Chapter 4

EVOLUTION AND PHYLOGENY

1. MORPHOLOGICAL EVOLUTION

The major difficulty in tracing paths of evolution and phylogenesis hides in the fact that we evaluate the extent of primitiveness of particular characters basing on our notions about the primitiveness of taxa that possess those characters, and, at the same time, we decide on the primitiveness of the taxa basing on the primitiveness of their characters. Here we find ourselves in a vicious circle, where we can build as many phylogenetic schemes as we like, but their main feature, the direction of changes, will then always remain doubtful. In order to stop this meaningless rotation, we have to stick to something that lies beyond that orbit. This may be either distinct paleontological evidence or observation of characters that appear to be an obvious indication of relations between taxa. So far, the search for the origin of the

69 amentiferous plants on the whole and particularly the Salicaceae has not been very promising. However, tracing major evolutionary paths within the Salicaceae family can be more successful. Naturalness of the family Salicaceae as well as close relation between the willows and poplars are beyond question, even though there are distinctions in their pollen morphology (Kupriyanova 1965). Consequently, we get a solid base for our decisions regarding the extent of the primitiveness of particular groups within the genus *Salix*. Obviously, the most primitive groups are those closest to the poplars. Apparently, this is the subgenus *Salix*. Therefore, the most primitive characters are those of the subgenus *Salix*, particularly, those resembling features of the poplars. We can as well partially rely on observations of ontogenesis, teratological study, and general ideas when evaluating some of the characters.

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

Relying on the characters listed in Table 3, one may evaluate the extent of primitiveness or progressiveness of particular sections. Of course, one should keep in mind that these evaluations will always be largely hypothetical. First of all, characters evolve independently,

70 so that a taxon may appear to be primitive with regard to some of its characters and advanced when taking others into consideration. For example, *S. cardiophylla* is by all means very primitive as far as the structure of its buds and flowers is concerned. At the same time, its leaves show advanced anatomical structure. However, primitive characters definitely predominate in *S. cardiophylla*, so that the conclusion about general primitiveness of that species is hardly disputable.

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

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

Table 3. Major directions of morphological evolution in the willows

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

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

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

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

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

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

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

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

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

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

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

Along with those features that may be with certain confidence qualified as primitive or advanced, there are, of course, scores of those that cannot be approached that way. They just reflect the variability of certain ways of development in particular species (to some extent, that variability was described in chapter 3, section 3; one can find more detail in the keys to sections and species). Within particular small groups, there are also occasions when one may try to consider some of characters as primary, others derived. However, these speculations would be much more hypothetical, since here we find ourselves too far away from the initial statements, that is, the idea of the common filiation of the willows and poplars and the notion about the primitiveness of the subgenus *Salix*. It is impossible, for instance, to tell with confidence, which of the two extreme types of catkin structure in the section *Arbuscella* is primary and which is more advanced: *S. pulchra* or *S. arbuscula* type. Probably, it is an intermediate structure which is primary. *72*

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

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

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

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

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

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

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

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

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

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

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

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

While studying the segregation of the hybrid *S. caprea* × *S. viminalis*, in the F_2 generation, N. Nilsson (1931) found a specimen that resembled *S. cinerea* in many ways. He concluded that he had managed to reconstruct *S. cinerea* and called his new plant *S. neocinerea*. According to N. Nilsson, *S. cinerea* is an apophytic species, which has just recently emerged polytopically (i. e., simultaneously in different places) in areas of human activities through multiple crossings between *S. caprea* and *S. viminalis*. "*S. neocinerea*" cannot form hybrids with its parental species. That fact was supposed to confirm N. Nilsson's success in the artificial imitation of the natural speciation. This work by N. Nilsson has been frequently referred to in the literature devoted to more general issues as an example of species "synthesis" (Cain 1944, Scharfetter 1953).

