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MONOGRAPH & ICONOGRAPH OF

NATIVE BRITISH ORCHIDACEÆ

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Godfery: Monograph and Iconograph of British Native Orchidaceae

ADDENDA ET CORRIGENDA

p. x, line 35. For Pls. A, D, E, F read Pls. A, E, F, G.

p. xi, ,, 8. ,, Pl. G ,, Pl. H.

,, ,, 12. ,, Pls. H and I ,, Pls. D and K.

p. xiv, ,, 28. ,, *prætermissa* ,, *latifolia.*

,, ,, 30. ,, *latifolia* ,, *prætermissa.*

p. 5, last line. ,, Pl. 58 A ,, Pl. 58 C.

p. 6, line 1. ,, Pl. 39 B ,, Pl. 39, 2.

p. 7, line 6. ,, fig. B ,, fig. 2.

p. 10, footnote. Add: *Vide* also footnote 1, p. 11.

p. 93, line 7. For Pl. D, fig. 2, shows the S. Irish form read Pl. D, fig. 1, shows the N. Irish form.

,, ,, 13. ,, Pl. D, fig. 1, the N. Irish form read Pl. D, fig. 2, the S. Irish form,

p. 96, line 26. After sensitive insert beneath.

p. 98 ,, 24. Insert comma after stalk.

p. 119, line 24. Add: A specimen about 3 in. high was found in flower in Oxon on May 20th, 1926, an extraordinarily early date, the usual time of flowering on the Continent being from July to September. Another specimen 9 in. tall with three flowers was found in the same county growing in the stump of a rotten tree filled with decaying beech-leaves on June 28th, 1931. I have seen photographs of both these, which are preserved in the Reading Museum.

p. 125, line 11. For Pl. 22 B read Pl. 22 A.

p. 126. After line 27 insert:

CŒLOGLOSSUM VIRIDE Hartman, *Handb. Skand. Fl.* ed. 1, p. 329 (1820). SATYRIUM VIRIDE L. (1753). ORCHIS VIRIDIS Crantz (1769). HABENARIA VIRIDIS R. Br. (1813). PLATANTHERA VIRIDIS Lindl. (1835). PERISTYLUS VIRIDIS Lindl. (1835).

p. 131, line 17. For fig. 4 read fig. 5.

p. 132, ,, 16. ,, fig. 4 ,, fig. 5.

,, ,, 24. ,, Pl. 22 A ,, Pl. 22 B.

p. 144, ,, 22. ,, Pl. 28 A ,, Pl. 28, figs. 3 and 4.

p. 145, ,, 10. Delete (Pl. 26 B).

p. 165, last line but 2. Insert comma after blotches.

,, ,, ,, 1. Delete comma after ringed.

p. 168, line 12. Delete (Pl. 34 A 1).

p. 170, footnote. Insert vol. ix, after ed. 3.

p. 176, line 33. For eight read six.

,, ,, 34. ,, four ,, three.

p. 178, ,, 16. ,, Pl. 39 B ,, Pl. 39, fig. 2.

p. 181, ,, 20. ,, p. 159 ,, p. 179.

p. 188, ,, 9. ,, immaculatis ,, maculatis.

,, ,, 33. ,, fig. 6 ,, fig. 4.

p. 191, Pl. G, Fig. 4. For *prætermissa* read *latifolia.*

,, ,, Fig. 6. ,, *latifolia* ,, *prætermissa.*

,, line 6. For fig. 4 read fig. 6.

,, ,, 23. ,, fig. 4 ,, fig. 6.

p. 216, ,, 1. Delete O. before *purpurella.*

p. 217, ,, 22. For p. 188 read p. 201.

p. 256, ,, 7. ,, K 3 ,, K 2.

,, ,, 18. ,, G 6 ,, G 4.

,, ,, 20. ,, G 4 ,, G 6.

,, ,, 30. ,, G 4 ,, G 6.

H. M. Godfery pinx.

CYPRIPEDIUM CALCEOLUS L.
Lady's Slipper Orchid

PLATE I

(Frontispiece)

Cypripedium calceolus L. Bex, Switzerland, May 15th, 1913.

MONOGRAPH & ICONOGRAPH OF NATIVE BRITISH ORCHIDACEÆ

BY

COLONEL M. J. GODFERY, F.L.S.

WITH FIFTY-SEVEN
COLOURED PLATES FROM WATER-COLOUR
DRAWINGS OF LIVING PLANTS
BY
HILDA M. GODFERY

CAMBRIDGE
AT THE UNIVERSITY PRESS
1933

PRINTED IN GREAT BRITAIN

Dedicated to the memory of

HILDA MARGARET GODFERY

my wife, companion, and enthusiastic fellow-student of Orchids, by whom this book is illustrated, and without whom it would never have been written

CONTENTS

PREFACE

NO MONOGRAPH OF BRITISH ORCHIDS WITH COLOURED PLATES HAS hitherto been published. In general Floras the imperative need of brevity restricts the characters given to the minimum essential for identification. Orchids deteriorate so much in desiccation, and the delicate mechanism of the column becomes so distorted or destroyed, that descriptions based on herbarium material are seldom satisfactory, and usually stop short at the floral envelopes, only the briefest mention, if any, being made of the column, which is the most essential part of the flower. The descriptions in the present work, as also the illustrations, were made from living plants, not only British but continental, watched and studied year after year in widely different habitats.

The coloured plates are life size, from water-colour drawings by my late wife. Of her 245 drawings of European orchids, 184 exhibited in London in 1925 were awarded the Royal Horticultural Society's gold medal, and 229 were shown at the Fifth International Botanical Congress at Cambridge in 1930.

The work is arranged to indicate the trend of evolution from the more simple and ancient types to comparatively recent and more specialised forms. Most works begin with the latter, inverting the natural sequence. The varied and wonderful floral mechanisms and their methods of working are described, and also the extraordinary relations between orchids and their visiting insects. Only a few synonyms likely to be of interest to British readers are given.

Readers should not be in haste to decide that a plant is not the one described, because it does not agree in every particular. Orchids often vary considerably in minor points such as height, shape of leaves, length of bracts, density of spike, etc., in different localities. It should be remembered that all spotted-leaved orchids are occasionally unspotted, though the reverse does not always hold good. Cases of reversion of the lip to a petal, making three petals, or of the development of both petals into lips, making three lips, occur, though very rarely, as also the development of two additional anthers. Very rarely also there are two lips side by side, sometimes with a third lip just beneath them.

Thirteen genera are only represented by one species in Britain, three only by two, two by three, one by four, one by six and the largest (*Orchis*) by twelve: total 47 species. Even in Europe the latter has only 42 species. Dr R. S. Rogers, late President of the Royal Society of Australia, is much struck by the absence of large genera in Europe. In the Malay Archipelago *Dendrobium* and *Bulbophyllum* have each some 500 species, and there are huge numbers of *Liparis*, *Microstylis*, *Oberonias*, etc.

In the diagnosis of each genus the essential peculiarities distinguishing it from other genera are given in the first paragraph. In the next follows a sketch of more general characters not necessarily confined to it.

Orchids are perhaps the most elusive of all flowering plants, and many a theory tentatively advanced or dogmatically laid down has been proved by time to be erroneous. One must enter the shrine of their closely guarded secrets with an open mind, ready to discard the most cherished preconceived ideas if necessary.

A viewer specially made to enable readers to see Herr Pfeiffer's photographs with stereoscopic clearness and perspective (but not adapted for ordinary stereographs) may be obtained from the Thornton-Pickard Manufacturing Co. Ltd., Altrincham, Cheshire, price 1*s*. 6*d*. each plus 3*d*. postage in the United Kingdom.

I desire to express sincere thanks to the following: Prof. Oakes Ames of Harvard University, U.S.A., for help in respect of *Spiranthes Romanzoffiana* and for text-figure 9A. Sir Maurice Abbot Anderson for interesting specimens of Dorsetshire orchids. Messieurs R. Bénoist and L. Berland of the Paris Muséum d'Histoire Naturelle for identifying insects taken visiting orchids. Mlle A. Camus for much helpful information and for permission to reproduce text-figures from the *Iconographie des Orchidées d'Europe*. The late Mr E. N. Carrothers of Belfast for observations on Irish orchids. Mrs E. Coleman of Blackburn, Victoria, for notes on the pollination of Australian orchids. Dorothy, Countess of Cranbrook, for specimens of rare forms of orchids. The late Dr G. C. Druce, F.R.S., for valuable information and rare specimens of British orchids. Mr T. A. Dymes, F.L.S., whose studies of the seeds of orchids were of great interest. Colonel G. H. Evans, F.L.S., and Mrs Evans for active help in discovering the visiting insects of several orchids. Prof. M. L. Fernald of Harvard University, U.S.A., for aid in identifying the Irish *Spiranthes* with the American *S. Romanzoffiana*. Colonel C. T. Green for the photographs on Pl. C. Mr P. M. Hall for valuable help in the field. Prof. J. W. Heslop Harrison, F.R.S., for notes on chromosomes and rare Durham orchids. Monsieur Houzeau de Lehaie for information as to British orchids growing also in Belgium. Dr Gottfried Keller of Aarau, who told us of many orchid stations in Switzerland and Italy. The late Mr Wilfrid Matheson for observations on Somersetshire orchids. Monsieur Meslin of Caen, who discovered *Epipactis dunensis* Godf. on the French coast. Mr H. Mousley of Ontario for notes on Canadian orchids. Herr F. Pfeiffer-Wellheim of Vienna for permission to reproduce the beautiful stereographic photographs on Pls. A, D, E, F. Prof. E. B. Poulton, F.R.S., for the determination of visiting insects. Monsieur M. Pouyanne, first discoverer of the method of pollination of *Ophrys*, for information as to the fertilisation of Algerian orchids. Dr A. B. Rendle, F.R.S., for help and encouragement and for publishing much of our work in the *Journal of*

Botany. Dr R. S. Rogers of Adelaide, S. Australia, for valuable observations on the pollination of orchids. Herr Josef Ruppert of Heidelberg Rohrbach, who sent us specimens, and was the finder of the remarkable spike figured in Pl. 2, fig. 3. Rev. T. Stephenson and his son Dr T. A. Stephenson, who showed us rare orchids in their habitats, and sent us specimens from time to time. Mr W. H. St Quintin of Scampston Hall, Yorks., who successfully cultivated many rare orchids which we sent him, enabling us to study the spikes in successive years, and supplied the photographs on Pl. G. Mr C. B. Tahourdin for his notes on British orchids and for help in the field. Herr P. Vermeulen of Amsterdam for information as to marsh orchids growing in Holland. Prof. E. F. Weiss, F.R.S., P.L.S., for valuable botanical aid. Mr Gurney Wilson, F.L.S., who helped us in many ways, and gave permission to reproduce several photographs from the *Orchid Review* (Pls. H and I).

M. J. GODFERY

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LIST OF MONOCHROME PLATES

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SIGNS AND ABBREVIATIONS

×	Between two names indicates a hybrid between them, but their sequence does not indicate which is the pollen parent.
×	Before a name shows that the plant is a hybrid.
××	Before a name indicates a hybrid between two genera. It is not really necessary, as the compound name is sufficient indication.
!	Means that the author has found or seen the plant in or from the locality named.
Ait. *Hort. Kew.*	Aiton's *Hortus Kewensis*, ed. 2 (1810–13).
A. and G.	Ascherson and Graebner, *Synopsis der mitteleuropäischen Flora*, III.
Bab.	Babington.
B.E.C.	*Reports Botanical Society and Exchange Club of British Isles.*
Bot. Mag.	Curtis' *Botanical Magazine.*
Camus, *Icon.*	Camus, *Iconographie des Orchidées d'Europe* (text), 1928. The album of drawings was published in 1921.
Darwin, *Fert. Orch.*	Darwin, *On the various contrivances by which orchids are fertilised*, ed. 2.
Dr.	Druce.
E.B.	Sowerby's *English Botany*, ed. 3, IX.
E.B.S.	Supplement to the same, the plates of which were incorporated in the 3rd edition.
Fl.	Flora.
J.B.	*Journal of Botany.*
J.L.S.	*Journal of Linnean Society*, Botany.
Lindl.	Lindley.
L.	Linnæus.
Man.	Manual.
N.H.S.	Natural History Society.
O.R.	*Orchid Review.*
R. Br.	Robert Brown.
Rchb. p.	Heinrich Gottlieb Ludwig Reichenbach.
Rchb. f.	Heinrich Gustav Reichenbach. His son.
Sp.	Species.
Sp. pl.	Linnæus, *Species plantarum* (1753).
Sub-sp.	Sub-species.
Top. Bot.	Watson's *Topographical Botany.*
Var.	Variety.

C. = common; F. = frequent; L. = local; R. = rare; V.R. = very rare.

I. INTRODUCTION

MAINLY FOR NON-BOTANICAL READERS

I AM frequently asked "What is an orchid?" As I hope that among my readers will be some with little botanical knowledge, I will briefly mention the outstanding points of difference between orchids and other families of flowers. The popular term "Orchid" includes all members of the great family Orchidaceæ. *Orchis*, however, is a name belonging to one particular genus out of the 500 genera of the Orchidaceæ.

If you look at any ordinary flower you will see in the middle a number of stamens, consisting of thread-like stalks (filaments) each with an anther at the top, which when ripe emits a quantity of very fine usually yellow dust-like pollen. In some species the anthers have no stalks, and are sessile. They vary in number from two in *Veronica* to very many in St John's Wort. In the centre of these there is a thicker stalk, called a style, which is a prolongation of the ovary (seed-vessel), and is either sticky at the top or covered with little protuberances (papillæ), whose function is to retain any pollen-dust brought to it by wind or insects. This rough or sticky area is called the stigma. Sometimes it is on the top of the ovary without any style or styles.

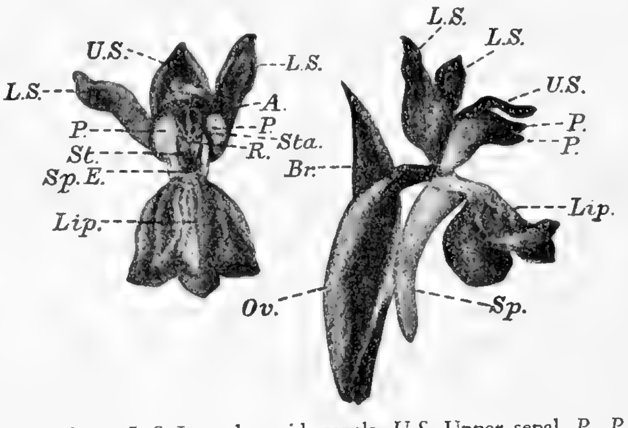
In the flower of an orchid there are no free stamens or styles. The filaments of the stamens and the style are fused together to form a solid central body called the **column**. This is the great distinguishing feature of the family Orchidaceæ. Also the pollen is never dusty, but consolidated into masses called pollinia, except in the Diandræ. Ground orchids, with which alone we have to do, there being no tree orchids in Europe, consist of two sub-families—so distinct that they would be considered separate families, but that both have the column in common.

The first of these, the **Diandræ**, comprises only the Cypripediums and their allies, of which *Cypripedium calceolus*, the Lady's Slipper Orchid, with its yellow calceolaria-like lip, is our only British representative (Pl. 1). The Diandræ have a branched column ending in a large staminode, with only two anthers, each on a side branch of the column, brimming over with a very sticky semi-liquid paste in which the single pollen-grains are embedded (Pl. A, fig. 4). The large stigma, which consists of three stigmas joined into one, is on a branch of the column and faces downward. It is dry and rough with papillæ in our species.

All the rest of our orchids belong to the sub-family **Monandræ**, with only one fertile (pollen-producing) anther at the summit of the column, with the stigma just below it, recognisable by its glistening sticky surface. The pollen-grains are built up into two pollinia (rarely four, in some exotic genera eight), which are bodily removed by insects. The only other family of plants having pollinia is the Asclepiadaceæ. There is also, in all our genera except *Cephalanthera*, a wonderful mechanism for affixing the pollinia to visiting insects, called the rostellum. It may be a simple ball of viscid matter enclosed in a tender skin, as in *Epipactis latifolia* (Pl. A, fig. 5), in the middle of the upper edge of the stigma, or, in its highest development in Britain, consist of one or two pouches filled with liquid in which the viscid discs to which the pollinia are attached are kept moist (Pl. 2, fig. 5, the two balls at the foot of the central anther).

Text-fig. 1 shows the different parts of the flower in the genus *Orchis* of the Monandræ which contains 52 species, 42 being European, but only 12 British.

Each flower springs from the axil of a small leaf called a bract (*Br.*, Text-fig. 1). What appears to be the stalk of the flower is really the ovary (*Ov.*). Within it three narrow, longitudinal, forked wings are thickly covered with a multitude of tiny ovules, which after being fertilised, develop into seeds. These wings are called parietal placentæ (from Lat. *paries*, a wall). Usually the ovary is sessile, but in some genera it is stalked. When the flower first opens the lip points upwards, but the ovary later twists through a half-turn, so that the lip is finally directed downwards. If the ovary has a stalk, it is the stalk which does the twisting. In a few genera the ovary does not twist, and the flower remains pointing upwards.



Text-fig. 1. *L.S.* Lateral or side-sepals. *U.S.* Upper sepal. *P.*, *P.* Petals. *Lip.* Labellum. *A.* Anther, with the two dark pollinia showing through. *Sp.* Spur. *Sp.E.* Spur-entrance. *St.* Stigma. *Sta.* Staminode. R. Rostellum. *Br.* Bract. *Ov.* Ovary.

The flower consists of three sepals, an upper (*U.S.*) and two lateral or side-sepals (*L.S.*), two petals (*P.*, *P.*), and a labellum or lip, a development of what was originally the third petal. These together form the perianth, or floral envelopes. The lip is often spurred, is usually the most conspicuous part of the flower, and frequently 3-lobed. It not only attracts insects by its size and colour, but affords them a convenient platform on which to alight, and assures their assuming the right position to come in contact with the rostellum, and thus to carry off the pollinia. In the Monandræ, in the centre of the flower is the column. On its summit is the only fertile anther (A^1, Text-fig. 2), with its two cells, which split down the front, so that the pollinium in each cell is visible. In the genus *Orchis* and in the Ophrydeæ generally, each of the two pollinia tapers into a **caudicle** (stalk), the end of which is attached to a tiny disc of membrane with a layer of extremely adhesive matter beneath, always kept moist within the pouch of the rostellum. If a pointed pencil is gently pushed into the mouth of the spur, it will be found on withdrawal that the viscid discs adhere to the pencil, and the attached pollinia are drawn neatly out of the anther. They stand erect on the discs at first, but soon begin to move downwards till they point forwards, parallel with the pencil. If this pretty experiment succeeds with any flower, you may be quite sure it is an orchid. Exactly the same thing happens when an insect touches the rostellum. Just below the anther is the stigma (*St.*), glistening with a sticky secretion, and often bordered by a coloured line. In Text-fig. 1 it is situated on the inside surface of the roof or back of the chamber forming the spur-entrance, and is shield-shaped, with a violet line on each side. If touched by a pollinium, packets or little masses of pollen adhere to it so firmly, that they become detached and remain on the stigma. In *Cypripedium* there are three stigmas, all united into one. In the Monandræ there are two, usually also united, the upper stigma having been transformed into the rostellum. In some genera, e.g. *Gymnadenia* (Pl. F, fig. 2), the two stigmas are separate; the column has a lobe on each side of the anther, and a stigma is situated on the front surface of each of these oval-shaped lobes.

If the flower is fertilised, the ovary swells, and develops into the seed-capsule. When ripe this opens in fine weather by three longitudinal slits, the valves thus formed remaining joined both at base and summit. The minute seeds, resembling sawdust in appearance, are shaken out and carried away by the wind. In wet weather the capsule lengthens, and the valves close up again, till fine weather returns, when the capsule contracts lengthwise, once more opening the valves.

Pl. 3 B shows a much-enlarged column of *Cephalanthera grandiflora*, with the anther at the summit, and the four half-pollinia leaning forward over the upper edge of the glistening stigma immediately below it. There is no rostellum in this genus.

This work does not go into microscopic detail, but as so much is said nowadays about chromosomes and their numbers, and their possible use for authoritatively discriminating between species,[1] it may be of interest to state what is referred to. Herr Pfeiffer-Wellheim's beautiful stereograph in Pl. A, fig. 2 (p. 6), shows six consecutive phases in cell-division taken from the root-tip of *Allium cepa* L. Beginning at the top, they are as follows:

1. **Spireme.** Nucleus breaking up into a thread from which chromosomes are formed.

[1] "It thus becomes apparent that with the help of the chromosome numbers the hitherto undecided controversy as to the systematic position of different series will be probably easy to determine." (Translated from K. M. Hoffmann, "Beiträge zur Cytologie der Orchidaceen" in *Planta, Archiv für wissenschaftliche Botanik*, Band x, Heft 3, p. 593.)

2. **Metaphase.** Formation of spindle with chromosomes on equatorial plate.

3. Early anaphase.

4. **Anaphase.** The chromosome halves have separated, one complete set going to each pole.

5. **Telophase.** Each new group of chromosomes is arranging itself into a thread, and a cell-wall is appearing between the two groups.

6. Division into two cells complete.

In 4 the chromosomes are connected by fine colourless filaments of cytoplasm.[1]

As to how far the chromosome numbers may prove of service in discriminating between critical species it is perhaps as yet too early to decide. In the Diandræ the numbers in the species already explored are 8–9, 10, 11, 12, 16 and about 24. As the Diandræ have only four genera, so extremely alike that they were formerly all put under *Cypripedium*, there seems to be a hopeful variety of chromosome numbers. In the Monandræ, however, in the species so far examined, there seems to be much less variation. The following species of the genus *Orchis—coriophora*, *incarnata*, *latifolia*, *maculata*, *mascula*, *morio*, *Traunsteineri* (var. *gigas* 20), and *ustulata* all have the same chromosome number, 10, as also have *Anacamptis pyramidalis*, *Gymnadenia conopsea* and *G. odoratissima*, according to Fuchs and Ziegenspeck.[2] The hybrids *Orchis incarnata* × *latifolia*, *latifolia* × *maculata*, *latifolia* × *morio* and *latifolia* × *palustris* also have 10 chromosomes. This does not look as if chromosome numbers will be very helpful in distinguishing between critical species of *Orchis*, or between such species and their hybrids, or even between the genera *Orchis*, *Anacamptis* and *Gymnadenia*.

The chromosome numbers for *Gymnadenia conopsea* are given as 16 by Strasburger, 10 by Fuchs and Ziegenspeck, and 8 by Chodat, which seems to indicate difficulty in arriving at the correct numbers, or possibly the occurrence of different numbers in the same species. Similarly *Listera ovata* has the chromosome numbers 16, 17, and 18 assigned to it by various authors.[3]

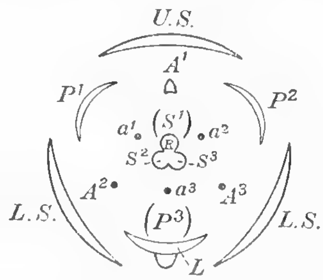
[1] That is, protoplasm of the cell, as opposed to nucleoplasm, protoplasm of the nucleus.

[2] K. Hoffmann, *Archiv für wissenschaftliche Botanik*, Band x, Heft 3, p. 590.

[3] Prof. F. E. Weiss, F.R.S., P.L.S., tells me that one of his assistants in Manchester working at the chromosome numbers in Cruciferæ found that in the common watercress collected from different countries the chromosome number is considerably more variable than in *Listera ovata*.

II. EVOLUTION OF THE ORCHID FLOWER

The flower in the Orchidaceæ has been extraordinarily modified from its original form. Text-fig. 2 is a diagram of the flower of the Monandræ (all orchids except the Diandræ). There are three sepals, two petals, and a labellum, or lip (an often 3-lobed development of the former petal, *P*3). There is only one anther (*A*1) and two stigmas, the original third stigma having been transformed into the rostellum, a delicate mechanism for affixing the pollinia to the heads of insects.



Text-fig. 2. *U.S.* Upper sepal. *L.S.* Lateral sepal. *P*1, *P*2. Petals. *L.* (*P*3) Lip. *A*1. Fertile anther. *A*2, *A*3. Suppressed anthers of outer whorl. *a*1, *a*2, *a*3. Suppressed anthers of inner whorl (*a*1, *a*2 often represented by staminodes). *S*2, *S*3. Fertile stigmas, usually confluent. *R.* Rostellum, evolved from *S*1. *A*1, *A*2, *A*3 on same radii as sepals, *a*1, *a*2, *a*3 on same radii as petals.

This flower has been derived from the typical flower of the Monocotyledons, which consists of five whorls, each of three similar organs, i.e. three sepals, three petals, an outer whorl of three stamens (*A*1, *A*2 and *A*3 in the diagram), an inner whorl of three stamens (*a*1, *a*2 and *a*3), and three stigmas (*S*1, *S*2 and *S*3). Evolution has resulted in the Monandræ in the following changes: (1) The conversion of the petal *P*3 into a labellum or lip. (2) The suppression of five out of the six anthers (the rudiments of two of which often appear as a little knob (staminode) on each side of the base of the column). (3) The conversion of the upper stigma *S*1 into the rostellum.

A still more important change, which probably preceded the others, is that the filaments (stalks of the anthers) and style (stalk-like prolongation of the ovary on which the stigmas are situated) have become fused together to form a solid central body called the column, or gynostemium, which is the outstanding feature of the Orchidaceæ. In the course of these changes the regular flower of the Monocotyledons has become so irregular that it can only be divided into symmetrically similar halves from back to front down the middle (zygomorphic).

In the Diandræ there are two fertile anthers, *a*1 and *a*2; the only fertile anther in the Monandræ (*A*1) has been changed into a large more or less petaloid staminode (Pl. A, fig. 4), which forms a shield sheltering the column, and probably a landing-stage for insects leading to the entrance of the bag-like lip.

That the flower of the Monandræ was originally regular is shown by the Australian genus *Thelymitra* (Pl. 2, fig. 1, *T. venosa*) with three sepals and three petals—an orchid with regular flowers persisting to the present day—and by the very exceptional reversion of the lip to a petal in various genera, e.g. *Platanthera bifolia*, *Orchis morio*, *O. ustulata*, *Ophrys apifera*, etc. (Pl. 58 A). That a petal can develop into a lip is shown on Pl. 39 B, in which a flower of *O. morio* with three lips is figured. This conversion of both petals into lips, as also the reversion of the lip to a petal, giving rise to three lips or three petals, is called peloria. A spike of *Orchis purpurea*, found near Chambéry, had sepals which remained closed, and a lip exactly like the petals (Pl. A, fig. 1), which moved down to a horizontal position forming a platform on which insects could alight and find access to the flower. The flower with spreading sepals was forcibly opened to show its construction. Pl. 2, fig. 3, shows a spike of *Ophrys arachnitiformis* found near Hyères, France, in which the lip has reverted to a petal, and, like the sepals and petals, is white with a green nerve, a striking example of peloria. Pl. 2, fig. 2, shows the typical flower of this species (enlarged), which has pink or white sepals and petals, and a dark purple lip with a metallic shield. These are not accidental malformations, but throw-backs to a remote ancestor.

The evidence that the orchid flower originally had six anthers is apparently conclusive. On each side of the base of the column in some genera is a little knob called a staminode, which is the rudiment of a suppressed anther.[1] Usually it is the anthers a^1 and a^2 (Text-fig. 2) which are thus represented. Pl. 2, fig. 8, shows a much-enlarged column of *Cephalanthera grandiflora* in which these obsolete anthers were fully developed and had pollinia (from Bauer's *Illustrations of Orchidaceous Plants*). I found a somewhat similar specimen at Hyères in 1920. Even in the most highly specialised genus, *Ophrys*, cases occur, though very rarely, of partial reversion to a 6-anthered flower. Pl. 2, fig. 5, shows an enlarged column of *Ophrys arachnitiformis* from Hyères with three anthers developed. In another spike of the same species also found there, no less than four anthers were developed, three being the same as in Pl. 2, fig. 5, and the fourth being the anther a^3 (*vide* Text-fig. 2), face to face with the usual fertile anther A^1, and so close that their beaks overlapped! The development of the anther a^3 is of the most extreme rarity, no doubt because it was the first to be got rid of when the lip became a landing-stage, as owing to its position it obstructed access to the rostellum by insects, and hindered cross-pollination. It was so in this case, the stigma being a cup surrounded by the four anthers. A beautiful example of the development of the anther a^3 is shown in Pl. 58 C,[2] from a spike of *Ophrys apifera* sent me from Dorset by Sir Maurice Abbot Anderson in July, 1930. Pl. 2, fig. 4, taken from the *Journal of the Linnean Society*, 1865, Pl. IX, fig. 18, shows a column (enlarged) of a species of *Isochilus* common in Trinidad, in which no less than five anthers were developed, and the sixth (a^3) represented by a filament. Had the latter developed its anther, it would have been a case of complete reversion to the ancient 6-anthered form[3].

[1] Pl. K, fig. 1, A3 shows a staminode (*st*) abnormally developed, with a yellowish rudimentary pollinium (*p*) visible within.

[2] p. 237.

[3] M. Maire (*Revue gén. Bot.* p. 316 (1909)) mentions a case of *Orchis militaris* and also of *Ophrys tenthredinifera* found near Algiers with six anthers.

PLATE 2

1. **Thelymitra venosa** R. Br. Flowers delicate blue. From *Introduction to the Study of S. Australian Orchids*, by Dr R. S. Rogers, M.A.

2. **Ophrys arachnitiformis** Grenier and Phillippe. Single flower enlarged, typical form. Hyères, France, March 3rd, 1920.

3. **Ophrys arachnitiformis.** Peloric form. Hyères, April 4th, 1926.

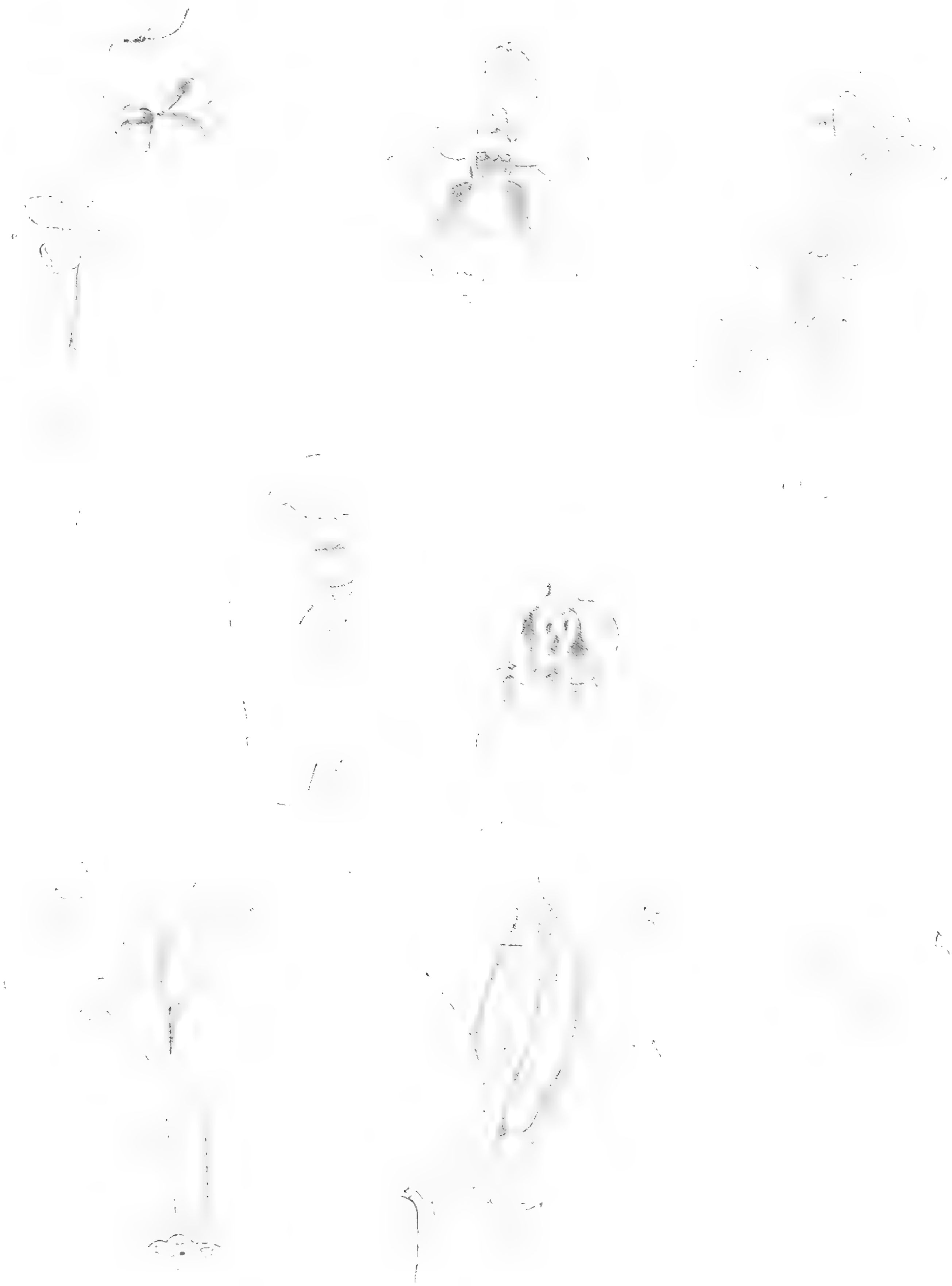
4. Column of a species of **Isochilus** (enlarged), with five anthers and a filament (*Journ. Linn. Soc. Bot.* vol. VIII, 1865, Pl. IX, fig. 18).

5. **Ophrys arachnitiformis.** Column with three anthers and three rostellar pouches (enlarged). Hyères, March 21st, 1920.

6. **Apostasia nuda** R. Br. Forcibly opened bud (× 10).

7. The same, sepals and petals removed, and one anther pulled back, showing style with three stigmas at tip, in groove of opposite anther (× 20). *A*, *A*, anthers; *S*, style; *St.*, stigmas. Both from Bauer's *Illustrations of Orchidaceous Plants*, Table XV.

8. **Cephalanthera grandiflora** (L.) Bab., with three perfect anthers (*A*, *A*, *A*). Table XX, fig. 19 of the same work (× 6).



K. W. Fairbrother del.

1. THELYMITRA VENOSA R. Br.
2, 3, 5. OPHRYS ARACHNITIFORMIS Grenier and Phillippe
4. ISOCHILUS sp.
6, 7. APOSTASIA NUDA R. Br.
8. CEPHALANTHERA GRANDIFLORA (L.) Bab.

Fig. 1. Peloric form of *Orchis purpurea*, the lip reverted to a petal. Challes-les-Eaux, Savoie.

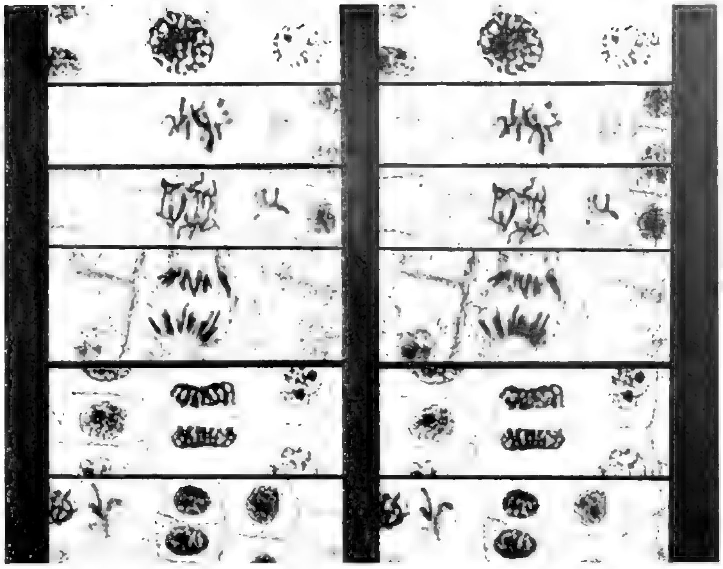


Fig. 2. Phases of cell-division from root-tip of *Allium cepa* L. (1) Spireme; nucleus forming a thread. (2) Metaphase; thread divides into chromosomes. (3) Early anaphase; chromosomes split into halves. (4) Anaphase; halves assemble in two sets. (5) Telephase; halves re-form a thread, new cell-wall appears. (6) Division completed. (440/1.)

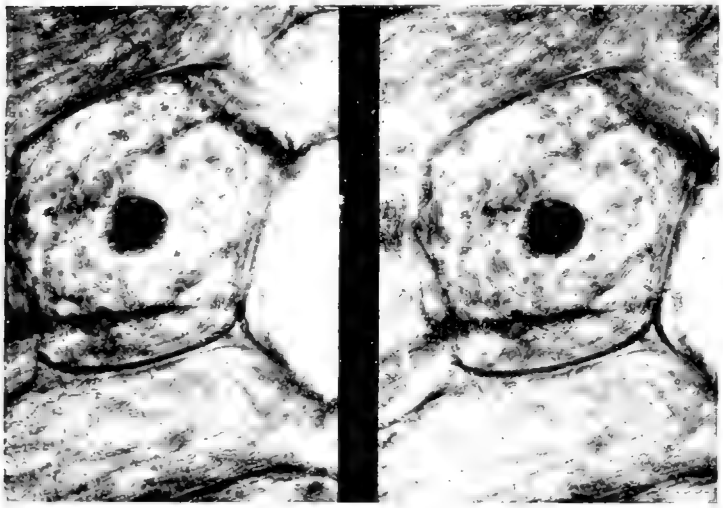


Fig. 3. Mycorrhiza in root-cells of *Epipogon aphyllum*. (190/1.)

Fig. 4. Column of *Cypripedium calceolus*. (2·5/1.)

Fig. 5. *Epipactis latifolia*, front and side views of column. (2·5/1.)

Fig. 6. *Epipactis leptochila*, front and side views of column. (4/1.)

Above stereographs reproduced by the kind permission of Herr F. Pfeffer-Wellheim of V[illegible]

Darwin believed that the obsolete anthers A^2 and A^3 (Text-fig. 2) had become petaloid and incorporated with the lower petal (P^3) to form the lip, whence its frequently 3-lobed form. He based his opinion on the spiral vessels running into each petal, anther, etc., believing that those formerly running to the anthers A^2 and A^3 had been diverted into the lip. Further experience shows that flowers of *Orchis morio* (Pl. 39, fig. B), *Ophrys arachnites*, *Anacamptis*, etc., occur in which both the upper petals P^1 and P^2 have developed into lips, sometimes complete with spur.[1] All three petals thus seem capable of developing into lips without outside assistance. Further, flowers occur, though very rarely, with two additional lips side by side, immediately above and almost touching the true lip, which is present and unchanged. From their position these superfluous lips could only have been developed through the agency of the group of vessels formerly supplying the obsolete anthers A^2 and A^3. It is therefore clear that not only can the true lip be developed by the vessels running into the petal P^3 without any aid from those of the anthers A^2 and A^3, but that the group of vessels belonging to each of the latter is itself capable of building up a perfect lip. I have seen this phenomenon in such widely separated genera as *Epipactis* and *Ophrys*. Sometimes the true lip is absent (and there are then two lips side by side), sometimes it reverts to a petal.

Development of the rostellum

When the transition from pollen in the form of very fine dust to pollinia built up of many thousands of pollen-grains (over 120,000 in the two pollinia of *Orchis morio*) took place, some new method of attaching the pollinia to insects became necessary, as they were too large to be carried merely entangled in their hairs. In the Monandræ this problem was solved by the evolution of a special organ, the **rostellum**, secreting viscid matter which sets hard on exposure to the air and cements the pollinia to visiting insects.

In *Cephalanthera* there is no rostellum. Insects entering the tubular flowers smear their backs (thorax) with the sticky secretion of the stigma, and by its means pick up the pollinia projecting from the face of the anther. In *Cattleya* there is a thick layer of viscid matter not distinctly separated from the stigma, whose use is to affix the pollinia to insects.[2] In *Malaxis paludosa* a little mass or drop of viscid fluid occurs on the upper edge of the stigma to which the tips of the pollinia become attached.[3] In the Indian *Microstylis rhedii* there is a tongue-shaped projection formed of cells which, when slightly disturbed, resolves itself into a drop of viscid matter. In *Epipactis* the viscid matter has become enclosed in an extremely tender skin which bursts on the slightest touch, glueing the pollinia to the touching object.

[1] A spike of *Orchis morio* s.sp. *picta*, found by Colonel Evans at Valescure, had one flower with three lips, each with a spur (each petal developed into a perfect lip), the other 15 flowers being normal.

[2] Darwin, *Fert. Orch.* ed. 2, p. 248.

[3] *Ibid.* p. 132.

In *Listera* and *Neottia* the rostellum is a tongue-shaped organ immediately below the anther, which deposits the pollinia on its upper surface. The rostellum encloses a series of longitudinal tubes charged with adhesive fluid at high pressure. Its under-surface is sensitive and, when touched by the head of an insect, a sort of miniature explosion occurs. Two drops of liquid glue are violently expelled, coalesce, and attach themselves simultaneously to the head of the insect and the thin ends of the pollinia, solidifying almost instantly. This mechanism is peculiar to these two genera.

In *Spiranthes* the rostellum is a green projection from the top of the stigma with a detachable brownish linear gland, very viscid below, to the upper surface of which the pollinia become attached. Its linear shape enables it to adhere lengthwise to the proboscis of insects. When removed, the green supports are left behind like a two-pronged fork. In *Goodyera* the rostellum is similar, except that the viscidium is circular and truncate above, and the prongs of the fork curved.

We now come to the Ophrydeæ, the most highly organised and specialised tribe of the Monandræ. In *Herminium* the rostellum, hitherto always single, divides into two separate viscidia with a pollinium attached to each. These are shaped so as to fit like a cap on a joint or elbow of the leg of very small insects. They are hollow beneath and filled with adhesive matter, and rest on a strip of membrane, easily pushed aside, which keeps the viscid matter from drying up, and is the forerunner of the pouch of *Orchis*, etc. In *Cœloglossum* there is a further development. Darwin says the oval ball of viscid matter is enclosed in a small pouch.[1] In *Platanthera* there is an extraordinary development. The viscidia or discs are large, attached to the ends of the caudicles sideways, so that they look inwards, facing each other, and become attached to the eyes or sides of the base of the proboscis of moths. The viscid matter is naked. In *Gymnadenia* the viscidia are also uncovered, and form part of the roof of the mouth of the spur. They are linear and designed to adhere longitudinally to the proboscis of Lepidoptera. In *Neotinea* the tiny viscid discs are enclosed in a little pouch full of liquid, in which they lie free. It has the stigmas of *Gymnadenia*, and seems to be a half-way house to *Orchis*, of which it has the anther and rostellum. In *Anacamptis*, which seems to be the climax of the *Gymnadenia* line of descent, the linear viscidia of the latter appear, by a half-turn outwards, to have become joined by their broader ends, with the pollinia rather close together. When withdrawn their free ends curl round, grasp, and become cemented by their viscous under-surface to the proboscis of Lepidoptera. The stigmas are on each side of the column, at a little distance from each other. The curling action of the viscidium makes the pollinia diverge a little, so that their tips become slightly wider apart, and are in the right

[1] Darwin, *Fert. Orch.* p. 63. This is not a pouch left behind when the pollinia are removed, as in *Orchis*, etc., but the skin of the viscidium, removed with it, and no doubt a forerunner of the pouch of the rostellum.

position to come into contact with the stigmas, which, if they remained parallel, as at first, they would not do. The viscidium is kept moist in a bursicule, as in *Orchis*.

In *Orchis* the viscidia are disc-like, and enclosed in a common moisture-filled pouch. This is a beautiful piece of mechanism, supported by a spring hinge at the back. On the slightest touch the pouch moves downwards and backwards, exposing the viscid discs, which thus come in contact with the insect's head, and are withdrawn when it retires. The pouch then resumes its original position, so that if by chance only one of the two pollinia has been withdrawn, the viscid matter of the other is kept moist and ready for action (Pl. B, fig. 1, D, E, p. 21).

Finally, in *Ophrys*, each viscid disc is protected from the air by a separate pouch, which does not return to its normal position after displacement by an insect, as the removal of one disc does not expose the other. Further, attraction by honey etc. is replaced by a more subtle allurement. The labellum mimics the female of the visiting insect plausibly enough to induce the male to pounce upon it, as described on p. 17.

The genus *Ophrys* thus appears to show the highest degree of specialisation yet attained in the evolution of terrestrial orchids. Well might Darwin write: "The more I study nature, the more I become impressed with ever-increasing force, that the contrivances and beautiful adaptations slowly acquired...transcend in an incomparable manner the contrivances and adaptations which the most fertile imagination of man could invent".[1]

One must be credulous indeed to believe that such marvellous examples of co-ordination between flowers and insects, "transcending the most fertile imagination of man", could happen haphazard without the guidance and planning of some directing Intelligence.

[1] *Ibid.* p. 286.

III. EVOLUTION OF GENERA AND SPECIES

Every orchid is descended from a long series of ancestors. The slender thread of life has come down to us unbroken through thousands, perhaps millions, of years. Most genera are the embodiment of a special idea or constructional plan. Tribes like Neottieæ, Ophrydeæ, etc., are not composed of genera based on a common architectural scheme, but of genera often widely differing in conception and construction which have a few characters of a general nature in common. Evolution is from the simple to the complex. It is not always continuous, but appears to stop when the end in view has been attained. In this work an ancient genus means one which has probably existed from remote ages in more or less its present form.

As no help is obtainable from fossil remains the comparative age of a genus can only be inferred from the following considerations:

(1) The simplicity or complexity of its organisation, and the degree of specialisation exhibited.

(2) The extent to which it has become differentiated from the type of its tribe.

(3) The number of species into which it has had time to expand.

(4) The extent of territory occupied. The wider its distribution the greater the time required for such extensive colonisation. Genera having their headquarters in America and two or three outposts in Europe, such as *Corallorhiza*, *Spiranthes*, etc., or headquarters in Europe with a species or two in America, such as *Epipactis*, indicate an antiquity going back to the remote geological era when there was no impassable barrier against the migration of plants between the Eastern and Western hemispheres.

The Orchidaceæ belong to the Monocotyledons in which the basal type of flower has six stamens and three stigmas, but of which some families have the stamens reduced to three.

The following considerations suggest that the Orchidaceæ may be descended from the Apostasiaceæ, a family of Indo-Malayan plants considered to be orchids by R. Brown, Bentham, etc. The latter assigned them to the Diandræ, doubtless because in *Apostasia*, the first genus to be discovered, the anthers a^1 and a^2 are fertile, as in the Diandræ, and in some species the anther A^1 is reduced to a staminode. They both have the minute seeds of the Microspermæ. Lindley, however, and H. N. Ridley (who had the great advantage of seeing nearly all the species in their native habitats) consider the Apostasiaceæ a distinct family.[1]

The subsequent discovery of the Apostasian genus *Neuwiedia* with three fertile anthers altered the position, as it could not logically be included in the Diandræ. Pfitzer there-

[1] *J.B.* p. 355 (1886), and *Flora of the Malay Peninsula* (1924).

fore changed the name of the latter to Pleonandræ, so as to cover *Neuwiedia*, and thus altered the main character of the group, all the genera of which have flowers like *Cypripedium*, and totally unlike those of the Apostasiaceæ (Pl. 2, figs. 6 and 7).

The Apostasiaceæ have regular flowers, *free* anthers (in *Neuwiedia* versatile), a long *free* style with three very small stigmas at the tip, a trilocular ovary with axile placentation, and dry dust-like pollen. There is nothing comparable with the column of the Orchidaceæ.

The Diandræ[1] have very irregular flowers, sessile anthers filled with viscid fluid in which the sticky pollen-grains are embedded, three large confluent stigmas, and unilocular ovaries (except *Selenipedium*) with parietal placentation.

The Apostasiaceæ conform with the structural plan so frequent in non-orchidaceous families, of flowers fertilised by insects which carry off the dusty pollen entangled in their hairs. They have little in common with the Diandræ except the two anthers of the genus *Apostasia*, and even these are of different shape and position. The whole conception of the flower is different from that of the Diandræ.

Starting with the genus *Neuwiedia*, which but for the three anthers and the seeds[2] might have belonged to the Liliaceæ, we find that it combines the only fertile anther (A^1, Text-fig. 2) of the Monandræ with the two (a^1 and a^2) of the Diandræ. The first step towards the Diandræ is shown by the genus *Apostasia* (see Text-fig. 3, p. 12), in which the anther A^1 is reduced to a staminode in some species and suppressed altogether in others. The two other anthers have closed together and embraced the style. Next comes a big gap to the genus *Selenipedium* with the anthers and stigmas of the Diandræ, but the trilocular ovary of *Apostasia*. The next step is to *Cypripedium*, in which the ovary is unilocular with parietal placentæ.

On the path of evolution towards the Monandræ no intermediate stage has yet been discovered, unless the closing up of the anthers a^1 and a^2 around the style in *Apostasia* be regarded as a step towards their fusion into a column. The stamens and style of *Neuwiedia* adhere for a very short distance at the base, which may be a first step towards their consolidation into a column, though in no wise as yet comparable with the column of the Monandræ. Just as the Diandræ may have been derived from *Neuwiedia* by the conversion of the anther A^1 into a staminode, so also the Monandræ may have arisen from the same source by the reduction to staminodes of the anthers a^1 and a^2, and by the conversion of the upper stigma into a rostellum.

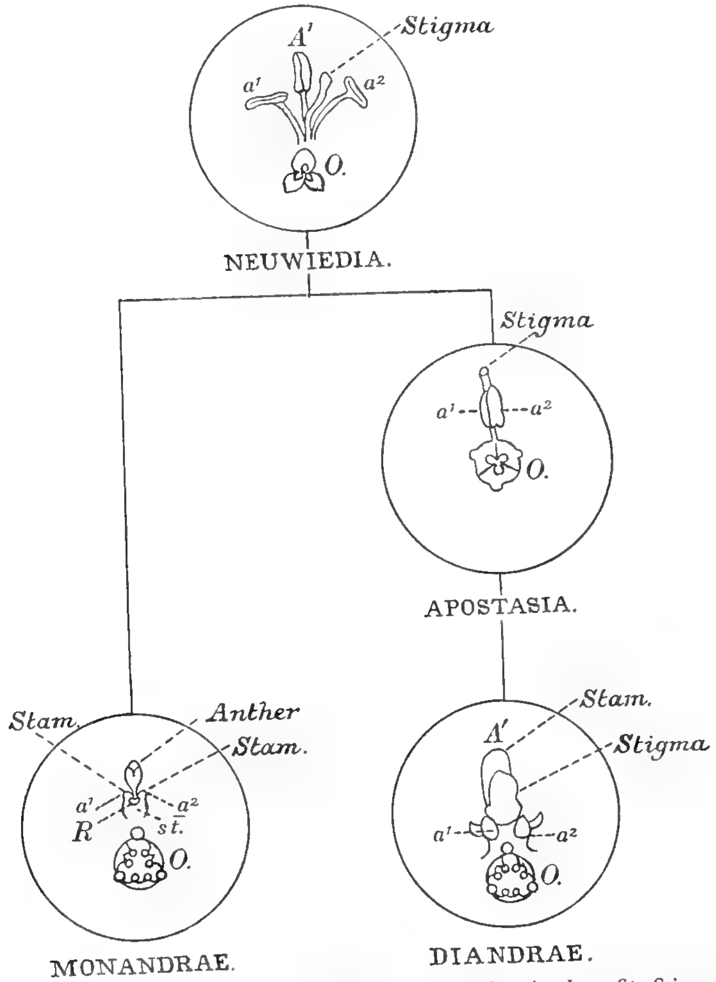
It may be objected that European orchids could hardly have been derived from wholly tropical plants peculiar to the Indo-Malayan region. According to Geikie, however, the flora of the mouth of the Thames in the Eocene period was "the most

[1] For a fuller account *vide* *O.R.* p. 355, Dec. 1932.

[2] Wallich, who found only fruiting specimens of *Neuwiedia Curtisii*, put it down as a Liliaceous plant as, like *Asparagus*, it has a red berry.

tropical in general aspect which has yet been studied in the Northern hemisphere". Thus the fruits of *Nipadites*, the fossil representative of the Nipa palm, now restricted to Indo-Malaya, are found in the London clay (Miocene) at the mouth of the Thames,

APOSTASIACEAE.



Text-fig. 3. A^1, a^1, a^2. Fertile anthers. *Stam.* Staminode. *St.* Stigma. *O.* Section of ovary. Sepals and petals omitted as unessential from these diagrams. In lower left-hand figure a^1 and a^2 are reduced to staminodes.

and in similar beds on the south coast of England, as well as in Central Europe.[1] Similarly the cinnamon (*Cinnamomium*) is now confined to Indo-Malaya, but in the Oligocene and Miocene periods was widely distributed in Europe, including the south

[1] Rendle, *Classification of Flowering Plants*, I, 260.

of England. *Engelhardtia*, a tropical genus of the walnut family (Juglandaceæ), now confined to Malaya and Central America, occurred in Miocene times both in Europe and N. America. Later, in Pliocene times, the climate became more temperate, and many of the tropical plants of the earlier Tertiary period disappeared, and in Gliostene times even the sub-tropical forms of the Mediterranean region mostly died out. *Ramondia pyrenaica* in the Pyrenees and *Haberlea rhodopensis* in the Balkans, both of which belong to the Gesneriaceæ, now restricted to tropical or sub-tropical regions, persist in these localities to the present day, probably because, being adapted to alpine conditions, they could better stand the change of climate.[1]

The Diandræ and the Monandræ form two great parallel lines of descent. The great antiquity of the Diandræ is shown by their world-wide distribution, tropical as well as temperate, in Asia (their probable centre of distribution), Europe, and America. They have rhizomes and roots, but no tubers, no pollinia and no rostellum, and have single pollen-grains immersed in a sticky paste secreted by the anther. The fact that they have only branched into four very closely related genera seems to show that evolution has long ago reached its climax and stopped. Darwin says that *Cypripedium* "differs from all other orchids far more than any other two of these do from one another". It forms "a record of a former and more simple state of the great Orchidean Order".[2]

In the Monandræ the most ancient and primitive genus appears to be *Cephalanthera*. It is the least differentiated from the monocotyledonous type of flower, for the anther is suspended from a filament, the pollen-grains do not cohere in tetrads, and there is no rostellum, in which points it differs from all other genera of the sub-order. It resembles *Cypripedium* by its rhizome and numerous roots, and by the employment of a narrow passage to compel insects to smear the thorax with very adhesive matter, and thus carry off the crescent-shaped pollinia affixed to their sticky backs. It came as a surprise to find that the ancient types of ground orchids, such as *Cypripedium*, *Cephalanthera*, *Epipactis*, *Listera*, *Neottia*, etc., are characterised by rhizomes and monostelic fungus-infected **roots**, and that we only meet with polystelic mostly fungus-free **tubers** in the more recent and more highly specialised Ophrydeæ.

Cephalanthera is the most ancient and I think the only genus of terrestrial orchids known to obtain the adhesive matter for affixing the pollinia to insects—not from the anther, as in *Cypripedium*—but by utilising the ordinary secretion of the stigma, whose normal function is the detachment of pollen from pollinia brought into contact with it by insects. In all other genera of the Monandræ (with rare exceptions), the upper stigma is transformed into a special organ, the rostellum, which secretes

[1] For most of the above information I am indebted to Prof. F. E. Weiss, President of the Linnean Society.

[2] Darwin, *Fert. Orch.* ed. 2, p. 226.

the necessary sticky material.[1] *Cephalanthera* thus enables us to understand how cross-fertilisation by the aid of insects could be brought about, before a rostellum had yet been evolved in the Orchidaceæ. Its antiquity is confirmed by its wide distribution from Britain to the Himalayas and N. America (*C. oregana* Rchb.).

Epipactis has sometimes been united with *Cephalanthera*, but the flower is constructed on a totally different plan. A rostellum now makes its appearance—a simple ball of viscid matter with a skin which bursts at the slightest touch, the adhesive material setting hard on exposure to the air, and cementing the pollinia to the head of the insect, not to the thorax, as in the two previous genera. In *E. leptochila* Godf. and *E. dunensis* Godf. the rostellum disappears soon after the flower opens, and indeed is often absent. In the continental *E. Muelleri* Godf. there is no rostellum. The stigma is horizontal and thrust back *under the base* of the overhanging anther, which thus deposits the pollinia directly upon its upper surface. In all three cases the failure or absence of the rostellum is made up for by self-pollination. In *Cephalanthera* cross-pollination by insects occurs in spite of the absence of a rostellum. The antiquity of *Epipactis* is shown by its wide distribution from Britain to Japan, N. Africa and N. America.

Listera and *Neottia*, both constructed on the same principle, constitute an entirely different conception from the preceding genera, and must have come from different ancestors. Just beneath the anther projects forward a tongue-shaped rostellum, containing liquid cement in a high state of tension in parallel tubes. Its under-surface is sensitive, and on the slightest touch the adhesive matter is explosively expelled, glueing the pollinia to the insect's head. *Listera* extends throughout Europe, Siberia, E. Asia and N. America; *Neottia* from Britain to Japan.

Goodyera, with the lip of *Epipactis* and the habit and flower-spike of *Spiranthes*, links these together. Curiously enough the pollen-tetrads cohere in packets bound together by elastic threads, and there is a definite detachable viscidium (viscid disc of Darwin), so that *Goodyera* foreshadows the Ophrydeæ, and forms a link between them and the Neottieæ. The foreign *G. discolor* actually forms long caudicles, resembling in form those of an *Orchis*,[2] but apical, not basal. America, with several species, is probably the centre of distribution. Only one species, *G. repens*, has reached Europe, extending through Asia to Japan.

Spiranthes strongly resembles *Goodyera*, but the narrow linear-lanceolate viscidium is adapted to adhere longitudinally to the proboscis of insects.[3] It has the cylindrical thickened roots of the Neottieæ invaded by *Rhizoctonia* (fungi), but in *S. autumnalis*,

[1] Darwin thought that the whole of the upper stigma was transformed into the rostellum. Pl. 2, fig. 5, shows a case of three pouches with viscid discs, and Lady Cranbrook found another specimen with four, attached by stalks to the upper edge of the stigma, so that in some cases the whole of the upper stigma is apparently not exhausted. *Fert. Orch.* ed. 2, p. 248.

[2] *Ibid.* p. 105.

[3] Pl. E, fig. 4, p. 108.

with its dry habitats, the roots are shorter and thicker, suggesting the tubers of *Platanthera chlorantha*, but monostelic with a single central cylinder (Text-fig. 9, p. 88). All the above, with the continental *Limodorum*, form the tribe Neottieæ Lindl.

Spiranthes has its headquarters in N. America, with about 24 species, of which one, *S. Romanzoffiana*, has an outpost in Ireland, and perhaps in the Western Scottish Isles, but is found nowhere else in the Old World. Europe has only four species, of which *S. æstivalis* extends to Asia Minor and Algeria, *S. autumnalis* to Transcaucasia, Asia Minor, Tunis and Algeria (Camus), whilst *S. australis* only occurs in Europe in the Caucasus, extending to Asia, Australia, Tasmania and New Zealand. This very wide distribution of the genus points to an extremely ancient origin, especially the extension of *S. australis* to Australia and New Zealand.

The tribe Malaxideæ Lindl. is characterised by waxy pollinia. Many exotic epiphytes belong to this tribe, of whose 350 genera only five are European. These five, except *Corallorhiza*, have a swelling of the stem (pseudo-bulb), the leaves embracing which contain abundant elongated cells for storing water, a useful provision for plants growing in wet ground which dries up in some seasons. It is a quite independent line of descent, as compared with the Neottieæ. *Malaxis paludosa* has probably the simplest form of rostellum in existence—a mass of cells which resolves itself into a viscid drop. *Corallorhiza* is a leafless saprophyte of low organisation with a coral-like rhizome and no roots. America seems to be the place of origin of *Liparis*, *Malaxis* and *Corallorhiza*, whose antiquity is shown by the fact that one species of *Corallorhiza* has had time to colonise Europe, and one each of *Liparis* and *Malaxis* to spread through Europe to Japan. There are large numbers of *Liparis* in New Guinea and the adjacent islands. *Epipogon* is allied to *Corallorhiza* by its similar rhizome and leafless flower-stem, and is probably descended from ancestors very near the latter. While, however, *Corallorhiza* has stood still, *Epipogon* has attained a high degree of evolution in the direction of *Orchis*, having beautiful flowers with a large but inverted spur, pollinia on long caudicles, and a heart-shaped rostellum, which foreshadows the division of the latter into two separate viscidia in the Ophrydeæ. It has perhaps been evolved since the isolation of America, for it is confined to Europe and Siberia, and is probably the summit of a long line of descent. Like *Corallorhiza* it is really a subterranean plant, increasing underground by runners, sometimes for several years, and only throwing up a flower-spike in favourable seasons to renew the vigour of the species by cross-pollination. It is the earliest example in the European flora of an empty spur with liquid stored between its walls.

We now come to the Ophrydeæ in which evolution has made enormous strides. The hitherto simple rostellum[1] now develops into a separate viscidium for each

[1] Darwin thought that the single viscidium was arrived at by the cohesion of two separate viscidia, which is the case in *Aceras*, and perhaps in *Himantoglossum*. But as we have seen, the rostellum is

pollinium. The two pollinia, erect when first withdrawn, move downwards till they point forwards horizontally, the correct position for ensuring contact with the stigma. This movement is timed, not being completed soon enough to admit of contact with the stigma of flowers on the same spike, but the right position being attained by the time the next spike is reached.

The small honey-scented *Herminium* has slightly distant viscidia, specialised to fit on the joint of the leg of very small insects, only one pollinium being removed at a time. *Cœloglossum* has still more distant viscidia, with a ridge down the lip, compelling insects to enter on one side and remove one pollinium at a time. The downward diverging anther-cells foreshadow those of *Platanthera chlorantha*, to which genus it was assigned by Lindley. *Platanthera* is organised to attract Lepidoptera by free honey in a long spur, and is remarkable for the large naked viscidia facing each other, and thus becoming attached to the sides and not to the front of the head or proboscis of moths. It is the climax of a long series of very ancient forms, for several species occur in N. America.

Gymnadenia also secretes free honey in its spur, *G. conopsea* catering (like *Platanthera*) for Lepidoptera with a long proboscis, and *G. odoratissima* and *G. albida* for short-tongued insects. It is remarkable for the lateral position of the separate stigmas on side-wings of the 3-lobed column, instead of in the centre of the flower as in all our other orchids, except *Herminium* in which separation is incomplete, there being two transverse stigmatic surfaces meeting by their points in the middle, and *Anacamptis* and *Neotinea*, which are really *Gymnadeniæ* which have evolved the rostellar pouch, viscidia, and tubers of *Orchis*. *Anacamptis* appears to be descended from *G. conopsea* (to which it bears an extraordinary likeness) or some extinct collateral species, and *Neotinea* perhaps from *G. albida* or some nearly allied collateral. For the reasons supporting this conclusion see below, under *Serapiadinæ*. Darwin considered that in no other plant was the correlation of the various parts with the habits of such widely remote organisms (Lepidoptera) more complete than in *Anacamptis*. It is of comparatively recent origin, extending only to the Caucasus, Asia Minor, and N. Africa, but not America.

In *Orchis* no free nectar is secreted, and the spur is dry, which suggested to Delpino degeneration and incipient extinction. A store of potable liquid, however, exists between the walls of the spur, the inner skin of which is easily pierced. Delpino maintained that this was not honey, but sap. Whatever its nature, it acts as a powerful attraction, for *Orchis* has not only evolved the largest number of species (75) of any genus of the Old World, but these transcend all others in abundance. The genus is apparently absent from America, *Orchis rotundifolia* Pursh. and *O. spectabilis* L.,

simple in the Neottieæ, Malaxideæ, etc., and we do not come to cases of two viscidia till we reach the most highly evolved tribe of all, the Ophrydeæ.

according to Schlechter (*Mon. Orch.* p. 158) certainly forming a genus of their own. *Orchis*, *Ophrys*, *Anacamptis* and the continental *Serapias* have attained the apex of evolutionary success. No new genera seem now to be in the making, evolution, as far as European terrestrial orchids are concerned, being apparently now confined to the expansion of existing genera.

In *Ophrys* it seems as if the object in view has been to restrict the number of insect visitors to an extraordinary degree. All the usual attractions, such as honey, potable liquid, edible tissue, etc., have been discarded. The labellum has been modified to resemble the female of certain fossorial Hymenoptera, the males of which emerge some time before the females, and carry out a furiously eager search for a possible mate. Specialisation has been carried to such a degree as to mimic the females of one particular genus, in the case of the N. African *Ophrys speculum* one particular species, *Dielis ciliata*.[1] In consequence insect visits are few, and limited not only to the short time between the dates of emergence of the sexes, but to the males only, and to the range of their wanderings from the ground where the females still lie in the pupa state, from which they do not venture far.

Thus we see that *Ophrys* has gone considerably further in evolution than *Orchis*. Instead of the two viscid discs being enclosed in a common pouch, each has a pouch to itself, and a much higher degree of specialisation has been realised in its relation to the insect world.

The field of European orchids is too limited to illustrate all the steps in the path of evolution. The lines of descent are nearly always parallel and quite independent. While we can visualise a steady line of development through a succession of different genera, which form as it were milestones, we cannot trace the multitudinous intermediate steps.

If *Cephalanthera* be taken as the starting-point of the evolution of the Monandræ, all the genera fall into line in a natural order of progression. There is a steady march of development from the simple to the complex. Nothing of this sort is perceptible, when, as is usually the case, systematic works begin with *Orchis*, *Ophrys*, *Serapias*, or *Platanthera*, which have respectively reached their highest point of evolutionary perfection. *Cephalanthera*, *Epipactis*, *Listera* and *Spiranthes* are independent lines of descent, but *Neottia* is identical with *Listera* in its floral mechanism. Each is the offspring of a different conception. *Goodyera*, however, is a *Spiranthes* which has left that genus behind by the development of its linear viscidium into a roughly quadrangular one—a move in the direction of *Himantoglossum*—and the evolution of its pollinia into separate packets of pollen tied together by elastic threads as in the Ophrydeæ. It is a change in the internal mechanism whilst the external facies remains that of *Spiranthes*. *Goodyera* seems to be the culminating point of the *Spiranthes* idea.

[1] *J.B.* p. 33 (1925).

In the Malaxideæ *Liparis* and *Malaxis* may probably be early exponents of waxy pollinia and of pseudo-bulbs, at first intended to bring these humble and inconspicuous plants of boggy habitats through recurrent periods of drought by the storage of water in tracheids (elongated closed cells). Later the evolution of pseudo-bulbs enabled plants to colonise rocks and even trees, and become the ancestors of some of the marvellous epiphytes of to-day. *Corallorhiza* belongs to a different line of descent —an ancient type (headquarters in N. America) of low organisation and a saprophyte, whose development seems to have stopped at an early stage. *Epipogon* is a unique type. In its low vegetative organisation and coralloid rootless rhizome it is allied to *Corallorhiza*. The large basal water-storage cavity replaces the numerous tracheids of *Liparis*. The floral organisation, however, is extremely high, on a par with that of *Orchis*. It is the apotheosis of the saprophyte.

In the Ophrydeæ *Herminium* caters for very small insects, and for the first time we come across two separate viscidia (fitting like caps on the joint of the leg) and lateral stigmas. It shows an early stage in the evolution of the Ophrydeæ. *Cœloglossum* has distant viscidia but a central stigma, with a supplementary honey-gland beneath each viscidium. It leads us on to *Platanthera*, the culmination of this line of descent, specialised for Lepidoptera by its long spur with free honey at the apex and lateral viscidia which adhere to the sides of the head. *Gymnadenia* is from a different line of descent, for the stigmas are lateral, and the viscidia central and linear for attachment to the proboscis of Lepidoptera. *G. albida* leads on to *Neotinea intacta*, which resembles it rather closely, but has evolved the viscidia and pouch of *Orchis*, whilst retaining the 3-lobed column of *Gymnadenia*, with its stigmas on the face of the side-lobes, and also its free honey.

Anacamptis pyramidalis is of special interest as it affords clear evidence of descent through an existing less highly organised genus. Though sometimes regarded as an *Orchis* on account of the pouch of the rostellum, it has the 3-lobed column with the stigmas on the face of the side-lobes, the flat 3-lobed lip, the small spur-entrance, and the long slender spur of *Gymnadenia conopsea*. The extraordinary resemblance of the flower to that of the latter is easily understood if we recognise that it is a *Gymnadenia* which has evolved the rostellar pouch, the rounded tubers and the dry spur of *Orchis* with liquid stored between its walls. It is the climax of the *Gymnadenia* line of descent.

Gymnadenia albida leads us on to *Neotinea* (obviously a connecting link), which in its turn leads us through *Aceras* to the *Militares* sub-section of *Orchis* (*O. simia*, *militaris*, etc.) with which *Aceras* is closely connected, its leaves smelling of coumarin like those of *O. simia*, *militaris* and *purpurea*. There appears to be no earlier genus from which the descent of the rest of the genus *Orchis* can be suggested. The pollinia with their packets of pollen were foreshadowed by *Goodyera*, the dry spur with liquid between the walls by *Epipogon*, the two separate viscidia and the downward movement of the pollinia by *Herminium* and *Cœloglossum*, but the actual line of descent remains obscure. The same is the case with *Ophrys*, perhaps the most astounding conception of all, based on the mimetic resemblance to the females of a particular genus or even species of Hymenoptera, the climax of specialisation.

It is not intended to imply that orchids are descended from existing species of the Apostasiaceæ, but merely that these indicate probable lines of descent from some closely allied ancestral forms. *Neuwiedia* suggests the facility with which the forking of the Orchidaceæ into their two great sub-families may have been brought about by the reduction of anthers to staminodes, a proceeding of undoubted occurrence in the Orchidaceæ. It must be admitted that the basic idea of the Apostasiaceæ differs from that of the Orchidaceæ, but if creation has taken place through evolution existing forms must have arisen from ancestors differing from them in conception as well as execution.

IV. POLLINATION AND FERTILISATION

Pollination simply means the placing of pollen on the stigma of a flower, and is the first step towards fertilisation. When a pollinium brought by an insect touches the stigma, some of the pollen adheres to the tenaciously sticky secretion with which the stigma is covered, the pull of which is sufficient to break the threads by which the pollen-grains or packets are bound to the pollinium, but not as a rule sufficient to detach the whole pollinium. The insect goes on to other flowers, distributing pollen on various stigmas, till nothing but the stump is left.

Under the stimulus of the stigmatic secretion the packets of pollen disintegrate into the tetrads (groups of four grains) of which they are composed, and finally as a rule into single grains. Each grain puts forth a pollen-tube, which grows down like a root into the ovary till it reaches an ovule (a seed in its earliest stage) which it enters by a microscopic aperture called the micropyle, and there discharges its protoplasmic contents. This process is called fertilisation, and without it the ovule can never develop into a fertile seed. The pollen-tubes enter the ovary by a passage called the stigmatic canal, and are united into a bundle by a mucilage formed by the cells of its walls, and convey the protoplasm with its nuclei to the ovules. Partitions are formed in the pollen-tubes behind the protoplasm, in long tubes very numerous ones.[1] The time required for the germination of the pollen-tubes is sometimes only 2–3 days (*Listera ovata*), 5–6 days in many species of *Orchis*, 9–10 days in *Ophrys*,

[1] Camus, *Icon.* p. 73.

and longer in the case of waxy pollinia. It takes from 3 to 6 weeks for the pollen-tubes to reach the ovules.[1]

In 1764 Linnæus asked whether the influence of the pollen may not be communicated internally to the ovary of the same flower. According to Sprengel he mistook the pouch of the rostellum for the stigma. Sprengel himself at first thought that the stigma was a honey-secreting organ. In 1755 Kolreuter had said that the fecundating matter is imparted to the inner surface of the anther-cells. In 1791 Batsch stated that in *Orchis*, etc., the only way pollen can act on the ovarium is by retrogradation of the impregnating power through the caudicle (stalk) of the pollinium to the gland (pouch of the rostellum). In 1802 Richard thought that fecundation operated without change of place of stamina. In 1824 Prof. Link expressed the opinion that the rostellum of Richard is without doubt the true stigma. In 1829 Lindley suggested that fertilisation occurred by absorption of fecundating matter from the pollen-masses through their gland into the stigmatic channel.[2]

All the above thought that orchids were self-fertilising. Lindley, however, in his preface to Bauer's *Illustrations of Orchidaceous Plants* (1838), in which Bauer figured supposed perforations through which the fertilising power of the pollen passed out from the pouch of the rostellum to the stigma, finally rejected this interpretation, and, following Robert Brown, adopted the theory that impregnation occurred through contact of the pollinia with the stigma. Even then the part played by insects does not appear to have been suspected, though Sprengel in 1793[3] had published observations of the visits of insects to *Orchis latifolia*, *O. morio*, *Platanthera bifolia*, *Gymnadenia conopsea*, *Listera ovata*, *Epipactis palustris*, and *E. latifolia*, and figured the removal of pollinia by them.

It is curious that in Sprengel's days there were two schools of opinion as to the nature and use of honey. Some thought it kept the ovary moist and supple, and preserved the seeds, and that bees were therefore robbers. On the other hand Krunitz said[4] that nectar was hurtful if not removed by bees, so that these were beneficent scavengers.

Orchids are never anemophilous (wind-fertilised), the pollen not being dusty, but consolidated into pollinia in the Monandræ, or immersed in viscid fluid in the Cypripediums. They are entirely entomophilous, i.e. pollinated by insects. Some method of attaching the pollinia to insects is therefore essential. Pl. B, fig. 1, from Darwin's immortal work *The various contrivances by which orchids are fertilised by insects*, shows the floral mechanism for this purpose of *Orchis mascula*. The genus *Orchis* is here dealt with first, although it is the summit of evolutionary progress, because it

[1] Camus, *Icon.* p. 74 (1928).
[2] R. Brown, *Trans. Linn. Soc.* XVI, 687 (1831).
[3] Sprengel, *Das entdeckte Geheimniss der Natur*, p. 403 (1793).
[4] *Œconom. Encycl.*

Fig. 1. *Orchis mascula* L. A. Side view of flower, sepals, petals, half of lip and part of spur removed. B. Front view, sepals and petals removed. C. Pollinium on its viscidium (viscid disc). D. Viscidia in pouch of rostellum, its front pushed down. E. Section through one side of viscidium. F. Pollen-packets with stretched elastic threads. (After Bauer.)

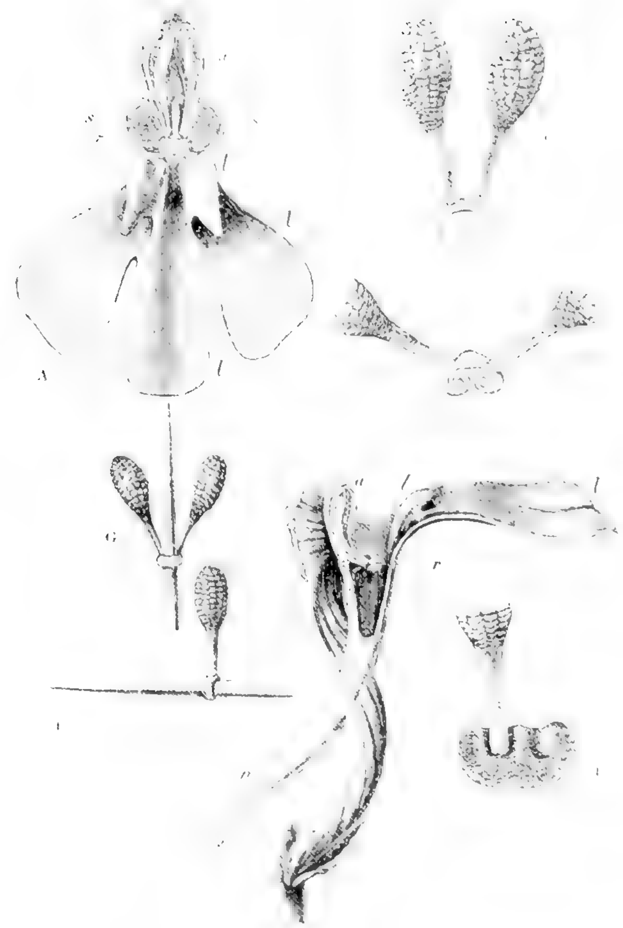


Fig. 2. *Anacamptis pyramidalis* Richard. A. Front view of flower, sepals and petals removed. B. Side view, sepals, petals, half of lip and part of spur removed. C. Pollinia attached to strap-shaped viscidium. D. Viscidium curling under with no object to grasp. E. Viscidium from above, flattened, showing depression which effects downward movement of pollinia. F. Pollinia removed on a needle. G. The same after downward movement. The uppermost "*l*" should read "*l'*".

a. anther.	*p*. pollinium.
c. caudicle.	*r*. rostellum.
d. viscidium.	*s*. stigmas.
l. labellum.	*l'*. guiding plate.
n. spur.	

From Darwin's *Various contrivances by which orchids are fertilised.*

contains more British species than any other genus, and specimens can easily be found. Also, knowing the end in view, the steps by which it has been attained can be better understood.

The anther, *a* (Pl. B, fig. 1), has two cells which split down the front so that the pollen-mass or pollinium in each cell is visible. Its caudicle (stalk), *c*, is at first free, but later becomes firmly attached to the cap of the viscidium, *d*, which has beneath a ball of very adhesive matter. This is immersed in liquid in the rostellum, *r*, a pouch which holds both the viscid discs as Darwin called them. In D the pouch has been pressed down a little so as to show the viscidia, which are otherwise concealed as in B. This is necessary as the viscid matter sets hard like cement on exposure to the air. E in Pl. B, fig. 1, shows a section of the rostellum. When the bee inserts its proboscis into the spur, its head pushes against the pouch, cunningly placed like a trap in a rabbit run. Being supported on an elastic hinge, the pouch moves back, the balls of viscid matter come in contact with the insect's head, and at once adhere. When it withdraws, it carries off the pollinia standing erect on the adherent discs. The bee works up the spike visiting other flowers, but owing to their erect position the pollinia are merely pushed against the face of the anther, and cannot touch the stigma, *s*, the dark-shaded space surrounding the pouch in B. Meanwhile the pollinia are executing a downward movement, and by the time the bee reaches another spike of flowers, are pointing forwards horizontally. When the insect enters a flower on the new spike, their tips are pushed against the tenaciously sticky stigma, to which some of the packets of pollen adhere, and are held with such strength that the slender threads by which they are bound to the pollinia give way and break. F shows these threads when they are extended. It is a pretty experiment to pull the tip of a pollinium, and see how easily the threads stretch, and observe the packets of pollen. It will also be found that the caudicles themselves stretch to a surprising extent, and spring back when released. The object of this elasticity is to prevent the packets being snatched away from the stigma through the sudden jerk of the insect leaving the flower. The pollen-packets left on the stigma are easily visible with a lens, or often with the naked eye. The stigmatic secretion has a marked effect upon the pollen-packets, which soon break up into the component tetrads and grains. These all put forth a pollen-tube, like a seed in a seed-bed, which grows down to the ovary, and enters an ovule by the tiny micropyle, and thus fertilises it by the emission of its protoplasm. The presence of pollen on the stigma stimulates the ovules, which begin at once to develop, and the ovary swells visibly, so that by the time the pollen-tube reaches the ovule, the latter is ready to receive it. This takes about three weeks, or more, especially with waxy pollinia.

It is a curious fact that the viscid disc to which the pollinium is fixed is not, as formerly supposed, a part of the pollinium (which is the male organ), but is developed from the upper stigma, a female organ—the caudicles being at first free, but later becoming attached. Thus one of the original three stigmas actually provides the mechanism for the transport of the pollinia to stigmas on another spike, and so prevents them from reaching its sister stigmas.

Sprengel spoke of *Orchis morio* and *O. latifolia* as "Scheinsaftblumen"—false honey flowers—which entice insects by the promise of nectar which their dry and empty spurs do not fulfil.[1] The spur, he said, was the true honey gland and also the honey receptacle, but though he examined many flowers, he could find no honey. He considered that no honey could be secreted, as the inside of the spur was covered with hairs, whereas nectar-secreting surfaces must be glabrous and smooth. The spurs of *Platanthera chlorantha*, etc., however, which contain free honey, have hairs on their inner surface. Delpino[2] spoke of the illusory spurs of *O. morio* and other species of *Orchis* as formerly melliferous but now dry—a sure sign, he said, of organic degeneration, whose pernicious effect was only too evident from the small number of seed-capsules produced. He regarded *O. mascula*, *morio*, etc., as on the verge of extinction! Darwin also examined all our common British species of *Orchis* and could find no trace of nectar, and concluded that the spurs never contain any.[3] He found, however, that the spur had an outer and an inner wall, separated from each other to a surprising extent, that the inner skin was extremely delicate and could be penetrated with the greatest ease, and that between the two membranes a quantity of fluid was contained. If the end of the spur be cut off and the latter gently squeezed, large drops of fluid are exuded. He therefore concluded that insects pierce the delicate inner membrane and suck the copious fluid. This was a bold hypothesis, for no case was then known of Lepidoptera[4] penetrating even the most delicate membrane with the proboscis. At the Cape of Good Hope, however, moths and butterflies do much damage to peaches and plums by puncturing their unbroken skins. He observed that various kinds of bees kept the proboscis inserted in the spur of *O. morio* for a considerable time and in constant movement. The same thing was noticed in the case of a fly, *Empis livida*, on *O. maculata*, and minute brown specks were sometimes seen on the inner skin, where punctures appeared to have been made.[5] Delpino[6] said that Darwin suggested that honey was secreted between the spur-walls. This was a misunderstanding—Darwin stated quite clearly that he could find no trace of honey. Delpino contended that the liquid between the spur-walls was not honey, but merely "linfa"

[1] Sprengel, *Das entdeckte Geheimniss der Natur*, p. 403 (1793).

[2] *Appar. d. fecondaz. n. piante* (1867).

[3] Camus states that in *Orchis coriophora* there is an abundant secretion of nectar inside the spur (*Icon.* p. 180 (1928)). Also that in the Lizard Orchid, before the expansion of the flower, nectar is secreted, but that it has almost entirely disappeared when the lip unrolls (*ibid.* p. 121).

[4] Some species of orchids are pollinated by butterflies.

[5] *Ann. Nat. Hist.* p. 143 (1869).

[6] *Appar. d. fecondaz. n. piante* (1867).

(sap), and suggested that insects visited the flowers for the sake of the pollen, which they find so conveniently packed for transport in pollinia! Anyone, however, who has watched insects with pollinia, will have often seen how hard they try to scrape them off, but rarely with any success, except before the viscid matter has had time to set hard. Whether the fluid secreted be, as Delpino suggested, merely *acqua di traspirazione* or sap, it is certain that bees of various kinds are attracted. One often comes across a tiny trickle of water on sandy ground, with numbers of bees eagerly quenching their thirst. In most places such trickles are rare, and the liquid contained in the spur of *Orchis* is probably sought to satisfy thirst. Darwin mentions 10–16 pollinia found on hive-bees visiting *O. morio*. I have watched humble-bees searching out insignificant little plants of *Pedicularis palustris* evidently for honey, but entirely ignoring the more abundant and much more conspicuous flowers of *O. morio*. Nevertheless I saw some visiting *O. morio*, and the number of fertilised ovaries showed that visits must have been much more frequent on other days. Honey-collecting must be thirsty work on a hot day, and *Orchis* flowers very convenient drinking fountains.

A few species—relatively very few—are self-fertilised. In almost every case the faculty of self-pollination appears to have been subsequently added to a flower already organised for cross-pollination by means of a rostellum, and the two processes exist concurrently. Thus in *Cephalanthera grandiflora* if the pollinia are not removed by insects, they crumble and fall on the stigma. This occurs so often that the species is commonly regarded as always self-fertilising. As will be seen later it is visited by at least two species of Hymenoptera. In *Epipactis leptochila* Godf. and *E. dunensis* Godf. there is a rostellum when the flower first opens, but it disappears by the time the next flower unfolds, and often fails to develop at all. A good deal of pollen, however, slides over the sloping upper edges of the stigma on to its effective surface. In the continental *E. Muelleri* Godf. the anther base projects well over the base of the stigma which is there horizontal, and deposits the pollinia directly on its sticky surface. There is no rostellum, but in bud there is a rounded protuberance in the middle of the upper edge of the stigma which looks like a rudimentary rostellum, and a few drops of nectar are secreted in the basal cup of the lip. In *Neottia nidus-avis*, if the pollinia are not removed, some of the pollen finds its way over the rostellum to the stigma. *Ophrys apifera* habitually pollinates itself (*q.v.*), but the machinery for the removal of the pollinia is still in perfect working order, and hybrids arise between it and other species. Mr C. S. Garnett, F.L.S., of Derby, saw several bees visiting the flowers in 1930. *Neotinia intacta* is also self-pollinating, but the pollinia are attached to viscid discs kept moist in the pouch of the rostellum, and can be withdrawn on a bristle—with difficulty, it is true, as they are so minute. There is free honey in the spur, but so far there is no record of insects having been seen visiting the flowers. Five British species are partly self-fertilising, most of them mainly so.

Pl. B, fig. 2, illustrates the pollination of *Anacamptis pyramidalis*, the Pyramid Orchid. A shows the 3-lobed column above the lip, with the 2-celled anther in the longer upper lobe, and the pollinia showing through the fissure in the front of each cell. At its foot is the rostellum, *r*, a pouch containing the viscidium, shown in C and D, to which the pollinia are attached so firmly that they stand erect. On the oval surface of each side-lobe of the column is one of the two stigmas, *s*, *s*, which are quite separate. At the base of the 3-lobed lip are two guiding plates, *l′*, *l′*, which appear in the figure to be flat. They really stand erect at right angles to the lip, and converge towards the rostellum where they nearly meet.

As might be imagined from the long spur, the flowers are visited by butterflies and moths—Darwin enumerated 23 visiting species—and the pollinia are invariably attached to the proboscis. As this organ is very slender and thread-like, and repeatedly curled and uncurled like a watch spring, the ordinary rounded disc-like viscidium of *Orchis*, which answers admirably for attachment to a flat surface, would be insufficient to secure a firm hold on a thin mobile proboscis. The viscidium is therefore strap-like—Darwin called it saddle-shaped—and the two ends curl round the moth's proboscis on withdrawal, just meeting round it, and grasping it firmly. As the viscid matter beneath it rapidly sets hard like cement, there can be no turning round sideways, and the hold is firm and rigid. Darwin found that if the pollinia were withdrawn by their caudicles, the ends of the strap, having nothing to grasp (Pl. B, fig. 2, D), curled inwards till they touched each other in nine seconds, and in nine more closed up into an apparently solid ball.[1] A naturalist, who sent him a moth with several viscidia attached to its proboscis, remarked that the moth had cleverly bored through the exact centres of the sticky glands of some orchid.

As in *Orchis*, the pollinia after withdrawal move downwards through an angle of nearly 90°, so that they then lie in the same plane as the needle or proboscis, F and G. The curling movement of the viscidium incidentally brings about a beautiful adjustment. The two pollinia originally stand erect and nearly parallel. If they remained parallel after the downward movement when attached to a proboscis, on insertion into another flower they would be too close together, and would be pushed against the rostellum, which would be useless. But the curling movement of the viscidium makes them diverge a little, so that they come in contact with the two lateral stigmas, and leave packets of pollen adhering to them.

It is essential that the insect's proboscis should touch the under-surface of the viscidium exactly in the middle, or the pollinia would be attached crookedly. As the entrance of the spur is spacious compared with a moth's proboscis, the rostellum is placed lower down in the mouth of the spur than in *Orchis*, and restricts the entrance to a narrow passage. To secure the necessary accuracy a special device, found in no

[1] Darwin, *Fert. Orch.* ed. 2, p. 21.

other European orchid, is provided in the shape of two erect guiding plates (*l'*) on the base of the lip converging towards the narrowed spur-entrance, which acts like an old wife's gadget for threading a needle. In several species of *Orchis*, etc., a groove in the base of the lip answers a similar purpose, but with less accuracy. If a fine bristle is inserted between these plates, it is automatically guided till it pushes against the pouch of liquid in which the viscidium is immersed. This swings back and exposes the strongly adhesive under-surface of the disc. The bristle, or in the case of Lepidoptera the proboscis, slides along the centre of the viscidium which coils round it and cements itself thereto. The proboscis of *Acontia luctuosa* figured by Darwin[1] bore seven pairs of pollinia arranged with perfect symmetry. The moth *Caradrina blanda* had no less than eleven pairs. The flowers are well visited by insects. Darwin found that six plants in Devonshire had had both pollinia removed from 102 flowers. A spike from Folkestone with 49 flowers produced 48 seed-capsules. Not without reason did Darwin remark, "How well moths and butterflies perform their office of marriage priests!"[2] Even a human hair is stiff enough to depress the pouch, and the strap-shaped viscidium adheres to it. If the pouch be pushed only slightly, it springs back to its original position.

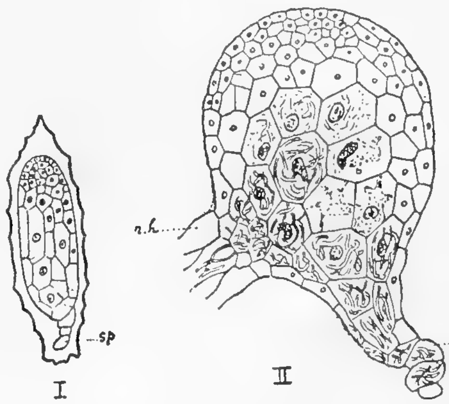
I saw *Apis mellifica* ☿ (hive-bee) withdraw two pairs of pollinia at Guildford from a spike of this species, and saw *Cœlioxys rufescens* Lep. ♂ visit another without withdrawing pollinia. The spur of *A. pyramidalis* contains no free nectar, but is dry inside. The outer and inner walls are, however, separated to an unexpected degree, and the inner skin is extremely delicate and easily pierced. If a spur from which the tip has been cut off is gently pressed, large drops of fluid are expelled. On the other hand in the very similar spur of *Gymnadenia conopsea*, which is full of nectar for at least one-third of its length, the inner and outer skins of the spur are closely united, though the inner presents the same structure and papillæ as those of *A. pyramidalis*.[3] It does not follow that the liquid between the walls of the latter species is nectar. The spur may be simply an alluring drinking fountain on a thirsty day, the visitors piercing the tender inner skin to suck their fill. The immense value of this may be easily realised by anyone who has noticed the numbers of bees and butterflies settling on sandy soil with a tiny trickle of water beneath. The author some years ago saw by the roadside in the Malay Peninsula what appeared to be a large circular white flower variegated with blue, the like of which he had never seen before. On his eager approach it dissolved into a cloud of white and blue butterflies settled round a patch of wet sand.

[1] *Ibid.* p. 31, Fig. 4. [2] *Ibid.* p. 34. [3] *Ibid.* p. 40.

V. THE LIFE OF AN ORCHID

In 1838 Lindley wrote that nothing certain was known of the germination of the Orchidaceæ. Seeds will not germinate under the ordinary conditions of moisture, warmth, light and soil. Seedlings sometimes appeared in pots in which the parent plant was growing, but when seeds were sown in such pots the results were very uncertain. The seed of a grass consists mainly of a large store of nutriment (albumen), and the embryo has a radicle and plumule ready to develop into a root and seed-leaf respectively on germination. The abundant albumen enables the seedling to grow till it can fend for itself.

The embryo of an orchid[1] consists of a mass of undifferentiated cells (Text-fig. 4, I). There is no sign of rootlet or seed-leaf, and no albumen. The small oily food-content is used up long before germination is completed.[2] The embryo cannot germinate without the aid of certain species of fungus, the thread-like filaments (mycelium) of which enter the seed through the suspensor (*sp.* Text-fig. 4) and aid in the nutrition of the embryo. It has been found that germination results from invasion by the fungus *Rhizoctonia repens* or other allied species. M. Beau[3] made the following experiment. A watchglass, convex face downwards, was placed on gelose (vegetable jelly), and mycelium on the latter, when its filaments rapidly climbed over the glass. Seeds were then sown on the mycelium, so that they had no contact with the gelose. The mycelium penetrated into the embryos which germinated normally. If the filaments were destroyed growth stopped. They evidently conveyed nutritive matter from the gelose to the embryo.



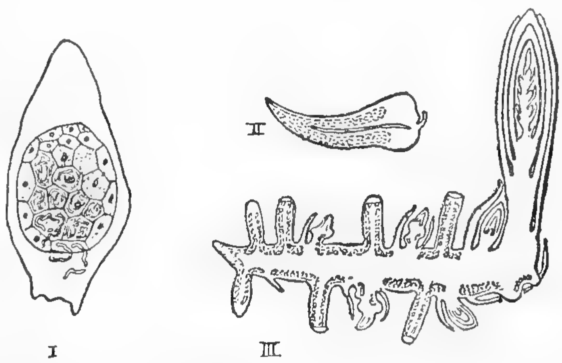
Text-fig. 4. I. Seed of *Odontoglossum* enclosing the oval embryo. *Sp.* Suspensor. II. Seedling of *Odontoglossum*. *Sp.* Suspensor through which the fungus enters the seedling. The filaments of the fungus are shown in the cells adjoining the suspensor, and are passing out through the root-hairs (*r.h.*) on the left-hand side. The filaments in the upper cells are less distinct, being in process of digestion by the cells. From Noel Bernard's "Études sur la tubérisation", *Revue générale de Botanique*, XIV (1902), by kind permission of the editor.

When thus invaded by the endophyte (a plant growing within a living plant), the embryo swells into a **protocorm** (Text-fig. 5, II), a greenish or whitish tubercle hardly visible to the naked eye, with a small peg on the top, the rudiment of the first leaf. Numerous absorptive hairs (*r.h.* Text-fig. 4, II) are produced at the base

1 Rendle, *Classification of Flowering Plants*, ed. 1, Monocoty. pp. 346–9.
2 Clement, *O.R.* p. 360 (1924).
3 Beau (Clovis), "Sur le rôle trophique des endophytes d'Orchidées" (*C.R. Ac. Sc.* 1920, p. 675).

of the protocorm, and the fungal filaments pass in and out through them. The cells near the suspensor are attacked, but the parasitic fungus is prevented from invading the whole plant by the latter's power of digesting it. The nuclei of the cells swell, put out pseudopodia (extensions like a glove-finger) which enclose the fungus, reducing it to a dead amorphous mass, which seems finally to disappear.[1] The growing hyphæ (filaments) of the fungus form coils (Text-fig. 4, II) or balls[2] within the cells which are invaded by degrees, coils being formed in each cell before passing on to the next. The fungus only attacks cells almost fully developed, and those invaded no longer grow perceptibly. There is no growing point in the infected area. Cells containing chlorophyll, tannin, mucus, raphides and other crystals are never invaded.[1] The meristematic cells (nascent or very young tissue) are never entered, the only cells infected still capable of growth by division being those of the seed, where the first entry is made.[1] The hyphæ do not as a rule extend from the seed to the root, the latter becoming later invaded from the soil through the root-hairs. In *Neottia*, however, the fungus passes from the protocorm into the rhizome and infects the successive roots (Text-fig. 5, III). The digesting cells are recognisable by the degenerating mass which more than half fills them.[1]

Reissek (1846) first recognised the fungal nature of the coils, and was followed by Irmisch, Fabre, Wahrlich (who proved their presence in 500 exotic species), Chodat, Ramsbottom and many other observers, but it is to Noel Bernard's researches that we are largely indebted for our present knowledge. His "Études sur la tubérisation" (1902) showed that the seeds of orchids can only germinate in the presence of the fungus, and that the seedling is infested in its earliest stages. He isolated the fungus from the orchid root and grew it on nutrient media, and showed that orchid seeds would germinate without difficulty if the appropriate fungus was supplied. His great work, "L'évolution dans la symbiose" (*Annales des Sciences nat.* sér. 9, IX, 196), appeared in 1909, and in the same year Burgeff's comprehensive work, *Die Wurzelpilze der Orchideen*, saw the light. These researches



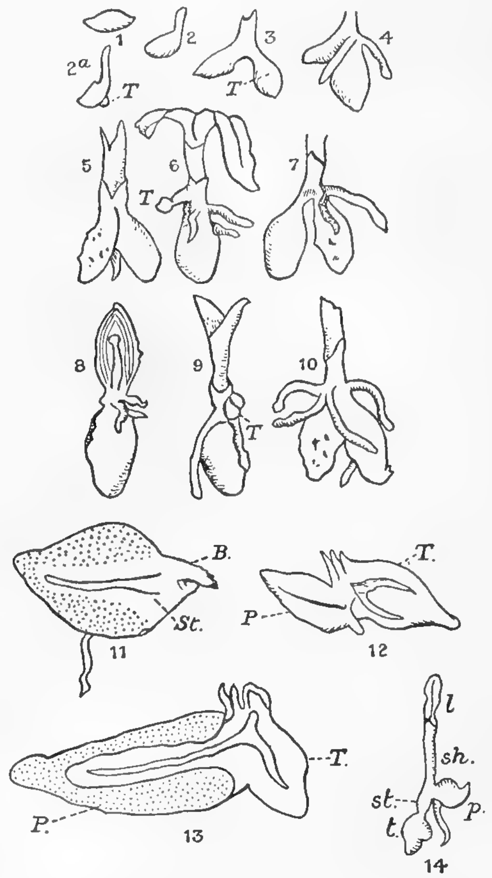
Text-fig. 5. I. Seed of *Neottia* showing oval embryo already invaded by fungal filaments. II. Protocorm of *Neottia*. Dotted area shows region penetrated by fungus. III. Plant of *Neottia* with young flowering axis. Area infected indicated by dots. From Noel Bernard's "Études sur la tubérisation" *Revue générale de Botanique*, XIV (1902), by kind permission of the editor.

