**VACCINIUM VITIS-IDAEA L. SUBSP. MINUS (G. LODD.) HULTÉN (ERICACEAE), AN OVERLOOKED CIRCUMPOLAR-ARCTIC TAXON OF THE ALPS**

by

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Resumen

Vaccinium vitis-idaea s.l. está representado en los Alpes por dos subespecies, las cuales se distinguen por varias características (tabla 1). La subespecie minus es un taxon ártico-circumpolar que se encuentra principalmente en el Empetro-Vaccinietum Braun-Blanq. 1926 y asociaciones relacionadas, entre los 2000-2400 m; la subespecie vitis-idaea se encuentra en los bosques de coníferas de la taiga en toda Eurasia, excepto en el extremo oriental. A altitudes de más de 2000 m prefiere lugares más calientes, cubiertos por la nieve en invierno.

Palabras clave: Spermatophyta, Ericaceae, Vaccinium vitis-idaea, distribución ártico-circumpolar, Empetro-Vaccinietum, Alpes.

Abstract

Vaccinium vitis-idaea s.l. is represented in the Alps by two taxa which are distinguished by various characteristics (table 1). Subspecies minus, a circumpolar-arctic taxon, is mainly restricted to the Empetro-Vaccinietum Braun-Blanq. 1926 and related associations between 2000 and 2400 m, whereas subsp. vitis-idaea is present within a wide area of the coniferous belt and is distributed in the taiga of Eurasia (except the Far East). At altitudes of more than 2000 m it prefers warmer sites which in winter are covered with snow.

Key words: Spermatophyta, Ericaceae, Vaccinium vitis-idaea, circumpolar-arctic distribution, Empetro-Vaccinietum, Alps.

INTRODUCTION

In mid September of 1994, Prof. Dr. K. Urbanska and I spent a few days in the regions of Davos and the Engadine showing the flora and vegetation of the Swiss Alps to guests of our institute, Prof. Dr. B.A. Yurtsev and Dr. A.E. Katenin of St. Petersburg, Russia. One day, while we were eating our lunch sitting on a northern exposed slope below the Albula Pass, Prof. Yurzev suddenly pointed to a *Vaccinium vitis-idaea* plant and commented that in his opinion, the specimen was identical to the subsp. minus (G. Lod. Hultén, a taxon which he knew well from his studies in eastern Siberia. Not far from the site of this taxon, our guests also found specimens of the subsp. vitis-idaea. Until this sighting, the

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taxon subsp. *minus* went mostly unrecognized in the Alps. As to my knowledge, no flora of the Alps or of alpine countries of this century distinguishes the taxon. In the *Flora Europaea* (Tutin & al., 1972: 12-13) the subsp. *minus* is cited only from northern Russia. Hultén (1958: 78-79) also records it from northern Scandinavia and, with some reservation, from Scotland. As an exception, Schroeter (1926: 240-248) published a drawing of a plant from high altitude (3000 m) which he thinks is similar to the var. *pumilum* Hornem. (subsp. *minus*) from Lapland.

If the subsp. *minus* really exists in the Alps, there must be some reason why it has been overlooked until now, since many excellent plant taxonomists have been studying the flora of the Alps for over two hundred years. This has made the study of the position of this taxon in the Alps quite exciting. It was my intention to answer the following questions:

- What are the morphological differences between the two taxa in regions where they have been distinguished? Can plants with similar characters be found within the Alps?
- Are there differences in chromosome numbers between the two taxa?
- Have the two taxa different ecological characteristics and geographical distribution?
- Why was this taxon not recognized earlier in the Alps?

**MATERIAL AND METHODS**

Three populations of eight plants with characteristics of subsp. *minus* and of subsp. *vitis-idaea* were collected on September 20, 1994 and transplanted to a climatic chamber in Zürich. The three localities where both subspecies were collected are situated in the Grisons, Switzerland, above the actual timberline: Albula pass, Julier pass, Bernina pass. The exact locality is shown in table 2. Samples of a seventh population consisting of subsp. *vitis-idaea* were taken from a Larici-Pinetum cembrae at Morteratsch (1850 m altitude). At this locality no subsp. *minus* was growing near by.

