PHENOTYPIC VARIATION OF *EPIPACTIS HELLEBORINE* x *E. ATRORUBENS* HYBRIDS IN ANTHROPOGENIC CONDITIONS

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(Received: May 25, 1995. Accepted: July 20, 1995)

ABSTRACT

Hybrid index has revealed the hybrid nature of helleborine populations growing on disturbed habitats in Białowieża Forest and its western foreland. An analysis of eight traits has revealed that hybrids are morphologically more similar to *E. helleborine*. Hybrids differ from the typical *E. helleborine* first of all by: a very pubescent inflorescence axis, a considerable length of the subinflorescence internode.

Also the range of phenotypical variation in these populations is shown.

KEY WORDS: *Epipactis helleborine*, *E. atrorubens*, *E. x schmalhauseni*, *Orchidaceae*, hybridization, poplar plantations, apophytism, Białowieża Forest.

INTRODUCTION

Hybridization is an important mechanism of evolution. Different investigators (see Stebbins 1958; Wagner 1968; Stace 1975, 1993 and the literature cited in them) attribute different importance to it. Hybridization and its frequent companions – introgression (Heiser 1973) and polyploidization (Stace 1993) are the source of new combinations of adaptations which make colonization of new habitats possible. These processes often are the first stage of the formation of new taxa. Particularly numerous hybrid forms occur in situations where catastrophic natural factors or man's activity have created new habitats, breaking existing ecological barriers.

Polish investigators have devoted much attention to the effects of hybridization (Staszkiewicz & Tyszkiewicz 1969, 1972; Staszkiewicz 1977, 1991, 1992; Staszkiewicz et al. 1993; Wójcicki 1991; Wójcicki and Marhold 1993; Kuta 1991 and others). This phenomenon usually followed disturbances in natural systems (communities and habitats), caused by man's activity. It is believed that the factor responsible for the intensification of hybridization of *Viola epipsila* and *V. palustris* was the reclamation of peatbogs (Kuta 1991). Starting the culture of cherry-trees (*Prunus cerasus*) was followed by the appearance, over a considerable part of Europe, of swarms of hybrid *Prunus x eminus* (*P. fruticosa* x *P. cerasus* – Wójcicki 1991; Wójcicki and Marhold 1993). Most vulnerable to the "dilution" by hybrid swarms are marginal populations, isolated from the main range e.g. *Quercus pubescens* at Bielinek on the Odra River (Staszkiewicz 1977), *Prunus fruticosa* in the western, discontinuous part of the species area (Wójcicki 1991). Hybrid forms often occur in areas where the altitude ranges of closely related species overlap, e.g. of *Lonicera nigra* and *L. xylosteum* (Staszkiewicz 1991), *Centaurea jacea*

and *C. oxylepis* (Staszkiewicz 1992). Investigations into the variation of *Betula humilis* have revealed, in addition to the effects of its crossing with *B. pendula* and *B. pubescens*, paleointrogression from *B. nana* and *B. tortuosa* (Staszkiewicz et al. 1993).

Orchidaceae seem to be a group with relatively weak genetical barriers. They readily interbreed in culture, and the hybrids most often are fecund. In the literature an increasing number of artificial orchid crossings have been reported (Hunt et al. 1975 – about 45 000; Stace 1993 – about 75 000). In spite of the considerable specialization of the family *Orchidaceae*, e.g. in the selection of pollinators (Faegri and van der Pijl 1979) and ecological requirements, representatives of its species and even genera (Hunt et al. 1975; Sundermann 1975) relatively often interbreed also under natural conditions. Bernacki (1989) reports from Poland on 40 interspecific and 39 intergeneric hybrids, the number of native orchids being equal to 50.

Herbarial material collected in 1988 from forest roadsides in the Białowieża Primeval Forest (Adamowski 1990) and from poplar plantations near Czeremcha (Adamowski and Conti 1991) was originally identified as *E. helleborine*. After a closer analysis and consultations with specialists it has appeared that at least part of the specimens collected have traits of the hybrid *E. helleborine* (L.) Cr. x *E. atrorubens* (Hoffm.) Schult. (= *E. x schmalhauseni* Richt.). Helleborines collected earlier on primeval-forest roadsides have also been identified as *E. x schmalhauseni* by Dr. L. Bernacki during a taxonomical revision.

