

STUDIES IN THE BRITISH EPIPACTIS

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I. EPIPACTIS DUNENSIS AND E. PENDULA

The three last decades have seen a steady advancement in our understanding of the self-fertilised or autogamous *Epipactis*, which had previously, in common with the rest of the genus, been thoroughly misunderstood. Godfery, in 1920-6, described *E. leptochila*, *E. dunensis* and the Continental *E. Muellerei*, and clearly distinguished the essential characteristics of each. However, only in the last eight years or so has it been recognised that other, and highly distinct, species exist. Brooke and Rose in 1940 pointed out that plants, particularly notable for their very pendulous flowers, and which had previously been dismissed as "degenerate" forms of *E. leptochila*, were actually unrelated to the latter; to cover these they used the name *E. vectensis*, based on the varietal name used earlier by Stephenson and Stephenson (1918). The following year Thomas (1941) reported that a related plant, which he named *E. pendula*, grew with *E. dunensis* in the plantations on the Lancashire sand-dunes, and a similar one—still *sub judice*—occurred in South Wales.

It seems opportune to make a survey of some of the autogamous British species, adding some further observations which will serve to distinguish them. One may state at the outset, however, that the study of these plants is still very far from complete, and the understanding of their origin and affinities even more so. For this reason, the time is not yet ripe for any major modifications in taxonomy, which may have to be made later. The present survey will therefore be almost entirely descriptive, and so will be from the field botanist's point of view. However, as further material is badly needed for the continuance of the study of the genus, if this account encourages interest in the search for further examples of this group of plants, it will have served its purpose.

Epipactis leptochila may be dismissed briefly, not as being well understood, but rather because it is at least better known than the other autogamous species, and is much less locally distributed, occurring in England over a broad band from Kent and Bedford to Shropshire and into South Wales. It is, like *E. Helleborine* Crantz, a rather variable plant. In this connection it should also be noted that, as is commonly the case with self-fertilised and apomictic groups, and especially where, as here, the plants occur in small and widely-separated colonies, different colonies tend to acquire diverging characters, so that it is frequently difficult to decide the precise taxonomic status of different races. A plant, apparently closely related to *E. leptochila*, is described by C. Thomas in Riddelsdell, Hedley and Price (1948), as *E. cleistogama*.

