

no doubt referring to the Solander specimen and the one placed next to it in Linnaeus's herbarium.

Most of the species described by Linnaeus in manuscript in his interleaved copy of the *Species Plantarum* were incorporated into his second edition, but that of *C. angustifolia* was struck out and discarded. This corresponds with the change of epithet on the 'type' sheet, and it seems certain that Linnaeus changed his mind about this being a distinct species, hesitantly referring it to his *C. filiformis*.

At this point it may be of interest to quote from Th. Holm, "Studies in the Cyperaceae, XVIII." (1903, *Amer. Journ. Sci.*, Ser. 4, 15: 147): "It is a well known fact that a large number of the specimens collected by Linnaeus do not correspond with the diagnosis, written by himself, and the reason for this is thus explained: Linnaeus did not preserve such material as he had already described, and which he described in the field, but he preserved such specimens which were either very rare and not readily accessible or such as he thought differed somewhat from those already described. These he laid into his herbarium with the intention of comparing and studying them later."

The above evidence appears sufficient to dispose of the view of Goodenough and certain later authors that the Solander specimen from Lapland represents the true *C. filiformis* L. There is, however, further proof. Solander's specimen cannot have been the *Flora Suecica* plant, on which, with Scheuchzer's, *C. filiformis* was founded, because Solander was only nine years old when the *Flora Suecica* was published, and his specimen was collected in Lapland (for which country *C. filiformis* L. was not recorded), probably in 1755, two years after this species was published in the *Species Plantarum*.

It is, therefore, reasonably certain that the plant described in the *Flora Suecica*, no. 760, to which Linnaeus gave the name *C. filiformis* in the *Species Plantarum*, p. 976, but of which no specimen was preserved, is that known hitherto to British and other European botanists as '*C. tomentosa* L.' I therefore formally typify *C. filiformis* L. in this sense, choosing as lectotype Scheuchzer's description and figure.

## STUDIES IN THE BRITISH EPIPACTIS.

By D. P. YOUNG.

### III. EPIPACTIS PHYLLANTHES G. E. SM., AN OVERLOOKED SPECIES

In 1852 Gerard Smith described in the *Gardeners' Chronicle* a new species of *Epipactis*, to which he gave the specific epithet *phyllanthes*. In view of the complete oblivion into which his observations have fallen, no apology is needed for repeating his note in full:

#### EPIPACTIS PHYLLANTHES

The recent notice of an *Epipactis* in your pages, as being sent to you by Mr. Harcourt, of Westdean House, has led me to send you a copy of the lithograph of an *Epipactis*, and of the MS. notes upon it, which I collected in the upper part of Phillis Wood, near Westdean, Sussex, in the years 1838-9, and described by comparison at the time. I do not doubt that Mr. Harcourt's plant and mine are the same. In its lip, flowering season, and general structure, it differs widely from *E. latifolia*. I named it *phyllanthes*, for distinction's sake. Some notes in addition I have given on the same sheet with the description. Gerard Smith, Ashton Hayes Parsonage, September 29.

#### "EPIPACTIS PHYLLANTHES, G.E.S.

(GREEN-FLOWERED HELLEBORINE. PHILLIS WOOD, SUSSEX.)

Spec. char.: Root leaves sheathing, broad-elliptic-ovate: upper ovate-lanceolate, all firm, keeled, smooth. Flowers secund, cernuous. *Lip ovate, undivided, pointed, convex and keeled on the back. Stigma rounded-angular.*

#### COMPARATIVE DESCRIPTION OF

<i>E. phyllanthes.</i>	<i>E. latifolia.</i>
<i>Plant.</i> scattered in groups, or solitary, 6 to 18 inches high.	The same, on similar stations.
<i>Roots.</i> copious, zigzag, uniform, simple, blunt, downy.	
<i>Stems.</i> erect, wavy, round and purple at the base, angular and yellowish-green above. Young shoots pink. Stem occasionally glandular, downy above.	The same, but dull grey-green or purple, and downy.
<i>Leaves.</i> broadly elliptic below, with smooth sheaths, narrowing upwards into the lanceolate bractees: their substance firm, scarcely plaited, but rather striated: with 1 to 3 principal, and many smaller parallel veins, edged with minute glandular hairs, obtusely pointed.	Substance thin, plaited. Principal veins many; edges serrulate.
<i>Raceme.</i> of alternate cernuous flowers, on longish green stalks.	<i>Flower-stalks</i> shorter, and purplish in many cases.
<i>Germen</i> obovate taper, roughish.	The same, but short.
<i>Flower bud.</i> triquetrous; point long deflexed.	<i>Bud</i> with a short straight point.

*E. phyllanthes.*

*Sepals* ovate, taper pointed, often cohering at the points, pale green; keels, darker green.

*Petals* ovate, concave, keeled, yellowish green.

*Lip*, similar in form and texture to the petals, *ovate, pointed*, presenting a smooth gibbous convexity at the back, and *keeled*.

*Pollen masses*, in two close, ovate cells. *Stigma* rounded angular, *point prominent*.

Flowering at least one month earlier than *E. latifolia*, and in seed when *E. latifolia* was in full bloom.

Flowers scentless, Sept. 1838, July 1839.

*E. latifolia.*

*Sepals* broader, green or purple.

*Petals* purplish, or pink.

*Lip* of two portions. 1, the upper, cup-shaped, crenate, shining and ribbed on the convex back; 2, the lower, uniform, with an obtuse, recurved point; above communicating by a channel which has callosities on either side with the cup-shaped superior portion.

*Pollen masses* the same. *Stigma* squarish, *point flattened*.

*E. latifolia* had scarcely expanded its dark-green cluster, on every locality as to elevation, when *E. phyllanthes* was in perfection.

This pretty plant was gathered from a single locality, upon the elevated part of Phillis Wood, near Westdean, Sussex, on a gravelly soil, where it occurred with *Galium verum*, *Fragaria vesca*, &c., under the shade of dwarf Sallows and Birches, first in seed in Sept. 1838, and the second time in blossom July, 1839; and was regarded as a variety of *E. latifolia* in which the lip had been replaced by a petaloid leaf. The form of this part has proved uniform in all the specimens examined.

I have specimens of *Ophrys fucifera* E.B.S. to 2649, in which the lip is replaced by a sepal; and this year I gathered at Killin, in Perthshire, a plant of *Habenaria bifolia* with a sepaliform lip.

But there are points in the structure, texture, and flowering season of *E. phyllanthes*, G.E.S., which render its distinctness from *E. latifolia* possible.

The lip and petals being uniform, the plant in description approximates *Goodyera*, and when I gathered it, it occurred to me that this might be the plant mentioned in Camden as *G. repens*.

Excepting the crenulated lip, the following species closely resembles our plant:—

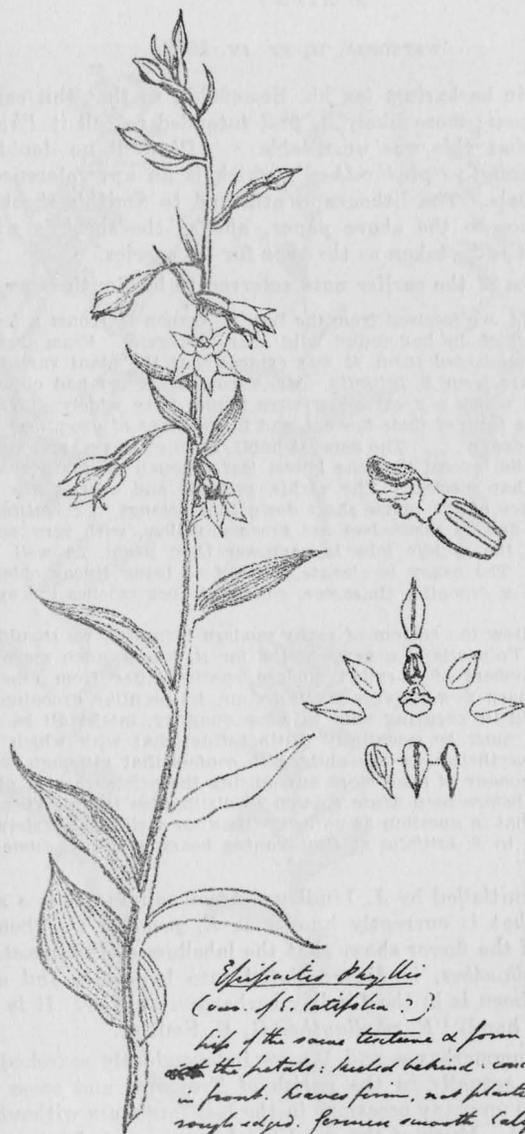
*Serapias microphylla*, fol. caulinis ovato-lanceolatis, inferioribus brevissimis, flor. cernuis, labello ovato acuto crenulato, cal. subaequali. Ehrhart Beitrage [sic], 4, p. 42. Habit. in sylvis montosis. Persoon. Syn. Pl. 1807, 1990, 2.

Sir James E. Smith, under *E. latifolia*, Engl. Flora, vol. iv, 418, 1, p. 41, observes, "a specimen in which the lip is perfectly entire, was sent me from Worcestershire many years ago as a new species."

The examination of a large number of specimens of *E. latifolia* has not afforded a single instance of approximation to *E. phyllanthes*, in the form of the lip.