An abundant occurrence of helleborines and other orchids in secondary or disturbed habitats and in new communities is characteristic of the phenomenon which Faliński (1966, 1968, 1986) defined as apophytism. The phenomenon is treated in a

similar way in my studies (Adamowski 1990; Adamowski and Conti 1991).

Epipactis helleborine most often occurs in broad-leaved forests and scrub. It is more tolerant to soil pH and moisture than *E. atrorubens*, requires better trophical conditions, but can thrive in shaded sites (Oberdorfer 1983; Zarzycki 1984; Rameau et al. 1993; Table 1). In eastern Kazakhstan it is found in river valleys, moist meadows and among shrubs and trees on streamsides (Kovalevskaja 1971). In Poland it grows in broad-leaved forest communities of the order *Fagetalia*, most often in thermophilous beech forest (Matuszkiewicz W. and Matuszkiewicz J. mscr.). In central Poland *E. helleborine* is much more frequent than *E. atrorubens* (Mowszowicz 1978; Nowak 1983). In the Białowieża Primeval Forest it has been known from isolated localities in oak-linden-hornbeam and bog spruce forests (Sokołowski 1966, 1968, 1981).

Epipactis atrorubens occurs far more often than *E. helleborine* in non-forest communities: scree-covered sites, grass-covered rock, xerothermic grassland and dunes, particularly seaside dunes (Hegi 1925; Oberdorfer 1983; Tabaka et al. 1988; Grabherr and Mucina 1993). It is the only orchid species growing on the steppe grassland found in areas between the rivers Danube and Tisza (Keller and Schlechter 1940). The species occurs also in thermophilous scrub and forest communities. It prefers soils rich in carbonates, sandy or rocky, dry and rather poor in nutrients and humus. It often grows in fully insolated sites. In France it is most abundant in the subalpine zone (Rameau et al. 1993). It can grow at higher al-

titudes than *E. helleborine* (Table 1). *E. atrorubens* is rare in the east-European part of its range (Hulten and Fries 1986). In contrast to *E. helleborine*, in eastern Kazakhstan it grows on open, stony mountain slopes (Kovalevskaja 1971). In Poland, it is found in thermophilous scrub and grassland communities on limy substrates (Michalik 1978, Zarzycki 1981). Sometimes it occurs in large numbers on seaside dune grasslands (Wojterski 1957; Piotrowska 1966; Filingier 1992). Less often than *E. helleborine* it occurs in thinned forest communities (pine-oak forests, thermophilous oak forests, thermophilous form of the oak-linden-hornbeam forest – Czerwiński 1978). It sporadically occurs outside the Baltic coast and limy terrains (Mowszowicz 1978; Nowak 1983). In the Białowieża Primeval Forest it seldom appears in the thermophilous forms of the oak-linden-hornbeam forest (Sokołowski 1981) and thermophilous oak forest (Matuszkiewicz 1955).

Epipactis x schmalhauseni Richt. (= *Epipactis helleborine* x *E. atrorubens*) is found in many European countries (Hunt et al. 1979; Rothmaler 1988). It is most frequent of the four hybrids found within the genus *Epipactis*, known from Poland (Bernacki 1988, 1989). It interbreeds with the parent species, and the resultant introgressive forms are difficult to distinguish from the typical species. For this reason, most floristic papers lack information on its occurrence. In the Tatra Mountain localities described by Bernacki (1988), *Epipactis x schmalhauseni* occurred at the edge of scrub communities, on a vegetation-covered brash at an altitude of 1120-1180 m

TABLE 1. Conditions under which *Epipactis helleborine* and *E. atrorubens* occur in Europe (on the basis of Oberdorfer 1983, Moravec et al. 1982, Zarzycki 1984, Rameau et al. 1993, Mucina et al. 1993 and others).