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

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

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

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

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

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

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

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

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

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

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

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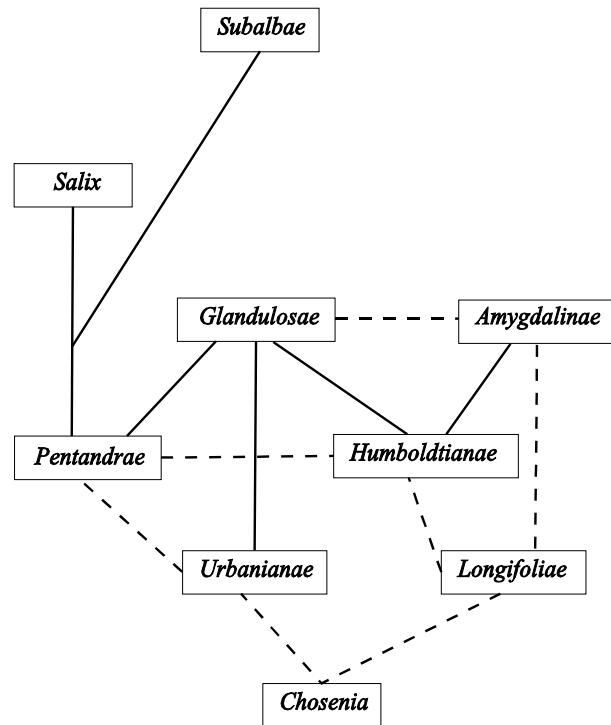
Probable evolutionary relations of the sections belonging to the subgenus *Salix*

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

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

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

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

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

the central sections in the subgenus *Vetrix*, as we will see later.) A Himalayan alpine section *Lindleyanae*, the major representative of *Chamaetia* in Southeast Asia, is clearly connected with the section *Eriostachyae*, which is as well Himalayan. One can tell with enough confidence that the section *Glaucae* has also originated from *Eriostachyae* or *Glabrella*; *Retusae* might have had a common root with *Glaucae* (however, they also have some affinity with *Myrtosalix*). Finally, the species of *Myrtosalix* are akin to *Hastatae* in many characters, although their direct derivation from *Hastatae* is hardly probable. *Chamaetia*, the most isolated section of the subgenus *Chamaetia*, retain a few especially primitive features *78* regarding the stamen, ovary, and stigma structure and are also known to have very specific, unique leaf anatomy. Presumably, this section constitutes a separate branch of development, which had become distinct long before the rest of the sections of the subgenus *Chamaetia* diverged from ancestral stems of the subgenus *Vetrix*. So far, it has been impossible to trace the closest relations of the section *Chamaetia*.

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

Possible evolutionary ways of the *Chamaetia* sections are depicted in the illustration.
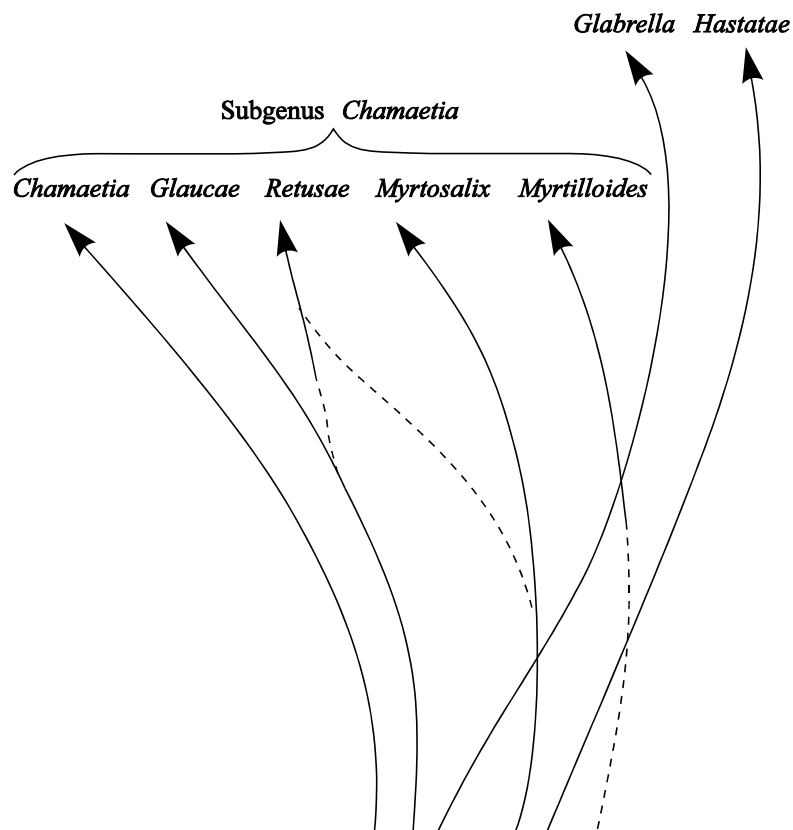
Probable evolutionary relations of the sections within and around the subgenus *Chamaetia*