[1] Ramsbottom, *Orchid Mycorrhiza* (Charlesworth & Co.'s Catalogue, 1922), reprinted in *Trans. Brit. Mycol. Soc.* VIII, 28 (1922).

[2] Pl. A, fig. 3, if properly focused, shows the fungus filaments with ball-like spores and the large nucleus floating in the midst of the cell, taken from a rhizome of *Epipogon aphyllum* (p. 6).

enabled the cultivation of orchids from seeds to be carried out on a large scale by Charlesworth and others.

This living together of two organisms in close association is termed **symbiosis.** A well-known example of this is the lichen, which is a composite plant formed of a fungus and an alga in definite union. Germination of orchid seeds without the aid of a fungus has now been carried out successfully by Charlesworth and Clement[1] in England, by G. and M. Ballion in Belgium,[2] and by M. Bultel in France,[3] amongst others. Germination appears always to be preceded by invasion by the fungus. In *Orchis*, for instance, the embryo swells and bursts its transparent covering, and forms the protocorm or germ-tubercle, shaped like a peg-top lying on its side (Text-figs. 4, II; 5, II and 6, *1*, *11*). The pointed end (suspensor) becomes invaded by the fungus, the infection spreading on all sides (but not in the centre) about half-way to the rounded end with its little peg (incipient leaf). On the lower side of the germ-tubercle rather long silky absorbent hairs enter the soil. A central cylinder (stele) begins to form (Text-fig. 6, *11*). The peg develops into a bud, *B.*, but often only a single leaf is formed during the first year. One or two adventitious roots break through near the base (Text-fig. 6, *4*, *6*), the first root lengthening downwards, contracting and drawing the germ-tubercle beneath the soil. The first real tuber forms within the germ-tubercle, below the bud, and emerges just beneath it (Text-fig. 6, *13*). At the end of the first year it becomes separated, together with the bud, from the germ-tubercle, being then hardly more than a few millimetres long. In the second or early third year it gives rise to a fresh tuber on a short stalk (Text-



Text-fig. 6. 1. Protocorm of *Orchis*. 2, *2a*. Later stages. *T*. New tuber appearing. 3. Latter more developed. 4. Roots appear. 5. Protocorm shrivelling. 6. Plant early in third year. *T*. New tuber on a little rhizome. 7. New tuber developed, the old one shrivelling. 8. An adult *Orchis*, about September, the young flower-spike already exists in bud. 9. Next stage about January, in S. France. 10. About May or June, old tuber withered, new developed. 11. Protocorm of *Orchis militaris*. *B*. Terminal bud. *St*. Stele. 12. Protocorm of *Platanthera chlorantha*, section in spring (after Bernard). 13. The same in May. *P*. Protocorm. Dotted area invaded by fungus. 14. Seedling in June (after Irmisch). For explanation of lettering, see p. 29.

[1] O.R. p. 360 (1924). [2] *Ibid.* p. 103 (1928).
[3] *Revue hort.* pp. 318, 334, 359 (1925).

fig. 6, *6*), almost as broad as the tuber, both furnished with absorbent hairs, which pushes the tuber beneath the soil. The latter has several steles and is free from endophytes. Adventitious roots (Text-fig. 6, *10*) are put forth above the tuber, which grow horizontally or obliquely, and become infected with mycorrhiza from the soil. Each year a stronger tuber is produced, and the old one shrivels away, gradually however, for sometimes the remains of two decaying tubers are found. The young plant grows vegetatively from 4 to 7 years (much longer in some exotic genera), building up a larger store of nutriment, till at length it is able to flower. A few species normally put forth two new tubers yearly, e.g. *Herminium monorchis* (which sometimes has 2–5 new tubers), *Ophrys bombyliflora*, *Serapias gregaria*, etc. This also sometimes happens with unusually vigorous plants of other genera, e.g. *Orchis mascula*.

The protocorm is at first almost globular, less than $\frac{1}{3}$ mm. long, and lies on its side, except in *Cypripedium*, in which it is erect. Text-fig. 6, *11* shows a section of a magnified protocorm of *Orchis militaris*; *B.* is the bud, *St.* the stele, and the dots show the area invaded by the fungus (after Irmisch). *12* is a section of a plantlet of *Platanthera chlorantha*, *P.* protocorm, *T.* tuber of second year; *13* shows a still more enlarged section of another plant of the same species in May (after Bernard). In Text-fig. 6, *2* shows bud developing; *2a*, first sign of new tuber; *3*, development of the latter; *4*, appearance of roots; *5*, protocorm shrivelling; *6*, plant of third year with tiny new tuber at tip of a stalk; *7*, the latter full grown, and old tuber shrivelling up; *8*, section of bud in autumn with rudimentary flower-spike visible; *9*, plant about January (south of France), old tuber gone, new tuber (*T.*) beginning; *10*, the same in May or June, old tuber withering and the new well developed; *14*, seedling in June, *p.* protocorm, *t.* first tuber, *st.* stalk, *sh.* sheath, *l.* first leaf.

Bletilla hyacinthina of Eastern Asia can germinate either with or without fungus, but in the latter case no bulb is formed.[1] Although it is possible to induce germination on richly nutritive media, the only method in nature appears to be fungal invasion. It is said that very rarely the fungus invades the whole plant and destroys it, but normally it is confined to the limited areas where its presence is beneficial.[2] As *Cynips* produces galls on a leaf, so perhaps invasion of an orchid by a fungus gives rise to the tuber.[3]

Cypripedium increases by annual zigzag growths of the rhizome, which is usually free from fungus, the roots only being infected. Irmisch figures a plant which has had six annual growths without being yet strong enough to flower.[4] *Cephalanthera rubra* in loose, calcareous soil is sometimes found with branched roots, the older ones

[1] Weiss, "Seeds and seedlings of Orchids", *Trans. Manchester Micros. Soc.* (1917).
[2] Camus, *Icon.* pp. 32, 35, 47.
[3] Constantin, *La vie des Orchidées*, p. 155.
[4] Irmisch, *Beiträge zur Biologie und Morphologie der Orchideen.*

only slightly invaded, the others with undigested coils in the cortex-cells.[1] Adventive buds have been found on roots still in living connection with the plant.[2]

Penetration of the roots and often of the rhizome is usual in the Neottieæ. In *Epipactis rubiginosa* the roots are very numerous and long, deeply penetrating the creviced limestone, with flat spear-shaped tips adhering to the rock. Swellings occur, giving rise to new roots and a new shoot (Pl. 11, F), showing how a rhizome can be formed deep in the rock. Pl. 11, figs. D and E, show that a shoot can even be formed at the tip of a root. In *Listera*, mycorrhiza form coils in the cells of the cortex, and are present in the root-hairs, but in *L. cordata*, according to Chodat and Lendner,[3] they do not extend outside the hairs. In *Neottia* (Text-fig. 5), symbiosis is continuous, the fungus infecting rhizome, roots, and sometimes the base of the stem. Increase may occur through buds at the tips of the roots.[3] W. H. Herbert found that some of the fleshy roots, though dead at the base, were alive and beginning to protrude young fibres at the tip,[4] the extreme point becoming the eye or shoot. There is no chlorophyll, the leaves being reduced to brown sheathing scales, probably due to the very extensive invasion by endophytes, which convey so much nutriment from decaying organic matter that leaves have become superfluous. *Bognisia crocea* (Burmanniaceæ) has a similar root-system, which is a sign of saprophytism, found also in our *Epipactis violacea* (Pl. 8) and the continental orchid *Limodorum abortivum*.

Goodyera repens inhabits the layer of needles and moss in pine-woods, and has a long creeping rhizome, in which the endophyte *Rhizoctonia Goodyeræ repentis* is abundant. The specimen figured (Pl. 13) is the only one we ever found or heard of with a bulb-like tuber, and shows the possibility of a slender rhizome giving rise to such. In *Spiranthes* the roots are long and cylindrical in species growing in wet ground, e.g. *S. æstivalis*, but thicker in those inhabiting drier places,[5] e.g. *S. autumnalis*, in which they resemble the tubers of *Platanthera bifolia* in shape. They are not true tubers, however, being monostelic and infected by fungi, but indicate a passage from the roots of the Neottieæ (to which the above belong) to the tubers of the Ophrydeæ.

Malaxideæ. In *Malaxis* and *Liparis* the roots are slender. There is a bulb-like swelling at the base of the stem above the leaves surrounded by several thick tunics, with many tracheids (elongated closed cells) for storage of water. They are slender frail plants, and this provision is necessary to bring them through dry periods when the sphagnum or boggy ground in which they grow dries up. *Corallorhiza* has no roots, but a whitish coral-like rhizome with short lobe-like branches largely infected by endophytes. That curious plant *Geomitra episcopalis* (Burmanniaceæ) has a similar

[1] Camus, *op. cit.* pp. 32, 35, 47.
[2] Irmisch, *op. cit.*
[3] R. Chodat et A. Lendner, *Bull. Herb. Boissier*, IV, 265 (1896).
[4] Leighton, *Fl. Shropshire*, p. 434 (1841).
[5] Mr Mousley found that near Hatley, Quebec, the roots of *Spiranthes Romanzoffiana* were much thicker in dry ground than in wetter places.

rhizome. The European and American *Calypso borealis* (*bulbosa*) has a pseudo-bulb, but in old plants sometimes develops a coralloid rhizome, strongly infected, apparently an effort to supplement insufficient nourishment by increase of absorptive surface and fungal assistance.[1] It is a sure sign of saprophytism.

Epipogon has a similar coral-like rhizome, which sends out thread-like runners which give rise to fresh rhizomes (Pl. 21). It is essentially an underground plant, sometimes growing for several years without appearing above the soil. The leaves are reduced to sheaths without chlorophyll, and the plant is saprophytic. A swelling at the base of the stem forms a large reservoir for the storage of water. It is extraordinary that a plant of such low organisation vegetatively should have evolved such highly organised flowers, which have attained a level of perfection equal to that of *Orchis*. Both it and the preceding have absorbent hairs on the rhizome. It only flowers in very favourable seasons, just often enough to maintain the vigour of the species by cross-pollination. A bunch of small independent rhizomes may sometimes be found at the base of a flowering stem.

We now come to the highly organised Ophrydeæ, in which rhizomes and monostelic fungus-infected roots are replaced by tubers. The palmate tubers of *Cœloglossum*, *Gymnadenia* and the Dactylorchid group of *Orchis* form a transition to the rounded entire polystelic fungus-free tubers of *Orchis* and *Ophrys*, in which, according to Bernard,[2] a very diffusible substance[3] stops the development of endophytes, though the free tips of palmate tubers often contain mycorrhiza. As a rule only the adventitious roots are infected, *Rhizoctonia repens* being the most common fungus. *R. violacea* is found in potato tubers. In ling, *Calluna vulgaris*, a fungus invades the whole plant, and waits in the seed-coat to infect the young seedling.[4]

As soon as the flower opens the beautiful and very varied floral mechanisms for automatically attaching the pollinia to visiting insects come into play, and the latter distribute the pollen on the stigmas of flowers, in almost every case growing on separate plants. About ten European species are self-fertilising. It is remarkable that they were all previously organised for the removal of the pollinia by insects, and, with perhaps one exception, have not been always self-fertilising (see Pollination and Fertilisation). In the few European species capable of self-pollination, cross-pollination by insects still occasionally occurs. The ripe seed-capsules open by longitudinal

[1] Camus, *op. cit.* pp. 32, 35, 47. [2] Bernard, *Ann. Sc. nat. Bot.* p. 221 (1911).

[3] Noel Bernard placed a sterilised fragment of a tubercle of *Himantoglossum* or of an *Ophrys* at the bottom of a tube which he partly filled with jelly made from salep (extract from the tubers of an *Orchis*). On its surface he sowed *Rhizoctonia repens*, the fungus which invades the Ophrydeæ. This at first developed well and then growth stopped. The soluble fungicide substance of the fragment of tubercle diffused itself in the jelly and stopped the development of the fungus long before its filaments had reached the tubercle. The fungicide acts well in the case of *Rhizoctonia repens*, but had no effect on *R. mucoroides*, the fungus which invades *Vandas*. Camus, *op. cit.* p. 36 (1928).

[4] Weiss, *op. cit.*

slits dividing them into six valves—three broad bearing the seeds, and three narrow, often reduced to a single nerve, which are sterile. The valves remain joined together both at base and summit. In dry weather the capsule contracts, opening the slits, and the wind blowing through carries out the ripe seeds, easily wind-borne for long distances owing to their extreme lightness. The vibration of the stiff stems displaced by sudden gusts shakes out the seeds as from a pepper-pot. In some genera of epiphytic orchids there are elater-like hairs on the valves which jerk out the seeds.[1] In wet weather the capsule lengthens, closing the valves, and protecting the seeds till fine weather once more opens the slits.

The number of seeds produced is enormous. Darwin found that a capsule of *Orchis maculata* held 6200 seeds, so that a plant with 30 capsules would bear 186,000. Allowing 400 bad seeds for each capsule, an acre would be thickly clothed by the progeny of a single plant, the grandchildren would cover the island of Anglesey, and the great grandchildren, at the same rate of increase, would nearly clothe the whole land surface of the globe with one uniform carpet of green.[2] This is eclipsed by Fritz Müller, who found 1,756,440 seeds in a single capsule of a *Maxillaria*, and the plant sometimes bears six such capsules. The reason for this stupendous production of seed appears to be that not a single seed can germinate unless it falls on ground where the appropriate species of *Rhizoctonia* is present, and unless hyphæ actually find their way into the extremely minute micropyles of the embryos.

Pl. F, fig. 5 (p. 123), is a beautiful stereograph of the seed of *Limodorum abortivum* which shows in a wonderful way the glass-like inflated testa with its reticulations, whose excessive lightness makes the transport of the seed by air very easy.

VI. HYBRIDISM

In 1820 Reichenbach pat. wrote "naturam enim purissimam tales impuritates non gignere...certi sumus".[3] Natural hybrids were regarded as an offence against the purity of nature. This idea blinded the eyes of botanists to their existence. As any union between two distinct species would be unnatural, the finding of a plant intermediate between them was supposed to prove that the two species were one and the same—the marriage was legalised by uniting them. Thus Hooker[4] wrote to Darwin: "The dismal fact you quote of hybrid transitions between *Verbascum thapsus* and *nigrum*, and its bearing on my practice of lumping species through intermediate specimens, is a very horrible one, and would open my eyes to my own blindness

[1] Rendle, *op. cit.* pp. 346–9.
[2] Darwin, *Fert. Orch.* ed. 2, p. 278.
[3] *Mon. gen. Aconiti*, p. 51.
[4] Hooker's *Life and Letters*, II, 34.

if nothing else could....Perhaps my intermediates between *Habenaria* (*Platanthera*) *chlorantha* and *bifolia* (of which I retain a lively recollection) were of this hybrid nature". Hybrids between genera were still more unthinkable. Wettstein urged the inclusion of *Cephalanthera* in the genus *Epipactis* on the strength of a single specimen of the cross *C. grandiflora* (*pallens*) × *E. rubiginosa*, maintaining that the very existence of this hybrid pleaded for the union of these two genera.[1]

One of the first natural hybrids recognised was *Gymnadenia conopsea* by *Nigritella nigra*, found near Grenoble in 1787, and named *Orchis suaveolens* by Villars.[2] Neither of the parents is now regarded as belonging to the genus *Orchis*. This was followed by *Orchis hybrida* Bonningh. in 1830, found growing amongst the parents, *O. militaris* and *O. purpurea*, and regarded by Lindley as a mere variety.[3] In 1852 a consignment of *Phalænopsis aphrodite* (*amabilis*) contained a plant which Lindley regarded as *P. amabilis* × *P. rosea* (×*P. intermedia*). Later Seden fertilised *P. amabilis* with pollen from *P. rosea*. Only one seedling was successfully raised, which flowered in 1886, and turned out to be identical with the wild plant, confirming Lindley's determination. This appears to have been the first actual proof by experiment of the hybrid parentage of a wild orchid.

Some species cross much more readily than others. *Orchis morio* crosses fairly frequently with *O. laxiflora*, forming ×*O. alata* Fleury (Pl. 42), but very rarely with *O. mascula* (Pl. 40), though they often grow together. Of the British marsh orchids *Orchis incarnata*, *latifolia*, *prætermissa* and *purpurella* hybridise not infrequently with *O. maculata*, and to a less extent among themselves. They are similar enough in appearance to attract, at any rate sometimes, the same insects. Wherever they grow together in any quantity there is a good chance of finding a hybrid, perhaps several. In some localities the intermediate hybrid forms vary so much as to give some plausibility to the theory that they all belong to one polymorphic species, but the various species are stable enough over very wide areas of distribution. The great variety in our marshes is probably due, not only to primary hybrids being sometimes nearer one parent, sometimes the other, but to back-crossing of these with one or other parent. A chain of intermediates between two forms does not necessarily prove that they belong to the same species. It is much more likely to be due to hybridism. When a first generation hybrid is crossed with a third species, great variation results, even seedlings from the same capsule showing wide divergence. If the hybrid $A \times B$ be crossed with C, some of the offspring resemble the hybrid $A \times C$, and some $B \times C$, while the rest will form various combinations of the three species concerned, as in the well-known case of *Cypripedium aureum* (*C. insigne* × *villosum* crossed with *C. spicerianum*). Artificial hybrids involving no less than six different species have been

[1] *Œster. Bot. Zeitung*, pp. 395–9 (1889).
[2] *Pl. Dauphin*, II, 38, t. 1.
[3] *Gen. et Spec. Orch.* p. 271.

successfully raised.[1] Incidentally it may be remarked that species between which natural hybrids practically never occur are remarkably faithful to type, whilst species prone to hybridisation, such as *Orchis maculata*, present a perfect riot of variation (Pl. 50).

When the existence of natural hybrids was at length admitted, it was still maintained that only crosses between races or varieties were fertile, that those between species were sterile, and that none could arise between genera. Experiment has shown that not only can hybrids occur between genera (of which indeed *Gymnigritella suaveolens* mentioned above was an example), but that various hybrids have been raised involving three distinct genera. A list of thirteen and coloured plate of nine European bi-generic natural hybrids appeared in *Genetica*, IX, 24 (1927). The belief that the existence of bi-generic hybrids amounted to a proof of the identity of the parent genera has no foundation in fact.

European orchids, except about ten wholly or partly self-fertilised species, are mainly visited by Hymenoptera. They alight at the base of the spike and work upwards, thus assuming the right position for the removal of pollinia, and nearly always confine themselves to the species which they first begin to visit on starting their round. This selective instinct plays a great part in keeping species true to type, and the fidelity with which they carry out this principle is remarkable. A natural hybrid is an accident, and as far as my experience goes, such accidents are rare, often extremely rare (with the partial exception of the marsh orchids). Bees do not often appear to change over in the course of their round from one species to another, unless the species with which they began proves too few and far between. Hence the conditions most favourable for the production of hybrids are not when both parents are abundant, but when one is plentiful and the other scarce, or when few plants of the one are in flower whilst the other is in full bloom. Of some hybrids only a single specimen has ever been found, whilst others, e.g. *Cœloglossum viride* × *Gymnadenia conopsea*, have only occurred in one or two localities, though the parents often grow together. This may be due to the presence of an insect in the localities in question which is absent from continental stations, or to pure accident.

Transmission of characters. All the characters of each parent are rarely traceable in a hybrid. One or more characters must be perceptible, or they could not, if growing wild, be recognised as hybrids. Even conspicuous characters may disappear in crosses between different genera, e.g. in all hybrids between *Orchis* and the spurless S. European *Serapias*, the spur of *Orchis* appears to be entirely suppressed. There was once an idea that the leaves of a hybrid resembled those of one parent, and the flowers those of the other. An example of this is seen in Pl. 30, B, *Orchis incarnata* × *O. maculata*, in which the leaves were those of *incarnata*, and the flowers were much like those of *maculata*. This, however, is quite exceptional. One plant of *Orchis papilionacea* ×

[1] *Genetica*, IX, 26 (1927).

Serapias neglecta found by us near Pisa had the narrow curly leaves of the *Serapias* parent, and another the broader flat leaves of an *Orchis*. On the Lago di Como the form of *Orchis mascula* prevalent there has innumerable short red lines on the leaves, and the yellow-flowered *Orchis provincialis* small rounded blackish spots. In a hybrid found there between them both kinds of markings were present on the same leaf.

The irregular manner in which the characters of the parents may be combined is seen in Text-fig. 10 (p. 128), showing three different types of *Cœloglossum viride* × *Gymnadenia conopsea*. The lip of *A* is near that of *G. conopsea*, that of *B* near *C. viride*, while that of *C* is between the two. *A* has the long slender spur of *G. conopsea*, that of *B* is much shorter, but as thick as and longer than that of *C. viride*, while that of *C* is very near the spur of the latter, and from some flowers absent altogether. All the single flowers are considerably enlarged.

Relation of variation to hybridisation. It is found that, in cultivation, crossing acts as a strong stimulus to variation. It assembles in the offspring a number of different, sometimes conflicting characters, in a state of more or less unstable equilibrium, even seeds from the same capsule varying considerably. This tendency to variation is a marked feature of hybrids, so that when some exceptionally fine hybrid orchid has been produced, it usually becomes necessary to perpetuate it by vegetative processes.[1]

Fertilisation of a hybrid by its own pollen. If a primary hybrid is artificially fertilised with its own pollen, partial reversion to one or other parent may occur, as in the case of *Epidendrum Kewense* (*E. evectum* × *E. xanthinum*), of which one seedling strongly resembled *E. Kewense*, another showed partial reversion towards the purple *E. evectum*, and a third towards the yellow *E. xanthinum*.[2] This seems to indicate a tendency to reversion, even if seeds are produced by self-pollination.[3]

VII. NOMENCLATURE

I have given reasons for the employment of any names which are open to controversy. The Rules adopted by the International Botanical Congress at Vienna in 1905 form on the whole an admirable code of regulations. It is doubtful, however, whether Art. 15, placing every name, however widely accepted, at the mercy of anyone who can find an older one even though still-born, has not been a direct temptation to replace living names by dead synonyms.

The Rules have now been over 25 years in force. So far as orchids are concerned,

[1] Rolfe, *O.R.* p. 104 (1912). [2] *O.R.* p. 127 (1909).

[3] In the case of two or three wild hybrids I have observed that after a few years' cultivation the characters of one of the parents become less and less marked.

the results have not fulfilled expectations. *Epipactis* has been changed to *Helleborine* by Druce, to *Serapias* in Gray's *New Manual of Botany*, ed. 7 (1908), and to *Amesia* by Nelson and Macbride—three names in the field at once, each claiming to be the "only valid" one. The name *Epipactis* has been transferred to *Goodyera* in America, though there can hardly be a more fruitful source of confusion than the transfer of a name of over 160 years' standing to a different genus of plants. *Cephalanthera grandiflora* was originally named *Serapias Helleborine β longifolia* by Linnæus in 1753. In 1767 he transferred the name *longifolia* to *Epipactis palustris*, and renamed our plant *Serapias grandiflora*, which, however, also included *C. ensifolia*. In 1769 Crantz named it *Epipactis alba*. Later Junz called it *Serapias pallens* (1791). It first appeared under its present genus as *Cephalanthera pallens* Richard in 1818. In 1843 Babington reverted to the Linnean specific name of 1767, naming it *C. grandiflora*. In 1906 Druce renamed it *C. Damasonium* from *Serapias Damasonium* of Miller's *Gardeners' Dictionary*, and in 1907 Janchen named it *C. latifolia* from the same horticultural work. Before the 1905 Congress there were practically only two names in use, *pallens* and *grandiflora*. Now there are in addition to these *longifolia*, *alba*, *Damasonium* and *latifolia*, each being considered by its sponsor the only valid name.

In the case of hybrids in this work the names of the parents are placed in alphabetical order, and not in the order of dominance. Rouy[1] protests against the giving of what he calls pseudo-generic names like *Orchigymnadenia*, but these do not pretend to be the names of genera. They are simply a combination of the generic names of both parents, and accurately represent the actual state of the case. His contention that a bi-generic hybrid should be attached to the genus of which it shows the most salient character would result in hybrids between the same parents being allotted to different genera. Thus the specimen of *Gymnadenia conopsea* by *Orchis maculata* from Sevenoaks mentioned on p. 144 would have been placed under *Gymnadenia* on account of the linear viscidia forming the roof of the spur-entrance and having no pouch, while that from Teesdale (Pl. 26 A), with viscidia enclosed in a pouch, would have been put under *Orchis*.

[1] *Flore de France*, XIII, 97.

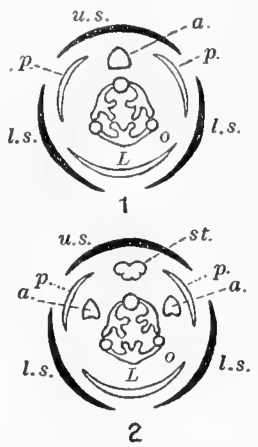
VIII. DESCRIPTION OF GENERA AND SPECIES

Family ORCHIDACEÆ Lindl.

The Orchidaceæ belong to the Monocotyledons (plants with only one seed-leaf and parallel leaf-veins), and form part of the minute-seeded Microspermæ.

The flowers are hermaphrodite, with both pollen-bearing and seed-bearing organs in the same flower, irregular,[1] zygomorphic,[2] situated above the ovary, usually resupinate.[3] The perianth consists of three sepals, and alternate with them two petals and a labellum or lip, generally larger and more conspicuous, very often 3-lobed, frequently spurred. In the centre of the flower is the column or gynostemium (formed by the fusion of stamens and style into a solid body), usually facing forwards or downwards. The number of anthers and stigmas differs in the two sub-families. In the Diandræ there are two fertile anthers, one on each side of the column at the base of the lip, containing pollen in single grains immersed in an adhesive paste, a large petaloid staminode terminating and protecting the column, and three united dry non-viscous stigmas, all functioning as receivers of pollen.

In the Monandræ there is only one fertile anther, at the apex of the column, containing two (rarely four or eight) pollinia, built up of tetrads, i.e. pollen-grains coherent in fours (except in *Cephalanthera*, in which they are single); two stigmas functioning as such, united or separate; and a rostellum or apparatus for affixing the pollinia to insects (evolved from the third stigma). In some species two small staminodes (vestiges of suppressed anthers) are present, one on each side of the column at the base. Beneath the perianth in both sub-families is the ovary, apparently formed of three fertile and three sterile carpels, usually unilocular (1-celled), bearing innumerable minute ovules (young unfertilised seeds) on three usually forked low ridges (parietal placentæ). Fruit a dry dehiscent capsule opening by the separation (except at the base and apex) of the valves from the intervening ridges, leaving slits through which the seeds escape, either shaken out by the wind, or in certain exotic orchids "scattered by the aid of elater-like hairs developed on the interior of the valves, the movements



Text-fig. 7. 1. Diagram of the Monandræ. 2. Diagram of the Diandræ. *l.s.* Lateral sepal. *u.s.* Upper sepal. *p.* Petal. *L.* Lip. *a.* Anther. *o.* Section of ovary. *st.* Staminode. From *Iconographie des Orchidées d'Europe*, by permission of Mlle A. Camus.

[1] Except in a few exotic species.

[2] Only divisible into symmetrically similar halves in one plane, down the middle from back to front.

[3] Reversed by twisting of the ovary or its stalk, placing the originally upturned lip downwards.

of which, due to their remarkable hygroscopic character, jerk out the seeds".[1] Seeds (Pl. F, fig. 5) scobiform (like sawdust), innumerable, minute, with a thin, loose, netted covering (testa) as transparent as glass, and an oval, dark-coloured embryo, without endosperm (albumen).

CONSPECTUS OF GROUPS OF BRITISH SPECIES

Family: **ORCHIDACEÆ** Lindley.

Sub-family: **DIANDRÆ** Salisbury. Fertile anthers 2

Tribe: **Cypripedieæ** Lindley.

Genus: Cypripedium.

Sub-family: **MONANDRÆ** Swartz. Fertile anther 1

Acrotonæ Pfitzer.

Pollinia without or with only apical caudicles, anther detachable.

Tribe I: **Neottieæ** Lindley.

Genera: Cephalanthera, Epipactis, Listera, Neottia, Goodyera, Spiranthes.

Tribe II: **Malaxideæ** Lindley.

Malaxis, Liparis, Corallorhiza.

Tribe III: **Epipogoneæ** Parlatore.

Epipogon.

Basitonæ Pfitzer.

Pollinia with basal caudicles, anther in one piece with column.

Tribe IV: **Ophrydeæ** Lindley.

Sub-tribe 1: ***Gymnadeniinæ*** Engler.

Viscidia not enclosed in a pouch left behind when they are removed.

Herminium, Cœloglossum, Platanthera, Gymnadenia.

Sub-tribe 2: ***Serapiadinæ*** Engler.

Viscidia kept moist in a pouch left behind when they are withdrawn.

Neotinea, Anacamptis, Himantoglossum, Aceras, Orchis, Ophrys.

[Sub-tribe 3: ***Habenariinæ*** Engler (***Habenarieæ*** Pfitzer).

Stigmas projecting forwards in distinct often long processes.

Habenaria, etc. About 400 species of warm climates.

No European representative.]

[1] Rendle, *Classification of Flowering Plants*, 1, 371.

POPULAR KEY TO BRITISH SUB-FAMILIES AND GENERA

A. Fertile anthers two, on horn-like side-lobes of column which ends in a large staminode.

Sub-family **Diandræ**

1. Lip inflated, yellow, calceolaria-like; sepals and petals brown-purple; side-sepals joined together behind lip; staminode white spotted red. **Cypripedium**

B. Fertile anther one only, at apex of column.

Sub-family **Monandræ**

I. Pollinia without caudicles (stalks) at base.

2. Column long; *rostellum none*; *pollinia crescent-shaped*; flowers white or rose; lip with parallel coloured crests. **Cephalanthera**
3. Column short; pollinia club-shaped, deposited in shallow cup (clinandrium) beneath the anther; *lip with basal cup* (hypochile) *glistening with nectar*, and triangular or heart-shaped apex (epichile). **Epipactis**
4. Leaves two only, nearly opposite, some way up stem. Lip narrow, forked; anther depositing pollinia on the tongue-shaped rostellum; ovary nearly globose; *nectar-filled groove down middle of lip.* **Listera**
5. *Whole plant smoky brown* without leaves or chlorophyll. Anther and rostellum as in 4. Crowded fleshy roots. **Neottia**
6. *Rhizome slender*, *creeping*. Flowers small, white, glandular, hairy, in a slightly twisted spike; lip with *deep bag-like base and long spout-like epichile.* **Goodyera**
7. Roots 2–6, thick. Flowers small, white, tubular, sweet-scented, in a twisted spike; column horizontal, ending in a *linear brown or grey viscid gland, leaving a green fork behind when withdrawn.* **Spiranthes**
8. Small marsh plant. Stem with bulb-like swelling at base. Leaves two, oblong, erect, glossy. Flowers green with slender sepals and petals and *much broader upcurved lip.* **Liparis**
9. Very small marsh plant. Leaves two, small, concave, with *tiny buds at apex.* Flowers very small, green, with *lip pointing upwards.* **Malaxis**
10. Stem with sheaths but no leaves. *Rhizome branched, coral-like.* Flowers small, yellowish green, with white, tongue-shaped, red-spotted lip. **Corallorhiza**

II. Pollinia attached to viscid glands by caudicles.

11. Stem without leaves, much swollen at base. *Rhizome with flattish coral-like branches.* Flowers large, *inverted*, yellowish, with erect red-tubercled lip and *thick spur.* **Epipogon**

12. Tubers palmate. Leaves short, rather broad. Flowers small, green (often edged red) or reddish brown; *lip narrow, strap-shaped, 3-toothed at apex*, with *short bladder-like spur*. **Cœloglossum**

13. Very small plant with one nearly globose tuber and *one or more long-stalked incipient tubers*. Spike short, prickly-looking; flowers very small, green, scented, obconical, with *dagger-shaped lip*. **Herminium**

14. Leaves two, long, broad. Spike conspicuous; flowers white or greenish white, with strap-shaped lip and long slender spur; viscid discs, yellow, *facing each other*, not in a pouch. **Platanthera**

15. Tubers fingered or fascicled. Stigmas 2, on side-lobes of column. *Viscidia nearly linear, not in a pouch*. Flowers small, pale lilac or rose (rarely white or magenta) with long slender spur (*G. conopsea*), or very small white with short thick spur (*G. albida*). **Gymnadenia**

16. Tubers ovoid. Stigmas 2, on side-lobes of column. Viscidia very small round *enclosed in a pouch*. Leaves bluish green often spotted along the nerves. Flowers very small, white or pink, scarcely opening. Spur short bladder-like. Irish plant. **Neotinea**

17. Tubers ovoid. Stigmas 2, on side-lobes of column. Pollinia attached to a *strap-shaped* viscidium. Spike dense *conical*. Flowers resembling *G. conopsea*, pink or rose-red. Lip *with erect guiding plates*. Spur long slender *dry*. **Anacamptis**

18. Spike stout, dense; flowers many, with *very long, narrow, ribbon-like lip curled up like a watch-spring in bud*, green, whitish and red-spotted at base; both pollinia attached to one viscid gland; smells like a goat. **Himantoglossum**

19. Leaves oblong, glossy. Spike narrow, cylindrical; flowers many, small, green, often edged red; lip green, brown-red or yellow, *man-like*, with two arms and two legs; spur none; viscid glands often coherent. **Aceras**

20. Flowers many, with showy 3-lobed lip, and spur without free honey; stigma on roof or back of chamber forming spur-entrance; *viscid glands disc-like, enclosed in the same pouch*. **Orchis**

21. Flowers few (1–7), with green or coloured sepals, velvety, dark-coloured lip, *no spur*, and each viscid gland enclosed in a *separate* pouch. **Ophrys**

Sub-family *DIANDRÆ* Salisbury

Fertile anthers two, stigmas three, confluent.

DIANDRÆ Salisb., *Prodr. stirp. hort.* chap. vig. (1796). CYPRIPEDIEÆ Lindley (1826). PLEONANDRÆ Pfitzer (1903).

Pleonandræ was probably adopted to cover the genus *Neuwiedia* (Apostasiaceæ) which has three fertile anthers. The recognition of the latter as a separate family makes the older name more accurate (*vide* "Evolution of genera and species", p. 11).

Tribe I CYPRIPEDIEÆ Lindley

Fertile anthers two. Pollen-grains single, immersed in a viscid paste. Stigmas three, united.

CYPRIPEDIEÆ Lindl., *Orchid. scelet.* 1, 18 (1826).

Genus I CYPRIPEDIUM L.

Column cylindrical at base, then forking; upper branch a large stalked staminode; lower branch 3-lobed, the mid-lobe expanding obliquely into a broad obtusely triangular dry **stigma**, the side-lobes horn-like, each bearing an anther. Pollen-grains single, immersed in a viscous paste within the anther.

Perennial herbaceous erect plants, with short creeping rhizome, leaves inrolled in bud, and large, usually solitary, flowers. Lateral sepals united lengthwise behind the lip. Petals long, spreading. Lip inflated into a large bag or pouch, spurless.

About 30 species inhabit northern temperate regions (of which *C. passerinum* Richardson extends north to Hudson Bay and the Yukon, and one species to Mexico).

Sticky pollen is rather uncommon in other families of plants, being apparently found only in certain genera of Onagraceæ, e.g. *Fuchsia*, *Epilobium*, *Œnothera*, and in the genus *Rhododendron* (including *Azalea*). In these plants the grains are held together either singly or in fours (tetrads) by means of slender sticky threads, the whole being adhesive, but not to the extent that obtains in the Diandræ. In Asclepiadaceæ the pollen is massed together in pollinia as in the Monandræ, but these pollinia are not themselves sticky. Stigmas with papillæ on the surface are fairly general throughout flowering plants, and such papillæ usually indicate the precise extent of the stigmatic surface, particularly where style and stigma are not otherwise easily separable. The papillæ, however, are not usually sharp-pointed, but rather blunt. Sticky stigmas, as found in the Monandræ, are, on the other hand, relatively rare among other families of plants.

The pollen-grains are immersed in a semi-fluid paste, and there is no rostellum, the adhesive matter being secreted by the anther. All three stigmas are receptive to pollen.

In addition to *C. calceolus*, widely distributed in Europe, *C. guttatum* Sw. and *C. macranthum* Sw. are found in Russia, and extend to Japan. The ancient character of the genus is shown by its wide distribution throughout Europe, temperate and tropical Asia, and N. America.

1. Cypripedium calceolus L.

Pl. 1; Pl. A, fig. 4 (p. 6). *Lady's Slipper, Sabot de Vénus*

Tubers none. **Rhizome** thick, short-jointed, creeping, often branching and forming new shoots; roots numerous, cylindrical, sinuous. **Stem** 20–50 cm., tall, erect, flexuous, round, downy, with 3–4 short broad obtuse brown or green leafless sheaths at base. **Leaves** 3–5, large (up to 12 cm. long or more), somewhat folded, embracing the stem, broadly ovate or ovate-lanceolate, acute, green (paler beneath), margins wavy, shortly ciliate, with ± 11 principal nerves and many intermediate ones, and short scattered hairs below and sometimes above, chiefly on the nerves. **Flowers** hanging from the tip of the curved ovary, solitary (rarely two), large, with bright yellow pouch-shaped inflated lip, and brownish purple (very rarely yellow, white, or greenish) sepals and petals, and a sweet orange-like smell. **Bracts** broadly lanceolate, more or less resembling the leaves. **Ovary** long, slender, curved, stalked, 6-ribbed, with short erect hairs. **Sepals** lanceolate to ovate-lanceolate, long, tapering, acute, several-nerved, brown-purple (rarely yellow), downy on inner face, hairy at the base, with wavy sometimes reflexed edges; upper sepal broader, erect, lower two joined together (except at the 2-toothed tip) pointing downwards. **Petals** slightly longer and narrower, of the same colour, ribbon-like, linear-lanceolate to linear, tapering, acute, twisted, with downy mid-rib and long hairs at the base in front. **Lip** yellow, inflated, bag-shaped, curved forwards and slightly compressed from back to front, with a rounded opening in front with inrolled edges, a small ear-shaped aperture on each side between the base of the lip and the column, and several concentric nerves; on its floor are lines of crimson spots and a central band of hairs denser towards its base, of which some secrete tiny drops of fluid at their tips, which form a brittle crust when dry. **Column** (Pl. A, fig. 4)[1] yellowish green, 3-lobed; base short, thick; side-lobes short, curved, horn-like, each bearing an anther on its lower surface; mid-lobe long, curved obliquely downwards, expanding into a large thick body whose under-surface forms the stigma. Back of column prolonged into a stalk bearing a greatly enlarged staminode (modified anther), petaloid, oblong, sub-cordate at base, trough-like with upturned sides above, strongly

[1] *Vide* p. 6.

keeled below, yellowish or white, with crimson spots and obtuse apex. **Stigma** close to and facing the hairy base of the lip, triangular with rounded angles, somewhat convex, but depressed in the centre, dry, non-viscous, covered with papillæ pointing obliquely downwards, and really consisting of three confluent stigmas. **Anther** cup-shaped, open, 2-celled, filled with very adhesive material in which the single non-coherent pollen-grains are imbedded. Fruiting capsule large, 6-ridged.

The short broad leaves, resembling those of *Convallaria majalis*, when once seen can be recognised at a glance. The large solitary flowers (rarely two on the same stalk) with claret sepals and petals and big yellow calceolaria-like lip cannot be mistaken for any other European orchid. The edges of the lip curl inwards, and there are two shallow rounded auricles at the base making the central opening rather violin-shaped. There are 7–9 yellow nerves spreading fan-wise from the base of the lip to its mouth, with reddish irregular tubercles, surmounted by 2–3 short hairs, at intervals. The crimson-spotted staminode partly closes the mouth of the lip. Colour-variations of the flowers have been named as varieties, e.g. *album* Pfitz., *citrinum* Hergt (with lemon-yellow sepals and petals), *flavum* Rion, *fulvum* Christ, and *viridiflorum* Schulze. These appear to be individual variations hardly worthy of varietal rank.

It is remarkable that the species nearest to *C. calceolus* are to be found, not in Asia, but in N. America, where there are several species whose close relationship cannot be disputed.[1] Glandular hairs are mixed with the ordinary hairs on the stem, leaves, ovary, and perianth,[2] and serve to keep out undesirable wingless insects.

Habitat. Shady woods and bushy slopes, more rarely in the open, usually in mountain regions, generally on calcareous soil. It seems to prefer a northern aspect, shade, and moisture, and has been found up to 1700 m. in the Tyrol.

Distribution. Formerly in Durham, Yorks. and Westmorland. Now extinct or nearly so, though a few plants may linger in places inaccessible to the public. Northern and Central Europe including Scandinavia, Denmark, Germany, Austria, Switzerland, E. and Central France, Pyrenees, N. Italy, N. Balkans, N. Greece, all Russia and the Caucasus. In Asia it extends throughout Siberia to Saghalien, and finds its southern limit in the Himalayas.

Cypripedium calceolus L., *Sp. pl.* p. 951 (1753).

Fertilisation. The staminode with its conspicuous crimson spots appears to serve as a landing-stage leading to the central opening of the lip. Attracted by the scent and colour of the flower small bees of the genus *Andrena* lick and bite the hairs on the floor of the lip, which are tipped with minute drops of honey.[3] These serve as

[1] Schlechter und Keller, *Mon. Orch. Eur.* I, 86.
[2] Camus, *Icon.* p. 511.
[3] H. Müller, *Fert. Flowers*, English translation, p. 539 (1883).

a bait, the lip being really a trap to imprison insect visitors for a time. These cannot escape by the way they came in, owing to the incurled slippery edges of the mouth of the lip, bees not being able to cling to glass-like surfaces like flies.

Darwin watched a specimen of *Andrena parvula* making vain efforts to escape from *C. pubescens*, but always falling backwards from the polished margins. The only way of escape is by one or other of the two small openings at the base of the lip. To reach these a bee must crawl through the passage roofed by the stigma, which is so low that its back must rub against it. The dry stigma, rough with minute teeth (papillæ), acts like a rake to scrape off and retain any pollen brought by the bee from some previously visited flower, which in nearly every case is on another plant, as there are rarely two flowers on the same stem. It is therefore an advantage in this case to have solitary flowers, as it ensures cross-fertilisation.

Müller considered that the light entering through the above mentioned basal openings guided bees to these exits, and that the staminode screened off the light from the base of the lip, thus making them more visible. The band of hairs on the floor of the lip affords good foothold, and assists bees to crawl up the steep and slippery surface to the only way of escape. Considerable exertion is necessary on the part of the bee to squeeze through the opening. The column being rigid, the stiff but slightly elastic lip has to be forced down a little to make the aperture large enough. Müller's attention was attracted from some distance by the frantic efforts of a small bee (*Andrena pratensis*) to escape. It tried at least twenty times to get out by the large central opening, but fell back every time. It then went to one of the small apertures, but thought it too narrow. After trying the main entrance and the narrow exits once or twice more, it finally made a determined attempt with great energy at the left-hand small opening, and exerting all its strength at last succeeded in forcing a passage. In doing so its left shoulder was smeared with a good quantity of pollen, for bees cannot avoid rubbing against the convex sticky surface of the anther so cunningly placed in the gangway.

Müller relates that he visited a colony of about 30 plants of *C. calceolus* on the Stromberg Hills at 6 a.m. on May 26th, 1868, when the temperature was only 1° C. above freezing-point. In each of three flowers he found a bee in a torpid condition, which had evidently passed the night there. These were so drowsy that when thrown on their backs they scarcely made an effort to regain their feet. He expresses a doubt as to whether they were stupefied by the scent of the flowers, or merely benumbed by the cold. The latter is the more probable, for, as Darwin pointed out in a letter to Müller, any narcotic effect would cause delay, and render the bees less fit for the transport of pollen, and would thus be a disadvantage to the plant. Müller suggested that the bees possibly used the flowers as a shelter, and in view of the fact that certain species of *Serapias* in the Mediterranean region appear to be entirely fertilised by bees which make a habit of passing the night in their flowers, it is quite probable that the flowers of *C. calceolus* fulfil a similar purpose. The lip of *Serapias* is covered with erect somewhat yielding hairs, which may conduce to warmth and comfort for the bees esconced among them, by supporting the weight of the body and resting the legs of the insect. The lip of *C. calceolus* is similarly furnished, though some of the hairs secrete a tiny drop of fluid at the tip, which may be edible, though Kurr states he was unable to detect nectar within the labellum.[1] It is at least certain that various species of *Andrena* enter the lip, and some spend the night there, and that none can leave the flower without carrying off some of the pollen, and also depositing on the stigma any pollen previously collected.

The following species of *Andrena* were observed by H. Müller to visit the flowers. *A. nigroænea* K. ♀, *A. fulvicrus* K. ♀, *A. albicans* K. ♀, *A. atriceps* K. ♀, and *A. pratensis* Nyl. ♀. The fact that these were all females is in favour of the secretion of nectar. *A. parvula* K. ♀ was repeatedly found dead within the labellum, probably owing to frost, for a specimen placed by Darwin five times within the lip of *C. pubescens*, always managed to crawl out, covered with pollen. Various flies were also found dead, viz. *Empis punctata*, a *Cheilosia* (Syrphidæ), an *Anthomyia* (Muscidæ), and considerable numbers of *Spilogaster semicinerea* Wied. (Muscidæ). Small beetles (*Meligethes*) are able freely to creep out of the labellum, but sometimes stick on the anther-face and die.[2]

Sub-family *MONANDRÆ*

Only one anther (A^1, Text-fig. 2), normally fertile; lateral anthers of inner whorl (a^1 and a^2) absent, or rudimentary (staminodes), very rarely developed through atavism. Fertile stigmas two, confluent or lateral, the upper converted into a rostellum (except in *Cephalanthera*).

MONANDRÆ Swartz, *Vet. Acad. Nya Handl. Stock.* XXI, 205 (1800).

The pollen-grains are dry, compressed into tetrads (fours), except in *Cephalanthera*, and built up into pollen-masses (pollinia). The adhesive matter for attaching them to insects is secreted, not by the anther, as in the Diandræ, but by the upper stigma, which is transformed into the rostellum, a beautiful piece of mechanism peculiar to the Monandræ, and found in no other family of plants. The stigmas are coated with an extremely adhesive secretion, to which the pollen-groups adhere so firmly on contact, that they are torn away from the pollinia when these are withdrawn.

[1] *Bedeutung der Nektarien*, p. 29 (1833). Darwin could detect no nectar in the six species he examined, *C. barbatum*, *purpuratum*, *insigne*, *venustum*, *pubescens* and *acaulis* (*Fert. Orch.* ed. 2, p. 229).

[2] Müller, *loc. cit.* pp. 539, 541.

The sub-family contains over 500 genera and 17,000–20,000 species (Schlechter, *Mon. Orch. Eur.* p. 71), and presents an extraordinary variety of floral construction. Evolution has been extremely active, on many distinct lines, in marked contrast with the Diandræ, in which it has stopped at four genera. The Monandræ embody a number of totally different ideas, the devices employed to secure the transport of pollinia having sometimes baffled the great Darwin himself.

The sub-family embraces two great groups:

(1) Epiphytes, normally growing on trees, with roots exposed to the air. With very few exceptions these are tropical, and far surpass the ground orchids in number.

(2) Terrestrial or ground orchids, chiefly found in the temperate zones, but also in the tropics, the roots or tubers of which are buried in the soil. All the European orchids are terrestrial, a class mostly confined to the temperate regions of Europe, Asia and N. Africa, comparatively few genera extending to N. America.

Tribe I NEOTTIEÆ Lindl.

Only fertile anther at apex of column, often hinged. Pollinia without basal caudicles. Rostellum usually present. Plants with thickened fleshy fungus-infected and partially tuberised roots, without tubers, but often with rhizomes.

In *Cephalanthera* there is no rostellum. It appears to be absent from *Epipactis* in *E. Muelleri* Godf. (continental only), and evanescent or sometimes absent in the case of *E. leptochila* and *E. dunensis*. In *Spiranthes autumnalis* the roots are usually two, looking like tubers, but monostelic as in the Neottieæ, not polystelic as in the Ophrydeæ.

NEOTTIÆ Lindl. *Gen. and Spec.* p. 441 (1835).

KEY TO SUB-TRIBES

A. *Rostellum none. Pollen-grains single.*

1. Flowers large, erect, conspicuous; lip erect (making them tubular), turned down at tip, with yellow crests; column long, erect; stigma oblong; pollinia crescent-shaped. **Cephalantherinæ**

   Cephalanthera.

B. *Rostellum present.*[1] *Pollen-grains in tetrads.*

2. Flowers smallish, horizontal or drooping, inconspicuous; lip with open nectariferous cup (hypochile) and tongue-like apex (epichile); column short; stigma oblong; pollinia club-shaped. **Epipactinæ**

   Epipactis.

[1] Evanescent (or even absent) in *Epipactis leptochila* and *dunensis*.

3. Flowers similar to 4, but with lip of *Epipactis*; column rather short; stigma orbicular; rostellum truncate above, rounded below; pollinia built up of pollen-packets. **Physurinæ**
   Goodyera.

4. Flowers small, white, sweet-scented, trumpet-shaped, horizontal, spirally arranged; column horizontal; stigma orbicular; rostellum nib-shaped; pollinia flat, attached to a linear dark-coloured viscidium. **Spiranthinæ**
   Spiranthes.

5. Flowers green; rostellum small, tongue-like, with parallel cells charged with liquid cement at high tension. **Listerinæ**
   Listera, Neottia.

Sub-tribe *CEPHALANTHERINÆ*

Genus II CEPHALANTHERA Richard

Column long, with a tapering point (filament) behind, to which the anther is fixed below the middle of the back. **Stigma** on front of column just below the anther, transversely oblong. **Rostellum** absent. **Pollinia** slender, nearly or wholly split into two, without caudicles, pollen-grains not united in tetrads, single. **Flowers** large, sessile, erect, white or rose. **Lip** jointed, basal half (hypochile) erect, parallel with column and embracing it by two rounded lobes (making the flower tubular), concave at base; forward half (epichile) turned down at the tip like a spout, with 3–5 parallel yellow crests.

CEPHALANTHERA Richard, *Mém. Mus. Paris*, IV, 51 (1818). SERAPIAS L., *Sp. pl.* ed. 1 (1753), which also included *Epipactis* and the present genus of the Ophrydeæ *Serapias*. EPIPACTIS Crantz (1769) (*Cephalanthera* + *Epipactis*).

KEY TO THE SPECIES OF CEPHALANTHERA

1. Flowers large, bright rose. Leaves distant, oblong, spreading. **C. rubra**

2. Flowers smaller, pure white. Leaves alternate in two opposite ranks, long, narrow, sword-shaped. **C. ensifolia**

3. Flowers large, creamy white, opening but little. Leaves broad, ovate-lanceolate, distant. **C. grandiflora**

Dr R. von Wettstein (*O.B.Z.* p. 395 (1889)) included *Cephalanthera* in the genus *Epipactis*, in which he was followed by Schulze (*Orchid. Deutschlands*, Pl. 56). Now that the method of fertilisation and the reason for the peculiar construction of *Cephalanthera* are understood, it is clear that the flower embodies a different conception, and is designed on a different plan from that of *Epipactis*. The latter belongs to a different line of evolution. *Cephalanthera* is a very ancient genus which shows us how cross-pollination was possible in the Monandræ before a rostellum had yet been evolved in the Orchidaceæ. *Epipactis* exhibits a large and very efficient rostellum, though of simple construction.

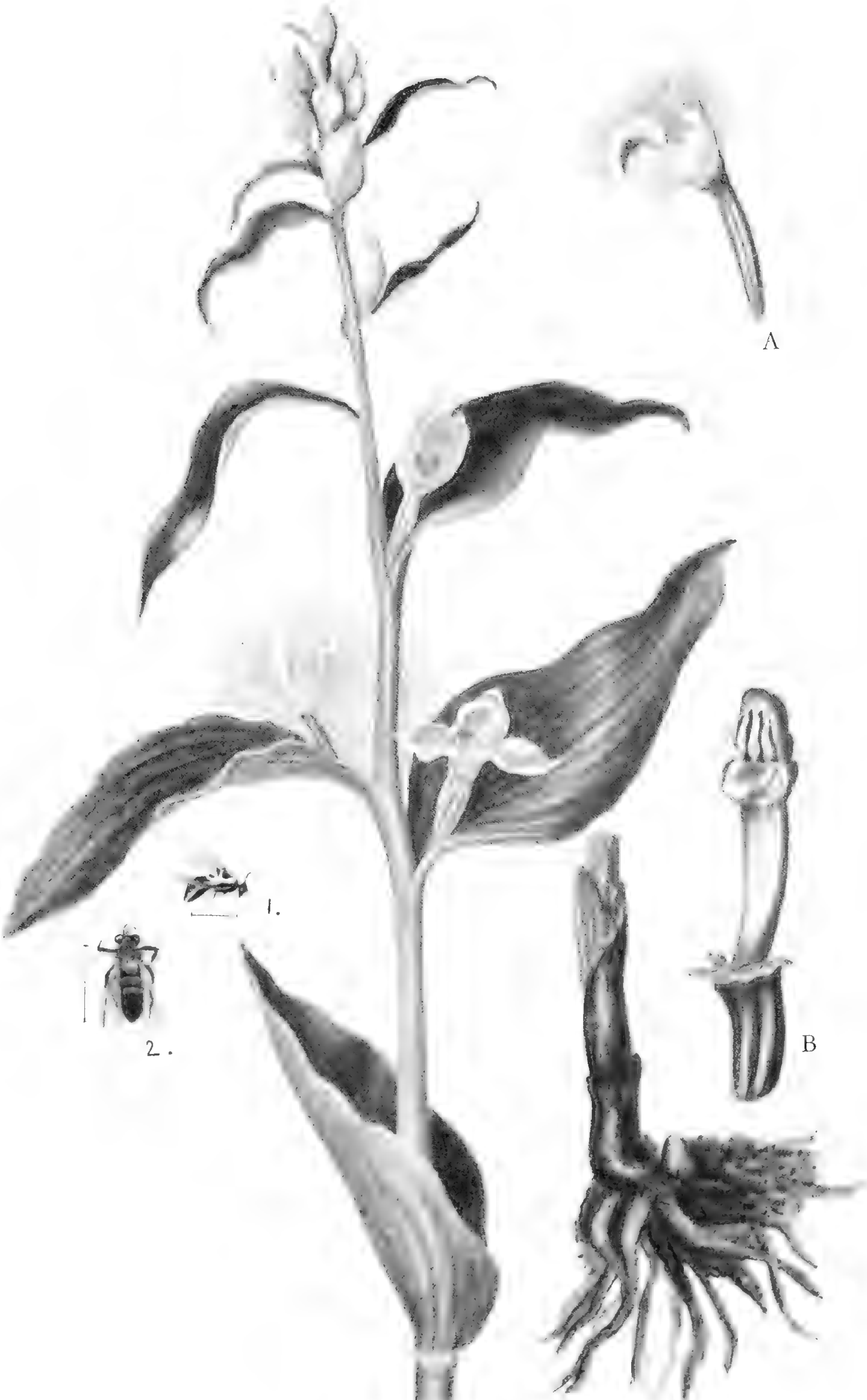
Cephalanthera approaches the Liliaceous type of flower, and differs from the prevailing Orchidaceous type in the following points: (1) The anther is suspended from the summit of a filament (stalk). (2) The pollen-grains are single, not united to form tetrads. (3) There is no *rostellum*.

Cephalanthera shows a transition from the mechanism of the Diandræ (Cypripediums) to that of the Monandræ. It is akin to *Cypripedium* in that it makes use of a narrow gangway to compel an insect making its exit from a flower to smear itself with adhesive matter by friction against a highly viscous surface. In *Cypripedium* the viscid matter is secreted by the anther, and contains the pollen-grains within itself. It can be drawn out into threads. In *Cephalanthera* there is no viscid matter in the anther. The viscous fluid secreted by the stigma is sufficiently abundant to smear the insect's thorax, so that in passing the face of the anther immediately above the stigma the protruding centres of the bowed-out pollinia are picked up and carried off. This transfer of function from anther to stigma is noteworthy, for it is the beginning of a long chain of evolution, in which the upper stigma ceases to function as such and develops into a *rostellum*, a new organ peculiar to the Monandræ, varying from the simple ball of *Epipactis* to the beautiful mechanism of *Orchis* and *Ophrys*.

1. CEPHALANTHERA GRANDIFLORA (L.) Babington

Pl. 3; Pl. C, fig. 1 (p. 50). ***Cephalanthera pallens*** Rich.
Large White Helleborine

Rhizome hard, short, woody. **Roots** many, short, stiff, corky. **Stem** 15–50 cm., nearly round, erect, rigid, solid, often flexuous, angled, and rough above with translucent ridges, leafy throughout, with 2–3 loose-fitting brown membranous ribbed sheaths at base, the upper sometimes green-tipped, the new bud arising at the junction of rhizome and stem. **Leaves** few, distant, passing gradually into bracts, dull or greyish green, ovate-oblong to oblong-lanceolate, obtuse or acute, often wavy-edged,



H. M. Godfery pinx.

CEPHALANTHERA GRANDIFLORA (L.) Bab.
Large White Helleborine

PLATE 3

Cephalanthera grandiflora (L.) Bab. Bex, Switzerland, May 29th, 1913.

A. Ovary, column and lip (enlarged).

B. Column (much enlarged), showing four half-pollinia leaning forwards over upper edge of stigma.

1. **Halictus malachurus** K., with four half-pollinia.

2. **Andrena florea** F., ♀. (Both enlarged.)

with prominent parallel nerves, rarely more than 8 cm. long by about 4 cm. broad; the upper lanceolate often narrow, the lowest short (± 6 cm.), ovate-lanceolate. **Spike** sometimes occupying nearly half the stem, the lower flowers distant, the upper close together. **Flowers** few (3–12), large, erect, stalkless, ovoid, creamy white, scentless, tubular at base, often closed, but for a short time the side-sepals spread and the lip turns down at the apex. **Bracts** ovate-lanceolate to lanceolate, the lower leaf-like, often much exceeding the flower, the uppermost linear, slightly longer or shorter than the ovary. Sometimes the lower bracts are so like the leaves that the flowers appear to be axillary and solitary. **Ovary** erect, stalkless, spindle-shaped, 6-ribbed, rough, twisted. **Sepals** oblong, obtuse, 5-nerved, creamy white, edges entire or minutely toothed. **Petals** shorter, oblong-lanceolate, rounded at tip, 5-nerved, slightly clawed, edges usually smooth. **Lip** shorter than petals, basal half sack-shaped with a deep yellow or orange patch within, and a rounded lobe on each side clasping the column, making the flower tubular; forward half (epichile) heart-shaped, obtuse, rounded, finely crenate often mucronate, narrowed to a hinge, ± 4 mm. wide at the base, broader than long, trough-like above, curved downwards at the tip, with three or five parallel orange-yellow interrupted longitudinal crests. **Column** tall (± 1 cm.), curved, semi-cylindrical, flat in front, whitish, ending behind in a point like the nib of a pen, to which the anther is fixed, with a small finger-like staminode (rudimentary anther) on each side. **Stigma** on front of column immediately below the anther (of which it partly conceals the base), oval, broader than long, concave, glistening, greenish white. **Rostellum** none. **Anther** suspended below the middle of the back from a nib-like filament, semi-ovoid, obtuse, hood-like, rough outside with minute papillæ, each of the two cells with a partition lengthwise. **Pollinia** two, each divided into separate halves, cylindrical, curved, without caudicles, yellowish white. Pollen-grains ovoid, pitted, separate, not joined into tetrads.

Whole plant glabrous, smooth except for papillæ on the upper part of the stem and on the ovary. Ripe *seed-capsule*, erect, ± 3 cm. long, slightly curved, hexagonal. *Seeds* with oblong transparent reticulated fine-meshed testa.

Pl. C, fig. 1, shows a Sussex specimen, May, 1927 (Col. C. T. Green).

Two colour-forms are mentioned by Camus,[1] one with yellowish white flowers (*C. ochroleuca* Rchb. f.), and one with flowers "d'un beau blanc" (*C. lonchophyllum* Rchb. f.). Each is said to occur to the exclusion of the other in their respective stations.

Forma *Duffortii* Camus, with smaller flowers and lip similar to the petals, is a partial reversion to the primitive type of the orchid flower before the lip had become differentiated from the petals. I found a plant at Hyères with three anthers, in which

[1] Camus, *Icon.* p. 437.

the two upper anthers of the inner whorl (as in Pl. 2, fig. 8), ordinarily absent, had been developed. Three plants were found in Kent[1] and one in Surrey with creamy white stems and leaves without any tinge of green (chlorophyll), resembling *Monotropa hypopytis*, and probably due to the same cause, saprophytism. I have seen the same thing in *Serapias lingua*, *S. longipetala*, and *S. neglecta* in France and Italy, but it is extremely rare in that genus. Specimens of *C. grandiflora* were found in two localities in Surrey with three lips.[2] Of these the central is the true lip, the side ones being extremely rare developments of the obsolete anthers A^2 and A^3 (Text-fig. 2). Incidentally this shows that Darwin's theory, that the lip is built up of a petal and these two anthers, is unnecessary. Not only has the original petal developed into a perfect lip without assistance, but each anther has been able to produce a lip by itself.

A specimen found by me near Wye had four buds on the upper part of the rhizome, which might perhaps have given rise to four stems the next year, but I have never seen the stems tufted as in *Epipactis violacea* (*purpurata*) and *E. leptochila*. The usual number of flowers is 6–8. I have found specimens occasionally with flowers wide open and sepals spreading, but never in flowers examined at night. The ovary is sometimes found with fine papillæ, and a ripe capsule was once seen with a very short stalk. Two spikes found near Salisbury had flowers as wide open as in *C. ensifolia*, as also were some flowers seen in Surrey.

Habitat. Woods and shady places on calcareous soil. I have seen it flourishing in the open among bushes or where it had shade during part of the day from trees. Flowers May to June.

Distribution. Not infrequent in S.E. England, rare and local elsewhere. Extends from Kent to Somerset, Wilts. and Dorset, and northwards to Cambridge (*B.E.C.* 1923), Warwick (*J.B.* 1905), and W. Cumberland (*Top. Bot.* p. 1041). Absent from Ireland. S. Sweden and Central Russia to the Mediterranean and N. Africa (Algeria), Caucasus, Transcaucasia, Asia Minor.

Cephalanthera grandiflora Babington, *Man. Brit. Bot.* p. 296 (1843). Serapias grandiflora L., *Syst.* ed. 12, p. 594 (1767). Cephalanthera pallens Richard, *Mém. Mus. Paris*, iv, 60 (1817). C. damasonium Dr. See p. 36.

Fertilisation. Self-pollination takes place as a rule, and almost every flower sets a capsule. The pollinia each divide into two and lean forward over the edge of the stigma, to which they become anchored by pollen-tubes. If not removed by insects they crumble, and pollen falls on the stigma. It has been generally regarded as always self-fertilised.

I saw two or three flowers visited by *Bombus lucorum* in Surrey, and found several flowers there, and also in the environs of Paris and Nice, from which one or both

[1] Tahourdin, *Notes as to British Orchids*, p. 11 (1923). [2] *Ibid.* p. 10 (1926–7).

Fig. 1. *Cephalanthera grandiflora* L. (*pallens*). Arundel, May, 1927.

Fig. 2. *Cephalanthera ensifolia* Richard. Border of Oxon. and Bucks., June, 1927.

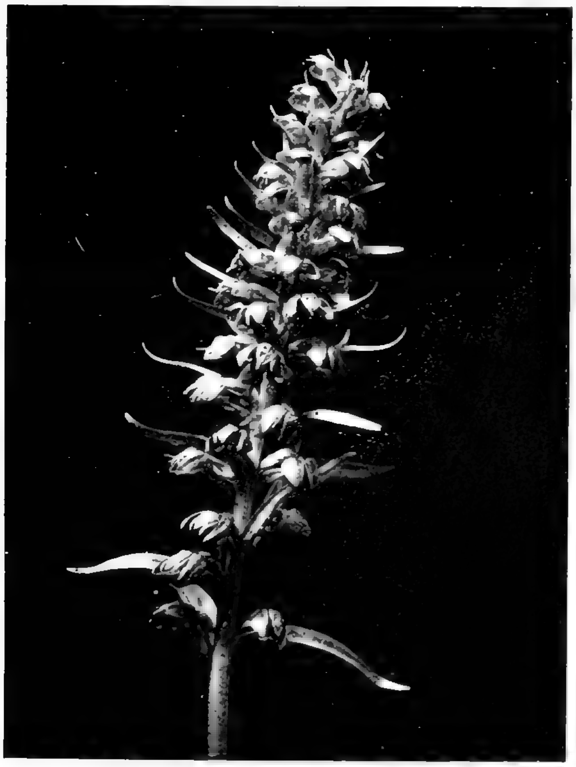


Fig. 3. *Cœloglossum viride* Hartm. var. *bracteatum*. Height 14 in. Leete valley near Mold, June 4th, 1927.

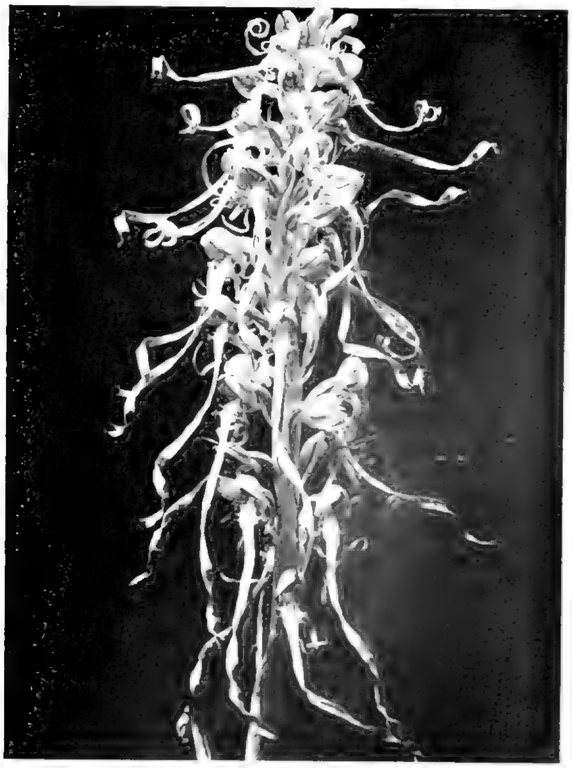


Fig. 4. *Himantoglossum hircinum* Sprengel. Sussex downs, June, 1926.

Reproduced by kind permission of Colonel C. T. Green of Birkenhead

pollinia had been removed. At Challes-les-Eaux, France, Colonel G. H. Evans, F.L.S., my wife and myself saw *Andrena florea* F. ♀ several times enter flowers exposed in a vase, which evidently had a strong attraction for this species. On one day when all the flowers were closed, a number of these bees came, and alighted on adjacent foliage, as if waiting for them to open, and one or two tried to find an entrance to the closed flowers. *Halictus malachurus* K. f. *longulus* Sn. was taken emerging from a flower with the four half-pollinia arranged neatly on the thorax as shown on Pl. 3. Darwin found that the yellow ridges on the lip, which taste like vanilla, were eaten, and found small fragments bitten off in the flower. It thus appears to be the only European species providing solid food for insects.[1] It is occasionally visited and cross-pollinated by at least two species of Hymenoptera. Darwin found that the pollen is extremely friable, and that the grains are tied together by a few weak elastic threads, but are not cemented together to form compound pollen-grains (tetrads) as in most of the Monandræ.[1] He considered this to be evidence of degradation, and thought that *Cephalanthera* was a degraded *Epipactis*. It was unfortunate that it was the only species of the genus which he examined, and that the above opinion was based on an exceptional species which, as far as was then known, was supposed to be entirely self-fertilised. Had he examined *C. ensifolia* and *C. rubra*, he would certainly have realised that cross-fertilisation is the rule in the genus, to which *C. grandiflora* is a partial exception, and also that the plan of construction of the flower is quite different from that of *Epipactis*, and based on a different idea. If a dry camel's hair brush is inserted into a flower, and withdrawn so that it sweeps upwards across the middle of the stigma and of the anther just above it, it will be found that it becomes smeared with the viscid secretion of the stigma, and comes out with the pollinia adhering to it. If, however, the pollinia have already become rooted to the upper edge of the stigma by pollen-tubes, only their upper parts will thus be withdrawn.

That effective cross-pollination by insects occurs is shown by the hybrid *C. grandiflora* × *ensifolia* found on Mont Salève near Geneva,[2] at Vence above Nice,[3] and near Grimaud in the Var,[4] the two last by Mlle Camus, a hybrid which may appear wherever the parents grow together. It is figured in *O.R.* for April, 1924, p. 101. The bi-generic hybrid *C. grandiflora* × *Epipactis rubiginosa* was once found in Austria, and flowered several times in the botanic gardens at Vienna.[5] These hybrids could not possibly have occurred in a state of nature, except by effective visits by the same insect to both parents in each case.

In protesting against the inclusion of the genus *Cephalanthera* in *Epipactis* I adopted Darwin's view and said:[6] "*Cephalanthera* is a decadent genus which has fallen from

[1] *Fert. Orch.* ed. 2, pp. 80–2.
[2] A. and G. *Syn.* III, 877.
[3] A. Camus, *Riviera Scient.* p. 19 (1919).
[4] *Bull. Soc. Bot. de France*, LXX, 451 (1923).
[5] A. and G. *Syn.* III, 883.
[6] *J.B.* p. 71 (1920).

its high estate, assuming that it is really the case that it is entirely self-fertilised". Now that I have witnessed the visits of insects to *ensifolia*, *rubra*, and also *grandiflora*, I no longer believe there has been any degeneration in *Cephalanthera*, but that it presents a case of persistence to the present day of an extremely ancient method of cross-pollination, which possibly prevailed in the Orchidaceæ before a rostellum had been evolved in that family. The absence of a rostellum and the single pollen-grains are signs not of degeneration, but of a very early phase of evolution.[1]

2. Cephalanthera ensifolia Richard

Pl. 4; Pl. C, fig. 2 (p. 50). *Sword-leaved Helleborine*

Rhizome knotted, with stiff wiry roots. **Stem** 20–50 cm., leafy throughout, pale green, slightly ridged above through decurrence of edges of bracts, with short internodes (1–2 cm.), and 2–4 whitish or green-tipped sheaths at base. **Leaves** alternate, mostly in two opposite ranks, obliquely erect or horizontally spreading, often folded, long (7–10 cm.), narrow (± 1·5 cm.), oblong, tapering, stiff, acute, glabrous, with 3–5 prominent and numerous fainter nerves; lowest leaves shorter, obtuse, upper linear, very narrow, acute, sometimes exceeding the spike. **Spike** lax. **Flowers** 3–15 or more, pure white, obliquely erect, smaller and opening wider than those of *C. grandiflora*. **Bracts** triangular, acute, 1-nerved, very short, but the lower one or two sometimes up to 8 cm. long, linear, acute, very narrow, with 3–5 principal and some intermediate nerves. **Ovary** 1–1·5 cm. long, sessile, cylindrical, slender, glabrous, twisted, 6-ridged. **Sepals** lanceolate, keeled, acute, faintly 1–5-nerved, 1–1·5 cm. long. **Petals** shorter and broader, oval, obtuse, 3–5-nerved. **Lip** shorter than sepals, jointed; basal half somewhat sack-shaped with two rounded ears embracing the column (making the flower tubular), white with an orange blotch at base, front half (epichile) somewhat heart-shaped, broader than long, curved, trough-like, white, with 3–5 orange-yellow, parallel crests and turned down, rounded orange tip, covered with dense papillæ. **Column** long, erect, flat in front, rounded behind, with a nib-like filament at the back from the tip of which the anther is suspended below the middle of its back. **Anther** whitish, ovoid, rounded, flat in front, tilted forward and firmly pressed against the back of the stigma, with an obtuse white staminode (rudimentary anther) on each side at the base, tending to keep it in position. **Pollinia** two, long, curved, yellowish white, sometimes split in two, or nearly so, their convex centres projecting slightly from the cells of the anther, where they remain till removed by insects. **Stigma** on the front of the column just below the anther, transversely

[1] *Journn. Linn. Soc. Bot.* XLV, 511 (March, 1922).

PLATE 4

Cephalanthera ensifolia Richard. Bormes, Var, France, March 31st, 1908.

A. Column (much enlarged).

1. **Halictus politus** Schenk., ♀ (enlarged).

2. **H. Smeathmannellus** K., ♀. Both bear a pair of pollinia (enlarged).

H. M. Godfery pinx.

CEPHALANTHERA ENSIFOLIA Rich.
Sword-leaved Helleborine

oval or reniform, concave, whitish, glistening, with thickened edges. Testa of seed oblong, transparent, with very fine mesh.[1]

Pl. C, fig. 2, shows a specimen from border of Oxon. and Bucks. photographed by Col. C. T. Green, early June, 1927.

HABITAT. Woods and shady places, bushy slopes, etc. Flowers May to July according to latitude, elevation, and season. Sometimes disappears for some years. Favours calcareous soil, but is abundant on schist in the south of France. Ascends to 4000 ft.

DISTRIBUTION. "Local over greater part of Britain from Hants. and Sussex to Fife, Perth and Argyllshire" (Sowerby, *E.B.*). Apparently now very rare. In Ireland recorded for eight of the twelve botanical districts, but not recently found in the north-east. First recorded for Ireland by W. Sherard, near Ballynahinch, Co. Down, in 1694.[2] Europe from Scandinavia to the Mediterranean, N. Africa, Siberia, the Urals, Caucasus, Asia Minor, Persia, Afghanistan, Kashmir, Japan.

> CEPHALANTHERA ENSIFOLIA Richard, *Mém. Mus. Paris*, IV, 60 (1817). SERAPIAS HELLEBORINE var. LONGIFOLIA L. (in part), *Sp. pl.* (1753). CEPHALANTHERA LONGIFOLIA Fritsch (1888).

FERTILISATION. In March, 1920, at Hyères, where *C. ensifolia* was frequent, on dissecting its flowers I found in many cases that the pollinia had disappeared without leaving a trace behind. In one flower both pollinia were intact in the anther, but a whole pollinium and portions of another were adhering to the stigma. These must evidently have come from another flower. It was clear (1) that the pollinia are removed from a large number of flowers, (2) that pollen is deposited on the stigma from some outside source. This seemed to indicate that probably insects removed the pollinia and transferred them to the stigmas of other flowers, but how could this be possible, there being no rostellum to provide the necessary viscid material to fasten the pollinia to insects?

I next observed that if the anther was pressed back on its hinge, it at once sprang back to its former position when released. Normally it leans forward, so that the lower part of the curved pollinia rests on the upper edge of the stigma. To ascertain whether they became anchored there by pollen-tubes, as described by Darwin in the case of *C. grandiflora*, I pressed back the anther with a needle. It moved easily, carrying the pollinia with it. These were quite free, with no trace of adhesion to the stigma. When I released the anther it sprang smartly back, with so much elasticity that in one case both pollinia were flung bodily out of the flower. What is the object of this elastic spring-hinge?

Delpino suggested that the viscid secretion with which the stigma is always covered

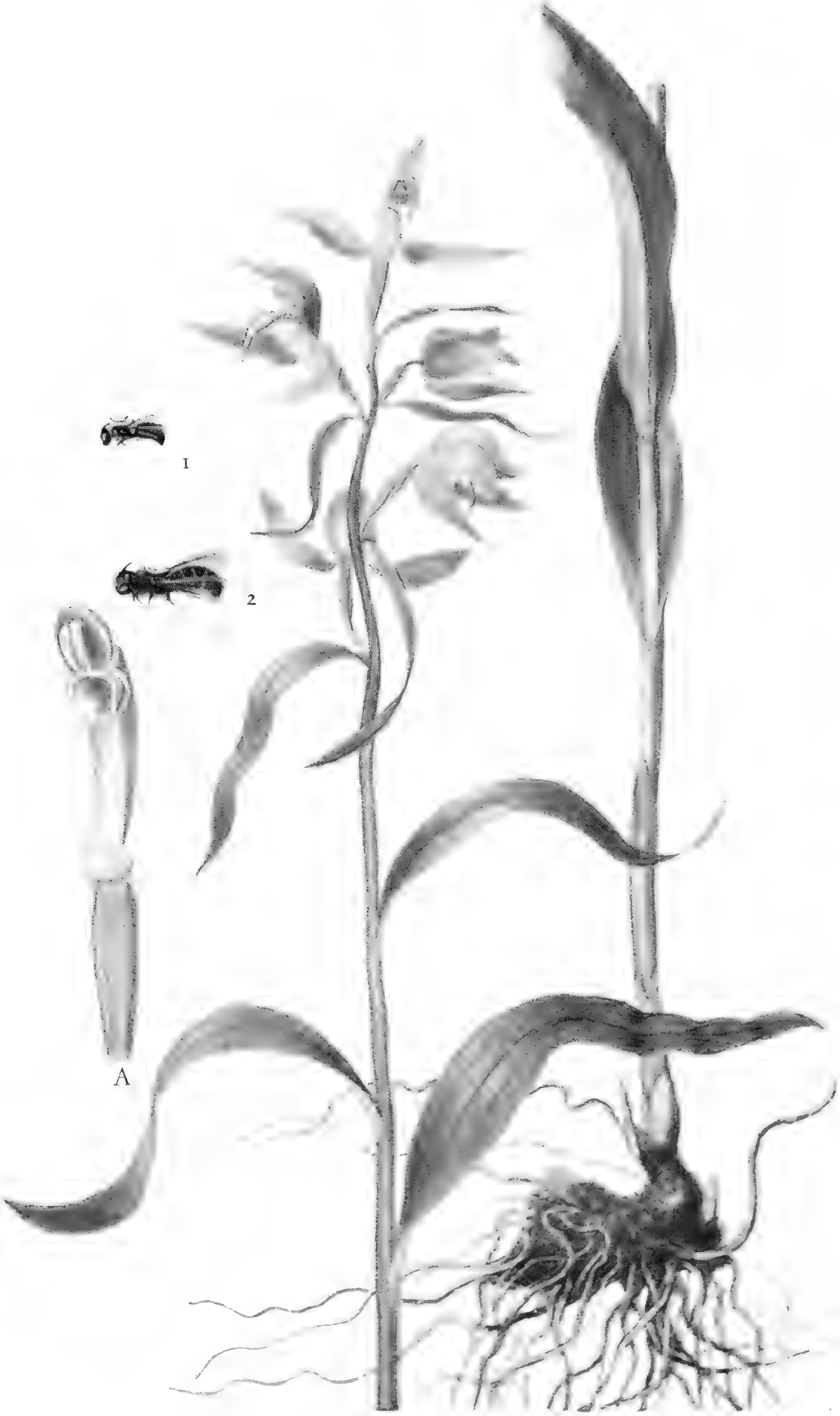
[1] Rchb. *Icones*, XIII, Pl. 118. [2] *Cybele Hibernica* (1898).

might be sufficient, if an insect became smeared with it, to remove the pollinia. To test this I inserted a dry camel's hair brush into a flower, causing it to sweep gently upwards along the middle of the stigma and the face of the anther, which is just above it. It came out with one whole pollinium attached to it by the middle of its convex side, the ends pointing outwards. With a lens I could see a little viscid matter glistening on the brush. On looking to see why only one pollinium was brought away, I found the anther empty—evidently one pollinium had been previously withdrawn. I did the same thing with another flower, and this time both pollinia were easily removed. I repeated the experiment with flower after flower, always with the same result. To make sure that this was really due to the viscid matter of the stigma, I passed a clean brush over the face of the anther in several flowers, without first touching the stigma. This had no effect—the pollinia would not adhere to a dry brush. The object of the elastic hinge now became apparent. The anther must be pressed against the edge of the stigma, so that the pollinia may project far enough forward to ensure that an insect, retreating backwards from the tubular flower, after smearing his back with the viscid secretion of the stigma, shall also brush against the pollinia. These at once adhere by their convex centres, their tips pointing forwards. It is these projecting ends which come into contact with the stigma of the next flower visited. This explains the curious fact that pollinia are very occasionally found adhering to the stigma by their extreme tips, their curved centres standing away quite clear of its surface.[1]

Although always on the watch for insects visiting the flowers, it was nine years before I saw this happen. In May, 1929, Colonel G. H. Evans, F.L.S., my wife and I systematically watched cut spikes of *C. ensifolia*, together with those of other orchids, on the terrace wall of an hotel garden at Challes-les-Eaux, France. We saw the flowers of *ensifolia* visited a number of times by a small Hymenopteron, *Halictus Smeathmannellus* K. ♀, and the still smaller *H. politus* Schenck ♀, which carried off the white pollinia attached by their convex centres to the thorax, and not to the head as I expected. These insects were so small that I saw them going to the flowers without suspecting that they were big enough to touch the stigma while crawling on the lip, until my wife saw one with white pollinia on its back. These little bees took no notice of the flowers of *C. grandiflora* exposed in the same vase. They are figured in Pl. 4. A British spike of 17 flowers had 13 pollinia removed.

[1] *Journn. Linn. Soc. Bot.* XLV, 511 (March, 1922).

PLATE 5



H. M. Godfery pinx.

CEPHALANTHERA RUBRA Rich.
Red Helleborine

PLATE 5

Cephalanthera rubra Rich. Bex, Switzerland, July 1st, 1912.

A. Column (much enlarged).

1. **Heriades campanularum** Kirby.
2. **Heriades nigricornis** Nyl.

3. Cephalanthera rubra Richard

Pl. 5. *Red Helleborine*

Rhizome descending with numerous moderately thick fleshy roots, mostly from the base of the stem, where the new bud also arises. **Stem** 2–5 dm., erect, solid, striate and clothed with short glandular hairs above, rather rough to the touch, with loose-fitting leafless sometimes green-tipped 7–9-nerved sheaths at the base. **Leaves** few, distant, sheathing at the base, much longer than the internodes, linear-lanceolate, alternate, spreading, acute, glabrous, often folded, dark green above, paler beneath, with 3–5 prominent and several intermediate nerves; the lowest often oval-oblong, concave, the uppermost almost linear, tapering, acute. **Spike** lax, flowers 3–10 or more, large, conspicuous, bright rose, not scented, sessile or nearly so, opening rather wide. **Bracts** linear-lanceolate, tapering, acute, usually exceeding the ovary, the lower sometimes longer than the flowers, 3–7-nerved, glandular-hairy. **Ovary** short ($\pm$ 1 cm.), slender, sessile or short-stalked, twisted at base, glandular-hairy, with violet-tinged ridges. Ripe capsule, erect, $\pm$ 2 cm. long, rather trigonous, with six cord-like ridges. **Sepals** lanceolate, tapering, acute, keeled, bright rose, glandular-hairy outside, glabrous within, paler at the base, 5–7-nerved, spreading rather wide, with tips turned outwards, the upper arched over the column. **Petals** lanceolate, shorter and broader, bright rose, paler at the base, darker (often with red-violet streaks) at the tip, 5–7-nerved, loosely connivent over the column. **Lip** erect, $\pm$ parallel with column at base (making the flower tubular), then curving outwards, jointed; basal part forming a rounded bag, with an erect rounded lobe on each side, white, glabrous, with several irregular yellowish ridges diverging fan-wise to the edges; apical part lanceolate, narrow, tapering, white, edged and tipped with violet-rose, with 7–9 thin erect parallel sinuous frilled or toothed crests, the outer pair sometimes faint. **Column** erect, slender, slightly curved, half as long as the lip, flat in front, rounded behind, violet-rose (as also the anther and stigma), with a triangular tooth to which the anther is affixed by the middle of its back, and ending in a tooth at each side. **Anther** leaning forwards at the top of the column against the back of the stigma, broad, hood-shaped, covered with papillæ outside. **Pollinia** two, long, narrow, somewhat crescent-shaped, whitish, greyish blue or violet-rose, their centres projecting slightly from the anther-cells. Pollen-grains solitary, oval, pitted. **Stigma** on front of column immediately below the anther, transversely oval, concave, glistening. Testa of seed transparent, reticulate, mesh larger and more open than in the other two species.

C. rubra, like *C. ensifolia* and *C. grandiflora*, while preserving several evidently ancient characters, appears to be free from any tendency to develop new ones. It seems to have reached the limit of its evolution, and to have settled down as a thoroughly stable species. The only variations known are such as generally occur in all plants through the influence of unusually favourable, or unfavourable, circumstances, such as vigour of growth, height of stem, size of leaves, and number and size of flowers. In shady places it is often tall—I found one specimen in damp open woods above Sallanches, Haute Savoie, 68 cm. high, with a spike 18 cm. long with 15 flowers. A few white-flowered specimens have been found abroad.

HABITAT. "In England steep slopes in beech-woods on oolite or pea-grit at about 500–600 ft. elevation. The proportion of flowering plants is very small—in one year only two out of 30. It disappears when the beeches are felled" (Wilfred Mathieson).

DISTRIBUTION. Apparently now only found in Gloucestershire; formerly found on the Quantock Hills, Somerset (1836), and on Hampton Common. Europe from Scandinavia southwards to Spain, Italy, etc., Caucasus, Asia Minor, Persia.

CEPHALANTHERA RUBRA Richard, *Mém. Mus. Paris*, IV, 60 (1818). SERAPIAS HELLEBORINE δ. L., *Sp. pl.* ed. 1, p. 949 (1753). S. LONGIFOLIA Hudson (1762) in part. S. RUBRA L., *Syst. Nat.* ed. 12, II, 594 (1767). EPIPACTIS PURPUREA Crantz (1769). E. RUBRA All. (1785), Wettstein (1889).

FERTILISATION. *C. rubra*, like *C. ensifolia*, is entirely dependent on insects for fertilisation—unvisited flowers set no seed-capsules—and the method of pollination is the same in both. I inserted a dead bee, *Osmia leaiana* ♂, into a flower of *C. rubra*, withdrawing it so that it brushed lightly against the stigma and the face of the anther. Both pollinia were removed with ease (*J.L.S.* XLV, 513 (March, 1922)). I watched *C. rubra* in woods where it was frequent, and several times exposed cut flowers in various likely places, but always without success. On June 11th, 1922, near Challes-les-Eaux, Savoie, while my wife was carrying several spikes in her hand, on passing the place where we had previously gathered them, a red humble-bee came and visited three flowers, but having no net, we could not catch it. Six days later, on a very wet morning, a similar bee came to *C. rubra* in a mixed bunch of flowers on my window-sill. I had no net, but he was so engrossed in the third flower I saw him visit, that I caught him in a glass-lidded pill-box. He was identified by Monsieur L. Berland of the Paris Museum as *Bombus agrorum* F.

Colonel Evans, F.L.S., at Anneçy, Haute Savoie, took the following bees visiting *C. rubra* in June, 1930: *Heriades nigricornis* Nyl. (taken by Mrs Evans), bearing pollinia; *Heriades campanularum* Kirby. This small bee was very persistent in its visits, and was taken in three distinct localities. Several were caught bearing remains of pollinia on the thorax. It is the most frequent visitor of all. *Eucera longicornis* persistently flew round and round the flowers, but was too timid to visit them. *Heriades rapunculi* L. and *Osmia cœrulescens* ♂ were also taken on the flowers bearing pollinia at Anneçy by Colonel Evans.

Sub-tribe *EPIPACTINÆ*

Genus III EPIPACTIS Adanson

Labellum of two dissimilar parts, basal half (hypochile) cup-like, apical half (epichile) cordate or triangular. **Stigma** quadrangular, rostellum nearly globular on upper edge of stigma. Anther leaning over a shallow cup (clinandrium). Pollinia two, without caudicles.

Herbs with numerous fleshy roots, with orbicular to lanceolate leaves, and usually one-sided raceme of dull-coloured or greenish flowers.

SECTIONS

Arthrochilium Irmisch.

Hypochile large, oval, petaloid, with two ears. Epichile broad, frilled, with raised yellow plate at base, joined to hypochile by an elastic spring-hinge. Stigma bi-lobed.

Eu-epipactis Irmisch.

Hypochile cup-shaped. Epichile only separated by a fold, rigid, with bosses at the base. Stigma not bi-lobed.

The genus *Epipactis* is remarkable for the open cup, glistening with nectar, forming the basal half of the lip, resembling that of *Goodyera*, but the latter is deeper and more pouch-like. The triangular forepart of the lip is also like that of *Goodyera*, but that of *E. palustris* more resembles the broad frilled lip of *Spiranthes*. Another peculiarity is the shallow cup (clinandrium) at the top of the column, over which the anther leans forward, and on its opening by the turning back of a flap on each side, deposits the two pollinia leaning against the back wall of the stigma, their upper ends becoming attached to the rostellum, or viscid gland. The latter is remarkable for its comparatively large size and simple construction. In early bud it is rough outside and consists of a mass of cells, but develops later into a soft smooth membrane, lined inside with extremely adhesive matter, which sets hard in from 5 to 10 minutes on exposure to the air. It is therefore one of the simplest and oldest forms of rostellum extant, being only a mass of viscid material enclosed in a skin so tender that it can be pierced by a human hair. The globular granules of pollen cohere in fours, but without affecting their shape—the first stage towards the compression of the pollen-grains into tightly packed groups of four (tetrads) to secure economy of space for transport. *Cephalanthera* is a still older form in which the grains of pollen are quite separate. *Epipactis* appears to follow it next in order of sequence with its primitive rostellum, including two or three species in which the rostellum disappears soon after the flower opens, or is even altogether absent.

One European species, *E. Muelleri* Godf.,[1] has no rostellum, and is probably the most ancient form of *Epipactis*. It is entirely self-fertilising. The stigma curves backwards to such an extent that it roofs over the clinandrium, its upper edge being pushed well *beneath the base of the anther*, which projects so far above it that it deposits the two pollinia nearly on the middle of its upper surface, where they stand erect on their bases. This unique plant was published as a new genus (*Parapactis epipactoides*) by Zimmerman,[2] but it appears to be rather a phase of development in *Epipactis* than a distinct genus. There are two British species (*E. leptochila* G. and *E. dunensis* G.) which are intermediate between *E. Muelleri* and the other species of *Epipactis*, in which the rostellum is present in bud and sometimes in the flower when it first opens, but disappears after a few hours, the upper part of the pollinia sliding over the edge of the stigma on to its viscous surface. The antiquity of the genus *Epipactis* is indicated by its wide geographic range. *E. palustris* extends through Europe and Asia to Japan, and southwards to N. Africa. *E. gigantea* inhabits N.E. Asia and N. America, where *E. latifolia* also occurs, but was introduced into Canada, perhaps also into the States. Unless therefore it is assumed that the genus *Epipactis* was evolved independently in the old and new worlds (which is improbable, there being only one species indigenous in America), it must have existed as a genus when plant migration was possible between the two hemispheres.

KEY TO THE GENUS EPIPACTIS

Section I Arthrochilium Irmisch

Hypochile with an ear on each side; epichile separated by a deep incision, only attached by an elastic hinge.

1. Rootstock creeping. Flowers white, streaked with violet-rose within, often brownish outside; epichile rounded, with a yellow plate at base. Marsh plant. **E. palustris**

Section II Eu-epipactis Irmisch

Hypochile without ears; epichile only separated by a fold, rigid, without basal plate.

A. Rostellum nearly globular, conspicuous.

2. Roots in a tassel. Leaves large, soft, elliptical to ovate-lanceolate with tapering point; bracts long. Ovary not hairy; sepals green; petals and lip pale rose (rarely all violet-red). Borders of woods. **E. latifolia**

[1] *J.B.* p. 101 (1921).
[2] *Mitt. Bad. Landesv. Natkd. Freiburg*, N.F. 1, 232 (1922), and Fedde, *Repertorium*, XVIII, 283 (1922).

3. Rootstock long, vertical, knotted; roots thickening downwards. Stems clustered. Leaves small, often tinged violet. Flowers large, greenish white; bracts long; ovary rough with short hairs. Shady woods. **E. violacea**

4. Rootstock short; roots long, slender, many. Stem (in Britain) short, stumpy. Leaves short, stiff, in two opposite ranks; bracts short. Ovary hairy; flowers rather small, wine-red; lip with tubercled sometimes toothed hunches. Rocky ground on limestone. **E. rubiginosa**

B. Rostellum none, or only visible in newly opened flowers, quickly vanishing.

5. Rootstock vertical with many fleshy roots. Stems 1–5. Leaves ovate, flat, internodes short. Raceme long, graceful. Flowers rather large, wide open, yellowish green; sepals and petals long, pointed; lip long, narrow, pointed, tip not reflexed. Woodland plant. **E. leptochila**

6. Rhizome short. Roots few, hard, wiry, deeply buried. Leaves oblong, folded, stiff. Flowers small, yellow-green, few, in a short raceme; sepals and petals connivent, short, broad; forepart of lip cordate, triangular, as broad as long, tip recurved. Plant of sandy dunes. **E. dunensis**

The section *Arthrochilium* forms a natural connecting link with the previous genus, *Cephalanthera*, with which it shares the following peculiarities. The flowers are less open and more conspicuously coloured than in *Eu-epipactis*, the lip is jointed, the basal cup has an ear on each side, and the epichile is crenate with a yellow ridged plate at the base, like the crests of *Cephalanthera*. The American *E. gigantea* belongs to this section.

EPIPACTIS Adanson, *Fam.* II, 70 (1763). R. Brown in Ait. *Hort. Kew.* ed. 2, V, 201 (1813). HELLEBORINE Druce (1909). AMESIA Nelson and Macbride (1913).

In *Epipactis* the *generic* characters are so striking that they quite eclipse the much less conspicuous characters which distinguish the various species from each other. This dominant family likeness makes the specific differences seem insignificant by comparison. Similarly the conspicuous generic characters of the genus *Ophrys* appeared to Linnæus to so far outweigh the specific characters, that the latter appeared to be only of varietal value, and all the forms known to him were included in one species—*Ophrys insectifera* L.

FERTILISATION. Within the single genus *Epipactis* the whole range of development from total self-fertilisation to entire dependence on insects for pollination is exhibited. It presents an epitome of the evolution of a flower from self-fertilisation to cross-pollination, including some intermediate methods, i.e.

(1) Total self-fertilisation, *E. Muelleri* Godf. (non-British).

(2) Normal self-fertilisation, with the possibility of occasional cross-pollination, *E. dunensis* G., *E. leptochila* G.

(3) Normal cross-pollination by insects, with self-fertilisation in reserve if insects fail to visit the flowers, *E. microphylla* (non-British).

(4) No self-fertilisation, but entire dependence on insects for pollination, *E. latifolia*, *E. violacea*, *E. rubiginosa*.

