

HYBRIDISATION BETWEEN DIPLOID AND TETRAPLOID SPECIES OF *EUPHRASIA*

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The chromosome numbers of the British species of *Euphrasia* have been tabulated in a previous paper (Yeo, 1954). Five species are diploid with $n = 11$. They are *E. rostkoviana* Hayne, *E. montana* Jord., *E. rivularis* Pugsl., *E. anglica* Pugsl. and *E. hirtella* Jord. These constitute the series *Hirtellae*, characterized by the possession of long glandular hairs, which in Britain only occur exceptionally outside the *Hirtellae*. In other groups, only the tetraploid number, $n = 22$, has been found, and it is probable that this is the chromosome number of all the other British species.

Warburg (1952) lists four hybrids whose parents are now known to be diploid and tetraploid respectively. Such hybrids would be expected to be sterile triploids and to occur only as occasional isolated individuals. However, in at least some cases, they are fertile and form populations of more or less numerous plants. Several populations of this type, representing various forms, have now been investigated. Observations made at Withypool, S. Somerset, will be reported first.

Diploid-Tetraploid Hybrids at Withypool

The plants concerned were found on a heath at 1200 feet elevation near Withypool, Exmoor (grid. ref. 21/826367), in August, 1952.

Four forms of *Euphrasia* were present; their characters and habitats are given in Table 1, and herbarium specimens are shown in plate 17, fig. 1.

The flower measurements for *E. anglica* given in the table represent a population (E.180) about a mile nearer Withypool than that (E.187B) which accompanied the hybrids. The specimens in the photograph were also taken from this population since the plants of E.187B show slight traces of the hybrid influence which is present in E.187A. Owing to their occurring in grazed turf, it is difficult to find intact plants of *E. anglica* late in the season, and neither of the two plants in the photograph is intact; that on the left has been drawn up by long grass but has been included because it shows the leaves relatively well.

It will be seen from Table 1 and Plate 17, fig. 1, that there were two species present, *E. anglica* and *E. micrantha* Rchb., which are widely different morphologically, and which differ in habitat. The dwarf habit of *E. anglica* is correlated with its short-turf habitat, while the tall *E. micrantha* is found in the immediate vicinity of *Calluna vulgaris* and *Erica cinerea*. In addition there was a single triploid hybrid, very like *E. micrantha* but with a slightly larger flower, and some stalked glands, which, together with the chromosome number, indicate *E. anglica* as the other parent. Finally, there was a population of a diploid form which is rather variable, but which possesses some of the characters of *E. anglica* and some of *E. micrantha*. In the characters listed in Table 1 it resembles *E. anglica* in four, *E. micrantha* in four, and is intermediate in three. It also differs from *E. anglica* in growing in taller grass. In its extreme form (No. 3 in Plate 17, fig. 1) it is very similar to the triploid. The morphological distinctness of this form would qualify

* The work reported in this paper was carried out during the tenure of a Research Scholarship at the University College of Leicester.

TABLE 1.
Characters of the Euphrasias at Withypool

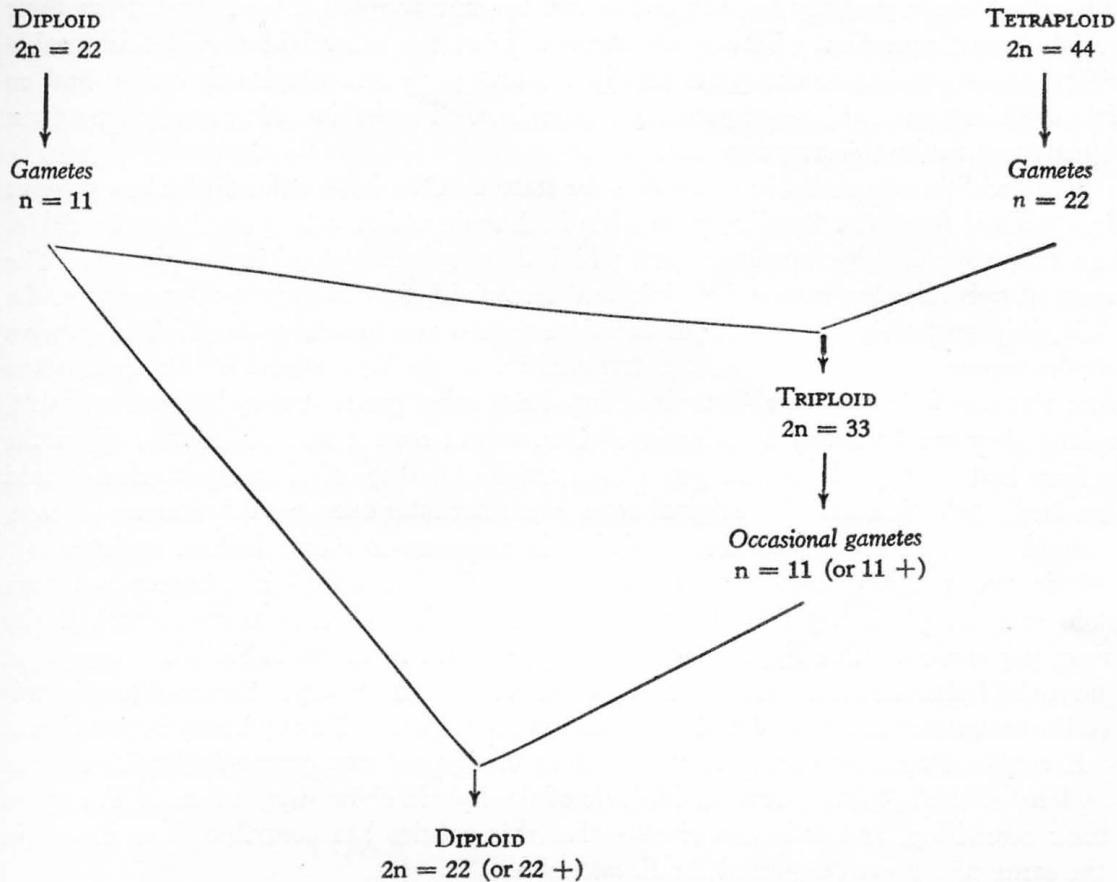
Name	<i>E. anglica</i>		<i>E. anglica</i> × <i>micrantha</i>	<i>E. micrantha</i>
Collector's Number	E 187B	E 187A	E 185C	E 185A
Internodes	Short	Long	Long	Long
Position and length of branches	Basal, not much exceeded by main stem	Central, much exceeded by main stem	Central, much exceeded by main stem	Central, much exceeded by main stem
Leaf shape	Broad	Narrow	Narrow	Narrow
Anthocyanin in				
(a) Leaves	None	Upper surface in some plants	Upper surface	Upper surface
(b) Stems	Little	Much	Much	Much
Foliar glands	Long, dense	Long, dense	Shorter, sparse	None
Corolla length	6.5-8 mm.	6.5-7 mm.	Smaller than E187A	5.6-5 mm.
Corolla-lip breadth	5.5-6.5 mm. (E 180, cult.)	4.5-5 mm. (cult.)	—	3.5-4.5 mm.
Corolla colour	White, upper lip sometimes lilac	White, upper lip sometimes lilac	Faint lilac	White, with magenta upper lip, or medium lilac, or intense red-purple
Capsules	Large, broad	Large, broad	None	Small, narrow
Normal-looking pollen	98 per cent.	98 per cent.	3 per cent.	95 per cent.
Chromosomes at meiosis	Not counted, but 11 bivalents in this sp. at several other localities	n = 11 (Plate 18, fig. 2)	Approximately 11 bivalents and 11 univalents	About 22 bivalents
Habitat	Closely grazed turf and paths	Longer grass around bushes of <i>Calluna</i> , <i>Erica cinerea</i> , <i>Rubus</i> and <i>Ulex</i>	One plant only, with E 185A	Periphery of <i>Calluna</i> and <i>Erica cinerea</i> bushes.

it for specific recognition. This is ruled out, however, on account of its distribution as at present known.

