*) and *Incubaceae*, as well as in a Himalayan willow *S. salwinensis*.

A few lowermost leaves on a young shoot, those next to the prophylls (the bud scale), usually are small and underdeveloped. Quite often, they do not even turn green and are fugacious in the majority of species. The most correct name for these lowermost abortive leaves is *cataphylls* (*cataphylla*). The cataphylls are lacking in some arctic-alpine species, like *S. reticulata*, which are limited to have only 2–5 leaves on each shoot per season, and these are fully preformed in a bud. Taking a short growing season into consideration, we understand that the cataphylls are an unacceptable luxury for the like species. The cataphylls are as well lacking in the second set of shoots produced in the axils of the same-year leaves (sylleptic shoots).

Among the rest of leaves on a shoot, it makes sense to distinguish the inferior ones (*folia inferiora* v. *primigena*), which attain neither the normal size nor shape typical for a species, though they are fully developed; the medium leaves (*folia successiva* or *Folgeblätter* in German), which may rather be called ordinary (*folia ordinaria*), since they cover not only the middle part but most of the shoot (these ones are most developed); and, finally, the superior leaves (*folia ultima*), which typically deviate from regular shape and size, being somewhat smaller. To avoid any misunderstanding and inconsistency, one must keep in mind that in all the keys and diagnoses in this book, only the ordinary leaves are implied, unless there is a special remark.

46 The stipules in the willows may be developed to a variable extent; however, there is a variability range typical for each species. In epicormic shoots, stipules are most developed; in short lateral shoots and those belonging to the oldest parts of crowns, stipules are least developed. Shape of stipules is much more important and stable than their size. The shape may vary from narrowly linear-subulate to round. Besides this general characteristic, which is not always sufficiently depicting all the significant peculiarities, one should consider the stipule midrib. It is important if the midrib is prominent or not, if it is straight or curved, if a stipule is more or less symmetric with respect to its midrib or it is conspicuously inequilateral. It is as well of significance if a stipule has a distinct apex and, if it does, then what is the apical shape. It is also crucial to notice if there are any glands on the upper stipule surface, and, finally, consider the margin (specify, if it is entire, glandular, or dentate; flat or revolute).

Stipules mostly fall off earlier than leaves they belong to. However, occasionally they persist longer than the leaves, even till the subsequent growing season. In the section *Daphnella*, stipules are adnate to petioles at their bases, hence they always shed together with leaves. In a number of species, stipules are reduced to tiny rudimentary outgrowths less than 1 mm long.

The petioles in the willows are generally shorter than in the poplars, and in some species leaves are sessile. On the transection, petioles are either round, with a convex upper side (like in most species of the subgenus *Vetrix*), or narrowly channeled above (like in most species of the subgenus *Salix*), or fully channeled (like in most species of the subgenus

Chamaetia and some of the section *Helix*). The majority of species from the subgenus *Salix* have a pair (occasionally two or three pairs) of glands sitting on the upper petiolar surface at the base of a leaf blade. In epicormic shoots, these glands frequently turn into botryoidal or foliolaceous outgrowths.

The leaf blades may have various shapes ranging from round (even reniform, as in *S. kurilensis*) to narrowly linear. An important quantitative characteristic describing the leaf shape is the length-to-breadth ratio. It may vary from 0.7 (in *S. kurilensis*) to 30 (in *S. wilhelmsiana*, *S. gordejewii*). Another essential character is the location of the broadest part of the leaf blade: either above, about, or below the middle of the blade. Leaf shape may not change all the way along the shoot, sometimes, from the very cataphylls to the uppermost leaves (as in *S. caprea*, *S. bebbiana*, *S. taraiensis*, *S. reticulata*, and others), or it may gradually change, mostly so that the lowermost leaves are the shortest and broadest of all, more obtuse than others, with the broadest part above the middle; and the closer leaves are to the top of the shoot, the closer their maximal breadth is to bases of their blades, and the more acute blade apices are. In some species of the section *Vetrix* (*S. caucasica*, *S. kuznetzowii*), the change of the leaf shape along the shoot is so pronounced that, if one collects shoots during the spring and then the upper shoot parts from the same specimen during the fall, he will hardly believe that these samples belong to the same species (Fig. 5).

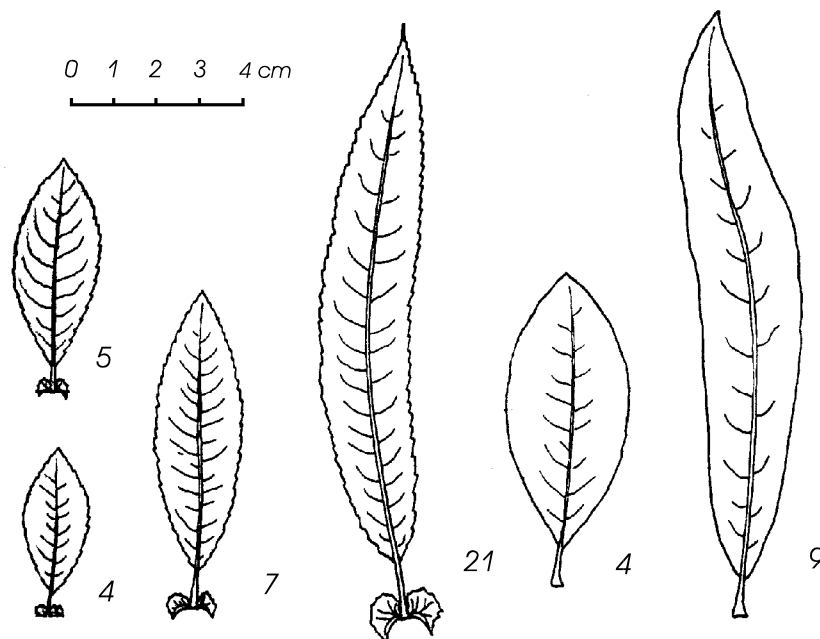


Fig. 5. Change of leaf shape along a shoot of *Salix caucasica* (the four leaves on the left) and *S. kuznetzowii* (the two leaves on the right)

Numbers refer to leaf count starting from the base of the shoot.

Leaf color is rather special and constant in each species, therefore, with enough of practice one can recognize many species even from a distance. Unfortunately, these peculiarities of foliage color, visible for a trained eye, can be hardly described verbally. The existing color scales are as well too rough for this purpose. Leaf surface may vary from

absolutely dull (as in *S. kochiana* or *S. myrtilloides*) to lustrous (as in species belonging to the sections *Pentandrae*, *Glabrella*, *Arbuscella*). The underneath of a leaf blade may be almost the same as the upper surface (as in *S. coesia*, *S. pycnostachya*, *S. pseudopentandra*, or *S. fedtschenkoi*), or it may be rather different in its color and pubescence. These differences in color between the two sides of leaf blades depend mainly upon whitish or bluish waxy bloom that may be present underneath, but lacking or inconspicuous above. This bloom can either be evenly distributed on the lower surface of all the leaves on the shoot (like in the section *Arbuscella*), or gradually changing along the shoot (which is particularly typical of *S. myrsinifolia*). In some species and even entire species groups (the section *Pentandrae*), there is absolutely no any waxy bloom on the leaf blade surface. However, the presence or absence of the bloom may as well be a completely facultative character (for example, in *S. triandra*).

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It is the position of veins within the mesophyll which is of major interest when one considers the venation: veins may hide inside the mesophyll, and then they would be conspicuous neither beneath nor above (at least on a live leaf); otherwise, veins may be rather impressed above and prominent beneath. This character is usually critical for large systematic groups: sections or even groups of closely related sections.

Leaf margins may be either flat or more or less revolute. When they are flat, then on the leaf transection one can see the similar structure of the upper and lower epidermis within the area next to the margins. When margins are revolute, then the epidermis and underlying layer of the collenchyma is more developed above than beneath. Flat margins usually occur along with veins submerged in the mesophyll; revolute margins, with veins prominent beneath. A revolute part of the leaf is usually rather callous-firm (due to the development of the marginal collenchyma). A flat margin may as well be callous, or otherwise thinned, as if it was sharpened (as in *S. kirilowiana* or *S. niedzwieckii*). See Fig. 6.

In the majority of species, leaf margins are more or less dentate, with minute glands located on each denticle. Perfectly entire leaves are quite rare; solitary, small glands may be scattered even along entire margins. Glands may be located on denticle apices or on the very margin (in species with flat leaf margins belonging to the sections *Salix*, *Subalbae*, *Helix*). We will call this arrangement of glands *marginal*. Glands may as well be located not on the very margin of the leaf blade, but rather very close to it (as close as fractions of 1 mm), yet in accordance with the arrangement of denticles. This type of glands will be called here *submarginal*. It is typical for the majority of species with conspicuously revolute leaf margins from the sections *Vetrix* and *Vimen*. Finally, glands may be completely removed from the revolute margin to upper leaf surface, so that they do not correspond to any marginal denticles. This arrangement of glands will be named *extramarginal*. It is characteristic of some species from the section *Vimen*. Marginal denticles may be either uniform and regular (as in the sections *Salix*, *Pentandrae*, *Subalbae*, *Daphnella*, *Helix*, and *Myrtosalix*) or irregular (as in *Vetrix* and *Glabrella*). In the majority of species, the closer to the leaf apex, the smaller the denticles, and the more densely they are arranged. In some species, denticles, if any, are located only on the lower half of the leaf blade (*S. arctica*, *S. fuscescens*). Generally, the closer to the top of the shoot, the more leaf dentation is pronounced, although in some few species it is vice versa (e. g., *S. recurvigemmis*).

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The lower leaf surface is always dotted with multiple scattered stomata; there are also many stomata on the upper cataphyll surface, although in the majority of species, they are lacking from the upper side of ordinary leaves. Therefore, the presence of stomata on the upper side of regularly developed leaves usually can be a reliable diagnostic character. This

is mostly typical of xeromorphic leaves (in some species from the sections *Helix*, *Retusae*). Stomata are visible under a strong magnifying lens as small light-colored spots (these are aerial cameras under stomata, which transmit light). Unfortunately, sometimes (under some undefined conditions), stomata become hardly detectable on drying. Therefore, if stomata are not found on the upper leaf surface, one should check cataphylls in addition. Sometimes, wetting of the leaf helps to detect stomata.

Leaves may be either absolutely glabrous or pubescent to a variable extent. Types of leaf pubescence are generally similar to those of shoot pubescence; however, there is also something special about the leaves. Pubescence is sericeous or silvery when all the trichomes are appressed in the same direction. White tomentose pubescence consists of thin, white, tangled trichomes corresponding to that of the arachnoidal type on the shoots, however, being more even on the leaves, so that it usually does not look floccose. Velvety, offset pubescence is very rare in the leaves and, probably, is pronounced only in *S. caprea* and occasionally some other species of the section *Vetrix* (*S. kuznetzowii*, *S. pedicellata*). Short tomentose pubescence of the kind that is typical for the shoots (dense, grayish) hardly occurs on the leaves; instead there is another type frequently found, consisting of loose, fine, grayish, often tangled trichomes. This type, when strongly developed, might be called gray arachnoidal. It occurs mostly on the upper leaf surface in such species as *S. hastata*, *S. caprea*, *S. bebbiana*, and others.

Cataphylls and inferior leaves occasionally have some fugacious pubescence beneath consisting of long sericeous trichomes. Ordinary leaves, glabrous in their mature stage, frequently are clothed with pubescence when very young. These may be straight or tangled trichomes either on one or both sides. In some species (*S. silesiaca*, *S. caucasica*), pubescence is very dense on young leaves, but then totally disappears.

Leaf anatomical structure is rather diversified in the willows (Fig. 7). Upper epidermis may be either similar or markedly different from lower one. In case the upper leaf surface looks dull, the upper epidermis may have parallel grooves or crests found on a microscopic

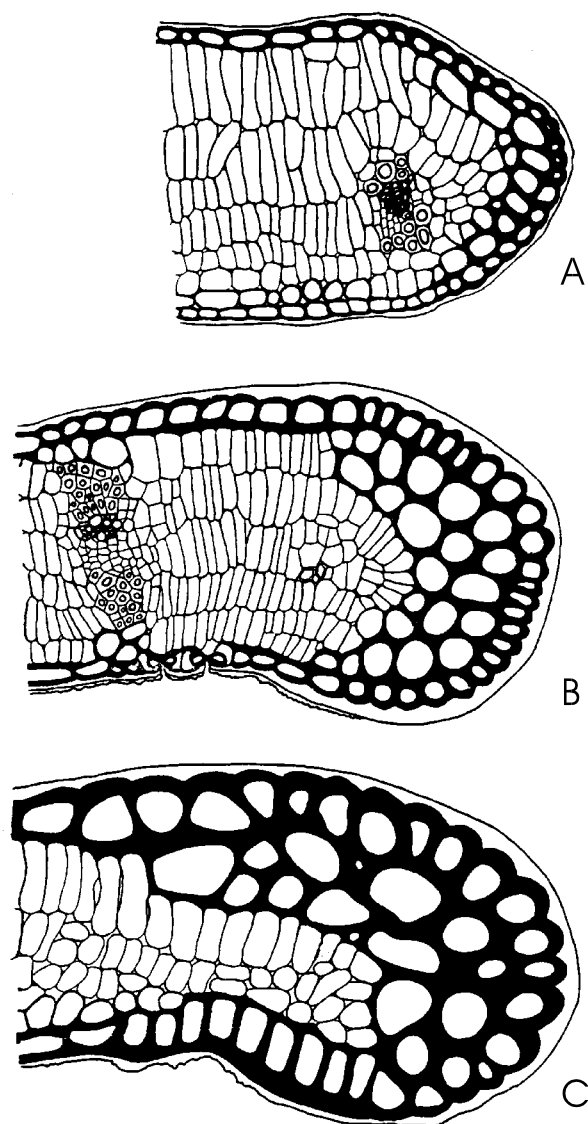


Fig. 6. Anatomical structure of the leaf margin

A—symmetric margin with faintly developed collenchyma in *Salix arbuscula*;
B—subsymmetric margin with pronounced collenchyma in *S. miyabeana*;
C—asymmetric margin in *S. glabra*.

transection (like in *S. triandra*). Mesophyll at times may be very dense, palisade, at times with a very loose spongy parenchymal layer. Some groups are distinguished by a pronounced chlorophyll-deficient hypodermal layer under the lower epidermis. (For more detail on the leaf anatomy, see: Skvortsov, Golysheva 1966.)

In some arctic willows, dead leaves do not abscise in the fall remaining on branches and deteriorating very gradually during subsequent years. This character is most typical and constant for some species from the section *Myrtosalix*, although occasionally in high arctic environments it may as well be pronounced in other species (*S. pulchra*, *S. polaris*, *S. nummularia*, *S. reptans*).

Time sequence of shoot and catkin development may vary. One should distinguish the following sequence types.

1. Catkins are precocious (*amenta praecocia*). Flowering occurs while vegetative buds just start to expand.

2. Catkins are subprecocious (*amenta subpraecocia*). A considerable part of vegetative buds are open and cataphylls partially expand by the start of the flowering.

3. Catkins are coetaneous (*amenta coetanea*). Not only cataphylls but also inferior leaves are expanded by the start of the flowering. However, axes of vegetative shoots are not yet considerably elongated.

4. Catkins are serotinous (*amenta serotina*). Axes of vegetative shoots are considerably long by the start of the flowering.

These types in a way correspond to the extent of floriferous shoot development as well

as to the bud types: precocious catkins are sessile or subsessile, with few cataphylls at base; the buds are mostly of the type 3. Serotinous catkins are terminating more or less foliated shoots, and the corresponding bud types are usually 1 or 2.

In the arctic belt and alpine zones, the species with the serotinous and coetaneous catkins drastically predominate (and the most frequent bud type is the type 2). There, the precocious catkins occur only in some few species (*S. pulchra*, *S. apoda*, *S. lanata*). In moderately cold climates of the boreal belt, it is the precocious catkin type which is dominant (along with the bud type 3). Farther to the south, especially in Middle Asiatic regions as well as warm

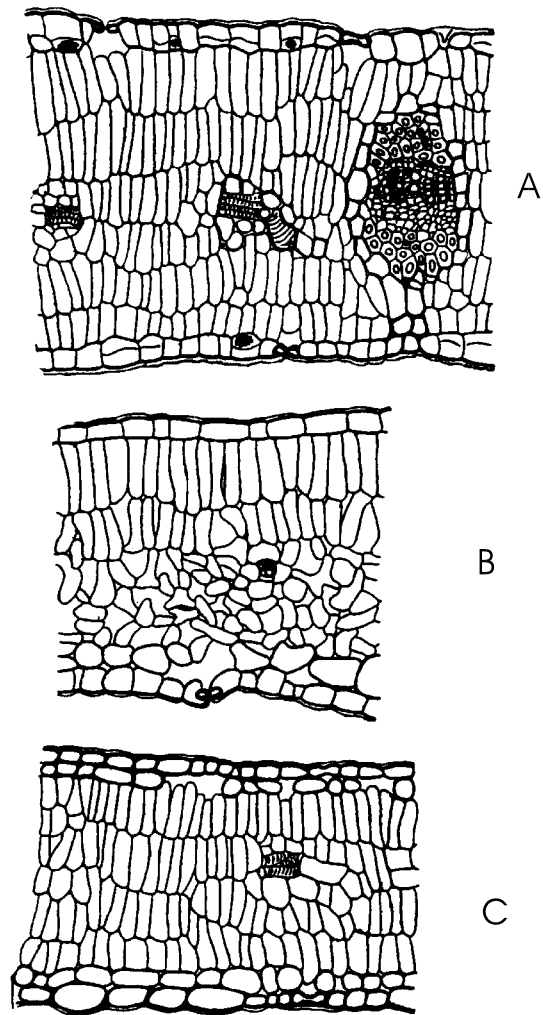


Fig. 7. Mesophyll structure

A—isolateral type (mesophyll of only palisade parenchyma without hypodermis) in *Salix miyabeana*;
 B—bilateral type (mesophyll of palisade and spongy parenchyma with lower hypodermis) in *S. lanata*;
 C—isolateral type with bilateral hypodermis in *S. interior*.

temperate regions elsewhere in Asia, the serotinous catkins again become very widespread, but this time along with the bud type 1.

The catkin type is not something absolutely determinate in each particular species. For example, in some species with the precocious or subprecocious catkin type (*S. caprea*, *S. myrsinifolia*, *S. phylicifolia*), the catkin development slows down in the northernmost parts of their distributional areas, so that catkins become "coetaneous". Local conditions may also affect the spring development, for instance, a very thick layer of snow or long-lasting spring flood may induce transformation from the typical precocious type to coetaneous and even serotinous, as it happens to *S. pulchra* in some arctic regions or *S. viminalis* in the flood plains of the Lower Volga and Lower Don. There also occur deviations that may hardly be interpreted as being induced by any particular external factor. For example, *S. pyrolifolia* specimens in Prebaykalia may exhibit either the precocious or coetaneous catkin type.

One should keep in mind that willows with the precocious catkin type do not necessarily expand catkins the earliest in spring, although it is true to a certain extent. For example, in *S. aurita*, catkins of the precocious type expand not only later than those in *S. cinerea* and *S. caprea* (which are as well precocious), but often even later than those in *S. starkeana* (which are coetaneous).

In any particular location, there exists a rather constant sequence for species to flower, recurrent every year. Early-flowering species are especially precise as regards "observing their turn" in the sequence. For instance, in Moscow Oblast, *S. caprea* always starts to flower 2–4 days earlier than *S. cinerea*; *S. dasyclados* is 3–5 days ahead of *S. viminalis*. Late bloomers have their flowering time less restricted and more prolonged. For example, in *S. aurita* growing at a particular locality near Moscow in a totally uniform environment, specimens may differ in their expansion time as much as 7–8 days.

In precocious species, the flowering period for any single specimen lasts 3–5 days; in typical serotinous species (*S. wilhelmsiana*, *S. capusii*), the flowering may be prolonged to 8–10 (up to 15) days.

Male catkins usually fall off soon after flowering; female ones, after seed ripening and capsule dehiscence. Precocious catkins usually shed together with their short stalks and cataphylls, abscising directly from annotinous shoots. The abscission of both serotinous and coetaneous catkins often follows two stages: first the catkin itself detaches at its base and falls off, then the rest of the floriferous shoot does. In some relatively few species, normal buds develop in axils of floriferous shoots, and then the lower parts of the shoots do not fall off. This phenomenon is particularly typical of the section *Chamaetia* as well as a Himalayan one, *Lindleyanae*, although it is as well known in *Retusae* and some primitive species of the subgenus *Salix*. Sometimes, precocious or subprecocious catkins fall off in a two-step mode (for instance, in *S. rosmarinifolia* and *S. coesia*). This fact might mean that the like species could have developed their precocious catkins relatively recently.

Bracts in female catkins fall off soon after flowering in most species of the subgenus *Salix* found in this country as well as in some of *Helix*. In the rest of our willows, bracts are persistent; they just contract when drying. Bracts may be either pale (yellowish, greenish, reddish, or light pinkish) or blackish (completely or just in their upper parts). Dark-colored bracts are mostly associated with precocious catkins; pale ones, with serotinous. These are always pale bracts, which are fugacious.

Both the size and shape of bracts are highly variable in any particular species, hence these characters are not very suitable for diagnostic purposes. The bract pubescence is a little more

stable. The two extremes in types of pubescence are either long, straight trichomes, mostly on the upper outer surface of a bract, or short, usually ruffled ones, mostly on the lower inner surface. In-between these extremes, there exist all kinds of intermediate and mixed types. Sometimes, bracts are glabrate. A peculiarity of *S. rorida* and species from *Pentandrae* is that there is one or two (up to four) glands on each of their bracts.

In the subgenus *Vetrix*, nectaries are arranged adaxially, one in a flower. Exceptions are very rare, encountered only as individual abnormalities. The shape of nectaries in this subgenus is characteristic for species and even sections. In the subgenera *Salix* and *Chamaetia*, both the number and shape of nectaries may vary within each species as well as between species. A considerable number of species from these subgenera have two nectaries in each male (and occasionally also in female) flower: the anterior (abaxial) and posterior (adaxial) one. Quite often, the an abaxial nectary is connected with adaxial one at base, and additional lobes may develop in-between.

In *S. cardiophylla*, there is usually the abaxial nectary and two identically small adaxial ones. Some authors (Sugaya 1960) expressed an opinion that this arrangement is the most primitive stage, the one, which reveals the origin of adaxial nectaries from a pair of prophylls. Then, one should treat the abaxial nectary as a homologue of a phyllome located next to prophylls on the flower axis. This approach, to my opinion, is most convincing and realistic. It provides a clue for understanding the morphological nature of the nectaries in the willows as well as perianth disks in the poplars.

Nectaries are mostly greenish or yellowish; however, in the section *Cheilophilae* and subsection *Purpureae* of *Helix*, they are purple, and in the rest of the section *Helix*, usually brownish (though the color, of course, is not always well preserved in herbarium specimens).

As for the stamen number, there are three possible variations in the willow flowers: two stamens, three stamens, and a fluctuating number (three or more). Deviations from the number typical for any particular species are extremely rare. The most common one is a form of *S. alba* with many stamens instead of two; multistaminate flowers are also encountered in *S. fragilis*; a very rare deviation is *S. acmophylla* flowers with two or three stamens. There is no doubt that the polyandrous flowers constitute a more primitive stage in the willows. Presumably, the reduction of stamen number took place independently in different phylogenetic branches. The two-staminate flower is also subject to stamen reduction; however, instead of elimination of the second stamen, both stamens become connate, as if they were one. Either a complete or partial, facultative or constant fusion of stamen filaments is encountered in the sections *Subvinales*, *Canae*, *Vimen*, *Daphnella*, *Flavidae*, *Helix*, and *Cheilophilae*. As an abnormality, a partial fusion of stamen filaments also occurs in other sections of the subgenus *Vetrix*.

52 The morphology of the willow stamens is rather uniform. Stamen filaments may be glabrous or pubescent. Anthers may or may not have purple pigmentation before dehiscence; they also may be of variable sizes. Those of larger sizes and with more pigmentation are most typical of species with precocious catkins; smaller and less pigmented anthers usually correlate with the serotinous catkin type. However, in arctic and alpine species, anthers are mostly bright colored; not infrequently, stamen filaments are also colored orange or purple. Yet it appears that the stamen pigmentation cannot be considered as a constant character in any single species. As for anther sizes, this is a rather reliable feature that can be often used as a diagnostic character. Since in herbarium one mostly has to deal with emptied anthers, it makes

sense to provide adequate information concerning sizes of dry, empty ones. Alive anthers are approximately by $\approx 1/2$ longer.

The pollen morphology in the willows so far provides a very few hints for the systematics of the genus. Assumed differences between species are not distinct enough and technically difficult to observe. One can find more detail in works specifically dedicated to the subject, reviewed by L. Kupriyanova (1965).

Ovaries may be sessile but more frequently stipitate. Stipes (as well as capsules) usually grow somewhat larger after flowering. In many species of the section *Vetrix*, stipes elongate to a considerable extent: in *S. bebbiana*, *S. pedicellata*, and *S. silesiaca* they may attain the length of 4–5 mm by the time when capsules are ripe. Since sizes of ovaries, styles, and stigmas also change during the period of time between the flowering and ripening, it is necessary to accept a conventional time for making measurements of all the gynoecium parts for diagnostic purposes. A convenient time is that after the flowering, close to capsule ripening. Shapes and sizes of mature willow capsules do not vary very much. The most deviating capsule parameters are encountered in *S. erythrocarpa* with its broadly ovoid, obtuse capsules 3–4 mm long; on the other hand, in *S. bebbiana* with narrow, nearly subulate capsules up to 10–11 mm long. Capsules may attenuate into styles either abruptly or gradually.

The presence or absence of the pubescence on ovaries is a constant character in the majority of our willows; however, in some 20 species of our flora, it is facultative. Usually, the pubescence consists of rather short, more or less appressed trichomes, all pointing forward, and therefore it looks silky. Occasionally, trichomes are ribbon-like, flexuous (which is particularly typical for the section *Myrtosalix*). Pubescence of this kind looks grayish when one examines it without a magnifying lens. Under a powerful lens, trichomes look opalescent because of strong refraction. Ovary pubescence consisting of thin, tangled, white trichomes is characteristic of the section *Villosae*. In *S. alata*, ovaries are clothed by coarse, thick trichomes.

Styles are always more or less connate, at least at the very base. Their length may vary from 0 to 2–3 mm. Stigmas are mostly two-lobed or two-parted; their length varies from very short, 0.10–0.15 mm, to 1 mm and even more. The length of styles and stigmas fluctuates in a very restricted range in each species. The extent of style fusion as well as stigma partition is also subject to fluctuations. Not infrequently, stigmas look entire during the flowering, but on drying they split nearly throughout. Sometimes, stigma lobes belonging to different carpels seem to be more closely fused than those of the same carpel. On that basis, M. Wichura (1848) and then A. Eichler (1878: 46) distinguished two different types of the arrangement of stigmas on the willow flower diagram: the sagittal and transversal type. However, it is quite obvious that the difference is purely secondary or even merely seeming. As there are no corresponding morphological structures, this illusion should not be depicted on the flower diagram. The real position of stigmas is transversal, corresponding to the position of carpels.

Seeds are very uniform in all the willows and, according to our present understanding, they do not exhibit any differences valuable for purposes of the systematics.

Willow chromosomes are small, short, monotonous, and difficult to study. Counts of chromosome numbers so far have not promoted any significant progress in the willow systematics, according to available literature data (Blackburn, Heslop-Harrison 1924; Wilkinson 1944; Almeida 1946; Håkansson 1955; Löve, Löve 1961). In many instances, a few different chromosome numbers may be reported for a single species; on the other hand, many different species may have same chromosome numbers. J. Wilkinson (1944) reasoned

that the subgenus *Salix* was entirely tetra- or polyploid; however, his assumption was invalidated by later studies (Suda 1958).

4. VARIABILITY AND TAXONOMICAL VALUES OF CHARACTERS

In the previous section of this chapter, some notes concerning the variability of characters in the willows were already made. Now we would treat this important issue in more detail. Many authors, particularly those who opposed the recognition of superfluous species and hybrids, like W. Koch, R. Buser, and, more recently, C. Ball (1946), made valuable observations and significant conclusions on the variability of the willows. Yet, on the whole, the problem has not been approached close enough.

If one would examine any large population of willow species in any region, especially when applying the method of taxonomical transects, that is, trying to evaluate every specimen on one's way rather than dealing with some selected specimens, then he would notice a significant morphological diversity. The easiest way to explain this diversity is to assume large plasticity and flexibility in the willows when they are adapting to variable environmental conditions. "Solum palustre, arenosum, alpestre, calidum mutavit mira metamorphosi species". ["Either paludal or sandy, alpine or warm soil alters species miraculously" (Linné 1753: 1022)]. However, this explanation sounds too general today. We have to understand, which part of the variation is of the phenotypical nature and which is genetically determined. It is possible to detect and describe the phenotypical variability while watching the same clone growing in a variety of habitats. In this case, changes in the willows occur in the same general manner as in any other plants. In the shade, leaves grow larger and thinner, their pubescence less pronounced. In the full sun, on the contrary, leaves of the same clone would grow smaller but thicker, more firm, and more pubescent. In the excess moisture situations, shoots would become longer, leaves larger; in the lack of water, shoots are shorter, leaves smaller, and so on. There is no doubt that just a little experience would be enough for any botanist to distinguish the phenotypical nature of these fluctuations. However, dealing with herbarium specimens may lead to problems, as one has to consider a single branchlet there, not being aware of what the whole plant looked like. Even an experienced investigator may easily make a mistake in this situation. For instance, the description of *S. korshinskyi* Goerz was based on a purely phenotypical deviation, a nourishing shoot of *S. pycnostachya*.

54 However, only a minor part of morphological diversity in the willows fits within limits of the like phenotypical variations. It happens that within a single habitat, where no visible environmental gradients can be detected, each willow specimen has its own peculiarities distinguishing it from other surrounding specimens of the same species—and these differences may be rather dramatic. At the same time, a single clone, whatever shape and size it would attain, whatever habitat, different in terms of water availability and substrate nature it may spread to, and no matter where and how it may be propagated, would still retain its major features, so that it will be possible to recognize this particular clone.

Therefore, from observations in nature, one can definitely conclude that these are polymorphic genotypes of willows rather than their reaction to environmental factors, which make them vary. Observations of cultivated plants prove the same. Removing of plants from their native places to the Moscow Nursery did not induce any significant morphological changes in them. Of course, not all of the transplanted willows were performing in the nursery as well as in their original habitats: some were damaged by the frost, others were growing too slowly or never succeeded to flower. Presumably, the cultivated plants were not

developing leaves of the exact size they would develop in their native environment. Neither were they adding the same annual accretion. Probably, they even developed their pubescence to a somewhat different extent. However, all peculiarities distinguishing any particular clone or genetic *household*¹ were perfectly retained in the nursery environment. For example, once, at the lower reaches of the Selenga, I found two different clones of *S. udensis* (which is not a common species there) far away from one another. In one clone, plants had a habit of shrub-like trees with short stems and low, wide crowns. Trees in the other clone looked petite, graceful, and were narrow crowned. I took cuttings from both clones, and, what grew in Moscow, were again the same wide shrubs and narrow-crowned slender trees. An unusual semi-weeping specimen was once found among spreading, loosely-branched shrubs of *S. michelsonii* growing along the Ili River. The semi-weeping habit was retained in Moscow in that particular specimen amidst other bushes of usual appearance. Also, on the Ili, some specimens had shoots of a bright yellow color, others were orange. These features remained unchanged in the Moscow Nursery. Cuttings of an abnormally large-leaved form of *S. taraiensis* were taken in the northern Sikhote-Alin along with cuttings from a normal specimen. When grown in Moscow, one bush was still characterized by leaves of a medium size, another one had unusually large leaves. It is possible to provide many more examples like these.

The stability of morphological characters in cultivated clones allows to make some conclusions, which are as well important for herbarium studies. The first one is that the variability of herbarium samples collected in nature adequately depicts the genotypic polymorphism of species. The second is that samples of cultivated plants can be used for purposes of the taxonomy as well as samples collected in nature (of course, if origin of cultivated plants is well documented).

Not only are morphological characters constant and genetically determined in the willows, but also features of their physiology. Nursery observations most clearly reveal the stability of developmental rhythms. Specimens of the same species originating from different elevations vary in their growing period duration finishing their seasonal growth at different times. *S. pycnostachya* from Dzhamantal Stov in the Pamirs (where the elevation is about 3,800 m) would complete its growing cycle, turn yellow, and drop its leaves somewhat earlier than the majority of indigenous Moscow species. Plants of the same species taken from Chigirchik Mountain Pass vicinity (located south of Osh, at about 2,300 m) would finish their growing season simultaneously with Moscow willows. Neither the Dzhamantal nor Chigirchik plants were subject to frost damage in Moscow. Three other clones coming from Ak-Terek Forestland near Dzhahalal-Abad, that is, from the walnut forest zone at elevations 1,400–1,500 m, usually did not manage to complete processes of preparation for the winter and to drop their leaves on time. Therefore, their shoots often were damaged by the frost. Observations of this kind were also made for *S. turanica* and *S. iliensis* in our collection.

The same pattern of differences was found in samples of one species taken from northern and southern localities. *S. phyllicifolia* originating from the vicinity of Denezhkin Kamen (the Northern Urals) turned yellow and dropped leaves somewhat earlier than indigenous Moscow plants of the same species. Specimens of *S. phyllicifolia* from the Khibins (the Kola Peninsula), grown in Moscow, finished their vegetation season 3–5 weeks ahead of native Moscow willows. In the climatic conditions of Moscow, early completion of the vegetation

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¹ As opposed to a larger population. See the explanation of this term on page 61 (translator's note).

cycle was especially striking in alpine and high arctic plants. *S. alata* and *S. karelinii* would go a month ahead of indigenous Moscow willows. In *S. lanata* and *S. arbuscula* from the Khibins, leaves fall usually in the middle of August, and in *S. reticulata* and *S. polaris* originating from the same region, the abscission takes place early in August or even in July, so that a two-month period of summer dormancy is added to the period of winter dormancy.

Other features, like different patterns of the root growth or different numbers of shoot generations per season, are also genetically determined. *S. phylicifolia* specimens from the Khibins, once brought to Moscow as young rooted plants, were so miserable and depressed for some 3–4 years that they did not grow taller than 15 cm. It was even difficult to identify these dwarf plants with plants of the same species that occur around Moscow (for example, in Solnechnogorsk) and have a habit of a shrub as tall as man's height. Eventually, it became obvious that the problem of the plants from the Khibins was extremely slow growth of their prostrate, shallow root systems. This shallow root pattern, genetically determined, beneficial in the cold and damp climate of the Kola Peninsula, turned out to be harmful in Moscow, where upper soil layers dry out most easily in the summer, even if the soil is occasionally watered. It took those plants from the Khibins some 5 years to develop deeper root systems. However, once they attained a stage of appropriate root growth, they started to normally develop and produce flowers, so that at last one could identify them with *S. phylicifolia*. Yet even in 14 years the Khibinic plants did not grow as tall and never made their annual accretions as large as indigenous *S. phylicifolia* plants.

Willows originating from Middle Asia, of course, do not feel as comfortable as native species in Moscow. Nevertheless, they usually succeed to develop two or three (and sometimes four) generations of shoots per season, while Muscovites with the like growing pattern and in similar growing conditions manage to produce only one or two shoot generations.

Also, the starting time in spring for the flowering and leaf expansion is genetically determined. Clones of *S. triandra* and *S. viminalis* from the lower reaches of the Volga started flowering some 2–3 weeks later than the rest of these species samples represented in the nursery. This curious feature of plants from the Lower Volga Flood Plain was first noticed by P. Pallas (1776), then studied in more detail and described by A. Fursayev (1937) and V. Sukachev (1935, 1953). The latter researcher found an appropriate name for these forms: he called them "late-inundation ecotypes". Indeed, the differences described above, such as those in the growing season duration, pattern of root growth, and number of shoot generations per season are to be treated in terms of the concept of the ecotype. Peculiarities of shoot bark color in alpine plants mentioned earlier, in section 3 of this chapter, are of the same nature.

However, genetic differences in the rhythm of development as well as morphological characters may also be inherited purely individually. As it was already mentioned in section 3, specimens with varying flowering schedules were found in *S. aurita* within a single habitat. T. Trofimov planted some seeds from one specimen of *S. aurita* in our Botanical Garden and found out that the progeny had a range of flowering initiation time as long as a week. The most attentive examination of each plant did not reveal a sign of the hybrid nature: all of them were perfect *S. aurita* specimens.

What are patterns of variability within populations and entire species? Is it possible to describe that variability in terms of any infraspecific taxa? To answer these questions, one should mention first of all that it is the individual variability, which prevails in the willows.

As it was said in the beginning of this section, while closely examining any population, one would find peculiarities that make a single specimen different from any other one. However, if one would compare any two populations, large enough and isolated from each other, then it would become obvious that ranges of morphological characters and variants are the same in both of them. Fig. 8 shows parallel ranges of variability in leaves of *S. caprea* growing in different locations remote from each other.

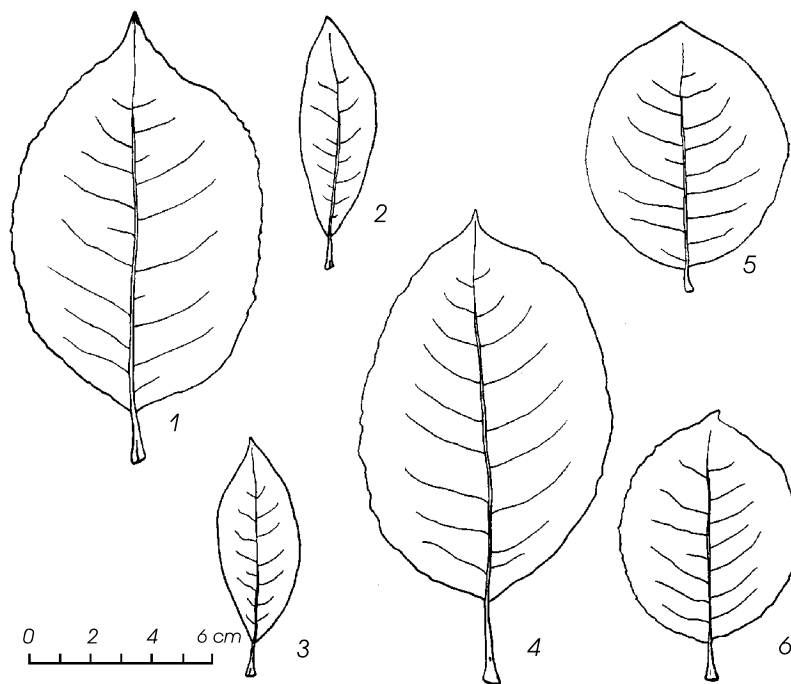


Fig. 8. Parallelism in individual genotypic variability of leaf shape in *Salix caprea*

All of the leaves taken from middle parts of moderately developed shoots.

1 and 2 —extreme variants collected in the vicinity of Kirovakan (now Vanadzor: northern Armenia); 3 and 4 —same, collected near Golitsyno (Moscow Oblast); 5 and 6 —leaves of suborbicular shape, a rather rare variation, 5 collected in Kamyshin District (Volgograd Oblast), 6 collected in the French Massif Central.

This striking individual variability within populations hides the characters typical for each population on the whole and makes them extremely difficult to be observed, so that these population features are pronounced in comparatively few instances. Naturally, it is easier in this situation to find common distinctive features in isolated populations of small sizes, which may be compared to *households*.

Characters typical of larger populations are indistinct, if they can be detected at all. For instance, pubescent leaves of moderate size prevail in *S. pycnostachya* from the Western Tien Shan (at the northern limit of this species' distribution), so that without catkins it is even difficult to distinguish it from *S. olgae*. Plants with glabrous, comparatively small and narrow leaves prevail in the alpine zone of the Pamirs. In southern Kirghizia, in the area of the

walnut forests, it is a large-leaf form which predominates. Many samples originating from Kulyab (Tadjikistan) are characterized by pronounced leaf pubescence. In some regions (for instance, in the Eastern Pamirs), glabrous capsules are typical for *S. pycnostachya*; pubescent capsules predominate in other localities. However, all of these differences can be traced only statistically. They are too general to use them as criteria for drawing any geographical or morphological borders within the species. Therefore, I would not consider any infraspecific taxa within *S. pycnostachya*.

In *S. viminalis*, one can detect rather obscure contours of slightly surfacing races. Plants from the Western Altai usually have rather broad leaves with particularly dense pubescence, which may even lose its typical sericeous appearance. It was that form that was described under the name of *S. polia* Schneid. Yet it is impossible to recognize it as a race: one of our colleagues, N. Suvorova, brought a whole series of samples from the same place (the Ulba River in the Western Altai) that looked exactly like European ones. Yet another deviation of *S. viminalis* morphology is found in the steppe area of the Southern Urals and Turgay Plateau. Plants that predominate there are characterized by particularly narrow leaves and pronounced silvery pubescence, their petioles and midribs often rufescent beneath. However, to my opinion, in *S. viminalis* it is impossible to draw borders between races in order to assign any taxonomical value to them, so that the only way to depict the variability is to verbally describe geographic distribution of particular characters.

Yet there are some few opposite examples of distinctly pronounced limits of willow subspecies: in *S. berberifolia*, *S. pulchra*, *S. alba*, and others. These differences will be considered in appropriate parts of the systematical treatment of the genus.

Not only the individual variability predominates over geographical one in the willows, but it may even mask differences between species. While infraspecific variability in willows is obvious and striking, differences between species are difficult to understand and articulate. This phenomenon constitutes the major hardship in the systematics of the willows. That is why the willows have been assigned a title of "botanicorum crux et scandalum". It is probably in the willows rather than any other genus, that one should refrain from any decisions on taxonomical values of particular characters a priori, without testing each character in every particular case. About a dozen of superfluous species were included in the flora of our country merely due to the fact that the presence or absence of the capsule pubescence was considered to be a diagnostic character a priori. Actually, as it was mentioned before, the capsule pubescence is a facultative character at least in some 20 species of our flora. Also, the concept of an absolute stability in the shape and number of nectaries typical of any particular species led to descriptions of a number of superfluous species. In reality, these characters may vary in the subgenera *Salix* and *Chamaetia*. Even such a distinct character as the presence or absence of the style cannot be treated as an important diagnostic one without testing. In *S. coesia*, *S. miyabeana*, *S. acmophylla*, and *S. tetrasperma* Roxb., the style length may vary from 0 to 0.5–0.7 mm.

Although limits of willow species are often masked by wide ranges of individual variations; although characters that are usually considered to be reliable often appear to be not reliable in the willows, still, the taxonomical situation in the genus *Salix* is very different from one, say, in the genus *Hieracium*. This is not a surprise though, since the willows do have normal sexual reproduction as opposed to the hawkweeds. With enough of experience and training, it is quite possible to distinguish willow species nearly "from the first glance" and in a number of cases even identify them dealing merely with a single leaf.

This fact proves that species limits are just masked by individual variability of willows, but these limits do really exist. In fact, they are as real as limits of species in any "perfect" and "easy" taxa. The willow species are by all means "perfect" as well. The difficulty in distinguishing willow species is that characters easy to recognize and describe, those which we are used to, which are sufficient when dealing with other groups, often "do not work" with the willows. On the other hand, there is a number of constant diagnostic characters of the shape, size, and color that are comparatively difficult to notice and even more difficult to articulate. One has to get used to these characters, train oneself to distinguish them.

Species identification in the willows often has to be based on inconspicuous characters that may seem "insignificant" or "not essential" a priori. For instance, *S. pentandra* is different from *S. pseudopentandra* in the appearance of the marginal pubescence of the lowermost cataphylls. That character proved to be very constant across the entire huge geographical areas of both species. The appearance of the cataphylls also turned to be critical for distinguishing *S. recurvigemmis*. In the section *Myrtosalix*, the angle at which buds are deviating off shoots works for distinguishing *S. saxatilis*. The main feature that makes *S. fedtschenkoi* different from *S. karelinii* is its nearly concolorous, somewhat lustrous leaves with stomata on their both sides. One might treat these differences as "unimportant" and unite both species, as it was done by P. Polyakov (1960). However, in the Western Hemisphere, there exists a whole group of mountain species from the section *Hastatae*, distinguished from the rest of the section by exactly the same characters that make *S. fedtschenkoi* different from *S. karelinii*. We have to conclude that in our flora, *S. fedtschenkoi* is the only representative of the group of species restricted mainly to the Rocky Mountains in North America, and by no means it is a form of *S. karelinii*. This is one more striking example proving that it is truly unacceptable to evaluate the significance of any character a priori.

Sometimes, however, it is impossible to find even those "small" characters which might be completely constant within a species. The only way to deal with this situation is to use combinations of characters in identification keys and species diagnoses. Let us consider differences between *S. viminalis* and *S. dasyclados* as an example of distinguishing species by a combination of characters, none of which is absolutely constant. There is no question that these species are closely related; they grow in the same habitats; their geographical areas almost completely overlap. They have been being constantly confused, and so far there is no sufficient approach to distinguish between these species, neither in the relevant literature nor herbaria.

Habitats. Both species are alluvial. *S. viminalis* is rare in non-alluvial habitats, occurring there exclusively on the sand. Apart from alluvial habitats, *S. dasyclados* would also grow along small streams and even on slopes of valleys where ground water reaches the soil surface.

Habit. *S. dasyclados* is primarily a tree, unless it is subject to damage. *S. viminalis* is a tall shrub occasionally looking like a tree.

Wood. In *S. viminalis*, the wood is always smooth under the bark; in *S. dasyclados*, it is frequently with distinct striation. However, the striae are not equally pronounced in every specimen. In European Russia, this character is more common in the south and absent in the north of the species distributional area.

Shoots. In *S. viminalis*, biennial shoots are glabrous, light yellow or grayish. In *S. dasyclados*, not infrequently they are clothed with remains of pubescence (glabrous ones are more common in the north), their color is usually tawny or tawny-brown. Annotinous

shoots are tomentulose or glabrous, 1.2–2.0 mm in diameter in *S. viminalis*; densely velvety-tomentose or glabrate, 1.8–3.0 mm in diameter in *S. dasyclados*. In *S. viminalis*, shoots are thin and flexible, harvested for rods; in *S. dasyclados*, they are coarse and less flexible.

Floriferous buds in *S. viminalis* are 6–10 × 2–3 × 1.5–2.5 mm; in *S. dasyclados*, they are 8–15 × 2.5–5.0 × 2.5–3.0 mm.

Stipules are crescent in *S. dasyclados*; in *S. viminalis*, they are linear, however, on vigorous epicormic shoots, stipules are frequently as well crescent.

Leaf blades are 5–15 mm (on vigorous epicormic shoots up to 25 mm) broad in *S. viminalis*; in *S. dasyclados*, 15–40 mm.

Leaf pubescence beneath is always densely sericeous in *S. viminalis*; in *S. dasyclados*, it is densely sericeous to nearly lacking.

Glands at leaf margins are extramarginal in *S. viminalis* (marginal only in lowermost leaves); in *S. dasyclados*, they are marginal, occasionally with some solitary extramarginal ones.

Catkins are precocious in both species; however, in *S. viminalis*, there are also serotinous ecotypes. *S. dasyclados* starts to flower a few days earlier when the two species occur together.

In *S. dasyclados*, **bracts** are black (occasionally brown), mostly acutish, densely covered with trichomes, which exceed the apex of the bract by 1.5–3.0 mm. In *S. viminalis*, bracts are brown (occasionally completely black), mostly obtuse or coarsely incised at apex, loosely covered with trichomes, which exceed the apex by 0.3–1.5 mm.

Anthers are 0.5–0.7 mm long in *S. viminalis*; in *S. dasyclados*, 0.7–1.0 mm.

In *S. viminalis*, **capsules** are sessile, either not or insignificantly compressed, 5–7 mm long when ripe (to 8 mm in serotinous ecotypes), mostly clothed with dense silvery pubescence. In *S. dasyclados*, capsules are sessile to stipitate (stipes are up to 0.8 mm long), mostly rather compressed, 7–9 mm long when ripe, usually comparatively faintly puberulent and, therefore, green, not silvery.

In *S. viminalis*, **styles** are 0.4–0.8 mm long, which is shorter or, rarely, equal to stigmas (stigmas are 0.8–1.5 mm long). In *S. dasyclados*, styles are 0.8–1.8 mm long, either longer, equal, or shorter than stigmas (which are 0.7–1.5 mm long).

As one can see, there are many distinguishing characters, but all of them vary in such a way that their extreme values overlap. However, a mass-scale study in herbaria and nature shows that both species are distinct and it is always possible to distinguish between them when there is enough of perfect, complete samples in a herbarium collection.

A combination of the most constant characters, like the color of biennial shoots, shape of stipules, leaf breadth, location of marginal glands, bract color, shape and size of capsules, and style length, may be accepted as diagnostic and used in a key.

5. INTERSPECIFIC HYBRIDIZATION

As it was mentioned before (chapter 1, section 3), J. Scopoli was the first to state that hybrids existed in the willows. He came to this conclusion as early as 1760. A hundred years ago, it was recognized that the willows may form a variety of natural hybrids as well as artificial ones, which are easy enough to obtain. The progress was achieved by A. Kerner (1860), F. Wimmer (1853, 1866), and particularly M. Wichura (1854, 1865), who accomplished experimental studies. Later, R. Buser (1887, 1909, 1940) contributed to better

understanding of the natural hybridization in the willows. In various "floras" and numerous floristic and taxonomical papers, willow hybrids were mentioned abundantly. During the first half of the 20th century, these were H. Nilsson (1918, 1928, 1930, 1937, 1954), S. Ikeno (1918, 1922), and V. Sukachev (1934, 1939, unpublished data) who got involved in studying particularly willow hybrids and experimenting with them.

There is no doubt that the willows belong to a genus with a great abundance of interspecific hybrids. There are very many hybrids between species of different, even very remote sections. A possibility of hybridization between dwarf shrubs from the sections *Retusae* or *Chamaetia* and tall representatives of *Arbuscella*, *Lanatae*, or *Villosae* is especially striking. Hybrids are often fertile and give birth to a whole range of various forms through subsequent genetic segregation.

B. Floderus (1931) mentioned as many as 177 willow hybrid combinations of different kinds from Fennoscandia; K. Rechinger (1957) named 181 from Central Europe; E. Wolf (1900) listed more than 70 from European Russia; D. Syreishchikov (1907) named and depicted 16 hybrids from Moscow Government. In the "Flora of the USSR", M. Nazarov accepted a total of 210–220 possible interspecific hybrids for the entire USSR territory. A significant number (about 60) of interspecific hybrids was published in the "Herbarium of the USSR Flora".

According to West European as well as Russian authors (Wimmer 1866; Seemen 1908–1910; Enander 1905–1910; Camus, Camus 1904, 1905; Görz 1922, 1928, 1934; Floderus 1912, 1923, 1926, 1931; Hultén 1928, 1943; Chassagne 1928, 1956; Rechinger 1957; Schmalhausen 1875; Wolf 1900; Lakschewitz 1911, 1914; Nazarov 1926, 1936; Drobov 1953; Shlyakov 1956; Popov 1959; and others), not only do willows form multiple hybrid combinations, but produce these combinations in abundant numbers. That is to say, willow hybridization naturally takes place en masse. B. Floderus stated his belief that specimens of hybrid nature even predominated over "pure" species in some places, such as Greenland, the Kamchatka Peninsula, Novaya Zemlya, and partly even northern Scandinavia. M. Nazarov's (1926) notion about the hybridization on Novaya Zemlya was close to that of B. Floderus. According to these authors' interpretation, the polymorphism in the willows is to a large extent the result of hybridization.

However, in spite of the prevailing concept that recognized willow hybridization en masse and proposed its significant impact on the willow morphology and evolution, some authors suggested a more moderate view on the role and abundance of natural hybrids. M. Wichura, a researcher who provided the very basis of our knowledge on willow hybrids, was, at the same time, the first one to point at restricted significance of hybridization in nature (Wichura 1854, 1865). First of all, he found out that any particular willow species would not form or be able to form a hybrid with any other species at random. Not only many willow species and entire groups of species never hybridize with one another naturally, but it is impossible to obtain hybrids between them in an experiment. Also, hybrids do not occur too frequently in nature. According to M. Wichura's estimation made for the most common hybrids, such as *S. purpurea* × *S. viminalis* or *S. aurita* × *S. repens*, there was one hybrid specimen for every 300–500 specimens of parental species. And a ratio of *S. triandra* × *S. viminalis* hybrid occurrence to that of the parental species was 1 : 50,000, as estimated by M. Wichura. Next, M. Wichura emphasized that it was difficult or even impossible to identify triparental and tetraparental hybrids relying only on morphological characters: "Even a gift of the keenest insight is hardly enough to reveal the nature of compound hybrids" (Wichura 1854). Finally, he also was the first to understand that many hybrids are characterized by low vitality and

fertility and usually are more poorly adapted to environmental conditions than their parental species (Wichura 1865). Therefore, hybrids do not have a future in natural settings. While hybridomania was rapidly spreading following M. Wichura and F. Wimmer, R. Buser came up with sharp criticism of that approach (Buser 1887, 1909, 1940). He demonstrated that a large number of hybrids named by his contemporaries (including those described by A. Kerner) actually were not hybrids. Instead, they were merely variants within species variability ranges. He did not treat hybridization as a major cause of polymorphism. R. Buser also emphasized that natural hybridization was by no means universal, taking place only in some particular types of habitats, namely, those naturally unstable or disturbed. T. Nakai (1930) also pointed out that hybrids were rather rare in the flora of East Asia.

Unfortunately, R. Buser's works did not get appropriate attention, as was mentioned here before. M. Wichura's works were also neglected soon after they were published. There are still plenty of triplets and quadruplets listed in the literature, no matter that N. Nilsson (1928), again relying on experimental data, made one more reminder concerning the impossibility of detecting compound hybrids. B. Floderus, for example, named 111 of tri- and tetraparental hybrids (and even a five-parental one!) from Fennoscandia (Floderus 1931); K. Rechinger (1957) listed 38 of them for the territory of Central Europe.

Relying upon my own experience in the willow studies, I have come to the conclusion that both the frequency of hybrids in nature and role of the hybridization in the origin of the willow polymorphism are actually very different from what is depicted in the current Russian and West European literature. M. Wichura and R. Buser definitely made more accurate assessments of hybridization.

To get evidence of the fact that hybridization in willows does not take place en masse in any particular habitat, one may consider any willow thickets in which one or two willow species are especially different from other participating willows. For example, near the upper limit of the spruce forest on the northern slope of the Terskey Alatau in the vicinity of Przhhevsk, there are very extensive, nearly pure willow shrublands composed of *S. tianschanica*, *S. alata*, and *S. karelinii*. There is also *S. argyracea* growing along streams. The latter species is particularly different from all the rest. It is very unlikely that a researcher studying willows might overlook a plant with characters intermediate between *S. argyracea* and any of the other three species. However, I did not manage to find even a single individual with any intermediate features.

S. acutifolia is quite common in the Oka Valley downstream of Serpukhov. This is also the species that looks very different from the rest of willows occurring in the valley. Any plant that might exhibit characters somewhat intermediate between *S. acutifolia* and any other willow species would be immediately noticed, even from a distance. However, no hybrids were found in the Oka Valley.

Within the range of *S. aegyptiaca* on the former USSR territory (the Talysh and Upper Sumbar in the Kopet-Dag), apart from *S. aegyptiaca* itself, there occur only willows belonging to the subgenus *Salix*. Members of the subgenus *Salix* never hybridize with those of the subgenus *Vetrix*. In spite of the fact that there are no willows to hybridize with, *S. aegyptiaca* still exhibits its "normal" range of variability. Indeed, the variability of *S. aegyptiaca* is hardly less pronounced than that of any species from the European temperate climate belt, like *S. caprea* or *S. cinerea*.

62 Now let us have a closer look at a false example of hybridization commonly cited in the literature. It has been known since the time of W. Koch, that in *S. myrsinifolia* there are two forms, both of which occur across all of the species range. One is characterized by glabrous

capsules; the other, by pubescent capsules. W. Koch and then F. Wimmer and R. Buser considered this character to be facultative in *S. myrsinifolia*. However, S. Enander (1910) came to the conclusion that the only "pure" *S. myrsinifolia* was the one with glabrous capsules, whereas the capsule pubescence was an alien character exhibited exclusively due to hybridization of *S. myrsinifolia* with other species. Although his judgment was not supported by any serious observations in nature, it was trusted by Russian authors (P. Lakschewitz, M. Nazarov) as well as others. In 1957, K. Rechinger still considered that statement to be S. Enander's "achievement" (Rechinger 1957: 88). Not one of the hybridization apologists was discouraged by the absence of any serious arguments in S. Enander's treatment or the fact that S. Enander's competence could not even be compared with that of W. Koch, F. Wimmer, or R. Buser. They also ignored the problem of loosing distinct species limits in *S. myrsinifolia* when switching from the concept accepted by W. Koch, F. Wimmer, and R. Buser to the one proposed by S. Enander. Let us consider S. Enander's explanation and try to understand, where *S. myrsinifolia* might get its pubescence from. The answer was that the pubescence originated from either some species of the section *Vetrix* or *S. phyllicifolia*. In fact, *S. myrsinifolia* often grows together with *S. caprea*, *S. cinerea*, and *S. aurita* in the temperate belt of this country as well as Central Europe and Scandinavia. However, according to R. Buser's observations (Buser 1940), *S. caprea* never hybridizes with *S. myrsinifolia* at all. Nor did I observe any plants that could be considered as the like hybrids. Hence, the only possibility left for *S. myrsinifolia* is to gain its pubescence from either *S. cinerea* or *S. aurita*. However, if this is the case, then why is the capsule pubescence the only character transferred? Why does not *S. myrsinifolia* acquire any other characters from these species, such as the growth habit, wood striation, bud shape, peculiarities of leaf pubescence, leaf color, sizes of gynoecium parts, and others? Indeed, it is absolutely impossible to assume that these characters altogether might depend on one gene that might get suppressed in crossings as a recessive one. Specimens with pubescent capsules occur quite frequently in any large population of *S. myrsinifolia*. However, specimens that exhibit any other common character, either with *S. cinerea* or *S. aurita*, have never been found. If, however, there occur some solitary specimens with a set of characters intermediate between *S. cinerea* and *S. myrsinifolia* (I found them occasionally in Moscow Oblast and the Southern Urals), then they are easily distinguished as hybrids. These specimens demonstrate that the rest of characters are by no means recessive. Finally, the distributional area of *S. myrsinifolia* is considerably exceeding those of *S. aurita* and *S. cinerea* in the Urals as well as on the Kola Peninsula. However, specimens with pubescent capsules occur there with the same frequency or even more often (on the Kola Peninsula).

Nor can the other assumption that *S. myrsinifolia* might get its capsule pubescence from *S. phyllicifolia*, stand up under scrutiny. *S. phyllicifolia* is known to have completely glabrous leaves with a whitish glaucescent color beneath. However, *S. myrsinifolia* native to the Kola Peninsula differ from Moscow plants in the opposite way: their leaves are more pubescent and more green beneath. Moreover, true hybrids *S. myrsinifolia* × *S. phyllicifolia*, which are not infrequent in Leningrad Oblast as well as north of Moscow and Vladimir, appear to be particularly rare on the Kola Peninsula. Besides, a species closest to *S. myrsinifolia*, an Italian willow *S. apennina* A. Skv., also exhibits capsule pubescence as a facultative character. Some species of groups closest to the section *Nigricantes*, namely, the section *Glabrella* and subsection *Vulpinae*, also appear to have their capsule pubescence as a facultative character (these are *S. jennisensis* and *S. reinii* in *Glabrella*, *S. silesiaca* and *S. pedicellata* Desf. in

Vulpinae). Should we again try to imagine, where these species could have received their pubescence from?

63 Hence, following S. Enander's idea, we will face more and more contradictions to real facts. In order to justify a single artificial concept developed prior to real experience, we will have to pile up more and more assumptions. However, once we return to the treatment approved by W. Koch, F. Wimmer, and R. Buser, everything immediately falls into place, and *S. myrsinifolia* again becomes a distinct and by all means clear species.

It was very common for S. Enander, B. Floderus, R. Görz, and others to consider *S. purpurea* as one parental species of a number of proposed "hybrids". As a ground for their assumptions, they used just a single character: stamen filaments of "hybrid" plants were partially connate. However, as we have already noticed in section 3, the tendency for stamen filaments to become connate is paralleled in a number of groups and may be expressed to a variable extent. If connate filaments are normal, for example, in *S. sitchensis* Sanson from the section *Vimen* or in *S. sieboldiana* Blume from *Vetrix*, then why cannot they occur in other species of these sections as individual abnormalities which have nothing to do with hybridization? It is in *S. cinerea* and *S. rosmarinifolia*, where this abnormal filament fusion appears to occur most frequently. What reason can one find to treat these specimens as hybrids? Often, they grow as far as a hundred or even thousand kilometers from the nearest population of *S. purpurea* or *S. vinogradovii* and do not exhibit any other characters that could prove their hybrid origin. I must say that M. Nazarov (1936) also understood the absurdity of such conclusions. He refrained from making decisions on the hybrid nature of plants relying only upon the connate stamen filaments.

B. Floderus stated (Floderus 1926) that hybrids prevailed among willows on Kamchatka. Vast herbarium collections of willows from Kamchatka have been accumulated since then. Indeed, the central part of the peninsula is now to be considered as one of the regions best represented in herbaria. On studying of these collections, one inevitably comes to the conclusion that hybrids are extremely rare on the Kamchatka Peninsula. With the exception of a few (as a rule, poorly collected) specimens, it is very easy to assign the entire material to appropriate species. Numerous labels by B. Floderus in the St. Petersburg Herbarium demonstrate that plants which he treated as hybrids do not show any signs of hybrid origin. For instance, a sample of *S. arctica* ssp. *crassijulis* (No 1665 of the Swedish Expedition to the Kamchatka Peninsula) was treated by B. Floderus as a four-parental hybrid "*S. arctica* × *chamissonis* × *cuneata* × *glauca*". There is hardly any specimen of *S. arctica* from Kamchatka correctly identified by B. Floderus. Neither could he distinguish *S. pulchra* ssp. *parallelinervis* from *S. udensis* burying both species in multiple hybrid combinations. S. Enander's treatment of willows from Kamchatka was not any better. It is quite obvious that both B. Floderus and S. Enander merely failed to understand the Kamchatkan willows.

According to R. Görz (1928, 1934), there are also many hybrids in the Caucasus. Most frequently, he found those of *S. silesiaca*. Some herbarium samples reminded R. Görz of *S. silesiaca*, and therefore he decided that the species was distributed across the Caucasus. However, the majority of specimens from the Caucasus did not fit in the variation range of *S. silesiaca*, so that R. Görz was forced to imagine all kinds of hybrid combinations and describe three "new" species (*S. palibinii*, *S. paracaucasica*, and *S. daghestanica*). Hence, according to R. Görz, the cycle of *S. silesiaca* was represented in the Caucasus by an extremely intricate conglomerate of four species and their multiple hybrids. However, an objective treatment of the Caucasian willows in nature and herbaria clarifies the status of the Caucasian "*S. silesiaca*". There is only one species in the Caucasus, very distinct and

"perfect" by all means, which is related to *S. silesiaca*, though both species are markedly different. The species actually does not hybridize with any other Caucasian willow. That is *S. caucasica*.

Also, the section *Helix*, according to R. Görz, is represented in Transcaucasia by complex combination of a few species (*S. purpurea*, *S. tenuijulis*, *S. caspica*) and their hybrids. An objective treatment shows again that neither *S. tenuijulis*, nor *S. caspica* are found in Transcaucasia. Neither the European *S. purpurea*, nor its hybrids are present there. Instead there is only one species, an endemic of the Caucasus, Asia Minor, and Iran, *S. elbursensis* Boiss., which had been long ago described by E. Boissier and then undeservedly neglected. Normal variations of that species were mistakenly treated at times as *S. tenuijulis*, at times as *S. caspica*, or *S. purpurea*, as well as all kinds of hybrids.

R. Görz noticed a difference between the Adzharian "*S. phyllicifolia*" and European one and explained it by hybridization between some Adzharian species and the "typical" *S. phyllicifolia*, which he assumed to be present in the Caucasus. Actually, there is no *S. phyllicifolia* there at all, and what R. Görz took for the hybrid, was another, quite distinct species, an endemic of the mountains of Colchis, *S. kikodseae*. While trying to treat Caucasian willows as hybrids of Central European species, R. Görz overlooked some more endemic species in the Caucasus. As a researcher of the Aschersonian school, R. Görz ignored geographical data. A lack of scope in the botanical geography badly affected his treatments.

The discussed examples appear to illustrate the idea clearly enough, so that there is no need to recall more of them.

Why is the role of hybrids in the willows exaggerated as much as it is? The reasons for that overestimation are quite obvious.

1. Taxonomical usefulness of characters is evaluated a priori. The concept of species is purely typological: the variability of species and their ranges are ignored; species are viewed as certain "types", each with a set of characteristics that is considered to be an ideal morphological sample. What does not fit, according to a researcher's opinion, within the limits of this ideal type is placed as a "hybrid". If an author decided that the "typical" *S. myrsinifolia* should have glabrous ovaries, then inclusion in the "pure" species is denied to specimens with pubescent ovaries. If an author is determined to consider glabrous leaves as "typical" for *S. myrsinites*, then samples with pubescent leaves, of course, cannot be anything but hybrids. And it does not matter that there is not any other evidence of their hybrid nature: once the resemblance to the ideal type is incomplete, there is no way to assign that specimen to the "pure" species. If an author assumes that the leaves of *S. polaris* are completely entire, then any denticles, indeed, prove its hybridization with *S. herbacea*. Therefore, those imaginary hybrids with *S. herbacea* show up in the Urals and even at the Ob River, despite the fact that *S. herbacea* actually is not distributed farther east than the Pechora Mouth.

2. Another cause for overestimation of hybridization in willows is insufficient knowledge of species, especially when researchers have not dealt with species in nature or have not observed them in their natural habitats. S. Enander, B. Floderus, and R. Görz repeated the same mistake over and over again: they treated species that they were less familiar with as hybrids of those more familiar to them. We have already considered here some examples; there are many more of them. For instance, B. Floderus treated dozens of *S. glauca* samples from the Kola Peninsula as hybrids *S. glauca* × *S. reptans* merely because he did not have a distinct notion of *S. reptans*. In fact, none of these samples have any characters of *S. reptans*.

He also decided that *S. nummularia* × *S. herbacea* hybrids were distributed in northern Norway up to 20° E. However, all of Stockholm samples of these "hybrids" that I had an opportunity to see were either *S. polaris* or *S. herbacea* and had nothing to do with *S. nummularia*.

I have to confess that not infrequently and particularly during my early years of studying the willows, I also considered those samples that did not fit within my concepts of species to be hybrids. However, in the majority of cases, I had to change my opinion later, as I found out that these were not hybrids. Instead I had to accept that my own understanding of species had been incomplete. It took me an especially long time to find the border between *S. viminalis* and *S. dasyclados*. Over and over again, I was drawn to the conclusion that these species hybridized in Siberia and the Urals en masse. Finally, I found out that my concept of *S. viminalis* morphological range, which had been developed from my experience on the Oka River and in Moscow Oblast, was insufficient for the entire species range and had to be broadened. Once I got to that point, the material immediately fell exactly to particular species leaving nearly no doubtful remainders.

3. Selective collecting is one more cause of exaggerations in assessment of the role of willow hybrids in nature. In collections of any expedition from any particular region, usually, there are no or very few hybrid samples. Hybrids usually show up in a collection when a researcher works at the same station for a long time and tries to give the most complete presentation of morphological diversity of willows in a particular area. Also, if a salicologist looks particularly for hybrid willows, he certainly finds them, and not just a few. And if one keeps cutting all these hybrid specimens for exsiccatae and mailing them out to herbaria, then, of course, the percentage of hybrid samples in herbaria becomes very different from occurrence of these hybrids in nature.

Taking all these critical remarks into account, let us now summarize the author's views on the natural hybridization in the willows.

1. Every single species cannot hybridize with any other one. For many pairs of species, hybrids have never been found (for example, *S. purpurea* × *S. myrsinifolia*; *S. caprea* × *S. myrsinifolia*; *S. hastata* × *S. glauca*; and others are unknown). Willows from the subgenus *Salix* nearly never form hybrids with representatives of the other two subgenera. Only one hybrid like this is known with certainty: *S. triandra* × *S. viminalis*. This is a vigorous shrub with the bark like the one in *S. triandra*, glabrous leaves, their shape resembling the leaf shape in *S. viminalis*. It develops flowers rather abundantly though never producing vital seeds. Members of the subgenera *Chamaetia* and *Vetrix* may hybridize not infrequently, including *S. reticulata*, the most isolated species in *Chamaetia*. The reader can find more detail on hybrid combinations, their possibility, vitality of hybrid offspring, etc. in the works by M. Wichura and R. Buser already cited here, as well as those by H. Nilsson (1918, 1930, 1937, 1954), S. Ikeno (1918, 1922), and V. Sukachev (1934, 1939). Most of hybrids published in the "Herbarium of the Russian Flora" were identified correctly. Presumably, most of the hybrid combinations mentioned by A. Kimura are also true. As for any other specifications of hybrids in the literature, one must treat them with great deal of caution. Even F. Wimmer somewhat exaggerated the significance of hybrids. Neither can we trust all of remarks on hybrids made by M. Nazarov (1936). M. Nazarov collected many hybrids, mostly in Vladimir Oblast, and correctly identified many of them. However, he was often mistaken while dealing with material from the Caucasus, Siberia, and Middle Asia. Besides, in the "Flora of the USSR", he often used data from E. Wolf's works as well as Western literature sources that were not reliable enough.

A revision of all known hybrid combinations is not an aim of this book, neither is a review of all available data on hybrids. To fulfill this task would mean to postpone another, much more important one: a revision of the willow species systematics in the USSR ad calendae graecae. However, since there is still very few data available on hybrids from the Asiatic part of Russia and Asiatic Republics, a list of these hybrids is provided here (see Table 2). All of them were studied by the author and many (those marked with an asterisk) observed in nature. 66

Although the list is by no means exhaustive and gives a rather incomplete picture of the willow hybridization on the Asiatic territory studied here, there is still some evident analogy with data on the willow hybridization in Europe. For instance, on our list, there are no hybrids between species of the section *Vetrix*, neither between members of *Vetrix* and *Glaucæ*, *Lanatae* and *Myrtosalix*. On the contrary, there are whole sets of *Vetrix* × *Vimen*, *Vetrix* × *Helix*, and *Vimen* × *Helix* hybrids.

Table 2. List of hybrid combinations for Asiatic Russia and adjacent Asiatic countries

- S. berberifolia* × *S. saxatilis* (Eastern Sayans*, Lower Lena)
- S. tschuktschorum* × *S. saxatilis* (Chukotka, Indigirka)
- S. fedtschenkoi* × *S. iliensis* (Tadjikistan)
- ? *S. pyrolifolia* × *S. myrsinifolia* (Northern Urals*)
- S. caprea* × *S. schwerinii* (Southern Maritime Province*)
- S. caprea* × *S. lapponum* (Northern Urals*)
- S. caprea* × *S. integra* (Maritime Province)
- S. cinerea* × *S. tenuijulis* (Ili*)
- S. cinerea* × *S. vinogradovii* (Southern Urals)
- S. armeno-rossica* × *S. elbursensis* (Armenia*)
- S. armeno-rossica* × *S. caprea* (Armenia*)
- S. turanica* × *S. iliensis* (Western Pamirs)
- S. turanica* × *S. tenuijulis* (Kirghizia*)
- S. viminalis* × *S. phyllicifolia* (Northern Urals*)
- S. viminalis* × *S. pulchra* (Lower Lena)
- S. alaxensis* × *S. pulchra* (Lower Lena)
- S. viminalis* × *S. miyabeana* (Irkutsk Oblast*)
- S. dasyclados* × *S. miyabeana* (Transbaykalia)
- S. dasyclados* × *S. abscondita* (Transbaykalia*)
- S. gracilistyla* × *S. schwerinii* (Southern Maritime Province*)
- S. acutifolia* × *S. rosmarinifolia* (Kazakhstan)
- S. brachypoda* × *S. integra* (Southern Maritime Province*)
- S. acmophylla* × *S. excelsa* (Kopet-Dag*)
- S. triandra* × *S. songarica* (Prebalkhashia)
- S. nummularia* × *S. reptans* (Chukotka)
- S. polaris* × *S. pulchra* (Arctic Yakutia)
- S. fuscescens* × *S. pulchra* (Chukotka)
- ? *S. fuscescens* × *S. arctica* (Lower Lena)
- S. fuscescens* × *S. udensis* (Sakhalin*, Kurils, Kamchatka)
- ? *S. arctica* × *S. chamissonis* (Ratmanov Island)
- ? *S. arctica* × *S. phlebophylla* (Wrangel Island)
- S. glauca* × *S. phyllicifolia* (Northern Urals*)

2. Hybridization takes place in particular areas and habitats. It is restricted to appropriate conditions and rarely occurs beyond them. Hybrids are rather common in European cultivated landscapes. According to R. Buser (1940), upper zones in the Alps, especially glacial

moraines and taluses, are rich in hybrids. Northern Fennoscandia is also hybrid rich: "Lapponia est terra hybridarum feracissima" (Wimmer 1866: XLIX). Probably, the abundance of hybrids in the Alps and Fennoscandia is of common origin: both territories have been freed from the glacier just recently, so that the vegetation and flora of these regions are not yet set stable. However, in the Polar Urals, for example, hybridization does not take place. According to available herbarium material, it is also insignificant in Siberian Arctic. The Caucasus, Middle Asia, the Far East, and major part of Siberia are as well hybrid deficient. In Prebaykalia, hybrids occur somewhat more frequently, yet there, as well, we are dealing with hybridization just between some few species.

3. Even in those areas that are comparatively hybrid rich, hybrids never predominate over parental species (except some special cases to be discussed below).

67 4. Hybridization is not the essential cause of infraspecific variability. This statement has been already discussed here in more detail.

5. As it was noticed first by R. Buser, willows that easily hybridize are not necessarily those of close filiation. On the contrary, most common are hybrids between representatives of different sections¹. This is a true fact, however paradoxical it may seem, and my own observations also confirm it by all means. The reader already had a chance to notice that the majority of hybrids cited on the Asiatic Territory List are intersectional ones. Contrary to all major concepts of his time including an opinion of as big an authority as that of F. Wimmer, R. Buser denied the existence of natural hybrids between *S. caprea* and *S. cinerea* (Buser 1940). Here, once again, R. Buser demonstrated his outstanding capability to make observations. In herbarium material, I have found many samples identified as *S. caprea* × *S. cinerea* (for example, there are a number of them in "Salices Brandenburgenses" by R. Görz). When I looked through those samples, I could not find a single specimen that might be considered as a hybrid of *S. caprea* and *S. cinerea*. All of them appeared to belong to either one or another of the two species. Neither did I ever find the hybrid in nature, although *S. caprea* and *S. cinerea* are very common and constantly occur close together in willow populations of the temperate climate belt in European Russia, the kind of communities that I have studied many times. I never met a *S. caprea* × *S. aurita* hybrid, although these species as well occur together in the non-chernozem belt almost at every step. Likewise, I never had a chance to see such hybrids as, for instance, *S. michelsonii* × *S. tenuijulis*, *S. turanica* × *S. argyracea*, *S. abscondita* × *S. caprea*, *S. miyabeana* × *S. integra*, *S. schwerinii* × *S. udensis*, no matter that the appropriate pairs of species grow together very frequently. On the other hand, intersectional hybrids between these particular species are real. Among those that I had a possibility to observe in nature were *S. tenuijulis* × *S. turanica*, *S. tenuijulis* × *S. cinerea*, *S. miyabeana* × *S. viminalis*, *S. integra* × *S. brachypoda*, *S. schwerinii* × *S. caprea*, *S. abscondita* × *S. dasyclados*.

6. As it was emphasized above, hybridization in willows generally does not occur en masse, except some particular occasions that deserve special treatment. There are four of them in our flora.

The first one is the case of *S. starkeana* and *S. bebbiana*. The relation between these two species, as mentioned in chapter 2, section 1, is absolutely similar to that of the Siberian and European spruces, which was studied in detail by E. Bobrov (1944). *S. bebbiana* is distributed across all of Siberia. In the north of the forest belt, it also invades Europe as far as

¹ Actually, this conclusion could be drawn from M. Wichura's data, but it was R. Buser, who first articulated it clearly.

Scandinavia. A European species *S. starkeana* goes east to the Urals and in some places farther, reaching the West Siberian forest-steppes. Hence, the northeastern limit of *S. starkeana* overlaps the southwestern limit of *S. bebbiana*. The species easily hybridize across the entire area of their contact, so that it is nearly impossible to distinguish between them within that zone. The most realistic explanation of the phenomenon is probably the one proposed by E. Bobrov for the spruces: the species, which had been isolated during the glaciation, started to expand during the subsequent postglacial period. Since they did not appear to have diverged far enough, ecologically as well as genetically, they again started to mix in the contact zone. It is quite possible that their current status is not yet stable and one of them (namely, the European one) is replacing the other.

S. repens and *S. rosmarinifolia* present one more case of the same nature, yet in another geographical setting. One of them has the Atlantic distribution, the other one is boreal Eurosiberian, continental. *S. repens*, unlike *S. starkeana* that survived during the glaciation somewhere in the south of Central Europe or the Balkans, spent the glacial period on the Atlantic Coast. Consequently, it did not reach the Urals after the glaciation and met *S. rosmarinifolia* in Central Europe. The area of their contact extends from Bavaria to Czechia, western Poland, the Baltic Coast, and Finland.

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The third case of mass-scale hybridization between two closely related species is quite different from the previous ones. *S. alba* is a European-West Siberian species that is reaching the Mediterranean Sea; *S. excelsa* is an Iranian species. Both have been widely cultivated from time immemorial in arid and semiarid regions of eastern Asia Minor, Transcaucasia, and Middle Asia (that are, as a matter of fact, the oldest regions of plant cultivation). Natural limits of their areas in these regions were deleted and messed up long ago by human activities. As a result, we have to deal with a tremendous number of intermediate forms, besides, so intricately scattered around that an idea to unite both species and treat them as a single one does not appear very inappropriate¹.

Finally, the fourth, very special occasion of hybridization en masse is of particular interest. Here, we are dealing with *S. fragilis* and *S. alba*. The first one is an endemic of Asia Minor that somehow penetrated to Europe, presumably, not later or, still more likely, earlier than the Middle Ages. There, in Europe, it became widely distributed, mostly vegetatively (the branches of *S. fragilis* are known to break off and root very easily). *S. fragilis* and *S. alba* hybridize everywhere in Central Europe as well as in western and temperate European Russia on such a grand scale that, according to many observers, their hybrids are much more common than "pure" *S. fragilis*. However, *S. fragilis* and *S. alba* appear not to hybridize that much in Asia Minor, as far as it could be concluded from the analysis of the scanty herbarium material available.

Obviously, each of these special cases of mass-scale hybridization in our flora has its own, specific grounds, and it is only in the first two cases that these grounds are of natural origin. Therefore, none of the cases can be an argument against the statement about fairly limited importance of the hybridization in the willows. Indeed, they even prove once more that the hybridization in the willows is hardly more significant than in other genera of the flowering plants similar to the genus *Salix* in terms of species number and manner of distribution.

The question about a possible role of the hybridization in the evolution of the genus *Salix* will be approached in the section 1 of the next chapter.

¹ See footnote on page 118.

Chapter 4

EVOLUTION AND PHYLOGENY

1. MORPHOLOGICAL EVOLUTION

The major difficulty in tracing paths of evolution and phylogenesis hides in the fact that we evaluate the extent of primitiveness of particular characters basing on our notions about the primitiveness of taxa that possess those characters, and, at the same time, we decide on the primitiveness of the taxa basing on the primitiveness of their characters. Here we find ourselves in a vicious circle, where we can build as many phylogenetic schemes as we like, but their main feature, the direction of changes, will then always remain doubtful. In order to stop this meaningless rotation, we have to stick to something that lies beyond that orbit. This may be either distinct paleontological evidence or observation of characters that appear to be an obvious indication of relations between taxa. So far, the search for the origin of the amentiferous plants on the whole and particularly the Salicaceae has not been very promising. However, tracing major evolutionary paths within the Salicaceae family can be more successful. Naturalness of the family Salicaceae as well as close relation between the willows and poplars are beyond question, even though there are distinctions in their pollen morphology (Kupriyanova 1965). Consequently, we get a solid base for our decisions regarding the extent of the primitiveness of particular groups within the genus *Salix*. Obviously, the most primitive groups are those closest to the poplars. Apparently, this is the subgenus *Salix*. Therefore, the most primitive characters are those of the subgenus *Salix*, particularly, those resembling features of the poplars. We can as well partially rely on observations of ontogenesis, teratological study, and general ideas when evaluating some of the characters.

On the basis of these initial assumptions, major trends of the morphological evolution within the genus *Salix* may be presented as follows (see Table 3).

Relying on the characters listed in Table 3, one may evaluate the extent of primitiveness or progressiveness of particular sections. Of course, one should keep in mind that these evaluations will always be largely hypothetical. First of all, characters evolve independently, so that a taxon may appear to be primitive with regard to some of its characters and advanced when taking others into consideration. For example, *S. cardiophylla* is by all means very primitive as far as the structure of its buds and flowers is concerned. At the same time, its leaves show advanced anatomical structure. However, primitive characters definitely predominate in *S. cardiophylla*, so that the conclusion about general primitiveness of that species is hardly disputable.

To make a decision on the status of the section *Helix* is a far more difficult task. Here, we find an overall predomination of advanced characters (the buds of type 3, no distinct hypodermis in the leaves, black, persistent bracts, one nectary, connate stamens, etc.). However, along with these, there are also primitive features (flat denticulate leaves and colorless fugacious bracts in some species). One can think of two possible explanations: either

this group has preserved some primitive characters while generally it developed advanced structures, or the primitive characters might have been secondarily acquired.

Table 3. Major directions of morphological evolution in the willows

<i>Primitive characters</i>	<i>Advanced characters</i>
Alluvial habitats	Non-alluvial habitats
Habit: erect trees	Habit: shrubs or dwarf shrubs
Bud scale margins distinct	Bud scale margins connate, scale cap-like
Lower cataphylls broad, their veins parallel	Lower cataphylls narrow, their veins pinnate, as in regular leaves
Bud size gradation of type 1 (<i>alba</i>)	Bud size gradation of type 2 (<i>arctica</i>) or 3 (<i>caprea</i>)
Petioles channeled above, glandular at leaf base	Petioles convex above, eglandular
Young leaves produce odorous pitch	Leaves not pitchy
Leaves acuminate	Leaves obtuse or short-pointed
Veins prominent neither beneath, nor above; leaves flat	Veins impressed above, prominent beneath; leaf margins revolute
Leaf denticles small and uniform	Leaf denticles coarse and irregular or lacking
Glands marginal	Glands submarginal or extramarginal
Distinct hypodermal layer in mesophyll	Hypodermis not distinct
Catkins narrowly cylindrical, long, sparsely flowered, more or less drooping	Catkins more stout and short, erect, compactly flowered
Bract connate at base to ovary stipe, abaxial nectary, and stamens	Bracts quite distinct
Bracts colorless, abscising in female catkins after flowering	Bracts colored (brown or black), persistent
Bracts puberulent on the inside, particularly at base	Bracts clothed with long trichomes, mostly at apex
Nectaries two, or three, or glandular disk replacing individual nectaries	Solitary adaxial nectary
Stamens multiple (three or more), their number fluctuating	Stamens three or two, their number constant; further evolution leading towards coalescence of stamen filaments
Stamen filaments comparatively short, pubescent	Stamen filaments comparatively long, glabrous
Anthers small, not pigmented	Anthers large, pigmented
Ovaries stipitate	Ovaries sessile
Styles partially or entirely distinct, separated	Styles entirely connate

In some cases, one can speculate on the secondary nature of generally primitive characters with more confidence. For instance, all of possible relations of the section *Vimen* are with non-alluvial groups; however, the section *Vimen* itself consists almost entirely of alluvial species. Apparently, we can consider the shift to alluvial habitats to be secondary in *Vimen*. We may as well treat the habit of an upright tree in *S. caprea* and *S. dasyclados* and also the loss of bract coloration in *S. starkeana* and *S. bebbiana* as other examples of secondarily acquired characters.

Atavistic features in willow phenotypes or physiology are not infrequent. They give evidence of evolutionary paths overcome by taxa. At the same time, atavistic features demonstrate occasional possibilities for taxa to develop in "the opposite direction". For example, in seedlings of *S. pycnostachya*, I once found some latent buds at bases of lateral shoots with their bud scales not connate. In the proleptical catkins (i. e., those that expand during the fall), bud scales are usually colorless, even in species that generally have black scales. In the sections where all of species normally have one nectary in each flower, some specimens with two nectaries are found (in our collection, there was one *S. argyracea* male clone like that). A multistaminate form of *S. alba* is not infrequent, although two stamens are normally characteristic of *S. alba* flowers; occasionally multistaminate flowers may also occur in *S. fragilis*. There are more examples like these.

Some characters evolve to a large extent in parallel to each other. For example, short, pubescent stamens are usually correlated with bracts puberulent on the inside, yet without long trichomes at the apex. On the contrary, if stamens are long and glabrous, then bracts usually have dense trichomes at the apex. That contingency in the development of pubescence might be connected with mechanisms of pollination by insects, as pollen is accumulated on trichomes.

Precocious flowering is usually correlated with the bud type 3 (*caprea*), sessile catkins, as well as pigmented bracts and anthers; serotinous flowering is typical for plants with the bud type 1 (*alba*) or 2 (*arctica*), elongated and more or less foliated catkin stalks, and also pale bracts and anthers.

Precocious catkins develop to a more advanced stage inside buds, and therefore floriferous buds become considerably larger than vegetative ones. Pigmentation of bracts and anthers might provide more absorption of sunlight, which may be critical for precocious catkins and not that important for serotinous ones. However, this correlation is not absolute in the subgenus *Salix*, where precocious species do have colorless bracts.

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As for the time of flowering, this feature itself appears to be of no particular, common for all groups evolutionary significance. All the European species of the subgenus *Salix* are comparatively serotinous. Therefore, R. Scharfetter (1953) tried to treat that character as primary one. However, *S. pierotii* from the section *Subalbae* has precocious catkins, and there are some species in the section *Humboldtianae* (*S. tetrasperma*, *S. bonplandiana*) that occasionally flower as early as November or December, when new leaves have not yet appeared and there are still old leaves on branches. In many sections (especially *Helix* and *Arbuscella*), there are species with extremely precocious catkins along with ones characterized by serotinous catkins. As it has been shown in chapter 3, section 4, considerable differences regarding the time of flowering may exist even within a single species.

In various branches of the genus *Salix*, similar morphological progress was achieved in parallel, in a number of directions. In the subgenus *Salix*, species of the sections *Amygdalinae* and *Longifoliae* have independently converted their arboreal habit to one of shrub. Since we

are quite confident that shrub species from the subgenera *Vetrix* and *Chamaetia* originate neither from *Amygdalinae* nor from *Longifoliae*, we can state that these have also acquired their shrub habit independently.

Within the section *Humboldtianae*, one can observe a transition from bud scales with distinct overlapping margins to connate, cap-like ones: in an African species *S. subserrata* Willd. as well as in American *S. amygdaloides* Anderss., there occur some bud scales with their margins only partially connate. The section *Pentandrae* has evolved to acquire the connate bud scale margins absolutely independently from *Humboldtianae*. This is quite obvious, because *Pentandrae* are more primitive than *Humboldtianae* in a number of characters, such as leaves producing pitch or the presence of the hypodermal layer in leaves. In any case, it is impossible to derive *Pentandrae* from *Humboldtianae*. The third group that has by all means independently acquired cap-like scales is an American section *Longifoliae*. This is a very isolated group with absolutely original leaf structure (the hypodermis is isolateral, chlorophyll deficient, like the one in *Chosenia* or *Turanga* poplars); one cannot derive *Longifoliae* from either *Humboldtianae* or *Pentandrae*.

The reduction in stamen number also took place in different groups, in parallel. There are at least three of them known: an isolated American section *Longifoliae* (which has been just mentioned above), a group of related sections *Pentandrae*—*Salix*—*Subalbae*, and the subgenera *Vetrix* and *Chamaetia*, none of which may in any case be derived from *Longifoliae* or *Salix*—*Subalbae*. The subsequent evolutionary process with regards the androecium, that is, the fusion of the two stamens (see chapter 3, section 3), also took place independently and in parallel in a number of phylogenetic lines. We can notice similar processes as regards the evolution of the nectaries. Although the change from a few nectaries to a pair and then single one of a constant shape has been completed only in the subgenus *Vetrix*, the trend is quite obvious in other branches: the sections *Salix*, *Subalbae*, *Humboldtianae*, and *Glaucæ*.

Along with those features that may be with certain confidence qualified as primitive or advanced, there are, of course, scores of those that cannot be approached that way. They just reflect the variability of certain ways of development in particular species (to some extent, that variability was described in chapter 3, section 3; one can find more detail in the keys to sections and species). Within particular small groups, there are also occasions when one may try to consider some of characters as primary, others derived. However, these speculations would be much more hypothetical, since here we find ourselves too far away from the initial statements, that is, the idea of the common filiation of the willows and poplars and the notion about the primitiveness of the subgenus *Salix*. It is impossible, for instance, to tell with confidence, which of the two extreme types of catkin structure in the section *Arbuscella* is primary and which is more advanced: *S. pulchra* or *S. arbuscula* type. Probably, it is an intermediate structure which is primary.

Even those characters that cannot be used as criteria of evolutionary advancement may still be useful for general judgements about morphological evolution in the willows. They provide abundant data demonstrating that parallel and convergent development is very common in the willows. To take an example, in our country, it is only in *S. lanata* and *S. brachypoda* where we find bract pubescence of a golden color. It is absolutely impossible to assume a common origin of the sections *Incubaceae* and *Lanatae*, to which the species belong, as these sections are strikingly different in almost every respect. In other sections, which might be considered as a missing link, that bract pubescence color is not encountered. Indeed, it never occurs even in other species within the same sections. Another example is the

opposite leaf arrangement in one species of a Himalayan section *Daltonianae* (*S. salwinensis* Hand.-Mazz.), some species of the section *Helix*, and *S. subopposita* Miq. from *Incubaceae*. It is again impossible to treat the three sections as closely related; on the other hand, there are no species with the opposite leaf arrangement in any other sections. The only realistic explanation for the same golden color of bract pubescence as well as opposite leaf arrangement in different sections would be an acknowledgment of totally independent, convergent development of these characters.

Table 4 is a list of characters that appear to have developed in parallel or convergently, independently in different groups.

Table 4. Similar characters developed in different sections of willows as a result of parallel or convergent evolution

<i>Characters</i>	<i>Sections in which these characters are found</i>
Wood striation (raised striae)	<i>Vetrix</i> ; less developed in <i>Vimen</i> , <i>Arbuscella</i>
Yellow phloem color	<i>Hastatae</i> , <i>Lanatae</i> , <i>Daphnella</i> , <i>Helix</i>
Pruinose shoots	<i>Amygdalinae</i> , <i>Villosae</i> , <i>Daphnella</i> , <i>Helix</i>
Buds with recurved beaks	<i>Myrtosalix</i> , <i>Vetrix</i> , <i>Lanatae</i> , <i>Daphnella</i> , <i>Arbuscella</i>
Stipules orbicular, equilateral	<i>Hastatae</i> , <i>Daphnella</i>
Stipules narrowly lanceolate or linear	<i>Salix</i> , <i>Glaucæ</i> , <i>Arbuscella</i> , <i>Vimen</i> , <i>Helix</i>
Stipules wide, distinctly inequilateral, abscising together with narrowly lanceolate leaves	<i>Humboldtianae</i> , <i>Amygdalinae</i> , <i>Salix</i> , <i>Subalbae</i> , <i>Arbuscella</i> , <i>Vimen</i>
Stipules persistent after leaf abscission	<i>Arbuscella</i> , <i>Lanatae</i>
Stipules adnate to petioles	<i>Eriostachyae</i> , <i>Daphnella</i>
Leaves approximately opposite	<i>Daltonianae</i> , <i>Incubaceae</i> , <i>Helix</i>
Golden color of catkin pubescence	<i>Lanatae</i> , <i>Incubaceae</i>
Species with pale and black bracts within one section	<i>Retusae</i> , <i>Myrtilloides</i> , <i>Glaucæ</i> , <i>Hastatae</i> , <i>Vetrix</i> , <i>Arbuscella</i> , <i>Helix</i>
Species with glabrous and pubescent capsules within one section	<i>Urbanianae</i> , <i>Subalbae</i> , <i>Chamaetia</i> , <i>Retusae</i> , <i>Myrtilloides</i> , <i>Glaucæ</i> , <i>Myrtosalix</i> , <i>Glabrella</i> , <i>Nigricantes</i> , <i>Vetrix</i> , <i>Arbuscella</i> , <i>Daphnella</i> , <i>Helix</i> , <i>Incubaceae</i> , <i>Cheilophilae</i>
Nearly isolateral chlorenchyma in leaves	<i>Humboldtianae</i> , <i>Amygdalinae</i> , <i>Retusae</i> , <i>Incubaceae</i> , <i>Cheilophilae</i> , <i>Helix</i>
Bilateral mesophyll along with nearly isolateral structure of epidermis and leaf margin	<i>Pentandrae</i> , <i>Salix</i> , <i>Glaucæ</i> , <i>Arbuscella</i> , <i>Villosae</i> , <i>Helix</i>
Diploids and polyploids within one section (according to literature data)	<i>Amygdalinae</i> , <i>Subalbae</i> , <i>Retusae</i> , <i>Glaucæ</i> , <i>Myrtosalix</i> , <i>Glabrella</i> , <i>Nigricantes</i> , <i>Vetrix</i> , <i>Arbuscella</i> , <i>Vimen</i> , <i>Villosae</i> , <i>Helix</i>

Of course, it is impossible to attribute the examples of convergence listed above merely to "a similarity of conditions". Although this explanation works, say, for a cushion habit in *Astragalus*, *Onobrychis*, *Acantholimon*, and *Convolvulus*, or leafless shoots in *Ephedra*, *Haloxylon*, *Calligonum*, and *Eremosparton*, or round floating leaves in *Caldesia*, *Hydrocharis*, *Limnanthemum*, and *Nuphar*, one would not succeed to detect any "similarity of conditions" in order to explain the resemblance of the golden catkin pubescence in an arctic species *S. lanata* and meadow species from the Far East *S. brachypoda*. 73

It is impossible to point to any "similar conditions" while trying to explain a peculiar leaf arrangement in *S. integra*, *S. subopposita*, and *S. salwinensis*. Neither it is reasonable to mention the "similarity of conditions" in order to explain the same bright yellow phloem color in a wetland species *S. pyrolifolia*; an arctic species growing near streams, *S. lanata*; a species of arid sandy territories, *S. caspica*; and the alluvial *S. rorida* (mind that none of alluvial species growing together with *S. rorida* including a closely related one, *S. kangensis*, exhibit that phloem coloration). We also find much similarity in the anatomical leaf structure of *S. chaenomeloides* Kimura and *S. alata* (the only difference is in the cell size). Yet there is hardly anything in common between the subalpine zone of the Tien Shan (the environment of *S. alata*) and moist subtropical forests of southern Japan, Taiwan, and East China (the natural setting for *S. chaenomeloides*). Apparently, we have to conclude that in various lines (and on different levels) of phylogenesis, similar structures may have completely different ecological significance.

It is a well-known fact that interspecific and intersectional hybrids are not infrequent in the willows, and many of them are fertile. Hence, the question naturally arises, whether the evolutionary process in willows is to any extent induced by the hybridization. Particularly, is it possible by any chance that the described facts of convergence and parallelism are results of distant hybridization? In other words, is the evolution in the willows of the so-called *reticulate* nature?

Our notions about phylogeny are always and inevitably hypothetical to a considerable extent, and consequently, any assertions regarding paths of the phylogenesis are by all means inappropriate, especially in the lack of paleontological evidence. Therefore, one cannot absolutely deny a possibility of intersection of evolutionary paths, that is, existence of *reticulate* areas. However, so far no one succeeded to find any particular evidence, examples that could demonstrate the role of hybridization in the evolution of the willows. All data that at the first glance appear to be such evidence indicate the opposite when considered more closely.

In the Western and also, to some extent, in the Russian literature, an opinion on the hybrid nature of *S. dasyclados* has become widespread (Rechinger 1964; Popov 1959). According to it, *S. dasyclados* is a feral (reverted to wilderness) hybrid of *S. viminalis* and a species from the section *Vetrix*, most likely, *S. cinerea*. Indeed, the shoots and leaves of *S. dasyclados* look somewhat intermediate between those of *S. viminalis* and *S. cinerea*. Also, in *S. dasyclados* usually there are raised striae on the wood, a feature particularly typical for *S. cinerea*. However, this intermediate position of *S. dasyclados* turns out to be false on more careful analysis. *S. dasyclados* is a tree up to 20 m tall and 90 cm in stem diameter. It is absolutely impossible to assume that either of the proposed "parental" species can ever attain that size. The bud shape and leaf pubescence in *S. dasyclados* do not at all resemble the *Vetrix* type. The flower in *S. dasyclados* is not like that in *S. cinerea*. Hence, the only common character to rely on is the wood with the raised striation. However, one should consider the presence of vague and sparse striae on the wood in species from the sections *Arbuscella* and

Nigricantes, which means that this feature is not exclusively typical for the section *Vetrix*. Then why is it so impossible to find striae in the section *Vimen* as well? To make a long story short, there is no reliable proof of *S. dasyclados* hybrid nature with regards the species morphology. Within the whole range of its huge distributional area, *S. dasyclados* occupies its own particular niche in nature, including absolutely intact natural habitats, and is normally reproduced by seeds. Finally, there is a number of species related to *S. dasyclados* in the mountains of Asia. These are a Siberian species *S. sajanensis* (which is of especially close filiation), *S. argyracea* from the Tien Shan, and a Himalayan species *S. obscura* Anderss. Consequently, here we deal not with a single "hybrid", but rather with a whole group of species characterized by very distinct geographical features. According to its distribution, the group is scarcely younger than *S. viminalis*. In the light of these facts, the idea about hybrid origin of *S. dasyclados* is deprived of any foundation.

M. Popov (1959) believed in hybrid nature of *S. bebbiana* (*S. starkeana* × *S. caprea*), *S. udensis* (*S. viminalis* × *S. miyabeana*), *S. sajanensis* (*S. viminalis* × *S. saxatilis*), and *S. vestita* (*S. reticulata* × *S. krylovii*). None of these assumptions stand up under scrutiny. In North America, where *S. bebbiana* is widespread, there is no *S. caprea* or *S. starkeana*. At the same time, in temperate European Russia, where *S. caprea* and *S. starkeana* commonly grow together, there is no *S. bebbiana*. M. Popov also did not notice that the leaf pubescence in *S. bebbiana* is absolutely different from that in *S. caprea*. A hybrid of *S. viminalis* and *S. miyabeana* is indeed encountered in Prebaykalia; however, it has nothing to do with *S. udensis*. Capsules in both proposed parental species are sessile, however, *S. udensis* is characterized by elongated capsule stipes. *S. sajanensis* does not have any characters resembling *S. saxatilis*. The only common feature of these species is that they both grow in the subalpine zone of the Sayans and Barguzinskiy Range. *S. sajanensis* is a quite typical member of the section *Vimen*, according to the set of its characters. There is a species very close to *S. sajanensis* in the Himalayas (*S. obscura* Anderss.); however, there is no *S. saxatilis* or any other species from the section *Myrtosalix*. *S. vestita* is known to have major parts of its distributional area in North America (the largest on Labrador and a smaller one in the Rocky Mountains), and American samples of this species are absolutely identical to those from Prebaykalia. As for *S. krylovii*, it is not distributed in North America. In accordance with its very peculiar leaf and floriferous shoot structure, *S. vestita* is a perfect member of the section *Chamaetia* and has nothing to do with *S. krylovii*. It remains unclear, which characters resembling *S. krylovii* were noticed in *S. vestita* by M. Popov.

