Chapter 2

MATERIAL AND METHODS

1. NOTION OF SPECIES THAT THE AUTHOR COMPLIES WITH

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

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

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

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

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

some too "large", and some too "small". In certain cases, differences between species may appear to be "significant", while in others, "insignificant". We don't have to worry about these results. Indeed, we cannot demand that nature should arrange all the species to our convenience, so that *23*
they would be easy to distinguish and besides appear neither too big nor small to us.

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

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

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

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

3. Genetic characters provide the direct biological connection between specimens. The panmixis, i. e., normal sexual reproduction, is the mechanism that promotes biological coherence and stability of species. Barriers that restrict the panmixis break this coherence. If these barriers last long, then the stream of life, which is initially whole, becomes eventually separated into individual streamlets, each of them with its own history. That is to say, one species gets divided *24*
into several ones.

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

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

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

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

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

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

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

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

Also, I have strong objections against some deviations in treating the notion of the polytypic species. Not infrequently, a complicated group, which an author has either ignored or failed to understand, is presented as "a polytypic species". In so doing, the author piles up everything to
subspecies, whether these are real subspecies, cultivars, valid species, morphological variants *26*
without any particular geographical destination, vague taxa described a long time ago and not understood by anybody at present, or even pure synonyms. Formally, it all looks excellent: the system appears to be elaborated "in detail", there are even some new combinations proposed; however, the actual result is a mess. Particularly, the West European literature is sinful of "polytypic species" of that kind.

In plants that demonstrate normal sexual reproduction, it makes no sense to distinguish further taxonomical groups within subspecies: these groups would be too obscure. The general notion of population is sufficient to describe all parts of species smaller than subspecies. Any conspicuous, constant, or in a way interesting peculiarities, which are not necessarily restricted to a particular population, are to be treated as a variety. At present, this notion is accepted rather in a morphological sense, as its taxonomical content is fairly indefinite (when speaking of wild plants; in cultivated plants this term has a certain special meaning). The "form" is equally vague, although, following common practice, they have listed it along with variety in the "International Rules of Nomenclature" together with other taxonomical units.

2. OBSERVATIONS IN NATURE

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

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

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

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

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

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

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

3. HERBARIUM MATERIAL

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

A. Major Domestic Depositories

Herbarium in the Botanical Institute of the USSR Academy of Sciences in Leningrad (St. Petersburg): Main (1964), European Russia (1963), Siberia and the Far East (1964), the Caucasus (1963), Middle Asia (1960), East Asia (1965);
Moscow University: the entire collection (1963);
Tomsk University: Transbaykalia and Krasnoyarsk Province (1955), Mongolia (1960), major part of West Siberian collection (1955);
Tashkent University: the entire collection (1959);
Botanical Institute of the Georgian Academy of Sciences in Tbilisi: the Caucasian collection (1962);
Botanical Institute of the Armenian Academy of Sciences in Yerevan: the Caucasian collection (1962);
Botanical Institute of the Azerbaijanian Academy of Sciences in Baku: the entire collection (1962);
Botanical Institute of the Kazakh Academy of Sciences in Alma Ata: the entire collection (1965);
Botanical Institute of the Tadjik Academy of Sciences in Dushanbe: the entire collection (1962);
Botanical Institute of the Ukrainian Academy of Sciences in Kiev: the Ukrainian collection of the Soviet period (1957);
Institute of Biology of the USSR Academy of Sciences, the Urals Branch in Sverdlovsk (Yekaterinburg) (1953 and a part of later collections).

B. Domestic Depositories of Smaller Magnitude[1]

Main Botanical Garden in Moscow (1966);
All-Union Institute of Medicinal Plants (1966);
Geographical Department of the Moscow University (1963);
Lvov University: a part of the collection (1957);
Lvov Museum of Nature (1957);
Perm University: a part of the collection (1953);
Polar-Alpine Botanical Garden in the Khibins: a part of the collection (1956);
Chernovtsy University (1962);

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

Dagestan University in Makhachkala (1962);
Batumi Botanical Garden (1962);
Botanical Institute of the Uzbek Academy of Sciences in Tashkent: a part of the collection (1956–1959); 29
Leninabad (Khodzhent) Pedagogical Institute (1962);
Leningrad (St. Petersburg) Academy of Forest Technology (1961);
Far East Branch of the USSR Academy of Sciences in Vladivostok (1967);
Sakhalin Science Institute (1967);
Yakutian Branch of the USSR Academy of Sciences (1967);
Novosibirsk Botanical Garden of the USSR Academy of Sciences (1964);
Caucasian National Preserve (1962);
Ashkhabad Botanical Garden of the Turkmenian Academy of Sciences (1959).

C. Material from Foreign Herbaria

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

D. Other Material

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

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

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

4. OBSERVATIONS OF CULTIVATED PLANTS

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

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

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

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

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

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

5. COMPILATION OF SPECIES DISTRIBUTION MAPS

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

6. NOMENCLATURE, AUTHENTIC SPECIMENS, SYNONYMY

The species' names by C. Linnaeus are accepted here without revision, in the sense that was established as long ago as the early last century, based primarily on interpretations of J. Smith, G. Wahlenberg, and E. Fries. It is worth mentioning that there are still some concerns regarding at least three of the species epithets by C. Linnaeus: *arbuscula*, *arenaria*, and *rosmarinifolia*. Linnaean Herbarium was mostly preserved in England, so that some prominent subsequent researchers did not have access to it when writing on the willows of Scandinavia and Central Europe. They had to judge the Linnaean species relying upon diagnoses by C. Linnaeus, which were extremely short, and notes by J. Smith, who had the Linnaean Herbarium at his disposal. Anyway, the "method of types" did not yet exist in the last century, and authentic herbarium samples did not have the significance they have nowadays. The "legible contents" of diagnoses was usually considered to be of more importance. F. Wimmer (1866: LVI) articulated that concept as follows: "Herbarii Linnaeani … auctoritas est nulla, ubi verba Linnaei contradicunt." ("The authority of Linnaean *32*
Herbarium equals zero if it contradicts Linnaeus' words"). C. Linnaeus himself did not assign any critical significance to the herbarium. His herbarium is far from being completely consistent with the text of "Species plantarum", and the labeling is insufficient, according to

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

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

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

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

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

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

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

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

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

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