The cultivated plants were kept in climate chambers (12 hours daylight at 20 klux, 18 °C day temperature, 10 °C night temperature). The plants began to flower after one to three months.

Morphological observations were performed in nature (fruits, leaves), on cultivated plants (flowers, newly formed leaves), and on herbarium specimens.

One relevé, according to the method of Braun-Blanquet, was taken from each locality of the three passes (Julier, Bernina, Albula). An area of 25 m² was selected in which subsp. *minus* was represented in the cover by at least 10%. The nomenclature of the vascular plants is taken from Hess & al. (1967-1972).

Chromosome counts were performed from squashed root tips.

*V. vitis-idaea* s.l. specimens of the herbaria Z, ZT and B were searched for indications of the distribution area of subsp. *minus* within Switzerland and for morphological characteristics.

**RESULTS**

**Morphology and chromosome numbers**

The observed morphological differences between the two taxa are summarized in table 1. The cultivated plants of the two taxa displayed most of the same differences, except that the young leaves of subsp. *minus* grew much bigger than in nature (up to about 1.4 cm in diameter compared with 1.5-1.8 cm in subsp. *vitis-idaea*). The size of the leaves is determined to a certain degree by ultraviolet light which reduces the elongation growth of the cells. Under the culture conditions in the climate chamber, no UV light is present. This might explain the larger size of the leaves (fig. 1). On the other hand, the reddish colour of the lower surface of young leaves is still very pronounced in subsp. *minus*, whereas subsp. *vitis-idaea* only very rarely displays a slight reddish colour.

Most of the morphological results are in accordance with the indications in the literature (cf. Fernald, 1950: 1134 for subsp. *minus*, Schiskin & Bobrov, 1952: 100-102, and Tu-
TABLE 1
MORPHOLOGICAL CHARACTERISTICS OF Vaccinium vitis-idaea subsp. vitis-idaea and subsp. minus

<table>
<thead>
<tr>
<th>Character</th>
<th>vitis-idaea</th>
<th>minus</th>
</tr>
</thead>
<tbody>
<tr>
<td>length of the largest leaves</td>
<td>&gt; 1.5 cm</td>
<td>0.8-1.2 cm</td>
</tr>
<tr>
<td>reticulate nerves on the lower surface</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>main nerves on the upper surface depressed</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>main nerves on the lower surface distinct</td>
<td>+</td>
<td>-,(+)</td>
</tr>
<tr>
<td>young leaves with anthocyanin</td>
<td>-,(+)</td>
<td>++</td>
</tr>
<tr>
<td>length of longest petioles</td>
<td>1.5-4 mm</td>
<td>0.8-1.5 mm</td>
</tr>
<tr>
<td>colour of the bracts in the flowering stand</td>
<td>whitish</td>
<td>reddish</td>
</tr>
<tr>
<td>no. of flowers in the raceme</td>
<td>3-8</td>
<td>1-4</td>
</tr>
<tr>
<td>length of corolla</td>
<td>5-7 mm</td>
<td>3-4 mm</td>
</tr>
<tr>
<td>incision of corolla compared with length</td>
<td>1/3</td>
<td>1/2</td>
</tr>
<tr>
<td>length of style</td>
<td>6-10 mm</td>
<td>3-4 mm</td>
</tr>
<tr>
<td>length of stamens</td>
<td>4-5 mm</td>
<td>3-4 mm</td>
</tr>
<tr>
<td>length of pollen sacs</td>
<td>c. 2 mm</td>
<td>c. 1 mm</td>
</tr>
<tr>
<td>length of tubes of stamens</td>
<td>c. 2 mm</td>
<td>c. 1 mm</td>
</tr>
<tr>
<td>length of hairs of filaments</td>
<td>0.3-0.4 mm</td>
<td>0.1-0.2 mm</td>
</tr>
<tr>
<td>diameter of fruits</td>
<td>5-8 mm</td>
<td>3-5 mm</td>
</tr>
<tr>
<td>length of seeds</td>
<td>1.4-1.8 mm</td>
<td>1.0-1.3 mm</td>
</tr>
</tbody>
</table>