While studying the segregation of the hybrid *S. caprea* × *S. viminalis*, in the F₂ generation, N. Nilsson (1931) found a specimen that resembled *S. cinerea* in many ways. He concluded that he had managed to reconstruct *S. cinerea* and called his new plant *S. neocinerea*. According to N. Nilsson, *S. cinerea* is an apophytic species, which has just recently emerged polytopically (i. e., simultaneously in different places) in areas of human activities through multiple crossings between *S. caprea* and *S. viminalis*. "*S. neocinerea*" cannot form hybrids with its parental species. That fact was supposed to confirm N. Nilsson's success in the artificial imitation of the natural speciation. This work by N. Nilsson has been frequently referred to in the literature devoted to more general issues as an example of species "synthesis" (Cain 1944, Scharfetter 1953).

However, these conclusions by N. Nilsson by no means stand up under scrutiny. First of all, on two excellent photos appended to the article, one can see a plant with an obscure habit instead of *S. cinerea*. The leaves of *S. cinerea* are very specific on every phase of their

development from the spring to fall; however, one cannot notice this specificity in Nilsson's plant. The plant does not have any distinct wood striation, although N. Nilsson tried to prove its presence. There is something very vague on the picture, whereas in *S. cinerea* the raised striae become very distinct as early as the end of the first year. Shortly, morphological similarity with *S. cinerea* is rather arbitrary. The statement about an apophytic origin of *S. cinerea* shows that N. Nilsson was not familiar with the species in its natural setting. *S. cinerea* has its particular place in intact natural landscape: swarding muddy banks of slow streams. The notion about multiple emergence of *S. cinerea* as a result of crossings between *S. caprea* and *S. viminalis* is not at all corresponding to the geographical distribution of the two species. In southern Kazakhstan, for example, both "parents" are missing; however, *S. cinerea* is not infrequent there. If *S. cinerea* is a product of hybrid segregation, then why don't we see other products of the same segregation ranging from *S. caprea* to *S. viminalis*? And then how should we treat species close to *S. cinerea*, such as *S. pseudomedemii* from the Caucasus and Asia Minor, the Atlantic *S. atrocinerea*, and the western North American *S. scouleriana*? Finally, it remains unknown if "*S. neocinerea*" is able to survive in nature, in the environment usual for *S. cinerea*.

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Taking the overall morphological, ecological, geographical, and systematical data into consideration, one cannot help judging N. Nilsson's conclusions on the reconstruction of *S. cinerea* as well as his assessment of the species nature as hasty and naive.

Stability of characters in the majority of willow species within huge geographical ranges (see chapter 3, section 4) constitutes one of the major arguments against the significance of the distant hybridization in the evolution of the willows. For example, samples of *S. coesia* from the Pamirs and Alps are absolutely similar, although *S. coesia* grows together with totally different plants in the Alps and Pamirs. There are no known hybrids of *S. coesia* from the Pamirs, but there are ones from the Alps. In spite of this fact, the morphology of the Alpine *S. coesia* and one from the Pamirs is identical. *S. myrtilloides* often forms hybrids with *S. aurita* and *S. lapponum* in Europe. In Maritime Province, there is no *S. aurita*, or *S. lapponum*, or any other species close to these. However, *S. myrtilloides* from Maritime Province looks exactly alike the European one. Again, this proves that the hybridization with *S. lapponum* or *S. aurita* does not lead to any introgression or have any influence on the evolution of *S. myrtilloides*. One can provide still more examples like these.

2. PHYLOGENETIC RELATIONS BETWEEN MAJOR TAXONOMICAL GROUPS: A TRIAL RECONSTRUCTION

To elucidate phylogenetic relations is the most tempting goal for a taxonomist. However, this attractive goal may turn out to be rather deceptive. In our attempts to reconstruct the evolutionary process, we cannot get along without hypotheses; yet proposing a hypothesis is not that far from mere fantasizing. Hence, one should not overestimate the significance of any phylogenetic schemes and always keep in mind that, as regards their reliability, these schemes do not equal those elementary facts on which they are based.

Taking this reasoning into consideration, let us try to clarify major phylogenetic connections within the genus *Salix*. From the very beginning, I have to emphasize that the majority of the following conclusions will be of preliminary nature, as I am still far from having studied all of the world's willows in detail. On the other hand, it is absolutely impossible to rely on the literature data, since treatment of many important groups of willows, particularly Chinese ones, is still far from satisfactory. The information on limits of sections,

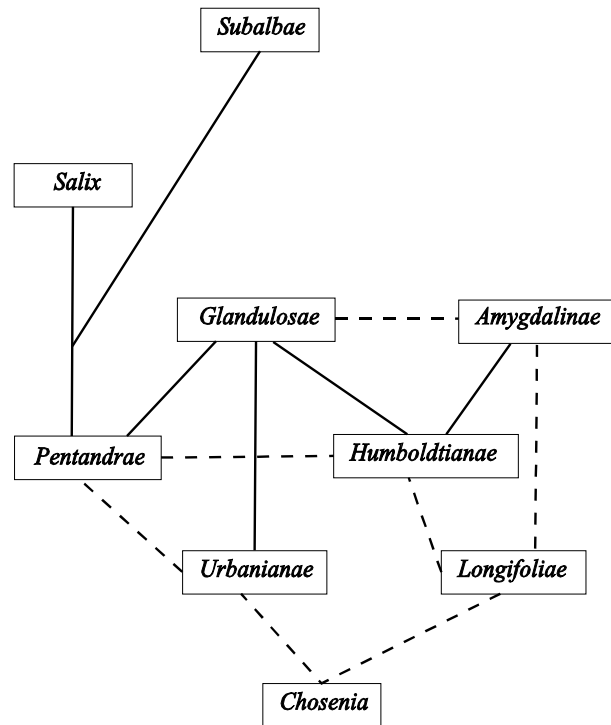
diagnostic characters of species, and other data in major sources on Chinese willows (Schneider 1916b; Hao 1936) appear to have serious errors when being critically compared with real material.

76 The subgenus *Salix*, as it was mentioned above, is the closest to the poplars and, therefore, to a primary common root of the family. The majority of its members are alluvial trees distributed mostly in warm temperate (and partially also tropical) regions, exhibiting primitive features in the structure of the bracts, nectaries, androecium, and gynoecium. No matter that the subgenus *Salix* appears to be natural (not polyphyletic), one can find a considerable divergence of individual types within it (see the illustration). However, none of these types can be treated as the most primitive in every particular respect. Some sections are more primitive as regards certain characters, others—as regards other ones.

An American section *Longifoliae* is particularly adapted to the arid climate: all the species have small and narrow leaves characterized by isolateral xeromorphic structure, much alike species from a Middle Asiatic section *Helix*. The willows from the section *Longifoliae* have retained general primitive organization of the flower; however, the stamen number is reduced to two. This is also the only section that, presumably because of tolerating the arid climate, has retained the isolateral, almost completely chlorophyll-deficient hypodermis, quite similarly to the chosenias and *Turanga* poplars. An ability to produce root offspring, so typical of poplars, has been as well preserved only in this section. The section *Longifoliae* apparently never produced any descendants. There is no doubt that its similarity with *Helix* mentioned above is completely convergent.

The section *Humboldtianae* is distributed in the Old as well as New World, in tropical, subtropical, and partially warm temperate regions. It has a rather obscure relation with *Longifoliae* and much more obvious one with *Glandulosae* and *Amygdalinae*. The latter section is especially close to American *S. amygdaloides* Anderss. Indeed, *Amygdalinae* could even be treated as derivatives of *Humboldtianae*, if it were not their unique bark structure that is not known in other willows (being only akin to that in the chosenias). *Longifoliae*, *Humboldtianae*, and *Amygdalinae* constitute mostly xeromorphic lines of evolution, their representatives restricted to dry, arid climates. *S. triandra* and an American species *S. interior* Rowlee (section *Longifoliae*) are those that managed to penetrate into areas of colder climates farther than the others.

The rest of the groups in the subgenus are mostly of the humid type. An East Asiatic section *Glandulosae* is obviously linked to *Humboldtianae* and, on the other hand, to



Probable evolutionary relations of the sections belonging to the subgenus *Salix*

Pentandrae. In some species of *Glandulosae* (*S. chaenomeloides*, *S. mesnyi*), the second bud scale is visible under the first one, so that the bud structure in this section appears to be most close to that in the poplars. That gave grounds to T. Nakai (1928) to segregate it in a separate genus *Pleiolepis*. There is no doubt that the sections *Pentandrae*, *Salix*, and *Subalbae* are of close filiation. Morphologically, the most primitive of these is *Pentandrae*, no matter its representatives are non-alluvial species distributed in cold climate areas. Both *Salix* and *Subalbae* can be easily derived from *Pentandrae* and are more xeromorphic in comparison with it.

Connections of the section *Urbanianae* with other groups of the subgenus are not yet clear enough; the most probable is some affinity with *Glandulosae*. The monotypic section *Urbanianae* is extremely primitive in terms of the flower structure: the ovary stipe base and stamen bases are connate to the base of the bract, which resembles the poplars very much. However, the leaves in this section are of the *Vetrix* type.

The subgenus *Salix* is well separated from the other two subgenera: there is no doubt that all of its sections are indispensable to it and none can belong to any other subgenus. The only change that might be worthy of consideration is further division of the subgenus, for example, segregation of *Urbanianae* (*Toisusu*) and *Longifoliae* as distinct subgenera.

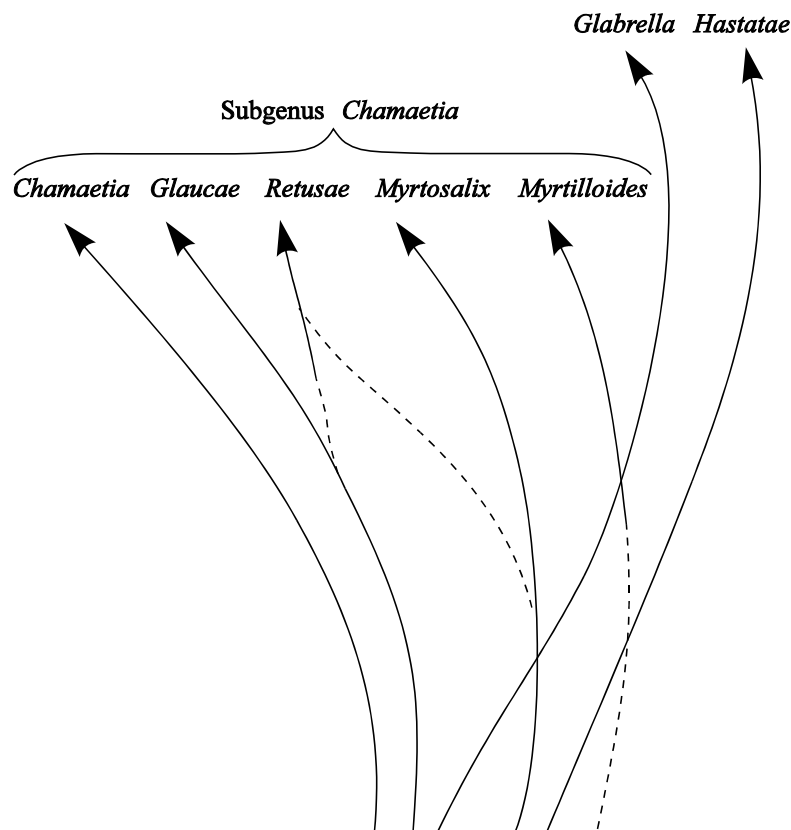
The situation is absolutely different with regards the subgenera *Vetrix* and *Chamaetia*. One can set limits for these subgenera only arbitrarily and with some major reservations. Many characters typical for the subgenus *Chamaetia* may be treated as adaptive ones. They might have emerged during transitions to extreme northern or alpine environmental conditions, probably, in some few phylogenetic lines. This is the clue explaining the late flowering as well as structure of buds and shoots. We also know that even precocious species produce late-developing ecotypes with altered structure of buds and floriferous shoots at northernmost locations of their distributional areas. There is no doubt that the bud type 2 (*arctica*-type) is also correlated with the specific way of shoot development in extreme conditions: everything that is supposed to expand in the following season is most prepared in the bud; at the same time, less urgent structures (latent buds, cataphylls), are largely reduced. A simplified leaf shape and peculiar arrangement of veins (vein origins are constricted to the base of the leaf blade, so that leaves appear to be nearly palmate-veined), particularly, in *S. reticulata*, *S. kurilensis*, *S. phlebophylla*, obviously result from some reduction process. To speak more correctly, this is a certain stage of neoteny (approximation to the structure of the inferior leaves). To take some examples, reduction (or neoteny) of this kind can be very well traced within the section *Myrtosalix* (*S. myrsinites* → *S. rectijulis* → *S. phlebophylla* → *S. rotundifolia*) or *Glaucæ* (*S. glauca* → *S. arctica* → *S. sphenophylla* → *S. kurilensis*). However, it is difficult to engage a secondary adaptation in order to explain, say, the primitive structure of nectaries in the majority of *Chamaetia* species. In addition to these considerations, one should keep in mind that features common to all *Chamaetia*, such as the habit of the plants, rhythms of development, bud and leaf structure, as well as their ecological and geographical unity, predominate so much that they mask the characters connecting *Chamaetia* with *Vetrix*. In some sections (particularly, *Retusae*), morphological reduction has gone such a long way, that their relations now appear to be absolutely obscure. Therefore, for the time being one should not give up the segregation of the subgenus *Chamaetia*. It is just necessary to bear in mind that this subgenus is much closer to *Vetrix* than *Salix* and might be of polyphyletic origin.

Of all the groups of *Vetrix*, Eurasiatic sections *Eriostachyae* and *Glabrella* and an Asiatic-American boreal section *Hastatae* are the closest to *Chamaetia*. (These are, at the same time,

the central sections in the subgenus *Vetrix*, as we will see later.) A Himalayan alpine section *Lindleyanae*, the major representative of *Chamaetia* in Southeast Asia, is clearly connected with the section *Eriostachyae*, which is as well Himalayan. One can tell with enough confidence that the section *Glaucæ* has also originated from *Eriostachyae* or *Glabrella*; *Retusæ* might have had a common root with *Glaucæ* (however, they also have some affinity with *Myrtosalix*). Finally, the species of *Myrtosalix* are akin to *Hastatæ* in many characters, although their direct derivation from *Hastatæ* is hardly probable. *Chamaetia*, the most isolated section of the subgenus *Chamaetia*, retain a few especially primitive features regarding the stamen, ovary, and stigma structure and are also known to have very specific, unique leaf anatomy. Presumably, this section constitutes a separate branch of development, which had become distinct long before the rest of the sections of the subgenus *Chamaetia* diverged from ancestral stems of the subgenus *Vetrix*. So far, it has been impossible to trace the closest relations of the section *Chamaetia*.

The status of the section *Myrtilloides* is rather obscure. It partially resembles *Retusæ*; however, it might as well be merely a comparatively recent derivative of the subgenus *Vetrix* (particularly, the section *Vetrix* or *Incubaceae*), which has emerged as a result of some reduction process.

Possible evolutionary ways of the *Chamaetia* sections are depicted in the illustration.



Probable evolutionary relations of the sections within and around the subgenus *Chamaetia*

Finally, we are proceeding to the largest and most complex of the subgenera, the subgenus *Vetrix*. In the flora of this country, within the subgenus, one can easily segregate the core unit, from which the majority of the sections may naturally be derived. This core unit embraces the sections *Glabrella*, *Nigricantes*, and *Hastatæ*. There is little doubt about the

close filiation of these sections. One can trace the line from *Glabrella* to *Arbuscella* rather well and go further on, from *Arbuscella* to *Vimen*, although the latter connection is not that obvious. *Subviminales*, *Villosae*, and *Canae* evidently have close relations with *Vimen*. *Lanatae* constitute a direct derivative from *Hastatae* as well as *Vetrix* from *Nigricantes*. Relations of the sections *Incubaceae* and *Daphnella* are less distinct. Some American species (such as *S. humilis* Marsh.) appear to provide evidence of connection between the sections *Incubaceae* and *Vetrix*. F. Wimmer used to associate *Daphnella* with *Lanatae* in accordance with the catkin structure; however, flat denticulate leaves and persistent subequilateral stipules would rather demonstrate close connections between *Daphnella*, *Hastatae*, and particularly the group *S. pyrolifolia*—*S. mackenzieana*.

The majority of American species and a considerable part of Chinese ones as well fit within *Glabrella*—*Hastatae* filiation unit.

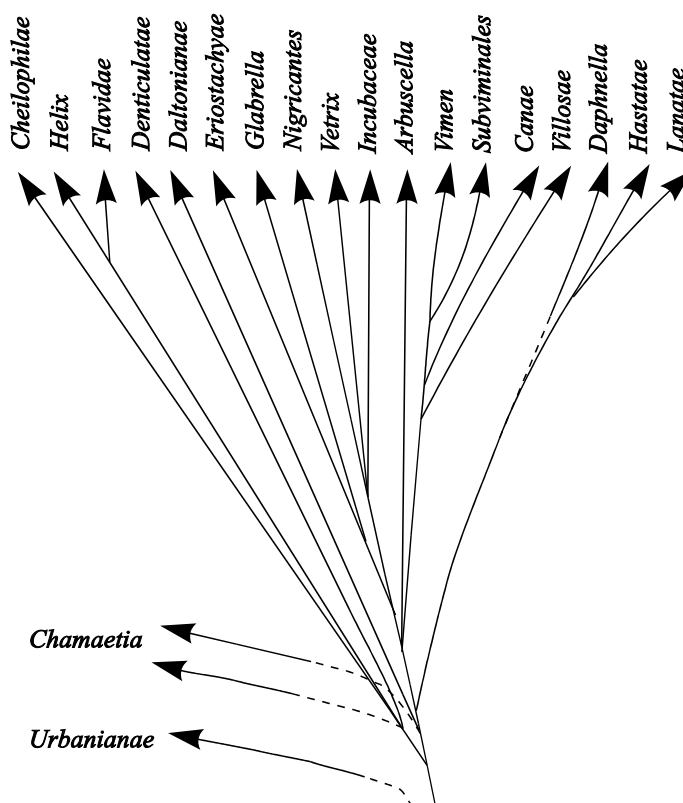
The section *Helix* (together with adjoining sections *Flavidae* and *Cheilophilae*) appears to have the most obscure status and relations; this group is to be placed totally apart from others. Coalescence of stamens, of course, does not constitute its major peculiarity, since this character is also encountered in other groups. The matter is that in *Helix* there are many characters that are generally considered to be primitive in the willows. These are flat denticulate leaves; short stamens; small bracts, usually puberulous on the inside and fugacious in many species; a potential habit of a rather large tree in some species (e. g., *S. pycnostachya*, *S. linearifolia*, and a Himalayan species *S. sericocarpa*); rather southern distribution of the whole group. One might consider a possibility of direct links to *Salix*, if it were not advanced characters, too many of which are encountered in *Helix* along with the primitive ones. These are the absence of the hypodermis in the leaves; black persistent bracts in the majority of species; the single nectary; bright yellow phloem color in some species (the character that is not known in the subgenus *Salix*); etc. The group *Helix*—*Flavidae*—*Cheilophilae* has exclusively Eurasiatic distribution with the center of diversity in Asia. It probably emerged right there in very remote ages from some primitive ancestors of the subgenus *Vetrix*.

At this point, we are inevitably approaching the question about the very origin of the subgenus *Vetrix*. In the floras of the former USSR territory, Western Europe, and North America, none of the groups within the subgenus *Vetrix* could be related with confidence to any particular group within *Salix*. However, there are groups like that in the flora of mountainous Southeast Asia. As regards the sections *Eriostachyae* (which includes *S. ernestii* Schneid. and *S. eriostachya* Anderss.) and *Daltonianae* (including *S. daltoniana* Anderss. and *S. salwinensis* Hand.-Mazz.), I find enough grounds for bringing them close together with the section *Urbanianae*. The catkins look very similar: they are long, often rather drooping, their bracts large, scarious. The ovaries are also very similar: lanceolate, gradually attenuating into elongated, almost entirely distinct styles, their stigmas cleft into linear, mostly curved parts. There are two nectaries in the majority of *Eriostachyae* and *Daltonianae* species, which is absolutely unusual for the subgenus *Vetrix* and is considered to be a rather primitive character. Some of these species also have petiolar glands located near the leaf blade base. On the other hand, the leaf structure in *S. cardiophylla* resembles one in the section *Vetrix*, as it has been already mentioned. There remain, of course, the differences in the bud scale structure and stamen number. However, we know that the difference in stamen number does also exist between the sections *Pentandrae* and *Salix*; nevertheless, there is no doubt in close filiation of these sections. As for the difference in the extent of fusion of the bud scale margins, it may

exist even between specimens of one species (for example, in *S. amygdaloides* Anderss., *S. subserrata* Willd., or *S. mesnyi* Hance). The section *Glabrella* can be derived directly from *Eriostachyae*; a further development of *Glabrella* might have led to *Nigricantes* and *Hastatae*.

There is high probability that the Himalayan section *Denticulatae* may be a connecting link between *Daltonianae* and *Helix*. The section *Denticulatae* (represented by *S. denticulata* Anderss., *S. longiflora* Anderss., *S. luctuosa* Levl.), which is obviously very close to *Daltonianae*, differs mostly in shortened styles and stigmas and small leaves. The leaves of *Denticulatae* are particularly akin of those in the subsection *Caesia*, catkins resemble those in the subsection *Purpureae* of *Helix*.

The illustration depicts hypothetic evolutionary connections of groups within the subgenus *Vetrix*.



Probable evolutionary relations of the sections within and around the subgenus *Vetrix*

3. DISTRIBUTIONAL TYPES OF SPECIES

The species geographical areas compiled by the author appear to be rather distinct. This makes it possible to try to arrange them in natural groups. Of course, the distributional range of each species is absolutely unique in detail. However, one cannot ignore obvious affinity between many of the distributional areas. The groups were formed on the basis of these common features.

According to the helpful remark by A. Tolmachev (1962), any geographical classification of plant distributional areas totally depends upon the size of the territory under consideration. For example, if one considers the territory of Moscow Oblast alone, then ranges of, say, *Hepatica nobilis* and *Delphinium elatum* would appear to belong to the same distributional

type. However, their overall ranges are absolutely different. *Koeleria grandis* and *Veronica incana* provide another example. Again, their areas totally match within the limits of Moscow Oblast, while their general ranges are strikingly different. When comparing Fig. 29 and Fig. 55, one would notice that the areas of *S. saxatilis* and *S. alaxensis* look similar. However, in North America, there is the second part of *S. alaxensis* area, which is about the same size. As for *S. saxatilis*, it is not distributed in North America at all. Hence, if one compares the ranges of these two species on the whole, he would never assign them to the same distributional type. In accordance with the range of the study, the proposed grouping of the species areas was made for the Old World territory.

Classification of species ranges may also significantly vary depending on interpretation principles. Two opposite approaches to the treatment of areas have been presented by E. Hultén (1937, 1950, 1958) and H. Meusel (Meusel 1943; Meusel, Jäger, Weinert 1965). H. Meusel emphasized ecological grounds that cause any particular distribution; accordingly, he considered latitudinal parameters of particular areas to be their major characteristics. E. Hultén found historical grounds to explain development of distributional areas. Therefore, he laid the main emphasis on shapes of areas. His goal was to find centers of origin and directions of expansion that might be common for entire groups of species. H. Meusel's causal treatment implied an undeniably true message: a plant is found only at places where it is able to grow; if it inhabits a particular place, then there are sufficient conditions for it to exist. Yet it is absolutely clear that the opposite is not always true: if a plant is absent from any particular area, that does not necessarily mean that it is unable to survive there: it is as well possible that the plant merely did not have enough time to reach the area. This is the case where the causal approach is useless. On the other hand, a historical treatment is always reasonable, as species areas are products of historical development in any case, without exceptions (including adventitious and introduced species). In a causal, ecological treatment, the species geography actually constitutes just a starting point, and all further reasoning, i. e., elucidating of particular conditions that define the species existence, is to be shifted to the field of pure ecology, so that any historical facts are left aside. Hence, historical development of particular distributional areas and entire floras appears to be naturally beyond the sphere of H. Meusel's attention. However, the goal of any systematist is to reveal filiation of taxa associated with their history. Therefore, the historical approach is more attractive to a taxonomist. Yet in this concept there is also a drawback, a dangerous possibility of engaging some preconceived notions when uniting distributional areas into groups. For instance, we may treat the area of *S. cinerea* as the one originating from a European center, but it is as well possible to decide that this species has expanded from Dzungaria. The area of *S. myrsinifolia* may be traced back to the Alps as well as Scandinavia. *S. nummularia* might originate from either Arctic or barren heights of South Siberia. Results of grouping will depend on the decision to accept one or another notion, that is to say, the grouping will depict the hypothetical development of species areas instead of their real affinity. In order to avoid subjecting real facts to hypotheses, I think, it makes sense to unite distributional areas using the concept of geographical floristic elements, which were also called *geoelements* by I. Kleopov and H. Walter (Walter 1954: 137). While grouping distributional areas, one should consider only real geographical resemblance and avoid introducing any deductive speculations or hypotheses in the procedure. Hypotheses may be developed later on, in order to explain results of the grouping. Titles of groups must only depict geographical facts.

With these general concepts in mind, we can group the studied species according to their distribution in the Old World in the following types (see Table 5).

Table 5. Types of species distribution (continued on next page)
The species distributed in North America are marked A.

1. Mediterranean and South Atlantic	
<i>S. pedicellata</i>	<i>S. salvifolia</i>
<i>S. atrocinerea</i>	<i>S. amplexicaulis</i>
2. Central and South European Mountain and Alpine	
a. Broad Central and South European	
<i>S. elaeagnos</i>	<i>S. retusa</i>
b. Alpine	
<i>S. serpyllifolia</i>	<i>S. mielichhoferii</i>
<i>S. appendiculata</i>	<i>S. helvetica</i>
	<i>S. laggerii</i>
c. Alpine-Pyrenean	
<i>S. foetida</i>	<i>S. breviserrata</i>
d. Pyrenean and Central French	
<i>S. pyrenaica</i>	<i>S. basaltica</i>
<i>S. tarraconensis</i>	
e. Apennine	
<i>S. apennina</i>	<i>S. crataegifolia</i>
f. Alpine-Carpathian-Balkan	
<i>S. alpina</i>	<i>S. glabra</i>
<i>S. waldsteiniana</i>	<i>S. silesiaca</i>
3. European Arctic and Arctic-Alpine	
a. Arctic-Alpine European	
<i>S. herbacea</i> (A)	
b. Arctic European	
<i>S. myrsinites</i>	<i>S. arbuscula</i>
4. European and Eurasiatic Boreal	
a. Atlantic and Central European	
<i>S. repens</i>	<i>S. purpurea</i>
<i>S. daphnoides</i>	
b. European-West Siberian	
<i>S. pentandra</i>	<i>S. phyllicifolia</i>
<i>S. myrsinifolia</i>	<i>S. lapponum</i>
<i>S. cinerea</i>	<i>S. starkeana</i>
<i>S. aurita</i>	
c. Eurasiatic Boreal	
<i>S. rosmarinifolia</i>	<i>S. caprea</i>
<i>S. dasyclados</i>	<i>S. myrtilloides</i>
<i>S. viminalis</i>	
d. Boreal-Mediterranean	
<i>S. alba</i>	<i>S. triandra</i>
e. Sarmatian	
<i>S. vinogradovii</i>	<i>S. acutifolia</i>
<i>S. caspica</i>	
5. East Asiatic Boreal	
a. Manchurian	
<i>S. integra</i>	<i>S. kangensis</i>
<i>S. pierotii</i>	<i>S. cardiophylla</i>
<i>S. gracilistyla</i>	<i>S. miyabeana</i>

Table 5. Types of species distribution (continued on next page)
The species distributed in North America are marked A.

b. Japanese-Kuril	
<i>S. gilgiana</i>	<i>S. kurilensis</i>
<i>S. vulpina</i>	<i>S. nakamurana</i>
<i>S. reinii</i>	
c. East Asiatic Boreal (in strict sense)	
<i>S. brachypoda</i>	<i>S. rorida</i>
<i>S. taraikensis</i>	<i>S. schwerinii</i>
<i>S. abscondita</i>	<i>S. pseudopentandra</i>
<i>S. udensis</i>	<i>S. dshugdshurica</i>
6. Siberian Boreal and Alpine	
a. Broad Siberian Boreal	
<i>S. bebbiana</i> (A)	<i>S. pyrolifolia</i>
<i>S. jensisseensis</i>	
b. Central Siberian Mountain and Alpine	
<i>S. nasarovii</i>	<i>S. rectijulis</i>
<i>S. turczaninowii</i>	<i>S. divaricata</i>
<i>S. vestita</i> (A)	<i>S. sajanensis</i>
<i>S. berberifolia</i>	<i>S. saposhnikovii</i>
c. Central Siberian-Mongolian Lowland	
Eastern:	Western:
<i>S. kochiana</i>	<i>S. microstachya</i>
<i>S. ledebourana</i>	<i>S. gordejevii</i>
<i>S. rhamnifolia</i>	
7. Siberian and Eurosiberian Arctic and Arctic-Alpine	
a. Siberian	
<i>S. nummularia</i>	<i>S. reptans</i>
<i>S. arctica</i> (A)	<i>S. recurvigemmis</i>
<i>S. polaris</i> (A)	
b. Eurosiberian	
<i>S. lanata</i> (A)	<i>S. glauca</i> (A)
<i>S. hastata</i>	<i>S. reticulata</i> (A)
8. Northeastern Subarctic-Arctic and Alpine	
a. Extreme Northeastern (Beringian)	
<i>S. ovalifolia</i> (A)	<i>S. rotundifolia</i> (A)
b. Northeastern	
<i>S. erythrocarpa</i>	<i>S. sphenophylla</i> (A)
<i>S. tschuktschorum</i>	<i>S. fuscescens</i> (A)
<i>S. chamissonis</i> (A)	<i>S. alaxensis</i> (A)
<i>S. phlebophylla</i> (A)	
c. East Siberian Arctic-Subarctic	
<i>S. pulchra</i> (A)	<i>S. boganidensis</i>
d. East Siberian Mountain and Alpine	
<i>S. saxatilis</i>	<i>S. krylovii</i>
9. Middle Asiatic	
a. Middle Asiatic-Mongolian	
<i>S. alatavica</i>	<i>S. turanica</i>
<i>S. tenuijulis</i>	<i>S. coesia</i>
b. Middle Asiatic-Himalayan	
<i>S. karelinii</i>	

Table 5. Types of species distribution (continued)
The species distributed in North America are marked A.

c. Middle Asiatic Eastern (Tien Shan Type)	
<i>S. tianschanica</i>	<i>S. michelsonii</i>
<i>S. argyracea</i>	<i>S. iliensis</i>
<i>S. kirilowiana</i>	
d. Middle Asiatic Western (Pamir-Alay-Afghan Type)	
<i>S. pycnostachya</i>	<i>S. fedtschenkoi</i>
<i>S. linearifolia</i>	<i>S. capusii</i>
e. Middle Asiatic Central	
<i>S. songarica</i>	<i>S. niedzwickii</i>
<i>S. olgae</i>	
10. Iranian	
<i>S. wilhelmsiana</i>	<i>S. aegyptiaca</i>
<i>S. excelsa</i>	<i>S. acmophylla</i>
11. Caucasian-Minor Asian	
<i>S. apoda</i>	<i>S. kuznetzowii</i>
<i>S. armeno-rossica</i>	<i>S. elbursensis</i>
<i>S. caucasica</i>	<i>S. pantosericea</i>
<i>S. fragilis</i>	<i>S. pentandroides</i>
<i>S. kazbekensis</i>	<i>S. pseudodepressa</i>
<i>S. kikodseae</i>	<i>S. pseudomedemii</i>

Of course, the proposed group titles as well as the groups themselves are appropriate only for distributional areas of willow species and by no means are they to substitute the general classification of elements of the flora. Time has not yet come to create such general classification, since we do not yet have enough of areas drawn in detail on the basis of elaborate taxonomical analysis of groups.

The following conclusions can be made on the grounds of the proposed area grouping of willow species.

1. We can accept the idea that species from the same group are very likely to have a common recent history outline, that is to say, not only do they represent a unified geographical element, but also, in certain limits, a unified genetic element of a certain flora.

2. Differences between area types might depict the process of flora composition through compilation of elements originating from various regions and centers, at least in the late glacial and postglacial time. Of course, the very centers could also migrate under the influence of climatic changes, however, presumably, not too far away. The largest shifts might have been possible in Northern Europe, where the glaciation expanded on the vastest areas. However, that does not mean that we have to consider the groups 2, 3, 4a, and 4b of the European species to be aliens of the postglacial time originating from elsewhere beyond Europe.

3. Some of the groups appear to be not distinctly delimited; there are intermediate, transitional distributional types. For instance, the East Asiatic Boreal Group (5c) may be treated as a result of the Manchurian Group (5a) north and west expansion, and the group 6a, as a result of the group 6b expansion. The group 6a (*S. pyrolifolia* → *S. dasyclados* → *S. myrtilloides*), expanding in its turn, particularly to the west, grades into 4c. Presumably, all these transitions constitute another evidence of some affinity in species historical development. However, this affinity partially originates from such remote past that it is hardly possible to interpret it now without forced statements and arbitrary assumptions.

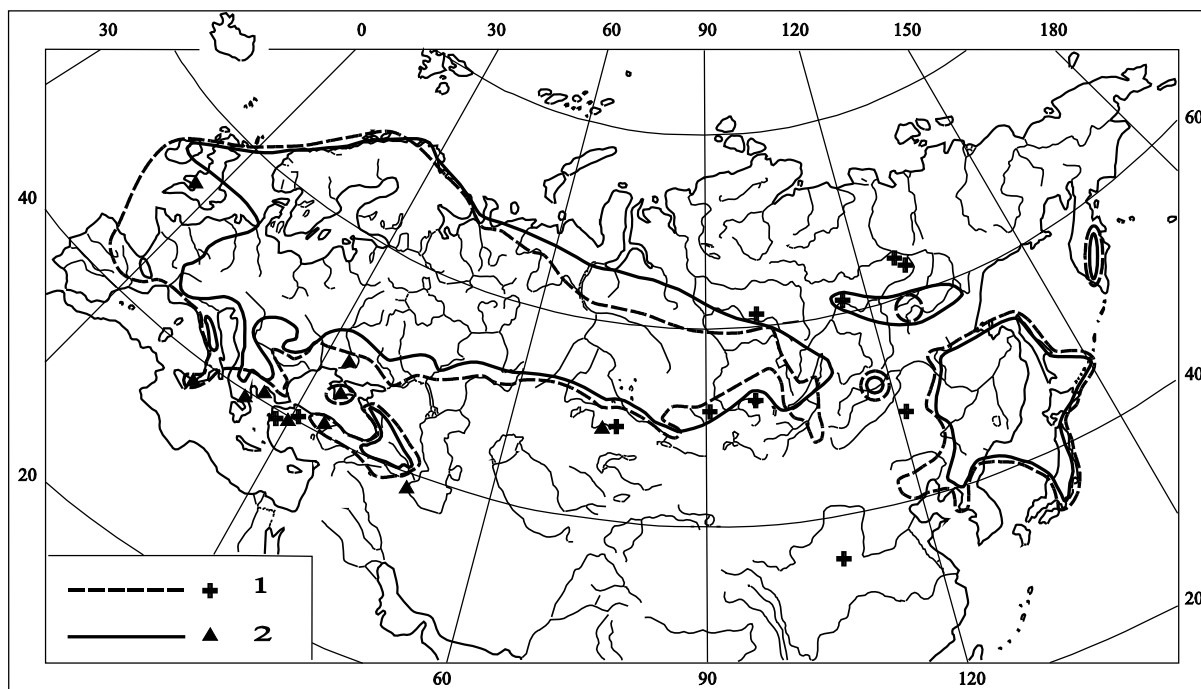


Fig. 9. Distribution areas of *Salix caprea* (L.) (1) and *Ramischia secunda* (L.) (2)

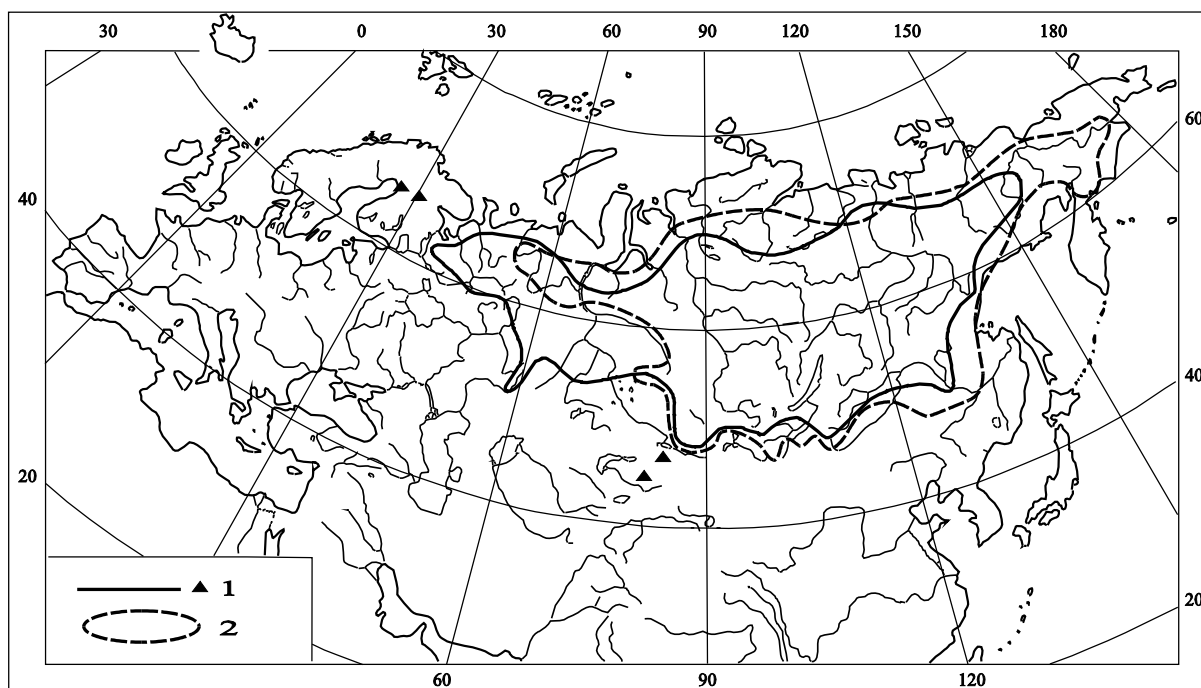


Fig. 10. Distributional areas of *Salix pyrolifolia* Ledeb. (1) and *Ramischia obtusata* (Turcz.) Freyn (2)

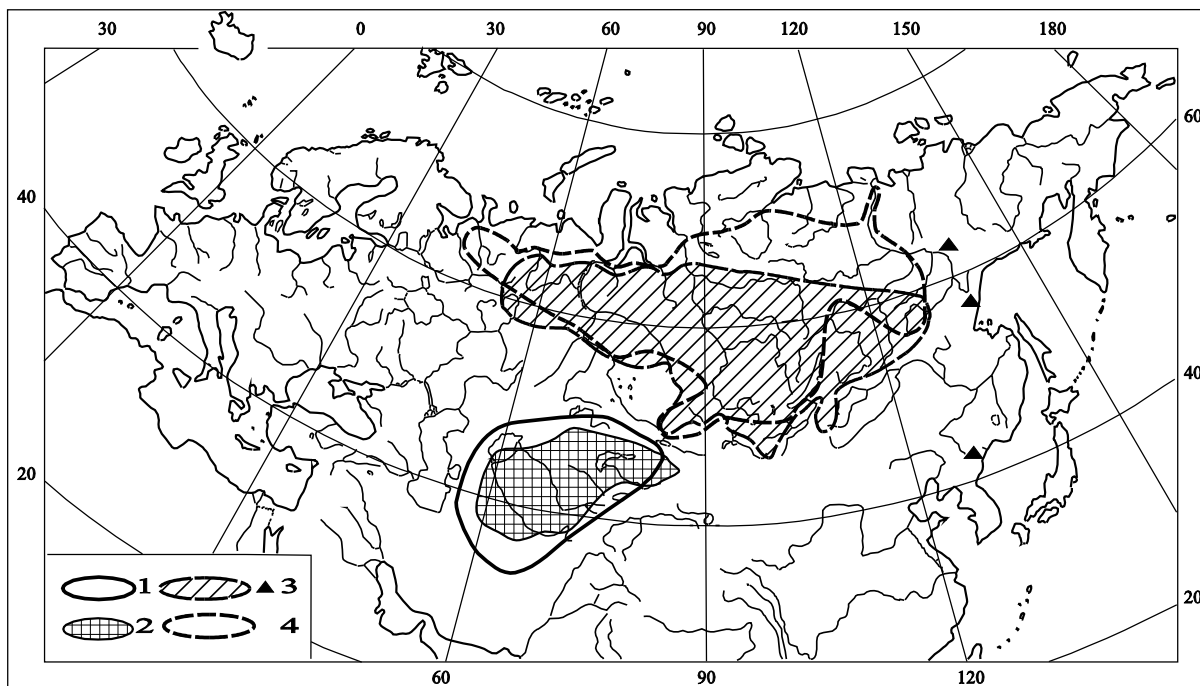


Fig. 11. Middle Asiatic Center of *Artemisia* (Krasheninnikov 1946) (1) and distributional areas of *Salix songarica* Anderss. (2), *Pinus sibirica* (Rupr.) Mayr. (Tikhomirov 1946, Shumilova 1962) (3), and *Salix jensiseensis* (Fr. Schmidt) Flod. (4)**Fig. 9.** Distribution areas of *Salix caprea* (L.) (1) and *Ramischia secunda* (L.) (2)

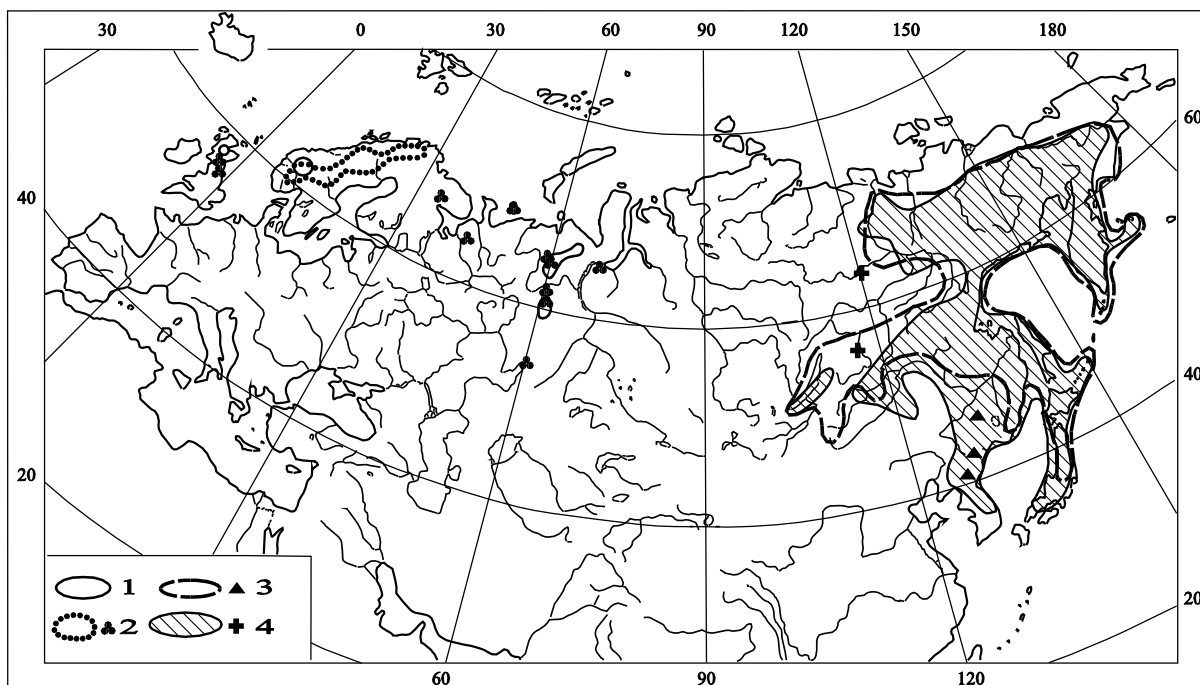


Fig. 12. Distributional areas of *Artemisia norvegica* Fries (Hultén 1954, Tolmachev 1962) (1); *Salix arbuscula* L. (2); *Pinus pumila* (Pall.) Rgl. (Tikhomirov 1946, Tolmachev 1962) (3); and *Salix udensis* Trautv. et Mey. (4)**Fig. 10.** Distributional areas of *Salix pyrolifolia* Ledeb. (1)

4. The species that are closely related (such as, for example, *S. viminalis*—*S. turanica*—*S. armeno-rossica*; *S. hastata*—*S. karelinii*—*S. apoda*; *S. daphnoides*—*S. acutifolia*—*S. rorida*) are usually attributed to different geographical groups. This fact proves that the groups are comparatively young formations as far as their present composition is concerned. However, it is quite clear that the group composition is a result of complex and long formation process, which included many changes, and therefore each group contains some ancient elements as well as more recent ones. Dominance of an old (presumably, autochthonous) core is particularly characteristic of the Middle Asiatic species group (which comprises the whole subsection *Tenuijules* and almost all of *Kirilowianae*) as well as the Manchurian (4a) group (which contains the endemic, primitive, monotypic section *Urbanianae*, the section *Subviminalae*, and also *S. kangensis* that may be easily segregated in a monotypic subsection).

If one compares distributional areas of willows with areas of other plants, even those very different as regards their ecology, some striking similarities can be found. This fact confirms the geographical distinctiveness and historical determinacy of willow distributional areas.

The reader can find some examples of these comparisons on Figs. 9–12. Perhaps, the most remarkable is the congruence of the ranges in *Pinus pumila* and *Salix udensis* (Fig. 12), while the ecology of these two species is quite different. *S. udensis* is a lowland or low-elevation species restricted to banks of streams. Mountain pine, on the contrary, avoids banks of streams and damp bottoms of *pad's* being restricted to upper mountain levels.

The consistency of the area of *S. songarica* with the Middle Asiatic distributional center of wormwoods (*Artemisia*, Fig. 11) is also quite didactic. There are no reasons to consider *S. songarica* as an alien species in the Turkestan Desert Area or to think of it as a species that has somehow colonized the area via streams coming down from mountains. There is no doubt that *S. songarica* is a true lowland species preferring clayey or sandy-clayey sediments of lowland rivers. It may ascend to mountain elevations forming there small colonies, but only very rarely and not high. *S. songarica* is not less typical for the Middle Asiatic Desert Area, than any of tamarisks, wormwoods, or anabases. The only difference is that the habitats suitable for *S. songarica* are of extremely restricted distribution in the area.

These examples illustrate the statement, which was also emphasized by E. Hultén (1958): the fact of belonging to the same distributional type does not necessarily mean the equality of ecological and coenological species characteristics. This is quite obvious, since any natural floristic area consists of many types of plant communities and ecological conditions within it are far from uniform.

Distribution of willow species confirms a number of boundaries in botanical geography. To take an example, it appears that none of truly Caucasian willows are found north of the border that goes along the foothills of the Greater Caucasus, south of Anapa, toward Maikop, south of Nevinnomysskaya, toward Mineralnyye Vody, along the right bank of the lower Terek, toward Groznyy, Khasavyurt, and Makhachkala. On the other hand, Eurosiberian species distributed on the plains of Ciscaucasia (the Northern Caucasus), such as *S. cinerea*, *S. acutifolia*, *S. viminalis*, or *S. caspica*, never violate the described border. They never ascend up the Caucasian Mountains, although they may approach the foothills of the Caucasus very closely.

In southeastern Transcaucasia, the limit of Hyrkanian Flora is very clearly marked by the congruence of the southeastern limits of *S. caprea* and *S. pseudomedemii* and northwestern

limit of *S. aegyptiaca*. It is interesting that in southern Armenia, *S. aegyptiaca* occurs exclusively together with *Platanus orientalis* and *Euonymus velutina*, whereas in Talysh, it is common everywhere from nearly the sea level (the area of moist forests) to the very zone of the beech forests, and even in the arid climate of Diabarskaya Depression.

The Middle Asiatic groups of willows also have rather distinct distributional limits. Eurasiatic Boreal and Sarmatian species (such as *S. pentandra*, *S. alba*, *S. viminalis*, *S. caprea*, *S. bebbiana*, *S. acutifolia*, *S. vinogradovii*, *S. caspica*) have their southern area limits north of the Aral, in the Kazakh Uplands, and Tarbagatay Range. True Middle Asiatic species, conversely, nearly never enter the territory of the Tarbagatay and Uplands. Hence, in accordance with willow distribution, one should consider the Tarbagatay as a part of Siberia, and Dzungarskiy Alatau as one of Middle Asia.

Willow distributional areas also follow a boundary, very important in botanical geography, that is the border between West and East Siberia along the Yenisei River. *S. pentandra*, *S. phylicifolia*, *S. lapponum*, and *S. cinerea* have their eastern limits close to the Yenisei; *S. pseudopentandra* and *S. saposchnikovii* have their western limits there. Locations of *S. pentandra* and *S. cinerea* east of the Yenisei, in the Yeniseiskiy Kryazh as well as those of *S. alba* and *S. cinerea* in Minusinskaya Depression represent the easternmost outposts of the European-West Siberian Flora.

In the forest flora of northeastern European Russia, the Siberian component is represented by *S. jenisseensis*, *S. pyrolifolia*, and *S. recurvigemmis* reaching there. The Central European component in the flora of the Baltic Republics is represented by *S. daphnoides*, *S. purpurea*, and *S. repens*. We could find more and more illustrations of the ways various willow distributional areas depict patterns of botanical geography, well-known ones along with those just starting to emerge. However, the reader can easily find them while viewing the distribution maps.

4. HISTORICAL DEVELOPMENT OF THE GENUS: MAJOR FEATURES

The representatives of the genus *Salix* existed at least as early as the mid Cretaceous (Krishtofovich 1957; Graham 1964) and probably even earlier. Already in the late Pliocene, contemporary species inhabited Eastern Europe, the Caucasus, and Siberia (Baranov 1950; Dorofeyev, Mezhvilk 1956; Nikitin 1957).

88 In the interglacial deposits, contemporary species are as well the only ones that can be confidently detected. There are, indeed, some findings of willows in the mid and lower Tertiary deposits; however, they cannot be identified with enough confidence. Hence, there are almost no reliable data as far as the development of the genus in the Tertiary is concerned. Yet the Tertiary was the most critical epoch for the development of Angiosperms. This fact justifies an attempt to trace some of the most important features of the genus' history relying upon available data in the systematics and geography of contemporary groups.

R. Scharfetter (1953) tried to build a similar reconstruction for the European willows. According to his hypothesis, the species of the subgenus *Salix* emerged in the Tertiary; those belonging to *Chamaetia*, in the late Tertiary and early Pleistocene; and the ones constituent of the subgenus *Vetrix*, at the end of the glaciation and later on. These speculations appear to be rather reasonable; however, they have some significant drawbacks. The notion about intensive speciation process in the postglacial time sounds totally outdated. Nowadays, it

hardly makes any sense to argue against the statement by A. Krishtofovich (1957: 439) saying that "during the period of the Quaternary Glaciation, which lasted about 500,000 years, the Earth's vegetation did not acquire anything really new, and indeed, its current composition had been complete long before that period, as far as genera and even species are concerned."

Some more initial malalignments brought R. Scharfetter to a blunder concerning the time of filiation for the majority of species. First, he overestimated the phylogenetic significance of developmental rhythms in the willows, particularly, the relation between the time of flowering and that of vegetative shoots' growth. As it was demonstrated here above (chapter 3, section 4), rhythms of development belong to the kind of adaptive characters that may dramatically change within a section and even single species. Precocious species may belong to very primitive groups (like *Humboldtianae*). Second, R. Scharfetter absolutely ignored a possibility of close relations between European species and those of other continents. He considered all the European species of the subgenus *Vetrix* as a unitary group of taxa with their common origin dating back to the end of the Glacial.

Due to these misinterpretations, it is impossible to accept the general scheme of development proposed by R. Scharfetter for the genus *Salix*. One may accept it only partially. Say, a quite agreeable idea is the filiation of *Chamaetia* from some branches of *Vetrix*, more primitive than those represented in Europe now.

Besides bare paleontological evidence, disjunctions in distributional areas may as well serve as points of reference for evaluation of contemporary species' age. For example, the distributional area of *S. coesia* has a gap from the Alps to Tien Shan and Altai. Obviously, *S. coesia* could overcome the gap only at a time when the climate on all the space from the Alps to Altai was very much alike that of the contemporary Chuyskaya Steppe and the *syrt*'s of the Tien Shan. It is difficult to imagine that such climatic conditions could exist later than the epoch of the maximal glaciation. Since the time of disjunction, no detectable differences between the Alpine and Altai plants have appeared. Hence, *S. coesia* might be at least much older than the time of the maximal glaciation.

The distribution of *S. vestita* is characterized by a colossal disjunction from the Canadian Rocky Mountains to Prebaykalia. As this is not an Arctic species, it might have not been able to pass across Alaska and the Chukchi Peninsula in climatic conditions similar to contemporary. Some observations (Malyshev 1965) along with the analysis of its area shape in North America (Raup 1943, 1959) demonstrate that *S. vestita* is confined to regions with the humid climate. It might hardly survive in the contemporary climate of the northeastern territory in-between the Verkhoyanskiy and Kolymskiy ranges. Hence, the current disjunctive distribution of *S. vestita* in the Asiatic Northeast and Alaska may be attributed only to the former significant climatic fluctuations. And again, one can hardly imagine any significant fluctuations of climate other than those connected with the glaciation in North America. The American *S. vestita* looks absolutely identical to that from Prebaykalia. Hence, in this case, too, the species has to be at least much older than the time of the maximal glaciation. These conclusions conform to paleontological data.

Some disjunctions are found between close willow species that are difficult to discriminate, such as pairs *S. apoda* and *S. karelinii*, *S. amplexicaulis* and *S. integra*, *S. reinii* and *S. glabra*. The latter one is especially peculiar (see Fig. 35): the first species of the pair is distributed on the islands of Japan and Kuril Archipelago, the second occurs on the Balkan Peninsula and in the Eastern Alps. However, one can find a rather close analogy to that unusual case, that is, the pair *Picea glehnii*—*P. omorika*. Both the willows and spruces are

fairly cryophilic. As to the age of such disjunctions, the most recent time one might consider is the Mindel-Riss Interglacial, when there were still many species in Europe common with East Asia. However, the presence of these species in Europe at that time might not mean that their ranges were continuous from Europe all the way to East Asia. The ranges presumably had been unified earlier, in the Pliocene.

A relation between *S. amplexicaulis* and *S. integra* is rather similar to the one discussed above (see Fig. 63). However, these species are more thermophilic, so that their disjunction reminds rather of those between some of *Forsythia* (*F. ovata*, *F. viridissima* in Korea and *F. europaea* in the Balkans) or *Syringa* (*S. oblata* in North China and Korea as opposed to *S. vulgaris* in the Balkans). The Tertiary age of disjunctions like these is still more obvious.

If we pay close attention to the disjunction between *S. apoda* and *S. karelinii* (see Fig. 34), then we will have to admit that this one, too, dates back to the Tertiary. Both species are alpine-subalpine. During the Pleistocene, the mountain glaciation on the territory of Iran never covered areas large enough to provide a possibility for an alpine species to spread continuously from the Caucasus to Pamir-Alay. For instance, the entire territory of Khorasan Province at that time apparently had an arid climate, indeed, as arid as it is now (Sinitsyn 1962). Therefore, we have to assume that *S. apoda* and *S. karelinii* could only have a unified range as late as the Pliocene, the time, when the climate within the territory of Iran was more humid, although the mountains were somewhat lower.

The examples of disjunctions mentioned above referred to some fairly young groups. If we now turn our attention to disjunctions found in the primitive groups of the subgenus *Salix*, then we will notice that these are of much older ages (and, respectively, the involved species are older).

S. tetrasperma Roxb. from the section *Humboldtianae* is a Paleotropical species distributed at low elevations in India, South China, and Indochina, reaching Java. A corresponding Neotropical species is *S. bonplandiana* Kunth distributed in Mexico and Guatemala and ascending somewhat higher in the mountains (as high as 2,000 m). The species are closely related and may be treated as one series. When might a disjunction, like that, appear? As for the probable time of connection between Paleo- and Neotropical regions, it did not last later than Paleogen, according to E. Wulf (1944). He accepted the idea that the connecting link was the African Continent. However, in Africa, there is absolutely nothing like *S. tetrasperma* or *S. bonplandiana*. Hence, if we try to date the disjunction back at least as late as the end of the Paleogen, we will need to pile up more assumptions. Therefore, we have to date it earlier, perhaps, back to the early Tertiary.

In the section *Humboldtianae*, there are three closely related species, all of them growing in arid subtropical areas: *S. acmophylla* (distributed in Iran, Turkmenia, and Northern India), *S. laevigata* Bebb (growing in California), and *S. subserrata* Willd. (found in Africa from the Nile Delta to Cape Province, which means it also grows in tropical regions). For that group, the scheme of Paleogenic connection via Africa works much better (although the Iranian and Californian species are apparently more closely related to one another than to the African willow).

Divergence between series naturally took place earlier than within series, just the same way as one between sections happened much earlier than between series. Consequently, if any two closely related species of the same series belonging to one of the sections from the subgenus *Salix* became separated at least in the Paleogen (including the upper Paleogen), then we obviously have to date the origin of the major sections of the subgenus *Salix* back to the very beginning of the Tertiary.

There are just about ten willows that are real tropical species: some four or five of them in the section *Humboldtianae*, three or four in *Glandulosae*, and one or two in *Longifoliae*. However, these sections contain species of the temperate climate as well. As we have already seen here, the subgenus *Salix* is a group of rather diversified sections, each of them having its own primitive as well as advanced features. Some of the sections are entirely confined to temperate regions. (The same is in the genus *Populus*, where tropical species are as well found only in some few groups). Consequently, there are no grounds to accept tropical origin of the genus *Salix* (and the entire family). The genus most likely originated from warm temperate or subtropical regions, then partially penetrated to the tropical and mainly temperate and then cold climatic belt. The subgenus *Vetrix*, the richest one in sections and species, does not have any representatives in the tropics.

The subgenus *Vetrix* appears to have passed two stages in its development. First, primary sections, like *Eriostachyae*, *Daltonianae*, and *Denticulatae* mentioned above, emerged in the early Tertiary. Representatives of these sections participated in the formation of the so-called "arctic-tertiary" flora of a warm temperate climate. Then, in the second half of the Tertiary, geographical ranges of these groups dramatically shrank due to a cold spell in Northern Eurasia. They receded to Southeast Asia, where they have survived till now. Of course, some of the species became extinct. At the same time, another, younger and hardier formation of the subgenus *Salix* expanded across the Holarctic being represented by a number of boreal sections. Thinking about that process, the reader should by no means imagine that the thermophilic groups felt cold and, facing the need to escape to warmer areas, rushed to "give birth" to hardy sections. This is an obvious nonsense. Undoubtedly, by that time, the hardy groups had already been formed to some extent (presumably, at intermediate and upper mountain levels). When the climate became colder and the thermophilic groups either became extinct or moved south, the hardy ones stayed and drastically expanded their ranges gaining an opportunity of long-distance migrations, which, of course, was a stimulus to further speciation.

A number of boreal sections and subsections are missing from Southeast Asia, the preservation locus for arctic-tertiary types. This fact proves that the boreal groups of *Vetrix* are relatively young and they have largely developed only in the recent climatic conditions, mostly, in new centers of expansion in the boreal Eurasia and America. In the flora of the southeastern Himalayas and Southwest China, which is extremely rich in willow species, there is not even a single representative of the sections *Hastatae*, *Nigricantes*, *Arbuscella*, *Subviminalis*, *Villosae*, *Lanatae*, *Daphnella*, *Incubaceae*, and the boreal subsections of the section *Vetrix*. There is no doubt that the development of the boreal groups of the subgenus *Vetrix* (as well as some few boreal groups of the subgenus *Salix*) took place in a number of regions in Holarctic, including Europe, Asia, and North America, rather than in one particular center. One can find evidence of that multiregional filiation in the existence of endemic sections and subsections, such as *Canae*, *Salix*, and *Kuznetzowiana* in Europe and Western Asia; *Urbanianae* and *Subviminalis* in Manchuria; *Caesia*, *Kirilowiana*, and *Tenuijules* in Central Asia; *Pentandrae* subsect. *Lucidae* and others in North America.

On the other hand, there is also evidence of vast intercontinental connections. For example, the section *Hastatae* is only represented in Eurasia by five species aggregating in three isolated groups: *S. hastata*—*S. karelinii*—*S. apoda*; *S. fedtschenkoi*; and *S. pyrolifolia*. However, the section *Hastatae* is very species rich in North America. Besides, there one can find connecting links between those groups that appear to be isolated within the Old World. One can as well trace parallel development of boreal groups from the section *Vetrix* in Europe

and North America. *S. caprea*, *S. cinerea*, *S. aurita*, *S. taraiensis*, and the entire subsection *Vulpinae* do have closely related American species, and *S. bebbiana* has nearly Holarctic distribution.

As we have noticed in section 2 of this chapter, one cannot consider the subgenus *Chamaetia* to be a derivative of some boreal groups of the subgenus *Vetrix*, because the sections of *Chamaetia* have a common root only with the most primitive groups of *Vetrix*. Consequently, one has to suppose that the time and place of *Chamaetia* emergence was close to that of the filiation of the primitive groups from *Vetrix*. Presumably, those were upper mountain levels in same regions where the primary groups of *Vetrix* emerged at lower elevations. *Chamaetia* benefited then from the expansion of a colder climate enlarging their distributional ranges and enriching the species composition, although not to the extent it happened in the subgenus *Vetrix*. The younger, "secondary formation" is not as distinct in *Chamaetia* as it is in *Vetrix*. Representatives of *Chamaetia* have been unable to reach many mountain regions of the temperate belt, such as the Caucasus, mountains of Asia Minor and Iran, and the Pamir-Alay.

Along with Eurasia, the North American continent is rich in willows (about 120 species), and there they also grow in nearly every climatic belt and region. However, Eurasia is exceeding North America not only in the number of species (there, 230–250 species are found), but also in diversity of systematic groups. The subgenus *Chamaetia* is less represented in North America (20–23 species as compared to 30–35 in Eurasia). Note that the southern mountain ranges of North America are particularly deficient of *Chamaetia* representatives in contrast to the mountains of South Siberia and the Himalayas. The subgenus *Salix* is also much less diversified in North America: there are only three sections as compared to seven in Eurasia. Yet the most striking fact is that the arctic-tertiary groups that constitute connecting links between *Salix*, *Vetrix*, and *Chamaetia* are absolutely missing from North America. The great majority of North American willows are boreal representatives of the subgenus *Vetrix* belonging to same sections as Eurasiatic species or very close ones.

One can definitely distinguish two major floristic elements in the North American willows. These two elements correspond to two stages of the genus' development on the North American Continent. The first one comprises ancient, late Cretaceous or early Tertiary tropical and arid subtropical groups: *Humboldtianae* (which is a common group with the Old World tropics) and *Longifoliae* (an endemic, presumably, autochthonous one). The second element is composed of younger, boreal and arctic groups. Here belong the sections of the subgenera *Vetrix* and *Chamaetia* and also the only one boreal section of *Salix* found in North America, that is, *Pentandrae*. These two floristic elements are totally isolated from each other in North America: no connecting links between them are found there, all of them left in Asia. Consequently, we have to conclude that in North America, the development of the genus *Salix* was divided into two stages separated by an enormous time period, whereas in Eurasia, it was never interrupted. And hence we have to further conclude that boreal willows have traveled from Asia to North America, and they did it at the time when the climate in Beringia was cold enough not to let thermophilic species migrate that way. However, since the evolution of the boreal willows took place on the American continent as well, we have to assume that their migration from Asia did not occur "before the curtains", that is, not before the very start of the glaciation, but much earlier, presumably, at the beginning of the Neogen.

Part Two: Systematic Overview

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Salix L. 1753, Sp. pl.: 1015; 1754, Gen. pl.: 447.

T y p u s: *Salix alba* L. (Britton, Brown, 1913, 1: 591).

KEY TO SECTIONS

1. Bud scales with distinct, overlapping margins on adaxial side 2
- Bud scales cap-like, with connate margins 3
2. Buds positioned at acute angle to shoot, triangular, not compressed, 3–5 mm long. Leaves 6–25 mm broad. Styles short, stigmas two-lobed, subsessile 1. HUMBOLDTIANAE
- Buds accumbent to shoots, lanceolate, 5–10 mm long. Leaves 25–60 mm broad. Styles long, filamentous, distinct almost to their bases, stigmas linear, two-parted 3. URBANIANAE
3. Stamens three or more, distinct 4
- Stamens two, distinct or connate 5
4. Bark exfoliating from old branches and stems in patches of irregular shape. Persistent part of bark remains smooth. Young leaves not producing pitch. Stamens three 2. AMYGDALINAE
- Bark on old stems with coarse longitudinal fissures, not exfoliating in patches. Young leaves glandular, producing pitch. Stamens 4–10 (rarely 3) 4. PENTANDRAE
5. Bracts pale: yellowish, greenish, reddish, or brownish, but not black. In female catkins either all or some of bracts fall off by time when capsules ripen 6
- Bracts persistent 7
6. Stamens two, distinct 5. SALIX
- Stamens two, entirely connate 25. HELIX
7. Stamens connate either partially or completely 8 93
- Stamens distinct 13
8. Leaves narrowly lanceolate, with revolute margins, their lower surface clothed with dense white tomentum composed of extremely thin, tangled trichomes 19. CANAE
- Either leaves glabrous or trichomes look different 9
9. Leaves with numerous prominent parallel veins beneath. Veins clothed with appressed silvery trichomes; frequently the rest of leaf blade beneath is also silvery pilose. By fall, leaf petioles with axillary floriferous buds become abruptly ventricose, embracing their buds. Nectaries linear 18. SUBVIMINALES
- Veins beneath neither prominent nor looking different due to pubescence. Petioles not abruptly ventricose by fall. Nectaries square or rectangular 10
10. Capsules stipitate; stipes 0.5–1.0 mm long. Styles 1.2–2.5 mm long 22. DAPHNELLA

- Styles 0–1.0 mm long 11
11. Leaves linear to linear-lanceolate, 2.0–6.0 mm broad. Stamen filaments glabrous 12
- Stamen filaments pubescent (sometimes inconspicuously, at their very bases, but in that case leaves more than 6.0 mm broad) 25. HELIX
12. Leaves 50–120 mm long, glabrous, emarginate-dentate, bicolorous 24. FLAVIDAE
- Leaves 30–60 mm long, mostly sericeous, delicately serrulate, concolorous 26. CHEILOPHILAE
- 13(7). *Arctica*- or transitional to *alba*-type of bud size gradation along shoot (see chapter 3, section 3 for the description of these types) 14
- *Caprea*-type of bud size gradation 23
14. Prostrate or depressed shrubs without subterranean stolons. Floriferous and vegetative shoots have same size and foliated to same extent. Floriferous shoots with normal axillary buds, which add to stem growth during subsequent year. Leaves exstipulate, round to broadly elliptic, distinctly bicolorous, their margins inconspicuously crenate or entire. Bracts pale or reddish (not black). Capsules small, ovoid, obtuse, subsessile to sessile, styles short or lacking, stigmas short, mostly laterally recurved, two-lobed 7. CHAMAETIA
- Characters not as above. Either subterranean stolons existing, or vegetative shoots more developed and foliated as compared to floriferous ones, or leaves distinctly dentate, or leaves concolorous, lustrous green, or capsules distinctly stipitate, or styles elongated 15
15. Low or totally depressed cushion shrubs. Abundant dead leaves of two, three, or more previous years persistent on branches 11. MYRTOSALIX
- Old leaves not persistent. (Occasionally, in extremely unfavorable conditions, leaves remain during one subsequent year, but fall off if plant removed from substrate.) 16
16. Numerous leafless stolons growing and gradually becoming woody inside substrate 8. RETUSAE
- Stolons lacking 17
17. Leaves green and lustrous on both sides (though occasionally rather pubescent), small (6–30 mm long) 18
- Leaves dull, rather glaucous beneath (if green, then larger: 30–60 mm long; in that case, stamen filaments densely pubescent, male flowers having two nectaries) 19
18. Leaves stipulate 11. MYRTOSALIX
- Leaves exstipulate 8. RETUSAE
19. Leaves exstipulate, ovate to obovate, small (10–35 mm long), entire or with few minute denticles, mostly on their lower half. Female catkins loosely flowered. Capsule stipes 1.0–2.5 mm long, approximately as long as bracts, 1.5–3.0 times longer than nectaries, and also 1.5–3.0 times longer than style length + stigma length (which is 0.5–0.8 mm). 9. MYRTILLOIDES
- Capsule stipes usually not longer than 1 mm. Style length + stigma length exceeding 0.8 mm 20
20. Two nectaries in male flowers, stamen filaments pubescent 10. GLAUCAE
- One nectary in male flowers; if two, then stamen filaments glabrous 21

21. Vegetative shoots much longer and more foliated than floriferous ones. Leaves lustrous above, dull and glaucous beneath, more or less dentate at margins (at least superior ones). Alpine, subalpine, and forest-tundra habitats, but not tundra itself 22
 — Floriferous shoots almost as long and leafy as vegetative ones. If vegetative shoots considerably longer, then plants are prostrate tundra dwarf shrubs. Leaves entire or with some few obsolete denticles, mostly on lower parts of leaf blades 10. GLAUCAE
22. Small shrubs with slender (1–2 mm in diameter), mostly reddish shoots. Floriferous buds up to 7 mm long. Leaves 6–20 mm broad. Anthers 0.3–0.4 mm long 16. ARBUSCELLA
 — Larger shrubs (of moderate height to tall), their shoots more stout (1.7–2.5 mm). Floriferous buds 5–10 mm long. Leaves 20–50 mm broad. Anthers 0.5–1.0 mm long. 13. GLABRELLA
- 23(13). Branches pruinose. Stipules adnate to petioles and fall off together with them (particularly, in leaves with axillary floriferous buds) 22. DAPHNELLA
 — Stipules not adnate to petioles and fall off separately 24
24. Young shoots villous; trichomes rather long, white, either upright or more or less tangled. Leaves beneath covered with dense white tomentum composed of thin tangled trichomes 20. VILLOSAE
 — Leaf pubescence not as above 25
25. Trees or tall shrubs. Leaves lanceolate or narrowly lanceolate, long-tapering toward apices, regularly serrate at margins, flat beneath (veins not prominent), glabrous or puberulous, 70–150 mm long. Stipules acute, semicordate or lanceolate 26
 — Characters not as above 27
26. Floriferous buds 4–7 mm long, ovoid or broadly elliptic, obtuse. Bracts pale; capsules sessile to subsessile 6. SUBALBAE
 — Floriferous buds 8–15 mm long, triangular-lanceolate, their beaks more or less recurved, bracts black; capsules stipitate; stipes 0.5–1.5 mm long 22. DAPHNELLA
27. Leaves elongated, 6–20 (seldom 3–5) times as long as broad, with numerous prominent parallel veins beneath, more or less silky villous, denticulate or entire at margins. Catkins precocious to subprecocious. Capsules sessile to subsessile. Nectaries linear or narrowly rectangular, considerably exceeding capsule stipes. Styles elongated; style length + stigma length exceeding 1.4 mm 28
 — Characters not as above 29
28. Floriferous buds with long, more or less recurved beaks. Leaves mostly broadest above middle. Leaf veins conspicuous beneath, clothed with appressed silvery trichomes. Styles very long (1.5–3.0 mm) 18. SUBVIMINALES
 — Floriferous buds without long beaks. Leaves mostly broadest about or below their middle. Leaf veins obscure, not prominent due to pubescence 17. VIMEN
29. Young shoots clothed with dense, rather long, white trichomes turning gray with age. Stipules distinct, subequilateral, long-tapering. Leaves 1–3 times as long as broad, more or less pubescent, mature ones with prominent reticulation beneath. Catkins precocious, sessile. Capsules sessile, glabrous or puberulous, gradually attenuating into elongated styles 21. LANATAE
 — Either leaf venation, or capsules, or both not as above 30

30. Stipules always persistent, subequilateral, more or less lanceolate. Leaves not large (15–40 mm long), mostly densely glandular-dentate at margins, lustrous at least on upper or on both surfaces. Female catkins erect on distinct stout stalks. Ovaries more or less pubescent, their trichomes flexuous, ribbon-like, strongly refractive (to watch light refraction use a highly magnifying lens) 11. MYRTOSALIX
 — Either ovary pubescence or leaves not as above 31
- 95 31. Stipules equilateral to subequilateral. Leaves densely denticulate at margins. Capsules glabrous, acute. Either capsule stipes or styles elongated 12. HASTATAE
 — Either stipules distinctly inequilateral, or leaves not dentate, or capsules not as above 32
32. Low shrubs with slender (0.8–1.7 mm) shoots. Floriferous buds ovate or lanceolate, faintly pointed, not at all or slightly compressed, up to 8 (rarely 10) mm long. Stipules lacking or small, lanceolate, equilateral, acute. Leaves on short (2–8 mm) petioles, small (10–60 mm long), entire or with few obscure denticles. Styles and stigmas short (style length + stigma length = 0.5–0.8 mm) 33
 — Either stipules distinctly inequilateral, or leaves distinctly dentate and larger, or styles and stigmas longer 34
33. Leaves, at least young ones, more or less silvery pubescent. Stipules always persistent on vigorous shoots. Veins rather prominent beneath mature leaves 23. INCUBACEAE
 — Either all of leaves glabrous or young ones not silvery pubescent. Stipules mostly rudimentary. Veins not prominent beneath mature leaves 9. MYRTILLOIDES
34. Capsule stipes considerably elongating when capsules ripen, reaching length of 2–4 mm, which is larger than bract length. Capsules slender, linear-lanceolate, pubescent; styles and stigmas short (style length + stigma length = 0.6–1.0 mm) 15. VETRIX
 — Characters not as above 35
35. Leaves linear-lanceolate, 6–12 times as long as broad (inferior leaves sometimes considerably broader), more or less revolute, either entire or wavy and delicately emarginate. Numerous veins considerably prominent beneath mature leaves. Stipules, if any, linear. Capsule stipes 0.5–1.5 mm long 17. VIMEN (*Salix udensis*)
 — Leaves not as above 36
36. Floriferous bud apices mostly compressed. Leaves bright green, lustrous above, whitish beneath, their veins delicate, inconspicuous. Either none or obsolete leaf shape gradation along shoots. Capsules acute, gradually attenuating into styles 16. ARBUSCELLA
 — Floriferous bud apices mostly not compressed (or, if apices compressed, then leaf shape gradation pronounced). Leaves distinctly reticulate-veined, often clothed with dense pubescence beneath 37
- 96 37. Leaves flat, rather lustrous above, young ones blackening on drying. Stipes of ripe capsules not considerably elongating. Capsules acute, styles distinct, stigmas shorter than styles 14. NIGRICANTES
 — Leaves may be rather rugose with impressed veins, mostly dull above (occasionally mature ones lustrous), not blackening too much on drying. Stipes of ripe capsules mostly elongating. Styles short: 0.1–0.5 mm, occasionally up to 0.7–0.8 mm, but in that case not longer than stigmas. Stigmas mostly not parted 15. VETRIX

SUBGENUS *SALIX*

Subg. *Amerina* Dum. 1862, Bull. Soc. Bot. Belg. **1**: 145. —Subg. *Protitea* Kimura, 1928, Bot. Mag. Tokyo **42**: 290. —Genus *Toisusu* Kimura, 1928, Bot. Mag. Tokyo **42**: 287.

T y p u s: *Salix alba* L.

Trees, often quite large, or tall shrubs. Petioles more or less channeled above, mostly with 1–3 pairs of glands sitting close to base of leaf blade. Leaves linear-lanceolate to subovate, long-tapering, regularly dentate at margins. Catkin rachises soft, often rather pendulous. Bracts pale, mostly abscising by the time capsules ripen. Nectaries mostly two (at least in male flowers), sometimes connate into glandular disk. In female flowers nectary frequently solitary. Stamens distinct, two or more.

The subgenus is the most primitive, having most in common with the poplars. It is impossible to distinguish it (nor the other subgenera) using any single diagnostic character. On the other hand, attempts to divide the subgenus *Salix* into a few subgenera cannot be accepted. The section *Urbanianae* seems to be somewhat more apart from the rest of the subgenus, yet it hardly makes sense to treat it separately. *S. cardiophylla* differs from other species of the subgenus in its reproductive organs; *Amygdalinae* are distinguished by their bark resembling *Chosenia*; *Longifoliae* are different in their leaf anatomy which is also close to that of *Chosenia*.

Sect. 1. *Humboldtianae*

Pax, 1889, in Engler et Prantl, Natürl. Pflanzenfam. **3**, 1: 36.

T y p u s: *Salix humboldtiana* Willd.

Trees, mostly medium-sized; old bark with coarse longitudinal fissures. Floriferous buds similar to vegetative ones, short, triangular, small. Bud scale margins distinct, not connate. Petiolar glands obsolete. Leaves broadly lanceolate to sublinear, flat, serrulate at margins. Bracts small, distinctly pubescent (pubescence short); in female flowers either some or (rarely) all of the bracts abscising. Nectaries two in male flowers; in female ones, nectary solitary, short, broad, truncate. Stamens 3–10, their filaments pubescent at bases, anthers small, nearly globular. Capsules ovoid, stipitate. Styles very short or lacking, stigmas small, two-lobed.

The species of this section are widespread in tropical and subtropical areas of the Old and New World. Of 12–14 species, there is only one in the flora of this country.

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1. **S. *acmophylla*** Boiss. 1846, Diagn. pl. or. **7**: 98; id. 1879, Fl. Or. **4**: 1183; Hook. f. 1890, Fl. Brit. Ind. **5**: 628; Parker, 1924, Forest fl. Punjab: 505; Post, 1933, Fl. Syr. **2**: 529; Nazarov, 1936, Fl. SSSR **5**: 194; Görz, 1937, Fl. Turkm. **2**: 16; Parsa, 1950, Fl. Iran. **4**: 1347; Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR **20**: 72; id. 1962, Bot. mat. Gerb. in-ta bot. AN UzbSSR **17**: 59; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 110. — *S. persica* Boiss. 1846, op. cit. **7**: 99; id. 1879, op. cit. **4**: 1183; Nazarov, 1936, op. cit. **5**: 195; Parsa, 1950, op. cit. **4**: 1348. — *S. dealbata* Anderss. 1851, K. sv. vet. handl. **1850**:

472. —*S. glaucophylla* Anderss. 1851, op. cit. **1850**: 474. —*S. basraënsis* Toepffer, 1920, Sal. Exs.: N 456. —*S. pseudo-safsaf* Camus et Gombault, 1939, Bull. Soc. Bot. Fr. **86**: 136; eid. 1942, op. cit. **89**: 24. —*S. louisii* Camus et Gombault, 1942, op. cit. **89**: 29. —? *S. daviesii* Boiss. 1846, op. cit. **7**: 98; id. 1879, op. cit. **4**: 1183. —? *S. dinsmorei* Enander ex Post, 1933, op. cit. **2**: 529.

T y p u s: "In alpe Kuh-Daë na, Kotschy Pl. Pers. Austr. N 620 et prope urbem Schiraz id. N 323" (G, LE!, JE!, W! et alibi).

HABIT: A medium-sized or small tree (up to 8–10 m tall, but mostly shorter, since the top is usually pruned similarly to our white willow).

HABITATS: Banks of rivers and streams, mostly in the piedmont or mountains (reaching the elevation of 1,200–1,500 m in Turkmenia and on the Pyandzh River; 2,000 m in central Iran; 2,100–2,200 m in Afghanistan, Pakistan, and India).

DISTRIBUTION: The Sinai Peninsula, Israel, Jordan, northern Syria, southeastern Turkey, Iraq, Iran, Afghanistan, northern regions of western Pakistan (including northern Baluchistan), northern India (to Dehra Dun and Tirich Garhwal). Within the territory of the former USSR, it is encountered throughout the Kopet-Dag (being common everywhere east of Kazandzhik), on the Tedzhen and Kushka rivers (close to the border of Tadjikistan and Iran), in the Kugitangtau, and in southern Tadjikistan (where it is very rare, known only from two locations: Shaartuz District and Dzharf on the Pyandzh). It is commonly cultivated, for instance, in nearly every village in and around the Kopet-Dag. Although the natural area of *S. acmophylla* extends very close to the Mediterranean, Caspian, and Persian Gulf shores, this willow never approaches the immediate zone of maritime climate, being entirely restricted to arid continental regions. (Fig. 13.)

NOTE. *S. daviesii*, as it was mentioned earlier (Skvortsov 1960a: 74), is most likely an abnormal form of *S. acmophylla* with 2 or 3 stamens. It also could be a hybrid with *S. excelsa*, which is, however, less likely. *S. dinsmorei*, too, appears to be a hybrid of *S. acmophylla* either with *S. alba* or with *S. excelsa* (compare Post 1933; Camus, Gombault 1939). It also might be merely one more form of *S. acmophylla* (I had no chance to see the type of *S. dinsmorei*). There is no doubt that hybrids of *S. acmophylla* with *S. alba* and *S. excelsa* do exist (I saw herbarium specimens from Palestine as well as three live plants in the Firyuzinskoye Gorge in the Kopet-Dag). The identity of the rest of the synonyms is beyond question.

Sect. 2. *Amygdalinae*

Koch, 1837, Syn. fl. germ. helv.: 644.

T y p u s: *Salix triandra* L.

Tall shrubs, occasionally small trees with short stems and wide crowns. Bark on old branches (larger than 4–6 cm in diameter) exfoliating in patches of irregular shape, not forming coarse longitudinal fissures. Floriferous buds similar to vegetative ones, compressed, obtuse. Petioles distinctly glandular in their upper part. Leaves lanceolate, flat. Catkins serotinous, borne on long, leafy-bracted stalks, narrowly cylindrical, mostly curved or somewhat pendulous. Bracts pale; in female flowers, either all or some of them abscising by the time capsules ripen. Stamens three, their anthers crooked when emptied (because both pollen sacks face forward rather than sideways). Capsules on long (1–2 mm) stipes, subfusiform, small (3–4 mm when ripen). Styles very short, stigmas recurved, very short, two-lobed.

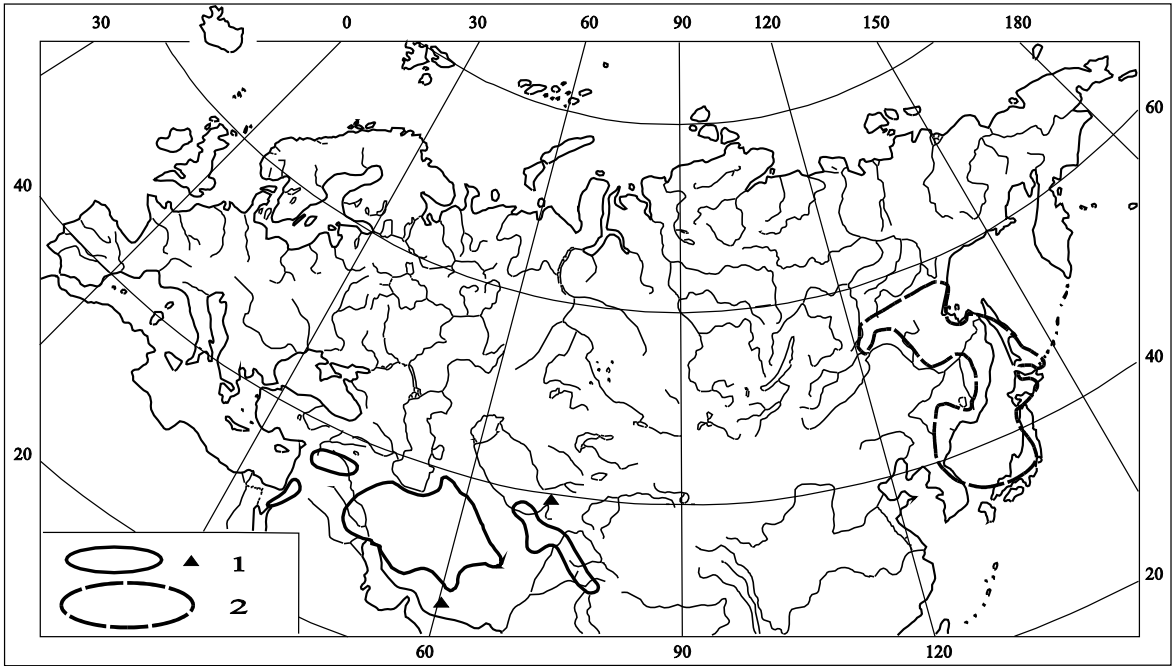


Fig. 13. Distributional areas of *Salix acmophylla* Boiss. (1) and *S. cardiophylla* Trautv. et Mey. (2)

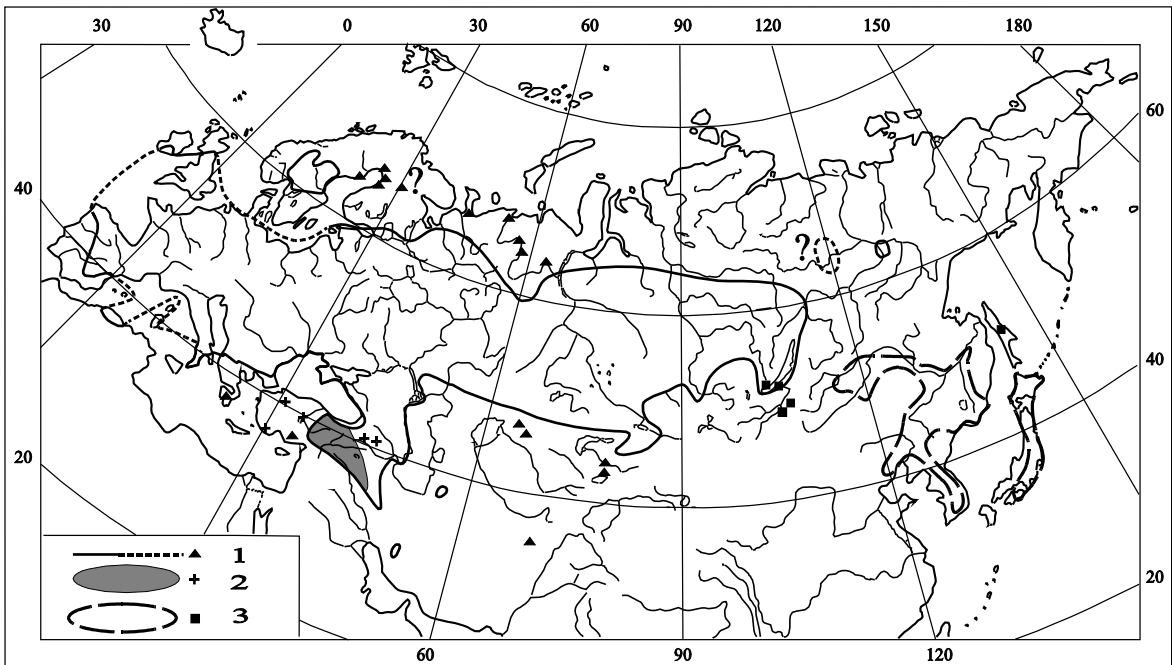


Fig. 14. Distributional areas of *Salix triandra* L. (1),
S. triandra ssp. *bornmuellerii* (Hausskn.) A. Skv. (2),
and *S. triandra* ssp. *nipponica* (Fr. et Sav.)

The section appears to contain only the Old World species. The American species *S. amygdaloides* Anderss., which has been traditionally placed here, should be excluded and removed to the section *Humboldtianae*, since it differs significantly from *S. triandra* in its bud and flower structure. Additionally, stem bark of *S. amygdaloides* is that of the common type, with coarse fissures.

Key to Species and Subspecies

1. Leaves either entire, or irregularly glandular, or irregularly denticulate; occasionally, shallowly emarginate, crenate; rarely some leaves regularly dentate. Petiolar glands minute, punctate, sitting as far as 0.5–2.0 mm down from leaf blade base. Catkin rachises below lowermost flowers 0.4–0.6 mm thick. Dry anthers 0.3–0.5 mm long 3. ***S. songarica***
 — All leaves (except cataphylls) densely regularly dentate at margins. Petiolar glands conspicuous, sitting close to leaf blade. Catkin rachises below lowermost flowers 0.6–0.8 mm thick. Dry anthers 0.5–0.7 mm long 2
 2. Shoots and leaves more or less puberulent 2. ***S. triandra* ssp. *bornmuellerii***
 — Shoots and leaves glabrous 3
 3. Epicormic shoots pruinose 2. ***S. triandra* ssp. *nipponica***
 — Epicormic shoots not pruinose 2. ***S. triandra* ssp. *triandra***

2. ***S. triandra*** L. 1753, Sp. pl.: 1016; Wimmer, 1866, Sal. Eur.: 12; Anderss. 1867, Monogr. Salic.: 23; Krylov, 1930, Fl. Zap. Sib. 4: 733; Wolf, 1930, Fl. Yu.-V. 4: 39; Nakai, 1930, Fl. sylv. Kor. 18: 87; Nazarov, 1936, Fl. SSSR 5: 184; Buser, 1940, Ber. Schweiz. bot. Ges. 50: 632; Grossheim, 1945, Fl. Kavk. 2 ed. 3: 24; Vicioso, 1951, Salic. Españ.: 37; Nazarov et al. 1952, Fl. URSR 4: 63; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. 2 ed. 3, 1: 71; Popov, 1959, Fl. Sredn. Sib. 2: 793; Polyakov, 1960, Fl. Kazakhst. 3: 15; Maire, 1961, Fl. Afr. Nord 7: 53; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR 17: 60; id. 1964, in Mayevsk. Fl. sredn. pol. 9 ed.: 186; id. 1966, Trudy Bot. In-ta AN ArmSSR 15: 113; Rech. f. 1964, Fl. Eur. 1: 46. —*S. amygdalina* L. 1753, op. cit.: 1016; Ledeb. 1850, Fl. Ross. 3, 2: 600; Schmalhausen, 1897, Fl. Sredn. i Yuzhn. Ross. 2: 432; Seemen, 1908, in Aschers. et Graebn. Synopsis 4: 74; Schneider, 1916, in Sarg. Pl. Wilson. 3, 1: 106. —*S. nipponica* Fr. et Sav. 1876, Enum. Jap. 2: 502; Tolmachev, 1956, Der. i kustarn. Sakhal.: 58. —*S. bornmuellerii* Hausskn. 1890, Mitt. bot. Ver. Gesamtthü ringen 9: 21; Görz, 1930, Feddes Repert. 28: 119; id. 1933, op. cit. 32: 393; id. 1934, op. cit. 36: 22, 36; Post, 1933, Fl. Syr. 2: 531; Skvortsov, 1966, op. cit. 15: 115. —*S. kinashii* Levl. et Van. 1905, Bull. Soc. Bot. Fr. 52: 141. —*S. medwedewii* Dode, 1908, Bull. Soc. Bot. Fr. 55: 652; Toepffer, 1925, Sal. Exs.: N 539; Nazarov, 1936, op. cit. 5: 186; Skvortsov, 1960, Bot. mat. Gerb. Bot. In-ta AN SSSR 20: 75. —*S. hamatidens* Levl. 1909, Bull. Soc. Bot. Fr. 56: 301. —*S. armena* Schischk. 1929, Izv. Tomsk. un-ta 81: 436. —*S. subfragilis* auct. (non Anderss. 1858, Mem. Amer. Acad. 6: 450): Kimura, 1943, Acta Phytotax. et Geobot. 13: 188; Ohwi, 1965, Fl. Jap.: 364.

T y p u s: "In Helvetia, Sibiria. Haller Helv.: 152; Gmel. Sib. 1: 155 et tab. 34 fig. 3".

Ssp. **nipponica** (Fr. et Sav.) A. Skv. comb. nova. —*S. nipponica* Fr. et Sav. 1876. —*S. triandra* var. *nipponica* Seemen, 1903, Sal. Jap.: 27; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 424; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 401; Sugawara, 1939, Ill. Fl. Saghal. **2**: 666. —*S. amygdalina* var. *nipponica* Schneid. 1916, in Sarg. Pl. Wilson. **3**, 1: 106.

T y p u s: "Nippon media circa Yokoska,—Savatier N 1139; Niigata id. N 2717" (P). [Isosyntypus (Savatier N 2717) LE!].

Ssp. **bornmuellerii** (Hauskn.) A. Skv. comb. nova. —*S. bornmuellerii* Hauskn. 1890. —*S. repens* auct. fl. As. Minor (non L.): Anderss. 1868, in DC. Prodr. **16**, 2: 237 (quoad pl. As. Minor); Boiss. 1879, Fl. Or. **4**: 1190 (pl. As. Minor).

T y p u s: "Asia Minor, Amasia, in humidis fl. Jeschil Irmak, 350 m.—17. VII 1889. J. Bornmueller" (JE!) (Ic. photogr. typi: Toepffer, Sal. Exs. N 362, LE! et alibi).

HABIT: A tall shrub or tree of small to moderate size (some specimens from the Ob are up to 14 m tall).

HABITATS: Banks of rivers and streams, bayou banks on flood plains; occasionally, secondary habitats, such as ditches and gullies. Its vertical range is from lowland to moderate mountain elevations: in the Pyrenees, it ascends as high as 1,700 m; in the Alps, to 1,600(–1,800?) m; in the Carpathians, to 1,200 m; in the Greater Caucasus, to 1,300–1,500 m; in the Lesser Caucasus, to 2,100 m; in the Urals, Tien Shan, Altai, Sayans, and east of these, only to foothills. In China, Japan, and on the Korea Peninsula also not higher than the foothills.

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DISTRIBUTION: The greater part of Spain, a minor area in Algeria, all of France, England, southern Ireland, Italy, Central Europe, the Balkan Peninsula (except Greece, where it is missing or extremely rare); central Sweden and southern Norway (a disjunct part of the area), Finland (some sporadic locations near the Gulf of Bothnia). It is missing from the rest of Fennoscandia. European Russia (nearly everywhere except Karelia and the forest-tundra belt), the Caucasus, Asia Minor, northern Iran; the Kopet-Dag, southern Iran and eastern Afghanistan (some isolated fragments of the area). Northern and eastern Kazakhstan, West and Central Siberia (to latitude 64–65° N), southern Transbaykalia, southern Amur Oblast, Maritime Province, and central Sakhalin. A disjunct fragment of the area on the Lena, around Yakutsk. Northeast China, Korea, and Japan.

Ssp. *bornmuellerii* is distributed in Asia Minor; ssp. *nipponica*, in Prebaykalia (typical specimens are found around Irkutsk) and all the way east of Prebaykalia. According to I. Koropachinskiy and A. Skvortsova (Koropachinskiy, Skvortsova 1966: 92), it is a sporadic but trivial species in Tuva. Yet I never saw any specimens from there. (Fig. 14.)

NOTE. *S. triandra* leaves may be either green, without any glaucous bloom beneath (f. *concolor*), or whitish, glaucous beneath (f. *discolor*). This character is persistent in all leaves of any single specimen, invariable, and very conspicuous. Consequently, C. Linnaeus treated the forms as two different species (*S. triandra* L. and *S. amygdalina* L.), and later some authors supported that point of view (Dumortier 1862; Wołoszczak 1889, 1912, 1920; Szafer, Kulczyński, Pawłowski 1953). There is some difference in the distribution of both forms, f. *concolor* dominating in mountainous locations of Western and Central Europe and the Caucasus, while f. *discolor* being more common there in the lowland. Also, f. *discolor* occurs more often in the south of the Central Russian Upland, and f. *concolor* in the north. It is f. *discolor* which prevails in East Siberia and the Far East. However, in spite of these fluctuations, both forms are distributed across the entire species range (including the areas of the subspecies). Actually, both forms can be found in

any large population. There are no other differences between the forms, except the color of leaves beneath. Intermediate forms with lower leaves green and upper leaves glaucous are not very infrequent. Therefore, I agree here with the majority of authors and do not recognize *S. amygdalina* as a distinct species. There is no doubt though, that *S. triandra* still needs investigation. It would make sense to test the way its leaf color is inherited through a genetic experiment. A. Neumann's proposal (1955), supported by E. Janchen (1956) and K. Rechinger (1957, 1964), to treat the forms of *S. triandra* as subspecies absolutely does not stand up under scrutiny: it is obvious that these forms can be anything but subspecies.

Each of the two subspecies recognized here by me (ssp. *bornmuellerii* and ssp. *nipponica*) actually also has just a single diagnostic difference: one, pubescent shoots and leaves, the other, pruinose epicormic shoots. However, in this case, each diagnostic character is confined to an appropriate geographical area and does not occur within the rest of the species range. On the other hand, both the pruinose bloom and pubescence may be developed to a variable extent, sometimes being very obsolete. Therefore, neither *S. bornmuellerii* nor *S. nipponica* can be treated as a distinct species.

103 It would probably make sense to distinguish one more subspecies consisting of populations from the Caucasus and Iran. They are characterized by more delicate, slender shoots and catkins as well as smaller buds and leaves.

According to the description of *S. armena* Schischk., no one would expect this name to be a synonym of *S. triandra*. Yet it is *S. triandra* that attained an unusual habit of a thick bush with small leaves, probably, due to multiple damage either by cattle or stones in a mountain stream. Its type has been found and preserved in the St. Petersburg Herbarium.

3. ***S. songarica*** Anderss. 1867, Monogr. Salic.: 53 et tab. 3, fig. 34; id. 1868, in DC. Prodr. **16**, 2: 213; Wolf, 1903, Trudy SPb. bot. sada **21**: 181; Nazarov, 1936, Fl. SSSR **5**: 204; Parsa, 1950, Fl. Iran. **4**: 1354; Drobov, 1953, Fl. Uzb. **2**: 53; Polyakov, 1960, Fl. Kazakhst. **3**: 16; Skvortsov, 1960, Bot. mat. Gerb. Bot. In-ta AN SSSR **20**: 75; id. 1962, Bot. mat. Gerb. In-ta bot. UzbSSR **17**: 60; Skvortsov, Derviz-Sokolova, 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4515; Sagitov, 1962, Uzb. biol. zhurn. **3**: 27. —*S. hypericifolia* Goloskokov, 1960, Fl. Kazakhst. **3**: 434.

T y p u s: "In Songaria ad Ajagus et in ripis fl. Tschu et Ili—Schrenk" (LE!).

HABIT: A tall shrub (to 8–10 m) or tree with a short, lowly branching stem and wide crown.

HABITATS. The species is strictly alluvial and is associated with fine sandy or muddy drifts. Hence, it is widespread and abundant only at lower reaches of the largest rivers.

DISTRIBUTION: The rivers of Lake Balkhash Basin; the Chu and Talas; Syr Darya (from Ferganskaya Valley to Dzhusaly); Amu Darya (sporadically, mostly extinct at its upper and middle reaches, yet common at the Lower Amu Darya); Murghab and Tedzhen rivers. There are a few rare locations in mountainous areas: the Shorlok River in the Kopet-Dag, Sotchkhar in the Shugnan, Okhotnichye on the Narynkol River, the Ulutau (isolated location). It is also encountered on the Hari Rud River in Iran, near Aq Chah in northern Afghanistan, and in Sinkiang. (Fig. 15.)

NOTE. The species is rather uniform throughout its entire, rather limited, range. *S. hypericifolia* is nothing but an individual deviation (mutation) characterized by obtuse leaf apices. There are no specimens collected, other than the type.

Sect. 3. *Urbanianae*

(Seemen) Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 103.

T y p u s: *Salix cardiophylla* Trautv. et Mey.

Tall trees reproducing only by seeds. Bark on old stems with coarse longitudinal fissures. Floriferous and vegetative buds similar: lanceolate, compressed. Bud scale margins not connate. Petioles glandular. Leaves broad, mature ones with veins conspicuously prominent beneath. Catkins pendulous, long-stalked. Leaves on catkin stalks normally developed. Bracts large, pale, at base more or less connate either with stamens or ovary stipes. In female flowers, bracts abscising after flowering. Nectaries mostly three: two of them transverse, adaxial, and one abaxial. Stamens 5–10, their filaments glabrous to puberulous. Ovaries stipitate; styles elongated, laciniate (cleft); stigmas two-lobed; lobes linear, acute. Stylodes (style branches) breaking off after flowering. This presumably is a monotypic section.

