

TAXONOMY AND DISTRIBUTION OF *CIRCAEA* (ONAGRACEAE) IN THE USSR¹

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ABSTRACT

In the USSR, five species of *Circaea* are recognized: *C. alpina* L., *C. caulescens* (Kom.) Hara, *C. lutetiana* L., *C. cordata* Royle, and *C. mollis* Sieb. & Zucc. Also, the sterile hybrid *C. × intermedia* Ehrh. is known from several regions. Distribution areas of all these taxa are presented on maps based on herbarium materials studied by the author. Among these materials, no specimen of *C. erubescens* Franch. & Savat. has been detected, though this species had been reported from southern Sakhalin previously. *Circaea caucasica* A. Skvortsov, described by the author earlier, is now regarded to be a disjunct fraction of *C. caulescens*.

The genus *Circaea* has few species, and they are sharply delimited taxonomically and very distinct and uniform morphologically and ecologically. All *Circaea* species are tender, broad-leaved, shade- and moisture-loving herbs. The overall area of the genus closely coincides with the area of temperate mesophilic (broad-leaved, mixed, and dark-coniferous) forests of the northern hemisphere. Hence, from the study of taxonomic interrelations within the genus *Circaea*, one could expect to get interesting suggestions regarding the history of mesophilic temperate forest in general.

I have been interested in *Circaea* for many years, and have previously published a few short notes on the subject (Skvortsov 1970, 1971, 1977). The present paper provides a general taxonomic and geographical review of this genus within the USSR.

I have studied *Circaea* both in the field and in herbaria. Field observations have been made chiefly in the following regions of the USSR: central part of the European territory (provinces of Moscow, Kaluga, Smolensk); Ukrainian Carpathians; Crimea; central part of the Great Caucasus; Altai Mountains; southern part of the Soviet Far East (Primorski Province). Outside the USSR, I have had the opportunity to observe and to collect *Circaea* species in Sweden, in the Indian Himalayas, and in the southern Appalachians.

Herbarium materials of the following institutions have been studied in full: Komarov Botanical Institute in Leningrad (LE); Botanical Institutes in Kiev (KW), Minsk (MSK), Erevan (ERE), and Wilnius; Biological Institutes in Riga (LATV), Syktyvkar (SYKO), and Vladivostok (VLA); Institute of Zoology and Botany in Tartu (TAA), Institute of Ecology in Sverdlovsk (SVER), Siberian Institute of Plant Physiology and Biochemistry in Irkutsk (IRK), Main Botanic Garden in Moscow (MHA), Central Siberian Botanic Garden in Novosibirsk (NS); Universities of Moscow (MW), Leningrad (LECB), Tartu (TU), Riga (RIG), Wilnius (WI), and Vladivostok. In part, materials also have been studied from the Universities of Uppsala (UPS) and Lund (LD).

¹ I am deeply grateful to colleagues in charge of the herbaria from which materials have been used for the present study. Also, I wish to thank Dr. P. H. Raven for many interesting discussions by correspondence and for the friendly invitation to submit the present paper for the publication in this journal.

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The distribution maps presented in this paper are based on herbarium specimens I have examined.

1. *CIRCAEA ALPINA* L.

Among the members of the genus, this species has the largest area of distribution. The distribution area of *Circaea alpina* has been depicted earlier by Tolmachev (1954: 71), Hultén (1971: map 86), and Jäger (1969: 404). As compared with these earlier maps, my map (Fig. 1) provides some necessary additions and corrections.

In the most generalized manner, the distribution of *Circaea alpina* may be termed circumpolar holarctic-boreal. A closer examination reveals some interesting details. In the middle of the Eurasian continent the zone occupied by *C. alpina* is the narrowest: less than 10° of latitude. In contrast, towards the western and eastern flanks of Eurasia, along with the decrease of the continentality and increase of the "maritimity" of the climate, the latitudinal span of the *C. alpina* area reaches nearly 30° (in the West from 40–41° N in Italy, northeastern Turkey, and Soviet Armenia to 70°N in Norway; in the East from 32–33°N in Kyushyu and Quelpaert Islands to 59°N in Koraginski Island. A similar pattern may be observed in the Western Hemisphere also.

In Transbaicalia there seems to exist a considerable (250–300 km wide) gap in the distribution of *Circaea alpina*. The region in question is by no means an unexplored one; thus, even if *C. alpina* will be some day found here, there will be only isolated localities. Though the chorology of the forest flora in Transbaicalia is yet far from fully worked up, still a few other Eurasian mesophytic forest species can be mentioned which have quite similar gaps in their areas, viz., *Salix caprea* (map: Skvortsov, 1968: figs. 9, 40), *Pyrola secunda* (maps: Skvortsov, 1960, 1968: fig. 9), *Oxalis acetosella* (map: Tolmachev, 1954: 64).