Trait/Species	<i>E. helleborine</i>	<i>E. atrorubens</i>
Light	shaded and half-shaded sites	insolated and half-shaded sites
Soil pH	weakly acidic to basic (alkaline)	most often basic (alkaline)
Carbonate substrate	++	+++
Soil richness (fertility)	rich soils	poor and moderately rich soils
Soil moisture	"fresh" (medium moist) soils	dry and "fresh" (medium moist) soils
Altitude range	Tatras 1300 Alps 1800	Tatras 1650 Alps 2400 S Norway 1200
Plant communities and formations	broad-leaved forests and scrub of the order <i>Fagetalia</i> , more frequent in orchid beech forests (<i>Cephalanthero-Fagenion</i>), less frequent in thermophilous scrub (<i>Prunetalia</i>) and heliophilous forests (<i>Quercetalia pubescentis</i>) and forest-edge communities (<i>Trifolio-Geranietea</i>).	xerothermic grasslands (<i>Festuco-Brometea</i>), grass communities of sands (<i>Helichryso-Jasionetum</i>) and rocks, vegetation of screes and rock crevices (<i>Thlaspietea rotundifolii</i>), forest-edge communities (<i>Trifolio-Geranietea</i>), thermophilous scrub (<i>Prunetalia</i>), heliophilous oak and pine forests (<i>Quercetalia pubescentis</i> , <i>Empetro nigri-Pinetum</i> , <i>Erico-Pinetea</i> , <i>Pulsatillo-Pinetea</i>), thermophilous forms of mixed coniferous forests and oak-linden-hornbeam forests.

TABLE 2. Key to 8 investigated traits.

Trait/points	<i>E. helleborine</i>	<i>E. x schmalhauseni</i>	<i>E. atrorubens</i>
	1	2	3
A			
Pubescence of inflorescence axis	poor	moderate	strong
B			
Comparison of the length of the last internode and the length of the last but one internode	more or less equal	the last internode clearly longer	last internode at least twice as long
C			
Leaf arrangement on the stalk	at an angle greater than 60 degrees	at an angle of 31-60 degrees	rising at an angle smaller than 30 degrees
D			
Shape of lower stalk leaves	elliptical, blunt, broadest in the middle	egg-elliptical, slightly tapering, broadest below the middle	lancet-shaped, clearly tapered, broadest close to the base
E			
Shape of the convexity on the epichile	smooth	slightly wrinkled	clearly wrinkled
F			
Flower colour	whitish-green, greenish-pink, pinkish-green	pink, pinkish-purple	intensively purple
G			
Flower fragrance	unsmellable	weakly smellable	distinct, similar to that of the lily of the valley
H			
Stalk colour	green	pink	purple

a.s.l. Fairly often the hybrids appear in secondary habitats (railway embankments, forest roadsides – Dr. L. Bernacki, oral communication). Their habitat in the Białowieża Primeval Forest is similar.

AIM OF STUDY

In foreign papers, especially those from highly developed countries, there have been an increasingly large number of reports on *Orchidaceae* encroaching upon habitats disturbed by man (e.g. Rossi 1988; Leten 1989; Dickson 1990), and even on a geographical expansion of some of the species (Alessandrini 1984; Light and Macconail 1994).

My findings also disagree with the common opinion that *Orchidaceae* are a dying-off plant group (Michalik 1975; Świeboda 1976; Żukowski 1976). Particularly noteworthy is the considerable abundance of local helleborine populations and its increase during the last 5 years. In 1993 about 8000 individuals were found in a permanent plot in a poplar plantation near Wólka Terechowska, and in 1989 there had been 1800. On account of the rapid increase in numbers, and the

association of this taxon with anthropogenic habitats, it was decided to carry out wide-scope studies of orchids in secondary and disturbed habitats. The aim of the study was to prove the hybrid nature of the populations under observation and establish the range of phenotypical variation in them.

MATERIAL AND METHOD

A hybrid index was used to prove the hybrid nature of the populations studied and establish the range of their phenotypical variation. The paper by Bernacki (1988), keys, descriptions and drawings (Mądalski 1977; Hamel and Walther 1986; Rothmaler 1987, 1988) and the author's own observations were used to select traits by which parent species could be distinguished (Table 2).