4. ***S. cardiophylla*** Trautv. et Mey. 1856, in Middendorff, Reise Sibir. 1, **2**: 77 et tab. 19–20; Anderss. 1867, Monogr. Salic.: 37; Wolf, 1903, Trudy SPb. bot. sada **21**: 177; Koidzumi, 1913, Bot. Mag. Tokyo **27**: 97; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 103; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 424; Nazarov, 1936, Fl. SSSR **5**: 107; id. 1937, Fl. Zabayk. **3**: 13; Tolmachev, 1956, Der. i kustarn. Sakhal.: 58; Kimura, 1950, Symb. Iteol. **10**: 546. —*S. urbaniana* Seemen, 1896, Bot. Jahrb. Beibl. **52**: 9; id. 1903, Salic. Jap.: 24; Schneider, 1916, op. cit. **3**, 1: 103; Makino, 1956, Fl. Jap.: 670; Tolmachev, 1956, op. cit.: 58. —*S. maximowiczii* Kom. 1901, Trudy SPb. bot. sada **18**: 442; id. 1903, op. cit. **22**: 25 et tab. 1; Schneider, 1916, op. cit. **3**, 1: 100; Nakai, 1930, Fl. sylv. Kor. **18**: 72; Komarov, Alisova, 1931, op. cit. **1**: 424; Nazarov, 1936, op. cit. **5**: 207. —*Toisusu cardiophylla* Kimura, 1928, Bot. Mag. Tokyo **42**: 288; id. 1934, in Miyabe, Kudo, Fl. Hokkaido **4**: 396; Sugawara, 1939, Ill. Fl. Saghal. **2**: 662. —*Toisusu urbaniana* Kimura, 1934, op. cit. **4**: 397; Sugawara, 1939, op. cit. **2**: 664; Ohwi, 1965, Fl. Jap.: 362.

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T y p u s: "Ad fl. Polowinnaja prope Udskoj 7.VI 1844; ad sin. Ujakon 23.III–1.IX 1844. A. Middendorff" (LE!).

Ssp. ***urbaniana*** (Seemen) A. Skv. comb. nova. —*S. urbaniana* Seemen 1896. —*S. cardiophylla* var. *urbaniana* Kudo ex Makino, 1956, Fl. Jap.: 67.

T y p u s: "Japonia, prov. Nambu, in subalpinis ad rivulos, a. 1865 Tschonoski" (B, LE! et alibi).

HABIT: A large, straight-stemmed tree up to 30–35 m tall and 1 m in diameter.

HABITATS: Banks of small streams. The species never reaches high elevations ascending to 800 m in the Sikhote-Alin and to 600–700 m in the Stanovoy Range. Throughout its entire area, it occurs sporadically, either solitary or in small clusters, never growing en masse.

DISTRIBUTION: From the Upper Olekma Basin to Ayan, central Sakhalin, Kunashir, Maritime Province, northeastern North Korea, southeastern part of Northeast China, Hokkaido, and the mountains of Hondo.

Ssp. *urbaniana*: Japan, Kunashir, and southern Sakhalin. Plants from central Sakhalin are to be assigned to ssp. *cardiophylla*, which comprises the continental part of the species' range. (Fig. 13.)

NOTE. According to V. Komarov and M. Nazarov, *S. maximowiczii* should differ from the "typical" *S. cardiophylla* in its somewhat narrower leaves and also in the length of its ovary stipe. Yet, while analyzing massive material, one comes to the conclusion that these characters are not consistent and reliable. Still more bizarre was the placement of *S. maximowiczii* in the section *Pentandrae* and *S. cardiophylla* in *Urbanianae*, as C. Schneider (1916) did! Earlier, in 1903, O. Seemen had mentioned that he had not been able to distinguish *S. maximowiczii* from *S. cardiophylla*. Yet he had recognized *S. urbaniana*, which is hardly more distinct. The distinguishing feature was the leaf pubescence and occasionally also capsule pubescence. However, these characters vary considerably: sometimes the leaf pubescence disappears even before the leaves expand. Neither any other diagnostic characters, such as the stipule and leaf base shape, nor catkin length, mentioned by A. Tolmachev (1953), are consistent.

Sect. 4. *Pentandrae*

(Borrer) Schneider, 1904, Handb. 1: 29.

T y p o s: *Salix pentandra* L.

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Trees, sometimes (in unfavorable conditions) nearly shrubs. Bark on old stems with coarse longitudinal fissures. Floriferous buds similar to vegetative ones; bud scale margins connate, scales cap-like. Petioles always glandular; glands conspicuous, two or three pairs positioned at blade base. Glands often developing into foliolaceous outgrowths. Leaves lustrous above, densely glandular-dentate at margins. Glands of young leaves producing odorous pitch (resembling poplars). Catkins serotinous, borne on leafy stalks, dense, rather stout. Bracts mostly with one or two glands at apex; in female flowers, bracts abscising by the time when capsules ripen. Nectaries two; occasionally in male flowers a few nectaries forming cup-like structures around bases of stamens. Stamens 3 to 10. Ovaries stipitate, styles short, stigmas two-lobed, deflected to sides. Mature capsules large.

The section consists of 7 or 8 species and is widely distributed in regions with the temperate cold climate in Eurasia and North America. The two distinct species groups within the section may be considered as subsections. One group consists of three species belonging to the flora of this country and a Chinese species (*S. paraplesia* Schneid.) that are closely related, as well as one North American species (*S. serissima* Fern.). The other group includes two or three boreal North American species (*S. lucida* Muhl., *S. lasiandra* Benth., *S. caudata* Heller).

Key to Species

1. Buds narrowly triangular-lanceolate, narrowly acuminate. Lowermost cataphylls pubescent along margins as well as at apices on the outer side, their dense, persistent trichomes exceeding margins by approximately 2.0–2.5 mm 6. **S. pseudopentandra**
- Buds lanceolate or ovoid, obtuse or faintly short-pointed. Margins of lowermost cataphylls silky ciliate. Trichomes about 1 mm long, fugacious 2
2. Leaves dark green above, pale beneath, distinctly bicolorous. Buds lanceolate, acuminate 5. **S. pentandra**
- Leaves not distinctly bicolorous. Buds ovoid, obtuse 7. **S. pentandroides**

5. **S. pentandra** L. 1753, Sp. pl.: 1016; Ledeb. 1850, Fl. Ross. **3**, 2: 597 (p. p. excl. pl. Sib. Or. et Caucasi!); Wimmer, 1866, Salic. Eur.: 22; Anderss. 1867, Monogr. Salic.: 35 (p. p. !); Seemen, 1908, in Aschers. et Graebn. Synopsis **4**: 61; Wolf, 1930, Fl. Yu.-V. **4**: 37; Krylov, 1930, Fl. Zap. Sib. **4**: 727; Floderus, 1931, Salic. Fennoscand.: 158; Perfilyev, 1936, Fl. Sev. kr. **2-3**: 32; Nazarov, 1936, Fl. SSSR **5**: 205 (ex parte: excl. pl. Sib. Or., Orientis Extr. et Caucasi); Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 627; Vicioso, 1951, Salic. Españ.: 34; Nazarov et al. 1952, Fl. URSR **4**: 73; Shlyakov, 1956, Fl. Murm. **3**: 55; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. 2 ed. **3**, 1: 65; Polyakov, 1960, Fl. Kazakhst. **3**: 15; Skvortsov, 1960, Trudy MOIP **3**: 249; Rech. f. 1964, Fl. Eur. **1**: 45.

T y p u s: "In Europae paludibus montosis duris. Hort. cliff. 454; Fl. Suec.: 792; Fl. Lapp.: 370 et tab. 8 fig. 3".

HABIT: A tree up to 15–18 m tall in favorable conditions.

HABITATS AND DISTRIBUTION: Graminoid forest fens dominated by *Carex* and *Calamagrostis*; transitional zones around *Sphagnum* bogs (*S. pentandra* plays an essential role there forming open canopies together with *Betula pubescens*); meadows that develop after logging on early stages of the vegetation recruitment, especially in valleys, hollows, and places where ground waters come out to the surface. At southern limits of its range, in West Siberian forest-steppes, the species occurs in *kolki* growing in *zapadina*'s. In the steppes of southern European Russia, it is found in lower parts of flood plains and also in *zapadina*'s amidst inland sandy territories, such as those between the Archeda and Don or along the Middle Dnieper. In Central and Western Europe, it is encountered mostly in the mountains, ascending to 2,000 m in the Alps (even to 2,400 m in the Italian Alps); to 1,400 m in the French Massif Central; to 1,000–1,200 m in the Sudetes and Carpathians. In the Urals and Altai, it goes up nearly to the timberline. (Fig. 16.)

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NOTE. *S. pentandra* exhibits its characters rather consistently across its nearly entire range. Yet the specimens originating from the Pyrenees, French Massif Central, and Alps have their buds somewhat more stout, resembling those of *S. pentandroides*. There is an option of treating these populations as a subspecies (besides, they are geographically isolated). Unfortunately, cultivated plants were often used for the earliest herbarium collections in Western Europe. This makes it difficult to evaluate the actual range of *S. pentandra* in that area, so that it still remains obscure. Therefore, it is impossible so far to segregate the West European subspecies with confidence. Plants from the Balkans appear to be not different from Scandinavian, Central Russian, or Siberian ones.

6. **S. pseudopentandra** Flod. 1933, Ark. bot. **25A**, 10: 12; Skvortsov, 1960, Trudy MOIP **3**: 250; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3221; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 92. —*S. pentandra* ssp. *pseudopentandra* Flod. 1926, Ark. bot. **20A**, 6: 57; Hultén, 1928, Fl. Kamtch. **2**: 17; Karavayev, 1958, Konsp. fl. Yak.: 84; Malyshev, 1965, Fl. Vost. Sayana: 110. —*S. pentandra* auct. fl. Sibir. Orient. et Orientis Extremis non L.: Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 371; Maxim. 1859, Primit. Fl. Amur.: 242; Komarov, 1929, Fl. Kamch. **2**: 7; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 424; Nakai, 1930, Fl. sylv. Kor. **18**: 82; Nazarov, 1937, Fl. Zabayk. **3**: 193; Grubov, 1955, Konsp. fl. Mong.: 101; Tolmachev, 1956, Der. i kustarn. Sakhal.: 62; Popov, 1959, Fl. Sredn. Sib. **2**: 792; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 22 (p. p.).

T y p u s: "Kamtchatka, Opala volkano, 19.VII 1921. E. Hultén N 2225" (S) (isotypus: LE!).

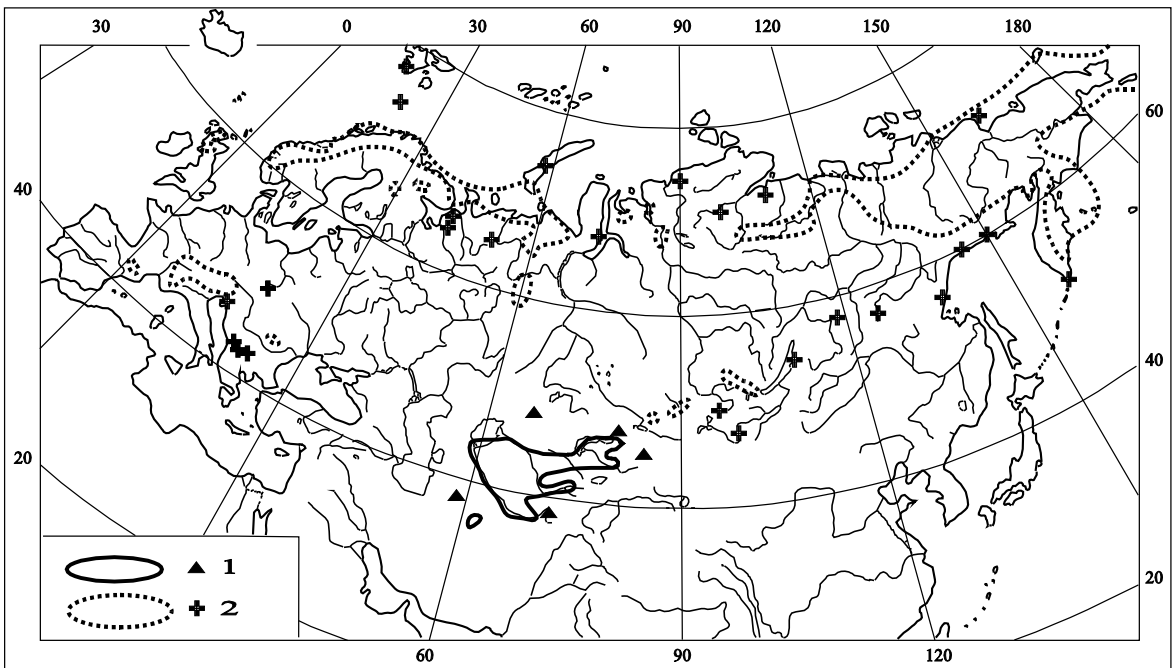


Fig. 15. Distributional areas of *Salix songarica* Anders. (1) and *S. reticulata* L. (2)

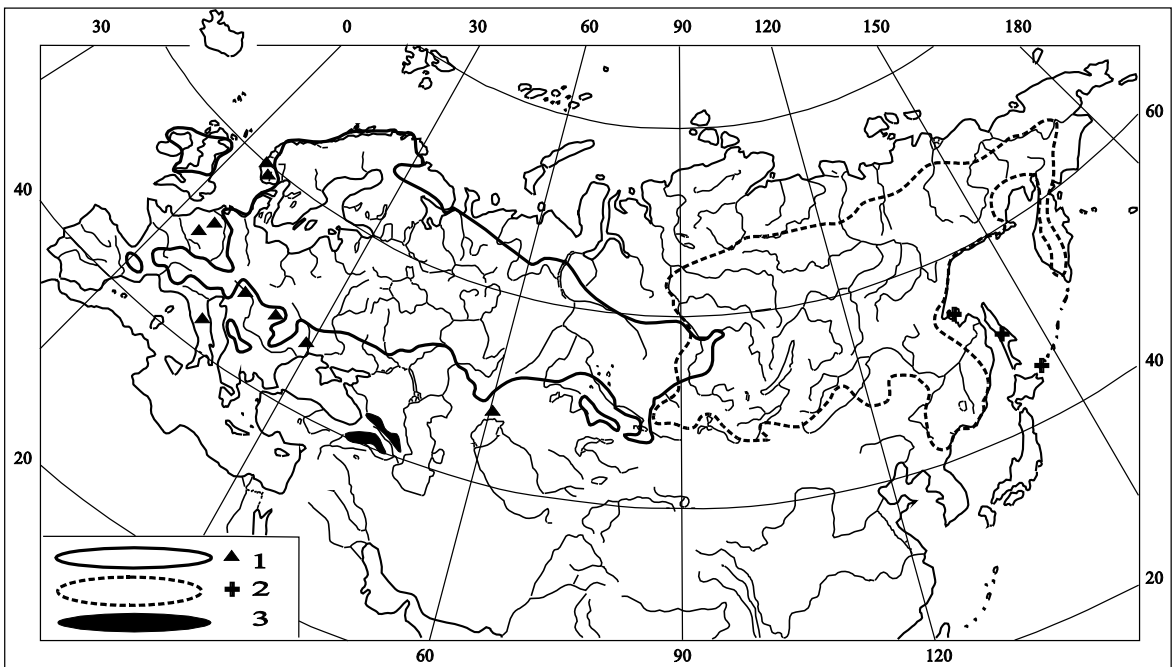


Fig. 16. Distributional areas of *Salix pentandra* L. (1), *S. pseudopentandra* Flod. (2), and *S. pentandroides* A. Skv. (3)

HABIT: A small tree, usually 2–5 m tall (up to 8–10 m and 12–15 cm in stem diameter).

HABITATS: Damp depressions, bog edges, and paludal open woodlands from lowland to near the upper forest limit. The species is not uncommon; however, in most places, it occurs sparsely, not growing en masse.

DISTRIBUTION. The left bank of the Yenisei is the westernmost point on the plain. 107
In the mountains, it is distributed farther west, across the southern Altai. The southern part of the range includes northern Mongolia and much of Northeast China. The northeastern Korea Peninsula, Maritime Province (common, but no collections from the Lower Amur available so far), Sakhalin (a single known locality at the middle reaches of the Tym), the Kurils (another single finding on Iturup), the Shantar Islands, Sea of Okhotsk Coast, Kamchatka (nearly everywhere), the Anadyr River down to the mouth of the Belaya (so far not found on the Koryak Plateau). The northern border of the species range almost exactly follows the parallel of 68–69° N, which is close to the limit of the forest-tundra belt. In the Sayans and Altai, it ascends to 1,800–2,100 m; in the Stanovoye High Plateau, to 900–1,000 m. (Fig. 16.)

NOTE. The specific distinctness of *S. pseudopentandra* is absolutely beyond question. Morphological differences between *S. pentandra* and *S. pseudopentandra* are even more pronounced than those between *S. pentandra* and, say, the Chinese species *S. paraplesia* Schneid. or between *S. pentandra* and the American *S. serissima* Fern. However, this is not the only point. Of more importance is the fact that within the area of their range overlap, both *S. pentandra* and *S. pseudopentandra* remain completely distinct.

7. ***S. pentandroides*** A. Skv. 1960, Dokl. AN ArmSSR **31**: 299; id. 1960, Trudy MOIP **3**: 253; id. 1961, Feddes Repert. **64**: 74; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 111. —*S. pentandra* auct. fl. Caucasi et Asiae Minoris, non L.: Boiss. 1879, Fl. Or. **4**: 1184; Görz, 1930, Feddes Repert. **28**: 113; id. 1933, op. cit. **32**: 389; id. 1934, op. cit. **36**: 226; Nazarov, 1936, Fl. SSSR **5**: 206 (quoad pl. caucas.); Grossheim, 1945, Fl. Kavk. **3**: 27; Makhatadze, 1961, Dendrofl. Kavk. **2**: 51.

T y p u s: "Caucasus septentr., prov. Kuban, pineto-betuletum in angust. Dshalan-Kol, 22.V 1908, N. et E. Busch. (♂)" (ERE, LE). "Caucasus septentr., Balkaria, in ripa rivuli Baschyl-sugusu, alt. 1950 m., 1.IX 1939. R. Jelenevski (♀)" (MW).

HABIT: A small, delicate tree.

HABITATS: Mostly damp and paludal minor valleys and slopes within the elevation range 800–2,300 m in the forest and subalpine zones.

DISTRIBUTION: Nearly all across the Greater Caucasus (although not that common in the eastern part, particularly, in Azerbaijan). In the Lesser Caucasus, it is more sporadic, known only from a few locations in northern Armenia, Borzhomi and Bakuriani vicinity, and Lake Geck-Gel. In Turkey, it grows on oozes in Kars, Erzurum, Bayazit, and Gü mü shane provinces. (Fig. 16.)

Sect. 5. *Salix*

T y p u s: *Salix alba* L.

Large or moderate-sized trees. Bark on old stems with coarse longitudinal fissures. Floriferous buds look similar to vegetative ones. One pair of petiolar glands sitting near leaf blade base. Leaves lanceolate, narrowly acuminate, serrulate at margins, not producing pitch, flat, stoutish. Catkin stalks leafy. Bracts pale, eglandular at apex, abscising in female

flowers after flowering. Nectaries two in male flowers and mostly one in female ones. Stamens two, their filaments densely pubescent. Capsules glabrous, moderate-sized, stipitate; stipes short, styles rather short, stigmas recurved, two-parted.

108 This section consists of only three species, of which *S. fragilis* to some extent resembles *S. pentandra* (in its bud shape and structure, as well as shape of the stipules). This fact reveals close relationship between the two sections. Besides, both in *S. alba* and *S. fragilis* there occur some specimens with an abnormally large number of stamens (up to four or even eight in a flower). A traditional treatment of these specimens as hybrids with *S. pentandra* is not always reasonable. This point was made long ago by A. Kerner and N. Andersson (Andersson 1867: 42). The multistaminate specimens I have inspected by no means could be treated as hybrids with *S. pentandra*. These abnormalities are more likely atavistic features, which could be one more proof of close relation between the sections *Salix* and *Pentandrae*.

Key to Species

1. Mature shoots light-colored, grayish-yellow or nearly ivory, glabrous, rather lustrous, growing at nearly right angles to branches, getting broken off at bases very easily. Buds acute, rather convex on adaxial side and therefore not appressed to shoots, either entirely or partially blackening by wintertime. Stipules broad, semicordate. Leaves yellowish-green, glabrous. Capsule stipes 1–1.5 mm long 10. **S. fragilis**
- Mature shoots of different colors, never growing at right angles and never too fragile, except crowns of really old trees. Buds flat on their adaxial side, closely appressed to shoots, colored similarly to shoots, never blackening by winter. Stipules lanceolate or subulate. Foliage coerulescent, leaves sericeous, at least superior ones. Capsule stipes 0.2–1.2 mm long 2
2. Buds lanceolate-oblong, to 2 mm broad, their abaxial side flattened. Bracts up to 1 mm broad. Anthers 0.5–0.7 mm long. Mature capsules 4–5 mm long. Style length + stigma length = 0.5–1.0 mm 8. **S. alba**
- Buds ovoid-lanceolate or ovoid-triangular, about 2.5 mm broad, distinctly convex on their abaxial side. Bracts mostly more than 1 mm broad, with straight, long, fugacious cilia at margins. Anthers 0.7–0.9 mm long. Mature capsules 5–7 mm long. Style length + stigma length = 0.8–1.5 mm 9. **S. excelsa**

8. **S. alba** L. 1753, Sp. pl.: 1021; Ledeb. 1850, Fl. Ross. **3**, 2: 598; Wimmer, 1866, Salic. Eur.: 16; Anderss. 1867, Monogr. Salic.: 47; Wolf, 1930, Fl. Yu.-V. **4**: 42; Krylov, 1930, Fl. Zap. Sib. **4**: 730; Nazarov, 1936, Fl. SSSR **5**: 188; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 629; Grossheim, 1945, Fl. Kavk. **3**: 26; Vicioso, 1951, Salic. Españ.: 42; Nazarov et al. 1952, Fl. URSR **4**: 66; Skvortsov, 1955, Bull. MOIP **60**: 121; id. 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR **20**: 78; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 117; Andreyev, 1957, Der. i kustarn. Mold. **1**: 80; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 68; Rasinš, 1959, Ivy Latv.: 90; Polyakov, 1960, Fl. Kazakhst. **3**: 17 (excl. var. *australior*); Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 21; Maire, 1961, Fl. Afr. Nord **7**: 54; Rech. f. 1964, Fl. Eur. **1**: 45. —*S. vitellina* L. 1753, op. cit.: 1016. —*S. massalskyi* Goerz, 1930, Feddes Repert. **18**: 116.

T y p u s: "Ad pagos et urbes Europae. Hort. Cliff. 473; Fl. Suec. N 812; It. Scan.: 200".

Ssp. **micans** (Anderss.) Rech. f. 1963, Öst. bot. Z. **110**: 338. —*S. micans* Anderss. 1867, op. cit.: 49; Nazarov, 1936, op. cit. **5**: 190; Grossheim, 1945, op. cit. **3**: 26. —*S. massalskyi* Goerz, 1930, op. cit. **18**: 116. —Non *S. micans* auct. fl. Europ. nec auct. fl. Asiae Mediae.

T y p u s: "Caucasus—Nordmann; Asia Minor—Wittman" (LE!).

HABIT: A large tree: up to 30 m tall and 1 m in stem diameter.

HABITATS: River banks and valleys (on sandy and especially sandy-muddy drifts). Near northern limits of its range, it occurs only in valleys of large rivers, whereas in the south, particularly within the steppe belt, it is common even along the smallest streams. On flood plains of many southern rivers, it forms groves extending for many kilometers, often together with poplars. It naturally ascends to 900–1,000 m in the Alps and 700–800 m in the Carpathians. When cultivated, it goes up for additional 200–300 m. In the Pyrenees, Caucasus, and Asia Minor, it is encountered as high as 1,800–1,900 m; in Morocco, at 2,400 m; in the Urals and Altai, presumably not higher than 600 m.

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DISTRIBUTION. On the British Isles, *S. alba* appears to be naturally distributed only in eastern England (and probably southeastern Ireland), although, according to some British authors (White 1890; Elwes, Henry 1913), it is doubtful if there are any natural occurrences. The area includes France, the Iberian Peninsula, maritime part of Algeria, mountains of Morocco, Central and Southern Europe, the largest Mediterranean islands (including Crete and Cyprus), Asia Minor, and the Caucasus. In Europe, the northern limit of the continuous area is not yet enough clarified. Some localities in northern Netherlands and the Northern German Lowlands are presumably beyond this border. This is a common species in Latvia, whereas in Estonia as well as Pskovskaya, Leningradskaya, and Novgorodskaya oblast's it does not occur naturally. It is rare in Tver(-skaya), Yaroslavl (Yaroslavskaya), and Kostroma (Kostromskaya) oblast's (on the banks of the Volga or close to it). In Pre-Uralia, it reaches nearly 60° N (at Usolye) growing along the Kama River, although in the Urals, it is not distributed farther than 55° N. The northernmost locality is at the confluence of the Irtysh and Ob. To the south, it penetrates as far as the Chinese part of the Black Irtysh; to the east, as far as the Chulyshman. A disjunct part of the area is on the Yenisei around Minusinsk. In Siberia, the southern border of the area goes via the Kazakh Uplands (probably excluding the Ulutau); it nearly reaches the Aral Sea going down the Turgay River and across the Mugodzhary. Along the Ural River (except its lowermost reaches) as well as down the Lower Volga (including the delta), *S. alba* is a very common species. Ssp. *micans* is distributed in western Transcaucasia and Turkish Lazistan.

Everywhere within and beyond its natural distributional range, *S. alba* is favored for cultivation on residential lots, at roadsides, on banks of reservoirs, in parks, and sometimes also forest plantings. For instance, it is common around St. Petersburg as a cultivated species. Another large cultivation locus is found in Semirechye, where *S. alba* is one of the most common plants in spite of the fact that it does not grow there naturally. It is also cultivated around Irkutsk. (Fig. 17.)

NOTE. Across the major part of its range, *S. alba* is exhibiting a very uniform set of characters. The plants, say, from Algeria look absolutely alike those from the Volga or Minusinsk. However, two important exceptions are to be mentioned. First, the populations from Colchis Floristic Area form a very distinct race of a subspecies rank, characterized by smooth, slender shoots and relatively broad, short, conspicuously silvery pubescent leaves (ssp. *micans*). This is a strict endemic race of Colchis. Other localities of ssp. *micans*, such as South European (Rechinger 1963, 1964), or Central Asiatic, or Iranian (Bornmüller

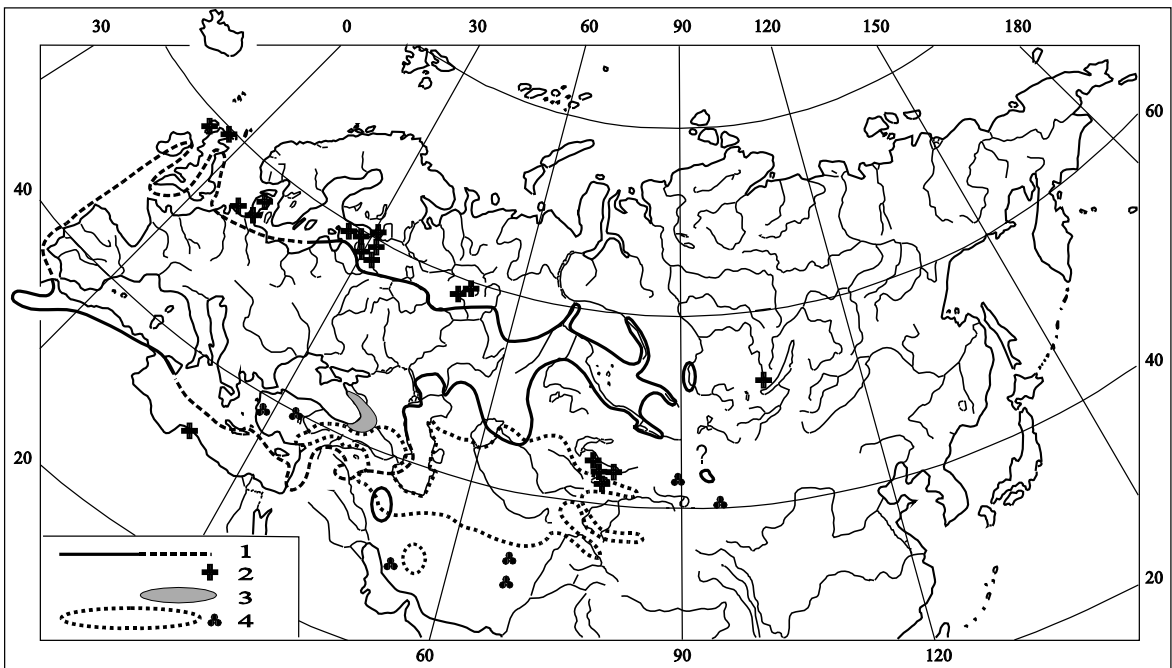


Fig. 17. Distributional areas of *Salix alba* L. (1), *S. alba*, undoubtedly cultivated (2), *S. alba* ssp. *micans* (Anderss.) Rech. f. (3), *S. excelsa* S. G. Gmelin, wild and cultivated (4)

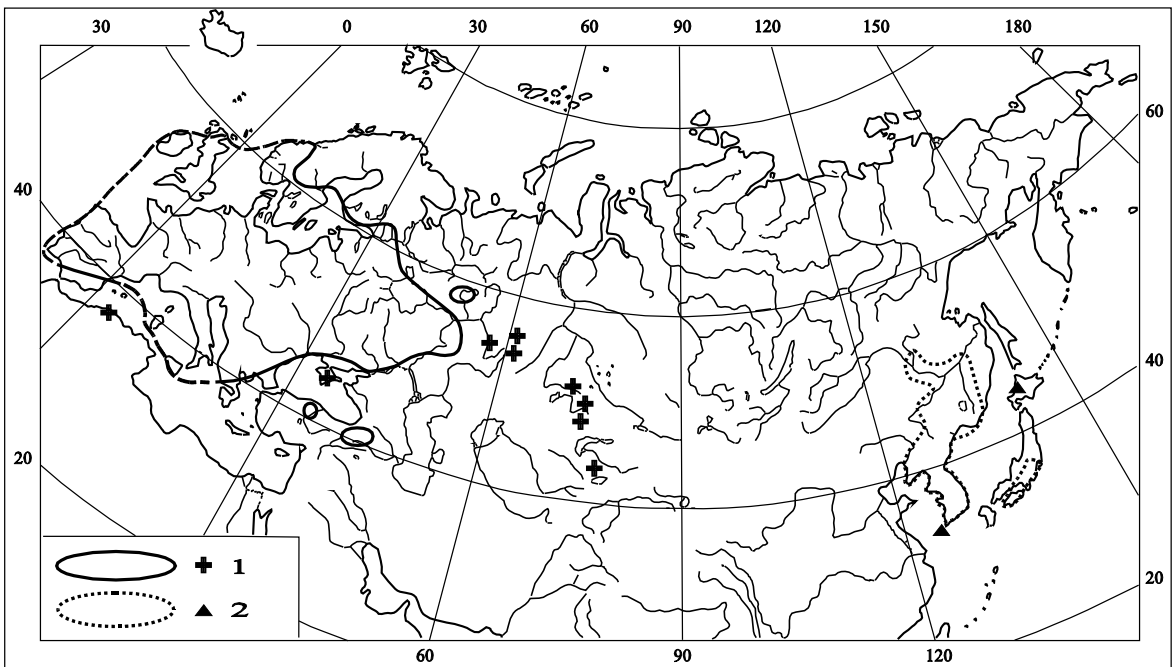


Fig. 18. Distributional areas of *Salix fragilis* L. including its hybrids with *S. alba* L. (1) and *S. pierotii* Miq. (2)

1915; Nazarov 1936; Drobov 1953), were reported due to misunderstanding of the subspecies' characters. Another major deviation from the uniformity is attributed to hybridization of *S. alba* and *S. excelsa* en masse in Asia Minor, Syria, the Caucasus, and also to some extent in Middle Asia (see details in the note concerning the next following species).

On most of the European part of its distributional area, *S. alba* also hybridizes en masse with an adventive species *S. fragilis*. Yet it is important that this hybridization has led to the swamping of both species only in places where there are no natural habitats left for *S. alba* to grow. There *S. alba* has lost its characteristic features. However, the typical *S. alba* still exists in localities where natural habitats are available for it and its natural regeneration is possible, such as Moskovskaya (Moscow), Kaluzhskaya (Kaluga), Tulsкая (Tula), and Voronezhskaya oblast's. Hybrids *S. alba* × *S. fragilis* are as well abundant in the same territories, being restricted to various secondary and disturbed habitats.

Numerous varieties (cultivars) of *S. alba* have been bred as ornamental plants. The most popular are those with bright yellow shoot color, which is persistent till the age of 3–5 years or even longer (the so-called var. *vitellina*), and also those of bright orange-red color (var. *brizensis*, var. *coccinea*). There also exists a weeping variant of var. *vitellina*: "*vitellina pendula*" = *S. chrysocoma* Dode. All these ornamental cultivars are obviously products of ancient peoples' selection and originate from Central and Southern Europe. Their poor hardiness in Moscow Oblast as well as southern pattern of their seasonal growth are proofs of their southern origin (in Moscow, they still manage to produce three or four shoot generations per season and keep growing throughout the entire season). Var. *vitellina* was widespread in Europe already at the time of C. Linnaeus, who treated it as a distinct species, *S. vitellina* L.

9. ***S. excelsa*** S. G. Gmelin, 1774, Reise 3: 308 et tab. 34, fig. 2; J. Gmelin, 1791, in Linnaei, Syst. Naturae, 13 ed. 2, 1: 74; Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR 20: 76 et fig. 1; id. 1962, Bot. mat. Gerb. In-ta AN UzbSSR 17: 61; id. 1966, Trudy Bot. in-ta AN ArmSSR 15: 118. —*S. australior* Anderss. 1867, Monogr. Salic.: 43; Görz, 1930, Feddes Repert. 28: 114; id. 1937, Fl. Turkm. 2: 18; Nazarov, 1936, Fl. SSSR 5: 191; Grossheim, 1945, Fl. Kavk. 3: 16. —*S. fragilis* δ *australis* Anderss. 1868, in DC. Prodr. 16, 2: 210. —*S. fragilis* auct. fl. orient., non L.: Boiss. 1879, Fl. Or. 4: 1184; Post, 1933, Fl. Syr. 2: 530; Parsa, 1950, Fl. Iran. 4: 1351; Makhatadze, 1961, Dendrofl. Kavk. 2: 51. —*S. variifolia* Freyn et Sintenis, 1902, Bull. Herb. Boissier 2, 11: 907; Parsa, 1950, op. cit. 4: 1353. —*S. lisopclados* Dode, 1908, Bull. Soc. Bot. Fr. 55: 651 et fig. H. —*S. oxica* Dode, 1908, op. cit. 55: 653; Lakschewitz, 1914, Spisok rast. Gerb. russk. fl.: N 2453; Nazarov, 1936, Fl. SSSR 5: 193; Grossheim, 1945, Fl. Kavk. 3: 27; Drobov, 1953, Fl. Uzbek. 2: 51. —*S. neodaviessi* Bornm. et Goerz, 1934, Feddes Repert. 35: 283. —*S. dischgensis* Goerz, 1934, op. cit. 35: 284. —*S. litwinowii* Goerz ex Nasarov, 1936, op. cit. 5: 708, 120; Görz, 1937, Fl. Turkm. 2: 33. —*S. euapiculata* Nasarov, 1936, op. cit. 5: 713, 192; Drobov, 1953, op. cit. 2: 51.

Т y п у с: "Persia, Rescht. S. G. Gmelin" (LE!).

HABIT: A large tree (as large as the previous species).

HABITATS: River banks (same habitats as those of *S. alba*).

DISTRIBUTION. Defining limits of *S. excelsa* natural range is even more complicated a task than doing it for *S. alba*, as *S. excelsa* was widely cultivated since ancient times. There is no doubt that its modern area of cultivation is very different from the original, natural one. One can tell with confidence that it is growing wild in Iran, occasionally in the Kopet-Dag, and probably at some locations in Afghanistan and Middle Asia. It appears to

be quite natural in Middle Asia growing solitarily and in clusters on river pebbles and in ravines (*say's*) near streams, yet I did not succeed in finding any young populations which could be confidently considered to have originated from seeds, except in the Kopet-Dag. V. Drobov (1953) stated that wild growing *S. alba* or any species close to it were absolutely missing from Uzbekistan. That opinion may turn out to be true; however, it is also quite possible that the majority of natural groves have been merely exterminated.

S. excelsa is cultivated on the territory extending from Israel and Syria to Kashgaria, Kashmir, and western Gansu. In the Elburz Mountains, it ascends to 2,500 m; in Middle Asia, to 2,000 m (in the Darvaz and western Pamirs, to 2,200 m); to 2,800 m around Kabul. (Fig. 17.)

NOTE. Numerous intermediate forms are found in the areas where *S. excelsa* is cultivated within the range of *S. alba* and particularly where both willows have been cultivated for a long time, such as Syria, eastern Asia Minor, central and eastern Transcaucasia, and partially Middle Asia. These forms, which are difficult to identify, appear to be hybrids¹.

10. ***S. fragilis*** L. 1753. Sp. pl.: 1017; Ledeb. 1850, Fl. Ross. **3**, 2: 598 (p. p.); Wimmer, 1866, Salic. Eur.: 19; Anderss. 1867, Monogr. Salic.: 41; Seemen, 1908, in Aschers. et Graebn. Synopsis **4**: 70; Nazarov, 1936, Fl. SSSR **5**: 201; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 629; Nazarov et al. 1952, Fl. URSR **4**: 71; Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR **15**: 116; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. 2 ed. **3**, 1: 66; id. 1964, Fl. Eur. **1**: 45. —Haud *S. fragilis* sensu Boiss. 1879, Fl. Or. **4**: 1184. —*S. decipiens* Hoffm. 1791, Hist. Salic. **2**: 9 et tab. 30; White, 1890, J. Linn. Soc. **27**: 348, 371; Linton, 1913, Brit. will.: 16 (p. ssp.). —*S. australior* var. *pseudofragilis* Goerz, 1933, Feddes Repert. **32**: 393 (Sal. Asiat. N 37).

T y p u s: "In Europae borealibus. Fl. Lapp. N 394 et tab. 8 f. B; Fl. Suec. N 795; Iter. Scan.: 200".

HABIT: A moderate-sized or, occasionally, quite tall tree (up to 15–18 m).

HABITATS: Banks of mountain streams.

DISTRIBUTION: Northern Asia Minor and the Armenian High Plateau (scattered). Within the territory of the former Soviet Union, it is known only from the vicinity of Akhaltsikhe (Georgia).

In Europe, it is widespread in cultural and semicultural landscapes, but is absolutely missing from undisturbed habitats. It is common along river banks, on shores of reservoirs, in damp depressions, along roads and ditches, and on residential lots. It is easily propagated and self-dispersed by rooting of wind-broken branches. As a result, it is distributed on major European territory outside this country (excluding southern Spain, the southern Balkan Peninsula, and most of Fennoscandia; known in Norway only south of 65° N; in Finland, only near the Gulf of Finland). In this country, the border of the continuous distribution of *S. fragilis* (together with hybrids *S. fragilis* × *S. alba*) runs across the Karelian Isthmus, the cities Nizhniy Novgorod, Samara, Rostov-on-Don, and the lower reaches of the Dnieper and Dniester. Beyond that territory, there are just a few isolated locations or small locuci of hybrids *S. fragilis* × *S. alba*, which appear to have been recently introduced there. These are locations in the Urals, Crimea, northern Kazakhstan, Semirechye, and the Upper Vyatka Basin. In the Carpathians and Alps, *S. fragilis* ascends

¹ In later years, I preferred to synonymize *S. excelsa* with *S. alba*. Most probably, what had been called *S. excelsa*, are several robust clones of *S. alba* very widely cultivated (author's note to the English edition).

to 800–1,100 m. Hybrids with *S. alba* are also widely distributed in the boreal belt of North America. (Fig. 18.)

Var. **sphaerica** Hryniewiecki, 1933, Tent. Fl. Lith.: 67 = var. *capitata* Snarskis, 1954: 225 = var. *bullata* hort. (see also Kobendza 1935; Rasinš 1959). This is an outstanding ornamental variety with a short trunk and dense spherical crown that looks as if trimmed. It has been known in the Baltic Countries since the late 18th century and is still rather popular in Lithuania; it is also occasionally found in Poland, Latvia, and around St. Petersburg (for instance, in Zelenogorsk and Luban). Of course, it deserves to be introduced more widely.

NOTE. As it was mentioned in chapter 3, section 5, in Europe *S. fragilis* most frequently hybridizes with *S. alba*. Long before scientists learned about the ability of willows to form hybrids, many of *S. fragilis* × *S. alba* hybrids had been assigned specific names, some of which occasionally may still be found in the literature, for example, *S. rubens* Schrank, 1789, Baier Fl. 1: 226; *S. russelliana* Sm. 1804, Fl. Brit. 3: 1045; *S. viridis* Fr. 1828, Novit. fl. Suec. 2 ed.: 283; *S. fragilissima* Host, 1828, *Salix*: 6; *S. palustris* id. 1828, op. cit.: 7.

According to results of multiple observations made by different researchers in various regions of Europe, the "pure" *S. fragilis* occurs there much more rarely than its hybrids with *S. alba* (Wimmer 1866: 133; Wołoszczak 1889: 292; Petunnikov 1901: 38; Szafer 1921: 33; Görz 1922: 31; Nazarov 1936: 203; Buser 1940: 630; Lawalrée 1952: 38; Chassagne 1956: 259; Rechinger 1957: 66). My own observations in the European temperate belt and Carpathians have led me to the same conclusion. More than that, a revision of the West European literature makes it clear that on many occasions hybrids of *S. fragilis* were mentioned under the name of "pure" *S. fragilis*. Consequently, data on the range of the "pure" *S. fragilis* in Europe need to be radically revised and reduced. For example, in the old as well as recent editions of the "British Flora" (Linton 1913; Moss 1914; Clapham et al. 1962), "*S. fragilis*" is, for certain, a collection of hybrids. The real *S. fragilis*, known in the British literature under the name of var. *decipiens*, is infrequent in England, occurring mostly in its southern parts. There is no doubt that botanists of the Iberian Peninsula, as well, have listed mostly hybrids under the name of *S. fragilis* (that was noticed by R. Görz as early as 1929). The same is true for the flora of the Balkans. Relying on this information, one can say with enough confidence that hybrids of *S. fragilis* prevail over the species within the European part of its range.

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Sect. 6. *Subalbae*

Koidzumi, 1913, Bot. Mag. Tokyo 27: 88.

T y p u s: *Salix pierotii* Miq.

Trees of moderate size. Bark on old stems with coarse longitudinal fissures. Floriferous buds considerably different from vegetative ones. Petiolar glands obsolete. Leaves lanceolate, narrowly acuminate, densely and sharply serrate at margins. Catkins precocious or coetaneous, short-stalked, small. Bracts persistent. Nectaries two in male flowers, one or two in female ones. Stamens two, their filaments short, anthers small, globular. Capsules sessile, ovoid, small, glabrous or pubescent; styles variably developed: nearly none to 1 mm long; stigmas small, two-lobed or two-parted.

This is an East Asian section, parallel to the European-West Asian section *Salix*. It appears to consist of just two species.

Key to Species

1. Floriferous buds broadly ovoid, occasionally nearly round, rather flat on their adaxial side, conspicuously convex on the back. Stipules slightly inequilateral, flat, shorter than petioles, mostly fugacious. Anthers bright orange when alive. Capsules pubescent, styles elongated, often cleft 11. **S. pierotii**
— Floriferous buds oblong-ovoid or ovate, nearly equally convex on both sides. Stipules distinctly inequilateral, their margins revolute, usually more persistent. Anthers yellow when alive. Capsules glabrous or rather pubescent. Styles very short * **S. babylonica**

11. **S. pierotii** Miq. 1867, Ann. Mus. Lugd.-Bat. **3**: 27 et seorsim (Prolusio Fl. Jap.) **4**: 215; id. 1871, Bijdr. Fl. Jap. **4**: 6; Toepffer, 1909, Salic. Exs. **4**: N 181; Koidzumi, 1926, Bot. Mag. Tokyo **40**: 346. —Non *S. pierotii* auct.: Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 426; Nazarov, 1936, Fl. SSSR **5**: 128 (these notes actually refer to *S. kangensis* Nakai). —*S. koreensis* Anderss. 1868, in DC. Prodr. **16**, 2: 271; Komarov, 1903, Fl. Manchzh. **2**, 1: 24; Koidzumi, 1913, Bot. Mag. Tokyo **27**: 89; id. 1916, op. cit. **30**: 332; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 111; Nakai, 1930, Fl. sylv. Kor. **18**: 164; Nazarov, 1936, op. cit. **5**: 201; Ohwi, 1965, Fl. Jap.: 365. —*S. eriocarpa* Fr. et Sav. 1876, Enum. Jap. **2**: 503; Koidzumi, 1913, op. cit. **27**: 88; Schneider, 1916, op. cit. **3**, 1: 108; Ohwi, 1965, op. cit.: 364. —*S. mixta* Korsh. 1892, Trudy SPb. bot. sada **12**, 8: 391; Komarov, Alisova, 1931, op. cit. **1**: 424. —*S. dolichostyla* Seemen, 1901, Bot. Jahrb. Beibl. **67**: 39; id. 1903, Salic. Jap.: 26 et tab. 2; Nazarov, 1936, op. cit. **5**: 198; Hao, 1936, Syn. Chin. *Salix*: 65. —*S. jessoënsis* Seemen, 1903, Salic. Jap.: 31 et tab. 3, fig. F-L; Schneider, 1916, op. cit. **3**, 1: 110; Miyabe, Kudo, 1921, Icon. forest tr. Hokkaido **1**: N 14; Ohwi, 1965, op. cit.: 365. —*S. pogonandra* Levl. 1912, Feddes Repert. **10**: 437. —*S. hondoensis* Koidz. 1913, op. cit. **27**: 87 (p. p.); Schneider, 1916, op. cit. **3**, 1: 110 (p. p.). —*S. hirosakensis* Koidz. 1913, op. cit. **27**: 264. —*S. pseudokoreensis* Koidz. 1926, op. cit. **40**: 346. —? *S. feddei* Levl. 1912, op. cit. **10**: 436. —? *S. pseudo-jessoënsis* Levl. 1912, op. cit. **10**: 436.

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T y p u s: "Japonia: in Monte Iwajama—Siebold; ins. Kiusiu, promont. Nomo-Saki—Pierot" (U!) (fragmenta typi—LE!).

HABIT: A tree of a moderate size (to 15–18 m tall and 50–60 cm in stem diameter).

HABITATS. Often it is found close to running water; however, even more frequently, solitary trees or small groves are scattered amidst wet graminoid meadows dominated by *Calamagrostis*, which are very common on flat bottoms and slanting slopes of valleys in the south of the Russian Far East (it is a very typical landscape plant there). In this country, it never ascends high up in the mountains (it is found as high as 750 m in the southern Sikhote-Alin).

DISTRIBUTION: Southern Amur Oblast (at the Lower Zeya and Amur, downstream of its confluence with the Zeya); Birobidzhan; the Amur immediately downstream of Khabarovsk; southern Maritime Province and its marginal zone bordering the Ussuri River; the southeastern part of Northeast China (not found west of the Sungari and Liao Ho). *S. pierotii* also occurs on the Korea Peninsula and in Japan, from southern Hokkaido (Sapporo) to Kyushu. (Fig. 18.)

* **S. babylonica** L. 1753, Sp. pl.: 1017; Anderss. 1867, Monogr. Salic.: 50; Boiss. 1879, Fl. Or. **4**: 1185; Hook. f. 1890, Fl. Brit. Ind. **5**: 629; Seemen, 1903, Salic. Jap.:

29; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 42; Hao, 1936, Synops. Chin. *Salix*: 65; Nazarov, 1936, Fl. SSSR **5**: 196; Grossheim, 1945, Fl. Kavk. **3**: 17; Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR **20**: 82; id. 1962, Bot. mat. Gerb. in-ta bot. AN UzbSSR **17**: 62; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 119; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 70; Ohwi, 1965, Fl. Jap.: 364. —*S. subfragilis* Anderss. 1858, Mem. Amer. Acad. **6**, 2: 450. —*S. lasiogyne* Seemen, 1903, op. cit.: 32; Koidzumi, 1913, Bot. Mag. Tokyo **27**: 265. —*S. pseudogilgiana* Levl. 1912, Feddes Repert. **10**: 436. —*S. pseudolasiogyne* Levl. 1912, op. cit. **10**: 436; Nakai, 1930, Fl. sylv. Kor. **18**: 168. —*S. matsudana* Koidz. 1915, Bot. Mag. Tokyo **29**: 312; Schneider, 1916, op. cit. **3**, 1: 107; Hao, 1936, op. cit.: 66; Ohwi, 1965, op. cit.: 364. —*S. neolasiogyne* Nakai, 1928, Bull. Soc. Dendr. Fr. **66**: 47. —*S. dependens* Nakai, 1928, op. cit. **66**: 49; id. 1930, op. cit. **18**: 170. —*S. jeholensis* Nakai, 1936, Rep. Sci. Exped. Manchoukuo **4**, 4: 74. —*S. ohsidare* Kimura, 1946, Symb. Iteol. **9**: 79; id. 1958, op. cit. **16**: 113. —*S. pseudomatsudana* Chou et Skvortz. 1955, in Liou Tchen ngo, Ill. Fl. Tr. Shr. Northeast China: 552 et tab. —*S. capitata* Chou et Skvortz. 1955, op. cit.: 551. —? *S. pseudo-jessoënsis* Levl. 1912, op. cit. **10**: 436.

T y p u s: "In Oriente. Hort. Cliff.: 454; Royen Lugd.—bat.: 84; Tournef. Coroll.: 41".

HABIT: A tree up to 15 m tall, sometimes taller.

HABITATS AND DISTRIBUTION. The species originates from arid and semiarid regions of Central and North China: Gansu (Kansu), Ningxia (Ningsia), Shaanxi (Shensi), Shanxi (Shansi), Suiyuan, and Jehol, growing there along rivers, on damp valley bottoms, in depressions amidst sand, and other similar habitats. There, huge specimens (up to 20 m tall and more than 1.75 m in diameter) were found by S. Chetyrkin (collections of 1909) in the oases of A-la Shan (Ho-lan Shan).

It is cultivated nearly everywhere in temperate regions of the world. In Eurasia, northernmost localities of its successful cultivation match limits of commercial peach orchards area and include southern England, Belgium, southern Germany, Czechia, Hungary, southern Romania, the Crimea and Caucasus, Uzbekistan, piedmont Kirghizia, the warm central part of Northeast China, major part of the Korea Peninsula, and Japan. Also, there are some cultivated specimens on southern Sakhalin around Kholmsk. In southern Middle Asia, it is successfully grown as high as 2,000–2,200 m in the mountains (in Vanch and Khorog); in northern India, at 2,700 m.

NOTE. *S. babylonica* was probably introduced to Europe from the Near East in the 17th century. An originally introduced female clone with weeping branches is still the only one that appears to grow everywhere in Europe. The same clone was brought (presumably from Europe) to the Crimea and Black Sea Coast. However, there are at least three different clones existing in Middle Asia, one of which is a male. This fact supports the idea that *S. babylonica* was independently introduced to Middle Asia directly from China. In China as well as Japan and Korea, there are even more cultivars known, and this explains the abundance of existing synonyms. It is in China where one can find non-weeping forms, which are quite common there. They prevail in herbarium collections brought from the area of the species original distribution, although these collections as well appear to mostly represent cultivated specimens.

A couple of very special horticultural varieties, which are occasionally found in arboreta, are, undoubtedly, products of ancient Chinese selection. These are var. *annularis*, its leaves curved into rings, and var. *tortuosa* with its irregularly tortuous shoots.

Sometimes, *S. cantoniensis* Hance and *S. heteromera* Hand.-Mazz. are mentioned in the literature as synonyms of *S. babylonica*. This appears to be wrong.

Besides *S. babylonica*, there are a few more ornamental weeping willows. One of them, a cultivar of *S. alba*, "*vitellina pendula*" = *S. chrysocoma* Dode, has been mentioned here. The other two are *S. blanda* Anderss. and *S. salomonii* Carrière.

S. blanda Anderss. 1867, Monogr. Salic.: 50; Skvortsov, 1962, Bot. mat. Gerb. In-ta Bot. AN UzbSSR **17**: 62; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 120. — *S. elegantissima* K. Koch, 1871, Wochenschr. Ver. Beförd. Gartenb. Preuss. **14**: 380; Seemen, 1908, in Aschers. et Graebn. Synopsis **4**: 73, 213; Dostá I, 1950, Květ. ČSR **2**: 881; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 68. — *S. petzoldii* hort. — *S. sieboldii* hort.

This willow is known only as a cultivated plant. There exist a few clones, at least three or four. Traditionally, it is considered to be a hybrid of *S. babylonica* and *S. fragilis*. Yet some of its characters do not fit well within this concept. It is more likely that one parent was *S. babylonica* and the other one was a hybrid from the series *S. alba* × *S. fragilis*. *S. blanda* appears to be selected relatively recently, somewhere in Europe. K. Koch (op. cit.) assumed that this willow was of Japanese origin, and this opinion of his has been occasionally referred to in the literature. However, there is no evidence in support of that hypothesis. Although *S. blanda* is considerably inferior to *S. babylonica* regarding its ornamentality, it is much more hardy. It is doing quite well in the Baltic States and retains its ornamental qualities even in Moscow if grown at sheltered sites.

S. salomonii Carrière, 1872, Rev. Hortic. **64**: 115; Schneider, 1904, Hand. **1**: 36; Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR **15**: 120. — *S. sepulcralis* Simonkai, 1889, Termesz. Fü z. **12**: 157; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 204; Dostá I, 1950, Květ. ČSR **2**: 883; Vicioso, 1951, Salic. Españ: 53.

One can say with much confidence that this form is a hybrid *S. alba* × *S. babylonica*. It is nearly as hardy as *S. blanda* or *S. alba* var. *vitellina* and at the same time almost as ornamental as *S. babylonica*. It is rather common in Azerbaijan (Baku) and also occasionally found in Armenia, Georgia, as well as Lithuania (in Vilnius and its suburbs).

SUBGENUS CHAMAETIA

(Dum.) Nasarov, 1936, Fl. SSSR 5: 31.

T y p u s: *Salix reticulata* L.

Low or procumbent, very rarely medium-sized shrubs, their stems sometimes completely submerged in substrate. *Arctica*-type of bud size gradation along shoots. Petioles usually channeled above, eglandular. Leaves moderate-sized to small, relatively broad, often round. Veins originating mostly in lower half of leaf blades, highly curved, arching. Number of leaves on shoot per growing season usually limited. Catkins serotinous, terminating floriferous shoots, which are often nearly as large and foliated as vegetative ones. Bracts persistent. Nectaries rather large, not infrequently lobed, sometimes two or more. Stamens two, distinct.

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Sect. 7. *Chamaetia*

Dum. 1825, Bijdr. Natuurk. Wetensch. 1, 1: 156 (p. p.)

T y p u s: *Salix reticulata* L.

Low or procumbent shrubs. Floriferous and vegetative buds look similar: obtuse, broadly elliptic or obovoid. *Arctica*-type of bud size gradation along shoots. Leaves and buds on floriferous shoots absolutely alike those on vegetative shoots. Floriferous shoots normally growing thicker and becoming woody up to superior leaves, their catkins detach above uppermost leaf scar. Cataphylls lacking; inferior leaves usually of normal shape, different only in their size. Stipules rudimentary. Leaf blades broadly elliptic or round, entire or obscurely crenate, contrastingly bicolorous, their reticulation distinctly prominent beneath. Bracts not blackening. Nectaries two or more in male and female flowers. Capsules ovoid, small; styles obsolete, nearly none; stigmas short, two-lobed, laterally recurved.

This is a section of arctic-alpine distribution, consisting of only four species (three in the Old World and one, *S. nivalis* Hook., in North America).

Key to Species

1. Leaves small (5–15 mm long), flat above; dry foliage of previous seasons persistent on branches. Catkins few-flowered, their rachises and bracts puberulous or glabrous. Stamen filaments glabrous. Capsule stipes distinct, glabrous 14. **S. erythrocarpa**
- Leaves large (mostly more than 20 mm long), distinctly rugose above due to impressed reticulation. Catkins dense, their rachises and bracts more or less densely puberulent. Stamen filaments pubescent. Capsules pubescent, sessile or subsessile 2
2. A shrub up to 30–70 cm tall, its branches upright. Annotinous and biennial shoots yellowish (not red). Petioles 5–12 times shorter than leaf blades. Mature leaves mostly long setulose-sericeous beneath. Catkin stalks (measured from the uppermost leaf scar) considerably shorter than catkins 13. **S. vestita**

- Stems procumbent, rooting. Annotinous and biennial shoots, petioles, and catkin stalks mostly reddish. Petiole length = $\frac{1}{4}$ – $\frac{2}{3}$ of leaf blade length. Mature leaves mostly glabrous. Catkin stalks approximately as long as catkins or even longer
 12. ***S. reticulata***

12. ***S. reticulata*** L. 1753, Sp. pl.: 1018; Ledeb. 1850, Fl. Ross. **3**, 2: 623 (p. p.: excl. *β villosa*); Wimmer, 1866, Salic. Eur.: 129; Krylov, 1930, Fl. Zap. Sib. **4**: 773 (p. p.: excl. var. *villosa*); Floderus, 1931, Salic. Fennoscand.: 19; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 26; Nazarov, 1936, Fl. SSSR **5**: 32; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 782; Vicioso, 1951, Salic. Españ.: 59; Shlyakov, 1956, Fl. Murm. **3**: 58; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 72; id. 1964, Fl. Eur. **1**: 46; Raup, 1959, Contrib. Gray Herb. **185**: 43. —*S. orbicularis* Anderss. 1868, in DC. Prodr. **16**, 2: 300; Rydberg, 1899, Bull. N. Y. Bot. Gard. **1**: 259; Nazarov, 1936, op. cit. **5**: 33.

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T y p u s: "In alpibus Lapponiae, Helvetiae. Fl. Lapp. N 359 et tab. 8 fig. L, tab. 7 fig. 1–2; Fl. Suec. N 801; Hall. Helv. N 154".

HABIT: A procumbent dwarf shrub with rooting branches.

HABITATS: Rocks, stone-fields, scarps, and glacial deposits in the alpine and partially subalpine zones as well as tundras, particularly, stony and dry short-grass ones. In the forest-tundra belt, it occasionally grows in stony well-drained areas covered with open woods. Usually, it prefers conditions of moderate moisture, but also occurs near tundra and alpine streams. It avoids stagnant water as well as acidic and oligotrophic substrate, being restricted to basic bedrock.

DISTRIBUTION: The mountains of Scotland (600–1,100 m), Alps (across the entire mountain system at 1,800–3,200 m), Tatras (900–2,300 m), Romanian Carpathians (rare in the east and common in the south), mountains of Albania and Macedonia (sparsely scattered), Rila and Pirin in Bulgaria (higher than 2,500 m), and Pyrenees. The Spitsbergen and Bear Island, the mountains of Scandinavia, Kola Peninsula (the arctic coast and inland alpine tundras), northwestern Karelia and the adjacent part of Finland (the Myansielkia Ridge), gypsic rocks and limestones of the Soyana, Pinega, Sotka, and Pizhma rivers, the northern Kanin Peninsula, Kolguyev Island, Malozemelskaya and Bolshezemelskaya tundras, the Novaya Zemlya, Vaygach, the Polar and Prepolar Urals, Northern Urals (sporadically, down to Konzhakovskiy Kamen). It is rather sparse within the territory between the Urals and Kotuy River. Starting from the Olenek Basin, it becomes more common again and is widespread in the appropriate habitats across the Northeast from the Verkhoyskiy Range to Wrangel and Ratmanov islands, Kamchatka, and the Commander (Komandorskiye) Islands. It is not infrequent in the Eastern Sayans (at 1,650–2,450 m), but rather sparse in the Western Sayans, Altai, Tuva (Tannu-Ola), and the Khangai. It is also sparsely distributed in the Barguzinskiy Range, on the Vitim-Olekma High Plateau, along the Upper Aldan, and around Ayan. (Fig. 15.)

NOTE. The report by A. Tolmachev (1956) that *S. reticulata* was distributed on the barren heights of the Eastern Sakhalin Range appears to be doubtful. I could not find any evidence of this species' presence in the Ukrainian Carpathians (Bradis 1965; Nazarov et al. 1952).

S. reticulata is rather common in American Arctic.

13. ***S. vestita*** Pursh, 1814, Fl. Amer. Sept. **2**: 610; Hook. 1840, Fl. Bor.-Amer. **2**: 152; Anderss. 1868, in DC. Prodr. **16**, 2: 300; Rydberg, 1899, Bull. N. Y. Bot. Gard. **1**:

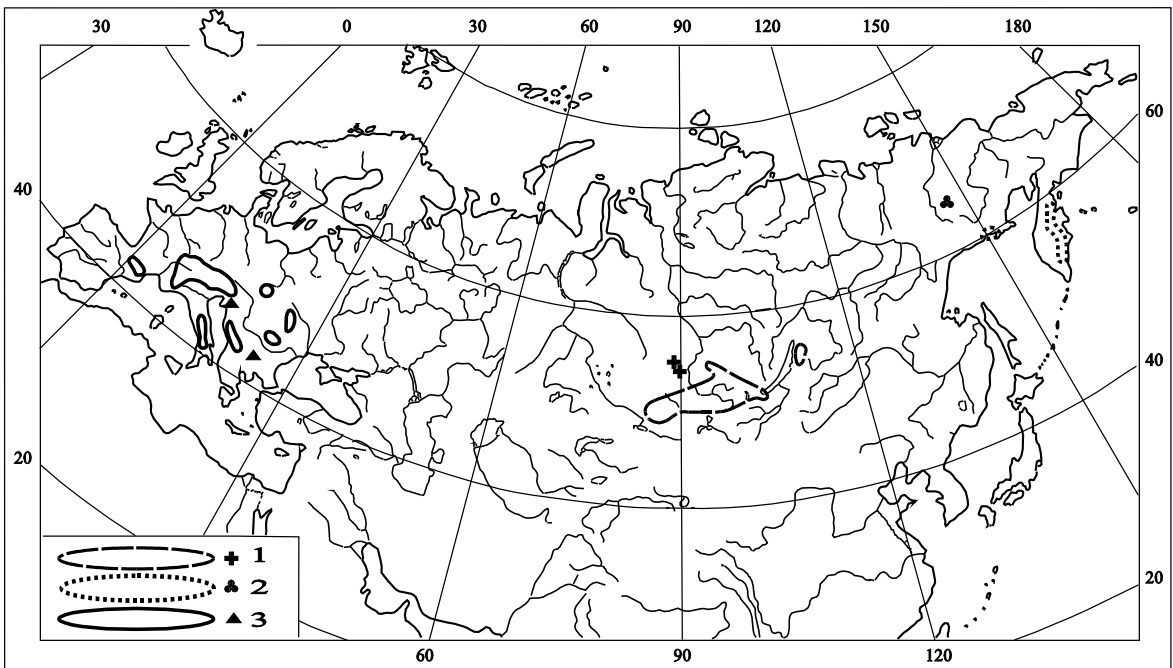


Fig. 19. Distributional areas of *Salix vestita* Pursh (1), *S. erythrocarpa* Kom. (2), and *S. retusa* L. (3)

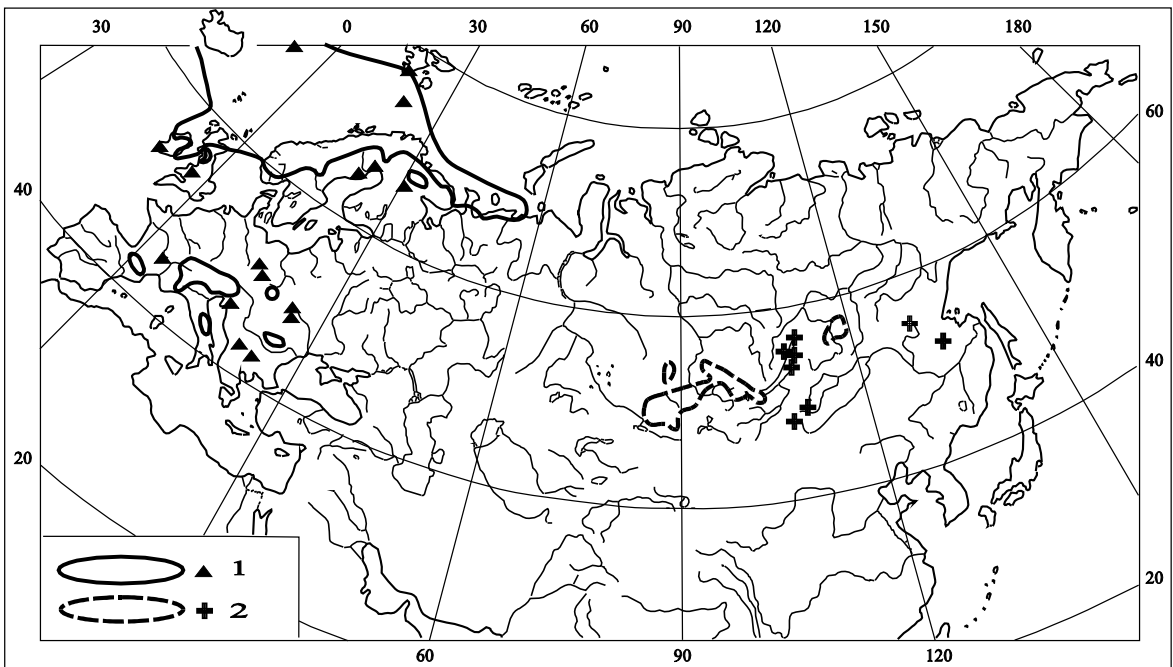


Fig. 20. Distributional areas of *Salix herbacea* L. (1) and *S. turczaninowii* Laksch. (2)

259; Schneider, 1919, Bot. Gaz. **67**: 45; Nazarov, 1936, Fl. SSSR **5**: 34; id. 1937, Fl. Zabayk. **3**: 220; Raup, 1959, Contrib. Gray Herb. **185**: 44; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 12; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3231; Malyshev, 1965, Fl. Vost. Sayana: 103. —*S. reticulata* β *villosa* Trautv. 1833, in Ledeb. Fl. Alt. **4**: 291; Ledeb. 1850, Fl. Ross. **3**, 2: 623; Turcz. 1854, Fl. Baic.-Dah. **2**: 395; Krylov, 1930, Fl. Zap. Sib. **4**: 774; Popov, 1959, Fl. Sredn. Sib. **2**: 808.

T y p u s: "Labrador. Herb. Lambert et Banks" (n. v.).

HABIT: A low shrub with short, stout branches.

HABITATS: Rocks, taluses, runoff hollows, and cirques within the alpine and subalpine zones (occasionally descending to lower elevations when growing on rocks). The species needs fair moisture along with good drainage. It is likely to form continuous shrublands, either pure or in mixture with *S. hastata*, *S. recurvigemmis*, or *S. lanata*. The thickets, however, are not very extensive. *S. vestita* is confined to basic bedrock, particularly, limestone.

DISTRIBUTION: The Altai, Western and Eastern Sayans, Khamar-Daban, nearly all of the ranges in Tuva, the Haan Höhey, Kuznetskiy Alatau (Saraly Basin), Barguzinskiy Range and the adjacent part of the Vitim High Plateau. According to L. Malyshev (1965), its altitudinal range in the Eastern Sayans is 1,700–2,350 m. (Fig. 19.)

There are also two disjunct areas in North America: one, in the Rocky Mountains, another one, around Hudson Bay, on the Labrador Peninsula, and Newfoundland. No distinctions between American and Siberian plants have been detected.

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14. *S. erythrocarpa* Kom. 1914, Feddes Repert. **13**: 165; Floderus, 1926, Ark. bot. **20A**, 6: 12; Hultén, 1928, Fl. Kamtch. **2**: 11; Komarov, 1929, Fl. Kamch. **2**: 29; Nazarov, 1936, Fl. SSSR **5**: 55. —*S. rubricapsula* Toepffer, 1916, Öst. bot. Z. **66**: 402.

T y p u s: "Kamtschatka: circa lacus Natschika et Kronotzkoje et ad font. fl. Kamtschatka aa. 1908–09 leg. Komarov" (LE!).

HABITATS: Rocky and stony outcrops within the alpine zone; mountain tundras. So far, it is hardly possible to present more data on this species' ecology, since both of its major collectors, V. Komarov and P. Novograbenov, used to omit habitat information on herbarium labels.

DISTRIBUTION: the Kamchatkan barren heights, vicinity of Magadan, and Ulakhan-Chastay Range (Moma Basin). V. Vasilyev (1957: 84) mistakenly considered it to be found on the Commander Islands. (Fig. 19.)¹

Sect. 8. *Retusae*

Kerner, 1860, N.-Öst. Weid.: 195.

T y p u s: *Salix retusa* L.

Small, prostrate, procumbent, cushion-like, or submerged in substrate dwarf shrubs. Floriferous and vegetative buds look similar, broadly elliptic or ovoid; *arctica*-type of bud size gradation along shoots. Stipules reduced. Leaves small, obtuse, round to oblanceolate,

¹ Due to scarcity of available material, the circumscription of *S. erythrocarpa* was admitted too broad in 1968 and included specimens that were later placed to other species: *S. khokhriakovii* A. Skv., *S. darpirensis* Jurtz. et Khokhr., and *S. magadanensis* Nedoluzhko. Thus *S. erythrocarpa* appears to be restricted to Kamchatka only (authors' note to the English edition).

with few veins. Floriferous shoots about as leafy as vegetative ones. Bracts pale to black. Stamen filaments glabrous. Capsules lanceolate or narrowly lanceolate, rather gradually attenuating into distinct styles. Stigmas two-lobed, not large, recurved.

This arctic-alpine, mostly Eurasiatic section consists of some 8–10 species. It might be heterogeneous. Its relations to other sections are not yet clear; the most probable connection is that with *Glaucæ*, connection with *Myrtosalix* is less obvious.

Key to Species

1. True stolons submerged in substrate (either moss or soil): pale, with small scales instead of leaves, gradually becoming woody and rooting on second or third growing season. Older stolons keep growing in substrate (unless they are exposed due to erosion). Epiterranean shoots uniformly short, poorly foliated, ones with elongated internodes lacking 2
 - Plants not producing leafless stolons in substrate. Old stems and branches rooting only when reaching age of 5–10 years. Epiterranean vegetative shoots of two kinds found in normally developed, not too suppressed specimens: short, poorly foliated along with elongated, virgate, multifoliate ones 5
2. Leaves entire or with sparse denticles (2–5 per 1 cm of leaf margin length) mostly on lower half of leaf blade. Bracts black, black-purple, or blackish-brown 3
 - Leaf margins with dense denticles (6–10 per 1 cm of leaf margin length) either regularly scattered along margins or more dense on upper half of leaf blade. Bracts yellowish to light brown. Ovaries glabrous 4
3. Leaves 12–40 mm long, 7–25 mm broad, dull, glaucous beneath. Catkins mostly cylindrical, 10–40 mm long when ripening. Dry anthers about 0.4 mm long. Styles 0.2–0.5 mm long 18. **S. nasarovii**
 - Leaves 7–20 mm long, 6–18 mm broad, rather concolorous, green, lustrous. Catkins mostly globular or ovate, 8–20 mm long when ripening. Dry anthers 0.5–0.6 mm long. Styles 0.3–0.6 mm long 17. **S. polaris**
4. Petioles 2–15 mm long, leaves 10–50 mm long, 7–30 mm broad, mostly obovate, cuneate at base. Catkins cylindrical. Styles obsolete (0.1–0.2 mm) 16. **S. turczaninowii**
 - Petioles 2–7 mm long, leaves 7–20 mm long, 5–20 mm broad, round or broadly elliptic, abruptly narrowing or subcordate at base. Catkins globular or broadly elliptic. Styles 0.3–0.6 mm long 15. **S. herbacea**
5. Leaves round or broadly elliptic, abruptly narrowing or cordate at base. Nectaries 2–4 times as long as capsule stipes. Capsule stipes very short. Anthers 0.3–0.4 mm long 19. **S. nummularia**
 - Leaves obovate or oblanceolate, gradually cuneate at base. Nectaries not larger than capsule stipes 6
6. Catkins of 3–6 flowers, hidden in foliage. Stamen filaments 1.5–2.5 mm long. Anthers 0.4–0.5 mm long, yellow. Capsules ovoid, short (2.5–3.5 mm long) 21. **S. serpyllifolia**
 - Catkins with more flowers, mostly broadly elliptic or cylindrical. Stamen filaments 3–5 mm long. Anthers 0.5–0.7 mm long, mostly purple before dehiscence. Capsules lanceolate-conical, 4–7 mm long 20. **S. retusa**

15. **S. herbacea** L. 1753, Sp. pl.: 1018; Ledeb. 1850, Fl. Ross. **3**, 2: 624 (p. p. excl. pl. Sibir.); Wimmer, 1866, Salic. Eur.: 125; Seemen, 1908, in Aschers. et Graebn. Synopsis **4**: 64; Floderus, 1931, Salic. Fennosc.: 21; Nazarov, 1936, Fl. SSSR **5**: 36; Perfilyev, 1936, Fl. Sev. kr. **2-3**: 25; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 757; Vicioso, 1951, Salic. Españ.: 57; Nazarov et al. 1952, Fl. URSR **4**: 30; Shlyakov, 1956, Fl. Murm. **3**: 59; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 74; id. 1964, Fl. Eur. **1**: 46.

T y p u s: "In alpihus Lapponiae, Helvetiae. Fl. Lapp. N 355. et tab. 8 fig. N, tab. 7 fig. 3, 4. Fl. Suec. N 800. Roy. Lugdhat.: 82; Hall. Helv.: 155".

HABITATS: Carpet-like alpine meadows, moss and short-grass tundra meadows, tussocky and hillocky tundras, rocks, stabilized moraines, taluses, clayey outcrops, banks of streams, and particularly places where the snow stays long during the summer. The species needs rather high moisture, especially air humidity, and good drainage. In the majority of locations, it is definitely restricted to siliceous (acidic) bedrock, however, occasionally it may as well grow on limestone.

DISTRIBUTION: Iceland (up to 1,000 m), the Faroe Islands, Jan Mayen Island, and Bear Island; the mountains of Ireland (250–900 m), Scotland (100–250 m), and Wales; the Pyrenees, French Massif Central (1,800 m), Apennines, Alps (up to 3,300 m), Sudetes, Tatras (1,500–2,600 m), Eastern and Southern Carpathians (1,700–2,500 m), Macedonia and western Bulgaria (2,300–2,600 m). It is widespread in the mountains of Scandinavia. The northern Kola Peninsula (close to the Barents Sea), the western Kola Peninsula (mountain tundras: Chuna-Tundra and Monche-Tundra), the Myansielkia Ridge; central and northern Kanin, Kolguyev, and Malozemelskaya Tundra. Multiple references for this species' locations in Bolshezemelskaya Tundra and the Polar Urals have turned out to be erroneous. The species is common in eastern American Arctic including Greenland. (Fig. 20.)

16. **S. turczaninowii** Lakschewitz, 1914, Spisok rast. Gerb. russk. fl. **8**, 50: N 2495; Krylov, Steinberg, 1918, Fl. Kansk. u.: 44; Krylov, 1930, Fl. Zap. Sib. **4**: 778; Nazarov, 1936, Fl. SSSR **5**: 37; id. 1937, Fl. Zabayk. **3**: 218; Grubov, 1955, Konsp. fl. Mong.: 102; Karavayev, 1958, Konsp. fl. Yak.: 80; Popov, 1959, Fl. Sredn. Sib. **2**: 808; Polyakov, 1960, Fl. Kazakhst. **3**: 37; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 12; Malyshev, 1965, Fl. Vost. Sayana: 104. —*S. liliputa* Nasarov, 1936, op. cit. **5**: 707, 37; id. 1937, op. cit. **3**: 218; Popov, 1959, op. cit. **2**: 809.

T y p u s: "Distr. Kansk, in alpinis ad fl. Kan super. 13. VII 1911. I. V. Kusnetzov. — Herb. Fl. Ross. N 2495" (LE!, MW! et alibi).

HABITATS: Rocks, taluses, moraines, moist slopes, moss-covered banks of small alpine streams, and cirques within the alpine and subalpine zones (1,300–2,600 m); also, mountain tundras, particularly, at places where the snow stays late during the summer. Presumably, it is associated with acidic bedrock.

DISTRIBUTION: The Altai, Kuznetskiy Alatau, Western and Eastern Sayans, Khamar-Daban, Barguzinskiy and Baykalskiy ranges, Vitim-Olekma High Plateau, Kentei, and Sokhondo; the Stanovoy and Dussye-Alin ranges and Upper Zeya Basin (isolated locations). (Fig. 20.)

17. **S. polaris** Whlbn. 1812, Fl. Lapon.: 261 et tab. 13, fig. 1; Ledeb. 1850, Fl. Ross. **3**, 2: 625; Wimmer, 1866, Salic. Eur.: 127; Krylov, 1930, Fl. Zap. Sib. **4**: 777; Floderus, 1931, Salic. Fennosc.: 30; Perfilyev, 1936, Fl. Sev. kr. **2-3**: 27; Nazarov, 1936, Fl. SSSR **5**: 40; id. 1937, Fl. Zabayk. **3**: 218; Shlyakov, 1956, Fl. Murm. **3**: 64; Raup, 1959, Contr. Gray Herb. **185**: 45; Rech. f. 1964, Fl. Eur. **1**: 46. — *S. pseudopolaris* Flod. 1926, Ark. bot. **20A**, 6: 8; Hultén, 1928, Fl. Kamtch. **2**: 18;

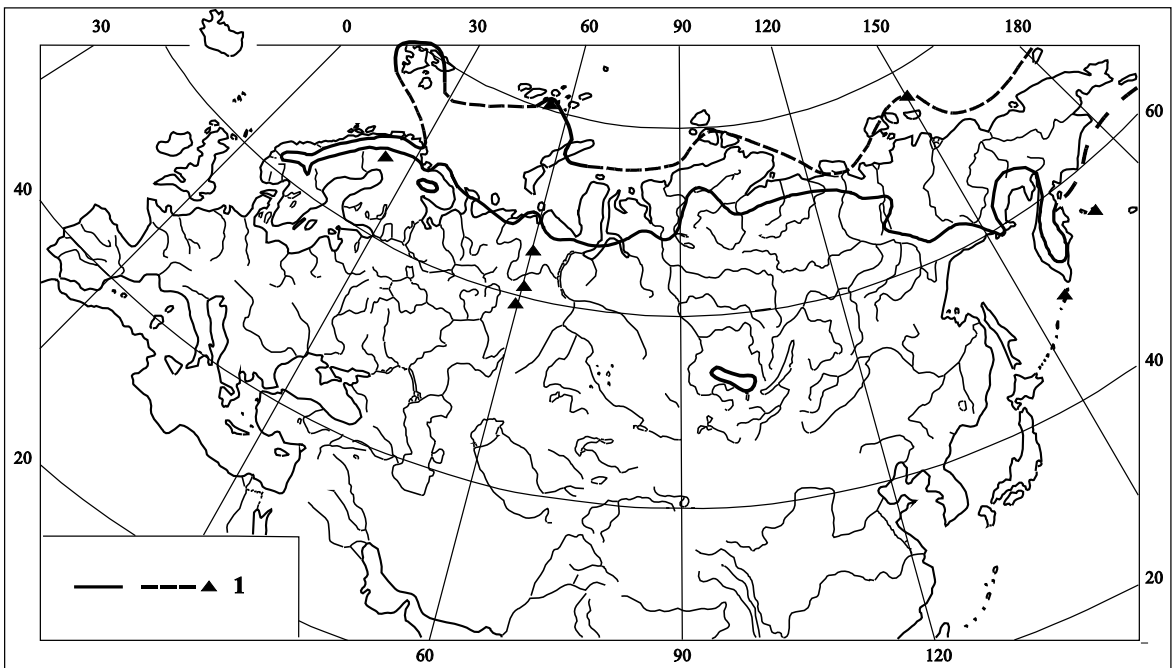


Fig. 21. Distributional area of *Salix polaris* Whlbn.

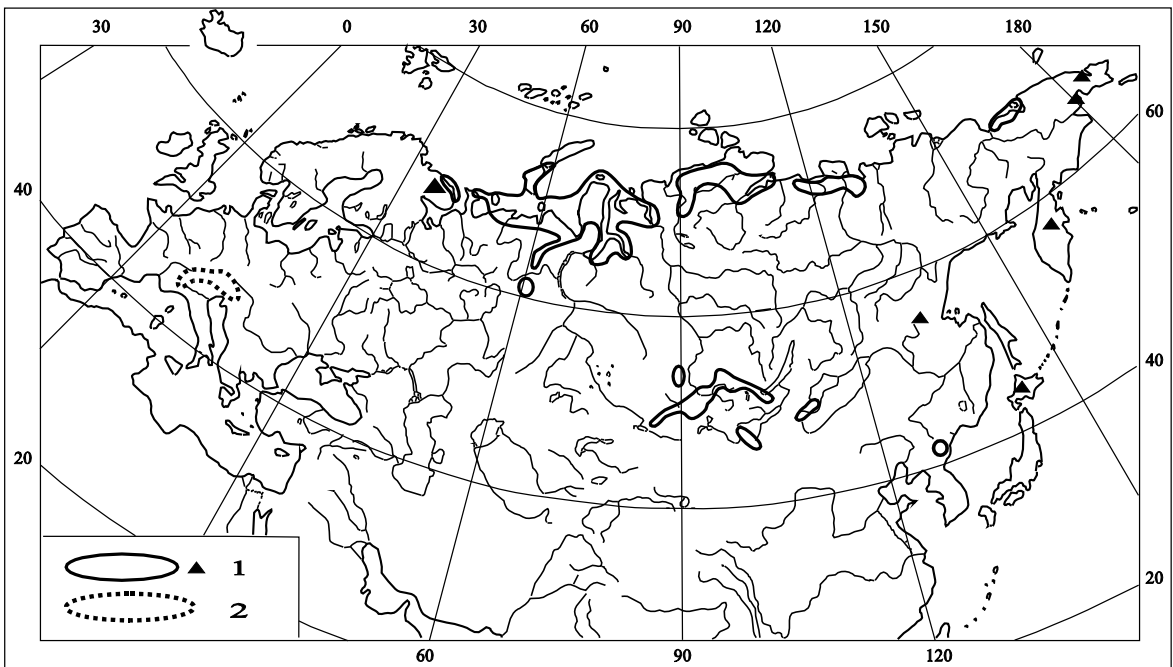


Fig. 22. Distributional areas of *Salix nummularia* Anders. (1) and *S. serpyllifolia* Scop. (2)

Komarov, 1929, Fl. Kamch. **2**: 33; Porsild, 1951, Botany S.-E. Yukon: 139; id. 1955, Vasc. Pl. W. Canad. Arch.: 100; id. 1957, Ill. Fl. Canad. Arct. Arch.: 67; Hultén, 1960, Fl. Aleut. 2 ed.: 161; Wiggins, Thomas, 1962, Fl. Alask. Arct.: 148.

T y p u s: "Finmarkia orient. ad Rastakaisse; ad lacum Tornensem (Wahlenberg)" (n. v.).

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HABITATS: Tundras with cryptogam vegetation; hillocky and spotty tundras; taluses, moraines, rocks, and outcrops; cirques and snowbanks. It tolerates much more dry climatic and habitat conditions as compared to *S. herbacea* showing its preference to basic bedrock and avoiding quartzite, especially in the western part of its range. It penetrates to extremely high latitudes in the Arctic, considerably farther than any other willow species.

DISTRIBUTION: The mountains of Scandinavia; inland mountains of the Kola Peninsula (the Khibins, Chuna-Tundra, and the tundras around Lovozero); the Spitsbergen; Franz Josef Land; northern Kanin; Kolguyev, the Novaya Zemlya, and Vaygach; Malozemelskaya and Bolshezemelskaya tundras, the Polar Urals; the entire territory of Siberian Arctic including the Severnaya Zemlya, Novosibirskiye, Bennett, and Wrangel islands; the barren heights of the Northeast and Kamchatka (including the southern Verkhoyskiy Range, Magadan, and the islands Mednyy and Paramushir in the south). Sporadically, it also occurs in the Northern and Prepolar Urals and Eastern Sayans. It was listed for northeastern Karelia by M. Ramenskaya (1960); however, I never saw any material from there.

Altitudinal ranges: to 1,000 m in the Khibins and Polar Urals (the Shchuchya and Sob basins); to 860 m in the Verkhoyskiy Range (at latitude 70° N); to 500–600 m near Korf Bay; 600–1,400 m on the Kamchatka Peninsula; 1,950–2,700 m in the Eastern Sayans. (Fig. 21.)

It is rather widespread in western American Arctic.

18. *S. nasarovii* A. Skv. 1956, Bull. MOIP **61**, 1: 76, cum fig.; Malyshev, 1965, Fl. Vost. Sayana: 105.

T y p u s: "Montes Sajanenses Orientales, jugum Tunkinski, prope pag. Arshan, in lapidosis reg. alpinae, 7.VIII 1936 leg. A. Korovkin" (MW).

HABITATS: Taluses, moraines, rocks, snowbank spots, etc. (similar to those of *S. turczaninowii*). However, it is associated with somewhat dryer conditions, more pronounced topography, and basic bedrock.

DISTRIBUTION: Tuva (Sangilen, rather sparsely), the Eastern Sayans (1,700–2,500 m), Barguzinskiy Range, and Stanovoye High Plateau. (Fig. 23.)

19. *S. nummularia* Anderss. 1868, in DC. Prodr. **16**, 2: 298; Krylov, 1930, Fl. Zap. Sib. **4**: 777; Nazarov, 1936, Fl. SSSR **5**: 38; id. 1937, Fl. Zabayk. **3**: 216; Floderus, 1941, Sv. bot. tidskr. **35**: 351; Popov, 1959, Fl. Sredn. Sib. **2**: 808; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3232. —*S. retusa* var. *rotundifolia* Trautv. 1847, in Middendorff, Reise Sibir. **1**, **2**: 152; Ledeb. 1850, Fl. Ross. **3**, 2: 624. —*S. rotundifolia* auct. non Trautv. 1832: Trautv. 1871, Acta Horti Petropol. **1**, 1: 79; Schmidt, 1872, Fl. Jeniss.: 118; Lundström, 1877, Weiden Now. Sem.: 10; Tolmachev, 1930, Trudy Polyarn. kom. **2**: 19; Nakai, 1930, Fl. sylv. Kor. **18**: 146; Krylov, 1930, op. cit. **4**: 775; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 25; Nazarov, 1936, op. cit. **5**: 39 (p. max. p.); Rech. f. 1964, Fl. Eur. **1**: 47. —*S. herbacea* var. *flabellaris* Anderss. 1868, in DC. Prodr. **16**, 2: 298. —*S. vulcani* Nakai, 1916, Bot. Mag. Tokyo **30**: 140. —*S. pauciflora* Koidz. 1918, Bot. Mag. Tokyo **32**: 61; Kimura, 1934, in Miyabe, Kudo, Fl. Hokkaido a. Saghal. **4**: 411; Ohwi, 1965, Fl.

Jap.: 365. —*S. polyadenia* Hand.-Mazz. 1932, Öst. bot. Z. **81**: 306; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 145. —*S. tundricola* Schljakov, 1954, Bot. mat. Gerb. Bot. in-ta AN SSSR **16**: 67; id. 1956, Fl. Murm. **3**: 63. —*S. tschanbaischanica* Chou et Chang, 1955, in Liou Tchen ngo, op. cit.: 557.

T y p u s: "In Sibiria arctica ad fl. Boganida: Middendorff; in Sibiria altaica in alpebus ad fl. Tschuja: Bunge" (utra LE!).

HABITATS. Exposed, relatively dry or at least well-drained ones: stony, moss-lichen, and moss tundras; polygonal tundras; clayey, sandy, and stony outcrops; maritime and riverine sediments (habitats that are neither invaded by larger plants nor flooded); exposed dune sand. *S. nummularia*, as opposed to *S. herbacea*, *S. polaris*, and *S. turczaninowii*, is restricted to habitats, the snow is blown away from, rather than those where the snow stays longer. It is also associated with acidic bedrocks, such as silicate or granite. 123

DISTRIBUTION: The Kola Peninsula (the tundras around Lovozero, northeastern coast including Teriberka in the west); northern Kanin; Kolguyev; the Novaya Zemlya (up to the Matochkin Shar); Vaygach; Malozemelskaya and Bolshezemelskaya tundras; the Polar and Prepolar Urals; the barren heights of the Northern Urals (including mounts Isherim and Chuval in the south); the Yamal Peninsula (up to Belyy Island); the coast of the Ob Inlet and all the way east of the Ob across Arctic regions to the northern Verkhoyanskiy Range (reaching the Lower Nizhnyaya Taimyra as the northernmost location). It becomes less common and rather sparsely distributed farther east: east of the Kolyma Mouth, on Ayon Island and Cape Vankarem, and along the coast of the Gulf Kresta. It is also scattered (being not infrequent) across the barren heights of South Siberia and Mongolia: the Altai, Kuznetskiy Alatau, Western and Eastern Sayans, Khamar-Daban, Sokhondo, Kentei, Khangai, Haan Höhey, and Tannu-Ola. It is occasionally found solitary in the eastern Stanovoy Range, on the Kamchatka Peninsula (at the drainage divide between the Sedanka and Yelovka), Hokkaido (in the Daisetsu Mountains), and in the Pai T'ou Shan Mountains on the border of China and North Korea.

In the Sayans, its range is 1,700–2,700 m (Malyshev 1965); in Tuva, it ascends to 3,000 m; in the Polar Urals, to 200–700 m. (Fig. 22.)

20. ***S. retusa*** L. 1763, Sp. pl. 2 ed.: 1445; Wimmer, 1866, Salic. Eur.: 121; Camus, 1904, Saul. Eur.: 117; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 84; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 793; Pawłowski, 1946, O niekt. wierzb.: 17; id. 1956, Fl. Tatr **1**: 183; Vicioso, 1951, Salic. Españ.: 54; Nazarov et al. 1952, Fl. URSR **4**: 26; Beldie, 1952, Fl. Rom. **1**: 293; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 76; id. 1964, Fl. Eur. **1**: 46. —*S. kitaibeliana* Willd. 1806, Sp. pl. **4**, 2: 683; Görz, 1926, Magyar Bot. Lap. **25**: 196; Nazarov et al. 1952, op. cit. **4**: 27; Pawłowski, 1956, op. cit. **1**: 184; Rech. f. 1964, op. cit. **1**: 46.

T y p u s: "In alpebus Helvetiae, Austriae, Italiae".

HABIT: A depressed, usually procumbent dwarf shrub.

HABITATS: Rocks, taluses, moraines, and sodded swales on a vast variety of bedrocks (sometimes, limestone) within the alpine and subalpine zones (occasionally at lower elevations).

DISTRIBUTION: The Pyrenees (to 2,700 m), Alps (1,200–3,000 m), Apennines, Tatras (1,300–2,400 m), Eastern Carpathians (both the Ukrainian and Romanian parts), Southern Carpathians, alpine zones in the mountains of Bosnia and Herzegovina, Montenegro (Crnagora), Albania, Macedonia, western Bulgaria (the Rila Mountains). Its altitudinal range in the Balkans is 1,200–2,600 m. (Fig. 19.)

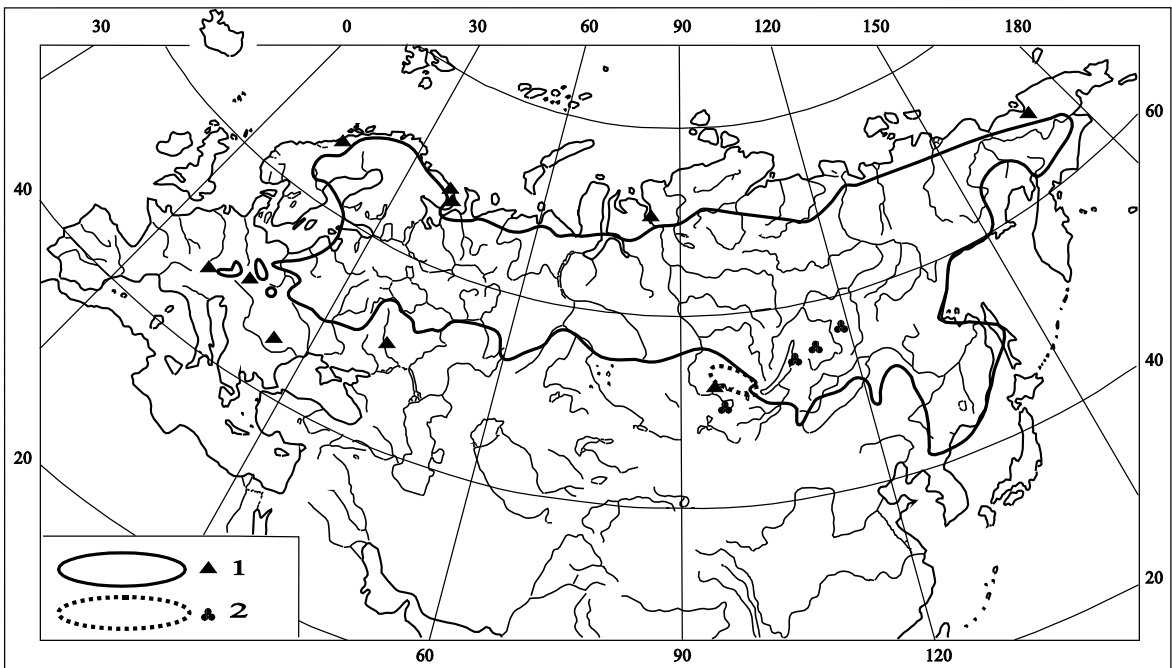


Fig. 23. Distributional areas of *Salix myrtilloides* L. (1) and *S. nasarovii* A. Skv. (2)

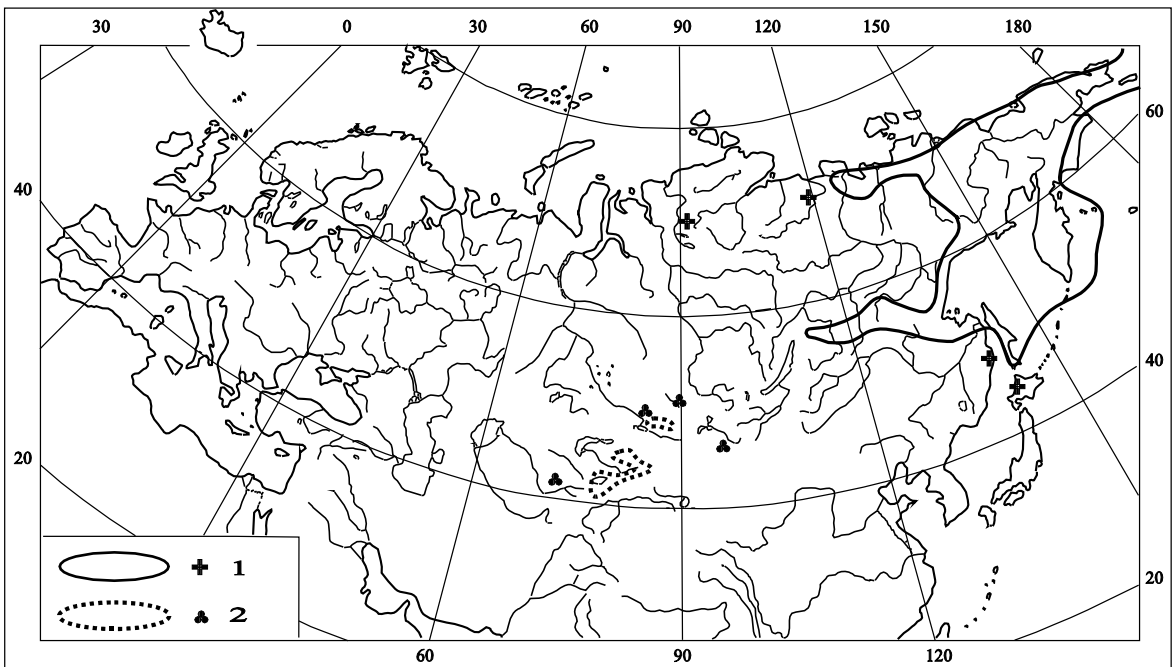


Fig. 24. Distributional areas of *Salix fuscescens* Anderss. (1) and *S. alatavica* Kar. ex Stschegl. (2)

NOTE. *S. kitaibeliana*, which is sometimes considered to be a distinct species (or subspecies), is only different in purely quantitative characteristics. These characters are also extremely obscure and inconstant, so that each author interprets them in his own way. While analyzing the material at my disposal, I could not justify the segregation of *S. kitaibeliana* either as a species or subspecies.

21. ***S. serpyllifolia*** Scop. 1772, Fl. Carn. 2: 255 et 3: tab. 61, fig. 1207; Jaccard, 1895, Catal. Valais.: 324; Buser, 1940, Ber. Schweiz. bot. Ges. 50: 742; Becherer, 1956, Fl. Valais. Suppl.: 135; Janchen, 1956, Catal. fl. Austr. 1: 102; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. 3, 1: 78; id. 1964, Fl. Eur. 1: 47. —*S. retusa* var. *serpyllifolia* Wahlenb. 1813, De veget. Helv.: 183; Wimmer, 1866, Salic. Eur.: 123; Camus, 1904, Saul. Eur. 1: 122; Fiori, 1923, Nuova fl. Ital. 1: 347; Seemen, 1909, in Aschers. et Graebn. Synopsis 4: 87. —*S. retusa* ssp. *serpyllifolia* Rouy, 1910, Fl. Fr. 12: 220; Toepffer, 1914, in Vollmann, Fl. Bayern: 193.

T y p u s: "In alibus Vochinensibus" (n. v.).

HABIT: A tiny dwarf shrub appressed to substrate, resembling *S. retusa* very much, however, more miniaturized. 124

HABITATS: Rocks, moraines, taluses, and other habitats in the subalpine and alpine zones, much alike *S. retusa*. However, it is associated with more exposed, dry spots and calcareous substrates (although occurs on slatestone and serpentinite). Unlike *S. retusa*, it avoids acidic bedrock.

DISTRIBUTION: Nearly all across the Alps from France and Bavaria to Slovenia. However, it is absent in the Jura and, presumably, Apennines. Its altitudinal range is 1,600–3,200 m. (Fig. 22.)

NOTE. I treat *S. serpyllifolia* as a distinct species, primarily following R. Buser, who repeatedly observed this species along with *S. retusa* in nature and resolutely favored its distinctness. The material that I managed to study enabled me to distinguish *S. retusa* from *S. serpyllifolia* (unlike the case of *S. retusa* and *S. kitaibeliana*).

Sect. 9. *Myrtilloides*

Koehne, 1893, Dendr.: 89, 102.

T y p u s: *S. myrtilloides* L.

Low shrubs with ascending, rooting stems. Floriferous buds similar to vegetative ones. Either *arctica*- or transitional to *alba*-type of bud size gradation along shoots. Leaves on short, channeled petioles, small, relatively broad, subentire. Catkins terminating foliated shoots; however, floriferous shoots less foliated and much shorter than vegetative ones. Bracts small, obtuse. In both sexes, nectaries mostly one in each flower. Stamen filaments short, glabrous. Capsules on long stipes, narrowly lanceolate. Styles very short, stigmas short, two-lobed.

This is a group of boreal and subarctic distribution consisting of 4 or 5 species (2 or 3 of them North American).