This plant is evidently the same with that figured in the *Gardeners' Chronicle*, No. 34, p. 536 [sic] 532, for August 21, 1852, as having been received from the Hon. and Rev. L. V. Harcourt, of Westdean-house, and described in that number, as well as referred to again in No. 35, p. 549, for Aug. 28."

In the Borrer herbarium at Kew is a sheet with four stems of what is undoubtedly Gerard Smith's plant (see Plate 5). It is labelled in his handwriting, "*Epipactis Phyllis*. Phillis Wood, Sussex, 1839." Attached to it is a copy of a lithograph, evidently the one to which he refers (Fig. 1). This also bears the name "*E. Phyllis*", as does another



*Epipactis Phyllis*  
(var. of *E. latifolia*?)  
Lip of the same texture & form as  
with the petals: keeled behind, concave  
in front. Leaves firm, not pliant,  
roughly edged. Foremen smooth (along &  
petals often cohering at the points, &  
somewhat irregular in proportion in  
different flowers. Color pale yellowish green.  
Phillis wood, Sussex, July, 1839.

Fig. 1.

Gerard Smith's lithograph of *Epipactis phyllanthes* ("Phyllis").

Courtesy of Royal Botanic Gardens, Kew.

copy in the main herbarium (ex hb. Bromfield), so that this can hardly be a *lapsus calami*; more likely he first intended to call it *Phyllis*, but later decided that this was unsuitable. "*Phyllis*" no doubt led by mental suggestion to "*phyllanthes*", which is an apt reference to the thick green tepals. The lithograph attached to Smith's sheet further bears a reference to the above paper, and so the sheet is without a shadow of doubt to be taken as the type for his species.

The substance of the earlier note referred to by Smith is as follows:

"In August, 1851, we received from the Rev. L. Vernon Harcourt a few flowers of an *EPIPACTIS*, which he had found wild near Chichester. From these, and a sketch which accompanied them, it was evident that the plant varied in some striking particulars from *E. latifolia*. Mr. Vernon Harcourt had observed that the specimens, of which a great many were found, were widely different from that species in the form of their flowers, and in the want of downiness upon the flower-stalks and ovary . . . The general habit, form of leaves, and stature, are those of *E. latifolia*; except that the lowest leaf is much narrower than in the usual forms of that species. The rachis, pedicels and ovaries are perfectly smooth, not a trace of the coarse short down that belongs to *E. latifolia* being observable. The flowers themselves are greenish-yellow, with very acute divisions; in the lip the middle lobe is narrower than usual, as well as much sharper pointed. The ovary is clavate, instead of being linear oblong. The raceme itself has a drooping character, which at once catches the eye of the observer.

Were we to follow the custom of many modern botanists, we should at once declare that our *Epipactis* is a new species, for it differs much more from *E. latifolia* than numbers of so-called modern species differ from others. Its smoothness, its sharp flower-divisions, its colour, its peculiar drooping flowers, and we might add its occurring wild in some quantity, might all be regarded as proofs that it must be essentially distinct from that with which we have compared it. Nevertheless we are obliged to confess that although we should be proud of the honour of once more announcing the existence of a plant that no one had ever before been acute enough to distinguish in this kingdom, yet we must regard that in question as no better than an accidental variety, having the same relation to *E. latifolia* as *Rosa cantina* bears to the *R. dumetorum* of Woods [sic]."

The note is initialled by J. Lindley. Accompanying it is a splendid engraving of what is currently known as *E. pendula* C. Thomas; an enlarged view of the flower shows that the labellum of this plant, unlike Smith's *E. phyllanthes*, is differentiated into hypochile and epichile. Harcourt's specimen is in the Lindley herbarium at Kew. It is labelled (not in Smith's hand) "*E. phyllanthes* G. E. Smith".

Mr. V. S. Summerhayes and I have independently searched Phillis Wood (which is actually in the parish of Treyford, and some 3 miles from West Dean) on many occasions in the last few years without re-finding Smith's plant. Much of the wood has been converted into a conifer plantation, and the small area which is on a drift of gravel (most of the wood is directly on chalk) and so answers to his description, is very overgrown now. One may hope that diligent search will nevertheless turn up *E. phyllanthes* in its *locus classicus*.

Only two other sheets of the same plant from the same locality have come to light. These are two small specimens in Herb. Druce (Oxford), ex herb. N. Tyacke, and are undated. Tyacke lived at Chichester from



*Epipactis phyllanthes* G. E. Sm., type specimen.

1840 till 1900; the specimens look nearer 100 years old than 50. One is labelled "*E. latifolia*, var. Lip replaced by a concave calycine leaf, nicked behind".

What is to be made of these plants?

Gerard Smith's description, figure, and specimens clearly refer to an *Epipactis* closely related to *E. pendula* C. Thomas and *E. vectensis* Brooke & Rose. In fact, the lithograph makes it plain that the anther is cylindrical and pedunculate—a detail confirmed by dissection of Smith's and Tyacke's specimens—which relate it more closely to the Kentish "*E. vectensis*" (cf. Part II; Young 1949). The sole difference is the labellum, which in the Kentish plant is degenerate but nevertheless shows some relics of differentiation, and in the Phillis Wood plant is completely undifferentiated, or as Tyacke remarks, with only nicks as the sign of division between hypochile and epichile. Smith does not comment on the discrepancy in the lip-form between *phyllanthes* and Harcourt's plant. It would be too much to say that he intended his species to include both forms, although he obviously realised that they were closely related. Since he lacked the conviction that it was a good species, he may have forborne from pressing the matter, especially in the teeth of criticism from Babington (see below)

Smith makes no mention of the fertilisation mechanism, which would hardly have been expected at that pre-Darwinian period. The "point" of the stigma probably refers to the protuberance carrying the rostellum or relics thereof. No sign of a rostellum can be seen in his drawing. It can be argued that the plant cannot have been insect-fertilised, since the sepaloid labellum would be unlikely to have secreted honey; the undifferentiated lip and the pendent and sometimes non-opening flowers would also discourage visits from insects. Nevertheless, it set good seed in the majority of capsules, as shown by Smith's specimens. Therefore it must have resorted to some form of autogamy. One may also appeal to analogy with the other British forms related to or apparently identical with Smith's plant, and which are known to be autogamous.

The relationship between the present plant and the other members of this group of *Epipactis* will be discussed in Part IV (following paper). It must first be established that Smith's name *Epipactis phyllanthes* is valid.

Despite the somewhat diffident tone of his paper, there can be no doubt that Smith definitely proposed and published the name therein. His description is clear and adequate, and is supported by type-material. If it be accepted—as can now be done unhesitatingly—that the plant is specifically distinct from *E. Helleborine*, *purpurata*, *atrorubens*, and (despite Smith's opinion) *microphylla*, it has no earlier synonyms. The remaining objection to its validity is that it is a monstrosity, on account of its sepaloid labellum.

Now, abnormalities are purely relative, in that their abnormality depends on rarity compared with the "normal". In the present case, all the plants in one colony appear to have been uniform in respect of the

sepaloid labellum, *teste* Smith, and supported by all extant specimens (eight plants in three gatherings). Plants of this group with similar lips have occurred at Wellow, Andover, Selborne, and Passfield (Hants), Byfleet (Surrey), Ascot (Berks), Melton (Suffolk), and Painswick (Glos.), either in uniform populations, in association with plants with "normal" (i.e. completely differentiated) labella, or with a series of intermediates with the completely undifferentiated form as one extreme (see Part IV following for further details). A variety of such frequency can hardly be classed as an abnormality. Nor can one regard it as abnormal on the ground that the modified lip interferes with reproduction, for this is simply not true. On the other hand, the form of *E. Helleborine* with a petaloid labellum which (I believe) occurs very rarely, can justly be regarded as an abnormality—a teratological sport—since it effectively prevents the normal means of reproduction.

The way in which Smith's paper has escaped further notice is very remarkable.

His name and specimen are referred to by Wolley-Dod (1937), who erroneously ascribes it to Borrer and states that it was never published. It is also mentioned without comment by Brooke (1950). Brooke & Rose (1940) refer to the specimen, which they include under their *E. vectensis*, without mentioning that it had previously been described.

The only contemporary comment that I have been able to trace is two letters to the *Gardeners' Chronicle* by Babington (1852); the first of these carries an editorial comment (by Lindley). Babington insisted that both Harcourt's and Smith's plants were his "*E. media*". His letters are polemical in tone and too long to repeat here, but they demonstrate that he himself had no clear conception of what "*E. media*" really was. He seizes upon the discrepancy in lip-form, but glosses over the question of the characteristic glabrous stem, remarking that he had never seen an *Epipactis* with a glabrous rachis. Since *E. media* Fries was a *nomen abortivum* (Fries cited two earlier valid specific names as synonyms), and Babington himself (*loc. cit.*) entertained grave doubts as to whether what he called *media* was the same thing as Fries's "species", his remarks have no sound basis at all.

It is tempting to speculate how the involved history of the study of *Epipactis* might have been altered had Smith and Lindley pushed their opinions more vigorously. They had grasped, more clearly than any author up to Brooke & Rose (1940), the essential features of this group of plants.

No doubt can now remain that *Epipactis phyllanthes* G. E. Smith must be regarded as a valid specific name and added to the British list. How this affects present nomenclature will be discussed in the following paper.

