

Epipactis leptochila GODF. — Its Occurrence in Switzerland and its Relationship to other *Epipactis* Species

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Zusammenfassung: Es wird über das Vorkommen von *Epipactis leptochila* (GODF.) GODF. im Berner Jura berichtet. Die verwandtschaftlichen Beziehungen dieser für die Schweizer Flora neuen *Epipactis* zu den nächst verwandten Arten der Gattung werden besprochen.

1. Introduction

Both in the general works on the middle European flora and in the critical compendium on European orchids by KELLER and Soó (1936) five *Epipactis* species have been described for Switzerland. These are *E. Helleborine* (L.) Cr. (= *E. latifolia* (L.) ALL.); *E. atrorubens* (HOFFM.) SCHULT. (= *E. atropurpurea* RAFIN.); *E. purpurata* SM. (= *sessilifolia* PETERM.); *E. microphylla* (EHRH.) Sw. and *E. palustris* (L.) Cr. A further species closely related to *E. Helleborine*, i.e. *E. Muelleri* GODF., is mentioned without indication of its habitat, but the occurrence of this plant has only recently been verified.

As reported by GODFERY (1933), a complete series of transitional species with self-fertilization besides those with cross-fertilization by insects (*E. Helleborine*, *E. atrorubens*, *E. purpurata*) has been observed. This distinctive biological behavior is clearly marked in the morphological structure of the column in which a rostellum that hinders self-fertilization is more or less developed but sometimes is completely lacking. The autogamous plants, i.e. the *Epipactis* species with self-fertilization, are distributed especially in England and in Northern Europe. As regards their vegetative variations some species stand close to *E. Helleborine* which, because it is so widespread and grows in various habitats, itself presents many forms.

Representatives from the group of autogamous *Epipactis* species are distinguished also by more or less striking characteristics in their exterior form apart from the differences in structure of the column and in their biological behavior. In Switzerland — where the group of autogamous *Epipactis* species in contrast to Northern Europe is only sparsely developed — they seem to have been subordinated to the group of the closely related *E. Helleborine*. After thorough observation of the *Epipactis* species in the Swiss Jura the autogamous species *Epipactis leptochila* (GODF.) GODF. has now been observed. We shall report in this paper on this species and show how it differs from the common Central European *Epipactis* and how it is related to the other Northern forms, which are not known in Switzerland. We also report a confirmation of previous old and unlocalized reports of *E. Muelleri* in Switzerland. It is, however, possible that, through further study of the genus *Epipactis* within the Swiss flora, other autogamous species may also be observed.

At the end of July and the beginning of August at heights of 800 to 1000 meters one can see many plants of *E. atrorubens* and *E. Helleborine* growing on the northwestern slopes of the Jura mountain ranges. *E. atrorubens* is at this time already in full bloom or in exposed places has already withered, whereas the lowermost blossoms of *E. Helleborine* are still closed or have only begun to open. In some places, and especially on northwesterly exposed slopes not far from the ridges or on wind-exposed north-south traverses, some *Epipactis* plants are found occasionally on stony ground in mixed beech-fir-woods which are quite different from the two mentioned above. They have fewer and smaller leaves wide apart from each other, and pale green, mostly drooping, slightly opened blossoms. Most of these plants are characterized by a dwarfed growth and loose spikes with few blossoms. Only occasional plants reach a striking height and possess compact spikes with many blooms so that in their habit they look almost like *E. purpurata*. All these characteristics mentioned have been verified by observations made over a period of years in their natural habitat in the Bernese Jura. The absence of a rostellum on these blossoms is also characteristic, so that we have here one of the autogamous *Epipactis* species. Careful comparison of these plants from the Swiss Jura with North European and especially English autogamous species seems to prove that we are dealing with *E. leptochila* GODF.

The blossoming time of *E. leptochila* GODF. in the Bernese Jura occurs between that of the two allied plants, *E. atrorubens* and *E. Helleborine*, accompanying it in its habitat, i.e. between the end of July and the beginning of August.

From the following general survey of the autogamous *Epipactis* species it is seen how *E. leptochila* GODF. — which up to now was known only in England, Denmark and Germany — is different from the other closely related species. After a general review of the position and related characteristics of the autogamous forms within the genus *Epipactis* we have given an exact description of *E. leptochila* GODF. new to the Swiss flora. The other four representatives of this group — *E. Muellieri* GODF., *E. dunensis* GODF., *E. phyllanthos* G. E. SMITH, and *E. confusa* YOUNG, which today are recognized as good species and all of which are present in Northern Europe — have been characterized and compared with the hope of calling attention to these forms within the genus *Epipactis*.