Southern Yakutia, too, is not underexplored, especially as regards the valleys of the larger rivers. The scarcity of *Circaea alpina* here is to be explained by the dryness of the climate and the resulting very restricted distribution of the dark coniferous taiga.³

In the USSR *Circaea alpina* usually inhabits shady and humid, but not boggy or marshy, places in coniferous or mixed forests. Often it can be seen on decaying stumps, rocky outcrops, or stony debris (especially calcareous) amidst a forest, or in shady ravines. More rarely it can be found in broad-leaved deciduous forests or in birch groves. In the northern parts of its area and in Siberia it prefers the dark taiga; nearer to the southern edge of its area, especially in the European part, *C. alpina* often grows in wet (sometimes even swampy) alder groves ("Erlenbrüche" of the German authors). It always grows in patches, never forming a continuous layer in a given forest plot.

Only extremely rarely does *Circaea alpina* reach the alpine region. In the Caucasus it has been found in subalpine birch elfinwood groves or among rocks

³ In Russian literature, the term dark taiga denotes coniferous forest composed of more hydrophilic and densely crowned trees: spruce, fir, and Siberian cedar-pine (*Pinus sibirica*). Light taiga is formed by more loosely crowned and relatively xerophilic larches and *Pinus silvestris*. The distinction between these two types is very important ecologically and phytogeographically.

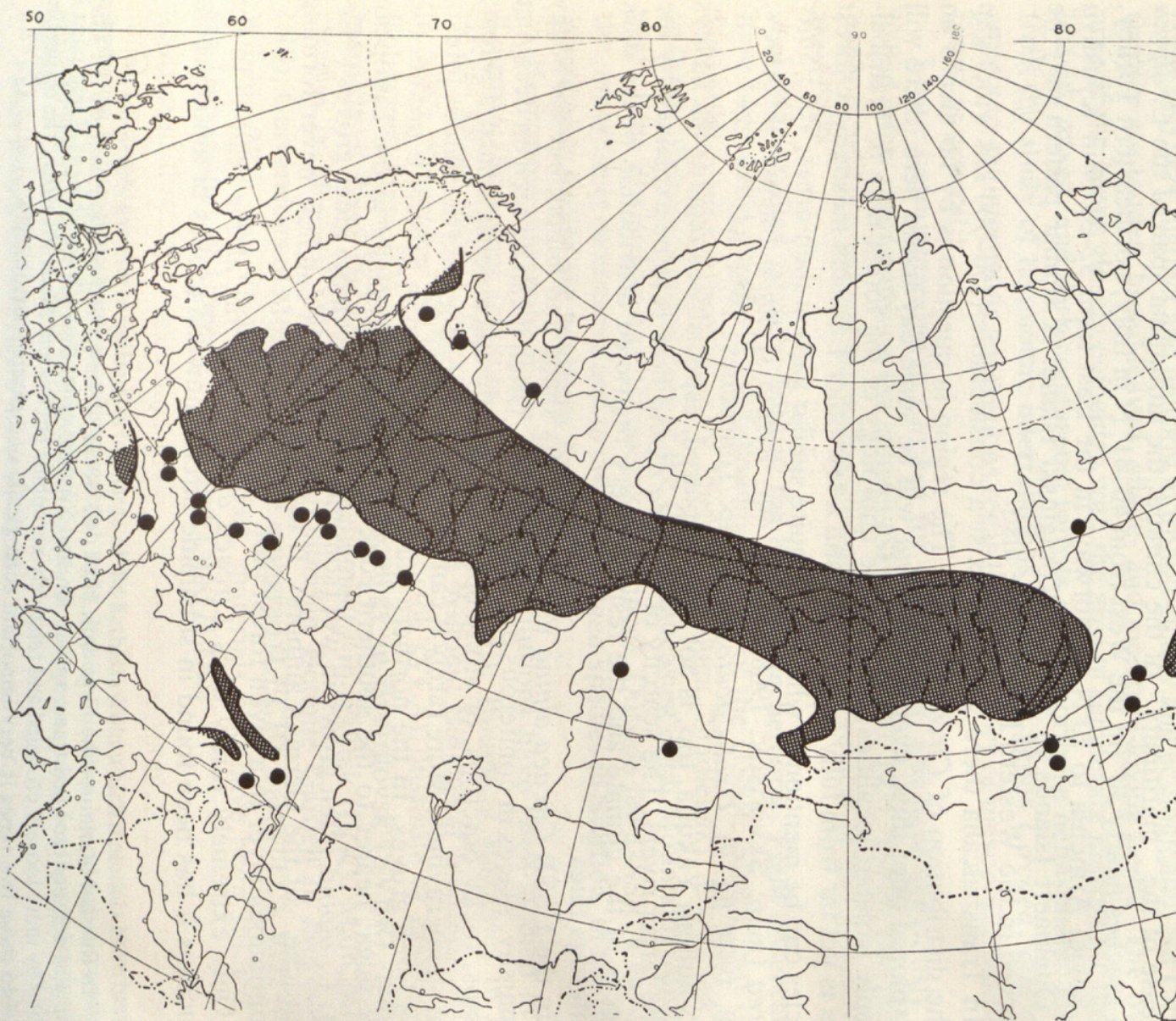


FIGURE 1. Distribution of *Circaea alpina* in the Soviet Union.

up to 2,300–2,400 m. In the Urals, or Siberian, or Far Eastern mountains no alpine or subalpine localities have been recorded. Excepting the northeastern extremity of its Asian range, nowhere else in the USSR does it approach northern forest limits.

