

## 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.<sup>1</sup> 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*).<sup>2</sup> 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

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<sup>1</sup> 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.

<sup>2</sup> 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.<sup>1</sup> The willows do not have real spurs (brachyblasts), although spurs are very pronounced, for example, in the balsam poplars.

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<sup>1</sup> 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 axils<sup>1</sup>, 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.

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<sup>1</sup> 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-leaved. 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. phyllicifolia*, 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.

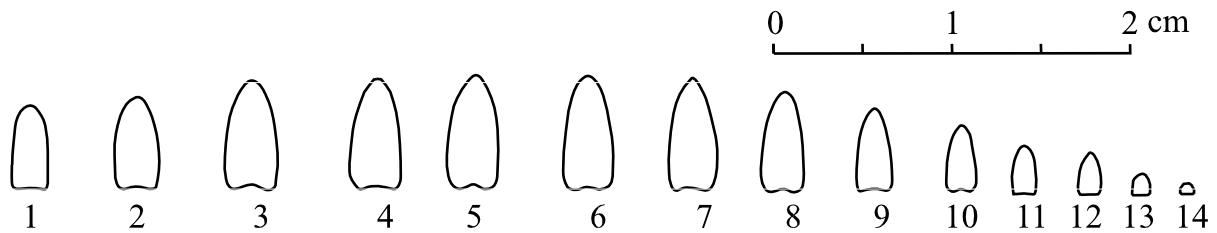
44 Type 2 (*arctica*-type, Fig. 3). The uppermost two or three (occasionally up to five-six) buds on the shoot are of almost identical size and shape: all are large (the very uppermost occasionally somewhat smaller). Further down the shoot there occurs a sudden pronounced change of bud size, and also 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).

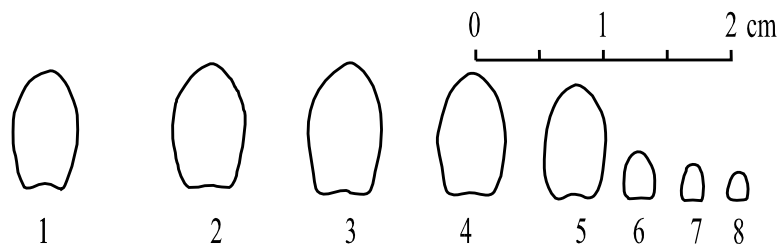
45 When considering the contents of a bud (which does not change much throughout the wintertime), one should, first of all, compare the size of the catkin primordium and leaf primordia. Frequently, the shape of leaf primordia is also of importance, as well as manner of their venation (it may be parallelinervous!) and pubescence. Certainly, the largest buds are the most suitable to see these peculiar details. There is an opinion (see, for example, Toepffer 1925; Rechingner 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).



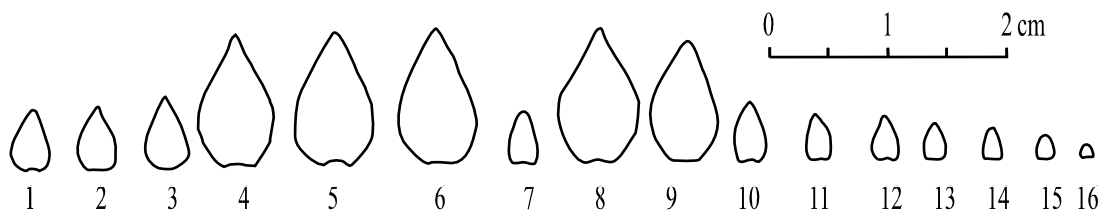
**Fig. 2.** Bud size gradation along a shoot of *Salix alba* (from the Altai)

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. jensseensis*, 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.