2. General aspects of autogamous *Epipactis* species

The self-fertilized or autogamous species of *Epipactis* have received much attention from English authors, but few continental botanists are well acquainted with them. In most floras they are either omitted or only mentioned briefly as varieties or subspecies of *E. Helleborine*. There are however at least five good species in the autogamous group, besides some forms that require further study. Their distribution is still incompletely known.

The well-known cross-pollinated species, *E. Helleborine*, *E. atrorubens*, and *E. purpurata*, have a prominent gland on the column, above the stigma and under the anther, called the rostellum. When the flower is visited by an insect (usually a wasp), this gland bursts under pressure and sticks the pollen-masses to the insect's head. In the autogamous species the rostellum is either completely absent, or else it only exists in the bud and disappears when the perianth

opens. As a consequence the pollinia cannot possibly be removed by insects, and they are eventually transferred to the stigma of the same flower. *Epipactis microphylla* (EHRH.) Sw. stands in an intermediate position, as its rostellum is functional when the flower is first open, but if cross-fertilization is not soon effected the rostellum dries up and self-fertilization takes place.

The autogamous *Epipactis* are not a homogeneous group, and are very likely polyphyletic. They fall into two groups, (I) with pubescent rachis and patent flowers, probably closely related to *E. Helleborine*, (II) with glabrous rachis and pendulous flowers, not obviously related to any European allogamous species but seemingly connected with oriental forms such as *E. persica* HAUSSKN. It should be emphasized that, besides flower characters, each species has its own vegetative characters that are constant and separate the species from one another and from *E. Helleborine*. Indeed, it is more difficult to distinguish for example the last named from *E. atrorubens* than from *E. phyllanthes*. The arrangements given by KELLER & Soó (1936) and KRÖSCHE (1936) give too much weight to unimportant forms and monstrosities, and too little to the species themselves. Besides being unnecessarily complicated, their treatments are rendered obsolete by newer discoveries.

It should be mentioned here that the name *E. viridiflora*, that has been much used in connexion with autogamous species, is quite worthless. The original epithet, *Serapias latifolia* * *viridiflora* HOFFM., may have referred to *E. confusa* YOUNG, but it is now impossible to typify, and it must be regarded as nomen ambiguum. Later authors have applied the specific name to various autogamous species, and also to various green-flowered forms of *E. Helleborine* and it is often difficult or impossible to tell what is meant. The nomenclature of the whole genus is very complicated; a good summary is given by NANNFELDT (1946).

3. Description of autogamous species

I. Flower-stem pubescent; flowers patent or inclined

A. Epichile longer than broad; flowers large.

1. *Epipactis leptochila* (GODF.) GODF.

B. Epichile not longer than broad; flowers small

2. *E. Muelleri* GODF.

3. *E. dunensis* GODF.

II. Flower-stem glabrous or with only a minute scattered adpressed pubescence; flowers strongly pendulous

4. *E. phyllanthes* G. E. SMITH

5. *E. confusa* YOUNG

1. *Epipactis leptochila* (GODF.) GODF.

GODFERY, 1921: J. Bot., 59, 146, *E. viridiflora* RCHB. var. *leptochila* GODFERY 1919: *ibid.*, 57, 37. *E. latifolia* ALL. AN *Godferyi* KRÖSCHE 1932: Feddes Repert., 30, 244.

Rhizome long, stout, often ascending; roots numerous, of medium thickness (1.4—2.8 mm.). Stems often clustered, strong, up to 70 cm. Leaves ovate, acute, flat. Flowers yellowish-green; hypochile reddish inside, containing nectar; epichile ca. 6 mm. long × 4 mm. broad, longly acuminate, ± sagittate, not reflexed. Anther on an erect pedicel or filament. Ovary pubescent. Fertilized by the entire pollinia descending on to the stigma.

In woods on strongly calcareous soils, usually under beeches. Southern England; Denmark (Møns Klint, compare the figur in HAGERUP and PETERSSON, 1956); Germany (Hannover, West-Braunschweig, Harz, Württemberg); now found in the Swiss Jura. Should be looked for in other limestone areas in central Europe and in France.

In Swiss Jura the following stations, all situated in the canton of Berne, have been observed:

1. On the pass between Tavannes and Sonceboz, on the way to Brahon, limestone, fir- and beech-wood, about 850 m,
August 12, 1951, no. 6525 in Herb. J. Renz.
August 1, 1953, no. 7936 in Herb. J. Renz.
2. La Caquerelle, on the way to "Chez Basuel", at the west end of the edge, in stony fir- and beech-woods, 920 m,
July 26, 1953, no. 7934 in Herb. J. Renz.
3. Jura mountain ranges between Courgenay and St. Ursanne, westerly of "Sur la Croix", limestone, beeches and fir-trees, in blossom on
August 15, 1954, no. 8286 in Herb. J. Renz.