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

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

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

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

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

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

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

The illustration depicts hypothetic evolutionary connections of groups within the subgenus *Vetrix*.
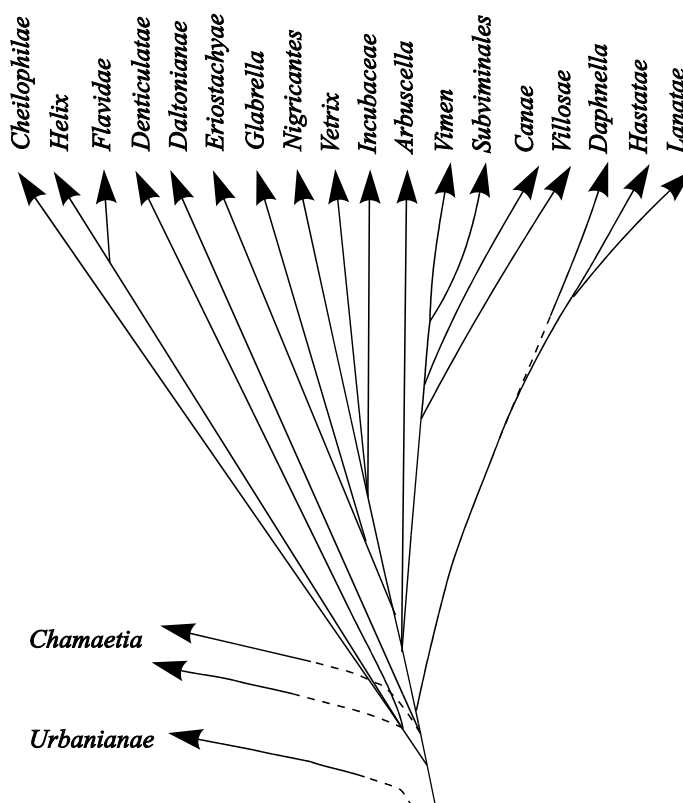
Probable evolutionary relations of the sections within and around the subgenus *Vetrix*