Key to Species

1. Leaves mostly obovate, dark green, lustrous above, usually with few denticles on lower half of leaf blade margin. Bracts blackish 23. ***S. fuscescens***

— Leaves mostly broadly elliptic, completely entire, light green, dull above. Bracts pale
 22. **S. myrtilloides**

22. **S. myrtilloides** L. 1753, Sp. pl.: 1019; Ledeb. 1850, Fl. Ross. **3**, 2: 613; Wimmer, 1866, Salic. Eur.: 112; Anderss. 1867, Monogr. Salic.: 95; Wolf, 1930, Fl. Yu.-V. **4**: 58; Krylov, 1930, Fl. Zap. Sib. **4**: 759; Nakai, 1930, Fl. sylv. Kor. **18**: 154; Floderus, 1931, Salic. Fennosc.: 93; Perfilyev, 1936, Fl. Sev. kr. **2-3**: 36; Nazarov, 1936, Fl. SSSR **5**: 112; id. 1937, Fl. Zabayk. **3**: 197; Nazarov et al. 1952, Fl. URSS **4**: 51; Shlyakov, 1956, Fl. Murm. **3**: 99; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 104; id. 1964, Fl. Eur. **1**: 51; Popov, 1959, Fl. Sredn. Sib. **2**: 804. —*S. elegans* Besser, 1822, Enum. Volhyn.: 77. —*S. lenensis* Flod. 1936, Sv. bot. tidskr. **3**: 393.

T y p u s: "In Suecia septentrionali. Fl. Lapp. N 357 et tab. 8 fig. J, K; Fl. Suec. N 804".

HABIT: A low shrub (20–150 cm) with rooting stems.

HABITATS: Mesotrophic wetlands, graminoid and shrub-dominated transitional zones at edges of *Sphagnum* bogs with *Carex* and *Calamagrostis*, damp meadows, *yernik*'s, damp and paludal pine and larch forests. Occasionally, it invades *Sphagnum* bogs and alpine tundras.

DISTRIBUTION: Northern Scandinavia (except ocean-facing slopes) and the Kola Peninsula (excluding its northern maritime part). Extending east to the Lower Anadyr, the area primarily matches the belt of forest-tundra. Its easternmost parts include the Penzhina Basin, Sea of Okhotsk and Sea of Japan coasts, and northeasternmost Korea Peninsula. The species is missing from Kamchatka and Pacific islands, except central Sakhalin (where it is found in the Upper Poronay Basin). The southern border of the species area embraces forested regions of the northern Northeast China, Transbaykalia (except the vicinity of Borzya), and the Kentei Range. West of Lake Baykal, the southern border crosses the foothills of the Eastern Sayans and, leaving some isolated localities in Tuva, reaches Kansk, Tomsk, and Kurgan. Then it goes round the Urals abruptly ascending to the Kama River, again descending from Ulyanovsk to Tambov, once more ascending when going round the northern Central Russian Upland, and leaving an isolated location in the Don Valley, near the Donskoye Belogorye Highlands, far beyond the area limits. Then the border runs via Kursk, Priluki, and Kiev, and, matching a parallel, reaches Poland. The western border of the continuous species range crosses the southeastern and northeastern Poland and the Baltic States (in a distance from the sea coast). There are also some small disjunct area parts in the mountains of southern Bavaria, the Sudetes, Tatras, and southern Carpathians.

In the Tatras, the species ascends as high as 900 m; in the Northern Urals, to 800 m; in the Polar Urals (the Sob River Basin), to 300 m; on the Stanovoye High Plateau, to 1,100 m, in Liaoning Province of China, to 900 m. (Fig. 23.)

23. **S. fuscescens** Anderss. 1867, Monogr. Salic.: 97; id. 1868, in DC. Prodr. **16**, 2: 230; Coville, 1901, Proc. Wash. Acad. **3**: 329; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 153; id. 1921, J. Arn. Arb. **2**: 83 et 199; Floderus, 1926, Ark. bot. **20A**, 6: 44; Hultén, 1928, Fl. Kamtch. **2**: 11; Komarov, 1929, Fl. Kamch. **2**: 13; Nazarov, 1936, Fl. SSSR **5**: 113. —*S. rhamnifolia* (non Pall. 1788) Hook. et Arnott, 1841, Bot. Beechey voy.: 117 et tab. 26. —*S. paludicola* Koidz. 1919, Bot. Mag. Tokyo **33**: 219; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 425; Ohwi, 1965, Fl. Jap.: 366. —*S. hebecarpa* Fern. 1924, Rhodora **26**: 123; Hultén, 1943, Fl. Al. **3**: 520. —*S. arbutifolia* auct. non Pall. 1788: Floderus, 1933, Ark. bot. **25A**, 10: 8; Kimura, 1934, op. cit. **4**:

423; Hultén, 1943, op. cit. **3**: 545; Kimura, 1952, Symb. Iteol. **19**: 196; Raup, 1959, Contrib. Gray Herb. **185**: 81. —? *S. poronaica* Kimura, 1934, op. cit. **4**: 426; Sugawara, 1936, Ill. Fl. Saghal. **2**: 677; Tolmachev, 1956, Der. i kustarn. Sakhal.: 68.

T y p u s: "Kamtschatka —captain Beechey". —K? —Cf. tab. 26 in Hooker and Arnott 1841.

Since the species name *S. fuscescens* Anderss. was proposed as nomen novum instead of *S. rhamnifolia* Hook. et Arnott, non Pall. and Beechey's sample was always first to be referred to by N. Andersson, apparently, it is to be considered as the holotype, and the rest of the cited samples (Alaska —Kastalski; the series from Uds koy District —Middendorff) are to be treated as paratypes.

HABIT: A low shrub (usually 8–30 cm tall, occasionally, on Sakhalin and at the Lower Amur, up to 80–100 cm) distinguished by obliquely ascending, rooting stems.

HABITATS: Wetlands, paludal meadows and tundras, occasionally (within maritime coastal zones) on dryer substrates, particularly, sand.

DISTRIBUTION. The species is very common on northern Sakhalin, the coast of the Sea of Okhotsk, Kamchatka, and in the Northeast from the Lower Lena and Indigirka to the Chukchi Peninsula, as well as on the islands and archipelagoes of Ratmanov, Commander, Shumshu, and Paramushir. The species is much more rare south and west of these regions, and its area becomes discontinuous there: some solitary locations are known in Maritime Province (the Botchi River) and on Hokkaido; it is scattered in the Stanovoy Range and on the Stanovoye High Plateau nearly reaching Lake Baykal. It was also found in the Putoran Mountains on the Taimyr Peninsula (the Chopko River). A sample was found among collections made by B. Gorodkov in Gydanskaya Tundra. However, the label was obscure. I. Koropachinskiy and A. Skvortsova (1966: 78) recorded the species in Tuva, which was apparently a mistake.

It is known to ascend to 1,600 m in the Stanovoy Range; to 2,100 m in the Kodar Range (the Stanovoye High Plateau); to 550 m in the Verkhoyanskiy Range at latitude 69° N. (Fig. 24.) It is also distributed in American continental Arctic, at least as far east as Hudson Bay.

NOTE. Hybrids with *S. udensis* are common on the Kamchatka and particularly Sakhalin. One of them was named *S. kudoii* Kimura 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 441 (see also Sugawara 1939: 687 et tab. 323). According to E. Hultén (1928: 12), *S. macilenta* Anderss. 1867, Monogr. Salic.: 141 is nothing but a hybrid of the same kind. Yet E. Hultén's opinion hardly seems to be true if one considers the illustration in N. Andersson's monograph. Although *S. macilenta* Anderss. was mentioned by M. Nazarov in the "Flora of the USSR" (1936: 83), the species remains obscure and puzzling. I had no chance to see its type ("Redovski Land"—Chamisso), which was preserved in the Berlin-Dahlem Herbarium.

On the northern coast of the Sea of Okhotsk, Sakhalin, and at the Lower Amur there occur unusually huge specimens with large leaves. These were the plants named *S. poronaica* by A. Kimura, according to his own description (Kimura 1934: 426) as well as the illustration in S. Sugawara's "Flora of Saghalin" (1936: pl. 315). Under this name, A. Kimura could also partially imply hybrids of *S. fuscescens* × *S. udensis* mentioned here above. These hybrids are considerably larger than *S. fuscescens* and quite common around Poronaysk. In any case, the available material does not provide enough grounds to recognize one more distinct species related to *S. fuscescens* existing on Sakhalin.

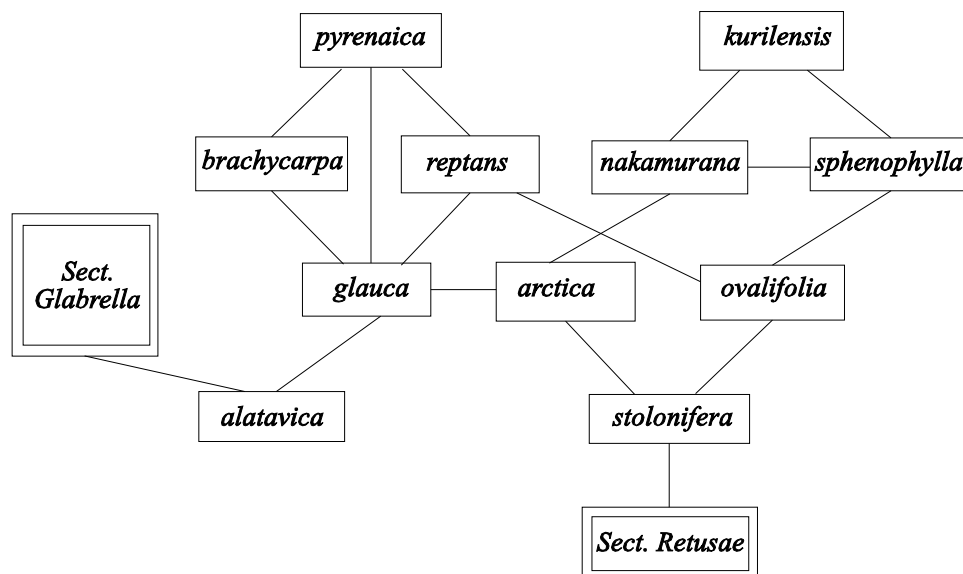
Sect. 10. *Glaucæ*

Pax, 1889, in Engl. et Prantl, Natürl. Pflanzenfam. 3, 1: 37 (p. p.).

T y p u s: *Salix glauca* L.

Low or depressed (occasionally moderate-sized) shrubs. Floriferous and vegetative buds look alike, ovoid or broadly elliptic. *Arctica*-type of bud size gradation along shoots. Leaves of variable shape, but mostly rather broad, entire or obscurely dentate, exstipulate or with lanceolate subequilateral stipules, their petioles channeled. Catkins borne on foliated stalks, rather large. Bracts pale to black. Nectaries one or two (sometimes more) in male flowers, mostly one in female ones. Adaxial nectary usually large, (1 mm long or more), frequently lobed. Capsules on short stipes, mostly large; styles distinct, often cleft; stigmas two-lobed or linear, two-parted.

At the first glance, the section, the way it is presented here, might appear rather heterogeneous. In fact, it is very difficult to admit close filiation of, say, *S. glauca* and *S. kurilensis*, as these species are very different both in their vegetative and floriferous parts. However, if one considers the section on the whole, then connections between all of its members become so obvious that it is even difficult to delimit subsections. The relations of the taxa within the section *Glaucæ* might be approximately outlined as follows.



Probable evolutionary relations within and around the section *Glaucæ*

The most natural approach to the division of the section could be the segregation of the species with pubescent capsules and cleft styles (*S. alatafica*, *S. glauca*, *S. reptans*, *S. arctica*, plus the West European *S. pyrenaica*) versus the species with mostly glabrous (or only partially pubescent) capsules and elongated, usually not cleft styles (these are *S. kurilensis*, *S. sphenophylla*, *S. nakamurana*, *S. ovalifolia*). These groups could be treated as subsections. One must say, this division is not absolute, since both *S. ovalifolia* and *S. nakamurana* greatly resemble *S. arctica* in their vegetative organs; *S. ovalifolia* is also close to *S. reptans* in the structure of its nectaries.

Some features of *S. alata* resemble those of *Glabrella* members: leaf and bud morphology, bract and capsule characters (bracts are large, scarious, truncate; capsules large, acute). It is quite possible that the sections *Glaucæ* and *Glabrella* are of close filiation. On the other hand, one can trace connection with the section *Retusæ* via *S. arctica*, *S. ovalifolia*, and particularly the Alaskan species *S. stolonifera* Coville. 129

Key to Species

1. Shrubs distributed mostly in subalpine and subarctic regions. Branches upright (except most unfavorable conditions). Stamen filaments pubescent 2
 - Shrubs of woodless tundras, rocks, and the alpine zone, their stems procumbent or ascending. Stamen filaments glabrous 3
2. Leaves dentate, lustrous above when alive. Bracts blackish-brown 24. **S. alata**
 - Leaves entire or with solitary glands along margins, dull or glittering when alive. Bracts pale or light brown (although there are some exceptions, such as the populations on Wrangel Island) 25. **S. glauca**
3. Stems procumbent, but almost never rooting. Leaves not large (10–30 mm), round to broadly elliptic, mostly cordate at base, exstipulate, their petioles 3–7 mm long, reticulation slightly prominent beneath. Catkins mostly short, globular or broadly elliptic. Capsules glabrous or with scattered pubescence 29. **S. ovalifolia**
 - Stems promptly rooting when procumbent. Leaves not as above. Catkins cylindrical 4
4. Branches ascending and rooting. Leaves (ob)ovate or (ob)lanceolate, mostly acutish or pointleted, light green or grayish-green, more or less pubescent, their petioles 2–5 mm long. Capsules pubescent. Styles cleft at least up to half of their length 5
 - Leaves mostly obtuse or rounded, mature ones mostly glabrous, their petioles longer than 5 mm. Styles not cleft or cleft on less than half of their length 6
5. Leaves mostly stipulate. Bracts black. Adaxial nectary usually deeply lobed. Mature capsules 7–9 mm long 26. **S. reptans**
 - Leaves exstipulate. Bracts pale. Adaxial nectary entire or shallowly lobed. Mature capsules 4–6 mm long 27. **S. pyrenaica**
6. Bracts mostly purple-brown. Ovaries acute, glabrous or pubescent in their upper parts. Styles mostly not cleft 7
 - Bracts black. Ovaries obtusish, entirely pubescent. Styles usually cleft 28. **S. arctica**
7. Petioles 10–40 mm long. Leaves broadly elliptic to reniform, mostly cordate at base; veins considerably curved; reticulation distinctly prominent beneath. Floriferous shoots short: their length (measured to catkin base) equal or less than leaf breadth on same plant 31. **S. kurilensis**
 - Petioles mostly not longer than 15 mm. Leaves cuneate at base. Floriferous shoots (measured to catkin base) longer than leaf breadth 8
8. Leaves light-colored, yellowish-green, dull above; reticulation distinctly prominent beneath mature ones. Bracts mostly equal or slightly longer than capsule stipes. Styles 0.3–1.0 mm long. Stigmas 0.2–0.3 mm long, with two short lobes 130

- 30. **S. sphenophylla**
 — Leaves dark green above, more or less lustrous. Reticulation not distinctly prominent beneath (leaves resemble those of *S. arctica*). Bracts much longer than capsule stipes. Styles 1–2 mm long. Stigmas 0.4–0.5 mm long, two-parted, their parts linear
 32. **S. nakamura**

24. **S. alata** Kar. ex Stschegl. 1854, Bull. Soc. Natur. Moscou **21**, 1: 197; Nazarov, 1936, Fl. SSSR **5**: 60; Skvortsov, 1962, Bot. mat. Gerb. in-ta bot. AN UzbSSR **17**: 63; Polyakov, 1960, Fl. Kazakhst. **3**: 35. —*S. spissa* Anderss. 1868, in DC. Prodr. **16**, 2: 283. —*S. karelinii* Wimm. ex Seemen, 1895, Bot. Jahrb. Beibl. **52**: 10. —Non *S. karelinii* Turcz. 1854. —*S. seemenii* B. Fedtsch. 1915, Rastit. Turkest.: 298.

T y p u s: "In lapidosis alpinum Alatau, Karelin et Kirilow a. 1842" (MW!, LE! et alibi).

HABIT: A low or medium-sized shrub (0.4–1.5 m tall) with short, stout branches.

HABITATS: Taluses, moraines, and moist slopes within the subalpine and partially alpine zones.

DISTRIBUTION: The Western Sayans (however, reliable data is available only from the Shapshalskiy Range, where it grows at 2,300–2,600 m), the western and southwestern Altai, western Mongolia (there is an isolated location in the Tayshir Ola Range within the larch forest zone). It is more common in the Tien Shan at 2,500–3,500 m (the Dzungarskiy Alatau, Borokhoro, Iren-Khabyrga, Zailiyskiy, and Ketmen ranges as well as those south of the Lake Issyk-Kul including the Atbashi Range in the west). There is an isolated location in the Talasskiy Alatau near Karabura Pass. (Fig. 24.)

25. **S. glauca** L. 1753, Sp. pl.: 1019; Ledeb. 1850, Fl. Ross. **3**, 2: 618; Wimmer, 1866, Salic. Eur.: 91; Krylov, 1930, Fl. Zap. Sib. **4**: 768; Floderus, 1931, Salic. Fennosc.: 37; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 41; Nazarov, 1936, Fl. SSSR **5**: 58; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 735; Raup, 1943, Sargentia **4**: 102; id. 1959, Contrib. Gray Herb. **185**: 54; Shlyakov, 1956, Fl. Murm. **3**: 75; Popov, 1959, Fl. Sredn. Sib. **2**: 805; Polyakov, 1960, Fl. Kazakhst. **3**: 35; Rech. f. 1964, Fl. Eur. **1**: 47; Argus, 1965, Contrib. Gray Herb. **196**: 1 et seq. —*S. pseudolapponum* Seemen, 1900, Bot. Jahrb. Beibl. **65**: 28. —*S. seemannii* Rydb. 1901, Bull. N. Y. Bot. Garden **2**: 164; Floderus, 1933, Ark. bot. **25A**, 10: 5; Nazarov, 1936, op. cit. **5**: 59. —*S. sericeo-cinerea* Nakai, 1919, Bot. Mag. Tokyo **33**: 43; id. 1930, Fl. sylv. Kor. **18**: 136; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 153. —*S. stipulifera* Flod. 1930, Bot. not.: 328; id. 1931, op. cit.: 35; Perfilyev, 1936, op. cit. **2–3**: 41; Nazarov, 1936, op. cit. **5**: 59; Shlyakov, 1956, op. cit. **3**: 72; Rech. f. 1964, op. cit. **1**: 47. —*S. glaucosericea* Flod. 1943, Sv. bot. tidskr. **37**: 169; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 83; id. 1964, op. cit. **1**: 47.

T y p u s: "In alpebus lapponicis. Fl. Lapp. N 363 et tab. 7 fig. 5, tab. 8, fig. P; Fl. Suec. N 802".

HABIT: A quite tall (up to 2–2.5 m) to nearly procumbent shrub, depending upon environmental conditions.

HABITATS are greatly variable: depressions, lowlands, river valleys, wetlands, bog edges; tundras of various types from paludal to rather dry; stone-fields, rocks, various outcrops, glacial moraines; banks of mountain and tundra streams, bypasses and channels with sluggish water flow. Usually, it avoids freshly deposited alluvia of large rivers. Although this species can survive on a vast variety of different bedrocks, it is mostly associated with acidic substrate staying away from carbonate. Usually, it forms extensive shrublands.

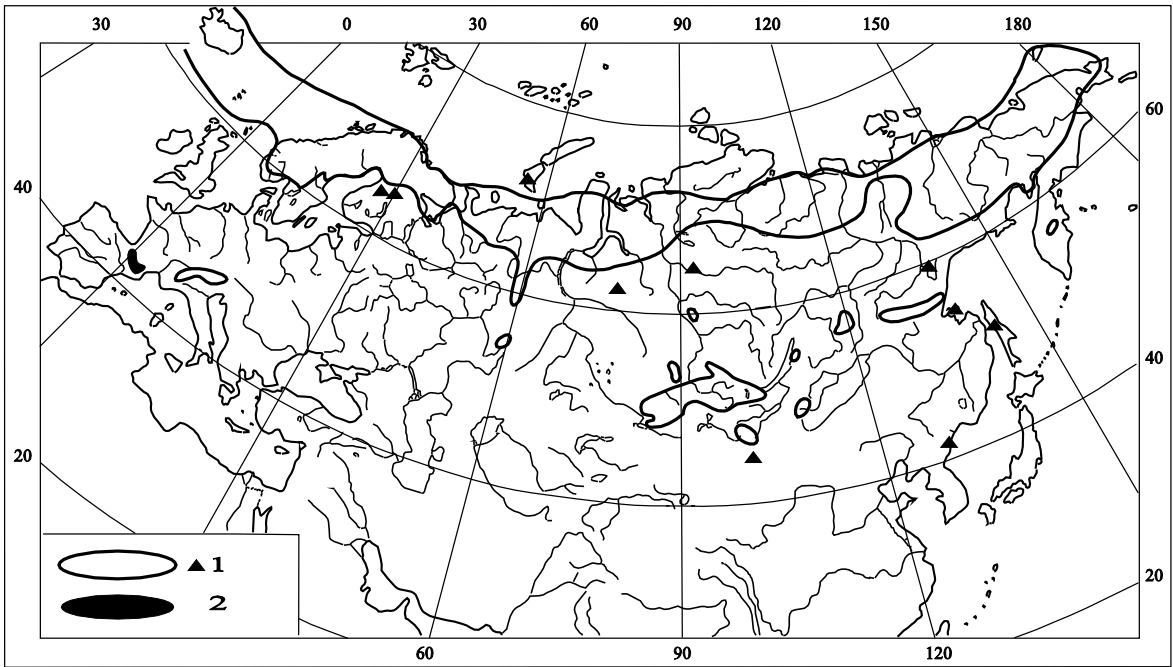


Fig. 25. Distributional areas of *Salix glauca* L. (1) and *S. pyrenaica* Gouan (2)

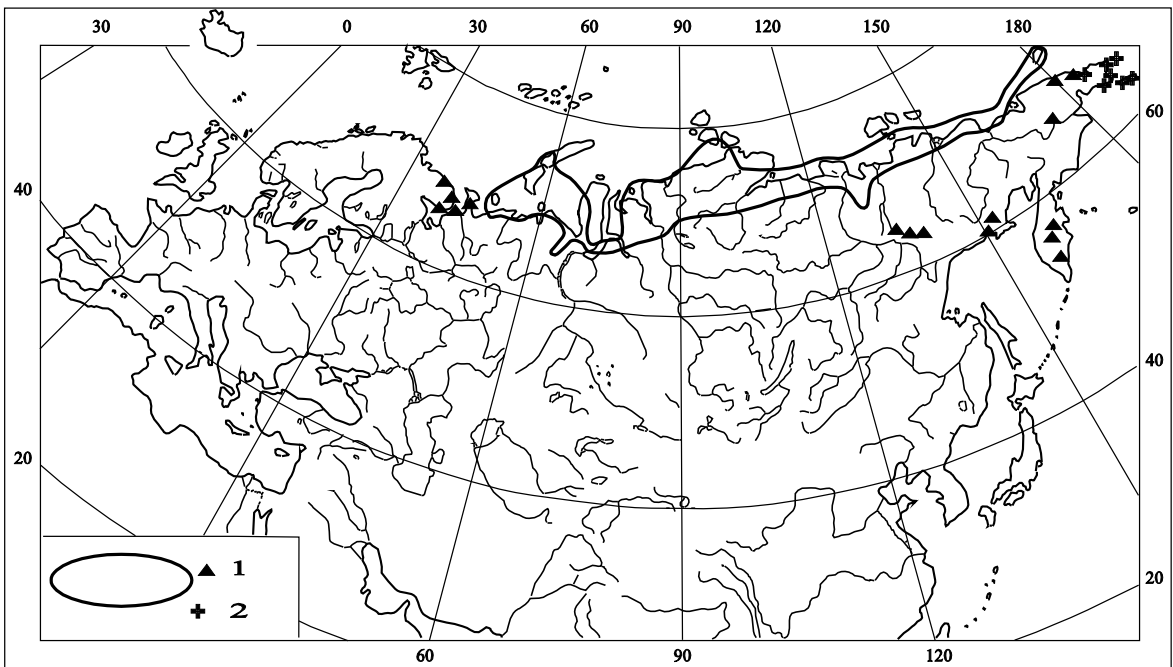


Fig. 26. Distributional areas of *Salix reptans* Rupr. (1) and *S. ovalifolia* Trautv. (2)

DISTRIBUTION: Iceland; major part of the Scandinavian Peninsula; northern Finland, the Kola Peninsula, and northern Karelia; the northernmost part of the forest belt, forest-tundra and southernmost tundra in European as well as Asiatic Russia. In the north, it reaches Southern Island of the Novaya Zemlya (occasionally, it is found there on the southwestern coast). It is encountered at latitude 62–63° N on the Yamal Peninsula and around the Yenisei Bay; on the Taimyr Peninsula in the Pyasina Basin, it reaches Tarea; east of the Khatanga River, it gets to the ocean coast almost everywhere, growing also on Ayon and Wrangel islands. It is scattered across the entire territory of the Northeast starting from the Verkhoyanskiy Range (except the coast of the Sea of Okhotsk). South of the area described above, it is encountered only in the mountains: the Alps, Urals (where it reaches Kytlym as the southernmost point and also occurs on many peaks in the Southern Urals), the Yeniseiskiy Kryazh, Kuznetskiy Alatau, Altai, Western and Eastern Sayans, Khangai, Kentei, Sokhondo, other barren heights of Transbaykalia, the Barguzinskiy Range, and Stanovoye High Plateau. There are some scattered locations in North Korea, on Sakhalin (Mount Lopatina), on the coast of the Sea of Okhotsk (Bolshoy Shantar Island and the vicinity of Ayan), and on the Kamchatka Peninsula (the Kamchatka River Basin).

Its elevation range in the Alps is 1,800–2,400 m; in the Southern Urals, 900–1,500 m; in the Northern Urals, 700–1,300 m, in the Altai and Eastern Sayans, 1,600–2,200 m; in Tuva, it ascends to 2,500 m and, according to I. Koropachinskiy and A. Skvortsova (1966), even to 3,000 m. (Fig. 25.)

NOTE. This is a rather polymorphic, manifold species. In every part of its area, one can easily find a vast diversity of forms. It was that high variability which caused many attempts to describe superfluous new species. However, the variability also made it impossible to distinguish those "species". Within the flora of this country, it is reasonable to distinguish the only one race growing on the barren heights of South Siberia from the Altai to Stanovoye High Plateau. These plants are generally characterized by relatively short, less pubescent leaves and short catkins borne on short stalks. Probably, it would make sense to treat those South Siberian populations as a subspecies. The plants from the Alps are not divergent that much, so that it does not appear reasonable to segregate them as a distinct species, as some of the European authors did. Particularly in North America many "species" were segregated within *S. glauca*. However, a thorough monographic study (Argus 1965) clearly demonstrated that there were not enough reasons for such division.

26. ***S. reptans*** Rupr. 1845, Fl. samojed. cisur.: 54; Ledeb. 1850, Fl. Ross. **3**, 2: 619; Lundström, 1877, Weiden Now. Sem.: 39; Lakschewitz, 1914, Spisok rast. Gerb. russk. fl. **8**, 50: N 2492; Floderus, 1926, Ark. bot. **20A**, 6: 31; Krylov, 1930, Fl. Zap. Sib. **4**: 775; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 36; Nazarov, 1936, Fl. SSSR **5**: 60; Shlyakov, 1956, Fl. Murm. **3**: 71. —*S. eriocalos* Lundström, 1888, K. sv. vet. handl. **22**, 10: 204; Grapengiesser, 1942, Sv. bot. tidskr. **36**: 161.

T y p u s: "In parte orientale ins. Kolgужew non longe ab ost. fl. Pestschanka, 8. VIII 1841, F. Ruprecht " (LE!).

HABIT: A low (10–40 cm), petite shrub with ascending, rooting, slender stems.

HABITATS: Damp and paludal tundras, particularly, those located on coastal plains and at lower reaches of rivers as well as maritime coastal meadows, maritime and riverine sand and pebbles (as long as they are not occupied by larger willows); occasionally, *layda*'s; graminoid and graminoid-moss tundras with *Carex* spp.; tussocky, hillocky, and spotty tundras. In the mountains, it is much more rare, found only in some few regions.

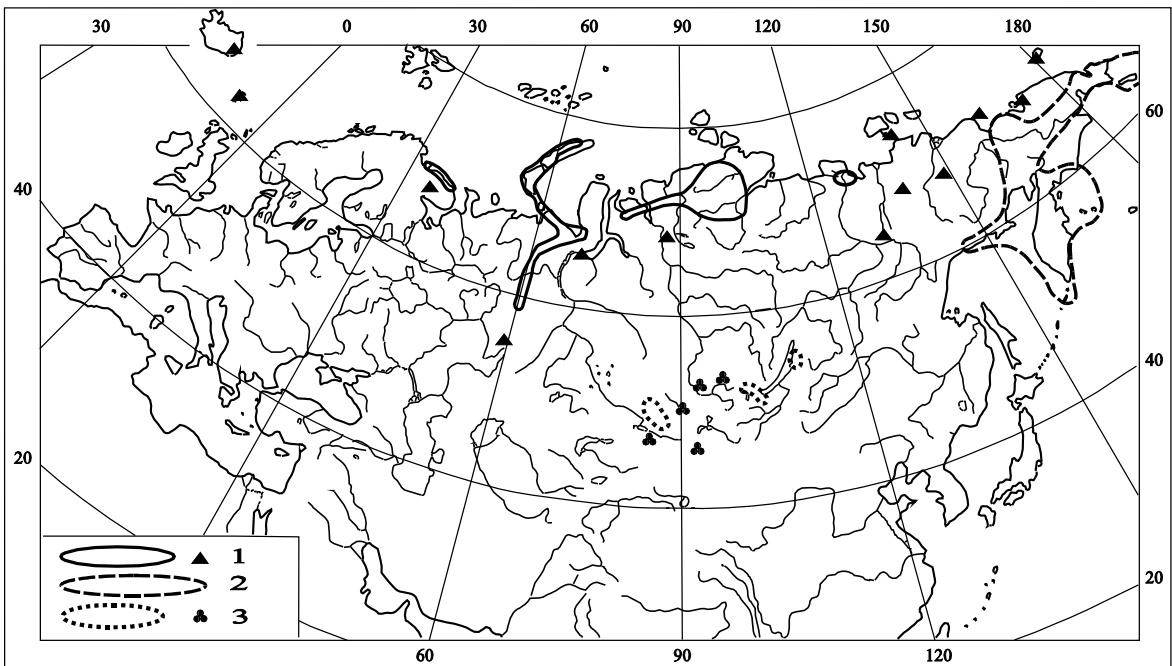


Fig. 27. Distributional areas of *Salix arctica* Pall. ssp. *arctica* (1), ssp. *crassijulis* (Trautv.) A. Skv. (2), and ssp. *torulosa* (Trautv.) A. Skv. (3)

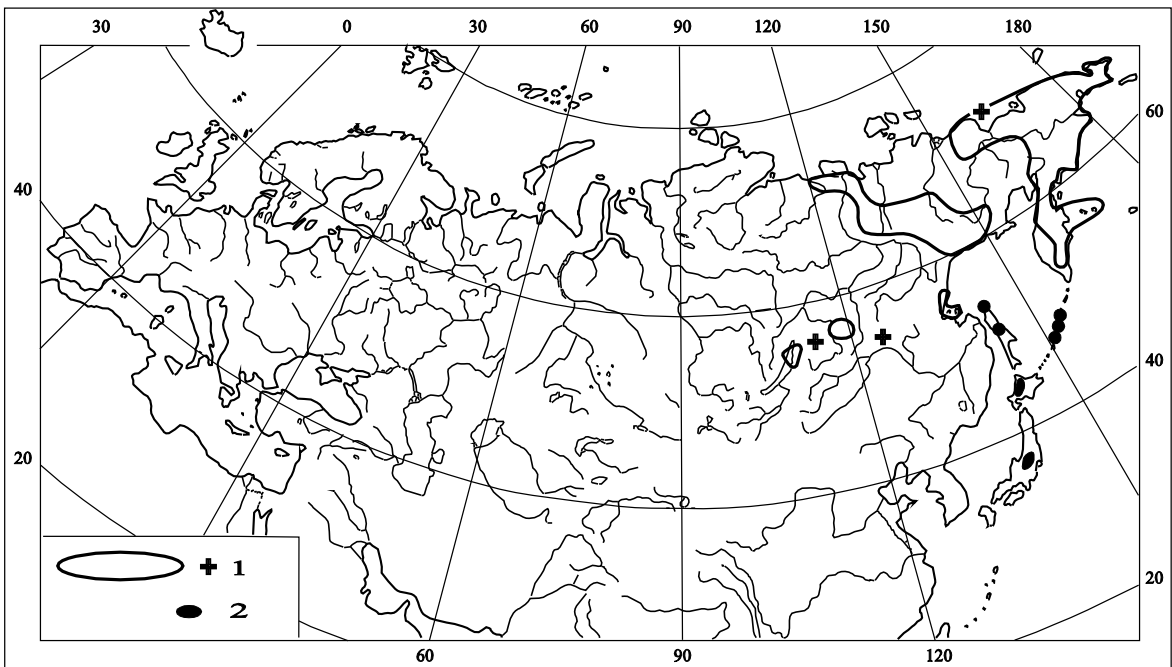


Fig. 28. Distributional areas of *Salix sphenophylla* A. Skv. (1) and *S. nakamurana* Koidz. (2)

DISTRIBUTION: The maritime zone on the Kola Peninsula (near Rynda, Ponoï, Tetrino, and on Kharlov Island, very rarely); the maritime zone between the Beloye (White) Sea Mouth (the Mayda River Mouth) and the Kara Inlet (rather sparsely); the islands Kolguyev, Vaygach, and Novaya Zemlya Archipelago including the southern part of its Northern Island (much more often); the Polar Urals, Yamal Peninsula, coast of the Ob and Taz Inlet, and Gydanskaya Tundra; the Lower Yenisei (very commonly); the Taimyr Peninsula and Severnaya Zemlya Archipelago (Bolshevik and October Revolution islands); the territory between the Khatanga River and Kolyma River Mouth including Bolshoy Lyakhovskiy Island in the north. East of that territory, it becomes sparse, however, it is known as far as Cape Vankarem, fairly common on Wrangel Island, found in many locations across the Verkhoyanskiy Range (Sakkyryrskiy District in the north, the Tompo and Bryangada basins in the south). There are also some isolated locations in the Northeast: around Magadan and Ust-Belaya on the Anadyr River and on the Kamchatkan *sopka*'s (Shiveluch, Klyuchevskaya, and Avachinskaya volcanoes).

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In the Polar Urals, it ascends as high as 600–700 m; on Klyuchevskaya Sopka, it is found at the elevation of 1,000 m; on Shiveluch, presumably, even at 2,600–2,700 m (according to a herbarium label by K. Stepanova, a collector). (Fig. 26.)

27. **S. pyrenaica** Gouan, 1773, Illustr.: 77; Wimmer, 1866, Salic. Eur.: 94; Bubani, 1897, Fl. Pyren. **1**: 61; Camus, 1904, Saul. Eur. **1**: 135; Rouy, 1910, Fl. Fr. **12**: 217; Görz, 1929, Saul. Catal.: 24; Cadevall, Font, 1933, Fl. Catal. **5**: 179; Vicioso, 1951, Salic. Españ.: 62.

T y p u s: "In Pyrenaeis ad juga montis Laurenti atque vallis Eynes, locis nivalibus" (n. v.).

HABIT: A depressed dwarf shrub with procumbent or ascending branches.

HABITATS: Moist and peaty meadows and pastures within the subalpine and alpine zones, at elevations (1,200–)1,400–2,500 m.

DISTRIBUTION: The Spanish part of the Pyrenees (Huesca, Lérida, and Gerona provinces), the French Pyrenees (nearly everywhere); the Corbières Range. The species is fairly common within its distributional area. (Fig. 25.)

NOTE. This is a Pyrenean endemic, quite distinct in its morphology. The closest to *S. pyrenaica* is Eurasian *S. reptans*; the closest American species is *S. brachycarpa* Nutt.

28. **S. arctica** Pall. 1788, Fl. Ross. **1**, 2: 86; Ledeb. 1834, Icon. **5**: 18 et tab. 460; id. 1850, Fl. Ross. **3**, 2: 619 (partim); Komarov, 1920, Fl. Kamch. **2**: 24; Krylov, 1930, Fl. Zap. Sib. **4**: 770 (p. p.: excl. var. *taimyrensis*); Nazarov, 1936, Fl. SSSR **5**: 44; Hultén, 1943, Fl. Al. **3**: 513; Raup, 1943, Sargentia **4**: 98; id. 1959, Contrib. Gray Herb. **185**: 47; Shlyakov, 1956, Fl. Murm. **3**: 67. —*S. diplodictya* Trautv. 1832, Salic. Frigid.: 307. —*S. crassijulis* Trautv. 1832, op. cit.: 308; Hultén, 1943, op. cit. **3**: 515. —*S. torulosa* Trautv. 1832, op. cit.: 309; Polyakov, 1960, Fl. Kazakhst. **3**: 36; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 13. —*S. pallasii* Anderss. 1868, in DC. Prodr. **16**, 2: 285; Nazarov, 1936, op. cit. **5**: 45. —*S. altaica* Lundström, 1877, Weiden Now. Sem.: 36; Nazarov, 1937, Fl. Zabayk. **2**: 212; Popov, 1959, Fl. Sredn. Sib. **2**: 807. —*S. brownei* Lundström, 1877, op. cit.: 37. —*S. ehlei* Flod. 1936, Sv. bot. tidskr. **30**: 386 et fig. 1. —*S. arctica* R. Br. 1823, Chloris Melvilleana: 24; id. 1823, ex Richardson, Franklin J.: 752; Trautv. 1832, op. cit.: 293. —*S. anglorum* Cham. 1831, Linnaea **6**: 541 (nom. nov. pro *S. arctica* R. Br. non Pall.). —*S. brownii* Bebb 1889, Bot. Gaz. **14**: 115.

T y p u s: "In plaga arctica secundum sinum Obensem et versus glaciale Oceanum legit Sujef" (n. v.). There are no samples of *S. arctica* from P. Pallas' collection in the

St. Petersburg Herbarium. Presumably, they are preserved in the British Museum or Berlin-Dahlem.

Ssp. **crassijulis** (Trautv.) A. Skv. comb. nova. —*S. crassijulis* Trautv. 1832, Salic. Frigid.: 308. —*S. pallasii* Anderss. 1868, in DC. Prodr. **16**, 2: 285. —*S. arctica* "sensu stricto" Rydb. 1899, Bull. N. Y. Bot. Gard. **1**: 265. —*S. arctica* × *glauca* et *S. arctica* × *cuneata* × *glauca* Flod. 1926, Ark. bot. **20A**, 6: 23, 26.

T y p u s: "Ad sinum St. Laurentii. Chamisso et Eschscholtz" (LE!).

Different from ssp. *arctica* in its vigorous growing habit, mostly ascending (not procumbent) branches, large leaves with distinct reticulation beneath, and densely pubescent catkins. Its young leaves are usually clothed with long sericeous trichomes.

Ssp. **torulosa** (Trautv.) A. Skv. comb. nova. —*S. torulosa* Trautv. 1832, Salic. Frigid.: 309. —*S. altaica* Lundström, 1877, Weiden Now. Sem.: 36.

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T y p u s: "Altai. Ledebour" (LE!).

Different from ssp. *arctica* in its mostly elongated, light-colored (yellowish-green) leaves and often in its reddish pigmentation of petioles and catkin stalks.

HABITATS: Well-drained graminoid or herb-dominated meadowy tundras; sometimes also moss and stony polygonal tundras; sodding clayey, sandy, and stony outcrops and deposits. On Kamchatka, it also descends to the forest zone, where it occurs in cold depressions and at wetland edges.

In the Southern Urals, it grows at about 1,500 m; in the Northern Urals, within 900–1,500 m; in the Polar Urals, it ascends only to 700–800 m; in the Sayans and Tuva, it is found at 1,800–2,600 m; in the Saur, at 2,150–2,400 m; on Kamchatka, from nearly the sea level to 1,700 m; in the Lower Lena Basin (the Kharaulakh Range), to 600–700 m.

DISTRIBUTION: Iceland (Mjoifjörður, very rare), the Faroe Islands (Kunø Island, very rare), the Kola Peninsula (the Khibins and northern coast, scattered), Yugorskiy Peninsula, Vaygach, and the Novaya Zemlya (to the Russian Harbor, common); the Polar Urals (very common), Prepolar Urals (rather infrequent), Northern Urals, (sporadically distributed), Southern Urals (only on Mount Iremel). East of the Urals, it is scattered across tundras. On the Taimyr Peninsula, it again becomes common, going north to the mouth of the Nizhnyaya Taimyra. So far it has not been found between the Khatanga and Lena; however, it is occasionally encountered at the Lower Lena and around Tiksi. It is found on Bolshoy Lyakhovskiy Island. East of the line connecting Okhotsk and the Kolyma Mouth, it again becomes considerably more common, particularly, on the Kamchatka Peninsula. The location on Wrangel Island is doubtful.

Ssp. *crassijulis*: Paramushir, the Commander Islands, Kamchatka, the Chukchi Peninsula, and Anadyr River Basin.

Ssp. *torulosa*: The barren heights of South Siberia (the Barguzinskiy Range, Eastern and Western Sayans, Altai, Tarbagatay). (Fig. 27.)

The species is widespread in North American Arctic: ssp. *crassijulis*, in Alaska and western Canada; plants from eastern Canadian Arctic and Greenland, presumably, are to be segregated in yet another subspecies.

NOTE. The species has an enormous range of individual variability, much alike *S. glauca*. N. Andersson (1868) brought about much confusion in the understanding of the species, since he included a whole series of completely alien components into *S. arctica*. These were actually some races from the *glauca*-cycle (*S. cordifolia* Pursh, *S. callicarpaea* Trautv.) and even some species from remote sections, like *S. saxatilis* Turcz., *S. divaricata* Pall., and *S. taimyrensis* Trautv. Some remnants of this confusion can be still found in the

literature. For example, in the "Flora of the USSR" and "Flora Europaea", *S. taimyrensis* = *S. pulchra* is still considered to be closely related to *S. arctica*. Still more complications emerged due to the fact that the species was described twice under the same name, however, absolutely independently: from Siberia by P. Pallas and from North America by R. Brown. The relation of these two "*S. arctica*" remained obscure for a long time. On our list, all the synonyms ascending to R. Brown's specimens are segregated at the end for the sake of the reader's better orientation.

It is a curious fact that the name *S. brownii* was also proposed two times, independently.

29. ***S. ovalifolia*** Trautv. 1832, Salic. Frigid.: 306 et tab. 13; Ledeb. 1850, Fl. Ross. **3**, 2: 620; Rydberg, 1899, Bull. N. Y. Bot. Gard. **1**: 275; Coville, 1901, Proc. Wash. Acad. **3**: 331; Schneider, 1918, Bot. Gaz. **66**: 138; Nazarov, 1936, Fl. SSSR **5**: 51 (p. min. p.: quoad pl. peninsulae Tschukot. tantum!!); Hultén, 1943, Fl. Al. **3**: 521; Raup, 1949, Contrib. Gray Herb. **185**: 51; Skvortsov, Derviz-Sokolova, 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4522. —Non *S. ovalifolia* auct.: Rgl. et Tiling, 1858, Fl. Ajan.: 117; Lundström, 1877, Weiden Now. Sem.: 15; Nazarov, 1936, op. cit. **5**: 51 (p. max. p.); id. 1937, Fl. Zabayk. **3**: 216; Karavayev, 1958, Konsp. fl. Yak.: 81 et al. —*S. glacialis* Anderss. 1858, Öfver. K. vet. förhandl. **15**: 131; id. 1868, in DC. Prodr. **16**, 2: 300. —*S. cyclophylla* Rydb. 1899, op. cit. **1**: 274.

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T y p u s: "Cap Espenberg. Eschscholtz" (LE!).

HABIT: A sprawling procumbent shrub with numerous branches spreading radially from a powerful caudex, almost never rooting.

DISTRIBUTION AND HABITATS. Within the Russian territory, it is known exclusively from the coast of the Chukchi Peninsula, where it grows on somewhat sodded sandy-pebbly deposits. So far, there are very few known localities: Uelen, Kolyuchin and Ratmanov islands, the Gulf of Lavrentiya, Provideniya (Providence) Bay, Senyavin Strait, and Arakamchechen Island. (Fig. 26.)

It is more widespread in North America: along the northern and western coasts of Alaska and on the Aleutian and Pribilof islands. According to E. Hultén (1943), it also occurs in the mountains of Alaska.

30. ***S. sphenophylla*** A. Skv. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4524 (nom. nov. pro *S. cuneata* Turcz. 1850 non Nutt. 1842); id. 1966, Arkt. fl. SSSR **5**: 62. —*S. cuneata* Turcz. ex Ledeb. 1850, Fl. Ross. **3**, 2: 623; Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 395; Komarov, 1929, Fl. Kamch. **2**: 27; Nazarov, 1936, Fl. SSSR **5**: 50; id. 1937, Fl. Zabayk. **3**: 212; Popov, 1959, Fl. Sredn. Sib. **2**: 807. —Non *S. cuneata* Nuttall, 1842, N. Am. Sylva **1**: 66. —*S. arctica* γ *leiocarpa* Ledeb. 1850, op. cit. **3**, 2: 619. —*S. arctica* α *nervosa* Anderss. 1868, in DC. Prodr. **16**, 2: 286. —*S. arctica* \times *cuneata* Flod. in Porsild, 1939, Rhodora **41**: 216. —*S. torulosa* (non Trautv.) Hultén, 1943, Fl. Al. **3**: 519.

T y p u s: "Inter Jakutsk et Ochotsk. —Turcz. pl. exs. a. 1835" (LE!).

Ssp. ***pseudotorulosa*** A. Skv. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4524; id. 1965, Arkt. fl. SSSR **5**: 63. A ssp. *sphenophylla* differt ramis saepe elongatis subascendentibus, foliis latioribus, capsulis plus minusve pubescentibus.

T y p u s: "Peninsula Tschukotka, prope pag. Uë len, tundra lapidosa, 8 VIII. 1959. leg. T. Derviz-Sokolova" (Herb. Fl. URSS, N 4524).

HABIT: A powerful, sometimes fist-sized woody caudex producing slender, short-living shoots. The development of this special habit is attributed to the impact of frost and wind erosion.

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HABITATS: Stony, gravelly, or gritty substrates on barren heights, particularly, taluses, rocky outcrops, and dry stony tundras; places where the snow is blown away from during the wintertime; occasionally, sandy and moss tundras.

DISTRIBUTION: The Siberian Northeast from the Lower Olenek, Lena, and Verkhoyanskiy Range to Uelen; Chetyrehstolbovoy and Ayon islands (yet missing from Wrangel Island); Kamchatka (common, to 1,000 m); Paramushir (according to A. Kimura; no samples in Russian collections); Commander and Shantar islands, Ayan, the Tukuringra and Baykal ranges, Stanovoye High Plateau (reaching the Barguzinskiy Range).

Ssp. pseudotorulosa is distributed east and northeast of the Kolyma Mouth and Lower Anadyr and scattered on the barren heights of western Alaska. M. Nazarov (1937: 212) mentioned that this species occurred in the Sayans, however, there is no evidence in herbaria. (Fig. 28.)

31. ***S. kurilensis*** Koidz. 1918, Bot. Mag. Tokyo **32**: 62; Hultén, 1928, Fl. Kamtch. **2**: 21; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 406; Nazarov, 1936, Fl. SSSR **5**: 34. —*S. longepetiolata* Flod. 1926, Ark. bot. **20A**, 6: 14; Hultén, 1928, op. cit. **2**: 15; Komarov, 1929, Fl. Kamch. **2**: 28. —*S. hidaka-montana* Hara, 1933, J. Jap. Bot. **9**: 512; Kimura, 1934, op. cit. **4**: 408; Ohwi, 1965, Fl. Jap.: 365. —*S. subreniformis* Kimura, 1934, op. cit. **4**: 409; id. 1937, Symb. Iteol. **4**: 312. —*S. phanerodictya* Kimura, 1934, op. cit. **4**: 449.

T y p u s: "Insula Shumshu, 29.VII 1903 K. Yendo" (TI?, n. v.).

HABIT: A procumbent small shrub with stout branches resembling *S. sphenophylla*, occasionally developing a strong caudex as large as in *S. sphenophylla*.

HABITATS: Rocks, scarps, damp meadows, and heaths.

DISTRIBUTION: Nearly all of the Kuril Islands from Shikotan to Shumshu (not found on Kunashir), southernmost Kamchatka, Bering Island, and the mountains of Hokkaido. On the central and northern Kurils, it descends almost to the sea level; on the southern Kurils and Hokkaido, it occurs only in the mountains. (Fig. 29.)

NOTE. A. Kimura considered *S. longepetiolata* Flod. to be a synonym of *S. kurilensis* (Kimura 1934: 407). It remains unclear if A. Kimura had compared the appropriate authentic specimens. In spite of numerous requests, I never had a chance to examine the type specimen of *S. kurilensis*, and the species description does not match our plants well enough. Consequently, the name of our plants is not yet decided, and it is quite possible that *S. longepetiolata* might become an accepted name. I have studied the authentic specimens of *S. hidaka-montana* from Hokkaido and found them absolutely identical with the plants from the Kurils.

32. ***S. nakamura*** Koidz. 1913, Bot. Mag. Tokyo **27**: 96; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 135; Kimura, 1928, Bot. Mag. Tokyo **42**: 574; id. 1931, Sci. Rep. Tohoku Univ. 4 ser. **6**, 2: 189; Makino, 1956, Fl. Jap.: 675; Ohwi, 1965, Fl. Jap.: 365. —*S. cyclophylla* (non Rydb. 1899) Seemen, 1902, Bot. Jahrb. Beibl. **67**: 41; id. 1903, Salic. Jap.: 69; Koidzumi, 1916, Bot. Mag. Tokyo **30**: 81. —*S. yezoalpina* Koidz. 1916, op. cit. **30**: 332; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 407; Ohwi, 1965, op. cit.: 365. —*S. neoreticulata* Nakai, 1930, Rep. Veget. Daisetsusan Mts.: 62; Kimura, 1934, op. cit. **4**: 408. —*S. ketoiensis* Kimura, 1934, op. cit. **4**: 410. —*S. rashuwensis* Kimura, 1934, op. cit. **4**: 450. —*S. aquilonia* Kimura 1934, op. cit. **4**: 405 (p. p.?).

T y p u s: "Prov. Sinano, Dailengezan, VIII 1912. Masao Nakamura" (TI n. v. Vidi specimina e loco classico e Hb. U. Tokyo missae).

HABIT: A compact procumbent shrub greatly resembling *S. arctica*.

HABITATS: Rocks and mountain tundras.

138 DISTRIBUTION: Sakhalin (the Schmidt Peninsula and Zatymovskiy Range); the Kurils (Shiashkhotan, Rasshua, Shimushir, and, according to A. Kimura, 1934, Ketoi); Japan (the mountains of Hokkaido and central Hondo). (Fig. 28.)

Sect. 11. *Myrtosalix*

Kerner, 1860, N.-Öst. Weid.: 203.

T y p u s: *S. myrsinites* L.

Small or dwarf shrubs. In majority of species, floriferous buds considerably different from vegetative ones; bud size gradation of type 3 (*caprea*) or transitional from 2 (*arctica*) to 3. Leaves mostly stipulate; stipules subequilateral, lanceolate or ovate. Petioles channeled. Leaves firm, stiff, lustrous above (and often as well beneath). In many species, dead leaves persistent on branches during wintertime. Catkins terminate more or less foliated shoots, bracts black or purple-brown. Nectaries two or one in male flowers. Ovaries glabrous or pubescent (in nearly all species, pubescence of ovaries is facultative). Pubescence consists of either flexuous or ruffled, ribbon-like trichomes highly refracting light. Styles distinct, stigmas vary in their length (0.2–1.0 mm).

This is a very solid and natural group of 13 or 14 species distributed across boreal Eurasia and North America, in tundras and alpine zones. There are just two species, *S. phlebophylla* and *S. rotundifolia*, that are somewhat different from the rest of the section members and resemble the species from *Retusae* because of considerable reduction of their organs. However, there is no doubt that these two also belong to *Myrtosalix*, as far as their foliage and pubescence are concerned. It is quite possible that *Myrtosalix* and *Retusae* are of close filiation (indeed, *S. retusa*, too, somewhat resembles the species from *Myrtosalix* in particular characters); still we are not confident about this relation. There also exists a possibility of close connection with *Hastatae*, which is revealed through the morphology of the leaves, stipules, buds, and partially gynoeceum.

Key to Species

1. Leaves green beneath. Dry leaves of previous seasons persistent on branches 2
 - Leaves deciduous 6
2. Plants form small, compact, cushion-like clumps. Annual accretion of epiterranean shoots insignificant. Elongated leafless stolons obliquely ascending inside substrate. Stipules lacking or obsolete, rudimentary. Leaves entire or obscurely dentate 3
 - Plants cushion-like or fruticose. Underground stolons lacking; all of annual accretion allocated to epiterranean shoots. Leaves stipulate, at least on vigorous shoots, distinctly dentate 4
3. Old specimens form powerful caudices, up to 1–2 cm thick. Leaves cuneately attenuating at base, 5–20 mm long. Old leaves disintegrating into fibers (reticulation) before total decay. Catkins of 6–10 flowers or more, mostly cylindrical, sticking out above foliage after flowering, at least female ones. Bracts mostly entirely pubescent; trichomes straight 41. **S. phlebophylla**

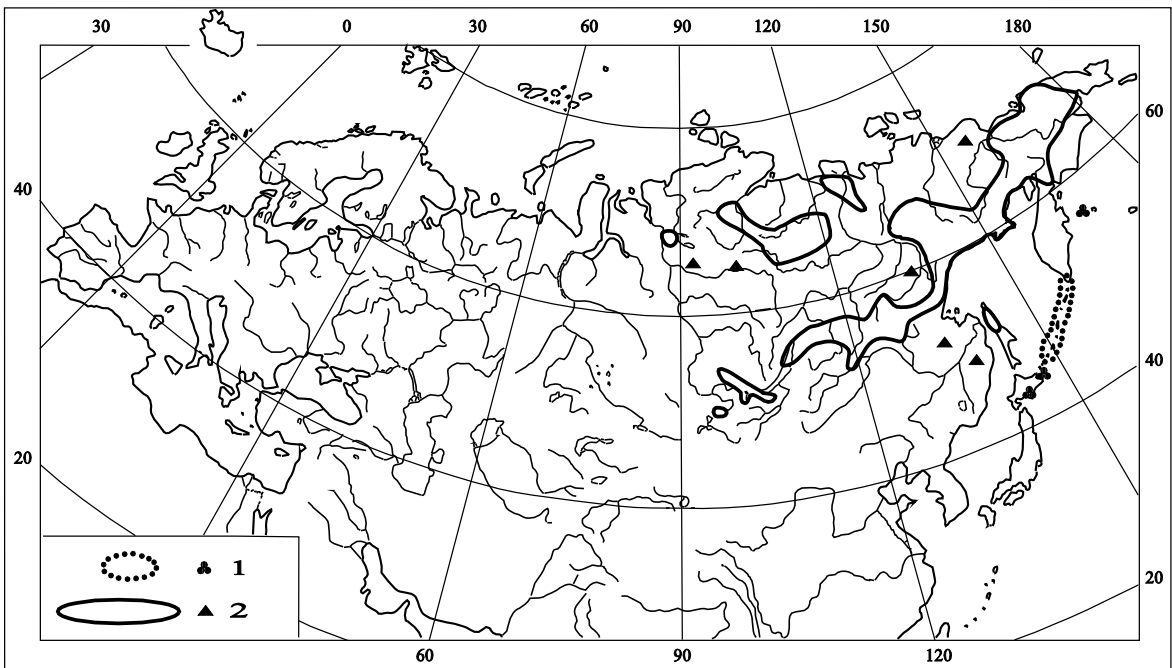


Fig. 29. Distributional areas of *Salix kurilensis* Koidz. (1) and *S. saxatilis* Turcz. ex Ledeb. (2)

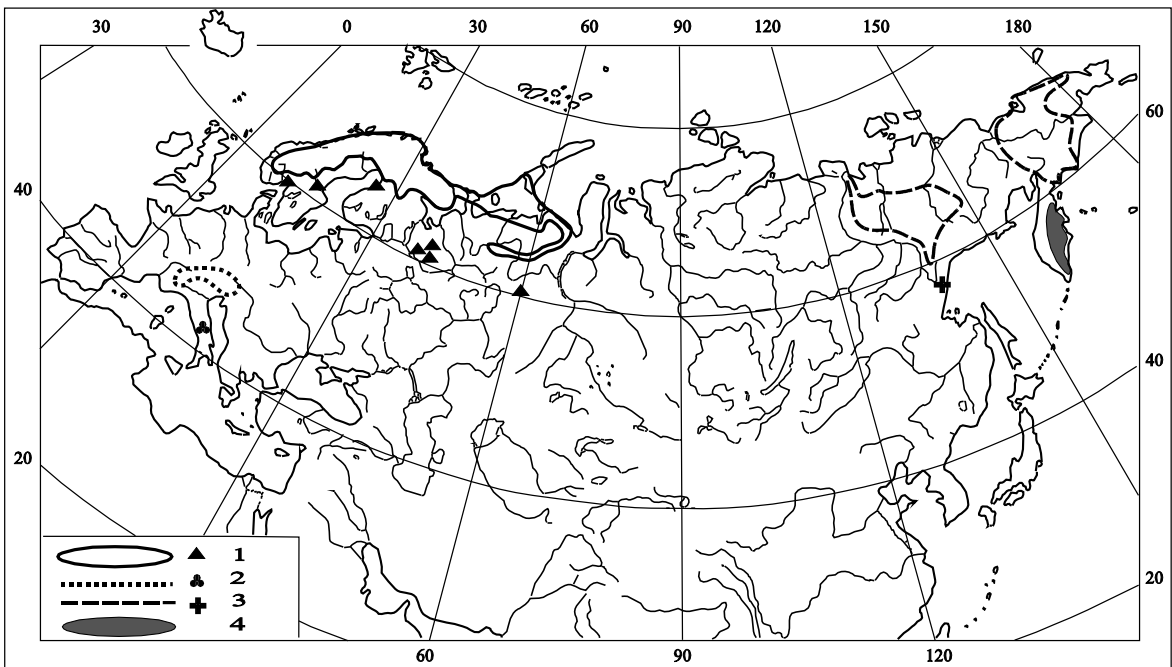


Fig. 30. Distributional areas of *Salix myrsinites* L. (1), *S. breviserrata* Flod. (2), *S. tschuktschorum* A. Skv. (3), and *S. berberifolia* ssp. *kamtschatica* A. Skv. (4)

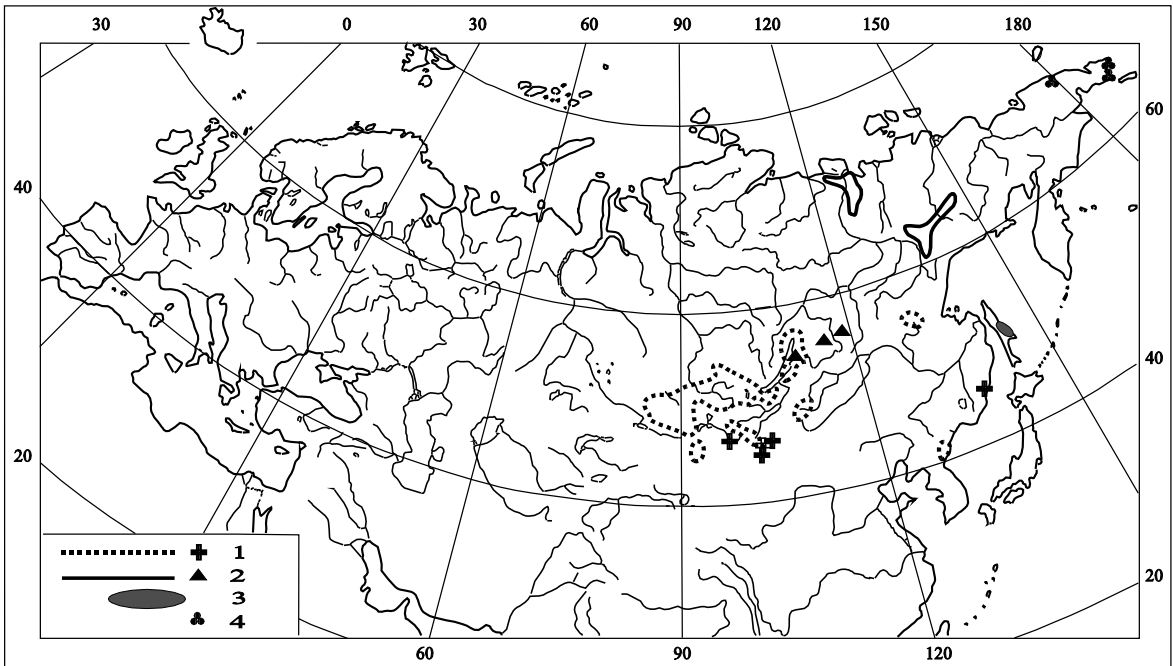


Fig. 31. Distributional areas of *Salix berberifolia* Pall. ssp. *brayi* et *berberifolia* (1), ssp. *fimbriata* A. Skv. (2), ssp. *kimurana* (Miyabe et Tatewaki) A. Skv. (3), and *S. rotundifolia* Trautv. (4)

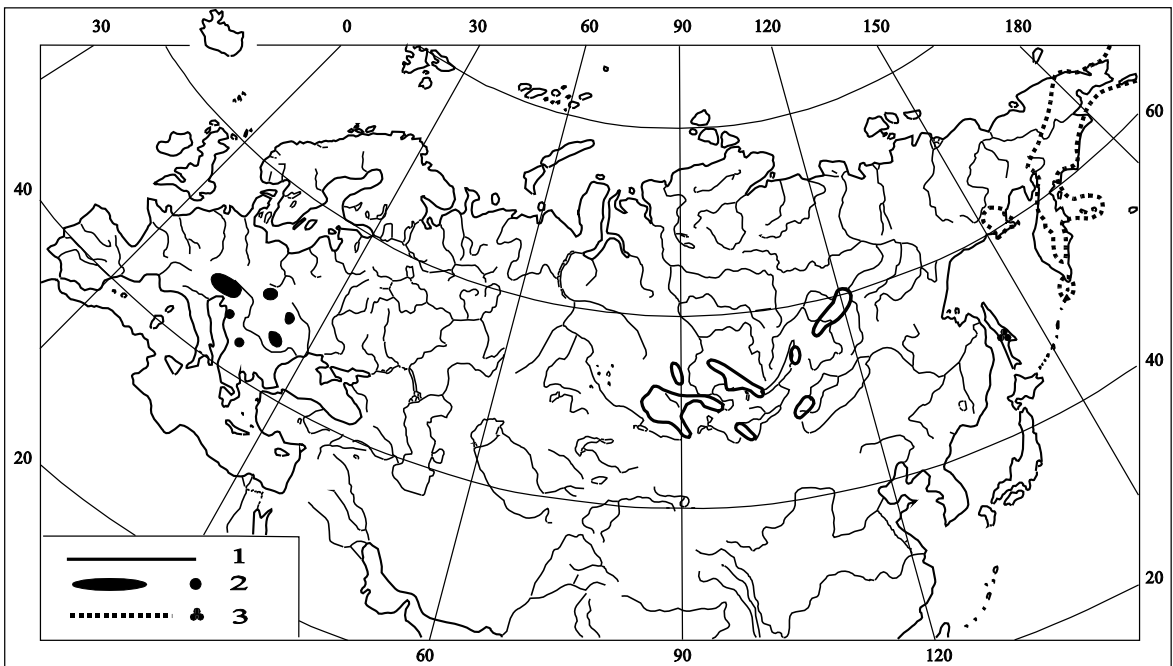


Fig. 32. Distributional areas of *Salix rectijulis* Ledeb. et Trautv. (1), *S. alpina* Scop. (2), and *S. chamissonis* Anderss. (3)

- Caudices never formed, even in oldest specimens. Leaves round to roundish, 2–5 mm long, abruptly cuneate at base. Old leaves persistent many years and decay totally, without previously disintegrating into fibers. Catkins of 2–6 flowers, not protruding out of foliage. Bracts crispy pubescent to puberulous at margins 42. **S. rotundifolia**
4. Plants procumbent, cushion-like. Leaves mostly obovate, cuneate at base. Anthers 0.4–0.5 mm long. Stigmas 0.2–0.3 mm long, short-two-lobed 34. **S. berberifolia**
- Plants fruticose. Leaves mostly broadly elliptic, abruptly cuneate or rounded, occasionally subcordate at base. Anthers 0.5–0.7 mm long. Stigmas 0.3–0.7 mm long, either deeply two-lobed or two-parted, linear 5
5. Leaves spiny-toothed (denticles to 0.5–1.5 mm long). Female catkins long-stalked, usually significantly protruding from foliage, rather loosely flowered, particularly at their lower parts. Ovaries glabrous, occasionally puberulent 35. **S. tschuktschorum**
- Leaf denticles not spiny, shorter than 0.3 mm. Catkins densely flowered, short-stalked, insignificantly protruding from foliage. Ovaries mostly densely pubescent (mature capsules sometimes glabrous) 33. **S. myrsinites**
6. Leaves glaucous dull beneath, at least superior ones. Bracts mostly lanceolate or ovate, acutish. Styles mostly considerably longer than stigmas 7
- All leaves green, lustrous beneath. Bracts usually broadly elliptic or ligular, either obtuse or rounded at apex. Styles mostly not longer than stigmas 8
7. Branches procumbent. Buds obtuse, accumbent to shoots; floriferous buds inconspicuously different from vegetative ones. Petioles 5–15 mm long. Leaves always denticulate 39. **S. chamissonis**
- Branches either upright or ascending. Floriferous buds significantly different from vegetative ones (*caprea*-type of bud gradation), ovoid, acute, growing at acute angle to shoot or at least recurved at their apices. Petioles 2–5 mm long; not infrequently, leaves subentire 40. **S. saxatilis**
8. Creeping habit. Leaves entire (rarely with sparsely scattered denticles). Catkin stalks slender (less than 1 mm thick) 38. **S. alpina**
- Leaves denticulate, at least ordinary ones. Catkin stalks mostly thicker than 1 mm 9
9. Leaves 5–15 mm broad, inferior ones (as well as cataphylls) always very densely denticulate; superior ones often partially entire. Female catkin stalks nearly as long as catkins or shorter (but not more than twice shorter), with 5–8 leaflets 36. **S. breviserrata**
- Leaves usually broader, inferior ones (as well as cataphylls) often subentire, ordinary ones with more distinct denticles. Female catkin stalks a few times shorter than their catkins, with 2–5 leaflets 37. **S. rectijulis**

33. **S. myrsinites** L. 1753, Sp. pl.: 1018; Ledeb. 1850, Fl. Ross. **3**, 2: 620 (p. p.: quoad pl. europaeas); Wimmer, 1866, Salic. Eur.: 97 (p. p.: excl. pl. centrali-europ.); Floderus, 1931, Salic. Fennosc.: 32; id. 1939, Ark. bot. **29A**, 18: 37; Perfileyev, 1936, Fl.

Sev. kr. 2–3: 28; Nazarov, Fl. SSSR 5: 49 (p. p.: excl. pl. Sibir. austr.); Shlyakov, 1956, Fl. Murm. 3: 68; Rech. f. 1964, Fl. Eur. 1: 47.

T y p u s: "In alpebus Lapponiae. Fl. Lapp. N 353 et tab. 8 fig. F, tab. 7, fig. 6; Fl. Suec. N 799".

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HABIT. The species usually forms dense thickets that are, however, neither extensive nor tall.

HABITATS: Banks of streams, well-moisturized slopes and depressions, damp rocks, and mesotrophic edges of wetlands. Presumably, it is associated with basic bedrock, particularly, limestone.

DISTRIBUTION: The mountains of Scotland (100–800 m) and Scandinavia (to 1,000 m in northern Norway); the entire Kola Peninsula (to 600 m in the Khibins); the northern Kanin Peninsula, Kolguyev Island, and Malozemelskaya Tundra; the western coast of Southern Island in the Novaya Zemlya. East of these territories, that is, in Bolshezemelskaya Tundra, on Vaygach Island, the Yugorskiy Peninsula, in Kara Tundra, as well as in the Polar and Prepolar Urals the species becomes much more rare and occurs only sporadically and almost exclusively on limestone. There are also some scattered locations restricted to limestone in drainage wetlands within the northern forest belt: in the Vaga Basin, near Lake Vozhe, in the Pizhma, Izhma, and Kozhva basins, and near Denezhkin Kamen in the Urals. (Fig. 30.)

34. *S. berberifolia* Pall. 1776, Reise 3: 444, 759; id. 1788, Fl. Ross. 1, 2: 84; Ledeb. 1850, Fl. Ross. 3, 2: 621; Nakai, 1930, Fl. sylv. Kor. 18: 149; Nazarov, 1936, Fl. SSSR 5: 55 (p. p.); id. 1937, Fl. Zabayk. 3: 216; Popov, 1959, Fl. Sredn. Sib. 2: 808; Polyakov, 1960, Fl. Kazakhst. 3: 36; Skvortsov, 1961, Bot. mat. Gerb. Bot. in-ta AN SSSR 21: 86. —*S. brayi* Ledeb. 1833, Fl. Alt. 4: 289; id. 1834, Icones 5: 15 et tab. 449; id. 1850, Fl. Ross. 3, 2: 621; Krylov, 1930, Fl. Zap. Sib. 4: 772. —*S. kimurana* Miyabe et Tatewaki, 1936, Trans. Sapporo Nat. Hist. Soc. 14: 255; Kimura, 1937, Symb. Itcol. 3: 103 et 4: 318; Skvortsov, 1961, op. cit. 21: 91. —*S. montis-lopatinii* A. Tolmatshev, 1956, Der. i kustarn. Sakhal.: 67.

T y p u s: "In summis alpium Sochondo leg. Sokolof" (LE!).

Key to Subspecies

- 141
1. Dead leaves of preceding season of bright brown or chestnut color, smooth, firm, spiny-toothed ssp. **kamtschatica**
— Dead leaves of preceding season dull, rather rumpled 2
 2. Leaves cleft to nearly half of distance from margin to midrib, with 3–8 denticles on each side. Styles 0.1–0.3 mm long ssp. **fimbriata**
— More leaf denticles of smaller size on each side. Styles not shorter than 0.3 mm 3
 3. Shoots stout, often more or less ascending. Leaves large (15–30 × 8–15 mm), without stomata on upper surface ssp. **kimurana**
— Shoots slender, procumbent. Leaves smaller, mostly with stomata on upper surface 4
 4. Leaves narrow (3–7 mm broad), with minute, sometimes obscure denticles. Bracts very shortly puberulent ssp. **brayi**
— Leaves broader (5–10 mm), with acute, distinct denticles. Bracts mostly clothed with longer, straight trichomes ssp. **berberifolia**

Ssp. **brayi** (Ledeb.) A. Skv. 1961, Bot. mat. Gerb. Bot. in-ta AN SSSR **21**: 88. — *S. brayi* Ledeb. 1833.

T y p u s: "Altai, in alpinis Terektensibus —Bunge" (LE!).

Ssp. **fimbriata** A. Skv. 1961, op. cit. **21**: 86 et fig. 3a.

T y p u s: "In valle fl. Lenae infer. ca 1800 km a Jakutsk, Adshergai pr. Atlach-Kaja, 6.VI 1914. V. A. Kaschkarov" (LE).

Ssp. **kamtschatica** A. Skv. ssp. nova. Foliis acute spinoso-serrulatis, emarcidis anni praecedentis rigidis castaneis sublucidis distinguitur.

T y p u s: "Kamtschatka, in alpinis Montis Krascheninnikovii, 21.VIII 1909. V. L. Komarov N 3265" (LE, MW).

Ssp. **kimurana** (Miyabe et Tatewaki) A. Skv. comb. nova. —*S. berberifolia* var. *kimurana* Miyabe et Tatewaki, 1935, Trans. Sapporo Nat. Hist. Soc. **14**: 84; Sugawara, 1939, Ill. Fl. Saghal. **2**: 695. —*S. kimurana* Miyabe et Tatewaki, 1936, l. c. —*Salix* an sp. n.? A. Tolmatshev, 1950, Bot. zhurn. **35**, 4: 347. —*S. montis-lopatinii* id. 1956, Der. i kustarn. Sakhal.: 67.

T y p u s: "Sachalin austr., Mons Sekaisan [Mons Sokolov] 2.VIII 1935. M. Kawashima" (Hb. Univ. Hokkaido, n. v.).

HABITATS: Well-drained dwarf-shrub, graminoid, or moss-dominated tundras (mostly on stony substrate), gravelly stone-fields, outcrops, and rocks (mostly on basic bedrock, particularly, limestone) within the barren heights zone in East Siberia at elevations 1,400–2,300 m in the Sayans and Altai, to 2,800–2,900 m in Tuva and Mongolia, to 2,300 m in the Stanovoy Range, and to 1,000 m on the Kamchatka Peninsula.

DISTRIBUTION: The barren heights of the Altai (including most of the Mongolian Altai), Western and Eastern Sayans, Khangai, Kentei, and southern Transbaykalia (common). The Baykal Range and the ranges of the Stanovoye High Plateau (more sporadically). The Stanovoy Range, Sikhote-Alin, and the mountains of North Korea (some solitary findings).

The plants from the Altai and part of the Western Sayan plants belong to ssp. *brayi*, the rest of the species area is occupied mostly by ssp. *berberifolia*. Ssp. *kimurana* is known only from three summits on Sakhalin (mounts Lopatina, Sokolov, and Orel). Ssp. *fimbriata* is distributed in the Verkhoyanskiy and Cherskogo ranges (however, some specimens also occur on the Stanovoye High Plateau). Ssp. *kamtschatica* is restricted to the Kamchatkan barren heights. (Fig. 31.)

NOTE. The systematics of *S. berberifolia* still needs more investigation. For instance, it is necessary to find out if the ssp. *fimbriata* is a distinct species, particularly, in the Stanovoye High Plateau. There is also a need for more material concerning the ssp. *kimurana*, since it is not improbable that this is yet another distinct species. The ssp. *kamtschatica* resembles the next species treated here below, *S. tschuktschorum*, in its firm dead leaves and stomata of large size. Hence, it is not unlikely that future studies may place the ssp. *kamtschatica* in *S. tschuktschorum*¹.

35. **S. tschuktschorum** A. Skv. 1961, Bot. mat. Gerb. Bot. in-ta AN SSSR **21**: 83, 90; id. 1961, Feddes Repert. **64**: 75. —*S. berberifolia* auct. fl. Ross. non Pall.: Trautv. 1879, Acta Horti Petropol. **6**, 1: 35; Nazarov, 1936, Fl. SSSR **5**: 55 (p. p.); Karavayev, 1958, Konsp. fl. Yak.: 81 (p. p.).

¹ As it was proposed in 1977 (Skvortsov 1977: footnote on p. 74), this subspecies might be rather related to *S. tschuktschorum* (authors' note to the English edition).

T y p u s: "Anadyr, montes Gorelovoy dicti, ad rivulum, 26.VI 1933. M. Vassiljeva" (LE).

HABIT: A dwarf shrub to 50 cm tall, different from the previous species in its rather upright habit; however, its branches are spreading, often nearly cushion-like. It resembles *S. myrsinites*, a European species.

HABITATS: Wet moss-dominated and stony tundras near streams; dwarf-shrub and cryptogam tundras that get enough water during the summer and snow during the winter; exposed dry slopes (much more rarely). Its ecological characteristics, like habitual ones, are divergent from those of *S. berberifolia* and close to *S. myrsinites*.

In the Moma Range, it ascends to 1,400 m; on Tarbaganakh Barren Height (the southern Verkhoyanskiy Range), to 2,100 m, appearing to be rather indifferent to bedrock acidity (or probably preferring acidic bedrock).

DISTRIBUTION: The barren heights of the Northeast from the Verkhoyanskiy Range to Koryak High Plateau and Anadyr Range. However, there are no collections from the coast of the Sea of Okhotsk and southern Kolymskiy Range. (Fig. 30.)

36. ***S. breviserrata*** Flod. 1939, Ark. bot. **29A**, 18: 44; Janchen, 1956, Catal. fl. Austr. **1**: 103; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 81; id. 1964, Fl. Eur. **1**: 47. —*S. myrsinites* auct.: L. 1753, Sp. pl.: 1018 (p. p.); Wimmer, 1866, Salic. Eur.: 97 (p. p.); Camus, 1904, Saul. Fr. **1**: 111 (p. p.); Rouy, 1910, Fl. Fr. **12**: 215; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 754; Vicioso, 1951, Salic. Españ.: 98. —*S. myrsinites* var. *serrata* Neilreich, 1859, Fl. Nied.-Öst.: 266; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 162. —*S. arbutifolia* auct. (non Pall. 1788): Willd. 1806, Sp. pl. **4**, 2: 682; Samuelsson, 1922, Vierteljahresschr. naturf. Ges. Zü rich **67**: 249.

T y p u s: "In alpinis Sabaudiae... Sub nomine *S. arbutifoliae* (♀) communicavit Flü gge" (Hb. Willdenow —B, n. v.).

HABIT: A low (but usually not procumbent) shrub 10–50 cm tall.

HABITATS: Peaty meadows, moist depressions, banks of streams, and stony spots in the crooked forest and alpine zones (the elevation range 1,600–2,500 m). Presumably, this species is associated with acidic, siliceous substrates. However, it also occurs on limestone, according to some authors (Buser 1940, Neumann 1960).

DISTRIBUTION: The central Pyrenees (presumably, just their French side), Alps (from the Maritime Alps to Carinthia), Abruzzi Apennines, and probably Picenum Apennines as well. (Fig. 30.)

NOTE. There are some complications with the type of *S. breviserrata*. B. Floderus did not designate the type of the species. Instead, when publishing the species name, he referred to pre-Linnaean descriptions of *S. breviserrata* made by J. Scheuchzer and A. von Haller and also to *S. arbutifolia* Willd. Obviously, the appeals to J. Scheuchzer and A. von Haller were relied on citations in C. Linnaeus' and C. Willdenow's works. However, neither C. Linnaeus, C. Willdenow, nor B. Floderus ever saw the original plants of J. Scheuchzer and A. von Haller. Therefore, it would be more appropriate not to treat those plants as type specimens. We would rather use the type of *S. arbutifolia* Willd., which is quite distinct and appears to belong to the species under consideration.

37. ***S. rectijulis*** Ledeb. ex Trautv. 1832, Salic. Frigid.: 313 (p. p. excl. pl. ex Ins. Sti Laurentii); Skvortsov, 1957, Spisok rast. Gerb. fl. SSSR **81**: N 4013; id. 1966, op. cit. **91**: N 4525; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3230; Malyshev, 1965, Fl. Vost. Sayana: 105. —*S. submyrsinites* Flod. 1936, Sv. bot. tidskr. **30**: 388 et fig. 2; id. 1939, Ark. bot. **29A**, 18: 47. —*S. myrsinites* auct. non L.: Trautv. 1833, in Ledeb. Fl. Alt. **4**: 284;

Ledeb. 1834, *Icones* **5**: 16 et tab. 455; id. 1850, *Fl. Ross.* **3**, 2: 620 (ex p.: quoad pl. altaicas); Nazarov, 1936, *Fl. SSSR* **5**: 49 (ex p.: quoad pl. Sibir. austr.); id. 1937, *Fl. Zabayk.* **3**: 214; Grubov, 1955, *Konsp. fl. Mong.*: 101; Popov, 1959, *Fl. Sredn. Sib.* **2**: 806; Polyakov, 1960, *Fl. Kazakhst.* **3**: 36; Cherepnin, 1961, *Fl. yuzhn. ch. Krasnoyar. kr.* **3**: 13.

T y p u s: "Prope Riddersk in Monte Crucis, in alpihus Sentelek et in summis alpihus Terektensibus" (Ledeb. 1834: 17) (LE!).

HABITATS: Rocks and stone-fields; stony, meadowy, and moss-dominated mountain tundras; banks of streams; spots near icefields and snowbanks (calcareous substrates preferred).

Elevation ranges: 1,700–2,500 m in the Eastern Sayans, to 2,900 m in the Tannu-Ola. Due to climatic inversions in the Barguzinskiy Range, the species descends to the coast of Lake Baykal at the mouth of the Sosnovka River and some other places.

DISTRIBUTION: On and around the barren heights of the Altai (including its Mongolian part), Sayans, Kuznetskiy Alatau, Tannu-Ola, Khangai, Kentei, Sokhondo, and Barguzinskiy Range. On the Stanovoye High Plateau, the species is quite rare: it was found in the Muya River Basin and also between Urteni and the Olekma River, according to P. Polyakov. (Fig. 32.)

38. *S. alpina* Scop. 1772, *Fl. Carniol.* 2 ed. **2**: 255 et tab. 61, fig. 1208 (p. p. ?); Floderus, 1939, *Ark. bot.* **29A**, 18: 49; Pawłowski, 1956, *Fl. Tatr* **1**: 185; Rech. f. 1957, in Hegi, *Ill. Fl. Mitteleur.* **3**, 1: 80; id. 1964, *Fl. Eur.* **1**: 47. —*S. fusca* (non L.) Jacq. 1778, *Fl. Austr.* **5**: 4. —*S. jacquinii* Host, 1797, *Synops. Austr.*: 529; Szafer, 1921, *Fl. Polska* **2**: 43; Pawłowski, 1946, *O niekt. wierzb.*: 13; Nazarov et al. 1952, *Fl. URSR* **4**: 28; Beldie, 1952, *Fl. Rom.* **1**: 312. —*S. jacquiniana* Willd. 1806, *Sp. pl.* **4**, 2: 692; Schur, 1866, *Enumer. Transsilv.*: 662; Zapałowicz, 1908, *Consp. Galic.* **2**: 78. —*S. myrsinites* auct. p. p. non L.: Wimmer, 1866, *Salic. Eur.*: 99; Seemen, 1909, in Aschers. et Graebn. *Synopsis* **4**: 162; Dostál, 1950, *Květ. ČSR*: 895 et al.

T y p u s: "In alpihus Carnioliae".

HABITATS: Moist rocks, taluses, meadowy slopes, and banks of streams in the alpine and subalpine zones (almost exclusively on limestone). 144

DISTRIBUTION: The Eastern Alps (Austria, Italy, Slovenia, and a part of Bavaria); Tatras, Eastern and Southern Carpathians (the only location within the Ukrainian territory is on Mount Bliznitse, at 1,800 m); Croatia and Macedonia.

The elevations are 1,700–2,500 m in the Alps, 1,100–2,150 m in the Tatra Mountains, 2,300–2,500 m in Macedonia. (Fig. 32.)

39. *S. chamissonis* Anderss. 1868, in DC. *Prodr.* **16**, 2: 290; Trautv. 1879, *Acta Horti Petropol.* **6**, 1: 35; Coville, 1901, *Proc. Wash. Acad.* **3**: 325; Floderus, 1926, *Ark. bot.* **20A**, 6: 29; Komarov, 1929, *Fl. Kamch.* **2**: 23; Nazarov, 1936, *Fl. SSSR* **5**: 49; Floderus, 1939, *Ark. bot.* **29A**, 18: 42; Hultén, 1943, *Fl. Al.* **3**: 509; Raup, 1959, *Contrib. Gray Herb.* **185**: 72; Skvortsov, Derviz-Sokolova, 1966, *Spisok rast. Gerb. fl. SSSR* **91**: N 4527. —*S. myrsinites* (non L.) Chamisso, 1831, *Linnaea* **6**: 540; Ledeb. 1850, *Fl. Ross.* **3**, 2: 620 (p. p. quoad pl. e Kamtschatka et Tschukotka). —*S. rectijulis* Trautv. 1832, *Salic. Frigid.*: 313 (p. p. quoad pl. ex ins. Sti Laurentii). —*S. pulchroides* Kimura, 1934, in Miyabe, Kudo, *Fl. Hokk. a. Saghal.* **4**: 446; id. 1940, *Symb. Itcol.* **8**: 414. —*S. kingoi* Kimura, 1940, *op. cit.* **8**: 405, fig. 3 et tab. 12.

T y p u s: "In sinu Sti Laurentii —Chamisso" (LE!).

HABIT: A prostrate shrub.

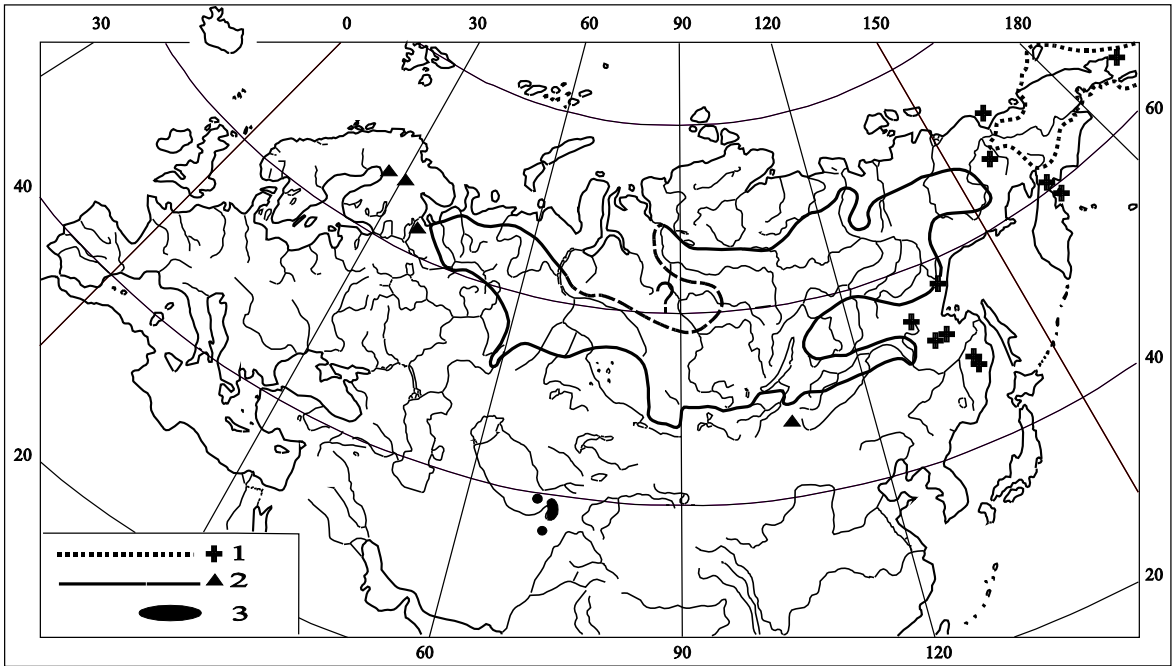


Fig. 33. Distributional areas of *Salix phlebophylla* Anderss. (1), *S. pyrolifolia* Ledeb. (2), and *S. fedtschenkoii* Goerz (3)

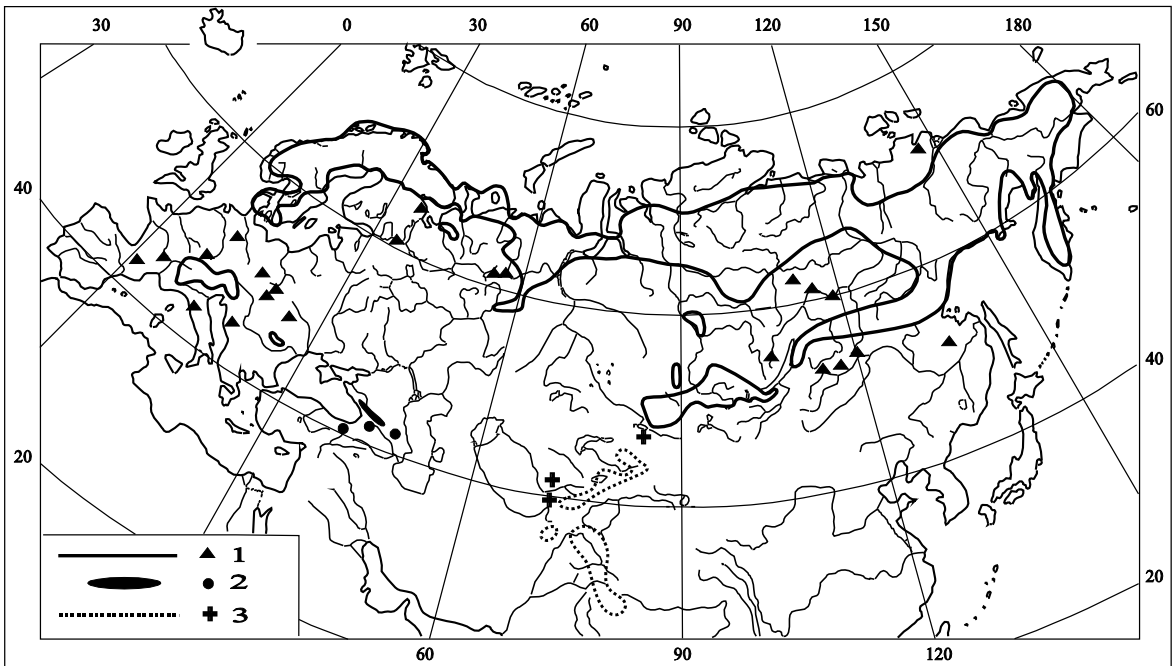


Fig. 34. Distributional areas of *Salix hastata* L. (1), *S. apoda* Trautv. (2), and *S. karelinii* Turcz. ex Stschegl. (3)

HABITATS: Moss-dominated and graminoid tundras in conditions where water supply is sufficient, but not stagnant; occasionally, somewhat paludal habitats (only on large tussocks). It appears to be a maritime species rather than inland one.

DISTRIBUTION: The Northeast (from Magadan and Cape Schmidt to Uelen and the Island of Ratmanov); the Kamchatka Peninsula (on and around the barren heights, to 1,200 m); the Commander Islands; Kurils (Shumshu and Paramushir); southern Sakhalin, (barren heights). (Fig. 32.) It also grows in Alaska.

40. *S. saxatilis* Turcz. ex Ledeb. 1850, Fl. Ross. **3**, 2: 621; Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 391; Nazarov, 1936, Fl. SSSR **5**: 52; id. 1937, Fl. Zabayk. **3**: 214. — *S. fumosa* Turcz. 1854, op. cit. **2**, 2: 384; Nazarov, 1936, op. cit. **5**: 51; id. 1937, op. cit. **3**: 214; Popov, 1959, Fl. Sredn. Sib. **2**: 803. — *S. arnellii* Lundström, 1888, K. sv. vet. handl. **22**, 10: 202. — *S. nyiwensis* Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 442; Tolmachev, 1956, Der. i kustarn. Sakhal.: 68. — *S. stoloniferoides* Kimura, 1934, op. cit. **4**: 448; Tolmachev, 1956, op. cit.: 69. 145

T y p u s: "In Sibiriae baicalensis rupibus ad torrentem Kudun—a. 1829 Turczaninow" (LE!).

HABIT: A low shrub (40–50 cm tall, specimens taller than that are rare), occasionally appressed to rocks.

HABITATS. It absolutely needs a good drainage and is restricted to stony or gravelly substrates. It grows under the canopy of open pine and larch stands or independently along mountain streams, on spring fens, near icefields, and in *yernik*'s, as long as there is a good supply of flowing water. On the other hand, it also occurs on fairly dry stony slopes, particularly, on calcareous rocks. It is mostly found around barren heights and in the forest-tundra; however, it may descend to the forest zone as well as partially ascend to barren heights and reach typical tundras.

DISTRIBUTION: The Eastern Sayans (to 2,400 m), Tannu-Ola and Sangilen (1,900–2,100 m), barren heights of southern Transbaykalia, Baykal Range, Stanovoye High Plateau (to 1,800–1,900 m), Stanovoy and Tukuringra ranges. There are solitary findings in the Bureyinskiy Range, northern Sikhote-Alin (Mount Tardoki-Yani, 1,700 m), and on northern Sakhalin (Mount Lopatina, to 1,200 m). It is common in the mountainous regions of the Northeast from the Verkhoyanskiy and Dzhugdzur ranges to the Gulf Kresta including the coast of the Sea of Okhotsk and reaching the Chaunskaya Inlet as the northernmost point. It is not found on Kamchatka. It is common in the forest-tundra and scattered in the northern forest belt of East Siberia from the Lena to Yenisei. (Fig. 29.)

NOTE. Across most of the species distributional area, its variability range remains fairly stable and rather narrow as compared to other species. However, there are two specific local forms standing out against that monotonous background.

1. In Amur Oblast and southern Yakutia, on pebbles of large rivers (particularly, the Zeya), there occur unusually tall (to 1–1.2 m) plants with abnormally elongated oblanceolate leaves. Unfortunately, all of a few (four or five) samples at my disposal were collected without catkins, so that one can hardly make any reliable assessments. Presumably, these are hybrids with one of riparian species (maybe, *S. udensis*).

2. On open sand dunes of northern Sakhalin, there occur plants with completely prostrate stems. These were described under the name of *S. stoloniferoides* Kimura. However, they do not exhibit any other specific characteristics except their prostrate habit and hence might be rather considered as a local ecotype adapted to certain conditions. Since

one can also find non-prostrate plants on Sakhalin, it is doubtful that "*S. stoloniferoides*" may be assigned of a taxonomic rank. More observations of this peculiar form are required.

Also, in the Dzhugdzur Range, there are many plants with strongly pubescent leaves, a feature that is extremely rare in the rest of the species distributional area.

41. ***S. phlebophylla*** Anderss. 1858, Öfver. K. vet. förhandl. **15**: 131; id. emend. 1868, in DC. Prodr. **16**, 2: 290 (nom. nov. pro *S. retusa* Hook. 1840, non L.); Coville, 1901, Proc. Wash. Acad. **3**: 336; Komarov, 1929, Fl. Kamch. **2**: 31; Nazarov, 1936, Fl. SSSR **5**: 56; Raup, 1959, Contrib. Gray Herb. **185**: 47; Skvortsov, Derviz-Sokolova, 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4520. —*S. buxifolia* Trautv. 1832, Salic. Frigid.: 301, non *S. buxifolia* Schleicher ex Seringe, 1815, Saul. Suisse: 54. —*S. anglorum* Cham. 1831, Linnaea **6**: 541 (quoad plantas citatas, nec ad synonyma). —*S. retusa* Hook. 1840, Fl. Bor.-Amer. **2**: 153. —*S. arctica* β *minor* Ledeb. 1850, Fl. Ross. **3**, 2: 619. —*S. palaeoneura* Rydb. 1899, Bull. N. Y. Bot. Gard. **1**: 267.

T y p u s: "Cap Mulgrave, captain Beechey" (K?, n. v.).

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HABITATS: Stony mountain slopes poorly covered with snow. Although it is mostly associated with granite, it is often found on limestone, as well.

DISTRIBUTION: The extreme Northeast from the mouths of the Indigirka and Penzhina to Cape Dezhnev (common, except the Koryak High Plateau, where it is not found); the islands Chetyrekhtolbovoy, Wrangel (to 500 m on Berry Peak), and Karaginskiy. After a large gap, the species again appears at a number of isolated locations on barren heights of the ranges Dzhugdzur, Stanovoy (the Upper Zeya, at 2,000 m), Dussye-Alin, and northern Sikhote-Alin (mounts Ko and Tardoki-Yani, at 1,800–2,000 m). (Fig. 33.)

The species is also distributed in Alaska and Yukon, reaching the Lower Mackenzie.

42. ***S. rotundifolia*** Trautv. 1832, Salic. Frigid.: 304 et tab. 2; Anderss. 1868, in DC. Prodr. **16**, 2: 299; Rydberg, 1899, Bull. N. Y. Bot. Gard. **1**: 276; Schneider, 1919, Bot. Gaz. **67**: 52; Kimura, 1934, J. Fac. Agric. Hokkaido Univ. **36**, 1: 32; Nazarov, 1936, Fl. SSSR **5**: 39 (p. min. p.!). Floderus, 1941, Sv. bot. tidskr. **35**: 351; Raup, 1959, Contrib. Gray Herb. **185**: 46; Hultén, 1960, Fl. Aleut. 2 ed.: 163. —Non *S. rotundifolia* auct. mult.: Trautv. 1871 et 1877; Schmidt, 1872; Lundström, 1877; Tolmachev, 1930; Krylov, 1930; Perfilyev, 1936; Rechinger, 1964; et al. (cf. supra sub *S. nummularia*). —*S. polaris* var. *leiocarpa* Chamisso, 1831, Linnaea **6**: 542. —*S. leiocarpa* Coville, 1901, Proc. Wash. Acad. **3**: 338.

T y p u s: "In sinu Sti Laurentii. Chamisso" (LE!).

HABIT: A tiny plant, the smallest of the willows in this country.

HABITATS: Rocky outcrops and moist, but well-drained mountain tundras on gravelly or clayey slopes. The species is apparently restricted to limestone.

DISTRIBUTION: Within the territory under consideration, it occurs only on Wrangel Island (where it is common), the Chukchi High Plateau, and occasionally in the maritime zone on the eastern coast of the Chukchi Peninsula, that is, along the Gulf of Lavrentiya, Senyavin Strait, on Arakamchechen Island, and around the Provideniya Bay. (Fig. 31.). It also grows in arctic and alpine tundras of Alaska.

SUBGENUS *VETRIX*

Dum. 1862, Bull. Soc. Bot. Belg. 1: 141.

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T y p u s: *Salix caprea* L.

Shrubs or moderate-sized trees. *Caprea*-type of bud gradation in majority of species. Petioles eglandular. Catkins mostly precocious, bracts black. One nectary typical for all groups of species within this country. Stamens two, their filaments either connate or distinct. A very large and diverse group embracing more than $\frac{2}{3}$ of the species in the genus.

Sect. 12. *Hastatae*

Kerner, 1860, N.-Öst. Weid.: 241.

T y p u s: *Salix hastata* L.

Low or moderate-sized shrubs, occasionally small trees. Floriferous buds significantly different from vegetative ones; *caprea*-type (type 3) of bud size gradation. Stipules distinct, equilateral or subequilateral. Leaves broad, denticulate at margins, their reticulation fine, not pronounced. Catkins precocious to serotinous. Nectary solitary, small, short-rectangular. Capsules glabrous, acute, gradually attenuating into a distinct style; stigmas two-lobed, not large (0.3–0.6 mm).

This is a boreal and arctic-alpine holarctic group consisting of 12–15 species, mostly American. The section is very natural, distinctly delimited from other sections, at least as far as the Old World flora is concerned. The most obvious links are those with *Lanatae*, *Nigricantes*, and *Glabrella*; more distant ones with *Myrtosalix*.

Key to Species

1. Buds lanceolate, acute, mostly attenuating into beaks. Stipules broad, round or reniform, not acuminate. Petioles 5–20 mm long, slender. Ovaries much reflexed (positioned at right or even obtuse angle to rachises). Stipes 1–2 mm long, two-four times longer than nectaries 47. **S. pyrolifolia**
— Buds ovoid, obtuse, not attenuating into beaks. Stipules ovate or lanceolate, acuminate, midribs pronounced, pointing to apices. Petioles up to 10 mm long. Ovaries less reflexed. Stipes 0.2–1.0 mm (occasionally to 1.5 mm), either shorter than nectaries or not more than twice as long 2
2. Leaves nearly concolorous, yellowish-green, rather lustrous, with stomata on their upper side 46. **S. fedtschenkoii**
— Due to waxy bloom, leaves whitish or glaucous beneath (occasionally excluding inferior ones); upper leaf surface light green, dull, without stomata 3
3. Catkins precocious or subprecocious, stalks short, stout (in female ones 2–12 mm long and not less than 1 mm thick), mostly with 1–3 leaflets. Leaflets abortive, densely

- glandular at margins. Bracts entirely black, 1.5–3.5 mm long, covered with dense, long trichomes. Stipes 0.2–0.5 mm, not exceeding nectaries 4
- Catkins serotinous or subserotinous, stalks in female ones 7–25 mm long and not more than 1 mm thick, with 2–4 leaflets. Usually, at least one or two leaflets are comparable with leaves of vegetative shoots in their size; lowermost leaflets abortive, entire or sparsely denticulate. Bracts 1–2 mm long, rufescent or brownish, occasionally blackish-purple at apices. Stipes 0.6–1.5 mm long, mostly exceeding nectaries 43. **S. hastata**
4. Stipules broadly (oblique-)ovate, mostly obtuse. Cataphylls glabrous beneath. Styles comparatively long (0.8–1.8 mm) 45. **S. apoda**
- Stipules (oblique-)ovate or lanceolate, acuminate. Cataphylls beneath clothed with long trichomes, at least on their central part. Styles comparatively short (0.5–1.5 mm) 44. **S. karelinii**

43. **S. hastata** L. 1753, Sp. pl.: 1017; Ledeb. 1850, Fl. Ross. **3**, 2: 612; Wimmer, 1866, Salic. Eur.: 83; Anderss. 1867, Monogr. Salic.: 170 (p.p.: excl. var. *himalayensis* et *viridula*); Krylov, 1930, Fl. Zap. Sib. **4**: 756; Floderus, 1931, Salic. Fennosc.: 211; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 33; Nazarov, 1936, Fl. SSSR **5**: 116 (p.p. excl. pl. Caucasi et Asiae Med.); Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 685; Shlyakov, 1956, Fl. Murm. **3**: 106; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 111; id. 1964, Fl. Eur. **1**: 52; Popov, 1959, Fl. Sredn. Sib. **2**: 802; Polyakov, 1960, Fl. Kazakhst. **3**: 28 (p.p.: quoad pl. altaicas tantum!). —*S. psiloides* Kom. 1929, Fl. Kamch. **2**: 18; Nazarov, 1936, op. cit. **5**: 117. —*S. hastata* ssp. *psiloides* Flod. 1926, Ark. bot. **20A**, 6: 54. —? *S. barclayi* (non Anderss.) Hultén, 1928, Fl. Kamtch. **2**: 8; Nazarov, 1936, op. cit. **5**: 121.