E. leptochila is of all the autogamous species the one most resembling *E. Helleborine*. Its general appearance is slightly different, however, and once known it can be recognized with some certainty at a glance. All except the strongest plants have the leaves in two ranks, whereas in *E. Helleborine* only the smallest and weakest examples have two-ranked leaves. The flowers are larger than in *E. Helleborine*, on a large and somewhat curving ovary, so that the flowers are more or less drooping (in *E. phyllanthes* and *E. confusa* the whole flower hangs almost vertically downwards). The appearance of the inside of the flower is characteristic. The perianth is entirely pale green without any purple or red shading, with the exception of the lip, which is reddish inside the hypochile, with the epichile white with faint markings of pale green and rose in the centre. The epichile also is of a characteristic shape; it is much longer than that of *E. Helleborine*, with an acuminate point that is not reflexed but directed forwards. The channel between it and the hypochile is wide and V-shaped, so that the epichile, seen from the front, appears to have the shape of an Arum-leaf. The absence of a rostellum in all flowers is obvious, and also the fact that the pollinia are always present (in the allogamous species, both rostellum and pollinia may be missing from older flowers, having been removed by insects). The column, seen from the side, is more elongated than in *E. Helleborine* the anther is usually on a "filament", which is really a somewhat conical structure directed forwards, so that there is a noticeable gap between the back of the anther and the column, underneath the filament. *E. leptochila* is an early-flowering species. In the Swiss Jura the flowering time lies between that of *E. atrorubens* and *E. Helleborine*.

Illustrations: GODFRERY 1933, t. 9; BUTCHER and STRUDWICK 1930, fig. 343; SUMMERHAYES 1951, t. 13 a.; YOUNG 1954, fig. 1.

Epipactis cleistogama C. THOMAS 1948 in RIDDELSDELL, HEDLEY & PRICE, Flora of Gloucestershire, 612 (Cheltenham) requires further study. It is large and robust with broad coriaceous leaves, and differs from *E. leptochila* in that the flowers are fertilized in the bud by scattering of friable pollen. Only known from one place in England (Gloucestershire), but may be the same as *E. leptochila* var. *praematura* KRÖSCHE 1929 (Feddes Repert., 26, 92) from Hannover and West-Braunschweig.

2. *Epipactis Muelleri* GODF.

GODFERY 1920: J. Bot., 58, 101. *Parapactis epipactoides* W. ZIMMERMANN 1922: Feddes Repert., 18, 283. "*Epipactis viridiflora* RCHB." H. MÜLLER 1868: Verhandl. N-H. Verein. preuß. Rheinl., 52, 7 et mult. auct. .

Rhizome stout, horizontal or ascending; roots of medium thickness. Stems often clustered, up to 85 cm. Leaves lanceolate, concave, undulate. Flowers pale green; inside of hypochile reddish, containing nectar. Epichile triangular, obtuse, $\pm$ reflexed, ca. 5×5 mm. Anther conical, usually with tip bent downwards, sessile; stigma very short, behind the anther so that the pollinia rest upon its surface and so fertilize it directly.

Warm lightly-shaded places such as forest borders, usually on basic soils; often amongst short grasses such as *Koeleria*. France (Alpes-maritimes, Pyrénées-orientales, Hte.-Savoie); Germany (Hannover, West-Braunschweig, Rheinland, Württemberg); Belgium (prov. Liège); Holland (Limburg); Luxemburg; Switzerland.

The plant was first recorded from Switzerland by GODFERY (1933, 73), who gave no locality. The record was repeated by KELLER and Soó (1936, 345), who stated that GRABER had found „ähnliche Formen“. In July 1955 Mr. C. SIPKES found a colony of about 20 plants of this species on the edge of an oak forest between Orbe and Vallorbe (canton of Vaud), thereby confirming its presence in Switzerland. Specimens are in Herb. Bot. Mus., Leiden, and in Herb. D. P. YOUNG (no. 5545). It should be looked for elsewhere in the Jura.

BECK's record (1890, 214) of "*E. viridiflora*" from Lower Austria was regarded by ZIMMERMANN (loc. cit.) as applying to *E. Muelleri* but further critical investigation is needed.

