STUDIES IN ORCHIS L.
II. ORCHIS TRAUNSTEINERI Saut. IN THE BRITISH ISLES

By J. Heslop-Harrison.

Introduction.

Of the various new dactylorchid taxa described from the British Isles during the last few decades, one of the most interesting—and taxonomically perplexing—has been Pugsley's *Orchis traunsteinerioides*. This plant was described from material originating in two Irish localities, the coastal marshes near Newcastle and Ballyman Glen, both in Co. Wicklow (Pugsley, 1936). Possibly impelled by a feeling that altogether too many new "species" of *Orchis* were being reported from Ireland at the period, Pugsley originally described the form as a subspecies under *O. majalis* Reichb., although recognising affinities with the Continental *O. Traunsteineri* Saut. ex Reichb., both in his account of the plant and his choice of name. At the time of the first description, Pugsley had not apparently seen the new plant in the field, and it seems not improbable that had he done so he would have refrained from suggesting any close association with the *majalis*-complex, and have accepted without reservation that this was indeed a plant to be connected rather with *O. Traunsteineri*. He did, ultimately, raise the plant to specific rank under the name *O. traunsteinerioides* (Pugsley, (1940) and later (1946) recorded it from Cothill in Berkshire and Odiham, N. Hants. A connection with *O. latifolia* var. *eborensis* Godfery (1933) had already been suggested by Pugsley (1936), and was affirmed by him after examination of a Yorkshire colony of this form (Pugsley, 1939).

In an account of the ecology of Athlone Bog by Osvald (1949), there appears a record for *O. Traunsteineri* Saut. There can, of course, be no doubt of Osvald's familiarity with the plant given this name in Scandinavia, and further, while the colony in question has not been refound, there seems every reason to believe now that it, also, would be referable to Pugsley's *O. traunsteinerioides*.

A further colony, in Scraw Bog, Co. Westmeath, was discovered by the writer in 1950 and recorded as *O. Traunsteineri* Saut. (Heslop-Harrison, 1950a), and in the same year, verbal intimation was received from Scandinavian and Central European members of the 9th Phytogeographical Excursion in Ireland of the occurrence of a plant, accepted by them as *O. Traunsteineri* Saut., in a fen north of the Curragh in Co. Kildare. This locality was visited in 1951, and the presence there of yet another large colony was confirmed.

Under the name *O. traunsteinerioides*, plants of the same affinity have been recorded from other Irish localities: from Fermanagh and Antrim (Summerhayes, 1951), and from near Lough Bunny, Co. Clare (Mrs. K. Gough, 1952).

Reasons are given below for referring all of the above records to *O. Traunsteineri* Saut. The nomenclature issue is, however, regarded as

secondary to the main purpose of this paper which is to demonstrate that the form in question, although possessing a remarkably discontinuous range in the British Isles, is nevertheless reasonably homogeneous, and as much meriting recognition as a distinct unit as other British marsh orchid "species" such as *O. purpurella* T. & T. A. Steph. and *O. praetermissa* Druce.

During the flowering-seasons (late May and early June) in 1949, 1950, 1951 and 1952, four colonies have been studied intensively, three Irish and one English. Biometrical investigation of these has been carried out by the methods adopted in previous studies of dactylorchid variation (Heslop-Harrison, 1948; 1952).

The Populations.

The distribution of the Irish and English colonies from which samples have been examined is indicated in fig. 1. The habitats of these quite widely separated colonies are all of the nature of rich fen, strongly affected by calcareous ground-water. Lists of associated plants, made within the actual sample areas at the time of collection of the population samples, are given in Table I. As will be seen, there is rather a close similarity between the plant associations in all of the localities.

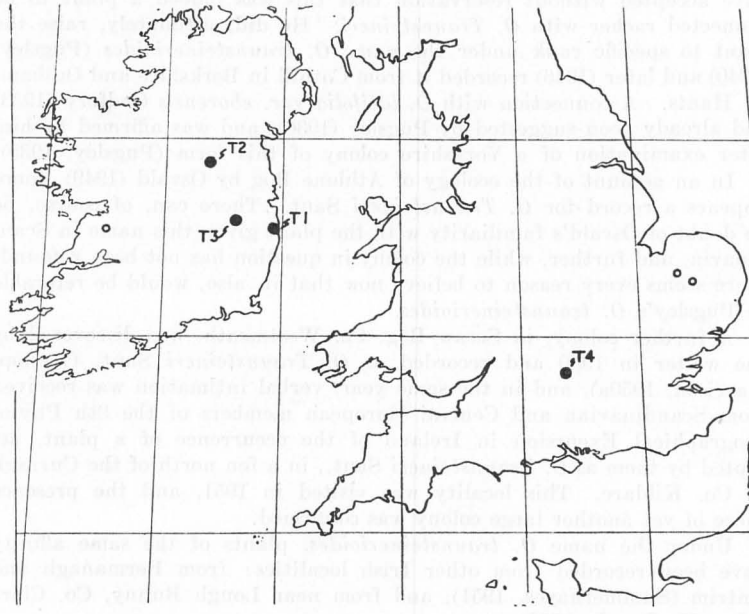


Fig. 1. Distribution of the colonies of *O. Traunsteineri* mentioned in the text. *Dots*: localities from which population samples have been examined; *open circles*: other colonies known to the author.

TABLE I.

Habitats of *Orchis Traunsteineri* Saut.

	T1	T2	T3	T4
Ranunculus Flammula L.	o	o	f	—
Caltha palustris L.	—	o	—	—
Cardamine pratensis L	o	o	o	o
Polygala vulgaris L.	—	—	r	—
Lychnis Flos-cuculi L.	f	o	—	—
Cerastium vulgatum L.	0	—	—	—
Filipendula Ulmaria (L.) Maxim.	o	f	o	f
Geum rivale L.	—	—	—	o
Potentilla erecta (L.) Räusch.	—	o	o	o
P. palustris (L.) Scop.	0	f	—	—
Drosera rotundifolia L.	—	r	—	r
D. anglica Huds.	—	r	—	—
Epilobium hirsutum L.	—	—	—	o
Hydrocotyle vulgaris L.	o	o	o	—
Angelica sylvestris L.	o	o	r	o
Oenanthe Lachenalii C. C. Gmel.	—	—	—	o
Galium uliginosum L.	—	f	—	o
Valeriana dioica L.	—	—	—	o
Succisa pratensis Moench	—	—	o	o
Eupatorium cannabinum L.	—	—	—	f
Cirsium palustre (L.) Scop.	o	—	o	o
C. dissectum (L.) Hill	—	o	—	f
Oxycoccus palustris Pers.	—	f	o	—
Erica Tetralix L.	—	o	f	—
Pyrola rotundifolia L.	—	la	—	—
Menyanthes trifoliata L.	f	a	la	—
Solanum Dulcamara L.	—	—	—	o
Pedicularis palustris L.	—	—	o	o
Pinguicula vulgaris L.	—	—	—	o
Mentha aquatica L.	o	—	—	o
Prunella vulgaris L.	o	—	—	o
Salix aurita L.	—	o	—	r
S. repens L.	—	o	—	—
Listera ovata L.	—	r	r	r
Ophrys insectifera L.	—	—	r	—
Epipactis palustris L.	—	—	—	o
Orchis latifolia L. sec. Pugsl.	o	—	—	r
Juncus inflexus L.	o	—	—	r
J. subnodulosus Schrank	la	—	ld	a
Typha latifolia L.	—	—	f	—
Triglochin maritima L.	o	—	—	—
Eleocharis palustris (L.) R.Br.	o	—	—	—
Scirpus maritimus L.	o	—	—	—
Eriophorum latifolium Hoppe	—	—	f	f
E. angustifolium Honck.	f	—	—	—
Schoenus nigricans L.	ld	d	ld	ld
Cladium Mariscus (L.) Pohl	ld	—	a	—
Carex disticha Huds.	a	o	—	—
C. diandra Schrank	—	f	o	—
C. appropinquata Schumacher	—	o	—	—
C. paniculata L.	—	—	a	o
C. nigra (L.) Reichard	a	f	o	o
C. elata All.	la	—	—	—
C. flacca Schreb.	o	o	o	f
C. limosa L.	—	r	—	—
C. panicea L.	f	f	o	f
C. Hostiana DC.	r	—	—	—
C. lepidocarpa Tausch	f	f	f	o
C. lasiocarpa Ehrh.	—	a	—	—
C. acutiformis Ehrh.	f	—	la	—
C. rostrata Stokes	—	o	la	o
Holcus lanatus L.	—	—	o	—
Phragmites communis Trin.	a	—	f	la
Molinia caerulea (L.) Moench	—	—	la	—
Briza media L.	—	—	r	o
Festuca rubra L.	—	—	o	—
Equisetum palustre L.	—	—	f	—
E. fluviatile L.	—	f	—	—
Sphagnum palustre L.	Bryophytes not recorded	a	—	—
S. squarrosum Crome		o	—	—
Fissidens adianthoides Hedw.		—	—	o
Mnium affine Bland., *s.l.*		f	—	o
M. cuspidatum Hedw.		—	—	o
M. undulatum Hedw.		—	—	o
Aulacomnium palustre (Hedw.) Schwaegr.		f	—	—
Climacium dendroides (Hedw.) Web. & Mohr		f	—	—
Acrocladium cuspidatum (Hedw.) Lindb.		a	a	f
Drepanocladus revolvens (Sm.) Warnst.		a	a	a
Scorpidium scorpioides (Hedw.) Limpr.		r	—	—
Campylium stellatum (Hedw.) Lange & C. Jens.		—	o	a
Cratoneuron commutatum (Hedw.) Roth		a	o	o
C. filicinum (Hedw.) Roth		—	—	o
Pscudoscleropodium purum (Limpr.) Fleisch.		—	o	o
Ctenidium molluscum (Hedw.) Mitt.		o	la	o
Rhytidiadelphus squarrosus (Hedw.) Warnst.		a	o	—
Hylocomium splendens (Hedw.) B. & S.		a	o	—
Aneura pinguis (L.) Dum.		—	—	o

