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***Viola epipsila* Ledeb., a vanishing species in Poland**

Elżbieta KUTA

1. INTRODUCTION

The present paper is based mainly on the results of the author's detailed analysis of Polish populations of *Viola epipsila* Ledeb. and *V. palustris* L. Some additional informations from the literature and from the herbarium material from several Polish and European herbaria were also taken into account.

Both taxa, *Viola epipsila* and *V. palustris* are the only representatives in the Polish flora of the large section *Plagiostigma* Godr. of the genus *Viola* L. They belong to the subsection *Stolonosae* Kupffer comprising mainly North American diploid species. The diploid *V. epipsila* ($2n=24$) and the tetraploid *V. palustris* ($2n=48$) have a wider area of distribution and their ranges are partly sympatric.

Viola epipsila is a circumboreal species whereas *V. palustris* is an Euro-American species with some isolated localities in North Africa. They are morphologically differentiated within their area of distribution and develop geographical and ecological races distinguished in subspecies or even species ranks.

Polish populations of *Viola epipsila*, *V. palustris* and their spontaneous hybrids have been the subject of very intensive biosystematic studies using morphological, karyological and embryological criteria (KUTA 1990a,b,c) and part of the investigations on evolutionary mechanisms of differentiation of Polish native populations of the *Viola* species (KUTA 1978, 1981).

2. GENERAL DISTRIBUTION OF *VIOLA EPIPSILA* LEDEB.

Viola epipsila is a circumboreal species with two subspecies whose ranges overlap a small part of Western Siberia. The type subspecies occurs mainly in Northern Europe. Scattered localities were found in Central Europe extending from West Germany to the Ural Mts. and to Western Siberia in the east (HEGI 1925, KOMAROV 1949, MEUSEL et al. 1978, SORSA 1968, VALENTINE et al. 1968, HULTEN and FRIES 1986). *V. epipsila* Ledeb. ssp. *repens* (Turczaninow) Becker prolongs the range of *V. epipsila* eastwards from Western Siberia to the Chukotka Peninsula and then from Alaska to the Hudson Bay (ANDERSON 1959, POLUNIN 1959, SORSA 1968, LOEVE and LOEVE 1975, TOLMACHEV and JURTSEV 1980).

3. *VIOLA EPIPSILA* LEDEB. IN POLAND

Viola epipsila prefers rather eutrophic habitats and is usually connected with associations of the alliance *Alno-Padion*. According to the previous reports *V. epipsila* has been noted from quite numerous stations from northeastern Poland to the Podlasie region in the south (GRAEBNER 1896, ABROMEIT 1898, STEFFEN 1940, CZUBINSKI 1950, POLAKOWSKI 1963, KEPCZYNSKI 1965, PIOTROWSKA 1966, SOKOLOWSKI 1968, 1969, LISOWSKI et al. 1970). Scattered localities are also known from central Poland (NOWAK 1967, MOWSZOWICZ 1978) and from Silesia (SZAFER et al. 1976). Some isolated localities in the Tatra Mts. (PAWLOWSKI 1956, DOSTAL 1958) and in the eastern Carpathians (SAVULESCU 1955) clearly indicate that in the past *V. epipsila* had probably a broader range.

Analysis of 34 natural populations from almost all over Poland (KUTA 1990a,c) as well as a critical revision of herbarium material drastically changed the picture of the occurrence of *V. epipsila*. It seems evident that *V. epipsila* is becoming rather rare. At the basis of detailed studies *V. epipsila* has been recognized only in 23 populations concentrated mainly in the northeastern Poland (Fig. 1). This might be an effect of two main phenomena: 1) the frequency of *V. epipsila* dramatically decreased since the end of the last century what is excellently supported by the revision of the old herbarium material from the northern lowland, 2) the previous records were partly erroneous and in fact they concerned forms of hybrid origin.

Natural hybrids of *V. epipsila* and *V. palustris* have been found quite frequently in Polish populations. Their occurrence in nature might suggest a

great morphological variability of *V. epipsila* and *V. palustris*. Hybrids were morphologically differentiated showing more or less intermediate characters between parental species or resembled predominantly *V. palustris*.