Interpretation of the Situation at Withypool

The observations show that it is possible for triploid hybrids between diploid and tetraploid species to occur. They also show strong evidence of the occurrence of plants of similar parentage which are fertile and have the diploid chromosome number. Meiosis in these plants is usually, at least, quite normal, as can be seen in plate 18, fig. 2, where at the end of the second meiotic division there are four groups of eleven chromosomes. The

occurrence of these diploids can be accounted for by supposing that triploids have occurred and have produced haploid gametes with eleven (or slightly more) chromosomes, which, by back-crossing with the diploid, have produced a fertile diploid of hybrid origin, containing germ-plasm derived from the tetraploid. This process is represented in the accompanying diagram; it will now be considered in more detail.



The production of gametes with a viable set of eleven chromosomes is only likely to happen, if, at meiosis in the triploid, eleven univalents and eleven bivalents are formed. For then the twenty-two chromosomes forming the eleven bivalents will separate regularly, while the others will either be scattered at random, or form a separate nucleus. In the former case, haploid (or slightly more than haploid) nuclei will occasionally be formed in accordance with the chance distribution of the unpaired chromosomes; in the latter, the other two haploid nuclei will produce four haploid pollen grains. In the Withypool triploid approximately eleven bivalents and eleven univalents were formed, and the univalents appear to be distributed at random (Yeo, 1954).

The eleven chromosomes coming from the triploid could be partly derived from the diploid parent, and partly from the tetraploid. In addition they would be affected by crossing over at meiosis in the triploid so that probably every one of them would contain some genes from the tetraploid parent. The sorting of the chromosomes and the positions of crossing-over in them would determine which genes were represented in the first diploid back-crossed individual. Since these factors operate more or less at random, the genetic constitution of this plant is unpredictable and could vary greatly between one occurrence of the process and another. The diploid back-crossed individual is likely to develop in the presence of the pure diploid, so that further back-crossing is possible. Owing to the heterozygosity of the first back-crossed generation, its progeny, whether

produced by self- or cross-fertilisation, will be highly variable. Thus a great source of variation in the diploid becomes available.

For this process to result in the production of a distinct form such as E.187A, there must be close at hand a plant community not occupied by a diploid species, to which the progeny of the back-crossed individual can gain access. This community must be one to which these progeny are adapted or can become adapted, by selection from their especially great variation. The genes derived from the tetraploid would thus enable their possessors to evade the parental diploid and grow in ecological isolation, and so obtain sufficient genetical isolation to remain distinct. The habitat of relatively long grass at Withypool fulfils this requirement.

Some additional possibilities can now be stated. One is that the diploid may result from a triploid fertilising itself by producing both male and female spores that are viable. There arise various other considerations which do not essentially alter the picture. The process of hybridisation between diploid and tetraploid, followed by back-crossing to the diploid, is presumably happening all the time with some low frequency. The process may also occur directly between the tetraploid and the new diploid. By both these means, the new form will be able to draw into itself other genes as they become available, provided they are favoured by selection. One would expect that ultimately, when the new form had "sampled" all the genes the tetraploid had to offer, an equilibrium would be reached. Selection after the original cross, and after later ones, would reduce variation, but could result in some variation persisting in response to minor habitat variation.

It is thus possible to explain the occurrence of a fertile diploid whose parents are diploid and tetraploid respectively, and to account for its existence as a morphologically distinct population. The hypothesis would appear still more probable if the suggested sequence of hybridisations could be made to occur experimentally. So far efforts in this direction have not even resulted in the production of a triploid. Finally it may be mentioned that *E. confusa* Pugsl. also grew on the heath at Withypool and approached quite near to the colony of the hybrid. Some individuals of the hybrid show suggestions of *E. confusa* in their branching, and it is conceivable that this species has contributed to its origin by the same process as suggested for *E. micrantha*.

EUPHRASIA VIGURSII DAVEY

This is the commonest and best known of the reported hybrids whose parents are respectively diploid and tetraploid. It was described as a species by F. H. Davey (1907), and was said to occur at Porth Towan and Perranzabuloe, both in v.c. 1, W. Cornwall, and at Roborough Down, v.c. 3, S. Devon. It is now well represented in herbaria, by specimens not only from the original localities, but from several others in Devon and Cornwall. Pugsley (1930) regarded it as a hybrid between *E. anglica* and *E. micrantha*. From the morphological point of view, this seems plausible, and Pugsley pointed out that in some gatherings a proportion of the capsules are malformed, though such capsules are not necessarily completely barren.

Observations on *E. vigursii* at Roborough Down

The following observations were made at Roborough Down, which is a tract of heathland extending along, and on both sides of, the Plymouth-Tavistock road, for a distance of about six miles. The area investigated extended for about three-quarters of a mile from the southern end, and was mostly to the west of the main road (grid ref. 20/5063-20/5064).

The *Euphrasiae* present were *E. confusa* (of which three very small colonies were found), *E. anglica*, *E. vigursii*, and a form which will be referred to as *E. nemorosa*, though,

since it is far from typical of that species, and to some extent resembles *E. micrantha*, the name will be used in quotation marks. It might conceivably be a hybrid between *E. micrantha* and *E. confusa* or *E. nemorosa* (Pers.) Mart., but it appeared quite uniform. *E. confusa* is not considered important and will not be mentioned further; the other three forms occurred in large quantity. Their characters are shown in Table 2, and photographs of *E. "nemorosa"* and *E. vigursii* are given in plate 17, fig. 2, numbers 1 and 2.

Of the characters listed in Table 2, *E. vigursii* resembles *E. anglica* exactly in only one (chromosome number), *E. "nemorosa"* in two, and is intermediate in three, being nearer *E. anglica* in two of these. In addition, it is outside the range of these two species in the four floral characters listed. It will be noted that the characters in which *E. vigursii* resembles *E. "nemorosa"* are those of habit.

TABLE 2.
Characters of the Euphrasias at Roborough Down

Name Collector's Number	<i>E. anglica</i> E198	<i>E. vigursii</i> E 197A	<i>E. "nemorosa"</i> E 196
Internodes	Short	Long	Long
Position and length of branches	Basal, not much exceeded by main stem	Central, much exceeded by main stem	Central, much exceeded by main stem
Leaf shape	Broad	Intermediate, rather broad	Narrow
Anthocyanin in leaves	Probably a trace	Less than in " <i>nemorosa</i> "	Usually present
Foliar glands	Dense, long	Dense, long, often less dense than in <i>E. anglica</i>	Occasional short stalked glands present
Corolla length	6-7.5 mm.*	7-8.5 mm.	5.5-6.5 mm.*
Corolla-lip breadth	5-5.5 mm.*	6.5-8 mm.	4-4.5 mm.*
Shape of lobes of lip	Nearly parallel-sided	Considerably dilated	Narrow, little dilated apically
Corolla colour	White, with upper lip lilac, or finally faint lilac throughout	Purplish red to pale lilac, sometimes white with upper lip lilac	Upper lip lilac, lower usually lilac, sometimes white
Capsules	Normal	Occasionally with reduced numbers of seeds, down to one	Normal
Normal looking pollen	93 per cent.	c. 64 per cent. but results inconsistent	100 per cent.
Chromosome Number (2n)	Not counted, but 22 in this sp. at several other localities	22 (Plate 18, fig. 1)	Over 22 (44 in its nearest relatives)

* These measurements (especially the lip-breadths) may be underestimated through being taken two days after collection

No clear chromosome count of *E. "nemorosa"* could be obtained, but it is very likely that the number is $2n = 44$ as in true *E. nemorosa* and *E. micrantha*. Meiosis in *E. vigursii* was seen at early anaphase of the first division (Plate 18, fig. 1), and metaphase of the second division, and appeared normal.