T1. Coastal marsh, between Five and Six Mile Point, south of Newcastle, Co. Wicklow. This is the type locality for Pugsley's *O. traunsteinerioides*. The railway embankment runs along the top of the shingle beach for several miles of this part of the Wicklow coast, and on the landward side of it there is a considerable area of fen. Large stretches are dominated by *Cladium* and *Phragmites*, alternating with sedge-meadow and smaller areas where *Schoenus nigricans* is prevalent. A certain maritime influence is revealed by the presence of *Triglochin maritima* and *Scirpus maritimus*. *O. maculata* subsp. *ericetorum* is present on drier banks, but apart from *O. latifolia* L. sec. Pugsl. which is occasional in the sedge meadows, *O. Traunsteineri* is the only dactylorchid in the area of fen. The sample was collected in a fairly uniform stretch of Schoenetum some two hundred yards inland from the railway embankment. The soil-pH here at tuber depth (determined colorimetrically) lay in the range 7.0-7.5.

T2. Scraw Bog, north-west of Mullingar, Co. Westmeath. This stretch of rich fen occupies a depression in the limestone about half a mile from Loch Owel, and is of interest in supporting a number of species many of which are singularly rare elsewhere in Ireland. The most striking is *Pyrola rotundifolia*, in great profusion here in one of its two Irish stations. *O. Fuchsii* occurs around the margin of the bog, and *O. latifolia* is present locally in small quantity. *O. Traunsteineri* is the only orchid growing in the central area, where it is abundant. The sample was taken in a very uniform stretch of scattered, non-tussocky *Schoenus*. The orchids root quite loosely in a thick moss carpet (composition given in Table I), and offer little resistance to plucking, so that they tend to come up complete with the extremely long, divaricate roots. Soil-pH, *c.* 7.0.

T3. Fen north-east of the Curragh, Co. Kildare. This area of fen has many points of resemblance with Scraw Bog, but is characterised by an extensive central stretch dominated by *Cladium* and *Phragmites*. The sample was drawn from a marginal area where *Cladium* is less frequent and where *Schoenus* assumes local dominance. The orchids were rooted loosely in a moss carpet similar in composition to that in Scraw Bog, with great local prevalence of *Ctenidium molluscum*. No other dactylorchids were encountered in the fen, but *Listera ovata* occurs, and *Ophrys insectifera*, here a typical rich-fen plant, as in many of its Continental stations. The pH of the ground-water was *c.* 7.2.

T4. Cothill Fen, Berkshire. *O. Traunsteineri* occurs throughout most of this small area of fen, but it is relatively sparse in the areas dominated by *Phragmites* and most abundant where *Schoenus nigricans* prevails. In the fen itself, *O. latifolia* occurs sparsely, and in a clearing in late-stage alder-carr on the south side, a small colony of *O. praetermissa* was encountered, with occasional plants of *O. Fuchsii*. The striking similarity between this habitat and the Irish ones will be clear from the lists of Table I. Here, as in Ireland, the plants of *O. Traunsteineri* root quite loosely in the bryophyte carpet. At the time when the sample was taken, the ground-water pH was *c.* 7.5.

Cytology.

Root-tip mitosis has been examined in several plants from each of the above colonies. Material was fixed in the field in Langlet's modification of Navashin's fluid, sectioned at 10 μ and stained according to the method of Newton. A chromosome number of 2n=80 has uniformly been observed, which implies that the form is tetraploid in respect to the base number, x=20, of the subgenus *Dactylorchis*. This count is agreement with the majority of Continental determinations for *O. Traunsteineri* Saut., including those made from material from the type locality, Kitzbühl in Austria (*fide* Vermeulen, 1949). Other counts reported from Continental plants referred to *O. Traunsteineri* include one of 2n=40 for a Swiss individual (Heusser, 1938) and another of 2n=122 for a plant originating in Esthonia (Vermeulen, 1938, 1947). It is not established whether entire populations exist possessing these chromosome numbers, populations which are morphologically indistinguishable from tetraploid *O. Traunsteineri*, and on the face of it, it would appear improbable that such should be the case. The existence of another diploid form with 2n=40, apart from the diploid section of the *maculata*-complex and the diploid *Latifoliae*, would have important phylogenetical implications (Heslop-Harrison, 1953, in press). Before accepting the possibility, further assurance would be desirable that the Swiss plant from which the count of 2n=40 was obtained was not merely an anomalous individual of *O. latifolia*.

In their monographic treatment of *O. Traunsteineri*, Fuchs and Ziegenspeck (1927), impressed no doubt by the wide variety of plants to which the name had been attached, concluded that they were dealing not with a "pure species", but with a complex of hybrids. With present-day knowledge of the ways in which pure-breeding groups can arise through hybridisation, a conclusion like this requires examination from more than one point of view. As is now well established, constant and pure breeding forms can arise through hybridisation followed by chromosome doubling; they have all the characteristics of Linnean species, and are justifiably recognised as such taxonomically. On the basis of cytological evidence, an origin of this nature has been suggested elsewhere (Heslop-Harrison, 1953, in press) for other tetraploid marsh orchids, namely *O. praetermissa* and *O. purpurella*. The possibility that tetraploid *O. Traunsteineri*, also, has arisen in this manner would appear to be strong. In this sense, the species might indeed be hybridogenous.