In the central and southern regions of the European part of the USSR the distribution of *Circaea alpina* seems to have been continuously shrinking during the nineteenth and twentieth centuries, and it is quite possible that the distribution presented in Fig. 1 in part reflects not entirely the present but perhaps even now some past situations. On the contrary, in the Far East *C. alpina* seems to fit quite well into the present ecological situation. So, it remains quite common in the southern part of the Primorski Province, including the nearest outskirts of Vladivostok, despite increasing human pressure.

In the course of the intensive floristic investigation of the Soviet Far East in the post-war period, *Circaea alpina* has been discovered in nearly all of the Kurile Islands, from Zeleny (Shihotsu) and Kunashir to Shumshu. Quite remarkable is the recent discovery of *C. alpina* on the completely treeless Koraginski Island (Voroshilov *et al.* in 1969, MHA); it grows there in low shrubby thickets amid herbaceous tundra. It is rather widespread in the Island of Sakhalin, as well as in Japan. Thus the opinion expressed by Hara (1934), Ohwi (1965), and, more reservedly, by Voroshilov (1966), that the Far Eastern distribution of *C. alpina* is predominantly continental, seems to be unjustified. On the contrary, *C. alpina* is more widespread in the maritime climate of the islands.

Especially interesting is the occurrence of *Circaea alpina* on Kyushyu. Two specimens I have seen from this island—Nagasaki-Simbaru (= Shimabara), Maximowicz in 1863, and Mount Hiko-san, Makino in 1906 (both LE)—undoubtedly belong to *C. alpina*. Equally interesting is the presence of this species on Quelpaert Island (Cheju-do) where it had been collected on Mount Hallaisan at altitudes from 1,300 to 1,700 m (Taquet 832, 4258, LE). This makes one suspect that *C. alpina* might be present even in Taiwan.

The morphological characters of *Circaea alpina* are rather uniform throughout its whole holarctic area. In Eurasian materials, I have been able to discover only one character having significant geographical variability: the quantity of glandular pubescence in the inflorescence. In Europe, Caucasus, and Siberia this pubescence is well developed, but in the Far East it is usually scarce or even absent.

The plants of Southwestern China, Tibet, and drier inner chains of the Himalayas, formerly referred to *Circaea alpina*, in my opinion should be regarded as a separate species, *C. micrantha* A. Skvortsov (1977). These plants have very small, entire or only slightly emarginate petals (resembling those of *C. erubescens* Franch. & Savat.). Between the areas of *C. alpina* and *C. micrantha*, there is a disjunction of about 1,000 km or even wider.

2. *CIRCAEA CAULESCENS* (Kom.) Hara

In 1905, V. L. Komarov, based on a plant collected by himself in northern Korea and two specimens collected by D. I. Litvinov in northeastern China described *Circaea alpina* var. *caulescens* Kom. As the chief distinction of the variety from the typical *C. alpina*, he emphasized its taller and more erect stem. In 1934, Hara raised the variety to the rank of species under the name *C. cau-*