TABLE 3.

Lists of species (not necessarily complete) occurring with *E. anglica* at Roborough, and with *E. vigursii* at various places.

Accompanying Species	<i>E. anglica</i> Roborough E(198)			<i>E. vigursii</i>									
				Roborough (E197)					Pensilva E374	Newlyn E360	Zela Hill E359	Polgoda E348-9	
	1	2	3	1	2	3	4	5					
A : with <i>E. vigursii</i> only													
<i>Agrostis setacea</i>				+	+	+	+	+	+	+	+	+	+
<i>Carex panicea</i>					?								+
<i>Erica cinerea</i>				+	+	+	+	+	+	+	+	+	+
<i>Molinia caerulea</i>				+						+		+	
<i>Potentilla erecta</i>				+	+	+				+	+		+
<i>Pteridium aquilinum</i>				+	+	+							+
<i>Ulex minor</i>													+
B : with <i>E. anglica</i> only													
<i>Achillea millefolium</i>		+	+										
<i>Lotus corniculatus</i>	+	+	+										
C : with <i>E. anglica</i> and <i>E. vigursii</i>													
<i>Calluna vulgaris</i>	+			+	+	+	+	+	+	+			
<i>Carex</i> sp.	+									+			
<i>Holcus lanatus</i>		+	+			+							
<i>Leontodon taraxacoides</i>	+		+		+	+	+			+			?
<i>Pedicularis sylvatica</i>		+				+							
<i>Plantago lanceolata</i>	+	+	+		+								
<i>Prunella vulgaris</i>			+			+							
<i>Sieglingia decumbens</i>	+	+				+	+			+			
<i>Thymus drucei</i>	+											+	
<i>Ulex gallii</i>	+			+	+	+	+	+	+	+	+		+
<i>Viola</i> sp. (subgen. <i>Melanium</i>)	+	+	+	+	+	+	+					+	

The three forms concerned were differentiated ecologically, as well as morphologically. Lists of species occurring with *E. anglica* and *E. vigursii* at Roborough are given in Table 3. *E. anglica* occupied its characteristic habitat of short turf. *E. "nemorosa"* was usually found in longer grass than *E. anglica*, round bushes of *Rubus fruticosus* agg. and *Ulex europaeus*, but it was also present in quite short grass by the roadside in places. *E. vigursii*, also a tall plant, grew in still taller vegetation. This was characteristically a heathy community consisting of *Agrostis setacea*, *Calluna vulgaris*, *Erica cinerea*, and *Ulex gallii*. It also grew in a grassy community with rather long grass, mostly *Agrostis setacea*, and more or less scattered fronds of *Pteridium aquilinum*. The first of these two communities occupied the greater part of the heath and *E. vigursii* is probably commoner than either of the other species.

The habitat differences keep the greater part of the populations of the forms apart. Occasionally, however, *E. anglica* and *E. "nemorosa"* were more or less intermixed. At such places no intermediate could be found. *E. vigursii* mixes less with these two than they do with one another, but in some places it met *E. anglica*, and, in intermediate habitats on the embankment of a side-road, plants intermediate between the two were found.

Interpretation of the Situation at Roborough Down

E. vigursii occurs at Roborough in company with diploid and tetraploid forms between which it might, on morphological grounds, be interpreted as a hybrid. It is a fertile diploid, differentiated in habitat from its presumed diploid parent. This situation appears to be analogous to that at Withypool, and the same hypothesis can be used to explain it.

There are, however, some differences between the Withypool and Roborough situations. At Roborough, *E. vigursii* is not so clearly intermediate between the two supposed parents as E.187A is. This can be explained by the complex series of crosses involved, causing the removal of genes from the tetraploid into a new genetic environment in which they may have a modified action.

E. vigursii is morphologically distinct from the fertile hybrid at Withypool. But, at least at localities other than Roborough, it appears to have *E. micrantha* as its tetraploid parent. The morphological difference between the two forms could be attributed to the transmission of different sets of genes from the tetraploid. Another possibility is that, as already suggested, *E. confusa* has been involved in giving rise to the hybrid at Withypool, as well as *E. micrantha*.

Though the tetraploid accompanying *E. vigursii* at Roborough is not true *E. micrantha*, the latter might nevertheless have been its original parent there, since *E. vigursii*, being fertile, can persist in the absence of its parents. *E. micrantha* may have subsequently died out on the heath, or it may still occur somewhere on the large part of the heath not explored.

The habitat which *E. vigursii* occupies at Roborough is different from that of E.187A, and is more clearly distinct from the habitat of *E. anglica*. In addition, *E. vigursii* forms an abundant population spread over a wide area. The importance of the ecological conditions in enabling the diploid population to become split into two different forms is again evident.

Further Examples of E. vigursii Populations

Some other populations of *E. vigursii* at more westerly localities will now be described. Species lists for the first four dealt with are given in Table 3. The habitats were similar to that of *E. vigursii* at Roborough but poorer in species, probably because of burning.

E. micrantha and *E. vigursii* were found at Pensilva, on the slopes of Caradon Hill, E. Cornwall, v.c. 2 (grid ref. 20/279695-283696). They are shown in Plate 17, figs. 2 Nos. 3 and 4 respectively. The profuse branching of the specimen of *E. micrantha* shown is due to its being luxuriant. The *E. vigursii* here was similar to that at Roborough. The greater part of the heath had been burnt over and *Ulex gallii* had not yet regenerated over the area as a whole, so that the vegetation consisted mainly of *Agrostis setacea* and *Molinia caerulea*. *E. micrantha* formed a small colony in a place where *Erica cinerea* and *Calluna vulgaris* were present (grid. ref. 20/282696). *E. anglica* was fairly common in the district but it was not found nearer the *E. vigursii* population than about a quarter of a mile.

The remaining populations to be described were in W. Cornwall, v.c. 1, in the neighbourhood of Perranzabuloe. At Zela Hill (grid. ref. 10/821529) *E. vigursii* much resembled that at Roborough and Pensilva. The vegetation had been recently burnt here also; the dominants were *Agrostis setacea* and *Erica cinerea*. The only other species of *Euphrasia* present was *E. confusa*, but this did not occur on the same ground as *E. vigursii*.