However, it is apparent that the statement of Fuchs and Ziegenspeck simply meant that they regarded the series of populations which had been grouped taxonomically as *O. Traunsteineri* as being all of independent, recent, hybrid origin—in other words, that the name "*O. Traunsteineri*" has been employed simply as a reference name for a series of hybrid-swarms. This possibility, too, requires serious consideration, since distinctive hybrid populations do arise not infrequently where dactylorchid taxa occur together. A parallel instance is afforded by *O. pardalina* Pugsl., which has been considered to be indistinguishable from

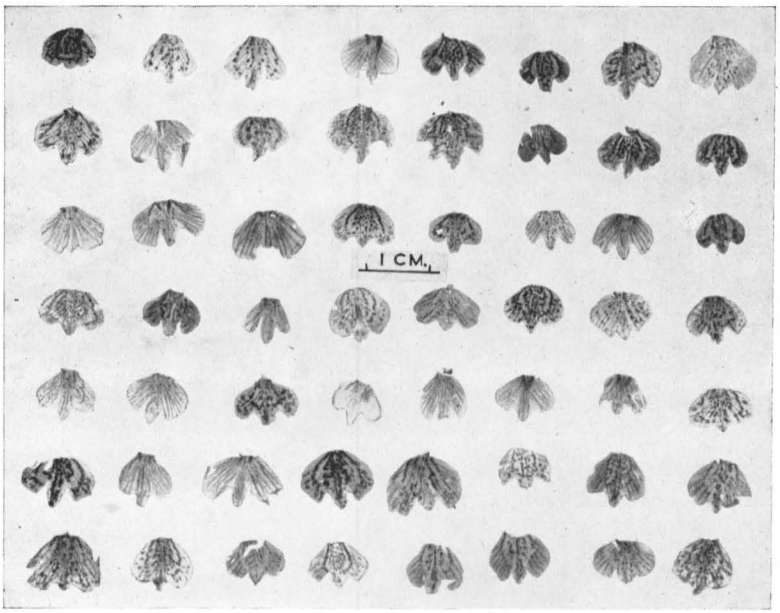
the hybrid *O. Fuchsii* × *O. praetermissa* (Clapham, 1952). However, as in *O. pardalina* (Heslop-Harrison, 1953, in press), the probability of the recent hybrid origin of the colonies ascribed here to *O. Traunsteineri* can be tested by observations of meiotic behaviour and fertility.

For this purpose, young buds were fixed from two of the populations involved in the present study, T2, Scraw Bog, Westmeath, and T4, Cothill Fen, Berkshire. Meiosis in all of the plants examined proved to be normal, with no suggestion of multivalent formation or of other irregularities such as might be expected to arise from hybridity. Estimation of pollen quality is naturally difficult in the dactylorchids because of the association of the pollen grains in massulae, but an assessment of fertility can be obtained from seed counts from well-pollinated ovaries. The percentage of perfect seeds produced by plants from the two Irish colonies, T2 and T3, observed during the period of seed maturation in the season of 1951, was 95% and 96%, figures of the same order as are commonly found, for example, in *O. Fuchsii*. All of this suggests that at least the Britannic colonies referred here to *O. Traunsteineri* represent fully fertile breeding-units, and not simply hybrid complexes of relatively recent origin. The cytological behaviour of the individuals examined was, in fact, of the typical "diploid" type, which, it may be noted, is suggestive of an allopolyploid rather than of an autopolyploid origin.

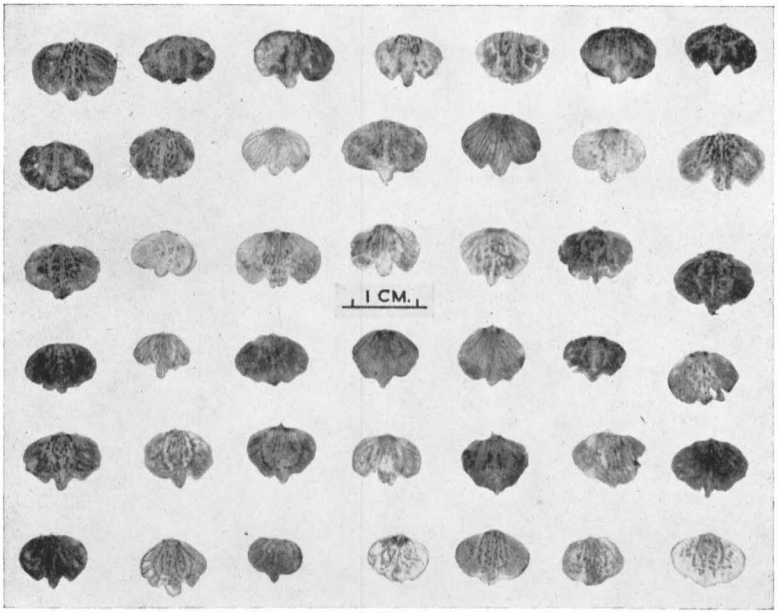
Further information on the latter point might be obtainable from observations of meiotic behaviour in hybrids between *O. Traunsteineri* and its possible progenitors, which may well have been the same as those suggested for *O. purpurella* and *O. praetermissa*, namely a diploid *maculata* form and a member of the *Latifoliae*. Hybrids of the putative parentages *O. Fuchsii* × *O. Traunsteineri* and *O. latifolia* × *O. Traunsteineri* have in fact been encountered during the present study, an individual of the former from Scraw Bog, and several of the latter from the Newcastle marshes. Mitotic chromosome counts of each have given the number 2n=60, a sufficient justification of the diagnosis based upon morphology. Unfortunately, it has not been possible so far to obtain satisfactory evidence of meiotic behaviour in any, so the question whether *O. Fuchsii* or *O. latifolia* (or related forms) have played any part in the origin of *O. Traunsteineri* remains open.

Analysis of Characters.

As is well known, the extreme local variability of dactylorchids reduces the value of taxonomic methods based upon the description and comparison of individual plants. Attention must be transferred from the individual to the local population if the pattern of variation is to be interpreted with any degree of objectivity, a change of emphasis which demands some form of statistical treatment. The purpose of biometrical analysis in the present case is two-fold: firstly, to show that the various colonies referred to *O. Traunsteineri* are as homogeneous amongst themselves in respect to the more important taxonomic characters as can be expected of any taxon within this subgenus, and, secondly, to show that,



A.



B.

Labellum mounts from homologous flowers.

A, 56 plants of *O. Traunsteineri* from colony T2, Scraw Bog, Co. Westmeath.
B, 42 plants of *O. praetermissa* from the Hampshire colony.

as populations, they are distinct from other tetraploid marsh orchids in the British Isles, namely *O. praetermissa*, *O. purpurella* and *O. majalis*.

The morphological differentiae which are of importance and which lend themselves to biometrical treatment are: (a) stature and leaf number, (b) leaf size and shape, (c) leaf marking, (d) labellum size and shape, and (e) spur size. Following methods described elsewhere (Heslop-Harrison, 1948, 52), statistical data for vegetative characters were recorded in the field as soon as possible after collection of the sample, while those for floral characters were recorded later from mounted dissections of homotypic flowers. The statistics recorded in the Tables are: N, the number of individuals examined; M, the arithmetic mean; σ, the standard deviation; S.E., the standard error of the mean and, in Table I, r, the coefficient of correlation. The graphical presentation of figs. 3, 4 and 5 follows that previously adopted in similar studies on *O. maculata* agg. Distances equivalent to $\pm$ 2 (S.E.) are marked off each side of the sample mean values for the variates plotted, and these can be used to give a rough estimate of the significance of the difference between means, since under the conditions in which the test is applied here, a difference between two means greater than twice the sum of their standard errors always indicates $P < .01$.

Comparison with other taxa.