T y p u s: "In Lapponia, Helvetia. Fl. Lapp. N 354 et tab. 8 fig. G; Fl. Suec. N 797; Haller Helv. N 151".

HABIT: A shrub 0.2–1.5 m tall (very seldom, a tree to 3 m tall).

HABITATS: Open birch, spruce, and larch stands (in the understory); *yernik*'s; banks of streams, drainage spring fens, and meadows; depressions and small mountain valleys; moraines, rocks, taluses; sometimes, exposed sandy territories. Being generally indifferent to the quality of the bedrock, it appears to be associated with limestone at southern limits of its distributional area. The species cannot tolerate water stagnation. Its area includes the northern part of the forest belt, the forest-tundra, and southern tundra regions; the subalpine and partially alpine zones of mountains. It is also encountered in the forest zone (on rocks and in cold depressions).

DISTRIBUTION: The Pyrenees, Alps, French Massif Central, Apennines (reliable data only from Mount Rondinayo in Tuscany, Italy), the Vosges, Harz, Sudetes, Tatras, Eastern and Southern Carpathians (also some doubtful indications in the Ukrainian Carpathians), and Bosnia. Nearly all of Scandinavia (including northern Denmark), northern Finland, the Kola Peninsula, tundras and forest-tundras of northern European Russia (missing from the Yugorskiy Peninsula and all of the islands except Kolguyev). The northern forest belt (only solitary locations; one of special interest in the Svir Basin near St. Petersburg); the Polar, Prepolar, and partially Central Urals; forest-tundras and southern tundras of West Siberia. East of the Yenisei, on major territory of East Siberia including the Stanovoy Range, coast of the Sea of Okhotsk, and Lower Anadyr, it occurs only sparsely, in the areas of pronounced mountainous landscape (avoiding the warmest lowlands). It is scattered across

the Kamchatka Peninsula. It is a common species in the mountains of South Siberia, however, missing from the Khangai, Sokhondo, and Kentei.

In the Alps, it ascends to 2,500 m; its vertical range in the Tatras is from 1,200 to 2,100 m; in the Khibins, it goes up to 500–600 m; in the Sayans, to 2,100 m. (Fig. 34.)

The literature data on this species concerning the Caucasus and Middle Asia are to be attributed to the following two species.

44. **S. karelinii** Turcz. ex Stschegl. 1854, Bull. Soc. Natur. Moscou **27**: 196; Turcz. 149
 ibid.: 393; Skvortsov, 1962, Bot. mat. Gerb. in-ta bot. AN UzbSSR **17**: 63. —
S. prunifolia Kar. et Kir. 1842, Bull. Soc. Natur. Moscou **15**: 183; non Sm. 1804, Fl.
 Brit. **3**: 1054. —*S. hastata* auct. florae Asiae Mediae necnon Himalayae, non L.: Anderss.
 1851, K. sv. vet. handl. **1850**: 479; id. 1860, J. Linn. Soc. **4**: 51; Hook. f. 1890, Fl. Brit.
 Ind. **5**: 630; Parker, 1924, Forest fl. Punjab.: 56; Hao, 1936, Syn. Chin. *Salix*: 83;
 Polyakov, 1960, Fl. Kazakhst. **3**: 28 (p. max. p., sed excl. pl. altaic. et syn.
S. fedtschenkoi). —*S. hastata* var. *himalayensis* Anderss. 1867, Monogr. Salic.: 173;
 Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 134. —*S. himalayensis* Flod. 1935, Geogr.
 ann. **17**: 306. —*S. adenophylloides* Flod. 1935, op. cit. **17**: 310. —*S. fedtschenkoi* (non
 Goerz) Protopopov, 1953, Fl. Kirgiz. **4**: 20.

T y p u s: "Alatau a. 1842 Karelin" (MW! LE! et alibi).

HABIT: A low, sparsely branched shrub (0.3–1.5 m).

HABITATS: Taluses, rocks, and moist slopes in the alpine and partially subalpine zones. Occasionally, it is found along streams.

DISTRIBUTION: The Tarbagatay, Dzungarskiy Alatau, Chinese Tien Shan, all of the Eastern and Central Tien Shan ranges within this country including the Ferganskiy Range. So far, it is not found in the Kirgizskiy Range, yet occurs in the western Talasskiy Alatau. The Pamir-Alay including the Petra Pervogo Range (Range of Peter I) in the west. Missing from the dry areas of the Pamirs, the species is again encountered in Nuristan, on Mount Chitral, and across the Himalayas from the Karakorum Range to central Nepal.

It is found at 2,800 m in the Talasskiy Alatau; in the Terskey, it ascends to 3,300 m; to 3,500 m in the Zaalayskiy Range; to 4,300–4,500 m, occasionally, to 4,900 m in the Karakorum and Nepal. (Fig. 34.)

45. **S. apoda** Trautv. 1866, Index Sem. Horti Petropol. a. 1865: 37; Medvedev, 1919, Der. i kustarn. Kavk.: 296; Nazarov, 1936, Fl. SSSR **5**: 117; Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR **15**: 121. —*S. hastata* var. *apoda* Laksch. ex Goerz, 1930, in Grossheim, Fl. Kavk. **2**: 6; Grossheim, 1945, Fl. Kavk. 2d ed. **3**: 22; Sosnovskiy, 1947, Fl. Gruz. **3**: 19. —*S. hastata* auct. fl. Caucas. non L.

T y p u s: "Caucasus, prope Pari, leg. Radde" (LE!).

HABIT: A low shrub.

HABITATS: Subalpine birch stands, *Rhododendron* shrublands, rocks, taluses, alpine meadows, and wetlands at 1,800–2,000 m in the alpine and subalpine zones.

DISTRIBUTION: The western part of the Greater Caucasus from the Fisht-Oshten Massif to Daryal Gorge (common). East of that region, it is encountered only at two locations in Dagestan. In the Lesser Caucasus, it is found only near Bakuriani; in Turkey, only in Gü mü shane Province. (Fig. 34.)

46. **S. fedtschenkoi** Goerz, 1931, Salic. As. **1**: 21, 25; id. 1933, Feddes Repert. **32**: 121; Nazarov, 1936, Fl. SSSR **5**: 118; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 64; Ikonnikov, 1963, Opred. rast. Pamira: 30.

T y p u s: "Schugnan. ad trajectum Schtam.—a. 1904 B. Fedtschenko" [Goerz, Sal. Asiat. (exs.) N 25] (LE!, TAK! et alibi).

HABITATS: Hollows, banks of streams, areas of alpine cryophilic vegetation at 3,000–3,900 m.

DISTRIBUTION: The Western Pamirs, Darvaz, the Range of Peter I, and Gilgit in northeastern Pakistan. Rare: so far, only about 25 samples are known in total. (Fig. 33.)

47. *S. pyrolifolia* Ledeb. 1833, Fl. Alt. **4**: 270; id. 1834, Icones **5**: 25 et tab. 476; id. 1850, Fl. Ross. **3**, 2: 613; Anderss. 1867, Monogr. Salic.: 169; Wolf, 1900, Izv. Lesn. in-ta **5**: 106; Krylov, 1930, Fl. Zap. Sib. **4**: 757; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 31; Nazarov, 1936, Fl. SSSR **5**: 115; id. 1937, Fl. Zabayk. **3**: 202; Popov, 1959, Fl. Sredn. Sib. **2**: 801; Polyakov, 1960, Fl. Kazakhst. **3**: 28; Rech. f. 1964, Fl. Eur. **1**: 52. — *S. subpyroliformis* Chang et Skvortz. 1955, in Liou Tchen ngo, Ill. Fl. Tr. Shr. Northeast China: 554 et tab. 42.

T y p u s: "Altai: Bystrucha; Koksa; Buchtorma inter pagos Sennoj et Maloj Narymsk. —Ledebour" (LE! omnes).

HABIT: A tall shrub or, more often, small tree, typically, with a few stems, their branches interlacing. I have found specimens to 25 cm in stem diameter in the Northern Urals.

HABITATS: Damp woods, eutrophic drainage fens, banks of streams, and shrublands on moist slopes in the forest belt. The species avoids acidic substrates and stagnant water and is associated with limestone, particularly, at limits of its distributional area. It does not ascend high up in the mountains never approaching the timberline. It is known to grow at 1,300–1,400 m in Tuva (Koropachinskiy, Skvortsova 1966: 79).

DISTRIBUTION: Northern Finland (some solitary findings); the northeastern Kola Peninsula (encountered, but no evidence in herbaria); the northern forest belt of European Russia (starting from Trans-Onega Region and the Northern Dvina Basin); nearly all of the Urals (reaching 65–66° in the north and the forest-steppe zone in the south); the West Siberian Plain (only in the southern forest belt); the ranges Dzungarskiy and Tarbagatay; the Altai and all of East Siberia. The northern area border in East Siberia runs via Dudinka, the Upper Vilyuy and Molodo rivers, Verkhoyansk, Druzhina on the Indigirka, and Srednekolymsk. Easternmost limits comprise the middle reaches of the Kolyma, the Maya (tributary of the Aldan), and Zeya. The species is also found in the northwestern part of Northeast China and northernmost Mongolia. (Fig. 33.)

Sect. 13. *Glabrella*

A. Skv. sect. nova. Novosti sist. vyssh. rast. 1968 describetur.

T y p u s: *Salix glabra* Scop.

Shrubs with stout short branches. Floriferous buds look similar to vegetative ones (type 2 of bud size gradation). Cataphylls (and occasionally also inferior leaves) beneath clothed with long sericeous trichomes. Stipules none or small, inequilateral. Leaves elliptic or obovate, flat, bright green, rather lustrous above, dull or glaucescent beneath, veins on lower surface of mature leaves somewhat prominent. Catkins large, stalked; stalks stout, not infrequently leafy. Bracts thin, scarious, pale or brownish. Nectary solitary. Capsules stipitate, acute, gradually attenuating into rather long styles.

Key to Species

1. Bracts large (2.5–3.5 mm long, 1.5–2.0 mm broad), densely pubescent, their apices broad, rounded, or truncate, or irregularly dentate. Anthers 0.9–1.2 mm long. Styles more or less cleft (often down to their middle or even more). Stigmas 0.6–1.0 mm long, cleft into slender, linear, twisted parts. Mature capsules ovoid, 5–6 mm long
 48. **S. crataegifolia**
 — Bracts not as above (either small, or glabrate, or their apices different). Anthers 0.8–0.9 mm long. Stigmas 0.4–0.6 mm long, their parts not twisted. Mature capsules lanceolate, (6–)7–8 mm long 2
2. Tall shrub. Buds flat on adaxial side, their carinas distinct, beaks flat. Leaves on vigorous shoots usually stipulate; stipules 3–5 mm long. Leaves 50–100 mm long. Bracts mostly acutish. Anthers 0.7–0.9 mm long
 51. **S. jennisensis**
 — Low shrubs. Buds without distinct carinas and flat beaks. Stipules none or inconspicuous. Leaves 20–60 mm long. Bracts obtuse, truncate, or more or less emarginate. Anthers 0.5–0.7(–0.8) mm long 3
3. All leaves rather regularly denticulate at margin. Bracts mostly pale (at least during flowering period), not less than 1 mm broad. Capsules glabrous. Style length + stigma length less than 1.2 mm 49. **S. glabra**
 — Leaves mostly entire, or partially entire, or obscurely and irregularly dentate; if dentation pronounced, then leaves spiny-toothed, their denticles pointing toward apex. Bracts not more than 1 mm broad, mostly dark brown or blackish at apices. Capsules often rather pubescent. Style length + stigma length not less than 1.1–1.2 mm . . .
 50. **S. reinii**

48. **S. crataegifolia** Bertoloni, 1814, Desv. J. Bot. **2**: 76; id. 1854, Fl. Ital. **10**: 312; Caruel, 1860, Prodr. Tosc.: 581; Parlatore, 1867, Fl. Ital. **4**: 244; Camus, 1905, Saul. Eur. **2**: 74; Negri, 1906, Sched. ad Fl. Ital. exs.: N 426; Pellegrini, 1942, Fl. Apuan.: 267; Floderus, 1944, Sv. bot. tidskr. **38**: 64; Rech. f. 1964, Fl. Eur. **1**: 49. —*S. glabra* var. *crataegifolia* Anderss. 1867, Monogr. Salic.: 175 (p. p.). —*S. phyllicifolia* var. *crataegifolia* Fiori, 1923, Nuova fl. anal. Ital. **1**, 3: 344.

T y p u s: "In suprema Tambura Alpium Apuanarum" (FI, vidi specim. a ipso Bertoloni lectum—an holotypus?).

HABIT: A low (to 1 m) shrub with stout, ascending branches.

HABITATS AND DISTRIBUTION: Calcareous rocks of the Apuan Alps (Apennines System, Tuscany Province) at 300–1,600 m. (Fig. 35.)

NOTE. This is a local endemic species remarkable for its restricted distribution. Still more striking is its extremely close affinity to *S. ernestii* Schneid., a species distributed in Southwest China. Treating *S. crataegifolia* as a variety of *S. glabra* or any other European species is by all means very inappropriate. On the contrary, it might make sense to withdraw *S. crataegifolia* from the section *Glabrella* and unite it with *S. ernestii*, *S. sikkimensis* Anderss., and probably with *S. daltoniana* Anderss. The only reason for me to refrain from doing it here is that sections of Chinese-Himalayan willow species have not yet been clearly delimited.

49. **S. glabra** Scop. 1772, Fl. Carn. **2**: 255; Wimmer, 1866, Salic. Eur.: 81; Anderss. 1861, Monogr. Salic.: 173; Parlatores, 1867, Fl. Ital. **4**: 253; Camus, 1905, Saul. Eur. **2**: 71; Beck, 1906, Fl. Bosn. Herc. **2**, 1: 98; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 158; Toepffer, 1914, in Vollman, Fl. Bayern: 192; Thommen et Rechinger, 1948, Ber. Schweiz. bot. Ges. **58**: 69; Janchen, 1956, Catal. fl. Austr. **1**: 103; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 112; id. 1964, Fl. Eur. **1**: 49.

T y p u s: "In montanis elatioribus Carnioliae" (n. v.).

HABIT: A medium-sized (to 1.5–2.0 m) shrub.

HABITATS: Rocks, taluses, banks of streams, and moist meadows on slopes, mostly in the subalpine and upper forest zones (1,400–1,800 m). However, it may also descend to 500 m, as well as ascend up to 2,200 m.

DISTRIBUTION: Limestones and dolomites of the Eastern Alps (including southern Bavaria, Tirol, and Canton Ticino); the mountains of the territory of former Yugoslavia including Herzegovina (scattered). The species was also listed for the flora of the High Tatras (Dostál 1950: 895), which appears to be a mistake, as it is not mentioned in Pawłowski's "Flora of the Tatras". Data on occurrence in the western Alps are as well rather doubtful. There is a sample labeled "In Monte Cenisio lecta ded. Hooker", LE, however, most likely, the label was mishandled. (Fig. 35.)

50. **S. reinii** Fr. et Sav. ex Seemen, 1903, Salic. Jap.: 41; Fr. et Sav. 1875, Enum. pl. Jap. **1**: 459 (nom. nud.); Koidzumi, 1913, Bot. Mag. Tokyo **17**: 91; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 127; Kimura, 1931, Sci. Rep. Tohoku Univ. 4 ser. **6**, 2: 189; id. 1934, in Miyabe, Kudo, Fl. Hokkaido **4**: 402; id. 1940, Symb. Itcol. **8**: 412; Ohwi, 1965, Fl. Jap.: 366. —*S. kakista* Schneid. in Sarg. Pl. Wilson. **3**, 1: 128. —*S. tontomussirensis* Koidz. 1916, Bot. Mag. Tokyo **30**: 81; Tatewaki, Kimoto, 1933, Acta Phytotax. Geobot. **2**: 227, 228; Kimura, 1934, op. cit. **4**: 449; Tolmachev, 1956, Der. i kustarn. Sakhal.: 70. —*S. hidewoi* Koidz. 1919, Bot. Mag. Tokyo **33**: 220; Kimura, 1934, op. cit. **4**: 403; Ohwi, 1965, op. cit.: 366. —*S. shikotanica* Kimura 1934, op. cit. **4**: 447.

T y p u s: "Insula Nippon media, in Monte Haksan —leg. Rein (Hb. Savatier N 2923, 2924)" (P; fragmenta LE!).

HABIT: A low (25–150 cm), occasionally prostrate shrub.

HABITATS: Rocks, taluses, scarps; moist slopes (amidst shrub alder, tall herbs, or bamboo thickets); secondary coppices and meadows at forest clearings; sometimes, maritime sand (together with *Rosa rugosa*).

DISTRIBUTION: The Kuril Islands (Shikotan, Kunashir, Iturup, Urup, and Shimushir, from the sea level to subalpine zone, common); Moneron, Hokkaido, and the alpine zone of Hondo. On the continent, it is known to occur in three localities: the southern Sikhotealin (Mount Sestra), the barren heights of the Tachin-Tchan Range (1,600–1,700 m), and Zarechye, a settlement in Khasanskiy District, where it descends nearly to the sea level. (Fig. 35.)

51. **S. jensiseensis** (Fr. Schmidt) Flod. 1936, Sv. bot. tidskr. **30**: 390 et fig. 3; Popov, 1957, Spisok rast. Gerb. Fl. SSSR **81**: N 4012; id. 1959, Fl. Sredn. Sib. **2**: 804; Skvortsov, 1959, Bot. mat. Gerb. Bot. in-ta AN SSSR **19**: 83. —*S. nigricans* var. *jensiseensis* Fr. Schmidt, 1872, Fl. Jeniss.: 117; Lundström, 1888, K. sv. vet. handl. **22**, 10: 201; Nazarov, 1936, Fl. SSSR **5**: 86. —*S. hastata* var. *viridula* Anderss. 1867, Monogr. Salic.: 173; id. 1868, in DC. Prodr. **16**, 2: 258. —*S. viridula* (Anderss.) Nasarov, 1936, op. cit. **5**: 119; id. 1937, Fl. Zabayk. **3**: 204. —Non *S. viridula* Anderss. 1858, Mem. Amer. Acad. **6**:

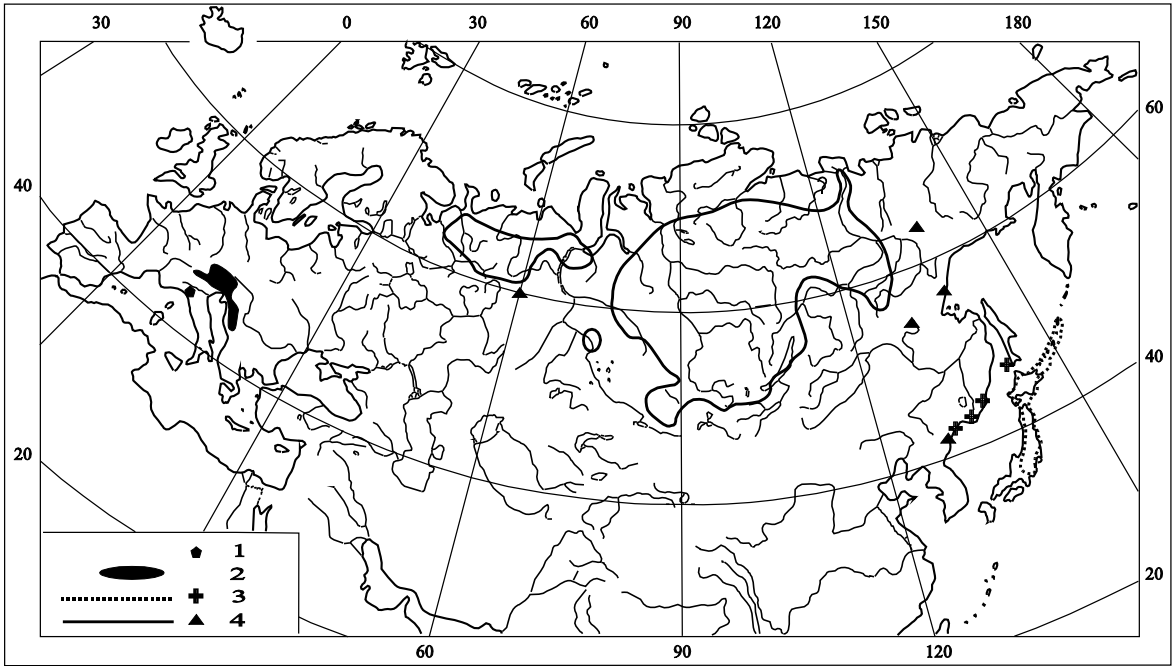


Fig. 35. Distributional areas of *Salix crataegifolia* Bertoloni (1), *S. glabra* Scop. (2), *S. reinii* Fr. et Sav. ex Seemen (3), and *S. jensseensis* (Fr. Schmidt) Flod. (4)

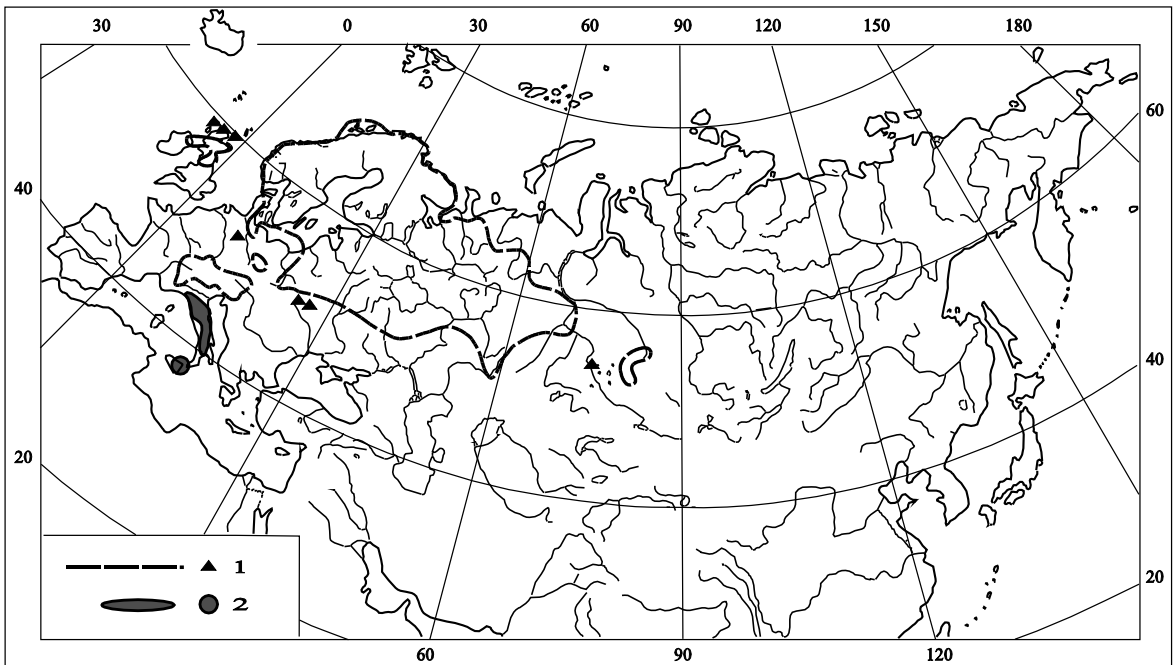


Fig. 36. Distributional areas of *Salix myrsinifolia* Salisb. (1) and *S. apennina* A. Skv. (2)

451. —*S. borealis* Nasarov, 1936, op. cit. **5**: 87 (p. max. p.). —*S. rectispica* Nakai ex Flod. 1939, Ark. bot. **29A**, 18: 26 et tab. 2.

T y p u s: "An Abhängen bei Dudino und Norilgebirge. —Fr. Schmidt" (LE!).

HABIT: A tall shrub or small tree (to 4–5 m tall).

HABITATS: Open woods, stony slopes and stone-fields, depressions, banks of streams (often together with *Alnus fruticosa*). Within its distributional area, it occurs extremely inconsistently being rather common in many parts and, at the same time, completely absent from large territories. That may be attributed to availability of appropriate substrates (the species is calciphilic).

DISTRIBUTION: The northeast of European Russia from the Northern Dvina and Vychegda rivers to the forest-tundra belt; the Urals (from 60° N at Mount Kumba to the Shchuchya Basin); the lower reaches of the Ob. East of a rather large gap, the species again occurs across the forest belt of Siberia starting from the Taz and Tara basins and the Altai, reaching the Lower Lena, Verkhoyanskiy Range, and Upper Aldan. There are solitary findings around Ayan, at the Upper Zeya, and in the mountains of the northern Korea Peninsula. The species is missing from most of Transbaykalia as well as Mongolia (except some few locations in its northern part).

In the Altai and Sayan Mountains, it occurs mostly in the subalpine zone, at 1,600–2,000 m (to 2,200 m in Tuva); on the Aldan High Plateau, it reaches 1,000 m. (Fig. 35.)

Sect. 14. *Nigricantes*

Kerner, 1860, N.-Öst. Weid.: 235.

T y p u s: *Salix myrsinifolia* Salisb.

Small or medium-sized shrubs. Floriferous buds greatly different from vegetative ones, ovoid, obtuse; *caprea*-type of bud size gradation. Stipules mostly fully developed, distinctly inequilateral. Leaves firm, bright green above, lustrous when alive, easily blackening when dried, their veins conspicuously prominent beneath. Nectary solitary, short, rectangular or square. Capsules stipitate, acute, attenuating into a pronounced style. Capsule stipes not elongating after flowering. Stigmas two-lobed or two-parted, comparatively small (0.2–0.6 mm), considerably shorter than styles.

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This is a small-sized group of some three or four species. Along with those mentioned below, one more might belong here. That is an Iranian willow *S. zygostemon* Boiss., a mysterious species which is still totally obscure.

As to its morphology, the section *Nigricantes* occupies an intermediate position between *Glabrella*, *Hastatae*, *Vetrix*, and *Arbuscella*.

Key to Species

1. All leaves of same color beneath: either dull, whitish or green, lustrous 2
- Inferior leaves green, superior ones glaucous beneath 52. **S. myrsinifolia**
2. Leaves green beneath 54. **S. mielichhoferii**
- Leaves glaucous beneath 53. **S. apennina**

52. ***S. myrsinifolia*** Salisb. 1796, Prodr. stirp. Allert.: 394 (nom. nov. pro *S. myrsinites* Hoffm. non L.); Schneider, 1916, Öst. bot. Z. **66**: 115; Grappengiesser, 1955, Bot. not. **108**: 327; Korchagin, 1957, Fl. Leningr. obl. **2**: 16; Rasinš, 1959, Ivy Latv.: 101; Skvortsov, 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4530; Krall, Viljasoo, 1965, Eestis kasv. pajud: 48. —*S. myrsinites* Hoffm. 1787, Hist. Salic. **1**, 4: 71 et tab. 17–19; Wulfen, 1788, in Jacquin, Collect. bot. **2**: 136. —Non *S. myrsinites* L. 1753. —*S. nigricans* Sm. 1802, Trans. Linn. Soc. **6**: 120; Koch, 1820, Flora **3**: 283; Ledeb. 1850, Fl. Ross. **3**, 2: 608 (excl. pl. Sibir. orient.); Wimmer, 1866, Salic. Eur.: 70; Anderss. 1867, Monogr. Salic.: 125; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 131; Enander, 1910, Salic. Scand. Exs. **3**: N 101–104; Krylov, 1930, Fl. Zap. Sib. **4**: 348 (excl. pl. altaic.); Wolf, 1930, Fl. Yu.-V. **4**: 47; Floderus, 1931, Salic. Fennosc.: 48; Nazarov, 1936, Fl. SSSR **5**: 85 (excl. var. *jenisseensis*); Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 693; Nazarov et al. 1952, Fl. URSS **4**: 35; Shlyakov, 1956, Fl. Murm. **3**: 84; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 87; id. 1964, Fl. Eur. **1**: 49. —*S. borealis* (Fries) Nasarov, 1936, op. cit. **5**: 87 (p. p. minore!); Floderus, 1936, Sv. bot. tidskr. **30**: 393; Shlyakov, 1956, op. cit. **3**: 86; Rech. f. 1964, op. cit. **3**: 48. —*S. kolaënsis* Schljakov, 1956, op. cit. **3**: 90, 364. —*S. phyllicifolia* L. 1753, Sp. pl.: 1016 (p. p. quoad var. β).

T y p u s: "Carinthia, Klagenfurth, am Fuß e des Schmalzbergels —F. X. Wulfen" (B?, n. v.).

G. Hoffmann described the plants he had received from F. Wulfen. The original plants are lost now, none of them found in Hoffmann's Herbarium in Moscow. However, there are many duplicates of F. Wulfen's collections in Willdenow's Herbarium in Berlin-Dahlem.

Ssp. ***borealis*** (Flod.) A. Skv. comb. nova. —*S. nigricans* ssp. *borealis* Flod. 1931, Salic. Fennosc.: 49; Hylander, 1945, Uppsala Univ. Arsskr. **1**, 7: 121. —*S. nigricans* var. *borealis* Fr. 1840, Bot. not.: 193. —*S. kolaënsis* Schljakov, 1956, Fl. Murm. **3**: 90, 364.

T y p u s: "In regionibus subsylvaticis et subalpinis Scandinaviae" (Fries Herb. Norm. fasc. 7, N 63, S, LE! et alibi).

The subspecies *borealis* is characterized on the average by larger leaves, their lower surface mostly green, pubescence more pronounced and often considerably sericeous.

HABITATS: Lighted, not too dry forests, edges of eutrophic and mesotrophic wetlands, as well as a whole range of secondary postforest habitats, such as clearings, coppices, openings, and forest edges. The species is quite common on residential lots and at roadsides. Being able to cope with almost any substrate acidity, it avoids only the most acidic and poorest grounds. Well-moisturized, but not overwatered soils are those preferred by this willow.

DISTRIBUTION: The northern British Isles and all of Scandinavia; Denmark and northwestern Germany (scattered); the Alps, Sudetes, and eastern Poland. The southern boundary goes along the border between Ukraine and Belarus (there are some solitary locations in northwestern Ukraine), then along the line connecting the cities Chernigov, Kursk, Tambov, and Ulyanovsk. Detouring the Bugulma Upland, the area boundary then descends along the Urals to Orsk; east of the Urals, it again steeply ascends northward, reaching Tobolsk and Khanty-Mansiysk; east of that area, there are some solitary findings, but not farther than the Ob. The northern boundary runs from Khanty-Mansiysk to the Konda River Basin, then via the northern meander of the Pechora and the southern Kanin Peninsula. On the Kola Peninsula, the species is encountered nearly everywhere. All data concerning the Altai, East Siberia, etc. are erroneous.

In the Alps, the willow ascends as high as 2,400 m; in Scotland, to 750 m; in northern Norway (around Tromsö), to 900 m; in the Khibins, to 400 m; in the Prepolar Urals, to 500–600 m; in the Southern Urals, to 800 m.

The ssp. *borealis* is distributed only in Fennoscandia; within the Russian territory, it occurs on the Kola Peninsula. (Fig. 36.)

NOTE. *S. myrsinifolia* is probably the most variable, manifold species of all the European willows. One can count scores of its synonyms, which were used by J. Smith, C. Willdenow, J. Forbes, and others for numerous repeated descriptions of this willow (not even to mention a hundred names by J. Schleicher and half a hundred by M. Gandoger). Not infrequently, *S. myrsinifolia* hybridizes with other willows, however, the majority of plants that have been treated as hybrids in the literature and herbaria, are by no means hybrids. Instead, they are normal variants within the species variability range. This is particularly true for those with pronounced pubescence. Even the most dense pubescence of the shoots, leaves, and capsules cannot be considered as a characteristic foreign to the species (see chapter 3, section 5).

Ssp. *borealis* is not very well delimited morphologically or geographically, and therefore it makes absolutely no sense to assign a species rank to this taxon.

Ssp. *alpicola* Buser ex Jaccard, 1895, Catal. valais.: 328 appears to be just an ecological form of the alpine zone and hardly deserves a special taxonomical treatment (cf. Handel-Mazzetti 1957).

53. **S. apennina** A. Skv. 1965, Novosti sist. vyssh. rast. **1965**: 90. —? *S. nigricans* var. *apennina* Borzi, 1885, Compend. fl. forest. ital.: 142. —*S. nigricans* (non Smith) auct. fl. ital. p. p. (quoad pl. apennin.); Bertoloni, 1854, Fl. Ital. **10**: 312; Parlatores, 1867, Fl. Ital. **4**: 250; Fiori, 1923, Nuova fl. analit. Ital. **1**, 3: 344 (pro var.) et al.

T y p u s: "Prov. Toscana, Apenninus Pistoriensis, ad. lacum Greppo, 9. VII 1888 leg. E. Levier" (FI).

HABIT: A low or medium-sized shrub.

HABITATS AND DISTRIBUTION: Damp and paludal places; on siliceous as well as calcareous substrates from 300 m to alpine elevations across the Apennines and on northeastern Sicily (the Etna Massif). (Fig. 36.)

54. **S. mielichhoferii** Sauter, 1849, Flora **32**: 662; Kerner, 1867, Öst. bot. Z. **17**: 85; Rech. f. 1947, Sitzungber. Österr. Akad. Math.-naturwiss. Kl. Abt. 1, **156**: 502; id. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 88; id. 1964, Fl. Eur. **1**: 49; Janchen, 1956, Catal. fl. Austr. **1**: 104. —*S. glabra* var. *mielichhoferii* Anderss. 1867, Monogr. Salic.: 175. —*S. nigricans* × *hastata* Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 235.

T y p u s: "Reitalpgraben auf dem Dungmahd der Schattbachalpe in der Tofern des Grossarltales, 5000' —Mielichhofer" (Wien Univ. Hb. Kerner, n. v.).

HABIT: A medium-sized (to 3 m) shrub.

HABITATS: Damp peaty meadows and banks of streams at 1,500–2,200 m mostly on acidic and siliceous substrates, but occasionally also on limestone, dolomite, slate, etc.

DISTRIBUTION: The Austrian Alps (Styria, Carinthia, Salzburg, Tirol); Italian Alps (Southern Tirol). (Fig. 37.)

NOTE. It may cause a problem to discriminate between this species, *S. myrsinifolia*, and *S. glabra*, if samples are incomplete or poorly dried. Since *S. mielichhoferii* occurs rather sparsely, it appears to be inadequately studied, as far as its morphological and geographical range is concerned. See also the note to *S. phyllicifolia*.

Sect. 15. *Vetrix*

Dum. 1825, Bijdr. Natuurk. Wetensch. **1**, 1: 55 (p. p.).

T y p u s: *Salix caprea* L.

Small or medium-sized trees or rather large shrubs. Wood under shoot bark often with longitudinal striae (excrescences). Floriferous and vegetative buds usually extremely different; *caprea*-type of bud size gradation; bud apices mostly abaxially recurved. Stipules mostly distinctly inequilateral. Petioles convex above. Leaves broad, entire, or coarsely and irregularly dentate, their veins usually conspicuously prominent beneath. Catkins precocious or subprecocious. Nectary solitary, short. Ovaries stipitate; stipes may elongate when capsules ripen. Styles mostly short (seldom more than 0.5–0.6 mm long); stigmas nearly as long as styles.

This is a large section (at least 30 species) which is widely distributed across forested areas of the temperate climate belt both in the Old and New World and missing from the arid and subtropical belts. It consists of six subsections, four of which are represented in this country (two more are Chinese-Japanese). The relation with the sections *Nigricantes* and *Hastatae* via the subsection *Vulpinae* is quite obvious.

Key to Species

1. Floriferous buds large (7–12 mm long), strongly flattened, their broad, flat apices markedly recurved off shoots. Stipules abortive, even on vigorous shoots, lanceolate, deformed, much shorter than petioles. Catkin stalks often foliated; leaves fully developed. Bracts pale or rufescent-brown, but not black, 1.5–3 mm long. Ovaries clothed with dense white pubescence 2
- Buds mostly different in shape from above. Stipules on vigorous shoots well developed, broad, distinctly inequilateral, semicordate. Bracts black, at least at apices; if pale, then 0.8–1.5 mm long 3
2. Bracts pale or rufescent. Anthers 0.7–0.8 mm long. Styles not shorter than stigmas 55. **S. kuznetzowii**
- Bracts brownish. Anthers 0.8–1.0 mm long. Styles usually significantly shorter than stigmas 56. **S. laggerii**
3. Catkins typically subprecocious, rather loosely flowered, their rachises exposed when ripen, at least in female ones. Bracts brownish or black at apices, 1–2 (seldom to 2.5) mm long. Capsule stipes mostly considerably elongating when ripening. Anthers 0.4–0.8 mm long. Stigmas 0.2–0.4 mm long 4
- Catkins precocious, densely flowered (rachises never exposed). Bracts black, densely pubescent, 2–3 mm long. Capsule stipes elongating inconspicuously when ripening. Ovaries always pubescent. Anthers 0.7–1.1 mm long. Stigmas 0.5–0.8 mm long 18
4. Leaves narrowly oblanceolate, all uniformly covered beneath with dense white tomentum consisting of extremely thin, tangled trichomes 68. **S. salvifolia**
- Pubescence on mature leaves looking different or leaves glabrous beneath, either partially or entirely 5
5. Cataphylls more or less dentate at margins. Bracts usually more pubescent on their inside than outside. Ovaries lanceolate, acute (gradually attenuating into styles), usually glabrous, seldom covered with tangled, crispy, white trichomes 6

- Cataphylls mostly entire at margins. Bracts equally pubescent on their inside and outside surfaces. Ovaries covered with grayish, sericeous, not tangled trichomes . . . 9
- 6. Stipules obtuse at apices. Bracts less than 1 mm long, densely covered with short, straight, often reddening trichomes that stick out above bract margins as far as 0.3–0.8 mm. Stamen filaments to 3 mm long, anthers 0.4–0.5 mm long. Capsule stipes mostly up to 1 mm long 61. **S. vulpina**
- Stipules acute at apices. Bracts sparsely covered with long, soft, white trichomes. Stamen filaments 4–6 mm long, anthers 0.5–0.7 mm long. Capsule stipes mostly longer than 1 mm 7
- 7. Leaf shape insignificantly changing along shoots. Young leaves in spring mostly of bright reddish color, not blackening on drying. Catkin rachises puberulous or glabrate. Anthers bright rust-colored before dehiscence, dark when dried . . . 57. **S. silesiaca**
- Leaf shape changing significantly along shoots: from obovate in inferior leaves to narrowly lanceolate in superior ones. Young leaves green in spring, easily blackening on drying. Rachises in female catkins densely pubescent. Before dehiscence, anthers yellow or partially purple, but not red 8
- 8. Low shrub. Leaves thin, glabrous beneath or pubescent along midrib. Capsule stipes 0.7–1.4 mm long 58. **S. caucasica**
- Tall shrub or tree. Leaves firm, at least some densely pubescent beneath, particularly in central part of leaf blade. Capsule stipes 2–5 mm long 60. **S. pedicellata**
- 9(5). Floriferous buds ovoid, without beaks. Leaf blades mostly broadest above their middle; leaf shape usually changing significantly along shoots. Mature leaves mostly with prominent reticulation beneath. Pubescence beneath more pronounced in central part of leaf blade, consisting mostly of highly flexuous, randomly oriented trichomes 10
- Floriferous buds lanceolate or oblong-lanceolate, their beaks either acute or obtusish, flattened. Leaves mostly broadly elliptic or elliptic, broadest about their middle, 1–2.5 times as long as broad; much more seldom, leaves obovate. Leaf shape constant along shoots. Leaf blades flat above, with inconspicuous reticulation beneath, either glabrous or uniformly covered with non-crispy, almost straight or slightly flexuous trichomes 13
- 10. Wood under bark without striae or with sparse, inconspicuous striation. Difference between floriferous and vegetative buds not obvious. Cataphylls and inferior leaves beneath covered with appressed, thin, sericeous trichomes. Capsule pubescence short, dense, tightly appressed, so that capsules look completely silvery 59. **S. appendiculata**
- Wood under bark with pronounced striation. Floriferous buds look strikingly different from vegetative ones. Pubescence on inferior leaves and capsules generally not sericeous or silvery 11
- 11. Low or medium-sized shrub. Shoots slender (1–1.5 mm), frequently reddish. Petioles slender, short, mostly not longer than stipules. Leaves obovate or (occasionally) oblanceolate, always broadest much above middle of blades, mostly coarsely wavy-dentate at margins, their upper surface distinctly reticulate-rugose . . . 67. **S. aurita**
- Tall shrubs or trees. Shoots 1.5–2.3 mm thick. Petioles stoutish (about 1 mm), typically much longer than stipules. Leaves oblanceolate or more or less elliptic, their upper surface usually flat, not rugose 12
- 12. Leaves mostly oblanceolate. Young leaves often with rufescent pubescence. Bracts comparatively large, mostly black at apices. Capsules more or less lageniform: their

- bases widened and upper parts narrowly oblong. Stigmas 0.3–0.5 mm long, usually longer than styles, pigmented 65. **S. atrocinerea**
- Leaves mostly elliptic (except inferior ones). Young leaves with white pubescence. Bracts comparatively small, mostly reddish-brown, not black at apices. Capsules lanceolate, gradually attenuating into styles. Stigmas 0.15–0.3 mm long, mostly shorter than styles, usually pale 60. **S. pedicellata**
13. Leaves small (7–30 mm long), broadly elliptic or round, often cordate at base 69. **S. tarraconensis**
- Leaves larger and more elongated 14
14. Bracts pale or diffusely reddish-brown, mostly not more than 0.5–0.6 mm broad 15
- Bracts black or at least conspicuously blackish at apices, mostly not less than 0.6 mm broad 17
15. Catkins extremely loose by the time capsules ripen; capsule stipes 2.5–5 mm long; capsules extremely narrow, nearly aciculiform 16
- Catkins only moderately loose by the time fruits ripen. Capsule stipes 1.5–2.5 mm long, capsules narrowly lanceolate 75. **S. pseudodepressa**
16. Mature shoots and leaves glabrous. Shoots mostly brightly colored. At start of flowering young catkins and cataphylls highly sericeous 70. **S. starkeana**
- Mature shoots and leaves more or less pubescent. Shoots mostly dull. Cataphylls and young catkins slightly sericeous 71. **S. bebbiana**
- 17(14). Mature shoots and leaves glabrous. Shoots, buds, and upper sides of leaves smooth, lustrous. Shoots and petioles mostly reddish or reddish-brown 72. **S. taraikensis**
- Shoots and leaves typically at least partially pubescent. Shoots, buds, and leaves dull, without red tones in coloration 74. **S. iliensis**
- 18(3). Floriferous buds lanceolate or oblong-lanceolate, their beaks conspicuous, either acute or obtusish, compressed; adaxial surfaces flattened (lateral carina in close proximity to adaxial surface at side view). Leaves mostly broadly elliptic or elliptic, with obscure reticulation beneath, either glabrous or clothed with thin, appressed, slightly flexuous trichomes (except midrib where pubescence frequently different). Wood striae sparse, scattered. 19
- Floriferous buds more or less ovoid, stout, neither attenuating into beaks nor compressed (lateral carina approximating to median of bud corpus at side view). Leaf veins conspicuously prominent beneath. Leaves pubescent not only on midribs but all over their surfaces, at least young ones; trichomes distorted, deviating off the surface 21
19. Young shoots glabrous or glabrate. Mature shoots, buds, and leaves glabrous, smooth. Bracts blackish-brown, either entirely or only at apices 72. **S. taraikensis**
- Young shoots densely pubescent; mature shoots, buds, and leaves retaining at least some pubescence. Bracts completely black, at least at time of flowering 20
20. Three- and four-year-old shoots olivaceous-tawny or blackish. Bud beaks mostly acute. Style length + stigma length = 1.2–1.7 mm; style length nearly = stigma length 73. **S. abscondita**
- Three- and four-year-old shoots light gray or yellowish. Bud beaks mostly obtuse, compressed. Style length + stigma length = 0.7–1.1 mm; stigmas typically longer than styles 74. **S. iliensis**
- 21(18). Trees 22

- Tall shrubs 24
22. Wood smooth or with short, sparse striae. Inferior (and often all) leaves elliptic, equally acuminate at both ends. Mature leaves uniformly pubescent all over their surface; trichomes bent at apices, but not ruffled, deviating off leaf blades. Anthers 0.9–1.2 mm long 62. **S. caprea**
- Wood with multiple striae. Inferior (and occasionally all) leaves obovate or oblanceolate, their broadest parts definitely above middle of leaf blades. Anthers 0.6–1.0 mm long 23
23. Leaves broad (20–50 mm; 1.25–3.5 times as long as broad), ordinary and superior ones mostly broadest about middle of blades; all leaves pubescent beneath, at least around midribs (rarely completely glabrous); trichomes white or grayish, deviating off leaf blades (as in *S. caprea*); pubescence on veins of second and third order, if any, not more dense than between veins 63. **S. aegyptiaca**
- Leaves narrower (12–30 mm; 2.5–4.5 times as long as broad); pubescence mostly rufescent, consisting of ruffled trichomes, conspicuously more dense on veins than in-between; frequently, leaves absolutely glabrous 65. **S. atrocinerea**
- 24(21). Wood striae mostly rather sparse; no conspicuous furrows on outside of bark. Mature leaves dark green, mostly glabrous above, glaucous beneath. Leaf blades mostly lanceolate or spear-shaped (narrowing more towards base than top), rarely oblanceolate or spatulate. Marginal denticles extending to very leaf blade base. Veins of third order obscure, reticulation not very dense beneath. Young leaves easily blackening on drying 66. **S. pseudomedemii**
- Wood striation usually very prominent; longitudinal furrows distinct on bark surface of four- or five-year-old and older branches. Mature leaves dull green, usually puberulent above and mostly ash gray (cinereous) beneath. Leaf blades oblanceolate, abruptly acuminate at apices, gradually attenuating towards bases (occasionally, nearly spatulate); denticles not extending to leaf base. Veins of third order distinct, reticulation dense beneath. Leaves not blackening on drying 64. **S. cinerea**

Subsect. *Kuznetzowianae*

A. Skv. subsect. nova. Novosti sist. vyssh. rast. a. 1968 describetur.

T y p u s: *Salix kuznetzowii* Goerz.

Subalpine shrubs with stout short branches. Floriferous buds strongly flattened, with flat, recurved apices. Stipules small. Leaves large, conspicuously changing their shape along vigorous shoots: inferior ones broad and short, superior ones narrow and elongated; beneath covered with dense, crispy pubescence. Catkins densely pubescent, bracts large, rufescent or brownish, but not black. Capsules densely lanate, white with pubescence.

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This is a rather isolated group consisting of just two species.

55. **S. kuznetzowii** Laksch. ex Goerz, 1930, in Grossheim, Fl. Kavk. 2: 9; Görz, 1934, Feddes Repert. 36: 231; Nazarov, 1936, Fl. SSSR 5: 98; Grossheim, 1945, Fl. Kavk. 2 ed. 3: 19; Sosnovskiy, 1947, Fl. Gruz. 3: 15; Karyagin, 1952, Fl. Azerb. 3: 53; Makhatadze, 1961, Dendrofl. Kavk. 2: 26; Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR 15: 129.

T y p u s: "Daghestan. Kaitago-Tabasaran". No specimen labeled like this was found in the St. Petersburg Herbarium. However, there is a nice sample "Chewsuretia ad lacum Tanes —Hb. Bayern" with an enclosed authentic diagnosis by P. Lakschewitz. That

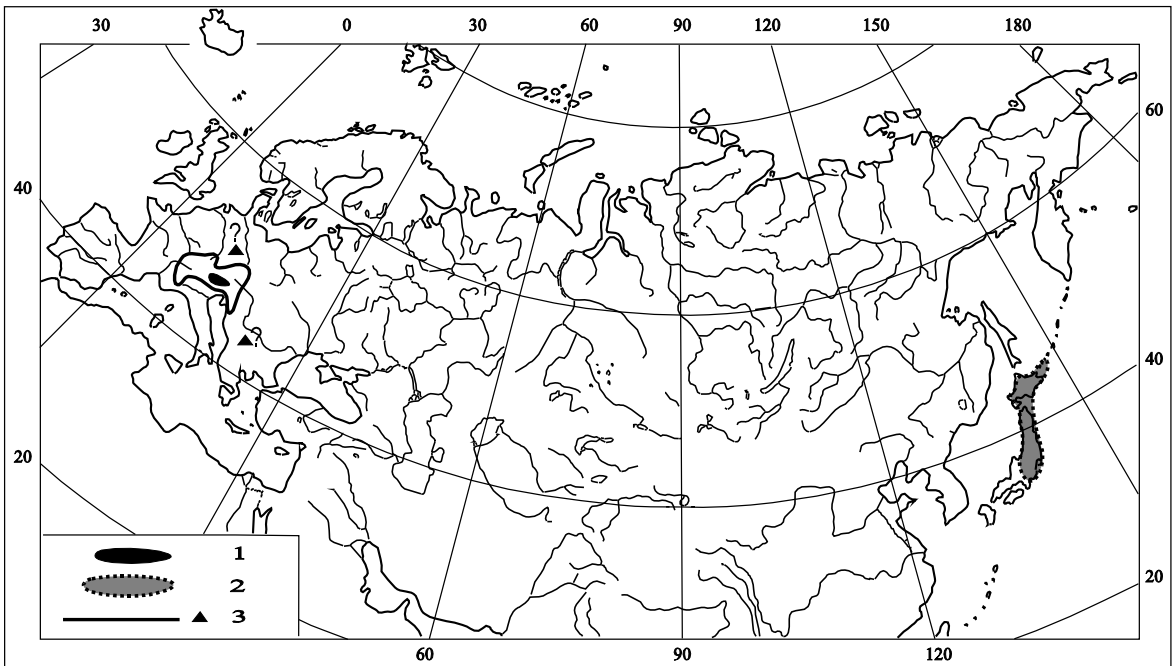


Fig. 37. Distributional areas of *Salix mielichhoferii* Sauter (1), *S. vulpina* Anderss. (2), and *S. appendiculata* Vill. (3)

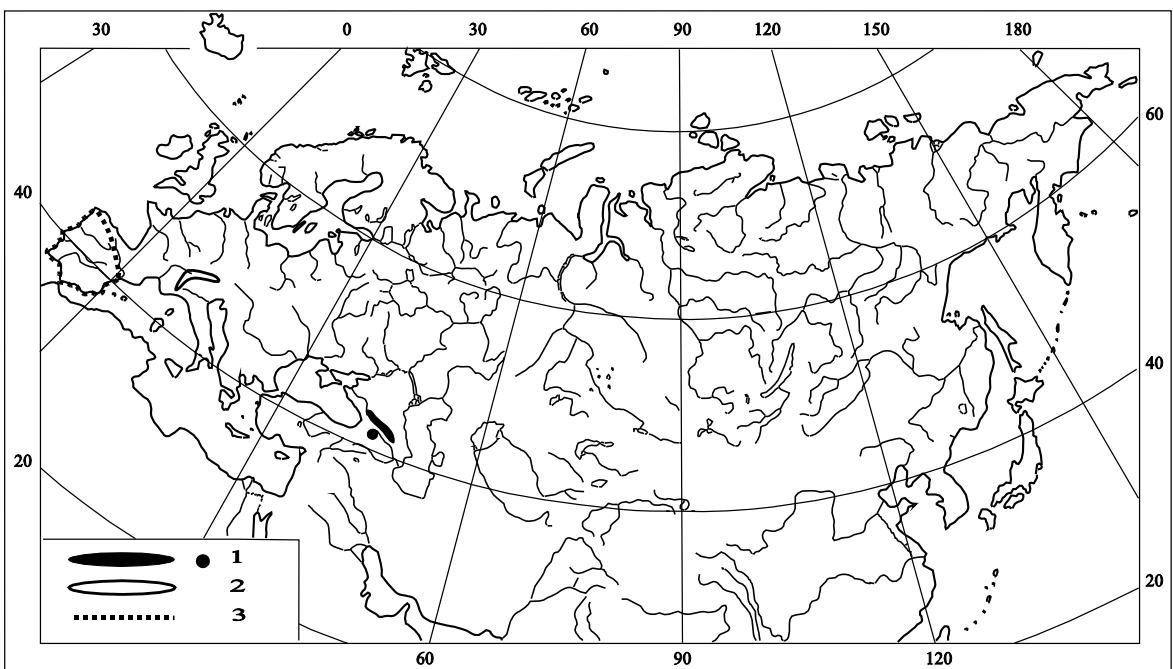


Fig. 38. Distributional areas of *Salix kuznetzowii* Laksch. ex Goerz (1), *S. laggerii* Wimm. (2),

specimen could be accepted as neotype.

HABIT: A medium-sized or fairly low shrub.

HABITATS: Rocks, shrublands, light birch and pine forests in the upper forest, subalpine, and partially alpine zones (1,600–2,600 m). The species apparently is restricted to limestone.

DISTRIBUTION: The Greater Caucasus from Uch-Kulan Gorge in Karachay to Mount Shakhdag in Azerbaijan (sporadically); the Trialeti Range (near Bakuriani and along the Tana River). There are just a little more than 30 locations known total. (Fig. 38.)

56. **S. laggerii** Wimm. 1854, Flora **37**, 11: 62; Rech. f. 1963, Öst. bot. Z. **110**: 339; id. 1964, Fl. Eur. **1**: 50. —*S. pubescens* Schleich. ex Kern. 1865, Herb. Öst. Weid.: N 30, 31; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 650; Rech. f. 1947, Sitzungber. Österr. Akad. Math.-naturwiss. Kl. 1, **156**: 499; id. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 102; Janchen, 1956, Catal. fl. Austr. **1**: 104. —*S. devestita* Arvet-Touvet, 1873, Essai pl. Dauphin.: 60. —*S. albicans* Bonjean ex Buser, 1897, in Dörfler, Schedae ad Herb. Norm. **32**: 83 (N 3230); Jaccard, 1895, Catal. valais.: 329; Becherer, 1956, Suppl. Valles.: 136. —*S. glauca* × *grandifolia* Wimm. 1866, Salic. Eur. : 256.

T y p u s: "Ad moles glaciales Rhodani (am Rhonegletscher), 1853, Dr. Lagger" (G, LE!, FI!).

HABIT: A low, distorted shrub.

HABITATS: Rocks, taluses, and banks of streams in the subalpine and alpine zones (1,500–2,100 m).

DISTRIBUTION: A comparatively small number of extremely scattered locations from the Maritime Alps to Austrian Tirol. (Fig. 38.)

Subsect. *Vulpinae*

Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Sagh. **4**: 403.

T y p u s: *Salix vulpina* Miq.

Small trees or, more frequently, shrubs. Floriferous buds ovoid, not very distinctly different from vegetative ones. Pubescence on young leaves pronounced, consisting of crispy trichomes, usually fugacious. Female catkins loose, bracts small, obtuse, light brown or blackish only at apices, mostly puberulent. Ovaries glabrous or pubescent, lanceolate, acute. Stigmas very short.

There are five species in the flora of this country. It is not improbable that the similarity between *S. vulpina* and the European species may be purely apparent, so that further studies may result in separating *S. vulpina* from the European species.

57. **S. silesiaca** Willd. 1806, Sp. pl. **4**, 2: 660; Wimmer, 1866, Salic. Eur.: 60; Anderss. 1867, Monogr. Salic.: 65; Wołoszczak, 1899, Öst. bot. Z. **39**: 331; Beck v. Mannagetta, 1906, Glasn. zem. muz. Bosn. Herc. **18**: 73; Seemen, 1909, in Aschers. et Graebner Synopsis **4**: 107; Görz, 1928, Feddes Repert. Beih. **52**: 1 et seq. (p. p.: excl. pl. caucas.); Nazarov et al. 1952, Fl. URSS **4**: 46; Beldie, 1952, Fl. Rom. **1**: 307; Pawłowski, 1956, Fl. Tatr **1**: 190; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 97; id. 1964, Fl. Eur. **1**: 49; Cmelař, 1963, Sb. Vys. šk. zem. Brne **2**: 119.

T y p u s: "In Silesiae montibus. Herb. Willdenow N 18116" (B, n. v.) (cf. Goerz, 1928: 19).

HABIT: A medium-sized or tall (1–4 m) shrub, occasionally almost a small tree.

HABITATS: Lighted woods, forest edges, openings, subalpine shrublands, as well as a whole range of secondary postforest habitats. It grows in the mountains, mostly within the distributional area of the spruce; on the plain, it is very rare.

DISTRIBUTION: The Sudetes, all of the Carpathians (Western, Eastern, and Southern), the mountains of Bosnia, Herzegovina, Crnagora (Montenegro), Albania (?), and western Bulgaria. In the Eastern Carpathians, it is encountered in the middle and upper forest zone, typically ascending to 1,700–1,800 m. There are some solitary locations on the plain in the vicinity of Lvov. In the Tatras, it occasionally ascends to 2,000 m (Chmelař 1963); also to 2,000 m in Montenegro. (Fig. 39.)

58. *S. caucasica* Anderss. 1867, Monogr. Salic.: 68; Nazarov, 1936, Fl. SSSR **5**: 101; Grossheim, 1945, Fl. Kavk. **3**: 21; Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR **15**: 122. —*S. silesiaca* var. *caucasica* Anderss. 1868, in DC. Prodr. **16**, 2: 219; Görz, 1930, in Grossheim, Fl. Kavk. **2**: 7; id. 1934, Feddes Reppert. **36**: 234. —*S. heterandra* Dode, 1908, Bull. Soc. Bot. Fr. **55**: 654. —*S. paracaucasica* Goerz, 1928, Feddes Repert. Beih. **52**: 28 et tab. 2; id. 1930, op. cit. **2**: 7; Nazarov, 1936, op. cit. **5**: 102. —*S. palibinii* Goerz, 1928, op. cit. **52**: 29 et tab. 3; id. 1930, op. cit. **2**: 7; Nazarov, 1936, op. cit. **5**: 102. —*S. daghestanica* Goerz, 1930, op. cit. **2**: 6; id. 1934, op. cit. **36**: 236.

T y p u s: "Caucasus —Nordmann" (LE!).

HABIT: A low or medium-sized (0.5–1.5, sometimes to 2 m) shrub, usually rather distorted.

HABITATS: Humid parts of the subalpine and upper forest zones (1,500–2,400 m). Occasionally, it may descend to considerably lower elevations, where it grows along streams or on cold spring fens (for instance, in the Bzyb River Gorge in Abkhazia it is encountered as low as 200–300 m).

DISTRIBUTION: The western Greater Caucasus (from the Fisht-Oshten Massif to Svanetia, very common). East of that area it occurs less often, being encountered all across the main range, its southeasternmost location in Ismaili District. Seven findings known from Dagestan and eight from Azerbaijan. It again becomes common in the Adzharo-Imeretinskiy and Adzharo-Shavshetskiy ranges, although it has never been found in other parts of the Lesser Caucasus. Within the territory of Turkey, the only known collections are from Chorukh (Artvin). (Fig. 39.)

59. *S. appendiculata* Vill. 1789, Hist. pl. Dauphin. **3**: 775; Timbal-Lagrave, 1856, Mem. Acad. Toulouse 4, **6**: 147; Schinz et Thellung, 1913, Vierteljahresschr. Naturf. Ges. Zü rich **58**: 49 (cf. Toepffer, 1913, Öst. bot. Z. **63**: 343); Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 99; id. 1964, Fl. Eur. **1**: 50. —*S. grandifolia* Seringe, 1815, Saul. Suisse: 20; Wimmer, 1866, Salic. Eur.: 66; Anderss. 1867, Monogr. Salic.: 60; Camus, 1904, Saul. Eur. **1**: 208; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 103; Rouy, 1910, Fl. Fr. **12**: 207; Toepffer, 1914, in Vollman, Fl. Bayern: 198; Rech. f. 1938, Feddes Repert. **45**: 88; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 647; Rech. f. 1953, Godišn. Biol. Inst. Sarajevu **5**: 335; Chmelař, 1963, Sb. Vys. šk. zem. Brne C, **2**: 119. —Excl. syn. *S. pubescens* Schleich., *S. albicans* Bonjean, *S. laggerii* Wimm.

T y p u s: "Dauphiné, bois de la Grande Chartreuse" (Herb. Chaix, P?, n. v.).

HABIT: A medium-sized or tall shrub or a small tree.

HABITATS: Rocks, taluses, moist slopes, and banks of streams in the montane forest and subalpine zones, mostly on limestone. It has also been encountered on peaty as well as siliceous substrates.

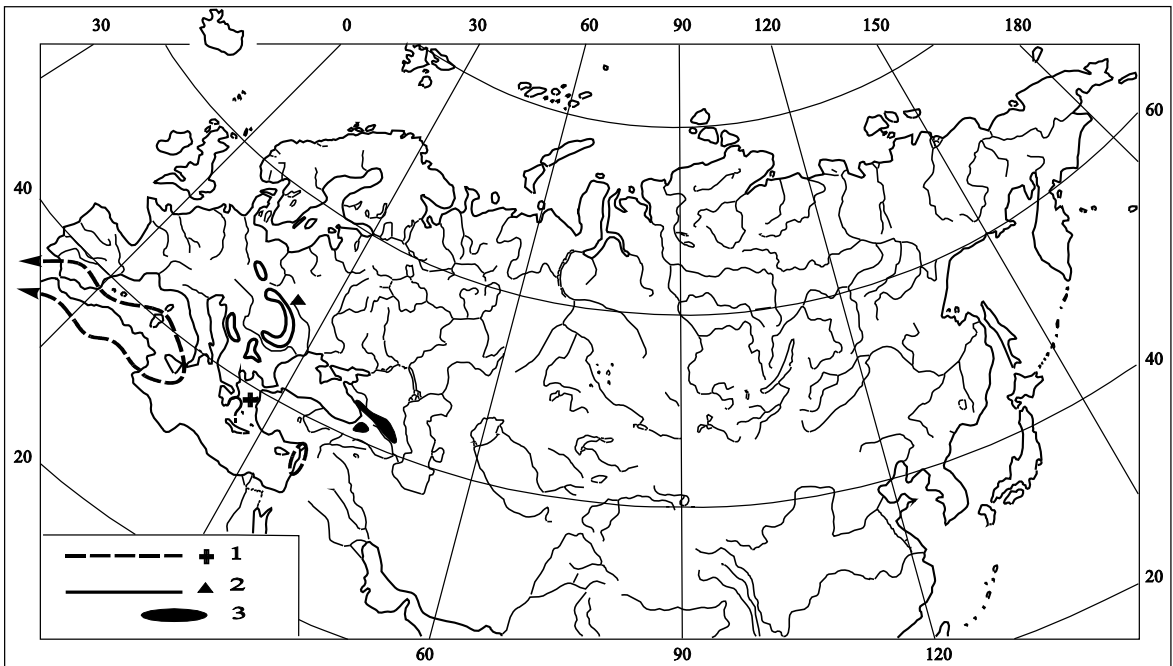


Fig. 39. Distributional areas of *Salix pedicellata* Desf. (1), *S. silesiaca* Willd. (2), and *S. caucasica* Anderss. (3)

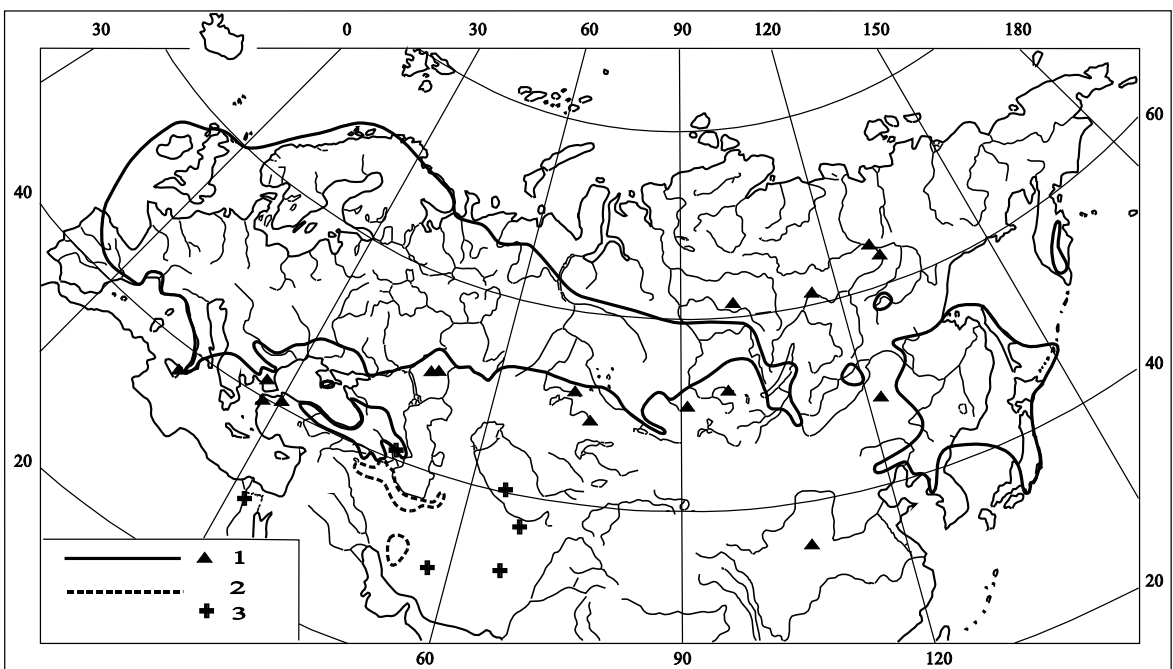


Fig. 40. Distributional areas of *Salix caprea* L. (1), *S. aegyptiaca* L. (2), and cultivated *S. aegyptiaca* (3)

DISTRIBUTION: All of the Alps from the Maritime Alps to Lower Austria and Slovenia; the Jura, Schwarzwald, Shumava, Bohemian-Moravian Highlands, Croatia (the Velebit Range); the Apennines (findings in Tuscany and Emilia, such as those from Boscolongo and Mount Rondinayo, are the only reliable ones; the rest have to be assigned to *S. apennina*). I also found some solitary samples from Thuringia (near Weimar), the Belanskiye Tatras, and southern Serbia (the Suva Planina); however, data from these localities need to be confirmed. (Fig. 37.)

60. *S. pedicellata* Desf. 1800, Fl. Atlant. **2**: 362; Anderss. 1867, Monogr. Salic.: 59; Boiss. 1879, Fl. Or. **4**: 1189; Post, 1933, Fl. Syr. **2**: 532; Vicioso, 1951, Salic. Españ.: 104; Maire, 1961, Fl. Afr. Nord **7**: 58; Skvortsov, 1966, Trudy Bot. In-ta AN ArmSSR **15**: 123. —*S. canariensis* Chr. Smith ex Buch, 1825, Physik. Beschr. Canar.: 159; Webb, 1850, Phytogr. Canar. **3**: 270 et tab. 215. —*S. nigricans* Boiss. 1879, op. cit. **4**: 1190, non Sm. —*S. libani* Bornm. 1914, Beih. Bot. Zbl. **31**: 259.

T y p u s: "Ad rivulos Sibibae in regno Tunetano" (n. v.).

Ssp. *canariensis* (Buch) A. Skv. comb. nova. —*S. canariensis* Chr. Smith ex Buch (1825) l. c.

T y p u s: "Insulae Canarienses, Chr. Smith" (n. v.).

HABIT: A tall shrub or small tree (to 8–10 m tall).

HABITATS: River banks and moist places.

DISTRIBUTION: Southern Spain including Huelva, Ciudad Real, and Almeria (so far, not found in Portugal); Sardinia, Sicily, and Malta; the mountainous regions of Tunisia; northern Algeria (including the Saharan Atlas) and Morocco (including the Anti-Atlas). Having an enormous distributional gap, it is found next in Lebanon, the mountains of western Syria, and Turkey (Hatay Province). It might have been found on Ikaria in the Aegean Sea (Rechinger 1943: 96), although these data need confirmation. Evidence from continental Italy as well as Corsica is hardly true (a few samples from Corsica, that I examined, appeared to be *S. atrocinerea*).

The vertical range in Northern Africa is from nearly the sea level to 2,400 m; on Sardinia, 0–700 m; in Lebanon, 300–1,100 m.

The area of ssp. *canariensis* comprises the Madeira and Canary islands (300–800 m). (Fig. 39.)

NOTE. I had an opportunity to examine a rather nice series of *S. canariensis* (11 samples without duplicates). Although the differences from *S. pedicellata* s. str. were quite obvious when considering the whole series, it was still impossible to identify each of the samples confidently. Therefore, *S. canariensis* would be more properly treated in the rank of subspecies. It is characterized by less pronounced pubescence on mature shoots, leaves, and buds; narrower and longer leaves; shorter capsule stipes (1.5–2.5 mm compared to 2–4.5 mm in ssp. *pedicellata*). I don't have enough reasons to distinguish the subspecies segregated by R. Maire (ssp. *antiatlantica*, ssp. *hesperia* Maire, 1961, op. cit. **7**: 60).

S. peloritana Prestrand ex Tineo, 1847, Plant. rar. Sicil. **2**: 31; Parlato, 1867, Fl. Ital. **4**: 246; Nicotra, 1904, Nuovo Giorn. bot. Ital. **11**: 47; Lojacono, 1904, Fl. Sic. **2**, **2**: 393. Cf. etiam: Camus, 1904, Saul. Eur. **1**: 281; Rouy et Foucaud, 1910, Fl. Fr. **12**: 230; Rouy, 1895, Ill. pl. Eur. rar. **6**: 48.

T y p u s: "Messina all' Ortora —Prestrand" (n. v.; vidi specimina in loco classico collecta).

This peculiar willow was described in the vicinity of Messina (Sicily), where it occurs on maritime marshes. It must be very rare nowadays, since L. Nicotra (op. cit.) reported

it to become rare due to extensive soil draining as early as 1904. I have examined 10 unicate samples (FI), which appear to be nearly all of collected material on this willow, and came to the same conclusion as A. Camus (Camus, l. c.). *S. peloritana* might be a hybrid of *S. pedicellata* and *S. purpurea*. Hybrids of *S. appendiculata* and *S. purpurea* look very much like *S. peloritana* (e. g., Kerner, Herb. Öst. Weid. N 76).

61. ***S. vulpina*** Anderss. 1858, Mem. Amer. Acad. **6**, 2: 452; Seemen, 1903, Salic. Jap.: 37; Koidzumi, 1913, Bot. Mag. Tokyo **27**: 89; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 130; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 404; id. 1957, Symb. Iteol. **14**: 9; Ohwi, 1965, Fl. Jap.: 336. —? *S. miquelii* Anderss. 1867, Monogr. Salic.: 166; id. 1868, in DC. Prodr. **16**, 2: 256.

T y p u s: "Yokohama legg. Williams and Morrow (♂)" (GH, S, n. v.). Icones photogr. typi apud Kimura, 1957 fig. 2 et tab. 3.

HABIT: A medium-sized shrub.

HABITATS: Forest edges, open woodlands, and prostrate pine (*Pinus pumila*) thickets.

DISTRIBUTION: The southern Kuril Islands (there are three different samples from Iturup; A. Kimura (1934) also enlisted it for Shikotan); Japan (Hokkaido and the mountains of Hondo). The species appears to be rather rare everywhere. (Fig. 37.)

Camus, 1904, Saul. Eur. **1**: 45

T y p u s: *Salix caprea* L.

Trees or large shrubs. Leaves mostly large, with prominent reticulation beneath, clothed with deviating or ruffled trichomes. Catkins precocious, mostly large, densely pubescent, usually with large black bracts. Capsules rather short-pubescent, their stipes not very much elongating on flowering.

62. ***S. caprea*** L. 1753, Sp. pl.: 1020; Ledeb. 1850, Fl. Ross. **3**, 2: 609; Wimmer, 1866, Salic. Eur.: 55; Komarov, 1929, Fl. Kamch. **2**: 11; Wolf, 1930, Fl. Yu.-V. **4**: 50; Krylov, 1930, Fl. Zap. Sib. **4**: 746; Floderus, 1931, Salic. Fennosc.: 73; Perfilyev, 1936, Fl. Sev. kr. **2-3**: 38; Nazarov, 1936, Fl. SSSR **5**: 90; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 646; Vicioso, 1951, Salic. Españ.: 106; Nazarov et. al. 1952, Fl. URSR **4**: 37; Skvortsov, 1966, Tr. Bot. in-ta AN ArmSSR **15**: 123; Shlyakov, 1956, Fl. Murm. **3**: 92; Andreyev, 1957, Der. i kustarn. Mold. **1**: 67; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 91; id. 1964, Fl. Eur. **1**: 50; Popov, 1959, Fl. Sredn. Sib. **2**: 795; Polyakov, 1960, Fl. Kazakhst. **3**: 30. —*S. hultenii* Flod. 1926, Ark. bot. **20A**, 6: 51; Nazarov, 1936, op. cit. **5**: 92; Ohwi, 1965, Fl. Jap.: 365. —*S. bakko* Kimura, 1928, Bot. Mag. Tokyo **42**: 568; id. 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 417; Ohwi, 1965, op. cit.: 365. —*S. coaetanea* Flod. 1930, Bot. not.: 331; id. 1931, op. cit.: 83; Nazarov, 1936, op. cit. **5**: 93; Shlyakov, 1956, op. cit. **3**: 95; Rech. f. 1964, op. cit. **1**: 50. —*S. hallaisanensis* (non Lév. 1912) Nakai, 1930, Fl. sylv. Kor. **18**: 129. —*S. idae* Goerz, 1930, Feddes Repert. **28**: 126.

T y p u s: "In Europae siccis. Fl. Suec. N 811; Fl. Lapp. NN 365, 367 et tab. 8 fig. N, S, U".

HABIT: A tree to 12–15 m tall; occasionally, due to some damaging impact, it may have a shrubby habit.

HABITATS: Woods on well-drained soils as well as a vast variety of secondary postforest habitats, such as clearings, forest edges, residential lots, roadsides; also, mountainous habitats near the timberline. The species avoids wet and, particularly, paludal soils.

DISTRIBUTION: Europe from northern Spain, southern Italy, Albania, and Macedonia to the extreme north of Scandinavia. In Eastern Europe and European Russia, its southern limit fits the line connecting Kishinev, Zaporozhye, Rostov, Volgograd, and Orenburg; in the north, it reaches the southern Kanin Peninsula and northern meander of the Pechora. The area comprises northern Asia Minor, the mountains of the Crimea Peninsula, and nearly all of the Caucasus (except the arid Kura Depression and Talysh). In Asia, the southern boundary goes from Orsk via Bayan-Aul to the foot of the Altai; then, approximating the border with Mongolia, it reaches the forested regions of Manchuria, North Korea and cuts the northern two-thirds of Hondo; in the north, the area includes the southern Kurils, entire Sakhalin, the Shantar Islands, Zeya, and Shilka; then the area boundary runs via Barguzin, the lower reaches of the Angara, and drainage divides between Ob and Taz, Ob and Pur, Ob and Nadym. North of that line, there are isolated fragments of the area at the Upper Aldan, on the Kamchatka Peninsula, as well as some scattered solitary locations along the Lena from Mukhtuya to Sangar. According to available data, in eastern Transbaykalia there is a considerable gap in *S. caprea* distributional area. There are some isolated locations far away southward: north of Beijing (the Weichang Plateau) and in the Qin Lin Range near Sian (Xi'an), Shansi (Shanxi) Province. (Fig. 40.)

In Scotland, it ascends to 750 m; in the Pyrenees, to 1,900 m; in the Alps to 2,100 m; in the Carpathians, to 1,400–1,600 m; in Bulgaria, to 2,500 m (never descending lower than 800 m); in the Caucasus and Asia Minor, its range is from 800 to 2,700 m (in the Karabakh and southern Zangezur mountain ranges, not lower than 1,500 m). In northern Norway, the species ascends to 400 m; in the Kola Peninsula, to 300 m; in the open forests of the Prepolar Urals, it goes up to 500 m; in the Northern Urals, to 800 m; in the Southern Urals, to 1,000 m. In the Altai and Sayans, where it is generally rather rare, it goes as high as 1,000 m up in the mountains; in the southern Sikhote-Alin, to 1,300 m; on southern Sakhalin, to 900 m.

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NOTE. Plants from the Far East usually differ in larger, rugose leaves. However, this difference is vague, so that it is impossible to use it for tracing any particular morphological or geographical limits. I have found plants with a typical "Far East" habit growing near Irkutsk; on the other hand, there are samples from Transbaykalia and Maritime Province having a completely "European" habit. Therefore, so far we would better refrain from segregating the Far Eastern plants in a distinct taxon.

S. coetanea is merely a very indistinct climatic ecotype of *S. caprea* that is characterized by a later time of flowering. No taxonomic rank is appropriate for *S. coetanea*.

63. ***S. aegyptiaca*** L. 1755, Cent. pl. 1: 33; Floderus, 1933, Ark. bot. 25A, 11: 1 et seq. p. p. (excl. syn. *S. pseudomedemii* et var. *cuneata* et *erosa*); Nazarov, 1936, Fl. SSSR 5: 94; (p. p.: excl. syn. *S. phlomoides*, *S. pseudomedemii* et *S. cinerea* var. *cuneata* et *erosa*); Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR 20: 82 (p. p.: excl. syn. *S. pseudomedemii*); id. 1962, Bot. mat. Gerb. in-ta bot. AN UzbSSR 17: 65; id. 1966, Trudy Bot. in-ta AN ArmSSR 15: 125. —Non *S. aegyptiaca* Rech. f. 1964, Fl. Eur. 1: 49. —*S. nitida* S. G. Gmelin, 1774, Reise Russ. 3: 283 et tab. 28. —*S. phlomoides* Marschall a Bieberstein, 1808, Fl. Taur.-Cauc. 2: 415; id. 1819, ibid. 3: 728, p. p. (quoad

pl. e Kizliar); Grossheim, 1945, Fl. Kavk. **3**: 19 (p. min. p.); Karyagin, 1952, Fl. Azerb. **3**: 50 (p. p. minore). —*S. medemii* Boiss. 1846, Diagn. **7**: 100. —*S. cinerea* var. *medemii* Boiss. 1879, Fl. Or. **4**: 1189. —*S. caprea* scrutatorum florum iranicae omnium, non L.

T y p u s: "In Aegypto (Febr. 1751) —Fr. Hasselquist" (UPS, n. v.). Icones photogr. typi apud Floderus 1933.

HABIT: A small tree to 8–10 m tall.

HABITATS: Lighted forests on slopes and banks of streams; secondary postforest plant communities at clearings, forest edges, and residential lots.

168 It is favored for cultivation, since it is easily propagated from cuttings, unlike *S. caprea*. Male catkins were commonly used in the East for making a drink.

DISTRIBUTION: The Caucasus (Talysh and Diabarskaya Depression, very ordinary, from the sea level to 1,800 m); the Karabakh and southern Zangezur (occasionally); extreme southeastern Turkey (Hakkâri and Bitlis); northern Iran (the Elburz and Kopet-Dag); the Turkmenian Kopet-Dag (gorges at the Upper Sumbar and near Nokhur, occasionally). The Zagros Mountains in southern Iran; Afghanistan and northern Pakistan (scattered, presumably, only as a cultivated species). It reaches 2,300 m in the Elburz.

There is no doubt that the plant from Egypt, after which the species was named, was also a cultivated specimen. The willow is cultivated at some locations in Azerbaijan and Middle Asia. (Fig. 40.)

NOTE. The species is close to *S. caprea*, morphologically as well as ecologically; the geographical areas of the two species are vicarious. They grow close together only in the Karabakh and Zangezur, however, being confined to different elevations: *S. caprea* occurs exclusively high up in the mountains (not lower than 1,500–1,600 m), and *S. aegyptiaca* grows only at lower levels. Erroneous reports of *S. aegyptiaca* from the Lower Volga, Kazakhstan, Crimea, etc., still occasionally appear in the literature (e. g., Rechinger 1964).

Two different species were hiding under the name of *S. phlomoides* M. B.: *S. cinerea* collected around Sarepta (near Volgograd) and cultivated *S. aegyptiaca* from Kizlyar. The samples from Sarepta have survived in the St. Petersburg Herbarium as well as in Moscow (in Trinius' Herbarium). I did not manage to find those from Kizlyar. However, B. Floderus was familiar with them and positively assigned them to *S. aegyptiaca*. According to B. Floderus (1933), the labels positively said that those samples had been collected from cultivated plants.

64. **S. cinerea** L. 1753, Sp. pl.: 1021; Ledeb. 1850, Fl. Ross. **3**, 2: 607; Wimmer, 1866, Salic. Eur.: 47; Boiss. 1879, Fl. Or.: 1189 (p. p.: excl. pl. Caucasi et Asiae Minor.); Wolf, 1930, Fl. Yu.-V. **4**: 54; Krylov, 1930, Fl. Zap. Sib. **4**: 744; Floderus, 1931, Salic. Fennosc.: 50; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 39; Nazarov, 1936, Fl. SSSR **5**: 99 (p. p.: excl. pl. caucas.); Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 644; Nazarov et al. 1952, Fl. URSS **4**: 40; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 94; id. 1964, Fl. Eur. **1**: 50; Polyakov, 1960, Fl. Kazakhst. **3**: 32. —*S. deserticola* Goerz ex Pavlov, 1935, Fl. Ts. Kazakhst. **2**: 26, 31 (nom. invalidum, sine descr. latina).

T y p u s: "In Europae nemoribus paludosis. Fl. Suec. N 805; Fl. Lapp. N 358".

HABIT: A tall (up to 4–5 m) shrub.

HABITATS: Eutrophic wetlands, muddy banks of stagnant or slow water bodies, floating bogs, damp depressions and *zapadina*'s in the steppe belt. In conditions of sufficient humidity, it becomes very common in various secondary habitats, such as ditches, ruts, embankments, forest edges and openings.

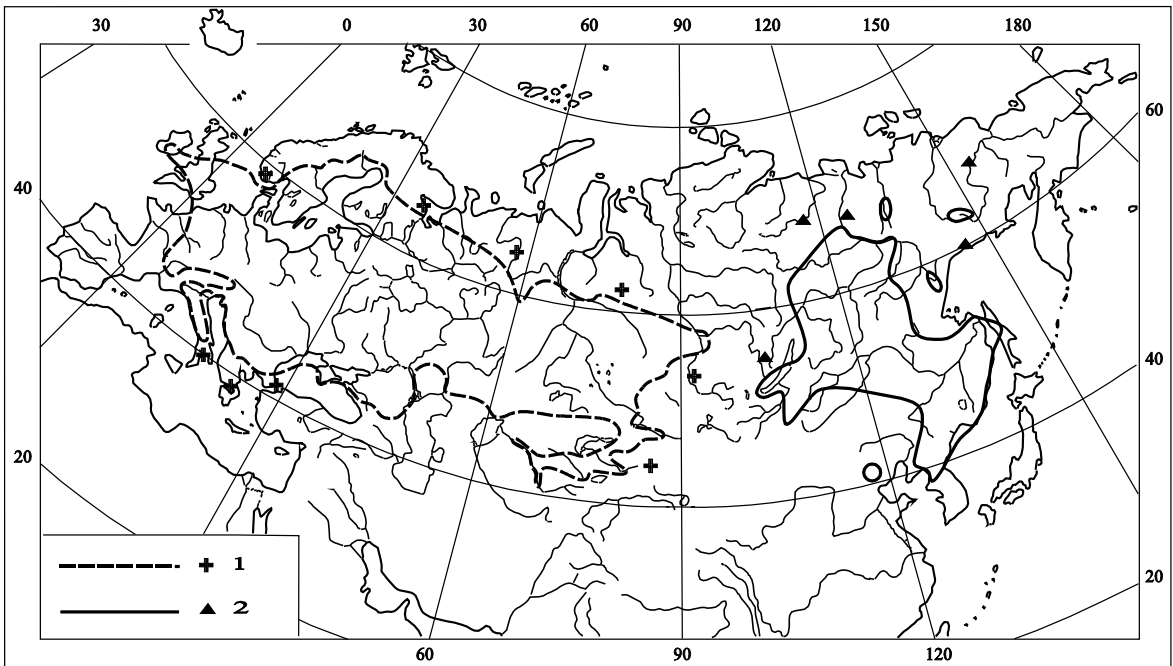


Fig. 41. Distributional areas of *Salix cinerea* L. (1) and *S. abscondita* Laksch. (2)

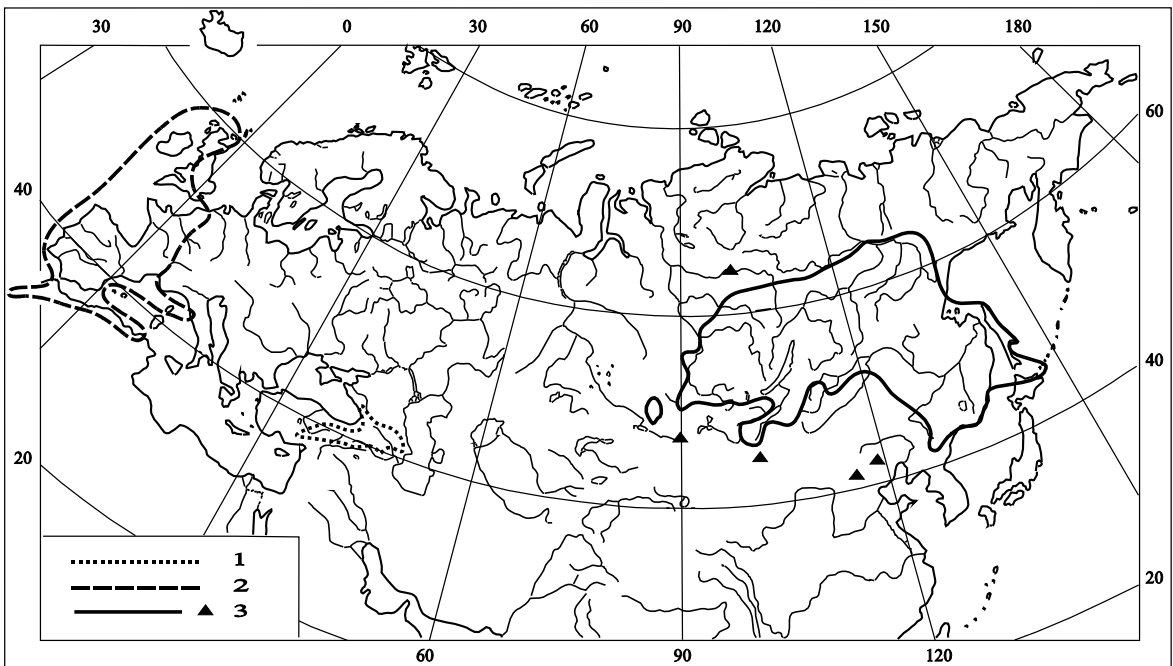


Fig. 42. Distributional areas of *Salix pseudomedemii* E. Wolf (1), *S. atrocinerea* Brotero (2), and *S. taraiakensis* Kimura (3)

DISTRIBUTION: Southeastern England, eastern France, nearly all of Italy (except the extreme south and the islands); the Balkan Peninsula (though very rare in Greece and the European part of Turkey); all of Central Europe; and southern Scandinavia. In Eastern Europe, it goes south to the Black Sea Coast, the foot of the Caucasus (the area includes the Lower Kuban River and Tersko-Kumskiy Sands), and the Volga Delta, nearly reaching the mouth of the Ural River. In Asia, the southern limit comprises the coast of the Aral, middle and lower reaches of the Syr Darya (with the southernmost location in the wetlands along the Chirchik River downstream of Tashkent), and the northern foot of the Tien Shan, occasionally penetrating into the mountains along river valleys and gorges. Along the valleys of the Ili and Black Irtysh, the species reaches the Chinese territory. In the east, the species limit is found along the foot of the Altai and Kuznetskiy Alatau and on the eastern bank of the Yenisei around its confluence with Angara. In Minusinskaya Depression, there is an isolated location. The northern limit matches the drainage divides between the Ob and Taz, Ob and Pur, Ob and Nadym, then going via the basins of the Pelym and Malaya Sosva, crossing the Urals south of Konzhakovskiy Kamen, and then proceeding via the Upper Pechora, Middle Mezen, Arkhangelsk, the Onega Peninsula, and central Karelia.

In the Alps, the species ascends as high as 1,000–1,100 m; in the Carpathians, to 1,100 m; in the Southern Urals, to 700 m; in the Zailiyskiy Alatau, to 1,800 m; in the Dzungarskiy Alatau, to 1,600 m. (Fig. 41.)

NOTE. All data on *S. cinerea* findings in the Caucasus and Asia Minor are attributed to *S. pseudomedemii* (Skvortsov 1966a). The northern limit of the species, as it was described by I. Perilyev (1936), that is, via the Pesh River, the entire Pechora Basin, and western Bolshezemelskaya Tundra, appears to be doubtful, inasmuch as it is not supported by any herbarium material. *S. cinerea* never reaches the forest limit: neither the northern one, nor altitudinal. The western species limit on the territory of France and England is not clarified. There, *S. cinerea* is still confounded with a closely related species, *S. atrocinerea* Brot. As I understand, all references to *S. cinerea* on Corsica, Sardinia, and Sicily have to be attributed either to *S. pedicellata* Desf. or *S. atrocinerea* Brot.

65. ***S. atrocinerea*** Brotero, 1804, Fl. Lusit. **1**: 31; Buser, 1894, Magnier Scrin. fl. sel. **13**: 327; Rouy, 1910, Fl. Fr. **12**: 203 (pro "race"); Guinier, 1912, Bull. Soc. Bot. Fr. **58**, suppl.: IX et seq.; Görz, 1929, Saul. Catal.: 43; Chassagne et Görz, 1931, Bull. Soc. Dendr. Fr. **80**: 69; Coutinho, 1935, Bol. Soc. Broter. **10**: 75; id. 1939, Fl. Portug. ed. 2: 191; Almeida, 1944, Publ. Serv. Florest. **11**: 125; Chassagne, 1956, Invent. fl. Auvergne **1**: 237; Rechinger, Lawalrée, 1960, Bull. Jard. bot. Bruxelles **30**: 367; Clapham et al. 1952, Fl. Brit.: 762; Rech. f. 1964, Fl. Eur. **1**: 50. —*S. oleifolia* Smith. 1804, Fl. Brit. **3**: 1065 (non Vill. 1789); Linton, 1913, Brit. willows: 57. —*S. rufinervis* DC. 1808, Mém. Soc. Agric. Dép. Seine **10**: 11. —*S. renecia* Dode, 1908, Bull. Soc. Bot. Fr. **55**: 656. —*S. cinerea* auct. non L.: Coutinho, 1899, Bol. Soc. Broter. **16**: 17; Cadevall, Font, 1933, Fl. Catal. **5**: 184; Franco, 1949, An. Inst. Super. Agron. **16**: 133; Maire, 1961, Fl. Afr. Nord **7**: 62; et al. —*S. aurita* auct. fl. hispan. et lusitan. non L. —*S. catalaunica* Sennen, in sched. ad "Pl. D'Espagne": N 4040, 5425 nom. nud. —*S. jahandiezi* Chassagne, 1938, Bull. Soc. Bot. Fr. **85**: 402 nom. nud. (sine descr. latina!).

T y p u s: "Margenes do Mondego. Brotero". (LISU, n. v.).

HABIT: A tree to 10 (occasionally even 15) m tall.

HABITATS: Damp places and wetlands; in regions with high humidity, it is found everywhere in lighted forests and various secondary habitats. It is associated with moderately acidic soils.

DISTRIBUTION: The British Isles (presumably, except southeastern England); Belgium; most of France (except the eastern part); the islands Corsica, Elba, and Sardinia (??); all of the Iberian Peninsula; Algeria and Tunisia (only rarely, in the mountain ranges closest to the sea), Morocco (not infrequently, ascending to the Grand Atlas).

In Atlantic Europe, its vertical range is from the sea level to 600 m in Wales and Scotland, to 1,600 m in the French Massif Central, to 1,600 m on the Iberian Peninsula; in Northern Africa, 800–2,400 m. (Fig. 42.)

NOTE. This species is morphologically very close to *S. cinerea*, so that in the regions where both species occur together (the British Isles, central France) it is often hard to distinguish samples. Only observations of live plants in nature will make it possible to delimit the species in these regions with confidence.

66. ***S. pseudomedemii*** E. Wolf, 1909, Trudy SPb. bot. sada **28**, 3: 397; Skvortsov, 1966, Trudy Bot. In-ta AN ArmSSR **15**: 126. —*S. eripolia* Hand.-Mazz. 1912, Ann. Naturh. Mus. Wien **26**: 132. —*S. alifera* Goerz, 1930, Feddes Reppert. **28**: 120; Nazarov, 1936, Fl. SSSR **5**: 100; Grossheim, 1945, Fl. Kavk. **3**: 20. —*S. fuscata* Goerz, 1930, op. cit. **28**: 122; Nazarov, 1936, op. cit. **5**: 100; Grossheim, op. cit. **3**: 20. —*S. cataonica* Goerz, 1930, op. cit. **28**: 123. —*S. neofuscata* Kimura, 1940, Symb. Iteol. **8**: 416. —*S. aegyptiaca* scrutatorum florum Caucasi necnon Asiae Minoris (non L.), p. max. p. —*S. cinerea* (non L.) scrutatorum florum Caucasi necnon Asiae Minoris omnium. —*S. phlomoides* auct. fl. caucas. (p. max. p.), non M. B. 171

T y p u s: "Leningrad, culta. Provenit e Tiflis" (Hb. Academiae Forestalis, Leningrad!).

HABIT: Usually a rather powerful and tall shrub (1.5–5 m).

HABITATS: Damp places; banks of streams in forested regions.

DISTRIBUTION: All across the Greater Caucasus (except the northwestern part behind the line Gagry–Karachay). The elevation ranges are from the maritime lowland in Abkhazia, Dagestan, and Azerbaijan and from the northern piedmont south of the line connecting Yessentuki and Khasavyurt to 1,000–1,100 m around Kislovodsk, 1,400–1,500 m in Dagestan, and to nearly 2,000 m in south Osetia. In the east it appears to be more common than in the west descending down to Shirvanskaya Steppe (near Agdash and at other places). It is not infrequent in the Lesser Caucasus occurring nearly all across the forested regions, except Adzharia, Karabakh, southern Armenia, and (?) Nahichevan (however, found in the mountain ranges south of Lake Sevan).

In Turkey, it is known from Kars, Erzurum, Agri, Gü mü shane, Malatya, Adana, Tunceli, Sivas, and Maras, as well as from the Cilician and Armenian Taurus. (Fig. 42.)

NOTE. As it was already mentioned in the note concerning *S. aegyptiaca*, the description of *S. phlomoides* M. B. had been based on the samples of *S. aegyptiaca* and *S. cinerea*. Therefore, *S. phlomoides* is a surplus name that should be abandoned.

All data on *S. cinerea* from the Caucasus and Asia Minor are to be attributed to *S. pseudomedemii*. As a matter of fact, *S. cinerea* and *S. pseudomedemii* are very different in their ecological ranges. *S. pseudomedemii* avoids muddy and paludal lake shores and banks of streams, whereas *S. cinerea*, on the contrary, is very rare on banks of mountain streams with rapid water flow.

I have studied the types of *S. eripolia*, *S. fuscata*, *S. alifera*, and *S. cataonica*; their identity with *S. pseudomedemii* is beyond question.

67. ***S. aurita*** L. 1753, Sp. pl.: 1019; Wimmer, 1866, Salic. Eur.: 51; Krylov, 1930, Fl. Zap. Sib. **4**: 755; Floderus, 1931, Salic. Fennosc.: 54; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 39; Nazarov, 1936, Fl. SSSR **5**: 101; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 645;

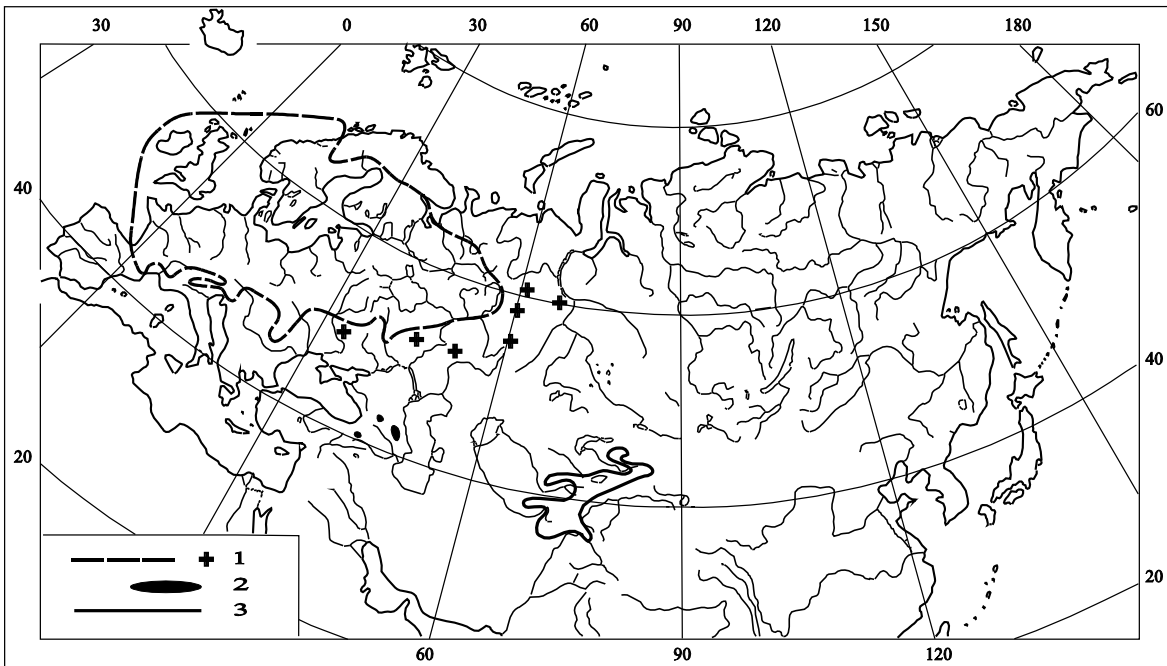


Fig. 43. Distributional areas of *Salix aurita* L. (1), *S. pseudodepressa* A. Skv. (2), and *S. iliensis* Rgl. (3)

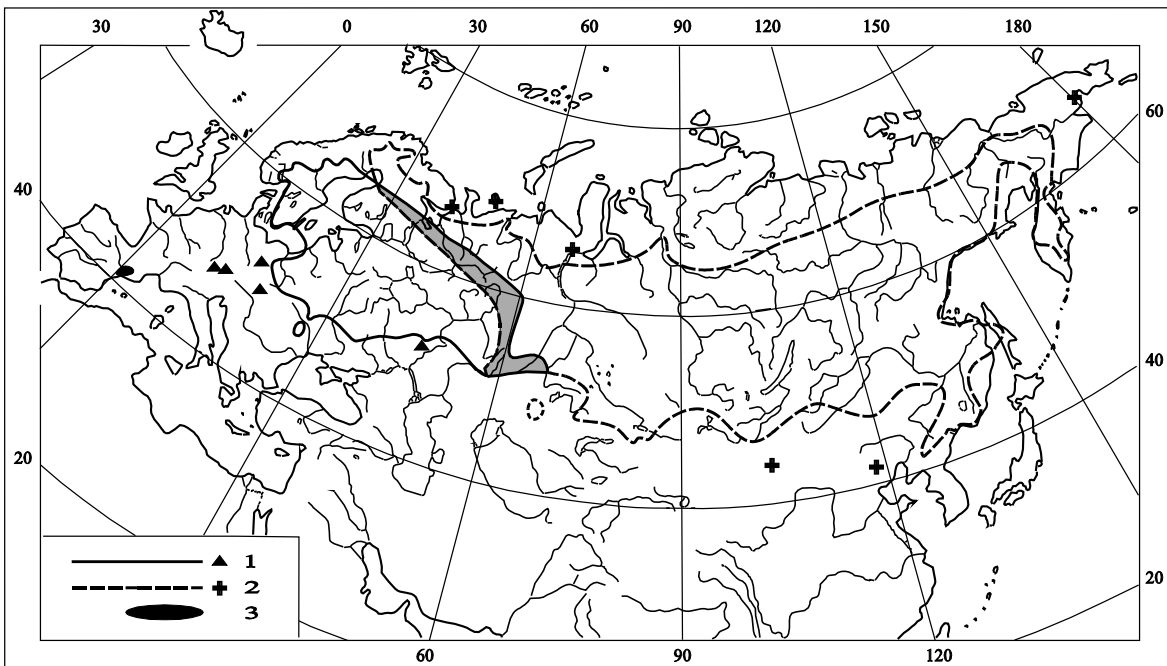


Fig. 44. Distributional areas of *Salix starkeana* Willd. (1), *S. bebbiana* Sarg. (2), transitional zone where these species hybridize (3), and area of *S. tarraconensis* Pau ex Font (4)

Nazarov et al. 1952, Fl. URSS **4**: 43; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 96; id. 1964, Fl. Eur. **1**: 50.