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## IV. A REVISION OF THE PHYLLANTHES-VECTENSIS-PENDULA GROUP

Part II of this series (Young 1949b) drew attention to the close similarity between *Epipactis vectensis* (T. & T. A. Steph.) Brooke & Rose and *E. pendula* C. Thomas (an illegitimate name; see p. 265). It was shown that supposed distinctions based upon stature or vegetative characters could not be upheld, and that the only constant difference lay in the floral structure. It was further suggested that these two species showed variations which approached one another. At the time that Part II was written, not enough stations for plants of this group were known to make it possible to decide whether a complete range of variation linked them.

Part III (pp. 253-259 above) calls attention to a further plant of the same group, *E. phyllanthes* G. E. Sm. Yet another related plant is *E. cambrensis* C. Thomas (but see p. 268).

A search of various herbaria and the kind co-operation of various botanists in the field has now brought to light a goodly number of further records for plants of this group, sufficient for it to be reviewed with some confidence. Forty-five stations, of which 25 are still extant, are now known in 22 vice-counties. Perhaps the most gratifying individual discovery has been the re-finding, by Dr. F. F. Laidlaw, of a colony in the Isle of Wight, which corresponds exactly as to plant, and very nearly as to locality, with Hunnybun's original *Helleborine viridiflora* f. *vectensis* T. & T. A. Stephenson (1918) which later formed the type for the species *E. vectensis*. (Since this discovery, however, Mr. E. H. White has told me *in litt.* that in 1930 he found a plant which P. M. Hall thought was this. His specimen appears to have been lost. The site was not the same as Dr. Laidlaw's, but only 2-3 miles removed.)

Wherever possible fresh material, or occasionally spirit material, has been examined. Otherwise, flowers from herbarium specimens have been dissected after soaking out in dilute ammonia; I am very grateful to those in charge of the various herbaria for permitting this to be done. The results of this research have amply demonstrated that a continuous range of variation exists, embracing the whole of this group of plants. The present classification of it has proved unsatisfactory to the point of being unworkable. The overall picture is therefore presented here without reference to nomenclature, and on the basis of it a new classification is proposed afterwards. To save repetition, a complete list of known stations and details of the plants therein is given at the end of this paper, each one numbered. In the body of the paper, these stations will be referred to by numbers in parentheses, thus (42).

The characters that unite the group may be briefly summarised first as: Stems rather stout, *glabrous* or *subglabrous*, sometimes in pairs or clusters from a single rhizome; roots *very stout* and copious; leaves small, *ovate*, *acuminate*, often concave, of a smooth thick texture, with minute *grouped ciliolae* on the margin; flowers *pendulous*, maturing early, *autogamous*, entirely *green* or with a white or pinkish epichile; tepals (except lip) persistent; ovary large, *pyriform*, shining-glabrous; seeds *long*. The variation found in vegetative characters is only what would be expected from varying habitat. It should be emphasised that weak or juvenile plants may give misleading characters. Weak states of the plant often have narrow leaves, narrow or flattened ovaries, and scarcely pendulous flowers, and can be very deceptive unless considered in relation to the population as a whole. Flowers from the top of the raceme, too, may show abnormalities which are not evident in the lower flowers; the descriptions which follow always refer to the lowest flowers of the raceme.

The distribution of the plant is shown in fig. 2. It is rather western and southern, although extending well into East Anglia. The continental European counterpart is discussed on p. 269.

The only variation of importance within the group is in the flower-structure. This variation is not only from one colony to another, but sometimes occurs within a single population. For instance, in a single wood on the Cotswolds (32), in an area of  $\frac{1}{4}$  square mile, can be found plants with perfectly formed or completely undifferentiated labella and various stages between, stipitate or sessile anthers, and open or cleistogamous flowers, and all these in various combinations. On the other hand, some other colonies are very uniform.

There is an ill-marked cline in the floral structure over the plant's geographical range. The plant attains its best development in the north-west (38-45), and incidentally its strongest colonies. This is the race called *E. pendula* by Thomas (1942). Its floral structure was detailed in Part II; briefly, the anther is sessile with the pollinia lying behind the vertical stigma (Fig. 3k), and the labellum is fully developed. It should be added that the hypochile is about 4 mm. long, and the epichile as long or slightly longer, and normally reflexed at the tip (Fig. 3a). The flowers open widely, and cleistogamic flowers are rare.

In the colonies which occur in the south, south-west, and east of England, the basic type of flower has a distinctly less well-developed labellum (3, 4, 12, 13, 16, 17, 19, 24-26, 28-32, 34, 37). It does not stand away from the column as in the north-western type, and often the hypochile embraces the stigma quite closely. The hypochile is smaller, seldom above 3 mm. long, and sometimes very deep in comparison, so that it becomes precisely hemispherical. The epichile is usually distinctly longer than the hypochile, sometimes markedly so, and then becomes long-cordate or -triangular. The tip is never reflexed, and the whole lip is usually porrect (Fig. 3b). The column-shape associated with this type of lip is much like the north-western type, but the anther is some-

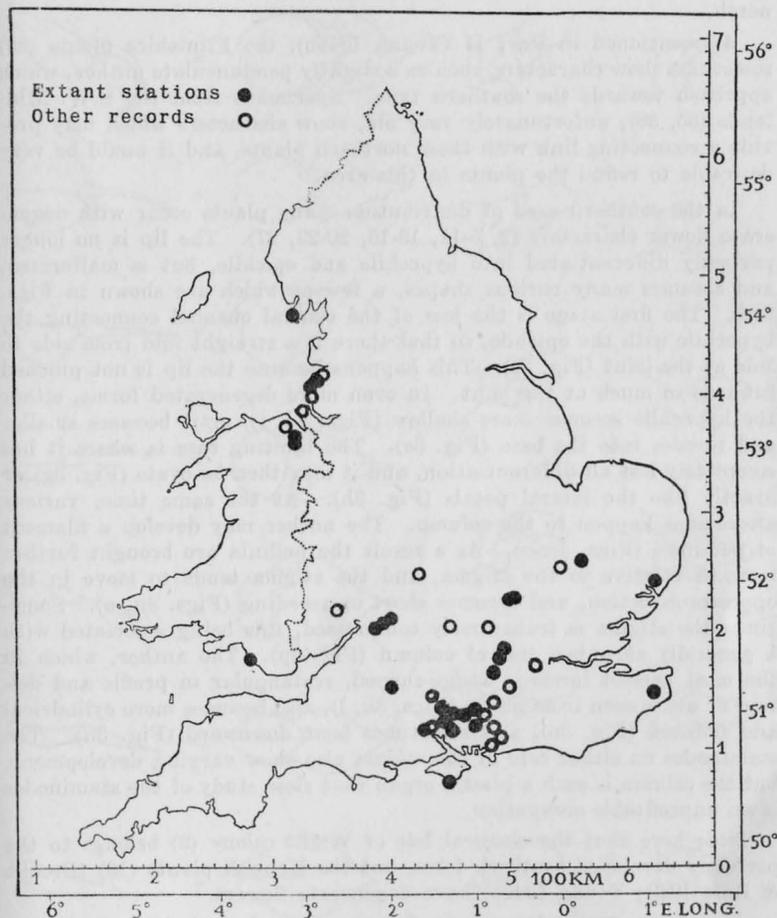


Fig 2.

Distribution of *Epipactis phyllanthes*.

Base-map by courtesy of "New Naturalist" Series.

times slightly pedunculate and the stigma tends to recede somewhat (Fig. 3l). Cleistogamy is very much more frequent in the south; the flowers either do not open at all until long past anthesis, or only part their tepals slightly; some, on the other hand, open as widely as in the north.

As mentioned in Part II (Young 1949b), the Flintshire plants (39) sometimes show characters, such as a slightly pedunculate anther, which approach towards the southern type. Specimens from the S.W. Midlands (35, 36), unfortunately very old, show characters which may provide a connecting link with these northern plants, and it would be very desirable to refine the plants in this area.

In the southern area of distribution many plants occur with degenerate flower characters (2, 5-11, 13-15, 20-23, 27). The lip is no longer perfectly differentiated into hypochile and epichile, but is malformed, and assumes many curious shapes, a few of which are shown in Figs. 3c-h. The first stage is the loss of the central channel connecting the hypochile with the epichile, so that there is a straight fold from side to side at the joint (Fig. 3e). This happens because the lip is not pinched inwards so much at the joint. In even more degenerated forms, either the hypochile becomes more shallow (Figs. 3d, f), or it becomes smaller and recedes into the base (Fig. 3e). The limiting case is where it has completely lost all differentiation, and it may then be ovate (Fig. 3g) or exactly like the lateral petals (Fig. 3h). At the same time, various alterations happen to the column. The anther may develop a filament or peduncle (Figs. 3m-o). As a result the pollinia are brought further forward relative to the stigma, and the stigma tends to move in the opposite direction, and becomes short or receding (Figs. 3n, o). Sometimes the stigma is transversely compressed, this being associated with a generally shrunken size of column (Fig. 3p). The anther, which in the most perfect forms is wedge-shaped, rectangular in profile and deltoid or ovate seen from above (Figs. 3k, l), also becomes more cylindrical and pointed (Fig. 3o), and sometimes bent downward (Fig. 3n). The staminodes on either side of the stigma also show varying development, but the column is such a plastic organ that close study of the staminodes is an unprofitable occupation.

Note here that the classical Isle of Wight colony (3) belongs to the perfectly developed southern form, but the Kentish plants (18) (Brooke & Rose 1940; Young 1949b) have degenerate flowers.