The other British tetraploid marsh orchids, namely *O. praetermissa*, *O. purpurella* and *O. majalis*, are themselves highly polymorphic and show enough ecological and regional variation to have given rise each to a certain amount of taxonomic confusion. Strictly, this variation should be taken into account in making comparisons, since no single local population can be regarded as "typical" of any of these forms. However, it is proposed to provide a more extensive account of the variation of the more widely distributed tetraploid marsh orchids in a further contribution, and since in any case the features in which *O. praetermissa*, *O. purpurella* and *O. majalis* show geographical and ecological variation, are not, for the most part, those which differentiate these species from *O. Traunsteineri*, it is considered sufficient to base comparisons here on three populations which, while not put forward as "typical", may be taken as occupying a roughly central position in the variation range of each. These are:

O. purpurella, a large colony near Dunfanaghy, Co. Donegal, growing in sedge-meadow at the south end of Lough Sessiagh. The plants here mostly conform to the Stephensons' "Form A" (T. and T. A. Stephenson, 1920).

O. praetermissa, a colony at Brambridge, growing in the water meadows on the west side of the river Itchen near Otterbourne, Hampshire. This colony, like most others of the species in Hampshire, includes a percentage of individuals conforming to the type description of *O. pardalina* Pugsl.

O. majalis, a colony growing near the type locality for the subsp. *occidentalis* Pugsl., Lisdoonvarna, Co. Clare, in open meadowland. In this, as in other Clare colonies, a proportion conforms to the type description of *O. kerryensis* Wilm.

(a) *Stature and leaf number.*

In all cases, plant stature has been measured from the base of the stem, just above the tubers, to the tip of the inflorescence at the time of flowering. In assessing the number of leaves, the lowest expanded green leaf has been taken as the first, and that immediately below the inflorescence as the last, even when scale- or bract-like.

Being quite sensitive to culture conditions, dactylorchid stature as a simple linear measure is of little taxonomic value. The data, for this attribute, given in Table II simply give a general impression of what are characteristic habits for the four tetraploid forms: *O. Traunsteineri* and *O. praetermissa*, both fen plants, are generally taller and relatively more slender than the meadow forms of *O. majalis* and *O. purpurella*.

TABLE II

Sample data for stature and number of leaves per plant.

Sample.	N	Stature in cm.			Leaf number.			r
		M	σ	S.E.	M	σ	S.E.	
O. Traunsteineri								
T1 ...	60	35.7	6.6	0.85	3.98	0.78	0.10	−.052 (P>.05)
T2 ...	75	32.3	6.2	0.71	4.32	0.75	0.09	+.021 (P>.05)
T3 ...	125	29.4	7.4	0.66	4.42	0.71	0.06	+.093 (P>.05)
T4 ...	90	32.6	6.3	0.67	3.83	0.70	0.07	+.153 (P>.05)
O. praetermissa								
Pr ...	70	45.2	6.6	0.78	6.17	0.75	0.09	+.351 (P<.05)
O. purpurella								
Pu ...	50	20.2	2.6	0.36	6.56	0.98	0.14	+.472 (P<.05)
O. majalis								
Ma ...	50	25.9	4.4	0.63	6.28	1.02	0.14	+.276 (P<.05)

However, two other attributes for which sample data are given in Table II constitute good differentiae. The more obvious is leaf number. The populations, here referred to *O. Traunsteineri*, are characterised by a mean leaf number in the neighbourhood of 4, an extremely small number for a tetraploid marsh orchid, and fewer even than in the most extreme of the diploid *Latifoliae* in British latitudes. This feature is absolutely diagnostic for *O. Traunsteineri* in comparison with other British tetraploids, which have almost invariably average leaf numbers greater than 6.

A less obvious feature is that in populations of *O. Traunsteineri* there is no significant correlation between leaf number and stature. As will be seen from the data of Table I, in *O. praetermissa*, *O. purpurella* and *O. majalis*, there is a significant positive correlation between stature and leaf number, a correlation to be expected from the simple consideration that variation in over-all height is likely to be linked not only with

internode length but with internode number (see Heslop-Harrison, 1952, for a discussion of this point in relation to *O. maculata sensu lato*). The absence of such a correlation in the populations of *O. Traunsteineri* investigated is connected, no doubt, with the small number of leaves produced per plant; variation in over-all height must be due entirely to variation in internode length.

(b) *Leaf size.*

The sample data given in Table III refer to the dimensions of the longest leaf of each plant. The data were recorded from fresh plants, length being measured from the opening of the sheath to the tip of the lamina, and width at the broadest part of the blade, generally about one-third of the leaf length from the base. In length of leaf, these *O. Traunsteineri* populations do not appear to differ to any marked extent from those of *O. purpurella* and *O. majalis* with which comparison is made in Table II, although the average leaf length in all of these colonies is evidently a good deal less than in the colony of *O. praetermissa* for which sample data are given.

TABLE III

Sample data for leaf length and width

Sample	N	Length in cm.			Width in cm.		
		M	σ	S.E.	M	σ	S.E.
O. Traunsteineri							
T1 ...	60	12.3	2.79	0.36	1.32	0.28	0.040
T2 ...	75	11.7	2.05	0.24	1.16	0.34	0.039
T3 ...	50	10.9	2.69	0.38	1.18	0.39	0.056
T4 ...	90	11.1	2.20	0.23	1.28	0.27	0.028
O. praetermissa							
Pr ...	70	15.4	2.93	0.35	2.33	0.40	0.048
O. purpurella							
Pu ...	50	12.5	1.88	0.27	1.99	0.33	0.047
O. majalis							
Ma ...	50	10.3	2.58	0.37	2.18	0.41	0.058

In leaf width, however, the *O. Traunsteineri* colonies differ significantly from all of the others. The character of very narrow lanceolate, or linear-lanceolate, leaves is, in fact, one of importance in discriminating *O. Traunsteineri* which is stressed in all of the Continental diagnoses of the species, including the two earliest, those of Reichenbach (1830) and Sauter (1837). The characteristic has no doubt encouraged the acceptance of one of the more widely used synonyms, *O. angustifolia* Lois. in Reichb., the name adopted by Klinge (1898) and E. G. & A. Camus (1928-29).

Taken together, the vegetative characters of leaf number and leaf width serve to separate the four colonies of *O. Traunsteineri* completely from those of the other tetraploid marsh orchids, as is shown graphically in fig. 2.

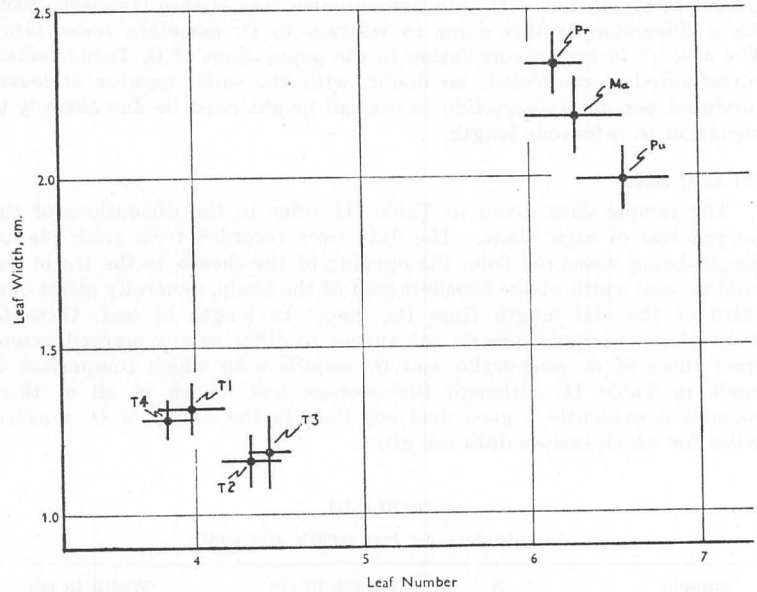


Fig. 2. Discrimination of *O. Traunsteineri* from other British tetraploid marsh orchids on the basis of leaf width and leaf number. The sample means are labelled to correspond with the notation in Tables II-VI.