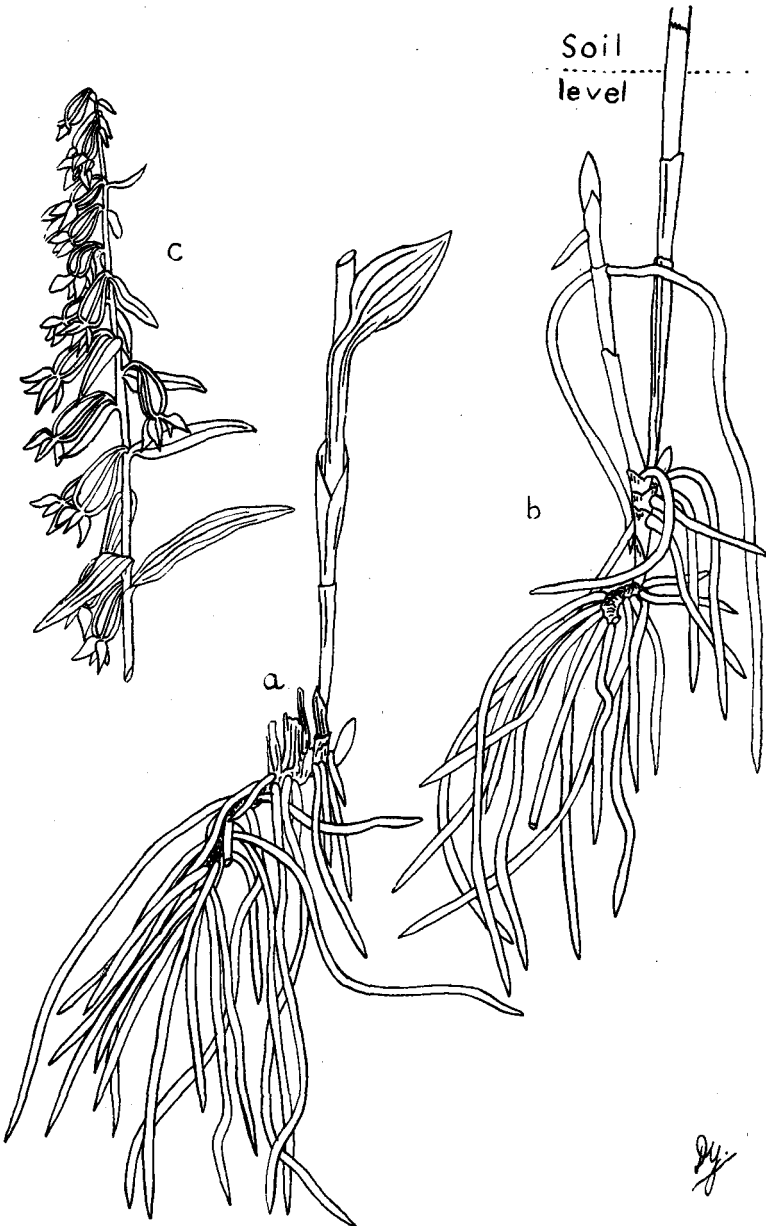


Fig. 1. *Epipactis pendula*: (a) normal root system; (b) branched rhizome; (c) fruit of Bedfordshire form. All $\times \frac{1}{2}$.

I will commence, then, with an account of the two Lancashire sand-dune species, and follow with a discussion of the relationship between *E. pendula* and *E. vectensis*.

E. dunensis, known in Britain only from Lancashire (v.-c.'s 59 and 60) and Anglesey (v.-c. 52), was first observed growing, usually amongst *Salix repens*, in somewhat peaty but not moist hollows in the coastal dunes. Here it answers to the description usually applied to it, viz., a weak slender plant, not much above 30 cm. in height, with rather small flowers, often 6-10 or less in number, and the whole plant of a characteristic yellow-green colour. As will be seen in a moment, this must really be regarded as a depauperate form resulting from the unfavourable nature of its ordinary habitat.

E. pendula was first discovered by Thomas in the pine plantations at Formby (v.-c. 59), and as it occurs in some quantity in this well-explored area, and is of distinct appearance, it is very curious that it had not been noticed previously.

Growing with it in the plantations is the robust dark-green form of *E. dunensis* that has arisen from continuous growth under the trees, which have been there for just over half a century; that the plants grow larger and of a richer green in the pine plantations has been noted previously (Godfery, 1931; Thomas, 1941), but no detailed account of this interesting state or form appears to have been published. It is proposed to call it f. *pinetorum*.

Epipactis dunensis (T. & T. A. Steph.) Godf., f. **pinetorum** forma nov. A typo differt habitu robustiore, 50-60 cm. altitudine; floribus numerosioribus; colore saturate viridi, nec flavo-viridi; foliis lanceolatis, flaccidioribus, plano-recurvis, nec plicatis nec undulatis. Caulibus nonnunquam aggregatis. Sub umbra pinetorum crescit, nec in arena aprica. Type in Herb. D. P. Young no. 1636.

This is a tall slender plant, 50-60 cm. high in its most typical form, mid-green in colour with little or no yellowish tinge. The leaves are lanceolate, the middle ones four times as long as broad; less rigid than in the typical form of the sand-dunes, neither plicate nor wavy-edged, but flat and recurved. Raceme long, 13-17 cm., with 20-25 flowers, pale clear green in colour; the hypochile* red-purple within and the epichilet nearly white with a pink flush in the centre (fig. 2). The roots are better developed than in the dune plants, and are more fully described below. Sometimes two or three stems grow in a cluster, which happens more rarely with the dune form. As might be expected, it flowers later than the last-named (end of July and beginning of August). *E. dunensis* f. *pinetorum* is interesting as representing the full stature of the plant under conditions more favourable to growth than the sand-dune habitat of the "typical" form, where growth of all plants is normally stunted and frequently chlorotic.