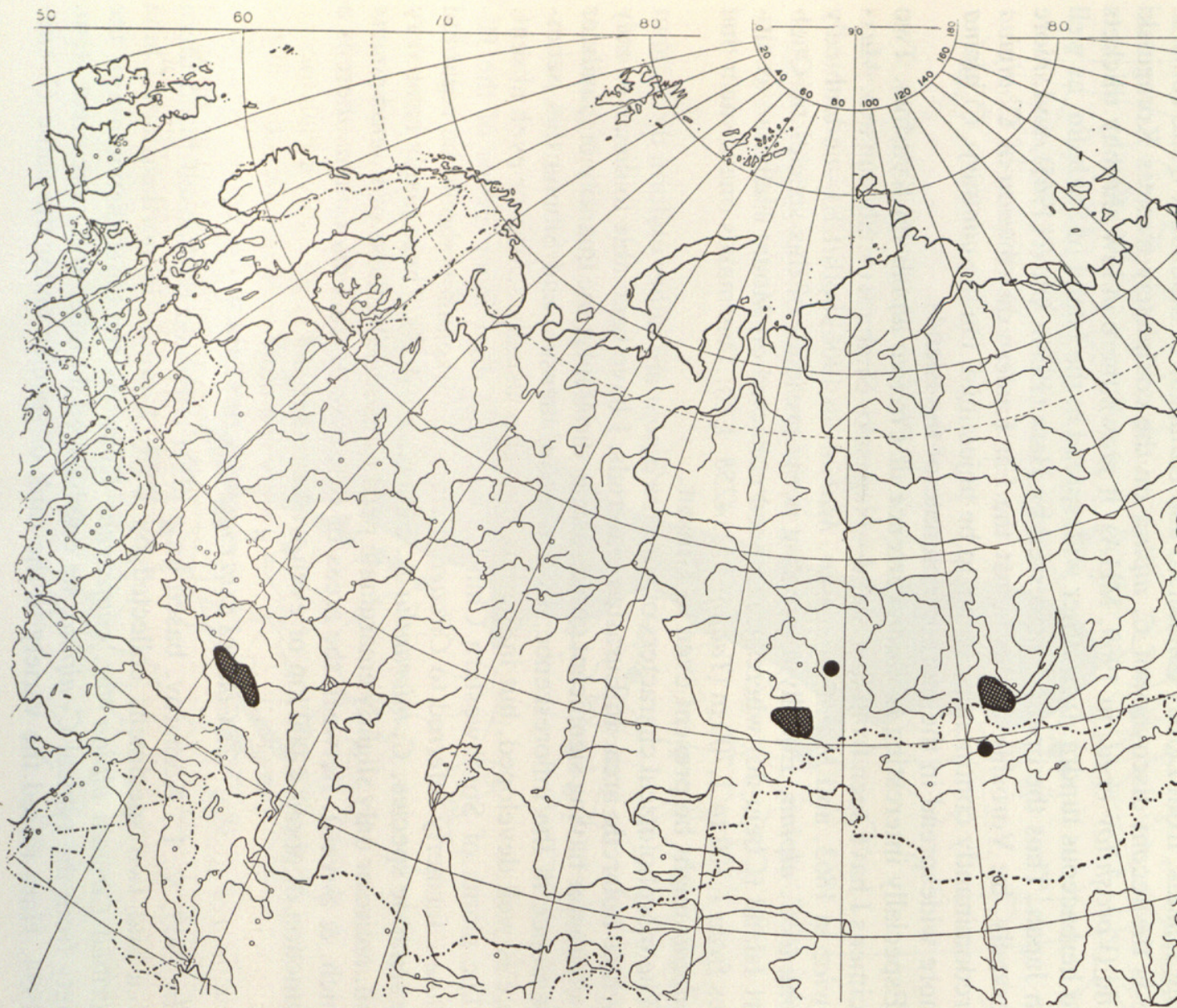


FIGURE 2. Distribution of *Circaea caulescens* in the Soviet Union.

lescens (Kom.) Nakai ex Hara. Neither Komarov nor Nakai nor Hara, however, properly clarified the morphological differences between *C. alpina* and *C. caulescens*. Consequently, Hara quite erroneously believed that these species are vicarious and that in Japan (and even in the entire Far East) only the latter species is widespread. This opinion was also expressed by Ohwi (1965: 655). Actually, as has been pointed out above, *C. alpina* is very widespread in the Far East. In contrast, *C. caulescens* has a very restricted area on the continent, and is absent from the Soviet Far Eastern islands. It also seems to be quite rare in Japan. Among herbarium materials from Japan that I have had access to, I detected specimens of *C. alpina* from ten localities, but not a single specimen of *C. caulescens*.

Circaea caulescens has a nonglandular pubescence of reflexed sicklelike hairs on the stems below the inflorescence. *Circaea alpina* never has such a pubescence on the stems. The flowers of *C. caulescens* are larger, usually pink or purplish, and open in a lateral position, whereas the small and usually purely white flowers of *C. alpina* open while directed upwards. The leaves of *C. caulescens* are darker and nontransparent, while the leaves of *C. alpina* usually are lighter colored and translucent when dried.

In 1970 I described what I believed to be a new species, *Circaea caucasica*. Since then, after having studied additional materials, especially from Siberia, I have concluded that *C. caucasica* should be included in *C. caulescens*. Whether it might be regarded a subspecies, remains to be seen.

The total area of *Circaea caulescens* consists of four widely disjunct fragments (Fig. 2): (1) Far East; (2) Baical and northern Mongolia; (3) Altai; (4) central and western part of the Great Caucasus. This is an extremely interesting and very rare type of distribution, that is probably most closely matched by the distribution of *Osmorhiza aristata* (Thunb.) Makino & Yabe (Umbelliferae). The latter species also has its main area of distribution in the Far East, with small fragments in the Altai and in the western part of the Great Caucasus.

Ecologically *Circaea caulescens* resembles *C. alpina* closely.

Quite often the two species grow intermingled; I have seen this many times in the Primorski Province, in the Altai, and in the Caucasus. But no intermediates have been observed in such cases, nor among herbarium specimens. It seems that *Circaea caulescens* generally prefers drier and warmer situations than does *C. alpina*.