(c) *Leaf marking.*

The incidence of leaf marking in the British tetraploid marsh orchids offers an interesting problem in variation. Whereas in the spotted orchids proper, intra-population variation in leaf marking follows more or less orthodox lines, in that frequency distributions of leaf-spot grades conform more or less with normality, in the tetraploid marsh orchids, L-, J-, and even U-shaped distributions are more often encountered. Furthermore, there are often peculiarities in leaf-spot shape not usually found in the *maculata*-complex, ring-spots commonly occurring. Since leaf-marking and flower-colour are often closely correlated, being presumably each reflections of the anthocyanin pigment system of the plant, the two modes in populations where J-shaped distributions prevail are often phenotypically very distinct. The taxonomic consequences that have arisen from this fact are well-known. In the *O. praetermissa* alliance, the original diagnosis of *O. praetermissa* (Druce, 1914) refers to the "anthocyanin-low" mode in a J-shaped distribution, and that of *O. pardalina* (Pugsley, 1935) to the usually smaller "anthocyanin-high" mode. Similarly, the "anthocyanin-low" mode of the *O. majalis* populations of western Ireland has been described as *O. kerryensis* (Wilmott, 1936), and the "anthocyanin-high" mode, as the subsp. *occidentalis* (Pugsley, 1935; the form was

later raised to specific rank as *O. occidentalis*, Wilmott, 1938). A possible explanation for these peculiarities in the incidence of leaf-marking may lie in the fact that probably all of the tetraploid marsh orchids are allopolyploid in origin, having had diploid *maculata*-forms as one progenitor. One may suspect that occasional aberrations in the mechanism of tetrasomic inheritance may well lead to the segregation of individuals in which *maculata*-genes are over-represented.

The incidence of leaf-marking in the *O. Traunsteineri* colonies studied is somewhat similar to that commonly encountered in colonies of *O. praetermissa* in the eastern parts of England, and in *O. majalis* towards the southern end of its western Irish range. The representation in the population samples of four arbitrary leaf-spot grades is shown in Table IV. The Scraw Bog, Wicklow and Cothill populations are evidently much alike in the representation of these grades, resembling somewhat the *O. praetermissa* population, in which the majority of individuals are unmarked. The Kildare population differs in that the bulk of individuals show some sign of leaf-marking. The shape of leaf-spots in *O. Traunsteineri* is unlike that found in *O. praetermissa*, taking usually the form of narrow transverse bars, as in the plant illustrated by Pugsley (1936). In the more deeply marked individuals, the upper part of the stem and the bracts are commonly suffused with pigment.

TABLE IV

Leaf marking. Percentage in four arbitrary grades: 1, unmarked; 2, light; 3, medium; 4 heavy. Shape and distribution of the marking not taken into account.

Sample	1	2	3	4
O. Traunsteineri				
T1	*77.5*	16	5	1.5
T2	*76.5*	17	6.5	—
T3	29	*44.5*	25	1.5
T4	*60*	*31*	8	1
O. praetermissa				
Pr	*78*	18.5	2.5	1
O. purpurella				
Pu	*57*	*43*	—	—
O. majalis				
Ma	*39*	*41*	17	3

Values in italic type where class contains 30% or more.

(d) *Flower characters: labellum size and shape.*

Sample data for the linear dimensions of the labellum, as illustrated in fig. 3, are given in Table V. The different colonies of *O. Traunsteineri* agree remarkably well in these dimensions, and the sample data for the *O. majalis* colony suggest that this lies also in the same general size range in respect to width and length. The mean values for the *O. praetermissa* sample are significantly greater, and, of course, those for *O. purpurella*, very much less. The relationships of the samples for these two dimensions are illustrated graphically in fig. 4.

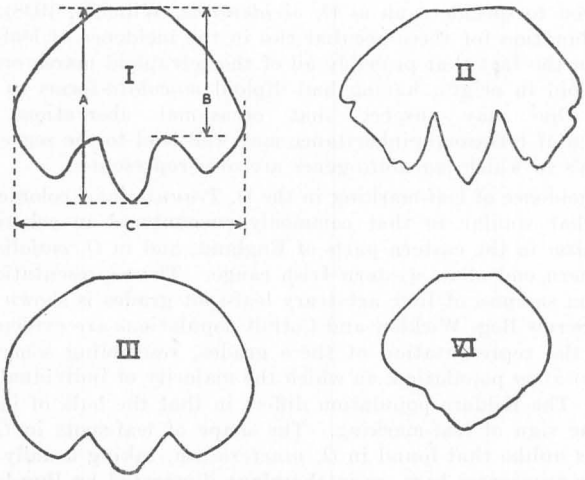


Fig. 3. Labellum shapes in tetraploid British marsh orchids. I, *O. Traunsteineri* Saut.; II, *O. majalis* Reichb. (a characteristic shape occurring in the subsp. *occidentalis* Pugsl.); III, *O. praetermissa* Druce; VI, *O. purpurella* Steph. The dimensions marked on the labellum in I are those for which data are given in Table V.

TABLE V

Sample data for labellum dimensions as in fig. 2; length (A), total length less sinus depth (B) and width (C); all in mm.

Sample.	N	(A)			(B)			(C)		
		M	σ	S.E.	M	σ	S.E.	M	σ	S.E.
O. Traunsteineri										
T1	50	8.37	0.77	0.11	6.05	0.68	0.01	10.00	1.12	0.16
T2	100	8.26	0.90	0.09	5.99	0.88	0.09	10.03	1.13	0.11
T3	100	8.62	0.65	0.07	6.07	0.73	0.07	10.11	1.56	0.16
T4	100	8.39	0.89	0.09	6.21	0.70	0.07	10.21	1.05	0.11
O. praetermissa										
Pr.	100	9.28	0.81	0.08	7.74	0.97	0.10	11.48	1.18	0.12
O. purpurella										
Pu	100	6.11	0.55	0.06	Sinus absent			7.93	0.66	0.07
O. majalis										
Ma	100	7.91	0.82	0.08	5.50	0.72	0.07	10.16	1.33	0.13

As indicated in fig. 3, the labella of the four tetraploids differ somewhat in shape, and this is, in the field, a more useful discriminant than size. *O. purpurella*, in its most common form ("Form A", Stephenson, 1920), is, of course, quite distinctive, the small labellum being rhomboidal and practically entire. The variation in *O. purpurella* is on the one hand towards *O. praetermissa* ("Form B," Stephenson, and the var. *pulchella* (Druce) Pugsley), and on the other in the direction of *O. majalis*, particularly in the west of Scotland and north-western Ireland, where the

cause may lie in actual hybridisation with *O. majalis* (Heslop-Harrison, 1952). *O. purpurella*, even in the broad sense, does not transgress the variation range of *O. Traunsteineri* for this character.

There is, however, some overlap in the variation ranges of both *O. majalis* and *O. praetermissa* with that of *O. Traunsteineri* for labellum-shape. This is apparent enough in the case of *O. praetermissa* from the samples illustrated in Plate 8. As emphasised by Pugsley in the original diagnosis of *O. traunsteinerioides*, there is a tendency towards a deltoid or obcordate shape in *O. Traunsteineri*, and the labellum is generally moderately incised so that there is a short, bluntly triangular, central lobe. In *O. praetermissa*, the labellum tends to be practically elliptical, only slightly incised, with a small, often almost obsolete, central lobe. Reference to the dimension "B" of fig. 3, which is a measure of the depths of incision, serves to discriminate the population of *O. praetermissa*, for which sample data are given in Table V, from those of *O. Traunsteineri*.