T y p u s: "In Europae borealis sylvis. Fl. Lapp. N 369 et tab. 8, fig. V; Fl. Suec. N 810".

HABIT: A shrub of a medium size (1–3 m).

HABITATS: Mesotrophic edges of wetlands, damp lowlands, and light forests. In regions with positive moisture balance, it is also found in a wide variety of secondary habitats, such as roadsides, ruts, embankments, clearings, burns, field boundaries, and abandoned meadows. It is associated with acidic and poor soils.

DISTRIBUTION: Major part of Central and Northern Europe including the British Isles, France (except the southeast), Spain (very rare, only in the Pyrenees), Switzerland, Austria, Slovenia, Czechia, Slovakia, Transilvania, Germany, Poland, southern half of Norway, and nearly all of Sweden and Finland. In northern European Russia, it reaches the Kandalaksha Bay, Arkhangelsk, and the Middle Mezen. Eastwards, it goes to Pre-Uralia (the Vycheгда and Kama river basins). There are some solitary locations in the Urals from Denezhkin Kamen to Kyshtym; behind the Urals, it is found in the Konda Basin. The southern limit of the species goes along the Lower Kama, then south of Ulyanovsk, Tambov, and Voronezh, via the southern part of Central Russian Upland, Kursk, and Kiev, towards the Carpathians. Some solitary locations are known south of this boundary, in sand dunes. The most remote one is in Buzulukskiy Bor. References to the Altai (Polyakov 1960) are erroneous. (Fig. 43.)

In Scotland, it ascends to 750 m; in the French Massif Central, to 1,750 m; in the Alps, it is known to reach 1,100 m, in the Tatras and Eastern Carpathians, 1,600 m. 172

68. **S. salvifolia** Brotero, 1804, Fl. Lusit. **1**: 29; Coutinho, 1899, Bol. Soc. Broter. **16**: 23; Merino, 1906, Fl. Galicia **2**: 619; Coutinho, 1939, Fl. Portugal.: 190; Almeida, 1944, Publ. Serv. Florest. **11**: 133, 141; Vicioso, 1951, Salic. Españ.: 101; Rech. f. 1964, Fl. Eur. **1**: 50. —An *S. salviaefolia* Link ex Willd. 1806, Sp. pl. **4**, 2: 688? —*S. oleifolia* Lange, 1870, in Willk. et Lange, Prodr. fl. Hisp. **1**: 229; Laguna, 1883, Fl. forest. Españ **1**: 148. —Non *S. oleifolia* Vill. 1789, nec Smith, 1804.

T y p u s: "Ad Mundae margines, Brotero". (LISU, n. v.).

HABIT: A medium-sized or tall shrub or a small tree.

HABITATS: Banks of streams and damp places.

DISTRIBUTION: All of Portugal and major part of Spain from Galicia to Burgos, Logroño, Castellón de la Plana, and Ciudad Real. (Fig. 38.)

Subsect. *Substriatae*

Görz, 1928, Feddes Repert. Beih. **52**: 140 (p. p.).

T y p u s: *Salix starkeana* Willd.

Shrubs or small trees with short trunks. Wood usually with short, scattered striae. Floriferous buds elongated, lanceolate or oblong-lanceolate, flattened on adaxial side, attenuating into somewhat recurved beaks. Leaves comparatively moderate-sized, elliptic, rarely obovate. Capsules narrowly lanceolate or sublinear, stipitate; stipes considerably elongating on flowering, usually longer than bracts.

69. **S. tarraconensis** Pau ex Font, 1915, Treb. Inst. Catal. Hist. Natur. **1**: 15 et tab. 2; Görz, 1929, Saul. Catal.: 41; Cadevall, Font, 1933, Fl. Catal. **5**: 183; Font, 1950, Fl. Cardá 75; Vicioso, 1951, Salic. Españ.: 73; Rech. f. 1964; Fl. Eur. **1**: 53.

T y p u s: "Tossa de Caro, penyals calissos a 1,400 m" (BC, n. v.).

HABITATS: Calcareous rocks in the mountains, mostly on northern slopes, at 800–1,400 m.

DISTRIBUTION: Southern Tarragona and northern Castellón de la Plana provinces in northeastern Spain. (Fig. 44.)

NOTE. This is a strict endemic species so far known only from a few localities. Thanks to the courtesy of Prof. O. de Bolós (Barcelona), I got fragments of three samples to examine; that was sufficient to admit *S. tarraconensis* as a distinct species. It appears to be quite obvious that the species is close to *S. starkeana*. Grounds for placing it close to *S. coesia* (Rech. f., l. c.) are provided by purely casual resemblance. Stamen filaments are partially connate in both species; there is no doubt that there also exist plants with distinct stamens.

70. *S. starkeana* Willd. 1806, Sp. pl. **4**, 2: 677; id. 1820, in Guimpel, Willd. Hayne, Abbild. Holz. **2**: 232; Besser, 1822, Enum. Volhyn.: 37; Floderus, 1943, Sv. bot. tidskr. **37**: 81; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 103; id. 1964, Fl. Eur. **1**: 51. — *S. livida* Wahlenb. 1812, Fl. lapp.: 272; Wimmer, 1866, Salic. Eur.: 108; Wolf, 1930, Fl. Yu.-V. **4**: 53; Nazarov, 1936, Fl. SSSR **5**: 105; Nazarov et al. 1952, Fl. URSR **4**: 48. — *S. depressa* auct. (non L. 1755, Fl. Suec. 2 ed.: 332), p. p. (quoad pl. folliis glabris): Fries, 1832, Mantissa **1**: 56; id. 1840, Bot. not.: 197; Ledeb. 1850, Fl. Ross. **3**, 2: 611; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 115; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 35; Skvortsov, 1964, in Mayevsk. Fl. sredn. pol. 9 ed.: 191. — *S. vagans* Anderss. 1858, Öfver. K. vet. förhandl. **15**: 121; id. 1858, Bot. not.: 45; id. 1867, Monogr. Salic.: 86, p. p.

T y p u s: "Silesia, prope Gurau, leg. Starke" (B, LE! K, S).

HABIT: A shrub of a medium size (1–3 m), which sometimes may grow as a small tree to 4 m tall.

HABITATS: Light forests (particularly, pine and birch ones), forest edges, clearings, burns; also field boundaries, roadsides, etc. (usually together with *S. aurita* or *S. myrsinifolia*).

DISTRIBUTION: Sweden, southern Finland, southern Karelia; the basins of the Sukhona, Vychegda, Kama, and Belaya. In the south, it reaches northern Saratovskaya Oblast, Voronezh, Kharkov, Kiev, Berdichev, and Lvov. In the Carpathians, it is encountered only in Bukovina; in eastern Poland and the Sudetes, it is distributed sporadically. There are some solitary locations in Slovakia and southern Germany. (Fig. 44.)

NOTE. Along the northern and eastern boundary of its distributional area, *S. starkeana* is hybridizing with *S. bebbiana* en masse (see the note to that species).

71. *S. bebbiana* Sarg. 1895, Gard. Forest **8**: 463; id. 1896, Sylva Amer. **9**: 131 et tab. 477 (nom. nov. pro *S. rostrata* Richardson, 1823); Schneider, 1920, J. Arn. Arb. **2**: 66; Floderus, 1933, Ark. bot. **25A**, 10: 7; Nazarov, 1936, Fl. SSSR **5**: 108; Hultén, 1943, Fl. Al. **3**: 544; Raup, 1943, Sargentia **4**: 116; id. 1947, ibid. **6**: 159; id. 1959, Contrib. Gray Herb. **185**: 79. — *S. rostrata* Richardson, 1823, in Franklin, Journey: 753. — Non *S. rostrata* Thuill. 1799, Fl. Paris: 516. — *S. livida cinerascens* Wahlenb. 1812, Fl. lapp.: 273. — *S. depressa* auct. (non L.) p. p. (quoad pl. folliis pubescentibus): Fries, 1832, Mantissa **1**: 56; id. 1840, Bot. not.: 197; Ledeb. 1850, Fl. Ross. **3**, 2: 611; Krylov, 1930, Fl. Zap. Sib. **4**: 753; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 38; Polyakov, 1960, Fl. Kazakhst. **3**: 29 (p. p.: quoad var. *cinerascens*). — *S. macropoda* Stschegl. 1854, Bull. Soc. Natur. Moscou **27**, 1: 197. — *S. vagans* Anderss. 1858, Öfver. K. vet. förhandl. **15**, 3: 121; id.

1867, Monogr. Salic.: 86, p. p. —*S. perrostrata* Rydb. 1901, Bull. N. Y. Bot. Gard. **2**: 163. —*S. cinerascens* Flod. 1926, Ark. bot. **20A**, 6: 48; id. 1926, in Lindman, Sv. Fanerogam-fl.: 209; Komarov, 1929, Fl. Kamch. **2**: 10; Nazarov, 1937, Fl. Zabayk. **3**: 106; Popov, 1959, Fl. Sredn. Sib. **2**: 794. —Non *S. cinerascens* Willd. 1806. —*S. xerophila* Flod. 1930, Bot. not.: 334; id. 1933, op. cit. **25A**, 10: 7; Nazarov, 1936, op. cit. **5**: 107; Schlyakov, 1956, Fl. Murm. **3**: 97; Rech. f. 1964, Fl. Eur. **1**: 51. —*S. floderii* Nakai, 1930, Fl. sylv. Kor. **18**: 123 (p. p.: excl. *S. abscondita* Laksch. et *S. taraiakensis* Kimura). —*S. orotchonorum* Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 444; Sugawara, 1939, Ill. Fl. Saghal. **2**: 689; Tolmachev, 1956, Der. i kustarn. Sakhal.: 65. —*S. starkeana* Willd. ssp. *cinerascens* (Wahlenb.) Hultén, 1950, Atlas: N 586; Benum, 1958, Fl. Troms.: 181. —*S. hsinganica* Chang et Skvortz. 1955, in Liou Tchen ngo, Ill. Fl. Tr. Shr. Northeast China: 556.

T y p u s: "Forest regions of Canada W. of Hudson Bay. —1819–1822, Richardson" (NY, K, GH, n. v.).

HABIT: A medium-sized shrub or, frequently, small (up to 5–6 m) tree with a short stem and wide crown.

HABITATS: Lighted forests (particularly, pine and larch stands), stony slopes, various secondary postforest habitats, dry to moderately paludal ones. The species copes with any kind of bedrock and can grow even on very poor soils.

DISTRIBUTION: Swedish and Finnish Lapland, northern Karelia, and the southern Kola Peninsula; the northern forest belt in European Russia (with the southern limit along the line Arkhangelsk–Syktyvkar); the entire Urals. In Asia, the southernmost locations are in the Ulu Tau, Karkaralinskiye Mountains, Tarbagatay, southern Tuva, the Khangai, Kentei, northernmost mountainous regions of Northeast China, and the extreme north of the Korea Peninsula. Isolated fragments of the area are located in the Gobi Altai and mountains of Jehol. In the north, the area includes the Anadyr Basin and Kamchatka, its limit nearly reaching the northern limit of the forest belt. Of all the Far East Pacific islands, it occurs only on Sakhalin. In the tundra and forest-tundra, it is encountered occasionally, presumably, as an anthropogenic plant (Kolguyev Island, the Pechora, Ob, and Kolyma mouths, and the Gulf Kresta). (Fig. 44.)

In the Southern Urals, it ascends to 800 m; in the Northern Urals (Kosvinskiy Kamen), to 600–700 m; in the Altai, Sayans, and Stanovoye High Plateau, to 1,600 m; in Oymyakon District, to 750 m.

NOTE. B. Floderus (1933) was the first to identify the plants from Asia (the Anadyr River Basin) with *S. bebbiana*. However, inconsistently and without any reason, he recognized one more species, *S. xerophila* growing at the same place, the Anadyr River Basin. It is absolutely impossible to treat the Siberian plants as two different species. At the same time, one cannot discriminate between the Siberian and American specimens. Apparently, we have to extend the name *S. bebbiana* to the entire Eurosiberian area. In the Urals and northern Europe, where the areas of *S. starkeana* and *S. bebbiana* come into contact, there is a wide transitional zone, apparently of hybrid nature. That makes it possible to treat *S. bebbiana* as a subspecies of *S. starkeana*. In that case, the valid name should be *S. starkeana* ssp. *cinerascens* Hultén, 1950.

One can occasionally find specimens with conspicuous pubescence on leaves and shoots even deep inside the area of *S. starkeana*. The presence of these plants has given grounds to enlist *S. bebbiana* (*S. xerophila*) for the territory of the European temperate belt, as it was done, for example, in the "Flora" by P. Mayevskiy (ed. 7, 8; 1940, 1954). However,

besides the pubescence, there are some other characters that help to discriminate between the two species, although these characters are rather indistinct: in *S. bebbiana*, shoots are of more dull, brownish color; leaves are more abruptly narrowing towards the base, their veins more pronounced beneath; the glaucous bloom on the leaves is less pronounced; also, the cataphylls are less sericeous. Pubescent specimens from the European temperate belt usually do not exhibit these features, and therefore, from a taxonomical point of view, we would rather treat them merely as specimens of *S. starkeana*. However, it is quite possible that the pubescence is a relict character inherited from *S. bebbiana*, which possibly had occupied the European temperate climate regions before, but then was superseded and taken up by *S. starkeana*. Spruces provide a similar example: within the European temperate belt, one may occasionally come upon spruces with cones approximating the *Picea obovata* type.

72. ***S. taraiensis*** Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 419; Sugawara, 1939, Ill. Fl. Saghal. **2**: 673; Tolmachev, 1956, Der. i kustarn. Sakhal.: 68; Ohwi, 1965, Fl. Jap.: 366. —*S. livida* var. *sibirica* Lakschewitz, 1914, Spisok rast. Gerb. russk. fl. **50**: N 2472. —*S. livida* auct. non Wahlenb. 1812: Nazarov, 1936, Fl. SSSR **5**: 105 (quoad pl. Sibiriae et Orientis Extrem.); id. 1937, Fl. Zabayk. **3**: 195; Grubov, 1955, Kosp. fl. Mong.: 101; Popov, 1959, Fl. Sredn. Sib. **2**: 794; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 16; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3226 (p. p.); Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 76. —*S. floderii* var. *glabra* Nakai, 1930, Fl. sylv. Kor. **18**: 126. —*S. starkeana* (non Willd.) Nazarov, 1936, op. cit. **5**: 106; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 171. —*S. abscondita* (non Lakschewitz) Flod. 1936, Sv. bot. tidskr. **30**: 398.

T y p u s: "Sachalin australis, Shikka, Siska, 7. VI et 21. VIII 1927. A. Kimura N 671 (♀); ibid. 11. VI et 22. VIII 1927. Id. N 700 (♂)" (Herb. Kimura, Sendai, Japonia, n. v.).

HABIT: A tall shrub or, frequently, tree to 10–12 m tall.

HABITATS: Light forests, forest edges, stony slopes, and a vast variety of secondary postforest habitats (much like *S. bebbiana*, however, avoiding very poor and paludal soils).

DISTRIBUTION: The Altai (sparsely in the Katun Basin, so far not known from Chuyskaya Steppe); Pechi on the Bukhtarma (the westernmost location); the Western Sayans, Kuznetskiy Alatau, and Tuva (rather scattered). It becomes fairly common east of the Yenisei. The northern area limit crosses the Angara Mouth, Tura on the Lower Tunguska, Elgyay on the Vilyuy, Sangar on the Lena, the southern Verkhoyanskiy Range (around Tompo), Ayan, and also Bolshoy Shantar, Sakhalin, and Kunashir islands. The southern boundary goes via northern Hokkaido, the very north of the Korea Peninsula, forested parts of Northeast China, the Kentei, and Lake Koso (Hövsögöl, Khöbsögöl) in Mongolia. Some isolated fragments of the area are found in the Chinese Altai, Khangai, Gurban Bogdo, and the mountains north of Beijing. (Fig. 42.)

In the Altai and Sayans, it ascends to 1,600–1,700 m; in the northern Sikhote-Alin and southern Verkhoyanskiy Range, to 600 m; in the southern Sikhote-Alin, to 800 m; in the southern Mongolian Altai (the Baga Bogdo), to 2,000 m.

NOTE. Although *S. taraiensis* is one of the most common willows in East Siberia and the Far East, it has been remaining unclarified and habitually confused with *S. starkeana*. A. Kimura considered *S. taraiensis* to be an endemic of Sakhalin and Hokkaido. However, there is no doubt at present that the plants from Sakhalin and the Kurils are identical to those growing in the Altai or around Irkutsk. That becomes obvious when one examines the bulky material from Sakhalin and Kunashir that is available now. I inspected

15 samples from Kunashir (A. Kimura had not had any material from there) as well as scores of samples from Sakhalin.

73. **S. abscondita** Lakschewitz, 1914, Spisok rast. Gerb. russk. fl. **50**: N 2471; Nazarov, 1936, Fl. SSSR **5**: 77. —*S. floderii* Nakai, 1930, Fl. sylv. Kor. **18**: 123 (p. p.). —*S. tatewakii* Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 422. —*S. sugawarana* Kimura, 1934, op. cit. **4**: 417; Sugawara, 1939, Ill. Fl. Saghal. **2**: 671. —*S. raddeana* Lakschewitz ex Nasarov, 1936, op. cit. **5**: 92, 107. —*S. oleninii* Nasarov, 1936, op. cit. **5**: 93, 108; Karavayev, 1958, Konsp. fl. Yakut.: 83. —*S. enanderii* Flod. 1936, Sv. bot. tidskr. **30**: 396.

T y p u s: "In urbe Czita. 10.V 1910 et 10.VIII 1910 leg. G. Stukov" (Herb. Fl. Ross. N 2471, LE!, MW! et alibi).

HABIT: A tall shrub or, more often, small tree (to 6–8 m) with a short stem and wide crown.

HABITATS: Forest openings, edges, and clearings; coppices on slopes of *sopka*'s and in damp depressions; ditches and roadsides. Quite often, it is found together with *S. taraiensis*, yet restricted to soils that are richer in humus. On the other hand, it may cope with more paludification and less light in comparison with *S. taraiensis*. Therefore, it is often found in river valleys or eutrophic wetlands that cover bottoms of *pad*'s. Presumably, it does not ascend to any considerable heights in the mountains.

DISTRIBUTION. The western border of the species area runs via Irkutsk, the interfluvium between the Angara and Upper Lena, the Chona Basin, and Middle Vilyuy. In the north and northeast, the species is distributed, presumably with some gaps, to the Middle Olenok, Srednekolymsk, the Upper Indigirka and Upper Kolyma, Okhotsk, the Maya (a tributary of the Aldan), and the mouth of the Amur (not yet collected near Ayan and in Udskoy District). On Sakhalin, it is found only in the Upper Tym and Upper Poronay basins. The southern limit is in the northernmost Korea, the forested regions of Northeast China, and the Shilka and Argun basins including the Kentei; isolated fragments of the area are in the mountains of Jehol, north of Beijing (Ch'aoyangwantzu [Chevantsze]). (Fig. 41.)

NOTE. While working in the Leningrad Herbarium, P. Lakschewitz put aside a large series of samples to be described under the name of *S. subphylicifolia*. In the publication, however, he changed that name to *S. abscondita*. The change itself did not cause any problems, but the trouble was that P. Lakschewitz mixed two different species under the name of *S. subphylicifolia*. Except the one distributed in exsiccatae under the name *S. abscondita*, P. Lakschewitz placed a considerable number of *S. taraiensis* samples there. The very epithet '*subphylicifolia*' was chosen to emphasize a resemblance to *S. phylicifolia*. Yet it is *S. taraiensis* that resembles *S. phylicifolia* and not *S. abscondita* sensu proprio. Also, in the original diagnosis of *S. abscondita*, one can definitely recognize some characters of *S. taraiensis*. Due to that, *S. abscondita* has been considered an obscure and doubtful species. However, since the type specimens belong to only one of these two species, the name *S. abscondita* Laksch. is valid.

74. **S. iliensis** Rgl. 1880, Acta Horti Petropol. **6**: 464; Nazarov, 1936, Fl. SSSR **5**: 111; Drobov, 1941, Bot. mat. Bot. in-ta, Tashk. **5**: 4; id. 1953, Fl. Uzb. **2**: 35; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 65. —*S. pseudolivida* Goerz, 1936, Trudy Tadzh. bazy **2**: 171. —*S. depressa* ssp. *iliensis* Hiitonen, 1950, Mem. Soc. F. Fl. Fenn. **25**: 82. —*S. depressa* var. *iliensis* P. Pol. et var. *macropoda* P. Poljakov, 1960, Fl. Kazakhst. **3**: 29. —*S. caprea*, *S. livida*, *S. depressa* in schedis et in operis impressis scrutatorum fl. Asiae Mediae, non L. nec Wahlenb. nec Fries.

T y p u s: "Sarybulak prope Kuldscha, 4,000'–6,000', 22.IV 1878. Regel" (LE!).

HABIT: A medium-sized or tall shrub or a small (to 7–8 m) tree with a short stem and wide crown.

HABITATS: Forest openings and open woodlands; stony alluvial cones, *sai*, and banks of small streams. Being mostly restricted to forested regions, it may spread to mountainous steppes along *sai* and streams, particularly at high elevations.

DISTRIBUTION: The entire Tien Shan including its Chinese part (except the Karatau northeast of the Syr Darya River); the Pamir-Alay Region including Kashgaria (nearly everywhere, except the westernmost part—the Baysun Mountains and Kashka Darya Basin); the Hindu Kush and Karakorum. (Fig. 43.)

In the Dzungarskiy Alatau and Zailiyskiy Alatau, the species descends to the lower limit of the spruce forests (1,200–1,400 m); in the Pamir-Alay, it presumably does not go any lower than 2,000 m; in the Karakorum and Eastern Pamirs, it is encountered as high as 3,900 m.

75. ***S. pseudodepressa*** A. Skv. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 127; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4536. —*S. livida* Goerz, 1930, in Grossheim, Fl. Kavk. **2**: 8; id. 1934, Feddes Repert. **36**: 232. —Non *S. livida* Wahlenb. —*S. xerophila* auct non Floderus, 1930: Grossheim, 1945, Fl. Kavk. 2 ed. **3**: 21. —*S. aurita* auct. non L.: Grossheim, 1945, op. cit. **3**: 20.

T y p u s: "Turcia, prov. Kars, prope Sarykamysch, in palude ad rivulum. 29.VI 1914 D. I. Litvinov" (Herb. Fl. URSS N 4536, LE, MW et alibi).

HABIT: A medium-sized or low shrub.

HABITATS: Pine and birch stands, rocks, and damp depressions in the upper forest and subalpine zones at 1,600–2,300 m.

DISTRIBUTION: The Caucasus. This is a rather rare plant. Its area consists of three isolated fragments: in Turkish Armenia (5 known locations), Dagestan (13 findings), and Balkaria (2 locations). (Fig. 43.)

NOTE. According to its morphological characters, *S. pseudodepressa* occupies a kind of intermediate position between *S. bebbiana* and *S. iliensis*. However, it can be identified with neither of these species. A completely isolated distributional area is one more argument in favor of its distinctiveness.

Sect. 16. *Arbuscella*

Seringe ex Duby, 1828, in DC. Bot. Gall. 2 ed.: 426 (p. p.).

T y p u s: *Salix arbuscula* L.

Low or medium-sized shrubs. Shoots typically of reddish colors. Floriferous buds different from vegetative ones, either slightly or considerably; in the latter case, attenuating into beaks. Most typical leaves contrastingly bicolorous: lustrous, dark green above, glaucous or whitish beneath, their veins very straight and slender. Leaf margins uniformly denticulate, rarely subentire. Catkins precocious to serotinous. Nectary solitary. Ovary acute, mostly covered with appressed sericeous trichomes, attenuating into distinct style.

This is a very compact, natural, and distinct group, which consists of some 16–18 species, primarily, from the Old World (there are two or three American species). The majority of species are restricted to subarctic and subalpine areas and have comparatively

small geographical ranges. The affinity with the sections *Glabrella* and *Nigricantes* is quite obvious; connection with *Vimen* is also possible.

Key to Species

1. Floriferous buds significantly different from vegetative ones, 7–12 mm long. Catkins precocious or subprecocious, sessile or stalked; stalks short, stout (about 1 mm thick), with a few underdeveloped leaflets. Bracts black, 1.5–3 mm long, densely covered with straight trichomes exceeding bract apex by 1–1.5 mm or more. Male catkins in bloom more than 10 mm thick. Dry anthers 0.6–0.7 mm long. (Subsect. *Bicolores*) 2
- Floriferous buds not that much different from vegetative ones, 4–7 mm long. Catkins coetaneous or serotinous, borne on slender, foliated stalks. Bracts mostly pale or brownish, rounded at apex, to 1.5 (rarely 2) mm long, sparsely covered with thin, uneven trichomes exceeding bract apex often not more than by 1 mm. Male catkins in bloom less than 10 mm thick. Dry anthers 0.3–0.4 mm long. (Subsect. *Arbusculae*) 7
2. Stipules mostly fully developed, narrowly lanceolate or linear-subulate, often persistent after leaf abscission. Leaves rhomboid-elliptic, equally acuminate at base and apex, entire or with very obscure, shallow denticles, their veins slender, very regularly parallel to each other. Bracts acute. Styles mostly not shorter than 1 mm 78. **S. pulchra**
- Either leaves exstipulate or stipules obliquely semicordate, conspicuously inequilateral. Leaves of different shape or leaf margins and veins not as above 3
3. Capsule stipes 0.6–1.8 mm long, not shorter than nectaries 4
- Capsule stipes 0.2–0.5 mm long, not longer than nectaries 5
4. Young leaves (and mostly shoots) pubescent. Veins of second and third order prominent beneath, especially on young leaves, so that leaves resemble those of species from section *Nigricantes* or *Vetrix*. Bracts mostly brown 77. **S. basaltica**
- Young leaves and shoots glabrous or covered with very sparse, fugacious pubescence. Only veins of second order prominent beneath. Bracts mostly black 76. **S. phylicifolia**
5. Leaves mostly broadest distinctly above middle of blades, large (40–80 mm long). Female catkins in fruit 50–80 mm long. Bracts and capsules ascending obliquely upward, not deflected. Stigmas 0.6–0.7 mm long, linear, two-parted 79. **S. kikodseae**
- Leaves lanceolate or elliptic, acute both at base and apex, broadest about their middle. Female catkins in fruit 25–50 mm long. In mature catkins, bracts mostly deflected backwards. Capsules deflected at right angle to rachises, mostly starting from time of flowering. Stigmas 0.3–0.5 mm long, two-lobed 6
6. Leaves entire, or very vaguely dentate, or coarsely and rather irregularly dentate. Female catkins rather loose at base. Styles 0.6–1.0 mm long 81. **S. divaricata**
- All leaves delicately serrulate; serration acute, regular nearly all along leaf margins. Female catkins compactly flowered at base. Styles 0.7–1.5 mm long 80. **S. tianschanica**
- 7(1). Leaf margins more or less revolute and undulate-dentate, 40–80 mm long. Catkins serotinous, their bracts rufescent-brown. Ovaries glabrous, either entirely or in their upper part 89. **S. rhamnifolia**

- Leaf margins neither revolute nor undulate. Ovaries entirely pubescent 8
8. Leaves narrowly elliptic or sublinear (4–8 times as long as broad), delicately and sharply serrulate, frequently covered with longitudinally appressed silvery trichomes. Inferior leaves often broader than ordinary and superior ones. Floriferous buds very different from vegetative ones, lanceolate, with flat beaks, mostly blackening by winter time. Catkins coetaneous or, more often, subprecocious, mostly on leafless or scantily foliated stalks, their bracts typically blackish 88. **S. boganidensis**
- Leaves not as above, 1.5–4 times as long as broad. Floriferous buds usually without distinct beaks, not blackening. Catkins coetaneous or serotinous 9
9. Leaves with numerous stomata above 10
- Leaves without stomata above 12
10. Floriferous buds conspicuously different from vegetative ones. When catkins expand from buds, bracts already blackish-brown or black, their width 1–1.5 mm in female flowers 84. **S. kazbekensis**
- Floriferous buds inconspicuously different from vegetative ones. Bracts pale or brownish, up to 1 mm broad 11
11. Leaves with rounded denticles and small, inconspicuous glands. Their reticulation very distinct, composed of delicate veins 82. **S. arbuscula**
- Leaves with very dense, acute denticles bearing large white glands; reticulation not that conspicuous 83. **S. foetida**
- 12(9). Low shrub with short branches. Leaves small (20–40 mm long), entire or with very slender, acute denticles. Styles 0.6–1.2 mm 85. **S. waldsteiniana**
- Branches rather elongated. Styles 0.1–0.4 mm 13
13. Floriferous buds 4–7 mm long. Leaves 30–70 mm long, mostly oblanceolate, crenate-dentate. Bracts brownish 86. **S. saposchnikovii**
- Floriferous buds 3–5 mm long, scarcely different from vegetative ones. Leaves 20–40 mm long, mostly broadly elliptic, entire or serrulate. Bracts pale 87. **S. dshugdshurica**

A. Skv. subsect. nova. Novosti sist. vyssh. rast. a. 1968 describetur.

T y p u s: *Salix phylicifolia* L.

Floriferous buds greatly different from vegetative ones, large (7–12 mm long), lanceolate, their beaks flattened. Catkins precocious or subprecocious, sessile or stalked; stalks short, stoutish, leafless or nearly leafless. Bracts black or blackish-brown, 1.5–3 mm long, pubescent on both sides, their trichomes dense, white, and straight. Male catkins in full bloom more than 10 mm in diameter. Dry anthers 0.6–0.7 mm long, oval.

76. **S. phylicifolia** L. 1753, Sp. pl.: 1016 (p. p.: excl. var. β); Ledeb. 1850, Fl. Ross. **3**, 2: 611; Wimmer, 1866, Salic. Eur.: 70; Anderss. 1867, Monogr. Salic.: 131 (p. p.); Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 140; Krylov, 1930, Fl. Zap. Sib. **4**: 750 (p. p.: excl. pl. altaic. et Sib. Or.); Perfilyev, 1936, Fl. Sev. kr. **2–3**: 35; Nazarov, 1936, Fl. SSSR **5**: 71; Floderus, 1931, Salic. Fennosc.: 45; id. 1939, Ark. bot. **29A**, 18: 1; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 707; Nazarov et al. 1952, Fl. URSS **4**: 33; Shlyakov, 1956, Fl. Murm. **3**: 80; Rech. f. 1964, Fl. Eur. **1**: 48; Krall, Viljasoo, 1965,

Eestis Kasv. pajud: 50. — *S. bicolor* Ehrh. ex Willd. 1796, Berlin. Baumz.: 339; Floderus, 1939, op. cit. **29A**, 18: 6; Dostál, 1950, Květ. ČSR **2**: 893; Beldie, 1952, Fl. Rom. **1**: 294; Pawłowski, 1956, Fl. Tatr **1**: 187; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 84; id. 1964, op. cit. **1**: 48. — *S. hegetschweileri* Heer, 1840, in Hegetschweiler, Fl. Schweiz.: 963 (p. p.: altera pars est *S. hastata* L. —cf. Buser, 1887: 66); Floderus, 1939, op. cit. **29A**, 18: 15; Janchen, 1956, Catal. fl. Austr. **1**: 20; Rech. f. 1957, op. cit. **3**, 1: 85; id. 1964, op. cit. **1**: 48, p. p. saltem. — *S. rhaetica* Kern. ex Anderss. 1867, op. cit.: 136. — *S. bifax* Wołoszczak, 1888, Öst. bot. Z. **38**: 225. — *S. arbuscula* auct. non L.: Wolf, 1900, Izv. Lesn. in-ta **5**: 91; Zapałowicz, 1908, Consp. Galic. **2**: 63. — *S. tatrorum* Zapałowicz, 1908, op. cit. **2**: 65. —? *S. hibernica* Rech. f. 1963, Öst. bot. Z. **110**: 340; id. 1964, op. cit. **1**: 48; Stelfox, 1965, Irish Natur. J. **15**, 2: 25.

T y p u s: "In Sueciae borealibus. Fl. Lapp. N 358 et tab. 8 fig. E: Fl. Suec. N 793".

Ssp. **rhaetica** (Flod.) A. Skv. comb. nova. — *S. bicolor* ssp. *rhaetica* Flod. 1939, Ark. bot. **29A**, 18: 10. — *S. bicolor* Willd. 1796. — *S. hegetschweileri* Heer, 1840. — *S. rhaetica* Anderss. 1867. — *S. bifax* Wołoszczak, 1888. — *S. tatrorum* Zapałowicz, 1908.

T y p u s: "Tirol, Sellrainer Tal: Kerner, Herb. Öst. Weid. N 119 a, b" (W, FI! et alibi). Eadem planta e loco classico in Fl. Exs. Austro-Hungarica N 3857 edita. (LE! MW! et alibi).

Ssp. *rhaetica* is different from the major subspecies in elliptic leaves, smaller catkins, and more explicit staminate pubescence.

HABIT: A medium-sized shrub.

HABITATS: Lighted forests, forest edges, clearings, banks of streams and lake shores, damp lowlands and depressions, edges of wetlands; also, willow shrublands in tundras (together with *S. glauca* and *S. lanata*). Being rather indifferent to the quality of the bedrock, it occurs on acidic as well as basic substrates, stony and peaty grounds, rather dry and paludal ones, and so on. However, at the southern limit of its area, it is found almost exclusively in paludal lowlands.

DISTRIBUTION. There are two major areas. The main subspecies has a continuous distributional range in northern Europe and West Siberia; the subspecies *rhaetica* has a discontinuous area scattered over the mountains of Central Europe. The solid part includes Iceland, Scotland, northern Ireland, and most of Scandinavia (except the very south). The southern boundary of the continuous area approximates the line connecting Riga, Moscow, Murom, Nizhniy Novgorod, and Perm; deviating south to Magnitogorsk in the Urals, it again runs northwards toward Turinsk, then approximately via Tobolsk, Tara, and Kolpashevo. The eastern limit is somewhere in-between the Taz and Yenisei (there are also samples from the Yenisei collected near Dudinka). In the western Yamal, it reaches 72° N, missing, however, from the Yugorskiy Peninsula, Vaygach, and possibly the Novaya Zemlya, where it is substituted by *S. pulchra*. Kolguyev Island and the entire Kanin and Kola peninsulas are included in the north.

The ssp. *rhaetica* occurs sparsely and not abundantly in the upper forest and subalpine zones of the Vosges, Harz, Sudetes, Alps, Tatras, and Eastern Carpathians (in Ukraine, at Chornogora). (Fig. 45.)

In Scotland and Iceland, it ascends to 600 m; in northern Norway (Tromsö), to 900 m; in the Khibins, to 600 m; in the Northern Urals (Denezhkin Kamen), to 1,000 m; in the Prepolar Urals (the Shchugor Basin), to 600 m; in the Polar Urals (the Sob and Khadata

basins), to 300–400 m. In the Tatras, its range is 1,600–1,900 m; in the Alps, 1,400–2,000 m.

NOTE. *S. phyllicifolia* was erroneously reported for the territories of East Siberia including Yakutia (e. g., Karavayev 1958, Popov 1959), the Altai and Tien Shan (Krylov 1930, Polyakov 1960), and the Caucasus (Grossheim 1945). These data are to be attributed to other species.

Some European authors (Floderus 1939; Rechinger 1957, 1964) treated plants from the mountains of Central Europe as distinct species: *S. bicolor* and *S. hegetschweileri*. I examined available Central European samples of *S. phyllicifolia* and related species from the herbaria of St. Petersburg, Prague, Wien, München, Paris, Florence, and Stockholm (LE, PR, W, M, P, FI, S). My opinion agrees with that of R. Buser (1940: 707 et seq.): we cannot accept *S. bicolor*, *S. rhaetica*, and *S. hegetschweileri* as distinct species. On the other hand, according to my opinion, the plants from the Pyrenees and French Massif Central, which were included in *S. bicolor* by B. Floderus and K. Rechinger, are to be treated as a distinct species *S. basaltica* (see the next species).

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In the material that I got from Wien, there were four curious samples collected by A. Neumann and K. Rechinger in the Ötztaler Alps (Gurgl Valley). Both K. Rechinger and A. Neumann identified those samples as *S. hegetschweileri*. Yet A. Neumann (personal communication) assumed that the species was approximating the section *Nigricantes* rather than *S. phyllicifolia*. In fact, the samples appeared to exhibit characters of *S. phyllicifolia* along with those of *S. mielichhoferii* and *S. glabra* (for instance, their capsules were glabrate or glabrous). They were probably hybrid plants (of three female samples, two had underdeveloped capsules). Another possibility is that they represented a restricted endemic species, not yet recognized. If this is the case, it is still absolutely impossible to identify it with *S. hegetschweileri*. The problem needs further investigation.

The description of *S. hibernica* Rech. f. from northeastern Ireland was based on only two samples that were different from *S. phyllicifolia* in their broader leaves and shorter capsule stipes, according to K. Rechinger. I did not have a chance to examine those samples; according to the description, the distinctness of that species appears to be doubtful.

77. ***S. basaltica*** Coste, 1896, Bull. Soc. Bot. Fr. **43**: 509. —? *S. semicordata* Dulac, 1867, Fl. Haut. Pyren.: 147. —*S. altobracensis* Coste, 1896, op. cit. **43**: 511. —*S. phyllicifolia* auct. fl. Galliae centr. et Mont. Pyren. non L.: Coste, 1906, Fl. Fr. **3**: 268; Rouy, 1910, Fl. Fr. **12**: 211 (excl. pl. e Mont. Vosges); Görz, 1929, Saul. Catal.: 36; Cadevall, Font, 1933, Fl. Catal. **5**: 182; Vicioso, 1959, Salic. Españ.: 93. —*S. bicolor* auct. non Willd.: Floderus, 1939, Ark. bot. **29A**, 18: 6 (p. p.: quoad pl. pyren. et Galliae centr.); Chassagne, 1956, Invent. Auvergne **1**: 232; Rech. f. 1964, Fl. Eur. **1**: 48 (p. p.: quoad pl. pyren. et Galliae centr.). —? *S. cantabrica* Rech. f. 1962, Öst. bot. Z. **109**: 374.

T y p u s: "Tourbières du plateau Aubrac, lisière supérieure du bois de Rigambal; montagne des Truques; sommet du bois de Laguiole. —J. Soulier et H. Coste" (P, vidi specim. ex Laguiole).

HABIT: A small or medium-sized (0.75–3 m) shrub.

HABITATS: Damp and peaty places.

DISTRIBUTION: The French Massif Central and Pyrenees at 1,000–1,800 m. It might also occur in the Cantabrian Mountains in northwestern Spain (see the note). (Fig. 45.)

NOTE. I examined 25 non-duplicate samples of *S. basaltica*; they provided enough evidence in favor of treating *S. basaltica* as a distinct species. It seems rather strange that

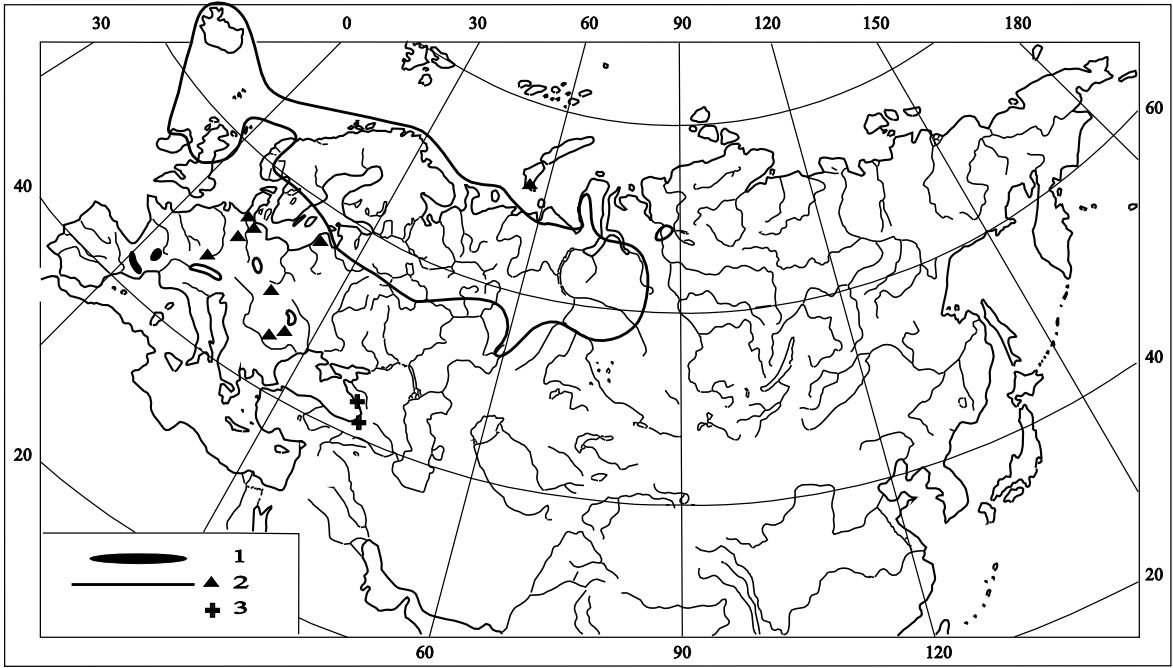


Fig. 45. Distributional areas of *Salix basaltica* Coste (1), *S. phylicifolia* L. (2), and *S. kikodseae* Goerz (3)

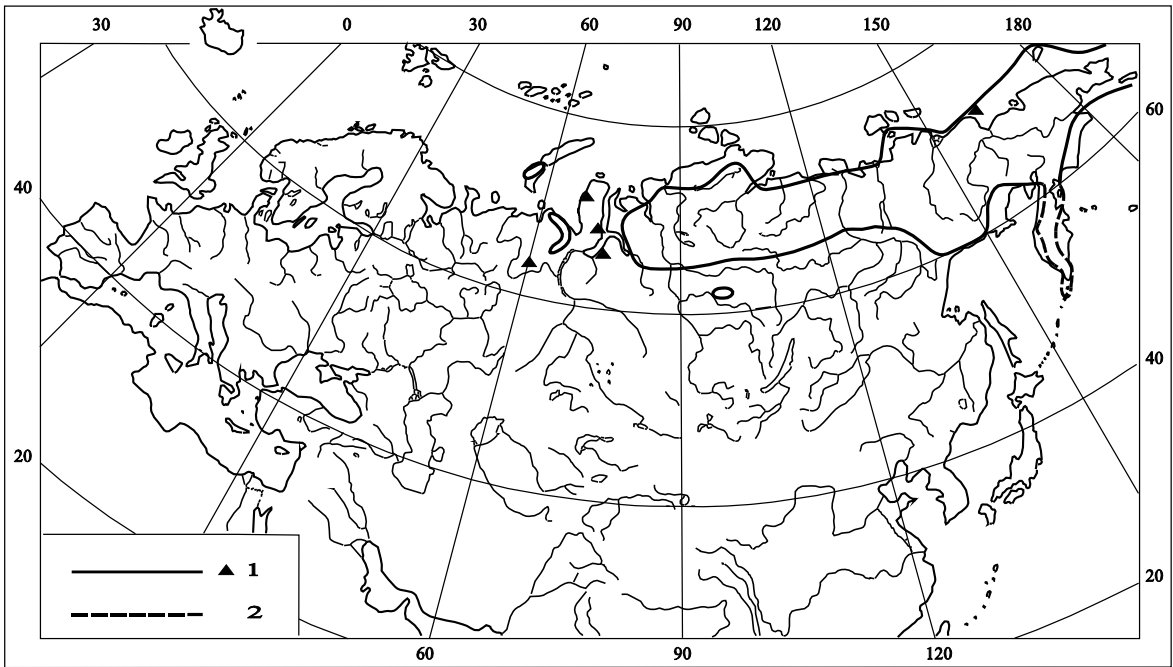


Fig. 46. Distributional areas of *Salix pulchra* Cham. (1) and *Salix pulchra* ssp. *parallelinervis* A. Skv. (2)

the West European authors, who tried to segregate *S. bicolor* and *S. hegetschweillerii* as distinct species without providing enough reasons, at the same time, never recognized such a good species as *S. basaltica*. The author of the species, H. Coste, considered *S. basaltica* to be a hybrid of *S. pentandra* and *S. aurita*, a combination that was never encountered and is hardly possible. He treated another species, *S. altobracensis*, which he described together with *S. basaltica*, as a hybrid of *S. pentandra* and *S. cinerea* (an equally impossible combination). As it is implied by an investigation of H. Coste's plants, *S. altobracensis* is nothing else but *S. basaltica*. Neither B. Floderus nor M. Chassagne admitted the hybrid nature of *S. basaltica* and *S. altobracensis* and assigned both to *S. bicolor* (Floderus 1939, Chassagne 1956). Apparently, A. Neumann was the only one who recognized *S. basaltica* as a distinct species (Neumann in litt.).

183 The plants from the Vosges are clearly different from *S. basaltica* and undoubtedly belong to *S. phyllicifolia* ssp. *rhaetica*.

S. cantabrica Rech. f. was described from the Cantabrian Mountains (northwestern Spain). Since the description was based on a single specimen, it remains dubious. Most probably, it is nothing other than *S. basaltica*.

In the literature, one can find the name *S. semicordata* Dulac. mentioned as a synonym of "*S. phyllicifolia*" from the Pyrenees (Rouy 1910, Vicioso 1951, Chassagne 1956). If this is true, then the correct name for *S. basaltica* is *S. semicordata*. I have not yet had an opportunity to verify if this is right.

78. ***S. pulchra*** Cham. 1831, *Linnaea* **6**: 543; Coville, 1901, *Proc. Wash. Acad.* **3**: 319; Schneider, 1919, *J. Arn. Arb.* **1**: 70; Floderus, 1933, *Ark. bot.* **25A**, 10: 5; id. 1939, *ibid.* **29A**, 18: 20; Nazarov, 1936, *Fl. SSSR* **5**: 46; Hultén, 1943, *Fl. Al.* **3**: 547; Raup, 1959, *Contrib. Gray Herb.* **185**: 88; Skvortsov, 1961, *Bull. MOIP* **66**, 4: 30; id. 1966, *Spisok rast. Gerb. fl. SSSR* **91**: N 4534. —*S. taimyrensis* Trautv. 1847, in Middendorff, *Reise Sibir.* **1**, **2**: 27 et tab. 5, 6; Ledeb. 1850, *Fl. Ross.* **3**, 2: 616. —*S. arctica* var. *taimyrensis* Anderss. 1868, in DC. *Prodr.* **16**, 2: 287; Krylov, 1930, *Fl. Zap. Sib.* **4**: 771. —*S. boganidensis* Trautv. 1847, in Middendorff, *Reise Sibir.* **1**, **2**: 154 (p. p.: quoad. pl. in tab. 3 depictas). —*S. boganidensis* var. *latifolia* Trautv. 1879, *Acta Horti Petropol.* **6**, 1: 34. —*S. fulcrata* Anderss. 1867, *Monogr. Salic.*: 139 (p. p.: quoad pl. e America septentr. tantum, nec ad pl. e Kamtchatka, nec in fig. 73 depicta). —*S. parallelinervis* Flod. 1926, *Ark. bot.* **20A**, 6: 35; Komarov, 1929, *Fl. Kamch* **2**: 14; Nazarov, 1936, *op. cit.* **5**: 73. —*S. anadyrensis* Flod. 1933, *op. cit.* **25A**, 10: 9 et fig. 3; Nazarov, *op. cit.* **5**: 69.

T y p u s: "Promontorium Espenbergii, inque insula Laurentii —Chamisso" [S (fide Floderus 1939), LE (insula Laur.)!].

Ssp. ***parallelinervis*** (Flod.) A. Skv. 1961, *Bull. MOIP* **66**, 4: 31. —*S. parallelinervis* Flod. 1926, *Ark. bot.* **20A**, 6: 35.

T y p u s: "Kamtchatka: Opala volc.; fluv. Tolmatchevaja; inter Petropavlovsk et Avatcha —Svenska Kamtchatka exped. N 2224, 3879, 1038" (S!).

The subspecies is different in its shorter stipules and subprecocious catkins borne on short stalks.

HABIT: A shrub to 1.5–3 m tall in favorable conditions; it may be as well completely procumbent when growing in severe environment.

HABITATS: Open larch and poplar forests, *yernik*'s, banks of streams, various depressions, edges of wetlands, meadows, as well as tundras of various kinds, like moss-,

lichen-dominated, or graminoid, tussocky, hillocky, stony, and polygonal, except extremely paludal ones and those in high arctic regions.

DISTRIBUTION: Southern Island of the Novaya Zemlya, the Yugorskiy Peninsula, Polar Urals; the Prepolar Urals (scattered); the Lower Taz, and Gydanskaya Tundra. East of the Yenisei, it becomes very common growing nearly all across the tundras and barren heights. In the north, it reaches the mouth of the Pyasina, Lake Taimyrskoye, the mouths of the Olenek, Lena, and Yana, and islands Bolshoy Lyakhovskiy, Chetyrekhstolbovoy, and Wrangel. It is sparsely distributed across the northern forest belt reaching the Chunya River, the drainage divide between the Olenek and Upper Vilyuy, and Zhigansk. It is rather common on the barren heights of the Northeast reaching Okhotsk, Magadan, and the territory south of Verkhoyansk. The easternmost point is Cape Dezhnev.

Ssp. parallelinervis is distributed on Kamchatkan barren heights (starting from Koraga) and Paramushir.

In the Prepolar Urals (the Shchugor Basin), it is found at 900 m; in the Polar Urals (the Sob Basin), it ascends to 500 m; on the Kamchatka Peninsula, to 1,000 m. (Fig. 46.)

S. pulchra is a common species in Arctic North America reaching the Coronation Gulf as the easternmost point.

NOTE. *S. pulchra* is rather polymorphous, especially in certain parts of its area, such as the Indigirka, Kolyma, Anadyr, and Penzhina basins. There, along with plants common to other Eurasian area parts, one can often find specimens with rather dense shoot pubescence, and sometimes even ones with pubescent leaves, particularly, the lower leaf surface. The pubescent forms are frequently characterized by rather large sizes and comparatively stout shoots. These powerful plants were described under the name of *S. anadyrensis* Flod. Yet, on the same territory, one can find perfectly normal *S. pulchra* which is absolutely identical to that from the Novaya Zemlya, Taimyr, or Chukotka, as well as all kinds of transitional forms. Therefore, we cannot segregate *S. anadyrensis* in a distinct species or even subspecies. Samples from the Lower Lena also occasionally exhibit conspicuous pubescence.

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Plants that appear to be "intermediate" between *S. pulchra* and *S. phyllicifolia* are rather common in the Lower Yenisei Basin, west of it (around the Ob and Taz Inlet), and particularly in the Polar Urals. These specimens may be of hybrid nature.

79. ***S. kikodseae*** Goerz, 1928, Feddes Repert. Beih. **52**: 133; id. 1930, Feddes Repert. **28**: 123; Skvortsov, 1961, Bull. MOIP **66**, 4: 31; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 129. —*S. phyllicifolia* auct. fl. caucas. non L.: Görz, 1934, Feddes Repert. **36**: 229; Grossheim, 1945, Fl. Kavk. 2 ed. **3**: 18; Dmitriyeva, 1959, Opred. rast. Adzhar.: 427; Makhatadze, 1961, Dendrofl. Kavk. **2**: 17.

T y p u s: Batumskiy District, the Machakhli-Tskhali River Gorge, near the Settlement of Yefrat. 7. VII 1913. E. I. Kikodze [in Russian] (LE!).

HABIT: A small (?) shrub.

HABITATS: Moist slopes in the subalpine zone.

DISTRIBUTION. This willow is one of the rarest in Eurasia. So far, only seven samples are known, of which five are from Adzharia (including Turkish Adzharia) and two from Abkhazia. (Fig. 45.)

80. ***S. tianschanica*** Rgl. 1880, Acta Horti Petropol. **6**: 471; Nazarov, 1936, Fl. SSSR **5**: 84; Skvortsov, 1961, Bull. MOIP **66**, 4: 31; id. 1962, Bot. mat. Gerb. in-ta bot. AN UzbSSR **17**: 66.

T y p u s: "Tian-Schan, in valle f. Tekes super., 6500', VII 1857 Semenov" (LE!).

HABIT: A shrub 1–3 m tall.

HABITATS: Openings and exposed slopes in the spruce forest zone, particularly, its upper part. Occasionally, it forms very extensive pure shrublands in the ecotone between the spruce forest and alpine zones on well-watered northern slopes.

DISTRIBUTION: The Tien Shan (the ranges Ketmen, Zailiyskiy, Kungey Alatau, and all those south of Lake Issyk-Kul including the Atbashi Range as the westernmost and the Halik Tau on the Chinese territory as the easternmost one). Presumably, it is not found any farther in China (there are only two samples from the Chinese Tien Shan). Besides, there are isolated localities in the Kirgizskiy Range and Chimgan.

It is encountered as high as 3,200 m, presumably, never descending lower than 1,800 m. (Fig. 47.)

NOTE. *S. tianschanica* is omitted in the "Flora of Kazakhstan" (Polyakov 1960). Probably, P. Polyakov considered it to be "*S. arbuscula*".

81. *S. divaricata* Pall. 1788, Fl. Ross. **1**, 2: 80; Turcz. 1854, Fl. Baic.-Dah. **2**: 388; Nazarov, 1936, Fl. SSSR **5**: 47; id. 1937, Fl. Zabayk. **3**: 212; Grubov, 1955, Konsp. fl. Mong.: 100; Skvortsov, 1961, Feddes Repert. **64**: 81; Malyshev, 1965, Fl. Vost. Sayana: 108. —*S. brevijulis* Turcz. 1854, op. cit. **2**: 387; Nazarov, 1936, op. cit. **5**: 80; id. 1937, op. cit. **3**: 200. —*S. leptocladus* Anderss. 1867, Monogr. Salic.: 144 et tab. 7 fig. 79; Nazarov, 1936, op. cit. **5**: 83. —*S. metaformosa* Nakai, 1919, Bot. Mag. Tokyo **33**: 42; id. 1930, Fl. sylv. Kor. **18**: 142 et tab. 30. —*S. orthostemma* Nakai, 1919, op. cit. **33**: 43; id. 1930, op. cit. **18**: 143 et tab. 31.

T y p u s: "In summo alpium Davuriae cacumine Sochondo lecta a cl. Sokolof" (LE!). The original label by N. Sokolov is still attached to the sample. It says: "On the top of Mount Sokhondo, amidst debries".

186 **Ssp. kalarica** A. Skv. comb. nova. —*S. pulchra* ssp. *kalarica* A. Skv. 1961, Bull. MOIP **66**, 4: 31.

T y p u s: "ad fluv. Kalar cursum superiorem prope lacum Ammudin, 5.VIII 1932. N. Savicz" (LE).

The subspecies is different in its large (up to 80 mm long) leaves that frequently are sericeous beneath.

HABIT: A shrub, either prostrate, appressed to substrate or upright, 1–2 m tall (in favorable conditions).

HABITATS: Taluses, moist slopes, banks of streams, and such, on and around barren heights. It may occasionally descend to foothills along cold and moist minor valleys and via wetlands.

DISTRIBUTION: The Altai and Tuva (rare, solitary findings on barren heights); the Khangai (more frequently); the east of the Eastern Sayans (rather frequently, ascending to 2,350 m, according to L. Malyshev, 1965); the Kentei and Borshchovochnyy ranges (most frequently); the coast of Lake Baykal and Stanovoye High Plateau including the Olekma Basin; the Stanovoy and Dzhugdzur ranges; the Amga and Aldan basins (found occasionally); the barren heights of North Korea (a disjunct fragment of the area).

Ssp. kalarica is restricted to the northeastern part of the species area: it is distributed from the Vitim River to Dzhugdzur Range. (Fig. 47.)

NOTE. The species is rather variable on and around the Stanovoye High Plateau. The segregation of the ssp. *kalarica* is the first and rough attempt to depict this variability. There is definitely necessity in further detailed study of the species in that part of its area.

Subsect. *Arbusculae*

Hayek, 1908, Fl. Steierm. **1**: 162, emend. A. Skv.

T y p u s: *Salix arbuscula* L.

Floriferous buds not much different from vegetative ones, 4–7 mm long. Catkins coetaneous or serotinous, borne on slender, foliated stalks. Bracts mostly pale or brownish, 1.5 (rarely 2) mm long, sparsely covered with thin, uneven trichomes exceeding bract apex often by not more than 1 mm. Male catkins in full bloom less than 10 mm in diameter. Dry anthers 0.3–0.4 mm long.

82. **S. arbuscula** L. 1753, Sp. pl.: 1018 (p. p.: var. γ tantum); id. 1755, Fl. Suec. 2 ed.: 348; Fries, 1840, Bot. not.: 205; Ledeb. 1850, Fl. Ross. **3**, 2: 622 (p. p.: quoad pl. europ.); Wimmer, 1866, Salic. Europ.: 102 (p. p.: excl. pl. centrali-europ.); Krylov, 1930, Fl. Zap. Sib. **4**: 752 (p. min. p.: quoad nonnullas pl. uralens. tantum); Floderus, 1931, Salic. Fennosc.: 99; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 34; Nazarov, 1936, Fl. SSSR **5**: 79 (p. p.: excl. pl. caucas. et sibir.); Shlyakov, 1956, Fl. Murm. **3**: 103; Skvortsov, 1961, Bull. MOIP **66**, 4: 32; Rech. f. 1964, Fl. Eur. **1**: 51. —Non *S. arbuscula* auct. fl. Europae centralis, Caucasi et Sibiriae.

T y p u s: "In Lapponiae campis arenosis. Fl. Lapp. N 360 et tab. 8 fig. M".

HABIT: A low (0.2–1.2 m), intensely branching shrub with slender shoots.

HABITATS: Gravelly and stony slopes, moraines, deluvial debries, as well as sandy grounds. Although it may occur on bedrock of variable acidity, basic one is preferred; all of southernmost localities appear to be associated with basic bedrock.

DISTRIBUTION: The mountains of Scotland (at 400–800 m) and the Scandinavian Peninsula (to 800 m in the south and 0–400 m in the north). In the Russian north, it is distributed very sparsely: in the Khibins (few localities at 300–400 m); on Kolguyev Island (many findings in its different parts); in the basin of the Pinega, the right tributary of the Northern Dvina (on limestone and gypseous rock); in the Prepolar Urals (on limestone of the western slope); in the Northern Urals (occasionally, on basic rock across the barren heights reaching Denezhkin Kamen as the southernmost point, found at 1,000 m there); and in the Southern Urals (the only one finding on Mount Iremel). There is also one finding reported from the Lower Ob (south of Salekhard), and another doubtful sample from Gydanskaya Tundra on the northeastern coast of the Yuratskaya Inlet. (Fig. 48.)

83. **S. foetida** Schleich. ex Lam. et DC. 1805, Fl. fr. 3 ed. **3**: 296; Gaudin, 1836, Syn. fl. helvet.: 265; Rech. f. 1938, Feddes Repert. **45**: 92; id. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 108; id. 1964, Fl. Eur. **1**: 52; Janchen, 1956, Catal. fl. Austr. **1**: 103. — *S. arbuscula* auct. non L.: Wimmer, 1866, Salic. Eur.: 102 (p. p.); Rouy, 1910, Fl. Fr. **12**: 213; Cadevall et Font, 1933, Fl. Catal. **5**: 181; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 714; Vicioso, 1951, Salic. Españ.: 95. —?? *S. glaucescens* Moench, 1802, Method. Suppl.: 116.

T y p u s: "Schleicher, Exs. Helvet., cent. I, N 95" (n. v.).

HABIT: A rather low shrub (30–120 cm, occasionally to 2 m).

HABITATS: Damp hollows and small drainage wetlands, moraines, pebbly bottoms of valleys, mostly on siliceous substrate in the subalpine and alpine zones.

DISTRIBUTION: The Alps at 1,600–2,600 m (from the Maritime Alps to Tirol reaching the Upper Piave River in the east); the Pyrenees (much more rare than in the Alps). (Fig. 48.)

NOTE. *S. glaucescens* Moench. was cited as a synonym by G. Rouy (1910). I did not have an opportunity to verify that name.

84. *S. kazbekensis* A. Skv. 1961, Feddes Repert. **64**: 78; id. 1961, Bull. MOIP **66**, 4: 27; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 130. —*S. arbuscula* auct. fl. caucas. omnium, non L.

T y p u s: "Circa Montem Kazbek, prope pag. Gherghety, regio subalpina, alt. 2500–2600 m, 12. VIII 1937, M. Nasarov" (MW).

HABIT: A low shrub.

HABITATS: Rocks, taluses, pebbles, glacial moraines, banks of streams, lake shores, alpine spring fens and meadows, *Rhododendron* shrublands, and occasionally birch and even pine forests in the subalpine and alpine zones, rarely in the upper forest zone (1,700–3,300 m).

DISTRIBUTION: All of the Greater Caucasus from the Fisht-Oshten Massif to the Andiyskiy Range and Salavat Pass southwest of Kuba (common nearly everywhere in the western half and comparatively rare and sparse in the east). In his notes, A. Grossheim showed a number of localities at the extreme southeastern part of the Main Range (Baba Dag); yet I did not see any samples from that region. Neither could I find any plants from the Lesser Caucasus. (Fig. 49.)

85. *S. waldsteiniana* Willd. 1806, Sp. pl. **4**, 2: 679; Schinz, Keller, 1900, Fl. Schweiz.: 137; Hirc, 1904, Rad Jugosl. Akad. **159**: 161; Rech. f. 1938, Feddes Repert. **45**: 90; id. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 109; id. 1964, Fl. Eur. **1**: 52; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 711; Janchen, 1956, Catal. fl. Austr. **1**: 103. —*S. arbuscula* auct. non L.: Wimmer, 1866, Salic. Eur.: 102 (p. p.: quoad var. α *waldsteiniana*); Beck, 1906, Glasnik zem. muz. Bosni i Herceg. **18**: 98; Hayek, 1924, Feddes Repert. Beih. **30**, 1: 85; Stoyanov, Stefanov, 1948, Fl. Blg.: 319.

T y p u s: "*S. myrsinites*? —Kitaibel in litt. —In alpiibus Croatiae" (Hb. Willdenow — B, n. v.).

HABIT: A low shrub with short branches.

HABITATS: Moist slopes, taluses, and rocks of the upper forest, subalpine, and lower alpine zones, mostly, on carbonate substrates.

DISTRIBUTION: The eastern part of the Alps from Canton Unterwalden to the Wiener Wald (900–2,000 m); the mountains of the former Yugoslavian territory from Slovenia to Crnagora (Montenegro); northern Albania; and western Bulgaria including the Vitocha, Rila, and Stara Planina. In the Balkans, its altitudinal range is 1,250–2,300 m. Apparently, all data in the old literature concerning findings in the Carpathians are erroneous. (Fig. 49.)

86. *S. saposhnikovii* A. Skv. 1961, Feddes Repert. **64**: 77; id. 1961, Bull. MOIP **66**, 4: 26; Malyshev, 1965, Fl. Vost. Sayana: 108; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 71. —*S. arbuscula* auct. non L.: Krylov, 1930, Fl. Zap. Sib. **4**: 752 (p. p.); Polyakov, 1960, Fl. Kazakhst. **3**: 33 (p. p.); Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 15. —*S. phyllicifolia* auct. non L.: Krylov, 1930, op. cit. **4**: 750, p. p. quoad pl. altaicas.

T y p u s: "Altai, ad font. fluv. Balykty-su, tundra montana muscoso-lichenosa, 28. VII 1915, P. N. Krylov" (MW, TK).

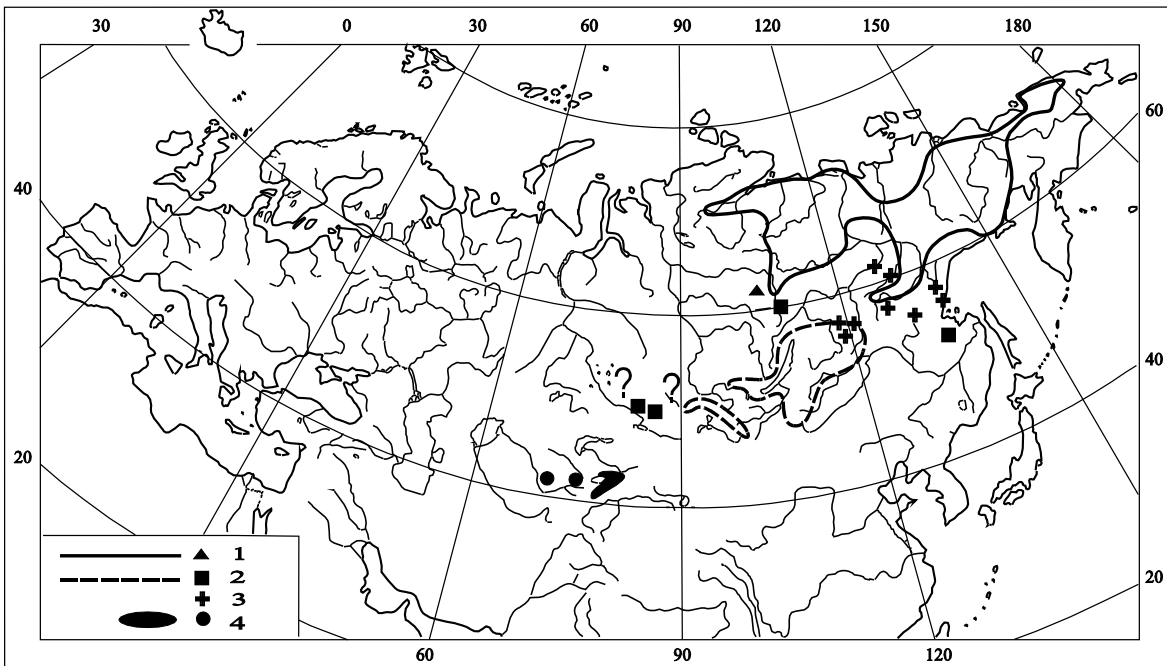


Fig. 47. Distributional areas of *Salix boganidensis* Trautv. (1), *S. divaricata* Pall. (2), *S. divaricata* ssp. *kalarica* A. Skv. (3), and *S. tianschanica* Rgl. (4)

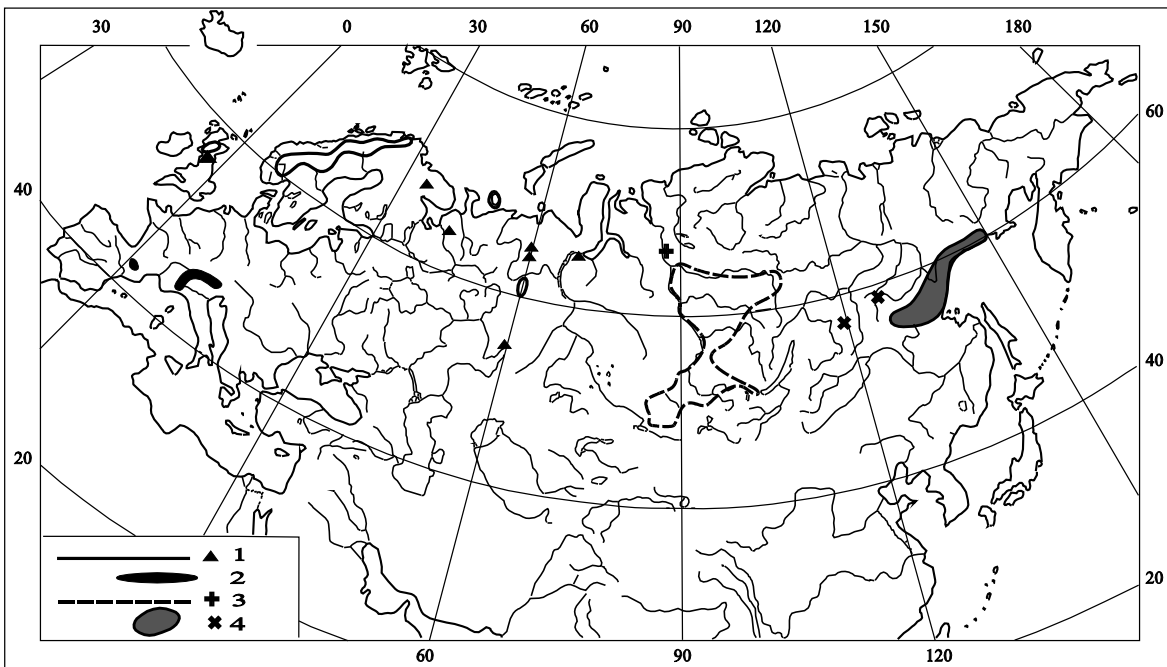


Fig. 48. Distributional areas of *Salix arbuscula* L. (1), *S. foetida* Schleich. ex Lam. et DC. (2), *S. saposhnikovii* A. Skv. (3), and *S. dshugdshurica* A. Skv. (4)

HABIT: A low or medium-sized shrub.

HABITATS: Alpine tundras, banks of streams, stony and sodded slopes within the alpine and subalpine zones (reaching 2,100–2,200 m in the Altai and Sayans). Occasionally, it may descend to the forest zone and grow there at damp hollows.

DISTRIBUTION: The Altai, Kuznetskiy Alatau, Western Sayans and the western part of Eastern Sayans (reaching the Pogranichnyy Range); also, in the Yeniseiskiy Kryazh and on the Central Siberian Plateau reaching the Nizhnyaya Tunguska in the north, the Upper Chunya and Upper Vilyuy Basin (the Ulakhan-Vava River) in the east. (Fig. 48.)

87. **S. dshugdshurica** A. Skv. 1961, Feddes Repert. **64**: 80; id. 1961, Bull. MOIP **66**, 4: 27. —*S. arbuscula* auct. fl. Sibir. p. p.

T y p u s: "Montes Dshugdshur, lariceto-betuletum in valle fluv. Matang. 16.IX 1953. V. N. Vassiljev" (LE).

HABIT: A small shrub with slender branches and small leaves, much alike *S. arbuscula*.

HABITATS: Bogs, *yernik*'s, larch forests with *Sphagnum* ground cover, and rock debris mostly in the lower part of the barren heights zone and upper forest zone (to 1,600 m).

DISTRIBUTION: The coast of the Sea of Okhotsk almost to the Tauyskaya Inlet, Yudomo-Mayskoye High Plateau, Dzhugdzur, Stanovoy, and Aldano-Uchurskiy ranges, and the eastern Stanovoye High Plateau. So far, only some thirty localities are known. It appears to be somewhat more common around Ayan. (Fig. 48.)

NOTE. This is a comparatively rare species that is distributed in a rather inaccessible region, therefore, it is still poorly known. More collections and observations are needed to clarify its morphology, ecology, and geographical distribution. Particularly, its delimitation from *S. boganidensis* in terms of morphology as well as geography has to be investigated. Early in spring, plants of the latter species may occasionally develop short and broad leaves that look very similar to those of *S. dshugdshurica*. Since the catkins in the two species also look alike, herbarium samples may be easily confused. However, *S. dshugdshurica* appears to be very different from *S. boganidensis* in ecological as well as geographical characteristics.

88. **S. boganidensis** Trautv. 1847, in Middendorff, Reise Sibir. 1, **2**: 154 (p. p.: quoad pl. fol. angustis subtus pilosis in tab. 2 depictas, nec in tab. 3); id. 1877, Acta Horti Petropol. **5**, 1: 105; id. 1878, op. cit. **5**, 2: 557. —*S. boganidensis* var. *angustifolia* Trautv. 1879, Acta Horti Petropol. **6**, 1: 34. —*S. chlorostachya* (non Turcz.) Trautv. 1877, op. cit. **5**, 1: 104. —*S. kolymensis* Seemen, 1908, Feddes Repert. **5**: 18; Nazarov, 1936, Fl. SSSR **5**: 75; Skvortsov, 1961, Bull. MOIP **66**, 4: 33.

T y p u s: "Ad. fl. Boganida a. 1843. —A. Middendorff" (LE!).

HABIT: A small tree (to 5 m tall at the Upper Kolyma) or shrub that can grow tall or low depending on environmental conditions.

HABITATS: River valleys and terraces (larch stands, chosenia groves, *yernik*'s; also, fresh alluvial deposits, mostly pebbles). It is more rare outside valleys. This is the only species in the section *Arbuscella* that clearly demonstrates a tendency to inhabit alluvial substrates. At the same time, it is obviously a mountainous species. A proof of the species' mountainous nature is, first of all, its confinement to pebbly deposits and avoidance of sandy ones or fine soil; and also its marginal penetration to arctic regions versus significant invasion up the mountains, even at high latitudes.

It ascends to 600 m in the northern Verkhoyanskiy Range near Sakhandzha; to 1,100 m in the Moma Range, close to the Arctic Circle.

DISTRIBUTION: The Taimyr Peninsula (the Kheta and Lower Kotuy basins), the Anabar, Olenek, and Vilyuy basins, a part of the Nizhnyaya Tunguska Basin; the Amga and Aldan basins; along the Lena downstream of Zhigansk. It is distributed nearly everywhere in the Verkhoyanskiy Range and east of it, reaching the Anadyrskiy Range, yet missing from the Penzhina and Anadyr basins except some tributaries of the Belaya. (Fig. 47.)

In Subarctic and Arctic North America, there is a species of very close filiation, *S. arbusculoides* Anderss.

89. ***S. rhamnifolia*** Pall. 1788, Fl. Ross. **1**, 2: 84; Skvortsov, 1957, Bot. mat. Gerb. Bot. in-ta AN SSSR **18**: 35, 36; id. 1961, Bull. MOIP **66**, 4: 33; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 15; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3224. —Non *S. rhamnifolia* auct.: Hook. Arnott, 1841, Bot. Beechey Voy.: 117; Ledeb. 1850, Fl. Ross. **3**, 2: 612; Anderss. 1867, Monogr. Salic.: 169; Nazarov, 1936, Fl. SSSR **5**: 120. —*S. chlorostachya* Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 373; Nazarov, op. cit. **5**: 76; id. 1937, Fl. Zabayk. **3**: 199; Grubov, 1955, Konsp. fl. Mong.: 100; Karavayev, 1958, Konsp. fl. Yak.: 82 (p. p.); Popov, 1959, Fl. Sredn. Sib. **2**: 803; Malyshev, 1965, Fl. Vost. Sayana: 108. —*S. podophylla* Anderss. 1867, op. cit.: 142; Nazarov, 1936, op. cit. **5**: 77.

T y p u s: "E *Selengia missa*" (Hb. J. G. Gmelin —LE!). In Gmelinii Flora Sibirica vol. 1 tab. 35 fig. 1A (1747) depicta. Cf. Skvortsov, 1957.

HABIT: A medium-sized shrub.

HABITATS: Mostly valley meadows, wet spots in flood plains of large rivers; wet, but not paludal bottoms of *pad'*s. It is quite common in somewhat saltish meadows and also in *zapadina*'s amidst the steppe vegetation. Growing primarily, at low elevations, it may reach the lower barren heights zone via suitable habitats (to 2,200 m in the Eastern Sayans). In Mongolia, it even ascends to *Cobresia* alpine meadows (to 2,600 m in the central Khangai).

DISTRIBUTION: The Altai (from Seminskiy Pass to the Kobdo River in Mongolia); southern Tuva; northern Mongolia including the Khangai and Kentei with their piedmont areas; Prebaykalia and Transbaykalia to the Tungir River in the east; southern Yakutia (the Aldan and Lena upstream of Yakutsk). The westernmost parts of the continuous area are the Kan and Lower Angara basins. An isolated part of the area is found at the northern foot of the Kuznetskiy Alatau, one more at the Lower Nizhnyaya Tunguska and Lower Yenisei. Some few isolated localities are known in these areas along the beaches of the named rivers and the Kureyka. One more disjunct area fragment is in the Weichang north of Beijing. (Fig. 49.)

NOTE. Plants from the Lower Yenisei are different from the rest in their broad elliptic leaves and completely glabrous capsules; besides, all of them grow on the beach, a habitat that is very unusual on the whole, within the entire area of *S. rhamnifolia*. If we assume that the populations at the lower reaches of the Yenisei have appeared merely due to seed dispersal by water, then the origin of the plants at the Lower Nizhnyaya Tunguska still remains unclear, as there is no *S. rhamnifolia* at the upper reaches of that river. The source of the population at the Kureyka is even more vague. It is very reasonable to assume that the Lower Yenisei fragment constitutes a distinct taxon of an infraspecific or probably even specific rank. However, there is not enough evidence to make the conclusion.

Plants from the Altai are also rather special. Their leaves are small, elliptic, and spiny serrate (as opposed to oblanceolate, crenate-serrate leaves in the rest of the species). Neither in this case can we speak of segregating even a subspecies, as there is not enough grounds: nice samples with catkins are missing from collections.

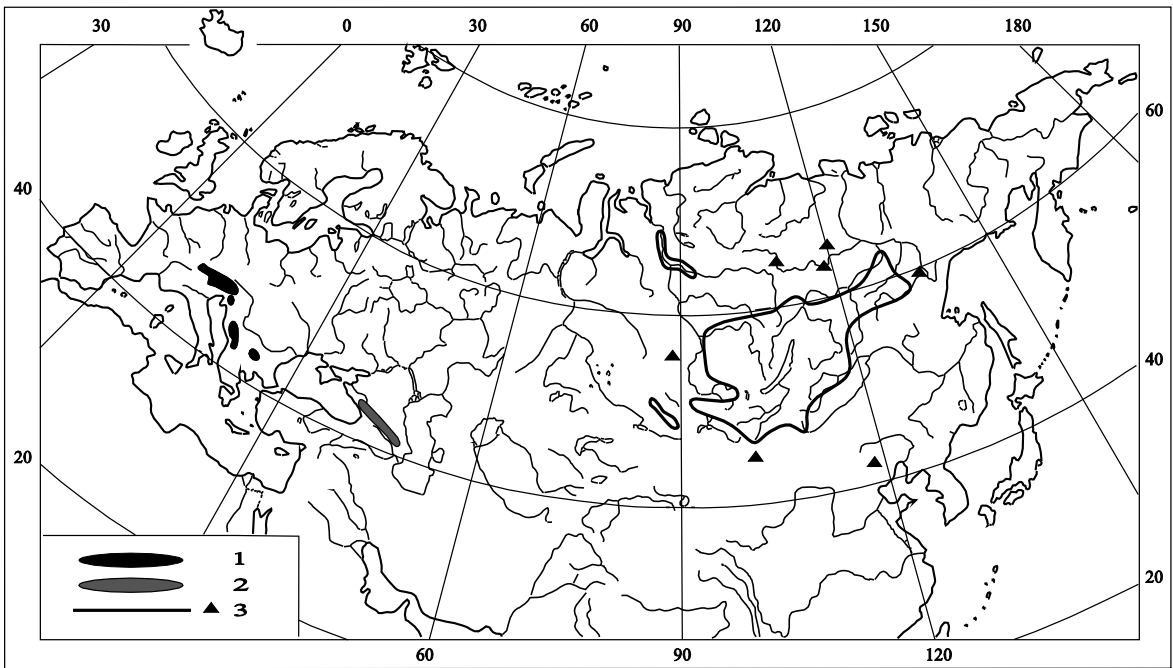


Fig. 49. Distributional areas of *Salix waldsteiniana* Willd. (1), *S. kazbekensis* A. Skv. (2), and *S. rhamnifolia* Pall. (3)

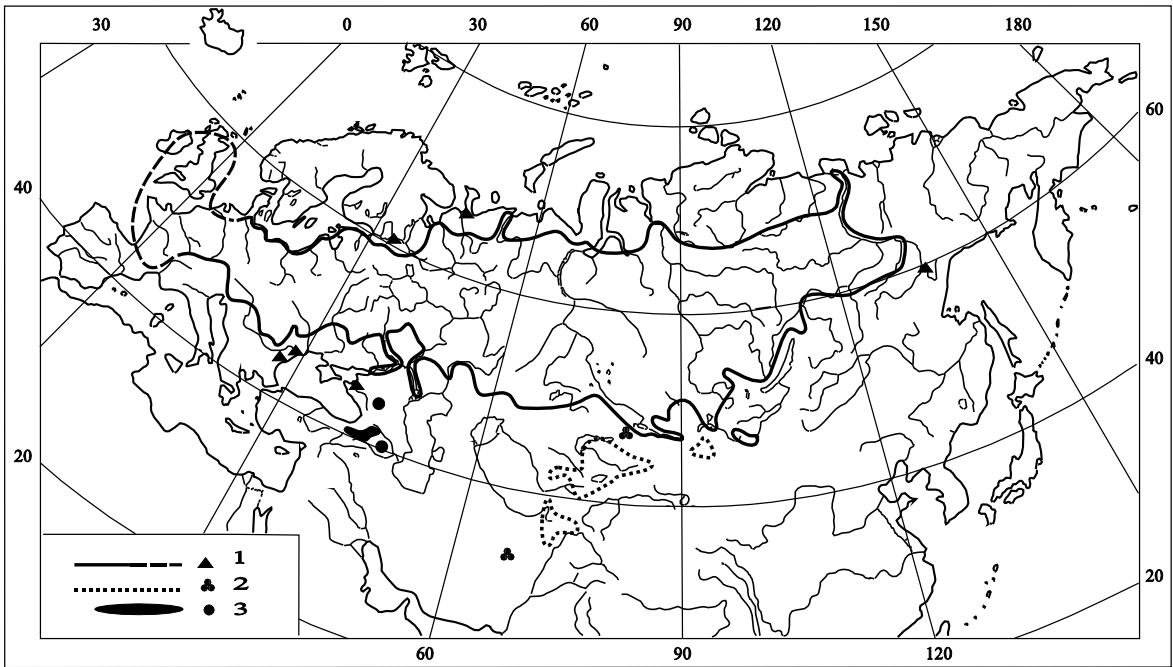


Fig. 50. Distributional areas of *Salix viminalis* L. (1), *S. turanica* Nas. (2), and *S. armeno-rossica* A. Skv. (3)

Dum. 1825, Bijdr. Natuurk. Wetensch. **1**, 1: 56 (p. p.).

T y p u s: *S. viminalis* L.

Trees or rather tall shrubs. Shoots mostly elongated, flexible, virgate. Floriferous buds strikingly different from vegetative ones, oval to nearly cylindrical, not flattened, their apices either straight or bent toward shoots. Stipules linear or falcate. Petioles that embrace floriferous buds usually become abruptly ventricose by fall. Leaves mostly narrow, with many parallel veins prominent beneath, entire or finely denticulate, usually silvery or silky beneath. Catkins precocious or subprecocious. Nectary solitary, rectangular or, more often, linear, 0.6–1.5 mm long. Capsules mostly short-stipitate or sessile, acute; styles elongated, stigmas two-parted.

Some 12–13 species are distributed in forested regions within the temperate climate belt (nine in and around this country, one in the Himalayas, and two or three in North America). The overwhelming majority of species are restricted to alluvial habitats. This is a very natural and compact section. The only species that stands somewhat apart is *S. udensis*, which approximates the section *Arbuscella* in some of its characters, such as short nectaries, elongated capsule stipes, scanty leaf pubescence. Close relations of *Vimen* with *Subviminales* and *Villosae* are obvious; those with *Canae* are also possible; others are more vague (most probable of them is one with *Arbuscella* via *S. udensis*, *S. boganidensis*, and *S. pantosericea*).

Key to Species

1. Bracts 1.0–1.8 × 0.5–0.8 mm, mostly puberulent; ovaries and stamens conspicuously protruding from pubescence. Ovaries finely pubescent with appressed trichomes and usually become deflected at right angle to catkin rachises as early as flowering period. Mature capsules 4.0–5.5 mm, their stipes 0.5–1.5 mm long, longer or just scarcely shorter than nectaries. Leaves not densely pubescent, often glabrous, frequently emarginate, crenate at margins 98. **S. udensis**
- Bracts mostly larger and with longer pubescence, ovaries and stamens not protruding much from pubescence. Ovaries mostly densely pubescent, positioned at acute angle to rachises. Capsule stipes not longer than 0.5–0.6 mm, at least twice as short as nectaries 2
2. Leaves conspicuously revolute, entire, occasionally undulate at margins; marginal glands sparse, all or majority of them removed from leaf margin to upper leaf surface (extramarginal type). Bracts black or brown, mostly obtuse. Anthers 0.4–0.7 mm long. Capsules mostly sessile, not compressed 3
- Mature leaves flat or subrevolute, entire or, more often, serrulate; glands on denticles directly at leaf margins. Bracts black, mostly acute. Anthers 0.6–1.0 mm long. Capsules often compressed, mostly stipitate; stipes to 0.5–0.6 mm long 6
3. Bracts brown or even rufescent, at least in lower parts of catkins. Styles 0.4–0.5 mm long, shorter than stigmas or, very rarely, as long as stigmas. Stigmas 0.8–1.5 mm long 90. **S. viminalis**
- All bracts mostly black. Styles 0.8–2.0 mm long, longer than stigmas 4
4. Two- and three-year-old shoots tawny-brown. Leaves very gradually narrowly acuminate, intensively dark green, rather lustrous above, not undulate at margins.

- Lower surface clothed with trichomes lying mostly parallel to midrib, more or less overlapping lateral veins. Styles mostly at least twice as long as stigmas
- 93. **S. schwerinii**
- Two- or three-year-old shoots mostly light green. Leaves dull green or grayish-green, mostly puberulent above. Leaf margins mostly undulate (nearly always, in epicormic shoots). Styles nearly as long as stigmas or not more than twice as long 5
5. Leaves stipulate on vigorous shoots. Leaf trichomes beneath comparatively short, nearly none of them parallel to midrib; veins mostly conspicuous against pubescence. Bracts black, 1.0–1.8 mm broad 91. **S. turanica**
- Leaves exstipulate even on vigorous shoots, pubescent beneath; their long, silvery trichomes lying parallel to midrib usually well developed; veins hidden in pubescence. Bracts mostly brownish, black at apices, 0.8–1.3 mm broad
- 92. **S. armeno-rossica**
- 6(2). Alpine shrubs or small trees. Petioles that embrace floriferous buds either not or only slightly ventricose. Mature capsules 4–6 mm long 7
- Trees or tall shrubs of large river valleys and lowlands. Leaves 80–150 mm long. Petioles that embrace floriferous buds usually abruptly ventricose by fall. Mature capsules 7–9 mm long 94. **S. dasyclados**
7. Floriferous buds shortly ovoid. Leaves broad (3 to 5 times as long as broad), rather pubescent above, although not as much silvery as beneath . . . 97. **S. pantosericea**
- Floriferous buds broadly elliptic or lanceolate. Leaves dark green, glabrous above, upper leaf surface strikingly different from lower one; the latter silvery pubescent 8
8. Distorted shrub. Leaves mostly entire, narrowly (ob-)lanceolate or linear-lanceolate, mature ones puberulent or glabrescent. Capsules somewhat compressed
- 95. **S. sajanensis**
- Usually small, long-branched tree. Leaves finely denticulate, lanceolate, broadly lanceolate, or elliptic, all densely silvery pubescent beneath. Mature capsules considerably compressed 96. **S. argyracea**

90. **S. viminalis** L. 1753, Sp. pl.: 1021; Ledeb. 1850, Fl. Ross. **3**, 2: 605; Wimmer, 1860, Salic. Eur.: 36; Wolf, 1930, Fl. Yu.-V. **4**: 45; Nazarov, 1936, Fl. SSSR **5**: 132; Nazarov et al. 1952, Fl. URSR **4**: 54; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 118; id. 1964, Fl. Eur. **1**: 52; Andreyev, 1957, Der. i kustarn. Mold. **1**: 73; Rasinš, 1959, Ivy Latv.: 112; Polyakov, 1960, Fl. Kazakhst. **3**: 25. —*S. serotina* Pall. 1776, Reise **3**: 759; id. 1788, Fl. Ross. **1**, 2: 77; Floderus, 1933, Ark. bot. **25A**, 11: 28, 29. —Non *S. serotina* auct.: Goerz, 1934, Feddes Repert. **26**: 26; Shlyakov, 1956, Fl. Murm. **3**: 118. —*S. gmelinii* Pall. 1788, op. cit. **1**, 2: 77; Ledeb. 1850, op. cit. **3**, 2: 606 (p. max. p. saltem!); Teploukhov, 1901, in Petunnikov, Krit. obz. Mosk. fl. **3**: 26 (p. max. p.); Syreishchikov, 1907, Ill. fl. Mosk. gub. **2**: 33; Krylov, 1930, Fl. Zap. Sib. **4**: 740; Perfilyev, 1936, Fl. Sev. kr. **2–3**: 40; Krall, Viljasoo, 1965, Eestis kasv. pajud: 72 —non *S. gmelinii* auct. fl. caucas. nec fl. extremiorient. —*S. polia* Schneid. 1916, in Sarg. Pl. Wilson. **3**, 1: 174; Hao, 1936, Syn. Chin. *Salix*: 89. —*S. veriviminalis* Nasarov, 1936, op. cit. **5**: 134. —*S. rossica* Nasarov, op. cit. **5**: 135; id. 1949, Fl. BSSR **2**: 44; Polyakov, 1960, op. cit. **3**: 26; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 18; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3222; Rech. f. 1964, op. cit. **1**: 52; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 83. —*S. splendens* (Turcz.) Nasarov, 1936, op. cit. **5**: 136 (p. p.); Sergiyevskaya, 1961, op. cit. **12**: 3222. —*S. rufescens* (Turcz.) Nasarov, 1936, op. cit. **5**: 137. —*S. strobilacea* (E. Wolf) Nasarov,

op. cit. 5: 141. —? *S. semiviminalis* E. Wolf, 1905, Izv. Lesn. in-ta 13: 51 et tabl. 4 (vel *S. viminalis* × *S. caprea*?).

T y p u s: "In Europa ad pagos. Fl. Suec. N 813".

HABIT: A tall shrub or multi-stemmed, wide-crowned tree to 6–8–(10) m.

HABITATS: River banks, mostly fresh deposits, either sandy or pebbly, near the running water. In older parts of flood plains, it is gradually replaced by other species. Also, ruts, ditches, and such, in areas of sufficient moisture on sandy soil. Mostly, on the plain; if ascending to mountains, then primarily along large rivers with wide valleys.

DISTRIBUTION. Natural boundaries in Western Europe are not yet clarified. Presumably, most of England and southeastern Ireland; also presumably, most of France (except its southeastern part); Belgium, Holland, Germany, eastern Austria, Slovenia, most of Hungary and Romania, Czechia, Slovakia, Poland. It is absent from the Alps; reports from Pyrenees and former territory of Yugoslavia (except Slovenia) are doubtful. It is absent from all of Scandinavia including Finland and Denmark and probably also from northern Holland. The northern area boundary runs via northern Estonia, southern Leningradskaya Oblast, Belozersk, the Onega River; then along the southern boundary of the forest-tundra belt toward the Polar Urals. There are some few solitary locations in the Svir and Vodla basins. From the forest-tundra, it penetrates to tundra belt along large rivers. Behind the Urals, in the north the area boundary runs from the Ob mouth to the mouth of the Taz, the Upper Olenek and Lower Lena; in the east, along the Lena and Aldan to the lower reaches of the Maya; in the south, via the Middle Aldan, Lower Olekma, Upper Lena (yet never reaching Lake Baykal), detouring the Eastern Sayans, entering Tuva and Mongolia (the Khangai) via the Western Sayans, reaching Tsetserlig as the southernmost point. The species area embraces nearly all of the Altai, reaching Chinese territory along the Black Irtysh, then via the Tarbagatay, Bayan-Aul, and the Ulutau, the boundary runs to the Mugodzhary and crosses the Ural River (south of Uralsk), Volga (south of Saratov), Don (around Voronezh), Dnieper (around Cherkassy), Dnestr, and Prut (around Kishinev). Besides that solid area, there are invasions down the Volga and Don (but not Dnieper!) to the very mouths of these rivers. There is a completely isolated locus at the Lower Kuban River. Also, isolated fragments of the area are encountered in the *plavni* of the Dnestr and Danube.

The species ascends to 900 m in Carpathians; to 600 m in the Southern and Central Urals; in the Altai, it reaches 1,500 m (Lake Markakol) and even 1,800 m (the Kaba River).

NOTE. The species is not completely uniform within its huge distributional range; yet differences are so vague that it is impossible to segregate any taxonomical units.

Plants from the steppes of the Southern Urals and Turgayskoye Plateau are characterized by narrow leaves that are silvery pubescent beneath. Relying upon this purely external character, M. Nazarov united these narrow-leafed forms with a species from the Far East, *S. schwerinii*, under the name of *S. pseudolinearis*.

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Conversely, plants from the Northern Urals and Siberia, particularly those from the Podkamennaya and Nizhnyaya Tunguska basins, are characterized on the average by unusually broad and strongly pubescent leaves, grayish on the upper surface. Forms with still broader leaves are encountered in the southwestern Altai and along the Irtysh upstream of Lake Zaysan. Plants from the Altai are particularly special in their dense lower side pubescence, which sometimes appears to be nearly velutinous rather than sericeous. However, "the typical" *S. viminalis* plants that dominate across the European temperate belt and Southern Siberia are encountered on the Turgayskoye Plateau, in the Altai, Northern Urals, and Siberia along with all kinds of intermediate forms.

There is a common opinion in the literature that *S. viminalis* growing in Russia is not the same as *S. viminalis* L. from Western Europe, but actually another species, *S. gmelinii* Pallas vel Teplouchov = *S. rossica* Nas. This idea was first proposed by F. Teploukhov (Petunnikov 1901) and then supported in the "Flora of the USSR" by M. Nazarov. Yet there are no serious arguments in favor of that notion. Naturally, M. Nazarov was unable to highlight, even approximately, the western limit for *S. rossica* and the eastern one for *S. viminalis*. It is a known fact that C. Linnaeus used cultivated specimens when describing *S. viminalis*. In Russian herbaria, *S. viminalis* from Western Europe is as well represented mostly by samples from cultivated plants. In fact, one cannot even compare the natural range and abundance of the species in Western Europe and this country. Therefore, we cannot expect that features of comparatively few samples known from Western Europe might embrace the whole range of the species morphological diversity within the vast territory including Belarus in the west, the Aldan River in the east, the Altai and Tuva in the south, and the mouths of the Ob and Lena in the north. On the contrary, if the understanding of the species variability range is based on material from Russia and the adjacent territories, then all the West European samples will easily fit within. Taking all these reasons into consideration, we have to treat *S. rossica* as a mere synonym of *S. viminalis*.

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A number of "species" described by M. Nazarov in the "Flora of the USSR", such as *S. splendens*, *S. rufescens*, or *S. strobilacea* were actually varieties proposed by N. Turczaninow and E. Wolf, which then were automatically assigned a species rank. An inspection of authentic specimens made it possible to conclude that most of them were nothing other than *S. viminalis* (in "*S. splendens*", there were also some belonging to *S. schwerinii*).

S. polia Schneid. is a densely pubescent form of *S. viminalis* from the Chinese part of the Black Irtysh.

Authentic specimens of *S. gmelinii* Pall.—plants from the Herbarium of J. Gmelin, the senior—also belong to *S. viminalis*. They had been long neglected till the author discovered them in the Herbarium of the Botanical Institute in St. Petersburg.

The populations from the Lower Volga and presumably also Lower Don and Lower Kuban constitute peculiar ecotypes that are different in their rhythm of the seasonal development: the so-called "late-inudation ecotypes" (Sukachev 1935, 1953; see also chapter 3, section 4). These plants require further investigation. According to my own observations around Volgograd, they are characterized not only by the late bud expansion, but also an unusually large range of variability as far as the time of spring development is concerned. Besides, one can often find catkins in bloom along with almost mature ones on a single specimen, simultaneously. Also, the contingency between the floriferous and vegetative shoot developmental schedule is rather variable. Although P. Pallas described these late-inudation forms as a distinct species, *S. serotina*, he himself admitted that they might be nothing other than a form of *S. viminalis*. Presently, it hardly makes sense to segregate these plants in a taxonomical entity of any rank. The name *S. serotina* was misused when applied to plants from the Caucasus (Görz 1934) and to *S. dasyclados* (Shlyakov 1956).

91. ***S. turanica*** Nasarov, 1936, Fl. SSSR 5: 709; Drobov, 1953, Fl. Uzb. 2: 36; Polyakov, 1960, Fl. Kazakhst. 3: 26; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR 17: 66; Ikonnikov, 1963, Opred. rast. Pamira: 90. —*S. viminalis splendens* 1° songarica Anderss. 1868, in DC. Prodr. 16, 2: 265. —*S. viminalis* auct. fl. As. Mediae, non L.: Kar. et Kir. 1842, Bull. Soc. Nat. Moscou 15: 182; Regel, 1880, Acta Horti

Petropol. **6**: 467; et al. —*S. stipularis* auct. fl. As. Mediae, non Sm.: Kar. et Kir. 1842, l. c.; Regel, 1880, op. cit. **6**: 468.

T y p u s: "Songaria ad ripas fl. Ili et Ajaguz leg. Schrenk" (LE!).

HABIT: A tall shrub or small tree (to 10 m).

HABITATS: Banks of rivers and small streams in *tugai*, mostly near the running water on sandy or pebbly deposits.

DISTRIBUTION: The Upper Zeravshan River, western Gissarskiy Range, nearly all of the Pamirs, Karakorum, and Hindu Kush. There are also specimens from central Afghanistan (Bamian Province). In the described part of the area, it is found at 1,400–3,800 m. The species area also embraces nearly all of the Tien Shan including its Kirghiz and Chinese parts (except the Kuraminskiy and Karatau ranges), where it presumably does not ascend higher than 2,000–2,200 m. Indeed, from the northern slopes, it descends to the piedmont and even lowland, reaching Lake Biylikol, the Chu River (around Bystrovka), and the very Lower Ayaguz via the Ili, Karatal, and Lepsa rivers. There are a few findings in southwestern Mongolia.

NOTE. Plants in the Pamir-Alay, Hindu Kush, and Karakorum are different from those in the Tien Shan and Prebalkhashia: the former ones grow mostly as trees, have yellowish bark and comparatively broad leaves; the latter are mostly tall shrubs with grayish bark and leaves shaped very much alike those in *S. viminalis*. It might be reasonable to treat the plants from the Pamir-Alay, Hindu Kush, and Karakorum as a distinct subspecies.

92. **S. armeno-rossica** A. Skv. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 30. — 196
S. viminalis auct. fl. As. Min. et Caucasi, non L. —*S. gmelinii* (non Pall.) Goerz, 1930, Feddes Repert. **28**: 127; id. 1930, in Grossheim, Fl. Kavk. **2**: 5. —*S. serotina* (non Pall.) Goerz, 1934, Feddes Repert. **36**: 26, 228. —*S. rossica* Nasarov in schedis, ined.

T y p u s: "Armenia turcica (olim Rossiae distr. Kaghyzman), in ripis fl. Kjaklik, 11. V 1914. leg. S. Turkewicz" (LE).