TIN & al., 1972: 12-13 for both taxa). The dimension of the fruits are generally larger in the literature, which is probably due to the larger size in herbaria specimens. The sizes in table 1 were measured on living fruits in nature. The only character of subsp. minus which could not be confirmed in the Alpine plants is the colour of the flowers. Whereas FERNALD (1950), MOSS (1958: 370-371) and TUTIN & al. (1972) describe the flowers as

![Fig. 1.-Drawings of leaves of Vaccinium vitis-idaea subsp. minus from above (a) and from below (b) and of subsp. vitis-idaea from above (c) and from below (d).](image-url)
“pink or reddish”, “rose-pink” and “bright pink” respectively, the colour of the flowers in the climatic chamber are more or less white. It could not be determined whether the colour of the Alpine representatives of subsp. minus are also white in nature, or if the absence of red pigment in the flowers of the cultivated plants is due to the lack of UV light in the chambers.

According to Schröeter (1926) V. vitis-idaea flowers twice a year at lower altitudes; in May (fruit ripens in August) and in August (fruit ripens in October). At higher altitudes there could be only one flowering. Our observations in midand late September show that at the same altitude, the fruits of subsp. minus were already ripe and deep red, whereas the fruits of subsp. vitis-idaea were still partly white. This might give an indication that at this high altitude subsp. vitis-idaea, which grows in warmer places than does subsp. minus, was already fruiting for the second time, while subsp. minus was fruiting for the first time in that season.

Hultén (1958: 78) writes that apparently the chemical composition of the berries of subsp. vitis-idaea and subsp. minus is different. “Jam made from Swedish lowland berries (apparently subsp. vitis-idaea) never moulds, probably on account of the benzoic acid, said to amount to 0.075 % of the weight. Jam made in the same way from berries collected by the writer on Mt. Fujiyama in Japan (apparently subsp. minus) however, moulded.”

Unfortunately, the plants did not develop many roots during the winter. Therefore, the cytological preparations showed rather poor results. One count from a plant of subsp. minus from Bernina amounted to about 2n = 24. This is in accordance with earlier chromosome counts. Loeve & Loeve (1975) cited the same chromosome number for both taxa from many places in the world.

Ecology and phytosociological position

Due to the Alpine distribution, it can be concluded that the altitudinal center of subsp. vitis-idaea is in coniferous forests and dwarf shrub communities from the montane belt up to the lower alpine belt. It is very rarely found below 1000 m, where it is restricted to raised moors. According to Schröeter (1926) it needs a snow cover in winter and cannot grow on sites with strong winds. The indication values show on what habitat the plant is mostly growing: F, humidity value (F 5, wet soils; F 1, very dry soils); R, reaction value (R 5, basic soils; R 1, very acid soils); N, nutrient value (N 5, soils with over-rich supply of nutrient; N 1, very poor soils); H, humus value (soils very rich in humus; H, raw soils); D, dispersion (and deficiency of aeration) value (D 5, clayey or peaty soils poor in oxygen; D 1, cliffs, rocks and walls); L, light value (L 5, full light; L 1, very shady); T, temperature value (T 5, warmest places; T 1, very cool areas; e.g. alpine zone); K, continentality value (K 5, continental climate; K 1, oceanic climate) (Landolt, 1977).

Subsp. minus occurs in its circumpolar distribution in the northernmost taiga and over its northernmost border. However, in eastern Siberia as well as in North America, where subsp. vitis-idaea is absent or very rare, it also grows in the open taiga forest and reaches its limit much further south. “In Kamchatka, subsp. typicum (apparently subsp. vitis-idaea) occurs only in the lowlands of the central valley, while subsp. minus is common everywhere else. The difference is very marked there” (Hultén, 1958).