3. DISTRIBUTIONAL TYPES OF SPECIES

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

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

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

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

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

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

1. *Mediterranean and South Atlantic*

S. pedicellata	*S. salvifolia*
S. atrocinerea	*S. amplexicaulis*

2. *Central and South European Mountain and Alpine*

a. Broad Central and South European

S. elaeagnos	*S. retusa*

b. Alpine

S. serpyllifolia	*S. mielichhoferii*
S. appendiculata	*S. helvetica*
	S. laggerii

c. Alpine-Pyrenean

S. foetida	*S. breviserrata*

d. Pyrenean and Central French

S. pyrenaica	*S. basaltica*
S. tarraconensis	

e. Apennine

S. apennina	*S. crataegifolia*

f. Alpine-Carpathian-Balkan

S. alpina	*S. glabra*
S. waldsteiniana	*S. silesiaca*

3. *European Arctic and Arctic-Alpine*

a. Arctic-Alpine European

S. herbacea (A)

b. Arctic European

S. myrsinites	*S. arbuscula*

4. *European and Eurasiatic Boreal*

a. Atlantic and Central European

S. repens	*S. purpurea*
S. daphnoides	

b. European-West Siberian

S. pentandra	*S. phylicifolia*
S. myrsinifolia	*S. lapponum*
S. cinerea	*S. starkeana*
S. aurita	

c. Eurasiatic Boreal

S. rosmarinifolia	*S. caprea*
S. dasyclados	*S. myrtilloides*
S. viminalis	

d. Boreal-Mediterranean

S. alba	*S. triandra*

e. Sarmatian

S. vinogradovii	*S. acutifolia*
S. caspica	

5. *East Asiatic Boreal*

a. Manchurian

S. integra	*S. kangensis*
S. pierotii	*S. cardiophylla*
S. gracilistyla	*S. miyabeana*

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

b. Japanese-Kuril

S. gilgiana	*S. kurilensis*
S. vulpina	*S. nakamurana*
S. reinii	

c. East Asiatic Boreal (in strict sense)

S. brachypoda	*S. rorida*
S. taraikensis	*S. schwerinii*
S. abscondita	*S. pseudopentandra*
S. udensis	*S. dshugdshurica*

6. *Siberian Boreal and Alpine*

a. Broad Siberian Boreal

S. bebbiana (A)	*S. pyrolifolia*
S. jenisseensis	

b. Central Siberian Mountain and Alpine

S. nasarovii	*S. rectijulis*
S. turczaninowii	*S. divaricata*
S. vestita (A)	*S. sajanensis*
S. berberifolia	*S. saposhnikovii*

c. Central Siberian-Mongolian Lowland

Eastern:	Western:
S. kochiana	*S. microstachya*
S. ledebourana	*S. gordejevii*
S. rhamnifolia	

7. *Siberian and Eurosiberian Arctic and Arctic-Alpine*

a. Siberian

S. nummularia	*S. reptans*
S. arctica (A)	*S. recurvigemmis*
S. polaris (A)	

b. Eurosiberian

S. lanata (A)	*S. glauca* (A)
S. hastata	*S. reticulata* (A)

8. *Northeastern Subarctic-Arctic and Alpine*

a. Extreme Northeastern (Beringian)

S. ovalifolia (A)	*S. rotundifolia* (A)

b. Northeastern

S. erythrocarpa	*S. sphenophylla* (A)
S. tschuktschorum	*S. fuscescens* (A)
S. chamissonis (A)	*S. alaxensis* (A)
S. phlebophylla (A)	

c. East Siberian Arctic-Subarctic

S. pulchra (A)	*S. boganidensis*

d. East Siberian Mountain and Alpine

S. saxatilis	*S. krylovii*

9. *Middle Asiatic*

a. Middle Asiatic-Mongolian

S. alatavica	*S. turanica*
S. tenuijulis	*S. coesia*

b. Middle Asiatic-Himalayan

S. karelinii	

c. Middle Asiatic Eastern (Tien Shan Type)

S. tianschanica	*S. michelsonii*
S. argyracea	*S. iliensis*
S. kirilowiana	

d. Middle Asiatic Western (Pamir-Alay-Afghan Type)

S. pycnostachya	*S. fedtschenkoi*
S. linearifolia	*S. capusii*

e. Middle Asiatic Central

S. songarica	*S. niedzwieckii*
S. olgae	

10. *Iranian*

S. wilhelmsiana	*S. aegyptiaca*
S. excelsa	*S. acmophylla*

11. *Caucasian-Minor Asian*

S. apoda	*S. kuznetzowii*
S. armeno-rossica	*S. elbursensis*
S. caucasica	*S. pantosericea*
S. fragilis	*S. pentandroides*
S. kazbekensis	*S. pseudodepressa*
S. kikodseae	*S. pseudomedemii*