Morphological, karyological and embryological analysis of such specimens supported their hybrid origin. Two types of hybrids have been identified in natural populations: highly sterile triploids ($2n=36$), morphologically intermediate (especially as to the characters of chasmogamous flowers) representing the F1-generation, and fully fertile tetraploids ($2n=48$) resembling *V. palustris* and originating probably via hybridization and subsequent introgression with *V. palustris* (KUTA 1990b). Since this supposition is based primarily on morphological, karyological and embryological data, conclusive documentation of introgression is rather difficult. In the light of new biochemical tech-

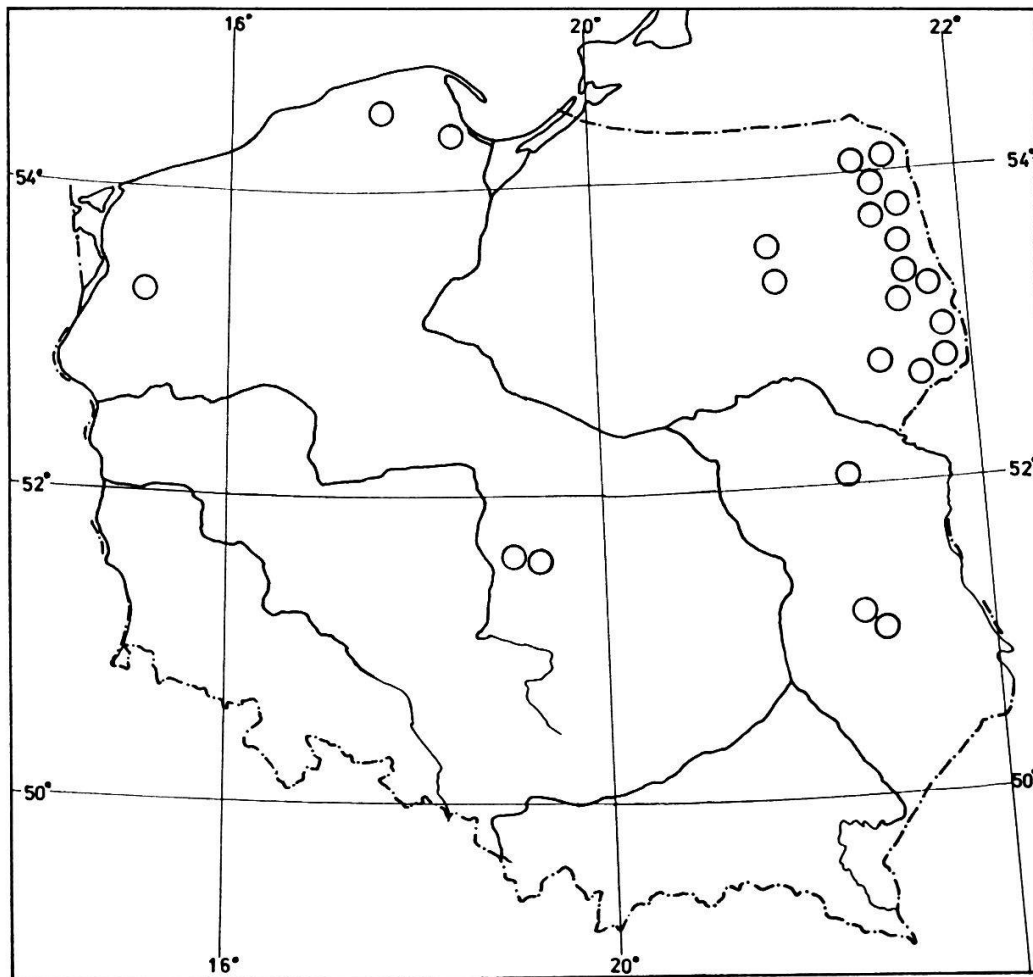


Fig. 1. Distribution of *V. epipsila* in Poland based on herbarium specimens and field studies.

niques only the use of precise genetic markers provided by allozyme and specific DNA (cpDNA, rDNA) variation may answer questions of introgression (RIESEBERG et al. 1988, SOLTIS and SOLTIS 1990).

Hybrids have been found growing together with both parental species, with *V. palustris* only or they were the only element of populations (no parental species in the vicinity) (KUTA 1990a,c). The frequency of hybrid forms was greater in northeastern Poland (data based on field studies and on herbarium material) than in western and southern Poland where *V. epipsila* has not been recorded so far (Fig. 2).

The occurrence of forms of hybrid origin in western and southern Poland supported also the hypothesis of the broader range of *V. epipsila* in the past.