In the Grisons, subsp. minus is restricted to a relatively small belt above the actual timberline, between 2000 and 2400 m, where it is relatively frequent. The lower altitudes were not thoroughly investigated in the present study. There are a few herbarium samples in the consulted herbaria from below 2000 m (from 1825 and 1990 m). Therefore, it is possible that the plant also occurs at lower altitudes, but rarely and only at special sites. Many more herbarium specimens can be found from high altitudes, up to 2780 m (Sertigfurka near Davos). Schroeter cites sterile plants from Piz Forun and Piz Linard (Grisons), at the highest recorded elevations of 3040 m and 3020 m (leg. J. Braun) respectively. Botanists generally prefer to collect plants from the up-
per limit of the distribution area. Therefore these regions are over-represented in herbaria.

In the study area, subsp. *minus* is found on siliceous parent rock with a well developed humus layer (ranker or crypto-podsol). It does not grow on southern exposed slopes, nor on hilltops, ridges, or moist depressions. However, contrary to subsp. *vitis-idaea*, it can tolerate conditions where snow is absent for some time during winter (transitions to ridges). Within the area of occurrence, three relevés were taken from places where the taxon was at its optimum (table 2). This provides, of course, only an indication of the typical ecological amplitude in the southern part of the Grisons and not a thorough insight into the ecological condition of the taxon within the Alps. Table 2 shows that the ecological optimum of subsp. *minus* stays within the Empetro-Vaccinietum Braun-Blanq. 1926, subass. cetrarietosum Kuoch 1970. Outside of this community type, the taxon has been observed in neighbouring transitional stages leading into other dwarf-shrub communities, pastures of the Nardion and Caricion curvulae type, as well as places around stones and below rocks.

| Relevé no. | No. of species | V. vitis-idaea | Li, Le | 2 | 3 |
|-----------|----------------|---------------|-------|
| 1         | 37             | 2             | 2     | 2 |
| 2         | 37             | 2             | 3     | 1 |
| 3         | 35             | 2             | 3     | 3 |

Additional species in one of the relevés (mosses and lichens are not complete).


Origin of the relevés

1) Julier Pass, 2330 m; coord. 798.600/143.650; morainic hill (mostly siliceous scree); NW exp., 30 % inclination. Soil: ranker. Vegetation cover: 70 %.

2) Bernina Pass, 2295 m; coord. 715.600/149.100; gneis; W exp., 40 % inclination. Soil: ranker. Vegetation cover: 80 %.

3) Albula Pass, 2200 m; coord. 782.150/161.450; morainic hill (siliceous scree with some dolomite components; the hill is in contact with dolomite rock); N exp., 50 % inclination. Soil: cryptopodsol. Vegetation cover: 90 %.
Based on my observations of subsp. minus sites, the indication values of the taxon should be expressed as follows: F 3, R 2, N 2, H 4, D 4, L 4, T 1, K 2.

Geographical distribution

According to HULTÉN (1958: 79), subsp. vitis-idaea has a Eurosiberian and subsp. minus a circumpolar-arctic distribution area. MEUSEL & al. (1978) give similar, but not identical distribution data. Subspecies vitis-idaea is generally restricted to the taiga, roughly between 50° N and 70° N. It has not been found growing in northeastern Siberia. South of the main distribution area, it occurs in the Caucasus and in the mountains of western, central, and eastern Europe (including northern England, Scotland, and Ireland). Subsp. minus is distributed in the northernmost part of the taiga and in a small band just north of the timberline. However, in regions where subsp. vitis-idaea does not occur (eastern Asia and North America) it penetrates the taiga far to the south (fig. 2).

Distribution within the Alps is so far unknown. From my experience in the Grisons it is rather widespread along the upper timberline. It seems that the taxon can be found throughout the inner chains of the entire Alpine Range on siliceous parent rock, and its area is similar to that of Loiseleuria procumbens or Empetrum hermaphroditum. The samples in the herbaria of Z, ZT and B are rather scarce. I saw specimens from the Grisons (many specimens), northern Ticino (Lukmanier; Val Mora), St. Gall (Pizol), and Bernese Oberland (Rötihorn).