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

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

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

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

3. Some of the groups appear to be not distinctly delimited; there are intermediate, transitional distributional types. For instance, the East Asiatic Boreal Group (5c) may be treated as a result of the Manchurian Group (5a) north and west expansion, and the group 6a, as a result of the group 6b expansion. The group 6a (*S. pyrolifolia* → *S. dasyclados* → *S. myrtilloides*), expanding in its turn, particularly to the west, grades into 4c. Presumably, all these transitions constitute another evidence of some affinity in species historical development. However, this affinity partially originates from such remote past that it is hardly possible to interpret it now without forced statements and arbitrary assumptions.
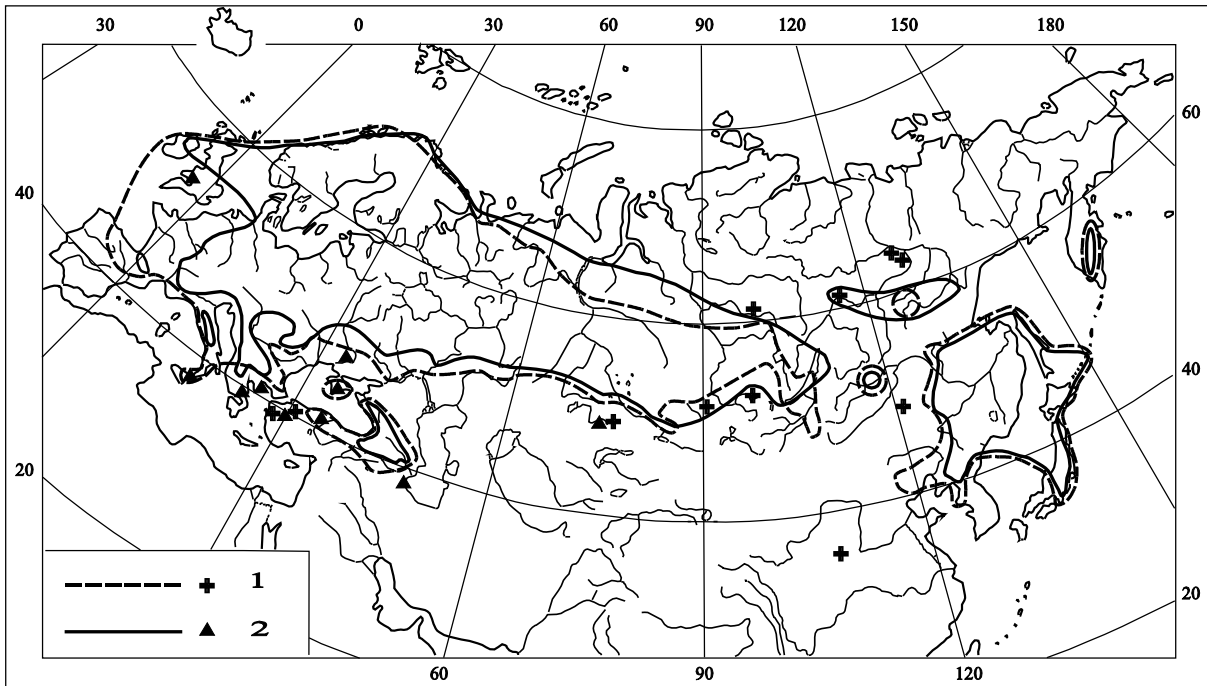
Fig. 9. Distribution areas of *Salix caprea* (L.)(1) and *Ramischia secunda* (L.) (2)
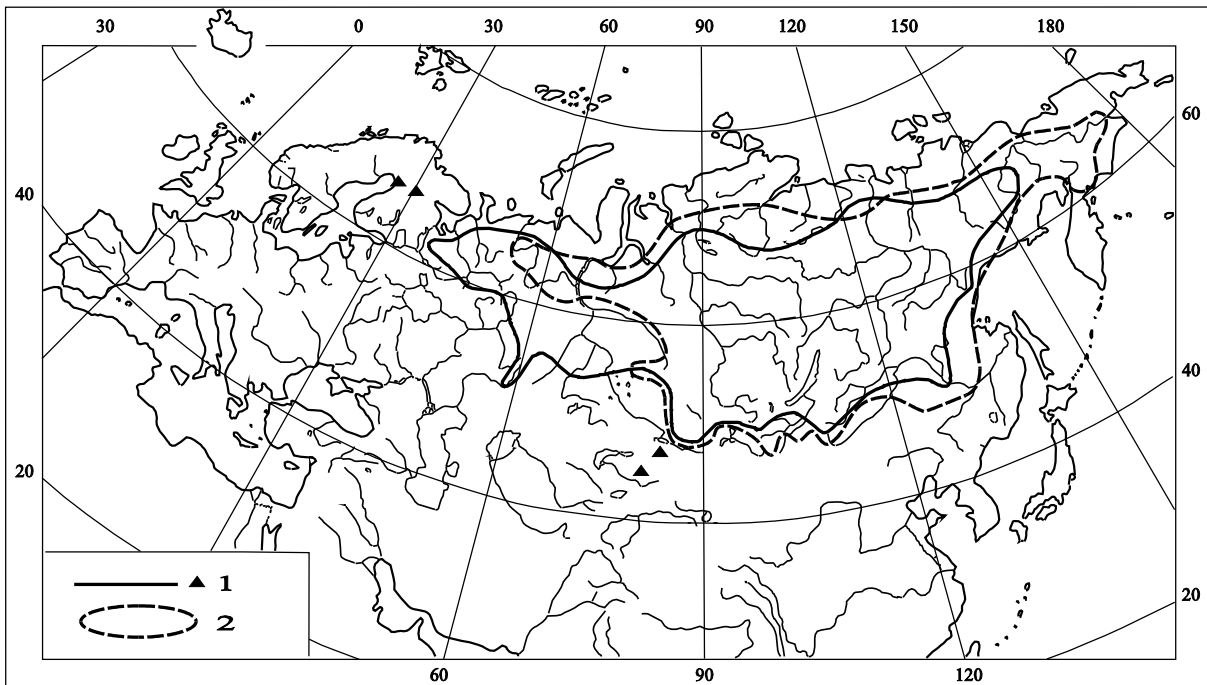