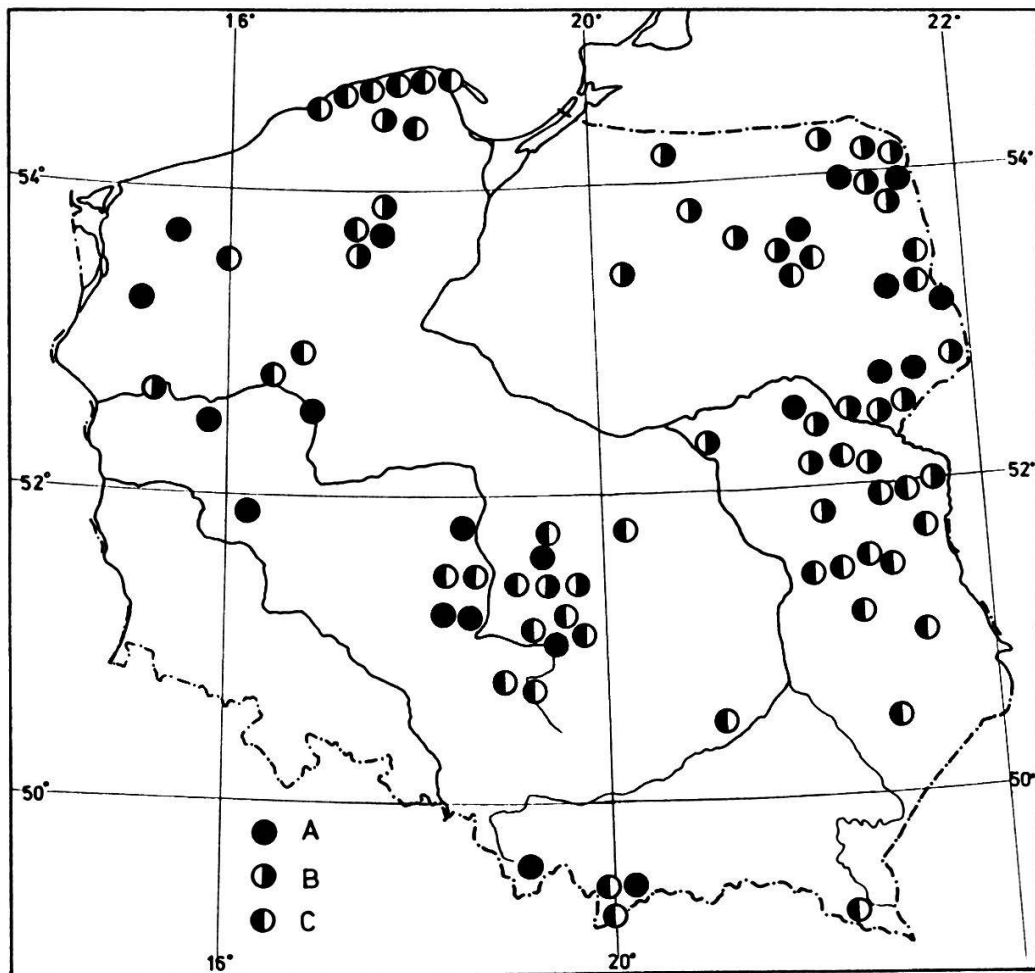


Fig. 2. Distribution of forms of hybrid origin in Poland.

A = hybrid of *V. epipsila* x *V. palustris* (material incomplete for precise determination)
B = *Viola* x *ruprechtiana*, C = *V. palustris* ssp. *pubifolia* (based on herbarium specimens of *V. epipsila* and *V. palustris* and field studies)

Based on these data, the migration of *V. epipsila* from the northern centre of its distribution to southern Poland during the old glacial period might be reconstructed. *V. epipsila* and *V. palustris* have probably been brought into contact, and mixed populations created excellent conditions for hybridization. Forms of hybrid origin which generally endure the climatic and ecological changes of the environment might have colonized new habitats and *V. epipsila* could have survived at higher altitudes after the retreat of the glaciers.

The actual distribution of *V. epipsila* in northern Poland is undoubtedly associated with the Baltic glaciation and can be considered in this area as glacial relict (STEFFEN 1931, CZUBINSKI 1950).

In conclusion, one might assume that *V. epipsila* is mainly endangered in Poland by the rapid change of habitats due to man's intervention in nature and is subsequently eliminated or replaced by more or less stabilized forms of hybrid origin. As both types of hybrids were often erroneously interpreted as *V. epipsila*, the author proposes to retain the name *Viola x ruprechtiana* Borb. for unstabilized triploid hybrids whereas stabilized tetraploid forms should be distinguished as *V. palustris* L. ssp. *pubifolia* Kuta (KUTA 1990c).