The Himalayan *Circaea imaicola* (Aschers. & Magnus) Hand.-Mazz. and the western North American *C. pacifica* Aschers. et Magnus are closely related to *C. caulescens*. All three should be regarded as descendants of a common ancestral stock, evidently a Tertiary warm-temperate one, whereas *C. alpina* and *C. micrantha* A. Skvortsov are descendants of another stock, probably a Pleistocene cold-temperate one. The third, and seemingly the most ancient relic stock of the *Uniloculares* group, is the Himalayan and South Chinese *C. repens* Wall. The origin of the *Uniloculares* (i.e., its divergence from the *Biloculares*) group must have taken place somewhere in southeastern Asia about the beginning of the Neogene.

3. *CIRCAEA LUTETIANA* L.

Like *Circaea alpina*, this species has a holarctic distribution but—in contrast to *C. alpina*—with many wide disjunctions. As has already been shown by Jäger (1969), the whole group *Biloculares*, to which *C. lutetiana* belongs, is very distinctly associated with the main regions of temperate deciduous broad-leaved and mixed (i.e., coniferous + broad-leaved) forests. The total range of the group resembles the area of the genus *Tilia* (Jäger 1969: figs. 4–5).

In the USSR, *Circaea lutetiana* has four main regions of distribution (Fig. 3): (1) Mixed and broad-leaved forests of the Russian Plain up to the foothills of the Urals; (2) mixed and broad-leaved forests of Crimea and Caucasus; (3) rich dark taiga or deciduous forest of the Altai-Sayan region of Siberia; (4) mixed and broad-leaved forests of the southern part of the Soviet Far East.

Besides these main fragments there are a number of disjunct isolated localities, the most interesting being those in the Saur Range (south of Lake Zaisan), in the Dzhungarian Range, and near Bayan-Aul in the hilly plateau (“Melkosopochnik”) of the northern Kazakhstan.

Among old nineteenth-century collections preserved at LE, there are three intriguing specimens of *Circaea lutetiana*:

1. “Türcomania, Karelin.” At present, the species is not known in Turcomania (Turkmenia), though the tip of its Iranian area approaches the USSR borders very closely. Perhaps Karelin collected the plant on what is now Iranian territory—or *C. lutetiana* may indeed have been growing in Turkmenia and subsequently died out.

2. “In deserto Kalmykorum inter Volgam et Ural, Sergatscheff (Reliq. Fischer).” Beyond the Volga towards the Ural River in the midst of dry treeless steppe, there is indeed a place where many forest plants find shelter—the so-called Saltovski Forest on sandy terraces of the Eruslan River (northeast of Kamyschin, at the border between the provinces of Saratov and Volgograd). Has the plant indeed been collected here? If so, this would be extremely interesting, and still more so because in its morphology the plant resembles mid-European or Caucasian specimens rather than eastern-European ones.

3. “In nemoribus humidis haud procul a Syuzma, Archangel, Bohuslaw in 1844.” Syuzma is situated west of Arkhangelsk at the White Sea coast. The record seems to be quite improbable because the locality is so far north. But one should keep in mind that even farther north, at the so-called Zimni Bereg (Winter Coast) of the White Sea, there is a disjunct fragment of the area of *Epilobium montanum* (Skvortsov, 1976), and a number of other temperate forest species (*Alnus glutinosa*, *Anemone ranunculoides*, *Corydalis solida*, *Viola mirabilis*, etc.) reach the southern coasts of the White Sea.

Circaea lutetiana requires rich, deep, and humid soil. In the European part of the USSR its usual habitat is in the bottoms of forested ravines, especially if they contain small rivulets; in Siberia the most usual habitat is alluvial forests.

If typical mid-European plants are compared with Far-Eastern ones, it can be easily seen that the latter are less pubescent, and have more elongated leaves and less attenuate bases of nutlets; the nutlets are conspicuously ribbed to grooved. Based on these differences, Maximowicz (1859:106) established for the Far-Eastern plants the “forma *quadrisulcata*”; Franchet & Savatier (1875:169) elevated