*Hypochile: the basin-shaped proximal part of the labellum, which in the cross-fertilised spp. contains nectar.

†Epichile: the cordate distal part of the labellum.

The differences between *E. pendula* and typical *E. dunensis* have been sufficiently well pointed out by Thomas (1941) in the original description. *E. pendula* is however very similar in superficial appearance to *E. dunensis* f. *pinetorum*, from which it is difficult to distinguish at a distance, but the specific characters, viz., the pendulous

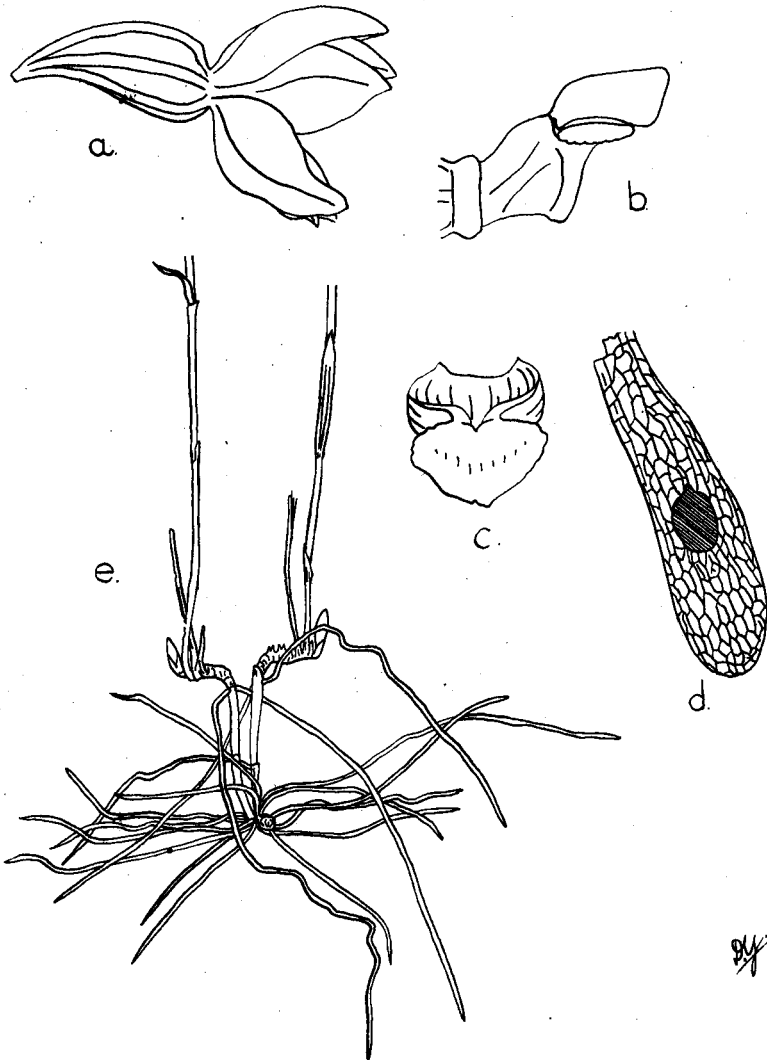


Fig. 2. *Epipactis dunensis* f. *pinetorum*: (a) branched rhizome, $\times \frac{1}{2}$; (b) flower, $\times 5$; (c) column, $\times 10$; (d) labellum, $\times 10$; (e) seed, $\times 50$.

flowers (appearing as if arising from weakness of the peduncles, but actually due to positive geotropism, as the peduncles are fairly rigid) entirely green within (and often without as well), ovate concave leaves of thick texture, and more frequently clustered stems and much stouter roots, will readily separate it. Two further characters may be useful for the determination of herbarium specimens: firstly, *E. pendula* has the upper part (and indeed the whole) of the stem very nearly glabrous, but *E. dunensis*, in common with all *eu-Epipactis* not belonging to the *pendula* group, has a good deal of short pubescence. This character is, however, somewhat variable, and must not be regarded as absolute. Secondly, the leaves of *E. pendula* show a rather characteristic sinuous edge with ciliola in regular groups, whereas other *Epipactis* have a more even fringe—in *E. dunensis* the cilia are so short as to be reduced to papillae, and are scarcely noticeable except under a high power.