At Polgoda Down (grid ref. 10/792525) *E. vigursii* grew mostly in parts of the heath where the vegetation was relatively thin with *Agrostis setacea* and *Erica cinerea* codominant. At this locality, *E. vigursii* was of an extreme form (Plate 18, fig. 3), with small elliptic cauline leaves with rounded teeth, strongly suggestive of *E. micrantha*. It was also rather small, and the anthocyanin pigmentation was strongly developed in the vegetative parts. It had the usual large purplish-red flowers. Growing with the glandular *E. vigursii* were eglandular plants which were not distinguishable except by this character, though on the average the plants were slightly less vigorous and had smaller leaves. Their flowers were identical with those of the glandular plant. The chromosome number of the eglandular plant is $n = 11$. The eglandular form must therefore be regarded as a form of *E. vigursii*. Apparently introgression of *E. micrantha* genes has gone so far that, in a proportion of the population, suppression of gland development has resulted. There was no gradation in the density of the glands between the strongly glandular and the eglandular types. The only other *Euphrasia* present at Polgoda Down was *E. confusa*.

A similar situation was found on a piece of heath-land about half-way between Zela Hill and Carland (grid ref. 20/837536), on the edge of Newlyn Downs. The *Euphrasias* occurred by paths and in other places where the vegetation was relatively thin. *E. micrantha* was present and in places grew with *E. vigursii*. A few plants of the eglandular form of *E. vigursii* were found growing with the normal form.

The eglandular *E. vigursii* is the only eglandular *Euphrasia* known to me which has the diploid chromosome number.

The observations on these four populations are considered to support the idea that *E. vigursii* is a hybrid, one of whose parents is *E. micrantha*, since in two of them *E. micrantha* was present, and, at Polgoda and Newlyn, the *E. vigursii* was an extreme form, showing a pronounced resemblance to *E. micrantha* in leaf-shape, indumentum (in a proportion of the plants), and habit.

A rather distinct form of *E. vigursii* was found on heathy slopes above the cliffs to the south-west of Perranporth. Here the dominant plant of the heathy ground is *Erica cinerea*. *Calluna vulgaris*, *Ulex* sp. (? *europaeus*), and *Molinia caerulea* were also present. *Euphrasia vigursii* grew in the grassier parts of the heathy area. It had the usual rather large reddish-purple flowers, and taller habit than *E. anglica*, but in its somewhat fleshy leaves, in the shape of these leaves, and in the formation of a dense flowering spike, it resembled *E. occidentalis* Wettst., a species which was very common in the short turf adjacent to the heath.

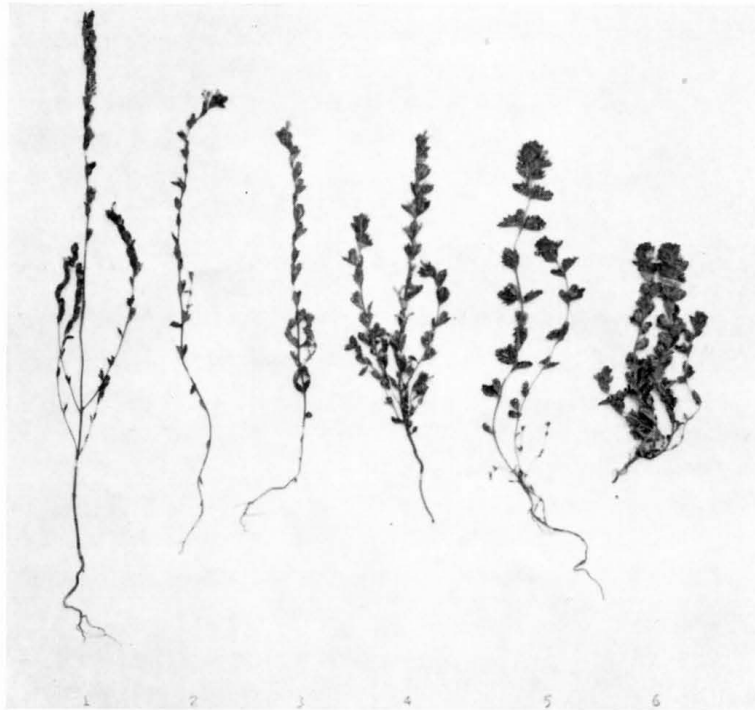


Fig. 1. Plants from Withypool : 1, *E. micrantha* (E185A); 2, *E. anglica* × *micrantha* sterile triploid (E185C) ; 3 and 4, *E. anglica* × *micrantha* fertile diploid (not *E. vigursii*) (E187A) ; 5 and 6, *E. anglica* (E180). In 2 note that calyces (teeth conspicuous) at nodes 1, 2 and 5 below lowest flower contain no capsules (compare corresponding nodes in 3).

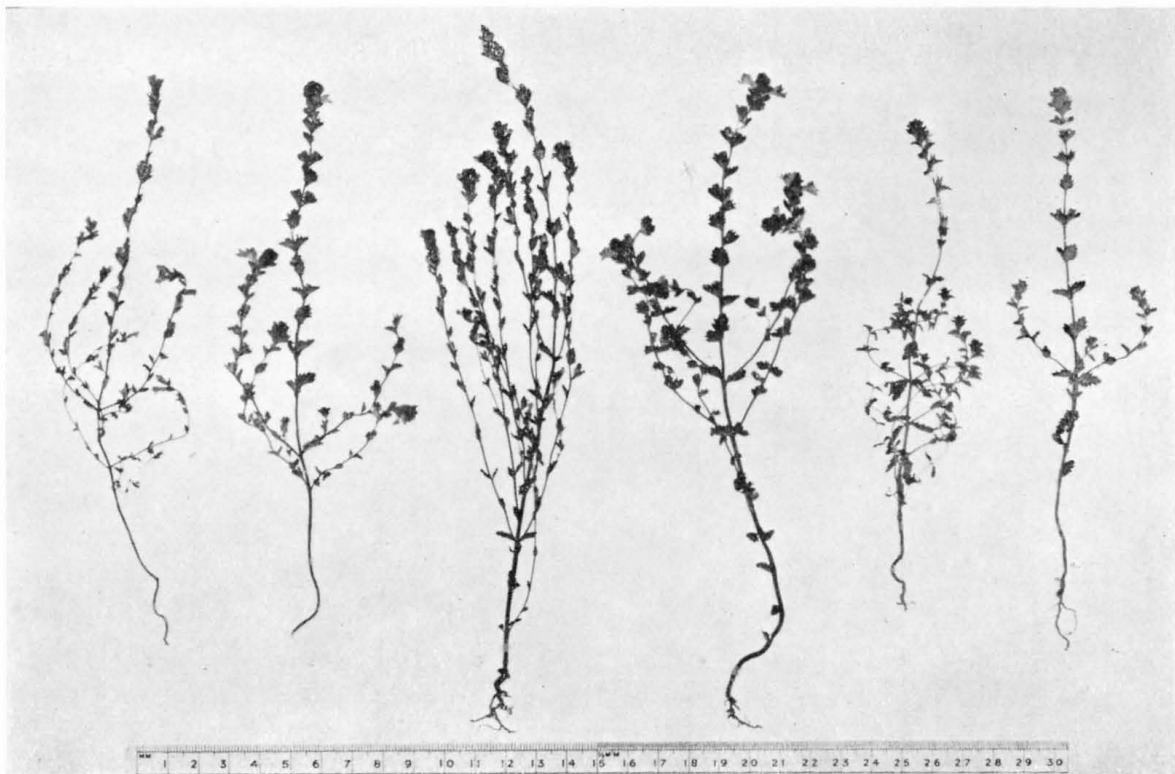


Fig. 2. 1, *E. "nemorosa"* (E196) Roborough Down; 2, *E. vigursii* (E197A) Roborough Down; 3, *E. micrantha* (E375) Pensilva ; 4, *E. vigursii* (E374) Pensilva ; 5, *E. nemorosa* (E334) Lane End Common; 6, *E. anglica* × *nemorosa* (E335C) Lane End Common.