HABIT: A tall shrub or small tree.

HABITATS: River pebbles at 1,200–2,200 m.

DISTRIBUTION: The central northern slope of the Greater Caucasus (around the summit of Beshtau); Dzhavakheti (a number of localities); Armenia (the Marmarik River and Dzhermuk Resort); Turkish Armenia (mostly Kars and Erzurum). (Fig. 50.)

93. **S. schwerinii** E. Wolf, 1929, Izv. Gl. bot. sada SSSR **28**: 421. —*S. viminalis* auct. non L.: Trautv. et Mey. 1856, in Middendorff, Reise Sibir. 1, **2**: 78; Regel, Tiling, 1858, Fl. Ajan.: 117; Seemen, 1903, Salic. Jap.: 50; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 157; Nakai, 1930, Fl. sylv. Kor. **18**: 175. —*S. viminalis* var. *angustifolia* Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 379. —*S. viminalis* var. *yesoënsis* Schneider, 1916, op. cit. **3**, 1: 158; Miyabe, Kudo, 1921, Icon. forest tr. Hokk. **1**: N 17. —*S. gmelinii* auct. non Pall.: Floderus, 1926, Ark. bot. **20A**, 6: 56; Hultén, 1928, Fl. Kamtsch. **2**: 13; Komarov, 1929, Fl. Kamch. **2**: 18; Görz, 1933, Feddes Repert. **32**: 387; Karavayev, 1958, Konsp. fl. Yak.: 83 (p. p.); Popov, 1959, Fl. Sredn. Sib. **2**: 795 (p. max. p. saltem). —*S. yesoënsis* Kimura, 1931, Bot. Mag. Tokyo **45**: 28; id. 1931, Sci. Rep. Tohoku Univ. 4 ser. **6**, 2: 190; id. 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 430; Sugawara, 1939, Ill. fl. Saghal. **2**: 681; Tolmachev, 1956, Der. i kustarn. Sakhal.: 660. —*S. serotina* (non Pall.) Flod. 1933, Ark. bot. **25A**, 10: 11. —*S. stipularis* (non Sm.) Nakai, 1930, op. cit. **18**: 179. —*S. pseudolinearis* Nasarov, 1936, Flora SSSR **5**: 137 (p. p.: quoad pl. dahuricas et extremorientales tantum!). —*S. rossica* Nasarov, 1936, op. cit. **5**: 135 (p. p.: quoad pl. dahuricas et extremorientales tantum!). —*S. pet-susu* Kimura, 1937, Symb. Iteol. **4**: 317;

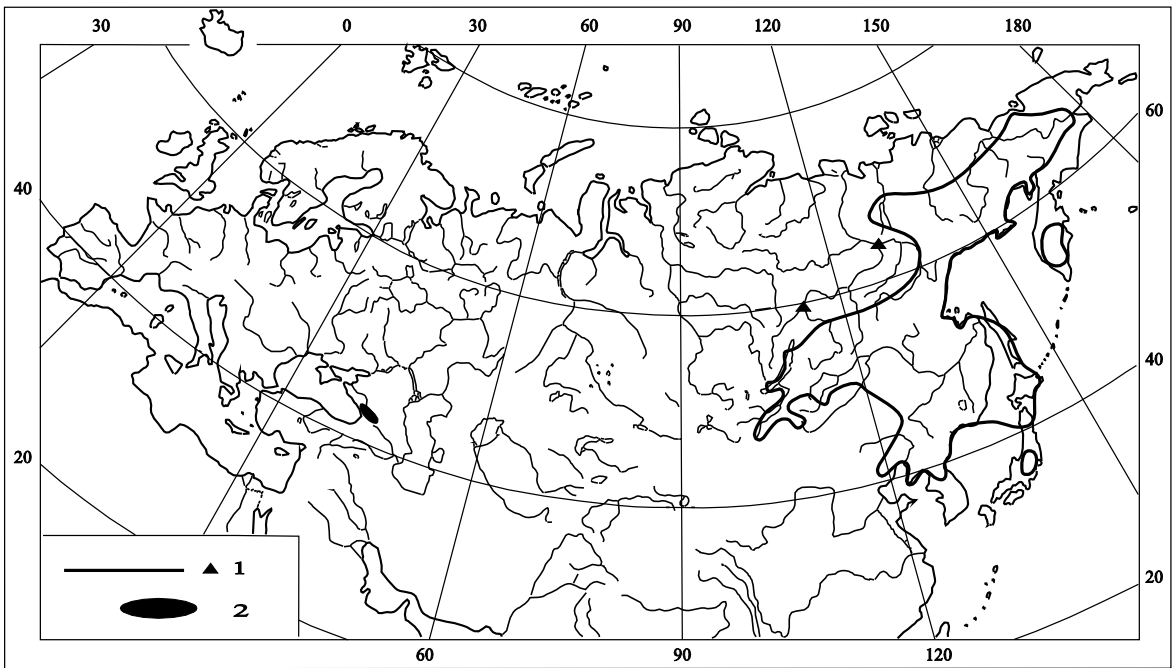


Fig. 51. Distributional areas of *Salix schwerinii* E. Wolf (1) and *S. pantosericea* Goerz (2)

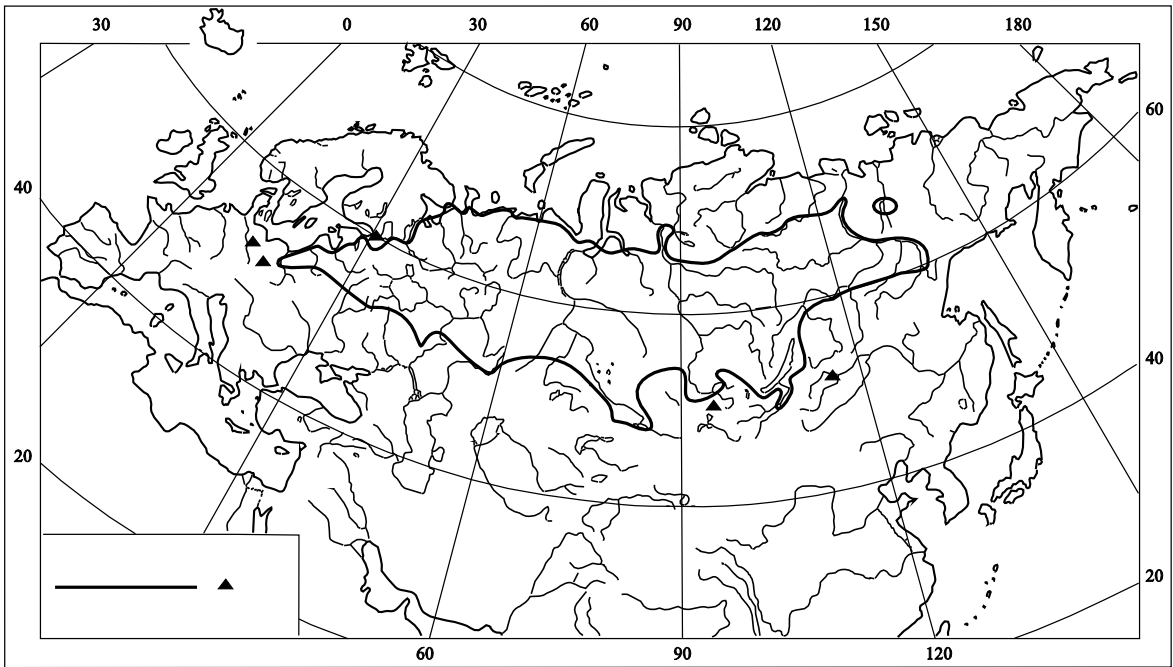


Fig. 52. Distributional area of *Salix dasyclados* Wimm.

Ohwi, 1965, Fl. Jap.: 367. —*S. kinuyanagi* Kimura, 1940, Symb. Iteol. **8**: 401; Ohwi, 1965, op. cit.: 367.

T y p u s: From the Zeya River [in Russian] (the Herbarium of the Academy of Forest Technology in St. Petersburg!). This is probably a cultivated specimen grown in Leningrad (St. Petersburg).

HABIT: A tall shrub or tree to 12 m.

HABITATS: Fresh alluvial deposits along rivers and streams.

DISTRIBUTION: Lake Baykal Coast and Transbaykalia; Mongolia (the Orhon and Upper Kerulen basins); Northeast China, North Korea, and Maritime Province; the Upper Aldan Basin; the Coast of the Sea of Okhotsk; the Yana, Indigirka, Kolyma, Anadyr, and Penzhina basins; the southern half of the Kamchatka Peninsula; Sakhalin; Hokkaido and northern Hondo.

The species does not ascend high in the mountains: it is known to reach 600 m in the Chara (Charskaya) Depression, 800 m in the Sikhote-Alin. (Fig. 51.)

NOTE. This boreal East Asian species is vicarious to *S. viminalis*. Although the areas of the two species get to contact in many regions, they appear not to grow together often.

Plants from Kamchatka, Sakhalin, and Japan are different in comparatively broad leaves; they might be segregated as a variety or subspecies.

94. ***S. dasyclados*** Wimm. 1849, Flora **32**: 35; Seemen, 1899, in Aschers. et Graebn. Fl. N.-O. Deutsch.: 238; id. 1909, in Aschers. et Graebn. Synopsis **4**: 177; Petunnikov, 1901, Krit. obz. Mosk. fl. **3**: 28; Syreishchikov, 1907, Ill. fl. Mosk. gub. **2**: 35; Litvinov, 1917, in Mayevsk. Fl. Sredn. Ross. 5 ed.: 584; Szafer, 1921, Flora Polska **2**: 45; Krylov, 1930, Fl. Zap. Sib. **4**: 743; Perfilyev, 1936, Fl. Sev. kr. **2-3**: 38; Nazarov, 1936, Fl. SSSR **5**: 147; id. 1937, Fl. Zabayk. **3**: 203; Skvortsov, 1955, Bull. MOIP **60**, 3: 126; id. 1964, in Mayevsk. Fl. sredn. pol. 9 ed.: 189; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4541; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 121; Rasinš, 1959, Ivy Latv.: 116; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 19; Krall, Viljasoo, 1965, Eesti kasv. pajud: 74. —*S. stipularis* auct. (non Sm. 1803): Trautv. 1832, Nouv. Mém. Soc. natur. Moscou **2**: 374; Ledeb. 1850, Fl. Ross. **3**, 2: 605; Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 380; Meinshausen, 1878, Fl. Ingr.: 317; Martyanov, 1933, Fl. Yuzhn. Yenis.: 144. —*S. acuminata* auct. (non Mill. 1768 nec Sm. 1804): Rupr. 1845, Fl. samojed. cisur.: 53; Ledeb. 1850, op. cit. **3**, 2: 606. —*S. longifolia* auct. (haud Host 1828): Wimmer, 1866, Salic. Europ.: 42; Wolf, 1900, Izv. Lesn. in-ta **4**: 74; Kupffer, 1901, Sched. ad Herb. Fl. Ross. **3**: N 739. —*S. viminalis* var. *nitens* Turcz. 1854, op. cit. **2**, 2: 380 (p. max. p. saltem). —*S. viminalis* var. *splendens* (non Turcz.) Lundström, 1888, K. sv. vet. handl. **22**, 10: 200. —*S. viminalis* auct. non L.: Trautv. 1889, Acta Horti Petropol. **10**: 532; Cajander, 1902, Acta Soc. F. Fl. Fenn. **23**, 1: 3 (p. p.: quoad f. *latifolia*). —*S. burjatica* Nasarov, 1936, op. cit. **5**: 137. —*S. jacutica* Nasarov, 1936, op. cit. **5**: 711 (p. max. p. saltem); Karavayev, 1958, Konsp. fl. Yak.: 84. —*S. serotina* (non Pall.): Shlyakov, 1956, Fl. Murm. **3**: 118; Opred. rast. Komi, 1962: 145.

T y p u s: "Silesia: Troppau, Scheitnich" (Wimmer et Krause Herb. Sal. N 7 —LE! et alibi).

HABIT: A tree to 20 m tall and 80–90 cm in stem diameter or a tall shrub.

HABITATS: Near the running water as well as in other parts of river flood plains.

DISTRIBUTION resembles that of *S. viminalis* very much. However, there are substantial differences: in the west, the species does not reach farther than northeastern Poland; there are also some solitary locations in Silesia and Brandenburg. The southern

limits of the area are in northern Belarus and the northern part of the chernozem belt; in the northwest, it reaches the Neva River, Lake Onega, and southeastern coast of the Kola Peninsula. The northern limit is close to that of *S. viminalis* in Europe as well as Siberia, approximating the limit of the forest-tundra belt with some invasions into tundras along rivers. In landscapes of the European northern forest and forest-tundra belt, it plays a particularly important role being the only large tree amidst the vegetation of river valleys that is composed of low willow thickets and *yernik*'s. It may frequently form real forests in river valleys of Bolshezemelskaya and Malozemelskaya tundras, the Polar Urals, and southern Yamal Peninsula, as well as in the Lower Ob Valley (see, for example, Vekhov, Uspenskiy 1959, where the plant is named *S. gmelinii*). The largest specimens to 20 m tall were encountered in the north. They were found along the Izhma River (Pechora Basin) by V. Andreyev (according to his notes on labels of 1929 collections). Specimens to 6–8 m tall are common in the valleys of the Khadata, Kara, and other rivers in the Polar Urals, where they grow beyond the northern limits of the larch and birch. The easternmost localities of *S. dasyclados* are in Verkhoyansk, at the Lower Maya, Lower Yudoma, and Shilka. The southern boundary runs from Kyakhta around the Eastern Sayans, via Tuva, around the Altai (not going into the mountains, as opposed to *S. viminalis*); then from Lake Zaysan, it proceeds along the Irtysh towards Ishim, Kurgan, Orsk, and Ulyanovsk. (Fig. 52.)

NOTE. Hybrids between *S. viminalis* and species of the section *Vetrix* (mostly *S. caprea* and *S. atrocinnerea*) are rather common in Western Europe, in nature and particularly in cultivation. Described under the names *S. stipularis* Sm., *S. acuminata* Sm., *S. longifolia* Host, *S. smithiana* Forbes, and *S. calodendron* Wimm., these hybrids resemble *S. dasyclados*. That was a reason for many authors to treat *S. dasyclados* also as a hybrid (Popov 1959, Rechinger 1964, and others). Yet an enormous distributional area, specific niche, absence of the hybrid segregation, and quite normal seed reproduction make all assumptions on hybrid nature of *S. dasyclados* completely improbable, whether they treat it as a single feral hybrid or a complex of various hybrids.

However, the question is if the authentic F. Wimmer's sample belongs to *S. dasyclados*. Unfortunately, we cannot give a positive answer: the specimen might be of hybrid origin. Strictly speaking, we could rename the species; however, it does not appear to be urgent. In 1866, F. Wimmer mentioned other samples as those belonging to the same species. The samples (which mostly originated from the territory of former East Prussia) were definitely not of hybrid origin. Later, the understanding of *S. dasyclados* was established in the literature in that revised meaning (Seemen 1899, 1909; Petunnikov 1901; and others)¹.

95. ***S. sajanensis*** Nasarov, 1936, Fl. SSSR 5: 710; id. 1937, Fl. Zabayk. 3: 206 and fig. 117; Popov, 1959, Fl. Sredn. Sib. 2: 797; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. 3: 18; Sergiyevskaya, 1961, Fl. Zap. Sib. 12: 3223; Malyshev, 1965, Fl. Vost. Sayana: 19; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 84.

T y p u s: "Montes Sajanenses in alpibus Tunkinensibus, 1929 leg. M. Nasarov N 12450, 12456, 12703" (LE!).

HABIT: A distorted shrub or wide-crowned small tree to 5 m tall.

¹ Following the present strict and formal requirements, the name *S. dasyclados*, apparently, is to be replaced by *S. burjatica* Nasarov, 1936 Fl. SSSR, 5: 137. —stat. et nom. nov. pro *S. viminalis* var. g Turcz. 1854, Fl. Baic.-Dahur. 2, 2: 380. Holotypus: LE, originating from the Irkut River (author's note to the English edition).

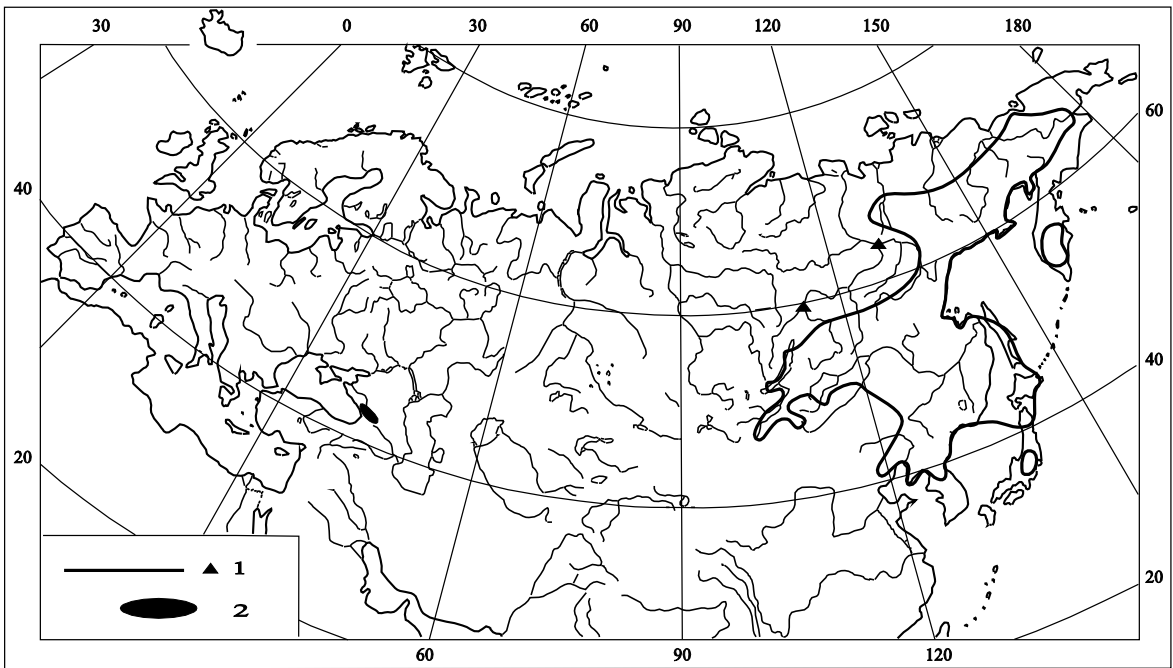


Fig. 53. Distributional areas of *Salix argyracea* E. Wolf (1), *S. sajanensis* Nas. (2), and *S. udensis* Trautv. et Mey. (3)

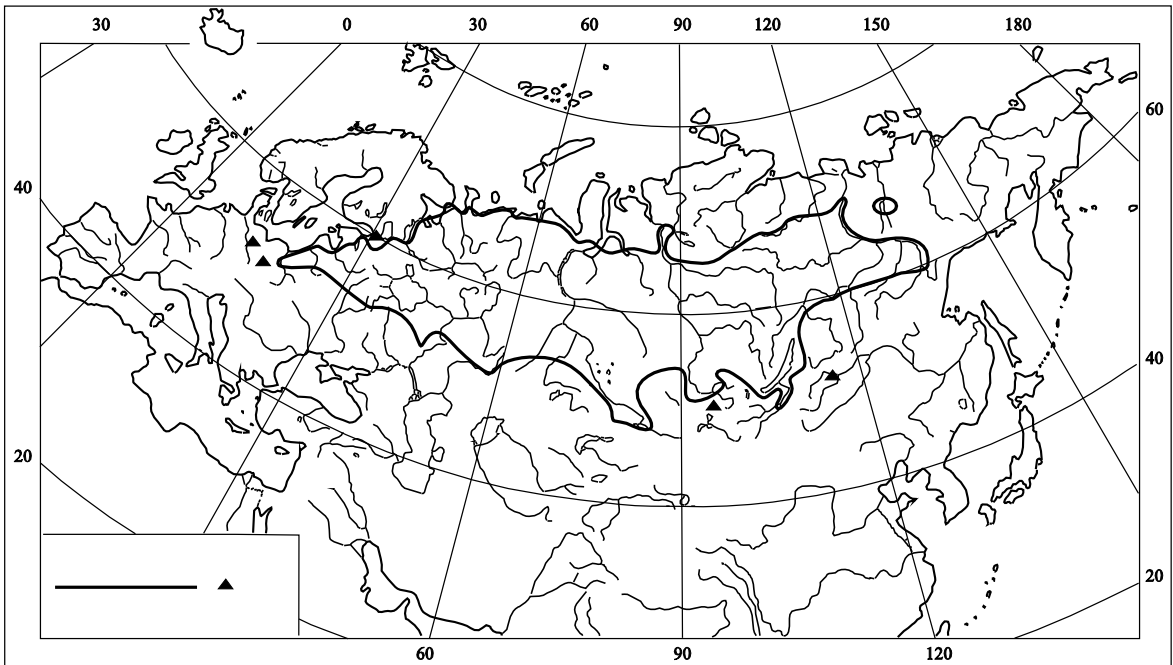


Fig. 54. Distributional areas of *Salix elaeagnos* Scop. (1) and *S. gracilistyla* Miq. (2)

HABITATS: Stone-fields; also, stony lichen-dominated and stony cushion plant (*Dryas*-dominated) tundras in the subalpine and alpine zones. According to L. Malyshev (1965), it is confined to acidic bedrock (avoiding limestone).

DISTRIBUTION: Nearly all of the Altai (rather sparsely); Western Sayans (rarely); Eastern Sayans and Sangilen (frequently); Barguzinskiy Range. It is found at 1,700–2,200 m (to 2,500 m in Tuva); however, on the Barguzin Coast of Lake Baykal, the place famous for its climatic inversions, it descends as low as the lake level together with other subalpine and alpine willows, such as *S. alaxensis*, *S. rectijulis*, and *S. hastata*. (Fig. 53.)

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96. ***S. argyracea*** E. Wolf, 1905, *Izv. Lesn. in-ta* **13**: 50, tabl. 3; Görz, 1934, Feddes Reppert. **36**: 27; Nazarov, 1936, *Fl. SSSR* **5**: 143; Polyakov, 1960, *Fl. Kazakhst.* **3**: 27; Skvortsov, 1962, *Bot. mat. Gerb. in-ta bot. AN UzbSSR* **17**: 67.

T y p u s: "In Leningrad culta. Provenit e vicin. Pischpeck (Frunse)" (the Herbarium of the Academy of Forest Technology in St. Petersburg!).

HABIT: A small tree or tall shrub.

HABITATS: Banks of alpine streams and rivers in the upper forest and subalpine zones at 1,600–3,200 m (rather scattered).

DISTRIBUTION: The Dzungarskiy Alatau, Chinese Tien Shan, and a part of the Kirghiz Tien Shan including the eastern Kungey Alatau, eastern Zailiyskiy Alatau and the Lower Atbashi (a tributary of the Naryn). (Fig. 53.)

97. ***S. pantosericea*** Goerz, 1934, Feddes Reppert. **36**: 229; Nazarov, 1936, *Fl. SSSR* **5**: 104; Kolakovskiy, 1939, *Fl. Abkhaz.* **2**: 22; Grossheim, 1945, *Fl. Kavk.* 2 ed. **3**: 21; Sosnovskiy, 1947, *Fl. Gruz.* **3**: 18; Makhatadze, 1961, *Dendrofl. Kavk.* **2**: 27; Skvortsov, 1966, *Trudy Bot. in-ta AN ArmSSR* **15**: 132. —*S. argyrophylla* Lakschewitz ex Goerz, 1930, in Grossheim, *Fl. Kavk.* **2**: 8. —Non *S. argyrophylla* Nutt. 1842.

T y p u s: Kubanskaya Obl., former Kutaisi Governm. [in Russian]. In the original description (Görz 1930), the type specimen was designated only as much as this. In the St. Petersburg Herbarium, there are the following samples, which were supposed to be described by P. Lakschewitz (marked by him): "The Rion Sources, 6,900'. —Sredinskiy N 15, 39"; "distr. Alagir et Radscha —7.IX 1861. Ruprecht"; "Klukhor Pass —11.VII 1905. Litvinov, N 440".

HABIT: A low shrub (0.5–2 m).

HABITATS: Banks of streams and lake shores, *Rhododendron* shrublands, alpine meadows, and glacial moraines within the alpine and subalpine zones (1,900–2,750 m).

DISTRIBUTION: From the Caucasian Preserve (Chugush, Bolshoy Bambak, Abago) to Mamison Glacier. (Fig. 51.) This endemic species of the western Greater Caucasus is rather scantily represented in herbaria so far. I managed to examine 37 samples total, excluding duplicates.

NOTE. *S. pantosericea* resembles species from the section *Arbuscella* in its general habit and ecology; they appear to have still more in common when one considers particular morphological features: their leaves, buds, and so on. Along with *S. udensis*, *S. pantosericea* may be treated as a connecting link between *Vimen* and *Arbuscella*.

98. ***S. udensis*** Trautv. et Mey. 1856, in Middendorff, *Reise Sibir.* 1, **2**: 81; Nazarov, 1936, *Fl. SSSR* **5**: 146. —*S. oblongifolia* Trautv. et Mey. 1856, op. cit.: 81; haud Nazarov, 1936, op. cit. **5**: 72. —*S. fulcrata* Anderss. 1867, *Monogr. Salic.*: 139 (p. p.: quoad pl. Kamtschat.); Nazarov, 1936, op. cit. **5**: 75 (p. p.?). —*S. phyllicoides* Anderss.

1867, op. cit.: 140 (quoad var. *angustifolia* et var. *attenuata* saltem); Floderus, 1933, Ark. bot. **25A**, 10: 11. —*S. sachalinensis* Fr. Schmidt, 1869, Reise Amur.: 173; Seemen, 1903, Salic. Jap.: 53; Miyabe, Kudo, 1921, Icon. forest tr. Hokk. **1**: N 18; Floderus, 1926, Ark. bot. **20A**, 6: 40; Komarov, 1929, Fl. Kamch. **2**: 20; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 431; Nazarov, 1936, op. cit. **5**: 145; Tolmachev, 1959, Der. i kustarn. Sakhal.: 60; Kimura, 1961, Symb. Iteol. **18**: 141; Ohwi, 1965, Fl. Jap.: 367. —*S. shikokiana* Makino, 1892, Bot. Mag. Tokyo **6**: 49. —*S. aequitriens* Seemen, 1896, Bot. Jahrb. Beibl. **53**: 52; id. 1903, op. cit.: 70. —*S. opaca* Anderss. ex Seemen, 1903, op. cit.: 50; Shirasawa, 1908, Icon. forest tr. Jap. **2**: tabl. 9; Nazarov, 1936, op. cit. **5**: 148. —*S. siuzevii* Seemen, 1908, Feddes Repert. **5**: 17; Wolf, 1911, Trudy SPb. bot. sada **28**, 4: 527; Lakschewitz, 1914, Spisok rast. Gerb. russk. fl. **50**: N 2488; Nakai, 1930, Fl. sylv. Kor. **18**: 180; Nazarov, 1936, op. cit. **5**: 144. —*S. mezereoides* E. Wolf, 1911, op. cit. **28**: 529; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kraya **1**: 426; Nazarov, 1936, op. cit. **5**: 84. —*S. amnicola* E. Wolf, 1911, op. cit. **28**: 529; Komarov, Alisova, 1931, op. cit. **1**: 426. —*S. paramushirensis* Kudo, 1922, J. Coll. Agric. Hokk. Univ. **11**, 2: 97; Hultén, 1928, Fl. Kamtch. **2**: 16; Kimura, 1952, Symb. Iteol. **11**: 192. —*S. parallelinervis* auct. (non Flod.), p. p. saltem: Hultén, 1928, op. cit. **2**: 16; Komarov, 1929, op. cit. **2**: 14; Vasilyev, 1957, Fl. Komandor.: 84.

T y p u s: "Udskoi 15.VI 1844. A. Middendorff" (LE!).

HABIT: A tall shrub or tree; specimens as tall as 30 m were encountered on the Kamchatka Peninsula (Komarov 1929) and ones to 8–10 m, in Magadan Oblast (Starikov 1958).

HABITATS: Banks of rivers, streams, and ditches; also, any exposed and damp habitats on Sakhalin.

DISTRIBUTION. The western boundary of the solid area runs via the Lower and Middle Lena, Upper Aldan, Middle Vitim, Ingoda, and Onon. The area embraces the forested regions of the Northeast China and North Korea; a major part of Japan (Shikoku, Honshu, and Hokkaido); Sakhalin, the Kurils, and Commander Islands; all of the Kamchatka Peninsula; the Coast of the Sea of Okhotsk; the Anadyr, Kolyma, Indigirka, and Yana basins (however, there are no collections available from the very lower reaches of the Kolyma, Indigirka, Yana, neither from the Lena Delta). There are also (isolated?) area parts on the Vilyuy downstream of its confluence with the Nyurba and around Lake Baykal (at the lower reaches of the Irkut and Selenga and in the Barguzin Basin). (Fig. 53.)

It is mostly confined to the lowland and piedmont and much more rarely encountered at lower and intermediary elevations in the mountains. However, it ascends as high as 1,100 m in the Stanovoye High Plateau (Kalarskiy District) and even to 1,600 m in the Sikhote-Alin (the Botchi Basin); also, to 900 m on southern Sakhalin.

NOTE. Some morphological characteristics of the species, such as the scanty or lacking leaf pubescence, elongated stipes of capsules, and short nectaries make it look similar to the species from *Arbuscella*. The vegetative parts may occasionally resemble those in *S. boganidensis* very much. In *S. udensis*, leaves on shortened shoots and even inferior ones on normal shoots may be much broader than ordinary leaves; that makes it look particularly similar to the species from the section *Arbuscella* and has brought about confusion with *S. parallelinervis* Flod.

Sect. 18. *Subviminales*

(Seemen) Schneider, 1904, Handb. 1: 65.

T y p u s: *Salix gracilistyla* Miq.

Shrubs or small trees. Floriferous buds strikingly different from vegetative ones, lanceolate, attenuating into long beaks. Petioles that embrace floriferous buds become abruptly ventricose by fall. Stipules broad, eglandular above. Leaves silvery pubescent beneath, pubescence mostly confined to veins, making them conspicuous. Catkins precocious, sessile, densely flowered, their bracts strongly pubescent. Nectary solitary, linear; stamen filaments glabrous, distinct or more or less connate. Capsules subsessile, not large, pubescent. Styles long (1.5–4 mm), several times exceeding two-lobed stigmas.

This is a very small East Asiatic group consisting of one species in this country and probably only one more, *S. blinii* Levl., in South Korea. It might be more reasonable to treat it as a subsection of *Vimen*.

202 99. **S. gracilistyla** Miq. 1867, Ann. Mus. Lugd.-Bat. 3: 26 et seorsum Prolusio fl. Jap.: 214; id. 1871, Bijdr. fl. Jap. 4: 5; Franch. et Sav. 1875, Enum. Jap. 1: 461; Koidzumi, 1913, Bot. Mag. Tokyo 27: 92; Nakai, 1930, Fl. sylv. Kor. 18: 104; Nazarov, 1936, Fl. SSSR 5: 129; Ohwi, 1965, Fl. Jap.: 368. —*S. thunbergiana* Blume ex Anderss. 1868, in DC. Prodr. 16, 2: 271; Komarov, 1903, Fl. Manchzh. 2, 1: 30; Seemen, 1903, Salic. Jap.: 61; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. 1: 422. —*S. graciliglans* Nakai, 1916, Bot. Mag. Tokyo 30: 274; id. 1930, Fl. sylv. Kor. 18: 102. —*S. gracilistylodes* Kimura, 1926, Bot. Mag. Tokyo 40: 8; id. 1928, ibid. 42: 571. —*S. nakaii* Kimura, 1926, op. cit. 40: 637. —*S. melanostachya* Goerz, 1933, Feddes Reperit. 32: 121.

T y p u s: "In Japonia detexit Buerger; Nagasaki —Oldham N 527, 719; Japonia —Pierot" (L, U, n. v.; fragmenta specim. Oldhamii N 527, 719 —LE!).

HABIT: A tall shrub or small tree.

HABITATS: Banks of streams and rivers, mostly small ones.

DISTRIBUTION: Southern Amurskaya Oblast (the Zeya downstream of Svobodnyy and Bureya downstream of Cheugda); the Amgun Basin; Maritime Province and nearly all of Khabarovsk Province, except the Lower Amur; the extreme southern part of Sakhalin (Yuzhno-Sakhalinsk); Japan (all the four large islands); North Korea and South Korea; eastern Northeast China. A solitary finding on the Kamchatka Peninsula is very peculiar. The label on the specimen, which was identified by V. Komarov as *S. caprea*, says: "along the Goltsovka R., in the vicinity of Bolsheretsk —8.V.1909, Zelenin". In the southern Sikhote-Alin, the species ascends to 900 m. (Fig. 54.)

Sect. 19. *Canae*

Kerner, 1860, N.-Öst. Wied.: 222.

T y p u s: *Salix elaeagnos* Scop.

Tall shrubs or, more frequently, small trees. Shape of buds and leaves similar to that in *Vimen* (*S. viminalis*, *S. schwerinii*, *S. udensis*); however, leaves with dense white tomentose pubescence beneath. Catkins coetaneous, slender, cylindrical, their bracts white, large, persistent. Nectary solitary, shortly rectangular or square. Stamen filaments more or

less pubescent at base and partially connate. Capsules on short stipes, not large, lanceolate, acute; styles and stigmas elongated.

The section appears to be represented by a single species. Being very close to the section *Vimen* in the vegetative parts structure, the species of the section *Canae* is strikingly different in the habit of its catkins. Therefore, it must be treated as a distinct entity connected with *Vimen* and *Villosae*.

100. **S. elaeagnos** Scop. 1772, Fl. Carn. 2 ed. 2: 257; Hayek, 1924, Prodr. Balc. 1: 86; Vicioso, 1951, Salic. Españ: 76; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. 3, 1: 122; id. 1964, Fl. Eur. 1: 53; Maire, 1961, Fl. Afr. Nord 7: 65; Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR 15: 133. —*S. incana* Schrank, 1789, Baier. Fl. 1: 230; Wimmer, 1866, Salic. Eur.: 25; Boiss. 1879, Fl. Or. 4: 1187; Camus, 1904, Saul. Eur. 1: 221; Seemen, 1909, in Aschers. et Graebn. Synopsis 4: 189; Buser, 1940, Ber. Schweiz. bot. Ges. 50: 637; Nazarov et al. 1952, Fl. URSR 4: 53.

T y p u s: "In montibus Carnioliae, ad scaturigines et rivulos" (n. v.).

HABIT: A small tree (to 8–10 m, rarely to 12 m); occasionally a tall shrub.

HABITATS: Coarse pebbles of large rivers; occasionally, moist stony slopes and scarps, bottoms of narrow gorges, etc. at intermediate and low levels in the mountains, sometimes descending to foothills. A calciphilic species.

DISTRIBUTION: Mountains of Northern Africa (rarely; Rif, at 1,500 m; the Middle Atlas, at 2,000 m); most of the Iberian Peninsula (except the southwestern part); southern France; all of the Alps (to 1,800 m); the mountains of the western Balkan Peninsula to the Peloponnese Peninsula; Bulgaria (800–1,600 m); the Southern, Eastern, and Western Carpathians (to 1,200 m); the Ukrainian Carpathians (mostly, in warm valleys, scattered, presumably not higher than 700–800 m). In northern Asia Minor, it occurs at 750–1,900 m. (Fig. 54.)

Sect. 20. *Villosae*

Rouy, 1910, Fl. Fr. 12: 200.

T y p u s: *Salix lapponum* L.

Shrubs or occasionally short-stemmed trees. Floriferous buds strikingly different from vegetative ones. Leaves elliptic or (ob-)lanceolate, entire or subdentate, more or less pubescent as well as shoots (covered with dense white tomentum); cataphylls and inferior leaves more or less silvery beneath. Catkins precocious or subprecocious, densely pubescent, rather thick. Nectary solitary. Capsules sessile or on short stipes, densely white pubescent; styles mostly elongated.

This boreal-arctic Eurosiberian-American group consists of five species (four in the Old World and one, *S. candida* Fluegge, in North America). Its relations to *Vimen* are obvious, connections with *Canae* and *Lanatae* are probable.

Key to Species

1. Leaf petioles embracing floriferous buds not ventricose. Floriferous buds oval or ovoid, obtuse, their apices not bent toward shoots. Catkins subprecocious, stalked; stalks leafy, with a few cataphylls. Capsule stipes 0.5–1.0 mm long, almost as long as shortly rectangular nectaries. Style length + stigma length = 0.7–2.0 mm 2

- Leaf petioles embracing floriferous buds become abruptly ventricose by fall. Floriferous buds pointleted or attenuating into beaks bent toward shoots. Catkins precocious, mostly quite sessile. Capsule stipes not longer than 0.5 mm, at least twice as short as nectaries. Nectaries narrowly rectangular or linear. Style length + stigma length = 1.4–4.0 mm 3
2. Due to impressed veins, leaves rugose above, their broadest part mostly above middle of blades. Veins, at least lateral ones, distinct beneath. Anthers 0.5–0.6 mm long. Style length + stigma length = 0.6–1.2 mm 103. **S. krylovii**
- Leaves not rugose above, their broadest part mostly about blade middle. Uniform pubescence makes veins nearly inconspicuous beneath. Anthers 0.6–0.7 mm long. Style length + stigma length = 1.2–2.0 mm 104. **S. helvetica**
3. Annotinous shoots 1.4–2 mm thick. Stipules mostly lacking or rudimentary. Leaves not large, mostly 10–20 mm broad, dull or grayish due to pubescence above. Female catkins 30–70 mm long when ripen 101. **S. lapponum**
- Annotinous shoots 2–3 mm thick. Stipules mostly well developed. Leaves large, mostly 20–40 mm broad, bright green above. Female catkins 70–130 mm long when ripen 102. **S. alaxensis**

101. **S. lapponum** L. 1753, Sp. pl.: 1019; id. 1755, Fl. Suec. 2 ed: 350; Ledeb. 1850, Fl. Ross. 3, 2: 617 (p. p.: excl. pl. altaic. et Sibiriae Or.); Wimmer, 1866, Salic. Eur.: 38 (p. p.: excl. syn. *S. helvetica* Vill.); Camus, 1904, Saul. Eur.: 147; Wolf, 1930, Fl. Yu.-V. 4: 46; Krylov, 1930, Fl. Zap. Sib. 4: 765; Floderus, 1931, Salic. Fennosc.: 132; Perfileyev, 1936, Fl. Sev. kr. 2–3: 32; Nazarov, 1936, Fl. SSSR 5: 65; Pawłowski, 1946, O niekt. wierzb.: 4; Montserrat, 1950, Collect. bot. 2, 3: N 24; Vicioso, 1951, Salic. Españ.: 86; Nazarov et al. 1952, Fl. URSR 4: 32; Shlyakov, 1956, Fl. Murm. 3: 114; Chassagne, 1956, Invent. fl. Auvergne 1: 253; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. 3, 1: 114; id. 1964, Fl. Eur. 1: 52; Polyakov, 1960, Fl. Kazakhst. 3: 34. — *S. daphneola* Tausch, 1837, Flora 20: 343. — *S. helvetica* ssp. *marrubifolia* (Tausch) Flod. 1943, Sv. bot. tidskr. 37: 77 — nom nov. pro *S. arenaria* θ *marrubifolia* Tausch, 1837, Flora 20: 339; Rech. f. 1957, op. cit. 3, 1: 118 (quoad pl. sudeticas). — *S. marrubifolia* Rech. f. 1964, op. cit. 1: 52 (p. p.: excl. pl. Mont. Tatararum). — *S. arenaria* auct. plur. vetustiorum (non L.): Trautv. 1832, Salic. Frigid.: 287; Tausch, 1837, op. cit. 20: 337–339; et al.

T y p u s: "In alpihus Lapponiae ubique. Fl. Lapp. N 366 et tab. 8 fig. T; Fl. Suec. N 808".

HABIT: A shrub to 1.5 m tall; rarely, to 2.0–2.5 m.

HABITATS: Eutrophic and mesotrophic wetlands, damp and paludal meadows and forest openings, paludal forests. It is particularly common in the forest-tundra belt and subalpine zone of northern mountains, where it forms extensive shrublands typical for these regions together with other willows, such as *S. phylicifolia*, *S. glauca*, and *S. lanata*. In the southern part of the area as well as at most paludal and peaty habitats, *S. lapponum* dominates the thickets giving way to *S. glauca* and *S. phylicifolia* at dryer places, *S. lanata* and *S. glauca* in the north.

DISTRIBUTION. The primary (solid) area embraces nearly all of Scandinavia (except southern Sweden) as well as the forest and forest-tundra belts in European Russia and West Siberia with some scattered locations in the forest-steppe belt. The southern area limit is

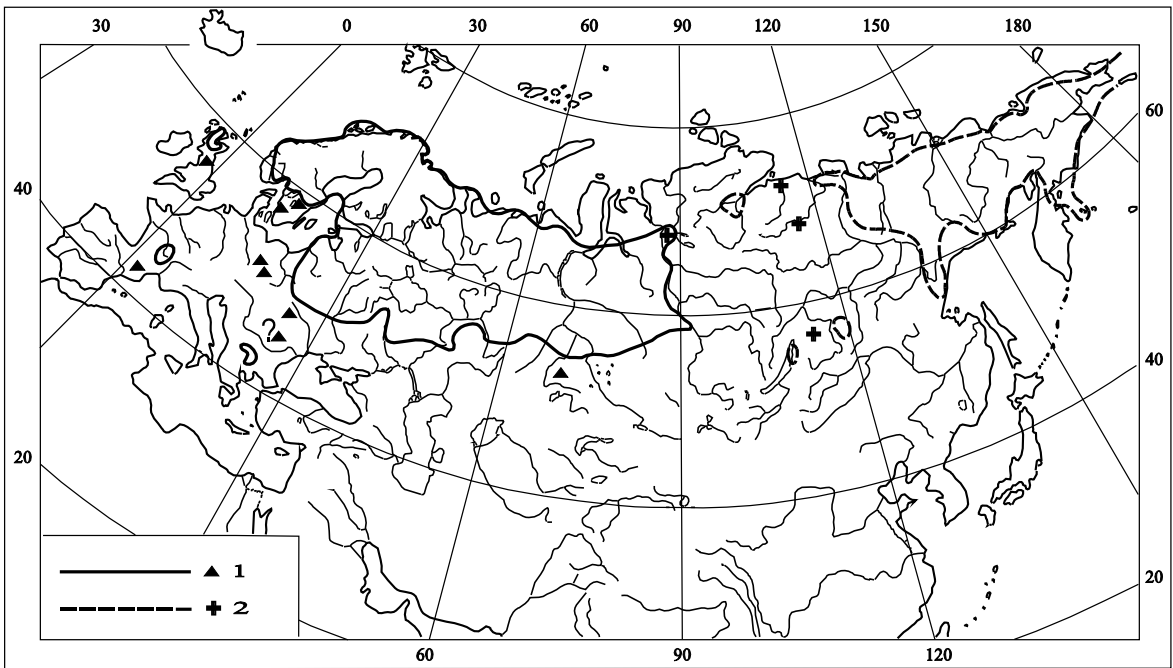


Fig. 55. Distributional areas of *Salix lapponum* L. (1) and *S. alaxensis* Coville (2)

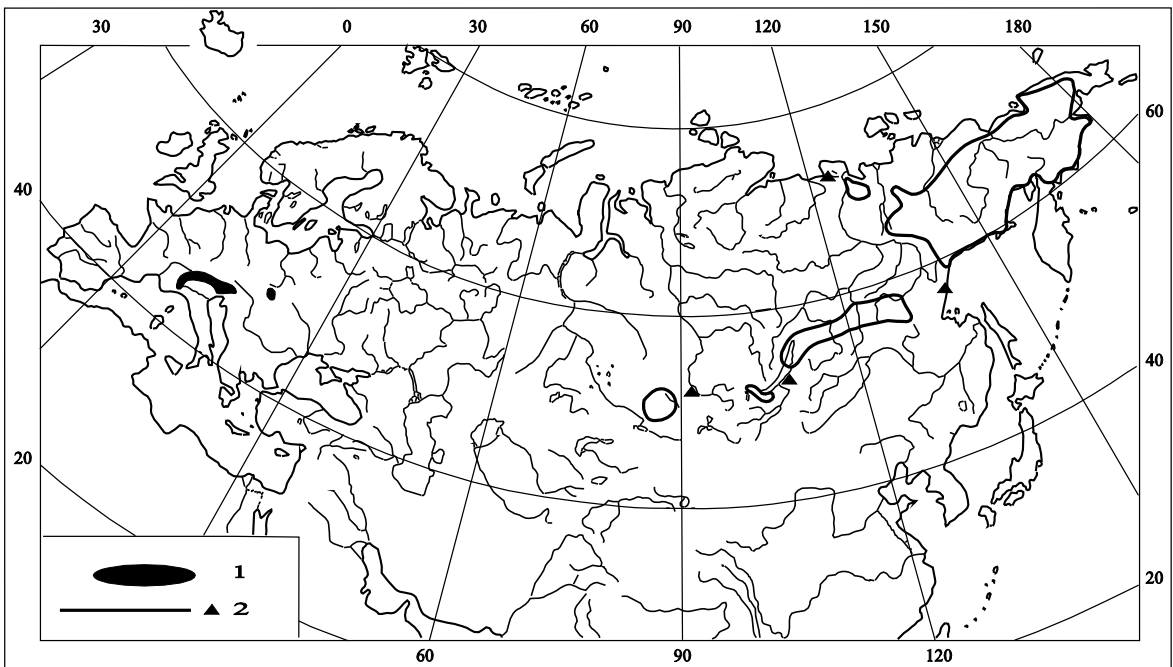


Fig. 56. Distributional areas of *Salix helvetica* Vill. (1) and *S. krylovii* E. Wolf (2)

found around Lvov, Kiev, Novgorod-Severskiy, Voronezh and Borisoglebsk, Samara, Chelyabinsk, Kurgan, Ishim, in northern Barabinskaya Steppe, Tomsk, and the Ket Basin with scattered locations in the Kazakh Uplands and northern piedmont of the Altai (the Salairskiy Kryazh, Kulundinskiy Bor). The eastern area boundary runs along the Yenisei reaching the eastern bank of the river only around Igarka and Dudinka. The northernmost parts of the area are the Ob Inlet, southern Yamal Peninsula, Kara Basin, and Lower Pechora, as well as all of the Kanin and Kola peninsulas. However, the species is absent from Kolguyev, Vaygach, the Yugorskiy Peninsula, and Novaya Zemlya. In the west, the area boundary reaches beyond the former USSR territory only in Scandinavia and eastern Poland.

In the Northern Urals (Denezhkin Kamen), it ascends to 900 m; in the Polar Urals (the Sob Basin), to 300 m; in the Khibins, to 500 m; in Norway (around Tromsö), to 1,100 m (Benum 1958).

In addition to that major area, there is a number of large and small fragmentary parts in European mountains: in Scotland and northern England (at 600–900 m); the eastern Pyrenees (2,000–2,400 m); French Massif Central (1,000–1,750 m); Sudetes (1,200–1,500 m); Eastern Carpathians (a solitary finding on a peatbog at the foot of Goverla); western Bulgaria (in the Vitocha, Rila, and Rhodopes at 1,800–2,500 m); Macedonia. (Fig. 55.)

All data from East Siberia and the Altai are to be attributed to *S. krylovii*.

NOTE. It is remarkable that the species is missing from the Alps and Western Carpathians, where it is replaced by *S. helvetica* Vill. Yet plants from the Pyrenees, Massif Central, Sudetes, Goverla, and Bulgaria are true *S. lapponum*. I had an opportunity to examine samples from all of these regions and came to this conclusion, although some authors (Pawłowski 1946; Rechinger 1957, 1964) had had other opinions on this matter.

The segregation of *S. marrubifolia* Rech. f. (1964) appears to be completely unjustified. B. Floderus (1943) found out that the so-called "*S. lapponum*" from the Tatras was actually *S. helvetica*. B. Floderus segregated plants from the Tatras in a subspecies: *S. helvetica* ssp. *marrubifolia* (Tausch) Flod. The segregation of the subspecies appears to be quite reasonable; however, I. Tausch's epithet was mistreated when applied to the Tatra plants, because the authentic Tausch's plants (PR! LE!) had originated from the Sudetes and were actually *S. lapponum*. Then K. Rechinger assigned a species rank to the ssp. *marrubifolia*; according to his treatment, plants from the Sudetes and Tatras both belong to that species. Hence, *S. marrubifolia* is actually a mixture of two different species: *S. lapponum* from the Sudetes (including the type of *S. marrubifolia*) and *S. helvetica* from the Tatras.

102. ***S. alaxensis*** Coville, 1900, Proc. Wash. Acad. **2**: 280; id. 1901, ibid. **3**: 311 et tab. 34 (nom. nov. pro *S. speciosa* Hook. et Arnott non Host); Hultén, 1943, Fl. Al. **3**: 539; Raup, 1947, Sargentia **6**: 158; id. 1959, Contrib. Gray Herb. **185**: 76; Porsild, 1951, Botany S.-E. Yukon: 145. —*S. speciosa* Hook. et Arnott, 1838, in Hook. Fl. Bor.-Amer. **2**: 145; eid. 1841, Bot. Beech. voyage: 130; Ledeb. 1850, Fl. Ross. **3**, 2: 625; Nazarov, 1936, Fl. SSSR **5**: 66; id. 1937, Fl. Zabayk. **3**: 210. —Non *S. speciosa* Host, 1828, *Salix*: 5 (quae est *S. triandrae* L. forma). —*S. lapponum* (non L.) Rgl. et Tiling, 1858, Fl. Ajan.: 118. —*S. lapponum* var. *ajanensis* Trautv. 1877, Acta Horti Petropol. **5**: 106; *S. longistylis* Rydb. 1901, Bull. N. Y. Bot. Gard. **2**: 163; Porsild, 1951, op. cit.: 145.

T y p u s: "Alaska, Kotzebue Sound, a. 1826 —captain Beechey" (K? n. v.).

HABIT: A vigorous, usually quite tall shrub with stout branches. In favorable conditions, it may grow as a small (to 6 m) short-stemmed tree with a wide crown.

HABITATS: Banks of mountain streams, flood plains of small and large rivers, nearly always close to running water; occasionally, taluses and runoff hollows with underground watercourses.

DISTRIBUTION: The alpine and subalpine zones of the Stanovoye High Plateau (sparsely; in the Kodar Range, to 1,800 m; in the Barguzinskiy Range, down to Lake Baykal level due to temperature inversions). The northern East Siberia from Dudinka to the Lower Anabar and Middle Olenek (sparsely). All of the Northeast from the Lena Delta, Verkhoyanskiy Range, Maya Basin, and Ayan to the very eastern Chukchi Peninsula (rather common); the Koryakskoye High Plateau, Karaginskiy and Bering islands. Yet it is missing from the Kamchatka Peninsula south of Koraga, Arctic Ocean islands, and northern coast of the Chukchi Peninsula. (Fig. 55.)

It is as well distributed in the arctic and subarctic regions of Alaska and Canada reaching the Hudson Bay.

103. **S. krylovii** E. Wolf, 1911, Trudy SPb. bot. sada **28**: 537 (nom. nov. pro *S. pseudolapponum* Wolf non Seemen); Krylov, 1930, Fl. Zap. Sib. **4**: 767; Nazarov, 1936, Fl. SSSR **5**: 65; Polyakov, 1960, Fl. Kazakhst. **3**: 34; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 15; Malyshev, 1965, Fl. Vost. Sayana: 107; Skvortsov, 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4540. —*S. lapponum* auct.ross. vetustior. non L.: Ledeb. 1850, Fl. Ross. **3**, 2: 617 (quoad. pl. altaic. et baicalens.); Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 289. —*S. speciosa* var. *trautvetteriana* Anderss. 1868, in DC. Prodr. **16**, 2: 276. —*S. lapponum* var. *trautvetteriana* (Anderss.) Glehn, 1876, Acta Horti Petropol. **4**: 80. —*S. pseudolapponum* E. Wolf, 1909, in Krylov, Fl. Alt. **5**: 1226. — Non *S. pseudolapponum* Seemen, 1900, Bot. Jahrb. Beibl. **65**: 28 (quae est *S. glaucae* forma). —*S. baicalensis* Turcz. ex Nasarov, 1937, Fl. Zabayk. **3**: 210; Popov, 1959, Fl. Sredn. Sib. **2**: 805. —*S. baicalensis* Turcz. in sched. inedit.; Floderus, 1933, Arc. bot. **25A**, 10: 11 (nom. nud.). —*S. helvetica* Vill. ssp. *krylovii* Flod. 1943, Sv. bot. tidskr. **37**: 75.

T y p u s: The alpine zone of the Altai [in Russian]. The description is based on samples from the Herbarium of the University of Tomsk (TK).

HABIT: A medium-sized or low shrub (to 2–2.5 m tall).

HABITATS: Stony taluses and screes, stony tundras, cirques, shallow drainage wetlands, damp depressions, *yernik*'s, banks of streams, flood plains of larger rivers (in the latter case, usually not close to running water); also, larch and poplar stands (in the undergrowth and at edges). Some contingency with acidic bedrock. Similarly to many other alpine willows distributed in the extreme Northeast, this species reaches high elevations in the mountains though not expanding its range to high latitudes.

DISTRIBUTION: The Altai (in the alpine and subalpine zones, to 2,500 m); the Western Sayans (only two findings known); Eastern Sayans (in the southeastern part only, at 1,700–2,200 m); Khamar-Daban (700–2,000 m); Baykalskiy Range; Stanovoye High Plateau (to 1,800–1,900 m); Aldanskoye High Plateau; Lower Lena; across the Northeast from the southern Verkhoyanskiy Range and Ayan to Cape Schmidt and Ugolnaya Gavan. In the Upper Kolyma Basin, *S. krylovii* ascends to 900 m. It is missing from the Kamchatka and Chukotka peninsulas. (Fig. 56.)

NOTE. M. Nazarov (1937) was first to use the name *S. baicalensis* Turcz. on legitimate grounds, although it had been introduced much earlier. Before 1937, it had been a nomen nudum. For more detail, see the appropriate note in the "Arctic Flora of the USSR", 5.

104. **S. helvetica** Vill. 1789, Hist. pl. Dauphin. **3**: 783; Wimmer, 1866, Salic. Eur.: 89; Camus, 1904, Saul. Eur. **1**: 151; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 719;

Floderus, 1943, Sv. bot. tidskr. **37**: 73 (excl. ssp. *krylovii*); Pawłowski, 1946, O niekt. wierzb.: 4; id. 1956, Fl. Tatr **1**: 186; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 116; id. 1964, Fl. Eur. **1**: 52. —*S. marrubifolia* Rech. f. 1964, op. cit. **1**: 52 p. p.: quoad pl. Mont. Tatarum.

T y p u s: "Suisse (Helvetia)" (n. v.).

HABIT: A low shrub (0.8–2.0 m), its branches short and stout.

HABITATS: Moist slopes, cirques, bottoms of depressions, and rocks in the subalpine and alpine zones. Occasionally, it may form shrublands, either solely or together with *S. glauca*, *S. hastata*, *S. foetida*, and *S. breviserrata*. The species is associated with acidic substrate.

DISTRIBUTION: The Alps (from the Maritime Alps to Tirol, at 1,700–2,700 m); the Tatras (rarely, confined to granite, at 1,600–2,000 m). (Fig. 56.)

NOTE. B. Floderus (1943) and B. Pawłowski (1946) both noticed that the plants from the Tatras, which had been treated as *S. lapponum*, were actually *S. helvetica*. However, the epithet "*marrubifolia* Tausch" was misused by B. Floderus when he applied it to those plants (see the note to *S. lapponum* above).

Sect. 21. *Lanatae*

Koehne, 1893, Dendrol.: 87, 93 (p. p.).

T y p u s: *S. lanata* L.

Shrubs with stout, usually densely pubescent branches. Floriferous buds strikingly different from vegetative ones, thick. Stipules subequilateral to slightly inequilateral. Leaves broad, entire or densely denticulate, usually more or less pubescent, their reticulation prominent beneath. Catkins precocious, sessile, their bracts clothed with long trichomes. Nectary solitary. Stamen filaments glabrous. Capsules sessile or subsessile, acute; styles elongated, stigmas linear.

The section consists of two or three Eurasiatic species (besides the two ones in this country, there is, presumably, *S. nuristanica* A. Skv., which is very poorly known so far) and also some two or three American species. However, the delimitation of *Lanatae* and other related groups (first of all, *Hastatae*, which is very abundant in species in the New World) has not yet been fully accomplished within the flora of North America.

The relation of *Lanatae* to the section *Hastatae* is quite obvious; *S. recurvigemmis* resembles *Myrtosalix* in some of its characters, such as lustrous leaves or ovaries clothed with strongly refractive trichomes. Indeed, the section *Myrtosalix* might be as well related to *Hastatae*, as it was already mentioned here.

A North American species, *S. hookeriana* Barr., undoubtedly belonging to *Lanatae*, was erroneously reported from the Anadyr (Floderus 1933) and Zhigansk (Nazarov 1936: 63).

Key to Species

1. Buds ovoid, obtuse. Stipules persistent on leaf abscission. Leaves matte (opaque) above. Ovaries glabrous 105. **S. lanata**
- Buds with reclined beaks. Stipules abscising not later than leaves. Mature leaves more or less lustrous above. Ovaries pubescent, at least partially 106. **S. recurvigemmis**

105. *S. lanata* L. 1753, Sp. pl.: 1019; Ledeb. 1850, Fl. Ross. **3**, 2: 616; Wimmer, 1866, Salic. Eur.: 2; Krylov, 1930, Fl. Zap. Sib. **4**: 764; Floderus, 1931, Salic. Fennosc.: 130; Perfilyev, 1936, Fl. Sev. kr. **2-3**: 29; Nazarov, 1936, Fl. SSSR **5**: 61; id. 1937, Fl. Zabayk. **3**: 209; Shlyakov, 1956, Fl. Murm. **3**: 112; Popov, 1959, Fl. Sredn. Sib. **2**: 806; Polyakov, 1960, Fl. Kazakhst. **3**: 35; Rech. f. 1964, Fl. Eur. **1**: 48; Malyshev, 1965, Fl. Vost. Sayana: 107. —*S. depressa* L. 1755, Fl. Suec. ed. 2: 352. —Non *S. depressa* Fries. et auct. poster. —*S. richardsonii* Hook. 1838, Fl. Bor.-Amer. **2**: 147 et tab. 182; Coville, 1901, Proc. Wash. Acad. **3**: 315; Floderus, 1933, Ark. bot. **25A**, 10: 8; Nazarov, 1936, op. cit. **5**: 63; Raup, 1943, Sargentia **4**: 112; id. 1959, Contrib. Gray Herb. **185**: 74. —*S. glandulifera* Flod. 1926, in Lindman, Svensk Fanerogam-fl. 2 ed.: 212; id. 1930, Bot. not.: 338; id. 1931, op. cit.: 127; Perfilyev, 1936, op. cit. **2-3**: 30; Nazarov, 1936, op. cit. **5**: 62; Shlyakov, 1956, op. cit. **3**: 110; Rech. f. 1964, op. cit. **1**: 48.

T y p u s: "In alpinibus Lapponicis. Fl. Lapp. N 368 et tab. 8 fig. X; tab. 7 fig. 7; Fl. Suec. N 809".

HABIT: A shrub to 2–2.5 m tall in favorable habitats and almost procumbent in severe environmental conditions.

HABITATS: Banks of water courses (from small mountain streams to large rivers on the plain), moist hollows and slopes, flood plains and alluvial plains, damp yet not paludal tundras (on well-moisturized, but well-drained stony, gravelly, or alluvial substrate). Being associated with eutrophic substrate and basic bedrock, it nearly never occurs on bogs and avoids quartzite. It is most common in the forest-tundra and southern tundra, where it may form extensive shrublands, either alone or with *S. glauca*, *S. phylicifolia*, and *S. pulchra*. Outside that major arctic area, the species is much more rare, being occasionally found in alpine zones of mountains.

DISTRIBUTION: Iceland (to 600 m); the Highlands of Scotland (600–900 m); the alpine zone and arctic belt in Scandinavia (to 1,000 m in northern Norway); the Kola Peninsula (the northern and mountainous central parts, reaching 600 m in the Khibins); the Myansielkia Ridge; the Kanin Peninsula, Kolguyev, and the Novaya Zemlya (reaching the Matochkin Shar); Malozemelskaya and Bolshezemelskaya tundras; within the forest belt, the Pechora and Upper Mezen (sporadically); Vaygach, the Yugorskiy Peninsula, and Polar Urals (to 500–600 m); the Prepolar and Northern Urals (occurring at 600–1,200 m in the Northern Urals and reaching Konzhakovskiy Kamen in the south); the Yamal Peninsula (except its northern part). East of these regions, it becomes rather common occurring across the tundra and forest-tundra and sparsely in the northern forest belt and reaching the mouth of the Taz, the Kureyka, and Middle Olenek as southernmost points; Gydanskaya Inlet, Pyasina Mouth, Lake Taimyrskoye, the Anabar and Olenek mouths, and Lena Delta as northernmost points. Some isolated area fragments are found in the Bolshoy Pur and Upper Vilyuy basins. It occurs in the Verkhoyanskiy Range (scattered, ascending to 860 m in its northern part); at the Lower Yana, Lower Indigirka, Middle and Lower Kolyma; in Chaunskaya Inlet and Anadyr basins; on Wrangel Island; on the Chukchi Peninsula; at the Korf Bay, on Koraga and Karaginskiy Island (south of these destinations, it is missing from the Kamchatka Peninsula). Neither are there any samples from the Penzhina and Omolon basins and the Coast of the Sea of Okhotsk. Very sparsely, it is distributed on the barren heights of the Aldanskoye High Plateau, Barguzinskiy Range, Eastern Sayans (1,600–2,200 m), and Altai. (Fig. 57.)

It is very common in Arctic North America.

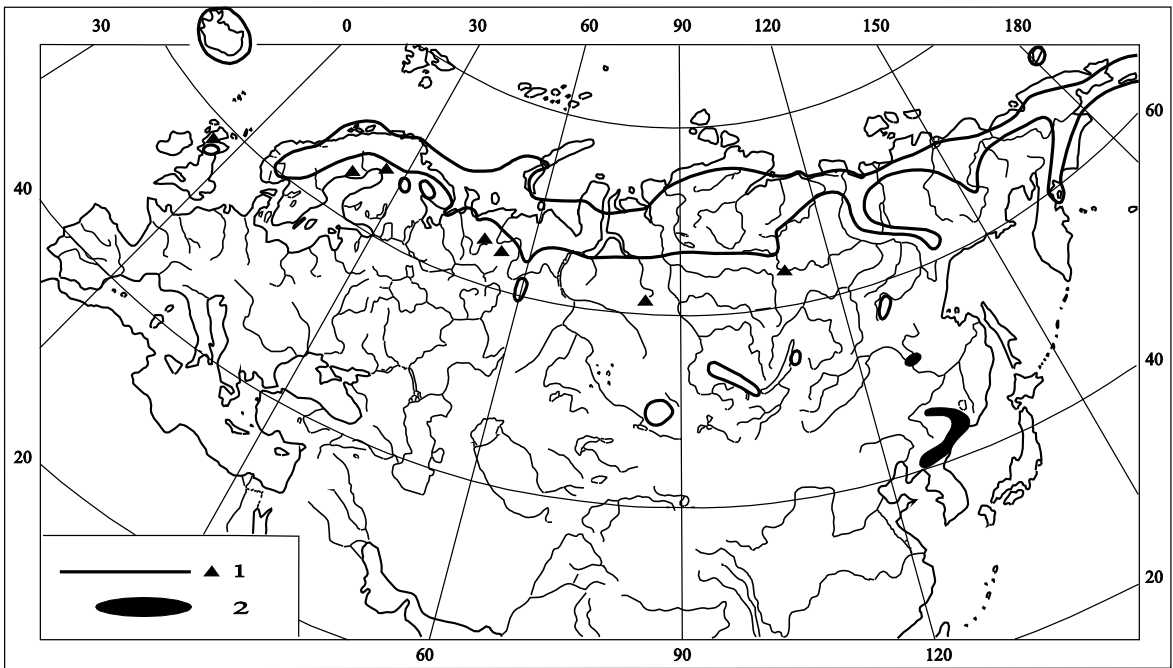


Fig. 57. Distributional areas of *Salix lanata* L. (1) and *S. kangensis* Nakai (2)

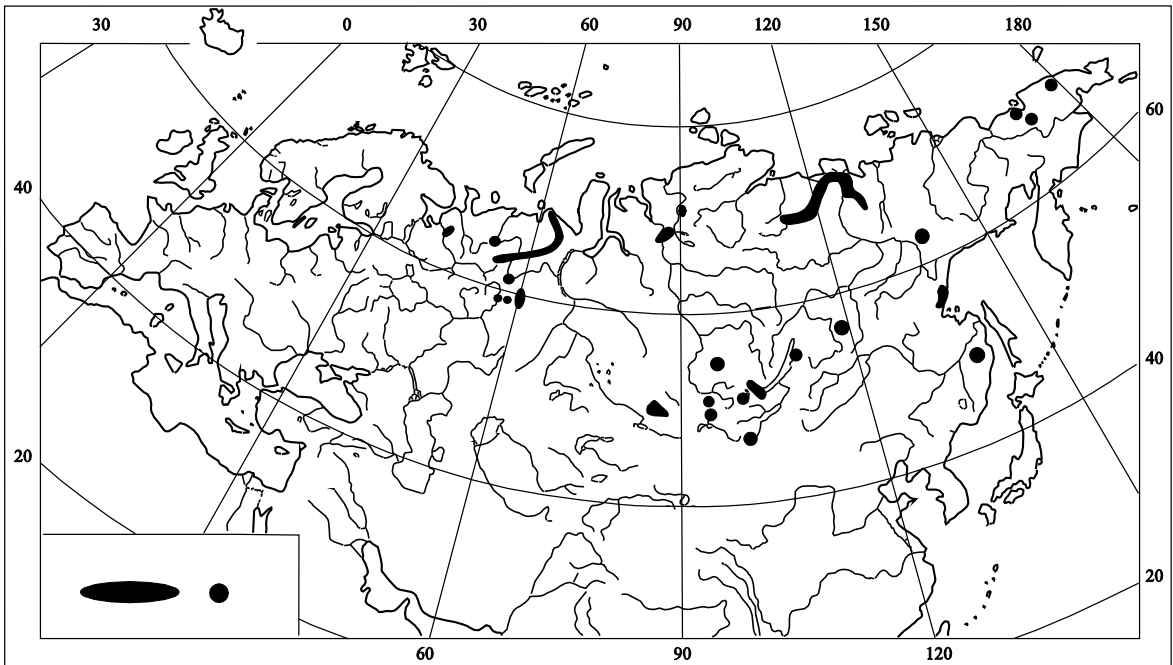


Fig. 58. Distributional area of *Salix recurvigemmis* A. Skv.

NOTE. The plants from North America and Northeast Asia (including the Lena or probably the Khatanga Basin) are different in their catkins, that are whitish with pubescence, and also smaller leaves having less pubescence and fewer denticles. It would make sense to distinguish these plants as ssp. *richardsonii* (Hook.) A. Skv. comb. nova (= *S. richardsonii* Hook. l.c.). The subspecies type is "Fort Franklin on the Mackensie River, —Richardson". Herb. Torrey, GH (n. v.).

106. **S. recurvigemmis** A. Skv. 1956, Sistem. zamet. gerb. Tomsk. un-ta **79–80**: 13 (nomen); id. 1957, Bot. mat. Gerb. Bot. in-ta AN SSSR **18**: 37 et fig. 1–2 (descriptio; hic sphalmate "*recurvigemmata*"); id. 1961, Feddes Repert. **64**: 76; Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3228; Opred. rast. Komi, 1962: 147; Malyshev, 1965, Fl. Vost. Sayana: 107; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 69. —*S. rhamnifolia* auct. non Pallas: Nazarov, 1936, Fl. SSSR **5**: 120; id. 1937, Fl. Zabayk. **3**: 204 (regarding vegetative parts only, as catkins were originating from another species!); Karavayev, 1958, Konsp. fl. Yak.: 83.

T y p u s: "Provincia Perm, prope pag. Dobrjanka in decliviis gypsaceis ad fl. Kama, 21.IV et 24.VIII 1899 leg. F. Teplouchow" (MW).

HABIT: A low, usually rather distorted shrub at times completely appressed to the substrate, at times (in favorable conditions) to 1–1.5 m tall.

HABITATS: Only well-drained, occasionally even fairly dry substrates, like rocky, stony, or gravelly ones in tundras with dwarf-shrub (particularly *Dryas*) or cryptogam vegetation; also in tundras with *Kobresia* cover and spotty tundras. It is clearly restricted to basic bedrock, such as limestone, gypsum, or gabbro.

DISTRIBUTION: Northern European Russia and Siberia (scattered across tundras and occasionally the forest belt, restricted to appropriate rock outcrops); barren heights of South Siberia (also scattered and restricted to suitable substrate). The Pinega, Pechora, and Kama basins (on limestone and gypsum outcrops); the Urals from Konzhakovskiy Kamen to the Yugorskiy Peninsula (in stony tundras); the Lower Yenisei, Pyasina, Middle Olenek, Lower Lena, and northern Verkhoyanskiy Range (on limestone). Following a large gap, it is again found in the Chauna Inlet Basin, on the Chukchi High Plateau, in the Moma, southern Verkhoyanskiy, and Dzhugdzur ranges, in the northern Sikhote-Alin (Mount Tardoki-Yani), on the Stanovoye High Plateau, and in the Barguzinskiy Range. It is rather common in the Eastern Sayans and Southern Tuva; a number of localities is known in the southern Altai as well as Mongolia: in the Haan Höhey, Khangai, and near Lake Koso (Hövsogöl).

It ascends as high as 1,200 m in the Northern Urals (Konzhakovskiy Kamen and Denezhkin Kamen); in the Eastern Sayans, its range is 1,700–2,300 m; on Mount Tardoki-Yani, 1,500–1,900 m; in the northern Verkhoyanskiy Range, at about 70° N, it reaches 700 m. (Fig. 58.)

Sect. 22. *Daphnella*

Ser. ex Duby, 1828, in DC. Bot. Gall. 2 ed.: 424.

T y p u s: *Salix daphnoides* Vill.

Tall shrubs or trees. Shoots frequently pruinose. Floriferous buds strikingly different from vegetative ones, large, broadly elliptic or lanceolate, their beaks acute or flattened. Leaves persistently stipulate, lanceolate or linear-lanceolate, finely acuminate, flat, regularly and densely serrate at margins, not revolute, their veins not prominent beneath.

Catkins extremely precocious, sessile, plump, cylindrical; bracts black, with dense, long trichomes. Capsules borne on short stipes, acute, gradually attenuating into elongated styles.

This boreal Eurasiatic section is very distinct and small: it contains only four species. One of them, *S. kangensis*, is rather different from the rest, so that it might reasonably represent a monotypic subsection. Filiation of this section is not yet clear. F. Wimmer placed it close to *Lanatae* according to similarity in the catkin structure. Yet connection with *Hastatae*, particularly, the group of *S. pyrolifolia*, *S. rigida* Muhl., and *S. mackenzieana* Anderss. appears to be more probable.

Key to Species

1. Shoots without pruinose bloom. Bast whitish. Floriferous buds narrowly triangular-lanceolate. Stipules free, not adnate. Stamen filaments often more or less connate. Capsules not flattened, frequently rather pubescent 110. **S. kangensis**
— Shoots pruinose. Shoot and particularly root bast bright lemon yellow. Floriferous buds broadly elliptic or lanceolate. Stipules adnate to petiole bases. Stamen filaments distinct. Capsules laterally flattened, glabrous 2
2. Stipules broadly elliptic or round, mostly obtuse. Petioles 3–13 mm long, not becoming abruptly ventricose when embracing floriferous buds. Bracts with whitish marginal glands at base. Stigmas 0.8–1.5 mm long 109. **S. rorida**
— Stipules lanceolate, acute. Bracts eglandular (lower ones in catkins may be occasionally glandular) 3
3. Shoots more or less pubescent, at least in their upper parts. Annotinous shoots 1.7–2.4 mm thick. Floriferous buds broadly lanceolate, abruptly short-pointed. Petioles embracing floriferous buds become markedly ventricose by fall. Leaves conspicuously pubescent (at least young ones), 10–35 mm broad, 2.5–6 times as long as broad. Capsule stipes 0.3–0.7 mm long, not longer than nectaries. Stigmas 0.4–0.7 mm long, considerably shorter than styles 107. **S. daphnoides**
— Shoots glabrous (except the youngest ones that may occasionally be loosely pubescent). Annotinous shoots 1.2–1.8 mm thick. Floriferous buds lanceolate, gradually acuminate. Petioles that embrace floriferous buds not becoming ventricose. Leaves glabrous, 6–20 mm broad, 5–15 times as long as broad. Capsule stipes 0.7–1.5 mm long, longer than nectaries. Stigmas at least as long as styles 108. **S. acutifolia**

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107. **S. daphnoides** Vill. 1789, Hist. pl. Dauphin. **3**: 765 et tab. 50 fig. 7; Wimmer, 1866, Salic. Eur.: 4; Camus, 1904, Saul. Eur. **1**: 227; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 167; Szafer, 1921, Fl. Polska **2**: 44; Floderus, 1931, Salic. Fennosc.: 144; Nazarov, 1936, Fl. SSSR **5**: 180; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 683; Dostál, 1950, Květ. ČSR **2**: 896; Vicioso, 1951, Salic. Españ.: 88; Nazarov et al. 1952, Fl. URSR **4**: 60; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 125; id. 1964, Fl. Eur. **1**: 54 (cf. adnot. nostram!); Rasinš, 1959, Ivy Latv.: 106; Krall, Viljasoo, 1965, Eesti kasv. pajud: 64. —Non *S. daphnoides* auct. plur. fl. Sibiriae Or. et Orientalis Extrem. (quae est *S. rorida* Laksch.), nec *S. daphnoides* auct. fl. Himalayae (quae est *S. sericocarpa* Anderss. = *S. oxycarpa* Anderss.). —*S. cinerea* Willd. 1806, Sp. pl. **4**, 2: 690; non L. —*S. pomeranica* Link, 1822, Enum. hort. Berol. **2**: 414. —*S. pulchra* Wimm. 1866, op. cit.: 7.

T y p u s: "Commune dans tout le Champsoir, Devoluy, Valgaudemar". Verosimiliter in Hb. U. Grenoble (n. v.). Specimen inscriptum "Dauphiné. Villars" in LE!

HABIT: A straight-stemmed tree to 15 m or tall shrub.

HABITATS: Banks of mountain rivers (on sandy, pebbly, and bouldery alluvia, often together with *S. elaeagnos*, *Myricaria germanica*, and such). It may descend from mountains to lowlands along the largest rivers, like the Rhine or Visla. It is as well found on the loose dune sand.

DISTRIBUTION. The area consists of three disjunct parts, each of them as well more or less fragmented. 1. Mountains of Central and partially Southern Europe: the central Pyrenees (seldom, at 1,600–1,700 m); all of the Alps (to 1,800 m and 2,000 m in the Italian Alps) and surrounding territories of Elsass, a part of Germany, Moravia, and the Sudetes; the Northern Apennines; the Carpathians (rarely and sparsely: in the Western Carpathians, around Skszyczin on the Raba; in the Eastern Carpathians, around Kolomyia; in the Southern Carpathians rarely, in Muntenia). Data from the Danube Valley within Serbia (Španović 1954) appear to be very doubtful. 2. The eastern part of the Baltic Region: the Eastern Baltic Sea Coast in Poland; the Baltic Sea Coast in Kaliningrad Oblast, Lithuania, and Latvia; Hiiumaa and Saaremaa islands. In Latvia, Estonia, (? and Lithuania), it is as well encountered on inland sand, far away from the sea, for example, along the Zapadnaya Dvina and around lakes Chudskoye and Pskovskoye. The dunes of the Karelian Isthmus; sandy shores of Lake Ladoga. 3. Southern Norway and southern Sweden (mostly on pebble deposits of mountain streams, the habitats resembling those in Central Europe). (Fig. 59.)

NOTE. The species has been commonly cultivated for a long time, hence it is often difficult to say if particular localities constitute parts of the natural area. The task becomes even more complicated if one has to make his decision relying only on herbarium collections and not making observations of live plants. Examples of such doubtful area parts are locations in Luxembourg, northeastern Germany, on Gotland Island and at other destinations in southern Sweden, central Poland, Lithuania, Estonia, Pskovskaya and Leningradskaya oblasts. The fact that natural limits of *S. daphnoides* in the Baltic Region are so obscure brings about some confusion in our understanding of relations between *S. daphnoides* and *S. acutifolia*. Plants in the Baltic Region are different from Central European and Scandinavian ones in their shrub-like habit and more pronounced morphological similarity with *S. acutifolia*. They were once segregated under the name of *S. pomeranica* Link or *S. daphnoides* var. *pomeranica* Koch (1828: 23); it appears reasonable to consider them as a subspecies. The name *S. pulchra* Wimm. (non Cham.) is still encountered in dendrological collections. Actually, it is the typical *S. daphnoides* of the Central European type which is cultivated under that name. This is a very vigorously growing tree, its crown of nearly pyramidal shape.

The data on *S. daphnoides* distribution in the "Flora Europaea" by K. Rechinger (1964) appear perplexing. There, the species is considered to have natural distribution only in Scandinavia; the Central European part of its area is attributed to naturalization; as for the Baltic part, it is not mentioned at all.

108. **S. acutifolia** Willd. 1806, Sp. pl. 4, 2: 668; Ledeb. 1850, Fl. Ross. 3, 2: 601; Wolf, 1930, Fl. Yu.-V. 4: 44; Krylov, 1930, Fl. Zap. Sib. 4: 735; Perfilyev, 1936, Fl. Sev. kr. 2–3: 30; Nazarov, 1936, Fl. SSSR 5: 181; Grossheim, 1945, Fl. Kavk. 3: 34; Nazarov et al. 1952, Fl. URSR 4: 61; Polyakov, 1960, Fl. Kazakhst. 3: 18; Rech. f. 1964, Fl. Eur. 1: 54. —Non *S. acutifolia* auct. fl. Asiae Mediae: Wolf, 1903, Trudy SPb. bot.

sada 21: 195; Fedchenko, 1915, Rastit. Turkest.: 297; Protopopov, 1953, Fl. Kirgiz. 4: 30; and others. —*S. daphnoides* auct., non Vill.: Perfilyev, 1936, op. cit. 2–3: 30; and others.

T y p u s: "Hab. ad mare Caspium?" (B?). Live cultivated samples were used for the description.

HABIT: A tall shrub growing occasionally nearly as a tree to 6 m tall.

HABITATS: Loose, unsodded sand only. Consequently, it is almost entirely restricted to valleys of comparatively large rivers within the forest belt. In the steppe belt, it may as well occur apart from river valleys at sandy areas including hillocky ones.

DISTRIBUTION: The southern shore of Lake Onega, the Upper and Middle Northern Dvina Basin (down the Dvina uncluding its delta); the middle reaches of the Mezen; the Indega River in Malozemelskaya Tundra; the Upper Pechora. Nearly all of the Volga Basin including the Kama, Vyatka, and Oka, but excluding the Belaya (down the Volga nearly to its delta). The middle and lower reaches of the Don, Donets, and other rivers of the Azov Upland; the Lower and Middle Dnieper with the tributaries including the Pripyat Basin; up the Dnieper to the mouth of the Berezina; along the Western Bug within Lublin Province (Fijałkowski 1964: 454). The sandy territories of the Northern Caucasus; the Volga-Ural Sands and the Ural River (up the Ural to Orsk); the sandy areas of Western Kazakhstan (nearly reaching the Aral Sea).

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It is probably even more favored for cultivation than *S. daphnoides*. It is particularly popular in northern Belarus, Smolensk, Tver, and other oblast's of northwestern European Russia and the Baltic Republics. Hence, it is very difficult to define northwestern area limits when only referring to herbarium material without making numerous observations in nature. Presumably, there are no natural populations in the Neman and Zapadnaya Dvina basins and in Pskov Oblast. It is commonly used for sand fixing in the forest-steppe and steppe belts of southern European Russia and Ukraine, and, to some extent, in Kazakhstan. There is no doubt that findings of this species in northeastern Kazakhstan (Polyakov 1960) are to be considered as those of cultivated plants. All the evidence from West Siberia (Krylov 1930) and Krasnoyarskiy Province (Cherepnin 1961) are as well to be attributed only to feral or cultivated plants. N. Pavlov's (1935: 29) statement that *S. acutifolia* occurs along streams and in valleys of the crystalline area in the Kazakh Uplands appears to be doubtful and is not supported by any collected material. All references for *S. acutifolia* from Middle Asia are based on erroneous identifications, mostly, of *S. tenuijulis*. (Fig. 59.)

NOTE. Many authors (Meinshausen 1878, Floderus 1931, Hultén 1950, Korchagin 1957) considered plants from Lake Ladoga, the dunes of Sestroretsk, Lake Chudskoye, and such, to be *S. acutifolia*. To my opinion, they are to be considered as *S. daphnoides*, whereas *S. acutifolia* distributional area extends only to Lake Onega and the Volga Basin. In other words, I consider the areas of *S. acutifolia* and *S. daphnoides* to be separated and never overlapping. I treat samples of *S. acutifolia* collected within the area of *S. daphnoides* as cultivated or feral. However, that might be a kind of simplification. D. Smalukas showed me his collections from the vicinity of Vilnius, which he considered to be natural *S. acutifolia*. The samples from the Cherekha River near Pskov published in the "Herbarium of the Russian Flora" (N 2476) also appear to have been collected from wild-growing specimens. To make the final decision concerning this problem, one needs more observations in nature, particularly, around Ladoga and Lake Chudskoye and in the vicinity of Pskov.

109. **S. rorida** Lakschewitz, 1911, Spisok rast. Gerb. russk. fl. 46–47: N 2329; Schneider, 1916, in Sarg. Pl. Wilson. 3, 1: 155; Nakai, 1918, Bot. Mag. Tokyo 32: 216;

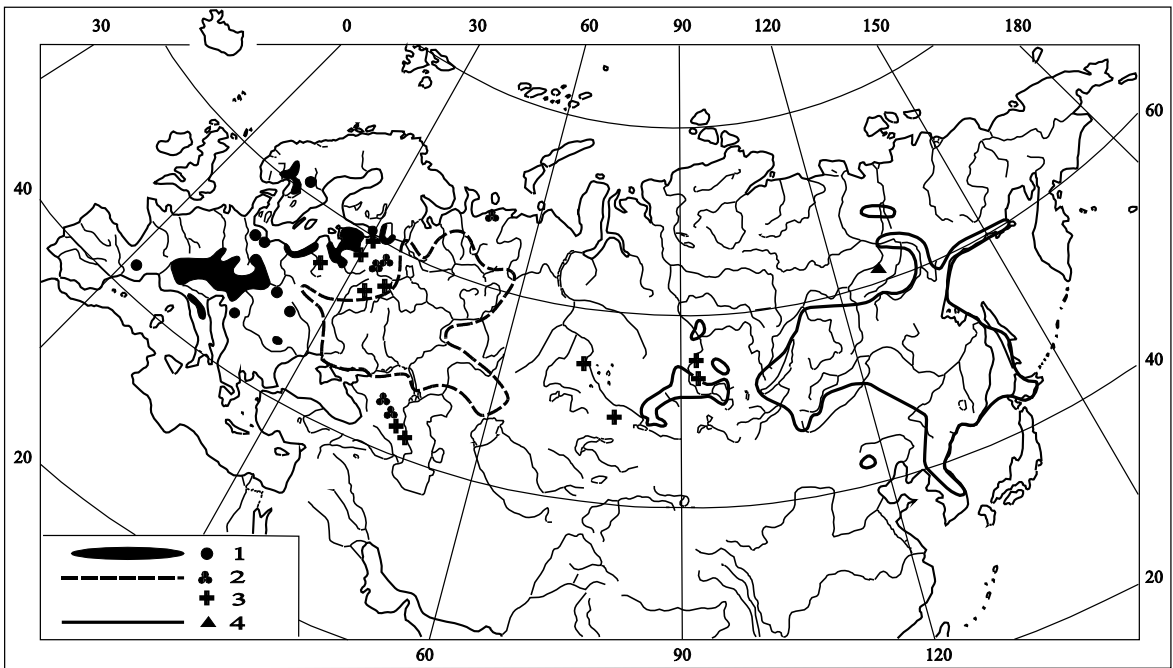


Fig. 59. Distributional areas of *Salix daphnoides* Vill. (1), *S. acutifolia* Willd. (2), cultivated *S. acutifolia* (3), and *S. rorida* Laksch. (4)

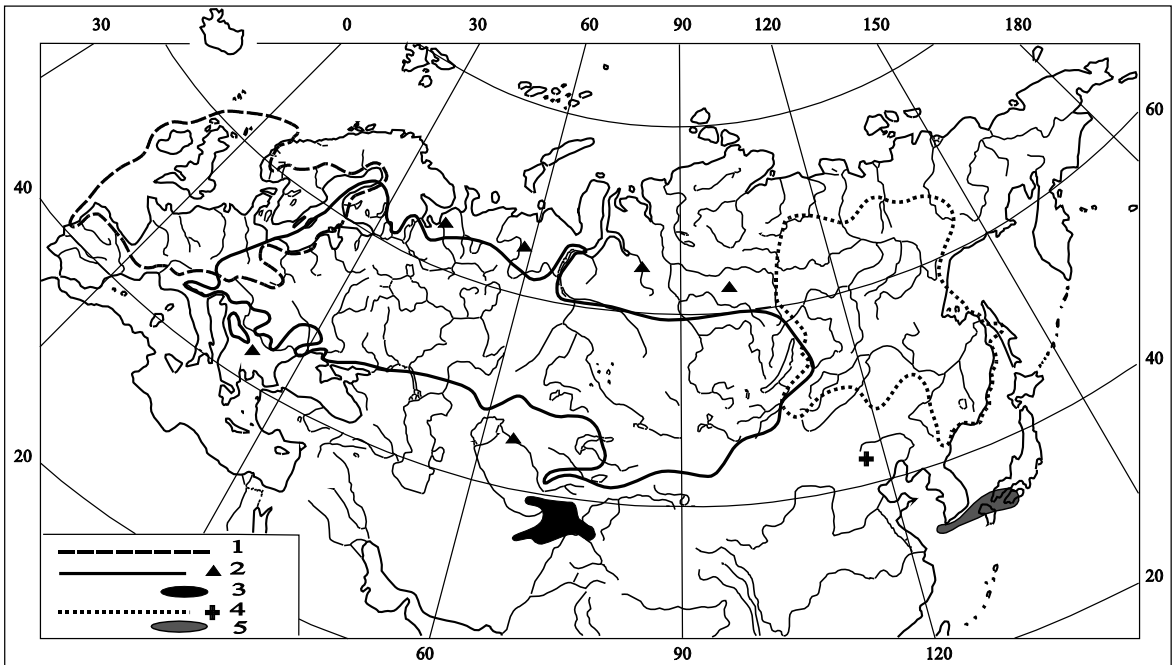


Fig. 60. Distributional areas of *Salix repens* L. (1), *S. rosmarinifolia* L. (2), *S. rosmarinifolia* ssp. *schugnanica* (Goerz) A. Skv. (3), *S. brachypoda* (Trautv. et Mey.) Kom. (4), and *S. subopposita* Miq. (5)

id. 1930, Fl. sylv. Kor. **18**: 92; Krylov, 1930, Fl. Zap. Sib. **4**: 736; Nazarov, 1936, Fl. SSSR **5**: 182; Popov, 1959, Fl. Sredn. Sib. **2**: 793; Polyakov, 1960, Fl. Kazakhst. **3**: 19; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 21; Ohwi, 1965, Fl. Jap.: 367. — *S. daphnoides* auct. non Vill.: Ledeb. 1850, Fl. Ross. **3**, 2: 602 (p. p. quoad pl. altaic. et Sib. Or.); Seemen, 1903, Salic. Jap.: 49; Hao, 1936, Syn. Chin. *Salix*: 84. — *S. acutifolia* (non Willd.) Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 374. — *S. lakschewitziana* Toepffer, 1916, Öst. bot. Z. **66**: 402; Kimura, 1931, Sci. Rep. Tohoku Univ. 4 ser. **6**: 185; id. 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **2**: 681. — *S. roridaeformis* Nakai, 1919, Bot. Mag. Tokyo **33**: 5; id. 1930, op. cit. **18**: 36 (p. p.—sed typo excluso!).

T y p u s: "Prov. Irkutsk, distr. Balagansk, a. 1902. N. Maltzev" (Herb. Fl. Ross. N 2329—LE!, MW! et alibi).

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HABIT: A tree to 20 m or tall shrub.

HABITATS: Sandy and pebbly banks of rivers and streams (solitary or in small groves).

DISTRIBUTION: The Altai, Kuznetskiy Alatau, Tuva (rarely), Minusinskaya Depression, the Yeniseiskiy Kryazh, and the foothills of the Eastern Sayans (sparsely). It becomes rather common east of Irkutsk and all the way to central and southern Sakhalin. The line of the northern area limit runs via the mouth of the Vitim, Upper Aldan, the territory south of Verkhoyansk, and the northern coast of the Sea of Okhotsk (the area reaching the Yama River). There are some solitary findings at Stolby on the Lena, in Verkhoyanskiy and Sakkyryrskiy districts. The area includes Hokkaido, northern Honshu, the northeastern Korea Peninsula, the major part of Northeast China, the Tola and Upper Kerulen rivers in Mongolia. An isolated part of the area is located on the Weichang Plateau north of Beijing (Jehol).

The species does not ascend high in the mountains never approaching the upper forest limit, reaching 1,200 m in Tuva, 1,300–1,400 m in the Kentei, 900–1,000 m in the Sikhote-Alin, 400 m on southern Sakhalin. (Fig. 59.)

NOTE. The name *S. lakschewitziana* Toepffer was proposed instead of *S. rorida* Lakschewitz merely because the epithet "*rorida*" had been used by M. Gandoger in his infamous "Flora of Europe" (1890: 148). However, as it has been already mentioned here, the names suggested by M. Gandoger do not have validity at any rank.

110. **S. kangensis** Nakai, 1916, Bot. Mag. Tokyo **30**: 275; id. 1930, Fl. sylv. Kor. **18**: 101; Kitagawa, 1939, Lineam. fl. Mandsh.: 159; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 176; Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR **20**: 85; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4539. — *S. roridaeformis* Nakai, 1919, Bot. Mag. Tokyo **33**: 5; id. 1930, op. cit. **18**: 96. — *S. fenghuanschanica* Chou et Skvortz. 1955, Liou Tchen ngo, op. cit.: 555. — *S. pierotii* auct. non Miq.: Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 426; Nazarov, 1936, Fl. SSSR **5**: 128.

T y p u s: "Korea prov. Heihok (Phyöng-an), Kangei. —R. G. Mills N 301" (TI, n. v.).

HABIT: A small tree (the largest ones I have seen were 8–10 m tall and to 25 cm in stem diameter; there is no doubt that there exist even larger specimens).

HABITATS: Banks of rivers (solitary specimens or small groups of trees growing on solid sandy or pebbly substrate).

DISTRIBUTION: Southern Maritime Province (south and west of Ussuriysk), the southern part of Northeast China; two known localities within Amur Oblast: near Busse on the Amur and near Svobodnyy on the Zeya. (Fig. 57.)

NOTE. *S. roridaeformis* is actually a mixture of *S. kangensis* and *S. rorida* samples. Its type ("At the foot of Mt. Setsurei, Nakai N 6851." —TI!) proved to belong to *S. kangensis*. *S. rorida* var. *roridaeformis* Kimura, 1931, Sci. Rep. Tohoku Univ. 4 ser. 6: 187 has nothing to do with *S. kangensis*. Apparently, there is no *S. kangensis* on the Islands of Japan.

Two samples of *S. kangensis* (from Askold Island and Furugelm Island) were mistakenly identified by V. Komarov as *S. pierotii*. Those two samples provided the only ground for listing *S. pierotii* in the guide to the plants of the Russian Far East by V. Komarov and Ye. Klobukova-Alisova (Komarov, Alisova 1931) as well as in the "Flora of the USSR" (Nazarov 1936). Actually, the name *S. pierotii* belongs to a different species (see species 11).

Sect. 23. *Incubaceae*

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Kerner, 1860, N.-Öst. Weid.: 264.

T y p u s: *Salix repens* L.

Low shrubs with slender shoots. Floriferous buds rather small, yet distinctly different from vegetative ones, ovoid, frequently positioned at acute angle to shoot. Stipules lanceolate, subequilateral, acute. Leaves sessile, small, entire or with few shallow denticles, more or less pubescent beneath or on both surfaces; trichomes silvery, appressed, pointing forward; reticulation finely prominent beneath. Catkins precocious or subprecocious, small, round or shortly cylindrical. Capsules stipitate, styles and stigmas very short.

This is a boreal section presented both in the Old and New World. Of four species distributed in the Old World, three are found in this country and one more, *S. subopposita* Miq., in southern Japan.

The American counterpart of the section is less known. Also, relations to other sections need clarification: it is impossible to gain fair understanding of these relations using material from Eurasia alone. We might approach better knowledge of the section's origin after a careful study of the North American willows. According to the structure of the gynoecium, common filiation with *Vetrix* and, on the other hand, with *Myrtilloides* appears to be most probable.

Key to Species

1. Pubescence on young catkins and leaves more or less golden. Capsule stipes 0.5–1.0 mm long, not more than twice as large as nectaries. Ovary pubescence mostly opaque white 113. **S. brachypoda**
- Pubescence on young catkins and leaves without golden tint. Capsule stipes 1.0–2.5 mm long, more than twice as long as nectaries. Ovary pubescence mostly grayish and silky or may be lacking at all 2
2. Leaves narrow (5–10 times as long as broad), entire (sometimes with sparse glands but never with denticles). Catkins precocious, sessile (their stalks less than 3 mm long). Bracts black. Capsules entirely pubescent 112. **S. rosmarinifolia**
- Leaves broader (1.5–5 times as long as broad), usually at least some of superior ones with few sparse denticles. Catkins subprecocious, female ones on stalks 2–12 mm long.

Bracts mostly blackish, but not completely black, or not black at all. Capsules frequently glabrous or partially pubescent 111. **S. repens**

111. **S. repens** L. 1753, Sp. pl.: 1020; Ledeb. 1850, Fl. Ross. **3**, 2: 614 (p. p.); Wimmer, 1866, Salic. Eur.: 114 (p. p.: excl. var. *rosmarinifolia*); Anderss. 1867, Monogr. Salic.: 113; Camus, 1904, Saul. Eur. **1**: 160; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 123 (quoad var. *eurepens*); Linton, 1913, Brit. willows: 58; Floderus, 1931, Salic. Fennosc.: 96; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 674; Vicioso, 1951, Salic. Españ.: 126; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 105 (p. p.: quoad subsp. *argentea*, *repens* et *galeifolia*); id. 1964, Fl. Eur. **1**: 51; Rasinš, 1959, Ivy Latv.: 99; Mang, 1962, *Salix*-Sektion *Incubaceae*: 35 et al.; Krall, Viljasoo, 1965, Eesti Kasv. pajud: 55. —*S. argentea* Sm. 1804, Fl. Brit. **3**: 1059. —*S. arenaria* auct. haud L.: Floderus, 1931, op. cit.: 101; Pawłowski, 1946, O niekt. wierzb.: 2; Lawalrée, 1952, Fl. Belg. **1**, 1: 50; Chassagne, 1956, Invent. fl. Auvergne **1**: 250; Rech. f. 1964, op. cit. **1**: 51; Krall, Viljasoo, 1965, op. cit.: 58. —*S. leiocarpa* Mang, 1962, op. cit.: 32.

T y p u s: "Inter montes Sueciae, locis humidis. Fl. Suec. N 814".

HABIT: A low shrub (0.3–1.0 m) with ascending and rooting stems.

HABITATS: Slightly sodded or loose sand dunes; sandy and peaty damp meadows; light birch and pine forests; edges of wetlands; bogs (occasionally).

DISTRIBUTION: Within the area under consideration, only the marine zone on the Baltic Coast in Kaliningrad Oblast, Lithuania, Latvia, and on the Estonian islands (most abundantly, on Kurshskaya Kosa). The vicinity of Sestroretsk is one more probable location. In other European countries, it may be found inland, sometimes rather high up in the mountains. The Bothnical Coast of Finland, southern Sweden and southern Norway, the British Isles; coastal Portugal, northern Spain, nearly all of France (excluding the Mediterranean part), Switzerland, Austria, Germany, Czechia, and western Poland.

In Scotland, it ascends to 800 m and to 1,700–1,800 m in the Alps. (Fig. 60.)

NOTE. The species is rather polymorphic. The size of leaves, their breadth-to-length ratio, and the intensity of the leaf pubescence are subject to striking variability. However, it does not appear reasonable to recognize some two or even three species instead of one (adding *S. arenaria* and *S. leiocarpa*). In any large population, one may find a full assortment of these "species" as well as all kinds of intermediate forms. The fact that plants from coastal dunes usually demonstrate more silvery pubescence and a more pronounced creeping habit should not be overemphasized and cannot provide grounds for acknowledgment of *S. arenaria*. It is well known that sea coasts are among those classic habitats that may induce specific ecotypes most frequently. Silvery, round-leafed specimens originating, say, from Portugal and Lithuania may look very much alike; yet they have developed in parallel, absolutely independently, from different populations. To my opinion, *S. arenaria* cannot be treated even in the rank of subspecies (ssp. *argentea* of the English or ssp. *dunensis* of the French).

The easternmost part of the *S. repens* area overlaps the westernmost part of the area of *S. rosmarinifolia* nearly all along the contact line. In Central Europe (southern Germany, Czechia, Poland), there exists a wide zone where it is extremely difficult to discriminate between the two species. Apparently, this is the area where hybridization commonly takes place. In Russia and the Baltic Republics, *S. repens* appears to be more distinct, as it is almost completely isolated there due to its confinement to the dunes of the sea coast. In Finland, however, the situation again becomes more obscure. That relation between

S. repens and *S. rosmarinifolia* might be most reasonably explained in the following way. Originally, there existed a single species, which was divided by the glaciation in Central Europe. The two parts diverged morphologically and, to some extent, ecologically. Yet they were not genetically different enough. After the retreat of the glacier, they shared the territory again, and it was then that the described hybridogeneous transitional zone was formed. Consequently, the treatment of *S. repens* and *S. rosmarinifolia* as two subspecies of a single species is as well acceptable.

112. ***S. rosmarinifolia*** L. 1753, Sp. pl.: 1020; Ledeb. 1850, Fl. Ross. **3**, 2: 615; Anderss. 1867, Monogr. Salic.: 115 (excl. var. *flavicans*); Nazarov, 1936, Fl. SSSR **5**: 123; id. 1937, Fl. Zabayk. **3**: 198; Pawłowski, 1946, O niekt. wierzb.: 2; Já vorka et Soq 1951, Magyar növ. kéz.: 832; Nazarov et al. 1952, Fl. URSR **4**: 52; Beldie, 1952, Fl. Rom. **1**: 311; Rasinš, 1959, Ivy Latv.: 98; Popov, 1959, Fl. Sredn. Sib. **2**: 800; Polyakov, 1960, Fl. Kazakhst. **3**: 27; Rech. f. 1964, Fl. Eur. **1**: 51; Krall, Viljasoo, 1965, Eesti kasv. pajud: 53. —*S. repens* var. *rosmarinifolia* Koch, 1828, Salic. Eur.: 48. —*S. repens* ssp. *rosmarinifolia* Celak. 1871, Fl. Böhmen **2**: 137; Wolf, 1930, Fl. Yu.-V. **4**: 57; Dostá l, 1950, Květ. ČSR **2**: 892; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 107. —*S. sibirica* Pall. 1788, Fl. Ross. **1**, 2: 78 et tab. 81 fig. 3; Wolf, 1906, Izv. Lesn. in-ta **14**: 193; Lakschewitz, 1914, Spisok rast. Gerb. russk. fl. **50**: N 2465; Nazarov, 1936, op. cit. **5**: 125; id. 1937, op. cit. **3**: 198; Polyakov, 1960, op. cit. **3**: 27; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. **3**: 18; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 82. —*S. angustifolia* Wulfen, 1789, in Jacquin, Collect. bot. **3**: 48. —*S. repens* ssp. *angustifolia* Neumann ex Rech. f. 1957, op. cit. **3**, 1: 105. —*S. canaliculata* Besser, 1822, Enum. Volhyn.: 77. —*S. volgensis* Anderss. 1868, in DC. Prodr. **16**, 2: 314. —*S. turgaiskensis* E. Wolf, 1912, Feddes Repert. **10**: 477. —*S. schugnanica* Goerz, 1936, Trudy Tadj. bazy AN SSSR **2**: 173; Nazarov, 1936, op. cit. **5**: 126; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 67; Ikonnikov, 1963, Opred. rast. Pamira: 90.