In (1) the stigma curves backward and extends *beneath the base of the anther*, which deposits the pollinia on its frontal surface, standing erect on their bases. In (2) the pollinia are deposited in the clinandrium, and their upper parts slide over the sloping upper edge of the stigma on to its effective surface, but the cup glistens with nectar, and a rostellum appears in at least some flowers when they first open, though it soon vanishes. In (3) there is always a rostellum, by which the pollinia are readily removed by insects, but if this fails to occur, a certain quantity of pollen comes over the upper edge of the stigma, as in *dunensis* and *leptochila*, causing self-fertilisation. In (4) the flowers are well visited and the pollinia removed by insects. If this does not happen the pollinia wither *in situ*, and no seed-capsules are produced.

1. Epipactis palustris Crantz

Pl. 6. *Marsh Helleborine*

Rhizome cylindrical or irregularly thickened, often creeping horizontally, giving off one or more stolons, from the ends of which new buds arise. **Roots** slender, rather long, pale brown. **Stem** 20–60 cm., erect, solid, angled and more or less clothed with short whitish hairs above, green, sometimes streaked with violet-red below, leafy below the middle, with one or more acute (rarely obtuse), close-fitting, sometimes loose or even funnel-shaped leafless sheaths at the base. **Leaves** 4–8, with rather long sheaths, more or less folded, erect, slightly spreading, ovate-oblong to linear-lanceolate, rigid, acute, sometimes hooded at the stiff tip, glabrous, yellow-green or grey-green, not glossy, much exceeding the internodes, with 3–5 thickened keel-like nerves beneath, and several intermediate translucent ones. Lowermost leaf or leaves short, ovate or oblong, rounded, concave, embracing the base of the next leaf, dull red beneath, the uppermost linear-lanceolate, tapering, acute, bract-like. **Raceme** lax, 7–14-flowered, at first drooping, turned to one side. Flowers moderately large, bell-shaped, then opening wider, at first drooping, then horizontal, finally pendent, creamy white, more or less tinged or streaked with violet-red or brown, scentless. **Bracts** lanceolate, acute, tapering, the lowest about equalling or slightly exceeding the ovary, the upper much shorter, nerves 5–7. **Ovary** long, slender, spindle-shaped, tapering into a stalk, not as a rule twisted, brownish or dull green, rough with short hairs, with six obtuse ridges, finally pendent, stalk twisted, brownish

PLATE 6

Epipactis palustris Crantz. Anglesey, July 28th, 1917.

H. M. Godfery pinx.

EPIPACTIS PALUSTRIS Crantz
Marsh Helleborine

Sepals keeled, lanceolate, concave, the lateral slightly longer than the median and rounded out on one side, obtuse or acute, brownish, whitish or dull green and rough with short hairs outside, violet-red and glabrous within, with 3–5 prominent nerves and faint sometimes branched veins (best seen when pressed). **Petals** slightly shorter, lanceolate, obtuse, glabrous, white, flushed violet-red at base with 3–7 sometimes branched nerves. **Lip** equal to sepals; basal half (hypochile) cup-like, shallow, cut low in front, with an upright triangular ear on each side, white with rosy parallel veins and many bright yellow raised spots down the middle, perhaps glands for the secretion of honey, with which the cup becomes filled; front half (epichile) joined on by a narrow elastic hinge (the edges passing within the erect ears of the basal cup), broadly oval, rounded or truncate, flat or slightly folded, with wavy frilled upturned edges, white with rose-red nerves, with a quadrangular furrowed yellow plate with 3–4 teeth in front projecting over its base. **Column** short, expanding upwards, yellowish green (with a rather large staminode on each side of the anther), at an obtuse angle with the ovary. **Stigma** transversely oval or sub-quadrangular, slightly bi-lobed below, with rounded corners above. **Rostellum** nearly globular, projecting from the middle of the upper edge of the stigma, leaving behind a small square stump when removed. **Anther** relatively large, oval, hood-shaped, obtuse, yellowish, sessile, projecting slightly over the edge of the stigma, its apex rounded, empty. **Pollinia** oval, yellowish white, friable, without caudicles, partially, sometimes wholly, divided into two; pollen-grains cohering in fours but not compressed, tetrads tied together by fine elastic threads, which join to form a brown line down the front of the pollinium. **Seeds**: testa transparent, short, broad, ovoid, mesh open; embryo small, lemon-shaped, yellow, half as broad as testa.

HABITAT. Bogs, marshes, moist grassy places, damp sandy ground between dunes. Flowers June, July.

DISTRIBUTION. England, Wales and Scotland, from Cornwall and Kent to Perth and Fife. Generally distributed, sometimes locally abundant. In Ireland found in most districts, but said to be rather rare. Europe (except Arctic), N. Africa, Caucasus, Asia Minor, Persia, the Himalayas, Siberia, Japan.

> EPIPACTIS PALUSTRIS Crantz, *Stirp. Austr.* p. 462 (1769). SERAPIAS HELLEBORINE η PALUSTRIS L., *Sp. pl.* p. 950 (1753). S. LONGIFOLIA L., *Syst.* ed. 12 (1767). EPIPACTIS LONGIFOLIA Allioni (1785). ARTHROCHILIUM PALUSTRE Beck (1890).

Var. **ochroleuca** Barla. Flowers yellowish white, lip pure white. Freshfield, Lancs., and probably elsewhere with the type; Kenfig pool, Glamorgan.

Var. **ericetorum** A. and G. *Syn.* III, 811. A dwarf few-flowered form often only 10 cm. high, with white or rosy flowers, sometimes abundant in flat rather moist sandy ground between dunes. Coasts of S. Wales, Lancashire, etc., Wexford (Druce).

Fertilisation. The rostellum consists of a ball of very adhesive material enclosed in a membrane so excessively tender that it can be pierced by a human hair, and the pollinia are firmly attached to its upper surface or cap. If a small feather is brushed lightly upwards against the rostellum, the membrane bursts, and the cap comes away with a certain quantity of the friable pollen attached, but the pollinia are not withdrawn as a whole; but if the feather is so held that at the same time it slightly pushes up the blunt end of the anther, the pollinia are set free, and are as cleanly removed as they are by insects.[1]

The flower when ready for visitation stands out at right angles to the stem. Both before and after this it is drooping, so that an insect can see at once which flowers are best for its purpose. The front part of the lip forms a convenient platform to alight on, and is joined to the cup containing nectar by a flexible elastic hinge, which is depressed even by the weight of a fly, but springs back smartly when the weight is removed. The flowers are mainly frequented by hive-bees. When a bee alights, the lip bends down, opening the way to the nectar-filled cup; when he takes flight, the lip springs back, throwing the bee slightly upward, like a spring-board, ensuring that he pushes up the end of the anther, and enabling the pollinia to be removed unbroken. This beautiful and delicate mechanism is not found in any other European *Epipactis*; in all other species the front part of the lip is rigid and fixed, there being no need for the anther to be lifted up as the pollinia lie free in the clinandrium.

E. palustris is the only European *Epipactis* pollinated by hive-bees. Darwin's son watched hundreds of plants for some hours on three occasions, but although many humble-bees were flying about, not a single one alighted on a flower, but he saw about a score of flowers visited by hive-bees. He also saw the carrion-loving *Sarcophaga carnosa* on the flowers, and two had pollinia on their foreheads.[2] They were probably seeking to deposit eggs or larvæ amongst aphides in the flower, as observed in the case of a blow-fly by Mr Burton on *Aceras anthropophora* (p. 163). Several smaller flies (*Cœlopa frigida*, which haunts sea-weed) were seen visiting the flowers, with pollen-masses adhering rather irregularly to the thorax, and three or four kinds of Hymenoptera, one of small size being *Crabro brevis*, perhaps seeking small beetles with which to provision its nest. These may be regarded as accidental visitors, though they may sometimes bring about pollination, but they do not remove the pollinia so effectively as hive-bees, which are the main agents of pollination. It is curious that the nectar is unattractive to humble-bees.

The American "Chatterbox", *Epipactis gigantea*, belongs to this section, and is very like *E. palustris*. A large clump of it in Mr St Quintin's rock-garden, near Malton in Yorkshire, flowered freely, but I could never see any insects going to it. The hinge

[1] Darwin, *Fert. Orch.* ed. 2, p. 98.
[2] *Ibid.* p. 100.

H. M. Godfery pinx.

EPIPACTIS LATIFOLIA Allioni
Broad-leaved Helleborine

PLATE 7

Epipactis latifolia Allioni. Surrey, August 7th, 1918.

1. Single flower (enlarged).

of the lip is so elastic that it bobs up and down if the flower is shaken, whence the American popular name.

2. Epipactis latifolia Allioni

Pl. 7; Pl. A, fig. 5 (p. 6); Pl. K, fig. 1 (p. 220). *Broad-leaved Helleborine*

Roots numerous, moderately thick, brownish white, cylindrical, in a tassel (Text-fig. 8) at the foot of the stem; rhizome, if present, small, woody. **Stem** 30–80 cm., tall, solid, round, leafy, often tinged with violet below, hoary above with short whitish hairs and with two or more ribbed leafless sheaths at the base. **Leaves** broadly ovate to ovate-lanceolate, sometimes nearly circular (var. *orbicularis* Richter), decreasing in size upwards; lowest usually small, rounded, uppermost bract-like, lanceolate, with long tapering tip, the transition either gradual or abrupt; all spreading, the lower arranged spirally round the stem at an angle of about 120° with each other, i.e. three leaves to one turn of the spiral, dull green, not glossy, minutely toothed, much longer than the internodes, their ribbed sheaths closely enclosing the stem, with ± 5 principal nerves strongly raised beneath the rather weak and flaccid leaf, and several transparent ones between, nerves and leaf-edges rough. The upper leaves are rather irregularly arranged. **Flowers** 15–50 in a long loose or dense one-sided spike-like raceme, at first nodding, finally erect, greenish to dull red-violet (var. *purpurea*), drooping, rather bell-shaped, later opening wide, according to Max Schulze smelling of valerian, but generally scentless. **Bracts** spreading, lanceolate, acute, the lower often exceeding the flowers, 9–19-nerved, the upper about equal to ovary, ± 3-nerved. **Ovary** green, somewhat pear-shaped, often humped at the back, ± 1 cm. long, 6-ridged, glabrous or with a few scattered hairs, tapering into a short twisted stalk, finally pendent. Ripe capsule hanging, oblong-ovate, about 11 mm. long, shortly stalked. Lateral **sepals** obliquely ovate to lanceolate, ± 1 cm. long, keeled, acute, concave, green or dull red-violet, 3–5-nerved. **Petals** ovate, slightly broader, ± 8 mm. long, acute, keeled, semi-transparent, 5–7-nerved, green tinged with rose or red-violet. **Lip** shorter than sepals, basal half (hypochile) cup-shaped, 5-nerved, green outside, dark brown (rarely dark green) and glistening with nectar within, the front edges turned down in a fold connecting it with the apical half (epichile), which is heart-shaped or triangular with reflexed acute tip, and with two wart-like smooth or wrinkled humps at the base, rose to violet-rose, rarely dirty white. **Column**[1] short, squat, the thin green walls forming a shallow cup (clinandrium) on the summit, and ending on each side in a whitish rounded staminode (rudimentary anther) almost touching the back of the stigma. **Stigma** transversely oblong, angles rounded, lipped below, facing forwards. **Rostellum** large, milky white, sub-globose, seated on a

[1] Pl. A, fig. 5 (p. 6); Pl. K, fig. 1 (p. 220).

square green projection. **Anther** yellowish, sessile or nearly so, in back view ovoid, in profile rhomboidal, leaning forwards over the clinandrium, in which the pollinia are deposited on their sides when the anther opens in the bud, by the turning back

Text-fig. 8. A. Tassel of roots (two separate plants) of *Epipactis latifolia*, without rhizome. B. Roots of *Epipactis violacea*, springing from nodes of rhizome.

of a flap on each side. **Pollinia** club-shaped, yellow, not friable, firmly attached to the rostellum. Covering of **seed** (testa) long, narrow, obtuse, transparent; embryo lemon-shaped, narrower than testa.

There is no descending rhizome giving off roots at various depths as in *E. violacea* and *E. leptochila*, so that the plant is easily dug up, the roots forming a tassel round the base of the stem, which is single, rarely if ever clustered. The new bud has two rootlets, one at each side. The leaves are very variable, but the arrangement of the three lower leaves in a spiral equidistant from each other sideways is characteristic. The colour of the flowers is not due to the amount of light, green-flowered forms sometimes occurring in full sunlight, and red-violet ones in shade. The basal cup of the lip may be circular or elliptical, shallow or relatively deep, and the epichile varies from cordate to triangular, also in the smoothness or rugosity of the basal bosses, and in the presence or absence of a central boss or ridge.[1] The sepals and petals may be broad and rather obtuse, or narrower and acute.[2] Any of these variations may be combined with any of the variations in the shape of the leaves—they do not appear to be correlated. *E. violacea*, *E. rubiginosa* and *E. leptochila* being very local, there is usually no other species present with which *E. latifolia* can hybridise. Its numerous forms seem therefore due to an inherent tendency to variation.

A. D. Webster says that a form of *E. latifolia* with creamy white flowers grows in some of the Welsh woodlands. Except for the colour of the flowers it resembles the type, but the stem is of an ashy yellow. I found one or two specimens there with dirty white flowers, the inside of the cup of the lip green. In Canada, where the plant appears to have been introduced, Mr Mousley found specimens with the whole plant—stem, leaves and flowers—snow-white (except for a faint violet tinge in places), and appearing to be devoid of chlorophyll, probably owing to saprophytism.

Richter's *E. orbicularis* (as species) with almost circular lower leaves was considered by Wettstein, who gathered it with its author, an unimportant variety. It occurs with the type in Britain (var. *platyphylla* Irm.).

Var. ***purpurea*** Celak., flowers dirty red-purple, is a colour-form not due to sunlight, as it also occurs in the shade.

E. Crowtheri Druce, described as a hybrid between *E. latifolia* and *E. rubiginosa*, judging from the specimen at Kew, appears to belong to this variety. I have seen similar plants in Surrey, where *E. rubiginosa* does not grow.

E. atroviridis W. R. Linton (as new species) is distinguished by "two side hunches and one median linear hunch descending lower than the side ones".[3] This peculiarity also occurs in the type.[4]

"*E. media* (Fries!) Babington." An *Epipactis* from Bomere Pool, Salop, was identified by Babington as *E. viridiflora* Rchb.,[5] but was later published by him as *E. media* Fries,[6] probably because Fries cited *E. viridiflora* Rchb. as a synonym of *E. media* "according to Koch".

[1] *J.B.* Pl. 555 (1920).
[2] *Ibid.* p. 35 (1921), text-figure.
[3] *Fl. Derbyshire* (1903), with plate.
[4] *J.B.* p. 36 (1921).
[5] Leighton, *Fl. Shropshire*, p. 434 (1841).
[6] *Man. Brit. Bot.* p. 295 (1843).

The late Mr R. F. Burton of Longner Hall, Salop, kindly explored Bomere Pool, and sent me specimens of the only *Epipactis* he could find growing there.[1]

The drawing of *E. media* in *E.B.S.* 2775 was made from a specimen of *E. violacea* (*E. purpurata* Smith) from Woburn Abbey, Bedford (*E.B.* ed. 9, p. 124).

Habitat. Open woods, clearings and borders of woods, occasionally edges of fields and hedge-banks, rarely sandy warrens. Essentially a woodland plant, it prefers neither deep shade nor full sunlight, though sometimes found in both. Flowers late July to early September.

Distribution. Generally distributed in Great Britain and Ireland. Occurs throughout most of Europe, N. Africa, Asia Minor, Persia, Siberia, Himalayas, Japan,[2] N. America (Montreal, Toronto, N.Y. and Pa.), where it is usually considered to have been introduced.

> Epipactis latifolia Allioni, *Fl. Pedem.* ii, 151 (1785). Serapias Helleborine α latifolia L. (1753). S. latifolia Hudson (1762). Helleborine latifolia Druce (1907). Amesia latifolia Nelson and Macbride (1913).

Fertilisation. The anther opens in bud and deposits the two pollinia in the clinandrium, their upper ends becoming firmly attached to the cap of the rostellum. The latter, on being touched by an insect, bursts, and the liberated adhesive matter instantaneously attaches the pollinia to its head. The nectar in the cup is very attractive to wasps, but not to bees or humble-bees. They do not visit the flowers in the rapid business-like manner of bees, but linger on them some time. The viscid matter therefore sets slowly. Darwin watched a colony of plants near his house for several years, but although hive- and humble-bees were constantly flying over them, he never saw a bee or a fly visit the flowers.[3] If a flower is not visited the pollinia wither in the clinandrium. There is no self-fertilisation.

3. Epipactis violacea Dur. Duq.

Pl. 8; Pl. K, fig. 1 (p. 220). *Violet-leaved Helleborine*
Clustered Helleborine

Rhizome descending, deeply buried, often with enlarged knots and blackish scales; roots worm-like, fleshy, thickening downwards, springing from the various nodes at different depths. Top of rhizome thickened in old plants, giving rise to several (one plant had 38) flowering stems. New bud at base of stem with a stout densely hairy rootlet on each side. **Stems** often clustered, 20–70 cm. tall, erect, rigid, solid, rather slender, grey-green flushed with violet, with dense short whitish hairs above

[1] *J.B.* (1919), p. 81. These turned out to be *E. leptochila*.
[2] A. and G. *Syn.* iii, 865.
[3] *Fert. Orch.* ed. 2, p. 101.

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H. M. Godfery pinx.

EPIPACTIS VIOLACEA Durand Duquesnay
Violet-leaved Helleborine

PLATE 8

Epipactis violacea Durand Duquesnay. Surrey, September 7th, 1916.

1. Lip and column (enlarged).

(giving a curious livid mealy appearance) and 2–3 rather loose brown leafless sheaths at base, the upper often green-tipped. **Leaves** small, few, distant, rough, ovate-lanceolate to lanceolate ($\pm$ 6 cm. $\times$ 2 cm.), dull grey-green, often (but not always) flushed with violet, not keeled, with 3–7 principal and numerous fainter nerves, fringed with short translucent papillæ, and with long sheaths, so that the leaves do not much exceed the internodes. Lowest leaf very small, concave above, the uppermost bract-like. **Raceme** long (up to 18 cm.), many-flowered, rather dense, one-sided, at first nodding, finally erect. Flowers pale greenish white, horizontal, rather large, opening wide, with a white lip and faint almost imperceptible scent. **Bracts** lanceolate to linear, tapering, acute, spreading or pointing downwards, often flushed with violet, the lower sometimes very long, with usually three principal nerves and several subsidiary ones, the edges minutely toothed. **Ovary** club-shaped, about 1 cm. long, straight, tapering gradually to the twisted stalk ($\pm$ 5 mm.), dark green tinged with violet, hispid with short hairs, with six cord-like ridges. Ripe capsule large (1·50–1·70 cm. long), broad, trigonous, sides nearly flat, thickest near the rounded apex, rough with the bases of worn-off hairs, horizontal, not as a rule pendent. **Sepals** lanceolate (10–12 $\times$ 5 mm.), obtuse or somewhat acute, hooded or drawn together at the tip, concave, green outside, smooth and whitish green within, obscurely 5-nerved with a green keel, edges sometimes rough. **Petals** ovate-lanceolate, obtuse or acute, whitish, sometimes faintly tinged with rose, or greenish white, translucent, shorter than sepals, green-keeled in the lower part only, obscurely 5-nerved. **Lip** slightly shorter than sepals, basal cup (hypochile) rather elliptical ($\pm$ 5 mm. long, 4 mm. broad, $3\frac{1}{2}$ mm. deep), glossy, pale green slightly tinged with violet outside, olive-green mottled with violet within (sometimes with no trace of violet inside or out), obscurely 5-nerved, rugose inside, glistening with nectar, with transparent, whitish or colourless edges. Tongue of lip (epichile) broader than long, cordate, acute, finely toothed, tip reflexed, dull white with 2–3 more or less confluent smooth hunches and a cord-like central boss, faintly tinged with violet or rose. **Column**[1] short (2 mm.) with a shallow cup (clinandrium) at the top enclosed by a low semi-circular wavy-edged wall, ending on each side in a rounded staminode almost touching the back of the stigma. **Stigma** in front of column, oblong, quadrangular, with rounded corners, its lower edge turned up in a lip, with a keel at the back running up to the whitish globular rostellum, which is rather smaller than that of *E. latifolia*. **Anther** sessile, *narrow*, laterally compressed, obtuse, granular outside, pale yellowish cream, leaning forward over the clinandrium. **Pollinia** short (2 mm.), thick, ovoid, yellowish white, adhering to the rostellum just below their apex. **Seed** similar to that of *E. latifolia*. Testa long, very narrow, straight or curved, obtuse, narrow-meshed. Embryo lemon-shaped much narrower than testa.

[1] Pl. K, fig. 1, *C* 1, *C* 2 and *C* 3.

Var. **purpurata** Smith (as species), *English Flora*, IV, 41; *E.B.S.* 2775 (colours quite wrong).

Smith described his *E. purpurata* from a single specimen found by the Rev. Dr Abbot in 1807 "parasitical on the stump of a maple or hazel in a wood at Leigh, Worcestershire", of which he says: "Perennial. June. Root certainly parasitical, whole plant when fresh glowing with a beautiful red-lilac colour". A similar form, *rosea* Erdner, was found in Bavaria, the whole plant rosy, as in *Lathræa squamosa*.[1] In July, 1919, another was found near Horsham, Sussex, now in the British Museum (Nat. Hist.), London. *E. violacea* is a saprophyte, agreeing with parasites in deriving its nourishment from organic material, but differing in growing on dead, not living organisms, and only assimilating matter in a state of decay. The flush of violet appears to be due to this cause, the same coloration occurring in the continental orchid *Limodorum abortivum*, in *Lathræa*, etc., which are also saprophytes. Many of the English plants have no tinge of violet except on the stem, but where much decaying organic matter is present the leaves are shot with violet. The extreme limit of saprophytism is reached when the plant is compelled to derive its nourishment entirely from organic matter, as in the Leigh and Horsham plants.

The figure of *E. media* in Sowerby's *Eng. Bot.* was drawn from a specimen of *E. violacea* from Woburn Abbey, Bedford.[2] According to Webster the species *E. purpurea* of some botanists is not *E. violacea* but a dark purple form of *E. latifolia*.[3] *E. violacea* is easily distinguishable from *E. latifolia* by (1) the deep vertical knotted rootstock, with roots from the nodes at different depths, not in a tassel at the base of the stem; (2) the tufted stems of the older plants; (3) the shorter narrower distant leaves, never orbicular or ovate; (4) the violet flush on the leaves (not always present); (5) the broader raceme of greenish white flowers; (6) the violet, not dark brown, interior of the cup of the lip; (7) the large thick heavy-looking seed-capsules. Some authors state that it is distinguishable by its robust habit, but *E. latifolia* and *leptochila* also are sometimes 70 cm. tall. Whilst the flowering head is often dense, plants are not infrequent in which it is not more dense than in *E. latifolia*, but it often has a bunchy appearance through two, three, or even four flowers being close together, almost as if in whorls.

Richter[4] regards *violacea* as a hybrid between *E. latifolia* and *E. microphylla*, but the total absence of the last-named from Britain puts it out of court as a parent, and *violacea* also occurs abroad where both the supposed parents are absent.[5] *E. violacea* appears to be uniform and constant in Britain, not varying in the shape of the leaves and the colour of the flowers like *E. latifolia*. It is a rarer and more local plant than

[1] A. and G. *Syn.* III, 864.
[2] *E.B.* IX, 124.
[3] Webster, *Brit. Orchids*, ed. 1, p. 26.
[4] *Pl. europ.* I, 284.
[5] Hoffmann, *Allg. Bot. Zeit.* No. 12 (Dec. 1907).

the latter, both at home and abroad. It differs from *E. leptochila* as follows. Bud with two rootlets, not one only. Stem violet, not pale green; internodes long. Leaves small, distant, not ovate. Epichile white, cordate, curved downwards, not green, tapering, straight. Anther not stalked. No incision between front and rear of column. Rostellum visible in all flowers, on lightly touching which the pollinia are easily removed. For fuller comparison, with figures, see *J.B.* p. 40 (1919) and Pl. K, p. 220.

Habitat. Essentially a woodland plant, preferring rather deep shade, where there is little undergrowth. Fleischmann and Rechinger say (*O.B.Z.* p. 267 (1905)) that it lives in the twilight of the beech-woods, thick with fallen leaves, usually away from paths, appearing suddenly like a wood spirit in the deep solitude of the woods. In Britain it is not confined to beech-woods, but occurs in copses of mixed growth, and, as far as I have seen, on calcareous soil. Flowers August to September. The Horsham *purpurata* was found in July, and Smith's specimen in June, which was extraordinarily early—is it possible that extreme saprophytism favours early flowering? Rare and local.

Distribution. Southern counties from Kent to Gloucester, Berks., Bucks., Oxon. (stems 20–30, Druce), Bedford, Worcester. Not recorded from the Isle of Wight. Early records are unreliable, as the plant was confused with *E. leptochila* (under the name *E. media*). France, Germany, Austria, Switzerland, Russia.

Epipactis violacea Durand Duquesnay, *Cat. pl. Lisieux*, p. 102 (1846), as E. latifolia var. violacea. Boreau, Babington (*Man. Brit. Bot.* ed. 8, p. 350), Schinz and Keller, E. Helleborine c Ep. varians Crantz (1769). E. sessilifolia Petermann (1844). E. Helleborine 5. violacea Reichenbach fil. (1851). E. purpurata Smith, *Engl. Fl.* iv, 36 (1828).

Crantz's *Ep. varians* is the oldest name, but such eminent orchid monographers as Reichenbach fil. and Camus thought his plant was *E. viridiflora*. Fleischmann and Rechinger made out a strong case for its identity with *violacea*, but admitted that universal agreement on this point could hardly be expected. *E. sessilifolia* is two years earlier than *violacea*, but Petermann himself abandoned it. Smith's *E. purpurata* was not based on typical *violacea*, but on an anomalous specimen so rare that no other example was found in Britain till 1919, and is best restricted to the form to which it was originally given.

Fertilisation. *E. violacea* is fertilised by wasps in exactly the same manner as *E. latifolia*, and is extremely well visited by these insects. Near Guildford on August 23rd, 1918, I saw a wasp assiduously visit 12 flowers on one spike, and was surprised to see that it carried no pollinia, until I found that all the pollinia had been previously removed from the flowers. Examination of a number of spikes showed that the pollinia had been carried off from nearly all the flowers, except the most recently opened ones. In one case a complete pair of pollinia was adhering to the stigma, the flower's own pollinia being still intact, so that it is possible for pollination to occur without withdrawal of the pollinia. Pollen was observed on many stigmas, and in October the stems were heavy with large ripe capsules.

EPIPACTIS LATIFOLIA × E. VIOLACEA

× E. Schulzei Camus

A specimen of this hybrid, found near Selborne on August 8th, 1931, by me in company with Mr P. M. Hall, differed manifestly from the plants of *E. violacea* amongst which it grew by its very stout stem, broad ovate *latifolia*-like leaves, very dense spike, and remarkably long bracts. The leaves from the base upwards measured (1) 6 × 4 cm., (2) 8 × 4·5 cm., (3) 8·5 × 3·2 cm., (4) 8·6 × 1·7 cm., (5) 7 × 1·2 cm. There was also a leaf-like tip to the basal sheath about 6 cm. long. The lowest bract was 6·5 × 1·2 cm. No flowers were yet open, but on dissection the buds differed from those of pure *E. violacea* as follows. The transverse wavy violet ridges on the floor of the basal cup characteristic of *E. violacea* were absent, but it was longitudinally streaked with closely parallel transparent veins, and was entirely green. The boss on each side of the terminal tongue was like that of *E. latifolia*, and showed no trace of the parallel furrows, like those between the fingers of the human hand, which are distinctive of *E. violacea*.

But for the above exceptions, the plant closely resembled *E. violacea*. The stem and leaves were flushed with violet. Perhaps a specimen in the herbarium of the late Mr C. E. Salmon, labelled *E. latifolia*, Ashburnham Park, August 4th, 1894, with a long spike of large flowers with very long bracts, belonged to this hybrid, and possibly also the "*E. purpurata* Sm. bracteis longissimis. Surrey. Kellermann! Box-hill Rach." mentioned by Reichenbach.

4. EPIPACTIS LEPTOCHILA Godfery

Pl. 9; Pl. A, fig. 6 (p. 6); Pl. K, fig. 1 (p. 220). *Slender-lipped Helleborine*

Rhizome descending, deep, knotted, with dark brown scales and numerous long fleshy sinuous light brown roots springing from the nodes, in old plants often thickened above, with several flower-stems, each with a bud at the base with a *single* very hairy rootlet. **Stem** 20–70 cm. tall, round, erect, rigid, solid, sometimes rather woody at the base, not more than 5 mm. in diameter as a rule, pale green, covered with often dense whitish hairs above, less so below, where it is whitish tinged with violet, with two or three ribbed violet-tinged leafless sheaths at the base, later turning brown. **Leaves** broadly ovate (7 × 5 cm. to 5 × 4 cm.), sometimes broadly lanceolate

PLATE 9

H. M. Godfery pinx.

EPIPACTIS LEPTOCHILA Godfery
Slender-lipped Helleborine

PLATE 9

Epipactis leptochila Godfery. Horsley, Surrey, July 29th, 1918.

A. Enlarged single flower.

B. Part of fruiting raceme.

($10 \times 3\frac{1}{2}$ cm. to 6×2 cm.), acute, often numerous, rather close together with short internodes, in two ranks on opposite sides of the stem, often wavy-edged, rigid, rather rough to the touch, yellow-green or dark green, neither grey-green nor glossy, with three strongly raised nerves on each side of the thick mid-rib, and 4–8 translucent nerves between each pair; upper leaves lanceolate to linear-lanceolate, tapering, often bract-like. **Raceme** long (up to 23 cm.), drooping, finally erect, narrow, one-sided, rather lax. Flowers pale yellow-green, scentless, rather larger than in *E. latifolia*, with spreading pointed sepals and petals and long narrow lip. **Bracts** linear-lanceolate, sessile, spreading, tapering, acute, yellow-green or dark green, the lower many-nerved (up to 11), often twice as long as the flowers, the upper 3-nerved, equalling or exceeding the ovary. **Ovary** spindle-shaped, narrowing gradually to the twisted stalk, green, rough with irregular tubercles, with sparse short (sometimes black) hairs (as also its stalk), and six prominent cord-like ridges, continuous with the keels of the sepals and petals. Ripe capsule horizontal or drooping, yellow-green, elliptical, with six prominent ridges; stalk $\pm$ 6 mm. long. **Sepals** long, spreading, lanceolate, with acute tapering point ($12–15 \times 4$ mm.), concave, pale green with transparent edges and 3 green nerves, keel rough with minute projections. **Petals** shorter and broader ($10–11 \times 5–6$ mm.), ovate-lanceolate, acute, glabrous, pale whitish green with bright green cord-like keel and 2–3 faint sometimes branched nerves on each side, edges transparent, minutely toothed. **Lip** long, narrow, acute, usually pointing straight forward ($\pm\ 10 \times 4$ mm.). Basal cup circular (4 mm. diam., 3–4 mm. deep), pale green outside with a raised darker keel and three nerves on each side and irregularly toothed semi-transparent wavy edges, green mottled with red inside, sometimes with a few short hairs outside. Tongue of lip cordate at base with a long sharp point not as a rule recurved, narrow (4 mm.), green bordered with white, with a raised keel and two obscure nerves on each side, semi-transparent minutely toothed upturned edges and two white, more or less distinct, smooth or irregularly wrinkled hunches at the base sometimes tinged with rose, with a rather deep channel between them leading into the basal cup. **Column**[1] short (5 mm.), divided into two parts at the apex by a **V**-shaped incision on each side, with a curved nib-shaped stalk at the back supporting the anther; the front wall on each side ending in a staminode almost touching the back of the stigma. The base of the column in front is quadrangular, its sides curving somewhat outwards and slightly winged. **Anther** stalked, ovate with a rather acute empty tip, projecting for about half its length over the upper edge of the stigma, cream-coloured or yellowish green, convex behind, more or less flat in front, minutely papillose outside, the membrane in front of each cell turning back like a flap, and becoming brown. **Pollinia** creamy white, joined at the apex, thicker, rounded, and slightly divergent at the base, split for most of their length; in early

[1] Pl. A, fig. 6 (p. 6); Pl. K, fig. 1, *A* 1, *A* 2 and *A* 3 (p. 220).

bud smooth and glistening, but rapidly becoming fluffy, owing to the swelling of the globular pollen-grains, united in tetrads. **Stigma** transversely oblong, leaning slightly backwards, not supported on a pedestal as in *E. latifolia*, the upper edge sloping slightly downwards on each side, the lower edge with a wavy irregular lip. **Rostellum** globular, always present in bud, and frequently when the flower first opens, but quickly disappearing, leaving a small brownish mark. The flowers, except perhaps the last opened one or two, then appear to have no rostellum at all. **Seeds**: testa long, narrow, obtuse, about eight or ten times as long as broad; mesh narrow, cell-walls thick. Embryo lemon-shaped, narrow, not much more than half as broad as testa, opaque.

The only *Epipactis* with which *E. leptochila* can be confused is *E. latifolia*, from which it differs as follows:

(1) Rhizome descends deep, giving off many roots at different levels; *latifolia* has a tassel of roots round the base of the stem.

(2) Each bud has only one rootlet instead of two.

(3) The leaves are in opposite ranks, i.e. at an angle of 180° with each other. In *latifolia* the lower leaves are so to speak in a spiral whorl of three, i.e. at an angle of 120° with each other.

(4) The flowers are yellow-green, with longer more acuminate sepals and petals.

(5) The epichile is long, narrow, acuminate, projecting forwards, not heart-shaped, as broad as long, with tip curled underneath, as in *latifolia*.

(6) There is an incision on each side of the column separating the back from the front (Pl. A, fig. 6 (p. 6); Pl. K, fig. 1 (p. 220)).

(7) The anther is on a nib-shaped stalk, not sessile as in *latifolia*, and projects well forward over the upper edge of the stigma.

(8) The upper parts of the pollinia slide over the top of the stigma, and form a rough horseshoe on its face, so that the flower is pollinated by its own pollen, which never happens with *latifolia*.

(9) The rostellum very soon disappears, so that all but the last opened flowers appear to have no rostellum.

(10) Practically every flower sets a seed-capsule. In *latifolia* no flower sets a capsule unless pollen from another flower is brought to the stigma by insects.

(11) It is mainly self-fertilised, *latifolia* never so.

I first found *E. leptochila* near Horsley, Surrey, on June 29th, 1918, and supposed it to be *E. viridiflora* Rchb., as it agreed with the diagnoses of Reichenbach and Hoffmann, though these were too meagre for positive identification. H. Müller, however, had stated that in *E. viridiflora* there was no rostellum, the pollinia were deposited on the stigma of the same flower, and self-fertilisation was inevitable. These unusual characters appeared to confirm the above identification, but I was still puzzled to know why nearly all authors considered *E. viridiflora* a mere variety of *E. latifolia*. In June, 1920, I went to Thorenc above Grasse, where Mlle Camus (joint-author of her father's monograph of European orchids) had told me *E. viridiflora* was frequent. I found that, so far from being self-fertilising, it had a conspicuous rostellum, was freely visited by wasps (the pollinia being removed from almost every flower) and showed no signs of self-pollination. I at once sent specimens to Mlle Camus, who identified them as *E. viridiflora*. Dr Keller of Aarau, joint-author with Dr Schlechter of the latest monograph of European orchids, kindly sent me specimens of *E. viridiflora* from some Swiss stations, which showed similar characters—the reverse of those of *E. leptochila*. They evidently were nothing more than a variety of *E. latifolia*. It was clear that *E. leptochila* was not the continental *E. viridiflora*.

Müller had said that in *E. viridiflora* the pollinia were deposited standing *erect upon their bases* on the front of the stigma. This seemed impossible, as in *Epipactis* the anther leans forward face downwards over a shallow cup (clinandrium) on the top of the column *behind the back* of the stigma, depositing the pollinia lying on their sides in this cup. Later I found an *Epipactis* at Thorenc at once recognisable as Müller's plant. I found to my surprise that only the lower part of the stigma faced forwards as in *Epipactis*, the upper part curving backwards at right angles and quite roofing over the clinandrium, its edge pushed underneath the base of the anther, nearly reaching the back of the column. The anther was erect, and its broad base projected forwards well over the surface of the stigma (which here faced upwards) and deposited the pollinia erect on their bases just as Müller described. His plant was not *E. viridiflora* Rchb., but an unsuspected new species to which I gave the name *E. Muelleri* in honour of his researches. It has since been found in Savoie, Switzerland! (Evans), Germany (Höppner) and the Pyrenees (Mlle Camus). Ascherson and Graebner's statement that *viridiflora* had no rostellum and was self-fertilised was not based on observation, but solely on Müller's most interesting paper (*Verh. N.H. Verein des preuss. Rheinlands*, 1868). For *E. Muelleri*, see *J.B.* p. 101 (1921). *E. leptochila* was therefore raised to specific rank, as it was clearly neither *E. viridiflora* nor *E. Muelleri*, and there was no other European *Epipactis* under which it could be reasonably placed.

The late Mr C. E. Salmon, F.L.S., examined large numbers of *E. leptochila* in Gloucestershire, and was convinced that, though varying in a few minor details, they belonged to this species, the reproductive organs and the form of the epichile remaining constant. He particularly noted the tall robust stems (1–5), ovate lower leaves, and large wide-open flowers. The side view of the reproductive organs exactly matched Pl. K, fig. 1, *A* 1, p. 220 (*J.B.* Pl. 553). The rostellum was practically useless—in no case could the pollinia be withdrawn on a pencil as is so easily done with *E. latifolia* (*J.B.* p. 21 (1921)).

Var. *vectensis* Stephenson (*J.B.* p. 1 (1918); Pl. 555, fig. 2 (1920); p. 205 (1921)). Plant slender, delicate. **Stem** solitary, nearly glabrous below, slightly pubescent above. Basal sheaths several, adpressed, upper often funnel-shaped. **Leaves** few, greyish green, not strongly ribbed, minutely ciliate, nerves smooth or ciliate. Lower leaves lanceolate to elliptic-lanceolate, upper linear-lanceolate to linear, acute. Lower **bracts** never much exceeding the flowers. Flowers in a lax few-flowered raceme, much more drooping, yellowish green, sometimes very faintly brownish outside. **Petals** and **sepals** longer, narrower and more acuminate than in *E. dunensis*. **Lip** whitish green, triangular, cordate, acuminate, straight or slightly recurved, bosses two, low, slightly wrinkled. **Ovary** large, almost glabrous. **Pollinia** friable, overhanging the stigma; rostellum a functionless rudiment. The above is abbreviated from the original diagnosis. The figure of the lip in the text is not acuminate, but nearly as broad as long. The original specimens were found in shade on chalk towards the end of July near Ventnor, Isle of Wight (where it was scarce and threatened with extinction by ivy), by the late Mr Hunnybun. The locality is unknown, and attempts to rediscover it were unsuccessful.

Drs T. and T. A. Stephenson named this plant *Helleborine viridiflora* (Rchb.) Wheldon and Travis forma *vectensis*, i.e. as a form of the dune plant now known as *Epipactis dunensis*. Later they transferred it to the subsequently described *E. leptochila* as a variety (*J.B.* p. 205 (1921)). In August, 1927, a small colony of abnormal *E. leptochila* was found near Nonington, Kent, which Dr Stephenson said were in exact agreement with his *vectensis* as far as stem and leaves were concerned, but the flowers had perished. In 1919 I found five plants of *E. leptochila* near Mold in which the flowers were pendent, and only opened at the tip, resembling Fig. D, *J.B.* p. 3 (1918) (*vectensis*). I now think this was probably *vectensis*, or very near it. I could not find a trace of it in subsequent years. It had completely disappeared. I believe that both it and the Nonington plants were degenerate and dwindling forms of *E. leptochila*, rather than varieties, and were starved plants on the verge of extinction. Probably *vectensis* was in the same condition, abnormal and struggling for existence. In 1931 (August 8th), Mr P. M. Hall showed me a very scattered colony of similar plants near Winchester, very dwarf, frail and inconspicuous, with few, pendent flowers, which in some cases did not open at all. It had evidently a hard struggle for existence in spite of self-fertilisation. In this form the lip is very small and triangular, not acuminate as in the type, and almost flat, not properly developed into hypochile and epichile, the former being a mere shallow depression.

The original Latin diagnosis was as follows (*J.B.* p. 38 (1919)):

"*Epipactis viridiflora* Rchb. var. nov. *leptochila* a typo differt caulibus altioribus (2–7 dm.) sæpe aggregatis; foliis inferioribus sæpe ovatis; sepalis acuminatis, 12–15 mm. longis, 4 mm. latis; labello protinus prominente; hyperchilio orbiculari, 4 mm.

diam., 3–4 mm. alto; epichilio cordato acuminato (cuspide longa acuta) angustissimo (± 8 mm. longo, 4 mm. lato, ubi latissimum est) viridi albo-marginato; callis duobus irregulariter rugosis albis interdum pallide roseis; rostello evanescente" (*J.B.* p. 38 (1919)).

The "type" referred to was *E. dunensis*, at that time supposed to be *E. viridiflora* Rchb.

Habitat. Shady woods. Horsley, Surrey! Oxon., Tahourdin! Maidenhead! Gloucester, W. Mathieson! Salop, C. E. Salmon (*J.B.* p. 21 (1921)). Sussex, Tahourdin. Luton, Kent, Babington. Bomere Pool, Salop, Babington, Burton!

Epipactis leptochila Godfery, *J.B.* p. 146 (1921). E. viridiflora Rchb. var. leptochila Godf., *J.B.* p. 37 (1919), with analytical Pl. 553; and p. 67 (1926), with Pls. 575 and 576. "E. media Fries" Babington (?).

Fertilisation. The nectar in the cup of the lip, and the presence of a rostellum in some of the newly opened flowers, show that these were organised to attract insects and secure the transport of the pollinia from one plant to another. In specimens from Marden Park, Surrey, on July 24th, 1925, both pollinia had been removed from three flowers, leaving a little pollen along the top edge of the stigma. In some spikes from Maidenhead, June 21st, 1925, one flower had no pollinia and no pollen on stigma, and another had no pollinia, but had a slight fringe of pollen on the upper edge of the stigma. Mr W. Mathieson of Shepscombe, Gloucester, once saw a wasp visit *E. leptochila*, and afterwards go to a flower of *E. latifolia* with pollen on its head. The rostellum is usually present in bud, and in the flower when it first opens, though sometimes it appears not to have been developed. I once saw a rostellum still existing in the two topmost flowers, but these may have opened simultaneously. Generally it has disappeared by the time the next flower above it has opened. If touched with a pencil a few strings of viscid matter can be withdrawn, but the pollinia do not come away smartly as in *E. latifolia*. Nevertheless I succeeded in removing one whole pollinium in this manner, but it needed long contact with the pencil to secure adhesion. Wasps, however, remain a long time on a flower sucking nectar, so that the weak viscid matter has time to set. Pollinia are sometimes, though as far as I have seen very rarely, removed by insects, but this can only happen within a few hours of the opening of the flower, owing to the early disappearance of the rostellum.

The flowers, however, appear to be mainly self-fertilised. The anther juts forward for about half its length over the slanting upper edge of the stigma, causing the pollinia also to project forwards. They are joined at the apex, thicker and slightly divergent downwards. In all other British species of *Epipactis* (except *E. dunensis*), the apex of the pollinia comes in contact with the rostellum and becomes firmly attached to it. In *E. leptochila* the anther projects too far forward, with the result that it often happens that the rostellum lies in the fork between the pollinia without touching them. The pollinia appear to slide over the edge of the stigma, which slopes down on each side, and come to rest on its adhesive surface, forming an inverted V (or horseshoe) in the angle of which is a brown irregular mark—the remains of the withered rostellum. The pollinia swell visibly and become fluffy, probably through the outgrowth of pollen-tubes. The disintegration and distribution of the pollinia over the surface of the stigma are apparently assisted by the small and active larvæ (thrips?) which are often found crawling about them. The pollen-tubes find their way to the ovary and fertilise the ovules in the usual way. Whether the rostellum is in course of evolution but not yet perfected, or whether it is losing a former efficiency and gradually disappearing, remains to be seen.

EPIPACTIS LEPTOCHILA × E. LATIFOLIA

× **E. Stephensonii** Godfery

In one specimen dug up by me in Surrey, there was no rhizome, and the roots were in a dense but shallow ring round the clustered stems, which were eight on the same plant. The flowers had been cut, and were not seen. *E. latifolia* and *E. leptochila* grew in the same wood, but in different parts. The supposed hybrid grew between the two habitats, and was the only *E. latifolia*-like plant I have ever seen with several stems. Horsley, Surrey! Generally speaking the hybrids are tall and robust with *latifolia*-like leaves, broader and less acuminate sepals, broader triangular epichile, standing straight out and not recurved at the tip. Gloucestershire, Salmon (*J.B.* p. 21 (1921)).

Dr Stephenson, who examined one of the specimens, wrote: "Much stouter and more latifolia-like...than any we have had before. The pollen is very overhanging and friable, falling on to the stigma of itself, and the rostellum is visible as a rudiment in the bud only, having vanished in the open flower" (*loc. cit.* p. 20).

5. EPIPACTIS DUNENSIS Godfery

Pl. 10. ***Dune Helleborine***

The original diagnosis (*J.B.* p. 68 (March, 1926), Pl. 574) was as follows:

"EPIPACTIS DUNENSIS, sp. nov. *Caulis* 20–40 cm. long. profunde descendens, vaginis basalibus laxis, radicibus paucis brevibus tenuibus rigidisque. *Folia* disticha oblongo-lanceolata rigida sæpe plicata. *Racemum* laxum floribus paucis, parvis, flavido-viridibus; bracteis lineari-lanceolatis, inferioribus flores superantibus. *Ovarium* breviter pedicellatum glabrum, vel pilis brevibus parcissime indutum. *Sepala* ovario breviora ovata obtusa carinata cucullata. *Petala* sepalis similia sed magis acuta translucentia.

H. M. Godfery pinx.

EPIPACTIS DUNENSIS Godfery
Dune Helleborine

PLATE 10

Epipactis dunensis Godfery.

1, 2. Complete plant. S. Lancashire coast, July 21st, 1917.

3. Single flower (enlarged).

4. Root of another plant.

5, 6, 7. Side, front and back view of column (much enlarged). July 26th, 1925.

p. Pollinia.

Labellum sepalis breviore, hypochilo dilute viride intus roseo-maculato, epichilo deltoideo acuto albido vel roseo-tincto apice recurvato, callis binis humilibus levibus interdum deficientibus. *Stigma* oblongum marginibus superioribus pronis. *Rostellum* deficiens vel mox evanidum. Pollinia primum fragilia, clinandrio tumescentia et super marginem stigmatis effusa.

"HAB. Sand-dunes amongst *Salix repens*, on the coast of Lancashire and Anglesey. In flower June–July."

Rhizome short, with few short wiry roots, buried very deep in the sand. **Stem** erect (20–40 cm.), solid, slender, stiff, green and downy above, violet-tinged and glabrous below, and with 2–3 ribbed loose sometimes funnel-shaped or green-tipped sheaths. **Leaves** in two opposite ranks, oblong-lanceolate, stiff, acute, slightly mucronate, often folded, sometimes wavy-edged, twice or thrice as long as the internodes, the lowest broadly ovate, obtuse, the uppermost bract-like; principal nerves $\pm$ 4 on each side of mid-rib, with fainter intermediate ones. **Raceme** spike-like, flowers 7–19, small, yellowish green, inconspicuous, horizontal, later drooping. **Bracts** linear-lanceolate, acute or obtuse, spreading, lower longer than the flowers. **Ovary** ($\pm$ 1 cm.) short-stalked, tapering to the base, spindle-shaped to pyriform, almost glabrous, yellow-green, shining, finally pendent. **Sepals** short ($\pm$ 7 mm.), ovate, obtusely pointed, concave, slightly hooded, keeled, firm, glabrous, yellow-green. **Petals** similar, slightly shorter and narrower, pale, translucent, not keeled. **Lip** greenish white or flushed rose, base cup-shaped, olive-green mottled with rose-red within, 7–9-nerved, edges turned down in a fold in front; epichile broadly triangular with recurved tip, finely toothed, white tinged green or rose, with two nearly smooth bosses and often a small central ridge. **Column** short, stout. **Anther** almost sessile, yellowish. **Pollinia** yellowish, almost split, pollen-grains finely netted. **Stigma** transversely oblong, upper edges sloping downwards, lower forming a lip. **Rostellum** globular if present, but usually absent. **Seeds** slug-shaped with rounded apex, nearly twice as long as and narrower than those of *E. rubiginosa*, but only about half as long as and broader than those of *E. latifolia*; mesh of testa open with very slender "wires"; embryo lemon-shaped, dark coloured, opaque. Distinct in appearance from those of all other species, their rounded contour, open mesh, and clean-cut brownish embryo are neat and pleasing, and make them easy to recognise.

HABITAT. Sand-dunes, or sandy ground between the dunes, amongst *Salix repens*. Flowers June to July.

Colonel C. T. Green, who has known the Lancashire plant for over 40 years, says its proper habitat is amongst *Salix repens* in the open. It also now grows among the more recently planted fir copses, where it is much larger owing to their shelter, but in all cases was growing there before the trees were planted.

DISTRIBUTION. Coasts of Lancashire! and Anglesey! Coutainville (Manche), France (Meslin, *J.B.* p. 217 (1928), with plate). Colonel A. M. Forbes thinks it is identical with plants found by him on sand-dunes near Le Coq-sur-Mer in Belgium. Nieuport Bains, Belgium (Houzeau de Lehaie, in lit.). Pomerania (*J.B.* p. 273 (1928)).

EPIPACTIS DUNENSIS Godfery, *J.B.* p. 66 (1926) (with plate). HELLEBORINE VIRIDIFLORA Wheldon and Travis, *J.B.* pp. 307, 343 (1913). EPIPACTIS LEPTOCHILA Godf. var. DUNENSIS T. and T. A. Stephenson, *J.B.* p. 205 (1921).

There is no creeping rhizome or root. There is sometimes a small irregular mass at the base of the stem in old plants. The root-system is extremely poor, the roots often only 4–6, though one specimen had ten. The leaves arch outwards, and spring back smartly if displaced. Lower bracts up to 9-nerved. Ovary with a few short hairs in its earlier stages. The flowers are more or less campanulate, and never open wide, in bad weather sometimes not at all. The cup glistens with nectar. The pollinia are at first friable, globules of pollen falling into the flower. Their upper parts swell and come over the edge of the stigma on each side, forming a fluffy yellow mass. There is a small projection in the middle of the upper edge of the stigma which supports the rostellum, if the latter is developed, which is not often the case. The viscid secretion of the stigma is very copious and thickens into a lip below; it sometimes forms a sort of stalactite at one or both sides, or in the middle.

Messrs Wheldon and Travis first observed this plant in Britain, and published an excellent description under the name *Helleborine viridiflora* (*J.B.* p. 343 (1913)), and it was identified by the late Mr Rolfe at Kew as *E. viridiflora* Rchb. As shown under *E. leptochila*, *E. viridiflora* Rchb. is a mere variety of *E. latifolia*, has a large rostellum, and is entirely fertilised by insects. It is also a woodland plant.

E. dunensis differs from *E. latifolia* as follows:

E. latifolia	**E. dunensis**
Roots numerous in a tassel, rather thick, soft, starting near the surface.	Few, slender, wiry, hard, deeply buried.
Sheaths at base of stem close-fitting.	Loose, often obliquely funnel-shaped.
Leaves all round the stem at an angle of 120° with each other, weak, not folded.	Leaves in two opposite ranks, stiff, resilient, ± folded.
Flowers large, opening wide.	Smaller, remaining bell-shaped.
Sepals long, spreading.	Shorter, not spreading.
Petals pale rose or red-purple.	Green.
Epichile rose or dull red-purple.	White, tinged green.
Rostellum conspicuous in all flowers, large, pollinia at once affixed to anything touching it.	Usually absent, if present, weak and ineffective.
Never self-fertilised.	Nearly always self-fertilised.
Pollen never coming over the edge on to the stigma.	Pollen always coming over.
Testa of seed 8–10 times as long as broad, narrow. Mesh compressed laterally.	4–5 times as long as broad. Mesh open. Easily distinguishable from *latifolia*.

Wheldon and Travis' diagnosis says: "Rhizome slender, far creeping". I searched carefully for this but could never find it. I once thought I had done so, but the supposed slender creeping rhizome turned out to be an underground shoot of grass which had pierced right through the middle of the *Epipactis* stem! Later Mr Travis wrote to me that he was now convinced that the plant had no creeping rhizome.

E. dunensis differs from *E. leptochila* as follows:

E. leptochila	E. dunensis
Root-system strongly developed.	Very poor.
Rhizome large, knotted, descending.	A small irregular mass, very deeply buried at the base of the stem.
Roots very numerous, rather thick, fleshy.	Few, slender, wiry, hard.
Flowers larger, wide open; sepals and petals long, tapering gradually to an acute point.	Sepals and petals short, broad, narrowing suddenly to an obtuse point. Flowers not opening wide.
Epichile long, narrow, pointing straight forward.	Short, as broad as long, with recurved tip.
No pollen-globules fall into the flower.	Globules of pollen fall into the flower.
Seed-testa long and narrow, 8–10 times as long as broad; cells narrow, compressed sideways, cell-walls thick.	Testa broader, only half as long, cells not compressed, cell-walls very thin.

E. dunensis resembles *E. leptochila* in the upper parts of the pollinia coming over the upper edge of the stigma on to its viscous surface, and was placed under it as a variety by Drs T. and T. A. Stephenson (*J.B.* p. 205 (1921)), before it was raised to specific rank.

Fertilisation. Mostly, if not entirely, self-fertilised. The pollinia are at first friable, and little globules of pollen fall on the sepals, petals, lip, and no doubt also on the stigma, even in bud, effecting self-pollination. The main method, however, is as follows. The pollinia emerge from the anther and lie in the clinandrium or shallow cup at the apex of the column beneath the anther. Here they swell and disintegrate, and appear to become matted together by pollen-tubes, so that they cease to be friable. The upper parts of the pollinia come over the sloping edge of the stigma on either side, probably pushed over by the expansion of the pollen, and thus reach its frontal viscid surface, resulting in fertilisation in the ordinary way. Little masses of pollen become rooted to the upper part of the stigma by pollen-tubes, for on attempting to remove them with a needle, it is found that they have to be moved backwards and forwards several times before they become detached. As a rule there is no rostellum, but occasionally it is developed, and in one case, on touching the rostellum with a pencil, the pollinia came away, spreading themselves like a little mat over the point of the pencil. There is therefore a possibility of cross-fertilisation occasionally through attachment of the pollinia to an insect visiting a flower for the nectar contained in the hypochile. This infrequent development of a rostellum is a very curious fact. Is it incipient or disappearing—an early stage of development, or the reversion of a previously insect-fertilised plant to self-fertilisation? Extended observation alone can show. It is possible that *E. dunensis* was a wholly self-fertilising form which became crossed with *E. latifolia* at some time in the past, and that the rare occurrence of a rostellum is a relic of hybridity.

6. Epipactis rubiginosa Crantz

Pl. 11. *E. atrorubens* Schultes
Dark red Helleborine

Rhizome thick, hard, dark brown, 1- rarely 2-stemmed. **Roots** many, long, slender, sinuous, acute, pale brown, sometimes forming a swelling from which fresh rootlets spring, and no doubt also a fresh plant; younger roots have dense short hairs. **Stem** (in Britain) short, stumpy (often tall abroad), stiff, erect, solid, flexuous, violet-red below, clothed with rather dense short whitish hairs, especially above, and with 2–3 loose-ribbed somewhat funnel-shaped basal sheaths, the uppermost often with green tip. **Leaves** 5–7 in two opposite ranks, each clasping the base of the next, the lowest short, broad, often concave above, red beneath, the rest ovate-oblong to ovate-lanceolate, keeled, folded, rather short, but longer than the short internodes, stiff, sharply pointed, many-nerved; the uppermost bract-like, narrow. **Flowers** in a stiff spike-like raceme, with (in Britain) 8–18 rather small wine-red, rarely dull rose or greenish, at first bell-shaped, later wider open, flowers, with a conspicuous yellow anther, and said to smell of vanilla, but the scent is often difficult to detect. **Bracts** small, lanceolate, acute, 3–7-nerved, short as compared with those of *E. latifolia*, the lower exceeding the ovary or even the flowers, often reddish at the base. **Ovary** short ($\pm$ 6 mm.), pear-shaped, 6-ridged, rough with short hairs, shortly stalked, olive-green often tinged with red. **Sepals** ovate, concave, hooded, keeled, dark wine-red (rarely dull rose or greenish), inside greenish with red veins, the upper shorter, arching over the column. **Petals** broadly ovate, slightly shorter and more obtuse, keeled, minutely and irregularly toothed, 3–5-nerved, of similar colour. **Lip** shorter than sepals, hypochile cup-shaped, projecting slightly forwards below, green, its red edges folded down in front leaving a triangular entrance to the cup, which is spotted inside with violet-red or brown, and glistening with nectar; epichile transversely oval, brighter and often darker in colour, minutely toothed with a small acute reflexed tip, its basal bosses forming a raised triangular central area often brighter and darker in colour than the lip, strongly wrinkled, sometimes almost tubercled or with tooth-like triangular folds ("carina plicato-crenata" of *E. media* Fries). **Column** very short

PLATE II

Epipactis rubiginosa Crantz.

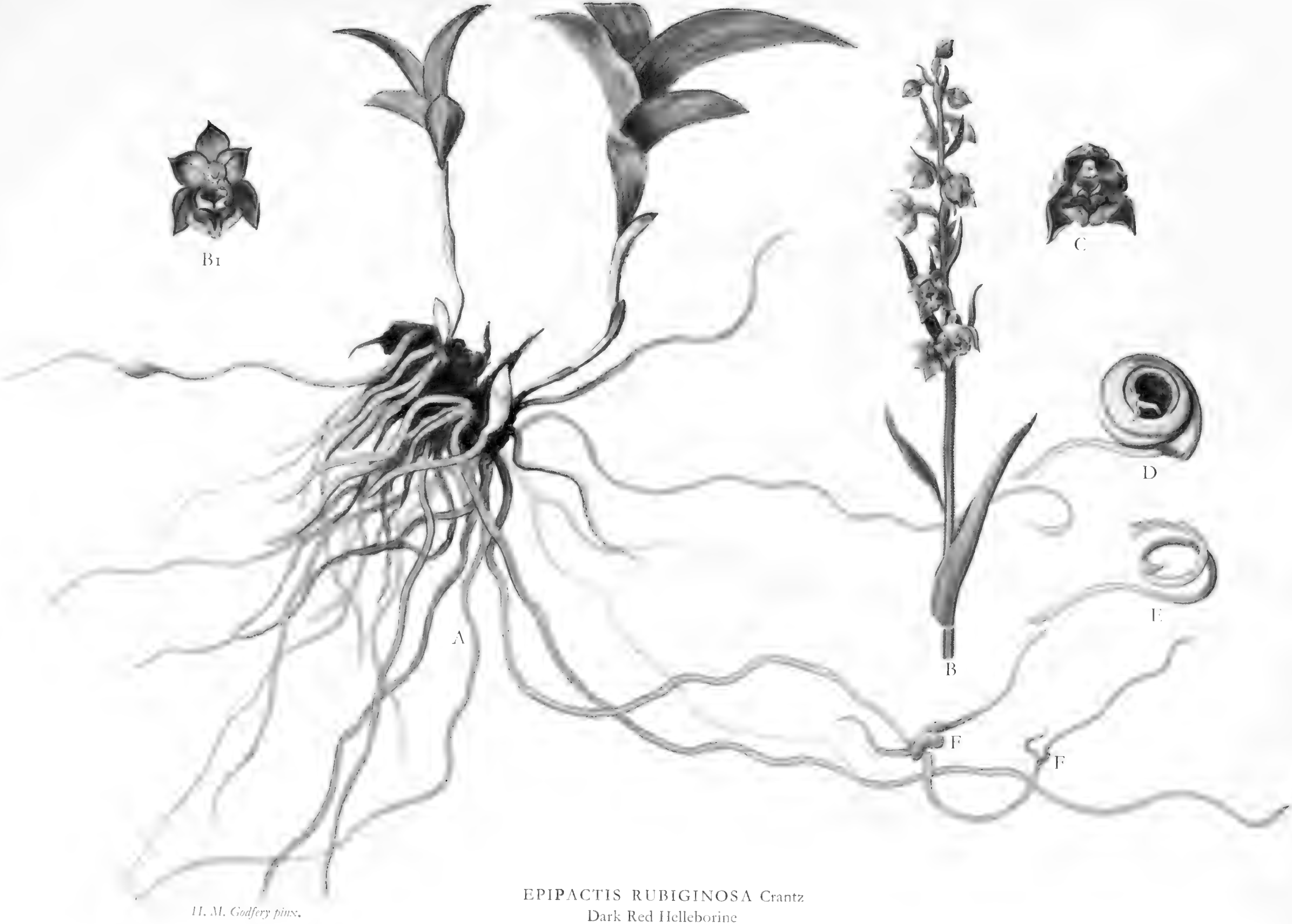
A. Non-flowering plant. North Wales, August 17th, 1917.

B, B 1. Spike and enlarged flower. N. Wales, July 7th, 1919.

C. Enlarged flower from Ballyvaughan, Ireland, July 25th, 1919.

D, E. Root emerging from a buried snail-shell as a young shoot. Brides-les-Bains, France, July, 1926.

F, F. Thickening of root probably giving rise to a new shoot, and forming a new rhizome.



EPIPACTIS RUBIGINOSA Crantz
Dark Red Helleborine

(about 2 mm.), white, convex behind, green and flat in front below stigma, with a shallow cup (clinandrium) at the apex below the anther, its low walls ending in a white translucent staminode on each side. **Stigma** transversely oblong with a tooth at each upper corner, and a small projection in the centre on which the whitish oval rostellum rests. **Anther** yellow, hood-like, obtuse, hinged at the back, minutely papillose outside. **Pollinia** creamy white, maggot-shaped, without caudicles (stalks), deposited in the clinandrium with their thin ends attached to the rostellum. **Capsule** small, hanging, ovoid, downy. Testa of seed short, broad, transparent, broad-meshed (only half as long as in *E. latifolia*), embryo broadly oval, not lemon-shaped, yellow.

It took over an hour to dig up the root-system of the plant shown in Pl. 11, which had over 40 roots. It appeared to grow in the solid rock, but this was really a mosaic of closely fitting angular fragments, like a Chinese puzzle, the very narrow crevices between them full of soil. The roots were long, some over 20 cm., with flat spear-shaped tips adherent to the rock. Two or three of the roots had a rounded swelling towards the end from which two or three roots grew, one growing upwards, probably to form a new bud. Figs. D, E show a curious discovery made at Brides-les-Bains, Savoie, in July, 1926, when digging up a plant of *E. rubiginosa.* One of the roots had entered an old snail-shell underground, full of earth, had made two turns inside, and come out through a hole in the apex of the shell in the form of a young blanched shoot with incipient leaves. The number and length of the roots in the British plant figured were very striking. The stem became very slender below, only 1 mm. thick at the junction with the rhizome, as against 4 mm. just below the lowest leaf.

In Britain *E. rubiginosa* is easily distinguished from *E. latifolia* by its dwarf stiff habit (it is often much taller abroad), the short stiff folded leaves with a sharp tip, growing in two opposite ranks, the short stiff few-flowered spike, the shorter and narrower bracts, the short broad dark red sepals and petals, the short hairy ovary, and the tubercled sometimes almost toothed bosses at the base of the forepart of the lip. The variety *purpurea* of *E. latifolia* is sometimes mistaken for it, but the colour is not the same, and the other characters of *E. rubiginosa* are absent.

HABITAT. Bare limestone rocks in full sunlight, often in company with *Helianthemum canum*, *Veronica spicata*, and other limestone plants. Rare and local in Britain and Ireland, where it is neither a dune nor a woodland plant. It is frequent on the Continent, especially in and on the borders of open woods, but it also grows on limestone rocks and slopes up to 2000 m. in the Tyrol. Although it occurs in such widely different localities it varies but little except in size. In mountain woods in Savoie at 1400 m. it is as tall as *E. latifolia* (40 cm.) and with leaves nearly as broad. In Britain it is a dwarf stumpy plant with small dull-coloured flowers. The woodland plant of Switzerland and Southern France is more luxuriant with more brilliantly coloured flowers. It has, though rarely, been found with yellowish green and greenish white flowers.[1] Webster says[2] that when transferred to a sheltered garden, its habit is not in the least changed, even after a number of years, and that it flowers in mid-July. The wild plant flowers in June and July.

DISTRIBUTION. Carnarvonshire! Yorks. (Settle, Grassington). Limestone pavement, Ben Suardal, Skye (Druce, *J.B.* p. 167 (1916)), Durness, Sutherland (*E.B.*), Burram and other hills, Co. Clare, Ireland (*E.B.*). Westmorland (Watson, *Top. Bot.*). Ballyvaughan (abundant), Cappanawalla mountain (abundant). Sparingly, rocky valley near Cong. Ascends to 1000 ft. in Burren (*Cyb. Hibern.*). Recorded for Little Doward Hill, Hereford, but this appears to have been *E. atroviridis* W. R. Linton. Scandinavia to Spain, Italy, the Balkans, Russia, Caucasus, N. Persia.

> EPIPACTIS HELLEBORINE α E. RUBIGINOSA Crantz, *Stirp. Austr.* VI, 467 (1769). SERAPIAS LATIFOLIA * ATRORUBENS Hoffmann (1804). EPIPACTIS ATROPURPUREA Raf. (1810). E. ATRORUBENS Schult. (1814). E. LATIFOLIA β RUBIGINOSA Gaud. (1829). E. MEDIA Fries (1839). E. OVALIS Bab. (1843). E. RUBIGINOSA "Gaud." Koch (1844). HELLEBORINE ATROPURPUREA Druce.

Babington identified what is now known as *E. leptochila* Godf. as "*E. media* Fries", and described the British form of *E. rubiginosa* as a new species (*E. ovalis* Bab.), apparently overlooking the fact that Fries himself cited *E. atrorubens* (*E. rubiginosa*) as synonymous with his *E. media*.

Fries gave three colour-forms of his *E. media*, (*a*) "floribus albis", (*b*) "floribus viridibus", (*c*) "floribus roseo-rubris". That he regarded (*c*) as the type is clear from his lengthy comparison of *E. media* with *E. latifolia*. He states that in *E. media* the basal leafless sheaths are open and funnel-shaped, the bracts shorter than the flowers, the flowers smaller (than in *E. latifolia*), the lip-bosses plicate-crenate, the ovary hairy—all distinguishing characteristics of *E. rubiginosa*. As the latter sometimes occurs with greenish flowers (I have once seen it so in Britain), these would naturally form his variety (*b*) with which *Serapias viridiflora* Rchb. was synonymous, *according to Koch*. Fries, however, remarked that it was doubtful to which (i.e. *E. latifolia* or *E. media*) *S. viridiflora* most probably belonged, and it is now regarded as a form of *E. latifolia*.

Crantz was the first to differentiate *E. rubiginosa* from the two allied species, and the fact that he named it *E. Helleborine* α *E. rubiginosa* shows that he did not regard it as a variety (in which case he would have written *E. Helleborine* α *rubiginosa*), but as a species. It seems contrary to the spirit of the Vienna rules to ignore the priority of the name given to it by its first discoverer, on the ground that it was only that of a variety, especially when he apparently leaned to the view that it was a species, but might alternatively be regarded as a variety.

FERTILISATION. *E. rubiginosa*, like *E. latifolia*, is entirely dependent on insects for

[1] A. and G. *Syn.* III, 867.

[2] *Brit. Orchids*, p. 23 (1898).

H. M. Godfery pinx.

EPIPACTIS LATIFOLIA × RUBIGINOSA

E. Schmalhausenii Richt.

PLATE 12

Epipactis latifolia × **rubiginosa**, × **E. Schmalhausenii** Richter.
Deganwy, North Wales, July 18th, 1911.

pollination. If not visited by them, no seed-capsules are produced. Self-fertilisation does not occur. The brighter colour of the flowers and their scent attract insects more readily than the other species of *Epipactis*, and result in the visits of a larger variety of species. At Sils Maria, in the Engadine, at 6000 ft. elevation, in a very open larch-wood, on August 7th and 8th, 1924, I caught no less than five bees and a wasp visiting the flowers, and failed to catch two other bees and a wasp. These were identified by M. Lucien Berland, of the Paris Museum, as *Bombus mastrucatus* Zerst., *B. pyrenæus* J.P. ♂, *B. pratorum* S. ♂, *B. jonellus* K., *B. hypnorum* L. ☿, and *Vespa saxonica*. It is noteworthy that all the bees were *Bombi*, which seem never to be attracted by *E. latifolia*, the latter being exclusively and freely visited by wasps, whereas although wasps visit *E. rubiginosa*, they do not appear to do it so frequently as *Bombi*. It would therefore seem that the honey produced by *E. rubiginosa* is not the same as that of *E. latifolia*.

EPIPACTIS LATIFOLIA × E. RUBIGINOSA

× Epipactis Schmalhausenii Richter

Pl. 12

Pl. 12 shows a plant growing wild in a shrubbery near Deganwy, N. Wales, July 18th, 1911. Its habit and general appearance were those of *E. latifolia*, of which it had the ovate-lanceolate tapering lower, and long narrow upper leaves, the long bracts, longer ovaries and longer many-flowered spike. It resembled *Epipactis rubiginosa* by its horizontal rhizome with many slender roots, its not very tall stem, with an open funnel-shaped sheath at the base, its short sepals and petals, transversely oval hypochile, and short heart-shaped epichile, broader than long, with two dark red bosses at its base. The colour of the two petals and upper sepal, as well as of the lip, was that of *E. rubiginosa*, but the pendent flowers and long tapering down-trending bracts resembled those of *E. latifolia*. Speaking generally it had the stem, leaves and bracts of the latter, with the small red flowers of *E. rubiginosa*. Time of flowering nearer that of *E. rubiginosa* (June to July) than that of *E. latifolia* (August to September). One specimen was found at Tongue, W. Sutherland, in 1900 on limestone by the Rev. E. S. Marshall.[1] Originally recorded from Russia in 1874 by Schmalhausen; Grassington, Yorks. (*J.B.* p. 11, Pl. 555, fig. 5 (1920)).

× Epipactis Schmalhausenii Richter, *Plant. Eur.* 1, 284 (1890).

[1] *J.B.* p. 298 (1907); *O.R.* p. 142 (1919).

Sub-tribe *PHYSURINÆ*

Distinguished from the Spiranthinæ by the pollinia built up of packets of pollen. Mostly found in tropical Asia, a few in Africa and America. Only one European species.

Genus IV GOODYERA R. Br.

Column short, horizontal. **Stigma** facing the lip, rostellum apical supported between curved horns. **Anther** leaning forward over rostellum, to which the stalkless pollinia become attached; pollinia built up of oval packets of pollen-tetrads.

Small herbs with creeping rhizome, ovate stalked leaves and small flowers with bag-like hypochile and recurved epichile, in a spike-like raceme.

Goodyera resembles *Epipactis* in the shape of the lip, but its plan of construction is essentially that of *Spiranthes*, which it closely resembles as far as the inflorescence is concerned. It shows a remarkable evolutionary trend in the direction of the Ophrydeæ by the development of pollinia built up of packets of pollen tied together by elastic threads, which coalesce at the apex of the pollinium into a flattened truncate ribbon adhering to the back of the rostellum, but not forming a caudicle, except in the foreign *G. discolor*, which has long apical caudicles.[1] The attachment of the anther to a filament by its back resembles that of *Cephalanthera*.

GOODYERA R. Br., in Ait. *Hort. Kew.* ed. 2, v, 197 (1813). SATYRIUM L. (1753). EPIPACTIS Boehm. (1760).

1. GOODYERA REPENS R. Br.

Pl. 13; Pl. H, fig. 2 (p. 219). *Creeping Lady's Tresses*
Creeping Goodyera

Rhizome creeping, short-jointed, with white slender runners extending through the layer of pine-needles without entering the soil, often emitting other runners, and ending in a rosette of leaves so that a plant may give rise to a number of others all connected together. **Roots** few, short, thickly clothed with hairs, brown, descending. Flowering stem 10–25 cm. tall, erect, stiff, cylindrical, ridged above (through decurrence of the nerves of the bracts), pale green, glandular-hairy, with a whitish veined leafless sheath at the base, sometimes with a leaf-like tip. Basal **leaves** almost in a rosette, ovate or ovate-lanceolate, obtuse or acute, firm, rigid, keeled, narrowing into a winged stalk sheathing the stem, dark green often marbled with lighter green, 5-nerved, conspicuously net-veined, persisting through the winter; upper leaves

[1] Darwin, *Fert. Orch.* ed. 2, p. 105.

H. M. Godfery pinx.

GOODYERA REPENS R. Br.
Creeping Lady's Tresses

PLATE 13

Goodyera repens R. Br. Bex, Switzerland, July 7th, 1912.

1. Enlarged flower, front view.
2. Side view, right-hand sepal removed.
3. Pollinia attached to viscid gland ($\times$ 10).
4. Stigma turning brown after pollination, showing horns supporting viscidium ($\times$ 6).
5. Tuber with young shoot, formed on rhizome.

bract-like, tapering, rather acute, 3-nerved, adpressed to stem. **Raceme** spike-like, one-sided, narrow, rather dense, straight or slightly twisted, up to 10 cm. long. **Flowers** small, white, sweet-scented, with numerous gland-tipped hairs, rather tubular, nearly at right angles with the ovary. **Bracts** linear-lanceolate, tapering, acute, 10–15 mm. long, 1-nerved, ciliate, sometimes glandular-hairy, pale green, whitish and glossy within, embracing and slightly exceeding the ovary. **Ovary** shortly stalked or sessile, short ($\pm$ 9 mm.), top-shaped, slightly bent forward at the apex, compressed laterally, later somewhat triangular, pale green, glandular-hairy, with three cord-like ridges, slightly twisted if sessile, if not the stalk is twisted; capsule distinctly stalked, pear-shaped. **Sepals** ovate, obtuse, concave, short, white or tinged green, glandular-hairy outside, the lateral slightly spreading, the upper rather longer, horizontal, 1–2-nerved. **Petals** lanceolate, obtuse, very narrow, 1-nerved, glabrous, lying close to the upper sepal and about the same length. **Lip** shorter than sepals, undivided, the basal half (hypochile) forming a deep rounded bag-shaped pouch, the forward half (epichile) narrow, tongue-shaped, obtuse, slightly, sometimes considerably shorter than the basal pouch, furrowed and curved sharply down in front, almost parallel with the hypochile. **Column** short, broad, projecting forwards with a triangular nib-shaped filament at the back, to the summit of which the anther is fixed by its back. **Stigma** nearly circular, not fringed with hairs at the base, prolonged at the apex into a rostellum, consisting of two short acute curved horns enclosing and supporting the viscid gland, which is nearly circular but truncate at the apex. **Anther** stalked, brownish, hood-shaped, 3-toothed in front, resting on the upper surface of the rostellum. **Pollinia** two, short, yellow, ovoid, without caudicles, attached to the viscid gland.

Habitat. Mossy pine-woods, generally in mountain regions. Flowers July to August.

Distribution. Scotland from Berwick to Ayr, Ross,[1] and Moray Firth, Culbin Sands (abundant), Cumberland. It has been found in Norfolk, perhaps introduced when pine plantations were formed, as was the case in Germany, Denmark, Holland and Belgium.[2] Scandinavia to the Pyrenees and Balkans, Russia, Asia Minor, Afghanistan, Siberia, Japan, N. America. *G. repens* is the only European species.

G. repens is easily distinguished from *Spiranthes autumnalis*, the only British orchid for which it could possibly be mistaken, by its creeping rhizome and stolons, net-veined leaves, deep sack-shaped base of the lip, and its spout-like undivided apex. The specimen figured, found by us near Bex, Switzerland, had a small top-shaped bulb, from the top of which a new shoot was growing. I have never seen or heard of a similar occurrence in the Neottieæ. It appears to be quite free from variation, and to be a pure-blooded stable species, perhaps because, owing to its habitat in mossy mountain woods, there are no other orchids with which it can hybridise. No

[1] Pl. H 2 shows specimens from Ross.

[2] A. and G. *Syn.* III, 896.

hybrids have yet been recorded. In some Swiss specimens there was no leafless sheath beneath the lowest leaf, which sheathed the stem down to the first joint of the rhizome, the joints of which are slightly constricted, and separated by a brownish ring.

> GOODYERA REPENS R. Br., in Ait. *Hort. Kew.* ed. 2, v, 197 (1813). SATYRIUM REPENS L. (1753). EPIPACTIS REPENS Crantz (1769). EPIPACTIS (L.) Crantz, Oakes Ames (1908). Crantz's *Epipactis* was mainly *Cephalanthera* and *Epipactis* (as understood by all European authors). *Goodyera* was probably included on account of the shape of the lip resembling that of *Epipactis*.

FERTILISATION. Nectar is secreted in the cup at the base of the lip, and the sweet scent of the flowers calls attention to its presence. They are visited by *Bombus pratorum*, many of which were seen in the north of Scotland by Mr R. B. Thomson frequenting the flowers, and carrying pollinia.[1] Hermann Müller saw one visited in the Alps by *Bombus mastrucatus* ☿. Mr St Quintin of Scampston Hall, Yorks., tells me that many plants of *Goodyera* in a greenhouse in which the windows were open day and night, set full capsules in 1918. The flower is tubular, the sepal and petals forming the roof, and the lip the base of the tube. At first the passage between the lip and the column is contracted, with only a small opening between. This prevents a bee from reaching the nectar without touching the viscidium with its proboscis, owing to the narrowness of the channel. On contact the viscid disc at once adheres to the upper surface of the proboscis, and is withdrawn by it, together with the two attached pollinia, leaving behind the two curved horns which formerly supported it. The viscid matter soon sets hard, cementing the pollinia firmly to the proboscis. Later the front of the lip turns down, widening the passage into the flower, and enabling a proboscis bearing pollinia to enter easily and rub against the stigma, which is so sticky as to break the strong threads by which the packets of pollen are bound to the pollinia, and detach those which come in contact with it.

Sub-tribe *SPIRANTHINÆ*

Genus V SPIRANTHES Richard

Flowers small, tubular, sweet-scented, horizontal, in a twisted spike. **Column** horizontal. **Stigma** on its under-surface, circular, with a nib-shaped beak (rostellum) enclosing a linear viscid gland. **Anther** hinged, lying face downwards on the back of the rostellum; pollinia, each with two leaves of pollen, becoming attached to upper surface of viscid gland.

Small herbaceous plants with 2–6 (rarely more) fleshy cylindrical or carrot-shaped

[1] Darwin, *Fert. Orch.* ed. 2, p. 105.

roots, ovate or linear leaves, and spirally arranged flowers, with spreading side-sepals, connivent upper sepal and petals, trough-like lip with expanded frilled reflexed tip, and two nectar-secreting globular nipples at the base.

The genus contains about 80 species, chiefly inhabiting the northern temperate regions, but extending into tropical Asia, and in America as far south as Chile. Sixteen species occur in the United States and Canada, and one in Australia. This extraordinarily wide distribution is a proof of the very ancient character of the genus. *S. Romanzoffiana*, which has its home in N. America, is found in N. Ireland, but nowhere else in Europe.

KEY TO GENERA

A. Flowering stem without leaves (or with withered remains) at the *side* of the rosette of leaves (which will flower next year).

1. Leaves short, in a rosette, flowers small, arranged spirally in a single rank. **S. autumnalis**

B. Flowering stem surrounded by the more or less long erect leaves.

2. Flowers in a single rank. **S. æstivalis**
3. Flowers in three ranks. **S. Romanzoffiana**

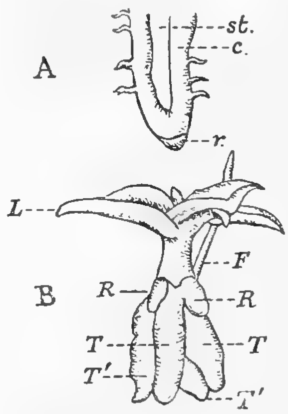
1. SPIRANTHES AUTUMNALIS Richard

Pl. 14 (p. 88). *Lady's Tresses*

Roots two, rarely 3–5, carrot-shaped, thick, tapering to an obtuse point, hard, smooth, pale brown, with short transparent hairs, monostelic (Text-fig. 9). **Stem** 7–15 cm. (up to 32 cm. abroad), with or without remains of last year's leaves at base, round, solid, with transparent glandular hairs extending to the leaf-sheaths, pale green, with several bract-like sheathing lanceolate close-fitting upper acuminate leaves with membranous edges and 3–5 nerves. **Leaves** about four or five, in a rosette on one side of the flowering stem (not surrounding it) which lasts through the winter and flowers the next year, short, ovate, pointed, with a broad sheathing stalk and thick keel, acute, mucronate, stiff, bluish green, glabrous, transparent-edged, with 5–7 rarely 9 nerves. **Spike** 3–12 cm. long, 7–20-flowered, slender, flowers very small, white, sweet-scented by day, in a single rank, twisting spirally round the axis,[1] more rarely all turned to one side. **Bracts** lanceolate, tapering, sheathing the ovary, and about the same length, incurved, white-edged, 3-nerved. **Ovary** short, slug-shaped, bent at the apex (making the flower stand out at right angles), green, as a rule not twisted, with three rounded ridges, gland-tipped hairs, and a stalk adherent

[1] It is really the axis which twists.

to the stem (forming a thick ridge), so that the ovary is sessile (except sometimes in two or three of the lowest flowers) and applied to the stem by its side. **Sepals** oblong, broadest at base, slightly tapering, obtuse, with a faint green nerve, ciliate or minutely toothed, slightly glandular-hairy outside, white and crystalline under a lens, the lateral spreading, the upper inclined downwards over the lip. **Petals** strap-shaped, obtuse, 1-nerved, adhering to the slightly longer upper sepal, together forming an upper lip to the flower, with recurved tips. **Labellum** oblong, trough-like, enlarged, rounded and turned down at the tip, forming a trumpet-like tube with the united upper sepal and petals, light green with a broad white crystalline jagged edge, closely embracing the column at the base, where there are two white glistening rounded honey-secreting glands, each with a ring of papillæ round the base, and a shallow receptacle below. **Column** obconical, horizontal, green, tapering to an acute point (rostellum). **Stigma** on under-surface of column, slanting gently upwards, shield-shaped, rounded and fringed with white hairs below, with a short point at each upper corner, and in the middle of the upper edge the rostellum, a brown or greyish linear viscid gland supported between two rather long very narrow teeth, left behind like the prongs of a fork when the viscidium is removed, and soon withering. A membrane extends backwards from the edge of the stigma over the back of the anther, forming a clinandrium or shelter for the pollinia. **Anther** sessile, resting face downwards on upper side of column, ovate-acute, already brown and shrunken when the flower opens, with a dark line down the centre. In bud the anther is green and covers the pollinia, which are cream-coloured, long, narrow, tapering from a rounded base to an acute apex projecting well beyond the shrunken anther, and attached to the back of the viscidium. According to Darwin each consists of two leaves of pollen, free at the ends but united in the middle by elastic threads (*Fert. Orch.* p. 109). Each leaf consists of a double layer of pollen-grains joined together in fours, and is very brittle, large fragments breaking off and adhering to the stigma on contact. Usually there are only two roots, whose thickness suggests analogy with the tubers of *Orchis*, but the development of two young roots (later tuberised) at the base of the new bud in *S. Romanzoffiana*, in exactly the same way as occurs in *Epipactis*, shows a nearer analogy with the roots of the latter genus. A specimen of *S. autumnalis* dug up near Nice had three large plump roots, and two very much shrunken old ones. Dr Keller informs me that the roots of some large



Text-fig. 9. *Spiranthes autumnalis*. A. Section of young root. *st*. Stele. *c*. Cortex. *r*. Root-cap. B. Plant, early November, S. France. *L*. Rosette of leaves to flower next year. *F*. This year's withered flowering stem. *R*. Young root. *T*. This year's root. *T'*. Last year's root. From *Iconographie des Orchidées d'Europe* by permission of Mlle A. Camus.

PLATE 14

Spiranthes autumnalis Rich.

A. Plant from Deganwy, N. Wales, September 6th, 1908.

B, B. Plant from Nice, France, October 12th, 1929.

1, 2. Forcibly opened flowers from A.

3. Bract and column showing ends of membranous clinandrium simulating long prongs to fork of rostellum.

4. Stigma fringed with hairs below, with white adherent pollen, showing fork of rostellum after removal of viscidium with pollinia.

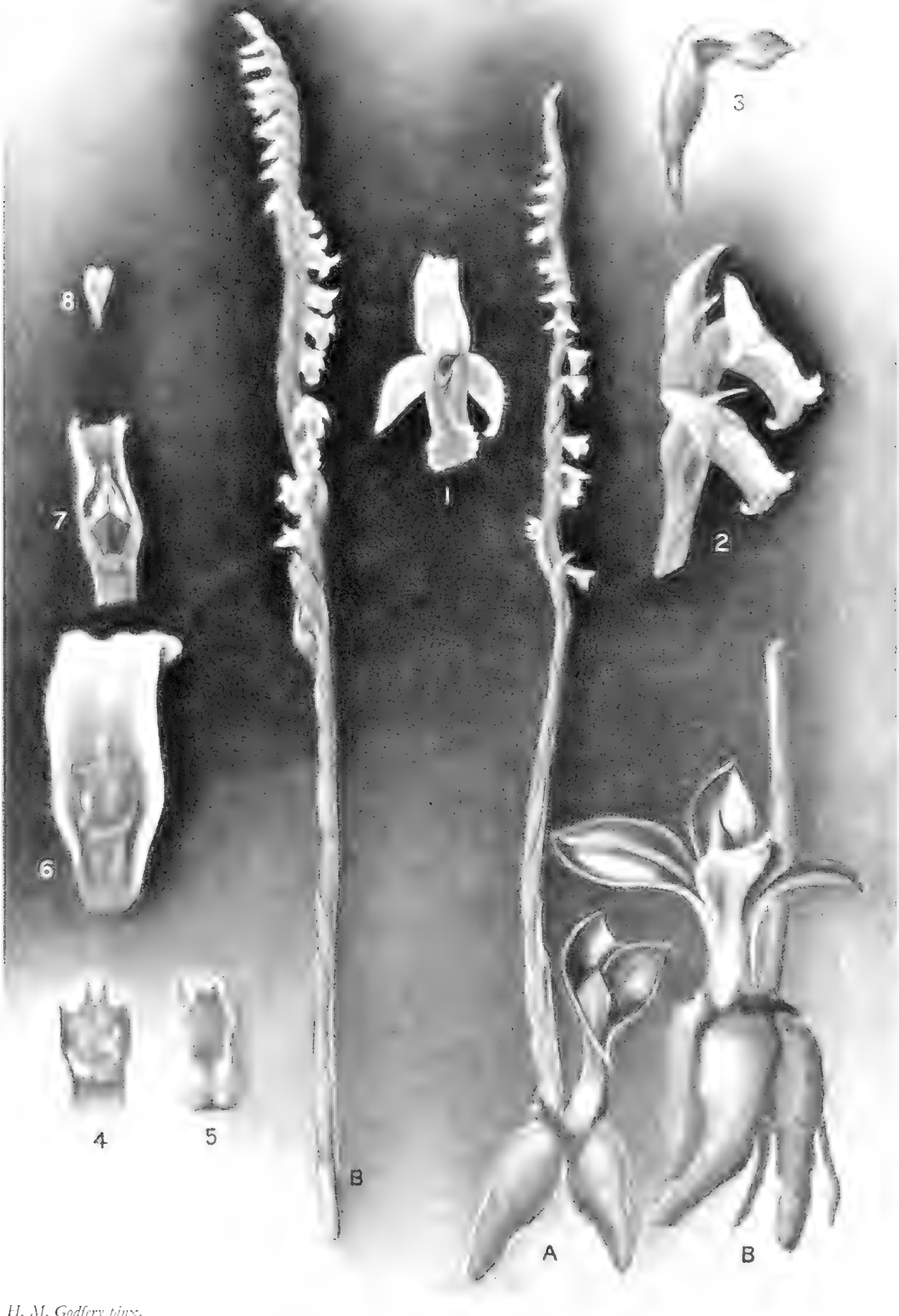
5. Nectar-secreting glands at base of lip seen from above.

6. Upper sepal, two petals, stigma and rostellum *in situ*.

7. Column from above with viscidium, pollinia (white) and brown shrunken anther.

8. Pollinia attached to viscidium.

Figs. 1–8 enlarged.



H. M. Godfery pinx.

SPIRANTHES AUTUMNALIS Rich.
Autumn Lady's Tresses

specimens from the Caucasus were like those of *Neottia nidus-avis*. Text-fig. 9 shows the present and last year's roots, and two very young, for next year. The flower-stem does not clearly arise from one root and the new rosette of leaves from another, as in *Orchis*, but both seem to arise from a sort of crown where the roots unite at their bases. *S. autumnalis* is unique in that the new rosette of leaves (which will persist through the winter and flower next year) is already well developed at the time of flowering. Last year's leaves, from the centre of which the present year's flower-spike arose, have then entirely disappeared, or left only withered remains. The gland-tipped hairs clothing the stem, leaf-sheaths, bracts, neck of ovary and outside of the flowers are for the exclusion of small insects whose visits would be of no service to the plant. The fringe of hairs round the lower edge of the stigma serves the same purpose, closing the shallow passage leading to the nectary, but offering no obstacle to the proboscis of bees, etc. There is no similar fringe of hairs in *S. æstivalis* or *S. Romanzoffiana*, perhaps because they grow in marshy localities, where ground insects are less frequent. The prongs of the green fork which support the viscidium and are left behind after its withdrawal often seem much longer than they really are owing to the membranous sides of the clinandrium being also left behind and appearing to form a continuation of the fork on each side. The fork is also shorter in the upper flowers than in the lower, sometimes nearly as short as in *S. æstivalis*. The long horns of the latter, as figured by Schulze and Hegi, look as if they had been drawn from *S. autumnalis*, as in reality they are very short. This is the last of our native orchids to flower, *S. æstivalis* and *S. Romanzoffiana* being then quite over. It is at once known by the spiral spike of very small white sweet-scented flowers in a single rank. It is easily distinguished from *Goodyera repens*, which somewhat resembles it, by the *Epipactis*-like lip of the latter, with its deep basal pouch and long spout-like apical half, as well as by their different habitats and time of flowering.

Habitat. Hilly pastures, open downs, moist meadows, usually on chalk or limestone, grassy or sandy ground near the sea, sometimes in sand. On the French Riviera it occurs in open cork woods on schist, as at Hyères, or in bushy waste calcareous land, as at Nice. Flowers August and September; in the south of France, where the time of flowering depends on the date of the earliest rains, in September and October.

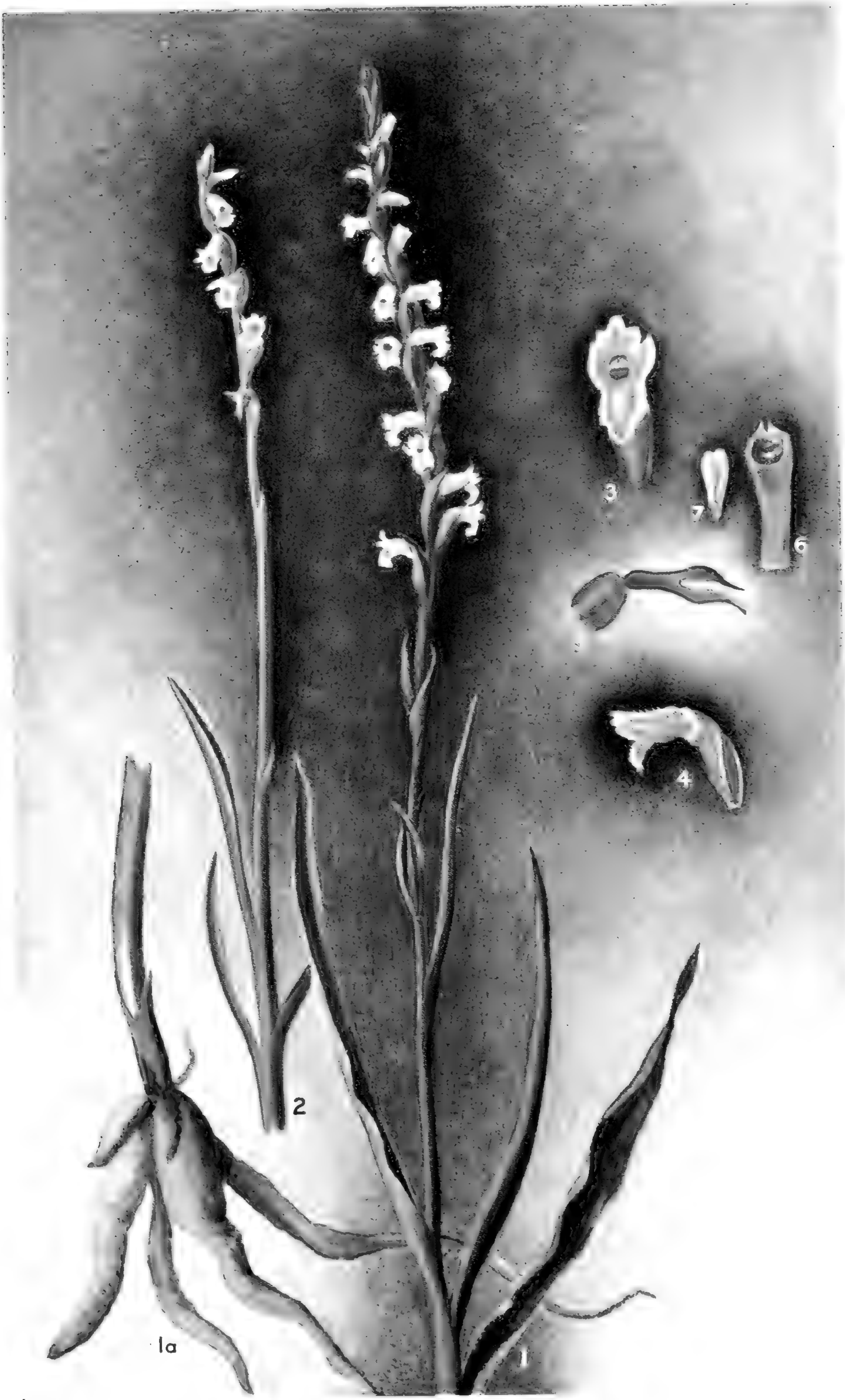
Distribution. England, Wales and Ireland Records north of the Humber perhaps doubtful. In Ireland found in eight of the twelve botanical districts (*Cybele Hibernica*, p. 338), Channel Islands (*B.E.C.* p. 130 (1917)). Europe from Denmark and Central Russia southwards, Transcaucasia, Asia Minor, N. Africa.

Spiranthes autumnalis Rich., *Mém. Mus. Paris*, iv, 59 (1818). Ophrys spiralis α L., *Sp. pl.* ed. 1, p. 945 (1753). O. autumnalis Balb. (1801). Spiranthes spiralis Koch (1839).

Spiralis, as used by Linnæus, was not the name of a species, but of a genus mistaken for a species, and was not intended to apply solely to *S. autumnalis*. To replace the latter by *S. spiralis* Koch is to give priority to a name of 1839 over one of 1818.