Fig. 1. *E. vigursii* from Roborough Down (E197A) : metaphase of first division, pollen mother cell meiosis ($\times 1000$).

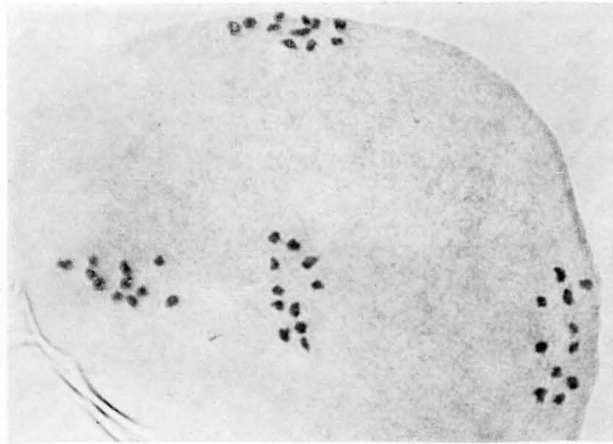


Fig. 2. E187A (see fig. 1) : anaphase of second division, pollen mother cell meiosis ($\times 1000$).



Fig. 3. *E. vigursii* (E348) extreme form, Polgoda Down, W. Cornwall.
Other species seen are *Agrostis setacea*, *Erica cinerea* and *Ulex gallii*.

This suggests either that the plant is a hybrid whose parents are *E. anglica* and *E. occidentalis*, or that *E. vigursii* arose from *E. anglica* and *E. micrantha* in the usual way, and that subsequently, by the same process, there has been introgression into it by *E. occidentalis*. The first alternative would not account for the purple flowers. The second gets some support from the presence of *E. micrantha* in the cliff-top heath, though this was found only at a point about one and a half miles from Perranporth, and was not adjacent to the *E. vigursii* population.

With the glandular *E. vigursii* form here, an eglandular plant with purple flowers was found; in one example a very few glands were present. In addition a small isolated colony consisting entirely of dwarf eglandular plants with fairly large purple flowers was found near the cliff-top. These may both be analogous to the eglandular *E. vigursii* at Polgoda Down.

At one of Davey's original *E. vigursii* localities, Porth Towan, the form present is markedly different from that at other places in its short internodes and broad rounded leaves. Davey first considered that the two forms should be distinguished as varieties. Since Porth Towan is a coastal locality it seems possible that this form has been introgressed by *E. occidentalis*, as suggested for the Perranporth form.

Distribution and Status of Euphrasia vigursii

A list of localities from which *E. vigursii* has been recorded is given in the appendix. At several of these *E. micrantha* is recorded, and, at a few, *E. anglica* has been found.* Its association with these two species supports the strong morphological evidence that it is a hybrid between them. Therefore, as regards the origin of *E. vigursii*, I accept Pugsley's view. A knowledge of the chromosome numbers of the three forms has, however, necessitated a special hypothesis to explain this origin.

The appendix shows that *E. vigursii* occurs in 7 of the 8 floristic divisions of Cornwall (see Davey, 1909), and that it thus occurs widely in the two vice-counties of Cornwall, as well as in part of a third (v.c. 3, S. Devon). Though in some places it is found with *E. micrantha* or *E. anglica*, it can exist independently of either. I did not see *E. anglica* at all in the Perranporth-Perranzabuloe district, and according to Rilstone (1923) it† is rare in this part of Cornwall, being unknown in District 8 (Land's End) and very rare in District 5 (North Coast), the district which includes Perranzabuloe. (There is, however, in the Cambridge herbarium, a gathering made by Curnow and Ralfs at Tregarrest, Penzance, in District 8). *E. vigursii* has a distinct habitat, namely heath with *Agrostis setacea*, and some or all of the following: *Calluna vulgaris*, *Erica cinerea*, *Molinia caerulea*, *Ulex gallii*. The only other *Euphrasia* found with it in this habitat is *E. micrantha*, from which it differs in chromosome number. It is morphologically very distinct and easily recognisable. It thus has the appearance of being a species. Davey's description of it as a species was based on his and Vigurs' knowledge of it in the field. Vigurs (1908) noted the constancy of its habitat, saying: "All the known localities but one . . . are heathy and furzy downs and crofts." In order, therefore, to signify its species-like status, I have adopted Davey's name, rather than Pugsley's hybrid formula.

E. vigursii may have had either a multiple or a single origin. If one supposes that it is of fairly recent origin, it is easier to imagine that it arose repeatedly in various localities, than to imagine its having migrated from one spot to the various areas of moorland which

* At localities not visited by me the absence of records or specimens of the presumed parents does not necessarily mean that they are absent.

† Rilstone used the name *E. rosthoviana* Hayne. The southern English plant known by this name was distinguished as *E. anglica* by Pugsley in 1930.

it now inhabits. If this is so, one must assume that in some areas *E. anglica* was once present and has now become extinct, probably owing to the elimination of its habitat.

Diploid-Tetraploid Hybridisation as a Source of New Species

E. vigursii is in effect a new species, assuming the hypothesis offered to account for its origin is correct. This suggests that other species may have been formed in the same way. The two forms most likely to have arisen in this way would appear to be *E. brevipila* Burnat & Greml. var. *notata* Pugsl. and var. *reayensis* Pugsl., since they combine characters typical of tetraploid species with the long-glandular indumentum of the diploids. The former occurs in central Scotland and is best known around Loch Tay. Here there also occurs a diploid species, *E. hirtella*. *E. brevipila* var. *reayensis* occurs along part of the north coast of Scotland, in Caithness and West Sutherland. No diploid species has, however, been reported north of the Loch Tay area. These two varieties of *E. brevipila* were investigated in 1953 and both were found to be tetraploid, as already reported (Yeo, 1954).

It is conceivable that *E. rivularis* may have arisen from *E. rostkoviana* and *E. curta* (Fr.) Wettst. var. *rupestris* Pugsl.

There are several other cases of apparent hybrids between diploid and tetraploid species, and these will be considered in the next two sections.

Further forms analogous to E. vigursii

Under this heading hybrids in which the habit of the diploid is modified will be dealt with. When these have been seen in the field the habitat has also been found to be modified. When they have not it is nevertheless to be expected that in fact the habitat is modified. All such forms are thus thought to be strictly analogous to *E. vigursii*.

(1) *E. anglica* × *nemorosa*

Pugsley (1930) described a form from Piltdown Common, E. Sussex, v.c. 14, as *E. anglica* × *pseudokernerii* Pugsl. A modified form of *E. anglica* has also been collected at Lane End Common, two and a half miles west of Piltdown (*Milne-Redhead & Summerhayes*, No. 1085, 1937, in Herb. Kew). The herbarium specimens from both these places are long-glandular, like *E. anglica*, but rather tall and large-flowered, and differing from *E. anglica* in leaf shape.