For the analyses 200 intact flowering individuals were collected from a poplar plantation which is about 25 years old, set up on abandoned farmlands near the village of Wólka Terechowska (near Czeremcha – Fig. 1). For comparisons, a sample (21 individuals) was collected from a forest-road and railway embankment near the Nieznany Bór Reserve (com-

FLORA OF THE BIAŁOWIEŻA FOREST
AND ITS WESTERN FORELAND
Epipactis helleborine (L.)
Cr. x *Epipactis atrorubens* (HOFFM.) SCHULT.

Fig. 1. Sites of occurrence of hybrid helleborine populations in the Białowieża Forest and its western foreland (on the basis of herbarial specimens).

partments 487 and 488, Nieznanowo range, Białowieża Forest – Fig. 1). A more detail description of the above habitats can be found in earlier papers (Adamowski 1990, Adamowski and Conti 1991).

Each of the traits was evaluated according to a 3-degree scale: 1 – typical of *E. helleborine*, 2 – intermediate (*E. x schmalhauseni*), 3 – typical of *E. atrorubens* (Table 2). This way each individual have scored 8 to 24 points. Since some of the traits are not preserved in the herbarium specimens, or are difficult to assess (flower fragrance, shape of the convexi-

ty on the epichile and arrangement of leaves of the stalk), for the analyses living plants were used. The above-ground parts of the individuals analysed have been deposited at the herbarium of the Białowieża Geobotanical Station of Warsaw University. It was impossible to collect a larger sample from the Nieznany Bór population, because at that locality material was collected only once, the orchids varied phenologically and their inflorescences were damaged by vehicles or animals.

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Fig. 2. Diagrams showing combinations of 8 investigated traits in the sample from the poplar plantation (Wólka Terechowska; $n = 200$) and forest roadside (Nieznany Bór; $n = 21$). Explanations: numbers – denote number of individuals representing each combination; letters – denote combinations common in both samples.

RESULTS

1. Hybrid index has revealed hybrid origin of investigated populations (Fig. 3, Fig. 4).
2. An analysis of 8 traits has revealed (Table 3) that hybrids are morphologically more similar to *E. helleborine*.
3. Hybrids differ from the typical *E. helleborine* first of all by: a very pubescent inflorescence axis, a considerable length of the last internode (Fig. 5).
4. Traits of *E. atrorubens*: purple-coloured stalks, a flower fragrance similar to that of the lily of the valley (*Convallaria majalis*), purple-coloured petals occurred sporadically (Table 3; Fig. 5).
5. The value of the hybrid index for particular individuals varies between 10 and 18, on average 13.5 points (Fig. 3). This indicates that the sample analysed did not contain even one individual with the traits of a pure *E. atrorubens* (total value 24) and even one individual with the traits of a pure *E. helleborine* (total value 8).
6. Most frequent in the sample were individuals whose total value was 14 (32% – Fig. 3).
7. Individuals with the lowest total value are much more similar to *E. helleborine* while individuals with the highest total value are slightly more similar to *E. atrorubens* (Fig. 4).
8. In a sample of the size of 200 individuals from the Wólka Terechowska population 89 different combinations of traits have been found (Fig. 2).
9. The most numerous combination was represented by 12 individuals, and two others by 11 individuals each (Fig. 2).
10. Individuals representing three most abundant categories attained the maximum evaluation value for inflorescence-axis pubescence, medium or maximum for the length of the subinflorescence internode, and a medium value for the arrangement of leaves on the stalk (Fig. 2).
11. 55 combinations were represented by single individuals.

DISCUSSION AND CONCLUSIONS

Hunt et al. (1975) are doubtful about the presence of hybrids between *E. helleborine* and *E. atrorubens*. They are of the opinion that *E. x schmalhauseni* recorded earlier in Great Britain were forms of *E. atrorubens* grown in shaded places, and call attention to the fact that the ranges of variation of both parent taxa overlap, but the taxa are partially isolated because they differ in flowering dates and ecological requirements.