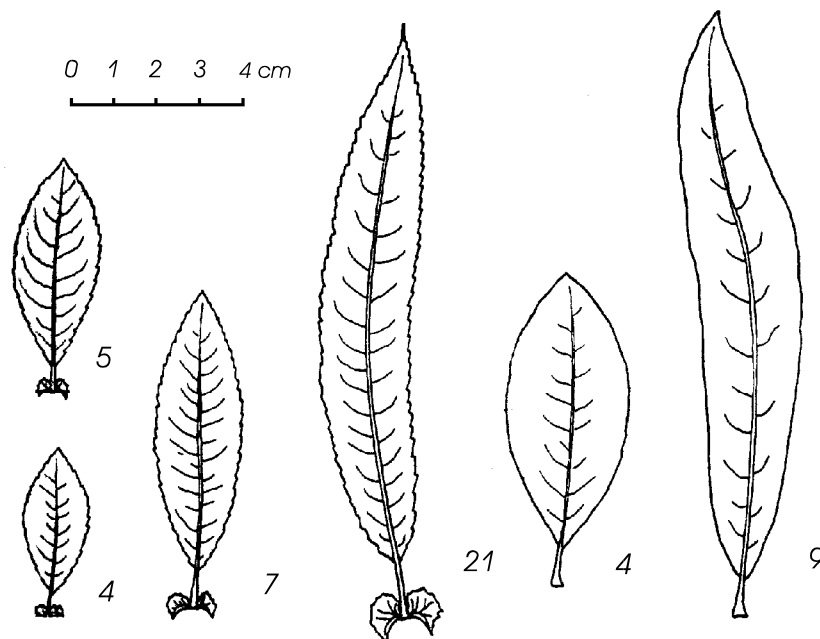
46 The stipules in the willows may be developed to a variable extent; however, there is a variability range typical for each species. In epicormic shoots, stipules are most developed; in short lateral shoots and those belonging to the oldest parts of crowns, stipules are least developed. Shape of stipules 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*).

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*).