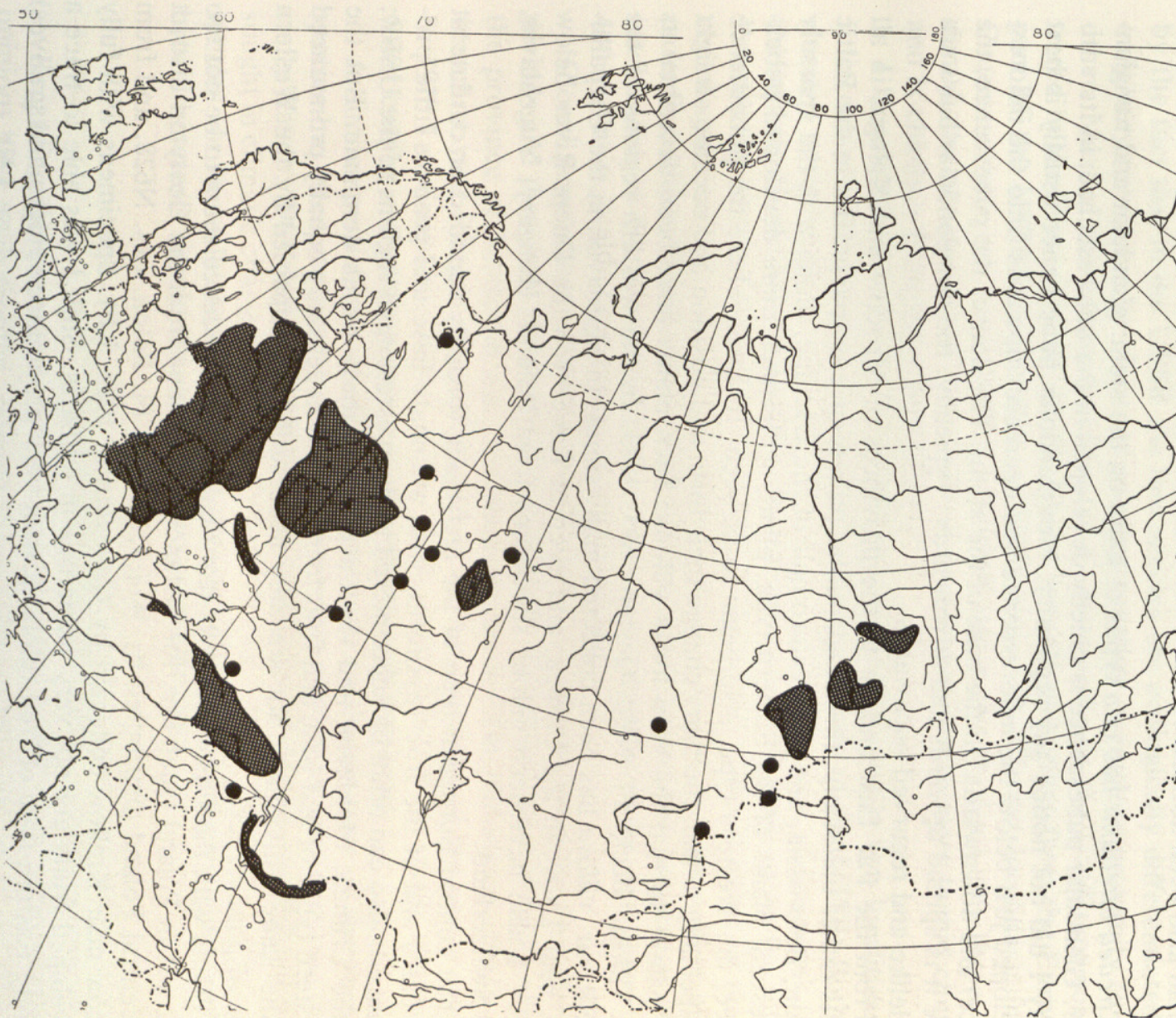


FIGURE 3. Distribution of *Circaea lutetiana* in the Soviet Union.

it to specific rank. Following them, twentieth-century Russian literature usually accepts the existence of two vicarious species: the European-Caucasian *Circaea lutetiana* L. s. str., and the Far-Eastern *C. quadrisulcata* (Maxim.) Franch. & Savat. Many foreign authors regard the latter as a variety or subspecies. The status of the Siberian populations remains obscure from any viewpoint; usually they are tacitly accepted as belonging to the European race.

I long ago had come to the conviction that *Circaea quadrisulcata* cannot be maintained as a species. But as to recognition of subspecies, the situation seemed to me doubtful. The pattern of morphological variability had to be carefully considered against the geographical background. Hence, in the course of preparation of the present paper the variability of *C. lutetiana* has received special attention.

A most surprising fact is that plants from the central region of the European part of the USSR look more like Far-Eastern than central-European ones. This fact had also been noticed by Dr. P. H. Raven, who insistently drew my attention to it.

Circaea lutetiana has two types of hairs on the stem: glandular and nonglandular. Glandular pubescence is chiefly developed in the inflorescence; in its variability I did not notice any regularity. Nonglandular pubescence usually is best developed just below the inflorescence and decreases upwards (into the inflorescence) and downwards (to the base of the stem). The denser the pubescence, the more it is spread upwards and downwards. Typically, the nonglandular hairs are sicklelike and recurved backwards.

From the Far East and up to the provinces of Moscow and Kaluga, in all plants rather uniformly, the nonglandular pubescence is sparse. But in the Baltic region, Belorussia, and the western half of the Ukraine, along with the sparsely pubescent plants of the Eastern type, plants with much more developed pubescence, the Western type, also begin to be seen. In cases where the pubescence is especially dense, the hairs change their form and position and become straight and patent so that the stem looks villous. Such plants have been described as var. *villosa* Beck, Fl. Nied.-Oesterr. 695. 1893. In the western regions of the USSR var. *villosa* has been collected many times: in Moldavia, in the Carpathians, near Lvov, in the Crimea, and even at Kanev (on the Dnepr River below Kiev). I also have seen villous specimens from Poland, Hungary, Yugoslavia, and Switzerland.