4. DISCUSSION

Comparing the actual distribution of *V. epipsila* in Poland with that in other countries, it seems evident that *V. epipsila* is rather rare in all Europe and even extinct in some regions. The general pattern of differentiation of all investigated populations of *V. epipsila* and *V. palustris* is almost the same as the process of hybridization plays a main role in evolutionary changes. The two species are closely related (even the allotetraploid origin of *V. palustris* with part of *V. epipsila* genome as one of the parental species was postulated) and natural hybrids have been found almost throughout the whole overlapping range. Forms of hybrid origin have been reported from Norway and Finland (EKLUND 1934, 1958, SORSA 1965, BRANDRUD and BORGES 1986), from Austria (PACHER 1894) and from Germany (HEGI 1925). Hybrids have also been found in herbarium material from Hungary (BP), Rumania (BP) and western Russia (KRA, KRAM) (abbreviations of herbaria according to HOLMGREN et al. 1990). In North America some morphologically less typical populations of *V. palustris* evidently indicate the influence of *V. epipsila* ssp. *repens* genes (SORSA 1968).

Hybrids are more or less stabilized, but due to vegetative reproduction by stolons, they are very expansive and in changing disturbed habitats they usu-

ally eliminate step by step *V. epipsila*. The frequency of *V. epipsila* gradually decreases from the northern centre of its distribution in Fennoscandia towards south. It is less rare, although not yet endangered, in southeastern Norway (BRANDRUD and BORGES 1986) than in Finland where *V. epipsila* is threatened with extinction and replaced by hybrid populations (SORSA 1965). An extreme example represents the southwestern archipelago of Finland where only forms of hybrid origin have been recognized with the complete extinction of *V. epipsila* (EKLUND 1934, 1958). In Poland the situation seems to be very similar to that in Finland although the hybrid populations do not show the same morphological and karyological variation. The populations in Finland probably represent later hybrid derivatives and different stages of introgression.

In North America, the occurrence of closely related diploid species belonging to the same subsection *Stolonosae* might be involved in hybridization with *V. epipsila* ssp. *repens*. The data is too scanty to take any general conclusions (CLAUSEN 1964, SORSA 1968).

The importance of hybridization in the evolutionary process of plants at, above and below the species level has been discussed since KERNER (1894-1895) stated it (GRANT 1981). It is evident that hybridization is a very common process among higher plants and one of the major routes in the evolution of species.

The role of hybridization in differentiation of particular groups of the genus *Viola* has been pointed out by CLAUSEN (1951, 1964) and VALENTINE (1962, 1976).

On the one hand, hybridization is involved in the origin of new species via polyploidy and there are a lot of examples of allopolyploids within *Viola* sections based on still existing diploid putative parental species. Such polyploids might come into contact with sympatric diploids or other polyploids resulting in partially sterile hybrids or more or less stabilized modified polyploid forms. These phenomena were observed in European sympatric populations of *V. riviniana* Rchb. with *V. reichenbachiana* Jordan ex Bureau (VALENTINE 1941, KUTA 1978), with *V. uliginosa* Bess. (KUTA 1978), with *V. canina* L. (CLAUSEN 1931, BRUUN 1932, MOORE 1959, VALENTINE 1975, KUTA 1981), and with *V. lactea* Sm. (MOORE 1959).

On the other hand, a large group of blue flowering North American violets belonging to the subsection *Boreali-Americanae* and the small subsection *Blandae* with only two white flowering species (*V. blanda* Willd. and *V. incognita* Brain) should be considered. All species represent the same ploidy

level and have the same chromosome number (*Boreali-Americanae* $2n=54$ and *Blandae* $2n=44$). The species within each group are closely related and hybridize easily in nature yielding fertile hybrids which may give rise to hybrid swarms where parental species become connected phenetically by every possible intermediate types. As a consequence, in many areas it is difficult to match the natural populations of "pure" species (BRAINERD 1904, 1924, RUSSEL 1954a,b, 1955, ANDERSON 1954, MCKINNEY and BLUM 1978, 1981, KUTA 1988). Hybridization in the larger sense might be regarded as 1) the route of formation of new species mainly via polyploidy, although several other modes of hybrid speciation in plants are known (GRANT 1981), 2) a factor introducing a great morphological variation within populations of related species forming hybrid swarm so that one species grades almost imperceptibly into the other, 3) enrichment of the gene pool of already successful species via introgression or in case of vanishing species they may save their genes by introducing them gradually into the other, and 4) a threat to the survival of small populations of endangered species.

SUMMARY

The distribution of *Viola epipsila* in Poland is compared with that in other regions. It seems evident that *V. epipsila* is becoming rather rare throughout the whole European distribution area, being even already regionally extinct. The significance of interspecific hybridization in evolutionary changes of populations with special attention to the genus *Viola* is discussed.

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