Although *E. pendula* often has aggregated stems, they do not by any means always spring from a single rhizome as in *E. purpurata* Sm., but rather resemble the arrangement of *E. Helleborine*. A cluster of seven stems was found to consist of as many separate rhizomes, each bearing one stem and one bud at the base. The whole clump was held together by the interlacing roots, but no physical connection could be traced between the different stems, although one may have existed at an earlier stage of development. A typical root-system (all roots described herein were taken in late September) is shown in fig. 1a. The rhizome is variable in length, nearly horizontal or ascending, sending out numerous short and long fleshy roots, white when young, 2.5-3 mm. in diameter. The bud for the next season's growth normally arises at the base of the old stem, but sometimes the underground portion of the stem itself also sends out buds and adventitious roots.* Fig. 1b shows an example where a branch stem, ending in a bud and bearing adventitious roots, has arisen 3 cm from the base of the flowering stem, at the fourth node, and another bud has formed at the node immediately below.

The root-system of *E. dunensis* f. *pinetorum* is essentially similar but of very different appearance; the rhizome is shorter and more slender than in *E. pendula*, and the roots, although more numerous than in the type form, are far less numerous than in *E. pendula*, less than half the diameter, wiry, not so straight nor so uniformly descending, but tending to radiate in all directions from the rhizome. It appears that this plant also is capable of budding from the buried portion of the flowering stem, as several examples have been seen of a rhizome sending up a vertical stolon a few cm. long, terminating in another

*This is the normal manner of growth of all British *eu-Epipactis*, varying slightly in detail. Evidence is accumulating, however, that the bud does not necessarily develop during the year immediately following, but may remain dormant for one or several seasons. To this cause may often be attributed the erratic manner of appearance of these plants.

rhizome. This could only have arisen from a bud off the stem, which latter had not decayed but remained as the stolon. For example, fig. 2a shows an interesting branched rhizome bearing two stems, which looks as if it had originally branched by the formation of two buds side by side on the original rhizome (visible at the base where the two stolons divide); the following season each of the two resulting stems produced a bud at the second node, which later developed into two horizontal rhizomes connected to the first, the original, by vertical stolons.

Similar roots might be expected with *E. pendula*. If the connecting stolons decayed the result would be a pair or cluster of separate rhizomes. The same result, of course, might arise from germination of several seeds in close proximity, but the rather frequent appearance of such clumps suggests that this is not the explanation. The soil in this station consists of nearly pure sand, covered by a layer about 3 cm. deep of decayed pine-needles. This abnormal underground branching may therefore be the result of the plant's search for humus, and also possibly to efforts to keep pace with the gradual rise in soil level as the layer grows thicker with time. It is hoped to discuss the morphology of the root-systems of various *Epipactis* more fully at a later date.

In the "typical" *E. dunensis* of the open sandhills, the root system, as has been described by Godfrey, is much reduced; the rhizome is usually no more than a knob, and sends out very few roots indeed. *E. pendula* also sometimes grows in the open dunes, although it does not seem to have been observed far from trees. This is rather curious, because, as the trees have only been planted in recent times, it raises the question, was *E. pendula* a native of the dunes before they were afforested? In the open this plant, like *E. dunensis*, becomes dwarfed and yellowish, but is then a rather stouter plant than the latter.

The ripe capsule of *E. pendula* retains the pendulous habit and rigidity, modified somewhat by its increased girth, and is pyriform to almost lagenoid in shape. The seeds (fig. 3d) are quite different from those of *E. dunensis* (fig. 2e; seeds of type and f. *pinetorum* appear to be identical), and more nearly resemble those of *E. Helleborine* or *E. purpurata*. Testa long (1-1.5 mm.), narrow, tapering at each end, cells irregular, elongated; embryo lemon-shaped, rather narrow, opaque.

The foregoing has referred entirely to material from the type-locality. A word may now be said about examples from the few other localities for these two species. The other British station for *E. dunensis*, in Anglesey, is similar to the Lancashire dunes, and the plants there are the same "typical" dunal form. Slight differences from the type have been noted for Continental examples (Meslin, 1928).