T y p u s: "In Europae campis depressis". Fide Smith, 1804, Fl. Brit. **4**: 1062, specimina originalia Linnaeana e vicin. Abo (Turku) proveniunt.

Ssp. ***schugnanica*** (Goerz) A. Skv. comb. nova. —*S. schugnanica* Goerz, 1936.

T y p u s: "Darwas, Masar—Lipsky N 3816; Schugnan, Shtam—a. 1904 O. et B. Fedtschenko, etc." (LE!).

HABIT: A low or medium-sized shrub (0.3–2.5 m).

HABITATS: Damp and peaty meadows and coppices, eutrophic and mesotrophic wetlands, floating bogs (in conditions of sufficient moisture but poor drainage); also, sand covered with *bor*'s, kettles amidst loose hillocky sand, steppe *zapadina*'s, and *sazy* at high elevations.

DISTRIBUTION: Northern Italy (very rarely); lower Austria, the territory of the former Yugoslavia, Hungary, Romania, Czechia, Slovakia, eastern Germany, Poland, Finland, southern Sweden (?). Within the Russian territory, the northern area border crosses southern Karelia reaching Arkhangelsk and the middle reaches of the Pechora, then traverses the Urals proceeding further east approximately along the 60° latitude (there is one prominence or maybe an isolated locus at the Lower Ob including its estuary). The eastern border is located between Baykal and Chita. In the south, the species reaches Jirgalanta and the Middle Khangai in Mongolia, Sant'anghu (near Hami) in Sinkiang Uighur; then along the Tien Shan, the southern border deviates back to the territory of

Kirghizia and Kazakhstan. The species is rather common in the Eastern and Central Tien Shan. It becomes more rare in the Western Tien Shan, where it is known mostly from the Chatkalskiy Range. From the Kirgizskiy Range and Zailiyskiy Alatau, the border descends to the piedmont plain. Crossing the plain and Lake Balkhash, it proceeds along the northern edge of the Kazakh Deserted Area towards the Bolshiye Barsuki Sands and Mugodzhary, via the northern edge of the Ryn Sands, south of Volgograd, and towards Rostov. So far, the species has not been found in Donbass (the Don Coal Basin) and the northern Azov Upland; however, it is distributed along the Black Sea Coast reaching the mouth of the Danube.

In Bulgaria, Romania, and the former Yugoslavian territory, it ascends to 1,000 m; in Poland (the Tatras), to 900 m. In the Urals, it almost never ascends to the mountains; in the Eastern Sayans, it reaches 900 m; in Tuva, 1,200 m; in the Altai, 1,700 m; in the Zailiyskiy Alatau, 2,500 m; in the Terskey Alatau and on Khan-Tengri, 3,600 m.

Ssp. *schugnanica* is rather common in the Pamir-Alai (ascending to 4,300 m in the Eastern Pamirs); it is also encountered in the Hindu Kush and Karakorum. (Fig. 60.)

NOTE. The species hybridizes with *S. repens* along the western limit of its area (cf. above: the note regarding *S. repens*). Within the rest of its area, *S. rosmarinifolia* demonstrates large morphological variability. Plants from Siberia (particularly those from East Siberia) are different in their leaves, which are on the average broader and mostly less pubescent. Siberian plants are also different in their cylindrical catkins (ones on European plants are nearly always orbicular). Siberian plants were described by P. Pallas as *S. sibirica*; however, it is completely impossible to segregate them even in the rank of subspecies. Plants from the Altai, Mongolia, and the Tien Shan are usually characterized by stout shoots (as stout as in *S. schugnanica*) and large leaves, often with rather prominent veins beneath. That race might be segregated in a taxon, however, there are not enough data to do it now. Of course, *S. rosmarinifolia* needs a thorough monographic study in its Asiatic part, especially within the area between the Pamirs and Tuva.

113. **S. brachypoda** (Trautv. et Mey.) Kom. 1923, Trudy Gl. bot. sada **39**: 49; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 422; Nazarov, 1936, Fl. SSSR **5**: 122 et 709; Kimura, 1937, Symb. Iteol. **4**: 316; Kitagawa, 1939, Lineam. fl. Mandsh.: 159; Skvortsov, 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4542. — *S. repens* var. *brachypoda* Trautv. et Mey. 1856, in Middendorff, Reise Sibir. 1, **2**: 79. — *S. sibirica* var. *brachypoda* Nakai, 1930, Fl. sylv. Kor. **18**: 158. — *S. repens* auct. non L.: Komarov, Alisova, 1931, op. cit. **1**: 423; Tolmachev, 1956, Der. i kustarn. Sakhal.: 69. — *S. rosmarinifolia* var. *flavicans* Anderss. 1867, Monogr. Salic.: 116. — *S. finalis* Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 451. — *S. flavicans* Hao, 1936, Syn. Chin. *Salix*: 97 (p. p.: excl. pl. Pamir.).

T y p u s: "Ad. fl. Appatyn 1.V; ad fl. Ujan 23.V; Ogus-Baha 25.V; Ulachan-Köch-Ueräch 26.V; ad fl. Solurnaj 3.VI; Udskoj 22.V 1844. — A. Middendorff" (LE, vidi omnia!).

HABIT: A low shrub (0.3–1.5 m).

HABITATS: Damp meadows, edges of wetlands, damp light forests.

DISTRIBUTION. The western area limit is at the Lower Selenga, Mukhtuya on the Lena (not reaching Baykal), the Upper Vilyuy, and Upper Olenek. The northern boundary runs from the Olenek to Verkhoyanskiy District and the Upper Indigirka; in the east, the boundary proceeds from the Upper Indigirka to Ayan. The species area includes the entire

Maritime Province, the northernmost part of the Korea Peninsula, and the major part of Northeast China. In Mongolia, *S. brachypoda* is distributed only in the Kentei and lower reaches of the Orhon. Of the islands, it is known from Bolshoy Shantar and central Sakhalin. There is an isolated area fragment on the Weichang Plateau in Jehol. (Fig. 60.)

NOTE. In Transbaykalia, the species area partially overlaps that of *S. rosmarinifolia*; however, according to available material, the two species remain separated even within the shared territory. In other words, there is no evidence of a hybridogeneous transitional zone, like the one existing between *S. rosmarinifolia* and *S. repens* in Central Europe. Samples of *S. brachypoda* can always be reliably distinguished from those of *S. rosmarinifolia* if the collections are thorough and complete.

Sect. 24. *Flavidae*

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Chang et Skvortz. 1955, in Liou Tchen ngo, Ill. Fl. Tr. Shr. Northeast China: 557.

T y p u s (et species unica): *Salix gordejewii* Chang et Skvortz.

This is a monotypic section; the section description matches that of its single species.

Low or medium-sized shrubs with slender, smooth branches. Floriferous buds distinctly different from vegetative ones, ovoid, their apices rather recurved off the shoot. Leaves very short-petioled, linear, distinctly emarginate-serrate all along margins. Catkins precocious or subprecocious, their bracts black, densely pubescent. Nectary solitary, subsquare. Stamen filaments glabrous, either distinct or more or less connate. Capsules sessile, small, ovoid, obtuse, abruptly attenuating into styles; styles 0.5–1.0 mm long.

There is no doubt the section is closely related to *Helix*; indeed, *Flavidae* may even be treated as a subsection of *Helix*. However, the section *Helix* appears to be rather large even without *Flavidae*. Therefore, it is helpful to consider the most isolated parts of *Helix*, the groups *Flavidae* and *Cheilophilae*, as distinct sections.

114. **S. gordejewii** Chang et Skvortz. 1955, in Liou Tchen ngo, Ill. Fl. Tr. Shr. Northeast China: 553 et tab. 63. —*S. flavida* Chang et Skvortz. 1955, *ibid.*: 557. —*S. mongolica* auct. non Siuzev: Grubov, 1955, *Konsp. fl. Mong.*: 101 (p. p.); Skvortzov in schedis a. a. 1955–1962 (ined.).

T y p u s: "Mongolia Inter., in arenosis prope rivulum Khandagai-gol, 10.III 1934 T. P. Gordejew; prope Zagan-nor 13.VIII 1934. id." (Hb. Inst. Sylviculturae et Soli Acad. Sinicae Mukden!). Three paratypes were mentioned when the species was first described. A duplicate of one of those paratypes is kept in Moscow ("prov. Liaoning, prope Dschangatai, T. N. Liou N 5461").

HABIT: A spreading shrub with slender branches.

HABITATS: Extensive sand areas only.

DISTRIBUTION. Within the territory of Russia, sandy hills around Borzya Railway Station in Transbaykalia appear to be the only known location. There the plant was first collected by N. Kuznetsov in 1909, and later, in 1949, by L. Sergiyevskaya with colleagues. Central and eastern Mongolia, central arid regions of Northeast China, Jehol and Suiyuan. The species appears to be rather sparsely distributed across the entire area. (Fig. 63.)

Sect. 25. *Helix*

Dum. 1825, Bijdr. Natuurk. Wetensch. 1, 1: 56.

T y p u s: *Salix purpurea* L.

Medium-sized or large shrubs or small trees. Shoots mostly slender, flexible, virgate. Stipules lanceolate, or subulate, or completely reduced. Leaves mostly narrow, entire or serrulate, flat, their margins not revolute, veins not prominent (however, on drying, veins in mature leaves become equally prominent, filament-like on both sides), upper leaf surface often dotted with stomata. Catkins precocious to serotinous, mostly narrowly cylindrical. Nectary solitary, short, subsquare. Stamen filaments connate, pubescent in lower parts. Capsules small to medium-sized; styles and stigmas short; stigmas often sessile.

This is a large Eurasiatic section consisting of 28 to 30 species. It is widely distributed in comparatively warm regions of the temperate forest belt as well as non-tropical arid regions, particularly, mountainous ones. The majority of species is restricted to Central and East Asia (there are only five species in Europe).

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Species of this section often differ from each other in rather subtle characters; besides, they are frequently encountered in close proximity to each other, a few of them at a time. Hence, of all the Eurasiatic willows, this section is one of the most difficult (if not the most difficult) to treat. The abundance of synonyms reveals the extent of confusion in this section's taxonomy and the way it was overloaded with unclarified species names. For example, there are five synonyms for *S. kirilowiana*, six for *S. tenuijulis*, eight for *S. miyabeana*, and eleven for *S. pycnostachya*. Relations to other sections are rather obscure. The only group that can be positively placed close to *Helix* is a Himalayan-Chinese section *Denticulatae*.

Within the section *Helix*, one can notice large diversity of morphological types, particularly those of the catkin structure and development. This diversity provides natural grounds for distinguishing four subsections: *Caesiae*, *Purpureae*, *Tenuijules*, and *Kirilowianae*. Of these, the former two are more closely related to each other, as well as the latter two. Hence, there are two major stems within the section, the first one consisting of *Caesiae* and *Purpureae*, the second, *Tenuijules* and *Kirilowianae*. The stems approach each other very closely in some of their representatives, such as *S. vinogradovii* from *Purpureae* and *S. caspica* from *Kirilowianae*; or *S. miyabeana* from *Purpureae* and *S. tenuijulis* from *Tenuijules*. So far, it is difficult to decide whether this proximity is due to a common filiation or it should rather be attributed to the convergence.

Key to Species

1. Bracts pale or rufescent (occasionally some of bracts in catkin blacken by end of flowering), mostly truncate, emarginate, or irregularly dentate at apex. At least some of bracts or all of them fall off by the time capsules ripen 2
- Bracts persistent when capsules ripen 7
2. Floriferous buds distinctly different from vegetative ones, 4–9 mm long. Leaf primordia in buds shorter than catkin primordia. Leaves 45–100 mm long 3

- Floriferous buds inconspicuously different from vegetative ones, 4–9 mm long. Leaf primordia in mature buds at least as long as catkin primordia or longer. Stipules mostly none. Leaves 25–50 mm long 6
- 3. Capsules glabrous 4
- Capsules pubescent 5
- 4. Shoots often slightly pruinose. Leaves mostly silky beneath, 4–10 times as long as broad. Bracts pale or pinkish 128. **S. kirilowiana**
- Shoots not pruinose. Leaves glabrous, 10–20 times as long as broad. Bracts brownish or blackish 131. **S. michelsonii**
- 5. Mature shoots olivaceous-green or yellow, not variegated, more or less pubescent. Stipules fully developed, lanceolate, 1.0–2.5 mm broad. Bracts pale, never blackening. Capsules mostly obtusish, stigmas subsessile 126. **S. olgae**
- Mature shoots glabrous, mostly dark red or reddish-brown, with light yellow variegation in their lower parts; more rarely, entirely yellowish. Stipules none or small, subulate, not more than 1 mm broad. Bracts partially darkening by the end of flowering period, however, becoming mostly pale in mature catkins. Capsules acute, styles usually distinct 127. **S. linearifolia**
- 6(2). Shoots with white waxy bloom. Bracts 1.0–1.5 mm long. Anthers 0.3–0.4 mm long. During flowering period, ovaries narrowly lanceolate, nearly subulate 130. **S. capusii**
- Shoots without bloom. Bracts 1.6–3.0 mm long, obcuneate, mostly truncate at apex, completely deciduous immediately after flowering in female catkins. Anthers 0.4–0.6 mm long. Ovaries lanceolate or ovoid-lanceolate 129. **S. niedzwieckii**
- 7(1). Petioles 1–2 (rarely 3) mm long. Leaves opposite, broad, 2–4 (rarely to 5) times as long as broad, their bases broad, more or less cordate 8
- Leaves alternate; if (rarely) opposite, then their shape different and petioles longer 9
- 8. Upper epidermis strikingly different from lower one only close to leaf margin. Leaf margin symmetrical with respect to upper and lower leaf surface. Mesophyll consists of five cell layers, upper layer constituting about one-third of total mesophyll height 121. **S. amplexicaulis**
- Upper epidermis strikingly different from lower one across entire leaf surface. Leaf margin asymmetrical (collenchyma overlapping upper surface more than lower surface). Mesophyll of four cell layers, upper layer constituting nearly half of total mesophyll height 122. **S. integra**
- 9. Leaf petioles 2–5 mm long, leaves opaque on both sides, rather broad (1.5–4.0 times as long as broad), their bases rounded or cordate, stomata lacking from upper leaf surface, leaf margins slightly dentate or entire. Cataphylls broadly elliptic, rounded or cordate at base as well as leaves 10
- Leaves narrower (4 and more times as long as broad). Cataphylls cuneately narrowing towards their bases 11
- 10. Shrub of medium size. Floriferous buds appressed to shoots, ovoid-lanceolate, conspicuously compressed on adaxial side, their lateral carinas pronounced. Leaves 30–80 mm long. Stamen filaments entirely connate 116. **S. kochiana**

- Low shrub. Mature floriferous buds usually positioned at acute angle to shoot, ovoid, nearly not compressed, their carinas obscure. Leaves 10–40 mm long. Stamen filaments not entirely connate 115. **S. coesia**
11. Bracts rounded. Nectaries of intensive purple color. Capsule stipes none or not longer than 0.5 mm; capsules shortly ovoid, obtuse, abruptly attenuating into short styles (or stigmas sessile). Stamen filaments pubescent only at very bases 12
- Bracts mostly acuminate or irregularly incised at apices. Nectaries mostly greenish or brownish. Capsule stipes 0.5–1.5 mm long; capsules lanceolate-conoidal, gradually attenuating into styles. Stamen filaments pubescent on lower $\frac{1}{4}$ – $\frac{1}{2}$ of their length 17
12. White waxy bloom on branches and buds becoming particularly intensive by fall. Leaf blades broadest about middle, of same light glaucous-green color on both sides, entire or partially and irregularly serrulate 133. **S. ledebourana**
- Branches and buds without waxy bloom. Leaves distinctly bicolorous: green above, more or less glaucescent beneath, serrate all along margins, either regularly or more densely towards apices 13
- 223 13. Mature annotinous shoots not very flexible, 1.3–2.0 mm thick, frequently having tomentose pubescence; young shoots usually densely short-tomentose. Leaves mostly broadest about middle, nearly regularly serrate all along margins, stomata lacking from the upper surface. Styles conspicuous (0.3–0.5 mm long) 123. **S. gilgiana**
- Shoots slenderer (0.7–1.5 mm thick), flexible, glabrous. Leaves broadest considerably above middle; marginal denticles more dense towards apex and sparse towards base 14
14. Floriferous buds 2.5–4.0 mm in diameter, mostly ovoid. Leaves mostly with fully-developed linear-subulate stipules; stomata numerous on upper leaf surface, margins distinctly serrate to very base of blade, in mature leaves conspicuously thickening, callous 120. **S. miyabeana**
- Floriferous buds 1.8–2.8 mm in diameter, broadly elliptic or oblong. Leaves exstipulate, serration usually only on their upper half, margins not thickening . . . 15
15. Medium-sized shrub (1.0–2.5 m). Floriferous buds broadly elliptic or subovoid, 4–7 mm long; lateral carinas mostly inconspicuous in mature ones. Leaves 190–210 μ thick, their upper surface dotted with numerous stomata, each as large as 18–21 μ . Mesophyll mostly of six cell layers. Capsule stipes mostly short (0.2–0.5 mm) 118. **S. vinogradovii**
- Tall shrubs or small trees (to 5–6 m). Floriferous buds oblong, their sides almost parallel, in mature ones lateral carinas conspicuous, apices often compressed or bent towards shoot. Leaves 140–170 μ thick, stomata either lacking from upper leaf surface or as large as 15–17 μ . Mesophyll of four or five cell layers 16
16. Floriferous buds 4–8 mm long. First cell layer tallest one in mesophyll. Stalks to 15 mm long in female catkins and to 6 mm in male ones. Bracts strikingly different in male and female catkins: in male, mostly black, densely pubescent, particularly on inside surface, 1.0–1.5 mm broad; in female catkins, bracts less colored, less pubescent, 0.6–1.0 mm broad. Capsules often on short stipes . . . 119. **S. elbursensis**

- Floriferous buds 6–12 mm long. Second cell layer tallest one in mesophyll. Stalks to 5 mm in female catkins, to 3 mm in male ones. Bracts in male and female catkins not conspicuously different. Capsules sessile 117. **S. purpurea**
- 17(11). Annotinous shoots 0.5–1.0 mm thick, light colored. Stipules either lacking or very small, filamentous. Leaves very narrow (10–20 times as long as broad); if somewhat broader, then broadest part of blade considerably above its middle. Mature capsules 4–5 mm long 132. **S. caspica**
- Annotinous shoots 1.0–2.2 mm thick, mostly dark colored. Stipules usually fully developed. Leaves lanceolate or linear-lanceolate (3–10 times as long as broad), broadest about or somewhat above middle. Mature capsules 5–7 mm long 18
18. Leaves mostly distinctly bicolorous, young ones more or less lustrous above when alive; mature ones never densely pubescent. Margins somewhat callously thickening in mature leaves, serration rather coarse, but regular. Bracts mostly obtuse-angled at apices. Ovaries always pubescent 124. **S. tenuijulis**
- Leaves mostly concolorous, always dull, either glabrous or pubescent, sometimes rather densely. Leaf margins sharp, not callous; leaves entire or rather irregularly serrate, their denticles very slender. Bracts mostly rounded or irregularly incised at apices. Ovaries glabrous or pubescent 125. **S. pycnostachya**

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Subsect. *Caesia*

(Kerner) A. Skv. comb. nova. —Sect. *Caesia* Kerner, 1860, N.-Öst. Weid.: 205.

T y p u s: *Salix coesia* Vill.

Low shrubs, their branches spreading in different directions. Leaves on short petioles, not large (10–60, rarely to 80 mm long), relatively broad, mostly obtuse or rounded, dull, glaucescent above. Catkins very dense, stalked; stalks short, densely clothed with broad, sessile cataphylls. Stamen filaments connate entirely or partially or, more rarely, distinct. Capsules short-ovoid, obtuse, sessile.

Species of this subsection are typical for non-alluvial habitats. They are distributed in central, rather arid, mostly mountainous regions of Asia (an isolated fragment of *S. coesia* area is accounted in the Alps). Besides the two species distributed in the area under consideration, there are three in China.

115. **S. coesia** Vill. 1789, Hist. pl. Dauphin. **3**: 768 et tab. 50 fig. 11; Kar. et Kir. 1842, Bull. Soc. nat. Moscou **15**: 452; Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 394; Wimmer, 1866, Salic. Eur.: 100; Camus, 1904, Saul. Eur. **1**: 139; Nazarov, 1936, Fl. SSSR **5**: 177; id. 1937, Fl. Zabayk. **3**: 223; Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 697; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 89; id. 1964, Fl. Eur. **1**: 53; Popov, 1959, Fl. Sredn. Sib. **2**: 800; Polyakov, 1960, Fl. Kazakhst. **3**, 19; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 68. —*S. sibirica* (non Pall.): Trautv. 1833, in Ledeb. Fl. Alt. **4**: 287; Ledeb. 1850, Fl. Ross. **3**, 2: 622. —*S. myricaefolia* Anderss. 1851, K. sv. vet. handl. **1850**: 483; id. 1860, J. Linn. Soc. **4**: 53; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 172; Parker, 1924, Forest fl. Punjab: 510; Hao, 1936, Syn. Chin. *Salix*: 109. —*S. divergens* Anderss. 1868, in DC. Prodr. **16**, 2: 316; Hook. f. 1890, Fl. Brit.

Ind. 5: 637. —*S. minutiflora* Turcz. ex Wolf, 1903, Trudy SPb. bot. sada 21: 141; Krylov, 1930, Fl. Zap. Sib. 4: 737. —*S. pubescens* Hao, 1936, op. cit.: 108. —*S. tuvinensis* Gudoschn. 1965, Sistem. zamet. gerb. Tomsk. un-ta 83: 3.

T y p u s: "Sur le Lautaret, le long des ruisseaux" Verosimiliter in Hb. Grenoble, n. v. (specimen inscriptum "Dauphiné —Villars. 1768" —LE!).

HABIT: A low (0.2–1.5 m) shrub, its short branches spreading in different directions.

HABITATS: Damp, occasionally subsaline meadows; *syr't*'s at high elevations, *sazy*, glacial moraines; more rarely, alpine meadows or banks of alpine streams.

DISTRIBUTION: The Alps (rather sparsely at 1,500–2,000 m from Savoy to Italian Tirol). The species area in the Alps closely matches that of the xerophilic vegetation, the way it is depicted by J. Braun-Blanquet (1961). The major part of the area is in Central Asia: the Pamir-Alai (at 3,000–4,200 m rather sparsely from the Range of Peter I to Kzylrabat); Karakorum (3,500–4,200 m). The Tien Shan (1,800–3,100 m): the western ranges (very rare, known only from the Talasskiy Alatau); the central and eastern ranges (more common, including the Dzungarskiy Alatau and Chinese Tien Shan); the extreme eastern spurs (near Hami and in the Range of Humboldt within Nan Shan). The Tarbagatay, Altai, Western and Eastern Sayans, Kuznetskiy Alatau, Tannu-Ola, and mountainous regions of northern Mongolia. Here it becomes common even in the steppes on bottoms of wide valleys, such as Chuyskaya Steppe (1,600–1,800 m), Shargyn-Gobi Desert (1,000 m), and the depression around Lake Ubsa Nuur (800 m).

The species ascends to 2,400 m in Mongolia; to 2,000 m in the Tannu-Ola and Eastern Sayans. At lower elevations, it occurs in Transbaykalia as well as on the Stanovoye and Aldanskoye high plateaus, being very sparsely distributed. (Fig. 61.)

116. **S. kochiana** Trautv. 1836, Salicetum: 26 et tab. 1 (nom. nov. pro *S. pontederiana* Trautv. non Willd.); Ledeb. 1850, Fl. Ross. 3, 2: 602; Turcz. 1854, Fl. Baic.-Dah. 2, 2: 375; Anderss. 1868, in DC. Prodr. 16, 2: 314; Wolf, 1903, Trudy SPb. bot. sada 21: 143; Krylov, 1930, Fl. Zap. Sib. 4: 738; Nazarov, 1936, Fl. SSSR 5: 178; id. 1937, Fl. Zabayk. 3: 222; Grubov, 1955, Konsp. Fl. Mong.: 100; Popov, 1959, Fl. Sredn. Sib. 2: 798; Polyakov, 1960, Fl. Kazakhst. 3: 19; Cherepnin, 1961, Fl. yuzhn. ch. Krasnoyar. kr. 3: 19; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 89. —*S. pontederiana* (non Willd. 1806) Trautv. 1833, in Ledeb. Fl. Alt. 4: 263.

T y p u s: "Ad fl. Karagai, ad fl. Koksam in alpinis, ad fl. Tscharysch in subalpinis, —Ledebour" (Trautv. in Fl. Alt. 4: 263). The original sample from E. Trautvetter's collection, which is apparently to be considered as the holotype, was labeled just "Altai. Herb. Trautvetter" (LE!).

HABIT: A low or medium-sized (0.5–2.5 m) shrub distinguished by the opaque coerulescent foliage color in live plants.

HABITATS: Damp meadows on bottoms of *pad*'s, lower parts of flood plains, but not close to the flowing water and apart from fresh deposits (mostly at low elevations; however, ascending to the timberline at wide valleys, such as Chuyskaya Steppe or Tunkinskaya Valley).

DISTRIBUTION: The Altai, Western Sayans, and Tuva; the Eastern Sayans and their piedmont (including Krasnoyarsk, Kansk, and Zayarsk in the north); Transbaykalia (reaching the Barguzin, Upper Vitim, and Shilka rivers in the north); northern Mongolia (to 47° N); the northern steppe part of Northeast China; a bit of the Russian territory near Blagoveshchensk; an isolated (?) location near Lake Dalai Nur. (Fig. 61.)

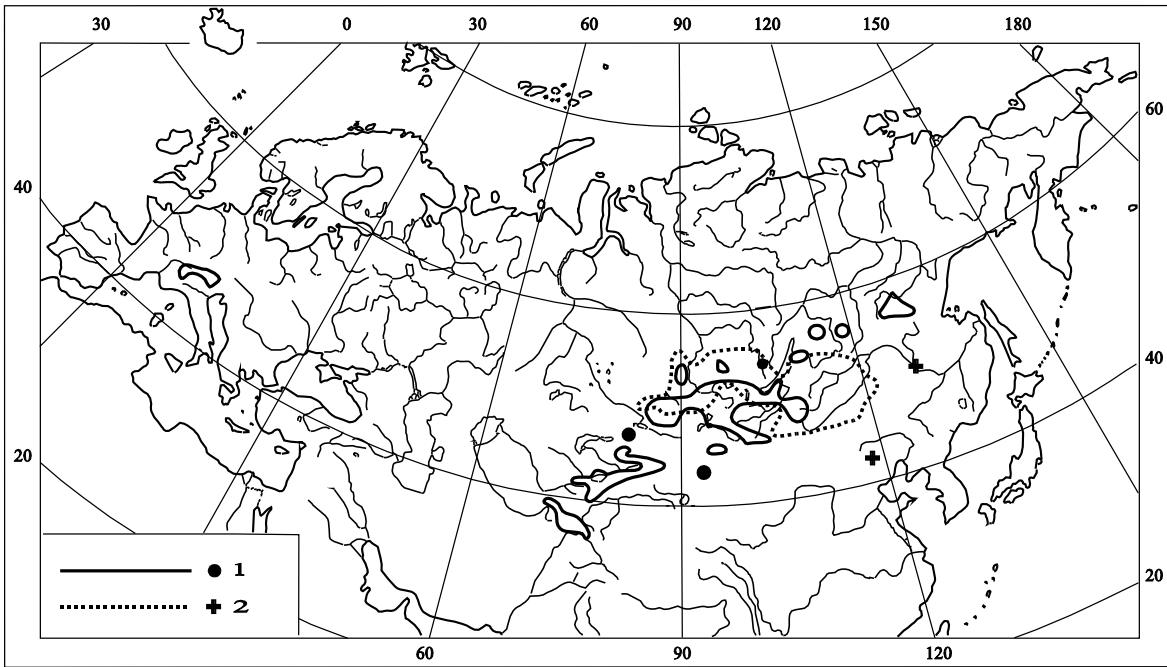


Fig. 61. Distributional areas of *Salix coesia* Vill. (1) and *S. kochiana* Trautv. (2)

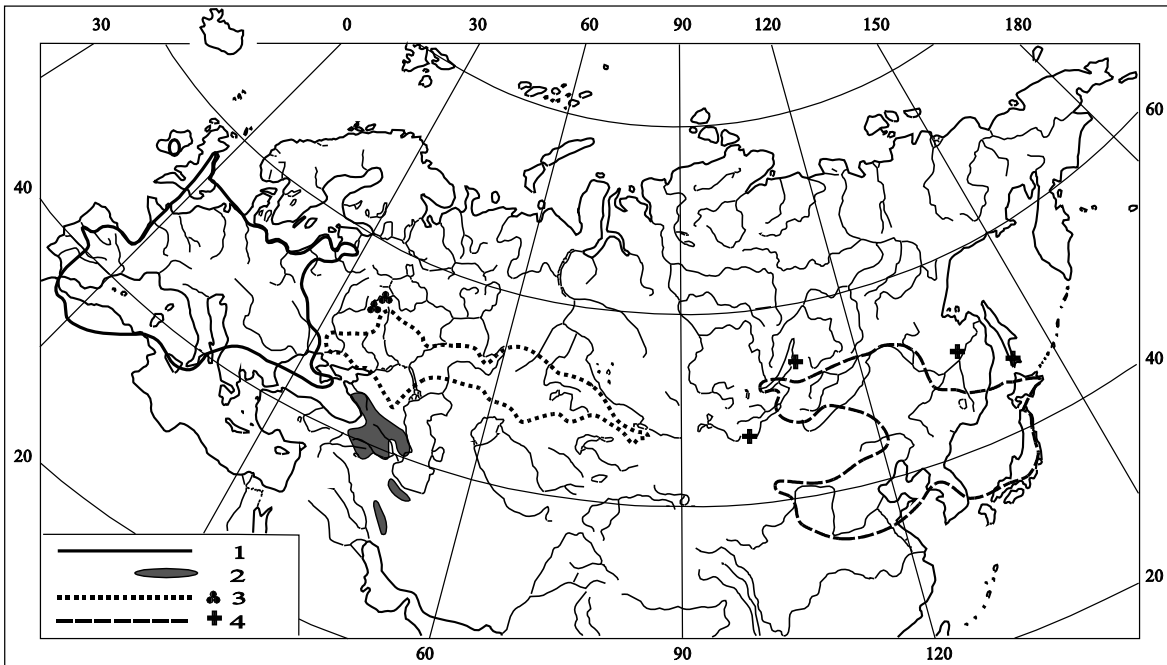


Fig. 62. Distributional areas of *Salix purpurea* L. (1), *S. elbursensis* Boiss. (2), *S. vinogradovii* A. Skv. (3), and *S. miyabeana* Seemen (4)

(Hayek) A. Skv. comb. nova. —Sect. *Meliteae* subsect. *Purpureae* Hayek, 1908, Fl. Steierm. **1**: 154.

T y p u s: *S. purpurea* L.

Usually rather tall shrubs or small trees. Floriferous buds strikingly different from vegetative ones (two or three times longer). Leaves usually distinctly bicolorous, bright green above. Catkins precocious or subprecocious, densely flowered, their bracts mostly rounded, black at apices. Nectaries mostly bright purple. Stamen filaments slightly or considerably pubescent at their very bases. Capsules rather small, ovoid, obtuse, sessile or subsessile.

This is a rather large group (10 species) that is distributed within the southern boreal belt and partially in warm temperate regions of Eurasia. The species are very much alike each other, however, well different in their geographical distribution.

117. **S. purpurea** L. 1753, Sp. pl.: 1017; Ledeb. 1850, Fl. Ross. **3**, 2: 502 (p. p.); Wimmer, 1866, Salic. Eur.: 29; Seemen, 1909, in Aschers. et Graebn. Synopsis **4**: 192 (p. p.); Nazarov, 1936, Fl. SSSR **5**: 153 (p. p.); Buser, 1940, Ber. Schweiz. bot. Ges. **50**: 634; Görz, 1947, in Wulf, Fl. Kryma **2**, 1: 120; Vicioso, 1951, Salic. Españ: 67; Beldie, 1953, Fl. Rom. **1**: 290; Nazarov et al. 1952, Fl. URSR **4**: 57 (p. p.); Andreyev, 1957, Der. i kustarn. Mold. **1**: 74; Rasinš, 1959, Ivy Latv.: 118; Rech. f. 1957, in Hegi, Ill. Fl. Mitteleur. **3**, 1: 123; id. 1964, Fl. Eur. **1**: 53 (partim); Maire, 1961, Fl. Afr. Nord **7**: 67; Skvortsov, 1966, Novosti sist. vyssh. rast.: 52. —Non *S. purpurea* auct. fl. Graeciae, Asiae Minoris, Caucasi, necnon Rossiae mediae et australis, vel Sibiriae et Orientis Extremis. —*S. caesifolia* Drob. 1941, Bot. mat. Bot. in-ta, Tashk. **3**: 23; id. 1953, Fl. Uzb. **2**: 47.

T y p u s: "In Europae australioribus. Iter Scan. 252; Raj. Angl. 450".

HABIT: A medium-sized or tall shrub that, if not damaged, may often grow as a small tree to 6–8 m tall.

HABITATS: River valleys and banks of streams (in close proximity to the flowing water as well as in other parts of valleys where there is sufficient water supply).

DISTRIBUTION: Northern Africa (mostly in the mountains, to 2,500 m), the major territory of the Iberian Peninsula (except the western part), France, southeastern England, nearly all of the territory of the former Yugoslavia (except Macedonia), northern Bulgaria, Romania, Hungary, Czechia, Slovakia, Austria, Switzerland, Holland, Germany (except Schleswig-Holstein and, probably, a part of the Northern German Lowlands), Kaliningradskaya Oblast, major territories of Lithuania and Latvia (rather common), southern Estonia, the vicinity of Pskov (the Cherekha River), Belarus (its naturalness is doubtful there, being more probable only near the western border), Western Ukraine and Moldavia (not infrequent, particularly in the Carpathians, ascending there to 1,100 m), the mountainous part of the Crimea Peninsula. (Fig. 62.)

In the Alps, the species ascends to 2,200 m (some specimens encountered at 2,400 m); in the Western Carpathians, to 1,350 m. It is missing from Denmark as well as the rest of Scandinavia.

S. purpurea is commonly cultivated across all of Europe, sometimes becoming nearly feral. All findings in the forested regions of central European Russia are to be attributed to

cultivated or feral plants. Data from the forest-steppe and steppe regions of European Russia and Kazakhstan are to be referred to *S. vinogradovii*; those from the Caucasus and Iran, to *S. elbursensis*, those from Transbaykalia and the Far East, to *S. miyabeana*; those from Japan, to *S. miyabeana*, *S. koriyanagi*, or *S. gilgiana*.

* **S. koriyanagi** Kimura ex Goerz, 1931, Sal. Asiat. **1**: 17; Görz, 1933, Feddes Repert. **32**: 119; Makino, 1956, Ill. Fl. Japan.: 672; Kimura, 1954, Symb. Iteol. **13**: 209; Ohwi, 1965, Fl. Jap.: 368. —*S. purpurea* var. *japonica* Nakai, 1928, Bull. Soc. Dendr. Fr. **66**: 14; id. 1930, Fl. sylv. Kor. **18**: 117; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 185.

T y p u s: "Japonia, Sendai, cult. —28.III et 3.VII 1930 leg. A. Kimura" (Görz, Sal. Asiat. N 18) (LE!, TAK! et alibi).

HABIT: A shrub (or small tree?) known only in female specimens and only in cultivation.

DISTRIBUTION. It is commonly grown in Japan for rod harvesting and as an ornamental plant. It is also known from the Korea Peninsula, Northeast China, southern Sakhalin, and the southern Kurils. Most probably, this is a strict endemic Korean or Japanese species, its natural populations not yet found.

118. **S. vinogradovii** A. Skv. 1966, Novosti sist. vyssh. rast.: 55. —*S. purpurea* auct. non L.: Wolf, 1930, Fl. Yu.-V. **4**: 60; Polyakov, 1960, Fl. Kazakhst. **3**: 20; et al.

T y p u s: "Prov. Lipetsk, ad flum. Tanain (Don) in reservatione naturae "Galitschja Gora", 9.V 1963 leg. S. V. Golitsin" (MW).

HABIT: A medium-sized shrub (1–4 m tall) that appears never to grow as a tree.

HABITATS: River banks and valley meadows in the forest-steppe and steppe belt.

DISTRIBUTION: The forest-steppe and steppe regions of European Russia and Ukraine, including the basins of the Don with Donets and Lower Dnieper in the west. Some isolated fragments are found on the Oka River in Kaluga and Moscow oblasts. The northern area limit is in southern Ryazan Oblast, around Penza and Samara. In the south, the species area reaches the Azov Sea Coast, Kalmykia, and the northern edge of the Ryn Sands. The species is found in the Southern Urals reaching as far north as the Upper Belaya and Uy rivers. Within the forest-steppe and steppe belt of West Siberia and Northern Kazakhstan, the northernmost point is around Kurgan, northeastern limit is the Irtysh River, and southern one matches the southern edge of the Mugodzhary, then running via Karsakpay and the Kzyl-ray Hills. The species also occurs in the Chingiz-Tau Hills and Tarbagatay. (Fig. 62.)

119. **S. elbursensis** Boiss. 1853, Diagn. **12**: 117 (sphalma typographicum: "*elbrusensis*"); Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR **15**: 134; id. 1966, Novosti sist. vyssh. rast.: 58. —*S. purpurea* auct. omnium florum Caucasicae necnon Iranicae, non L. —*S. tenuijulis* Goerz, 1930, in Grossheim, Fl. Kavk. **2**: 10; id. 1930, Feddes Repert. **28**: 128; id. 1934, ibid. **36**: 30, 238. — Non *S. tenuijulis* Ledeb. — *S. ledebourana* auct. non Trautv.: Görz, 1930, op. cit. **28**: 128; id. 1934, ibid. **36**: 239. — Non *S. ledebourana* Trautv. — *S. roopii* Grossh. 1945, Fl. Kavk. 2 ed. **2**: 23.

T y p u s: "In Monte Elburs prope Derbend. 15.V 1843. —T. Kotschy, Pl. Pers. bor. N 154" (LE! JE! W! et alibi).

HABIT: A medium-sized or large shrub that may as well grow as a tree to 8–10 m tall if there is no major damage.

HABITATS: Banks of rivers and streams, bottoms of hollows, ravines, and valleys with sufficient water supply.

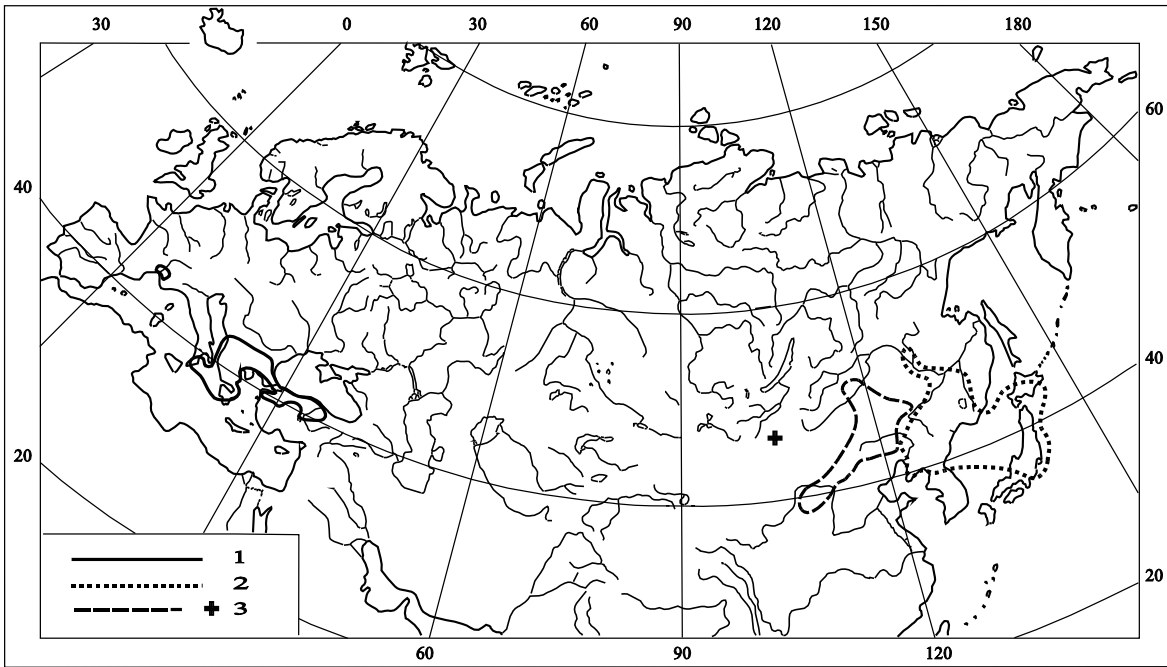


Fig. 63. Distributional areas of *Salix amplexicaulis* Bory et Chaubard (1), *S. integra* Thunb. (2), and *S. gordejvii* Chang et Skvortz. (3)

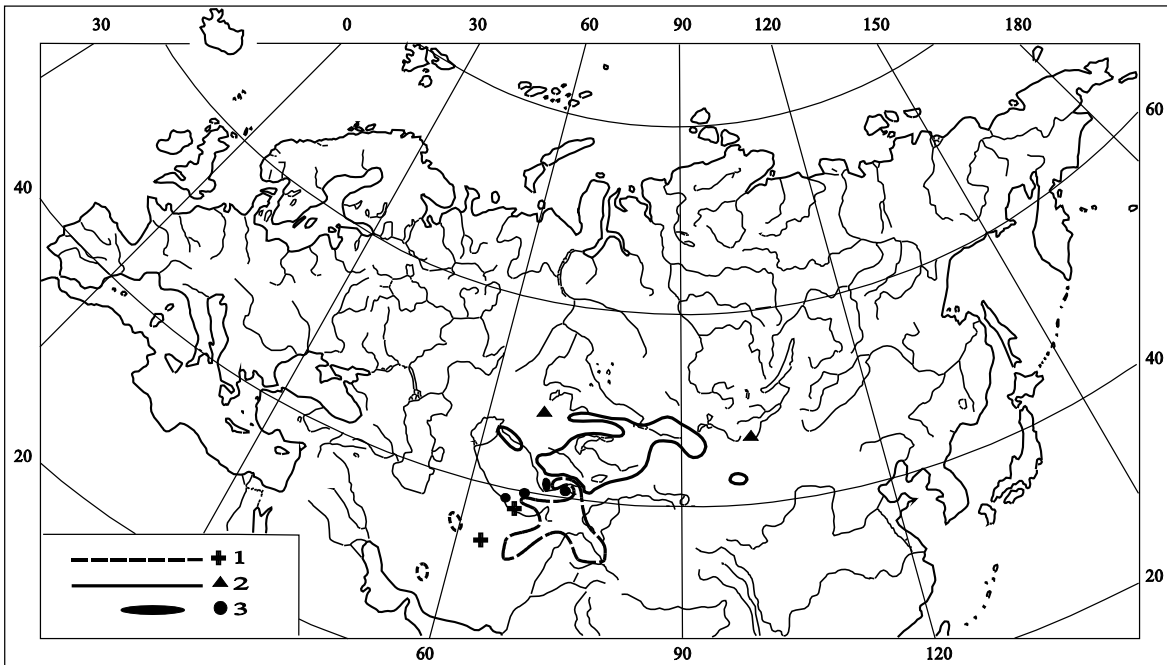


Fig. 64. Distributional areas of *Salix pycnostachya* Anderss. (1), *S. tenuijulis* Ledeb. (2), and *S. olgae* Rgl. (3)

DISTRIBUTION: From the sea level to the upper forest zone (reaching 1,800 m in the Greater Caucasus and 2,000–2,100 m in Armenia). Being encountered across nearly all of the Caucasus, it is more rare in damp, thickly forested areas and more common in dryer ones, such as Kakheta, Armenia, and Azerbaijan. Within Azerbaijan, it has not been found along the Kura River; neither did I manage to identify any samples from Adzharia and Talysh. Within Asia Minor, it is found only in the eastern part: the eastern Gü mü shane (along the Coroch River), Erzurum, Kars, Van, and Agri provinces of Turkey; the Elburz and Zagros Mountains in Iran. It might also be distributed in Iranian Azerbaijan, but there is no evidence from there. (Fig. 62.)

120. *S. miyabeana* Seemen, 1896, Bot. Jahrb. Beibl. **53**: 50; id. 1903, Salic. Jap.: 57 et tab. 12 fig. A-E; Tokubuchi, 1896, Bot. Mag. Tokyo **10**: 69; Miyabe, Kudo 1921, Ic. forest tr. Hokk. **1**: N 19; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 435; Hao, 1936, Syn. Chin. *Salix*: 113; Ohwi, 1965, Fl. Jap.: 368; Skvortsov, 1966, Novosti sist. vyssh. rast.: 59. —*S. purpurea* auct. fl. Asiae Orient. non L.: Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 375; Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 167, p. p.; Hao, 1936, op. cit.: 114. —*S. purpurea* var. *stipularis* Franch. 1884, Pl. David. **1**: 284. —*S. purpurea* var. *smithiana* (non Trautv.) Nakai, 1930, Fl. sylv. Kor. **18**: 115; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 185. —*S. lepidostachya*, Seemen, 1896, Bot. Jahrb. Beibl. **53**: 51; id. 1903, op. cit.: 58; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 425; Nazarov, 1936, Fl. SSSR **5**: 195; Liou Tchen ngo, 1955, op. cit.: 186. —*S. tenuifolia* (non Smith, 1792) Turcz. ex Wolf 1903, Trudy SPb. bot. sada **21**, 2: 145; Lakschewitz, 1914, Spisok rast. Gerb. russk. fl. **50**: N 2497, 2498; Komarov, Alisova, 1931, op. cit. **1**: 423; Nazarov, 1936, op. cit. **5**: 154; id. 1937, Fl. Zabayk. **3**: 222; Liou Tchen ngo, 1955, op. cit.: 182; Popov, 1959, Fl. Sredn. Sib. **2**: 798. —*S. mongolica* Siuzev, 1912, Trudy Bot. muz. **9**: 90, 135; Komarov, Alisova, 1931, op. cit. **1**: 423; Nazarov, 1936, op. cit. **5**: 156; Liou Tchen ngo, 1955, op. cit.: 179. —*S. dahurica* Turcz. ex Lakschewitz, 1914, op. cit. **50**: N 2496; Komarov, Alisova, 1931, op. cit. **1**: 423; Nazarov, 1936, op. cit. **5**: 155; id. 1937, op. cit. **3**: 220; Liou Tchen ngo, 1955, op. cit.: 185; Popov, 1959, op. cit. **2**: 798. —*S. linearistipularis* Hao, 1936, op. cit.: 102. —*S. gracilior* Nakai, 1936, Rep. First Sci. exped. Manch. 4, **4**: 7. —*S. neotenuifolia* Kimura, 1946, Symb. Iteol. **9**: 85. —*S. sungkianica* Chou et Skvortz. 1955, in Liou Tchen ngo, op. cit.: 552.

T y p u s: "Yezo, prov. Ishikari, Sapporo —a. 1891 leg. Y. Tokubuchi" (B, SAP, n. v.). Specimina authentica depicta: Tokubuchi, 1896, op. cit. tab. 6 —optime; Seemen, 1903, op. cit. tab. 12 fig. A-E —sat bene; Hao, 1936, op. cit. fig. 86 —sat bene.

HABIT: A tall shrub or small tree.

HABITATS: Banks of rivers and streams, flood plains, damp meadows (exhibiting no restriction to alluvial substrates, but on the other hand, no tolerance to water stagnation). The species does not go in the mountains any further than low elevations.

DISTRIBUTION. The northern area boundary runs along the line connecting Irkutsk, the Barguzin River, Chita, Dzhalinga, Svobodnyy on the Zeya, and finally reaching the Iman River (a tributary of the Ussury). The species area includes southernmost Sakhalin, Hokkaido, the northern part of Honshu, the northwestern Korea Peninsula, all of Northeast and North China (Shaanxi, Shanxi, Hopeh, Honan, Shantung, and Suiyuan provinces). It is rather sparsely distributed across northern Mongolia reaching Tsetserlig in the west. In North China, it is encountered mostly as a cultivated plant. T. Nakai (1930: 207) listed this species for the territories of the Amgun and Uda basins, which was definitely a mistake.

On a previous map compiled by the author (Skvortsov 1966), the western area boundary within Mongolia was treated as approximate, shown as a dotted line. Some additional material from the eastern Mongolia and Outer Mongolia has made it possible to draw that segment of the boundary more precisely. (Fig. 62.)

121. **S. amplexicaulis** Bory et Chaubard, 1832, Expéd. sci. Morée, **3**, 2: 277; id. 1838, Nouv. fl. Pelop.: 64; Halácsy, 1904, Consp. fl. Graec. **3**: 138; Rech. f. 1943, Fl. Aegaea: 95; Skvortsov, 1966, Trudy Bot. in-ta AN ArmSSR **15**: 133. —*S. purpurea* var. vel ssp. *amplexicaulis* auct.: Boiss. 1879, Fl. Or. **4**: 1186; Hayek, 1924, Prodr. Balc. **1**: 87; Görz, 1930, Feddes Repert. **28**: 128.

T y p u s: "Graecia, Morea, leg. J. B. M. Bory" (P, n. v.).

HABIT: A medium-sized or tall shrub.

HABITATS: River valleys, banks of streams.

DISTRIBUTION: Calabria, the southern Balkan Peninsula (including Albania, Macedonia, and central Bulgaria), northwestern Asia Minor, southeastern France (a fragmentary part, its shape not yet known). (Fig. 63.)

The vertical range is from nearly the sea level to 1,100–1,200 m in Greece and 1,700–1,800 m in Asia Minor.

122. **S. integra** Thunb. 1784, Fl. Jap.: 24; Sieb. et Zucc. 1846, Fl. Jap. fam. **4**: 211; Nakai, 1930, Fl. sylv. Kor. **18**: 113; Komarov, Alisova, 1931, Opred. rast. Dalnevost. kr. **1**: 425; Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 434; Nazarov, 1936, Fl. SSSR **5**: 179; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 173; Ohwi, 1965, Fl. Jap.: 367. —*S. purpurea* auct. non L.: Franch. et Sav. 1875, Enum. Jap. **1**: 462; Seemen, 1903, Salic. Jap.: 55 (p. p.). —*S. purpurea* ssp. *amplexicaulis* var. *multinervis* Schneider, 1916, in Sarg. Pl. Wilson. **3**, 1: 168. —*S. multinervis* Franch. et Sav. 1876, op. cit. **2**, 1: 504; Komarov, 1903, Trudy SPb. bot. sada **2**: 25; Hao, 1936, Syn. Chin. *Salix*: 114. —*S. savatieri* Camus, 1904, Saul. Eur. **1**: 326.

T y p u s: "Japonia. Thunberg" (UPS, n. v.).

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HABIT: A medium-sized shrub (1–4 m). In damp hay-meadows on bottoms and slopes of large *pad'*s, it often has a suppressed habit growing not taller than 0.3–0.8 m due to annual mowing (the same habit is exhibited by *S. brachypoda* and *S. bebbiana*).

HABITATS: Damp lowlands. The species is tolerant to some paludification, at the same time, staying away from alluvial river deposits, particularly fresh ones, so that it is never found close to the flowing water. In the southern Sikhote-Alin, it occurs in damp logged areas and secondary meadows, ascending to 800 m. In China (Liaoning Province), it is encountered at the same height.

DISTRIBUTION: Southern Amur Oblast (going up the Amur to Korsakov and up the Zeya to the mouth of the Tygda); Birobidzhan; the Ussuri Valley (?except the lower reaches) and southern Maritime Province (reaching the Sudzukhe River in the east); the southeastern part of Northeast China; the northern Korea Peninsula (reaching Pyongyang in the south); Hokkaido and the major part of Honshu. (Fig. 63.)

123. **S. gilgiana** Seemen, 1903, Salic. Jap.: 59 et tab. 13 fig. A-D; Schneider, 1916, in Sarg. Pl. Wilson. **3**: 169; Nakai, 1930, Fl. sylv. Kor. **18**: 112 (p. p. —cf. adnot. nostram); Kimura, 1934, in Miyabe, Kudo, Fl. Hokk. a. Saghal. **4**: 437; Makino, 1956, Fl. Jap.: 671; Ohwi, 1965, Fl. Jap.: 368; Skvortsov, 1966, Novosti sist. vyssh. rast.: 63. —*S. purpurea* var. *sericea* (non Wimmer) Seemen, 1903, op. cit.: 56; Koidzumi, 1913, Bot. Mag. Tokyo **27**: 92; Schneider, 1916, op. cit. **3**, 1: 167.

T y p u s: "Japonia, Yedo, 15.III, 23.IV, 8.VI 1874 leg. Hilgendorf" [KYO et olim (et nunc?) etiam B] N. v.

HABIT: A tall shrub.

HABITATS: Damp meadows, banks of streams.

DISTRIBUTION: Japan (Hokkaido, Honshu, Shikoku, and Kyushu); the Korea Peninsula. T. Nakai (1930: 212) also listed this species for southern Maritime Province, however, it is missing from there. He could mistakenly treat samples of *S. miyabeana* with fully developed styles as those of *S. gilgiana*. Japanese authors never listed this species for the Kurils. However, *S. gilgiana* was collected on Zelenyy Island by N. Popov and A. Chernyayeva in 1960 (the Herbarium of the Sakhalin Science Institute).

Subsect. *Tenuijules*

A. Skv. Novosti sist. vyssh. rast. a. 1968 describetur.

Tall shrubs or trees growing on alluvia in arid regions. Floriferous buds greatly different from vegetative ones. Stipules usually fully developed. Petioles relatively long (6–15 mm); leaf blades (linear-)lanceolate, broadest about middle. Catkins precocious or subprecocious. Nectary yellowish-olivaceous. Capsules short-stalked, lanceolate, acute, mature ones 5–7 mm long.

T y p u s: *Salix tenuijulis* Ledeb.

124. **S. tenuijulis** Ledeb. 1833, Fl. Alt. **4**: 262; id. 1834, Icon. **5**: 16 et tab. 453; Wolf, 1903, Trudy SPb. bot. sada **21**: 146; Krylov, 1930, Fl. Zap. Sib. **4**: 740; Pavlov, 1935, Fl. Ts. Kazakhst. **2**: 30; Nazarov, 1936, Fl. SSSR **5**: 158; Polyakov, 1960, Fl. Kazakhst. **3**: 21; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 69. — *S. regelii* Anderss. 1868, in DC. Prodr. **16**, 2: 309. — *S. albertii* Rgl. 1880, Acta Horti Petropol. **6**: 462; Nazarov, 1936, op. cit. **5**: 172. — *S. serrulatifolia*, E. Wolf, 1903, op. cit. **21**: 163; Nazarov, 1936, op. cit. **5**: 165; Polyakov, 1960, op. cit.: 24. — *S. przewalskii* E. Wolf, 1907, Izv. Lesn. in-ta **15**: 179 et tabl.; Nazarov, 1936, op. cit. **5**: 169. — *S. verticilliflora* E. Wolf, 1909, Trudy SPb. bot. sada **28**: 400. — *S. spinidens* E. Wolf, 1909, op. cit. **28**: 403; Nazarov, 1936, op. cit. **5**: 161; Polyakov, 1960, op. cit. **3**: 22.

T y p u s: "In arenosis ad fl. Bekun et Kurtschum. —C. A. Meyer" (LE?). I did not have a chance to see that sample; probably, it is lost. If that is the case, then it is reasonable to consider an excellent image in C. Ledebour's work as the type. 231

HABIT: A tall shrub (to 6 m) or wide-crowned tree (to 6–8 m).

HABITATS: *Tugai* along rivers, bottoms of *sai* at places where ground waters come to the surface or near underground streams. The species is associated with pebbly, sandy, and sometimes muddy-clayey substrate.

DISTRIBUTION: The southern Kazakh Uplands and northern coast of Lake Balkhash (occasionally). It becomes rather common south of Zaysan and Balkhash, along rivers from their mouths to elevations of 2,000–2,200 m (to 2,400 m at the Upper Chilik). It is particularly common in the basins of the Lepsa, Karatal, and Ili. The southwestern border of the species high occurrence area runs via Naryn, the Koke-Meren, Susamyr, and Upper Talas rivers and then across the Boroldaytau. It is sporadically encountered all across the Karatau and at the Lower Syr Darya downstream of Kzyl-Orda. It has never been found at the middle reaches of the Syr Darya, nor along the Arys. Within the Altai Mountains, it is

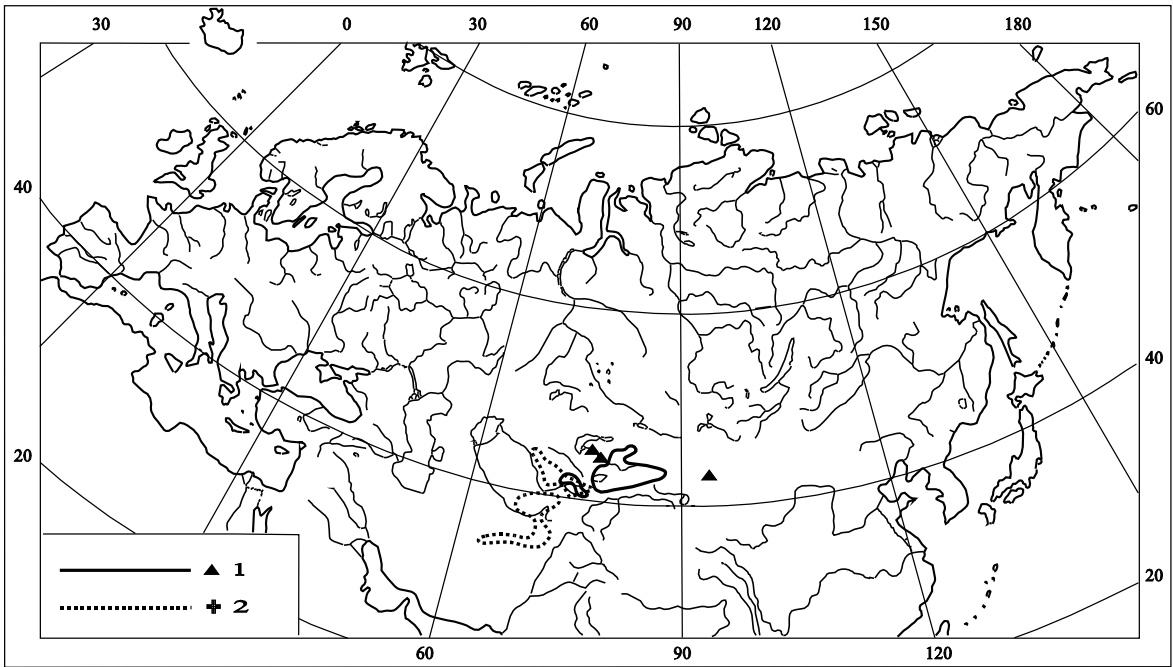


Fig. 65. Distributional areas of *Salix linearifolia* E. Wolf (1) and *S. kirilowiana* Stscheegl. (2)

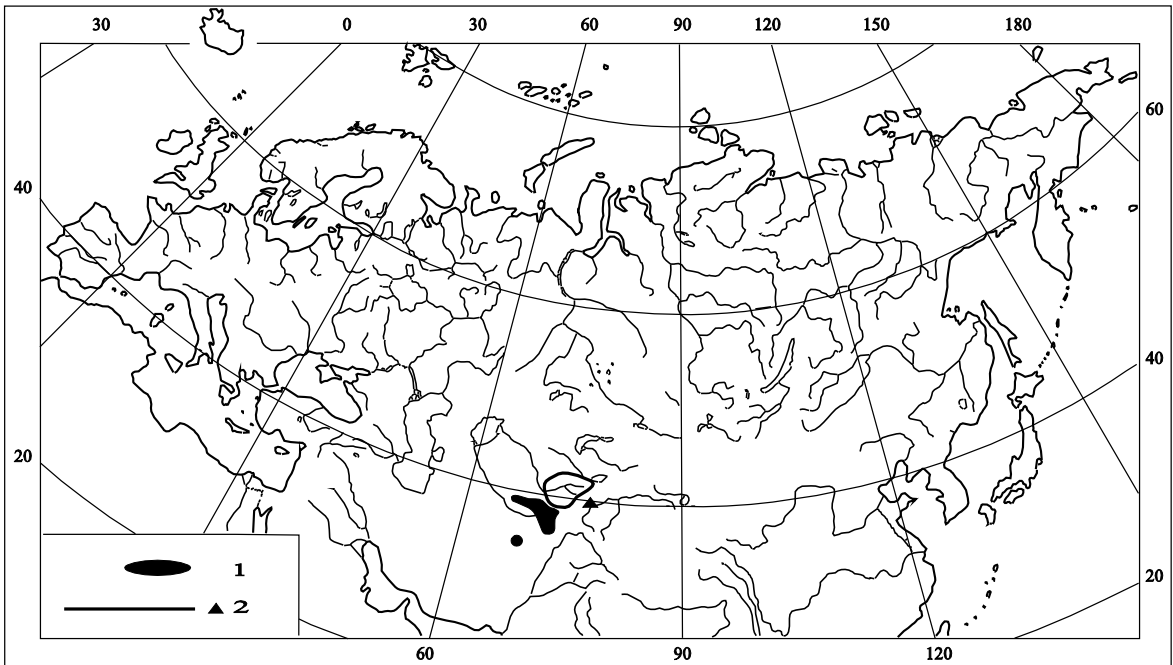


Fig. 66. Distributional areas of *Salix capusii* Franch. (1) and *S. niedzwieckii* Goerz (2)

listed only for the extreme southwestern part. The area includes western Sinkiang (primarily, the Ili Basin and the banks of the Black Irtysh); the Mongolian Altai (reaching Trans-Altai Gobi Desert in the southeast); the Khangai (near Zayin-geygen, solitary). (Fig. 64.)

125. *S. pycnostachya* Anderss. 1860, J. Linn. Soc. **4**: 44; id. 1868, in DC. Prodr. **16**, 2: 309; Hook. f. 1890, Fl. Brit. Ind. **5**: 636; Parker, 1924, Forest fl. Punjab: 510; Görz, 1934, Feddes Repert. **36**: 34; Nazarov, 1936, Fl. SSSR **5**: 163; Parsa, 1950, Fl. Iran. **4**: 1359; Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR **20**: 83; id. 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 69; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4548; Ikonnikov, 1963, Opred. rast. Pamira: 90. —*S. sarawschanica* Rgl. 1882, Izv. Ob-va lyubit. yest. **34**, 2: 80; Nazarov, 1936, op. cit. **5**: 160. —*S. iranica*, 1920, Bornm. ex Toepffer, Salic. Exs.: N 471. —*S. margaritifera* E. Wolf, 1903, Trudy SPb. bot sada **21**: 162; Nazarov, 1936, Fl. SSSR **5**: 173. —*S. macrostachya* E. Wolf, 1903, op. cit. **21**: 163; Nazarov, 1936, op. cit. **5**: 172. —*S. komarovii* E. Wolf, 1903, op. cit. **21**: 195; Nazarov, 1936, op. cit. **5**: 166. —*S. holargyrea* Goerz, 1936, Trudy Tadj. bazy **2**: 175. —*S. korshinskyi* Goerz, 1936, op. cit. **2**: 178; Nazarov, 1936, op. cit. **5**: 176. —*S. ferganensis* Nasarov, 1936, op. cit. **5**: 176, 713. —*S. rubrobrunnea* Drobov, 1941, Bot. mat. Bot. in-ta, Tashkent **5**: 15. —*S. pamirica* Drobov, 1941, op. cit. **5**: 16.

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T y p u s: "India, Zanskar, alt. 13000' —Thompson" (K!).

HABIT: A tall shrub or, if there is no damage, a tree, sometimes as tall as 10–12 m and to 40 cm in stem diameter.

HABITATS: Banks of rivers and streams.

DISTRIBUTION: The western ranges of the Tien Shan (the Ferganskiy, Chatkalskiy, Pskemskiy, Ugamskiy, and western Talasskiy ranges, at 1,200–2,500 m); the Pamir-Alay (all the ranges, reaching the Kashka Darya Basin in the west, at 1,400–4,300 m, being especially common in the Pamirs); the Kugitangtau; southern Kashgaria; Kashmir; Afghanistan (at high elevations); Iran (two small locations, one in Khorasan Province in the northeast, another one in the Kuhrud Mountains in the south.) (Fig. 64.)

NOTE. This is one of the most polymorphic willows. Such characters as the leaf breadth, intensiveness of pubescence on leaves and capsules, shoot color, and size of floriferous buds are greatly variable. Differences may be exhibited by individual plants as well as entire populations. Some characteristics appear to be contingent with certain ecological conditions, for example, a very dark color of shoots and rather narrow leaves with scanty pubescence dominate in high-altitude populations. Yet it is impossible to distinguish any particular races or subspecies.

The type of *S. holargyrea* Goerz (from Kulyab: Divnogorskaya) belongs to *S. pycnostachya*; as for other samples cited by R. Görz, they belong to *S. schugnanica*.

126. *S. olgae* Rgl. 1882, Izv. Ob-va lyubit. yest. **34**, 2: 79 (p. p.: quoad pl. 1.IV 1871 Lectas tantum); Wolf, 1903, Trudy SPb. bot. sada **21**: 152 (?); Nazarov, 1936, Fl. SSSR **5**: 170 (p. p.); Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 70; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4549. —*S. pseudalba* E. Wolf, 1903, op. cit. **21**: 167; Nazarov, 1936, op. cit. **5**: 171; Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR **20**: 84. —*S. angrenica* Drobov, 1941, Bot. mat. Bot. in-ta, Tashkent **3**: 22; id. 1953, Fl. Uzb. **2**: 36. —*S. coerulangrenica* Drobov, 1941, op. cit. **3**: 9; id. 1953, op. cit. **2**: 39. —*S. olgangrenica* Drobov, 1941, op. cit. **3**: 9; id. 1953, op. cit. **2**: 47.

T y p u s: "Ad fl. Salar prope Taschkent. 1.IV 1871. O. Fedtschenko" (LE!).

HABIT: A tall shrub or small tree.

HABITATS: River pebbles at low elevations in the mountains and on piedmont plains.

DISTRIBUTION is fairly discontinuous: The Chirchik Basin (along the Chirchik near Tashkent and Gazalkent, rather abundantly at the lower reaches of the Chimganka); the wide stony bottom of the Angren River Valley (extensive thickets); the *tugai* between Almalyk and Angren (the dominating species); the Zeravshan River and Zeravshan(-skiy) Range around Samarkand (sparsely); the vicinity of Kokand; the Karasu River in the Ferganskiy Range (?—only vegetative specimens); the vicinity of Beshir in Chardzhou Oblast. It has never been encountered higher than 1,500 m in the mountains; on the other hand, it is missing from sandy-muddy deposits of lowland rivers. Its scanty area is likely to be attributed to the cutting of *tugai* forests, which has been most intensive at piedmont and low mountain elevations. (Fig. 64.)

127. *S. linearifolia* E. Wolf, 1903, Trudy SPb. bot. sada **21**: 160, cum fig.; Nazarov, 1936, Fl. SSSR **5**: 169; Drobov, 1953, Fl. Uzb. **2**: 43; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 71; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4550. — *S. blakii* Goerz, 1934, Feddes Repert. **36**: 31; Nazarov, 1936, op. cit. **5**: 162; Drobov, 1953, op. cit. **2**: 41; Polyakov, 1960, Fl. Kazakhst. **3**: 23. — *S. olgae* Rgl. 1882, Izv. Obva lyubit. yest. **34**, 2: 79 (p. p.); Drobov, 1941, Bot. mat. Bot. in-ta, Tashkent **5**: 11; id. 1953, op. cit. **2**: 44. — *S. blakolgae* Drobov, 1941, op. cit. **5**: 8. —? *S. tenuijulis* auct. non Ledeb.: Drobov, 1953, op. cit. **2**: 37.

T y p u s: "Hissar montes Babatag prope Akmetset, 1.V 1883. A. Regel" (LE!).

HABIT: A tall shrub or occasionally tree. (In the Zeravshanskiy Range, I have seen specimens to 10 m tall and 25–30 cm in stem diameter).

HABITATS: Banks of streams and rivers in the mountains and piedmont (on pebbly, sandy, and sandy-muddy drifts).

DISTRIBUTION. The northern limit is found in the northernmost Karatau; the eastern border runs via the Susamyr River, Naryn, Daraut-Kurgan, and Vanch; the westernmost localities are around Tashkent, Samarkand, and in the Kugitangtau. The species apparently is missing from lowlands: along the Chirchik, it is found only upstream of Tashkent; along the Arys, only upstream of Tamerlanovka; along the Kashka Darya, only upstream of Kitab, and so on. It is as well missing from the alpine zone (particularly, in the Pamirs), ascending not higher than 2,200 m (sometimes, 2,400 m). Within the territory of Afghanistan, it is distributed in the Paropamisus and western Hindu Kush. (Fig. 65.)

Subsect. *Kirilowianae*

A. Skv. Novosti sist. vyssh. rast. 1968 describetur.

Shrubs or small trees, their shoots slender, smooth, often covered with pruinose bloom. Floriferous buds slightly different from vegetative ones. Stipules usually lacking. Leaves small, dull on both sides, nearly concolorous, pale, bluish. Catkins serotinous, narrowly cylindrical, somewhat loosely flowered. Stamen filaments densely pubescent. Capsules stipitate, small (mature ones 4–6 mm long), mostly acute, conoidal.

T y p u s: *Salix kirilowiana* Stschehl.

128. *S. kirilowiana* Stschehl. 1854, Bull. Soc. Nat. Moscou **27**, 1: 148; Skvortsov, 1960, Bot. mat. Gerb. Bot. in-ta AN SSSR **20**: 80; id. 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 72; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4544. — *S. alba-*

viminalis Rgl. 1880, Acta Horti Petropol. **6**: 460. —*S. issykiensis* Goerz ex Nasarov, 1936, Fl. SSSR **5**: 712. —*S. lipskyi* Nasarov, 1936, op. cit. **5**: 712; Polyakov, 1960, Fl. Kazakhst. **3**: 25. —*S. niedzwieckii* auct. non Goerz: Polyakov, 1960, op. cit. **3**: 23 (p. p.). —*S. coerulea* auct. non E. Wolf: Polyakov, 1960, op. cit. **3**: 22 (p. p.).

T y p u s: "In montosis Alatau ad fl. Lepsa et Sarchan, a. 1841 Karelin et Kirilow N 1967; a. 1842 et 1844 Karelin" (LE!).

HABIT: A tall shrub or small, short-stemmed tree with a wide round crown (to 6–8 m tall).

HABITATS: Banks of mountain streams and rivers, screes and taluses, deluvial cones, etc. (either on coarse pebbles or at places where ground waters reach the surface). Being characteristic of intermediate elevations, it may also descend to lowlands along large rivers. The upper limit is at 2,500 m.

DISTRIBUTION: The Saur Range; the entire Eastern Tien Shan including its Kazakh, Kirghiz, and Chinese parts as well as an isolated Karlyktag Massif near Hami. The western limit of the species continuous distribution matches that of the spruce forests. West of that boundary, it occurs rather sparsely, reaching the Talasskiy and Chatkalskiy ranges. There are some few localities at the lower reaches of the Ili. The species is not found on the territory of the Pamir-Alay System. (Fig. 65.)

129. **S. niedzwieckii** Goerz, 1931, Salic. Asiat. **1**: 18; id. 1933, Feddes Repert. **32**: 120; Nazarov, 1936, Fl. SSSR **5**: 161 (p. p.); Drobov, 1953, Fl. Uzb. **2**: 39; Protopopov, 1953, Fl. Kirg. **4**: 25; Polyakov, 1960, Fl. Kazakhst. **3**: 23 (p. p.); Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 72; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4545. —*S. olgae* Rgl. 1882, Izv. Ob-va lyubit. yest. **34**, 2: 79 (p. p.). —*S. coeruleiformis* Drobov, 1941, Bot. mat. Bot. in-ta, Tashkent **3**: 22; id. 1953, op. cit. **2**: 39 et tab. 1 fig. 1. —*S. coerulea* auct. non E. Wolf: Polyakov, 1960, op. cit. **3**: 22 (p. p.).

T y p u s: "Ad fl. Tschimganka 1.V 1921 leg. P. Gomolitzky (Goerz Sal. Asiat. N 19 et 20) (LE! TAK! et alibi).

HABIT: A small tree to 6–8 m tall.

HABITATS: River banks (mostly on coarse pebbles). It is encountered more often at intermediate mountain elevations (1,000–2,500 m); however, it may descend to piedmont plains along rivers.

DISTRIBUTION: The Western Tien Shan including Angren, Tashkent, Lenger, Dzhambul, and Gulyayevka on the Chu (rather frequently); the Central Tien Shan (less frequently, reaching the southwestern shore of Issyk-Kul, the Town of Naryn and apparently missing from the Susamyr and Upper Talas); the eastern and southern Ferganskaya Valley, Ferganskiy and Alayskiy ranges (again becoming more common). The westernmost part of the area includes the Karavshin and Isfara basins; the southern limit is near Daraut-Kurgan and on the northern slopes of the Zaalayskiy Range (Altynmazar) and the Range of Peter I (Sarykosh). Within Kashgaria, it is found in the Kyzylsu Basin upstream of Kashgar. (Fig. 66.)

130. **S. capusii** Franch. 1884, Ann. Sci. Natur. **6**, **18**: 251; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR **17**: 73; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4546. —*S. coerulea* E. Wolf, 1903, Trudy SPb. bot. sada **21**: 157, cum fig. (non Smith 1812); Nazarov, 1936, Fl. SSSR **5**: 159; Drobov, 1953, Fl. Uzb. **2**: 38. —Non *S. coerulea* auct.: Polyakov, 1960, Fl. Kazakhst. **3**: 22. —*S. egberti-wolfii* Toepffer, 1916, Öst. bot. Z. **66**: 402.

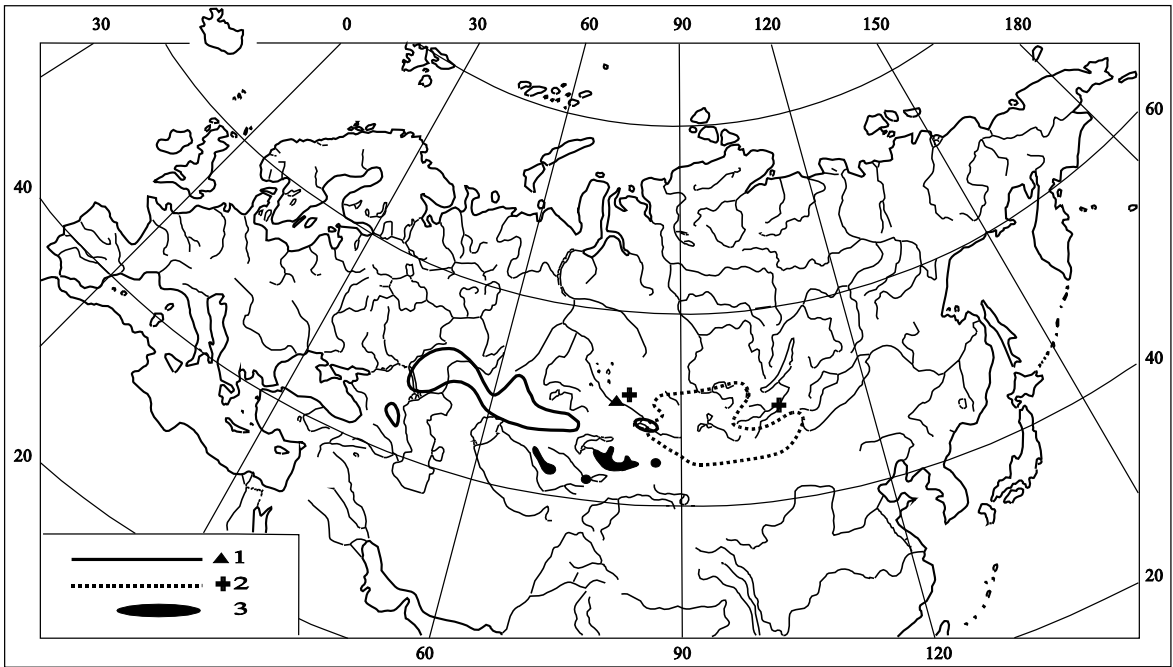


Fig. 67. Distributional areas of *Salix caspica* Pall. (1), *S. ledebourana* Trautv. (2), and *S. michelsonii* Goerz ex Nas. (3)

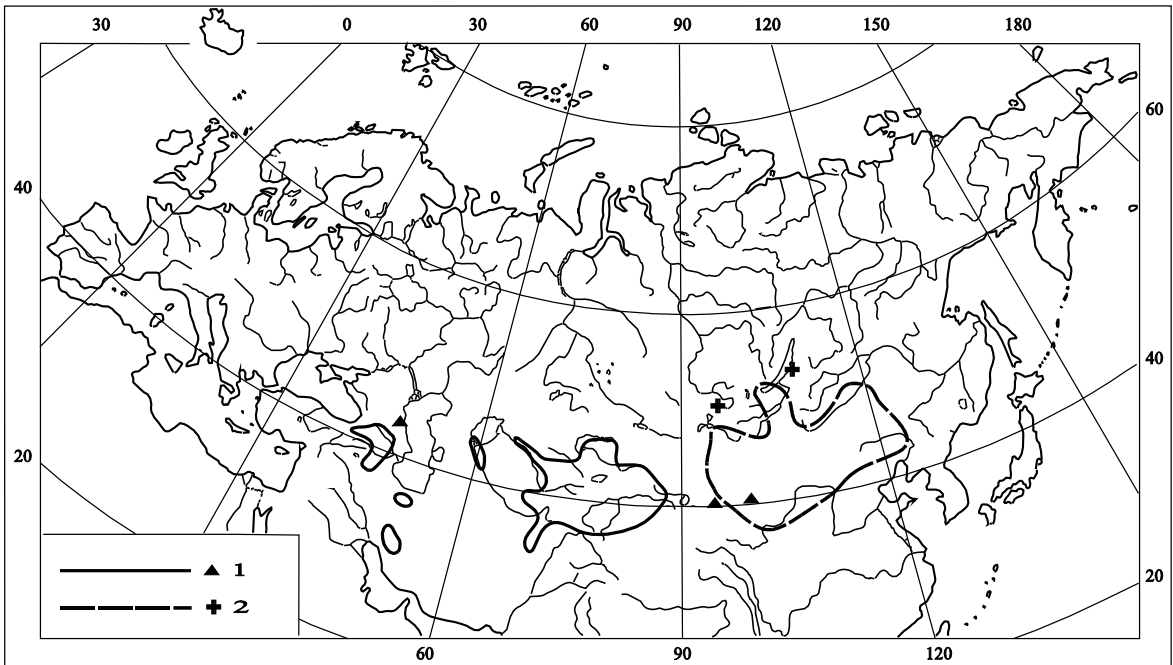


Fig. 68. Distributional areas of *Salix wilhelmsiana* M. B. (1) and *S. microstachya* Turcz. ex Trautv. (2)

T y p u s: "Bords du Zeravchane près de Dardar, 17.VI 1881 Capus N 1200; Iskanderkoul 7.VII id N 1201" (P!; N 1201 etiam LE!).

HABIT: A small tree with a wide crown to 6–8 m tall or a wide, spreading, dense shrub.

HABITATS: Banks of rivers and streams; *sai* and irrigation ditches. The elevation range is from nearly the lowland to 3,400 m.

DISTRIBUTION: The Zeravshan Basin (along the Zeravshan from Matcha to Samarkand); the Gissar(-skiy) Range (seldom, reaching the border with Uzbekistan in the west); the Vaksh(-skiy) Range; the Darvaz(-skiy) Range (reaching Kulyab in the west); the Western Pamirs (in the east reaching Lake Sarezskoye, the Gunt River at the confluence with the Tokuzbulak, and the Upper Pyandzh). In the Hindu Kush, it is found on the territory of Afghanistan as well as northwestern Pakistan. (Fig. 66.)

131. **S. michelsonii** Goerz ex Nasarov, 1936, Fl. SSSR 5: 711; Skvortsov, 1962, Bot. mat. Gerb. In-ta bot. AN UzbSSR 17: 71; id. 1966, Spisok rast. Gerb. fl. SSSR 91: N 4543. —*S. caspica* var. *michelsonii* Poljakov, 1963, Fl. Kazakhst. 3: 21.

T y p u s: "Dsharkent (nunc Panfilov), limen Dshijdelik 2.VIII 1910 A. Michelson, N 2494" (LE!).

HABIT: A tall shrub, its branches spreading in different directions.

HABITATS: *Tugai* along rivers (mostly on the sand and fine pebbles) on the plain or at low elevations in the mountains (not higher than 1,400–1,500 m).

DISTRIBUTION: The Karatau from Turkestan District to Dzhambul (sparsely); Buam(-skoye) Gorge (the Chu River); the Ili Basin, particularly, the Ili River upstream of Bakanas and its tributaries, such as the Kunges, Charyn, and Chilik (much more frequently). North and east of that territory, along the Aksu and Borotala rivers at the northern and southern foothills of the Dzungarskiy Alatau, the species is distributed more sparsely. In Chinese Dzungaria, it has been found near Manas. (Fig. 67.)

132. **S. caspica** Pall. 1788, Fl. Ross. 1, 2: 74; Trautv. 1876, Salicetum: 27; Ledeb. 1850, Fl. Ross. 3, 2: 604; Wolf, 1909, Trudy SPb. bot. sada 28, 3: 405; id. 1930, Fl. Yu.-V. 4: 61; Nazarov, 1936, Fl. SSSR 5: 157 (p. p.: excl. syn. *S. ledebourana* Trautv.); Grossheim, 1945, Fl. Kavk. 3: 23 (p. p.: excl. pl. e reg. Colch. et Iran); Ivanov, 1949, Opred. der. i kustarn. Zap. Kazakhst.: 31; Polyakov, 1960, Fl. Kazakhst. 3: 20 (p. p.: excl. var. *michelsonii*); Sergiyevskaya, 1961, Fl. Zap. Sib. 12: 3221; Rech. f. 1964, Fl. Eur. 1: 53.

T y p u s: "In arenis inter australem Volgam et Rhyminum... itaque ad Sarpa et Kuma". In St. Petersburg, there is a sample labeled "Ryn-peski. Pallas" ("The Ryn Sands. Pallas") (!), and obviously there is a good reason to consider it as the holotype.

HABIT: A shrub or small tree (to 4–5 m tall) in favorable conditions.

HABITATS: Hillocky sand in steppes and semi-deserts.

DISTRIBUTION: The eastern part of the Northern Caucasus; the Volga-Ural Sands; the middle reaches of the Ural (occasionally), Yeruslan River, and Buzulukskiy Bor; sandy territories of Northern Kazakhstan. It appears to be distributed across all of sand areas that are large enough, however, according to the data available so far, rather sparsely and discontinuously. The southern area limit is found on the northern coast of the Aral Sea, in northern Betpak-dala, and near Lake Balkhash; the northernmost point is near Kushmurun; the easternmost one is at Zaysan(-skaya) Depression. (Fig. 67.)

NOTE. The species has been frequently confused with *S. vinogradovii* ("*S. purpurea*" auct.), both in the literature and herbaria. Particularly, N. Pavlov (1935: 29) and P. Polyakov (1960: 20) assigned a considerable number of *S. vinogradovii* samples to *S. caspica*. V. Ivanov (1949) succeeded much more in the delimitation of these species. He articulated very well the major ecological difference between the species, that is, the confinement of *S. vinogradovii* to river banks and *S. caspica* to hilly sand areas. However, another statement made by V. Ivanov as well as preceding authors about "an extraordinary ability" of *S. caspica* to tolerate high soil salinity appears to be doubtful. As far as one can judge relying on the range of known habitats, the one exhibiting more salinization tolerance is *S. vinogradovii* rather than *S. caspica*. *S. vinogradovii* has been frequently found amidst subsaline meadows on soils of considerable salinity.

237 133. **S. ledebourana** Trautv. 1836, Salicetum: 25 (nom. nov. pro *S. pallida* Ledeb. non Salisb. 1796 nec H. B. K.); Ledeb. 1850, Fl. Ross. **3**, 2: 603; Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 337; Wolf, 1903, Trudy SPb. bot. sada **21**: 150; Krylov, 1930, Fl. Zap. Sib. **4**: 739 (p. p. ?); Sergiyevskaya, 1961, Fl. Zap. Sib. **12**: 3221; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 86. —*S. pallida* Ledeb. 1833, Fl. Alt. **4**: 261; id. 1834, Icon. **5**: 16 et tab. 454 (non *S. pallida* Salisb. 1796, Prodr. Allert.: 394). —*S. caspica* auct. (quoad pl. altaicas, sajanens. et mongolicas) non Pall.: Nazarov, 1936, Fl. SSSR **5**: 157; Sobolevskaya, 1953, Konsp. fl. Tuvy: 65; Grubov, 1955, Konsp. fl. Mong.: 99.

T y p u s: "In insulis fl. Tschuja —Bunge" (LE!).

HABIT: A medium-sized or tall shrub (to 4–5 m), its branches spreading.

HABITATS: River banks, valley meadows, sometimes considerably subsaline.

DISTRIBUTION: The Saur Piedmont; valley steppes in the Altai (particularly common in Chuyskaya Steppe), southern and central Tuva, and the major part of Mongolia (reaching the Upper Kerulen in the east). The only places within the Russian territory east of Tuva where the species is found are the Oka River in the Eastern Sayans and the vicinity of Kyakhta. M. Nazarov listed this species in his "Flora of Transbaykalia" (3: 222) for the basins of the Barguzin and Uda in Buryatia and the Nercha Basin in Dahuria, yet this is not supported by any collected material.

The species ascends to 1,700 m in the Altai; to 2,200 m, in southern Tuva; in Mongolia, it has been encountered even higher than that. (Fig. 67.)

Sect. 26. *Cheilophilae*

Hao, 1936, Syn. Chin. *Salix*: 102, emend. A. Skv.

T y p u s: *Salix cheilophila* Schneid. (sec. Hao, l. c.).

Medium-sized or rather tall shrubs, occasionally small trees. Shoots slender, multifoliate, young ones mostly covered with silky, appressed trichomes. Leaves on very short petioles (1–3 mm), small (10–60 × 3–8 mm), dirty green, more or less covered with silky, appressed pubescence. Catkins serotinous, short (15–50 mm long), cylindrical, their rachises densely white pubescent, bracts obtuse, pale, persistent. Nectary solitary, trapeziform or narrowly triangular, mostly colored. Stamen filaments entirely connate, glabrous. Capsules small, sessile, styles and stigmas short.

This is a small Asiatic group. Besides the two species described here, there are two Chinese ones: *S. cheilophila* Schneid. distributed in the central, arid regions of China and *S. variegata* Franch. from South China.

Key to Species

1. Shrub, its branches vigorously spreading in different directions at nearly right angles, shoots arching. Leaves 3–4 (–5) mm broad. Ovaries clothed with dense, compact, silky pubescence 134. **S. wilhelmsiana**
— Shrub not exhibiting any unusual branching habit or small tree. Leaves 4–6 mm broad. Ovaries glabrous 135. **S. microstachya**

134. **S. wilhelmsiana** Marschall a. Bieberstein, 1819, Fl. Taur.-Cauc. **3**: 627; Trautv. 1836, Salicetum: 21 et tab. 3; Wolf, 1903, Trudy SPb. bot. sada **21**: 153; Görz, 1934, Feddes Repert. **36**: 28, 29; Nazarov, 1936, Fl. SSSR **5**: 164; Grossheim, 1945, Fl. Kavk. **3**: 23; Drobov, 1953, Fl. Uzb. **2**: 43; Polyakov, 1960, Fl. Kazakhst. **3**: 23; Skvortsov, 1962, Bot. mat. Gerb. Bot. in-ta AN UzbSSR **17**: 73; id. 1966, Trudy Bot. in-ta AN ArmSSR **15**: 135; id. 1966, Spisok rast. Gerb. fl. SSSR **91**: N 4547. —*S. angustifolia* Willd. 1806, Sp. pl. **4**, 2: 699; M. B. 1808, Fl. Taur.-Cauc. **2**: 414; Ledeb. 1850, Fl. Ross. **3**, 2: 604 (p. p.); Boiss. 1879, Fl. Or. **4**: 1184. —Non *S. angustifolia* Wulfen, 1789, in Jacquin, Collect. bot. **3**: 48. —*S. dracunculifolia* Boiss. 1846, Diagn. **7**: 99. —*S. trautvetteriana* Rgl. 1880, Acta Horti Petropol. **6**, 2: 465.

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T y p u s: "Iberia —Wilhelms" (LE!).

HABIT: A shrub with vigorously spreading branches, to 4–5 m tall, greatly resembling the sea buckthorn (*Hippophaë rhamnoides*) and often growing together with it.

HABITATS: Sandy or clayey-loamy-sandy river deposits, from lowland to alpine elevations.

DISTRIBUTION. The species area consists of two isolated parts: Caucasian-Iranian and Middle Asian. The Caucasian-Iranian part includes the eastern arid regions of the Caucasus (where the species is rather sparse): the Kura Valley from the Lower Aragva to Lower Iori and Gäncä (formerly Kirovabad); Nahichevan Republic and Armenia: the Debed River and Mount Bogutli (some solitary findings); eastern Turkey: Olti, Bayburt on the Coroch, the Zab River in Hakkâ ri Province (rarely); the arid northwestern part of Iranian Azerbaijan; the western Elburz and Zagros (occasionally). The species is missing from the eastern half of Iran and all of Turkmenia. It is common in northeastern Afghanistan (the Hindu Kush). Not infrequently, it is found in Kashgaria, in the mountains as well as lowland (along the Tarim River); some solitary findings have been reported from the Karakorum (Baltistan). Within the territory of the Middle Asia, it is very common at the lower reaches and estuary of the Amu Darya and in the Sultanuzdag Mountains; it is also encountered along the Syr Darya from Yany-Kurgan to Dzhusaly and occasionally in the Karatau. East of the Kafirnigan River, Shakhriyabz, Samarkand, Tashkent, and Chimkent, the distributional area becomes nearly continuous, reaching the Lepsa River in the east and the Lower Talas and Lake Balkhash in the north. Along the Ili and Kunges rivers, the species extends its area to Chinese Dzungaria.

In the Caucasus, it does not ascend higher than 1,500 m; in the Tien Shan, it goes up to 2,200 m; in the Pamirs, to 3,500 m; in the Karakorum, even to 3,600 m. (Fig. 68.)

NOTE. In Kashgaria, within the Upper Ili Basin including its Kazakh part, there occur some specimens resembling *S. microstachya* either in their glabrous capsules or tree-like habit. Such specimens, for example, have been found in Sarytogoy on the Charyn (see the note to *S. microstachya* description).

135. *S. microstachya* Turcz. ex Trautv. 1836, Salicetum: 22 et tab. 4; Turcz. 1854, Fl. Baic.-Dah. **2**, 2: 377; Wolf, 1903, Trudy SPb. bot. sada **21**: 156; Nazarov, 1936, Fl. SSSR **5**: 136; id. 1937, Fl. Zabayk. **3**: 223; Hao, 1936, Syn. Chin. *Salix*: 103; Liou Tchen ngo, 1955, Ill. Fl. Tr. Shr. Northeast China: 178; Grubov, 1955, Kosp. fl. Mong.: 101; Popov, 1959, Fl. Sredn. Sib. **2**: 797; Koropachinskiy, Skvortsova, 1966, Der. i kustarn. Tuvy: 87. — *S. angustifolia* β *leiocarpa* Ledeb. 1850, Fl. Ross. **3**, 2: 604. — *S. stenophylla* Sukacz. 1931, Trudy issled. po lesn. op. delu **10**: 13, 20 cum fig. — *S. bordensis* Nakai, 1936, Rep. First Sci. Exped. Manch. 4 sect. **4**: 74.

T y p u s: "In sabulosis ad fl. Irkut. —Turczaninow" (LE!).

HABIT: A shrub or small tree.

HABITATS: Sandy river banks; occasionally, sandy areas apart from any rivers or streams.

DISTRIBUTION: Within the Russian territory, only southern Tuva, Prebaykalia (around Irkutsk, in Tunkinskaya Valley, along the Barguzin, in the Selenga Basin upstream of Ulan Ude), and southern Dahuria. The area includes Mongolia; the eastern and southeastern part of Northeast China; Jehol; Ordos; Gansu Province; ?Kashgaria (see the note).

In Russia, the species hardly ever occurs in the mountains (it is known to ascend to 800 m); in Gansu Province, to 2,500 m. (Fig. 68.)

NOTE. Delimitation of *S. wilhelmsiana* and *S. microstachya* has constituted a problem since the time of M. Nazarov (1936). Indeed, one can find specimens very much resembling *S. microstachya* even within the area of *S. wilhelmsiana* continuous distribution (on the Charyn River). Material from Sinkiang is even more challenging. *S. wilhelmsiana* appears to reach the Nan Shan; on the other hand, *S. microstachya* appears to be distributed all the way to Kashgar. A number of samples cannot be attributed to either of the two species with confidence. Hence, it is quite possible that we will have to consider *S. microstachya* in the rank of subspecies. However, to make a reasonable decision, we need more Chinese material. Within the territory treated in this book, the areas of the two species are far from each other, so that their delimitation is not a real problem.

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FROM THE AREA TREATED IN THE BOOK**

1. *Salix kalarica* (A. Skv.) Worosch. 1966, Flora Sovetskogo Dalnego Vostoka: 144. — *S. pulchra* ssp. *kalarica* A. Skv. 1961, Bull. Soc. Natur. Moscow 66 (4): 31. Holotypus: LE. — Transbaykalia, Kalar Range.
2. *S. trabzonica* A. Skv. 1971, Nov. syst. pl. vasc. 8: 120. Holotypus: E. — NE Turkey.
3. *S. gracilistyliformis* Korkina, 1971, Nov. syst. pl. vasc. 7: 90. Holotypus: LE. — Russian Far East, Ussuriysk vicin.
4. *S. vorobievii* Korkina, 1971, Nov. syst. pl. vasc. 7: 83. Holotypus: LE. — Vladivostok vicin.
5. *S. kamtschatica* (A. Skv.) Worosch. 1971, Bull. Glavn. Bot. Sada 84: 31. — *S. berberifolia* Pall. ssp. *kamtschatica* A. Skv. 1968, Willows of the USSR: 141. Holotypus: LE, iso: MW. — Kamchatka.
6. *S. jurtzevii* A. Skv. 1972, Nov. syst. pl. vasc. 9: 96. Holotypus: LE, iso MHA. — NE Siberia, Magadan Oblast.
7. *S. khokhriakovii* A. Skv. 1972, Nov. syst. pl. vasc. 9: 99. Holotypus: LE, iso MHA. — N coast of the Sea of Okhotsk.
8. *S. dailingensis* Y. L. Chou et C. Y. King, 1974, Acta Phytotax. Sin. 12 (1): 8 et tab. 3. Holotypus: Herb. Acad. Sylvicult. Harbin. — NE China, Heilongjiang.
9. *S. humaënsis* Y. L. Chou et R. C. Chou, 1974, Acta Phytotax. Sin. 12 (1): 5 et tab. 2. Holotypus: Herb. Acad. Sylvicult. Harbin. — NE China, Heilongjiang.
10. *S. liangshuiensis* Y. L. Chou et C. Y. King, 1974, Acta Phytotaxon. Sin. 12 (1): 11 et tab. 4. Holotypus: Herb. Acad. Sylvicult. Harbin. — NE China, Heilongjiang.
11. *S. darpirensis* Jurtzev et Khokhryakov, 1976, Flora i rastitelnost Magadanskoy oblasti: 33. Holotypus: MHA. — Yakutia, Moma River Basin.
12. *S. neolapponum* Ch. Y. Yang, 1980, Bull. Botan. Labor. NE Forest Inst. 9: 92. Holotypus: Herb. Coll. Agric. August 1, Xinjiang. — Xinjiang, Chinese Altai.
13. *S. burqinensis* Ch. Y. Yang, 1980, Bull. Botan. Labor. NE Forest Inst. 9: 102. Holotypus: Herb. Coll. Agric. August 1, Xinjiang. — N Xinjiang, Chinese Altai.
14. *S. paraphylicifolia* Ch. Y. Yang, 1980, Bull. Botan. Labor. NE Forest Inst. 9: 92. Holotypus: Herb. Coll. Agric. August 1, Xinjiang. — Xinjiang, Chinese Altai.
15. *S. metaglauca* Ch. Y. Yang, 1980, Bull. Botan. Labor. NE Forest Inst. 9: 89. Holotypus: Herb. Coll. Agric. August 1, Xinjiang. — Xinjiang, Chinese Altai.
16. *S. yanbianica* C. F. Fang et Ch. Y. Yang, 1980, Bull. Botan. Labor. NE Forest Inst. 9: 103. — Holotypus: Herb. Inst. Sylv. et Pedol. Acad. Sin. — NE China, E. Jilin.
17. *S. fimbriata* (A. Skv.) Czerepanov, 1981, Plantae vasculares URSS: 459. — *S. berberifolia* Pall. ssp. *fimbriata* A. Skv. 1961, Notulae systemat. herb. Inst. Komarov 21: 86. Holotypus: LE. — Yakutia, Lena inferior.
18. *S. pseudotorulosa* (A. Skv.) Czerepanov, 1981, Plantae vascul. URSS: 459. — *S. sphenophylla* ssp. *pseudotorulosa* A. Skv. 1966, Schedae ad Herb. fl. URSS 16: 62. Holotypus: LE, isotypi: Herb. Fl. URSS No 4524. — Chukotka Peninsula.
19. *S. alexii-skvortsovii* Khokhryakov, 1984, Bull. Soc. Natur. Moscow 89 (4): 108. Holotypus: MW. — N coast of the Sea of Okhotsk.
20. *S. flabellinervis* Khokhryakov, 1984, Bull. Soc. Natur. Moscow 89 (4): 108. Holotypus: MW. — Magadan Oblast.
21. *S. sichotensis* Charkevich et Vyshin, 1985, Bot. Zhurn. 70 (8): 1120. Holotypus: VLA, isotypi LE, MHA, NS. — Khabarovsk Province, Sikhote-Alin Mountain Range.
22. *S. hastatella* Rech. fil. — K. H. Rechinger, 1987, Anales Jard. Bot. Madrid 44 (2): 597. — Holotypus: W, isotypi: G, MA. — Spain.
23. *S. gussonei* Brullo et Spampinato, 1988, Willdenowia 17: 5. Holotypus: CAT. — Sicilia.
24. *S. magadanensis* Nedoluzhko, 1989, Bull. Glavn. Bot. Sada 153: 29. Holotypus: MHA. — N coast of the Sea of Okhotsk.
25. *S. integerrima* (Worosch.) Nedoluzhko, 1990, Horologia i taxonomia rastenij Sovet. Daln. Vostoka: 99. — *S. chamissonis* Anderss. ssp. *integerrima* Worosch. 1981, Bull. Glavn. Bot. Sada 119: 26. Holotypus: MHA. — Sakhalin.
26. *S. xanthicola* Christensen, 1991, Willdenowia 21: 105. — Holotypus: C, iso: B, W. — NE Greece.
27. *S. rizeënsis* A. Güner et J. Zeliński, 1993, Karaca Arbor. Mag. 2 (1): 2. Holotypus: HUB, iso: KOR. — NE Turkey.
28. *S. brutia* Brullo et Spampinato, 1993, Candollea 48: 291. Holotypus: CAT. — Calabria.
29. *S. oropotamica* Brullo, Scelsi et Spampinato, 1995, Flora Mediterranea 5: 58. Holotypus: CAT. — Calabria.

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