The data set out in Table 1 disprove the last argument assuming that interbreeding is impossible because of ecological requirements differences. The flowering dates of both species in the Białowieża Primeval Forest and those reported in the literature (Keller and Schlechter 1940, Sundermann 1975) also coincide at least partially. In addition, in the managed part of the Białowieża Forest *E. atrorubens* could easily encroach on road embankments adjacent to well-preserved oak-linden-hornbeam forest communities where *E. helleborine* occurred. Both species have common pollinators – the wasps (Judd 1971, Faegri and van der Pijl 1979), and both show a tendency towards apophytism (Nikolaeva and Zefirov 1971, Hamel and Walther 1986). Due to their occurrence in the vicinity of each other, the parent forms could interbreed and produce hybrids which subsequently populated suitable habitats.

In the populations under observation parent forms are not present. The hybrids more often are more similar, morpho-

Fig. 3. Histograms of the value of hybrid index of helleborines from the poplar plantation (Wólka Terechowska) and forest roadside (Nieznany Bór).

gically, to *E. helleborine*. Their hybrid origin is indicated by traits typical of *E. atrorubens* e.g.: marked pubescence of the inflorescence axis found in about 70% of individuals, considerable elongation of the subinflorescence internode (about 50% of individuals), and traits intermediate between the parent species: shape of leaves (about 50% of individuals) and their arrangement on the stalk (about 85% of individuals; Table 3).

It seems that the Wólka Terechowska helleborine population has already passed at least through several generations of interbreeding and selection. This is indicated by the occurrence, as a result of recombinations, of individuals with very variable combinations of the traits analysed (Fig. 2). Fairly numerous also were individuals with a green interior of the hypocyle. They can be considered recombinations which did not inherit (from either parent) genes responsible for the synthesis of the respective pigments (typical *E. helleborine* has a brown, and *E. atrorubens* a violet hypocyle interior – Małal-

ski 1977, Rothmaler 1988). As colours can mask each other, it was impossible to distinguish individuals which had inherited these genes from both parents. For this reason, this trait has been omitted.

All the above observations also apply to the Nieznany Bór population in the Białowieża Forest. In a sample consisting of 21 individuals there were 17 combinations of traits (Fig. 2), of which 9 were common to that sample and the Wólka Terechowska sample. The Nieznany Bór sample has a similar range of variation of the traits considered (Fig. 2, Fig. 5), although the mean value of the hybrid index is slightly lower (12,8 versus 13,5 point). This indicates a greater similarity of this population to *E. helleborine*. This fact can be attributed to the presence near by of well-preserved forest communities in which typical forms of this species occur. The building of a road network in the Forest, and setting up of poplar plantations in its foreland considerably disturbed the environment. Poplar plantations in particular, because they are systems con-

TABLE 3. Frequency of the values of particular traits, used for the evaluation of the hybrid index in the Wólka Terechowska sample; n = 200.

Trait/points	1	2	3
Pubescence of inflorescence axis	1	57	142
Comparison of length of the last internode and length of the last but one internode	25	80	95
Leaf arrangement on the stalk	16	174	10
Shape of lower stalk leaves	95	102	3
Shape of the convexity on the epichile	120	76	4
Flower colour	154	43	3
Flower fragrance	162	33	5
Stalk colour	195	5	0

siderably transformed by man. Prior to the plantation of poplars the existing plant cover had been destroyed, drainage of the area had been carried out, and deep ploughing, soil liming and fertilization had been applied. Of some importance to the growth of the herbaceous vegetation under the poplar canopy may also be the enrichment of the soil with nitrogen compounds by the lupine (*Lupinus polyphyllus*) sown there. The effect of the poplar litter, derived from hybrids of non-native poplar species reduces the competition of other herbaceous species (Adamowski, Conti 1991), which favours the growth of orchids whose competitive abilities most often are poor (Leten 1989).