Discussion

The present study shows that there are two different morphological taxa of Vaccinium vitis-idaea s.l. in the Alps which correspond to subsp. vitis-idaea and subsp. minus from Northern Europe, Asia, and North America. The two taxa can be distinguished by quite a few characteristics in nearly the same way in the Alps as in other regions of their distribution area. Therefore, it is feasible that the two taxa be acknowledged in the Alps as well. If the small-leaved taxon is regarded as a separate species, the correct name is Vaccinium
Table 3

Species pairs of a taxon with mainly Eurasian and one with mainly arctic distribution, with chromosome numbers

<table>
<thead>
<tr>
<th>(circumpolar) arctic (-alpine) species</th>
<th>2n</th>
<th>eurasian-(northamerican) species</th>
<th>2n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vaccinium vitis-idaea subsp. minus</td>
<td>24</td>
<td>V. vitis-idaea subsp. vitis-idaea</td>
<td>24</td>
</tr>
<tr>
<td>Vaccinium gaultherioides</td>
<td>24</td>
<td>V. uliginosum</td>
<td>48</td>
</tr>
<tr>
<td>Juniperus nana (sibirica)</td>
<td>22</td>
<td>J. communis</td>
<td>22</td>
</tr>
<tr>
<td>Veronica tenella (humifusa)</td>
<td>14</td>
<td>V. serpyllifolia</td>
<td>14</td>
</tr>
<tr>
<td>Gnaphalium norvegicum</td>
<td>56</td>
<td>G. silvaticum</td>
<td>56</td>
</tr>
</tbody>
</table>

minus (Lodd.) Maksimova. Table 3 shows species pairs whose distribution patterns are similar to the two taxa of V. vitis-idaea.

It is interesting to note that the Eurasian taxon with its need for higher temperatures was not always able to colonize North America. It is probable that the origin of most of these species pairs is in North America. Therefore, the circumpolar arctic taxon is probably the older one. If the two taxa have different chromosome numbers (V. uliginosum s.l.), then the arctic species has the lower ploidy level. Apparently, gene exchange is possible between most of these pairs. Hybrid swarms or even morphological transitions (e.g. Juniperus communis and J. nana) can be observed. Where both V. vitis-idaea subsp. vitis-idaea and subsp. minus grow, plants with combinations of characteristics occur. However, the occurrence of populations of both taxa within 20 m distance shows that there must be some barriers between the taxa preventing the two from mixing. As was pointed out earlier, the flowering times of the two taxa are somewhat different, but probably still overlap. Schröter (1926) gives some indication that the stigma of subsp. minus reaches about the same level as the anthers, whereas the stigma of subsp. vitis-idaea is much longer and by far surpasses the anther. He concludes that subsp. minus must be self-pollinating, in contrast to subsp. vitis-idaea. This characteristic is widespread among arctic species and leads to some isolation of the taxa.

What is the reason for subsp. minus having gone thus far unrecognized in studies of alpine flora?

- The distinguishing characters are not always clearly recognizable. In nature, both taxa can grow together, implying that the morphological differences belong to a normal variation within a population of one taxon.
- The differences between characters of the taxa (mostly smaller size of various organs) could just as well be caused by environmental factors (UV light, cooler temperatures, etc.).
- Many herbarium samples contain specimens of both taxa on the same sheet which leads to the conclusion that the differences are intrapopulational.

Prof. Yurtsev's observation, that some of the plants in the Alps look exactly the same as the plants of subsp. minus in eastern Siberia, led to the present study and to the conclusion that subsp. minus is a genuine taxon in the Alps, overlooked until now.

There are still some details which must be cleared up. What is the exact distribution of subsp. minus in the Alps? Does the taxon occur in other mountains of central and southern Europe as well (e.g. Pyrenees Carpathians)? How much does the flowering time of both taxa overlap? Is the colour of the flower a distinguishing feature under natural conditions?

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REFERENCES