In colonies with degenerate flowers, a good deal of variation in flower structure is found from plant to plant, and to a lesser extent from

Fig. 3.

Some lip and column forms in *E. phyllanthus*. (Numbers in parentheses refer to the list of stations). Labella in profile and plan view: a, Freshfield (42); b, Stetchworth (29); c, Lavington (2); d, Ascot (22); e, Winchester (7); f, Crawley (8); g, Byfleet (20); h, Wellow (5). Columns in profile and plan view: k, Freshfield (42); l, Ventnor (3); m, Winchester (7); n, Ascot (22); o, Womenswold (18); p, Melton (27). The floral axis is horizontal in all cases.

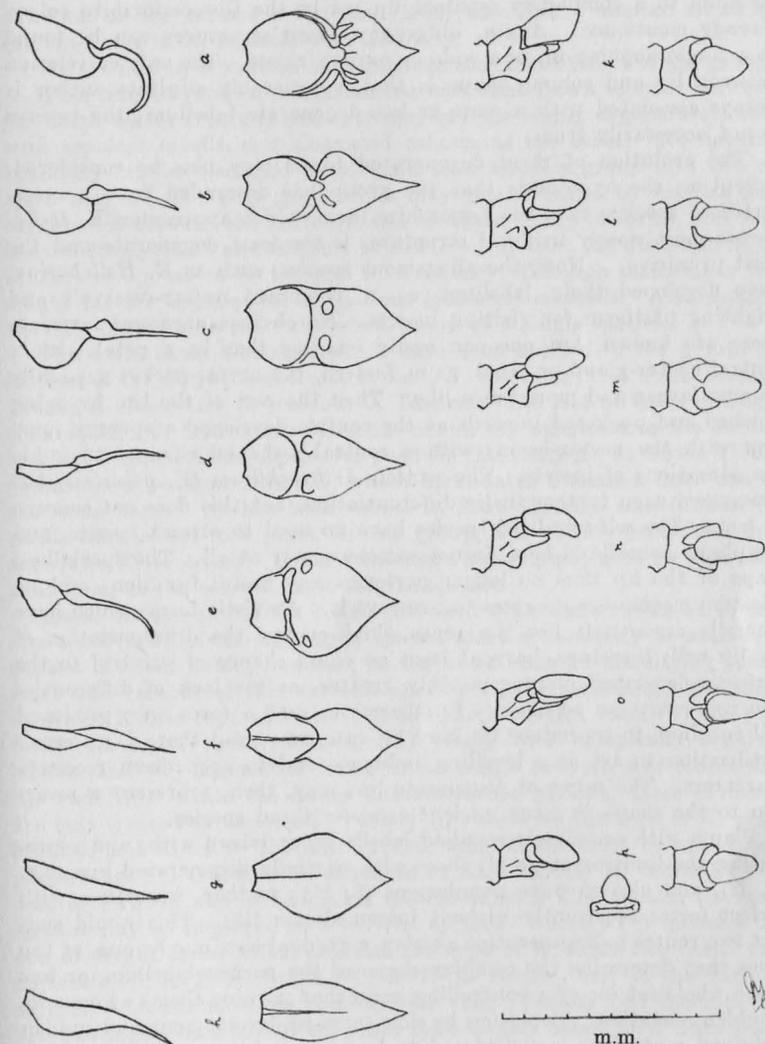


Fig. 3. (For explanation see foot of opposite page.)

flower to flower in one raceme. Degeneration in flower structure is also sometimes associated with malformation, e.g. fusion of two or more tepals. The range of variation which can be found may not be large, or it may embrace the entire gamut from perfect differentiation of the labellum to a completely sepaloid lip, as in the Gloucestershire colony already mentioned. Again, different column structures can be found in a single population, in a wide or narrow range. The only correlation between lip and column shape is that a noticeably stipitate anther is always associated with a more or less degenerate labellum; the reverse is not necessarily true.

The evolution of these degenerated forms may now be considered. Accepting the hypothesis that the group has descended from a cross-fertilised species, then the Lancashire form, which approaches *E. Helleborine* most closely in floral structure, is the least degenerate and the most primitive. Now, the allogamous species, such as *E. Helleborine*, have developed their labellum as a combined nectar-reservoir and alighting platform for visiting insects. No obvious ancestral forms to these are known, but one can easily imagine that in a petal with a central nectar-gland or canal, as in *Listera*, the nectar-pocket gradually became larger and more basin-like. Then the rest of the lip, by being pinched and puckered inwards at the centre, developed a springy junction with the nectar-basin, with a central-V-shaped channel to guide the attentions of insects. The section *Arthrochilium* (*E. palustris*) has progressed even further in lip-differentiation, but this does not concern us here. The self-fertilised species have no need to attract insects, and the plants considered here do not secrete nectar at all. The specialised shape of the lip thus no longer performs any useful function, and no selection mechanism operates to preserve it. Atavistic forms which have partially or entirely lost the genes which control the differentiation of the lip will, therefore, have at least an equal chance of survival to the perfectly-developed plants; possibly greater, as the lack of differentiation represents an economy. Furthermore, such a form once produced will continue to reproduce its kind by autogamy, and there is no cross-fertilisation to act as a levelling influence and to keep down recessive characters. The series of degenerate lips may, then, represent a reversion to the shape in some ancient cross-fertilised species.

Plants with completely sepaloid labella occur mixed with, and representing the limiting stage of, those with partially degenerated lips (e.g. 27, 32), and also in pure populations (5, 15); further, sometimes with perfect forms apparently without intermediates (13). This would suggest two routes to degeneration: either a gradual loss, one by one, of the genes that determine the complex shape of the perfect labellum, or loss of the whole set (or of a controlling gene that governs them) at once by a sudden mutation. Evolution by slow forward development and sudden backward mutations is considered to be a normal process (cf. Darlington & Mather 1947).

The reason for the alteration in the column is not so clear. In *E. leptochila* (Godf.) Godf., which regularly has a stipitate anther, this de-

velopment is of service in allowing the pollinia to fall on the stigma. The same may be (or have been) true of the present series, but the form of the column often looks as if it were due to mechanical pressure from the perianth in bud, in its reduced and malformed condition, leading to attrition of the column. Krösche (1936) describes a similar series of column-forms in *E. leptochila* in Germany.

We are now in a position to reconsider the classification of the group.

A continuous range of variation has now been shown to exist between the north-western form as one extreme, and the highly degenerate forms with sepaloid labella and elongated column as the other. No natural boundary can be discerned that would separate this group into two or more species. The only gap—which may yet be closed by further discoveries—is between the northern and southern group of forms, and this is exceedingly small and difficult to define. Nor does the distribution of characters appear to be bimodal in frequency, although material is too scanty for the application of rigorous biometric methods. Accordingly, the only course is to treat the whole group as a single species.

There are three binomials which have been applied to the group, or sections of it: *E. phyllanthes* G. E. Sm., *E. vectensis* (T. & T. A. Steph.) Brooke & Rose, and *E. pendula* C. Thomas. The last of these is illegitimate; Mr. V. S. Summerhayes has drawn my attention to the earlier and valid combination *Epipactis pendula* (Maxim.) A. A. Eaton (1908) (= *Goodyera pendula* Maxim.), which invalidates Thomas's later use of the same name. As has been shown in Part III, the combination *E. phyllanthes* refers to a plant in this group, was validly published, and antedates *E. vectensis*. It must therefore be adopted, with an extended definition, as the correct name for the species.

Again, on account of the continuous and even distribution of forms, any subdivision of the aggregate species must of necessity be artificial. Such a division would, however, be useful at least for classifying specimens and records of this variable species. It is accordingly proposed to divide it into four varieties: (i) the north-western race, (ii) the perfectly developed southern race, (iii) plants with completely sepaloid labella, and (iv) degenerate forms intermediate between and connecting (ii) and (iii). Since the flower characters are genetic, these divisions are best treated as varieties. Variety (iii) includes the type of *E. phyllanthes*, and so under the new International Rules must be called var. *phyllanthes* if a trinomial is employed at all. Variety (i) is the *E. pendula* of Thomas, and although his specific name is illegitimate, the same epithet may be employed as a varietal epithet. Variety (ii) includes the Isle of Wight form, which provides the type of *E. leptochila* Godf. var. *vectensis* (T. & T. A. Steph.) T. & T. A. Steph., and so the varietal epithet *vectensis* must be retained for this. Variety (iv) includes the Kentish plant, on which Brooke and Rose largely based their description of *E. vectensis* (as species). They cited *E. leptochila* var. *vectensis* T. & T. A. Steph. as synonym, and referred to their name as "comb. nov." only. No question of a new type (they did not designate one) therefore arises; the type of *E. vectensis* remains the Isle of Wight plant (Hunny-

bun's specimen at the British Museum). No earlier separate name therefore exists for variety (iv), and it is proposed to call it var. *degenera*. In fairness to Brooke and Rose, it should be pointed out that they clearly intended their species to cover the same range as is here included under *E. phyllanthes*.