Habitats with new properties have thus formed intermediate, as it were, between the requirements of the parent species. Better light conditions in the ground-cover vegetation layer of the poplar plantations and roadsides than in the ground vegetation of forests provide better conditions for the development of hybrid helleborine populations. They are also favoured by the presence of carbonates in the substrate, and a high pH le-

vel of the latter. In the case of roadsides, the pH level is determined by the gravel derived from deep unleached deposits and used for road repairs. In the plantations, substrates rich in basic substances have been brought to the surface by the deep ploughing. Liming additionally raised the pH level of the top layers of the soil. The high soil moisture in the plantations (in spring 1994 waterlogging could be seen), unfavourable for the pure forms of *E. atrorubens*, is readily tolerated by hybrids. Owing to the possession of *E. helleborine* traits, they also can better utilize the soil nutrients (cf. Table 1).

Spontaneously produced hybrids have colonized habitats created, as it were, for them. The presence of helleborines on roadsides in the Białowieża Forest has been observed before (herbarial collections and J. B. Faliński's floristic notes in the Białowieża Geobotanical Station). Preserved specimens (Fig. 1) indicate that in a considerable proportion of cases they were hybrid populations. It seems that under the conditions of forest roadsides and poplar plantations: on nutrient-rich, medium moist or temporarily moist soils containing carbona-

Fig. 4. Ordination of *Epipactis helleborine* x *E. atrorubens* hybrid individuals on the basis of the share of parental species traits.

Fig. 5. Comparison of the mean values of particular traits of samples from Wólka Terechowska and Nieznany Bór populations.

tes, in sites half-shaded or shaded for only a part of the day, helleborine populations combining the traits of the forest *E. helleborine* and the scrub-grassland *E. atrorubens* (cf. Table 1) find optimum conditions for growth.

Hybridization may, however, endanger the parent species: *E. helleborine* and *E. atrorubens* – both not so common in the Białowieża Primeval Forest. The progressing exploitation of the Forest causes destruction of habitats that favour the presence of pure "forest" *E. helleborine* populations (closed-canopy broad-leaved forests), and breaks the ecological barriers and thereby enables the parent species to occur in common habitats (road embankments, forest edges and suchlike). As a result, hybridization intensifies, which may lead to the extinction of the genetically pure parent forms through their "dilution" by swarms of hybrid forms.

To sum up, it may be stated that the apophytism and hybridization of helleborines in the Białowieża Primeval Forest are a sign of an intensifying synanthropization of the plant cover (Faliński 1966, 1968, 1986). Orchids are sensitive indicators of the state of the environment, although, luckily enough, they do not always respond to disturbances in it by dying-off.

ACKNOWLEDGEMENTS

I wish to thank the staff of the Białowieża Geobotanical Station who participated in the field work regardless of the difficulties and weather which was not always clement and to Prof. J. B. Faliński for his permanent interest in the progress of the study and discussions on the form and scope of the article. My thanks are due to Prof. J. Staszkiwicz and Prof. K. Zarzycki for their critical comments on the earlier version of the article, and to Dr. J. J. Wójcicki for making books and papers on hybridization available to me.

My thanks are extended to Dr. L. Bernacki for the identification of helleborines from secondary localities, revision of archival herbarial materials of this genus and valuable informations and comments which have been used in the article.

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FENOTYPOWA ZMIENNOŚĆ MIESZAŃCÓW *EPIPACTIS HELLEBORINE* X *E. ATRORUBENS*
W WARUNKACH ANTROPOGENICZNYCH

STRESZCZENIE

Indeks mieszańcowości wykazał mieszańcowe pochodzenie populacji kruszczyków rosnących w Puszczy Białowieskiej i na jej zachodnim przedpolu, na siedliskach przekształconych przez człowieka. Analiza ośmiu cech wykazała, że mieszańce są bardziej podobne morfologicznie do *E. helleborine*. Od typowych form *E. helleborine* różnią się one przede wszystkim silnym owłosieniem osi kwiatostanu i znaczną długością międzywęzła podkwiatostanowego.

W artykule przedstawiono także zakres zmienności fenotypowej w badanych populacjach.

SŁOWA KLUCZOWE: *Epipactis helleborine*, *E. atrorubens*, *E. x schmalhausonii*, *Orchidaceae*, hybrydyzacja, plantacje topolowe, apofityzm, Puszcza Białowieska.