On visiting these two places, I was unable to find pure *E. anglica*, but at Piltdown (grid ref. 51/444224-446226) two forms of the glandular plant were found. One was only slightly modified; it had green leaves as in *E. anglica*, but the leaves were narrower and the internodes longer. It grew in grass of moderate length. The other form was much more modified, being taller and stouter-stemmed, and having a good deal of anthocyanin in the vegetative parts. It looked much like the Roborough form of *E. vigursii*, but the flowers were white with the upper lip lilac. This form grew in a grass-heath community, and with it was found a small colony of a form of *E. nemorosa*. This form was rather small-leaved and usually had lilac flowers; it is possibly var. *transiens* Pugsl. The same form was found at Lane End Common and a specimen from there is shown in Plate 17, fig. 2, No. 5.

At Lane End Common (grid ref. c. 51/404223), *E. nemorosa* (Plate 17, fig. 2, No. 5) was much commoner than at Piltdown, growing in short turf along the edges of the paths. The apparent hybrid showed variation according to habitat, tending towards *E. anglica*

on the one hand and *E. nemorosa* on the other (Plate 17, fig. 2 No. 6). Its commonest form, however, was intermediate between the extremes, being tall but with little anthocyanin, and very distinctive in appearance. It grew in long grass where *Pteridium aquilinum* was present, with the fronds well spaced out. The variation of the apparent hybrid might be due either to selection in response to habitat variation, or to phenotypic responses to different conditions. Probably both causes operate.

The glandular plant from Lane End Common has the diploid chromosome number, and at meiosis two of the larger chromosomes quite frequently occur as univalents, instead of as one bivalent.

The glandular plant at these two localities is presumably derived from *E. anglica*, by crossing with the form of *E. nemorosa* present, since it distinctly resembles the latter in its more extreme modifications. *E. anglica* is presumed to be the diploid parent because it is the only diploid species known in southern England. The modification of *E. anglica* is comparable in extent to that which *E. vigursii* shows, and it enables the glandular plant to grow in communities in which normal *E. anglica* would not be expected to occur. The hybrid populations are thus closely analogous to *E. vigursii*.

Like *E. vigursii*, the Sussex plant has rather large flowers, and this evidently led Pugsley to regard it as a hybrid between *E. anglica* and *E. pseudokernerii*. The nearest place to Piltown where the latter is likely to occur is the South Downs, six miles away. *E. pseudokernerii* is therefore much less likely to be the parent than *E. nemorosa*. Owing to the unpredictable results of the process of crossing involved, the parentage of these fertile hybrid-populations should be inferred from the species associated with them, and not from the hybrids' morphology alone.

(2) *E. anglica* × *brevipila*

At Street Heath, N. Somerset, v.c. 6, two forms were found (grid ref. 31/396461). One is *Euphrasia brevipila*, a plant with long internodes, rather few branches, short-stalked glands on the leaves, and medium-sized flowers (6-7.5 mm. across the lower lip). The other is a long-glandular plant, similar in habit to *E. brevipila*, and attaining a very large size and having very large flowers, 7-11 mm. across the lower lip. The plants were found in moderately long grass, in two separate clearings, about 50 yards apart, in the fen carr which occupies most of Street Heath. *E. brevipila* was found by a peat cutting, the other plant in a relatively acid spot, with *Myrica gale*, *Erica tetralix* and *Calluna vulgaris*. The long-glandular plant is similar to *E. rostkoviana* Hayne, but the fine leaf- and calyx-teeth of some plants suggest that it is a hybrid.

Mr. C. C. Townsend has kindly sent me specimens of a plant collected at Street Heath and reported as *E. anglica* in *Proc. B.S.B.I.*, 1, 59 (1954). These plants resemble *E. anglica* in habit and flower size, but appear somewhat modified in habit, and more distinctly so in the fine teeth of the leaves and calyx. These plants tend to confirm that the very tall and large-flowered plant is in fact *E. anglica* × *brevipila*.

The hybrid parallels *E. vigursii* in having larger flowers than either parent, and in having a modified habit and habitat, as compared with *E. anglica*.

Two records of this hybrid from the Somerset peat moors have been obtained from herbaria. They are: (1) Sharpham, near Street, with *E. brevipila*, in low peaty pasture, V. S. Summerhayes, 19/7/1928 (Herb. Kew); (2) "Carex evoluta enclosure," Turfmoor, with *E. brevipila* and more or less normal *E. anglica*, H. S. Thompson, 1922 (Herb. Univ. Cantab. and Herb. N. D. Simpson). These two gatherings are probably both from the same place, which is probably the Sharpham Reserve of the Society for the Promotion of Nature Reserves.

(3) *E. confusa* × *rostkoviana*

This hybrid is one of those listed by Warburg (1952). The specimens to be described were collected in a "damp pasture near Whinlatter road, bottom of Hobcarton Gill, v.c. 70," Cumberland, by S. M. Walters.

E. rostkoviana is a tall plant of hayfields, with rather few branches and large flowers. It was not collected at this locality. *E. confusa* is a dwarf plant with flexuous branches, rather narrow, finely toothed leaves, and small flowers. The plants collected (No. 53/76) represent a rather sparingly branched form. The apparent hybrid (No. 53/77) was growing with it. It is long-glandular and has large flowers, 8-10 mm. long, like *E. rostkoviana*, but has numerous slender flexuous branches and is dwarf in habit. The capsules are longer and narrower than in *E. rostkoviana*, the leaves are smaller and narrower, and the teeth of the bracts and calyces are finer. In all these characters it approaches *E. confusa*.

Here, the tall hayfield species, *E. rostkoviana*, has been modified in such a way as to enable it to grow in a grazed pasture, that is, to become like *E. anglica*. The situation is therefore the converse of that at Street. *E. rostkoviana* is absent from Somerset, and *E. anglica* is absent from Cumberland.

(4) *E. rostkoviana* × *salisburgensis*

Specimens in Herb. Kew from fields near Innsbruck, collected by A. Kerner, show clear indications of the modification of *E. rostkoviana*, or an allied species, by a small form of *E. salisburgensis* Hoppe. Of the six plants on the sheet one is correctly determined by Pugsley as *E. salisburgensis*. The others resemble this plant in their relatively short, thin, wiry stems and branches and their long narrow leaves, deeply cut and with the teeth directed towards the apex, but are large-flowered and long-glandular plants.

The occurrence of this hybrid is interesting since *E. salisburgensis* is not closely related to the other tetraploids mentioned in this paper.

Diploid-Tetraploid Hybridisation Resulting Only in Introgression

Where a diploid and a tetraploid hybridise in the manner suggested for *E. vigursii* but without change of habit in the diploid, the process can be regarded simply as the introgression of genes from the tetraploid into the diploid. The absence of habit modification may be either because the diploid and the tetraploid are the same in habit, or, if they are not the same, because there is no habitat not occupied by the diploid parent to which it could become adapted by acquisition of genes from the tetraploid. However, even in the absence of habit modification, there might be physiological changes which would alter the diploid's tolerance with respect to environmental factors other than tallness of vegetation. The forms to be described now are, therefore, those in which there has been introgression of ecologically neutral characters, and possibly also of characters significant with respect to habitat factors not easily observed with the eye.