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

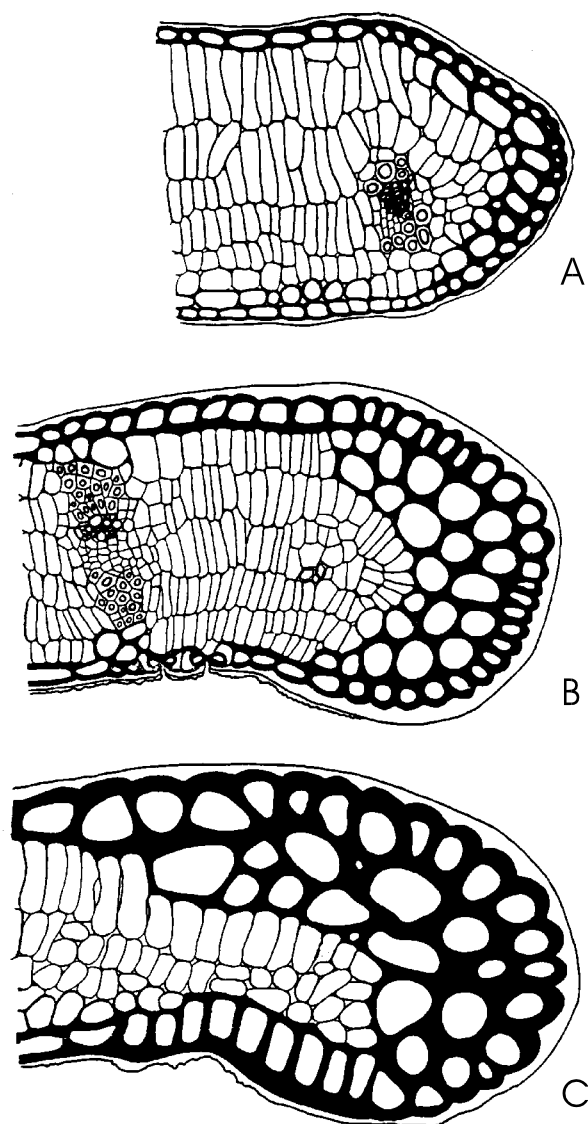


Fig. 6. Anatomical structure of the leaf margin

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

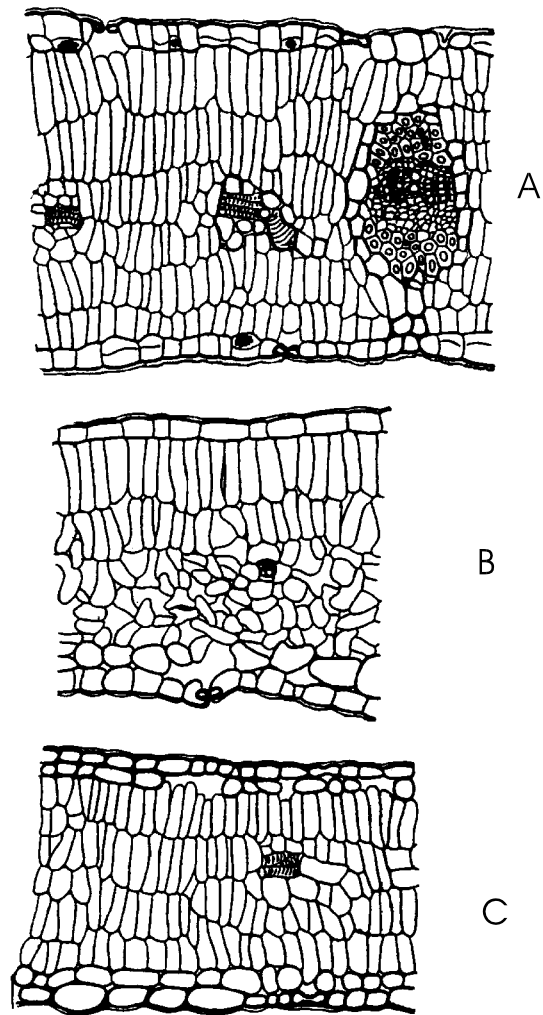


Fig. 7. Mesophyll structure

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*<sup>1</sup> 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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<sup>1</sup> 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.

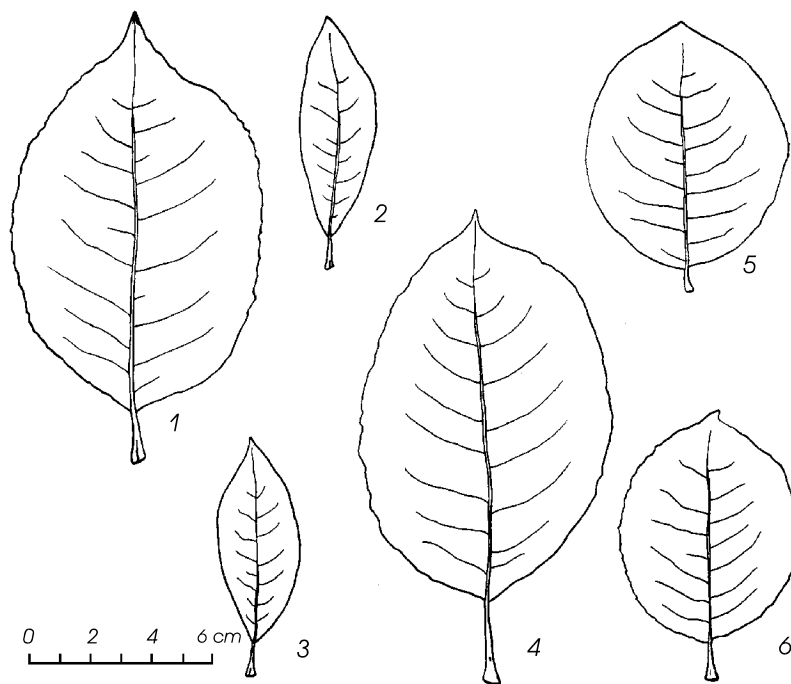
Willows originating from Middle Asia, of course, do not feel as comfortable as native species in Moscow. Nevertheless, they usually succeed to develop two or three (and sometimes four) generations of shoots per season, while Muscovites with the like growing pattern and in similar growing conditions manage 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. jennisseensis* 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* × *glauc*". 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 and calendars graecas. 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 sections<sup>1</sup>. 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

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<sup>1</sup> 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 inappropriate<sup>1</sup>.

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.

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<sup>1</sup> See footnote on page 118.