In *O. majalis*, there is a considerable range of variation in labellum shape both within colonies and between different ones throughout the western Irish range. In general, Pugsley's description of "rotund-rhomboidal" (1936) is fitting. The degree of dissection is rather more marked than in *O. Traunsteineri* (cf. dimension "B" in Table V). A characteristic which readily serves as a discriminant in the field (although not one which lends itself to biometrical treatment) is that

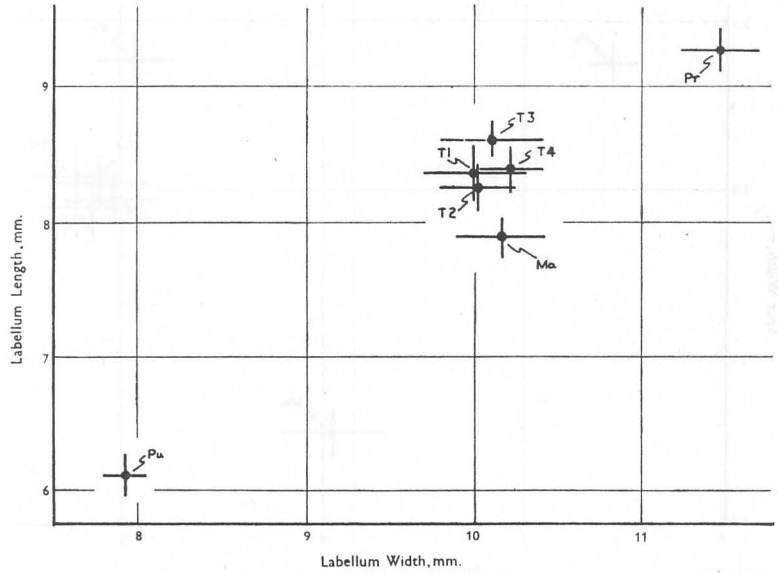


Fig. 4. Relationship of labellum width to labellum length. Labelling as in Tables II-VI.

the lateral lobes of the labellum, smoothly rounded in *O. Traunsteineri* as in *O. praetermissa*, tend to be angular, notched, or even laciniate, in *O. majalis*.

(e) *Spur size and shape.*

The sample data for spur dimensions given in Table VI refer to length from mouth to tip, and width at about a millimetre from the mouth when flattened. The "width" figure represents, therefore, not the diameter, but approximately half the circumference at this point. The samples are compared graphically for these attributes in fig. 5; clearly they serve to separate *O. Traunsteineri* quite satisfactorily from *O. purpurella* and *O. majalis*. The former possesses on the average a broader and much shorter spur, and the latter, one which is both somewhat shorter and a good deal more slender. An additional characteristic of the Irish populations of *O. majalis* is that in most plants the flower spur is rather strongly curved, sometimes quite abruptly, about one third of its length from the tip, a feature which is well shown in the drawings and photographs accompanying Wilmott's description of *O. kerryensis* (Wilmott, 1936). The spur of *O. Traunsteineri* is, in contrast, quite straight. Spur characters do not serve particularly well to discriminate *O. Traunsteineri* from *O. praetermissa*, although the data of Table VI suggest that the mean spur width, in the population of *O. praetermissa* for which data are given, is greater than in any of those referred to *O. Traunsteineri*.

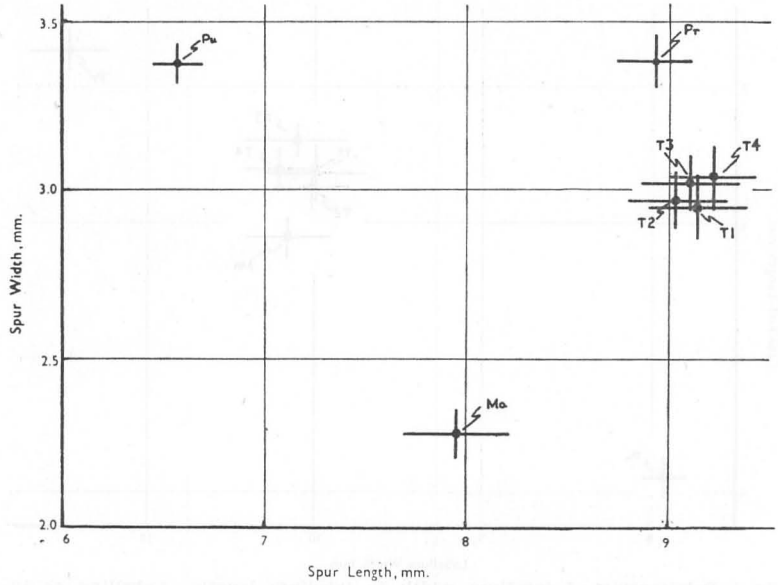


Fig. 5. Relationship of spur length to spur width. Labelling as in Tables II-VI.

TABLE VI

Sample data for spur length and width.

Sample	N	Length.			Width.		
		M	σ	S.E.	M	σ	S.E.
O. Traunsteineri							
T1 ...	70	9.14	1.01	0.10	2.95	0.38	0.046
T2 ...	100	9.03	1.15	0.12	2.97	0.40	0.040
T3 ...	100	9.10	1.19	0.12	3.02	0.41	0.041
T4 ...	100	9.22	1.04	0.10	3.05	0.45	0.045
O. praetermissa							
Pr ...	100	8.93	0.89	0.09	3.39	0.37	0.037
O. purpurella							
Pu ...	100	8.93	0.89	0.09	3.39	0.37	0.037
O. majalis							
Ma ...	100	7.95	1.13	0.11	2.29	0.36	0.036

Other characteristics.

It is useful at this point to consider other characteristics, apart from the more critical ones treated biometrically above, in which these populations of *O. Traunsteineri* show points of difference from those of the other British tetraploid marsh orchids.

Stem: in *O. majalis* and *O. praetermissa*, the stem cavity is usually rather large, equalling or exceeding half of the diameter of the stem just below the inflorescence. In *O. purpurella*, the cavity is generally considerably smaller, rarely exceeding one millimetre in diameter. *O. Traunsteineri*, similarly, possesses a small cavity, and in many plants the cavity is absent altogether throughout much of the length of the stem. The characteristic of stem flexuousness, stressed by Pugsley in the original diagnosis of *O. traunsteinerioides*, is not one which is very striking in the field, and it may have been exaggerated in the plants examined by him as a result of their passage through the post in a cramped container.

Leaves: Particularly in the meadow-land ecodemes of *O. purpurella* and *O. majalis*, the lower internodes are short, so that the sheaths of the lower three or four leaves are almost contiguous. In *O. praetermissa* and *O. Traunsteineri* growing in fen habitats (although not in the chalk down ecodemes of the former) the lower internodes are extended, so that the leaves are more equally spaced along the stem, a feature particularly obvious in the few-leaved *O. Traunsteineri*. In the latter, the upper bract-like leaves, usually found in tetraploid marsh orchids just below the inflorescence, are often entirely wanting, as in the plant illustrated by Pugsley (1936).

Inflorescence: In all of the colonies of *O. Traunsteineri* examined, a proportion of the plants was remarkable in possessing unusually lax, few-flowered inflorescences. This is a characteristic usually emphasised in Continental descriptions of the species. However, it appears to be one in which there is great variation; for in the Scraw Bog colony, the range of flower numbers encountered was from 8 to 29, with a mode between 12 and 14. This range is, nevertheless, low in comparison with the other British tetraploid marsh orchids.