The central European type of the leaf blade (broadly rounded or cordate at the base) and of the fruit (pyriform, with attenuate base and grooves little pronounced) also can often be encountered in the westernmost regions of the USSR; in the Crimea, Moldavia, and the Carpathians these forms dominate. But the Western types of leaf base and fruit form are not necessarily equally pronounced in the same individuals; nor are they necessarily accompanied by the Western type of pubescence.

Plants with the Eastern type of leaf blade and pubescence seem to be not too rare yet in Poland (such are, for instance, specimens from the Gostynin district in central Poland distributed by *Woloszczak* as Fl. Polon. exs. N628, and from Ojców near Krakow collected by *Ganeshin* in 1905, LE). Specimens with fully developed fruits are not very numerous in herbaria. Still, I was able to trace a purely Eastern type of fruit (globose with very pronounced ridges and grooves) as far west as the Alps ("Lienz in Tirol," *Gander*, without date, LE).

In the Caucasus, plants of the Western type are prevalent, though a wide range of variability can be observed. The villous type of pubescence is rather frequent. In the few Iranian specimens I have seen nonglandular pubescence is quite sparse.

To sum up, any distinct demarcation line between the Eastern and Western morphological types of *C. lutetiana* cannot be drawn. Hence, there seems to be no good reason to recognize any intraspecific taxonomic entities. The situation can be more adequately portrayed in a descriptive manner in terms of character geography and frequencies.

4. *CIRCAEA* × *INTERMEDIA* Ehrh.

This sterile hybrid between *Circaea alpina* and *C. lutetiana* is quite common in central and Atlantic Europe but rather rare in the USSR. This may be explained by the fact that in the USSR the two species are ecologically differentiated and only very rarely can be observed growing together or in close proximity to each other. Most of the known localities of *C. intermedia* in the USSR are concentrated in the West (Fig. 4). In all, I have seen 23 gatherings from the European part of the USSR (representing probably some 20 different localities); in the Caucasus there are seven known localities, and in the Far East only three. Evidently, the occurrence of *C. intermedia* is associated with more humid climates and is chiefly a European phenomenon.

I have observed *Circaea intermedia* in natural habitats in two localities that I discovered in the central region of the European part of the USSR. Both are situated in the valley of the Ugra River: one in the province of Smolensk (near the village Zhelanya), and another in the province of Kaluga (near the village Palatki). In both localities *C. intermedia* grows alone, without either of the parental species in its immediate neighborhood. In the first locality neither of the parents could be found closer than at least 1 km around the population of *C. intermedia*. In the second locality, *C. lutetiana* has been found at a distance of 400 to 500 m, but *C. alpina* was nowhere around.

Clonal populations of *Circaea intermedia* can persist for quite considerable periods and thus may have originated long ago. The above mentioned locality in the province of Smolensk was first seen by me in 1938 (Skvortsov, 1961)—the very first year I began plant collecting in the surroundings of my native village. In 1978 I revisited the place. Although the habitat had been much altered by wood cutting and cattle grazing, *C. intermedia* still persisted.

A similar persistence of *Circaea intermedia* in the absence of the parental species has been repeatedly recorded in western European literature (see especially Raven, 1963; Jungblut, 1967). The explanation of this phenomenon may be sought in climatic changes or in interference of man causing the decline of parental species, or in an interaction of both factors. But fairly certainly some kind of hybrid heterosis should also be taken into consideration.

5. *CIRCAEA MOLLIS* Sieb. & Zucc.

Regarding the presence of this species in the USSR flora, very divergent opinions have existed. The situation was clarified in my previous paper (Skvort-