E. pendula is also found in Flintshire (v.-c. 51) in an ash-oak wood on carboniferous limestone, and a specimen exists from the Wirral (v.-c. 58). The Flintshire specimens are small but agree closely with the Lancashire plants, except that the anther is, more frequently than in the latter, slightly pedunculate (an approach to *E. vectensis*). There

is thus a compact area of distribution in the north-west, which suggests that the plant may have colonised the coastal plantations from some other source in this area. From the exsiccata and pickled material in Herb. Kew, the plant recorded by Thomas (1941) from the Cotswolds (v.-c. 33) is also a small example of this species. *E. pendula* is further known in Bedfordshire (v.-c. 30), where a distinctly different type occurs in a few small colonies under beech woods on the chalk. Here the plants do not attain the size which they often do in Lancashire, being 20-30 cm. in height and rather slender. The structure of the essential organs agrees well with the northern plants, but the labellum is very small, being about the same size as that of *E. vectensis* although perfectly developed (cf. Part II), and as in the latter species it embraces the stigma. The flowers are usually cleistogamic, but the perianth after fertilisation opens and is then extraordinarily persistent, being fresh and green (except for the labellum) when the seeds are being shed (fig. 1c). The seeds are similar to those of the Lancashire plant. Clearly, *E. pendula* is quite catholic as to habitat, and although its original and main station is on the coast its distribution is not markedly maritime. *E. dunensis*, on the other hand, whatever its earlier distribution may have been, is now exclusively coastal so far as is now known.

The reported occurrence of *E. vectensis* in the Lancashire dunes is commented on in Part II.

Brooke, B. J., and Rose, F.: 1940: *J. Bot.*, 78, 81.

Godfrey, M. J.: 1920: *J. Bot.*, 58, 101.

—; 1921: *J. Bot.*, 59, 146.

—; 1926: *J. Bot.*, 64, 65.

—; 1931: *Monograph and Iconograph of the Native British Orchidaceae*, 77.

Meslin, R.: 1928: *J. Bot.*, 66, 217.

Riddelsdell, H. J., Hedley, G. W., and Price, W. R.: 1948: *Flora of Gloucestershire*, 612.

Stephenson, T., and Stephenson, T. A.: 1918: *J. Bot.*, 56, 1.

Thomas, C.: 1941: *J. Bot.*, 79, 200.

II. THE DIFFERENTIATION OF *E. PENDULA* FROM *E. VECTENSIS*

As has been shown in Part I, *Epipactis pendula* and *E. dunensis*, although growing together in their main station and superficially alike, are in reality distinct in numerous particulars, and are probably not very closely related at all. *E. vectensis*, on the other hand, is only separated with difficulty from *E. pendula*.

The original Ventnor station of *Epipactis leptochila* Godf. var. *vectensis* T. & T. A. Steph. has most unfortunately been lost. In the circumstances, Brooke and Rose (1940), in raising the Stephensons' plant to the rank of species, described specimens from the colony at Nonington (v.-c. 15), which they considered to be identical with the Isle of Wight plants. The only authentic living material of *E. vectensis* (T. & T. A. Steph.) Brooke & Rose, therefore, is to be obtained from the

Nonington station, and such specimens have here been used as standards of comparison. The question of their absolute identity with the Ventnor plants will be referred to again later.

Although previous descriptions have tended to emphasise that *E. vectensis* is a small and slender plant, this is hardly in fact the case. One plant seen at Nonington was nearly 40 cm. tall; it had 14 flowers. Although it remains to be seen whether *E. vectensis* can attain the very robust stature that *E. pendula* shows in the Lancashire pinewoods, its habit is very similar indeed to the *E. pendula* which grows in beech woods—an entirely comparable habitat—in Bedfordshire. Furthermore, the vegetative portions—stem, leaves, and root—of comparably-sized plants of the two species appear to be completely indistinguishable. So far as can be ascertained, the practical differences lie entirely in the floral structure.