Fertilisation. Nectar has already collected in the hollowed base of the lip when the flower opens. This attracts humble-bees, of which Darwin saw two species visit the flowers. In one case the pollinia were attached to the upper surface of the proboscis, as well as three viscid discs without pollinia, so that the bee had removed the pollinia from four flowers and distributed all the pollen from three of them on the stigmas of others. I saw the moth *Plusia gamma* visit some flowers, but without withdrawing the pollinia. When the flower first opens, the rostellum lies so near the lip that the space between them will only admit a fine bristle, so that a bee's proboscis cannot reach the nectar without touching the viscidium, which at once adheres, becoming well glued to it in four or five seconds, the attachment being wonderfully strong when the cement sets hard, which it does in about a minute. This early stage of the flower is the most favourable for the removal of the pollinia. In a day or two the opening becomes wider, the lip turning more downwards, and, according to Prof. Asa Gray, the column moving back from the lip. The passage is now large enough for a proboscis bearing pollinia to enter. The pollen-leaves are very brittle, and large pieces easily break off and adhere to the sticky stigma. Thus in a newly expanded flower the pollinia can readily be removed, but pollen cannot be placed on the stigma, which moreover is not so viscid as it is later. The anther-cells are pressed against the back of the rostellum and open in bud, so that the pollinia come in contact with the viscidium, to which they become firmly fixed by their projecting threads. Later the anther-cells shrivel up, leaving the pollinia naked and free, ready for removal. The narrow boat-shaped viscidium, filled with a milky extremely adhesive fluid, originally forms an integral part of the rostellum. The groove beneath the latter is sensitive, and if touched by a bristle or by the proboscis of an insect, instantly splits along its whole length, the fissure running all round the edges of the viscidium, setting it free for removal. This does not occur spontaneously, and if insects are excluded, fails to take place. The flowers are freely visited soon after expansion. Darwin found that six out of seven open flowers on one spike, and all the eight expanded ones on another had had the pollinia removed.[1] The long narrow viscidium is intended to adhere longitudinally to the upper surface of a flat proboscis, as in humble-bees, and is in contrast with the strap-shaped disc of *Anacamptis pyramidalis*, which curls round and clasps the cylindrical proboscis of Lepidoptera.

[1] Darwin, *Fert. Orch.* ed. 2, p. 111.



H. M. Godfery pinx.

SPIRANTHES ÆSTIVALIS Rich.
Summer Lady's Tresses

PLATE 15

Spiranthes æstivalis Rich.

1, 1*a*. Plant from St Martin Vésubie, above Nice, July 22nd, 1914.

2. From near Geneva, July, 1929.

3, 4. Enlarged flowers of latter.

5. Column, side view.

6. Front view, after removal of viscidium.

7. Pollinia attached to viscidium.

Figs. 5–7 much enlarged.

2. Spiranthes æstivalis Rich.

Pl. 15; Pl. E, fig. 6 (p. 108). *Summer Lady's Tresses*

Tubers 2–6, thick at base, tapering downwards. **Roots** few, short. **Stem** 10–20 cm. or more, erect, glandular-hairy above with remains of withered leaves at base. **Leaves** erect, short (5–8 cm.), narrow (5–9 mm.), the lower sheathing the base of the stem, linear-obtuse, slightly trough-like, glabrous, bright green, glossy on both sides, with one or more nerves on each side of keel and numerous cross-veins; the upper 1–2 distant, very short, bract-like, tapering, adpressed. **Spike** 6–18-flowered, slightly twisted, glandular-hairy. **Flowers** small, tubular, pure white, slightly scented at night. **Bracts** lanceolate, tapering, 3–5-nerved, clasping and exceeding the ovary. **Ovary** short (± 9 mm.), sessile, 6-ridged, slightly twisted, usually glandular-hairy. Ripe capsule oblong. **Sepals** forming a tube with the lip, linear obtuse, white with a greenish keel, slightly glandular-hairy outside, the lateral often curving outwards. **Petals** shorter, linear obtuse, somewhat spatulate, 1-nerved. **Lip** oblong, trough-like, exceeding sepals, expanded turned down and irregularly toothed at the tip, forming a slight sack or receptacle with the ovary at the base, pure white, with two nectar-secreting nipples. **Column** horizontal, green, slender, acute, shorter than sepals. **Stigma** at apex of its lower surface shield-shaped, green, rounded below (without the fringe of hairs of *S. autumnalis*), truncate above with two short central acute teeth supporting the short brown linear viscidium, and left behind when it is removed, and a pale transparent line down the centre. **Anther** at apex of upper surface of column, nib-shaped, brown, acute, with a short thick curved filament or stalk attached to the grooved middle of its back. A very delicate whitish transparent membrane forms a tooth lying flat on the anther on each side of this filament, and then runs along the edge of the column to the corner of the stigma, forming a clinandrium for the protection of the pollinia, and often ending in a small tooth on each side. This tooth is represented in some works by a little circle suggestive of a staminode, but no staminode exists. This membrane appears to enclose the under-surface of the column up to the edges of the stigma like a transparent skin. **Pollinia** rather long, yellowish white or sulphur-yellow, parallel with and attached to the upper surface of the viscidium.

Habitat. Marshy ground amongst rushes, sedges, and other water-loving plants. Flowers July to August.

Distribution. Now only found in the New Forest, Hants., and verging on extinction. Not seen in Wyre Forest, Worcestershire, since it was gathered at the margin of the great bog in August, 1854, though this is a small area well known to botanists. It also grows in Jersey, but is very local and rare. Only eight specimens were seen by me in August, 1931, in one of the New Forest stations. Central and Southern Europe, from Belgium and Germany southwards, Corsica, Sardinia, Algeria and Asia Minor.

SPIRANTHES ÆSTIVALIS Rich., *Mém. Mus. Paris*, IV, 58 (1818). OPHRYS SPIRALIS γ L., *Sp. pl.* ed. 1, p. 946 (1753). O. ÆSTIVALIS Lam. (1797).

FERTILISATION. The floral mechanism is the same as in *S. autumnalis*, but the visiting insect is not yet known. The flowers are scentless by day, becoming slightly fragrant in the evening, from which it is probable that it is fertilised by moths or other nocturnal insects, probably the former, as linear viscid glands are specially adapted for adhesion to the proboscis of Lepidoptera.

NOTE. The prongs of the green fork left behind when the viscidium is removed, as figured by Max Schulze, and recently by Hegi, appear to be too long, these being in reality very short. Pl. E, fig. 6, shows the flowers enlarged (3/1).

3. SPIRANTHES ROMANZOFFIANA Chamisso

Pl. 16; Pl. D, figs. 1, 2 (p. 94); Pl. E, fig. 4 (p. 108). *Three-ranked Lady's Tresses Irish Lady's Tresses, Hooded Ladies' Tresses* (American name)

Roots 2–6, long, cylindrical, thick. **Stem** up to 20 cm. or more, erect, pale green, obscurely triangular and sparsely downy above. **Leaves** linear, nearly erect, long, narrow, tapering, acute, glabrous; uppermost bract-like, short, lanceolate, tapering to a fine point, 3-nerved, loosely sheathing the stem. **Spike** slightly twisted, dense, many-flowered. **Flowers** large for a *Spiranthes*, in three ranks curving spirally, white, scented like hawthorn. **Bracts** lanceolate concave, sheathing the ovary, gradually tapering, acute, 3-nerved (sometimes with branched intermediate nerves), the lower ($\pm$ 3 cm.) exceeding the flower, the upper the ovary, the uppermost forming a tuft in early flower. **Ovary** cylindrical ($\pm$ 1 cm.), very shortly stalked, not twisted, turned to one side, flat in front, convex behind, with three cord-like ridges, pale green, glandular-hairy, bent at the tip, so that the flower stands out nearly at right angles. **Sepals** and petals adherent, their tips free and turned up, side-sepals joined together beneath the lip, sheathing its base, lanceolate, acuminate, $\pm$ 12 mm. long, white, greenish at the base with three green nerves, glandular-hairy outside. **Petals** strap-shaped, linear obtuse, narrow ($\pm$ 2 mm.), 3-nerved, adherent to sepals. **Lip** tongue-shaped, trough-like at base (where there are two short nectariferous glands), curving downwards to the broader rounded frilled finely toothed apex, white with green nerves, giving it a greenish tinge, and with minute papillæ below. **Column**

PLATE 16

Spiranthes Romanzoffiana Chamisso.

1, 1, 1. Plant without roots, and two enlarged flowers from N. Ireland.

2, 2, 2, 2, 2. *Spiranthes cernua* from Hatley, Quebec, sent as a seedling by Mr Mousley.

3, 3. *Spiranthes Romanzoffiana*, also sent by him as a seedling. Both were grown on and flowered by Mr St Quintin at Scampston Hall, Malton, Yorks., as also 1 above.

H. M. Godfery phot.

SPIRANTHES ROMANZOFFIANA Chamisso
Irish Lady's Tresses

short (± 4 mm.), horizontal, ending in a sharp dark brown beak. **Stigma** crescent-shaped, glistening, slanting gently upwards, with a green nib-shaped rostellum ending in a linear viscid gland, supported by green tapering sides, left behind like the prongs of a fork, when the gland is removed. **Anther** cordate, brown, resting face downwards on the back of the rostellum. **Pollinia** wax-like, cream-coloured, split at the apex, without caudicles, lying horizontally on the upper surface of the viscid gland, and attached to it by their centres. Pl. D, fig. 2, shows the S. Irish form.

Pl. E, fig. 4, shows a N. Irish flower (enlarged 3/1) with the side-sepals spread out, and the flower opened so as to show the glistening stigma tapering above into two acute points which support the long linear very adhesive viscidium. When the latter is removed (together with the two pollinia attached to its back, concealed behind the stigma) the supports are left behind like a two-pronged fork.

Pl. D, fig. 1, the N. Irish form was evidently taken from a specimen in which the flowers, especially the lips, were partly withered, which makes them look shorter and more globular than when in perfect condition.

In 1926 Mr A. J. Wilmott, of the British Museum of Natural History, saw about 12 plants in Co. Cork and 6 in Co. Kerry and about 200 of the northern form in Co. Armagh.[1] He considered the two forms to be specifically distinct, renaming the northern one *Spiranthes stricta* Rydberg and retaining Smith's name *S. gemmipara* for the southern plant. The characters relied on to distinguish the latter as a separate species were: shorter stature, broader leaves, acute but not acuminate bracts, denser spike, smaller shorter fatter flowers of a purer white, and shorter and broader lip. Pl. D, fig. 2.

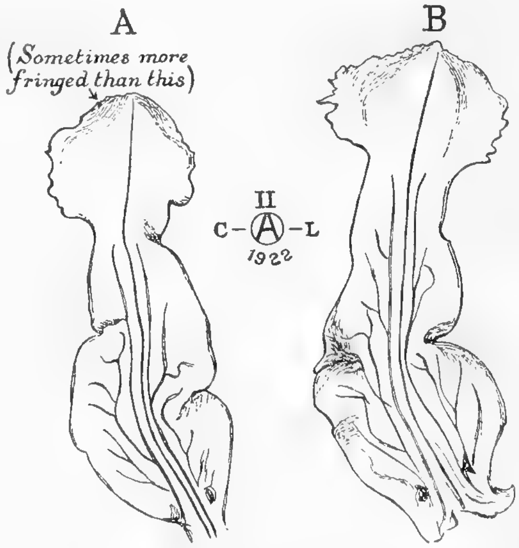
Prof. Oakes Ames, the well-known American orchidologist, to whom photographs of both forms were sent, wrote that, judging from the photographs, there did not appear to be any tangible consistent differences between them. Even if the differences were as striking as they were claimed to be, he did not consider them specific in value. He kindly sent me a camera lucida drawing (Text-fig. 9 A) of the lip of a N. Irish specimen and of a Newfoundland one selected at random, identical even to the veining.

Prof. Fernald of Harvard told me at the Fifth Botanical Congress at Cambridge, in 1930, with reference to Mr Wilmott's statement[2] that the N. American *S. Romanzoffiana* is not the same as Chamisso's Unalaskan plant, that Chamisso's material was very poor and dwarf, and forms no criterion by which to judge the Alaskan plant. He has compared plenty of material from Alaska with U.S.A. specimens, and could find no specific differences between them—they are in his opinion identical. He considers the Irish plant is *S. Romanzoffiana*, as does also Prof. Oakes Ames of Harvard University, and states that both the N. and the S. Irish forms are found in N. America, that they are there connected by many intermediate forms, and that the differences

[1] *J.B.* p. 145 (1927). [2] *Ibid.* p. 148.

between them count for nothing in America. Rydberg's name *Gyrostachys stricta* is not generally accepted in the U.S.A. He did not describe the plants or specify the differences between them, but merely said that the U.S.A. species was not the same as the Alaskan, and that he therefore named it *G. stricta*. Being unsupported by a diagnosis, this name does not appear to be valid (Art. 37, International Rules, 1905).[1]

Mr Mousley sent a few young seedlings of *Spiranthes Romanzoffiana* from Canada. The first to flower was painted, but on examination turned out to be *S. cernua*, which accounts for the presence of this American plant on Pl. 16. In the early stage at which it was collected it was probably impossible to distinguish between the two species.



Text-fig. 9 A. Camera lucida drawing from Prof. Oakes Ames (Harvard) of the lip of (A) a Newfoundland specimen (Fernald and Wiegand 5232) picked out at random, and (B) an Irish specimen (Præger, July, 1895) of *Spiranthes Romanzoffiana* Chamisso. "Aspect under microscope as to tissues and veins identical!!" The claw of B was torn in dissection.

Habitat. Moist pastures, rushy meadows, worked-out peat-bogs. Wet spongy pastures liable to flood in winter, often with a substratum of sand. Cold damp bogs in usually upland situations. Very rare and local, but in some stations in moderate numbers. Flowers July to August.

Distribution. In various places all round Lough Neagh, and near some of its tributary streams. It has descended the river Bann to Coleraine. Armagh, Derry. Colonsay (Lady Strathcona, *J.B.* p. 346 (1930)). Possibly Coll, J. B. Simpson (*B.E.C.* p. 213 (1923), recorded as *S. autumnalis*). Confined to Ireland, and possibly the western Scottish Isles, and found nowhere else in Europe. In N. America extends from the Atlantic to the Pacific, and from Unalaska southwards to California and Colorado.

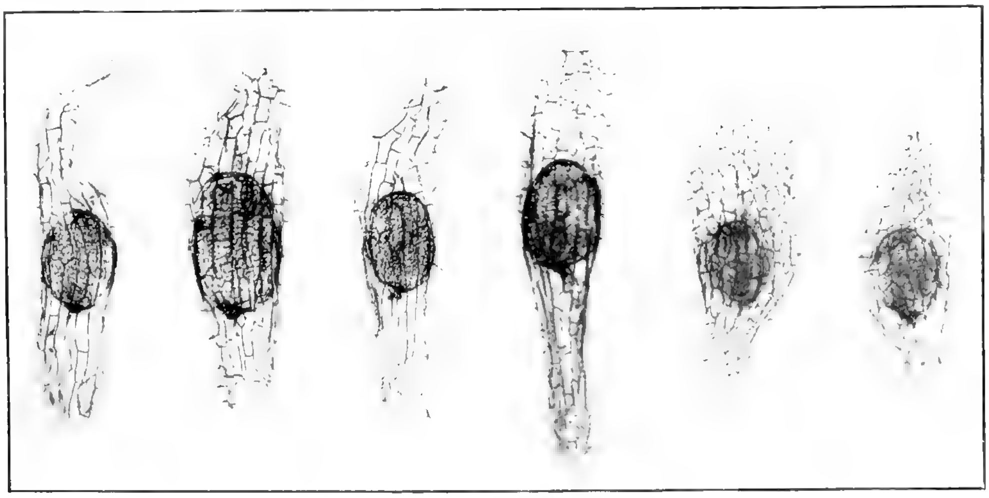
Spiranthes Romanzoffiana Chamisso, *Linnæa*, III, 32 (1828). Neottia gemmipara Smith, *Engl. Flora*, ed. 1, IV, 36 (1828). Spiranthes gemmipara Lindl., *Syn. Brit. Flora*, ed. 1, p. 257 (1829). S. cernua Hooker, *Bot. Mag.* 5277 (1829). Gyrostachys stricta Rydberg (1900).[1] S. stricta Wilmott.

The biological sequence of the buds and tuberous roots in *S. Romanzoffiana* is as follows. A single bud is formed at the foot of the flower-stalk in each plant, at first

[1] Dr Druce wrote (*B.E.C.* p. 369 (1930)): "It is quite evident that Rydberg's *S. stricta* will have to be degraded from specific if not from varietal rank, which was all I gave it in the *List*. The northern and southern plants do not appear to me to vary more than the eastern (fen) and western (dunal) form of *Liparis*". Rydberg's name was *Gyrostachys stricta*, not *Spiranthes stricta*.

Fig. 1. *Spiranthes Romanzoffiana.* North Irish form.
Photo by E. J. Bedford. *O.R.* October, 1930.

Fig. 2. *Spiranthes Romanzoffiana.* South Irish form.
Photo by E. J. Bedford. *O.R.* October, 1930.



(1) (2) (3) (4) (5) (6)

Fig. 3. Seeds of the Marsh Orchids. (1) *Orchis maculata.* (2) Sub-sp. *elodes* (*ericetorum*). (3) Var. *O'Kellyi.* (4) *Orchis praetermissa.* (5) *O. incarnata.* (6) *O. purpurella.*
Orchid Review, November, 1923.
Reproduced by kind permission of the Editor.

concealed amongst the sheathing bases of the leaves. This bud arises from the same roots as the flower-stalk, i.e. those of the previous year, which thus precede the bud. At the base of the new bud are two little knobs, which develop into a pair of tuberous roots, thus enabling the bud to throw up its flowering stem and produce a new bud in the following year. The same thing happens in *Epipactis latifolia*, two short roots covered with root-hairs being found at the base of the new shoot, which develop into two cylindrical roots. In this sense the bud precedes the roots or, more strictly speaking, they are developed simultaneously. The plant thus produces two new tuberous roots every year. The pair of the previous year may also persist, and often one or two of the year before, so that there may be from one to six tubers. In Canada Mr Mousley has twice found a plant with 12 tubers due to the formation of two separate root-systems. In the N. Irish plants the usual number is 2–6.

The plant is not gemmiparous. Drummond in 1810 said: "Buds destined to flower the following year are formed among the leaves at the bottom of the flower-stalk. The following spring each bud...becomes a separate plant". This was taken to mean that *each plant* produced several adventitious buds, and each bud a new plant. The name *gemmipara* was given by Smith under this misapprehension. In the United States increase takes place by single shoots (Ames). In Canada, where it is abundant, two buds have several times been found on a plant, but did not separate and become separate plants, only throwing up a second flower-spike on the same plant. Only once were three buds found on a plant.[1]

The thickness of the tuberous roots appears to depend on the moisture of the soil. Mr Mousley found that at Hatley, Quebec, in very wet ground the roots were slender, and widely divergent, spreading horizontally. As a rule only two were developed in the autumn, but sometimes one or two more in the spring. On high dry ground, however, most of the plants have three or four new roots each season, and the tuberisation is more developed; the roots becoming much stouter, descending vertically instead of spreading, no doubt in search of moisture. Similarly *S. æstivalis*, which grows in wet ground, has long rather slender roots, whilst *S. autumnalis*, a plant of dry places, approaches *Platanthera* and *Orchis* in the thickness of its highly tuberised roots, usually only two in number. Articles were published in the *O.R.* p. 261 (1922); p. 358 (1924); and p. 291 (1930) (Godfery); pp. 71, 296 and 326 (1924) (Mousley), all with photographs; and in the *Irish Naturalists' Journal*, p. 2 (1928), by Miss M. C. Knowles, with a coloured plate by Miss E. Barnes.

Fertilisation. This species is entirely dependent on insects for pollination. Mr W. H. St Quintin, who has cultivated several N. Irish specimens for some years at Scampston Hall, Yorkshire, in a cool house with a northern aspect, and put them out-of-doors on warm nights when many insects were flying about, found that they

[1] Mousley, *O.R.* p. 74 (1924).

were left severely alone, and produced no seed-capsules, whereas *Goodyera* in the same house was extremely well pollinated. An attempt to fertilise *S. Romanzoffiana* by artificial pollination also failed. This seems to show that the necessary insect was absent, and that, in spite of their marked fragrance, the flowers were unattractive to local insects.

If a pencil is inserted into a flower, the viscidium adheres to it, and is withdrawn, with the attached pollinia, without difficulty. These lie horizontally on the upper surface of the gland, and as the latter, which is long and narrow, adheres longitudinally to the insect's proboscis, the pollinia are already in position to touch the stigma of the next flower visited, so that no downward movement occurs after removal. When the flower first opens the column lies close to the trough of the lip, and only the tips of the pollinia and the brown front of the anther, on the upper side of the column, are visible. There is only room to insert a bristle beneath the column, but that is sufficient to remove the pollinia. Later the lip turns more downward, and the column moves back from the lip, when the *under*-surface of the rostellum with its brown viscid gland becomes visible, pointing upwards. If at this stage a finely pointed pencil bearing pollinia is thrust gently into the flower, it readily reaches the stigma, and fragments of pollen at once adhere to it. If the flower has not been previously visited, its own viscid gland adheres to the pencil, which brings away a new pair of pollinia affixed to the remains of the first one.

Mr Henry Mousley, of Montreal, Canada, took the following insects visiting the flowers of *S. Romanzoffiana* (the first-named with the pollinia of that species attached to its head), at Hatley, Quebec: *Chlorhalictus smilacini* Rob. ♀, *Halictes provancheri*. In August, 1926, he took *Bombus vagans* F. Smith at the same place, also bearing pollinia.

Sub-tribe *LISTERINÆ*

Rostellum small, tongue-like, membranous, sensitive, explosively ejecting on being touched two drops of very adhesive fluid, quickly solidifying and cementing the pollinia to the touching insect's head.

KEY TO GENERA

1. Plant green, leaves two, broad, nearly opposite. **Listera**
2. Plant brown, leaves none. **Neottia**

Though sometimes included in the Spiranthinæ, *Listera* and *Neottia* have nothing in common with *Spiranthes*, being the embodiment of a totally different idea, unique in the Orchidaceæ. The floral mechanism is the same in both, but owing to the pronounced saprophytism of *Neottia*, the plants are so different in appearance that they are generally regarded as forming distinct genera. No other European orchids display a tongue-shaped rostellum with longitudinal cells like gun-barrels loaded with extremely viscid fluid, simultaneously discharging their contents when a *sensitive* portion of the under-surface of the rostellum is touched.

Genus VI LISTERA R. Br.

Column short. **Anther** hinged to column, persistent, sessile. **Pollinia** club-shaped, yellow, without caudicles, bi-partite, or divided into two. **Stigma** on face of column just below the rostellum, transversely oval or kidney-shaped.

Small herbs with numerous rather fleshy roots and a very short rhizome. **Leaves** two only, nearly opposite. **Flowers** green, or purplish red, inconspicuous. **Bracts** shorter than the twisted stalk of the ovoid, short untwisted ovary. **Sepals** and **petals** loosely connivent or spreading, exceeded by the narrow strap-shaped forked lip. Ripe capsule ovoid or nearly globular. **Seeds** oblong, testa transparent, netted, cells not striate, embryo small, without suspensor (stalk).

Easily recognised by the single pair of apparently opposite short flat rounded leaves, the small green or reddish flowers with a narrow forked lip, the stalked short nearly globular ovary, and the bunch of rather fleshy roots. *Platanthera* is the only other British genus with but two nearly opposite leaves, but the flowers are white and have a long spur. About 12 species are known.

KEY TO SPECIES

1. Plant tall, with a single pair of large oval leaves, and a long many-flowered spike-like raceme of green flowers. **L. ovata**
2. Plant short, frail, very slender, with two small heart-shaped leaves and a short loose raceme of very small dull purplish red flowers. **L. cordata**

1. Listera ovata R. Br.

Pl. 17 (p. 98). *Twayblade*

Rhizome short, creeping, deeply buried. **Roots** many, long, sinuous, moderately thick. **Stem** erect, tall (20–60 cm.), pale green, solitary, downy above with 1–2 small green triangular bract-like leaves, glabrous, whitish and thicker below, with 2–3 membranous scale-like sheaths at the base. **Leaves** two, spreading horizontally, just below the middle of the stem, almost opposite, broadly oval, sheathing at the base, obtuse, mucronate, rather thick, glabrous, green, with five or more principal nerves.

Raceme long, spike-like, erect, many-flowered, finally lax. **Flowers** inconspicuous, stalked, spreading, yellowish green, rather small. **Bracts** very small, ± 3 mm. long, shorter than the stalk of the ovary, ovate, tapering, green, glabrous or nearly so. **Ovary** almost globular, not twisted, shorter than its curved erect twisted stalk, green or tinged violet, glabrous or hairy, with six slight ridges. **Sepals** ovate obtuse, green or violet edged, concave, loosely connivent with the much narrower linear rather acute yellow-green petals. **Lip** green, 2–3 times as long as sepals, wedge-shaped at base with two small tooth-like erect side-lobes, slightly broadening downwards and deeply divided at the apex into two linear obtuse yellow-green lobes, rarely with an intermediate tooth. It projects forwards at the base (where the edges are slightly turned up at each side, the space between them often glistening with nectar), and then turns sharply downwards almost at right angles. A nectar-secreting furrow runs down the centre, referred to by some authors as a green callus, but if the nectar be wiped off, it is seen to be a furrow. **Column** short (2 mm.), rising at the back into a pale green white-edged notched hood, arching over the anther; in front the white rostellum curves forward, in profile like the spout of a jug, on which lie the two pollinia. **Stigma** on the front of the column immediately below the rostellum, transversely oval, convex, prominent, looking like a wide drop of clear green liquid. **Rostellum** (if the pollinia are removed) rather broadly tongue-shaped, very finely striate under a strong lens, with two longitudinal very shallow furrows in which the pollinia lie. **Anther** ovate, wide open in front, with a shallow partition between the cells, shrivelling early and best seen in bud. **Pollinia** oblong, pale yellow, without stalks, each divided or nearly divided into two. Ripe capsule globular on an upward curved stalk with three flat ridges. Testa of seed 3–4 times as long as broad, reticulate, not striate, suspensor not developed. The continental varieties *alternifolium* Peterm. (leaves more distant), *trifoliata* A. and G. (three leaves), *parvifolia* A. and G. (leaves ± 5 cm. long), and *multinervia* Peterm. (leaves 17–18-nerved) appear to be only individual variations. A curious form with ivory-white sepals and lip, and dark purple-red petals found by Dr Beauverd in Savoie was named by him sub-sp. *eburneo-rosea.*

The stem is sometimes glandular-hairy and sticky to the touch. The band of nectar extends to the base of the lip, and often covers the basal part. The fruiting spike looks like a spray of green currants, the resemblance being accentuated by the withered flower at the apex of each capsule. When shaken, the dust-like seeds come out like pepper from a pot. A specimen found at Chambéry, France, was 70 cm. tall with a spike 28 cm. long.

Var. **platyglossa** Peterm. Lip short (6–8 mm.), broadening downwards into two oblong obtuse slightly diverging lobes, sometimes with a tooth between. Sand-dunes, S. Wales.

PLATE 17

Listera ovata R. Br. Twayblade. Complete plant from Challes-les-Eaux, France, May 7th, 1928.

1. Side view, ovary, column and lip.

2. Front view of complete flower.

2*a*. Base of lip and column after removal of pollinia.

3. *Eucera longicornis* L.

4. *Empis tesselata* F.

Figs. 1–4 enlarged. *a*. anther; *r*. rostellum; *h*. hood of column.

H. M. Godfery pinx.

LISTERA OVATA R. Br.
Twayblade

HABITAT. Woods and shady places, hedge-banks, moist pastures. Frequent and locally abundant. Flowers June to July.

DISTRIBUTION. Throughout Great Britain and Ireland to Orkney and Shetland. Europe from Scandinavia to Spain, Italy, Corsica, the Balkans, Mid- and S. Russia, the Urals, Caucasus, Siberia.

> LISTERA OVATA R. Br. in Ait. *Hort. Kew.* v, 201 (1813). OPHRYS OVATA L., *Sp. pl.* ed. 1, p. 946 (1753). EPIPACTIS OVATA Crantz (1769). HELLEBORINE OVATA Schmidt (1794). NEOTTIA LATIFOLIA Rich. (1818).

FERTILISATION. One might easily jump to the conclusion that the green inconspicuous flowers of *L. ovata* were self-fertilised, but this is far from being the case. Although apparently uninteresting, they are provided with a wonderful mechanism for attaching the pollinia to insects, somewhat suggestive of a contact mine which explodes when touched. Down the centre of the lip above the fork there is a glistening streak of free nectar which is so attractive to small bees and flies that the flowers are visited over and over again. I have even seen hive-bees going to them. Darwin saw a *Hæmiteles* and a *Cryptus* crawl into the flowers, and suddenly retreat with a pair of bright yellow pollinia adhering to their foreheads.[1] The rostellum consists of a tongue-like membrane growing from the upper edge of the stigma, at first directed obliquely upwards, its point near the tip of the anther. Its upper surface is concave, and the anther, just above it, opens in bud, and deposits the two pollinia upon it, where they lie free, their thin ends near its tip. The tips of the anther, the rostellum, and the pollinia are nearly touching. The rostellum is internally divided into a series of cells which contain very adhesive matter, and have the power of violently expelling it. The rostellum is sensitive, and if touched ever so lightly beneath, a kind of explosion occurs. A drop of very adhesive fluid is instantly expelled from each of the two little hollows near the tip, at once coalescing to form a bigger drop which catches the two ends of the pollinia and fastens them to the touching object. The fluid is at first somewhat milky, but in less than a second a film forms over it, and in two or three seconds it sets hard in a solid mass. The rostellum is so exquisitely sensitive beneath that a touch from the thinnest human hair is enough to cause the explosion, and so accurate is the adjustment that the tips of the pollinia are always caught and attached to the touching object. Never once did Darwin find this fail. Moreover, so rapidly is this done that it is difficult to touch the rostellum with a needle, however quickly, without removing the pollinia.[2]

The arrangements for leading the unsuspecting insect into this trap are as ingenious as the trap itself. The insect crawls up the lip, following the trail of honey till it reaches the angle where the lip bends, almost at right angles, towards its base. There

[1] Darwin, *Fert. Orch.* ed. 2, p. 122. [2] *Ibid.* p. 118.

it is so near the underside of the rostellum that it is sure to touch its sensitive surface. It should be noted that the lip narrows gradually upwards, so that the insect is infallibly led to the exact position in which it must touch the rostellum. Immediately it does so the miniature explosion takes place, and the startled insect flies off, carrying the pollinia to another plant. If he now alights on a flower from which the pollinia have already been taken, the trail of honey will lead him right to the base of the lip, where the pollinia on his head will come in contact with the sticky stigma, to which little masses of pollen will adhere, as the pollen-grains are only fastened to the pollinia by weak easily broken threads.

Nor are the delicate mechanical adjustments even now exhausted. When the anther has deposited the stalkless pollinia on the back of the rostellum, the latter curves a little downwards, to avoid the tip of the anther being caught by the viscid drop, and thus glued to the rostellum, locking up the pollinia for ever. The rostellum also bends quickly downwards at the moment of the explosion—an additional precaution against the above danger. In its new position it also tends to keep off pollinia-bearing insects from the stigma, which does not mature quite so early as the pollinia. In the course of some hours after, the rostellum slowly rises until it is well out of reach of any insect crawling up the lip, leaving the way to the stigma clear. An insect arriving with pollinia is therefore no longer checked by touching the rostellum, but goes on to the base of the lip, when the pollinia come in contact with the stigma, whose sticky surface, by this time mature, is able to detach and retain little masses of pollen. These disintegrate into tetrads, and these again into single grains, which emit pollen-tubes in the usual way, the latter penetrating the ovary and fertilising the ovules.

Sprengel several times saw Ichneumon flies withdraw the pollinia.[1] One stayed long on a flower, and, on holding another flower near it, crawled to it, sucked the nectar, and on reaching the bend of the lip, touched the rostellum. Immediately the pollinia became affixed to its head. He also saw a small beetle carrying pollinia.

One sunny afternoon in May, 1867, Hermann Müller watched about 20 plants simultaneously, and often on each three or more insects were busy sucking honey. He concentrated his attention on a single insect, and did not catch it until it had accomplished at least one act of pollination, and in most cases three or four. One specimen of *Grammoptera lævis* was already laden with pollinia when he first saw it. It visited six flowers, carrying off pollinia from four, and leaving pollen on the stigmas of two, which had already lost their own pollinia. Judging from the number of hardened discs on its head, it must have already fertilised many flowers before he began to watch it.[2] Spiders appear to have observed how attractive the flowers are to insects, for their webs are frequently found on *Listera ovata*.

The marvellous co-ordination of parts in this exquisite and complicated piece of

[1] *Das entdeckte Geheimniss der Natur* (1793). [2] Müller, *Fert. of Flowers*, p. 530.

H. M. Godfery pinx.

A. LISTERA CORDATA R. Br.
Lesser Twayblade

B. MALAXIS PALUDOSA Swartz
Bog Orchid

PLATE 18

A. **Listera cordata** R. Br. Les Plans, Switzerland, July 24th, 1912.

1. Enlarged flower with ovary and bract.

B. **Malaxis paludosa** Swartz. New Forest, Hants., July 17th, 1916.

2. Side view of flower *in situ*.
3. Front and back view of flower.
4. Leaf with fringe of adventive bulbils.

All enlarged.

mechanism is worth noting—a co-ordination not only of construction, but also of function and time. The insect is unconsciously led to the exact spot where he cannot avoid springing the concealed mine, whose explosion frightens him away with the pollinia attached to his head, so that he does not go on to the stigma of another flower on the same spike but flies away to another plant. So delicate is the adjustment of the mine that Darwin found one which had been exploded by an extremely minute Hymenopterous insect, smaller than the pollinia themselves, which was struggling to escape, its head firmly cemented to the end of the rostellum and the tips of the pollinia.

The following insects were taken May 31st, 1930, visiting the flowers (from which they removed pollinia) at Anneçy, Haute Savoie: *Eucera longicornis* L. by Mrs Evans, and *Empis tesselata* F. by Colonel G. H. Evans. H. Müller took also the following insects with pollinia on their heads: *Ichneumon uniguttatus* (1), *Alysia* (1), *Cryptus* (8, belonging to 3 species), *Phagedon* (2), *Tryphon* (2), *Campoplex* (1), *Microgaster rufipes* F. (3), and saw *Bombus agrorum* licking honey on several flowers without removing the pollinia.[1] I took the sawfly *Dolerus picipes* Kl. ♀ on *Cephalanthera ensifolia* and placed it in a box containing flowers of *Listera ovata*. I found later it had withdrawn four pollinia on its proboscis.

2. Listera cordata R. Br.

Pl. 18 A. *Lesser Twayblade*

Rootstock slender, creeping, with a few whitish thread-like short-haired roots. **Stem** erect, slender, rarely more than 20 cm. tall, thickened below the leaves by decurrence of their nerves and edges, with 1–2 brownish scale-like lanceolate close-fitting leafless sheaths at the base, and also the new bud; stem above the leaves angled, fluted, glabrous or slightly downy, pale green often reddish, resembling a long peduncle. **Leaves** two, about the middle of the stem, appearing opposite, sessile, spreading horizontally, triangular with rounded corners and broadly wedge-shaped base, rounded at the apex, entire, often with incurved or wavy edges, glabrous, green and shining above, paler rather grey-green below, 5-nerved, the mid-rib ending in a fine point, with numerous netted veins on each side. **Flowers** few (usually 6–12), very small, inconspicuous, green more or less suffused with red, in a short loose feeble slender raceme. **Bracts** nearly triangular, ovate acute, shorter than the stalk of the ovary, obscurely 1-nerved. **Ovary** nearly globular, shorter than its twisted stalk, angular, light green, glabrous, with six reddish ridges. **Sepals** oblong, rounded at the tip, green, rather spreading, persisting on the fruit. **Petals** very similar and

[1] Müller, *loc. cit.*

nearly as long, green outside, red-purple within. **Lip** linear, exceeding sepals, horizontal or pendent, with an erect lanceolate acute tooth on each side at the base, divided about the middle into two linear tapering divergent terminal lobes, brownish red. Fruiting capsule globular. **Column** thick, very short with a curious leaf-like hood at the apex protecting the anther. **Stigma** kidney-shaped. **Rostellum** oblong, 2–3-toothed at apex. **Anther** oblong, with a small obtuse tooth at apex. **Pollinia** two, bi-partite, without caudicles, club-shaped. **Seeds** without suspensor, cells of hyaline testa rectilinear without striæ.

A frail slender inconspicuous little plant easily recognised by its pair of small heart-shaped stalkless almost opposite leaves, its tiny green flowers with forked reddish lip (looking at the first glance as if withered), and its small stalked globose ovary. Very rarely a third leaf is produced above the usual pair. According to Rouy (*Fl. de France*, XIII, 215) it smells of musk, especially at night.

HABITAT. Mountain woods (especially pine-woods) and turfy moors under heather, also in spongy cushions of wet moss. Boggy heaths in mountain districts in Ireland. Flowers July to September.

DISTRIBUTION. From N. Devon northwards, rare in the south, almost all Scotland to Orkney and Shetland. Rather rare in Ireland, but found in most districts, descending to 150 ft. in Antrim (*Cyb. Hib.* p. 338). Europe from Iceland and Scandinavia to the Pyrenees and Apennines, Mid-Russia, Transcaucasia (A. and G.), N. Asia, N. America (Hooker).

> LISTERA CORDATA R. Br. (1813). OPHRYS CORDATA L. (1753). EPIPACTIS CORDATA Allm. (1785). HELLEBORINE CORDATA Schmidt (1794). NEOTTIA CORDATA Rich. (1818).

I first saw this plant at Les Plans, in Switzerland, in rather dry places under Scotch firs, and afterwards in the Boréon Valley above Nice, amongst spongy cushions of wet moss, where it was almost twice as tall as at Les Plans, but did not differ otherwise. No variation was produced by the warmer climate of the Alpes Maritimes (both stations are a little over 1000 m. above the sea), or by the much wetter habitat, except in height. It is abundant near Chamonix, and is essentially a plant of mountain forests, often found growing with *Corallorhiza*.

FERTILISATION. Similar to that of *L. ovata*. The tooth-like basal lobes curving up on each side of the lip cause a visiting insect to approach from straight in front. As soon as it touches the sensitive rostellum the viscid matter is explosively discharged, and cements the pollinia to the head of the intruder. The rostellum then bends downwards, protecting the virgin stigma, subsequently rising up and leaving the way of access open to the next visitor. The flowers are frequented by minute Diptera and Hymenoptera (Darwin, *Fert. Orchids*, p. 124).

H. M. Godfery pinx.

NEOTTIA NIDUS-AVIS Rich.
Bird's Nest Orchid

PLATE 19

Neottia nidus-avis Rich. Bex, Switzerland, July 5th, 1912.

Genus VII NEOTTIA Swartz

Column long, at right angles to lip. **Rostellum** strap-shaped, projecting forwards, parallel with and just above the stigma, sensitive, ejecting a viscid drop of fluid when touched. **Stigma** on frontal lip of column. **Anther** leaning forwards, attached by a very short hinge to back of column. **Pollinia** bi-partite, pollen reticulate.

Saprophytic plants without leaves or green colouring matter, only the flower-stem appearing above ground. Rhizome quite concealed by densely crowded short thick fleshy roots. **Stem** enclosed in sheathing scales. **Raceme** spike-like, flowers smoky brown, rather large, spurless. **Sepals** and **petals** sub-similar, connivent in an open canopy. **Lip** hollowed out at base with two curved widely divergent lobes at apex.

Neottia shares with *Listera* an outstanding peculiarity—the development of the rostellum into a sensitive organ, ejecting two drops of viscid fluid on being touched—which differentiates them so completely from all other orchids that Reichenbach fil. (*Icones*, XIII, 145) united the two genera into one (*Neottia*). Lindley confessed that there was nothing that could be regarded as a satisfactory distinctive mark except their habit, but that this was so dissimilar that he thought it unwise to unite them.

1. Neottia nidus-avis Richard

Pl. 19. *Bird's Nest Orchid*

Whole plant, including the flowers, yellowish brown, without chlorophyll. **Root-stock** short, entirely concealed by a dense mass of crowded short thick obtuse fleshy roots, popularly supposed to resemble a bird's nest. The tips of the roots are said by various writers to give rise to adventive buds. **Stem** 2–4 dm. tall, erect, stiff, cylindrical, usually stout, slightly viscid above with glandular hairs, covered below with oblong or lanceolate close-fitting or loose brown sheaths, the lower short, acute, the upper longer, lanceolate, obtuse, sometimes large and loosely surrounding the stem, with many parallel nerves connected by branching cross-veins. **Leaves** none. **Raceme** spike-like, cylindrical, long, dense above, lower flowers distant. **Flowers** moderately large, yellowish brown, honey-scented, the lip ending in two broad divergent lobes. **Bracts** lanceolate, tapering, acute, reaching about the middle of the ovary, 1-nerved. **Ovary** not twisted, on a twisted stalk half its length or more in lower flowers, ovate, with sparse or plentiful shortly stalked glands, and six longitudinal ridges. **Sepals** and **petals** free, similar (the latter slightly smaller), spreading in a nearly erect fan or open helmet, obovate with minute rounded teeth at apex, 1-nerved. **Lip** twice as long as and darker brown than sepals, directed obliquely forwards, at right angles to column, hollowed out into an oval cup glistening with tiny drops of honey, and with two small tooth-like side-lobes at the base, oblong, then dividing into two broad widely spreading curved oval or strap-like often crenulate lobes, rounded at apex and glandular-hairy beneath. Drops of nectar, rather bitter, are also sometimes found on the limb of the lip. **Column** nearly in line with ovary, but sloping slightly backwards, cylindrical in section with a long-waisted body, pale brownish white, ending at the back in a short rounded tooth, projecting in front in a spout-like slightly notched lip, on the upper surface of which is the narrow kidney-shaped **stigma**, which appears **V**-shaped viewed from in front. **Rostellum** projecting forwards immediately above the stigma, and extending some distance beyond it, strap-shaped, trough-like, grooved above, and curving downwards at the tip. **Anther** oblong, slightly cordate, papillose outside, hinged to the back of the column, projecting forwards over stigma nearly at right angles to column. **Pollinia** two, bi-partite, linear-oblong, pale yellow, friable, consisting of compound grains (tetrads) tied together by very weak threads; they lie free, unattached to any viscid gland, in the trough of the rostellum. Seed-capsule erect, ovate, nearly 3-sided, with six ridges, of which three are more prominent, ± 12 mm. long. **Seeds** oblong with netted transparent testa.

The varieties *pallida* Wirtgen, pale yellow or whitish; *sulphurea* Weiss, sulphur-yellow; *nivea* Magnus, snow-white, are mere colour-forms, which might also occur in Britain. The plant varies very little, except in size and robustness.

Habitat. Shady woods, especially under beech, more rarely in pine-woods. Flowers June to July.

Distribution. Generally distributed in England, Wales and Scotland as far north as S. Aberdeen, Banff, and E. Inverness. Throughout Ireland in shady woods and thickets, but rather rare. Europe from Scandinavia to Spain, Italy and the Balkans, Russia (middle and south), Caucasus, Transcaucasia, Ural.

Neottia nidus-avis Rich., *Mém. Mus. Paris*, iv, 59 (1818). Ophrys nidus-avis L., *Sp. pl.* ed. 1, p. 945 (1753). Epipactis nidus-avis Crantz. Helleborine nidus-avis Schmidt. Listera nidus-avis Hooker.

The whole plant is of a yellowish brown colour, and, even in its freshest condition, looks dead and withered, like a faded *Orobanche*. The supposed resemblance to a bird's nest is rather fanciful. There is no nest-like hollow on the upper surface of the closely packed mass of roots. The absence of leaves and of green colouring matter has often caused it to be mistaken for a parasite. It is, however, only a saprophyte, subsisting on dead and decaying leaves or other organic matter, but never on living plants. The brown colouring matter must be nearly allied to chlorophyll, for when dipped in boiling water it becomes a yellowish green.[1] A clump of 13 fruiting spikes dug up by me at Thorenc was found to consist of separate plants, though growing intermixed. The short rhizome is covered with densely packed thick fleshy roots, two root-systems being often found back to back, closely adpressed. This comes from a second bud giving rise to a new root-system on the lower side of the rhizome, opposite the main bud at the foot of the stem, which is always at one end of the mass of roots. The 13 plants referred to might conceivably have grown from the tips of decaying roots, but they might also have come from seed.

Leighton[2] states that the Rev. W. H. Herbert's observations showed that *Neottia* "is capable of reproducing a new plant from the point of each of its fibres after they have fallen apart, the extreme point becoming the eye or shoot". Ascherson and Graebner (*Syn.* p. 893) also state that after the ripening of the fruit the plant usually dies, but the dried flower-spike persists, sometimes for several years. They never found living roots beneath such stems, but state that adventive buds are found at the tips of the roots. While no doubt these observations were correct for the rhizomes observed by them, they are not universally true. We have never found, among the few specimens dug up, any sign of adventitious buds at the ends of the roots, but have always seen a strong bud (sometimes more than one) at the foot of the flowering stem, and occasionally a last year's dead stem—proving that the same rhizome may give rise to flowering stems for at least three years. Sometimes there are two such buds, on opposite sides of the rhizome. Each bud seems to form a separate cluster of roots, which explains the not infrequent occurrence of two back-to-back systems of densely packed roots. No doubt each individual plant finally dies of exhaustion, and dried stems with dead roots thus occur, but ordinarily a new bud is found at the base of the stem, as is the rule with *Listera*, *Epipactis*, *Corallorhiza* and nearly all ground orchids. Noel Bernard found that the number of plants of *Neottia* underground was much greater than above the soil, and is said to have thought that many of them led an entirely subterranean existence, even flowering below ground.[3] This idea was probably based on accidentally buried stems, of which he himself tells us[4] he found one whose seeds had germinated in the capsule. The little plants were club-shaped, the acute end still affixed to the torn tegument of the seed, their surface smooth without absorbent hairs. The buried stem was moist, and contained a close network of mycelium of the fungus *Rhizoctonia repens*, which extended into the capsule and surrounded the seeds. The latter, which cannot germinate without the aid of the fungus, were therefore favourably situated in this respect. Whilst these mycorrhiza disappear in later stages of growth from the tubers of *Orchis*, the roots of *Neottia* are permanently infected. This symbiosis is most complete in *Neottia*, *Epipogon* and

[1] A. and G. *Syn.* III, 293.
[2] *Fl. Shropshire*, p. 434 (1841).
[3] Constantin, *Vie des Orchidées*, p. 110.
[4] *Acad. Sc. Paris*, p. 1253 (1899).

Corallorhiza, in which the fungus establishes itself from the beginning, entering the seed by way of the suspensor, permeating the rhizome and making its way into all roots as they appear.[1]

Fertilisation. The anther opens in bud, and deposits the pollinia on the upper surface of the horizontal rostellum. In a newly opened flower no viscid gland can be seen, but the pollinia lie quite free, their thin upper ends forward in the groove of the rostellum, the tip of which turns down a little, leaving a slight space between itself and the ends of the pollinia. It was found that if the underside of the rostellum was gently stroked in an upward direction with a camel's hair brush, or touched with a needle, a large drop of milky looking liquid was instantaneously ejected, big enough to fill up the space between the end of the rostellum and the tips of the pollinia, which were caught and held by it. This drop was sufficiently viscid to adhere to the touching object and to bring with it the pollinia, rapidly setting brown and hard like cement. The simplicity and never-failing efficiency of this ingenious device are most striking. The mechanism is identical with that of *Listera*.

The adhesive liquid is contained within the cells of the rostellum. Darwin states that there are about six rough points on the crest of the rostellum which seem particularly sensitive to a touch, causing the expulsion of the viscid matter.[2] After about four days the rostellum loses its sensitiveness, and fails to eject the liquid. Its tip turns black, and a hard ball of matter can be seen and felt—the viscid material has set hard *in situ*. After the flower has been open for a few days the pollinia swell and disintegrate, overhanging the sides of the rostellum, and sliding down on to the stigma which lies immediately beneath. This gives rise to self-fertilisation, a result also brought about by the presence of minute insects (thrips), which may be seen crawling about the flowers dusted all over with pollen.[2]

Insects are attracted by the honey-like smell, and the tiny drops of nectar on the lip eventually lead them to the cup at its base, where it is more plentiful. They thus touch the sensitive rostellum, and the pollinia become cemented to the head or thorax. Hermann Müller saw the plant visited by flies in considerable numbers, and several of the spikes were covered with spiders' webs. He saw *Spilogaster cinerea* and small Muscidæ sucking the honey, but without removing the pollinia. Finally he saw a larger yellow fly (*Helomyza affinis* Mgn.) crawl up the lip to its base, licking the honey on its way, till it came in contact with the rostellum, thereby cementing the pollinia to the front of its thorax. It flew away, startled, but was caught in a spider's web.[3] One cold wet season Darwin could not find a drop of honey, though he searched several times.

We noticed that in a number of flowers (but not in all) after a time the rostellum

[1] Weiss, Presidential Address, Manchester Micr. Soc. (1917).
[2] *Fert. Orch.* ed. 2, pp. 125–6.
[3] H. Müller, *Fert. of Flowers*, p. 532.

rises up, greatly widening the space between the stigma and itself, leaving the former quite free and open to insect visitors. This has happened both in flowers from which the pollinia have been removed and in others in which they are intact, but the viscid material has set into a hard black ball. This seems to show that the stigma does not become ripe for the reception of pollen for some time after the flower opens, and until this occurs insects are fended off by the rostellum, which covers it like a roof. As soon as the pollinia have been removed, or the power of ejecting viscid matter has ceased, the rostellum moves up out of the way, so that nothing may hinder pollinia-bearing insects from coming into contact with the stigma.

That insect visits are frequent is shown by the number of flowers from which the pollinia are found to have been removed. Darwin records a spike of 41 flowers which produced 27 large seed-capsules, besides some smaller ones. I found a last year's spike with 36 developed capsules. In addition, several capsules were missing, presumably having failed to develop and dropped off. Propagation is unusually well assured—cross-pollination by insects, self-fertilisation if this fails to occur, and vegetative reproduction by adventive buds at the ends of the roots.

Tribe II MALAXIDEÆ Lindl.

Pollinia compact, waxy, bi-partite, without caudicles. Pseudo-bulbs formed by a swelling of the stem, except in *Corallorhiza*.

KEY TO GENERA

1. Pseudo-bulbs two, one above the other, distant. Lip directed upwards. Column very short, not winged. Pollinia four, flat, in pairs, face to face. **Malaxis**
2. Pseudo-bulbs two, side by side. Lip curving upwards. Column long, slender, winged. Pollinia four, globose, in pairs, side by side. **Liparis**
3. No pseudo-bulbs. Rhizome coralloid. Lip curving downwards. Pollinia four, sub-globose. **Corallorhiza**

The immense antiquity of the Malaxideæ, like that of the Neottieæ, is shown by their vast geographical distribution, which extends to N. America. When we find species on both sides of an impassable barrier like the Atlantic Ocean, and yet identical, whether gathered in Europe or America, it should enable us to realise the extreme antiquity of the species in question, which must date back to a period when it was possible for the plant to spread from the eastern to the western hemisphere, or *vice versa*. Incidentally it also shows the extraordinary permanence of the species in question, which after separation for such untold ages still remain identical.

Genus VIII MALAXIS Swartz

Column minute. **Anther** at back of column, **pollinia** four, in superincumbent pairs. **Stigma** on face of column, **rostellum** a small viscid mass at its apex.

Small herbs in Britain mostly growing in *Sphagnum* with two pseudo-bulbs one above the other, with small leaves sometimes fringed with adventive buds, and very small green flowers with lip pointing upwards.

Only our species in Europe. Closely allied to *Liparis* and *Microstylis*. In the *Orchids of the United States and Canada* (Oakes Ames, 1924) the last-named genus is included in *Malaxis*.

1. Malaxis paludosa Solander *ap.* Swartz

Pl. 18 B (p. 101); Pl. E, fig. 1. *Bog Orchid*

Rhizome short, connecting the two pseudo-bulbs, which are ovate, somewhat four-sided, the new bulb embraced by the leaves, 1–2 cm. above the old, which is as large as a pea, clothed with brownish acute scales, and tapering below into a slender root (Pl. E, fig. 1). **Stem** erect, 6–12 cm. tall, 3–5-angled above, like the whole plant glabrous. **Leaves** 3–4 (often only two fully developed, the lowest one or two reduced to sheaths), small, short, concave, spoon-like, ovate or oblong, sub-obtuse or sub-acute, rather thick, 3–7-nerved, pale yellow-green, fringed near the tip (as also sometimes the sheaths) with little gland-like bulbils capable of producing new plants. The new pseudo-bulb is produced in the axil of the uppermost leaf. **Raceme** slender, spike-like, many-flowered, rather dense, later becoming lax. **Flowers** very small, yellow-green, inconspicuous, lip pointing upwards. **Bracts** small, lanceolate acute, longer than the twisted stalk of the small top-shaped untwisted **ovary**, scarcely longer than its stalk. Lateral **sepals** erect, ovate or broadly lanceolate, somewhat triangular, obtuse, 1-nerved, tips recurved, median pointing downwards, slightly longer and broader, obtuse. **Petals** two, linear-lanceolate, 1-nerved, narrower and shorter, spreading, with tips curved back. **Lip** erect, longer than petals, but shorter, firmer, and sometimes darker than the sepals, undivided, ovate, sub-obtuse, with a (sometimes bifid) little point, concave, 3-nerved, embracing the column. **Column** minute, with a green obtuse membranous lobe, concave within, on each side at the apex, forming a clinandrium to shelter the pollinia, making the column appear toothed at apex. **Anther**, seen from behind in the bud, heart-shaped, obtuse, united to column by its broad base; in the open flower shrivelled downwards into a shallow wrinkled mass in which the broad ends of the otherwise free pollinia rest as in a

Fig. 1. *Malaxis paludosa* Swartz. Showing bulbils on tips of sheath and leaves.

Fig. 2. *Liparis Loeselii* Richard.

Fig. 3. *Corallorhiza innata* R. Br.

Fig. 4. *Spiranthes Romanzoffiana* Chamisso. Side-sepals separated to show stigma with adherent pollen and linear rostellum. (3:1.)

Fig. 5. Flower of *Epipogon aphyllum* Swartz. Enlarged 2·5:1, in natural position, half of lip cut away, and anther bent back to show pollinia and caudicles detached from rostellum.

Fig. 6. *Spiranthes [illegible]* Richard. (3:1.)

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cup. **Pollinia** two, waxy, each composed of two flat separate face-to-face broad-based tapering very thin leaves of pollen, built up of angular compound grains which never separate.[1] **Stigma** on front of column, in the horseshoe-like space between the sides of the clinandrium, continued downwards as a pocket-shaped cavity behind the oblong projection on the front of the column, and covered with a thin layer of viscid material. **Rostellum** a minute tongue-shaped mass of viscid matter on the apex of the stigma which, by the time the flower opens, has become attached to the thin upper ends of the pollinia.[2]

M. paludosa, the smallest British orchid, is so inconspicuous as to be hard to see. I have mostly found it embedded in cushions of *Sphagnum*. It is easily recognised by the tiny flat triangular-looking green flowers, with two sepals standing up like ears, by the erect trowel-shaped much shorter lip, embracing the column, and the larger triangular sepal pointing downwards. The only British orchid at all like it is *Herminium monorchis*, the Musk Orchid, a plant of dry hills with a prickly-looking spike, and flowers with a 3-fid lip pointing downwards. Moreover its bulb is underground, whilst in *Malaxis* the flowering bulb is a swelling of the stem above the leaves, their sheathing bases fitting round it like a glove. Pl. E, fig. 1, compared with Pl. F, fig. 3, will show the difference at a glance. *Malaxis* and *Liparis* are our only genera with flowers upside down (except *Epipogon*), and *Malaxis* is our only gemmiparous orchid, for the edges of the leaf-tips and often of the leafless sheaths are fringed with tiny gemmæ, each capable of producing a new plant.

Mr T. A. Dymes, F.L.S., states that *Malaxis* passes the winter as a greenish bulbil at the base of the flowering stem, enclosed in the remains of the sheath of the upper leaf, which contains tracheids (long closed cells) for storing water. The bulbils are heavier than water, and in the winter rains are apt to sink in the *Sphagnum*, which would be fatal, were it not that the bulbil grows a stalk (rhizome) which pushes it up to the right position. Hence the distance between the bulbs of successive years.

Darwin regarded the membranous expanse between the side-lobes at the apex of the column as the rostellum. He, however, stated that it is covered with a thin layer of viscid material "*which is of no use for the transportal of pollen*", and that he found pollinia glued to it, with a large number of pollen-tubes penetrating the stigmatic tissue.[3] It therefore functions as a stigma and not as a rostellum, and its position, size, and viscid layer are those of a normal stigma. The little mass of viscid material at the apex of the stigma, which becomes attached to the pollinia, and later to a visiting insect, is the true rostellum. It is apparently not essential that the pollinia

1 Darwin, *Fert. Orch.* ed. 2, p. 133.
2 The description of the column is based on Darwin (*loc. cit.* p. 130).
3 *Ibid.* p. 134.

should be pushed into the narrow pocket which Darwin alone regarded as the stigma, though this may often happen; it is enough if they come in contact with what he considered to be the rostellum. In the great majority of European genera the lip is directed upwards in the bud, but through the twisting of the ovary (or of its stalk), the flower turns round through an angle of 180°, so that the lip points downwards, the position most convenient as a landing-place for insects. In a few genera, e.g. *Epipogon*, *Liparis*, *Malaxis*, *Nigritella*, etc., the lip normally points upwards. The downward movement of the lip has been called geotropic (relating to the influence of gravity on growing organs). In *Malaxis* the flower makes a complete revolution, so that the lip regains its original position, and points upwards. The movement is more probably due to a natural tendency to twist in the ovary or its stalk.

HABITAT. Wet peat-bogs or marshes, usually growing in cushions of *Sphagnum* standing in water. Ascends to 1500 ft. in N. Britain. Flowers July, August, or even September in the north.

DISTRIBUTION. From Kent to Devon northwards to Ross, Sutherland, and the Hebrides. Rare and local, more frequent in the north. In Ireland widely distributed, but rare and local. Scandinavia, Denmark, Finland, Central Russia, France (rare), Switzerland (very rare), Siberia, Dahuria (Hooker), N. America (Oakes Ames).

MALAXIS PALUDOSA Swartz, *Act. Holm.* p. 235 (1800). OPHRYS PALUDOSA L. (1753). STURMIA PALUDOSA Rchb. p. (1828).

FERTILISATION. Although the flowers of *Malaxis* are so hard to see, they are very attractive to insects. Darwin found that the pollinia had been removed from all the flowers he examined, except one or two top ones. In some spikes every single pollinium had been carried away. Sometimes an insect removes only one of the two pairs. He noticed a pollinium in the stigmatic cavity of one flower, whose own pollinia were still *in situ*. This must have been brought by an insect from another flower. Plenty of seed is produced, one spike having 13 large capsules. He transplanted some specimens to a bog about two miles from their original habitat, and most of the pollinia were immediately removed.[1] The insects which visit *Malaxis* must be of small size. I can trace no record of what they are. The middle sepal, which normally stands at the top of the flower, points downwards in *Malaxis*, and replaces the lip as a landing-place for insects. The two petals are curved backwards out of the way, leaving the flower quite open and flat. The sharp-pointed trowel-like lip embraces the column with its curved base, and affords some slight protection from the weather. The lobes, one on each side of the anther at the top of the column, resemble the anther in shape and form a clinandrium to prevent the naked pollinia from being blown away. These lobes are developments of the obsolete anthers

[1] *Fert. Orch.* ed. 2, pp. 32 and 134.

a^1 and a^2 of the inner whorl, here utilised for the benefit of the flower. When the flower opens the pollinia have already become attached to the sticky drop at the top of the stigma. On an insect inserting its proboscis into the narrow space between the upright lip and the rostellum, it will infallibly touch this projecting viscid mass, and when it flies away will carry off the pollinia. This can easily be tested by inserting any object of suitable size. When it visits another flower the pollen-leaves are thrust into the pocket or against the viscous surface of the stigma above it, to which they adhere. If the waxy pollen-leaves are placed in water for three or four days, the tetrads readily fall apart, but the four grains of which each is formed still firmly cohere.[1]

Genus IX LIPARIS Rich.

(*Mém. Mus. Paris*, IV, 52 (1818))

Flowers not reversed, so that lip is uppermost. **Column** long, winged above on each side of stigma. **Anther** inclined over top of column like a lid, soon falling off. **Pollinia** two pairs, waxy, without caudicles, each pair attached to a viscidium. **Stigma** transversely oblong. **Rostellum** with two viscidia, evanescent.

In Europe small inconspicuous herbaceous plants with two pseudo-bulbs side by side, angled stem, two greasy-looking leaves and rather small yellowish green flowers in a terminal raceme with slender sepals and petals and relatively much broader lip, its base nearly parallel with column and apical half bent nearly at right angles. The two round but distinct viscidia disappear early, which led Richard to state in his diagnosis that the genus has no rostellum. About 100 species, some epiphytic, widely spread in temperate and warmer regions.

1. Liparis Lœselii Rich.

Pl. 20 A (p. 112); Pl. E, fig. 2 (p. 108). *Fen Orchid*

Pseudo-bulbs two, above ground, side by side, the older enveloped in the reticulate remains of last year's leaves. In young plants there is a short rhizome emitting thread-like roots; in older plants the roots are thicker, very hairy, and grow down through the envelope of decaying leaf-bases. **Stem** erect, 6–20 cm. tall, smooth, glabrous with usually three (rarely four or five) almost winged angles above, and 2–3 greenish or whitish basal leafless sheaths. At the base between the leaves the stem swells into an elliptical green shining bulb, with one (or more) new bulbs enveloped in soft pale scales, with simple wavy rootlets; above the leaves the stem is a long naked

[1] *Ibid.* p. 258.

peduncle. **Leaves** two, nearly opposite, erect, oblong, rather acute, keeled, many-nerved, shining, greasy-looking (whence the name *Liparis*, from the Greek *liparos*, greasy), about half as long as the flowering stem, with elongated sheathing bases. **Raceme** loose, few-flowered (1–10, sometimes up to 18). **Flowers** rather small (but much larger than those of *Malaxis*), greenish yellow, inconspicuous, with very narrow sepals and petals, and broader lip. **Bracts** small, lanceolate, keeled, very short (± 1 mm.), 1-nerved, the lowest sometimes longer, or even foliaceous. **Ovary** spindle-shaped, rather 3-angled, 6-ribbed, straight or slightly twisted at the base, erect in fruit, stalk rather long, twisted, 3-angled, furrowed. **Sepals** linear, narrow, acute or obtuse, spreading, slightly inrolled, yellowish or yellow-green. **Petals** similar, narrower, often shorter. **Lip** usually but not invariably pointing upwards, curved, oblong or oblong-ovate, obtuse, folded, trough-like, usually crenate, sometimes wavy-edged, undivided, petaloid, much broader than and nearly as long as the sepals, yellowish, of a deeper shade, without spur. **Column** erect, flat in front above, but rounded out at the base, narrowed in the middle, with rounded crenate forward-directed side-wings at the apex, protecting the anther and stigma, a clinandrium or shallow cup at the apex, in which the pollinia are deposited, and a furrow down the front. **Stigma** small, quadrangular, transversely oblong, depressed, with rather prominent edges. **Rostellum** minute, horizontal, toothed (Reichenbach). **Anther** sessile at apex of column, deciduous (Hooker), ending in a deciduous membranous appendage, 2-celled, cells bi-locular. Pollen-masses four, waxy, globose, laterally compressed, side by side in contiguous pairs, each pair attached to an evanescent viscidium. Fruiting capsules rather large, spindle-shaped.

Pl. E, fig. 2, gives a good idea of the habit of the plant, and of the greater conspicuousness of the lip. Small bog-plants with yellowish green inconspicuous flowers with very narrow sepals and petals, much broader lip bent at right angles in the middle, and two erect shining greasy-looking leaves; also two green pseudo-bulbs, side by side, surrounded by the decaying remnants of leaves. Very hard to see, owing to its small greenish flowers, and more easily detected by searching for the leaves, which differ in shape and by their lighter colour from the surrounding marsh plants. Richard said that it has no rostellum, and that the ovary is usually imperfect and abortive. This was probably based on plants from which the evanescent rostellum had already disappeared, and in which the abortion of the ovary was an accidental occurrence. I found it with well-developed fruit on the shores of the Lake of Geneva, whilst the Rev. H. J. Riddelsdell found it in Wales in good quantity and in excellent fruit.[1]

Var. **ovata** Riddelsdell. Leaves broad, elliptical, obtuse.

Habitat. Spongy or sandy bogs, often in cushions of moss. Hence it is liable

[1] Riddelsdell, *J.B.* p. 274 (1905).

PLATE 20

A. **Liparis Lœselii** Rich.

1. Plant from Villeneuve, Switzerland, June 1st, 1913.
2. Same locality, June 9th, 1925.

3, 4. Slightly enlarged flowers of latter, side and front views.

B. **Corallorhiza innata** R. Br. Solalex, Switzerland, July 15th, 1912.

5. Ovary and flower (enlarged).
6. Flower from Les Diablerets, Switzerland (still more enlarged).

H. M. Godfery pinx.

A. LIPARIS LŒSELII Rich.
Fen Orchid

B. CORALLORHIZA INNATA R. Br.
Coral-root Orchid

to extinction through drainage or cultivation. With it commonly grow rushes, sedges, bog-bean, *Anagallis tenella*, *Hydrocotyle*, *Scutellaria*, *Epipactis palustris*, *Orchis incarnata*, *O. latifolia*, *O. prætermissa*, etc. In the Welsh station the ground was dry when *Liparis* was found, but was evidently wet in winter, a case in which the water-storing tracheids in the coverings of the pseudo-bulbs would be of immense value.

Distribution. Norfolk, Suffolk, Cambs., Hunts., Surrey, Kent (?), Glamorgan,[1] Carmarthen. In Norfolk it occurred in 1883 in great profusion, as many as 6–10 plants in a clump, with abundant *Carex paradoxa*; in Cambridge it is much less plentiful and more scattered. It is believed to be extinct in the Kent locality (Sowerby, E. B.), and is nearly exterminated in several localities through the drainage of the fens. Not recorded for Ireland or Scotland. Southern Scandinavia, Denmark, Germany, Austria, France, Upper Italy, Central and S. Russia, N. America.

Liparis Lœselii, Rich., *Mém. Mus. Paris*, iv, 60 (1818). Ophrys Lœselii L., *Sp. pl.* (1753). O. latifolia L. (1755). O. paludosa, *Flora Danica* (1782). O. trigona Gil. (1792). Cymbidium Lœselii Swartz (1799). Malaxis Lœselii Swartz (1800). Serapias Lœselii Hoffm. (1804). Sturmia Lœselii Rchb. p. (1826).

Included by Linnæus in his *Flora suecica* in the genus *Herminium*.[2] In the *Species plantarum* both were included in *Ophrys*.

Fertilisation. There is no sign of self-pollination, and the species must therefore depend on the agency of small insects for the transport of the pollinia from flower to flower, but I can trace no record of actual observations of their visits. Owing to the rarity of the plant, and the inconspicuousness of the flowers, such observations are extremely difficult. The maturing of numerous seed-capsules shows that the flowers are well visited by insects. Two plants sent by me from Switzerland in 1925 to Mr St Quintin of Scampston Hall, Yorks., had four and five flowers respectively in 1929, but set no seed-capsules, whilst two Canadian specimens in the same green-house in a contiguous pan, with seven and six flowers respectively, each set four capsules. It seems therefore certain that *L. Lœselii* is not self-fertilising, even in the absence of insect visits. It is curious that insects should have been attracted by the Canadian plants, to the exclusion of the Swiss ones, which were quite healthy.

Genus X CORALLORHIZA Haller

Column long, erect, not winged. **Anther** kidney-shaped, hinged to back of column and soon falling off, each of the two cells divided by a partition. **Pollinia** four, sub-globose. **Stigma** triangular or oval, in front of column just below anther. **Rostellum** small, globular.

[1] Riddelsdell, *loc. cit.*

[2] A. and G. *Syn.* iii, 805.

Small leafless herbaceous plants with branched coral-like rhizome, 2–3 leafless sheaths loosely clasping the stem, and small yellowish flowers with a white tongue-shaped lip. Essentially underground plants (like *Epipogon*), growing and increasing beneath the soil, feeding on organic matter in a state of decomposition (dead leaves, decaying wood, etc.) and only throwing up a flower-stem to produce seeds to colonise fresh ground, and maintain the vigour of the species by cross-fertilisation. About 12 species known in Europe, temperate Asia, N. America and Mexico, but only our species in Europe.

1. Corallorhiza innata R. Br.

Pl. 20 B (p. 112); Pl. E, fig. 3 (p. 108). *Coral-root*

Rhizome coral-like, horizontal, fleshy, cream-coloured, with knob-like rounded branches. **Flowering-stem** leafless, arising from a branch of the rhizome, erect, slender, short (up to 20 cm.), solid, glabrous, pale yellow-green, with 2–4 long membranous brown whitish or green obtuse or acute mucronate brown-nerved leafless sheaths, often reaching the middle of the stem, loose and slightly open at the tip. Bud springing from the axil of a sheath just above the junction of stem and rhizome. **Raceme** spike-like, lax. **Flowers** 4–12, small, inconspicuous, greenish yellow with white lip with reddish markings at the base. **Bracts** very small, membranous, sometimes shorter than the stalk of the ovary, rarely half as long as the ovary itself, triangular acute or truncate, 1-nerved, sometimes with 1–2 short teeth. **Ovary** spindle-shaped ($\pm$ 7 mm. long), untwisted, flattened in front with three prominent and three lesser longitudinal obtuse ridges, stalk short, twisted. Seed-capsules pendent, spindle-shaped. Side **sepals** curving forwards on each side of lip, linear-lanceolate with incurved edges making them trough-like, yellow or yellowish green, sometimes with a reddish edge; upper sepal concave leaning forward over petals, 1-nerved. **Petals** nearly flat with a little spur-like depression at the base, elliptic-oblong, obtusely pointed, 1-nerved, yellowish spotted with reddish brown within, sometimes streaked with violet. **Lip** small, oblong, tongue-shaped, directed upwards and then turning sharply downwards, as long as but broader than the sepals, white, crystalline, with crimson blotches, lines or dots and two broad distant longitudinal slightly raised ridges at the base; side-lobes small, rounded or tooth-like, at the base of the lip, sometimes absent; mid-lobe obtusely pointed or notched with irregularly eroded edges often turned up. **Column** long, slightly curved forwards, convex behind, flat streaked with violet in front, truncate at apex, not winged. **Anther** hinged to back of column and soon falling off, nearly flat, with two hollows above the cells, small, yellowish, turning brown (sometimes even in bud), without beak. **Pollinia** ovoid, almost globular, each divided into two, or bi-partite. **Stigma**

oval or triangular, in front of column just below anther. **Rostellum** small, globular. It is well seen in the two flowers facing forwards in Pl. E, fig. 3.

Habitat. In damp woods, generally on bare soil, amongst fallen leaves, in cushions of moss, in peaty marshes amongst alders, or in damp places amongst sand-dunes. Rather gregarious. Not parasitic, but a saprophyte, living on decaying organic matter. Flowers June to July. Usually a mountain species. In early places it may flower in May, in later ones in August, according to elevation.

Distribution. Apparently confined to Scotland: Aberdeen, Berwick, Edinburgh, Fife, Forfar, Inverness, Kincardine, Perth, Ross. Northern, Central, and parts of Southern Europe (Alpes Maritimes, Bosnia and Dalmatia), Siberia, N. America. Only one European species, but six species in the United States and Canada.

Rouy[1] says the plant is a parasite on the roots of beech. He probably employs the word in a general sense, including saprophytes. It occurs in beech-woods, for the thick layer of dead leaves is favourable to it, but it does not draw nourishment from living plants, and is not therefore a true parasite. It is a saprophyte, without special organs for parasitism. It occurs also on moist ground among sand-dunes, as on the sands of Barry and on Culbin sands, where there are no trees.

Barla says that the pollinia are immediately applied to the stigma,[2] and Camus that it has no rostellum,[3] statements probably due to herbarium material, or possibly to specimens of living plants sent from a distance, from which the rostellum had already been removed by insects. Inconspicuous as they are, the flowers are organised to attract insects, as shown by the white lip spotted with red, the short saccate spur, the groove along the centre of the lip enclosed by parallel ridges leading to the spur, and the viscidium for attaching the pollinia to insect visitors.

The wide distribution—Europe, Asia, and N. America—shows the great antiquity of the species.

Corallorhiza innata R. Br. in Ait. *Hort. Kew.* v, 208 (1813). Ophrys Corallorhiza L., *Sp. pl.* ed. 1, p. 945 (1753). Epipactis Corallorhiza Crantz (1769).

Fertilisation. According to H. Müller (*Alpenblumen*, 1881) the small yellow-green flowers, with only the lip white, appear to indicate that the visitors are small insects with short proboscis, who crawl up the groove in the middle of the lip to the sharp bend near its base (where it turns downwards towards the nectary) and there come in contact with the rostellum, which, together with the attached pollinia, becomes affixed to the head of the insect. There is thus a certain similarity with the lip of *Listera ovata*, which also has a median groove and a sharp bend near the base,

[1] *Fl. de France*, xiii, 218.
[2] *Icon. Orch. Alpes Maritimes*, p. 19 (1868).
[3] Camus, *Icon.* p. 435.

but in *Listera* this groove secretes honey, and there is a relatively large leaf-like rostellum, whilst in *C. innata* no honey is secreted there, and the rostellum is very small. Both are founded on the idea of leading the insect up to a definite point (the angle where the lip bends) where it is bound to come in contact with the rostellum.

Tribe III Epipogoneæ Parlatore

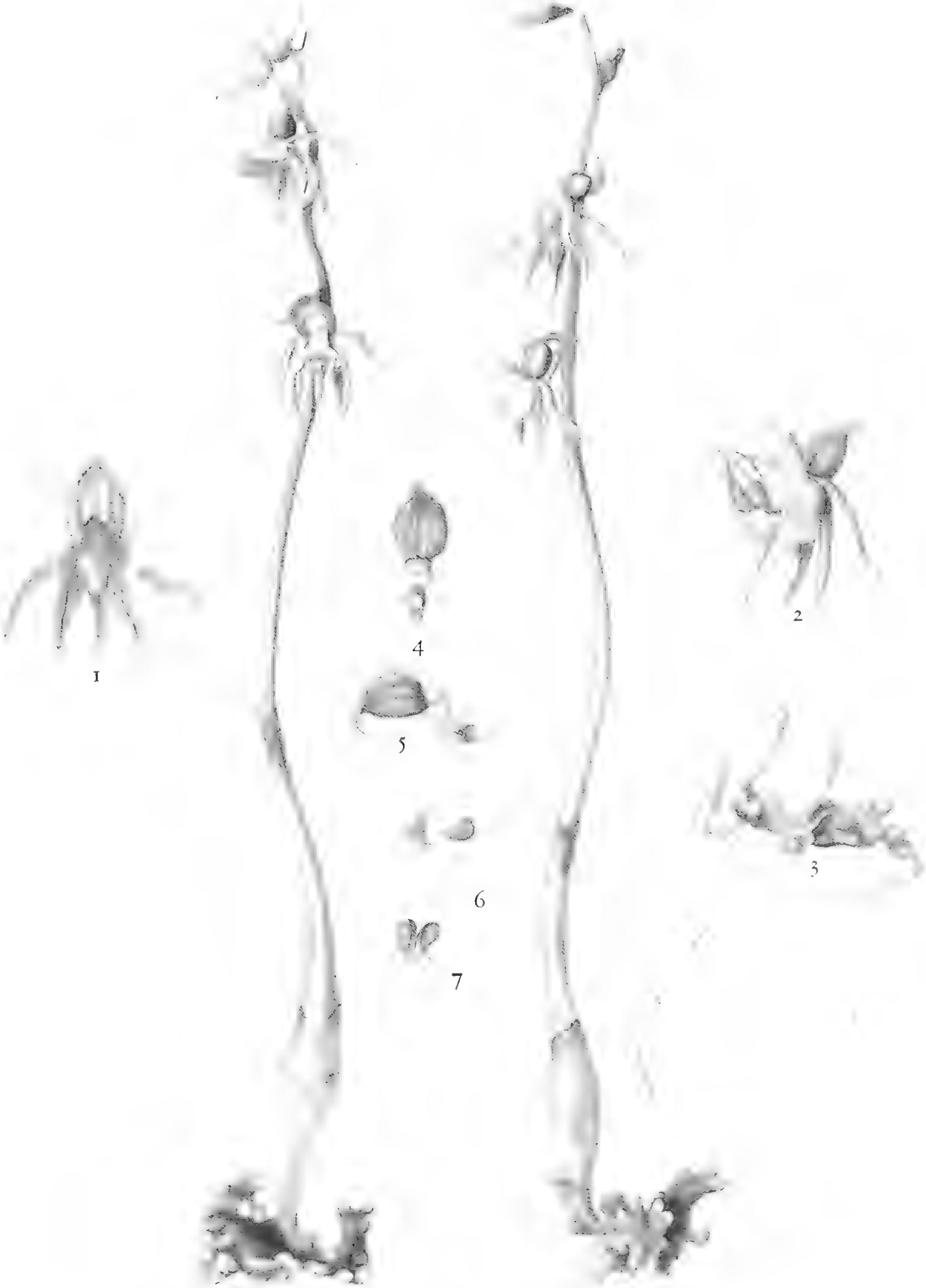
Stigma on projecting foot of column; rostellum heart-shaped. Pollinia pear-shaped, compact, dependent on long caudicles arising from base of pollinium and running up to its apex. Subterranean plants with coralloid rhizome emitting runners but no roots, without leaves or chlorophyll, and with large non-reversed flowers. Only one genus and one species.

Epipogon was considered as a species of *Satyrium* by Linnæus, of *Epipactis* by Crantz, and of *Limodorum* by Swartz. It has been assigned to the Arethuseæ by Reichenbach f., the Gastrodieæ by Lindley, and the Neottieæ by various authors. It really stands alone, and forms a tribe of itself. The following characters are peculiar—the large inverted spur, the downward-facing stigma on the overhanging base of the column, the large rostellum with its cordate viscidium in a V-shaped incision at the apex of the column, and the suspension of the pollinia on long elastic caudicles.

Genus XI EPIPOGON Rich.

Flowers pendent, non-reversed, lip uppermost, sharply bent upwards in the middle, with a rounded lobe on each side, mid-lobe cordate, erect, with tubercled ridges. Spur inflated, erect. **Column** pointing downwards with overhanging base, on which is the stigma, and a deep clinandrium at the apex. **Anther** non-deciduous. **Pollinia** two, pear-shaped, caudicles flat, running up from base nearly to summit. Pollen-grains in tetrads bound together by elastic threads. **Rostellum** large, heart-shaped. Saprophytic subterranean plants without chlorophyll, only the flower-stem appearing above ground, often at intervals of several years. **Rhizome** branched, coral-like, emitting thread-like runners.

> Epipogon Rich., *Mém. Mus. Paris*, IV, 42, 50 (1818). Epipogum Gmelin, *Fl. Sibir.* I, t. 272 (1747).



H. M. Godfery pinx.

EPIPOGON APHYLLUM Swartz
Spurred Coral-root

PLATE 21

Epipogon aphyllum Swartz. Pralognan, Haute Savoie, France, August 14th, 1926.

1. Flower (enlarged), front view.
2. Three-quarter side view.
3. Rhizome, with runners.
4. Column, front view.
5. Side view, with ovary and stalk.
6. Pollinia.
7. Pollinia attached to viscidium.

Figs. 4–7 enlarged.

1. Epipogon aphyllum Swartz

Pl. 21; Pl. E, fig. 5 (p. 108)

Spurred Coral-root, Banana Orchid (German name)

Rhizome without roots, whitish, much branched, resembling coral, branches very short, forked or tri-lobed, lobes rounded at apex, often spreading in a fan like an elk's horn. It sends out one or two long (5–7 cm.) thread-like sinuous whitish runners, with buds at intervals (protected by semi-transparent scales) which give rise to new rhizomes.[1] It is small in proportion to the flowering stem, which is much swollen above its junction with it. A specimen dug up by me at Pralognan, Savoie, grew in a little nest of 6 or 7 small rhizomes. One had two new incipient shoots (Pl. 21, fig. 3). **Stem** up to 20 cm. tall, rarely more, semi-translucent, white, tinged with dull rose or pinkish brown, with numerous short pale rose dashes, sinuous, frail, slightly hollow and tensely full of liquid, much swollen at the base (where there is a cavity for water-storage), tapering suddenly to the rhizome, the attachment sometimes so weak that it falls down if the layer of decayed leaves is gently removed. There are 2–3 yellowish or brownish short sheaths at the base, and 1–2 long close-fitting sheaths on the stem, usually dark-edged, according to Barla sometimes open and funnel-shaped.[2] **Flowers** (1–7) usually only 2–4, distant, large, hanging on a slender stalk, of remarkable appearance, upside down, the mid-lobe of the lip and spur uppermost, the sepals and petals pointing downwards, yellowish, more or less tinged with rose; the thick inverted spur and the heart-shaped deeply concave lip with its dark rose tubercled ridges giving a rather uncanny appearance. The scent is said to resemble that of a banana or the orchid *Stanhopea*. **Bracts** oblong or rhomboidal, obtuse, membranous, semi-transparent, 3-nerved, or without nerves, sheathing the whole bud except the spur. **Ovary** ovoid, short, thick, yellowish, streaked or spotted with violet, without hairs, stalk short, ± 5 mm., curved. **Sepals** long, linear, trough-like through incurved edges, yellowish, sometimes tinged red. **Petals** twice as broad, lanceolate obtuse, trough-like, yellowish with a few short violet lines, semi-transparent and curving downwards like the sepals. **Lip** bent back sharply in the middle so that the back of the epichile (apical half) nearly touches the spur, both pointing obliquely upwards. Hypochile (basal half) with two short rounded lobes directed forwards. Epichile heart-shaped, rather pointed, very concave, with eroded or entire edges, white with violet spots, with irregularly tubercled violet-tinged crests, making it deeply channelled down the middle. Spur erect, ± 8 mm. long by 4 mm. thick, wide, sack-shaped, rounded, white tinged with yellow, sometimes lilac or reddish,[3]

[1] Kerner, *Pflanzenleben* (English translation), II, 111 (1897).

[2] *Icon. Orch. Alpes Maritimes*, Pl. 11.

[3] A. and G. *Syn.* III, 881.

with lines of violet spots inside, faintly visible from without, glabrous and shining within. At the junction of the lip and ovary is a narrow bright yellow ridge with tender skin and hexagonal cells filled with rather viscous sugar-containing fluid, which on gentle pressure flows out in some quantity. **Column** with broad protruding flat-topped foot, above which it is broad and rather flat expanding into a deep cup at apex. **Stigma** on the foot and partly on the face of column. **Rostellum** large, white, heart-shaped, in a fork at the apex of the column (Pl. E, fig. 5), below the stigma in the natural reversed position of the flower. **Anther** helmet-like, rounded, sessile in the concave summit of the column with a slight protruding point just above the rostellum, fastened to the back of the column by a narrow band, not falling off. **Pollinia** pear-shaped, granular, pale yellow, caudicles long, elastic, ribbon-like, attached to base of pollinia and running up nearly their whole length, each fastened to the heart-shaped rostellum. Ripe capsules almost globular, pendent, opening by short slits not reaching base or apex of capsule.

Pl. E, fig. 5, shows a flower (enlarged $2\frac{1}{2}/1$) in its natural hanging position with a sepal and half the lip cut away. The anther has been pushed down a little so as to show the pollinia with their ribbon-like caudicles, which have been detached from the white heart-shaped rostellum.

This extraordinary plant, without roots, leaves, or chlorophyll, is regarded by some authors as parasitic on the roots of *Abies*, beech, and *Vaccinium*,[1] but although found among them, it appears to have no organs adapted for drawing nourishment from them. It is really a saprophyte, deriving support only from decaying organic matter, such as leaves, etc. In this it resembles *Corallorhiza*, *Neottia*, and *Monotropa hypopitys*, its appearance in early stages being so like the last-named that it might easily be mistaken for it at a distance. It is hard to realise that an orchid can be an underground plant, growing and increasing, and giving rise by runners to new plants beneath the soil, going for years without flowering, and only doing so in exceptionally favourable seasons in order to maintain the vigour of the race by cross-fertilisation, after which it usually dies. Roots are replaced by the tabular epidermal cells of the rhizome, whose walls are so thin that they are quite as well adapted for absorbing nutriment as root-hairs. On digging up a plant one finds it growing amongst several living but not stem-bearing rhizomes. The spur in profile is straight in front and curved at the back, with a coloured line down the back and sometimes the front, and its apex is slightly channelled. It contains no free honey. The inner wall is very tender, and there are hexagonal cells between the two walls, where sugary liquid accumulates (and also in the expansion at the junction of lip and ovary) which is exuded on the least pressure. In the swelling at the base of the stem is a large reservoir for water-storage.[2]

[1] Rouy, *Fl. France*, XIII, 216.

[2] Camus, *Icon.* p. 462.

Habitat. Shady woods; in Britain under oak, on the Continent under beech, and sometimes under pine, singly or in colonies. In the few stations in which I have seen it, it has been on ground free from undergrowth. It often disappears from its stations abroad, sometimes for several years, growing and increasing underground by thread-like runners, and then, when a favourable season occurs, suddenly bursting into flower. Flowers July to August. In England it has once been found in June, and once as late as September 3rd.

Distribution. First found in Britain by Mrs W. Anderton Smith in 1854 on a path at the foot of a very steep bank at Tedstone Delamere, near Bromyard, Herefordshire (*Phytologist*, p. 118 (1855)), and figured (*Bot. Mag.* t. 4821 (1854)) from a drawing by the finder, later reproduced in the *Flora of Herefordshire* (1889). On August 23rd, 1854, the Rev. W. Anderton Smith found a colony of it near the original locality, who, fearing its destruction by timber carting, removed it to his garden, where it no doubt soon died. The first specimen found was sent to Prof. Babington, and is in the Cambridge Herbarium. There is a note on the Babington sheet at Cambridge, where there is a painting of the Salopian plant dated August, 1881, that it was seen by a retired chemist named Cockney, who thought it was a deformed Bee Orchid. In 1876 a specimen was found by Miss Lloyd in a wood near Ludlow, Salop, and another in 1878. On September 3rd, 1892, a small flowering specimen was found by Dr G. C. Druce in the same locality, and is now in his herbarium. A solitary example is said to have been found near Ross on Wye, Herefordshire, in 1910. In June, 1924, two small specimens were found in an Oxfordshire wood. The following month Dr Druce was fortunate enough to find a specimen still in flower, but past its best,[1] now in the British Museum Herbarium, S. Kensington.

Continental distribution: Scandinavia, Germany, Austria, Switzerland, France, Pyrenees, Italy, Serbia, Central and S. Russia, Caucasus, Siberia, Himalayas.[2]

> Epipogon aphyllum Swartz, *Summa Veg. Scand.* p. 32 (1814). Satyrium epipogium L., *Sp. pl.* ed. 1, p. 945 (1753). Epipogon Gmelini Rich. (1818). E. epipogium Karsten (1883).

Fertilisation. The flowers have an attractive banana-like scent, resembling that of *Stanhopea*, and secrete nectar. They are wholly dependent on insects for pollination, and are never self-fertilised, which indeed would be impossible, as the pollinia are enclosed with only the tips of their caudicles (stalks) showing, and the stigma is *above* the anther. Some outside agency is therefore essential to withdraw the pollinia from their hiding place and carry them up to the stigma, which must always be that of another flower, as the pollinia are only withdrawn on the departure of the insect. Very few capsules are produced.

[1] *B.E.C.* p. 330 (1923) and p. 453 (1924).
[2] Camus, *Mon. Orch. d'Europe*, p. 364 (1908).

Paul Rohrbach (Prize Essay on *Epipogium Gmelini*, 1866) saw it twice visited by *Bombus lucorum*, which alighted on the thick rounded end of the inverted spur, and crawled over the adjoining tip of the lip, and down its deeply channelled centre to its base, guided by the coloured ridges on each side, and by the spots within the spur (honey-guides). There the lip turns sharply upwards, and the bee on rounding the bend finds itself at the mouth of the spur, and can bore through the tender inner wall, and suck the sweet juice. On retreating from the flower it crawls down the column, and its head comes into contact with the rostellum, the tender skin of which bursts at the slightest touch. The very adhesive matter gushes out, and attaches the viscidium, to which the ends of the caudicles are affixed,[1] to the forehead of the insect, so that the pollinia are thus withdrawn. These would be liable to damage by scraping from the pressure of the anther, were it not for a projecting point on the front of the latter, so arranged that the bee pushes against it on leaving, pressing down the anther, and giving free passage for the easy withdrawal of the pollinia. A similar provision is made in *Epipactis palustris*, from which the pollinia are not cleanly withdrawn unless the apex of the anther is pressed upwards, which is automatically done by the bee on quitting the flower.

Occasionally only one pollinium is withdrawn, but as it contains enough pollen to fertilise a number of flowers, no great harm is done. The viscidium with its ribbon-like caudicles is attached to the bee between the eyes, and the weight of the pollinia makes these lie flat on its head, so that the pollinia project forwards like a pair of club-shaped antennæ. When the bee visits another flower, and pushes his head upwards to reach the nectar, the pollinia come in contact with the projecting stigma, the viscid material of which is sufficiently adhesive to detach a certain quantity of pollen, by breaking the slender threads by which they are fastened to the pollinia. Incidentally it may be mentioned that the lip, if displaced, springs back to its original position near the column. But for this, a humble-bee, pushing his way in, might so widen the space between lip and column that the next visitor carrying pollinia would fail to deposit any of his precious burden on the stigma.

Epipogon is one of the most extraordinary of terrestrial orchids. It affords a combination of characters peculiar to such widely different tribes that it is hard to say what its natural affinities are. Its rootless rhizome and leafless stem resemble those of *Corallorhiza* (Malaxideæ), but the pollinia are like those of the highly evolved Ophrydeæ. It thus combines a character of the Basitonæ with those of the Acrotonæ, and the basal origin of the caudicles also is related to the former of these two great

[1] Rohrbach (*Blutenbau und Befruchtung von Epipogium*, p. 10) states that very seldom do the caudicles fail to become attached to the viscidium which usually emits a little viscid matter which fastens them to it, so that they appear to be covered with a thin white membrane. If they remain free, one or both become attached to the insect by the bursting of the tender skin on being touched and the outflow of the viscid matter. Rohrbach's Prize Essay with two plates is worthy of study.

divisions. The position of the flower with the lip uppermost finds its counterpart in *Liparis* (Malaxideæ) and *Nigritella* (Gymnadeniæ). R. Brown placed it in the Gastrodiæ, especially on account of the deciduous anther, but Rohrbach, who devoted much study to the plant, maintains that the anther is persistent, in which Endlicher concurs. It is often placed in the Neottieæ, having an epichile and clinandrium as in *Epipactis*, but not a cup-like hypochile. None of the Neottieæ has inverted flowers or a coralloid rhizome, however, nor is any genus constructed on the same plan as *Epipogon*. The pollinia are built up of pollen-packets as in the Physurinæ, but there is no other resemblance to that sub-tribe. The coloured ridges of the lip are suggestive of *Cephalanthera*, but nothing could be more different from the latter than the pollinia, long caudicles, and large rostellum of *Epipogon*.

Tribe IV OPHRYDEÆ Lindl.

Anther in one piece with column. Pollinia two, built up of packets of pollen-tetrads attached by elastic threads, and affixed by caudicles in a few species to one viscidium, but as a rule to two separate viscidia.

Sub-tribe I GYMNADENIINÆ Engler, *Syllab.* (1892)

Viscidia not enclosed in a pouch left behind when they are withdrawn.

EBURSICULATÆ Rchb. f.

Sub-tribe II SERAPIADINÆ Engler

Viscidia enclosed in a pouch left behind when they are withdrawn.

BURSICULATÆ Rchb. f.

This division is based on a single character, and is to a certain extent artificial, the latter sub-tribe including the genera *Anacamptis* and *Neotinea*, which have the 3-lobed column and separate lateral stigmas of the genus *Gymnadenia*.

Sub-tribe I *GYMNADENIINÆ*

KEY TO GENERA

A. *No spur.*

1. Plant small, spike slender, prickly-looking. Flowers very small, green; sepals, petals and 3-fid lip connivent. **Herminium**

B. *Spur short, bladder-like.*

2. Flowers green (often edged red), or red-brown. Lip hanging, strap-shaped, 3-toothed at tip. **Cœloglossum**

C. *Spur long, slender.*

3. Leaves two, broad, spike loose; flowers rather large, white or greenish white, lip strap-shaped, undivided; viscid glands round or oval, yellow, facing each other, attached *sideways* to caudicles by their backs. **Platanthera**

4. Leaves several, narrow, spike long, cylindrical, flowers many, small with short 3-fid lip, viscidia linear, pollinia erect on their forward ends. **Gymnadenia**

Genus XII **HERMINIUM** R. Br.

Column very short. **Stigma** bi-lobed, viscidia large, somewhat triangular, with broad upturned edges. **Anther-cells** divergent downwards. **Pollinia** relatively large, elliptical, with very short elastic caudicle.

Small plants with only one fully developed tuber at time of flowering, and 1–4 immature tubers on rather long stalks. **Leaves** two, sometimes 3–4. **Spike** erect, slender, usually dense. **Flowers** small, drooping, green, sub-campanulate, scented. **Ovary** twisted, tapering and bent downwards at apex. **Lip** 3-lobed.

HERMINIUM R. Br. in Ait. *Hort. Kew.* ed. 2, v, 191 (1813). OPHRYS (species) L., *Sp. pl.* p. 1342 (1753). EPIPACTIS Schmidt.

Though included in the Gymnadeniinæ through the viscid glands not being enclosed in a pouch, *Herminium* is not nearly related to any other genus of the sub-tribe. The size, shape and texture of the viscid glands, and their method of attachment to the legs of insects are very remarkable, and find no counterpart in any other European genus.

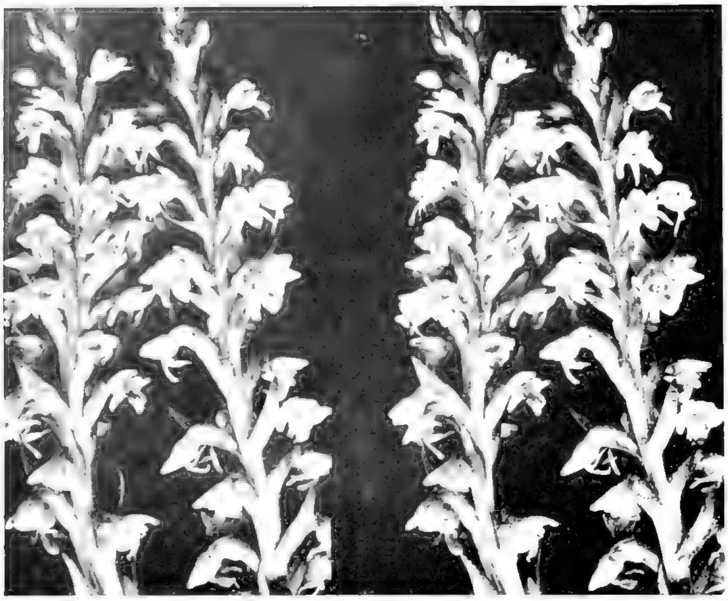


Fig. 1. *Gymnadenia albida* Richard.

Fig. 2. *Gymnadenia conopsea* R. Br. Flower enlarged (5/1), showing concave lateral stigmas on side-lobes of column, and staminodes on each side of anther above stigma.