Flower colour and patterning: The colour range of *O. Traunsteineri* flowers is somewhat similar to that of *O. praetermissa*, tending on the whole to rather darker shades, but never reaching the intensity characteristic always of *O. purpurella*, or even of that of the *O. majalis* populations of Clare or Galway. As may be seen from Plate 8, the labellum patterning is of a similar nature to that found in *O. praetermissa*, but is generally more intense and occupies a greater proportionate area. There is no similarity to the pattern of short, intense, broken bars characteristic of the small rhomboidal labellum of *O. purpurella*, nor to that found in the deeper hued *occidentalis*-type plants of the Irish *O. majalis*. Somewhat similar patterns are, however, found in the *kerryensis*-type plants of the latter.

A characteristic of the living plants is obscured in labella mounted flat as in Plate 8, namely a tendency for the lateral lobes of the labellum to be reflexed in *O. Traunsteineri*, somewhat in the manner of *O. latifolia*. This is absent in *O. praetermissa* and *O. purpurella*, but generally shown in Irish *O. majalis*.

Taxonomic Notes.

The facts stated in the foregoing demonstrate that the four colonies which have been investigated may be grouped to form a fairly natural unit which is morphologically separable from other British tetraploid dactylorchid taxa. The justification for referring this to the Continental species, *O. Traunsteineri* Saut., remains to be examined.

Recently, Vermeulen (1949) has given a full account of the nomenclatural problem of *O. Traunsteineri*, and a detailed discussion is not therefore required here. The earliest description of a plant under the name of *O. Traunsteineri*, with Sauter quoted as the authority, is that given by the elder Reichenbach (1830, *Flora Germanica Excursoria*). The description by Sauter himself appeared seven years later (Sauter, 1837), and contains a reference to the earlier one of Reichenbach which is clearly accepted as referring to the same plant. The circumstances of the first description are, therefore, somewhat unusual, but it seems that there is justification in accepting Vermeulen's conclusion that Reichenbach's description of 1830 must be taken as the authoritative one, and Kitzbühl in Austria, whence came the material upon which it was based, as the type locality. Plants from Kitzbühl and Zell am See were originally distributed by Traunsteiner, and were known to Sauter, whose own description (1837), however, is based upon material from Bregenz (rather more than a hundred miles from Kitzbühl) which he accepted as being conspecific. Characters which are diagnostic in the earlier descriptions are (a) the sparse, very narrow leaves, and (b) the large flowers, with bluntly three-lobed labellum, the lateral lobes of which are reflexed. The former characters serve to differentiate the plant from any form of *O. majalis* Reichb. (=*O. latifolia* auct. mult.), and the larger flowers from the forms of *O. latifolia* L. sec. Pugsl. (=*O. incarnata* auct. mult.).

Later treatments of *O. Traunsteineri* suggest that the "species" quickly became a repository for forms not readily placed elsewhere in the subgenus. Klinge (1899) regarded *O. Traunsteineri* Saut. as synonymous with "*O. angustifolia* Lois.", of Reichenbach, 1830, and adopting the latter name, grouped under it numerous minor varieties and geographical races from well outside of the original Alpine area of *O. Traunsteineri.* Later, Fuchs and Ziegenspeck, in their monograph of *O. Traunsteineri* (1924, 1927) extended the use of the name to cover a polymorphic mass of hybrids and other dubious forms, declaring that "*Orchis Traunsteineri* non est species, sed forma ex gregibus *Dactylorchideis* hybridis vel 2, vel 3, vel 4 speciebus vel hybridis specierum ipsis composita, quam legit olim Traunsteiner et Sauter descripsit." Von Soó (in Keller & Schlechter, 1930-40) accepts the possibility of *O. Traunsteineri* being " eine hybridogene Art," but declines to follow Fuchs and Ziegenspeck in placing under it almost every type of dactylorchis hybrid. His subdivision of the species owes much to Klinge, the two major types recognised being an "alpine" one, subsp. *Traunsteineri,* and a "Baltic-northern" one, subsp. *Russowii.* Under each of these are placed several varieties and forms, mostly of somewhat dubious taxonomic significance. Collectively, the subsp. *Russowii* (Klinge) Aschers. & Graebn. is said to differ from the subsp. *Traunsteineri* in being more robust, and in possessing a greater number of leaves, a denser inflorescence and a labellum usually broadest at the centre rather than at the apex. It is doubtful whether distinctions of this nature can have much meaning, when applied in so general a manner to such extensive population systems, and certainly the characteristics referred to were not well developed in the Scandinavian *O. Traunsteineri* seen by me in 1950. Both in habit, and in the variation range of most of the critical taxonomic features, this appeared somewhat similar to the Irish plant, although material for more precise statistical comparison was unfortunately not obtained.

Vermeulen (1949) provides a careful and detailed "general description" of *O. Traunsteineri,* based apparently upon first-hand study of plants from the type area rather than upon literary research. This description gives some indication of the range of variation to be expected in various characters, and for most of these it may be said that the ranges indicated would include the bulk of the plants in the Britannic colonies described above.

With this group of dactylorchids, however, the fitting of plants to descriptions is a singularly unsatisfactory procedure, and ideally, before assuming the complete identity of the Britannic and Austrian forms, it would be desirable to conduct a biometrical comparison along the lines developed above. Nevertheless, as there is at the moment no evidence of morphological or other differences, it is necessary to accept the conspecificity of the two, recognising that more critical evidence may eventually suggest the desirability of segregating the British forms as a subspecies, for which the appropriate name would be subsp. *traunsteinerioides.*

DISTRIBUTION.

Stations for *O. Traunsteineri* in the British Isles known to the writer are listed in full below. These have been entered on the map, fig. 1, which replaces that published for "*O. majalis* subsp. *traunsteinerioides*" (Heslop-Harrison, 1949). The latter was prepared when the plant was imperfectly understood, and omits some Irish and southern English records, and includes some northern ones which now require re-examination. These northern records refer to Godfery's *O. eborensis* (Godfery, 1933), considered by Pugsley (1939) to be conspecific with *O. traunsteinerioides*. Judging from herbarium material, the possibility remains that some of these are, in fact, localities for *O. Traunsteineri*, but the matter requires investigation in the field.

V.-c. 22, Berkshire. Cothill Fen (Colony T2 in this paper).

V.-c. 28, West Norfolk. (1) Foulden Common; (2) water-meadows near Snetterton. Herbarium specimens collected on Foulden Common by J. E. Little in 1922 exist in the Cambridge University Herbarium, and a search made in June 1952 after inspection of this material revealed the presence there of a number of small colonies growing with *Schoenus* and *Cladium* in several small patches of fen over an area of about 1 sq. mile. Another Norfolk locality from which plants, probably of *O. Traunsteineri*, collected by J. E. Little, exist in the Cambridge herbarium is Marham Fen, but this has apparently suffered much drainage recently, and the plant was not observed there in 1952. *O. Traunsteineri* was, however, seen during this season near Snetterton, growing in small quantity in company with *O. Fuchsii*. It seems likely that the plant will be found elsewhere in Norfolk, for certainly many highly suitable localities exist in the county.

V.-c. H9, Clare. Fen near Lough Bunny, the locality from which it was reported by Mrs. K. Gough (1952) under the name *O. traunsteinerioides*. This colony was visited after its discovery by Mrs. Gough. *O. Traunsteineri* occurs sparsely in *Schoenus*- and *Cladium*-dominated fen at the north-east corner of the lake, and also at other points around it. There are many similar habitats in Co. Clare, and there is a strong likelihood of the plant occurring elsewhere.

V.-c. H19, Kildare. Fen north of the Curragh (T3 above).

V.-c. H20, Wicklow. Coastal marshes near Newcastle (T1 above). The Ballyman Glen colony, also in this vice-county, which was included by Pugsley in *O. traunsteinerioides*, has not been seen by the writer.

V.-c. H23, Westmeath. Scraw Bog (T2 above).

Mention has already been made of other Irish records for what is probably *O. Traunsteineri*, for v.-c. H25 (Roscommon) by Qsvald (1949), and for v.-cs. H33 (Fermanagh) and H39 (Antrim) by Summerhayes (1951).