Apart from the characteristic large, shining-glabrous and pendulous ovary, the flowers of *E. pendula* are fairly like those of *E. dunensis*. The perianth more or less resembles that of *E. Helleborine*, apart from being entirely green; the essential organs (fig. 3b) are, apart from the lack of rostellum, what might be termed normally shaped, and are similar to those of *E. dunensis* (fig. 2c). The stigma is squarish and nearly perpendicular to the floral axis, and the pollinia lie in the clinandrium* in the normal manner, under the anther-cell, which is rectangular in profile and ovate in plan view, and sessile (or, rarely, on a very short filament); the pollinia thus lie behind the stigma. The mode of fertilisation is a little obscure. The pollen is very scanty, even more so than in *E. dunensis*, and after rupture of the enclosing membrane the pollinium is no more than a little mat of grains inside the clinandrium. It appears that an adequate number of grains work their way to the top edge of the stigma, possibly by gravity, and there germinate.

The floral structure of *E. vectensis*, on the other hand, is distinctly degenerate, as has been observed by Godfrey (1931). The perianth segments are narrower than those of *E. pendula*, and the lateral ones are noticeably crooked. They are of the same thick, waxy consistency and green colour as in the latter species, and have the same prominent midribs. The labellum, though, is extremely debased (fig. 4c). The hypochile is shallow, dish-like, and the long, acute, white and membranous epichile is separated from it, not by the usual form of constriction flanked by folds so as to form a central channel, but simply by a latitudinal fold extending almost the width of the lip, and with little sign of a central channel. The hypochile closely embraces the stigma. The flowers do not open widely, and frequently not at all; *E. pendula*, on the other hand, usually opens its flowers normally, and is rarely cleistogamic.

*Clinandrium: the depression on the column, underneath the anther-cell and behind the stigma, in which the pollinia lie.

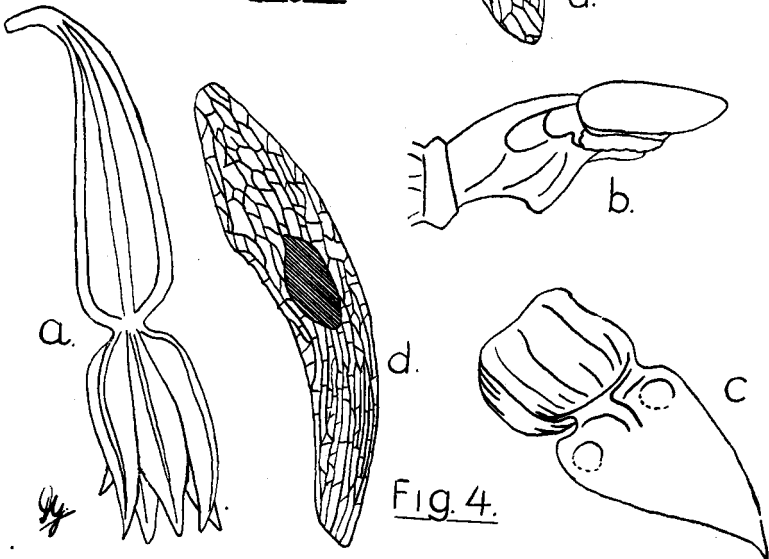
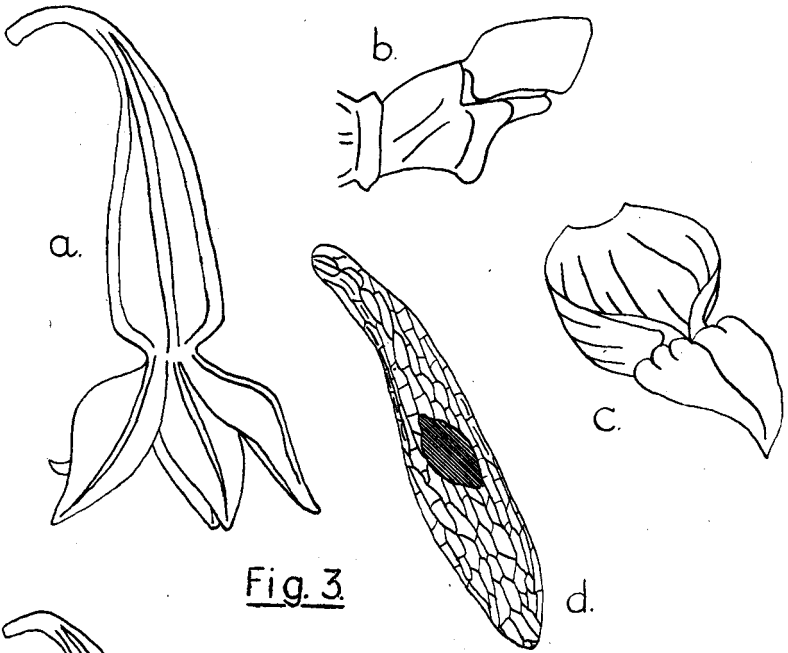