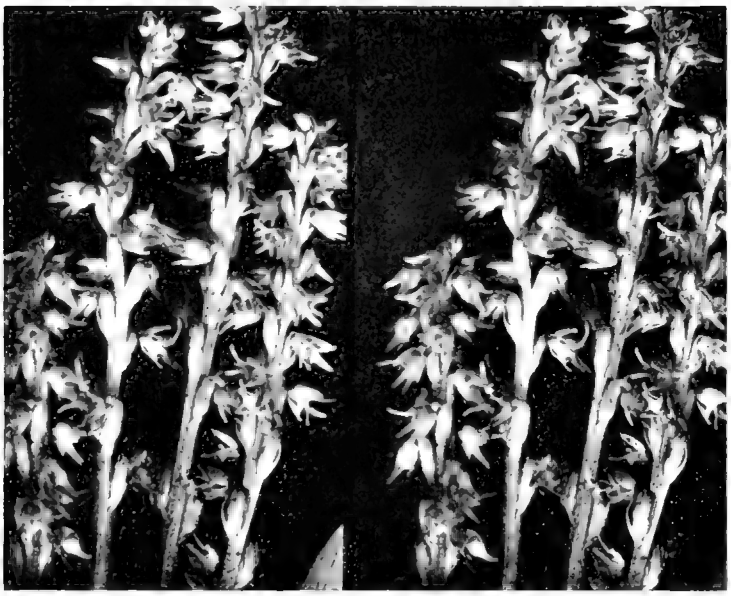


Fig. 3. *Herminium monorchis* R. Br.

Fig. 4. *Neotinea intacta* Rchb. f. (2·6/1.) Lowest left-hand flower shows lateral stigmas as in fig. 2 above, pouch of rostellum, and pollinia *in situ* in the anther.

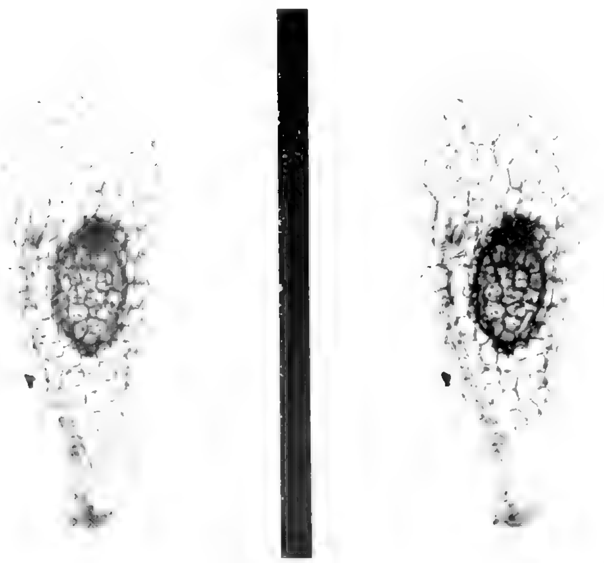


Fig. 5. Seed of *Loroglossum hircinum*, 55/1.

Fig. 6. *Anacamptis pyramidalis* Richard.

1. Herminium monorchis R. Br.

Pl. 23 B (p. 130); Pl. F, fig. 3. *Musk Orchid*

Tubers globose, as big as a pea, sometimes twice or thrice that size, the flowering one sessile, the rest, usually 2–3, sometimes 4–5, on long stalks (up to 10 cm.), semi-transparent, slug-like, immature; roots few, rather slender. **Stem** 8–20 cm. tall (sometimes more), stiff, erect, slender, rounded, glabrous, angled above, yellow-green or dark green with one or two close-fitting leafless sheaths at base. **Leaves** two, sometimes 3–4, oblong, obtuse or acute, keeled, flat or slightly folded, spreading, glabrous, yellowish or bluish green, with one principal, and fainter intermediate nerves on each side; upper leaves 1–3, sessile, small, bract-like, tapering, acute. **Spike** 1–5 cm., slender, cylindrical, erect, many-flowered, dense, "sometimes very lax" (Webster), often one-sided. **Flowers** very small ($\pm$ 4 mm.), drooping, sub-campanulate, yellow-green or green, sweet-scented, the lower somewhat distant. **Bracts** usually shorter than ovary, but the lowest sometimes as long as the flowers, lanceolate, tapering, 1-nerved, green. **Ovary** sessile, erect, cylindrical, slightly twisted, prolonged and bent downwards at apex, pale green. **Sepals** connivent, making the flower almost tubular, the upper broader, oval, rounded at tip, the lateral ovate-lanceolate, obtuse, 3-nerved. **Petals** longer and narrower with a rounded angle or tooth on each side, then suddenly narrowed, strap-shaped, obtuse. **Lip** equal to or slightly longer than petals, 3-lobed, dagger-shaped, with a small cup-like hollow at base; side-lobes short, widely divergent or curved downwards, mid-lobe longer and broader, linear obtuse. **Column** small, short, broad. **Anther** rounded, cells slightly divergent at base, with a large plate-like quadrilateral staminode on each side, with rounded angles. **Pollinia** oval, white, relatively large, packets of pollen rounded, suggesting a microscopic bunch of grapes, caudicles short, thick, elastic, vertically attached to the hinder end of the viscidium, which is large, obscurely triangular, with the edges turned up, very sticky beneath and resting on a narrow strip of membrane, easily pushed away. **Stigma** transversely 2-lobed, the broad part of each lobe directly beneath the viscid gland, surrounded by glabrous thickened walls. Seed-capsule oblong, tapering at the base, with six ridges. **Seeds** short, extremely small, nearly linear (figured in Reich. f. *Icones*, Pl. 63, fig. 23), ripe about mid-September (Webster). Pl. F, fig. 3, gives a good idea of the habit of the plant.

As a rule only 3 or 4 inches tall, with 2–3 short leaves and a stiff little prickly-looking spike of green curiously scented flowers. Though called the Musk Orchid, the flowers do not smell of musk, but have a honey-like indefinable scent with a faint suggestion of cobbler's wax. The only British orchid resembling it is *Malaxis paludosa*, which has wide-open flowers with the lip pointing upwards, and is only found in boggy ground, usually growing in *Sphagnum*. In the plains *Herminium* rarely seeds, but increases by the supplementary tubers.[1]

HABITAT. Chalk downs, mountain pastures, grassy hills, meadows, "dunes, plains, sub-alpine marshes", usually on calcareous, but sometimes on clayey damp soils (Camus). It usually occurs in colonies, owing to the production of additional tubers. It ascends to 5000 ft. in Switzerland and Savoy, and 8000 ft. in the Caucasus, according to Schlechter. Flowers June to July. Rare in Britain, and very local.

DISTRIBUTION. Southern and Eastern England, Kent, Surrey, Sussex, Hants., Dorset, Somerset, Gloucester, Wilts., Bucks., Beds., Northants., Cambridge, Suffolk, Norfolk, Oxford (Sowerby, *E.B.*). Most of Europe, from Norway and Sweden to the Mediterranean, Caucasus, Himalayas, throughout Siberia in both dry and damp meadows (Reich.), Yunnan, Eastern Mongolia (Camus).

> HERMINIUM MONORCHIS R. Br. in Ait. *Hort. Kew.* ed. 2, v, 191 (1813). OPHRYS MONORCHIS L., *Sp. pl.* ed. 1, p. 947 (1753). ORCHIS MONORCHIS All. EPIPACTIS MONORCHIS Schmidt. HERMINIUM CLANDESTINUM Grenier et Godron, *Fl. France* (1856).

FERTILISATION. The flowers, though very small and inconspicuous, emit a strong honey-like odour, and are highly attractive to minute insects not as a rule exceeding one-twentieth of an inch in length. They are visited by very small Hymenoptera, the most frequent of which is *Tetrastichus diaphantus*, by flies, and by *Malthodes brevicollis*, a beetle.[2] Hermann Müller saw them visited in the Alps by small Braconidæ and Pteromalidæ, parasitic Hymenoptera with similar habits to Ichneumonidæ.[3] They enter the drooping flower at a corner between the lip and a petal, crawling in with their backs to the lip, and inserting their heads and forelegs into the basal cup. In doing so the projecting joint formed by the coxa and the femur of one of the front legs readily slips into the hollow base of the viscid gland, the adhesive matter of the latter gluing it firmly to the elbow or to the surface of the femur. The pollinium then moves downwards till it projects just beyond the tibia. The insect, on entering another flower, can hardly fail to deposit pollen on the stigma, which lies just beneath the viscid gland on either side. The extraordinary shape of this gland is therefore clearly an adaptation to enable it to fit like a cap on the projecting joint of the insect's foreleg.

[1] Camus, *Icon.* p. 364.
[2] Darwin, *Fert. Orch.* ed. 2, p. 61.
[3] *Alpenblumen*, p. 72 (1881).

H. M. Godfery pinx.

A. CŒLOGLOSSUM VIRIDE Hartmann
Frog Orchid

B. CŒLOGLOSSUM VIRIDE × ORCHIS MACULATA
Orchicœloglossum mixtum A. and G.

PLATE 22

A. **Cœloglossum viride** Hartm. Winchester, July 12th, 1917.

1, 2. Single flowers (enlarged).

B. **Cœloglossum viride** × **Orchis maculata.**

Orchicœloglossum mixtum A. and G. Winchester, July 15th, 1918.

3, 4. Flowers, front and side views.

5. Flower of another type. Winchester, June 26th, 1916.

Figs. 3, 4 and 5 enlarged.

Genus XIII CŒLOGLOSSUM Hartman

Column short, anther broader than long, cells divergent downwards, pollinia with short ribbon-like caudicles, viscidia little broader than caudicles, one on each side of the central stigma on the back of the spur-chamber.

Small herbs with palmate tubers, ovate or oblong leaves, small green or brown flowers, sepals connivent in a helmet, strap-shaped lip, and short saccate nectariferous spur.

Hartman, *Handb. Scand. Flora*, ed. 1, p. 329 (1820). PERISTYLUS Lindl. (1835). Included in HABENARIA by R. Br. (1813).

1. CŒLOGLOSSUM VIRIDE Hartman

Pl. 22 B; Pl. C, fig. 3 (p. 50). *Frog Orchid*

Tubers two, thick, palmate with two (rarely three) carrot-shaped segments; roots few, short. **Stem** 6–25 cm. tall, solid, erect, cylindrical, angled above with often reddish ridges, and with 1–2 brown obtuse leafless sheaths at base. **Leaves** alternate, 3–5, bluish green, ovate to oblong, rather obtuse, with winged stalk, and 3–5 nerves on each side of mid-rib with numerous cross-veins; the upper 1–2 lanceolate acute, sessile, with long sheath. **Spike** usually short (sometimes up to 9 cm. or more), few- or many-flowered, loose or rather dense. **Flowers** rather small, inconspicuous, distant or close together, green, sometimes more or less edged or suffused with reddish brown, or wholly red-brown, faintly scented. **Bracts** lanceolate to oblong, rather obtuse, green or suffused with reddish brown, 3-nerved with irregular cross-veins, very variable in length, usually longer than ovary, sometimes 2–3 times as long. **Ovary** cylindrical or spindle-shaped, twisted, green or brownish, with six slight ridges. **Sepals** short, ovate obtuse, forming a semi-globular hood, the upper slightly shorter, 3–5-nerved, free or partly adherent. **Petals** linear-lanceolate, very narrow, 1-nerved, acute, often protruding from the helmet. **Lip** linear-oblong, slightly enlarged downwards, thick, flat, green often edged red, hanging or bent backwards, 3-toothed at apex, side-teeth 1–3 mm. long, lanceolate, pointed, curved forwards, middle tooth shorter, obtuse, often reflexed, with an obtuse keel down the centre in front and two shallow thickened ears where it joins the column, forming a chamber at the mouth of the spur. **Spur** very short ($\pm$ 2 mm.), bladder-like, semi-transparent, greenish white, flattened from back to front, rounded, sometimes grooved at the apex, which is slightly curved forward, with a green band running from the column down the middle of the back and up the front. **Column** short, broad, viewed from behind like the ace of clubs. Staminodes whitish, large, obtuse. **Anther**

broader than long, cells club-shaped, brownish, touching at apex, divergent below. **Pollinia** pale greenish yellow, together with the straight ribbon-shaped caudicle just under 2 mm. long. Viscidia two, oval, separated by a thickened arched ridge, each enclosed in a tender skin. **Stigma** kidney-shaped, on back of chamber at base of lip, bordered by dark side-lines.

Easily recognised by the green flowers with almost globular green or red-brown helmet, and the strap-shaped often red-edged lip, ending in three teeth, the middle one shorter and broader than the side ones. Rarely more than 8 in. (20 cm.) tall in Britain. Varies but little except in the very variable length of the bracts, sometimes short (var. *microbracteatum* Schur), sometimes considerably exceeding the flowers (var. *bracteatum* K. Richt.), sometimes very long and leaf-like (var. *macrobracteatum* Schur), and in the amount of red-brown with which the flowers are suffused. Reichenbach states that it is the first orchid to reappear in fields when turned into meadows, and holds its own tenaciously in meadows turned into woods, which perhaps explains its presence in such an unusual habitat. It sometimes remains underground for two or three years and then reappears in plenty. The name Frog Orchid appears to be rather fanciful, but the side-view of the flower is sometimes faintly suggestive of a frog. Pl. C, fig. 3, shows a specimen of the var. *bracteatum* from near Mold, N. Wales, photographed by Col. C. T. Green, June 4th, 1927.

Habitat. Moist or dry pastures, chalk downs, grassy hillsides especially on calcareous soil, also (rarely) in woods, and occasionally on sandhills. Flowers June to August.

Distribution. Frequent in Northern England, Scotland and Ireland, where it occurs at sea-level in N. Donegal and Kerry, and ascends to 1000 ft. (349 m.) in Derry, Dublin and Clare. Not so frequent in Southern England and Wales. Most of Europe, from Iceland and Scandinavia to Spain, Italy and Northern Balkans; Mid- and S. Russia, Caucasus, Asia Minor, Siberia, China, N. America.

Fertilisation. The spur contains free nectar, which can be seen to rise on pressure. Just below the viscid disc at the foot of each pollinium there is also a shallow depression glistening with nectar. The ridge down the middle of the lip causes an insect to crawl up on one or other side of it, and thus guides it to the exposed drop of nectar on that side. In licking this up it is almost sure to touch the viscid disc immediately above it, and carry off the pollinium attached to its head. It then goes to the small orifice leading to the spur, where it finds ample provision of nectar. The pollinium moves downwards very slowly, and does not reach the position in which it can touch the stigma for about 20 minutes or more. An insect can thus visit all the flowers open on the spike, and perhaps some of those on another plant, without depositing any of the pollen on their stigmas, but when once the pollinium has moved down to the right position, some of its pollen will be left on each stigma subsequently visited.

Darwin thought that an insect might visit all three nectaries, but this is improbable in view of the abundant contents of the spur. An insect alighting on the opposite side of the lip would similarly remove the other pollinium.

I can find no record of what insects visit this species, but on the Col de Granier above Chambéry, on June 11th, 1924, my wife saw a long slender insect with black thorax, orange abdomen and black tail, subsequently identified at the Paris Museum as *Tenthredopsis tarsata* F., visit two or three flowers of *C. viride*, and emerge with pollinia on its head. She caught it in her fingers and put it into a match-box. The pollinia were attached to the head between the eyes and beneath the antennæ. Below were the remains of another pollinium with most of the pollen gone.

CŒLOGLOSSUM VIRIDE × GYMNADENIA CONOPSEA

Gymnaglossum Jacksonii Rolfe, *O.R.* p. 117 (1919)
Cœloglossogymnadenia Jacksonii A. Camus (1928)
Gymplatanthera Jacksonii Quirk, *Winchester Coll. N.H. Rep.* p. 33 (1911)

Pls. 23 A (p. 130) and 29 B (p. 146)

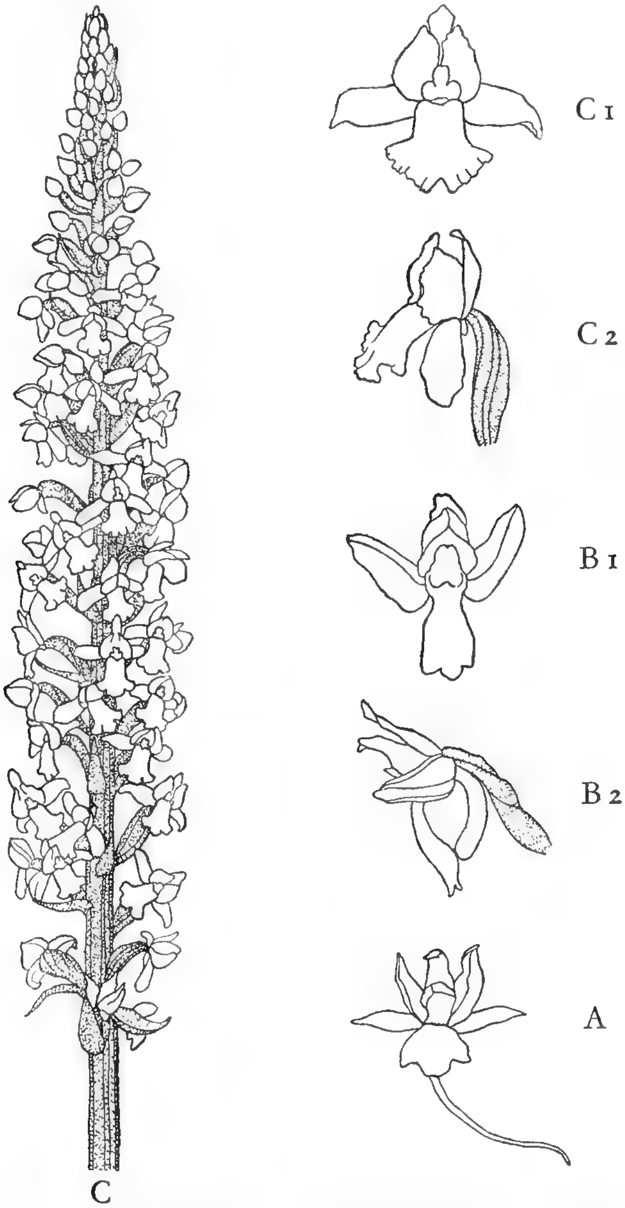
Three types of this hybrid have been found in England:

(1) A form first found in 1909 by Mr Jackson near Winchester, and described by the Rev. R. Quirk as follows: "Much shorter than *G. conopsea*. Flower-spike either pink tinged with green, or dull livid red. Corolla pink or purplish, but overspread with a marked tinge of pale yellowish green. Bud blunter and squarer, as in *C. viride*. Sepals and petals not connivent in a helmet, but open and spreading, exposing the column, thus differing from both parents. Spur shortened, but not to the small blunt pouch of *C. viride*. Bracts as a rule larger and more leaf-like, as in the latter. Described from an indifferent specimen, no good specimen having been found this year".[1] (Text-fig. 10 A.)

To the above may be added the following description of a cut spike sent to us, July 17th, 1917, by Donald Lowndes, then a boy at Winchester College (Pl. 23 A). Stem about 10 cm. tall. Lower leaves not seen, upper leaves several, erect, bract-like, linear-lanceolate, acute, the lower bracts exceeding the flowers, the upper the ovary. Spike cylindrical, dense, flowers small. Sepals sub-equal, pale lilac rose, in some flowers greenish tinged with rose, the lateral spreading incurved, not recurved at the tip as in *G. conopsea*. Petals oblong, slightly longer than sepals, nearly erect, in some of the lower flowers forming a loose hood with the upper sepal. Lip broadly oblong, the mid-lobe tongue-shaped, broad, slightly emarginate, the side-lobes barely

[1] *Winchester Coll. N.H. Soc. Rep.* p. 33 (1909–11).

reaching the middle of the lip, narrow with obtuse tip, the mid-lobe slightly arched, with a somewhat ribbed appearance due to very shallow longitudinal ridges and



Text-fig. 10. *Cœloglossum viride* × *Gymnadenia conopsea*. A. Winchester, 1909. B 1, B 2. Winchester, 1915. C, C 1, C 2. Salop, 1912. Pen-and-ink drawing by Dr T. A. Stephenson, O.R. April, 1922.

furrows. Spur shorter and stouter than in *G. conopsea*, about twice as long as the rather short ovary, curved forwards in nearly a semicircle. Anther apparently abortive.

(2) A second form was also found near Winchester in June, 1915, by the Rev. R. Quirk (Text-fig. 10, B 1 and B 2) and described as follows[1]: "The inflorescence is more like *viridis*; the spur is short (5–6 mm. when fully developed, less in the younger flowers); the labellum is shaped like that of *viridis*, and when first open, the rose-purple coloration appears on the lateral lobes only, the rest of the labellum being a delicate primrose-green, which gradually changes to rose-purple almost all over. The tilt of the flowers is marked".

From the accompanying figure it appears that the sepals are oblong, broad and obtuse, the lateral spreading obliquely, the upper conniving with the petals to form a hood, the lip is oblong, wedge-shaped, ending in three rounded teeth, without side-lobes, and the spur is cylindrical, thick, curved forward with rounded end. This form is much nearer to *C. viride* than the preceding one, especially in the sepals, the more or less closed hood, the shape of the lip and the spur, all of which show clearly the influence of the *Cœloglossum* parent. Another form was found closely resembling *G. conopsea*, except for the presence of the green colour, and also one in which the labellum was almost undivided and green, though the spur remains long. It is possible that these were crosses between a first generation hybrid and one or other of the parents.

(3) This remarkable form was found near Cressage, Salop, on June 26th, 1912, growing in company with both parents, by the late Mr R. F. Burton of Longner Hall, Salop, who transferred it to his garden. A pen-and-ink drawing of the 1916 spike of this plant, with front and side views of enlarged flowers, by Dr T. A. Stephenson, appeared in the *O.R.* p. 101 (1922) (Text-fig. 10, C 1 and C 2). In that year's spike the sepals were pale green and obtuse, and the lip and petals rose-lilac. Pl. 29 shows the spike of July, 1919, which was only 6 cm. long, that of 1916 having been 16 cm. in length and that of 1917 16½ cm. The stem in the latter year reached the extraordinary height of 74 cm. (2 ft. 5½ in.) which seems to have exhausted the plant, for in 1919 it was only 24 cm. tall, as received in a cut state. Its general appearance was that of *G. conopsea*, and the great stature of the 1917 plant made me at first extremely sceptical of its hybrid origin. I was inclined to concur with Mr Burton, who called it a spurless *G. conopsea*. On further study, however, the following points appeared strongly to indicate the part-parentage of *C. viride*. (1) The pale green sepals of the 1916 spike. Those of 1919 were pale rose, but in flowers which opened in the house they were greenish. (2) The undivided lip, wedge-shaped at base, fan-like at apex. In some flowers a slightly projecting acute tooth at the apex of the lip was strongly recurved, making the lip look bi-lobed, whilst the shallow rounded side-lobes pointed forwards, and were, together with the shape of the lip, very suggestive of *C. viride*. (3) The spur was as small as in *C. viride* and of similar

[1] *Winchester Coll. N.H. Soc. Rep.* p. 9 (1913–15).

shape, sometimes even smaller, and indeed absent from some flowers, showing that the spur-building mechanism was thrown out of gear, sometimes failing to work, sometimes forming a spur resembling *C. viride*. The time of flowering, July, agrees with the latter species. The lower bracts were lanceolate, just exceeding the ovary; the flowers about the size of *G. conopsea*, pale rose and scented, but not like *G. conopsea*;[1] the side-sepals spreading and recurved, the upper erect; the petals ovate-acute, keeled, not so broad at the base as in *G. conopsea*, but erect and spreading, thus differing from both parents. Mlle Camus has named this form var. *biloba*.[2]

Habitat. Chalk downs, together with the parents.

Distribution. Hants. (Winchester!); Salop! It has never been found on the Continent.

CŒLOGLOSSUM VIRIDE × ORCHIS LATIFOLIA

Orchicœloglossum Drucei Camus

Pl. 23 C

Tubers not dug up, doubtless palmate as in both parents. **Stem** 18–21 cm., solid. Lower **leaves** oblong-lanceolate, rather short and broad, with faint transverse sometimes ringed spots in some plants and small faint sparse spots on others; upper two bract-like, narrow, acute. **Spike** nearly cylindrical, 5–7 cm., rather dense or somewhat lax at the base, with about 25 dull rose flowers. **Bracts** linear-lanceolate, tapering to a fine point, lower longer than flowers. **Sepals** lanceolate, erect, spreading, dull rose (in one specimen greenish in the middle and slightly spotted). **Petals** at first connivent with upper sepal to form a hood, later nearly erect, dull rose unspotted. **Lip** longer than sepals, oblong or slightly obovate, 3-toothed at apex with two broad longitudinal stripes of continuous or interrupted rose colour on a whitish ground occupying most of the lip. **Spur** short, barely half as long as ovary, rather thick, rounded at tip. **Pollinia** brownish, *viscid glands not enclosed in a pouch.*

The parentage of *C. viride* is clearly shown by the habit, low stature, short broad leaves, oblong 3-toothed lip, often with side-teeth curved forward, and short rather sack-like spur. That of *O. latifolia* is suggested by the ring-spotted or spotted leaves, rather dark-coloured flowers, erect spotted sepals, small mid-lobe of the lip, and by the spur, longer and less saccate than in *Cœloglossum*.

The plant is evidently a hybrid of *Cœloglossum viride* with a spotted-leaved orchid, and the only two such present with it being *O. latifolia* and *O. maculata*, the second parent must be one of these. Two hybrids of *C. viride* with *O. maculata* were found in the locality (*vide* Pl. 22), and in both the resemblance to *O. maculata* was at once

[1] *O.R.* p. 103 (1922). [2] *Icon.* p. 378.

PLATE 23

A. **Cœloglossum viride** × **Gymnadenia conopsea. Gymnaglossum Jacksonii** Rolfe. Winchester, July 17th, 1917.

1, 2. Enlarged flowers.

B. **Herminium monorchis** R. Br. Winchester, July 12th, 1917.

3. Enlarged flower.

C. **Cœloglossum viride** × **Orchis latifolia. Orchicœloglossum Drucei** Camus. Winchester, June 26th, 1916.

H. M. Godfery pinx.

A. CŒLOGLOSSUM VIRIDE × GYMNADENIA CONOPSEA
Gymnaglossum Jacksonii Rolfe

B. HERMINIUM MONORCHIS R. Br.
Musk Orchid

C. CŒLOGLOSSUM VIRIDE × ORCHIS LATIFOLIA
Orchicaloglossum Drucei Camus

recognisable by the deeply trifid lip characteristic of the form of *O. maculata* abundant on the downs. *O. latifolia* is essentially a marsh orchid, but strangely enough a few plants of it grew on the dry chalk downs near the hybrid. The spotting of the leaves most resembled that of *O. latifolia*, some spots being green in the centre, a frequent occurrence in *O. latifolia* but very rare indeed in *O. maculata*, and perhaps even then due to previous crossing with *O. latifolia*. The solid stem is, however, in favour of *O. maculata*, but though the stem of *O. latifolia* is hollow in marshy places, the form on the downs is of shorter stature and has a nearly solid stem. The author regrets that he did not make sections of the stem of the hybrid, but formed his opinion of its solidity by its non-compressibility, a test not always reliable, as the walls may be thick enough to resist compression, even with a tube down the centre.

Dr Keller of Aarau, whose work on European orchids is in course of publication, wrote with reference to the above: "J'ai la conviction que les deux plantes qui sont peintes entières [Pl. 23 and another] sont des *C. viride* × *O. latifolia*. Le rouge foncé, la longueur du tige, les feuilles, la forme du labellum; enfin tout plaide pour un hybride avec *latifolia*. Quant à la troisième plante qui n'est représentée que par une fleur isolée [Pl. 22, fig. 4]...je crois que c'est un hybride *Cœloglossum* × *O. maculata*. C'est surtout la couleur, le rouge plus pale, beaucoup moins foncé qui disparaît presque devant le vert saturé de *Cœloglossum*, qui plaide pour l'*O. maculata*, en outre la forme du labellum qui rappelle beaucoup plus les formes plus aiguës de *maculata* que de *latifolia*. Étrange hasard cependant de trouver en même temps 2 exemplaires de *Cœloglossum* × *latifolia*, avec un exemplaire de *Cœloglossum* × *maculata*! J'ai une aquarelle de *Cœloglossum* × *maculata* trouvé en France; cette plante ressemble beaucoup à votre fleur isolée mais nullement à une des autres de vos 2 plantes entières. En tout cas ce sont des plus beaux et étranges hybrides que j'ai jamais vus".

Distribution. So far only known from chalk downs in the neighbourhood of Winchester. It has never been found on the Continent.

Mlle A. Camus (*Iconographie*, p. 377 (1928)) gave the name *Orchicœloglossum Drucei* to *C. viride* × (*O. incarnata* × *maculata*). This is the same plant as the present hybrid, the difference in parentage being due to Dr Druce's opinion that British *O. latifolia* is the hybrid *O. prætermissa* × *maculata*, the form of *O. incarnata* referred to being later named *Orchis prætermissa* by Dr Druce (*B.E.C.* p. 340 (1913)), 1914. I therefore retain the name in honour of that eminent botanist.

CŒLOGLOSSUM VIRIDE × ORCHIS MACULATA

Orchicœloglossum mixtum A. and G.

Pl. 22 B (p. 125)

This very rare hybrid combines the characters of both parents in varying manner in different plants. The first specimen recorded was found near Morpeth in July, 1891, and described by the late R. A. Rolfe under the name *Habenari-orchis viridi-maculata*. It resembled *O. maculata* in the general shape of the flower, the spreading sepals and obovate lip. The *Cœloglossum* parent was evidenced by the strong suffusion of green in the pale lilac flower, the tooth-like mid-lobe, and the short forward-curved somewhat club-shaped spur, and especially by the viscid discs not being enclosed in a pouch in the column (*c*), though they are clearly so in the flower (*a*) of the original illustration.[1] A specimen found by me near Winchester, June 26th, 1916, had greenish flowers with faint purple streaks on the lip, the latter with narrow pointed side-lobes curved forward at the tip, and longer narrow tapering mid-lobe, the sepals and petals spreading acute. The leaves were faintly spotted, and the bracts, buds and sepals brownish outside (Pl. 22, fig. 4). Another specimen from the same locality, July 15th, 1918, was 12 cm. tall, with faintly spotted leaves, narrow spike, with 17 dull rose flowers with a whitish streak down the lip, ovate-lanceolate spreading sepals with recurved tips, a wedge-shaped lip with rhomboidal side-lobes curved forward at the tip, a slightly longer tongue-shaped mid-lobe, and a rather thick cylindrical obtuse spur, two-thirds the length of the ovary, with a triangular entrance. The viscid discs were not enclosed in a pouch, the pollinia were dull olive-green, and the stigma was on the roof of the chamber beneath the anther, with a purple line on each side (Pl. 22 A).

Another plant found on the Winchester downs by Mr Comber, G. Philipson Stow and myself in June, 1916, was $13\frac{1}{2}$ cm. tall, with short rather broad spotted leaves, and a short lax 6-flowered spike. Flowers like *O. maculata*, but side-lobes of lip, which was green with purplish edges and spots, curved forwards, and the mid-lobe curved backwards as in *C. viride*, while the thick sack-like but rather long forward-curved spur was intermediate between those of the parents. The viscid discs were not enclosed in a pouch.[2]

Two specimens were found in a field at Levally in Ireland in July, 1919.

Ten years after the first specimen referred to above a single example found on the frontier of Bohemia was described by Domin[3] as *Orchis mixta*, and was later named

[1] *Ann. Bot.* Pl. 18 (1892).
[2] *Winchester Coll. N.H. Soc. Rep.* Plate facing p. 12 (1915–17).
[3] *Sitzb. Böhm. Ges. Wiss.* No. XXII, p. 7.

Orchicœloglossum mixtum by Ascherson and Graebner,[1] and *Orchicœloglossum Dominianum* by Camus.[2]

HABITAT. Chalk downs, rarely in fields. V.R.

DISTRIBUTION ABROAD. Riesengebirge, E. Prussia (one specimen), Bohemia, France (Masseube), where the only specimen found resembled a large and superb *O. maculata*. The habit of British plants is nearer that of *C. viride*. Although both parents were abundant at Sils Maria, in the Engadine, I could find no hybrid.

Genus XIV PLATANTHERA Rich.

Anther united with column, open at apex, cells parallel or divergent downwards. **Pollinia** stalked. Viscidia round or oval, naked, without pouch, placed laterally in the flower, facing each other, attached to the side of the caudicles, not to the tip. Small or medium-sized herbs with the habit of *Orchis*. **Tubers** undivided, tapering. **Stem** erect. **Leaves** unspotted, in our species two (rarely three), near base, broad, upper 2–4 bract-like. **Spike** loose, many-flowered, flowers of medium size, white, sweet-scented. **Side-sepals** spreading, upper sepal and petals forming a shallow arch protecting the column. **Lip** undivided, strap-shaped, spur (in our species) long, slender with free nectar.

PLATANTHERA Rich., *Mém. Mus. Paris*, IV, 48 (1818). ORCHIS L. (1753). HABENARIA R. Br. in part (1809).

KEY TO SPECIES

1. Pollinia sloping backwards, divergent downwards, 4 mm. long, caudicle longer than pollen-mass. Viscid discs, large, circular, $\pm$ 4 mm. apart. Anther flat, truncate above. **P. chlorantha**
2. Pollinia vertical, parallel, about 1 mm. apart, caudicle shorter than pollen-mass. Viscid discs small, oval, 1 mm. apart. Anther folded vertically forwards, like an inverted letter **U** in horizontal section. **P. bifolia**

1. PLATANTHERA CHLORANTHA Rchb. p.

Pl. 24 (p. 134). *Greater Butterfly Orchid*

Tubers two, entire, tapering downwards, obtuse, sometimes tailed; roots few, stout, brown. **Stem** 20–40 cm. tall (up to 60 cm. abroad), erect, rigid, robust, solid, angled or ridged above through decurrence of the mid-ribs and edges of the bracts and

[1] *Syn.* III, 847 (1907).

[2] *Mon. Orch. Eur.* p. 322 (1908).

leaves, with 1–3 oblong brown ribbed leafless sheaths at base. **Leaves** basal, two (very rarely three), broadly oblong to oval-oblong, 6–18 cm. long by 3–7 cm. broad, narrowing towards the base, obtuse, pale usually yellowish green, glabrous, glossy beneath and sometimes above, strongly keeled, with ± 7 transparent parallel veins on each side of the thick mid-rib, with numerous translucent dashes between; upper leaves 2–6, sessile, linear-lanceolate, bract-like, narrow. **Spike** cylindrical, lax. **Flowers** larger than those of *P. bifolia*, 10–25, greenish at first, then greenish white, rarely pure white, with green-tipped lip, sweet-scented, but only at night as a rule. **Bracts** 5–10 mm., green, lanceolate, equalling or half as long again as the ovary, 1-nerved, with numerous longitudinal dashes. **Ovary** not stalked, slender, cylindrical, curved, ± 15 mm. long, twisted, with six obtuse ridges. Lateral **sepals** 10–13 mm. long, 5–6 mm. broad, ovate-lanceolate or lanceolate, obtuse, obscurely 3-nerved; upper sepal shorter and slightly broader, triangular with rounded angles, about 8 × 8 mm., obscurely 3-nerved, slightly inclined forward. **Petals** (7–9 × 2 mm.) linear-lanceolate, curved, somewhat sickle-shaped, rounded out in front at base, their tips nearly touching, with three hardly visible nerves, forming with the upper sepal a shallow Gothic arch over the column. **Lip** (12–15 × 3–4 mm.) hardly longer than the sepals as a rule, linear, strap-shaped, slightly narrowing towards the rounded tip, firm in texture, faintly 5-nerved, white, with green tip, sometimes mostly greenish (in long-opened flowers sometimes nearly pure white), directed downwards. **Spur** very long ($2\frac{1}{2}$–3 cm. or more), about twice as long as ovary, compressed from above at the base, so that the entrance is transversely oval, often flattened and somewhat club-shaped at the obtuse tip, yellowish white more or less suffused with green, horizontal or directed downwards, but both positions, and sometimes an ascending spur also, may be found on the same spike. **Column**, basal wall curving round in a white-tipped wing overlapping the stigma on each side. **Stigma** resembling a scallop-shell, concave, green-edged above, situated on the trumpet-shaped throat of the flower above the spur-entrance. **Anther** flattened out, truncate above, the green wavy "connective" furrowed down the back separating the two cells, which slope backwards and diverge downwards, the foot of each cell resting on the outer edge of the stigma. Viscidia two, facing each other, one on each side of the stigma, 3–4 mm. apart, thin, flat and circular, with a tiny drum or pedicel on the non-viscous side, to which the end of the caudicle is attached by its side, its tip projecting like a little tail. **Pollinia** pale yellow, split in two, shorter than the transparent bright yellow caudicles, the whole 4 mm. long. Outside the base of each anther-cell is a rather large hyaline staminode. The tip of the spur is filled with nectar for 4 mm. or more—on squeezing the liquid can be seen to rise in the tube. There is only one wall to the spur—no inner layer as in *Orchis*. In section it is not circular, but bluntly **V**-shaped below and semi-circular above, with a row of erect short hairs within, which possibly

PLATE 24

Platanthera chlorantha Rchb. p. Challes-les-Eaux, France, June 2nd, 1928.

H. M. Godfery pinx.

PLATANTHERA CHLORANTHA Rchb. p.
Greater Butterfly Orchid

secrete nectar. Fruiting capsule spindle-shaped with three acute angles, brown, shining, erect, $\pm$ 2 cm. long, dehiscing along the narrow rib in the middle of each of the three sides.

P. bifolia and *P. chlorantha* are so similar in general appearance as to have been frequently regarded as forms of one species. They are easily distinguished as a rule by the anther-cells, which are erect, parallel and close together in *P. bifolia*, sloping backward, divergent and much wider apart at the base than at the summit in *P. chlorantha*. In the latter the stem is taller, stouter (diameter about 5 mm. or more in well-grown plants), the spike broader (owing to the longer ovaries), the flowers rather larger, often much more tinged with green (especially when first open), only scented by night as a rule, and the spur is longer, stouter, often flattened and club-shaped at tip, curved and usually horizontal or directed downwards. In *P. bifolia* the diameter of the stem is 2–3 mm., the ovaries are shorter, the spike narrower, flowers rather smaller, purer white, scented by day, and the spur is very slender, nearly straight and horizontal.

P. chlorantha	**P. bifolia**
Anther. Wide open, flat, truncate, grooved at back, cells 3–$4\frac{3}{4}$ mm. long, divergent, leaning back.	Folded forward in a ∩, ridged at back, cells 2–$2\frac{1}{2}$ mm. long, parallel, close together, erect.
Pollinia. Total length 4 mm., caudicle longer than pollen-mass.	Total length 2 mm., caudicle shorter than pollen-mass, much shorter than in *chlorantha*.
Viscid discs large, circular, $\pm$ 4 mm. apart, with drum-like pedicel, becoming attached to the side of the head of large moths (often to the eye).	Smaller, oval, drum-like pedicel replaced by a longitudinal ridge, only 1 mm. or less apart, becoming attached to the base of the proboscis of smaller moths.

HABITAT. Clearings and borders of woods, hillsides, grassy slopes, less frequently in marshy ground and moist pastures. Flowers June to July, according to Camus (*Icon.* p. 406) about 20 days before *P. bifolia*.

DISTRIBUTION. Throughout Great Britain and Ireland, found up to 1000 ft. elevation in Derry. Locally abundant, but not common as a rule.

Lusus **ecalcarata.** Without spur. Berks.[1]

Europe: Scandinavia and Russia (except in the extreme north) to the Mediterranean and its islands. Siberia, Caucasus, China, Japan.

PLATANTHERA CHLORANTHA Rchb. p. (Mössl. *Handb.* II, 1565 (1828)). ORCHIS BIFOLIA γ L. (1753). PLATANTHERA BIFOLIA Rich. (1818). ORCHIS CHLORANTHA Custer (1827). O. VIRESCENS Gaud. (1829). O. OCHROLEUCA Rchb. p. (1830). HABENARIA BIFOLIA β Hooker (1830). H. CHLORANTHA Bab. (1837). PLATANTHERA VIRESCENS Koch (1849). P. MONTANA Rchb. f. (1852). HABENARIA CHLOROLEUCA Ridley. H. VIRESCENS Dr.

[1] *B.E.C.* p. 399 (1921).

In the copy of *E.B.* in the Royal Horticultural Society Library is a drawing of a *Platanthera* with three long slender spurs found with a group of Butterfly Orchids at Inwood, June 16th, 1909, which looks like *P. chlorantha*.

Sir J. D. Hooker expressed his pleasure at finding specimens intermediate between *P. bifolia* and *chlorantha*, and following his usual practice, pronounced them conspecific on the strength of it. Later he confessed: "Perhaps my intermediates between *Habenaria chlorantha* and *bifolia* (of which I retain a lively recollection) were of this hybrid nature".[1] This is interesting as showing that even very great botanists were not always free from bias when they lumped together species previously regarded as distinct, on the ground that intermediate forms occurred.

Bentham[2] says of *chlorantha*: "The anther-cells are broadly diverging at the base. But intermediates passing gradually from the broad to the narrow forms have been frequently seen in great numbers at High Force in Teesdale in 1865".

The anther-cells in *chlorantha* are not always equally wide apart—the angle of divergence varies—but only within narrow limits. Any specimens in which it was less than the average would appeal to a botanist anxious to reduce the number of species as opportune examples of "intermediate forms", though they might in all other respects be pure *chlorantha*. Intermediates of hybrid origin also occur, but are, as far as my experience goes, extremely rare. The two species are organised for pollination by different species of moths, as Darwin so clearly showed. The differences between them go much deeper than the parallelism or divergence of the anther-cells.

FERTILISATION. The length of the spur, one-quarter to one-third full of free nectar, the white flowers so easily seen in the dark, and the strong sweet scent emitted by night, all show that this species depends for pollination on the larger moths. To these the flowers are evidently attractive, for spikes are found with almost all the pollinia removed. In Dorset on May 30th I found several plants with last year's spikes still persisting and bearing numerous seed-capsules (one had 17). As the slits are so narrow it is remarkable that no seeds were left inside, but the valves open wide when it is fine and close in wet weather through the lengthening of the capsules. Owing to the distance between the viscid discs it often happens that only one pollinium is removed at a time. On one spike Darwin found three flowers from which both pollinia, and eight from which only one had been removed. He saw a specimen of *Hadena dentina* with one eye covered by a disc, and one of *Plusia gamma* v. *aureum* with a disc fixed to the edge of the eye. Mr Marshall[3] took 20 specimens of *Cucullia umbratica* on an island in Derwent Water, half a mile by water from any spot where *P. chlorantha* grew, of which no less than seven had pollinia of this species affixed to their eyes. The discs are so adhesive that if a bunch of the flowers be carried in

[1] Hooker's *Life and Letters*, II, 34.
[2] *Handb. Brit. Flora*, ed. 6, p. 445.
[3] *Nature*, p. 393 (Sept. 12th, 1872).

H. M. Godfery pinx.

A. GYMNADENIA ALBIDA Rich.
White Mountain Orchid

B. PLATANTHERA BIFOLIA Rich.
Butterfly Orchid

PLATE 25

A. **Gymnadenia albida** Rich. Les Plans, Switzerland, July 31st, 1912.

1, 2. Front and side views of flower (enlarged).

3. A flower from Yorkshire, June 15th, 1918 (enlarged).

B. **Platanthera bifolia** Rchb. Strensall, Yorks., July 4th, 1909.

the hand, numbers of pollinia are removed by the viscid discs touching the sepals of their neighbours. The reason the pollinia are affixed to the eye or proboscis in Lepidoptera is that the discs do not adhere well to a very hairy or scaly surface (scales being so easily detached), but in Hymenoptera the naked forehead or proboscis affords a good hold.[1] On withdrawal the pollinia are more or less vertical. A few seconds later, one side of the drum contracts, causing the pollinia to move inwards (i.e. towards each other, if both have been withdrawn together). At the same time the drum rotates through nearly a quarter of a circle, causing the pollinia to move downwards till they finally point forwards, and are thus in the right position to come in contact with the stigma of the next flower visited.[2]

2. PLATANTHERA BIFOLIA Rchb. p.

Pl. 25 B. *Lesser Butterfly Orchid*

Tubers two, ovoid, abruptly tapering into an obtuse tail; roots few, short. **Stem** 20–30 cm., erect, slender, angled above, solid (towards the end of summer often hollow), with 2–3 brown or whitish tapering membranous ribbed sheaths at base. **Leaves** two at base, about 7–13 cm. long by 2–3 cm. broad, oblong or oblong-lanceolate, obtuse or moderately acute, keeled, glabrous, glossy, bright or grey-green, sometimes wavy-edged, with numerous nerves with transparent parallel dashes between them, tapering below to a flat whitish winged stalk pressed against the stem; upper leaves small, bract-like, erect, slightly decurrent, linear-lanceolate with 3–5 obscure nerves. **Spike** narrow, cylindrical, 7–15-flowered, but sometimes up to 9 cm. long, usually lax. **Flowers** white, smaller than in *P. chlorantha*, very sweet-scented by day and especially at night. **Bracts** lanceolate to ovate-lanceolate, obtuse, somewhat keeled, slightly decurrent, about as long as the ovary (or longer) with 3–5 scarcely visible nerves. **Ovary** linear, twisted, shorter than in *P. chlorantha* (making the spike narrower), curved (sometimes like an S), tapering. **Sepals**, the lateral spreading, lanceolate, rather narrow, obtuse, white (crystalline under the lens), the upper erect, heart-shaped, slightly stalked, obtuse, broader and slightly shorter than the lateral. **Petals** white or greenish white, linear-lanceolate, somewhat sickle-shaped, much narrower and slightly shorter than the sepals, erect, more or less arched over the column, about twice as long as the latter. **Lip** linear-oblong, strap-shaped, obtuse, entire, longer than the sepals, directed obliquely downwards, white with greenish tip. **Spur** long ($1\frac{1}{2}$–$2\frac{1}{2}$ cm.), very slender, acute, sometimes slightly club-shaped at apex, usually horizontal, greenish at least at the tip, which is filled with nectar. **Column** small, 3 mm. tall; basal part whitish, curving round on each side

[1] Darwin, *Fert. Orch.* ed. 2, p. 72. [2] *Ibid.* p. 71.

with a long whitish staminode at base; upper part (anther) an upright green membrane (connective) curved forwards like a horseshoe (in section), convex (not grooved) behind, ending on each side in a white anther-cell. Cells erect, parallel, ± 2 mm. long, close together, partly concealing the stigma. **Pollinia** small (including caudicles, 2 mm. long), twice as long as caudicles, cream-coloured, divided to base into two parallel leaves, in side-view pear-shaped, attached sideways to the small oval orange-yellow viscid discs by one corner of the truncate foot of the caudicle, the other corner projecting like a tiny spur. **Stigma** on lower front of column, not extending below entrance of spur, magnet-shaped in horizontal section, with very thick edges.[1]

HABITAT. Woods, heaths, hillsides, pastures and marshes, with a fondness for damp places. Flowers late May to July.

DISTRIBUTION. Throughout Great Britain and Ireland, except perhaps in the extreme north of Scotland. Europe from Scandinavia and Mid-Russia to the Mediterranean and N. Africa; Siberia, Caucasus, Asia Minor, China.

PLATANTHERA BIFOLIA Rchb. p., *Fl. Germ. exc.* p. 120 (1830). ORCHIS BIFOLIA L. (p.p.) (1753). O. ALBA Lam. (1778). HABENARIA BIFOLIA R. Br. (1809). LYSIAS BIFOLIA Salisb. (1812).

FERTILISATION. Darwin examined two moths, *Agrotis segetum* and *Anaitis plagiata*, one with three pollinia, the other with five, attached, not to the eye or the side of the face, as in *P. chlorantha*, but to the base of the proboscis. The distance between the viscid discs, which is only about a quarter of that in *P. chlorantha*, is thus nicely adjusted to coincide with the space between the points of attachment. To accomplish this, the anther appears to have been folded sideways, until in section it is like a magnet, or the letter **U** inverted. Darwin found that the viscid matter of the disc, after having been dried for several months, when moistened became as adhesive as ever.[2]

Platanthera bifolia × *Orchis maculata* (p. 217), vide *Orchis maculata*.

PLATANTHERA BIFOLIA × CHLORANTHA

× P. hybrida Brug.

A specimen found by me near Chambéry, Savoie, June 8th, 1928, resembled *P. chlorantha* in its habit, stout stem, broad spike, large flowers, broad bracts, and green-edged stigma, and *P. bifolia* in its narrower sepals, column bent into a **U**, ridged at the back, and parallel anther-cells only 2 mm. apart (in one or two flowers 3 mm.). Roughly speaking, it had the general appearance of *P. chlorantha*, intermediate flowers,

[1] A specimen without spurs (lusus *ecalcarata*) was found near Exeter. *B.E.C.* p. 149 (1920).
[2] *Fert. Orch.* ed. 2, p. 251.

but the reproductive organs of *P. bifolia*. The hybrid is sometimes nearer one parent, sometimes the other.

It is recorded (*J.B.* p. 95 (1910)) that *P. chlorantha* occurred in Flintshire with plenty of *P. bifolia*, but that careful search revealed no intermediates. This was to be expected, hybrids between the two being very rare. A specimen of *P. chlorantha* was exhibited to the Linnean Society with all three petals spurred—a case of true peloria. A specimen figured in their *Journal* (*Bot.* XXXVIII, t. 1) had three sepals spurred—false peloria —a really extraordinary accident.

A single specimen of this hybrid found amongst multitudes of both parents at Sligachan, Skye, differed from *P. bifolia* by its longer spur and slightly divergent anther-cells, and from *P. chlorantha* by its colour, and the shape of the sepals and spur (*B.E.C.* p. 508 (1910)). With it was found a peloriate specimen of *P. chlorantha* in which the lip had reverted to a spurless petal.

Sowerby (*E.B.*) states that he found specimens on Reigate hills difficult to assign to *P. bifolia* or *chlorantha*, but that he did not then know of the differences in the pollinia, caudicles, viscid discs, and stigmas.

Genus XV GYMNADENIA R. Br.

Column short with an oval lobe on each side, on the front of which the stigmas are situated. **Pollinia** erect on forward ends of the two parallel linear viscid glands.

Herbs with palmate or fascicled tubers, long narrow or ovate-oblong leaves and cylindrical spikes of small flowers with spreading side-sepals, petals connivent with upper sepal, short 3-lobed lip, and spur with free honey.

About 12 known species, of which four inhabit Europe, and the rest Central and Eastern Asia to Japan. *Gymnadenia* R. Br. in Ait. *Hort. Kew.* ed. 2, V, 191 (1813) was included in *Orchis* by Linnæus (*Sp. pl.* ed. 1, p. 942 (1753)) and in *Habenaria* by Bentham and Hooker. The latter genus is now restricted to exotic orchids with projecting stigmatic processes, and has no European representative. A few authors still cling to the genus *Habenaria*—a heterogeneous collection of widely differing genera, including *Gymnadenia*, *Platanthera*, *Cœloglossum* and *Neotinea*.

Meyer[1] created a new genus, *Leucorchis*, for *G. albida*, the following being a translation of his diagnosis: "Lip through connivence with the other perianth-segments almost campanulate. Each pollen-mass attached erect to a separate, naked gland. Everything else as in *Gymnadenia*". As each pollinium is similarly attached to a naked gland in *Gymnadenia*, Meyer's new genus is only based on the sepals, petals and lip

[1] *Preuss. Pflanzengatt.* (1839).

being less spreading than in *Gymnadenia*, which, although it alters the appearance of the flower, is hardly a ground for generic differentiation.

Schlechter[1] adopts Meyer's genus, which he endeavours to support by two new characters: (1) Viscid glands sub-orbicular instead of linear or oblong as in *Gymnadenia*. (2) Rostellum erect, forked, with an ear on each side at the base surrounding a naked round viscid gland. In *Gymnadenia* he gives "rostellum at base with two upright or slightly diverging little plates with the two naked oblong or linear viscid glands resting on the lightly forked outer edge".

As to (1), in all the living specimens of *G. albida* I have seen in France, Switzerland and Britain the pollinia were inserted at the forward end of a *linear* gland, as in *Gymnadenia*, and Darwin records the same of British specimens.[2] It therefore appears to be a true *Gymnadenia* in this respect. The second character needs a dissecting microscope to detect, and appears to be too unimportant to justify the creation of a new genus, being merely a slight difference in the method of support of the viscidium.

Fertilisation. *Gymnadenia* is organised for visitation by Lepidoptera, as shown: (1) by the viscid glands to which the pollinia are attached being long and narrow so as to adhere longitudinally to the proboscis, and thus secure a firmer hold; (2) in the case of *G. conopsea*, by the length of the spur, containing nectar only at the apical part, which prevents all insects except those with a long proboscis from reaching it.

There are no guiding plates on the lip as in *Anacamptis* (which is also specially adapted for Lepidoptera), so that there is nothing to compel the insect to stand on the exact centre of the lip. This is not necessary, as it is an advantage rather than otherwise for the viscid gland to be affixed to the side of the proboscis, as the pollinia are then in better position to come in contact with the lateral stigmas. The pollinia when withdrawn are erect, i.e. at right angles with the narrow viscidium. After the downward movement, they become parallel with the viscidium and therefore also with the straightened proboscis to which it is affixed. If the pollinia are withdrawn on a bristle, and if this be inserted, after the movement of depression, into the spur of a flower, the two ends of the pollen-masses will accurately strike the two very adhesive stigmatic surfaces, situated on each side of the mouth of the spur.[3]

1. Gymnadenia conopsea R. Br.

Pls. 26 B, 27 and 29 A; Pl. F, fig. 2 (p. 123). ***Fragrant Orchid***

Tubers two, palmate, with 3–6 rather thick tapering obtuse segments; roots few, short, rather thick. **Stem** erect, 15–40 cm. (up to 60 cm. abroad), round, green, leafy, angled or smooth, sometimes tinged with violet and slightly hollow above,

[1] Fedde, *Repert.* XVI, 266, 269 (1919).
[2] *Fert. Orch.* ed. 2, p. 68.
[3] *Ibid.* p. 67.

H. M. Godfery pinx.

A. GYMNADENIA CONOPSEA × ORCHIS MACULATA
St Quintin's Orchid
3, 4. GYMNADENIA CONOPSEA × ORCHIS PURPURELLA
Orchigymnadenia varia Steph. p. and f.
B, 5. GYMNADENIA CONOPSEA R. Br.
Fragrant Orchid

PLATE 26

A. **Gymnadenia conopsea** × **Orchis maculata. Orchigymnadenia St-Quintinii** Godf. Teesdale, July 5th, 1930.

1, 2. Single flowers (enlarged).

3, 4. **Gymnadenia conopsea** × **Orchis purpurella. Orchigymnadenia varia** Steph. p. and f. Teesdale, July 5th, 1930.

B. **Gymnadenia conopsea** R. Br. Baveno, N. Italy, June 22nd, 1912.

5. Single flower (enlarged).

glabrous with 2–3 close-fitting brown membranous sheaths at base. **Leaves** erect, slightly spreading, linear, rather sword-shaped, about 9–16 cm. long, usually narrow ($\pm$ 1 cm.) in Britain (often broader abroad), the lower obtuse or somewhat acute, slightly hooded, strongly keeled, more or less folded, glabrous, rather thick and firm, opaque with 1–2 or more transparent nerves on each side of mid-rib, and several lesser ones, depressed and more visible below, with abundant minute whitish dots and minutely toothed edges. Lower leaves 3–5, near together on opposite sides of stem; upper 2–3 sessile, lanceolate, bract-like, tapering to a fine point. **Spike** long (6–10 cm. or more), many-flowered, usually lax, sometimes dense, conspicuous. **Flowers** small, long-spurred, pale mauve, red-lilac or rose, rarely pure white or bright magenta, strongly scented, agreeable to some persons, displeasing to others, sometimes scented like a clove-carnation (var. *densiflora*). **Bracts** lanceolate, tapering to a fine point, 1–3-nerved, green, often tinged violet, longer than ovary (lower often as long as ovary and flower combined), dotted with minute papillæ. **Ovary** slender, cylindrical, twisted and curved, with three longitudinal ridges (later with six), green tinged violet. **Sepals** ovate to ovate-lanceolate, obtuse, the lateral spreading horizontally with rolled-back edges (making them look narrow), the upper forming a hood with the petals. **Petals** broader and shorter, rounded out on the exterior side, slightly hooded at the tip, connivent. **Lip** usually broader than long, but sometimes wedge-shaped longer than broad, about as long as sepals, 3-lobed, lobes subequal, rounded, sometimes obscurely crenate or minutely toothed. **Spur** long, slender, tapering, $1\frac{1}{2}$ times to twice as long as ovary, curved downwards, half-full (or more) of free nectar, the entrance circular. **Column** very short. **Anther** pear-shaped, obtuse, cells with a small stigmatic fold between them at base. **Staminodes** whitish, prominent. **Pollinia** pale green or greenish yellow, affixed near the forward end of the narrow strap-shaped viscidium, which is nearly as long as the caudicles. **Stigmas** two, on inner surface of side-wings of column on each side, separated by the foot of the anther, which projects downward and partly hides the entrance to the spur.

Pl. F, fig. 2, shows an enlarged flower (5/1), in which the two concave stigmas on side-wings of the column, the large staminodes between them and the sides of the anther, and the absence of a pouch to the rostellum, are well shown.

Continental authors have named many forms or varieties, such as *angustifolia* with almost linear leaves, *clavata* with short club-shaped spur, *crenulata* with broad crenulate side-lobes, *sibirica* with a rather long wedge-shaped base to the lip, etc. These appear to be fluctuating characters not confined to the named variety in question, but sometimes appearing in other varieties or in the type itself. Others appear to be teratological forms, e.g. *ecalcarata*, without spur, *inodora*, lower bracts without flowers, etc. I have only met with three well-marked varieties on the Continent, apart from the type: (1) a very tall late-flowering form with long very loose spike (borders of woods on mountains), (2) *densiflora* with long dense spike of rose-red flowers (wet places), and (3) *alpina*, a dwarf few-flowered form of high altitudes.

HABITAT. Grassy places, chalk downs (often abundant), banks, pastures, etc., generally on limestone. In Ireland also on clay banks, pastures and heaths (*Cybele Hibern.*). Occasionally in marshy meadows, and wet slipping ground. Flowers June to August, according to locality.

DISTRIBUTION. Not common though locally plentiful in Great Britain, and known in most counties, extending throughout England, Wales, and Scotland to Shetland, where it is very scarce (Watson, *Top. Bot.* p. 1054). In Ireland frequent and locally abundant, extending from sea-level in Antrim and Kerry to 900 ft. in Clare, rarer in the south.

GYMNADENIA CONOPSEA R. Br. in Ait. *Hort. Kew.* ed. 2, v, 191 (1813). ORCHIS CONOPSEA L., *Sp. pl.* ed. 1, p. 942 (1753). HABENARIA GYMNADENIA Dr.

Conopea has been substituted for *conopsea* by most continental authors, on the ground that the latter is grammatically incorrect (A. and G. *Syn.* III, 812). *Conopsea*, however, was the name given by Linnæus.

G. conopsea sub-sp. **densiflora** (Marsh Fragrant Orchid) Lindl., *Gen. and Spec.* p. 275 (1835), as variety. Generally attributed to Dietrich (1839). Spike dense, often long (8–16 cm.), flowers touching, bright rose-red or magenta, with a pleasant clove-like scent quite different from that of the type, and flowering later (mid-July). Stem tall, hollow above. Leaves long, sword-shaped, broad or narrow. Spike cylindrical, at first pyramidal. Flowers darker than in the type. Pl. 27.

Isle of Wight, July 12th, 1916. Fine spikes of large red-purple flowers, lip whitish in centre, side-lobes truncate, finely toothed! Anglesey, July 9th, 1919. Small pyramidal spikes of bright magenta flowers, with rather short spur (± 12 mm.), but these were in early flower! forma **monensis** (Pl. 29 A, A 1) (p. 146). The former occurred on wet slipping ground on cliffs, the latter in damp meadows near water. Perhaps "*Habenaria Gymnadenia* Druce, small specimens with dark coloured flowers"[1] belonged to the last-mentioned form. Billingham, Durham;[2] Rievaulx, Yorks.

I saw this sub-species in some quantity in July and August, 1929, at Trient, Switzerland. It was entirely confined to marshy ground, near runnels of cold glacier water, and began to flower in mid-July when the type, abundant some 400 yards away, was in fruit, and was practically over even 2000 ft. higher up. The stem was up to 45 cm. tall, hollow above, the leaves distant, 10–19 cm. long by 8–23 mm. broad, the spike dense, long (8–16 cm.), the flowers bright rose-red and clove-scented, the spur 15–18 mm. long. The leaves are not always broad, the spike is not always long, and the spur is not always short, as described in continental floras. It

1 "Fl. Zetlandica", *B.E.C.* p. 523 (1921). 2 *Ibid.* p. 170 (1917).

PLATE 27

Gymnadenia conopsea sub-sp. **densiflora** Lindley. Trient, Switzerland, July 23rd, 1929.

1. Enlarged flower.
2. Column with two stigmas on side-lobes (magn.).
3. Pollinia, erect on linear viscidia.
4. *Ino statice* L. ♂, taken on *G. conopsea* (type) with pollinium on proboscis.

H. M. Godfery pinx.

GYMNADENIA CONOPSEA sub-sp. DENSIFLORA Lindley
Marsh Fragrant Orchid

was remarkably uniform in appearance and colour, the variations recorded above being only the natural result of differences in the age and vigour of the plants. There were no hybrids, and no intermediate forms between it and the type, which was abundant a short distance away.

Var. **borealis** Dr. Plant about 15 cm. high, leaves about 5 mm. broad, spur thick, about as long as ovary, flowers very sweet-scented, dark purple, 3 mm. long by 2·5 mm. broad, middle lobe relatively larger than the lateral. Upland pastures near Watendlath, Cumberland, 1907.

I have not seen this plant, but the description resembles in some respects the Anglesey form of the sub-species *densiflora*.

Gymnadenia conopsea × *albida*, vide *G. albida*.

Fertilisation. The viscid gland is as long as the caudicle, which stands erect at its forward end. The under-surfaces of the two glands form part of the roof of the mouth of the spur, so that when the moth bows its proboscis to fit the arched spur, it is bound to come in contact with them. At the broad end of each viscid gland there is a deep depression bordered by a slight ridge. The foot of the caudicle is attached to the steep sides of this ridge and depression. On exposure to the air the ridge sinks down flat, taking with it the pollinium, till the latter lies parallel with the viscidium. The action is hygrometric, for if the gland is placed in water, the ridge rises together with the pollinium, and when re-exposed to the air sinks down again. The two stigmas are separate; each situated on an oval wing or lobe of the column, and glistening with adhesive matter, often covered with packets of pollen. The elastic threads binding the latter to the pollinia are unusually weak, to avoid the possibility of the whole pollinium being dragged off by the stigma through the viscid material not setting hard and dry as quickly as in *Orchis*. If a fine bristle be inserted into the spur, the long narrow viscidia will adhere to it, slightly on one side, and the pollinia will then move down till they are parallel with it. If the bristle be now inserted into the spur of another flower, the ends of the pollinia will touch the stigmas, and leave packets of pollen adhering to them.

Darwin wrote:[1] "My son George went at night to a bank where this species grows plentifully, and soon caught *Plusia chrysitis* with six pollinia, *P. gamma* with three, *Anaitis plagiata* with five, and *Triphæna pronuba* with seven pollinia attached to their proboscides. I may add that he also caught the first named moth in my flower-garden, with the pollinia of this *Orchis* attached to its proboscis, but with all the pollen-grains removed, although the garden is a quarter of a mile distant from any spot where the plant grows. Many of the above moths had only a single pollinium attached, somewhat laterally to their proboscides; and this would happen in every

[1] *Fert. Orch.* ed. 2, p. 67.

case, unless the moth stood directly in front of the nectary and inserted its proboscis exactly between the two discs".

At Trient, on July 26th, 1929, my wife and I saw *Papilio machaon* visit the flowers of the variety *densiflora*, and also an orange-brown skipper butterfly, which, when approached, flew away to another spike of the same orchid. Unfortunately we had no net with us. On June 23rd, 1930, I took a green Zygænid moth, *Ino statice* L. ♂, with one pollinium of the type on its proboscis (Pl. 27), and a Dipteron, *Empis livida*, with one pollinium on its proboscis, both at Lewes, Sussex.

GYMNADENIA CONOPSEA × ORCHIS MACULATA

Orchigymnadenia Heinzeliana G. Camus (1892)

Pls. 26 A (p. 141) and 28

Tubers oblong, flattened, thick, with two short lobes at apex. **Stem** about 20 cm. tall, round, slightly hollow below, glabrous. **Leaves** 2–4, resembling those of *G. conopsea*, linear, narrow (7 mm.), rather acute, strongly keeled, folded, usually spotted, upper 1–2 bract-like. **Spike** oval (4–7 cm.), rather lax. **Flowers** like those of *O. maculata*, but smaller, pale rose, with rather long narrow often spotted side-sepals, spreading horizontally as in *G. conopsea*, and slender slightly curved spur considerably longer than in *O. maculata*. **Lip** rather deeply 3-lobed, lobes sub-equal, rounded, slightly crenate, pale rose faintly spotted.

Two specimens found by me in Hants. and Surrey respectively agreed with the above description. In another specimen found in Surrey at the same station (Pl. 28 A), the lip was broader than long, its whole area, with the exception of a pale lilac border, dark red-violet. Flowers June to July.

A specimen found at Winchester, July 3rd, 1928, resembled *O. maculata* by the spotted leaves, side-sepals and lip, and short dense spike, and *G. conopsea* by the linear folded leaves, horizontally spreading side-sepals, broad-based petals, small flowers, short broad equally 3-lobed lip, long very slender spur, and oval viscidia. Another from Sevenoaks had a stout spur without honey, with viscidia twice as long as broad, forming roof of spur-entrance, and without pouch.[1]

ORCHIS HEINZELIANA Reichardt (1876).

[1] O.R. p. 274 (1899).

PLATE 28

Gymnadenia conopsea × **Orchis maculata. Orchigymnadenia Heinzeliana** G. Camus. Surrey, June 28th, 1917.

1, 2. Enlarged flowers of the same.

3, 4. Enlarged flowers of another specimen. Same place and date.

H. M. Godfery pinx.

GYMNADENIA CONOPSEA × ORCHIS MACULATA
Orchigymnadenia Heinzeliana Camus

Orchigymnadenia St-Quintinii Godfery

Pl. 26 A, figs. 1, 2 (p. 141)

Two specimens found in Teesdale, nearer to *G. conopsea* than *O. maculata*, may be briefly described as combining the narrow erect leaves and long slender many-flowered spike of *G. conopsea* with diminutive flowers of *O. maculata*. **Stem** 28 cm. **Leaves** erect, linear-lanceolate, with small spots near the edges. **Flowers** scarcely bigger than those of *G. conopsea*. **Lip** 3-lobed, lobes sub-equal, lilac with red-violet streaks, and a few spots on the mid-lobe. **Spur** long (± 11 mm.), slender, curved. Three ovaries visibly fertilised. The second specimen had a shorter spike ($7\frac{1}{2}$ mm.), but was otherwise similar, and had six ovaries fertilised (Pl. 26 B). This would have been placed by me under ×× *Orchigymnadenia Legrandiana* G. Camus, but that the viscid glands were *enclosed in a pouch*, and the spike was long instead of short and few-flowered.

GYMNADENIA CONOPSEA × ORCHIS MACULATA s.sp. ELODES

Orchigymnadenia souppensis G. Camus, *Journ. de Bot.* VI, 477 (1892)

Pl. 30 A (p. 150); Pl. K, fig. 2 (p. 220)

Leaves narrow, linear-lanceolate, acute, rather greyish green, with small faint spots. **Spike** conical, ± 5 cm. long, but not yet fully out. **Flowers** intermediate in size, nearer *O. maculata*, but with a very slender spur much longer than in *elodes*, white faintly tinged with violet, with many very small violet spots on lip, sweet-scented. **Sepals** spreading upwards with rolled-back edges, appearing narrow as in *G. conopsea*, sometimes faintly spotted; upper sepal nearly erect. **Petals** ovate obtuse, 1-nerved, white, with faint violet tinge, forming a close hood. **Lip** broader than long, with side-lobes rounded out, and short narrow mid-lobe (recalling that of *O. elodes*), white faintly flushed with violet, with minute spots, and sometimes pale detached lines faintly indicating a vague loop-pattern. **Spur** long (10 mm. or more), very slender, acute, horizontal or slightly descending.

HABITAT. Mountain pastures, Devil's Bridge, Aberystwyth, N. Wales, growing with both parents, June 30th, 1919. Five specimens seen, in company with Dr T. Stephenson. Teesdale!

× GYMNADENIA SOUPPENSIS G. Camus, *Bull. Soc. Bot. Fr.* XXXVIII, 157 (1891). ORCHIS EVANSII Dr., *B.E.C.* p. 199 (1906). ORCHIGYMNADENIA EVANSII Stephenson, *J.B.* (1922), *Icon. J.B.* Pl. 559, fig. 24 (1921), and *O.R.* p. 131 (1921).

GYMNADENIA CONOPSEA × ORCHIS MASCULA

Orchigymnadenia Robsonii Harrison, *B.E.C.* p. 638 (1928)

Habit of *O. mascula*, of which it was a paler coloured miniature. **Leaves** unspotted. **Spike** lax. **Flowers** "intermediate between the rich purple of *O. mascula*, and the rose-purple of *G. conopsea*", scented like, but more faintly than, the latter. **Bracts** purple, paler in the middle, 1-nerved. **Side-sepals** spreading, upper connivent with petals. **Lip** unspotted, 6·25 mm. long by 8 mm. broad, mid-lobe longer and narrower, slightly cleft. Throat as in *O. mascula* but smaller. **Spur** slender, as long as in *G. conopsea*, in some flowers 2–3 mm. shorter.

Found (one specimen only) in a mixed colony of the parents, both then in flower, on June 12th, 1927, on the coast of Durham, by Prof. J. W. Heslop Harrison.

GYMNADENIA CONOPSEA × ORCHIS PRÆTERMISSA

Orchigymnadenia Wintoni A. Camus, *Icon.* p. 393 (1928)

Pl. G, fig. 3 (p. 191)

Stem $32\frac{1}{2}$ cm., slender, angled and purplish above, slightly hollow (with pinhole in centre). **Leaves** linear-lanceolate, distant, acute to acuminate, the upper two bract-like, acuminate with short transparent dashes, tinged violet. **Spike** short (6 cm.), about 18-flowered, rather lax. **Flowers** pale, violet, a little larger than in *G. conopsea*, resembling *O. prætermissa* in miniature. **Bracts** lanceolate acuminate, lowest 2 cm. long. **Ovary** ± 10 mm., twisted, curved, flushed violet. **Sepals** oblong, obtuse, unspotted, the lateral obliquely erect, spreading, the upper connivent or erect. **Petals** broad at base as in *G. conopsea*, and slightly bowed out, connivent. **Lip** with three shallow apical lobes, mid-lobe tongue-shaped, obtuse, bluish pink (rose in newly opened flowers), with white throat and faint radiating lines of violet dots as in *O. prætermissa*. **Spur** slender, intermediate in length, about equal to ovary, widened at throat, tapering gradually. **Column** white, **anther** purplish red, **pollinia** small purplish, caudicles slender at base thickening upwards attached near forward end of the viscidium, which is longer than broad. **Stigmas** somewhat lateral but not on side-lobes of column as in *G. conopsea*. Inside surface of spur with short sparse papillæ, with no free nectar.

Hampshire, June 16th, 1931. Described from one of three plants found by P. M. Hall, with a faint but distinct scent resembling *G. conopsea*. In my opinion an undoubted hybrid, with the general appearance of *G. conopsea* but *prætermissa*-like flowers. It has the pouch of *Orchis* but the lengthened viscidium of *Gymnadenia*.

PLATE 29

A. **Gymnadenia conopsea** R. Br. sub-sp. **densiflora** Lindl. forma **monensis** Godfery.

1. Enlarged flower. Anglesey, July 9th, 1919.

B. **Cœloglossum viride** × **Gymnadenia conopsea. Gymnaglossum Jacksonii** Rolfe.

2, 3. Enlarged flowers.

H. M. Godfery pinx.

A. GYMNADENIA CONOPSEA R. Br. sub-sp. DENSIFLORA
forma MONENSIS

B. CŒLOGLOSSUM VIRIDE × GYMNADENIA CONOPSEA
Gymnaglossum Jacksonii Rolfe

A form with thick stem, broad spike, and flowers resembling those of *G. conopsea*, with a long narrow slender curved spur is figured in the frontispiece, *Winchester Coll. N.H. Soc. Rep.* 1913–15, and reproduced in *B.E.C.* Pl. 10 (1917), as *Habenaria Wintoni* Druce, but on too small a scale to show any recognisable characters of *O. prætermissa*.

GYMNADENIA CONOPSEA × ORCHIS PURPURELLA

Orchigymnadenia varia Steph. p. and f.[1]

Pl. 26 A, figs. 3 and 4 (p. 141); Pl. K, fig. 3 (p. 220)

Three plants growing close together in Arran in early July, 1921, were described by Dr Stephenson[2] as follows. The tallest was about 20 cm. high, the whole plant yellowish green with narrow unspotted leaves. Flowers larger than in *G. conopsea*, but the colour, strong scent and long spur clearly showed the parentage of that species. The regular lip-pattern of broken lines, the stout spur rather darker than the flower, and the short spike showed the influence of *O. purpurella*. Dr Stephenson admits that the *Orchis* parent might possibly have been *O. latifolia*, which was present but scarce, but the spur of the latter is paler and more slender, and he considers the balance of evidence to be in favour of *O. purpurella* (Pl. K, fig. 3). A second form was found, July 9th, 1921, which was nearer to *O. purpurella*—a slender dwarf plant about 10 cm. high with narrow spotted leaves, and a lip very similar to that of *O. purpurella*, but scented, and with a long and stout spur, very large in comparison with the size of the flower. Dr Stephenson found two specimens at Teesdale in 1929, *O. purpurella* being plentiful there.

A few specimens were found by me in Teesdale, July 3rd–6th, 1930:

(1) Like an unspotted-leaved *O. purpurella*, but flowers smaller. Spur curved, more slender, and as long as ovary.

(2) Leaves spotted. Spike longer (8 cm.) and more slender (22 mm.). Flowers like *O. purpurella* but much smaller. Spur slender, as long as ovary (Pl. 26 A, fig. 3). Fig. 4 is from another spike.

(3) Leaves with small spots near edges. Spike longer (8 cm.) and more slender than in *O. purpurella*, almost as long and nearly as slender as in a fine spike of *G. conopsea* compared at the time with it.

(4) Leaves nearly as broad as in *O. purpurella* (all the above had narrow leaves) with small spots. Spike cylindrical, narrow (7·5 × 2·5 cm.). Flowers like *O. purpurella*, but not so dark-coloured and much smaller. Spur curved, longer and much slenderer than in *O. purpurella*.

[1] *J.B.* p. 33, Pl. 561 (1922). [2] *O.R.* p. 132 (1921).

In all the above *O. purpurella* is the dominant parent, the signs of *G. conopsea* being much less evident. They are (1) longer and more slender spike, (2) smaller, paler flowers, (3) longer much more slender spur. The actual difference in length is small, but the much greater slenderness gives the impression of greater length than the measurement suggests.

G. conopsea × *albida*, p. 150. *G. conopsea* × *Anac. pyramidalis*, p. 156. *G. conopsea* × *Cœloglossum viride*, p. 127.

2. Gymnadenia albida Rich.

Pl. 25 A (p. 137); Pl. F, fig. 1 (p. 123). *White Mountain Orchid, Small White Orchid*

Tubers widely divergent, long, thickened and joined at base, gradually tapering; roots long, fleshy, much thinner. **Stem** 10–30 cm., erect, stiff, solid, cylindrical, slightly angled above, glabrous, pale green, with 2–3 brownish or whitish leafless sheaths at base. Lower **leaves** ± 4, somewhat distant, sheathing at base, oblong-ovate to oblong-lanceolate, shortly pointed, tapering at base, often broadest above the middle, keeled, firm, rather thick, glossy above, with 4–6 parallel veins on each side of mid-rib, and rows of very numerous short translucent dashes between the nerves, densely dotted below with papillæ; upper leaves 1–2, small, bract-like, acute, narrow. **Spike** 3–6 cm., cylindrical, dense, rather one-sided. **Flowers** many, very small, almost tubular, white and faintly scented, with hanging trifid lip. **Bracts** slightly exceeding ovary, lanceolate, sessile, tapering, obtuse, green, glabrous, 1–3-nerved, the lowest about 7 mm. long. **Ovary** short (± 7 mm.), slightly twisted, side next to stem flat, glabrous, with three rather broad ridges. Ripe capsule 6–7 cm. long. **Sepals** short (2–3 mm.), ovate obtuse, keeled, 1-nerved, white (sometimes yellowish or greenish white), loosely connivent with petals to form a more or less bell-shaped or tubular flower. **Petals** ovate obtuse, concave, rounded out on the outer side, shortly clawed, 2-nerved, hooded at apex. **Lip** directed forwards, white, yellowish or greenish white, equalling or exceeding the sepals, as a rule deeply 3-lobed, edges entire; side-lobes linear, rather acute, often as long as mid-lobe (rarely reduced to a tooth on each side), more or less divergent, sometimes incurved; mid-lobe tongue-shaped, rather broader and usually longer than side-lobes, rounded at apex, rarely acute. **Spur** pendent, very short, rounded, compressed from back to front, yellowish, rarely half as long as ovary, with free nectar. **Column** short, erect. **Anther** broad, obtuse or with a little point, greenish white, cells nearly parallel, club-shaped, their bases narrow and rather wide apart, separated by a stigmatic fold. **Pollinia** very small, less than 1 mm. long, pale cream, the packets of pollen rounded, relatively large, caudicles very short, affixed to the minute slightly elongated viscid glands, which are not enclosed in a pouch. **Stigma** transverse, more or less kidney-shaped with lateral lobes, or oblong with rounded angles. Staminodes large, short, rather flat. Cells of testa very faintly striate. Fruiting spike dense, 4–6 cm. long, nearly all the flowers setting a capsule, somewhat like a plantain, but thicker. Capsule cylindrical, glabrous, slightly glossy, with three rather broad ridges, 7–10 mm. long.

Var. **tricuspis** Beck, side-lobes of lip as long as or longer than mid-lobe, appears scarcely worthy of varietal rank, as the relative sizes of the lobes of the lip are not constant. I found a plant on Lago Maggiore, Italy, with an undivided lip.

Habitat. Mountain pastures and grassy slopes. Abundant on granite above Chamonix at about 5000 ft. Flowers June to July, according to elevation and latitude. In N. Wales I found it practically over on June 28th.

Distribution. England from Lancashire and Yorkshire northwards. Records for Sussex, E. Hants., Worcester, Salop, Northants. and Cheshire require confirmation. N. Wales, Scotland to Shetlands and Western Hebrides. Widespread (but rather rare) throughout Ireland, except N. Tipperary, King's County, W. Meath and Longford. In Europe from Greenland and Iceland, Scandinavia, Denmark and Mid-Russia to the Pyrenees, Maritime Alps, N. Italy and Northern Balkans.

Gymnadenia albida Rich., *Mém. Mus. Paris*, iv, 57 (1818).

The plant was placed under *Satyrium* by Linnæus, and under *Orchis* by various authors. It was transferred to *Habenaria* in 1814 by Swartz, but this genus is now restricted to exotic orchids with projecting stigmatic processes. Hartman included it in his new genus *Cœloglossum* probably because of the resemblance of the spur, and of its habit and foliage to *C. viride*. Lindley placed it under *Platanthera* (1829) and later under *Peristylus*. Parlatore made it the type of his new genus *Bicchia* (1858). It appears, however, to be a true *Gymnadenia* by the three-lobed and short column, spur with free nectar resembling that of *G. odoratissima*, and especially by the attachment of each pollinium to one end of a more or less *linear* viscid gland, and their downward and forward movement after withdrawal till they lie parallel with it. It hybridises with *G. conopsea* and *G. odoratissima*. In *Cœloglossum* the viscid glands are oval, little broader than the caudicles, enclosed in a thin skin, and placed one on each side of the stigma. In *G. albida* they are placed *between* the stigmas.

As to *Leucorchis*, vide *Gymnadenia* (genus).

Fertilisation. The white sweet-scented flowers, and the presence of a spur with free nectar, show that the flower is organised for the attraction of insects. Its great efficiency in this regard is proved by the fact that almost every flower sets a seed-capsule, in which respect it resembles self-fertilising plants, but this fecundity is due to the visits of insects. The occurrence of flowers here and there setting no capsules shows that, in the absence of such visits, fertilisation does not take place. On July 11th, 1929, at Trient, Switzerland, I took the following Hymenoptera visiting the flowers:

Halictus calceatus ♀ (which bore a single pollinium of *Orchis maculata*) and *Lindenius albilabris* F. ♂. I also took a small Hymenopteron with ruby-red metallic abdomen, which unfortunately escaped. No pollinia were removed, and the visits may perhaps have been of an experimental nature, but more probably the pollinia had been previously removed.

GYMNADENIA ALBIDA × CONOPSEA

× G. Schweinfurthii Hegelmaier

Tubers divided to base, segments ± 4, short, narrow. **Leaves** ± 5, ovate-oblong to lanceolate like those of *G. albida*. **Spike** ± 4 cm. long, sometimes one-sided, broader than in the latter. **Flowers** intermediate in size between the parents, pale rose or white tinged with rose. **Sepals** and **petals** spreading, not connivent, larger than in *G. albida*. **Lip** wedge-shaped with broadish base, rather deeply trifid at apex with nearly equal lobes, or with longer mid-lobe. **Spur** rather thick, longer than in *G. albida*. Sometimes nearer to one parent, sometimes to the other, usually resembling *G. albida* in foliage, *G. conopsea* in the sepals and petals, and *G. albida* in the lip. Austria, Germany, Switzerland (Albula Pass). Flowers July. V.R.

Two or three specimens found amongst the parents near Arisaig, W. Inverness, in late June were identified at Kew by Rolfe, who said they were substantially identical with the plant of the Alps, and describes them as follows. Leaves intermediate, but the spike resembles that of *G. albida*. Flowers rose-purple. Spur stout, only twice as long as the lip, which is nearly intermediate in shape.[1] According to A. H. Woolley Dod it had the general aspect of *G. conopsea*, but with a much shorter and stouter spur. The locality was half a mile from the sea, and not more than 100 ft. above it.

Sub-tribe II *SERAPIADINÆ* Engler, *Syllab.* (1892)

Viscidia two, rarely one, enclosed in a common pouch left behind when they are withdrawn, or (in *Ophrys*) each viscidium in a separate pouch.

> SERAPIADEÆ Lindl., *Veg. King.* p. 182 (1847). ANGIADENIEÆ Parlatore, *Fl. ital.* (1858). BURSICULATÆ Rchb. f., *Icones* (1851). SERAPIEÆ Benth. and Hooker (1883). ANGIADENINÆ Camus (1908). Lindley's name is retained amended to end in -inæ in accordance with the Vienna rule for sub-tribes.

A very natural sub-tribe, characterised by the highest development of the rostellum —a pouch filled with liquid to keep the viscid glands from losing their adhesiveness, which swings back and exposes them when pushed by an insect, so that they adhere to its head or proboscis.

[1] *O.R.* p. 238 (1898); *J.B.* p. 352 (1898).

PLATE 30

A. **Gymnadenia conopsea** × **Orchis maculata** sub-sp. **elodes.**

1. Enlarged flower. Aberystwyth, July 9th, 1919.

B. **Orchis incarnata** × **maculata.**

2. Part of hollow stem. Anglesey, July 9th, 1919.

H. M. Godfery pinx.

A. GYMNADENIA CONOPSEA × ORCHIS MACULATA (ELODES)
Orchigymnadenia souppensis Camus
B. ORCHIS INCARNATA × MACULATA × *Orchis ambigua* Kerner

There are two anomalous genera placed under this sub-tribe because the pollinia are enclosed in a common pouch—*Anacamptis* and *Neotinea.* They both have a 3-lobed column with two separate stigmas situated on the side-lobes, as in *Gymnadenia*, instead of the central compound stigma on the roof of the spur-entrance as in *Orchis*. *Anacamptis* is really a *Gymnadenia* as far as the sepals, petals, lip, spur, and 3-lobed column with lateral stigmas are concerned. It has, however, taken three steps forward in evolution in the direction of *Orchis*. (1) The linear horizontal backward pointing viscid glands of *Gymnadenia* have taken a half-turn outwards, and the broader ends have united, forming a transverse strap-shaped viscidium with the erect pollinia rather close together in the middle. (2) It has evolved a pouch like that of *Orchis*, to keep the viscid gland moist and sticky. (3) It has ceased to provide free nectar in the spur, and secretes liquid instead between the spur-walls as in *Orchis*.

Neotinea resembles *G. albida* in the one-sided spike of small almost tubular (usually) white flowers with connivent sepals and petals, 3-lobed lip, short honey-filled spur, lateral divergent stigmas on side-lobes of column, and very small pollinia with relatively large rounded pollen-packets and extremely short caudicles. It has, however, evolved the rounded entire tubers, and the orbicular viscidia enclosed in a common pouch, of *Orchis*.

KEY TO THE GENERA

A. *Both pollinia attached to a single viscidium enclosed in a pouch* (*bursicula*).

1. Flower very like *Gymnadenia conopsea*, long-spurred, but with two erect guiding plates on base of lip. Viscidium strap-shaped, the ends curling round and clasping the proboscis of Lepidoptera. **Anacamptis**
2. Flowers green with long narrow ribbon-like lip and short spur. Viscidium large, flat. **Himantoglossum**

B. *Each pollinium attached to a separate viscidium.*

3. Flower without spur. Viscidia sometimes accidentally coherent (but often removed singly by insects). **Aceras**
4. Flower spurred, without free nectar. **Orchis**
5. Side-sepals saccate at base. Spur very short, nectariferous. Stigmas two, on side-lobes of column. **Neotinea**
6. No spur. Each viscidium in its own separate pouch. Stigmas confluent on inner surface of chamber forming foot of column. **Ophrys**

Genus XVI NEOTINEA Rchb. f.

Column very small, 3-lobed, with a stigma on each side-lobe. Pollinia 2, with relatively large loosely attached pollen-packets and very short caudicles. Viscidia 2, enclosed in a pouch.

Small herbs with entire tubers, dense spike, and very small flowers with coherent sepals and saccate spur. Only one species.

The structure of the flower is hard to make out. The plant has been allotted to the following genera by various authors: *Orchis*, *Satyrium*, *Ophrys*, *Gymnadenia*, *Habenaria*, *Cœloglossum*, *Himantoglossum*, *Aceras*, *Peristylus*, *Tinea* and finally *Neotinea*.

Whilst declaring himself a decided opponent of the view that the same generic name could not be used both in the animal and vegetable kingdom, Reichenbach f. nevertheless quite unnecessarily changed the name of the genus from *Tinea* (a genus of moths) to *Neotinea*. *Neotinea* is a connecting link between *Gymnadenia* and *Orchis*, combining the stigmas of the former with the anther, pollinia, and rostellum of the latter. *Vide* also second paragraph of previous page.

NEOTINEA Rchb. f. in *De pollin. Orch. gen. ac struct.* p. 9 (1852).

1. NEOTINEA INTACTA Rchb. f.

Pl. 31; Pl. F, fig. 4 (p. 123). *Irish Orchid, Dense Flowered Orchid*

Tubers two, ovoid; roots few, short. **Stem** 20–30 cm. or more, erect, often flexuous, cylindrical, basal sheaths brownish, acute, membranous. Basal **leaves** 2–3, near together, oblong obtuse, mucronate, spotted (spots small, often in interrupted lines parallel with the nerves), sometimes unspotted, with about three principal transparent nerves on each side of mid-rib, with a fainter nerve between each pair. Stem leaves erect clasping the stem, narrower, acute, the uppermost bract-like, adpressed. **Spike** cylindrical, narrow, dense, often one-sided. **Flowers** very small, white, more rarely pink, ovoid in appearance, as they do not open wide. **Bracts** membranous, ovate-lanceolate or lanceolate, whitish or reddish towards the tip, acute, sometimes with a tooth at the side, 1–3-nerved, from two-thirds to nearly as long as the ovary. **Ovary** short (under 1 cm.), twisted, pale green, glabrous, spindle-shaped, with three slightly raised ridges. **Sepals** connivent, forming a nearly closed helmet, coherent at base, free at the tip, lanceolate to ovate-lanceolate, acute, greenish white or pale rose, the lateral concave at base. **Petals** linear, very narrow, acute, greenish, 1-nerved. **Lip** very small, equal to or exceeding sepals, 3-lobed, spreading or pendent, white or rose, with two or three pale rose or violet markings at the deeply channelled base, side-lobes very narrow, linear, acute, usually shorter than mid-lobe—the latter linear

PLATE 31

A. **Neotinea intacta** Rchb. f. Irish specimen, May 23rd, 1918.

B. Specimen from Hyères, France, April 24th, 1908.

1. Diagram of enlarged column, front view. *S*, *S*, stigmas. *R*, pouch of rostellum. *Sp.*, spur-entrance.

2. Back view. *L*, *L*, side-lobes, on front of which the stigma is situated.

H. M. Godfery pinx.

NEOTINEA INTACTA Rchb. f.
Irish Orchid. Dense-flowered Orchid

or tongue-shaped, notched at the apex (sometimes with a tooth in the notch) and twice as broad as the side-lobes. **Spur** very short (± 2 mm.), conical, obtuse, flattened laterally. **Column** very short, notched at apex, anther-cells parallel, contiguous, ovoid, splitting in front in the usual manner. **Pollinia** extremely small, pale green, consisting of few globular relatively large packets of pollen, loosely tied together; caudicle very short, shorter than pollinia, viscid discs globular, enclosed in the pouch of the rostellum. Capsule moderately thick, tapering at both ends, 3-ridged. **Seeds** with transparent netted testa.

HABITAT. Lowland rocky pastures on limestone. Castle Taylor, Kinvarra, Ballyvaughan, Loch Corrib, etc., in Galway, Clare, and Mayo. Absent from Britain. Flowers May to June. Reaches its extreme northern limit in Ireland. First found by Miss F. M. More at Castle Taylor, Galway, in 1864.

DISTRIBUTION ABROAD. Portugal, Spain, Balearic Islands, Sardinia, Corsica, Sicily, the shores of the Mediterranean from France to Italy and Greece, Cyprus, Asia Minor, Algiers, Morocco, Madeira, and the Canary Islands. A Mediterranean and Atlantic plant, flowering from April to June.

On the Riviera, both French and Italian, the plant is frequent, and occurs not only on limestone, but also on schist and mica-schist, some of the tallest plants being found on the latter. Reichenbach records it from Serra da Cintra, Portugal, as growing in steep granitic places and in arid sand near Coina (Welwitsch). The admirable stereograph (Pl. F, fig. 4) by Herr F. Pfeiffer-Wellheim, of Vienna, is a great achievement, for no one without actual dissection of the flower can realise the difficulty of rendering the inside of the flower visible without causing the pollen-packets to fall on the stigma. It shows clearly the spur-entrance, the anther with the two pollinia, each joined to a separate viscid gland (concealed in the pouch of the rostellum), and the two lateral stigmas reaching half-way up the anther. The complete absence of the plate concealing the base of the anther, pollinia and rostellum figured by Reichenbach[1] will be noted.

Reichenbach f.,[2] following Lindley, placed the plant under *Aceras*, never having seen the rostellum or caudicle. Later he published a coloured plate[1] in which he showed a heart-shaped plate occupying the middle of the flower and two pollinia attached to a long branched caudicle, but did not know whether the latter was constant.

I have dissected a number of flowers—a difficult task owing to their very small size and the tenacity with which the sepals and petals adhere—and found that:

(1) Each of the two pollinia is attached to a separate viscid disc, both discs enclosed in a tiny pouch, as in *Orchis*.

[1] Seemans, *J.B.* p. 1, Table XXV (1865), reproduced in *E.B.* ed. 3, IX, Pl. MCCCCLXV.
[2] *Icones*, XIII, 2, Tab. 148 (1851).

(2) The caudicles are extremely short, scarcely more than half as long as the minute pollinia. I succeeded in withdrawing one of the pollinia on a bristle, but not both. No doubt this could be done if the bristle could be inserted exactly in the middle.

(3) I could find no trace of the central plate shown in Reichenbach's Fig. 6.[1] The space there is clear, and the entrance to the spur visible, also anther, rostellum and stigma (Pl. F, fig. 4 (p. 123)).

(4) The two divergent stigmas are situated on the front surface of a short lobe of the column on each side, as in *Gymnadenia*, i.e. the column is 3-lobed (Pl. 31, B 1 and B 2).

(5) The globules of pollen detach themselves very easily from the pollinia, and fall on the stigma just below them. It is difficult to open a flower without causing this to take place.

Reichenbach's Figs. 6, 7 and 9[1] must have been taken from a very abnormal plant (he only had a few buds from a cultivated specimen to examine), and cannot be reconciled with the Riviera plant. Mlle A. Camus informs me that in the numerous plants gathered at St Tropez, Var, France, the presence of the pouch of the rostellum never appeared doubtful, and that she had never seen a trace of the disc-like organ shown in Reichenbach's Fig. 6.

Neotinea intacta Rchb. f., *De pollin. Orch.* p. 20 (1852), who revived the specific name intacta first given by Link in *Schrad. Journ.* p. 322 (1799). Satyrium maculatum Desf. (1800). S. densiflorum Brot. (1804). Orchis atlantica Willd. (1805). O. secundiflorum Bert. (1806). O. densiflora Desf. (1808). Gymnadenia Linkii Presl. (1826). Himantoglossum secundiflorum Rchb. p. (1830). Aceras secundiflora Lindl. (1832). Tinea cylindrica Biv. (1833). Ophrys sagittata Munby (1847). Aceras intacta Rchb. f. (1851).

Fertilisation. The white or rose-coloured flowers, the presence of a spur filled with free honey, and the mechanism for attaching the pollinia to visiting insects, show that the flower is organised for cross-pollination by their agency. While this no doubt occurs through minute insects, it is difficult to observe, and has not been recorded. The plant, however, fertilises itself by its own pollen. The pollen-packets are very lightly attached to the pollinia, and automatically fall on the sticky stigmas, placed like baskets just below to receive them. It is hard to find open flowers in which this has not occurred. Nearly every flower produces a seed-capsule.

[1] Seemans, *loc. cit.*

Genus XVII ANACAMPTIS Rich.

Stigmas two, lateral, on inner face of side-wings of column, as in *Gymnadenia*. **Rostellum** with a single pouch (as in *Orchis*), enclosing a transverse strap-shaped viscidium to which both pollinia are attached.

Herbs with globose tubers, conical spike of small long-spurred flowers, deeply 3-lobed lip with two converging guide-plates at base, and a viscid gland which curls round and cements itself to the proboscis of the insect withdrawing it. There are two species, both European.

> ANACAMPTIS Rich., *Mém. Mus. Paris*, IV, 47 (1818). ORCHIDIS species L., *Sp. pl.* p. 940 (1753). ACERAS sect. ANACAMPTIS Rchb. f., *Icones*, XIII, 6 (1851). ORCHIS sect. ANACAMPTIS Bentham and Hooker, *Gen.* III, 620 (1883).

Though sometimes placed under *Orchis*, it appears to be a *Gymnadenia*, which in the course of further evolution has acquired the undivided tubers and pouch of the rostellum of *Orchis*. Reichenbach says that the tubers are sometimes almost lobed at the apex, and it is just as credible that *Gymnadenia* could develop a pouch as that the pouch of *Orchis* could have been evolved from a rostellum without one. The two linear viscid glands of *Gymnadenia* joined by their broader ends would give the unusual viscidium of *Anacamptis* with its free curling tips, which the circular discs of *Orchis* if cohering would not do. The flower and spur are extraordinarily like those of *Gymnadenia conopsea*, and the very small circular spur-entrance is as different as possible from the wide spur-mouth of *Orchis*, with the compound single stigma on the roof or back of the spur itself, while the two separate stigmas on side-wings of the column are the counterpart of those in *Gymnadenia*.

Anacamptis fully deserves generic rank, and has reached a very high degree of evolution and adaptation to the structure of a particular class of insects. The strap-shaped viscid gland, exactly encircling the slender proboscis of Lepidoptera, ingeniously solves the difficult problem of attaching the pollinia firmly and always in the same position to a very mobile thread-like organ. *Vide* also first paragraph, p. 151.

