

## 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20th century, these were H. Nilsson (1918, 1928, 1930, 1937, 1954), S. Ikeno (1918, 1922), and V. Sukachev (1934, 1939, unpublished data) who got involved in studying particularly willow hybrids and experimenting with them.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. Reching (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 Przhevalsk, there are very extensive, nearly pure willow shrublands composed of *S. tianschanica*, *S. alata*, and *S. karelinii*. There is also *S. argyrea* 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. argyrea* 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 losing 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 gynoeceum parts, and others? Indeed, it is absolutely impossible to assume that these characters altogether might depend on one gene that might get suppressed in crossings as a recessive one. Specimens with pubescent capsules occur quite frequently in any large population of *S. myrsinifolia*. However, specimens that exhibit any other common character, either with *S. cinerea* or *S. aurita*, have never been found. If, however, there occur some solitary specimens with a set of characters intermediate between *S. cinerea* and *S. myrsinifolia* (I found them occasionally in Moscow Oblast and the Southern Urals), then they are easily distinguished as hybrids. These specimens demonstrate that the rest of characters are by no means recessive. Finally, the distributional area of *S. myrsinifolia* is considerably exceeding those of *S. aurita* and *S. cinerea* in the Urals as well as on the Kola Peninsula. However, specimens with pubescent capsules occur there with the same frequency or even more often (on the Kola Peninsula).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

---

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

as 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.

68

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>2</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.

---

<sup>2</sup> See footnote on page 118.