In England, the dactylorchids of Greywell Fen, near Odiham, Hants., have been investigated, following up Pugsley's report of *O. traunsteinerioides* from this locality (1946). In the highly polymorphic *O. praetermissa* population of this fen there are individuals which approach the *O. Traunsteineri* variation range in sparsity and narrowness of leaves, and in labellum shape and pattern, but nothing has been found in this locality comparable, for example, with the very distinctive Cothill Fen colony.

The taxonomic confusion which has surrounded *O. Traunsteineri* practically since its first description makes it difficult to formulate any picture of the extra-British distribution except in the broadest possible terms. The following points, however, seem reasonably clear:

(1). The "typical" form of the species (*O. Traunsteineri* subsp. *Traunsteineri* [von Soó]; var. *eu-Traunsteineri* Asch. & Graebn.; *O. angustifolia* var. vel ssp. *Traunsteineri* Klinge; *Dactylorchis Traunsteineri* subsp. *typica* Vermeulen etc.) occurs in the Alps and throughout the associated mountain systems, where according to Keller (quoted by von Soó, 1930-40) "ist die Art eine Characterpflanze der mineralstoffreichen Flachmoore, besonders der subalpinen Gehängemoore."

(2). Associated forms occur in southern and central Germany, probably westwards into lowland France (where, however, the species is either rare or generally overlooked), and, sparsely, even in Holland (Vermeulen, 1949).

(3). A second series of populations, placed by Ascherson and Graebner (1907) under subsp. *Russowii* (Klinge), but treated in standard Scandinavian floras simply as *O. Traunsteineri* Saut. or *O. angustifolia* Lois. in Reichb. (non Wimm.), occurs in northern Germany and the Baltic countries, throughout most of Scandinavia to a latitude of *c.* 65° N, and eastwards, in Russia, into western Siberia.

Hultén (1950) refers *O. Traunsteineri* to his distributional-type 26, "West-European — Middle-Siberian Plants", in the subgroup, "Present in Caucasus, absent east of the Urals." As is clear from the distributional map given by Hultén for *O. Traunsteineri*, this is based upon an interpretation of the species in the widest possible sense, including even *O. pseudocordigera* Neum., *O. lapponica* Laest. and *O. Blyttii* Soó. Accepting a rather less wide interpretation of the species than this, and assuming that the above summary of distribution is at least approximately corrected, it would appear that the species would be better placed in Hultén's group 35, "East-European continental species with connections to Scandinavia through the Baltic countries".

Throughout its European range, *O. Traunsteineri* appears to retain a predilection for rich fen habitats, and many authors comment upon the strongly calcareous nature of the ground water in localities in which it occurs. This characteristic is certainly apparent in the British

Isles, and it would possibly be more appropriate to seek for an explanation of the present highly disjunct distribution of the species in relative rareness of suitable habitats rather than to invoke historical explanations. Nevertheless, it is clear that, like *O. cruenta* (Heslop-Harrison, 1951), *O. Traunsteineri* may have been much more common in the British Isles at a time when fen habitats were available more widely—in Ireland, particularly, before the growth of ombrogenous bog over the central limestone plain.

ACKNOWLEDGMENTS.

Thanks are due to the Central Research Fund of the University of London for a grant towards travelling expenses during the conduct of this work, and to the authorities of the Kew, British Museum and Cambridge University Herbaria for their co-operation.

I wish also to tender thanks to my wife, Dr. Y. Heslop-Harrison, for assistance in the field and biometrical work, to Miss J. Bilby for general technical assistance, and to Mr. R. Brinsden, A.R.P.S., who took the photographs of the flower parts.

LITERATURE CITED.

ASCHERSON, P., & GRAEBNER, P., 1907, *Synopsis der Mitteleuropäischen Flora*, **3**. Leipzig.

CAMUS, E. G. & A., 1928-29, *Iconographie des Orchidées d'Europe*. Paris.

CLAPHAM, A.R., 1952, in CLAPHAM, A. R., TUTIN, T. G., & WARBURG, E. F., *Flora of the British Isles*. Cambridge.

DRUCE, G. C., 1914, Notes on the Marsh Orchids, *Rep. Bot. Soc. & E.C.*, **3**, 340.

FUCHS, A., & ZIEGENSPECK, H., 1927, Monographie des Orchis Traunsteineri Saut. (Zusammenfassung), *Bot. Arch.*, **19**, 264.

GODFERY, M. J., 1933, *Monograph and Iconograph of the Native British Orchidaceae*. Cambridge.

GOUGH, K., 1952, Orchis Traunsteinerioides Pugsl. in Co. Clare. *Irish Nat. Journ.*, **10**, 273.

HESLOP-HARRISON, J., 1948, Field studies in Orchis L. I. The structure of dactylorchid populations on certain islands in the Inner and Outer Hebrides, *Trans. Bot. Soc. Edinb.*, **35**, 26-66.

——, 1950a, Notes on some Irish dactylorchids, *Irish Nat. Journ.*, **10**, 81-82.

——, 1950b, Orchis cruenta Müll. in the British Isles, *Watsonia*, **1**, 366-375.

——, 1951, A comparison of some Swedish and British forms of Orchis maculata L. sens. lat., *Svensk Bot. Tidskr.*, **45**, 608-635.

——, 1952, [written 1949] Notes on the distribution of the Irish dactylorchids. *Veröff. d. Geobotanischen Inst. Rübel, Zürich*, **25**, 100-113.

——, 1953, Microsporogenesis in some dactylorchid hybrids, *Ann. Bot.* (in press).

HEUSSER, C., 1938, Chromosomenverhältnisse bei schweizerischen basitionen Orchideen, *Ber. Schweiz. Bot. Ges.*, **48**, 562.

KLINGE, J., 1898, Dactylorchidis, etc., *Acta Horti Petropolitani*, **17**.

OSVALD, H., 1949, Notes on the vegetation of British and Irish Mosses, *Acta Phytogeogr. Suecica*, **26**.

PUGSLEY, H. W., 1935, On some Marsh Orchids, *Journ. Linn. Soc. Bot.*, **49**, 553-592.

——, 1936, New British Marsh Orchids, *Proc. Linn. Soc.*, Session **148**, 121-125.

——, 1939, Recent work on dactylorchids, *J. Bot.*, **77**, 50-56.

——, 1940, Further notes on British dactylorchids, *J. Bot.*, **78**, 177-181.

——, 1946, Orchis Traunsteinerioides Pugsl. in Britain, *The Naturalist*, No. 819, 47.

REICHENBACH, H. G. L., 1830, *Flora Germanica Excursoria*. Lipsiae.

SAUTER, J., 1837, *Flora* **20**, Beibl. 3, p. 36.

SOÓ, R. von, 1930-40, in KELLER, G., & SCHLECHTER, R., *Monographie und Iconographie der Orchideen Europas und des Mittelmeergebietes*, **2**, 201-261. Berlin-Dahlem.

STEPHENSON, T. & T. A., 1920, A new Marsh Orchis, *J. Bot.*, **49**, 164-170.

SUMMERHAYES, V. S., 1951, *Wild Orchids of Britain*. London.

VERMEULEN, P., 1938, Chromosomes in Orchis. *Chron. Bot.*, **4**, 107-8.

——, 1949, Varieties and forms of Dutch orchids, *Ned. Kruidk. Archief*, **56**, 225-242.

WILMOTT, A. J., 1936, New British Marsh Orchids, *Proc. Linn. Soc.*, Session **148**. 126-130.

——, 1938, Orchis occidentalis (Pugsley) Wilmott in CAMPBELL, M. S., Further botanising in the Outer Hebrides, *Rep. Bot. Soc. & E.C.*, **11**, 551.