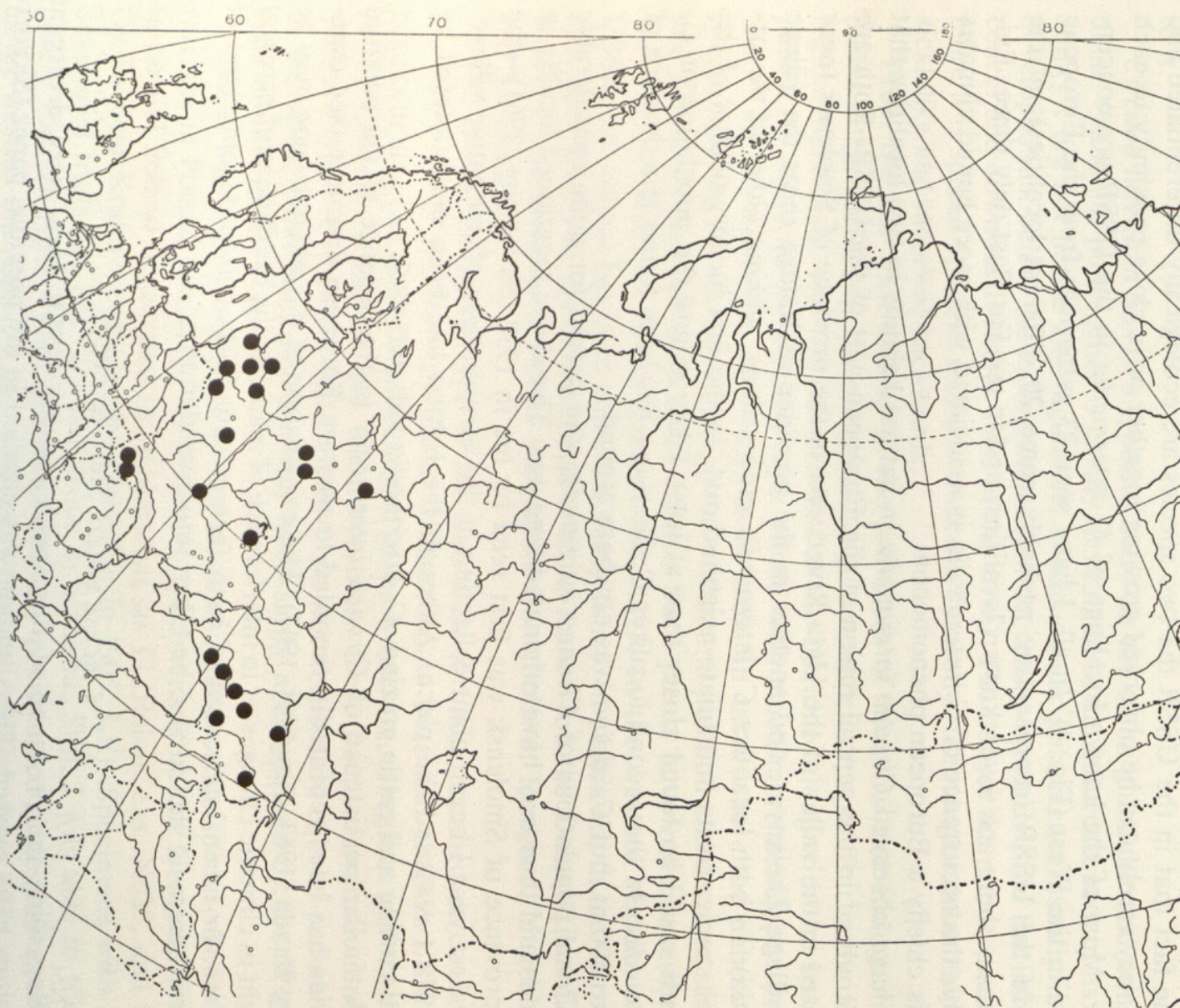


FIGURE 4. Distributions of *Circaea* \times *intermedia* (dots), *C. mollis* (asterisk) and *C. cordata* (shaded area)

sov, 1977). The species has been collected in the USSR twice, both localities being situated near the southern edge of Lake Hanka (Fig. 4).

6. *CIRCAEA CORDATA* Royle.

This species is rather common in the southernmost part of Primorski Province, including the islands in the Gulf of Peter the Great. Towards the north it quickly becomes rare; the northernmost locality is Mount Vandan about 60 km north of Khabarovsk. The species has not been found on Sakhalin Island, but occurs on the small Moneron Island near the southwestern edge of Sakhalin, and on Kunashir Island.

Compared with *Circaea lutetiana*, *C. cordata* prefers better drained and open habitats, often along forest edges. In spite of its quite extended distribution, the species seems to display no significant geographical variability. Specimens I collected in several localities in Kashmir cannot be discriminated from plants collected near Vladivostok.

7. *CIRCAEA ERUBESCENS* Franch. & Savat.

According to Hara (1934: 592), this species was collected by Sugawara near Toyohara (now Yuzhnosakhalinsk). In the USSR herbaria (LE, MHA) there are two specimens collected near Yuzhnosakhalinsk which could have been suspected to belong to *Circaea erubescens*: (1) An unidentified Japanese collector, 30. Aug. 1931 (ex Herb. Saghalien Experim. Station); (2) V. N. Voroshilov, 7 Oct. 1953. Voroshilov (1966) evidently influenced by Hara's views, believed these specimens to be *C. erubescens*, and consequently included the species in his *Flora of the Soviet Far East*. But at the same time Voroshilov thought that *C. erubescens* might have originated as a hybrid between *C. alpina* and *C. quadrisulcata*. In my opinion, both specimens are *C. × intermedia* and differ distinctly from *C. erubescens*. Thus there is no evidence of the existence of *C. erubescens* in the USSR.

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