***Epipactis phyllanthes*** G. E. Smith (1852), emend. et ampl. *E. vectensis* (T. & T. A. Steph.) Brooke & Rose (1940).

Autogamous. Rhizome short, horizontal or ascending, with numerous thick fleshy roots (2.5-3 mm. diameter) emerging from it and sometimes from the buried portion of the stem. Stems solitary or more rarely 2-3 together from the same rhizome, (8-) 20-45 (-65) cm. above ground level plus another 5-20 cm. below, stout, glabrous or with very sparse short pubescence. Leaves few (3-6), obscurely bifarious, rather small, orbicular, ovate, or lanceolate, 3.5-6 (-7) cm. long, smooth and thick in texture, acuminate; the lowest reduced to sheaths, the uppermost lanceolate and sometimes reduced to sterile bracts; lower leaves with rather long sheaths; edges interruptedly ciliolate, often undulate; main ribs few, not prominent. Raceme of up to 35 flowers, sometimes aggregated, with lower bracts much longer than the flowers. Flowers cernuous or, most characteristically, hanging vertically downwards. Ovary large (0.9-1.3 cm. long), pyriform, shining-glabrous, with 6 prominent ribs, tapering insensibly into a short curved peduncle. Perianth thick and waxy in texture, entirely pale green or with a slight dull violet tinge, except the epichile which may be whitish or pinkish and is sometimes thin and papery; opening widely or not, sometimes remaining closed until after anthesis is complete; persistent, except the labellum, which with the column rapidly decays after anthesis. Labellum variously shaped (see under vars.). Anther sessile or stipitate, cuneiform or cylindrical; glandular rostellum absent, except sometimes in bud, represented by a horn-like projection above the stigma. Fruit pyriform; seeds long (1.0-1.5 mm.), tapered at each end, areolation elongated. In flower from mid-July to end of August.

*Type* in Hb. Borrer (Kew): Phillis Wood, Sussex, 1839, *G. E. Smith*.

*Hab.* and *exsicc.*, see list of stations at end of this paper.

*Icon.* See below, under individual vars.

*α* var. ***phyllanthes***. *E. phyllanthes* G. E. Smith, sensu stricto. "*E. Phyllis*" G. E. Smith MS.

Labellum completely undifferentiated, ovate or lanceolate, with a central rib, in form, colour, and texture like the lateral petals. Anther sessile or stipitate. Flowers not rarely cleistogamous.

*Hab.* Woods in S. England, often with vars. *vectensis* and *degenera*.

*Icon.* Part III (preceding paper), Fig. 1; (dissections) this paper, Figs. 3g, h.

*β* var. ***vectensis*** (T. & T. A. Stephenson), comb. nov. *E. leptochila* (Godf.) Godf. var. *vectensis* (T. & T. A. Steph.) T. & T. A. Stephenson (1921), et syn.; *E. vectensis* (T. & T. A. Steph.) Brooke & Ross sensu stricto quoad nomen, haud descr.

Labellum embracing the stigma  $\pm$  closely; hypochile small, 2.5-3.0 (-3.5) mm. long, hemispherical, entirely green; epichile cordate-deltoid, longer than the hypochile, usually elongated and acuminate, often whitish or pinkish, usually with two lateral bosses; joint with the epichile perfectly formed, with a central sinus. Anther sessile or subsessile. Flowers not rarely cleistogamous.

*Type* in Hb. Mus. Brit.: Isle of Wight, 1917 [*E. W. Hunnybun*].

*Hab.*: as var. *phyllanthes*, but more frequent.

*Icon.* *Gardeners' Chronicle*, 1852, 532; *Watsonia*, 1949, 1, 103, Fig. 1c; Brooke (1950), t. 7 (as *E. cambrensis*); Summerhayes, 1951, t. 13b; (dissections) *J. Bot.*, 1918, 56, 3; this paper, Figs. 3b, 1.

*γ* var. ***degenera***, var. nov. *E. vectensis* Brooke & Rose (1940), quoad descr.

A var. *vectensi* recedit labello in hypochilium epichiliumque imperfecte fincto; anthera saepe stipitata.

Labellum imperfectly differentiated, lanceolate or ovate, with a shallow or ventricose depression at the base representing the hypochile; constriction dividing hypochile from epichile absent, or at most imperfect, with no central sinus; coloured as in var. *vectensis*; often with two lateral bosses. Anther sessile or frequently  $\pm$  longly stipitate, cuneiform or ovate-cylindrical. Flowers not usually opening widely, and often not at all until after anthesis.

*Hab.*: as var. *vectensis*.

*Type* in Hb. Kew: Market Lavington, Wiltshire, 23 Aug. 1950, *E. M. Marsden-Jones*.

*Icon.* Brooke, 1950, t. 6 (as *E. vectensis*); Summerhayes, 1951, t. 14; (dissections) *J. Bot.*, 1940, 78, 82, Figs. B, D, E; 83; *Watsonia*, 1949, 1, 110, Fig. 4; this paper, Figs. 3c-f, m-p.

*δ* var. ***pendula***, var. nov. *E. pendula* C. Thomas (1942), non A. A. Eaton (1908).

A var. *vectensi* differt floribus raro cleistogamis; labello magno, patente; epichilio hypochilium (4 mm. longum) aequante vel vix superante, cordato, acuminato, reflexo. Anthera cuneiformis, sessilis.

Labellum perfectly differentiated, large, patent; hypochile 4 mm. long; epichile as long or scarcely longer, cordate, rugose at the base or with two bosses, acuminate, usually strongly reflexed. Anther cuneiform, sessile. Rarely cleistogamous.

*Type* in Hb. Mus. Brit.: near Formby, Lancs., Aug. 1941, *C. Thomas*.

*Hab.* Woods, plantations, and sand-dunes in N.W. England.

*Icon.* *J. Bot.*, 1941, 79, 201, Fig. a; Brooke, 1950, t. 10 (as *E. pendula*); (dissections) *Watsonia*, 1949, 1, 110, Fig. 3; this paper, Figs. 3a, h.

It should be made clear that the plant interpreted in Part II as *E. vectensis* is here named var. *degenera*, and that var. *vectensis* is not the same thing but was included under *E. pendula* in Part II.

The Isle of Wight examples of var. *vectensis* are unlike other material in having narrow flaccid leaves with poorly developed marginal ciliolae, and are more pubescent than usual on the rachis. The plants

seen were growing in unusually dense shade, which may be a factor in producing the unusual habit. It is difficult to know how much importance to place upon this, but the leaf characters of *Epipactis* are so variable that it is better disregarded taxonomically.

I do not understand *E. cambrensis* C. Thomas, and have left it out of account here. Thomas's type in Hb. Mus. Brit. is immature; specimens in various other herbaria determined (by him or others) as *E. cambrensis* appear to me to be *E. phyllanthes* var. *vectensis*, which he himself (1950) records (as *E. pendula*) from the same locality (37). On several visits to the Kenfig dunes I have not been able to find plants corresponding exactly to his description of *E. cambrensis* (especially further points emphasised *in litt.*), although *E. phyllanthes* was seen both on tops of dunes and in the stacks. More definite evidence that *E. cambrensis* is distinct from *E. phyllanthes* and not just a dwarfed state of it would be welcome.

*E. pendula* var. *minor* Brooke (1950, 122) refers to various weak and juvenile states of vars. *pendula* and *vectensis*, and is not worth retaining.

Finally, the ecology of *E. phyllanthes* may be discussed. Its distribution (Fig. 2) follows in a general way the calcareous areas of the country, but it is not confined to chalk or limestone areas. Nevertheless, where samples have been available from stations which are away from calcareous districts (2, 5, 22, 27), the soil has proved to have a surprisingly high calcium content, and has often contained visible particles of chalk. The sand-dunes in which it also flourishes are also highly calcareous with comminuted shells. Soils supporting the plant have always proved to be alkaline (pH 7-8). The plant, then definitely favours an alkaline calcareous soil. As to moisture it seems to be fairly indifferent; of 28 stations for which information is available (not including dunes), 8 are moist or beside water, whilst some others are exceedingly dry. It has often been noted as growing amongst ivy, in fact in 12 stations this forms a close ground-cover through which the plant grows. In the dunes it grows characteristically amongst *Salix repens*\* mixed sometimes with *Rubus caesius*. In other inland stations it is associated with a low open ground-flora of *Viola Riviniana*, *Sanicula europaea*, *Fragaria vesca* and *Asperula odorata*. It appears that it can tolerate, and possibly benefit from, a closed bushy cover, provided that this is not too tall (not above 15-20 cm.) and with roots not too closely spaced. It cannot tolerate such plants as *Mercurialis perennis* or *Nepeta hederacea* as associates, except in very small quantity, possibly because their roots occupy too much of the soil, or else because their requirements are in some way different. Still less can it tolerate tall rank undergrowth. As to the kind of tree cover it appears to be indifferent provided that the ground cover is to its liking. Besides beech it occurs under birch, ash, hazel, or planted trees, but rarely under oak which usually encourages a ground-flora that is too vigorous. It shows a

\*The plant referred to here as *S. repens* is that regarded by Floderus as *S. arenaria* L. and hybrids of *S. repens* L. therewith.

marked preference for small woods or copses, tree-belts, or the shelter of tall hedges bordering woods; of 32 woodland stations for which information is available, 22 are in such situations. A curious feature is that no less than 13 stations are under trees (native or exotic) known to be planted, or else to have colonised the spot quite recently. It may be that the plant requires more light than is to be found in the middle of large woods, and is happier in small woods where light enters on all sides, or in marginal situations. Possibly some of the associations in which it occurs are not ecologically stable, but only represent one stage of development in the woodland community; if so this would explain the plant's frequent occurrence in comparatively new plantations or woods.