1. ANACAMPTIS PYRAMIDALIS Rich.

Pl. 32 (p. 156); Pl. F, fig. 6 (p. 123); Pl. K, fig. 4 (p. 220). *Pyramidal Orchid*

Tubers two, globose or oblong; roots few, short. **Stem** erect (20–50 cm.), solid, often somewhat sinuous, slightly angled above, green, glabrous, often slender, with 2–3 brown truncate or tapering leafless sheaths at base. **Leaves** linear-lanceolate, acute, narrow (10–15 cm.), tapering gradually, keeled, glabrous, green, with numerous parallel nerves and short cross-veins; the basal few, sometimes withered at time of flowering, the upper loosely embracing each other, the uppermost bract-like, sessile, acuminate, sometimes membranous. **Spike** dense, many-flowered, short, conical, lengthening later and becoming ovate or oblong. **Flowers** small, crowded, pale or bright rose, carmine or brilliant rose-red or violet-red, rarely white. **Bracts** linear-lanceolate tapering to a slender point, narrow, 1–3-nerved, green or coloured, slightly exceeding the ovary. **Ovary** sessile, cylindrical, twisted, glabrous, green, often flushed red-violet. **Sepals** free, ovate-lanceolate to lanceolate, acute or obtuse, keeled, 1-nerved, the lateral curved, spreading but not reflexed, the upper connivent with the slightly shorter ovate or lanceolate somewhat hooded 1-nerved **petals** to form a rather long helmet. **Lip** flat, broadly wedge-shaped, deeply 3-lobed, ± 6 mm. long, lobes oblong, nearly equal, truncate or rounded, usually entire, sometimes slightly crenate or toothed, side-lobes divergent. The side-wings of the column run down the lip in the form of two slightly divergent plates with a prolonged rounded apex, acting as guide-plates converging towards the entrance of the spur. **Spur** slender, long, often exceeding the ovary, with no free honey. **Column** short (2 mm.), obtuse, with a concave wing on each side, white, more or less tinged with colour. **Anther** ovate, granular outside, white tinged with pale rose, cells parallel, separated at the base by the rounded low-waisted stigmatic fold. **Stigmas** two, oval, white, on the concave side-wings of the column, with a whitish or pinkish rugose staminode between each and the anther. The foot of the anther and the rostellum which it embraces are low down in the flower, partly blocking up the entrance to the spur and separating the two stigmas. Pouch of rostellum hollowed out in the middle beneath.[1] Viscidium single, transversely strap-shaped, the two caudicles fastened to its upper surface rather close together in the centre. **Seeds** oblong, cells of transparent testa transversely netted.

Var. **sanguinea** Druce. Flowers bright blood-red instead of rosy pink (*B.E.C.* p. 639 (1928)).

Pl. K, fig. 4 (p. 220). An abnormal form without spur and with almost entire lip, found by Dr T. Stephenson near Winchester in July, 1926. It did not appear to be a hybrid. The flowers were pale rose, and the leaves short and yellowish. Forma *ecalcarata* Ruppert.[2]

A. pyramidalis is at once recognisable by the short dense conical spike of bright-coloured flowers, by the two erect guiding plates on the base of the lip, found in no

[1] "duabus foveis pro cruribus unicae glandulae", Rchb. *Icones*, XIII, 8.

[2] A specimen of *Anacamptis pyramidalis* × *Gymnadenia conopsea* was found by the Rev. T. Stephenson on the downs near Winchester in July, 1925, and was seen by me. The spike was oblong, not pyramidal, the flowers of the colour of *G. conopsea*, and the lip not so deeply divided as in *A. pyramidalis*, but with the guide-plates peculiar to the latter species. Pl. 32, fig. 1, shows a flower from the hills behind Genoa which appeared to me to be this hybrid, but I failed to note whether the tubers were palmate, and the pollinia on separate viscidia. It was scented like *G. conopsea*, but the facies was nearer that of *A. pyramidalis*. *Gymnanacamptis Aschersonii* Camus, *Mon. Orch. Eur.* p. 95 (1908).

PLATE 32

Anacamptis pyramidalis Rich. Deganwy, North Wales, July 18th, 1908.

1. **Anacamptis pyramidalis** × **Gymnadenia conopsea.** Granarolo, Genoa, May 22nd, 1914.

H. M. Godfery pinx.

ANACAMPTIS PYRAMIDALIS Rich.
Pyramidal Orchid

1. ANACAMPTIS PYRAMIDALIS × GYMNADENIA CONOPSEA

other British orchid, and by the long slender spur. The only one of our orchids it could be mistaken for is *Gymnadenia conopsea*, but the latter has no guide-plates. The upper surface of the lip is minutely velvety with erect extremely short hairs or papillæ, which perhaps help to give the lip its extraordinary brilliancy of colour.

Darwin received six spikes from Folkestone without any spur. None of the pollinia had been removed. He also found that, in about a dozen other flowers either having short spurs or the guiding plates absent or over-developed and foliaceous, the pollinia had only been removed from one flower and the ovary of another was swelling. The perfect flowers on the same spikes had all been fertilised and the pollinia removed.[1] Plants were pushing up in the rock-garden at Scampston Hall, Malton, Yorks., on November 2nd, 1931. They increase rapidly under cultivation.

Habitat. Chalk downs, sunny slopes, especially on limestone, banks, pastures, and rarely on sand-hills. Flowers June to July.

Distribution. Generally distributed but local in England and Wales, frequent throughout Ireland, Scotland only in the south, few records. Wigton, Berwick, Colonsay (Watson, *Top. Bot.* No. 1050). Europe from Southern Scandinavia and Central Russia to Spain, Italy, the Mediterranean islands, the Balkans, Caucasus, Asia Minor, Syria, Palestine, Persia, N. Africa.

Anacamptis pyramidalis Rich., *Mém. Mus. Paris*, iv, 41 (1818). Orchis pyramidalis L., *Sp. pl.* ed. 1, p. 940 (1753). Aceras pyramidalis Rchb., *Icones*, p. 6 (1851).

Fertilisation. See "Pollination and Fertilisation", p. 24.

Genus XVIII **HIMANTOGLOSSUM** Sprengel

Rostellum pouch-like, containing only one viscidium, to which both pollinia are attached. **Labellum** curled up like a watch-spring in bud, mid-lobe very long and narrow; spur short, conical, sack-like.

Herbs with undivided tubers, stout stem, oblong leaves, cylindrical spike-like raceme, and greenish flowers with connivent sepals and petals.

It is difficult to decide the genetic position of *Himantoglossum*. In S. Europe the monotypic genus *Barlia* has both pollinia attached to a common viscidium, and was placed under *Himantoglossum* by Schlechter on that account, and the larger Mediterranean genus *Serapias* with about seven species possesses the same character. They appear to be survivals of an independent line of descent parallel with *Orchis*. Probably their common ancestor had both pollinia attached to a single viscidium, but whilst *Himantoglossum*, *Barlia* and *Serapias* have retained this character, and have failed to diverge into numerous species, the rest of their ancestral group has evolved two

[1] Darwin, *Fert. Orch.* ed. 2, p. 38.

separate viscidia, and given rise to the large genera *Orchis* and *Ophrys*, and also the Gymnadeniinæ. The single viscidium in the above genera may possibly have arisen from the coherence of two viscidia, but is more probably a connecting link between the single rostellum of more primitive tribes and the two viscidia of *Orchis*, etc.

> HIMANTOGLOSSUM Sprengel, *Syst.* III, 675 (1826). LOROGLOSSUM Rich., *Mém. Mus. Paris*, IV, 54 (1818) (which included ACERAS). Included by Linnæus in SATYRIUM, by Crantz, Robert Brown, etc., in ORCHIS, and by Lindley, in which he was followed by Reichenbach f., in ACERAS.

1. HIMANTOGLOSSUM HIRCINUM Sprengel

Pl. 33; Pl. C, fig. 4 (p. 50). *Lizard Orchid*

Tubers ovoid or oblong, undivided; roots short, rather thick. **Stem** usually robust (sometimes rather slender in English specimens), 20–40 cm. tall (recorded up to 90 cm. abroad), solid, cylindrical, glabrous, smooth, obscurely angled above, pale green faintly mottled with purple, leafy. **Leaves** firm, basal (4–6), 6–12 cm. long, 3–5 cm. broad, oval- to oblong-lanceolate, rather obtuse or moderately acute, keeled, glabrous, erect or spreading, light green or dark green, often yellowish or fading at time of flowering; upper sessile, tapering, acute, many-nerved, with branching cross-veins. **Raceme** spike-like, 10–25 cm. long, stout, erect, cylindrical, many-flowered, usually dense. **Flowers** greenish with very long ribbon-like twisted lips, at first coiled up like a watch-spring, finally hanging obliquely downwards, the lower somewhat distant, the upper crowded, becoming less so through lengthening of the axis, with a strong goat-like smell and somewhat tangled and untidy appearance. **Bracts** linear, narrow, tapering, acute, more or less membranous, often with inrolled edges, pale green or whitish often tinged rose, lowest about 5 cm. long, equalling the flowers, with green central nerve and about three others on each side near the edge, the upper slightly exceeding the ovary. **Ovary** shortly stalked, somewhat spindle-shaped, twisted, ± 1 cm. long, smooth, glabrous, pale green, with three slight longitudinal ridges. Capsule long, rather 3-sided, tapering at base, with marked ridges. **Sepals** forming a helmet, cohering at base, free or not at the tip, oval, rounded at apex, concave, 3–4-nerved, whitish green sometimes flushed with violet, paler inside with numerous violet-red lines and spots; upper sepal arched forward, rather boat-shaped. **Petals** slightly shorter, linear, very narrow, adhering to edges of upper sepal for most of their length, spotted, 1-nerved. **Lip** linear, very long, wedge-shaped and broader at base, with green strongly undulate (crimped) edges continued on the linear short (± 1 cm.) narrow acute curly green or reddish side-lobes; mid-lobe ribbon-like, very long (4–5 cm.) in proportion to its breadth (± 2 mm.), at base trough-like, white spotted red-violet with a dense fur of minute white papillæ

PLATE 33

Himantoglossum hircinum Sprengel. Allaman, Switzerland, May 18th, 1913.

1. Single flower (enlarged). Kent, June 20th, 1918.

H. M. Godfery pinx.

HIMANTOGLOSSUM HIRCINUM Sprengel
Lizard Orchid

as far as the junction of the side-lobes, the rest of the lip pale green, glabrous to its bifid, notched or 2–4-toothed apex. **Spur** short (± 4 mm.), conical, sack-like, rounded at apex, directed downwards, with thick green walls, its interior surface covered with extremely minute short papillæ. **Column** short. **Anther** pear-shaped, greenish white, cells somewhat distant, staminodes small, rounded, fold between anther-cells bright green, short or rather long. **Pollinia** short, pear-shaped, pale olive-green, caudicles thick, yellow, longer than pollinia, bent at apex, fixed to the centre of the elliptical or somewhat quadrangular viscid gland. **Stigma** obtusely four-cornered or heart-shaped, bordered by a dark line.

Pl. C, fig. 4 (p. 50), shows a spike from the Sussex downs.

Camus states that before the flower opens, nectar is secreted in the spur, but that it has almost entirely disappeared when the lip uncoils.[1] Is this always the case? The visits of hive-bees suggest the presence of honey. Plants were pushing up in a garden in Yorkshire on November 2nd, 1931.

Habitat. Edges of woods, near paths in woods, amongst bushes, in fields, etc., mostly on calcareous soils. Flowers May to July.

Distribution. Least rare in Kent, where about 20 stations are known; Surrey (*B.E.C.* 1921 and 1924); Sussex, Cuckmere district (*J.B.* 1911 and *B.E.C.* 1921); Hants. (*B.E.C.* 1925); Sussex (*B.E.C.* p. 399 (1921)); Dorset (?) (*B.E.C.* 1923); N. Somerset (*B.E.C.* 1923); W. Gloucester (*B.E.C.* p. 129 (1917)); N. and S. Wilts. (*J.B.* 1908); Oxon. 1 plant (*B.E.C.* 1921); Berkshire (*B.E.C.* 1921); Cambridge (*B.E.C.* 1921 and 1924); E. Norfolk (*B.E.C.* 1923); Jersey (*B.E.C.* 1919, 1920 and 1921). Mostly sporadic. The first record for Britain appears to be "nigh the highway between Crayford and Dartford", Johns, *Merc. Bot. pars alt.* p. 27 (1641). It was collected at Dartford by Banks, and the figures in *English Botany* and in *Flora Londonensis* are from Dartford specimens. Prof. F. Darwin told Webster that a flowering specimen suddenly appeared in the Cambridge Botanical Garden, where, so far as was known, it had never been noticed before. It is said to be difficult to cultivate, usually dying after flowering. It seems to be spreading. Its northern limit appears to be Holland. It extends to Germany, Austria, France, Spain, Italy, the Balkans, Asia Minor, and N. Africa.

Himantoglossum hircinum Sprengel, *Syst.* iii, 694 (1826). Satyrium hircinum L., *Sp. pl.* ed. 1, p. 944 (1753). Orchis hircina Crantz. Loroglossum hircinum Rich. (1818). Aceras hircina Lindl.; Rchb. f.

Fertilisation. The floral mechanism for the removal of the pollinia is much the same as in *Orchis*, but the two pollinia are attached to one undivided viscid disc, on which account it has sometimes been united with *Aceras*, in spite of its spur. The

[1] Camus, *Icon.* p. 121 (1928).

pollinia go through the same downward movement as in *Orchis*, through an angle of 90°. This movement takes place in about 30 seconds according to Darwin, but I found that in one specimen the pollinia required from $1\frac{1}{2}$ to 2 minutes to complete the movement, which is caused by the sinking down of the front part of the disc till it is separated from the hinder part by an abrupt step.[1] Darwin was surprised at the degree to which the inner and outer walls of the spur were separated, and at the quantity of fluid contained between them.[2] Hildebrand saw this species fertilised by a bee.

Mr J. Jacob, of Dover, tells me that the man in charge of a colony of *Himantoglossum* had continually seen a wasp-like fly (*Odynerus parietum*) visiting the flowers, but did not notice whether the pollinia were carried off.

On May 6th, 1931, not far from Cannes, France, I caught a hive-bee (worker) on *H. hircinum* bearing seven pollinia, and saw two others come and look at it without alighting. I also saw a smaller bee alight but failed to take him.

Genus XIX ACERAS R. Br.

Column very short, forming a little chamber, on the roof and walls of which is the stigma. **Pollinia** small, with very short caudicles. Viscid glands two, touching and sometimes coherent, but often separately withdrawn, enclosed in a pouch. **Lip** without spur.

Small plants with habit of *Orchis*. Sepals and petals partly adherent forming a nearly globose helmet. Lip hanging, anthropoid, grooved at base, joined to column by two thick rolls enclosing a shallow cup with two slight depressions.

ACERAS R. Br. in Ait. *Hort. Kew.* ed. 2, v, 191 (1813). OPHRYS (species) L., *Sp. pl.* p. 948 (1753). LOROGLOSSUM (species) Rich. (1818). HIMANTOGLOSSUM (species) Sprengel (1826).

Though the genus *Aceras* owes its name to the absence of a spur, the most important character in all previous diagnoses has been the attachment of both pollinia to a single viscid disc. Reichenbach f. adopted it as the type of all species with only one viscid gland, and transferred to it *Anacamptis*, *Himantoglossum*, etc. The two discs lie touching each other in the pouch of the rostellum, and sometimes cohere, but are frequently removed separately by insects, as I have observed both at home and abroad. Darwin pointed this out so long ago as 1862 (*Fert. Orch.* p. 26), adding in a foot-note: "The separation of this genus is evidently artificial. It is a true *Orchis*, but with a very short nectary". Nevertheless in the most recent works Schlechter and Keller say: "Pollinia...viscidio rotundato communi affixa",[3] and E. G. and A. Camus, "rétinacles soudés en un seul".[4]

[1] Darwin, *Fert. Orch.* ed. 2, p. 26.
[2] *Ibid.* p. 39.
[3] *Mon. Orch. Eur.* p. 130 (1925).
[4] Camus, *Icon.* p. 110 (1929).

H. M. Godfery pinx.

A. ACERAS ANTHROPOPHORA R. Br.
Man Orchid

B. ORCHIS MILITARIS × SIMIA
O. Beyrichii Kerner

PLATE 34

A. **Aceras anthropophora** R. Br. Kent, June 9th, 1918.

1. **Formica fusca** L.

B. **Orchis militaris × simia, × Orchis Beyrichii** Kerner. Allaman, Switzerland, May 18th, 1913.

Whether the absence of a spur is sufficient to justify the separation of *Aceras* from *Orchis* is open to doubt. It appears to be the only important point in which the two genera differ. That *Aceras* is very closely allied to *Orchis militaris*, *purpurea* and *simia* is shown by the characteristic odour of coumarin (as in woodruff) common to the leaves of them all when dried, by the resemblance of the helmet to that of these three species, and of the lip to that of *O. simia*, and by the readiness with which hybrids occur with the latter species when they grow together, which shows that they are not infrequently visited by the same insects.

1. Aceras anthropophora R. Br.

Pl. 34 A. *Man Orchid*

Tubers thick, ovoid or sub-globose; roots several, moderately thick. **Stem** erect (20–30 cm.), solid, cylindrical, slightly ridged above, pale green, glabrous, with obtuse membranous leafless sheaths at base. **Leaves** sub-erect or spreading, sheathing at base, oblong or oblong-lanceolate, but little narrowed at the base, 6–12 cm. long by $1\frac{1}{2}$–$2\frac{1}{2}$ cm. broad, keeled, more or less acute, glabrous, dark green or grey-green, glossy on both sides, with innumerable whitish dots beneath, smooth to the touch, of a rather firm consistency, with 3–4 nerves on each side of the mid-rib, usually with a fainter nerve between each pair. Basal leaves close together, the upper erect clasping the stem, with sometimes a narrow membranous acute bract-like leaf above. **Spike** erect, long, narrow, cylindrical. **Flowers** many, close together except at the base, small, green often edged red, with green, yellow or dull red lip. **Bracts** half as long as ovary, or less, membranous, 1-nerved, tapering, acute. **Ovary** stalkless, erect, slightly spreading, cylindrical or slightly triangular, $\pm$ 1 cm. long, twisted, glabrous, green with six cord-like ridges. **Sepals** 6–7 mm. long, forming with the petals a short globose or ovoid helmet, adherent for about half their length, free at the tip, ovate to ovate-lanceolate, obtuse or moderately acute, 1-nerved, light green edged violet- or brownish red. **Petals** slightly shorter and much narrower, linear, rather obtuse, greenish, 1-nerved, covering the edges of the sepals internally, and making the helmet water-tight. **Lip** without spur, pendent, narrow, oblong, greenish or yellowish often edged with brownish red, sometimes pure yellow or crimson-red, twice as long as the sepals, shaped like the body of a man, with two linear long very narrow side-lobes and two shorter equally narrow terminal lobes sometimes with a small tooth between. At the base the lip divides into two whitish shining thickened folds (with a narrow V-shaped passage between them) which curve round and join the base of the column, enclosing a shallow cup on the floor of which are two small depressions (visible beneath as little humps) which, according to Darwin, are the nectaries. **Column** very short. **Anther** short, ovate obtuse, yellowish green. **Staminodes** small. **Stigma** on roof and sides of the stigmatic chamber formed by the base of the lip and the column. **Pollinia** small, very short (1 mm.), pale sulphur-yellow, caudicles transparent darker yellow, viscid discs colourless, nearly globular, touching or cohering, caudicle ribbon-shaped where it joins the viscidium.

Forma *flavescens* Zimm. Sepals without red edging; lip pale, sulphur-, or bright yellow. Wye! Gomshall! (lip bright yellow). Figured by Ruppert in *Deutsche Monatssch.* Pl. 128, fig. 31 (1912).

Forma *virescens* Ruppert (*loc. cit.*). Helmet and lip greenish white.

I have seen specimens of enormous stature on the Lake of Geneva, growing in long hay-grass, doubtless drawn up in the effort to reach the light. The flowers are said to have an unpleasant smell, not always noticeable. It is extremely constant to type, only varying in such trifling points as height, density of the spike, and colour of the lip. The leaves when dried develop a strong smell of woodruff, due to coumarin, like *Orchis militaris*, *purpurea* and *simia*. The resemblance of the lip to the body, arms and legs of a man has given rise to the botanical (*anthropophora*) as well as the popular names Man Orchid, Homme pendu (French) and Ballerino (Italian). No hybrids have so far been found in England, but crosses with *Orchis militaris*, *purpurea* and *simia* have occurred on the Continent, the last two in some numbers in a few localities.

In Smith's *Catalogue of the Plants of South Kent* (1829) we read: "Mr Price sent me a specimen of this crimson-lipped variety bearing 87 flowers...the greater part appear in perfection at the same time. The flowers emit a fragrance more aromatic but less sweet than those of the honeysuckle, strongest in the evening, and then not pleasant" (p. 51).

Plants were already pushing up in the rock-garden at Scampston Hall, Yorks., on November 2nd, 1931.

Habitat. Chalk downs, grassy slopes, amongst bushes, undisturbed borders of fields, rarely in open woods, on calcareous soil. Flowers June to July. Rare in Britain.

Distribution. Eastern and south-eastern counties of England, extending according to Watson[1] as far north as Yorks. Appears to be absent from the west of England, Wales, Ireland, and Scotland. Europe from Germany southwards to the Mediterranean, extending from Spain to the Balkans; Cyprus, N. Africa (Morocco to Tunis).

Aceras anthropophora R. Br. in Ait. *Hort. Kew.* v, 191 (1813). Ophrys anthropophora L., *Sp. pl.* ed. 1, p. 948 (1753). Orchis anthropophora All. (1785). Loroglossum anthropophorum Rich. (1817). Aceras anthropomorpha Steud. (1840). Himantoglossum anthropophorum Spreng. (1826).

[1] *Top. Bot.* p. 1058.

Fertilisation. The small flowers, the unusually short caudicles, and the two very shallow depressions in the base of the lip which act as nectaries[1] show that the insects which carry off the pollinia are probably small, but no actual visits seem to have been witnessed or recorded, except as stated below. On a spike of 27 flowers found by me near Gomshall, Surrey, both pollinia had been removed from 11 flowers, and one pollinium only from each of four flowers, leaving the second *in situ* in the anther, whilst there was pollen on the stigmas of five flowers. The lower 24 flowers of a long spike found by me near Hyères, France, had seven flowers with both pollinia removed, three with only one removed, and 14 intact, whilst there was pollen on eight stigmas. This is of special interest as showing that the two pollinia are not attached to one and the same viscid disc, as stated by practically all writers on the subject except Darwin,[1] who recorded that a single pollinium is sometimes removed by insects. On grasping a pollinium with forceps and gently withdrawing it from the anther, the author found, in the case of several flowers thus tested, that it came away with a perfect viscid gland at the foot of the caudicle, quite free from the second pollinium and its viscid disc, which remained behind undisturbed. The plant appears to be well visited and fertilised.

On May 12th, 1928, Colonel G. H. Evans and I watched vases containing cut spikes of *Ophrys muscifera* on the terrace-wall of the Hôtel du Château, Challes-les-Eaux, Savoie, France. Amongst them I had placed two or three spikes of *A. anthropophora*. Ants were running about, and with their usual inquisitiveness, they now and again explored the flowers in the vase. To my astonishment I noticed an ant going down the stalk of *Aceras* with a pair of pollinia attached very neatly to its head (*Formica fusca* L.). I thought at first this was accidental, but on other days the same thing happened, so it may be concluded that some of the insect-visitors which play a part in the pollination of *Aceras* are certainly ants. This may explain the absence of a spur from this plant—the two very shallow depressions in the base of the labellum being admirably adapted for presenting honey to such small creatures as ants. Pl. 34, A 1.

They are probably not the only visitors. Hybrids between *Aceras* and *Orchis militaris*, *simia*, *purpurea* and *undulatifolia* (*Italica*) are not infrequent, so that the Hymenoptera which visit these latter may also visit *Aceras*, though of course ants bearing the pollinia of the latter may carry them to the other orchids mentioned.

The late Mr Burton, of Longner Hall, Salop, told me that while sitting in his glass-house he saw flies (*Platychirus manicatus*) visiting *Aceras*, and depositing eggs amongst aphides in the flowers. He watched to see whether they removed pollinia, and in every case found pollinia on their heads. Later he found larvæ of *Platychirus* energetically destroying the aphides. This curious case of the pollination of the flowers of an orchid through the attraction, not of any product of the plant itself,

[1] Darwin, *Fert. Orch.* ed. 2, p. 26.

but of aphides infesting it, may throw light on the visits of *Sarcophaga carnosa*, a fly which frequents decaying animal matter, to the flowers of *Epipactis palustris*, which so puzzled Darwin. Mr Burton was a most successful cultivator of British orchids.

Spikes of *A. anthropophora* were exposed at Challes-les-Eaux, Savoie, France, in May, 1929, together with *Listera ovata*, *Cephalanthera grandiflora*, five species of *Orchis* and four of *Ophrys*. The following Hymenoptera came (in very small numbers) and visited one or other (rarely more than one) of the above species: Hive-bees, *Bombi* (two species), *Halictus* (three species), *Andrena* (two species), *Eucera tuberculata*, *Gorytes mystaceus*; also the following Diptera, *Echinomyia magnicornis* and *Volucella inflata*. Not one of these took the slightest notice of *Aceras anthropophora*.

Genus XX ORCHIS L.

Column erect, surmounted by the non-detachable anther. **Stigma** central, on front of column, which forms roof of spur-entrance. **Pollinia** two, caudicles attached to separate viscidia, enclosed in the same pouch.

Herbs with entire or forked tubers, entire glabrous leaves, numerous rather small flowers in a spike, connivent or spreading sepals, 3-lobed lip and honeyless spur with liquid between its walls.

ORCHIS L., *Gen. pl.* ed. 1, p. 270; ed. 5, p. 405 (1754).

By far the largest genus of European orchids, and except *Ophrys*, the most highly developed and specialised. About 80 species are known, inhabiting Europe, temperate Asia, N. Africa, the Canary Islands, and (three species) the United States and Canada (Oakes Ames, *Orchids of the United States and Canada*, p. 83 (1924)), but according to Schlechter these latter constitute a separate genus.

FERTILISATION. See "Pollination and Fertilisation", p. 21.

KEY TO SPECIES

A. TUBERS ENTIRE (**Euorchis** Klinge)

Section I HERORCHIS Lindl.

Sepals and Petals forming a helmet.

Sub-section 1 *Militares* Parl.

Lip anthropoid, mid-lobe bi-lobed, longer than side-lobes. Bracts short, membranous. Sepals more or less coherent.

1. Helmet greyish, flushed violet or rose; side and terminal lobes of lip violet or rose-red, long, narrow, of similar shape. **O. simia**

2. Helmet greyish rose; mid-lobe of lip with two widely divergent rounded darker lobes, broader and shorter than side-lobes. **O. militaris**

3. Helmet dark red-purple; lip broad, with violet tufts, and broad diverging terminal lobes; flowers large. **O. purpurea**

4. Flowers very small; helmet dark red-brown; lip narrow, white with crimson spots. **O. ustulata**

Sub-section 2 *Moriones* Parl.

Sepals free; side-lobes of lip broad, rounded, mid-lobe shorter, truncate.

5. Sepals with conspicuous green or bronze-purple veins. **O. morio**

Section II ANDRORCHIS Lindl.

Side-sepals spreading or reflexed.

Sub-section 3 *Masculæ* Parl.

6. Flowers red-purple; mid-lobe of lip longer than side-lobes. **O. mascula**

7. Flowers dark violet; mid-lobe much shorter than the reflexed almost touching side-lobes; spur long, straight, often notched. **O. laxiflora**

B. TUBERS FORKED (**Dactylorchis** Klinge)

Leaves always unspotted.

8. Stem hollow, walls thin. Leaves erect, tapering, hooded at tip, broadest just above base; bracts long, incurved. Flowers small, narrow-looking, rose or violet; sepals erect, back to back, sides of lip much reflexed, mid-lobe small, apical, markings square-ended loops; spur short, stout, conical. **O. incarnata**

9. Stem-walls thicker. Leaves spreading, oblong-lanceolate, firm; lower bracts long. Flowers larger; sepals not reflexed; side-lobes of lip not reflexed, mid-lobe small, markings radiating dots (or streaks); spur stout, longer. **O. prætermissa**

Leaves usually spotted.

10. Stem not so hollow as 8. Leaves oblong-lanceolate, rather thin, with blotches ringed, or small spots. Sepals erect; lip shallowly lobed, mid-lobe small, markings parallel loops; spur rather long, conico-cylindrical. **O. latifolia**

11. Stem solid. Lowest leaf short, oval, the upper longer with conspicuous transverse oval spots; bracts inconspicuous, narrow. Flowers pale lilac or rose, sepals erect; lip 3-lobed divided to middle, side-lobes rhomboidal, mid-lobe long (basic soils) or lobes sub-equal (limestone); spur straight, somewhat enlarged at base. **O. maculata**

11*a*. Like 12, but lower leaf like the others, leaf-spots faint. Sepals narrow, horizontal or drooping; lip broad, side-lobes rounded out, mid-lobe very short, narrow; spur straight, very slender, hardly enlarged at base. **O. maculata** sub-sp. **elodes**

12. Dwarf (10–20 cm.). Leaves short, $\pm 2\frac{1}{2}$ cm. broad, spotted at tip. Flowers rich dark purple with crimson markings; spur conical, short, stout. **O. purpurella**

13. Dwarf ($\pm$ 12 cm.). Leaves very narrow, frequently ring-spotted. Spike short, few-flowered (9–20); bracts coloured; flowers dull red-purple with reflexed side-lobes, and small mid-lobe; spur stout conical. **O. latifolia** var. **eborensis**

1. ORCHIS SIMIA Lamarck var. MACRA (Lindl.)

Pl. 35. *Monkey Orchid*

Tubers ovoid; roots few, short, rather thick. **Stem** 15–30 cm., round, solid, angled, glabrous, greyish green, often purplish above, with 2–3 close-fitting acute sheaths at base. **Leaves** about four, oblong, broad, rather obtuse, mucronate, folded, keeled, slightly hooded, grey-green, unspotted, glabrous, glossy, with parallel nerves depressed beneath, the upper oblong-lanceolate, acute, wrapped round the stem, the uppermost thin, membranous, lanceolate acuminate, sometimes bract-like. **Flowers** of medium size, white, lobes of lip violet. In the type the helmet is ashen grey more or less tinged, streaked and spotted with violet, the lip-segments bright rose-red (as in Pl. 34 B) to red-violet. **Bracts** membranous, semi-transparent, greenish, rose or whitish, awl-shaped, tapering, acute, often ending in a rather long point, $\frac{1}{4}$–$\frac{1}{3}$, rarely half as long as ovary. **Ovary** $\pm$ 10 mm., cylindrical, twisted, curved, with six violet-tinged ridges. **Sepals** lanceolate acute, partly adherent, tips free, forming a rather long open helmet, white or pale violet with minute violet dots, and 2–3 raised white nerves. **Petals** shorter, linear acute, very narrow (1 mm.), minutely denticulate, white edged violet, adherent to sepals for half their length. **Lip** longer than sepals with a long slender upturned linear violet arm-like segment on each side near the base; mid-lobe straight, narrow, with parallel sides, forking into two narrow linear divergent up-curled segments (legs) with a short tail-like appendix between, all deep

PLATE 35

Orchis simia Lamarck var. **macra** Lindl. Oxfordshire, May 29th, 1918.

1. Flower (enlarged).
2, 3. **Apis mellifica** L., ♀ carrying two pairs of pollinia.

H. M. Godfery pinx.

ORCHIS SIMIA Lamarck var. MACRA Lindl.
Monkey Orchid

violet shading into white at the base. Mid-lobe sprinkled with minute tufts of violet rather long papillæ, the white surface crystalline with densely studded very short white papillæ. **Spur** pointing downwards about half as long as ovary, narrow at the neck, flattened from back to front, wider at the truncate sometimes notched apex. **Column** short, white at the back, with two dark purple eye-like spots at apex, forming a chamber over the mouth of the spur, with a rounded violet staminode on each side at the base. **Anther** oblong, truncate at apex, sometimes with a short beak. **Stigma** on the back of the chamber above the spur, bordered by a purple line, and appearing cordate owing to the projection of the rostellum downwards.

The British plant differs from the type by its darker more grey-green leaves, more cylindrical spike, bluer lip-segments, broader mid-lobe with smaller spots, and whiter spur. One or more, however, of these characters may be occasionally found in some continental specimens. I have therefore named it *O. simia* var. *macra*, retaining Lindley's specific name. I found one specimen at Challes-les-Eaux, Savoie, France, with similar colouring to the British plants, amongst hundreds of the type. Sometimes it is pure white and very beautiful. Lindley wrote[1] that he had no doubt that the British plant was altogether distinct from the *O. tephrosanthos* of continental writers (*O. simia*). He says that *O. macra* "independent of its more slender habit, narrow few-flowered spikes and bluntish leaves, is quite remarkable for the exceedingly large cells of the tissue of the lip, which project and have a watery appearance, as if the whole surface were covered with crystalline warts; the lip is moreover destitute of the hispid line which invariably runs through its centre in all the varieties of *militaris* or *tephrosanthos* I have examined".

A. Camus[2] writes of *O. simia* that the papillæ of the upper surface of the lip are extremely developed, those of the violet spots 200–250μ long, but that at the base of the lip there is a central furrow without papillæ. Towards the middle of the lip the central area forms a crest furnished with papillæ. The plant smells of woodruff when dried. A curious character is the opening of the flowers from the top downwards, not from the base upwards, as in all other British species.

O. militaris × *simia*, vide *O. militaris*.

ORCHIS SIMIA Lam., *Fl. Franc.* III, 507 (1778). O. MILITARIS ε L. (1763). O. TEPHROSANTHOS Vill. (1787). O. BRACHIATA var. CINEREA Gilib (1792), etc. O. MILITARIS, *E.B.* t. 1873. O. MACRA Lindl., *Syn.* ed. 2, p. 260 (1835).

HABITAT. Grassy places on hillsides, among bushes, and on borders of fields on limestone or chalk; rather dry and wooded hills.

DISTRIBUTION. Apparently now confined to Oxfordshire, formerly found in Berkshire. There is a single record for Kent, the Rev. S. L. Jacobs having found it near

[1] *Syn. Brit. Flora*, ed. 2, p. 260.

[2] Camus, *Icon.* p. 166 (1929).

Chilton, which, if not an error of identification, must have been due to a wind-borne seed.

Mid- and Southern Europe: Alsace Lorraine, Baden, Belgium, France, Italy, Spain, Switzerland. South Tyrol, ascending to 2000 ft. near Trient, Balkan peninsula, Crimea, Caucasus, Asia Minor, Palestine, Syria, Cyprus, N. Africa, Persia.

FERTILISATION. See "Fertilisation and Pollination". I saw a hive-bee at Challes-les-Eaux, Savoie, in May, 1929, go to *Cephalanthera ensifolia*, which it immediately deserted for *Orchis purpurea*, from which it withdrew a pair of pollinia from one flower. It then went to *O. simia*, from which it also withdrew a pair of pollinia, and afterwards to *O. ustulata*, on which I took it before it had time to remove any pollinia. I also took a hive-bee, *Apis mellifica*, bearing seven pollinia, all belonging to *O. simia*, at Challes-les-Eaux in May, 1929 (Pl. 34, A 1). The unusual conduct of the first bee mentioned was probably due to all the spikes being in the same vase. It was apparently not satisfied with any of them, for it did not visit a second flower on any spike.

2. ORCHIS MILITARIS L.

Pl. 36. *Soldier Orchid, Military Orchid*

Tubers two, ovoid; roots few, short. **Stem** 30–40 cm., round, light green, slightly angled and often tinged with violet above, with 2–3 membranous acute sheaths at base. **Leaves** close together at base of stem, unspotted, oblong to oblong-lanceolate, acute or obtuse, rather broad and thick, light green and glossy above, paler and slightly glaucous beneath, the upper erect loosely clasping the stem. **Spike** oval or conical, later cylindrical, many-flowered, dense or rather lax. **Flowers** rather large, rose or pale red-violet, honey-scented, opening from below upwards. **Bracts** 4–6 times shorter than the ovary, membranous, pellucid, rose-coloured, nearly triangular, acute, obtuse or somewhat truncate. **Ovary** slender, linear, sessile, much twisted, often violet-tinged. Seed-capsule oblong with six prominent ridges. **Sepals** elliptic-lanceolate, acute or sub-obtuse, connivent in an ovate or ovate-lanceolate acute helmet, pale ashen grey flushed rose or violet outside, veined and spotted with darker red-violet within, their bases coherent. **Petals** very narrow, linear acute, 1-nerved. **Lip** rather longer than sepals, or equalling them, rose, nearly white in the centre with scattered tufts of red-violet hairs, 3-lobed, lobes bright rose or red-violet, darker, side-lobes short, narrow, linear obtuse or slightly spatulate, mid-lobe broadly linear with more or less parallel sides, variable in length, but usually longer than the side-lobes, ending in two widely divergent oblong or elliptic entire or minutely toothed lobelets, shorter and 2–4 times broader than the side-lobes, with a short

PLATE 36

Orchis militaris L. Challes-les-Eaux, Savoie, France, May 20th, 1929.

1, 2. Enlarged flowers.

3. **Andrena curvungula** Th. ♀.

H. M. Godfery pinx.

ORCHIS MILITARIS L.
Soldier Orchid

narrow acute tooth between. **Spur** descending, cylindrical, sack-like, obtuse, slightly curved forwards, pale rose or violet, barely half as long as ovary. **Column** obtuse. **Stigma** cordate, pouch of rostellum and viscid glands yellowish white. **Anther** ovoid, violet-purple with contiguous parallel cells, pollinia dark bluish green. **Seeds:** testa transparent, oblong, rounded at apex, reticulate, cells not striate, cell-walls thick.

Specimens found by me in Savoie had a delicious honey-like scent. Camus (*Icon.* p. 169) says they smell slightly of coumarin, like woodruff (*Asperula odorata* L.). The tubers yield salep.

O. *militaris*, *purpurea* and *simia* were regarded as varieties of one species by Linnæus, a view adopted by Hudson[1] and some other authors. Smith[2] thought that O. *militaris* and *purpurea* were good species, but was doubtful about O. *simia*. No doubt all three sprang from a common ancestor. When dried they all smell of coumarin. So also does *Aceras anthropophora* in a still more marked degree, and probably arose from the same stock as O. *simia*, which its lip somewhat resembles. All are now regarded as good species.

Schulze[3] figures a flower with three sepals alternating with three lips, making the flower appear regular (peloria). He does not say whether the petals transformed into lips had spurs. Camus[4] describes and figures a flower with the two side-sepals turned into incomplete lips, each with a spur.

A small colony with pure white flowers of great beauty was found by me near the Lac de Thuile, Savoie, in May, 1927. The species is much less variable than O. *purpurea*.

Habitat. Grassy hills, banks, field borders and edges of woods on chalk or limestone. Flowers mid-May to mid-June. On the Continent occurs also in turbaries (Camus, *Icon.* p. 171 (1929)).

Distribution. Formerly found in the Thames Valley in Oxford and Berks., and also at Harefield, now nearly extinct.[5] Long extinct in Kent (Hanbury, *Fl. Kent*). There is some doubt whether the Kent plants were not a form of O. *purpurea*. Extends from S. Sweden to Spain, Portugal, Italy as far south as the Abruzzi, the northern part of the Balkan peninsula, Central and Southern Russia, Siberia, Caucasus, Transcaucasia.

Druce (*Fl. Oxfordsh.* (1886)) says: "...Native. Chalkwoods in Thames District. V.R. Almost extinct"..."I have found it during the last four years very sparingly. It only appeared in a barren state in 1886".

Orchis militaris L., *Sp. pl.* (1753). O. Rivini Gouan (1775). O. galeata Lam. (1789). The connivence of the sepals and petals in a helmet probably gave rise to the name militaris.

1 *Fl. Anglica*, ed. 2, p. 384 (1778).
2 *Engl. Flora*, p. 16 (1828).
3 *Orch. Deutsch.* 9 (1894).
4 *Icon.* p. 171, Pl. 130, fig. 20 (1928, Planches (1921)).
5 Formerly abundant in Hertfordshire. Pryer's *Fl. Herts.* (1887).

Fertilisation. See "Fertilisation and Pollination". At Challes-les-Eaux, Savoie, France, on May 25th, 1929, Colonel G. H. Evans, F.L.S., took *Andrena curvungula* on *O. militaris* with a pair of pollinia on its head. Near the same place I saw the large black Carpenter Bee, *Xylocopa violacea*, come twice to the flower, but it did not alight. I also took a rather small humble-bee, black with a yellow collar, but it bore no pollinia—perhaps these had been already removed. A small *Bombus* with yellow collar and red tail (*B. lapidarius*) flew round my head in bed in the early morning, and then went to *O. militaris* on the window-sill. I took it, but as it bore no pollinia, I placed the box containing it on the window-sill, and took off the lid. It then went to *O. militaris*, *O. maculata* and *O. latifolia*—to one flower of each in turn—and then to *O. mascula*, from which it withdrew two pairs of pollinia and then flew away.

Sprengel stated (*Das entdeckte Geheimniss*, p. 404) that *O. militaris* is imperfectly fertilised in Germany, but as he mentions five spikes with 31 set capsules, an average of over six a spike, he seems to have expected nearly every flower to bear a capsule, as in *Gymnadenia conopsea*, with which he contrasted it. As it is abundant in Central and Southern Germany, it is evidently well fertilised there.

ORCHIS MILITARIS × O. SIMIA

O. Beyrichii Kerner

Pl. 34 B (p. 161)

I have not seen a British specimen of this hybrid, but have found it at Mantes in France and Allaman in Switzerland. It varies much, being sometimes nearer to one parent, sometimes to the other. Some plants have the general appearance of *O. simia*, but are more robust, with a usually longer and more oblong spike. The mediastin (undivided part of the mid-lobe) is broader than in *O. simia*, but narrower than in *O. militaris*, the lobes often curled upwards and more or less spatulate, and the terminal lobes more widely divergent, as in *O. militaris*, but much narrower, though broader than in *O. simia* (× *O. Chatini* Camus). Other plants are near *O. militaris* in appearance, but have long narrow spatulate terminal lobes, and side-lobes longer than the mediastin (× *O. Grenieri* Camus).

There is great diversity of form, but always a departure from the type of *O. simia* in the direction of *O. militaris*, or *vice versa*. None of the plants I found agreed exactly with published figures or descriptions.

According to Sowerby,[1] in localities where *O. simia* and *O. militaris* grew together in the Thames Valley, hybrids occurred, but in stations where only one or the other of them grew there were no hybrids. In France I have several times found hybrids

[1] *E.B.* ed. 3, p. 96.

H. M. Godfery pinx.

ORCHIS PURPUREA Hudson
Brown-winged Orchid. Lady Orchid

PLATE 37

Orchis purpurea Huds. Kent, May 29th, 1919.

1. Enlarged front view of darkest flower.
2. Side view of palest flower seen.

where the two species occur together, and also in Switzerland. As these are sometimes nearer to one parent and sometimes to the other, it would be possible to find a series of intermediate forms, which would give some colour to the idea that both belong to the same species, especially in the early days when the existence of hybrids was doubted. Sir J. E. Smith in his *English Flora* (1828) said that he had long thought them to be one species, and was still dubious on the matter. Intermediate forms, however, *only* occur where the two species grow together. In some localities O. *militaris* abounds, but O. *simia* is entirely absent, in others O. *simia* is plentiful, but there is no O. *militaris*. In both these cases no intermediate forms arise. If both belong to the same species, these polymorphic forms ought to occur wherever either species is abundant.

3. Orchis purpurea Huds.

Pl. 37. *Brown-winged Orchid, Maids of Kent, Lady Orchid*

Tubers ovoid; roots thick, short, numerous. **Stem** 20–40 cm. (up to 80 cm. abroad), round, solid, glabrous, pale green below, angular, channelled and often dark dull purple above, sometimes with lines of green cells like a pattern on a snake's skin. **Leaves** long, 3–5, oblong or oblong-lanceolate, the lower erect, slightly spreading, obtuse, bright or grey-green, glabrous and shining as if varnished above, paler, glossy and greyer green below, the upper acute clasping the stem, which extends some distance above it, and sometimes has a small bract-like leaf. **Spike** 6–10 cm. long, ovoid to oblong, lax or dense. **Flowers** many, large, flat, not scented, conspicuous by the contrast of the dark red-purple helmet with the pale-coloured lip. **Bracts** narrow, very short, ovate or triangular, thin, membranous, pellucid, purplish, usually 1-nerved. **Ovary** long (10–18 mm.), linear, sessile, twisted, often curved, glabrous, green or tinged with purple, with six sometimes purple-spotted ridges. Helmet short, rather open. **Sepals** coherent towards the base, but easily separated, the tips slightly spreading, ovate, acute or obtuse, 3-nerved, heavily blotched with dark red-purple outside, green or whitish mottled with purple within; upper sepal boat-shaped. **Petals** narrow, linear, ribbon-like, acute, rarely spatulate, whitish or pale violet with violet spots, partly adherent and caulking the seams between the sepals. **Lip** pendent, 3-lobed at base, broad, flat, longer than the sepals, white above, the edges more or less suffused with violet or pale rose (especially on open ground), plentifully spotted with tiny tufts of rather long violet papillæ, and white beneath sometimes edged violet or rose; side-lobes narrow, linear, curved, spotted with violet tufts, rounded, pointed, truncate or spatulate at the tip; mid-lobe broad, widening gradually from the base downwards, ending in two short broad divergent rhomboidal or rounded often truncate irregularly toothed or crenate lobes, with a short tooth between. The base of the lip curves up on each side to form a heart-shaped chamber, on the roof of which is the stigma, bordered by a purple line. **Spur** descending, cylindrical, sack-like, curved forwards, compressed from back to front, enlarged, truncate, notched or slightly bi-lobed at the obtuse tip, less than half as long as the ovary. **Column** very short, nearly as broad as long, white or rose. **Stigma** cordate, glistening, pouch of rostellum white, viscid discs oval, hyaline. **Anther** ovoid, purple-eyed, cells parallel, with a stigmatic fold between. **Pollinia** pale green, caudicles flat, ribbon-like, pale yellow; packets of pollen large, obconical, rounded at apex, very pale green. **Seeds**: cells of transparent testa nearly rectilinear, not striate.

Var. **pseudo-militaris** Druce.[1] Flowers smaller, lobes of the lip much narrower than the type. Repeatedly mistaken for *O. militaris* when dried, but easily distinguished from it when fresh by the dark helmet, and the colour and shape of the lobes of the lip.

Var. **albida** Camus. Flowers white.

Near Wye non-flowering plants had only two leaves, lying flat on the ground, possibly through drought. The prevailing colour scheme was dark red-violet or brown-purple helmet and pale-coloured lip, but the following variations were noted. Helmet green flecked with purple; helmet dull rose outside, green within with pale rose markings, lip white with very pale spots; helmet greenish white with pink nerves, lip pure white with extremely faint spots; helmet dark red-purple, lip broadly mottled at the edges with bright purple. Some continental specimens have a broad red-violet border on the under-surface of the lip, so that the pale whitish spike when turned upside down looks bright violet. Flowers growing in the open are generally darker, nevertheless a specimen with rather pale rose helmet grew in the open, amongst a colony of dark-coloured forms. In Kent the lip is usually white or very pale in the shade. The lip is at first horizontal, then obliquely pendent. It varies very much in shape. Camus gives 27 named varieties, but some of these are much alike, and some are dwarf or abnormal forms. There are two marked forms: (*a*) mid-lobe inversely heart-shaped with broad rounded lobes with a shallow sinus between (var. *obcordata* Wirtgen); (*b*) mid-lobe wedge-shaped with nearly straight sides and oblong almost parallel-sided entire or more or less deeply toothed lobes, separated by a mere notch or by a deep triangular indentation extending half-way to the base of the lip (var. *triangularis* Wirtgen). The side-lobes vary in length, are usually narrow, enlarged or not towards the apex, acute, obtuse, or obliquely truncate at the tip, curved or straight, entire or with one or two teeth. Very rarely they are absent, as in a specimen found by me above Grasse, which had a wedge-shaped lip with a rather long tooth

[1] *B.E.C.* p. 318 (1927).

between the two shallow apical lobes. A curious peloric form I saw at Challes-les-Eaux had long narrow sepals which remained closed, the lip reverted to a petal which turned down between the two lateral sepals, and gave a narrow entrance to the flower (Pl. A, fig. 1). Brébisson[1] mentions a plant with 3-lipped flowers, each petal transformed into a spurred lip. The tooth between the terminal lobes of the lip seems to be practically always present.

In Savoie, France, *O. purpurea* hybridises not infrequently with *O. simia*, and the combinations of the dark helmet of the former with the slender "arms and legs" of the latter are quaint and pleasing. It crosses occasionally with *O. militaris*, producing very beautiful rich-coloured spikes, handsomer than either of the parents, with the lip of *O. militaris* and the helmet of *O. purpurea*.

Habitat. Copses, open woods, more rarely open downs, on chalk or limestone. Very local in distribution, now apparently found only in Kent. Anne Pratt[2] says that Kentish people called it the Lady Orchid, owing to the resemblance of the flower to a lady in a widespread gown and close bonnet. It was sometimes so plentiful that it was carried into the towns for sale. This authoress gathered a specimen near Chatham with a stem 2 ft. 5 in. high, and a spike so large that two hands could scarcely enclose it. Webster states[3] that less than a quarter of a century ago, in all shades from dull white to very deep mulberry, it was abundant in Kent on forest slopes facing east. Hanbury and Marshall[4] say that *O. purpurea* is a marked feature of the thickets and copses on the chalk downs, and that it is infinitely more plentiful in Kent than elsewhere. Luxford[5] says that it was once found on Buckland Hill by the Rev. W. Wood, Prebendary of Canterbury. A single specimen is reported to have been recently found in the Ouse district, near Lewes, Sussex. Blackstone mentions[6] that it grew in the chalk-pit near the paper-mill at Harefield, Middlesex. Bicheno[7] says that since Blackstone's time it has been gathered frequently in Middlesex, but Peter and Michael Collinson's MS. (about 1790) states that they diligently searched the chalk-pit, but could never discover it or *O. militaris*. Its disappearance may perhaps be explained by the following remark of Peter Collinson quoted by Dillwyn in the *Hortus Collinsonianus*, p. 36: "There is...a parson of Cowley, near Uxbridge who is orchis-mad, takes up all, leaves none to seed, so extirpates all wherever he comes, which is cruel, and deserves chastisement".[8] It is stated[9] that *O. purpurea* was formerly reported from Berkshire, Surrey, Sussex, Middlesex and even Lincolnshire, but that the last named is probably an error. The author said

[1] *Fl. Normandie*, ed. 3, p. 295.
[2] *Flowering Plants of Great Britain.*
[3] *Brit. Orch.* ed. 2, p. 84 (1898).
[4] *Fl. Kent* (1899).
[5] *Fl. Reigate* (1838).
[6] *Fasc. plant. circa Harefield* (1737).
[7] *Trans. Linn. Soc.* XII, 30.
[8] Dyer and Trimen, *Fl. Middlesex*, p. 270 (1869).
[9] O.R. I, 164 (1893).

that he had seen authentic specimens from Box Hill gathered in 1842, and from Berkshire found early in the nineteenth century. Flowers May to early June.

DISTRIBUTION. Now almost confined to Kent. Denmark, France, Spain, Italy, Balkan peninsula, Central and Southern Russia, Caucasus, Asia Minor, Corsica.

> ORCHIS PURPUREA Huds., *Fl. Anglica*, p. 334 (1762). O. MILITARIS β L., *Sp. pl.* ed. 1, p. 943 (1753). O. FUSCA Jacq., *Fl. Austr.* IV, 307 (1776). O. MILITARIS β PURPUREA Huds., *Fl. Anglica*, ed. 2, II, 384 (1778). O. MILITARIS, *Fl. Danica*, t. 1277 (1806), etc.

FERTILISATION. See "Pollination and Fertilisation". Mr J. Jacob, of Dover, watched a colony of *O. purpurea*, and saw it visited continually by a wasp-like fly, *Odynerus parietum*, which entirely ignored *O. mascula*, growing with it. I watched a colony in the open near Wye, but nothing came to it. I saw a hive-bee withdraw a pair of pollinia from one flower at Challes-les-Eaux, France, and then visit a flower of *O. simia*, from which it also withdrew the pollinia, showing how easily hybrids may arise between these two species. Darwin examined two fine spikes from Kent with 62 flowers, but both pollinia had only been removed from three flowers and one from five. He found that 10 spikes only produced 11 capsules. Five of these still had their own pollinia *in situ*, and were evidently fertilised by pollen from other flowers. I found one spike at Wye with both pollinia removed from the four lowest flowers, but the few other spikes gathered had no pollinia removed, though there was pollen on the stigmas of one or two flowers in two or three spikes. Insects seemed to be scarce or indifferent to the flowers in that year (1919).

4. ORCHIS USTULATA L.

Pl. 38. *Burnt Orchid*

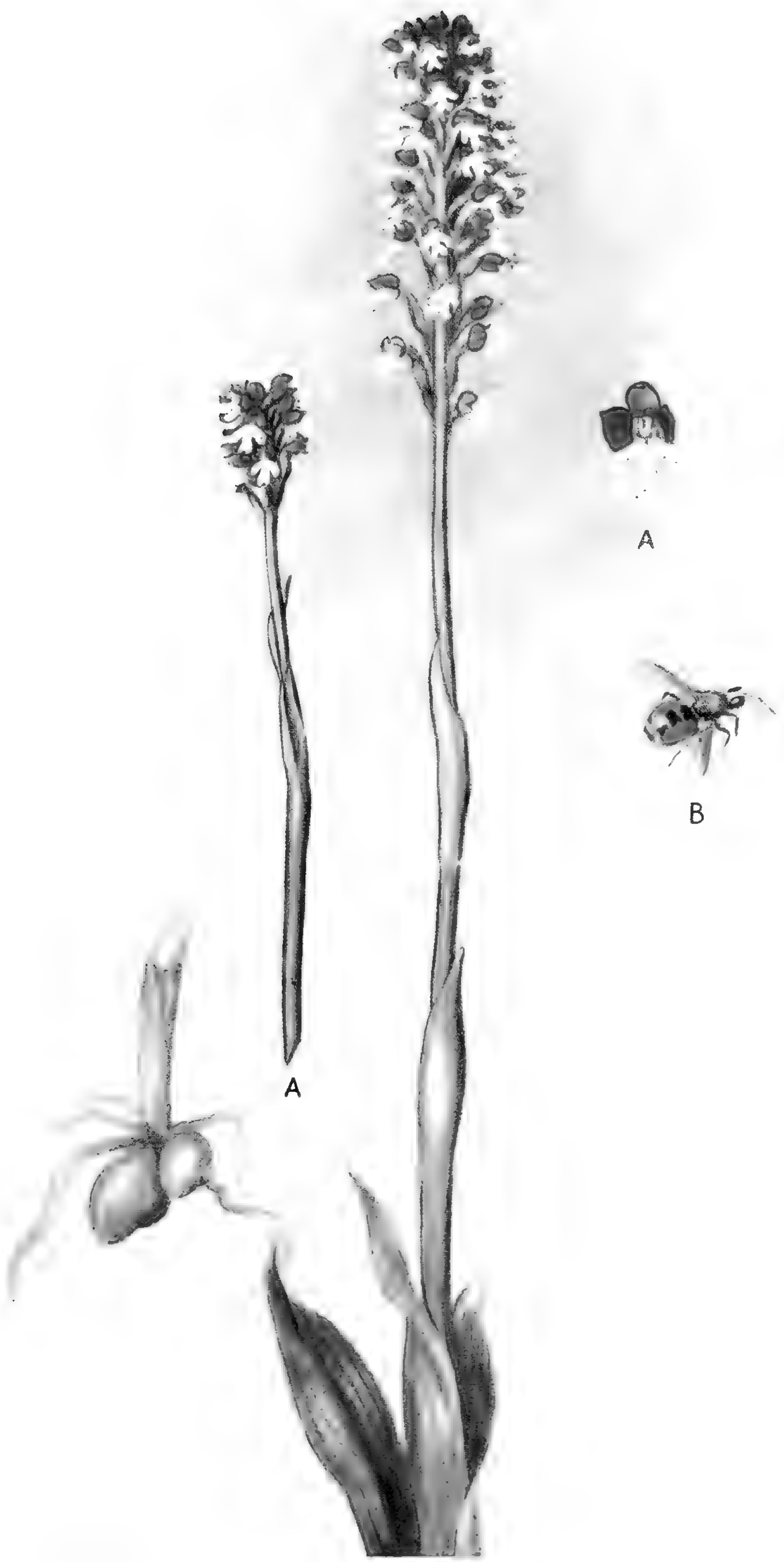
Tubers sessile, globose or ovoid. **Stem** short (10–20 cm. in Britain) (abroad, 20–30 cm.), slender, cylindrical, solid (in stout specimens slightly hollow), angled above, somewhat striate and channelled, with 2–3 white membranous sheaths at base. **Leaves** oblong to oblong-lanceolate, erect or spreading, keeled, folded, acute, glabrous, rather bluish green, unspotted, with numerous parallel nerves sometimes connected by cross-veins; the upper more or less loosely embracing the stem, the uppermost bract-like, membranous, 3-nerved. **Spike** ovoid at first, gradually lengthening, dense, many-flowered. **Flowers** very small, honey-scented, with nearly globular dark brownish red helmet, later becoming much paler (sometimes nearly white), and pure white crimson-spotted lip. **Bracts** lanceolate, acute or obtuse, membranous, purplish red, lower keeled, shorter than ovary (± 10 mm. long), 1–3-nerved, nerves green or reddish. **Ovary** sessile, cylindrical, twisted, glabrous,

PLATE 38

Orchis ustulata L. Baveno, N. Italy, May 14th, 1912.

A, A. Specimen from Sussex, and enlarged flower, June 4th, 1918.

B. **Echinomyia magnicornis** Meigen, with six pollinia on the under surface of proboscis.



H. M. Godfery pinx.

ORCHIS USTULATA L.
Burnt Orchid

green, with six scarcely raised longitudinal ridges. **Sepals** ovate, obtuse, keeled, 3-nerved, dark purplish or brownish red outside, greenish within, conniving with petals to form a helmet. **Petals** small, of paler colour, shorter and narrower than sepals, linear-spatulate, obtuse, 1-nerved, apex sometimes notched or slightly toothed. **Lip** slightly longer than sepals, directed forwards and downwards, 3-lobed, somewhat concave, with a groove at the base leading into the spur, white (rarely tinged with rose) with a few irregular bright crimson spots; side-lobes divergent, rather broad, oblong, rounded or squarish at apex, often crenate; mid-lobe longer and often broader, widening downwards, and ending in two short more or less divergent crenulate lobules, sometimes with a tooth between. **Spur** very short ($\pm$ 2 mm.), conical, rounded at apex, compressed from back to front, directed downwards and forwards. Throat of flower shaped like a key-hole. **Column** very short, whitish. **Anther** ovate, pale yellow, cells contiguous, separated by a fold at base. **Pollinia** very short, pale lemon-yellow, caudicles short, brighter yellow. **Stigma** partly concealed by pouch of rostellum. Seed-capsule cylindrical with three obtuse ridges, about 10 mm. long. **Seeds** oblong, slightly attenuated above. Cells of transparent testa transversely striate.

Smith[1] says that *O. ustulata* imitates the delicious scent of heliotrope.

The smallest flowered species of *Orchis* in Europe. The dark brownish red buds give the top of the spike a charred appearance, whence the name Burnt Orchid. The pure white lip contrasts well with the dark-coloured helmet, in which respect it resembles in miniature *O. purpurea*. It varies very little. On the Continent in favourable conditions the spike becomes long and cylindrical, and the plant is much taller than in England, where it is usually dwarf. The lip is sometimes faintly flushed with rose, and white-flowered forms have, though rarely, been found. A curious peloric form, with the spurless lip exactly like the petals, was gathered by us at Aix-les-Bains, the sepals and petals greenish with a narrow reddish edge, like *Aceras anthropophora*—suggesting a reversion to a primitive type in which the lip had not yet been differentiated from the petals. A white variety was found near Chiswell, Berks.[2]

Webster[3] says that both pollinia are attached to a common gland, as in the Lizard Orchid. Colonel G. H. Evans, F.L.S., a skilled microscopist, dissected a number of flowers from different spikes with me on May 17th, 1929. We found that each pollinium was attached to a separate disc, and that *in situ*, in the pouch of the rostellum, the two discs are separated by an appreciable space. Webster's specimen was not normal, but a case of accidental adherence of the two discs, which also occurs not infrequently in *Aceras*. If both pollinia were attached to the same disc, *O. ustulata* would not belong to the genus *Orchis*, as now understood, but to *Himantoglossum*.

[1] *Cat. Plants S. Kent* (1829). [2] *English Flora* (1828).
[3] *Brit. Orch.* ed. 1, p. 15 (1886).

HABITAT. Grassy calcareous slopes or cliffs, chalk downs, rather dry meadows and pastures. More frequently a plant of the mountains or hills. Flowers June to July.

DISTRIBUTION. Widely distributed, but local, and usually rare. In Kent fairly frequent in some districts.[1] Webster says that on some Kentish hills it is very abundant, and quite enlivens the landscape. Isle of Wight and southern counties to Northumberland and Cumberland, in widely scattered localities. Europe from Scandinavia and Mid-Russia to Northern Spain, Italy, the Balkans, and Caucasus; Urals, Siberia.

> ORCHIS USTULATA L., *Sp. pl.* ed. 1, p. 941 (1753). OPHRYS ANTHROPOPHORA, *Fl. Danica* (1763), not L. ORCHIS AMŒNA Crantz (1769). O. PARVIFLORA Willd. (1805). HIMANTOGLOSSUM PARVIFLORUM Sprengel (1826). The last name looks as if Sprengel also may have found a spike in which the viscid discs were adherent, as he placed it under HIMANTOGLOSSUM.

FERTILISATION. Hermann Müller, that prince of observers of the fertilisation of flowers, says[2] that the very narrow entrance to the spur indicates that butterflies visit the flowers, the crimson spots and contrast of colour between the helmet and the lip pointing to day-flying Lepidoptera, whilst the sweet smell and the whiteness of the lip probably also attract night-flyers. He did not succeed in seeing the flowers visited, and there appears to be no record of any other observer having done so.

The arrangements for pollination somewhat resemble those of *Anacamptis pyramidalis*. The erect converging guiding plates of the latter are replaced by the deep groove at the base of the lip, which answers the same purpose. There are also two lateral stigmas, as in *pyramidalis*, but these are connected by a narrow rim of true stigmatic tissue.[3] The downward motion of the pollinia is rapid, taking place in about 15 seconds, and they also diverge slightly, so that their tips become wider apart, and are thus in position to touch the separated stigmas of the next flower visited. They are, however, often slightly divergent when first withdrawn.

On May 9th, 1929, I was watching some orchids at Challes-les-Eaux, Savoie, France, in the forenoon, when a large fly, *Echinomyia magnicornis* Meigen, alighted on the top of a spike of *O. ustulata*, and began thrusting his proboscis into the flowers, working downwards. I netted him, but did not expect that he could have removed any pollinia, owing to his upside-down position. I was surprised to find a bunch of eight pollinia attached to the under-surface of his jointed proboscis, near the base of its apical half, just above the joint. He had thus visited at least four flowers.

If *O. ustulata* is usually pollinated by this insect, or by other allied Diptera which visit the flowers in a similar manner, it would account for the unusual coloration of the spike, for the dark-coloured apex of the Burnt Orchid is conspicuous and

[1] Hanbury and Marshall, *Fl. Kent* (1899).
[2] *Alpenblumen* (1881).
[3] *Fert. Orch.* ed. 2, p. 25.

PLATE 39

H. M. Godfery pinx.

ORCHIS MORIO L.
Green-veined Orchid

PLATE 39

Orchis morio L.

Two colour varieties from Strensall, Yorkshire, June 8th, 1909.

1. Slightly enlarged flower from Dorset, May, 1918.
2. Enlarged flower with three lips, Dorset, May, 1918.

unlike any other orchid (except *O. purpurea*, which has equally dark-coloured buds). The rounded top of the spike forms an admirable landing-stage for the fly, which is many times bigger than the individual flower, and the nearly white flowers when open show the visitor clearly where to begin work. One would never have suspected that a plant with such tiny flowers would be visited by a fly as large as a bluebottle.

The change of colour of the sepals from dark almost blackish red-purple to nearly white is most striking, the line of demarcation clearly indicating the most advantageous flowers for the insect to visit. I afterwards saw a similar fly come once or twice to the flowers but failed to catch it.

5. Orchis morio L.

Pl. 39. *Green-veined Orchid*

Tubers globose or ovoid; roots few, short. **Stem** (10–30 cm.) erect, round, more or less hollow, angled and tinged with violet above, with 2–3 whitish membranous sheaths at base. **Leaves** lanceolate to oblong-lanceolate, acute or obtuse, keeled, unspotted, broad-sheathed at base, green or bluish green, the lower spreading or recurved, the upper 2–3 erect, rather broader, loosely clasping the stem, the uppermost bract-like, membranous, acute, often purplish; nerves 1–2 on each side of midrib with fainter nerves between and numerous cross-veins. **Spike** short, few-flowered (6–12), lax. **Flowers** rather large, very faintly scented, red-purple, blue-purple, lilac or pale mauve, rarely pink, still more rarely white, the sepals with conspicuous green veins, the middle of the lip paler and spotted. **Bracts** lanceolate, acute or rather obtuse, membranous, glossy, more or less tinged with purple, the lower 3–5-nerved, the upper shorter, 1-nerved, all sheathing the ovary, which they equal, slightly exceed, or sometimes fall short of. **Ovary** sessile, rather long, curved and twisted at the summit, often purplish; ripe capsule long, triangular, with salient ridges. **Sepals** forming a short almost globular helmet, ovate-oblong, concave, keeled, rounded at the tip, with 3–7 conspicuous green or bronze-purple nerves, the upper sepal narrower, oblong, 3–5-nerved. **Petals** paler, shorter and narrower, linear-oblong, rounded and concave at the tip, 1–3-nerved, forming an interior hood beneath the helmet. **Lip** transversely oblong, broader than long, side-lobes broadly rounded out and folded back, mid-lobe short, broad, truncate, sometimes notched, usually shorter than but sometimes equalling or slightly exceeding the side-lobes, edges toothed or slightly crenate, the surface densely covered with very short minute papillæ. **Spur** cylindrical, rather long but shorter than the ovary, thick, horizontal or slightly curved upwards, flattened, club-shaped, truncate and often notched at the tip, densely covered inside with minute papillæ. **Column** short, purplish. **Stigma** on the roof of the throat of the flower, bordered with a purple line, depressed and greenish in the middle. Pouch of rostellum whitish, tinged with purple. **Anther** purple, pollinia greenish (in white flowers yellow), caudicles yellow, viscidia disc-like. Testa of seed hyaline, long, rather narrow; embryo oval, not much longer than broad (Dymes). Cells of testa with wavy walls, very striate (Camus). The bulbs yield salep.

Var. **Bartlettii** Heslop Harrison. Flowers only half the linear dimensions of the type.[1]

On May 22nd, 1918, near Broadstone, in a damp meadow amongst rushes, I found plants of remarkable size and beauty. The stem was hollow beneath the spike, the lip bright violet, nearly flat and very broad (17–21 mm.), the side-lobes deeply toothed, the mid-lobe slightly longer and truncate (Pl. 39 A). At first they were thought to be *O. latifolia* × *morio*, the former being also present, but no other definite signs of *O. latifolia* could be found than the hollow stem, and the stem of *O. morio* itself is often hollow. A specimen found by me in Dorset[2] had 3-lipped flowers, each petal having developed into a lip, but without a spur (Pl. 39 B). Flowers with three lips, each with a spur, and others in which the lip is reduced to its original form of a spurless petal have also occurred, making the normally irregular flower appear regular (peloria).

The plant may be tall (30 cm.) or dwarf (10 cm.), and may have unusually large flowers as above, or only half the usual size. The shape and colour of the lip are very variable. The mid-lobe may be slightly longer or shorter than the side-lobes, but it is usually truncate. The central area is white or pale-coloured with purple spots. The sepals are nearly always connivent in a helmet, and the side-sepals have conspicuous green nerves. The spur is cut off square at the tip, or sometimes more or less notched.

Habitat. Abundant in rather moist meadows, pastures, etc., where it sometimes forms large colonies, field borders, open woods, and grassy slopes. Flowers May to June.

Distribution. Local in Britain, but widely distributed and often abundant where it occurs, but not as yet recorded for Scotland. In Ireland rather rare, reported absent from the north and south-west, but found in the centre, where it is scarcer in the west than in the east. Europe from S. Scandinavia to Spain and to within a few miles of the Mediterranean (where it is replaced by *O. picta* and *O. Champagneuxii*), Italy, Balkan peninsula, Caucasus, Asia Minor, Siberia, Transcaucasia, Cyprus.

Orchis morio L., *Sp. pl.* ed. 1, p. 940 (1753). O. crenulata Gilibert (1792). Singularly free from synonyms.

[1] *B.E.C.* p. 638 (1928). [2] *J.B.* p. 75 (1918).

1

2

H. M. Godfery pinx.

ORCHIS MASCULA L.

Early Purple Orchid

1, 2. ORCHIS MASCULA × MORIO

× *Orchis morioides* Brand

PLATE 40

Orchis mascula L. Deganwy, N. Wales, May 31st, 1909.

1, 2. **Orchis mascula** × **morio**, enlarged flowers. Shifnal, Salop, May 16th, 1928. × **Orchis morioides** Brand.

Fertilisation. See "Pollination and Fertilisation". Delpino's idea that *O. morio* (and *mascula*) are more or less on the verge of extinction through the absence of honey shows the danger of making deductions from a mere theory. Besides the hive-bee, Darwin and Müller saw the following visit the flowers: *Bombus lapidarius*, *B. muscorum*, *B. confusus*, *B. hortorum*, *B. pratorum*, and *B. silvarum*, *Eucera longicornis*, and *Osmia rufa*. Some of the hive-bees bore 10–16 pollinia, and the *Eucera* eleven, and it is certain they would never have visited the same species so frequently had they not found what they wanted. Six spikes gathered by me at Verwood had no less than 44 ovaries fertilised, an average of over seven to each spike. My experience is that *O. morio* is one of the most widely distributed and locally abundant of European orchids, with several allied species or sub-species which are equally plentiful. *Andrena curvungula* Thoms with five pollinia of *O. morio* was taken by me at Sus in 1930 (p. 208 and Pl. 36, fig. 3).

Judging by the comparatively few specimens I have seen, rose-coloured and white flowers seem to be less attractive to insects than the type, but further research may probably modify this.

6. Orchis mascula L.

Pl. 40. *Early Purple Orchid. Regals* (Dorset)
Soldiers' Jackets (Dorset), *Kettle-cases* (Isle of Wight)

Tubers rather large, ovoid or globular; roots few, rather slender. **Stem** 12–35 cm. (up to 50, very rarely 60 cm. abroad), erect, stout, cylindrical, angled above, glabrous, pale green (often purplish above), unspotted, in large specimens sometimes hollow at the base, with 2–3 leafless sheaths. **Leaves** oblong-lanceolate, narrowing downwards, slightly enlarged towards the summit, acute or obtuse, keeled often folded, bright or greyish green, unspotted or with large dark irregular blotches or spots, very glossy beneath, less so above, with about three transparent nerves on each side of the mid-rib, with fainter nerves between; the surface sometimes wavy, giving the lip a crimped appearance. Lower leaves close together, spreading, upper erect, loosely clasping the stem, the uppermost thin, membranous, acute, often purplish. **Spike** finally cylindric, often long (up to 15 cm.), rather lax, especially below, many-flowered (10–45). **Flowers** rather large, red-violet, magenta, lilac, rose, pale pink or very rarely pure white with yellowish, whitish, or greenish throat, with a slight unpleasant smell suggesting cats, sometimes becoming offensive after some time in water. **Bracts** linear-lanceolate, acute, membranous, 1-nerved, equalling or slightly exceeding the ovary, purple tinged, in white flowers transparent with a green nerve. **Ovary** sessile, cylindrical, curved, twisted, often flushed violet with six ridges. Seed-capsules erect, $\pm\ 2\frac{1}{2}$ cm. long, with prominent ridges. **Side-sepals** erect, almost back to back, obliquely ovate-lanceolate, obtuse or acute, 1–3-nerved, upper sepal broadly lanceolate, arching forward over the **petals**, which are ovate obtuse, overlapping at tip, shorter and paler than sepals, faintly 1-nerved. **Lip** pointing downwards and forwards, wedge-shaped at base, nearly as broad as long, convex (the reflexed sides making it look longer than broad), longer than sepals, deep red-violet to pale rose, yellowish or white in the centre, velvety with erect papillæ at the base, with a few interrupted lines or spots formed of dense tufts of bright red-violet hairs; side-lobes more or less rhomboidal, minutely toothed or crenate towards the tip, mid-lobe slightly longer, broadened, and with two entire or crenate lobelets at the apex, sometimes with an intermediate tooth. The lip arches upwards at each side at the base to form a wide oval chamber. **Spur** rather broad, about as long as the ovary, cylindrical, slightly curved upwards, enlarged and club-shaped at the tip, nearly in the same plane with the lip. **Column** short, with a little point at apex. **Stigmas** two, confluent, on the roof and sides of the chamber, edged with a purplish line. **Anther** ovate, purplish or greenish grey; pollinia dark green (yellow in white flowers); caudicles yellow, transparent. **Rostellum** (pouch) rose-violet. **Seeds** rounded at apex, testa transparent, cells not striate, cell-walls appearing double.

A plant with spotted leaves sometimes occurs in a clump of plain-leaved ones. In some localities spotted, in others unspotted leaves prevail. The flowers are said to smell of elder. In Britain the sepals are usually acute, sometimes obtuse (var. *obtusiflora* Koch). The stem in August is hollow and compressible, like a reed, full of loose transparent material. A plant 19 in. tall with over 40 flowers was found in E. Sussex, and another with the lip replaced by a petal, without spur, in Kent, probably a reversion to a primitive type before the lip had been differentiated from the petals. In contrast with this was a plant above Grasse, in which both petals had been transformed into lips,[1] a case of ultra-development. The British plant differs from that of Southern France, Italy, Switzerland and Germany, in which the leaves (often on both sides) and sometimes the stem are in their lower parts covered with innumerable reddish linear spots or dashes, without the large purple-black blotches often found in Britain. I have, however, seen plants spotted like ours at Falaise (Brébisson, *Fl. Normandie*, says the leaves in that part of France are usually spotted), Aix-les-Bains and near Chambéry, and Schulze[2] mentions two places near Jena where the leaves were thus blotched. Webster[3] never saw the red-spotted form in England, nor have I ever done so. The leaves of this form are often broader than in the British plants. A white-flowered specimen with dark blotches on the leaves was received from Ireland, which is very unusual. An ordinary *O. mascula* cultivated by the late Mr Burton of Longner Hall, Salop, in some years produced two new bulbs instead of one, the additional bulb flowering the second year. A double-flowered specimen

[1] A. Camus, *Riviera Scientif.* p. 7 (1918).
[2] Schulze, *Orch. Deutsch.* p. 13.
[3] *Brit. Orch.* p. 63 (1898).

of *O. mascula* found at the Bridge of Allan, Scotland, was described by Dr Masters.[1] On Lake Como, April 28th, 1925, I found a specimen in which each side-sepal had developed a spur, about half the length of the normal spur, which was also present.

HABITAT. Rather moist meadows and pastures (often with cowslips), open woods, banks in woods, copses, thickets, and shady places. Flowers April to June according to locality. In west of England flowers two weeks earlier than *O. morio*.[2] Ascends to 2300 ft. on Brandon, Ireland, but is rarely seen above 1000 ft. (Scully, *Fl. Kerry*). Occurs in Sussex on white sand (Tahourdin).

DISTRIBUTION. Throughout Great Britain and Ireland, extending to the Orkney and Shetland Islands. Locally frequent, sometimes abundant. Channel Islands, native, hillsides and thickets. Very local and rare in Jersey; rather rare in Guernsey; Sark. Southern Scandinavia to the Iberian and Balkan peninsulas, Italy, Central and S. Russia, Caucasus, Asia Minor, Persia, Urals, N. Africa, taking it as an aggregate species, including *O. speciosa* Host and *O. Olbiensis* Reuter, the former of which possibly and the latter most probably are deserving of specific rank.

ORCHIS MASCULA L., *Fl. Suec.* ed. 2, p. 310 (1755). O. MORIO δ MASCULA L., *Sp. pl.* ed. 1, p. 941 (1753).

ORCHIS MASCULA × MORIO

O. morioides Brand *ap.* Koch[3]

Pl. 40, figs. 1, 2 (p 159)

Leaves unspotted (but if the *mascula* parent had spotted leaves, the hybrid would probably also have them). **Sepals** spreading, with strong green veins, more acute than in *O. morio*. Mid-lobe of lip longer than side-lobes.

I have seen two forms of this. (1) Among a few spikes of *O. mascula* sent me by Dr Stephenson from Shifnal, Salop, I found most unexpectedly a spike of this hybrid, nearer to *O. mascula* than to *O. morio*, single flowers of which are shown in Pl. 40, figs. 1 and 2. Flowers pale rather bluish rose. Lateral sepals spreading with marked green veins. Lip broader than long, toothed, paler and slightly spotted in the middle, side-lobes broader than in *O. mascula*, mid-lobe broad, truncate, shallow as in *O. morio*, but longer than the side-lobes. Spur shorter than in *O. mascula*, straight. The general appearance and colour were so like *O. mascula* as to be easily passed over as being that species, but the spreading green-veined sepals and the broad truncate mid-lobe of the lip showed clearly the parentage of *O. morio*. A single specimen was found at Blackhall Rocks, Durham, by Prof. Heslop Harrison.[4] (2) A specimen found by me near Martigny, Switzerland, was like *O. morio* in colour and form, but the spreading sepals, longer mid-lobe, and very upcurved spur, as

[1] *Journ. Linn. Soc. Bot.* p. 349 (1867).
[2] White, *Fl. Bristol*, p. 555.
[3] *Syn.* éd. Hall et Wohlf, p. 2427 (1904).
[4] *B.E.C.* p. 638 (1928).

well as the small keyhole-shaped throat of the flower, showed the influence of *O. mascula.* Most continental specimens are nearer to *O. morio.* The hybrid is surprisingly rare, since the parents grow together so frequently.

Fertilisation. For detailed account see "Pollination and Fertilisation". *O. mascula* was the species the study of which enabled Darwin to understand and explain the wonderful mechanism of the flower of *Orchis*, with all its subtleties of adjustment and accuracy of timing—an achievement all the more remarkable as he had never seen any insects visit the flowers. This was first witnessed by Dr Hermann Müller on May 6th, 1869, on Stromberg Hill. He saw a humble-bee, apparently *Bombus terrestris*, alight on the base of a spike of *O. mascula*, thrust its head into three flowers in succession, and withdraw it in each case with a pair of pollinia attached. It then paused and tried in vain to scrape them off its head. He next saw *Bombus hortorum* suck three or four flowers of *O. mascula* and then go to another spike, on which he found several stigmas pollinated and the anther-cells empty. Within two hours three more visits were observed, two by *Bombus lapidarius* and one by *Psithyrus campestris*. These were caught and had a number of pollinia on their heads, some already pointing forwards, in the right position to touch the stigma of the next flower visited, a few still erect. Out of 97 humble-bees caught that day, 32 bore pollinia. It was noticed that when the pollinia had moved downwards, captured bees were sometimes able to tear them off with their mandibles. These occasionally successful efforts explain why pollinia are sometimes found attached to the sepals, petals, etc., by their viscid discs—the bees have succeeded in scraping them off before the cement has had time to set firm. I have on several occasions seen bees succeed in getting rid of pollinia, but only after much effort. This renders untenable the theory of the Italian botanist Delpino that bees visit the flowers of *Orchis* for the sake of the pollen which they find so conveniently packed for transport! Quite true, but for transport to another flower, not to the hive or nest. Müller's observations showed that the three or four seconds spent by a bee on a flower are enough to permit the cement to harden, and to fix the pollinia firmly to its head, which can easily be confirmed by withdrawing the pollinia from *O. mascula* on the point of a pencil. The downward motion is completed in about 40 seconds—very rarely it is accomplished in 25 seconds. A bee spends three to four seconds on each flower, and about two in passing from flower to flower. It thus takes about 18 to 22 seconds to visit three or four flowers on a spike, and the bee passes to another plant before the downward motion of the pollinia is effected. There is therefore no danger of a stigma being loaded with pollen from another flower on the same spike, as the pollinia are not in a position to touch the stigma until the downward movement is completed.[1]

The inside of the spur is densely covered with papillæ, but quite dry. The outer

[1] H. Müller, *Fertilisation of Flowers.*

1

H. M. Godfery pinx.

ORCHIS LAXIFLORA Lamarck
Jersey Orchid

PLATE 41

Orchis laxiflora Lamarck.

1. Basal part of another plant. Challes-les-Eaux, France, May 26th, 1928.

skin is very thin, and the inner lies close to it but can be separated by rolling between the finger and thumb. If the spur is cut and squeezed, liquid is pressed out from between the walls. Müller's observations confirmed Darwin's view that insects pierce the delicate tissue of the spur and suck the included fluid. Kerner[1] also states that repeated observations show that the spurs of *O. mascula*, etc., are pierced and sucked by insects. This is a much more natural explanation than Sprengel's idea that the spurs of *O. mascula*, *O. morio*, etc., are sham nectaries which induce insects to visit the flowers by the promise of nectar which they cannot supply.

I examined four spikes of *O. mascula* gathered near Bournemouth and found that pollinia had been removed from 41 flowers, and that four flowers had pollen on the stigma. On May 9th, 1918, near Corfe Castle, I saw six large humble-bees visit *O. mascula*. This occurred at long intervals and the bees only visited two or three flowers on a spike as a rule.

Four spikes of *O. mascula* received from the late Mr Burton of Longner Hall, Salop, in August, 1918, bore no less than 62 ripe capsules. I saw *Bombus lapidarius* withdraw two pairs of pollinia from *O. mascula* in a mixed bunch of orchids on my window-sill at Challes-les-Eaux in May, 1929.

7. Orchis laxiflora Lamarck

Pl. 41. *Jersey Orchid, Loose-flowered Orchid*

Tubers sessile or stalked, oblong or nearly globose, and roots short. **Stem** 20–40 cm. or more, straight or slightly sinuous, round, glabrous, angled, rough and purple above, with rather loose brownish basal sheaths. **Leaves** erect, slightly spreading, linear-lanceolate, tapering, acute, keeled and more or less folded with prominent parallel nerves, green and shining, 12–17 cm. long, 1–2 cm. broad; upper small, bract-like. **Spike** loose, cylindrical, 7–16-flowered, up to 20 cm. long and 5 cm. in diameter. **Flowers** large, dark purple (rarely rose or white and then smaller), with centre of lip white, scentless. **Bracts** slightly longer than ovary, linear-lanceolate, acute, somewhat membranous, tinged with purple, lower 7-nerved. **Ovary** long, linear, curved, twisted, stalkless, tinged purple, ripe capsule spindle-shaped. **Sepals** free, ovate obtuse, dark purple, 3–6-nerved, the lateral erect, back to back, the upper oval obtuse, concave, 5-nerved, curving upwards. **Petals** two-thirds as long as sepals, obliquely oblong, rather obtuse, 3–6-nerved, forming a hood. **Lip** dark purple with keeled white centre and channel leading into the spur, and strongly reflexed sides almost touching behind; when flattened out transversely oval, broader than long with rounded more or less crenate or toothed side-lobes separated by a broad ($\pm$ 5 mm.) truncate wavy-edged mid-lobe much shorter than they, sometimes absent,

[1] *Pflanzenleben* (English translation), II, 171 (1895).

making the lip two-lobed. **Spur** curving upwards, $\frac{1}{2}$–$\frac{2}{3}$ as long as ovary (± 16 mm.), expanding into a chamber at the mouth, obtuse, squarish or notched at the tip, flattened, dark purple, with no free honey. **Column** short (4 mm.), white. **Stigma** 2-lobed on roof of spur, violet-edged, rostellum pouch-like, violet. **Anther** pear-shaped, obtuse, violet, with a white fold between the cells at base. Pollinia greenish, caudicles hyaline, whitish, flattened, with pollen-grains visible inside. Viscid discs oval, transparent, colourless. **Seeds** oblong, rounded at apex; testa transparent, cells more or less striate.[1]

Easily recognised by the erect sword-shaped leaves and large dark purple flowers with a white streak down the middle of the lip. Sometimes the mid-lobe has two shallow lobules, making the lip slightly 4-lobed, sometimes it is wanting, owing to the absence of the two short incisions which separate it from the side-lobes. There is a slight resemblance to *O. morio*, but the latter is easily distinguished by its shorter broader leaves and green-veined sepals. The two species hybridise readily, and the cross (× *O. alata*) may usually be found where they grow together. A curious form with three sepals, three petals (one replacing lip) and no spur, making the flower peloric (apparently regular) is figured by Camus, *Icon.* Pl. 36, figs. 9 and 10 (1921). The flowers remain purplish when dried.

In June, 1872, F. Arnold Lees found a few specimens in extensive mounds and flats north of Hartlepool, known as the ballast-hills, on damp ground, obviously from France or the Channel Islands, for the orchid grew with *Sinapis cheiranthus*, *Bromus maximus*, *Cynosurus echinatus*, *Lagurus*, etc.[2] Several orchids occur occasionally on the ballast, and a few have obtained a permanent footing. Prof. Heslop Harrison informed me that he found *O. laxiflora* on cliffs, mid-Durham, and suggested that it came from the ballast-heaps several miles away.

HABITAT. Marshes and moist meadows. Flowers May to June.

DISTRIBUTION. Native in the Channel Islands, accidentally introduced with ballast near Hartlepool, where it was recorded as growing on ballast-heaps by Webster, Arnold Lees and others. Cliffs, mid-Durham, Heslop Harrison. Essentially a Mediterranean species, with headquarters from Portugal to Greece, and extending to Palestine, Asia Minor, N. Africa, Mesopotamia and Persia, also northward (like *Himantoglossum* and *Limodorum*) to S. Germany, Switzerland and Austria.

ORCHIS LAXIFLORA Lamarck, *Fl. Franc.* III, 504 (1778). O. ENSIFOLIA Villars (1787).

FERTILISATION. As in *Orchis* generally, see "Pollination and Fertilisation". I have seen it on two or three occasions visited by Hymenoptera (bees), but without being able to catch them.

1 Camus, *Icon.* p. 190 (1929).

2 *J.B.* p. 209 (1873).

H. M. Godfery pinx.

ORCHIS LAXIFLORA × MORIO

× *Orchis alata* Fleury

PLATE 42

Orchis laxiflora × **morio**, × **Orchis alata** Fleury. Sus, Basses Pyrénées, May 13th, 1930.

1. Enlarged flower.

ORCHIS LAXIFLORA × MORIO

Pl. 42. × **Orchis alata** Fleury

Tubers ovoid. **Leaves** narrow, linear-lanceolate, tapering to an acute point. **Spike** short, few-flowered. **Flowers** rather large, ranging from pale lilac to rather dark red-purple. **Bracts** shorter than or equal to ovary. **Sepals** spreading, ovate-lanceolate to lanceolate, with green or dark purple nerves. **Petals** shorter, forming a hood over column. **Lip** more or less folded lengthwise, sometimes nearly flat, wedge-shaped at base, with more or less rhomboidal obtusely angled side-lobes, and distinctly shorter truncate broad often emarginate mid-lobe, paler in the middle with numerous darker spots. **Spur** curved slightly upwards, rather long, compressed, thickened at the rounded or truncate end.

The veins of the sepals are not always easily seen, except by transmitted light. Most of the specimens I have seen were nearer to O. *morio*, which they resembled by their few-flowered spike, smaller and lighter coloured flowers (as compared with O. *laxiflora*), green- or purple-veined sepals, spotted lip, and enlarged tip of spur. They differed from O. *morio* by the longer narrower more acute leaves, larger flowers, sepals not connivent in a helmet, but open and spreading in one plane, and slightly longer spur, which show the influence of O. *laxiflora*. A plant found near Pisa in June, 1924, looked like a dwarf O. *laxiflora*, and had large rich purple flowers, broad lip with dark unspotted central area, and but slightly reflexed sides, rounded side-lobes, much shorter mid-lobe, rather long flattened spur notched at the tip, and erect grey-green stem-clasping leaves.

A remarkable form of × O. *alata* found by us near Pisa, May 7th, 1914, had a spike of seven large flowers, in some of which the side-sepals were transformed into lips, giving the flower a very showy appearance. There was only one spur, longer than in O. *laxiflora*. According to Penzig lateral sepals replaced by lips have been seen in O. *laxiflora*, *Aceras* and *Anacamptis*.[1]

Habitat. Moist meadows and pastures, with the parents. Flowers May to June.

Distribution. Channel Islands. Still in existence in 1923. France, Italy, Switzerland. V.R.

8. Orchis incarnata L.

Pl. 43 (p. 186). *Hooded-leaved Marsh Orchid*

Tubers thick, flattened, forking into 2–4 tapering segments, short- or long-tailed, rarely carrot-shaped, long, tapering; roots numerous, horizontal, sometimes very long. **Stem** stiff, stout, very hollow and compressible, angled, often purplish above,

[1] *Considérations générales sur les anomalies des Orchidées* (1894).

with 2–3 membranous acute brownish sheaths at base, the upper sometimes with a green leaf-like tip; height 10–35 cm. (a plant from Brimsfield Bog, Glos., measured 51 cm.), in sandy ground near sea usually dwarf. **Leaves** 4–7, stiff, erect, long, lanceolate, broadest about 2 cm. above base, tapering gradually to the acute hooded tip, strongly keeled, glossy, glabrous, yellowish rarely bluish green, firm, sometimes almost fleshy, always unspotted, 2–4½ cm. broad at base, sometimes narrow (± 2 cm.), the middle leaves usually reaching or exceeding the base of the spike, the lowest leaf short, trough-like, the uppermost sometimes bract-like. Nerves 2–3 on each side of mid-rib, with fainter nerves between, and irregular transverse veins, with innumerable minute whitish dots between. **Bracts** lanceolate, tapering to a fine point, keeled green or purplish, usually 3-nerved, the lower much exceeding the flowers, curving upwards (sometimes forming a sort of cage from which the flowers protrude), the upper longer than the buds so that the young spike ends in a tuft of bracts; they often turn abruptly upwards, forming a rounded elbow below the middle. **Spike** ovate, finally cylindrical, thick, dense, many-flowered, bracts conspicuous in the early stage, but later the flowers stand out more prominently, and are sometimes arranged (especially abroad) in slightly slanting ranks. **Flowers** usually smaller than in other British marsh orchids, often appearing narrow and somewhat lozenge-shaped through the reflexed sides of the lip, pale rose with carmine markings (flesh-coloured), bright rose fading into dirty white, lilac or violet with red-purple markings, bright purple with bright carmine markings (var. *pulchella* Druce), rarely pale yellowish, rich dark Indian red (forma *atrirubra*) or white. **Ovary** sessile, cylindrical, with three broad and three narrow ridges. Lateral **sepals** erect, reflexed, often back to back, obliquely lanceolate or ovate-lanceolate, often spotted, 3-nerved; upper sepal narrower, lanceolate, obtuse, hooded, 1-nerved, unspotted, connivent with petals, or only arched forwards. **Petals** shorter, broad-based, oblong-lanceolate with 1–3 obscure nerves, connivent. **Lip** as long as or longer than broad, obovate when flattened, appearing narrow and often oblong through the much reflexed sides (but sometimes almost flat), often nearly entire, with short rounded rarely pointed mid-lobe only slightly separated from the side-lobes, but sometimes more or less clearly 3-lobed at the apex, with rounded irregularly crenate or even dentate side-lobes; sometimes wedge-shaped, widening downwards into three sub-equal shallow denticulate lobes. Markings two ± parallel loops with square or rounded apex formed by continuous or interrupted crimson or violet lines, sometimes faint or absent. Rarely the loops are replaced by spots or broken lines, which also often occur in conjunction with them. The upper surface towards the base is densely covered with minute erect papillæ. **Spur** short, conical, wide-mouthed, rounded at tip often slightly curved, $\frac{1}{2}$–$\frac{2}{3}$ as long as the ovary, directed downwards, with two walls, the outer coloured, the inner colourless, thickly studded inside with minute erect papillæ, with a considerable quantity of liquid between the

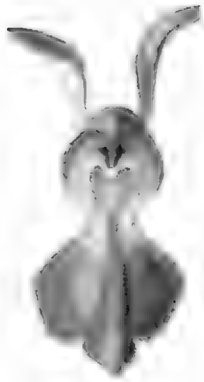
PLATE 43

Orchis incarnata L.

1, 2. Enlarged flowers. Surrey, June 16th, 1919.

H. M. Godfery pinx.

ORCHIS INCARNATA L.
Hooded-leaved Marsh Orchid



1

2

H. M. Godfery pinx.

ORCHIS INCARNATA L. forma ATRIRUBRA Godf.

PLATE 44

Orchis incarnata L. forma **atrirubra** Godf.

South Wales, June 20th, 1928.

1, 2. Enlarged flowers.

walls containing sugary products.[1] **Column** short, small. **Stigma** longer than broad, with purple edge, very viscous and glistening. **Anther** ovate, coloured like the petals, pollinia emerald or grey-green. **Rostellum** rose or violet, with a fold between the anther-cells. **Seeds** with short broad testa, enlarged and rounded above, mesh small, embryo oval, considerably narrower than testa,[2] cell-walls broad, raised, giving the appearance of marginal papillæ here and there, cells not striate.[3] Pl. D, fig. 3 (5).[4]

Var. **pulchella** Druce. A beautiful colour-form with violet flowers and bright crimson markings, the labellum sometimes less reflexed, strongly marked with darker interrupted lines.[5]

Var. **dunensis** Druce.[6] A dwarf form found on sand-dunes, sometimes (as on the sands of Barry) in great abundance, in a "series of bright colours from pure white, various shades of rose-red and crimson to darkest purple".

Forma **atrirubra** (Pl. 44). Dwarf (9–15 cm.) but one giant was 20 cm. high, spike 8 cm. Stem but slightly hollow. Leaves thick, gradually tapering, somewhat acute, unspotted, often exceeding the oblong sometimes one-sided dense spike. Flowers small, rich dark rose-red, of most beautiful and brilliant colour. Bracts brownish, not much exceeding flowers. Side-sepals erect, back to back. Sides of lip reflexed, irregularly toothed or crenate. Spur short, conical, obtuse, truncate or emarginate. A few plants have narrow leaves and a lax few-flowered spike. Dunes amongst dwarf willows, S. Wales, in sandy black comparatively dry soil. Flowers June. Locally fairly abundant.

Var. **albiflora.** Flowers pure white. New Forest.

Habitat. Bogs, turbaries, and marshy ground, sometimes growing in standing water, also found locally abundant in damp sandy flats between sand-dunes, amongst *Salix repens*, etc. The variety *pulchella* Dr. occurs in *Sphagnum* and peat bogs, but also in ordinary marshy ground. According to Camus in the environs of Paris *O. incarnata* prefers calcareous marshes or ground watered by calcareous streams.[7]

Flowers May to June. In Southern England it is the first marsh orchid to flower, blooming before *O. latifolia* and *O. prætermissa*, but according to Camus[7] *O. latifolia* flowers 20 days before *O. incarnata* in the neighbourhood of Paris.

Distribution. Throughout Great Britain and Ireland, including the Shetlands (Trail, *Ann. Scot. Nat. Hist.* p. 230 (1906)). Almost all Europe except in the extreme south. A small colony with purple flowers was found in Asturias by Dr Stephenson,[8] but it appears to be absent south of the Pyrenees. Caucasus, Siberia.