Fig. 10. Distributional areas of *Salix pyrolifolia* Ledeb. (*1*)
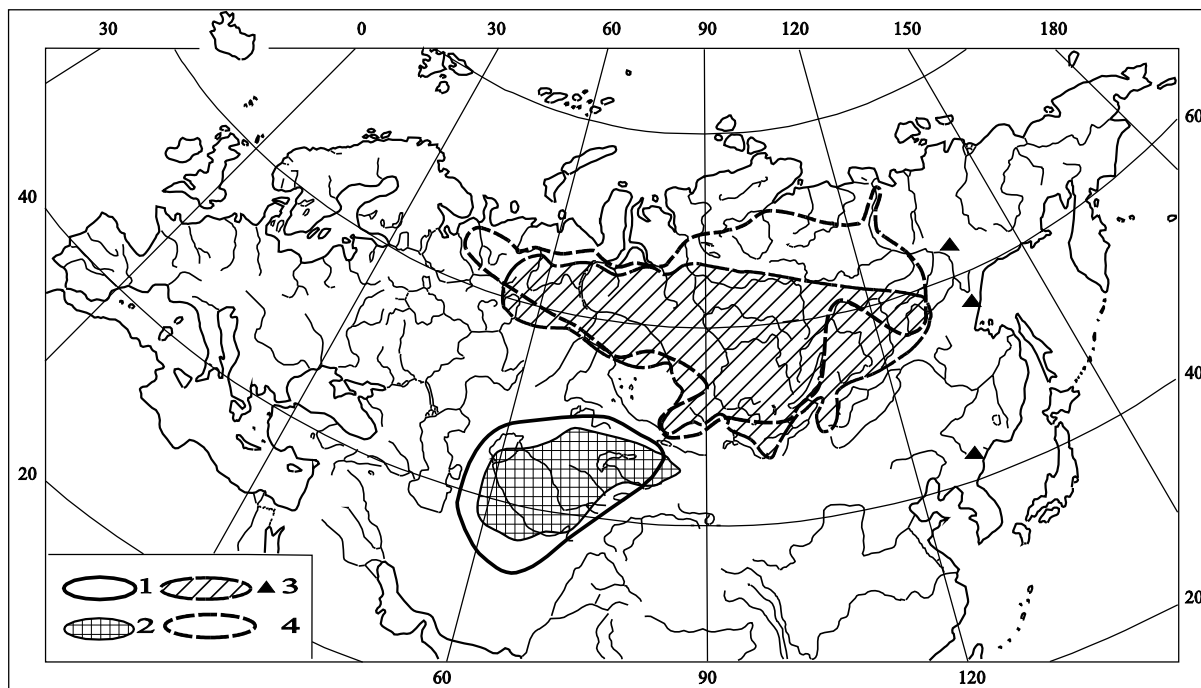and *Ramischia obtusata* (Turcz.) Freyn (*2*)