Since Part I (Young 1949a) was written, it has become clear that sand-dunes are a normal habitat for *E. phyllanthes*. Besides the Formby locality (42), the plant has been recorded from three other dune habitats (37, 41, 45) where no tree plantations exist. It has evidently spread to, or persisted in, the plantations at Formby from the dunes. Mr. Thomas mentions *in litt.* that he has found it also under a birch copse, apparently natural, behind the dunes. He thought that this was perhaps its original habitat. Some information *in litt.* from Mr. F. W. Holder suggests that the conditions for establishment and optimum growth may not be the same. At Ainsdale (43), he says, he had not noticed the plant until 1942, the year after part of the plantations had been burned down. In the clearing, *E. phyllanthes* var. *pendula* appeared in great vigour and quantity, one plant having 46 stems in a cluster. From what is known of the rate of growth of *Epipactis* (cf. Ziegenspeck 1936), these plants must have been nearly 10 years old at least, and must have escaped notice before the trees were destroyed. Subsequently, and presumably as the site became overgrown, they decreased greatly in numbers and size. *E. dunensis* f. *pinetorum*, on the other hand, in the same spot made little response to the changes. When growing in open dunes, *E. phyllanthes* assumes a chlorotic and stunted appearance, as most plants do in such situations.

A related plant is quite widespread in the countries around the Baltic, especially Denmark, and was identified by Nannfeldt (1946) as *E. persica* (Soó) Hausskn. ex Nannf. As pointed out in Part II, *E. persica* is described (Soó 1927) as having a rostellum. With the kind co-operation of Dr. J. Renz and the Kew Herbarium, I have been able to see a set of Persian material of *E. persica*, and it is clearly different from the European plant. It is characterised by very long bracts (longer even than in *E. phyllanthes*) and very small, not pendulous, flowers which develop into large fruit. It is doubtless allogamous. Spirit material supplied by Dr. Nannfeldt appeared also to show a rostellum, but according to specimens and information kindly supplied by Dr. O. Hagerup, there is no doubt that the Danish plants are self-fertilised. Tentatively, the continental plant may be assigned to *E. phyllanthes*, but it does not agree with any of the British forms. It is hoped to study this plant further.

I am very much indebted to many botanical colleagues who have supplied specimens and information, and given other assistance. My particular thanks are tendered to Dr. J. L. Farmer, Miss E. P. A. and Mr. T. Jones, and Dr. F. F. Laidlaw for hospitality and transport; and to Mr. V. S. Summerhayes of Kew and to the botanical staff at the British Museum for their co-operation in bringing new records to my notice.

#### SUMMARY OF PARTS III AND IV.

Attention is drawn to *Epipactis phyllanthes* G. E. Smith, a name which has been overlooked since the time of its publication (1852). This plant, *E. vectensis* (T. & T. A. Steph.) Brooke & Rose, and *E. pendula* C. Thomas (*nomen illegitimum*) all represent parts of an aggregate species which presents a continuous range of variation. The valid name for the aggregate species is *E. phyllanthes*, and an artificial division into four varieties, based on the form of the labellum and column, is proposed, as follows:

Labellum imperfectly differentiated. Anther sessile to longly stipitate.

Labellum completely sepaloïd ..... var. *phyllanthes*.

Labellum with rudimentary hypochile ..... var. *degenera*.

Labellum perfectly formed. Anther sessile or very shortly stipitate.

Epichile longer than hypochile, porrect. Southern ..... var. *vectensis*.

Epichile about equalling hypochile, reflexed. Northern ..... var. *pendula*.

It grows in woods (usually marginally) and sand-dunes in England, and requires a calcareous soil. It is only associated with certain types of ground-flora, especially closed communities of *Hedera Helix* (in woods) or *Salix repens* (in dunes). A Scandinavian plant, which has been incorrectly called *E. persica* (Soó) Hausskn. ex Nannf., appears to belong under or near *E. phyllanthes*, but requires further study.

#### LIST OF STATIONS.

Information is given for each station in the following order:

*Name of station.* In the case of extant localities, only the name of the parish is given for security reasons. This may differ from the locality as named on herbarium sheets or in other records, but the names may be reconciled by consulting Ordnance Survey maps showing parish boundaries. All available details are given for localities which have not been refound.

*Records.* Names of discoverers not previously acknowledged are in italics, with date when first noted (this may be earlier than any specimen). Names in roman type and dates in parentheses are literature references. ! indicates that I have seen the plant *in situ*, but not necessarily in the year stated. All known exsiccata are listed, but full collection data are only given for non-extant localities. Abbreviations for herbaria: B = British Museum, C = Cambridge Univ., K = Kew, O = Oxford Univ., S = South London Botanical Inst., W = Nat. Museum of Wales (Cardiff), Y = Hb. D. P. Young. The following herbaria have been searched but contained no *E. phyllanthes*: Harrow school, Holmesdale N.H. Soc. (Reigate), Derby, Haslemere, Taunton, and Torquay museums.

*Present status.* Colonies seen within the last three years are noted as "still extant"; absence of this remark implies that it has not been seen since the last date mentioned. Present size of colony: \* = less than 10 plants, \*\* = 10-100 plants, \*\*\* = hundreds of plants.

*Nature of locality.* (i) Tree cover, (ii) ground flora (G.F.), (iii) geological formation (Geol.), (iv) nature of soil (sample taken from around roots; pH determined with B.D.H. Universal Indicator; Ca = total calcium). Conventions used for G.F.: thin ivy = *Hedera Helix* in open association, thick ivy = *H. Helix* dominant in closed association, violet = mostly *Viola Riviniana*, sanicle = *Sanicula europaea*.

*Description of plants.* (i) Range of height, (ii) frequency of cleistogamous flowers (cleisto.), (iii) description of column (col.), (iv) of labellum (lab.), (v) other noteworthy features.

*Determination,* based on examination of fresh material from extant colonies, otherwise on dissected herbarium material or sketches when available.

Other abbreviations: *E.* = *Epipactis*, *H.* = *Helleborine*, *lat.* = *latifolia*, *lepto.* = *leptochila*, *med.* = *media*.

#### V.-c. 3 OR 4, DEVON.

(1) "Devonshire", Brook & Rose (1940). Specimen lost and no details traceable.

#### V.-c. 8, S. WILTS.

(2) Market Lavington, *C. Rheinganum*, comm. *E. Marsden-Jones*, 1950 (K). Still extant \*\*. Margin of wood, under *Alnus*, *Salix*, *Acer*, and conifers, and under *Crataegus* hedge; near a stream. G.F.: ivy. Geol.: Lower Greensand. Soil: loam, pH 7.5-8, Ca high. 20-65 cm. Not cleisto. Col.: anther pointed, shortly pedunculate; stigma receding. Lab. incompletely differentiated; hypochile hemispherical; epichile cordate with 2 bosses; not constricted at the joint, no central channel. Var. *degenera* (type).

#### V.-c. 10, I. OF WIGHT.

(3) Ventnor, *E. W. Hunnybun* 1913 (C), 1917 (B); T. & T. A. Stephenson (1918); *E. H. White* 1930? (see p. 259); *F. F. Laidlaw* 1950! (C). Still extant\*. (Laidlaw's locality:) small plantation of *Tilia*, *Ulmus glabra*, *Populus canadensis*, rather heavily shaded. G.F.: thick ivy, with *Phyllitis* and *E. Helleborine*. Geol.: chalk? (landslip). Soil: dark poor loam; pH 6.5; Ca present. Flowers not opening widely, sometimes cleisto. Col.: anther almost rectangular in profile, on very short erect peduncle. Stigma vertical. Lab. completely differentiated but small; hypochile deepest towards front, close to ventral side of col.; epichile cordate, acuminate, long, with 2 elongated hunches. Leaves narrow, flaccid; rachis slightly pubescent. Var. *vectensis* (type).

#### V.-c. 11, S. HANTS.

(4) Romsey, *F. Townsend*, 1878 (as ?*E. med.*) (S). May refer to the following station, but the flower structure is different. Wood. Geol.: Eocene sands. 30-40 cm. All cleisto. Anther rectangular in profile, sessile. Lab.: hypochile small, rather shallow; epichile cordate, with 2 elongated bosses. Differentiation appears perfect. Var. *vectensis*.

(5) Wellow, *Miss M. Howard*, 1951! (K). Still extant\*. Roadside, under hedge bordering beech wood and spinney. G.F.: thick ivy; with *E. Helleborine*. Geol.: Eocene sands. Soil: loam with Eocene pebbles and fragments of chalk; pH 7.5; Ca present. 15-30 cm. Anther slightly pedunculate. Lab. completely sepaloïd (Fig. 3h). Var. *phyllanthes*. Mr. G. W. Pierce tells me that he has seen the plant in another spot in the same parish.

(6) Owslebury, *G. W. Pierce*, 1929; Godfery (1933)! (B, K, O). Disappeared about 1935, but reappeared in 1949 and is still extant\*. Beech wood. G.F.: sanicle, *Asperula odorata*; with *E. Helleborine*. Geol.: chalk. Soil: chalky loam; pH 8; Ca high. 5-20 cm., never larger. Frequently cleisto. Col. small, short; anther subsessile; stigma receding. Lab. brownish, degenerate; lanceolate to ovate, with or without median constriction; hypochile a small depression in the base, embracing the stigma. Var. *degenera*.