E. Muelleri has a characteristic tall slender habit. The leaves are narrower than in *E. Helleborine*, rather stiff, concave and undulate. The flowers are at first glance much like those of *E. Helleborine* in shape and size, having a short triangular recurved epichile, but they are coloured as in *E. leptochila*. The chief distinguishing feature is the structure of the column. The horizontal hollow on the top of the column, behind the stigma (Clinandrium, Androklinum, Pollenschüssel), in which in all other *Epipactis* species the pollinia lies, is here almost or completely absent; the stigma is level with the point of attachment of the sessile anther, so that the bases of the pollinia are pressed against its surface. The plant flowers at the same time as *E. Helleborine*.

Epipactis latifolia ALL. *At singularis* KRÖSCHE 1932, Feddes Repert. 30, 244, from West-Braunschweig, differs from *E. Muelleri* in having the pollinia lying behind instead of upon the stigma. It may be a separate species, but requires further study.

3. *Epipactis dunensis* GODF.

GODFERY 1926: J. Bot., 64, 65. *Helleborine viridiflora* (HOFFM.) WHELDON & TRAVIS f. *dunensis* T. & T. A. STEPHENSON 1918: ibid., 56, 2.

Rhizome short, horizontal; roots thin (1.3—2.0 mm.), wiry. Stems rarely clustered, slender, up to 60 cm. (but in open habitats only 20—30 cm.). Leaves lanceolate, recurved, in open habitats becoming concave. Flowers yellowish-green; hypochile red-purple inside, without nectar; epichile cordate, white marked with rose. Anther sessile, behind the stigma. Fertilized by pollen becoming friable and scattering on to the stigma.

Sand-dunes, either amongst *Salix repens* or in lanted pine-forests. Britain (Lancashire, Anglesey), has been reported from France (Manche), Belgium and Germany (Pommern), but these lack confirmation. So far as is known, this is exclusively a maritime plant.

4. *Epipactis phyllanthes* G. E. SMITH.

G. E. SMITH 1852: Gardeners' Chronicle, 660. *E. vectensis* (T. & T. A. STEPH.) BROOKE & ROSE 1940: J. Bot., 78, 81. *E. pendula* C. THOMAS 1941: ibid., 79, 200 non A. A. EATON 1908.

Rhizome horizontal; roots copious, thick (2,0—3,5 mm.). Stems stout, often clustered, up to 50 cm. Leaves small, ovate-acuminate, concave, undulated, of a thick and smooth texture. Ovary obconical or pyriform, large and rapidly swelling. Flowers pale green; interior of hypochile always green. In English forms the lip is often degenerate, being mis-shapen or even exactly like the sepals (var. *phyllanthes*). Plants from outside England that have so far been examined have all had perfect lips with cordate epichile (var. *pendula* Young). Lip and column rapidly decomposing; rest of perianth persistent in fruit. Anther sessile or pedunculate. Pollen germinating early, on the edge of the stigma, so that fertilization occurs as soon as the bud is mature. Often the flowers do not open.

Woods on basic soils, but not always on limestone often marginal; also in sand dunes amongst *Salix repens* or under planted pines. England and Wales (in many places although rarely in large quantity): Ireland; France (Vendée, Charente-maritime, Basses-Pyrénées, Hte.-Garonne, Pyrénées-orientales); Denmark (Jütland, Funen). Should be sought elsewhere, especially in northern France, the limestone areas of Germany, and in Switzerland.

Illustrations: SUMMERHAYES (1951), t. 13 b and 14; NANNFELDT (1946), t. e (as *E. leptochila*); YOUNG (1953), fig. 2 b.

Epipactis cambrensis C. THOMAS 1950: *Watsonia* 1, 283, from sand dunes in Wales (Glamorgan), appears to be a habitat-form of *E. phyllanthes*.

5. *Epipactis confusa* YOUNG.

YOUNG 1953: Bot. Not., 263. *E. persica* HAUSSKN. sec. NANNFELDT (1946: ibid., 1) p. p., haud *Helleborine persica* (HAUSSKN.) SOÓ.

"*E. microphylla*", "*E. viridiflora*", "*E. varians*" of Danish authors.

Rhizome ascending; roots of medium thickness, 2,1—3,0 mm. Stems solitary, slender, to 55 cm. high. Leaves lanceolate, recurved, not undulate nor acuminate. Ovary clavate, not swelling until the flower starts to wither; perianth not persistent. Flowers pale green; inside of hypochile reddish or less often green; epichile cordate, recurved. Fertilized as in *E. dunensis*.

Woods, especially of beech or conifers, often marginal. Germany (Schleswig-Holstein, Pommern, Berlin); Denmark (fairly widespread); southern Sweden (frequent). The eastern and southern limit of this species is at present unknown, but it does not appear to occur any further westward, and it is unlikely to be found in Switzerland.

Illustrations: NANNFELDT (1946), t. 1; YOUNG (1953) fig. 2 a, (1954) fig. 2.

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