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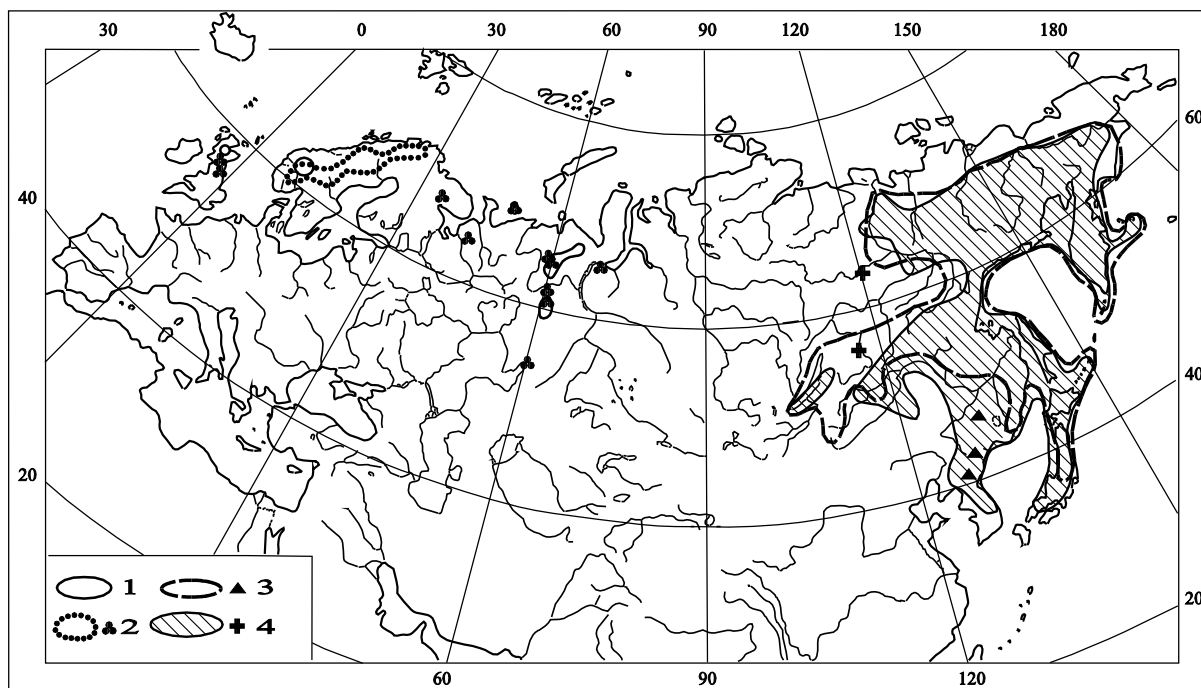

Fig. 12. Distributional areas of *Artemisia norvegica* Fries (Hultén 1954, Tolmachev 1962) (*1*); *Salix arbuscula* L. (*2*); *Pinus pumila* (Pall.) Rgl. (Tikhomirov 1946, Tolmachev 1962) (*3*); and *Salix udensis* Trautv. et Mey. (*4*)**Fig. 10.** Distributional areas of *Salix pyrolifolia* Ledeb. (*1*)

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

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

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

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

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

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

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

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

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

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

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

4. HISTORICAL DEVELOPMENT OF THE GENUS: MAJOR FEATURES

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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