1 Camus, *Icon.* p. 224 (1928). 2 *O.R.* p. 267, fig. 5 (1923) (Dymes).
3 *B.E.C.* p. 434 (1921) (Dymes). 4 *Vide* p. 94. 5 *B.E.C.* p. 167 (1917). 6 *Ibid.* p. 212 (1915).
7 Camus, *Icon.* p. 225 (1928), quotes me as saying that *O. incarnata* is absent from calcareous ground. What I said was that it had not so far been found on chalk downs, i.e. away from marshes. Mr P. M. Hall has since told me that he has found one or two specimens on chalk downs. *J.B.* p. 49 (1918).
8 *J.B.* p. 72 (1927).

Var. *pulchella*. New Forest, Teesdale, Wales, Scotland, including the Shetlands (Druce, *B.E.C.* p. 523 (1921)).

Var. *albiflora*. New Forest (rare). I saw two or three plants in two localities there in 1931.

Orchis incarnata was included by Linnæus under *O. latifolia* in all his works up to the 1st ed. *Fl. suecica* (1745) and *Sp. pl.* (1753), but in the 2nd ed. *Fl. suecica*, he separated it from *O. latifolia* as follows: "Præcedenti [i.e. 801, *latifolia*] simillima, a qua differt. Foliis pallide viridibus immaculatis; nec saturate viridibus immaculatis. Caule dimidio breviore. Bracteæ vix flore aut germine longioribus. Corollis pallide incarnatis; nec rubris. Petalis dorsalibus totaliter reflexis; nec tantum patulis, nec maculatis. Nectarii labium structura convenit". He did not realise the existence of colour-varieties other than the flesh-coloured one from which he derived its name. Reichenbach p. reversed Linnæus' action and presented *incarnata* as the type of *O. latifolia*, giving the new name *O. majalis* to the spotted marsh orchid which was the type of *O. latifolia* L.;[1] but his son rejected this change of names and types, and figured and described true *incarnata* as such.[2] In the earlier British Floras *O. latifolia* was mainly *incarnata* (including *prætermissa*). Babington was the first to separate it from *O. latifolia* as a variety,[3] and later as a distinct species.[4]

ORCHIS DIVARICATA Rich. (1822). O. LATIFOLIA Rchb. p. (1828). O. LATIFOLIA b ANGUSTIFOLIA Babington, *Man. Brit. Bot.* p. 291 (1843).

FERTILISATION. As in *Orchis* generally. The flowers are well visited, and many seed-capsules are produced. I saw it visited near Christchurch, Hants., on May 14th, 1918, by *Bombus lapidarius* and *B. terrestris*. The former had two pairs of pollinia on the front of the head. On the spikes on which I took them the pollinia had been removed from six flowers, and three stigmas had been pollinated in one case, and two pairs of pollinia removed and two stigmas fertilised in the other. On May 28th, 1918, I saw the variety *pulchella*, near Hamworthy Junction, visited by a *Bombus*, with a pair of pollinia on its head, which I think was *B. agrorum* F. On June 17th, 1919, some spikes of *O. incarnata* in a vase on a verandah at Guildford were visited by two humble-bees, who took no notice of spikes of *O. prætermissa* in the same vase.

ORCHIS INCARNATA × LATIFOLIA

Pl. G, fig. 6 (p. 191). × **Orchis Aschersoniana** Hausskn.

Stem not so hollow as in *O. incarnata*. **Leaves** erect, linear-lanceolate, tapering from base, sometimes with ringed spots, sometimes with many small dull purple spots, rarely unspotted, slightly concave at tip, sometimes rather bluish green, sometimes narrow (11 mm.). **Spike** rather short, about 6 cm. **Flowers** resembling those of

[1] *J.B.* pp. 35–41 (1924). Wimmer and Grab, *Fl. Silesia*, II, 2, 250, n. 1319 (1829).
[2] Reich. *Icones*, XIII, 51 (1851).
[3] *Man. Brit. Bot.* ed. 2, p. 310 (1847); ed. 4, p. 318 (1854). [4] *Ibid.*

1

2

H. M. Godfery pinx.

ORCHIS INCARNATA (PULCHELLA) × LATIFOLIA

PLATE 45

Orchis incarnata var. **pulchella** × **latifolia.**

1, 2. Enlarged flowers. Winchester, June 21st, 1917.

O. incarnata, but slightly larger. Lower **bracts** exceeding the flowers, sometimes suffused with purple. **Sepals** erect, reflexed, spotted. **Lip** lozenge-shaped, broader than in *O. incarnata*, fairly dark red-lilac with pronounced red-purple lines and spots, mid-lobe but little longer than side-lobes as a rule. **Spur** rather longer than in *O. incarnata*, stout, conico-cylindrical, coloured. The parentage of *O. latifolia* is suggested by the ringed spots, or numerous small spots on the sometimes bluish-green leaves, the bright colour of the flowers, the conspicuous lip-markings, and the length and stoutness of the spur in some cases.

Pl. G, fig. 6, shows one of a group of 11 exactly similar plants found by P. M. Hall in June, 1931. The parentage of *O. incarnata* is shown by the wide spur-mouth, coloured incurved bracts and long yellowish green leaves. He considered the other parent to be *O. maculata*, but the ringed leaf-spots, conspicuous loop-patterns on the lip, the unusual length and stoutness throughout of the spur plead in favour of *O. latifolia*. The two upper central flowers suggest *O. maculata* by the marked tri-lobed lip, but the left-hand flowers are very like *O. latifolia*. Hants., Surrey. Flowers June.

ORCHIS INCARNATA var. PULCHELLA × LATIFOLIA

Pl. 45

Tubers not dug up. **Stem** hollow, 30 cm. tall, angled above. **Leaves** erect, lowest with recurved tip, long, narrow, keeled (15–18 cm. × 1·20–1·40 cm.), slightly hooded, entirely suffused with violet above, about the same width for two-thirds of their length, gradually tapering to an acute tip, very slightly narrower at the base than in the middle. **Spike** short, ovate, lax, few-flowered. **Flowers** rather large, violet, the whole central area of the lip occupied by a dark red-violet patch of solid colour. **Bracts** green, linear-lanceolate, tapering to an acute point, lower nearly twice as long as ovary, upper exceeding the buds. **Sepals** long, narrow, lanceolate, pointing forwards, upper more or less connivent with petals. **Petals** lanceolate obtuse, nearly equal to sepals, connivent. **Lip** obovate, entire with a slightly projecting small obtuse lobe at apex, bright red-purple with pale violet margins. **Spur** short, conical, half as long as ovary, which is twisted, with purple ridges. Throat of spur gaping. **Stigma** bordered by a red-violet line.

A striking plant owing to the long narrow upright leaves flushed with violet (as in *Epipactis violacea*), and the long obovate lip with its conspicuous red-purple central area. Only one specimen was seen. I visited the spot twice in subsequent years, but could find no trace of it. The lip with its striking red-purple centre so exactly resembles Pl. 49, fig. 7, of Barla's *Iconographie des Orchidées*, which is labelled "*O. latifolia* variety with dark purple flowers", that there can be little doubt that *O. latifolia* was one of the parents. The other appears to be *O. incarnata*, on account of the long erect narrow tapering hooded leaves. The flush of violet on their upper surface has not been recorded for any species of *Orchis*, and may possibly be due to saprophytism, as in *Epipactis violacea*. The rich colour of the centre of the lip suggests the parentage of *O. incarnata* var. *pulchella*, with its brilliant crimson markings, a specimen of which was growing close by. Winchester marshes! June 21st, 1917.

ORCHIS INCARNATA × MACULATA

Pl. 30 B (p. 150); Pl. H, fig. 1 (p. 219). × **O. ambigua** Kerner (1865)

Taller, less hollow and not so stout as *O. incarnata*. **Leaves** shorter and more spreading, with small scattered spots, or unspotted. **Spike** oval, dense, rather short in Britain. **Bracts** purplish. **Lip** flat, 3-lobed, dark blue-purple with red-purple lines and spots. **Spur** longer and more slender than in *O. incarnata*, which it otherwise resembles. The second parent was *O. maculata*. I could not find either *O. latifolia* or *O. prætermissa* in the locality. Anglesey! July 9th, 1919.

The following example was found at the same time and place. **Stem** hollow, stout. **Leaves** very broad, erect, unspotted, broadest in middle (3·3 cm.), tapering to both ends, thick and firm, of *O. incarnata* type. **Spike** dense. **Bracts** narrow, exceeding flowers. **Flowers** pure white, almost exactly like *O. maculata*. **Lip** deeply 3-lobed, side-lobes rhomboidal, mid-lobe long, triangular, markings two very faint loops formed of microscopic pale violet papillæ. **Spur** ± 8 mm., cylindrical, rather conical at base. The stem and leaves were clearly those of the *O. incarnata* parent, whilst the flowers were nearly typical *O. maculata*, but pure white, interesting as an example supporting the old theory that the leaves of a hybrid resemble one parent and the flowers the other, a combination of rare occurrence (Pl. 30 B).

× *O. curtisiana* Dr.

ORCHIS INCARNATA × MACULATA sub-sp. ELODES

× **Orchis carnea** Camus (*Icon.* p. 276)

Pl. 52 A (p. 215)

Lower leaves not seen, upper bract-like with a few tiny spots, flowers bright rather dark red-violet, larger than those of *incarnata*, lip nearly flat, with side-lobes broadly rounded out and mid-lobe small, pale in the middle with parallel lines of spots. Spur wide-mouthed, slender, curved, 7–10 mm. long. The cylindrical spike, long rather broad bracts, wide-throated spur, dark red-violet lip and slightly hollow stem gave good indications of *incarnata*, whilst the spotted leaves, broad flat lip, narrow mid-lobe, and slender spur as long as the ovary, showed clearly the influence of *elodes*.

[illegible] Lower Austria.

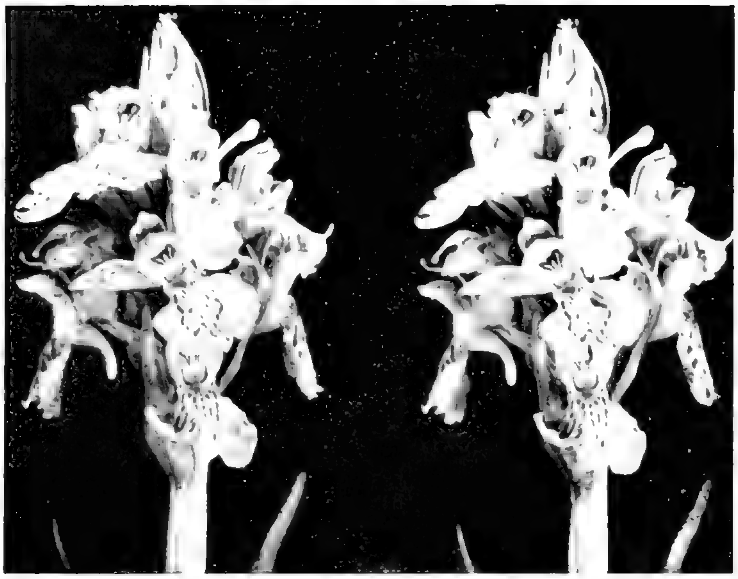
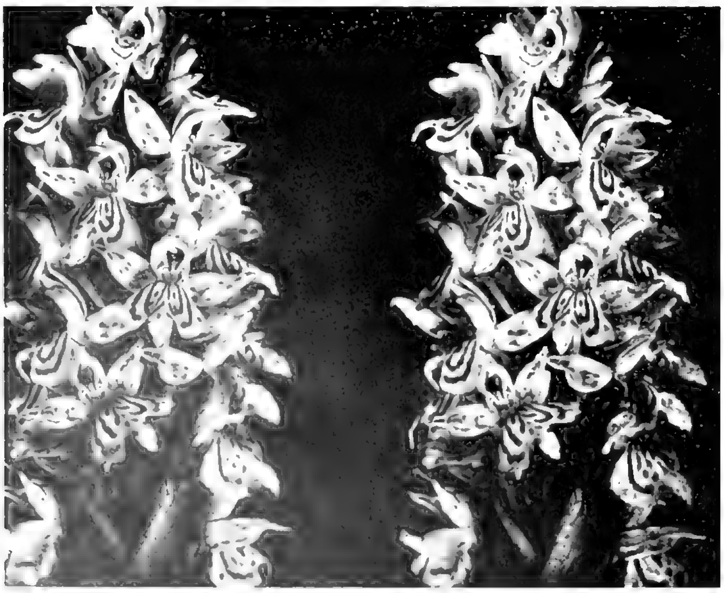


Fig. 2. [illegible]

Fig. 3. *Gymnadenia conopsea* × *Orchis praetermissa.* Slightly enlarged. Hants., June, 1931.

Fig. 4. *Orchis incarnata* × *praetermissa.* Hants., June, 1931.



[illegible]

Fig. 6. [illegible] Hants., June, 1931.

[illegible]

Two plants only were found by Mr St Quintin in a field near the sea-cliffs at Buckton, Flamborough, Yorks., on June 15th, 1918, growing amongst *O. elodes*, of which they were twice the size. About half a mile away in a marshy hollow was a colony of *O. incarnata*.

ORCHIS INCARNATA × PRÆTERMISSA

Pl. G, fig. 4

It much resembles *O. prætermissa*, of which it has the pale lilac flowers whitish at the throat, and more distinctly 3-lobed lip with dotted markings, but the erect yellowish green hooded leaves, narrow cylindrical spike, smaller flowers with erect reflexed sepals, and narrower more lozenge-shaped lip point to the part parentage of *O. incarnata*. Stem moderately hollow, spur conico-cylindrical, moderately stout.

Marshy ground with the parents. Rare. I have found it at Frensham, Surrey, and West Drayton, Middlesex. Cothill, Berks. Hambledon, Hants. (*B.E.C.* p. 157 (1917)). Chippenham, Cambs. (Dr Stephenson, "parents plentiful, hybrids very rare"). Flowers May to June.

Since the above was written Mr P. M. Hall showed me this hybrid in Hants. Its general appearance was that of *O. prætermissa*, but the smaller flowers with narrow wedge-shaped rather more deeply lobed lip struck the eye. The parentage of *O. incarnata* was shown by the long erect yellow-green leaves with a slight concavity at the tip, the narrow cylindrical spike, the long somewhat incurved bracts, the erect back-to-back sepals (in some flowers), the narrow lip with sometimes a tendency towards the pattern of *O. incarnata*, and the stout spur with a gaping mouth. It was going over, while *O. prætermissa* was only in early flower (June 13th) (Pl. G, fig. 4).

ORCHIS INCARNATA var. PULCHELLA × PRÆTERMISSA

A very handsome hybrid found by the author in Winchester water-meadows on June 19th, 1919. The parentage of *O. incarnata* was suggested by the very hollow stem, the erect hooded yellow-green unspotted leaves, the purple-tinged bracts exceeding the flowers and buds, the erect reflexed spotted sepals, the deflexed side-lobes making the lip appear lozenge-shaped, and the conspicuous bright red-purple markings (loops enclosing interrupted lines) on a bright violet ground, which are suggestive of the var. *pulchella*. The influence of *prætermissa* is indicated by the dense pyramidal spike, the larger flowers, and the broad side-lobes of the lip. Another specimen was nearer to *incarnata*, the lip being longer, narrower and more lozenge-shaped. Another had similar lips, but the markings consisted entirely of dots and dashes, and covered the whole lip, closely resembling those of typical *prætermissa*.

ORCHIS INCARNATA var. DUNENSIS × PRÆTERMISSA

Resembles *O. prætermissa*, but with pale pink flowers as small as those of the var. *dunensis*, erect back-to-back faintly spotted side-sepals, and short conical slightly curved spur resembling that of flesh-coloured *O. incarnata*. Leaves 16½–18½ cm., erect, unspotted, broadest 2 cm. above base. Lip-markings in one specimen like *O. incarnata*, in the other like *O. prætermissa*. Two plants only seen, sand-dunes, S. Wales, with the parents. June 20th, 1928. *J.B.* Pl. 556, fig. 8 (coloured), Nov. 1920 (as *O. prætermissa*).

9. ORCHIS PRÆTERMISSA Dr.

Pl. 46. *Flat-lipped Marsh Orchid*

Tubers 2, palmate, 3–4-fid, with short or long tails; roots long, rather stout. **Stem** 20–40 cm., in long herbage sometimes nearly twice as tall, robust, more rarely slender, 4–9 mm. in diameter at the base with 2–3 brownish sheaths, hollow, but with thicker walls than *O. incarnata*, green, glabrous. **Leaves** about five, 10–14 cm. long by 1·50–2·50 cm. broad, "up to 21 cm. and 5·5 cm." respectively (Druce), oblong-lanceolate, moderately acute, "thickened or slightly hooded" (Druce) at the tip, not narrowed at the base, often broadest above the middle, firm, glabrous, green, often grey-green or dark green, always unspotted, long-sheathed and rather distant, erect, more or less spreading. **Spike** ovate to cylindrical, 5–10 cm., "rarely up to 17 cm. long" (Druce). **Flowers** many, large, conspicuous, rather flat-lipped, pale mauve or lavender, pale or dark red-violet, "dull rose, purple, often of the colour of *Rhododendron ponticum*, reddish, rarely dark crimson, purple, or white" (Druce). **Bracts** broad to rather narrow, spreading, not elbowed and incurved as in *O. incarnata*, as long as or longer than the flowers, "sometimes leafy" (Druce), often coloured, the lower often considerably exceeding the flowers, the upper short, coloured. **Ovary** spindle-shaped, 6-ridged, glabrous, twisted. **Side-sepals** spreading horizontally or semi-erect, not as a rule back to back, the upper connivent with the petals or erect, narrowly lanceolate, obtuse or acute, 1–3-nerved, as a rule unspotted. **Petals** shorter, ovate-lanceolate, obtuse, concave, tips overlapping, forming a hood. **Lip** large, broad, flat with upturned edges in early flower (later somewhat reflexed), very shallowly 3-lobed at apex ("mid-lobe when present up to 2 mm. long", Druce), broadly obovate or elliptical, sometimes wedge-shaped at base, as broad as or broader than long, variable in size ["usually about 12 mm. broad by 9 mm. long" (Druce), 6–8 mm. long by 7–12 mm. broad (Stephenson)], thin in texture, range of colour as above, paler in the centre, with very numerous minute spots often in radiating lines, more

PLATE 46

Orchis prætermissa Dr.

1, 2, 3. Enlarged flowers. Surrey, June 24th, 1916.

H. M. Godfery pinx.

ORCHIS PRÆTERMISSA Dr.
Flat-lipped Marsh Orchid

rarely with streaks, heavy lines or blotches. Sometimes the pattern is geometric with single or double loops, but these are probably due to lingering traces of hybridity. Side-lobes rounded out, mid-lobe small, rather broad, tongue-like or wedge-shaped (separated by an obtuse sinus rather than an incision), sometimes almost absent, rarely long and prominent (var. *macrantha*). **Spur** conico-cylindrical, obtuse, straight or very slightly curved, about two-thirds as long as ovary, or less. **Seeds** with long straight somewhat club-shaped transparent testa, rounded at apex, larger meshed than in *O. incarnata*; cells with broad raised walls, not striate; embryo oval nearly as broad as testa[1] (Pl. D, fig. 3 (4) (p. 94)).

In Southern England *O. prætermissa* flowers usually 10–14 days later than *O. incarnata*, but in Durham Prof. Heslop Harrison gives it as flowering before *O. incarnata*.[2] Figures of single flowers are given in *B.E.C.* Pl. 1 (1917), and by the Stephensons (*J.B.* Pl. 559 coloured (1920) and Pl. 566 (1921)), and an exhaustive study with photograph was published by the latter.[3] The grandchildren of the original specimen of *O. prætermissa* (figured as *O. incarnata* in the *Report of the Ashmolean Society* in 1904) flowered in 1926 in the garden of Mr B. S. Ogle, at Steeple Aston, and showed no appreciable variation except in stature. Their parents flowered in 1913.

Although so long confused with *O. incarnata*, *O. prætermissa* appears to be more closely allied to *O. latifolia*. Dr Stephenson says: "The habit is precisely similar, but *O. latifolia* is distinguished by the spots or rings on the leaves, which are almost always present, and by the very distinct lip-pattern of continuous lines. By far the greatest number of plants of *O. latifolia* have paler tinted lips, often nearly white inside the lined pattern, not the soft purples or magenta of *O. prætermissa*, nearly always more slender spurs, and generally a different facies".[4]

During three years I observed a large colony of *O. latifolia* near Vence (about 1000 ft. above Nice), where it was the *only* dactylorchid present. *O. incarnata*, *O. prætermissa* and *O. maculata* have never been found in the neighbourhood, either by Mlle Camus, who published a list of orchids found there during two or three seasons (*Riviera Scientif.* p. 1 (1919)), or by myself, nor was any hybrid of *O. latifolia* ever discovered. It was therefore clear that any differences between individual plants were due to variation, and not to hybridisation. *O. latifolia* was here an isolated self-contained species, free from any taint of hybridity, and could not possibly be a hybrid between *O. prætermissa* and *O. maculata*, as Dr Druce claims to be the case with English *latifolia*. On May 10th, 1920, I found one specimen which would, I think, have been taken for *O. prætermissa* if found in England, with large pale mauve flowers, short conical spur not quite half as long as ovary, and quite unspotted leaves. Another specimen had a flat lip, of pale violet colour, covered with rows of

[1] O.R. p. 267, fig. 4 (1923).
[2] *B.E.C.* p. 170 (1917).
[3] *J.B.* p. 65 (1923).
[4] *Ibid.* p. 67 (1923).

tiny spots radiating like a fan, and very few tiny spots on the leaves. Much as these suggested *O. prætermissa*, they were only variants of *O. latifolia*.

On May 30th, 1923, above Aix-les-Bains where *O. latifolia* was abundant, I found a single specimen of which my wife and I at once said, "Why, here is *prætermissa*". The leaves were unspotted and rather glaucous, the flowers bright red-violet, the sepals spreading in a horizontal plane, the lip slightly tri-lobed at summit, the side-lobes reflexed with upturned edges, the markings a single loop on each side, enclosing more or less parallel lines of small red-purple spots, the spur conico-cylindrical, nearly as long as ovary. On closer inspection we concluded regretfully that it was only a form of *O. latifolia* with unspotted leaves. We searched the same ground in successive years but could never find another specimen. These experiences seem to show that the production of isolated specimens with a suggestive resemblance to *O. prætermissa* is within the scope of variation of *O. latifolia*. They perhaps both sprang from a not very remote ancestor, and the *prætermissa*-like specimens might conceivably be cases of partial reversion to a primitive type.

Mr T. A. Dymes wrote, October 10th, 1925: "The seeds [of *O. latifolia*] are quite different from any of the *maculata* group, but are very like *prætermissa*, and mixed seeds would be difficult to separate". They were taken from spotted-leaved plants (*B.E.C.* p. 784 (1925)).

Var. **pulchella** Druce.

Tubers two, flattened, palmate, with ± 4 long slender fingers; basal sheaths two, lower brown, upper white. **Stem** round, angled above, hollow with thick walls, average height 20–30 cm., in mid-Perth sometimes 60 cm. (R. Mackechnie). **Leaves** oblong-lanceolate, distant, spreading, obtuse or acute, firm rather thick, unspotted, keeled, with 3–5 parallel nerves on each side and anastomosing veins, rather yellow-green, the lowest short; average length ± 12 cm., width ± 2·5 cm. **Spike** 25–70 mm. long,[1] average about 5–6 cm., few-flowered (± 20); in mid-Perth massive spikes occur occasionally (R. Mackechnie). **Bracts** lanceolate, tapering, 2–3 cm., edged purple. **Ovary** cylindrical with three prominent ridges. **Flowers** smaller than those of the type, like those of *O. purpurella*, but with a wider range of colour, "bright tints of purple, purplish rose, dark bluish purple, rarely pale rose or white" (Druce).[1] **Sepals** erect, reflexed back to back, spotted, the median hooded, connivent with the paler ovate hooded petals. **Lip** cuneate at base, with a rounded elbow on each side, then truncate or rounded, slightly crenate; mid-lobe very short, triangular, obtuse, only separated by a slight notch; markings red-violet interrupted loops and spots. **Spur** conical, wide at base, ± 6–8 mm. long, dorsally compressed at tip, coloured, slightly spotted inside at base, spots showing through. **Column** white, forming a chamber at the mouth of the spur. **Stigma** shield-shaped, edged red, pouch of

[1] Druce, *B.E.C.* p. 577 (1919).

rostellum nearly white. **Anther** violet with greenish eyes. **Pollinia** sage-green, shorter than the pale yellow transparent caudicles. Capsule oblong, ± 17 mm. long.

Dr Druce at first called the plant Northern *incarnata*, perhaps on account of its firm unspotted leaves. I went with him to Hamworthy, Dorset, to see an orchid which he expected would prove to be *O. prætermissa*. On seeing it he said, "Yes, it is *prætermissa*", but later thought it *O. incarnata* var. *pulchella* Druce, which it undoubtedly was. In 1919 (*B.E.C.* p. 578) he wrote: "To this (*O. incarnata* v. *pulchella*) I formerly referred the Hamworthy plant. It is possible that further study may result in uniting both these forms under *prætermissa*, and therefore I have selected the same name (i.e. *pulchella*) for the northern plant, but definitely making it subordinate to *prætermissa*, as it is distinctly in closer alliance with that than *incarnata* under which for the time I leave the Hants. and Dorset plants".

Dr Stephenson found *O. purpurella* and *O. prætermissa* var. *pulchella* Dr. growing together in Arran, and wrote (*J.B.* p. 35 (1922)): "The flowers are of precisely the same type, the differences being that *O. purpurella* is dwarf, with minutely spotted leaves, whilst *O. pulchella* is much taller, stout or slender, and with unspotted leaves".[1]

In July, 1930, I saw *O. purpurella* growing in several localities in Teesdale. I found a number of the plants with firm unspotted leaves, so that, like all other European spotted orchids known to me, it has an unspotted form. One specimen of pure *O. purpurella* was $41\frac{1}{2}$ cm. tall, so that it may lose its dwarfness under favourable conditions. It appears very probable that *O. prætermissa* var. *pulchella* is the unspotted form of *O. purpurella* Steph.,[2] now recognised as a distinct species in the most recent continental works. On the other hand "the seeds of *purpurella* are the smallest of the group, with an abruptly pointed apex indented at the base, whilst those of *O. pulchella* are longer, with a rounded apex, only a little narrowed from the middle of the seed. This is in form precisely like those of the typical *prætermissa*, but for being a little more slender". Moreover they agree with the latter in having long loose testal cells, and not the closer mesh of *O. purpurella* whose small rather dusky seeds are easily distinguished from all others of the group.[2] *O. prætermissa* var. *pulchella* is figured in *J.B.* Pl. 556, fig. 7 (1920) (single flower only). All the specimens I have seen appear to me to be much nearer to *O. purpurella* than *O. prætermissa*, but I have not seen many.

Var. **macrantha** Sipkes (*De Levende Natuur*, June, 1921). Mid-lobe of lip with a long narrow extension. Pl. 1, *B.E.C.* (1917), appears to be this variety.

[1] "As far as I have seen there is no difference between *O. purpurella* without spots and *O. prætermissa* var. *pulchella*. I have never myself found the latter without the former present, and in such cases the tendency is for the unspotted forms to grow amongst the taller grass and the spotted forms where it is short. But I believe there are places in Yorkshire where you get nothing but the tall unspotted forms....I have seen great quantities of *O. purpurella* from the Orkney Islands, and there have been few tall plants and few without spotted leaves. The only variation is that in some lots the spots are rather large, and may be circular." Rev. T. Stephenson in lit. Aug. 23rd, 1932.

[2] *J.B.* p. 68 (1923).

Lusus *ecalcarata* Dr. Lip without spur. Pudmore, Surrey.[1]

Forma *albiflora* Dr. Flower pure white, a solitary specimen. Abington, Berks.[1]

HABITAT. Moist meadows, marshy ground, rushy or boggy places where it sometimes attains 2 ft. It does not like standing water. Flowers May to June, in the north June to July.

DISTRIBUTION. England, Wales, Scotland; Ireland in the north-east, apparently absent from the east and south-east. Occurs sparsely in Scotland as far north as the Shetlands. The var. *pulchella* is abundant in Scotland, extending to the Shetlands. The type occurs in Northern France, environs of Paris (Stephenson).[2] "Pas de Calais à Berck, Essarts le Roi, Vieux Moulin, Pierrefonds, Jouy-le-Comte, Arronville, jusqu'à Souppes dans le Sud de Seine et Marne."[3] Holland (Sipkes).[4]

ORCHIS PRÆTERMISSA Dr., *B.E.C.* p. 34 (1913).

Included in *O. incarnata* by all previous authors who recognise that species, and in *O. latifolia* L. by those who do not. Regarded as the type of *O. latifolia* L. by the late Mr Rolfe.[5]

O. prætermissa × *Gymnadenia conopsea*. See *Gymnadenia*, p. 146.
O. prætermissa × *incarnata*. See *O. incarnata*, pp. 191, 192.
O. prætermissa × *latifolia*. See *O. latifolia*, p. 202.
O. prætermissa × *maculata*. See *O. maculata*, p. 214.
O. prætermissa × sub-sp. *elodes*. See *O. maculata*, p. 216.

10. ORCHIS LATIFOLIA L.

Pl. 47 B; Pl. G, fig. 1 (p. 191). *Broad-leaved Orchis*

Tubers short, thick, forking into two widely divergent short thick tapering segments, either or both of which may again fork; roots above tuber several, 2–3 mm. thick by 5–10 cm. long. **Stem** erect (15–50 cm.), hollow, compressible, cylindrical, ridged above and often tinged with purple, with 2–4 whitish ribbed sheaths, sometimes green-tipped, at base. **Leaves** 4–6, more or less spreading, oblong or oblong-lanceolate, obtusely pointed (7–17 cm. by 2–4 cm. broad), keeled, flat or slightly hooded at tip, dark greyish or bluish green, more or less densely covered with purple-black spots often ringed (i.e. with green centres), more rarely unspotted; upper leaves sessile hardly sheathing, bract-like, linear-lanceolate, tapering to a fine point, often edged or suffused with purple. **Spike** usually dense, many-flowered, at first conical, then cylindrical, 6–11 cm. long. **Flowers** pale lilac to rose-violet with darker red-violet markings, showy, rather flat-lipped. **Bracts** lanceolate to ovate-lanceolate, tapering to a fine point, keeled, glabrous, microscopically toothed, the lower often exceeding the flowers and sometimes spotted, the upper slightly longer or shorter

[1] *B.E.C.* p. 159 (1917). [2] *J.B.* p. 96 (1925). [3] Camus, *Icon.* p. 219.
[4] *De Levende Natuur*, June, 1921. [5] *O.R.* p. 65 (1920).

PLATE 47

H. M. Godfery pinx.

A. ORCHIS MACULATA L.
Spotted Orchid

B. ORCHIS LATIFOLIA L.
Broad-leaved Orchid

PLATE 47

A. **Orchis maculata** L. N. Wales, June 10th, 1908.

B. **Orchis latifolia** L. Surrey, June 28th, 1918.

1. Enlarged flower. Winchester, June 18th, 1917.

than the buds, often purple-tipped, 3- or more nerved. **Ovary** slender, twisted, 6-ridged, often tinged purple. **Sepals** narrow, lanceolate, inner edge straight, outer rounded, the lateral erect, often back to back, spotted or not, the upper slightly shorter and broader, erect or arched forwards. **Petals** forming a hood, lanceolate, concave at tip, violet outside, paler within. **Lip** directed downwards and slightly forwards, flat, or sides gently sloping downwards, sometimes transversely oval, slightly broader than long, sometimes wedge-shaped at base with a more or less obcordate outline, shallowly 3-lobed at apex, side-lobes rounded, sometimes with an obtuse angle in the middle, often irregularly crenate or toothed; mid-lobe smaller, usually slightly longer, tongue-shaped or triangular, entire. Markings usually consisting of two single or double longitudinal loops (often of interrupted lines), with supplementary hieroglyphics, but sometimes of short lines and spots variously arranged. The centre of the lip is often paler or whitish, and the lip itself densely clothed with extremely minute erect acute papillæ. **Spur** conico-cylindrical, sometimes slightly curved, obtuse, equal to or shorter than the ovary, pointing downwards, sometimes spotted within. **Column** short, erect, anther oval, rose-violet, pollinia grey-green, caudicles yellow. **Stigma** on roof of mouth of spur, bordered by a purple line, very viscous. **Seeds** with transparent testa, cells most delicately and somewhat spirally reticulate (Rchb. *Icones*, XII, 57), "Very like those of *O. prætermissa*, but somewhat shorter and broader, and inclined to taper and curve in the apical half", and with smaller mesh, the differences being merely of degree. Seeds from plants at Chippenham Fen and near Winchester showed no sign of *O. maculata* or of hybridism (T. A. Dymes). Cells of the testa of adult seeds with rectilinear walls not striate in individuals growing isolated, sometimes having a few striæ in plants growing near *O. incarnata* and *O. maculata*, probably the result of crossing (Camus, *Icon.* p. 233 (1929)).[1]

A handsome marsh orchid with conspicuous ring-spotted leaves (i.e. spots with green centres) but also found with dark or faint often small transversely oblong or rounded spots, more rarely with unspotted leaves, and showy pale lilac or red-violet flowers. The tubers are said to be sometimes long-tailed in wet ground, but this may perhaps be due to crossing, e.g. with *O. incarnata*, as they are mostly described and figured as short. The stem is usually from 15 to 40 cm. tall, and is hollow, but not so much so as in *O. incarnata*, in which the stem is often a thin-walled tube; in dry soil it may be nearly solid, except for a narrow central tube. Though called *latifolia*, the leaves are often not broader than in the wood-form of *O. maculata*, and are not so thick and firm as in *O. prætermissa*. They narrow but little towards the base, and are broadest below the middle, the sides nearly parallel for some distance, and then tapering to an obtuse point. In the Engadine, at 6000 ft., the author found plants

[1] For var. **eborensis** *vide* p. 219 below.

with oval leaves, nearly as broad as long (var. *impudicus* A. and G.), but ordinarily they are much longer than broad. Of 35 specimens gathered in June, 1919, in the Winchester district, 21 had spotted leaves (of which 12 had ringed spots) and 14 were unspotted. All the stems, leaves, spikes, bracts, and flowers appeared to be alike. The lip-pattern was very similar in them all, two longitudinal loops with additional lines and spots—the lines often interrupted, but not broken up into innumerable dots as often occurs in *O. prætermissa*. Ringed spots are much more frequent in *O. latifolia* than in *O. maculata* or *elodes*, in which they are rare, and less frequent on the Continent than in England.

The spike when young is conical, sometimes ending in a pencil of bracts concealing the buds (comose) (var. *macrobracteata* Schur). The side-sepals are at first erect, later reflexed, spotted inside, the upper unspotted. It is very rarely found with white flowers. I once found what appeared to be a white-flowered specimen above Grasse, but on comparing it with a pure white *O. maculata*, it was seen to be very faintly tinged with violet. I found a beautiful specimen near the Lac de Bourget, with violet sepals and petals and white lip with very faint indistinct markings.

The late Rev. E. S. Marshall wrote as follows on receiving a plant of the Winchester *O. latifolia* gathered by Mr Comber and myself, June 26th, 1916: "This is *exactly* the spotted leaved plant (except that your plants have narrower foliage, somewhat, and smaller blotches), down to the markings of the labellum, of the plant figured by M. Schulze (Pl. 21) as *O. latifolia*". This plate represents typical *O. latifolia* as understood by the author of *Die Orchidaceen Deutschlands*. "Sowerby's plate 2308, *English Botany*, ed. 1, was...by error named by Smith as *O. latifolia* L., but it correctly represents the purple-flowered form of *O. incarnata*. The error had been pointed out by Babington, and a figure of *O. latifolia*, No. 2973, drawn by J. W. Salter appeared in *E.B. Suppl.* vol. v. The plate of *O. latifolia* in Curtis' *Flora Lond.* represents *O. incarnata*."[1]

Pl. G, fig. 1, shows a specimen from Lower Austria. Heer P. Vermeulen[2] states that there are two forms of *O. latifolia* in Holland.

(1) *O. latifolia majalis* Kittel. Flowers latter half of May (a plant or two end of April). Stem dwarf, mostly under 20 cm. Leaves short, broad, ovate-lanceolate with dots or rounded spots, about 8 per cent. unspotted. Flowers small, dark red-purple, mid-lobe often prolonged. Spur dark, slenderer than in the following. Habitat: meadows, sometimes dunes. Considered to be *O. purpurella* by some Dutch botanists. Four spikes received by me from Heer Vermeulen, June 12th, 1931, were certainly not *O. purpurella*. Plants sent to Dr T. Stephenson in 1929 were all considered by him to be *O. latifolia*, but differing somewhat from the British form.

(2) *O. latifolia junialis* Vermeulen. Blooms nearly a month later, about June 15th.

[1] Townsend, *Fl. Hants.* pp. 405–22 (1904).

[2] *Nederl. Kruid. Archief*, Afl. 2, pp. 147–54 (1930).

Stem taller; leaves long, narrow, lanceolate, tapering gradually, with ringed spots, very distinctive of the two forms. Flowers pale lilac with violet markings, lip broader than long, shallowly 3-lobed at apex, mid-lobe small, not prolonged. Spur thick, tapering. Habitat: marshes. Four plants sent to me at the same time, and others sent to Dr Stephenson, agreed well with English *O. latifolia.*

Heer Vermeulen does not think that *O. junialis* can be a hybrid between *O. praetermissa* Dr. and *O. maculata*, as the latter is entirely absent from the low turf-moor district where it occurred. Above Nice I found *O. latifolia* with small dots, or oval, transverse, or ringed leaf-spots, or unspotted, growing together, evidently pure, no other dactylorchid existing in the neighbourhood.[1]

Mr T. A. Dymes in his paper on the "Seeds of the Marsh Orchids" read before the Linnean Society, June 21st, 1923,[2] expressed a doubt whether the seeds of British plants sent to him as *O. latifolia* were not of hybrid origin. In a paper read before the same Society, June 19th, 1924, he stated, however, that he had since received plants from Chippenham Fen and from Winchester, agreeing in other respects with *O. latifolia* L., whose seeds were obviously pure, showing no sign of *O. maculata* or of hybridism, though the plants had spotted leaves. The seeds were "very close to *O. prætermissa*, the differences being merely in the degree of the qualities common to both". "The evidence of the seeds of these plants, which came from Winchester and Chippenham Fen, suggests that *O. latifolia* L. and *O. prætermissa* are close allies or forms of the same species."

For isolated specimens of *O. latifolia* at Vence, Alpes Maritimes, France, very similar in appearance to *O. prætermissa*, see above, under *O. prætermissa.* Mr S. A. Bennett[3] states that in a N. Irish station where *O. prætermissa* and *O. maculata* grow together hybrids occur in some quantity, but he has never seen any with ring-spotted leaves.

Habitat. Marshes, moist meadows, edges of swamps, slopes with trickles of water, etc. A few plants have been found on chalk downs, where they are accidental casuals which have survived unfavourable conditions. It has been observed up to 6000 ft. on the Continent. Flowers end of May to August, according to latitude, elevation and season, the main flowering period in England being in June.

Distribution. Probably throughout Great Britain, but said to be of doubtful occurrence in Ireland (*Cybele hibernica*, p. 345 (1898)). As *O. prætermissa*, and by some authors *O. incarnata*, were included in *O. latifolia* until recently, early records do not distinguish between them and *O. latifolia.* Nearly all Europe, Caucasus, Transcaucasia, Northern Persia.

Orchis latifolia L. (*Sp. pl.* p. 941 (1753)) was a composite species embracing *O. incarnata*, *O. latifolia* (as described above), and *O. sambucina*, a plant of dry alpine slopes

[1] *J.B.* p. 286 (1920). [2] *O.R.* p. 266 (1913). [3] *J.B.* p. 290 (1920).

in Central Europe which extends to S. Scandinavia, and has nothing to do with marsh orchids. Linnæus omits all mention of the leaves in his diagnosis of *O. latifolia* in his *Sp. pl.*, but cites his previous description in *Hort. Cliff.* (1734), which says "Variat foliis immaculatis", showing that in this, his earliest diagnosis, he regarded the spotted plant as the type. Linnæus evidently realised the composite nature of his species, for two years later (*Fl. suecica*, ed. 2 (1755)) he separated from it *O. sambucina* and *O. incarnata* as distinct species, *thus removing from it the only two forms with invariably unspotted leaves*,[1] and restricting *O. latifolia* to plants normally with spotted leaves, but occasionally with unspotted ones. Of his newly created *O. incarnata* he says: "Very similar to the preceding (i.e. 801, *latifolia*) from which it differs: leaves pale green unspotted, not dark green spotted". All European orchids with spotted leaves sometimes occur without spots.

The elder Reichenbach (*Icon. Pl. Crit.* VI, 7, no. 771 (1828)) tried to reverse Linnæus' action, transferring the name *O. latifolia* to *O. incarnata* L., and giving the new name *O. majalis* Rchb. to *O. latifolia* L. Happily this has fallen into disuse, owing to the inevitable confusion involved. Reichenbach's son regarded his father's *O. majalis* simply as a synonym of *O. latifolia* L.

ORCHIS LATIFOLIA L., *Sp. pl.* ed. 1, p. 941 (1753) as amended by Linnæus, *Fl. suecica*, ed. 2, p. 312 (1755). O. MAJALIS Rchb. p., *Pl. crit.* VI, 7 (1828).

O. latifolia according to Webster is *O. incarnata*, according to Rolfe *O. prætermissa*, according to Druce *O. maculata* × *O. prætermissa*, whilst as understood by most British authors it was an aggregate species including all the above, as well as true *latifolia*. The latter was the early Linnean point of view in the *Sp. pl.*, abandoned by him after two years' further study.

As far as my experience goes *O. latifolia* on the Continent is a widespread, abundant and stable species which not unfrequently occupies considerable areas to the exclusion of all other dactylorchids.[2] Like *O. maculata* it has a rather wide range of variation. In some stations the flowers are dark red-violet, in others pale lilac like most of the British plants.[3] The leaf-spots are variable, plants with many small spots, larger transverse spots and ringed spots with green centres all growing together. The last named are not signs of hybridism, and occur where no other species is present with which crossing could have taken place.[4] I have found ringed spots very frequent in *O. latifolia*, but extremely rare in *O. maculata* and its sub-sp. *elodes*.

FERTILISATION. As described under *Orchis mascula* in "Pollination and Fertilisation". In June, 1879, in Germany, Hermann Müller caught specimens of *Bombus Rajellus* ♀ and *B. pratorum* ♀ with numerous (up to 10) pollinia on their heads on

[1] *J.B.* pp. 35–41 (1924).
[2] *Ibid.* p. 138.
[3] *Ibid.* p. 287 (1920).
[4] Camus, *Icon.* p. 218 (1929).

H. M. Godfery pinx.

ORCHIS LATIFOLIA × MACULATA
× *Orchis Braunii* Halacsy

PLATE 48

Orchis latifolia × **maculata,** × **Orchis Braunii** Halacsy.
Thorenc, above Grasse, France, June 19th, 1920.

flowers of *Pedicularis verticillata*, but did not see them actually visit *O. latifolia*.[1] Darwin found that only 50 flowers out of 169 on nine spikes from Kent had had pollinia removed.[2] It cannot, however, be concluded that this is the usual proportion removed, for this varies not only with the abundance of the insect concerned, but also with the abundance of the plant. Darwin found that seven spikes with 315 flowers of *O. maculata* only set 49 capsules, or seven on each plant.[2] As the plants were in larger groups than he had ever seen before, he thought this was probably due to there not being enough insects to go round.

In his *Fertilisation of Flowers*, H. Müller gives from his own observations the following visitors: *Apis mellifica* L. ☿, *Bombus senilis* Sm., *B. fragrans* Poll., *B. confusus* Schenck., *B. hortorum* L., *B. lapidarius* L., *B. terrestris* L., *B. muscorum* L., *Eucera longicornis* L. ♂, *Halictus leucozonius* K. ♀, *Nomada sexfasciata* Pz. ♀ and *Osmia fusca* Chr. (= *bicolor* Schr.) ♀. Darwin states that it is also visited by Diptera.

ORCHIS LATIFOLIA × MACULATA. ×**Orchis Braunii** Halacsy

Pls. 48 and 50, fig. 19 (p. 206)

The characters of the parents may appear in varying combinations. **Stem** 20–40 cm., hollow, in plants nearer *O. maculata* with only a slender central tube. **Leaves** long, lanceolate, rather narrow, light green to darker grey-green with transverse oval, ringed, or small spots. **Spike** dense, flowers rather large, bright-coloured. **Sepals** spotted, usually erect or reflexed. **Lip** with rounded side-lobes and small apical lobe as in *O. latifolia* (or more or less deeply tri-lobed as in *O. maculata*), red-lilac to violet, with red-purple double loops, lines, or spots. **Spur** rather long, tapering.

Signs of *O. latifolia*: hollow stem, ring-spotted leaves, bright-coloured flowers (not pale as in *O. maculata*), small apical lobe of lip, and rather bright-coloured lip-markings; of *O. maculata*: nearly solid stem, long narrow transversely spotted leaves, rather slender spur, more deeply lobed lip.

To this hybrid probably belongs the Kilmarnock Orchid, often called *Orchis maculata superba*, cultivated as a hardy garden plant by Miss F. Hope of Wardie Lodge, Edinburgh, and figured in *O.R.* p. 113 (1920). It was remarkably handsome with pronounced dark leaf-spots and spikes 7–9 inches long (*O.R.* p. 177 (1918)).

A specimen found by us near Megève, Haute Savoie, was 40 cm. tall (including spike 22 cm.), and towered over the abundant parents, of which *O. latifolia* was dark red-purple and *O. maculata* nearly always pale lilac. The cross had hollow stem, dense transverse spots on the leaves, very long spotted bracts, and pale lilac flowers, larger than either parent, with bright red-violet markings, broad crenate side-lobes, small mid-lobe, and conico-cylindrical spur, as long as the ovary. Another specimen had

[1] H. Müller, *Alpenblumen*, p. 64. [2] *Fert. Orch.* ed. 2, pp. 33, 35.

tiny leaf-spots, hollow stem, purple bracts and red-purple flowers. A specimen at Thorenc, above Grasse, was 70 cm. tall! (spike 7 cm.), stem solid except for a central pin-hole, leaf-spots large, transverse, faint, ringed; flowers large, bright red-violet, side-lobes broad, toothed, mid-lobe pronounced, acute, spur short, truncate (Pl. 48). Another specimen had densely spotted leaves with a tendency to form ringed spots, long bracts and bright red-lilac flowers. One on the Col de Granier above Chambéry had bright violet flowers, larger than in either parent, lip broader than long, with rhomboidal side-lobes and short triangular mid-lobe, and spur longer than ovary. At Gryon, Switzerland, June 26th, 1925, a specimen had a spike 17 cm. long, large flowers (Pl. 50, fig. 19) and thick cylindrical spur 10 mm. long. Some of the above had transverse bands of darker green on the stem.

HABITAT. Marshy ground. May occur wherever the parents grow together. Flowers May to June.

DISTRIBUTION. Hants.! Ayr, Kilmarnock, Eton, Sevenoaks, and Co. Leitrim, Ireland (*O.R.* p. 177 (1918)). Surrey!

Townsend (*Fl. Hampshire*, p. 409) says: "Some plants have spur of *latifolia*, but solid stem[1] and spreading leaves of *maculata*, with the lower bracts longer than the flowers". White (*Fl. Bristol*, p. 556) says: "Mr Fry observes: This plant has the leaves of *maculata* but approaches *latifolia* in its hollow stem, much broader and more deeply cleft labellum, with the lateral lobes ultimately reflexed, and markings confined to the centre, and in its much thicker spur, longer and stouter germen, more reflexed lateral sepals, and much larger and more conspicuous bracts....Similar hybrids are on record from Devon".

ORCHIS LATIFOLIA × PRÆTERMISSA

Pl. 49 B

Stem hollow, mottled with lighter and darker green. Leaves unspotted. Flowers large, violet with pale centres; lip broader than long, markings bright red-violet, like those of *O. latifolia*; spur conical, spotted.

Another plant. Stem very hollow, leaves unspotted, spike long (13 cm.), flowers large, red-lilac, lip almost orbicular, with darker red-purple loops enclosing hieroglyphics, mid-lobe apical, very slightly indicated. Winchester marshes, June 21st, 1919!

Pl. 49 B. Another plant. Stem hollow, leaves faintly spotted. Flowers intermediate, red-lilac with dark *latifolia*-like markings. Winchester, June 18th, 1917.

[1] Var. **Townsendiana** Rouy, *Fl. France*, XIII, 173. Stem nearly solid, leaves unspotted. France, Great Britain.

PLATE 49

A. **Orchis maculata × prætermissa.** Winchester, June, 1917.

1, 2. Enlarged flowers.

3. Enlarged flower from Surrey.

B. **Orchis latifolia × prætermissa.**

4, 5. Enlarged flowers. Winchester, June 18th, 1917.

H. M. Godfery pinx.

A. ORCHIS MACULATA × PRÆTERMISSA
× *Orchis Mortonii* Druce
B. ORCHIS LATIFOLIA × PRÆTERMISSA

ORCHIS LATIFOLIA × PURPURELLA

× **Orchis insignis** Stephenson p. and f.[1]

Pl. 53 B (p. 217)

Stem usually tall, a fair number taller than either parent, a few dwarf like *O. purpurella*. **Leaves** 4–5, sub-erect, longer and sometimes broader than in *O. purpurella*, keeled and slightly hooded, mostly with larger often transversely oval blotches, sometimes with ringed spots, a few with small dots like *O. purpurella*, and some without spots. **Spike** short, ovoid, rather dense. **Leaves** small, about the same size as in *O. purpurella*, brightly coloured. **Sepals** erect, reflexed. **Petals** erect with crossed tips. **Lip** more distinctly 3-lobed at apex and slightly broader than in *O. purpurella*, paler, with brilliant carmine markings (double loops of continuous lines with detached spots outside), side-lobes rounded or slightly rhomboidal, rather coarsely and irregularly toothed or crenate, mid-lobe small, rounded. **Spur** rather long, conico-cylindrical, shorter than ovary.

When seen with the parents, at once recognisable as a hybrid between them. The general appearance is that of a modified *O. purpurella*, of which it has the short spike, brilliantly coloured flowers, similar lip, and sometimes the dwarf habit. The other parent is suggested by the somewhat taller stem, longer leaves, larger sometimes ringed spots, and shallowly 3-lobed lip, with the characteristic markings of *O. latifolia*, but much intensified in colour.

Habitat. Old pasture, Aberystwyth! amongst two or three colonies containing both parents; fairly numerous, some tall, some dwarf, some spotted. Pl. 556, *J.B.* 1920, shows the Aberystwyth form of *O. latifolia* (fig. 13), *O. purpurella* (fig. 9), and the hybrid between them, × *O. insignis* (fig. 11). Arran, Scotland (Stephenson), many stations near the shore, in fair numbers, with few, if any, dwarfs, and with large dark blotches (though sometimes faint) on the leaves. Flowers June to July.

O. latifolia × *Cœloglossum viride*, vide *C. viride*, p. 130.

O. latifolia × *O. incarnata*, vide *O. incarnata*, pp. 188, 189.

O. latifolia eborensis × *maculata*, p. 220.

11. Orchis maculata L.

Pls. 47 A (p. 197) and 50 (p. 206). *Spotted Orchid*

Tubers palmate, flattened, back to back, thick at the base with 2–4 tapering ± divergent segments; roots rather short, thick, cylindrical. **Stem** erect, sometimes slightly sinuous, cylindrical, 20–60 cm. tall, acutely ridged above (through decurrence of edges and mid-ribs of bracts), solid, non-compressible (rarely slightly hollow and compressible), glabrous, light green sometimes flushed with violet above, leafy to about the middle, with 2–3 brownish or whitish 3-nerved close-fitting leafless sheaths

[1] *J.B.* p. 33 (1922).

at base, the uppermost sometimes green-tipped and leaf-like. **Leaves** usually 6–10, erect, more or less spreading, distant, flat, slightly narrowed at base, broadest about the middle, oblong to oblong-lanceolate, up to about 16 cm. long × 3½ cm. broad, gradually decreasing in length and notably in breadth as they ascend the stem (the upper bract-like, awl-shaped, tapering to a fine point, sessile, 3-nerved, minutely denticulate, often spotted with purple at the edges); all acute or obtuse (sometimes with a little point or mucro), with large transversely oval or oblong sometimes confluent brown-purple spots, becoming smaller on the upper leaves (rarely all leaves unspotted), rather dark green or grey-green above, greyish or whitish green and somewhat glossy beneath. Lowest leaf (except in *elodes*) usually short, broad, rounded at apex. **Spike** conical or ovoid, later cylindrical, obtuse, dense, many-flowered. **Flowers** of medium size, pale lilac or rose with red-violet markings, sometimes so bright as to make the flower look dark-coloured, sometimes very faint, or even absent in pure albinos, sometimes very faintly scented. **Bracts** linear-lanceolate, gradually tapering to a fine point, green, sometimes tinged with violet, usually not conspicuous, the lowest sometimes exceeding the flowers, the upper generally shorter than, rarely exceeding, the buds, keeled, 1–3-nerved with faint cross-veins, edges minutely denticulate and spotted with purple, densely dotted beneath with minute whitish papillæ, and slightly so above. **Ovary** stalkless, cylindrical, twisted, often flushed with violet, with six rather acute longitudinal ridges. **Sepals** narrow, lanceolate, obliquely enlarged towards base, obtuse or acute, 1–3-nerved, pale lilac or rose, the lateral spotted, erect or spreading, the upper unspotted, connivent with petals to form a hood, or erect, concave. **Petals** with tips crossed (rarely erect and spreading), ovate-lanceolate to linear-lanceolate, more or less obtuse, shorter than sepals, 1- or faintly 3-nerved, unspotted, often edged with violet. **Seeds**: cells of testa most delicately spirally reticulate (Rchb. *Icones*, XIII, 66). Apex of testa curved and pointed. "Coils" (nearly straight transverse lines or wrinkles) "loose" (Dymes, *Seeds of the Marsh Orchids*, Linn. Society, June 21st, 1923) (Pl. D, fig. 3 (p. 94)).

From a slide prepared by Mr Dymes it appeared that some seeds were long and narrow, but others were shorter and broader. They were not always curved or pointed at the apex.

Sub-sp. *elodes*. Embryo about 30 per cent. larger than in the type, coils loose, less developed (Dymes, *loc. cit.*). Testa shorter and broader, cell-walls thin, embryo broadly oval, nearly as broad as testa in specimens on slide.

Var. *O'Kellyi*. Testa long, narrow, almost straight, coils close and pronounced (Dymes, *loc. cit.*). Slide showed some seeds with shorter and moderately broad testa, "coils" very marked and close together, and embryo nearly as broad as testa. These microscopic differences are of doubtful value for distinguishing between varieties.

Lip extremely variable, 3-lobed, with rounded shoulders (more rarely wedge-shaped at the base), flat or nearly so, pale lilac-rose, whitish or pure white, with darker usually symmetrical red-violet lines, loops, or spots, faint or absent in the case of albinos. Lip divided to about the middle with mid-lobe (often considerably) longer than side-lobes; or with three nearly equal lobes (*trilobata*); or only shallowly lobed at the apex, with mid-lobe usually considerably narrower and often shorter than side-lobes (*elodes*, Pl. 51). Side-lobes rounded, or oblong and divergent, with more or less parallel sides, rounded or obliquely truncate at apex, entire, irregularly toothed, or crenate. Mid-lobe longer than, equal to, or slightly shorter than side-lobes, tongue-shaped with rounded tip; or triangular and more or less acute; or like a broad dagger-blade; or small and tooth-like (*elodes*). **Spur** nearly as long as ovary, but variable (4–10 mm.), neither stout nor slender, slightly conico-cylindrical, enlarging gently towards the moderately wide mouth (slender with narrower mouth in *elodes*), straight or very slightly curved, directed downwards, usually pale violet. Throat of flower appearing cordate through downward projection of rostellum. **Stigma** on its roof, bordered by a violet line. **Rostellum** pouch-like, whitish, viscid discs colourless. **Anther** erect, pear-shaped, purplish. **Pollinia** dark green; caudicles yellow, transparent. In albinos pollinia are yellow. Each tuber divides into two fangs, either or both of which may again divide, so that there are 3–4 segments. The stem may be tall and robust in lowland woods, or dwarf and stunted in high and exposed positions. It is usually solid and not compressible, but in wet situations has been found with a very slender central tube. The leaves vary from broadly oblong to lanceolate, or linear-lanceolate, long and narrow (*elodes*), and may be strongly or faintly spotted, or quite unspotted. The spots may be large and transversely elliptical, or small and round, or reduced to tiny dots. The lower leaf is usually elliptical, short and broad compared with the others, or it may be much the same type as they (*elodes*). The bracts are usually almost hidden by the flowers, but sometimes exceed them, and form a tuft at the tip of the young spike. The ground-colour of the flowers is usually pale, but sometimes the markings are so strong as to give the spike a bright conspicuous colour. This was especially noticeable near the Argentière glacier above Chamonix, where *O. maculata* had flowers as dark and brilliant as the local *O. latifolia*, and very probably owed this to a strain of *O. latifolia* in its constitution (Pl. 50, figs. 5, 6 and 14) (p. 206).

In Britain there are four easily recognised forms of *O. maculata*, though the limits between them are not always very sharply defined.

(1) The tall (up to 60 cm.) woodland form of clayey and loamy soils with broad oblong heavily spotted leaves (the lowest short, broad and rounded at apex), conical spike, and deeply 3-lobed lip, the mid-lobe often considerably longer than the side ones.

(2) Sub-sp. **elodes** Grisebach (as species). Leaves linear to lanceolate (no short

broad lowest leaf). Lip broad, only shallowly lobed, side-lobes broad, mid-lobe small, tooth-like, usually shorter, spur slender. Plant of marshes, peat bogs and damp pastures, on acid soils.

(3) Var. **trilobata** Brébisson.[1] Medium height (20–35 cm.), leaves narrow, lanceolate or oblong, with or without short rounded lowest leaf. Spike short, ovoid or cylindrical, slender, with smaller flowers, lip with three deep nearly equal lobes, sometimes the mid-lobe longer; spur cylindrical, only slightly enlarged at base, somewhat (rarely considerably) shorter than ovary. Plant of open chalk downs and dry calcareous hillsides.

(4) Var. **O'Kellyi** (*Orchis O'Kellyi* Dr.). A form with lanceolate unspotted leaves, oblong obtuse spike and small almond-scented pure white flowers. Lip not very deeply 3-lobed, lobes sub-equal, or the mid-lobe slightly longer. Chalk downs and limestone hills. Perhaps an albino form of (3), as it occurs singly amongst hundreds of the latter in some stations,[2] but in Co. Clare, Antrim, Tyrone, etc., it is locally common in colonies. Inchnadamph, W. Sutherland, York, Durham, Winchester, Beds., Bucks., Oxford, etc.

Pl. 50. The enlarged flowers, Nos. 1–20, of *Orchis maculata* L. were all from districts where *elodes* was entirely absent. Nos. 1, 2, 6, 10, 12 and 16 would perhaps be identified as *elodes* by some botanists, but were isolated variants of what is sometimes known as *O. Fuchsii* Dr. Nos. 5, 6, 13 and 14 were from alpine stations where *O. latifolia* was abundant, and probably owe their striking colour to a strain of that species. No. 19 is *O. latifolia* × *O. maculata*. Nos. 21–25 *a* are chalk-down forms from Winchester. No. 24 is remarkable for the shortness of the spur.

Habitat. Woods, copses, pastures, field-borders, banks and marshes, but usually not in very wet ground. Colonies have been seen in *Sphagnum* (*J.B.* p. 124 (1921)), but this is unusual. I have several times observed in Surrey and Hants. that it is almost absent from marshes where *O. incarnata* and *O. latifolia* abounded, but frequent on adjoining drier ground. Prefers basic clayey soils and is usually a lowland plant. Recorded as ascending to 2800 ft. in Co. Kerry, Ireland (*Cyb. Hibern.* p. 345), but this includes *elodes*, which Scully says (*Fl. Co. Kerry*, p. 279) is as common as the type. In Arran confined to the lower levels, though *elodes* extends to highland bogs. At Kerry, Montgomery, N. Wales, both types occur on a rich loamy clay, with no peat.

Distribution. Throughout Great Britain and Ireland; our commonest orchid.

Sub-sp. *elodes*. Extends northwards from the southern counties, where it occurs chiefly on heaths, moors and peat bogs, to Wales, Northern England and Scotland,

[1] Brébisson's description was "var. b. épi grêle, fleurs petites, labelle à 3 lobes profonds presque égaux".

[2] "var. *trilobata* Bréb. has a slender spike of small flowers, the lip divisions nearly equal and is very close to *O'Kellyi*, but it has spotted leaves and tinted flowers" (Dr Druce in *B.E.C.* p. 167 (1917)).

PLATE 50

Orchis maculata L.

Enlarged flowers showing variation in the shape of the lip. The subspecies *elodes* was never seen by us in the district in the case of Nos. 1–20.

1–3. St Gervais-les-Bains, June, 1924.

4–9. Col de Balme, Switzerland, July, 1924.

10–16. Argentière, Switzerland, July, 1924.

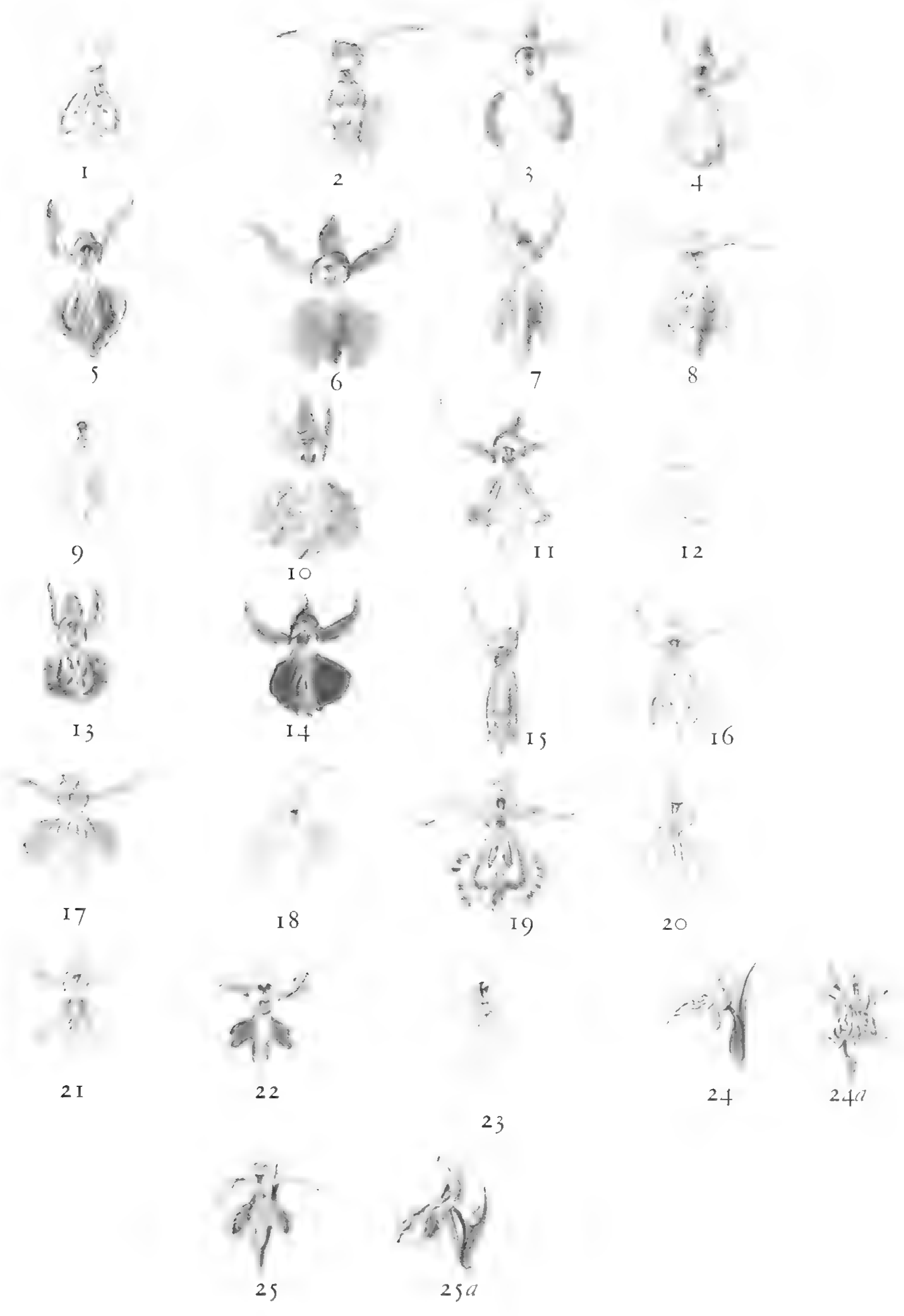
17. Sils Maria, Engadine, August 1st, 1924.

18–19. Gryon, Switzerland, June, 1925. No. 19 is the hybrid *Orchis latifolia* × *maculata*.

20. Aix-les-Bains, France, May, 1926.

21. S. Wales.

22–25 *a* (life-size). Chalk downs, Winchester.



H. M. Godfery pinx.

ORCHIS MACULATA L.

Lip-forms

19. *Orchis latifolia* × *maculata* (× *O. Braunii* Hal.)

in the north of which it is the predominant form. In Ireland as common as the type. *Vide* also p. 213.

Almost all Europe including Iceland, Northern Asia from Siberia to Kamtschatka, Asia Minor, Persia, N. Africa.

Orchis maculata L., *Sp. pl.* ed. 1, p. 942 (1753). O. Fuchsii Dr., *B.E.C.* p. 105 (1914) (in part). Sub-species elodes Grisebach (as species), *Göttingen Studien*, 1845. O. maculata præcox Webster, 1886. O. maculata sub-sp. ericetorum Linton, 1900.

Dr Druce restricts *O. maculata* L. entirely to the sub-sp. *elodes*. Linnæus' diagnosis in the *Sp. pl.* p. 942 (1753) is "labio plano petalis dorsalibus erectis" and further "Petala 3 exteriora erecta". In *elodes* the side-sepals are horizontal or drooping, not erect, but they are erect as a rule in *O. Fuchsii* Dr. (cf. *J.B.* p. 306 (1923)).

In his *Olandska Resa*, p. 48, Linnæus stated that on June 2nd, 1741, in a marsh at Rella in the island of Œland he found an *Orchis* "commonly called *O. palmata maculata*". In his *Fl. suecica*, ed. 2, after his diagnosis of *Orchis maculata* he quotes *It. œl.* p. 48, and *Sp. pl.* p. 942, definitely placing the Rella plant under this species. On June 19th, 1922, Mr W. N. Edwards of the British Museum (Nat. Hist.) visited the marsh at Rella and brought home a series of *O. maculata*, which was passed by Dr Druce as his *Orchis Fuchsii*. Thus Linnæus did not restrict his type to *elodes*.

Fertilisation. As in other species of *Orchis*, *vide* "Pollination and Fertilisation". H. Müller (*Fert. of Flowers*, Engl. transl. p. 539) witnessed the visits of *Bombus pratorum* (once only), *Psithyrus Barbutellus* (frequently), and *P. globosus*, also of *Volucella bombylans* L. (*Syrphidæ*) and *Eristalis horticola* Mgn.; Darwin (*Fert. Orch.* ed. 2, p. 16) and his son saw it frequently visited by a fly, *Empis livida*.[1] Six of these had the pollinia attached to their spherical eyes on a level with the base of the antennæ, in the most favourable position to come in contact with the stigma. A specimen of *Empis pennipes* had five pollinia attached to the thorax.

I saw it visited by *Bombus muscorum* and *B. hortorum* near Badbury Rings on May 30th, 1918, and by *Volucella bombylans* var. *plumata* on Mont Pèlerin, above Vevey; also by the orange-brown *Bombus agrorum* at Challes-les-Eaux, in this last case witnessing at close quarters the actual withdrawal of a pair of pollinia, which was most neatly done. Darwin detected minute brown specks where punctures had been made in the inner lining of the spur by an *Empis* (*Ann. Nat. Hist.* p. 143 (1869)).

On June 25th, 1929, I took a hive-bee on *Orchis maculata* above Montreux, Switzerland, bearing eight pollinia of that species on its head. I also took on *Gymnadenia albida* at Trient, Switzerland, a specimen of *Halictus calceatus* ♀ with a single pollinium of *O. maculata* on July 11th, 1929. On May 4th, 1930, I took *Halictus tumulorum* L. ♀

[1] Probably this refers to the sub-sp. *elodes*, often visited by *Empidæ*, and not distinguished from the type in Britain till 1886.

and *H. morio* F. ♀ on cut spikes of *O. maculata* in a garden at the Château de Sus, Sus, Basses Pyrénées, both with pollinia.

Halictus leucozonius Schr. ♀ was taken by me in a Surrey garden on *O. maculata.* On a cold May evening at Sus, Basses Pyrénées, in 1930, I saw a dark object hidden in a spike of white *O. maculata.* It had five pollinia of *Orchis morio* on its head, and turned out to be *Andrena curvungula* Thoms, evidently sheltering there for the night. I also saw *Bombus agrorum* var. *pascuorum* visit two or three flowers at Sus, bearing pollinia.

11A. ORCHIS MACULATA L. sub-sp. ELODES

Pl. 51. *Early Spotted Orchid, Spotted Heath Orchid*

Tubers with 2–4 ovoid divergent sometimes long-tailed segments. **Stem** usually 20–40 cm., sometimes attaining 1 m. (Stephenson),[1] in Webster's *præcox* 10–20 cm., solid or slightly compressible above through spongy central tissue, pale green sometimes purplish above, with 2–3 membranous sheaths at base. **Leaves** linear to linear-lanceolate, sometimes oblong, 10–20 cm. long by 1–2·5 cm. broad, tapering gradually, moderately acute, yellow or grey-green, paler below, strongly keeled, usually somewhat folded lengthwise and with rather faint often quite small spots, sometimes unspotted, the lowest not short and rounded at tip but resembling the others, the upper bract-like, acuminate. **Spike** 4–6 cm. (rarely 10 cm.), conical, later cylindrical, dense. **Flowers** fewer and larger than in the type, but sometimes closely packed and smaller, slightly scented, white or pale mauve with faint or bright violet markings. **Bracts** linear-lanceolate, fine pointed, 3–5-nerved, green or purplish, as long as the flowers, but finally almost hidden by them. **Ovary** 10–15 mm., cylindrical. **Sepals** spreading horizontally, narrow, lanceolate, 1-nerved, 8–10 mm. by ± 2 mm., sometimes slightly twisted, edges reflexed, the upper connivent with petals. **Petals** slightly shorter, 1- or obscurely 3-nerved, white or pale mauve edged violet. **Lip** flat, variable, broad and transversely oval, in some localities rather wedge-shaped at the base widening towards the apex, and then more or less obovate, shallowly lobed at the apex; side-lobes rounded out, slightly crenate or toothed, obtuse or somewhat pointed; mid-lobe usually small, tooth-like, and shorter than the side-lobes, but sometimes nearly as broad as their apex (measured at the same distance from the tip), and rarely longer than they. Colour white to pale mauve or moderately bright purple (*J.B.* Pl. 556, fig. 19), with variable pale or bright violet markings—small spots sometimes scattered over the whole lip, fine often interrupted lines, more rarely symmetrical double or single loops. **Spur** slender, usually shorter than ovary, sometimes slightly curved, but little enlarged at the mouth, only about 1 mm. in diameter. **Stigma** on roof of mouth of spur, edged with a violet line. **Rostellum** white, pouch-like,

[1] *J.B.* pp. 123–5 (1921).

PLATE 51

Orchis maculata sub-sp. **elodes** (**O. ericetorum Linton**).
Spotted Heath Orchid.

1, 2. Enlarged flowers. Surrey, June 10th, 1919.

3. Enlarged flower. Capel Curig, N. Wales, July 29th, 1919.

H. M. Godfery pinx.

ORCHIS MACULATA L. sub-sp. ELODES (Godfery)
Spotted Heath Orchid

projecting slightly downwards. Stigmatic fold white, grooved, equal to caudicles. **Anther-cells** red-purple, pollinia olive-green, caudicles yellow, transparent. **Seeds**: *vide O. maculata*. I saw two or three specimens with pure white flowers in the New Forest.[1]

Var. **macroglossa** Dr.[2] A large-flowered form with dark lilac markings, side-lobes much longer than the mid-lobe. Llandrindod, Harlech, etc. I have not seen this.

The distinguishing features of the sub-sp. *elodes* are:

(1) Leaves rather long, narrow, tapering, more or less folded and recurved.

(2) Lowest leaf similar to those just above it, not short, broad and rounded at the tip as in the type.

(3) Flowers usually larger.

(4) Sepals narrower, spreading horizontally, not erect, often slightly twisted.

(5) Lip broad, shallowly lobed at the apex, side-lobes usually rounded out, mid-lobe small, tooth-like, often shorter than side-lobes.

(6) Spur very slender, cylindrical, not wide-mouthed as in the type.

There are, however, exceptions to the above. The leaves are sometimes oblong and then up to 3 cm. broad. The flowers sometimes in a dense spike and then smaller, the lip sometimes obovate, wedge-shaped at base, widening downwards, and then not so broad (Text-fig. 11, Nos. 12, 13). The mid-lobe may be as long and nearly as broad as the side-lobe (Text-fig. 11, Nos. 3, 9, 18) or even longer (Text-fig. 11, Nos. 4, 10, 19, 25). One must be prepared to find one or two points of difference, though most of the characters agree. In the Basses Pyrénées its stout erect habit, short rather broad acute finely spotted *latifolia*-like leaves (the lowest rather short but acute), dense pyramidal spike, pale violet-rose flowers with broadly elliptical lip and curved broken lines of minute irregular spots, gave it a very distinctive appearance.

A plant from wet ground, Tregaron bog, N. Wales, had horizontal tubers with ovoid segments with long tapering tails (4–13 cm.). The stem rarely has a narrow central tube. Leaf-spotting does not appear to be due to melanism, as plants with dark-coloured flowers sometimes have unspotted leaves, and heavily spotted leaves occur with pale-coloured flowers. Leaves may be obtuse or rather acute, usually recurved, spots small, or large, *very* rarely ringed and then possibly due to a strain of *O. latifolia* in the plant. Flowers usually light-coloured. Bracts on large spikes sometimes as broad and long as in the marsh orchids. Sepals sometimes gently sloping upwards. The sides of the lip sometimes slope gently downwards, and the obtusely pointed tips of the side-lobes sometimes point inwards like callipers, rarely these lobes are almost frilled. Mid-lobe very variable, usually tooth-like and shorter than side-lobes, sometimes approaching them in width, and as long or even longer than they. Pale colours predominate, darker flowers are the exception. Lip varies in size, and has been found from 16 mm. broad by 10 mm. long to 4 mm. broad

[1] Sub. var. *leucantha* Dr. *B.E.C.* p. 167 (1917).

[2] *B.E.C.* p. 579 (1919).

by 5 mm. long.[1] The spur is sometimes described as filiform, but though slender, it is hardly thread-like, though of nearly the same diameter throughout.

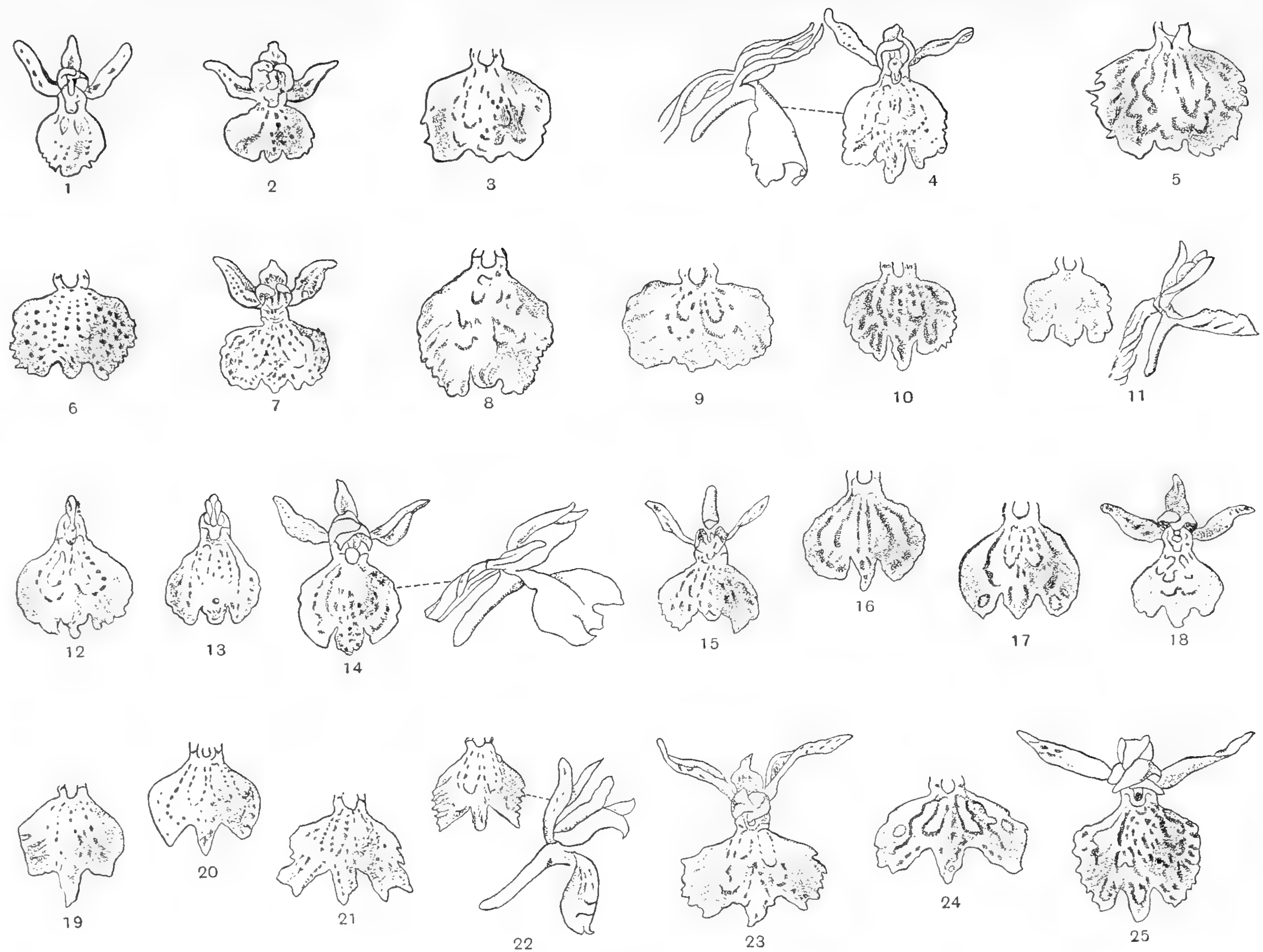
PROLIFERATION. A spike (1 inch long) from Dorset (Sir M. Abbot Anderson) had double flowers. One flower had nine sepals and petals and ten lips, all more or less 3-lobed, flushed pale mauve with yellowish centres and a few faint mauve spots, the lowest with a slender spur, and the three next with a rudimentary one, all arranged spirally round the lengthened axis, which ended in two whitish concave scales enclosing a terminal scale (or point in some flowers).

Text-fig. 11, by the late Prof. Lindman,[2] shows the great variation in the shape of the lip in *Orchis maculata* L. in Sweden. He does not recognise any named varieties, but says that they pass into each other without definite lines of demarcation. Nos. 1, 2, 7, 14 and 18 belong to what is regarded by European botanists generally as the type of the species, being the most widely distributed and best known form. They have the rather broader and more erect sepals of this type (*petala 3 exteriora erecta* of Linnæus' diagnosis in the *Sp. pl.*), but the lip in Nos. 2, 7 and 14 is rather broader than usual and a slight strain of *elodes* is possible. No. 1 is comparable with Nos. 4, 5, 13 and 14 of Pl. 50 (which does not include *elodes*), the lip being practically undivided, No. 2 with No. 2 (except that the latter has sepals nearer to *elodes*, though that sub-species was absent), No. 7 with No. 12, whilst No. 18 finds its counterpart in No. 8. Nos. 3, 5, 6, 9 and 15 are forms of *elodes*, and probably Nos. 12 and 13, though they somewhat resemble No. 16 of Pl. 50. The late Dr Druce told me that he spent five weeks in Norway and only saw *ericetorum* (*elodes*) there. No. 4 looks like a cross between the two forms, and is near No. 20 (Pl. 50), whilst No. 20 is not far from No. 9, and No. 24 from No. 17. Nos. 19–25 (Text-fig. 11) all appear to be hybrids within the species, and the heavy markings of Nos. 5, 10, 16, 17 and 25 also suggest the same origin (cf. Pl. G, fig. 5). The narrower, often twisted sepals of *elodes* are usually more horizontal than in Nos. 4, 15, 23 and 25, but Nos. 2, 3, 8, 9, 11, 17 and 25 of Pl. 50 show that they also occur in isolated specimens amongst the type.

Ninety-two years passed before any botanist seems to have suspected that *O. maculata* L. comprised two forms of possibly specific value, when the existence of this interesting plant was first brought to notice by A. Grisebach in *Ueber die Bildung des Torfs in den Emsmooren*, p. 25 (1846) (reprinted from *Göttingen Studien* (1845)). His original description is translated below.

Orchis elodes new sp. Tubers twin, palmatifid, leaves (4–5) lanceolate acuminate, decreasing upwards, bracts nerved, exceeding the ovary, flowers flesh-coloured, painted (i.e. adorned with markings), segments of perianth semi-lanceolate, the exterior spreading, lip tri-lobed, spur descending, filiform, acuminate, half as long as

[1] *J.B.* pp. 123–5 (1921).
[2] Lindman, *Bihang till K. Svenska vet.-akad. Handlingar*, Band XXIII, Afd. 3, No. 1, Stockholm, 1897.



Text-fig. 11. *Orchis maculata* L. Lip-variations.

By permission of the Royal Academy of Science, Stockholm. (From *Bihang* 23, III, No. 1.)

ovary. Spur $\frac{1}{2}'''$ in diameter at the base, very slender, tapering towards the rather obtuse apex, straight, pendent. External divisions of perianth similar to the interior, and of the same length. Labellum as long as broad, the mid-lobe a little shorter than the outer ones. Stature the span-length of *O. latifolia*. Distinguished from *O. maculata* L., with which it agrees in the tapering spur, solid stem, and uppermost leaves decreasing and rather distant from the spike: (1) lower leaves lanceolate (not oblong), all spreading; (2) number of leaves more than twice as small; (3) bracts all exceeding the ovary and not the median almost equalling the ovary; (4) segments of perianth narrower; (5) spur much more slender, filiform, narrower than half a line in the middle; (6) but especially in the shortness of the spur, half as long as ovary (and not exceeding it). Habitat. Turfy heaths, sparsely, throughout the whole Bourtangensian swamp. Flowers May and June (much earlier than *O. maculata*).[1]

A. D. Webster[2] was the first British botanist to distinguish *elodes* from *O. maculata* L. He found it in cold exposed marshy ground at 700 ft. elevation in the Snowdon range of mountains, where it was a dwarf and stunted plant, and showed living specimens before the Botanical Society of Edinburgh, June 10th, 1886, where it was promptly turned down as a mere variety of *O. maculata*. Whilst strongly of opinion that it was a distinct species, he published it as *O. maculata* var. *præcox* in deference to this decision. He transferred six plants from a mountain meadow to his garden, where, under the most favourable circumstances of soil and situation, they failed to attain any larger size. He found its average height at 700 ft. did not exceed 6 inches, that of *O. maculata* on the same estate being 18 inches. Webster's *præcox* agreed well with Grisebach's *elodes*, except that the spur of the latter was only half as long as the ovary, whilst that of *præcox* is nearly as long as the ovary. As, however, the spur of *elodes* varies in Britain from 4 to 10 mm.[3] this discrepancy is of no importance.

In 1900 E. F. Linton, in his *Fl. Bournemouth*, described under the name of *O. ericetorum* a new sub-species of *O. maculata*. He evidently did not know that a form of his plant had already been named *O. præcox* by Webster. The latter's publication appears to have been overlooked, for various authors have adopted the later name of *ericetorum*. There was for a time doubt as to whether the two were identical, but it is now generally admitted that this is the case, in spite of the tall and luxuriant habit of the south of England plants. I sent Mr Webster specimens of *ericetorum* from Snowdon, which he said were like his *præcox*, but could not be the latter, on account of their larger size. To him it was a dwarf mountain plant, braving the roughest weather at from 500 to 1000 ft. elevation, and he did not realise that its stunted growth was due to unfavourable conditions.

It has been shown[1] that *O. maculata præcox* and *O. ericetorum* are identical with

[1] *J.B.* p. 306 (1921), in which the original Latin diagnosis is given.
[2] *Brit. Orch.* ed. 1, pp. 54–6 (1886).
[3] Stephenson, *J.B.* p. 123 (1921).

O. elodes Grisebach, whose unusually exhaustive diagnosis agrees with Webster's and Linton's descriptions, whilst the habitat and early period of flowering also coincide.

The question as to whether *elodes* is a distinct species was discussed by me, with a leaning towards specific rank, mainly on the ground that in Britain they occupy different areas, and usually grow on different soils.[1] I am now inclined to take the more usual view that it is a sub-species of *O. maculata*, from which it is separated by differences which are small in comparison with those between *O. maculata* and other species of *Orchis*. The immense variability of the lip in both *O. maculata* and *elodes* shows how little reliance can be placed on its shape and lobing as a ground for establishing a separate species, as may be seen from Pl. 50 and Text-fig. 11. That both sprang from a common ancestor there can be no doubt, an ancestor that probably occurred throughout Britain. Possibly the cumulative effect of long periods of growth on heavy basic soils, acid peat and heaths, and chalk downs respectively, has differentiated it into the tall woodland form with long mid-lobe to the lip, the broad-lipped shallow-lobed *elodes*, and the equal-lobed type of the chalk downs. If these are not yet distinct species, they are probably races or sub-species in process of evolution into species. Ascherson and Graebner state that *elodes* is very difficult to cultivate, easily dying off, and resenting any change of environment, but nevertheless shows great constancy under cultivation.[2]

Habitat. Marshes, damp pastures, moors, and wet ground, usually on peaty and acid soils, but not rigidly confined to them. Both the type and *elodes* occur in a field at Kerry, Montgomery, in a rich loamy clay with no peat. Rarely colonies exist in pure bog, in *Sphagnum*, though the zone between wet and dry levels is usually preferred.[3] Upland moors on coal measures (Riddelsdell). On limestone, W. Sutherland (Marshall, *B.E.C.* p. 398 (1908)). Great Scar Limestone at Cam Houses, 1580 ft. (J. Cryer, *B.E.C.* p. 127 (1911)). Menmarsh, Oxon., on Oxford Clay (Druce). Absent from large parts of the central and eastern counties.[3] "Only form of *maculata* we found in the Highlands" (Marshall and Shoolbred). In Sweden[4] it grows in hay-fields mown yearly in July, and very few plants escape the scythe, or produce more than one tuber. Dr Stephenson found *elodes* in the Charente[5] district of France, in a few patches on sandy peat, and "countless thousands of the slender form familiar on English heaths" above Covadonga in Asturias, Spain, north of the Pyrenees, "where both flora and climate are very much like those of England".[6] He also found it to the south of Limoges, and in large numbers in the valley of the Tarn, in the Cevennes, and in returning northward towards Puy and Limoges. In a circuit of about 1200 kil. along the sides of a triangle having Limoges as its apex and the valley of the Tarn as its base, *elodes* occurred in countless numbers but only one group of

[1] *J.B.* p. 306 (1921).
[2] A. and G. *Syn.* III, 748.
[3] *J.B.* pp. 123–5 (1921).
[4] Lindman, *loc. cit.* (*vide* p. 210).
[5] *J.B.* p. 97 (1925).
[6] *Ibid.* p. 72 (1927).

O. maculata was seen.[1] In late May, 1930, I found it on heathland covered with *Ulex Galii* at Sus, Basses Pyrénées, France, where it was scarce, and so different in appearance that at first I thought it was something new. Formerly supposed to be a northern plant, its occurrence so far south seems to show that the peaty or sandy soil of heaths is the chief essential for its presence.[2]

FERTILISATION. I took a specimen of *Bombus terrestris* L. ♂ on a Dutch specimen of *elodes* in Mr St Quintin's greenhouse at Scampston Hall, Malton, Yorks., in June, 1930, and saw it visited once by *Bombus agrorum* at Sus, and several times by *Empis tesselata* ♂, ♀ (Diptera: Empidæ), each fly with one or more pollinia on its head in the New Forest, June 13th, 1931.

ORCHIS MACULATA × sub-sp. ELODES

Pl. G, fig. 5 (p. 191). ×O. transiens Dr.

Fig. 5 has flowers like a heavily marked *O. maculata* with the long very slender spur of *elodes*. Side-sepals spreading; side-lobes of lip broad, crenate, mid-lobe long, projecting. Aberystwyth, June, 1928 (T. Stephenson). A similar specimen from a neighbouring locality had much fainter markings.

Dr Druce saw many intermediates, some with leaves of *O. maculata*, but flowers of nearly typical *elodes*, growing together on Oxford Clay at Menmarsh, Oxon.

A plant found by me in Teesdale, July, 1930, had nearly white flowers with bright violet loops and spots on the wedge-shaped lip, with broad truncate side-lobes, and shorter mid-lobe, narrow sepals and straight cylindrical spur as in *elodes*, but not so slender. The transverse oval leaf-spots were like those of *O. maculata*.

ORCHIS MACULATA × PRÆTERMISSA

Pl. 49 A (p. 202); Pl. G, fig. 2 (p. 191). ×O. Mortonii Dr.

(1) **Stem** 40 cm., hollow. **Leaves** narrower and more acute than in *prætermissa*, faintly spotted, the largest leaf 21 cm. × 2·5 cm., unspotted. **Spike** short, ovate, comose. **Flowers** very little larger than in *maculata*, pale mauve with bright red-violet lines of dots and dashes on the lip. **Lip** shaped as in *prætermissa*, whitish in the centre, shallowly 3-lobed, mid-lobe triangular, side-lobes rounded, edges turned up. **Spur** straight, nearly cylindrical, thicker than in *maculata*. **Bracts** very narrow, twice as long as flowers, upper longer than buds. It has the facies of *maculata*, but with larger flowers of the shape and colour of *prætermissa*.

Found near Godalming, July 1st, 1918!

1 *Bull. Soc. Bot. de France*, p. 484 (1928).

2 The occurrence of *O. elodes* Gr. on limestone in the two localities given is very remarkable, as it appears as a rule to shun calcareous ground.

H. M. Godfery pinx.

A. ORCHIS INCARNATA × MACULATA (ELODES)
× *Orchis carnea* Camus

B. ORCHIS MACULATA × PURPURELLA
× *Orchis venusta* Steph. p. and f.

PLATE 52

A. **Orchis incarnata** × **maculata** sub-sp. **elodes.**

1. Enlarged flower. Yorks., June 15th, 1915.
2. Single flower ovary and bract (life-size).

B. **Orchis maculata** × **purpurella.**

× **Orchis venusta** Steph. p. and f. South Wales, July, 1926.

(2) **Stem** 38 cm., very hollow. **Leaves** as in *O. maculata*, linear-lanceolate, tapering, acute, grey-green, plentifully spotted. **Bracts** (lower) much exceeding flowers, nearly 4 cm. long. **Spike** dense, 9 cm. long. **Flowers** larger than in *O. maculata*, mauve, exactly the colour of the prevailing shade of *O. prætermissa* in that locality. **Lip** clearly 3-lobed, side-lobes broad, rounded, somewhat rhomboidal, slightly crenate, mid-lobe not quite half as broad as side-lobes and slightly longer, tongue-shaped. **Spur** conico-cylindrical, almost equal to ovary, like that of *O. prætermissa* but more slender. Lip-markings a double loop on each side with a few scattered spots, red-violet. Facies of *O. maculata*, for which it was taken till it was noticed how very hollow the stem was. Eashing! Surrey, June 26th, 1917. Enlarged flower, Pl. 49 A, fig. 3.

(3) **Stem** 22 cm., solid at base except for a pinhole, hollow above. **Leaves** dark greyish green, oblong, 14–20 mm. wide, scarcely narrowing towards the base, gradually tapering towards the tip, with many small circular spots. **Spike** conical, becoming cylindrical. **Flowers** larger than in *maculata*, of the delicate pale mauve often seen in *prætermissa*. **Bracts** lanceolate, acuminate, green tinged purple. **Sepals** lanceolate, reflexed, spotted. **Lip** broader than long, paler in the middle, side-lobes rounded, mid-lobe half their breadth, slightly longer, tongue-shaped, obtuse, markings two loops made up of dotted lines. **Spur** rather long, nearly equal to ovary, cylindrical, widening at the throat, stouter than in *O. maculata*. Facies of *O. maculata*, but the large pale lilac flowers with their broad nearly flat shallowly 3-lobed lip and dotted pattern at once suggest the parentage of *prætermissa*, to which the plant is nearer than any other hybrid I have seen. Found near Winchester. The spike was given to me by the Rev. S. A. McDowell, of Winchester College, June 22nd, 1917 (Pl. 49 A).

(4) This hybrid occurs in considerable numbers in a station near Belfast where both the parents are plentiful, but *O. incarnata* is absent. All the hybrids have spotted leaves, but *none* have ringed spots.

(5) The beautiful marsh orchid (*O. latifolia*) with (often) ring-spotted leaves frequent near Winchester is considered by Dr Druce to be *O. maculata* × *O. prætermissa*. This is discussed under *O. latifolia*. The preceding paragraph shows that in a station where the latter hybrid occurs in some abundance, no ring-spotted plants have been found.

For *O. maculata superba* Syme (*Eng. Bot.* IX, 101), vide *Orchis latifolia*.

ORCHIS MACULATA × PURPURELLA

Pl. 52 B. ×**Orchis venusta** Steph. p. and f.[1]

Although *O. maculata* grows in some numbers in a wood near *O. purpurella* at Aberystwyth, no hybrid between them was found by Dr Stephenson during his two or three years' stay there, although hybrids with *elodes* occurred. A fine example of *O. macu-*

[1] *J.B.* p. 34 (1922).

lata × *O. purpurella* was received by him from Ambleside, and it frequently occurred in Arran. There is the same fine colour as in the case of ×*O. insignis* (*O. latifolia* × *purpurella*), but the side-lobes of the lip are nearly always narrower, and the mid-lobe is large and deeply divided from the side-lobes. The leaves are heavily or faintly blotched, and the lip-pattern is of more or less broken lines. Only one of the specimens found had the dwarf habit and small spots of *O. purpurella*, the flowers, however, being intermediate. A fine specimen was found at Llandovery in 1926, and cultivated by Mr St Quintin, at Scampston Hall, the spike of July, 1928, being figured in Pl. 52.

Several handsome specimens were seen by me in Teesdale in July, 1930, with the taller stem, conical spike and oval leaf-spots of *O. maculata*, but flowers shaped, coloured and marked as in *O. purpurella*, though paler.

ORCHIS MACULATA sub-sp. ELODES × PURPURELLA

Pl. 53 C. ×**Orchis formosa** Steph. p. and f.[1]

Resembles the preceding. Leaves rather darker, greyish green. Spike small. Flower distinctly suggestive of *O. elodes* by the long narrow spreading sepals, longer ob-cordate lip with rounded crenate side-lobes and small mid-lobe, by the disconnected lines and spots, not so brilliant as in the preceding, but reproducing the fine colour of *O. purpurella*, and by the longer almost cylindrical spur, nearly equalling the ovary, and but little enlarged at the throat.

Habitat. Old pasture, Aberystwyth! Arran (Stephenson). Only about six plants seen altogether. One specimen was seen by me in Teesdale in July, 1930, in a marsh where both parents grew.

ORCHIS MACULATA sub-sp. ELODES × PRÆTERMISSA

×**O. Hallii** Dr.