(7) Winchester, G. W. & G. G. Pierce, 1949! (Y). Still extant\*. Planted beech belt. G.F.: thick ivy. Geol.: chalk. Soil: leaf-mould over loam; pH 8; Ca high. 15-30 cm. Flowers scarcely opening. Anther pointed, shortly pedunculate, forward of stigma. Lab. imperfectly differentiated; hypochile very small; epichile cordate, much broader than hypochile, separated from it by a pair of curved ridges, and with 2 small bosses, green with pink edges (Figs. 3e, m). Var. *degenera*.

## V.-c. 12, N. HANTS.

(8) Crawley, G. G. Pierce & Mrs. E. W. Churches, 1951! (Y). Still extant \*\*. Beech belt. G.F.: nil; with *E. Helleborine*. Geol.: chalk. Soil: leaf-mould over chalk; pH 8; Ca high. 10-30 cm. Flowers scarcely opening. Col.: anther pedunculate, pointed; stigma slightly receding. Lab. imperfect; hypochile shallow, oval, embracing stigma; epichile ovate, acute; median folds absent. (Fig. 3f). Var. *degenera*.

(9) Headbourne Worthy, M. P. Dann, comm. G. G. Pierce, 1951! Still extant \*. Small spinney beside stream; *Aesculus*, *Crataegus*, *Salix fragilis*, *Betula*. G.F.: thick ivy. Geol.: chalky alluvium. Soil alluvial; pH 8; Ca high. 30 cm. Usually cleisto. Col. short; anther ovoid, on a short erect peduncle; stigma transversely compressed. Lab. small, very imperfect; lanceolate or ovate, with median constriction; hypochile a small wide depression; epichile  $\pm$  concave, whitish with green centre. Var. *degenera*.

(10) Easton, Miss M. Jaques, 1951! (Y). Still extant \*. Hedge beside stream; *Salix alba*, *Taxus*, *Ulmus*. G.F.: thick ivy, *Caulis Anthriscus*. Geol.: alluvium. Soil: alluvial, chalky; pH 7.5-8; Ca high. 12-35 cm. Usually cleisto. Col.: anther pointed, pedunculate; stigma receding. Lab. small, differentiation imperfect; hypochile deep; epichile cordate, without bosses, greenish white with pink edges. Var. *degenera*.

(11) Andover, F. Townsend, 1860, 1864 (S); *idem* (1883); C. B. Clarke, 1877 (K) (all as *E. med.*). "Canal Swamp", now a meadow by the railway; possibly under *Salix*. Geol.: alluvium. 25-35 cm. Doubtfully cleisto. Anther sessile or nearly so, short, deltoid from above. Lab. sepaloïd, lanceolate. Var. *phyllanthes*.

(12) Colemore, 1938, Hall (1942) (as *E. lept.*); 1950! (B, Y). Still extant \*. Small coppice colonising old clay (or chalk?) pit; hazel, beech, oak. G.F.: thick ivy. Geol.: chalk. Soil: chalky loam; pH 8-8.5; Ca high. 30 cm. Not cleisto. Col.: anther sessile, rectangular in profile; stigma almost vertical. Lab. perfectly differentiated; hypochile hemispherical, 3.5 mm.; epichile about as long as hypochile, cordate-orbicular, not reflexed, green with white edge, with 2 prominent pinkish bosses and median ridge. Var. *vectensis*, approaching *pendula*.

(13) Selborne, P. M. Hall & M. J. Godtery, 1931 (as *E. lept.*); 1951! (B, Y). Still extant \*. Beech wood on escarpment. G.F.: thin ivy. Geol.: chalk. Soil: loam, apparently leached; pH 6.5; Ca present, low. 20-30 cm. Col.: anther subsessile or shortly pedunculate, rectangular in profile or somewhat compressed; stigma rather receding. Lab.: sometimes perfectly differentiated, hypochile small, deep; epichile long-deltoid, pale green with 2 pinkish bosses; sometimes completely undifferentiated, sepaloïd, lanceolate. Vars. *vectensis* and *phyllanthes*.

(14) Passfield, E. C. Wallace, 1938 (as *E. purpurata*) (Hb. Ips.). Side of lane. Geol.: Lr. Greensand. 40 cm. Not cleisto., opening widely. Col.: anther sessile, ovate-rectangular in profile; stigma receding diagonally. Lab. completely sepaloïd, lanceolate, or with faint trace of hypochile at base in form of a small depression. Var. *phyllanthes*.

## V.-c. 13, W. SUSSEX.

(15) Treyford; Phillis Wood, 1838 (K, O). See Part III. Geol.: gravel over chalk. 15-45 cm. Anther cylindrical, shortly pedunculate; stigma receding. Lab. completely sepaloïd or with faint trace of hypochile at base. Var. *phyllanthes* (type).

(16) Near Chichester, L. Vernon Harcourt, 1851 (K), see Part III. May refer to localities (15) or (17). 20 cm. Not cleisto. Anther sessile, ovate, pointed. Lab. completely differentiated. Cf. var. *vectensis*.

(17) West Dean, W. Wallinger, 1852 (as *E. med.*) (K). Geol. probably chalk, 20 cm. Not cleisto. Anther pointed, shortly pedunculate. Lab. differentiated; hypochile small; epichile long-cordate, acuminate. Cf. var. *vectensis*.

## V.-c. 15, E. KENT

(18) Womenswold, Brooke & Rose (1940), Young (1949b)! First record 1926, seen irregularly since (S, K, Y). Still extant \*. Small beech wood. G.F.: thick ivy. Geol.: chalk. 15-40 cm. Flowers scarcely opening. Anther cylindrical, usually longly pedunculate; stigma very receding (Fig. 3o). Lab.; differentiation imperfect; see *loc. cit.* Var. *degenera*.

## V.-c. 17, SURREY.

(19) Waverley, Miss Parker, 1838 (as *E. lat.*) (C). Geol.: Lr. Greensand. 15-25 cm. Flowers not opening widely. Col.: anther sessile; stigma almost vertical. Lab.: hypochile small, shallow; epichile deltoid; differentiation complete. Var. *vectensis*.

(20) Between Byfleet and Ripley (this may be in Pyrford parish), C. E. Britton 1927 (K). Canal towpath: presumably under hedge trees, or on margin of a coppice (felled about 1948). Geol.: Bagshot Sands (alluvium?). 40 cm. Flowers not opening widely. Col.: anther pedunculate; stigma receding diagonally. Lab. completely undifferentiated, ovate-acuminate with central rib (Fig. 3g). Var. *phyllanthes*.

(21) Mortlake, J. T. Syme, 1853 (as *E. lat.*). Between Kew and Mortlake, M. Moggridge, 1870 (as *E. lat.* var. *foliis minoribus subcoriacets*) (B). Geol.: London Clay. 30 cm. Flowers not opening widely. Col.: anther pedunculate, pointed; stigma very receding. Lab. imperfectly (sometimes perfectly?) differentiated, lanceolate, constricted  $\frac{1}{2}$  way from base, hypochile a shallow depression, epichile with 2 bosses. Var. *degenera*.

## V.-c. 22, BERKS.

(22) Ascot, J. S. Wilkinson 1945! Young (1949b) (B, K, Y). Still extant \*. Birch wood. G.F.: violet, sanicle, *Fragaria*; with *E. Helleborine*. Geol.: Bagshot Sands (brick earth). Soil: rather moist; pH 6-7; Ca present. 20-40 cm. Invariably cleisto. Anther usually pedunculate, pointed, often depressed at end; stigma receding. Lab. degenerate, variable; lanceolate with  $\pm$  median constriction; hypochile a basal depression or almost absent (Fig. 3d, n). Var. *degenera*, approaching *phyllanthes*.

## V.-c. 23, OXFORD.

(23) Oxford: The Parks, G. C. Druce, 1909 (as *H. lat.* var. *angustifolia*) (O). Geol.: Oolitic clay? 20-30 cm. Flowers not opening widely. Anther cylindrical, pointed, shortly pedunculate. Lab. degenerate, lanceolate with constriction  $\frac{1}{2}$  way from base; hypochile a shallow depression. Var. *degenera*.

Druce (1927) records from Shotover "*E. lat.* A var. with smooth germen and entire lip" which may belong here.

## V.-c. 24, BUCKS.

(24) Dorney, W. C. Worsdell, 1917 (as *E. lept.*); V. S. Summerhayes 1950! (K, Y, Hb. J. Renz). Still extant \*\*. Plantation belt on river bank; mainly *Aesculus*. G.F.: thick ivy. Geol.: alluvium. Soil: loamy; pH 8; Ca high. 20-40 cm. Usually cleisto. Col.: anther subsessile, rectangular in profile; stigma receding or transversely compressed. Lab. perfectly differentiated; hypochile small; epichile long-deltoid, pale yellow-green with whitish bosses. Tepals with purplish flush inside and out; frequently imperfectly formed, fused together. Var. *vectensis*.

(25) Beaconsfield, *E. F. Taylor*, comm. *D. I. Gatfield*, 1950! (B, Y). Still extant\*. Grass verge of residential road, bordered by remains of beech woods. G.F.: planted turf. Probably a relic, although the locality has been unchanged for 25 years. Geol.: margin of chalk and London Clay. Soil: loam; pH 7-7.5; Ca high. 30 cm. Flowers not opening widely. Col.: anther sessile, rectangular in profile; stigma slightly receding. Lab. perfectly differentiated; hypochile small, deepest at front; epichile long-cordate, with 2 bosses. Var. *vectensis*.