Fig. 3. *Epipactis pendula*; Fig. 4. *Epipactis vectensis*: (a) flower, $\times 5$; (b) column, $\times 10$; (c) labellum, $\times 10$; (d) seed, $\times 50$.

The structure of the column of *E. vectensis*, however, shows the most remarkable difference from that of *E. pendula*. In the present plant, the column appears elongated and attenuated. The stigma slopes much more steeply backwards, and the long-ovoid, pointed anther-cell, and hence the pollinia, are thrust far forward at the end of a detached filament (fig. 4b). The pollinia actually do not lie in the clinandrium, which appears as an empty hollow on either side of the rear of the anther, but instead lie astride, as it were, the horn-like projection which carries the vestiges of the rostellum. They are thus forward of the stigma, and might fertilise it by dropping or sliding back on to it. The very rapid decay of the column, however, lends doubt to whether fertilisation takes place at all, and the plant may well be parthenogenetic; the same remark applies to *E. pendula*. The ovary seems to be a trifle smaller than in *E. pendula*, and although the writer has not had the opportunity of seeing ripe fruit *in situ*, it appears from material and photographs kindly supplied by Messrs Brooke and Rose that the fruit is also rather smaller and more distinctly lagenoid. The seeds closely resemble those of *E. pendula* (fig. 4d).

It is clear that *E. pendula* and *E. vectensis* are very closely related, and must have been derived from a common ancestor at a comparatively recent date. The more orthodox floral arrangements of the former species point to it as being the more ancient type. The essential organs of *E. vectensis* bear a remarkable resemblance to those of *E. leptochila*, which has the same stipitate anther-cell and general arrangement. As these two species do not appear to be closely related in other respects—*E. leptochila* lies perhaps nearer *E. dunensis* in the matter of foliage, pubescence, and patent and not pendulous flowers—this must be regarded as an interesting example of parallel development.

The different structure of the column in *E. vectensis*, although in principle only a difference in development, has led to an apparently important distinction in the fertilisation arrangements, which would justify the specific separation of the two. If, as has just been foreshadowed, the plants should be parthenogenetic, this does not affect the argument, as the development of the column has clearly been dictated by the requirements of fertilisation.

Epipactis persica (Soó) Hausskn. ex Nannf. (Soó, 1927), a plant of northern and eastern Europe, also bears a strong resemblance to *E. vectensis* and *E. pendula* in its pendulous flowers and glabrous stem, for instance, but it differs in a most important and interesting respect in possessing a rostellum. Nannfeldt (1946) has placed *E. vectensis* (and also *E. troödi* Lindb. f.) under it as a synonym; however, the presence of a rostellum, quite distinctly stated in the original diagnosis and clearly shown by Swedish specimens (in alcohol) kindly supplied by Dr Nannfeldt, disposes of any question of synonymy. As a matter of fact, the perfect labellum and almost sessile anther-cell make it nearer to *E. pendula*, and its ovary seems to be smaller than either. *E. persica* is, however, of extraordinary interest as being apparently the cross-

fertilised counterpart, and possible progenitor, of the autogamous *vectensis* group.

Judging from exsiccata in Herb. Kew (Cyprus: Lindberg *iter* 1939), *E. troëdi* is quite unlike *E. persica*, and could hardly be synonymous, as suggested by Nannfeldt, with the latter, still less with *E. vectensis*.