Dr Druce believes that this combination was present in plants found at Perranwell (Cornwall), Wool (Dorset), Odiham (Hants.), Charlbury (Oxon.), Cothill (Berks.), Hornstock (Northants.), etc., and usually occurred in a greater percentage than *O. maculata* × *O. prætermissa*. The lip varied from 14 mm. broad at Wool to 11 mm. at Odiham, the markings being more variable and not so well defined as in the hybrid with *O. maculata*, than which it is often a more handsome plant, owing to the broad labellum and large side-lobes. The whole flower is often suffused with a brighter colour than *O. prætermissa* (*B.E.C.* p. 157 (1917)). Hants. (*loc. cit.* p. 166).[2]

[1] *J.B.* p. 33 (1922).
[2] P. M. Hall (after whom this hybrid was named) found a good station for it in Hants. in 1932, where there was no other orchid to suggest a different parentage.

H. M. Godfery pinx.

A. ORCHIS PURPURELLA Steph. p. and f.
Dwarf Purple Orchid

B. ORCHIS PURPURELLA × LATIFOLIA
Orchis insignis Steph. p. and f.

C. ORCHIS MACULATA (ELODES) × PURPURELLA
Orchis formosa Steph. p. and f.

PLATE 53

A. **Orchis purpurella** Steph. p. and f.
A 1. Enlarged flower.

B. **Orchis purpurella × latifolia.**
B 1. Enlarged flower.

C. **Orchis maculata (elodes) × purpurella.** Enlarged flower.

All from Aberystwyth, June 29th, 1919.

ORCHIS MACULATA × PLATANTHERA BIFOLIA (?)
Orchiplatanthera Chevallieriana A. Camus

This plant is said to have looked from a distance like *Platanthera bifolia*, the spike being lax and not pyramidal. Tuber 3-lobed, leaves spotted. Comparison with parents showed that in the general shape of flower, 3-lobed lip and short spur it closely approached *O. maculata*, though the flower was rather larger and the colour greenish white, as in *P. bifolia*—not lilac and not spotted. Found by Arthur Reid, July 2nd (1897), on a large moor carpeted with both parents, 600 ft. above sea-level, near Glen Almond, Perth (*O.R.* p. 234 (1897)).[1]

No character of *P. bifolia* is given except the lax non-pyramidal spike, and the slightly larger greenish white unspotted flowers. No mention is made of the leaves, except that they were spotted (which are only two and of characteristic shape in *P. bifolia*), or of the pollinia, which in the latter have yellow oval discs attached sideways and are not enclosed in a pouch as in *Orchis*. The evidence of the parentage of *P. bifolia* is therefore inconclusive. It was not stated whether the *Orchis* parent was *O. maculata* type or the sub-species *elodes*, which latter might be expected on an elevated Scottish moor.

Cœloglossum viride × *O. maculata*, vide *Cœloglossum viride*, p. 132.
Gymnadenia conopsea × *O. maculata*, vide *G. conopsea*, p. 144.
G. conopsea × *O. maculata* sub-sp. *elodes*, vide *G. conopsea*, p. 145.
O. incarnata × *maculata*, vide *O. incarnata*, p. 190.
O. latifolia × *maculata*, vide *O. latifolia*, p. 188.

12. ORCHIS PURPURELLA Steph. p. and f.
Pl. 53. *Dwarf Purple Orchid*

Tubers palmate with 2–4 slender segments. **Stem** usually 10–20 cm. (one giant was 41 cm. tall), erect, hollow (walls as thick as diameter of central tube), fluted above. **Leaves** about 4, 2·5 cm. broad, lanceolate, often acute, rather distant, sheaths long, blade loosely embracing stem, slightly spreading, firm and rather thick, dull green above, pale and rather glossy below, with sparse small faint spots at apex, sometimes unspotted. **Spike** short (4–7 cm.), broad, ovate to cylindrical, often flat-topped, usually dense. **Bracts** narrow, lanceolate, tapering (± 2 cm. × 6 mm.), edged or flushed with purple, with numerous gland-like dots. **Ovary** cylindrical, twisted,

[1] R. A. Rolfe (*O.R.* p. 235, 1913) identified a plant found in a hayfield in Somerset as the above. Flowers white, unspotted, side-lobes of lip ample, rounded, mid-lobe elongated, spur nearly as short as in *O. maculata*, which it also approached in shape of spike. No character suggesting *Platanthera* was given, though it was stated that the plant showed an unmistakable combination of the two parents. *Orchiplatanthera somersetensis* A. Camus, *Icon. Orch. d'Europe*, p. 410 (1928).

± 10 cm. long, erect, with six often purple-spotted ridges. **Flowers** 11–15 mm. long, 7–10 mm. broad. **Sepals** ovate to lanceolate, keeled, 3-nerved, slightly hooded, the lateral erect, reflexed (rarely spreading) with irregular red-violet rings or lines. **Petals** ovate obtuse, concave, entire or minutely crenate, 1-nerved, connivent with upper sepal. **Lip** flat, transversely oval or lozenge-shaped, 7–10 mm. broad by about 7 mm. long with upturned edges at first; side-lobes rounded or with an obtuse elbow (making the lip diamond-shaped), finely crenate, mid-lobe short, tongue-shaped, separated by a short acute notch (± 2 mm.) or hardly separated at all. Surface of lip bright violet with darker often brilliant red-violet or crimson double loops, often broken up into rather heavy lines. **Spur** short, conical, wide-mouthed, obtuse, ± 3 mm., rather quadrilateral in section at the base, violet outside, whitish with dense very short erect hairs within. **Column** short (5 mm.), nearly white, forming a chamber over the spur-entrance. **Anther** hood-like, violet, with darker eyes. **Stigma** shield-shaped, glistening, edged violet. **Rostellum** oval, pouch-like, pale violet, projecting downwards. **Pollinia** pear-shaped, sage-green; caudicles transparent, pale yellow, slightly longer, viscid discs very small. **Capsule** oblong, ± 15 mm., with three prominent ridges. **Seeds** the smallest of the marsh orchids, with a pointed apex, indented on one side, close-meshed, rather dusky in colour (Pl. D, fig. 3 (6), p. 94).[1]

The plant is easily recognised by its very dark purple flowers, dwarf habit, and short spike. The "clear-cut diamond" shape of the lip in Welsh plants is due to the suppression of the notches which separate the mid-lobe from the side-lobes in the Teesdale plants.

HABITAT. It grows freely in marshy ground, and occurs sparingly on sloping banks in fields. It is found in company with *Orchis latifolia*, *maculata*, *elodes*, *Gymnadenia conopsea* and *Listera ovata*. Flowers June.

> ORCHIS PURPURELLA T. and T. A. Stephenson (*J.B.* p. 164, Pl. 566, figs. 9 and 10 (1920), and Pl. 559, figs. 9 and 10 (1921). *O.R.* p. 163 (1921)).

DISTRIBUTION. Aberystwyth, about 200 plants in one pasture, but found nowhere else in the district. In the same field were small colonies of *O. latifolia* (only known from one other station) and *prætermissa*, absent from the rest of the region. Portmadoc (Druce). Llandovery (St Quintin). Borrowdale, Watendlath (H. Goss). Durham (Druce). Ambleside (Stephenson). Arran (Stephenson). Orkneys (plentiful), Firth of Forth, Teesdale (Stephenson, in great abundance, but not plentiful in 1930, Godfery). South Tyne. Holland (Sipkes).[2]

It was several times identified as *Orchis cruenta* Müller, doubtless because it appeared to be nearer to the descriptions of that plant than to any other European

[1] *O.R.* p. 267 (1923).

[2] According to P. Vermeulen the plant considered to be *O. purpurella* in Holland is not that species, but was identified by Dr Stephenson as *O. latifolia*, *q.v.* (*Nederl. Kruidkundig Archief*, Afl. 2 (1930)).

Fig. 1. *Orchis incarnata* × *maculata*. Yorkshire, June, 1927.

Fig. 2. *Goodyera repens* R. Br. Ross-shire. The leaves are beautifully veined. July, 1927.

Fig. 4. *Orchis latifolia* var. *eborensis* Godfery. Yorkshire, June 6th, 1929. Life-size.

Fig. 3. *Orchis latifolia* var. *eborensis* × *maculata*.

Reproduced by kind permission of Mr W. H. St Quintin of Scampston Hall, Yorkshire, by whom the photographs were taken species. Dr Stephenson, who studied a sheet of *O. cruenta* from Sweden, states quite definitely that the plants are not the same, *O. cruenta* being much nearer to *O. incarnata* and having heavy spots or purple blotches on *both sides* of the leaves, very different from the sparse small spots of *O. purpurella*, which also has broader leaves, a larger flatter lip with a very different pattern, and a more slender spur.[1]

O. purpurella × *Gymnadenia conopsea*, vide *G. conopsea*, p. 147.
O. purpurella × *O. latifolia*, vide *O. latifolia*, p. 203.
O. purpurella × *O. maculata*, vide *O. maculata*, p. 215.
O. purpurella × sub-sp. *elodes*, vide *O. maculata* sub-sp. *elodes*, p. 216.

13. ORCHIS LATIFOLIA var. eborensis var. nov.
Pl. H, fig. 4. *The Mystery Orchid*

Tubers forked. **Stem** hollow, ± 12 cm. tall. **Leaves** long, very narrow (± 14 cm. × ± 10 mm.), folded, spreading, moderately acute, ± 7-nerved, bluish or yellowish green with rather faint ringed or smaller solid spots or sometimes unspotted, slightly concave at the tip. In some plants one basal leaf is broader, as seen in Pl. H, fig. 4. **Spike** short, 4–5 cm. long, 9–20-flowered. **Bracts** ± $2\frac{1}{2}$ cm. long, awl-shaped, narrow, gradually tapering, acute, dull green, edged and flushed with dull red-violet, the lowest often exceeding the flowers. **Ovary** about $1\frac{1}{2}$ cm. long, 6-ridged, ridge on flat side adpressed to stem, little developed, making section of ovary pentagonal. **Flowers** small, dull red-violet with red-violet darker markings, resembling those of *O. incarnata* in shape and size. **Sepals** ± 7 × 3 mm., obliquely lanceolate, obtuse, 1–3-nerved, dull red-violet with numerous faint spots, spreading or erect back to back, the upper connivent with petals. **Petals** similar, ± 5 × 2–3 mm., lanceolate obtuse, slightly hooded, 1-nerved, dull red-violet, connivent. **Lip** about 6–7 by 6–8 mm. with reflexed sides, shallowly 3-lobed, side-lobes narrow, rounded, mid-lobe rounded, sub-equal, or triangular, slightly longer and sub-acute as in the above plate. **Spur** conico-cylindrical, varying on the same spike from 6 to 9 mm. in length.

LEADING FEATURES. Dwarf habit (the photograph is life size), very narrow usually spotted leaves, short few-flowered spike, coloured bracts, small dull red-violet flowers with reflexed side-lobes and small often produced mid-lobe, and stout conical spur. Also its early flowering before any other orchid in the valley except *O. mascula*.

HABITAT. A rough pasture in an upland Yorkshire valley in a peaty patch of boggy ground only about 12 yards square, with a few outlying specimens. *Orchis incarnata, maculata, elodes, mascula, Gymnadenia conopsea, Ophrys muscifera, Listera ovata* and *Epipactis palustris* occur in the same field, but no other orchids. Flowers first week in June.

DISTRIBUTION. Neighbourhood of Helmsley, Yorkshire! Durham, on coast north of Hartlepool! Castle Eden Dene (Stephenson), eight plants!

[1] *O.R.* p. 164 (1921); *J.B.* p. 35 (1922).

It was first observed in a withered state by Mr St Quintin of Scampston Hall, Malton, Yorks., on July 4th, 1928, who transferred two plants to his greenhouse, where I saw it in flower in 1930. On June 6th, 1929, he found 11 plants in flower, often with immature plants forming a tuft with them. I saw twelve flowering plants *in situ* in June, 1930, and a few on the Durham coast some days later, all restricted to a very limited area and nearly over. At first I thought they might be *Orchis incarnata* × *maculata*, but they differed considerably from a spike of that hybrid from the same valley (Pl. H, fig. 1), and showed no definite signs of *O. maculata*; also they exhibited none of the variation usual among hybrids. As the flowers and ring-spotted leaves recalled those of *O. latifolia*, the plant suggested *O. latifolia* var. *pumila* Freyn, which also has a dwarf habit and narrow spotted leaves, but neither the description nor the time of flowering given by Ascherson and Graebner[1] supported this view, and it seemed very unlikely that a plant of high altitudes should occur but little above sea-level in Britain. In 1931 I specially noted a pan of six dwarf non-flowering plants with long and very narrow ring-spotted leaves. In 1932 I was astonished to find that these dwarf plants had attained an average height of 30 cm. (one was 36 cm. tall), with much broader (27 mm.) leaves, and spikes ± 10 cm. long! The Mystery Orchis, as Mr St Quintin called it, had revealed what it could have been but for the adverse conditions under which it grew. I could no longer doubt that it was a stunted form of *O. latifolia* and therefore named it var. *eborensis*. It certainly is not *O. incarnata*, *maculata*, *prætermissa* or *purpurella*. As shown above it does not appear to be a hybrid. It must therefore be either a new species or a form of *O. latifolia*. As its main differences from the latter are dwarfness and narrowness of leaf, which disappear under more congenial surroundings, it can hardly be regarded as a new species.

ORCHIS LATIFOLIA var. EBORENSIS × MACULATA

Pl. H, fig. 3

Tubers palmate; stem solid. **Leaves** narrow, more acuminate and erect than in *O. eborensis*, with rather larger not ringed spots, the upper linear-lanceolate, acuminate with small spots. **Spike** short (± 6 cm.), lax, few-flowered (± 15). **Bracts** lanceolate, narrow, acuminate, the lowest 2·5 cm. × 4·5 mm. **Flowers** like those of *O. maculata*, but for the spur. **Sepals** lanceolate obtuse, the lateral spotted. **Petals** slightly shorter and broader. **Lip** 3-lobed, pale with rather bright red-violet loops, dots and streaks; side-lobes rounded but not very broad, mid-lobe tongue-shaped, 3–4 mm.

[1] *Syn.* III, 737. Plant small, only 10–15 cm. Leaves three, narrow, up to 3·5 cm. long....Plants from the Alps retained their distinctive habit in the Botanical Garden. Apart from the later flowering period they differed much from the form of the plains cultivated with them by the tongue-shaped abruptly acuminate leaves and the large brightly coloured flowers, which stand out well. (Translation.)

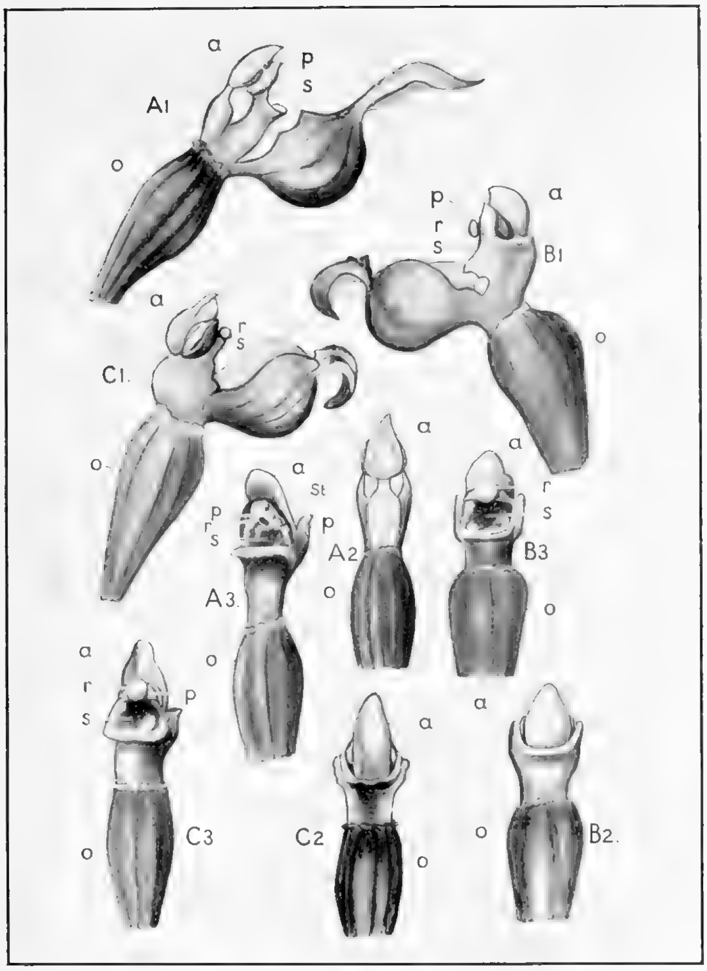


Fig. 1. A. *Epipactis leptochila* Godfery. B. *E. latifolia* All. C. *E. violacea* Dur. Duq. 1. Side view of column, lip, and ovary. 2. Back view. 3. Front view. *a*, anther; *p*, pollinia; *r*, rostellum; *s*, stigma; *st*, staminode; *o*, ovary. In A3 the staminode (*st*) is abnormally developed, with a yellow rudimentary pollinium (*p*) within.
Reproduced from *Journal of Botany*, Pl. 553, by permission of the Editor.

Fig. 2. *Gymnadenia conopsea* × *Orchis maculata* sub-sp. *elodes* (*ericetorum*).
Photo by E. W. Tattersall. *O.R.* November, 1921.

Fig. 3. *Gymnadenia conopsea* × *Orchis purpurella.*
Photo reduced by E. W. Tattersall. *O.R.* November, 1921.

Fig. 4. *Anacamptis pyramidalis*. A. Type. B. Forma *ecalcarata*.
O.R. February, 1926.

long. **Spur** stout, about 9 mm. long, compressed laterally. **Pollinia** very small, split almost to base, yellowish brown, perhaps abortive, as they left no pollen-packets on the sticky stigma, which is bordered by a coloured line. Flowers in June.

The hybrid retains the very dwarf habit, narrow leaves, small lax few-flowered spike and thick spur of *O. eborensis*, but has acquired the more deeply lobed pale-coloured lip with red-violet markings of *O. maculata*. It is curious that the influence of the latter, which is a much taller plant in the same valley, has not modified the dwarf habit or broadened the leaves.[1]

Genus XXI **OPHRYS** Swartz

Column with stigma on inner surface of basal chamber, anther in one piece with column and each viscidium in a separate pouch.

Herbs with ovoid tubers, mostly basal leaves, 4–7 rather distant flowers with petaloid or herbaceous sepals, densely velvety usually dark-coloured spurless lip, and two shining eye-like staminodes (except in *Pseud-ophrys*).

Easily recognised by the spurless velvety lip, resembling an insect (hence the names Fly Orchid, Bee Orchid, etc.), the separate pouch for each viscid disc, and the resemblance of the column, in profile, to the head and neck of a bird, with two eyes and (usually) a beak. There are two sections:

I. **Eu-ophrys** Godf. Lip without basal cavity, with two shining eye-like staminodes at the base, and geometrical often metallic markings. Pollinia removed by Hymenoptera on the head. All the British species belong to this section.

II. **Pseud-ophrys** Godf. Lip with basal cavity hispid inside, without eye-like staminodes, with two leaden bluish or purplish loops of different colour from the rest of the lip. Pollinia carried off by Hymenoptera on the tip of the abdomen.[2] Non-British. In *Eu-ophrys* the whole lip mimics an insect sucking honey in the centre of the flower. In *Pseud-ophrys* only the differently coloured central portion represents an insect resting upside down, in a reversed position. The visiting male insect places himself in the same position, and thus withdraws the pollinia on the end of the abdomen.

OPHRYS L., *Gen. pl.* ed. 1, p. 272; ed. 5, p. 406 (1754).

The genus OPHRYS L. contained no less than ten different genera, NEOTTIA, CORALLORHIZA, SPIRANTHES, LISTERA, LIPARIS, MALAXIS, HERMINIUM, CHAMÆORCHIS, ACERAS and OPHRYS. The species OPHRYS INSECTIFERA corresponds with the modern genus OPHRYS.

OPHRYS Swartz, *Act. holm.* p. 22 (1800); Benth. and Hooker, *Gen. pl.* III, 621.

[1] Pl. H, fig. 3, shows two plants from a tuft gathered June 26th, 1929, by Mr St Quintin and Dr Stephenson, in the same locality, which appeared to them to be hybrids between the Mystery Orchis and *O. maculata*, which grew a few yards away.

[2] *J.B.* pp. 33–6 (1928).

Distribution. The headquarters of the genus is in the Mediterranean region—Southern Europe, Asia Minor and N. Africa. Two species (*O. bombyliflora* and *O. lutea*) extend to Persia, and four to the British Isles, of which one, *O. muscifera*, reaches as far north in the Scandinavian peninsula as 67° N. *O. muscifera* and *O. apifera* occur in Ireland, but are rare. *O. arachnites* is confined to Kent and Surrey, and *O. aranifera* to Southern England. All our species except *O. muscifera* appear to find their northern limit in the British Isles. About 29 species are known.

KEY TO SPECIES

Sepals green, herbaceous, firm.

1. Petals linear, thread-like (edges rolled back), velvety, dark brownish red; lip 3-lobed, flattish, with a transverse bluish band in the middle. **O. muscifera**
2. Petals strap-shaped, flat, truncate, green, with wavy edges; lip nearly entire, very convex, often with two hairy hunches at the base. **O. aranifera**

Sepals rose, violet-rose, or rarely white, petal-like.

3. Petals rose, rarely white, short, dagger-shaped, with two rounded lobes at base, velvety in front; lip broad, nearly flat, with a 3-fid appendix *turned up in front* of the lip. **O. arachnites**
4. Petals short, triangular, or long, almost tubular through rolled-back edges; lip 5-lobed, margins rolled back, making it look like a rounded bag, appendix sting-like turned up *behind* the lip, out of sight. **O. apifera**

4*a*. Similar, but sepals white and lip greenish yellow. **O. apifera var. chlorantha**

4*b*. Lip long, very narrow with two auricles (side-lobes) at base, tapering into a slender appendix not turned up, with irregular yellow and brown markings. **O. apifera var. Trollii**

Fertilisation. With the exception of the Bee Orchid (*O. apifera*), all European species are entirely dependent on insects for pollination. If the flowers are not visited by insects, the ovaries fall off, and no seed-capsules are produced. The fact that few capsules are developed shows that the non-fertile flowers have not been visited, and are also incapable of self-pollination. In self-fertilised flowers, however (accidents apart), practically every flower sets a capsule. No honey is secreted. The attraction they offer to insects is of a different kind.

Darwin said that the two shining "eyes" at the base of the lip in *O. muscifera*—"curiously like a drop of fluid or nectar"—suggested "sham nectaries" more plausibly than the honeyless spurs of *Orchis*, so named by Sprengel, but he was evidently not satisfied enough with this hypothesis to adopt it.

Monsieur A. Pouyanne, Président of the Court of Appeal at Algiers, made the important discovery that in Algeria *Ophrys speculum* Link. is solely pollinated by the males of *Dielis ciliata* F., a bee rather larger than a hive-bee, each segment of whose abdomen is fringed with long red hairs. These emerge from the buried pupæ some time before the females, and engage in ceaseless quest for the latter, pouncing eagerly on any which may appear. If a few spikes of *O. speculum* are taken in the hand where the female pupæ lie buried, males come quickly and alight on the flowers. They do not bring the proboscis into play, or attempt to seek nectar. They evidently mistake the lip of the flower for a female *Dielis*, which it resembles by its fringe of long red hairs, and by the violet-blue metallic sheen of the oval shield in the middle of the lip, very suggestive of the reflections from the closed blue wings of the female. The males have colourless wings. The resemblance of the lip to an insect, embodied in the Linnean name *Ophrys insectifera*, is not a mere fancy of the imagination, and the popular names Bee Orchid and Fly Orchid show that the likeness was widely recognised. Some have hazarded the suggestion that the resemblance to an insect was to prevent cattle from grazing on the plants, others that it was to keep insects from the flowers. Both are wide of the mark. A full account of M. Pouyanne's twenty years of observation, which was first published in 1916,[1] supplemented by my own observations in the south of France, was given in *J.B.* pp. 33–40 (Feb. 1925). In the section *Pseud-ophrys* Godf., which contains *O. fusca*, *O. lutea*, etc., the markings on the lip (and not the whole lip itself) represent an insect on the flower in the "reverse position", i.e. with the head turned towards the tip of the lip, and the abdomen in the centre of the flower. The male on alighting turns round and assumes the same position, thrusting its abdomen into a cavity lined with hairs at the base of the lip, keeping it in constant movement, and finally carrying off the pollinia on the tip of the abdomen. These remarkable observations were naturally received with some scepticism, but they were unexpectedly confirmed by the discovery that an Australian orchid, *Cryptostylis leptochila*, is pollinated by *Lissopimpla semipunctata* Kirby, an ichneumon-fly, in a similar manner, the insect being attracted by sexual appeal, and the pollinia being carried off on the tip of the abdomen.[2]

Each pollinium stands erect on a minute disc with a ball of extremely adhesive material beneath. This is enclosed in a pouch filled with fluid, as it sets hard like cement on exposure to the air. On the slightest touch by an insect the pouch swings back and exposes the viscid matter, which at once adheres to the insect's head with sufficient firmness to withdraw the pollinia from the anther-cells. The visitor carries off one or both pollinia standing upright on its head. The usual downward movement of the pollinia after withdrawal, through nearly a right angle, is slow (in

[1] Correvon and Pouyanne, *Journ. d'Hort. de France*, p. 5 (Févr.–Mars, 1916).
[2] *J.B.* p. 97 (1929), with coloured plate.

O. muscifera about six minutes according to Darwin).[1] As the insect usually spends some time on the flower, this prevents pollination of another flower on the same spike, for until the downward movement is completed the pollinia cannot touch the stigma. The pollinia then point horizontally forward, but the slight bend or elbow in the caudicle causes the two pollen-masses to incline slightly upwards, so that they are in exactly the right position to come in contact with the stigma, which is on the inner surface of the ceiling and walls of the little arched chamber formed by the base of the column. It is easily distinguished by its glistening surface, due to the viscid secretion, and is often bordered by a coloured line. The secretion is sufficiently tenacious to detach packets of pollen from the pollinia. Stimulated by the stigmatic fluid, these disintegrate into their component pollen-grains, which put forth pollen-tubes. These grow down like roots in a seed-bed to the ovary, each tube entering an ovule (immature seed) by the micropyle, and discharging its life-giving contents, without which the ovule could never develop into a fertile seed.

The rostellum consists of the two small cup-shaped pouches, each enclosing a viscid disc. In *Orchis* both discs are enclosed in the same pouch and, on the withdrawal of the insect, the pouch moves back to its former position, so that if only one viscidium is removed, the other is again immersed in liquid and kept from setting hard. As the pouch in *Ophrys* only holds one pollinium, it does not need to resume its position, and does not do so. In *Orchis* the stigma is vertical, and the straight pollinia only need to point horizontally forwards to come in contact with it. In *Ophrys* it is partly on the ceiling of the little chamber. The tips of the pollinia must therefore point upwards—hence the beautiful adjustment of an elbowed stalk, which is of the greatest service to the plant. If the pollinia are withdrawn on a pencil, it will be seen that the elbow finally rests on the pencil, tilting the pollinia slightly upwards.

The European Orchidaceæ attain their highest stage of evolution in the genus *Ophrys*. The high degree attained by *Orchis* is surpassed by the provision of a separate pouch for each of the two viscid discs instead of a common pouch to hold both, and by the substitution of sexual allurement for that of edible matter. Having no honey, the flowers are shunned not only by insects generally, but even by the females of the particular species by the males of which the flowers are pollinated. Certain species of *Ophrys* are so highly specialised that they mimic the females of one particular species of insect, and are solely visited by the males of that species. To this category belong *Ophrys speculum* of N. Africa, and probably also our *O. muscifera*, which, as far as is at present known, is only visited by *Gorytes mystaceus*.

[1] *Fert. Orch.* ed. 2, p. 46.

H. M. Godfery pinx.

OPHRYS MUSCIFERA Hudson
Fly Orchid

PLATE 54

Ophrys muscifera Huds.

1, 2. Enlarged flowers. Challes-les-Eaux, France, June 1st, 1928.

3. **Gorytes mystaceus** L. ♂.

1. Ophrys muscifera Huds.

Pl. 54. *Fly Orchid*

Tubers two, globose or ovoid, the younger often stalked; roots short, rather thick. **Stem** erect, 25–40 cm., sometimes over 60 cm.,[1] slender, round, solid, with whitish or brownish obtuse ribbed basal sheaths, rarely green-tipped. **Leaves** oblong-lanceolate to lanceolate, more or less acute, keeled, folded, bluish green, about 13-nerved with numerous cross-veins, the upper narrow tapering clasping the stem. **Flowers** 2–10, distant, in a long lax spike, small unscented green with purple- or red-brown lip. **Bracts** erect, lanceolate, folded, with inrolled edges, ± 6-nerved, the lowest exceeding the flowers. **Ovary** sessile, erect, long, slender, 6-ridged, light green, glabrous. **Sepals** narrow, lanceolate, obtuse, glabrous, yellow-green, 3-nerved, spreading, with rolled-back edges. **Petals** shorter, linear, very narrow, velvety in front, purplish or brownish red, the edges rolled back making them thread-like. **Lip** longer than sepals, 3-lobed, velvety, purplish or reddish brown with a quadrangular bluish iridescent (rarely cream or white) glabrous shield in the middle, and two dark shining eye-like knobs (staminodes) at the base; side-lobes short, narrow, oblong, slightly convex, densely velvety, mid-lobe broadening downwards, bi-lobed or deeply notched, rarely with a short tooth in the middle, lobes obtuse or acute. Lip on the whole nearly flat with slightly reflexed margins, longer than broad. **Column** shorter than petals with a short blunt beak (often with none), surmounted by the red-celled anther, and with an arched chamber at its base, on the inner surface of the roof and sides of which the stigma is situated. **Rostellum** with two cup-shaped whitish pouches enclosing the viscid discs. **Pollinia** bright yellow with transparent yellow elbowed caudicles. **Seeds** with netted transparent testa, its cells with transverse nearly parallel sometimes forked striæ.

O. muscifera owes its popular name to its resemblance to a fly—Linnæus declared that only the buzz was wanting. Flies, however, do not have long antennæ, of which the thread-like petals are strongly suggestive, resembling those of the insect which actually pollinates it. The species is very constant to type, showing little variation. The var. *bombifera* Brébisson[2] appears to be *O. aranifera* × *muscifera*, as suggested by Camus, whilst *parviflora* Schulze seems only to be a dwarf form with small flowers due to dry ground. The forms *apiculata* with an intermediate tooth, *rotundata* with very short side-lobes, and *dubia* with very long ones seem to be of small account. The colour-forms *ochroleuca* with small yellowish white flowers and *virescens* Rolfe with green flowers and a whitish shield (Pl. 55) seem to be accidental sports. The discoverer of the latter took me in 1919 to the place where he found it, but not a

[1] Townsend, *Fl. Hants.*

[2] Brébisson, *Fl. Normandie*, ed. 3, p. 279.

trace could be seen. A curious form near Orpington, Kent, with white or very pale green bracts, and pure white sepals has been recorded.[1]

Teratological forms occasionally occur. One with both petals transformed into lips is relatively not very rare, according to Camus (*Icon.* p. 301).[2] A specimen found near Canterbury had no petals and two additional anthers,[3] each with pollinia, doubtless developed from two ancestral anthers of the inner whorl, fertile in the Diandræ, suppressed in the normal flower of all the Monandræ. This triandrous condition not infrequently occurs in *Ophrys*, usually without suppression of the petals. In a plant found near Münster each flower had five lips, and this did not change under cultivation. Another, found in Germany, had three sepals, three petals (all alike) and three columns. The lip had reverted to the primitive petal from which it was evolved.

HABITAT. Open woods and clearings, sometimes in shade, banks, field-borders, chalk downs, sometimes in marshy ground, as in Anglesey! and Ireland, where it also (rarely) occurs in bogs (*Cyb. Hibern.* p. 346), turbaries (very rarely) (Camus, *Icon.* p. 301). Flowers May to July.

DISTRIBUTION. Rather rare, sometimes locally abundant. From Kent and Dorset to Durham and Westmorland. Wales. Denbigh (Dallman, *J.B.* Supp. p. 45 (1911)). Anglesey! Scotland. Perth (E. Pickard, *B.E.C.* p. 399 (1921)). Dr Druce says a friend of his found leaves and a tuber in W. Ross, which turned out to be *O. muscifera*. E. Perth (*B.E.C.* p. 399 (1921)). In Ireland only in the centre, where it is rare. Its great rarity in Scotland is remarkable, as in Scandinavia it extends to 67° N. latitude, i.e. just within the Arctic circle. Scandinavia and Central Russia (further north in the Onega region, Camus) to Northern Spain, N. Italy, N. Balkan peninsula, N. Greece. In the Mediterranean region it is only found in the mountains, and appears not to extend to N. Africa.

> OPHRYS MUSCIFERA Huds., *Fl. anglica*, ed. 1, p. 340 (1762). O. INSECTIFERA α MYODES L., *Sp. pl.* p. 948 (1753). O. MYODES Jacquin (1781), who was the first to use MYODES as a specific name, though Linnæus had used it in a varietal sense. As the latter did not recognise it as a species, and as MUSCIFERA has passed into universal botanical language, it is not in the interests of science to replace it by a name less generally known, and not adopted by the greatest modern monographists Camus and Schlechter, or by Ascherson and Graebner or Rouy.

FERTILISATION. As described under *Ophrys*. H. Müller stated[4] that in sunny weather drops of nectar are secreted on the lip as in *Neottia nidus-avis*, and that he once saw a fly (*Sarcophaga*) licking up these drops, but it did not remove the pollinia. This was perhaps honey-dew, for Darwin could never find any trace of nectar, nor did he ever see any insects approach the flowers, often as he watched them.[5] He knew that

[1] *J.B.* p. 267 (1908).
[2] Tahourdin records a Kentish specimen with three lips, *Native Orchids of Britain* (1925).
[3] *O.R.* p. 101 (1920). [4] *Nature*, p. 22 (1878). [5] *Fert. Orch.* ed. 2, p. 47.

insects visited them, for he twice found abundant pollen on the stigma with both pollinia intact in the anther. He suspected that they were attracted by the shining "eyes", "curiously like a drop of fluid or nectar". He noticed very minute punctures in these, but was not certain that they were not due to the spontaneous bursting of superficial cells.[1] These conjectures have now been superseded by actual observation. It appears to be efficiently fertilised in Britain. In certain localities it is frequent, and in some seasons abundant. I found plenty of evidence from pollinia removed, pollen on stigma and developed ovaries that it is not infrequently visited. Darwin indeed remarked that in 1861 it was extraordinarily plentiful, but that eleven marked plants only produced seven capsules. Probably the plants were so abundant that there were not insects enough to go round, for *Ophrys* does not attract such numbers or varieties as honey-bearing plants. The hybrid *O. aranifera* × *muscifera* proves that both these species are, even though rarely, visited by the same insect.

In May, 1928, and again in 1929, at Challes-les-Eaux, near Chambéry, France, Colonel Evans, F.L.S., my wife and I watched *O. muscifera* for many hours on suitable days, and saw it visited by *Gorytes mystaceus* L. a number of times, witnessing the actual withdrawing of the pollinia. It is a small burrowing wasp placed by Westwood in the Crabronidæ. It preys on the larvæ of the Cuckoo-spit or Frog-hopper insect. At present it is the only known instance of an *Ophrys* being pollinated by a wasp. It is hard to see when quiescent on the flower, the closed wings agreeing with the contour of the lip, the gap between the thorax and abdomen seen through the wings giving much the same impression as the leaden oblong marking on the middle of the labellum, and the antennæ resembling the thread-like petals. It alights on the lip head uppermost, and rests there with quivering wings and waving antennæ, doubtless a preliminary phase of courtship, sometimes for three minutes. Its actions made it quite clear that the wasp regarded the lip as a female of its own species. Only males visited the flowers. In both years *Gorytes* suddenly ceased to appear. Probably the females had begun to emerge, and the flowers lost their attraction. Although *O. aranifera*, *O. arachnites* and *O. litigiosa* were exposed at the same time, sometimes in the same vase, *Gorytes* took no notice of them. No other kind of insect came to *O. muscifera*.[2] *G. mystaceus* is figured in Pl. 54.

O. muscifera × *aranifera*, p. 230.

[1] *Ann. Nat. Hist.* p. 144 (1869).

[2] *J.B.* pp. 298–302 (1929).

2. Ophrys aranifera Huds.

Pl. 55 B. *Spider Orchid*

Tubers two, entire, globose or ovoid. **Stem** 1–3 dm. (rarely 4–6 dm. abroad), erect, round, often flexuous, glabrous, yellow-green. **Leaves** ovate-lanceolate to oblong, rather short in Britain, somewhat obtuse, often with a small point (mucro), spreading or recurved, green or grey-green, the upper lanceolate, acute, clasping the stem; nerves 10–14 with irregular cross-veins. **Spike** erect, lax, few-flowered (1–7); flowers distant, of medium size, scentless, finally turning a yellowish brown. **Bracts** lanceolate, slightly obtuse, concave, pale green, glabrous, 7–9-nerved, the lower long. **Ovary** long, curved, 6-ridged, not, or but slightly twisted. **Sepals** yellow-green, oblong, obtuse, 3-nerved, with rolled-back edges, the lateral spreading, the upper erect, slightly arched forward. **Petals** spreading, strap-shaped, rounded or squarish at the tip, wavy-edged, narrower and shorter than the sepals, 1-nerved, green or brownish, glabrous or with very short hairs in front. **Lip** about equal to sepals, rounded, oval-oblong or oval-triangular, nearly orbicular when flattened, strongly convex, notched at the tip, sometimes with a tooth in the notch, with or without two obtuse conical hunches near the base, their outside surface and the sides of the lip densely clothed with rather long brown-purple hairs, forming a kind of fur collar round the velvety central area, the edge of the lip often paler or yellowish green. Markings leaden, glabrous, rather glossy, consisting of two parallel lines, sometimes attached to a collar or joined in the middle forming an **H**. On each side of the base of the column is a small shining eye-like staminode. **Column** nearly at right angles to lip, slightly curved forward, sometimes a little hispid at the back, forming a small arched chamber at the base, on the inside surface of which is the glistening stigma. **Anther** like the head of a bird with yellowish eyes and a short obtuse beak. **Pollinia** and caudicles yellow. **Rostellum** of two separate pouches, each enclosing a viscid disc. Ripe capsule oblong with prominent ridges. **Seeds**: cells of the transparent testa with undulate walls and abundant transverse striæ.[1]

The so-called variety *fucifera*, the Drone Orchid,[2] cannot be maintained. It was defined as having the petals minutely rough or downy in front, the lip without lobes, and as flowering six weeks to two months later. The lobing is variable in both forms, and both forms have been collected in flower from April to early June; the roughness or downiness of the petals is the only real difference.[3] Mlle Camus,[4] however, who has done so much microscopical research on orchids, says that the petals in *aranifera* are never completely glabrous, but are papillose, sometimes briefly pubescent.[5]

[1] Camus, *Icon.* p. 332.
[2] Smith, *English Flora*, IV, 31 (1828).
[3] *E.B.* ed. 3, pp. 112–13 (1869).
[4] Camus, *Icon.* pp. 331–4.
[5] *Vide* also C. B. Tahourdin, *O.R.* p. 230 (1928).

PLATE 55

A. **Ophrys aranifera × muscifera.**

1. Enlarged flower. Kent, May 28th, 1919.

2. **Ophrys muscifera** var. **virescens** Rolfe. Enlarged flower. Same place and date.

B. **Ophrys aranifera** Huds.

3. Enlarged flower. Dorset, May 29th, 1917.

B

H. M. Godfery pinx.

A. OPHRYS ARANIFERA × MUSCIFERA
× *Ophrys hybrida* Pokorny

B. OPHRYS ARANIFERA Hudson
Spider Orchid

2. OPHRYS MUSCIFERA var. VIRESCENS Rolfe

Reichenbach's *fucifera*[1] is defined as having two hunches, his *genuina* having none. This character is a variable one, hunches being present in some individuals and absent from others in several species of *Ophrys*. The flowers change colour quickly after flowering to light brown or dirty yellow, the column moves down till it lies on the lip, and the withered sepals and petals close up, as in other species of the genus, returning to their original function of protection. According to Camus[2] the flowers are scented, especially in the low dry warm mountains of Southern France. It is possible, however, that green-petaled forms of *O. arachnitiformis*, which is slightly fragrant, have been regarded as *O. aranifera*. Camus[2] mentions 30 named varieties, sub-varieties and forms, mostly founded on very slight and variable characters, such as shades of colour, varying length of various parts, etc. One suspects that several of these might be found growing in one field, and that plants occur combining the characters of two or more of these forms. Anomalous flowers with three anthers, or without petals, or with three lips, or three petals, occasionally occur.[3]

G. E. Smith[4] describes a teratological form of *O. aranifera* found at Ospringe as follows: "In place of a stigma and lip were three staminals, each complete, placed upon a triangular base, their anthers and base turned inwards, two combined sepals representing the lip, of which no trace was visible in any of the four flowers on the spike".

Habitat. Sunny open downs, grassy slopes, etc., on calcareous or marly soils. Flowers April, May and June.

Distribution. Extremely local, and usually found in colonies. Mostly confined to the southern counties from Kent to Dorset and perhaps Wilts. Dr Druce states (*in lit.*) that he has seen specimens from Northants. (? now extinct), Oxford (1919), and Denbigh. Colwyn Bay, 1891. Jersey (*B.E.C.* (1918)). Said to have been formerly found in Essex and Suffolk. Absent from Scotland and Ireland.

In Europe it extends from Belgium (where it occurs singly on the coast dunes) and Germany to Spain, Portugal, France, Italy to Turkey, Greece, the Mediterranean islands, and, according to Ascherson and Graebner, Asia Minor. Absent from Algeria and Tunis.

Ophrys aranifera Huds., *Fl. Angl.* ed. 2, p. 392 (1778). O. sphegodes Mill.

The proposal to replace it by a name from a gardening dictionary (Miller's (1768)) has not been adopted by any of the monographists of the Orchidaceæ, or by the most recent Floras of France and Germany. It seems hardly in the interests of science to substitute dead synonyms for living and generally accepted names. The popular name is derived from the resemblance of the lip to the garden spider.

Fertilisation. See *Ophrys*. The stalk of the pollinium is nearly straight but

[1] Rchb. *Icones*, xiii, 89.
[2] Camus, *Icon.* pp. 331–4.
[3] Masters, *Journ. Linn. Soc. Bot.* viii, 209 (1863).
[4] *Catalogue of Plants S. Kent* (1829).

slightly curved forwards at the apex, without the elbow or double curve of some species, but the result is the same, the pollinia remaining slightly tilted upwards after the downward movement. The pouch containing the viscid disc is enclosed within the foot of the anther-cell, and is thus kept damper than in *O. muscifera*, and the downward movement is more rapid. The plant is entirely dependent on insects for pollination. I watched flowers of this species, in May, 1929, at Challes-les-Eaux, Savoie, together with those of *O. arachnites* and *O. muscifera*, but although both the latter were a number of times visited by Hymenoptera, nothing came to *O. aranifera*. Delpino stated[1] that in Liguria hardly one flower in 3000 sets a capsule. As, however, it occurs in thousands and does not appear to multiply vegetatively, his observations were probably made in a bad season for insects. M. Houzeau de Lehaie states that after a very unfavourable spring in Belgium hardly a capsule was to be found on any of the species of *Ophrys* except the self-fertilised *O. apifera*. I examined 18 spikes of *O. aranifera* near Swanage, with 27 open flowers, of which four had both pollinia removed and six had pollen on the stigma. As only one flower was as yet open on most of these spikes there had not been time for many visits. There can be little doubt that the flowers are visited (probably by a Hymenopteron), and that the attraction is a suggested resemblance of the lip to the female of the visiting insect concerned.

OPHRYS ARANIFERA × MUSCIFERA

Pl. 55 A. × **O. hybrida** Pokorny

Stem rather tall, up to 35 cm. **Leaves** erect, slightly spreading, broadly lanceolate acute, grey-green. **Spike** lax, flowers few, distant, clearly intermediate between the parents. **Sepals** long, green, spreading, oblong, the upper erect, edges rolled back. **Petals** narrow, rather long, brownish velvety in front. **Lip** broad as in *O. aranifera*, with pronounced side-lobes like *O. muscifera*, slightly hispid, mid-lobe broad, deeply notched, with or without appendix, velvety, brown. Markings a collar and shield, glabrous, leaden, bordered with a whitish line. Anther with a short beak, as in *O. aranifera*. A second specimen had a broader chestnut-brown lip with an olive-green margin.

In general appearance it is nearer to *O. aranifera*, but the influence of *O. muscifera* was clearly visible in the narrow dark velvety petals with rolled-back edges, the conspicuous side-lobes of the flatter lip, and the quadrangular shield.

Two specimens were found in an open wood near Wye, Kent, and were handsomer than either of the parents, which grew close at hand. Both pollinia had been removed from two flowers, but no pollen had been left on the stigma.

[1] *Ult. osserv. s. Dicog.* Parte 1, 177.

H. M. Godfery pinx.

A. OPHRYS ARACHNITES L.
Late Spider Orchid

B. OPHRYS APIFERA Hudson
Bee Orchid

C. OPHRYS APIFERA × ARACHNITES
× O. *Albertiana* Camus

PLATE 56

A. **Ophrys arachnites** L. Kent, June 17th, 1930.

B. **Ophrys apifera** Huds. Sussex, June 23rd, 1930.

C. **Ophrys apifera** × **arachnites**, × **Ophrys Albertiana** Camus. Kent, June 17th, 1930.

1, 2. **Eucera tuberculata** F., ♂ (enlarged), bearing pollinia.

The lowest left-hand figure in *E.B.S.* No. 2649, called in the third edition *O. aranifera* var. *β fucifera*, appears to be this hybrid.

Ophrys arachnites × *aranifera*, vide *O. arachnites*, p. 234. *O. aranifera* × *apifera*, p. 241.

3. Ophrys arachnites (L.) Rich.
(O. fuciflora Reich. p.)
Pl. 56 A. *Late Spider Orchid*

Tubers two, ovoid; roots rather thick, sinuous, tapering to a narrow flattened point. **Stem** $1\frac{1}{2}$–4 dm., erect, solid, round, sinuous, glabrous. **Leaves** 2–5, the basal spreading or erect, the upper 1–2 erect, loosely clasping the stem, the basal (sometimes withered at time of flowering) oblong-lanceolate to ovate-oblong, obtuse or subacute, glabrous, grey-green, sometimes wavy-edged, with ± 15 nerves and numerous cross-veins. **Spike** lax with 2–6 rather large flowers with petaloid sepals and broad conspicuously marked lip. **Bracts** green, concave, lanceolate, acute or obtuse, longer than the ovary, the lowest sometimes leaf-like. **Ovary** sessile, linear, 6-ridged, curved, rather long, slightly twisted. **Sepals** oval-oblong, obtuse, keeled, with 1–3 green nerves, glabrous, petaloid, usually pale rose, rarely white, the edges rolled back, the lateral spreading, the upper arched forward. **Petals** short, obtusely triangular with two rounded auricles at the base, making them somewhat dagger-shaped, faintly 3-nerved, rose, rarely white, densely velvety with short hairs. **Lip** broad, often subquadrangular and broader towards the tip, entire, rarely with a slight incision on each side, red-brown, dark brown, or brown-purple, velvety, with two slight or prominent basal hunches, a small shining eye-like knob on each side of the base of the column, and a thick trifid appendix turned sharply up in front of the lip. The latter is relatively but slightly convex, broader and flatter than in *O. apifera*, adorned with a complicated glabrous shining pattern of yellow lines often enclosing three circles, prolonged in a kind of collar round the base of the lip. **Column** as long as the petals, forming an arched chamber surmounted by the anther. **Stigma** on the inside surface of this chamber, the rostellum formed of two slightly oval yellowish pouches, each enclosing a colourless viscid gland, to which the pollinium is attached in front of its centre. **Pollinia** and caudicles bright yellow, the latter short, translucent, ribbon-shaped, elbowed in the middle. Seed-capsule slightly enlarged towards the tip, with three more or less prominent ridges. **Seeds**: cells of netted transparent oblong testa marked with nearly parallel transverse striæ.

The lip is rarely sub-orbicular, with the sides more reflexed. The flower is very variable. Camus (*Icon.* pp. 309–12) gives over 30 named varieties and forms, some of which are very slight. The variety *albescens* Brébisson has white sepals instead of rose. Mlle Camus found that rose-coloured sepals became white when cultivated in a pot in the shade, and I have repeatedly observed that the coloured sepals of all *Ophrys* become white if the flower has opened in the house. I received beautiful specimens of the var. *albescens* from Folkestone from Mr H. Walker, June 17th, 1930.

This species is easily distinguished from *O. apifera*, of which it has been considered by some botanists to be a variety, by the short rose or white dagger-shaped petals, the flat broad undivided lip, the thick trifid appendix turned up in front of the lip, and not behind it as in *O. apifera*, the short straight beak of the anther, and the flat stiff ribbon-like caudicles, only about half as long as the thread-like flexible caudicles of *O. apifera*.

Occasionally, in late-flowering plants, the basal leaves are withered, or apparently absent, at the time of flowering, as in a plant gathered at Shorncliffe, June 23rd, 1918. This plant also had a very broad lower bract and very dark-coloured lip. A specimen sent me at the same time had three anthers and three columns, the latter coherent almost to the summit. Each of the side-anthers had only one pollinium, and no viscid disc, and was open to the base showing the ends of the caudicles. The middle anther was normal, but the caudicle of one pollinium was not yet attached to its viscid disc. Max Schulze[1] figures a flower with two complete lips. This happens also in other species and genera. I have seen it in *Epipactis latifolia*. The two lips are side by side. In such cases the true lip is absent, and the two obsolete lower stamens of the outer whorl have developed into lips. Sometimes the true lip is also present, immediately below the other two.

O. arachnites develops three anthers more often than other species, though they are of very rare occurrence. They are due to the exceptional development of the two suppressed anthers a^1 and a^2 (Text-fig. 2), and are a partial reversion to the ancestral 6-anthered flower. A specimen of *O. arachnitiformis* at Hyères had four anthers, three identical with those of some English plants, and one ($a3$, Text-fig. 2) face to face with the normal fertile anther. Pl. 58 C shows an example of this in a British *O. apifera*.

HABITAT. Chalk downs, meadows and hedges on chalk. Flowers May to June.

DISTRIBUTION. Rare and very local in Britain, restricted to Kent, and the only orchid peculiar to that county.

Central and Southern Europe. Austria, France, Germany, Italy, Spain and the Balkan peninsula.

OPHRYS ARACHNITES Rich., *Fl. moen.-franc.* II, 89 (1772); Lamarck, *Fl. Franç.* III, 515 (1778); Rouy, *Fl. France*, XIII, 110. O. FUCIFLORA Haller, *Icon. pl. Helv.* t. 24, figs. 2, 3 (1795); Reich., *Fl. Germ. exc.* t. 1, p. 128 (1830). O. INSECTIFERA η ADRACHNITES L., *Sp. pl.* ed. 1, p. 949 (1753), subsequently corrected

[1] *Orch. Deutschlands*, pl. 27.

by Linnæus in *Systema Naturæ*, ed. 10, 1759, to ARACHNITES. O. INSECTIFERA ARACHNITES α Haller, *Ic. pl. Helv.* p. 26.

Haller's *fuciflora* only dated from 1795, and included *O. apifera*. It was long forestalled by Richard and Lamarck. *Arachnites* was used by a long series of authors, and it is difficult to see how the substitution of *fuciflora* by the elder Reichenbach in 1830 can be justified. Haller says it becomes notably changed during the summer. The median tooth of the labellum is bent back against the concave face of the latter, so that the outline appears to be continuous and without appendix! He thought that his *O. fuciflora* changed into *O. apifera* later in the year.

FERTILISATION. On May 12th, 1929, my wife and I were carrying home the earliest opened spikes of *O. arachnites* at Challes-les-Eaux, France, when a grey bee with long antennæ came to the flowers in my hand, and after much hesitation alighted on one. Immediately another bee of the same kind pounced on him and tried to push him off, but he held on, and his assailant flew away. We then watched the first bee, and saw him withdraw the two pollinia, attached to his head, and fly away. We kept perfectly still. Several similar bees circled round and sometimes alighted but never stayed. Weary of waiting we moved away, but a bee followed us and settled on a flower in my wife's hand. I boxed him just as he had withdrawn the pollinia, and he was identified at the Paris Museum as *Eucera tuberculata* F. ♂. He tried hard to scrape the pollinia off with his feet, and succeeded in getting rid of one of them.

The next day several similar bees came to the flowers but did not alight. The following day we took the flowers down to the gate where we first encountered the bees. In a few minutes at least five *Eucera* appeared, circled round the flowers and made off. They had quickly become aware of the presence of *O. arachnites*, though it has no perceptible smell. At intervals single bees arrived, and two settled on the flowers. I watched one carefully. He seemed to be exploring the turned-up appendix at the apex of the lip with the tip of his abdomen, which he kept moving actively about. On May 23rd we again took fresh flowers to the gate. A few *Eucera* appeared, but were manifestly less keen. Only three alighted, and these left at once. After that no more came to the flowers. The previous year we had seen the same kind of bee come several times to flowers held in the hand, but I was unable to catch one. We noted the promptness with which *Eucera* became aware of the presence of *O. arachnites*, and its excessive wariness and caution. It entirely ignored *O. muscifera*, *aranifera* and *litigiosa*, as well as various species of *Orchis*, *Aceras*, *Listera* and *Cephalanthera*, exposed at the same time with *O. arachnites*. In both years the bees suddenly ceased to appear about the same date. From observations made on various species of *Ophrys* in S. Europe and N. Africa, this appears to be due to the emergence of the females from the pupa state, which happens some time after the males appear. Hence the early flowers of *Ophrys* are more frequently fertilised than the later ones, which are neglected as soon as the female insects appear.

At Challes about May 24th a yellowish spotted-winged fly, *Volucella inflata* Fabr., began to visit *O. arachnites*, and remained long on the flower. On alighting it immediately began a series of frantic movements, clawing at the labellum as if it were on an extremely slippery surface requiring desperate efforts to secure a foothold. It kept turning round and round sideways, now facing upwards, now downwards, sometimes resting as if exhausted, and then furiously resuming the same erratic movements. A bee sucking honey remains still on the flower. A male bee visiting an *Ophrys* at once takes up the proper position, facing the centre of the flower and withdrawing the pollinia on his head in all species except *O. fusca* and *O. lutea*, in which the labellum suggests an insect facing the tip of the lip, and the pollinia are carried off on the end of the abdomen. In both cases the visitor buzzes with its wings, waves its antennæ, and explores the flower with the tip of the abdomen, otherwise remaining motionless. The disordered movements of *Volucella* are entirely different, and suggest a frantic search for something it is unable to find. Often as I saw it visit the flowers it never removed the pollinia.[1]

OPHRYS ARACHNITES × ARANIFERA
Pl. 57 D. × **Ophrys Aschersonii** De Nanteuil

This is thus described in the *Catalogue of Plants of S. Kent*, p. 58 (Rev. G. E. Smith): "The tone of its pale citron-green, in both herbage, calyx and petals, closely resembles that of *O. fucifera* (a form of *aranifera*) with which I have figured it. The lip is variable in form, the margin deep and pale, and the gland (appendix) large, and in several cases distinctly trifid. Is it possible that a plant of *arachnites* can receive pollen transferred by an insect from *fucifera*? Upon the 17th May in the past year (apparently 1828), a year remarkable for the early flowering (as well as from continued rains about June for the long continuance in flower of many plants), I had specimens of *arachnites* and *fucifera* blooming together. If this be the case—but let it be regarded as supposition—the varieties in *fucifera* may be thus explained. Mr A. Matthews collected *O. arachnites* several years since at Ospringe, whence the varieties of *O. fucifera* were procured. The terminal gland, the variable lip, the marking and the petals of *O. fucifera* exhibit traces of this (*arachnites*). The purple-rose colour of *O. arachnites* is...suppressed in these varieties. This supposition may be regarded as chimerical; it is at least plausible; and will furnish a new motive of interest in these singular and beautiful plants".

Referring to the above in their *Flora of Kent* (1899) Messrs Hanbury and Marshall

[1] *J.B.* pp. 298–302 (1929).

PLATE 57

A. **Ophrys apifera** var. **Trollii.** Bex, Switzerland, May 24th, 1913.

B. **Ophrys apifera**, varying in the direction of **Trollii.** Wiltshire, June 27th, 1928.

C. **Ophrys apifera** var. **chlorantha.**

D. **Ophrys arachnites** × **aranifera**, × **Ophrys Aschersonii** De Nant. Bex, Switzerland, May 14th, 1913.

1. Enlarged flower of specimen from Saarbrücken, 1926.

A B C D

I

H. M. Godfery pinx.

A. OPHRYS APIFERA var. TROLLII
Wasp Orchid

B. OPHRYS APIFERA (versus TROLLII)

C. OPHRYS APIFERA var. CHLORANTHA

D. OPHRYS ARACHNITES × ARANIFERA
× *O. Aschersonii* De Nanteuil

say: "The excellent figure of the above-mentioned specimen leaves no doubt in our minds about the suggestion being correct...*aranifera* was seen by Marshall 1st June 1882 at Folkestone, still just in flower, *arachnites* being then in perfection, and a good many specimens of *apifera* having already expanded their blossoms".

Smith's description confirms this conclusion. The green sepals and petals are characteristic of *O. aranifera* whilst the broad lip and trifid appendix are equally so of *O. arachnites*. This hybrid must necessarily be very rare in Britain, where *O. aranifera* ordinarily flowers in April and early May, and *O. arachnites* in late May and early June, for their time of flowering only overlaps in exceptional years. The circumstances are very favourable for intercrossing, however, when but few specimens of one species remain in bloom, whilst the other parent is in full flower.

On June 25th, 1930, I received from Mr H. Walker from Folkestone a specimen of *O. arachnites* with green herbaceous sepals. As it showed no other recognisable characters of *O. aranifera*, it might possibly be a sport of *O. arachnites*, but more probably it was this hybrid back-crossed with *O. arachnites*, but still retaining the green sepals of *O. aranifera*.

The following is a description of a specimen found at Bex, Switzerland, May 14th, 1913 (Pl. 57 D). Height 16 cm. Leaves grey-green. Flowers three, rather large, distant. Sepals green, obtuse, spreading. Petals green, short, triangular. Lip rather quadrangular (with two slight hunches at base and a broad very short appendix turned up in front), brown, shading off at the broad apex into a rather wide yellowish green margin. Markings a combination of the pattern of *O. arachnites* with the H-like marking of *O. aranifera*. The single flower marked D 1 is from a specimen from Saarbrücken sent me by Herr J. Ruppert who named it *O. fuciflora* var. *Walteri* Rupp. *in schedis*. For the following reasons this appears to be the hybrid *O. arachnites* × *O. aranifera*. The petals were broad all along the basal half, in one spike almost to the apex, with darker and wavy edge, a marked character of *O. aranifera*, as well as their green colour, and that of the sepals. In one spike the sides of the lip were much reflexed, making it appear oval, and the marking simple and more like *O. aranifera*, for which it might easily have been mistaken at a little distance, but for the rather large appendix. In another spike the lip resembled *O. arachnites*, but was slightly emarginate with a very small almost rudimentary appendix. In another the hunches were low, except in a flower with dark wavy-edged petals, which are in themselves evidence of the part parentage of *O. aranifera*.

Ophrys arachnites × *apifera*, vide *O. apifera*, p. 241.

Ophrys arachnites × *muscifera*, not yet recorded for Britain, might well occur in Kent.

4. Ophrys apifera Huds.

Pls. 56 B, 57, 58. *Bee Orchid*

Tubers two, ovoid or globose. **Stem** 2–4 dm., solid, round, somewhat sinuous, glabrous, often stout. **Leaves** oblong-lanceolate to ovate-lanceolate, keeled, many-nerved, glabrous, paler and slightly glossy below, the lower obtuse, spreading, the upper acute, more or less embracing the stem. **Spike** lax, flowers 2–8, moderately large, rather distant. **Bracts** lanceolate acute, the lower sometimes exceeding the flowers, the upper nearly equalling the buds. **Ovary** sessile, curved forward, not twisted, linear, rather 3-sided, glabrous, green. **Sepals** spreading, finally much reflexed, oblong obtuse, petaloid, pale rose to bright violet-rose, rarely white, more or less hooded at tip, with 3–5 green nerves, the mid-nerve pronounced. **Petals** about half as long as sepals or less, linear with rolled-back edges (making them semi-tubular), green or purple-brown, covered in front with whitish hairs. **Lip** 5-lobed (the lobes strongly curved back out of sight behind the lip, so that in front view it looks bag-shaped), velvety, red-brown or dark purple, with a broad glabrous brownish or purplish collarette encircling the red-brown (or red) oval-shaped base of the lip, and ending in two very short lobes at the angles below, the whole pattern edged with yellow or white; there are often also two or three yellowish spots near the apex of the lip, and sometimes an indefinite yellowish blotch on each side. The upper side-lobes are long, tapering and triangular, cut out and turned back behind the lip, forming also a densely hairy cone, glabrous on the inside surface, on each side of the lip above; the lower side-lobes short, truncate, green-edged, reflexed, and the mid-lobe prolonged into a rather long green glabrous moderately acute appendix, turned up and concealed, like the other lobes, behind the lip. At the base of the column on each side is a greenish obtuse dark-tipped knob, like the eye of a snail. **Column** long, green, at right angles to lip, its base forming a hemispherical chamber, on the inside surface of which is the stigma. **Rostellum** with two separate pouches, each enclosing a viscid disc with its attached pollinium. **Anther** with a long flexuous beak. **Pollinia** yellow, pear-shaped; caudicles long, very slender, thread-like, flexible, elastic, yellow. Seed-capsule large, long, oblong with prominent ridges. **Seeds:** testa transparent, usually straight, nearly of equal width throughout; cells long, fairly wide, striate with well-marked nearly parallel sometimes forked transverse striæ, closer and easier to see than in *O. maculata* (T. A. Dymes).

The continental monographists agree in describing the petals as very short (Schlechter says about 3 mm.) and triangular or nearly lanceolate in typical *O. apifera*, and this is markedly so on the French Riviera, where they are shorter than the column. In Britain the petals are usually much longer, about half as long as the sepals,

H. M. Godfery pinx.

OPHRYS APIFERA Hudson

A. Peloric form B. var. *Trollii*

C. Flower with anther a^3 fully developed

PLATE 58

A. **Ophrys apifera** Huds., peloric form. Sussex, June 23rd, 1930.

B. **Ophrys apifera** var. **Trollii.** Gloucestershire, June 30th, 1930.

C. **Ophrys apifera**, single flower (enlarged) with anther a^3 fully developed. Dorset, July 14th, 1930.

sometimes lanceolate, sometimes oblong-linear, with the edges so much rolled back that they appear tubular, resembling antennæ, and are then often dark reddish purple, suggesting a resemblance to those of *O. muscifera*, but too frequent and widely distributed to be due to hybridity. This is probably the same as *O. apifera β aurita* Moggridge,[1] which according to J. Ruppert is as frequent in Germany as the type (*E.B.* t. 65). Isle of Wight. Surrey! Somerset! In Moggridge's figure (reproduced by Schulze in *Orch. Deutschlands*) the petals are flat and acute, not rolled into a tube. They are said to be green, sometimes with rosy edges. Plants near Salisbury had green petals.

Var. **chlorantha** Hegets. (Pl. 57 C). Sepals greenish white, whole lip yellowish green, usually without markings. White (*Fl. Bristol* (1912)) calls it forma *albida* and says it grows in fair numbers amongst the type. About a dozen were seen in bloom at Rancomb, Glos., in 1760.[2] Hegetschweiler's plant[3] was apparently a diseased abnormal form, with but moderate resemblance to the var. *chlorantha* as now understood, which is apparently due to a kind of albinism. A very similar form of *O. arachnitiformis* was found by Mr St Quintin at Hyères.

Var. **Trollii** Heg. (Pls. 57, 58). Wasp Orchid. Lip long, very narrow, tapering into the appendix, which is not turned up behind the lip, markings yellow and brown, very irregular, side-lobes very small. In the excellent figure in White's *Flora of Bristol* the petals are long and very narrow. In the specimen figured from Bex they were extremely short, as in the continental type of the species. In Hegetschweiler's original plant they were long,[4] and the plant looks abnormal, as if diseased, which prompted Prof. Chodat to say to me: "Perhaps there was only one Trollii". It is not a stable form, but varies according to the type of *O. apifera* from which it is a sport. Plants occur in some numbers at Winchester, Reigate and Salisbury which are intermediate between *Trollii* and *O. apifera*, of which a specimen from the last-named place is figured on Pl. 57 B. Regel considered it to be the hybrid *O. arachnites* (*fuciflora*) × *muscifera*, but in the English localities given above *O. arachnites* is unknown. Reichenbach thought it a form of *O. apifera* due to growth in deep shade, but it is found in the full blaze of the sun. The Winchester form approaching *Trollii* may be described as follows: sepals narrower than the type, much reflexed; petals about half as long as sepals, almost tubular, green tinged with red. Lip rather ovate, the apex like the toe of a shoe, from which the appendix projects like a sting, and often shows some tendency to curl backwards; the side-lobes are short, triangular, rounded at the base, not raised into hunches, densely hairy, the lower side-lobes very shallow, turned down. Markings irregular, sometimes with a shield-shaped darker area at the base of the greenish yellow lip, and a darker blotch at the tip.

[1] Moggridge, *Verh. Leop.-Carol. Acad. Naturf.* xxxv, 13 (1870).
[2] *Phyt.* p. 176 (1866). [3] Schulze, *Orchideen Deutschl.* Pl. 31*b*. [4] *Ibid.* Pl. 31*c*.

Mr C. B. Tahourdin[1] saw a specimen in Hants. with the long narrow lip and short side-lobes of *Trollii* and an indefinite appendix. The flower was white, faintly washed with yellow-green. He thought it might be fairly described as a white *Trollii.* He also found in Sussex a peloric form of *O. apifera* (Pl. 58 A), in which the lip was pink and petal-like (but much larger than the petals) and in shape suggestive of that of *Trollii.*[2] Mlle Camus found at Vence, above Nice, a spike in which one flower was normal *O. apifera*, whilst the other flowers showed the same variation as *Trollii.*[3] A spike from Dorset (Sir M. Abbot Anderson) showed Darwin's hypothetical anther *a*3 (probably the first anther to be suppressed) fully developed with pollinia (Pl. 58 C), of which I have only known one previous instance (in a spike of *O. arachnitiformis* at Hyères). The flowers of the former were more or less deformed, and showed an approach to *Trollii.* A second spike also from him was similar, the bottom flower in each spike practically normal.

Var. **albida** Garnier and Poulter (var. *albiflora* Rolfe).[4] Sepals white. Still grows near Bordean, Hants. (!), whence it was originally described 133 years ago. In all species of *Ophrys* with coloured sepals that I have seen the sepals are occasionally white, in the case of *O. arachnitiformis* in some places and seasons predominantly so.

Habitat. Usually a calcicole plant, thoroughly at home on chalk downs, limestone and oolite, and (rarely) also found in sand, as at St Ouen's Bay, Jersey, from which island chalk and limestone are entirely absent. Perhaps the plant benefits from calcareous fragments of shells, for *Spiranthes autumnalis*, another limestone plant, occurs in similar circumstances. It is, however, not confined to calcareous soils, being found on the Greensand in Kent (Smith's *Cat. Pl. S. Kent*, p. 53), also on stiff Lias Clay, Kimmeridge Clay and Oxford Clay (Druce, letter of May 22nd, 1922). Owing to its self-pollinating ability, it is often abundant where it occurs. In Ireland it occurs in pastures, drift banks, sandhills, etc., and is rather rare, but is abundant on clayey ground about Youghal. Sandhills near Rush (*Cyb. Hib.* p. 345). Flowers June to July.

Distribution. Not infrequent from Kent to Devon, extending to N. and S. Wales, York, Durham and Westmorland (*B.E.C.* p. 394 (1913)), and has been found in Lanark (Druce).

Var. **chlorantha.** Bristol. Gloucester (1760). Isle of Wight (P. M. Hall, as *flavescens*). A form with white sepals and cowslip-yellow lip was found in Kent in 1873 (Hanbury, *Fl. Kent*).

Var. **Trollii.** Bristol (White), V.R. Warwick (*B.E.C.* p. 129 (1917)). Seaton,

[1] Tahourdin, *Notes on British Orchids*, 1926–7.

[2] *Ibid.* Notes for 1924 and 1925. A similar form was found at Seaton, N. Devon, and another at Reigate, which latter, according to Mr J. G. Baker, was figured by Reichenbach as *O. Trollii. J.B.* p. 248 (1882).

[3] Camus, *Icon.* p. 325 (1929).

[4] *Annual Hampshire Repository*, vol. 1 (1799).

S. Devon (*J.B.* p. 248 (1882)). Forms varying towards *Trollii* occur at Salisbury! Winchester! and Reigate.

Fertilisation. The flowers of the Bee Orchid were primarily designed for cross-pollination by insects, the mechanism for the transport of the pollinia being exactly similar to that of all other species of *Ophrys* wholly dependent on insects for pollination.

Nevertheless self-pollination is the rule. The pollinia emerge from the anther-cells (their viscid discs, however, remaining *in situ* in the two pouches), and dangle on their long thread-like flexible caudicles just in front of the stigma. According to Darwin this takes place in the course of a few hours. The slightest breath of air makes them oscillate, till they touch the stigma, and are caught and held by its viscid secretion. He found that the pollinia of a spike in a still room remained free, suspended in front of the stigma, till the flowers withered, and said, "it can hardly be doubted that *O. apifera* was at first constructed to be regularly cross-fertilised".[1]

Robert Brown was the first to observe that the Bee Ophrys is capable of self-fertilisation, and erroneously believed that this peculiarity was common to the genus. Darwin pointed out that even now the pollinia can be withdrawn on a pencil in the same way as those of other species of the genus (sometimes even after they have adhered to the stigma) and also go through the same motion of depression till they assume the exact position for touching the stigma of another flower. If the pencil be then inserted into another flower, several packets of pollen adhere to the stigma, and the elastic threads fastening them to the pollinia break, leaving them on its viscid surface. The mechanism for the transport of the pollen is thus still in good working order. No wonder that Darwin was surprised that none of its parts showed any tendency to abortion, in spite of their uselessness to a self-fertilising plant. He, however, overstated the case when he said that *O. apifera* has "almost certainly been propagated in a state of nature for thousands of generations without having been once intercrossed".[2]

That cross-fertilisation actually occurs in nature at the present day is proved by the fact that natural hybrids have been found between *O. apifera* on the one hand and *O. arachnites* (Pl. 56), *aranifera*, *litigiosa* and *scolopax* respectively, on the other. These could not possibly have arisen without the effectual visit of the same individual insect to both the parents concerned. For one such visit to two different species of *Ophrys* in succession, there must be very many more in which the insect confines itself solely to *O. apifera* in conformity with the usual habit of bees. Darwin[3] states that out of 106 flowers gathered in Surrey three had lost one pollinium, and that out of 136 flowers in the Isle of Wight 10 had lost both pollinia and 14 had lost one.

[1] Darwin, *Fert. Orch.* ed. 2, p. 58.
[2] Darwin, *Cross- and Self-fertilisation*, p. 439.
[3] Darwin, *Fert. Orch.* ed. 2, p. 55.

In 11 of these the caudicles had been gnawed by snails. Omitting these, there still remained 13 flowers from which one or both pollinia had been removed. In 1922 at Vence above Nice I found a spike from the lowest flower of which both pollinia had been removed, and two others from the lowest flower of which one pollinium had been taken. Three days later, on May 17th, I found three spikes from a flower of which both pollinia, and two spikes from a flower of which one pollinium had been cleanly removed. This could only have been due to the agency of insects, and shows that their visits are not so rare as might be supposed. Long and often as Darwin watched plants of the Bee Ophrys, he never saw one visited by any insect. Smith, however, in his *Catalogue of Plants of S. Kent*, p. 25 (1829), says: "Mr Price has frequently witnessed attacks made upon the Bee Orchis by a bee, similar to those of the troublesome *Apis muscorum*". What this sentence means Darwin could not conjecture,[1] for in those days the existence of any other lure than honey or edible tissue had never been suspected. In the light of the recent observations of M. Pouyanne on Algerian species of *Ophrys* (see *Ophrys*) and my own discoveries of the visits of *Gorytes mystaceus* to *O. muscifera*, and of *Eucera tuberculata* to *O. arachnites*, Mr Price's statement is easily intelligible. He had the great good fortune to witness the visits of some male Hymenopteron to *O. apifera*, attracted by the resemblance of the lip to a female of its species. He probably watched plants growing near a bank containing pupæ of the not yet emerged females, on ground over which the earlier developed males were carrying on their eager quest for a mate. Well might he refer to these visits as attacks, for to an onlooker the bee appears to be trying to sting the labellum of the *Ophrys*. The reason why it is so extremely difficult to witness the visits of Hymenoptera to *Ophrys* is that there is very little chance of doing so unless the plants are growing, or unless cut flowers are taken, near the ground in which the burrows of the insect concerned are situated. The males seem not to wander far as a rule from the banks, etc., where the females still lie in the pupa state.

G. E. Smith[2] states that the pollinia are withdrawn by the contraction of the caudicles with so much elasticity that they strike the stigma, and C. B. Clarke[3] speaks of the same thing, but as the length of the caudicles *in situ* is greater than the distance from the base of the pollinia to the rostellum, and as the pollinia are so frequently found dangling free in front of the stigma, this appears to be an exceptional occurrence. It might perhaps be due to an abnormal lengthening of the column.

O. apifera shares with *Cephalanthera grandiflora* the distinction of having been organised for two distinct but concurrent methods of pollination—(1) cross-pollination by insects in the usual manner, (2) self-pollination if no insects of the right size visit the flowers. Hitherto it has been regarded as wholly self-fertilised.[4]

[1] Darwin, *Fert. Orch.* ed. 2, p. 56.
[2] *Cat. Pl. S. Kent*, p. 53.
[3] *J.B.* p. 369 (1882).
[4] *J.B.* p. 285 (1921).

OPHRYS APIFERA × ARACHNITES
× Ophrys Albertiana Camus
Pl. 56 C (p. 231)

A specimen sent to me by Mr H. Walker from Folkestone, July 15th, 1919, now in the herbarium of Mr F. J. Hanbury of East Grinstead, showed the following characters. Stem 24 cm. tall, leaves lanceolate acute, spike 6-flowered, 10 cm. long, bracts lanceolate acute. The part-parentage of *O. apifera*, which the flowers resembled in general appearance, was suggested by the strongly convex lip, the long narrow deflexed sepals (broader, shorter, more elliptical and spreading in *arachnites*) and by the rather long distinctly curved beak of the anther, which is short and blunt in the last-named species. It resembled *O. arachnites* in the short triangular petals with rounded basal lobes dark rose in colour, the undivided lip, and the short toothed appendix turned up in front of the lip. The caudicles, a little less than twice as long as the pollinia, were flat and ribbon-like at base, as in *arachnites*, and thread-like at the apex, as in *apifera*, standing erect when withdrawn, and moving down quickly. One flower had been pollinated.

A second specimen from Mr Walker on June 15th, 1930, had almost exactly the lip of the Bee Orchid in front view, but with the broad 3-toothed appendix turned up in front of *O. arachnites*. The hunched side-lobes were like those of *O. apifera*, and the anther had the long beak with the peculiar curve of that species. The petals were livid, green flushed with rose. The pollinia did not descend on the stigma. Pl. 56 C.

OPHRYS APIFERA × ARANIFERA
× Ophrys epeirophora Peter

Two specimens of this hybrid are recorded as having been gathered near Shoreham, Kent, in 1898, by Mr G. L. Bruce, in Hanbury and Marshall's *Fl. Kent*, p. 334. Cf. G. E. Smith, *Cat. Pl. S. Kent*, p. 58. No description was given. I have never seen this hybrid.

ADVENTIVE SPECIES
GYMNADENIA ODORATISSIMA Rich.

Tubers bifid, segments usually bifid. Stem 20–40 cm. Leaves linear, narrower than in *G. conopsea*, rather glaucous, erect or arched, minutely denticulate, the lower thick, more or less folded, keeled, the upper bract-like. Spike slender, dense except at the base, cylindrical but rather short. Bracts lanceolate acuminate, about equal to ovary. Flowers very small (5–8 mm. long), pale rose-red to lilac, sweet-scented, like vanilla.

Lip slightly longer than broad, 3-lobed, mid-lobe longer, obtuse, rarely acute. Spur slender, curved, slightly swollen at the apex, scarcely as long as the ovary. Pollinia greenish yellow, caudicles white. Viscidia longer than broad. Stigmas on face of side-lobes of column.

Habitat. Humid calcareous ground. A solitary specimen of this is recorded as having been found "Between Juniper Hill and Box Hill, Surrey, June 28th, 1833".[1] A second specimen is reported to have occurred in the south of England, "but some error may have arisen through the circumstance of *conopsea* differing much in scent according to soil or humidity".[2]

Prof. J. W. Heslop Harrison[3] writes: "In July 1912, I picked a very large and unusual spike of what I took to be the Fragrant Orchis (*Gymnadenia conopsea*) at the Black Hall Rocks. However, as it failed to answer to that plant in my floras, I ran it down in several continental books to *Gymnadenia odoratissima*, a continental plant not previously recorded from Britain. Subsequent search has failed to reveal further specimens. It is worth noting that the habitat was a correct one—on limestone—and one which has almost a monopoly of certain lime-loving plants in our islands". This was on Magnesian limestone in E. Durham.[3]

Prof. Heslop Harrison kindly sent me the dried specimen and a dissected flower mounted on a slide. The leaves agreed with *G. odoratissima*, and were very finely denticulate, but this is also the case with *G. conopsea*. The bracts, sepals, petals and spur also agreed, and especially the lip, longer than broad, with produced mid-lobe. Continental writers, however, agree that the spike is rather short and slender, and the longest spike I have seen was 8·5 cm. In the Durham specimen it was about 16 cm. long, and rather strongly curved, whereas in *G. odoratissima* it is very straight and tapering. Had I found this specimen abroad I should have put it down as *G. conopsea* × *G. odoratissima*. A seed might easily be carried on the foot of a water-bird.

ORCHIS PALLENS L.

Tubers ovoid, leaves broadly oblong, bracts yellowish with membranous edges, equalling or exceeding the ovary. Flowers rather large, sulphur-yellow, smelling of elder. Lip broad, shallowly 3-lobed, brighter yellow, not spotted. Spur cylindrical, yellowish white, ascending or horizontal.

Mrs Tristram (née Cardew) informed me that two or three specimens suddenly appeared and flowered for several years on a wild bank above her grandmother's tennis-court at Liss, Hants., who was herself somewhat of a botanist, and knew every plant which had been introduced into the grounds. Some cartloads of soil from

[1] W. Pamplin and A. Irvine in *Mag. Nat. Hist.* IX, 475 (1836).
[2] *Cybele Brit.* II, 429.
[3] *The Vasculum*, pp. 18, 31 (June, 1915).

Woolmer Forest, three miles away, had been unloaded there 35 years before the *Orchis* appeared. It was at first thought to be a yellow *O. mascula*, but Mrs Tristram examined a good many dried specimens of *O. pallens* from Germany, which she concluded were identical with the Liss plant, in which the late Mr C. E. Salmon of Reigate concurred. I sent her a water-colour drawing by my late wife of *O. pallens* from Switzerland, and she said that except that the Liss flowers were rather more yellow, the plants were exactly the same. She sent me a dried specimen of it, which in my opinion was *O. pallens*. She mentioned that it had a very distinct smell, and Mr Salmon wrote: "Scent strong and peculiar". *O. pallens* would have deserved the name *sambucina* much more than *O. sambucina* itself, on account of its elder-flower smell. The last time Mrs Tristram saw them there were three plants, two of which were flowering. Her grandmother, just before her death, ordered the remaining plant to be sent to her, but it arrived without the new tuber. She suggests that seeds may have been brought over on the claws of birds. In any case it is remarkable that a sub-alpine plant like *O. pallens* should have sprung up spontaneously in England.

Orchis laxiflora Lam.

Adventive near Hartlepool. See *O. laxiflora*.

Serapias neglecta De Notaris

Tubers ovoid. Stem 10–30 cm. Leaves linear-lanceolate, acute, not spotted. Bracts oval, acute, often tinged violet, equalling or slightly exceeding the helmet. Flowers with a peculiar scent, large, 2–6, in a short spike. Sepals and petals connivent in a helmet, joined at the base, free at the tip. Lip 3-lobed, the rounded side-lobes curved upwards, projecting forwards a little from the helmet, mid-lobe more or less reflexed, large, oval, with wavy edges and bristling as well as its base with long hairs, and with two nearly parallel dark red callosities at the base, forming a channel leading to the column. Colour very variable, yellow or buff (with red or rose edges), brick red, or deep rose-red, very rarely pure yellow throughout.

A plant of this grew for a time in a field in the Isle of Wight, but has disappeared. As this is a Riviera and Italian plant, it is difficult to believe that it was introduced without human agency. *B.E.C.* p. 309 (1918).

APPENDIX

TABLE SHOWING THE NUMBER OF SPECIES IN EACH GENUS IN BRITAIN

Names of genera	No. of species
1. *Cypripedium*	1
2. *Cephalanthera*	3
3. *Epipactis*	6
4. *Goodyera*	1
5. *Spiranthes*	3
6. *Listera*	2
7. *Neottia*	1
8. *Malaxis*	1
9. *Liparis*	1
10. *Corallorhiza*	1
11. *Epipogon*	1
12. *Herminium*	1
13. *Cœloglossum*	1
14. *Platanthera*	2
15. *Gymnadenia*	2
16. *Neotinea*	1
17. *Anacamptis*	1
18. *Himantoglossum*	1
19. *Aceras*	1
20. *Orchis*	12
21. *Ophrys*	4
Total	47

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(Abbreviations used in the text are shown in brackets)

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GLOSSARY

Mainly for non-botanists. Gives only the sense in which the words are used in this work.

Abortive. Imperfectly developed.
Acuminate. Gradually diminishing to a drawn-out point.
Acute. Sharply pointed, but not drawn out.
Adherence, adherent. The union by adhesion of two different kinds of organs, e.g. sepal to petal; cf. **Coherence.**
Adpressed. Pressed flat against.
Adventitious roots. Those springing direct from the stem.
Adventive. Introduced, not native.
Albumen. Nutriment stored in the seed for nourishment of the young seedling.
Alternate. Placed opposite the spaces between the members of the next whorl of a flower; in the case of leaves placed alternately on opposite sides of the stem.
Amplexicaul. Embracing or sheathing the stem.
Anastomosing. Union of one vein with another—net-veining.
Anther. The part of a flower which produces the pollen, usually 2-celled and stalkless in orchids; when attached to a filament (stalk), the two together constitute a stamen.
Apex. The end furthest from the point of attachment.
Auricle. A little ear-shaped lobe.
Axil. The upper angle between stem and leaf.
Axile. Belonging to the axis.
Axis. An imaginary line round which the organs of a plant or flower are placed.

Base. The end of an organ nearest the point of attachment.
Bifid. Divided half-way into two lobes.
Bipartite. Divided nearly to the base.
Bracts. Small leaves from the axil of which the flower springs.

Callus. An abnormally thickened part.
Capsule. A dry many-seeded dehiscent seed-vessel.
Channelled. Folded or upcurved, forming a gutter.
Chlorophyll. The green colouring matter of leaves, etc.
Ciliate. Fringed with hairs.
Clavate. Club-shaped. Thickened upwards from a slender base.
Clinandrium. A shallow cup at the apex of the column, in which the pollinia are deposited in *Epipactis*, etc.
Coherence, coherent, cohering. Adhesion of two organs of the same kind, e.g. sepal to sepal.
Confluent. Blended into one, e.g. the stigmas of many orchids.
Conical. Tapering upwards, in transverse section circular.
Connate. Firmly united.
Connective. The membrane connecting the two cells of an anther.
Connivent. Converging together.
Cordate. Heart-shaped.
Cortex. Bark. The ground tissue between the stele and epidermis.
Cotyledon. A seed-leaf, of which monocotyledons have one, and dicotyledons two.
Crenate. With rounded teeth—scalloped.
Crenulate. Minutely crenate.
Cuneate. Wedge-shaped.
Cylindric. Elongated, with a circular cross-section.

Deciduous. Falling off in due season.
Decurrent. Prolonged down the stem, like the mid-rib and often the edges of bracts.
Dehiscence. The opening of an anther or of a seed-capsule by slits or valves.
Deltoid. Triangular, with nearly equal sides.
Dentate. Toothed.
Denticulate. Minutely toothed.
Diagnosis. A summary of the important characters of a species, genus, tribe, etc.
Diandrous. Having two anthers.
Dicotyledon. Plant having a pair of seed-leaves (cotyledons).
Dicotyledonous. Having a pair of seed-leaves.
Disc, viscid. Darwin's term for the disc-like membrane, very sticky beneath, to the top of which the pollinia are attached by their caudicles in *Orchis*, *Ophrys*, etc. The viscidium.
Distichous (of leaves). Arranged alternately one above another in two opposite rows.
Divergent. Gradually separating so as to form an angle with each other.
Dorsal. Belonging to the back.
Dorsally compressed. Compressed from back to front.

Downy. With soft hair or down.

Elliptical. Oblong with rounded ends.
Elongate, elongated. Lengthened.
Emarginate. Having a notch at the apex.
Embryo. The part of a seed which develops into a plant.
Endophyte. A plant living within another plant, as certain fungi within the roots or seeds of orchids.
Entire. With unbroken edges, without teeth or lobes.
Epidermis. The outer skin.
Epiphyte. A plant growing on another plant, but not deriving nutriment from it.
Erect. Ascending vertically, upright.
Erecto-patent. More or less erect, but slightly spreading.
Exotic. Not native, introduced from abroad.

Facies. The general aspect of a plant.
Family. A group of tribes, genera, etc., formerly called an order.
Fascicled. In a bundle.
Fertile. (Anther) producing pollen. (Ovary) producing viable seeds.
Fertilisation. The fecundation of an ovule by protoplasm from the pollen-grain conveyed by the pollen-tube.
Filament. The stalk of an anther.
Filiform. Thread-shaped, thread-like.
Floral envelopes. Sepals and petals.
Foliaceous. Leaf-like.
Fusiform. Spindle-shaped.

Genus. A natural group of plants built up of species.
Germen. Linnæus' term for the ovary.
Germination. The first act of growth of a seed; sprouting.
Glabrous. Without hairs.
Gland. A secreting organ.
Glandular-hairy. With hairs tipped with glands.
Glaucous. Bluish or whitish green, like a cabbage-leaf.
Globose. Nearly spherical.

Habit. The general appearance of a plant.
Helmet. The hood formed by the connivence and often partial adherence of sepals and petals.
Herbaceous. Green, and with the more or less opaque texture of a leaf, as opposed to petaloid, white or coloured with the translucent texture of a petal.
Hermaphrodite. Having both pollen-bearing and seed-bearing organs in the same flower.
Hispid. Covered with rather stiff short hairs.
Hoary. Grey or whitish from fine pubescence (soft hair or down).
Homologue. The equivalent in one plant of a somewhat dissimilar organ in another.
Hooded. With a concavity or hood at the tip.
Hyaline. Colourless and translucent, glass-like.
Hybrid. A cross between two different varieties, species or genera.
Hypha, pl. hyphæ. The thread-like growth of certain fungi.

Icones. Pictures or figures of plants.
Incision. A notch or indentation in the margin.
Indigenous. Native, not introduced.
Inferior. Below, as the ovary is below the sepals in the Orchidaceæ.
Inflorescence. The flower-cluster.
Internode. The space between two nodes of the rhizome or stem.

Keel. A prominent ridge.
Kernel. The embryo of the seed of an orchid, the dark rounded body within the glass-like testa.

Labellum. The lip of an orchid, a development of the third petal, often the most conspicuous part of the flower.
Lanceolate. Narrow, tapering at each end.
Lateral. Placed on the side, e.g. a lateral sepal is a side-sepal.
Laterally compressed. Compressed sideways.
Lax. Loose—the opposite of dense.
Limb. The expanded part of a leaf, sepal, petal, etc.
Line. The twelfth part of an inch = 2·1167 millimetres.
Linear. Long and narrow with nearly parallel sides.
Lip. See **Labellum.**
Lobe. A 2-lobed, 3-lobed, etc., organ is one cleft into two or more often rounded more rarely acute divisions, e.g. the lip of an orchid.
Lobelet, lobule. A small lobe.

Micropyle. The minute aperture by which the pollen-tube enters the embryo.
Mid-rib. The principal nerve in a leaf.
Mon- (prefix), one. **Monandrous.** Having one anther.
Monocotyledon. Plant having only one seed-leaf.
Monostelic. Having but one stele or central cylinder (pith).
Monstrosity. A departure from the usual natural structure.

Morphological. Concerning the shape or form.
Morphology. The study of shape or form.
Mucronate. Tipped with a short straight point.
Mycorrhiza. Fungi living in symbiosis in the roots or seeds of orchids.

Naturalised. Introduced, but establishing itself as if a native.
Nectar. Honey.
Nectary. The organ which secretes honey, usually the spur in orchids.
Nerves. The principal veins of a leaf, sepal, petal, etc.
Netted. Reticulated, net-veined.
Node. A knot in a stem or root.
Normal. The ordinary usual condition.
Nucleus. The kernel (embryo) of the seed. The minute body in a cell which plays a leading part in cell-division.

Ob- (prefix). Inversely.
Obconic. Conical, but attached by the narrower end.
Ob-cordate. Inversely heart-shaped.
Oblique. Slanting.
Oblong. Longer than broad, with nearly parallel sides.
Obovate. Inversely ovate.
Obscure. Difficult to see.
Obsolete. Wanting or rudimentary.
Obtuse. Blunt or rounded at the tip.
Opposite. At the same height on the stem, but on opposite sides (of leaves); one organ in front of another, as a stamen in front of a petal.
Orbicular. Round and flat.
Oval. Oblong with rounded ends, about twice as long as broad.
Ovary. The immature seed-vessel, formerly called the germen.
Ovate. Egg-shaped, but flat.
Ovule. The young seed before fertilisation.

Palmate. Roughly hand-shaped, with finger-like lobes.
Papillæ (Lat. a nipple). Small superficial protuberances.
Papillose. Covered with papillæ.
Parasite. A plant subsisting on the living tissues, sap, etc., of another plant.
Parietal. Borne on or belonging to a wall.
Parietal placentæ. The forked organs bearing the ovules which arise from the walls of the ovary.
Patent. Spreading.
Peduncle. The flower-stalk.
Peloria (Gr. a monster). An irregular flower abnormally assuming an appearance of regularity, as an orchid-flower with three petals or three lips. Adj. **peloric.**
Pendent. Hanging down.
Perianth. The floral envelopes, i.e. sepals and petals.
Petaloid. White or coloured, with the semi-transparent texture of a petal.
Petals. The inner whorl of the floral envelopes, in orchids only two, the third having been transformed into the lip.
Petiole. The stalk of a leaf.
Placenta. The part of the ovary which bears the ovules.
Pollen. The male element (pollen-grains) produced by the anther.
Pollen-tetrads. Pollen-grains cohering in fours.
Pollination. The placing of pollen on the stigma.
Pollinium, pl. **pollinia.** The body or bodies built up of pollen-tetrads (or single pollen-grains in *Cephalanthera*) in the Monandræ.
Polystelic. With more than one stele. See **Stele.**
Pseudo- (prefix), false. **Pseudo-bulb,** a thickened and bulb-like internode in some orchids.
Pubescent. Clothed with soft hair or down.

Raceme. A spike with stalked flowers.
Radical. Arising from the root or its crown.
Raphides. Needle-shaped crystals in some cells of certain plants.
Recurved. Curved backwards or downwards.
Reflexed. Bent or turned backwards or downwards.
Reniform. Kidney-shaped.
Reticulate. Forming a network.
Retuse. With a shallow notch at the rounded apex.
Rhizome. Rootstock—subterranean stem producing roots and shoots.
Rhomboidal. Obliquely square or oblong.
Rib. A primary vein of a leaf, especially the central or mid-rib.
Rostellum. The floral mechanism of an orchid for attaching the pollinia to visiting insects by means of a viscid secretion which quickly sets hard like cement.
Round. As applied to the stem, circular in section (terete).
Rudiment. An imperfectly developed and functionless organ.
Rudimentary. Imperfectly developed.
Rugose. Wrinkled.

Salep (salop, saloop). Food prepared from the dried tubers of certain orchids.

Saprophyte. A plant subsisting on decaying organic matter, but not drawing nourishment from a living plant.

Scale. A thin dry membranous body, not green, usually an undeveloped or degenerate leaf.

Secund (of an inflorescence). Turned to one side.

Segment. One of the divisions into which a leaf, tuber, etc., may be cleft.

Self-fertilised. A flower fertilised by its own pollen.

Sepal. A member of the outer whorl of the perianth, or floral envelopes.

Sessile. Sitting close, stalkless.

Sheath. The tubular base of a leaf enclosing the stem. **Leafless sheaths.** Those at the base of a stem which have not developed a leaf-blade, but sometimes have a green tip.

Sinuate. Wavy: with a wavy margin.

Sinuous. Sinuate.

Sinus. A recess, e.g. the space between two lobes.

Stele. Pith or medulla.

Sterile. Barren, as an anther without pollen, or an ovary not producing seeds.

Stigma. The female organ of a flower which detaches and retains portions of the pollinia, in the Monandræ glistening with a sticky secretion, in the Diandræ dry and often rough with backward-pointing papillæ.

Stigmatic. Belonging to or secreted by the stigma.

Stolon. A runner or underground shoot rooting and forming a new plant.

Striæ. Markings, ridges or furrows presenting the appearance of lines.

Striate. With fine parallel lines.

Sub- (prefix). Almost, e.g. sub-acute, almost acute.

Sub-species. A permanent race of a species, hardly yet sufficiently differentiated to deserve specific rank, but probably evolving into a distinct species.

Suspensor. The end of the loose transparent covering (testa) of the seed, by which it was attached to the ovary.

Symbiosis. Living together of dissimilar organisms, e.g. plant and fungus.

Synonym. Another name for the same plant which has failed to secure general acceptance.

Teratology. The study of malformations and monstrosities. Adj. **teratological.**

Ternate. In threes.

Testa. The loose transparent netted outer covering of the seed.

Transverse. Cross-wise—the opposite of longitudinal.

Tribe. A group of plants whose units are genera.

Trifid. Three-cleft to about half-way down.

Tripartite. Three-cleft nearly to the base.

Trivial. The second or specific name, e.g. *mascula* in *Orchis mascula.*

Truncate. Square at the end, as if cut off.

Tuber. The rounded, palmate, or more rarely carrot-shaped underground bulb-like offshoot of an orchid, from which the leaves and flower-stem of next year's plant spring.

Tubercle. A little tuber.

Tubercled. Covered with warty excrescences.

Tuberisation. Thickening of a root through invasion by mycorrhiza, such as *Rhizoctonia repens*, etc. Adj. **tuberised.**

Tuberous. Thickened as above, tuber-like.

Unilateral. Turned to one side.

Variety. A form differing from the type of a species.

Vegetative reproduction. Increase by development or division of the plant itself, not by seed.

Veins. Conducting vessels in flat organs such as leaves, etc.

Vermiform. Worm-shaped.

Versatile. Turning freely on its support, as many anthers on their filaments.

Vessel. A duct or tube.

Viable (of seeds). Capable of germination.

Viscid. Tenaciously sticky.

Viscidium. The tiny membrane to which the pollinia are attached, which adheres to insects by its viscid under-surface.

Whorl. The arrangement of organs in a circle round an axis.

Whorled. Arranged in whorls.

Winged. Having a wing-like usually membranous expansion.

Zygomorphic. Divisible into similar halves in one plane only.

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Synonyms in italics. Figures in black type refer to the main entry.

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