(26) Ellesborough: Warley Wood, Chequers Park, *F. L. Foord Kelcey*, 1910 (as *E. lat. med.*) (B). Beech wood; with *E. lepto*. Geol.: chalk. 20 cm. Not cleisto. Anther sessile, pointed. Lab.: hypochile 3.5 mm. long, deep; epichile 4 mm., ovate-acuminate; differentiation perfect or nearly so. Cf. var. *vectensis*.

V.-c. 26, E. SUFFOLK.

(27) Melton, *Miss N. Churchman*, ca. 1944! (K, Y). Still extant\*. Small group of planted trees; *Aesculus*, beech, oak. G.F.: thick ivy. Geol.: Pliocene. Soil: sandy loam; pH 7-7.5; Ca high. 15-40 cm. Invariably cleisto. Col.: anther cylindrical, often depressed or bent, on arching filament; stigma sometimes transversely compressed (Fib. 3p). Lab. very degenerate, lanceolate, with or without median constriction, variable. Var. *degenera*, varying through to *phyllanthus*.

V.-c. 29, CAMBRIDGE.

(28) Cambridge: Robinson Crusoe's I., *A. S. Stubbs*, 1899 (as *E. med.*) (C). Willow holt? Geol.: alluvium. 40 cm. Anther sessile? Lab.: hypochile small; epichile long-deltoid; differentiation  $\pm$  perfect. Var. *vectensis*.

(29) Stetchworth, *F. Rose*, 1941! (Y). Still extant\*. Beech belt. G.F.: thick ivy. Geol.: chalk. Soil: poor loam; pH 8; Ca present. 30 cm. Usually cleisto.? Col.: anther rectangular in profile, slightly pointed, sessile; stigma vertical, pollinia behind stigma. Lab. perfectly differentiated; hypochile small, hemispherical; epichile long-cordate, with 2 bosses (Fig. 3b). Var. *vectensis*.

V.-c. 30, BEDFORD.

(30) Streatley, 1926, Dony (1946)! (Hb. Luton Mus.). Still extant\*. Beech wood. G.F.: thin ivy. Geol.: chalk. 15-30 cm. Other details as (31), which is not far away.

(31) Barton-in-the-Clay, *R. G. Crabb*, 1929 (B); Dony (1946)! (K, Y, Hb. Luton Mus.). Still extant\*. Beech wood. G.F.: thin ivy. Geol.: chalk. 15-40 cm. Frequently cleisto. Col.: anther sessile, rectangular in profile, deltoid in plan; stigma vertical, behind pollinia. Lab. perfectly differentiated; hypochile small, hemispherical, embracing stigma; epichile long-cordate, with 2 bosses. See also Young (1949b). Var. *vectensis*.

V.-c. 33, E. GLOS.

(32) Painswick, *Lady Davy*, 1935 (as *E. lepto.*), 1950! (O, Y). Still extant\*\*. Beech plantation. G.F.: thin ivy, sanicle, *Hieracium*; with *E. Helleborine*. Geol.: Oolitic limestone. Soil: leaf-mould over loam; pH 7.5-8; Ca high. 20-40 cm. About half cleisto. Col.: anther cuneiform or ovoid, sessile or shortly pedunculate, or sometimes (in flowers with sepaloïd labellum) longly pedunculate. Stigma  $\pm$  receding. Lab. variable; some perfectly differentiated, with ventricose hypochile, and long-cordate epichile, with 2 bosses; some with median constriction  $\pm$  absent; some  $\pm$  completely undifferentiated, lanceolate, with slight or no depression at base. Tepals sometimes imperfectly formed, fused together. Var. *vectensis* varying through *degenera* to *phyllanthus*.

(33) Brimpsfield, *C. Thomas*, 1947. Still extant?\*. Beech wood. G.F.: thin ivy, sanicle, *Hieracium*; with *E. Helleborine* and *lepto*. Geol.: Oolitic limestone. No specimens seen.

(34) Cowley, Thomas (1941) (K). Not seen recently. Beech wood. G.F.: violet, sanicle, thin ivy; with *E. Helleborine*. Geol.: Oolitic limestone. 20-25 cm. Col.:

anther sessile, ovoid; stigma vertical, rather behind pollinia. Lab. completely differentiated; hypochile ventricose; epichile cordate, as long as hypochile. Var. *vectensis*, approaching *pendula*.

V.-c. 36, HEREFORD.

(35) Walford, *W. H. Purchas*, ca. 1870? (O). Geol.: Carb. limestone? (or Devonian). 45 cm. Anther apparently sessile. Lab. perfectly differentiated? Var. *vectensis* or *pendula*.

V.-c. 38, WARWICK.

(36) Charlcote, *T. Fleetwood* (?), 1857 (B). Geol.: Trias? 20 cm. Not cleisto.? Anther cuneiform, sessile. Lab. perfectly differentiated; hypochile 3 mm. long; epichile cordate, as long as hypochile, with 2 small bosses. Var. *vectensis*, approaching *pendula*.

V.-c. 41, GLAM.

(37) Kenfig, Thomas (1950)! (B, K, W, Y). Still extant\*\*. Sand dunes; no tree cover. G.F.: *Salix repens*, *Rubus caesius*; with *E. Helleborine* and *cambrensis*. Geol.: maritime sand. Soil: calcareous sand; pH 7.5-8; Ca high. 20-40 cm. Frequently cleisto. Col.: anther sessile, rectangular in profile; stigma vertical. Lab. completely differentiated; hypochile small, embracing stigma; epichile long-deltoid, apple-green with 2 pinkish bosses. Whole plant chlorotic. Var. *vectensis*.

V.-c. 51, FLINT.

(38) Llyn Helig, 1906, Young (1951) (W). Geol.: Carb. limestone. 15 cm. Not cleisto. Flower not examined. Probably var. *pendula*.

(39) Mold (Rural), Jones & Young (1949)! (Y, Hb. E. P. A. Jones). And in another spot, *Miss E. P. A. Jones* 1948! (K, Y, Hb. ips.). (a) Still extant\*. Mixed woods of ash, oak, *Ulmus glabra*. G.F.: thin ivy, violet, sanicle; with *E. Helleborine*. (b) Still extant\*\*. Small copse (ash, oak, birch). G.F.: *Fragaria vesca*, violet, *Rubus Thalictrum collinum*; or thick ivy; also in adjoining ditch in thick ivy, under *Crataegus*, etc. Both spots: Geol., Carb. limestone. 20-30 cm. Less than 10% cleisto. Col.: anther sessile or subsessile, cuneiform, rectangular in profile; stigma receding. Lab. perfect; hypochile ventricose, patent, 4 mm.; epichile cordate, acuminate, as long or slightly longer than hypochile, frequently but not always reflexed. Var. *pendula*.

V.-c. 58, CHESHIRE.

(40) Near Birkenhead, 1925, Jones & Young (1949) (K). Habitat not stated, but sand-dunes implied. 20 cm. Not cleisto. Lab. fully differentiated; flowers not dissected. Cf. var. *pendula*.

V.-c. 59, S. LANCs.

(41) Crosby (incl. Hightown), *J. A. Wheldon* & *W. G. Travis*, 1913 (as *H. viridiflora*; mixed with *E. dunensis*) (B, O, W); *C. B. Tahourdin*, 1925 (as *E. lepto*. var. *dunensis*) (S). Sand dunes; no tree cover. An extension of (42), q.v. Var. *pendula*.

(42) Formby (incl. Freshfield), Thomas (1941)! Earliest record: *W. G. Travis*, 1914 (as *H. viridiflora*) (B). Other exsicc.: B, K, Y, Carlisle and Leicester museums, E. P. A. Jones, J. Renz. Still extant\*\*\*. (a) Open dunes. No tree cover. G.F.: *Salix repens*, *Rubus caesius*. Geol.: maritime sand. Soil: calc. sand; pH 7; Ca present. (b) Plantations; under *Pinus nigra* vars., also birch coppice. G.F. nil. Soil: thin pine-needle mould over calc. sand; pH 7-7.5; Ca present. With *E. dunensis* in both habitats. 10-40 cm. Rarely cleisto. Floral structure see Young (1949b). Whole plant chlorotic in (a). Var. *pendula* (type).

(43) Ainsdale, *H. Britten*, 1924 (B). Other exsicc.: Y, Southampton Bot. Mus., F. W. Holder, J. E. Lousley. Still extant\*\*\*. In open dunes and plantations (*Pinus nigra*, *Acer Pseudoplatanus*); an extension of (42), q.v. Var. *pendula*.

(44) Southport: Hesketh Park, *F. W. Holder*, 1935 (Hb. ips.). Destroyed 1940. Shrubbery; G.F.: grasses. A relic: the park was made over sand-dunes. Soil: sandy; sampled 1951, pH 5; Ca low. 30 cm. Flowers not opening widely; not dissected. Cf. var. *pendula*.

V-c. 69b, N. LANCs.

(45) Dalton-in-Furness, *B.S.B.I. excursion*, 1951 (Y. Carlisle Mus., I. W. Evans, A. W. Westrup). Still extant\*\*. Sand dunes; no tree cover. G.F.: *Salix repens*. Geol.: maritime sand. Soil: sand, not so calc. as at Formby. 20-30 cm. Not cleisto. Lab. fully differentiated. Col. not examined. Cf. var. *pendula*.

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