The first of these to be described was found at Friday Street, Surrey. This is the locality of another plant determined by Pugsley (1933) as *E. anglica* × *pseudokernerii*. The specimens of this were originally collected by Salmon in 1899. They have short internodes, and since both *E. anglica* and *E. pseudokernerii* have short internodes they are more plausibly regarded as *E. anglica* × *pseudokernerii* than the tall Piltdown plant. Salmon's plant is very like *E. pseudokernerii* in habit and foliage, and its flowers are very large, larger, in fact, than is usual in *E. pseudokernerii*. In 1953 I found what may be the locality of Salmon's plant (grid ref. 51/132461). The only *Euphrasia* present apart from the

supposed hybrid was *E. nemorosa*, which was abundant. No pure *E. anglica* was found at Friday Street, though it is common in Surrey. The apparent hybrid was found to occupy only a few square yards of ground, over which it occurred quite densely in short grass. It differed from *E. anglica* primarily in its small, narrow, ovate leaves. The corolla lobes were unusually narrow for *E. anglica*; this might have resulted from hybridisation but it was not a character of the *E. nemorosa* population here. The colony was visited in July and late September, and on neither occasion were the flowers large. The difference between my specimens and Salmon's in this respect may be attributed either to the evolution of a smaller flower-size in the last fifty-five years, or to my not having found the same population as Salmon.

Friday Street is on acid sandy soil, unsuitable for *E. pseudokernerii*, which is not likely to occur less than two miles away, on the North Downs, so that it seems as if the tetraploid parent must be *E. nemorosa*.

E. anglica × *confusa* occurs quite frequently. These two species are both dwarf in habit, so that hybridisation results in no change in stature. *E. anglica* affected by introgression from *E. confusa* tends to show the flexuous branches of the latter, but the main indication of hybridity is seen in the leaf shape. The occurrences of this hybrid known to me are:

V.c. 5, S. Somerset: round Withypool, visited in 1952, *E. anglica* was almost invariably accompanied by *E. confusa*, and in some populations it appeared to be modified by introgression from that species. At Elworthy in 1951 Mr. M. C. F. Proctor collected, as well as more or less normal *E. anglica*, plants that were strongly modified, especially in leaf shape. *E. confusa* was collected at the same place.

V.c. 6, N. Somerset: at Gorse Bigbury, N.E. of Cheddar (grid ref. 31/479559), *E. anglica* and *E. confusa* were found growing together, and the former showed definite characters of the latter. Herbarium specimens collected by Turrill (in Herb. Kew) from Mendip Moors, near Cheddar, 1930, appear to represent this hybrid, as do those of Bucknall from "boggy ground, in thick spongy turf on Mendips, near Rowberrow," as "*E. rechingeri*, with the parents," 1916. The parents of *E. × rechingeri* Wettst. are *E. kernerii* Wettst. and *E. rostkoviana*, and Bucknall (1917), citing earlier gatherings from here, said it occurred with these two species. His description of "*E. kernerii*" suggests that it was *E. confusa*, and *E. anglica* was usually called *E. rostkoviana* at that period. Pugsley (1930, 540) regards the Rowberrow plant as abnormal *E. anglica*.

V.c. 39, Stafford, and v.c. 57, Derby: at Stanshope, near Wetton (v.c. 39) (grid ref. 43/126544) and at Thorpe (v.c. 57) (grid ref. 43/151506), populations of *E. anglica* were found which showed, in their habit and foliage, indications of introgression from *E. confusa*, which was growing with it in both places.

E. anglica is a very variable species, in spite of its nearly always being easily identified, and part of this variation is probably due to introgression from various tetraploid species.

In the British Isles, the diploid *E. rostkoviana* is usually accompanied by the tetraploid *E. brevipila*, and some of its variation may be due to introgression from that species. A probable indication of this is the variation in capsule shape, which is typically short and broad but is sometimes longer and narrower. The two species are similar in habit, both being tall.

Much Continental material of *E. rostkoviana* shows characters recalling those of tetraploids, but field observation is needed to assess the significance of this.

DISCUSSION

The main conclusion drawn from the observations described in this paper is that genes can pass from tetraploid species of *Euphrasia* into diploid species. A hypothesis

is offered to account for the achievement of fertility, in the diploid state, of forms whose ancestry includes both diploid and tetraploid forms. Such a result has not been achieved experimentally and it is therefore of interest to enquire whether a comparable process is known in any other group.

Anderson & Hubricht (1938) demonstrated, by morphological investigation, introgression from the tetraploid *Tradescantia canaliculata* into the diploid *T. bracteata*. This state of affairs is comparable with that described in some *Euphrasia* populations. Unfortunately, the chromosome numbers of the forms in the population investigated were not stated. The authors add that the case needs further investigation, since *T. bracteata* presents the most complicated pattern of intraspecific variation yet encountered among American *Tradescantias*.

The second example is also provided by wild plants and is more fully investigated than the first. It concerns hybrids between *Polystichum lonchitis* and *P. lobatum*, described by Manton (1950). These two species are diploid and tetraploid respectively. Plants of the putative hybrid, *P. illyricum*, from a locality where the other two species grow together, formed an almost continuous series of morphological intermediates between *P. lonchitis* and *P. lobatum*. Cytological investigation showed that some plants of *P. illyricum* were triploid, but one, which resembled *P. lobatum* more closely, was tetraploid, and one, which resembled *P. lonchitis* more closely, was diploid or nearly so. The behaviour of the chromosomes at meiosis in the triploid showed that *P. lobatum* is an allotetraploid, one of whose parents is *P. lonchitis*. The diploid plants, referred to *P. illyricum*, thus appear to have originated in the way suggested for the *Euphrasia* hybrids discussed in this paper. Manton says: "That some signs of hybridity still persist in such progeny would merely seem to imply that some extra chromosomes belonging to one or other species are still present or that a measure of gene exchange can occur between the chromosomes of the two species." It is not clear whether the second alternative concerns the sets which pair at meiosis in the triploid or those that usually do not. However, one can assume that the sets which pair in the triploid, while being cytologically homologous, are not genetically identical. In that case, since there will have been crossing-over between the chromosomes that paired in the triploid, characters found in the tetraploid will be expected to appear in the back-crossed diploid.

Müntzing (1937) obtained a partially fertile diploid in *Dactylis* by crossing the tetraploid *D. glomerata* with the diploid *D. polygama* (*D. aschersoniana*) and back-crossing the resulting triploid with the diploid parent. In this case *D. glomerata* itself forms quadrivalents frequently at meiosis and the triploid forms a high proportion of trivalents. Pollen fertility in the triploids was between 4 and 10 per cent. This indicates a closer relationship between the haploid set in the diploid with both sets in the tetraploid than is the case in *Euphrasia*.

The cross *Viola reichenbachiana* × *riviniana* provides a final example. Valentine (1950) crossed these two species, the first of which is a tetraploid with $2n = 40$ and the second a diploid with $2n = 20$, and thereby produced a triploid.

The commonest arrangement of the chromosomes at meiosis consisted of ten bivalents and ten univalents. The triploid was highly sterile, but most of its few offspring had a diploid chromosome number between 18 and 21. These varied from weak and non-flowering, through flowering but sterile, to slightly fertile. They were produced cleistogamously, so that the process involved differs from that suggested for *Euphrasia* (p. 255), but the selfing of the triploid is an alternative possibility for *Euphrasia* that has been mentioned (p. 256). The fertility of the diploid is very low, but might increase in later generations. It is interesting to note that Valentine, in his discussion, considers the possible achievement of fertility in hybrids between species differing in chromosome

number. He envisages repeated back-crossing leading to fertility, resulting in introgression by which one or other of the original species may be progressively modified. It would seem, however, that introgression into the diploid, by this process, is of rare occurrence.

No definite indications of introgression from diploid into tetraploid have yet been encountered in *Euphrasia*.