Other records for *E. vectensis* have mostly not been critically determined with reference to the above criteria, but plants which certainly come under this species occur in Berkshire (v.-c. 22), in a birch-wood on the Bagshot sands. Here the plants are uniformly cleistogamic, the sepals adhering by the tips and persisting so until the seed is ripe. The column and labellum closely resemble those of the Kentish examples, but the former is a trifle less elongated and the anther filament very arched, and the epichile is less acuminate and less papery, green with purplish edges.

As already mentioned, fresh material of the Stephenson's original Isle of Wight plant is no longer available, and the existing descriptions and exsiccata are not really adequate for a critical comparison. However, their description (1918) speaks clearly of long, narrow, acuminate tepals, a shallow hypochile, and of the pollinia overhanging the stigma; the accompanying diagram, although not very clear, suggests that although a filament may be present, the essential organs are not so elongated as in the Nonington plants, although they might more resemble those of the Ascot colony. The specimens in Herb. Mus. Brit. confirm that the tepals are like those of the Kentish plant. On the whole, it may be said provisionally that the Ventnor plant, as compared with the Nonington plant, may have features that approach *E. pendula*—just as, in Bedfordshire, *E. pendula* shows by its small labellum and tendency to cleistogamy and, in Flintshire, by a slightly stipitate anther, features approaching *E. vectensis*.

E. vectensis has also been recorded from the Formby dunes (Travis, 1943), but all the Lancashire material named as *E. vectensis* that I have seen has been a small form of *E. pendula*, and it seems probable that the record was based on such plants. Until it can be confirmed that plants with the characteristics given above do occur in Lancashire, the record must be regarded as doubtful.

Those records which can be assigned to *E. pendula* have already been listed in Part I. Exsiccata of this group are frequently impossible to determine critically, and it is to be urged that specimens should include flowers pickled in alcohol. Pending re-examination of the numerous herbarium records, it may be of interest to give a list of vice-counties for which records, of one sort or another, exist for the *vectensis-pendula* aggregate: 3 (or 4), 10, 11, 12, 13, 15, 17, 22, 29, 30, 33, 41, 51, 58, 59. The apparent continuous geographical variation between the two extremes of the aggregate which might be deduced from the examples given in the present paper, should be regarded with considerable reserve for the moment.

As has been said in Part I, the time is not yet ripe for a reconsideration of the taxonomy of the group. Only study of a much larger number of examples than are at present available can determine whether the *vectensis-pendula* aggregate is to be regarded as a single polymorphic species, or whether it may be divided into recognisable segregates. As matters stand at present, however, it must be stressed that naming of specimens is very critical and must be carried out by meticulous comparison with type-material. Too much emphasis has in the past been placed on relative stoutness or frailty of growth as a distinguishing character. From what has been said here, it is plain that *under comparable conditions* there is little to choose between the stature of *E. dunensis*, *E. pendula*, or *E. vectensis*, or, for that matter, *E. leptochila*. Whilst it is, of course, perfectly correct to describe a plant in the form in which it occurs in its usual habitat, too little attention seems to have been paid to the fact that not only do these, like any other plants, vary very considerably in size between individuals, but also that the characters of different habitats inevitably impress themselves upon the growth of the plants therein.

To sum up, real structural differences exist between *E. dunensis*, *E. pendula*, and *E. vectensis*, and the significance of these may become apparent on closer study and lead to an understanding of their relationships with one another and with other members of the genus. The last two are very closely related, and their further relationship to the (presumably) allogamous *E. persica* indicates that they come from a line of descent that diverged from that leading to *E. leptochila* and *E. dunensis* at a stage before they lost their rosetta. Putting this more succinctly: we have evidence that the autogamous *Epipactis* are polyphyletic in origin.

Besides those mentioned in the text, I wish to thank various colleagues, too numerous to name individually, for their kind assistance in field and herbarium work.

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Travis, W. G.; 1943: *N.W. Nat.*, 18, 326 (see also *B.E.C. 1943-44 Rep.*, 756, 1946).