The conclusions drawn with regard to hybridisation mean that gene exchange is possible between two groups which would be expected to be genetically isolated on account of polyploidy. In Turesson's terminology of experimental taxonomy, forms that would be expected to belong to two coenospecies belong to the same one. A difference of chromosome number may in some cases mark the separation of two coenospecies, while in others, such as that of *Euphrasia*, it will not. It is therefore perhaps preferable to use the new terminology of Gilmour & Heslop Harrison (1954), which in its general definitions is explicitly elastic, but which is made precise in any particular case by the qualifications introduced by the user. According to this terminology *E. anglica* and *E. micrantha* may be said to constitute two different hologamodemes (within which all individuals are able to interbreed with a high level of freedom), which are not completely discontinuous and therefore belong to one coenogamodeme. Gene exchange between the two hologamodemes is at present only known to go in one direction. In a particular population *E. anglica* and *E. micrantha* form two gamodemes which are largely, but not completely, isolated genetically, while the diploid hybrid forms another gamodeme genetically isolated from *E. micrantha* (which may be called a cytogamodeme) and ecologically isolated from *E. anglica* (which may be called an ecogamodeme). Though the frequency of transfer of genes from the tetraploid to the diploid population is low, individuals showing intermediate characters may be very numerous. In spite of the abundance of intermediate individuals and the possibility of their closely resembling the tetraploid parent, the two gamodemes will be able to persist as largely discontinuous breeding units because of the difference in their chromosome numbers, which cannot be bridged by intermediates as the morphological differences can.

Finally, attention is drawn to the occurrence of hybrid forms with flowers larger than those of either parent. This is so frequent as to suggest that such forms may be selected for some reason.

SUMMARY

The parents of some reported hybrids are now known to be diploid and tetraploid respectively. The hybrids, however, are fertile and numerous.

Such a hybrid is described from Withypool, Exmoor. It looked intermediate between *E. anglica* and *E. micrantha* which accompanied it, and it grew in longer grass than the dwarf diploid *E. anglica*. It was diploid. A single triploid individual was also found, evidently a hybrid between *E. anglica* and *E. micrantha*.

Probably the diploid hybrid arose through the back-crossing of a triploid to the parental diploid by means of a haploid gamete. If this hybrid possesses characters derived from the tetraploid which enable it to grow in a habitat not occupied by the parental diploid, it may form an independent population of a new diploid type with distinct morphology and habitat.

The plant described as *E. vigursii*, and regarded as *E. anglica* × *micrantha* by Pugsley, was investigated, and presented an analogous situation, but no triploid was found. *E. vigursii*, though morphologically different from the Withypool plant, appears to have the parentage suggested by Pugsley. *E. vigursii* occurs in three vice-counties, is distinct in morphology and habitat, and resembles a species.

At one locality *E. vigursii* itself appears to have been modified by introgression from another tetraploid species.

Four other hybrids analogous to *E. vigursii* are described. In addition, there occur hybrids of similar origin, but in which there is merely introgression of characters with no apparent ecological significance, and no isolation of hybrids from the diploid parent.

Reported cases are mentioned of diploids in four other genera whose immediate ancestry includes a diploid and a tetraploid; in two cases the occurrence was natural.

In spite of the abundance of intermediate individuals derived from the kind of hybridisation described, the two original populations cannot merge into one, owing to the difference of chromosome number.

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APPENDIX : Localities for *E. vigursii*

Cornish records are grouped according to the floristic divisions of Davey (1909). The following abbreviations are used to indicate the sources of records : BM, the British Museum (Nat. Hist.) Herbarium; CGE, Cambridge University Herbarium; DF, Davey's (1909) *Flora of Cornwall*; K, the Kew Herbarium; PM, Pugsley's (1930) monograph; S, Mr. N. D. Simpson's herbarium.

All specimens collected by me are in my herbarium, and most gatherings are also in the herbaria of the University College of Leicester and Cambridge University.

Records of *E. anglica* and *E. micrantha* from localities for *E. vigursii* are also included.

V.c. 1. W. CORNWALL

District 7 : Lizard Downs, *Salmon*, 1926 (BM).

District 6 : edge of Newlyn Downs between Carland and Zela Hill, *Yeo*, 1953 (locality for *E. micrantha*, *Yeo*, 1953).

District 5 : Perranzabuloe, *Babington*, 1839 (CGE), (locality for *E. micrantha*, *Babington*, 1839 (CGE)); Reen Common, Perranzabuloe, *Vigurs*, 1907 (CGE), (locality for *E. micrantha*, *Vigurs*, 1907, (CGE)); Ventongimps, Perranzabuloe, *Rilstone*, 1918 (K); Goonhavern, *Davey*, 1906 (CGE), *Tresidder*, 1909 (CGE), (locality for *E. micrantha*, *Tresidder*, (DF), *Rilstone*, 1922 (PM)); Mill Down, Goonhavern, *Thurston*, 1916 (K); Polgoda Downs, *Lousley*, 1936, (K), *Yeo*, 1953; Newlyn Downs, *Thurston*, 1916 (K); Shepherds, *Druce*, 1917 (BM); Zela Hill, *Yeo*, 1953; Droskyn Point, Perranporth, *Thurston*, 1916 (K), *Yeo*, 1953; downs near Perranporth, *Rilstone*, 1918 (CGE); Quintrell Downs, near Newquay, *Vigurs*, 1907 (K), (locality for *E. micrantha*, *Vigurs*, (DF), *Hume* (PM)); Connor Downs, (DF); Porth Towan, *Davey*, 1905 (CGE).

District 4 : St. Issey Downs, near Padstow, *Riley*, 1906 (K), (locality for *E. micrantha*, *Riley*, 1906 (K)).

V.c. 2. E. CORNWALL

District 3 : Helman Tor, *Rilstone*, 1923 (? *E. vigursii*); Cheesewring Down, Minions, *Rilstone*, 1920 (BM); opposite Duchy Terrace, Minions, *Thurston*, 1923 (K), (Minions is a locality for *E. micrantha*, *Thurston*, 1923, (K), *Yeo*, 1953, and for *E. anglica*, *Yeo*, 1953); slopes of Caradon Hill, *Rilstone*, 1920 (BM) and *Yeo*, (Pensilva), 1953, (locality for *E. micrantha*, *Yeo*, 1953); Herod Down, near Pillaton, *Jenkins* (DF).

District 2 : Kit Hill, Callington, Rilstone, 1917 (K), Rilstone & Thurston, 1923 (K), (locality for *E. anglica* (as *E. rostkoviana*), Hammond (DF)).

District 1 : Kittows Moor, near Treneglos, Little, 1924 (BM, CGE, PM), (locality for *E. micrantha*, Little, 1924 (CGE, K, PM)); Wilsey Down, near Treneglos, Little, 1924 (C); Laneast Downs, Marsden-Jones, 1929 (K).

V.c. 3. S. DEVON.

Roborough Down, Vigurs, 1906 (CGE), Sara, 1907 (CGE), Simpson, 1939 (S), Yeo, 1953 (locality for *E. cf. micrantha* (*E. "nemorosa"* in this paper); Simpson, 1939 (S), Yeo, 1952, and for *E. anglica*, Yeo, 1952); Horrbridge, Roborough Down (N. end), Stephenson, 1937 (BM); Yelverton, Williams, 1925 (CGE, K, S); Yannadon Down, Yelverton, Hume, 1902 (BM), (locality for *E. micrantha*, Hume, (PM)); near Hand Tor, Dartmoor, Stephenson, 1937 (S); Lydford, Dartmoor, Martin (BM).

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